THE STATUS OF *HIMALAYASAURUS TIBETENSIS* (ICHTHYOPTERYGIA)

Ryosuke Motani[1], Makoto Manabe[2], and Zhi-Ming Dong[3]

[1]University of California Museum of Paleontology, 1101 VLSB, Berkeley, California 94720
[2]National Science Museum, 3-23-1 Hyakunin-cho, Shinjuku-ku, Tokyo 163-0073 Japan
[3]Institute of Vertebrate Paleontology and Palaeoanthropology, Academia Sinica, 142 Xizhimenwai St., Beijing 100044, China

ABSTRACT

A reexamination of the type specimen of *Himalayasaurus tibetensis* reveals that the bone previously identified as a coracoid is more likely a radius. This bone clearly shows a synapomorphy of the Shastasaurinae, which confirms a shastasaurid affinity previously proposed for the species. *H. tibetensis* is diagnostic for having remarkable cutting-edges on its flattened tooth crowns, which is otherwise unknown for ichthyopterygians. *Himalayasaurus* is among the largest ichthyopterygians known, rivaling the closely related *Shonisaurus*.

INTRODUCTION

Himalayasaurus tibetensis was originally described based on a partial skull and some associated postcranial elements (Dong, 1972). This Norian (Upper Triassic) species is comparable in size to the slightly older *Shonisaurus* from the Carnian (Upper Triassic) of Nevada, which is one of the largest ichthyopterygians thus far reported (Camp, 1980; Kosch, 1990; McGowan, 1991, 1996; McGowan and Montani, 1999). This is the youngest of the three ichthyopterygian genera reported from China (Young, 1965; Young and Dong, 1972; Callaway and Massare, 1989a; Montani and You, 1998). Dong (1972) suggested a shastasaurid affinity for *H. tibetensis*, but poor preservation prevented further testing of this hypothesis. Also, the relationships among various ichthyopterygians were poorly understood at that time, which made a phylogenetic study of *H. tibetensis* difficult.

Callaway (1989) ws the first to propose a phylogenetic hypothesis that included *Himalayasaurus*. A generally accepted assumption of the time was that the so-called "Shastasauridae", which always contained *Shastasaurus*, *Californosaurus*, and *Merriamia* (now considered *Toretocnemus*; see Montani, in press), formed a natural group. This view, initiated by Merriam (1902, 1908), was followed by most reviewers (e.g., Kuhn, 1934; von Huene, 1951,1956; Mazin, 1982; Kirton, 1983; Callaway, 1989; Dal Sasso and Pinna, 1996), although they variously included some or all of the following taxa in the Shastasauridae in addition to the three core genera listed above:

Pessosaurus, *Cymbospondylus*, *Besanosaurus*, *Shonisaurus*, and *Himalayasaurus*. With this assumed monophyly, Callaway (1989) analyzed a data matrix with 33 characters coded for seven "Shastasauridae", plus *Grippia* and *Petrolacosaurus* as the outgroup. He found a single most parsimonious tree in which *Himalayasaurus* was the basal taxon of the subclade Shastasaurinae (Figure 1A), whose sister taxon was *Shonisaurus* (Callaway, 1989). Dal Sasso and Pinna (1996) reanalyzed Callaway's (1989) data matrix by adding *Besanosaurus* and obtained six most parsimonious trees. They figured one of the six, which suggested that *Himalayasaurus* and *Shonisaurus* might form a clade of their own (Figure 1B). Montani (in press) recently proposed a more comprehensive phylogenetic hypothesis for ichthyopterygians by analyzing a data matrix with 104 characters coded for 27 better known ichthyopterygians and five outgroups. Based on the strict consensus of 12 most parsimonious trees, he found that the "Shastasauridae" was not monophyletic as traditionally assumed (Motani, in press); *Californosaurus* and *Toretocnemus*, two of the three core taxa, were more closely related to parvipelvians than to *Shastasaurus* (Figure 1C). Motani (in press) did not include *Himalayasaurus* in his analysis because the genus was too poorly known at the time.

