First palaeanodont (?pholidotan) mammal from the Eocene of Europe

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We report the discovery in the early Eocene French locality of Le Quesnoy (MP7, Neustrian) of the first palaeanodont from the Eocene of Europe, and the first metacheiromyid from outside of western North America. The species, known from a dentary and a few postcranial bones, belongs to the genus *Palaeanodon,* and it is one of several North American immigrant taxa that characterize the Paleocene–Eocene faunal turnover in Europe. *Palaeanodon* sp. from Le Quesnoy is close in size to *P. nievelti* from the early Wasatchian of North America. However, it shows noticeable primitive features such as a more prominent ventral keel on the metacarpal III and a probably elongated and bilobed pc4 (= p4), although this is inferred from the infilled alveolus. Additional original features are also noticed on the tentatively referred astragalus. These minor differences suggest that the Le Quesnoy form represents a new species, but the available material remains inadequate to name it. The morphology and the size of the metacarpal are actually closer to *P. parvulus* (Clarkforkian)—*P. nievelti* (Wasatchian) intermediates, suggesting a sister-group relationship with the latter (if *Palaeanodon* sp. from Le Quesnoy is not shown to belong to a distinct European lineage). This would indicate a dispersal at least as old as *P. nievielti* and a correlation of Le Quesnoy not later than early Wasatchian. The discovery of *Palaeanodon* in Le Quesnoy fits paleobiogeographically well with the hypothesis of a relationship of palaeanodonts to pholidotans, which have their earliest record in the middle Eocene of Europe (Messel).

Key words: Mammalia, Palaeanodonta, paleobiogeography, Neustrian, Eocene, Le Quesnoy, Europe.

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Introduction

The locality of Le Quesnoy, from the early Eocene (MP7, Neustrian Fahlbusch 1976 = Sparnacian of paleomammalogists) of the Paris Basin (Oise, France), has yielded one of the most diversified floristic and faunal assemblages from the Paleogene (Nel et al. 1999). It provides a relatively unbiased picture of an early Eocene continental paleoecosystem. The mammal fauna from Le Quesnoy has been only briefly reported. Here we describe an unexpected taxon, a metacheiromyid palaeanodont (see Fig. 1), previously reputed to be a relatively uncommon taxon of early Paleogene North American mammal assemblages. Its discovery in Le Quesnoy provides additional evidence of the exceptional nature of its fossiliferous assemblage in Europe.

In 1998, during the sorting of crocodilian and other unidentified bones recovered from Le Quesnoy following our washing and screening operations of 1997 and 1998, one of us (EG) identified a fragmentary lower jaw as that of a palaeanodont mammal, the first discovered in the Eocene of Europe. This record was mentioned in our preliminary paper on the locality as "cf. Edentata indet." (Nel et al. 1999). Since this initial discovery, several postcranial bones from Le Quesnoy, probably belonging to the same palaeanodont species, were identified (by KDR and MG).

Palaeanodonts are otherwise known mostly from the Late Paleocene–Eocene of North America, with additional marginal occurrences known in the early Oligocene of Europe (Heissig 1982; Storch and Rummel 1999) and in the early Eocene of Asia (Tong and Wang 1997). As a whole, they are uncommon mammals, even if recent field work in North America has shown that they are not so rare as previously thought (Gingerich 1989; Rose et al. 1991; Rose et al. 1992).

Institutional abbreviations.—MNHN, Muséum national d'Histoire naturelle, Paris; UM, University of Michigan, Museum of Paleontology, Ann Arbor, Michigan; USGS, U.S. Geological Survey collections, now at USNM; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Other abbreviations.—MDE, Mammalian Dispersal Event; NALMA, North American Land Mammal Ages; QNY, Le Quesnoy (Creil) France, QNY 2: channel 2 (see Nel et al.
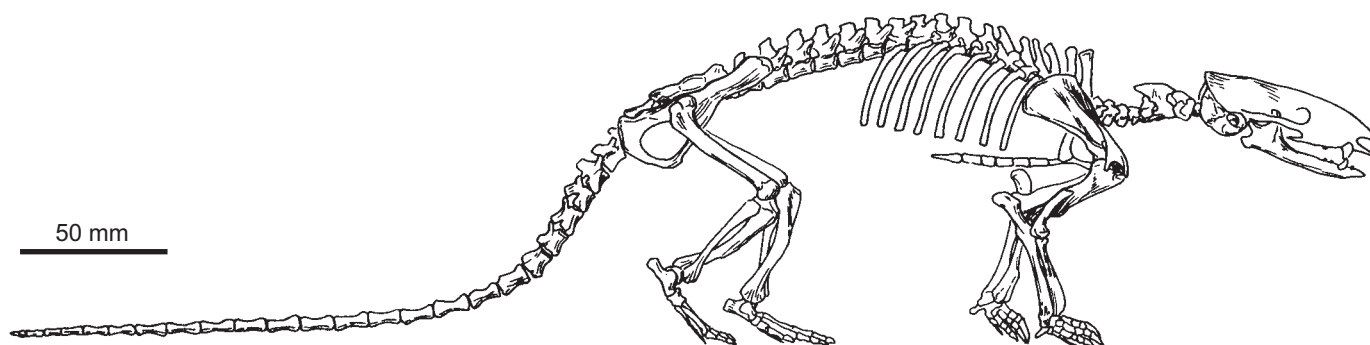
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50 mm

Fig. 1. Reconstruction of the skeleton of *Metacheiromys* (modified by Rose and Emry 1993 after Simpson 1931: fig. 1), a palaeanodont from the Middle Eocene of North America. Palaeanodonta means "ancient edentate", in reference to the highly reduced dentition (except for the large canines) in specialized genera such as *Palaeanodon* and *Metacheiromys*, which probably reflects a dietary preference for ants and termites. Palaeanodonts were digging and burrowing mammals thought to have been armadillo-like in their habits, and they are currently considered as the probable ancestors of the pangolins (Rose et al. 2005).

