Research paper

Silurian atmospheric O$_2$ changes and the early radiation of gnathostomes

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Abstract

The number of known Silurian gnathostome fossils has increased significantly during the last two decades, and greatly improved our understanding of the early diversification of gnathostomes (jawed vertebrates). Primitive gnathostome remains from the Silurian of China are of special interest in bridging morphological gaps between osteichthyans and non-osteichthyan gnathostome groups. A review of these early fishes shows that gnathostomes had already obtained a wide distribution and experienced an early radiation in the Middle-Late Silurian.

Environmental conditions in the Silurian are inferred from recent advances in geochemistry and paleoclimate models. Atmospheric oxygen concentration, an environmental factor critical in organismal evolution, rose gradually during the Silurian and reached modern levels for the first time. Compared to the Middle Ordovician when invertebrates and agnathans underwent a great radiation, the Middle-Late Silurian is distinctive for its high atmospheric oxygen level. We suggest that the rise of the atmospheric oxygen concentration would have triggered the early radiation of jawed vertebrates in the Silurian, which paved the way for the high generic diversity of vertebrates in the Devonian.
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1. Introduction

Gnathostomes, or jawed vertebrates, are traditionally divided into four major clades: the Placodermi, the Acanthodii, the Chondrichthyes (cartilaginous fishes), and the Osteichthyes (actinopterygians and sarcopterygians), although recently both Placodermi monophyly and Acanthodii monophyly have been challenged by Brazeau (2009). The total-group Gnathostomata also includes several extinct jawless groups ('ostracoderms' such as heterostracans, osteostracans, and galeaspids) (Janvier, 2007). The origin of jaws is a pivotal morphological innovation, which marks a transition to a predatory lifestyle. For the purpose of correlating morphological innovations with environmental changes, here we adopt the traditional apomorphy-based Gnathostomata, which is defined on the basis of the presence of jaws, and includes the crown-group gnathostomes and some stem gnathostomes (placoderms) (Fig. 1).

Despite the earliest record of gnathostomes possibly extending to the Late Ordovician (Sansom et al., 2001; Turner et al., 2004), Silurian gnathostome remains have been few and fragmentary for a long time (Blieck and Janvier, 1991). However, recent decades have seen a growth of fossil evidence of gnathostomes in the Silurian (e.g., Blieck and Turner, 2000), which is improving our understanding of early gnathostome distribution and evolution. These data suggest an early radiation pattern of Silurian gnathostomes.

In this paper, we will summarize the taxa and geographical distribution of Silurian gnathostomes. Close attention is paid to the new discoveries of the past two decades. Recent advances in geochemistry and paleoclimate models have provided considerable information on Phanerozoic climates and atmosphere (e.g., Veizer et al., 2000; Berner, 2006; Trotter et al., 2008), thus making it possible to examine biological events in more definite environmental backgrounds. Finally, we will discuss the possible relationship between environmental changes and the gnathostome radiation during the Middle-Late Silurian.

2. Geographical distribution of Silurian gnathostomes

Until recently, fossils of gnathostomes have been scarce in the Silurian (Blieck and Janvier, 1991). The fossil record of
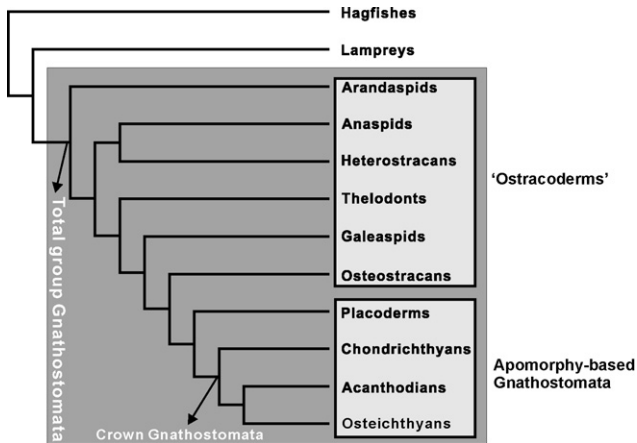

Fig. 1. Vertebrate phylogeny, showing the total-group Gnathostomata (i.e., stem-group Gnathostomata plus crown-group Gnathostomata) and the apomorphy-based Gnathostomata (defined on the presence of jaws), simplified from Janvier (1996, 2007).

Silurian vertebrates was dominated by agnathans including heterostracans, osteostracans, thelodonts, and galeaspids. However, recent studies show that gnathostomes are more diversified and widely distributed in the Silurian than previously thought. IGCP 328, IGCP 408, and the work carried out by the Subcommission on Silurian Stratigraphy greatly advanced the research on Silurian vertebrates, some of which were summarized in the book '*Palaeozoic Vertebrate Biostratigraphy and Biogeography*' (Long, 1993) and the final report of IGCP 328 (1991–1996) (Blieck and Turner, 2000). Since then, many new discoveries related to IGCP 491 (2003–2007) have continued to highlight the early evolution of gnathostomes. To better understand the earliest history of gnathostomes, herein we update all these recent findings.

The distribution of Silurian gnathostome taxa is shown in Fig. 2. Although most are based on microfossil remains or disarticulated specimens, their gnathostome affinities can be confirmed to a large extent by means of histological studies or by comparison to articulated fossils (e.g., Gross, 1947, 1971; Karatajūte-Talimaa, 1998). With reference to the palaeogeographical reconstruction of Scotese and McKerrow (1990), the majority of Silurian gnathostomes are from low-latitude areas. Some possible gnathostomes have been reported from Bolivia and Brazil (Janvier and Suárez-Riglos, 1986; Janvier and Melo, 1988); however, they are fragmentary and debatable in age. The uppermost part of the Tarabuco Formation in Bolivia yielded many fin spines and jaw bones of acanthodians, but this part has been dated as Early Devonian based on chitinozoans (Grahn, 2002). Brazilian fossils from the upper section of the Pitinga Formation have been recently dated as Ludlow to early Pridoli in age (Grahn, 2005), although the fossils themselves suggest an Early Devonian age (Janvier and Melo, 1988). Thus, the Brazilian fossils possibly represent Silurian gnathostomes from the high-latitude area of Gondwana.

Young (1981) illustrated five Early Devonian vertebrate provinces, based mainly on the endemic agnathan faunas. Early gnathostomes except placoderms do not display significant endemism, possibly due to the enhanced dispersal ability of
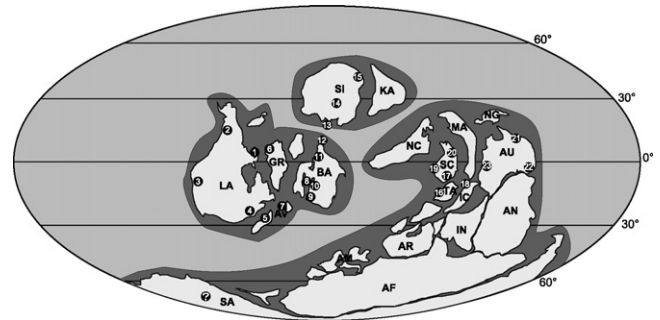

