

Chapter 10

The Edentulous Skull of the North American Pangolin, *Patriomanis americanus*

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ABSTRACT

The previously unknown preorbital part of the skull of *Patriomanis americanus* shows that by the end of the Eocene, this North American pangolin was already like all extant pangolin species in being completely edentulous. The skull, like the postcranial skeleton, has defining pangolin characters imposed on a morphology that is otherwise quite generalized and primitive. The absence of teeth in *Patriomanis* reinforces its close relationship to living pangolins, but also means that some morphologic information that might have shed light on the question of pangolin origins is absent.

INTRODUCTION

The opportunity to contribute to this volume honoring Malcolm C. McKenna has prompted me to write this supplement to a paper published more than 30 years ago, when I was a graduate student, Malcolm was my advisor, and I was working to finish my dissertation at the AMNH. Not wanting to miss an identifiable specimen in the Frick Collection from the Flagstaff Rim area of Wyoming, I had faced up to a drawer of unidentified miscellaneous material. There I encountered a most unusual braincase, with some associated postcranial elements, equally unusual. The specimen had been collected in 1957, labeled “? immature carnivore” in the field, and sent with other carnivore specimens directly to Childs Frick at his Millstone Laboratory in Roslyn, Long Island. There someone had written “NOT carnivore” on the label, and had sent it back to the Frick Laboratory in the AMNH, where it ended up in the drawer of miscellaneous material from Flagstaff Rim. The shape of the strange cranium suggested an anteater, but the associated postcranial elements were not like those of any xenarthran, and soon I had convinced myself that this “NOT carnivore” could only be a fossil pangolin. This was sur-

prising because extant pangolins, or scaly anteaters, live only in sub-Saharan Africa, and in southern Asia from India to China, Borneo, and Java, and fossils were known only from Africa and Eurasia. I took the specimen and my evidence to Malcolm, who seemed less surprised than I had been by the idea of a North American pangolin, but nevertheless, being my advisor, he offered advice that was something like “better be sure before you say that in print”. When all of the less counterintuitive comparisons had failed, the specimen became the holotype of *Patriomanis americanus*, the first record of a pangolin in North America (Emry, 1970).

Although the holotype included the braincase, most of the compelling evidence for identifying *Patriomanis americanus* as a pangolin was in the postcranial anatomy (Emry, 1970). The preorbital part of the skull was missing, so the question of whether *Patriomanis* was edentulous, like extant pangolins, remained unanswered. When additional specimens were found during the 1970s and 1980s, the postcranial skeleton became almost completely known, and finally in 1990 a skeleton was discovered that includes the preorbital part of the skull and the mandible. The new material shows that, in fact, *Patriomanis* was very much like mod-

ern pangolins in being completely edentulous and was presumably an obligatory feeder on colonial insects such as ants and termites. The skull and mandible are described and illustrated below.

MATERIAL

The skull of *Patriomanis* described here, USNM 494439, is associated with a nearly complete skeleton, largely still articulated. Gaudin and Wible (1999) mentioned some characters of this skull and mandible in their phylogenetic analysis, but in their list of specimens examined (Gaudin and Wible, 1999: 59), they cited USNM 299960, which pertains to another nearly complete postcranial skeleton that lacks the skull and mandible. Comprehensive description of the postcranial skeleton of *Patriomanis*, based on these two specimens and several others less complete, is included in a study now underway by Timothy Gaudin and myself, which will also include a phylogenetic analysis of all pangolins, living and fossil, and their possible relatives.

USNM 494439 is from the White River Formation in the Flagstaff Rim area of central Wyoming (Emry, 1973). It was discovered only a few meters from the site that produced the holotype of *P. americanus* (Emry, 1970: 466) and at virtually the same stratigraphic level (15 feet above Ash F; Emry, 1973: 29). The age at this level is within the middle part of the Chadronian North American Land Mammal Age. When the original material was described (Emry, 1970) the Chadronian NALMA was thought to correlate with the early Oligocene, but it is now regarded as latest Eocene.

