New Archostemata (Insecta: Coleoptera) from the French Paleocene and Early Eocene, with a note on the composition of the suborder

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Abstract. The paper deals with descriptions of four new species of Archostemata from the Paleocene and Earliest Eocene amber, *Cupes manifestus* **n. sp.**, *C. orbiculatus* **n. sp.**, *C. ponomarenkoi* **n. sp.** and *Micromalthus eocenicus* **n. sp.**, the latter representing the oldest member of genus *Micromalthus* Leconte 1878 (Micromalthidae). The position, composition and origin of the genera *Cupes* and *Micromalthus* are considered. *Cupes* seemed to appear during Cretaceous or very close to this period, while *Micromalthus* could originate somewhat later. The synonymy of Cupedini and Priacmini is grounded. The genus *Crowsoniella* Pace 1975 (Crowsoniellidae) could be excluded from the suborder Archostemata and transferred into the infraorder Cucujiformia (Polyphaga).

Résumé. Nouveaux Archostemata du Paléocène et de l'Eocène basal de France (Insecta : Coleoptera). Quatre nouvelles espèces d'Archostemata, *Cupes manifestus* n. sp., *C. orbiculatus* n. sp., *C. ponomarenkoi* n. sp. et *Micromalthus eocenicus* n. sp., sont décrites, les deux premières du Paléocène de Menat (Puy-de-Dôme) et les deux autres de l'ambre éocène basal de l'Oise. *M. eocenicus* est le plus ancien fossile connu du genre *Micromalthus* beconte 1878 (Micromalthidae). La position, composition et origine des genres *Cupes* et *Micromalthus* sont discutées. *Cupes* semble être apparu dans le Crétacé alors que *Micromalthus* pourrait être plus récent. La synonymie entre Cupedini et Priacnimi est proposée. Le genre *Crowsoniella* Pace 1975 (Crowsoniellidae) pourrait être exclu du sous-ordre Archostemata et transféré dans l'infra-ordre Cucujiformia (Polyphaga).

Keywords: Cupedidae, Micromalthidae, Polyphaga, Crowsoniellidae, new species.

If Mesozoic Archostemata are rather common, Paleogene representatives of this group are not very frequent, being recorded from Eocene Baltic amber and Middle Eocene of Messel (Germany) (Troester 1993; Kirejtshuk 2005), and also from Middle Miocene Pochlovice (Ponomarenko 1973a). France is known by many compression and amber insect outcrops of different ages (Lacroix 1910; Schlüter 1978; Nel et al. 2004). Since 1996 a great number of amber inclusions has been obtained in the outcrop with the Lowermost Eocene sediments in the Oise Department. Specialists of different groups of animals and plants (Nel et al. 2004; etc.) recently started to investigate these inclusions. The crucial differences of this source from Baltic amber are connected with age and group of resin producing plant. Very numerous insect impressions have been recently obtained in the Paleocene lacustrine outcrop of Menat (56 Myr old), thanks to the field researches of the Association Rhinopolis.

The ages of Menat paleolake and the "French"

from "thermoera" to the "crioera", while Baltic amber could coincide with the beginning of the latter. The infrared spectrum of "French" amber is rather similar to the recent *Hymenaea* copal (Nel *et al.* 2004), while the resin for Baltic amber seemed to be produced by coniferous plants. This difference can have a crucial importance for the composition of the entomofauna (Nel & Bourguet 2006).

amber in Oise fall to the earlier stages transition

Some references to the coleopterous inclusions in the Baltic amber have been published by Spahr (1981), Kirejtshuk (2005), and Ponomarenko & Kirejtshuk (2009). Before this study only Archostematan species of the genus Cupes Fabricius 1801 (Cupedidae) were described from Baltic amber. The family Micromalthidae was recorded from the Lebanese, Dominican, and Mexican amber. The suborder Archostemata sensu stricto [families Cupedidae, Ommatidae, Triadocupedidae, Jurodidae, and Micromalthidae] was rather common in fossils through the Mesozoic and, perhaps, in the Palaeogene, however during the Neogene the representation of this group in the global biota seemed to have decreased. As an example, there is only one record of a specimen of Cupedidae in the Late Oligocene lacustrine outcrop of Aix-en-Provence for thousands of

E-mail: agk@zin.ru, kirejtshuk@gmail.com, anel@mnhn.fr, Collomb.Francois-Marie@wanadoo.fr Accepté le 2 avril 2009 specimens belonging to other coleopteran groups (Nel pers. obs.). In contrast to the other Coleoptera, species of most groups of this suborder from Mesozoic and Cenozoic (and also groups of Archecoleoptera or Protocoleoptera from Paleozoic) can be easily determined due to comparatively large body size and characteristic structure of elytra maintaining some remains of initial venation and primary membrane. Because of the wide distribution in the past, inhabitance in wood and easy recognition many species and genera have been described from many sites of different ages. At the same time the rather small members of the suborder (Micromalthidae) are more problematical for deposition

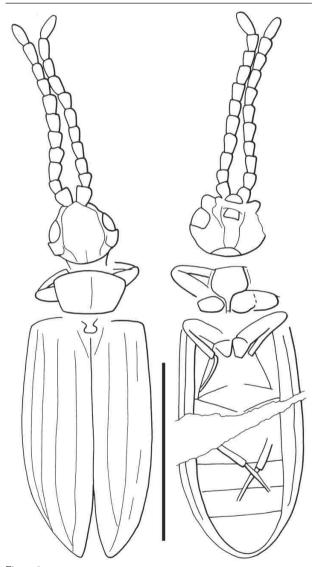


Figure 1 *Cupes manifestus* **n. sp.**, holotype MNT-06-902-A. A, print dorsal view; B, counterprint ventral view. Scale bar represents 6 mm.

in water basins sediments and their scarcity or absence in known fossils could be caused by this circumstance. Thus, the description of the new species of the genus *Micromalthus* LeConte 1878 from the Early Eocene is rather valuable to understand the dynamics in the evolution of the family Micromalthidae.

