

An arctomorph carnivoran skull from the Phosphorites du Quercy and the origin of procyonids

MIECZYŚLAW WOLSAN and BRIGITTE LANGE-BADRÉ



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The size and morphological characteristics of a skull of an arctomorph carnivoran mammal from Mouillac (old collection of the Phosphorites du Quercy, of unknown age) in France closely match those of the holotype of the earliest known procyonid *Pseudobassaris riggsi* and another skull referred to this species, both from old collections of the Phosphorites du Quercy (Caylus and Mouillac), probably earliest Late Oligocene in age. The skull is more primitive in morphology than those of *Pseudobassaris riggsi* and every other known procyonid, plausibly approaching a hypothetical primitive procyonid morphotype. The only, but methodologically fundamental, departure from this morphotype is the lack of the procyonid suprameatal fossa, which is the crucial synapomorphy of the family Procyonidae. To explain the phylogenetic and taxonomic status of the arctomorph represented by the skull, three competing hypotheses are put forward. Hypothesis A, which considers the arctomorph as an individual of *Pseudobassaris riggsi*, assumes that the procyonid suprameatal fossa first appeared in a common ancestor of *Pseudobassaris* and other procyonids but was still of variable occurrence within *Pseudobassaris riggsi*. Hypothesis B, which proposes the arctomorph as a member of a new *Pseudobassaris* species ancestral to *Pseudobassaris riggsi*, concludes that the procyonid suprameatal fossa arose in *Pseudobassaris riggsi* and in the Procyonidae independently, excluding *Pseudobassaris* from the procyonids. Hypothesis C, which recognizes the arctomorph as a representative of a new species of a new genus of the paraphyletic procyonid stem group, presumes that the procyonid suprameatal fossa originated in a common ancestor of *Pseudobassaris* and other procyonids after the new genus had become detached from the ancestral stock of the Procyonidae.

Key words: *Pseudobassaris*, Procyonidae, Oligocene, Quercy, France.

Mieczysław Wolsan, Instytut Paleobiologii PAN, al. Żwirki i Wigury 93, 02-089 Warszawa, Poland.

Brigitte Lange-Badré, Laboratoire de Paléontologie des Vertébrés et Paléontologie Humaine, Université Pierre et Marie Curie (Paris VI), 4 place Jussieu, 75252 Paris Cedex 05, France.

Introduction

The arctomorph carnivoran mammals constitute a monophyletic taxon encompassing ursoids, pinnipeds, and musteloids. They are united by the derived development of the suprameatal fossa in the middle ear and the derived loss of the third upper molar (Wolsan 1993a). Their fossil record dates back to the late Eocene of North America (early Chadronian, about 36–37 Ma) from where the primitive ursoid *Parictis* has been reported (Stucky 1992). The early arctomorphs are, however, best documented from mid-Cenozoic strata of Europe, where they first appeared about 33–34 million years ago, following the Grande Coupure faunal turnover event at the Eocene–Oligocene boundary. The most abundant and best preserved material of Oligocene arctomorphs has been collected from phosphorite beds in southern France, the Phosphorites du Quercy.

The collections of fossil mammals from the Phosphorites du Quercy consist of old collections, which were established during the second half of the past century and in the early decades of this century, and new collections, which have originated within the last 30 years (Vianey-Liaud 1980; Legendre & Marandat 1986; Legendre *et al.* 1992). They cover the timespan from the Early-Middle Eocene transition to the late Early Miocene (Remy *et al.* 1987; Sigé *et al.* 1991). In contrast to the new collections, which are chronologically homogeneous and of known provenance and age, the old collections generally constitute mingled assemblages of faunas coming from different fillings of unknown exact location and age (Sigé *et al.* 1979; Vianey-Liaud & Legendre 1986). Both the old and new collections include remains of the earliest known musteloid arctomorphs.

The musteloids are distinguished by the apomorphic loss of the third lower molar (Schmidt-Kittler 1981). The major subgroups among the musteloids are the Mustelidae and the Procyonidae. The concept of these families has recently been refined by Wolsan (1993a, 1993b) who rediagnosed them on the basis of uniquely derived anatomical patterns of the suprameatal fossa. In contrast to ursoids, early pinnipeds, and non-mustelid and non-procyonid musteloids, which all retained the primitively shallow suprameatal fossa of small volume, as well as later pinnipeds, in which it is secondarily lost, the suprameatal fossa of mustelids and procyonids is enlarged, so that either its lateral wall is perpendicular to the roof of the external auditory meatus or it is excavated laterally into the squamosal bone dorsal to the meatal roof. Both these patterns make the fossa deep in appearance. Unlike mustelids, in which the lateral wall of the suprameatal fossa extends further ventrally than the medial wall, which may not be differentiated at all, the procyonid suprameatal fossa has both walls well developed and nearly equal in ventral extension. As evidenced by the rich fossil record of early musteloids from the Oligocene and Lower Miocene of Europe, the deep suprameatal fossae evolved independently in mustelids and procyonids (contrary to Schmidt-Kittler 1981). The mustelid suprameatal fossa originated in consequence of great

ventral elongation of its lateral wall, so that the lateral wall is higher than the medial one, whereas the procyonid suprameatal fossa developed through deep dorsal expansion of the roof of an initially shallow fossa and thereby preserved about equally high lateral and medial walls (Wolsan 1992, 1993a, 1993b, 1994).

The earliest and only Paleogene musteloid to exhibit the procyonid suprameatal fossa is *Pseudobassaris riggsi* from the lowermost part of the Upper Oligocene (earliest Chattian, about 29–30 Ma) of the Phosphorites du Quercy. The oldest Neogene procyonids are *Angustictis* and *Broiliana*, whose lineages evolved during the Early Miocene (Agenian and Orleanian) in Europe (Wolsan 1993a). All other known members of the Procyonidae are more advanced and restricted to North and South America, including the earliest New World procyonid, *Edaphocyon lautus*, from the upper part of the Lower Miocene (early Hemingfordian) of Nebraska (Baskin 1982, 1989). This pattern of procyonid occurrences strongly suggests Eurasia as the source area for the Procyonidae and the Oligocene epoch as the time of their divergence from primitive musteloids. Finds of Oligocene musteloid arctomorphs in Europe and Asia, especially their skulls, are therefore essential for solving the enigma of procyonid origin. A skull of such an arctomorph is described in this paper and its implications for procyonid ancestry are presented.

Abbreviations for collections: AMNH – American Museum of Natural History, New York, USA; BMNH – The Natural History Museum (formerly British Museum (Natural History)), London, England; BSP – Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; FSL – Centre des Sciences de la Terre, Université Claude Bernard (Lyon I), France; FSM – Laboratoire de Géologie, Université de Provence, Marseille, France; FSP – Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, Université de Poitiers, France; ISEZ – Instytut Systematyki i Ewolucji Zwierząt PAN, Cracow, Poland; MGHN – Musée Guimet d'Histoire Naturelle, Lyon, France; MHNM – Musée d'Histoire Naturelle, Montauban, France; MHNT – Muséum d'Histoire Naturelle, Toulouse, France; MNHN – Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France; MNHU – Museum für Naturkunde, Humboldt-Universität, Berlin, Germany; NMB – Naturhistorisches Museum, Basel, Switzerland; NMW – Naturhistorisches Museum, Vienna, Austria; PDV – private collection of D. Vidalenc, Saint Gaudens, France; PMR – private collection of M. Rummel, Weißenburg, Germany; PVPH – Laboratoire de Paléontologie des Vertébrés et Paléontologie Humaine, Université Pierre et Marie Curie (Paris VI), France; SMF – Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; VSGM – The Vernadsky State Geological Museum, Moscow, Russia; YPM-PU – Princeton University Collection, Yale Peabody Museum, New Haven, USA; ZM – Zoologisk Museum, Copenhagen, Denmark.

Other abbreviations: C – upper canine; I1, I2, I3 – upper incisors; M1, M2, M3 – upper molars; P1, P2, P3, P4 – upper premolars.