Any reference or comparison below to *Manis javanica* is to USNM 198852 (mammalogy collections), an adult male from Borneo, and any reference or comparison to *M. pentadactyla* is to USNM 240168 (mammalogy collections), an adult individual from China.

DESCRIPTION

The skull of USNM 494439 (figs. 10.1A, B; 10.2A; 10.3A) is not perfectly preserved. Some of the individual bones of the skull are broken and displaced, especially in the inter-

orbital region and the dorsal part of the braincase, and the skull is distorted. Nevertheless, the skull is sufficiently well preserved to show that it is narrow and elongate (figs. 10.1, 10.2, 10.3), more closely comparable in its proportions to that of the Java-Borneo pangolin, *M. javanica*, in which the rostral or preorbital part is relatively longer (figs. 10.1C, 10.2B, 10.3B), than to the Chinese pangolin, *M. pentadactyla*, which has a relatively shorter rostrum (figs. 10.1D, 10.3C).

Because the braincase is not as well preserved in USNM 494439 as it is in the holotype (FAM 78999) already described (Emry, 1970), I will concentrate here on the preorbital part, which has not been reported previously.

Neither of the premaxillary bones was in place in USNM 494439, although both were preserved near the skull. The right one was found in matrix several centimeters ahead of the skull, and the left one was displaced just slightly outward and backward from its natural position; it is shown in this position in figure 10.4B. The premaxillaries are completely edentulous and their shape is closely comparable to those of *M. javanica*: overall outline of the facial portion is rhombic, with the anterior margin (border of the nares) roughly parallel to the posterior margin, which contacts the maxilla (fig. 10.4C, D). The premaxillary-maxillary contact is posterodorsally-anteroventrally inclined, similar to its orientation in *M. javanica*, whereas this suture is more nearly vertical in *M. pentadactyla*. The dorsal margin has a substantial contact with the nasal. In *M. javanica*, each premaxilla has a slender posteromedian process that forms the medial border of the incisive foramen, and both continue backward, exposed on the palate as a slender wedge protruding between the anterior ends of the maxillaries. This process is broken and missing on both premaxillaries of USNM 494439 (fig. 10.4E, F), so its extent cannot be determined directly; however, the slender gap between the anterior ends of the preserved maxillaries (figs 10.2A, 10.4A) suggests that this process of the premaxillaries was essentially like that of *M. javanica*.

The maxilla of *Patriomanis* is also closely comparable to that of *M. javanica* in most

