

骨舌鱼超目的系统发育关系¹⁾

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摘要:通过对中国化石骨舌鱼类及骨舌鱼类现生主要类群的比较研究,用 PAUP 软件对 31 个分类单元的 65 个特征进行了分析,得到了 16 个最简约的分支图(步长为 206,一致性指数为 0.4320,保留指数为 0.7194)。严格合意树显示,中国早白垩世的骨舌鱼类(酒泉鱼、狼鳍鱼、固阳鱼、吉南鱼、同心鱼、西夏鱼、昆都仑鱼和华夏鱼)主要为骨舌鱼超目中不同等级的干群;与一般的观点不同,始舌齿鱼与蛟河鱼组成了姊妹群关系;骨舌鱼目由 *Thaumaturus*、弓背鱼亚目和骨舌鱼亚目组成;弓背鱼类与象鼻鱼类关系更近;*Ostariostoma* 为弓背鱼科的姊妹群;副狼鳍鱼与[骨舌鱼亚科+犁齿鱼亚科]组成了姊妹群,该姊妹群关系的建立,将骨舌鱼科的历史延伸到了早白垩世。

关键词:骨舌鱼超目,系统发育

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PHYLOGENY OF OSTEOGLOSSOMORPHA

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Abstract Based on extensive morphological studies of the Chinese fossil osteoglossomorphs as well as the representatives of the major lineages of living osteoglossomorphs, I present the result of a cladistic analysis of 65 characters in 31 taxa, conducted using PAUP software (version 4.0b10). Strict consensus tree of 16 equally parsimonious trees (tree length of 206 steps, consistency index of 0.4320, retention index of 0.7194) shows that the Chinese Early Cretaceous osteoglossomorphs (*Jiuquanichthys*, *Lycoptera*, *Kuyangichthys*, *Jinanichthys*, *Tongxinichthys*, *Xixiaichthys*, *Kuntulunia* and *Huashia*) are mostly stem-groups of the superorder at different levels; *Eohiodon* and *Jiaohichthys* are interpreted as sister group rather than generally accepted *Eohiodon* and *Hiodon*; Osteoglossiformes consists of *Thaumaturus*, Notopteroidei and Osteoglossoidi; Notopterids are more closely related to mormyrids than to osteoglossids; *Ostariostoma* is the sister group to Notopteridae; Osteoglossoidi is coextensive with Osteoglossidae; *Paralycoptera* is a sister group to [Osteoglossinae + Phareodontinae]. The suggestion of a sister group relationship between *Paralycoptera* and [Osteoglossinae + Phareodontinae] extends the range of Osteoglossidae back to Early Cretaceous.

Key words Osteoglossomorpha, Phylogeny

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1 Introduction

Osteoglossomorphs are primitive teleosts and were once suggested to be the sister group of all other teleostean fishes (Patterson and Rosen, 1977; Lauder and Liem, 1983). All extant osteoglossomorphs are distributed in the tropical or subtropical fresh waters of southern continents except for *Hiodon* which lives only in North America. Fossil osteoglossomorphs were found from fresh water deposits (*Brychaetus* may live in brackish water) in all the continents save Antarctica. Explanation for such a transoceanic distribution of fresh water fishes is a challenge for paleogeography and historical biogeography. Due to their geographical and geological distributions and their morphological and biological diversities, osteoglossomorphs have received a considerable attention on their phylogenetic relationships.

The study on the classification of osteoglossomorphs mainly started at the beginning of the last century when Ridewood (1905) summarized the history of the systematics of Osteoglossidae. According to his summary, some authors associated Osteoglossidae to Hiodontidae, and Notopteridae to Mormyridae, but others related Osteoglossidae to Albulidae. Regan (1909) referred Osteoglossidae, Notopteroidei and Mormyroidei to his Isospondyli. Gregory (1933) put Hiodontidae, Mormyridae and Notopteridae into Mormyroidea, but included Osteoglossidae and Pantodontidae in Osteoglossidae. Berg (1940) referred Osteoglossidae to Clupeiformes and separated Mormyroidea from Clupeiformes and named a new order, Mormyiformes. Gosline's (1960) Clupeiformes included Osteoglossidae and Clupei, the former including Hiodontidae, Notopteridae and Osteoglossidae and the latter including the other fishes of the order. Greenwood (1963) raised the rank of Gosline's Osteoglossidae to Osteoglossiformes. Both Greenwood and Gosline noticed the close relationship between Osteoglossiformes and Mormyiformes.

Osteoglossomorpha was defined by Greenwood et al. (1966). Their superorder is consisted of Osteoglossiformes and Mormyiformes, the former including Osteoglossidae (Osteoglossidae and Pantodontidae) and Notopteroidei (Hiodontidae and Notopteridae) and the latter including Mormyridae and Gymnarchidae. Since the concept and principle of cladistics were introduced to the study of ichthyology, the investigations on the phylogeny of osteoglossomorphs were carried out at length (e. g. Chang and Chou, 1976; Patterson and Rosen, 1977; Lauder and Liem, 1983; Bonde, 1996; Shen, 1996; Li and Wilson, 1996b, 1999; Arratia, 1997, 1999; Taverne, 1998 and Hilton, 2003).

Patterson and Rosen's (1977) Osteoglossomorpha and Osteoglossiformes are coextensive and include the same subgroups, Osteoglossidae and Notopteroidei (Notopteroidea, Hiodontidae). Lauder and Liem (1983) grouped Osteoglossidae, Notopteroidea and Hiodontidae in his Osteoglossomorpha. In the cladogram of Li and Wilson (1996b), *Lycoptera* is a stem-group of Osteoglossomorpha, and Osteoglossiformes consists of Osteoglossidae and Notopteroidei (including Mormyroidea). Taverne's (1998) Osteoglossomorpha contains Hiodontiformes, Mormyiformes (Notopteroidei, Mormyroidei), Osteoglossiformes and three fossil families, i. e., Hua-shiidae, Kipalaichthyidae and Singididae. His Hiodontiformes includes Ostariostomidae, Lycoperidae and Hiodontidae. In the analysis of Hilton (2003), *Lycoptera* is either the sister group of all other osteoglossomorphs or that of *Eohiodon* plus *Hiodon*. Mormyrids are the sister group of notopterids plus osteoglossids.