The lacustrine material from Menat is stored in the Musée of Menat (MNT), Puy-de-Dôme, France. The amber material under consideration is deposited in the Department de Paléontologie, Muséum national d'Histoire naturelle, Paris.

The type strata and localities are as follows: for lacustrine impressions. Paleocene, circa 56 Myr, (Vincent *et al.* 1977; Russell 1982), spongo-diatomitic paleolake of maar, Menat, Puy-de-Dôme, France; for inclusions in amber. Lowermost Eocene, *circa* - 53 Myr, Sparnacian, level MP7 of the mammal fauna of Dormaal, Farm Le Quesnoy, Chevrière, region of Creil, Oise department (north of France).

Note. The authors checked the paratype of *Crowsoniella* relicta Pace 1975 (sent to us by Dr. Mauro Daccordi and Dr. Leonardo Latella) (Crowsoniellidae Iablokoff-Khnzorian 1983) formerly regarded as a member of the suborder Archostemata and found that this specimen has only one suture on the underside of prothorax (pronotosternal suture - figs 15 and 16) and its metepisterna could not reach mesocoxal cavities (fig. 17), therefore, it could be excluded from this suborder and transferred to the suborder Polyphaga. Pace (1975) wrote that the 'notopleural sutures not distinguishable' and Crowson (1975) decided that *Crowsoniella* 'would be go with Ommadinae' because some other structural similarities 'short laterally inserted antennae, lack of free labrum, contiguous front coxae, simple tarsi, etc.'. Strict argumentation to put this genus into Archostemata has not been published in this paper and later, although till now this genus is regularly put into this suborder (Hörnschemeyer 2009 and many earlier publications). The combination of characters of C. relicta Pace 1975 coincides with that in some Cerylonidae Billberg 1820 (particularly bulged preapical palpomeres, type of formation of mesocoxae, type of antennal insertions, elongate trochanters, structure of antennae, character of depressions for reception of legs on thoracic and abdominal sclerites as well as depressions at anterior angles of pronotum as well as depressions at base of elytra congruous to posterior angles of prothorax, tendency to reduction of eyes, even some features in the structure of aedeagus: Slipinski, 1990) rather than with other coleopterous groups, although the metacoxae of Crowsoniella relicta are paradoxically similar to those in species of the genus Tetraphalerus Waterhouse 1901 and other Archostemata (fig. 17). Crowsoniella relicta differs also from other Cerylonidae in the reduced labrum, reduced ultimate maxillary and labial palpomeres, five-segmented tarsi, and peculiar structure of all coxae. This species could be tentatively placed into Cucujoidea (Polyphaga: Cucujiformia). On the other hand, small remains of propleura seem to be exposed outer from the procoxal cavity of *C. relicta* demonstrating some similarity to that in the prothorax of some members of the suborder Myxophaga (sharing also with *C. relicta* tendency in reduction of different structures), however, in contrast to them, *C. relicta* has lateral dilatations of the prosternal process closing the procoxa posteriorly and laterally.

Order Coleoptera

Family Cupedidae Laporte 1836

Genus Cupes Fabricius 1801

Cupes Fabricius 1801: 66 (Type species: Cupes capitatus Fabricius 1801, by monotypy).

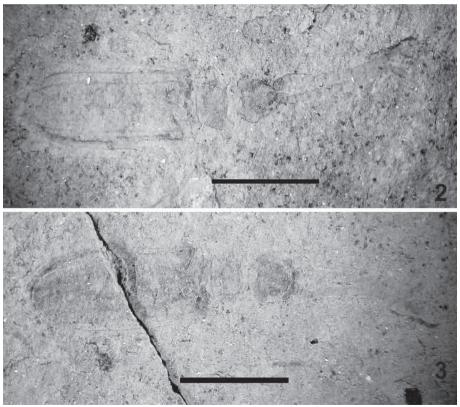
Cupoides Motschulsky 1856: 27 (type species: Cupoides tesselatus Motshulsky 1856, by monotypy).

Tenomerga Neboiss 1984: 448 (type species: *Cupes mucidus* Chevrolat 1829, by subsequent designation).

Distocupes Neboiss 1984: 457 (type species: Cupes varians Lea 1902, by subsequent designation).

Notes. This genus is here interpreted in the wide sense proposed by Kirejtshuk (2005), who after study the intensive materials on this genus in Baltic amber came to conclusion that the "tarsal" grooves on prosternum and level of development of tubercles on the dorsal surface of head cannot be used for generic discrimination as it was supposed by Neboiss (1984). The specimens examined for this paper have different level of preservation of the diagnostic characters, although all their characters exposed are correspondent with those in other members of the genus *Cupes*. All of them have narrowly separated antennal insertions. The holotype of Cupes manifestus **n. sp.** also demonstrates the separated procoxae, separated gular sutures and tarsal grooves on ventral sides of prothorax characteristic of members of the genus, while its lateral sides of head more gently arcuate than in most species and dorsal surface of head subflattened (see the discussion below).