Fig. 2. Locality map for Silurian gnathostome occurrences. The palaeogeographical reconstruction is based on Scotese and McKerrow (1990). (1) Canadian Arctic Archipelago; (2) Western Northwest Territories, Canada; (3) Nevada, western USA; (4) Pennsylvania, north-eastern USA; (5) Eastern Canada; (6) North Greenland; (7) Great Britain: Welsh Borderland, South Wales, West Midlands; (8) Scania and Gotland, Sweden; (9) East Baltic-derived erratics, Northwest Europe; (10) Baltic states; (11) Timan-Pechora; (12) Eastern European Russia: Novaya Zemlya Archipelago, Central Urals; (13) Severnaya Zemlya Archipelago, Russia; (14) Siberia; (15) Russian Tuva and Mongolia; (16) Tarim, northwestern China; (17) Yunnan, southwestern China; (18) northern Vietnam; (19) Gansu, China; (20) Lower-Middle Reaches of the Yangtze River, South China; (21) north-eastern Australia and Indonesia; (22) south-eastern Australia; (23) western Australia; (?) Amazon Basin, Brazil.
LA, Laurentia; AV, Avalonia; GR, Greenland; BA, Baltica; SI, Siberia; KA, Kazakhstan; NC, North China; MA, Malaya; SC, South China; NG, New Guinea; TA, Tarim; IC, Indochina; AU, Australia; AN, Antarctic; IN, India; AR, Arabia; AM, Armorica; SA, South America.

nectonic gnathostomes relative to that of demersal agnathans. Silurian placoderms have a very limited distribution in South China and Vietnam, which may correspond to their lower dispersal ability. By contrast, the acanthodians *Nostolepis* and *Gomphonchus* have a worldwide distribution during the Middle-Late Silurian (Fig. 1 and Appendix A). Thus, the five provinces of Young (1981) adopted below do not necessarily represent the biogeographic provinces of gnathostomes.

2.1. Laurentia and West Avalonia (1–6 in Fig. 2)

This area covers a majority of North America, Greenland and West Avalonia. Sites yielding Silurian gnathostome microfossils include the Canadian Arctic Archipelago, west Northwest Territories, eastern Canada, Pennsylvania, Nevada, and Greenland.

Many islands of Arctic Canada have yielded acanthodian remains (Soehn et al., 2000). Putative articulated chondrichthyans have been reported from this region (Märss et al., 2006), but they lack any definite gnathostome features; thus, their assignment to chondrichthyans is doubtful. The MOTH locality of the Mackenzie Mountains in western Northwest territories is famous for articulated fossils of Early Devonian acanthodians and various agnathans. Recently a second fish-bearing layer below the traditional Lower Devonian fish layer, the B-MOTH, has been discovered. Some gnathostome fossils have been reported, including acanthodian fin spines and jaw bones dated as early Sheinwoodian on the basis of graptolites (Soehn et al., 2000; Hanke et al., 2001). In eastern Canada, acanthodian microfossils have been discovered in New Brunswick (Turner, 1986a) and Nova Scotia (Legault, 1968) belonging

to the Avalonia terrane, although those remains mentioned by Turner (1986a) have not been described in any detail.

Some putative acanthodian scales from the Bloomburg Formation of Pennsylvania have been illustrated by DeWindt (1974), but their histological structures are unknown. Burrow (2003a) described the acanthodian *Poracanthodes* from the Roberts Mountains Formation (Late Silurian) of Nevada; many other acanthodian remains from the same region have only been mentioned but are yet to be described (Burrow, 2003a).

Blom (2000) summarised the occurrences of Silurian vertebrates in Greenland. Only the Chester Bjerg Formation at Halls Grav, Hall Land, and the Monument, central Hall Land have yielded some fragmentary materials of acanthodians, of probable Pridoli age.

2.2. Baltica and East Avalonia (7–12 in Fig. 2)

The current Silurian vertebrate biozonal scheme was erected based on the research of Silurian vertebrates in the Baltic region (Märss, 1986; Märss et al., 1995). Early studies concerned erratic boulders from northwest Europe, which shared similar vertebrate assemblages with the Baltic states. The most common gnathostomes from this region are acanthodian and basal osteichthyan microfossils, whereas placoderms and chondrichthyans are rare and putative.

The Silurian deposits of the Timan-Pechora Basin, central Urals and Novaya Zemlya Archipelago have also yielded rich vertebrate microfossils (Märss and Gagnier, 2001; Valiukevicius, 2003a), and the gnathostomes are represented by diversified cosmopolitan acanthodians and a few osteichthyans. The Ural Mountains and their northward extension into Novaya Zemlya belonged to Baltica during the Silurian (Cocks and Torsvik, 2005).

In the Welsh Borderland of Britain, many acanthodians and putative chondrichthyans have been reported from late Pridoli rocks (Vergoossen, 1995, 1999), but their histology is still unknown.

2.3. Siberia (13–15 in Fig. 2)

Gnathostomes from the Siberian Platform consist mainly of acanthodian and chondrichthyan microfossils, with an age of Llandovery to Wenlock (Karatajūte-Talimaa and Predtechenskyj, 1995).

Recently the acanthodian remains from the same area and the adjacent Tuva and northwestern Mongolia have been thoroughly studied (Karatajūte-Talimaa and Smith, 2003) as a result of the good preservation; and these scales possibly possess many primitive acanthodian or even gnathostome characters.

It is noteworthy that Early Silurian chondrichthyans from the Siberian Platform are very similar to those from South China and Tarim (Wang et al., 1998; Sansom et al., 2000); no other places have yielded such forms. At present there are few records of Early Silurian gnathostomes outside South China and Siberia, which may be due to insufficient fieldwork, or may indicate that these two places represent the distribution center.

New palaeomagnetic data show that the Severnaya Zemlya region was an exotic microcontinent south of Siberia and north of Baltica (Metelkin et al., 2005). The Late Silurian acanthodian fauna in this region is very similar to that of Baltica (Valiukevicius, 2003b). Its earliest record extends to the Ludlow.

2.4. Pan-Cathaysian landmass group and Indochina (16–20 in Fig. 2)

Recently, an articulated gnathostome has been discovered from the Silurian of the Qujing district, Yunnan, China (Zhu et al., 2009). This is the first time that we can examine a Silurian gnathostome as a complete organism, which is essential for understanding early gnathostome history. The same region has also yielded many other gnathostome remains, including articulated placoderms and acanthodian jaw bones. This newly discovered fauna (Xiaoxiang Fauna in Zhu et al., 2009) evidently shows the pattern of early gnathostome radiation. A recent summary of Silurian vertebrates from China shows that all major gnathostome groups already occurred in this region (Zhu and Wang, 2000), together with the endemic galeaspids. Some Llandovery taxa, like the contemporary Siberian forms, are among the earliest gnathostomes. The presence of abundant early placoderms and sarcopterygians is the most significant feature in this region. Further investigation on the Xiaoxiang fauna and materials from the adjacent areas will definitely give us a clearer view of the early gnathostome radiation.

The basal member of the Do Son Formation in the north of central Vietnam, which is dated as the Late Silurian, has yielded yunnanolepiform-like antiarchs and '*Wangolepis*'-like placoderms (Janvier et al., 2003). Although this region is north of the Song Ma suture, it has strong connections with the Indochina Block indicated by lithological and faunal similarities with the Ly Hoa sandstones of central Vietnam (Young and Janvier, 1999). The Late Silurian Dai Giang Formation in central Vietnam has yielded some similar forms of placoderms and osteichthyans to those in South China (Tông-Dzuy et al., 1997; Janvier and Tông-Dzuy, 1998), indicating a close link between the South China Block and the Indochina Block at that time.

Tarim and South China are rich in Early Silurian sinacanth fin spines as well as chondrichthyan scales that closely resemble those from Siberia (Wang et al., 1996, 1998; Sansom et al., 2000). Given that the sinacanth fin spines have not been reported in Siberia, the proximity between the Pan-Cathaysian landmass group and Siberia needs further consideration.

2.5. East Gondwana (21–23 in Fig. 2)

Silurian records of gnathostomes in Australia are sparse and fragmentary, with the acanthodians being the most common group (Burrow and Turner, 2000). Other remains include putative osteichthyans and placoderms that are hard to identify (Burrow and Turner, 2000). The best-preserved fossil is a putative acanthodian from the Late Silurian Yea Formation in Victoria, which is partially articulated as only part of the trunk has been preserved (Burrow and Young, 1999).

