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On *Sacabambaspis janvieri* and the vertebrate diversity in Ordovician seas

Pierre-Yves Gagnier* and Alain Blicek**

* Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, Québec, Canada H3A 2K6.

** Université des Sciences et Techniques de Lille-Flanders- Artois, Sciences de la Terre, URA 1365 du CNRS, 59655 Villeneuve d'Ascq Cedex, France.

Abstract. In this short review of Ordovician vertebrates, the authors summarize preliminary data on *Sacabambaspis* from the Ordovician of Bolivia (age, taphonomy, morphology). This is the base for comparisons with the Ordovician vertebrates of North America and Australia. Finally, the palaeogeographical problem of this distribution is settled.

Introduction

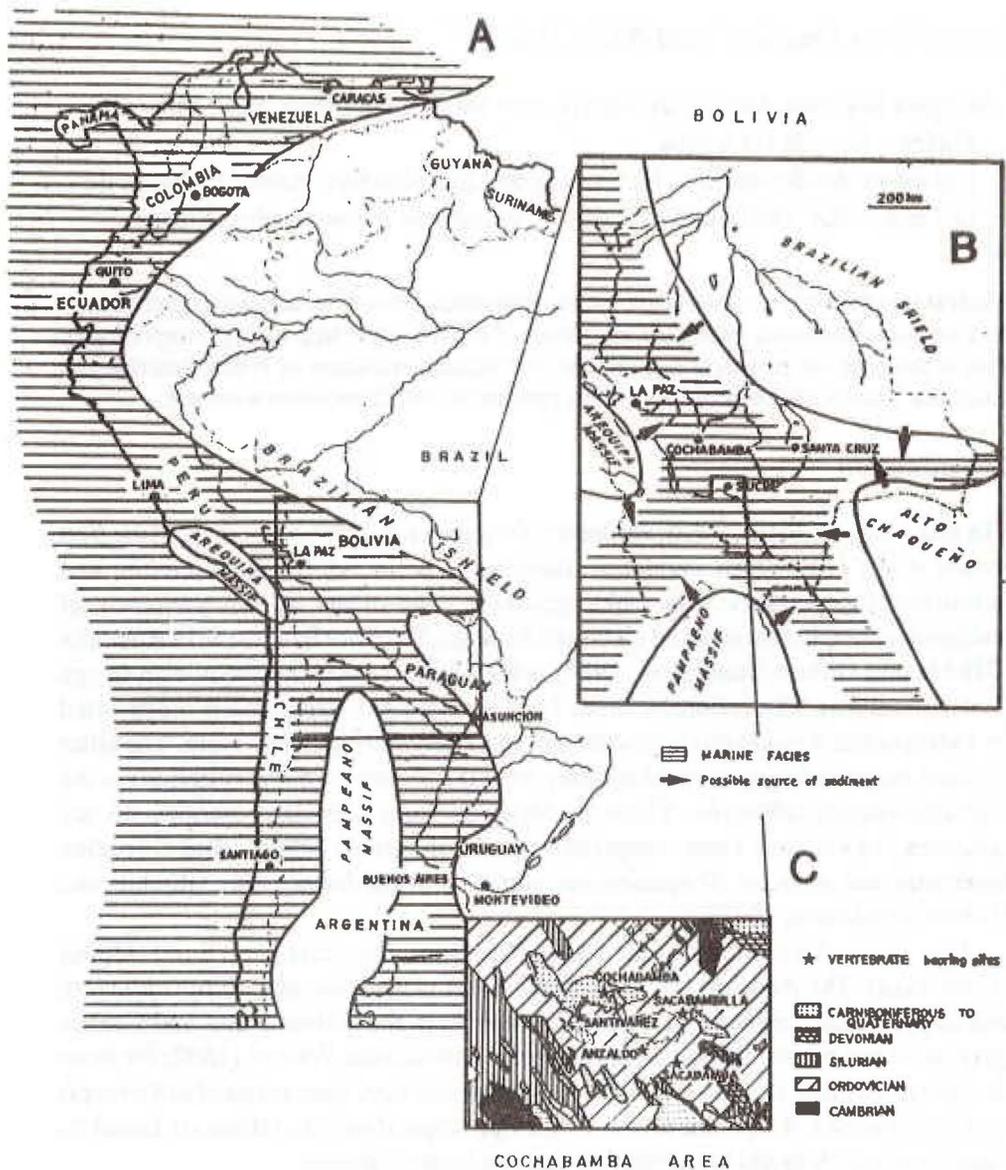
The discovery of *Sacabambaspis janvieri* Gagnier et al. (1986) represented the first record of an Ordovician vertebrate showing most of the dermal skeleton, and permitting comparisons with other agnathans. The oldest known testimony of undisputed vertebrates is based on fossils from the Stairway Sandstone in Australia (Ritchie and Gilbert-Tomlinson, 1977), which is Early Middle Ordovician in age (Early Llanvirn). The vertebrate fauna from the Stairway Sandstone is represented by two species: *Arandaspis prionotolepis* and *Porophoraspis crenulata*. The latter is based on plate fragments which differ from the former by the perforations in the diamond-shaped tubercles. These perforations form crenulate margins on the tubercles, which have been compared to those of various Silurian and Devonian heterostracans such as *Traquairaspis plana* or *Weigeltaspis alta* (Ritchie and Gilbert-Tomlinson, 1977).

