

Chapter 28

Palaeobiogeography of Early Palaeozoic vertebrates

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Abstract: The oldest known Palaeozoic vertebrate record currently is Early Cambrian in age. The first taxa with mineralized exoskeletons are at least Ordovician in age, followed by a sporadic fossil record with Talimaa's Gap of c. 3 myr in the Rhuddanian (earliest Silurian). Ordovician and Silurian vertebrate faunas are dominated by 'agnathans'. Early Palaeozoic vertebrates occupied a wide range of environments: nearshore marine to restricted marine in the Ordovician, and on the marine epicontinental shelves of the Silurian. Silurian vertebrates are useful biostratigraphical indicators, as well as good markers of palaeocontinental margins. Two main palaeobiogeographical units are renamed for the Ordovician: a Gondwana Realm and a Laurentia–Siberia–Baltica Realm. Vertebrate fossil localities are more numerous in the Silurian; therefore a series of palaeobiogeographical provinces and realms are defined on Laurentia, Baltica, Avalonia, Siberia, South China and East Gondwana. More discoveries of Silurian vertebrate-bearing localities should certainly help to define additional provinces, in particular along the northern margins of Gondwana and in SE Asia.

Interpreting the earliest vertebrate fossil record is difficult, particularly considering that the Early Palaeozoic fossil record begins with a paraphyletic group of jawless vertebrates, also known as 'agnathans'. Furthermore, it is probable that vertebrates have a Precambrian (Neoproterozoic) origin according to the molecular analysis of major proteins of enamel (Delgado *et al.* 2001). The oldest known record of vertebrates is represented by controversial fossils such as the Early Cambrian *Myllokunmingia* (syn. *Haikouichthys*, Shu *et al.* 1999, 2003; and perhaps also *Zhongjianichthys*, Shu 2003 – see Hou *et al.* 2002), and some latest Cambrian–Early Ordovician phosphatic microremains, such as *Anatolepis* pro parte (see references in Turner *et al.* 2004). The vertebrate fossil record from the beginning of the Palaeozoic Era is very limited and incomplete, and therefore highly interpretative, particularly regarding that from the Cambrian and Ordovician systems.

The conodonts (euconodonts) have also been repeatedly claimed recently as vertebrates, but this assignment must be considered with caution as some early vertebrate experts do not include them within the vertebrates; conodonts are treated either as 'stem gnathostomes' (Donoghue *et al.* 2000) or as basal chordates (Turner *et al.* 2010; Blicek *et al.* 2011). Therefore, we do not include conodonts in this chapter, first of all in order to clarify our palaeobiogeographical definitions, and also to avoid further discussion following the latest critical re-analysis of phylogenetic relationships within the group by Turner *et al.* (2010; also Blicek *et al.* 2011).

Early vertebrates are classically divided into an early, basal (paraphyletic or monophyletic) group of jawless taxa known as cyclostomes, including hagfishes and lampreys, which are not known before the Devonian (Gess *et al.* 2006); another basal (paraphyletic) group of jawless and toothless vertebrates, that is, 'agnathans' ('ostracoderms' e.g. Janvier 1996a); and gnathostomes or jawed vertebrates, which are regarded as a monophyletic group (clade) – both latter groups are known from the Early Palaeozoic. Most of the higher rank Early Palaeozoic vertebrate taxa are still poorly defined, and their phylogenetic relationships are under continuing study. Within the Early Palaeozoic record, *Pikaia*, a 'worm-like' organism from the Middle Cambrian Burgess Shale Fauna of British Columbia (Canada), has never been properly and fully described; *Yunnanozoon*, another 'worm-like' organism from the Early Cambrian Chengjiang Fauna of

the Yunnan Province (China), has been attributed to a great variety of taxa (see, e.g. Donoghue & Purnell 2009); *Myllokunmingia* (syn. *Haikouichthys*), from the Early Cambrian Chengjiang Fauna (Fig. 28.1), is sometimes interpreted as the first vertebrate (Shu *et al.* 2003), but some of its features are problematic and it might well be a basal chordate; *Zhongjianichthys* from the same area of China, although attributed to a myllokunmingiid by Shu (2003), is even more problematic as a vertebrate.

Several major steps in the evolution of vertebrates can be documented in the Early Palaeozoic: (1) an origin starting perhaps in the Neoproterozoic (but this requires a separate discussion); (2) the possible fossil record starting with the Cambrian; (3) a first adaptive radiation during the Great Ordovician Biodiversification Event; (4) the 3 myr-long, Rhuddanian, Talimaa's Gap (Turner *et al.* 2004); and (5) a renewed diversification in the Silurian, which continued into the Devonian, giving rise to 'The Age of Fishes' (for details, see Kaljo & Märss 1991; Märss 1992a; Kaljo *et al.* 1996). Ordovician and Silurian vertebrates both thrived in the warm waters of the tropical and subtropical palaeoseas, which may have been spread across considerably wider latitudes than today. Different Ordovician and Silurian vertebrate palaeobiogeographical units have been proposed (Blicek & Janvier 1999; Blicek & Turner 2003; Sansom 2009a). All of them were dominated by 'agnathans' (Long 1995; Blicek 2005, 2009), but acanthodians, a group of jawed vertebrates, were among the key vertebrate predators of the time (e.g. in the East Baltic Silurian: Märss & Einasto 1978; Kaljo & Märss 1991; Valiukevičius 2003, 2004a, b, 2005, 2006). Note that acanthodians are most recently considered as a paraphyletic grouping by Brazeau (2009). The Silurian record of vertebrates appears to be much richer than previously thought, which has helped to develop a biostratigraphical scale correlated to the standard conodont zonation (Märss *et al.* 1995, 1996, and references in Blicek & Turner 2000). This is confirmed by recent discoveries in China (references in Zhao & Zhu 2007, 2010). From what is currently known, by the Late Cambrian and Early Ordovician vertebrates had developed their mineralized exoskeleton, and Early Palaeozoic vertebrate fossils are often mainly represented by micromeric taxa, collected in the field as phosphatic (apatite) microremains of dermal exoskeleton, not exceeding 5 mm in length (if we leave conodonts apart). However, collection and study of microremains of vertebrate origin have greatly enhanced the fossil record of the