Elytral venation. The elytra of most Archostemata have distinct ribs (primary, secondary and transverse veins) and cells (remains of primary wing membrane). The authors follow the terms elaborated by Ponomarenko (1969) who considered that only four veins can still be traced in the elytra of the Cupedidae. The vein M is located along plane of the elytron and at its



Figures 2–3

Cupes manifestus n. sp., holotype MNT-06-902-A. 2, print dorsal view. Scale bar represents 5 mm. 3, counterprint ventral view. Scale bar represents 5 mm.

subvertical lateral slope. Between the suture and vein M, there are disposed the vein Cu and vein A2, which end by a joined rib meeting with the vein M before the elytral apex. Finally, the vein A3 is represented by a short and partly smoothed prescutellar oblique rib. Between the main primary veins M, Cu, and A2, one intermediate (secondary) vein is seen quite clearly and sometimes these secondary veins are raised as primary ones. In contrast to the primary veins, the secondary elongate veins and the transverse veins originated from the archedictyon. These veins can have, as primary veins, a configuration rather stable among close relatives.

Cupes manifestus n. sp. (Figs 1-3)

Type material. Holotype MNT-06-902-A: imprint of dorsum of the complete beetle with exposed antennae and anterior

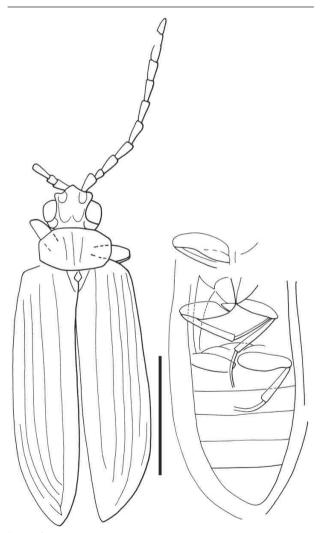


Figure 4 *Cupes orbiculatus* **n. sp.**, holotype MNT-05-198, A, print dorsal view; B, counterprint ventral view. Scale bar represents 6 mm.

legs as well as with traces of outlines of profemora, mesocoxae, part of posterior legs and also edges of abdominal ventrites; and counterimprint of underside of almost complete beetle obliquely broken behind the metaventrite with exposed antennae, right anterior leg, left profemur, intermediate legs, and part of metatibiae with metatarsi as well as with trace of outline of elytral edges and part of venation.

Etymology. The epithet of this new species means "noticeable", "evident", "remarkable", "clear".

Diagnosis. This species is very distinct from all the congeners due to the combination of rather wide and long antennae with much smoothed cells along the middle of elytra and subflattened pronotal disk. This species is preliminarily put in the genus Cupes, and its proper position in the subfamily Cupedidae should be clarify after a further comparative study of variability in the structure of antennae among different members of the subfamily. From the another new species obtained from the same outcrop it differs also in the smaller body size, smaller eyes, longer temples, longer head, structure of head surface, thicker antennae with thicker and shorter antennomeres, antennomere 2 slightly shorter than others, shape of pronotum, narrower elytra, much narrower epipleura, and shorter hypopygidium. The shape of pronotum and thick antennae of this new species is partly similar to that in some recent congeners, but the subflattened pronotum and peculiarities of elytra make this new species and C. orbiculatus n. sp. rather different from all congeners (see the discussion below).

Note. The smoothness of elytral cells, particularly along the middle of elytra is evident as for this new species as for the following one, because "microtuberculation" (probable remains of scales are clearly visible) has a good expression on elytra.

Description. Length 12.2 mm, head 2.2 mm long and 2.6 mm wide, body width 3.7 mm. Elongate oval, apparently moderately convex dorsally and ventrally; integument of dorsum somewhat smoothed.

Head without prominent tubercles along the middle, median part of frons and occiput apparently subflatted and elevated with more rugose and more coarse sculpture (probable remains of recumbent suboval scales) and somewhat explanate anterior part above antennal insertions, but on each temple a characteristic and weakly raised tubercle clearly visible. Eyes comparatively small, markedly shorter than temples. Antennae seemingly at least reaching basal third of elytra (posterior edge of ventrite 1); all antennomeres rather broad and of comparable width; scape somewhat shorter than apical antennomeres, antennomere 2 only slightly shorter than scape, antennomeres 3–9 comparable in length, antennomeres 10 and 11 longest. Labrum somewhat visible on counterpart and apparently convex at anterior edge. Pronotum transverse (1.7 x 2.5 mm), subquadrangular and clearly widened anteriorly, anterior and posterior angles with more or less distinct tops, anterior edge gently convex and posterior one nearly straight; plane of pronotum apparently subflatted and with coarse sculpture (somewhat similar to that on median part of head: probably also remains of recumbent scales) and a very weak median carina apparently dividing disk along the entire length. Elytra 8.2 × 3.7 mm, with clearly raised veins Cu and A2 joining and meeting together; intermediate veins between veins M and Cu not risen; vein A3 distinct; cells (remnants of primary membrane) are slightly expressed only along the lateral parts of elytra where they arranged in more or less regular double rows along lateral slopes and between main veins M and Cu, but two rows of cells between the veins Cu and A, and along the suture, the sculpture is similar to that on head and pronotum (probably remains of recumbent scales).

