

# Redescription of †*Paralycoptera wui* Chang & Chou, 1977 (Teleostei: Osteoglossoidei) from the Early Cretaceous of eastern China

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†*Paralycoptera wui* Chang & Chou, 1977 from the Early Cretaceous of China is redescribed herein through a re-examination of the original materials, as well as observations on some newly collected specimens. The use of the peeling method has revealed much of the new or revised information on its osteology, e.g. aspects of the nasal, infraorbitals, retroarticular, preopercle, extrascapular, basihyal toothplate, epineural, pelvic fin, caudal skeleton and scales. The phylogenetic relationships of †*Paralycoptera* and other osteoglossomorphs are re-evaluated. The cladistic analysis largely agrees with the previous hypothesis that †*Paralycoptera* is not a †lycopterid, but rather a stem osteoglossoid. †*Paralycoptera* is excluded from notoapteroids and exhibits the following derived characters of the Osteoglossoidei: (1) palatal area behind and below orbit completely covered by infraorbitals; (2) jaw articulation under posterior portion of orbit; (3) opercle depth twice or more its width; (4) first pectoral fin ray much enlarged and long, extending posteriorly beyond origin of pelvic fin. †*Singida* and †*Phareodus* are regarded as different levels of osteoglossoids above †*Paralycoptera*. †*Singida* shares the following derived characters with †*Phareodus* plus extant osteoglossoids: (1) jaw articulation posterior to orbit; (2) anterior process of hyomandibula in contact with entopterygoid; (3) subopercle small and anterior to opercle. †*Phareodus* shares the following derived characters with extant osteoglossoids: (1) supraorbital and otic sensory canals connected; (2) one uroneural; (3) reticulate furrows present over entire scale.

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ADDITIONAL KEYWORDS: Early Cretaceous – East Asia – Osteoglossoidei – osteology – phylogeny.

## INTRODUCTION

The Osteoglossomorpha is a basal group of teleosts that comprises about 218 extant species, referred to 28 genera in four families (Nelson, 2006). Almost all recent osteoglossomorphs are freshwater fishes, a few (notopterids) of which occasionally enter brackish water. Extant osteoglossomorphs are confined to the tropical regions of southern continents and South-East Asia, except for a North American subgroup, Hiodontiformes, thus showing a disjunct pattern of distribution (Greenwood *et al.*, 1966; Patterson, 1975). Abundant fossil osteoglossomorphs have been

discovered from all continents except Antarctica. The earliest records of the group can be dated back to the Early Cretaceous (Berg, 1948; Liu *et al.*, 1963; Chang & Chou, 1977; Taverne, 1979; Ma, 1980; Liu, Ma & Liu, 1985; da Silva Santos, 1985). The majority of fossil osteoglossomorphs have been found in freshwater deposits. Thus, the group is presumed to be primary freshwater fishes, i.e. unable to move across oceanic barriers. They are considered to have been widespread before the supercontinent Gondwana broke up some 135 Mya (Greenwood & Wilson, 1998).

The Osteoglossomorpha has long attracted the attention of ichthyologists for its distinctive features in morphology and physiology (and hence its apparent monophyly), its long history with relatively

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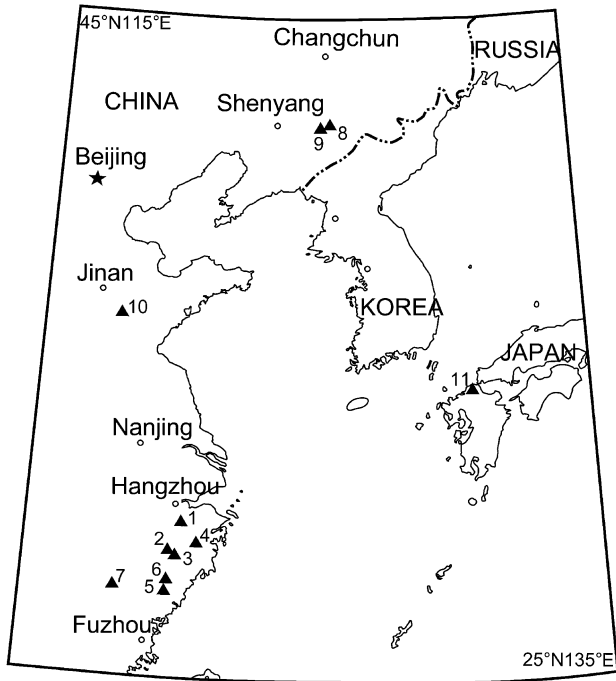
comprehensive and widespread fossil records, and its restriction to freshwater. All of these provided a basis for investigating interesting phylogenetic and related biogeographical problems. Studies on the Osteoglossomorpha have increased rapidly in the last few years. They have shed new light on the morphology, systematics and distribution of the group through studies of newly discovered fossils and structural details of living forms, as well as reviews of previously described forms (e.g. Maisey, 2000; Newbrey & Bozek, 2000; Taverne, 2000; Cavin & Forey, 2001; Hilton, 2002, 2003; Pouyaud, Sudarto & Teugels, 2003; Zhang, 2004, 2006; Kumar, Rana & Paliwal, 2005; Moritz & Britz, 2005; Murray & Wilson, 2005). This group of fishes has also attracted the attention of molecular biologists. Consequently, molecular systematic studies of the group have increased rapidly (Kumazawa & Nishida, 2000; Lavoué *et al.*, 2000; Al-Mahrouki *et al.*, 2001; Lavoué & Sullivan, 2004).

Although relatively abundant, the fossil osteoglossomorphs have not been studied in detail in general. The only comparatively well-studied taxa are †*Eohiodon* and †*Phareodus* from the early to middle Eocene Green River Formation of Wyoming (Taverne, 1977, 1978; Grande, 1984; Li, Grande & Wilson, 1997a; Li, Wilson & Grande, 1997b). †*Brychaetus* is similar to †*Phareodus* and is known from marine deposits of Europe and Africa (Woodward, 1901; Roellig, 1974; Taverne, 1974; Murray, 2000). Li & Wilson (1996a) suggested that †*Brychaetus* might be better assigned to the genus †*Phareodus*, but this was not accepted by Taverne (1998) because †*Brychaetus* seems to be more derived than †*Phareodus* with upper hypurals fused with the last centrum. Other Palaeogene fossil records include: †*Joffrichthys* from the Palaeocene of Alberta (Canada) and North Dakota (USA) in North America (Li & Wilson, 1996b; Newbrey & Bozek, 2000); †*Singida* and †*Chauliopareion* from the Eocene lacustrine shale of Tanzania in East Africa (Greenwood & Patterson, 1967; Murray & Wilson, 2005); possible †*Phareodus* (once revised as †*Phareoides*, see Taverne, 1973) from the Eocene to Oligocene Redbank Plains Formation in Australia (Hills, 1934; Taverne, 1978, 1998; Li, 1994); †*Musperia* from the Eocene of Sumatra in South-East Asia (Sanders, 1934); †*Sinoglossus* from the Palaeogene of north Sichuan (Su, 1986); and possible †*Phareodus* (only afterbody preserved) from the Eocene of Hubei (Zhang, 2003) of China. The Cretaceous fossil records are also quite common. †*Laeliichthys* from the Early Cretaceous of Brazil has been suggested to be related to extant osteoglossiforms (Taverne, 1979; da Silva Santos, 1985), although it needs further study (see Hilton, 2003: 9: 'the published description of †*Laeliichthys* evidently reports several features that cannot be confirmed on the known specimens'). †*Palaeonotopterus*

from the late Albian or early Cenomanian of south-east Morocco in north-western Africa might be a fossil record of Notopteroidei with a mixture of notopterid and mormyrid characters (Forey, 1997; Taverne & Maisey, 1999; Taverne, 2000, 2004; Cavin & Forey, 2001). †*Lycoptera* is the best-known Early Cretaceous stem osteoglossomorph, and is endemic to northern China, Mongolia and Siberia (Berg, 1948; Liu *et al.*, 1963; Yakovlev, 1965; Gaudant, 1968; Greenwood, 1970; Ma, 1987; Jin, Zhang & Zhou, 1995). After its establishment, more than a dozen generic names were given to †*Lycoptera*-like fishes from China (Chang & Chou, 1976, 1977; Ma, 1980; Liu *et al.*, 1985; Zhang, 1998, 2004). Among them, †*Paralycoptera wui* from the Early Cretaceous of Zhejiang Province was the only genus that occurred in south-eastern China.

†*Paralycoptera wui* was originally described and assigned to †Lycopteridae by Chang & Chou (1977) (in Chinese with a short English summary) based on specimens collected in the 1960s from the sedimentary intercalations in the Lower Cretaceous volcanic deposits of the Guantou Formation in Zhejiang Province of China (Fig. 1). However, it should be noted that, in a paper (Chang & Chou, 1976) submitted later, but published earlier than Chang & Chou (1977), †*P. wui* was actually designated as a primitive osteoglossoid, although there was a lack of comprehensive comparisons with other osteoglossiforms, living or fossil. By the end of the 1980s, more materials similar to †*P. wui* were found from the corresponding strata in the north-eastern part of China. Ma & Sun (1988) named a new species (†*P. changi*) of the genus based on specimens uncovered from the Hengtongshan Formation at Sankeyushu section close to Tonghua City in Jilin Province. Before long, Jin (1991) named a new genus and species, †*Tanichthys ninjiagouensis*, based on specimens from the Fenshuiling Formation at Ningjiagou section in the vicinity of Xintai of Shandong Province. The generic name, however, was later changed to †*Tanolepis* by the same author (Jin, 1994) as it was a junior homonym of *Tanichthys* Lin 1932, a living cyprinid. Then, however, Jin *et al.* (1995) suggested that †*Tanolepis ninjiagouensis* was, in fact, the synonym of †*P. changi*, because the distinctions between †*Tanolepis* and †*Paralycoptera* mentioned in Jin (1991) did not exist. †*Paralycoptera* was also discovered later from the corresponding strata (Baiyashan Formation) of Fujian Province of China (G.-H. Xu and M.-M. Chang, pers. observ. on undescribed materials housed in the Zhejiang Museum of Natural History). These discoveries extended the range of the distribution of †*Paralycoptera*.

Although †*Paralycoptera* has been incorporated in the phylogenetic analysis of the Osteoglossomorpha



**Figure 1.** Fossil localities of †*Paralycoptera* and †*Aokiichthys* in East Asia. 1–10, Localities of †*Paralycoptera* from China. 1–6, From Zhejiang Province: 1, Xiaoxisi, Zhuji City; 2, Yongkang; 3, Jinyun; 4, Jiuliping, Tiantai City; 5, Sixi, Taishun County; 6, Shiyuan, Wencheng County. 7, Chong'an (renamed as Wuyishan) City, Fujian Province; 8, Sankeyushu, Tonghua City, Jilin Province; 9, Xinbin County, Liaoning Province; 10, Ningjiagou, Xintai County, Shandong Province. 11, Locality of †*Aokiichthys* (a genus very similar to †*Paralycoptera*) from Japan.

in the phylogenetic investigations of a few authors (Shen, 1996; Li *et al.*, 1997b; Zhang, 1998, 2004, 2006; Li & Wilson, 1999; Zhang & Jin, 1999), a number of characters were not available, or not properly coded. The materials of †*P. wui* are fairly well preserved. With the improved techniques of preparation and newly collected specimens, more details were revealed, which enabled us to recognize more characters and to change the coding of some others. The purpose of this study is to re-examine and redescribe †*P. wui* Chang & Chou and re-evaluate its systematic relationships with other osteoglossomorphs.

## MATERIAL AND METHODS

### MATERIAL

This paper summarizes new information on the osteology of †*Paralycoptera* based on a re-examination of the original described materials studied by Chang & Chou (1977), Ma & Sun (1988) and Jin (1991), and observations on some specimens

collected recently. The specimens IVPP V2989.2–181, V2990.2–20, V2992.2 and V2999.3 were collected by the second author at several localities of Zhejiang Province in the 1960s (several of these specimens are now missing). The specimens IVPP V8493–8494 were collected by F.-Z. Ma and J.-R. Sun at Sankeyushu section, Tonghua City, Jilin Province in 1985–1986. IVPP V8948.1–12 were collected by F. Jin and D.-Z. Su at Ningjiagou section, near Xintai City, Shandong Province in 1986. IVPP V14964.1–25 were collected by J.-Y. Zhang, F. Jin and M. Shen at several localities in Zhejiang Province in the 1990s. IVPP V14965.1–20 were collected during fieldwork undertaken by the first author and Q.-S. Chen at Getangxia section, Zhejiang Province in 2003.

In addition to the specimens of †*Paralycoptera* listed in the systematic section, the following materials were used for comparison. Fossil taxa are marked with daggers (†) preceding their names.

*Cleared and stained extant specimens:* *Scleropages jardinii* IVPP OP302.

*Specimens preserved in alcohol:* *Hiodon alosoides* IVPP OP310–315; *Gnathonemus petersii* IVPP OP317.