3. Taxonomic review of Silurian gnathostomes

3.1. Placoderms

Placoderms are an extinct group of gnathostomes characterized by a massive armor of dermal bony plates that cover the head and the anterior part of the trunk (Janvier, 1996; Goujet, 2001; Janvier, 2007). The head armor articulates with the trunk armor in several groups including arthrodires, antiarchs, petalichthyids, and ptyctodonts (Janvier, 1996). The jaws comprise distinctive denticle-bearing dermal bones, or so-called gnathal bones. Placoderms are known from the Early Silurian (Telychian, Llandovery) to the Late Devonian (Famennian) when they underwent a sudden extinction. They were once regarded as chondrichthyan relatives (Stensiö, 1963; Miles and Young, 1977) or osteichthyan relatives (Forey, 1980; Gardiner, 1984), but they are currently placed as the sister group to all other jawed vertebrates (Janvier, 1996, 2007; Goujet, 2001; Goujet and Young, 2004), thus being basal among jawed vertebrates. Recently, the traditional view of placoderm monophyly (Young, 1986; Goujet and Young, 1995; Janvier, 1996) was questioned by Johanson (2002) and Brazeau (2009), who suggested the hypothesis of placoderm paraphyly (Downs and Donoghue, 2009). However, Goujet and Young (2004), and Young (2008) still adhere to the hypothesis of placoderm monophyly.

Placoderms are the most diverse and abundant fish group during the Devonian, with about 400 known species ranging from 10 mm to 6–7 m in total length (Janvier, 2007). The high diversity of antiarch placoderms in the earliest Devonian (Zhu, 1996; Zhao and Zhu, 2007) suggests an earlier history of placoderms in the

Silurian, which has been confirmed by the discovery of diversified placoderm materials from the Silurian of China and Vietnam (Pan, 1986a,b; Pan and Dineley, 1988; Wang, 1991, 1993; Tông-Dzuy et al., 1997; Janvier and Tông-Dzuy, 1998; Zhu and Wang, 2000). Wang (1991) described two yunnanolepiform antiarchs (*Shimenolepis* and an indeterminate form of the Chuchinolepidae) from the Xiushan Formation of Lixian, Hunan Province. Although these two forms are poorly known, they represent the earliest record of placoderms and highlight the divergence between antiarchs and other placoderm groups as early as the Telychian. *Silurolepis platydorsalis* (Fig. 3D) from the Ludlow Kuanti Formation of Qujing, Yunnan (Zhang et al., 2010) represents the best-preserved Silurian antiarch. It is a large-sized antiarch, distinguishable from other antiarchs in that its anterior median dorsal plate overlaps the posterior median dorsal plate. From the same formation were also reported numerous small-sized yunnanolepiform specimens (Pan, 1986a).

Pan (1986a,b) reported abundant 'arthrodire' specimens from the Wenlock Yuejiashan Formation of Xundian and Qujing, eastern Yunnan, and the Wenlock Xiaoxiyu Formation of Sangzhi, Hunan, but gave no description except a *nomen nudum* (*Wangolepis sinensis*). Specimens of the same taxon were also collected from the same horizons and sites by Wang Junqing, and are under the study of Wang and Goujet (personal communication). Although the name '*Wangolepis*' was later cited by Wang (1993), Zhu and Wang (2000), and Janvier et al. (2003), thus far this arthrodire-like placoderm has not been formally described. Janvier and Tông-Dzuy (1998) and Janvier et al. (2003) described '*Wangolepis*'-like specimens (Fig. 3A and B) from the Late Silurian (Ludlow-Pridoli) of Central and North Vietnam. Recently, more '*Wangolepis*'-like remains have been
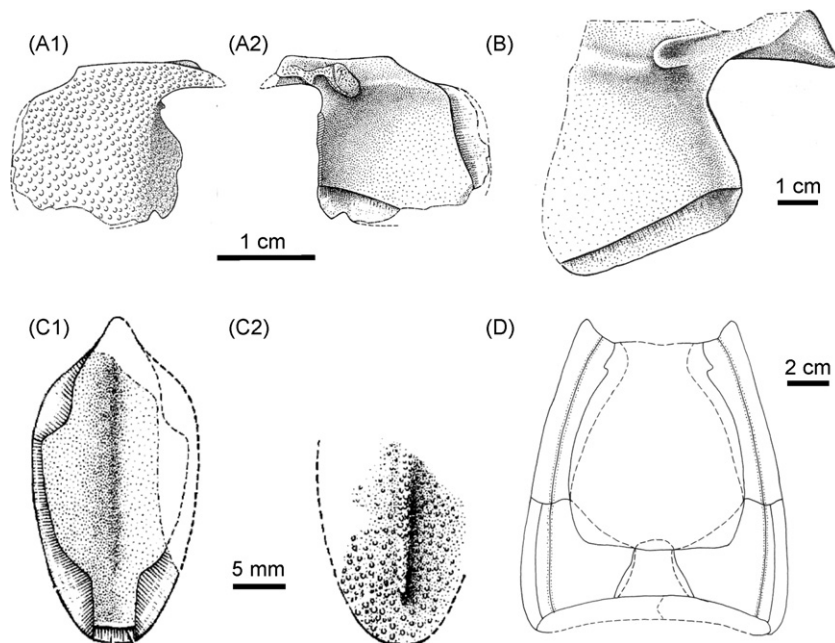

Fig. 3. Silurian placoderms. (A) '*Wangolepis*'-like form, left anterior ventrolateral plate from Locality 17 (A1 in external view, A2 in internal view); (B) '*Wangolepis-like*' form, anterior ventrolateral plate from Central Vietnam (Locality 18), in internal view; (C) *Myducosteus anmaensis*, median dorsal plate from Locality 18 (C1 in internal view, C2 in external view); (D) *Silurolepis*, from Locality 17, in external view. (A after Janvier et al., 1994; B after Janvier and Tông-Dzuy, 1998; C after Tông-Dzuy et al., 1997; D after Zhang et al., 2010.)
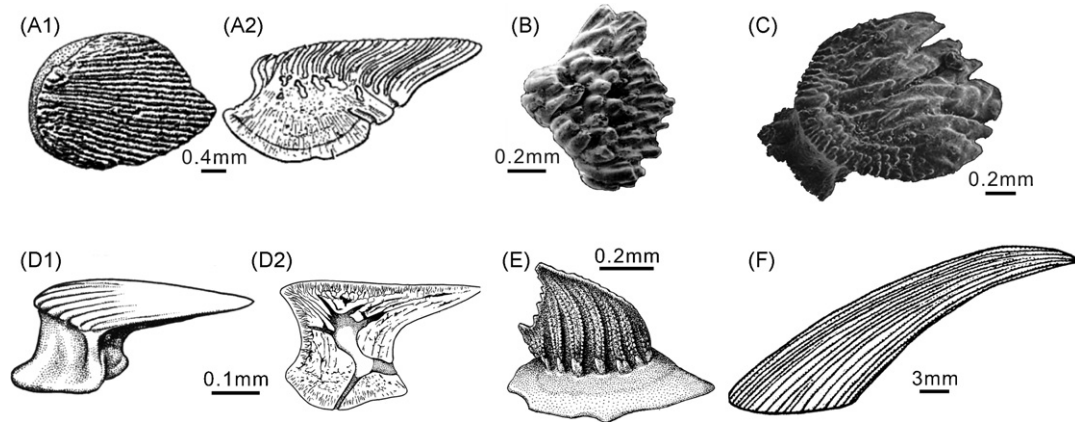
Fig. 4. Silurian chondrichthyans. (A) *Mongolepis rozmanae*, scale from Mongolia (Locality 15) (A1 in crown view; A2 vertical thin section); (B) *Xinjiangichthys pluridentatus*, scale from Tarim (Locality 16), in crown view; (C) *Shiqianolepis hollandi*, scale from Guizhou Province (Locality 20); (D) *Elegestolepis grossi*, scale from Tuva (Locality 16) (D1 in lateral view; D2 thin section); (E) *Pilolepis margaritifera*, scale from Canadian Arctic Archipelago (Locality 1); (F) *Sinacanthus wuchangensis*, fin spine from Hubei Province (Locality 20), in lateral view. (A after Karatajūte-Talimaa et al., 1990; B after Wang et al., 1998; C after Sansom et al., 2000; D after Karatajūte-Talimaa, 1973; E after Thorsteinsson, 1973; F after Pan, 1964.)

collected from the Ludlow Kuanti Formation of Qujing, in association with the oldest articulated osteichthyan *Guiyu* (Zhu et al., 2009).

