Ants (Hymenoptera: Formicidae) of Formation Green River and some other Middle Eocene deposits of North America

Муравьи (Hymenoptera: Formicidae) формации Грин Ривер и некоторых других среднеэоценовых отложений Северной Америки

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КЛЮЧЕВЫЕ СЛОВА: ископаемые муравьи, эоцен, свита Грин-Ривер, Formicidae.

ABSTRACT. Middle Eocene ants collected in Green River, Kishenehn and Klondike Mountain Formations in western North America are reviewed. 18 species and 12 genera (7 formal ones) are recorded, 6 genera and 15 species described as new (*Mianeuretus eocenicus* sp.n., *Proiridomyrmex vetulus* gen. sp.n., *Dolichoderus kohlsi* sp.n., *Myrmecites rotundiceps* gen. sp.n., *Solenopsites minutus* gen. sp.n., *Ponerites eocenicus* gen. sp.n., *P. coloradensis* sp.n., *P. hypoponeroides* sp.n., *Pachycondyla labandeirai* sp.n., *Eoformica magna* sp.n., *E. globularis* sp.n., *Klondikia whiteae* gen. sp.n., *Kohlsimyrma laticeps* gen. sp.n., *K. longiceps* sp.n., *K. gracilis* sp.n.). Key to genera is given for ant wingless impression fossils in Middle Eocene of N. America. Problems of preservational state and parataxonomy of ant impression fossils are discussed. General ant history is outlined based mainly on the Eurasian material, N. American data are considered on that background, and 4 main stages of ant history are identified: (1) later Early Cretaceous through latest Cretaceous: ancient ant fauna, (2) Paleocene and Early Eocene: old ant fauna, (3) Middle Eocene through at least Early Oligocene: formation of the modern fauna, and (4) Oligocene or Miocene through now: essentially modern fauna).

РЕЗЮМЕ. Переописаны муравьи среднего эоцена из формаций Грин Ривер, Кишенен и Клондайк Маунтин запада С. Америки. Установлено 18 видов 12 родов (в том числе 7 формальных родов), 6 родов и 15 видов новые для науки (*Mianeuretus eocenicus* sp.n., *Proiridomyrmex vetulus* gen. sp.n., *Dolichoderus kohlsi* sp.n., *Myrmecites rotundiceps* gen. sp.n., *Solenopsites minutus* gen. sp.n., *Ponerites eocenicus* gen. sp.n., *P. coloradensis* sp.n., *P. hypoponeroides* sp.n., *Pachycondyla labandeirai* sp.n., *Eoformica magna* sp.n., *E. globularis* sp.n., *Klondikia whiteae* gen. sp.n., *Kohlsimyrma laticeps* gen. sp.n., *K. longiceps* sp.n., *K. gracilis* sp.n.). Приведена определительная таблица для родов среднеэоценовых муравьев, известных по отпечаткам тела без крыльев. Обсуждаются проблемы сохранности и паратаксономии отпечатков муравьев. Дан анализ общей истории муравьев и места в ней североамериканских ископаемых. Выявлены 4 основных этапа в истории муравьев: (1) конец раннего мела — конец мела: древнейшая фауна, (2) палеоцен и ранний эоцен: древняя фауна, (3) средний эоцен — олигоцен (по меньшей мере ранний олигоцен): становление современной фауны, (4) олигоцен или миоцен–ныне: существенно современная фауна.

Introduction

Ants are one of the most important and intriguing insect groups whose role is beyond doubts concerning both the human welfare (through their versatile environmental control and conditioning) and world outlook (for their paradigmatic diligence and role as a model for biosociological and biopsychological researches, to mention only the most apparent aspects). At the same time, our knowledge of the ant history is far from even, although the known fragments are inspiriting [E. Wilson, 1985; Dlussky, Fedoseeva, 1988; Dlussky, 1998; Rust, Andersen, 1999].

The most sound historical information based on a rich fossil record is only available for the north European Late Eocene (due to the Baltic amber and its inclusion [Wheeler, 1915; Dlussky, 1997]) and, to a lesser extent, for the earliest Oligocene of North America (Florissant in Colorado [Carpenter, 1930]). Other intervals of ant history are either badly undercollected (Eurasian and North American Cretaceous, Paleocene and, partially, Eocene, North American Neogene and all the rest world throughout), or huge accumulated material is left not re-visited since long ago.

Last decade (since 1991) a large collection of fossil insects from the famous Green River Formation (Middle Eocene of western USA) has been amassed at the National Museum of Natural History (Smithsonian Institution, Washington, DC, USA), due to enthusiastic efforts by Mr. David Kohls (Rifle, Colorado), supported by a few scientists and volunteers, primarily by Dr Conrad Labandeira and the late Dr. Louis Pribyl. Courtesy these three outstanding people, we are able to study practically all the Green River ants collected and inventoried by 1997. The types of the earlier described ant species from Green River and other Middle Eocene North American deposits kept at the above museum have been studied as well. This new material, although incomparably more limited than available for the Baltic amber and Florissant, nevertheless makes possible to elucidate more basic features of somewhat older, Middle Eocene stage of ant history in North America, and to compare the resulted picture with what is possible to draw from the general fossil record of ants.

Additionally to the above collection and thanks to the same three persons, a representative collection of the Green River insects collected by one of us (APR) jointly with Mr. Kohls in 1997 has been provided to be kept at the Paleontological Institute RAS, Moscow. The ants in that collection are also considered here. Three fossil ants from the Middle Eocene Klondike Mountain Formation of Republic in Washington, USA, studied courtesy Dr. Wesley C. Wehr (Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington), are included into the present study as well.

Source deposits

Green River Formation. Deposits of the Green River Formation are widespread across western USA (Utah, Colorado, Wyoming). They are rich in various fossil including the insects. The insectiferous beds of past lakes Uinta, Gossuite and Fossil Lake belong to Parashute Member accumulated mostly during the Middle Eocene [Bradley 1964; Franczyk *et al.* 1992]. Best collected are deposits from the Piceance Creek Basin (eastern bay of the Uinta Lake) with some 12,000 rock pieces with about 80,000 insect fossils housed in the Paleobiology Department, Smithsonian Institution, Washington DC; further material is kept in a number of other institutions. Dominating the fauna are dipterans (~40%) followed by beetles (~20%), hemipterans (~10%), and hymenopterans (~4%). Some 300 insect species have been named [M. Wilson, 1978, Grande, 1984] including four ants: *Eoformica pinguis* (Scudder), *Archimyrmex rostratus* Cockerell, *Lasius terreus* Scudder (a synonym of *E. pinguis*, see below), and *Myrmica* sp. [Scudder, 1878] whose identity is obscure. Calculations by one of us (APR, 1997) based on the above collection at the Smithsonian Institution give the ant share of hymenopterans as 17%.

Kishenehn Formation. Insectiferous oil shale of the Middle Eocene (Lutetian) Kishenehn Formations are formed in a deep stratified lake and widespread in Montana and British Columbia [Constenius et al., 1989, age after Labandeira, pers. comm.] They are little studied paleoentomologically. Two ant fossils are described herein collected in the Middle Coal Creek Member at Disbrow Creek locality, Pinnacle Quadrangle, Garfield County, Montana, USA.

Klondike Mountain Formation. In the Middle Eocene Klondike Mountain Formation at Republic in Washington State, USA, 16 insect orders are collected including 5 hymenopteran families Braconidae, Ichneumonidae, Sphecidae, Megachilidae, and Formicidae mentioned by Wehr, Barksdale [1996], Rhopalosomatidae [Dlussky, Rasnitsyn, 1999], and Cimbicidae figured by Lewis [1992] as unidentified hymenopteran. Numerical data provided by Lewis [1992] imply that 535 insect fossil are collected totally and 25 of them (out of 373 identified by orders) are hymenopterans. These include 5 leaves characteristically damaged by megachilid bees, and among 20 remaining fossils 10 belong to ants, the share unusually high for the Paleogene [cf. Dlussky, Fedoseeva, 1988].

Taxonomic approach: preservation state and parataxonomy

Preservation state of fossils affects profoundly the taxonomist's approach to routine procedures of creation and description of taxa [Rasnitsyn, 1996]. Ant fossils are known mainly either as amber inclusions or as impression fossils which differ much in respect of both taphonomy and preservation state. Buried in resin are mostly worker ants running about on tree trunks, with those of smaller size having more chance to be buried there. As a result, the herpetobiotic ants of larger size and soil and litter dwellers have little chance to became an amber inclusion. Inclusion fossils are appreciated for their preservation state which is often comparable with that of extant ants.

Unlike them, the impression fossils are always of more or less imperfect preservation state, both in terms of body parts preserved and morphological details possible to discern on the parts preserved, with the extent of above imperfectness being highly variable depending on subtleties of the pre-burial and post-burial environments. Still more striking are differences in composition of the ant assemblages of impression *vs.* inclusion fossils. To became impression fossils, an ant should be buried in the bottom deposits of an ancient lake. The allochthonous insects (those lived outside the target lake) find their way to future tomb mostly from the air [M. Wilson, 1980, 1988; Zherikhin, 2002]. That is why the chance to became an impression fossil is higher for winged ants, and particularly for those practicing aerial swarms (mating flight with copulation started in air, as opposed to the ground swarm when males and females copulate only after the dispersal flight is over [Kannowski, 1963]). Indeed, aerial swarms are often involve numerous ant sexuals which could be drawn far from their start area (swarm transfer for tens of kilome-

ters beyond the ant northern limits is recorded in tundra [Dlussky, 1967]). In contrast, ground swarming female ants execute comparatively short flight while males are flying low over the ground to seek females by odor. Their chance to become impression fossils is lower.

Body size of ants also affects their chance to turn into an impression fossil but in reverse mode than in case of the inclusion fossil: the insects of larger size (and with more durable integument) more likely survive fossilization and are noticed by a collector.

We can conclude that both types of fossil assemblages, the amber inclusions and impression fossils, are strongly but differently biased taphonomically, and so they can be used for the mutual control to try and approach toward a less biased picture of structure of the past ant communities.

Another aspect of ant taphonomy is that it can heavily affect taxonomy and nomenclature of the fossil ants. Amber inclusions are often preserved well enough to be studied and described like living ants, and both of them are commonly and successfully studied by the same students. Unlike this, impression fossils reveal only a part, often a small part of the characters used by taxonomists dealing with the extant ants. That is why these taxonomists are usually reluctant to work with impression fossils. Indeed, the impression ant fossils rarely permit proper comparison with extant taxa and so their position in the ant system rarely can be correctly identified.

Ant impression fossils often fall into one of two main preservational categories, either detached wings or bodies lacking wings (often also other appendages) entirely or almost entirely. Preservation of detached wings presumably took place in water bodies rich in autochthonous aquatic animals that consumed ant bodies and left wings not eaten (e.g., in Vishnevaya Balka in N. Caucasus). In contrast, the wingless bodies (sometimes with the thickest R vein present to an extent) are characteristic of localities (e.g., Green River and Khetana in Russian Far East) where insect fossils look pale (faded out). These deposits are probably formed in hydrochemically aberrant water bodies whose water was chemically affecting (discoloring) insect integument and particularly so the weakly sclerotized ant wings.

Any of these two types of the preservationally deficient ant fossils cause taxonomic problems, because the affected fossils often cannot be assigned to a particular genus or even subfamily because of this deficiency. At the same time, these fossils can be of considerable scientific and applied importance:

(i) They can inform us about taxonomic, morphological and adaptational diversity of the past ant faunas.

(ii) Composition of even imperfectly preserved ant fossils often can shed a light on the depositional environments (climate, relief, vegetation, etc. (see, for example, Dlussky [1981]). This holds particularly true when the life forms of the ants can be appreciated, which is not a particularly rare occasion.

(iii) In some cases similarity of even imperfectly preserved fossils can be useful in correlation of the source deposits.

It is true that available descriptions of ant impression fossils are often poor (based on the general appearance of the fossils at the best) and so are of little use in respect of the above goals. There are more successful attempts based on the best preserved impression fossils [e.g., Carpenter, 1930; Dlussky, 1983; Lutz, 1986; Zhang, 1989; Rust, Andersen, 1999] which, however, are hardly expectable applied to a less perfect material. The latter needs special approach which is available from parataxonomy.

Parataxonomy is a special version of taxonomy addressed to the material which is so imperfect, for one reason or another, that it cannot be involved into standard taxonomic procedure, and which nevertheless deserves classification [Rasnitsyn, 1996]. Parataxonomy is traditional and respactable tool in the fields where its necessity is apparent since long ago, particularly in paleobotany (primarily as classification of detached and dispersed plant parts and organs like leaves, wood, pollens etc.), mycology (classification of Fungi imperfecti which lack sexual part of the life cycle that is crucial for normal fungal taxonomy) and parasitology (classification of larval parasitic worms whose adults are not identified yet).

Rasnitsyn [1996] defines 3 kinds of parataxa: taxon incertae sedis, formal taxon and collective group. Incertae sedis is the most common and most familiar parataxon. It differs from an *orthotaxon* (normal taxon) in that its incomplete characteristics make it impossible to specify its position at a particular level of the hierarchy. For instance, a genus *incertae sedis* can be assigned to an order (or family), but not, at least for the moment, to any particular family (subfamily, tribe etc.).

A **formal taxon** can be treated as if it is an orthotaxon, but only in the framework of a special system which is parallel to the general one and completely independent of it (except for the principle of homonymy). These are taxa in systems mentioned above as created to classify immature parasitic worms, Fungi imperfecti, fossil detached plant and animal parts and animal traces and other their works (e.g., caddis cases), or an unassociated sex in highly dimorphic animal groups with classification traditionally based on the opposite sex. Parataxon differs from orthotaxon in that it is possibly (or even certainly) a synonym of an orthotaxon, and yet it should not be synonymized with the latter.

A **collective taxon,** the poorest kind of parataxon, usually of generic rank, can be assigned to a higher taxon but cannot be organized there in a special system of above sort. For instance, *Cercaria* O.F. Müller is the collective group name used for any trematode larvae that cannot be placed with certainty in known genera.

Taylor [1964] was the first who applied the concept of parataxon and particularly of formal taxon to ant fossils, when he proposed to consider *Poneropsis* Heer, 1867 a form-genus embracing detached ant wings with the complete (for ants) array of closed cells. The approach was further developed by Dlussky [1981] who has introduced formal genus *Camponotites* Dlussky for ants with the *Camponotus*-like wing venation whose taxonomic position is not clear (also due to insufficient preservation state), and informal names "*Ponerites*" for small-sized, non-

specialized Ponerinae of obscure taxonomic position (due to insufficient preservation state), and "*Formicites*" for ants with one-segmented petiole, again with the preservation state insufficient for correct identification of their taxonomic position. The approach is maintained herein because of the characteristically imperfect preservation state of the Green River ant fossils.

Technics

LINE DRAWINGS. The fossil specimens were scanned using projecting scanner ScanNex II, and enlarged outprints were hand traced by pen with the visual control of the specimen under stereomicroscope MBS–9. The resulted draft drawing was scanned with ScanExpress 6000 PS and improved finally using the program CorelDraw 8. Shown as light filled are areas of the original fossil that differ in color from the rock matrix, and those dark filled denote the preserved, even if chemically modified, original sclerites. Solid lines trace boundaries of visible sclerite, dashed lines — supposed sclerite boundaries and visible lines other than sclerite boundaries (deformation folds, occasionally superimposed objects, elements of sculpture, and so one. In the case when both part and counterpart fossil are available the better preserved one is used for illustration or, sometimes, both of them are used. In these cases a drawing based on the part is completed with details better preserved on the counterpart (or vice versa).

TERMINOLOGY of ant morphology is after Bolton [1994].

MEASUREMENTS. Ant impression fossils are found significantly deformed resulted in that the calculated measurements and their ratios are more variable than it is expectable in intact ants. This obscures real differences of taxa, and yet their discrimination is found possible in many cases (for instance, in case of *Eoformica pinguis* vs. *E. globularis*, or *Kohlsimyrma laticeps* vs. *K. longiceps*). Worth mentioning are some measurements which are found less affected by deformation than the others, e.g., the length of alitrunk in comparison to its width and height.

The measurements are referred to as follows: AL — alitrunk (mesosoma) length from junction with head to that with petiole; AH — alitrunk height; AW — maximum alitrunk width; F2 — middle femur length; F3 — hind femur length; HL — head length without mandibles; HW— maximum head width; MdL — mandible length; n — number of specimens measured; PtL — petiole length; PtH — maximum petiole height; PtW — maximum petiole width; PptL — postpetiole length; PptH — maximum postpetiole height; PptW — maximum postpetiole width; SL — scape length; WL — fore wing length.

STATISTICS of the living and extinct genera and species are after Bolton [1995] corrected to consider missed [Rossi de Garcia, 1983; Zhang, 1989] and succeeding publications.

MUSEUMS keeping types and other vaucher specimens are referred to as follows: AMNH — American Museum of Natural History, New York, New York, USA; MCZ — Museum of Comparative Zoology, Harvard, Massachusetts, USA; PIN — Paleontological Institute RAS, Moscow, Russia; SIC — Stonerose Interpretive Center, Republic, Washington, USA; SNHSD — State Natural Hystory Survey Division, Section of Faunistic Surveys and Insect Identification, Champaign, Illinois, USA; USBM — Burke Museum of Natural Hystory & Culture, University of Washington, Seattle, Washington, USA; USNM — United States National Museum, Washington, D.C., USA.

Taxonomic paleontology

For comparison of genera of the Middle Eocene North American ants based on wingless impression fossils see key on p.20.

FAMILY FORMICIDAE Latreille, 1802

Subfamily ANEURETINAE Emery, 1912

DIAGNOSIS (for wingless impression fossils). Antennae geniculate in females and workers, filiform in males. Workers with no ocelli. Mandibles triangular with dentate masticatory margin. Hind tibiae with one simple or feebly pectinate spur. Waist of one segment (petiole), narrowly attached to gaster. Petiole more than twice as long as wide, pedunculate, with node at its posterior part. Gaster without constriction between first and second segments. Pygidium simple, convex in side view. Sting present.

