

Rencunius zhoui, New
Primate from the Late
Middle Eocene of Henan,
China, and a Comparison
with Some Early
Anthropoidea

7

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Introduction

Late Eocene primates of Asia are often mentioned in discussions of anthropoid origins. This is in part because of the distinctive morphologies of Asian Eocene primates that document an otherwise hidden diversity of potential anthropoid ancestors. Asia also draws our attention as a large, centrally placed

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geographic region that is still inadequately known paleontologically. Asia and its Eocene primates are important for understanding both the phylogenetic and biogeographic history of primate and anthropoid diversification.

Amphipithecus and *Pondaungia* from Burma (reviewed by Ciochon and Holroyd, Chapter 6, this volume) have generated the most interest. *Hoanghonius* from the Chaili Member in the upper part of the Heti Formation in Shanxi Province, China, has also received some attention. It has never been labeled an anthropoid, but similarities to the early African anthropoid *Oligopithecus* are interesting. Gingerich (1977) and more recently Rasmussen and Simons (1988) have interpreted *Hoanghonius* as an adapid showing affinities with *Oligopithecus*. Dental similarities between these two taxa are part of the evidence favoring an adapid origin of Anthroproidea. Here we redescribe Chinese specimens previously referred to *Hoanghonius* and place these in a new genus and species, *Rencunius zhoui*.

Hoanghonius stehlini

Hoanghonius stehlini was first described by Zdansky (1930, p. 75) from his Locality 1, the so-called "River Section" locality, on the north bank of the Huanghe [Huang Ho or Yellow River] near Yuanqu city in southern Shanxi Province. This locality is in what is now called the Chaili Member of the upper Heti Formation, which was regarded as late middle Eocene in age by Russell and Zhai (1987, p. 212–215), but is now regarded as late middle Eocene (Holroyd and Ciochon, Chapter 5, this volume). The type specimen is a left dentary with M_{2-3} , and Zdansky also referred an upper molar to this genus and species (for illustrations see Zdansky, 1930, Fig. 7, plate 5, pp. 16–18; Szalay and Delson, 1979, Fig. 136). *Hoanghonius* takes its name from the Yellow River.

The most distinctive characteristics of *Hoanghonius stehlini* noted by Zdansky are the double-cusped trigonid (protoconid and metaconid present, but no paraconid) and the anteriorly sloping "cross-yoke" paracristid connecting these on M_{2-3} . The trigonid is little higher than the talonid. The hypoconid is larger than the entoconid. Anteriorly the hypoconid is connected to the protoconid. The hypoconulid on M_2 is as large as the entoconid and close to it, forming the posterior corner of the tooth. The talonid is broader than the trigonid, and there is a labial cingulid running along the lateral side of the tooth. M_3 has a strong hypoconulid forming a strong third lobe on the tooth. The labial cingulid on M_3 borders the trigonid and talonid but not the third hypoconulid lobe. The referred upper molar is tritubercular, with the paracone and metacone equally large. The protocone has the appearance of a well-proportioned half-moon with small but distinct conules (paraconule and metaconule) on each arm. The cingulum is complete (as far as preserved),

with two inner cusps. Zdansky (1930) referred to these inner cusps as the hypocone and "protostyle"; the latter is now called a pericone.

Zdansky (1930) classified *Hoanghoni* as *incertae sedis* but found that the lower teeth resembled *Smilodectes* most closely and the upper molar resembled *Washakius* or *Hemiacodon*, all now clearly and unquestionably members of the order Primates. *Smilodectes* is a well-known North American middle Eocene notharctine adapid, and *Washakius* and *Hemiacodon* are North American omomyids known since the last century. Uncertainty about the systematic position of *Hoanghoni* within Primates has continued since it was first named. Simpson (1945, p. 64) classified *Hoanghoni* as Prosimii of uncertain infraorder or family. Hill (1955, p. 274) included it "for convenience" in Omomyinae. Romer (1966, p. 382) classified it in Omomyidae. Simons (1972, p. 287) classified it in Omomyidae? *incertae sedis* (see also Conroy and Brown, 1975). Szalay (1974, p. 53) was the first to classify *Hoanghoni* as "probably an adapid," writing "I would not classify it as an omomyid, based upon admittedly scanty material."

In 1975, Gingerich studied the original specimens of *Hoanghoni* in Uppsala and made sharp epoxy casts distributed to colleagues for comparison with other primates. He independently corroborated Szalay's referral of *Hoanghoni* to Adapidae (Gingerich, 1976) and illustrated the close similarity of its M_2 to that of *Oligopithecus* (M_2 was the only comparable tooth known at the time; Gingerich 1977, p. 177). Szalay and Delson (1979, pp. 269–271) confirmed similarity to *Oligopithecus* but reclassified *Hoanghoni* in Omomyidae, *incertae sedis*, writing "Contrary to Gingerich's view, there is no character or combination of characters which would mandate adapid ties for *Hoanghoni*." A few sentences later they wrote: "Nevertheless, the possible adapid ties of *Hoanghoni*, and also *Oligopithecus*, cannot be dismissed. Were they to be corroborated by better samples of these forms, then *Oligopithecus* should clearly be taken out of the Catarrhini."

