The Entotympanic of Pangolins and the Phylogeny of the Pholidota (Mammalia)

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Entotympanics are independent elements present in the auditory bullae of various eutherians. An entotympanic has been reported for extant pangolins of the Order Pholidota, but the actual distribution of this element remains uncertain, in part, because it is a small, loosely attached structure that is often lost in macerated skulls. Consequently, it is unknown whether or not the entotympanic characterizes Pholidota primitively or has evolved within the group. This report addresses the morphology and distribution of the entotympanic among living and extinct pholidotans. An entotympanic occurs in the African pangolins Manis gigantea, M. temminckii, and in one specimen of M. tricuspis. In each, it is a small, nodular bone that occupies a distinct fossa primarily on the basioccipital, the presence of which allows us to assess the occurrence of an entotympanic even in specimens in which the bone has fallen out. Both the entotympanic and the basioccipital facet are lacking in the four remaining extant pangolin species and in the late Eocene pangolin Patrionanus. To assess the significance of this entotympanic distribution, a phylogenetic analysis of extant pangolins plus Patrionanus based on 67 cranial characters was performed. Four different outgroup analyses all resulted in the same single most parsimonious tree, in which the three extant Asian pangolins form a monophyletic clade and the four extant African pangolins fall into a paraphyletic assemblage. Optimization of the entotympanic distribution onto this tree results in two patterns, dependent on the outgroup choice. If Patrionanus is the sole outgroup to the extant pangolins, the entotympanic arises within pangolins as a synapomorphy of Manis gigantea and M. temminckii, convergently acquired in some M. tricuspis. If Xenarthra and Palaeocondylura are employed as outgroups, the entotympanic optimization is ambiguous: the pattern is either as above or the entotympanic is present primitively within Pholidota and lost secondarily in Patrionanus and a clade comprising M. tricuspis, M. tetradactyla, and the Asian forms.

KEY WORDS: Pholidota; entotympanics; pangolins; phylogeny.

INTRODUCTION

Entotympanic bones are independent ossifications that are found in the floor of the tympanic cavity in various mammals (van Kampen, 1905; van der Klaauw, 1931; Novacek, 1977; MacPhee, 1979). Generally considered to be restricted to certain Eutheria (MacPhee,

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1979; Maier, 1989), entotympanics are broadly distributed taxonomically among some extant and extinct eutherian groups, including, for example, Scandentia, Chiroptera, Dermoptera, Hyracoidea, Xenarthra, Carnivora, Macroscelidea, Leptictida, and Palaeanodonta (Novacek, 1977, 1986, 1993). Entotympanics have been reported for some marsupials based on macerated skulls [e.g., Dromiciops gliroides (Hershkovitz, 1992), Phalanger orientalis (Norris, 1993)], but to date the presence of an entotympanic has not been confirmed from histological preparations for any marsupial (or monotreme).

Entotympanics are exceedingly variable in composition, size, and form. Where known, all entotympanics develop endochondrally (MacPhee, 1979), with the possible exception of that in the xenarthran Bradypus, which may develop like intramembranous bone (Schneider, 1955). However, the number of centers of entotympanic chondrification varies from one [e.g., the scandentian Tupai glis (Spatz, 1966; MacPhee, 1981)] to a maximum of four [e.g., the megachiropteran Pteropus edulis (van der Klaauw, 1922)]. Entotympanics sometimes form intimate associations with neighboring elements; for example, in Tupai glis, the entotympanic fuses with the cartilage of the auditory tube, tegmen tympani, and caudal tympanic process of the petrosal (MacPhee, 1981), whereas in Pteropus sp. it fuses with the tympanohyal (van Kampen, 1915). Entotympanics may form a very small part of the floor of the tympanic cavity [e.g., the chrysoclorid Amblysomus hottenrotius (MacPhee and Novacek, 1993)] or underlie the entire tympanic cavity and also contribute to the tympanic roof [e.g., Tupai glis (Spatz, 1966; MacPhee, 1981)]. Two categories of entotympanics are generally recognized based on their embryonic positions in the tympanic floor (van der Klaauw, 1922): rostral, which may develop from multiple centers, and caudal, which appears to always have a single center. Such morphological variability has led some authors (e.g., Novacek, 1977, 1993; Wible and Novacek, 1988) to conclude that not all entotympanics are homologous and that independent elements have been added to the tympanic floor on several occasions within Eutheria. Others (e.g., Hershkovitz, 1992) consider entotympanics to be primitive eutherian (or therian) characters.

Usually included in the list of eutherians possessing an entotympanic is the Old World order Pholidota, the pangolins or “scaly anteaters” (Novacek, 1977, 1986; MacPhee and Novacek, 1993). This peculiar group of toothless myrmecophagous mammals, with their extraordinary covering of overlapping epidermal scales, is represented by seven extant species distributed across sub-Saharan Africa, the Indian subcontinent, and southeast Asia, including parts of Indonesia (e.g., Sumatra, Java, Borneo) and the Palawan Islands of the Philippines (Barlow, 1984; Nowak, 1991). The group has a meager fossil record extending back to the Eocene and is represented by scattered and isolated remains (though some specimens represent nearly complete skeletons) from Cenozoic deposits in Asia, Europe, Africa, and North America (Rose and Emry, 1993).

The presence of an entotympanic in pangolins is most often attributed to van Kampen’s (1905) observation of the bone in two African species, Manis tricuspis and M. gigantea. In both, the entotympanic was reported as a small element caudal to the auditory tube that contacts, but is not sutured to, the petrosal dorsally and the ectotympanic ventrally; it also contacts the basioccipital and basioccipital in M. gigantea. In an alcohol specimen of M. tricuspis dissected by van Kampen (1905), the entotympanic was said to lie lateral to the internal carotid artery and to form a small portion of the medial wall of the tympanic cavity, whereas it is expanded medially and underlies the carotid sulcus to enclose a carotid canal in a macerated skull of M. gigantea. Van Kampen (1905) did not find an entotympanic in
the other five extant pangolin species, but suggested that because it is a small free element, the entotympanic may have been lost from the dry skull. MacPhee (1994; Fig. 8) illustrated (but did not discuss) a very different type of entotympanic for a third African species, *M. tetradactyla*; the well-developed auditory bulla was labeled as a composite formed by the fused entotympanic and ectotympanic. An entotympanic has not been described in the skull of any other extant or extinct pangolin.

The question of whether an entotympanic is more widely distributed among extant and extinct pangolins, or indeed is a primitive characteristic of the order, is of particular relevance for studies of the interordinal relationships of the Pholidota. Recent phylogenetic hypotheses have linked the Pholidota to the Neotropical order Xenarthra (Novacek, 1986, 1992; Novacek and Wyss, 1986; McKenna, 1992; Norman and Ashley, 1994), resurrecting in modified form earlier concepts of a supraordinal cohort Edentata [see Hoffstetter (1982) and Glass (1985) for reviews of edentate classification]. Pholidota has also been purported to share a close common ancestry with the small, predominantly North American early Tertiary group Palaeanodonta (Emry, 1970; Rose and Emry, 1993). Both the Xenarthra and Palaeanodonta are characterized by large entotympanic bones (Matthew, 1918; Simpson, 1931; Patterson et al. 1989, 1992; Gaudin, 1995). Simpson (1931) and Patterson et al. (1992) use the absence of a well-developed entotympanic in pangolins to justify their alliance of palaeanodonts and xenarthrans to the exclusion of the Pholidota. Gaudin (1995) assumes an entotympanic to be characteristic of the Pholidota, but uses differences in the morphology of the pangolin element and that of palaeanodonts and xenarthrans to again support the monophyletic grouping of the latter two taxa. If an entotympanic does in fact characterize the Pholidota primitively, it is possible that the presence of an entotympanic is diagnostic at an even higher taxonomic level, as a synapomorphy of the entire cohort Edentata (*sensu* Novacek et al., 1988), including pholidotans, xenarthrans, and palaeanodonts.