Mentum subtrapezoid, narrowing anteriorly. Gular sutures somewhat arcuate and V-shaped. Prosternum apparently swollen and its median part restricted by paramedian tarsal grooves, its intercoxal process very narrow and subparallel-sided, not far extended behind them. Mesoventrite without distinct outlines of sclerites. Metaventrite with a comparatively clear transverse median depression at metacoxae. Hypopygidium about twice as long as each of ventrites 2–4, somewhat shorter than wide and widely rounded at apex.

Tibiae rather narrow, about as wide as epipleura at base and wider than antennomeres. Pro- and mesofemora at least twice as wide as tibiae. Meso- and metatarsi apparently narrower than tibiae.

Cupes orbiculatus n. sp. (Figs 4–6)

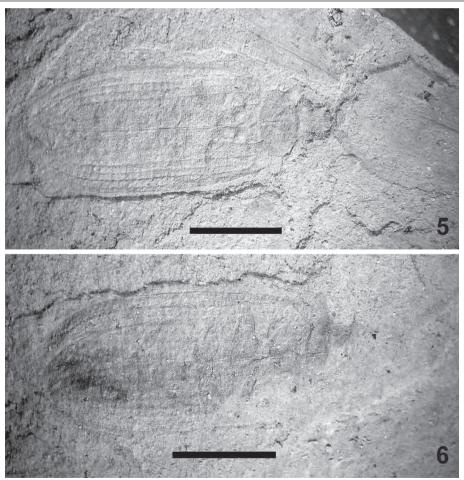
Type material. Holotype MNT-05-198: Imprint of dorsum of the complete beetle with exposed entire right antenna,

base of left antenna and anterior femora as well as with traces of outlines of base of profemora, thoracic and abdominal sclerites, intermediate and posterior legs; counterimprint of the underside of pterothorax, abdominal ventrites, intermediate legs, right metafemur and left posterior leg; as well as with traces of outline of elytral lateral edges and epipleura.

Etymology. The epithet of this new species means 'roundish', 'rounded' referred to suboval outline of the prothoracic segment.

Diagnosis. This new species can be diagnosed from the other species from the same outcrop after the characters mentioned above (see the diagnosis to *Cupes manifestus* n. sp.). The suboval outline of its pronotum is reminiscent only of *C. weitschati* Kirejtshuk, 2005, although the subflattened pronotum and peculiarities of elytra make this new species quite different from the latter. If this new species is somewhat similar to the species described in *Mesocupes* Martynov, 1926 (Ponomarenko 1969; Tan et al. 2007) in the shape of its pronotum, but it is at least clearly distinct from them in the level of separation of antennal insertions and length of antennae.

Description. Length 18.2 mm, head 2.6 mm long and 3.0 mm wide, body width 7.3 mm (elytra apparently enlarged because

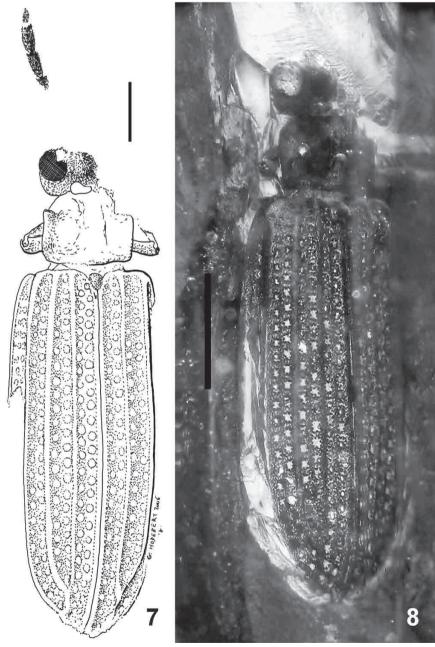


Figures 5–6
Cupes orbiculatus n. sp., holotype MNT-05-198. 5, print dorsal view. Scale bar represents 5 mm. 6, counterprint, ventral view. Scale bar represents 5 mm.

of turning during fossilization). Elongate oval, apparently moderately convex dorsally and ventrally; integument of dorsum somewhat smoothed.

Surface of head without prominent tubercles, although median part of frons and anterior part of occiput apparently elevated and anterior part somewhat explanate above antennal insertions; sculpture finely microtuberculate (i.e. with probable remains of scales). Eyes rather large, about 2.5 times as long as temples. Antennae seemingly almost reaching the middle of elytra (base

of ventrite 1); all antennomeres elongate and of comparable width; scape somewhat shorter than most antennomeres, antennomere 2 about half as long as scape, antennomeres 3–9 comparable in length. Labrum not visible. Pronotum transverse $(2.0 \times 3.7 \text{ mm})$, suboval and subequally rounded anteriorly and posteriorly, angles without distinct tops, anterior and posterior edges gently convex; plane of it apparently subflattened and with coarse sculpture (somewhat similar to that on median part of head: probably also remains of recumbent scales) and



Figures 7–8

Cupes ponomarenkoi n. sp., holotype PA 6457. 7, drawing of habitus, dorsal view. Scale bar represents 1 mm. 8, photograph of habitus, dorsal view. Scale bar represents 2 mm.

a very weak median carina apparently dividing the disk along the entire length. Elytra 4.2 × 2.5 mm, with clearly raised veins Cu and A2 joining and meeting together; intermediate vein between veins M and Cu (also joining with Cu and A2) and vein A3 more or less distinct; cells (remnants of primary membrane) are hardly expressed throughout the whole elytral plane; sculpture looking like much more smoothed than that on head and pronotum (probably remains of recumbent scales here much sparser and somewhat larger).

