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Coryphodon anthracoideus (de Blainville, 1846) from the Upper Paleocene of Orp-le-Grand, Belgium

by Spencer G. LUCAS*

Abstract

An incomplete skeleton of *Coryphodon* from the Sables d'Orp at Orp-le-Grand in eastern Belgium is the most complete specimen of this genus available from western Europe. This specimen is assigned to *C. anthracoideus* (BLAINVILLE, 1846) because of its relatively large size, incomplete lingual cingulum on M^3 and relatively small M_3 entoconid. *C. anthracoideus* apparently is restricted to pre-Ypresian strata in the London and Paris Basins. Its occurrence at Orp-le-Grand suggests a Late Paleocene (Thanetian) age for the Sables d'Orp.

Introduction

Coryphodon OWEN, 1845, is one of the most widely distributed early Cenozoic mammals. Its fossils are known from upper Paleocene and/or lower Eocene strata in western Europe (England, Belgium, France), North America (western United States, Ellesmere Island) and Asia (People's Republic of China, Mongolian People's Republic). In 1812, the French comparative anatomist Georges CUVIER first describes a specimen of *Coryphodon.* According to CUVIER (1812, p. 7), the complete skeleton of a mammal nearly as large as a bull was discovered in 1807 between Soissons and the Vauxbrun valley in France. CUVIER thought that this skeleton pertained to a perissodactyl similar to *Palaeotherium.* He only illustrated its left M^2 (CUVIER, 1812, pl. I, fig. 6) because the workmen who discovered the skeleton saved little of it. Thereby, the most complete specimen of *Coryphodon* discovered in Europe was lost; specimens discovered subsequently consist almost entirely of isolated bones and teeth, an incomplete skull and a lower jaw (e.g., HÉBERT, 1856; CAILLEUX, 1945).

However, in 1933 an incomplete skull and lower jaw and some postcrania of a single *Coryphodon* individual was discovered in eastern Belgium at Orp-le-Grand (Fig. 1). Although QUINET (1969) briefly discussed this specimen, it never has been fully described despite the fact that it is the most complete specimen of *Coryphodon* now available from Europe. This paper describes the *Coryphodon* from Orp-le-Grand and discusses its biostratigraphic significance. The following institutional abbreviation are used:

BMNH – British Museum (Natural History), London;
IM – Ipswich Museum, Ipswich;
IRSNB – Institut Royal de Sciences Naturelles Belgique, Brussels;
MNHN – Museum Nationale d'Histoire Naturelle, Paris.

Measurements and nomenclature of the cusps on *Coryphodon* cheek-teeth follow LUCAS (1984, figs. 1-2).

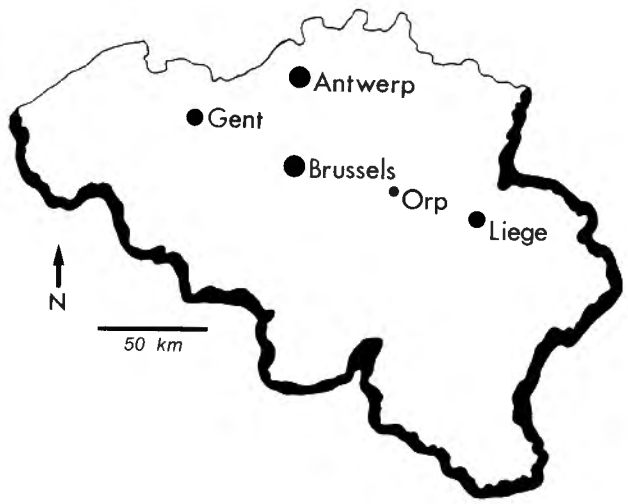


Figure 1. – *Map of Belgium showing the location of Orp-le-Grand (Orp).*

* Department of Geology, University of New Mexico, Albuquerque, New Mexico 87131 U.S.A..

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA LINNAEUS, 1758
Order PANTODONTA COPE, 1873
Family CORYPHODONTIDAE MARSH, 1876 (1873)
Genus *CORYPHODON* OWEN, 1845

Coryphodon anthracoideus (de BLAINVILLE, 1846)
(Plates I - VI)

1969 — *Coryphodon eocaenus* — G.E. QUINET, p. 48.

REFERRED SPECIMEN

IRSNB n° M 1461: incomplete skull (in two pieces) with incomplete right C^1, left P^2 and P^4 roots, damaged left P^3 and M^{1-3}, damaged right P^2 and partial roots of right P^{3-4}; incomplete lower jaw with roots of left I_1, I_3 and C_1, complete left I_2, left P_2-M_3 and right M_3; incomplete left scapula, radius and ulna; a cervical vertebra; a magnum, scaphoid and metacarpals from the left manus; and fragments of centra, ribs and foot bones.

LOCALITY AND HORIZON

IRSNB n° M 1461 was bought by the Institute in June 1933 from E. Battard, foreman of the brickyards at Orp-le-Grand, Belgium (Fig. 1). FEUGUEUR (1963, fig. 96) applied the name "Sable fluvio-marin de Landen" to about six meters of glauconitic and clayey sand at Orp-le-Grand that contains lignite in its uppermost part. This unit hereafter is referred to as the Sables d'Orp. It unconformably overlies the "Tuffeau à *Pholadomya konincki*" and is unconformably overlain by Quaternary muds. The lignitic preservation of IRSNB n° M 1461 suggests it may have been derived from the upper part of the Sables d'Orp.