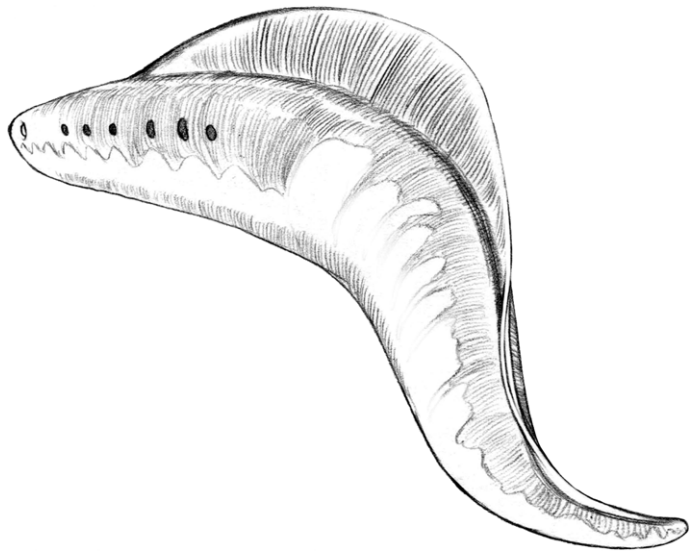


Fig. 28.1. Artist's reconstruction of *Myllokunmingia* (syn. *Haikouichthys*), by courtesy of Philippe Payet (Paris) ©; the animal is c. 2.5–3 cm long.

entire clade, be they from fragmentary components of the head-shields, tesserae of macromeric taxa (such as pteraspidomorphs and osteostracans) and fin spines (derived from acanthodians and putative chondrichthyans), or complete body scales from micromeric taxa (such as thelodonts, acanthodians and putative chondrichthyans), together with other skeletal components such as teeth, branchial denticles and lepidotrichia. These remains are often called 'ichthyoliths', 'vertebrate microremains' or 'micro-vertebrates'. All the bony parts of Ordovician–Silurian vertebrates are composed of several superimposed hard tissues, including bone, dentine, lamelline, enameloid or enamel. However, Early Palaeozoic vertebrates are still relatively rare. This is probably due to the fact that most of the earliest vertebrate taxa lacked larger mineralized elements, and therefore left few fossils (Sansom *et al.* 2010b).

Preliminary nomenclatural note

Comparison of different palaeobiogeographical models based upon different methods, and on different higher taxa, is elusive, particularly concerning the Palaeozoic fossil record (see Blicek 1990). Thus the editors of this volume (Harper & Servais 2013) have suggested following the recommendations of Westermann (2000), Cecca & Westermann (2003) and Servais & Sintubin (2009) for both palaeobiogeographical and palaeogeographical nomenclature. In this chapter, we do not define Cambrian palaeobiogeographical units for vertebrates because of their very restricted record (i.e. localities in a single Early Cambrian region of South China), and the fact that the vertebrate nature of Cambrian taxa is not definitely established. The two palaeobiogeographical units that have been defined for Ordovician vertebrate assemblages by Blicek & Turner (2003) are renamed as realms: thus we propose here to rename those two main Ordovician vertebrate palaeobiogeographical units the Gondwana Realm and the Laurentia–Baltica–Siberia Realm (LBSR). For the Silurian, the various units that have been defined either by Blicek & Janvier (1999) or Lucas (2001), after a previous analysis by Karatajūtė-Talimaa (1978, p. 172), are renamed as provinces which may be grouped under four different Realms (see the corresponding section below). Finally it must be noted that this new nomenclatural procedure may be extended to the Devonian palaeobiogeographical units of Young (1981–2003), which could be renamed as realms as well. However, all these units are

simply qualitatively defined. They have not been defined on the basis of quantitative (statistical) analyses of an Early Palaeozoic vertebrate database, which is clearly required. This might be a good topic for future research in order to proceed with palaeobiodiversity, palaeobiogeography (palaeochorology) and palaeoecology studies, in order to understand and define geobiological patterns of early vertebrate distributions. Finally, for simplicity, in this chapter we do not consider the conodont fossil record, except if otherwise mentioned.

Possible vertebrates of the Cambrian

As already noted, many badly preserved Cambrian fossils have been tentatively attributed to vertebrates, which may in some cases be incorrect. Amongst the presumed Cambrian vertebrates, the following are still problematic for various reasons and are not (provisionally?) retained as vertebrates. *Pikaia*, from the Middle Cambrian Burgess Shale Fauna of British Columbia (Canada), is considered as a possible cephalochordate (a taxon that is generally interpreted as the sister-group of craniates), but has not yet been properly and fully described; as reconstructed with its two tentacles, it looks more like *Tullimonstrum gregarium* (Richardson 1966) from the Pennsylvanian Mazon Creek fauna of Illinois, which has variously been compared with annelids, arthropods and molluscs (see e.g. Beall 1991; and references in Turner *et al.* 2010). *Yunnanozoon*, from the Early Cambrian Chengjiang Fauna of the Yunnan province (China), has been given a wide array of phylogenetic positions from stem-bilaterians to craniates (Donoghue & Purnell 2009, and references therein), and may be interpreted as a sclerite-bearing organism, having nothing to do with vertebrates (Bergström *et al.* 1998). *Haikouella*, represented by more than 300 specimens in the Early Cambrian Haikou locality near Kunming, only about 35 km NW of the Chengjiang Fauna (Chen *et al.* 1999), does resemble *Yunnanozoon* in several anatomical features and has been interpreted as a craniate-like chordate or an even more derived animal, but is as problematic as *Yunnanozoon*. *Myllokunmingia* (syn. *Haikouichthys*: Hou *et al.* 2002), also an unossified, naked and jawless organism from the Early Cambrian Chengjiang Fauna (Fig. 28.1), is sometimes interpreted as the first vertebrate, characterized by the presence of eyes, branchial sacs and possible vertebral elements (Shu *et al.* 2003; Janvier 2003), but some of its features are problematic and it might well be a basal chordate (craniate?). *Zhongjia-nichthys* from the same area of China, although attributed to a myllokunmingiid by Shu (2003), is even more problematic, and might be a badly preserved *Myllokunmingia*. All Cambrian fossils are soft-bodied and strongly flattened, which is the main reason for misinterpretation and misidentification, as discussed by Donoghue & Purnell (2009).

However a series of phosphatic microremains with possibly vertebrate histology has been reported and described at the Cambrian–Ordovician transitional time slice. It includes the problematic taxon from the Gola Beds of Western Australia, part of what has been called *Anatolepis*, and *Fenhsiangia* (see a review in Turner *et al.* 2004, and references therein). Yet, these records remain controversial: the Gola Beds taxon is re-interpreted as a secondarily phosphatized arthropod; *Anatolepis* is not always accepted as a vertebrate; and *Fenhsiangia* has perhaps nothing at all to do with vertebrates (Turner *et al.* 2004). Puzzling is the fact that there are no ossified vertebrate exoskeleton remains that would firmly establish vertebrates in the Cambrian, although all major phases of biomineralization, including the phosphatic mode, do appear in the 'Early Cambrian' (between –535 and –510 Ma, Nemakit–Daldynian to Botomian of the older Cambrian stratigraphical scale, that is, Terreneuvian plus Cambrian Epoch 2: Kirschvink & Hagadorn 2000; Ogg 2008; Haq & Schutter 2008). Therefore, taking into account a possible Precambrian origin for vertebrates (Delgado *et al.* 2001; see critical reviews

by Donoghue *et al.* 2003; Benton *et al.* 2009), we may hope to find more basal unossified or ossified vertebrates in the Cambrian.