*Prepared dry skeletons:* *Scleropages formosus* IVPP OP80; *S. leichardti* IVPP OP81; *S. jardinii* IVPP OP303–307; *Osteoglossum bicirrosus* IVPP OP308–309; *Chitala chitala* IVPP OP316.

*Fossil specimens:* †*Lycoptera davidi* IVPP V10636.1, 3–4, 6–20; V10651.1–12, 16–19. †*Lycoptera (Asiatolepis) sinensis* IVPP V367.1, 8–9, 12, 36, 90; V10637.7, 16; V10667.1–6. †*Sinoglossus lushanensis* IVPP V6354.1–6. †*Phareodus (?) songziensis* IVPP V 12751. †*Paralycoptera (?)* sp. IVPP V10666.1–4, V10668.1–3. †*Huashia gracilis* IVPP V2995.1, 15, 42; V2996.1; V2989. 95. †*Jinanichthys longicephalus* IVPP V8475.1–5; V10645.2–5. †*Kuyangichthys microdus* IVPP V.5668.1–2, 17, 25. †*Tongxinichthys microdus* IVPP V11373.1, 8; V2332.1. †*Xixiaichthys tongxinensis* IVPP V131114.1–2. †*Kuntulunia longipterus* IVPP V8556.1–3, 28–29.

The materials used in this study are kept in the collections of the Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences (IVPP, CAS), Beijing, China.

### METHODS

Fossil specimens were prepared mechanically and latex peels were made from cleaned impressions.

Comparative materials of extant fishes included dried skeletons, specimens fixed in formalin or preserved in alcohol, and specimens cleared and double-stained. Dried skeletons were prepared first by hand with a blade to remove the scales and most of the muscles, and then continued using insect larvae to graze away the remaining soft tissue. Bleached scales were scanned in an optical scanner quickly before they curled. Latex peels were photographed immediately after they had been coated with ammonium chloride. Drawings were executed under a Wild M7A microscope with a camera lucida attachment.

## ABBREVIATIONS

### ANATOMICAL

ang-art, angulo-articular; ao, antorbital; bfr, branched fin ray; bhtp, basihyal toothplate; bpt, basipterygoid process; br, branchiostegals; ch, ceratohyal; den, dentary; dpt, dermopterotic; dsp, dermosphenotic; ecp, ectopterygoid; enp, endopterygoid; epn, epineural; es, extrascapular; fr, frontal; h1–h6, first to sixth hypurals; hh, hypohyal; hm, hyomandibula; iol–io4, first to fourth infraorbitals; iop, interopercle; mx, maxilla; na, nasal; nspu1, neural spine on pu1; nsu1, neural spine on u1; op, opercle; pa, parietal; pas, parasphenoid; ph, parhypural; pmx, premaxilla; pop, preopercle; pt, post-temporal; pu1–pu3, first to third preurals; qu, quadrate; rart, retroarticular; scl, supraclathrum; smx, supramaxilla; soc, supraoccipital; sop, subopercle; sy, symplectic; u1 and u2, first and second urol centra; u1a, anterior part of u1; u1p, posterior part of u1; un, uroneural.

### MEASUREMENTS

AFBL, anal fin base length; BD, body depth; CPD, caudal peduncle depth; CPL, caudal peduncle length; DFBL, dorsal fin base length; FL, caudal fin fork length; HD, head depth; HL, head length; PAL, preanal length; PDL, predorsal length; PPL, prepectoral length; PVL, prepelvic length; SL, standard length; TL, total length.

### MERISTICS

AFR, principal anal fin rays; AP, anal pterygiophores; BR, branchiostegals; CFR, principal caudal fin rays; CV, caudal vertebrae; DFR, principal dorsal fin rays; DP, dorsal pterygiophores; EP, epurals; H, hypurals; PCV, precaudal vertebrae; PFR, pectoral fin rays; SN, supraneurals; TV, total vertebrae; UN, uroneurals; VFR, pelvic fin rays.

## SYSTEMATIC PALAEOLOGY

### SUBDIVISION TELEOSTEI MÜLLER, 1846

### SUPERORDER OSTEOGLOSSOMORPHA GREENWOOD ET AL., 1966

### ORDER OSTEOGLOSSIFORMES REGAN, 1909

### SUBORDER OSTEOGLOSSOIDEI REGAN, 1909

### GENUS †*PARALYCOPTERA* CHANG & CHOU, 1977

*Emended diagnosis:* A stem osteoglossoid possessing the following derived characters of Osteoglossoidei: (1) palatal area behind and below orbit completely covered by infraorbitals; (2) jaw articulation under posterior portion of orbit; (3) opercle depth twice or more its width; (4) first pectoral fin ray much enlarged and long, extending posteriorly to origin of pelvic fin, but lacking the following derived characters of crown group osteoglossoids: (1) extrascapular much reduced; (2) jaw articulation posterior to orbit; (3) anterior process of hyomandibula contacting entopterygoid; (4) subopercle small, anterior to opercle; (5) otic and supraorbital sensory canals in connection; (6) supraorbital sensory canal not entering parietal; (7) one pair of uroneurals; (8) reticulate furrows over entire scale; (9) most upper hypurals fused with last centrum; (10) caudal fin unforked.

*Type species:* †*Paralycoptera wui* Chang & Chou, 1977.

### †*PARALYCOPTERA WUI* CHANG & CHOU, 1977

(FIGS 2–5, 6A–C, 7–9)

*Paralycoptera wui* Chang & Chou, 1974: 183 (name only).

*Yungkangichthys hsitanensis* Chang & Chou, 1974: 183 (name only).

*Paralycoptera wui* Chang & Chou, 1976: 150, 152, text figs 2, 4; fig. 4, pl. 1.

*Paralycoptera wui* Chang & Chou, 1977: 8–16, text figs 5–9; figs 4–5, pl. 4; pls. 5–8; fig. 1, pl. 9.

*Yungkangichthys hsitanensis* Chang & Chou, 1977: 16–19, text fig. 10; figs 2–3, pl. 9.

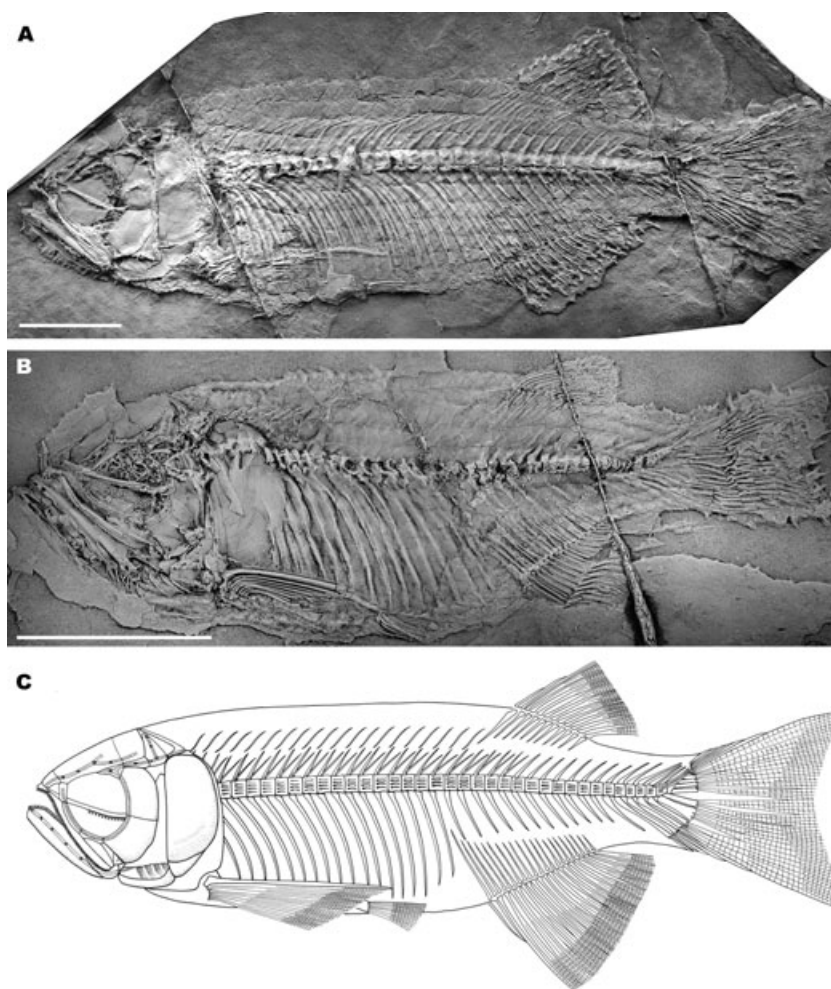
*Paralycoptera changi* Ma & Sun, 1988: 702–704, text fig. 6; pl. 6, figs 1–4.

*Tanichthys ningjiagouensis* Jin, 1991: 46–51, figs 1–3, pl. 1.

*Tanolepis ningjiagouensis* Jin, 1994: 70.

*Paralycoptera changae* (Ma & Sun) – Jin *et al.*, 1995: 185.

*Remarks:* The genus and species name ‘†*Paralycoptera wui*’ first appeared in a brief report (Chang & Chou, 1974), but no description and illustrations were provided. It was not until 1977 that the original description was published (Chang & Chou, 1977).



**Figure 2.** †*Paralycoptera wui*: A, B, two complete specimens, showing the body shape, shape of fins and vertebral column; A, IVPP V2990.20, holotype; B, IVPP V2989.31. C, Restoration of the skeleton of †*P. wui* mainly based on the holotype, modified from Chang & Chou (1977: fig. 5). Scale bars, 1 cm.

Thus, †*P. wui* was considered to be formally established in Chang & Chou (1977).

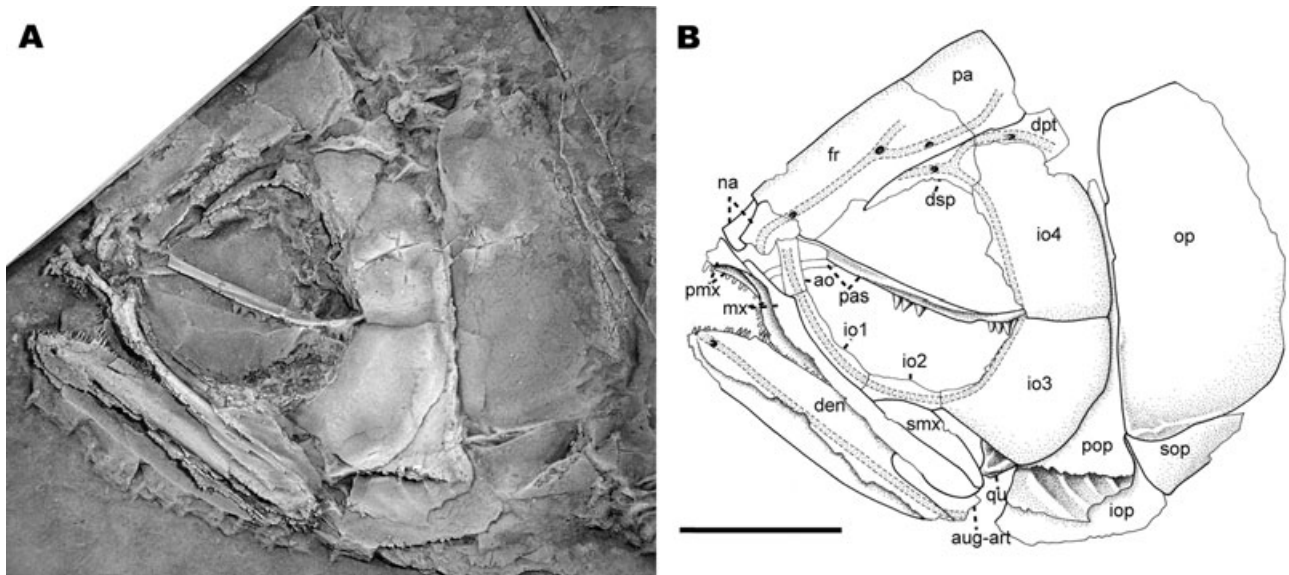
*Emended diagnosis:* As genus, monotypic. D. II+10, P. I+8, V. 7, A. III+18, C. I+8/7+I.

*Holotype:* IVPP V2990.20.