The other Ordovician vertebrates are from the Caradoc (Early Upper Ordovician). The Anzaldo Formation of Bolivia yielded *Sacabambaspis janvieri*, and the Harding Sandstone and other formations in the United States and Canada gave up *Astraspis desiderata* and *Eriptychius americanus* Walcott (1892; for more details refer to Elliott et al., 1991). Two other species have been referred to *Astraspis* and *Eriptychius*, *A. splendens* and *E. oervigi*, respectively, but these are based on fragments which might be referred to the two former species.

Recently Ritchie (1985) gave a redescription of *Arandaspis* and Elliott (1987) reassessed *Astraspis* on the base of new specimens.

We now have clearer representation of most of the Ordovician forms, permitting an hypothesis on their relationships. So we intend here to highlight those relationships and show what palaeogeographic problems they lead to.

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Text-fig. 1. Map of western South America showing the distribution of Ordovician rocks on a present geography (A). An interpretation of Ordovician highlands and seaways of Bolivia is given in (B) with arrows showing the possible sediment sources (after Suarez-Soruco, 1976). (C) is a simplified geological map of Cochabamba, based on the Mapa Geologico de Bolivia (GEOBOL) [Note that these schemes do not care of the tectonic structure of the Andes, nor their original Ordovician relationships].

I - On *Sacabambaspis janvieri*

A) Geological setting and age

The most complete sequence of Ordovician rocks in Bolivia occurs in the Eastern Cordillera (Text-fig. 1), which extends from the Peruvian border to Argentina. All the localities where *Sacabambaspis* was found (Text-fig. 1), occur in the Anzaldo Formation (the term of Cuchupunata Formation is used by some authors, but it represents the same unit: it is only a question of priority in the name) which could reach a thickness of 2000 metres. In the Cochabamba area, Steinmann and Hoek (1912) were the first to distinguish different Ordovician rocks, based principally on their associated fauna. They described three levels, viz. from the base to the top, "Bilobites Sandstein", "Lingula Sandstein" and "oberer Quarzit". Later the upper sandstone received the name of the San Benito Formation, and the two lower ones now form the Anzaldo Formation (Text-fig. 2).

Division of Steinmann & Hoek 1912	SYSTEM	CENTER OF EASTERN CORDILLERA	
		Cochabamba Sucre	Chapare
Upper Quartzite	upper	Ashgill	
Sandstone with Lingula		Caradoc	Mizque / San Benito Anzaldo / Anzaldo
Sandstone with Bilobites	middle	Llandeilo	Capinota / Capinota
Level with Geodes		Llanvirn	Independencia
	lower	Arenig	Limbo Group / Avispas
		Tremadoc	Putintiri

Text-fig. 2. Simplified stratigraphical sequence of the Ordovician of the central Eastern Cordillera of Bolivia (modified from Rivas, 1971 in Suarez-Soruco, 1976). The location of the lingulid sites is indicated in grey.