The relationships of Osteoglossomorpha with other teleosts are still disputable. Greenwood et al. (1966) considered that Osteoglossomorpha, Elopomorpha, Clupeomorpha and Protacanthopterygii are derived respectively from pholidophoroid holosteans. In the cladistic analysis of Patterson and Rosen (1977), Osteoglossomorpha is the sister group of all other living teleosts and this view was followed by Lauder and Liem (1983), Forey et al. (1996), Taverne (1998) and Inoue et al. (2001). Arratia (1991) found that Osteoglossomorpha is not the most primitive

teleosts and recognized that elopomorphs are more basal than osteoglossomorphs within Teleostei when she studied the caudal skeletons of teleosts. Her later more extensive studies (Arratia, 1997, 1999) still bolstered up the conclusion. This new arrangement can be seen in the subsequent cladograms of Li and Wilson (1996b, 1999) and Shen (1996).

Besides the morphological systematic studies of Osteoglossomorpha, the researches on molecular phylogeny of the superorder have been becoming active (Forey et al., 1996; O'Neill et al., 1998; Sullivan et al., 2000; Kumazawa and Nishida, 2000; Al-Mahrouki et al., 2001; Inoue et al., 2001; Lavoué and Sullivan, 2004 and Albert et al., 2005). Among them Lavoué and Sullivan presented the first comprehensive molecular phylogenetic analysis and assessed osteoglossomorph monophyly and interrelationships of all major osteoglossomorph lineages.

Based on Greenwood's (1970) hypothesis about a sister group relationship between *Lycoptera* and the extant *Hiodon*, numerous fossils similar to *Lycoptera* recovered from Early Cretaceous of China were assigned to different subgroups of Osteoglossomorpha respectively, e. g. *Huashia* and *Kuntulunia* to Osteoglossiformes, *Tongxinichthys* and *Lycoptera* to Lycoperidae, *Jiuquanichthys* to Hiodontoidea, *Yanbiania* to Hiodontidae and *Sinoglossus* to Osteoglossidae. Some fossils such as *Jiaohichthys*, *Jinanichthys* and *Kuyangichthys* were treated as Osteoglossomorpha *incertae sedis*. Also referred to the superorder are some poorly preserved fossils such as *Changichthys*, *Nieerkunia*, *Plesiolycoptera*, *Pulinia*, *Suziichthys*, *Tanolepis* and *Che-tungichthys*.

Many Chinese early osteoglossomorphs are stem-groups but some genera form monophyletic groups such as the sister group of *Yanbiania* and *Hiodon*, the clade of *Sinoglossus* + [*Arapaima* + *Heterotis*] and the sister group of *Kuntulunia* and *Huashia*. The inclusion of fossil taxa in the cladistic analysis can make remarkable changes in the topologies (Shen, 1996). Therefore, fossil taxa have important positions in the phylogeny of Osteoglossomorpha. Most of early osteoglossomorphs were found in China (*Lycoptera* is the earliest known representative of the superorder). China is probably the key area for the study of the origin, evolution and the biogeography of osteoglossomorphs. Incommensurate with the findings, few cladistic analyses of osteoglossomorphs deal with Chinese fossil taxa except those of Shen (1996), Li and Wilson (1996b, 1999) and Zhang (1998, 2004). We still know little of the interrelationships of the early osteoglossomorphs.

Based on extensive morphological studies of the Chinese fossil osteoglossomorphs (including a newly found genus) as well as the representatives of the major lineages of living osteoglossomorphs, I present the result of a cladistic analysis of 65 characters (listed in Appendix and scored from published informations (Li and Wilson, 1996b; Zhang, 1998, 2004) and personal observations of specimens) in 31 taxa (ingroup and outgroup), conducted using PAUP software (version 4.0b10; Swofford, 1998) and using DELTRAN character-state optimization. The trees obtained using the heuristic search option and tree-bisection-reconnection (TBR) was employed as the branch-swapping algorithm. All the characters were unweighted, unordered, and considered to be simple and independent of one another. Missing characters or unclear conditions owing to the quality of preservation were coded as "?". For character states see Fig. 1. The cladogram shown in Fig. 2 represents the strict consensus tree of the 16 equally parsimonious trees.

All Chinese fossil taxa listed in Fig. 1 are deposited in the collection of Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, in Beijing. *Huashia*, *Jiaohichthys*, *Jinanichthys*, *Jiuquanichthys*, *Kuntulunia*, *Kuyangichthys*, *Lycoptera*, *Paralycoptera*, *Sinoglossus*, *Tongxinichthys* and *Xixiaichthys* were considered in the analyses as part of the ingroup because these genera are comparatively well preserved relative to other early osteoglossomorphs. Some genera (e. g. *Plesiolycoptera*, *Tanolepis* and *Yanbiania*) appearing in the cladograms of Li and Wilson (1996b, 1999) and Shen (1996) are not included in the

present analysis. *Plesioleptoptera*, from a drilling core, was supposed to be a stem-group of Hiodontiformes (Li and Wilson, 1999), but Chang (1999) argued that the preservation of the specimens is insufficient to allow interpretation of several character states observed by Li (1987) and Li and Wilson (1999). To clarify these characters collection of better specimens is required. *Tanolepis* was set up by Jin (1991, 1994) and referred to Hiodontidae. He and his colleagues (Jin et al., 1995) later reexamined the specimens of the genus and corrected some mistakes in his original description and thus considered *Tanolepis* a junior synonym of *Paralycoptera*. Li et al. (1997) and Li and Wilson (1999) reaffirmed the validity of *Tanolepis* based only on Jin's original description and figures. The matrix of the specimens of *Tanolepis* is sandstone, which hinders the observations of detailed morphology. Again we need better specimens to clarify its taxonomic validity. *Yanbiania wanqingica* (Li, 1987) shares many features with *Jiaohichthys pulchellus* (Ma, 1983). Chang (1999) and Chang and Miao (2004) suggested that the two forms may belong to the same genus and *Yanbiania* is most probably a junior synonym of *Jiaohichthys*. I, therefore, include only *Jiaohichthys* in my analysis.

