

# The oldest sarcopterygian fish

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The study of basal sarcopterygians is crucial to an understanding of the relationships and interrelationships of sarcopterygians, including their relationship to tetrapods. The new material from Qujing, Yunnan, southwestern China, represents the oldest known sarcopterygian fish and extends the record of sarcopterygians to the Late Silurian, or about 410 Ma. The new form is close to *Youngolepis* and *Powichthys* at the base of the Crossopterygii. Similarities among the lower jaws of onychodonts, porolepiforms, *Youngolepis*, *Powichthys* and the new form support a position of onychodonts within the Crossopterygii. Four characters in the character matrix of Cloutier & Ahlberg (1996, in Stiassny *et al.*: *Interrelationships of Fishes*, Academic Press) are reviewed, and sarcopterygian interrelationships are studied on the basis of their data with minor modifications. The new scheme of sarcopterygian interrelationships differs markedly from Cloutier & Ahlberg's scheme. Neither actinistians nor onychodonts are situated at the base of Sarcopterygii, but within the Crossopterygii. *Youngolepis* and *Powichthys* are at the base of the Crossopterygii, instead of being the sister group of dipnoans plus *Diabolepis*. □Sarcopterygii, Late Silurian, China, phylogeny.

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Sarcopterygian interrelationships and the relationship of tetrapods have been discussed at length during the last two decades, and many contrasting hypotheses have been proposed (Schultze 1994). The relationship of tetrapods to Elpistostegalia (panderichthyids) and osteolepiforms and the monophyly of tetrapods are generally accepted (Ahlberg & Milner 1994; Ahlberg *et al.* 1996), whereas interrelationships of sarcopterygians are still controversial (Rosen *et al.* 1981; Gardiner 1984; Janvier 1986; Maisey 1986; Panchen & Smithson 1987; Schultze 1987, 1994; Chang 1991a; Forey *et al.* 1991; Cloutier & Ahlberg 1995, 1996; Chang & Yu 1997). In addition to careful analysis of characters, a good knowledge of the basal taxa such as those from the Lower Devonian of China is crucial to resolve controversial hypotheses (Schultze 1987, 1994; Huelsenbeck 1991). Basal taxa shorten the evolutionary distance between groups and carry less 'background noise', such as reversals and parallelisms of characters, produced during evolution (Schultze 1995). In addition, the oldest known taxa provide the minimum age of the group.

Sarcopterygians and actinopterygians are the two main divisions of the osteichthyans. The oldest known actinop-

terygians, *Andreolepis hedei* from Gotland, Sweden (Gross 1968), and *Ligulalepis yunnanensis* and *Naxilepis gracilis* from Yunnan, China (Wang & Dong 1989), are of Ludlow (Late Silurian) age. On the basis of scale morphology and histology, *Lophosteus superbus* from the Pridoli (Late Silurian) of Saremaa, Estonia (Gross 1969), is considered the most primitive osteichthyan, which cannot be placed with either actinopterygians or sarcopterygians (Schultze 1977). However, *Lophosteus* as an osteichthyan was recently questioned by Burrow (1995), who suggested its possible affinity with placoderms. All these Silurian osteichthyan remains are represented by scales and teeth. The oldest known skeletal material of actinopterygians is that of *Dialipina markae* (Schultze 1992), described from the Lochkovian (Lower Devonian) of Siberia. Up to this report, the fossil record of the sarcopterygians begins with the Lochkovian (Schultze 1993), and the oldest known sarcopterygians are *Youngolepis* (Chang & Yu 1981; Chang 1982, 1991b; Chang & Smith 1992), *Powichthys* (Jessen 1975, 1980), and the dipnoan-like *Diabolepis* (Chang & Yu 1984; Smith & Chang 1990; Chang 1995). These three fish were originally reported from the upper Lochkovian of southwestern China and Arctic Canada;

*Youngolepis* has recently been found in China in beds dated as early Lochkovian (Zhu & Fan 1995).

The material reported here represents a new, unnamed sarcopterygian. It was collected from the Yulongsi and the overlying Xishancun formations in one section of Qujing, Yunnan, China. The older occurrence is in the uppermost part of the Yulongsi Formation, about 7 m below the top of the formation. The sarcopterygian remains include a parietal bone (V11253.1, Fig. 1), a left ramus of lower jaw (V11253.2, Fig. 2), and a fin spine (V11253.3, Fig. 3). In addition, this horizon contains galeaspid agnathans and petalichthyid placoderms. The younger occurrence in the Xishancun Formation, about 24 m above the base of the formation, yielded a right ramus of a sarcopterygian lower jaw (V11254, Fig. 4), as well as remains of the galeaspid *Polybranchiaspis yulongensis* (Liu 1975) and of yunnanolepiform antiarchs. The earliest occurrence of *Youngolepis* (Zhu & Fan 1995) lies also in the Xishancun Formation of the same section, but about 54 m above the base.

The boundary between the Yulongsi and Xishancun formations is generally considered as Silurian–Devonian (S–D) boundary (Zhu *et al.* 1994), as the latest Silurian conodont *Ozarkodina crispera* was found in the middle part of the Yulongsi Formation (Wang 1981). This subdivision was recently corroborated by the conodonts *Ozarkodina excavata*, *Dentacodina* sp. and cf. *Ligonodina elegans detorta*, all of which have been found in the uppermost part of the Yulongsi Formation (Fang *et al.* 1994). Since *Ozarkodina crispera* characterizes a zone of Ludlow age (and may reach into early Pridoli according to O.H. Walliser, personal communication, 1996), it is reasonable to consider the age of the uppermost part of the Yulongsi Formation as Pridoli, about 410 Ma. The S–D boundary may be within the Xishancun Formation in Qujing; nevertheless, we take the conservative position and consider the age of the Xishancun Formation as early Lochkovian, since no index fossil has been discovered in the formation. In conclusion, the material reported here from the Yulongsi Formation represents the oldest known sarcopterygian, and it is the only record of sarcopterygians from the Silurian. The lower jaw from the Xishancun Formation is accepted as Lochkovian and is thus the oldest record of sarcopterygians in the Devonian. All of the specimens are housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

Yu (in press) describes a new sarcopterygian genus from the Xitun Formation of Qujing, Yunnan. The specimens in this study are suggestive of Yu's new genus, even though there exist some differences, which we consider of specific significance (e.g., lack of the first coronoid *sensu* Yu in our lower-jaw specimens). The Xitun Formation overlies the Xishancun Formation, so Yu's material is younger than ours.

## Description of the specimens

The right parietal bone (V11253.1, Fig. 1) is long and narrow, and similar to the parietal of osteolepiforms and some primitive actinopterygians (Jarvik 1980). In the anterior third, the median suture of the parietal shows the right half of a relative large pineal foramen (f.pi, Fig. 1A). A pineal foramen is considered as the primitive condition in osteichthyans (Ahlberg 1991); nevertheless, it is absent in primitive actinopterygians (Schultze 1992), *Youngolepis*, porolepiforms, *Diabolepis* and most dipnoans. The anterior pit line (a.pl, Fig. 1A) is situated in the posterior half of the bone, and its position relative to the pineal foramen or pit is similar to that in *Youngolepis*, *Powichthys*, porolepiforms and the osteolepiform *Kenichthys* (Chang & Zhu 1993). This is presumably the primitive osteichthyan character. In advanced osteolepiforms, such as *Eusthenopteron* (Jarvik 1980), the anterior pit line lies lateral to the pineal foramen, since the latter has migrated posteriorly.

