

New data on the Oxyaenidae from the Early Eocene of Europe; biostratigraphic, paleobiogeographic and paleoecologic implications

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ABSTRACT

The locality of Le Quesnoy (France; MP7) has yielded a diversified mammal fauna including especially large mammals. Oxyaenidae are well documented with two species identified: *Oxyaena woutersi* and *Palaeonictis gigantea*. The Le Quesnoy material illustrates almost the entire dentition of these species. Its study supports the generic attribution of *Oxyaena woutersi*. Its M_2 is more secant than in the primitive *Dipsalidictis*, but the M_1 appears to be slightly less secant than in the earliest species of *Oxyaena*. *Oxyaena woutersi* is a morphological intermediate between the Clarkforkian-Wasatchian *Dipsalidictis* and the Wasatchian *Oxyaena*. The M_2 of *Palaeonictis gigantea* is compared to the sole known molar of *Dormaalodon woutersi*. *Dormaalodon* is here demonstrated to be a junior synonym of *Palaeonictis*. Several postcranial elements of *Oxyaena woutersi* and *Palaeonictis gigantea* are described: they are the first described for European oxyaenids. The oxyaenid species from Le Quesnoy and Dormaal show a close affinity and support an age very close to MP7 for Le Quesnoy. The Le Quesnoy oxyaenids are morphologically close to the North American species of Wa0, which supports correlation with this level. We revised the European Oxyaenidae previously described from younger localities. Fossils from Meudon, Sinceny and Abbey Wood (MP8+9) are referred to *Oxyaena* sp. A North American origin of the Oxyaenidae is confirmed. Our study supports a single dispersal event of oxyaenids from North America to Europe followed by a short endemic local evolution. Oxyaenidae rapidly disappeared from Europe. This disappearance could support the distinction between the MP7 and MP8+9 reference levels.

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KEY WORDS: Creodonta; Oxyaenidae; Le Quesnoy; Europe; Eocene; MP7

INTRODUCTION

Oxyaenidae is one of the families included in the diphyletic order “Creodonta”, with the Hyaenodontidae. Oxyaenidae represent the largest specialized carnivorous mammals from the Early and Middle Eocene, whereas Mesonychidae represent the largest non-specialized carnivorous mammals. They were distinctly larger and possessed a more specialized shearing dentition than the hyaenodontids. Four subfamilies are known: Tythaeinae, the most primitive group; Ambloctoninae (= Palaeonictinae) characterized by a reduced M_2 and broad premolars; Oxyaeninae characterized by a large and bladelike M_2 ; and the hypercarnivorous Machaeroidinae characterized by a very bladelike M_2 and long upper canines protected by a ventral flange at the front of the jaw (Gunnell 1998). However, the placement of Machaeroidinae is presently uncertain, because they may belong to Oxyaenidae or to Hyaenodontidae. The group appeared in North America during the Late Paleocene (Gingerich 1980). Its diversification occurred mainly on this continent. It disappeared from North America during the Middle Eocene. Oxyaenidae appeared in Europe right after the Paleocene/Eocene transition (Smith and Smith 2001), and they disappeared rapidly there. Only oxyaenines and paleonictines are known in Europe. The Oxyaenidae are poorly known in Europe because they are rare and represented by very poor material (Rich 1971; Gunnell and Gingerich 1991).

The fossil locality of Le Quesnoy (Oise, Early Eocene, MP7) is located in the Paris Basin (Nel et al. 1999). This fossiliferous locality, located near Houdancourt (Creil area) (Figure 1), is one of the richest known for the Early Eocene of Europe. It provides information concerning the environment, the flora and the arthropod and vertebrate fauna and is important for the understanding of the mammalian fauna of the earliest Eocene in Europe. Nel et al. (1999) have already identified 24 species of mammals representing 20 families. The mammalian fauna appears well diversified and is similar to the Dormaal assemblage. The faunas share some taxa (e.g., *Teilhardina* aff. *belgica*, *Landenodon* sp., *Paschatherium* sp.), but differences do exist. The

large species are better represented in Le Quesnoy, which is less biased taphonomically.

Thanks to this locality, our knowledge of the earliest Oxyaenidae is greatly increased. Nearly complete dentitions of oxyaenids are known from Le Quesnoy, allowing a new look at the fossils of Oxyaenidae previously discovered in Europe (Van Valen 1965; Rich 1971; Hooker 1998) and to a discussion of the evolution of this group in Europe.

Abbreviations

AMNH: American Museum of Natural History, New York

ARP: Argiles à lignites du Soissonnais, collection of the MNHN

BMNH: British Museum of Natural History, London

IRSNB M: Mammals, collection of types and figured specimens of the IRSNB

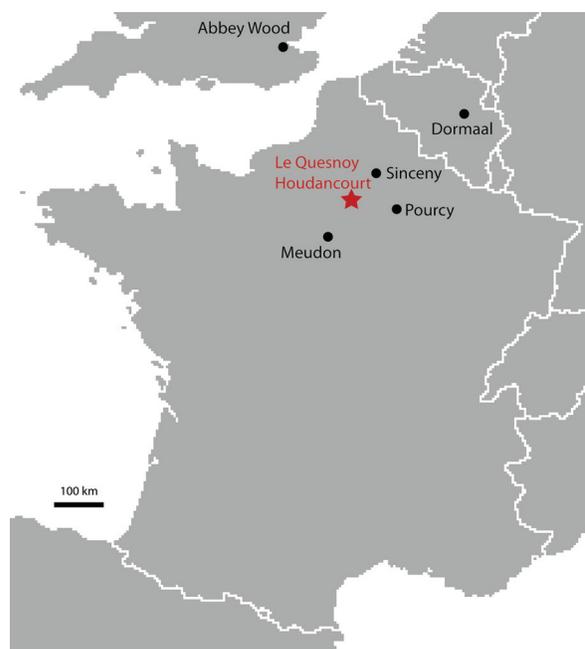


FIGURE 1. Map with location of the European localities of Oxyaenidae: Le Quesnoy/Houdancourt (red star), Sinceny, Pourcy, Meudon (France), Abbey Wood (England) and Dormaal-Hoegaarden (Belgium). Syntypes of *Palaeonictis gigantea* (MNHN ARP 52, 53, 54) have no precise location.

IRSNB: Institut Royal des Sciences Naturelles de Belgique, Bruxelles

MNHN: Muséum National d'Histoire Naturelle, Paris

QNY1 and QNY2: Le Quesnoy, collections of the MNHN

UM: University of Michigan, Ann Arbor

UCMP: University of California, Museum of Paleontology, Berkeley

YPM-PU: Princeton collection at Yale Peabody Museum, New Haven

M: mean, and OR: observed range; L: Length and W: Width

R: right; L: left

MATERIAL AND TERMINOLOGY

Material of Le Quesnoy

The fossils were collected during field work undertaken in 1997 and 1998. The fossils come from two different channels (numbered QNY1 and QNY2). The second channel (QNY2) has yielded the major part of the vertebrate material. All the material is housed in the collection of the Muséum National d'Histoire Naturelle of Paris.

Some postcranial material has been found in Le Quesnoy. Unfortunately they have been found isolated. However, comparison with postcranial material of Oxyaenidae housed in the collections of AMNH, and UM allows their identification as oxyaenids.

Terminology and Measurement

Terminology of the molar dental cusps and crests follows Van Valen (1966). The terminology of Ginsburg (1999) is used to describe the premolars. Instead of the term "metastyl", we used the term "postmetacrista", which is more adequate functionally. We compared the fossils from Le Quesnoy with casts of the North American and European oxyaenids. The measurements (in cm) followed those used by Gingerich and Deutsch (1989) for hyaenodontids. The parameters provided are only the observed range (OR) and the mean (M). The evolution of the shape of the trigonid of the lower molars and of the M¹ follows Gunnell and Gingerich (1991, figures 12, 13, 14).

SYSTEMATICS

Order "CREODONTA" Cope, 1875
Family OXYAENIDAE Cope, 1877

Subfamily OXYAENINAE Cope, 1877

Genus OXYAENA Cope, 1874

Diagnosis. *Oxyaena* differs from *Dipsalidictis* Matthew, 1915 in having a well-developed carnassial shearing dentition including a long postmetacrista on M¹, and a long, often flaring, paralophid on M₂. It also differs from *Dipsalidictis* in having lower molar trigonids longer than wide, in having reduced metaconids on lower molars, in having heavier premolars and in having a more anteroposteriorly compressed M² that lacks a metacone.

Type species. *Oxyaena lupina* Cope, 1874

Other species. *Oxyaena forcipata* Cope, 1874; *Oxyaena gulo* Matthew, 1915; *Oxyaena pardalis* Matthew, 1915; *Oxyaena intermedia* Denison, 1938; *Oxyaena simpsoni* Van Valen, 1966; *Oxyaena woutersi* (Lange-Badré and Godinot, 1982)

Distribution. Early Eocene-Middle Eocene

Oxyaena woutersi (Lange-Badré and Godinot, 1982)

Figures 2, 3, 4, 5 and 6

Synonymy.

v. 1982 *Arfia woutersi* Lange-Badré and Godinot; p. 295-300, pl. 1, fig. 1; non pl. 1, figs. 2-4.

Emended diagnosis. Smallest species of the genus. Morphologically intermediate between *Dipsalidictis* and *Oxyaena*. Shares with *Dipsalidictis* a trigonid wider than long on M₁, lower molar cingulids and upper molar lingual cingula present but poorly developed and a postmetacrista on M¹ less elongated than in other species of *Oxyaena*. It is closer to *Dipsalidictis transiens* Matthew, 1915 than to other species of that genus in the longer paracristid on the lower molars, a paraconid with a base more lingual on the lower molars, and a developed postmetacrista on M¹. Shares with other species *Oxyaena* a trigonid longer than wide on M₂ and a talonid more robust on P₃ and P₄ (features also distinctive from *Dipsalidictis transiens*). Its closest *Oxyaena* species are *Oxyaena* sp. and *Oxyaena gulo* Matthew, 1915. It differs from later species of *Oxyaena* such as *Oxyaena gulo* by a trigonid much longer than wide on M₂.

Lectotype. M¹ (or DP⁴?), IRSNB M1319 (L), figured as WL1147 by Lange-Badré and Godinot (1982; pl. I, fig. 1a-b).

Referred dental material from Le Quesnoy. MNHN QNY2-2568, right maxillary with P⁴ and M¹

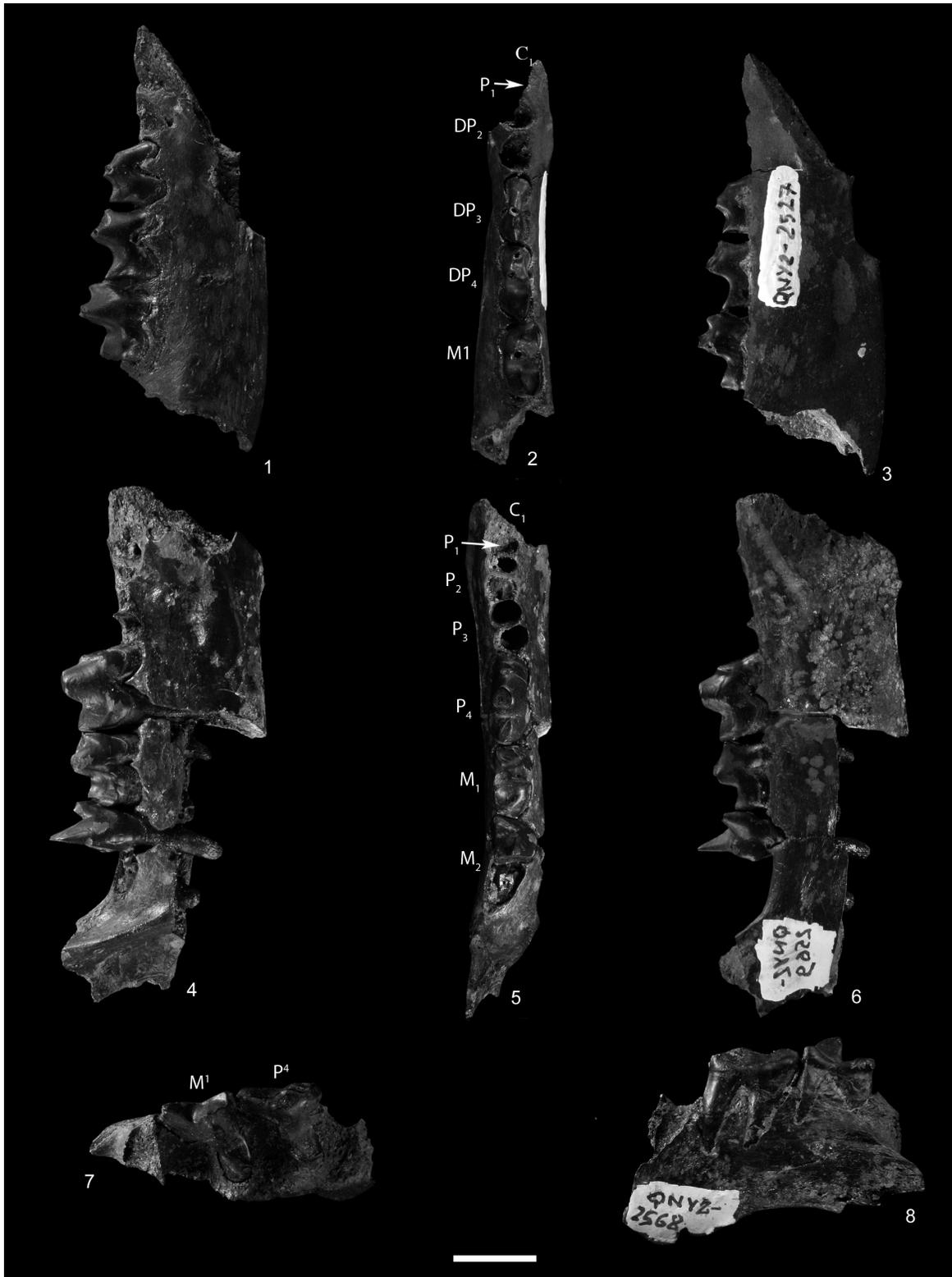


FIGURE 2. *Oxyaena woutersi* (Lange-Badré and Godinot 1982). 1-3. MNHN QNY2-2527, left lower jaw bearing DP₃, DP₄ and M₁, and alveoli of DP₂, P₁ and C₁ in 1. labial, 2. occlusal, 3. lingual views. 4-6. MNHN QNY2-2569, right lower jaw bearing P₄-M₂ and alveoli of C₁ and P₁-P₃ in 4. labial, 5. occlusal, 6. lingual views. 7-8. MNHN QNY2-2568, right upper jaw bearing P⁴-M¹ in 7. occlusal, 8. lingual views. Reversed views: 1, 6. Scale bar equals 10 mm.

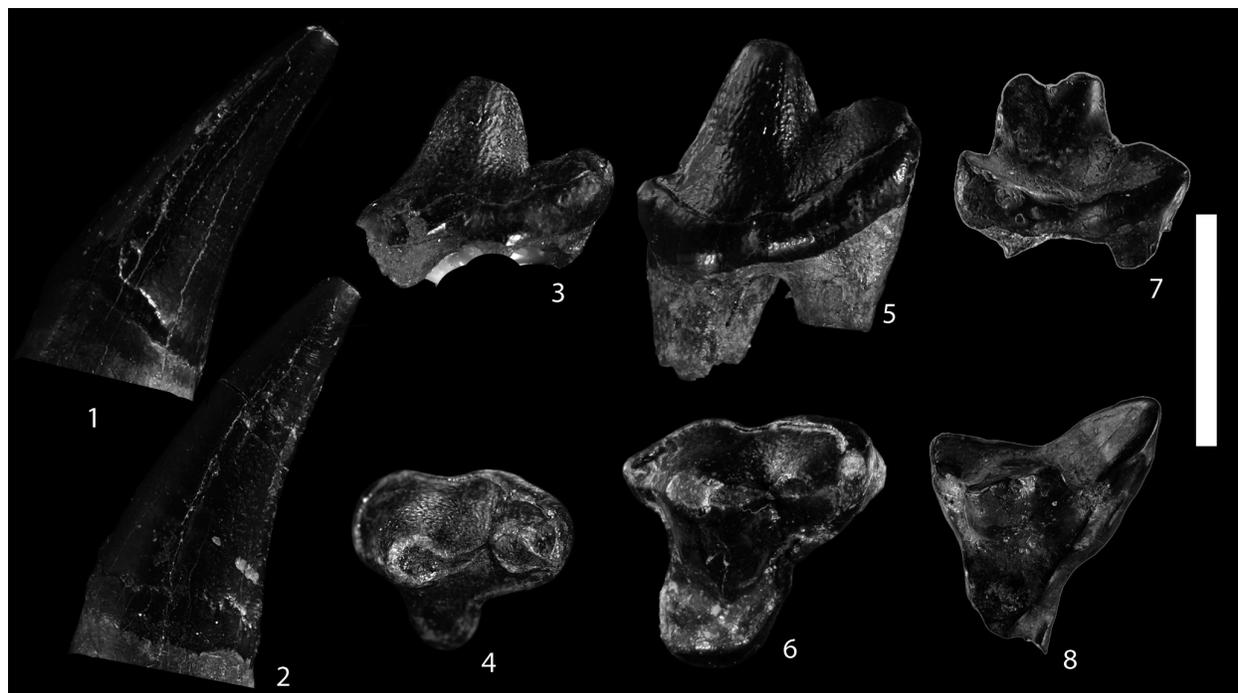


FIGURE 3. *Oxyaena woutersi* (Lange-Badré and Godinot 1982). Reconstruction of the C¹, P³-M¹ series from isolated upper teeth from Le Quesnoy. 1-2. MNHN QNY2-2586, right C¹ in 1. labial, 2. lingual views. 3-4. MNHN QNY2-2598, left P³ in 3. labial, 4. occlusal views. 5-6. MNHN QNY2-2574, right P⁴ in 5. labial, 6. occlusal views. 7-8. MNHN QNY2-2573, left M¹ in 7. labial, 8. occlusal views. Reversed views: 1, 3, 6, 7. Scale bar equals 10 mm.

MNHN QNY2-2527, left mandible with DP₃, DP₄ and M₁, and alveoli of C₁, P₁ and DP₂

MNHN QNY2-2569, right mandible with P₄, M₁ and trigonid of M₂, and alveoli of C₁, P₁, P₂ and P₃

C¹, MNHN QNY2-2561 (R), MNHN QNY2-2603 (L), MNHN QNY2-2584 (L), MNHN QNY2-2586 (L)

P³, MNHN QNY2-2598 (L)

P⁴, MNHN QNY2-2551 (L), MNHN QNY2-2571 (R), MNHN QNY2-2574 (R), MNHN QNY2-2590 (R)

M¹, MNHN QNY2-2572 (R), MNHN QNY2-2573 (L), MNHN QNY2-2600 (L)

P₃, MNHN QNY2-2503 (L), MNHN QNY2-2549 (R), MNHN QNY2-2622 (R)

P₄, MNHN QNY2-2565 (L), MNHN QNY2-2595 (R)

M₁, MNHN QNY2-2579 (R)

M₂, MNHN QNY2-2524 (L)

Referred postcranial material from Le Quesnoy.

MNHN QNY2-2526, left distal humerus; MNHN QNY2-2636, right calcaneum; MNHN QNY2-2633, right astragalus; MNHN QNY2-2635, right astragalus; MNHN QNY2-2638, cuboid

Type locality. MP7, Dormaal (Belgium)

Distribution. MP7, Dormaal (Belgium), Le Quesnoy (France).

Description

Measurements: Table 1

Upper dentition. Canines: Three canines have been referred to *Oxyaena woutersi*. They are too small to belong to *Palaeonictis gigantea* de Blainville, 1842 which is also present in Le Quesnoy. In *Oxyaena*, the upper canine is almost straight whereas the lower canine is curved. The canines found in Le Quesnoy are only slightly curved, suggesting that they belong to the upper dentition. They have a small cingulum, which runs around the tooth, curves and joins the disto-lingual crest. A second crest, distal, is sharper. A wear facet is visible along the mesio-labial part of the teeth. This is probably due to the occlusion with the lower canine. The root is wider than the crown.