<i>Leptolepis</i>	00000	00000	00000	00000	?0000	00000	00000	000??	?0000	00000	00000	00000	000??
<i>Arapaima</i>	00021	01112	01000	10011	00101	20020	01001	00010	11000	11132	12100	10200	21010
<i>Brychaetus</i>	20021	00110	01000	10000	?0?2?	21122	0110?	101??	??0??	?????	?????	?????	?1???
<i>Eohiodon</i>	0?000	001?0	0?001	00010	?0?0?	20010	0000?	210?0	01100	12320	01001	?0110	10???
<i>Heterotis</i>	10021	01112	11000	10011	10101	20020	01000	10010	11001	11132	12100	10200	21110
<i>Hiodon</i>	01010	00110	01001	00011	00101	20010	00000	22010	01100	11020	01001	10110	10010
<i>Huashia</i>	10000	00110	01000	00110	1010?	21021	0100?	101?0	01010	11030	01100	10?00	10???
<i>Jiaohichthys</i>	00000	001?0	0?001	00010	?0?0?	20010	0000?	2?0??	01100	11320	01000	10200	10???
<i>Jinanichthys</i>	00000	00110	01000	00000	10100	20020	01000	201?0	01000	11020	00000	10200	200??
<i>Jiuquanichthys</i>	01000	10100	00000	00010	1010?	20020	00000	200?0	01100	11020	00000	00100	10???
<i>Kuntulunia</i>	10020	00110	01000	00110	10101	21020	01000	101?0	01010	11030	01001	10100	10???
<i>Kuyangichthys</i>	00000	00?10	0?000	00001	?0100	20020	0000?	101?0	01110	11?00	01000	10200	10???
<i>Lycoptera</i>	00000	00110	00000	00000	?0100	20020	00000	201?0	01000	11020	00000	10200	100??
Mormyridae	00020	00101	11110	00010	11101	20010	00000	20011	01001	11032	12100	10200	11010
<i>Notopterus</i>	01021	00101	11110	00010	11101	21140	01000	20010	01001	11133	12101	10201	20010
<i>Ostariostoma</i>	010?0	00101	11110	00010	1010?	20100	0000?	100??	??0??	10321	1?10?	10200	20???
<i>Osteoglossum</i>	00021	00110	01000	11010	10121	11130	11011	20011	01001	11132	12100	11200	21111
<i>Pantodon</i>	11020	00100	00000	10010	00121	11132	01001	20011	01110	11132	12100	11200	20?10
<i>Papycrocranus</i>	01021	00101	11110	00010	11101	21140	01001	20010	010??	11133	12100	10301	30010
<i>Paralycoptera</i>	000??	0?110	0?000	10000	?0111	20021	01?0?	200??	01000	11???	01100	10?00	201??
<i>Phareodus 1</i>	20020	00110	21000	10010	1012?	20132	01100	101?1	01000	11223	12100	11200	211??
<i>Phareodus 2</i>	2002?	?011?	21000	10010	?0?2?	20132	0110?	101??	?????	1????	?????	?1200	21???
<i>Phareodus 3</i>	20021	00110	01000	10010	1011?	21132	01101	100?1	01000	11223	12100	11200	212??
<i>Scleropages 1</i>	00121	00110	01000	11010	10121	11132	11011	20011	01001	11132	12100	11200	21211
<i>Scleropages 2</i>	00121	00110	01000	11010	10121	11132	11011	20011	01001	11132	12100	11200	21111
<i>Singida</i>	0??2?	?0110	01000	10?10	?0?2?	2?132	1100?	10???	??000	11121	01100	11200	20???
<i>Sinoglossus</i>	0??2?	?1?12	21000	1001?	?0?0?	2?020	0????	?????	01???	?????	?????	102?0	21???
<i>Thaumaturus</i>	010??	00100	11000	00111	1010?	20020	00?1?	200??	??2??	11333	12100	1??00	10???
<i>Tongxinichthys</i>	00020	10110	00000	00000	10101	20020	0000?	200??	01100	11020	01000	10200	10???
<i>Xenomystus</i>	00021	00101	11110	00010	11101	20140	01000	20010	1010?	10333	1210?	10301	30010
<i>Xixiaichthys</i>	00020	00100	0?00?	00010	?0101	20020	0??00	201??	01100	11130	01011	101?0	00???

Fig. 1 Data matrix of 65 morphological characters (Appendix) for 31 taxa of fossil and extant teleosts. 0, plesiomorphic character state, 1~4, apomorphic character states; ?, unclear owing to preservation of the specimens or not applicable; outgroup is *Leptolepis*; *Phareodus 1* = *P. encaustus*, *Phareodus 2* = *P. queenslandicus*, *Phareodus 3* = *P. testis*, *Scleropages 1* = *S. formosus*, *Scleropages 2* = *S. leichardti*

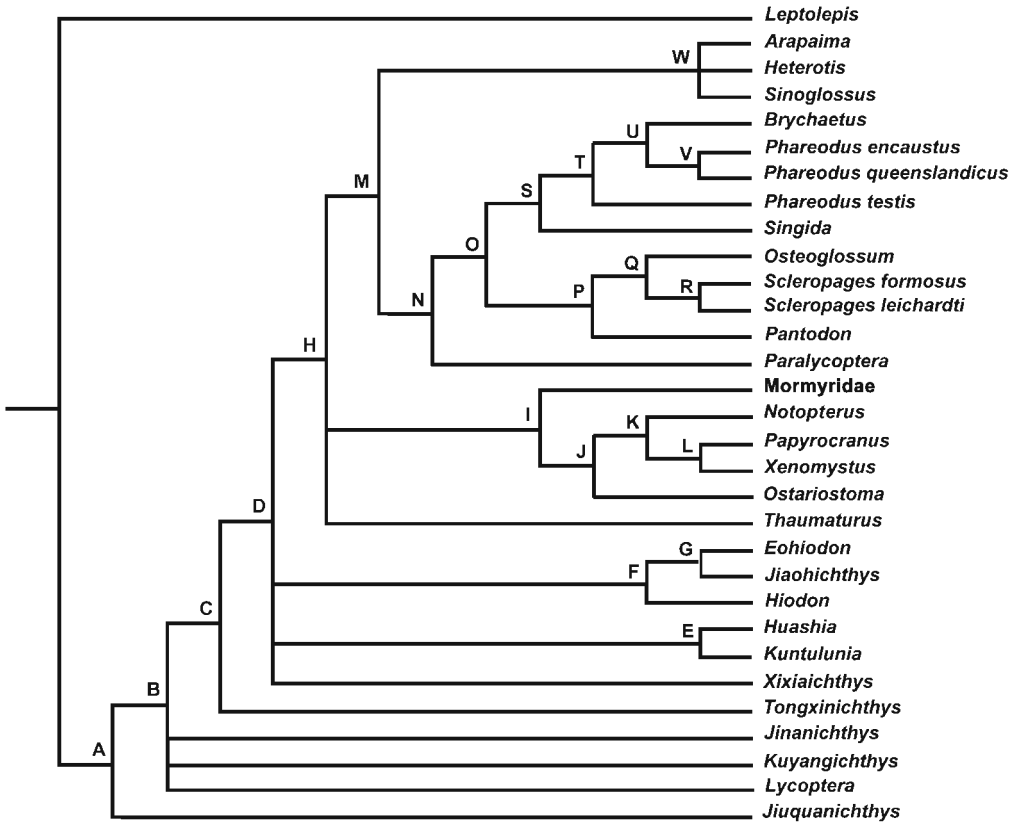


Fig. 2 A hypothesis of the phylogeny of Osteoglossomorpha based on the result of this analysis. Strict consensus tree of 16 equally parsimonious trees, with the tree length of 206 steps, consistency index (CI) of 0.4320 (0.4179 excluding uninformative characters), homoplasy index (HI) of 0.5680 (0.5821 excluding uninformative characters), retention index (RI) of 0.7194 and rescaled consistency index (RC) of 0.3108; numbers outside square brackets represent the characters and those in square brackets represent the state of characters; for explanation of characters see Appendix; uniquely derived characters are indicated with an asterisk (*)