Rasmussen and Simons (1988, p. 182), describing new specimens of *Oligopithecus*, favored adapid ties for *Hoanghoni*, writing:

Among prosimians, the upper teeth of *Oligopithecus* very closely resemble those of *Protoadapis* and allied forms (*Europolemur*, *Mahgarita*, *Periconodon*, *Hoanghoni*) but differ substantially from other prosimian taxa. Most of the dental and osteological resemblances between *Oligopithecus* and the *Protoadapis* group are derived features, thus favoring the hypothesis that *Oligopithecus* and other Anthropoidea are descended from Adapidae.

Thus, *Hoanghoni* is inextricably bound up in the nexus of genera and morphological characteristics connecting the origin of Anthropoidea backward in geological time to Eocene ancestors.

The type specimen of *Hoanghoni stehlini* (unnumbered in Paleontological Museum, University of Uppsala, Sweden) is a left dentary with M_{2-3} . M_2 measures 4.0 mm in anteroposterior length and 3.4 mm in breadth; M_3 measures 4.6 mm in anteroposterior length and 2.8 mm in breadth; and the mandibular ramus is 7.9 mm deep beneath M_1 (measured on original). The

referral specimen (also unnumbered in Uppsala) is an isolated right M^2 that measures 3.9 mm in length and 5.9 mm in breadth.

Rencunius zhoui

Woo and Chow (1957) described four new specimens from "Jentsen" [Rencun], a locality on the opposite side of the Huanghe [Yellow river] and 5 km upstream from the *Hoanghoni* type locality. Woo and Chow referred these to *Hoanghoni* *stehlini* but had no possibility of direct comparison to the original specimens in Uppsala. Study of original specimens of *Hoanghoni* and the referred material and comparison of sharp epoxy casts of these with other Eocene primates indicates that the referred specimens represent a new genus and species: Family Adapidae, Subfamily **Hoanghoniinae**, new subfamily.

Asian *Hoanghoni* and *Rencunius*, described here, differ from other subfamilies of Adapidae in combining strongly developed pericones and hypocones on the lingual cingulum of upper molars with well-developed twinned entoconids and hypoconulids at the posterolingual corners of lower molars. The new *Hoanghoni*-like genus from Thailand (Suteethorn *et al.*, 1988; Ducrocq, 1992) probably belongs in this subfamily as well.

Rencunius zhoui: new genus and species (Figs. 1B, 2C, and 3B)

Holotype: Institute of Vertebrate Paleontology and Paleoanthropology [IVPP] 5312, left dentary with P_4 – M_2 (Figs. 1B and 2C). This was also illustrated by Woo and Chow (1957) in their text Figure 2 and plate figures 3a,b, 4a,b, and 5a,b.

Referred specimens: IVPP 5311, right dentary with M_{1-2} , and IVPP 5313, right maxilla with P^4 – M^1 . Woo and Chow (1957) illustrated a fourth specimen (their Fig. 6, not seen by us) and described this as an isolated left M_1 ; it is almost certainly a right M_3 .

Type locality: Rencun (= Jentsun, or Jentsen of Woo and Chow, 1957; Locality 7 of Zdansky, 1930), Mianchi County, Henan Province, east central China. Latitude and longitude of this locality are approximately 35°03'N, 111°47'E. Chow *et al.* (1973, p. 170, Fig. 2), Li and Ting (1983, p. 32, Fig. 10), and Russell and Zhai (1987, p. 212, Fig. 123) published maps showing this locality.

Age and distribution: Late middle Eocene. The type locality of this genus and species is in the lower part of the Heti Formation, and it is thus older than the type locality of *Hoanghoni* *stehlini* in the upper part of the Heti Formation. *Rencunius zhoui* is presently known only from the type locality in east central China.

