Anatomy of the Temporal Bone in the Oligocene Anthropoid *Apidium* and the Origin of Anthropoidea

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Abstract. An associated group of cranial fragments and upper teeth of *Apidium phiomense* from the Oligocene of Egypt includes two fragments of the right temporal bone. The petrosal fragment preserves part of a large unbranched carotid canal similar to that of all Anthropoidea. The squamosal fragment demonstrates that there was no ossified ectotympanic lateral to the bulla, and that the anterior crus of the tympanic annulus was not fused to the squamosal. This suggests the presence in *Apidium* of a free tympanic ring within the bulla similar to that of Eocene lemuroid primates. Osteological and paleontological evidence favors the view that Anthropoidea evolved directly from lemuroid ancestors, without passing through an intermediate tarsioid stage.

Key Words
Oligocene Anthropoidea
Apidium
Os temporale
Origin of Anthropoidea

Introduction

The first primate specimen from Oligocene sediments of the Fayum Province of Egypt, a partial mandible, was described by OSBORN [1908] and named *Apidium phiomense*. OSBORN cautiously did not assign the species to any order, but suggested a possible relationship to Primates or to certain Eocene artiodactyls. SCHLOSSER [1910, 1911] described three additional primate species from the Egyptian Oligocene and proposed that OSBORN's mandible of *Apidium* represented a primate related to early cercopithecid monkeys. This suggestion was further discussed and supported by GREGORY [1920–21]. Later PIVETEAU [1957] and HÜRZELER [1958, 1968] disagreed, stating that the *Apidium* mandible belonged to a condylarth, not a primate. More recently Yale expeditions to Egypt have collected a large number of new specimens of *Apidium*, and SIMONS [1960, 1962, 1971, 1972] has discussed at length the dental and cranial evidence demonstrating that *Apidium* is an anthropoid primate.

Apidium phiomense is the most common mammal found in Yale Quarry I in the Upper Fossil Wood Zone of the Jebel el Qatrani Formation, Egypt. In 1967, SIMONS found an associated group of cranial fragments and upper teeth of *Apidium phiomense* (Yale Peabody Museum No. 23968) at Quarry I. This assemblage includes a broken frontal which demonstrates that the more complete frontal previously described by SIMONS [1959] belongs to *A. phiomense* [SIMONS, 1970]. The find also includes two fragments of a right temporal bone of *Apidium*, which with careful preparation have revealed details of the temporal anatomy of *A. phiomense*. The temporal anatomy of *Apidium* is particularly important as it provides new evidence on the origin of Anthropoidea.

Petrosal

The larger of the two temporal fragments (fig. 1) is a right petrosal preserving the cochlea and the semicircular canals of the inner ear. The petrosal fragment is broken in front of the internal acoustic meatus and immediately behind the posterior semicircular canal. On its anterodorsal surface the hiatus of the facial canal and a sharp petrosal crest are preserved, but the internal opening of the carotid canal is broken away. The internal acoustic meatus, which contained the facial (VII) and acoustic (VIII) cranial nerves, and the subarcuate fossa penetrating the semicircular canals are both intact.
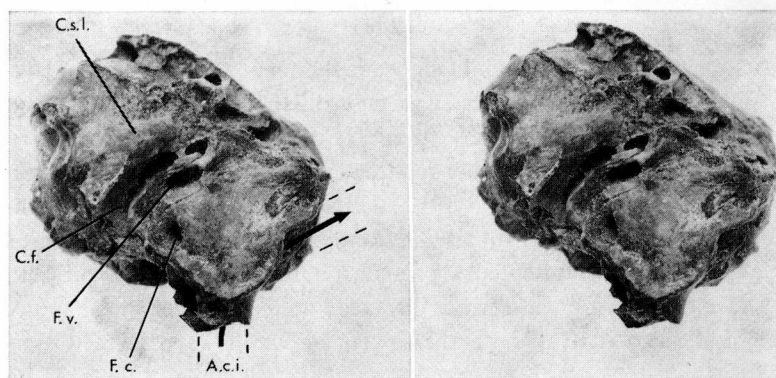

Fig. 1. Stereophotograph of lateral view of right petrosal of *Apidium phiomense* (YPM 23968, ×4.0). A.c.i. = Arteria carotis interna; C.f. = canalis facialis; C.s.l. = canalis semicircularis lateralis; F.c. = fenestra cochleae; F.v. = fenestra vestibuli.