Description

The skull (Figs 1–4, Table 1) is stored in PVPH under catalogue number PVQ70-2. It comes from an old collection of the Phosphorites du Quercy. As indicated by the inscription on the specimen ('Mouillac'), it was excavated in the vicinity of the village Mouillac in southwestern France. The accurate location of this fossil site and the age of the skull are unknown.

Preservation (Figs 1–4). — The cavities and canals of the skull are filled with red marlstones and calcite crystals. The bones and tooth enamel are colored yellowish to light-brown with some black spots. The skull lacks the anterior and anterolateral parts of the rostrum, on the right side in particular; both zygomatic arches; a large portion of the dorsal surface of the interorbital and postorbital regions, especially on the right side, including the right supraorbital (or postorbital) process and the tip of the left one, as well as much of the frontal crests; fragments of the sagittal and nuchal (or lambdoidal) crests; small portions of the right temporal fossa; the antorbital process (or facial process of the lacrimal) on both sides; a part of the medial wall of the left orbit; the median palatal spine; both pterygoid hamulae; much of the glenoid (or mandibular) fossa and the postglenoid process on the right side, as well as their lateral parts on the left side; the right temporal crest; the right mastoid process; the posterior portion of the bony shelf between the mastoid and paroccipital processes on both sides; the right paroccipital process and the distal part of the left one; and the ventral surface of the left auditory bulla. The facial-palatal portion of the skull is divided by a conspicuous oblique fissure. Of the dentition, only fragments of roots of the left P1 and left and right P2, as well as partial crowns and roots of the left and right P3–M1, are retained.

Dorsal aspect of the skull (Fig. 1). — The skull is narrow and moderately dorsoventrally flattened. Its rostrum is pronounced. Judging from the preservation of the side walls of the rostrum, they were originally almost parallel to each other between the levels of C and P2. The nasal bones as preserved are elongated, nearly parallel-sided, with rounded posterior borders. They are posteriorly wedged in between the frontals for an extent of 8.5 mm to the level of the lacrimal fossa, being slightly less extended posteriorly than the ascending ramus of the maxillary bone. The sutures of the nasal and frontal bones, as well as the maxilla-jugal suture, remain unfused.

The postorbital constriction is marked. The bones of the postorbital constriction region and the interorbital area are partially broken away so that a natural cast of the nasal cavity is exposed in part. The supraorbital process, though devoid of its tip, is prominent, being shaped like a tetrahedron. As deduced from the preserved fragments of the frontal crests, they were marked and met each other slightly behind the postorbital constriction. The sagittal crest, which is well developed, deflects slightly from the midline towards the left side, some 5 mm anterior to its junction with the nuchal crest, making the posterodorsal portion of the

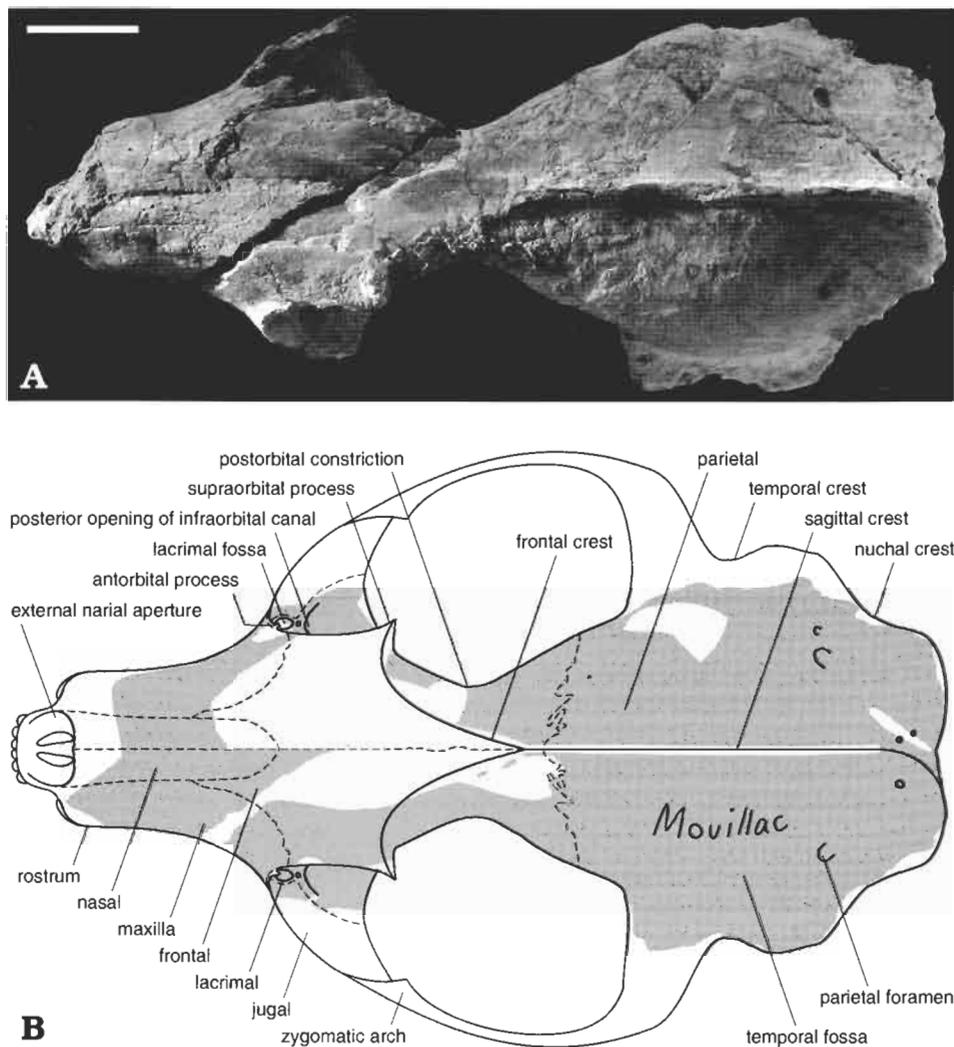


Fig. 1. Dorsal aspect of the arctomorph skull PVPH PVQ70-2 from Mouillac (old collection of the Phosphorites du Quercy). **A.** Original specimen dusted with ammonium chloride. **B.** Restoration, shaded areas indicate intact and exposed bony surfaces. Scale bar equals 10 mm.

cranium bilaterally asymmetrical in appearance. The nuchal crest is strong and overhangs the occiput to an extent of approximately 1–2 mm. The temporal crest is sharp and prominent where preserved.

The surface of the temporal fossa is rugged. In the posterodorsal quarter of either temporal fossa, within the parietal bone, there is a conspicuous elliptic parietal foramen measuring about 1.5 mm in greatest diameter and facing posteromediodorsad. The right parietal foramen is accompanied by a minute opening located 2.5 mm lateroventral to it.

Other tiny openings lie at the posterodorsal corner of the temporal fossa, one on the left side and two on the right side.

Lateral aspect of the skull (Fig. 2). — The dorsal profile of the skull rises at an angle of less than 15 degrees from the external narial aperture posteriorly to the posterior half of the sagittal crest, where it attains to its maximum height.

The anterior opening of the infraorbital canal, the infraorbital foramen, is about 3.5 mm high by 2 mm wide and elongated in a dorsolateral to ventromedial direction. Its lateral margin is positioned above the interalveolar septum between P3 and P4. Behind the infraorbital foramen, on the lateral surface of the zygomatic process of the maxillary bone, there is an extensive depression that is deepest between the lateral roots of P4. Another depression, the nasolabialis fossa, is situated above the infraorbital foramen directly in front of the orbit.