In addition, Tông-Dzuy et al. (1997) described two placoderm fishes from the Ludlow to Pridoli of Central Vietnam (thus on the Indochina Block). One is *Myducosteus* (Fig. 3C) that does not belong to any of the major placoderm orders known to date, and the other is an acanthothoracid placoderm. Zhu and Wang (2000) reported a petalichthyid placoderm from the Pridoli Yulungssu Formation of Qujing. All these early records indicate that the placoderms underwent early divergences in the Silurian, most likely in a region comprising the South China and Indochina blocks.

3.2. Chondrichthyans

Living chondrichthyans include two major groups: the Elasmobranchii and the Holocephali; they are characterized by many features such as prismatic endoskeletal calcification and a dermal skeleton made up of placoid scales (Nelson, 2006). The Silurian chondrichthyans are all represented by microfossils, most of which are isolated scales with characteristic features of the group: the crown comprising single or closely set odontodes attached to a growing base, with several basal and neck canals (Zangerl, 1981; Janvier, 1996). However, a unique feature of chondrichthyans, the prismatic calcified cartilage, is unknown in these Silurian taxa, due either to its possible absence in basal chondrichthyans or to unfavorable preservation potentials (Janvier, 1996).

Märss and Gagnier (2001) summarized the Silurian chondrichthyan taxa from a few regions of the world, mostly in Asia. Mongolepids are the most common chondrichthyan group in the Silurian. They were first discovered in West Mongolia (Karatajūte-Talimaa et al., 1990), and then in the Siberian Platform, Tuva (Karatajūte-Talimaa and Predtechenskyj, 1995), the Tarim Basin (Wang et al., 1998), and South China (Sansom et al., 2000). The mongolepids are only known from scales, with crown composed of many closely set odontodes with

atubular dentine (Fig. 4A). By comparison, the elegestolepids from the Siberian Platform and Tuva (Karatajūte-Talimaa, 1973; Karatajūte-Talimaa and Predtechenskyj, 1995), usually found in association with the mongolepids, have a single odontode in the scale crown (Fig. 4D), closely resembling the typical placoid scales of chondrichthyans. The elegestolepids extend the earliest occurrence of the Chondrichthyes back to the lower Llandovery (Melichan Formation in Siberia) (Karatajūte-Talimaa and Predtechenskyj, 1995).

The sinacanths (Fig. 4F), based on fin spines from the Silurian of South China, were originally assigned to the Acanthodii (Pan, 1959; Denison, 1979; Pan and Dineley, 1988). They were later found from the Silurian of Tarim, suggesting palaeogeographic proximity between Tarim and South China during the Silurian (Liu, 1995; Wang et al., 1996). The occurrences of sinacanths in Australia (Talent and Spencer, 1963; Turner, 1986b; Burrow, 2003b), Bolivia (Gagnier et al., 1988), and North America (Blieck and Turner, 2003; Turner et al., 2004) are doubtful or need further investigations (Sansom et al., 2005). Based on the histological examination of these Chinese fin spines, Zhu (1998) assigned the sinacanths to the Chondrichthyes. This new assignment was partially corroborated by Sansom et al. (2005), who placed the sinacanths crownwards of the placoderms, and possibly within the total-group Chondrichthyes. Other mongolepid scales (Fig. 4B and 4C) have also been found in Tarim and South China (Wang et al., 1998; Sansom et al., 2000). One puzzling question here is the relationship between sinacanths and mongolepids. In Tarim and South China, both groups with chondrichthyan affinity (one based on scales, and the other based on fin spines) were found in association from late Llandovery (Telychian) to early Wenlock (Zhu and Wang, 2000). It is not unlikely that mongolepids and sinacanths belong to the same basal chondrichthyan group, however we are in need of articulated specimens to test this hypothesis.

The teeth of chondrichthyans are poorly known in the Silurian. Teeth of *Stigmodus gracilis* and *Plectrodus hamatus* from the Pridoli of the Baltic region (Brotzen, 1934) might represent the oldest chondrichthyan teeth known so far (Turner and

Miller, 2008). They are tentatively referred to the Protodontidae by Turner and Miller (2008) based on the morphology of tooth base and cusp, although Denison (1979) placed them within the Acanthodii.

The putative chondrichthyan *Pilolepis* (Fig. 4E) was found from the latest Wenlock of Cornwallis Island, Arctic Canada (Thorsteinsson, 1973). *Pilolepis* is supposed to represent bradyodont shark scales, but they also resemble the heterostracan scales from Nevada (Thorsteinsson, 1973). Gross (in Reif, 1982, p. 307) regarded it identical with the acanthodian genus *Nostolepis*. Burrow et al. (1999) tentatively assigned a scale from the same region (Ludlow-Pridoli) to *Arauzia*, but its chondrichthyan affinity is weakly supported. Other putative placoderm remains were also mentioned (Burrow et al., 1999), but in the absence of more material and histological information, their status cannot be confirmed now.

Some articulated specimens from the Canadian Arctic Archipelago have been tentatively assigned to the Chondrichthyes based on morphological similarities of their scales to other putative chondrichthyan scales (Märss and Gagnier, 2001; Märss et al., 2006). However, they look remarkably similar to thelodonts. Nevertheless, the specimens do not possess real jaws and fin spines, which are characteristic of early jawed vertebrates. Thus we exclude Kannathalepididae and Wellingtonellidae from our data.

3.3. Acanthodians

Acanthodians, sometimes called 'spiny sharks', are distinguished by their fin spines in front of all fins except the caudal fin (Janvier, 1996). Their bodies are covered by minute scales, with a distinct histological structure that is similar to a set of matryeshka (Russian doll) and a bulging base. They lived from the Late Ordovician to the Early Permian (Janvier, 1996). Their records in the Ordovician and Silurian are all based on isolated scales, fin spines, jaw bones, or tooth whorls (Denison, 1979; Smith and Sansom, 1997; Turner et al., 2004), with the exception of an articulated specimen (*Yealepis*) from Australia (Burrow and Young, 1999).