1999); UMR, Unité Mixte de Recherche. Lower case letters are used to designate lower teeth (p = lower premolar; m = lower molar; pc = lower postcanine tooth).

Systematic paleontology

Order ?Pholidota Weber, 1904
Suborder Palaeanodonta Matthew, 1918
Family Metacheiromyidae Wortman, 1903
Genus *Palaeanodon* Matthew, 1918

Palaeanodon sp.
Figs. 2–6.

Locality, horizon, and age: Le Quesnoy, Argiles à Lignites du Soissonnais Formation, Early Eocene (MP7, Neustrian) of the Paris Basin, France.

Referred material.—MNHN QNY 2-275, right fragment of dentary with the distal postcanine tooth. MNHN QNY 2-276, right metacarpal III. MNHN QNY 2-279, left first metatarsal I.

Questionably referred material.—MNHN QNY 2-278, right astragalus.

Description

The dentary and lower dentition (Figs. 2, 3; Table 1).— MNHN QNY 2-275 is a fragment of right dentary preserving the distal part of the horizontal ramus and the posterior postcanine tooth. The coronoid and angular processes, and the articular condyle are broken, as is typical of palaeanodont dentaries. Only one tooth, the posterior postcanine, is preserved.

The genus *Palaeanodon*, to which the Le Quesnoy specimen is referred, has five postcanine teeth pc1–5 (e.g., based on UM 66243, referred to *P.* cf. *ignavus* by Rose 1981). These teeth are interpreted as p1–4, and m1 by Secord et al. (2002), implying that teeth were lost from the back of the sequence in metacheiromyids. Following this interpretation,

the postcanine tooth preserved in MNHN QNY 2-275 is identified as pc5 (= m1).

The pc5 has only one root and is typically peglike and small. It is signicantly smaller than its alveolus (Figs. 2A, 3A, B) as is usual in *Palaeanodon*. The crown is strongly worn by abrasion. Its occlusal outline is slightly oval with a mesio-distal long axis. Although the sharp rim of the abraded crown suggests that enamel may have been present as seen in *Alocodontulum* (Rose et al. 1992), microscopic (SEM) examination reveals no evidence of enamel. Enamel was still present, though thin, on the cheek teeth of the epoicotheriid *Tubulodon* (including *Alocodontulum*) (Jepsen 1932; Rose et al. 1991; Rose et al. 1992). Radiographic views (Fig. 3) show that the root is massive and robust, and longer than wide (tranverse section oval). It is slightly recurved posteriorly. It is nearly four times higher than the worn crown. In lateral view the root appears only slightly narrower at its lower part than near the base of the crown.

The dentary preserves the distal edge of the alveolus of a more anterior tooth, just where the lower jaw is broken (Fig. 1A). The preserved vertical section of this alveolus indicates a tapered root. This tooth and pc5 are separated by an apparent diastema. However, a cavity in this diastema suggests the remnants of the alveolus for the postcanine tooth pc4 (= p4), which is in the course of infilling by remodeled bone. The

Table 1. Dimensions of the dentary MNHN QNY2-275 (mm).

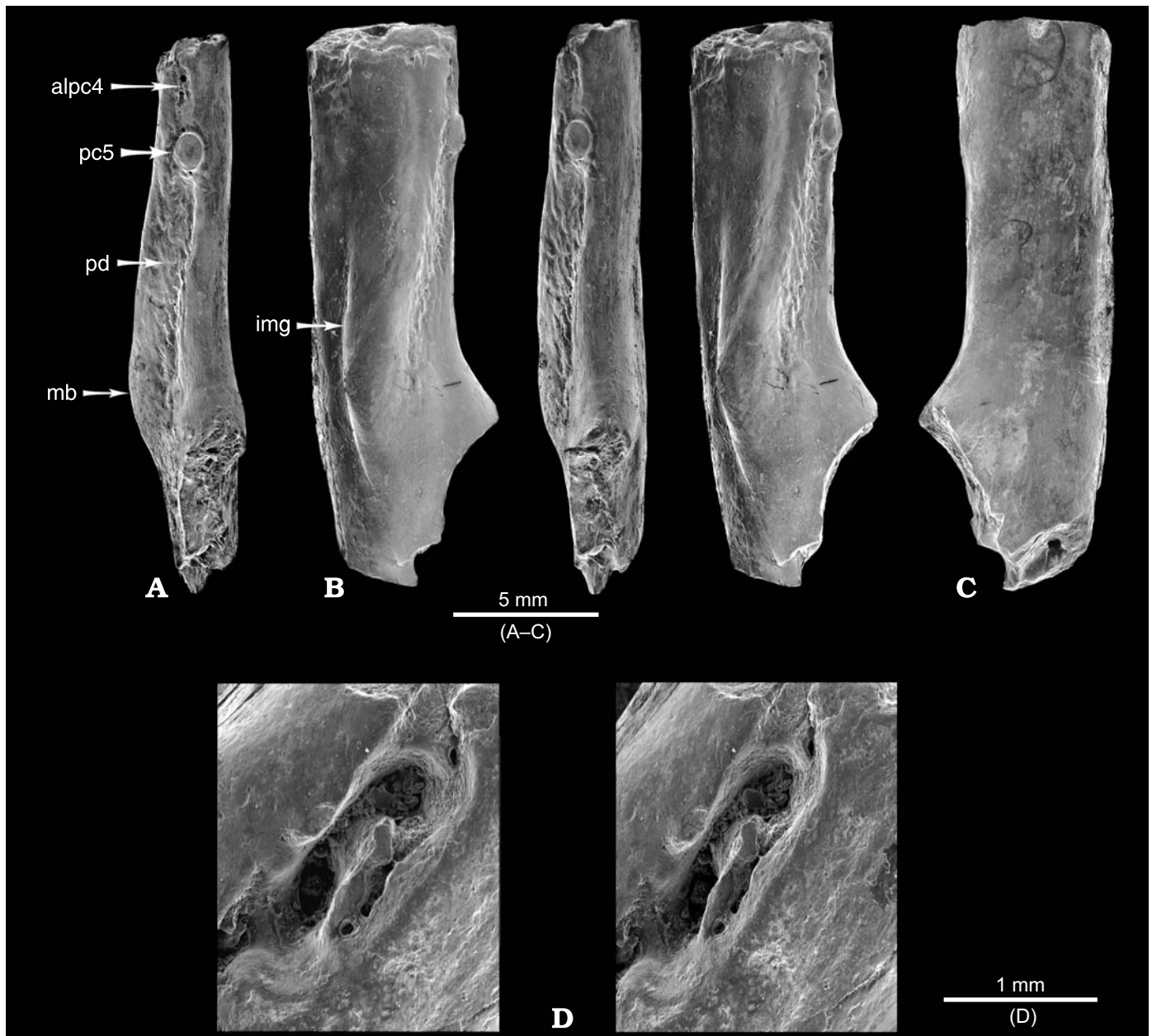|	length	width	height
pc5	1.4	0.8	?
Alveolus of pc4	1.5	?	–
Posterior diastema	6.5 (to ascending ramus) – 8.2 (to medial buttress)	–	–
Horizontal ramus	–	3.2 at pc5 – 3.9 at medial buttress	5.2 below pc4 and at medial buttress