The anterior part of the medial wall of the orbit is concave and rounded. Its anteriormost portion is made up of a relatively large lacrimal bone that is in contact with the maxilla anteriorly and ventrally, the frontal dorsally and posterodorsally, the palatine posteroventrally, and the jugal laterally. Of the lacrimal sutures, only the lacrimal-palatine suture and the posterior (or orbital) portion of the lacrimal-maxilla suture are obliterated. The lacrimal bone entirely encompasses the lacrimal fossa that is a conspicuous, very deep funnel-shaped pit. Beneath the lacrimal fossa, on the posterior surface of the horizontal shelf between the fossa and the infraorbital canal, lies a minute orifice with a diameter of less than 0.5 mm. About 3 mm posteroventral to the lacrimal fossa there is a tiny, anteroposteriorly elongate depression delimited ventrally by the infraorbital ridge. The infraorbital ridge, which borders the medial wall of the orbit ventrally, is well pronounced in its anterior half.

The sphenopalatine and pterygopalatine canals open into a common fossa immediately below the infraorbital ridge and posteromedial to the posterior outlet of the infraorbital canal. Whereas the sphenopalatine foramen is placed on the vertical part of the lateral face of the skull, the pterygopalatine foramen lies within its horizontal part, so that only the former opening is visible in lateral view. The sphenopalatine and pterygopalatine foramina are separated from each other by a thin horizontal septum, with the latter aperture located posterolateroventral to the former. The sphenopalatine foramen is elongated anteroposteriorly and measures about 2 mm in greatest diameter. The pterygopalatine foramen is approximately half this size.

The ethmoid foramen is an ovate opening with a greatest diameter of almost 1 mm. Its posterior border is ventrally produced into a short, incompletely preserved ridge. Posteroventral to the ethmoid foramen, at the level where the braincase is narrowest, there is an elliptical, anteroposteriorly elongate fossa that contains the optic foramen at its posterior corner. The optic foramen is oval, elongated from anteromedial to posterolateral, and facing anterolaterad. The fossa for the optic foramen is

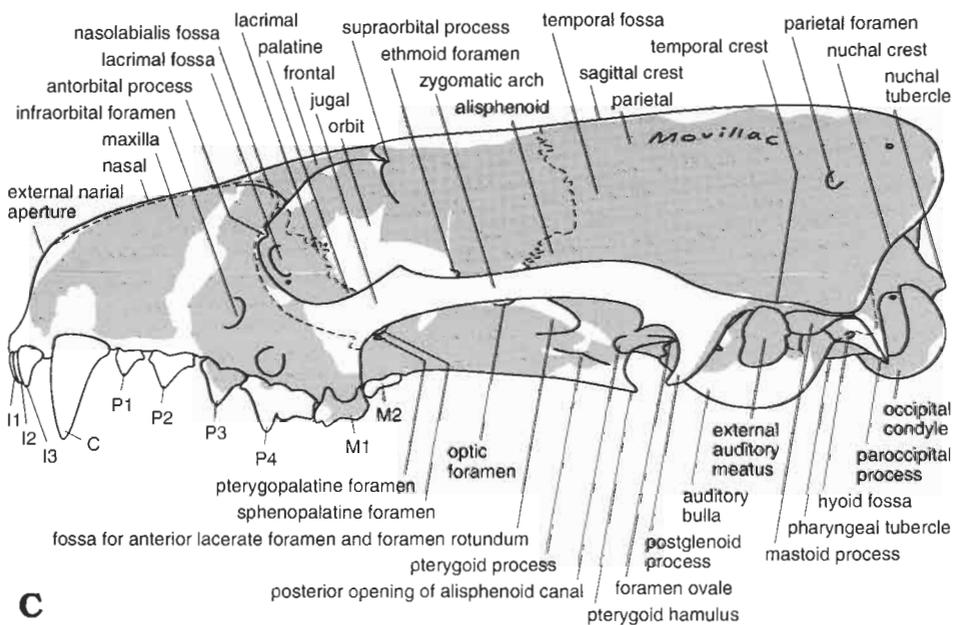


Fig. 2. Lateral aspects of the arctomorph skull PVPH PVQ70-2 from Mouillac (old collection of the Phosphorites du Quercy). **A.** Right lateral aspect of the original specimen dusted with ammonium chloride. **B.** Left lateral aspect of the original specimen dusted with ammonium chloride. **C.** Restoration of the left lateral aspect, shaded areas indicate intact and exposed bony and dental surfaces. Scale bar equals 10 mm.

dorsally separated by a distinct ridge from a small, anteroposteriorly elongate depression situated just posterior to the ethmoid foramen. Above this depression, within the temporal fossa, there is another, more extensive concavity in the frontal bone.

The anterior lacerate foramen (or orbital fissure) and the foramen rotundum lie in a common spacious fossa that is elongated from anteromedial to posterolateral and faces anterolaterad. Directly above this fossa there is a low, ridge-like elevation.

Ventral aspect of the skull (Fig. 3). — The palate is arched dorsad, both longitudinally and transversely. Its posterior margin is medially excavated to the level of the lingual alveolus of M2. Of the anterior palatine (or incisive) foramina, only the posterior parts of the left anterior palatine foramen and the median anterior palatine foramen are preserved. The palatine sulci are distinct. At the level of the anterior border of M1, either palatine sulcus is posteriorly terminated into the posterior palatine foramen that constitutes the anterior outlet of the pterygopalatine canal. Behind the right posterior palatine foramen lie five minute palatine foramina, whereas on the left side there are only four. The palatine tuberosity, which medially flanks the lingual alveolus of M2, is well developed. It is medially contiguous with a pronounced palatine notch. A shallow groove running from the palatine notch to a fossa between P4 and M1 can be distinguished on each side. The medial wall of this groove is posteriorly and ventrally continued into a ridge that passes posteriad to form a sharp ventral edge of the lateral wall of the nasopharyngeal fossa.

The pterygoid process is small and anteroposteriorly elongate. The posterior opening of the alisphenoid canal and the foramen ovale are placed in a common elongate fossa that is shallower on the left side. The glenoid fossa is elongated transversely and has a smoothly curved articular surface of semicircular shape in paramedian section. The postglenoid process, which buttresses the glenoid fossa posteriorly, is strong and overlaps the fossa to an extent of about 1 mm in ventral view.

The axial plate of the basicranium, which is formed by the presphenoid (lack of suture closure), basisphenoid, and basioccipital bones, as well as the ventral parts of both exoccipitals, becomes wider from the nasopharyngeal fossa posteriad. It is broadly concave between the auditory bullae, partly overlapping their medial surfaces. Posteriorly and medially, it is produced into a pharyngeal tubercle that is prominent and separated from the occipital condyles by a transversely oriented crescent-shaped depression. The pharyngeal tubercle tapers anteriorly and continues as a median ridge extending far anteriorly to a point between the levels of the foramen ovale and the posterior opening of the alisphenoid canal. Between the pharyngeal tubercle and the auditory bulla, two small tubercles can be identified. The posterior of them is located at the isthmus between the posterior opening of the carotid canal and the fossa containing the posterior lacerate foramen. The anterior tubercle is situated 5 mm anterior