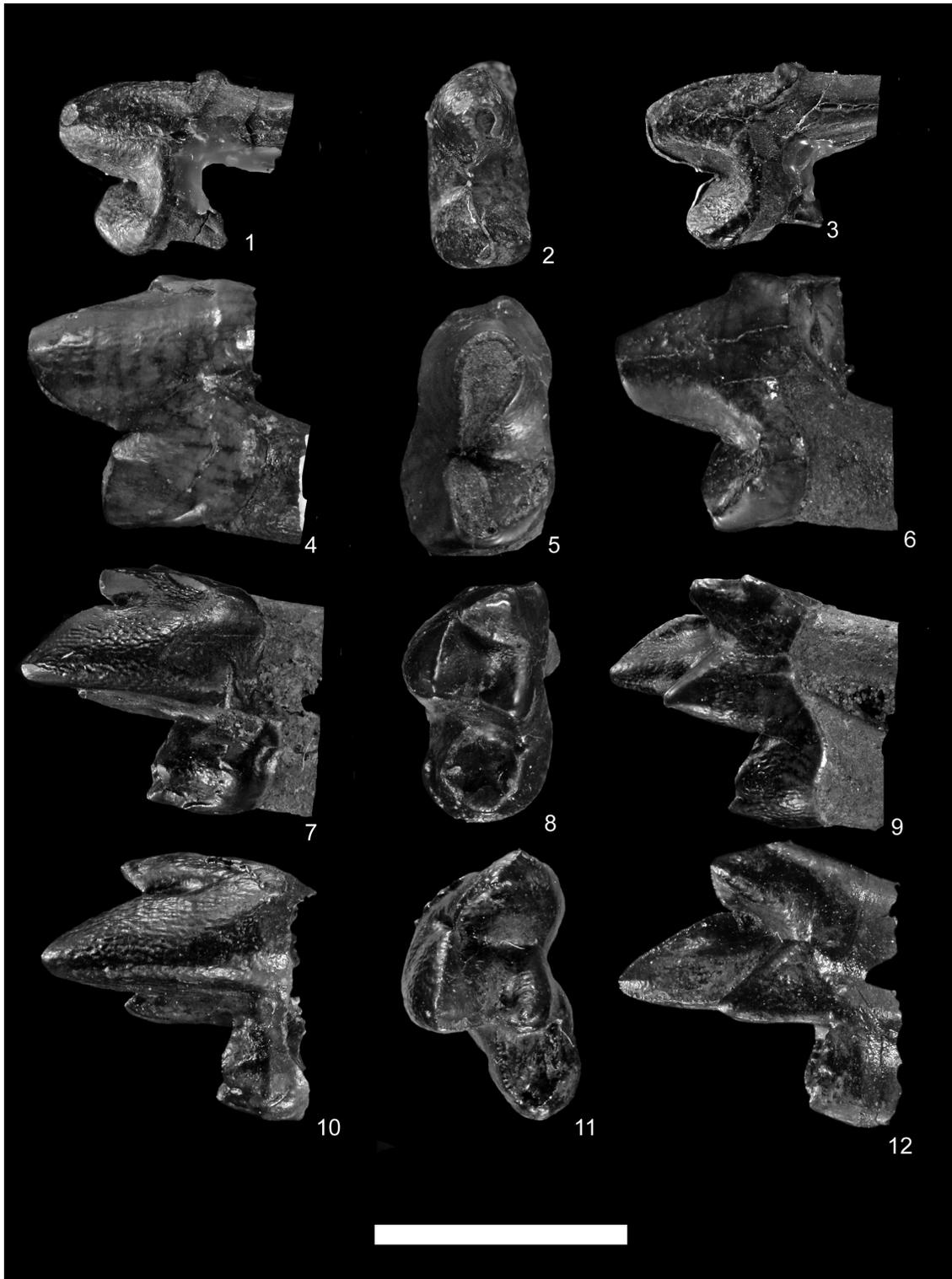


FIGURE 4. *Oxyaena woutersi* (Lange-Badré and Godinot 1982). Reconstruction of the P₃-M₂ series from isolated lower teeth from Le Quesnoy. 1-3. MNHN QNY2-2622, right P₃ in 1. labial, 2. occlusal, 3. lingual views. 4-6. MNHN QNY2-2565, left P₄ in 4. labial, 5. occlusal, 6. lingual views. 7-9. MNHN QNY2-2579, right M₁ in 7. labial, 8. occlusal, 9. lingual views. 10-12. MNHN QNY2-2524, left M₂ in 10. labial, 11. occlusal, 12. lingual views. Reversed views: 2-4, 8-10. Scale bar equals 10 mm.

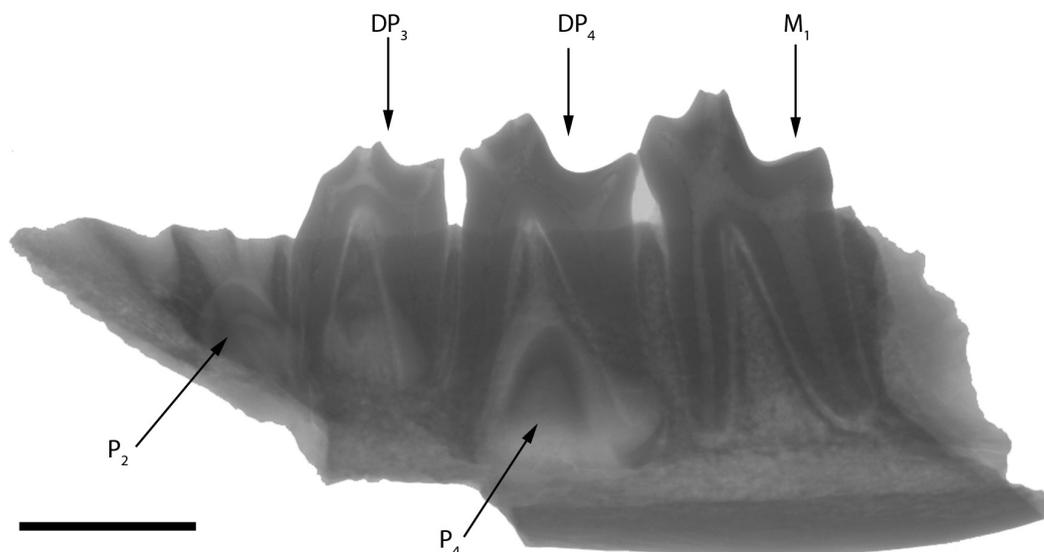


FIGURE 5. *Oxyaena woutersi* (Lange-Badré and Godinot 1982). MNHN QNY2-2527, x-ray image of labial view of left lower jaw bearing DP₃, DP₄ and M₁, and permanent teeth not erupted P₂ and P₄. Scale bar equals 10 mm.

Premolars: As for all the teeth of *Oxyaena woutersi*, the enamel is slightly crenulated. Only P³ and P⁴ are known in Le Quesnoy. Both teeth have three roots and are morphologically similar. The P³ is distinctly smaller than the P⁴. The protocone is less developed on P³ than on P⁴: only a swelling is present lingually on P³ (no apex is present) while the protocone on P⁴ is well individualized and mesio-distally as long as the paracone. Contrary to the internal swelling on P³, the protocone of P⁴ is shifted mesially. On the two teeth, the lingual structure is located much lower than the paracone. The parastyle is absent on P³ and only poorly developed on P⁴. Both teeth present distally a very elongated and high postmetacrista separated from the paracone by a carnassial notch. The paracone is two-times higher than the postmetacrista. Its apex is tilted distally on the two teeth. P³ and P⁴ are surrounded by a tiny cingulum (slightly more pronounced on P⁴ than on P³).

Molars: Only the M¹ is known for this species. As seen on the fragmentary maxillary MNHN QNY2-2568, the M¹ is similar in size to P⁴. The metacone and paracone are connate and are of equal development. The paracone is slightly higher than the metacone. The preparacrista is developed (but much smaller than the postmetacrista). It is mesio-labially oriented. It is separated from the paracone by a carnassial notch. The postmetacrista is very

elongated and separated from the metacone by a deep carnassial notch. It is shifted distally (notably on MNHN QNY2-2573). The ectoflexus is very deep. The styler shelf is very short labially. The protocone is transversally relatively narrow and is equal to the protocone of P⁴. Mesio-distally, it is shorter than the paracone and metacone, is shifted mesially and is also lower than the paracone and metacone (as for the premolars). The protocone is surrounded by pre- and postcingulum, but we do not know if they were linked lingually. The metaconule and paraconule are well developed. They seem to have a similar development. No internal crest is visible. The paraconule is linked to the parastyle by the preparaconule crista. The metaconule reaches the top of the postmetacrista at its half-length.

Excavations in the maxillary between the P⁴ and M¹ and between the M¹ and M² are visible on MNHN QNY2-2568, probably to accommodate the tips of the lower molars (Gunnell and Gingerich 1991).

Dentary. The two fragments of mandible found in Le Quesnoy show that the teeth were closely appressed. The mandible is slender and not very high. The symphysis extends below P₃. It seems to have been very developed. Mandibular foramina are present below the P₁ (near the tooth's crown) and the posterior root of P₃. The coronoid crest is very pronounced and vertical.

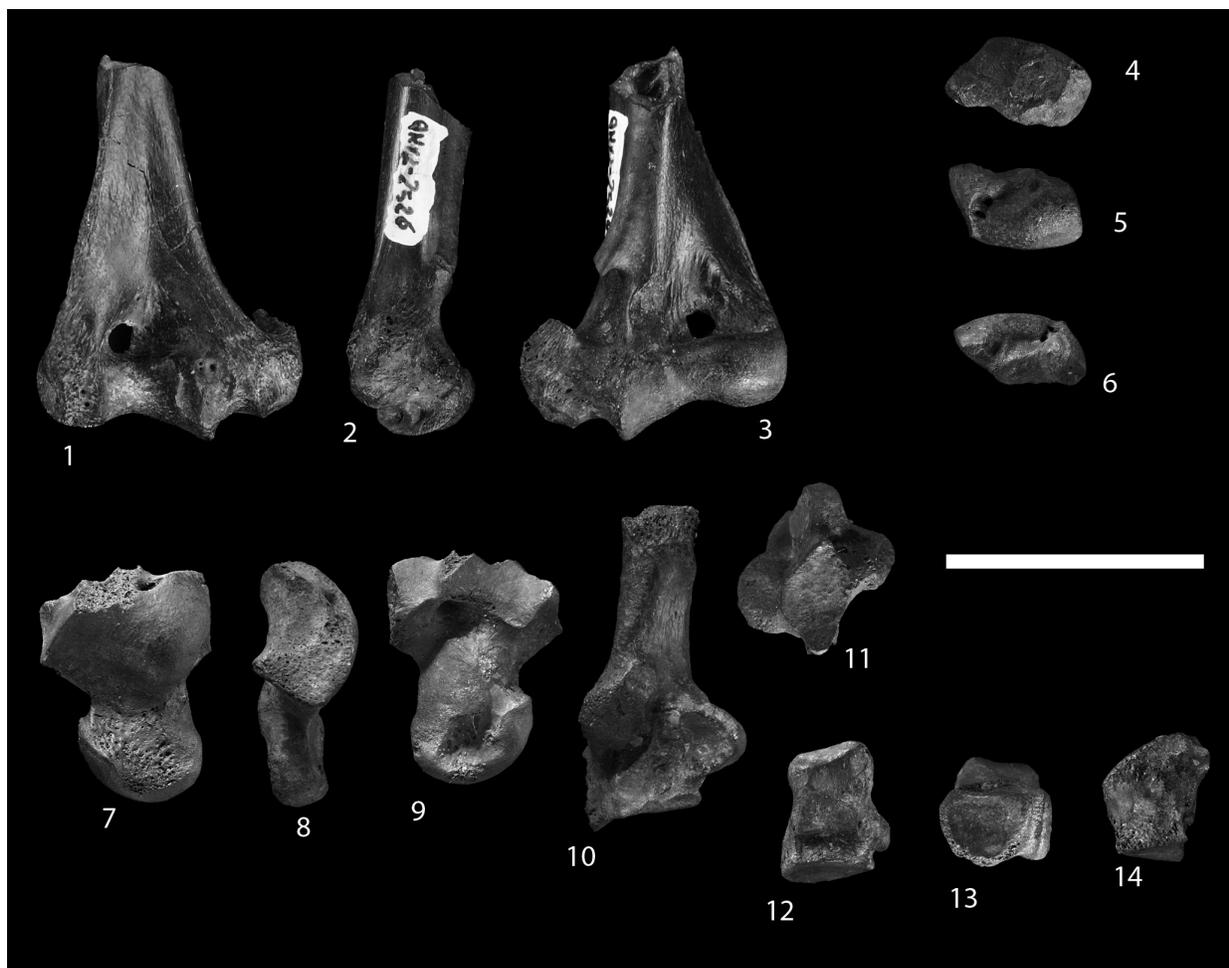


FIGURE 6. *Oxyanea woutersi* (Lange-Badré and Godinot 1982). Postcranial elements of *Oxyanea woutersi* (Lange-Badré and Godinot, 1982) from Le Quesnoy. 1-3. MNHN QNY2-2526, left distal humerus in 1. posterior, 2. lateral, 3. anterior views. 4-6. MNHN QNY2-2637, left scaphoid in 4. posterior, 5. dorsal, 6. ventral views. 7-9. MNHN QNY2-2635, right astragalus in 7. dorsal, 8. lateral, 9. ventral views. 10-11. MNHN QNY2-2636, right calcaneum in 10. dorsal, 11. anterior views. 12-14. MNHN QNY2-2638, cuboid in 12. lateral, 13. ventral, 14. anterior views. Scale bar equals 10 mm.

Lower dentition. Deciduous teeth: Two deciduous teeth (DP₃ and DP₄) are present in MNHN QNY2-2527. The teeth are very worn. Permanent teeth are visible inside the mandible (Figure 5). The DP₃ and DP₄ are compressed transversally and elongated mesio-distally, as is the typical morphology of deciduous teeth. The DP₃ has a very low paraconid, probably poorly developed. The talonid is high, long (as long as the protoconid) and secant. The DP₄ has a trigonid widely open lingually with a metaconid more distal than the protoconid. The paraconid is very slightly lingual. It seems to have been smaller than the metaconid. The talonid is as long as the trigonid and slightly narrower. The post-fossid is much narrower than the trigonid. The talonid cusps are distally located, with a hypoconulid

much more posterior than the hypoconid and entoconid.

Premolars: Only the P₁ is single-rooted. P₂, P₃ and P₄ are double-rooted. The P₃ is inserted obliquely in the dentary (the mesial part is lingual while the distal part is labial). Only P₃ and P₄ are known for this species. The teeth are morphologically similar but the P₃ is distinctly smaller than the P₄. The teeth are rather bulbous with a wide and short talonid. On P₃ there is a fold in the mesio-lingual part of the protoconid but no distinct cusped paraconid. The talonid is half as high as the protoconid. A carnassial notch on the cristid obliqua separates the protoconid from the hypoconid. The talonid has only one cusp, the hypoconid, which has a very

TABLE 1. Measurements (in cm) of the specimens of *Oxyaena woutersi* (Lange-Badré and Godinot, 1982) from Le Quesnoy.

Locus		n	OR	M
P ³	L	1	1.134	-
	W	1	0.808	-
P ⁴	L	3	1.13-1.21	1.176
	W	2	1.09-0.95	0.808
M ¹	L	2	0.9-1.04	1.085
	W	1	0.948	-
C ₁	L	2	0.814-0.87	0.849
	W	2	0.67-0.682	0.677
P ₃	L	4	0.658-0.804	0.718
	W	3	0.33-0.422	0.371
P ₄	L	2	0.902-1.024	0.963
	W	3	0.458-554	0.499
M ₁	L	3	0.88-0.93	0.909
	W	3	0.492-0.596	0.527
M ₂	L	1	1.024	-
	W	1	0.658	-
DP ₄	L	1	0.898	-
	W	1	0.332	-
MD	H	1	1.573	-

wide base. The cristid obliqua is mesio-distal and curves into a posterior, ventro-lingually inclined, crest. Pre- and postcingulids are present. A tiny lingual cingulid is present along the talonid. A paraconid shelf is more developed on P₄ than on P₃ but is still not cusplate. The talonid of P₄ is more elongated than on P₃, but they are morphologically similar (e.g., orientation of the crest). The talonid is bulbous and wider than the protoconid. The cingulid on the lingual side of the talonid is more developed than on P₃. A very tiny entoconid was possibly present. A very thin cingulid labially links the paraconid to the hypoconid. The mesial and distal parts of the tooth are very straight as on P₃.

Molars: The M₁ has almost the same size as the P₄. The trigonid is compressed mesio-distally. The bases of the paraconid and metaconid are in contact. The apices of the two cusps are slightly divergent. The apex of the metaconid is slightly more posterior than the apex of the protoconid, and it is slightly tilted lingually. The prefossid is more closed than on deciduous premolars. The metaconid is only slightly higher than the paraconid. The protoconid part of the paracristid is directed mesio-dis-

tally; the paraconid part is much more transverse: the paraconid is not shifted mesially. Its base is slightly less salient lingually than the base of the metaconid. The protoconid is not much higher than the metaconid and paraconid and is not as sharp but is more robust. The paracristid and protocristid present a carnassial notch. A tiny cusp "e" is present on the mesio-lingual flank of the paraconid. The talonid is shorter than the trigonid, but, it is nearly as wide as the trigonid. The postfossid is narrow. The three cusps of the talonid are well developed. Two notches separate them. The separation is more pronounced between the hypoconulid and hypoconid than between the hypoconulid and entoconid. The hypoconulid is closer to the entoconid than to the hypoconid. The hypoconulid and entoconid have nearly the same height and are higher than the hypoconid. The base of the hypoconid is the largest. The cristid obliqua is disto-labially oriented. The part near the trigonid is worn, so it is impossible to know if a carnassial notch was present (a real possibility). The cristid obliqua runs along the trigonid distal wall toward the protocristid notch. The entocristid is oblique (distally shifted lingually) and closes the postfossid lingually. The curvature of the orientation of the entocristid and of the cristid obliqua renders the postfossid almost circular. The hypoflexid is deep. A pre-, ecto- and postcingulid link the paraconid to the hypoconulid. The M₂ is higher, longer and sharper than the M₁ and clearly represents the major carnassial tooth. Contrary to M₁, the paraconid is slightly higher than the metaconid. The paracristid is less transverse than on M₁: the paraconid is more shifted mesially. Its base is more extended lingually than that of the metaconid. A very tiny cusp "e" is present on the mesio-lingual flank of the paraconid. Moreover the protoconid is much taller than on M₁ and secant. As on M₁, the apex of the metaconid is slightly more distal than the apex of the protoconid. The metaconid is more reduced than on M₁. The prefossid is more open than on M₁. The paracristid and protocristid present a carnassial notch. The talonid of the M₂ is more elongated mesio-distally than on M₁ but it is distinctly narrower. The talonid cusps are also less developed than on the M₁. Their apices are poorly defined. Numerous very tiny cusps are present along the crests of the three cusps. Only a groove on the posterior wall of the basin separates the hypoconid from a hypoconulid part. This latter is the highest. The cristid obliqua and entocristid are mesio-distally oriented. Only a pre- and postcingulid are visible, but the

base of the tooth is broken, so an ectocingulid may have been present.

Discussion

The fragment of mandible MNHN QNY2-2569 and the isolated molars MNHN QNY2-2579 and MNHN QNY2-2524 show clearly that the M_1 is smaller than the M_2 and that no M_3 is present. On the maxillary fragment MNHN QNY2-2568 and on the isolated upper molars MNHN QNY2-2572 and MNHN QNY2-2573, the M^1 has a well-developed postmetacrista. All these characters refer to the Oxyaenidae subfamily Oxyaeninae.

The fossils differ from the genera *Patriofelis* Leidy, 1870 and *Protopsalis* Cope, 1880 by a less secant pattern of the molars and premolars: postmetacrista less developed on P^4 and M^1 , protocone less reduced on P^4 and M^1 , metaconid less reduced on lower molars. They are morphologically similar to Late Paleocene and Early Eocene genera of oxyaenines: *Dipsalidictis* and *Oxyaena*. The fossils found in Le Quesnoy have nearly the same size as *Dipsalidictis platypus* Matthew, 1915 and are distinctly smaller than all the other species known for the two genera in North America.

By contrast to North American oxyaenines, our knowledge of European oxyaenines is very scarce. The best known European species is *Oxyaena woutersi* from the Belgian locality of Dormaal (MP7). *O. woutersi* is known by three teeth: two M^1 and a P_3 or P_4 (Smith and Smith 2001). The teeth from Le Quesnoy have the same morphology as *O. woutersi*, but are slightly larger (12% longer for the P_3) (Table 1). Our knowledge does not support species distinction based on this size difference between Le Quesnoy and Dormaal material. In oxyaenines species, the intraspecific variation in size can reach almost 10% (after Gunnell and Gingerich 1991, table 3).

The M^1 MNHN QNY2-2573 is more similar to IRNSB 1320 than to IRNSB 1319, which may be a DP^4 (Smith and Smith 2001), or a M^1 of Hyaenodontidae. They share a more pronounced ectoflexus, a more secant morphology, a more developed parastyle and a size larger than IRNSB 1319. The postmetacrista on M^1 is slightly longer and more distally oriented in the material of Le Quesnoy. The lower premolar IRNSB 1318 was considered by Smith and Smith (2001) as a possible P_3 or P_4 . Comparison of the material found in Le Quesnoy (notably the mandible MNHN QNY2-2569) shows that this specimen is a P_3 .

The Le Quesnoy material is more complete than that of Dormaal and allows for a further discussion of the phylogenetic relationships of *Oxyaena woutersi*.