Fig. 2. *Palaeanodon* sp., MNHN QNY 2-275, from Le Quesnoy, SEM micrographs. **A–C**. Right lower jaw in occlusal (**A**), lingual (**B**), and labial (**C**) views; mb, medial buttress; pd, posterior diastema; pc5, last lower postcanine tooth (= m1); alpc4, alveolus for pc4 (= p4); img, internal mandibular groove. **D**. Detail of the infilling alveolus of pc4 in occlusal view, showing its elongated and laterally compressed outline which is suggestive of an elongated p4 with bilobed root (or possibly two-roots). A, B, D, stereo micrographs.

occlusal outline of this infilled alveolus is elongated (especially with respect to pc5), slightly constricted in its mid-length and it shows two small pits. This configuration suggests that the missing tooth (p4) was elongate and had a bilobed root, or just possibly was two-rooted. This is confirmed by the X-ray views, especially the lateral one (Fig. 3). In front of pc5, the occlusal surface of the dentary is depressed by a double-concavity which is separated in the middle by a very slight vertical septum of dense bone, probably corresponding to the transverse alveolar wall present laterally between two more or less fused roots (but probably not completely separating

them). However, most of the alveolus is completely filled by bone of density similar to that of the rest of the jaw (e.g., diastema area), confirming that the tooth was prematurely lost during the life of the animal. The identification of this tooth alveolus as that for pc4 in MNHN QNY 2-275 indicates that the anterior alveolus corresponds to pc3 (= p3).

The horizontal ramus is slender and shallow. It is straight (lower and upper borders nearly parallel and horizontal), and it has nearly the same depth all along its preserved part. The medial buttress is strong, especially below the rising anterior part of the ascending ramus where it forms a promi-
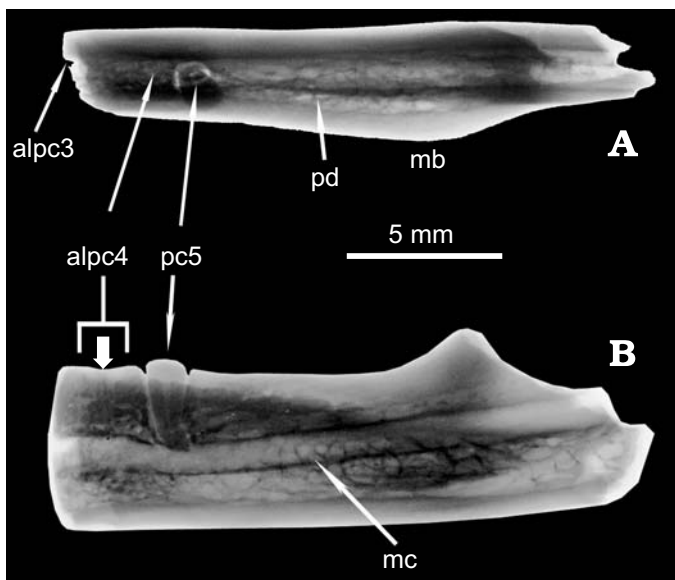
Fig. 3. *Palaeanodon* sp., right lower jaw MNHN QNY 2-275, from Le Quesnoy in occlusal (**A**) and lingual (**B**) X-ray views; alpc3, alveolus for pc3 (distal part); alpc4, infilled alveolus for pc4 (visible only in the higher part), the broad arrow indicates a dense transverse bony wall of the alveolus wall, probably indicating a bilobed root; pc5, m1; mb, medial buttress; mc, mandibular canal; pd, posterior diastema.