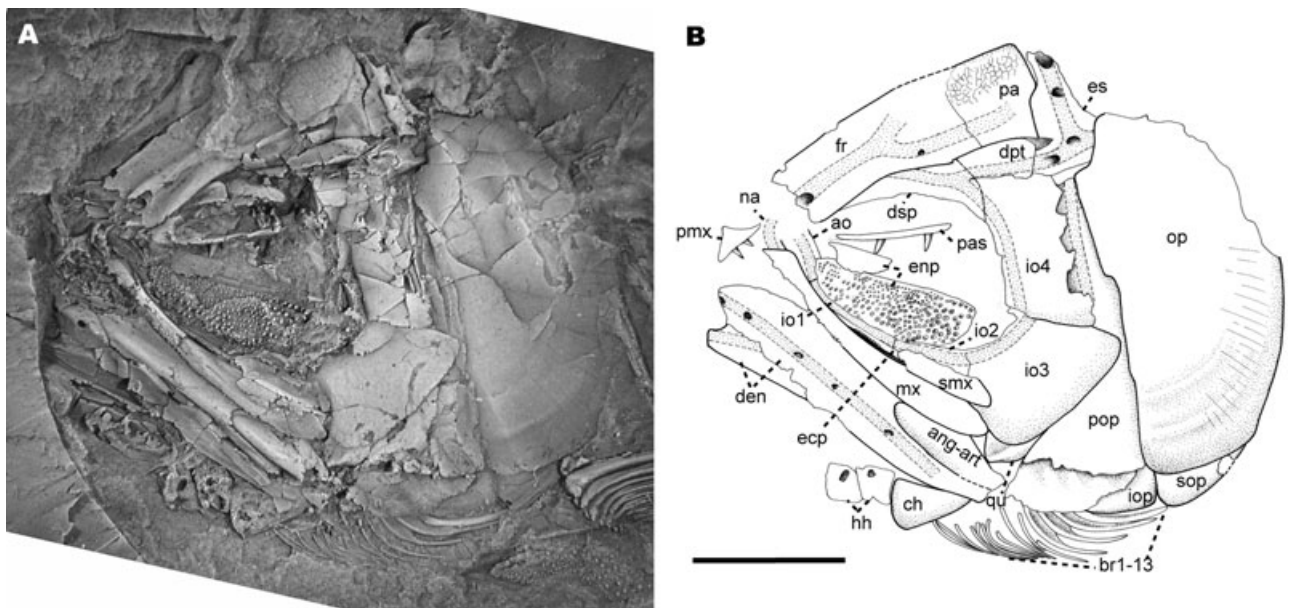
*Other specimens:* IVPP V2989.1–181, among them V2989.2–5, 7–8, 11–12, 14–22, 24, 26–43, 45–47, 49–50, 52–58, 62–65, 67, 69–70, 73, 75, 77–78, 80–85, 87, 89–94, 96–98, 101, 103, 108–110, 112–115, 118–122, 124–127, 132–133, 135–136, 138–145, 147–149, 171, 180–181 now still remain in the collections; V14964.1–15; V14965.1–20; V2990.1–19, among them V2990.2–4, 7, 17 now still remain in the collections; V2992.2; V2999.3; V8493; V8493.1; V8494; V8948.1–12.

*Localities:* Henancun, Getangxia and Xitan, Yongkang City; Houyueling, Shanqian Village and Datang, Huzhen, Jinyun County; Jiuliping, Tiantai City; Xiaoxisi, Zhuji City; Sixi, Taishun County; Shiyuan, Wencheng County, Zhejiang Province. Sankeyushu, Tonghua City, Jilin Province. Ningjiagou, Xintai City, Shandong Province. Xinbin, Xinbin City, Liaoning Province. Dongshanfu, Chong'an County (renamed as Wuyishan City), Fujian Province.

*Horizon and age:* Guantou Formation; since its establishment, the formation has been regarded as Early Cretaceous on the basis of fossil invertebrates (e.g. bivalves, gastropods, ostracodes, conchostracans) and plants (e.g. *Ruffordia-Onychiopsis* Flora) (see recent review by Gu, 2005). Several chronological data (110 ± 3 Mya, 110 Mya and 111 Mya) have been obtained from the Guantou Formation in different



**Figure 3.** †*Paralycoptera wui*, close-up of cranial skeleton in the holotype (IVPP V2990.20): A, photograph; B, explanatory drawing. Scale bar, 5 mm.



**Figure 4.** †*Paralycoptera wui*, cranial skeleton in lateral view (IVPP V2989.12): A, photograph; B, explanatory drawing. Scale bar, 5 mm.

basins of Zhejiang (Yu & Xu, 1999). Thus, the age of †*P. wui* is accepted as Early Cretaceous, and most probably Aptian and/or Albian, based on the absolute dating.

## DESCRIPTION

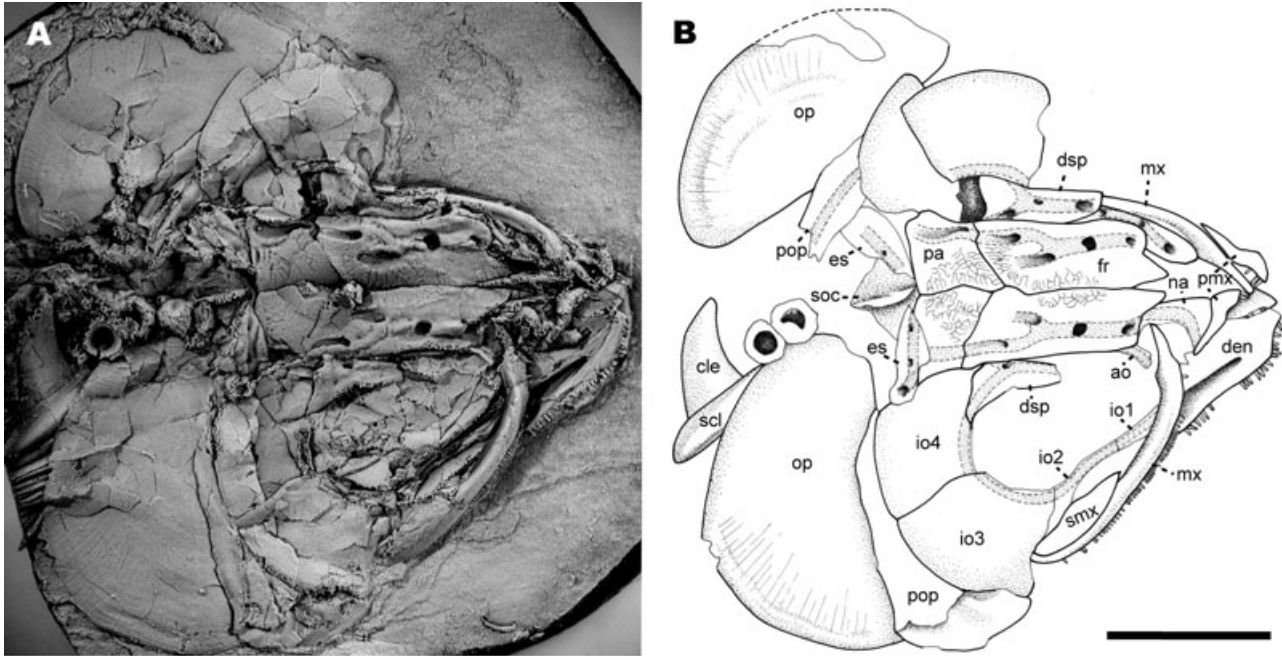
### GENERAL FEATURES

The body is fusiform (Fig. 2). Most specimens are preserved in lateral view, which indicates that it is

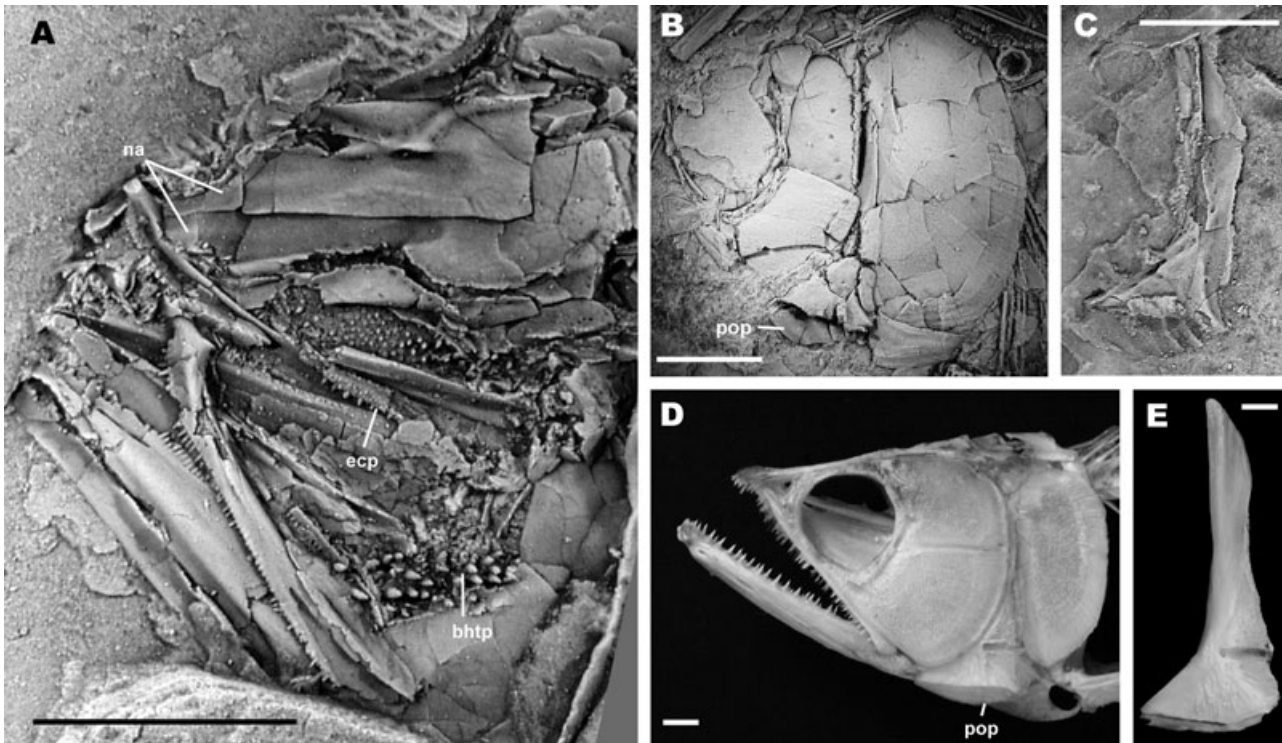
probably compressed laterally. The pectoral fin is greatly elongated and extends beyond the origin of the pelvic fin. The dorsal fin is situated far back, opposite the anterior part or the origin of the large anal fin. The caudal fin is moderately forked. The measurements and meristics are shown in Tables 1 and 2.

### SKULL ROOF

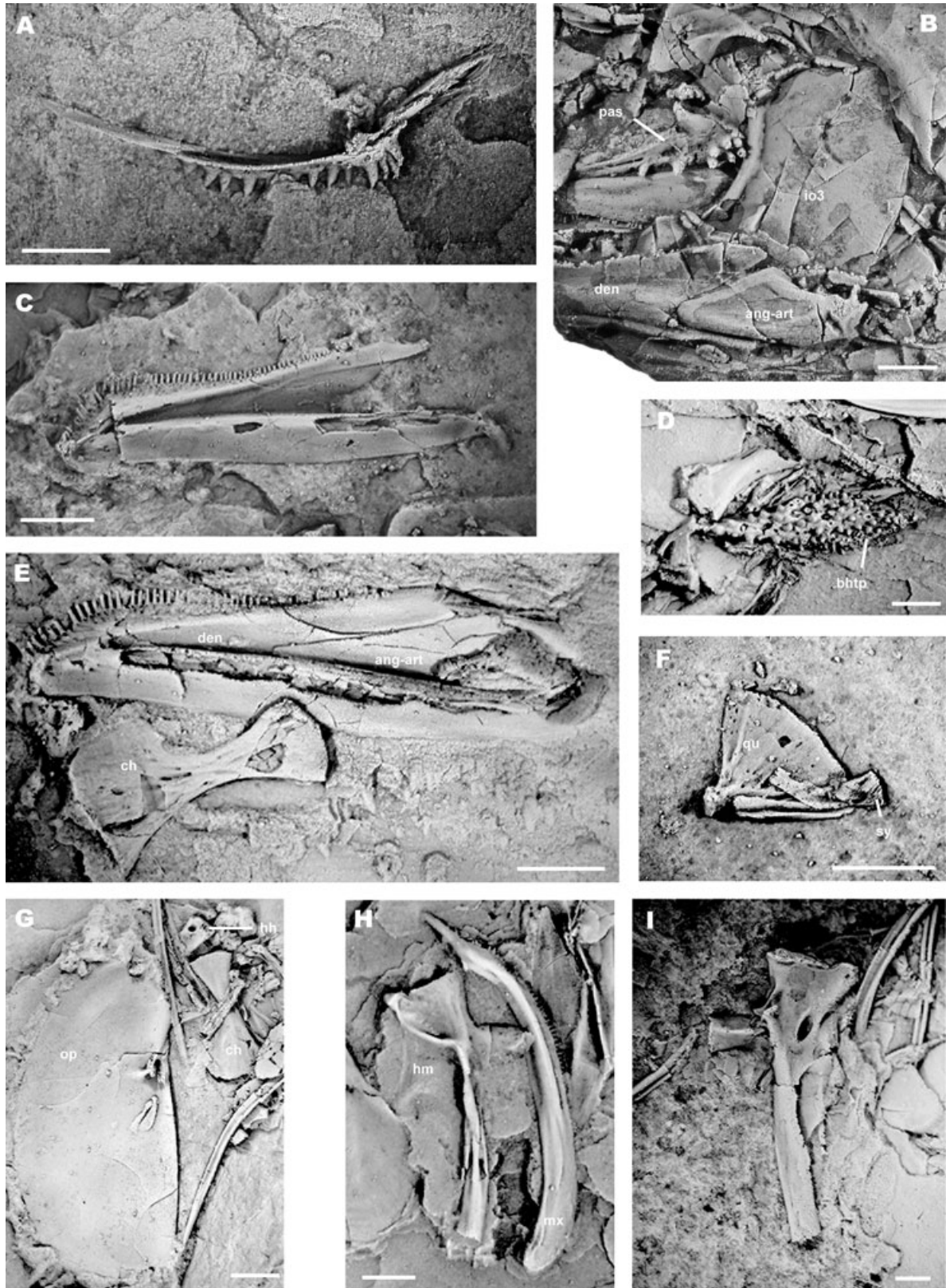
The supraoccipital was not described by Chang & Chou (1977), but revealed by our re-examinations



**Figure 5.** †*Paralycoptera wui*, cranial skeleton in dorsal view (IVPP V2989.182): A, photograph; B, explanatory drawing. Scale bar, 5 mm.