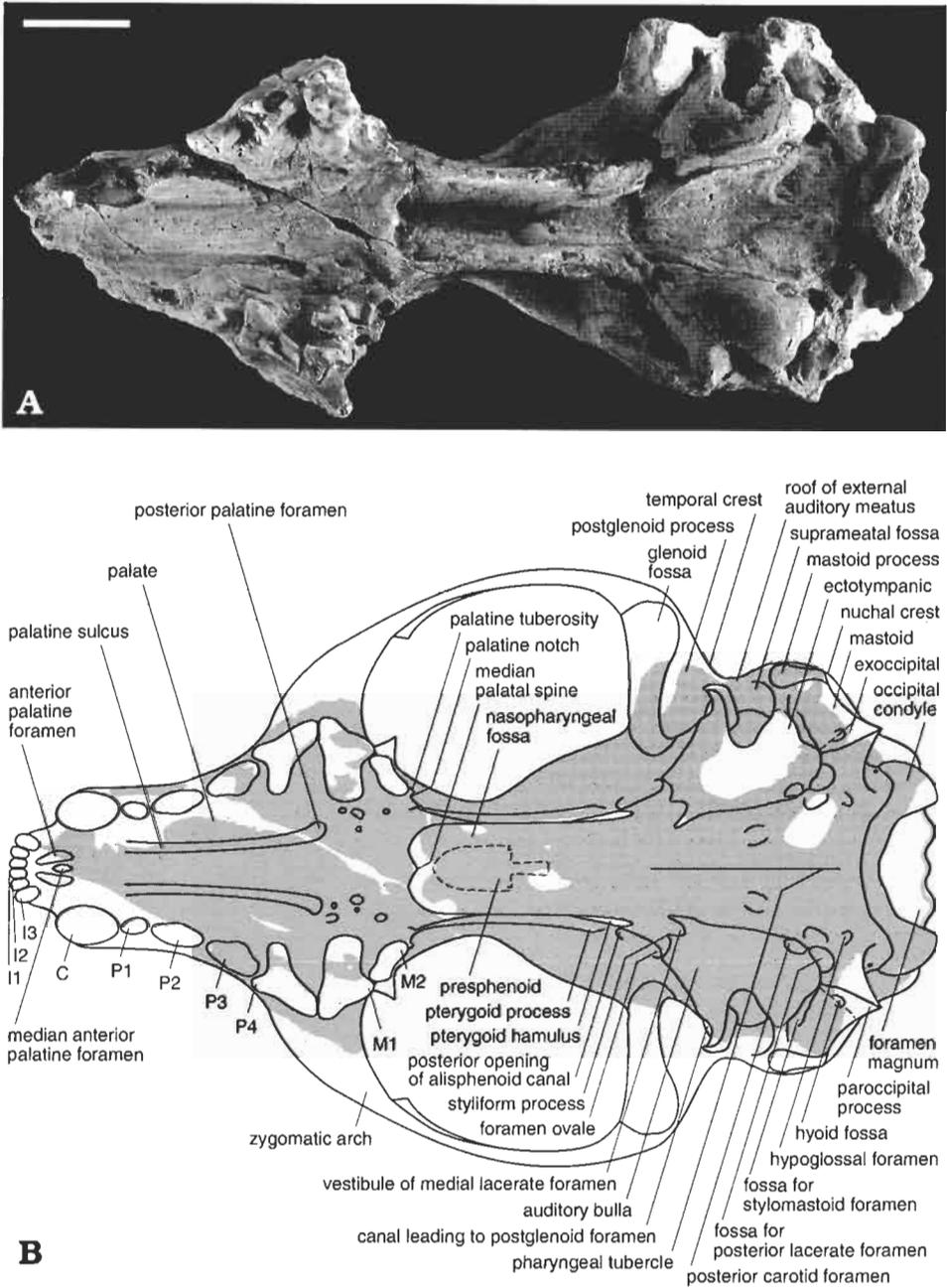


Fig. 3. Ventral aspect of the arctomorph skull PVPH PVQ70-2 from Mouillac (old collection of the Phosphorites du Quercy). **A.** Original specimen dusted with ammonium chloride. **B.** Restoration, shaded areas indicate intact and exposed bony and dental surfaces. Scale bar equals 10 mm.

and slightly medial to the posterior one. Between the posterior tubercle and the pharyngeal tubercle there is a depression.

The fossa that houses the posterior lacerate foramen lies at the posteromedial corner of the auditory bulla. It is a deep pit, with a roughly elliptic, approximately 3 mm by 1.5 mm diameter rim that is elongated from anteromedial to posterolateral. About 3 mm posteromedial to this fossa and within the basicranial axial plate lies the hypoglossal (or condyloid) foramen, which faces anterolateroventrad and is round with a diameter of about 1 mm.

The paroccipital process as preserved is broad, flattened, and directed posteroventrad. Its ventral surface and that of its base are divided into medial and lateral halves by a prominent anteroposterior ridge. On its posterior surface, the paroccipital process has a vertical swelling that dorsally curves posteromedial to reach the base of the occipital condyle. There is a well-defined fossa that is demarcated laterally and dorsally by this swelling, medially by the occipital condyle, and ventrally by a strong ridge running transversely from the paroccipital process to the base of the occipital condyle. In the dorsal part of this fossa lies a tiny foramen.

The paroccipital and mastoid processes are connected by a broad horizontal shelf that is mainly composed of the mastoid bone. While the lateral half of the ventral surface of this shelf is mostly bulged, the medial one is widely depressed. Within a deep recess at the bottom of this depression, immediately lateral to the ventral ridge that runs from the paroccipital process towards the auditory bulla, just on the unfused exoccipital-mastoid suture, sits the hyoid fossa. The mastoid portion of the paroccipital-mastoid shelf flanks posteriorly and posterolaterally a deep fossa leading to the stylomastoid foramen. This fossa is elongated from anterolateral to posteromedial and is larger than the fossa for the posterior lacerate foramen. On the right side, the tympanohyal is fused to the lateral wall of the fossa for the stylomastoid foramen to form the hyoid process that protrudes into the stylomastoid foramen.

The mastoid process is prominent, projecting laterad from the cranium. Its dorsal surface is flattened and made up of the nuchal crest. Ventrally, the mastoid process is bulged out into a rugose, approximately hemispheric swelling that flanks posterodorsally the external auditory meatus. In cross section the meatus is large, elliptical, and elongated from antero-medioventral to posterolaterodorsal. Directly over the meatus there is a horizontal shelf of the squamosal bone, measuring approximately 4 mm transversely. Its anterior portion, which is flanked anteromedially by the auditory bulla and anterolaterally by the postglenoid process, together with its very narrow lateral part, which is formed by the sharp temporal crest, constitute the bony roof of the external auditory meatus. The remainder of the horizontal shelf is occupied by the suprameatal fossa that is a part of the middle ear cavity.

The suprameatal fossa is elongated anteroposteriorly and is semicircular in shape both at the rim and in paramedian section. It lies in a plane

inclined to the horizontal plane so that its anterior half is positioned dorsally and its posterior half ventrally. Its posterior or ventral half, which is excavated into the medial base of the mastoid process, possesses the well-defined, edged posterior and lateral borders that received the tympanic membrane, which makes this part of the fossa well depressed in appearance. In contrast, the anterior or dorsal half of the suprameatal fossa, which takes up the posteromedial portion of the horizontal squamosal shelf posterior and medial to the roof of the external auditory meatus, has indistinct limits anteriorly and anterolaterally and appears to be only slightly depressed. As in many non-procyonid and non-mustelid arctomorphs, the suprameatal fossa is not excavated laterally into the squamosal dorsal to the roof of the external auditory meatus, nor is the lateral wall of the fossa perpendicular to the meatal roof. The fossa is roofed by the squamosal except for a small ventral part that is roofed by the mastoid bone. Along the line of their junction, the squamosal and the mastoid form a low transverse ridge, so that the suprameatal fossa effectively comprises two depressions.

The auditory bulla is single-chambered and inflated, particularly ventrally and posteriorly, attaining its maximum ventral inflation at the level of the external auditory meatus, where it projects approximately 5.5 mm below the interbullar plate of the basicranium. The external surface of the bulla is smooth except for the anterolateral portion where it is somewhat rugose. Although the ectotympanic and caudal entotympanic bones are coossified, the line of their juncture is discernible on the external surface of the bulla. This line passes from the vestibule of the medial lacerate foramen directly medial to the styliform process to the stylomastoid foramen, just medial to the longitudinal ventral elevation of the bulla. The ectotympanic contribution to the bulla is greater than that of the caudal entotympanic. The medial and posterior walls of the bulla, which are composed of the caudal entotympanic, slope steeper than the lateral wall made up of the ectotympanic.