Generic diagnosis: Most similar to *Hoanghoni* but differs in having a higher and more inflated M_2 crown and in retaining a small paraconid on M_2 (minute in the holotype, larger in IVPP 5311); has the twinned entoconid–

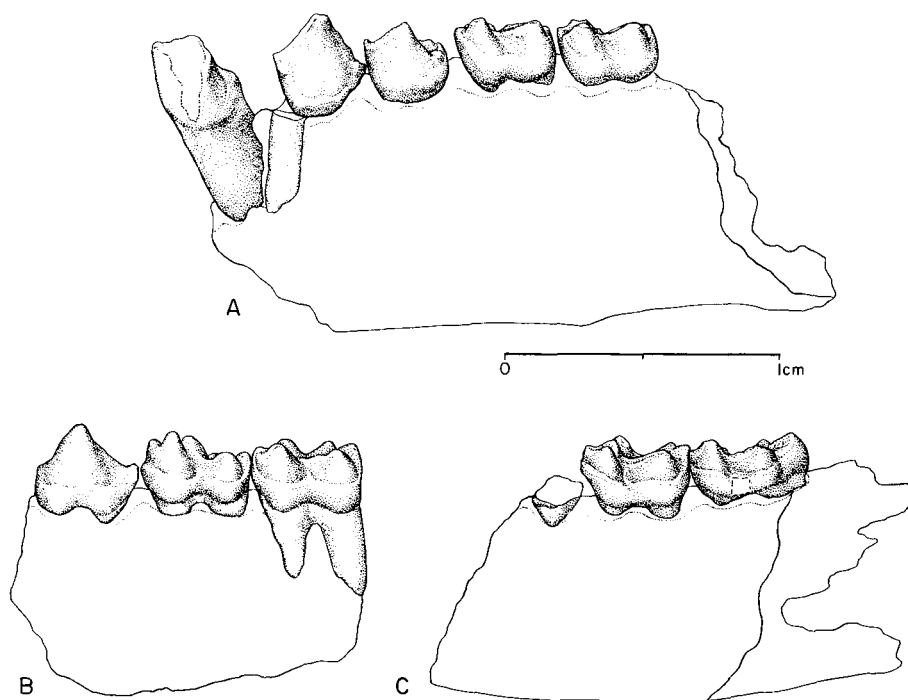


Fig. 1. Comparison of left dentaries of *Oligopithecus*, *Rencunius*, and *Hoanghoniuss* in lateral view. A: Type specimen of *Oligopithecus savagei*, Cairo Geological Museum 18000, from Quarry E, Fayum Province, Egypt. B: Type specimen of *Rencunius zhoui*, new genus and species, Institute of Vertebrate Paleontology and Paleoanthropology 5312, from Henan Province, China. C: Type of *Hoanghoniuss stehlini*, University of Uppsala (no number), from Shanxi Province, China. See Fig. 2 for comparison in occlusal view.

hypoconulid seen on M_2 in *Hoanghoniuss*, but these cusps are larger and more separated in *Rencunius*. The M_3 illustrated by Woo and Chow (1957, Fig. 6) has a trigonid resembling that of *Hoanghoniuss* in being short anteroposteriorly, narrow in comparison to M_2 , and lacking a paraconid, but the talonid is very different in retaining more distinct cusps with a narrower and less rounded hypoconulid lobe. M^1 in *Rencunius* resembles M^2 in *Hoanghoniuss* in having a large pericone and hypocone on the lingual cingulum but differs in having a much larger and more centrally placed paraconule and metaconule and in having a very distinctive flexure of enamel running along the posterolingual side of the paracone, a small centrocrista within the talon basin.

When *Rencunius* is compared to other primates, the relatively long and narrow P_4 distinguishes it from omomyids. A relatively long and narrow P_4 and M_1 , with a small metaconid on P_4 and an open trigonid on M_1 , distinguishes it from anthropoids. These are features of Adapidae. The reduced paraconid on M_2 and M_3 , twinned entoconid–hypoconulid on M_2 , bulbous