Node A: 8[1]*, 23[1]*, 26[2], 29[2], 36[2], 42[1]*, 43[1], 46[1]*, 47[1], 49[2], 58[1], 61[1]; Node B: 9[1], 38[1], 56[1]*, 58[2]; Node C: 4[2], 25[1]*, 38[0], 52[1]; Node D: 12[1], 19[1], 58[1]; Node E: 1[1], 18[1], 27[1], 32[1], 36[1], 43[0], 44[1]; Node F: 4[1], 15[1]*, 29[1], 37[1]*, 38[0]; Node G: 4[0], 48[3]; Node H: 11[1], 38[0], 48[1], 49[3], 50[2], 51[1], 52[2], 53[1]; Node I: 9[0], 10[1], 13[1]*, 14[1]*, 45[1]; Node J: 2[1], 28[1], 61[2]; Node K: 5[1], 22[1], 29[4], 32[1], 50[3], 60[1]*; Node L: 58[3], 61[3]; Node M: 5[1], 9[1], 16[1]*, 32[1], 61[2]; Node N: 11[0], 24[1], 30[1], 63[1]; Node O: 24[2], 27[1], 28[1], 29[3], 30[2], 40[1], 57[1]*; Node P: 26[1], 35[1]; Node Q: 17[1]*, 31[1], 34[1], 45[1], 62[1], 65[1]*; Node R: 3[1]*; Node S: 36[1], 49[2]; Node T: 1[2], 33[1]*, 48[2], 50[3], 62[1]; Node U: 38[1]; Node V: 11[2], 27[0]; Node W: 7[1]*, 10[2], 20[1], 36[1], 62[1]

2 Phylogeny of Osteoglossomorpha

2.1 Basal osteoglossomorphs

Jiuquanichthys Ma (1993) recognized that *Jiuquanichthys* shares a number of resem-

blances with both Hiodontidae and Lycopteridae but is closer to *Hiodon* than to *Lycoptera*. She named a new family, Jiuquanichthyidae, and placed it in Hiodontoidea (Greenwood, 1970). The synapomorphies, she listed, supporting the phyletic relationship between *Jiuquanichthys* and *Hiodon* include: lack of supramaxilla and supraorbital, the anterior part of supraoccipital separating the posterior part of the two parietals, the supraoccipital with a high crest, the parasphenoid without basiptyergoid process, the jaws with several rows of teeth and pectoral and anal fins relatively large.

These characters are not unique in *Jiuquanichthys* and *Hiodon* but manifest in the various taxa of Osteoglossomorpha. They, therefore, provide little evidence for interpreting the relationships of *Jiuquanichthys*. There is no synapomorphy to support the idea of a close phyletic relationship between the two genera in the present analysis. *Jiuquanichthys* is here proposed to be a stem-group of osteoglossomorphs, sister to all other osteoglossomorphs sampled.

Lycoptera It was first assigned to Esocidae (Müller, 1848). Later, Woodward (1895) referred it to Leptolepidae. Cockerell (1925) separated it from Leptolepidae and erected a new family Lycopteridae after reviewed the type specimen of *Lycoptera middendorffi* of Transbaikal based on the morphology of scales. Berg (1940) placed the family in Clupeiformes as a group coordinate with Leptolepidoidei. Yakovlev (1965) first noted the similarities of *Lycoptera* and *Arapaima*. Romer (1966) assigned both Lycopteridae and Leptolepidae to Leptolepiformes. Greenwood (1970) considered that *Lycoptera* is closest to Hiodontidae. Chang and Chou (1977) believed that *Lycoptera* is probably an early member of Osteoglossomorpha and established the Lycopteriformes.

Greenwood's (1970) suggestion of a close relationship between *Lycoptera* and *Hiodon* was followed by the subsequent investigators (Chang and Chou, 1976; Ma, 1980, 1993; Patterson and Rosen, 1977; Lauder and Liem, 1983 and Nelson, 1994). This relationship was based mainly on caudal skeleton and temporal fenestra, but a similar caudal skeleton was also seen in other taxa of Osteoglossomorpha and the temporal fenestra needs to be reconsidered.

The temporal fenestra in *Hiodon* is bordered by the parietal, epiotic and pterotic. Such a structure exists also in a number of early osteoglossomorphs such as *Tanolepis* (*Tanichthys*, Jin, 1991), *Kuyangichthys*, *Asiatolepis* (Ma and Sun, 1988), *Jiaohichthys* and *Tongxinichthys*. Ma and Sun (1988) therefore considered it a primitive character of Osteoglossomorpha. Taverne (1977, 1978) called the structure temporal fossa and he later (1998) believed that the temporal fenestra is a transformation of the posttemporal fossa that is located between the same three bones in elopids and albulids, *Pholidophorus* and *Leptolepis*.

Ridewood (1904) postulated that the temporal fenestra in *Hiodon* is probably homologous to the preepiotic fossa of clupeiforms, but Greenwood (1970) believed that the two structures are more likely to be analogous than homologous. Li and Wilson (1996b), following Ridewood (1904), suggested homology between the two structures and considered that the temporal fenestra cannot support the relationship of *Lycoptera* and *Hiodon*. Cavin and Forey (2001) discussed the temporal fenestra at length and suggested that the structure is a plesiomorphic character for osteoglossomorphs.

In the cladograms published in last decade (Bonde, 1996; Shen, 1996 and Li and Wilson, 1996b), *Lycoptera* nests deeply and is a stem-group osteoglossomorphs, whereas Taverne (1998) still set Lycopteridae and Hiodontidae as sister groups. In the present analysis, *Lycoptera* is positioned deep in the topology and its phyletic relationship is not resolved.

Kuyangichthys Liu et al. (1982) left the systematic position of *Kuyangichthys*, from the Guyang basin of Nei Mongol (Inner Mongolia), uncertain when they named it albeit they thought the fish is a primitive teleost like *Lycoptera* and *Leptolepis*. Ma (1983) referred

Kuyangichthys Osteoglossomorpha based on its caudal skeleton. After detailed comparisons between *Kuyangichthyidae* and *Lycoperidae* and *Leptolepidae*, Ma (1993) proposed that *Kuyangichthyidae* is closer to *Lycoperidae* based on caudal skeleton, hyoid arch, opercular series, lack of supraorbital and the position of fins and scales. Jin et al. (1995) thought that most characters of *Kuyangichthyidae* are either imprecisely defined or shared with *Lycoperidae*. They therefore argued that *Kuyangichthys* is probably a member of *Lycoperidae*.

