A new cyamodontoid placodont from Triassic of Guizhou, China

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Abstract A new cyamodontoid placodont is named (*Pse*phochelys polyosteoderma gen. et. sp. nov.) and described based on a three-dimensionally preserved specimen. The material comes from the Wayao Member of the Falang Formation (Carnian, Late Triassic) in Guizhou Province, southwestern China. The skull of Psephochelys shows a unique combination of characteristics observed in Psephoderma and Placochelys, and the carapace is diagnostic of a new taxon as well. The ventral dermal armor of Psephochelys differs from all other known cyamodontoids in that it comprises irregular marginal osteoderms in loose contact with each other, and gastralia between them. The cranial suture pattern is in part difficult to analyze due to apparent co-ossification of elements, or poor delimitation of sutures. This affects primarily the demarcation of the nasal from the prefrontal, and the relation between the anterior part of the parietal, posterior ends of the frontals, and postfrontals. However, the postfrontal appears to enter the anteromedial margin of the upper temporal fenestra, a characteristic otherwise known from Placodus, but not from other cyamodontoids. However, given the difficulties of interpretation of this skull, additional material is required to unequivocally assess some details of the pattern of cranial sutures.

Keywords: placodont, Triassic, Guizhou.

For a long time the placodonts, sister-group of all other Sauropterygia^[1], were believed to be restricted to coastal stretches of the western periphery of the Triassic Tethys, and to epicontinental seas of central Europe^[2]. Reports of cyamodontoids from China^[3, 4] extend the distribution of these Triassic marine reptiles to the eastern Tethyian faunal province. All placodonts that have so far been found in China are referred to the Cyamodontoidea. Recently, along with many ichthyosaurs^[4, 5] and thalattosaurs^[6, 7], another well-preserved cyamodontoid placodont has been found at the same locality of Guizhou Province, preserving a complete skull of seemingly peculiar structure, as well as parts of the postcranial skeleton comprising a well-preserved carapace.

1 Systematic paleontology

Class Reptilia Linnaeus, 1758 Order Placodontia Cope, 1871 Suborder Cyamodontoidea Nopcsa, 1923 Family Placochelyidae Romer, 1956 Genus *Psephochelys* gen. nov.

Etymology. The genus name refers to the unique combination of cranial characters this taxon shares with *Psephoderma* and *Placochelys*.

Type species. *Psephochelys polyosteoderma* gen.et. sp. nov.

Diagnosis. As for the type and only known species. *Psephochelys polyosteoderma* gen. et. sp. nov. (Plate I)

Etymology. The species name derived from Greek, and refers to the numerous small osteoderms (in the carapace).

Holotype. IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences) V 12442. A complete skull and carapace, and parts of the appendicular skeleton.

Type locality and horizon. Xinpu, Guanling County, Guizhou Province, southwestern China; Wayao Member of Falang Formation, Carnian of Upper Triassic.

Diagnosis. Elongated and narrow rostrum spatulate, edentulous; two maxillary teeth; posterior (nasal) processes of the premaxilla enlarged and extending backwards to contact frontals; postfrontal appears to enter the anteromedial margin of the upper temporal fossa. Carapace composed of relatively small and numerous hexagonal and pentagonal osteoderms meeting each other in interdigitating sutures; osteoderms with a flat surface ornamented with a pattern of radiating pits and ridges; carapace with a central longitudinal depression and a vaulted zone on either side of it, dorsolateral ridge flat and formed by enlarged, keeled osteoderms; nuchal concavity deeply excavated, flanked on either side by an enlarged, tuberculiform osteoderm. Lateral wall 5 rows of hexagonal osteoderms deep, terminating in a ventrolateral ridge formed by enlarged, keeled osteoderms. Plastron absent, but 3 rows of marginal, loosely distributed osteoderms flank the gastralia on either side.

Comments: Psephochelys shares with other placochelyids the squamosal buttress receiving the distal end of the paroccipital process. *Psephochelvs* is unique among cyamodontoids by the apparent entry of the postfrontal into the anteromedial margin of the upper temporal fossa. It shares with *Placochelys* the spatulate and edentulous premaxillary rostrum. With Psephoderma it shares the presence of two maxillary teeth; upper temporal fenestrae relatively long and narrow, squamosals projecting far posteriorly; tuberculiform osteoderms fused to the squamosals at their posterior extremity only; posterior (nasal) processes of the premaxilla enlarged and extending backwards to contact the frontals (convergent in Prothenodontosaurus). The (estimated) proportion of the posterior palatine tooth plates is plesiomorphic relative to Psephoderma, and the short palatal exposure of the pterygoid is plesiomorphic relative to the Placochelyidae.