DESCRIPTION

The bones of IRSNB n° M 1461 are dark-brown to black and lignitic. The skull (Pl. I; Pl. II, fig. 1) is incomplete, distorted and broken into two pieces. One piece (Pl. I) consists of the rostrum, facial region, some of the maxillary cheek teeth, anterior root of the left zygomatic arch and the skull roof dorsal to the orbits. The other piece (Pl. II, fig. 1) consists of the basicranium and posterior skull-roof, severely compressed and distorted dorso-ventrally.

The skull of IRSNB n° M 1461 closely resembles that of other *Coryphodon,* especially that of *C. molestus* (COPE, 1877; LUCAS, 1984), although the Belgian skull is larger and more robust than the skull of this North American species. The posterior skull-roof of IRSNB n° M 1461 is broad and has distinct parasagittal crests (Pl. II, fig. 1). The nasals are damaged and essentially absent (Pl. I, fig. 1), and, as in most adult skulls of *Coryphodon* (LUCAS, 1984), many cranial sutures are fused and obliterated. Damage to IRSNB n° M 1461 has artificially produced a doming of the maxillary region of the skull dorsal to the cheek-tooth row (Pl. I, figs. 1, 3). Distinct supraorbital crests are present dorsal to the anterior portions of the orbits (Pl. I, fig. 3). IRSNB n° M 1461 bears a well-excavated nasal incision and a flaring rostrum (Pl. I).

On the left external surface of the skull of IRSNB n° M 1461 (Pl. I, fig. 3) the alveolus for the left C^1 is large and deep, extending posteriorly to a point dorsal to P^4. There is a distinct postcanine diastema, and the anterior root of the zygomatic arch is robust. Its dorsal edge forms a distinct suborbital crest.

On the ventral surface of the skull of IRSNB n° M 1461, anterior palatine foramina are present along the maxillary-premaxillary sutures (Pl. I, fig. 2). The basicranium (Pl. II, fig. 1) has closely appressed mastoid-paroccipital and postglenoid processes that bound a deep and antero-posteriorly narrow external auditory meatus. A shallow, slightly concave and transversely elongate glenoid fossa is anterior to the postglenoid process. The large occipital condyles and foramen magnum are produced posteriorly from the basioccipital. Paired hypoglossal foramina perforate the basioccipital antero-external to the condyles. The basisphenoid and orbitosphenoids are anterior to the basioccipital, and the roofs of the internal nares in the palatines are preserved. The presphenoid is absent, having broken along its suture with the anterior edges of the basisphenoid and orbitosphenoids. The epitympanic recess is a depression between the basioccipital and external auditory meatus. The foramen ovale is preserved in the external edge of the orbitosphenoid. Poor preservation precludes the further elucidation of the basicranial structure of IRSNB n° M 1461.

The lower jaw of IRSNB n° M 1461 (Pl. II, fig. 2) has a stout mandibular symphysis that extends posteriorly to the juncture between P_3 and P_4. The flaring rostrum and subparallel cheek-tooth rows of this lower jaw are features characteristic of all *Coryphodon* (LUCAS, 1984).

The only upper teeth of IRSNB n° M 1461, left P^2-M^3 and right P^2 (Pl. I, fig. 2; Pl. III, fig. 1), are damaged and eroded. P^3 has the V-shaped ectoloph and lingual protocone bearing distinct pre- and postprotocristae typical of all *Coryphodon* (LUCAS, 1984). The remnants of P^2 and P^4 present suggest teeth similar to P^3 morphologically. M^1 and M^2 closely resemble each other morphologically. They conform to the M^{1-2} morphology of other *Coryphodon* (LUCAS, 1984) except that their preparacristae appear to be connected to their parastyles. M^2 has a posterolingual cingulum, a variable feature among *Coryphodon* (LUCAS, 1984). M^3 is so badly