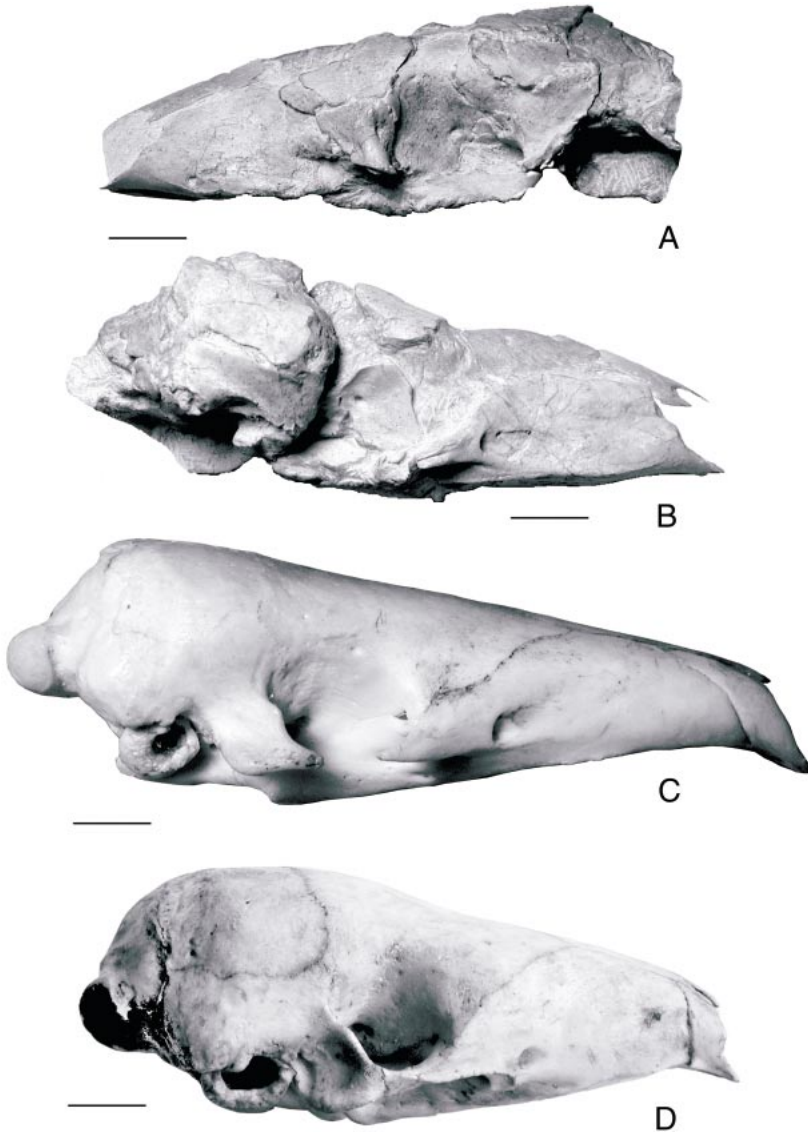


Fig. 10.1. Lateral views of skulls of three pangolin species. **A**, *Patriomanis americanus*, USNM 494439, left lateral view; **B**, *Patriomanis americanus*, USNM 494439, right lateral view; **C**, *Manis javanica*, USNM 198852, right lateral view; **D**, *Manis pentadactyla*, USNM 240168, right lateral view. All approximately $\times 1$; scale bars = 1 cm.

respects but does differ in some details. It is completely edentulous: the palatal part of the right maxilla is preserved completely, to the rear of the palate, and there are no indications of alveoli anywhere along the “alveolar border”. Anteriorly, the lateral edge of the palate (“alveolar border”) is a rounded crest that becomes broader and flatter posteriorly (fig. 10.4A). Just medial to this edge, a shal-

low, narrow longitudinal groove appears to run the whole length of the palate. The small ridge that forms the medial border of this shallow groove is also the lateral margin of a shallow, medial longitudinal palatal trough formed by both maxillaries. Posteriorly, the central part of the palate is broken and the palatine bones are missing; it cannot be determined whether the maxillaries are broken

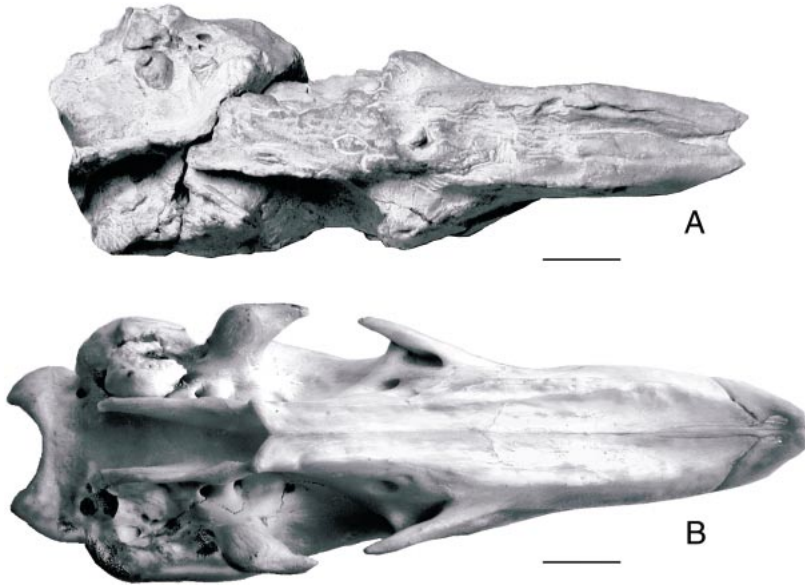


Fig. 10.2. Ventral views of skulls of two pangolin species. **A**, *Patriomanis americanus*, USNM 494439; **B**, *Manis javanica*, USNM 198854. Both approximately $\times 1$; scale bars = 1 cm.