The precise age of the Anzaldo Formation is debated: Suarez- Soruco (1976) considers it is Caradoc in age, but G. Rodrigo de Walker and M. Toro (pers. comm.) argue for a Llanvirn-Llandeilo age based on the generic reattribution of a trilobite encountered in this formation. Gagnier (1987) thought that the vertebrate from those localities is related to the forms from Australia which are of Early Llanvirn age (Ritchie and Gilbert-Tomlinson, 1977; Webby, 1981). There is no fossil known to date from this formation, but the Capinota Formation, below, is Llanvirn- Llandeilo in age (Suarez-Soruco, 1976) or Llanvirn (Aceñolaza and Baldis, 1987), on the base of the graptolite *Didymograptus murchisoni* and the trilobite *Hoekaspis matacencis*; and the San Benito Formation, above, is Caradoc after the bivalve *Ctenodonta cochabambensis*.

Sacabambaspis was first described from Sacabamba, from the basal part of the local section composed of 300 metres of lutites, well-bedded yellowish sandstones with limonite alteration and grey to greenish grey and yellow sandstones. A few metres below and above the vertebrate-bearing levels are phosphorite levels, principally composed of crushed lingulid shells, in which some small vertebrate fragments were found. Rodrigo de Walker and Toro (1987) correlated the Sacabamba section (Anzaldo Formation) with the one from Cerro Chakeri (Cuchupunata Formation) near Sacabambilla, where the most complete vertebrate remains have been found. For the Cerro San Pedro (in the town of Cochabamba) no correlation was made for the moment with the other localities, but it is part of the Anzaldo Formation.

Important highlands emerged in South America during the Ordovician epoch (Text-fig. 1). These highlands provided the sediment which formed thick epicontinental marine sequences in South America (cf. Suarez-Soruco, 1976).

B) Taphonomical remarks

The localities Anzaldo, Santivañez, Cerro San Pedro (Cochabamba), Cerro Chakeri (Sacabambilla) and Rio Challaque (Sacabamba), contain large concentrations of disarticulated but well preserved inarticulate brachiopods, identified as *Lingula ellipsiformis*, *L. muensteri*, *Bistramia elegans* (Suarez-Soruco, 1976). These lingulids are under revision by M.G. Bassett and C. Emig. A trilobite, *Homalonotus (Brongniartella) bistrami*, and the vertebrate, *Sacabambaspis janvieri* Gagnier et al. (1986) occur together with the lingulids. The invertebrate fauna corresponds to a Benthic Assemblage 1 or 2 sensu Boucot (1975), i.e., to a marine, intertidal or subtidal environment. A similar marine environment has also been suggested for the North American and Australian Ordovician taxa (Elliott et al., 1991).

Concerning lingulids, Emig (1986) suggests three processes for mass mortality outside their burrows: a sudden drop of salinity, an inflow of sediment with particles bigger than 0.5 mm, and/or the destruction of substratum by a storm. Since the sediment in the vertebrate-bearing level of Sacabambilla is fine-grained, Gagnier (1987) proposed that massive inflow of fresh water brought by a storm or a nearby

river, may have produced the mortality of the lingulids and, to some extent, the vertebrates. However it does not explain entirely the fossilization process, which requires a massive input of sediment (Emig, pers. comm.). The quality of the articulated vertebrates is good. The *Sacabambilla* locality yielded about 30 articulated specimens, concentrated in a small area, many of them being packed side-by-side and some one-over-the-other.

C) General external structure of *Sacabambaspis janvieri*

Preliminary studies of *Sacabambaspis janvieri* were based on fragmentary material and the discovery of more complete specimens requires reinterpretation of some earlier observations. Gagnier et al. (1986) and Gagnier (1987) described some fragments thought to be ventral shields (e.g., the holotype MNHN BOL V-3282), but which are in fact from dorsal shields (Gagnier, 1989).