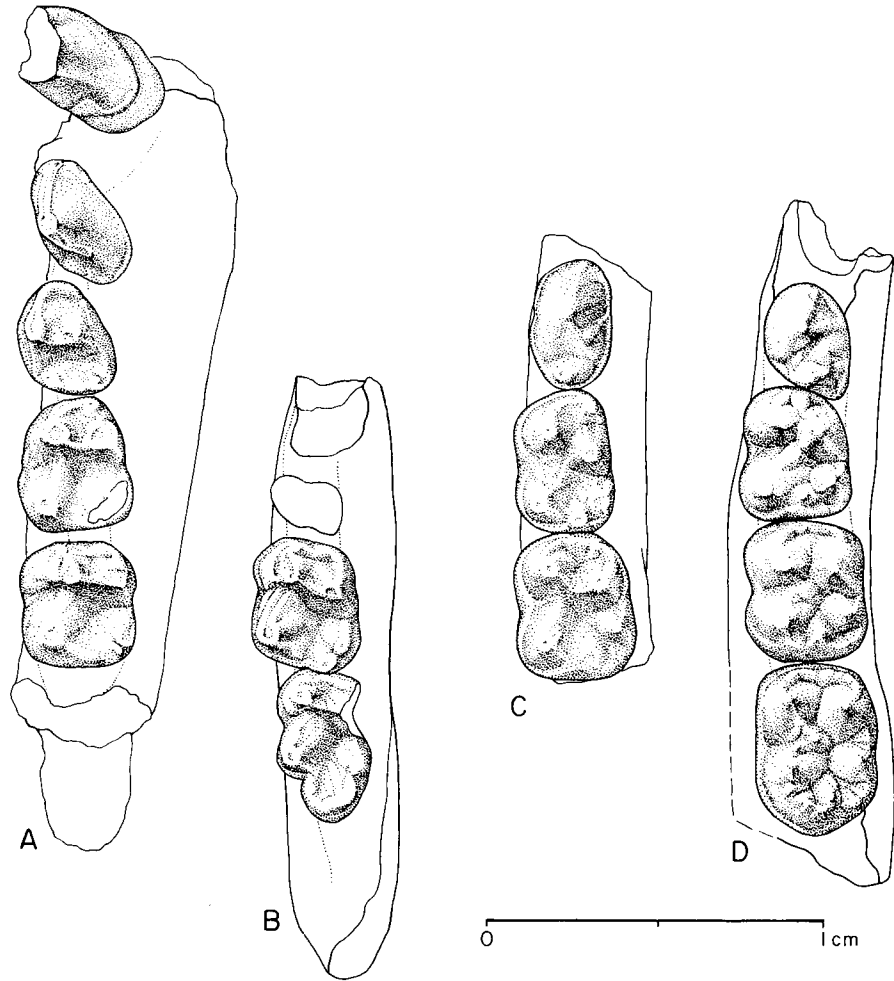


Fig. 2. Comparison of left dentaries of *Oligopithecus*, *Hoanghoniuss*, *Rencunivus*, and *Apidium* in occlusal view. A: Type specimen of *Oligopithecus savagei*, Cairo Geological Museum 18000, from Quarry E, Fayum Province, Egypt. B: Type of *Hoanghoniuss stehlini*, University of Uppsala (no number), from Shanxi Province, China. C: Type specimen of *Rencunivus zhoui*, Institute of Vertebrate Paleontology and Paleoanthropology 5312, from Henan Province, China. D: Type specimen of *Apidium phiomense*, American Museum of Natural History 13370, from Fayum Province, Egypt. Note anteroposteriorly elongated P_4 and M_1 and the large paraconid on M_1 distinguishing *Rencunivus* from anthropoids *Oligopithecus* and *Apidium*. Note larger size, retention of very small paraconid on M_2 , more bulbous cusps, and wider separation of hypoconulid and entoconid distinguishing *Rencunivus* from *Hoanghoniuss*. All four genera share a reduced paraconid and twinned hypoconulid-entoconid on M_2 that gives them a general resemblance in spite of other distinctive specializations.

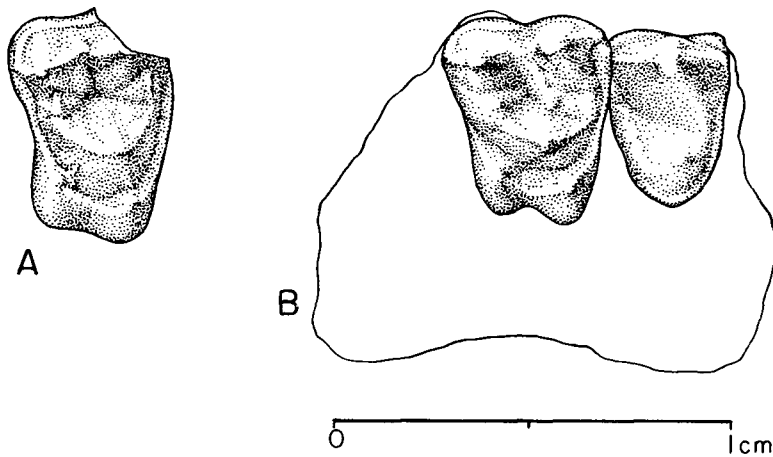


Fig. 3. Comparison of right maxillary cheek teeth in *Hoanghoniuss* and *Rencunius* in occlusal view. A: Referred M² of *Hoanghoniuss stehlini*, University of Uppsala (no number), from Shanxi Province, China. B: Referred maxilla fragment with P⁴–M¹ of *Rencunius zhoui*, Institute of Vertebrate Paleontology and Paleoanthropology 5311, from Henan Province, China. Note larger, more centrally placed conules and flexure of enamel or centrocrista posterolingual to the paracone on M¹. P⁴ in *Rencunius* is simple, with a distinct protocone, a single large labial cusp, but no conules or other accessory cusps (if a parastyle was originally present, it has been removed by breakage).

cusps on an inflated crown on M₂ (especially IVPP 5311), distinct talonid cusps on M₃, and large pericone and hypocone on M¹ are resemblances to Anthropoidea that distinguish *Rencunius* from most adapids.