or whether this separation occurred at the palatine-maxillary suture.

The facial portion of the maxillary is high and relatively featureless except for the small zygomatic process placed far to the rear. Just ahead of this process is the infraorbital foramen at the forward end of a short infraorbital canal. The zygomatic process is broken on the left, but completely preserved on the right side; it is a blunt, weak process projecting obliquely outward and slightly downward, very much like that of *M. javanica* in its conformation. However, unlike *M. javanica*, its posterodorsal surface is irregular and appears to be a sutural surface for the jugal, although the jugal itself is not preserved (or at least is not in place and has not been recognized among the displaced fragments) in USNM 494439. In *M. javanica* the zygomatic process of the maxillary terminates in a smooth point, the jugal is missing altogether, and the zygomatic arch is incomplete. However, the jugal is retained in some species of extant pangolins, *M. pentadactyla* for example, as can be seen in figure 10.1D.

Both nasal bones are present in USNM 494439. The anterior parts are well preserved, but the posterior extremities of both are missing, along with most of the frontals.

The two nasals together form an anteriorly pointing wedge at the midline. Each nasal has a deeply concave anterior border, and each has a narrow lateral process that extends anteroventrally to form part of the lateral margin of the nares. In extant pangolins, this lateral process is the surface expression of a flange that folds inward along the whole lateral margin of each nasal to form a partial longitudinal septum of the nasal cavity. Presumably this is also the case in USNM 494439, although the nasal cavity has not been prepared sufficiently to reveal this. In the parts preserved, the nasal bones of USNM 494439 do not differ in any important way from those of *M. javanica* and *M. pentadactyla*.

Parts of both dentaries are present and were preserved in their approximate original positions. The left dentary is the most nearly complete, missing only the posterior extremity (fig. 10.5A, B, D). The ramus is long and thin, abnormally so if compared to those of most mammals, but in fact somewhat more robust than it is in extant pangolins. The dentary, like the skull, is completely edentulous, and its dorsal edge is a thin, sharp crest with no indication of alveoli. The two dentaries were separated at the symphysis, but it is