**Figure 6.** †*Paralycoptera wui*: A, IVPP V14964.1, showing two nasals meeting at mid-line; B, IVPP V2989.21, opercle and orbital series; C, IVPP V14964.2, left preopercle in lateral view. D, E, *Scleropages jordinii*: D, IVPP OP304, skull in left view; E, IVPP OP306, left preopercle in lateral view. Scale bars, 5 mm.





**Figure 7.** †*Paralycoptera wui*, disarticulated bones: A, IVPP V2989.37, parasphenoid in lateral view; B, IVPP V2989.34, posterior portion of skull, showing parasphenoid in ventral view; C, IVPP V2989.180, dentary in medial view; D, IVPP V14964.4, basihyal toothplate in dorsal view; E, IVPP V2989.138, dentary, angulo-articular and ceratohyal in external view; F, IVPP V2989.180, quadrate and symplectic; G, IVPP V2989.180, opercle in medial view, hypohyal and ceratohyal; H, IVPP V14964.2, maxilla and hyomandibular in external view; I, IVPP V2989.21, hyomandibular in medial view. Scale bars, 2 mm.

(Fig. 5). It is somewhat rectangular in outline. The occipital crest in the middle is low, differing from that of hiodontids.

The extrascapular (Figs 4, 5) lies behind the parietal and is slightly triangular and much broader than that of extant osteoglossids. The supratemporal commissural canal is enclosed in this bone.

The dermopterotic, contacting the parietal medially, is a small elongated bone. Its posterior part is slightly broader than the anterior part. The infraorbital sensory canal comes into the dermopterotic from the dermosphenotic, traverses the bone longitudinally, and then goes back and enters the extrascapular (Figs 4, 5).

The parietal is relatively large and trapezoidal in shape (Figs 2–5). The two parietals meet at the mid-line and are not separated by the supraoccipital. The parietal length is about one-half of the frontal length.

The frontal is long. Its anterior part is slightly narrower than the posterior part. The suture between the two frontals is relatively straight. The supraorbital sensory canal enters the frontal from the nasal, and then runs posteriorly along a line parallel to the lateral margin of the bone, and gives off a short branch medially, at a distance from its anterior margin of about two-thirds of its total length (Figs 3–5). The short branch does not reach the mid-line. At least four pores of the supraorbital sensory canal are visible in the frontal. Similar to that of †*Lycoptera* and *Hiodon*, but different from that of most other osteoglossiforms, the supraorbital sensory canal runs into the parietal in †*Paralycoptera*.

The nasal was not described by the previous authors because this region was often not well preserved. In our studies, well-preserved nasals were observed in specimens collected by J.-Y. Zhang and M. Shen in the 1990s (Fig. 6A). The nasal is relatively broad and is longer than wide, rather than tube-like and slender as that in *Hiodon*. Its medial margin is straight, whereas the lateral margin is slightly convex. The nasal carries the anterior part of the supraorbital sensory canal. Its posterior margin contacts the anterior margin of the frontal, and the suture between the two bones is straight. Similar to those of most osteoglossoids and notopterids, but different from those of hiodontids, the two nasals meet each other at the mid-line.

#### CIRCUMORBITAL BONES

The orbit is large (Figs 3–5, 6A, B). Its length is approximately one-third of the head length. The circumorbital series consists of six bones, including an antorbital, four infraorbitals and a dermosphenotic.

The antorbital is a subrectangular bone, partly lying on the dorsal edge of the maxilla. It contacts the frontal and nasal dorsally and the first infraorbital ventrally.

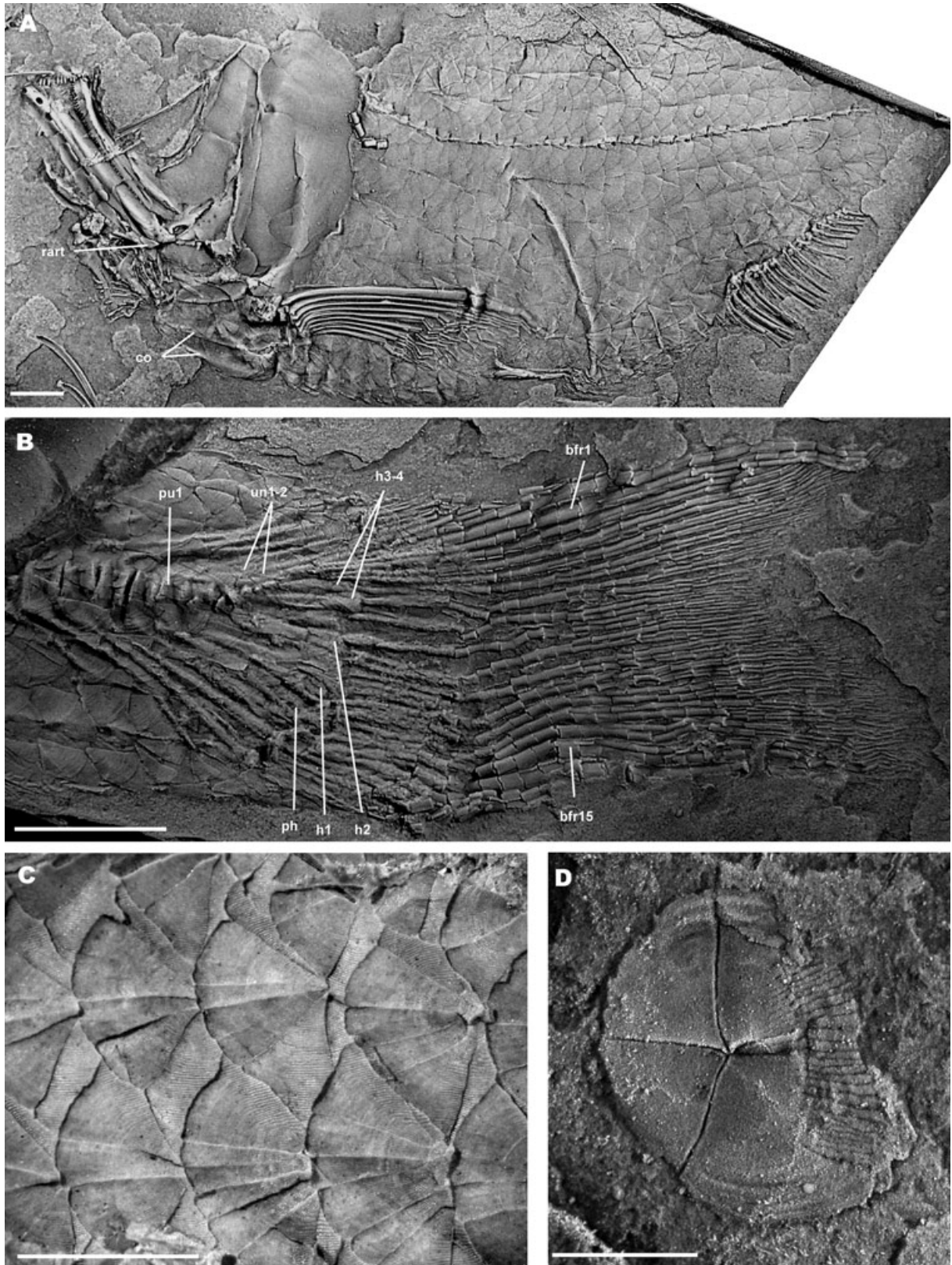
The first infraorbital (io1) is narrow and elongate. The second infraorbital (io2) is also narrow, but becomes slightly deeper posteriorly. The bone io1 contacts io2 posteriorly, and the two form the ventral margin of the orbit.

The two posterior infraorbitals (io3 and io4), covering the hyomandibular, metapterygoid, symplectic and most of the quadrate, are very broad in †*Paralycoptera*, and are similar to those in extant osteoglossids (Fig. 6D). io3 is very prominent. io4 lies dorsal to io3, and is slightly deeper than io3.

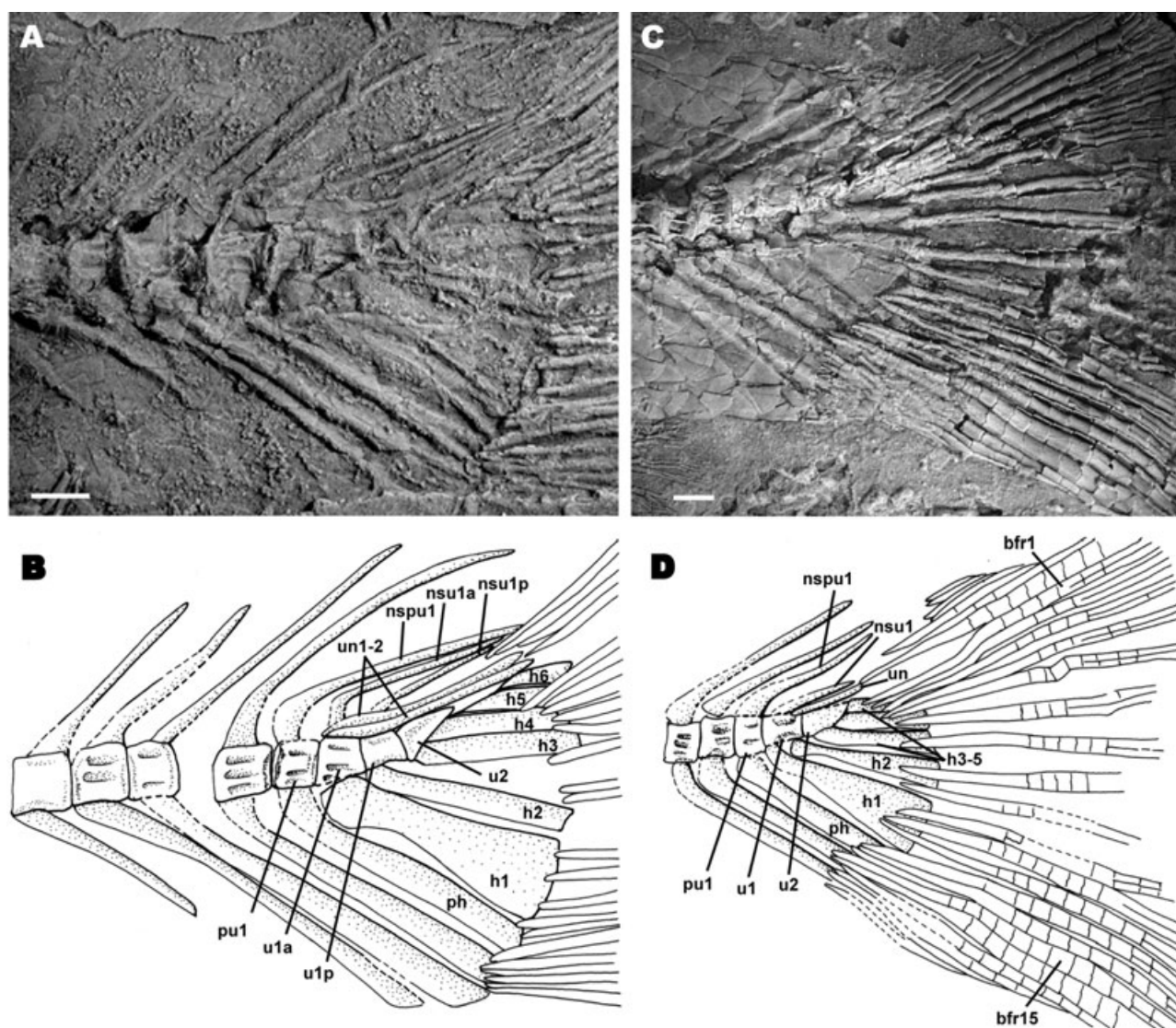
The dermosphenotic is an elongate subtriangular bone (IVPP V2989.12, 83, 181, V2990.20). It contacts the posterolateral edge of the frontal dorsally, and the anterior edge of io4 and the dermopterotic posteriorly.