Adaptive radiation of vertebrates in the Ordovician

The first Ordovician vertebrate discoveries were made from the Late Ordovician succession of the Harding Sandstone (Colorado, USA) in the late nineteenth century (Walcott 1892), with many more discoveries in the late twentieth century (see reviews in Sansom *et al.* 2001; Blicek & Turner 2003). These taxa, together with discoveries in Canada, Australia, South America, Oman and Russia, are the first well-documented vertebrate fossils with an ossified exoskeleton. They are represented, amongst others, by (1) jawless taxa such as Pteraspidomorpha – arandaspids (*Arandaspis* and *Sacabambaspis*), which occur in Bolivia, Argentina, Oman and Australia, astraspids (*Astraspis*) and *Eriptychius*, which occur in North America (Turner *et al.* 2004; Sansom *et al.* 2009); Osteostraci and Thelodonti; and (2) gnathostome groups, including possible Placodermi, Mongolepidida, Chondrichthyes and Acanthodii (references herein below). Nevertheless, all in all, the Ordovician vertebrates display a low specific diversity. They are all animals with zero, one or two pairs of lateral fins, armoured by an external bony carapace of plates and scales.

The fossil record

The Lower Ordovician displays a relatively poor vertebrate record. *Fenhsiangia* (upper Tremadocian of the Hupeh Province, Yangtze Platform, China) and partly what has been called *Anatolepis* (references in Turner *et al.* 2004) might be considered the only vertebrates of the Tremadocian if they are confirmed. In the Floian, an enigmatic form called *Piranchaspis* has been recorded in southern Bolivia (Erdtmann *et al.* 2000), and *Porophoraspis* sp. indet., together with another undetermined vertebrate, have been referred from the Amadeus Basin, central Australia (Young 1997).

The Middle Ordovician contains the first records of the most common Ordovician vertebrates. Their earliest representatives, *Arandaspis prionotolepis* and *Porophoraspis crenulata*, are known from the Middle Ordovician of central Australia, near Alice Springs (Ritchie & Gilbert-Tomlinson 1977; Ritchie 1985, 1991; Young 1997), where they occur as impressions in fine-grained sandstone. When these fossils were first discovered in the mid-1960s, the strata were considered to be Devonian in age, because Ordovician vertebrates were virtually unknown at that time (Long 1995). *Arandaspis* sp. is also recorded from the Darrivilian of western New South Wales, Australia (Young 2009). The first nearly complete Ordovician vertebrate was discovered by Gagnier (1993a, b, 1995) in central Bolivia, and named *Sacabambaspis*. It is slightly younger than the Australian taxa (Gagnier *et al.* 1996), but shows most of the articulated armour and body shape (Fig. 28.2). *Sacabambaspis* is assigned to the arandaspids, a taxon which has subsequently been recorded in Argentina and Oman (Ramirez *et al.* 1992; Albanesi *et al.* 1995; Sansom *et al.* 2009). A small fragment of a supposed vertebrate exoskeleton has been recorded by Wang & Zhu (1997) from the Zhuozishan Formation of Inner Mongolia, China. This formation is dated as 'lower Middle Ordovician' (Llanvirn: Wang & Zhu 1997), but we do not know how the strata were correlated. Additionally Sansom *et al.* (2000) considered this specimen to be 'similar to specimens which have undergone secondary phosphatisation' and suggested 'an arthropod assignment'.

In the Upper Ordovician vertebrates become more and more abundant worldwide. *Sacabambaspis* sp. is recorded in central Australia, being the last Ordovician occurrence of vertebrates on Gondwana; vertebrates do not reappear on Gondwana until the mid-Late Silurian (Young 1997). More species occur in North America, and mainly in the USA: in the Harding Sandstone

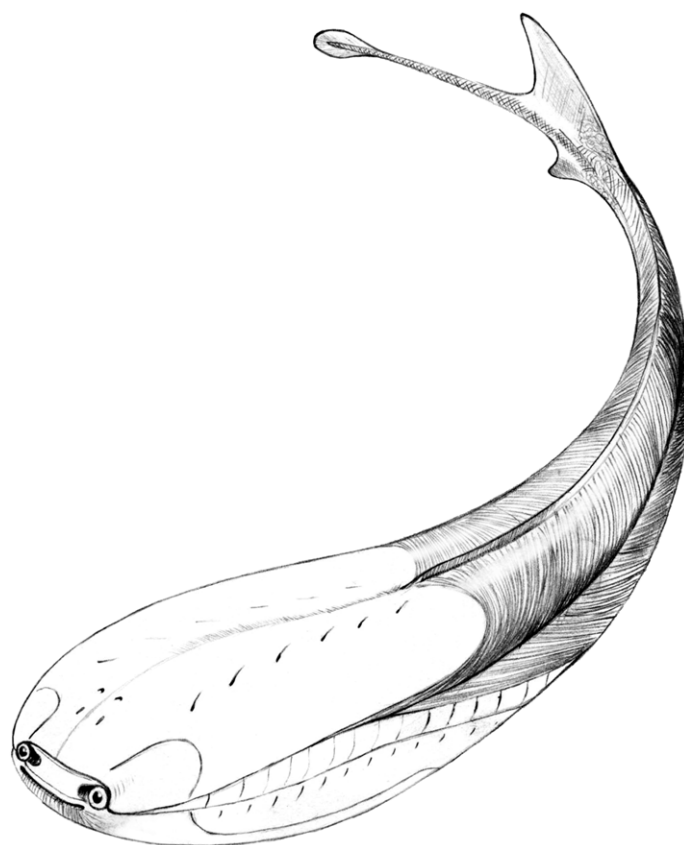


Fig. 28.2. A new artist's reconstruction of *Sacabambaspis*, after Gagnier (1993a, b, 1995) and Pradel *et al.* (2006), by courtesy of Pierre Bourcier (Paris) ©; the animal is c. 25–30 cm long.