The average length of the animal is about 35 cm, of which the head shield represents more than a third. The shield is about 8 cm broad. The overall morphology is quite similar to that of *Arandaspis* from Australia, with two large bone units covering the head, and rows of lateral platelets. The body shape vaguely resembles that of a tadpole.

In this paper, we do not intend to provide a full description of *Sacabambaspis janvieri*. We will just highlight some of its major features (Text-fig. 3) and compare it to the other Ordovician forms. A more complete description will soon be published by one of us (P.-Y. G.).

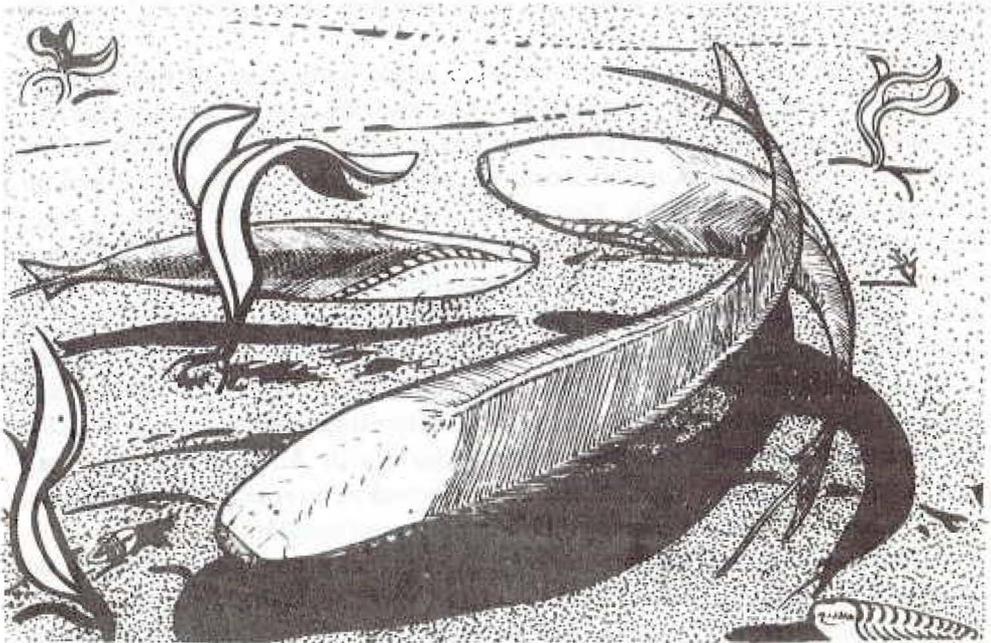
The dorsal and ventral shields are large single units made of tiny platelets (tesserae) that are fused by a basal layer. These platelets have an average size of 2 mm and are roughly hexagonal in shape. Their external surface is ornamented with oak-leaf-shaped tubercles, a kind of ornamentation which is encountered in various heterostracans (*Traquairaspis*, *Tesseraspis*, *Lepidaspis*) and the crown of some thelodont scales. The bone in the medial part of the tesserae is enclosed by individual walls and the inner part of it is filled with spongy bone. There is no trace of fusion on the undivided basal layer of the shield, which shows small nutrient foramina that might have served for vascularization of the bone. As to the structure of the exoskeleton itself, the first observation hypothesized cellular bone without any cover of dentine contrarily to what is known in heterostracans and other Ordovician vertebrates (*Astraspis* and *Eriptychius*) from North America. However all specimens are strongly recrystallized, so it is hazardous to conclude on this matter until further investigation is made on better preserved material.

The dorsal shield delimits anteriorly an elliptical space which contains the eyeballs and articulate with a "T"-shaped bone which separates two openings that could be interpreted as nostrils. The posterior end of the dorsal shield makes transition with the body scales. In this region there is a low median crest followed posteriorly by dorsal median ridge scales.