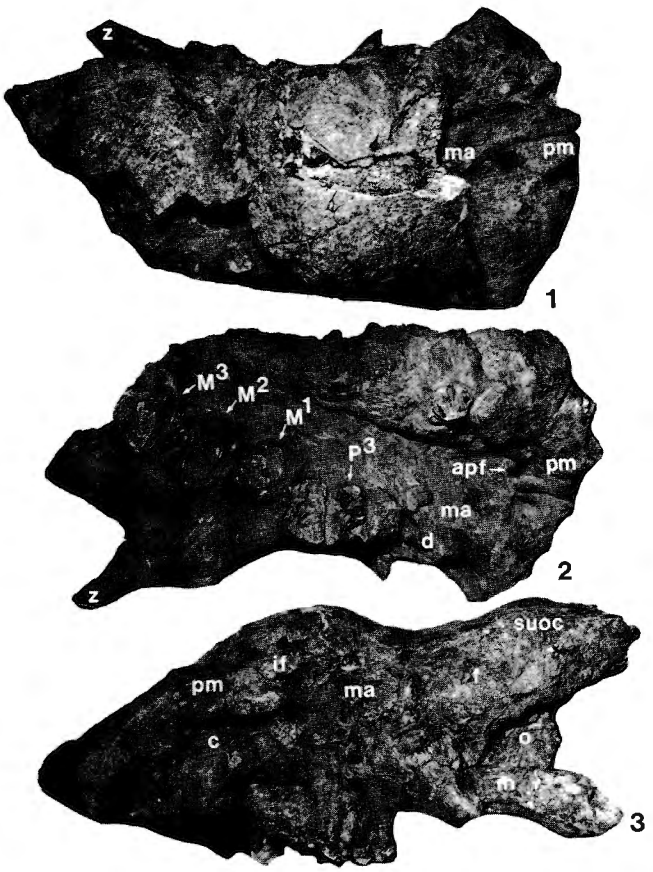


PLATE 1

Anterior portion of the skull of IRSNB n° M 1461, C. anthracoideus *from Orp-le-Grand, Belgium.*

Fig. 1. – *Dorsal view.*
Fig. 2. – *Ventral view.*
Fig. 3. – *Left external view.*

All figures × 1/4. Abbreviations are: apf - anterior palatine foramen, c - canine alveolus, d - diastema, f - frontral, if - infraorbital foramen, m - malar, ma - maxillary, o - orbit, pm - premaxillary, suoc - supraorbital crest, z - zygomatic arch.

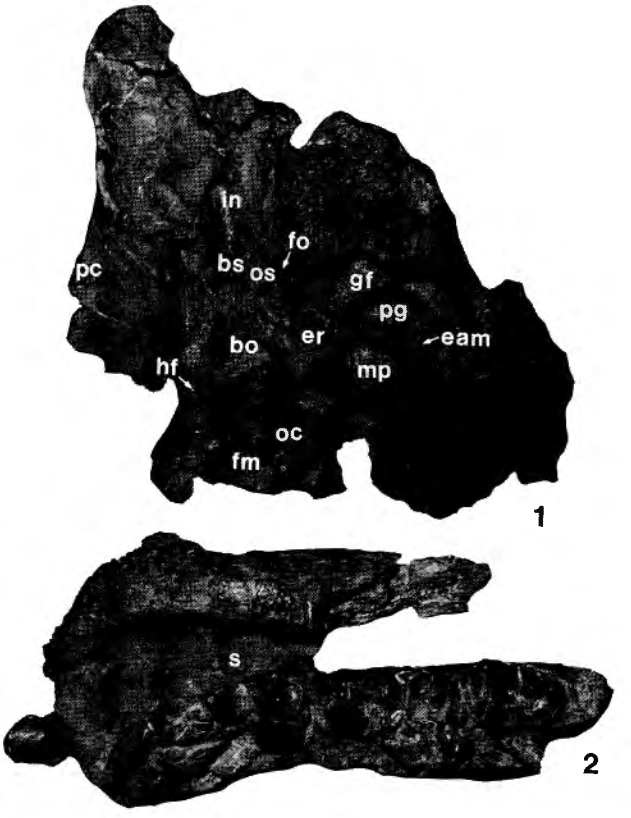


PLATE 2

Posterior portion of skull and incomplete lower jaw of IRSNB n° M 1461, C. anthracoideus *from Orp-le-Grand, Belgium.*

Fig. 1. – *Basicranium, ventral view, × 1/4.*
Fig. 2. – *Lower jaw, occlusal view, × 3/10.*

Abbreviations are: bo - basioccipital, bs - basisphenoid, eam - external auditory meatus, er - epitympanic recess, fm - foramen magnum, fo - foramen ovale, gf - glenoid fossa, hf - hypoglossal foramen, in - internal nares, mp - mastoid-paroccipital process, oc - occipital condyle, os - orbitosphenoid, pc - parasagittal crest, pg - postglenoid process, s - symphysis.

damaged that, beyond the fact that it well corresponds to the M^3 morphology typical of *Coryphodon,* little can be said.

The left I_2 (Pl. II, fig. 2) is spatulate and procumbent. Based on alveolar size, it is the largest of the three lower incisors of IRSNB n° M 1461, as it is in all *Coryphodon* (LUCAS, 1984). The roots of left C_1 and P_1 (Pl. II, fig. 2) indicate a stout, single-rooted P_1 separated from the large C_1 by a distinct diastema. The left $P_{2\text{-}4}$ (Pl. IV, fig. 1) are similar teeth morphologically that increase in size posteriorly. The $P_{2\text{-}4}$ trigonids are shallow lingually, becoming deeper from P_2 through P_4 as the paracristids and metalophids become more prominent and more labio-lingually oriented. The talonids of $P_{2\text{-}4}$ are short heels that bear median, antero-posteriorly oriented cristids that may be the homologues of the molar cristids obliquae. M_1 (Pl. IV, fig. 1) is so damaged that it can only be describes as a sub-bilophodont tooth with a posterior cingulid. M_2 (Pl. IV, fig. 1) is also sub-bilophodont but is larger than M_1. It, too, bears a posterior cingulid, and it has a low cristid obliqua that runs lingually and anteriorly from the hypoconid to a point low on the posterior face of the metalophid. M_3 (Pl. IV, figs. 1-2) has a similar cristid obliqua, but its talonid cusp and cristid morphology differs from that of M_2. On M_3, the talonid is "triangular." Thus, the hypoconid is relatively anterior, the hypoconulid is central and posterior and an oblique hypolophid connects the two cuspids; from the hypoconulid, a cristid runs antero-lingually and bears a small entoconid preceded by a smaller entoconulid. On the right M_3 of IRSNB n° M 1461 (Pl. IV, fig. 2) there