Formation and its contemporaneous deposits of the Cordilleran region of Colorado, as well as other localities in Alberta, British Columbia, Ontario, Quebec, Michigan, Minnesota, Montana, Oklahoma, South Dakota and Wyoming (references in Sansom *et al.* 2001; Turner *et al.* 2004). Vertebrates in these assemblages comprised the pteraspidomorphs *Astraspis* and *Eriptychius*, thelodont and chondrichthyan-like scales (Sansom *et al.* 1995, 1996, 2001; Sansom & Elliott 2002), as well as *Skiichthys*, an enigmatic genus (Denison 1967; Smith & Sansom 1997), and unidentified gnathostome and acanthodian remains together with some fin spines attributed to *Sinacanthus* by Turner *et al.* (2004, p. 331; 'isolated spine' in Sansom *et al.* 2001, fig. 10.4i). The Late Ordovician thelodont *Sandivia* occurs in the Bratsk region of Siberia (Turner 1985; Karatajūtė-Talimaa 1997), and in the Timan–Pechora province, Russia (Karatajūtė-Talimaa 1997). Some thelodont scales reminiscent of *Sandivia* are also known from Quebec (Turner *et al.* 2004). Another thelodont record, *Stroinolepis*, is from the Severnaya Zemlya Archipelago, Russia (Märss & Karatajūtė-Talimaa 2002). Even if the fossil record is less diverse as compared with the pre-Hirnantian, it is not certain that a real mass extinction affected vertebrates in the Hirnantian (Turner *et al.* 2004). However, the globally incomplete record of Late Ordovician to Early Silurian vertebrates precludes a clear answer to this problem.

Biogeography of Ordovician vertebrates

Early vertebrates occurred mainly around Gondwana during the Early and Middle Ordovician, where they almost disappeared during the Late Ordovician; they do not reappear on Gondwana until the mid-Late Silurian, and come back only significantly later in the Devonian. The disappearance of Gondwanan taxa in

the Katian overlaps with the incoming of vertebrates in North America, but with only one taxon, *Sacabambaspis* sp., persisted for a brief time. Most of the Ordovician vertebrates are known from the last 15–20 myr of the Late Ordovician. The maximum diversity occurred during the early Katian (formerly time slice 5b of the Caradoc in Turner *et al.* 2004, fig. 30.1) when several taxa appeared on Laurentia (western USA). Based upon these data, Blicek & Turner (2003) have proposed to distinguish two endemic palaeobiogeographical units, viz., an earlier ‘Gondwana Endemic Assemblage’ from a later ‘Laurentia–Baltica–Siberia Assemblage’. They are renamed here as the Gondwana Realm and the LBSR, the latter with two subrealms: a Laurentia Subrealm and a Baltica–Siberia Subrealm (Fig. 28.3). Arandaspids are the dominant and most typical taxon of the Gondwana Realm (Young 2000, 2009; Blicek & Turner 2003), whereas LBSR has been considered as a major centre of origination of different vertebrate clades either for the Ordovician (see the ‘out of Laurentia’ scenario of Smith *et al.* 2002, who considered dispersal to be related to adult mobility) or for the Silurian (Blicek & Janvier 1993; Žigaitė & Blicek 2006).

Climatic context of Ordovician vertebrates

Owing to the sparse and fragmentary vertebrate Ordovician fossil record, it is difficult to say whether the ‘Hirnantian crisis’ (defined as a glaciation and prominent mass-extinction event at the end of the Ordovician) had a pronounced effect on vertebrate biodiversity. In the latest Ordovician, the last 2 myr (Hirnantian) has shown a significant changeover and upsurge of new taxa, indicating a biodiversification among thelodonts, pteraspidomorphs and acanthodians (Turner *et al.* 2004; but again, this hypothesis is hampered by a poor fossil record). Almost everywhere a gap of *c.* 3 myr in the vertebrate fossil record does follow this recovery between the latest Ordovician to earliest Silurian (Rhuddanian), which was named Talimaa’s Gap by Turner *et al.* (2004). Changes in sea-

level owing to the late Ordovician (Hirnantian) glaciation may have played an important role in masking part of the Ordovician ecosystem by simply reducing continental shelves, and particularly the nearshore siliciclastic marine environments, where all the known Ordovician taxa lived (Allulee & Holland 2005; Davies *et al.* 2007; Holland & Allen 2008; Davies & Sansom 2009). However, some Hirnantian vertebrate taxa (*Tesakoviaspis* and possible astraspids) continued through to the Silurian, but *Stroinolepis* did not, nor did *Sandivia* – contrary to Turner *et al.* (2004); see Märss *et al.* (2007). Later in the earliest Silurian vertebrates underwent a substantial adaptive radiation. All the localities of the LBSR are in the equatorial and tropical warm waters of the Ordovician World, whereas the Gondwana Realm localities are much more widely spread from low-latitude (tropical) to high-latitude (cold) regions (Fig. 28.3). Consequently, the end-Ordovician extinction of vertebrates was probably stronger than previously thought.

Diversification of vertebrates in the Silurian

The fossil record

The Silurian is considered as the second period of diversification of vertebrates, although much more important than the Ordovician in terms of species diversity. The taxonomical composition increases significantly, and Silurian vertebrates become more abundant worldwide. Nearly all the major Palaeozoic vertebrate groups are present in the Silurian: a variety of jawless armoured taxa attributed to ‘agnathans’ (‘ostracoderms’), together with gnathostomes such as chondrichthyans and acanthodians already known from the Ordovician, and others, like placoderms, osteichthyans and actinopterygians (e.g. Zhu *et al.* 2009). During the Silurian, most vertebrate communities are dominated by ‘agnathans’. Their diversity increased steadily throughout the Silurian, and no major extinction event has been recognized at the family level (see Long 1993; based upon Benton’s 1993 database; and for a critical review, Blicek 2011). This increase in diversity is also seen at a generic level for gnathostomes and may be related to an increase in atmospheric oxygen content and in sea surface temperature (Qu *et al.* 2010). However, several prominent extinctions and taxonomic turnovers can be recognized at the species level, such as the Lau event in the Late Ludlow, wiping out nearly two-thirds of vertebrate taxa (see Märss 1992a; Kaljo *et al.* 1996; Eriksson *et al.* 2009; and references therein). It is particularly well documented in Baltoscandia, and is also known for being associated with the largest positive stable carbon isotope ($\delta^{13}\text{C}$) excursion in the Phanerozoic (e.g. Saltzman 2001; Martma *et al.* 2005). Despite numerous recent discoveries of new Silurian fossil vertebrate sites (e.g. Zhu & Wang 2000; Lucas 2001 for China; Blom *et al.* 2002 for Greenland; Märss & Gagnier 2001; Märss *et al.* 2002, 2006 for the Canadian Arctic), vertebrate-bearing localities are still relatively scarce, and display local biodiversity fluctuations that may be linked with environmental conditions. The known fossil record of Silurian vertebrates probably does not mirror Silurian vertebrate biodiversity, but rather reflects the lack of good conditions for preservation as well as, to some extent, the poor preservation potential of the individuals, many of which had a micromeric to mesomeric exoskeleton that left only dispersed microremains in the sediments (Blicek & Janvier 1991). The earliest Silurian (Rhuddanian) Talimaa’s Gap may be contradicted by few exceptions, particularly the earliest Silurian of Siberia with *Tesakoviaspis* (Karatajūtė-Talimaa 1978; Karatajūtė-Talimaa & Predtechenskyj 1995). This may mean that the gap is purely fiction, or merely that the Rhuddanian did correspond to a strong decrease in diversity, rather than a real gap.