Previous studies of this group mainly depended on articulated specimens of the Devonian or younger (Hanke and Wilson, 2004, 2006), while the only connection between the
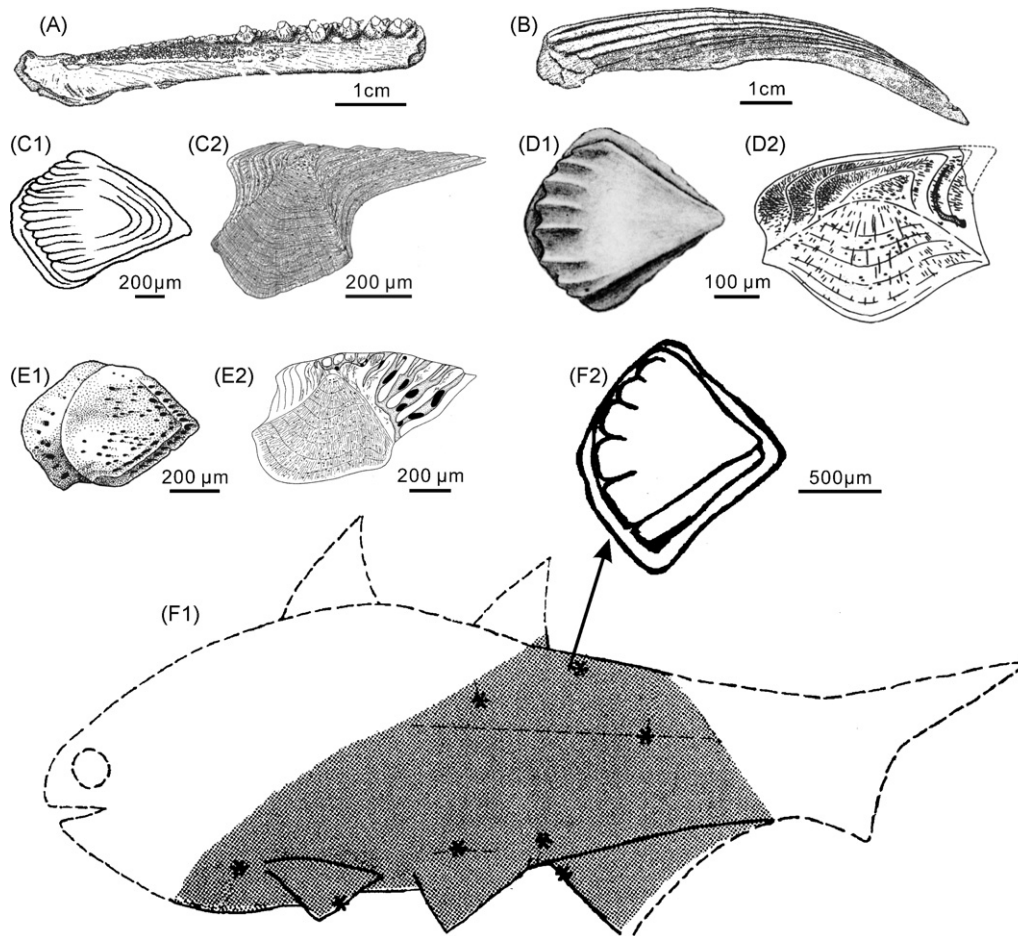

Fig. 5. Silurian acanthodians. (A) *Xylacanthus kenstewarti*, jaw bone from southern Mackenzie Mountains (Locality 2), in lateral view; (B) *Granulacanthus joenelsoni*, fin spine from southern Mackenzie Mountains (Locality 2), in lateral view; (C) *Tchunacanthus obruchevi*, scale from Southern Siberia (Locality 14) (C1 in crown view; C2 vertical thin section); (D) *Nostolepis striata*, scale from Germany (Locality 9) (D1 in crown view; D2 vertical thin section); (E) *Poracanthodes punctatus*, scales from North Germany (Locality 9) (E1 in crown view; E2 vertical thin section); (F) *Yealepis douglasi*, hypothetical reconstruction and a scale impression from Victoria, Australia (Locality 22). (A and B after Hanke et al., 2001; C after Karatajūte-Talimaa and Smith, 2003; D after Gross, 1947; E1 from Denison, 1979 after Gross, 1971; E2 after Gross, 1956; F after Burrow and Young, 1999.)

Silurian and Devonian taxa lies in isolated scales (Fig. 5C–F), jaw bones (Fig. 5A), fin spines (Fig. 5B), and tooth whorls (e.g., Valiukevicius, 1992; Hanke et al., 2001; Burrow, 2003a). Their scales look like some bony fishes but the body forms resemble chondrichthyans (Fig. 5F). Many isolated fin spines referred to acanthodians are possibly basal chondrichthyans, as suggested by histological studies (Zhu, 1998; Sansom et al., 2005). Teeth formerly assigned to acanthodians have been reassigned to chondrichthyans based on an articulated Early Devonian chondrichthyan specimen (Miller et al., 2003). Janvier (2007) proposed that the acanthodians possibly comprise both stem osteichthyans and stem chondrichthyans. Brazeau (2009) also challenged the monophyly of the Acanthodii, based on a restudy of the Early Devonian acanthodian *Ptomacanthus anglicus*. Further investigations on early representatives of this group will solve this debate and revise the deep gnathostome phylogeny. However, we still use the term acanthodian here for brevity.

Acanthodian microfossils are the most abundant among Silurian gnathostomes, and are very important in stratigraphical correlations. In an early attempt of the Silurian biozonal scheme, *Nostolepis gracilis* and *Poracanthodes punctatus* were used as index fossils (Märss et al., 1995). The Silurian acanthodian material from Lithuania has also proved to be useful for erecting standard biostratigraphy (Valiukevicius, 2005), which may be a research direction in the future.

Articulated acanthodians from the Early Devonian (Lochkovian) indicate a high diversity of this group (Gagnier and Wilson, 1996; Gagnier et al., 1999; Hanke and Wilson, 2004, 2006). These fossils mainly come from the MOTH locality, Canada, and are extremely well preserved. This diversification certainly roots into the Silurian, but such information still depends on microfossils at present. Nevertheless, microfossils from many localities have confirmed that the acanthodians became more abundant throughout the Silurian, and were dominant in Late Silurian (Ludlow-Pridoli) deposits (Märss, 1986; Valiukevicius, 2003a,
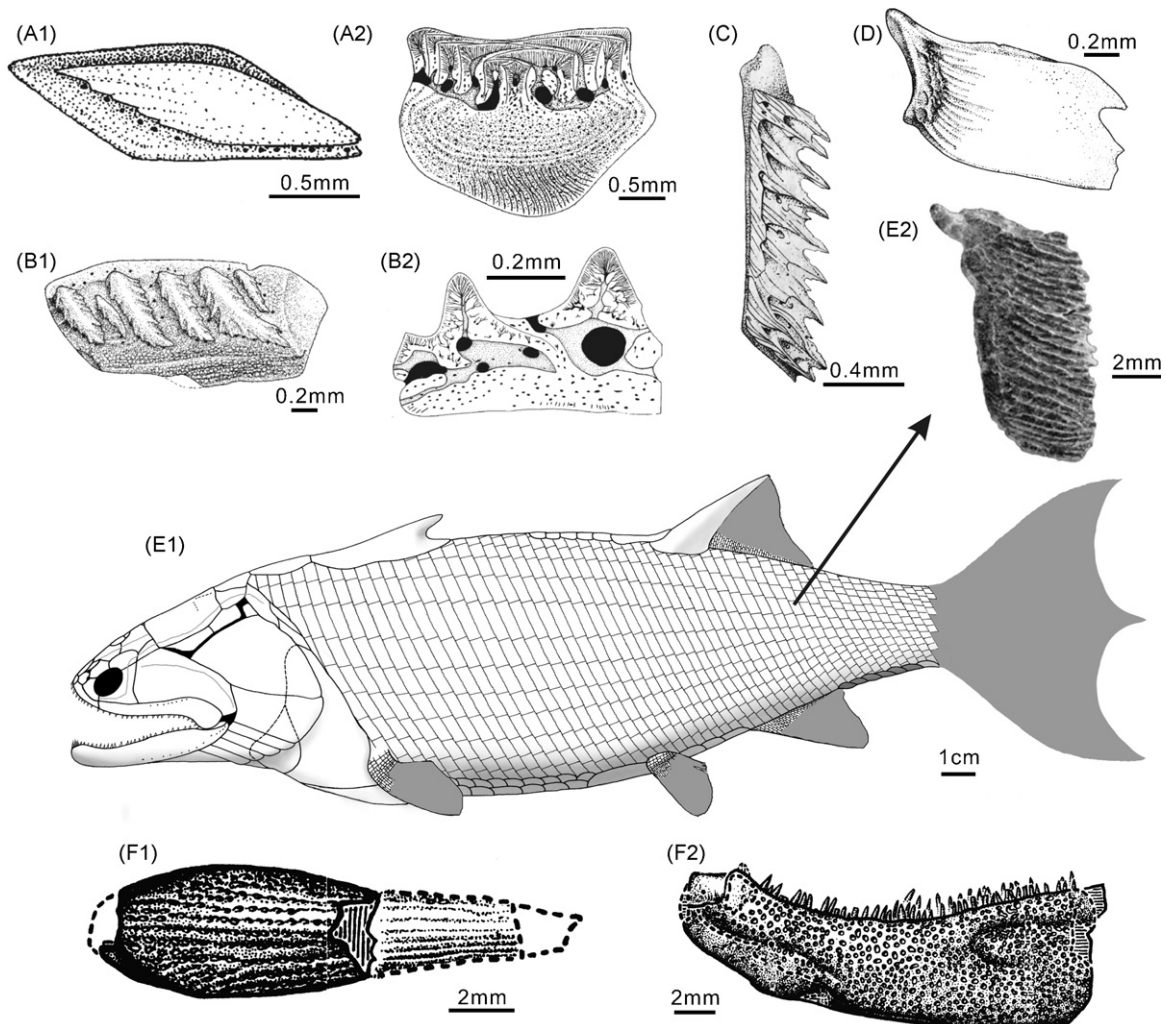

