

BIOSTRATIGRAPHIC SIGNIFICANCE OF SOME UPPERMOST DEVONIAN PLACODERMS

by

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(1 figure)

ABSTRACT. - A review of the biostratigraphic and paleogeographic distribution of Famennian fish faunas emphasizes the significance of placoderms. (Abstracted by the editors).

RESUME. - Le papier discute la distribution biostratigraphique et paléogéographique des faunes de poisson famenniennes, mettant l'accent en particulier sur la distribution des placodermes, le groupe qui fournit le plus de renseignements.

1. - INTRODUCTION

The regressive period of the Late Devonian in the Belgian Ardenne is associated with arenaceous shallow marine deposits where fishes were relatively abundant, but not well preserved. In these Famennian sequences the fish fauna is well known since a long time. An important number of papers has been written on Belgian ichthyofauna (Fourmarier, 1899; Lohest, 1882, 1888, 1895; Malaise, 1875; Newberry, 1889). A synthesis by Leriche (1931) was one of the last papers on Belgian Devonian fishes.

Several groups have been recognized : the Placoderms *Bothriolepis* sp., *Bothriolepis lohesti*, *Phyllolepis undulata*, *Dinichthys belgicus*; the lungfishes *Dipterus fourmarieri*, *Dipterus nelsoni*, some poorly preserved remains of Selachians and the Crossopterygians : *Holoptychius*, mostly represented by scales and teeth.

This late Devonian fish assemblage is well known from other sites (Scotland, Greenland, Baltic Provinces, southeastern England, northeastern United States) in the Old Red Continent and supports the hypothetical paleogeographic reconstructions of an important Old Red Continent situated to the North. From Gondwana this typical fish fauna was described more recently and is partly known in the Famennian of China (Wang shitao & Turner, 1985; P'an Kiang, 1956, 1957, 1981; Pan Jian *et al.*, 1980), Australia (Campbell & Bell, 1982; Long, 1983, 1984; Young, 1974, 1981, 1984) and Turkey (Janvier, 1984) although the Upper

Devonian paleogeographic position of this last region is not clearly established. Our review is not intended to be exhaustive for many reasons such as the lack of direct age control by invertebrate faunas since the association of fishes and stratigraphically important invertebrates is not common. Fish-bearing sediments with typical marine invertebrates are generally interpreted as marine whereas fish-bearing strata without marine invertebrates are incorrectly interpreted as deposited in fresh-water environment.

The wide geographic distribution of certain placoderms such as : *Groenlandaspis*, *Bothriolepis*, *Phyllolepis*, *Remigolepis*, or Dipnoans : *Soederberghia*, or the occurrence of the first Amphibians in Greenland, Brazil (Leonardi, 1983), Australia (Campbell & Bell, 1977) and the U.S.S.R. (Lebedev, 1985) often associated with the same placoderms may be a tool for long-distance correlations between marine and non-marine sequences throughout the regions mentioned above. But some questions remain such as the first - poorly dated - appearance of these fishes in the stratigraphic sequences throughout the world.

Although some species seem to be endemic, particularly in China and in Australia, the wide distribution of some of the above mentioned fishes, has kept the attention in order to establish ways of migration or dispersal. The occurrence of ichthyofaunas usually consi-

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dered to be restricted to the Old Red Continent has led to envisage other centers of origin than those traditionally supposed to occur around this continent (see Young, 1981 : 225). These new early vertebrate faunas give rise to new models in biogeography, while "traditional" paleogeographic reconstructions stand approximately in their European- North American views : a certain kind of immobilism.

To discuss the interest of biostratigraphic and paleogeographic data for Famennian fish faunas, in connection to the aim of the present symposium, we consider mainly the distribution of placoderms which appear to be the most informative.

2. - THE SIGNIFICANCE OF SOME FAMENNIAN PLACODERMS AS BIOSTRATIGRAPHIC INDICATORS

It is well known that the Placoderms became extinct by the end of the Famennian. Among the last placoderms, the antiarchs *Bothriolepis* and *Remigolepis*, and two other placoderms *Phyllolepis* and *Groenlandaspis* have a biostratigraphic importance. These four genera have been reported from all continent with the exception of Africa and South America (Young, 1974) where they are unknown, although Termier has mentioned the presence of *Asterolepis* in the Adrar. This fossil is undeterminable as an antiarch (see Lehman, 1956 : 10).