Kuyangichthys appeared in some cladograms as stem-group osteoglossomorphs (Zhang, 1998, 2004) or as a sister group of *Jiuquanichthys* (Li and Wilson, 1999). The sister group relationship of *Kuyangichthys* and *Jiuquanichthys* is supported by only two homoplasies (presence of 'urodermals' and possible presence of upper caudal scutes). These characters, except the urodermal of *Jiuquanichthys*, need to be clarified again since they are never observed by other investigators. There are grounds for questioning a judgment based on a single character that is only possibly present. *Kuyangichthys* lies at the base of the tree just above *Jiuquanichthys* in the present analysis. Its relationship is still uncertain.

Jinanichthys Ma and Sun (1988) described *Jinanichthys longicephalus* based on the materials from Tonghua, Jilin and thought that *Lycopera longicephalus* from western Liaoning and *Jinanichthys longicephalus* are actually the same species. Su (1992) disagreed with Ma and Sun (1988) and argued that *Lycopera longicephalus* is different from both *Jinanichthys* and *Lycopera*. He coined a new name for it, *Liaoxiichthys*. Zhang et al. (1994) examined the specimens from Jilin and found no difference between the fish and *Lycopera longicephalus* but recognized that *Lycopera longicephalus* differs from the other species of the genus in having a long and narrow frontal, relatively large supramaxilla, hyandibular with a prominent process on its lower end, the lower limb of preopercular relatively long, dentary with a high coronoid process and a short mouth cleft. They supported the opinion of Ma and Sun (1988) for separating *Lycopera longicephalus* from *Lycopera* and establishing a new genus, *Jinanichthys*, whereas *Liaoxiichthys* was regarded as a junior synonym of *Jinanichthys*.

Ma and Sun (1988) noted the affinities of *Jinanichthys* and *Kuyangichthys*. Zhang et al. (1994) referred *Jinanichthys* to *Kuyangichthyidae* based on hyandibular, the form of preoperculum, coronoid process on dentary, mouth cleft and teeth on the jaws, but Jin et al. (1995) suggested that *Jinanichthys* is a lycoperid. *Jinanichthys* appears to be a highly derived taxon among basal osteoglossomorphs in the published cladograms (Zhang, 1998, 2004; Zhang and Jin, 1999) but forms an unresolved polytomy with other early osteoglossomorphs in this cladogram. No synapomorphy was found to support the phyletic relationship between *Jinanichthys* and *Kuyangichthys* or between *Jinanichthys* and *Lycopera*.

Tongxinichthys Ma (1980) placed *Tongxinichthys* in *Lycoperidae* when she described the fish. Her placement was based mainly on primitive characters found in various early osteoglossomorphs, which cannot demonstrate close phyletic links with *Lycoperidae*. Li and Wilson (1994) first studied the phylogenetic systematics of *Tongxinichthys* and in their cladogram *Tongxinichthys*, *Lycopera* and the clade [*Yanbiania* + [*Plesiolycoptera* + [*Eohiodon* + [*H. consteniorum* + *Hiodon*]]]] consist an unresolved tricotomy. *Tongxinichthys* is stem-group osteoglossomorphs in Shen's (1996) cladogram but forms polytomy with other osteoglossomorphs in Zhang (2004). The fish was interpreted as the sister group of *Jiuquanichthys* plus *Kuyangichthys* in the result of Li and Wilson (1999). This sister group relationship is supported by one synapomorphy (anterior supraneurals dorsally moderately broader and leaf-shaped). The supraneurals are markedly large in *Kuntulunia* and *Huashia*, but "moderately broader" supraneurals are also present in *Xixiaichthys*, some specimens of *Lycopera davidi* besides *Tongxinichthys*, *Jiuquanichthys* and *Kuyangichthys*. Hilton (2002, 2003) pointed out that other taxa coded as

plesiomorphic by Li and Wilson (1999) also possess anterior supraneurals that could be regarded as 'leaf-shaped' (or at least dissimilar to the posterior ones in shape) with slender posterior supraneurals (e. g. *Hiodon*, *Elops*). As Li and Wilson (1999) conceded, the evidence for this clade is admittedly weak. *Tongxinichthys* was considered to be the sister group to *Jiuquanichthys* by Zhang and Jin (1999). One derived character weakly supports this sister group relationship. In the present cladogram, although *Tongxinichthys* is more derived than other basal osteoglossomorphs mentioned above, it is still a stem-group of osteoglossomorphs.

Xixiaichthys It was recovered from the Madongshan Formation, Liupanshan group of Tongxin County, Ningxia Autonomous Region. The strata yielding *Xixiaichthys* contact conformably with the underlying *Lycoptera*-bearing strata of the Liwaxia Formation. The phylogenetic analysis of Zhang (2004) shows that *Xixiaichthys* is the sister group of Osteoglossiformes ([[*Notopterus* + *Osteoglossum*] + [*Huashia* + *Kuntulunia*]]). This sister group relationship is characterized by one derived character (epural absent) and one homoplasy (supramaxilla absent). *Xixiaichthys* was assigned to Osteoglossiformes in Zhang (2004) but forms a polytomy with the clade [*Huashia* + *Kuntulunia*], Hiodontiformes and Osteoglossiformes in the present result.

2.2 Hiodontiformes

Hiodontids were thought to be closely related to notopterids (Greenwood, 1963, 1970; Greenwood et al., 1966; Cavender, 1966; Nelson, 1968; Patterson and Rosen, 1977; Grande, 1979 and Lauder and Liem, 1983) because they share a special swimbladder-ear connection. However, Li and Wilson (1996b) considered that this connection is not a uniquely derived character state present only in Hiodontidae and Notopteridae.

Taverne (1979) erected Hiodontiformes, which consists of Hiodontidae and Lycoperidae. The relationship between the two taxa is not supported by the recent cladograms. Li and Wilson's (1996b) Hiodontiformes includes only Hiodontidae. In their analysis Hiodontiformes and Osteoglossiformes (including Osteoglossoidei and Notopteroidei) were tied as sister group. Two synapomorphies support the relationship (absence of supramaxilla, and fusion of infraorbital 4 with 5). In this study, the strict consensus tree shows a polytomy among Hiodontiformes, *Xixiaichthys*, the clade [*Huashia* + *Kuntulunia*] and Osteoglossiformes. Most interestingly, *Eohiodon* and *Jiaohichthys* are interpreted as sister group rather than generally accepted *Eohiodon* and *Hiodon* (Chang and Chou, 1976; Li and Wilson, 1994, 1996b, 1999; Bonde, 1996). This result is only weakly supported by two homoplasies (nasal tubular but straight, neural spine on u1 + 2 absent).