Specific diagnosis: Only species known; diagnosis as for genus.

Etymology: Named for Rencun locality, which is named in turn after Rencun village nearby. Specific name honors Zhou Minchen, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, who collected these specimens 30 years ago, in recognition of his important contributions to paleomammalogy and paleoprimatology.

Description: The holotype, IVPP 5312 with P₄–M₂, is the most complete specimen of *Rencunius* (Figs. 1B and 2C). P₄ is relatively long and narrow, like *Cantius* and other adapids. Illustrations by Woo and Chow (1957) show that it had a single high central cusp, the protoconid (now broken), with a small but distinct metaconid posterolingual to the protoconid. There is no paraconid on P₄, but there is a small cusp at the base of the crown (hypoconid?). P₄ is bordered labially and lingually by a narrow cingulid. The crown of P₄ in the holotype measures 3.7 mm in anteroposterior length and 2.6 mm in breadth.

M₁ in the holotype is relatively long and narrow by comparison to M₂, with the talonid a little broader than the trigonid. The protoconid, paraconid, and metaconid on the trigonid are all large and well separated. The paraconid is little worn, but enamel at the tips of the protoconid and metaconid is perforated by wear. The hypoconid at the posterolabial corner of the tooth is

the largest cusp on the talonid, but the twinned entoconid and hypoconulid at the posterolingual corner of the talonid are also large and subequal in size. The cristid obliqua joins the hypoconid to the metaconid rather than the protoconid or middle of the metacristid (this may be related in some way to development of a distinctive flexure of enamel or centrocrista on M^1). There is a well-developed labial cingulid on M_1 but no lingual cingulid. The crown of M_1 in the holotype measures 3.9 mm in anteroposterior length and 3.0 mm in breadth. M_1 in IVPP 5311 is now broken and adds little to knowledge of *Rencunius*.

M_2 in the holotype is longer and considerably broader than M_1 . The trigonid has distinct protoconid and metaconid cusps, but the paraconid is reduced to a minute cusp on the holotype. IVPP 5311 differs in having a larger paraconid. The paraconid is part of a continuous paracristid connecting the protoconid to the metaconid and, with the metacristid, enclosing a distinct anterior fovea. The talonid on M_2 is broader than the trigonid. Enamel at the tips of the protoconid and metaconid is perforated by wear. As in M_1 , the hypoconid is large, filling the posterolabial corner of the talonid, and the entoconid and hypoconulid are twinned at the posterolingual corner of the talonid. The latter cusps are both relatively large, and they are more separated than in *Hoanghoni* or *Oligopithecus* (Fig. 2). In *Oligopithecus* and in *Catopithecus* the entoconid is larger than the hypoconulid, and it is more anteriorly positioned. Enamel on the hypoconulid is perforated by wear. The cristid obliqua joins the metacristid a little closer to the protoconid than to the metaconid. There is a well-developed labial cingulid on M_2 and just a hint of a cingulid present on the lingual side of the trigonid (the labial cingulid is stronger, and there is no trace of a lingual cingulid in IVPP 5311). The crown of M_2 in the holotype measures 4.1 mm in anteroposterior length and 3.5 mm in breadth. The crown of M_2 in IVPP 5311 measures 4.0 mm in anteroposterior length and 3.9 mm in breadth. It is broader than M_2 in the type and consequently looks more anthropoid in its proportions.

M_3 is not preserved in the specimens studied, but Woo and Chow (1957) illustrated a tooth (their specimen no. 3, illustrated in their Fig. 6a,b) that appears to be an isolated right M_3 . This has the anteroposteriorly short trigonid expected of M_3 , with no paraconid and a paracristid connecting the protoconid and metaconid and enclosing a small fovea like that on M_2 . The hypoconid, hypoconulid, and entoconid are all relatively large and well separated. Woo and Chow (1957) give measurements (anteroposterior length 4.5 mm, breadth 2.9 mm) indicating that this tooth is much longer than M_1 or M_2 in *Rencunius* and that it is a little shorter and broader than M_3 in *Hoanghoni*.

P^4 is preserved in the right maxillary fragment of referred specimen IVPP 5313 (Fig. 3B). It is simple, with a distinct protocone and a single large lingual cusp (paracone) but no conules. A parastyle may have been present at the anterolabial corner of the crown, but this is broken. A high robust preprotocrista connects the protocone and paracone. The crown is bordered by

weak labial and lingual cingula. P_4 measures about 3.1 mm in anteroposterior length (estimate), and 4.2 mm in breadth.