The two lower jaws (V11253.2, Fig. 2; V11254, Fig. 4) are well preserved; however, both lack the posterior portion. The lower jaws agree well with those of *Youngolepis*, *Powichthys*, porolepiforms and osteolepiforms in overall structure and shape. The dentary (De), splenial (Spl), and postspenial (Pspl) are identified in V11254 (Fig. 4A–B), and two pit lines are evident in V11253.2 (Spl.pl, m.pl, Fig. 2A). The posterior pit line (m.pl, Fig. 2A) is comparable to the horizontal part of the mandibular line in *Youngolepis* (Chang 1991b); however, its anterior end forms a down-turning curve. The pores of the mandibular sensory canal are lined up near the ventral margin of the lower jaw; they are not easily distinguished from the

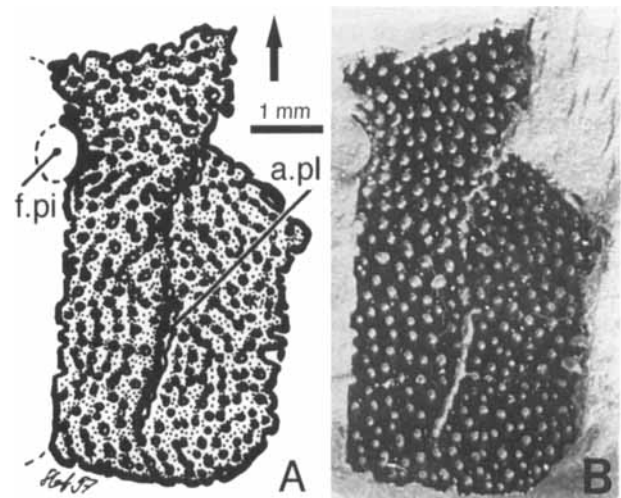


Fig. 1. Right parietal bone of a sarcopterygian from the Upper Silurian of China (V11253.1). □A. Sketch. □B. Photograph,  $\times 10$ . Abbreviations: a.pl, anterior pit line; f.pi, pineal foramen.

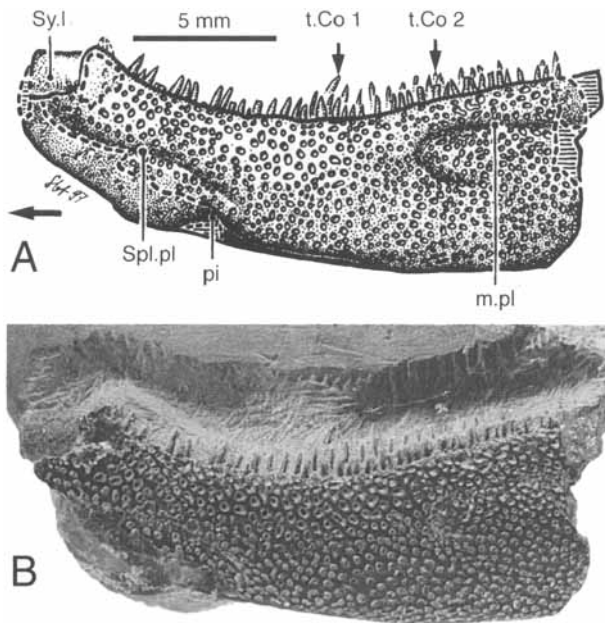


Fig. 2. Left ramus of a sarcopterygian lower jaw from the Upper Silurian of China (V11253.2). □A. Sketch. □B. Photograph,  $\times 4$ . Abbreviations: m.pl, mandibular pit line; pi, pit of lower jaw; Spl.pl, pit line of splenial; Sy.l, parasymphysial lamina; t.Co 1, tusk of coronoid 1; t.Co 2, tusk of coronoid 2.

large pores of cosmine. In some cases they are inferred from the inner side of the infradentaries. Immediately posterior to the suture between the splenial and postsplenial, there is a pit (pi, Figs. 2A, 4B) which is followed by a posteroventrally extending groove. The groove forms a narrow descending lamina at the ventral margin of the lower jaw. This kind of pit is also found in the lower jaws of *Youngolepis*, *Powichthys* and of the porolepiforms *Lacognathus* and *Holoptychius* (Jarvik 1972), and in the cheek bones of *Youngolepis* and the osteolepiform *Kenichthys* (Chang & Zhu 1993). However, a groove following the pit is only present in *Youngolepis* and *Kenichthys*.

The dentary is equipped with two rows of teeth, as is the case in *Youngolepis* and *Powichthys*. The teeth of the outer row are tiny and form the transition from the superficial cosmine layer. The teeth of the inner row are large and striated at their base. Where broken, the teeth exhibit a free pulp cavity. Anteriorly, the dorsal margin of the dentary is devoid of teeth and forms a notch at the anterior margin of the lower jaw; thus the parasymphysial lamina of the mentomeckelian bone (Sy.l, Figs. 2A, 4A) can be seen in lateral view. In *Youngolepis* (Chang 1991b) and *Powichthys* (Jessen 1980), a parasymphysial lamina supporting the parasymphysial tooth whorl is also present; however, it is not visible in lateral view, because the lamina is below or at the same level as the dorsal margin of the lower jaw. In porolepiforms and onychodonts, the dentary forms a dermal anteromedial

lamina as support of the parasymphysial tooth whorl. In dorsal or mesial view, the parasymphysial lamina is fairly broad, similar to the dermal anteromedial lamina in the porolepiform *Holoptychius*. In *Youngolepis* and *Powichthys*, the parasymphysial lamina is not so strongly developed as the dermal anteromedial lamina in *Holoptychius* and onychodonts. The upper face of the parasymphysial lamina is strongly arched and bears longitudinal grooves and ridges for the attachment of the parasymphysial tooth whorl, as does the anteromedial lamina in porolepiforms. In mesial view, the parasymphysial lamina displays a symphysial pit.

Anteroventrally, the lower jaw of the new form has a large ventral lobe. The right ramus of the lower jaw in V11254 possesses an area overlapped by the left ramus of the lower jaw (oa.j, Fig. 4B); the area is visible in its large anteroventral lobe. The anteroventral lobe of the left ramus of the lower jaw V11253.2 has no overlapped area (Fig. 2). This kind of overlap between two rami of the lower jaw is also found in the onychodont *Strunius rolandi* (Jessen 1966) and the porolepiform *Holoptychius*. In *Holoptychius*, the overlapped lamina is more or less a medial structure and cannot be seen in external view. The large anteroventral lobe of the lower jaw is probably related to the development of the parasymphysial tooth whorl and its support, judging from the occurrence of tooth whorls in the new form, in onychodonts and porolepiforms.