The ventral or tympanic surface of the petrosal (fig. 1) is in remarkably good condition, especially considering that the specimen was preserved in a sandy sediment. Much of the facial canal (C.f.) has been broken open, and its external opening, the stylomastoid foramen, is not preserved. Above the facial canal is a large convexity, the lateral semicircular canal (C.s.l.). Below and in front of the facial canal are the oval vestibular fenestra (F.v., length = 1.2 mm, width = 0.4 mm) and the round cochlear fenestra (F.c., diameter = 0.8 mm). A distinct groove, apparently part of the tympanic plexus, begins behind and just above the cochlear fenestra and crosses the promontorium below the vestibular fenestra. At the anteroventral corner of the vestibular fenestra the groove penetrates a bony process via a canal (now partially plugged with sediment) and continues anteriorly. Immediately in front of the vestibular fenestra is a fossa, from which the tensor tympani muscle originated. Behind the vestibular fenestra is a circular depression for the origin of the stapedial muscle. Just below and slightly in front of the cochlear fenestra are three small denticles, the function of which is unknown.

The most interesting feature of the *Apidium* petrosal fragment is the preserved ventral portion of the canal for the internal carotid artery (A.c.i., represented by dashed lines and an arrow in figure 1). A 2-mm length of the carotid canal is intact, including part of its lower aperture. The internal diameter of the canal is 1.0 mm, which is approximately the size of the canal in a similar sized monkey such as *Aotus trivirgatus*. There clearly was no stapedial branch of the internal carotid artery. This is an important characteristic in which *Apidium* resembles higher primates or Anthropoidea, and differs from *Tarsius* and all other prosimians [except *Phaner*, see SABAN, 1963]. In *Tarsius* the promontory or entocarotid branch of the internal carotid carries the chief arterial supply to the brain. In anthropoids the same is true, but the internal carotid is greatly enlarged, a development correlated with increased brain size [VAN DER KLAAUW, 1931]. The presence of an enlarged internal carotid artery in *Apidium* is thus an indication that this Oligocene primate had reached an anthropoid grade of cerebral size and organization.

Squamosal and Ectotympanic

The second temporal fragment of *Apidium phiomense* is a portion of the right squamosal (fig. 2), including the posterior part of the mandibular fossa (F.m.), the retroarticular process (P.r.) and the retroarticular foramen (F.r.). The medial surface of the fragment articulated with the greater wing of the
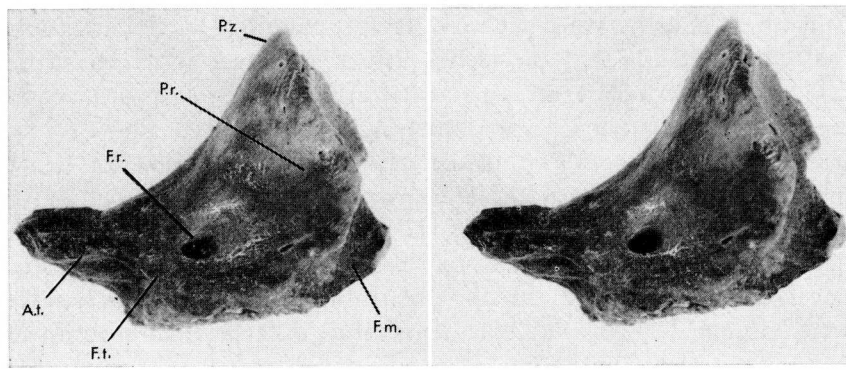
Fig. 2. Stereophotograph of ventral view of right squamosal of *Apidium phiomnsee* (YPM 23968, ×4.0). A.t. = Anulus tympanicus; F.m. = fossa mandibularis; F.r. = foramen retroarticulare; F.t. = fossa tympanica; P.r. = processus retroarticularis; P.z. = processus zygomaticus.

sphenoid. On the ventral surface, behind the retroarticular foramen, the proximal end (posterior crus) of the tympanic ring (A.t.) is preserved, fused to the squamosal. Just posterior to this fusion the ring is broken, and most of it is missing. A small facet (F.t.) just behind and slightly medial to the retroarticular foramen received the distal end (anterior crus) of the tympanic annulus, which was not fused to the squamosal. The tympanic annulus was oriented nearly vertically on the skull, and placed just behind the medial edge of the retroarticular process. This position of the ring is typical of most primates.

