First complete fossil Scleropages (Osteoglossomorpha) postprint

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Abstract

一种骨舌鱼科新种，中华硬骨舌鱼（Scleropages sinensis sp. nov.），发现于中国湖南下湾铺组与湖北洋溪组的早始新世地层。该新种被归入硬骨舌鱼属（Scleropages），骨舌鱼科的一个现生属，因其在头骨、尾骨骼、鳍的形状与位置以及网纹鳞片等方面与该属极为相似。这种新鱼与现生硬骨舌鱼属非常相似，区别在于：鼻骨似乎无装饰；眶前骨中的感觉孔较大；后眶下骨并未完全覆盖前鳃盖骨的上肢；前鳃盖骨的后腹角延伸成尖状；鳃盖骨的后腹缘呈凹形，且该骨的腹端延伸成尖状；胸鳍很长，延伸至腹鳍 fm 起点后方很远；脊椎数约为 46 — 8；椎体横突较短，且上下尾鳍条几乎与中央鳍条等长。该新鱼与其亚洲近亲美丽硬骨舌鱼（S. formosus）的亲缘关系，比与其南方近亲利氏硬骨舌鱼（S. leichardti）更近。美丽硬骨舌鱼栖息于天然湖泊、沼泽、被淹没的森林以及有悬垂植被覆盖的河流缓流深水区。其为肉食性鱼类，食物主要包括昆虫、鱼类、蠕虫、小型两栖动物、小型哺乳动物甚至鸟类。中华硬骨舌鱼可能生活在相同的自然环境中，并具有相似的食性，只是不包括最大的那些猎物。中华硬骨舌鱼可能存在两性异形现象。推测的雄性个体具有更纤细且更浅的身体、相对较大的头部以及更深的口裂。中华硬骨舌鱼（Scleropages sinensis sp. nov.）的发现将硬骨舌鱼属与骨舌鱼属的分化时间推至不晚于早始新世。

Full Text

Preamble

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First Complete Fossil Scleropages (Osteoglossomorpha)

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Abstract

A new species of osteoglossid fish, *Scleropages sinensis* sp. nov., is described from the Early Eocene Xiwanpu Formation in Hunan and the Yangxi Formation in Hubei, China. The new species is attributed to *Scleropages*, an extant genus of Osteoglossidae, based on its close resemblance to the genus in skull bones, caudal skeleton, fin shape and position, and reticulate scales. The new fish closely resembles extant *Scleropages* except for the following features: the nasals do not appear to be ornamented; the sensory pore in the antorbital is large; the posterior infraorbitals do not fully cover the dorsal limb of the preopercle; the posteroventral angle of the preopercle is produced to a point; the posteroventral margin of the opercle is concave and the ventral end of the bone is produced to a point; the pectoral fin is very long and extends well behind the beginning of the pelvic fin; the vertebral count is about 46–48; the parapophyses are shorter; and the upper and lower caudal rays are nearly as long as the inner rays. The new fish is closer to its Asian neighbor, *S. formosus*, than to its southern relative, *S. leichardti*. *Scleropages formosus* inhabits natural lakes, swamps, flooded forests, and slowly moving, deep parts of rivers with overhanging vegetative cover. It is a carnivorous fish whose diet consists mainly of insects, fishes, worms, small amphibians, small mammals, and even birds. *S. sinensis* likely lived in a similar natural environment and had a comparable diet, though probably excluding the largest prey items. Sexual dimorphism may have existed in *S. sinensis*; the presumed male has a slimmer and shallower body, a relatively larger head, and a deeper mouth cleft. The discovery of *Scleropages sinensis* sp. nov. dates the divergence of *Scleropages* and *Osteoglossum* to no later than the Early Eocene.

Key words: Hunan, Hubei, China; Early Eocene; Xiawanpu Formation; Yangxi Formation; Osteoglossidae

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1. Introduction

Scleropages, an extant genus of Osteoglossidae, is a freshwater fish with a transoceanic distribution in Southeast Asia and Australia. It comprises four species: *S. formosus* (Müller and Schlegel, 1844) and *S. inscriptus* (Roberts, 2012) distributed in Sumatra, Kalimantan, Peninsular Malaysia, Thailand, and Cambodia; and *S. jardinii* (Saville-Kent, 1892) and *S. leichardti* (Günther, 1864) in Australia and New Guinea. Pouyaud et al. (2003) described three closely related new species of *Scleropages* based on coloration, molecular data, and morphometric characters, but these were subsequently questioned and regarded as synonyms of *S. formosus* by Kottelat and Widjanarti (2005) and Roberts (2012). Pouyaud et al. (2003) also designated a neotype for *S. formosus* in their redescription, though Martien et al. (2013) considered this designation unnecessary because the original types are still extant.

The Asian arowana (*Scleropages formosus*), known as the dragon fish, is one of the most prized and expensive aquarium fishes in the world. Some Asians believe that the arowana brings good luck and fortune and can even cast out evil spirits. This belief persists in Thailand, China (Taiwan and Hong Kong), and Japan, despite the species being listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) as a highest-class protected fish. At present, only captive-bred dragon fish (F2 generation) may be traded.

Fossil *Scleropages* are known from the Maastrichtian of India (Hora, 1938; Rana, 1988; Kumar et al., 2005; Nolf et al., 2008), the Maastrichtian/Late Paleocene of Africa (Taverne, 2009), the Paleocene of Europe (Taverne et al., 2007), the Eocene of Sumatra (Sanders, 1934; Forey and Hilton, 2010), and the Oligocene of Australia (Hills, 1934, 1943; Unmack, 2001). All these earlier records consist of scales, otoliths, and isolated bone fragments. Here we report the first skeletons of fossil *Scleropages* from Lower Eocene strata in Xiangxiang, Hunan Province and Songzi, Hubei Province, China. Some specimens are complete and well preserved. A local farmer in Xiangxiang first collected the specimens and sent them to the IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences). Later, Li Chun from IVPP obtained a beautiful specimen (the holotype) from a farmer in Songzi. Zhang Miman of IVPP first recognized these specimens and encouraged and advised the first author to study them (including one piece from Xiangxiang sent by Song Changqi, a senior geologist), as she often helps young researchers study specimens in her care. Thereafter, the first author and his colleagues from IVPP collected dozens of specimens of the fish along with other fishes during three field seasons—one in Xiangxiang and two in Songzi.

The specimens from Xiangxiang were found in gray-black shale of the lacustrine Xiawanpu Formation, which consists predominantly of greenish, blue-gray claystone and grey-black shale, grey-black paper shale, with marlstone lenses. The geological age of the Xiawanpu Formation was considered to be Eocene or probably somewhat later (Liu et al., 1962; Cheng, 1962), or Early Eocene to early Middle Eocene (ECSLC, 1999). In addition to osteoglossids, other fishes (Cheng, 1962) including "*Osteochilus*" *hunanensis* (originally described as a cyprinid fish by Cheng (1962) and later revised to *Amyzon hunanensis*, a catostomid, by Chang et al. in 2001), *Aoria* (a genus of bagrid catfishes), *Tungtingichthys* (Perciformes), and *Cyclurus* (Amiidae, Chang et al., 2010), as well as ostracods and plants, were also found in the formation.

The Songzi specimens, including the holotype, were collected in the Yangxi Formation, which is 100–150 m thick and contacts conformably or disconformably with the underlying Paomagang Formation and the overlying Pailoukou Formation. The Yangxi Formation comprises shallow lacustrine deposits consisting of finely laminated mudstones and siltstones. Tons of slabs of fossil fishes (most are

Jianghanichthys, a cypriniform fish) were unearthed by farmers and commercial collectors. Many vertebrate fossils have been found at this locality, including the osteoglossid *Phareodus songziensis* (Zhang, 2003), *Jianghanichthys* (Liu et al., 2015), catfishes, perciforms, two rail-like birds *Songzia heidangkouensis* and *S. acutunguis* (Hou, 1990; Wang et al., 2012), and a pantodont mammal *Asiocoryphodon* cf. *A. conicus* (Chen and Gao, 1992). In addition, the oldest known primate was found in the same formation near this locality (Ni et al., 2013). Other fossils seen at the locality include ostracods, gastropods, charophytes, spores, and pollen. The age of the strata is Early Eocene (ECSLC, 1999).

2. Material and Methods

The specimens studied are deposited in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences. Comparative materials of extant *Scleropages* (*S. formosus*, IVPP V OP 80; *S. leichardti*, IVPP V OP 81) were purchased at a fish market in Beijing and are also deposited at IVPP. *Scleropages jardinii* and *S. inscriptus* were not available at the Beijing fish market.

3. Systematic Paleontology

Teleostei Müller, 1846
Osteoglossomorpha Greenwood et al., 1966
Osteoglossidae Bonaparte, 1832
Scleropages Günther, 1864
***Scleropages sinensis* sp. nov.** (Figs. 1-5, 7)

Etymology. The specific name refers to China where the specimens were found.

Holotype. IVPP V 13672.2, a complete skeleton.

Referred specimens. IVPP V 12749.1-8, V 12750, V 13672.1, 3.

Locality and horizon. Specimens V 13672.1-3 and V 12750 are from Songzi County, Hubei Province, China; Yangxi Formation, Lower Eocene. Specimens V 12749.1-8 are from Xiangxiang, Hunan Province, China; Xiawanpu Formation, Eocene.

Diagnosis. A fossil species of *Scleropages* differing from extant species of the genus in: nasals not appearing to be ornamented; sensory canal exposed in prominent groove on nasals; supraorbital sensory canal enclosed in bone on frontal only for middle third of its length; unornamented posterior portion of parietal is only 1/4 of length rather than 2/3; commissure in extrascapular tubes rather than passing through parietals; pterotic thicker in lateral portion; sensory pore in antorbital larger than in extant species; posterior infraorbitals not as large as in extant species and not quite covering dorsal limb of preopercle, with width-to-height ratio about 0.75 rather than 1-1.2; preopercle posteroventral angle produced to point, unlike condition in extant species; posteroventral margin of opercle concave and ventral end of bone produced to point; supracleithrum recurved; dorsal process of cleithrum long and strong; pectoral fin very long and extending well behind beginning of pelvic fin; vertebrae about 46-48; parapophyses shorter; neural spine on U1 partly doubled; upper and lower caudal rays nearly as long as inner rays.

4. Description

The body of the fish is fusiform in adults, with median fins posteriorly positioned and pelvic fins in abdominal position. Skull bones are thick and squamation is heavy. The standard length of the largest specimen is 175 mm, that of the holotype is 140 mm, and that of the smallest is 78 mm. Unless otherwise indicated, the following description is based on the holotype (Fig. 1 [Figure 1: see original paper]), which is the best-preserved example.

Cranium. The bone interpreted as the probable dermethmoid has an elongate, spear-point shape, with a pointed anterior end and a long, tapered posterior end (Fig. 4 [Figure 4: see original paper]). The nasals are large and suture in the midline along the anterior half of their length but are separated by the tapered frontals posteriorly. The nasals are not noticeably ornamented, unlike the condition in extant *Scleropages formosus* (Taverne, 1977:fig. 73 [Figure 73: see original paper]) and *S. leichardti* (IVPP dried skeleton). Also unlike the condition in the two extant species examined, the sensory canal appears to be exposed in a prominent groove in the fossil species.

The frontal is similar in shape and ornamentation to that of extant species of *Scleropages* (Taverne, 1977:fig. 73; IVPP dried skeleton of *S. leichardti*). It is long and subrectangular, with an anterior embayment for reception of the nasal and a posterior sinuous suture with its opposite member. In proportions it is slightly shorter and wider than that of *S. leichardti* and more like that of *S. formosus*. The lateral margin is embayed to conform to the medial margin of the dermosphenotic. Parallel to the lateral margin, the sensory canal is enclosed in bone for the middle third of its length, while being exposed in deep grooves for the anterior and posterior thirds. In *S. leichardti* and *S. formosus*, in contrast, the canal is enclosed in bone to or almost to its entry into the nasal.

As in other species of the genus, the parietal is subrectangular and sutures with its opposite at the midline and with the pterotic laterally. The surface of the anterior three-quarters of the bone is sculptured, while the posterior quarter lies at a lower level, beneath the canal-bearing extrascapulars, and is not sculptured. Length-to-width proportions of the parietal are about 2:3, similar to those of *S. formosus* but unlike the 1:1 ratio seen in *S. leichardti*.

The external portion of the pterotic is a little larger and thicker than in extant species of *Scleropages*. The anterior half of the bone, lateral to the parietal, is sculptured and bears the temporal sensory canal in an open groove, whereas it is a simple tube in *S. formosus* (Taverne, 1977:fig. 73). The epiotic, supratemporal, and supraoccipital are not visible in the available specimens.

Scleropages sinensis appears to have its extrascapular sensory commissure carried within tubular 'extrascapulars' situated dorsal to the unsculptured area of the parietals, rather than passing directly through the parietals as seen in extant species (Taverne, 1977:fig. 71 [Figure 71: see original paper]). In both fossil and extant species, the canal is carried in paired extrascapular tubes between the previously mentioned bones and the posttemporals.

The orbital portion of the parasphenoid is toothless, moderately broad, and parallel-sided (V 12749.5). The remainder is covered by infraorbitals in available specimens.

The circumorbital series (Fig. 4) is composed of six bones: an antorbital, four infraorbitals, and a dermosphenotic. A supraorbital is absent. The antorbital, infraorbitals 1, 3, and 4, and the dermosphenotic are all prominently sculptured, while infraorbital 2 is not preserved well enough for assessment of its sculpture.

The antorbital is polygonal, making contact with the dermopterotic posterodorsally, the frontal and parietal dorsomedially, and the first infraorbital ventrally. The concave anterior and orbital margins are free. The shape is similar to that of *S. formosus* (Taverne, 1977:fig. 71). Dorsally, the circumorbital sensory canal enters the antorbital via a short, broad groove, then passes through the bone in a tube, entering the first infraorbital where a large pore communicates with the exterior. In *S. formosus* as illustrated by Taverne (1977:fig. 71), the latter pore is small and the canal is completely enclosed in bone throughout its length. The antorbital in *Osteoglossum bicirrhosum* (Taverne, 1977:fig. 42 [Figure 42: see original paper]) is more tubular and parallel-sided and unornamented; in *S. leichardti* (IVPP dried skeleton) it is also less polygonal but is ornamented.

