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STRATIGRAPHIC OCCURRENCE OF SOME PLACODERM FISHES IN THE MIDDLE AND LATE DEVONIAN

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(not for publication)

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By Gavin C. Young,

with 3 figures.

Abstract: Recent work on antiarchan fishes in the Baltic and northwest Russian Devonian dates the replacement of *Asterolepis* by *Bothriolepis* as early Frasnian. Other sequences encompassing this change are continental deposits and cannot be precisely dated on marine invertebrates, but in both North America and Australia *Bothriolepis* is associated with late Givetian - early Frasnian conodonts. In southern China, however, it occurs in Eifelian strata, which compares with the earliest European antiarch occurrence of *Gerdalepis* in the Mühlenberg Beds of the Rhineland. There is also evidence that *Asterolepis* in China extends well into the Famennian. In Australia the first appearances of antiarchs *Bothriolepis* and *Remigolepis* and arthrodires *Phyllolepis* and *Groenlandaspis* may be earlier than in Europe, and an antiarch occurrence in Victoria isotopically dated at 362±6 m.y. may approximate the Middle/Late Devonian rather than the Devonian/Carboniferous boundary.

Zussammenfassung: Kürzliche Forschung an Antiarchan Fischen im baltischen und nordwest russischen Devon datiert den Austausch von *Asterolepis* gegen *Bothriolepis* als frühes Frasnian. Andere Sequenzen die diese Änderung einschliessen sind kontinentale Deposite und können nicht präzise an marinen Invertebraten datiert werden, sind aber im nord-amerikanischen und australischen *Bothriolepis* assoziert mit späten Givetian/frühen Frasnian Conodonten. Es erscheint in Süd-China in Eifelian Strata, was vergleichbar ist mit den frühesten europäischen Antiarch Vorkommen von Gerdalepis in den Mühlenberg Schichten vom Rheinland. Dort ist auch Beweis, dass *Asterolepis* in China reichte weit in das Famennian. Das erste Auftreten von den Antiarchen *Bothriolepis* und *Remigolepis* und Arthrodiren *Phyllolepis* und *Groenlandaspis* in Australien kann früher sein als in Europa und ein Antiarch Vorkommen in Victoria ist isotopisch datiert worden als 362±6 m.y. was vergleichsweise das mittlere/späte Devon ist, denn die Devon/Karbon Grenze.

1. Introduction

The replacement of the Middle Devonian placoderm fish *Asterolepis* (Class Placodermi, Order Antiarchi) by the Late Devonian antiarch *Bothriolepis* has long been recognized as an important biostratigraphic horizon in the fish-bearing Old Red Sandstone strata of Western Europe (Traquair, 1895; Westoll, 1951). The use of antiarchs in conjunction with the psammosteid heterostracans (Class Agnatha, the jawless fishes) and other placoderms (especially the arthrodire *Phyllolepis*) has enabled the broad correlation of Middle-Late Devonian non-marine sequences throughout western Europe, Greenland, and eastern North America. Correlation with the standard Devonian marine succession has remained a problem, however, and only in the Baltic region has it been possible to date changes in the vertebrate fauna using associated marine invertebrate assemblages.

The wide geographic distribution of *Bothriolepis* is also well established; species of the genus have been reported from all continents except Africa and South America. *Bothriolepis* occurs most typically and abundantly in continental deposits of probable fluviatile or lacustrine origin, but is known in one case from marine strata (the Gogo Formation in northwest Australia), whilst a number of occurrences are associated with marine intercalations containing datable invertebrates. The date of its first appearance over the limits of its geographic range has not been closely examined, however, and the purpose of this paper is to review the stratigraphy of *Bothriolepis* occurrences throughout the world in an attempt to determine the accuracy with which its dispersal can be dated using associated invertebrate assemblages.

The review is not intended to be comprehensive, and several important faunas for which direct invertebrate age control is lacking are only briefly mentioned. Detailed consideration is restricted to those sequences where the *Asterolepis* - *Bothriolepis* transition is shown or where occurrences of either genus in continental deposits can be dated on associated marine assemblages.

Other antiarchs are in general too poorly known or too limited in geographic distribution to be considered at length, and the few well-dated marine genera such as *Gerdalepis* and *Grossaspis* (Middle Devonian of the Rhineland), and *Lepadolepis* (Frasnian of Bad Wildungen), are of little use in dating continental occurrences at this stage. Other placoderms commonly associated with *Bothriolepis* are considered in relation to Australian occurrences as the overall affinity of these assemblages has a direct bearing on their age assessment. In this context the relationships and stratigraphic significance of the European antiarch *Remigolepis* and arthrodires *Phyllolepis* and *Groenlandaspis*, the Chinese antiarch *Dianolepis*, and the Australian antiarch *Hillsaspis* and arthrodire *Wuttagoonaspis* (both endemic) are briefly considered.