Oxyaena and *Dipsalidictis* are poorly distinguished, and they often have been grouped together (Gunnell and Gingerich 1991). *Dipsalidictis* is the most primitive and appears during the Clarkforkian with *Dipsalidictis krausei* Gunnell and Gingerich, 1991 (Cf1-Cf3). *Oxyaena*, which appears during the Wasatchian with *Oxyaena gulo* (Wa2-Wa3), differs in having more secant upper and lower molars and more robust premolars. A difference between *Dipsalidictis* and *Oxyaena* is the absence of metacone on the M^2 of the latter (Gunnell and Gingerich 1991). Unfortunately no M^2 has been found in Le Quesnoy, and the presence/absence of the metacone on M^2 can not be checked.

Gunnell and Gingerich (1991, figures 12, 13, 14) proposed also several ratios of the two lower molars and M^1 that allow distinguishing the two genera. These ratios reflect the development of a secant dentition in the earliest Oxyaeninae (e.g., trigonid wider than long in *Dipsalidictis*, trigonid longer than wide in *Oxyaena*). The material of Le Quesnoy provides measurements of lower molars only (Table 2). The ratio evaluated for the M_1 fits in the values of *Dipsalidictis*. Conversely, the ratio for the M_2 is typical of *Oxyaena*. It reaches values intermediate between *Oxyaena intermedia* Denison, 1938 (Wa4-Wa6) and *Oxyaena forcipata* Cope, 1874 (Wa5-Wa6) (Figure 7), which is due to the prominence of the paraconid, which is well developed and shifted mesially on M_2 , correlated to the reduction of the metaconid, in *O. woutersi*.

Some characters of the Le Quesnoy material are known in typical *Oxyaena* species. The P_3 and P_4 have a talonid enlarged labio-lingually as in *Oxyaena*. A maxillary excavation between the dental embrasures of M^1 and M^2 is typical of *Oxyaena* species. This character, which is derived in the oxyaenines, is linked to the strongly elevated M_1 and M_2 trigonid (Gunnell and Gingerich 1991). This maxillary excavation is distinctly present in MNHN QNY2-2568. The parastyle of P^4 is smaller than in *Dipsalidictis*, similar in size to that of *O. gulo*. The postmetacrista of the M^1 of *O. woutersi* is more elongated and shifted distally than in *Dipsalidictis* (but less than in *O. gulo*). *O. woutersi* is closer to *O. gulo*, the most primitive species of the genus, than to any other species of *Oxyaena*: they share a

TABLE 2. Mean measurements of upper and lower teeth reflecting the development of efficient shearing dentitions in *Dipsalidictis* and *Oxyaena*. Measurements, except for *Oxyaena woutersi* (Lange-Badré and Godinot, 1982) and *Oxyaena* sp., are from table 12 of Gunnell and Gingerich (1991). L/W = Length/Width; PALD = M_2 paralophid length divided by M_2 trigonid width (Gunnell and Gingerich 1991; Figure 12, 13 & 14). Sample size N is given in parentheses.

Genus and species		M_1 trigonid L/W	M_2 trigonid L/W	PALD
<i>Dipsalidictis krausei</i> (Cf1-Cf3)	<i>D kr</i>	0.90 (5)	0.87 (4)	1.15
<i>Dipsalidictis aequidens</i> (Cf2-Cf3)	<i>D ae</i>	0.91 (6)	0.86 (7)	1.16
<i>Dipsalidictis platypus</i> (Cf2-Wa0)	<i>D pl</i>	0.89 (4)	0.86 (3)	1.16
<i>Dipsalidictis transiens</i> (Wa0-Wa2)	<i>D tr</i>	0.93 (5)	0.91 (8)	1.23
<i>Oxyaena woutersi</i> (MP7)	<i>O wo</i>	0.99 (1)	1.14 (1)	1.28
<i>Oxyaena</i> sp. (MP7)	<i>O sp</i>	1.02	-	-
<i>Oxyaena gulo</i> (Wa2-Wa3)	<i>O gu</i>	1.06 (4)	1.07 (5)	1.23
<i>Oxyaena intermedia</i> (Wa4-Wa5)	<i>O in</i>	1.09 (2)	1.08 (2)	1.25
<i>Oxyaena forcipata</i> (Wa5-Wa6)	<i>O fo</i>	1.14 (5)	1.24 (5)	1.33

Genus and species		Ln P_4 LxW	Ln M_1 LxW	Ln M_2 LxW
<i>Dipsalidictis krausei</i> (Cf1-Cf3)	<i>D kr</i>	3.85 – 4.25	3.95 – 4.375	4.325 – 4.75
<i>Dipsalidictis aequidens</i> (Cf2-Cf3)	<i>D ae</i>	4.35 – 4.75	4.2 – 4.6	4.55 – 5.0
<i>Dipsalidictis platypus</i> (Cf2-Wa0)	<i>D pl</i>	3.35 – 3.8	3.6 – 4.00	3.9 – 4.3
<i>Dipsalidictis transiens</i> (Wa0-Wa2)	<i>D tr</i>	4.00 – 4.4	4.2 – 4.6	4.4 – 4.875
<i>Oxyaena woutersi</i> (MP7)	<i>O wo</i>	3.87	3.88	4.21
<i>Oxyaena</i> sp. (MP7)		-	-	4.41
<i>Oxyaena gulo</i> (Wa2-Wa3)	<i>O gu</i>	4.4 – 4.85	4.4 – 4.8	4.65 – 5.05
<i>Oxyaena intermedia</i> (Wa4-Wa5)	<i>O in</i>	4.5 – 4.9	4.6 – 5.00	5.0 – 5.4
<i>Oxyaena forcipata</i> (Wa5-Wa6)	<i>O fo</i>	4.9 – 5.3	5.0 – 5.4	5.25 – 5.65

less-developed shearing dentition and narrower M_2 talonid.

On the other hand, some features of the upper teeth of the Le Quesnoy species recall the genus *Dipsalidictis* in having similar (and primitive) features: protocone on P_4 more shifted mesially than on *Oxyaena* (this primitive morphology is also found in *Tytthaena* Gingerich, 1980); protocone of the M_1 is less reduced than in *O. gulo*; deep ectoflexus on M_1 ; parastyle developed on M_1 . The M_1 trigonid is more compressed than in *O. gulo*. The labial cingulids of the M_1 and M_2 and pre- and postcingulum of the M_1 are less developed than in *O. gulo* and other *Oxyaena* species.

The presence of a small and poorly developed paraconid on P_4 is known in some *Dipsalidictis* and the first species of *Oxyaena*, *O. gulo*. It is more developed in younger *Oxyaena* species.

In general, *Oxyaena woutersi* has hypercarnivorous adaptations as known in *Oxyaena* (e.g., postmetacrista oblique and elongated, paracristid elongated on M_2) however, some characters (e.g.,

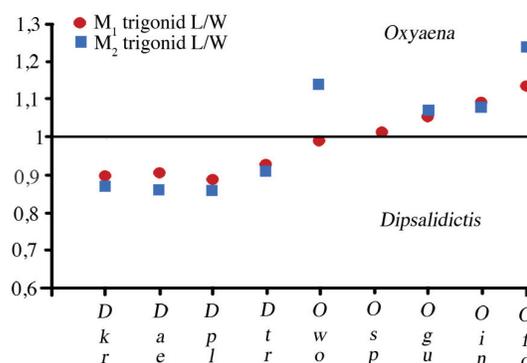


FIGURE 7. Comparison of the trigonid shape of M_1 and M_2 (M_1 trigonid L/W; M_2 trigonid L/W) between *Dipsalidictis* species, *Oxyaena woutersi* (Lange-Badré and Godinot, 1982), *Oxyaena* sp. and oldest species of *Oxyaena*. See values on Table 2. L = length; W = width. *D kr* = *Dipsalidictis krausei*, *D ae* = *Dipsalidictis aequidens*, *D pl* = *Dipsalidictis platypus*, *D tr* = *Dipsalidictis transiens*, *O wo* = *Oxyaena woutersi*, *O sp* = *Oxyaena* sp., *O gu* = *Oxyaena gulo*, *O in* = *Oxyaena intermedia*, *O fo* = *Oxyaena forcipata*.

paraconid lingually located and trigonid compressed in M_1 , which are primitive, recall also *Dipsalidictis*. The dental morphology of *O. woutersi* is intermediate between *Dipsalidictis* and *Oxyaena*, notably between *D. transiens* and *O. gulo*.

Four species of *Dipsalidictis* are known: *Dipsalidictis krausei* (Cf1-Cf3), *Dipsalidictis aequidens* (Matthew, 1915) (Cf2-Cf3), *Dipsalidictis platypus* (Cf2-Wa0) and *Dipsalidictis transiens* (Wa0-Wa2). They are notably distinguished by their size. Except *D. platypus*, the *Dipsalidictis* species are larger than *O. woutersi*. *O. woutersi* differs from them notably by a longer paracristid on M_2 and slightly longer postmetacrista on M^1 which are derived features toward increased carnivory, which is characteristic of *Oxyaena* (see above). *D. transiens* has the most shearing teeth in the genus. Gunnell and Gingerich (1991) root *Oxyaena* in *D. transiens*.

Dipsalidictis aequidens has a maxillary excavation between M^1 and M^2 , as in *Oxyaena* species, including *O. woutersi*. Gunnell and Gingerich (1991) consider that this character is convergent with *Oxyaena*. *D. aequidens* has excessively larger and robust premolars (notably P_4 with a well developed paraconid) and molars to be at the origin of *Oxyaena*, and of *O. woutersi* which has much more slender premolars and molars. This is in accordance with Gunnell and Gingerich (1991).

The teeth of *O. woutersi* are much more secant than those of *D. krausei*. They differ notably in the paraconid of P_4 more developed and in the protocone of the M^1 and P^4 less robust and mesiodistally elongated. These derived characters of *O. woutersi* are shared with *D. platypus* and *D. transiens*.

For Smith and Smith (2001), *Oxyaena woutersi* and *Dipsalidictis platypus* are close because they share a shorter postmetacrista and more slender molars than in *D. transiens*. The postmetacrista of *O. woutersi* is not as short as in *D. platypus*, but is as long as in *D. transiens*. Gunnell and Gingerich (1991, figures 9, 10, 11) used three measurements of length and width of P_4 , M_1 and M_2 , which reflect the evolutionary changes in size during the evolution of oxyaenine lineages in the Bighorn Basin and Clarks Fork Basin (Table 3). The values obtained for *O. woutersi* are similar to those of *D. platypus* (Figure 8) except for the P_4 (Figure 9). Concerning the M_1 and M_2 this is not surprising because the two species share a small size. The difference in the P_4 reflects that this tooth is larger and more robust in *O. woutersi* than in *D. platypus*.

The robustness of the P_4 is characteristic of *Oxyaena*. The slender aspect shared by *O. woutersi* and *D. platypus* seems to be related with the small size of both species. The differences between *O. woutersi* and *D. platypus* are the more robust P_4 and the base of the paraconid of the molars which is much more developed lingually and shifted mesially in *O. woutersi* than in *D. platypus*. These latter features are derived among Oxyaeninae. The premolars closely appressed are observed in *D. krausei* and *D. transiens*. The premolars are more spaced in *D. platypus*. However, the P_3 , which is obliquely inserted in the mandible, has a peculiar position, also similarly seen in *D. platypus* (YPM-PU 21215). However, the position of the premolars along the mandible is variable and therefore is uninformative for establishing clear phylogenetic relationships.

The peculiar development of the paraconid (base developed lingually and shifted mesially) of the molars of *O. woutersi* is shared with *D. transiens* and *O. gulo*. They also share a long postmetacrista. They share a more robust P_3 and much more developed cingula around the protocone than in other *Dipsalidictis* species. All these features are indicative of affinities with the genus *Oxyaena*. *O. woutersi* also shares with *D. transiens* a more pronounced ectoflexus on the upper molars. We think that the species of *Dipsalidictis* closest to *O. woutersi* is *D. transiens*. Both *O. woutersi* and *D. transiens* present notably a development toward secant lower and upper molars. *O. woutersi* differs from *D. transiens* by a more derived dentition toward carnivory (e.g., paracristid more developed and metaconid more reduced on M_2), and a P_3 and P_4 with a talonid more robust as in *Oxyaena* (derived features).

Our comparison suggests that the European *O. woutersi* continued to develop the shearing dentition which appeared in *D. transiens*, at the beginning of the Eocene. Among oxyaenines, *O. woutersi* is a structural intermediate between *D. transiens* and *O. gulo*. However, *O. woutersi* is distinguished by a M_2 more secant than in *O. gulo* (known in one specimen only).

If the European reference-level MP7 is correlated to the North American Wa0 as proposed by Smith and Smith (2001), the known North American *Oxyaena* species are younger than *O. woutersi*. In this regard it is not surprising that *O. woutersi* appears more primitive (Figure 10).

We retain the generic attribution of *O. woutersi* because its dentition is more specialized for

TABLE 3. Evolutionary change in size of P_4 , M_1 and M_2 between *Oxyaena woutersi* (Lange-Badré and Godinot, 1982), *Oxyaena* sp., North American *Oxyaena* and *Dipsalidictis* species. (L = length; W = width). Measurements for North American *Oxyaena* and *Dipsalidictis* species are taken from Gunnell and Gingerich (1991; figures 9, 10 and 11).

Genus and species		Ln P_4 LxW	Ln M_1 LxW	Ln M_2 LxW
<i>Dipsalidictis krausei</i> (Cf1-Cf3)	<i>D kr</i>	3.85 – 4.25	3.95 – 4.375	4.325 – 4.75
<i>Dipsalidictis aequidens</i> (Cf2-Cf3)	<i>D ae</i>	4.35 – 4.75	4.2 – 4.6	4.55 – 5.0
<i>Dipsalidictis platypus</i> (Cf2-Wa0)	<i>D pl</i>	3.35 – 3.8	3.6 – 4.00	3.9 – 4.3
<i>Dipsalidictis transiens</i> (Wa0-Wa2)	<i>D tr</i>	4.00 – 4.4	4.2 – 4.6	4.4 – 4.875
<i>Oxyaena woutersi</i> (MP7)	<i>O wo</i>	3.87	3.88	4.21
<i>Oxyaena</i> sp. (MP7)		-	-	4.41
<i>Oxyaena gulo</i> (Wa2-Wa3)	<i>O gu</i>	4.4 – 4.85	4.4 – 4.8	4.65 – 5.05
<i>Oxyaena intermedia</i> (Wa4-Wa5)	<i>O in</i>	4.5 – 4.9	4.6 – 5.00	5.0 – 5.4
<i>Oxyaena forcipata</i> (Wa5-Wa6)	<i>O fo</i>	4.9 – 5.3	5.0 – 5.4	5.25 – 5.65

Genus and species		Ln P_4 LxW	Ln M_1 LxW	Ln M_2 LxW
<i>Dipsalidictis krausei</i> (Cf1-Cf3)	<i>D kr</i>	3.85 – 4.25	3.95 – 4.375	4.325 – 4.75
<i>Dipsalidictis aequidens</i> (Cf2-Cf3)	<i>D ae</i>	4.35 – 4.75	4.2 – 4.6	4.55 – 5.0
<i>Dipsalidictis platypus</i> (Cf2-Wa0)	<i>D pl</i>	3.35 – 3.8	3.6 – 4.00	3.9 – 4.3
<i>Dipsalidictis transiens</i> (Wa0-Wa2)	<i>D tr</i>	4.00 – 4.4	4.2 – 4.6	4.4 – 4.875
<i>Oxyaena woutersi</i> (MP7)	<i>O wo</i>	3.87	3.88	4.21
<i>Oxyaena</i> sp. (MP8+9)		-	4.41	-
<i>Oxyaena gulo</i> (Wa2-Wa3)	<i>O gu</i>	4.4 – 4.85	4.4 – 4.8	4.65 – 5.05
<i>Oxyaena intermedia</i> (Wa4-Wa5)	<i>O in</i>	4.5 – 4.9	4.6 – 5.00	5.0 – 5.4
<i>Oxyaena forcipata</i> (Wa5-Wa6)	<i>O fo</i>	4.9 – 5.3	5.0 – 5.4	5.25 – 5.65

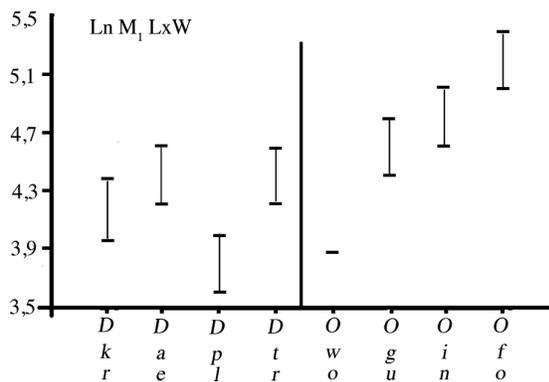


FIGURE 8. Comparison of Ln M_1 LxW between *Dipsalidictis* species, *Oxyaena woutersi* (Lange-Badré and Godinot, 1982) and oldest species of *Oxyaena*. See values on Table 3. *Oxyaena* sp. is not included. L = length; W = width. *D kr* = *Dipsalidictis krausei*, *D ae* = *Dipsalidictis aequidens*, *D pl* = *Dipsalidictis platypus*, *D tr* = *Dipsalidictis transiens*, *O wo* = *Oxyaena woutersi* (blue), *O gu* = *Oxyaena gulo*, *O in* = *Oxyaena intermedia*, *O fo* = *Oxyaena forcipata*.

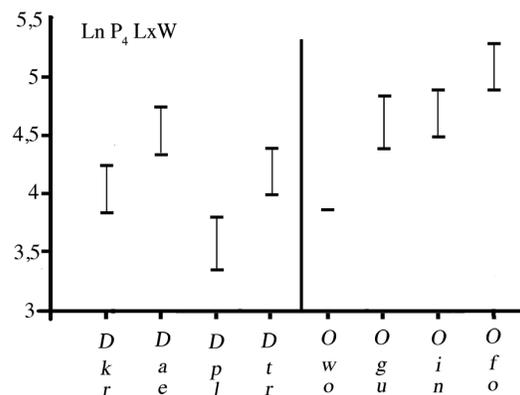


FIGURE 9. Comparison of Ln P_4 LxW between *Dipsalidictis* species, *Oxyaena woutersi* (Lange-Badré and Godinot, 1982) and oldest species of *Oxyaena*. See values on Table 3. *Oxyaena* sp. is not included. L = length; W = width. *D kr* = *Dipsalidictis krausei*, *D ae* = *Dipsalidictis aequidens*, *D pl* = *Dipsalidictis platypus*, *D tr* = *Dipsalidictis transiens*, *O wo* = *Oxyaena woutersi* (blue), *O gu* = *Oxyaena gulo*, *O in* = *Oxyaena intermedia*, *O fo* = *Oxyaena forcipata*.

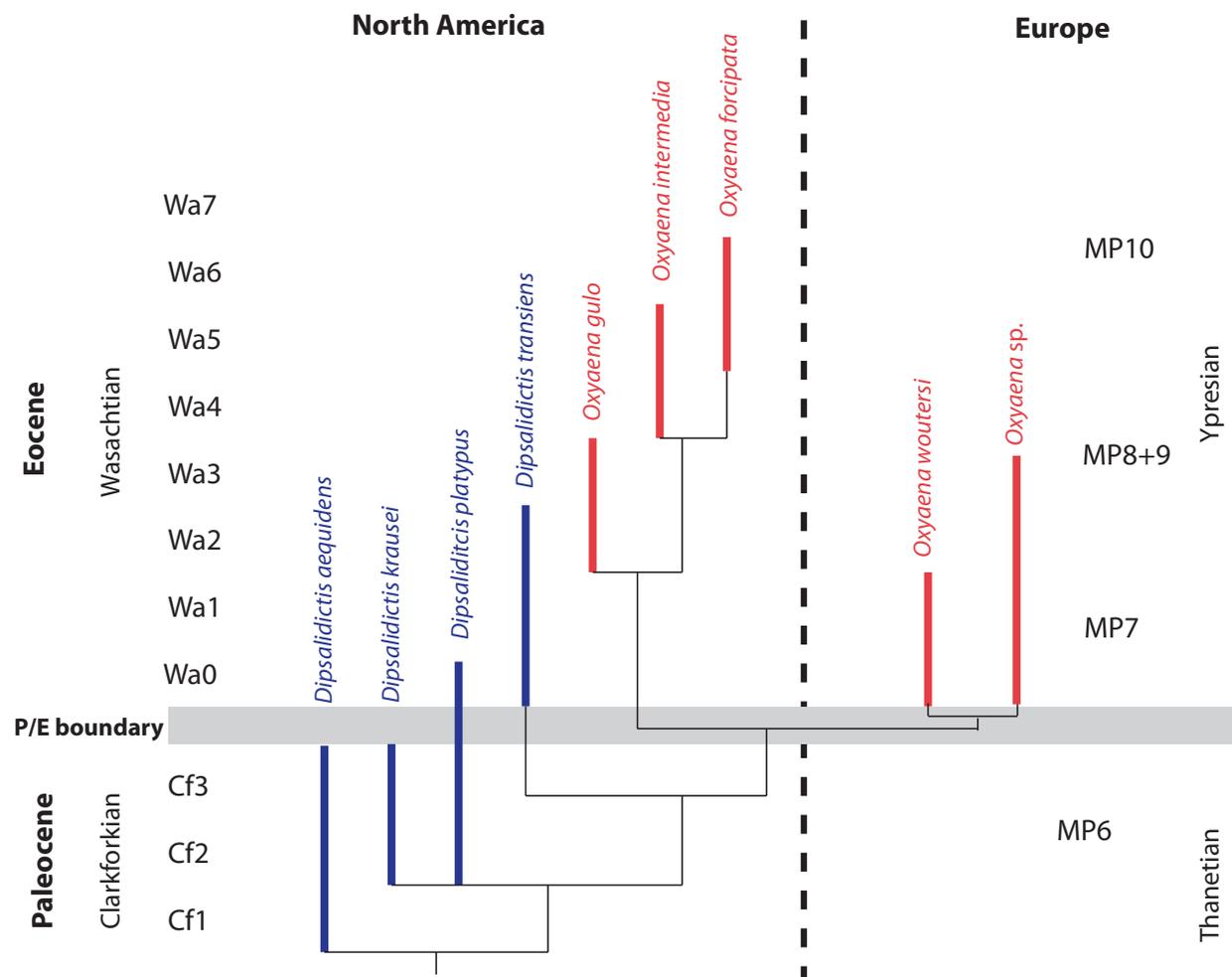


FIGURE 10. Phylogenetic relationships of Oxyaeninae with indications of stratigraphic and geographic repartition of the Late Paleocene and Early Eocene *Dipsalidictis* and *Oxyaena*. The phylogenetic relationships are based on Gunnell and Gingerich (1991) and Gunnell (1998). Note: *Dipsalidictis* is a paraphyletic genus.

shearing than *Dipsalidictis* (e.g., M_2 paracristid enlarged), even if this concerns only the M_2 .