The infraorbital canal runs in a tube along the orbital margin. When it enters the dermosphenotic from io4, it bifurcates into two branches. One branch runs up near its dorsal margin and the other runs posteriorly and enters the dermopterotic. The infraorbital sensory canal and otic sensory canal do not connect with the supraorbital sensory canal in †*Paralycoptera*, which is different from those in †*Phareodus* and extant osteoglossoids, but similar to those in the basal osteoglossomorphs (e.g. †*Lycoptera* and hiodontids).

As in extant osteoglossomorphs, the supraorbital is absent. When complete dermosphenotics were found in well-preserved specimens (e.g. IVPP 2989.43, 83, 181), we realized that the ‘supraorbital’ identified by Chang & Chou (1977) on the holotype was, in fact, the anterior part of the dermosphenotic in front of its sensory canal. Moreover, io4 was broken into two parts in the holotype, which caused the misinterpretation of the anterodorsal part of io4 as the ‘dermosphenotic’ (Chang & Chou, 1977: fig. 6).



**Figure 8.** †*Paralycoptera wui*: A, IVPP V2989.43, showing jaws and cheek bones, large pectoral fin, body scales and lateral line; B, IVPP V2989.46, caudal skeleton and fin; C, IVPP V14964.6, scales in posterior part of body; D, IVPP V2989.41, close-up of a single scale. Scale bars, 2 mm.



**Figure 9.** Caudal skeletons of †*Paralycoptera wui*: A, B, IVPP V2989.105, showing h1 and h2 in contact with u1a and u1p, respectively; A, photograph; B, explanatory drawing. C, D, IVPP V14964.5, both h1 and h2 in contact with u1; C, photograph; D, explanatory drawing. Scale bars, 1 mm.

**Table 1.** Measurement data (in mm)

Specimen (TL)	SL	FL	BD %SL	HL %SL	HD %SL	PPL %SL	PVL %SL	PDL %SL	PAL %SL	CPL %SL	CPD %SL	DFBL %SL	AFBL %SL
V2989.31 (~40)	35	39	13 37.1%	13 37.1%	12 34.3%	9 25.7%	17 48.6%	24 68.6%	24 68.6%	6 17.1%	5 14.3%	3 8.6%	6 17.1%
V2990.20 (~85)	67	75	22 32.8%	19 28.4%	18 26.9%	15 22.4%	27 41.5%	47 70.1%	45 67.2%	10 14.9%	8 11.9%	10 14.9%	14 20.9%
V8494 (~130)	110	126	38 34.5%	29 26.4%	28 25.5%	24 21.8%	55 50.0%	75 68.2%	78 70.9%	~20 18.2%	14 12.7%	16 14.5%	~19 17.3%

**Table 2.** Meristic data

Specimen	BR	TV	PCV	CV	SN	PFR	VFR	DFR	DP	AFR	AP	CFR	H	EP	UN
V2989.31	13	~39	~19	20	?	~8	~7	12	~12	18	~20	17	~5	?	~2
V2990.20	?	~39	~20	19	~20	9	7	10	12	18	21	17	6	0	~2
V8494	?	~40	~20	~20	?	9	5+	12	~12	15+	16+	17	6	0	~2

#### VENTRAL AND LATERAL PORTIONS OF THE BRAINCASE

The parasphenoid is a long, slightly curved bone that passes through the orbit and has paired posterior wings (Fig. 7A). Anterior to the posterior wings, it bears paired ascending processes on the dorsolateral sides and paired basipterygoid processes on the ventrolateral sides (IVPP V2989.8, 34, 45). The parasphenoid is toothed on its ventral side. The conical teeth bend forward slightly (IVPP V2989.12, 16, 33). There is only a single row of large conical teeth (about 12 in number) anterior to the basipterygoid process and two rows of teeth (about three in a row) in the area from the base of the basipterygoid process to that of the ascending process (Figs 2, 7A, B).

A semicircular orbitosphenoid has only been observed in a single specimen (IVPP V8493) from Jilin (Ma & Sun, 1988). The epiotic, intercalar and exoccipital are obscure.

#### JAWS

The upper jaw consists of the premaxilla, maxilla and supramaxilla (Figs 3–5, 7H, 8A). The premaxilla is small, elongate and triangular in lateral view. It is well toothed with at least seven conical teeth (e.g. IVPP V2989.8, 31).

The maxilla is elongate and well preserved on both disarticulated and complete specimens (e.g. IVPP V2989.31, V14964.4; V2990.20). Its anterior portion curves slightly upwards, forming an elongate narrow process that articulates with the premaxilla (Fig. 7H). Many conical teeth are present on the oral margin of the maxilla. About 60 conical teeth can be counted in well-preserved specimens (e.g. IVPP V2989.16, 31, 43). The teeth gradually decrease in size towards the back of the maxilla.

Similar to that of †*Lycoptera*, the supramaxilla is posterodorsal to the maxilla. It is a slender bone, tapering at both ends (IVPP V2989.8, 12, 31, 43; V2990.20; V8494; V8948.1, 7; Figs 2–6). The state of the supramaxilla in †*Lycoptera* was coded first as ‘absent’ by Li & Wilson (1996a), but this was changed later (see Li & Wilson, 1999). Hilton (2003) coded the state of the supramaxilla in †*Lycoptera* as unknown, which is different from most observations by other

authors (e.g. Liu *et al.*, 1963; Greenwood, 1970; Ma, 1987; Jin *et al.*, 1995), ours included. In addition to †*Paralycoptera* and †*Lycoptera*, many other fossil osteoglossomorphs possess a supramaxilla, such as †*Tongxinichthys* and †*Kuyangichthys* from Asia (Ma, 1980; Liu *et al.*, 1985; Zhang, 1998), †*Phareoides* from Australia (Taverne, 1978) and †*Brychaetus* from Europe (Roellig, 1974; Taverne, 1978, 1998). Thus, we can conclude that ‘supramaxillae absent’ must be a derived state of supramaxilla in osteoglossomorphs.

The lower jaw consists of the dentary, angulo-articular and retroarticular. The strong dentary forms the anterior part of the mandible. On several specimens, isolated dentaries are found well preserved (Fig. 7C, E). The anterior end of the bone is inturred to meet its counterpart to form the symphysis. No noticeable coronoid process is seen. The oral margin of the dentary bears numerous sharp conical teeth. About 60 teeth can be counted on IVPP V2989.180. The teeth at the anterior portion are of approximately equal length. Their sizes decrease gradually towards the rear (IVPP V2989.180). No medial wall of the Meckelian fossa is shown on the medial side of the dentary, as is the case in *Hiodon*, †*Eohiodon* and †*Lycoptera* (Hilton, 2003).

The angular appears to have fused with the articular and the angulo-articular bone inserts into the deep posterior notch of the dentary (Fig. 7B, E). A well-developed socket is situated at the posterodorsal side of the angulo-articular for receiving the articular process on the quadrate (Fig. 8A).

Our re-examination using the peel method clearly reveals the retroarticular. It is a small bone lying posteroventral to the angulo-articular (IVPP V2989.16, 43, 138; Fig. 8A). The retroarticular in †*Paralycoptera* is excluded from the articular facet for the quadrate, which is similar to the observations in most extant osteoglossiforms (except *Pantodon*, *Arapaima*, *Heterotis*). †*Lycoptera* might be similar to †*Paralycoptera* in this character (Ma, 1987; Jin *et al.*, 1995), whereas the retroarticular is fused with the angular and is included in the jaw joint in *Hiodon* (Hilton, 2003).

The mandibular sensory canal enters the angulo-articular from the preopercular, and then runs into the dentary. Five pores of the mandibular sensory canal can be observed in the dentary (Fig. 4).

## PALATO-PTERYGO-QUADRATE ARCH

The endopterygoid has a straight upper edge and an arched lower edge. It bears a broad tooth patch with numerous densely set conical teeth on its inner surface (Figs 4, 6A).

The ectopterygoid lies to the external anterior side of the endopterygoid. It is slender and toothed (Figs 4, 6A). The dermopalatine and ectopterygoid are separated in *Hiodon*, whereas they are fused into one element in extant osteoglossiforms. It is hard to know whether or not the ectopterygoid of †*Paralycoptera* is fused to the dermopalatine.

The metapterygoid is still unclear because it is often covered by the posterior infraorbitals.

The quadrate and the symplectic are not easily visible in complete specimens, but are well preserved as detached bones found on some specimens (Fig. 7F). The main part of the quadrate is fan shaped, with an elongated ventral process. The anteroventral end of the bone bears a process that articulates with the socket on the posterodorsal side of the angulo-articular. The symplectic is a small, long strip-like bone. Its slender anterior end fits into the deep notch between the main part and the long ventral process of the quadrate (Fig. 7F).

## HYOID ARCH

The hyomandibula, which serves for the suspension of the jaw from the neurocranium, has a large triangular dorsal portion, a long vertical ventral shaft, a rather extensive, thin anterior plate, and a robust posterior process which articulates with the anterodorsal socket of the opercle (Fig. 7H, I). The dorsal margin of the triangular dorsal portion, which articulates with the ventrolateral part of the neurocranium, is broad and slightly curved. It has two continuous heads as in most osteoglossomorphs (except *Hiodon* and heterotidins). The external surface of the vertical shaft bears a longitudinal ridge (Fig. 7H), whereas the inner surface is relatively smooth (Fig. 7I). The strong opercular process projects from the posterior margin of the hyomandibular, approximately at the level between the dorsal triangular portion and the shaft. From the anterior margin of the triangular portion and the shaft, a thin plate extends forwards. The anterior tip of the thin plate does not seem to be in contact with the endopterygoid, based on available specimens. At the level of the opercular process, a large, oval foramen on the inner side of the dorsal portion of the hyomandibular can be seen (Fig. 7I). It is interpreted as the opening for the hyomandibular ramus of the facial nerve (VII) and the efferent hyoidean artery to traverse.

The hypohyal is often preserved together with the anterior ceratohyal. There is a foramen for the

hyoidean artery on the lateral face of the hypohyal (Fig. 7G).

The anterior ceratohyal is comparatively flat and hourglass shaped (Figs 7D, E, G, 8A). The posterior ceratohyal is only partially preserved.

Disarticulated, elongate, fusiform, bisymmetrical toothplates with large, randomly set teeth are found in several specimens (e.g. IVPP V14964.1, 14964.4; Figs 6A, 7D). One of these toothplates is next to the ceratohyal. A bone with a similar shape and structure was found in two specimens (IVPP V2328.6, V2328.9) of †*Lycoptera davidi*, named as the basi-hyal toothplate and illustrated by Ma (1987: fig. 8). The bone in both †*Paralycoptera* and †*Lycoptera*, however, also looks somewhat like the anterior basibranchial toothplate in *Arapaima* (Hilton, 2003: fig. 30C). Thus, more information on its exact position is needed to determine whether it is a basi-hyal or basibranchial toothplate.

## OPERCULAR SERIES AND BRANCHIOSTEGAL RAYS

A complete opercular series is preserved on the holotype, and portions of it on many other specimens (Fig. 6B).

The preopercle is curved. Its vertical limb is narrower and much longer than the horizontal limb (Fig. 6B, C). The preoperculo-mandibular canal goes down along the anterior margin of the vertical limb, and then turns anteroventrally along the dorsal margin of the horizontal limb until it enters the angulo-articular. On the horizontal limb, the canal sends off four to five branches posteroventrally to the very ventral margin of the preopercle. The dorsal sections of the branches are shaded by a bony cover which ends halfway to the ventral margin of the horizontal limb, leaving the ventral sections of the branches lying in open grooves. This situation is very similar to that in most osteoglossiforms (e.g. †*Singida*, †*Phareodus*, *Pantodon*, notopterids and osteoglossins). For instance, in the specimens of extant *Scleropages* that we examined (Fig. 6D, E), the canal also gives off about four branches on the horizontal limb. Unlike those in †*Paralycoptera*, the branches do not leave any grooves on the surface of the ventral portion of the horizontal limb, and not all branches extend posteroventrally. In *Scleropages*, the anterior two branches turn anteroventrally, the third goes ventrally, and only the posterior branch turns slightly posteroventrally. The situation in *Osteoglossum* and *Notopterus* is more or less the same (Taverne, 1977, 1978). Furthermore, on the lower portion of the canal on the vertical limb, a large pore opens posteroventrally in *Scleropages*, *Osteoglossum* and *Notopterus*, whereas no such structure has been found in †*Paralycoptera*. Instead, quite a few small

pores of various sizes are distributed along the canal. They most probably carried small branches of the preopercular canal. The anterior margin of the preopercle is covered slightly by the posterior margins of the two broad posterior infraorbitals (IVPP V2989.12, 21, 181; IVPP V2990.20).