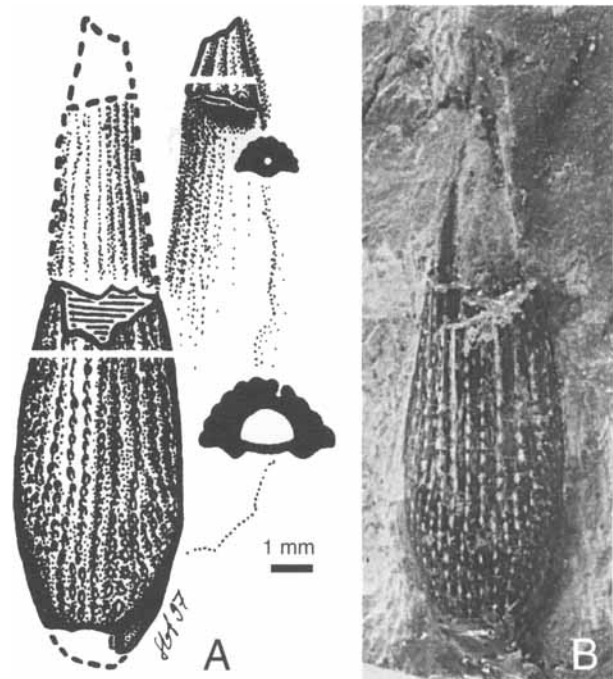


Fig. 3. Fin spine of a sarcopterygian from the Upper Silurian of China (V11253.3). □A. Sketch. □B. Photograph,  $\times 6$ .

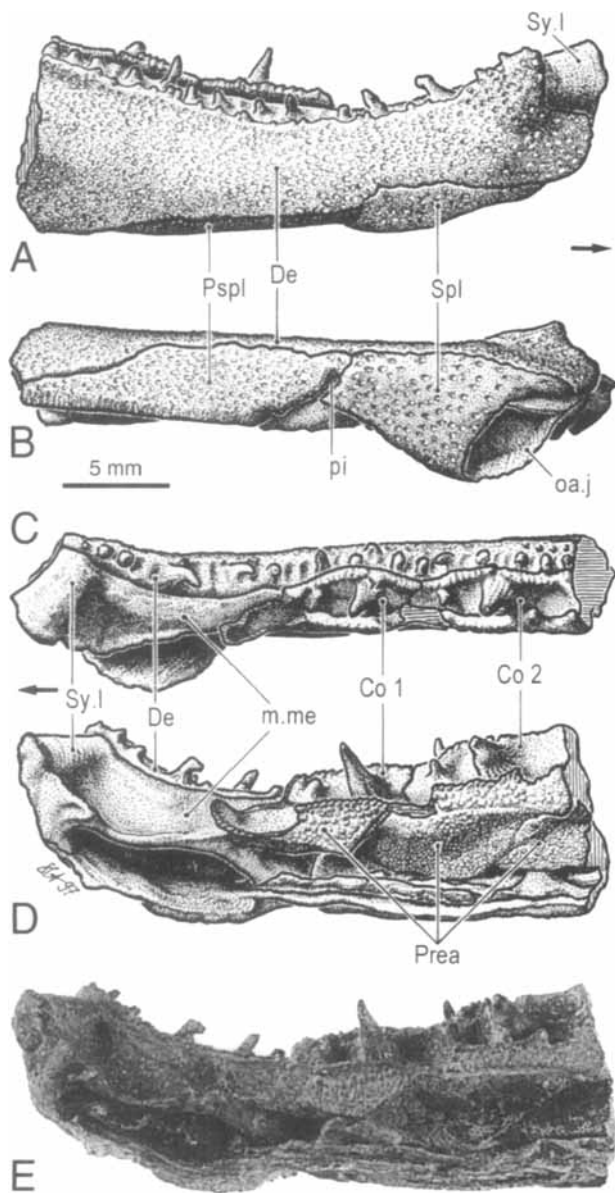


Fig. 4. Right ramus of a sarcopterygian lower jaw from the lower Lochkovian (Lower Devonian) of China (V11254). □A. Sketch in lateral view. □B. Sketch in ventral view. □C. Sketch in dorsal view. □D. Sketch in mesial view. □E. Photograph in mesial view,  $\times 3$ . Abbreviations: Co 1, coronoid 1; Co 2, coronoid 2; De, dentary; m.me, mentomeckelian bone; oa.j, overlapped area by lower jaw; pi, pit of lower jaw; Prea, prearticular; Pspl, postsplenial; Spl, splenial; Sy.l, parasymphysal lamina.

The coronoids and prearticular bone (Co 1, Co 2, Prea, Fig. 4C–D) are very similar to those in *Youngolepis* and *Powichthys*. The main difference is that the lateral portions of the coronoids in the new form bear only two or three rows of small teeth, whereas more than four rows of small teeth are present in *Youngolepis* and *Powichthys*. Two coronoid tusks are preserved in the available speci-

mens. In V11254, the first tusk is sharply pointed and thin, and the second tusk is somewhat swollen in its lower part. As in *Youngolepis*, the coronoid tusk displays a central pulp cavity, which is not filled by osteodentine.

The fin spine (V11253.3, Fig. 3) is referred to this unnamed fish because it bears the same cosmine as the parietal bone and lower jaws. The spine is relatively short and straight. Its base is very short and devoid of the superficial cosmine layer. In cross section, the spine is more or less semicircular in shape and displays a central cavity. Its anterior face is gently arched and exhibits about 15 ridges and grooves. The large cosmine pores are distributed along the grooves. Its posterior face is somewhat flat and without cosmine pores.

The dermal bones of the new form show large round pores on the surface, which is covered by shiny enamel. However, the big size of pores produces a rough surface. The thin section shows that the enamel does not dip into the pore canal as in osteolepiforms.

### Sarcopterygian interrelationships

To place the new Late Silurian sarcopterygian, we use the data set of Cloutier & Ahlberg (1996) in the analysis of sarcopterygian interrelationships. Cloutier & Ahlberg (1996) obtained their scheme of sarcopterygian interrelationships on the basis of detailed character analysis. They selected 33 taxa (including five outgroup taxa) and 140 osteological characters for their phylogenetic analysis. Being different from other cladograms of sarcopterygians (Gardiner 1984; Panchen & Smithson 1987; Schultze 1987, 1994; Long 1989; Chang 1991a; Forey *et al.* 1991; Chang & Smith 1992; but Janvier 1986, Maisey 1986, Chang & Yu 1997), their consensus tree shows that *Powichthys* and *Youngolepis* are sister groups of dipnoans plus *Diabolepis*; the Dipnoiformes (Cloutier 1990) encompass these basal sarcopterygians and dipnoans; the Dipnoiformes is the sister group of the Porolepiformes (Cloutier & Ahlberg 1996). This cladogram agrees well with their previous studies (Cloutier 1990; Ahlberg 1991). In selecting characters and taxa for phylogenetic analysis, one can easily be influenced by one's previous studies (Schultze 1994). To avoid subjectivity in the selection of taxa and characters, we therefore use the Cloutier & Ahlberg data set, so that we are not biased by previous cladograms proposed by one of us (Schultze 1987, 1994). The other reason for using Cloutier & Ahlberg's data set is that so far it is the most complete and detailed one of sarcopterygian interrelationships. This does not mean that we accept all characters and codings of Cloutier & Ahlberg (1996). We will review some of them and make minor modifications to their data set before carrying out our phylogenetic analysis.