2.3 Osteoglossiformes

Composition and synapomorphies of Osteoglossiformes Greenwood et al.'s (1966) Osteoglossiformes includes Osteoglossoidei and Notopteroidei (Hiodontidae and Notopteridae). Nelson's (1994) Osteoglossiformes consists of Osteoglossoidei, Notopteroidei (Hiodontidae and Notopteridae) and Mormyroidei. In the cladogram of Patterson and Rosen (1977), Osteoglossiformes is formed by Osteoglossoidei and Notopteroidei ([Notopteridae + [Hiodontidae + Lycoperidae]]). In Li and Wilson's (1996b) scheme, only *Tanichthys*, Osteoglossoidei and Notopteroidei were left in their Osteoglossiformes after Hiodontidae and Lycoperidae were removed. While in Taverne's (1998) classification, Osteoglossiformes is nearly coextensive with Osteoglossoidei.

In the present study, Osteoglossiformes consists of *Thaumaturus*, Notopteroidei and Osteoglossoidei and is defined by eight homoplasies (shape of io3 subrectangular 11[1], hyomandibula anteriorly not extended 38[0], one full neural spine on u1 + 2 48[1], no epurals 49[3],

first uroneural reaches ural centra 50[2], two or more uroneurals not extending forward beyond the "second" ural centrum (U3 + 4) 51[1], one or no uroneural 52[2] and six or less hypurals in adult individuals 53[1]).

Notopteroidei Notopterids and mormyrids usually are considered more closely related to each other than to any other group (Greenwood, 1973; Lauder and Liem, 1983; Li and Wilson, 1996b, 1999). However, different schemes also appeared in recently published cladograms. Hilton (2003) proposed that mormyrids are the sister group of notopterids + osteoglossids. Of the cladograms based on molecular data, Lavoué and Sullivan's (2004) suggested a sister group relationship between Notopteridae and Mormyridae + Gymnarchidae, while Kumazawa and Nishida's (2000) interpreted Notopteridae to be related to *Pantodon*.

My result agrees with Li and Wilson (1996b) on that notopterids are more closely related to mormyrids than to osteoglossids but differs from them in that *Ostariostoma* is the sister group to Notopteridae in my analysis but to Notopteridae + Mormyroidea in Li and Wilson (1996b).

The monophyly of Notopteroidei ([Mormyridae + [*Ostariostoma* + [*Notopterus* + [*Papycranus* + *Xenomystus*]]])) of the present analysis is supported by two derived characters (infraorbital ledge formed by lateral extension of orbital margin of iol and io2 present 13[1], infraorbital canal on iol to io2 in open groove 14[1]) and three homoplasies (without a large posteroventral infraorbital bone representing the third and the fourth infraorbitals of other teleosts 9[0], second infraorbital medium-sized and rectangular 10[1] and neural arches of most abdominal vertebrae with fused halves of the neural arch forming a median neural spine 45[1]).

Osteoglossoidei It comprises Osteoglossidae and Pantodontidae in Greenwood et al.'s (1966) classification. Later, Greenwood and Patterson (1967) erected Singididae and placed it in Osteoglossoidei. Lauder and Liem's (1983) Osteoglossoidei contains Osteoglossidae, *Pantodon* and Arapaimidae. Nelson's (1994) Osteoglossoidei includes only Osteoglossidae and Pantodontidae. The Osteoglossiformes of Taverne (1998) is almost coextensive with Osteoglossoidei and includes Arapaimidae, Pantodontidae and Osteoglossidae, while Singididae is a sister group to Mormyriiformes (include Notopteroidei and Mormyroidei) plus Osteoglossiformes.

Li and Wilson (1996b) argued that the characters considered diagnostic of Pantodontidae by Nelson (1994) and of Singididae are mainly autapomorphies of *Pantodon* and *Singida* and they therefore included the two genera in the Osteoglossinae (Li and Wilson, 1996b, 1999). The result of my analysis is congruent with Li and Wilson (1999) in most respects except the positions of *Singida* and the Huashiidae (*Huashia* plus *Kuntulunia*). *Singida* was considered to be the sister group to Osteoglossinae by Li and Wilson's (1999) and was interpreted as the sister group to *Phareodus* (include *Brychaetus*) in the present study. With respect to the relationship of Huashiidae Chang and Chou (1977) proposed that *Huashia* seems to be on the line of evolution from primitive teleosts to Euteleostei and noticed the resemblances between the genus and *Chanos* in broad skull, jaws and infraorbitals. Ma (1986) referred *Huashia* to Osteoglossomorpha according to the caudal skeleton and a large ventral posterior infraorbital. In the published cladograms Li and Wilson (1996a, 1999) suggested *Huashia* and *Kuntulunia* are the ancestral lineages of the Heterotidinae while Taverne (1998) considered them to be a sister group to the clade ([Kipalaichthyidae + [Singididae + [Mormyriiformes + [Osteoglossiformes]]])) and Shen et al. (1991), Shen (1996) and Zhang (2004) thought them to be related to the clade ([*Notopterus* + *Osteoglossum*]). In the present analysis, Huashiidae forms a polytomy among *Xixiaichthys*, Hiodontiformes and Osteoglossiformes, and its systematic position is therefore not resolved.

Osteoglossoidei is characterized by one derived character (pterygo-quadrate area behind and below orbit completely covered by infraorbitals 16[1]) and four homoplasies (the two

nasals contacting each other 5[1], presence of a large posteroventral infraorbital bone representing the third and the fourth infraorbitals of other teleosts 9[1], subopercle missing or atrophied, lies below the anteroventral corner of opercle 32[1] and principal branched caudal fin rays 15 or fewer 61[2]) in this study.

Paralycoptera Chang and Chou (1977) described *Paralycoptera wui* in Lycoperidae and placed Lycoperidae to their new order, Lycoperiformes. They found that *Paralycoptera* shares more specializations with osteoglossiforms than *Lycoptera* in having a longer mouth cleft, more teeth on lower jaw, two large posterior infraorbitals and 15 branched caudal fin rays (Chang and Chou, 1976). Ma and Sun (1988) named *Paralycoptera changi* based on the specimens from Tonghua, Jilin and first noticed that the scales of *Paralycoptera* bear some simple reticulae, which, although very different from the typical osteoglossid reticulation patterns, probably have a tendency towards the latter. Jin et al. (1995) described *Paralycoptera* sp. from western Liaoning and also found reticulations on their scales. They considered in the same paper that *Paralycoptera* is closely related to Osteoglossidae based on the following features: its mouth cleft large and upturned, mouth margin with thick conical teeth, two large posterior infraorbitals, opercle high and narrow, the lower limb of the preopercle short and broad and scales with reticulations. Yabumoto (1994) described *Aokiichthys* from Fukuoka Prefecture, Japan and suggested that it is close to *Paralycoptera*. The two fishes are almost identical except the number of vertebrae and ribs. The number of vertebrae is 40 to 42 in *Paralycoptera* but 34 to 36 in *Aokiichthys*. Strangely, the vertebrae are 34 to 36 in Yabumoto's description but show 38 in the restorations (his figures 36, 37 and 50).

