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目录

Earliest complete dentition of an anthropoid primate from the Late Middle Eocene of Shanxi Province, China

摘要 (Abstract): The complete lower dentition of a new species of the basal anthropoid genus Eosimias shows a combination of primitive and derived traits unknown in other living or fossil primates. Eosimiids document an early structural phase in the evolution of higher primates.

全文文献: The extinct primate family Eosimiidae was first described in 1994 on the basis of fossils collected from the middle Eocene Shanghuang fissure-fillings of southern Jiangsu Province, China (1). Although fossils documenting several species of Eosimiidae are known, only one of these, Eosimias sinensis, has been described to date. Eosimias sinensis was originally interpreted as a member of an early basal radiation of anthropoid or higher primates, the taxon that today includes New and Old World monkeys, apes, and humans. Subsequently, the phylogenetic hypothesis that Eosimias is a basal anthropoid has been widely criticized, and several workers have even doubted its primate affinities (2-4). Here we describe a new eosimiid species, Eosimias centennicus (5), on the basis of fossils collected during May 1995 fieldwork in the Eocene Heti Formation, Yuanqu Basin, southern Shanxi Province, China (Fig. 1). (Figure 1 omitted) These new specimens include the first complete lower dentition of eosimiid primates ever found. The anatomical information yielded by these fossils confirms the anthropoid affinities of Eosimiidae, thus providing new data on temporal, biogeographic, and phylogenetic aspects of anthropoid origins.

Historically, the Heti Formation in the Yuanqu Basin yielded the first Eocene vertebrates (including the primate Hoanghonius stehlinii) to be discovered in China (6). The mammalian fauna from the Heti Formation is usually correlated with the Sharamurunian Land Mammal Age of Asia (7) and is therefore probably late middle Eocene in age. The cricetid rodent Pappocricetodon schaubii from Locality 1 in the Zhaili Member of the Heti Formation (8), the same locality that yielded the eosimiid primate fossils described here, is morphologically more derived than is P. antiquus, which occurs in the Shanghuang fissure-fillings (9). Indeed, all available biostratigraphic evidence suggests that the new eosimiid fossils from the Yuanqu Basin are somewhat younger than E. sinensis from Shanghuang. This interpretation is consistent with the anatomy of the eosimiids themselves, because the dentition of E. centennicus is slightly more derived than that of E. sinensis (5).

The most complete specimen of E. centennicus from the Heti Formation consists of left and right dentaries of a single individual (Figs. 2 and 3). (Figures 2 and 3 omitted) The symphysis and all lower tooth crowns (I sub 1 through M sub 3) are preserved on the right side, whereas only the crowns of the incisors are missing from the left. Additionally, the posterior part of the left dentary, including the coronoid process, condyle, and angle, is preserved.

The symphysis is unfused in E. centennicus, as is the case in other basal anthropoids such as Catopithecus from the Fayum, Egypt (4). In this primitive feature Eosimias also resembles many Eocene omomyids and adapiforms, although some adapiform taxa evolved fused mandibular symphyses in parallel with derived anthropoids. However, Eosimias differs from Eocene omomyids and adapiforms (and resembles other anthropoids) in having a symphyseal region that is dorsoventrally deep and anteroposteriorly abbreviated. In Eocene omomyids and adapiforms, the symphyseal region is more gracile in the dorsoventral dimension and is noticeably procumbent. Even adapiform taxa in which the symphysis is fused (for example, Notharctus, Mahgarita, and Adapis) show this primitive, gracile, and procumbent symphyseal morphology.

The two lower incisors are vertically implanted in Eosimias, and I sub 1 is smaller than I sub 2 , as is the case in other early anthropoids for which the lower incisors are known. Vertical implantation of the lower incisors is undoubtedly a derived resemblance between Eosimias and other early anthropoids, because omomyids and

adapiforms possess lower incisors that are invariably implanted in at least a slightly more procumbent position. The angle of implantation of the lower incisors is probably correlated with the differences in symphyseal morphology noted earlier. On the other hand, I sub 1 <I sub 2 likely represents the primitive condition in primates, because this character also occurs in adapiforms and omomyids suck as Washakius (10).

The morphology of the lower incisor crowns has figured prominently in debates on anthropoid relationships (4, 11). In Eosimias, I sub 1 and I sub 2 have slightly convex labial surfaces and moderately concave lingual surfaces. I sub 2 bears a lingual cingulid that completely surrounds the concave lingual surface of the crown. A similar lingual cingulid appears to have been present on I sub 1 , but the morphology of this crown is slightly obscured by wear. Mesiodistally, both incisor crowns are widest near their bases. The apex of I sub 2 is pointed; a similar condition may well have characterized I sub 1 . The roots of both incisors are remarkably long and are much wider in the labiolingual dimension than mesiodistally. The crowns of I sub 1 and I sub 2 in Eosimias differ morphologically from both the spatulate condition common in Eocene adapiforms and many anthropoids, and the more conical, pointed condition found in many omomyids (11, 12). However, only subtle differences in lower incisor morphology distinguish Eosimias from such undoubted anthropoids as Arsinoea. The incisors of Eosimias are smaller relative to the cheek teeth than is the case in other basal anthropoids. It seems likely that the nonspatulate morphology and relatively small size of the lower incisors in Eosimias are primitive with respect to other anthropoids.