Unfortunately, given the paucity of information on the true distribution of entotympanics among various pholidotan taxa, it is difficult to evaluate the reliability of this feature as a systematic character, or to ascertain at what taxonomic level it might be useful. The problem is exacerbated by the lack of any clear understanding of phylogenetic relationships within the Pholidota. Even at the alpha taxonomic level, substantial confusion exists in the literature as to the proper allocation of the various pangolin species. The seven extant pangolin species are classically placed together in a single genus *Manis* (Simpson, 1945), an arrangement followed by most modern mammalian systematists (Emry, 1970; Barlow, 1984; Corbet and Hill, 1991; Nowak, 1991; Schlitter, 1993). However, the species have been allocated to as many as six different genera (Pocock, 1924). The proper specific epithet for the three Asian species has been a source of controversy, with one group of authors referring to the species from the Indian subcontinent as *M. pentadactyla* and the species from southern China as *M. aurita* (Frechkop, 1931; Emry, 1970; Patterson, 1978), whereas a second group of authors refers the Indian species to *M. crassicaudata* and the Chinese species to *M. pentadactyla* (Pocock, 1924; Grassé, 1955; Barlow, 1984; Corbet and Hill, 1991; Nowak, 1991; Schlitter, 1993).

There have been few attempts to elucidate genealogical relationships among the various extant pangolin species, a notable exception being Patterson's (1978) study. Patterson advocated splitting the extant species into two monophyletic genera, one for the African forms (*Phataginus*) and the other for the Asian species (*Manis*). He further suggested
two clades within the African genus, one to include the large bodied terrestrial species *Phataginus gigantea* and *P. temminckii*, the second to include the smaller arboreal species *P. tricuspis* and *P. tetradactyla (=longicaudata)*. Unfortunately, Patterson (1978) did not attempt to resolve relationships within the Asian clade, and he provided few clearly derived features to support his various pholidotan subgroups. In fact, many of the features utilized by Patterson to diagnose his African and Asian subgroups are soft tissue characters unique to pangolins (e.g., scale patterns and xiphisternum morphology), which are difficult to polarize and which do not facilitate comparison with fossil specimens. Despite the fact that a number of the fossil species within the Pholidota are represented by extensive skeletal material, including *Eomanis krebsi* and *E. waldi* from the middle Eocene of Germany (Storch, 1978; Storch and Martin, 1994), *Necromanis franconica* from the Oligocene and Miocene of Europe (Koenigswald and Martin, 1990), and *Patriomanis americanus* from the late Eocene (Chadronian) of western North America (Emry, 1970; Rose and Emry, 1993), little effort has been made to incorporate these taxa explicitly into a comprehensive scheme of pholidotan phylogeny. The above authors merely assert that each of these extinct pholidotans is more primitive in certain aspects of its morphology than are the living taxa. On the other hand, McKenna and Bell (1997) without explanation include these extinct taxa with the Asian pangolins to the exclusion of the African forms.

The goals of the present study are twofold. First, we describe the distribution and morphology of entotympanics among all living pholidotan species, including a consideration of basicranial ontogeny. Second, we generate a phylogeny of the Pholidota based upon morphological features drawn from the skull of living and extinct pangolins. Using this phylogenetic scheme, we attempt to discern whether the entotympanic is present primitively in the Pholidota as a whole or evolved independently within Pholidota on one or more occasions.

**MATERIALS AND METHODS**

Our observations of adult pholidotan auditory region morphology and cranial anatomy were carried out largely at the Division of Mammals of the Field Museum of Natural History, Chicago, the Division of Mammals and Department of Paleobiology of the National Museum of Natural History, Smithsonian Institution, Washington, DC, and the Department of Mammalogy of the American Museum of Natural History, New York. Serially sectioned prenatal and neonatal specimens were studied at the Anatomisches Institut, Goethe-Universität, Frankfurt am Main, Germany, and the Duke University Comparative Embryological Collection, Durham. Specimens are referred to in the text using the following abbreviations: AIF, Anatomisches Institut, Frankfurt am Main; AMNH, American Museum of Natural History, New York; DUCEC, Duke University Comparative Embryological Collection, Durham; FMNH, Field Museum of Natural History, Chicago; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC; and YPM-PU, Princeton University collection housed at Peabody Museum, Yale University, New Haven, CT.

A phylogenetic analysis of relationships among the seven living pangolin species and the late Eocene North American pholidotan *Patriomanis* is performed based on 67 discrete cranial morphological characters derived from direct observations of relevant speci-
mens (listed in Table A1). Other relatively well-preserved fossil pholidotans, including the European taxa Euramis and Necromantis, are omitted from this phylogenetic assessment as they are represented by fragmentary or poorly preserved cranial material (Storch 1978; Koenigswald and Martin, 1990; Storch and Martin, 1994) and hence cannot be coded for the vast majority of characters. For the purposes of discussion, we follow Simpson (1945) and others in considering all extant pangolin species to pertain to the single genus Manis. Similarly, we will follow Nowak (1991) and others in using the specific epithet M. pentadactyla to refer to the Chinese pangolin species, and M. crassicaudata to refer to the Indian form.

The 67 morphological characters (listed in Table AII) which make up our data matrix include 19 multistate characters, of which 12 could be ordered along structural, positional, or numerical morphologies. Following Gaudin (1995) and Gaudin and Branham (1998), four weighting and ordering schemes are applied to the multistate characters in order to test for their effect on the analysis: (1) all multistate characters unordered, all character state changes weighted equally; (2) all multistate characters unordered, all characters weighted equally; (3) multistate characters ordered or unordered, all character state changes weighted equally; and, (4) multistate characters ordered or unordered, all characters weighted equally. As each weighting and ordering scheme will of necessity change the tree length, the preferred scheme is that which maximizes consistency index (CI) and retention index (RI).

The data matrix (Table AIII) is analyzed using the computer program PAUP [Version 3.1.1 (Swofford, 1993)]. The bulk of the analyses are carried out using PAUP’s branch and bound algorithm, although the preferred tree is confirmed using PAUP’s exhaustive search option. Characters are optimized using PAUP’s DELTRAN option [for justification see Gaudin (1995)]. In those instances in which interspecific variation is noted in a given character for a given taxon, the taxon is coded for all the relevant states and treated as polymorphic in all PAUP analyses.

Characters are polarized via comparison to two outgroups, the Xenarthra and Palaeanodontia, which together with the Pholidota have been suggested to form a monophyletic cohort Edentata (Novacek et al., 1988; see also Matthew, 1918; Simpson, 1931; Rose, 1979; Cifelli, 1983; McKenna, 1992). The Palaeanodontia is represented by the well-known and relatively unspecialized metaceiromyid genus Metaceiromys (Table A1). The Xenarthra is represented by six species (Table A1), drawn from two armadillo genera (Tolypeutes matacus and Euphractus sexcinctus), two anteater genera (Tamandua mexicana and Cyclopes didactylus), and one sloth genus (Bradypus variegatus and B. tri-dactylus). The relationships among xenarthran taxa are constrained a priori in all PAUP analyses following Engelmann (1985) and Gaudin (1993, 1995). Because of the controversy surrounding relationships among the various edentate taxa, four separate outgroup analyses are performed. In the first, Metaceiromys is constrained to be the sister taxon to Xenarthra following Simpson (1931, 1945), Szalay (1977), Patterson et al. (1992), and Gaudin (1995), and this monophyletic xenarthran-palaeanodont clade is used as the sole outgroup to Pholidota. In the second outgroup analysis, Metaceiromys is constrained to be the sister taxon to Pholidota, following Emry (1970) and Rose and Emry (1993), and Xenarthra is employed as an additional outgroup to this pholidotan-palaeanodont clade. In the third outgroup analysis, the relationship among Pholidota, Xenarthra, and Metaceiromys is left as an unresolved trichotomy. In the fourth and final outgroup analy-
sis, the nonpholidotan outgroups are omitted, and *Patriomanis* is employed as an outgroup to the living pangolins following Emry (1970).