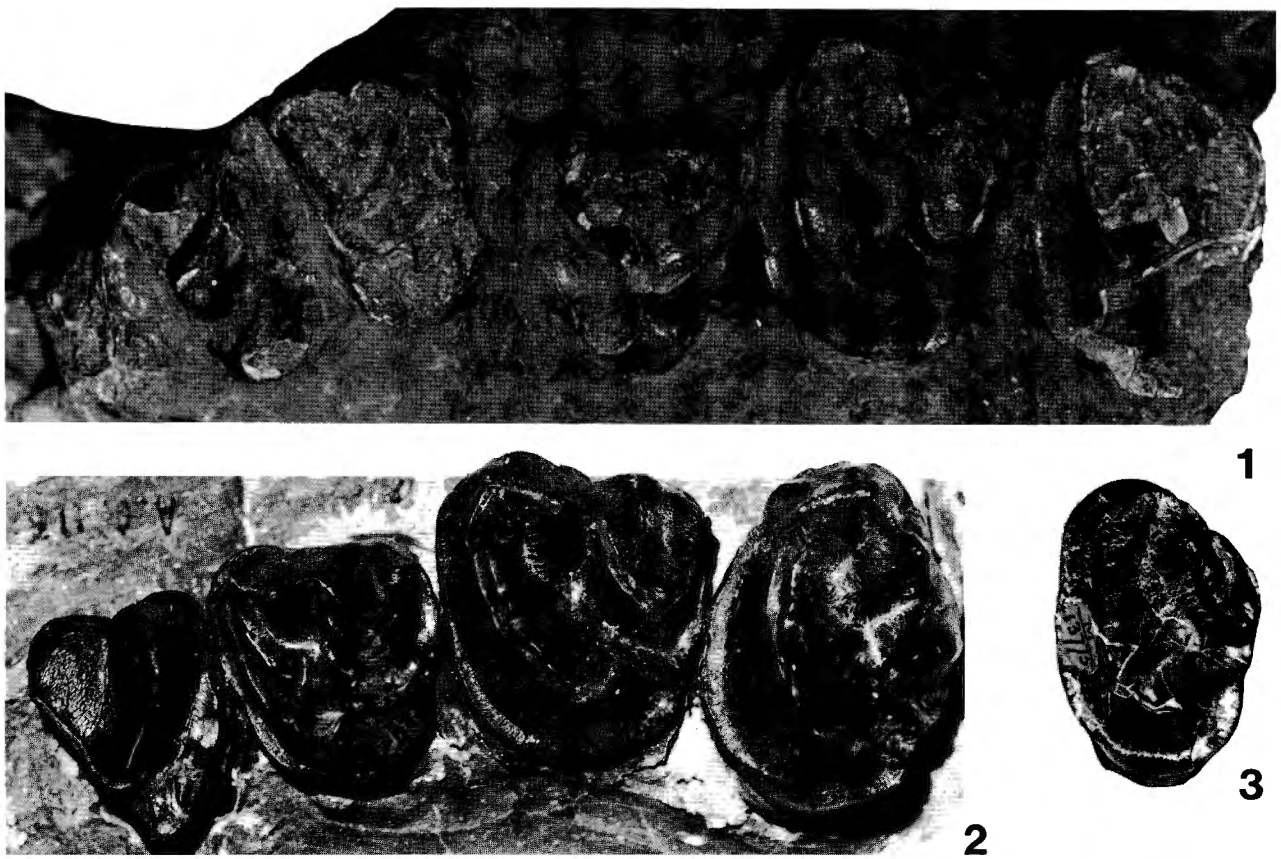


PLATE 3

Upper cheek teeth of C. anthracoideus *and* C. eocaenus *from western Europe.*

Fig. 1. – *IRSNB n° M 1461, left P^2-M^3, occlusal view,* C. anthracoideus *from the Sables d'Orp, Orp-le-Grand, Belgium.*

Fig. 2. – *MNHN ARP 58, left P^4-M^3, occlusal view,* C. anthracoideus *(lectotype) from the Argiles à lignites, Soissonnais, France.*

Fig. 3. – *BMNH M 13775, left M^3, occlusal view* C. eocaenus *from the Blackheath Beds, Abbey Wood, England.*

All figures × *1.*

are two closely-appressed cuspulids in the position of the entoconulid, whereas the left M_3 (Pl. IV, fig. 1) has only one cuspulid in this position. M_3 has a very weak posterior cingulid.