A good review of the stratigraphic interest of the antiarchs *Asterolepis* and *Bothriolepis* for the Middle and Upper Devonian was published by Young (1974). The new data especially on *Bothriolepis* (considered to flourish during the late Devonian) add no further information since Young's review. We refer to his conclusions and present the new data concerning this genus.

During the late Devonian (Upper Famennian) of Europe *Bothriolepis* is known from the Baltic States where its first appearance in the Pakrojis level of the Kaliningrad region in Lithuania is dated as Lower Famennian. This genus occurs throughout the Famennian until the Tournaisian, in the Latij Horizon, where it is associated with crossopterygians, such as *Holoptychius*, and dipnoans. In Greenland (Bendix-Almgreen, 1976) *Bothriolepis* appears at the base of the Famennian in the *Phyllolepis* series and is restricted to the lower part of the overlying *Remigolepis* series, considered to be at the base of the Strunian. The association with *Holoptychius* is the same as in Baltic States, with the difference that the species *Phyllolepis nielseni* is restricted to the Zagere Horizon in Lithuania, this is a much older level than in Greenland but equivalent to the upper part of the Rosebrae beds of Scotland.

In Australia (Young, 1974) the same assemblage of *Bothriolepis* together with *Remigolepis*, *Groenlandaspis* and *Phyllolepis* is known. But recent discoveries of new phyllolepid genera by Long (1984) and Ritchie

(1984) prove that the phyllolepid already appeared in the Frasnian, particularly in the Mt. Howitt (Victoria) where the assemblage exhibits the presence of *Bothriolepis*, *Groenlandaspis* sp., together with Acanthodians, dipnoans, paleoniscids and crossopterygians.

This new Australian fauna suggests a geographic extension of the typical Famennian ichthyofauna from Greenland to Australia, but there appearing already in the Frasnian whereas this ichthyofauna is unknown at that age in Greenland. This placoderm assemblage - *Bothriolepis*, *Remigolepis*, *Phyllolepis*, *Groenlandaspis* - ranges into the Uppermost Famennian - both in Euramerica and Australia. But, it seems likely that detailed morphological studies will show important geographical endemism and will allow a revision of the classical biostratigraphic importance of this assemblage.

During the Late Devonian of China, the occurrence of both *Asterolepis* and *Bothriolepis* gives a different aspect of the question discussed here. In Euramerican regions, *Asterolepis* is considered to be of Middle Devonian to Frasnian age; moreover *Bothriolepis* appears earlier in China than in Euramerica.

In the Wutung series (P'an Kiang, 1957, 1981) *Asterolepis sinensis* is associated with two endemic species of the antiarch genus *Sinolepis*. The Wutung flora, with *Leptophloeum rhombicum* is considered to indicate a late Devonian - early Carboniferous age. The fishes (antiarchs and *Holoptychius*) come from the upper part of the Wutung series, in black shales, associated with the plant *Lepidodendropsis hirmeri* dated as Lower Carboniferous in Bavaria (RFA) and in the Pocono Formation (USA) (Allen *et al.*, 1976).

More recently Pan Jiang *et al.* (1980) mentioned the occurrence of both *Bothriolepis* and *Remigolepis* in the region of Ningxia Hui in Northwestern China. The stratigraphic sequences, red beds, occur in the upper part of the Zhongning Formation where *Remigolepis zhongningensis* and *Bothriolepis* are associated with *Leptophloeum rhombicum* indicating a late Devonian-early Carboniferous age.

P'an Kiang (1981) and Yang Shi-Pu *et al.* (1981) revised the age of the antiarch-bearing strata (*Asterolepis*, *Bothriolepis*, *Sinolepis*, *Remigolepis*) and the associated flora as being late Devonian age. For these Chinese authors the Upper Devonian is characterized by two assemblages :

- The *Sinolepis*-*Asterolepis sinensis* assemblage, occurring in the upper part of the Wutung series and associated with *Leptophloeum rhombicum*.
- The *Remigolepis* assemblage, occurring in South China in the Sandstone member of the Shetienschiao Formation of East Hunan and South Kiangsi. In Northwestern China the *Remigolepis* assemblage is considered slightly older in the Chunging (= Zhangning) Formation of Ningxia. In both assemblages the presence of *Holoptychius* is known, and so this genus seems to have a "cosmopolitan" distribution. P'an

Kiang dated the last occurrence of the *Remigolepis* assemblage as Frasnian. But it should be kept in mind that his biostratigraphic conclusions may be influenced by the fact that China is considered to be the center of origin for antiarchs on the simple stratigraphic argument that the oldest antiarchs are found in China. This interpretation doesn't take into account other definitions of centers of origin. Therefore biostratigraphic data may only indicate the change of biogeographic barriers with time (see Young, 1984).

