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The first record of *Helicoprion* Karpinsky (Helicoprionidae) from China

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A new species, *Helicoprion jingmenense* sp. nov., from the Lower Permian Qixia Formation of Hubei Province, China, is described based on a nearly complete symphyseal tooth spiral preserved as part and counterpart. The specimen is a large elliptical symphyseal tooth spiral with $4^1/_3$ volutions, with cutting blade being relatively wide, and its width being greater than the height after $3^1/_2$ volution, middle portion being higher than the cutting blade, narrowed base being short. There is a distinct space not covered by enameloid in two adjacent tooth crowns in the outermost two volutions; the height of the compound root is moderate, and the ventral groove is about 1/10 of the same tooth crown. In comparison with other known *Helicoprion* species of the world, the new species resembles *H. ferrieri* and *H. bessonowi.* However, it can be easily distinguished from *H. ferrieri* by the wider cutting blade, the shorter narrowed base and lower compound root, and also from *H. bessonowi* by its more narrowed compound root and less than 39 tooth crowns per volution. *Helicoprion jingmenense* sp. nov. is obviously different from helicoprionid species previously found in China in general shape, size and histology. However, it is very difficult to identify their relationships because of the fragmentary nature of holotypes of the latter. Because the new specimen is the first record of *Helicoprion* and the most complete fossil dentition of helicoprionids from China, the new species is of significance for biostratigraphy and paleobiogeography.

Permian, *Helicoprion*, Hubei Province

1 Introduction

Helicoprion, a bizarre and enigmatic shark taxon, can be easily distinguished by its unique tooth spiral. *Helicoprion* was first reported from the Ural Mountains area by Karpinsky in 1899[1]. Afterwards, this kind of fantastic shark fossils were successively found in California, Nevada[2], south-east Idaho[3] and West Texas[4,5] of United States of America, northern Wandagee Mountain of western Australia[6], Canadian Rocky Mountains, western Canada, and Canadian Arctic archipelago[7,8], Puebla of Mexico[9] and others area[2,6], except for South America and Africa. *Helicoprion* was regarded as one of the most important fossils in subdivision and correlation of the middle part of the Lower Permian on a global scale.

Hitherto, there was no record of *Helicoprion* from China, although other taxa of helicoprionids have been found. *Sinohelicoprion changxingensis* was first described from the Upper Permian Changxing Limestone of Zhejiang by Liu and Chang[10]. Later, *S. qomolangma* Chang 1976, *S. macrodontus* Lei 1983, and *Hunanohelicoprion xiandongensis* Liu 1994, were successively reported from the Lower Triassic of Dingri of Tibet[11], the Upper Permian of Jiahe of Hunan[12], the Permian Maokouian Stage of Lianyuan, Huana and Weining of Guizhou[13,14], respectively. Well-preserved helicoprionids fossils were also found in a series of coal beds at Yezhou of Jianshi, Hubei Province and the Per-

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mian of Gufu Mountain, Zhijin, Guizhou Province, respectively. In addition, some new material of *Sinohelicoprion changxingensis* was collected from Changxing, Zhejiang Province, by Liu and Wang[15]. A fossil collected from Yezhou of Jianshi, Hubei Province possesses three volutions including about 110 tooth crowns[16] but has never been described in detail. It may belong to *Helicoprion*. The material from the Permian of Gufu Mountain is a section of a tooth spiral bearing 16 tooth crowns and also has not been studied (hhp://www.gz.xinhua.org/tppd/2003-9/16/content-948258.htm). The most well-preserved fossils of all specimens which have been described and reported from China only preserve a row of 11 tooth crowns[15]. Obviously, they are regional elements occurring from the Middle Permian to Triassic.