On the dorsal shield, there is a paired depression located 2.5 cm from the anterior median margin of the shield. Posterior to this paired depression, the tubercles of the tessellated units are smaller and their orientation gives a false impression that there is a separate plate. It is interpreted as a paired pineal- parapineal apparatus because of the modified ornamentation of the surrounding platelets (Gagnier, 1989).

The ventral shield is deep and convex. The anterior 2.5 cm are made up of square-shaped platelets aligned in rows to form the exoskeletal mouth apparatus. This may represent an arrangement of scales on the lip or a postoral field as in some cephalaspids (*Hirella*; Heintz, 1939). In ventral view, it is oval in shape. It is strongly convex anteriorly and becomes flattened posteriorly, so that in lateral view it appears higher anteriorly and slopes posteriorly, disappearing at the posterior end. Its posterior end is a median, rounded, convex lobe onto which body scales are attached and form a ventral median ridge.

On each side of the head, the dorsal and ventral shields are united by a series of marginal plates. These are diamond-shaped (lozangic), with a little posterior knob at mid height; they are about 20 in number and extend from approximately the level of the pineal openings to the posterior end of the ventral shield. They probably are covers for the branchial external openings.



Text-fig. 3. Artist's illustration of *Sacabambaspis janvieri* swimming in an Ordovician sea of Bolivia. The tail is extrapolated from three partially articulated specimens (from Gagnier, 1989; courtesy of Nation. Geogr. Res.).

The remainder of the body is covered with rows of thin, elongated scales ornamented with oak-leave-shaped tubercles similar to those of the shields but arranged in parallel rows. There are four main scale rows covering the flank parts of the body, plus two small ones which form the dorsal and ventral median scale ridges. The four main rows are arranged two-by-two in "chevrons". There are more than a hundred scales along the chevrons axes. The scaled part of the body is about twenty five cm long, of which ten make the tail. The ventral median ridge scales seem to end before the tail, in the region interpreted as the cloacal opening. The tail seems to have a long "rat-tail-shaped" cordal extension.

The sensory-line system of the dorsal shield is represented by two anterolaterally curved grooves previously described in the holotype and on specimen YPFB PAL-6206 (Gagnier, 1987). These sensory grooves may possibly be supraorbital and infraorbital lines. There is also a discontinuous paired medial sensory groove (the medial dorsal line) which runs from the back to the shield near the paired pineal-parapineal depression; at this point it turns laterally. In front of the paired depression, there are two small pit-lines. On the ventral shield, the sensory-line pattern consists of a paired medial discontinuous line turning laterally near the mouth border, and forming the postoral line. In the lateral part of the shield there is another discontinuous groove which runs posteriorly from the oral region on the posterior two thirds of the shield and which turns ventromedially. A series of laterally placed transversal commissures (18 to 20 in number) are situated ventrally to each marginal plate. There is a pair of ventral lateral lines on the body scales which run from the ventral shield for two thirds of the length of the body. They are marked by a continuous and straight groove on the surface of the scales.

II - Ordovician vertebrates and their relationships

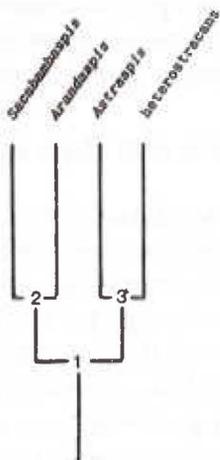
The first record of Ordovician vertebrates was from North America (*Astraspis* and *Eriptychius* Walcott, 1892). These taxa were identified as heterostracans on the basis of their histology, especially the presence of cancellous or spongy aspidin (an acellular bone) which is classically regarded as typical for the heterostracans. The Australian genus *Arandaspis* was also identified as heterostracan (Ritchie and Gilbert-Tomlinson, 1977) but no bone structure was preserved; this attribution was based on the presence of two large shields covering the head and the detail of the ornamentation resembling that of some heterostracans.