The vertebrate groups that occur in the Silurian are represented by heterostracans, thelodonts, osteostracans, anaspids,

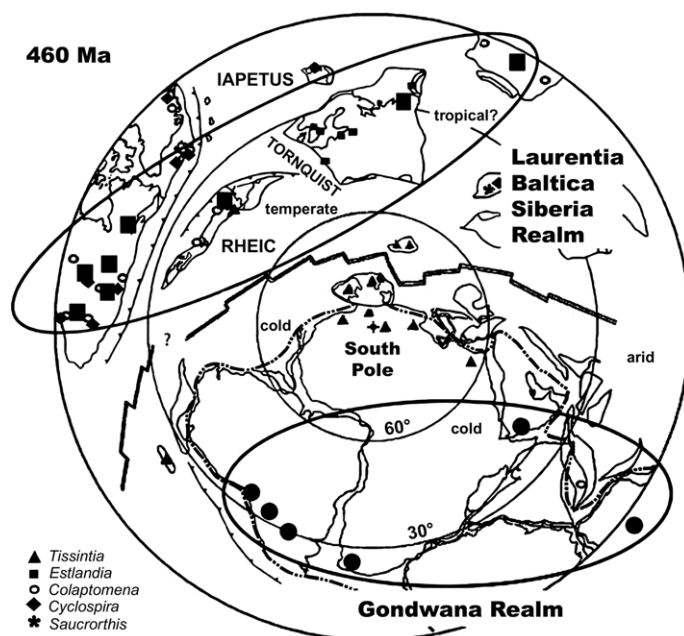


Fig. 28.3. The Gondwana Realm and the Laurentia–Baltica–Siberia Realm for vertebrates in the Ordovician. Palaeobiogeographical distributions on the palaeocontinental reconstruction of Cocks & Torsvik (2002, fig. 5, for mid-Ordovician at 460 Ma), with palaeoclimatic zones according to Scotese (2002, Middle and Upper Ordovician). Black dots, Gondwana Realm vertebrate localities; black squares, Laurentia–Baltica–Siberia Realm vertebrate localities; smaller symbols, some Late Ordovician (Caradoc) key brachiopod genera.

galeaspids and gnathostomes, which include acanthodians, chondrichthyans, placoderms and osteichthyans (actinopterygians + sarcopterygians). Thelodonts comprise a number of species of jawless vertebrates which all possess a micromeric exoskeleton (see the latest revision by Märss *et al.* 2007). Silurian thelodonts occur first in the lower Llandovery of Siberia, and thrive throughout the entire Silurian Period, becoming most diverse in the Pridoli. Thelodonts become extinct in the Upper Devonian, before the Frasnian/Famennian crisis. As is evident from their stratigraphical and palaeogeographical distributions, it appears that thelodonts were the most widely distributed Silurian vertebrates (Märss 1986, 1989; Blicek & Janvier 1991). Most likely this is due to their nektonic lifestyle (Märss 1986; Märss *et al.* 2007). Therefore thelodonts are considered to be one of the most cosmopolitan groups, contrasting with the majority of other Silurian vertebrates, which show a highly endemic distribution (see e.g. galeaspids on South China, osteostracans and heterostracans on Laurentia–Baltica–Siberia). This pattern of endemism has been placed within a morphological and phylogenetic framework by Smith *et al.* (2002) and Sansom (2009b). Osteostraci and Galeaspida both appear in the Silurian, and are characterized by large, fused, cephalic shields which, combined with their large range of environments, give them a high preservation potential and thus extensive record (from freshwater to shallow marine, Sansom 2009a; or only in marine carbonate and terrigenous deposits, Märss 1992b).

Galeaspids range from the Early Silurian (late Llandovery) to Late Devonian (Frasnian) and are distributed across China and northern Vietnam, with a potential additional locality in southern Siberia (Karatajūtė-Talimaa & Žigaitė 2005). The most primitive galeaspid is *Hanyangaspis* (Janvier 1984), known from the Wenlock, although the earliest occurrence of galeaspids is *Dayongaspis*, which has a first appearance in the Llandovery (Blicek & Janvier 1991). Both latter genera belong to the older Early Silurian group of galeaspids, that is, the Huananaspidoformes, and the other, younger and more advanced galeaspids (Eugaleaspidoformes) diversified only in the Late Silurian. The ‘basal’ galeaspids (Hanyangaspididae, Xiushuiaspididae and Dayongaspididae; see Sansom 2009a) are known from the Tarim basin, southeastern China and northern Vietnam, and the Silurian Eugaleaspidoformes are known exclusively from SE China (see references in Zhu & Wang 2000; Zhao & Zhu 2007, 2010; Sansom 2009a). This limited distribution of galeaspids makes the group one of the most palaeogeographically restricted among the Silurian vertebrates. However, recent discoveries of microremains of tessellated hanyangaspid galeaspids in the upper Llandovery–Wenlock of southern Siberia (Karatajūtė-Talimaa & Žigaitė 2005), expands the palaeobiogeographical distribution of Silurian galeaspids to outside the Chinese palaeocontinents.

Osteostracans range from the mid-Silurian (earliest Wenlock) to the Late Devonian (Frasnian) and have a range across the Northern Hemisphere (North America, Spitsbergen, Northern Europe, Eastern Europe and Siberia). They are distinguished by their well-ossified, both endo- and exoskeletal head shield with characteristic ‘cephalic fields’ on their dorsal surface. Both the most primitive (*Ateleaspis*) and the most derived (Tremataspidoformes) groups of osteostracans (Sansom 2009b) are known from the late Wenlock. This indicates that most of the diversification of the group had occurred earlier, at least in the earliest Silurian (Blicek & Janvier 1991). Osteostracans are present mainly in Laurentia–Avalonia–Baltica (on the Old Red Sandstone Continent, ORSC, at the dawn of the Devonian), their easternmost representatives being timanaspids from the Upper Silurian of North Timan, Russia (Afanassieva 2004; Afanassieva & Karatajūtė-Talimaa 2009).