The new specimen, split into part and counterpart (Figure 1) described in this paper was found accidentally by workers of the Yichang Chaoyue Road & Bridge Co. during construction of a highway from Xiangfan County to Jingmen County at Ziling village, in the northeastern part of Jingmen County, Hubei Province. The exact stratigraphic position of the find is not clear. However, the matrix indicates that the specimen may come from the Lower/Middle Permian Qixia Formation. The rock is split naturally along the fossil layer, so both the components of the tooth spiral and the external mold are in two parts (Figure 1). After taking photos and studying the specimen carefully, we selected one tooth crown for cutting polished section (the white line in Figure 1(b) shows the sample location). Using an OLYMPUS SZ-ST stereomicroscopy, we studied the histological structure as visible in the polished section. The new specimen is impportant not only because it is the most complete tooth

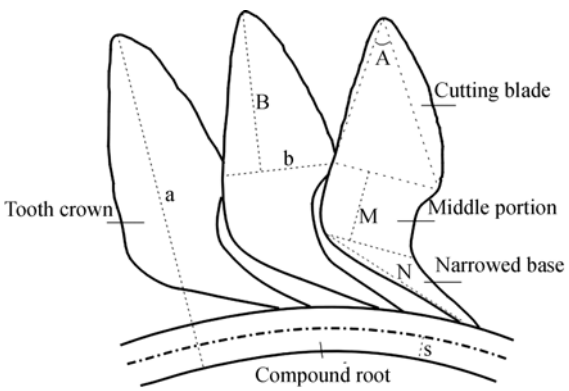


Figure 1 *Helicoprion jingmenense* sp. nov. (YIGM–V 25147). (a) Left part; (b) right part. The dotted line shows the location of the polished section.

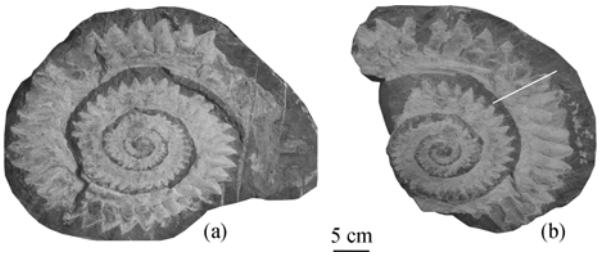


Figure 2 Morphological terminology of *Helicopri*on (adapted from refs. [2,3,6]). (a) Height of volution; (b) width of cutting blade; A, apical angle; B, height of cutting blade; M, height of middle portion; N, length of narrowed base; s, height of compound-root.

spiral of the Helicoprionidae from China, but also because it contributes to helicoprionid taxonomy, biostratigraphy and biogeography.

2 Morphological terminology

Based on first description of *Helicoprion* by Karpinsky[1], Wheeler[2] proposed a special morphological terminology for specimen descriptions. However, Teichert[6] pointed out that the tooth spiral of *Helicoprion* formed one solid structure. The “teeth” are actually the enameloid portion of the tooth spiral, and the “interdental space” is only a gap or curved depression which is not covered by enamel. Bendix-Almgreen[3] also thought that the “teeth” (or “denticles”) and so-called “shaft” were inadequate terminology. Consequently, these terms were replaced by Bendix-Almgreen[3] by “tooth crown” and “compound root”, respectively (Figure 2).

Since Karpinsky[1] first recognized that *Helicoprion* belongs to the shark group, Karpinsky[17], Teichert[6], Bendix-Almgreen[3], and Zangerl[18] have discussed its taxonomy successively. Karpinsky[17] tried to establish a Helicoprionidae referred to Edestoidea in 1911. This idea was also accepted by Hay (in Teichert, 1940[6]) and some Chinese researchers[11−14], but a number of other authors, including Wheeler[2], Logan and McGugan[7], Kelly and Zangerl[4], and Chron[5] still support Karpinsky’s original suggestion that *Helicoprion* should be referred to the Edestidae among Selachii because of the specialization of the symphyseal row of tooth crowns and the histological structure. However, Bendix-Almgreen[3] concluded that the microscopic structure of the tooth crowns cannot provide significant evidence for the systematical position of *Helicoprion* when he described the paleohistology and anatomical features of *Helicoprion ferrieri*. According to him, *Helicoprion* has closer affinities to selachians than to edestids based on