Sacabambaspis shares several features with heterostracans – large ventral and dorsal shields covering the head; a dermal shield structure which consists of polygonal units; ornamentation of oak-leaf-shaped tubercles; anterior position of two nostrils; preanal median ridge scales; a pineal sensory line; and (only in a few heterostracans) a grooved sensory-line. From these characters, only the covering of the head with at least two large shields may be regarded as a synapomorphy of *Sacabambaspis* and heterostracans. The polygonal structure of the dermal skeleton and the pineal lines are also encountered in osteostracans. The galeaspids show

grooved sensory lines. The preanal median ridge scales are certainly a primitive condition for the craniates since they may correspond to the preanal ridge of myxinooids and cephalochordates, and are probably related to the absence of unpaired fins (cf. Janvier, 1981).

Comparison of the vertebrate from Sacabamba and Sacabambilla with those of the other Ordovician localities reveals the following similarities and differences. The sculpture of the shield ornamentation shows a gradation between *Arandaspis*, *Porophoraspis* and *Sacabambaspis*, starting from diamond-shaped-tubercles which would be sculptured into an oak-leaf tubercle (G. C. Young, pers. comm.). The elongated tubercles of *Eriptychius* seem closer to this pattern than the stellate ornamentation of *Astraspis*. *Sacabambaspis* shares with *Arandaspis* the branchial opening arranged in a slanting row, each one being covered by a platelet, whereas these seem to form a horizontal row in *Astraspis* (Elliott, 1987). The double pineal depression in *Sacabambaspis* and *Arandaspis* is not visible on *Astraspis*. The elongated shape of the body scales occurs also in *Eriptychius* (Sawin, 1959; Pl. II fig. 3), but is closer to that in the rhombic scales of *Astraspis* (Elliott, 1987). The eye ring of *Sacabambaspis* is not known in other Ordovician taxa.

The comparison of these three taxa shows that *Sacabambaspis* and *Arandaspis* are closer to each other than to the North American genus *Astraspis*, and thus can be united in the same group (Text-fig. 4).



Text-fig. 4. Hypothesis of phylogenetic relationships of Ordovician vertebrates.

1: Large plates covering the head, long and thin rod scales, strictly pelagic forms, development of oral plates.

2: Sensory line system born in surface grooves on the cephalic region and on the body scales; individual platelets on the branchial openings; pineal and parapineal apparatus.

3: Reduction of the number of branchial openings, development of dentine tissue (mesodontine) and the pineal-parapineal organs get arranged antero-posteriorly. Heterostracans and *Astraspis* are individualized by the presence of acellular bone and the dorsalisation of the branchial openings.

The anterior position of the olfactory capsules and possibly paired nostrils in the heterostracans, as argued by Novitskaya (1975), refutes the hypothesis of the presence of prenasal sinus (Stensiö, 1927, 1964, 1968; Janvier, 1975, 1981). This feature, shared with *Sacabambaspis*, would be closer to the gnathostome condition than to the nasohypophyseal or nasopharyngeal opening of lampreys and hagfishes. If this relation to gnathostomes is accepted, it would mean that muscularized fins in gnathostomes and osteostracans appeared twice in vertebrate history or, on the contrary, that the nasohypophyseal opening is primitive.

Among characters which differentiate *Sacabambaspis* and *Arandaspis* from the heterostracans, are the paired pineal- parapineal openings side-by-side. Bjerring (1975) could not find any embryological evidence to define this condition as primitive or apomorphic. The large number of branchial openings is a widespread character, and probably primitive among craniates. The presence of a single opening corresponds to an apomorphy for the heterostracans (sensu Lankester, 1868-70).