The first and second infraorbitals are narrow and tubular. The first is slightly expanded, longer, and more ornamented than the second, but the latter is not well preserved.

The two posterior infraorbitals (third and fourth) are very large but do not quite reach the size of those in extant *Scleropages* and *Osteoglossum*, in which they extend posteriorly to the articulation of the opercle, completely concealing the dorsal end of the preopercle and covering the posterior suspensorium. In *S. sinensis* there is a narrow gap through which the dorsal limb of the preopercle may be seen. The two posterior infraorbitals have a width-to-height ratio of about 0.75, compared to about 1.0-1.2 in the two extant species. The two bones are nearly equal in size, like those in extant *Scleropages* but differing from *Osteoglossum*, in which the lower one is much larger than the upper. The infraorbital sensory canal is carried in a tube near the orbital margin of both posterior infraorbitals, with only a single small pore opening externally near the anteroventral end of the third infraorbital, as in the specimen of *S. formosus* figured by Taverne (1977:fig. 71). In *O. bicirrhosum* the pore is much larger and directed posteroventrally into a large groove (Taverne, 1977:fig. 42).

The complete or near-complete enclosure by infraorbitals of the cheek posteroventral to the orbit is considered a synapomorphy of Osteoglossidae by Li and Wilson (1996) and Hilton (2003). Among early osteoglossomorphs, this character is found only in *Paralycoptera*. Accordingly, *Paralycoptera* was considered to be closely related to or included within Osteoglossidae by different authors (Chang and Chou, 1977; Ma and Sun, 1988; Jin et al., 1995; Zhang, 2002).

The dermosphenotic is large, thick, sculptured, and approximately triangular. It bears the infraorbital canal internally near its posterior margin. The canal emerges from the posterodorsal corner of the dermosphenotic, where it enters the frontal to join with the supraorbital sensory canal near the anterior end of the posterior sensory groove of the frontal. In *S. formosus* the canal also joins within the frontal, but within a bone-enclosed tube. In V 12749.5 there is a suggestion of a branch in the infraorbital canal within the dermosphenotic, but the course of this branch cannot be detailed. Taverne (1977:fig. 71) did not show any branching within the dermosphenotic.

Jaws. The premaxilla is small, approximately triangular, and sculptured. It bears a blunt ascending process in its anterior half. There are seven teeth on the left premaxilla of the holotype, with the anterior three teeth being much larger than the posterior ones. The number of teeth on the premaxilla of extant *Scleropages* has been counted differently: 4–5 by Ridewood (1905), 3–5 by Kershaw (1976), and 11 by Taverne (1977). In the four specimens of extant *Scleropages* that we examined, this number is 6–8, a condition agreeing with that of *S. sinensis*.

The maxilla is long and slender, and forms an angle of about 45º with the long axis of the fish when the mouth is closed. It extends posteriorly nearly to the level of the mandibular articulation and ends well behind the posterior margin of the orbit. The posterior end is slightly expanded and downturned, especially immediately posterior to the marginal teeth. Ornament is present all along the external surface but is most prominent at the anterior and posterior ends. As in all living osteoglossomorphs, there is no supramaxilla.

The maxilla bears 40 conical teeth in an external row in the holotype, resembling *S. formosus* in number and differing from *S. leichardti*, in which the teeth number about 35 (IVPP dried skeletons). The teeth decrease in size steadily from anterior to posterior. Here and there, a few smaller teeth seen behind and between these marginal teeth might represent replacement teeth.

The mandible is also very long, makes a 45º angle with the long axis of the fish, lacks a distinct coronoid process, and consists of three bones: dentary, anguloarticular, and retroarticular. The dentary forms the great majority (3/4) of the length of the mandible. Anteriorly, the dentary curves medially to meet its opposite at a shallow symphysis. As for the premaxilla, the anterior five or six teeth of the dentary are much larger than the posterior ones.

As in extant *Scleropages* (Taverne, 1977:fig. 71), the angulo-articular is relatively small, articulates with the quadrate as seen in lateral view, and the posterior tip of the retroarticular is visible laterally posterior to the quadrate articulation. Both dentary and angulo-articular bear longitudinal ridges on their lateral surfaces.

The mandibular sensory canal extends the length of the dentary and angulo-articular within a canal, with one pore located near the ventral end of the suture between the angulo-articular and dentary, as in *S. formosus* (Taverne, 1977:fig. 71), and three more pores evenly spaced and opening onto posteriorly directed grooves more anteriorly in the dentary, as in *S. formosus* and *S. leichardti* (IVPP dried skeletons).

Palato-quadrate arch. The toothed palato-ectopterygoids are preserved in V 12749.5, both bearing a row of uniform-sized small teeth on their lateral margins. On the right side, more medially an area of much smaller teeth can be seen. Both conditions are matched in extant *S. formosus* (Taverne, 1977:fig. 83 [Figure 83: see original paper]) and *S. leichardti* (IVPP dried skeleton). According to Taverne (1977:134–135), the anterior end of this bone in *S. formosus* includes the fused dermopalatine, with the autopalatine ossified only in the largest, oldest individuals. We were unable to confirm these details in *S. sinensis*.

The entopterygoid in extant species of *Scleropages* is triangular, with a single row of large conical teeth on the medial edge and fine denticles covering the remainder of the surface. The detailed shape is not seen in the fossils of *S. sinensis*, but part of the medial row of large teeth on the right entopterygoid is visible in the holotype. These teeth are larger posteriorly than anteriorly, and each is curved slightly ventrolaterally, as in *S. leichardti* (IVPP dried skeleton). In V 12750 the medial row and more lateral denticles are visible in cross section. The metapterygoid, symplectic, and most of the quadrate are covered by the posterior infraorbitals in available specimens, although the quadrate and symplectic are exposed in inner view in V 12750.

Hyoid arch and branchiostegals. Only a very small part of the hyomandibular can be seen in the holotype. The tip of a bone protruding from beneath the anterior margin of the fourth infraorbital in the holotype might be the entopterygoid process of the hyomandibular as characteristically seen in extant osteoglossids, but it seems rather too stout. On the other hand, it is not oriented appropriately to be identified with the basipterygoid process of the parasphenoid, which might be expected to occur in the same area of the fossil.

A small triangular hypohyal, most of the anterior ceratohyal, and basihyal are seen in V 12749.5. There are nine slender, acinaciform branchiostegal rays in the holotype, and at least two broad, spatulate ones. In *S. formosus*, Taverne (1977:fig. 84 [Figure 84: see original paper]) illustrates nine acinaciform and seven spatulate branchiostegals; thus we might estimate that *S. sinensis* had a similar number, perhaps 16 in total, given that only two spatulate branchiostegals are preserved.

Opercular series. The preopercle is similar but not identical to that in extant species of *Scleropages*. The upper limb is not completely covered by posterior infraorbitals as it is in extant species (Taverne, 1977:fig. 71). The dorsal limb tapers uniformly dorsally, as far as can be seen, and is about twice as long as the ventral limb. The latter is bluntly rounded anteroventrally. The posteroventral angle of the preopercle is produced posteriorly to a point, located immediately below the ventral extremity of the opercle. This last feature is not seen in the preopercles of extant species but is met with in a more extreme form in some African osteoglossiforms such as *Chauliopareion* Murray and Wilson, 2005, and *Singida* as redescribed by Murray and Wilson (2005).

The preopercular sensory canal in *S. sinensis* has features typical for osteoglossids. The canal is open ventrally beneath a long, horizontal shelf. On the shelf, and dorsal to it, the preopercle is sculptured, but ventral to it the surface is smooth. From the posterior end of this shelf to the dorsal end of the vertical limb, the preopercular canal is enclosed in bone beneath the anterior edge of the exposed portion of the bone, except for a single, large pore at about half the height of the preopercle. This pore opens posteriorly from the main canal into a prominent groove directed posteroventrally. In other osteoglossids the relative height of this single pore varies, but essentially the same feature is seen, where preservation permits, in many genera of Osteoglossidae and Notopteridae including extant species of *Scleropages* and fossil taxa such as *Phareodus* and *Musperia* (e.g., Taverne, 1977, 1978). *Arapaima* and *Heterotis* do not exhibit the shelf and single large pore, showing instead a bone-enclosed canal opening via pores, while the condition in *Pantodon* is perhaps somewhat intermediate (Taverne, 1978).

The opercle in *S. sinensis* is large and nearly semicircular in shape, but differs from that in extant species of *Scleropages* and *Osteoglossum* in having its ventral end produced to a point and its posteroventral margin concave. The opercle is also prominently sculptured except for its anterior margin and dorsal extremity. In the holotype, the opercle has a height of 24 mm and a maximum width, at right angles to the anterior edge, of 13 mm. The hyomandibular facet is located at a height of 19 mm from the ventral end, judging by the arrangement of ornamental ridges on the external surface. The subopercle and interopercle are not visible.

Appendicular skeleton. The pectoral girdle is partially seen in the holotype and in V 12749.8. The posttemporal is a forked bone with the dorsal limb longer than the ventral one. The lateral line runs near the ventral margin of the bone and probably goes into the trunk scales directly, without passing through the supracleithrum, as in living osteoglossids.

The supracleithrum is strap-like dorsally and broadens ventrally; it is recurved rather than following a uniform curve as seen in extant species. In *Osteoglossum* the bone broadens ventrally but is not recurved (Taverne, 1977). A small postcleithrum is present and lies medial to the junction between the supracleithrum and cleithrum.

The cleithrum is best exposed in specimen V 12749.8, where it is seen to have a long dorsal limb of uniform width, terminating dorsally in a long, rod-like process. In contrast, the cleithrum of extant species (Taverne, 1977:fig. 86 [Figure 86: see original paper]; IVPP dried skeletons) has only a smaller, acuminate dorsal extremity, much shorter and more slender than that of *S. sinensis.* The coracoid, scapula, and mesocoracoid have not been observed.

Four proximal pectoral radials that support the pectoral rays (except for the first ray) can be recognized in the holotype, with the first thick and stout and the others becoming smaller posteriorly.

The pectoral fin (Figs. 1, 3C) is very long and extends well behind the beginning of the pelvic fin, a difference from extant species where it does not reach the beginning of the pelvic fin. In the holotype the longest rays are 47 mm long, whereas the pelvic fin originates 35 mm posterior to the origin of the pectoral fin. The pectoral fin contains seven rays, resembling *S. formosus* rather than *S. leichardti* where the fin has eight rays (IVPP dried skeletons). All rays are branched and segmented except the first one, which is exceptionally thick and unbranched, though segmented. Adjacent to the base of the smallest ray there is a claw-shaped bone.

The pelvic girdle and fin are very small. The pelvic fin originates slightly closer to the anal fin than to the pectoral fin. The pelvic bone (seen in V 12749.8) is short and flat. There appear to be six pelvic fin rays, all branched but the first, a condition agreeing with *S. leichardti* and differing from *S. formosus*, which has five fin rays in specimens examined.

Dorsal and anal fins. Both dorsal and anal fins are rounded in outline and located posteriorly. The dorsal fin is small and originates posterior to the origin of anal fin, opposite the middle of the anal fin. In the holotype there are two short procurrent dorsal rays, the second one segmented, followed by one full-length unbranched ray and 11 branched rays, the last one apparently double, for a total of 12 principal rays. Fourteen short dorsal pterygiophores can be counted, matching the fin rays one-to-one. Other specimens (V 12749.1,2) may have slightly more principal rays, 12–15 in available specimens, with 14–17 pterygiophores.

The anal fin is much larger than the dorsal fin, with three very small, unsegmented procurrent rays and 22 principal rays, supported by 23 anal pterygiophores in the holotype, and 21–24 anal pterygiophores in other specimens (V 12749.1,4). This resembles the condition in *S. formosus* and differs from *S. leichardti*, in which 28 principal fin rays are present.

Vertebral column and caudal fin. There are 46–48 vertebrae in available specimens, of which in the holotype about 22 are abdominal and 24 are caudal including the two ural centra. This number is much less than in extant osteoglossids and agrees more with early osteoglossomorphs such as *Kuntulunia* and *Xixiaichthys* (Zhang, 1998, 2004). The first three centra are covered by the opercle. The centra are slightly deeper than long.

The first four neural spines are paired, and the remainder anterior to the dorsal fin are fused into a single element. In extant *Scleropages* and *Osteoglossum*, this condition varies, with neural spines being fused beginning with the third in *S. formosus* and with the eighth in *O. bicirrhosum* (e.g., Taverne, 1977:108, 147). Parapophyses are difficult to see but appear (V 12749.8) to be much shorter than in extant *Scleropages*, *Osteoglossum*, and *Phareodus* (Li et al., 1997) and even shorter than in most early osteoglossomorphs (Zhang and Jin, 1999; Zhang, 1998, 2004).

There are 22 pairs of pleural ribs, which extend to the ventral margin of the trunk, except for the last pair, which is only about half the length of the more anterior ones. Long, slender epineurals are present, their proximal ends not fused with the neural arches. The last epineural is related to the second vertebra following the last abdominal vertebra.

Some 22 long, slender supraneurals are seen in specimen V 12749.8, anterior to the dorsal fin and lying at a shallow angle to the long axis of the body so that each one overlaps the dorsal end of one or two neural spines.

The caudal skeleton (Figs. 3D, 5) is very similar to that of extant species of *Scleropages* with a couple of exceptions. Unfortunately, these details can only be seen in a single specimen of *S. sinensis* (V 12749.8). The caudal skeletons in the two examined extant species (Fig. 6 [Figure 6: see original paper]) display important differences, each resembling that of *S. sinensis* in some ways but not in others.