M^1 is also preserved in the referred maxillary fragment, IVPP 5311. M^1 of *Rencunius* is similar in shape to M^2 of *Hoanghoni*, but it is relatively narrower and a little more massively constructed. The protocone, paracone, and metacone enclose a trigon basin, but this is not as simple and open as that of *Hoanghoni*: the paraconule and metaconule are both larger and more centrally positioned, and there is a distinct flexure of enamel or centrocrista located posterolingual to the paracone. The pericone and hypocone are very well developed on the lingual cingulum, and there is a weak labial cingulum as well. M^1 measures 4.2 mm in anteroposterior length and 5.3 mm in breadth.

Discussion. Dashzeveg and McKenna (1977, p. 131) singled out the type specimen of *Rencunius zhoui* (dentary IVPP 5312) from the rest of the Rencun sample and claimed that this specimen is an artiodactyl rather than a primate. No justification was given for separating one specimen from the rest of the sample, and no justification was given for considering this to be an artiodactyl. Delson (1977, p. 49) published a similar conclusion, also without justification. Woo and Chow (1957) considered the IVPP 5312 dentary and the IVPP 5311 maxilla to be parts of the same individual animal, which may or may not be true (see below). Another Eocene mammal from China, *Lantianius*, was originally described as an adapid (Chow, 1964) but later reclassified as an artiodactyl because of its anteroposteriorly elongated premolars, unlike those of any primate (Gingerich, 1976). None of the *Rencunius* specimens has elongated artiodactyl-like premolars. The combination of the moderate length of P_4 , the open trigonid and distinct paraconid on M_1 , the reduced paraconid and the paracristid enclosing an anterior fovea on the trigonid of M_2 , and the basined talonids on M_1 and M_2 indicate that *Rencunius* is a primate. *Rencunius* is an adapid rather than an omomyid because of its (1) relatively large size, (2) longer and narrower P_4 than is typical of omomyids, (3) reduced paraconid on M_2 (and presumably M_3), and (4) twinned hypoconulid–entoconid as found in other Adapidae including *Hoanghoni*, the Thailand adapid, *Indraloris*, and *Sivaladapis*.

Woo and Chow (1957) referred the primate specimens they described from “Jentsen” or Rencun to *Hoanghoni stehlini*. This was conservative and reasonable given the inaccessibility of the *Hoanghoni* type material and an unquestioned general morphological resemblance. It is only by studying originals directly and being able to compare them using sharp epoxy casts that it is evident two genera and species are represented.

Woo and Chow (1957) indicated that the four specimens they described belong to at least three individuals, and they suggested that their specimens no. 2 (IVPP 5312, holotype dentary) and no. 4 (IVPP 5311, maxilla) might belong to a single individual. This appears unlikely because IVPP 5312 is more heavily worn than IVPP 5311; it is the only specimen with perforated enamel on the tips of cusps.

Geology and Mammalian Succession of the Heti Formation

Chow *et al.* (1973, p. 171, Table 1) divided the Heti Formation into two members, an upper Chaili Member and a lower Rencun Member, separated by an unconformity, and each of these members was further subdivided into two stratigraphic intervals. The Heti Formation is about 600 m thick (Li, 1984). *Hoanghoniuss stehlini* is from the uppermost subinterval (IVPP 5301), whereas *Rencunius zhoui* is from the lowermost subinterval (IVPP 5311-5314; Li and Ting, 1983, pp. 31–32). The most recent review of these faunas (Tong, 1989) indicates that they share a single species, the anthracotheriid artiodactyl *Anthracoeryx sinensis*, and the record from Rencun is recorded as questionable. Thus, it is clear that *Rencunius* is older than *Hoanghoniuss*. How much older is a difficult problem, but the thickness of the formation, separation of the two genera in distinct faunas at the bottom and top of the formation, and an intervening unconformity, taken together, mean *Rencunius* is probably much older.

Russell and Zhai (1987) and Tong (1989) correlated the Rencun fauna with the Shara Murun fauna in Inner Mongolia, on which the Sharamurunionian land-mammal age is based. There are relatively few taxa shared in common between the two faunas, and the correlation is based instead on the high proportion of perissodactyls in both faunas. The Sharamurunionian land-mammal age is considered early late Eocene by Russell and Zhai (1987) and late middle Eocene by Tong (1989), which probably reflects recent expansion of the middle Eocene to include the Bartonian marine stage/age. Holroyd and Ciochon (Chapter 5, this volume) consider both Heti Formation faunas, the Chaili Member fauna and the Rencun member fauna, to be late middle Eocene in age.