**RESULTS**

**Ontogeny of the Tympanic Floor**

The ontogeny of the tympanic floor can be reconstructed from several literature sources for only one pangolin species, *Manis javanica*. The entire chondrocranium and osteocranium have been described for this form based on serially sectioned specimens from two fetal stages (Starck, 1941) and one neonate (Jollie, 1968). The details of the composition of the tympanic floor and the pattern of the cranial arteries in these three specimens along with a serially sectioned fetus of *Manis sp.* have been reported by Wible (1984). Finally, some details of the tympanic floor in a serially sectioned adult *M. javanica* are included by Eschweiler (1899). The pertinent results of these studies are summarized below.

In the older fetal stage of *Manis javanica* (AIF 17; crown–rump length = 95 mm) and the one fetal stage of *Manis sp.* (DUCEC 8321; crown–rump length = 70 mm), the only hard-tissue structure in the floor of the tympanic cavity is the simple, ring-shaped ectotympanic, the bulk of the floor being completed by a loose, ill-defined fibrous membrane (Wible, 1984), the fibrous membrane of the tympanic cavity of MacPhee (1981). The internal carotid artery runs longitudinally in a shallow sulcus beneath the anteromedial aspect of the otic capsule, the cartilaginous precursor of the promontorium of the petrosal; the artery lies medial to the fibrous membrane except at the anterior pole of the otic capsule where the artery runs through the membrane in a fibrous carotid canal that extends to the carotid foramen (Wible, 1984). The left side of the younger *M. javanica* fetus (AIF 14; crown–rump length = 70 mm) has an extra element in its tympanic floor, a small, round accessory cartilage within the fibrous membrane in the posteromedial corner (Starck, 1941; Wible, 1984). This cartilage does not resemble the entotympanses described for *M. tricuspis* and *M. gigantea* (van Kampen, 1905) and illustrated for *M. tetradactyla* (MacPhee, 1994), as it lies wholly posterior to the internal carotid artery. Beyond that, the meaning of this transient cartilage is uncertain. Starck (1941) suggested it might be a remnant of Reichert’s cartilage, but this homology seems unlikely in light of the accessory cartilage’s proximity to the central stem of the chondrocranium, an unusual position for Reichert’s cartilage in mammals (De Beer, 1937).

The neonate of *Manis javanica* (AIF 105-108; crown–rump length = 120 mm) shows several major advances with regard to the composition of the tympanic floor (Fig. 1). First, the ectotympanic is expanded both medially and laterally, and therefore contributes more to the tympanic floor (Wible, 1984). Second, in the interval between the ectotympanic and promontorium of the petrosal, the fibrous membrane is better defined, as a dense mass of connective-tissue fibers; also better defined is the fibrous carotid canal, which surrounds a longer section of the artery in its course below the promontorium (Wible, 1984). Third, a well-developed cartilage of the auditory tube lies in a horizontal plane within the fibrous membrane at the anteromedial corner of the tympanic floor, ventral to the fibrous carotid canal (Fig. 1) (Jollie, 1968; Wible, 1984). The cartilage has a complex shape with a wider medial portion bent such that it shields the auditory tube on its dorsal, rostral, and ventral
surfaces at the nasopharyngeal junction and a thinner lateral portion which extends first laterally and then posteriorly dorsal to the auditory tube (Wible, 1984).

The most significant advance visible in the serially sectioned adult Manis javanica is the further expansion of the ectotympanic both medially and laterally within the tympanic
floor (Eschweiler, 1899, Figs. 17 and 19). This expansion results in a fairly extensive osseous auditory bulla (see Jollie, 1968, Fig. 15). The expanded ectotympanic along with the complex-shaped cartilage of the auditory tube are still the only hard-tissue structures in the adult tympanic floor (Eschweiler, 1899).

To summarize, the ontogeny of Manis javanica shows that (1) there is no entotympanic in the interval between the petrosal and ectotympanic as described for M. tricuspid and M. gigantea by van Kampen (1905), and (2) there is only a single bony element in the auditory bulla, the ectotympanic. Therefore, in the absence of sutures in the auditory bulla, we see no reason to identify the manid bulla as a composite structure with both an entotympanic and ectotympanic, as MacPhee (1994, Fig. 8) did for M. tetradactyla.

**Morphology and Distribution of the Entotympanic in Adult Skulls**

In our studies of macerated adult skulls, we found an accessory ossification in the tympanic floor in only three forms: Manis gigantea, M. temminckii, and M. tricuspid. In each, the extra ossification is in the same position and shows essentially the same morphology. Although there is a positional resemblance to the entotympanics described by van Kampen (1905) for M. gigantea and M. tricuspid, there are some striking differences as well (see below). We also found no support for MacPhee's (1994) identification of a composite auditory bulla (fused entotympanic and ectotympanic) in M. tetradactyla or any other manid.

The element that we observed in Manis gigantea, M. temminckii, and M. tricuspid is identified here as an entotympanic because it fits the definition of that structure as an independent tympanic floor ossification. We note, however, that it is unlike most entotympanics that occur in other eutherians in one major aspect: it is a chunky, rectangular piece of bone, whereas entotympanics in other eutherians are usually laminar. Yet stocky entotympanics are known for some other forms [e.g., the dermopteran Cynocephalus (Wible and Martin, 1993)]. The manid entotympanic is best developed in the largest of the living species, the giant pangolin M. gigantea, as noted by van Kampen (1905). We describe the entotympanic in this species first and then discuss its morphology and distribution in other living and extinct pangolins.

The entotympanic in Manis gigantea is a chunky bone, longer anteroposteriorly than it is wide, and slightly extended ventrally (Figs. 2 and 3). Its dorsal surface fits into a deep, sharp-edged depression on the basioccipital (Fig. 2). This entotympanic fossa or facet is formed predominantly by the ventral portion of the lateral wing of the basioccipital, with a smaller contribution from either the petrosal (AMNH 53858) or basisphenoid (USNM 269706). [The alisphenoid, basisphenoid, and pterygoid are fused in pangolins (Jollie, 1968), and we describe these elements based on their positional relationships in other living taxa for which the individual ossification centers are known.] There is no facet on the free ventral edge of the entotympanic, nor is there a facet on the dorsal edge of the ectotympanic. The ectotympanic and entotympanic may be separated from one another by a small gap (AMNH 53849) or contact one another via a simple abutment (AMNH 53850). Contra van Kampen (1905), the entotympanic lies medial rather than lateral to the internal carotid artery in all of our M. gigantea specimens. The course of the artery is indicated by a deep, well-defined groove, the sulcus caroticus, on the ventromedial edge of the petrosal. The sulcus is open ventrally, although its walls approximate
one another in the central portion of the groove (Fig. 3). The sulcus ends in a well-defined carotid foramen situated on the suture between the petrosal and alisphenoid. There is a small basioccipital contribution to the postero medial portion of the sulcus, but there is no entotympanic contribution, nor any true canalis caroticus, again in contrast to van Kampen's (1905) description.
Like *Manis gigantea*, all the specimens of *M. temminckii* that we examined bear either an entotympanic bone or an entotympanic facet on the basioccipital. As shown in the figured specimen (Fig. 4), the entotympanic is smaller in this species than in *M. gigantea*; its facet is smaller, shallower, and directed laterally rather than ventrally. As in *M. gigantea*, the entotympanic facet may receive a small contribution from either the basisphenoid (FMNH 38144, 34610) or petrosal (FMNH 35682). The entotympanic itself extends ventrally toward the ectotympanic, but there is no facet on the ventral entotympanic surface for the ectotympanic, nor is there an entotympanic facet on the dorsomedial surface of the ectotympanic. Rather, the two bones are presumably joined by a fibrous connective tissue membrane. In contrast to *M. gigantea*, the entotympanic of *M. tem-
minckii forms a partial bony floor of a carotid canal, in conjunction with the medial most portion of the ectotympanic. Only the middle portion of the carotid canal is floored by bone. The anterior and posterior sections of its course are likely floored by membrane. The entire course of the internal carotid artery, however, is roofed by a well-defined sulcus caroticus lying between the petrosal, basisphenoid, and basioccipital (the petrosal comprising the lateral wall of the sulcus, the latter two the medial wall). The carotid foramen lies at the junction of the petrosal, squamosal, and alisphenoid/basisphenoid (Fig. 4). That portion of the entotympanic which extends ventral to the internal carotid may participate in the medial wall of the tympanic cavity, as in van Kampen’s (1905) specimens.