A recent reexamination of the type specimen of *Himalayasaurus tibetensis* revealed several anatomical features that are phylogenetically informative. The purpose of the present contribution is to reevaluate the phylogenetic relationships of this species based on the new knowledge.
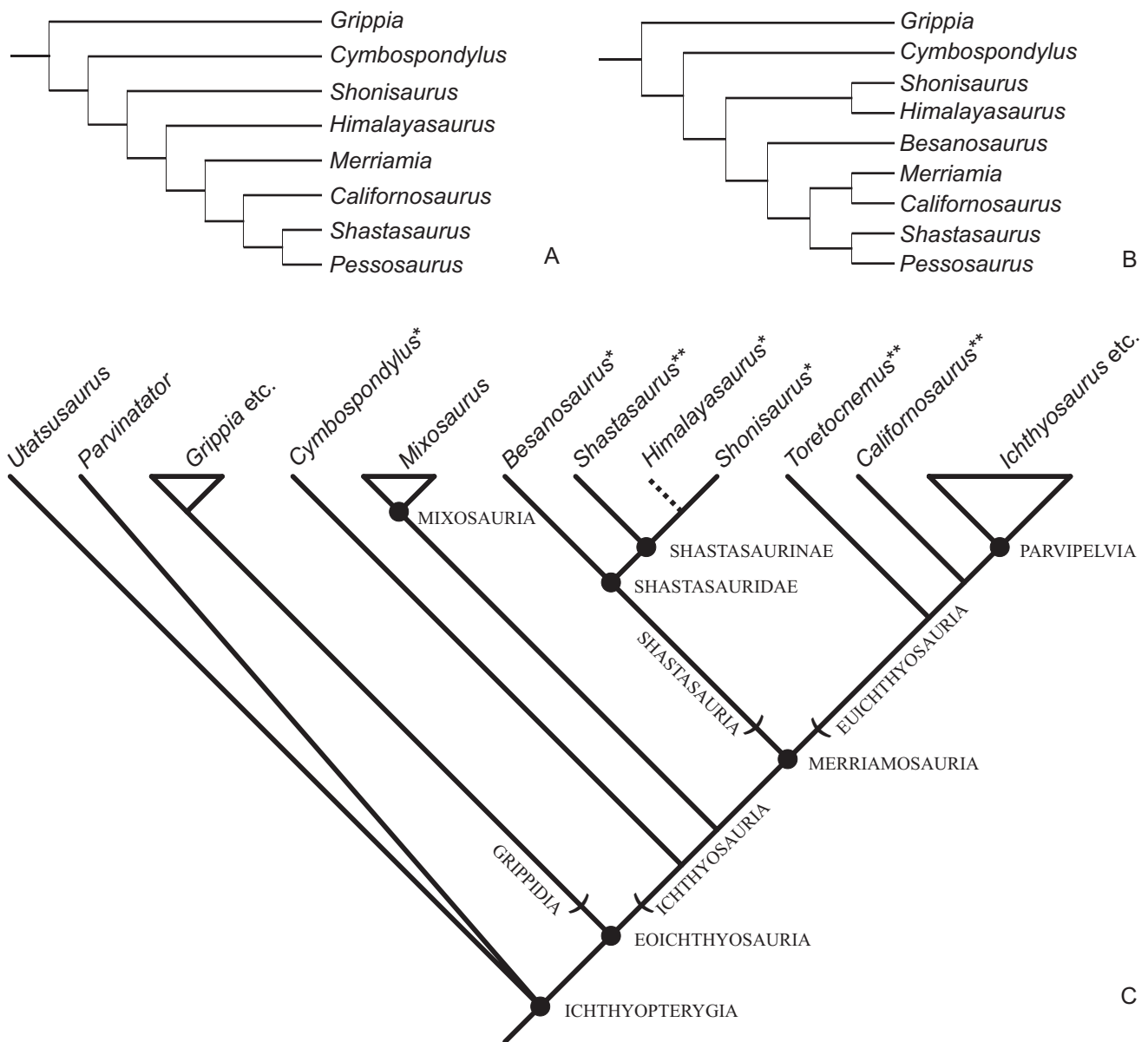
FIGURE 1. A, Phylogenetic hypothesis proposed by Callaway (1989) for the traditional Shastasauridae. B, Phylogenetic hypothesis proposed by Dal Sasso and Pinna (1996) for the traditional Shastasauridae. C, Simplified phylogeny of the Ichthyopterygia based on Motani (in press). Black dots indicate node groups, and brackets stem groups. Three of the clades are represented by reversed triangle to save space, with the name of a typical constituent genus attached to each. Taxa with asterisks had been included in the Shastasauridae by at least one author, and those with double asterisks are the three core taxa of the traditional Shastasauridae mentioned in the text. *Himalayasaurus* is connected to the cladogram by a dotted line because the genus is poorly known. See text for the discussion of the phylogenetic position of the genus.

MATERIALS AND METHODS

The type and only specimen of *Himalayasaurus tibetensis* is stored at the Institute of Vertebrate Paleontology and Palaeoanthropology, Academia Sinica, China (IVPP V4003). The specimen comprises of five parts: IVPP V4003-1 (a slab with a partial skull and vertebrae), V4003-2 (fin element), V4003-3 and -4 (caudal vertebrae?) and V4003-5 (radius). It was not possible to examine V4003-3 and -4 in the present study. Comparisons were made with shastasaurian specimens stored at Berlin-Ichthyosaur State Park, Nevada (BISP); the Marjorie Barrick Museum of Natural History, University of Nevada at Las Vegas (FZVE); the Royal Ontario Museum, Toronto, Canada (ROM); and the University of California Museum of Paleontology, Berkeley (UCMP).