Rencunius Compared to Hoanghoniuss and Early Anthropoid Primates

Rencunius is compared to the Chinese adapid *Hoanghoniuss* and primitive Egyptian Fayum anthropoids *Oligopithecus* and *Apidium* in Figs. 1–3, supplemented by reference to features of *Catopithecus* recently described by Simons (1989). All five genera are similar in size and, to the extent they can be compared, in general primate morphology. Unfortunately, the only tooth identified with certainty that is preserved in common in both *Rencunius* and *Hoanghoniuss* is M_2 . This is generally similar in both. M_2 of *Rencunius* differs from that of *Hoanghoniuss* in being a little larger, retaining a very small paracoid, having more bulbous cusps, and having a wider separation of the

hypoconulid and entoconid. M^1 of *Rencunius* is like M^2 of *Hoanghoni* in that both have conspicuous pericones and hypocones on the lingual cingulum. These teeth differ some in proportion, and M^1 of *Rencunius* has larger conules than M^2 of *Hoanghoni*.

Resemblances of *Hoanghoni* to *Oligopithecus* have been detailed elsewhere (Gingerich, 1977; Rasmussen and Simons, 1988), but here again comparison is limited to M^2 . This tooth is a little longer and narrower in *Hoanghoni*, but the two are otherwise very similar in size and shape. Both have the trigonid compressed anteroposteriorly, lacking a paraconid, and both have the twinned hypoconulid and entoconid positioned close together. On the basis of this one comparable tooth, one would expect Asian *Hoanghoni* to have been very similar overall and probably closely related to African *Oligopithecus*. Another slightly older African genus, *Catopithecus*, qualifies these similarities and postulated relationships somewhat. *Catopithecus* and *Oligopithecus* both have a dental formula of $2?-1-2-3$, and there is no evidence that *Hoanghoni* or *Rencunius* had reached this advanced state of dental reduction. *Catopithecus* has an M_2 that is similar to that of both *Hoanghoni* and *Oligopithecus*, but it also preserves an M_3 that is conspicuously shorter in length than the M_3 of *Hoanghoni* (relative to M_1 or M_2).

Teeth of *Rencunius* can be compared to those of *Catopithecus* and *Oligopithecus* at four tooth positions. P_4 , M_1 , and M_2 are all longer anteroposteriorly and narrower buccolingually. P_4 has a buccal cingulid that is lacking in *Oligopithecus*. The metaconid on P_4 is much less developed, and the posterior margin of the tooth is narrower. The paraconid on M_1 is large and well separated from the metaconid. The paracristid on M_2 extends farther forward, and the trigonid is not as compressed anteroposteriorly on either M_1 or M_2 . In the upper dentition, M^1 of *Rencunius* differs markedly from that of *Oligopithecus* (Rasmussen and Simons, 1988) and *Catopithecus* (Simons, 1990) in having a large pericone and a large hypocone on the lingual cingulum, with a large paraconule and metaconule, in contrast to the simple *Protoadapis*-like upper M^1 of *Oligopithecus* and *Catopithecus*.

Teeth at five positions in *Rencunius* can be compared to those of *Apidium*. P_4 , M_1 , and M_2 are all longer anteroposteriorly and narrower buccolingually. P_4 has a buccal cingulid that is lacking in *Apidium*, and, as in *Oligopithecus*, the metaconid is less strongly developed. The paraconid on M_1 is much stronger than that in *Apidium*, in which the paraconid is positioned close to the protoconid and metaconid (and the whole trigonid is much shorter). The position of talonid cusps on M_1 is generally similar. The closest resemblance between *Rencunius* and *Apidium* is in M_2 , where the trigonid is a little narrower relative to the talonid, but most cusps and crests are similarly developed and similarly positioned. *Rencunius* lacks the centroconid between the protoconid, metaconid, and hypoconid that is a distinctive characteristic of *Apidium*. P^4 in *Rencunius* differs markedly from P^4 in *Apidium* in lacking any trace of the large centroconule so distinctive of *Apidium*. M^1 is generally similar but differs in

having a pericone and hypocone approximately equal in size: the pericone is small in *Apidium*, and the hypocone is greatly enlarged.

Anthropoid Origins

Chinese *Rencunius zhoui* and *Hoanghoniuss stehlini* are not well enough known, by themselves, to contribute very much to clarification of anthropoid origins. Rather, *Rencunius* and *Hoanghoniuss* are representative of a general direction and grade of evolution in adapid primates, showing that there was greater morphological and taxonomic diversity in Asia than previously recognized.

The strongest evidence that African *Oligopithecus* is an anthropoid comes from its reduced catarrhine dental formula, with a canine hone on P₃, and from its close dental resemblance to *Catopithecus*, a genus with anthropoid cranial characteristics that include frontal fusion, postorbital closure, and an ectotympanic in the lateral wall of the bulla (Simons, 1990). *Apidium* has the frontal fusion, postorbital closure, and carotid circulation of an anthropoid (Simons, 1959, 1971, 1990; Gingerich, 1973). These cranial characteristics are evolutionarily “derived” or advanced characteristics of early anthropoids that distinguish them from adapids and other prosimian primates. Calling them “derived” or “advanced” means that they are characteristics that appeared later in geological time than adapid and other prosimian cranial characteristics appeared. *Rencunius* and *Hoanghoniuss* might turn out to be anthropoids when their skulls are known, but this appears unlikely given present evidence. There is no reason to attribute derived character states indicative of anthropoid rank to either *Rencunius* or *Hoanghoniuss* in the absence of evidence that such diagnostic characteristics had evolved by the late middle Eocene.