median keel, flanked by grooves separating it from small tubercles at the medial and lateral margins of the articular surface. The keel is somewhat more prominent than in *Palaeanodon ignavus* Matthew, 1918 and at least some *P. nievelti* Gingerich, 1989 in projecting palmarly slightly beyond the tubercles, and the grooves appear to be more constricted. A stronger keel is found in the basal palaeanodont *Escavadodon* Rose and Lucas, 2000, as well as in the earliest species of *Palaeanodon*, Clarkforkian *P. parvulus* Matthew, 1918. At the proximodorsal border of the distal articular surface is a
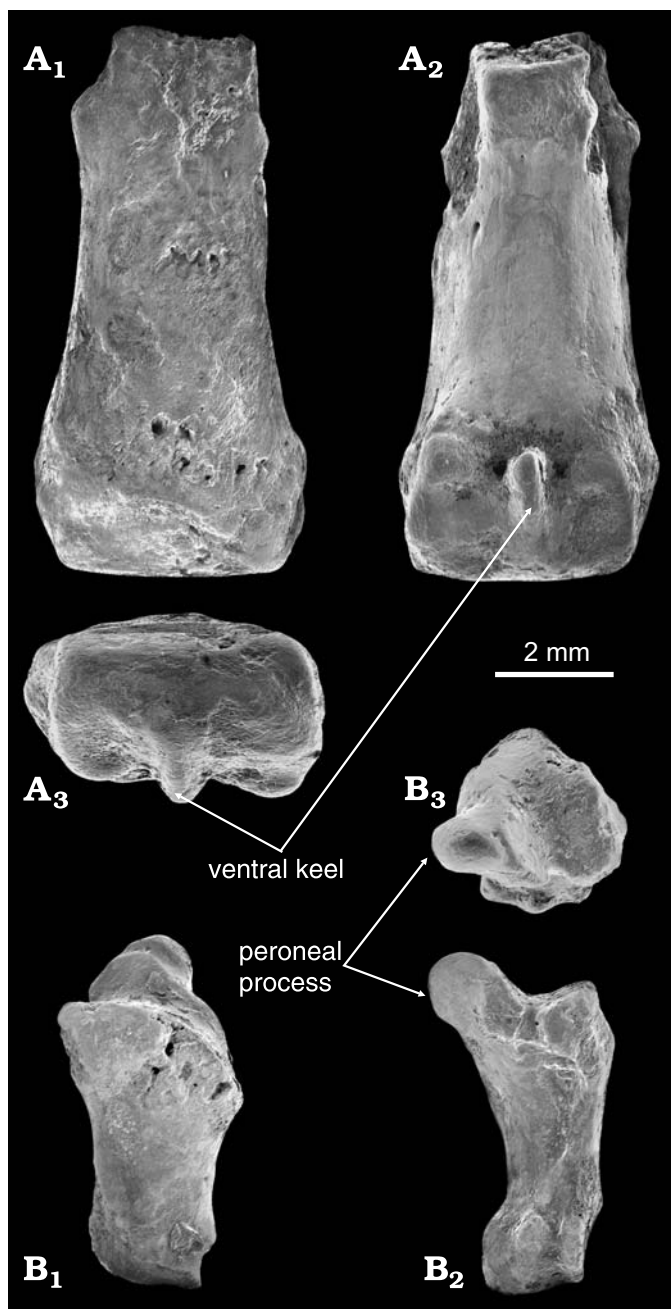
nent bulge lingually. From this bulge an inflated oblique ridge diverges anteriorly and upwards. It joins the alveolar margin at or in front of the posterior postcanine tooth (pc5). The upper surface of the medial buttress is rough and marked by a series of irregular striations of the bone which are oriented more or less mesio-lingually, and which may be related to the attachment of a horny plate, as hypothesized for palaeanodonts by Matthew (1918) and Rose (1981). The X-ray view (Fig. 3A) shows that the bone is apparently cancellous in this area. It shows also a large mandibular canal and the medial buttress which is distinct as an oblique darker zone of dense bone (Fig. 3B). Below the medial buttress, a distinct horizontal mandibular groove extends at least as far as the level where the lower jaw is broken, well anterior to pc5. Between pc5 and the vertical ramus (at maximum width of the medial buttress), is a conspicuous posterior diastema, characteristic of *Palaeanodon*. The lowest part of the masseteric fossa is distinct and well excavated. It extends as low as about the middle depth of the horizontal ramus. Its anterior margin seems not to be vertical, but is inclined posteriorly. A small posterior mental foramen occurs between pc4 (infilling alveolus) and pc3, as in described species of *Palaeanodon* (though the position of this foramen might be variable).

Metacarpal III (Fig. 4A).—MNHN QNY 2-276 is a right mc III which displays typical metacheiromyid morphology. It is short and robust, forming a gentle arch in the sagittal plane (concave on the palmar surface). The distal articulation is highly characteristic, consisting of a broad cylindrical surface that terminates on the palmar aspect in a short spine-like

Fig. 4. *Palaeanodon* sp. from Le Quesnoy, postcranials. **A**. MNHN QNY 2-276, right metacarpal III in dorsal (A$_1$), ventral (A$_2$), and distal (A$_3$) views. **B**. MNHN QNY 2-279, left metatarsal I in dorsolateral (B$_1$), ventromedial (B$_2$), and proximal (B$_3$) views. SEM micrographs.

Table 2. Dimensions of the metacarpal and metatarsal (mm).

	distal width	midshaft width	proximal width	length
Metacarpal III, MNHN QNY 2-276	4.6	2.5	> *3.6 (proximal part missing)	> 9.6 (proximal part missing)
Metatarsal I, MNHN QNY 2-279	≥ 2.2 (distal part damaged)	2.3	3.3	6.7

* estimated measurement.

shallow extensor fossa, which served to limit the degree of extension of the proximal phalanx. The dorsal surface of the shaft is damaged in the region of the extensor tubercle, as is the proximal articulation, but preserved features indicate that the element was essentially identical in all significant details to mc III of *Palaeanodon* from western North America.

