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The Anatomical Characteristics of a Giant Miocene Amphicyonid (Carnivora) Humerus from Pakistan

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Abstract.- A recently discovered distal humerus shows that very large bodied amphicyonids existed in Pakistan in the Early Miocene. Movements on their elbow joint are interpreted to be very similar to those of modern bears. They had powerful front limbs, which were probably used to grasp the prey. Taxonomic affinities of the specimen are also discussed.

Keywords: Paleontology, Pakistan, carnivora, elbow joint, movement, Miocene

INTRODUCTION

Amphicyonids were important members of the carnivore fauna in Eurasia during the Oligocene and most of the Miocene. They first appear in the Eocene fossil record, and soon show great diversity both in number of taxa and morphologic displays in the Late Oligocene (Hunt, 1996). The family became extinct in the Late Miocene (Werdelin, 1996). The Amphicyonidae, as did many other groups, faced a major extinction at the Oligocene-Miocene boundary, and the other one at the end of the Early Miocene (Springhorn, 1977). The surviving and newly evolving species were all relatively large and less predatory than the earlier forms (Springhorn, 1977; Viranta, 1996).

Intraspecific variation is common in amphicyonids (Viranta, 1996) and considerable sexual dimorphism has been demonstrated (Ginsburg, 1961). Some truly gigantic individuals of species such as *A. major* and *A. giganteus* are known from Europe (Ginsburg and Telles Antunes, 1968). These animals were comparable to the largest bears (Ursidae) of today. Like the amphicyonids, the bears display enormous intraspecific variation in size. In the Brown or Grizzly bear (*Ursus arctos*) the body mass of the largest individuals is up to ten times the body mass of the smallest individuals (Nowak, 1991). In this paper we describe a gigantic amphicyonid humerus from the Manchar Formation (Miocene) in the Gaj River area, Sind in Pakistan (Figs. 1, 2). We also discuss functional morphology of the corresponding elbow joint and possible taxonomic affinities of the specimen.

Fig. 1. Location of the Gaj-River area in Pakistan. Arrow indicates the area shown in Fig. 1. (adopted from Romein *et al*., 1983)

DESCRIPTION OF THE LOCALITY AND SPECIMEN

Lithology and age of the lower Manchar Formation

HGSP8311 was found during the 1983 field season of Howard University-Geological Survey, Pakistan. The specimen was found in sediments belonging to the basal part of the Manchar Formation (Fig. 2.), near Gaj river in the southern Pakistan. The Manchar Formation is represented by reddish brown clays with interbedded gray sandstone units (Fig. 3). The base of the lower

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Manchar Formation is particularly dominated by sandstone units and is highly fossiliferous (Khan *et al.*, 1984).

Fig. 2. Simplified geological map of the Gaj river area (adopted from Romein *et al.*, 1983).

Fig. 3. Gaj River section of the Manchar Formation.

The exact age of these sediments remain unknown, but they have been suggested to be 15 or 16 million years old (Raza *et al.*, 1984) or even older (Bernor *et al.*, 1988). Paleomagnetic work by Khan *et al.* (1984) placed the basal (lower) Manchar in Chron 15 suggesting an age of 13.7 to 15 Ma.

Morphology of the specimen

HGSP8311 is a distal fragment of a right humerus (Fig. 4.). Almost complete distal epiphysis is preserved, while the shaft is missing some 5 cm proximal of the entepicondylar fossa. It has a prominent entepicondyle and very wide entepicondylar foramen (max height = 34.9 mm). The trochlea appears small relative to the capitulum. The coronoid fossa is large and its borders are difficult to distinguish. It is a shallow fossa, except in the distal margin (that contacts the capitulum), where it appears well excavated. The olecranon fossa is deep. Since the bone is broken at the lateral border of the fossa, the extent of this border is unknown. It seems that bone may have extended medially over the fossa, as is in case of extant bears.