There are three distinct superfamilies of prosimian primates living today: Tarsioidea, Lemuroidea, and Lorisioidea (Gingerich, 1984a,b). These are commonly classified in the infra- or suborders Tarsiiformes (Tarsioidea) and Lemuriformes (Lemuroidea + Lorisioidea), which are matched in turn to Eocene Omomyidae and Adapidae, respectively (e.g., Fleagle, 1988). It is not clear whether Lemuroidea and Lorisioidea are grouped together because they belong together or because this grouping is required to make the number of groups of living prosimians match the number of groups of Eocene prosimians. One alternative would be recognition that lorisooids are very different anatomically from lemurooids in spite of their shared tooth comb. Whatever the reason for grouping the living forms, Eocene omomyids were not modern living tarsiers, and Eocene adapids were not modern living lemurs or lorises. Omomyids are sufficiently similar to tarsiers that it is plausible that they are broadly ancestral to tarsiers, and, likewise, adapids are sufficiently similar to lemurs and to lorises that it is plausible they are broadly ancestral to both.

However, no adapid has a tooth comb, and this must have evolved from spatulate incisors if lemurs and lorises are descendants of adapids. Alternatively, the spatulate incisors of adapids may have evolved as a derived characteristic from the procumbent pointed incisors of an earlier primate that independently gave rise to lemurs and lorises. The presence of pointed incisors in Paleocene proprimates, Eocene omomyids, and later colugos, tree shrews, tarsiers, lemurs, and lorises suggests that pointed incisors are primitive in primates. Whether omomyids and adapids are ancestral to living prosimians or not, omomyids and adapids were generally similar to each other in evolutionary grade, and both were generally similar in grade to prosimians living today. In spite of their similarities, adapids consistently differ from omomyids, where these characteristics are known, in having a primitively free ectotympanic in the middle ear and in having a derived anterior dentition with overlapping canines and spatulate upper and lower incisors.

Anthropoids are different from both adapids and omomyids in many characteristics. Living anthropoids are clearly a third group distinct from living tarsiiform and lemuriform primates, but this does not mean that they were so clearly distinct from Omomyidae and Adapidae in the Eocene. Anthropoids are widely recognized to be more advanced in grade than living prosimians, with different behaviors and life history strategies and, as a consequence, different morphological specializations such as enlarged brains, frontal fusion, and postorbital closure. These anthropoid characteristics are unknown in undisputed Eocene primates, which means that anthropoids are more advanced than most, and possibly all, Eocene primates. Enlarged brains, frontal fusion, and postorbital closure are unknown in putative anthropoids *Biretia* (Bonis *et al.*, 1988) and *Algeripithecus* (Godinot and Mahboubi, 1992); the age of *Biretia* is poorly constrained, and the Eocene age of the early anthropoid *Catopithecus* is also debatable (Simons, 1989; Gingerich, 1993).

Conservatively, it is not possible to trace the origin of anthropoids farther and farther back in time as a "third group" separate from adapids and omomyids without some clear evidence that such a third group existed in the Eocene. Anthropoids may have been part of a third group of primates in the Eocene, but, if so, such a third group will not be very interesting until it is known from fossils unequivocally different from omomyids or adapids. *Renuncius* joins *Hoanghoni*, *Amphipithecus*, and *Pondaungia* in Asia (Szalay, 1970; Gingerich, 1981; Ciochon *et al.*, 1985), *Oligopithecus* and other Fayum taxa, *Algeripithecus*, *Djebellemur*, and possibly *Biretia* from North Africa (Rasmussen and Simons, 1988; Simons, 1971, 1989, 1992; Godinot and Mahboubi, 1992; Hartenberger and Marandat, 1992; see also Bonis *et al.*, 1988), *Cercamoni* in Europe (Gingerich, 1975), and *Mahgarita* in North America (Rasmussen, 1990) as intermediate fossils of uncertain systematic position. Some appear to link anthropoids to a broadly adapoid origin, but this may reflect convergence in dental and gnathic morphology related to similar diets and behavioral strategies. Knowing which are anthropoids, which are adapoids, and which might represent a new third group of Eocene primates different from omomyids

and adapids will require better Eocene fossils that preserve anatomic evidence from the cranium as well as the dentition.

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