### Dentition on coronoids

Cloutier & Ahlberg 1996: Character 10

It has been suggested that the parasymphysial dental plate of dipnoans, porolepiforms and osteolepiforms belongs to the coronoid series (Jessen 1966; Schultze 1969; Thomson & Campbell 1971; Miles 1977; Gardiner 1984). The coronoids *sensu stricto* of *Youngolepis*, *Powichthys*, porolepiforms, osteolepiforms, elpistostegalians and tetrapods (coronoids 1–3 of Jarvik 1937, 1980) are homologous with the posterior members of the coronoids in basal actinopterygians; e.g., the coronoids 2–4 in *Mimia* and *Moythomasia* (Gardiner 1984; Fig. 5A). In this paper, Jarvik's (1937, 1980) definition of sarcopterygian coronoids is followed. The dentition on sarcopterygian coronoids applies strictly to the coronoids behind the parasymphysial dental plate.

Cloutier & Ahlberg (1996) proposed that the broad marginal 'tooth field' on coronoids is an advanced character within osteichthyans. In their cladogram, this character is one of the synapomorphies of their supposed 'Dipnoiformes' and is lost in *Diabolepis* and dipnoans. In their data set, the broad marginal 'tooth field' is only recorded in *Youngolepis* and *Powichthys*, and most of the other taxa including the actinopterygians are described with narrow marginal tooth row on coronoids.

Cloutier & Ahlberg (1996) were correct to state that both *Powichthys* (Jessen 1980; Fig. 5H) and *Youngolepis* (Chang 1991b; Fig. 5G) have the broad marginal 'tooth field' on coronoids, but the limited distribution of this character does not imply that it is apomorphic. Instead, we consider the broad marginal 'tooth field' as a plesiomorphy for the sarcopterygians, as implied by Jessen (1980). First, by outgroup comparison small teeth on the lateral lamina of coronoids of *Youngolepis* and *Powichthys* can be directly compared with numerous teeth on coronoids of the actinopterygians, such as *Polypterus bichir* (Jarvik 1980; Fig. 5E), *Moythomasia durgaringa*, *Mimia toombsi* (Gardiner 1984; Fig. 5A) and *Amia* (Jarvik 1980; Fig. 5C). The difference between them is that *Youngolepis* and *Powichthys* have coronoid tusks on their mesial lamina of coronoids. In actinistians where coronoid tusks are absent, the coronoids also have many small teeth (Millot & Anthony 1958; Jessen 1966; Lund & Lund 1985; Cloutier 1996; Fig. 5B, D, F), as in actinopterygians. Second, the marginal 'tooth field', or tooth rows, on coronoids in sarcopterygians is serially homologous with a shagreen of numerous small teeth on the parasymphysial dental plate (Jessen 1966; Jarvik 1972; Fig. 5J). The small teeth on the parasymphysial dental plate become fewer in advanced forms, such as *Eusthenopteron* (Jarvik 1972).

In the sarcopterygians with coronoid tusks, there are four genera with a broad marginal 'tooth field' on coronoids. Three of them (*Youngolepis*, *Powichthys* and *Kenichthys*; Fig. 5J) are found in the Lower Devonian, and

the osteolepid *Medoavia* from an unknown locality (Lebedev 1995) is assumed to be of Late Devonian age. Double rows of small teeth on the lateral portions of coronoids are found in *Lamprotolepis* (Vorobyeva 1977) and an unnamed osteolepid from the Emsian of Iran (Janvier 1980). Other osteolepiforms, porolepiforms, rhizodontids, elpistostegalians and early tetrapods have exclusively only one row of small marginal teeth on coronoids. It is clear that when tusks of coronoids are developed in sarcopterygians, the lateral tooth field of coronoids is decreased to two or one row of small marginal teeth. The coronoid tusks are secondarily lost in early tetrapods (Fig. 5I).

In our new analysis, we have made a modification of this character in Cloutier & Ahlberg's character matrix. This is the only modification of characters in our new analysis. The broad marginal 'tooth field' on coronoids is regarded as a plesiomorphy of osteichthyans, and is coded 0 in actinopterygians, actinistians, *Youngolepis* and *Powichthys*.

### Position of premaxilla

Cloutier & Ahlberg 1996: Character 17

Cloutier & Ahlberg (1996) suggested that the ventral part of the premaxilla turning in is a shared character of *Youngolepis* and *Diabolepis*. In their cladogram, this character is one of the synapomorphies uniting *Youngolepis*, *Diabolepis* and Dipnoi. It is true that the ventral part of the premaxilla in *Diabolepis* is turned in and forms an inward tooth pad which merges posteriorly with the vomerine tooth pad (Chang & Yu 1984). However, the similar state cannot be observed in *Youngolepis* (Chang & Yu 1981; Chang 1982). The snout of *Youngolepis* is not different from that of *Porolepis* (Jarvik 1972) and *Osteolepis* (Jarvik 1948). We consider the ventral part of the premaxilla turned in as an autapomorphy of *Diabolepis*.

### Fossa autopalatina

Cloutier & Ahlberg 1996: Character 78

In porolepiforms, the pars autopalatina of the palatoquadrate has two anterior articular processes (Jarvik 1972). The ethmoidal process articulates with a small depression on the lateral portion of the postnasal wall, and the anteromedial lamina articulates with the fossa autopalatina on the ventral side of the interorbital wall. In osteolepiforms, the palatoquadrate has only one anterior process, the apical process (Jarvik 1942, 1972; Long 1985; Lebedev 1995), which articulates with a facet on the postnasal wall. This facet, the articular area for the apical process, is fairly unique in osteolepiforms in regard to shape, size and position (Jarvik 1942; Long 1985; Fox *et al.* 1995; Lebedev 1995). It is oval or bean-shaped, rather large, and is situated on the middle portion of the postnasal wall.