Heterostracans have a similar temporal range to osteostracans and galeaspids. The taxon Heterostraci, which can be characterized by dorsal and ventral shields composed of acellular bone (aspidine), and paired external branchial openings, is divided into two

major phylogenetic groups, the ‘CA group’ (Blicek & Janvier 1991; Cyathaspidiformes of Janvier 1996b), which comprises cyathaspids and amphiaspids, and the ‘APP group’ (Blicek & Janvier 1991; Pteraspidoformes of Janvier 1996b), composed of anchipteraspids, protopteraspids, pteraspids and psammosteids, the phylogeny of the latter having been revised by Pernègre & Elliott (2008). Silurian heterostracans are known from the latest Llandovery–earliest Wenlock in the Canadian Arctic, represented mainly by cyathaspids as well as by taxa of uncertain (basal?) affinities such as corvaspids or traquairaspids. In the Pridoli, the Pteraspidoformes diversified, becoming more abundant than the Cyathaspidiformes, which became extinct in the Early Devonian. Heterostracans occur only in Europe, North America and Siberia, with a possible occurrence in Algeria and unverified records from Morocco, Kazakhstan and the Russian Far East (Blicek *et al.* 2002; Märss & Karatajūtė-Talimaa 2009; Elliott & Swift 2010). Anaspids were small Palaeozoic vertebrates with an ossified head shield, known from the Silurian until the Early Devonian (see e.g. Blom *et al.* 2002). The organisms rarely exceeded 15 cm in length; their exoskeleton mainly consisted of scales and smaller plates, for example, *Birkenia* and *Pharyngolepis*. The interest in anaspids is because their overall morphology (elongated body, numerous gill openings, hypocercal tail) is also found in some naked Silurian and Devonian vertebrates that are thought to be related to lampreys as well as thelodonts (Blicek & Janvier 1991). The Wenlock *Jamoytius kerwoodi*, after having been regarded as a ‘protocraniate’ (White 1946) and as a naked anaspid (Ritchie 1964), was later regarded as a close relative of lampreys, or even a true lamprey (Janvier 1981). It has recently been restudied and considered as basal to the clade (anaspids – thelodonts (other ostracoderms + gnathostomes)) by Sansom *et al.* (2010a). Anaspid remains are known from deposits that are variously interpreted: either from freshwater sediments, without excluding the possibility that they may have spent a phase of their life living in marine conditions (Long 1995), or from marine deposits (Blom *et al.* 2002; Miller *et al.* 2004). Silurian anaspids were palaeogeographically restricted to the ORSC (Laurentia, Avalonia, Baltica).

There is evidence from the late Silurian of the two major extant taxa of gnathostomes, that is, Chondrichthyes and Osteichthyes. Placodermi, a major Devonian group of gnathostomes, also have their first appearance in the Silurian (Zhang *et al.* 2010). The most common among Silurian gnathostomes are Acanthodii, which are nearly cosmopolitan, and are fairly abundant in the Llandovery to Pridoli, where they occur mainly as isolated macro- and micro-remains (scales, spines, teeth; Burrow & Simpson 1995; Burrow *et al.* 1999; Hanke *et al.* 2001; Burrow 2003; Karatajūtė-Talimaa & Smith 2003). The two major Silurian acanthodian groups are the Climatida and Ischnacanthida (Denison 1979). The former are characterized by broad-based spines and a series of petal-shaped teeth, and the latter by toothed jaw bones and tooth whorls (Denison 1979; Blicek & Janvier 1991). Chondrichthyans are mainly known from placoid-like scales from the upper Ludlow and Pridoli of Tuva (central Asia), such as *Elegestolepis* (Karatajūtė-Talimaa 1973; Karatajūtė-Talimaa & Ratanov 2002) and *Tuvalepis* (Žigaitė & Karatajūtė-Talimaa 2008). They are also represented in the Wenlock of the Canadian Arctic by *Kannathalepis* on Baillie-Hamilton Island (Märss & Gagnier 2001), as well as by *Frigorilepis* and *Wellingtonella* on Cornwallis Island, both the latter being putative chondrichthyans (Märss *et al.* 2002, 2006). Evidence from the Silurian of Osteichthyes exists mainly as isolated scales, dermal bone fragments and teeth, such as *Andreolepis* and *Lophosteus*, known from the Ludlow and Pridoli of the Baltic area (Sweden and East Baltic area) and China (Gross 1968, 1969; Mark-Kurik 1969; Dineley & Loeffler 1993; Märss 2001; Schultze & Märss 2004). However, well-preserved osteichthyans occur as well in the Ludlow of southern China, Yunnan Province (Zhu *et al.* 2009). The oldest record of placoderms is from the late

Llandovery to Pridoli of southern China as well (references in Zhu & Wang 2000; Zhang *et al.* 2010). An articulated teleostome has been described from the Ludlow of Australia (Burrow & Young 1999).

The Silurian to Devonian transition shows remarkable taxonomic continuity as no higher vertebrate taxon disappeared by the end of the Silurian, and the diversification of both ‘agnathans’ (‘ostracoderms’) and gnathostomes continued through the Early Devonian (Benton 1993; Long 1993; Blicek 2011). However, many genera and species become extinct at or near the Silurian–Devonian boundary in some regions such as the Chinese terranes (Zhao & Zhu 2007; Zhao *et al.* 2011 – this point has been critically analysed by Blicek 2011).

Biogeography of Silurian vertebrates

Palaeogeographical reconstructions produced using palaeomagnetic and faunal data reveal that the Old Red Sandstone Continent (also known as Euramerica, Laureuropa, or Laurussia) formed in the Wenlock through to the Pridoli as a result of the collision of Avalonia, Baltica and Laurentia (Scotese & McKerrow 1990; Cocks & Torsvik 2002). During the Silurian, the Arctic archipelago of Svalbard was associated with Greenland as part of Laurentia, while Severnaya Zemlya migrated slightly north of Baltica (Cocks & Torsvik 2002, 2007). The majority of osteostracans and heterostracans were therefore distributed across the ORSC, which was associated with Severnaya Zemlya (Blicek *et al.* 2002, fig. 1). The non-ORSC osteostracans are known from the Tuva and Khakasia republics, in the south of present-day Siberia, Russia (Afanassieva & Janvier 1985; Sansom *et al.* 2008). Various authors (among others, Blicek & Janvier 1991; Smith *et al.* 2002) suggested that the heavy dermal skeleton of ‘ostracoderms’, such as heterostracans, galeaspid and osteostracans, limited their dispersal capacity. They are thus used as ‘continental’ indicators (Rosen 1974), that is, of palaeocontinental margins under epeiric seas (e.g. Blicek 2011 and references therein). The richest and most abundant Silurian vertebrate localities known and studied so far include the Canadian Arctic, Norway, southern Britain, Scotland, Saaremaa Island (Estonia),

