

THE DEVONIAN VERTEBRATES OF SOUTH AMERICA: MALVINOKAFFRIC FISHES AND GONDWANA-EURAMERICA FAUNAL INTERCHANGE

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INTRODUCTION

Most Devonian vertebrate assemblages are known from Euramerica, Siberia, South China and northern Gondwana, and are essentially represented by "ostracoderms" (armoured jawless fishes), placoderms (armoured jawed fishes) and osteichthyans (bony fishes). Despite local endemism in the Lower-Middle Devonian this faunal composition remains relatively stable, and becomes more and more homogeneous worldwide towards the Upper Devonian. This type of vertebrate assemblage is thought to be bound to intertropical, warm water environments, and is associated to either Old Red Sandstone-like facies (i.e. marginal marine environments) or marine carbonate platform facies. Albeit scarce the Devonian vertebrates from South America display two distinct major faunal assemblages: an Eifelian-Frasnian placoderm- and osteichthyan-dominated fauna of "intertropical belt" type in the northwest (Venezuela, Colombia; Janvier & Villarroel, 2000; Young & Moody, 2002), and a unique Lochkovian-Eifelian chondrichthyan- and acanthodian-dominated fauna south of the present-day equator (central Brazil, Bolivia; Janvier, 1991, 2004; Janvier & Melo, 1992) (Fig. 1).

Stratigraphical correlations with South Africa and the Falkland Islands (Malvinas) (Fig. 3) suggest that the latter faunal assemblage is within the geographic bounds of the particular invertebrate communities referred to as the "Malvinokaffric Realm" (see review in Boucot & Racheboeuf 1993, Janvier & Maisey, in press). In contrast, the Eifelian-Frasnian vertebrate faunas of Venezuela and Colombia strikingly resemble the placoderm- and osteichthyan-dominated faunas of the Devonian intertropical belt that widely occurs on the northern margin of Gondwana and the southern margin of Euramerica.

Although the Venezuelan and Colombian vertebrate faunas provide some indications of an interchange between the Gondwanan and Euramerican vertebrate faunas by the Late Devonian, the southern South American faunas from Bolivia and Brazil remain unique and probably represent the only available example of Palaeozoic circumpolar vertebrate faunas. Current palaeogeographic reconstructions for the Devonian (e.g. Cocks & Torsvik, 2006) preclude occurrences of comparable epicontinental marine environments in northern circumpolar position. The northernmost Devonian vertebrate assemblages from Euramerica, Siberia or North China do not fundamentally differ from those of the typical Devonian

“intertropical belt”, except for a few endemic taxa.

The Lower and Middle Devonian fish faunas recorded from Bolivia and Brazil during the past three decades consistently yield almost exclusively chondrichthyans (shark relatives) and acanthodians (Fig. 3), with only exceptional occurrences of a placoderm in the Eifelian and Famennian and scarce osteichthyan (actinopterygian) remains in the Givetian and Famennian (see review in Janvier, 2001, 2003; Janvier & Maisey, in press). In addition, these chondrichthyan-dominated faunas include some very odd endemic taxa, such as *Zamponiopteron* and *Pucapampella* that are only known elsewhere in the Emsian-Eifelian Tra Tra and Gydo Formations of South Africa (Anderson *et al.*, 1999a; Maisey & Anderson, 2001). The only placoderm from the Eifelian of Bolivia, *Bolivosteus*, is a rhenanid, a group also known from Euramerica, but always extremely rare (Janvier, 2003). In contrast, the only Famennian placoderm from the quartzites of the Colpacucho Formation of Bolivia is a dunkleosteid, a group of large arthrodires that are usually very abundant in the Frasnian-Famennian, marine warm water platform carbonates of the “intertropical belt”, notably in Euramerica and Morocco (Díaz-Martínez *et al.*, 1996) and is interpreted as an incidental occurrence at high southern latitudes.