Paralycoptera is visible in the recent cladograms. It was placed at the base of the trees of Shen (1996) and Bonde (1996) as stem osteoglossomorph, as stem osteoglossiform in the trees of Zhang (1998, 2004) but was regarded to be a sister group to *Tanolepis* and further the group (*Paralycoptera* + *Tanolepis*) is sister to Osteoglossoidae in Li and Wilson's (1999) analysis. In the present study, *Paralycoptera* is treated as a sister group to [Osteoglossinae + Phareodontinae], supported by four homoplasies (shape of io3 short and posteriorly deep 11[0], angle of jaws between middle vertical line and posterior edge of orbit 24[1], ratio of depth to width of opercle about 2.30[1] and number of lateral line scales 30 ~ 40.63[1]). The suggestion of a sister group relationship between *Paralycoptera* and [Osteoglossinae + Phareodontinae] extends the range of Osteoglossidae back to Early Cretaceous.

The morphology of reticulate scales in some osteoglossomorph fishes is discussed in Cockerell (1910, 1911), Nelson (1969), Taverne (1979), Gayet and Meunier (1983), Jolly and Sunil (1988) and Hilton (2003). The reticulate pattern is present over entire scales of *Heterotis*, *Arapaima*, *Osteoglossum*, *Scleropages*, *Phareodus*, *Brychaetus* (Bond, 1996) and *Sinoglossus*, but only on the posterior field of the scale of mormyrids (Taverne, 1971, 1972; Hilton, 2003). Jin et al. (1995) observed that obvious reticulation and sparse granules exist on the apical region of the scale of *Paralycoptera* sp. from western Liaoning. In my observation, reticulate furrows are present on the apical region of the scale of *Paralycoptera* sp., which form dense and irregular networks. The densely covered furrows of *Paralycoptera* vary highly in thickness, most of which are fine and weak while a few of them are relatively strong. This is considerably different from the typical osteoglossid ones, in which the furrows are regularly distributed and are the same in thickness. It remains unknown whether the specialization of *Paralycoptera* is homologous with the typical osteoglossid reticulation. Nevertheless, a scale with somewhat reticulated structure is only seen in *Paralycoptera* among early osteoglossomorphs.

3 Classification of Osteoglossomorpha

Based on the phylogeny of Osteoglossomorpha shown in Fig. 2, I propose the following classification:

- Superorder Osteoglossomorpha
 - Jiuquanichthys*
 - Lycoptera*
 - Kuyangichthys*
 - Jinanichthys*
 - Tongxinichthys*
 - Xixiaichthys*
 - Kuntulunia*
 - Huashia*
- Order Hiodontiformes
 - Family Hiodontidae
 - Hiodon*
 - Eohiodon*
 - Jiaohichthys*
- Order Osteoglossiformes
 - Thaumaturus*
 - Suborder Notopteroidei
 - Family Mormyridae
 - Family Ostariostomidae
 - Ostariostoma*
 - Family Notopteridae
 - Notopterus*
 - Papyrocranus*
 - Xenomystus*
 - Suborder Osteoglossoidei
 - Family Osteoglossidae
 - Subfamily Heterotidinae
 - Arapaima*
 - Heterotis*
 - Sinoglossus*
 - Unnamed group
 - Paralycoptera*
 - Subfamily Osteoglossinae
 - Pantodon*
 - Osteoglossum*
 - Scleropages*
 - Subfamily Phareodontinae
 - Singida*
 - Phareodus* (*Brychaetus*)

4 Conclusions

The Chinese Early Cretaceous osteoglossomorphs (*Jiuquanichthys*, *Lycoptera*, *Kuyangichthys*, *Jinanichthys*, *Tongxinichthys*, *Xixiaichthys*, *Kuntulunia* and *Huashia*) are mostly stem-groups of the superorder at different levels.

Eohiodon and *Jiaohichthys* are interpreted as sister group in contrast with the generally accepted sister group relationship between *Eohiodon* and *Hiodon*. This suggestion, however, is only weakly supported by two homoplasies (nasal tubular but straight, neural spine on u1 + 2 absent).

Osteoglossiformes consists of *Thaumaturus*, Notopteroidei and Osteoglossoidei and is defined by eight homoplasies (shape of io3 subrectangular 11[1], hyomandibula anteriorly not extended 38[0], one full neural spine on u1 + 2 48[1], no epurals 49[3], first uroneural reaches ural centra 50[2], two or more uroneurals not extending forward beyond the "second" ural centrum (U3 + 4) 51[1], one or no uroneural 52[2] and six or less hypurals in adult individuals 53[1]).

Notopteroidei are more closely related to mormyrids than to osteoglossids. *Ostariostoma* is the sister group to Notopteroidei. The monophyly of Notopteroidei is supported by two derived characters (infraorbital ledge formed by lateral extension of orbital margin of io1 and io2 present 13[1], infraorbital canal on io1 to io2 in open groove 14[1]) and three homoplasies (without a large posteroventral infraorbital bone representing the third and the fourth infraorbitals of other teleosts 9[0], second infraorbital medium-sized and rectangular 10[1] and neural arches of most abdominal vertebrae with fused halves of the neural arch forming a median neural spine 45[1]).

Osteoglossoidei is coextensive with Osteoglossidae and are characterized by one derived character (pterygo-quadrate area behind and below orbit completely covered by infraorbitals 16[1]) and four homoplasies (the two nasals contact each other 5[1], present a large posteroventral infraorbital bone representing the third and the fourth infraorbitals of other teleosts 9[1], subopercle missing or atrophied, lies below the anteroventral corner of opercle 32[1] and principal branched caudal fin rays 15 or fewer 61[2]) in this study.

Paralycoptera is a sister group to [Osteoglossinae + Phareodontinae], supported by four homoplasies (shape of io3 short and posteriorly deep 11[0], angle of jaws between middle vertical line and posterior edge of orbit 24[1], ratio of depth to width of opercle about 2.30[1] and number of lateral line scales 30 ~ 40 63[1]). The suggestion of a sister group relationship between *Paralycoptera* and [Osteoglossinae + Phareodontinae] extends the range of Osteoglossidae back to Early Cretaceous.