Only the relatively well-preserved postcranial elements of IRSNB n° M 1461 are described here. A badly damaged posterior cervical vertebra (Pl. V, figs. 3-4) lacks the neural spine and most of the transverse processes, including the portions that bound the external edges of the transverse foramina. On this vertebra, the large anterior and posterior zygopophyses and increase in centrum width posteriorly are features typical of all *Coryphodon.*

The distal (glenoid) portion of the left scapula of IRSNB n° M 1461 (Pl. V, figs. 1-2) has a prominent, pointed coracoid process and a cup-like glenoid fossa. Part of the scapular spine is present, but the acromion process is missing. The supra- and subscapular notches are shallow.

The incomplete left radius of IRSNB n° M 1461 (Pl. VI, figs. 5-6) has a shallow articular surface for the humerus. The anterior ridge is distinct, but the proximal ulnar facet is indistinct.

The partial left ulna of IRSNB n° M 1461 (Pl. VI, figs. 1-2) has a large semilunar (greater sigmoid) notch. The radial notch is relatively short and is located distal to the prominent coronoid process.

The left scaphoid of IRSNB n° M 1461 (Pl. VI, figs. 3-4) has a large, convex scaphoid-radius facet. The scaphoid tubercle is a blunt-edged flange. A pit is eroded in the concave proximal surface of the scaphoid between the tubercle and the scaphoid-radius facet. On the distal aspect of the scaphoid, the scaphoid-trapezoid and scaphoid-trapezium facets are distinct.

The left metacarpal 1 of IRSNB n° M 1461 (Pl. V, figs. 5-6) has a slightly convex proximal facet for the trapezium. This stout metacarpal is slightly concave ventrally and has a moderately well-formed

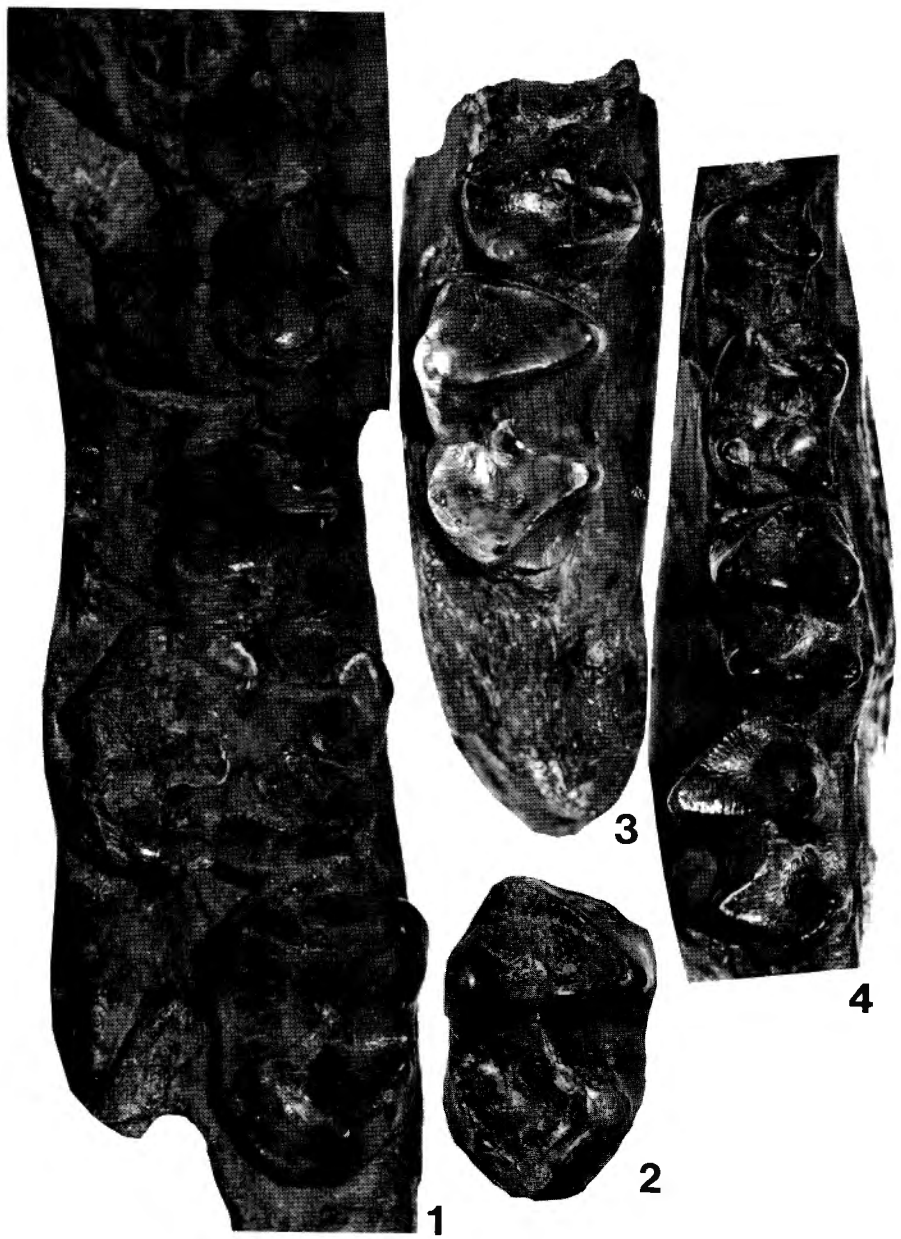


PLATE 4

Lower cheek teeth of C. anthracoideus, C. eocaenus *and* C. oweni *from western Europe.*

Figs. 1, 2. – *IRSNB n° M 1461, left P_2-M_3 (1) and right M_3 (2), occlusal views,* C. anthracoideus *from the Sables d'Orp, Orp-le-Grand, Belgium.*

Fig. 3. – *BMNH M 27848, incomplete right M_2 and complete M_3, occlusal view,* C. eocaenus *(holotype) from the London Clay near Harwich, England.*

Fig. 4. – *MNHN ARP 9, left P_4-M_3, occlusal view,* C. oweni *from the Conglomerat de Meudon, Meudon, France.*

All figures × *1.*

gynglymus distally for articulation with the proximal phalanx.