NOTES. Subfamily Aneuretinae includes the only unique extant species *Aneuretus semoni* Emery which inhabits Sri Lanka [E. Wilson et al., 1956]. There were also described 5 fossil species ascribed to Aneuretinae: *Aneuretellus deformis* Dlussky, 1988 (Paleocene, Sakhalin amber), *Protaneuretus succineus* Wheeler, 1915, *Paraneuretus longicornis* Wheeler 1915, *P. tornquisti* Wheeler, 1915 (Late Eocene, Baltic amber), and *Mianeuretus mirabilis* Carpenter, 1930 (latest Eocene or earliest Oligocene, Florissant). The incomplete *Burmomyrma rossi* Dlussky, 1996 (?Late Cretaceous Burmese amber) also may belong to this subfamily. The key traits of Aneuretinae separating them from Dolichoderinae are the presence of sting and pedunculate petiole with distinct node. However the sting is not visible in any of the above fossils except *Burmomyrma*, their attribution to Aneuretinae being based only on the petiole shape.

Genus *Mianeuretus* Carpenter, 1930

TYPE SPECIES: *Mianeuretus mirabilis* Carpenter, 1930.

DIAGNOSIS. Female. Head oval, widest behind midlength, with convex sides, without occipital corners. Eyes of moderate size, oval, situated nearly midlength of head sides. Mandibles triangular. Alitrunk nearly as wide as head. Petiole very long, much longer than wide, with small node near rear end. Gaster oval, without constriction between first and second segments. Wing venation unknown.

SPECIES INCLUDED. Type species only.

COMPARISION. Differs from *Protaneuretus* Wheeler and *Paraneuretus* Wheeler from the Late Eocene Baltic amber and from extant *Aneuretus* Emery in weak petiolar node. *Aneuretellus* Dlussky from the Paleocene Sakhalin amber has no petiolar node, but unlike the present genus as well as all other Aneuretinae *Aneuretellus* has antenna with distinct three-segmented clava, and its only known species *A. deformis* Dlussky is of very small size (body length about 3 mm, alitrunk length 0.88 mm).

Mianeuretus eocenicus Dlussky et Rasnitsyn, **sp.n.**
Figs 1, 2.

MATERIAL EXAMINED. Holotype: USNM #495959, dorsal imprint of female; Anvil Points Area, Kohls Site, Locality 41093, Garfield Co., Colorado, USA (coll. D. Kohls, 1991−93), Paratype: USNM #495957, Anvil Points Area, Labandeira Site, Locality 41075, Garfield Co., Colorado, USA (coll. C. Labandeira and D. Kohls, VIII.1995). Middle Eocene (Lutetian), Green River Formation.
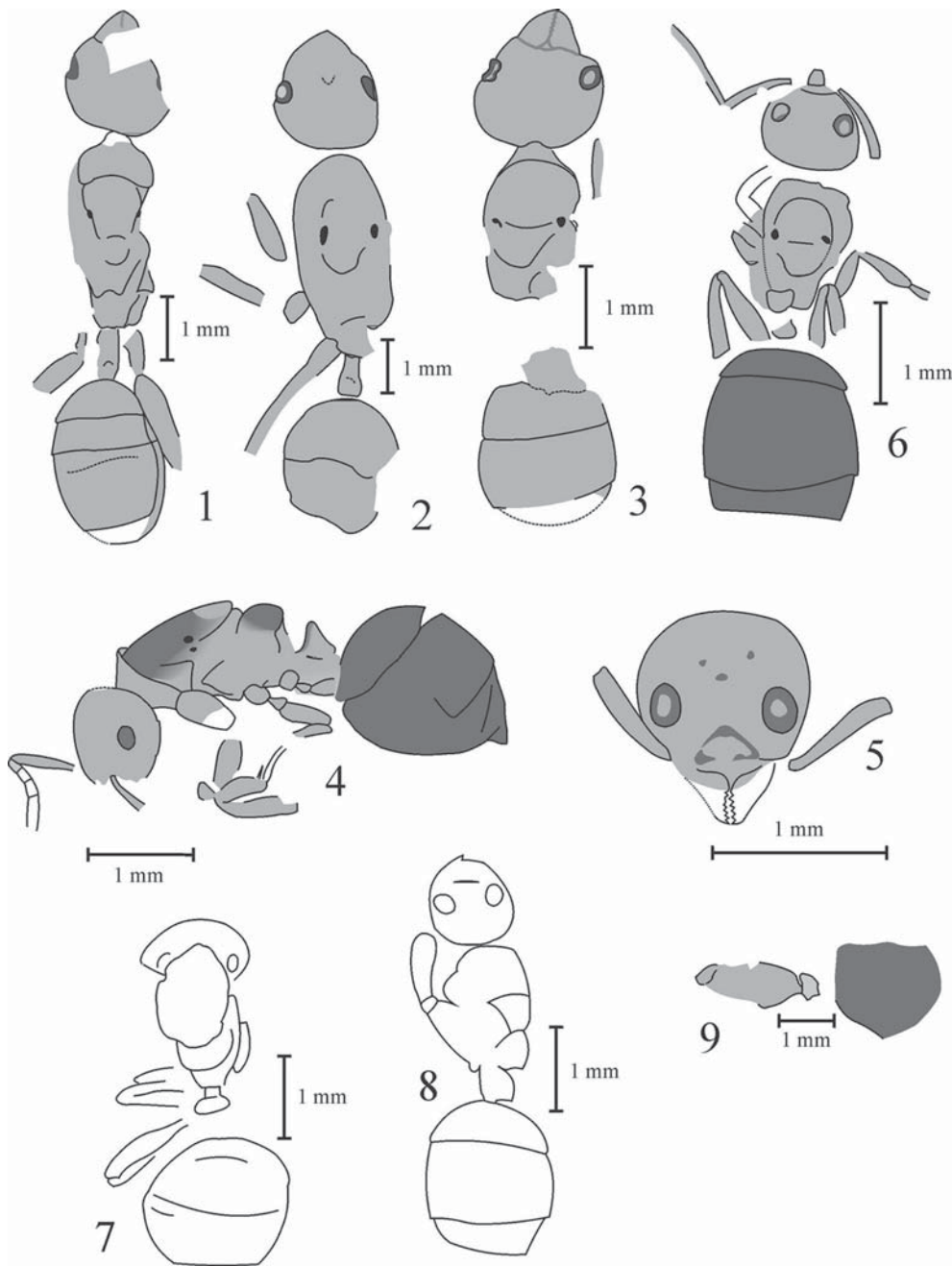
Figs 1−9. 1−2 — *Mianeuretus eocenicus* sp. n., dorsal imprint of female, holotype USNM # 495959 (1), paratype USNM # 495957 (2); 3 — *Proiridomyrmex vetulus* sp. n., dorsal imprint of female, holotype USNM # 495907; 4−8 — *Dolichoderus kohlsi* sp.n., lateral imprint of female, holotype USNM # 495905 (4), paratype USNM # 495952 (7), head of female in full-face view, paratype PIN # 4621/659 (5), lateral imprint of female, paratype USNM # 495889 (6), dorsal imprint of female body with head in full-face view, paratype USNM # 495901 (8); 9 — Dolichoderinae incertae sedis, preserved fragments of alitrunk, petiole, and gaster, PIN # 4621/639b.

Рис. 1−9. 1−2 — *Mianeuretus eocenicus* sp. n., дорзальный отпечаток самки, голотип USNM # 495959 (1), паратип USNM # 495957 (2); 3 — *Proiridomyrmex vetulus* sp. n., дорзальный отпечаток самки, голотип USNM # 495907; 4−8 — *Dolichoderus kohlsi* sp.n., латеральный отпечаток самки, голотип USNM # 495905 (4), паратип USNM # 495952 (7), голова самки сверху, паратип PIN # 4621/659 (5), латеральный отпечаток самки, паратип USNM # 495889 (6), отпечаток самки, тело в профиль и голова сверху, паратип USNM # 495901 (8); 9 — Dolichoderinae incertae sedis, сохранившиеся фрагменты мезосомы, петиолюса и брюшка, PIN # 4621/639b.

DESCRIPTION. Female. Body length 8.4–8.8 mm. Head oval, nearly as long as wide. Occipital margin straight. Eyes of moderate size, oval, situated somewhat before head midlength. Mandibles triangular. Alitrunk elongate, more than twice as long as wide. Pronotum nearly twice as wide as long. Scutum flattened, about as long as wide, not overhanging pronotum anteriorly. Scutellum small and flattened. Propodeum with pair of short, obtuse teeth. Petiole 2.5–3 times as long as wide, with long peduncle and small node. Gaster oval; gaster with apex missing.

MEASUREMENTS, mm. Holotype: AL 3.0; AW 1.3; HL 1.6; HW 1.65; PtL 0.875; PtW 0.275. Paratype: AL 3.3; AW 1.35; HL 1.8; HW 1.75; PtL 0.85; PtW 0.35.

COMPARISION. Closely resembling the type species in most of its visible traits but differs in larger size (alitrunk length about 3 mm as opposed to 2 mm in *M. mirabilis*) and proportionally shorter head (about as long as wide in *M. eocenicus* vs. 1.3 times as long in *M. mirabilis*).

NOTE. The poorly preserved specimen USNM #495914 (Anvil Points, location 40193) also can belong to *Mianeuretus*.

ETYMOLOGY. Species name is after Eocene.

Subfamily DOLICHODERINAE Forel, 1878

DIAGNOSIS (for impression fossils). Female and worker antennae geniculate; male antennae often with short scape or filiform, rarely geniculate. Anterior margin of clypeus usually straight or concave. Workers often with no ocelli. Mandibles triangular with dentate masticatory margin. Hind tibiae with one simple or pectinate spur, rarely without spur. Waist of one segment (petiole), narrowly attached to gaster. Petiole less than twice as long as wide, with scale inclined forward, or with spines (some *Dolichoderus* Lund, 1831), or triangular in side view, or subcylindrical; sometimes gaster overhanging petiole anteriorly; very rarely petiole with vertical scale. Gaster without constriction between first and second segments. Pygidium small or very small; often shifted to ventral surface of gaster, often overhung and concealed partially to almost entirely by fourth gastral tergite. Sting and acidopore absent.

NOTES. At present 22 extant and 18 extinct genera of Dolichoderinae are described embracing 554 extant and 111 fossil species. In contemporary ecosystems and in the Miocene deposits of Europe they are less abundant than Myrmicinae and Formicinae. In contrast, Dolichoderinae were dominant ant subfamily during Paleogene: 4 of 7 described ant species in the Paleocene Sakhalin amber, 64% of individuals and 18 of 92 species in the Late Eocene Baltic amber, and 63% of individuals and 14 of 32 species in the Lower Oligocene of Florissant belong to Dolichoderinae.

16 fossil species of 8 genera of Dolichoderinae were described from North America: *Eotapinoma macalpini* Dlussky, 1999 (Late Cretaceous, Canadian amber), *Iridomyrmex mapesi* Wilson (Middle Eocene, Arkansas amber), *Dolichoderus antiquus* Carpenter, 1930; *D. rohweri* Carpenter,1930; *Elaeomyrmex coloradensis* Carpenter, 1929; *E. gracilis* Carpenter, 1930; *Iridomyrmex florissantius* Carpenter, 1930; *I. obscurans* Carpenter, 1930; *Liometopum miocenicum* Carpenter, 1930; *L. scudderi* Carpenter, 1930; *Miomyrmex impactus* (Cockerell, 1927); *M. striatus* Carpenter, 1930; *Petraeomyrmex minimus* Carpenter, 1930; *Protazteca capitata* Carpenter, 1930; *P. elongata* Carpenter, 1930; *P. hendersoni* (Cockerell, 1906); *P. quadrata* Carpenter, 1930 (Lower Oligocene, Florissant). Two new species from Middle Eocene are described below.

Formal genus *Proiridomyrmex* Dlussky et Rasnitsyn, **gen.n.**

TYPE SPECIES. *Proiridomyrmex vetulus* sp.n.

DIAGNOSIS. Poorly preserved wingless female and worker fossils. Head elliptical, oval, heart-shaped, or subrectangular with rounded occipital corners, but never rectangular and longer than wide as in *Protazteca* and *Miomyrmex*. Eyes of moderate size. Mandibles triangular, dentate. Propodeum rounded in side view. Petiole with scale inclined forward. Integument thin, with shallow sculpture.

SPECIES INCLUDED. Recently Shatuck [1992] divided a very diverse former genus *Iridomyrmex* Mayr, 1862 on 7 separated genera, and his division was generally accepted [Bolton, 1995; Dlussky, 1997]. As a result, taxonomic status of some species based on poorly preserved or incomplete fossils became obscure. In addition to the type species, we propose *Proiridomyrmex* to cover such species, in particular *Iridomyrmex florissantius* Carpenter, 1930; *I. obscurans* Carpenter, 1930, and *I. mapesi* Wilson, 1985. Besides them, *Proiridomyrmex* should embrace other incompletely preserved Tapinomini originally attributed to *Liometopum* Mayr, 1861, *Forelius* Emery, 1888, etc. However the formal rearrangement needs study of the type material.

COMPARISION. *Proiridomyrmex* differs well from fossil representatives of some other dolichonerine genera. Less advanced of them (*Eotapinoma* Dlussky, 1988, *Technomyrmex* Mayr, 1872, *Tapinoma* Foerster, 1850) lack petiolar scale characteristic of *Proiridomyrmex*. Specialized *Protazteca* Carpenter, 1930, *Miomyrmex* Carpenter, 1930 and *Zherichinius* Dlussky, 1988 differ in having the head much longer than wide and either rectangular (in *Protazteca* and *Miomyrmex*) or with deeply excavated occipital margin (in *Zherichinius*). *Dolichoderus* Lund, 1831 is easily identifiable due to its dorsal and declivous propodeal surface being separated by a crest or ridge seen even in weak impressions. However, there are genera (*Anonychomyrma* Donisthorpe, 1947, *Forelius* Emery, 1888, *Iridomyrmex* Mayr, 1862, *Liometopum* Mayr, 1861, *Linepithema* Mayr, 1866, *Ochetellus* Shattuck, 1992, etc.), whose diagnostic traits (form of fore clypeal margin and of propodeum, development of thoracic sutures, palpal formula, presence of ocelli in worker ants, etc.) are rarely seen in impression fossils. So the poorly preserved fossils of these genera are to be described in the formal genus *Proiridomyrmex*.

Proiridomyrmex vetulus Dlussky et Rasnitsyn, **sp.n.**
Fig. 3.

MATERIAL EXAMINED. Holotype: USNM #495907, poorly preserved dorsal imprint of female. Anvil Points Area, Locality 40193, Garfield Co., Colorado, USA (D. Kohls, 1991−93). Middle Eocene (Lutetian), Green River Formation.

DESCRIPTION. Female. Body length 6.5 mm. Head wider than long, widest behind midlength, with convex sides, rounded occipital corners, and weakly concave occipital margin. Anterior margin of clypeus weakly concave. Eyes small: maximum eye diameter 0.2 head width. Mandibles comparative large, triangular, with small denticles. Alitrunk narrower than head. Scutum wider than long. Gaster oval. Distinct sculpture absent.

MEASUREMENTS. Holotype: AL about 2.3; AW 1.3; HL 1.25; HW 1.55; EL 0.325.

COMPARISION. Differs from all North American Paleogene ants of comparable preservation state and with one-segmented petiole in cordiform head.

ETYMOLOGY. Vetulus is the Latin for old.

Genus *Dolichoderus* Lund, 1831

TYPE SPECIES. *Formica attelaboides* Fabricius, 1775.

DIAGNOSIS (for impression fossils of females and workers). Head elliptical or oval, widest behind midlength of head sides; sometimes retort-shaped or subrectangular with rounded occipital corners, but never rectangular and longer than wide as in *Protazteca* Carpenter. Eyes of moderate size.

Mandibles triangular, dentate. Propodeum bispinate, bidentate, or distinctly angular in side view, with concave declivity. Petiole with scale proclined, or triangular in side view. Integuments thick, often coarsely sculptured. Forewing with closed cells 1r, 2r, rm and mcu; rm usually triangular.

NOTES. 140 extant and 40 fossil species of *Dolichoderus* are described, including three species from the lowermost Oligocene of Florissant [Carpenter, 1930] and 15 species from Late Eocene Baltic and Rovno amber [Dlussky, 2002a]. New species from the Green River Formation is the oldest in the genus (older than those from Baltic amber [Wheeler, 1915]).

Dolichoderus kohlsi Dlussky et Rasnitsyn, **sp.n.**
Figs 4–8.

MATERIAL EXAMINED. Holotype: USNM #495905, lateral imprint of female. Anvil Points Area, Locality 40193, Garfield Co., Colorado, USA (coll. D. Kohls, 1991−93). Paratypes: Garfield Co., Colorado, USA: USNM #495876, Old Mountains, Locality 40189, (coll. D. Kohls, 1991−93); USNM #495889, Mahaffey Trail, Locality 41219, (coll. D. Kohls, 1996); USNM ##495898, 495901, 495904, 495908, 495921, 495922, 495925, 495927, 495930, 495932, 495935, 495936, 495941, 495942, 495944, Anvil Points Area, Locality 40193 (coll. D. Kohls, 1991−93); USNM ##495945, 495952, Labandeira Site, Anvil Points Area, Locality 41075 (coll. C. Labandeira and D. Kohls, VIII. 1995); USNM ##495949, 495950, Anvil Points Area, Labandeira Site, Locality 41088, (coll. D. Kohls, 1995); USNM #495961 Anvil Points Area, Kohls Site, Locality 41089; PIN #4621/659 Anvil Points (coll. A. Rasnitsyn, 1997). Not in type series: USNM ##495912, 495928 (Anvil Points, Locality 40193; coll. D. Kohls, 1991−93). Middle Eocene (Lutetian), Green River Formation.