Metatarsal I (Fig. 4B).—MNHN QNY 2-279 is a left mt I which shows characteristic palaeanodont anatomy and is of appropriate size and structure to belong to the same species as the metacarpal III MNHN QNY 2-276. It, too, is short and robust, though more slender than mc III. It is expanded at the proximal articulation and tapers distally. The proximal end has a sellar joint for the entocuneiform and a prominent peroneal process on the lateroplantar side, thus resembling this joint in sciurids. The joint surface is dorsoventrally convex and transversely concave, suggesting a fair range of mobility, and is longer in the dorsoventral than the transverse plane. The dorsal margin of the bone is nearly flat, whereas the plantar side is longitudinally concave. The distal end, though slightly damaged medially, is narrower than the rest of the bone and asymmetric, with the lateral side (toward digit II) extending distally farther than the medial side. The articular surface for the proximal phalanx is restricted to the distal and plantar aspects and does not extend at all onto the dorsal aspect of the bone. A moderately well-developed keel is present on the plantar surface only.

Astragalus (Figs. 5, 6).—MNHN QNY 2-278 is a right astragalus of questionable reference to *Palaeanodon*. It is reported here because it resembles the astragalus of *Palaeanodon* in having a moderately broad and somewhat grooved trochlea, a distolateral flange on the trochlea, and a neck and head of similar proportions. Compared to astragali of *Palaeanodon* from Wyoming (USGS-Johns Hopkins collection at the USNM), however, there are several possibly significant differences. The trochlear rims are not parallel as in Wyoming *Palaeanodon*, but diverge distally, and the neck is somewhat narrower. Unlike *Palaeanodon*, there is a distal notch in the medial side of the trochlea, a resemblance to the astragalus of pantolestids. However, the Le Quesnoy astragalus differs from that of pantolestids in subtalar morphology. The ectal (posterior calcaneal) facet is oblique, broad proximally, and tapers distally. There is a wide tarsal canal between the ectal and sustentacular facets.
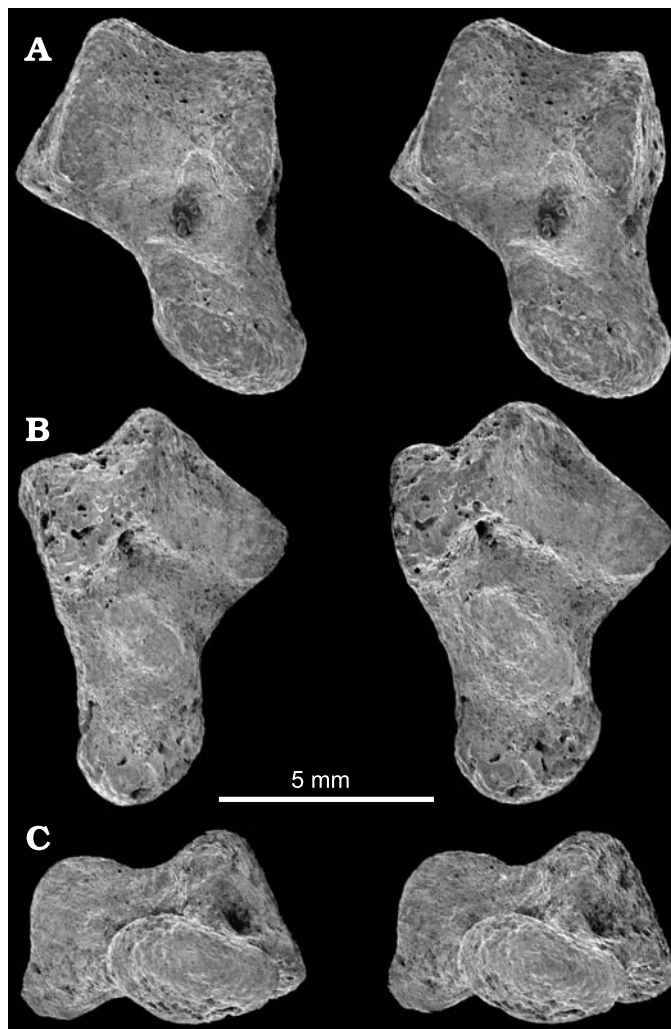

Fig. 5. ?*Palaeanodon* sp. from Le Quesnoy, MNHN QNY 2-278, right astragalus in dorsal (**A**), ventral (**B**), and distal (**C**) views. SEM stereomicrographs.

The latter appears to be separated from the navicular facet, but this area is badly eroded. In all these ways MNHN QNY 2-278 is closer (though not identical) to the astragalus of *Palaeanodon*.

Comparisons and discussion

The species from Le Quesnoy shows several significant features shared with the palaeanodont family Metacheiromyidae: postcanine teeth strongly reduced; medial buttress present and strong; alveoli significantly larger than the teeth they contain; postcanine teeth typically heavily abraded but without wear facets. The species also shares with *Propalaeanodon* and *Palaeanodon* the occurrence of an internal mandibular groove just belowe the medial buttress.

The strong medial buttress and the moderately long posterior diastema (indicating a reduced number of postcanines) clearly indicate closer affinity with *Palaeanodon* than with *Propalaeanodon* or any other genus of palaeanodonts. More-
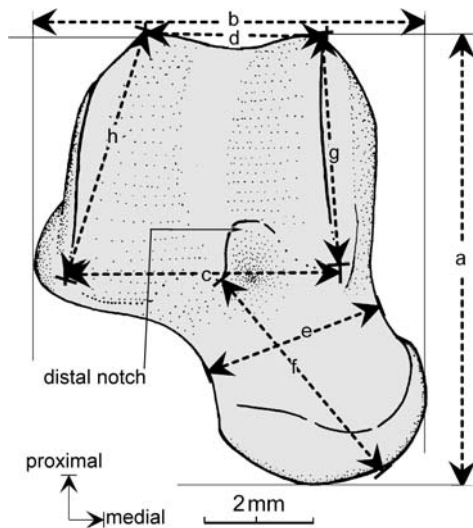
Fig. 6. ?*Palaeanodon* sp. from Le Quesnoy. Sketch of the astragalus MNHN QNY 2-278 and measurements which are taken here (see Table 3). The trochlea is oriented vertically.