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2 Description and comparison

The specimen here described includes a complete skull and the carapace, as well as parts of the appendicular skeleton. In terms of its skull morphology, *Psephochelys polyosteoderma* combines characteristics of the western Tethyan taxa *Placochelys* and *Psephoderma* with possible autapomorphies of its own. In dorsal view the skull has the shape of an isosceles triangle, with an elongate rostrum and a deeply excavated occiput. It is completely preserved without depression or distortion, and measures 140.3 mm in total length, 96 mm in maximal width, and 66 mm in height (fig. 1, Plate I-1).



Fig. 1. The skull of *Psephochelys polyosteoderma* gen. et. sp. nov. (IVPP V 12442). The nasal is not labeled here for the uncertainty of its position. Cor, coracoid; f, frontal; g, gastralia; hu, humerus; isc, ischium; j, jugal; l.w, lateral wall; m, maxilla; ost, osteoderm; p, parietal; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pub, pubis; qj, quadratojugal; sc, scapula; sq, squamosal; v, vertebra.

The paired premaxillae form a spatulate and edentulous rostrum that resembles the rostrum morphology seen in *Placochelys placodonta*^[8]. It has a long posterolateral process that forms the floor of the external naris medial to the anterior process of the maxilla that enters the lateral margin of the rostrum. The enlarged posterior (nasal) processes of the premaxilla meet the frontals at a level between the external naris and the orbit. The nasal cannot unequivocally be delimited either from the prefrontal, or from the premaxilla. The configuration of the posterior margin of the external naris therefore remains uncertain. It would be highly unusual, although perhaps not impossible, for a placodont to have a prefrontal entering the border of the nares. Such a relation of the prefrontal is observed within turtles^[9], where it is correlated with confluent external nares and the loss of the nasals, i.e. a truncation of the snout. The frontal is paired, long and narrow, and forms the dorsal margins of the orbits. The area of contact between the frontals, parietal, and postfrontals around the anteriorly damaged pineal foramen is again difficult to interpret. There is the appearance of a pair of enlarged postfrontals, which meet each other along the dorsal midline of the skull, separating the frontal from the parietal as they embrace the pineal foramen. This peculiar interpretation of the postfrontals requires confirmation by additional material. The parietals are fused, the parietal skull table has concave lateral margins. The maxilla carries two blunt teeth and bears a distinct ascending process. The shape of the postorbital is similar to that seen in other cyamodontoids, but its posteromedial process is short and appears to allow the postfrontal to enter the anteromedial margin of the temporal fossa. The posterolateral process of the postorbital tapers off along the dorsal margin of the upper temporal fossa at a level behind the midpoint of the longitudinal diameter of the latter. The jugal meets the maxilla at the ventral margin of the orbit below the midpoint of its longitudinal diameter. The suture between the quadratojugal and the squamosal is indistinct posteriorly, but the anterior tip of the quadratojugal is located at the ventral margin of the temporal arch at a level shortly behind the anterior margin of the upper temporal fossa. The ratio of the temporal fossa length (469 mm) to orbital length (264 mm) is 1.78. Enlarged tubercular osteoderms are secondarily fused only to the posterior surface of the temporal arch.

The carapace measures 265 mm in length and 271 mm in width. It has a rounded contour except for an anterior nuchal excavation and, as preserved, a biconcave posterior margin (fig. 2(a), Plate I-2). The outline of the carapace is somewhat similar to that of Psephoderma alpinum^[10] and Psephosaurus sp. described by Haas^[11]. A feature diagnostic of Psephochelys polyosteoderma is two enlarged, tuberculiform osteoderms flanking the nuchal excavation, one on each side. The dorsolateral ridge is formed by enlarged, keeled osteoderms. The lateral wall is 5 rows of osteodersm deep, which together with the distinct ventrolateral ridge osteoderms results in a total height of 88 mm (fig. 2(b), Plate I-3). The dorsal surface of the carapace is not entirely flat. It is moderately convex with a shallow longitudinal groove at the dosal midline. In contrast to Sinocyamodus xinpuensis^[3], the osteoderms of



Fig. 2. Carapace of *Psephochelys polyosteoderma*. (a) Dorsal view; (b) the lateral wall.