DESCRIPTION. Female. Body length 4.2–5.7 mm (average 4.68 mm; n 18). Head oval, about as long as wide, widest behind midlength of head sides; occipital margin feebly convex in full face view. Eyes of moderate size, oval, situated somewhat frontally and before head midlength. Mandibles robust, triangular; masticatory margin with 5–7 acute denticles. Anterior margin of clypeus feebly concave. Scape shorter than head (HL/SL 1.2–1.5; average 1.3; n 8). Alitrunk rather robust, somewhat longer than wide (AL/AW 1.3–1.8; average 1.6; n 8). Scutum and scutellum relatively small and feebly convex. Propodeum angular, with distinct carina separated propodeal dorsum and declivity; propodeal dorsum convex; propodeal declivity concave in side view. Posterior margin of propodeal dorsum weakly convex or straight in dorsal view. Femora and tibiae short and thick. Wings missed in all studied specimens. Petiole triangular in side view. Head and alitrunk with large, deep, circular or slightly elliptical foveolae, visible on most parts of fossils.

MEASUREMENTS, mm. Holotype: AL 1.68; AH 0.93; HL 0.93; SL 0.75; PtL 0.45. Paratypes: AL 1.15–1.88 (average 1.57; n 21); AW 0.80–1.13 (average 0.92; n 8); AH 0.85–1.30 (average 1.03; n 3); HL 0.80–1.13 (average 0.95; n 16); HW 0.75–1.13 (average 0.94; n 10); SL 0.68–0.80 (average 0.72; n 8).

NOTES. By its abundance *Dolichoderus kohlsi* is the second ant species after *Eoformica pinguis* in the Green River Formation. 26 (25%) from 104 randomly selected specimens belongs to this species. Majority of the fossils are well preserved indicating them to have thick integuments. Like the most of living *Dolichoderus* species, *D. kohlsi* seems to be dendrobiotic ant constructing its nests in wood. This inference is additionally supported by construction of the cranio-manibular system: the head widened behind correlates with large mandibular muscles, and massive triangular mandibles with strongly sclerotized teeth indicate burrowing galleries in hard substrate.

In a purely technical sense it is not possible to separate *D. kohlsi* from all other known species of *Dolichoderus*, but on the combined basis of its age, geographical location, and morphology this form can be safely treated as a distinct species.

COMPARISION. Differs from all known fossil *Dolichoderus* in having the head which is wider than long, in combination with a particular form of propodeum, viz. its dorsum is weakly convex in side view, and its hind margin is straight or weakly convex in dorsal view. All other species with similar propodeum have elongate head, and all species with short head have propodeal dorsum either strongly elevated, or bilobate, or bidentate.

ETYMOLOGY. The species is named in honor to David Kohls, who collected most of Green River ants, including the type specimen.

Dolichoderinae incertae sedis
Fig. 9

Poorly preserved fossil PIN # 4621/639b (Anvil Points, coll. A. Rasnitsyn, 1997), judging from the construction of petiole, seems to be a species of Dolichoderinae. It is not a species of *Dolichoderus* because of propodeum rounded in side view; it might be rather a species of *Proiridomyrmex*.

Subfamily FORMICINAE Latreille, 1802

DIAGNOSIS (for impression fossils). Antennae of females, workers and majority of males geniculate; rarely male antennae of with short scape but never filiform. Anterior margin of the clypeus convex, often angular. Workers with ocelli variable. Mandibles variable, often triangular with dentate masticatory margin. Hind tibiae with one simple spur. Forewing venation always with closed cells 1+2r+rm and 3r; cell mcu present or absent; crossvein r-m absent, and Rs5 and M4 branches off from the same point; crossvein cu-a meeting M+Cu proximal to junction of 1M and 1Cu for distance subequal to or longer than cu-a. Waist of one segment (petiole), narrowly attached to gaster. Petiole usually with scale vertical, rarely proclined or armed by spines or teeth (in *Polyrhachis* F. Smith, 1857). In some specialized, long-legged desert (*Cataglyphis* Foerster, 1850) and dendrobiotic (*Oecophylla* F. Smith, 1860, *Dendromyrmex* Emery, 1895) genera petiole lacking scale (nodiform, triangular in side view, or elongate). Gaster without constriction between first and second segments. Pygidium large and simple. Female and worker gaster ending in acidopore usually looking like a short tube with circlet of hairs (coronula); coronula sometimes concealed under last gastral sternite. Sting absent.

NOTES. 2458 extant and 224 fossil species are currently described in 49 extant and 11 extinct genera of Formicinae. In many contemporary ecosystems and in the Miocene of Europe Formicinae are the first or second (after Myrmicinae) dominating subfamily and always outnumber Dolichoderinae. In the Late Eocene through Early Miocene they were less abundant than Dolichoderinae (about one third of individuals in Baltic amber and Florissant). Before the Late Eocene Formicinae are rare.

10 fossil species of 7 genera of Formicinae were described from North America. The oldest known formicine ant is *Kyromyrma neffi* Grimaldi et Agosti, 2001 from the Turonian of New Jersey. Only two species, that can be placed with reasonable confidence to the Formicinae, are found in the Eocene deposits of the New World: *Protrechina carpenteri* Wilson, 1985 (Arkansas amber) and *Camponotites crausei* Dlussky et Rasnitsyn, 1999 (Republic, Washington). 6 species are described from the lowermost Oligocene deposits of Florissant: *Lasius peritulus* (Cockerell, 1927), *Camponotus microcephalus* Carpenter, 1930, *C. petrifactus* Carpenter, 1930, *Formica cockerelli* Carpenter, 1930, *F. grandis* Carpenter, 1930, and *F. robusta* Carpenter, 1930. *Pseudocamponotus elcoanus* Carpenter, 1930 comes from the Miocene of Elko in Nevada, USA.

Formal genus *Camponotites* Dlussky, 1981

TYPE SPECIES. *Camponotites macropterus* Dlussky, 1981.
DIAGNOSIS. Impression fossils with *Camponotus*-like forewing venation (closed cells 1+2r+rm and 3r; cell mcu absent; crossvein r-m absent, and Rs5 and M4 branches off from the same point; crossvein cu-a meeting M+Cu proximal to the junction of 1M and 1Cu for distance subequal to or longer than cu-a long), which cannot be identified to a genus.
NOTE. *Camponotites* should cover imperfectly preserved fossils of many Formicinae genera including all Camponotini, Oecophyllini, Plagiolepidini and some Lasiini (for example *Paratrechina* Motschoulsky, 1863 and *Prenolepis* Mayr, 1863) which have similar forewing venation.

Camponotites krausei Dlussky et Rasnitsyn, 1999
Fig. 10

MATERIAL EXAMINED. Holotype: USBM #78047, well preserved imprint of winged female. Golden Promise Mine, location B4876 Republic, Ferry Co., Washington, USA (coll. Rob Krause, 1994). Middle Eocene (Lutetian), Klondike Mountain Formation.
DESCRIPTION. Female. Body length 16.7 mm. Head subrectangular, 1.25 times as long as wide, with sides subparallel, occipital corners rounded, occipital margin feebly convex. Anterior margin of clypeus feebly convex. Eyes large, flattened; situated before midlength of head sides. Mandibles massive, subtriangular, dentate, with concave external margin. Antennae geniculate, 12-segmented, without clava, with scape as long as head. Alitrunk and petiole not armed. Scutum flattened. Petiole long (AL/PtL 2.5; PtL/PtW 2.7), with node or narrow, thin scale. Gaster large and soft. Integument with fine chagrinned sculpture.
MEASUREMENTS, mm. Holotype: AL 4.8; HL 2.75; HW 2.2; SL 2.75; PtL 1.9; PtW 0.7; WL about 16.
NOTE. In all available characters *C. krausei* agrees with *Camponotus* Mayr and differs from other genera of Camponotini, as well as of Oecophyllini and Plagiolepidini which have similar wing venation. However, the key trait of Camponotini (position of antennal insertion) is not visible in imprint, so we prefer to place it to *Camponotites* rather than to *Camponotus*.
COMPARISION. Fore wing similar to *C. macropterus* but differs in more wide cell 3r (length 5.7 width *vs.* 7 times in *C. macropterus*). Differs from all fossil ants described as *Camponotus* Mayr, 1861 (Camponotini) è *Plagiolepis* Mayr, 1861 (Plagiolepidini) in larger size and elongate head, from *Oecophylla* F. Smith, 1860 (Oecophyllini) — in head form (subrectangular and not distinctly widened behind).

Formicinae incertae sedis
Fig. 11.

MATERIAL EXAMINED. SNHSD #217/333−6846. Relatively well preserved imprint of alitrunk, petiole and gaster of ant female with head, wings and most parts of legs missing. Parachute Creek Mb. ,Rio Blanco Co. Colorado, USA. (coll. Mark B. DeBois). Green River Formation, Middle Eocene (Lutetian).
NOTES. Judging from the construction of petiole and general appearance, this ant seems to be a species of Formicinae. General appearance closely reminds some species of *Formica* Linnaeus, 1758, but the similarity well may be convergent. Sqamiform petiole differs the fossil from all others known from Green River Formation. Length of body without head 6.75 mm, AL 2.8 mm. Gaster, sides of scale, spot at scutellum and bands along notauli darker than legs and remaining portions of alitrunk.

Subfamily MYRMECIINAE Emery, 1877

DIAGNOSIS (for impression fossils). Female and worker antennae geniculate, male antennae filiform. Workers usually with ocelli. Mandibles linear with dentate masticatory margin. Hind tibiae always with two spurs, one (larger) pectinate, another simple. Forewing with closed cells 1+2r, 3r, rm, and mcu; cells rm and mcu pentagonal; 2M longer than RS+M; cua present; crossvein cu-a meeting M+Cu proximal of junction of 1M and 1Cu for distance subequal to vein thickness. Waist of two segments (petiole and postpetiole); postpetiole broadly attached to gaster. Pygidium simple, convex in side view. Sting present.
NOTES. Subfamily Myrmeciinae is now represented by the only genus *Myrmecia* Fabricius, 1804 with 89 species inhabiting Australia and nearest islands [Ogata, Taylor, 1991]. There were also described 5 genera and 6 species ascribed to Myrmeciinae: *Cariridris bipetiolata* Brandão et Martins-Neto, 1989 (Lower Cretaceous Santana Formation, Brazil), *Archimyrmex rostratus* Cockerell, 1923 (Middle Eocene Green River Formation, western U.S.A.), *Ameghinoia piatntzkii* Viana et Haedo Rossi, 1959 (Late Paleocene — Early Oligocene Ventana Formation, Rio Pichileufu, Argentina), *Polanskiella smekali* Rossi de Garcia, 1983 (Upper Paleocene — Lower Oligocene Ventana Formation, Rio Limay, Argentina), *Prionomyrmex longiceps* Mayr, 1868, and *P. janzeni* Baroni Urbani, 2000 (Upper Eocene Baltic Amber).
C. bipetiolata as described and figured by Brandão *et al.* [1989] looks very similar to an unnamed Santana fossil kept at the American Museum Natural History (New York, New York, USA) and described as belonging to either Sphecidae (Ampulicinae) or Dryinidae [Darling, Sharkey, 1990]. One of us (APR) jointly with W.J. Pulawski of the California Academy of Sciences (San Francisco, California, USA) have studied that fossil (AMNH 44108) and found it belonging to Sphecidae (probably to subfamily Ampulicinae) rather than to Formicidae. That is why we maintain here our earlier conclusion that *Cariridris* is a genus of Sphecidae [Rasnitsyn, 1990; Dlussky, 1998].
Ameghinoia and *Polanskiella* have been recently [Dlussky, Perfilieva, 2003.] synonymized under *Archimyrmex*, and the latter genus has been transferred from Myrmicinae [Carpenter, 1930; Bolton, 1995] to Myrmeciinae for the reasons explained there.
Baroni Urbani [2000] proposes to synonymise *Nothomyrmecia* Clark, 1934 under *Prionomyrmex* and, respectively, Notomyrmeciinae Clark, 1951 under Prionomyrmicinae Wheeler, 1915. We cannot agree with this proposal for the
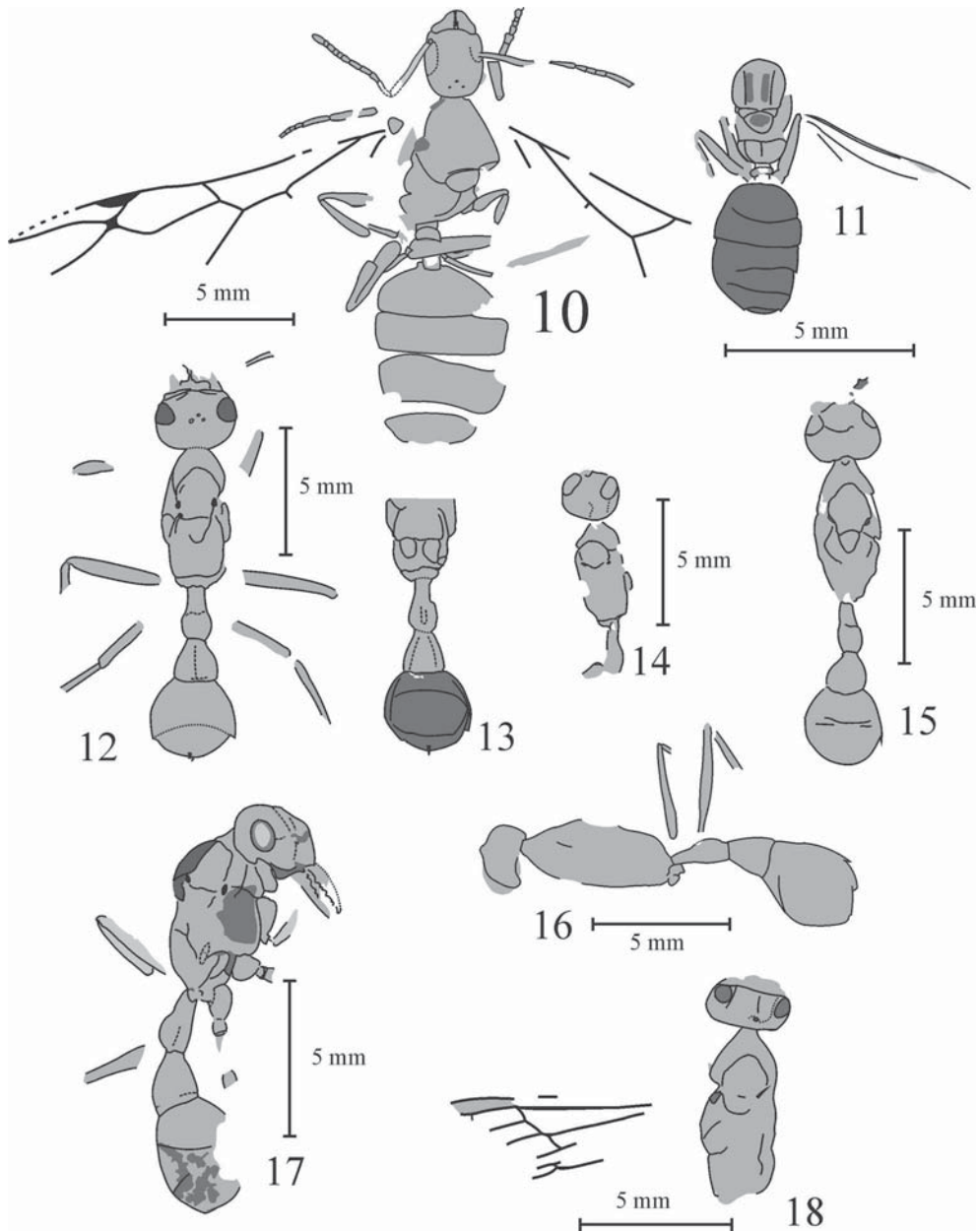
Figs 10−18. 10 — *Camponotites krausei* Dlussky et Rasnitsyn, holotype USBM # 78047, dorsal imprint of female; 11 — Formicinae incertae sedis, SNHSD # 217/333−6846, dorsal imprint of female, head missed; 12−18 — *Archimyrmex rostratus* Cockerell, USNM # 496002, obverse dorsal imprint of female (12), reverse imprint of female, propodeum, waist and gaster in ventral view (13), USNM # 495985, dorsal imprint of female, head, alitrunk, and petiole (14), USNM # 495986, dorsal imprint of female (15), USNM # 495902, lateral imprint (16), USNM # 496004, obverse lateral imprint of female (17), USNM # 495989, dorsal imprint of female, head, alitrunk, and fragment of forewing (18).

Рис. 10−18. 10 — *Camponotites krausei* Dlussky et Rasnitsyn, голотип USBM # 78047, дорзальный отпечаток самки; 11 — Formicinae incertae sedis, SNHSD # 217/333−6846, дорзальный отпечаток самки, голова не сохранилась; 12−18 — *Archimyrmex rostratus* Cockerell, USNM # 496002, прямой дорзальный отпечаток самки (12), обратный отпечаток самки, проподеум, стебелек и брюшко снизу (13), USNM # 495985, дорзальный отпечаток самки, голова, мезосома и петиолюс (14), USNM # 495986, дорзальный отпечаток самки (15), USNM # 495902, латеральный отпечаток (16), USNM # 496004, прямой латеральный отпечаток самки (17), USNM # 495989, дорзальный отпечаток самки, голова, мезосома и фрагмент переднего крыла (18).

following reasons. The above inference is based on the cladogram calculated after the matrix for 34 characters and 6 taxa (*Myrmecia,* Myrmicinae, *Nothomyrmecia*, Pseudomyrmecinae, *Prionomyrmex*, and Vespidae as the outgroup). The resulted cladogram (the unique most parsimonous one) shows *Nothomyrmecia* and *Prionomyrmex* as synapomorphous in a unique character, *viz.* worker and gyne with the lateral clypeal carina. This opposes to the similarity of *Myrmecia,* Myrmicinae, Pseudomyrmecinae and *Prionomyrmex* (but not *Nothomyrmecia*) in both worker and gyne with 3rd abdominal

segment forming the postpetiole. The cladogram identifies the above state as the ant groundplan. Baroni Urbani explicitly considers this interpretation as implausible (what we absolutely agree with), and yet he takes the resulted cladogram for the truth and so performs the above synonymisation.