Measurements less than 145 mm were taken using dial calipers and recorded to the nearest 0.1 mm. A plastic tape measure was used for larger measurements for *Himalayasaurus*, which were recorded to the nearest 10 mm. Larger measurements for *Shonisaurus* were made with large Vernier calipers and recorded to the nearest millimeter.

The range for the relative length of cervical vertebral centra was obtained in the following manner. Triassic ichthyosaurians has long necks (Massare ad Callaway, 1990), so the ratio between the maximum diameter of each centrum and its length was calculated for the first ten centra of each specimen, and the range of this MD/L ratio was listed. However, all ten centra were not always measurable with confidence, in which case the range was given based on a subset of the ten centra (those that were measurable).

Higher taxonomic names within the Ichthyopterygia follow Motani (in press). A phylogenetic tree with these names is provided as Figure 1. It should be noted that the names Shastasauridae and Shastasaurinae are differently defined from the traditional usage mentioned in the introduction.

SYSTEMATIC PALEONTOLOGY

Subclass Diapsida Osborn, 1903
Order Ichthyosauria de Blainville, 1835
Suborder Ichthyopterygia Owen, 1840
Family Shastasauridae Merriam, 1902
Subfamily Shastasaurinae Merriam, 1908
Genus *Himalayasaurus* Dong, 1972

Type and Only Species--*Himalayasaurus tibetensis* Dong, 1972.
Diagnosis--Large shastasaurian probably exceeding 15 m in total length; tooth crowns labiolingually flattened, with remarkable cutting edges on mesial and distal sides giving swollen outline in labiolingual view; radial shaft not reduced posteriorly and absent anteriorly; cervical vertebral centra short, with Width/Length ratio near 3.0.

Locality and Horizon--Upper Triassic (Norian) of Tibet.

Himalayasaurus tibetensis Dong, 1972.

Type and Only Specimen--IVPP V4003.
Diagnosis--As for genus.
Description--*Radius*: IVPP V4003-5 (Figure 2A), previously identified as a coracoid (Dong, 1972), is herein identified as a radius, because the outline of the bone is very similar to those of the shastasaurine radii (Figure 2) than to any ichthyopterygian coracoids. The bone is thicker proximally (87.2 mm) than distally (76.4 mm), and the decrease of the thickness is gradual between the two ends, as in most fin elements of *Shonisaurus* (McGowan and Motani, 1999). The distal margin of the bone is posteriorly curved (Figure 2A, bracket), where it forms a second, small facet. This area is much thinner (44.8 mm) than the main part of the distal end (76.4 mm), so the second facet is remarkably smaller than the distal facet. Such a small posterodistal facet is known for shastasaurine radii, in which it articulates with the ulna (Figure 2D-F).

The anterior margin is thin (26.0 mm), smooth, and convex without a notch. There is a wedge-shaped incision near the position where notches would occur in merriamosaurian radii (Figure 2A, arrow), but this is clearly a break: there is no thickening of the area that is usually associated with true notches. Surface striations are radial anteriorly, suggesting the loss of the plesiomorphic shaft in this area. The posterior margin is concave and the surface striations are parallel to the margin, so the plesiomorphic shaft is probably retained on this side of the bone. The co-occurrence of the complete loss of the radial shaft anteriorly and the complete retention posteriorly is unique to some shastasaurines, such as *Shonisaurus* and *Shastasaurus neoscapularis* (McGowan, 1994; Motani, 1999).

IVPP V4003-5 is wider (295 mm) than long (275 mm), as in most shastasaurine radii (one of the radii referred to *Shonisaurus* is longer than wide, probably because of distortion; Figure 2). It is also larger than any of the measured *Shonisaurus* radii (Table 1), but the difference is not remarkable.