Three neural and haemal spines in *S. sinensis* are lengthened to support the caudal fin rays; these haemal spines gradually thicken posteriorly. The first preural centrum bears a complete neural spine, while in some specimens of *S. leichardti* the centrum bears two. The first ural centrum (U1) appears to have two incompletely fused neural spines, with the first complete and the second shorter. The second ural centrum (U2) is fused with the proximal ends of hypurals 3-5. There are six hypurals. Hypural 1 is very deep and does not reach U1 proximally. Hypural 2 is less than half the width of the first and either articulates with or is fused to the centrum as in extant species. Hypurals 3 through 5 are fused proximally and fit tightly together distally. A rod-like bone dorsal to hypurals 3-5 is probably the sixth hypural. Just above this bone, a similarly shaped bone is interpreted here as fused uroneurals (see Hilton, 2003, for discussion of this unusual feature of osteoglossiforms).

In *S. leichardti*, centrum U1 supports three hypurals in every specimen available to us, a very unusual situation for a teleostean fish. The first two of these hypurals are fused to each other proximally but separated distally, and the combined first two hypurals do not reach U1. In contrast, both *S. formosus* and

O. bicirrhosum have the more usual situation of two lower hypurals, the first not reaching U1 and the second joining it.

The greatly enlarged first hypural in *S. sinensis* seems deep enough to correspond to the two partially fused hypurals of extant *S. leichardti* specimens. This hypural is as deep as the first two (of three lower) hypurals in *S. leichardti*. However, we do not see any evidence of a division into two hypurals in this specimen. The occurrence in *S. sinensis* of two incompletely separated neural spines on U1 might suggest an origin by fusion of centra. However, the neural spine of *S. leichardti* specimens examined by us is not doubled, whereas they have an extra lower hypural. Additional specimens showing the caudal skeleton of *S. sinensis* and a study of the development of the caudal skeleton in *S. leichardti* could be very informative in light of these findings.

The caudal fin is rounded. There are 16 principal caudal rays, the first and last being unbranched and almost as long as the remaining rays, whereas in living species of *Scleropages* and *Osteoglossum*, the upper and lower rays are only half the length of the innermost ones. One or two procurrent rays are present anterior to the principal rays.

Squamation. The scales are large (Figs. 2, 7), cycloid, oval, and exhibit the reticulate pattern, involving small units called squamules, typical of osteoglossids (Fig. 8 [Figure 8: see original paper]). The external surface of the scale shows circuli in the basal portion and granular ornamentation in the apical area. The squamules (Gayet and Meunier, 1983) are rhombic, polygonal, or irregular in shape. The mesial surface of each squamule may be smooth or bear 1–25 rounded, raised tubercles, each of which has a minute transversal pore (Jolly and Bajpai, 1988) at its center.

The lateral line (Fig. 2) runs just below the vertebral column, and the scales along the lateral line number about 24, a similar number to that in *S. formosus* and 10 scales fewer than seen in *S. leichardti* (IVPP specimens).

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5. Discussion

The new fish found in Hubei and Hunan provinces of China closely resembles *Scleropages* in skull bones, caudal skeleton, fin shape and position, and reticulate scales (Fig. 9 [Figure 9: see original paper]). Therefore, it must belong to the genus. *Scleropages* has four species: two in Australia and New Guinea (*S. jardinii* and *S. leichardti*) and two in Asia (*S. formosus* and *S. inscriptus*). *S. jardinii* and *S. leichardti* are very similar to each other, while *S. formosus* and *S. inscriptus* are nearly identical except that the latter has complex maze-like markings on the circumorbitals, opercular series, and scales. For this reason and because specimens of the other two species were not available to us, only *S. leichardti* and *S. formosus* were used as representatives of extant *Scleropages* for comparative study.

The new fish is very similar to *S. leichardti* and *S. formosus*, except for the following differences: the nasals do not appear to be ornamented; the sensory canal is exposed in a prominent groove on the nasals (unless this is a preservational artifact); the supraorbital sensory canal is enclosed in bone on the frontal only for the middle third of its length; the unornamented posterior portion of the parietal is only 1/4 of its length rather than 2/3; the commissure is in extrascapular tubes rather than passing through the parietals; the pterotic is thicker in its lateral portion; the sensory pore in the antorbital is larger than in extant species; the two posterior infraorbitals are not as large as in extant species, not quite covering the dorsal limb of the preopercle, and their width-to-height ratio is about 0.75 rather than 1–1.2; the posteroventral angle of the preopercle is produced to a point, unlike the condition in extant species; the posteroventral margin of the opercle is concave and the ventral end of the bone is produced to a point (in extant species the ventral end is not as produced and the posteroventral margin is not concave); the supracleithrum is recurved versus uniformly curved; the dorsal process of the cleithrum is long, strong, and rod-shaped versus shorter and acuminate in extant species; the pectoral fin is very long and extends well behind the beginning of the pelvic fin; vertebrae number about 46–48 versus ~60 in extant species and other Recent osteoglossids; the parapophyses are shorter; the neural spine on U1 is partly doubled; and the upper and lower caudal rays are nearly as long as the inner rays (versus much shorter). Based on these differences, a new species is established: *Scleropages sinensis* sp. nov.

Scleropages sinensis is similar to *S. formosus* but different from *S. leichardti* in that: length-to-width proportions of the parietal are 2:3 versus 1:1; antorbital proportions are similar to those in *S. formosus*, but in *S. leichardti* the antorbital is not as polygonal; maxillary teeth number about 40 versus about 35 in *S. leichardti*; principal anal rays are 21–24 versus 28 in *S. leichardti*; there are two lower hypurals versus three in *S. leichardti*; and there are 24 scales along the lateral line versus ~34 in *S. leichardti.*

Scleropages sinensis also shares some similarities with *S. leichardti* but differs from *S. formosus.* These characters include six pelvic rays versus five in *S. formosus*, and the first hypural being very deep (as deep as the first two in *S. leichardti*, and unlike the slender first hypural in *S. formosus*). Pelvic fin rays are seven in Hiodontidae, six principal plus one short in *Kuntulunia* and *Xixiaichthys*, and six in *Lycoptera* and *Asiatolepis* (Zhang, 2010: five in original description, but clearly six in V 11982.28a). Therefore, having more pelvic rays is likely a primitive condition in osteoglossomorphs. Centrum U1 supporting three hypurals in *S. leichardti* is a very unusual situation in teleosts. The same condition was noticed by Hilton (2003) in *S. jardinii* (152 mm SL) and by Xu and Chang (2009) in *S. jardinii* and *S. leichardti.* Hilton thought that study of more specimens was needed to confirm if this is due to ontogeny (i.e., if hypural 1 typically is composed of two elements) or is individual variation. Although the first hypural in *S. sinensis* seems deep enough to correspond to the first two hypurals in *S. leichardti*, no evidence of a possible division into two hypurals can be seen. The caudal skeleton is usually covered by scales in *S. sinensis*, making it difficult to determine if there is any variation in the hypural pattern.

According to the above comparison between *S. sinensis* sp. nov. and extant *Scleropages*, it is clear that the new fish is closer to its Asian neighbor, *S. formosus*, than to its southern relative, *S. leichardti*.

The Asian arowana *S. formosus* is distributed in the Mekong Basin in Vietnam and Cambodia, southeastern Thailand, Tenassarim (Myanmar), the Malay Peninsula from Sungai Golok southwards, Borneo, and Sumatra. It inhabits natural lakes, swamps, flooded forests, and slowly moving, deep parts of rivers with overhanging vegetative cover. The Asian arowana is a carnivorous fish whose diet consists mainly of insects, fishes, worms, small amphibians, small mammals, and even birds. It can jump very high in the wild to obtain food hanging in trees. *S. sinensis* may have lived in the same natural environment and could have had a similar diet, except for the largest items, considering the smaller body size of the new fish.

Arowanas are paternal mouthbrooders. The Asian arowana is not easy to sex. Scott and Fuller (1976) found no obvious external sexual differences in 170 specimens (32 were fry) they obtained in Malaya. However, Suleiman (2003) argued that the differences become apparent after maturity is reached at about 3–4 years of age. Sex determination is based on body shape and mouth cavity size. Males have a slimmer and shallower body depth (while females have a more rounded body), a bigger mouth, and more intense color than females. A larger mouth and deeper lower jaw in males are beneficial for holding more eggs and fry. These sexual differences can also be seen in *S. sinensis*. The holotype (Fig. 1) and another fish (Fig. 3A) have a slimmer and shallower body, a relatively larger head, and a deeper mouth cleft. In contrast, some other individuals (Fig. 2) have a more rounded body and a smaller head. This suggests possible sexual dimorphism in *S. sinensis*. The deeper mouth cleft in the holotype and V 12749.4 (Fig. 3A) also suggests the possibility of paternal mouthbrooding in *S. sinensis*. Unfortunately, no direct evidence such as eggs and fry can be found in the fossils.

Except for *Hiodon*, which lives only in North America, all other extant osteoglossomorphs are distributed in the tropical or subtropical fresh waters of southern continents. Fossil osteoglossomorphs have been found in freshwater deposits (some forms, such as *Brychaetus*, may have lived in brackish water or even marine environments) on all continents except Antarctica. The explanation for such a transoceanic distribution of freshwater fishes is a challenge for paleogeography and historical biogeography. Nelson (1969) argued that Africa was probably the center of the ancestral distribution of osteoglossomorphs. Greenwood (1970) and Chang and Chou (1976) supposed that East Asia might be the ancestral region of osteoglossomorphs. Gayet (1987) explained the present distribution by a hypothetical "lost Pacifica." All these hypotheses failed to resolve the transoceanic distribution of the superorder Osteoglossomorpha satisfactorily. Li (1997) and Xu and Chang (2009), in contrast, suggested that the early evolution of Osteoglossomorpha occurred in Pangaea.

The earliest fossil record of Osteoglossomorpha is *Lycoptera* (Barremian) (Swisher et al., 2002). Early osteoglossomorphs have mostly been recovered from China, but have also been found in other parts of the world, such as *Chandlerichthys* from North America (Cenomanian), *Laeliichthys* from South America (Aptian), and *Kipalaichthys* from Africa (Cenomanian). Since Osteoglossomorpha were already widely distributed on both northern and southern continents in the Early and mid-Cretaceous, it is reasonable to suggest that the superorder originated in Pangaea.

Li (1997) believed that the earliest members of the main lineages of Osteoglossomorpha had already extended their distribution to most parts of Pangaea before its final breakup, and that the recent relict distribution of the superorder resulted from extinction. Li conceived that the transoceanic dispersal and vicariance of Osteoglossomorpha did not happen after the final split of Pangaea. *Phareodus*, a very common genus of fossil osteoglossid also seen in the same formation with *S. sinensis*, has been found in Pakistan, India, Sumatra (*Musperia*), North America, and Australia. If transmarine migration never happened, a Pangaean origin would be the most likely model to interpret the transoceanic distribution of *Phareodus*. Based on their study of molecular phylogeny of osteoglossoids, Kumazawa and Nishida (2000) concluded that the divergence time between Asian arowana (*Scleropages formosus*) and Australian arowana (*S. leichardti* and *S. jardinii*) is about 138 million years, which is close to or slightly older than the probable time of the India-Madagascar separation from Gondwanaland (120–130 Ma, Smith et al., 1994). They consequently argued that the Asian arowana originated on a part of Gondwanaland and was carried to Eurasia by the Indian subcontinent. Therefore, the transoceanic migration of Osteoglossomorpha might have occurred after the split of Pangaea.

The Eocene collision of the Indian subcontinent with Asia has been accepted for a long time (Besse et al., 1984; Metcalfe, 1999), but recent data support the view that terrestrial continuity between India and mainland Asia was already established by the time of the K/T boundary, 65 Ma ago, or probably slightly earlier (Beck et al., 1995; Jaeger et al., 1989; Prasad et al., 1994; Rage et al., 1995). The discovery of *Scleropages* and *Phareodus* from mainland Asia suggests the possibility that the genus originated in Gondwana and dispersed to Asia through the Indian subcontinent, and that *Phareodus* then reached North America via the Bering Strait. The Eocene fish fauna along the coast of the Bohai Gulf, eastern China, shows striking similarity in composition to those of the same age along the west coast of North America, demonstrating a "transpacific" distributional pattern (Chang and Chen, 2000). The Arctic connection of the northern continents and the broad connection between Asia and North America in the Bering Strait area may have served as a passage for fishes from both sides of the Pacific (Chang and Chen, 2000). With those connections between the two places, *Phareodus* could have dispersed from Asia to North America. *Scleropages* has been found in the Maastrichtian, Paleocene, Eocene, and Oligocene, and *Phareodus* was cosmopolitan in the Eocene, but their Late Cretaceous representatives were only found in southern continents. The fossil records thus seem to support the view of a Gondwanan origin of osteoglossids.

However, a recent work (Lavoué, 2015) rejected the Gondwanan origin of *Scleropages*. Lavoué reported an age CI of *Scleropages* ranging from 79.9 to 101.4 Ma, which is significantly younger than the (138 ± 18) Ma age inferred by Kumazawa and Nishida (2000). Recent paleogeographical reconstructions (Gibbons et al., 2013; Scotese, 2014) give a latest possible age (115.0 Ma) for a direct connection of the Indian subcontinent to Australia–Antarctica. Lavoué' s result suggests that the divergence between the Sundaland–Indochina *Scleropages* and the Australia–New Guinea *Scleropages* is younger than 115.0 Ma. The early divergence of *Scleropages* therefore occurred after the final separation between India and Antarctica–Australia. Consequently, his study rejects the Gondwanan origin hypothesis to explain the distribution of *Scleropages*.