Description of the Referred Postcranial Material from Le Quesnoy

Measurements: Table 4

Forelimb. MNHN QNY2-2526; left distal humerus. Only the distal part of the humerus is known. A slight torsion of the diaphysis is reflected by a somewhat posterior inclination of the supinator crest (origin of the elbow flexor muscle brachioradialis, and the forearm and digital extensors), which is not salient laterally. The distal part is transversally elongated. On medial and lateral views, the fragment appears almost flat. The trochlea is poorly projected anteriorly. The elbow joint is transversally elongated: the trochlea is well developed and the posterior trochlear groove is proximally

deep and moderately concave. On the anterior side, the capitulum is less extended than the trochlea. The medial epicondyle is prominent and elongated medially. The entepicondylar foramen is very large. The medial lip of the trochlea is extended distally. In anterior view, there is a small and shallow radial fossa laterally to a round and large coronoid fossa. There is a hole in the coronoid fossa, although it does not seem to be the supratrochlear foramen, but rather the result of breakage. The pit for attachment of an ulnar collateral ligament is deep. The olecranon fossa is deep and wide.

MNHN QNY2-2637; left scaphoid. The scaphoid is elongated mediolaterally (in dorsal view) and flat dorsoventrally (in mesial view). It is strongly convex dorsally. The scaphoid tubercle extends ventrally. The articular facet with the lunate is elongated proximodistally. In ventral view, the artic-

TABLE 4. Measurements of the postcranial material of *Oxyaena woutersi* (Lange-Badré and Godinot, 1982) from Le Quesnoy.

Humerus	
Maximum transverse width of the distal extremity	2.63
Transverse width of the distal articular surface in distal view	1.67
Antero-posterior depth of the trochlea in distal view	0.52
Transverse width of the capitulum in anterior view	0.77
Proximal height of the capitulum in anterior view	0.78
Distance between the medial lip of the trochlea and the apex of medial epicondyle	0.97
Scaphoid	
Width	1.26
Calcaneum	
Total length	3.14
Length of the tuber calcanei	1.53
Transverse width of the ectal facet	0.82
Proximodistal length of the ectal facet	1.09
Transverse width of the sustentacular facet	0.65
Proximodistal length of the sustentacular facet	0.71
Maximal width at the level of facets	1.67
Transverse width of the calcaneocuboid facet	1.12
Astragalus	
Total length	2.27
Maximum transverse width	1.70
Astragalotibial length	1.28
Astragalotibial width	1.65
Astragalar head width (anterior view)	1.17
Astragalar head height (anterior view)	0.63
Cuboid	
Width	1.07
Length	1.34

ular facets with the centrale (laterally) and trapezium (medially) are wide and square. The proximal facet is more oblique than of the proximal facet. The distal facets are almost flat, contrasting with the convexity of the proximal facet.

Hindlimb. MNHN QNY2-2636; right calcaneum. The bone is short anteroposteriorly. The part posterior to the sustentacular facet is the longest; the anterior part to the facet is relatively short. The calcaneum is compressed mediolaterally, but dorsoventrally high. The tuber calcanei is wide, and worn laterally and medially. Posteriorly, there is a wide surface indicating a strong tendon insertion. The sustentacular facet (slightly concave) is more elongated anteroposteriorly than transversally. The facet is slightly inclined proximo-dorsally. The calcaneoastragalar facet (anteroposteriorly convex) is

elongated anteroposteriorly, narrow and is directed dorso-posteriorly. The sustentacular facet and calcaneoastragalar facet are close to each other. There is also a very small calcaneofibular facet, posterior to the calcaneoastragalar facet. The peroneal process is broken distally, but, the large size of its base suggests that it was well developed. In anterior view the peroneal process is thin. Ventrally a surface for insertion is visible (for the calcaneocuboid ligament?). The articular facet with the cuboid is at an acute angle with the antero-posterior direction and slightly concave. In anterior view, the facet is somewhat rectangular. An articulation facet for the astragalar head is visible on the antero-dorsal part of the calcaneum.

MNHN QNY2-2633, MNHN QNY2-2635; two right astragali. The astragali fit with the calcaneum in

morphology and size. The astragalus is slightly elongated antero-posteriorly. The astragalar trochlea for the articulation with the distal tibia is shallowly grooved. The body is wide medio-laterally. The neck is narrower. It is robust and short antero-posteriorly. The head is slightly wider than the neck. It is convex anteriorly, but flattened dorso-ventrally. The astragalar foramen is well developed and weakly shifted posteriorly. In medial view, the medial part is lower than the lateral part. The sustentacular facet (convex) is broad and wide, but short antero-posteriorly and is inclined proximo-ventrally. The ectal facet is strongly concave. It is wide, but very thin antero-posteriorly. The sustentacular and ectal facets are well separated. Lateral to the ectal facet, there is a deep groove for the tendon of the plantar flexor muscles: flexor hallucis longus and peroneus longus. The head of the astragalus has a large and laterally extended navicular facet.

MNHN QNY2-2638; cuboid. The cuboid is square except on the dorsal part. It is long proximodistally, but narrow transversally. The proximal facet, which articulates with the calcaneum, is convex and oblique. A triangular facet for the articulation with the astragalar head is present dorsally on the medial side. The articular facet with the navicular is extended anteroposteriorly, but short dorsoventrally. There is also a large articulation for the ectocuneiform. The plantar tubercle is well developed. It is laterally related to the distal articulation of the cuboid. The articular facet for the fourth and fifth metatarsals is transversally short and only slightly concave.

Discussion

The postcranial elements and the locomotion of the Oxyaenidae are well known. However, they have not been discussed in detail since the major work of Denison (1938). Only Rose (1990, 2001) and Gunnell and Gingerich (1991) discussed several points. A revision of the postcranium of the Oxyaenidae and a discussion of their locomotion are beyond the scope of this paper.

The material of the Oxyaenidae from Le Quesnoy has been especially compared with the material housed in the collection of the AMNH and the University of Michigan.

As explained previously, the Oxyaeninae are represented during the Paleocene and earliest Eocene by the genus *Dipsalidictis*, which is our main reference. The North American *Oxyaena* species are younger and more derived than the European *O. woutersi*.

On the humerus (MNHN QNY2-2526) the medial trochlear rim is more salient distally than in Hyaeodontidae, and agrees with the Oxyaenidae. A second distal fragment of Oxyaenidae (MNHN QNY2-2634) differs from MNHN QNY2-2526 by a larger size and a more robust morphology, but, the trochleae are similar in shape: it belongs to *Palaeonictis gigantea* (see below). The distal fragment of humerus (MNHN QNY2-2526) is morphologically similar to AMNH 15857 and UM 69474 referred to *D. platypus*. Their sizes are also similar: as noted previously the two species have almost the same size. We refer MNHN QNY2-2526 to *O. woutersi*.

The medial rim of the trochlea is not as extended distally as in *O. forcipata* and is more similar to *Dipsalidictis platypus*. The trochlea of MNHN QNY2-2526 is deeper posteriorly, less shallow than in *D. platypus*. The medial epicondyle (origin of muscle pronator teres and forearm and deep digital flexors), which is less well developed in terrestrial species than in arboreal and digging species (Taylor 1974; Argot 2003), is slightly more reduced than in *Dipsalidictis*. The radial fossa and the olecranon fossa are deeper than in *Dipsalidictis*. The lateral epicondylar crest, which is well developed in arboreal species (Heinrich and Rose 1997), is less developed in MNHN QNY2-2526 compared to *Dipsalidictis*. Moreover, the pit for attachment of the ulnar collateral ligament is slightly deeper. This ligament comes from the semilunar notch of the ulna, and it anchors the humerus and stabilizes the humeroulnar joint. The olecranon fossa and the great ulnar collateral attachment stabilize the elbow joint by reducing the axial rotation of the ulna. The supinator crest is less developed than in *Dipsalidictis*. The torsion of the diaphysis is less marked than in *Dipsalidictis* and is probably derived in comparison with the latter genus. All of these features are linked to a terrestrial locomotion that is slightly more pronounced in the forelimb of *O. woutersi* than in *Dipsalidictis*.

The scaphoid is more elongated transversally than in *Dipsalidictis*. The dorsal facet is more developed in *O. woutersi*, thus limiting the flexibility of the manus.

The calcaneum is similar in size to UM 66137 of *D. platypus*. It differs by a proximal articular facet that is extended proximo-distally and is more oblique (distolaterally oriented). Moreover the two articular facets with the astragalus are closer. The sustentacular facet is smaller. All these features are derived toward a less mobile ankle. A distinct fibular facet typical of the genus *Oxyaena* (Gunnell and Gingerich 1991) is also observable. The articu-

lar facet with the cuboid is flatter, elongated transversely and at an acute angle, which limits the movement between the two bones. This facet fits with the cuboid (MNHN QNY2-2638) found in Le Quesnoy. The proximal tuber extremity is worn. However, it may have been as large and developed as in *Dipsalidictis*. Its surface is more excavated than in *Dipsalidictis*.

On the astragalus, the ectal facet is deeper than in *D. platypus*. However, the trochlea is similar. The articular facets for the calcaneum are more developed. The articular facets for the cuboid and navicular are more developed than in *Dipsalidictis*. The sustentacular facet contacts the navicular facet. It also extends closer to the ectal facet. This is a derived character toward a more terrestrial locomotion. The neck is shorter, more robust and broader. The fibular process is larger. All these features correspond to those of *Oxyaena* as noted by Gunnell and Gingerich (1991). They indicate a more robust ankle, with less flexibility. The astragali found in Le Quesnoy are less robust than in *O. gulo*: the body is lower, the trochlea is shallower and the ectal facet is less concave. In *O. gulo*, it limits the movement of the pes to a dorsoventral plane.

The cuboid fits in structure and shape with the other fossils. The cuboid is shorter, but more robust than in *Dipsalidictis* (Gunnell and Gingerich 1991). As indicated above, its articulation with the astragalus is slightly more limited than in *Dipsalidictis*. On the whole, it appears that *O. woutersi* possessed more restricted articulations, which indicate movements more restricted to the parasagittal plane than in *D. platypus*.

The trends here described are also found in the North America *Oxyaena*. *O. woutersi* thus possessed a more terrestrial locomotion than *Dipsalidictis*.

Gunnell and Gingerich (1991) proposed that *Oxyaena* could be an ambulatory terrestrial predator, more terrestrial than *Dispalidictis*. Rose (2001) proposed the hypothesis that *Oxyaena* was semifossorial or scansorial, on the basis of an original combination of characters.

Denison (1938) and Gunnell (1998) considered the Oxyaenidae as plantigrade. However, Rose (1990) proposed that the earliest *Dipsalidictis* were subdigitigrade. The smallness and robustness of the calcaneum (notably the tuber calcanei) is typical of plantigrade species (Ginsburg 1961). Thus, *Oxyaena woutersi* was probably plantigrade.

One of the arguments used by Denison (1938) to propose an arboreal mode of life for *Oxy-*

aena was the development of the entepicondylar crest, here broken but surely developed. On this crest are inserted the pronation muscles.

The supinator crest is present on the only available fragment of humerus, but reduced. This supports arboreal and/or scansorial habits, but less developed than in *Dipsalidictis*. The medial trochlear rim is more developed than in arboreal species. The presence of a delineated coronoid fossa proximal to the trochlea suggests usual use of highly flexed forelimb postures (Heinrich and Rose 1995, 1997). The coronoid fossa is found in arboreal and primitive carnivores and is linked to highly flexed forelimb postures. Its presence in *O. woutersi* is probably a primitive retention. The peroneal tubercle is also a primitive feature of arboreal carnivorous mammals. The peroneal musculature allows eversion, abduction and plantarflexion of the pes (Heinrich and Rose 1997). The plantarflexion role is predominant in terrestrial carnivorous mammals, which is not the case here. Plantarflexion is also limited by the high position of the astragalar foramen. Moreover a laterally extended peroneal process increases the leverage of the muscle peroneus longus (abductor of the hallux) (Argot 2004).

The presence of a well-defined groove for the flexor hallucis longus tendon in the posterior side of the cuboid indicates that the flexor of the hallux was large. The hallux is somewhat divergent.

On the astragalus, the differences in size of the medial and lateral trochlear crests indicate simultaneous inversion and abduction at the tibioastragalar joint during plantarflexion (Jenkins and McClearn 1984). The astragalus can slide anteriorly below the tibia: this increases the abduction and eversion at the tibioastragalar joint, and therefore allows the reversion of the hindfoot. However, these movements were rather limited. The presence of a developed lateral articular surface on the head indicates an usual eversion.

Oxyaena woutersi, as *Dispalidictis* species, is clearly not cursorial. Many features can be related to an arboreal mode of life (e.g., divergent hallux, morphology of the astragalus). However, because the arboreal features are more developed in *Dispalidictis* species than in *O. woutersi*, we think that the arboreal features are primitive features. Moreover, the terrestrial features in *O. woutersi* are more developed than in *Dispalidictis* species.

If we apply the methodology proposed by Morlo (1999) for body mass estimation of the "Creodonta" only on dental data, *O. woutersi* is estimated to have weighed approximately 7 kg, which is not in contradiction with an arboreal niche. How-

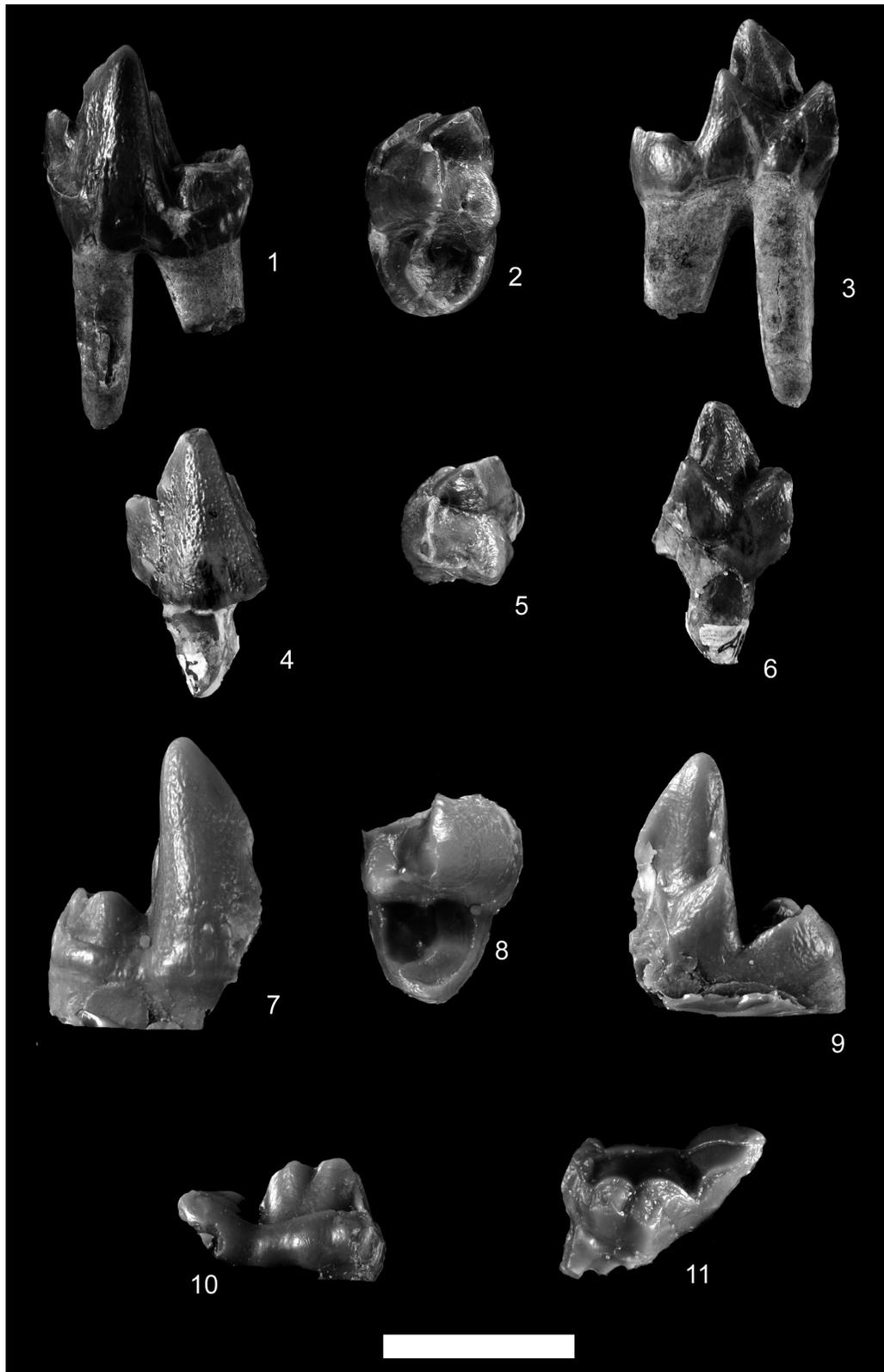


FIGURE 11. *Oxyaena* sp. 1-3. UCMP 83754, LM₁ in 1. labial, 2. occlusal, 3. lingual views. 4-6. ARP 5, LM₁ in 4. labial, 5. occlusal, 6. lingual view. 7-9. BMNH M13778 (cast), RM₂ in 7. labial, 8. occlusal, 9. lingual views. 10-11. BMNH M31877 (cast), LM¹ in 10. labial, 11. occlusal views. Scale bar equals 10 mm.

TABLE 5. Measurements (in cm) of the specimens of *Oxyaena* sp. from Abbey Wood (M¹ and M₂) and Sinceny (M₁).

Locus		n	OR	M
M ¹	L	2	0.878-1.154	1.016
	W	0	-	-
M ₁	L	1	1.16	-
	W	2	0.562-0.71	0.636
M ₂	L	0	-	-
	W	1	0.832	-

ever, *O. woutersi* was probably still capable of arboreal locomotion, but spending more time, possibly hunting, on the ground; this recent adaptative shift had not yet led to a marked terrestrial locomotion. However, several of the derived features of *O. woutersi*, compared to *Dipsalidictis*, are considered as adaptation to a more terrestrial locomotion. *O. woutersi* was probably a terrestrial ambulatory taxon.

Oxyaena sp.
Figure 11

Referred material from Sinceny (France). M₁, UCMP 83574 (L)

Referred material from Meudon (France). M¹, M-13-G (L)

M₁, MNHN ARP 5 (L)

Referred material from Abbey Wood (England). M¹, BMNH M31877 (L)

M₂, BMNH M13778 (R)

Distribution. MP8+9, Meudon, Carrière des Montalets (Conglomérat de Meudon), Sinceny (France), Lessness Shell Bed, Blackheath Beds, Abbey Wood (England).

Description

Measurements: Table 5

Upper dentition. Molars: Two fragmentary M¹ are known: M-13-G from Meudon (MP8+9) and BMNH M31877 from Abbey Wood (MP8+9). The trigon basin is missing on the M¹. M-13-G is worn. However, its morphology is distinctly observable. The two specimens are morphologically similar. The paracone and metacone are connate but their apices are individualized. They are almost equal in development. The preparacrista is very small. It is more transversal than labio-lingually oriented. The postmetacrista is very elongated. It may have been

separated from the metacone by a carnassial notch. It is shifted more distally than in *O. woutersi*. The ectoflexus is flat. The styler shelf is very narrow. The paraconule and metaconule are present, and close to the paracone and metacone. The paraconule is linked to the preparacrista via the preparaconule crista. On the mesial part of the paraconule, a weak precingulum is visible.