Although the outline of IVPP V4003-5 may resemble those of some euichthyosaurian coracoids, the bone lacks a typical feature of those coracoids: the presence of both scapular and glenoid facets. The above mentioned posterodiastal facet is too small to be either of the facets.
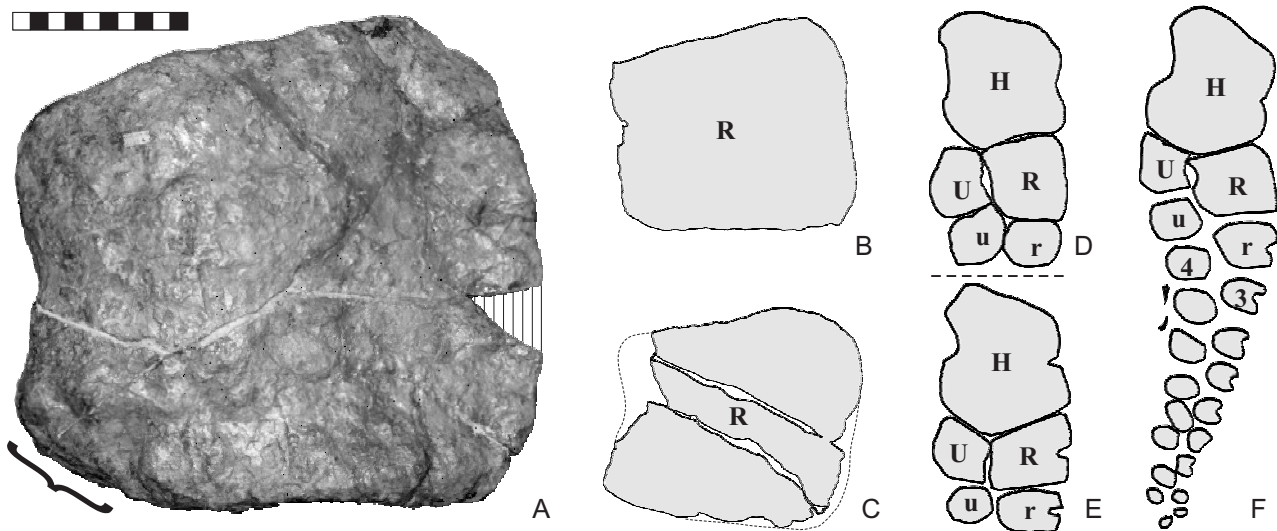
FIGURE 2. Radius and other forefin elements of shastasaurines. A, radius of *Himalayasaurus tibetensis* (IVPP V4003-5). Bracket indicates a smallposterodistal facet. Vertical stripes indicate the break mentioned in text. B-C, radii of *Shonisaurus* (modified from Camp, 1980). D, forefin of *Shonisaurus* (after McGowan and Motani, 1999). E, forefin of *Shastasaurus* (modified from Callaway and Massare, 1989b). F, forefin of *Shastasaurus neoscapularis* (modified from McGowan, 1994). Scale bar in A is 10 cm. B-F are laterally inverted for ease of comparison, and are not to scale.

Fin element: IVPP V4003-2 (Figure 3) was previously identified as a vertebral centrum. The outline of the bone is indeed very similar to that of a typical euichthyosaurian caudal centrum, which seems to support this identification. However, two features of the bone suggest otherwise. First of all, the bone is not amphiceolous, unlike ichthyopterygian vertebral centra. Second, the thickness distribution suggests that the supposed bilateral symmetry (Figure 3D) does not exist: the axis of bilateral symmetry, if any, should be as in Figure 3C. Moreover, a close inspection reveals that a slightly concave profile of the supposed dorsal margin of the bone is formed by unprepared matrix (Figure 3D, white area). Therefore, the interpretation given in Figure 3C is more reasonable than the one in Figure 3D. The thickness decreases gradually from the top of Figure 3B to the bottom (Figure 3A), and such a uniform decrease in thickness it typical of fin elements (McGowan and Motani, 1999). We conclude that IVPP V4003-2 is more likely a fin element than a vertebral centrum.

It is difficult to specify the position of this element within a fin, or whether it belongs to a forefin or hindfin. The element is not notched as in the leading-edge elements of the forefin of the Shastasaurinae, or widened as in digit-IV elements. It is possibly a digit-V element for these reasons, but too little is known about digit V of the Shastasaurinae to test this identification further. The relative size of the element with respect to the radius suggests that the

element was not very distal within a fin, judging from the only articulated forefin of the Shastasaurinae, *Shastasaurus neoscapularis* (ROM 41993; Figure 2F).

Skull and mandible--A very fragmentary and unprepared skull and mandible are preserved in IVPP V4003-1 (Figure 4C). At least two jaw rami are preserved, but it is difficult to judge (with confidence) whether they are derived from the upper or lower jaws. Therefore, the description will be given according to a tentative identification given in Figure 4C, which is based on the general distribution of bones. At least two vertebral centra are preserved near the dentigerous bones (Figure 4C), so it is likely that the specimen underwent disturbance during preservation.

The dentary is far from complete: only a part of dentigerous region is preserved. Fourteen better-preserved tooth positions can be confirmed over 680 mm, with less conspicuous ones preserved both anteriorly and posteriorly, making the total preserved count of 16. The ninth position is associated with a nearly complete tooth (Figure 4), but others are empty. There is a structure that appears to be a coronoid process in the posterior part of the bone, but this is probably unprepared matrix (Figure 4C, matrix): if this were a bony process, it would dorsally close the last four tooth positions.