Underside of head, prosternum and mesoventrite not preserved. Only mesocoxae apparently preserved. Metaventrite with a comparatively clear transverse median depression at metacoxae. Hypopygidium about 1.5 times as long as each of ventrites 2–4, somewhat shorter than wide and widely rounded at apex.

Tibiae rather narrow, about half as wide as epipleura at base and about as wide as flagellomeres. Pro- and mesofemora more than twice as wide as tibiae. Meso- and metatarsi apparently narrower than tibiae.

Cupes ponomarenkoi n. sp. (Figs 7–8)

Type material. Holotype PA 6457. The specimen is represented by a print with remains of dorsal surface of the most part of body (except of anterior and right part of base of head), the left protibia and femur and terminal segments of left antenna are also included in the amber piece. Above and behind of the beetles fossil there is located a small specimen of Diptera. The amber piece was polished mostly from above side of the beetle in order to study accessible structures of the latter.

Etymology. The epithet of this new species is devoted to A.G. Ponomarenko, greatest specialist on Cupedidae, whose contribution to our knowledge on the diversity and system the suborder Archostemata is most valuable during the 20th century.

Diagnosis. This species is distinct from all the congeners from Baltic amber in the subquadrangular pronotum with distinctly acuminate tops of its anterior and posterior angles (Kirejtshuk 2005); and from both extinct and modern species of the genus in the elevated median stripe of pronotum in basal half (Neboiss 1984), which is much weakened in the new species from amber. Besides it, in contrast to most species of the genus, the vein A3 of elytra in the new species is scarcely traced as well as, in contrast to many members of the genus, this new species has comparatively large eyes, although such large eyes occur also in some species of both extinct and extant faunas [C. anguliscutis Kolbe 1886; C. concolor Westwood 1835; C. groehni Kirejtshuk 2005; C. hoffeinsorum Kirejtshuk 2005; C. leucophaeus Newman 1839; C. mucidus Chevrolat 1829; C. rohdendorfi Iablokoff-Khnzorian 1960; C. trabeculus (Neboiss 1984)]. Finally, this new species is characterized by its intermediate veins of the elytra which are much less raised than the primary elytral veins.

Description. Length (from visible edge of head to elytral apices) 9.17 mm, head (incomplete) circa 1 mm long and 1.2 mm wide, body width 2.5 mm. Rather long, apparently moderately convex dorsally and ventrally; with extremely dense, yellowish grey scales (masking the darker coloration of body surface), without clear infuscation; preserved antennomeres with distinct and dense stout setae.

Surface of head with one posterior paramedian pair of tubercles

(longitudinal and comparatively wide, more elevated anteriorly than posteriorly and reaching the level of anterior third of eyes); interval between posterior tubercles apparently nearly as great as length of a tubercle. Eyes rather large, almost three times as long as temples. Antennae seemingly at least reaching basal 1/5 of elytra; preserved antennomeres (probably antennomeres 6 and 7 or 7 and 8) subcylindrical to subconical and about 2.5 times as long as thick. Pronotum transverse $(1.5 \times 2 \text{ mm})$, subquadrangular and nearly subparallel-sided in most length, but somewhat narrowing to both anterior and posterior angles as well as at base to junctions as with head as with pterothorax; with a median stripe rather and widely elevated in anterior half and strongly depressed in posterior one, although at scutellum it is again elevated as a prominent tubercle (without longitudinal median furrow), anterior angles subrectangular, posterior ones with blunt indistinct apices, its posterior edge subrectilinear. Scutellum moderately vaulted and rather widened before subtransverse posterior edge. Elytra 6.6 × 2.5 mm, with clearly raised veins Cu and A2 joining and meeting with vein M; intermediate veins between veins M and Cu very slightly risen along the entire length; vein A3 indistinct. Cells of elytra forming characteristic double rows between main and intermediate veins.

Protibia rather narrow, not compressed and scarcely widened at apex. Profemur less than twice as wide as tibiae.