southern Siberia, northwestern Mongolia and the Yunnan Province of China (references in Blicek & Turner 2000; Märss *et al.* 2006; Žigaitė *et al.* 2011). However, Silurian vertebrates are significantly more abundant in the Northern Hemisphere (North America, Greenland, western and northern Europe, the Ural Mountains, the Timan–Pechora region, northern and southern Asia), which is partly related to the presence in these regions of outcropping Silurian rocks, preserved fossils and palaeontologists working in these regions. By comparison, far fewer localities are known from the Southern Hemisphere, and particularly from southern Africa, which is devoid of Silurian vertebrates (at the time of writing). In contrast to the two palaeobiogeographical realms defined for the Ordovician, a series of separate palaeobiogeographical units, based upon endemic faunal elements, have been defined for the Silurian (Karatajūtė-Talimaa 1978; Blicek & Janvier 1991, 1999). We propose here to designate all these units simply as provinces grouped under their respective realms (Westermann 2000; Cecca & Westermann 2003). On Laurentia, Avalonia and Baltica, combined to form the ORSC, they include (Fig. 28.4): a Canadian Arctic Province (Blicek & Janvier 1999: cyathaspid-dominated), a mixed Canadian Arctic–European Russian Province (‘mixed Canadian Arctic–Western former USSR fauna’ of Blicek & Janvier 1999), a Baltic–European Russian Province (‘Western former USSR Province’ of Blicek & Janvier 1999: *Phlebolepis elegans*–*Thelodus schmidti* fauna), an Acadian–Anglo-Welsh Province (*Thelodus parvidens* and *Hemicyclaspis*–*Auchenaspis* faunas), and a Central Appalachian Province (*Americaspis* fauna). These five provinces may be grouped under the Laurentia–Avalonia–Baltica Realm. Two provinces have been defined for the Siberian palaeocontinent and its neighbouring palaeocontinental elements, that is, the Siberian Province and the Tuvan Province (Blicek & Janvier 1999; Fig. 28.4). Both latter provinces can be grouped under a Siberia Realm (see Žigaitė *et al.* 2011). Finally a South Chinese Province is defined after its endemic vertebrate elements (Lucas 2001; Fig. 28.4). This is perhaps the present single representative of the South China Realm. Additionally, Karatajūtė-Talimaa (1978, p. 172) discussed the Australian thelodont area that we redefine here as a province, and is at present the single representative of an East Gondwana Realm (Fig. 28.4). Other Silurian vertebrate records

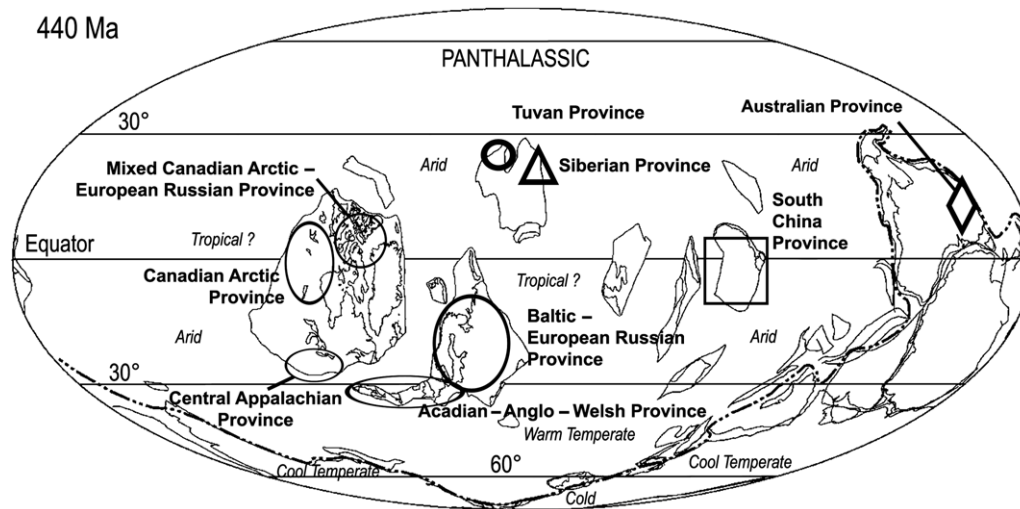


Fig. 28.4. Silurian agnathan vertebrate biogeographical provinces after Karatajūtė-Talimaa (1978), Blicek & Janvier (1999) and Lucas (2001), plotted on Cocks & Torsvik’s (2002, fig. 7, for latest Ordovician–earliest Silurian) palaeocontinental reconstruction with Scotese’s (2002) palaeoclimatic zones. Note that each symbol may not fit exactly the extent of each corresponding province; we provide herein a general view of Silurian vertebrate provinces. Tuvan Province + Siberian Province are grouped under a Siberia Realm; South China Province corresponds to the South China Realm; ‘mixed Canadian Arctic–European Russian Province’ + ‘Canadian Arctic Province’ + ‘Central Appalachian Province’ + ‘Acadian–Anglo–Welsh Province’ + ‘Baltic–European Russian Province’ are grouped under a Laurentia–Avalonia–Baltica Realm (Old Red Sandstone Continent in the Devonian). Other Silurian vertebrate records are known from outside those provinces, and particularly along the northern margin of Gondwana, but they have not yet been palaeobiogeographically defined (e.g. South America, Iran and Vietnam – see the text for the references).

are known from outside those provinces, and particularly along the northern margin of Gondwana (for a critical definition of Gondwanan margins, see Servais & Sintubin 2009), but they have not yet been palaeobiogeographically defined (see e.g. South American, Iranian and Vietnamese records in Janvier & Suarez-Riglos 1986; Janvier & de Melo 1988; Hamed *et al.* 1997; Janvier & Tong-Dzuy 1998; Hairapetian *et al.* 2008). Additionally, the Silurian vertebrate record of SE Asia (Shan–Thai and Indochina terranes) is very poor, but shows affinities with the South Chinese record (Wang *et al.* 2010). Apart from some widespread, fully nektonic species such as some thelodonts and acanthodians, which are useful for intercontinental biostratigraphical correlations (e.g. *Loganellia*: Märss *et al.* 1995, 1996, 2007; Žigaitė & Blicek 2006; Žigaitė *et al.* 2011), vertebrate endemism was well marked in the Silurian (Janvier & Blicek 1993; Blicek & Janvier 1993). This endemism may be explained by at least two features, that is, the limited dispersal ability of organisms and different palaeoenvironmental constraints (in addition to the limited Silurian fossil record, which certainly hampers any global interpretations).