Anteriorly, the auditory bulla extends to the posterior border of the foramen ovale. The anterior margin of the bulla is produced into three small but distinct projections that taper anteromediad. The most medial of these projections, which constitutes the anteromedial corner of the bulla, is formed by the caudal entotympanic, while the middle projection (or styliform process) and the most lateral one, which constitutes the anteriormost part of the bulla, are of the ectotympanic. Enclosed ventrally by the three anterior projections of the bulla and dorsally by the alisphenoid bone there is an irregular, horizontally elongate aperture facing anteromediad.

Laterally, the auditory bulla is widely excavated at the level of the external auditory meatus. It sends out an immense nodular projection of the ectotympanic, which ends about 2.5 mm medial to the edge of the temporal crest to flank the external auditory meatus anteriorly. The projection is broadly appressed to the dorsomedial part of the posterior

surface of the postglenoid process, bounding posteriorly an anteroposteriorly compressed canal that appears to lead to the postglenoid foramen. The dorsal extremity of this ectotympanic projection is slightly plunged into the squamosal anterior to the suprameatal fossa. Although the bulla appears to be firmly attached to the medial base of the mastoid process, the suture between the ectotympanic and mastoid bones remains unused.

The medial wall of the auditory bulla encloses the carotid canal, which opens posteriorly in front of and close to the fossa containing the posterior lacerate foramen. The posterior opening of the carotid canal, the posterior carotid foramen, is approximately elliptical in shape and elongated from anteroventral to posterodorsal, facing posteromedioventrad. On the left side it is completely surrounded by the caudal entotympanic, but on the right side the basioccipital contributes dorsally to its rim. The caudal entotympanic and the basioccipital are in contact immediately behind the posterior carotid foramen, so that the foramen and the fossa for the posterior lacerate foramen are actually separated from each other. This separation is, however, very slight because the caudal entotympanic-basioccipital contact measures approximately 1 mm in length on the left side and about 0.5 mm on the right side.

Posteriorly, the auditory bulla expands to a point between the level of the stylomastoid foramen and the level of the posterior border of the fossa for the posterior lacerate foramen. The posterior swelling of the bulla, which is formed by the caudal entotympanic, is medially bounded by the posterior carotid foramen, basioccipital, and fossa for the posterior lacerate foramen, posteriorly bounded by the exoccipital and mastoid, and laterally bounded by the fossa for the stylomastoid foramen. The least width of the swelling, measured between the fossa for the stylomastoid foramen and that leading to the posterior lacerate foramen, is smaller than the greatest diameter of the fossa for the stylomastoid foramen on both sides.

Posterior aspect of the skull (Fig. 4). — The foramen magnum is wide and dorsoventrally compressed, facing posteroventrad. Its ventral margin is broadly excavated. It is encircled by a bony band extending from the occipital shield for about 3–5 mm posteroventrad. The ventral half of this band, as well as that of the foramen magnum, are ventral to the plane of the basicranial axial plate. Laterally and ventrally, the band consists of the occipital condyles, the articular surfaces of which are continuous ventrally. Dorsally, the band is composed of a pair of prominent nuchal tubercles protruding posteroventrad and conjoined by a plate of bone that medially projects slightly posteroventrad. Immediately above this plate of bone, the occipital shield is transversely depressed. Directly over this depression there is a broad, vertically aligned median eminence that meets the nuchal crest at the dorsal corner of the occipital shield. This median eminence is flanked laterally by a pair of wide fossae that become narrower towards the roof of the foramen magnum. In turn, each fossa is bounded

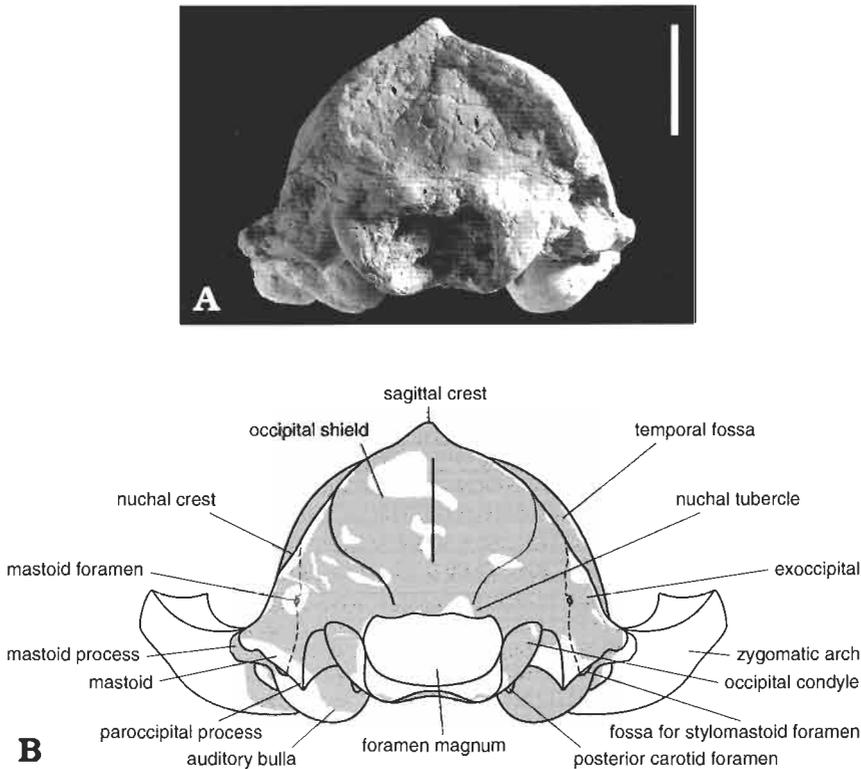


Fig. 4. Posterior aspect of the arctomorph skull PVPH PVQ70-2 from Mouillac (old collection of the Phosphorites du Quercy). **A.** Original specimen dusted with ammonium chloride. **B.** Restoration, shaded areas indicate intact and exposed bony surfaces. Scale bar equals 10 mm.

laterally by a broad swelling that tapers from the nuchal crest medioventrad to the nuchal tubercle. Lateral to that swelling, the occipital shield slopes considerably anterolaterad. The mastoid foramen is placed in the bottom of a deep, narrow fossa adjoining the suture between the exoccipital and mastoid bones.

Dentition (Figs 2–3, Table 1). — Of the incisor alveoli, only a part of the lateral wall of the alveolus for the left I3 is retained. The canine alveolus, which is partially preserved on the left side only, is voluminous and elongated from anteromedial to posterolateral.

The left P1 is represented by the basal portions of two roots, showing that the tooth was double-rooted. The retained fragment of the anterior root is situated slightly anterolateral to that of the posterior root and posterior to the canine alveolus. Its cross section measures merely 0.25 mm in greatest diameter, whereas for the posterior root the corresponding dimension is about 1.4 mm. On the right side neither P1 nor its alveoli are preserved.

P2 also had two roots, as indicated by their preserved basal parts.

P3 is double-rooted as well. Its crown, which is better preserved on the right side, is mostly formed by a large, buccolingually compressed cusp that is edged anteriorly and posteriorly. The occlusal part of this cusp is broken off on both sides, so that only the basal portions of its edges are retained. The anterior edge is straight, while the posterior one is arched linguad. Insofar as the base of the crown is preserved, it is encircled by a cingulum. Anteriorly and posteriorly, slightly lingual to its point of juncture with the anterior and posterior edges, respectively, the cingulum bulges out into a minor cuspsule. The lingual base of the crown is notably swollen medially, making its outline concave in front of and behind the swelling when viewed from the occlusal surface.

The crown of P4 is supported by three roots and has a prominent, tongue-like anterolingual or protocone wing that extends far linguad. A marked cingulum surrounds the base of the crown anteriorly and lingually, wherever it is preserved, except for the lingual part of the protocone wing, where the anterior cingulum vanishes into the anterior base of the protocone. Judging from its preservation, the protocone was approximately conical in form. There is no ridge from the protocone to the paracone.