The reason for the predominance of chondrichthyans and acanthodians in the Devonian of Bolivia and Brazil remains unknown, although it recalls the classically odd composition of the “Malvinokaffric” invertebrate faunas (e.g., paucity or absence of ammonoid cephalopods, bryozoans or colonial corals). The latter may have represented a very different food chain from that of the “intertropical belt”. Other possible explanations are the temperate to cold-water condition, the more contrasted seasons and light conditions in the polar and circumpolar areas, or the higher



Figure 1. The Devonian vertebrate localities of South America and the Malvinas (Falkland Islands). a, Sierra de Perijá, Maracaibo, Venezuela (Campo Chico Formation); b, Maturin Basin (borehole), Venezuela, (?Middle Devonian); c, Floresta area, Colombia (Floresta and Cucho formations); d, Cumaná Peninsula, Lake Titicaca, Bolivia (Colpacucho Formation); e, Altiplano, La Paz area (Calamarca, Pisacaviña, Ayo Ayo, Patacamaya, Chacoma-Chiarumani, Lahuachaca, Pujrivi, Belén, Sica Sica), Bolivia (Belén and Sica Sica formations); f, Andamarca, Lake Poopo, Bolivia (Huamampampa Formation); g, Subandean zone, Sucre area (Presto, Tarabuco, Padilla, Aiquile), Bolivia (Icla and Huamampampa formations); h, Seripona and La Higuera, Bolivia (Santa Rosa Formation); i, Yuquimba anticline, Chalana Vieja, Bolivia (Iquiri Formation); j, Sucuriju Creek, Para, Brazil (Manacapuru Formation); k, Picos, Piauí, Brazil (Pimenteira Formation); l, Jandiatura Sub-basin, Acre area (Barreirinha Shale; borehole); m, 12, Dunnoose Head, West Falkland Island (Port Philomel Formation); n, Roy Cove, West Falkland Island (Fox Bay Formation).

Pridoli	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian	
						Campo Chico Fm. (1)		Ve
				(2) Floresta Formation		? Cucho Formation (3)		Co
		? Belén Formation (Lower Member)		(4) Belén Formation (Upper Member)	(5) Sica Sica Formation ?		Colpacucho Formation (6) ?	Bo1
Tarabuco Fm. (7)	Sta Rosa Fm. (8) ?	Icla Fm. (Lower Mb) ?		Icla Fm. (Upper Mb) (9)	Huamampampa Formation ?		Iquiri Fm. (10)	Bo2
Manacapuru Formation (11)					Pimenteira Formation ? (12)		? Barrereirinha Shales (13)	Br
			? Fox Bay Formation (14)		? Port Philomel Formation (15)			Falk
				? Tra Tra, Gydo Formations (16)	? Klipbokkop & Adolphspoor formations (17)	? Wagen Drift Fm. (18)	? Witpoort Formation (19)	SA

Figure 2. Stratigraphical distribution of the main vertebrate-bearing formations (grey) in the Devonian of South America, the Falkland Islands and South Africa. Bo1, Bolivia (Altiplano); Bo2, Bolivia (Oriental Codillera and Subandean zone; Br, Brazil; c, Condoriquiña Quartzite; cl, Cruz Loma quartzite; Co, Colombia; Falk, Falkland Islands; SA, South Africa; Ve, Venezuela. The bold vertical lines indicate the position of the Condoriquiña and Cruz Loma quartzites in the Devonian of the Bolivian Altiplano. (From Janvier & Maisey, in press).

rate of siliciclastic sedimentation. Another feature of this vertebrate fauna is the abundance of apparently endemic taxa. Contemporary Devonian faunas from other areas include very few chondrichthyans, all being typically primitive elasmobranchs, such as antarctilamnids. Although antarctilamnids also occur in Bolivia, Brazil and South Africa, they are accompanied by other peculiar forms, such as *Pucapampella*, whose anatomy suggest that they are stem chondrichthyans. It is thus tempting to suggest that the main evolutionary radiation of chondrichthyans, that took place in the Famennian or Early Carboniferous worldwide, began in fact much earlier in the Devonian austral seas.

The Eifelian-Frasnian Devonian vertebrate faunas of the siliciclastic formations of Colombia and Venezuela are in many respects identical to those of the Middle and Upper "Old Red Sandstone" of northern Euramerica. They are dominated by placoderms (antiarchs, arthrodiros) and osteichthyans (actinopterygians and sarcopterygians), with very few chondrichthyans and acanthodians (Fig. 3). These faunas include some taxa (phyllolepid and groenlandaspimid arthrodiros, rhizodontid and megalichthyid sarcopterygians) that are typically Gondwanan before the Famennian, but expand into Euramerica after the collision between Gondwana and Euramerica. However, the Frasnian Cucho Formation of Colombia also yields the antiarch *Asterolepis* and the Sarcopterygian *Holoptychius* that are known since the Eifelian in Euramerica, and never recorded elsewhere in Gondwana. This suggests that an early southward dispersion of reputedly Euramerican endemics has preceded the Famennian northward dispersion of originally Gondwanan endemics.