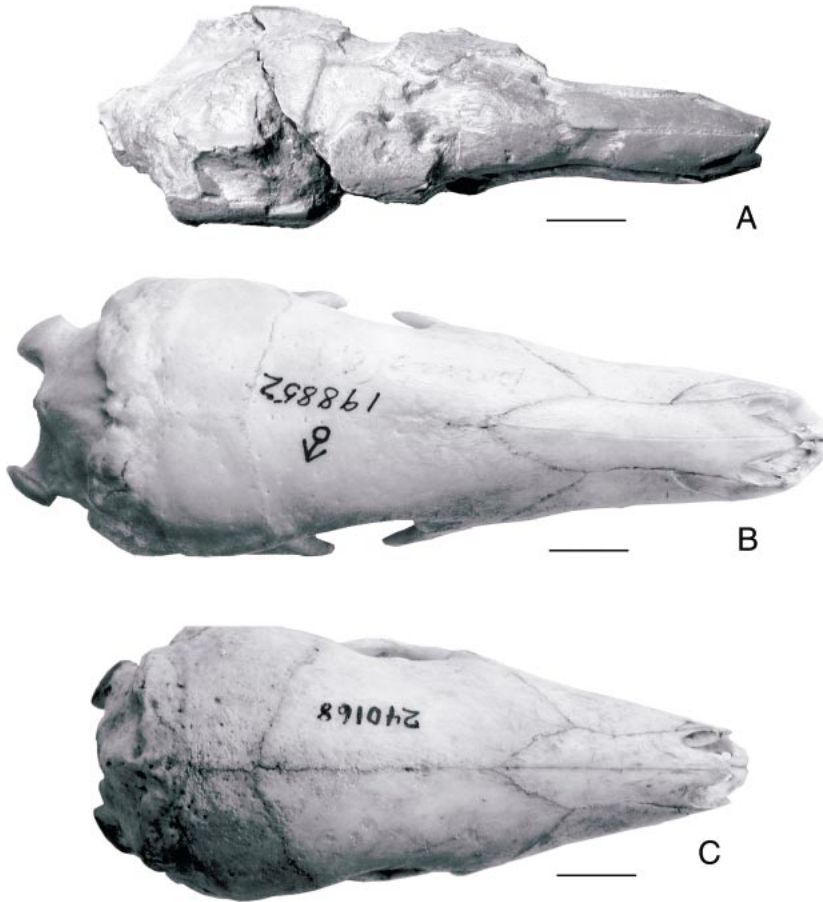


Fig. 10.3. Dorsal views of skulls of three pangolin species. **A**, *Patriomanis americanus*, USNM 494439; **B**, *Manis javanica*, USNM 198852; **C**, *Manis pentadactyla*, USNM 240168. All approximately $\times 1$; scale bars = 1 cm.

clear that the symphysis has a fairly strong interdigitating suture, much like that of extant pangolins. Above the symphysis on the dorsal margin, about where one would expect to see a canine tooth if teeth were present, is an anterolaterally projecting bony prong, just like that of extant pangolins. Posteriorly, the dorsal margin is elevated into a low but distinct coronoid process, much more prominent than in extant pangolins (compare fig. 10.5A and E), in which the coronoid is but a very slight elevation of the dorsal profile. The apex of the coronoid process in *Patriomanis* is a blunt point, and posterior to this the dorsal border is concave downward and continues to the broken edge. The posterior part is missing from both dentaries, so the mor-

phology of the condyle and angular process cannot be determined.

DISCUSSION

Emry (1970) and Rose and Emry (1993) demonstrated that in its postcranial skeleton *Patriomanis* has some advanced features that it shares with extant pangolins, but these are combined with other characters that are more primitive than those of any extant pangolin. USNM 494439 shows that the skull of *Patriomanis* has a similar mosaic of advanced and primitive characters. *Patriomanis* is comparable to modern pangolins in some of its skull characters (complete loss of teeth, long anterolateral prong