DISCUSSION

BLAINVILLE's (1846) species *"Lophiodon anthracoideum"* (= *Coryphodon anthracoideus*) was synonymized with *C. eocaenus* OWEN, 1845 by HÉBERT (1856, p. 97). Subsequent authors (an exception is COPE, 1877, p. 206) thus did not recognize BLAINVILLE's species (e.g., CAILLEUX, 1945). However, *C. anthracoideus* can be distinguished from *C. eocaenus* by its larger size (length M^{1-3} of *C. anthracoideus* is about 9.3 cm, length M^{1-3} of *C. eocaenus* is about 7.9 cm), its relatively small M_3 entoconid and lack of a complete lingual cingulum on M^3.

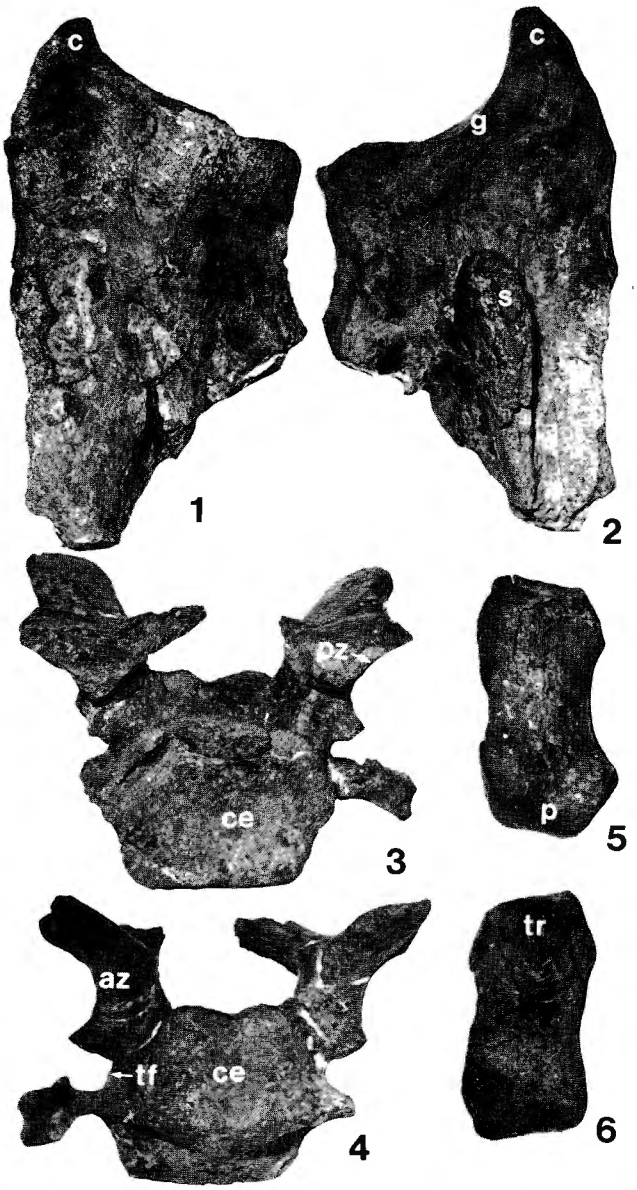


PLATE 5

Selected postcrania of IRSNB n° M 1461, C. anthracoideus *from the Sables d'Orp, Orp-le-Grand, Belgium.*

Figs. 1, 2. – *Glenoid portion of left scapula, internal (1) and external (2) views.*

Figs. 3, 4. – *Posterior cervical vertebra, posterior (3) and anterior (4) views.*

Figs. 5, 6. – *Left metacarpal 1, anterior (5) and posterior (6) views.*

All figures × 4/10. Abbreviations are: az - anterior zygopophysis, c - coracoid process, ce - centrum, g - glenoid fossa, p - articular surface for proximal phalanx, pz - posterior zygopophysis, s - scapular spine, tf - transverse foramen, tr - facet for trapezium.