Psephochelys polyosteoderma meet in interdigitating sutures with a tendency to fuse in the central part of the carapace. The osteoderms on the periphery of the carapace and the lateral wall remain distinct. Other than in *S. xin*- *puensis*, the surface of these osteoderms is quite flat, and ornamented with a pattern of radiating pits and ridges. The outline of the osteoderms varies between hexagonal and pentagonal, and the diameter of the carapacial os**NOTES**



Fig. 3. Ventral view of *Psephochelys polyosteoderma* (abbreviations as in fig. 1).

teodermsvaries from 9 mm to 14 mm. Due to the relatively small size of the osteoderms, the latter are distinctly more numerous in the carapace of *Psephochelys polyosteoderma* compared to *S. xinpuensis*.

No complete plastron is developed. The ventral sideof the specimen is composed of loosely distributed osteoderms along the periphery and the gastralia between them (fig. 3, Plate I-4). The ventral osteoderms are distinctly different from those of the carapace, in that they are of a elongate lanceolate shape (pointed anteriorly, concave posteriorly). There are between 19 and 21 gastralia exposed, each comprising three elements, a broad straight or only very slightly angulated medioventral one with a short collateral element on either side.

The coracoid, ischium and pubis are completely preserved (fig. 3, Plate I-4). They are all expanded and plate-like. Among them the coracoid is the only one covered by the carapace. There is no distinct evidence of the presence of a separate tail-shield covering the pelvic elements, as is known to be the case in *Psephoderma*. The proximal margin of the scapula is broad; it is 38 mm wide, while the minimal width of the scapula in the middle part is 10 mm. The humerus is broken, with a large and deep concavity on its proximal ventral surface.

3 Discussion

Psephochelys polyosteoderma is the third placodont described from China. The first one to be described in a

	Psephochelys	Psephoderma	Placochelys
Shape of skull	relatively wide	relatively narrow	relatively wide
Shape of rostrum	elongate, spatulate	elongate, narrow and pointed	elongate, spaulate
Number of teeth on maxilla	2	2	3
Fused tubercular osteoderms	on posterior end of squamosal only	on posterior end of squamosal only	on posterior and posterolateral surface of squamosal
Shape of palatal tooth	not distinctly elongate	distinctly elongate	not distinctly elongate
Palatal exposure of pterygoid	short	long	long

Table 1 A brief comparison on skull among Psephochelys, Psephoderma and Placochelys

very incomplete manner was Placochelys minutus by Yin and Luo^[4], shortly followed by the description of *Sinocvamodus xinpuensis*^[3]. It is likely that these two species are both junior and seemed to be similar to each other, given similar carapace size, and a similar osteoderm structure in the two specimens. But the ratio of length to width in carapace is clearly different (14.2 cm/13.6 cm in Placochelys minutus and 13 cm/17.5 cm in Sinocyamodus). For the time being, we refrain from formalizing this synonymy because one specimen is exposed in dorsal view, the other in ventral view, which renders comparison difficult, and because we did not yet have access to the holotype of *Placochelys minutus*. Whether one or two species, however, it (they) certainly cannot be referred to the genus Placochelys, which is why we here retain the generic name Sinocyamodus for that material. Psephochelvs differs from Sinocyamodus xinpuensis^[3] in having an elongated rostrum, an edentulous premaxilla, a relatively small and rounded orbit and tubercular osteoderm fused to the posterior end of the squamosal only. It also differs dramatically in the carapace structure.

As mentioned above, *Psephochelys polyosteoderma* combines characteristics of both *Psephoderma* and *Placochelys* in its skull structure (table 1), while the possible entry of the postfrontal into the anteromedial margin of the upper temporal fossa is an autapomorphy of this new taxon. The carapace as well as the ventral dermal armor likewise are unique among cyamodontoids in the detailed structure.

By virtue of the presence of a well-differentiated squamosal buttress on the lower surface of the squamosal, against which the distal end of the paroccipital process abutted, *Psephochelys polyosteoderma* can be referred to the Family Placochelsidae. However, its phylogenetic relationship within that family remains to be further investigated. **Acknowledgements** We would like to thank Ding Jinzhao and Wang Zhao for preparation of the material. We also thank Gao Wei for taking the photographs in plate and Yang Mingwan for drawing the illustrations. This work was supported by the National Natural Science Foundation of China (Grant Nos. 40072010, J9930095 and 49942006) and the Chinese Academy of Sciences (Grant No. KZCX3-J-02).

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