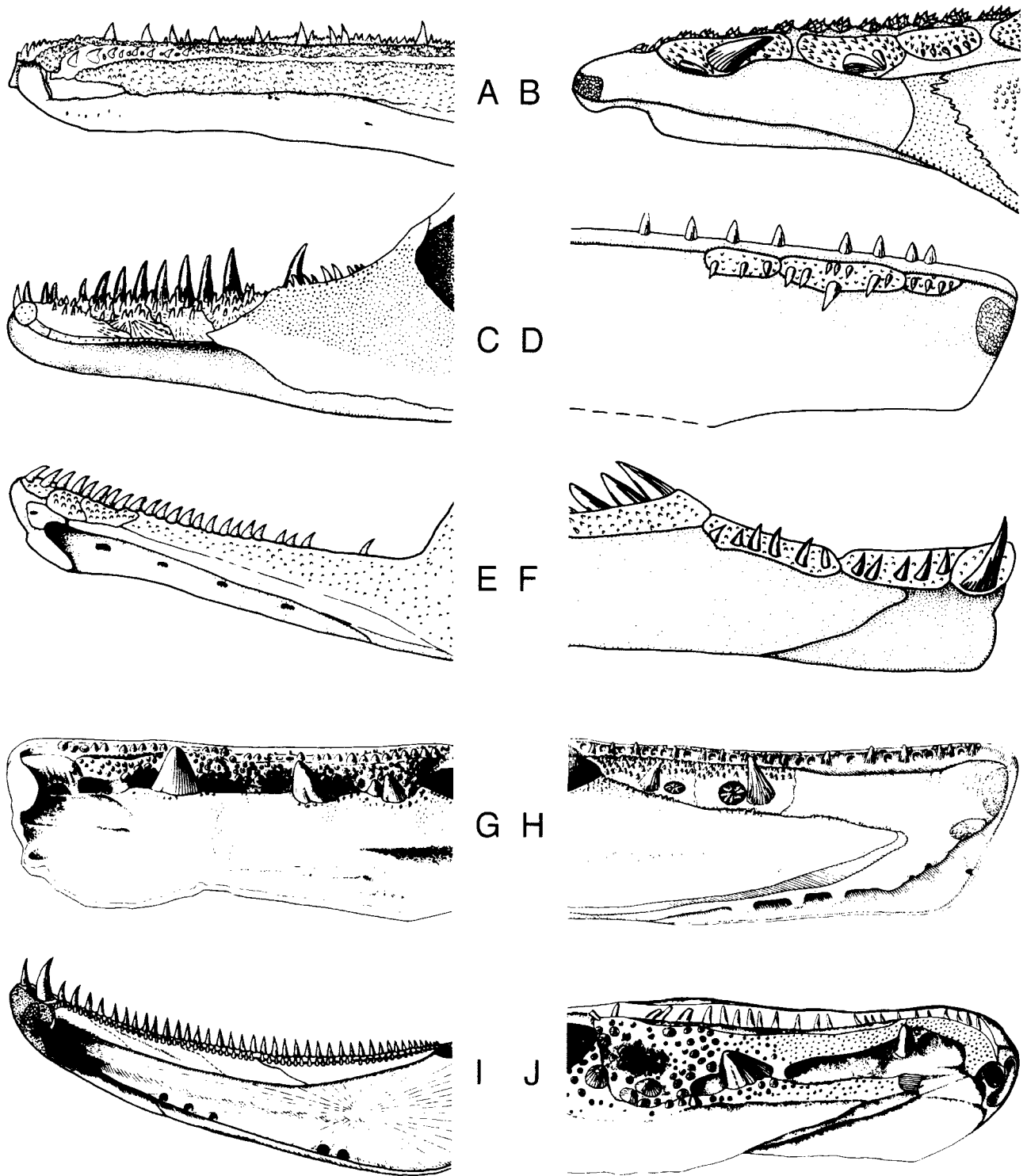


Fig. 5. Lower jaws in mesial view. Figures not to scale. □A. *Mimia toombsi*, after Gardiner (1984, Fig. 91). □B. *Latimeria chalumnae*, after Millot & Anthony (1958, Fig. 18). □C. *Amia calva*, after Jarvik (1980, Fig. 40C). □D. *Diplocercides heiligenstockiensis*, after Jessen (1966, Fig. 15I). □E. *Polypterus bichir*, after Jarvik (1980, Fig. 235D). □F. *Caridosuctor populosum*, after Lund & Lund (1985, Fig. 29). □G. *Youngolepis* sp., after Chang (1991b, Fig. 10C). □H. *Powichthys thorsteinssoni*, after Jessen (1980, Fig. 1C). □I. *Ichthyostega* sp., after Jarvik (1980, Fig. 174B). □J. *Kenichthys campbelli*, V11256.1.

The apical process of the palatoquadrate can be directly compared to the anterior process of the palatoquadrate in basal actinopterygians, such as *Polypterus*, *Mimia* and *Moythomasia* (Gardiner 1984). Their articular facets on the postnasal wall are also similar. The single rostro-palatine articulation was considered as a plesiomorphy for osteichthyans (Gardiner 1984). It is also found in actinistians, such as *Latimeria* (Milot & Anthony 1958) and *Rhabdoderma*. There is little doubt that double rostro-palatine articulations and the fossa autopalatina in porolepiforms are derived.

The fossa autopalatina has been used in the analysis of sarcopterygian interrelationships by many authors, but Maisey (1986, p. 232) doubted the value of this character and argued that it 'is no more variable than orbital articulation among Recent squalomorphs'. Gardiner (1984) considered the fossa autopalatina as a shared character of porolepiforms, *Youngolepis* and *Powichthys*. Forey *et al.* (1991) and Chang & Smith (1992) expanded the distribution of this character to include *Diabolepis* (Chang 1995). Recently, Chang & Yu (1997) even suggested the presence of the fossa autopalatina in basal osteolepids with comparison to the 'fossa autopalatina' in *Youngolepis* and *Powichthys*. However, Panchen & Smithson (1987) regarded the fossa palatina as absent in *Powichthys*. This opinion was followed by Cloutier & Ahlberg (1996), who meanwhile regarded the fossa autopalatina as present in *Youngolepis*. So the dispute in this regard is mainly on the distribution of the fossa autopalatina in *Youngolepis* and *Powichthys*.

We suggest that the fossa autopalatina is absent both in *Powichthys* and *Youngolepis*. Jessen (1980) considered *Powichthys* as a porolepiform, so he compared the endocranium of *Powichthys* mainly with that of *Porolepis*, *Holoptychius* and *Glyptolepis* (Jarvik 1972). As to the fossa autopalatina, which is a typical porolepiform character, Jessen argued that a faint shallow depression posteromedial to the strong anterior articulation may represent the fossa autopalatina, although he expressed his hesitation with a quotation mark ('fossa autopalatina', Jessen 1980). In fact, the rostro-palatine articulation reflected by the endocranium of *Powichthys* (Fig. 6B) resembles closely that of osteolepiforms. Its articulation facet on the postnasal wall is much more alike the articular facet receiving the apical process of the palatoquadrate in osteolepiforms than the articular facet receiving the ethmoidal process in porolepiforms. This can also be confirmed by the palatoquadrate of *Powichthys* (Jessen 1980). As stated by Jessen (1980, p. 82), the palatoquadrate of *Powichthys* (*Porolepiformes* gen. et sp. indet. in his work) 'in their general habitus somewhat remind of the palatoquadrate of *Eusthenopteron* and that of in this respect known osteolepids'. But once again, Jessen was misled by his assumption that *Powichthys* is a porolepiform and explained the palatoquadrate of *Powichthys* in a model of porolepi-