Lower dentition. Molars: One trigonid of a first molar is known from Meudon (MNHN ARP 5). UCMP 83754 from Sinceny is the only complete lower molar known in Europe for this species. It is slightly larger than MNHN ARP 5. However, the morphology of the two teeth is quite similar. They have a crenulated enamel. The trigonid is more elongated mesio-distally than in *O. woutersi*. The metaconid and paraconid are in contact. However their apices are divergent. The apex of the metaconid is slightly more distal than that of the protoconid. It is only very slightly titled lingually. The paraconid and metaconid are almost equal in height. The paracristid is distinctly less transverse than in *O. woutersi* and is also more elongated mesially. The paraconid projects mesially. The protoconid is not much higher than the paraconid and metaconid, but it is the highest cuspid.

On M₂, the lower carnassial tooth, the protoconid is much higher than the paraconid and metaconid. The paracristid and protocristid present a carnassial notch. The cusp "e" is present on the mesio-lingual flank of the paraconid but very slightly developed. The talonid is shorter than the trigonid. However, they have almost the same width. The postfossid is narrow and is surrounded by three well distinct cusps. The hypoconulid is more separated from the hypoconid than from the entoconid. These two cusps are close and have the same size. They are slightly higher than the hypoconid. The hypoconid has the largest base. The cristid obliqua is oblique (disto-labially oriented). No carnassial notch is present. The cristid obliqua extends on the trigonid wall towards the protocristid notch. The entocristid is oblique (distally shifted lingually) and closes lingually the postfossid. As in *O. woutersi*, thanks to the orientation of the entocristid and cristid obliqua, the postfossid seems to be almost circular. The hypoflexid is deep. A pre-, ecto- and postcingulid link the paraconid to the hypoconulid. The ectocingulid is well developed. The second lower molar here referred is a M₂ from Abbey Wood (BMNH M13778). Only the paraconid is missing. By contrast to the previously described M₁, the protoconid is tall and

pointed. As on M_1 , the protoconid is distinctly higher than the metaconid (almost twice the height), and the metaconid is more reduced than on M_1 . Its apex is slightly distal to the protoconid producing an open prefossid. The talonid is shorter and narrower than the trigonid. By contrast to M_1 , the talonid is longer than wide, so the talonid appears to be elongated mesio-distally. The hypoconid is distinct but the entoconid is not as individualized. A slightly visible notch marks the separation between the entoconid and the hypoconulid. Their apices are poorly defined contrary to M_1 . The hypoconulid is more distal than the two other cusps of the talonid. The entocristid is straight and aligned mesio-distally. The cristid obliqua is slightly oblique (distally shifted labially). The labial cingulids are well developed and are connected as on M_1 .

Discussion

The two teeth from Meudon MNHN ARP 5 (M_1) and M-13-G (M_1) (MP8+9, France) were not found during the same field campaign, but in the same facies ("Conglomérat de Meudon") and same locality. The other specimens here described and discussed are from Sinceny (MP8+9, France) and Abbey Wood (MP8+9, England).

Van Valen (1965) referred the specimens from Abbey Wood to cf. *Oxyaena* sp. Gunnell and Gingerich (1991) consider MNHN ARP 5 and BMNH M31877 as representatives of a small *Dipsalidictis* species, BMNH M13778 as a large *Dipsalidictis* species, and UCMP 83754 as a *Dipsalidictis* or *Oxyaena* species. Hooker (1998) considers BMNH M13778 and BMNH 31877 as European representatives of *O. gulo*, and UCMP 83754 as *Dipsalidictis transiens*.

The teeth have well-developed secant structures (e.g., very long postmetacrista and paracristid, trigonid on molars longer than wide), which clearly permit to refer them to the Oxyaeninae.

Oxyaena sp. has a paraconid more projected and a paracristid more elongated than in *Dipsalidictis*. The trigonid of the M_1 of *Oxyaena* sp. is distinctly longer than wide. This feature is distinct for *Oxyaena* (see above). It also shares with other *Oxyaena* species a reduced metaconid, equal in height to the paraconid and not projected lingually. The metaconid is even smaller than in some specimens of *O. gulo* (e.g., UM 63670).

The paraconid is broken on the M_2 . However, as noticed by Hooker (1998), the tooth belongs to the genus *Oxyaena*. The features shared with *Oxy-*

aena are the reduced metaconid compared to the protoconid, the talonid short and wide (but not as wide as the trigonid), the presence of well-developed postcingulid and ectocingulid.

In M_1 , the postmetacrista is more shifted distally than in *Dipsalidictis*. The preparacrista is also more reduced and the postmetacrista is longer than in *Dipsalidictis*. The ectoflexus and stylar shelf are narrower than in *Dipsalidictis*.

The derived morphology of the teeth of *Oxyaena* sp. permits to refer these teeth to the genus *Oxyaena* rather than to the primitive *Dipsalidictis*.

UCMP 83754 (M_1) from Sinceny is the only complete lower molar of an oxyaenine found in Europe, which is younger than the specimens of Le Quesnoy. UCMP 83754 is distinctly larger than the M_1 of *O. woutersi* from Le Quesnoy (27% longer). UCMP 83754 also differs from the M_1 of *O. woutersi* by a more secant morphology: the trigonid is longer than wide, the metaconid is more reduced (equal in height to the paraconid), the apex of the metaconid is projected less lingually and the paraconid is more shifted mesially. UCMP 83754 and MNHN ARP 5 (M_1 from Meudon) are clearly derived toward more shearing dentition compared to the M_1 of *O. woutersi*. The labial cingulid is more developed in the M_1 of *Oxyaena* sp. from Sinceny than on the one of Le Quesnoy. The M_1 of *Oxyaena* sp. is clearly more derived compared to the M_1 of *O. woutersi* because all its features (e.g., paraconid more projected mesially, metaconid reduced, ectocingulid more developed) are derived within the Oxyaeninae.

BMNH M13778 is the only M_2 of *Oxyaena* known for fossiliferous localities younger than Le Quesnoy in Europe. Compared to MNHN QNY2-2524 of *O. woutersi*, BMNH M13778 of *Oxyaena* sp. is distinctly larger (26% wider). BMNH M13778 has also more developed labial cingulid, reduced metaconid, and talonid shorter and wider. These are derived trends observed in the North American Oxyaeninae.

The upper molars of *Oxyaena* sp. from Meudon and Abbey Wood are distinctly bigger than those of *O. woutersi* (19% longer). *Oxyaena* sp. also differs by a more elongated and distally shifted postmetacrista, narrower stylar shelf, narrow ectoflexus, and very short parastyle. As for the lower molar of *Oxyaena* sp., all these features are derived within the Oxyaeninae.

We choose to group all the specimens in *Oxyaena* sp. despite their different origin, because they share similar morphology and derived features,

notably the mesial location of the paraconid on molars, and the elongation and distal location of the postmetacrista. Their derived features clearly distinguish the fossils of *Oxyaena* sp. from *O. woutersi*. The derived features are not restricted to *Oxyaena* sp. However they support a distinction between *Oxyaena* sp. from Meudon, Abbey Wood and Sinceny, and *O. woutersi* from Dormaal and Le Quesnoy. *Oxyaena* sp. is also larger than *O. woutersi*. Its size is closer to the oldest specimens of *O. gulo*. We prefer presently not to erect a new species because the specimens of *Oxyaena* sp. are fragmentary and few.

All the derived features of *Oxyaena* sp. (e.g., trigonid longer than wide on M₁, paraconid as high as the metaconid, cingulids developed, postmetacrista long and shifted mesially) are observed in *O. gulo*. However, UCMP 83754 shares with the M₁ of Le Quesnoy an unusual talonid, which distinguishes *Oxyaena* sp. from *O. gulo*.

- In the North American *Oxyaena* species, the entocristid and cristid obliqua are aligned mesio-distally.
- In the MNHN QNY2-2574 and UCMP 83754, the entocristid is oblique (mesially shifted labially), as the cristid obliqua (but distally shifted labially).

The combination of oblique entocristid and cristid obliqua, and the more distally projected hypoconulid, gives a rounded morphology to the talonid of the European *Oxyaena*. In the North American *Oxyaena*, the hypoconulid is more mesially located, and the talonid of the North American *Oxyaena* is wider and more squared. The M₁ from Sinceny appears to be morphologically closer to the European *O. woutersi* than to the North American *O. gulo*. This feature permits to distinguish *Oxyaena* sp. from *O. gulo*. The morphology of the talonid is the only present distinctive feature of the two European *Oxyaena* compared to *O. gulo*.

The two European *Oxyaena* species also share the absence of an individualized entoconid. In *O. gulo*, as in all younger North American *Oxyaena*, the entoconid is separated from the hypoconulid by a deeper notch than in *Dipsalidictis*.

The close entoconid/hypoconulid and the morphology of the talonid are primitive features within the Oxyaenidae: they are notably present in the oldest Oxyaenidae *Tythyaena lichna* (Rose, 1981) and in *Dipsalidictis*. The morphology of the European *Oxyaena* is primitive compared to *O. gulo*.

Oxyaena woutersi and *Oxyaena* sp. represent probably an endemic clade of *Oxyaena* characterized by the retention of primitive features (Figure 9). *Oxyaena* sp. is more derived than *O. woutersi* notably in having an M₁ more secant, which suggests that the evolution toward secant molars is convergent with the evolution observed in the North American *Oxyaena*. However, we prefer inclusion of the European oxyaenines within the single genus *Oxyaena*.

Conclusion on the European Oxyaeninae

The Oxyaeninae were poorly known before the discovery of Le Quesnoy material, because fossil oxyaenids are rare in Europe. The fossils from Le Quesnoy add further data on the dentition of the earliest European representatives of Oxyaenidae. Comparisons suggest that European *Oxyaena* represent a lineage different from North American *Oxyaena*. The two lineages from Europe and North America are derived from the same *Dipsalidictis* species: *D. transiens*. The difference between the North American and European *Oxyaena* lineages is based on the distinctive morphology of the talonid of M₁, which is more primitive in the European *Oxyaena*. However, the European *Oxyaena* species present other features related to the development of a specialized secant dentition. These features are similar to what is known in the North American *Oxyaena*, notably in the oldest species, *O. gulo*. Because of the more primitive morphology of *O. woutersi* compared to *Oxyaena* sp. from Meudon, Sinceny and Abbey Wood (e.g., M₁ wider than long in *O. woutersi*), we think that the development of secant structures in the European lineage is convergent with North American *Oxyaena*.

Aside from the development of the secant structures, European *Oxyaena* are characterized by an increase in the size; this is also observed for the North American *Oxyaena* (see Gunnell and Gingerich 1991). The larger size is recorded at the beginning of the MP8+9 with the fossils from Meudon, Abbey Wood and Sinceny. This species also corresponds to the last occurrence of Oxyaeninae in Europe.

Oxyaena woutersi and *Oxyaena* sp. provide evidence for an endemic evolution of the Oxyaeninae in Europe (Figure 10). This lineage supposes a single dispersal event of Oxyaeninae in Europe from North America, right near the Paleocene-Eocene boundary.

Subfamily AMBLOCTONINAE Cope, 1877
Genus *PALAEONICTIS* de Blainville, 1842

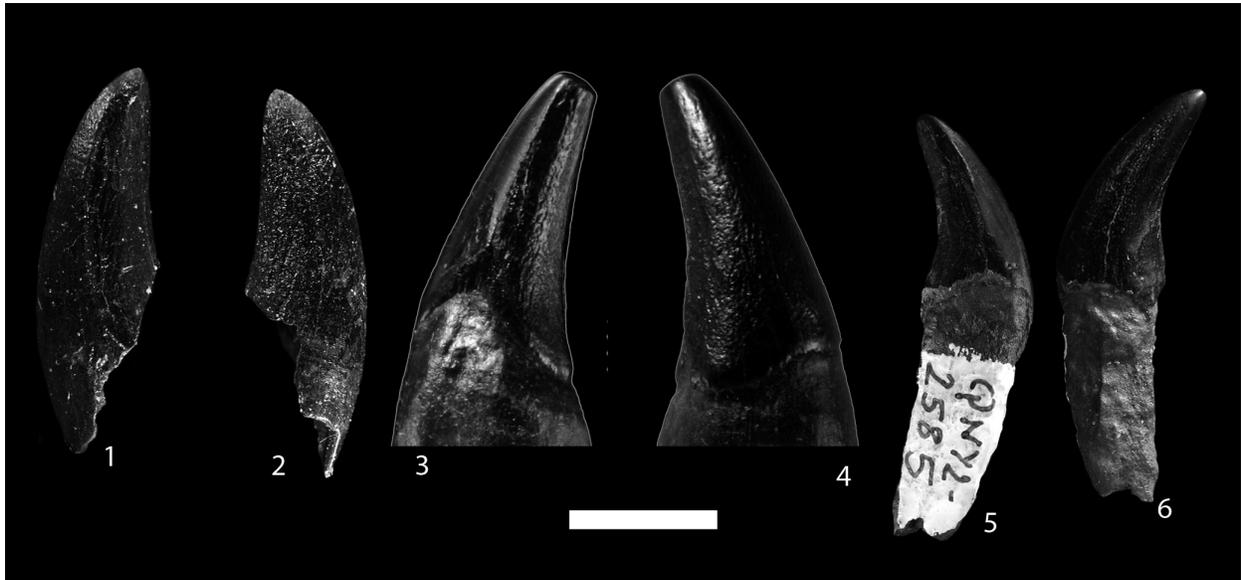


FIGURE 12. *Palaeonictis gigantea* de Blainville 1842. Isolated canine and incisor of *Palaeonictis gigantea* de Blainville 1842 from Le Quesnoy. 1-2. MNHN QNY2-2585, right I³ in 1. labial, 2. lingual views. 3-4. MNHN QNY2-2562, left C¹ in 3. lingual, 4. labial views. 5-6. MNHN QNY2-2626, right C¹ in 5. lingual, 6; labial views. Scale bar equals 10 mm.

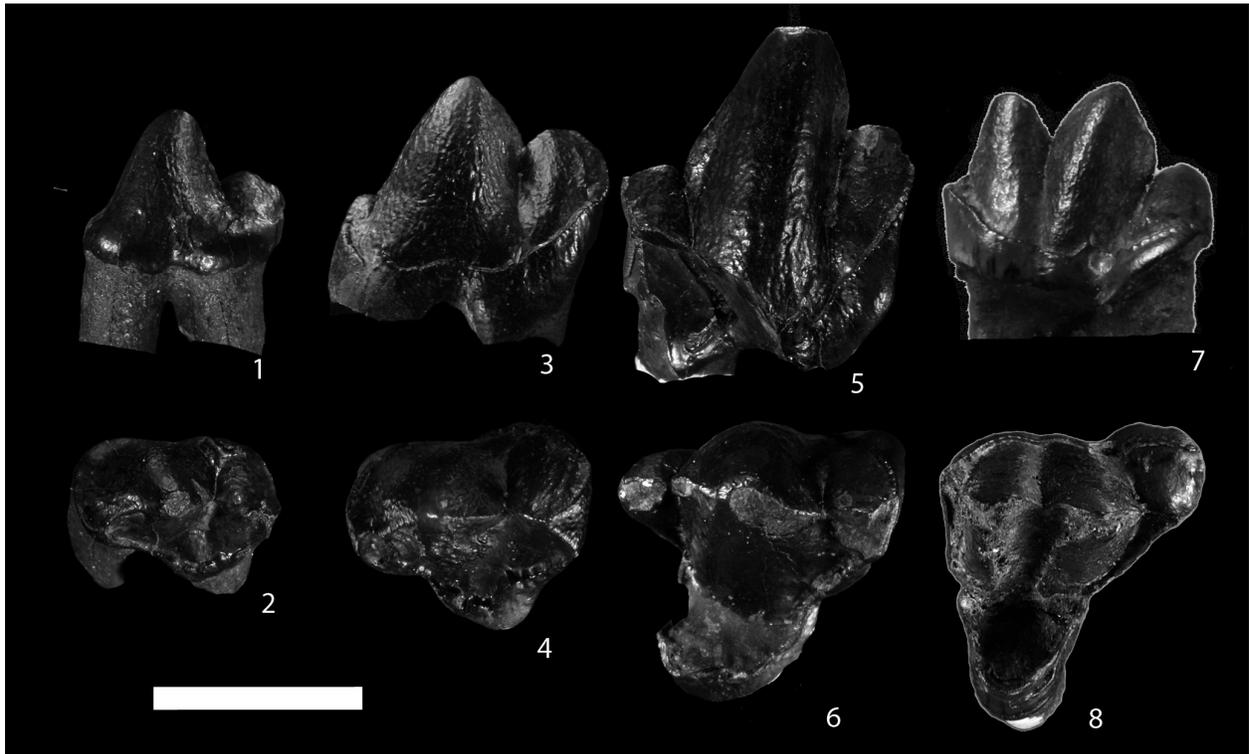


FIGURE 13. *Palaeonictis gigantea* de Blainville 1842. Reconstruction of the P²-M¹ series from isolated upper teeth from Le Quesnoy. 1-2. MNHN QNY2-2599, left P² in 1. labial, 2. occlusal views. 3-4. MNHN QNY2-2592, right P³ in 3. labial, 4. occlusal views. 5-6. MNHN QNY2-2564, right P⁴ in 5. labial 6. occlusal views. 7-8. MNHN QNY2-2567, right M¹ in 7. labial, 8. occlusal views. Reversed views: 1, 4, 6, 8. Scale bar equals 10 mm.

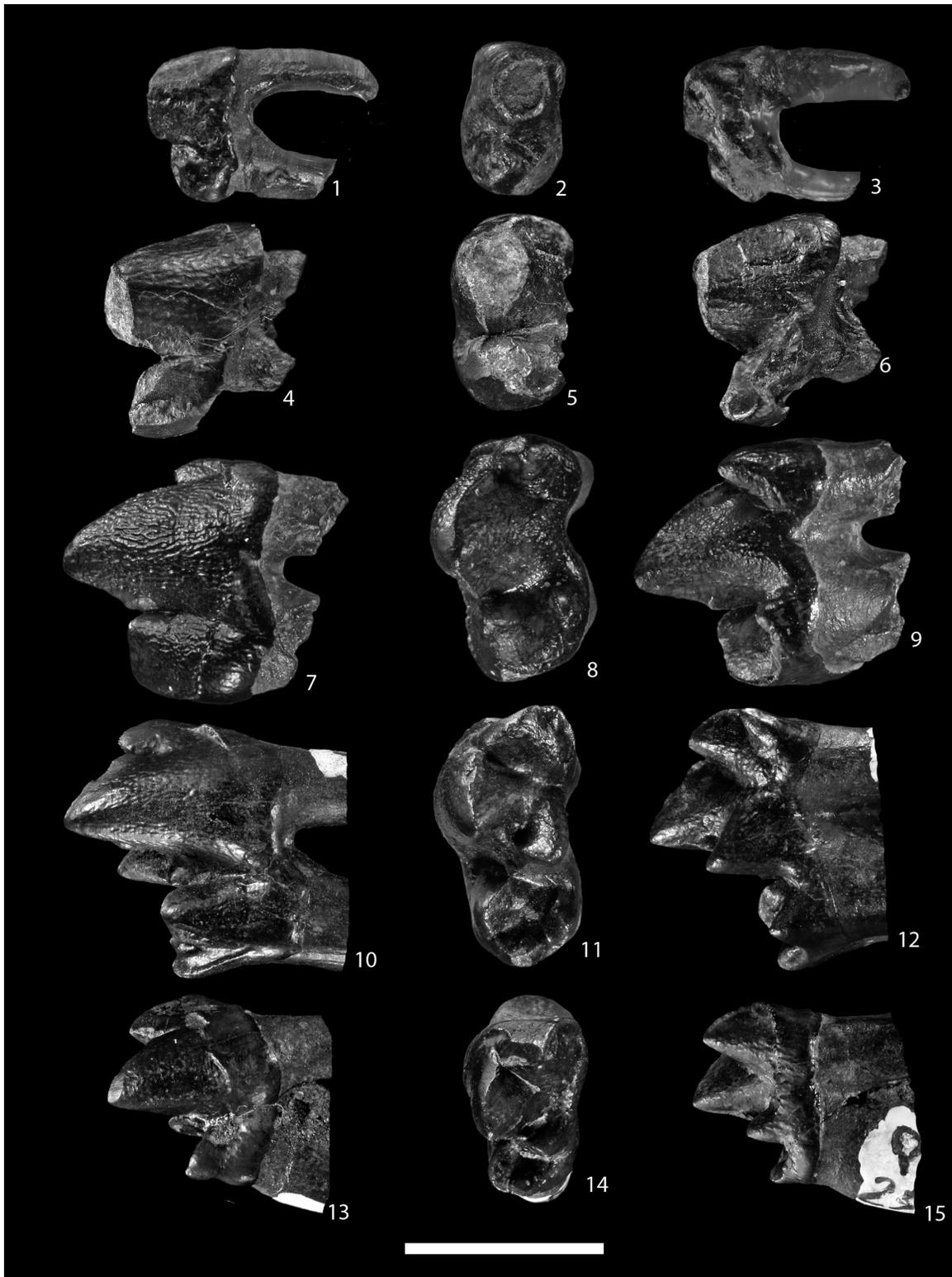


FIGURE 14. *Palaeonictis gigantea* de Blainville, 1842. Reconstruction of the P₂-M₂ series from isolated lower teeth from Le Quesnoy. 1-3. MNHN QNY2-2597, left P₂ in 1. labial, 2. occlusal, 3. lingual views. 4-6. MNHN QNY2-2591, right P₃ in 4. labial, 5. occlusal, 6. lingual views. 7-9. MNHN QNY2-2560, left P₄ in 7. labial, 8. occlusal, 9. lingual views. 10-12. MNHN QNY2-2550, left M₁ in 10. labial, 11. occlusal, 12. lingual views. 13-15. MNHN QNY2-2578, left M₂ in 13. labial, 14. occlusal, 15. lingual views. Reversed views: 1, 5-7, 10, 13. Scale bar equals 10 mm.