the anatomical features of the neurocranium and palatoquadrate[3]. Thus, Bendix-Almgreen[3] not only referred *Helicoprion* to a new family, the Helicoprionidae, but also placed *Helicoprion* and Edestidae into two different orders. Obviously, the definition of Helicoprionidae established by Bendix-Almgreen differs from that erected by Karpinsky. Consequently, Zangerl[18] created a new family-Agassizodontidae which, together with Edestidae, was referred to Eugeneodontida among Chondrichthyes. His diagnosis of Agassizodontidae includes the narrowed bases pointing forward in the tooth spiral.

3 Systematic palaeontology

Agassizodontidae Zangerl, 1981

Helicoprion Karpinsky, 1899

Helicoprion jingmenense sp. nov.

Etymology: Jingmen, Jinmen County of Hubei Province, referring to the name of the type locality.

Holotype: A nearly complete symphyseal tooth spiral preserved as part and counterpart. Yichang Institute of Geology and Mineral Resources, YIGM V 25147 (Figures 1, 3, 4(c)).

Locality and horizon: Lower Permian Qixia Formation; Ziling village, Jingmen County of Hubei Province, China.

Diagnosis: A larger elliptic symphyseal tooth spiral with $4^1/_3$ volutions; no wear marks on the smooth face of the cutting blade; the width being greater than the height of the cutting blade after $3^1/_2$ volutions; the middle portion being higher than the cutting blade; the narrowed base being short; there being a distinct space not covered by enameloid between adjacent tooth crowns in the two outermost volutions; the height of the compound root being moderate; the ventral groove being about 1/10 the size of the respective tooth crown; the lateral margin of the proximal portion of the compound root being smooth and straight; the distal portion of the compound root bearing four processes; the tooth crown consisting of four osteodentine layers; two distinct canals being located in the tubular layer; there being a large and long longitudinal canal in the tubular osteodentine layer outside the distal canal.

4 Description

The elliptic symphyseal tooth spiral has $4^1/_3$ volutions and consists of a large number of individual tooth crowns situated on a whole compound root. Most of components of the inner three volutions were lost to slight wear. The elements of the fourth and the last one third volutions are preserved very well (Figure 1). The greatest diameter of the specimen is 417.9 mm.

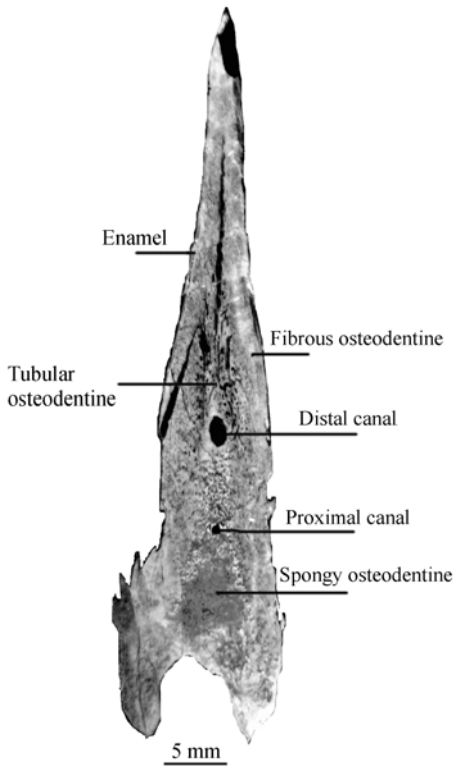


Figure 3 The polished section of *Helicoprion jingmenense* sp. nov., YIGM V 25147.