Resulted from Baroni Urbani's analysis we have two incompatible putative synapomorphies: the lateral clypeal carina for *Nothomyrmecia* + *Prionomyrmex*, and formation of postpetiole for *Myrmecia* + *Prionomyrmex* + Myrmicinae + Pseudomyrmecinae (as well as for Ponerinae and a few minor subfamilies). Baroni Urbani selects the former as the true synapomorphy, and rules out the postpetiole formation based on a varying degree of constriction between the postpetiole and the gaster in various ants. However, as Taylor [1978] has shown, the matter is not the constriction *per se* but the tubulation, that is, fusion of the basal parts of both tergum and sternum of the 4th abdominal (1st gastral) segment to form a short and wide tube. Taylor (l.c.) has found tubulation as always present in Ponerinae, Myrmeciinae, Myrmicinae, Pseudomyrmicinae, and relative subfamilies, and always absent in Formicinae, Dolichoderinae, Aneuretinae, and Notomyrmeciinae. No likely case of reversal has been discovered, and it was shown additionally that tubulation results in reduction of several muscles making reversion unlikely [Dlussky, Fedoseeva, 1988]. The tubulation is perfectly illustrated for *P. janzeni* [Baroni Urbani 2000, fig. 6], so relationship of the fossil to *Myrmecia* and not to *Nothomyrmecia* is beyond doubts. That is why we keep maintaining subfamilies Myrmeciinae and Notomyrmeciinae and genera *Nothomyrmecia* and *Prionomyrmex* as distinct and not closely related taxa.

Genus *Archimyrmex* Cockerell, 1923

Archimyrmex: Cockerell, 1923: 52.
Ameghinoia: Viana, Haedo Rossi, 1957: 119.
Polanskiella: Rossi de Garcia, 1983: 19.
TYPE SPECIES *Archimyrmex rostratus* Cockerell, 1923.
DIAGNOSIS. Female. Large, slender ants with elongate alitrunk and appendages. Head rounded or oval, without distinct occipital corners. Eyes large, oval, displaced forward. Mandibles linear, about as long as head; masticatory margin with coarse obtuse teeth and small denticles between them. Scutum small, weakly convex, longer than wide. Propodeum rounded in side view, without spines or teeth. Petiole elongate, with dorsal elevation beyond middle. Postpetiole robust, very broadly attached to gaster. Gaster compact.

SPECIES INCLUDED. Dlussky, Perfilieva [2003] include three species: *A. rostratus* Cockerell, 1923 from the Middle Eocene Green River Formation, U.S.A., *A. piatntzkii* (Viana et Haedo Rossi, 1959) and *A. smekali* (Rossi de Garcia, 1983), both from Ventana Formation, Argentina, tentatively dated as Late Paleocene — Early Oligocene [Petrulevicius, 1999]).

NOTES. Genus *Archimyrmex* differs easily from other fossil ants except *Prionomyrmex* from the Baltic amber in its campaniform postpetiole very broadly attached to the gaster. *Prionomyrmex* differs from *Archimyrmex* in the head form which is elongate with distinct occipital corners, in uniformly denticulated mandibles, bidentate propodeum, and high petiole.

Archimyrmex rostratus Cockerell, 1923
Figs 12–18.

Archimyrmex rostratus: Cockerell, 1923, p. 51–52; Wheeler, 1928, p. 117; Carpenter, 1930, p. 16–17, Plate II, fig. 5; Bolton, 1995, p. 75; Dlussky, Perfilieva, 2003, p. 44, fig. 2.

HOLOTYPE (not examined): University of Colorado collection, # 15174; lateral imprint of worker; reverse imprint USNM #69617. Roan Mountain (Ute Trail), Colorado, USA. Middle Eocene (Lutetian), Green River Formation.

MATERIAL EXAMINED. USNM #495902, Anvil Points Area, Locality 40193, Garfield Co., Colorado, USA (coll. D. Kohls, 1991−93); USNM ##495984, 495985, 495986: Anvil Points Area, Labandeira Site, locality 41677, Garfield Co., Colorado, USA (coll. D. Kohls, 1999); USNM #495989, Denson Site; locality 41220; Garfield Co., Colorado, USA (coll. D. Kohls, 1996); USNM ##496001, 496002, 496004, Anvil Points Area, Labandeira Site, Locality 41678, Garfield Co., Colorado, USA (coll. D. Kohls, 1999); USNM #496003, Anvil Points Area, Logan Wash Site, Locality 41236, Garfield Co., Colorado, USA (coll. D. Kohls, 1998); USNM #496005A, Anvil Points Area, Denson Site, Locality 41617, Garfield Co., Colorado, USA (coll. D. Kohls, 1998). PIN # 4621/634, Anvil Points (coll. A. Rasnitsyn, 1997). Middle Eocene (Lutetian), Green River Formation.

Specimens ##495602, 496004 and 2−98 are laterally, and the others are dorsoventrally preserved. Head of all dorsoventrally preserved fossils except ##495986 and 496002 is turned under (usual feature of the fossil ants with long mandibles) and so visible from behind. All studied fossils are incomplete, with middle and hind femurs and tibiae observable in #495602, fragments of mandibles in ##495986 and 496004, and fragment of forewing in #495989.

DESCRIPTION. Female. Body length 13.2–15.8 mm. Head rounded, wider than long. Mandibles with some coarse, obtuse teeth, and small denticles between them. Scape long, reaching far beyond occipital margin of head (implied from preserved fragment of antenna in specimen 496002 and from general appearance of ants). Alitrunk elongate, about twice as long as high and wide. Scutum small and flat, longer than wide. Legs long and thin. Hind coxae not touching each other. Propodeum rounded in side view, without teeth. Petiole pedunculate, about twice as long as high and wide, with feeble dorsal elevation beyond midlength. Postpetiole campaniform, broadly attached to gaster, about as long as high and wide. Gaster small, about as long as waist, and shorter than alitrunk. Sting short and thick.

MEASUREMENTS, mm. Holotype (after Cockerell, 1923): AL 5.3; HL+MdL 4.0; F2 3.7; USNM #495602: AL 5.5, AH 2.3, F2 3.6, F3 4.1, PtL 1.7, PtH 0.9, PptL 1.6, PptH 1.4; USNM #495894: AL 5.8, AW 2.1, HW 2.5, PtL 2.0, PtW 0.9, PptL 1.6, PptW 1.3; USNM #495985: AL 4.4, AW 1.9, HL 1.95, HW 2.3; USNM #495986: AL 5.3, AW 2.5, HL 2.2, HW 2.8, PtL 2.0, PtW 1.0, PptL 1.5, PptW 1.5; USNM #495989: AL 5.5, AW 2.3, HW 2.7, PtL 1.8; USNM #496001: PtL 2.0, PtW 1.0, PptL 1.4, PptW 1.5; USNM #496002: AL 5.3, AW 2.4, HL 2.3, HW 3.1, PtL 2.2, PtW 1.1, PptL 1.5, PptW 1.6; USNM #496003: AL 4.2, PtL 1.5, PptL 1.1; USNM #496004: AL 5.4, PtL 2.2, PtH 1.1, PptL 1.7; USNM #496004: AL 4.4, AW 2.0, HW 2.2, PtL 1.7.

NOTES. We have not seen the holotype, however the specimens studied are very similar to the description and photo of the holotype in size, proportions and form of waist segments. The only important difference is the shape of propodeum. According Cockerell's description the propodeum ("epinotum") is armed with large and obtuse "elevations" (i. e. teeth or spines), while all studied specimens have rounded, unarmed propodeum. The contradiction is explainable with Carpenter's [1930] observation on the holotype: "I believe that what appears to be an epinotal spine is merely the only part of the epinotum which is exposed to its dorsal surface, the adjoining parts of the epinotum being covered by the matrix of the rock. In as much as the specimen was a holotype, however, no attempt was made to test this conclu-
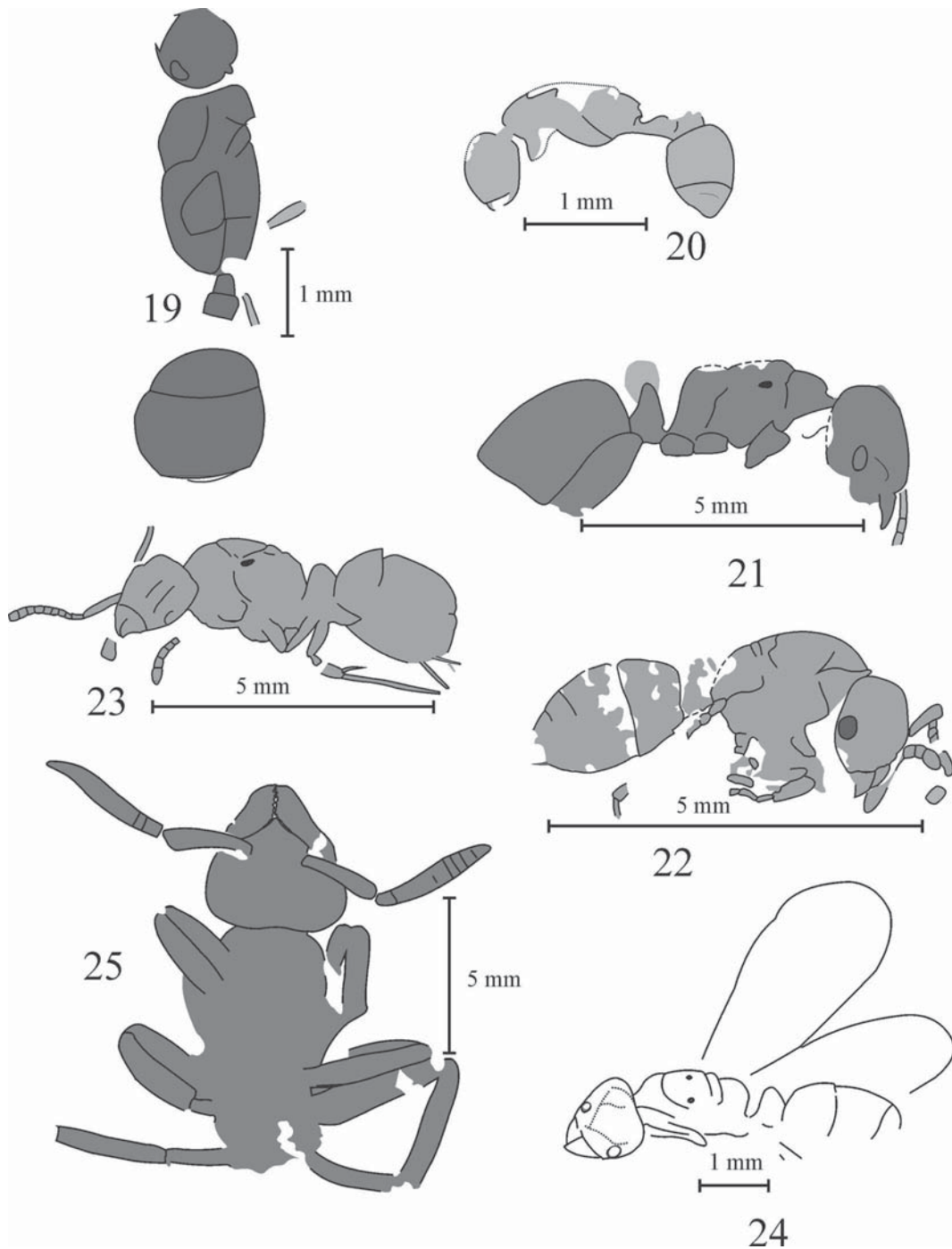
Figs 19−25. 19 — *Myrmecites rotundiceps* sp. n., ventral imprint, presumable female, holotype USNM # 495916; 20 — *Solenopsites minutus* sp. n., lateral imprint of female or worker, holotype USNM # 495933; 21 — *Ponerites eocenicus* sp. n., lateral imprint of female, holotype USNM # 495919; 22−23 — *Ponerites coloradensis* sp. n., lateral imprint of female, holotype USNM # 495896 (22), paratype USNM # 495895 (23); 24 — *Ponerites hypoponeroides* sp. n., holotype, USNM, combination of obverse(# 495991A) and reverse (# 495990) lateral imprints of the same female; 25 — *Pachycondyla labandeirai* sp. n., dorsal imprint of female, holotype USNM # 404747.

Рис. 19−25. 19 — *Myrmecites rotundiceps* sp. n., вентральный отпечаток, предположительно самки, голотип USNM # 495916; 20 — *Solenopsites minutus* sp. n., латеральный отпечаток самки или рабочего, голотип USNM # 495933; 21 — *Ponerites eocenicus* sp. n., латеральный отпечаток самки, голотип USNM # 495919; 22−23 — *Ponerites coloradensis* sp. n., латеральный отпечаток самки, голотип USNM # 495896 (22), паратип USNM # 495895 (23); 24 — *Ponerites hypoponeroides* sp. n., голотип, USNM, комбинация прямого (# 495991A) и обратного (# 495990) латеральных отпечатков одной и той же самки; 25 — *Pachycondyla labandeirai* sp. n., дорзальный отпечаток самки, голотип USNM # 404747.

sion by exposing the hidden part of the thorax". Based on this we believe, that the specimens we have studied belongs to the same species, the more so they were found in the same deposits.

Cockerell and Carpenter have described the holotype for a worker. All specimens we have studied that have head or top of gaster are females. As they are very similar to the description and photo of the holotype, it is possible that the holotype is the female too.

A. rostratus looks a common species in the Green River Formation comprising 6 (5.8%) of 104 randomly selected specimens. However the real share of this species might be less than that, for being of very large size, this ant may have higher chance to be both preserved as fossil and noticed by collectors.

Subfamily MYRMICINAE Lepeletier, 1835

DIAGNOSIS (for wingless fossils). Female and worker antennae geniculate, male antennae variable. Workers with no ocelli. Mandibles dentate or denticulate, not bidentate (linear and edentate in some extant parasitic species). Hind tibiae with single simple or pectinate spur, or with no spur. Waist of two segments (petiole and postpetiole); postpetiole narrowly attached to gaster. Pygidium simple, convex in side view. Sting always present, sometimes small.

NOTES. 4377 extant and 145 fossil species are known subordinated to 152 extant and 23 extinct genera. Myrmicinae dominate in many contemporary ecosystems, but rare in most of fossil deposits. The earliest fossil myrmicine ant is *Eocenidris crassa* Wilson, 1985 from the Middle Eocene Arkansas amber. In the Upper Eocene Baltic amber Myrmicinae comprise less than 2% of individuals and 25 of 92 species, in the Lower Oligocene deposits of Florissant 5% of individuals and 8 of 32 species. Only in the Miocene deposits the myrmicine share approaches to the contemporary one [Dlussky, 1981].

10 fossil species in 7 myrmicine genera are described from North America: *Eocenidris crassa* Wilson, 1985 (Middle Eocene, Arkansas amber); *Aphaenogaster donisthorpei* Carpenter, 1930; *A. mayri* Carpenter, 1930; *Cephalomyrmex rotundatus* Carpenter, 1930; *Eulithomyrmex* (=*Lithomyrmex*) *rugosus* (Carpenter, 1930); *E. striatus* (Carpenter, 1930); *Messor sculpturatus* Carpenter, 1930; *Pheidole tertiaria* Carpenter, 1930; *Pogonomyrmex fossilis* Carpenter, 1930 (Lower Oligocene, Florissant), and *Aphaenogaster praerelicta* de Andrade, 1995 (Miocene, Mexican amber). Two new species are described below from the Green River Formation.

Formal genus *Myrmecites* Dlussky et Rasnitsyn, **gen.n.**

TYPE SPECIES. *Myrmecites rotundiceps* sp.n.
DIAGNOSIS. Ant impression fossils with waist two-segmented and short (less than half as long as gaster and less than one third as long as alitrunk), petiole sessile, and postpetiole narrowly attached to gaster, which cannot be identified more precisely.

SPECIES INCLUDED. Type species only.

COMPARISION. In spite of poor preservation state of the only known specimen, it differs clearly from all known Eocene ants and from all New World fossil ants with two-segmented waist by the very short waist. However, the generic and tribal level characters are not available, and the general appearance is similar to various genera and tribes of Myrmicinae. That is why we have to describe it in a new formal genus.

ETYMOLOGY. From the ant genus *Myrmica*.

Myrmecites rotundiceps Dlussky et Rasnitsyn, **sp.n.**
Fig. 19

MATERIAL EXAMINED. Holotype, USNM #495916, poorly preserved ventral imprint, presumable female. Anvil Points Area, Locality 40193, Garfield Co., Colorado, USA (D. Kohls, 1991−93). Middle Eocene (Lutetian), Green River Formation.

DESCRIPTION. Presumably female. Body length 5.5 mm. Head round, without occipital corners, nearly as long as wide. Eyes of moderate size, oval, situated at midlength of head sides. Clypeus broad, with rounded anterior margin. Alitrunk elongate, about twice as long as wide. Petiole trapezoidal in dorsal view, widest at rear end, as long as wide. Postpetiole subrectangular in dorsal view, somewhat wider than long. Gaster oval. Sides of alitrunk with coarse chagrinned sculpture, postpetiole with longitudinal rugae.

MEASUREMENTS, mm. AL 2.0; AW 1.1; HL 0.75; HW 0.875; PtL 0.25; PtW 0.26; PptL 0.30; PptW 0.40.

ETYMOLOGY. Rotundiceps is the Latin for "with round head".

Formal genus *Solenopsites* Dlussky et Rasnitsyn, **gen.n.**

TYPE SPECIES. *Solenopsites minutus* sp.n.
DIAGNOSIS. Ant impression fossils with waist two-segmented and long (more than half as long as gaster and nearly half as long as the alitrunk), with propodeum unarmed, petiole pedunculate and postpetiole narrowly attached to gaster, which cannot be identified more precisely.

SPECIES INCLUDED. Type species only.

NOTE. In spite of poor preservation state, the fossil under description differs well from all fossil ants known in the New World because of its small body size (1.9 mm in contrast to 5 mm or more in other fossils) except about 1.5 mm long *Eocenidris crassa* Wilson which differs in bidentate propodeum and high (more high than long) petiole. General appearance is similar to that of some *Solenopsis* Westwood, 1840, but characters necessary for correct identification are not visible, and similarity may be convergent. That is why we describe this species in a new formal genus.

ETYMOLOGY. From the ant genus *Solenopsis*.