More recently, Lavoué (2016) used newly reconstructed time-calibrated phylogenetic trees based on a large dataset combining extant and fossil taxa and molecular and morphological characters to test whether the divergence of Osteoglossiformes was compatible with the breakup of Gondwana. He thought that the most convincing evidence that some osteoglossomorphs may have achieved their current transmarine distribution through marine dispersal is from the genus *Scleropages*. Marine dispersal in *Scleropages* was also mentioned by Cracraft (1974), Briggs (1979), and Wilson and Murray (2008). Taverne et al. (2007) argued that Recent freshwater Osteoglossiformes generally tolerate brackish waters and sometimes enter marine waters near estuaries. In contrast, Lavoué (2015) suggested that *Scleropages* species are highly intolerant of salt water according to the investigations of Gehrke et al. (2011) and Roberts (1978).

The distribution of osteoglossids remains a zoogeographical enigma. Marine fossils of *Scleropages* or an unknown vicariance event are needed to explain the intercontinental distribution of the genus. In this context, the discovery of *Scleropages sinensis* dates the divergence of *Scleropages* and *Osteoglossum* to at least as old as the Early Eocene, which is a significant step toward solving this zoogeographical puzzle.

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Therocephalian (Therapsida) and Chroniosuchian (Reptiliomorpha) from the Permo-Triassic Transitional Guodikeng Formation of the Dalongkou Section, Jimsar, Xinjiang, China

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Abstract

The Guodikeng Formation encompasses the terrestrial Permo-Triassic transition sequence in China. This formation crops out in the Dalongkou section, Jimsar, Xinjiang, where remains of the dicynodonts *Jimusaria* and *Lystrosaurus* were found. We describe here a therocephalian and a chroniosuchian from the Dalongkou section, representing the first records of these groups from the Guodikeng Formation. Diagnostic characters of the new therocephalian, *Dalongkoua fuae* gen. and sp. nov., include: maxillary ventral margin strongly concave in lateral view; incisors spatulated and rounded; incisors and canines with faint serrations; coronoid process of the dentary with a marked external adductor fossa; and triangular reflected lamina of the angular with two smooth concavities. Chroniosuchians are represented by several postcranial elements, and the vertebral morphology is similar to *Bystrowiana* and *Bystrowiella*. These remains are interpreted as representing Bystrowianidae indeterminate. The new findings increase the diversity of the Guodikeng Formation, which is now represented by three or four dicynodonts, one therocephalian, and one chroniosuchian. All these groups survived the massive Permian-Triassic extinction but disappeared from the fossil record in the Middle to Upper Triassic.

Key words: Dalongkou, Xinjiang; Permian; Triassic; Guodikeng Formation; chroniosuchian; therocephalian

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1. Introduction

The Dalongkou section, Jimsar, Xinjiang, is a famous terrestrial section with Permo-Triassic transitional sequences. The southern limb of the Dalongkou anticline section (SLS) has been suggested as a candidate for the global non-marine Permian-Triassic boundary (PTB) reference section (Cheng and Lucas, 1993; Liu, 1994). This section was originally known for its fossil vertebrate remains. The formation produced the dicynodonts *Jimusaria sinkianensis* and the first specimen of *Lystrosaurus* from China (Sun, 1963; Yuan and Young, 1934a, b); later, the co-occurrence of these taxa on the same horizon of the Dalongkou section was noted (Cheng, 1993). The lowest occurrence of *Lystrosaurus* at the SLS is at the base of bed 63 or 54 of the measured lithostratigraphic section

(Fig. 1), ~65 m below the base of the Jiucaiyuan Formation (Cheng, 1993; Liu et al., 2002). The exact position of the holotype of *Jimusaria sinkianensis* is unknown, but Cheng (in Yang et al., 1986) suggested it could lie within the top 20 m of the Guodikeng Formation. This is perhaps why Kozur and Weems (2011) located the stratigraphic position of this dicynodont 15 m below the base of the Jiucaiyuan Formation. Besides dicynodonts, the procolophonid *Santaisaurus yuani* and the archosauriform *Chasmatosaurus yuani* were discovered from horizons of the Jiucaiyuan Formation at the Dalongkou section (Koh, 1940; Li et al., 2008; Young, 1958, 1963).

The PTB in the Junggar Basin was traditionally positioned at the base of the Jiucaiyuan Formation, but a joint team of the Chinese Academy of Geological Sciences and the Xinjiang Bureau of Geology and Mineral Resources first proposed the PTB within the Guodikeng Formation (Yang et al., 1986). They tentatively located the PTB at the uppermost Guodikeng Formation; one major reason for this decision was the position of the lowest occurrence of *Lystrosaurus*. For a long time, *Lystrosaurus* was a Triassic index fossil, and its lowest occurrence marked (or at least approximated) the base of the Triassic (cf. Lucas, 1998).

Based on palynomorph evidence, Ouyang and Norris (1999) placed the PTB at the base of Unit 3 in the uppermost Guodikeng Formation, ~50 m below the base of the Jiucaiyuan Formation. Hou (2004) discovered an overlapping interval of sporomorphs from the middle part of the Guodikeng Formation at SLS and placed the PTB at the base of Bed 51 of the measured lithostratigraphic section 1 (Fig. 1). Furthermore, Pang and Jin (2004) observed a distinct turnover in ostracod assemblages between Bed 54 and 55 in the Guodikeng Formation (Fig. 1), approximately 10 m above the PTB suggested by the palynological analysis of Hou (2004). Foster and Afonin (2005) studied abnormal pollen grains from Russia and China and suggested that the latest Permian mass extinction level lies in the upper lower Guodikeng Formation, between Bed 63 to 65 on s1. Using conchostracan biostratigraphy, Kozur and Weems (2011) proposed the continental extinction event horizon at the middle part of the Guodikeng Formation at SLS, and they proposed that the first appearance datum (FAD) of *Falsisca verchojanica*, ~25 m below the base of the Jiucaiyuan Formation at SLS, correlates to the PTB. Based on paleomagnetic data, Li et al. (2003) placed the PTB between their Bed 41 and 42 at the SLS. Cao et al. (2008) suggested an isotopically defined PTB at the base of Bed 65 (Fig. 1).

In summary, there are distinct faunal and floral turnovers in the middle part of the Guodikeng Formation. As suggested by Kozur and Weems (2011), their relationships with the end-Permian mass extinction need to be studied carefully, but they must not be equated with the PTB.

A recent revision of *Dicynodon* restricted the name to two species from the African Permian, and *Jimusauria*, which was synonymized with *Dicynodon*, is considered a valid taxon distinct from *Dicynodon* (Kammerer et al., 2011). The phylogeny presented by Kammerer et al. (2011:fig. 156 [Figure 156: see original paper]) found *Jimusauria* as a basal form in a clade of Permian and Triassic dicynodonts. Metcalfe et al. (2009) point out the poor record of *Lystrosaurus* in the Guodikeng Formation in opposition to its rich representation in the overlying Jiucaiyuan Formation. Considering the faunal composition of the Permo-Triassic transition in South Africa, they argue that the combined presence of *Lystrosaurus* and *Jimusauria* more likely represents levels of the Late Permian, in which the former taxon is poorly represented (Smith and Botha-Brink, 2014). As a result, the PTB is interpreted as being at the top of the Guodikeng Formation, near the base of the Jiucaiyuan Formation. Recently, Gastaldo et al. (2015) reported a dicynodontoid skull of characteristically Permian aspect more than 10 m above the previous last occurrence of *Dicynodon* and a zircon age of (253.48 ± 0.15) Ma from a layer ~60 m below the current vertebrate-defined boundary from the Karoo Basin. They suggested the PTB should be higher than that recognized by Ward et al. (2005). The work in the Karoo Basin suggested an older occurrence of *Lystrosaurus*, and the PTB could be around the base of the Jiucaiyuan Formation in the Junggar Basin.

In 2000, some bones were collected from the SLS while digging a trench for paleomagnetic study. One specimen (IVPP V 23296) was recovered from a green mudstone close to the yellow sandstone in Bed 40. All bones of this specimen are badly weathered before being buried. Another specimen came from the red mudstone of Bed 70, including several vertebrae and a nearly complete humerus (IVPP V 23295). These materials were prepared and identified as a therocephalian and a chroniosuchian. Therocephalian therapsids were an important component of Middle Permian to Middle Triassic terrestrial faunas (Abdala et al., 2008, 2014; Huttenlocker et al., 2015; Ivakhnenko, 2011). In China, therocephalians are only known from the Triassic, including *Urumchia lii* recovered from the Jiucaiyuan Formation of Xinjiang, which was originally assigned as Late Permian (Li et al., 2008; Fig. 1). The new discoveries thus represent the first report of a Permian therocephalian from China. Chroniosuchians are an enigmatic and recent addition to the group of tetrapods. They were first reported from the Permian and Triassic of Russia (Golubev, 1998; Novikov and Shishkin, 2000; Shishkin et al., 2014), and later from the Permian of China (Li and Cheng, 1999; Young, 1979) and the Triassic of Kyrgyzstan and Germany (Schoch et al., 2010; Witzmann et al., 2008). The new material presented here represents a new Permian record for China and the first from Xinjiang.

Abbreviation. IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences.

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2. Systematic Paleontology

Therapsida Broom, 1905
Therocephalia Broom, 1903
Eutherocephalia Hopson & Barghusen, 1986

Dalongkoua fuae gen. et sp. nov.

Holotype. IVPP V 23296, incomplete left premaxilla with three teeth, incomplete right premaxillae with four teeth, snout and part of the orbital region with the maxilla on both sides featuring functional and replacement canines, isolated vertebrae, left humerus, two phalanges, and some bone fragments (Figs. 2–4).

Etymology. "Dalongkou," the name of the locality; "fu," dedicated to the preparator Ms. Fu Hua-Lin.

Diagnosis. Maxillary ventral margin strongly concave in lateral view; incisors spatulated and rounded; incisors and canines with faint serrations; coronoid process of the dentary with a marked external adductor fossa; triangular reflected lamina of the angular with two smooth concavities.

Description. The skull is strongly deformed as a flat plate and broken into small blocks. The anterior portions of the premaxillae are separated from the rest of the skull (Fig. 2). Both premaxillae are represented as independent elements, with the right being better preserved. It forms a curved plate housing the alveoli for four incisors (Fig. 2C). Posteromedially, it has the process for contacting the vomer. The posterolateral side of the palatal surface curves dorsally, forming the anterior margin of the palatal fenestra for the lower canine (Fig. 2C). There are four preserved teeth, three with the main axis of their bases oriented longitudinally, whereas the second is circular in section. The latter tooth is completely preserved, presenting a spatulated crown, concave lingually, and mesiolingual and distal smooth ridges (Fig. 2E). Remaining teeth are incomplete, lacking any ridge at their bases where the external surface is relatively smooth. Based on preservation, we interpret the probable presence of at least five incisors. Two replacement teeth lie on the lingual side of the first and third functional incisors (Fig. 2C). The crown of the first replacement incisor shows faint serrations on the medial margin. A tiny foramen lies posterior to the first replacing incisor. A long diastema separates the last incisor and the canine. The left premaxilla has three poorly preserved incisors and an extra alveolus for the fourth incisor, without a tooth. There are pits with replacement teeth behind the second and third incisors.

The maxilla is a long bone with a large facial plate. It extends anteriorly and covers the lateral surface of the premaxilla anterior to the canine. Ventrally, there is a concave ventral step. The maxilla is laterally expanded to encapsulate the canine, and the snout seems constricted behind the canine. On the right side, the facial plate is folded medially, and a remarkable longitudinal ridge is present, suggesting a well-exposed maxillary platform. The platform is posteriorly concave in lateral view, as in *Theriognathus microps* (Huttenlocker and Abdala, 2016). The root of the left canine is exposed posteriorly. An erupting replacement canine lies anteromedially to the canine on both sides. The maxillary ventral margin is strongly concave in lateral view. The postcanines are not observed on the skull, but some isolated teeth could be postcanines. Two of them preserve the base of the crown, and it is possible to see strong ridges on two margins without serration. One margin is remarkably concave, the other straight to slightly concave. One preserved tip of a postcanine has faint serrations on both margins of the cusp. The putative preserved postcanines are much smaller than the incisors.

The nasal is long and forms the dorsal surface of the snout. A middle ridge is present on the posterior portion of the nasal. It is sutured with the frontal at the level of the anterior margin of the orbit (Fig. 2A). Laterally, it contacts the maxilla and the prefrontal. The prefrontal, frontal, and postorbital form the dorsal margin of the orbit, whereas the postorbital bar is formed by the postorbital and jugal.

Lower jaw. The symphyseal region and posterior part of the left dentary are preserved, as well as the right reflected lamina of the angular (Fig. 3). The articular symphysis with the right dentary is broken, and the lower margin is incomplete (Fig. 3B). The symphyseal region bears a marked constriction lateral to the lower canine where the upper canine rests. The anterior part of this region bears pits and grooves, whereas the surface that contacts the medial side of the upper canine is smooth. The posteroventral portion of the dentary forms a thickened lower border that supports the angular in a trough on its medial surface (Fig. 3B). The posteroventral corner of the dentary forms an angle of 137°. The coronoid process is well developed, with a dorsal adductor fossa on the lateral surface (Fig. 3A). The posteroventral margin of the dentary, below the bulged ridge that limits the adductor fossa ventrally, forms a descending flange ending in a sharp ridge. Although the posterodorsal corner is incomplete, the preserved portion shows a nearly straight posterodorsal margin. Six teeth are preserved on the symphyseal region. The largest is the canine, and anteromedially there is a replacement canine partially wrapped by it (Fig. 3C). Faint serrations developed on the anterior margin of the replacement canine. There are four lower incisors, including three preserved teeth and one alveolus (Fig. 3C). A tiny tip of an erupting tooth lies immediately anterior to the canines. The last incisor is small and partially preserved, whereas two other incisors medial to the latter are also preserved. One of them is faceted, showing a well-developed ridge laterally (the medial side is not exposed). Very fine serrations, only visible under microscope magnification, are present on the margins of the larger two preserved incisors.