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Appendix Definitions of characters and character states used in cladistic analysis

1. Frontal: [0] long and narrowed anteriorly, [1] short and broad, [2] anterior portion at least twice as broad as posterior end.
2. Parietals: [0] posteriorly not separated by supraoccipital, [1] separated.
3. Post half of parietal sinks abruptly: [0] absent, [1] present.
4. Nasal: [0] tubular but straight, [1] tubular and strongly curved, [2] gutter-like or irregularly subrectangular.
5. Relationship between two nasals: [0] separated, [1] contact each other.
6. Supraoccipital with a long, narrow process on both its anterior and posterior margins: [0] absent; [1] present.
7. Antorbital and first infraorbital: [0] separate, [1] fused.
8. Supraorbital: [0] present, [1] absent.
9. A large posteroventral infraorbital bone representing the third and the fourth infraorbitals of other teleosts: [0] absent, [1] present.
10. Second infraorbital: [0] slender and small, [1] medium-sized and rectangular, [2] large, wide irregular trapezoid.
11. Shape of io3: [0] short, posteriorly deep, [1] subrectangular, [2] long, posteriorly shallow and fanlike.
12. Number of infraorbital bones including first infraorbital to dermosphenotic: [0] six or more, [1] five.
13. Infraorbital ledge formed by lateral extension of orbital margin of io1 and io2: [0] absent, [1] present.
14. Infraorbital canal on io1 to io2: [0] enclosed in bony tube, [1] in open groove.
15. Shape of dermosphenotic: [0] irregularly triangular or trapezoid, [1] triradiate.
16. Pterygo-quadrate area behind and below orbit: [0] not completely covered by infraorbitals, [1] completely covered by infraorbitals.
17. Mouth sharply upturned and the anterior end of mouth is nearly as high as the dorsal margin of fish body: [0] absent, [1] present.
18. Premaxilla nearly excluding maxilla from the mouth gape: [0] absent, [1] present.
19. Supramaxilla: [0] present, [1] absent.
20. Posterior end of maxilla: [0] lying on angular, [1] lying on dentary.
21. Retroarticular: [0] included in the articular facet for quadrate, [1] excluded from the articular facet for quadrate.
22. Mandibular (dentary) canal: [0] enclosed in bony tube, [1] in open groove.
23. Posterior opening of the mandibular sensory canal: [0] placed medial or posterior, [1] placed lateral to the angular portion of the jaw.
24. Angle of jaws: [0] anterior to middle vertical line of orbit, [1] between middle vertical line and posterior edge of orbit, [2] behind orbit.
25. Gular plate: [0] present, [1] absent.
26. Upper part of the upper limb of preopercle: [0] covered by suborbital, [1] covered by infraorbitals, [2] not covered.
27. The preopercular sensory canal on the lower limb of preopercle expanded as a raised area with several foramina opening lateroventrally: [0] absent, [1] present.
28. Branches of preoperculo-mandibular canal on horizontal arm of preopercle: [0] separate, [1] connected with each other to form a horizontal groove.
29. Opercle: [0] irregular trapezoid, [1] irregular parallelogram, [2] oval or kidney-shaped, [3] subsemicircular, [4] fan-shaped.
30. Ratio of depth to width of opercle: [0] less than 2, [1] about 2, [2] greater than 2.
31. Posteroventral margin of opercle: [0] rounded, [1] distinctly concave.
32. Subopercle: [0] lies below opercle, [1] missing or atrophied, lies below the anteroventral corner of opercle.
33. Shape of extrascapular when it is present: [0] expanded and more or less square or irregularly triangular, [1] slender and distinctly angular or branched.

34. Orbitosphenoid: [0] present, [1] absent.
35. Basisphenoid: [0] present, [1] absent.
36. Parasphenoid: [0] with small teeth, [1] almost toothless, [2] with large teeth.
37. Hyomandibular heads: [0] one, [1] two, separate, [2] two, connected.
38. Hyomandibula: [0] anteriorly not extended, [1] anteriorly extended to form a subtriangular anterior wing.
39. Paired tendon bones on 2nd hypobranchial: [0] absent, [1] present.
40. Basihyal tooth plate (when present) and basibranchial tooth plate: [0] separate from each other, [1] fused.
41. Tooth plate of basihyal: [0] present, [1] absent.
42. "Shearing bite" between the basihyal and lateral pterygoquadrate teeth: [0] absent, [1] present.
43. Dorsal arm of posttemporal: [0] less than 1.5 times as long as ventral arm, [1] more than twice as long as ventral arm, [2] other condition (no ventral arm).
44. Anterior supraneurals: [0] slender, [1] expanded.
45. Neural arches of most abdominal vertebrae: [0] with separate halves of the neural arch, [1] with fused halves of the neural arch forming a median neural spine.
46. Length of neural spine on pu2: [0] shorter than npu3, [1] as long as npu3.
47. Neural spine of preural centrum 1: [0] rudimentary or short, [1] long, close to, or reaching the dorsal margin of the body, [2] absent.
48. Neural spine on u1 + 2: [0] rudimentary, [1] one full, [2] two full, [3] absent.
49. Number of epurals: [0] three or more, [1] two, [2] one, [3] none.
50. First uroneural reaches: [0] preural centrum 2 or 3, [1] preural centrum 1, [2] ural centra, [3] no uroneural.
51. Two or more uroneurals extending forward beyond the "second" ural centrum (U3 + 4): [0] present, [1] absent.
52. Last uroneural (or the last ones) much shorter than the first one: [0] present; [1] absent; [2] other condition (only one or no uroneural).
53. Number of hypurals in adult individuals: [0] seven or more, [1] six or less.
54. Hypural 1 fused but hypural 2 autogenous with U1 + 2: [0] absent, [1] present.
55. Parhypural of adult individuals fused with preural centrum 1: [0] absent, [1] present.
56. Urodermals: [0] present, [1] absent.
57. First pectoral fin ray: [0] normal, [1] greatly enlarged and extremely long.
58. Pelvic fin rays: [0] more than seven, [1] seven, [2] six or fewer, [3] no separated pelvic fin.
59. Shape of anal fin: [0] similar in both sexes, [1] sexually dimorphic.
60. Anal fin and caudal fin: [0] separate, [1] connected.
61. Principal branched caudal fin rays: [0] 17 or more, [1] 16, [2] 15 or fewer, [3] no separated caudal fin.
62. Scales: [0] not reticulate, [1] reticulate.
63. Number of lateral line scales: [0] more than 40, [1] 30 ~ 40, [2] less than 30.
64. Intestine: [0] coiling to right of stomach, [1] coiling to left of stomach.
65. Mandibular barbels: [0] absent, [1] present.