In Manis tricuspis, we observed the entotympanic in a single specimen (USNM 450073), and only on the left side. Its entotympanic is a tiny nubbin sitting in a shallow facet on the basioccipital, contacting the petrosal medial to the sulcus caroticus (at the posterior end of the sulcus). The entotympanic and its facet were not found on the specimen’s right side or in any of the remaining M. tricuspis skulls examined, including all of
Fig. 4. Left basicranial region of Manis temminckii, FMNH 34610, in ventral view. Scale = 1 cm. bo, basioccipital; bs, basisphenoid; cf, carotid foramen; eam, external auditory meatus; ec, entotympanic; en, entotympanic; fo, foramen ovale; hf, hypoglossal foramen; jf, jugular foramen; pe, petrosal; pgf, postglenoid foramen; pt, pterygoid; sq, squamosal.

the remaining skulls listed in Table AI, as well as some 30 AMNH specimens not listed in the Appendix.

It is especially noteworthy that in Manis tricuspis, the one tiny entotympanic that was observed sat in a small but distinct basioccipital facet. Likewise in M. gigantea and M. temminckii, all the specimens in which an entotympanic was found also possessed a well-defined basioccipital facet, irrespective of the size of the entotympanic. An entotympanic was not observed in any of the remaining extant pangolin species. Neither was there a entotympanic facet on the basioccipital in any of these species. We take this (combined with the ontogenetic evidence presented above) as evidence that the presence of an entotympanic facet on the basioccipital is a reliable indicator of the presence of an entotympanic, even if the element itself is not preserved in the macerated skull. Likewise, the absence of such a facet implies that the entotympanic itself was not present.

The single skull of Patriomanis available (the type specimen, AMNH 78999) was examined for evidence of an entotympanic or an entotympanic facet on the basioccipital. No evidence for either structure was found. There is no published information on the basicrania of either Necromanis or Eomanis.
Phylogenetic Analysis

Each of the four outgroup arrangements resulted in the same single most parsimonious branching pattern within Pholidota, regardless of the weighting and ordering scheme employed (with a single exception, discussed below). The following summary of the phylogenetic results will focus on the third outgroup analysis, in which Metacheiromyidae and the Xenarthra are constrained to form a basal trichotomy with the Pholidota. It is our feeling that this represents the most conservative of the outgroup arrangements, as it allows us to use the other edentate taxa for the purposes of determining character polarity without an a priori preference for one of the two controversial schemes of edentate interrelationships (see Materials and Methods). The weighting and ordering scheme which maximized CI and RI in this instance was the first scheme, in which all multistate characters were unordered and character state changes were weighted equally. The single most parsimonious tree produced by this PAUP analysis had a length of 185 steps, a CI = 0.719 and a RI = 0.713 (Fig. 5). Characters will be referred to in the ensuing discussions following the numeration in Table AII.

Node 1. Pholidota. The described remains of the late Eocene genus Patriomnis include a single well-preserved braincase and basicranium broken approximately at the level of the glenoid fossa/posterior orbital wall (Emry, 1970). Dr. Robert J. Emry has, in his collection at the National Museum of Natural History, some undescribed material of this same taxon (USNM-P 299360), including much of the snout, hard palate, and lower jaw, which he kindly permitted us to examine in connection with the present study. The published material yielded four unequivocal synapomorphic resemblances between Patriomnis and the extant members of Pholidota: narrow contact between the orbitosphenoid and squamosal (character 17); lateral wings of the basisphenoid and basioccipital present (char. 42; see Fig. 2); elongate, ventrally directed zygomatic processes of the squamosal (char. 50; Fig. 2); and the absence of temporal lines (char. 53). The new material is astoundingly similar to extant pangolins. Like modern pangolins, this material shows Patriomnis to be completely toothless. In our phylogenetic analysis, the new Patriomnis specimens provided an additional six unambiguous cranial synapomorphies for the Pholidota (Table AIV), including medial and lateral nasal processes separated by a deep notch on the anterior edge of the nasal (char. 1); a posterodorsally inclined dorsal process of the premaxilla (char. 4); a deep median longitudinal palatal concavity (char. 8); an orbital shelf of the palate which extends anterolaterally toward the zygomatic process of the maxilla (char. 12; Fig. 2); a pair of anterolaterally directed prongs attached to the outer surface of the mandibular symphysis (char. 61), and a mandibular condyle situated at the level of the mandibular symphysis (char. 65).

Node 2. Monis. The monophyly of the extant genus Monis is supported by as many as 20 synapomorphies. Unfortunately, given the large amount of missing data on Patriomnis, only six of these synapomorphies can be unambiguously assigned to this node, including: a flat, weakly developed promontorium (char. 29; see Figs. 2 and 3); the fenestra cochleae directed laterally, situated immediately next to the fenestra vestibuli (char. 32; Figs. 2 and 3); the lambdoid crest rudimentary or absent (char. 47); absence of endocranial venous grooves (char. 57); the middle cranial fossa floored by the squamosal (char. 58); and the absence of a coronoid process on the mandible (char. 66).

Node 3. Unnamed. In the most parsimonious tree, the African pangolins form a
Fig. 5. Preferred phylogeny of the Pholidota based on PAUP analysis of 67 cranial characters in seven extant and one extinct pangolin species. Characters are polarized via comparison to two outgroups, the Palaenodontata (represented by the extinct genus Metacheiromys) and Xenarthra, which together are assumed to form a basal trichotomy with the Pholidota. Multistate characters are all unordered, and all character state changes are weighted equally. The single most parsimonious tree resulting from this analysis has a tree length = 185 (CI = 0.719; RI = 0.713). See Results and Table A1V for a listing of characters at each node.
paraphyletic assemblage in which a clade including the two arboreal African pangolins, *Manis tricuspid* and *M. tetradactyla*, is joined to a monophyletic Asian clade by three unambiguous synapomorphies: the lateral extension of the anterolateral palatine shelf so that it comes to lie directly posterior to the zygomatic process of the maxilla (char. 12); the posteroventral shielding of the fenestra cochleae by a flange of the petrosal (char. 33); and a circular foramen magnum (char. 45). The two terrestrial African pangolins, *M. gigantea* and *M. temmincki*, are each other’s closest relative, and together form a clade that is the sister group to the remaining extant forms. In an attempt to ascertain the robusticity of this paraphyletic arrangement versus Patterson’s (1978) suggestions of the monophyly of the African taxa, a separate analysis was run (using the same settings as the preferred tree) in which the monophyly of the African species was constrained a priori. This resulted in a single most parsimonious tree that was only a single step longer than the unconstrained tree. The African taxa were united in the constrained tree by similarities in the morphology of the auditory ossicles (as described in Segall, 1973), including a short stapedial columnella (char. 39) and the dorsal rotation of the malleal/inciped articulation (char. 37).

The monophyly of the *Manis temmincki*/*M. gigantea* clade, the equivalent of Pocock’s (1924) genus *Smutsia*, was supported by four unambiguous synapomorphies in the most parsimonious tree (Table AIV). The *M. tetradactyla*/*M. tricuspid* clade is the most strongly supported on the entire cladogram. These two taxa are united by 11 unambiguous synapomorphies in the most parsimonious tree (Table AIV).