There is a partially exposed tooth crown that points in the opposite direction to the one on the dentary, so the bone associated with this tooth crown is tentatively identified as a part of the upper jaw, rather
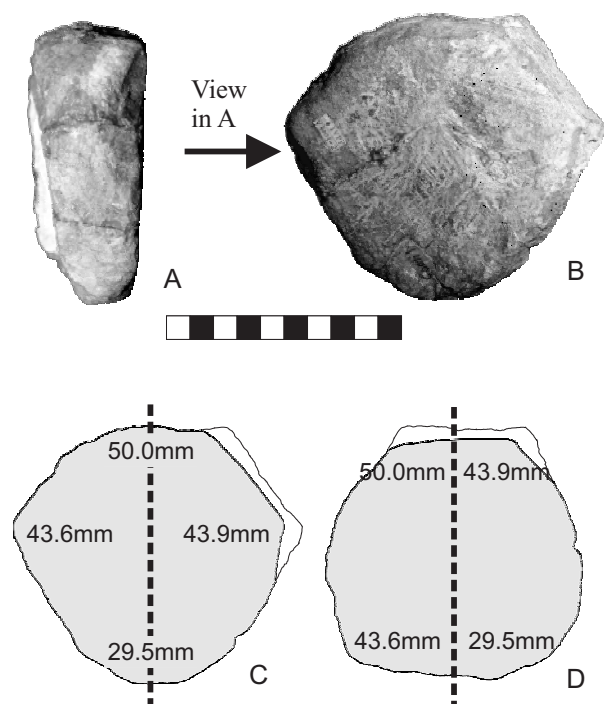
FIGURE 3. A fin element of *Himalayasaurus tibetensis* (IVPP V4003-2). A, horizontal view from the diredtion indicated by arrow in B. White area on theleft is plaster. B, planar view. C-D, two competing interpretations for the bilateral symmetry of the elements, with distribution of the thickness of the bone for four corners. The element was previously identified as a caudal vertebra. See text for explanation. Scale bar is 10 cm.

Dentition: Most characteristic of *Himalayasaurus tibetensis* is its dentition, especially the tooth crowns. Only one tooth that is well exposed in IVPP V4003-1, in association with the dentary. The crown looks like a thick dagger blade; it is labiolingually compressed and its cutting edges are remarkably well developed both mesially and distally (Figure 4A, B). Coarse and deep longitudinal striations run along the surface of the crown especially proximally. The pattern of enamel crystals can be observed with the naked eye on the surface, and these are elongated nearly perpendicular to the mesial and distal margins of the crown. The root is also coarsely striated, but it is not possible to judge whether this is because of folding of the dentine wall. The boundary between the crown and root is located at the level of the dentigerous margin of the dentary, so the gumline was probably not very high above this margin (only basal ichthyopterygians have high gum lines).

The entire tooth is 133.0 mm long, of which 59.7 mm is the crown. The crown appears more prominent than the root in labiolingual view: the maximum distomesial width of the tooth is 39.5 mm, for the swollen part of the crown, whereas the minimum for the constricted part of the root is 33.4 mm. This is unlike any other ichthyopterygians (see Massare, 1987): crowns are never larger than the roots. A labiolingaully compressed crown is not unique to *Himalayasaurus*. For example, *Temnodontosaurus* is occasionally known to have labiolingually compressed tooth crowns (thus the name of the type species *T. platyodon*), although such teeth are not necessarily persent in all individuals (McGowan, 1974; 1979; Massare, 1987).

Tooth implantation is difficult to establish. A bony fixation between the root and dentigerous bone cannot be established with confidence. Tooth positions are separated by ridges developed on dentigerous bones

than the other mandibular ramus. The upper jaw is less well preserved than the lower one. Nine tooth positions can be seen posteriorly (Figure 4C), but this jaw ramus is not well exposed anteriorly where the tooth just mentioned is located.

TABLE 1. Size comparison between *Himalayasaurus* and *Shonisaurus*. The width of the radius was measured at the distal part of the bone. The widths of the vertebral centra do not include parapophyses or diapophyses. The diameter of the tooth root in *Shonisaurus* is based on the maximumdiameter of four dental sockets, which should be an overestimation of the true value. The same for *Himalayasaurus* is based on the narrowest part of the root of the only exposed tooth, which should be a slight underestimation of the thickest part. McGowan and Motani (1999) refer BISP 1 to Camp's (1980) Specimen D, but this was a mistake made by RM. Asterisks indicate derivation from Camp (1980).