Angular. The right angular is nearly complete. This bone is flat and elongated posteriorly with a triangular-like reflected lamina (Fig. 3D, E). The large reflected lamina bears a deep 'U' -shaped dorsal notch which is posterodorsally directed (Fig. 3D). The lateral surface of the reflected lamina is ornamented by fine, radiating ridges and grooves and is divided into three parts by large grooves directed ventrally and posteriorly (Fig. 3D).

Prearticular. The prearticular lies on the medial side of the angular (Fig. 3E). It is an elongate element forming an anterior rod to contact the splenial. Posteriorly, it is a triangular plate whose posterior process contacts the articular.

Vertebrae. Two partial vertebrae including centra and a left partial neural arch are represented. The complete centrum in one of them, interpreted as a dorsal vertebra, is amphicoelous and deeply hollowed. The second element has an incomplete centrum, and a clear suture between the centrum and right partial neural arch shows lack of synostosis between them (Fig. 4A, B). The transverse process extends dorsolaterally and is angled posterolaterally, with a vertical flange on the ventral side. This is similar to the dorsal vertebra of *Promoschorhynchus platyrhinus* (Huttenlocker et al., 2011).

The isolated arch is possibly of a cervical vertebra, with its zygapophyses bearing more or less horizontal articulating surfaces (Fig. 4C, D). The transverse process is not preserved and should lie well down on the neural arches. The neural spine is robust and inclines anteriorly. This is similar to the cervical of *Olivierosuchus parringtoni* (Botha-Brink and Modesto, 2011).

Sternum. A partial posterior margin of the sternum is preserved (Fig. 4G, H). It is a large plate with a convex ventral surface and concave dorsal surface. There is no posterior notch, and a weak midline ridge is developed on the ventral surface, as in *Promoschorhynchus platyrhinus* (Huttenlocker et al., 2011).

Humerus. The humerus is robust with an expanded proximal end, missing the distal end and deltopectoral crest (Fig. 4I–L). The proximal half is curved dorsally relative to the shaft (Fig. 4J, L). A low ridge lies on the rough posterodorsal side, possibly representing part of the wide posteroventral ridge described by Kemp (1986). The long shaft is broken at the position of the entepicondylar foramen.

Phalanges. Two phalanges are well preserved (Fig. 4E, F). A longitudinal middle groove develops on the ventral surface. They are nearly as wide as long. Nearly quadrangular phalanges are represented in several therocephalians including the Scylacosauridae *Glanosuchus*, the Akidnognathidae *Olivierosuchus*, the Hofmeyriidae *Mirotenthes*, and the Whaitsiidae *Theriognathus* (Attridge, 1956; Boonstra, 1964; Botha-Brink and Modesto, 2011; Fourie and Rubidge, 2007; Abdala, pers. obs).

Chroniosuchia Tatarinov, 1972
Bystrowianidae Vjuschkov, 1957
Genus and species undetermined

Referred specimen. IVPP V 23295, five vertebrae, rib, gastral scales, partial ilium, left femur, and partial fibula (Figs. 5, 6).

Description. Three articulated vertebrae show two intercentra, two isolated pleurocentra fused to the neural arches, and three isolated intercentra. Four larger vertebrae are tentatively identified as dorsals and the smallest as caudal.

The morphology of the vertebrae is very similar to that of *Bystrowiana sinica* or *Bystrowiella schumanni* (Liu et al., 2014; Witzmann et al., 2008) (Fig. 5). The length of the large pleurocentrum is approximately 14 mm, whereas the length in the other two is 12 and 10 mm. The pleurocentra are roughly twice as long anteroposteriorly as the intercentra. The height of the pleurocentra is about 10 mm. All pleurocentra are deeply amphicoelous with a round cross-section, and they are not perforated by the notochord. In lateral view, the anterior and posterior margins of the pleurocentrum are curved but the ventral margin is nearly straight. A small knob (parapophysis) for the capitulum lies on the middle of the pleurocentrum anterior margin (Fig. 5B, E), and a longitudinal faint ridge runs posterior to it. The parapophysis is separated from the diapophysis by an anterodorsally directed incisure.

On the larger pleurocentrum, the ventral surface is slightly convex to smooth (Fig. 5E). On the smallest pleurocentrum, two anteroposteriorly directed low ridges delimit the faintly concave ventral margin (Fig. 5I), as in *Bystrowiella schumanni* (Witzmann et al., 2008).

The intercentra are about as tall as the pleurocentra in lateral view. The articular intercentra show smooth periosteal bone, without haemal arch on the ventral surface. They appear wedge-like in articulation (Fig. 5B, E) but are actually ball-like (Fig. 5K–M). On three free caudal intercentra, the ventral surface consists of slightly concave, smooth periosteal bone and bears the ventrolateral bases of the haemapophyses, as in *Bystrowiella schumanni* (Witzmann et al., 2008). The roughened dorsal surface of the intercentrum is convex and did not articulate with the neural arch, forming part of the base of the neural canal. The largest intercentrum measures 9.7 mm long, while the others range from 8 to 9 mm. The exposed length of them in ventral view is nearly 5 mm.

All neural arches are fused to the pleurocentrum, and the spines are only preserved at their base. The zygapophyses are widely spaced (Fig. 5D, E), and the facets slope medially at a small angle to the horizontal plane in anterior view. There are two pairs of well-developed paraneural canals at the base of the zygapophyses, with the anterior openings of the dorsal pair being larger than those of the lateral pair (Fig. 5A). As in *Bystrowiana permira*, the number and shape of the openings on the two sides could be different (Liu et al., 2014). The neural canal is compressed dorsoventrally. The short transverse process lies on the upper half of the pleurocentrum, bearing small, unfinished diapophyses (Fig. 5A–C).

Rib and gastral scales. A proximal rib fragment and some gastral scales are preserved on a bone plate (Fig. 5J). The gastral scales are thin, some ending in a sharp point.

Ilium. The preserved acetabular area of the right ilium is similar to that of *Dendrysecos helogenes* or *Chroniosaurus* (Clack and Klembara, 2009; Holmes et al., 1998; Schoch and Milner, 2014). The anterior margin is slightly concave (Fig. 6A). There is a distinct crescent supra-acetabular buttress, and anteroventrally a notch on the anterior margin of the acetabulum. The iliac blade is only preserved as a narrow base above the acetabular rim. On the medial side, a strong iliac ridge runs dorsoventrally and divides the medial surface into two portions (Fig. 6B).

Femur. The slender left femur is well-ossified and nearly complete (Fig. 6C–H). The general shape of the bone is the same as that of *Chroniosaurus* (Clack and Klembara, 2009). The length of the bone is 73 mm, and the width is 21 mm for both proximal and distal ends. The distal side deflects ventrally relative to the proximal part, so the bone is curved dorsally. The anterior margin is curved while the posterior margin is relatively straight. Differing from *Chroniosaurus dongusensis*, the articular surface on the proximal side is smoothly convex and dorsoventrally flattened (Fig. 6C). The dorsoventral height of the articular surface is near half its anteroposterior length (Fig. 6G). The proximal extensor surface of the femur bears some striations on the posterior side (Fig. 6C), indicating insertion for the ischiotrochantericus.

On the anteroflexor side, the ventrally directed adductor blade demarcates the anterior side of the deep intertrochanteric fossa (Fig. 6D, E). The broken internal trochanter is separated from the femoral head by a narrow ridge and continues distally as a low crest, the fourth trochanter (Fig. 6D). The anterior surface of the adductor blade is rugose with deep muscle scars. From the distal end of the fourth trochanter, the adductor crest follows a strongly diagonal course posteroventrally to a point distal to the middle of the shaft (Fig. 6E, F). A low ridge continues distally on the posterior side of the shaft, ending on the distal posterior corner. This ridge does not seem to be for muscle attachment. In other groups such as captorhinomorphs, seymouriamorphs, and temnospondyls, the adductor crest generally runs toward the popliteal area (Fox and Bowman, 1966; Klembara and Bartik, 2000; Pawley, 2007).

The popliteal area is pitted and concave on the flexor side (Fig. 6E). The fibular (posterior) condyle projects more distally than the tibial (anterior) condyle. Proximal to the fibular condyle is a narrow but deep fibular fossa. In extensor view, a deeply incised intercondylar fossa is oriented posteroventrally toward the midline of the fibular condyle (Fig. 6H).

Fibula. The proximal end of the left fibula is preserved (Fig. 6I–K). The head is convex to fit the concave articular surface of the femur. Small striae distribute around the proximal articular surface (Fig. 6I, K), indicating the presence of cartilage or perhaps ligamentous connective tissue. The extensor surface is incised by a cnemial trough, which is bordered anteriorly by the prominent cnemial crest (Fig. 6J). Another crest is on the posterior surface of the bone. A striate area on the medial side of this ridge, distal to the proximal articular surface, provided attachment for muscles.

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3. Discussion

The new therapsid specimen (IVPP V 23296) can be diagnosed as a therocephalian based on the presence of a palatal fenestra for the lower caniniform confluent with the choana and the posteroventral portion of the dentary forming a thickened lower border that extends below the angular bone and supports the latter in a trough on its medial surface. It has four lower incisors and can thus be diagnosed as a eutherocephalian (Huttenlocker, 2009). In addition, the shape of the reflected lamina, lacking an anterodorsal rounded portion in front of the notch that makes this structure circular in basal therocephalians, also indicates that the new species is a member of Eutherocephalia.

Dalongkoua fuae shows evidence of faint serrations on the margin of a replacement incisor and canine and on the tip of a postcanine. These findings are contrary to the assumed absence of serrations in the dentition of Eutherocephalia (e.g., van den Heever, 1994; Abdala et al., 2008; Huttenlocker, 2009; Huttenlocker et al., 2015, for incisors; and Huttenlocker and Sidor, 2012 for anterior dentition). The serrations in the teeth of *Dalongkoua fuae* are exceedingly faint, and it is clear that they would disappear with minimal wear, as demonstrated by the smoothly ridged crown of the preserved elements.

This specimen represents a new species based on the following characters: maxillary ventral margin strongly concave in lateral view; incisors spatulated and rounded; incisors and canines with faint serrations; coronoid process of the dentary with a marked adductor fossa; triangular reflected lamina with two concavities.

The maxillary ventral margin is convex or nearly straight in most therocephalians, but it is slightly concave in *Moschowhaitsia* (Ivakhnenko, 2011) and strongly concave in *Euchambersia* and *Theriognathus* (Broom, 1931; Huttenlocker and Abdala, 2016). Recent studies (e.g., Huttenlocker et al., 2015) indicate that spatulated incisors are restricted to a group of akidnognathids. In *Dalongkoua fuae*, the completely preserved second left incisor is spatulated, whereas remaining left incisors, although incomplete, show the crown sufficiently preserved to suggest the presence of rounded (non-spatulated) incisors. The adductor fossa is developed in the dorsolateral portion of the coronoid process, above the trough for the postdentary bones. This fossa differs from the one described on the lateral surface of the dentary in the bauriids *Microgomphodon oligocynus* (Abdala et al., 2014) and in the Russian *Notogomphodon danilovi* (Abdala, pers. obs.), as in these taxa there is no connection between the fossa and the trough for the postdentary bones. The incomplete left dentary of *Urumchia lii* also seems to have an adductor fossa, although less developed than in *D. fuae* (Fig. 7). A triangular reflected lamina is also present in the holotype of *Tetracynodon darti*, but the lamina shows a more complex lateral surface with several ridges and valleys. In the lamina of *D. fuae*, there is a posterior deep canal and a dorsoventrally oriented shallow and wide depression.

Urumchia lii is the only known therocephalian from Xinjiang, documented in the Jiucaiyuan Formation (Sun, 1991; Young, 1952). Diagnostic characters in this species are concentrated in the palate and postcanine morphology (Li et al., 2008; Sun, 1991). Unfortunately, both palate and postcanines are incompletely preserved in *Dalongkoua fuae*, with postcanines only represented by isolated fragments including two crown bases and one tip. However, there are a set of characters shared between these two species that may indicate relationships (Fig. 7): the medial margin of the frontal bones directed dorsally in *Dalongkoua fuae* indicates the presence of a central ridge in the posterior internasal and interfrontal sutures; the presence of a depressed facial area of the maxilla immediately above the dental series, also described recently in *Ichibengops* of East Africa by Huttenlocker et al. (2015); an apparent development of an adductor fossa, though clearly smaller, in the left dentary of *Urumchia lii*; and the presence of spatulated incisors. The putative relationship between these two taxa should be considered a working hypothesis, whose validation will require finding additional material.

The new specimen of Reptiliomorpha (IVPP V 23295) is referred to Chroniosuchia based on the characteristic ball-and-socket joint between pleurocentra and intercentra (Ivakhnenko and Tverdokhlebova, 1980). It can be further assigned to Bystrowianidae based on paired paraneural canals on the vertebrae (Novikov et al., 2000). The vertebrae show morphology similar to other bystrowianids, and the intercentrum is similar to that figured for *Bystrowiella schumanni* (Novikov and Shishkin, 2000; Witzmann et al., 2008). The morphology of the ilium, femur, and fibula is consistent with this taxonomic identity (Clack and Klembara, 2009; Ivachnenko and Tverdochlebova, 1980). Unfortunately, no dermal scute was discovered, preventing further identification.

Chroniosuchian specimens in China were first reported from the Upper Permian Jiyuan fauna (Young, 1979) and then from the Middle Permian Dashankou fauna (Li and Cheng, 1999). The new findings reported here represent the latest occurrence of chroniosuchians in China. This group is known from the Middle/Upper Triassic Madygen Formation of Kyrgyzstan (Schoch et al., 2010), indicating their continued presence in Laurasia after the Permian extinction.

These new findings allow us to recognize that tetrapod diversity near the Permo-Triassic boundary in China, particularly in Xinjiang, was higher than previously recognized. Only dicynodonts were previously reported from the Guodikeng Formation, including *Lystrosaurus*, *Jimsaria*, *Turfanodon*, and possibly *Diictodon* (Li et al., 2008). Both chroniosuchians and therocephalians crossed the P-T boundary; therocephalians became extinct in the Middle Triassic (Abdala et al., 2014), whereas the youngest record of chroniosuchians is in the Middle or Late Triassic (Schoch et al., 2010).