M1 has two smaller roots buccally and a large one lingually. The anterobuccal root stands more buccally than the posterobuccal one, so that the former is clearly visible in posterior view. The paracone and metacone are about equal in size. The long axis of the metacone appears to be oriented anteroposteriorly, whereas that of the paracone deflects towards the parastyle wing. Although the parastyle wing of the crown is broken away on both sides, the buccal position of the anterobuccal root supporting it indicates that the wing was well developed and protruded buccally. The buccal border of the crown, which is paralleled by a cingulum, is gently excavated buccal to the notch dividing the paracone from the metacone. The buccal cingulum is posteriorly continuous with the posterior edge of the metacone. At the place of their junction, the posterior surface of the crown is slightly swollen to form a tiny metastyle. From the level of the metacone and linguad, the crown becomes shorter anteroposteriorly. Its lingual half is moderately deflected posteriad and occlusad, giving the posterior margin of the crown a widely concave contour in occlusal view and making the crown convex basally in posterior and anterior views. The protocone culminates close to the lingual margin of the crown at the level of the paracone, having its anterior and lingual slopes directly continuous with the surface of the anterolingual base of the crown. The protocone is anteriorly prolonged into an anterocrista (or anterior protocone crest) that arches softly to border the crown anteriorly in front of the paracone. The posterocrista (or posterior protocone crest), which reaches the metastyle and borders the crown posterolingual to the metacone, does not contact the protocone. The metaconule is little in size and located near the metacone. The talon is small and positioned behind the protocone. The postcingulum (or posterior cingulum) is preserved only at the lingual border of the talon, where it corresponds in its position to

Table 1. Measurements of the arctomorph skull PVPH PVQ70-2, in mm. Parentheses indicate estimated values. When available, dimensions of the left side are entered first.

Condylbasal length (from a line connecting the anteriormost points of the premaxillae to a line joining the posteriormost points of the occipital condyles, in median plane)	(86)
Median distance from a line connecting the anteriormost points of the canine alveoli to a line joining the posteriormost points of the occipital condyles	(81.5)
Palatal length (from the median point of a line connecting the anteriormost points of the premaxillae to the posteriormost point of the median palatal spine)	(37.5)
Maxillary toothrow length (greatest distance between the alveolar rims of C and M2)	(32.8)
Greatest distance between the rims of the anterobuccal alveolus of P4 and the posterobuccal alveolus of M1	10.6; 10.6
Least distance between the infraorbital foramen and the posterior border of the zygomatic process of the maxilla	–; 11.6
Temporal fossa length (greatest distance between the frontal and nuchal crests)	51.5; –
Postpalatal length (from the posteriormost point of the median palatal spine to the median point of a line joining the posteriormost points of the occipital condyles)	(48.5)
Greatest distance between the anterior and posterior margins of the fossa containing the foramen ovale and the posterior opening of the alisphenoid canal	5.3; 5.0
Median distance from a line connecting the posteriormost points of the oval foramina to a line joining the posteriormost points of the occipital condyles	25.9
Bulla length (greatest distance between the anterior and posterior borders of the auditory bulla)	14.6; 14.9
Least distance between the posterior carotid foramen and the opening leading to the anterior carotid and medial lacerate foramina	9.0; 9.1
Infraorbital width (least distance between the infraorbital foramina)	(20)
Interorbital width (least distance between the orbital rims)	(20.5)
Greatest distance between the alveolar rims of P4s	(26.5)
Least distance between the alveolar rims of M1s	14.7
Postorbital constriction width (between the lateralmost points of the postorbital constriction)	12.1
Meatal width (least distance between the lateral borders of the cranium above the external auditory meatus)	(35.5)
Mastoid width (between the lateralmost points of the mastoid processes)	(38.2)
Interbullar width (least distance between the auditory bullae)	8.2
Bulla width (greatest distance between the lateral and medial borders of the auditory bulla, perpendicular to the long axis of the bulla)	11.6; 11.4
Condylar width (between the lateralmost points of the occipital condyles)	19.1
Foramen magnum width (between the lateralmost points of the foramen magnum)	12.0
Foramen magnum height (from the dorsal to the ventral margins of the foramen magnum, in median plane)	7.7
P3 length (greatest distance between the anterior and posterior borders of the P3 crown)	–; (5.1)
P3 width (greatest distance between the buccal and lingual borders of the P3 crown, perpendicular to the P3 length)	–; 2.9
P4 buccal alveolar length (greatest distance between the rims of the anterobuccal and posterior alveoli of P4)	7.1; 7.1
P4 lingual alveolar length (greatest distance between the rims of the anterolingual and posterior alveoli of P4)	8.7; 8.4
P4 alveolar width (least distance from a line connecting the buccalmost points of the rims of the anterobuccal and posterior alveoli of P4 to the lingualmost point of the rim of the anterolingual alveolus of P4)	4.8; 5.0
M1 length (least distance from the anterior border of the M1 crown to the posteriormost point of the metacone wing of the M1 crown)	(4.6); –
M1 alveolar length (least distance from a line connecting the anteriormost points of the rims of the anterobuccal and lingual alveoli of M1 to the posteriormost point of the rim of the posterobuccal alveolus of M1)	–; 3.7
M1 alveolar width (greatest distance between the rims of the anterobuccal and lingual alveoli of M1)	–; 7.3
M2 alveolar length (least distance from a line connecting the anteriormost points of the rims of the anterobuccal and lingual alveoli of M2 to the posteriormost point of the rim of the posterobuccal alveolus of M2)	–; (2.0)
M2 alveolar width (greatest distance between the rims of the anterobuccal and lingual alveoli of M2)	–; 4.9

the hypocone, disappearing anteriorly into the posterolingual base of the protocone. Occlusally, the postcingulum exposes a vast dentine facet. Judging from the thickness of its retained basal portion and the size of the wear facet, the hypoconal postcingulum was originally swollen. The pre-cingulum (or anterior cingulum) is absent, though it is not unlikely that a tiny portion of it might have been present anterior to the protocone at the place where the base of the crown is slightly convex, before it was removed by wear that produced an irregular facet extensively affecting the protocone, the lingual portion of the anterocrista, the paracone, the metacone, and the trigon basin of the left M1. On the right M1, the crown of which is mostly destroyed, the corresponding part is not preserved.

The right M2 was three-rooted as shown by its three alveoli. The anterobuccal alveolus is little larger than the posterobuccal one, while the lingual alveolus is distinctly the largest. The posterobuccal alveolus is positioned posterior and slightly buccal to the anterobuccal alveolus, whereas the lingual alveolus is situated posterolingual to the two buccal alveoli. The buccal alveoli, which are in contact occlusally, are placed behind the lingual part of the buccal half of M1. The lingual alveolus is located behind and somewhat lingual to the lingual root of M1. On the left side, the horizontal plate of the maxilla is broken off posteriorly so that only the anterior fragments of two alveoli of M2 are retained, one buccally and the other lingually.

Discussion

The skull PVPH PVQ70-2 has a suprameatal fossa and congenitally lacks M3, which indicates that it represents an arctomorph. A comparison with arctomorphs of the Phosphorites du Quercy revealed its close affinity to the earliest known procyonid *Pseudobassaris* (Table 2).

The genus *Pseudobassaris* was erected by Pohle (1917) for his new species *Pseudobassaris riggsi* based on the skull YPM-PU 11455 from an old collection of the Phosphorites du Quercy, labelled as excavated 'near Caylus'. In his revision of early European musteloids, Wolsan (1993a) referred one more skull (ZM 144) to *Pseudobassaris*. This skull was described by Winge (1895, 1924, 1941) under the name *Amphictis* and by de Beaumont (1968) as *Cynodictis compressidens* var. *viverroides*. It is also a part of the old collections of the Phosphorites du Quercy. According to its label, it comes from 'Mouillac'. The identity of the precise locality of ZM 144 and that of PVPH PVQ70-2 is uncertain, however, because the old collection of Mouillac (and also that of Caylus) encompasses fossils that come from various fillings of unknown accurate placement and age (Sigé *et al.* 1979; Vianey-Liaud & Legendre 1986).