Solenopsites minutus Dlussky et Rasnitsyn, **sp.n.**
Fig. 20

MATERIAL EXAMINED. Holotype: USNM #495933, poorly preserved lateral imprint of female or worker. Anvil Points Area, Locality 40193, Garfield Co., Colorado, USA (D. Kohls, 1991−93). Middle Eocene (Lutetian), Green River Formation.

DESCRIPTION. Body length 2.9 mm. Head subrectangular with rounded occipital corners and convex occipital margin; about one and a half times as long as wide. Alitrunk elongate, more than twice as long as high. Propodeum feebly convex, unarmed. Petiole pedunculate, with low node.

MEASUREMENTS, mm. AL 1.15; HL 0.63; HW 0.44; PtL 0.61; PtH 0.17.

ETYMOLOGY. Minutus is the Latin for small.

Subfamily PONERINAE Lepeletier, 1835

DIAGNOSIS (for wingless fossils). Female and worker antennae geniculate, male antennae with short scape, often filiform. Workers with no ocelli. Mandibles dentate or denticulate, not bidentate. Hind tibiae usually with two spurs, larger one being pectinate and shorter one simple; rarely with one

pectinate spur. Waist of one segment (petiole) of different shape. Gaster usually with constriction between first and second segments. Pygidium usually convex in side view, without denticles, teeth or spines; very rarely (in some extant genera) with few teeth or pair of spines. Sting always present; often large and strongly developed.

NOTES. At present 1299 extant and 81 fossil species are known in 42 extant and 9 extinct genera. They are common though never abundant in many contemporary tropical and subtropical ecosystems, rare or absent in the temperate ones. The earliest fossil ponerine ant was described from the Late Cretaceous fossil resin of New Jersey [Grimaldi et al., 1997]. Although Ponerinae are discovered in most Cenozoic fossil ant assemblages, they are abundant in no deposit. For example, in the Late Eocene Baltic amber they comprise less than 1% of inclusions and 8 of 92 described species; in the Lower Oligocene deposits of Florissant only two of 5594 ant impression fossils belong to one species of Ponerinae. The only exception is the Fur and Ølst Formations in Denmark (transitional between Paleocene and Eocene), where about a hundred imprints of *Pachycondyla rebekkae* Rust et Andersen were described [Rust, Andersen, 1999].

Three fossil species of Ponerinae are described from North America: *Brownimecia clavata* Grimaldi, Agosti et Carpenter, 1997 (Upper Cretaceous, Turonian, New Jersey amber), *Canapone dentata* Dlussky, 1999 (Upper Cretaceous, Campanian, Canadian amber), and *Archyponera wheeleri* Carpenter, 1930 (Lower Oligocene, Florissant). Brown [1953] have found *Pachycondyla* sp. in Mexican amber (Lower Miocene), but the species was not described. Six new species from Green River Formation are described below.

Formal genus *Ponerites* Dlussky et Rasnitsyn, **gen.n.**

"*Ponera* (?)": Popov, 1933: 17; Taylor, 1964: 134
"*Ponerites*": Dlussky, 1981: 67, informal name without taxonomic meaning.
TYPE SPECIES. *Ponerites eocenicus* sp.n.
DIAGNOSIS. Fossil ants preserved not well enough to fit orthotaxa, and with following combination of traits: size small or medium, head subrectangular with rounded occipital corners; eyes comparatively small, situated before midlength of head sides; mandibles triangular with denticulate masticatory margin; promesonotal and mesopropodeal sutures present in workers; conspicuous sculpture, denticles or spines absent from head, alitrunk and waist; petiole with thick scale; gaster with constriction between first and second gastral (III and IV abdominal) segments; second gastral (IV abdominal) tergite and sternite subequal, gastral apex not directed downwards; sting well developed.

SPECIES INCLUDED. Three species described below, and *P. umbrus* (Popov, 1932) from the Middle Miocene of North Caucasus. Evidently some European Miocene and Oligocene ants, described as *Ponera*, also deserve allocating here.

NOTES. Key traits used to distinguish extant genera of the tribe Ponerini (shape of ventral petiolar lobe, dentition of mandibular masticatory margin, number of spurs of middle and hind tibiae) are not visible on the most impression fossils of small, nonspecialized Ponerinae. Taylor [1964] designed these fossils as "*Ponera* (?)", and the informal name "*Ponerites*" has been later coined for them [Dlussky, 1981]. Now we propose to use the latter name as valid for a formal genus with the above diagnosis.

Extant genera *Ponera* Latreille, 1804, *Hypoponera* Santschi, 1938, and partially *Pachycondyla* F. Smith, 1858 and may be some other ponerine genera agree with the diagnosis of *Ponerites*.

The formal genus *Poneropsis* Heer, 1867 (type species *Ponera fuliginosa* Heer, 1849), has completely diferent coverage as interpreted by Taylor [1964]. Taylor proposed it to designate ant forewings described as *Ponera* Latreille, 1804. However, his re-definition of *Poneropsis* has resulted in its much wider application, *viz.* for all detached ant wings with complete venation. This is because Taylor has missed some important traits, and particularly position of cu-a, which permits to distinguish forewings of Ponerinae and several other ant subfamilies (Armaniinae, Sphecomyrminae, Myrmeciinae, Nothomyrmeciinae, Pseudomyrmecinae, Cerapachyinae, Dorylinae and Ecitoninae) from a group of the venationally advanced subfamilies (Myrmicinae, Aneuretinae, Dolichoderinae, Formicinae and Formiciinae). As a result, *Poneropsis* can accommodate majority of the ant wing fossils.

Further confusion is possible with the name *Poneropsis*, for Mayr [1867] re-examined three specimens identified by Heer as *Ponera fuliginosa* and found that they had two-segmented waist and might be females of *Aphaenogaster* Mayr, 1853, a genus of Myrmicinae. Therefore we refrain ourselves of using this name until the type specimen is re-studied.

Ponerites eocenicus Dlussky et Rasnitsyn, **sp.n.**
Fig. 21

MATERIAL EXAMINED. Holotype: USNM #495919, incomplete lateral imprint of female. Anvil Points Area, Locality 40193, Garfield Co., Colorado, USA (coll. D. Kohls, 1991−93). Middle Eocene (Lutetian), Green River Formation.
DESCRIPTION. Female. Body length about 9.5 mm. Eyes small, oval, situated near mandibular bases. Mandibles triangular. Scutum convex, distinctly separated from pronotum by promesonotal groove. Metanotal groove distinct, mesonotum and propodeal dorsum forming angular impression in side view. Propodeum angular in side view; propodeal declivity nearly twice as long as propodeal dorsum. Petiole triangular in side view, with rounded top, twice as high as long.
MEASUREMENTS, mm. AL 3.0; HL 2.1; PtL 0.55; PtH 1.12.
COMPARISION. Differs from *P. umbrus* (Popov) in larger body size (alitrunk 3 mm long *vs*. 2 in *P. umbrus*) and comparatively narrow, triangular scale of petiole.
NOTE. The species is superficially similar to some recent *Pachycondyla* but key diagnostic characters of the genus are not seen in the fossil.
ETYMOLOGY. Species name is after Eocene.

Ponerites coloradensis Dlussky et Rasnitsyn, **sp.n.**
Fig. 22, 23

MATERIAL EXAMINED. Holotype: USNM #495896; relatively well-preserved lateral imprint of female; Paleoburn, Locality 40190, Garfield Co., Colorado, USA (coll. D. Kohls, 1991−93). Middle Eocene (Lutetian), Green River Formation. Paratype: USNM #495895, lateral imprint of female; collected at the same locality.
DESCRIPTION. Female. Body length 6.2–6.7 mm. Head subrectangular with convex sides, nearly as long as wide; occipital corners distinct; occipital margin convex. Eyes nearly round, situated slightly before midlength of head sides. Mandibles triangular (dentition of masticatory margin is not visible). Scape about as long as head wide. 2–5 joints of funiculus a little longer than wide; apical joints thicker but not forming distinct clava. Alitrunk dorsum convex in side view, without distinct promesonotal and metanotal grooves. Pronotum longer than scutum. Propodeum rounded in side view. Legs relatively short and thick. Scale of petiole thick and high. Sting well developed.

MEASUREMENTS, mm. Holotype: AL 2.25; HL 1.3; HW 1.2. Paratype: AL 2.2; HL 1.3.

COMPARISION. Differs from other congeners in alitrunk robust and scale thick and rounded apically in side view.

NOTE. The fossil looks similar to some extant *Pachycondyla* but key diagnostic characters of the genus are not seen.

ETYMOLOGY. Species name is after Colorado State and River.

Ponerites hypoponeroides Dlussky et Rasnitsyn, **sp.n.**
Fig. 24

MATERIAL EXAMINED. Holotype: USNM #495991A (obverse) and #495990 (reverse), Denson Site; locality 41223 (coll. D. Kohls,1997); lateral imprints of the female with preserved forewings, but without visible venation.

DESCRIPTION. Female. Body length about 5 mm. Head subtrapezoidal, longer than width, with weakly convex sides, rounded occipital corners and straight middle part of the occipital margin. Eyes small, oval, situated distinctly before midlength of head sides. Mandibles triangular, probably with finely dentate masticatory margin. Alitrunk narrow. Pronotum elongate, not overhung by scutum. Scutum flattened. Propodeum angular, with dorsum and declivity forming rounded right angle. Petiole with thick scale, triangular in side view, with rounded top, less than twice as high as long. Gaster elongate, with weak but well-marked constriction between first and second segments.

MEASUREMENTS, mm. AL 1.8; HL 1.3; HW 1.15; PtL 0.38; PtH 0.61; FWL 3.8.

COMPARISION. Differs from other congeners in small size (alitrunk less than 2 mm long) and comparatively wide head.

NOTE. The species looks very similar to some recent *Hypoponera*, but key diagnostic characters of the genus (tibial spurs, mandibular dentition, shape of ventral petiolar lobe) are not visible.

ETYMOLOGY. From the ant genus *Hypoponera* Em.

Genus *Pachycondyla* F. Smith, 1858.

TYPE SPECIES. *Formica crassinoda* Latreille, 1802.

DIAGNOSIS (for wingless female fossils). Large or medium sized robust ants. Head subrectangular, subquadrate or subtrapezoidal with rounded occipital corners, and with feebly convex, straight or feebly concave occipital margin. Antennal fossae close to each other. Mandibles triangular with several rather large obtuse teeth on masticatory margin. Hind tibiae always with two spurs: larger spur pectinate, shorter one simple. No denticles or spines on head, alitrunk, and waist. Petiole with thick scale. Gaster with constriction between first and second segments; second gastral tergite and sternite subequal, gastral apex not bent downwards. Sting well developed.

NOTES. Diverse genus now distributed mainly in tropical regions. 201 extant and 8 fossil species are described, including 3 Eocene ones: *P. gracilicornis* (Mayr) and *P. succinea* (Mayr) from the Late Eocene Baltic amber and *P. rebekkae* Rust et Anderson, 1999 from Fur and Ølst Formations in Denmark which are transitional between Paleocene and Eocene.

Pachycondyla labandeirai Dlussky et Rasnitsyn, **sp.n.**
Fig. 25

MATERIAL EXAMINED. Holotype: USNM #404747, Little Mountain, Sweetwater County, Wyoming, locality 41427−25 (coll. P. Wilf ,1998); incomplete dorsal imprint of female with gaster and petiole missing. Middle Eocene (Lutetian), Green River Formation.

DESCRIPTION. Female. Large robust ant. Head subtrapezoidal with rounded occipital corners and feebly concave occipital margin. Anterior margin of the clypeus with medial denticle or rounded lobe. Mandibles massive, triangular, with 7 large obtuse teeth on masticatory margin. Scape thick. Funiculus thick in middle part and spicate to the top. Middle segments of funiculus twice as thick as long. Legs thick and comparatively short.

MEASUREMENTS, mm. AL 7.5; HL with mandibles 4.5; HL 3.5; HW 4.4; SL 2.7; funiculus length 40.

NOTES. Waist and gaster of the unique holotype are absent, so formally it cannot be placed to any ant genus or subfamily. However construction of the head and general appearance of the fossil is similar to some living species of *Pachycondyla* enough to include it, albeit not without some doubts, to this genus.

COMPARISION. New species differs from all described Paleogene Ponerinae except *P. rebekkae* in giant size (all other species have AL <3.5 mm). *P. rebekkae* is of approximately same size but has head longer than wide, mandibles about as long as head wide, and antennae longer and slender.

ETYMOLOGY. The species is named in honor to paleoentomologist Conrad C. Labandeira.

Formicidae incertae sedis

Formal genus *Eoformica* Cockerell, 1921

Liometopum: Scudder, 1877: 742 (nec Mayr, 1861).
Lasius: Scudder, 1878: 747 (nec Fabricius, 1804).
Eoformica Cockerell, 1921: 38, Wheeler, 1928: 117; Carpenter, 1930: 17; Bolton, 1995: 188.
"*Formicites*" Dlussky, 1981: 75, informal name without taxonomic meaning.

TYPE SPECIES. *Eoformica eocenica* Cockerell, 1921 (= *Liometopum pingue* Scudder, 1877).

DIAGNOSIS. Wingless impression fossils of male and female ants with waist one-segmented and narrowly attached to gaster and with gaster lacking constriction between first and second segments. Head suboval, subtrapezoidal, subrectangular (not elongate rectangular), hearth- or retort-shaped. Eyes well developed. Alitrunk unarmed. Scutum large and convex, taking near half alitrunk length. Petiole relatively small, sessile, without scale, subconical or subcylindrical with feebly convex sides in dorsal view; rounded dorsally in side view. Gaster not over-hanging petiole anteriorly. Sting never seen, probably absent. Male genital parts small and weakly sclerotized, rarely visible. Integument thin, lacking visible sculpture.

SPECIES INCLUDED: the type species and two species described below, all from the Middle Eocene of North America. Additionally, specimens USNM 495881 and 495885 (Savage, Colorado, Green River Formation) may belong to further species of *Eoformica*, but their preservation state is too poor to warrant description. Imprints of two or three species of "Formicites" from Miocene of Kirghizia (Chon-Tuz), that were drawn but not described [Dlussky, 1981], also agree with the diagnosis of *Eoformica*. Numerous other poorly preserved impression fossils described in *Formica*, *Lasius*, *Iridomyrmex* and possibly in other genera should be probably transferred to *Eoformica* as well.

NOTES. Study of the holotype of *Eoformica eocenica* reveals the head as incorrectly restored by Cockerell [1921] (cf. his fig. 9 and our fig. 26). We can also confirm the inference by

Carpenter [1930] that, contrary to Cockerell [1921], *Eoformica* shows no specific similarity to *Oecophylla* F. Smith, 1860 in construction of its legs and petiole (figs 26–31).

Taxonomic position of *Eoformica* within Formicidae is not apparent. One-segmented waist and gaster lacking constriction between the first and second gastral (III and IV abdominal) segments are characteristic of male and female Aneuretinae, Dolichoderinae, Formicinae, Dorylinae, Ecitoninae, Nothomyrmeciinae and Formiciinae. Females of Dorylinae and Ecitoninae are wingless, and general appearance of their males is specific and quite different from that of *Eoformica*. Formiciinae are giant ants (body length 40–70 mm), and their females have very large oval propodeal spiracles usually well seen in impression fossils. Subfamily Nothomyrmeciinae includes the only living species *Nothomyrmecia macrops* Clark, 1934 that differs easily in pedunculate petiole and unusual general habitus.

So Aneuretinae, Dolichoderinae and Formicinae are the only ant subfamilies that *Eoformica* is similar to. They differ in construction of apex of the female gaster and in some other characters (male tibial spurs, forewing venation, etc.) impossible to discern in many impression fossils. There is indirect evidence that may help identifying subfamilial position of some fossils. All known Aneuretinae have elongate petiole with distinct node and peduncle. Female Formicinae usually have squamiform petiole, while males often have petiole low triangular in profile view, and females of some desert (*Cataglyphis* Foerster, 1850) and dendrobiotic (*Oecophylla* F. Smith, 1860, *Dendromyrmex* Emery, 1895) genera often have nodiform petiole. However, dendrobiotic Formicinae differ from *Eoformica* in having longer legs and antennae. Many male and female Dolichoderinae are similar to *Eoformica* in form of scaleless petiole. Male Formicinae always have scape long unlike majority of the male Dolichoderinae which usually have short scape. Scape length of *Eoformica* is variable: it is short in E. *pinguis* and long in E. *magna*. So the indirect evidence identifies *Eoformica* as Dolichoderinae or aberrant Formicinae. In particular, it cannot be excluded that, being better known, some or many species included would agree with definition of the primitive dolichoderine genus *Eotapinoma* Dlussky, 1988, known from Late Cretaceous (Canadian amber) and Paleocene (Sakhalin amber). However proper comparison of the two genera is impossible because *Eoformica* is known only from imperfectly preserved impression fossils of males and females, and *Eotapinoma* from worker inclusions in fossil resins.

Eoformica pinguis (Scudder, 1877)
Figs 26–31

Liometopum pingue Scudder, 1877: 742;
Lasius terreus Scudder, 1878: 747; Bolton, 1995: 226; syn. n.
Eoformica eocenica Cockerell, 1921: 38;
Eoformica pingue: Carpenter, 1930: 17;
(Formicidae) *terreus*: Carpenter, 1930: 19; syn. n.
Eoformica pinguis: Bolton, 1995: 188.
HOLOTYPE. imprint of female, MCZ #2937 (not examined). Green River City, Wyoming, USA. Middle Eocene (Lutetian), Green River Formation.
MATERIAL EXAMINED. USNM #66932, male, Smith's Ranch, Colorado, USA (holotype of Eoformica eocenica Cockerell). Garfield Co., Colorado, USA: USNM ##495874 (male), 495875 (? male), Old Mountains, Locality 40189 (coll. D. Kohls, 1991–93); USNM ##495882 (male), 495884 (male), 495886a (? male), Savage, Locality 40192 (coll. D. Kohls, 1991–93);

USNM ##495887 (male), 495888 (? male), Mahaffey Trail, Locality 41087 (coll. D. Kohls, 1995); USNM #495890 (male), 495893 (female), Mahaffey Trail, Locality 40911 (coll. D. Kohls, 1991–93); USNM ##495897 (?), 495899 (? female), 495900 (male), 495903 (male), 495910 (4 males), 495913 (? male), 495915 (male), 495918 (male), 495920 (?), 495924 (? male), 495929 (? female), 495931 (female), 495934 (male), 495938 (male), 495960 (2 ? females), Anvil Points Area, Locality 40193 (coll. D. Kohls, 1991–93); USNM ##495946 (female), 495947 (male), 495951 (?), 495953 (male), 495954 (male), 495955 (male), 495956 (male), 495960 (2 ?females), Anvil Points Area, Labandeira Site, Locality 41088 (coll. D. Kohls, 1995); USNM #495962 (male), Anvil Points Area, Kohls Site, Locality 41089 (coll. D. Kohls, 1995); PIN ##4621/639 (female), 4621/674, 4621/833 (males), Anvil Points (coll. A. Rasnitsyn, 1997). Middle Eocene (Lutetian), Green River Formation. USNM ##495993 (female), 495994 (? male), Disbrow Creek locality, Site 10; locality 41621 (coll. N. Constenius ,1998); Pinnacle Quadrangle, Garfield County, Montana, USA; Middle Coal Creek Member, Kishenehn Formation, Eocene (Lutetian).