Fig. 6. Silurian osteichthyans. (A) *Andreolepis hedei*, scales from Gotland, Sweden (Locality 8) (A1 in outer surface view; A2 vertical thin section); (B) *Lophosteus superbus*, scales from Estonia (Locality 10) (B1 in outer surface view; B2 vertical thin section); (C) *Ligulalepis yunnanensis*, a scale from Yunnan Province (Locality 17) in outer surface view; (D) *Naxilepis gracilis*, a scale from Yunnan Province (Locality 17) in outer surface view; (E) *Guiyu oneiros*, fish restoration and a scale from Yunnan Province (Locality 17) in outer surface view; (F) *Psarolepis* sp., a fin spine and a lower jaw from Yunnan Province (Locality 17) (F1 in dorsal view; F2 in lateral view). (A after Gross, 1968; B after Gross, 1969; C and D after Wang and Dong, 1989; E after Zhu et al., 2009; F after Zhu and Schultze, 1997.)

2004; Vergoossen, 2003). The "Acanthodian Event" (Märss, 1992) witnessed the radiation of acanthodians in the Ludlow to Pridoli when they became a universal group of microfossils in many localities of the world (Märss, 2000). More evidence of the early diversification of acanthodians is anticipated, such as the partial articulated specimen from the Yea Formation of Victoria, Australia (Burrow and Young, 1999).

3.4. Osteichthyans

Osteichthyans, or bony fishes (piscine osteichthyans) and tetrapods, comprise two major groups—actinopterygians and sarcopterygians; the former are now the most diverse of the extant fishes, and the latter have only a few modern representatives (excluding tetrapods), consisting of six lungfish species and two coelacanth species. However, piscine sarcopterygians were common in the Middle to Late Palaeozoic waters; and by the Late Devonian, tetrapods had evolved from them.

Silurian osteichthyans have long been represented by *Lophosteus* (Fig. 6B) and *Andreolepis* (Fig. 6A), two genera based on fragmentary fossils from the Baltic Region (Gross, 1968, 1969; Janvier, 1978). *Andreolepis* was generally considered as a primitive actinopterygian (Gross, 1968; Märss, 2001), and *Lophosteus* was regarded as having a close affinity to acanthodians (Otto, 1991; Schultze and Märss, 2004). Recent studies support their phylogenetic position as stem osteichthyans (Botella et al., 2007; Zhu et al., 2009). *Andreolepis* occurred mainly in northern Europe, with some specimens known from northern Asia (Märss, 2001), and putative remains from Great Britain (Turner, 2000). It is used as an index fossil in the current Silurian vertebrate biozonal scheme (Märss et al., 1995), with a short duration in the Middle-Late Ludlow. *Lophosteus* has a much longer time range from Ludlow to Lochkovian (Schultze and Märss, 2004).

Wang and Dong (1989) and Gagnier et al. (1989) reported possible osteichthyan scales from the Yulungssu Formation in Qujing, South China, and more scales assigned to *Naxilepis* (Fig. 6D) and *Ligulalepis* (Fig. 6C) from the underlying Miaokao and Kuanti formations. Later the osteichthyan occurrences in the Late Silurian were confirmed by jaws and fin spines referred to as stem sarcopterygian *Psarolepis* (Fig. 6F) in South China and Vietnam (Tông-Dzuy et al., 1997; Zhu and Schultze, 1997; Zhu et al., 1999).

In addition to the above-mentioned fragmentary fossils, an articulated specimen named *Guiyu* (Fig. 6E) has recently been found from the Kuanti Formation (Ludlow) of Qujing (Zhu et al., 2009). It represents the oldest known near-complete gnathostome, and forms the index taxon of a newly discovered fish fauna, the Xiaoxiang Fauna; such a discovery displays the early diversification of gnathostomes. Such finding of a near-complete specimen is very important, because it was previously thought that the environment in the Silurian was not suitable for fossil preservation outside China (Janvier, 1996). Furthermore, the abundant gnathostome microfossils from the Late Silurian (Ludlow-Pridoli) also indicate the early diversity of basal gnathostomes in the South China Block.

4. Silurian atmosphere and climate

Compared with other periods of the Palaeozoic, the Silurian is shorter and comprises less than one tenth of the era, but it is a critical period for the evolution of life on the Earth. The earliest macrofossils of land plants were discovered in the Early Silurian (Gensel, 2008), although cryptospore records indicate an earlier land colonisation of plants (Rubinstein and Vaccari, 2004). The invasion of land by plants has significantly contributed to changing the Earth's landform, climate, and atmosphere ever since. The fossil record also demonstrates that the arthropods had already colonised the land in the Silurian (Engel and Grimaldi, 2004; Labandeira, 2005). As reviewed above, the early diversification of jawed vertebrates, which had far-reaching effects on our family tree, also occurred in the Silurian. An analysis of Silurian environmental changes may provide some hints on the causes of the above substantial events.

After the great glaciation event at the end of the Ordovician (Brenchley et al., 1994), global temperature began to rise. Scotese (2008) roughly estimated the temperature changes during the Phanerozoic based on Frakes et al. (1992), which showed that the temperature during the Silurian remained relatively stable, with the global average being about 25 °C, higher than the present day value (Fig. 7). Another estimate gave a similar conclusion that the temperature rose after the Llandovery (Veizer et al., 2000). A detailed analysis of the oxygen isotopic composition of single conodont elements using the SHRIMP II ion microprobe revealed that the surface sea temperature (SST) regained the modern equatorial level by the early Wenlock. In addition, the invertebrate faunas also indicated relatively high temperatures during the Early to Middle Ordovician and Middle to Late Silurian (Cocks, 2001). Thus, the global mean temperature during the Middle to Late Silurian was relatively high. Based on recent palaeogeographic reconstructions (Metcalfe, 1998; Chen and Boucot, 2001), South China was at low-latitude during most of the Silurian, and the agnathans experienced a slow radiation in this region during the Early Silurian (Zhao and Zhu, 2007). The newly discovered Xiaoxiang fauna, which was dominated by gnathostome remains with an age of late Ludlow (Zhu et al., 2009), could be well assigned to a warm, shallow marine or delta environment.