Discussion. Cupes manifestus n. sp. and C. orbiculatus n. sp. from Menat are characterized by the slightly tuberculate head, subflatted pronotum, reduced cellulation at least along the middle of elytra and rather wide antennae. Nevertheless, they should be considered in the composition of the genus Cupes because of its rather long antennae, comparatively narrowly separated antennal insertions, rather narrowed neck behind temples and more or less clear prosternal process. The elytra of both these new species demonstrate the type of venation which seems to be close to the basal state in the Cupedinae and very similar to that in most species in Cupes. However, clearly reduced cells in general and obsolete those along the middle of elytra are quite peculiar features of these new species. The peculiarities of these new species give some arguments to revise the state and composition of this genus. Particularly, the size of it can be increased by inclusion of some Mesozoic species. It seems that the most principal character for compression fossils to discriminate genera Cupes and Priacma remains only the level of separation of antennae. In this connection most species described as Priacma LeConte, 1861 (published by Ponomarenko 1986, 2000; Tan et al. 2006) and also as Furcicupes Tan & Ren 2006, Latocupes Tan & Ren 2006 and Mesocupes sensu Tan, Huan & Ren 2007, not Martynov, 1926 (species lastly mentioned taxa probably are mostly congeneric with true members of Priacma) should be revised, although Priacma sanzii Soriano & Delclos 2006 looks like rather different from the members of both Priacma and Cupes. The diagnostic characters of the tribes Priacmini Crowson 1962 (n. syn.) and Cupedini in antennae, prosternum and eyes demonstrate numerous exceptions and these tribal names should be regarded as synonyms. The differences between some genera of this united tribe are also frequently not so reliable for generic discrimination because of variability from species to species and therefore these generic taxa are certainly needed to be revised. On the other hand, the male genitalia of recent Priacma serrata LeConte 1861 show extremely unique structure, very different from those in other recent Cupedidae.

The reduction of the primary membrane in cells is expressed in different extant and extinct species. The level of expression of this tendency that is visible in Cupes manifestus n. sp. and C. orbiculatus n. sp. looks like close to the extreme, although in Priacma latidentatus Tan, Ren & Shin 2006 such reduction can also be traced. Besides, the trace of primary membrane of Miocupes rihai Ponomarenko 1973 seems to be completely evanescent [however the latter generic group is very distinct due to the clearly subparallel main and secondary longitudinal veins on elytra as well as due to the very large temples]. The subflattened pronotum is not characteristic of the species of Cupes known from the later time, although Cupes groehni Kirejtshuk 2005 from Baltic amber has very similar plane of its pronotum. On the other hand, the subflattened surface of pronotum, structure of antennae and other characters of the mentioned new species and Cupes ponomarenkoi n. sp., except for the weakened sculpture of elytra, are rather similar to that in the Cretaceous species with long antennae described by Tan et al. (2006) as members of the *Priacma*, differing from the latter only by the level of separation of antennae. Thus, it is thought that all generic taxa near Cupes and Priacma are needed to be

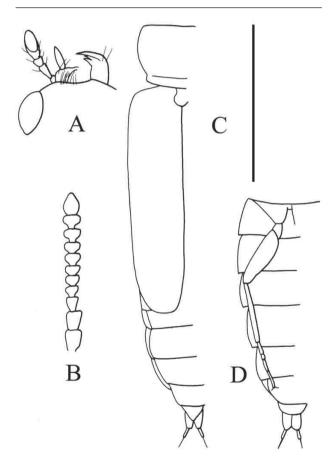


Figure 9 Micromalthus eocenicus n. sp., holotype PA 7870, drawing of details. A, anterodorsal view of head (scale bar represents 0.5 mm); B, antenna (scale bar represents 0.5 mm); C, dorsal view of thorax and abdomen (scale bar represents 1 mm); D, ventral view of abdomen with metacoxae and posterior legs (scale bar represents 1 mm).

revise after further re-study of the types of many species. It could be also supposed that appearance of both *Cupes* and *Priacma* took place at a comparable stage of historic development of Cupedinae, although the first has been for certain recorded only in Cainozoic and forms with *Priacma*-appearance are known in fossil record since the Middle Jurassic (Tan, Huan & Ren 2007).

As to the generic names *Priacmopsis* Ponomarenko 1966; *Cupedium* Ponomarenko 1968; *Gracilicupes* Tan, Ren & Chin 2006, and *Ovatocupes* Tan & Ren 2006 proposed for the groups with species rather similar to the species of the genus *Cupes*, it is thought to be reasonable to revise all of them as well, although they were proposed in three different tribes of the subfamily Cupedinae. However, it will be done after re-testing type material deposited in Russian and Chinese collections. Besides it, species of some other genera that are treated as "subfamilia incerta" in Ponomarenko & Kirejtshuk (2009), are needed to be revised in order to clarify their relation. The beetles of this genus are comparatively unusual in some compression deposits and more regular in Middle-Late Eocene Baltic amber (Motschulsky 1856; Peyerimhoff 1909; Iablokoff-Khnzorian 1960; Ponomarenko 1969; Kirejtshuk 2005 etc.).

Family Micromalthidae Barber 1913

Genus Micromalthus LeConte 1878

Micromalthus eocenicus n. sp. (Figs 9–14)

Type material. Holotype PA 7870, female (a complete beetle with a specimen of Ceratopogonidae (Diptera), situated aside from the ventral side of the holotype, included in the amber piece with some cracks at body of the latter along its plane). Paratype PA 1286, female (a complete beetle together with one specimen of Trichoptera, some coprolithes and many other small pieces of organic matter included in the amber piece, which has many cracks and a bigger crack approaching to the middle of the underside of the beetle; the dorsum of the beetle specimens is located near the amber surface that remained unpolished.).

Etymology. This new species is named after the time of amber deposition (Eocene).