Table 3. Dimensions of the astragalus MNHN QNY 2-278 (see measurements a–h in Fig. 6).

Measurement	mm
a: medial length	8.8
b: maximum width of the body	7.38
c: distal width of the trochlea	5.2
d: proximal width of the trochlea	3.2
e: minimum width of the neck	3.4
maximum diameter of the head (measured in distal view)	4.1
minimum diameter of the head (measured in distal view)	2.5
f: length of head and neck	4.2
g: medial length of the trochlea	4.4
h: lateral length of the trochlea	4.7

over, MNHN QNY 2-275 is significantly smaller than *Propalaeanodon schaffi* Rose, 1979.

The Le Quesnoy dentary can be confidently referred to *Palaeanodon* based on the following features: postcanine teeth small, very simple (peglike) and most with only one root (with possible exception of pc4), and separated by small diastemae; posterior diastema long; and medial buttress prominent. The position of the posterior mental foramen is also shared by *Palaeanodon*. Based on size and morphology, the metapodials described here (as well as the astragalus, if it is properly referred to *Palaeanodon*) can, with reasonable assurance, be attributed to the same palaeanodont species represented by the dentary MNHN QNY 2-275 from Le Quesnoy. Besides palaeanodonts, the only taxon known to show similar metacarpal III morphology is the supposed xenarthran *Eurotamandua* from the

middle Eocene of Messel, Germany, which may instead be related to palaeanodonts (Rose 1999).

Three species of *Palaeanodon*, all from western North America, have been described: *P. parvulus* Matthew, 1918 from the late Clarkforkian (Cf2–Cf3) and early Wasatchian (Wa0; Rose 1981; Gingerich 1989), *P. nievelti* Gingerich, 1989 from the early Wasatchian (Wa0–Wa2) and *P. ignavus* Matthew, 1918 from the middle Wasatchian (Wa3–Wa4).

Palaeanodon sp. from Le Quesnoy is significantly smaller than *P. ignavus*. Even the smaller specimens such as UM 66243, identified as "intermediate between *P. ignavus* and *P. parvulus*" (Rose 1981), are larger than MNHN QNY 2-275. UM 66243 differs also in having a somewhat weaker medial buttress (especially anteriorly), a less marked internal mandibular groove, a more anterior location of the posterior postcanine tooth (longer posterior diastema), and a wider dentary.

MNHN QNY 2-275 shares with *P. parvulus* its small size and its slender morphology. This is noticeable especially with respect to *P. ignavus*. However, MNHN QNY 2-275 falls in the lowest part of the range of *P. parvulus* from the Clark's Fork Basin (Gingerich 1989: fig. 43). The metacarpal III of the holotype of *P. parvulus* figured by Matthew (1918: fig. 57) is also significantly larger (length: 12.75 mm; distal width: 5.5 mm) than MNHN QNY 2-276, but is similar in having a relatively prominent distal keel.

MNHN QNY 2-275 is nearly the same size as the holotype of *P. nievelti* (depth × width of the dentary of the holotype = 5.2 × 3.6 mm; Gingerich 1989). Within the plot of the size and stratigraphic distribution of the different species of *Palaeanodon* from Clark's Fork Basin given by Gingerich (1989: fig. 43), MNHN QNY 2-275 falls within the upper range of *P. nievelti* (size of specimens from level 1800 m in the Clark's Fork Basin). Some undescribed USNM specimens of *Palaeanodon* from early Wasatchian (Wa1) strata of the Bighorn Basin, Wyoming, are also very similar to the Le Quesnoy dentary. Specimens from Wa2–Wa3 levels of the Clark's Fork Basin referred to "*Palaeanodon* n. sp." by Gingerich (1989) are larger. The metacarpal III MNHN QNY 2-276 is also very close in size to material referred to *P. nievelti*, such as UM 83478 (length: 10.1 mm; distal width: 4.5 mm; Gingerich 1989). Similarly, it is smaller than the metacarpal III of "*Palaeanodon* n. sp." from Clark's Fork Basin reported by Gingerich (1989).

Consequently, based principally on the criterion of size MNHN QNY 2-275 and MNHN QNY 2-276 are closer to the early Eocene North American species *Palaeanodon nievelti*, than to any other.

However, the metacarpal III MNHN QNY 2-276 differs from that of *Palaeanodon nievelti* in having a more prominent ventral keel. More strikingly, the dentary MNHN QNY 2-275 seems to display one feature previously unknown in other described species of *Palaeanodon*. It is distinguished by the occurrence of a probably elongated and bilobed pc4 (= p4). This is suggested by the shape of the infilling alveolus of pc4, which differs significantly from pc5 and its alveolus

(Figs. 2D and 3). Such a morphology of p4 has not been previously reported in *Palaeanodon*, but it is reminiscent of the p4 of primitive metacheiromyids such as *Propalaeanodon* and *Mylanodon*. If the p4 of the Le Quesnoy species has a bilobed root rather than two roots, as seems most likely, it would be at an intermediate evolutionary stage between these primitive metacheiromyids and the described species of *Palaeanodon* for this feature. However, we rely here on a single specimen and on a feature which seems to be anomalous (infilling alveolus) in this specimen. We cannot exclude individual variation in this feature in the Le Quesnoy species, as noticeable intraspecific variability is known in palaeanodonts (including individual variation and sexual dimorphism). For example, a bilobed root of pc3 was reported by Rose et al. (1991) in cf. *Palaeanodon* sp. from the Wind River Formation and in *P. ignavus* (USGS 21876) from the Willwood Formation. These minor differences between the Le Quesnoy *Palaeanodon* and the North American species suggest that it represents a distinct species, but we consider the existing sample inadequate on which to base a new species. In any case, the Le Quesnoy species remains closer to *Palaeanodon* than to any other palaeanodont genus.