In the past two decades, large amounts of basic geochemical data have been accumulated; these data have been used to calculate the atmospheric history of the Earth based on different kinds of models. The earlier versions of atmospheric O_2 changes of the Phanerozoic eon suggested that O_2 concentration during the Silurian was very stable, with a minor decrease based on rock abundance modeling (Berner and Canfield, 1989; Berner et al., 2000) or a slight increase based on isotope mass balance modeling (Berner, 2001). Details of the estimation models are provided in Berner (2004). All these previous results indicated that the O_2 levels in the Silurian were between 19% to 18%, lower than the present 21%. Recently, Berner (2006) gave another estimate of Phanerozoic atmospheric oxygen based on a new model GEOCARBSULF and some new isotopic data of both carbon and sulfur. The result showed a gradual increase of atmospheric O_2 from the end of Ordovician with a peak near the
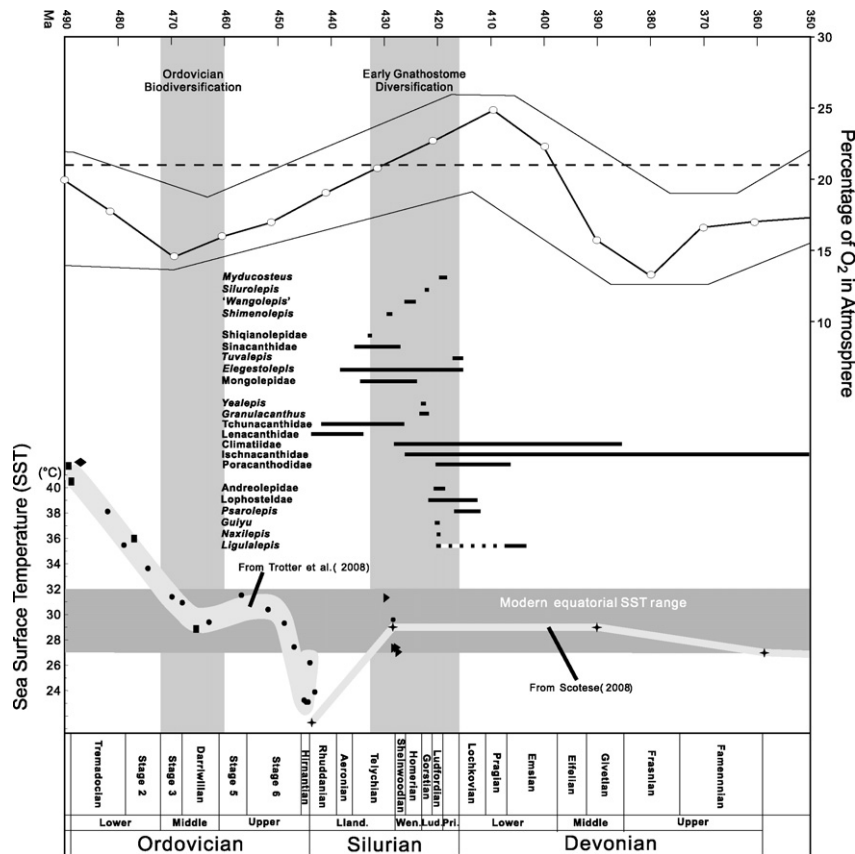
Fig. 7. The temperature curve and atmospheric O$_2$ concentrations from Ordovician to Devonian, with stratigraphic ranges of main gnathostome taxa. Two grey columns represent the Ordovician invertebrate diversification and the early gnathostome diversification. (Graph of oxygen levels from Berner, 2006; global temperature data presented by squares, circles, triangles, and rhombuses from Trotter et al., 2008 and others based on Scotese, 2008.)

Silurian/Devonian boundary, later decreasing during the Early to Middle Devonian with a lowest point in the Frasnian. This trend during the Silurian to Devonian was relatively stable under sensitivity analysis, which may confirm its presence (Berner, 2006). Furthermore, the analysis of fossil charcoal abundance from Silurian to end Permian has confirmed the improved accuracy of the new model for Phanerozoic atmospheric O$_2$ (Scott and Glasspool, 2006).

In summary, basic environmental settings during the Silurian were probably as follows: increasing O$_2$ levels that exceeded the modern level for the first time, decreasing atmospheric CO$_2$ but relatively warm climate.

5. Discussion

5.1. Radiation pattern of gnathostomes in the Silurian

The oldest record of gnathostomes possibly dates back to the Ordovician, with various microremains similar to those from articulated jawed vertebrates (Sansom et al., 2001). These remains include the placoderm-like or acanthodian-like *Skiichthys* and some chondrichthyan-like scales from the Harding Sandstone, USA (Sansom et al., 1996; Smith and Sansom, 1997). Other possible Ordovician gnathostome *Areyongalepis* from Australia was described by Young (1997), but Sansom et al. (2001) refuted its gnathostome affinities. The radiation of

gnathostomes in the Late Ordovician as suggested by Turner et al. (2004) seems unlikely.

Considering the available fossil data from the Silurian, we propose that the gnathostomes had their earliest radiation in the Silurian, and might have a close relationship with the change of climate, atmosphere, and environment during that period. Fig. 7 displays the radiation pattern of gnathostomes and the environmental backgrounds in the Silurian. After the middle-late Telychian, the number of genera increased and the older fauna (represented by mongolepids, elegestolepids, and sinacanths of the Chondrichthyes) was replaced by a new one. Primitive placoderms (early antiarchs and arthrodire-like forms) appeared in the South China Block in latest Telychian to early Wenlock, representing the first evidence for their radiation. Diverse acanthodian taxa evolved quickly after the Telychian, and became worldwide and dominant during the Ludlow to Pridoli. Stem osteichthyans have their earliest occurrences as low as the lower Ludlow in the Baltic region. *Guiyu* from the Ludlow of South China represents the earliest known crown osteichthyan, and indicates an earlier divergence event of actinopterygians and sarcopterygians, probably in the early Ludlow.

All available data suggest that the gnathostomes underwent a radiation throughout the Silurian, and this radiation became more significant during the Middle-Late Silurian when major divergent events probably occurred (e.g., the antiarch-arthrodire and actinopterygian-sarcopterygian divergences).

5.2. The rise of atmospheric O_2 as a possible trigger of early gnathostome radiation

During the Ordovician, the global marine biosphere underwent a significant diversification, with the genus and family numbers increasing approximately three-fold (Sepkoski, 1997). Webby (2004) described this event as "one of the two greatest evolutionary events in the history of life on Earth". During the Middle to Late Ordovician, surface water temperatures remained stable at levels similar to modern equatorial temperatures (Fig. 7), thus probably providing favorable climate conditions for the Great Ordovician Biodiversification Event (Trotter et al., 2008), including the early diversification of agnathans (Sansom et al., 2001).

Molecular clock estimates indicate the time of divergence of crown gnathostomes was much earlier than the Silurian (Donoghue et al., 2003). The fossil record also displays the possible occurrence of gnathostomes in the Ordovician. It is remarkable that, while the agnathans underwent some radiation in the Ordovician, the gnathostomes 'remained in silence' and did not diversify until the Middle-Late Silurian. Why did the Ordovician global biodiversity event involve marine invertebrates and agnathans but not gnathostomes? Why did the gnathostomes have their early radiation in the Silurian? We consider that possible causes lie in the environmental background, for instance, sea surface temperature, water salinity, and atmospheric oxygen concentration.