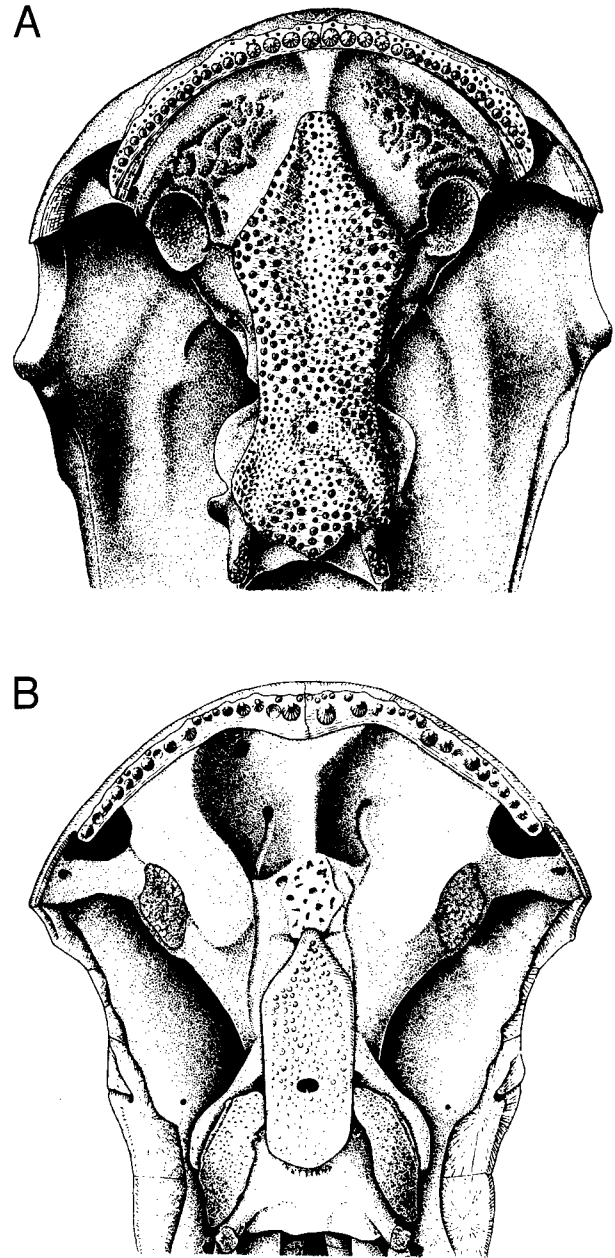


Fig. 6. Restoration of anterior cranium in ventral view. Figures not to scale. □A. *Youngolepis praecursor*, after Chang (1982, Fig. 7A). □B. *Powichthys thorsteinssoni*, after Jessen (1980, Fig. 4).

forms. But, as clearly shown by his plates (Jessen 1980, Pl. 1:1–2), the ethmoidal articular process and the anteromedial lamina at the anterior end of the pars autopalatina identified by Jessen are more suggestive of the apical process of osteolepiforms (Jarvik 1942, 1972; Lebedev 1995). In *Powichthys*, there is only one rostro-palatine articulation as in osteolepiforms, primitive actinopterygians and actinistians, as stated by Panchen & Smithson (1987) and Cloutier & Ahlberg (1996).

The problem of the fossa autopalatina in *Youngolepis* is similar. Chang (1982), in her detailed description of the endocranium of *Youngolepis* (Fig. 6A), observed the resemblance of rostro-palatine articulation between *Youngolepis* and osteolepiforms. She stated that, 'the area of articulation for ethmoidal process of palatoquadrate in *Youngolepis* is reminiscent of the articular area for the processus apicalis of the pars autopalatina of the palatoquadrate in the ethmoidal region of *Eusthenopteron foordi* and *Megalichthys nitidus* (art1m, Jarvik 1942; etha, Romer 1937). It is situated more or less medially and resembles more that of *Powichthys*.' This comparison was followed by Chang & Yu (1997). She also said (Chang 1982), 'it seems probable that in this fish the connection between the endocranium and the anterior part of the palatoquadrate is different from that of *Glyptolepis* and *Porolepis* but is closer to the situation in *Eusthenopteron* and *Megalichthys*'. In this original work, Chang (1982) was not quite certain of the fossa autopalatina in *Youngolepis*. She only borrowed the term from Jessen (1980), and stated that 'posteromedial to the art.e, the ventral side of interorbital wall contains a shallow depression, similar to the depression in *Powichthys* which Jessen designated as "fossa autopalatina"'. She was also correct to point out that the "fossa autopalatina" of *Youngolepis* 'corresponds positionally to the depressed area posteromedial to the articular area in *Eusthenopteron foordi*'. However, the "fossa autopalatina" of *Youngolepis* in Chang (1982) were replaced by the 'fossa autopalatina' (i.e. without quotation marks) in some later works (Forey *et al.* 1991; Chang & Smith 1992; Chang 1995; Cloutier & Ahlberg 1996; Chang & Yu 1997).

Although no palatoquadrate of *Youngolepis* has been found, a close resemblance between the articular facet on the postnasal wall and the depression posteromedial to the facet in *Youngolepis* and *Powichthys*, as well as in osteolepiforms, strongly supports the single rostro-palatine articulation and the absence of a fossa autopalatina in *Youngolepis*. In addition, the observation on some new specimens of *Youngolepis* shows that the so-called 'fossa autopalatina' of *Youngolepis* is unsuitable to be an articular area, since it is transversed by the crista suspendens ('olfactory ridge' in Chang, 1982), which merges posteriorly with the horizontal portion of the basiptyergoid process.

### Oral canal of lower jaw

Cloutier & Ahlberg 1996: Character 108

The oral canal is typically developed in dipnoans, where it is a canal parallel to the mandibular canal. In primitive dipnoans, the oral canal may have a connection with the mandibular canal anteriorly by a vertical canal, but it terminates posteriorly at or near the posterior end of the 'surangular' (Campbell & Barwick 1987). The connection

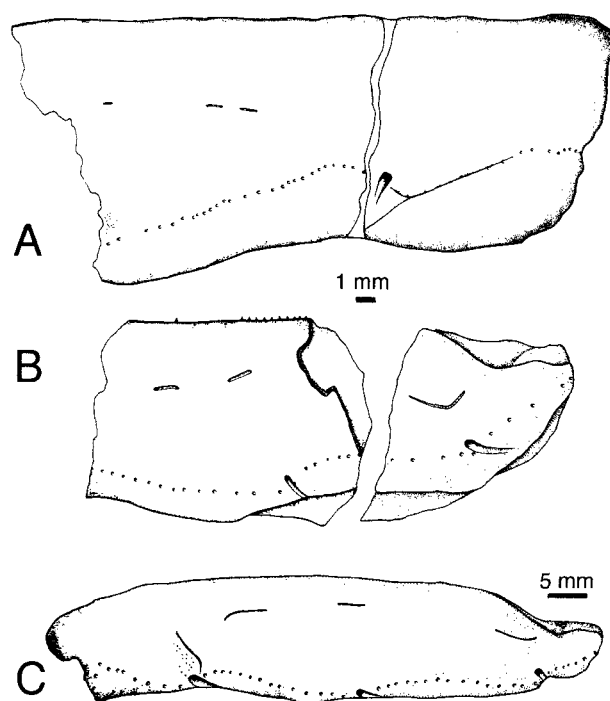


Fig. 7. Lower jaws of *Youngolepis* sp. in lateral view. □A. V11255.2. □B. V11255.3. □C. V11255.1.

between the oral and infraorbital canals, as in *Neocera-todus*, is derived. The term 'oral canal' was also used to represent a short canal which branches off the posterior portion of the mandibular canal in osteolepiforms (Jarvik 1948). This short canal is unlikely to be homologous with the oral canal of dipnoans, and it is better to use another term. However, the horizontal pit-line of the lower jaw is likely to have the same origin as the oral canal of dipnoans, as proposed by Cloutier & Ahlberg (1996).