**Node 4.** Asian Pangolins. In accordance with Patterson’s (1978) study, the monophyly of the Asian pangolins was supported in our analysis by five unambiguous synapomorphies. All the Asian species have a broad contact between the orbitosphenoid and squamosal (char. 17), an uninflated ectotympanic bone (char. 25), a closed canal in which the facial nerve travels after its emergence from the facial foramen on the lateral surface of the petrosal (char. 30), a stout rectangular incus with reduced crura (char. 38), and an exoccipital constriction (a condylar “neck”) immediately anterior to the occipital condyles (char. 44). Among the three Asian forms, *Manis javanica* and *M. pentadactyla*, the Chinese and Southeast Asian/Indonesian species, are allied in the preferred tree by only two unambiguous synapomorphies, including the loss of the median palatal concavity (char. 8) and a mandibular symphysis that is concave anteriorly (char. 60). In the three outgroup analyses in which Xerathra and *Metachiroonyms* are included, if the fourth weighting and ordering scheme is employed (multistate characters ordered or unordered, character state changes weighted equally), a second most parsimonious tree results. This second tree differs from the preferred tree only in relative position of the Asian taxa, allying *M. pentadactyla* with *M. crassicaudata* rather than *M. javanica*.

**DISCUSSION**

Our review of the ontogeny of the tympanic floor in *M. javanica* coupled with the discovery of a distinct basioccipital facet for the entotympanic in those taxa (and those individuals) in which the latter element is present has permitted us to assess the distribution of the entotympanic within Pholidota with some confidence. Among living species, the entotympanic is invariably present in *M. gigantea* and *M. temmincki* and occurs on one side of a specimen of *M. tricuspid* as well. There is no evidence indicating the pres-
ence of an entotympanic in the remaining extant species, including *M. tetradactyla* (contra MacPhee, 1994) and the three Asian species. Among fossil pholidotans, only *Patriomanis* is represented by sufficient cranial material to assess the presence or absence of the entotympanic. As in the majority of living species, this extinct pangolin apparently did not possess an entotympanic.

When the distribution of entotympanics among pholidotans is optimized onto the cladogram resulting from our phylogenetic analysis (Fig. 5), two patterns emerge, depending upon the choice of outgroups. If *Patriomanis* is used as the only outgroup to the living manids, the entotympanic is optimized as a feature absent from Pholidota primitively that evolves within the group on two separate occasions—once at the base of the *M. gigantea/M. temminckii* clade, and a second time in some *M. tricuspis*. If *Metachiromys* and xenarthrans are included as outgroups, two equally parsimonious optimization patterns emerge. The first (Fig. 6A) is similar to that resulting when *Patriomanis* is the sole outgroup. The entotympanic, which is present in both paleaeanodonts and xenarthrans (Patterson et al., 1992), may or may not be a synapomorphy of the supraordinal group Edentata (it is if these taxa are assigned to a basal trichotomy or if paleaeanodonts are allied with pholidotans, but not if paleaeanodonts and xenarthrans are arranged as sister-groups). However, the bone is not present at the base of Pholidota, but evolves independently in *M. gigantea/M. temminckii* and some *M. tricuspis*. The second optimization pattern (Fig. 6B) places the evolution of the entotympanic at the base of the Edentata, as an unequivocal synapomorphy of this clade. In this scheme, the entotympanic is also present at the base of the Pholidota. The bone is then lost independently within Pholidota in *Patriomanis* and a clade including the Asian pangolins plus *M. tetradactyla* and *M. tricuspis* (note that the entotympanic is secondarily reevolved or polymorphic in some *M. tricuspis*)

According to these results, it is not possible to state unequivocally whether the presence of an entotympanic is a primitive characteristic for the order Pholidota. The morphological dissimilarity between the entotympanic of pangolins and that found in xenarthrans and paleaeanodonts would tend to favor the argument that the bone originates independently in pangolins. The entotympanic of pangolins is small and blocky; that of paleaeanodonts and xenarthrans is large and laminar (Matthew, 1918; Simpson, 1931; Patterson et al., 1989, 1992; Gaudin, 1995). The entotympanic of pangolins is loosely attached to the surrounding elements and sits in a distinct fossa on the basioccipital (Figs. 2–4); that of paleaeanodonts and xenarthrans lacks a basioccipital fossa and is typically sutured to surrounding elements (Simpson, 1931; Patterson et al., 1989, 1992; Gaudin, 1995). The entotympanic of pangolins lies medial or ventral to the internal carotid artery in the specimens we observed [although van Kampen (1905) describes the element as situated lateral to or surrounding the internal carotid artery]; that of paleaeanodonts and xenarthrans is typically either lateral to the internal carotid artery or perforated by the artery (Wible, 1986; Patterson et al., 1989, 1992; Gaudin, 1995). The absence of the entotympanic in *Patriomanis*, the single early fossil pangolin for which such information could be obtained, further supports the idea of an independent origin of the entotympanic within Pholidota. Nevertheless, the pattern of entotympanic evolution in the Pholidota depends ultimately upon the choice of outgroups and the manner in which those outgroups are arranged. With the addition of paleaeanodonts and xenarthrans to the analysis, it becomes equally parsimonious to consider the condition in *Patriomanis* an independent loss of an entotympanic present primitively in Pholidota. Further information on the basicranium of other early
Cenozoic fossil pangolins, e.g., Necromantis and Eomanis, could resolve the issue definitively. However, given the present state of knowledge, it is not possible to resolve whether an entotympanic is primitive for the order Pholidota.

Likewise, until the pattern of entotympanic evolution within the Pholidota is clarified and the relationships among palaeocanodonts, pangolins, and xenarthrans are better understood, it is not possible to say with any certainty whether an entotympanic characterizes all edentatans primitively. The optimization of this character at the base of Edentata depends on how the three taxa are arranged relative to one another. Our preferred conservative arrangement, in which the three are joined at a basal trichotomy, results in the optimization of the entotympanic as a primitive feature of this supraordinal cohort (Fig. 6). However, if Simpson (1931, 1945) and others (Szalay, 1977; Patterson et al., 1992; Gaudin, 1995) are correct in aligning palaeocanodonts and xenarthrans to the exclusion of pholidotans, then parsimony dictates multiple evolution of the entotympanic within Edentata.

Whereas the present analysis has not been completely successful in clarifying the evolutionary history of the entotympanic within Pholidota or Edentata and hence the phylogenetic utility of this feature, the results are significant as regards the phylogenetic relationships within Pholidota. As noted in the Introduction, the present analysis is to our knowledge the first detailed cladistic study of the group, and the first to con-
sider formally fossil pholidotans along with the living taxa. The results strongly support
the monophyly of the order Pholidota. There are ten unambiguous cranial synapomor-
phies which serve to distinguish the group from xenathrans and palaeanodonts, including
such unique characteristics as a pair of anterior bony prongs on the outer surface of the
mandibular symphysis, a median longitudinal palatal concavity, and a ventrally directed
zygomatic process of the squamosal bearing a convex glenoid articulation on its distal
surface. Indeed, we find the pholidotan cranium to be highly distinctive, despite the sug-
gestions of several recent authors that pangolins may evolve within Xenarthra, based on
shared derived morphological (Engelmann, 1978, 1985; Reiss, 1996) and molecular simi-
larities (Norman and Ashley, 1994). Two of the morphological studies go so far as to
suggest a sister-group relationship between pangolins and myrmecophagid anteaters [i.e.,
the Vermilingua (Engelmann, 1978; Reiss, 1996)], although both authors retreat some-
what from this claim in subsequent publications (Engelmann, 1985; Reiss, 1997).