DESCRIPTION. Male. Body length 6.00–6.85 mm (average 6.35 mm). Head without occipital corners visible in full face view; wider than long. Anterior margin of clypeus concave (as seen in dorsal imprints USNM ##495915 and 495929). Eyes convex and very large, occupying most part of head sides. Scape (preserved in USNM #495953) shorter than head. Alitrunk elongate and relatively low: AL/AH 1.25–1.5. Scutum large and convex but not over-hanging pronotum anteriorly; pronotum visible as narrow band in all better preserved dorsal imprints. Petiole small (AL/PtL 4–6), subconical or subcylindrical, a little longer than high.

Female. Body length 7.3–7.5 mm. Head wider than long, subrectangular, widest behind midlength, with conspicuous, rounded occipital corners and straight or feebly convex occipital margin. Eyes of moderate size, oval, situated midlength of head sides. Anterior margin of clypeus convex. Scutum large and convex, not over-hanging pronotum anteriorly. Petiole as in male.

MEASUREMENTS, mm. Holotype (after Carpenter [1930]): BL 7.5; AL 3.0; AW 2.2; HL 1.2; HW 1.2; gaster length 2.7; gaster width 2.7. Holotype of *Eoformica eocenica* Cockerell: BL 6.3; AL 2.9; AH 2.0; HL 1.15; F3L 2.44; PtL 0.71; PtW 0.54. Variability: Males: AL 2.45–2.95 (average 2.73, n 13); AH 1.60–2.15 (n 2); HL 1.0–1.15 (n 2); HW 0.65–1.25 (average 1.03, n 6); SL 0.60 mm (495953); F2 1.75–2.00 (n 3); F3 2.25–2.35 (n 2); PtL 0.50–0.71 (average 0.59, n 11); PtW 0.48–0.65 (average 0.57, n 8); PtH 0.50–0.55 (n 2). Females (n 3): AL 3.15–3.50; PtL 0.60–0.68; PtH 0.60–0.65.

SYNONYMY. Scudder [1877] described this species as *Liometopum pingue*, based only on general appearance. It cannot be *Liometopum*, because male Liometopum have large and heavily sclerotized genital parts, which should left preserved in most fossils, and females have squamiform petiole. Later Cockerell [1921] described *Eoformica eocenica*. Carpenter [1930] has studied types of both species, found them conspecific and proposed the name *Eoformica pingue*. Bolton [1995] has corrected the name grammatically as *Eoformica pinguis*.

Description of *Lasius terreus* Scudder, 1878 does not contain any characters distinguishing this species from the female of *E. pinguis*. We have not seen the fossil, but Carpenter [1930] has studied the holotype (USNM 69618, Green River City, Wyoming, USA) and concluded that "The single specimen of this species is very poorly preserved, and since I have not been able to discern in the type many of the characters given by Scudder in the description". In this connection it seems to us expedient to consider this species as a junior synonym of *E. pinguis*.
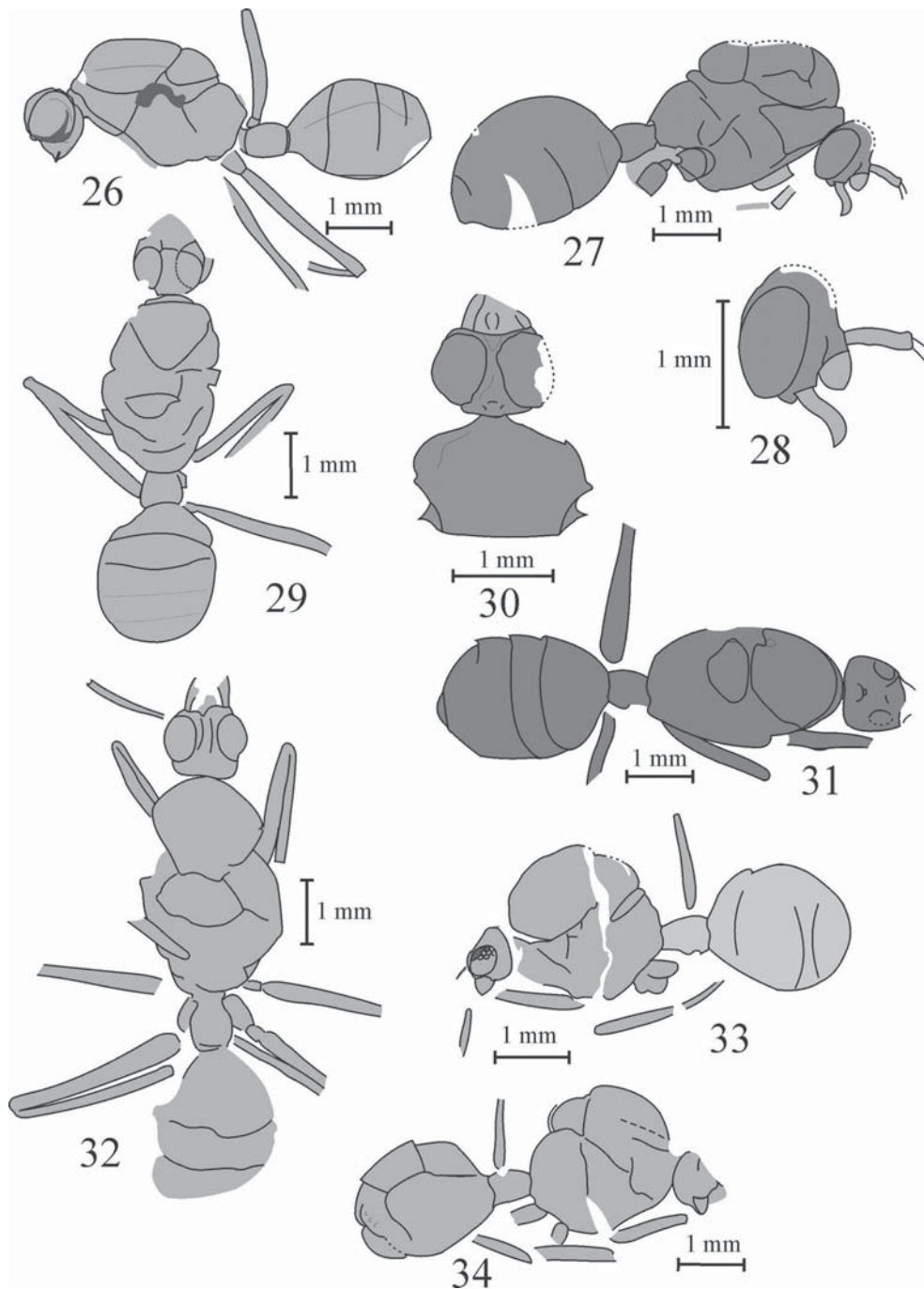
Figs 26–34. 26 — *Eoformica pinguis* (Scudder), USNM # 66932 (holotype of Eoformica eocenica Cockerell), lateral imprint of male; 27–31 — *Eoformica pinguis* (Scudder), USNM # 495953, lateral imprint of male (27), head of male in profile (28), USNM # 495934, dorsal imprint of male (29), USNM # 495915, head of male in full-face view (30), USNM # 495956, dorsal imprint of female (31); 32 — *Eoformica magna* sp.n., holotype USNM # 495917, combination of obverse and reverse dorsal imprints of male; 33–34 — *Eoformica globularis* sp. n., lateral imprint of male, holotype USNM # 495940 (33), paratype USNM # 495886b (34).

Рис. 26–34. 26 — *Eoformica pinguis* (Scudder), USNM # 66932 (голотип Eoformica eocenica Cockerell), латеральный отпечаток самца; 27–31 — *Eoformica pinguis* (Scudder), USNM # 495953, латеральный отпечаток самца (27), голова самца в профиль (28), USNM # 495934, дорзальный отпечаток самца (29), USNM # 495915, голова самца сверху (30), USNM # 495956, дорзальный отпечаток самки (31); 32 — *Eoformica magna* sp.n., голотип USNM # 495917, комбинация прямого и обратного дорзальных отпечатков самца; 33–34 — *Eoformica globularis* sp. n., латеральный отпечаток самца, голотип USNM # 495940 (33), паратип USNM # 495886b (34).

DISTRIBUTION. *E. pinguis* is the most abundant ant species in the Green River Formation, comprising 42 (40.4%) out of 104 randomly selected ant fossils. It is recorded in the following localities. Wyoming: Green River City. Utah, Uinta Co.: Wagon Hound Cañon, Fossil Cañon, White River Cañon, White River. Colorado: Cathedral Bluffs, Smith's Runch [Cockerell, 1921]; Rio Blanco Co.: Dripping Rock Cañon, Roan Mountains [Carpenter, 1930]; Garfield Co.: Old Mountains, Savage, Mahaffey Trail, Anvil Points.

Eoformica magna Dlussky et Rasnitsyn, **sp.n.**
Fig. 32.

MATERIAL EXAMINED. Holotype, USNM #495917, comparatively well preserved dorsal imprint of male. Anvil Points Area, Locality 40193, Garfield Co., Colorado, USA (D. Kohls, 1991−93). Middle Eocene (Lutetian), Green River Formation.

DESCRIPTION. Male. Body length about 7 mm. Head longer than wide above eyes, a little shorter than wide including eyes; occipital corners rounded; occipital margin feebly concave in full face view. Eyes convex, not as large as in *E. pinguis*; situated before midlength of head sides. Scape longer than head. Scutum large, about as long as wide; over-hanging pronotum anteriorly. Scutellum one and a half times as wide as long. Petiole small (AL/PtL 4.06), a little longer than wide, with sides convex in dorsal view, sharply narrowing anteriorly.

MEASUREMENTS, mm. AL 3.25; HW 1.1; F3L 2,6; PtL 0.8.

COMPARISON. Differs from male *E. pinguis* in somewhat larger size (alitrunk 3.25 mm long *vs.* 2.45–2.95 in *E. pinguis*) and scape longer than head (shorter than that in *E. pinguis*).

ETYMOLOGY. Magnus is the Latin for large.

Eoformica globularis Dlussky et Rasnitsyn, **sp.n.**
Figs 33, 34.

MATERIAL EXAMINED. Holotype, USNM #495940, lateral imprint of male, Anvil Points Area, Locality 40193, Garfield Co., Colorado, USA (D. Kohls, 1991−93). Paratype: USNM #495886b, Savage, Locality 40192, Garfield Co., Colorado, USA (D. Kohls, 1991−93). Middle Eocene (Lutetian), Green River Formation.

DESCRIPTION. Male. Body length 5.6 mm. Eyes convex, smaller than in *E. pinguis*; with large facets; situated near mandiblar base. Alitrunk round in side view, about as long as high. Scutum large and strongly convex, overhanging pronotum anteriorly. Scutellum also strongly convex, forming deep impression at boundary with scutum. Petiole relatively long (AL/PtL 3.2–3.6), subtrapezoidal in side view, with feebly convex dorsum.

MEASUREMENTS, mm. Holotype: AL 2.25; AH 2.3; PtL 0.7; PtH 0.6. Paratype: AL 2.3; AH 2.35; HL 0.85; PtL 0.65; PtH 0.55.

COMPARISON. Differs from other congeners in globular form of alitrunk and relatively long petiole (AL/PtL = 3.2–3.6 *vs.* >4 in *E. magna* and *E. pinguis*).

ETYMOLOGY. Globularis is the Latin for globular.

Formal genus *Klondikia* Dlussky et Rasnitsyn, **gen.n.**

TYPE SPECIES *Klondikia whiteae* sp.n.

DIAGNOSIS. Wingless impression fossils of male and female ants with waist one-segmented and narrowly attached to gaster and with gaster lacking constriction between first and second segments. Female head rectangular. Alitrunk elongate, unarmed. Petiole relatively small, subconical, sessile, without scale. Gaster not over-hanging petiole anteriorly. Sting invisible, probably absent. Male genital parts large and sclerotized. Integument thin, without visible sculpture.

COMPARISON. Differs from *Eoformica* in male sex in large sclerotized genitalia. Females are known only in *Eoformica pinguis* and *Klondikia whiteae*; they show no difference of undoubtedly generic level but clearly differ specifically in size (AL = 2.05 mm in *K. whiteae* and more than 3 mm in *E. pinguis*) and proportion of head (longer than wide in *K. whiteae* vs. wider than long in *E. pinguis*).

ETYMOLOGY. The genus name is after the Klondike Mountain Formation.

Klondikia whiteae Dlussky et Rasnitsyn, **sp.n.**
Fig. 35, 36.

MATERIAL EXAMINED. Holotype, SIC #SR−94−5−7, poorly preserved obverse and reverse imprints of male, location B4131, the Stonerose fossil site located in the City of Republic , Ferry Co., Washington, USA (coll. Pat White, 12.08.1997). Paratype, SIC #SR−94−4−24, poorly preserved ventral imprint of female, location B4599, Mt Elizabeth, approximately 15 miles north of Republic, Ferry Co., Washington, USA (coll. Grace Adams, 20.VIII.93). Middle Eocene (Lutetian), Klondike Mountain Formation.

DESCRIPTION. Male. Body length 4.8 mm. Scape distinctly curved near base, about as long as head wide. Funiculus filiform. Alitrunk about 2.5 times longer than wide. Legs rather short and thick. Petiole small, subtrapezoidal in dorsal view, widest behind midlength. Genital stipes massive, with rounded top and small denticle in the middle.

Female. Body length 5.5 mm. Head subrectangular, longer than wide, with subparallel sides and rounded distinct occipital corners. Scape distinctly curved near base. Alitrunk elongate (AL/AW 1.7). Legs rather short and thick. Petiole small (AL/PtL 4.2), subtrapezoidal in lateral view, widest behind midlength.

MEASUREMENTS, mm. Holotype AL 2.05; HW 1.03; SL 0.97. Paratype. AL 1.31; AW 0.75; HL 0.94; HW 0.86; PtL 0.31.

NOTES. Male and female, although found in different localities of the same Klondike Mountain Formation, are similar in general appearance and preservational features enough to be considered conspecific.

ETYMOLOGY. The species is named in honor to Pat White who has collected the holotype.

Formal genus *Kohlsimyrma* Dlussky et Rasnitsyn, **gen.n.**

TYPE SPECIES *Kohlsimyrma laticeps* sp.n.

DIAGNOSIS. Medium sized or comparatively large ants. Head subquadrate or subtrapezoidal, widest behind midlength, with rounded occipital corners. Antennae geniculate; funiculus filiform. Mandibles triangular. Propodeum unarmed. Waist of one segment (petiole), massive, without scale, narrowed toward both ends. Gaster oval, without visible constriction between first and second segments; gastral apex not bent downward. Integument thick. Sing never visible, probably lost.