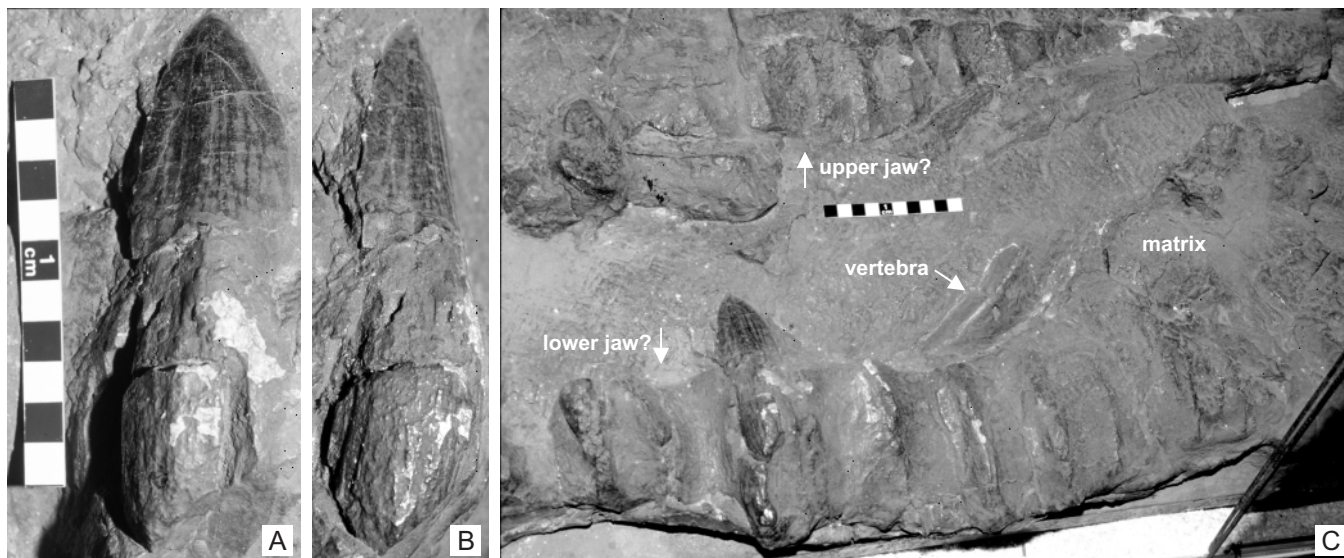| | | Radius | | Mid Cervical | | Root | Total |
		Length	Width	Width	Height	Diam	Length
Shonisaurus	BISP-1			202			>1450
	BISP-3	175	204				
	FZVE-1	240*	280*	150-200*	150-170*		
	FZVE-2	247	239	170-180*	140-180*		
	FZVE-3					<31.7	
Himalayasaurus	IVPP V4003	275	295	220	160	>33.4	

FIGURE 4. The main slab of the holotype of *Himalayasaurus tibetensis* (IVPP V4003-1). A, only complete tooth in the specimen in labiolingual view. Compare with B to see that the cutting edges are extremely well developed for an ichthyopterygian. B, same from slightly anterior direction. C, middle part of the slab. Anterior to the left. Unlabeled bones are not identifiable. Scale bars are 10 cm.

(Figure 4C), as in aulacodont ichthyosaurs such as *Leptonectes tenuirostris*. However, because of the incompleteness of the specimen, it is possible that these ridges may actually represent the remains of bony septa of thecodont or ankylothecodont tooth implantation that has been broken during preservation. In *Shonisaurus*, the teeth are set in separate sockets but the septa between sockets are thin (FZVE-C; reported as unnumbered by McGowan and Motani, 1999). Such thin walls of bone, even if they existed in life, are unlikely to be preserved in IVPP V4003-1, considering that dentigerous bones are halfway eroded in this specimen. It is also possible that the tooth implantation was subthecodont: it is inevitable that the dentary of *Utatsusaurus* would show similar interdental ridges once the teeth were removed (see Montani, 1996:fig. 3C). In short, the tooth implantation in *Himalayasaurus* could be any of the four types known for ichthyopterygians (Motani, 1997).

Vertebrae: One of the vertebral centra preserved in IVPP V4003-1 is sufficiently exposed. It has been removed from its life position, being associated wit the dentigerous part of the jaw. The centrum is 220 mm wide, 160 mm high, and 75 mm long. Because the centrum is wider than high, it is probably derived form the mid-cervical region. Preservation is too poor to elaborate on the identification.

DISCUSSION

Lucas and Gonzáles-Léon (1995:fig. 4) and Lucas (1997:fig. 3) considered *Himalayasaurus tibetensis* a *nomen dubium*. Although they provided no discussion of this designation, their views are understandable considering the incompleteness of the type and only specimen (IVPP 4003). However, the species is unique among ichthyopterygians in having teeth with remarkably well developed crowns. Furthermore, diagnostic features of the postcranial elements enable the phylogenetic discussion of the species as given below. In light of the new knowledge provided in the present contribution, we conclude that the species is diagnostic and valid.