The tympanic ring in *Apidium* was placed very near the lateral edge of the skull, which would preclude further lateral extension of the tympanic to form an auditory tube. In this character *Apidium* agrees closely with similar-sized South American monkeys. The primitive Oligocene hominoid *Aegyptopithecus zeuxis* also lacked an external auditory tube, even though the edge of the skull extends laterally almost 1 cm beyond the external border of the tympanic [SIMONS, 1972, fig. 93]. In *Aegyptopithecus*, as in many living and fossil primates, the tympanic was fused to the bulla and formed its lateral wall [SIMONS, 1969].

Discussion

Since publication of POCOCK's [1918] classification and GREGORY's monographs on fossil primates [GREGORY, 1920, 1920–21], most discussion of the

origin of Anthropoidea has divided the ancestral prosimians into two categories: 'lemuroids' and 'tarsioids'. SIMONS [1961] tabulated the dental and osteological characters by which living and fossil lemuroids and tarsioids are distinguished. The living *Tarsius* differs from lemurs and resembles higher primates in having postorbital closure, a short muzzle, a tubular ectotympanic extending out of the bulla, and the promontory branch of the internal carotid artery enlarged at the expense of the stapedial branch. These resemblances, together with the dry rhinarium, structure of the upper lip and nose, and nature of placentation led POCOCK [1918], HILL [1953], and others to propose that tarsioids and anthropoids are more closely related than either is to lemuroids. Thus the search for the ancestry of Anthropoidea has been largely confined to tarsioid fossil primates, and in particular to the Omomyinae. As it was described by SCHLOSSER [1911], the type mandible of *Parapithecus fraasi* from the Egyptian Oligocene seemed to link tarsioids and anthropoids, however, new specimens collected and described by SIMONS have clarified the mandibular morphology of this genus, demonstrating that the supposed tarsier-like character of the mandible was due to its incompleteness [SIMONS, 1972].

The characters of soft anatomy linking *Tarsius* and Anthropoidea cannot be identified in fossil specimens; thus it is very difficult to prove that they are characters acquired by a common ancestor of *Tarsius* and anthropoids after their separation from the lemuroid stock, and not primitive characters of primates retained by *Tarsius* and anthropoids or independently acquired characters. The osteological characters allying *Tarsius* with anthropoids can be determined in fossils and offer the best hope of solving the problem of tarsioid or lemuroid ancestry for Anthropoidea.

The earliest anthropoid primates are found in the Oligocene of Egypt [SIMONS, 1972]. It is clear from exceptionally well preserved skulls of the tarsioid *Necrolemur* [SIMONS and RUSSELL, 1960; SIMONS, 1961], and the lemuroids *Notharctus* [GREGORY, 1920] and *Adapis* [STEHLIN, 1912], together with related dental remains, that the ancestral stocks of tarsioid and lemuroid primates separated before middle Eocene time. These fossil skulls are also important in evaluating the osteological resemblances seen in the skulls of living *Tarsius* and Anthropoidea.

There is no evidence that any of the osteological resemblances distinguishing *Tarsius* and Anthropoidea from lemuroid primates are due to common inheritance. The manner of postorbital closure in *Tarsius* is different than that seen in anthropoids, implying that the postorbital closure of *Tarsius* parallels that of Anthropoidea and is not a character of common inheritance [SIMONS

and RUSSELL, 1960]. The earliest anthropoid skull *(Aegyptopithecus)* has a long lemur-like muzzle [SIMONS, 1972], which is atypical of tarsioid primates.