Biostratigraphical context

Correlations of Le Quesnoy fauna with European mammal reference levels and Neustrian Biozones (Hooker 1996, 1998).—Godinot et al. (1998) identified in Le Quesnoy a new *Plesiadapis* species (referred then to *Platychoerops*) that is closer to *P. tricuspidens* Gervais, 1877 from Berru (MP 6) than to *P. russelli* from Meudon (MP 8–9). This lineage is further defined and will be described in detail by Godinot et al. (in press). Based on this presumed lineage, a formal succession of the mammal localities in the Paris Basin was proposed: Cernay, Berru, Le Quesnoy, Meudon, Mutigny. This view was confirmed by a preliminary analysis of the faunal list, giving an age close to MP 7 (Nel et al. 1999). The MP 7 reference fauna is Dormaal in Belgium, which is almost lacking plesiadapids (one upper molar, referred to the problematic *Platychoerops georgei* Hooker, 1994, can as well be referred to the new Le Quesnoy species). A more precise estimation of the age of Le Quesnoy with respect to Dormaal needs more detailed systematic study of the lineages common to the two localities. However, taxa such as *Landenodon*, *Paschatherium,* and possibly *Arctocyon* give an ancient character to the Le Quesnoy fauna. This and the occurrence of a species of *Teilhardina* very close to *T. belgica* (Teilhard, 1927) indicates an earliest Eocene age, close to MP 7 (Godinot et al. 1998; Nel et al. 1999) and equivalent to Hooker's (1996, 1998) PE I Biozone. Le Quesnoy includes also taxa such as Esthonychidae (*Esthonyx*) and Paromomyidae, that were referred to higher Neustrian Biozones by Hooker (1996), but the overall mammal assemblage of the site supports that they belong to the earliest Neustrian faunas. They were not sampled in Dormaal

for taphonomic reasons; Dormaal has only small mammals, and a very peculiar composition, it differs for instance in the predominance of *Paschatherium*, and in the absence of coryphodontids, *Hyopsodus*, *Cantius*, and paromomyids, and near absence of multituberculates, plesiadapids, and perissodactyls (Smith and Smith 1995; Denys and Russell 1981). The very early Eocene age of Le Quesnoy is also supported by the reptilian fauna (Nel et al. 1999). We conclude that Le Quesnoy is indeed one of the earliest Neustrian faunas, close to the MP 7 reference fauna, and that it is the oldest known mammal fauna from the Eocene of the Paris Basin (Nel et al. 1999). This implies that *Palaeanodon* is a member of the earliest Eocene wave of immigrants in Europe.

Correlation of Le Quesnoy fauna with NALMA.—The palaeanodont described here provides a new element for the correlation of Le Quesnoy with NALMA. The fragments from Le Quesnoy referred to *Palaeanodon* most closely resemble the early Wasatchian North American species *P. nievelti* in size. They are slightly larger than basal Eocene (Wa0) samples of *P. nievelti* and more consistent with slightly younger samples of that species (especially from the Wa-1 interval in the southern Bighorn Basin and level 1800 m in Clark's Fork Basin (= Wa2); see Gingerich 1989: fig. 43). If the size of *Palaeanodon* is used as an indication of the age of the Le Quesnoy fauna (i.e., if the Le Quesnoy species belongs to the North American lineages of *Palaeanodon*, and especially to the lineage of *P. nievelti*), this would suggest a very early Eocene age, most likely equivalent to Wasatchian biozones Wa1 or possibly Wa2 in western North America.

However, the prominent palmar keel on the MC III of the Le Quesnoy *Palaeanodon* is similar to that of the Clarkforkian *P. parvulus*, which is slightly larger. This MC III morphology as well as the size of the Le Quesnoy specimens are closer to *P. parvulus*–*P. nievelti* intermediates than to *P. nievelti* material. It seems unlikely that the Le Quesnoy species represents the intermediate ancestral species of *P. nievelti* (which would also imply that Le Quesnoy is older than Wa0). More likely, the intermediate construction of the Le Quesnoy species could suggest that it is the sister species of *P. nievelti*, and that both species share a common ancestor close to *P. parvulus*. In this case, the direct comparison of *P. nievelti* and the Le Quesnoy species would be less significant biostratigraphically, but this phylogenetic scenario would suggest that the dispersal of *Palaeanodon* to Europe was at least as old as the oldest *P. nievelti* (Wa0). Additionally, it should be remembered that there are other features in the Le Quesnoy material (e.g., astragalus and elongated bilobed pc4; see above) which, if they are representative of the species, would suggest the presence of a primitive European lineage of *Palaeanodon* belonging to a distinct lineage from those known in North America.

Thus despite a close resemblance with *Palaeanodon nievelti*, a precise biostratigraphical correlation of the European species with North American lineages of *Palae-*

anodon requires a better knowledge of the Le Quesnoy species. Nonetheless, *Palaeanodon* sp. from Le Quesnoy indicates at least a correlation with NALMA that is not later than early Wasatchian.