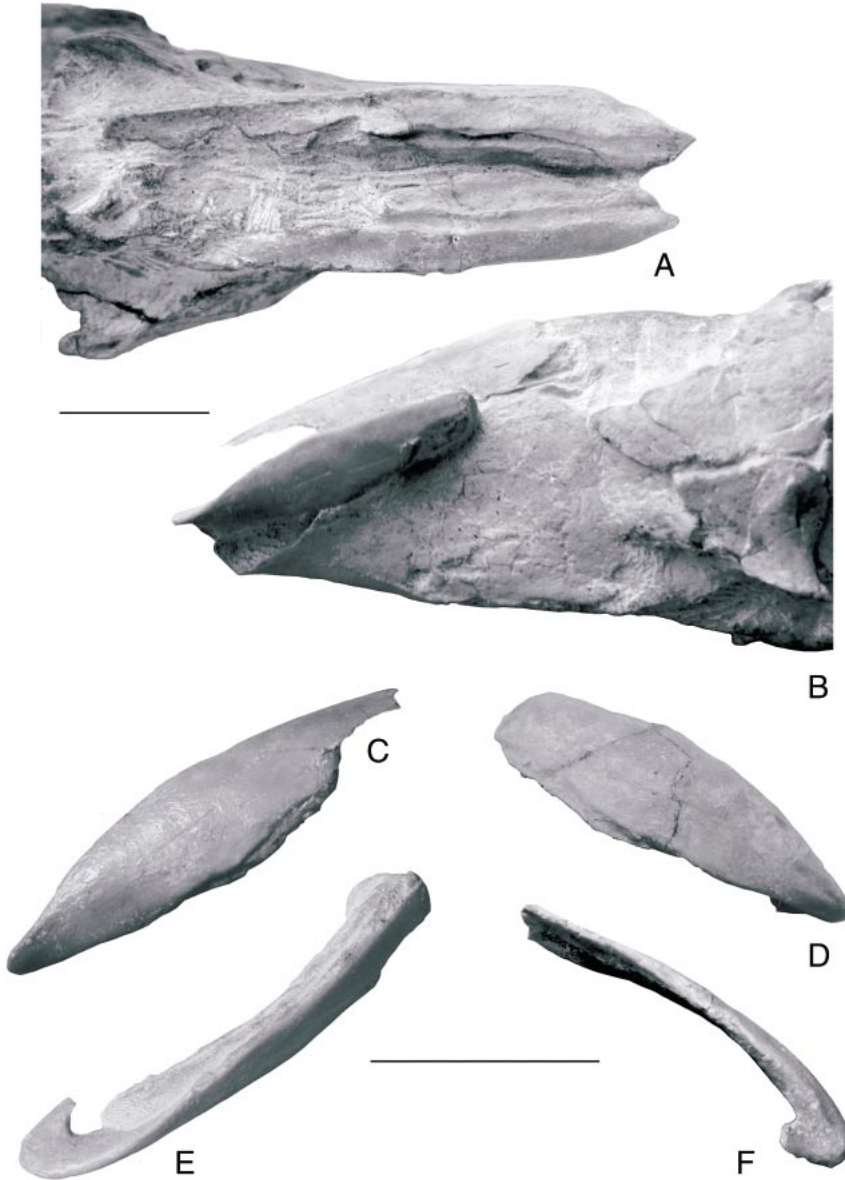


Fig. 10.4. *Patriomanis americanus*, USNM 494439. **A**, ventral view of palate, approximately $\times 2$; **B**, left lateral view of rostrum, showing left premaxilla as preserved slightly out of position, approximately $\times 2$; **C**, left lateral view of left premaxilla, approximately $\times 3$; **D**, right lateral view of right premaxilla, approximately $\times 3$; **E**, dorsal view of left premaxilla, with some matrix still adhering to inner surface, approximately $\times 3$; **F**, ventral view of right premaxilla, approximately $\times 3$. Scale bars = 1 cm.

of nasals, bony “canine” process of the dentaries). *Patriomanis* apparently retained a jugal bone in the zygomatic arch, which is present in some extant pangolin species and is completely lost in others. The dentary

of *Patriomanis* is advanced in being completely edentulous, but more primitive than that of any living pangolin in being more robust and in retaining a much more prominent coronoid process.