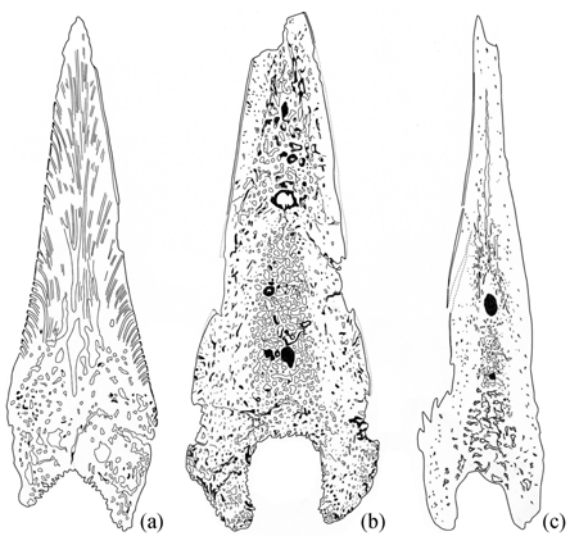


Figure 4 Comparison of the histological structure of the tooth spiral. (a) *Sinohelicoprion changhsingensis*; (b) *Heliocoprion bessonowi*; (c) *Helicoprion jinmenense* sp. nov. Scale bar: 5 mm.

The height of the tooth spiral, i.e. the distance from the base of the compound root to the tip of the cutting blade, is 10.8 mm at the end of the first volution. It increases gradually in the successive volutions and reaches about 80 mm at the end of the fourth volution. As best as it can be estimated, the umbers of tooth crowns in the first volution, is more than 27. The counts for the succeeding three and one third volutions are 35, 36, 36, and 12, respectively. The detailed measurements for each part are given in Table 1.

The tooth crowns are flat, thin, and symmetrical in lateral view. In the first two volutions, the tooth crowns are only divided into an upper part (corresponding to the cutting blade) and a lower part (including the middle portion and the narrowed base). From the third volution to the end of the spiral, the tooth crowns gradually reach maturity in that all three portions of the crowns, including the cutting blade, the middle portion, and the narrowed base, are clearly developed. The curved depression or space not covered by enameloid occurs between adjacent tooth crowns of the fourth and fifth volutions only.

The cutting blade is nearly triangular. The surface of the cutting blade is smooth, without traces of wear trace on its surface. The height of the cutting blade, together with the width, increases gradually with increasing height of the tooth crown. However, the width increases more rapidly than the height surpassing the height from the second half of the third volution onwards. The tip of the cutting blade points slightly backward. The anterior edge is longer and more convex than the posterior one, which is only slightly convex or straight. Crenulations are developed on the cutting edges. The apical angle of cutting blade is close to 30° at the end of the first volution. It increases rapidly, and reaches 64° at the end of the fourth volution. Successive tooth crowns contact each other in at the lower end of the cutting edges. The posterobasal edge possesses a small groove which embraces the anterobasal process of the succeeding tooth crown.

The height of the middle portion is slightly lower than that of the cutting blade. The anterior margin of the middle portion is strongly concave, whereas the posterior margin is slightly convex or straight. The distal part of the middle portion becomes narrow gradually towards basal to fit the narrowed base. The narrowed base is short and extends anterobasally to terminate at the level of the center of the succeeding tooth crown. The tip of the narrowed base contacts the compound root. The middle portion and narrowed base enclose an obtuse angle.

The compound root is a coiled element in symphyseal position, to which all tooth crowns are attached. There is a distinct semicircular longitudinal groove on the basal side of the compound root. The depth of the groove is about one-tenth of the height of the tooth spiral. The laterobasal margin of the compound root is smooth and straight. Apically, four processes extend laterally from the lateroapicalr portion of the compound root (Figure 3). The straight part of the compound root is as long as one sixth of the total height of the tooth crown.