Climatic context of Silurian vertebrates

When looking at the palaeobiogeographical distribution of Silurian vertebrates, it appears that, again, most localities were distributed in the equatorial and tropical warm waters of the Silurian World (Märss 1989; Fig. 28.4). However, as already mentioned, other localities are from the northern margins of Gondwana, which in some places were located in the cold to cold temperate palaeoclimatic zones (Fig. 28.4). If vertebrates are useful palaeocontinental indicators and allow discrimination between the various Silurian palaeocontinents (see preceding section), they may eventually become useful palaeoclimatic indicators. Silurian vertebrates have occupied a number of different ecological niches, ranging from marginal marine to the most distal marine environments (Märss & Einasto 1978; Schultze 1999; Blicek 2011). Differences in inhabited water depths or ecological niches occupied within the water column are crucial when reconstructing palaeoseawater temperatures and palaeoclimate using the stable isotopes. It already has been successfully applied to Late Silurian vertebrates (Žigaitė *et al.* 2010). The oxygen isotope values have been measured in thelodonts from the Upper Silurian (Pridoli) of Lithuania, and their apatite appeared to be depleted in ^{18}O , in comparison to those of conodonts, with an offset of around 2.5‰, which translates into a difference in palaeotemperature of around 10°C (Žigaitė *et al.* 2010). An explanation for the difference in the $\delta^{18}\text{O}$ values could be related to differences in the ultrastructure of the mineralized tissues, which would have affected the preservation of the primary $\delta^{18}\text{O}$ signals. Different tissues are being sampled with thelodonts being largely composed of an open and diagenetically susceptible tissue that is penetrated by tubules, whereas the tissue in conodonts is a denser and compact crystalline tissue. Different life habitats might be another explanation for the observed offset in conodont and thelodont $\delta^{18}\text{O}$ values, although the palaeohabitats of Silurian conodonts are not well known. Apart from suggestions that some conodonts were living close to the sediment surface, the nektonic lifestyle of most taxa within the upper water column is widely accepted (Sweet 1988). Silurian thelodonts are supposed to also have had mostly a nektonic lifestyle (Märss *et al.* 2007). Since temperatures decrease with increasing water depth, the offset between thelodont and conodont stable oxygen isotope values might be interpreted as an effect of the different water depths of their habitats. However, the thelodonts studied are assumed to have at least partly shared the palaeohabitats with conodonts. Therefore, the discrepancy of the $\delta^{18}\text{O}$ values cannot be explained by different life habitats, and differences in the ultrastructure of the mineralized tissues are more likely.

Palaeobiological remarks and implications for biostratigraphy

Silurian vertebrates have undergone different morphological adaptations, reflecting nektonic (demersal), nektonic and epinektonic lifestyles in a wide range of habitats (Märss 1986; Janvier 1996b; Märss *et al.* 2007). Some benthic species may have pursued specific infaunal life modes, and therefore may have been blind (as e.g. the Devonian amphiaspid heterostracan *Eglonaspis*; Novitskaya 1971). Others have developed complex sculptures on their bony exoskeleton, most likely reflecting particularly complicated aquatic environments, and were adaptations either to reduced mobility (Janvier 1996b; Blicek 2005, 2009) or to increased mobility conditions (Märss 1999). Their adaptations to various environments have been discussed by Fredholm (1992) and Turner (1999). Benthic vertebrate species usually have been strongly endemic, and are used in palaeogeographical reconstructions to characterize different Early Palaeozoic continents (see the previous chapters). In contrast, some Early Palaeozoic vertebrates are considered to have had a nektonic lifestyle (sometimes referred to as ‘pelagic’, but pelagic refers to both plankton and nekton), and have probably been able to spread between the oceans. This is, for example, the opinion of Belles-Isles (1987), indicating the transoceanic capacity of the Late Devonian osteostracan *Alaspis* and the Early Devonian heterostracan *Pteraspis*; however, this is in disagreement with both their restricted palaeobiogeographical distribution (a single locality of Quebec for *Alaspis*, and southeastern ORSC for *Pteraspis*) and recent physical experiments on *Errivaspis* (formerly known as *Pteraspis*: Botella & Fariña 2008). Nevertheless, we know of Early Palaeozoic vertebrate species (e.g. the loganelliid thelodonts and nostolepid acanthodians) which are found in rocks (of the same age) on different palaeocontinents, and are thus supposed to have been actively swimming species. These serve as excellent biostratigraphical indicators. (Once again transoceanic dispersal of larvae is untestable, therefore we prefer to base our interpretation on the known records of ossified individuals.) Another reason for the biostratigraphical use of microvertebrate remains is taphonomic: each individual fish (thelodont or acanthodian) left thousands of small characteristic scales in the sediment, which then can be treated as regular microfossils for dating the sediment. All these data help to define: (1) regional biostratigraphical schemes such as in the Late Ordovician to Early Silurian of northern Russia (Talimaa 2000) and in the Ordovician of Central Australia (Young in Shergold *et al.* 1991); and (2) a ‘global’ Silurian biostratigraphical scale based upon both thelodonts and acanthodians (Märss *et al.* 1995, 1996; and references in Blicek & Turner 2000).

Conclusions

In view of the most recently published data, the origin of vertebrates may date back at least to the Cambrian although the first confirmed record of mineralized exoskeleton is Ordovician in age. Ordovician and Silurian vertebrate faunas are dominated by ‘agnathans’ (‘ostracoderms’) and a few other unossified taxa. The Early Silurian vertebrate record contains Talimaa’s Gap of c. 3 myr in the Rhuddanian. Vertebrate fossils are useful biostratigraphical indicators mostly in Silurian marine successions (and later in the Devonian). They are also good indicators of palaeocontinental margins, as they occupied a wide range of environments: proximal marine to restricted marine in the Ordovician, and all along the marine epicontinental shelves of the Silurian. Two main palaeobiogeographical units are defined for the Ordovician: the Gondwana Realm, and the Laurentia–Siberia–Baltica Realm. In the Silurian, many more fossil localities are known, and a series of palaeobiogeographical provinces have been grouped under different realms on Laurentia, Avalonia,

Baltica, Siberia, South China and East Gondwana. More discoveries of Silurian vertebrate-bearing localities would certainly help to define additional provinces, in particular along the northern margins of Gondwana and in SE Asia.

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