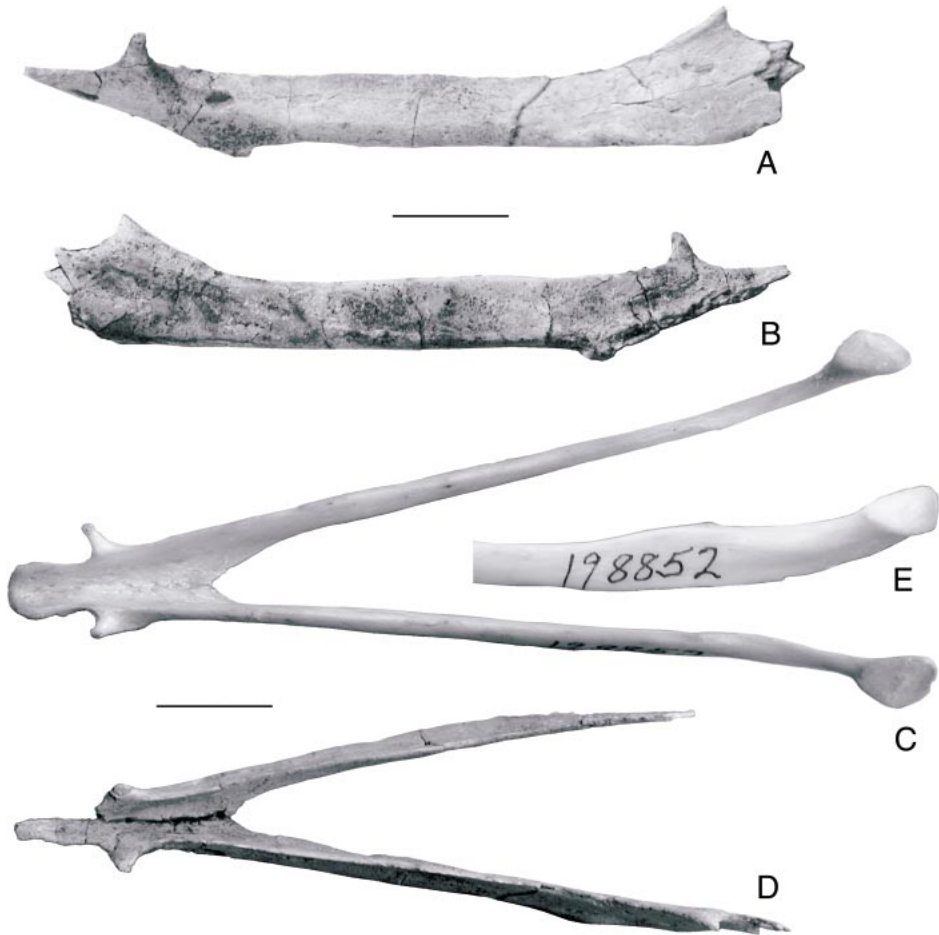


Fig. 10.5. Lower jaws of two pangolin species. **A**, *Patriomanis americanus*, USNM 494439, left lateral view of left dentary; **B**, *Patriomanis americanus*, USNM 494439, medial view of left dentary; **C**, *Manis javanica*, USNM 198852, dorsal view of mandible; **D**, *Patriomanis americanus*, USNM 494439, dorsal view of mandible; **E**, *Manis javanica*, USNM 198852, left lateral view of rear portion of left dentary. All approximately $\times 1.5$; scale bars = 1 cm.

Patriomanis had been confidently considered a pangolin, principally on the basis of postcranial characters. The presence of some advanced pangolin characters in its skull strengthens this conclusion and shows that 35 million years ago pangolins were already surprisingly modern in some ways. However, it is interesting to consider how much more enlightening *Patriomanis* might have been, had its skull been more primitive. In the contemporary world of systematics, where cladistic phylogenetic analysis permits only apomorphic characters to be accorded phylogenetic significance, the quest for useful

primitive characters might be seen as quixotic. However, the proposition that *Patriomanis* is a pangolin would not have been seriously weakened had teeth been present, and teeth with recognizable patterns of cusps with recognizable homologies might have provided some insight into the higher-level relationships of the Pholidota. Reduction or absence of dentition is a phylogenetically useful character at lower taxonomic levels, but is distributed so broadly among so many divergent groups of mammals that its phylogenetic importance is limited at higher levels. As pangolins acquired this apomorphic

character that makes them pangolins, they lost phylogenetic information.

Characters that could be described with the terms “loss of” (e.g., loss or reduction of teeth among mammals, loss or reduction of wings in flightless birds, reduction or loss of limbs in marine mammals) have too often been “red herrings”, much too obvious to have been used objectively by systematists. Just as a smoked herring dragged across a trail leaves a scent so intense that hunting dogs are confused and diverted from their real quarry, these red-herring characters have confused systematists, causing them to lose track of the less obvious but systematically more important characters.