The lower canine in Eosimias is robust, projecting well above the crowns of the remainder of the lower dentition. The crown itself is slightly recurved and daggerlike. A well-defined lingual cingulid is continuous from the apex of the crown mesially to near its base, where the cingulid also lines the distal margin of the tooth. The broken left canine reveals that the root of this tooth is long and voluminous, extending virtually to the inferior margin of the dentary.

Eosimias centennicus possesses three lower premolars (P sub 2 through P sub 4), as do other basal anthropoids and many omomyids and adapiforms. However, primitive omomyids and adapiforms retained an additional lower premolar (P sub 1) that was lost at some point in anthropoid phylogeny (13). Also as in other basal anthropoids and all omomyids, P sub 2 in Eosimias is single-rooted rather than double-rooted. In contrast, P sub 2 is double-rooted in primitive adapiforms, although such derived adapiforms as Mahgarita convergently attained the single-rooted condition. The crown of P sub 2 is diminutive in Eosimias, only slightly larger than that of I sub 2 . In this respect, Eosimias differs from many other basal anthropoids (for example, Arsinoea, Serapia, and many platyrrhines), but it is unclear whether the relatively small P sub 2 of Eosimias is primitive or derived with respect to other basal anthropoids. The morphologically simple crown of P sub 2 is dominated by a single cusp, and the crown as a whole is slightly canted mesially. Weak mesial and distal crests emanate from the apex of the P sub 2 protoconid, and a cingulid lines the lingual and distal bases of the crown.

Both P sub 3 and P sub 4 are obliquely oriented in the tooth row, with the mesial root labial in position with respect to the distal root. This condition was apparent on the basis of the alveoli of P sub 3 and the crown of P sub 4 in Eosimias sinensis (1), although some workers have questioned this (2). The crowns of P sub 3 and P sub 4 are similar in many respects, but P sub 4 is more nearly molariform in having a distinct paraconid and strong metaconid. In contrast, the trigonid of P sub 3 bears only a protoconid. P sub 3 further differs from P sub 4 in having a mesiodistally shorter talonid heel without a distinct hypoconid cusp. The crowns of both P sub 3 and P sub 4 bear weak, discontinuous labial cingulids and are slightly exodaenodont, as is common among basal anthropoids. A complete and well-defined lingual cingulid occurs on P sub 3 .

The lower molars of E. centennicus do not differ appreciably from those preserved in E. sinensis. Therefore, only M sub 3 , which was previously unknown in Eosimiidae, is described here. As is the case on M sub 1 and M sub 2 , the trigonid of M sub 3 bears three well-defined cusps. The paraconid is remarkably large and cuspidate and is well separated mesially from the metaconid. In having the M sub 2 and M sub 3 paraconids and metaconids widely splayed (not connate), Eosimias differs from most adapiforms and omomyids. Although

several other basal anthropoids retain lower molar paraconids, none of these taxa possess lower molar paraconids that are as robust as those of Eosimias. However, the smaller M sub 3 paraconid in Serapia does resemble that of Eosimias in being widely splayed from the metaconid. The M sub 3 trigonid is appreciably wider than the talonid, an uncommon condition in primates but one that is frequent in early anthropoids (2). The hypoconulid lobe of M sub 3 is highly abbreviated (both mesiodistally and buccolingually), and the entire distolingual margin of the talonid is reduced in comparison with omomyids and adapiforms. Similar reduction of the hypoconulid lobe and distolingual margin of M sub 3 occurs in other basal anthropoids (for example, Arsinoea, Serapia, and Catopithecus).

Posteroinferiorly, the dentary of Eosimias exhibits a rounded angle that is not developed into a projecting angular process, as is common among omomyids and adapiforms. In this derived character, Eosimias closely approximates other basal anthropoids. The articular surface of the condyle is broken, and the condyle is situated only slightly below the level of the relatively gracile coronoid process.

Like E. sinensis, E. centennicus was a tiny primate. Mean estimates of body mass for E. centennicus, based on regressions of body mass against M sub 1 area in living primates (14), are 91 to 179 g, depending on the regression model chosen. Thus E. centennicus was roughly the same size as the smallest extant anthropoid, Cebuella pygmaea. Its relatively low-crowned, bluntly crested cheek teeth suggest that E. centennicus subsisted primarily on a diet of fruits, supplemented with insects (15).