RESULTS

Comparisons and identification

The large carnivores known to be present in the early Middle Miocene of Eurasia are the hyaenodontids, hemicyonine bears and amphicyonids. A fourth carnivore family during this time with large body-sized members is the Percrocutidae. This family is known in the Middle and Late Miocene of Eurasia, and a relatively large species (*Percrocuta miocenica*) is present in Pasalar, Turkey in the early Middle Miocene (Schmidt-Kittler, 1976). Pasalar is correlative with lower MN 6, which suggests an age ca. 15 Ma (Bernor and Tobien, 1991; Steininger *et al.*, 1996). Very little postcranial material and no humeri have been described for percrocutids. This fact prevents any comparisons of HGSP8311 to percrocutids, and a possibility remains that the distal humerus actually represents a percrocutid.

We associate HGSP8311 with amphicyonids because of the entepicondylar foramen, large epicondyles, proximo-distally high olecranon fossa and a suggestion of the presence of supracondyloid ridge (Table I). The lateral edge of the olecranon fossa in HGSP8311 is rough, indicating dismemberment of the bony structure. It is probably the trace of a supracondyloid ridge, a structure that posteriorly covers the lateral aspect of the olecranon fossa in ursids and amphicyonids (Olsen, 1960). The entepicondylar foramen is present in felids, most of the amphicyonids and in the large Hyaenodontidae (Creodonta).

Fig. 4. Drawings of the amphicyonid distal humerus from the Manchar Formation (HGSP8311); A, posterior view; B, anterior view; C, is a distal view.

Body mass estimate

Because of the apparent functional similarity of bears and amphicyonids (Olsen, 1960), we used an equation calculated for bears (Viranta, 1994) to estimate the body mass of the amphicyonid represented by HGSP8311. This equation uses the width of the distal epiphysis to return a body mass estimate and it is calculated as log10 (body mass) = 0.98 log 10 (distal width)-4.89. In the case of HGSP8311, the body mass was estimated at 411 kg. The distal humeri provide a good estimate of the body mass for the Recent bears. The percent error (PE) of this equation was calculated as (observed body mass – predicted body mass) / predicted body mass for each taxa (Smith, 1981). For bears the PE using this equation is 13 (Viranta, 1994) and the body mass of the individual represented by HGSP8311 is 358-534 kg. This estimate range equals to the known body masses of large Polar bears.

We were also able to find a polar bear humerus (USNM 275124) that had approximately the same distal width as the HGSP8311 (Table II.). Unfortunately, the real body mass of this individual was not available, but based on the humerus we calculated it at 355-530 kg. Body masses as much as 800 kg have been recorded for the large Polar bears (Nowak, 1991).

Table I.- Diagnostic characters of the Miocene amphicyonid distal humerus from the Manchar Formation, Sind (HGSP8311) as compared to the distal humeri of other contemporary carnivores.

HUGSP8311	Entepicon-dylar foramen	Olecranon fossa	Epicondyles
Amphicyonidae	Present	High	Large
Ursidae	Present	High	Large
Felidae	Absent	Low	Normal
Percrocutidae	Not known	Not know	Not known
Hyaenodontidae	Present	High	Flat

Functional anatomical interpretations

All amphicyonids, except some extremely

cursorial forms of North America, retain the entepicondylar foramen. The entepicondylar foramen transmits the median nerve, and Landry (1958) has suggested that it prevents the nerve from lumping during abduction of the forelimb. It may also protect the nerve during pronation, typically performed by carnivores that take down large prey using their front paws.

Table II.- **Table of distal humeral maximum widths (max w.), widths of the distal articulation surface (art. w.) and minimum antero-posterior dimension (ant.-post.) in millimeters (mm) of the distal articulation surface in extinct and extant species. The Recent animals were all wild.**

Species	max. w.	art. w.	ant.-post.
HGSP8311 *Manchar amphicyonid*	141.4	93.3	40.2
USNM218230 *Ursus maritimus*	141.2	94.9	33.6
USNM260231 *Ursus maritimus*	118.3	82.7	28.5

Among extant carnivores the entepicondylar foramen is present in felids and most of the mustelids. The entepicondylar foramen has been lost in bears. In other respects, the functional similarity of amphicyonid and ursid humeri previously suggested (Hunt, 1972; 1996) appears valid here as well. The articular surfaces, lateral epicondyle and shape of the olecranon process of the large polar bear (*Ursus maritimus*) humerus (USNM218230) are similar to HGSP8311. It is, however, smaller in the anteroposterior dimension of the distal epiphyses and lacks the entepicondylar foramen.