NOTES. The unusual shape of petiole is a key character of *Kohlsimyrma*. There is no known recent and fossil Formicinae, Dolichoderinae, and Aneuretinae that have such massive petiole. Some recent Ponerinae and the fossil ponerine *Platythyrea primoeva* Wheeler, 1915 from the Baltic amber have massive petiole which is, however, either truncate posteriorly (in *Platythyrea* Roger, 1863, *Plectroctena* F. Smith, 1858, some *Pachycondyla* F. Smith, 1858), or bidentate (in *Diacamma* Mayr,1862) or else broadly attached to the gaster (in Amblyoponini). Fossil *Archiponera wheeleri* Carpenter, 1930 (Oligocene, Florissant) is the only known species with similar petiole shape, but it differs strikingly in trapezoid head widened forward (like in Amblyoponini) and very short and
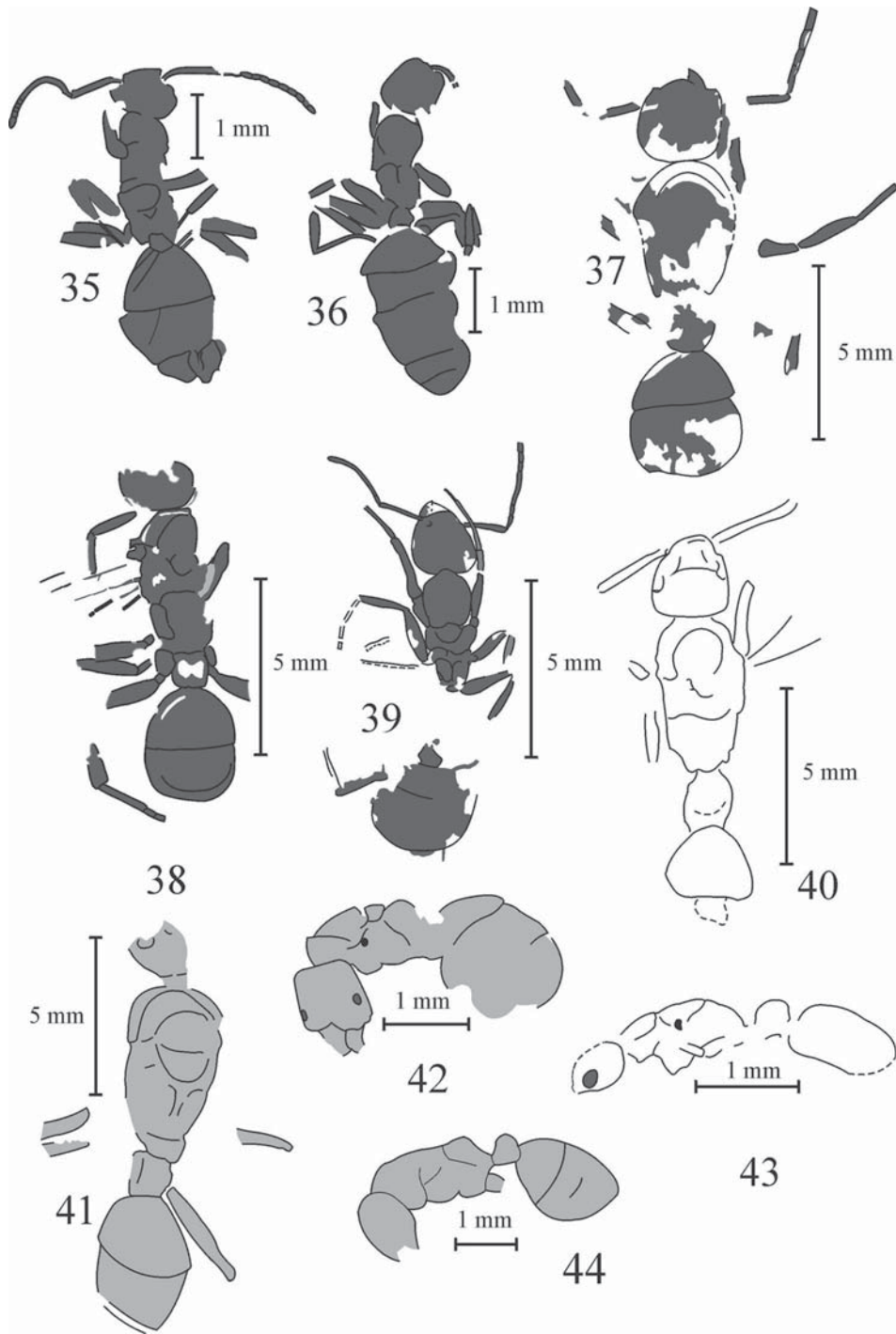
Figs 35–44. 35–36 — *Klondikia whiteae* sp. n., obverse dorsal imprint of male, holotype SIC # SR 94–5–7a (35), dorsal imprint of female, paratype SIC # SR 94–4–24 (36); 37 — *Kohlsimyrma laticeps* sp. n., dorsal imprint of female, holotype USNM # 495879; 38–39 — *Kohlsimyrma longiceps* sp. n., dorsal imprint of female, holotype USNM # 495878 (38), paratype USNM # 495877 (39); 40–41 — *Kohlsimyrma gracilis* sp. n., dorsal imprint of female, holotype USNM # 495906 (40), dorsal imprint, paratype USNM # 495911 (41); 42–44 — Formicidae incertae sedis, species A, PIN # 4621/637 (42), species B, PIN # 4621/638 (43), species C, USNM # 495923 (44).

Рис. 35–44. 35–36 — *Klondikia whiteae* sp. n., прямой дорзальный отпечаток самца, голотип SIC # SR 94–5–7a (35), дорзальный отпечаток самки, паратип SIC # SR 94–4–24 (36); 37 — *Kohlsimyrma laticeps* sp. n., дорзальный отпечаток самки, голотип USNM # 495879; 38–39 — *Kohlsimyrma longiceps* sp. n., дорзальный отпечаток самки, голотип USNM # 495878 (38), паратип USNM # 495877 (39); 40–41 — *Kohlsimyrma gracilis* sp. n., дорзальный отпечаток самки, голотип USNM # 495906 (40), дорзальный отпечаток, паратип USNM # 495911 (41); 42–44 — Formicidae incertae sedis, species A, PIN # 4621/637 (42), species B, PIN # 4621/638 (43), species C, USNM # 495923 (43).

wide alitrunk which is hardly longer than head. The key trait of Ponerinae, a constriction between first and second segments of the gaster, is seen nowhere but in the holotype of K. *laticeps*, where it is very shallow and so might be a result of postmortem deformation. The constriction is not visible at some extant Ponerinae as well (in *Centromyrmex* Mayr, 1866, some *Odontomachus* Latreille, 1804), so it cannot be excluded that *Kohlsimyrma* is an aberrant ponerine ant. Alternatively it can be an aberrant genus of Dolichoderinae or Aneuretinae.

ETYMOLOGY. The genus is named in honor to David Kohls who has collected the fossils described under this generic name.

Kohlsimyrma laticeps Dlussky et Rasnitsyn, **sp.n.**
Fig. 37.

MATERIAL EXAMINED. Holotype: USNM #495879, dorsal imprint of female. Old Mountains, Locality 41086, Garfield Co., Colorado, USA (coll. D. Kohls, 1995). Middle Eocene (Lutetian), Green River Formation.

DESCRIPTION. Female. Body length 12 mm. Head subquadrate, somewhat wider than long (HL/HW 0.87); sides and occipital margin feebly convex. Scape shorter than head. Alitrunk robust, about one and a half times as long as wide. Scutum not over-hanging pronotum anteriorly. Petiole wider than long. Gaster oval. Constriction between first and second segments of the gaster shallow, but well-marked.

MEASUREMENTS, mm. AL 4.25 mm; AW 2.8 mm; HL 2.25 mm; HW 2.6 mm; SL 2.0 mm; PtL 1.4 mm; PtW 1.5 mm.

ETYMOLODY. Laticeps is the Latin for "with broad head".

Kohlsimyrma longiceps Dlussky et Rasnitsyn, **sp.n.**
Figs 38, 39.

MATERIAL EXAMINED. Holotype: USNM #495878, dorsal imprint of female with fragment of fore wing and missing part of head, Old Mountains, Locality 40189 Garfield Co., Colorado, USA (coll. D. Kohls, 1991−93). Middle Eocene (Lutetian), Green River Formation. Paratype, USNM #495877, obverse and reverse ventral imprints of female with missing posterior part of alitrunk, most of petiole and part of gaster; collected together with holotype.

DESCRIPTION. Female. Body length 9–10 mm. Head subtrapezoidal, widest behind midlength, a little longer than wide (HL/HW 1.07); sides feebly convex; occipital margin straight. Scape shorter than head, weakly curved near base. Funiculus filiform, without clava. Mandibles triangular. Alitrunk rather slender, about twice or more than twice as long as wide. Hind coxae touching each other. Femora thick basally. Petiole subquadrate in dorsal view, about as long as wide. Gaster oval.

MEASUREMENTS, mm. Holotype: AL 3.7; AW 1.5; HW 1.8; PtL 1.0; PtW 1.05. Paratype: AL about 3,5; AW 1.3; HL 1.6; HW 1.5; SL 1.1; F3L 1.5.

COMPARISION. Differs from *K. laticeps* in subtrapezoid form of the head which is longer than wide (subquadrate and somewhat wider than long in *K. laticeps*) and slender alitrunk (twice or more than twice as long as wide) *vs.* robust alitrunk (about one and a half times as long as wide) in *K. laticeps*.

ETYMOLOGY. Longiceps is the Latin for "with long head".

Kohlsimyrma gracilis Dlussky et Rasnitsyn, **sp.n.**
Figs 40, 41.

MATERIAL EXAMINED. Holotype: USNM #495906, poorly preserved dorsal imprint of female. Anvil Points Area, Locality 40193, Garfield Co., Colorado, USA (coll. D. Kohls, 1991−93).

Middle Eocene (Lutetian), Green River Formation. Paratype: USNM #495911, dorso-lateral imprint with head and legs missing in part. Collected together with holotype.

DESCRIPTION. Female. Body length about 13.5 mm. Head subtrapezoidal, widest behind midlength, with distinct, rounded occipital corners and convex occipital margin. Scape longer than head. Alitrunk elongate, twice as long as wide. Scutum and scutellum small and flattened. Propodeum elongate. Petiole massive, a little longer than high; petiolar sides and dorsum feebly convex. Legs relatively long and slender.

MEASUREMENTS, mm. Holotype: AL 4.2; AW 2.0; HL 1.8; HW 2.1; SL 2.6; PtL 1.4; PtW 1.2. Paratype: AL 5.6; AW 2.8; F3L 3.9; PtL 1.3; PtH 1.2.

COMPARISION. Differs from congeners in relatively long scape (longer than head *vs.* short than that in *K. laticeps* and *K. longiceps*) and more elongated petiole.

ETYMOLOGY. Gracilis is the Latin for thin.

Formicidae incertae generis

In addition to the species described above there are three ant fossils from the Green River Formation, which are dissimilar to any species described there and evidently belong to different genera. However their poor preservation state permits neither attribution to a described genus nor description of a new one.

Species A
Fig. 42.

MATERIAL EXAMINED. PIN #4621/637, poorly preserved lateral imprint of female. Anvil Points, Garfield Co., Colorado, USA. (coll. A. Rasnitsyn, 1997). Middle Eocene (Lutetian), Green River Formation.

NOTES. Body length about 4 mm. Differs from other Green River ants in shape of head which is subtrapezoidal, widest behind midlength, with occipital corners distinct, occipital margin feebly concave, eyes small, situated somewhat before midlength of head sides. Scutum feebly convex, not over-hanging pronotum anteriorly. Propodeum angular, without teeth or spines. No characters are seen to permit attribution of the fossil to a subfamily.

Species B
Fig. 43.

MATERIAL EXAMINED. PIN 4621/638, poorly preserved lateral imprint of female. Anvil Points, Garfield Co., Colorado, USA. (coll. A. Rasnitsyn, 1997). Middle Eocene (Lutetian), Green River Formation.

NOTES. Body length about 3.5 mm. Differs from other Green River ants in shape of petiole which is large, nodiform, higher than long, rounded in side view. Eyes are medium-sized, oval, situated distinctly before midlength of head sides. Scutum and scutellum flat, scutum not over-hanging pronotum anteriorly. Propodeum rounded in side view, without teeth or spines. In general appearance this species is very similar to some Ponerinae, but have oval gaster without constriction between the first and second gastral tergites.

Species C
Fig. 44.

MATERIAL EXAMINED. USNM #495923, Poorly preserved lateral imprint of worker. Anvil Points Area, Locality 40193, Garfield Co., Colorado, USA. (coll. D. Kohls, 1991−93). Middle Eocene (Lutetian), Green River Formation.

NOTES. Body length about 5 mm. Differs from other Green River ants in form of propodeum and petiole. Propodeum angular in side view, with feebly concave declivity. Petiole nodiform with very short peduncle. In general appearance the fossil is similar to some extant *Neivamyrmex* Borgmeier, 1940 (Ecitoninae), but otherwise it shows no characters that would permit its attribution to a subfamily.

Key to genera of ant wingless impression fossils in middle Eocene of North America

1. Waist of two segments (petiole and postpetiole). Sting present 2
— Waist of one segment (petiole) 4
2. Postpetiole broadly attached to gaster. Large (13–16 mm) elongate ants. Mandibles linear, about as long as head, with large blunt teeth .... *Archimyrmex* Cockerell
— Postpetiole narrowly attached to the gaster. Mandibles triangular 3
3. Petiole sessile .... *Myrmecites* gen.n.
— Petiole pedunculate ....*Solenopsites* gen.n.
4 (1). Gaster with distinct constriction between first and second segments. Sting present 5
— Gaster without constriction between first and second segments 6
5. Large species (more 10 mm). Hind tibiae with two spurs. Mandibles triangular with several rather large obtuse teeth on masticatory margin ..... *Pachycondyla* F. Smith
— Smaller species (less then 10 mm). Hind tibiae with one spur. Mandibles triangular with numerous small denticles on masticatory margin .... *Ponerites* Dlussky
6 (4). Petiole pedunculate, 2.5–3 times as long as wide, with long peduncle and small node. Sting not visible (probably present but small) .... *Mianeuretus* Carpenter
— Petiole not pedunculate, nodiform, subconical, subcylindrical, or with scale. Sting absent 7
7. Propodeum bispinate, bidentate, or distinctly angular in side view, with concave declivity .... *Dolichoderus* Lund
— Propodeum rounded or weakly angular, with convex declivity 8
8. Petiole with scale. Anterior margin of clypeus straight or concave .... *Proiridomyrmex* gen.n.
— Petiole nodiform, subconical or subcylindrical 9
9. Petiole large and massive (figs 36–40) ....
.... *Kohlsimyrma* gen.n.
— Petiole comparatively small (figs 26, 27, 29, 31–36) .....
.... 10
10. Gaster with large male genitalia.*Klondikia* gen.n. (male)
— Gaster without visible male genitalia 11
11 Head rectangular, longer than wide. Eyes comparatively small. Scape distinctly curved near base (fig. 35) ....
.... *Klondikia* gen.n. (female)
— Head either wider than long (females), or rounded or rectangular with large eyes occupying most of head sides (males). Scape straight or weakly curved ....
.... *Eoformica* Cockerell

Discussion

Until recently the Early Oligocene ant assemblage from Florissant was the only one of larger size in the North America and so permitting comparison to the past Eurasian ant faunas. The Baltic amber ants are mainly used as a counterpart which was not quite correct because of great taphonomical differences between impression fossils and amber inclusions (see above: Taxonomic approach …). Now the material accumulated permits more correct comparison.

Subfamily level analysis of composition of the past ant assemblages is particularly relevant. Different preservation state of inclusion and impression fossils results in different levels of detalization of taxonomic descriptions. As a result the lower rank taxa, particularly genera and species, are incompletely comparable when established on different material. Unlike these, subfamilies are usually interpreted in similar way irrespective of impression *vs.* inclusion material involved.

In Eurasia the subfamily level turnover of ants can be outlined as follows. The first formicoids appeared in the top Early Cretaceous represented by Armaniinae which was accompanied by Sphecomyrminae in the Late Cretaceous. Both subfamilies were the least advanced morphologically and at most of lower eusocial level in behavior. Besides them there are incompletely known fossils which can belong elsewhere: *Burmomyrma rossi* Dlussky from the Burmese amber of debatable age (Late Cretaceous or earlier Paleogene [Zherikhin, Ross, 2000]), and *Petropone petiolata* Dlussky and *Cretopone magna* Dlussky from the Turonian of Kazakhstan which might belong to Ponerinae [Dlussky, 1975, 1983, 1987, 1996, 1999; Dlussky, Fedoseeva, 1988].

The extinct ant subfamilies all left in the Cretaceous (with a possible exception of *Haidomyrmex* Dlussky in the Burmese amber which possibly represents Sphecomyrminae), Paleocene fauna is composed of extant Aneuretinae, Dolichoderinae, Formicinae and Ponerinae. Sakhalin amber yields 6 Dolichoderinae out of total 9 specimens. Tadushi Formation in the Russian Far East has produced two wings probably belonged to Formicinae, and the ponerine *Pachycondyla rebekkae* Rust et Anderson is found abundant in the marine Fur Formation of Denmark. The latter case, with more than 100 winged ants found accompanied with not a single other ant, suggests burial of a huge mating swarm. All known genera are extinct, generally archaic and sometimes combine characters of different tribes. At the same time many of them show specializations attesting ants to be adapted to different forest tiers and different foraging behavior [Dlussky, 1988, Rust, Andersen, 1999].

Early and Middle Eocene is little known in Eurasia. Three species of giant ants from the genus *Formicium* of extinct, very short-lived subfamily Formiciinae are described from the Middle Eocene of Isle of Purbeck in England and Ölschiefer of Grube Messel in Germany [Lutz, 1986]. 225 ant fossils are found in Messel, 167 (75%) of them belong to females and males of two species of *Formicium*, 2 (1%) to Ponerinae, 5 (2%) to Myrmicinae and 43 (16%) to Formicinae + Dolichoderinae. A ponerine ant *Eomyrmex guchenziensis* Hong et al., also of the Middle Eocene age, is described from Fushun amber in Liaoning, China [Hong et al., 1974; Lutz, 1986].

Late Eocene Baltic amber has given the best known ant assemblage of the past. Wheeler [1915] presents data

on 11687 ant specimens. The senior author has provided a generic revision of the Baltic amber ants as well as a revision of some types (*Formica flori* Mayr, *Ponera atavia* Mayr, *Dolichoderus* spp.) [Dlussky, 1997, 2002a, 2002b], and additionally identified 1468 inclusions. Hence as many as 13146 Baltic amber ants are currently studied taxonomically. The subfamily composition summarized below is original but similar to that by Wheeler [1915]. The total material includes Aneuretinae (30 specimens, 0.2%), Dolichoderinae (8310, 63.2%), Formicinae (4343, 33.0%), Myrmeciinae (10, 0.1%), Pseudomyrmecinae (33, 0.3%), Ponerinae (118, 0.9%), Cerapachiinae (9, 0.1%) and Myrmicinae (233, 1.8%). Except for Myrmeciinae, all of them still frequent Eurasia, and only two additional subfamilies occur there nowadays but not in the Baltic amber times, viz. Aenictinae and Dorylinae. However, the contemporary and Late Eocene shares of various subfamilies differ profoundly, for now the Eurasian biocenoses are dominated by either Formicinae or Myrmicinae, while Dolichoderinae are never particularly abundant. At the same time, the Baltic amber ant assemblage differs much from the Paleocene ones in higher share of Formicinae and presence of Myrmicinae.

Of 49 ant genera recorded in the Baltic amber more than half (29) are extant and include 87 (77.7%) of 112 species known there (but not always described) and half (50.7%) the identified specimens. In extinct genera, only *Ctenobethylus goepperti* (Mayr) is abundant, and very much so (47% of all ant inclusions), while all the rest species of extinct genera comprise only 2.3% of total ant inclusions.