Cloutier & Ahlberg (1996) described the apomorphy of this character as the 'middle pit-line developed into enclosed oral canal or intermediate morphology'; we disagree with them only in the coding of *Youngolepis* and *Diabolepis*. It seems true that in one lower jaw of *Youngolepis* (V8743.3, Chang 1991b), the middle horizontal pit-line has been developed into the enclosed oral canal. But this should be an individual variation, and we do not consider an oral canal present in *Youngolepis*, since in a number of lower jaws at our disposal that can be referred to *Youngolepis* (Fig. 7) no similar pores in the position of the middle horizontal pit-line have been observed. The similar individual variation took place in *Holoptychius flemingi*. Jarvik (1948) showed that in one specimen of this species there is a sensory canal in the quadratojugal. This canal has a position roughly similar to that of the quadratojugal pit-line in other specimens of the same species (Jarvik 1948).

No oral canal has been described in the lower jaws of *Diabolepis* (Chang & Yu 1984; Chang 1995). New lower



jaws of *Diabolepis* do not show an oral canal either. Cloutier & Ahlberg (1996) were wrong to state an oral canal present in *Diabolepis*, and their codings of *Youngolepis* and *Diabolepis* are corrected in our analysis.

Based on the above discussion, we modified the character matrix of Cloutier & Ahlberg (1996) (Table 1). In order to make a direct comparison with their analysis, we adopted the same algorithm options. All characters were entered unordered and unweighted. The tree was rooted on a monophyletic outgroup including *Polypterus*, *Cheirolepis*, *Mimia*, *Moythomasia*, and *Howqualepis*. Using the heuristic search, we found 54 most-parsimonious tree at 276 steps (C.I.=0.580; C.I. excluding uninformative characters=0.572; R.I.=0.821), as did Cloutier & Ahlberg (1996). The Adams and Strict Consensus Trees show the same topology (Fig. 8). Four topological variants are the same as those of Cloutier & Ahlberg. The monophyly and the interrelationship of the Actinistia, Onychodontida, Dipnoi, Porolepiformes, Rhizodontida, Elpistostegalia and Tetrapoda are also the same as those of Cloutier & Ahlberg.

Table 1. The change of coding (in bold) of four characters in Cloutier & Ahlberg's (1996) character matrix. Character 10 in this analysis has the new polarization.

	10	17	78	108
<i>Acanthostega</i>	1	0	0	?
<i>Allenkypterus</i>	0	0	?	0
<i>Barameda</i>	1	0	?	?
<i>Beelarongia</i>	?	?	?	?
<i>Cheirolepis</i>	0	0	?	0
<i>Crassigyrinus</i>	1	0	?	?
<i>Diabolepis</i>	L	1	?	0
<i>Diplocercides kayseri</i>	0	0	?	0
<i>Diplocercides heiligenstockiensis</i>	0	0	?	0
<i>Dipnorhynchus</i>	L	L	L	1
<i>Dipterus</i>	L	L	L	1
<i>Elpistostege</i>	?	0	?	?
<i>Eusthenopteron</i>	1	0	0	0
<i>Glyptolepis</i>	1	0	1	0
<i>Gyroptychius</i>	1	0	?	0
<i>Holoptychius</i>	1	0	1	0
<i>Howqualepis</i>	0	0	?	0
<i>Ichthyostega</i>	1	0	0	?
<i>Miguashaia</i>	0	0	?	0
<i>Mimia</i>	0	0	0	0
<i>Moythomasia</i>	0	0	0	0
<i>Onychodus</i>	L	0	0	?
<i>Osteolepis</i>	1	0	0	0
<i>Panderichthys</i>	1	0	0	0
<i>Polypterus</i>	0	0	0	0
<i>Porolepis</i>	1	0	1	0
<i>Powichthys</i>	0	0	0	0
<i>Speonesydrion</i>	L	L	L	1
<i>Strepsodus</i>	1	0	?	?
<i>Strunius</i>	L	0	?	0
<i>Uranolophus</i>	L	L	L	1
<i>Ventastega</i>	1	0	?	?
<i>Youngolepis</i>	0	0	0	0

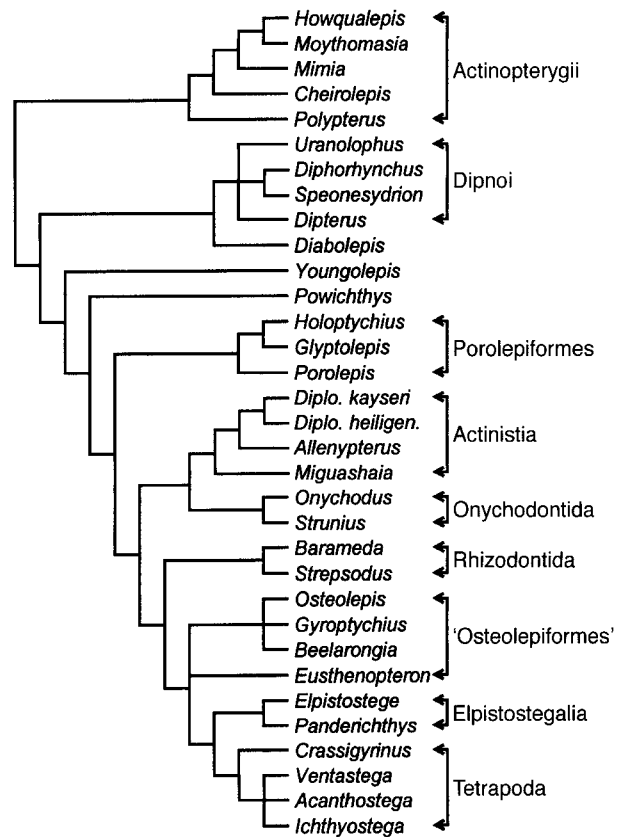


Fig. 8. Interrelationships of 28 sarcopterygian taxa (data set modified from Cloutier & Ahlberg, 1996). Strict consensus tree based on 54 most parsimonious trees at 276 steps.

Our new analysis gives us a rather new scheme of sarcopterygian interrelationships. The clade of *Diabolepis* + Dipnoi, rather than the Actinistia, is at the base of the Sarcopterygii (Schultze 1987). As in Cloutier & Ahlberg's (1996) analysis, *Diabolepis* is the sister group of the Dipnoi (Chang 1991b; Chang & Yu 1997). Among the remaining sarcopterygians, which is termed Crossopterygii (Andrews 1973) in this paper, *Youngolepis* and *Powichthys* form consecutive sister taxa at the base. Among the remaining crossopterygians, the Porolepiformes is the sister group of the clade including the Actinistia, Onychodontida and Choanata (=Tetrapodomorpha of Cloutier & Ahlberg 1996). The Actinistia and Onychodontida form a clade which is not at the base of the Sarcopterygii, but the sister group of the Choanata. The interrelationships of the Choanata in our analysis are the same as those of Cloutier & Ahlberg.