The olecranon fossa is proximo-distally elongated indicating a similarly elongated olecranon process. The olecranon process provides a momentum arm for the muscles extending the elbow joint. A long olecranon process is usually related to cursorial and fossorial adaptations in carnivores. Graviportal animals with heavy distal limbs also need powerful extensor group for the elbow joint.

The olecranon fossa is also deep, so the elbow joint was probably well stabilized. The large capitulum, however, indicates some degree of freedom in movement at the elbow joint. Pronation and supination were possible and the joint was not as fixed as in cursorial carnivors (e.g. living canids). Strong muscles must have stabilized the elbow joint and moved the forearm, as indicated by the enlarged epicondyles.

DISCUSSION

Taxonomic relationships

HGSP8311 is equivalent in size to the largest amphicyonids known in Eurasia. Unfortunately, taxonomic identification beyond the family level is not possible based on a humerus only. Pilgrim (1932) described a new species, *Amphicyon sindiensis*, from the basal beds of the Manchar Formation. The type of *A. sindiensis* is a mandible with m_2 and alveolus for m_3. As noted by Pilgrim (1932), the mandible is similar to those of the European contemporary species, *A. giganteus* and *A. major,* in overall morphology and size. Pilgrim (1932) used the posterior tapering of the m_2 and the double-rooted m_3 to erect a new species separate from the European ones. Although posterior tapering of the m_2 differs from that of *A. giganteus*, none of these characters can be used to rule out the possibility that *A. major* and *A. sindiensis* are a single species.

A. sindiensis was a large amphicyonid and may have had humeri the size of HGSP8311. Unfortunately, no taxonomic work on *A. sindiensis* beyond Pilgrim's preliminary description is available. No postcrania have been assigned to this species. Until more material is recovered our comments on systematics can only be preliminary.

If *A. sindiensis* is a valid species and we accept the hypothesis that HGSP8311 represents *A. sindiensis*, it suggests that there was a large bodied amphicyonid unique to Asia in the Middle Miocene. The other possibility is that HGSP8311 represents *A. major*, a species that is common in Europe during the entire Middle Miocene (Werdelin, 1996) and extends as far east as Turkey (Gürbüz, 1974). This species may have ranged as far as Sind, Pakistan. Dental material of a very large amphicyonid has also been recently described from lower Miocene of Vietnam (Ginsburg *et al*., 1992). This material was also insufficient for taxonomic identification beyond the family level.

CONCLUSIONS

HGSP8311 reveals that large bodied amphicyonids existed in Pakistan during the early Middle Miocene, while their presence in Europe has been demonstrated earlier (Ginsburg and Telles Antunes, 1968). These animals probably exhibited modes of locomotion and limb mobility quite similar to those exhibited by the modern bears. They hade powerful front limbs with high degrees of movement in the elbow joint. Like modern bears, they could have used the front paws to grasp and lacerate large bodied prey. Since no dental or cranial material was found in association of HGSP8311, its dietary preferences can not be studied. The large European amphicyonids have been interpreted to be mesocarnivorous, meaning that they were predators but supplemented plant matters to their diet (Viranta, 1996).

Similarly, owing to the lack of material, the taxonomic status of the large amphicyonid from the Manchar remains ambiguous. It may represent a large form of *A. sindiensis*, earlier described from the basal beds of the Manchar Formation. It is also possible that it is *A. major*, a large amphicyonid known from Europe during that time. Since no described dental characters separate *A. sindiensis* and *A. major*, they could also be a single species.

Barry *et al*. (1991) showed a peak of increased muroid and bovid diversity between 15-13 Ma in the Siwaliks, Pakistan. They were able to demonstrate that diversity increased as a result of migration of new species from Europe and Africa to Pakistan. It is possible that carnivores, included an amphicyonid, *A. major*, which participated in this migration event.

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