In the fossil tarsioid *Necrolemur* the bony tube for the promontory artery is only slightly larger than that for the stapedial artery [SIMONS and RUSSELL, 1960]. Considering this character in *Notharctus*, GREGORY [1920, p. 179] states that 'in *Notharctus*, as in *Adapis*, *Lemur*, *Propithecus*, and all other true lemurs except the Chirogaleinae, the main internal carotid (art. promontorii) was small', but this is misleading as it implies greater similarity of the internal carotid circulation of *Notharctus* to that of lemurs than in fact exists. In a Yale skull of *Notharctus* (YPM No. 11466) the bony stapedial and promontory canals are broken, which exposes a natural calcite cast of the interior of each canal, and permits their internal diameter to be measured. The internal diameter of the promontory canal of YPM 11466 is 0.6 mm, that of the stapedial canal is 0.4 mm. The cross-section of the promontory branch is thus more than twice that of the stapedial branch. For comparison, the diameter of each of these canals is approximately 0.4 mm in a specimen of *Lemur catta* (YPM No. 4987) of skull length equal to that of the *Notharctus* skull. According to HILL [1953, p. 82], in most Malagasy lemurs the stapedial is a large artery and the promontory artery minute. The skulls of *Necrolemur* and *Notharctus* demonstrate that the differences in internal carotid circulation which distinguish *Tarsius* from living lemurs had not appeared by the middle Eocene. Thus enlargement of the promontory artery and loss of the stapedial, characteristic of all anthropoids, could have occurred with equal probability in lemuroids or tarsioids.

The final osteological character shared by *Tarsius* and some anthropoids is an extended tubular ectotympanic. Most authorities [MAJOR, 1899; VAN KAMPEN, 1905; GREGORY, 1920; VAN DER KLAUUW, 1931; LE GROS CLARK, 1959; SIMONS, 1961, 1972; McKENNA, 1966; but not SZALAY, 1972] consider the lemur-like 'free' ectotympanic ring to be the primitive condition phylogenetically in Primates. Whether tree shrews are primitive Primates or primitive Insectivora, the fact that they have a free ectotympanic within the bulla substantiates this interpretation. *Necrolemur* [SIMONS and RUSSELL, 1960] and the early Oligocene omomyine *Rooneyia* [WILSON, 1966] both had a tubular ectotympanic similar to that of *Tarsius*. *Necrolemur* and *Rooneyia* are widely separated geographically and rather different morphologically, implying that a tubular ectotympanic was acquired early in the evolution of tarsioids. The primitive anthropoids *Apidium* and *Aegyptopithecus* and all living platyrrhine monkeys lack a tubular ectotympanic, which implies

that anthropoid primates were derived from a stock more primitive than any known tarsioid.

The tympanic of *Apidium* provides positive evidence that anthropoid primates evolved directly from a lemuroid ancestor. A U-shaped ectotympanic ossifies, and its posterior crus fuses to the squamosal early in ontogeny in all living primates. In those primates having the lateral margin of the bulla filled by the ectotympanic (i.e. all living anthropoids, lorisids, and *Tarsius*), the anterior crus also fuses to the squamosal early in ontogeny. This is presumably for structural reasons related to anchoring the bulla. In those forms having a 'free' ectotympanic ring enclosed within the bulla (lemuroids and tupaiids) the only function of the ring is to hold the tympanic membrane, and the anterior crus usually does not coossify with the squamosal. The fact that the anterior crus of the ectotympanic was not fused to the squamosal in *Apidium* suggests that *Apidium* had an ectotympanic similar in morphology and function to that of lemuroid primates.

Unfortunately the tympanic of *Apidium* is incomplete, but this primitive anthropoid apparently retained a 'free' ectotympanic while its contemporary *Aegyptopithecus* shows the more advanced condition (tympanic filling the lateral margin of the bulla) typical of living anthropoids. The tympanic morphology of *Apidium* and *Aegyptopithecus* indicates that a tarsioid origin of higher primates is unlikely, and suggests that anthropoid primates evolved from a lemuroid ancestor, possibly a species of the early Eocene *Pelycodus*, without passing through a tarsioid stage. The dental morphology of the earliest known catarrhine *Oligopithecus savagei* is consistent with this view [SIMONS, 1963, p. 73]. Furthermore, the presence of a fused symphysis and vertically implanted incisors in Eocene adapids is an important functional component of the feeding apparatus of early lemuroids linking them to the origin of Anthropoidea.

Finally, it should be noted that species of *Pelycodus* and its close relatives are common in the early Eocene of North America and Europe [RUSSELL *et al.*, 1967]; thus speculations about rafting anthropoid primates from Africa to South America [SARICH, 1970; HOFSTETTER, 1972] are probably unnecessary to explain the geographic distribution of living Anthropoidea.

Acknowledgements

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