Of the ten unambiguous pholidotan synapomorphies, only one is clearly present
in myrmecophagids, an orbital shelf of the palatine, and perhaps one more, basis-
phenoid/basioccipital wings, arguably present, although the differences in morphology
between the two groups (the basisphenoid/basioccipital wings are inflated and sutured to
the pterygoid ventrally in myrmecophagids but not pangolins) argue against their homol-
ogy. There are an additional eleven characters which may be pholidotan synapomorphies
but are not preserved in *Patriomantis* (chars. 6, 14, 23, 27, 28, 34, 36, 41, 51, 54, 67;
see Table AII). Of these, only character 54 (absence of postorbital processes) also clearly
characterizes vermilinguans, with character 41 (vomer not visible from choanae) arguably
present in both, although again there are morphological differences in the two groups
(in pangolins the vomer is covered by the palatine bones on the roof of the choanae,
whereas in myrmecophagids the vomer is not visible due to the extraordinarily elongate
hard palate). Nevertheless, the majority of unequivocal and potential pholidotan synap-
omorphies are not present in myrmecophagids. Recent cladistic studies of vermilinguan
phylogeny (Gaudin, 1993; Gaudin and Branham, 1998) reveal a similar pattern—a few
derived resemblances are shared by the pangolins and myrmecophagids (e.g., antepo-
steriorly elongate mandibular condyle, fusion of the basisphenoid, alisphenoid, and ptery-
goid early in ontogeny, anterior elongation of the neural spine of the axis, presence of an
tenepicondylar notch on the humerus), but the majority of vermilinguan synapomorphies
are absent in the Pholidota.

Perhaps even more troubling for the pangolin/myrmecophagid hypothesis is the
absence of higher level xenathran characteristics among pholidotans. Whereas pangolins
share with the Pilosa (sloths plus vermilinguans) an incomplete zygoma and a loosely
attached premaxilla, they lack most other synapomorphies of this group, including a con-
cave navicular facet on the astragalus [absent primitively in Pholidota (Rose and Emry,
1993 contra Engelmann (1985)]), a scapular fenestra (Engelmann, 1985), reduction or
absence of the postglenoid foramen (Engelmann, 1985; Gaudin, 1995) and pterygoid
hamulus, as well as a long list of ear region features and cranial synapomorphies identified
by Gaudin (1993, 1995). A brief survey of characters identified as synapomorphies for
the order Xenarthra by Engelmann (1978, 1985), Rose and Emry (1993), and Gaudin (1993,
1995) revealed over 20 characters that are present in all or nearly all xenarthrans but are
not found among pangolins. Pangolins differ strongly from xenarthrans in the morphology
of their axial skeleton, shoulder girdle, pectoral girdle, and auditory region and, to a lesser
extent, in the morphology of their pelvis, humerus, and manus. Although this study by no means rules out the possibility of a sister-group relationship between xenarthrans and pholidotans as proposed by Novacek (1986, 1992) and colleagues (Novacek et al., 1988; McKenna, 1992), we find little compelling evidence for a closer relationship between the two groups.

Within the Pholidota, the present study provides robust support for the monophyly of the seven living pangolin species, grouped here under the genus *Manis*, to the exclusion of the North American late Eocene fossil genus *Patriomani* (Fig. 5). Despite the large amount of missing data on the skull of *Patriomani* (25 of 67 characters, or 37%, coded as unknown), the living taxa are united by six unambiguous synapomorphies, including loss of the lamdoid crest and coronoid process on the dentary and a weakly developed promontorium of the petrosal. This node was the second strongest in our exhaustive search, collapsing only after the addition of four steps to the most parsimonious tree. We suspect that there is more structural diversity within the order Pholidota than is allowed for in existing classifications, which tend to lump fossil genera in the same family (Manidae) that contains the recent taxa (Emry, 1970; Storch, 1978). In addition to the cranial characters from the present study separating *Patriomani* from recent manids, we note, for example, that all Tertiary pangolins lack a concave navicular facet on the astragalus (Koenigsfeld and Martin, 1990; Rose and Emry, 1993) and that *Eoman* lacks the fissured unguals characteristic of all other pholidotans (Storch, 1978; Storch and Martin, 1994), including other Tertiary forms. We feel that the Tertiary pholidotans probably ought to be placed in a separate family from the recent forms (perhaps in more than one separate family). However, any definitive revision of family level relationships within the Pholidota must await further study. Such a study would need to incorporate not only additional taxa, but also additional postcranial characters, as postcranial remains constitute the bulk of preserved material for Tertiary taxa other than *Patriomani* (Emry, 1970; Storch, 1978; Koenigsfeld and Martin, 1990; Rose and Emry, 1993; Storch and Martin, 1994).

A novel systematic arrangement of extinct and extant pangolins was published recently by McKenna and Bell (1997). They identified two subfamilies: Smutsiinae for the African pangolins and Maninae for the Asian pangolins plus *Eoman*, *Necromani*, and *Patriomani*. Unfortunately, characters linking the early Tertiary taxa specifically with the Asian forms were not offered, but this scheme is not congruent with the results of our analysis.

Among extant manids, the derivation of Asian pangolins from a paraphyletic African stem group (Fig. 5) is weakly supported in the present analysis. In an exhaustive search, there are four trees that are one step longer than the most parsimonious tree. Included with these four is one tree in which the African pangolins form a monophyletic group *sensu* Patterson (1978), supported by derived characteristics of the auditory ossicles (chars. 37 and 39) described in Segal (1973). The most parsimonious tree allies *Manis tricuspid* and *M. tetradactyla* to the Asian pangolins on the basis of three unambiguous synapomorphies (see Results and Table AIV) taken from various regions of the skull. Similarly, although *M. temminckii* and *M. gigantea* are allied as sister taxa in the shortest tree, this relationship collapses with the addition of a single step in the exhaustive search. *M. gigantea* and *M. temminckii* share four unambiguous synapomorphies in the most parsimonious tree (see Results and Table AIV). The sister-group relationship between *M. tricuspid* and
M. tetradactyla, however, is the strongest node in the entire analysis. Six steps must be added to the shortest tree before this node collapses in the exhaustive search, and the two species are united by eleven unambiguous synapomorphies, the largest number of synapomorphies to be found at any node.

The monophyly of Asian pangolins (Fig. 5) receives moderately robust support from the present analysis. The node is supported by at least five unequivocal synapomorphies, and collapses in an exhaustive search in trees three steps longer than the most parsimonious tree. The relationships among the three Asian species are less clearly resolved. In the most parsimonious tree from the preferred analysis, the East Indian and Chinese pangolins (Manis javanica and M. pentadactyla) form a clade to the exclusion of the Indian species (M. crassicaudata). However, under certain weighting, ordering, and outgroup schemes (see Results above), an alliance of M. crassicaudata and M. pentadactyla to the exclusion of M. javanica is equally parsimonious. The latter arrangement also appears only the single step less parsimonious than the shortest tree under the preferred weighting, ordering and outgroup scheme.

In summary, the phylogenetic results for living pangolins show some similarities to the taxonomies of both Patterson (1978) and Pocock (1924). Patterson suggests grouping all extant Asian species in the genus Manis, and all African species in the genus Phataginus. Pocock placed each Asian species, as well as tricuspis and tetradactyla, into separate genera but allied gigantea and temminckii in the same genus, Smutsia. Our results indicate three major clades among living pangolins: (1) the Asian pangolin species crassicaudata, pentadactyla, and javanica; (2) the arboreal African pangolin species tricuspis and tetradactyla; and (3) the terrestrial African pangolin species gigantea and temminckii. As discussed above for fossil taxa, we believe that the living pangolins encompass a broader range of morphologies than is indicated by their currently accepted placement within a single genus. We suggest that the living forms might be divided into at least two and possibly three genera. Based strictly on the phylogenetic tree shown in Fig. 5, three genera would be indicated: (1) Manis, for the Asian species; (2) Phataginus, for the arboreal African species; and (3) Smutsia, for the terrestrial African species. However, we are hesitant to make any formal taxonomic pronouncements without the inclusion of a wider range of characters in the analysis, including not only postcranial skeletal features, but also soft tissue characters such as scale patterns, xiphisternal morphology, hair patterns, and the presence or absence of external ear pinnae, that have formed the basis for previous taxonomic studies of the living species (e.g., Pocock, 1924; Frechko, 1931; Patterson, 1978).