Neither Wolsan (1993a) nor we were able to inspect the original of YPM-PU 11455. Only a cast of this specimen was studied by him and the same cast is available to us. A comparison of ZM 144 with this cast and

with the descriptions and illustrations of YPM-PU 11455 published by Riggs (1898, as *Amphictis*), Hough (1948, as *Plesictis robustus*), and Schmidt-Kittler (1981, as *Mustelictis riggsi*) revealed no differences in size

Table 2. Distribution of craniodental character states in the arctomorph skull PVPH PVQ70-2 and the arctomorph genera of the Phosphorites du Quercy; after Wolsan (1993a) and on the basis of specimens from AMNH, BMNH, BSP, FSL, FSM, FSP, ISEZ, MGHN, MHNM, MHNf, MNHN, MNHU, NMB, NMW, PDV, PMR, PVPH, SMF, VSGM, and ZM. The cranial character states for *Pseudobassaris* are based on ZM 144 and a cast of YPM-PU 11455. The primitive state for each character is denoted by 'a', while 'b', 'c', and 'd' designate derived states. For each genus, the number of differences between its character state distribution and that of PVPH PVQ70-2 is given in parentheses following the generic name.

	Characters												
	1	2	3	4	5	6	7	8	9	10	11	12	13
PVPH PVQ70-2	a	a	a	a	b	a	a	a	b	a	a	b	a
<i>Amphictis</i> (4)	a	b	b	a	a	ab	a	ab	b	a	b	ab	a
<i>Amphicyonodon</i> (4)	a	a	a	a	a	a	a	b	b	a	b	a	a
<i>Bavarictis</i> (4)	a	a	a	a	a	b	a	b	b	a	b	b	a
<i>Cephalogale</i> (5)	a	a	a	a	a	b	a	b	b	a	b	a	a
<i>Mustelictis</i> (5)	a	b	a	a	a	a	c	b	a	a	ab	b	a
<i>Pachycynodon</i> (6)	a	a	b	a	a	b	a	b	b	a	b	a	a
<i>Plesictis</i> (10)	b	b	b	b	ab	b	c	b	ab	b	b	b	b
<i>Pseudobassaris</i> (2)	a	a	a	a	b	a	b	b	b	a	a	b	a

Definitions of the character states:

1. Dorsal cranial crests Y-shaped, so that a sagittal crest is present (a), or about parallel to each other, so that strong parasagittal crests are developed in adults (b).
2. Parietal foramen or foramina present (a) or absent (b).
3. Posterior border of the palate situated at the level of the posteriormost upper teeth in adults (a) or behind them (b).
4. Alisphenoid canal present (a) or absent (b).
5. Caudal entotympanic and basioccipital separated from each other behind the posterior carotid foramen in adults, so that the posterior carotid and posterior lacerate foramina lie in a common fossa (a), or meet each other directly behind the posterior carotid foramen so that the posterior carotid foramen is detached from the fossa leading to the posterior lacerate foramen (b).
6. External auditory meatal trough of ossified ectotympanic absent in adults, so that the auditory bulla is extensively excavated lateroventrally (a), or present (b).
7. Suprameatal fossa shallow, that is neither is it excavated laterally into the squamosal dorsal to the roof of the external auditory meatus nor is the lateral wall of the suprameatal fossa perpendicular to the meatal roof (a), or deep, that is, it is laterally excavated into the squamosal dorsal to the external auditory meatal roof or the lateral wall of the suprameatal fossa is perpendicular to the meatal roof, with the medial and lateral walls of the fossa being about equal in ventral extension (b) or with its medial wall absent or considerably smaller in ventral extension than it is in the lateral wall (c).
8. P1 double-rooted (a) or single-rooted (b).
9. P4 protocone angulated occlusally into a ridge running towards the paracone (a) or not angulated (b).
10. Anterior and posterior borders of the lingual half of the crown of M1 curved and diverging (a) or straight and parallel (b).
11. Precingulum and postcingulum of M1 not continuous (a) or continuous around the lingual base of the protocone (b).
12. M1 posterocrista complete (a) or discontinuous to absent (b).
13. M2 three- to double-rooted (a) or single-rooted to absent (b).

Table 3. Comparison of the arctomorph skull VVPH PVQ70-2 with those of *Pseudobassaris riggsi* (ZM 144 and a cast of the holotype YPM-PU 11455). The primitive state for each character is designated by 'a', while 'b' indicates the derived state. For definitions of conditions 7a and 7b (suprameatal fossa) see Table 2.

Character	VVPH PVQ70-2	YPM-PU 11455	ZM 144
Alisphenoid canal	prominent (a)	prominent (a)	reduced (b)
Caudal entotympanic	poorly inflated posteriorly, so that the posterior carotid foramen and the fossa for the posterior lacerate foramen are weakly detached from each other, and the least width of the auditory bulla between the fossa for the posterior lacerate foramen and the fossa for the stylomastoid foramen is smaller than the greatest diameter of the fossa for the stylomastoid foramen (a)	poorly inflated posteriorly, so that the posterior carotid foramen and the fossa for the posterior lacerate foramen are weakly detached from each other, and the least width of the auditory bulla between the fossa for the posterior lacerate foramen and the fossa for the stylomastoid foramen is smaller than the greatest diameter of the fossa for the stylomastoid foramen (a)	well inflated posteriorly, so that the posterior carotid foramen and the fossa for the posterior lacerate foramen are well detached from each other, and the least width of the auditory bulla between the fossa for the posterior lacerate foramen and the fossa for the stylomastoid foramen is greater than the greatest diameter of the fossa for the stylomastoid foramen (b)
Suprameatal fossa	shallow (7a)	?deep, of procyonid type (7b)	deep, of procyonid type (7b)
P1	double-rooted (a)	single-rooted (b)	single-rooted (b)
M1 precingulum	absent or poorly developed (a)	prominent (b)	absent or poorly developed (a)
M2	large and three-rooted (a)	large and three-rooted (a)	small and two-rooted (b)

or morphology, except some dissimilarities apparently resulting from individual variation, especially due to different ontogenetic ages (ZM 144 represents an adult animal, whereas YPM-PU 11455 is a subadult individual). This plainly confirms de Beaumont's (1968) supposition that the two skulls belonged to the same species. Unfortunately, the external auditory meatus of each bulla had been plugged up before the cast available to us was made, so that no details of the middle ear, including the suprameatal fossa, are visible. However, Hough (1948: 89), who studied the ear region of YPM-PU 11455, described it as having 'a deep suprameatal fossa', which has led us to assume, as did Wolsan (1993a), that the fossa of YPM-PU 11455 is shaped like that in ZM 144, that is, it is of the procyonid type. Although the exact age of the skulls is unknown, their approximate earliest Late Oligocene age can be estimated on the basis of the earliest Late Oligocene (earliest Chattian, Mammal Paleogene Reference Level MP 25) occurrences of remains attributable to *Pseudobassaris riggsi* in several new collections from the Phosphorites du Quercy (Belgarite 4A, M. Wolsan & C. Mödden, unpublished; Belgarric 1, de Bonis & Cirot 1995: fig. 9, as '*Mustelictis*' cf. *robustus*; Rigal-Jouet, de Bonis & Cirot 1995: fig. 8, as '*Mustelictis*' *robustus*).