The histological structure of the specimen can be observed in fracture surfaces because the 34th tooth crown of the third volution and the 21st—22nd and 33rd—234th tooth crowns of the fourth volution are broken longitudinally. The thin enameloid that covers the cutting blade and the surface of the middle portion is called the enamel osteodentine layer. The fibrous osteodentine layer is visible below the enamel osteodentine layer. Three canals can be observed from apical parts of their middle portions at the end of the third, the fourth, and the last volution.

Table 1 Measurements of *Helicoprion jingmenense* sp. nov. (mm)

	A	B	b	M	a	N	S
R_2-35th	35°	—	—	—	21.3	—	—
R_3-3rd	—	—	—	—	24.7	—	—
R_3-36th	—	—	—	—	44.2	—	—
R_4-10th	44°	19.8	17.0	—	56.6	—	—
R_4-22nd	54°	20.8	26.6	22.6	66.0	36.8	6.7
R_4-26th	56°	21.5	24.2	23.6	80.8	—	—
R_4-35th	64°	23.4	30.4	26.4	79.2	—	8.1
R_5-2nd	64°	—	37.5	29.6	80.0	—	8.8

R_2-22nd indicates the 22nd tooth crown of the second volution; other abbreviations as in Figure 2.

As can be seen in the polished section (Figure 3), the hard tissue histology of the new species is very similar to that of *Helicoprion bessonowi*, *H. davisii*, and *H. ferrieri* as described by Karpinsky[1], Teichert[6], and Bendix-Almgreen[3], respectively. The hard tissue can be easily divided into four osteodentine layers: the enamel osteodentine, the fibrous osteodentine (or true osteodentine layer), the tubular osteodentine (or inner osteodentine layer), and the spongy osteodentine layer. Among them, the enamel osteodentine layer is thin and compact and only covers the surface of the cutting blade and middle portion. The second layer, the fibrous osteodentine, is composed of pallial dentine[3]. It occupies almost the three fourth of the thickness of one tooth crown. Except for smaller pulp cavities, there are a few dentine tubes, which were described already by Karpinsky[1] and Bendix-Almgreen[3] in the fibrous osteodentine. The tubular osteodentine is the third layer, forming a meshwork. Two distinct longitudinal canals penetrate this layer. The distal canal, near the base of the middle portion, is much larger than the proximal one, at the upper part of the compound root. Both canals are surrounded by abundant irregular channels. The irregular channels surrounding the proximal canal are sparse, and some have different diameters or lengths. The larger and longer longitudinal channel occurs at the center of cutting blade, and its length exceeds the height of cutting blade. The fourth layer, the spongy osteodentine, is located between the proximal end of the canal and the ventral groove of the compound root. The spongy osteodentine is the most cancellous tissue.

5 Comparison and discussion

The new species described above belongs to *Helicoprion* Karpinsky 1899 because of the following characteristics: the presence of a symphyseal tooth spiral; the presence of a space not covered by enameloid between adjacent tooth crowns in the outer two volutions; and the presence of a spongy osteodentine layer at the center of the compound root. There are several species of *Helicoprion* that have been described before, i.e. *H. bessonowi*[1,6] from the western Ural, Russia, *H. ferrieri*[3−5] from south-eastern Idaho and western Texas, *H. ergassaminon*[3] from south-eastern Idaho, *H. nevadensis* and *H. sierrensis*[2], from Nevada and California, USA, and *H. davisii*[6] from Western Australia. The new species shows similarities and differences with these *Helicoprion* species.

The height of the tooth spiral of *H. jinmenensis* sp. nov. is greater than that of *H. nevadensis* and *H. sierrensis*[3], but it is about the same as in *H. ferrieri* at the corresponding portion of the tooth spiral.

The number of tooth crowns in each volution is less than 39 in *H. jinmenensis* sp. nov., which is about the same as in *H. ferrieri*, *H. davisii*, *H. nevadensis*, and *H. sierrensis*, but less than in *H. bessonowi* and *H. ergassaminon*. It is 48−50 in *H. ergassaminon* and 43 in *H. bessonowi*[1,3−5].