Diagnosis. The new species differs from the recent species in the frons very slightly projecting anteriorly before eyes and with the straight anterior edge, somewhat longer antennae, subacute ultimate antennomere, transverse pronotum, elongate scutellum with rounded apex, somewhat longer elytra and rather long tibial spur. Besides, *Micromalthus debilis* in contrast to the new species has the very shining integument, very acute apex of the last maxillary palpomere, last labial palpomere subconical about 1.5 times as long as wide at base and subacute, anterior edge of frons strongly concave, scutellum subtransverse to concave at apex, elytra with a distinct oblique thickening from the shoulder to the middle of the suture. This new species differs from *M. anansi* Perkovsky 2007 from Dominican amber in the characters mentioned for the recent M. debilis and also in the less transverse most antennomeres and not so transverse head.

Description. Holotype (female). Length 2.5 mm, width 0.6 mm, height 0.3 mm. Rather elongate, somewhat depressed

dorsally and rather convex ventrally; dorsum and appendages light brown; underside dark brown; integument feebly sclerotized (not even on pronotum and elytra), smooth to subalutaceous and glabrous, although few sparse and comparatively long hairs spread on elytral sides as well as sparse and shallower indistinct punctures visible on ventrites (their diameter about as great as eye facets in diameter).

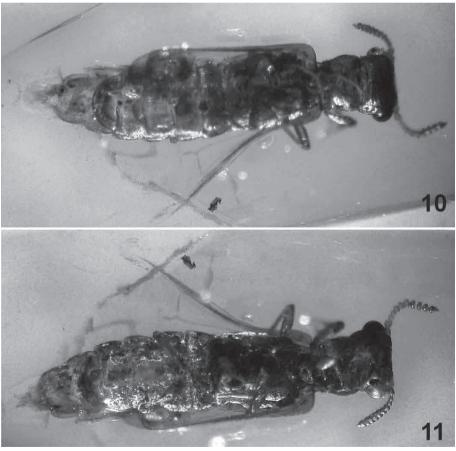
Head markedly wider than prothorax (about 0.6 mm), slightly wider than long and shorter than distance between eyes (which are moderately large), without temples, slightly convex dorsally, although with a weak depression at straight anterior edge; anterior part of frons not extended forwards beyond the level of anterior edge of eyes and antennal insertions, frons slightly elevated mesally from antennal insertions, which are disposed at anteromesal edge of eyes. Mandibles tridentate at apex. Mentum subquadrangular and about as wide as antennomeres 1 and 2 long combined. Gular sutures subparallel and apparently as widely separated as subtruncate part of frons. Maxillary palpi rather long, ultimate palpomere largest, obliquely truncate at apex and without clear cavity. Labial palpi moderately developed, ultimate palpomere largest, rather elongate and with acute apex and without clear apical cavity bearing sensilla. Antennae 11segmented, about as long as head wide, antennomeres 1-3 and 11 somewhat longer than wide, the rest ones more or less

transverse and antennomeres 7-10 subequal in shape and size.

Pronotum about three fourth as long as wide, widest at anterior third, without lateral carina (between pronotum and prohypomera), its sides subarcuately convex and with a small sinuation at base, its disk slightly convex, shallowly and irregularly grooved and with somewhat more impressed transverse groove along base, its anterior edge shallowly emarginate and posterior edge regularly convex. Scutellum distinctly longer than wide, not strongly widened before rounded apex. Prosternum and mesoventrite combined nearly three fourth as long as metaventrite, prosternum and mesoventrite moderately and metaventrite rather convex, prosternal process not raised, mesoventrite without trace of sutures, metaventrite transversely elevated before metacoxae.

Elytra about 2 and 1/3 as long as wide combined, with long longitudinal furrows and shallowly irregularly grooved, their plane with some narrow thickenings (longest one along the lateral edge and one crossing the plane from shoulder to the middle of suture), their rounded apices somewhat declined down. Three last abdominal segments completely and part of previous one exposed from under elytra.

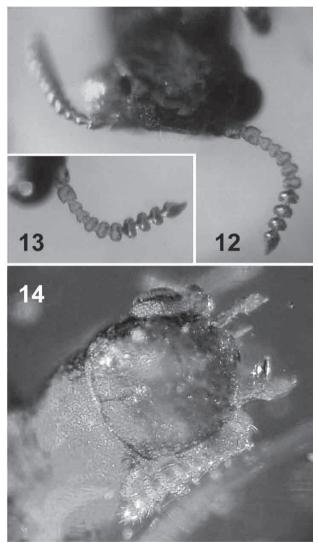
Procoxae subconical and long, oriented downwards and nearly contiguous, their cavities strongly transverse and posteriorly



Figures 10–11 Micromalthus eocenicus n. sp., holotype PA 7870, photograph of habitus. 10, dorsal view; 11, ventral view.

open. Mesocoxae oval and narrowly separated, almost as separated as metacoxae. Metacoxae transverse and medially subconical, oriented posteriorly. Legs very narrow and long. Trochanters rather elongate. Femora with slightly convex anterior and posterior edges, more than five times as long as wide, with a shallow furrow for reception of tibiae. Tibiae very long and almost as long as femora and about 10 times as long as wide, their outer surface simple and narrow apices with a distinct and rather long spur. Tarsi somewhat shorter than tibiae, all tarsomeres simple, tarsomeres 2–4 subequal in length and somewhat shorther than tarsomere 1, tarsomere 5 longest and about as long as tarsomeres 2–4 combined; claws long and narrow.

Abdomen with six completely exposed ventrites; ultimate ventrite not longer than others and with a widely rounded apex. Ovipositor with exposed apices of gonocoxites and rather long styli bearing a long apical seta (about as long as stylus).