The history of the classification of mammals without teeth, or with reduced teeth, illustrates how such a red-herring character can be inordinately influential. Simpson (1945), in a short review of the history of the term Edentata, noted that the classical conception of Edentata included sloths, anteaters, armadillos, pangolins, and aardvarks; that evidence had necessitated removing the pangolins and aardvarks; that Taeniodonta had been included and accepted for a time; and that Palaeanodonta had been added and surely belonged there. Earlier, Simpson (1931) had argued in favor of a close palaeanodont-xenarthran relationship. However, the characters cited by Simpson in support of this hypothesis were mostly “incipient” xenarthran characters of the palaeanodont *Metacheiromys*, and he admitted (Simpson, 1931: 371) that “*Metacheiromys* is so early and primitive that the specifically xenarthran characters are indicated rather than typically defined.” This was an example of the red-herring character (loss of dentition) overwhelming the real signal. Consider what might have happened had the skull been unknown for palaeanodonts, or alternatively, if the skull were known but had a normal complement of unreduced teeth. Would “incipient” and not “typically defined” xenarthran characters have been found in the palaeanodont postcranium, let alone seen as taxonomically important? Comparing palaeanodonts with xenarthrans was obviously prompted by the fact that the dentition is reduced in palaeanodonts (practically absent in *Metacheiromys*). Without this powerful red herring,

Simpson might have been more impressed by the typically defined palaeanodont characters of palaeanodonts, rather than unduly emphasizing their “incipient” or not “typically defined” xenarthran characters.

In more recent years, arguments have again been made for reuniting Pholidota and Xenarthra in a clade separate from all other eutherians (Novacek, 1986, 1990; Novacek and Wyss, 1986a, 1986b; Novacek et al., 1988). The fact that this clade emerged from a parsimony-based (PAUP) analysis of many characters, equally weighted, does not guarantee objectivity. Before the computer begins its objective work, plenty of subjectivity remains in the decisions involved with the identification of characters, interpretations of degree of similarity, coding of characters, and in the choice of characters to be used in the analysis (which amounts to weighting—those characters used, equally weighted, are obviously all weighted more heavily than characters not used). Especially where subjective judgment is used in assessing degree of similarity, the opportunity remains for overvaluing the degree of this similarity. As a possible example of this, Novacek et al. (1988) added a feature of the pelvic girdle to the list of possible synapomorphies for edentates and pholidotans suggested earlier by Novacek and Wyss (1986). To quote Novacek et al. (1988: 44), “The arrangement of the pangolin pelvic-sacral region closely resembles that in the xenarthrans: both groups have extensive regional fusion in the pelvic-sacral area, and the large sacro-ischiadic foramen. The only significant difference between the two groups is that pholidotes have an ischial-sacral connection that is not completely fused, but is ligamentous.” In reality, pholidotes do not have an ischial-sacral connection, ligamentous or otherwise; the ligamentous connection mentioned is between the ischium and expanded transverse process of anterior caudal vertebrae, usually the second free caudal vertebra behind the sacrum. The sacrum in pangolins normally consists of three fused vertebrae, which is not unusual, and is in contrast to the sacrum of xenarthrans where the number of vertebrae incorporated in the sacrum ranges from a low of four to six in anteaters to as many as 13 in some armadillos (Rose and Emry, 1993). In

the pelvic-sacral region, the rodent *Geomys* is much more closely comparable to xenarthrans than pangolins are. But *Geomys* has teeth (and undoubtedly many other characters) that let us know it is a rodent, not an edentate. The similarity of the pelvic-sacral region between *Geomys* and xenarthrans is discounted because of what we know about *Geomys*. Is the lesser degree of similarity between pangolins and xenarthrans overvalued because of what we do not know about pangolins? Is the red herring of dental reduction still throwing systematists off the track?

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