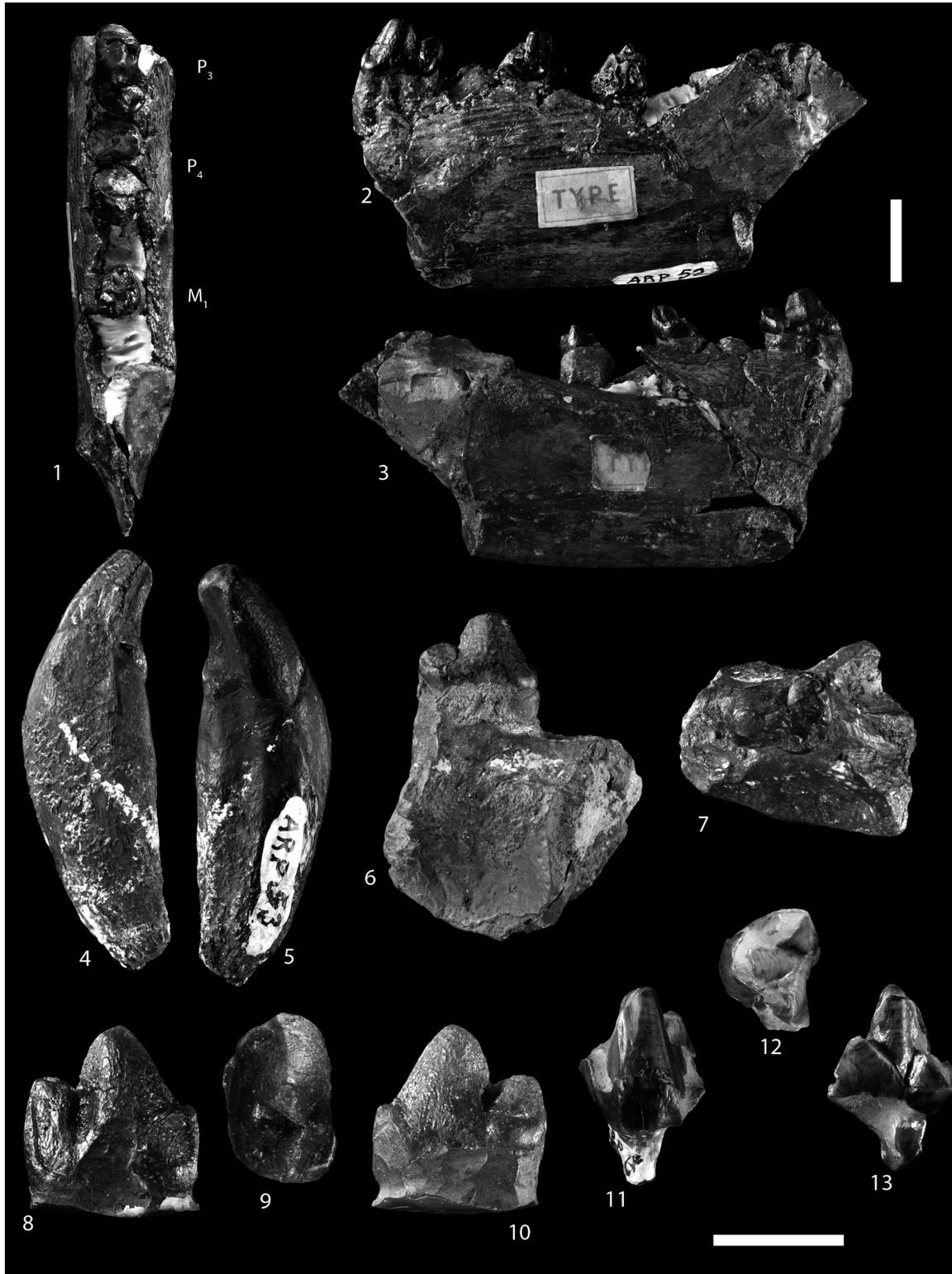


FIGURE 15. *Palaeonictis gigantea* de Blainville, 1842. 1-3. ARP 52 (Syntype), left mandible with P₃, P₄ talonid, and M₁ talonid in 1. occlusal, 2. labial, 3. lingual views. 4-5. ARP 53 (Syntype), left I³ in 4. labial, 5. lingual views. 6-7. ARP 54 (Syntype), left P² in 6. labial, 7. occlusal views. 8-10. L-PY-60 (cast), right P₄ in 8. labial, 9. occlusal, 10. lingual views. 11-13. ARP 6, left M₂ in 11. labial, 12. occlusal, 13. lingual views. Scale bar (top; 1-3): 10 mm. Scale bar (bottom; 4-13) equals 10 mm.

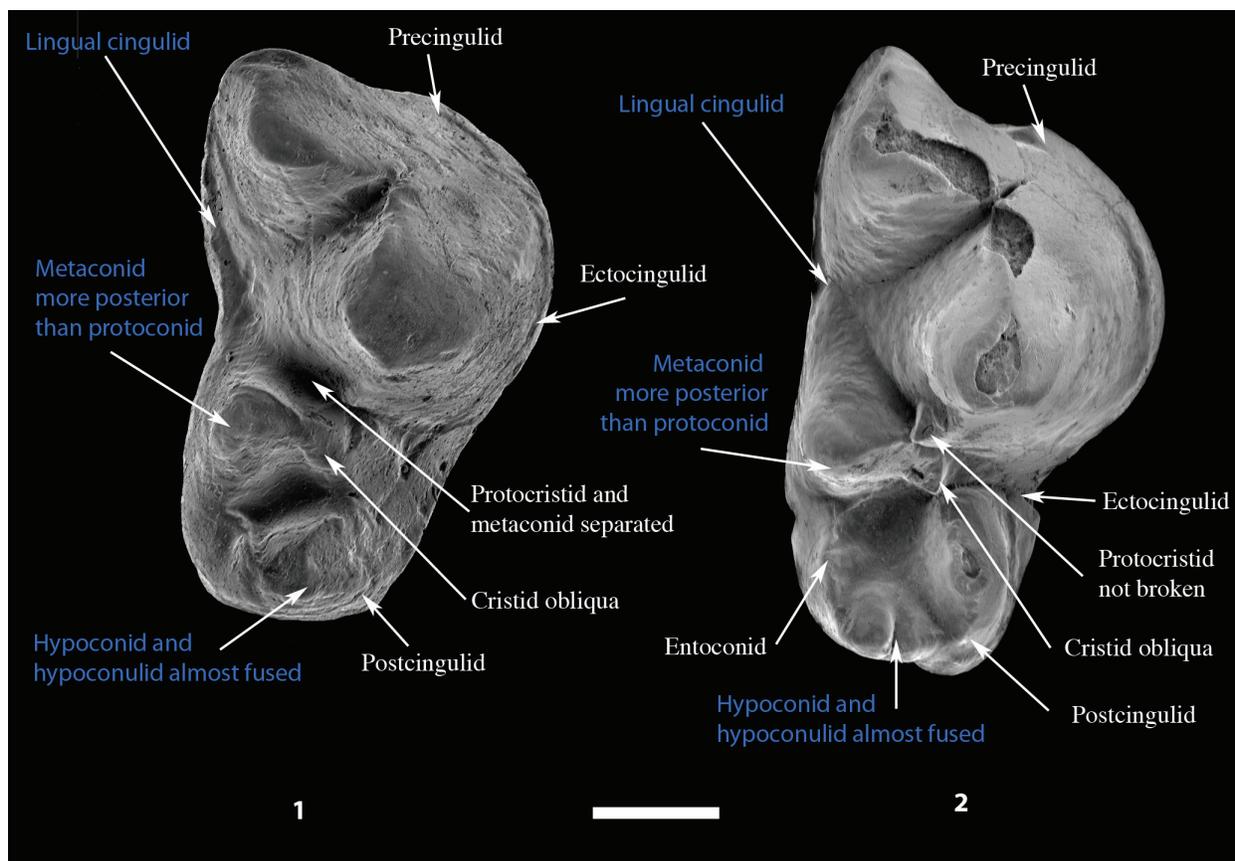


FIGURE 16. Comparison between 1. M_2 of “*Dormaalodon woutersi*” Lange-Badré, 1987 (IRSNB M1474) and 2. M_2 of *Palaeonictis gigantea* de Blainville, 1842 (MNHN QNY2-2513) in occlusal view. Characters noted in blue were used by Lange-Badré (1987) as diagnostic for *Dormaalodon woutersi* Lange-Badré, 1987. S.e.m. photographs. Scale bar equals 2 mm.

Diagnosis. *Palaeonictis* differs from *Dipsalodon* Jepsen, 1930 in having M_2 , much smaller than M_1 , in having a relatively smaller metaconid on M_2 , with a more open trigonid, and in having a less well-developed talonid on P_4 that lacks an entoconid cusp.

Type species. *Palaeonictis gigantea* de Blainville, 1842

Other species. *Palaeonictis occidentalis* Osborn and Wortman, 1892 ; *Palaeonictis peloria* Rose, 1981; *Palaeonictis wingi* Chester et al., 2010

Distribution. Late Paleocene-Early Eocene

Palaeonictis gigantea de Blainville, 1842
Figures 12, 13, 14, 15, 16 and 17

Synonymy.

v*1966 *Oxyaena* (?) *casieri* Quinet, p. 35, pl 5, figs. 4-6

v 1987 *Dormaalodon woutersi* Lange-Badré, p. 831, fig. 1

Syntypes.

MNHN ARP 52, left mandible with P_3 , P_4 talonid and M_1 talonid

I^3 , MNHN ARP 53 (L)

P^2 , MNHN ARP 54 (L)

Referred material from Le Quesnoy.

C^1 , MNHN QNY2-2562 (L), MNHN QNY2-2588 (R)

I^3 , MNHN QNY2-2581 (L), MNHN QNY2-2582 (R), MNHN QNY2-2583 (R), MNHN QNY2-2585 (R), MNHN QNY2-2601 (R)

P^2 , QNY1-1309 (L), MNHN QNY2-2589 (L), MNHN QNY2-2599 (L)

P^3 , MNHN QNY2-2555 (L), MNHN QNY2-2557 (L), MNHN QNY2-2559 (R), MNHN QNY2-2566 (R), MNHN QNY2-2592 (L)



FIGURE 17. *Palaeonictis gigantea* de Blainville, 1842. Postcranial elements of *Palaeonictis gigantea* de Blainville, 1842 from Le Quesnoy. 1-5. MNHN QNY2-2639, right radius in 1. posterior, 2. lateral, 3. anterior, 4. dorsal, 5. ventral views. 6-7. MNHN QNY2-2634, right humerus in 6. posterior, 7. anterior views. 8-10. MNHN QNY2-2604, left astragalus in 8. dorsal, 9. ventral, 10. lateral views. Scale bar equals 10 mm.

P₄, MNHN QNY2-2558 (R), MNHN QNY2-2563 (R), MNHN QNY2-2564 (R), MNHN QNY2-2587 (L)

M₁, MNHN QNY2-2567 (R), MNHN QNY2-2575 (R)

C₁, MNHN QNY2-2580 (R), MNHN QNY2-2621 (L), MNHN QNY2-2626 (R)

P₂, MNHN QNY2-2597 (L)

P₃, MNHN QNY2-2591 (R)

P₄, MNHN QNY2-2556 (L), MNHN QNY2-2560 (L)

M₁, MNHN QNY2-2550 (L), MNHN QNY2-2552 (R)

M₂, MNHN QNY2-2513 (R), MNHN QNY2-2576 (L), MNHN QNY2-2577 (R), MNHN QNY2-2578 (L)

Referred postcranial material from Le Quesnoy.

MNHN QNY2-2634, right distal humerus; MNHN QNY2-2639, right radius; MNHN QNY2-2604, left astragalus; MNHN QNY2-2605, left astragalus.

Referred material from Meudon.

M₁, MNHN ARP 6 (L)

Referred material from Pourcy.

P₄, MNHN L-PY-60 (R)

Type-locality. Muirancourt, Argiles à Lignites du Soissonnais (MP7) for MNHN ARP 52; unknown locality, Argiles à Lignites du Soissonnais (MP7) for MNHN ARP 53 and MNHN ARP 54.

Distribution. MP7, Muirancourt, Argiles à Lignites du Soissonnais, Le Quesnoy, Pourcy, Houdancourt (France), and Dormaal (Belgium); MP8+9, Meudon (France).

TABLE 6. Measurements (in cm) of the specimens of *Palaeonictis gigantea* de Blainville, 1842 from Le Quesnoy.

Locus		n	OR	M
I ³	L	4	0.554-0.642	0.598
	w	4	0.75-0.854	0.817
C ¹	L	1	1.126	-
	w	1	0.916	-
P ²	L	3	0.928-0.974	0.955
	w	3	0.62-0.702	0.667
P ³	L	3	1.328-1.466	1.388
	w	3	0.92-0.98	0.633
P ⁴	L	3	1.228-1.4	1.321
	w	2	1.336-1.338	1.337
M ¹	L	1	1.27	-
	w	1	1.48	-
C ₁	L	1	1.17	-
	w	1	0.956	-
P ₂	L	1	0.806	-
	w	1	0.53	-
P ₃	L	1	1.08	-
	w	1	0.736	-
P ₄	L	2	1.266-1.298	1.282
	w	2	0.76-0.806	0.733
M ₁	L	2	1.3-1.35	1.325
	w	2	0.72-0.746	0.733
M ₂	L	4	0.942-1.048	0.981
	w	4	0.57-0.654	0.617

Description of the dental material from Le Quesnoy

Measurements: Table 6

Upper dentition. Incisors: The I³ is caniniform and has a robust root. The tooth is very curved lingually. The main feature is the presence of a very strong wear facet in the disto-lingual part of the tooth. This facet is due to the occlusion with the lower canine, which indicates a strong occlusion of the anterior teeth.

Canines: Two specimens are known. The tooth is distinctly bigger than in *O. woutersi*. They are oval in horizontal section. The root is very large. The cingulum is poorly developed. However, it rises a little in the lingual part of the tooth and continues as a crest. The tooth is straighter than the lower canines, and the apex is slightly more shifted lingually. There is a second carina in the disto-lingual

face of the tooth. A wear facet is present in the mesio-labial part of the tooth.

Premolars: The P², P³ and P⁴ are known. Their size increases with the distal rank. The P² and P³ are two-rooted; the P⁴ has three roots. The premolars share the same pattern. The paracone is large and bulbous. Its apex is tilted distally (also slightly lingually on P² and P³). The parastyle is only marked by a fold in the mesio-lingual part of the tooth on P² and P³ - it is slightly more developed on P³, and much more developed and individualized on P⁴, where it is located mesial to the paracone. It reaches one-third the size of the paracone. The postmetacrista is very short and bulbous on all premolars. It reaches half the height of the paracone on P⁴. The protocone is marked on P² and P³ by a little fold. On P⁴, the protocone is well developed and functional. It is lower than the paracone, as seen on M¹. The protocone is slightly shifted mesially. A thin cingulum surrounds the teeth. It elevates distally to the postmetacrista and on P⁴ also mesially to the paracone.

Molars: Only M¹ is known in Le Quesnoy. The paracone and metacone are robust and almost fully separated. The styler shelf is absent. Only a little cingulum links labially the parastyle to the metastyle. The preparacrista is very reduced. Only a small enamel fold at the half height of the paracone represents the parastyle. The postmetacrista is more developed than the preparacrista, but very poorly elongated compared to what is seen in *Oxyaena*. The postmetacrista is almost aligned with the paracone and metacone. It is more than half the size of the metacone. The metacone is slightly higher than the paracone and also slightly larger. The protocone is lower than the labial part of the tooth. It is wider labio-lingually than mesio-distally. The metaconule and paraconule are present and well developed. They are connected respectively to the postmetacrista and preparacrista. No internal crest is present. The protocone is very weakly shifted mesially. The pre- and postcingulum are present but are poorly developed; they are linked lingually.

Lower dentition. Canines: Three lower canines are known. These teeth are more curved and slightly larger than the upper canines. Two crests are present in the lingual part and in the disto-labial part. On MNHN QNY2-2621 and MNHN QNY2-2580, a strong wear facet is visible in disto-labial position. This facet results from the occlusion with the upper canine. Another wear facet is visible on

the mesio-labial part of the tooth, as the result from the occlusion with the I³.

Premolars: As for upper premolars, the first premolar is unknown. The size of lower premolars increases with the distal rank. The teeth are two-rooted. The protoconid, which is very bulbous, constitutes the main structure of the teeth. The protoconid is tilted posteriorly and labially on P₃ and P₄ (probably also on P₂). The paraconid is marked by a fold in the mesio-lingual facet of the protoconid in P₂ and P₃. On P₄ it is well individualized. It is less high than the talonid. The talonid is short and bulbous. It reaches half the size of the protoconid. It is constituted by a single cusp (hypoconid) distally shifted lingually. It is separated from the protoconid by a carnassial notch. It is more shifted on P₃ and P₄ than on P₂. The talonid on P₄ is variable. The talonid extends up distally in MNHN QNY2-2556 and extends down in MNHN QNY2-2560. On P₄, an entoconid is present lingually. A cingulid surrounds the tooth on P₂ and P₃. Only a labial cingulid runs from the labial facet of the paraconid to the hypoconid on P₄.

Molars: The M₁ and M₂ are known. The teeth are two-rooted. The posterior root of M₂ is elongated mesio-distally. Contrary to *O. woutersi*, the M₁ is wider and higher than the M₂, and it represents the carnassial tooth. In M₁, the paraconid and metaconid have nearly the same height. The apices of the two cusps are very divergent. The pre-fossid is closed lingually by a small contact of the bases of paraconid and metaconid. The metaconid apex is distinctly more distal than the protoconid apex. The paraconid apex is much less lingual than its base. The paracristid is very short and almost transverse. These characteristics explain the shortness of the paracristid, almost only constituted by the protoconid crest. The paracristid and protocristid present a carnassial notch. There is an accessory cusp "e" in the mesio-lingual face of the paraconid. The protoconid is also very bulbous with a well-developed base. It is higher (but not very much) than the other cusps. The talonid is narrower and shorter than the trigonid. The talonid bears three well developed and separated cusps. All the cusps are high, the hypoconid being the highest. The hypoconulid is more distal than the two other cusps. Its distal facet is almost straight. The hypoconid is slightly more mesial than the entoconid. The cristid obliqua is very oblique (distally shifted labially). A carnassial notch is present near the trigonid. The cristid obliqua rises very high

on the distal facet of the trigonid toward the apex of the metaconid. The entocristid is aligned with the mesio-distal axis. The pre-, ecto- and postcingulid are present. Another cingulid runs lingually from the cusp "e" to the base of metaconid. M₂ looks like M₁. The apex of the paraconid is less lingual than its base, and the mesio-lingual facet is curved. The crest of the paraconid is less reduced than on M₁ but is also transverse. The metaconid apex is more distal than that of the protoconid. The metaconid is also distinctly smaller than the paraconid. The pre-fossid is opened: the base of the protoconid separates the paraconid and the metaconid. The protoconid is bulbous and not much higher than the paraconid. The paracristid and protocristid present a carnassial notch. The accessory cusp "e" in the mesio-lingual flank of the paraconid is less individualized than on M₁. The principal difference between the M₁ and M₂ is that the talonid is narrower, shorter and smaller than the trigonid on M₂. Only the hypoconulid and hypoconid are well developed on the talonid of M₂, and the two cusps are distally placed. They tend to fuse in some teeth (MNHN QNY2-2513). On some specimens, where the fusion is the less pronounced, an entoconid is visible. The cristid obliqua is oblique (distally shifted labially) and, on some teeth, it joins the apex of the metaconid. A carnassial notch is present. The distal facet of the talonid is very straight. The cingulids are similar to what is seen on M₁ (pre-, ecto- and postcingulid and labial cingulid between the cusp "e" and base of the metaconid).

Description of the Material from the Syntypes

Measurements: Table 7

Upper dentition. MNHN ARP 53 and MNHN ARP 54 have not been described by de Blainville (1842). These fossils may have been added posteriorly to the syntypes of *P. gigantea*. Their colours and appearance agree with fossils from the Argiles à Lignites. However, the exact locality remains unknown for them.

Incisive: MNHN ARP 53 represents an I³. This tooth is characterized by a strong occlusal facet in the disto-labial part of the tooth, which is caused by the occlusion with the lower canine as discussed above. MNHN ARP 53 does not differ from the fossils from Le Quesnoy, except by a slightly larger size.