Figures 12–14

Micromalthus eocenicus n. sp., holotype PA 7870. 12, photograph of mouthparts; 13, antenna; 14, head, dorsal view.

Variability (paratype, female). Head rather declined ventrally. Both antennae and all legs oriented more or less downwards. Abdomen with six ventrites with proportions somewhat different from those in the holotype (ultimate ventrite somewhat longer than the two previous taken separately). The ovipositor is exposed beyond the abdominal apex.

Discussion

The new species represents a third member of the genus described. However, triunguline larvae of this family were recorded from Mexican (Rosen 1971) and Lebanese (Crowson 1981) amber. It is very probably that these larvae belong to different species. The triunguline larva from Lebanon is very distinct from that of *M. debilis* and apparently from that in the Mexican amber and therefore it can be regarded as a member of a separate genus (Kirejtshuk & Azar 2008). Rosen (1971) regarded that the triunguline larvae from the amber of Chiapas (Mexico) as conspecific with that of recent M. debilis, however, it could belong to another species which had larvae similar to those in *M. debilis*. The age of the specimen from Mexican amber is about at a comparable time distance from both M. eocenicus **n. sp.** and *M. debilis* (according to Martínez-Delclós *et* al. 2004: Middle Oligocene-Miocene).

Poinar & Poinar (1999) mentioned Micromalthus also from Dominican amber with younger age (Middle Oligocene to Miocene) and Perkovsky (2007) described an imago of *Micromalthus* from this resource as a separate species (see the diagnosis to M. eocenicus n. sp.). Study of adults from that amber would be very advisable to solve the problem of species attribution of the larva. Hörnschemeyer et al. (2009) considered that the adults from Dominican amber could be regarded as conspecific with recent species. A.L. Tikhomirova and A.G. Ponomarenko found some prints of Micromalthidae among materials from Karatau (Mikhaylovka, Upper Jurassic). The recent re-examination supports this family attribution, although most of these prints have not very fair preservation and different in their body size and in the structure of some sclerites. Most of them have seven abdominal ventrites, one specimen demonstrates the characteristic posterior wing and some show metacoxae similar to those in the specimens here described.

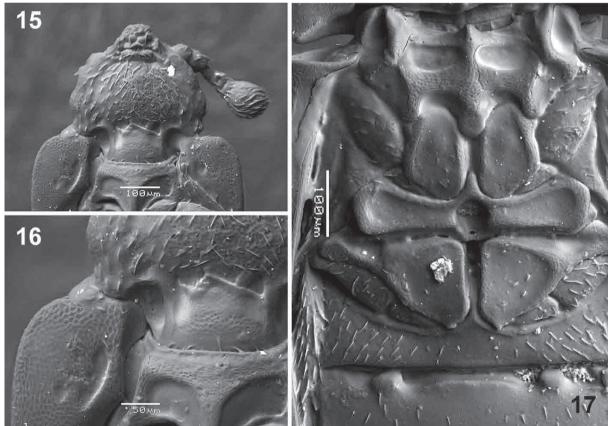
Thus, it is possible to claim that the family Micromalthidae appeared at least not later than the Lower Cretaceous and the genus *Micromalthus* – not later than Early Eocene.

Notes. The genus *Micromalthus* was proposed in the composition of the family Lymexylidae, then Barber (1913) erected for it a separate family near Lymexylidae, but after publication of Forbes (1926) this family is usually treated among the suborder Archostemata (Beutel & Friedrich 2008). Nevertheless, this position of this group has been frequently

discussed and up to now the relation of this family with other groups is not very clear. Some authors considered that it could be interpreted with some more relationship to the suborder Myxophaga (Ponomarenko 1973b) or Polyphaga [for example, superfamily Cantharoidea (Arnett 1963); Lymexyloidea (Barlet 1996) (see also Machatschke 1962 etc.)]. Perhaps, peculiarities of the larval structures are scarcely very reliable for phylogenetic interpretation because of a more evolutionary 'plasticity' of larval structures in general, although their peculiarities can provide with additional support to a certain viewpoint. In particular, its epicranial and mouthparts structures as well as male genitalia of adults seem to give a more obvious indication on the phyletic affinity of this family to Archostemata rather than other characters and can support a more or less clear relation of it to other coleopterous groups. However, the lack of maxillary lobes in adults of Micromalthus is characteristic only of this family of the suborder. The adults of Micromalthidae, in contrast to other groups of Archostemata, got the more or less expressed paedomorphic characters in many organs [in first turn, in the level of development of abdomen (general segmentation), partly venation of elytra, perhaps, sculpture of integument and so on], although certain reduction of some structures could be caused by general miniaturization. These peculiarities combine with not complete development of some other organs, like the reduced venation of posterior wings and missing prothoracic sutures. Nevertheless, the larval structures of *Micromalthus* are also in accordance with those in other recent groups of Archostemata (Grebennikov 2004).

Recorded frequency of occurrence of larvae of this genus (family) in amber (see above) can be explained by the bionomics of both active stages of the species within this family. They seem to be always associated with wood (as it is characteristic of the recent representatives).

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Figures 15–17

Crowsoniella relicta Pace, paratype, SEM picture. 15, head and anterior part of prothorax, ventral view; 16, right part of head and anterior part of prothorax, ventral view; 17, pterothorax, ventral view.

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