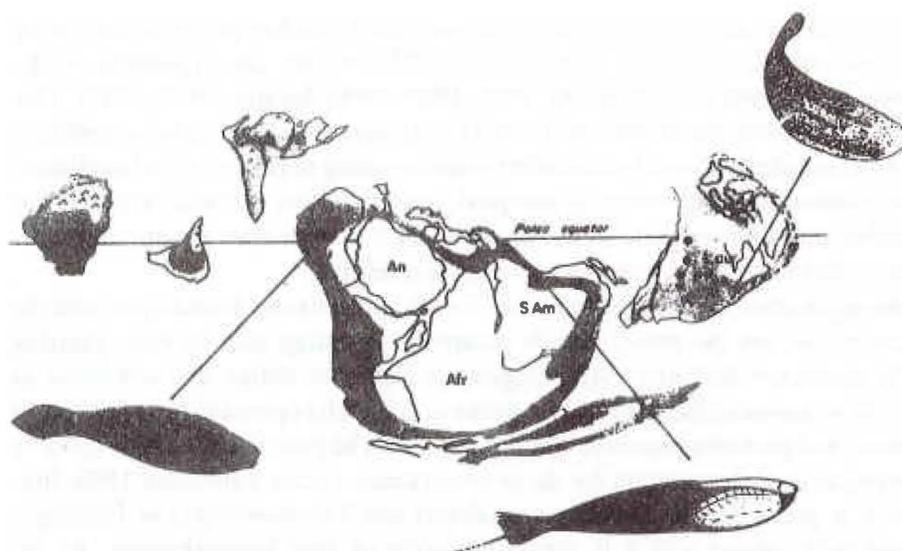
So it is preferable to consider *Arandaspis* and *Sacabambaspis* as forming a monophyletic group which is the sister-group of true heterostracans. As for *Astraspis* and heterostracans, a closer relationship seems probable (Text-fig. 4).

III - Palaeogeographical interpretation

As shown in Text-fig. 5, Ordovician vertebrates have been collected in three distant geographical areas, viz., central Australia (Amadeus Basin), Bolivia (Cochabamba region) and North America (USA and Canada). On most recent palaeogeographical reconstructions (e.g., Scotese, 1986), the three records fall within the warm Ordovician zones, near the palaeoequator. All are derived from lingulid- and *Cruziana*-bearing sandy facies, interpreted as near-shore, intertidal to subtidal marine. The problem is then to know if the observed distribution may be easily explained on the palaeogeographical reconstruction (Text-fig. 5).

Arandaspis and *Sacabambaspis* have been collected from countries which are thought to have been parts of a single continental platform, at the edge of Gondwana, in Ordovician times (Text-fig. 5: Australia and South America). As both taxa are phylogenetically related (Text-fig. 4), it seems that no strong problem arises here. However, *Astraspis* and *Eriptychius* come from North America which is supposed to have been separated from Gondwana. In this case, if Ordovician vertebrates, such as heterostracans, were unable of transoceanic migrations (Blieck, 1985; Blieck and Janvier, 1991), we need a more compact reconstruction of the Pangeic type, with a closed paleo-Pacific ocean (Gagnier et al., 1986), to explain the occurrence of the North American taxa.

Using a vicariant analysis better than a migratory one, we also need a pre-Mid Ordovician compact reconstruction, with a generalized distribution for the ancestral species to all Ordovician vertebrates (Elliott et al., 1991). As it is not the case on any published reconstruction (e.g., Scotese et al. 1979; Scotese, 1986), we conclude that the observed distribution does not fit the palaeogeographic reconstructions.



Text-fig. 5. Palaeogeographic reconstruction (after Scotese, 1986) for the Ordovician (Llandeilo-Caradoc) with location of the Middle and Upper Ordovician vertebrate records. Shallow seas (grey) slightly modified after Turner (1978). The black triangle refers to the *Arandaspis-Porophoraspis* assemblage from Australia (Ritchie, 1985). The black circles refer to the *Astraspis-Eriptychius* assemblage from North America (reconstruction of *Astraspis* in right lateral view after Elliott, 1987). The black star refers to *Sacabambaspis* from Bolivia (Gagnier, 1989).

Abbreviations: AFR Africa, AN Antarctica, AU Australia, IC Indochina, IN India, KAZ Kazakhstan, LAUR Laurentia, SAM South America, SIB Siberia.

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