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The Morphology of Chiappeavis magnapremaxillo (Pengornithidae: Enantiornithes) and a Comparison of Aerodynamic Function in Early Cretaceous Avian Tail Fans

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Abstract: Chiappeavis is the first enantiornithine discovered to preserve a fan-shaped tail, demonstrating that the rectricial bulb structure was already developed in relatively basal members of this clade. This study provides a detailed description of the skeletal morphology of the holotype of Chiappeavis magnapremaxillo. The palatal morphology of Chiappeavis is similar to Archaeopteryx but differs from the Late Cretaceous enantiornithine Gobipteryx. Even if rectricial bulbs were present, the pygostyle morphology of pengornithids suggests this structure was poorly developed. We estimated the lift generated by the fan-shaped tail feathers in Chiappeavis and compared it with other Early Cretaceous birds. The results show that the aerodynamic lift generated by the tail fan of Chiappeavis was less than that of sympatric ornithuromorphs, which may explain the general absence of aerodynamically functional tail feather morphologies in Enantiornithes.

Key words: Mesozoic, Jehol Biota, Aves, rectrix

Chinese Library Classification: Q 915.865 **Document code:** A **Article ID:** 1000−3118(2017)01−0041−18

Elephas cf. E. planifrons (Elephantidae, Mammalia) from Upper Siwalik Subgroup of Samba district, Jammu and Kashmir, India

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Abstract: A left M3 fossil of Elephas cf. E. planifrons is reported and described herein. The specimen was recovered from a mudstone horizon underlying a volcanic ash bed exposed near Nangal village, which represents an extension of the geochronologically dated (2.48 Ma) volcanic ash beds exposed at Barakhetar in the Nagrota Formation of the Upper Siwalik Subgroup, Samba district, Jammu and Kashmir, India. Based on crown morphological parameters (plate numbers, molar length and width, crown length, width and height, enamel thickness, dentine thickness, length and width of plates, lamellar frequency, hypsodonty index, and cement thickness), the specimen has been identified and tentatively referred to Elephas cf. E. planifrons (LM3). The recovery of this specimen is of great significance as it extends its upper limit of the range zone from 3.6–2.6 Ma to 3.6–2.48 Ma.

Key words: Jammu, India; Nagrota Formation, Upper Siwalik Subgroup; Elephas

Chinese Library Classification: Q915.878 **Document code:** A **Article ID:** 1000—3118(2017)01—0059-12

1 History of Research

Numerous researchers have conducted studies on the origin, evolution, paleoecology, taxonomy, distribution, classification, anatomy, ecology, behavior, phylogenetic analysis, and fossil lineages of elephants from various parts of the world. In the Indian subcontinent, the genus Elephas is represented by four species: E. planifrons, E. hysudricus, E. namadicus, and E. maximus. Among these, the first three are completely extinct, while E. maximus survives to the present day. Detailed studies on the geology, paleontology, phylogeny, and age of elephantoid faunas from the Siwaliks of India, Pakistan, and Burma have been carried out by many scholars.

In the Siwalik Province of Jammu, Jammu & Kashmir State, India, no detailed work on Elephantidae fauna was conducted except by a few researchers. Wadia (1925) first recovered a tusk (about 3.43 m) of Stegodon ganesa from near Jagti village in the Nagrota Formation of the Upper Siwalik Subgroup of Jammu. Ganjoo (1985) recovered dental remains of Stegolophodon sp., Stegodon insignis, Stegodon ganesa, and Elephas sp. from Pleistocene deposits of the Khanpur Formation (Pinjor Formation) and Tawi Formation (Boulder Formation) of the Upper Siwalik Subgroup of the Jammu region. Nanda (1994) commented on certain faunal discrepancies in Upper Siwalik mammalian faunas from Chandigarh and Jammu areas.

Many proboscidean specimens were collected by the Geological Survey of India from the Siwaliks of Jammu and other parts of India, published in Catalogue series no. 5 in 2002. Basu (2004) discussed the diversity and habitats of Siwalik mammals of the Jammu Sub-Himalaya. Recently, Kundal and Kundal (2011) recovered an upper right third molar (M3) of Elephas maximus indicus from post-Siwalik deposits of Jammu Province near Kharian village, Jammu and Kashmir, India. Several workers have conducted detailed studies on fossils recovered from mudstone horizons associated with geochronologically dated volcanic ash in the Upper Siwalik of Jammu and its depositional environment.

The present study examines the systematics and biochronology of Elephas cf. E. planifrons recovered from Nangal village in the Nagrota Formation, Upper Siwalik Subgroup, Samba district, Jammu and Kashmir. The study area is shown in Fig. 1A.

Geological, paleontological, and paleomagnetic studies of type sections of Siwalik in the Indian subcontinent have revealed that boundaries are time-transgressive between most formations of the Siwalik Group and that temporal mammal ranges are not usually fixed within the time limits of these formations. A generalized stratigraphic framework of Siwalik in the Indian Subcontinent is given in Fig. 1D.

The local classifications of the Upper Siwalik Subgroup of Jammu–Samba district are based on paleontology, magnetostratigraphy, and radiometric dates of ash beds. A volcanic ash bed occurring near Barakhetar and Nagrota villages has been geochronologically dated at 2.48 Ma. These ash beds straddle the Gauss-Matuyama boundary in the Siwalik of Jammu-Samba district, Jammu and Kashmir, India. The specimen described in this study was discovered from the mudstone horizon immediately underlying the geochronologically dated 2.48 Ma volcanic ash bed at Nangal village and is preserved in the vertebrate paleontology laboratory, Geology Department of Jammu University, under catalog number JU/GD/VPL/9001.

2 Systematic Paleontology

Class Mammalia Illiger, 1811
Order Proboscidea Gray, 1821
Family Elephantidae Gray, 1821
Genus Elephas Linnaeus, 1735
Elephas cf. E. planifrons Falconer & Cautley, 1845 (Fig. 2A–C)

Referred material: JU/GD/VPL/9001, left M3 with broken roots and broken anterior two plates.

Locality: River cutting section 15 km northwest of Samba city near Nangal village, J&K, India.

Stratigraphic horizon: Mudstone horizon underlying volcanic ash bed in Nagrota Formation (Ranga Rao et al., 1988)/Uttarbaini Formation (Gupta and Verma, 1988)/Pinjor Formation (Pilgrim, 1934).

Age: Late Pliocene–Early Pleistocene.

Measurements (in mm): Number of plates, 9 (2½ broken out + 6½ preserved); length of molar, 140+50 (broken anterior two plates); width of molar, 82; length/width ratio, 1.70; number of plates preserved, 6½ (4½ worn + 2 unworn); average length of plates (occlusal), 72; average width of plates (occlusal), 17.16; lamellar frequency (lf), 6; average enamel thickness (et) of worn plates, 3.5; average cement thickness (ct) between plates, 10; average dentine thickness (dt) of worn plates, 4.64; crown length, 140; crown width, 92; maximum crown height, 80; hypsodont index (H/W$×$100), 87.

Description: JU/GD/VPL/9001 has well-preserved plates with broken roots. The anterior two and a half plates of the molar are broken out. The molar tapers at the posterior end (ovate); molar curvature is straight; inclination of plates to occlusal surface is weak; molar roots are strong and broken; enamel height above the cement is high; enamel figures are parallel-sided with median loop, lateral sides of enamel are rounded and turn slightly anteriorly; the enamel is symmetrical in line with the long axis of the molar; medial edges of enamel of two middle plates are in contact, undulating folded; amplitudes of enamel folding in few plates are high to low; and spaces between enamel folds in few plates are tight to loose. The plates are well compacted with cement and are widely spaced. The plates are slightly slanting toward the posterior side. The specimen has four and a half worn plates and two unworn plates. The width of the molar increased from posterior to center and then decreased slightly toward the anterior side. Except for the four and a half worn plates, three plates have developed strong expansion of loops at the middle which are in connection with adjacent ones. The enamel layer is quite simple and thick.

3 Comparative Study of Specimen JU/GD/VPL/9001 with Allied Species of Elephas

Using dental morphological characters (number of plates, length of molar, height and width of crown, lamellar frequency, enamel thickness, and hypsodonty index), specimen JU/GD/VPL/9001 was compared with allied species of Elephas (E. namadicus, E. hysudricus, E. hysudrindicus, E. maximus, E. naumani, and E. planifrons) described previously. Detailed parameters are given in Table 1.

Elephas namadicus differs from JU/GD/VPL/9001 in number of plates (12–16), length of molar (223–317), width of crown (61–101), height of crown (137–218), enamel thickness (1.8–3.0), and hypsodonty index (135.6–298). Parallel lophs and absence of median expansion are characteristic of E. namadicus, differentiating it from JU/GD/VPL/9001.

Elephas hysudricus differs from JU/GD/VPL/9001 in number of plates (12–

15), length of molar (235-302), width of molar (93-107), height of crown (108-137), lamellar frequency (3.9-6.5), and hypsodonty index (112.5-147.2). Lack of median expansion and strong plication of lophs characterize E. hysudricus, differentiating it from JU/GD/VPL/9001.

Elephas hysudrindicus differs from JU/GD/VPL/9001 in number of plates (18-21), molar length (293.2-316.6), crown width (72.3-82.5), crown height (128.4-149.3), lamellar frequency (6.5), enamel thickness (2.6-2.7), and hypsodonty index (177.5-182.3). E. hysudrindicus is the most advanced member of the Palaeoloxodon namadicus group.

Elephas maximus differs from JU/GD/VPL/9001 in number of plates (22-27), molar length (244-282), crown width (80-98), crown height (187-214), lamellar frequency (5-9), enamel thickness (2.5-3.0), and hypsodonty index (150-250). JU/GD/VPL/9001 has anterior and posterior columns along the median line (lenticular) which are absent in E. maximus. E. maximus has narrow folding enamel structure, whereas JU/GD/VPL/9001 has thick folded enamel structures.

The molar characters of **Elephas naumani** show ranges of hypsodonty index (230-320), enamel thickness (2.0-3.2), lamellar frequency (6-7), crown height (195-251), crown width (81-95), molar length (211-278), and number of plates (17-19), whereas JU/GD/VPL/9001 has values of 87, 3.5, 6, 80, 92, 190, and 9 respectively, which differ from E. naumani.

Specimen JU/GD/VPL/9001 is broad and brachydont with expanded strong anterior and posterior columns along the median line (lenticular), which are characteristic features of Elephas planifrons. The average enamel thickness of the molar is 3.5 mm, which precisely equals that of E. planifrons at the Indian Museum, Calcutta. The lamellar frequency of E. planifrons given by different authors is: Osborn (1942): up to 6; Hooijer (1955): up to 5; Maglio (1973): 2.6-5.5.

The lamellar frequency of the studied molar is 6. This specimen was also compared with Elephas planifrons collected during Gupta's (1981-1982) field session from the Marikhui Member of the Uttarbaini Formation, published in GSI Catalogue No. 5 (pictorial catalogue of Siwalik vertebrate fossils from NW Himalaya, 2002, pp.130, figure 1). JU/GD/VPL/9001 was compared with the most primitive specimen (M3) of E. planifrons (number 19965, American Museum) collected by Barnum Brown from the Upper Pliocene Pinjor horizon of the Siwalik near Siswan, India. The specimen resembles JU/GD/VPL/9001 in outline as well as dental characters such as plate numbers, enamel thickness, and molar length. JU/GD/VPL/9001 was also compared with specimen No. WIF/A 423 (Nanda et al., 1991), which favors E. planifrons.

Based on comparative studies of parameters such as plate number, lamellar frequency, hypsodonty index, straight molar curvature, greatest crown height at posterior end, molar shape tapered at posterior end (ovate), thick cement on sides and valleys, highly crenulated enamel, strong and broken molar roots, high enamel height above cement, parallel-sided enamel with median loop expansion, rounded lateral sides of enamel symmetrical with the long axis of the molar, and discussion, JU/GD/VPL/9001 shows close affinity to Elephas planifrons and is tentatively referred to as Elephas cf. E. planifrons.

4 Biozones/Faunal Interval Zones

Various biostratigraphic interval zones of the Siwalik Group of Pakistan have been recognized based on fauna, lithology, and magnetostratigraphy by numerous workers. In India, Verma (1988) recognized two biozones based on his work in the Markanda valley of Himachal Pradesh: the Equus sivalensis-Elephas hysudricus (EE) Biozone and the Stegodon insignis-Hipparion theoboldi-Hexaprotodon sivalensis (SHH) Biozone.

The SHH biozone evidently corresponds to the Hexaprotodon sivalensis Interval Zone of the Potwar Plateau (Pakistan) ranging from 5.3-2.9 Ma B.P., while the EE biozone corresponds to the Elephas planifrons Interval Zone ranging from 2.9-1.5 Ma B.P. and the Pinjor Faunal Zone of the type area. The SHH biozone is restricted to the Saketi Formation and exhibits high frequency of aquatic forms in Himachal Pradesh, while the EE biozone is characterized by the presence of Equus, absence of Hipparion, presence of some aquatic forms, and terminates at the end of the Pinjor Formation.

The range of the Elephas planifrons Interval Zone was modified by Hussain et al. (1992) from 2.9-1.5 Ma to 3.4-2.7 Ma, and they also recognized a fifth zone known as the Elephas hysudricus Range Zone (2.7-? Ma). Later, Nanda (1997) proposed the upper limit of the E. hysudricus Range Zone up to 0.6 Ma based on fossils available in the Indian Siwalik. Agarwal et al. (1993) modified the lower limit of the E. planifrons Interval Zone and extended it up to 3.6 Ma based on dated E. planifrons. Nanda (1997) recognized two biostratigraphic interval zones of the Upper Siwalik Subgroup with their lower and upper limits as: 1) E. hysudricus Range Zone (containing most taxa of Pinjor fauna), 2.6-0.6 Ma; 2) E. planifrons Interval Zone (containing most taxa of Tatrot fauna), 3.6-2.6 Ma.