CONCLUSIONS

The Devonian of central and southern South America and South Africa offers a unique opportunity for studying circumpolar marine to marginal Devonian vertebrates, which were at the top of the unusual food chain composed by the characteristic invertebrate assemblages of the "Malvinokaffric Realm". These austral vertebrate faunas, notably in the Lower and Middle Devonian of Bolivia and Brazil, differ from those

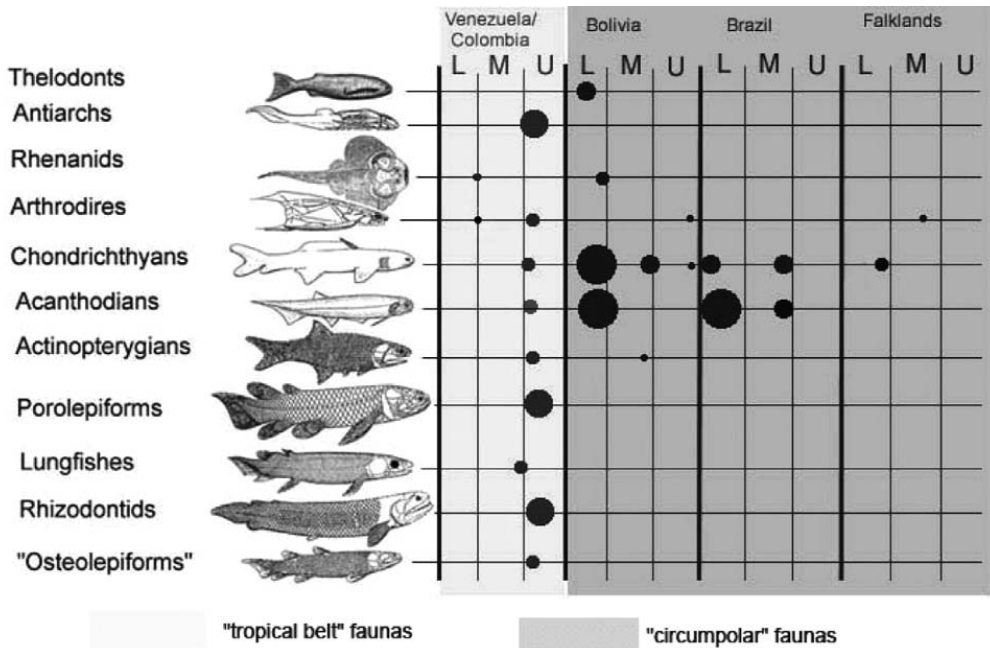


Figure 3. Relative abundance (black circles) of the major vertebrate groups in the Devonian of South America. Note the marked difference between the "tropical belt" (light grey) and "circumpolar" (dark grey) assemblages. Placoderms are represented by the antiarchs, rhenanids and arthrodires.

of the Devonian "intertropical belt" in being almost exclusively composed of chondrichthyans and acanthodians. It is still unknown whether this unique condition is linked to cooler environmental conditions, sedimentological biases, or a mere consequence of a different food chain. By the early Givetian, placoderm- and osteichthyan- dominated vertebrate faunas progressively develop in South Africa (Anderson *et al.* 1999b), but remain virtually absent in Bolivia and Brazil, suggesting the possible remanence of "Malvinokaffric" cool-water conditions in this particular part of western Gondwana.

In contrast, the Eifelian-Frasnian vertebrate assemblages from Venezuela and Colombia display the characteristic placoderm- and osteichthyan-dominated assemblages of the "intertropical belt", with Gondwanan endemics, but also some reputedly Euramerican endemics, which suggest a minor faunal interchange between Gondana and Euramerica as early as the late Frasnian.

This biogeographical pattern of the Devonian vertebrate faunas for northern and southern South America, respectively, needs to be further tested by the discovery of more extensive Lower-Middle Devonian occurrences in northern South America, and more extensive Upper Devonian occurrences in southern South America.

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