Over the time span of the Ordovician biodiversity event, the sea surface temperature (SST) remained stable near modern equatorial conditions (Trotter et al., 2008). The Late Ordovician saw a significant decrease of SST, coincident with the extinction event at the end of the Ordovician. Later the SST rose to modern equatorial values again and remained stable during the Middle-Late Silurian (Scotese, 2008; Trotter et al., 2008).

Another factor that influences the solubility of oxygen in water is water salinity; recent model estimation shows that the mean salinity of the ocean changed little during Ordovician to Silurian time (Hay et al., 2006).

Therefore, the remaining major difference between the environments of the two time intervals (indicated by two grey columns in Fig. 7) is reflected in atmospheric O_2 concentration. The oxygen estimate indicates that atmospheric oxygen concentration was well below modern levels during the Ordovician (Fig. 7), with the lowest level (about 15%) in the early Middle Ordovician (Berner, 2006). During the Silurian, atmospheric oxygen concentration increased gradually to modern levels in the Telychian (late Llandovery), and continued this incremental trend until the Early Devonian. This high level of atmospheric oxygen concentration coincides with the first radiation of the gnathostomes in the Silurian; the generic abundance of gnathostomes increased considerably from late Llandovery to Pridoli. We suggest that, after the O_2 concentration increased to modern levels, the environment became more favorable for early gnathostomes and possibly triggered the gnathostome radiation event.

Key events in vertebrate evolution during the Phanerozoic eon, e.g., the origin of tetrapods, the evolution of large placental mammals, the terrestrial Late Permian extinctions, and the appearance of the air-sacs system of modern birds in dinosaurs, have been considered to be related to O_2 concentration variations (Falkowski et al., 2005; Huey and Ward, 2005; O'Connor and Claessens, 2005; Clack, 2007). McNamara (2008) and Glikson (2008) also reviewed many critical transitions in evolutionary history, but they overlooked the origin and early diversification of gnathostomes. Here, we provide another example of a key evolutionary event possibly related to O_2 concentration variation.

It is recognised that the time coincidence by itself does not definitely indicate a causal relationship between the O_2 concentration variation and evolutionary events. We need to have some physiological interpretations for this relationship. A positive relationship between the origin of eukaryotic organisms and the rise of atmospheric oxygen concentration has long been a hypothesis based only on the coincidence of the two events. Research on the transmembrane proteins of modern organisms provided additional evidence for this hypothesis (Acquisti et al., 2007). Back to our case, many invertebrates and agnathans live a benthic life and their oxygen consumption is quite low, while most gnathostomes live a more active and energy-consuming life because of their innovative structures such as paired fins and three semicircular canals; thus, the oxygen concentration level is probably more critical for gnathostomes than for agnathans and invertebrates. Low oxygen levels would have caused physiological constraints on gnathostomes and delayed their radiation. The rise of oxygen concentration during the Middle-Late Silurian may have triggered the radiation of gnathostomes.

Abundant physiological experiments on extant fishes under hypoxic conditions show O_2 concentration plays an essential role in fish growth (e.g., Ishibashi et al., 2002; Herbert and Steffensen, 2005), although these extant fishes cannot fully represent their ancient ancestors. As many fishes live in environments in which O_2 concentrations change rapidly, many of them possess structures or strategies that enable them to survive in hypoxic conditions (Mandic et al., 2009). However, thus far we have known little about the influence of hypoxia on developmental processes, growth rate, mortality rate, and hatching time of fishes, especially the fish groups that may have closer relationships with early gnathostomes. Carefully designed experiments would be the key point for us to investigate how the early radiation of gnathostomes occurred.

6. Conclusions

The Middle-Late Silurian is distinct for its high oxygen levels, which surpassed the present day value for the first time. This review of Silurian gnathostomes adds to the knowledge of an early gnathostome radiation, which was contemporaneous with the rise of atmospheric oxygen concentration. We suggest that this oxygen rise would have triggered the early radiation of jawed vertebrates in the Silurian. Nevertheless, this causal relationship should be tested by research on modern fish groups, for instance, physiological experiments of fishes under hypoxic conditions.

Appendix A.

List of Silurian gnathostomes; numbers represent fossil fish localities. Data compiled from Blieck and Janvier (1991), Long (1993), Tông-Dzuy et al. (1997), Janvier and Tông-Dzuy (1998), Blieck and Turner (2000), Hanke et al. (2001), Märss (2001), Märss and Gagnier (2001), Burrow (2003a), Karatajūte-Talimaa and Smith (2003), Vergoossen (2003), Valiukevicius (2005) and Zhu et al. (2009). For numbers of the localities, see Fig. 1. Question mark indicates problematic taxonomy.

Pridoli:
Placoderms: *Myducosteus*[18]
Chondrichthyans: *Tuvalepis*[15], *Protodus*?[5], *Elegestolepis*[15]
Acanthodians: *Hanilepis*[17], *Vesperalia*[10], *Fecundosquama*[10], *Rohonilepis*[10], *Bracteatacanthus*[10], *Cheiracanthoides*[5,10,13], *Endemolepis*[10], *Monospina*[10,11], *Poracanthodes*[1,3,6,7,9,10,13], *Gomphonchoporus*[7,9], *Gomphonchus*, *Nostolepis*[1,7,8-11,13,17], *Radioporacanthodes*[9,17], *Monopleurodus*[10], *Climatius*[5,7,10,11], *Erriwacanthus*[7], *Ischnacanthus*[7]
Osteichthyans: *Andreolepis*?[7], *Lophosteus*[1,9,10], *Psarolepis*[17], *Osteichthyes indet.*[17], *Onychodus*?[5]

Ludlow:
Placoderms: *Silurolepis*[17], *Myducosteus*[18]
Chondrichthyans: *Elegestolepis*[15]
Acanthodians: *Hanilepis*[17], *Yealepis*[22], *Arenaceacanthus*[10], *Rohonilepis*[10], *Granulacanthus*[2], *Xylacanthus*[2], *Gomphonchus*[1,8,10,16,20,21], *Nostolepis*[8,16,22], *Poracanthodes*[1,8], *Radioporacanthodes*[8-10,17,22], *Climatius*[10], *Ischnacanthus*[17], *Gomphonchoporus*[8,10]
Osteichthyans: *Andreolepis*[8, 10-13], *Guiyu*[17], *Ligulalepis*[17], *Naxilepis*[17], *Lophosteus*?[21], *Elegestolepis*[15]

Wenlock:
Placoderms: '*Wangolepis*'[17,20]
Chondrichthyans: *Pilolepis*?[1], *Sinacanthus*[16,20], *Elegestolepis*[14]
Acanthodians: *Xylacanthus*[2], *Granulacanthus*[2], *Ischnacanthus*[19], *Nostolepis*[19], *Gomphonchus*[10]

Llandovery (Telychian):

Chondrichthyans: *Xinjiangichthyans*[16,20], *Shiqianolepis*[20], *Sinacanthus*[16,20], *Neosinacanthus*[16,20], *Tarimacanthus*[16], *Elegestolepis*[14], *Mongolepis*[15], *Teslepis*[15], *Sodolepis*[15], *Udalepis*[15], *Rongolepis*?[20], *Chenolepis*?[20]
Placoderms: *Shimenolepis*[20]
Acanthodians: *Tchunacanthus*[14,15]

Llandovery (Aeronian and Rhuddanian):
Chondrichthyans: *Elegestolepis*[14]
Acanthodians: *Lenacanthus*[14], *Tchunacanthus*[14,15]

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