Premolars: MNHN ARP 54 is a left fragment of maxillary with P². MNHN ARP 54 is also indistinguishable from MNHN QNY2-2597 of Le Quesnoy.

TABLE 7. Measurements (in cm) of the specimens of *Palaeonictis gigantea* de Blainville, 1842 from Paris Basin (except Le Quesnoy).

Number	Locality	Locus		Measurement
MNHN ARP 53	Argiles à Lignites	I ³	L	0.840
			w	0.554
MNHN ARP 54	Argiles à Lignites	P ₂	L	0.888
			w	0.610
MNHN ARP 52	Muirancourt	P ₃	L	1.062
			w	0.668
		P ₄	L	1.370
			w	0.664*
		M ₁	L	1.148**
			w	0.530**
MNHN ARP 6	Meudon	M ₁	L	-
			w	0.790
MNHN L-Py-60	Pourcy	P ₄	L	1.324*
			w	0.746

*: Estimated on the basis of the roots; **: estimated on a fragmentary specimen.

Lower dentition. Premolars and molars: MNHN ARP 52 corresponds to a fragmentary mandible. This fossil is the type of *P. gigantea* and was previously described by de Blainville (1842). Since this work, the fossil has been broken up. No foramen is visible on this fragment of mandible. The mandible is deep and robust as in all *Palaeonictis*. The lingual part is more robust than the labial part. The teeth are inserted in a parabolic way.

The first tooth of the specimen MNHN ARP 52 is a P₃. The morphology of the tooth (e.g., presence of a small paraconid) agrees with the P₃ of *P. occidentalis* and P₃ found in Le Quesnoy. The P₃ is the sole complete remaining tooth. The P₃ is robust and, as all the other teeth, has a crenulated enamel. The protoconid is bulbous. There is a paraconid mesio-lingually located. The paraconid is separated from the protoconid by a distinct notch and is one-third the size of the protoconid. The talonid is also separated from the protoconid by a notch. The talonid is half the size of the protoconid in height and length. However, the talonid is wider than the protoconid, notably lingually. The talonid has only one cusp. It is oblique (distally shifted lingually). Its distal part is higher than the mesial part. A cingulid is present lingually. Labially, only precingulid and postcingulid are present. They are not linked by an ectocingulid. On the lingual part of the talonid, two very small accessory cusps are present. They are located at the usual place of the

entoconid on the P₄. The P₃ preserved on MNHN ARP 52 only differs from the P₃ found in Le Quesnoy (MNHN QNY2-2591) by more developed paraconid and cingulids. The talonid of the P₄ is similar in structure to the talonid of P₃. The P₄ of MNHN ARP 52 differs also from the P₄ found in Le Quesnoy by a more pronounced cingulid around the talonid and less pronounced entoconid in the lingual part of the talonid. Our observations of the specimens of *Palaeonictis occidentalis* housed in the collections at the University of Michigan document that these characters are highly variable in this species. However, this reflects a tendency toward the reduction of the entoconid: in *Dipsalodon*, the entoconid is more elevated, while it is absent in the younger *Ambloctonus* Cope, 1875. As for the P₄, only the talonid is available for the M₁. The talonid of the M₁ has the same morphology as the fossils from Le Quesnoy. The derived genus *Ambloctonus* is characterized by an entoconid well isolated and low. This feature is not visible in MNHN ARP 52, as usually observed on M₁ of *Palaeonictis*.

Description of the Material from Meudon

Measurements: Table 7

Lower dentition. Molar: MNHN ARP 6 is a trigonid of first lower molar. MNHN ARP 6 is characterized by ambloctonine features such as the metaconid

distal to the protoconid and the trigonid robust. The strong specialization of the basic trigonid structure (metaconid well distal, very short and labial paraconid) permits reference of this tooth to the genus *Palaeonictis* rather than *Dipsalodon*. *Ambloctonus* differs in the cusps of the trigonid, which are nearly similar in size. MNHN ARP 6 remains primitive compared to *Ambloctonus*. MNHN ARP 6 very slightly differs from the M_1 found in Le Quesnoy by a metaconid more distal, an apex less projected lingually, a paraconid less lingual, a more pronounced labial cingulid and a prefossid more opened. These correspond to trends observed in North American *Palaeonictis* toward the unusual dentition of *Ambloctonus*. MNHN ARP 6 from Meudon is slightly more derived than the specimens from Le Quesnoy. However, MNHN ARP 6 is not distinctly larger than the M_1 from Le Quesnoy of *Palaeonictis gigantea*. As we do not know the entire dentition of this taxon and its variability, we refer MNHN ARP 6 to *P. gigantea*.

Description of the Material from Pourcy

Measurements: Table 7

Lower dentition. Premolar: The P_4 MNHN L-Py-60 from Pourcy is slightly larger than the fossils from Le Quesnoy, but slightly smaller than the P_4 of MNHN ARP 52 from "Argiles à lignites". A broken part suggests an individualized paraconid. MNHN L-Py-60 is referred by Gunnell and Gingerich (1991) to *Dipsalidictis*. By contrast this fossil is considered here as representative of *Palaeonictis*. MNHN L-Py-60 differs from *Dipsalidictis* species in being much more robust and in possessing a talonid much wider than the trigonid. It differs from *Oxyaena* by a talonid expanded lingually. In *Oxyaena* the talonid is widened lingually but also labially. Moreover, the tooth is more similar in size and structure to the P_4 of *Palaeonictis* found in Le Quesnoy, than to those of *Oxyaena*. It notably presents some small accessory cusps on the lingual part of the talonid. No similar cusps are visible on the P_4 of *Oxyaena* and *Dipsalidictis*. MNHN L-Py-60 is similar to MNHN ARP 52 in having a shorter talonid than in the P_4 from Le Quesnoy. The cingulids are less developed on MNHN L-Py-60 than on MNHN ARP 52 and recalls more the fossils from Le Quesnoy.

Affinities of *Dormaalodon*

In Dormaal, Lange-Badré (1986, 1987) has described a new genus, *Dormaalodon* Lange-Badré, 1987 from a very peculiar lower molar. This

genus has been only found in Dormaal. Lange-Badré (1987) described the lower molar (IRNSB M 1474) as the holotype and only known specimen of the ambloctonine *Dormaalodon woutersi*. This tooth presents some puzzling characters: metaconid posteriorly located, separated from the protoconid and integrated to the talonid; absence of entoconid; cingulid well developed, which reaches lingually the metaconid (Figure 16). The molar is considered by Lange-Badré (1987) as a M_1 because of the presence of a posterior interdental facet indicating a contact with a posterior molar, the M_2 . Our observations do not confirm the occurrence of this facet, and there are no features supporting IRNSB M 1474 as a M_1 . Comparison with the M_2 of *Palaeonictis gigantea* found in Le Quesnoy shows that IRNSB M 1474 is slightly shorter, as for the P_4 of Dormaal.

IRNSB M 1474 presents an important wear: notably the mesio-labial facet of the paraconid and protoconid (wear facet 2), distal facet of the trigonid (wear facet 1) and mesio-labial facet of the hypoconid (wear facet 3), which are very marked; for instance, the hypoconid is even partially truncated (Figure 16). These facets are similar to those observed on the M_2 from Le Quesnoy. Wear facet 3 is caused by the occlusion with the paracone of the M_2 . We can note the high development of the cristid obliqua, which runs along the distal facet of the trigonid toward the carnassial notch of the protocristid and apex of metaconid. The cristid obliqua visible on the M_1 is less developed than on M_2 but presents an almost similar morphology. Wear facet 1 is caused by the long and robust paracrista of the M_2 . Wear facet 2 is caused by the poorly elongated but high and robust postmetacrista and metacone of the M_1 . Wear facet 4 of the M_1 is caused by the occlusion with the metacone, which has almost the same size as the paracone on M_1 . This facet is not present on the M_2 from Le Quesnoy nor is it present on the only known molar of *Dormaalodon* due to the reduction of the metacone of the M_2 in the Oxyaenidae.

Contrary to IRNSB M 1474, the protocristid is not broken on the M_2 found in Le Quesnoy. The metaconid is linked to the protoconid and not included in the talonid. The cristid obliqua is well developed and, on some M_2 , it reaches the apex of the metaconid through the carnassial notch of the protocristid as on IRNSB M 1474 (Figure 16). On IRNSB M 1474, the inclusion of the metaconid to the talonid can be explained by the broken protoc-

ristid (effect of the wear facet 1) and strong development of the cristid obliqua.

On IRNSB M 1474, the hypoconid and hypoconulid are more or less fused in disto-lingual position as on some M_2 of Le Quesnoy. On the M_1 of ambloctonines, the talonid cusps are more developed and separated. The talonid is also wider and more basined.

IRNSB M 1474 and the M_2 of *P. gigantea* of Le Quesnoy also share: a metaconid more reduced than on M_1 and posterior to the protoconid, a prefossid well opened, a pre-, ecto- and postcingulid, and a lingual cingulid running from the base of the paraconid to the apex of metaconid.

The similarities of size, wear pattern and morphology with Le Quesnoy material support the identification of IRNSB M 1474 as an M_2 of *Palaeonictis gigantea*. *Dormaalodon woutersi* is here recognized as a junior synonym of *Palaeonictis gigantea*.

Discussion

de Blainville (1842) has described the first Ambloctoninae, *Palaeonictis gigantea* from a mandible MNHN ARP52 found near Paris in the "Argiles à lignites du Soissonnais". Even though some other specimens have been found during the XIXth century in the Paris Basin (Rat 1965), the European ambloctonines are very rare and poorly studied. The most recently described specimens of *Palaeonictis gigantea* (one P_4 and one DP_4) have been found in the Belgian localities of Dormaal and Hoegaarden (Smith and Hooker 1996; Smith and Smith 2001).

Our study of the material previously described from "Argiles à lignites" (MNHN ARP 52, MNHN ARP 53, MNHN ARP 54), Meudon (MNHN ARP 6) and Pourcy (MNHN L-Py-60) shows that these specimens are similar to the fossils found in Le Quesnoy. Contrary to the *Oxyaena* material, there are no distinctive characters which justify a specific separation of specimens from localities younger than Le Quesnoy (such as Meudon, Muirancourt and Pourcy). The specimens from these younger localities are slightly larger than those of Le Quesnoy. They also differ from the material of Le Quesnoy by a few features (e.g., metaconid more distal on M_1 , more pronounced labial cingula on premolars and molars) that correspond to trends observed in the North American ambloctonines.

Three genera of Ambloctoninae are known in North America: *Dipsalodon*, *Palaeonictis* and

Ambloctonus. Those genera form a lineage characterized notably by the reduction of the M_2 and of its talonid, by lower molar trigonid more secant with a reduction of the metaconid and by a molarization of the P_4 . Some of these features are probably linked to an omnivorous or durophagous diet.

The M_2 found in Le Quesnoy shows a reduced talonid and metaconid much more similar to *Palaeonictis* than to *Ambloctonus* and *Dipsalodon*. Four species of *Palaeonictis* are known: *P. gigantea* (MP7) from Europe; *Palaeonictis peloria* Rose, 1981 (Cf3), *Palaeonictis occidentalis* Osborn and Wortman, 1892 (Wa1-Wa4) and the recently described *Palaeonictis wingi* Chester et al., 2010 (Wa0) from North America. *P. peloria* is the oldest and biggest, and *P. wingi* is the smallest (Rose 1981; Chester et al. 2010).

The P_4 found in Le Quesnoy is morphologically close to *P. gigantea* known from Dormaal (IRSNB M1355) and the Paris Basin (MNHN ARP 52). It is slightly longer (almost 10%; Tables 6 and 7) than those of Dormaal and Paris Basin. The P_4 MNHN QNY2-2560 has a talonid slightly longer relative to the protoconid than seen in IRSNB M1355 and P_4 of the type of *P. gigantea*. The P_4 MNHN QNY2-2556 is more similar to the last two specimens. These slight differences do not justify the erection of a new species because the talonid of the P_4 seems to be variable and because we do not know the variation of size of *Palaeonictis* from Dormaal and the "Argiles à lignites du Soissonnais". The talonid of the M_1 from Le Quesnoy is very similar to the type specimen studied by de Blainville (1842). The larger size of Le Quesnoy fossils is within the size variation of the Ambloctoninae. In *P. occidentalis*, the difference in size can reach 16% for the M_1 (calculated after Rose 1981, table 34).

Rose (1981) and Smith and Smith (2001) proposed to root *P. gigantea* in the Paleocene *P. peloria* (Cf3), the older and most plesiomorphic species known in North America for this genus. Chester et al. (2010) proposed that *P. peloria* gave rise to *P. gigantea* and *P. wingi*.

- The P_4 is smaller compared to M_1 than in *P. occidentalis* and is also less molarized. The P_4 of *P. gigantea* is morphologically similar to *P. peloria*.
- In *P. gigantea* the ratio of M_1/M_2 is close to 1.36. This is intermediate between *P. peloria* (1.14) and *P. occidentalis* (1.34-1.44). This ratio is close to those calculated for *P.*

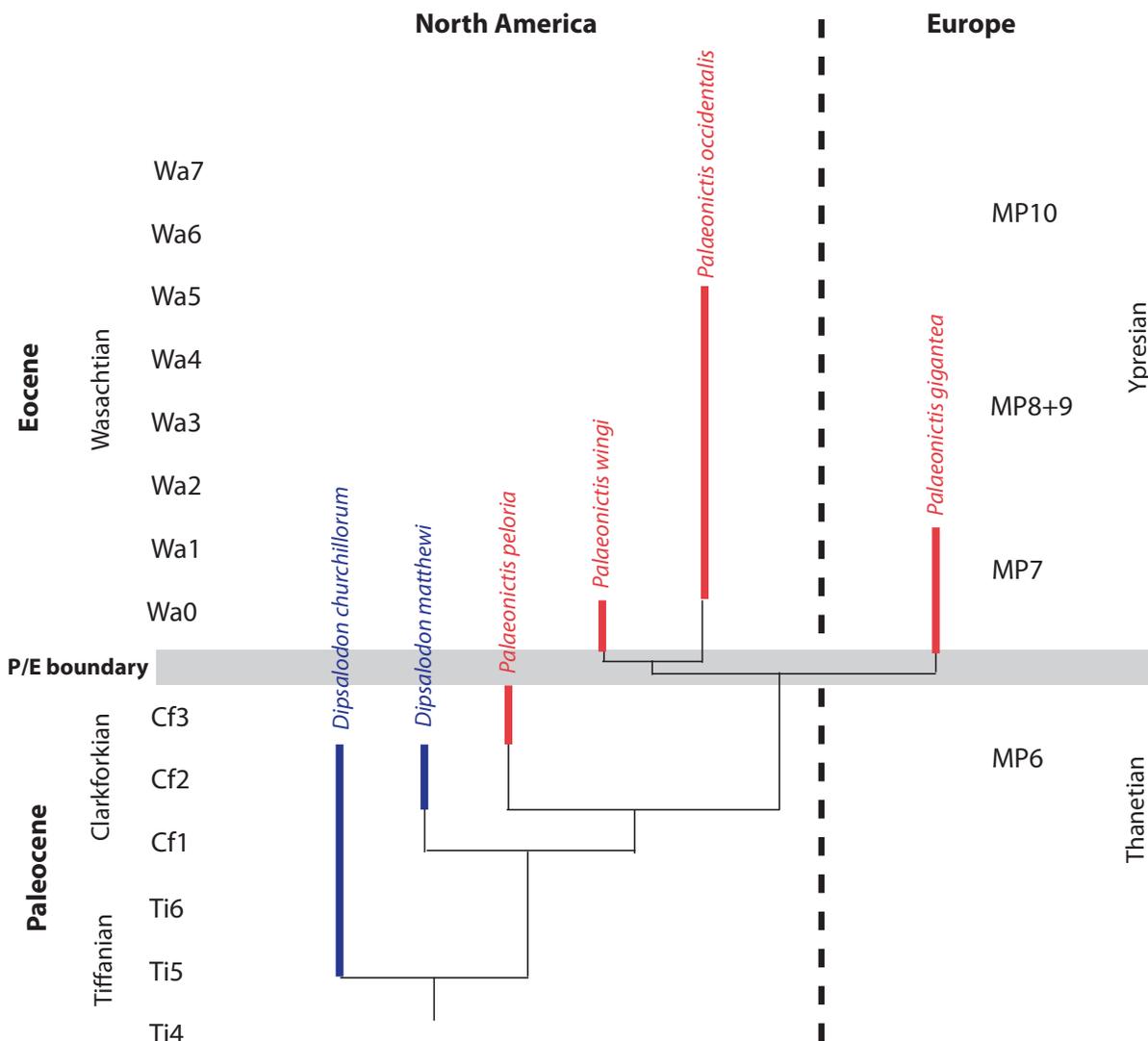


FIGURE 18. Phylogenetic relationships of Ambloctoninae with indications of stratigraphic and geographic repartition of the Late Paleocene and Early Eocene *Dipsalodon* and *Palaeonictis*. The phylogenetic relationships are based on Gunnell and Gingerich (1991) and Gunnell (1998). Note: *Dipsalodon* is a paraphyletic genus.

wingi (1.26 for left M₁-M₂ and 1.34 for right M₁-M₂). The reduction of the size of the M₂ is less important in *P. gigantea* and *P. wingi* than in *P. occidentalis*.

- The entoconid of the M₁ is less developed than in *P. peloria*, but more developed than in *P. occidentalis*. The entoconid of M₁ tends to reduce in Ambloctoninae. *P. gigantea* and *P. wingi* differ from *P. occidentalis* by less developed labial cingulids on M₁. This feature is primitive.
- *P. gigantea* and *P. peloria* are similar in the lesser reduction of the talonid of the M₂

and metaconid of M₁ and M₂, and in the narrower cheek teeth compared to *P. occidentalis*. *P. wingi* differs from *P. gigantea* and *P. peloria* by a more reduced metaconid on M₂ (Chester et al. 2010). In *P. gigantea* the talonid of the M₂ is less reduced, and the talonid of the M₁ is narrower and shorter than in *P. occidentalis* (Wa1-Wa4). The talonid reduction in M₂ and enlargement in M₁ are trends in the evolution of the Ambloctoninae. In these regards, *P. gigantea* is slightly more derived than *P. peloria*. However, *P.*

TABLE 8. Measurements of the postcranial material of *Palaeonictis gigantea* de Blainville 1842 from Le Quesnoy.

Humerus	Incomplete
Maximum transverse width of the distal extremity	3.54
Transverse width of the distal articular surface in distal view	2.24
Antero-posterior depth of the trochlea in distal view	0.81
Transverse width of the capitulum in anterior view	1.39
Proximal height of the capitulum in anterior view	1.02
Radius	
Total length	10.2
Anteroposterior length of the head	2.10
Transverse width of the head	1.28
Distance between the apex and the centre of the bicipital tuberosity (DFR)	1.72
Anteroposterior depth of the diaphysis at the level of the bicipital tuberosity	1.03
Mid-shaft anteroposterior diameter	0.92
Mid-shaft transverse diameter	0.99
Anteroposterior length of the distal extremity	1.69
Transverse width of the distal extremity	2.15
Astragalus	
Total length	3.15
Maximum transverse width	2.33
Astragalotibial length	1.23
Astragalotibial width	1.64
Astragalar head width (anterior view)	1.82
Astragalar head height (anterior view)	0.84

gigantea remains less advanced than *P. occidentalis* for all the following characters.

- The parastyle of P⁴ and M¹ is more reduced than in *P. peloria* but less than in *P. occidentalis*.
- In correlation to the wider talonid of P₄ and M₁, the protocone of P⁴ and M¹ are larger and more elongated mesio-distally than in *P. peloria*. The entoconid on P₄ is less important than on *P. occidentalis*.

P. gigantea and *P. wingi* are both characterized by a small size compared to *P. peloria* and *P. occidentalis*. However, *P. gigantea* differs from *P. wingi* by a more reduced P₃ (derived feature also present in *P. occidentalis*; see Chester et al. 2010). Contrary to Chester et al. (2010), we consider that the relative development of the precingulid on P₃ does not permit to distinguish *P. gigantea* and *P. wingi*, because this feature is highly variable in *P. gigantea* (paraconid developed on MNHN ARP 52 vs. very small on MNHN QNY2-2591).

P. gigantea is, in accordance to Rose (1981) and Smith and Smith (2001), closer to *P. peloria*

than to *P. occidentalis* (Figure 18). It is more derived (e.g., reduction of the M₂, reduction of the talonid of the M₂) and smaller than the earlier *P. peloria*. Its size and features (e.g., reduction of the M₂) indicate a close relationship with the recently described *P. wingi*. The two species, in accordance to Chester et al. (2010), originated in *P. peloria*. The small size of the two species could have been the result of an evolutionary “Dwarfing” event that occurred during the PETM (see Chester et al. [2010] for a discussion).