It is most likely that *Himalayasaurus* is closely related to shastasaurines, judging from the shape of the radius. Three features of the bone are particularly important: (1) the plesiomorphic shaft of the radius is completely lost or extremely reduced anteriorly (apomorphic within ichthyopterygians); (2) the plesiomorphic shaft is not reduced posteriorly (plesiomorphic for ichthyopterygians); and (3) the radius is wider than long (apomorphic within ichthyopterygians). Features 1 and 3 convergently occur in the Shastasaurinae and Parvipelvia (Figure 1), but feature 2 is primitively lost in the latter group (Motani, 1999, in press). Therefore, it is most likely that *Himalayasaurus* is closely related to the Shastasaurinae.

The next question is whether *Himalayasaurus* is the sister group of the Shastasaurinae or is nested within it. Only one feature is available to assess this question: the relative length of cervical vertebral centra. The only measurable cervical centrum of *Himalayasaurus* is much shorter than wide, with the Maximum Diameter/Length ratio of 2.93. Such short cervical centra are typical of *Shonisaurus* (MD/L = 3.19-3.23 for BISP Specimen 1; see Materials and Methods of the calculation of the range), whereas *Shastasaurus* has much longer cervical centra (DM/L = 1.90-2.17 for UCMP 9076). Cervical centra are not short in the outgroup, including *Mixosaurus* (MD/L = 1.56-1.68) and *Californosaurus* (MD/L = 1.67-2.05), so the shortened cervical central seem to be apomorphic within the Shastasaurinae (measurements unavailable for *Besanosaurus*). Given the absence of any opposing features, we conclude that it is most reasonable to consider shortened cervical centra as a synapomorphy of *Himalayasaurus* and *Shonisaurus*. Therefore, *Himalayasaurus* is probably more closely related to *Shonisaurus* than to *Shastasaurus*, a suggested in Figure 1 (dotted line). This conclusion accords with that of Dal Sasso and Pinna (1996), and is very close to Callaway's (1989) phylogenetic hypothesis. Nevertheless, it is desirable to obtain more data on *Himalayasaurus* in the future to test the present hypothesis: the shortness of the cervical centra may be related to large body size of the two genera.

Himalayasaurus was probably comparable to *Shonisaurus* in size. McGowan and Motani (1999) gave an estimated total length of 14.5 m for the most complete skeleton of *Shonisaurus* (BISP 1) which is close to what was estimated by Camp (1980) and Kosch (1990). Individuals larger than BISP 1 are known for *Shonisaurus*, being represented by incomplete material (McGowan and Motani, 1999). *Himalayasaurus* (IVPP V4003) is larger than BISP 1 in vertebral measurement, but not by more than 10% (Table 1). Therefore, *Himalayasaurus* was probably within the size range of *Shonisaurus*, assuming similar body proportions for the two closely related genera. The large size and extensive cutting edges of the teeth in *H. tibetensis* suggest that large vertebrates were probably among its prey items, as McGowan (1974) and Massare (1987) suggested for some large Jurassic ichthyosaurs.

The similarities between *Himalayasaurus tibetensis* and *Shonisaurus popularis*, as pointed out above, raise the question whether the two, given the limited material of *H. tibetensis*, are congeneric. The only difference between the two is the shape of the tooth crown, but this features alone does not warrant a separate generic status. If the two species are considered congeneric, the name *Himalayasaurus*

Dong, 1972 has priority over *Shonisaurus* Camp, 1976. However, it is also possible that the two species are considerably different in the region of the body that is unpreserved in *H. tibetensis*. Considering the poor preservation of *H. tibetensis*, we remain conservative and keep the two species in separate genera.

ACKNOWLEDGMENTS

LITERATURE CITED

Blainville, H. M. D. de. 1835. Description de quelques espéces de reptiles del la Califomie. Nouvelles Annales du Muséum d'Histoire Naturelle, Paris 4:233-296.

Callaway, J. M. 1989. Systematics, phylogeny, and ancestry of Triassic ichthyosaurs. Unpublished PhD dissertation, University of Rochester, 204 pp.

Callaway, J. M. and J. A. Massare. 1989a. Geographic and stratigraphic distribution of the Triassic Ichthyosauria (Reptilia; Diapsida). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 178:37-58.

Callaway, J. M. and J. A. Massare. 1989b. *Shastasaurus altispinus* (Ichthyosauria, Shastasauride) from the Upper Triassic of the El Antimonio district, northwestern Sonora, Mexico. Journal of Paleontology 63:930-939.

Camp, C. L. 1976. Vorläufige Mittelung über grosse Ichthyosaurier aus der oberen Trias von Nevada. Österische Akademie der Wissenschaften, Mathematisch-naturwissen-schaftliche Klasse, Sitzungsberichte, Abteilung 1, 185:125-134.

Camp, C. L. 1980. Large Ichthyosaurs from the Upper Triassic of Nevada. Palaeontolgraphica A 170:139-200.

Conybeare, W. D. 1822. Additional notices on the fossil genera *Ichthyosaurus* and *Plesiosaurus*. Transactions of the Geological Society of London, Series 2, 1:103-123.