Paleobiogeographical implications

The palaeanodont discovered in the Neustrian of Le Quesnoy documents a new taxon occurrence that marks the mammalian dispersal event at the beginning of the Eocene in Europe (MDE in Hooker 1998). The Le Quesnoy *Palaeanodon* remains constitute the first record of Metacheiromyidae from outside of western North America and the second palaeanodont family known from Europe. The only other palaeanodonts previously found outside North America are two epoicotheriids: *Molaetherium* from the early Oligocene of Europe (Heissig 1982; Storch and Rummel 1999) and *Auroratherium* from the early Eocene of Asia (Tong and Wang 1997). The Palaeanodonta (Torrejonian–early Oligocene) and especially the family Metacheiromyidae (Tiffanian–Bridgerian), have their earliest record and their highest diversity in North America, which suggests that this is their most likely center of origin and radiation.

However, the recent discoveries of *Molaetherium* and *Auroratherium* led Storch and Rummel (1999) to suggest an origin of palaeanodonts in Asia. They postulated the dispersal of several lineages: (1) colonization of North America in the Late Paleocene from Asia; (2) later dispersals of *Epoicotherium* and *Molaetherium*, respectively, in North America and Europe from a shared Asiatic epoicotheriid ancestor (presumably close to *Auroratherium*). The lack of a land connection between Europe and North America after the early Eocene was surely a factor in their hypothesis (point 2), even though they acknowledged close affinities of *Epoicotherium* and *Molaetherium*. The occurrence of the metacheiromyid *Palaeanodon* in France and a new epoicotheriid-like palaeanodont, *Arcticanodon*, from the early Eocene of Ellesmere Island, Canada (which was presumably on the corridor between North America and Europe) (Rose et al. 2004), now prompts reconsideration of the direction of dispersal of palaeanodonts to Europe. In North America there are more primitive metacheiromyids in the Paleocene and more primitive epoicotheriids in both the Paleocene and Eocene than the known European palaeanodonts. These factors suggest that both families reached Europe from North America, rather than from Asia where only a single early Eocene palaeanodont is known. This is a return to the more "classical" opinion of a North American center of origin and radiation of palaeanodonts. However, the new palaeanodonts discovered in Europe and Asia correspond probably to several distinct lineages and dispersal events of North American origin: (1) the epoicotheriid *Auroratherium* might correspond to an early Eocene dispersal to Asia; (2) the meta-

cheiromyid *Palaeanodon* from Le Quesnoy is probably an early Eocene immigrant to Europe (or a latest Paleocene immigrant if it would prove to be more primitive than *P. parvulus*); (3) the epoicotheriid *Molaetherium* (related to *Epoicotherium*) is an immigrant to Europe of uncertain origin (possibly from an early Eocene North American ancestor shared with its vicariant taxon *Epoicotherium*, or as an Asiatic immigrant following the Grande Coupure dispersal event—taking into account that all other early Oligocene immigrants to Europe are of Asiatic origin).

The metacheiromyid palaeanodonts can now be associated with the numerous Neustrian taxa of strict North American origin. Other taxa of such strict North American origin include one multituberculate genus (*Ectypodus*), marsupials (peradectids and "didelphids"), apatemyids, nyctitheriids, oxyaenids (including *Palaeonictis*), and phenacodontids (*Phenacodus*). To these should be added three groups, which seem to have immigrated to North America from Asia at the beginning of the Clarkforkian—ischyromyid rodents, tillodonts (*Esthonyx*), and coryphodontids (*Coryphodon*)—and dispersed to Europe at the beginning of the Eocene. Most of these immigrants from North America occur in Le Quesnoy (Nel et al. 1999). Other immigrants found in the European Neustrian and in the North American Wasatchian (primates, perissodactyls, artiodactyls) have their initial source in Asia (Beard 1998; Beard and Dawson 1999), but their dispersal is contentious, either through North America to Europe (Beard 1998; Beard and Dawson 1999), or from Asia to Europe (Hooker 1998; Hooker and Dashzeveg 2003; Godinot 1982; Godinot and Lapparent de Broin 2003). It should be noted that the exact timing of the immigrant taxa (i.e., number of dispersal events) found in the Neustrian is poorly known because the European record is discontinuous (e.g., a possible gap for part or all of Clarkforkian) and difficult to correlate. However, the Le Quesnoy fauna reinforces the view of one first earliest Eocene massive dispersals.

Although the affinities of Wasatchian and Neustrian faunas are well known (e.g., Simpson 1947; McKenna 1975; Godinot 1982; Savage and Russell 1983), and exemplify among the strongest intercontinental paleobiogeographical links known in the Paleogene, relatively few early Eocene Euramerican species are known (7–9 species according to Hooker 1998). This and the reputed poor dispersal abilities of fossorial mammals such as palaeanodonts (Storch and Rummel 1999) make remarkable the identification in Le Quesnoy of a species of *Palaeanodon* close in size to *P. nievelti*. Whatever its specific status, the palaeanodont from Le Quesnoy emphasizes again the importance of the dispersal event between North America and Europe at the Paleocene/Eocene boundary. It shows that the filtering nature of the dispersal route supported by Godinot (1982), in the way of a forested and humid continental North Atlantic "corridor", did not affect the dispersal of specialized fossorial mammals such as palaeanodonts. In this regard, Simpson (1931: 314) previously reported a probable "fairly humid" paleoenvironment for the palaeanodont *Metacheiromys*.

Finally, presence of *Palaeanodon* in the Neustrian of Europe strengthens the probability of a relationship between palaeanodonts and Pholidota, the oldest definitive representative of which is *Eomanis* from the Lutetian of Messel, Germany. Metacheiromyids share numerous derived features of the skeleton with primitive pholidotans (e.g., Emry 1970; Rose and Emry 1993; Rose et al. 2005), including the presence of a medial buttress on the back of the dentary (Storch 2003). The Le Quesnoy specimens for the first time document the probable sister taxon of Pholidota at an appropriate place and time.

Acknowledgements

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