Finally, the results of the present study have important implications for students of mammalian interordinal relationships. It is evident from our results that features like the entotympanic, which have been employed in previous studies of higher-level mammalian relationships, may vary significantly within individual orders. Gaudin et al. (1996) note similar difficulties with the characters used to establish the Edentata–Epitheria split among placental mammals. It is difficult to establish reliably relationships among various orders if the phylogeny within the respective orders is not well understood. Without such information, the primitive condition for a given character in a given order cannot be rigorously established, thus compromising its phylogenetic utility. The phylogenetic results reported here suggest that using a single pangolin species to represent the entire order Pholidota, as has been the case in several recent molecular studies of interordinal
relationships among placental mammals (e.g., Sarich, 1985; Miyamoto and Goodman, 1986; Czelusniak et al., 1990; Graur et al., 1996; Springer et al., 1997), may well result in misidentification of the primitive condition for this order, especially if that species is one of the derived Asian species (e.g., Sarich, 1985; Miyamoto and Goodman, 1986; Czelusniak et al., 1990). At least one Asian and one African pangolin species ought to be included in such analyses to adequately represent the diversity present in this order. Similarly, in morphological studies of interordinal relationships, the primitive condition for the order Pholidota is subject to misinterpretation without consideration of fossil taxa such as Patroimanus that lie outside the clade including living pholidotans. These fossil forms preserve a number of primitive characteristics no longer present in the living taxa.

**APPENDIX**

**Table A1. Specimens Examined in Connection with the Present Study**

<table>
<thead>
<tr>
<th>OTU</th>
<th>Specimen Nos.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Manis crassicaudata</em></td>
<td>FMNH 57338, 57404, 82823, 98232, 98264, 104032</td>
</tr>
<tr>
<td><em>M. gigantea</em></td>
<td>USNM 269706</td>
</tr>
<tr>
<td></td>
<td>AMNH 53847-9, 53850, 53854-5, 53858</td>
</tr>
<tr>
<td><em>M. javanica</em></td>
<td>AIF 14, 17, 105-8 (embryos)</td>
</tr>
<tr>
<td></td>
<td>FMNH 33550, 37989, 62919, 62921, 68742-3</td>
</tr>
<tr>
<td></td>
<td>USNM 257682, 300025</td>
</tr>
<tr>
<td><em>M. pentadactyla</em></td>
<td>FMNH 39384-8, 75874-9, 94945, 98909</td>
</tr>
<tr>
<td></td>
<td>USNM 238725, 332899, 356431</td>
</tr>
<tr>
<td><em>M. temminckii</em></td>
<td>FMNH 34610, 35682, 38144</td>
</tr>
<tr>
<td></td>
<td>USNM 268914, 314972, 368617</td>
</tr>
<tr>
<td><em>M. tetradactyla</em></td>
<td>FMNH 54447, 54682, 62209-10</td>
</tr>
<tr>
<td></td>
<td>USNM 481805-6</td>
</tr>
<tr>
<td><em>M. tricuspid</em></td>
<td>FMNH 42679-83, 62205-8, 62768</td>
</tr>
<tr>
<td></td>
<td>USNM 435022, 450073</td>
</tr>
<tr>
<td><em>Manis sp. (embryo)</em></td>
<td>DUCCE 8321</td>
</tr>
<tr>
<td><em>Patroimanus americana</em></td>
<td>AMNH 78999 (type), USNM-P 299960</td>
</tr>
</tbody>
</table>

**Outgroups**

| Metachiremys sp.     | USNM 26132, 452349                                 |
|                      | YPM-PU 18107                                      |
| *Typhus sullacu*     | FMNH 28341, 28345, 124569, 152052                  |
| *Euphractus sexcinctus* | FMNH 28350, 34348, 54325                           |
| *Bradypus variegatus* | FMNH 2032, 51871, 69589, 70813, 86761-2           |
| *R. tridactylus*     | FMNH 16557, 93297                                  |
| *Tamandua mexicana*  | FMNH 15163, 22397, 68924, 69597, 90063            |
| *Cyclopes didactylus* | FMNH 51931, 58802                                 |
Table AI. Listing of Characters and Character States

**1. Anterior border of nasal—convex (0), with shallow notch (1), or with deep notch forming
   elongate medial and lateral processes, with deep fossa on lateral process (2).
2. Nasal length—less than or equal to (0) or greater than one-third skull length (1).
3. Maxillonasal suture—subparallel (0) or convergent anterior to maxillofrontal junction (1).
4. Dorsal process of premaxilla—essentially erect, may be inclined anterodorsally or curved
   from posteroledger to anterodorsal (0), inclined posterodorsally (1), or absent (2).
5. Incisive foramen—within premaxilla (0) or between premaxilla and maxilla (1).
6. Palatine process of premaxilla extending posteriorly between maxillae—absent (0) or
   present (1).
7. Vomerine exposure on palate—absent (0) or present (1).
8. Maxilla with deep median longitudinal palatal concavity—absent (0) or present (1).
9. Alveolar sulcus on maxilla—absent (0) or present (1).
10. Maxilla with narrow posterior palatal process extending lateral to palatine—absent (0) or
    present (1).
11. Palatine foramina—multiple within palatine and maxilla (0), double within palatine (or
    posterior within palatine, anterior between palatine and maxilla) (1), single within maxilla
    (2), or double within maxilla (3).
12. Anterolateral shelf of palatine—absent (0), lies posterior to (1), or medial to zygomatic
    process of maxilla (2).
13. Palatines within choanae—subparallel, widely separated by presphenoid and/or vomer (0)
    or converging anteriorly, nearly contacting (1).
**14. Lacrimal bone and lacrimal foramen—both present (0), bone present, foramen absent (1),
    or both absent (2).
15. Lacrimal fenestra—absent (0) or present (1).
16. Ethmoid foramen—within frontal (0) or between frontal and orbitosphenoid (1).
**17. Orbitosphenoid/septomaxillary contact—absent (0), narrow, alisphenoid approximates frontal
    (1), or broad (2).
18. Small foramen posterior to optic foramen in orbitosphenoid—absent (0) or present (1).
19. Foramen rotundum and sphenorbital fissure—separate (0) or confluent, opening into same
    fossa (1).
20. Foramen suboval—absent (0) or present (1).
21. Foramen ovale—within alisphenoid (0) or between alisphenoid and squamosal (1).
22. Flange on pterygoid process behind foramen ovale—absent (0) or present (1).
**23. Pterygoid hamulus—distal tip anterior to aperture for auditory tube (0), distal tip extends
    to level of oval window (1), distal tip extends to level of anterior rim of jugular foramen
    (2), or absent (3).
24. Pterygoid/entotympanic contact—widely separated (0) or closely approximated or in
    contact (1).
25. Entotympanic inflation—present (0) or absent (1).
26. Entosphenoid or facet for entotympanic on basioccipital—present (0) or absent (1).
**27. Course of internal carotid artery—transpromontorial (0), on the ventromedial edge of the
    petrosal, lateral to the entotympanic if present (1), or within or medial to the
    entotympanic (2).
**28. Auditory tube aperture orientation—anteromedial (0), medial (1), or posteromedial (2).
29. Promontorium of petrosal—prominent, globular (0) or weakly developed, flat (1).
**30. Course of facial nerve—open sulcus, crista parotica weak (0), open sulcus, crista
    parotica prominent (1), or closed canal (2).
**31. Contact between distal tip of tympanic and lateral surface of promontorium—absent
    (0), present, but unfused (1), or fused (2).
32. Position of fenestra cochleae—well separated from the fenestra vestibuli, facing
    posteriorly and slightly laterally (0) or immediately next to fenestra ovalis, facing laterally
    and slightly posteriorly (1).
33. Shielding of fenestra cochleae—open posterovertrally (0) or shielded posterovertrally
    by flange on petrosal (1).
**34. Position of fossa incudis within epithympanic recess—in lateral wall, facing medially
    (0), in posterior wall, facing anteriorly (1) or in medial wall, facing laterally (2).
35. Squamosal participation in roof of epithympanic recess—absent or forming small part
    of lateral wall (0) or extensive, forming much of roof (1).
36. Shape of malleal/incudal facet—concave (0) or convex (1).
Table AII. Continued