Description of the Referred Postcranial Material from Le Quesnoy

Measurements: Table 8

Forelimb. MNHN QNY2-2634; right distal humerus. This humerus is larger than the humerus of *Oxyaena woutersi* (QNY2-2526). Only a distal fragment is known. The medial epicondyle area is broken. In medial and lateral views, the fragment appears to be almost flat. The trochlea is slightly projected anteriorly. The elbow joint is weakly elongated transversally. The trochlea is well developed and bears a deep and concave posterior trochlear

groove. The capitulum is small and almost flat. The medial lip of the trochlea is high. In anterior view, there is only a wide and transversally elongated coronoid fossa. The radial fossa is not visible (fused with the coronoid fossa?). No foramen is present on the fossa. The pit for attachment of an ulnar collateral ligament is deep and clearly visible in posterior view. The olecranon fossa is deep and transversally wide.

MNHN QNY2-2639; right radius. The radius is complete. The distal epiphysis is unfused, which indicates a juvenile individual. The diaphysis is slightly twisted. The distal part is more robust than the proximal part. The radial head is oval and transversally elongated. The capitular eminence is present, elongated and not very salient proximally. The ulnar proximal facet is slightly concave. There is a well-developed bicipital tuberosity. The area for insertion of the pronator teres is well developed and is curved. The ulnar distal facet is present and slightly concave. The distal part of the radius is more triangular and massive. It is elongated mediolaterally and is moderately deep and concave – the deeper part being near the styloid process. The styloid process is low. The tubercle of the radius (origination of the abductor pollicis longus) is well developed dorsodistally.

Hindlimb. MNHN QNY2-2604, MNHN QNY2-2605; two left astragali. Two complete astragali are known. The astragalus is slightly elongated antero-posteriorly and appears to be robust. The astragalar trochlea for the articulation with the distal tibia is very poorly grooved. The body is wide mediolaterally and short anteroposteriorly. The neck is slightly narrower. It is also very short anteroposteriorly. The head is anteroposteriorly wide and short. It is convex anteriorly. It is less flattened dorsoventrally than in the astragalus of *Oxyaena*. The astragalar foramen is weakly shifted posteriorly. In medial view, the medial part is lower than the lateral one. The medial surface is laterally extended. In dorsal view, the medial side is salient medially: this could represent a spiral facet which articulates with the medial malleolus of the tibia. On ventral view, the sustentacular facet (convex) appears to be wide and rounded. It is not extended anteroposteriorly. It is well separated from the navicular facet. Its disto-medial part is distinctly inclined ventrally. The ectal facet is strongly concave. It is wide and very short anteroposteriorly. The sustentacular and ectal facets are close. Lateral to the ectal facet, there is a deep (but transversally short) groove for the tendons of the plantar flexor muscles. The navicular facet is well extended transversely. It is rotated

medio-ventrally relative to the body. In MNHN QNY2-2604, a third articular facet with the calcaneum is visible ventrally, along the navicular facet.

Discussion

The postcranial bones of *Palaeonictis occidentalis* are well known. Sinclair and Jepsen (1929) described an almost complete specimen (number 13001 housed at the Geological Museum of Princeton University, now in Yale). The second species of *Palaeonictis* (*P. peloria*) is only known by dental material. Sinclair and Jepsen (1929) concluded that *Palaeonictis* was a robust terrestrial ambulatory predator.

The postcranial elements of *Palaeonictis* and *Oxyaena* are nearly similar (Sinclair and Jepsen 1929; Rose 1990). Our discrimination of the different postcranial elements of Oxyaenidae found in Le Quesnoy is based on size differences. *P. gigantea* is here compared to the oldest *Oxyaena* and *Dipsalidictis* species.

The humerus is larger than that of *Oxyaena woutersi* but is similar in morphology. It differs by a slightly steeper trochlea. The articulation with the head of the radius is antero-posterior deep. The great capitular eminence is well developed on the radius, so the humero-radial articulation is less flexible than in Oxyaeninae (Rose 1990). The deep radial and olecranon fossae on the humerus indicate an articulation with large antero-posterior mobility. All these features imply that the humero-ulnar joint had a strong stability.

The radius is smaller than the one published by Sinclair and Jepsen (1929) (102.17 vs. 104 mm long). This is not surprising because *P. gigantea* is slightly smaller than *P. occidentalis*. The diaphysis of the radius is straighter than in *Oxyaena* and *Dipsalidictis*, probably linked to its increased weight (and robustness). However, the diaphysis in *Palaeonictis* is slightly twisted as in the primitive species. The head is more ovoid (so more derived) than in *Dipsalidictis* (rounder) and *Oxyaena* (Rose 2001), which limits the degree of pronation and supination (Sinclair and Jepsen 1929; Denison 1938). The radius appears to be designed more for heavy weight-bearing. The distal part is wider anteroposteriorly and flatter than in *Dipsalidictis*, which increases the articulation of the radius with the carpus. The facet of articulation with the ulna is deeper and more developed, indicating a strong contact between the two bones and a limitation of the movement between them.

The astragalus is similar to what is known in *P. occidentalis*. The astragalus has a shallow and



FIGURE 19. *Palaeonictis* cf. *gigantea* de Blainville 1842. MNHN Hou 01, right lower jaw bearing worn P₃, P₄ and anterior part of M₁, and alveoli of C₁-P₂ and M₂ in 1. labial, 2. occlusal, 3. lingual views. Reversed view: 3. Scale bar equals 10 mm.

short trochlea. It is surprising that there is so little antero-posterior movement at the ankle. This morphology does not prevent entirely small rotatory movements. This conformation could be a primitive feature.

The broad and dorsoventrally compressed head and the short neck may be linked to a plantigrade locomotion (Denison 1938; Ginsburg 1961; Rose 1990). Moreover the neck of the astragalus is shorter in plantigrade species than in digitigrade species.

The more robust and weight-bearing morphology is not surprising because *Palaeonictis* is noticeably larger than *Oxyaena*, and implies more robust postcranial elements. As previously indicated, Sinclair and Jepsen (1929) considered *Palaeonictis* as a plantigrade and robust terrestrial ambulatory predator. This result agrees with that obtained for *Oxyaena woutersi* (see above).

The ancestors of Oxyaenidae are presently poorly known (no postcranial material has been found for the Paleocene *Tytthaena*), but based on the data available for *Dispsalidictis*, they could have been arboreal. The short limbs of Oxyaenidae (e.g., *Palaeonictis*) might not be necessarily an adaptation to semifossorial habits as proposed by Heinrich and Rose (1995), but rather retention of primitive and arboreal features.

The robust morphology of *Palaeonictis* and its joints indicate that *P. gigantea* was not cursorial. However, *Palaeonictis gigantea* appears – as does *Oxyaena* – to have a combination of arboreal (and primitive) and terrestrial features. The astragalus of *P. gigantea* does not show more adaptation toward a terrestrial locomotion than in *O. woutersi*. However, the elbow joint appears to be more restricted

TABLE 9. Estimated measurements (in cm) of specimens of *Palaeonictis* cf. *gigantea* from Houdancourt.

Locus		Measurement
P ₁	L	0.470
	w	0.560
P ₂	L	1.054
	w	0.670
P ₃	L	1.178
	w	0.696
P ₄	L	1.338
	w	0.782
M ₁	L	1.228
	w	0.722
M ₂	L	1.2
	w	0.512
MD	H	3.040

TABLE 10. Comparison of the mandibular depth (=MD) divided by the M₁ length (M₁ L) in several specimens of *Palaeonictis*. Measurements of North American species are taken from Rose (1981; table 34).

	<i>Palaeonictis peloria</i>	<i>Palaeonictis occidentalis</i>					<i>Palaeonictis gigantea</i>	<i>Palaeonictis cf. gigantea</i>
	YPM-PU 18077	AMNH 110 (type)	AMNH 15212	AMNH 15213	YPM-PU 14677	YPM-PU 17845	MNHN ARP 52	Houdancourt
M ₁ L	16.6	13.4	14.2	12.9	15	13.7	11.9	12.3
MD	42.5	30.4	25.5	34.5	34.4	31.5	26.9	30.4
MD/ M ₁ L	2.56	2.27	1.8	2.67	2.29	2.3	2.26	2.47

than in *O. woutersi*, which supports an ambulatory terrestrial locomotion for *Palaeonictis gigantea*. The calcaneum morphology of *P. gigantea* would possibly also reflect more limited ankle movements.

According to our weight estimation, *P. gigantea* approaches 10 kg. The Le Quesnoy's flora indicates a wet river forest habitat surrounded by semi-deciduous or deciduous woodlands (Nel et al. 1999). It is possible that *Palaeonictis gigantea* and *Oxyaena woutersi* were able to move on the ground as easily as in the trees (thanks to primitive features). Because of the diversity of environments in Le Quesnoy, the presence of various locomotor abilities (derived terrestrial abilities and primitive arboreal abilities) was probably an advantage for the Oxyaenidae.

Palaeonictis cf. gigantea

Figure 19

Referred material from Houdancourt.

MNHN Hou 01; right mandible with alveoli of P₁, P₂, M₁ and M₂, and very worn P₃ and P₄.

Locality. Exact locality unknown. Found near Houdancourt, which is 2.4 km from Le Quesnoy. Argiles à lignites du Soissonnais, MP7.

Description

Measurements: Table 9

Dentary and lower dentition: Only a right mandible has been found. The size and number of the teeth indicate that they correspond to permanent teeth. The dental alveoli for the canine, P₃, P₄ and the anterior part of the M₁ and M₂ are preserved but are very worn. All the teeth are closely inserted. The canine alveolus is very large. It extends distally far below the P₂. Except for the single-rooted P₁, all the premolars are two-rooted. The size of the premolars increases from P₁ to P₄. The P₄ is longer than the M₁. The M₁ is wider than the M₂. Teeth form a parabolic row in the horizontal ramus,

with the P₃ and P₄ very labially located. The canine is inserted close by the P₁ and P₂ and pushes them lingually. The horizontal ramus is high and robust. Its height slightly increases posteriorly. The symphysis is deep and massive, and extends between the P₂ and P₃. Three mental foramina are visible: below the crown of P₂, below the two roots of P₃ and below the anterior root of P₄. The anterior mental foramen marks the beginning of a mandibular canal. The alveolar canal is present ventrolabially to the alveolus of the canine. The distal opening of the mandibular canal is seen in the ventral part of the masseteric fossa. Anterior parts of the coronoid crest and masseteric fossa are present. The coronoid crest is worn but seems to have been strong and high. The M₂ extends to the coronoid crest. The masseteric fossa is deep.

Discussion

Numerous characters of *Palaeonictis* are visible on the mandible: the parabolic shape of the tooth row in occlusal view which is typical of the genera *Palaeonictis* and *Ambloctonus* by contrast to *Dipsalodon* where it is more straight; the dental formula (one large canine, four premolars of which the first one is single-rooted, and two molars); the relative size of the teeth (P₄ as robust as M₁ and M₁ longer and wider than M₂); and the mandible robust and deep. The two teeth present on the mandible are too worn to be described in detail. The teeth are slightly larger than in Le Quesnoy and in de Blainville's (1842) samples.

The teeth are slightly smaller than in *P. occidentalis* but more closely placed. They are slightly more closely located than the primitive *P. peloria* and *Dipsalodon*. The mandible shares with *P. peloria*, *P. occidentalis* and *Ambloctonus* the particular insertion of the P₂ which is a little transverse to the axis of the tooth row. The P₁ is more lingual than in *P. peloria* and *P. occidentalis* because of the proximity of the canine. This insertion gives a more parabolic aspect to the tooth row. The symphysis is

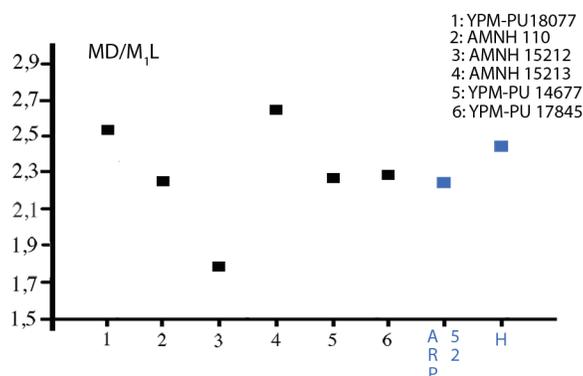


FIGURE 20. Comparison of the ratio between MD/M₁L for several mandibles of *Palaeonictis* species. See values on Table 10. MD = mandibular depth measured labially beneath M₁; L = length. H = specimen from Houdancourt (*Palaeonictis* cf. *gigantea*). The two European fossils are in blue.

shorter on the French fossil: it extends below the anterior root of P₃ (as in *Dipsalodon matthewi* Jepsen, 1930) whereas it is below the posterior root in *P. occidentalis*. *P. peloria* has a more robust mandible with a longer symphysis than *P. occidentalis*. The P₂ and P₁ are more developed than in *P. occidentalis*. These features are primitive for the ambloctonines. As for *P. occidentalis*, a mental foramen is located under the P₃.

As for *P. occidentalis* the mandible is shallower than in *P. peloria* but deeper than in the syn-type MNHN ARP 52 of *P. gigantea*. To compare the robustness of the mandible between the different specimens of *Palaeonictis*, we divided the mandibular depth (MD) by the length of M₁ (Table 10). The mandible is more robust than the type of *Palaeonictis gigantea* (MNHN ARP 52). However, the two specimens present values comparable to what is known in *P. occidentalis*. Only AMNH 15212 has a less robust mandible (Figure 20). The robustness in *Palaeonictis* is highly variable and Rose (1981) proposed a sexual dimorphism in *Palaeonictis* to explain these variations. The two mandibles found in Europe are probably male specimens, while AMNH 15212 is a female.

This specimen is referred to as *Palaeonictis* cf. *gigantea* because it is the only species of *Palaeonictis* known in Europe and because P₁ and P₂ are wider than in *P. occidentalis* (primitive feature). The specimen is not referred formally to *P. gigantea* because of its larger size compared to other specimens referred to *P. gigantea* and because the morphology of the teeth is unknown.

The Houdancourt specimen of *P. cf. gigantea* retains some primitive characters (e.g., P₁ and P₂

not reduced), but has also some derived characters (compression of the tooth row). These could be the peculiar characters of the European Ambloctoninae.

Conclusion on the European Ambloctoninae

Russell et al. (1982) listed *Oxyaena* and *Palaeonictis* in the faunal list of Mutigny (MP8+9). However, our study of the carnivorous mammals of this locality refutes this occurrence. All the material appears to represent hyaenodontids.

As for the Oxyaeninae, the Ambloctoninae were poorly known in the Early Eocene of Europe. They are documented by fragmentary material. The study of this new material, mostly from Le Quesnoy, allows a better understanding of the evolution of this group in Europe.

Our demonstration of the synonymy of *Dormaalodon* with *Palaeonictis* implies that the Ambloctoninae were only represented by the genus *Palaeonictis*.

By contrast to the Oxyaeninae, there is no support for an endemic evolution of the Ambloctoninae in Europe. A single dispersal of the Ambloctoninae from North America to Europe is suggested during the Paleocene-Eocene boundary, followed by an endemic evolution during the beginning of the Early Eocene, as for the Oxyaeninae. The European evolution of *Palaeonictis* is characterized by a slight size increase, and by morphologically similar trends to what is known in the North American lineage of *P. occidentalis* (e.g., paraconid more lingual, metaconid more distal, protoconid lower, P₄ with less individualized entoconid). European *Palaeonictis* evolved convergently with North American lineages. However, by

contrast to North American Ambloctoninae, which diversified and persisted until the end of the Early Eocene, the European Ambloctoninae remained restricted to one genus and rapidly disappeared.

GENERAL CONCLUSION

Biostratigraphic Implications

Before the discovery of the fossiliferous locality of Le Quesnoy, our knowledge of the European Oxyaenidae was poor and restricted to few complete or fragmentary teeth. The Le Quesnoy material increases significantly our knowledge of the first European oxyaenids, and their systematics and evolution.

The oxyaenids from Le Quesnoy are *Oxyaena woutersi* and *Palaeonictis gigantea*. They recall taxa from the Paleocene/Eocene transition of North America. They belong to species previously known in Dormaal, although slight size differences do exist between the two samples.

The presence of almost the same oxyaenid fauna at a stage of evolution similar to that of Dormaal supports the placement of Le Quesnoy very close to MP7. The larger size of the specimens from Le Quesnoy might be explained by a slightly younger age with respect to Dormaal.

O. woutersi departs from *Dipsalidictis* by its more advanced carnassial shearing adaptation and from *Oxyaena gulo* by its less secant M_1 . It seems intermediate between two Oxyaeninae from the early Wasatchian of North America, *D. transiens* (Wa0-Wa2) and *O. gulo* (Wa2-Wa3). *Palaeonictis gigantea* is less derived than the Wasatchian *P. occidentalis* (Wa1-Wa4) and appears closer to the latest Clarkforkian *P. peloria* (Cf3) and *P. wingi* (Wa0). However, *P. gigantea* and *P. wingi* are of same size and are probably equivalent in age.

The correlation of MP7 and Wa0 proposed by Smith and Smith (2001) is supported by the oxyaenids from Le Quesnoy fauna.

Le Quesnoy has yielded numerous specimens of the oldest European Oxyaeninae (*Oxyaena woutersi*). The species is more primitive than those from the "Conglomérat de Meudon", Sinceny, Pourcy and Abbey Wood.

Oxyaenidae are known in Dormaal (reference-level locality of MP7), but are unknown in Avenay (reference-level locality of MP8+9). Meudon, Sinceny and Abbey Wood are considered presently as MP8+9 localities. However, it seems that the carnivorous mammal faunas changed between Dormaal (MP7) and Mutigny (MP8+9),

because no oxyaenid is known in Europe after Mutigny. This turnover is notably characterized by the disappearance of the Oxyaenidae. As Meudon, Abbey Wood and Sinceny are considered as older than Mutigny (Hooker 1998), they may probably be considered as MP7 localities. Moreover, Oxyaenidae could be considered as a characteristic group of MP7 level.

Paleoecologic Implications

As indicated above, the MP7-MP8+9 transition is marked by the disappearance from Europe of the Oxyaenidae, but also by that of the largest hyaenodontid genera (*Arfia* Van Valen, 1965, *Galecyon* Gingerich & Deutsch, 1989 and *Prototomus* Cope, 1874; North American and partly European 'proviverrine' genera *sensu* Morlo and Gunnell [2003]); the two groups are well diversified in North America during Early and Middle Eocene. This decrease of diversity of Early Eocene carnivorous mammals from Europe is coincident with the disappearance of *Coryphodon* from Europe.

Only the smallest hyaenodontids, which belong to the 'True' Proviverrinae *sensu* Morlo and Gunnell (2003), and miacids span the MP7-MP8+9 transition in Europe. The 'True' Proviverrinae probably filled the larger body-size carnivorous niches in Europe after the disappearance of Oxyaenidae, because they represented the main group of carnivorous mammals in Europe during the Middle Eocene (Morlo 1999). The decrease of diversity is unknown for carnivorous mammals in North America and probably had significant implications for the ecology of European mammal faunas.

Chew (2009) has recently exemplified the existence of biotic turnover events in the Early Eocene mammalian fauna of the Willwood Formation (Wyoming, United States) during the earliest part of Early Eocene (Wa3-Wa5) (55-54 Ma). Chew (2009) identified increasing disappearance rates followed by a diversity crash and a subsequent faunal reorganization. This extinction event coincided with a climate cooling (decrease in MAT of 5-8 °C) between PETM and EECO evidenced by Wing et al. (1999). However, this cooling has not been presently recorded presently in Europe.

The age of the fossiliferous locality of Mutigny (MP8+9) is considered to be 54-52 m.y. (Neal 1996; Duprat 1997). This age is younger than the faunal turnover exemplified by Chew (2009). The faunal turnover, which affected the Early Eocene carnivorous mammals from Europe, and which is marked by the disappearance of *Prototomus*, *Galecyon*, *Arfia* and Oxyaenidae, could represent in

Europe the faunal response to the global cooling which succeeded the PETM. Moreover, the differences observed between North American and European carnivorous faunas could be explained by the fact that Europe mostly consisted of several isolated islands during the Early Eocene. Thus, the small size of the ecosystems was probably defavorable to the mammalian faunas when the climate has changed during the beginning of the the Early Eocene. However, these are preliminary results, which must be confronted with those obtained for the other groups of mammals.

Paleobiogeographic Implications

The North American origin of the Le Quesnoy oxyaenids is well supported. The European taxa are rooted in Clarkforkian oxyaenines and ambloctonines. The dispersal via Arctic Canada and Greenland (e.g., McKenna 1975) is supported by the discovery of *Palaeonictis* sp. from the Eureka Sound Group (Early Eocene, Ellesmere Island, Nunavut) (Eberle and McKenna 2002).

A revision of the European Oxyaenidae presently known supports a single dispersal followed by endemic and convergent evolution. However, European Ambloctoninae and Oxyaeninae evolution and diversification is much more limited than in North America.

The Oxyaenidae are present in Northern Europe, but absent in Southern Europe, supporting a North-South provincialism (Marandat 1997).

As in North America, the oxyaenids represent the largest specialized carnivorous mammals in the Early Eocene of Europe. They are distinctly larger than the hyaenodontids and "miacids". However, as for the other carnivorous mammals, European Oxyaenidae remain smaller than the North American ones.

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