Important novel feature of the Baltic ant assemblage is presence of a few species of particularly high abundance, when 9 species (of total 112) comprise more than 90% specimens (*Ctenobethylus goepperti* — 46.5%, *Lasius schiefferdeckeri* Mayr — 10.7%, *Formica flori* Mayr + *F. gustawi* Dlussky — 10,7%, *Iridomyrmex geinitzei* (Mayr) — 10.3%, *Prenolepis henschei* Mayr — 5.4%, *Dolichoderus tertiarius* (Mayr) — 4.0%, *Gesomyrmex hornesi* Mayr — 1.6%, *Camponotus mengei* Mayr — 1.0%, *Plagiolepis klinsmanni* Mayr — 0.8%). High density of these species most probably suggests that they had large colonies and hence high sociality level. *Ctenobethylus* Brues is an extinct genus close to living *Liometopum* Mayr and *Bothriomyrmex* Emery. *Iridomyrmex* Mayr and *Gesomyrmex* Mayr now occur in the Oriental and Indo-Australian Regions, and relatives of the rest 6 species (which comprise 32.6% of all ant inclusions) frequent Palearctic now.

Oligocene and Neogene insects of Eurasia are plenty in collections, and ants are numerous among them, but unfortunately they are mostly not identified yet or badly need revision and so of little use for our review. It is only possible to conclude tentatively that participation of Formicinae and especially Myrmicinae was growing since Eocene while abundance of Dolichoderinae was decreasing.

Better known are ants from Vishnevaya balka (Middle Miocene, Tchokrakian of Stavropol in North Caucasus). It resembles to the contemporary warm temperate Europe

[Dlussky, 1981]. Formicinae comprise 55.3% of all ant fossils, Myrmicinae — 40%, Dolichoderinae — 4%, Ponerinae — 3.7%. Generic level composition is difficult to assess because the incomplete preservation results in many fossils assigned to formal and collective genera.

A rich Middle Miocene fauna is known also from Shanwang in Shandong Province, China [Zhang, 1989; Zhang et al., 1994]. Unfortunately, only a part of the material is described, and general composition of the fauna is unknown. Worth to mention is that 13 out of 21 genera recorded there are extant and comprising 49 (82%) out of 60 described species.

As to the Sicilian amber, the ants described [Emery, 1891], though deserving revision, show evident differences from other Eurasian Tertiary and possibly belonged to the Afrotropical rather than Palearctic realm. We don't consider it further here. The Sicilian amber is now considered as of Early Oligocene and not of Miocene age [Skalski & Veggiani 1990].

To summarize the Eurasian ant turnover, it is possible to conclude that:

1. Armaniinae appeared in the latest Early Cretaceous, to die out before mid-Late Cretaceous (after Turonian).

2. Sphecomyrminae joined Armaniinae in the late Cretaceous to get lost by Paleocene.

3. There are problematic evidence of living subfamily(ies) in Late Cretaceous (*Cretopone* and *Petropone* in Turonian of Kazakhstan, *Burmomyrma* in Burmese amber).

4. Paleocene reveals only extinct genera belonged to extant subfamilies. Ants were comparatively rare, with Dolichoderinae highly dominated and Myrmicinae absent, and with no really abundant species present except for *Pachycondyla rebekkae* which represents a special case (see above).

5. No reliable data exist for the Early Eocene. Characteristic of the Middle Eocene is the ephemerally flourished Formiciinae that sometimes has produced as many as 75% of all locally collected ant fossils.

6. Late Eocene Baltic amber records the next turning-point in the ant history: ants became common, three quarter of species belonged to extant genera, and, except for *Ctenobethylus goepperti*, all the extinct genera combined comprised less then 3% of fossils. Dolichoderinae continued producing almost 2/3 of fossils, but Formicinae became numerous comprising most of the rest 1/3, and Myrmicinae have appeared. Sharp dominance of few (highly social) species became commonplace.

7. Oligocene is little known. It is possible hypothesize that the old (pre-Baltic) taxa were decreasing and participation of Formicinae and Myrmicinae was growing.

8. Miocene ant fauna looks modern with Formicinae and Myrmicinae dominating, Dolichoderinae taking far subordinate position, and no signs of ancient (pre-Baltic) taxa are traced.

9. Pliocene ants are practically unknown.

Processes experienced by North American ants were generally similar although differed in some details. The ant record starts here since Turonian. The oldest fossils

are collected at Cliffwood Beach in New Jersey, USA, as amber inclusions. Six of them belong to Sphecomyrminae, one to Ponerinae, and one to Formicinae [E. Wilson et al, 1967; Grimaldi et al., 1997; Grimaldi, Agosti, 2001]. Ponerine fossil and *Brownimecia clavata* demonstrates a number of specializations (saber-shaped mandibles, unique pennate maxillary palps, well formed petiole) and can be an ancestor of no other ponerine ants. At the same time *Kyromyrma neffi* looks like modern formicine ant, heving acidopore and coronula. The younger (Campanian) amber of Medicine Hat in Alberta and Cedar Lake in Manitoba, Canada, yields 3 species of Sphecomyrminae, Ponerinae and Dolichoderinae [E. Wilson, 1985; Dlussky, 1999]. Of them, *Sphecomyrma canadensis* Wilson is described formally, accompanied with figures showing no diagnostic characters of Sphecomyrminae, and with the holotype and paratype being evidently non-conspecific [Dlussky, Fedoseeva, 1988]. Unfortunately this material was not available for restudy. Two other species described are primitive in their subfamilies, and one of them belongs to a genus (*Eotapinoma* Dlussky, Dolichoderinae) survived in the Asian Paleocene (Sakhalin Amber [Dlussky, 1988]).

No Paleocene ants are known in the North America, and only the wing *Formicium berryi* (Carpenter) from Wilcox in Tennessee, USA is described in the Early Eocene [Carpenter, 1929; Lutz, 1986].

In contrast, the Middle Eocene ants are abundantly collected. Three species come from the Arkansas amber (Malvern, Arkansas USA [E. Wilson, 1985]) and represent Myrmicinae, Dolichoderinae and Formicinae. The myrmicine record is the oldest worldwide, but this should not imply the American origin of the subfamily until the Early Eocene ants are better studied in other territories. The dolichoderine fossil described as *Iridomyrmex mapesi* Wilson belongs most probably to the genus *Linepithema* Mayr (now in North and South America), and the formicine one, *Protrechina carpenteri* Wilson, represents a basal genus of its subfamily. *Protrechina* is one of very few formicine genera lacking acidopore and coronula (modified apex of the last gastral sternite in female sex). It was already noted that differences between the earliest Dolichoderinae (*Eotapinoma*, *Zherichinius*) and Formicinae (*Protrechina*, *Chimaeromyrma*) are almost elusive (petiole is squamiform in *Protrechina* and lacking node or scale in *Eotapinoma* [Dlussky, 1988]).

A bulk of the Middle Eocene ants are impression fossils, and vast majority of them come from the Green River Formation in the western USA (Utah, Colorado, Wyoming). These are dealt with in more details in this paper, as well as some other fossils of similar age (e.g., from Klondike Mountain Formation in Washington, USA). Worth mentioning additionally are undescribed ants from Tallahatta Formation in Mississippi, USA [Johnston, 1993]. Judging from photographs presented, these belong to Formicinae or Dolichoderinae, and one of them (Plate 1, fig. 5) evidently represents *Camponotites* Dlussky.

Preservation state of the Middle Eocene impression fossils of Green River and Klondike Mountain Formations is generally imperfect causing extensive use of formal taxa and resulting in problematic subfamilial attribution of many fossil ants. If to rely on 46 fossils whose subfamily attribution is more or less certain, the calculation gives 7% Aneuretinae, 61% Dolichoderinae, 4% Formicinae, 13% Myrmeciinae, 11% Ponerinae, and 4% Myrmicinae. Ascribing *Eoformica* and *Klondikia* to Dolichoderinae, and *Kohlsimyrma* to Ponerinae produces similar result: Aneuretinae — 3%, Dolichoderinae — 72%, Formicinae — 3%, Myrmeciinae — 6%, Ponerinae — 10%, Myrmicinae — 2% (97 fossils totally). In any case we have Dolichoderinae taking some 2/3 of the total material, comparatively high shares of Myrmeciinae and Ponerinae and low shares of Formicinae and Myrmicinae. Proportions are similar to those in the Baltic amber, except Formicinae are more numerous there. Similarly, there are a few species of particularly high abundance, with three of them taking 71% of all ants (*Eoformica pinguis* 40%, *Dolichoderus kohlsi* 25% and *Archimyrmex rostratus* 6%). *E. pinguis* might be a mixture of species, but majority of the males described under this name most probably belong to a single species. A share of extinct genera is not easy to assess. *Dolichoderus* and *Pachycondyla* are certainly extant genera, and *Mianeuretus*, *Kohlsimyrma* and *Archimyrmex* are doubtless extinct, but the state of the rest genera is obscure. The record of *Archimyrmex* is of particular interest, for the genus represents the subfamily Myrmeciinae whose the only extant genus *Myrmecia* is confined to Australian Region. Two other species of *Archimyrmex* come from the Late Paleocene or Early Eocene of Argentina [Dlussky, Perfilieva, 2003]. So it is possible to conclude that the North American Middle Eocene ant fauna looks less advanced than that of the Baltic amber but the characteristic features of the latter are already traceable there.

The next younger ant assemblage in the North America is that from the earliest Oligocene (or possibly latest Eocene) of Florissant in Colorado, USA. It is the second best known ant fauna of the past, whose study was based on 5593 fossils [Carpenter, 1930]. 32 species and 19 genera are described from Florissant. Of them, 11 genera (58%, as in Baltic amber) with 19 species (59.4%) are extant. The latter figure is less than 78% of species in extant genera recorded in the Baltic amber, but the difference is not necessary indicative, because taxonomy of impression fossils is by necessity less discriminative, and the resulted species were probably further split if found included in amber. More indicative is the difference in the share of specimens attributed to extant genera, which is higher in Florissant (68.3%) than in Baltic amber (50.7%). Proportions of Dolichoderinae (62.6%) and Formicinae (32.5%) are the same as in Baltic amber (63.6% and 32.5%, respectively). Unlike them, Myrmicinae are more common (4.8% vs. 1.8% in Baltic amber), other subfamilies being rare (Pseudomyrmecinae and Ponerinae are known by two specimens each, Aneuretinae by only one). Like in the Baltic amber, there are few highly dominated species, six of which take 93% of all fossils (*Protazteca elongata* Carpenter 26.8%, *Liometopum miocenicum* Carpenter 26.8%, *Lasius peritulus* Cockerell 25%, *Formica ro-*

busta Carpenter 7.2%, *Liometopum scudderi* Carpenter 3.6%, *Aphaenogaster mayri* Carpenter 3.6%). First of them belongs to an extinct genus, and the rest five (taking collectively 66.2% of fossils) to the extant ones. It is possible to infer that the Florissant fauna is generally similar to that of the Baltic amber, except for the shares of extant genera and of Myrmicinae which are higher in Florissant.

In parallel to changing participation of subfamilies in the ant assemblages through time, ants as a whole increased their participation in the entire insect assemblages, with explosive growth during Eocene and particularly Oligocene (Tab. 1, fig. 45). Decrease of the ant share in the Neogene is paradoxical and needs more study to be accepted as real event in the ant evolution.

Table 1. Ant participation in past insect assemblages.
Таблица 1. ....

Locality	Stratigraphy	Age (Myr)	Preservation*	Ant share	References
Khetana, Russia	M. Albian	100	IM	1.5%	orig.
Obeshchayushchiy, Russia	Cenomanian	95	IM	0.5%	orig.
Burmese amber	Cenomanian	95	FR	0.3%	Rasnitsyn, Ross, 2000; Shedrinsky et al., 2001
New Jersey, USA	Turonian	90	FR	0.05%	Grimaldi, Agosti, 2001
Kzyl-Zhar, Kazakhstan	Turonian	90	IM	0.7%	orig.
Orapa, Botswana	Turonian	90	IM	0.6%	Brothers, Rasnitsyn (in preparation)
Yantardakh, Russia	Santonian	85	FR	0.001%	Zherikhin in Grimaldi, Agosti, 2001
Canada amber	Campanian	75	FR	0.002%	Pike, 1995
Baikura, Russia	Maastrichtian	70	FR	1.6%	Rasnitsyn, Kulicka, 1990
Sakhalin amber, Russia	Paleocene	60	FR	1.2%	Dlussky, 1988
Tadushi, Russia	Paleocene	60	IM	0.05%	orig.
Oise amber, France	Early Eocene	50	FR	7%	Nel in Grimaldi, Agosti, 2001
Arkansas amber, USA	Middle Eocene	45	FR	1%	Sounders et al.,1974; Wilson, 1985
Green River, USA	Middle Eocene	45	IM	6.9%	Labandeira et al. (in preparation)
Klondike Mt Fm.,USA	Middle Eocene	45	IM	2%	Levis, 1992
Messel, Germany	Middle Eocene	45	IM	13.1%	Lutz, 1990
Eckfelder Maar, Germany	Middle Eocene	45	IM	1.1%	Lutz, 1993
Baltic amber	Late Eocene	40	FR	5%	orig.
Rovno amber, Ukraine	Late Eocene	40	FR	7.6%	Perkovsky (in press)
Florissant, USA	Early Oligocene	33	IM	20%	Carpenter, 1930
Biamo, Russia	Early Oligocene	33	IM	7%	orig.
Amgu, Russia	Early Oligocene	33	IM	0.2%	orig.
Sicily amber, Italy	Early Oligocene	30	FR	40%	Zherikhin, Eskov, 1999
Rubielos de Mora, Spain	Early Miocene	20	IM	3.6%	Penalver, 1998
Stavropol, Russia	Middle Miocene	16	IM	3%	orig.
Chon-Tuz, Kirghizia	Middle Miocene	16	IM	2%	orig.
Dominican amber	Miocene	15	FR	36%	Rasnitsyn (in preparation)
NE Japan	Late Miocene	10	IM	17.9%	Fujiyama, 1983
Willershausen, Germany	Late Pliocene	5	IM	7.8%	Zherikhin (unpublished)

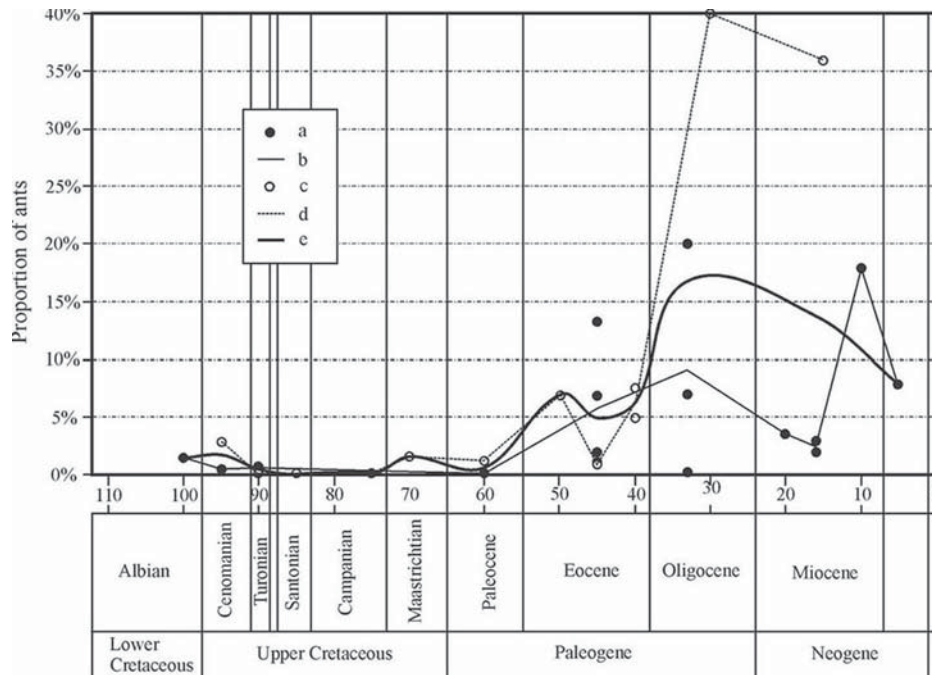*FR — inclusions in fossil resins; IM — impressions.

Fig. 45. Dynamic of proportion of ants among all insects in fossil deposits from Late Cretaceous to Pliocene: a — fossil imprints; b — average for fossil imprints, c — inclusions in fossil resins, d — average for fossil resins; e — average for all fossils.

Рис. 45. Динамика доли муравьев от всех насекомых в ископаемых отложениях от позднего мела до плиоцена: a — ископаемые отпечатки; b — среднее для всех отпечатков; c — инклюзы в ископаемых смолах; d — среднее для ископаемых смол; e — среднее для всех ископаемых.

Comparing the outlined ant history in North America and Eurasia, it is possible to note their essential similarity in spite that the respective faunas are different in terms of generic and species composition. At the subfamily level, following stages of the combined faunistic turnover can be preliminary defined.

I. *Later Early Cretaceous through the latest Cretaceous*: **ancient ant fauna**. Earliest ants appear (Armaniinae and then Sphecomyrminae) which have at most low eusociality. The earliest extant subfamilies Ponerinae, Formicinae, and Dolichoderinae come into existence toward the end of this interval.

II. *Paleocene and Early Eocene*: **old ant fauna**. No Armaniinae and Sphecomyrminae present. Instead, all major and many minor extant subfamilies appear (Aneuretinae, Dolichoderinae, Formicinae, Myrmeciinae, Ponerinae and Myrmicinae) accompanied with the short-lived extinct subfamily Formiciinae toward the end of the interval (known only in Early and Middle Eocene). Ant fossils are usually rare in deposits, and mass species are uncommon indicating low colony size. Almost all recorded genera are extinct.

III. *Middle Eocene through at least Early Oligocene (Green River — Baltic amber — Arkansas amber — Florissant)*: **formation of the modern fauna**. Ants are numerous and often a mass group. Extant genera become numerous and gradually oust old fauna. Massive dominance of few species (belonged mostly to extant genera)

is an ordinary feature of fossil ant assemblages. Unlike contemporary ant faunas, most abundant subfamily in fossil assemblages are Dolichoderinae.

IV. *Oligocene or Miocene through now*: **essentially modern fauna**. Participation of Dolichoderinae decreases and that of Myrmicinae increases. Ancient genera go extinct.

To close the discussion, it is worth to note once again that the above inference on the ant history on the north continents is very preliminary because of highly insufficient knowledge of the paleontological history of ants. This is the more so disappointing that the accumulated collections are huge and only need close study to make apparent history of these unique and attractive insects.

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