Remarks on the Placoderms *Groenlandaspis* and *Phyllolepis*

- The placoderm *Groenlandaspis*, first described by Heintz (1932) from the Uppermost Devonian of Greenland, has been reported from various other regions in Famennian layers :
- from Antarctica, South Victoria land (Ritchie, 1975);
 - from the Uppermost Devonian or Tournaisian of Kiltorcan beds in Ireland (Woodward, 1891);
 - from the Frasnian of Western Turkey (Janvier & Ritchie, 1976) and more recently from the Devonian/Carboniferous limit of Southeastern Turkey, Zap Valley (Janvier *et al.*, 1984).
 - some remains have been mentioned from the Uppermost Devonian of England (Ritchie, 1975);

- in New South Wales its occurrence is known from the Cloghan shale in Jemalong Range, dated as Famennian.

This genus is known both from Southern and Northern Hemispheres, but is probably much older in the first one. *Groenlandaspis* seems to be a useful biostratigraphic species for the Uppermost Devonian in Greenland and probably North America. However because of its appearance in the Upper Frasnian of Australia (Long, 1984; Young, 1974) this is not an ideal guide for the Famennian. A similar problem occurs with *Bothriolepis* and *Remigolepis*, the last genus considered as being exclusively Famennian (Young, 1984) in Australia. Since this genus is absent in the Upper Devonian placoderm fauna of Victoria this has been assigned to the Frasnian. Its presence in the Upper Devonian localities of New South Wales is accepted as indicative for a Famennian age.

The presence or absence of *Groenlandaspis* cannot be used for stratigraphic purposes. In the Devonian of Western Turkey the fossil localities with *Groenlandaspis* are dated as Frasnian. However, in Southeastern Turkey, *Groenlandaspis* is associated with an Uppermost Famennian fauna together with the crossopterygian *Strepsodus* and the actinopterygian *Cano-bius* (Janvier *et al.*, 1984).

The stratigraphic problems met with Australian phyllolepis resembles those for the Turkish localities. *Phyllolepis* is known both in Victoria and New South Wales, but restricted to Frasnian in Victoria and ranging from the Frasnian into Famennian in New South Wales. In this last region *Phyllolepis* does not reach the Uppermost Devonian (Long, 1983, fig. 3). In Euramerica the occurrence of *Phyllolepis* is restricted, until now, to the Uppermost Famennian and may be considered as a good biostratigraphic indicator for that interval.

		Greenland	Scotland	Baltic States	China	Australia		Turkey	Belgium
						Victoria	NSW		
LATE DEV	Stru								
	Fam								
	Fras								
MIDDLE DEV	Giv								
	Eif								

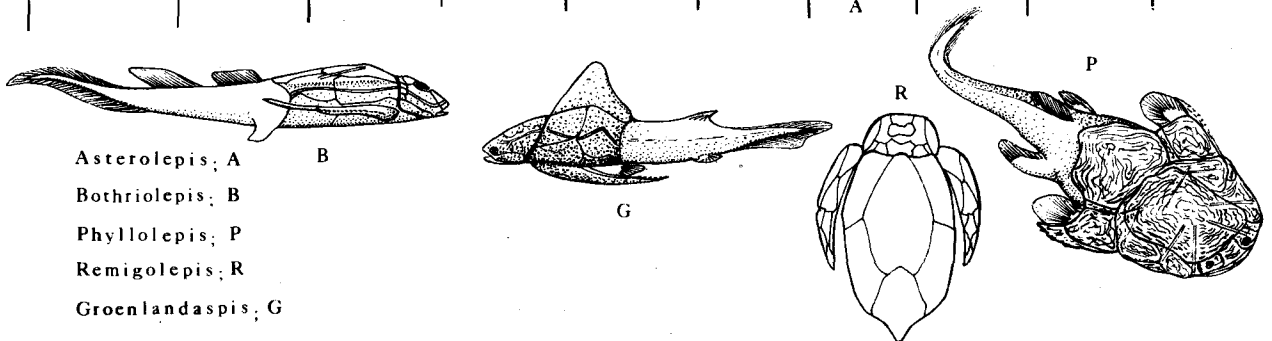


Fig. 1. Biostratigraphic extensions of some placoderms; adapted from Long, J., 1983.