Dal Sasso, C. and G. Pinna. 1996. *Besanosaurus leptrhynchus* n. gen. n. sp., a new shastasaurid ichthyosaur from the Middle Triassic of Besano (Lombardy, N. Italy). Paleontologia Lombarda, Nouva Serie 4:3-23.

Dong, Z.-M. 1972. An ichthyosaur fossil from the Qomolangma Feng region. Pp. 7-10 in C. C. Young and Z.-M. Dong (eds.) Aquatic reptiles from the Triassic of China. Academia Sinica, Institute of Vertebrate Paleontology and Palaeoanthropology, Memoir 9, Peking. [in Chinese]

Huene, F. von. 1951. Eine neue Ichthyosaurier-Gattung der mitteleren Trias. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 94:80-92.

Huene, F. von. 1956. Paläontologie und Phylogenie der niedreen Tetrapoden. Gustav Fischer Verlag, Jena, 716 pp.

Kirton, A. M. 1983. A review of British Upper Jurassic ichthyosaurs. Unpublished PhD dissertation, University of Newcastle, 239 pp.

Kuhn, O. 1934. Ichthyosauria. Pp. 75 in W. Quenstedt (ed) Fossilium Catalogus. 1: Animalia. Pars 63, Berlin, Junk.

Lucas S. G. 1997. Marine reptiles and Mesozoic biochronology. Pp. 423-434 in J. M. Callaway and E. L. Nicholls (eds.) Ancient Marine Reptiles. Academic Press, New York.

Lucas, S. G. and C. M. Gonzáles-Léon. 1995. Ichthyosaurus from the Upper Triassic of Sonora and the biochronology of Triassic ichthyosaurs. Pp. 17-20 in C. Jacques-Ayala, C. M. Gonzáles-Léon, and J. Roldan-Quintana (eds.) Studies on the Mesozoic of Sonora and Adjacent Areas. Geological Society of America Special Paper 301.

Massare, J. A. 1987. Tooth morphology and prey preferene of Mesozoic marine reptiles. Journal of Vertebrate Paleontology 7:121-137.

Massare, J. A. and J. M. Callaway. 1990. The affinities and ecology of Triassic ichthyosaurs. Geological Society of America Bulletin 102:409-416.

Mazin, J. M. 1982. Affinités et phylogénie des Ichthyopterygia. Geobios, Mémoire spécial 6:85-98.

McGowan, C. 1991. Dinosaurs, Spitfires,a nd Sea Dragons. Harvard University Press, Cambridge, 365 pp.

McGowan, C. 1994. A new species of *Shastasaurus* (Reptilia: Ichthyosauria) from the Triassic of British Columbia: the most complete exmplar of the genus. Journal of Vertebrate Paleontology 14:168-179.

McGowan, C. 1996. Geiant ichthyosaurs of the early Jurassic. Canadian Jouranl of Earth Sciences 33:1011-1021.

McGowan, C. and R. Motani. 1999. A reinterpretation of the Upper Triassic ichthyosaur, *Shonisaurus*. Jouranl of Vertebrate Paleontology 19:42-49.

Merriam, J. C. 1902. Triassic Ichthyopterygia from California and Nevada. University of California Publication, Bulletin of the Department of Geology 3:63-108.

Merriam, J. C. 1908. Triassic Ichthyosauria, with special reference to the American forms. Memoirs of the University of California 1:1-196.

Motani, R. 1996. Redescription of the dental features of an early Triassic ichthyosaur *Utatsusaurus hataii*. Journal of Vertebrate Paleontology 16:396-402.

Motani, R. 1997. Temporal and spatial distribution of tooth implantation in ichthyosaurs. Pp. 81-103 in J. M. Callaway and E. L. Nicholls (eds.) Ancient Marine Reptiles. Academic Press, New York.

Motani, R. 1999. On the evolution and homology of ichthyopterygians forefins. Journal of Vertbrate Paleontology 19:28-41.

Motani, R. In press. Phylogeny of the Ichthyopterygia. Journal of Vertebrate Paleontology.

Motani, R. and H. You. 1998. Taxonomy and limb ontogeny of *Chaohusaurus geishanensis* (Ichthyosauria), with a not on the allometric equation. Jouranl of Vertebrate Paleontology 18:533-540.

Osborn, H. F. 1903. The reptilian subclass Diapsida and Synapsida and the early history of the Diaptosauria. Memoirs of the Aemrican Museum of Natural History 1:449-507.

Young, C. C. 1965. On the revised determination of a fossil reptile from Jenhui, Kweichou with note on a new ichthyosaur probably from China. Vertebrata PalAsiatica 9:368-375.

Young, C. C. and Z.-M. Dong. 1972. Aquatic reptiles from the Triassic of China. Academia Sinica, Institute of Vertebrate Paleontology and Palaeoanthropology, Memour 9, Peking.