Similar to †*Singida*, †*Phareodus* and most extant osteoglossoids, the opercle of †*Paralycoptera* is tall. It has a straight anterior edge and a rounded, smooth posterior edge, without serrations. Its depth is about twice its width (Figs 6B, 7E). The surface is marked by weak striations radiating from the point of articulation.

The subopercle is large and lies ventral to the opercle (Fig. 6B), which is similar to the condition in †*Lycoptera*, *Hiodon* and mormyroids, but differs from the situation in †*Singida*, †*Phareodus* and extant osteoglossids, in which the subopercle is small and anterior to the opercle (Fig. 6D). In *Pantodon* and notopterids, the subopercle is absent.

A complete interopercle is preserved on IVPP V2989.180. It is triangular in shape.

About 13 branchiostegal rays are present (Fig. 4). The anterior ones are slender, whereas their width gradually increases posteriorly in the series.

No gular plates are found in the available specimens, which differs from the condition in †*Lycoptera*.

#### VERTEBRAL COLUMN

In the holotype (Fig. 2A), about 19 caudal vertebrae and about 16 abdominal vertebrae can be counted behind the opercle. If, as we suggest, there are about four vertebrae covered by the opercle, the total number of vertebrae is around 39 ( $-4 + 16 + 19$ ).

The well-ossified centra are amphicoelous and bear a relatively large opening in the centre for the notochord. They are slightly deeper than long, except for the two ural centra. There are about four to five longitudinal ridges on the lateral surface of the centra.

About 18 pairs of ribs extend to the ventral margin of the trunk and insert on the lower side of the abdominal vertebrae (Fig. 2). The anterior two pairs of ribs are often only partly exposed, extending from beneath the posterior edge of the opercle (e.g. IVPP V2989.12, 31). It is hard to see how exactly the ribs insert.

The supraneurals are thin, slightly sigmoid, with their proximal ends inserting between the neural spines of the abdominal vertebrae. About 20 supraneurals are present anterior to the dorsal fin (Fig. 2).

The neural arches on the first 24 vertebrae each bear a pair of epineurals that extend posterodorsally from the bases of the neural arches. The epineurals are long, slender rods with no bifurcation (Fig. 2).

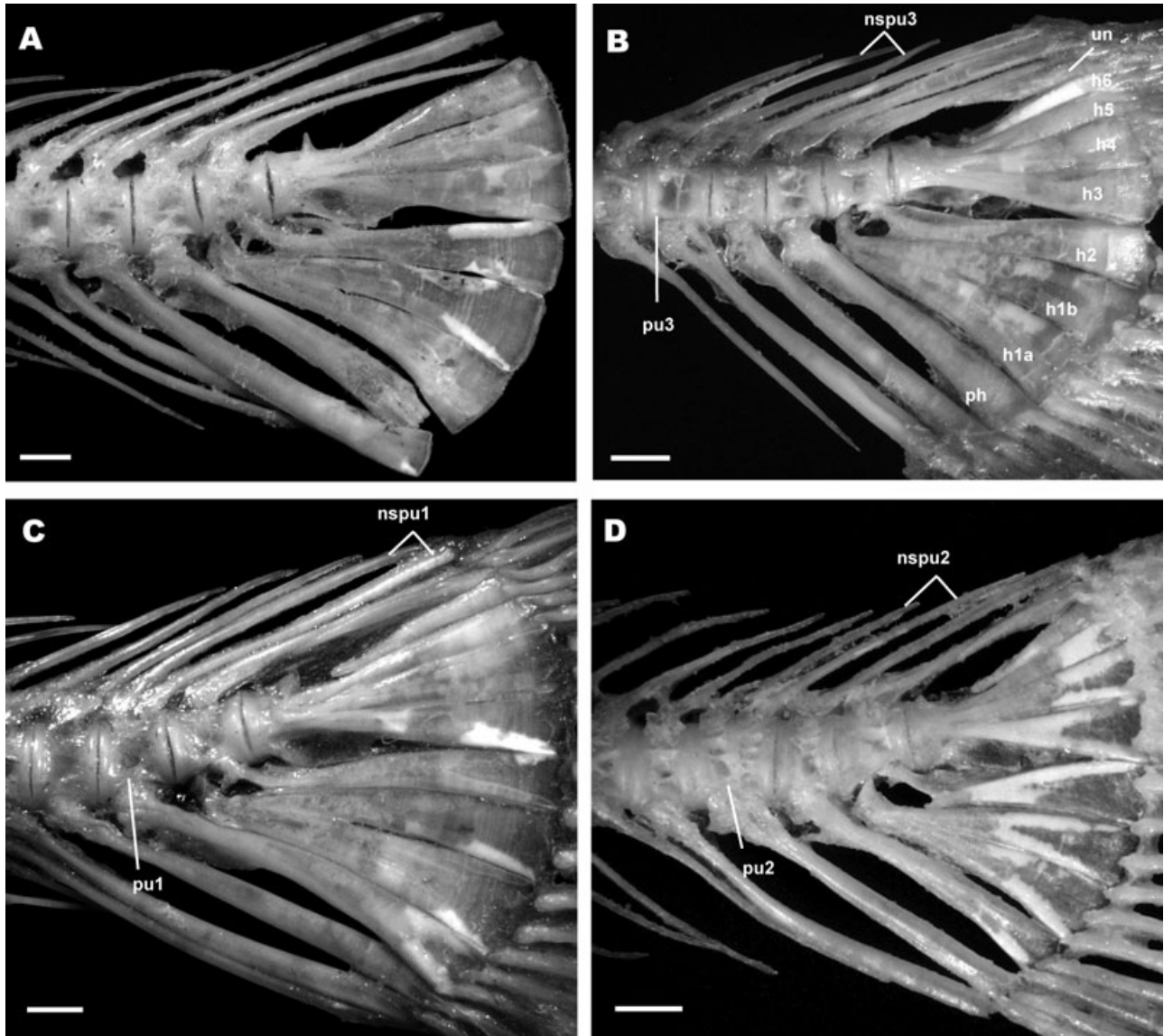
As for most osteoglossomorphs (except *Heterotis*), †*Paralycoptera* has no epipleurals.

#### CAUDAL SKELETON

Six hypurals are visible in the available caudal skeletons (Figs 8B, 9). The hypurals 1 and 2 support the caudal fin rays of the lower lobe. Their articulation with the ural centrum (a) and the number of ural centra show individual variations. Both hypurals articulate with a single ural centrum (u1) in some specimens (Fig. 9B), whereas each articulates with one ural centrum in others (Fig. 9A). Greenwood (1970: fig. 10) and Patterson & Rosen (1977: fig. 24) observed that the first ural centrum of some adult teleosts was composed of two distinct centra. Following the terminology used by Greenwood (1970: fig. 10) to describe †*L. davidi*, we use 'u1a' and 'u1p' to refer to the anterior and posterior components of the first ural centrum (u1) in this condition.

Hypurals 3–6 support the caudal fin rays of the upper lobe. Hypurals 3–5 articulate with the second ural centrum (u2), whereas hypural 6 might be free. Of the six hypurals, hypural 1 is the broadest and longest, with an expanded distal end (Fig. 9). The other hypurals are narrower and decrease in length posterodorsally. When we examined materials of extant *Scleropages* (Fig. 10), we found seven hypurals in *S. jardinii* and *S. leichardti* (species from Australia) and six hypurals (as in †*Paralycoptera*) in *S. formosus* (species from South-East Asia). In all materials of *S. jardinii* and *S. leichardti* examined, there are three hypurals connected with u1, the anterior two partly joined proximally. In contrast, only two hypurals are present in *S. formosus*. Hilton (2003) noticed that the element corresponding to hypural 1 in *S. formosus* was almost completely divided in *S. jardinii*, and interpreted it as two independent hypurals. More recently, however, Hilton & Britz (2007) regarded 'the possessing of the "third" hypural in the ventral portion of the caudal skeleton' of *S. jardinii* and *S. leichardti* 'as unique among osteoglossomorphs'.

Similar to most osteoglossiforms (except mormyroids) and *Hiodon*, †*Paralycoptera* bears a completely developed neural spine on u1 and pu1. No double neural spines on pu1–pu3, as those in †*Phareodus* (Taverne, 1978: fig. 13; Li *et al.*, 1997a: fig. 5) and extant osteoglossids (Leal & Brito, 2007), are found in our materials of †*Paralycoptera*. In extant *Scleropages*, we found that the positions of the doubled neural spines are variable in specimens in which they occur in *S. jardinii* and *S. leichardti* (Fig. 10B–D). For example, they occur on pu1 in IVPP OP81 (Fig. 10C), on pu2 in IVPP OP304 (Fig. 10D) and on pu3 in IVPP OP306 (Fig. 10B). In some specimens, there are no



**Figure 10.** Variation of caudal skeletons of *Scleropages*. A, B, D, *S. jardinii*; C, *S. leichardti*. Three hypurals (the two anterior ones partially fused) attached to u1 in all specimens. A, IVPP OP307, un and h6 were removed, no double neural spines occur; B, IVPP OP306, double neural spines on pu3; C, IVPP OP81, double neural spines on pu1; D, IVPP OP304, double neural spines on pu2. Scale bars, 5 mm.

doubled neural spines at all (Fig. 10A). Similar variations were also seen in *Osteoglossum bicirrhosum* (Leal & Brito, 2007).

Two or three slender uroneurals are present on each side of the caudal centra, and the most anterior one stretches forwards, at least to overlap the posterodorsal part of pu1 (Fig. 9). The number of uroneurals ranges between two and four in *Hiodon* (Hilton, 2002). Two or more uroneurals are also present in †*Lycoptera* and †*Singida*, whereas only one is present in †*Phareodus* and all extant osteoglossiforms except notopterids.

Epurals are not found in our materials of †*Paralycoptera*. *Hiodon* bears one epural, and †*Lycoptera* was also thought to have one to three epurals (Gaudant, 1968; Greenwood, 1970; Patterson & Rosen, 1977; Taverne, 1977), whereas extant osteoglossiforms do not have any (e.g. Taverne, 1968: fig. 16; 1977: fig. 66; 1978: fig. 54; Nelson, 1969: fig. 17; Hilton, 2003: figs 35–38; Fig. 10). 'Epurals absent' might also be a common feature in fossil osteoglossiforms. †*Singida* has an element identified as the epural (Greenwood & Patterson, 1967), but later interpreted as the neural spine on u1

(Taverne, 1998: fig. 19; Murray & Wilson, 2005: fig. 6). A small bone in the caudal skeleton of †*Phareodus*, identified as the epural by Li *et al.* (1997a), was interpreted as the uroneural by others (Taverne, 1978: fig. 13; Hilton, 2003: fig. 38).

#### PAIRED FINS AND GIRDLES

The post-temporal is a forked bone (IVPP V14964. 4). Its dorsal limb is longer than the ventral limb. The supracleithrum is an elongate bone (Fig. 5). The cleithra are well preserved in both complete specimens and as disarticulated bones (IVPP V2989.38, V14964.2). They have a curved, ridged external surface and a smooth inner surface. The angle formed by the vertical dorsal part and the horizontal ventral part is slightly larger than 90°.

The paired coracoid blade is partly preserved in IVPP V2989.43 (Fig. 8A). No coracoid fenestra is found in available materials of †*Paralycoptera*, whereas it is present in †*Singida*, †*Phareodus* and nearly all extant osteoglossiforms (except *Arapaima*) (Fig. 6D).

The pectoral fin contains nine rays. The first is unbranched but segmented distally, and is quite strong and long, extending beyond the origin of the pelvic fin (Figs 2, 8A). This is similar to those of †*Singida*, †*Phareodus* and extant osteoglossines. The other eight are branched and segmented.

The origin of the pelvic fin lies at about the midpoint between the pectoral and anal fin. The pelvic bone has an elongated triangular shape, with its posterior end enlarged. The small pelvic fin has seven branched and segmented rays (IVPP V2989.135).

#### DORSAL AND ANAL FINS

The dorsal fin is set well back on the body, approximately opposite to the anal fin (Fig. 2). It has 12 fin rays, the first two small ones of which are unbranched and unsegmented, whereas the third is long, unbranched, but segmented distally (IVPP V2992.2). The rest of the fin rays are all segmented and branched. Eleven dorsal pterygiophores (proximal radials) are observed, supporting the dorsal fin rays. All branched rays and pterygiophores decrease in length posteriorly.

The anal fin is larger than the dorsal fin. It consists of 18 segmented rays preceded by two small unsegmented rays (IVPP V2990.20, V2992.2). Of the 19 segmented principal anal fin rays, the first is unbranched, and the others are branched; 20–21 anal pterygiophores are seen, supporting the anal fin rays (IVPP V2992.2, V2990.20).