The apical angle in *H. jinmenensis* sp. nov. is rather larger (64°) in comparison to that in *H. ergassaminon* (25−35°), *H. ferrieri* and *H. sierrensis* (34−37°), *H. nevadensis* (37 − 45°) and *H. bessonowi* (40°)[3]. Unfortunately, it is impossible to compare the apical angle at the end of the fourth volution of *H. jinmenensis* sp. nov. to that of the other known species, because the latter have not so many volutions. Additionally, the apical angle of the cutting blade in all species, except for *H. ergassaminon*, becomes larger with the increasing size of the tooth crowns.

The cutting blade is slightly lower than the middle portion in *H. jinmenensis* sp. nov., which is similar to the condition in *H. bessonowi*. The other species have an inverse B/M ratio. Additionally, the height of cutting blade increases more slowly than its width and as a result, the width is more than the height from the beginning of the fourth volution.

The narrowed base is shorter in *H. jinmenensis* sp. nov. by comparison to the other known *Helicoprion* species. The height of the lower free lateral portion of the compound root is equal to about one-sixth of the total height of the tooth spiral at the same location. This ratio is about the same as in *H. ferrieri* (1/5−1/7), but greater than in *H. nevadensis* (1/10) and *H. bessonowi* (1/15). Additionally, there are four tooth processes of a uniform shape and different size in the upper part of the lateral margin of compound root.

The histological structure of the hard tissues in *H. jinmenensis* sp. nov. is very similar to that of *H. bessonowi*[1]. However, the latter shows dentinal tubes that are distributed randomly in the fibrous osteodentine layer. The dentinal tubes extend at nearly a right angle to the spiral and send out dichotomously branching tiny canals towards surface of spiral in *H. bessonowi*. The new species, on the other hand, does not exhibit such

dentinal tubes (Figure 4). Compared to *H. davisii* from Western Australia[6] and *H. ferrieri*[3] from Idaho, the spongy osteodentine layer occurs in the new species at the center of the compound root and the longitudinal canals at the center of the cutting blade. An unnamed species of *Helicoprion*, which was collected from the Permian Patlanoaya Formation of Puebla, Mexico, by Sour-Tovar et al.[9], is characterized by a thicker tubular osteodentine layer and a fibrous osteodentine layer with a number of pulp cavities. This is different from the new species.

In summary, the new species is close to *H. ferrieri* in the height of the tooth spiral, the count of tooth crowns per volution, and the apical angle of the cutting blade. However, the new species can be easily distinguished by its wider cutting blade, the shorter narrowed base, and the lower compound root. The new species is also similar to *H. bessonowi* in that the height of the cutting blade is slightly less than its width. However, the latter has broader compound root and more than 40 tooth crowns per volution.

Compared to the other known helicoprion genera and species from the Permian and Triassic of China, including *Sinohelicoprion changxingensis*, *S. qomolangma*, *S. Macrodontus*, and *Hunanohelicoprion xiandongensis*[11−15], the new species has thinner tubular osteodentine layer apart from the different silhouette of the longitudinal section cut from the center of the tooth spiral (Figure 4). Because the best helicoprionid fossil reported previously from China only has 11 tooth crowns[15], it is difficult not only to detect whether the series of tooth crowns describe an arc or a spiral, but also to decide how they contact the skull. Some characters in the diagnoses of *Sinohelicoprion* and *Hunanohelicoprion*, such as that the middle portion and narrowed base are not easily distinguished, that there is only a small spaces not covered by enameloid in adjancet tooth crown, and that there is a thick tubular osteodentine layer in the tooth spiral, are also seen in specimens of *H. ferrieri* from Idaho, USA, and *H.* sp. from Mexico[3,9]. It thus requires further study whether the helicoprionids genera and species previously described from China are valid or whether they are the same or different species of *Helicoprion*.

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