The original description of Eosimias as a basal anthropoid was based on fragmentary lower jaws preserving the crowns of P sub 4 through M sub 2 and alveoli for other tooth loci (1). Partly as a result of this incomplete knowledge of the dentition of Eosimias, its affinities with anthropoids have been widely disputed (2-4). The new fossils reported here make Eosimias one of the few Eocene primates to be represented by its complete lower dentition. As such, several additional derived characters of Eosimias are now known that reinforce the hypothesis that Eosimias is a basal anthropoid. These include (i) an anteroposteriorly abbreviated, dorsoventrally deep symphysis; (ii) vertically implanted lower incisors; (iii) large projecting canines; (iv) P sub 3 and P sub 4 being slightly exodaenodont and obliquely oriented in the tooth row; (v) the M sub 3 trigonid being appreciably wider than the talonid; (vi) the hypoconulid lobe on M sub 3 being reduced both mesiodistally and buccolingually; and (vii) a rounded, nonprojecting angular region providing expanded area for insertion of pterygoid muscles. All of this new anatomical information corroborates the original hypothesis that Eosimias is a basal anthropoid, whereas none of the new data point toward alternative phylogenetic reconstructions (that is, there are no crossing synapomorphies). We conclude that Eosimias is indeed a basal anthropoid. Alternative phylogenetic reconstructions for this taxon have erred in emphasizing its retention of primitive dental traits (such as lower molar paraconids). Although it is undeniable that Eosimias is more primitive than any other fossil anthropoid in several respects, symplesiomorphy alone is no reason to deny its anthropoid affinities.

The phylogenetic relationships of anthropoids have been debated for many years (1-4, 10, 16-18). One current hypothesis is that anthropoids are derived from cercamoniine adapiforms (3, 4, 16, 17), but it conflicts with the anatomy of Eosimias, which is unlike that of adapiforms in any meaningful way. If we are correct in interpreting Eosimias as a basal anthropoid, the hypothesis that anthropoids evolved from adapiforms can be rejected (1). An adapiform ancestry for anthropoids is also difficult or impossible to reconcile with the large body of neontological data suggesting that Tarsius is the nearest living relative of anthropoids (19). Moreover, early fossil anthropoids are now known to antedate many of the cercamoniine adapiforms that are alleged to have been their ancestors (1, 2, 20). Advocates of the view that anthropoids are derived from cercamoniine adapiforms have often complained that alternative hypotheses of anthropoid origins rely on the assumption that a long interval of anthropoid history remains undocumented paleontologically; that is, that undoubted anthropoids evolved from a poorly known third group of early Cenozoic primates that were neither adapiforms nor omomyids (17). We submit that Eosimiidae represent this third group of early Cenozoic primates, amply demonstrating that the anthropoid clade was distinct from both Strepsirhini (including Adapiformes) and

Tarsiiformes (including Omomyidae) by the middle Eocene if not earlier.

The fossil record of early anthropoid primates has been greatly augmented in recent years and is now sufficient to demonstrate that by the middle Eocene, higher primates ranged from western Algeria (2, 20) to eastern China. This wide geographic range and the high taxonomic diversity of early anthropoids imply that the anthropoid clade is Car more ancient than most workers have assumed. Nevertheless, this great antiquity for the anthropoid clade is consistent with the paleontologically documented antiquity of its likely sister group, the Tarsiiformes (18). Robust paleobiogeographic hypotheses regarding the continent of origin for Anthropoidea--either Asia or Africa--must be based on better paleontological data than are currently available.

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5. Order Primates, Suborder Anthropoidea, Family Eosimiidae, Eosimias centennicus. n. sp. Holotype: IVPP V11000, associated left and right dentaries of a single individual preserving right I sub 1 through M sub 3 and left C sub 1 through M sub 3 (Figs. 2 and 3). Dental measurements (in millimeters) for the right dentary are as follows: I sub 1 mesiodistal length (L) 0.60, labiolingual width (W) 0.45; 12 L 0.90, W 0.80; C sub 1 L 1.70, W 1.40; P sub 2 L 1.00, W 0.85; P sub 3 L 1.60. W 1.40; P sub 4 L 1.70, W 1.45: M sub 1 L 1.95, W 1.60; M sub 2 L 1.95, W 1.70; and M sub 3 L 2.35, W 1.55. Type locality: Locality 1. the "River Section" locality of Zdansky (6), Zhaili Member, Heti Formation, Yuanqu Basin, Shanxi Province. China (35degD4.95'N, 111deg50.99'E). Hypodigm: The holotype; IVPP V11001.1, right dentary preserving P sub 3 through M sub 3 ; and IVPP V11001.2, right dentary preserving P sub 4 through M sub 2 . Known distribution: Late middle Eocene of Shanxi Province, China. Diagnosis: Slightly larger than E. sinensis. P sub 4 differs from that in E. sinensis in having a trigonid with a distinct paraconid and a stronger metaconid. The P sub 4 metaconid is higher and more mesial in position than in E. sinensis. Etymology: In commemoration of the centennial of the Carnegie Museum of Natural History, celebrated in 1995-96.

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