LUCAS (1984) thus recognized three valid species of *Coryphodon* from western Europe: the small *C. oweni* (length M^{1-3} is about 7.1 cm), *C. eocaenus* and *C. anthracoideus* (= *C. gosseleti* MALAQUIN, 1899). *C. croydonensis* NEWTON, 1885, based on a single ulna, is a *nomen vanum.*

Comparison of the dentition of IRSNB No. M 1461 with other *Coryphodon* specimens from western Europe reveals that the Belgian specimen most closely resembles specimens of *C. anthracoideus* and should be assigned to that species. Thus, IRSNB n° M 1461 is much larger than specimens of *C. oweni* (Table 1; compare Pl. IV, figs. 1-2 with Pl. IV, fig. 4). IRSNB n° M 1461 also is larger than specimens of *C. eocaenus* (Table 1), appears to lack the complete lingual cingulum on M^3 characteristic of *C. eocaenus* (compare Pl. III, fig. 1 with Pl. III, fig. 3) and has a relatively smaller M_3 entoconid than does *C. eocaenus* (compare Pl. IV, figs. 1-2 with Pl. IV, fig. 3). Indeed, the upper cheek teeth of IRSNB n° M 1461 are essentially identical to those of MNHN ARP 58, the lectotype of *C. anthracoideus* (Table 1; compare Pl. III, fig. 1 with Pl. III, fig. 2).

Assignment of IRSNB n° M 1461 to *C. anthracoideus* makes this specimen the most complete specimen of *C. anthracoideus* from western Europe. In addition, the large supraorbital crests and canines and the robust skull and mandibular symphysis of IRSNB n° M 1461 suggest it is a male, since these are sexually dimorphic features characteristic of male *Coryphodon* (OSBORN, 1898; LUCAS, 1984). If this conclusion is valid, then IRSNB n° M 1461 documents the same type of sexual dimorphism in *C. anthracoideus* that is evident in other species of *Coryphodon* .

Biostratigraphy

LUCAS (1984) assigned specimens from western Europe, North America and eastern Asia to *C. anthracoideus.* In western Europe, *C. anthracoideus* occurs at Orp-le-Grand, the Suffolk Pebble Beds at Suffolk (England), the Blackheath Beds at Abbey Wood (England), the Sables d'Ostricourt at Vertain (France), the Argiles à lignites in the Soissonnais and Laonnais (France) and the Argiles Plastiques near Sarron on the Oise (France). In western North America, *C. anthracoideus* is restricted to the Gray Bull Biostratigraphic Zone (SCHANKLER, 1980) in the Bighorn Basin (Wyoming) and temporally equivalent units in other basins. In Asia, *C. anthracoideus* (= *C. tsaganensis* RESHETOV, 1976) is known from a single locality, the White Beds of the Naran Bulak Formation at Tsagan Khushu in the Mongolian People's Republic (RESHETOV, 1976; DASHZEVEG and MCKENNA, 1977).

PLATE 6

Selected postcrania of IRSNB n° M 1461, C. anthracoideus *from the Sables d'Orp, Orp-le-Grand, Belgium.*

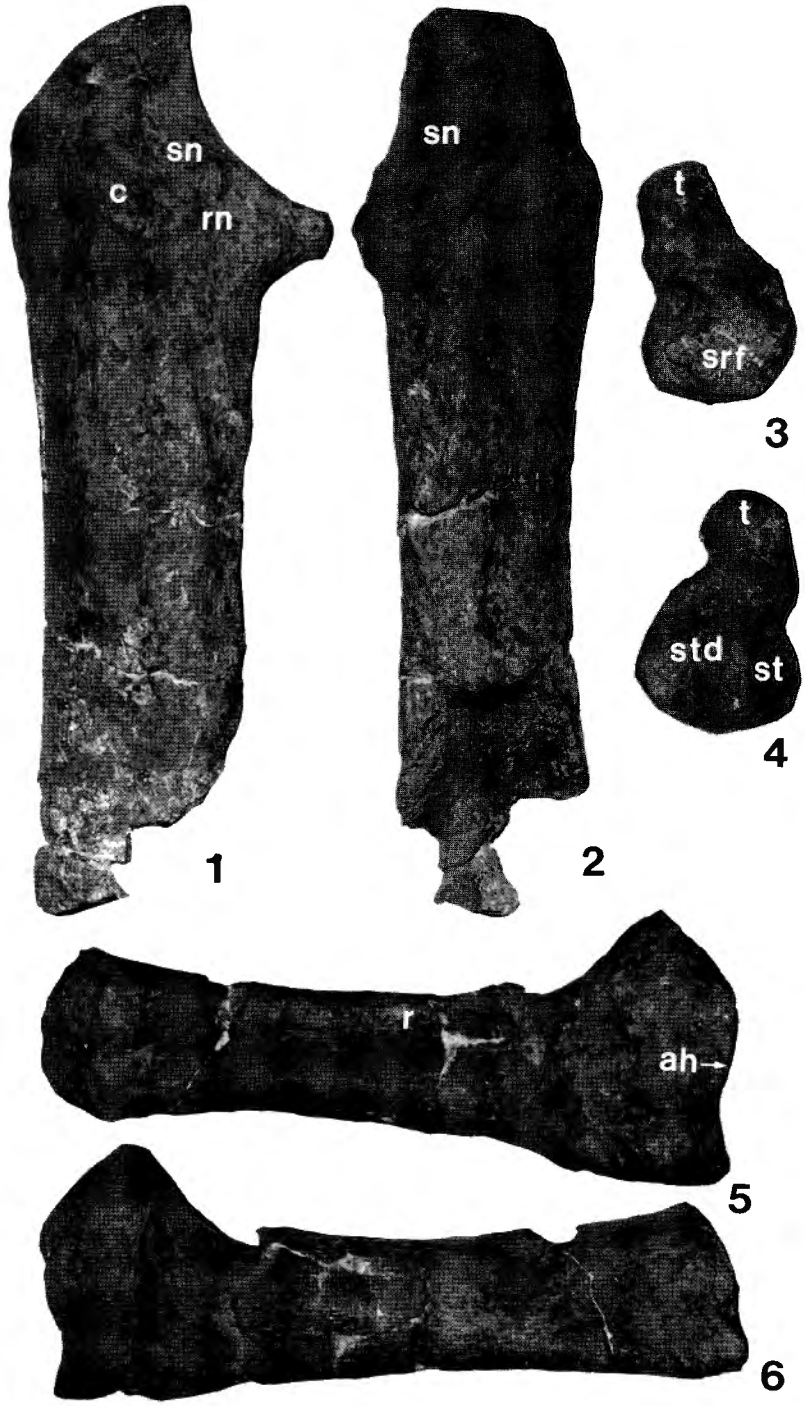
Figs. 1, 2. – *Incomplete left ulna, internal (1) and antero-external (2) views.*