Based on fauna in the Pabbi Hills of Upper Siwalik of Pakistan, Dennell et al. (2006) divided the Elephas hysudricus Range Zone of Hussain et al. (1992) into the Elephas hysudricus-Crocuta-Ursus-Panthera faunal zone (1.7-0.9 Ma) and the Elephas hysudricus-Sivatherium faunal zone (2.7-1.7 Ma).

As Elephas cf. E. planifrons in the present study was recovered from a mudstone horizon underlying geochronologically dated (2.48 Ma) volcanic ash beds, the upper limit of the range zone of Elephas planifrons may be extended from 2.6 Ma (Nanda, 1997) to 2.48 Ma (proposed). The biostratigraphic interval and range zones of elephant fauna by various authors and the proposed range zone of Elephas planifrons are given in Fig. 3.

5 Conclusion

The recovery of the Elephas cf. E. planifrons specimen from mudstone underlying geochronologically dated (2.48 Ma) volcanic ash beds indicates that the age of the specimen is not younger than the volcanic ash beds exposed in the Upper Siwalik Subgroup of Samba districts. The upper limit of the Elephas cf. E. planifrons Interval Zone is also extended from 2.6 Ma (Nanda, 1997) to 2.48 Ma (proposed) in the present study, as the specimen was recovered from underlying geochronologically dated ash beds.

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Small Mammal Taphonomy of Three Miocene Localities from Damiao, Nei Mongol, China

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Abstract: Predation is the most common cause of death in small mammals. It also causes the greatest modification to their remains. Other postmortem processes, such as weathering, trampling, and transportation all modify bones and contribute to the formation of assemblages. Here we examined three Miocene localities from Damiao, Siziwang Banner, Nei Mongol, China with different fluvial subenvironments. The ages span from early Miocene to early late Miocene (ca. 21–11.6 Ma). We describe the sedimentary context and taphonomic features of the small mammal assemblages, and identify the responsible agents for the fossil accumulations. Our study reveals predation as the primary means of accumulation for all three localities. However, there is overprinting of other means of accumulation such as fluvial transportation and possibly signs of trampling at the two younger localities. Results indicate possibly different predators for all localities; owls for the oldest one, and diurnal birds of prey or mammalian agents for the younger two. We also show that systematic excavation for small mammals can be done, and in this way it may be possible to reduce some of the damage collecting always produces.

Key words: Nei Mongol, Neogene, micromammals, digestion, predation, fluvial deposits

1 Introduction

Taphonomy, the study of preservational processes of organic remains, connects paleontology with biology and geology. Taphonomic processes begin at the moment of an organism' s death and continue until its recovery. These processes are sources of bias in the fossil record since they may remove some biological information but simultaneously produce information about past environments and fossilization. Taphonomic processes affecting fossil assemblages include predation, scavenging, transport, and weathering, and are manifested through different taphonomic features such as breakage, intrusive corrosion, rounding, polishing, cracks, staining, scrapes, weathering, root marks, pressure damage, and enamel pitting.

Due to their limited life range, small mammals are more sensitive to local-scale environmental changes than large mammals and therefore serve as useful indicators of past ecologies. One major cause of death in small mammals is predation, which also causes the greatest modification of their remains. Among different predators, mammals modify prey bones most extensively due to their shearing teeth breaking up prey before ingestion, making prey of mammalian predators less likely to become fossilized. Owls produce the least bone breakage, while diurnal birds of prey are intermediate bone breakers.

Shortly after a small mammal's death, secondary modifications of remains occur. These include decay and scavenging, which are not easily recognized in fossil samples, as decay leaves little modification and scavenging marks are not readily distinguished from predation modifications. Trampling is another source of modification beginning soon after death, resulting in dispersal, breakage, burial, or total destruction of remains. Weathering occurs when bones lie exposed without protection. However, small mammal remains are more likely to be trampled and broken or blown away than to remain exposed to weathering.

Transport of remains often results in bone breakage. Although pellets and scat structures may protect bones temporarily, when pellets disintegrate the skeletal material becomes exposed to weathering and dispersal. Small mammal remains are easily transported by flowing water.

This study examines small mammal taphonomy from three Miocene mammal localities in Damiao, Siziwang Banner, Nei Mongol. The site was identified in 2006 and excavated during three field seasons since, yielding over 30 fossil localities with three main fossil horizons magnetostratigraphically dated from early Miocene to earliest late Miocene. Although numerous, Neogene fossil mammal localities in Central Nei Mongol are scattered, lacking continuous vertical exposures, with few representatives of early Miocene mammals. Damiao constitutes one of the most continuous sequences in Nei Mongol with early, middle, and late Miocene fossil faunas in stratigraphic superposition. Damiao also hosts the latest occurrence of the humidity-favoring pliopithecid primate in Central Asia, in the late middle Miocene locality of DM01. Out of approximately 30 localities, three rich localities of different ages and sedimentology were chosen for closer inspection. While stratigraphy and some mammalian groups have been studied in detail, this is the first attempt to study small mammal taphonomy from the area.

This paper reports results of a taphonomic study of small mammals from three Damiao localities. The aims are to characterize the sedimentary context and taphonomic features of small mammal burials and identify the agent(s) responsible for fossil accumulations. This study also demonstrates that systematic excavation for small mammals can be done, potentially reducing some damage that always results from collecting.

2 Sedimentological and Paleontological Framework

The study area is located in central Nei Mongol, approximately 100 km north of Hohhot, near Damiao village in Siziwang Banner. The area is characterized by undulating topography ranging between 1250 m and 1350 m a.s.l. Damiao fossil localities are divided into eastern and western sides separated by the Wulanhua-Damiao motorway. All localities are only a few kilometers apart. The sedimentary sequence is characterized as a fluvial environment where fine-grained deposits represent well-drained floodplains.

DM16 is stratigraphically the lowest fossil site, paleomagnetically dated at 20-21 Ma. It occurs within a mudstone interval comprising the basal 16 m of the sequence, extending laterally over hundreds of meters. The sediment succession comprises rather monotonous and homogeneous red-brown claystone-fine siltstones with massive weathering appearance. Thin flat lamination and graded beds 1-4 cm thick occur in the upper portion. Slickensides and spherical mm-size manganese and calcium carbonate nodules occur throughout and are locally abundant. Some fine-scale alternation of red and green coloration appears in the lower portion.

The productive bed is approximately 1.2 m thick, with one approximately 9 cm thick fossil-rich horizon in the middle, associated with root traces and few desiccation cracks. The bonebed has yielded relatively well-preserved but fragmented vertebrate remains, mainly small mammal skeletal elements; dipodid and eomyid rodents are common, as are ochotonid lagomorphs with few insectivores. Large mammals are scarcer, represented by artiodactyls, rhinos, and a mustelid. Small mammals at this level are dominated by Oligocene genera, though by more derived species. In addition to vertebrate remains, the locality contains dense accumulations of fossil eggshell fragments, a few gastropod shell casts, and several bone-bearing pellets in the richest horizon.

Laterally extensive, massive, and finely laminated mudstones with various features indicating paleosol development characterize floodplain deposits. Sporadic desiccation cracks indicate that mudstones were probably deposited as ephemeral ponds/lakes at highest flood stage, with cracks developing during desiccation.

DM01, the richest and only primate-bearing locality, is associated with latest middle Miocene Tunggur fauna with an age estimate of approximately 12.1 Ma. The DM01 section is dominated by two clast-supported conglomerate beds stretching laterally over 60 meters. Well-sorted and densely packed clasts consist principally of spherical, well-rounded intraformational reworked calcium carbonate nodules up to 8 cm in diameter. The lower unit is up to 60 cm thick, composed of few-cm-thick beds often showing inverse grading from coarse sand to granules. The upper conglomerate shows variable bed thickness from 1 m to 1.6 m, consisting mainly of horizontally stratified pebble-granule conglomerate with subordinate layers of coarse sand and granules. Sand-dominated parts show trough and tabular cross-bedding. Lower boundaries are erosive with discrete local scours. These reworked pedogenic conglomerates show distinct rust and black color; concretions have black manganese staining, and manganese and goethite highlight bedding planes.

Sediments surrounding the conglomerates are mainly well-sorted reddish yellow (7.5 YR 6/6) to light brown (7.5 YR 6/4) fine sands and silts. Primary sedimentary structures, when present, include thin parallel lamination and cross-lamination. These sediments are often calcareous, but calcareous nodules are scarce and continuous concretion horizons are absent.

The nodule conglomerates are interpreted as resulting from avulsive emplacement of channels reworking and concentrating underlying calcic paleosols. Abundant goethite and manganese indicate impeded drainage and more humid conditions, although reworked pedogenic nodules indicate seasonally dry climate.

Fossils occur in sand-granule interbeds throughout the upper nodule conglomerate. In addition to the pliopithecid, more than 30 species and over one thousand skeletal elements were found. While large mammals are few and fragmentary, small mammals are abundant with well-preserved remains. Contrary to DM16 fauna, DM01 fauna comprises taxa from extant families lacking any Paleogene members.

DM02 locality represents early late Miocene with an estimated age of approximately 11.6 Ma. The DM02 section is predominantly fine-grained. Lithologies are mixtures of reddish brown (5 YR 4/4) to yellowish red (5 YR 4/6) silt and clay with variable calcium carbonate accumulation as distinct nodules and indurated layers. Most units exhibit no internal bedding structures. DM02 fossils occur in a 0.2–0.4 m thick lens-shaped sandstone body at the lowest portion of the local section. The fossiliferous unit erosionally overlies underlying mudstone and passes upward with a sharp conformable contact to overlying coarse siltstone. The sand lens is massive or displays few-centimeter-thick horizontal interbeds of silt to poorly sorted coarse-very coarse sand. Constituent grains are mostly angular quartz embedded in a silt matrix.

The fine-grained deposits encompassing the DM02 section are interpreted as pedogenically modified overbank deposits. Red coloration, carbonate nodules, pedogenic slickensides, and overall massive appearance suggest pedogenesis. The fossil find unit, with its erosional base and heterogeneous lithology, indicates sites of episodic coarse sediment injection on the floodplain surface. Fossil fauna at DM02 contains abundant and diverse rodents and lagomorphs, together with few large mammal specimens. In general, the fauna in DM02 is similar to DM01.

3 Material and Methods

Materials: Fossil specimens were collected from Damiao during three field seasons between 2007–2009. Material from DM01 consists of 185 fossil specimens, both teeth and postcrania. From DM02, 158 fossil specimens were analyzed, mainly teeth and a few jaw fragments. No postcranial material from DM02 was available for study. Fossil material from DM16 consists of 360 specimens from the grid, of which 255 specimens were taphonomically analyzed. Half of the analyzed specimens have full grid reference (coordinate and depth information). Most DM16 material is postcrania with few teeth and jaws.

Methods: At the pliopithecid-bearing locality DM01 and adjacent DM02, a restricted area was opened and sediments screened. Systematic sampling was conducted at locality DM16, where a grid with 27 squares of 1 m × 1 m was established and collected fossils were given specific grid references, with precise horizontal and vertical locations recorded for most specimens. Dry-sieving of excavated material was done at the site using coarse screens.

Investigated specimens from Damiao showed a wide variety of taphonomic modifications. To detect, measure, and score surface alterations, each element was carefully examined under a stereoscopic light microscope. Taphonomic features analyzed were breakage, intrusive corrosion, rounding, polishing, cracks, staining, scrapes, weathering, pressure damage, root marks, and surface (enamel) pitting.

All taphonomic features were scored on an ordinal scale of four modification stages developed for this study based on Andrews' (1990) work on small mammal taphonomy. Scorings depended on the degree of taphonomic modification: 0 = no modification; 1 = light modification; 2 = moderate modification; and 3 = strong modification. Additionally, to detect the microfossil accumulating agent, the ratio of major distal elements to proximal elements was calculated, as well as the ratio of cranial elements to postcranial elements following Andrews (1990).

Voorhies' Groups are a common method to examine skeletal elements according to their potential for fluvial transport. Degree of transport reflects different settling velocities of bone types. Voorhies' Groups have been recalibrated for micromammal studies, and the Generalized Sequence of Korth' s settling groups was applied to the present data.

Detailed sedimentological logging was done using conventional methods for lithofacies analysis. Vertical heights were measured with Jacob' s staff and Abney level, grain size was determined in the field and for selected fine-grained samples in the laboratory using a Malvern Mastersizer 2000, and sediment colors were defined as Munsell™ codes on fresh samples.

4 Results and Interpretation of Taphonomic Features

Proportions of taphonomic features on specimens at each locality are shown in Fig. 3, for bones and dental materials separately. The most prominent feature is the lack of skulls at all localities as well as the lack of postcranial material at DM02 (Table 2). The ratio of major distal limb elements to proximal elements for DM16 is higher than for DM01 (Fig. 5). The ratio of cranial element to postcranial is higher in DM01 than in DM16 (Fig. 6). Both teeth and bones from DM16 showed high incidence of breakage, intrusive corrosion, rounding, polishing, cracking, enamel pitting and staining (Fig. 3), the taphonomic features that indicate predation (e.g., Andrews, 1990; Andrews and Evans, 1983; Fernández-Jalvo, 1995; Reed and Denys, 2011). The straight and spiral fracture types in broken bone specimens provide further evidence for predation as a means of accumulation (Shipman et al., 1981). Results from DM16 were also inspected with respect to the richest fossil layer. This level showed even more specimens with features associated with digestion (breakage, intrusive corrosion, and scrapes) than layers below or above it. Cracking was detected only from specimens from the richest fossil horizon and below it, and was more common in teeth than bones. Nevertheless, this feature was less common than other predation features and could result from taphonomic agents other than predation, for example from weathering during subaerial exposure of the remains.