<table>
<thead>
<tr>
<th>Character Description</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>37. Orientation of mallear head/incudal facet—mallear head unrotated, incudal facet facing caudally and medially (0) or head rotated dorsad 90°, incudal facet facing dorsally, caudally and medially (1).</td>
<td></td>
</tr>
<tr>
<td>38. Incus—body gracile, may or may not be rectangular, crura elongate (0) or body stout and rectangular, crura short (1).</td>
<td></td>
</tr>
<tr>
<td>39. Stapedial columnella—elongate, height nearly equal to or exceeding greatest width of footplate (0) or short, height much less than greatest width of footplate (1).</td>
<td></td>
</tr>
<tr>
<td>40. Mastoid/exoccipital contact—broad, squamosal well separated from lateral rim of jugular foramen (0) or narrow, squamosal approximates lateral rim of jugular foramen (1).</td>
<td></td>
</tr>
<tr>
<td>41. Vomer—underlies pterygoid in posterior nasopharynx, visible through choanae (0) restricted to anterior nasal cavity, not visible from choanae (1).</td>
<td></td>
</tr>
<tr>
<td><strong>42. Lateral wings of basioccipital and exoccipital—both absent (0), only basioccipital wing present (1), or both present (2).</strong></td>
<td></td>
</tr>
<tr>
<td><strong>43. Basioccipital wing—weak, does not reach level of promontorium (0), moderate, even with promontorium (1), or prominent, ventral to promontorium (2).</strong></td>
<td></td>
</tr>
<tr>
<td>44. Exoccipital constriction anterior to condyle—present (0) or absent (1).</td>
<td></td>
</tr>
<tr>
<td>45. Foramen magnum shape—circular (0) or oval transversely (1).</td>
<td></td>
</tr>
<tr>
<td>46. Supraoccipital/parietals suture shape—subtends an angle greater than 90° (0) or less than or equal to 90° (1).</td>
<td></td>
</tr>
<tr>
<td>47. Lambdoid crest—strongly developed (0) or rudimentary to absent (1).</td>
<td></td>
</tr>
<tr>
<td><strong>48. Squamosal inflation—absent (0), weak, not clearly demarcated on external surface (1), or strong, with distinct lateral bulge on external surface (2).</strong></td>
<td></td>
</tr>
<tr>
<td>49. Position of alisphenoid/squamosal suture—widely separated from (0) or approximating base of zygomatic process (1).</td>
<td></td>
</tr>
<tr>
<td>*50. Orientation (and size) of zygomatic process of squamosal—laterally directed (0), ventrally directed, elongate (1), or ventrally directed, short (2).</td>
<td></td>
</tr>
<tr>
<td>51. Glenoid fossa—concave anteroposteriorly (0) or convex anteroposteriorly (1).</td>
<td></td>
</tr>
<tr>
<td>*52. Postglenoid foramen—on posterior aspect of zygomatic process (0), on lateral aspect of zygomatic process (1), posterior to zygomatic process (2), or absent (3).</td>
<td></td>
</tr>
<tr>
<td>53. Temporal lines—present (0) or absent (1).</td>
<td></td>
</tr>
<tr>
<td>54. Postorbital process—present (0) or absent (1).</td>
<td></td>
</tr>
<tr>
<td>55. Postorbital constriction—present (0) or rudimentary to absent (1).</td>
<td></td>
</tr>
<tr>
<td><strong>56. Tenorial ossification—absent (0), present but weak, developed only inferiorly on petrosal (1), or present, strongly developed, extends to roof of cranial cavity (2).</strong></td>
<td></td>
</tr>
<tr>
<td>57. Endocranial venous grooves—present (0) or absent (1).</td>
<td></td>
</tr>
<tr>
<td>58. Floor of middle cranial fossa—formed by splenoid (0) or formed by squamosal (1).</td>
<td></td>
</tr>
<tr>
<td>59. Mandibular symphysis length—long, extends well posterior to level of anterior mental foramen (0) or short, ends at or near level of anterior mental foramen (1).</td>
<td></td>
</tr>
<tr>
<td>60. Mandibular symphysis shape in lateral view—straight (0) or with anterior concavity (1).</td>
<td></td>
</tr>
<tr>
<td>61. Anterolaterally directed prongs on outer surface of mandibular symphyseal region—absent (0) or present (1).</td>
<td></td>
</tr>
<tr>
<td>62. Elongate medial perforation in mandibular canal—absent (0) or present (1).</td>
<td></td>
</tr>
<tr>
<td>63. Elongate lateral perforation in mandibular canal—absent (0) or present (1).</td>
<td></td>
</tr>
<tr>
<td>*64. Mandibular condyle—medially elongate (0), circular (1), or anteroposteriorly elongate (2).</td>
<td></td>
</tr>
<tr>
<td>65. Position of mandibular condyle—dorsal to (0) or at the level of the mandibular symphysis (1).</td>
<td></td>
</tr>
<tr>
<td>66. Coronoid process of mandible—present (0) or absent (1).</td>
<td></td>
</tr>
<tr>
<td>67. Angular process of mandible—present (0) or absent (1).</td>
<td></td>
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</tbody>
</table>

*Characters marked with a single asterisk are multistate; those marked with two asterisks are multistate and ordered in some analyses (see text).
<table>
<thead>
<tr>
<th>Species</th>
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</tbody>
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*The symbol "?" represents missing data; the symbol "n" is used in cases where a character is not applicable to a given taxon. The following symbols are used to represent character states in polymorphic taxa: a = (0, 1); b = (1, 2); c = (2, 3); d = (0, 2). Characters and character states are described in Table AII.*
Table AIV. Distribution of Apomorphies on the Single Most Parsimonious Tree Shown in Fig. 5a

| Node 1. Pholidota: 1(2), 4(1), 8(1), 11(2), 12(1), 17(1), 19(1), 42(2), 50(1), 53(1), 61(1), 65(1) |
| Node 3: 12(1), 26(1), 33(1), 45(0), 64(1) |
| Node 4. Asian pangolins: 17(2), 25(1), 30(2), 38(1), 44(0) |
| M. javanica + M. pentadactyla: 8(0), 15(1), 16(1), 60(1) |
| M. teiwincki + M. gigantea: 3(1), 5(0), 30(0), 52(1), 59(1), 63(1), 64(2) |

The apomorphies are based on a weighting and ordering scheme in which all multistate characters are unordered, and all character state changes are weighted equally. Characters are numbered according to the scheme provided in Table AIV, with numbered character states shown in parentheses. Unambiguous synapomorphies are shown in boldface.

ACKNOWLEDGMENTS

We are indebted to the following institutions and individuals for access to the specimens that formed the core of our study: Ross MacPhee and Nancy Simmons, American Museum of Natural History, New York; Larry Heaney, Bruce Patterson, and Bill Stanley, Division of Mammals, Field Museum of Natural History, Chicago; Bob Emery and Richard Thorton, National Museum of Natural History, Washington, DC; Prof. Dr. D. Starck, Anatomisches Institut, J. W. Goethe-Universität, Frankfurt am Main; and Matt Cartmill and Kathleen Smith, Department of Biological Anthropology and Anatomy, Duke University, Durham, NC. We also wish to thank Julia Scott, who so skillfully prepared the illustrations for this paper.

LITERATURE CITED


Entotympanic of Pangolins