The size and morphological characteristics of the arctomorph skull VVPH PVQ70-2 closely match those of *Pseudobassaris riggsi* (Table 3),

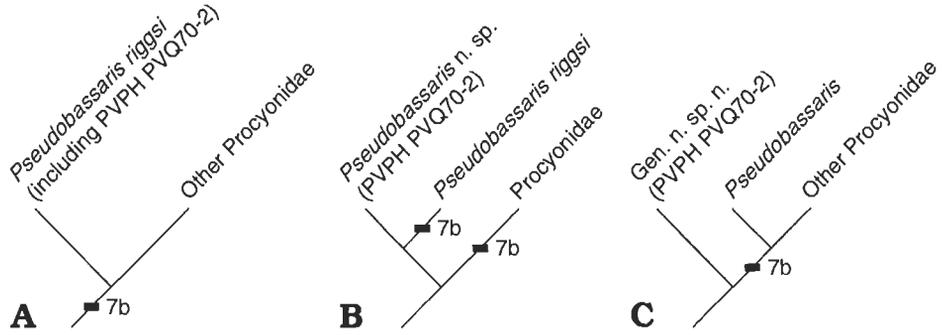


Fig. 5. Competing hypotheses for the relationships among the arctomorph represented by PVPH PVQ70-2, *Pseudobassaris riggsi*, and the Procyonidae. **A.** PVPH PVQ70-2 as an individual of the early procyonid species *Pseudobassaris riggsi*: the procyonid suprameatal fossa (7b, for definition see Table 2) first appeared in a common ancestor of *Pseudobassaris* and other procyonids but it was still of variable occurrence within *Pseudobassaris riggsi*. **B.** PVPH PVQ70-2 as a representative of a new *Pseudobassaris* species ancestral to *Pseudobassaris riggsi*: the procyonid suprameatal fossa (7b) appeared in *Pseudobassaris riggsi* and the Procyonidae independently. **C.** PVPH PVQ70-2 as a member of a new species of a new genus of the procyonid stem group: the procyonid suprameatal fossa (7b) appeared in a common ancestor of *Pseudobassaris* and other procyonids.

plausibly approaching a hypothetical primitive procyonid morphotype. The only, but methodologically fundamental, departure from this morphotype is the lack of the procyonid suprameatal fossa, which is the crucial synapomorphy of the Procyonidae (Wolsan 1993a, 1993b). Because the specimen PVPH PVQ70-2 differs from every known procyonid, including the individuals assigned to *Pseudobassaris riggsi* (Table 3), in plesiomorphic features only, three major competing hypotheses regarding its phylogenetic and taxonomic status can be put forward (Fig. 5).

Hypothesis A (Fig. 5A) proposes PVPH PVQ70-2 as a representative of *Pseudobassaris riggsi*. The procyonid suprameatal fossa first appeared in a common ancestor of *Pseudobassaris* and other procyonids but was still of variable occurrence within *Pseudobassaris riggsi*. The genus *Pseudobassaris* constitutes one of the earliest offshoots from the procyonid phylogenetic tree.

Hypothesis B (Fig. 5B) recognizes PVPH PVQ70-2 as an individual of a new species of *Pseudobassaris*, ancestral to *Pseudobassaris riggsi*. The procyonid suprameatal fossa arose in *Pseudobassaris riggsi* and in the Procyonidae independently. Thus, *Pseudobassaris* is not a procyonid.

Hypothesis C (Fig. 5C) envisions PVPH PVQ70-2 as a member of a new species of a new genus of the paraphyletic procyonid stem group. The procyonid suprameatal fossa emerged in a common ancestor of *Pseudobassaris* and other procyonids after the new genus had become detached from the ancestral stock of the Procyonidae, unless that genus is paraphyletic. The genus *Pseudobassaris* remains one of the earliest procyonids.

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Czaszka arktomorfa z fosforytów Quercy a pochodzenie szopowatych

MIECZYŚLAW WOLSAN and BRIGITTE LANGE-BADRÉ

Streszczenie

Arctomorpha stanowią monofiletyczną grupę ssaków drapieżnych odznaczających się dwiema synapomorfiami: obecnością *fossa suprameatale* w uchu środkowym oraz brakiem trzeciego górnego zęba trzonowego. Grupa ta obejmuje nadrodzinę niedźwiedzi i dużych pand (Ursoidea), płetwonogie (Pinnipedia) oraz Musteloidea. Te ostatnie odróżniają się od pozostałych Arctomorpha synapomorficznym brakiem trzeciego dolnego zęba trzonowego i reprezentowane są współcześnie przez trzy rodziny: małe pandy (Ailuridae), łasicowate (Mustelidae) i szopowate (Procyonidae).

Synapomorfia szopowatych, która odróżnia je od wszystkich innych Arctomorpha, jest w szczególności powiększona *fossa suprameatale*. Zwiększenie jej objętości u szopowatych było wynikiem znacznego wpuklenia się kości łuskowej, najpierw ku górze, a potem także odśrodkowo, toteż ściana wewnętrzna i zewnętrzna *fossa suprameatale* są mniej więcej tak samo wysokie, a także ściana zewnętrzna jest prostopadła do powierzchni

brzuszej stropu przewodu słuchowego zewnętrznego lub w ten strop zagłębiona ponad jego powierzchnią brzuszną. Chociaż naturalny zasięg szopowatych ogranicza się obecnie do Ameryki Północnej i Południowej, to jednak najwcześniejsi i najprymitywniejsi przedstawiciele tej rodziny znani są z dolnej części górnego oligocenu (rodzaj *Pseudobassaris*) oraz z dolnego miocenu (rodzaje *Angustictis* i *Broiliana*) Europy, co sugeruje, że Procyonidae wyodrębniły się z prymitywnych Musteloidea w oligocenie na kontynencie eurazjatyckim.

Opisana w tej pracy czaszka przedstawiciela *Arctomorpha* (Fig. 1–4, Tab. 1) pochodzi ze starej kolekcji z górnopaleogeńskich złóż fosforytów w południowej Francji (Phosphorites du Quercy). Jej porównanie z czaszkami arktomorfów znanych z fosforytów Quercy wykazało duże podobieństwo do *Pseudobassaris riggsi* (Tab. 2–3), będącego najwcześniejszym znanym szopowatym. Pod względem cech morfologicznych, czaszka ta jest prymitywniejsza zarówno od dostępnych okazów *Pseudobassaris riggsi*, jak i wszystkich innych znanych szopowatych, nieomal odpowiadając hipotetycznemu prymitywnemu morfotypowi rodziny Procyonidae. Jedyną — lecz pod względem metodologicznym zasadniczą — różnicą w stosunku do tego morfotypu jest brak w opisanej czaszce synapomorfii rodziny szopowatych. W jej miejscu występuje plezjomorficznie płytko *fossa suprameatale* prymitywnych *Arctomorpha*.

Aby ustalić pozycję filogenetyczną i status taksonomiczny arktomorfa reprezentowanego przez opisaną czaszkę, wysunięto trzy współzawodniczące hipotezy (Fig. 5). Zgodnie z hipotezą A (Fig. 5A), która traktuje tego arktomorfa jako osobnika gatunku *Pseudobassaris riggsi*, głęboka *fossa suprameatale* szopowatych pojawiła się wprawdzie po raz pierwszy u wspólnego przodka rodzaju *Pseudobassaris* i innych Procyonidae, lecz była jeszcze cechą zmienną w obrębie *Pseudobassaris riggsi*. Hipoteza B (Fig. 5B), według której dyskutowany arktomorf reprezentuje nowy gatunek rodzaju *Pseudobassaris*, będący gatunkiem macierzystym dla *Pseudobassaris riggsi*, sugeruje, że powiększona *fossa suprameatale* powstała niezależnie u *Pseudobassaris riggsi* i szopowatych, wyłączając w ten sposób rodzaj *Pseudobassaris* z rodziny Procyonidae. Hipoteza C (Fig. 5C), która uznaje omawianego arktomorfa za przedstawiciela nowego gatunku nowego rodzaju parafiletycznej grupy wyjściowej dla Procyonidae, zakłada, że głęboka *fossa suprameatale* szopowatych jest odziedziczona przez rodzaj *Pseudobassaris* i pozostałe Procyonidae po ich wspólnym przodku, który zaistniał w linii prowadzącej do szopowatych po oddzieleniu się od niej tego nowego rodzaju, chyba że rodzaj ten jest parafiletyczny.