3. - BIOSTRATIGRAPHIC SIGNIFICANCE OF OTHER ICHTHYOFAUNA

The worldwide importance of early vertebrate microremains, mainly scales and teeth, as biostratigraphic tools is known for the Silurian and Early Devonian (Blieck, 1978; Blieck *et al.*, 1984). Recently Wang Shitao & Turner (1985) described microfish remains from the Muhua section (Changshun County, SE China). The marine sequences are situated at the Devonian/Carboniferous boundary, on the evidence of the conodonts *Siphonodella praesulcata* and *Siphonodella sulcata*; the microfish remains were found associated with conodonts. They belong to several groups such as acanthodians, chondrichthyans and probably placoderms. The authors envisage the acanthodian: *Acanthodes guizhoniensis*, as "potential zone fossil" for the base of the Lower Carboniferous. But rhombic scales of Acanthodidae are known during the Devonian, although the histologic structure does not indicate that these belong to *Acanthodes*. The choice of a so debated genus as a guide for this boundary seems to be unfortunate.

During the Devonian the selachians are mostly known from scales, teeth and fine spines, for their cartilaginous skeleton is rarely preserved. They are considered to be marine dwellers and they become more and more diversified during the Uppermost Devonian. The selachians are worldwide distributed just as the placoderms and crossopterygians. An example is the new genus *Harpago ferox* (Turner, 1982; erected on teeth) from the late Famennian and late Tournaisian of Australia. Since its first discovery in Australia, *Harpago* has been mentioned from the Devonian/Carboniferous boundary of China (Wang Shitao & Turner, 1985) and from the Lower Carboniferous of Avesnois, France (Goujet, unedit.).

4. - A BRIEF ACCOUNT OF DEVONIAN FISH DISPERSAL

Young (1981, 1984) has examined possible dispersals for some of the Devonian fishes. He restricted the problem of placoderm dispersal to the early Devonian, during that period the endemism is more evident than during later periods. He envisaged a Phlyctaenioid/Actinolepid center of origin in Euramerica (North America, Greenland, Europe) whereas Australia is considered to be the center of origin for *Wuttagnaspis* + *Antarctaspis* + *Phyllolepis*. The presence of *Phyllolepis* in the Famennian, and maybe in the late Frasnian of Turkey, might be the result of dispersal, since the extinction of the psammosteid Heterostracan with a similar adaptation took place just before this dispersal.

The problem with the dispersal of *Groenlandaspis* of which no primitive related taxa are known, raises some questions, as its older occurrence in New South

Wales does not designate this region as the center of origin for that genus. Recently, Schultze (1984) considered *Tiaraspis*, from the lower Devonian of Germany as a possible primitive sister group of *Groenlandaspis*. If (following Schultze) we consider *Tiaraspis* as a good sister taxon, Europe may be considered as a possible center of origin for the *Groenlandaspis*-*Tiaraspis* assemblage. But a possible occurrence of *Groenlandaspis* is mentioned by Ritchie (1975) in the Middle Devonian of New South Wales, and raises the following problem: - the biogeographic barrier will operate for some placoderms such as the *Wuttagnaspis* assemblage but not for a similarly adapted placoderm such as *Groenlandaspis*.

The geophysical data suggest, that Gondwana approached Euramerica either during the Middle Devonian (Irving, 1977) or during the late Devonian (Scotese, 1985). Nevertheless, the opening of large oceanic basins during the Devonian is not consistent with the vertebrate distribution. Between these two models, and many others, an alternative model may be envisaged: a continuing Pangea during the Paleozoic (Crawford, 1982) on an Expanding Earth model. It has the advantage to reduce the opening of oceanic basins, which existence is not really demonstrated before the Jurassic. The expanding Earth model (Carey, 1976; Jordan, 1966; Owen, 1983; Shield, 1979) allows a better understanding of the distribution of vertebrates during the Middle and Upper Paleozoic although those distributions are generalised or disjointed. With the *Tiaraspis*-*Groenlandaspis* assemblage it is not necessary to envisage the closure of such oceanic basins for understanding their dispersal from a probable European center of origin toward Eastern Gondwana.

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