Our new cladogram closely resembles the cladogram of Schultze (1987, 1994). They differ only in the position of actinistians and onychodonts. According to Schultze (1987), actinistians and onychodonts are at the base of the Crossopterygii, whereas *Youngolepis* and *Powichthys* are more derived in the lineage of the Crossopterygii. This is

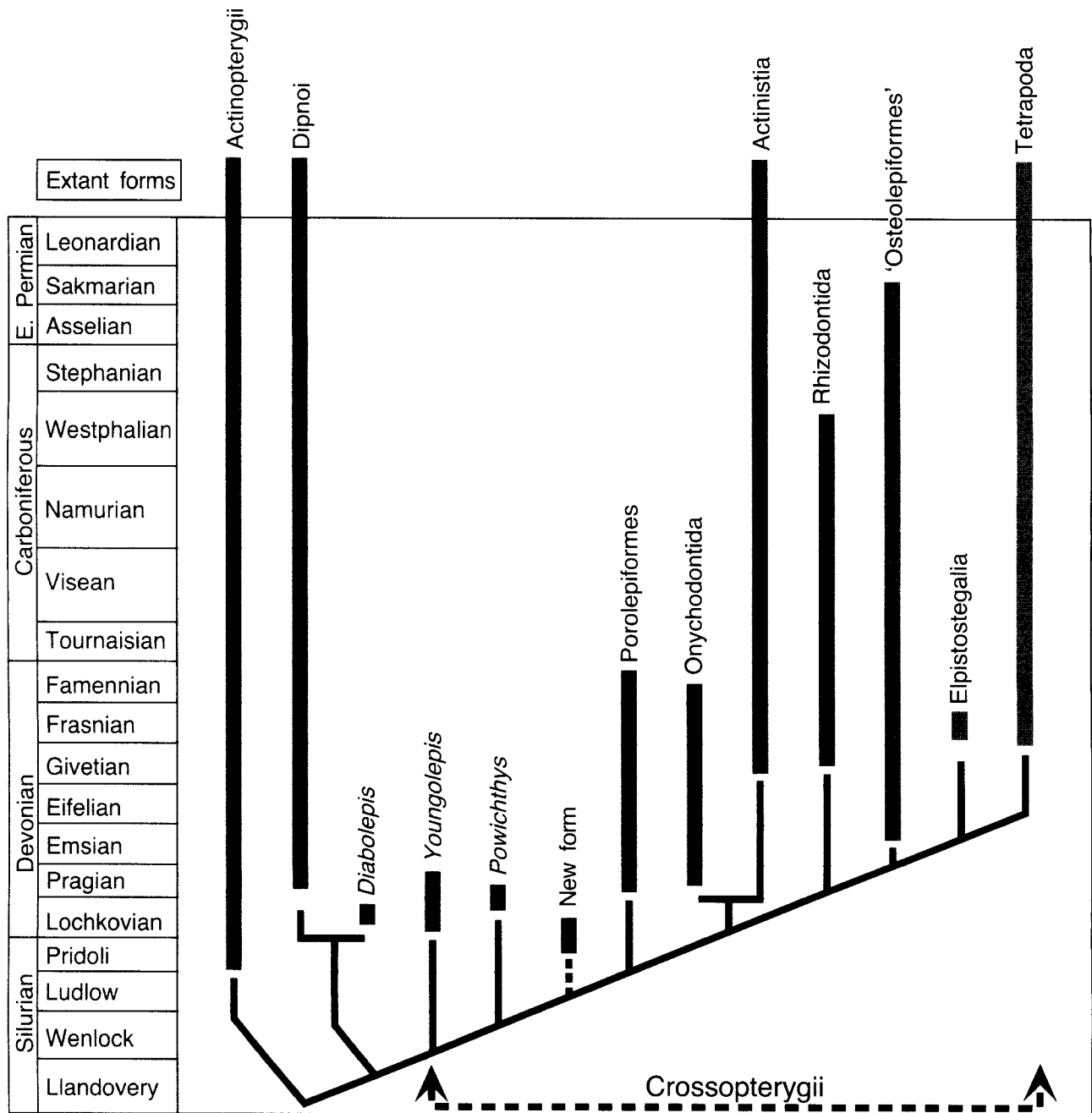


Fig. 9. Evolutionary tree of sarcopterygians with stratigraphic record. The possible position of the new form is added on the tree (dashed line).

not so compatible with the fossil record of sarcopterygians (Fig. 9). Until now, the oldest known actinistian is *Euporoosteus eifelianus* of Givetian age (Stensiö 1937), whereas the crossopterygians in the Lochkovian and Pragian (Lower Devonian) are mainly *Youngolepis*, *Powichthys*, *Porolepis* and related forms. The Silurian material described here also belongs to an allied form of *Youngo-*

*lepis* (see below). Considering the large amount of sarcopterygian fossils found in the Lower Devonian during the last three decades, the absence of actinistians in the Lower Devonian is hardly due to incompleteness of the fossil record. It is likely that the Actinistia is a crossopterygian group derived after the innovations of *Youngolepis*, *Powichthys* and porolepiforms.

## Discussion of the new form and conclusion

The new form exhibits clear sarcopterygian characters, such as cosmine, true enamel on teeth and bones, a mandibular canal that does not pass through the dentary, and possibly three coronoids with a prearticular separated from the dentary.

Crossopterygian characters are polyplocodont plicidentine, anterior pit line on the parietal, and a lower jaw with rhipidistian-type bone pattern (four infradentaries below a long dentary lateral to three coronoids). A parasymphysial lamina of the mentomeckelian bone for a parasymphysial tooth whorl can be found in the new form, as in *Youngolepis* and *Powichthys*; the teeth of the dentary do not extend to the anterior extremity of the lower jaw in either the new form or *Powichthys*. The dermal anteromedial lamina supporting the parasymphysial tooth whorl in porolepiforms and onychodonts, however, is formed by the lateral expansion of the dentary. Further characters shared with *Youngolepis* and *Powichthys* are the presence of more than two rows of small teeth on the lateral portions of coronoids (also in the osteolepiforms *Kenichthys* and *Lamprotolepis*) and the low position of the pit on the lower jaw with a groove following the pit (only in *Youngolepis*).

Unique characters of the new form are the lateral exposure of the parasymphysial lamina, only 2–3 rows of small teeth on lateral portions of coronoids, and possession of a fin spine.

Based on this character combination, the new sarcopterygian is more closely related to *Youngolepis* and *Powichthys* than to any other sarcopterygian. The new form, together with *Youngolepis* and *Powichthys*, is at the base of the Crossopterygii (Fig. 9). Similarities among the lower jaws of onychodonts, porolepiforms, *Youngolepis*, *Powichthys* and the new form support a position of onychodonts within the Crossopterygii (Figs. 8–9).

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