#### CAUDAL FIN

The caudal fin is moderately forked (Figs 2, 8B), similar to that of †*Singida* and †*Phareodus*. It has 17

principal rays, with the dorsal and ventral marginal principal rays distally segmented but not branched. The segmented and branched rays are 15 in total, seven in the upper and eight in the lower lobe. Hiodontids and mormyrids have 16 principal branched caudal fin rays, whereas most extant osteoglossids (except *Arapaima*) have 14 or fewer principal branched caudal fin rays (14 in *Scleropages jardinii*, 12 in *S. formosus*, 10 in *Osteoglossum* and 14 in *Heterotis*). Normally, the number of principal branched fin rays is 16 in †*L. davidi* (17 branched rays are observed occasionally), and 15 in †*L. sinensis*.

The proximal end of the lowermost principal ray contacts the hemal spine on pu2 (Fig. 9). There are about six procurrent rays in the upper lobe and five in the lower lobe.

#### SCALES

The body is covered with large cycloid scales. The lateral line is well demonstrated on several specimens (Figs 2A, 8A). At least 28 lateral line scales could be counted from the holotype and 29 from IVPP V2989.43 (Fig. 8A), roughly 20 from the origin of the anal fin to the posterior margin of the opercle. The total number of lateral line scales is about 40. There are four lines of scales above and five under the lateral line. On the surface of the scales, fine circuli are well shown in many specimens (Fig. 8), but no reticulate furrows, similar to those present in †*Phareodus* and extant osteoglossoids, were observed on any specimen. No such furrows were revealed in †*Singida* either (Greenwood & Patterson, 1967; Murray & Wilson, 2005). Ma & Sun (1988) claimed that reticulate furrows might have been present on the scales of †*Paralycoptera*, based on a single specimen (IVPP V8494) from Jilin, but gave no illustrations or detailed descriptions. We examined the specimen carefully, but failed to find any similar structures. Jin *et al.* (1995) also alleged that reticulate furrows were present on the anterior part of the scale of †*Paralycoptera* sp., based on their observations of a detached scale (IVPP V10666.3) from Liaoning. After examining the specimen, we are not convinced that the structures displayed on IVPP V10666.3 represent reticulate furrows, because they do not show a regular pattern, and are only restricted to the anterior portion of the scale. We would rather suggest that the structures were caused by crushing and/or weathering. Based on our examinations of the scales on well-preserved specimens (Figs 2, 8), we believe that no reticulate furrows are present on the scales of †*Paralycoptera*.

#### DISCUSSIONS OF SYNONYMIES

†*Yungkangichthys hsitansensis* was erected based on several specimens from the same localities as †*P. wui*.



Only two specimens now remain. Although the body of the holotype of †*Y. hsitanensis* (IVPP V2999.3) looks visibly higher, than that of †*P. wui*, this difference could be attributed to taphonomic distortion of the former. Another referred specimen (IVPP V2989.122) is incomplete, with only the posterior portion of the trunk preserved; this is almost the same as †*P. wui* in osteology. We are thus inclined to suggest that †*Y. hsitanensis* is probably synonymous with †*P. wui*.

When Ma & Sun (1988) erected a new species of †*Paralycoptera*, †*P. changi*, they believed that †*P. changi* was different from †*P. wui* in lacking the supramaxilla and bearing fewer anal pterygiophores. However, after re-examination of the materials of †*P. changi* from north-east China (Ma & Sun, 1988; Jin, 1991), we confirmed the presence of the following osteological characters in †*P. changi*: (1) one supramaxilla (e.g. IVPP V8494, V8948.1, 7); (2) palatoquadrate area behind and below orbit completely covered by infraorbitals; (3) opercle depth/width ratio about two; (4) anal pterygiophores about 18; (5) p<sub>1</sub> and u<sub>1</sub> bearing complete neural spines (IVPP V8494); (6) branched caudal fin rays 15 (e.g. IVPP V8948.9, 12). Thus, materials from north-east and south-east China may well be referred to the same species: †*P. wui*.

Jin *et al.* (1995) suggested that †*Tanolepis ninjiagouensis* was the synonym of †*P. changi* because the distinctions between †*Tanolepis* and †*Paralycoptera* mentioned in Jin (1991) did not exist. The distinctions between †*Tanolepis* and †*Paralycoptera* listed by Li *et al.* (1997b) are not credible according to Jin *et al.*'s (1995) and our re-examinations. †*Tanolepis* is regarded as synonymous with †*Paralycoptera* following Jin *et al.* (1995).

Among the recently described fauna from the Early Cretaceous Wakino Subgroup (Kwanmon Group) of Kitakyushu, Japan, †*Aokiichthys* is most similar to †*Paralycoptera*, but was thought to have fewer vertebrae (Yabumoto, 1994). However, the vertebral counts for different species of †*Aokiichthys* provided by Yabumoto (1994: 148, table 3) are quite similar to the number in †*P. wui*: †*A. toriyamai* (16–17 + 17–19), †*A. changae* (16–17 + 18–19), †*A. otai* (16–17 + 17–19), †*A. uyenoi* (16–17 + 17–18), †*A. praedorsalis* (17 + 18). We suspect that a few vertebrae were covered by the opercle, and thus were not included in the total number of vertebrae by Yabumoto (1994). If this is the case, there is no difference in the number of vertebrae between the two genera, and †*Aokiichthys* should also be synonymous with †*Paralycoptera*. Moreover, it seems that the differences in the number of vertebrae in the five species of †*Aokiichthys* mentioned above may not be of much systematic significance.

Jin *et al.* (1995) reported †*Paralycoptera* sp. based on incomplete specimens (IVPP V10666.1–4,

V10668.1–3) found in the Shahaai Formation in Fuxin County, West Liaoning. These incomplete materials are only disarticulated bones and are therefore difficult to identify.

#### PHYLOGENETIC ANALYSIS

Chang and Chou (1977) originally assigned †*Paralycoptera* to the †*Lycoperidae* (†*Lycoperiformes*), but mentioned its shared characters with osteoglossomorphs. In their 1976 paper (actually written after their 1977 paper was submitted for publication), Chang & Chou suggested that †*P. wui* might be a primitive member of the Osteoglossoidei, closely related to †*L. sinensis* but different from †*L. davidi*. However, no phylogenetic analysis was conducted in either paper. The phylogenetic position of †*Paralycoptera* remains uncertain in more recent analyses. It was regarded as the stem osteoglossomorph by Shen (1996) and Bonde (1996), stem osteoglossoid by Li *et al.* (1997b), stem osteoglossiform by Zhang (1998, 2004) and osteoglossid by Zhang (2006).

In order to reassess the phylogenetic position of †*Paralycoptera*, we performed a phylogenetic analysis. In addition to †*Paralycoptera*, †*Lycoptera* from the Early Cretaceous of north China (Liu *et al.*, 1963; Greenwood, 1970; Ma, 1987; Jin *et al.*, 1995; Zhang, 2002), †*Singida* from the Eocene lacustrine shale of Tanzania in East Africa (Greenwood & Patterson, 1967; Murray & Wilson, 2005), †*Phareodus* from the early to middle Eocene Green River Formation of Wyoming (Taverne, 1978; Grande, 1984; Li *et al.*, 1997a) and eight extant genera (*Hiodon*, *Osteoglossum*, *Scleropages*, *Arapaima*, *Heterotis*, *Pantodon*, *Notopterus* and *Gnathonemus*) were included in the analysis. Other fossil genera referred to the Osteoglossomorpha, such as †*Musperia* from South-East Asia (Sanders, 1934), †*Chanopsis* from Africa (Taverne, 1984), †*Laeliichthys* from South America (Taverne, 1979; da Silva Santos, 1985), †*Joffrichthys* from Alberta (Canada) and North Dakota (USA) in North America (Li & Wilson, 1996a; Newbrey & Bozek, 2000), †*Palaeonotopterus* (Forey, 1997; Taverne & Maisey, 1999; Cavin & Forey, 2001), and several marine genera redescribed by Taverne (1998) (e.g. †*Monopteros*, †*Thrissopterus* and †*Foreyichthys*) were not included in our analyses because they are not adequately known based on available materials at present. Some early osteoglossomorphs from China under study were also not included in this analysis.

†*Leptolepis*, *Elops* (Elopomorpha) and *Odaxothrissa* (Clupeomorpha) were selected as outgroups, based on previous hypotheses on the phylogenetic relationships of teleosts (e.g. Patterson & Rosen, 1977; Arratia, 1991, 1997). †*Leptolepis* has long been regarded as a basal teleost. The Osteoglossomorpha was suggested

by Patterson & Rosen (1977) as the most basal teleost group with living representatives, and Elopomorpha and Clupeomorpha as sequential sister groups to Euteleostei. Elopomorpha (represented by *Elops*) was suggested later by Arratia (1991, 1997) as more basal than osteoglossomorphs, but other recent studies (e.g. Forey *et al.*, 1996; Inoue *et al.*, 2001) upheld Patterson & Rosen's (1977) hypothesis.

#### CHARACTER SELECTION AND CODINGS

The 65 characters listed in Appendix S1 are mainly those used in previous analyses (e.g. Shen, Jin & Zhang, 1991; Li & Wilson, 1996b, 1999; Li *et al.*, 1997a; Taverne, 1998; Zhang, 1998, 2006; Hilton, 2003), some are combined or modified, and a few are used here for the first time. More than 20 species have been named under the genus †*Lycoptera*. This makes the coding for †*Lycoptera* complicated. In order to simplify the case, we selected †*L. davidi* as the representative of the genus. Its coding was based on our own observations and descriptions by previous authors (e.g. Liu *et al.*, 1963; Greenwood, 1970; Ma, 1987; Jin *et al.*, 1995). The characters of other fossil genera, †*Singida*, †*Phareodus* and †*Leptolepis*, were taken from other workers (Greenwood & Patterson, 1967; Nybelin, 1974; Patterson & Rosen, 1977; Taverne, 1978, 1979, 1998; Bonde, 1996; Li *et al.*, 1997a; Hilton, 2003; Murray & Wilson, 2005). The characters of extant genera were based on the studies of Taverne (1968, 1977, 1978), Kershaw (1970), Forey (1973), Grande (1985), Schultze & Arratia (1988), Arratia (1991), Hilton (2002, 2003) and Moritz & Britz (2005), as well as our own examinations on available materials of five genera (*Hiodon*, *Osteoglossum*, *Scleropages*, *Notopterus* and *Gnathonemus*).

Cladistic analysis was carried out using PAUP 4.0b10 (Swofford, 2002). All characters were unordered and equally weighted. Each of the states of a given character was placed in parentheses following the number of the character [e.g. 1(1) is character state 1 of character 1]. Missing or unknown data were coded by question marks in the data matrix (Appendix S2).

#### RESULTS

Our analyses (using the branch-and-bound search) generated one most parsimonious tree with a length of 151 steps, a consistency index (CI) of 0.5695 (0.5423 excluding uninformative characters), a retention index of 0.6977 and a rescaled consistency index of 0.3974 (Fig. 11). In this section, we explain the result and list the main characters (CI  $\geq$  0.5) that support the key nodes of the tree. Characters with an asterisk (\*) have a CI of 1.0.

The cladistic analysis largely agrees with previous hypotheses that †*Lycoptera* is the sister group of all

other osteoglossomorphs (Li & Wilson, 1996b), and the monophyly of Osteoglossomorpha is supported by the following derived characters: supraorbital absent 14(1)\*; epural one or absent 56(1)\*; intestine coiling to left of stomach 65(1)\*; four bones in infraorbital series, not including dermosphenotic or antorbital 18(1); and 16 principal branched caudal fin rays or fewer 62(1).