Weathering, in turn, is more common on bones than teeth but is altogether not a very common feature and can be separated from digestion by some unique features on the surface of the specimens. Weathering in small mammal remains can be identified from splitting that occurs along the collagen fiber orientation, flaking or exfoliation of the outer layer of bone (Fig. 4C) as well as chipping and splitting of teeth (Andrews, 1990). Of all the localities, discoloured dental specimens were found only from DM16.

The ratios of anatomical elements further suggest that predation contributed to the accumulation of the small mammals in DM16. The ratio of distal (tibia + radius) to proximal (femur + humerus) limb elements is low (Fig. 5), indicating predator assemblage, as does the ratio of postcranial to cranial elements (Fig. 6). The absence of more distal parts of limbs is a common feature in predator assemblages, as is the deviation from the average skeletal proportions of postcranial to cranial elements, which indicates preferential destruction of a skeletal group—or selection against it (Andrews, 1990)—in this case destruction of, or selection against, cranial elements. The lack of skulls is one main feature of trampled assemblages, although in small mammals evidence of natural trampling is nearly non-existent due to the fragile nature of their bones (Andrews, 1990). Also the low number of isolated teeth at this locality suggests a source of modification of material other than trampling, such as fluvial transportation.

For DM16, bones of all of Korth's settling groups are present (Table 3). However, group I (most easily affected by fluvial transport) is rather poorly represented whilst there is a high representation of least easily transported group III elements (lag deposit). The loss of group I likely results from winnowing of lighter elements during surface runoff. Less than half of DM16 fossil bones are weathered and when they are, they mostly represent stage 1. This together with even less weathered dental material means that DM16 small mammal remains likely experienced only a short duration of exposure to weathering agents before burial. Taphonomic processes after burial in DM16 are represented by light pressure damage that is present in most specimens, and some rare light root marks. Intrusive corrosion found on specimens is likely digestive in origin as fossils are only partially affected by corrosion (Andrews, 1990).

Both teeth and bone specimens from DM01 showed high incidence of modifications related to predation (breakage, intrusive corrosion, rounding, polishing, enamel pitting and staining; e.g., Andrews, 1990; Andrews and Evans, 1983; Fernández-Jalvo, 1995; Reed and Denys, 2011). Also a high proportion of broken bones together with straight and spiral fracture types indicate predation as a means of accumulation (Shipman et al., 1981). Bones from DM01 show highest incidence of stage 3 corrosion and dental material is mostly of stage 2. High incidence and high level of corrosion both on bone and dental material in DM01 suggest predation. However, the bimodal breakage distribution at DM01 could indicate two different agents forcing the accumulation. Primary means of accumulation would be predation with overprinting of other processes like transportation or trampling. It is said that much of the breakage of bone assemblages is due to transport before or after burial and transportation of small mammal bones produces high levels of breakage (Andrews, 1990). Trampling on the other hand is not well documented in small mammals since their bones are easily destroyed (Andrews, 1990). However, the lack of skulls together with a high number of isolated teeth, proximal femora and distal humeri (Fig. 7) is in accordance with the few observed trampled small mammal assemblages (Andrews, 1990). The low ratios of distal to proximal limb elements and postcranial to cranial elements in DM01 are characteristic features of many predator assemblages (Andrews, 1990) (Figs. 5, 6).

The members of group I of Korth' s settling groups in DM01 are absent (Table 3). This group is the one most easily affected by fluvial transport and might indicate DM01 is a lag assemblage (Behrenesmeyer, 1975). However, DM01 has rather low representation of group III (lag assemblage) specimens as well, and this suggests that the assemblage has been affected by fluvial transport. In DM01 more than half of the analyzed postcranial specimens showed signs of weathering, mainly stage 1. Dental material is less often weathered but more severely, mostly stage 2, indicating short duration of exposure, but longer than in DM16. Postdepositional modification in DM01 is represented by light pressure damage that is detected on most specimens as well as rare and light root marks. Intrusive corrosion in DM01 did not affect whole surfaces and therefore is interpreted to be digestive in origin (Andrews, 1990).

Locality DM02 contains only small mammals and features only isolated teeth (Table 2). The dental material from DM02 presented the same taphonomic features of digestion that strongly indicate predation as for the previous unit DM01 (Fig. 3). Trampling cannot be fully excluded as a factor affecting the DM02 small mammal fossil assemblage, since the lack of skulls may be associated with trampling (Andrews, 1990). The total absence of postcrania may also be due to trampling, since trampling causes dispersal of bones (Andrews and Cook, 1985) and in addition small mammal bones are fragile and easily broken when not protected by pellets (Andrews, 1990).

The dental material at DM02 is the least weathered of all studied localities, with only 4% of teeth at DM02 showing light modification. The near lack of signs of weathering in DM02 indicates short duration of surface exposure prior to burial. After burial DM02 dental material has experienced some pressure damage and root marks, however not severe. Intrusive corrosion is detected from all specimens but affecting only parts of the teeth, suggesting digestive origins (Andrews, 1990).

5 Discussion

The large lateral continuity of the DM16 sedimentary beds, their fine-grained lithologies and associated horizontally laminated structures indicate suspension settling in the distal floodplain with periodic input of fine sands. The small mammal remains represent larger grain sizes than the range represented in the sediment matrix and therefore are not likely to have experienced much fluvial transport to the site; the low representation of lighter elements is considered as resulting from winnowing during surface runoff. Sedimentological evidence suggests that conditions were at least periodically oxidizing and conducive for soil formation as evidenced by carbonate nodules, root traces and occasional presence of mottling. The presence of bird eggshells indicates nesting sites and consequently substantiates the subaerial conditions. However, the fairly unweathered bone and teeth surfaces in DM16 do not suggest a prolonged period of subaerial exposure during dry seasons prior to burial.

The sedimentological data indicate that fossil bearing beds at DM01 resulted from reworking of the resistant pedogenic carbonate nodules into an intraformational conglomerate by fluvial avulsion. Some mechanical damage produced by transport is evident in the remains, although in light to moderate stages. It is also easily observed that DM01 shows element sorting by transport processes. The lack of skulls and high proportion of isolated teeth, distal humerus, distal tibia, and proximal ulna as well as fragmentary mandibles (cf. Wolff, 1973; Andrews, 1990) all point to fluvial transportation as a means of accumulation (Fig. 7). Weathered specimens were more common at DM01 than at DM16 although their dominantly light to moderate stages do not indicate extended subaerial exposure. Therefore it is obvious that DM01 contains materials harvested from the floodplain but, based on the relatively well-preserved nature of the remains, they have probably not been transported very long nor far.

The stratified bed of poorly sorted sand that typifies DM02 suggests relatively high-energy injection of sediment to the floodplain. Taphonomical features at DM02 locality are identical to DM01, except that the most prominent feature of DM02 is the total absence of skulls and postcranial elements. This may be due to transportation of all the lighter, more easily moved material away leaving only molars and a few mandibles behind, however, with total absence of postcrania this is uncertain. Another option could be trampling, which could have destroyed the fragile small mammal bones. However, due to the fragile nature of small mammal bones, natural trampling is rarely evidenced in small mammals (Andrews, 1990).

Natural causes of death usually leave animals well preserved, with all parts of the skeleton unbroken and typically one or only a few species present at the bone accumulations (Andrews, 1990). In the three discussed localities from Damiao this seems not to be the case. The fossils are fragmentary, with missing skeletal elements. While the identifications of specimens are uncertain and in some cases impossible due to the fragmentary nature of material, a variety of species of small mammals were present (Tables 4–6).

Small mammal (fossil) assemblages most often result from predation (e.g., Andrews, 1990; Arcos et al., 2010; Fernández-Jalvo, 1995; Fernández-Jalvo et al., 2016). Owls are commonly cited as a source for accumulations of small vertebrate fossils (Andrews, 1990; Andrews and Evans, 1983; Dodson and Wexlar, 1979), but there is rich evidence of various other predators like diurnal raptors and mammalian carnivores involved in the accumulation of small mammal vertebrate remains as well (Andrews and Evans, 1983 and references therein). Predation seems to be a likely agent of accumulation for all localities in Damiao, however, there are differences in the intensities of digestion-associated features between localities (Fig. 3), which might point to different predator species as dominant accumulation agents. Mammalian carnivores have complete digestion and high levels of gastric acidity and therefore digestive corrosion (Andrews, 1990). Nocturnal owls, in turn, have relatively low levels of acidity of gastric juices and corrosion whilst diurnal birds of prey feature intermediate acidity and corrosion of bone and dental remains. Signs of intrusive corrosion in Damiao specimens are very great for both bone and dental material in all three localities, being most severe in DM01 (Fig. 3) and least pronounced but abundant in DM16. DM02 molars exhibit similar distribution of corrosion stages as dental material in both DM01 and DM16. However, incisors and molars are known to have different response to digestion (Andrews, 1990; Fernández-Jalvo et al., 2016) and when excluding incisors, it is evident that DM02 and DM01 are more alike. The high incidence of intrusive corrosion could also be of pedogenic rather than digestive origin. However, the former should affect all parts of the bone rather than just small parts of it (Andrews, 1990). Considering that the fossils from Damiao are partially affected by corrosion and show other abundant predation-related taphonomic features, corrosion seems more likely to be the result of digestion for these localities.

In addition to corrosion, indications of predation in Damiao localities are evidenced by several other taphonomic features. Nearly all of the dental material from the three localities showed signs of pitting. Breaking, rounding and staining of dental material were common features in DM01 or DM02 but less abundant in DM16. These taphonomic features on both dental specimens and bones indicate predation as an accumulating agent for all localities and possibly similar, more destructive predation for DM01 and DM02 than for DM16.

Relative proportions of skeletal elements may reveal the identity of the bone accumulator since all predators produce bone loss (Andrews, 1990; Andrews and Evans, 1983; Lyman, 1994). Mammalian predators produce the largest relative loss of distal limb parts, while the opposite occurs for owls. Diurnal raptors are set in between the two groups (Andrews, 1990; Lyman, 1994). The relatively high proportion of distal limb elements and low ratio of cranial to postcranial material together with lightly digested elements suggest the involvement of owls in DM16. Several fossilized predator pellets at or right above the richest fossil layer further support this interpretation. Additionally, a few discoloured teeth indicate that diurnal raptors may have contributed to the formation of the assemblage (cf. Andrews, 1990; Mayhew, 1977).

For DM01, the relatively low proportion of distal limb elements and high ratio of cranial to postcranial material point to diurnal raptor or mammalian predator as possible producers of the assemblage even without the discoloration which may be concealed by strong manganese coloration. Significant alteration by digestive processes in nearly all elements could favour a mammalian predator origin. For DM02 the teeth exhibit similar evidence of digestion as in DM01, perhaps suggesting the same predator implicated in the deposit formation.

At all localities some transportation of material is indicated, transportation of different duration for all localities and this results in selective loss and/or destruction of elements (e.g., Andrews, 1990; Behrensmeyer, 1975; Behrensmeyer et al., 2000; Korth, 1979). However, the fluvial transportation has not been extensive for any of the localities as the taphonomy and preservational state of specimens suggest.

All field collecting methods may play an important role in bone modification and some damage is always done (Andrews, 1990). In our study we conducted systematic excavation at DM16, and this material shows less severe stages of breakage compared to DM01 or DM02, both for bone and dental specimens. It seems likely that this method is slightly less destructive, but the differences are not statistically significant, preventing a definitive conclusion concerning the reason for breakage. The systematic sampling in DM16 did result in a clearly more representative set of specimens than DM01 (not to mention DM02) with more comprehensive representation of different skeletal elements (Table 2). However, it did not produce higher species diversity than at the two younger localities (Tables 4–6).

Large mammal fauna from Damiao has a relatively stable pattern through time with cervoids as ruling group excluding the dominance of widespread open environment for the sequence (Kaakinen et al., 2015). Indication of closed and humid environment for DM01 comes from the presence of the humid-favouring pliopithecoid primate (Zhang and Harrison, 2008) as well as anchitheriine horse and the cervid Euprox alticus (Kaakinen et al., 2015; Wang and Zhang, 2011). Sedimentological evidence also supports this with abundant goethite and manganese occurrence indicating more humid climate for DM01. However, the small mammal fauna in the entire sequence is dominated by rodents with only relatively few insectivores, which might indicate more dry and open environment (Klietmann et al., 2015; Van den Hoek Ostende, 2001) than that inferred from the large mammals. Taphonomy and preservational state of the specimens suggest that small mammals were collected within the fluvial system, however, the primary accumulators were predators. Predators, however, often prey outside their living habitats affecting the faunal composition of the fossil accumulation and further paleoecological interpretations based on the exposed fauna (e.g., Fernández-Jalvo et al., 2016) and therefore small mammals from Damiao may represent habitats of some distance away.

Yet many small mammal predators, even if hunting outside their living/nesting habitats, are rarely foraging far but within few kilometers distance depending on the stage of the breeding cycle and season (e.g., Hardey et al., 2009 and references therein). It can be hypothesized that all three localities were predator accumulations that encountered fluvial transportation to the final burial sites. Based on taphonomy, sedimentology and fauna the environment was likely predominantly closed with more open surrounding areas as a gallery forest with surrounding grassland. The youngest locality, DM01, was likely the most humid.

6 Conclusions

The bone material in Damiao was mainly accumulated by predators and deposited in a fluvial setting. Some reworking by fluvial process took place in DM01 and DM02. DM16 represents distal part of the flood plain whereas DM01 portrays a channel-fill, and DM02 is a result of an episodic flood discharge to the floodplain.

Accumulating predators were likely owls for DM16, and diurnal birds of prey for DM01 and DM02. However, mammals are not fully excluded for contributing to DM01 fossil assemblage.

Systematic sampling of DM16 resulted in a wider range of skeletal material, however, it did not produce taxonomically richer sample than the more traditional excavation methods used at DM01 and DM02. Breakage was less pronounced in the systematic sample, but the difference was not statistically significant.

Environmental conditions for Damiao were rather stable throughout. It represents fluvial system, with mosaic grassland-forest environment (perhaps gallery forest with surrounding grassland). DM01, the only primate bearing locality, seems to have been the most humid, although seasonally dry.

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