Figs. 3, 4. – *Left scaphoid, proximal (3) and distal (4) views.*

Figs. 5, 6. – *Incomplete left radius, anterior (5) and posterior (6) views.*

All figures × 1/2.

Abbreviations are: ah - articular surface for humerus, c - coronoid process, r - anterior ridge, rn - radial notch, sn - semilunar notch, srf - scaphoid-radius facet, st - scaphoid-trapezium facet, std - scaphoid-trapezoid facet, t - scaphoid tubercle.



The distribution of *C. anthracoideus* in the London Basin of England suggests that its occurrence elsewhere indicates a late Paleocene (Thanetian) age. Its distribution in the French Sparnacian thus is consistent with dinocyst-based correlations that suggest the French Sparnacian is of Thanetian age (COSTA and DOWNIE, 1976; COSTA *et al.*, 1978). Therefore, the occurrence of *C. anthracoideus* at Orp-le-Grand supports assignment of a Thanetian age to the Sables d'Orp. This assignment is consistent with QUINET's (1969, p. 48) determination of a late Landenian ("L2" = late Paleocene) age for the *Coryphodon* occurrence at Orp. It also is consistent with an argument made long ago by LERICHE (1905) that the upper Landenian of Belgium is equivalent to the French Sparnacian and of late Paleocene age.

Acknowledgements

Numerous colleagues facilitated my study of *Coryphodon* specimens in museums on three continents, and thereby made any publication on *Coryphodon* by myself possible. NSF Grant DEB-7919681 supported the research reported here.

Table 1.
Measurements (in cm) of the teeth of IRSNB n° M 1461 and selected Coryphodon *from France and England.*
AW = maximum anterior width, L = maximum antero-posterior length, PW = maximum posterior width. Asterisks (*) indicate approximate measurements of damaged or heavily worn teeth.

	MEASUREMENTS											
SPECIMEN	I_2L	I_2W	P_2L	P_2W	P_3L	P_3W	P_4L	P_4W	M_1L	M_1AW	M_1PW	
C. anthracoideus:												
IRSNB n° M 1461	1.71	2.59	2.02*	1.39*	2.70*	1.63*	2.85*	1.79*	3.03*			
C. oweni:												
MNHN ARP 8-9			1.58	0.93	1.59	1.11	1.74	1.22	2.23	1.51	1.42	
SPECIMEN	M_2L	M_2AW	M_2PW	M_3L	M_3AW	M_3PW	P^2L	P^2W	P^3L	P^3W	P^4L	P^4W
C. anthracoideus:												
IRSNB n° M 1461	3.88	2.15*	2.05*	4.38	2.76	2.67	1.98*	2.62*	2.29	3.18	2.32*	3.32*
MNHN ARP 58[a]											2.36	3.14
C. eocaenus:												
BMNH M 27848[b]			2.28	3.80	2.41	2.21						
C. oweni:												
MNHN ARP 8-9	2.81	1.88	1.68	3.08	1.92	1.73	1.35*	1.88*	1.58	2.29	1.64	2.44
MNHN ARP 10[c]											1.68	2.31*
SPECIMEN	M^1L	M^1AW	M^1PW	M^2L	M^2AW	M^2PW	M^3L	M^3AW				
C. anthracoideus:												
IRSNB n° M 1461	2.88*	3.41*	3.44*	3.35*	4.29	4.02	3.12*					
IM B3							2.98*	4.50*				
MNHN ARP 58[a]	2.83	3.28	3.06	3.37	4.01	3.71	3.15	4.35				
C. eocaenus:												
BMNH M 13775							2.77	3.81				
C. oweni:												
MNHN ARP 8-9	2.08	2.42	2.31	2.48	2.96	2.72	2.28	3.11				
MNHN ARP 10[c]	2.26	2.54	2.42	2.57	2.90	2.66	2.50	3.31				

[a] Lectotype of *C. anthracoideus.*
[b] Holotype of *C. eocaenus.*
[c] Lectotype of *C. oweni.*

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Department of Geology
University of New Mexico
Albuquerque (U.S.A.)