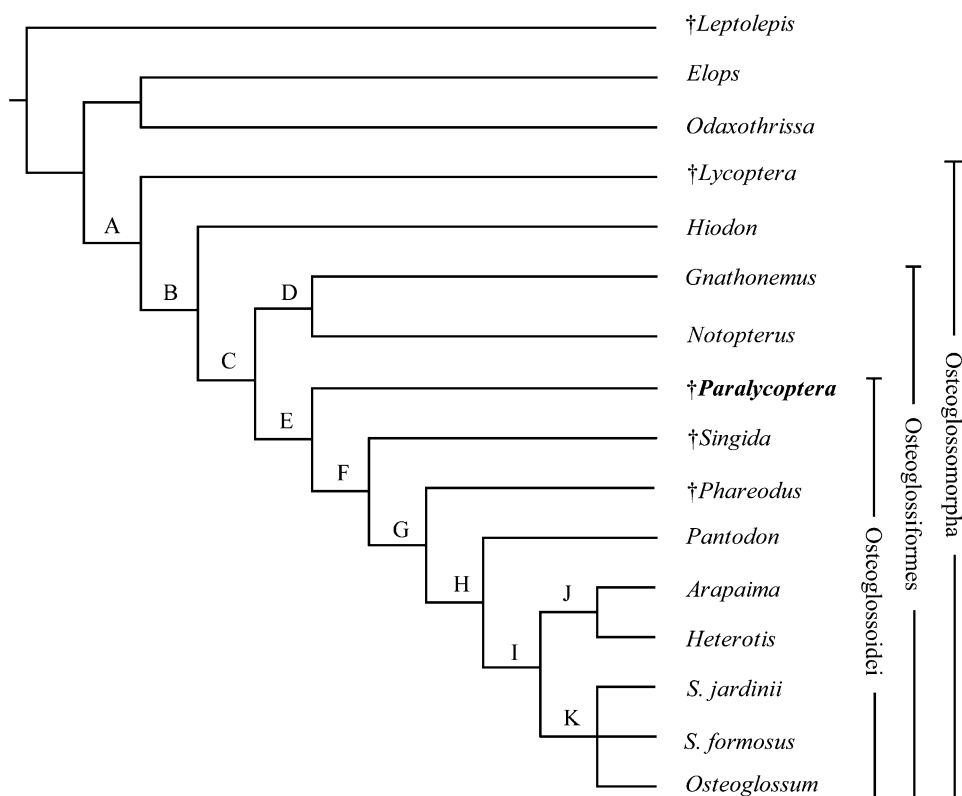
Within the Osteoglossomorpha, the Osteoglossiformes is the sister group of the Hiodontiformes. The monophyly of Osteoglossiformes is supported by the following derived characters: bony elements associated with the second ventral gill arch present as a bony process on second hypobranchial 31(2)\*; one ossified pair of hypohyals 35(1)\*; palatine and ectopterygoid fused 40(1)\*; four or fewer upper hypurals 59(1)\*; neural spine on u1 completely developed 55(1); and principal branched caudal fin rays 15 or fewer 62(2).

Of the two subgroups (Osteoglossoidae and Notopteroidei) of the Osteoglossiformes, †*Paralycoptera* shares more derived characters with the Osteoglossoidae. The monophyly of the Osteoglossoidae is supported by the following derived characters: palatoquadrate area behind and below orbit completely covered by infraorbitals 20(1)\*; jaw articulation under posterior part of orbit 25(2); basibranchial toothplate fused to basihyal toothplate 32(1); opercle depth twice or more its width 43(1); and first pectoral fin ray much enlarged and long, extending backwards beyond origin of pelvic fin 52(1). †*Paralycoptera* is the most basal osteoglossoid.

†*Singida* and †*Phareodus* are regarded here as different levels of osteoglossoids above †*Paralycoptera*. †*Singida* is more derived than †*Paralycoptera*, sharing the following derived characters of †*Phareodus* plus extant osteoglossoids: articulation of jaw posterior to orbit 25(2); anterior process of hyomandibula contacting entopterygoid 37(1); and subopercle small, anterior to opercle 41(1). †*Phareodus* differs from †*Singida*, sharing the following derived characters of extant osteoglossoids: supraorbital and otic sensory canals connected 9(1); one paired uroneural 57(2); and reticulate furrows present over entire scale 64(1).

Within the extant osteoglossoids, the sister group relationship between the Pantodontidae and Osteoglossidae is supported by the following derived characters: caudal fin unforked 63(1)\*, basisphenoid absent 7(1); and most upper hypurals fused with last centrum 60(1). Within the Osteoglossidae, the sister group relationship between the Osteoglossinae and Heterotidinae is supported by the derived character: temporal fossae bordered by epioccipital and pterotic 8(3)\*.

The monophyly of Notopteroidei has been supported by most phylogenetic hypotheses based on



**Figure 11.** The most parsimonious tree generated by PAUP 4.01b, showing the hypothetical phylogeny of Osteoglossomorpha. Characters supporting the nodes: Node A: 2(1), 4(1), 14(1)\*, 18(1), 56(1)\*, 62(1), 65(1)\*; Node B: 27(1), 36(1); Node C: 2(2), 31(2)\*, 35(1)\*, 40(1)\*, 45(1), 47(1), 55(1), 59(1)\*, 62(2); Node D: 1(1), 5(1)\*, 6(1), 8(1)\*, 10(1), 11(1), 17(1)\*, 29(1)\*, 57(2), 58(1), 60(1); Node E: 3(1), 20(1)\*, 25(1), 32(1), 43(1), 52(1); Node F: 12(1), 25(2), 37(1), 41(1); Node G: 9(1), 10(1), 49(1), 57(2), 64(1); Node H: 7(1), 60(1), 63(1)\*; Node I: 8(3)\*, 11(1), 24(1); Node J: 3(0), 16(1), 25(0), 28(1), 30(2), 32(0), 34(1)\*, 38(1), 39(1), 43(0), 45(0), 52(0); Node K: 4(0), 15(1)\*, 23(1). Character with asterisk has a consistency index (CI) of 1.0.

morphological data (e.g. Greenwood, 1973; Li & Wilson, 1996a; Taverne, 1998; but see Hilton, 2003) and molecular data (e.g. Lavoué & Sullivan, 2004). We used the genera *Notopterus* (Notopteridae) and *Gnathonemus* (Mormyridae) as representatives of the Notopteroidei. The monophyly of Notopteroidei is supported by the following derived characters in our analysis: supraorbital branch of otic sensory canal present 5(1)\*; temporal fossae bordered by epioccipital, exoccipital and pterotic 8(1)\*; infraorbital sensory canal in some infraorbitals open in groove 17(1)\*; mandibular canal open in groove 29(1)\*; nasal broad, gutter-like 1(1); otic and supraorbital sensory canal partially or completely in grooves 6(1); utriculus completely separated from sacculus and lagena 58(1); and most upper hypurals fused with last centrum 60(1).

## DISCUSSION

A number of schemes showing the relationships of the Osteoglossomorpha have been proposed in the past, based on both morphological (e.g. Greenwood *et al.*,

1966; Nelson, 1968, 1969, 1973; Greenwood, 1973; Patterson & Rosen, 1977; Taverne, 1979, 1998; Bonde, 1996; Li & Wilson, 1996a, b, 1999; Shen, 1996; Li *et al.*, 1997a, b; Zhang, 1998, 2004, 2006; Hilton, 2003) and molecular (e.g. Lavoué *et al.*, 2000; Lavoué & Sullivan, 2004) data. Hilton (2003) recently reviewed the history of the classification and systematic study of the osteoglossomorphs, and discussed the characters used in previous phylogenetic analyses of the Osteoglossomorpha. His hypothesis, based on 65 informative morphological characters drawn from 19 osteoglossomorph taxa and a single outgroup (*Elops*), differs from previous analyses in the placement of the notoapteroids as the sister group to the osteoglossoids, rather than to the mormyroids. This indicated that the Notopteroidei is not a monophyletic group. In recent years, the molecular analysis of the phylogeny of the Osteoglossomorpha has been well studied. Based on the analysis of more than 4000 characters from five molecular markers (mitochondrial cytochrome *b*, 12S and 16S rRNA genes, and the nuclear genes RAG2 and MLL), Lavoué & Sullivan

(2004) advocated a hypothesis of interrelationships for the living Osteoglossomorpha, largely agreeing with those based on morphological data (Taverne, 1979, 1998; Li & Wilson, 1996b), and differing mainly in the exclusion of *Pantodon* from a position within or as sister group to the Osteoglossidae. Our analysis based on morphological data differs from those of Greenwood *et al.* (1966), Nelson (1968) and Greenwood (1973), but agrees with those of Taverne (1979, 1998), Li & Wilson (1996b), Li *et al.* (1997b), Hilton (2003) and Zhang (2006) in the exclusion of the Hiodontidae from the Notopteroidei. It differs from those of Li & Wilson (1996b), Hilton (2003), Lavoué & Sullivan (2004) and Zhang (2006), but agrees with those of Greenwood *et al.* (1966), Nelson (1968) and Greenwood (1973) in supporting the sister group relationship of the Pantodontidae and the Osteoglossidae within the Osteoglossoidei. It differs from those of Greenwood *et al.* (1966), Nelson (1968) and Hilton (2003), but agrees with those of Greenwood (1973) and Taverne (1979, 1998) in supporting the sister group relationship of the Notopteridae and the Mormyroidea within the Notopteroidei.

†*Paralycoptera* was included in several recent cladistic analyses (Shen, 1996; Li *et al.*, 1997b; Zhang, 1998, 2004, 2006; Li & Wilson, 1999; Zhang & Jin, 1999), but many characters were not available, or not properly coded. Our re-examination added a large amount of new or revised information on osteology (e.g. nasal, infraorbital, retroarticular, preopercle, extrascapular, basihyal toothplate, epineural, pelvic fin, caudal skeleton and scales). Of Li *et al.*'s (1997b) 60 characters of †*Paralycoptera*, six unknowns (characters 3, 4, 9, 18, 53, 56) were resolved unequivocally, five (characters 20, 21, 30, 39, 41) were coded differently and two (characters 6, 46) were coded, but with uncertainty. Similar conditions exist in Zhang's (2006) codings. Of Zhang's (2006) 65 characters of †*Paralycoptera*, 10 unknowns (characters 4, 5, 7, 12, 21, 33, 48, 49, 50, 58) can now be resolved satisfactorily, one (character 32) is assigned differently and one (character 59) is not confidently resolved. The systematic position of †*Paralycoptera* based on our analysis is different from that of Shen (1996) and Zhang (2006), but similar to that of Li *et al.* (1997b), Li & Wilson (1999) and the non-cladistic hypothesis of Chang & Chou (1976), i.e. at the basal position of the Osteoglossoidei.

Mainly based on its extant distribution, Nelson (1969) suggested that the Osteoglossomorpha might have originated in the southern continents (Africa might be the centre of origin), and its subgroups in North America and Asia might be secondarily derived. However, it is difficult to interpret why the eastern Asiatic fossil records (e.g. †*Lycoptera*) are more primitive and older in age. Chang & Chou (1976), instead,

suggested that Asia and, in particular, eastern Asia might be the centre of origin of the Osteoglossomorpha. Because the osteoglossomorphs are mainly freshwater forms (Eocene marine forms might be secondarily derived; Nelson, 1969), it seems reasonable to believe that they are unable to move across oceanic barriers, and thus the vicariance caused by plate separations should be taken into account (Nelson, 1975). Geological evidence shows that Laurasia and Gondwana were almost completely separated by 160 Mya (Smith, Smith & Funnell, 1994), which made it impossible for freshwater fishes to migrate between the two supercontinents after that time. The widespread records of the Osteoglossomorpha on both southern and northern continents indicate that it might have a Pangean origin. †*Paralycoptera*, one of the oldest members of the Osteoglossoidei (~110 Mya), may provide direct fossil evidence for the earliest divergences among the subgroups of Osteoglossomorpha at or before the Early Cretaceous.

## CONCLUSION

In our re-examination of †*Paralycoptera*, a large amount of new or revised information on osteology (e.g. nasal, infraorbital, retroarticular, preopercle, extrascapular, basihyal toothplate, epineural, pelvic fin, caudal skeleton and scales) has been revealed. †*Yungkangichthys*, †*Tanolepis* and †*Aokiichthys* are regarded as possibly synonymous with †*Paralycoptera*, which indicates that this form has a wider distribution than previously thought. Some characters of †*Paralycoptera* that were coded with question marks or wrongly understood in previous analyses have been revised. Our cladistic analysis supports the previous hypothesis that †*Paralycoptera* was not a lycopterid, but a stem osteoglossoid (Chang & Chou, 1976; Li *et al.*, 1997b; Li & Wilson, 1999). †*Singida* and †*Phareodus* are regarded as different levels of osteoglossoids above †*Paralycoptera*. Within extant osteoglossiforms, the sister group relationships of Pantodontidae and Osteoglossidae, and Notopteridae and Mormyroidea, are supported.

†*Paralycoptera* has important implications for the morphological evolution of the Osteoglossiformes. It possesses highly derived characters of the Osteoglossoidei, although it still retains many primitive characters of the Osteoglossomorpha (e.g. supramaxilla present; supraorbital sensory canal ending in parietal; supraorbital and otic sensory canals separated; extrascapular expanded; subopercle large, ventral to opercle; uroneurals numerous; upper hypurals independent). Some characters once thought to be uniquely derived for the Osteoglossinae (e.g. opercle depth twice or more its width; first pectoral fin ray much enlarged and long), or for the Osteoglossidae

(e.g. nasals broad, irregularly subrectangular; palatoquadrate area behind and below orbit completely covered by infraorbitals), are now found in †*Paralycoptera*. Thus these characters now have a wider distribution, and may possibly be synapomorphies of the Osteoglossoidei. †*Paralycoptera* is one of the oldest osteoglossoids (~110 Mya). Future studies are expected to reveal more details about the earliest diversifications of the subgroups of Osteoglossomorpha at or before the Early Cretaceous.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Characters used in the analysis.

**Appendix S2.** Data matrix of characters.

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