This study was initiated during the course of describing new placoderm material from northwestern Australia, with a view to clarifying the biostratigraphic implications of numerous Australian occurrences of *Bothriolepis*. In this respect the study has been somewhat inconclusive, and it is clearly evident that a great deal of detailed taxonomic work is required before correlations based on placoderms can be accepted with any confidence. It is also evident, however, that only by relating vertebrate occurrences to invertebrate faunas, as is attempted below, will the utility of widespread forms such as *Bothriolepis* in intercontinental correlation of nonmarine Devonian strata be ascertained.

2. Age of the Asterolepis - Bothriolepis transition in Europe

The Middle and Upper Devonian in the Baltic region is stratigraphically and historically one of the most important sequences for understanding the vertebrate faunal succession in western Europe. The type species of *Asterolepis* (*A. ornata* Eichwald, 1840) and *Bothriolepis* (*B. ornata* Eichwald, 1840) were both originally described from this area, and subsequent taxonomic studies, especially by Gross (1931, 1933, 1940, 1941, 1942) led to detailed biostratigraphic subdivisions based mainly on changes in the antiarch and psammosteid components of the fish fauna (Gross, 1950; Obruchev, 1951, 1958; Karatajute-Talimaa, 1958, 1963; Tarlo, 1961, 1964). The most useful genera for the Givetian - Frasnian part of the sequence (Fig. 1), are the psammosteid heterostracans *Schizosteus* and *Pycnosteus* (Givetian), *Psammolepis* (Givetian - Frasnian), and *Psammosteus* (Frasnian), the antiarchs *Byssacanthus* (Givetian) and *Grossilepis* (Frasnian), and several species of *Asterolepis* and *Bothriolepis*. Of the four antiarch genera only the last two are sufficiently widespread outside the area to be useful in regional correlation.

Asterolepis ranges from the Givetian Narova (A_1) beds (Fig. 1) where *A. estonica* Gross, 1940 makes its first appearance, through to the Amata (A_4) beds, where *A. radiata* Rohon, 1900 is associated with the first two *Bothriolepis* species, *B. prima* Gross, 1942 and *B. obruchevi* Gross, 1942. Above this level *B. panderi* Lahusen, 1880 and *B. cellulosa* (Pander), 1846 occur, but *Asterolepis* is unknown, and the Amata horizon thus marks an important zone where the stratigraphic ranges of the two genera overlap.

Marine intercalations and the occasional mixing of vertebrate and invertebrate faunas have allowed correlation of this sequence with the marine succession of the central Russian Platform (Fig. 1), which in turn can be correlated on conodonts with the Belgian standard. Directly above the Amata, the Snetogor (B_1) and Pskov-Chudov marine layers contain an invertebrate fauna which correlates with the Khvorostan (Sargajev) horizon of the central Russian Platform. Common elements in the two faunas are the brachiopods *Chonetes* menneri Ljasch., and Ladogia meyendorfi (Verneuil) and the ostracod Acratia pskovensis Egorov (Liashenko & Liashenko, 1967, p. 518). The Khvorostan fauna also contains conodonts of the lower Frasnian Polygnathus asymmetricus Zone (Ziegler, 1971, p. 284), and is placed by Russian workers in the Timanites acutus - Hypothyridina calva Zone, which marks the top of the lower Frasnian substage (Aronova et al., 1967; Rzhonsnitskaya, 1967). The base of the Frasnian in Russia is taken at the base of the Kynov and Paschja horizons, which are correlated by Russian workers with the Gauja and Amata beds, and contain earliest lunulicosta Zone goniatites and conodonts of the Polygnathus varcus or Schmidtognathus hermanni - Polygnathus cristatus Zones. On this basis they can be approximately correlated with the Assise de Fromelennes of the Belgian type section (House, 1973, p. 4). According to Ziegler (1971, p. 261,2) the hermanni - cristatus Zone lies between the Givetian varcus and the Frasnian asymmetricus Zones, and is Givetian in its lower and possibly Frasnian in its upper part.

Figure 1 Beneath the Amata the uppermost Narova beds contain the brachiopod Emanuella pachyrincha Verneuil, which is also known from the middle Givetian Staryy-Oskol beds to the east, where it occurs with Stringocephalus burtini (Aronova et al., 1967).

The Givetian/Frasnian boundary must lie between these datable horizons but its precise position is uncertain, and various levels have been proposed. Gross (1950 and earlier works) and Westoll (1951) accepted the Snetogor as the lowest Frasnian horizon, with the Middle/Upper Devonian boundary, thus corresponding to the disappearance of Asterolepis from the fauna, and the zone containing both Asterolepis and Bothriolepis representing the uppermost Givetian. On this basis Bothriolepis has generally been cited as ranging from late Middle to late Upper Devonian in Europe (see for example Tomlinson, 1968 p. 212).

However, Obruchev (1951, 1958) and Karatajute-Talimaa (1958, 1963) have proposed a lower level, with the boundary lying at the top of the Tartu

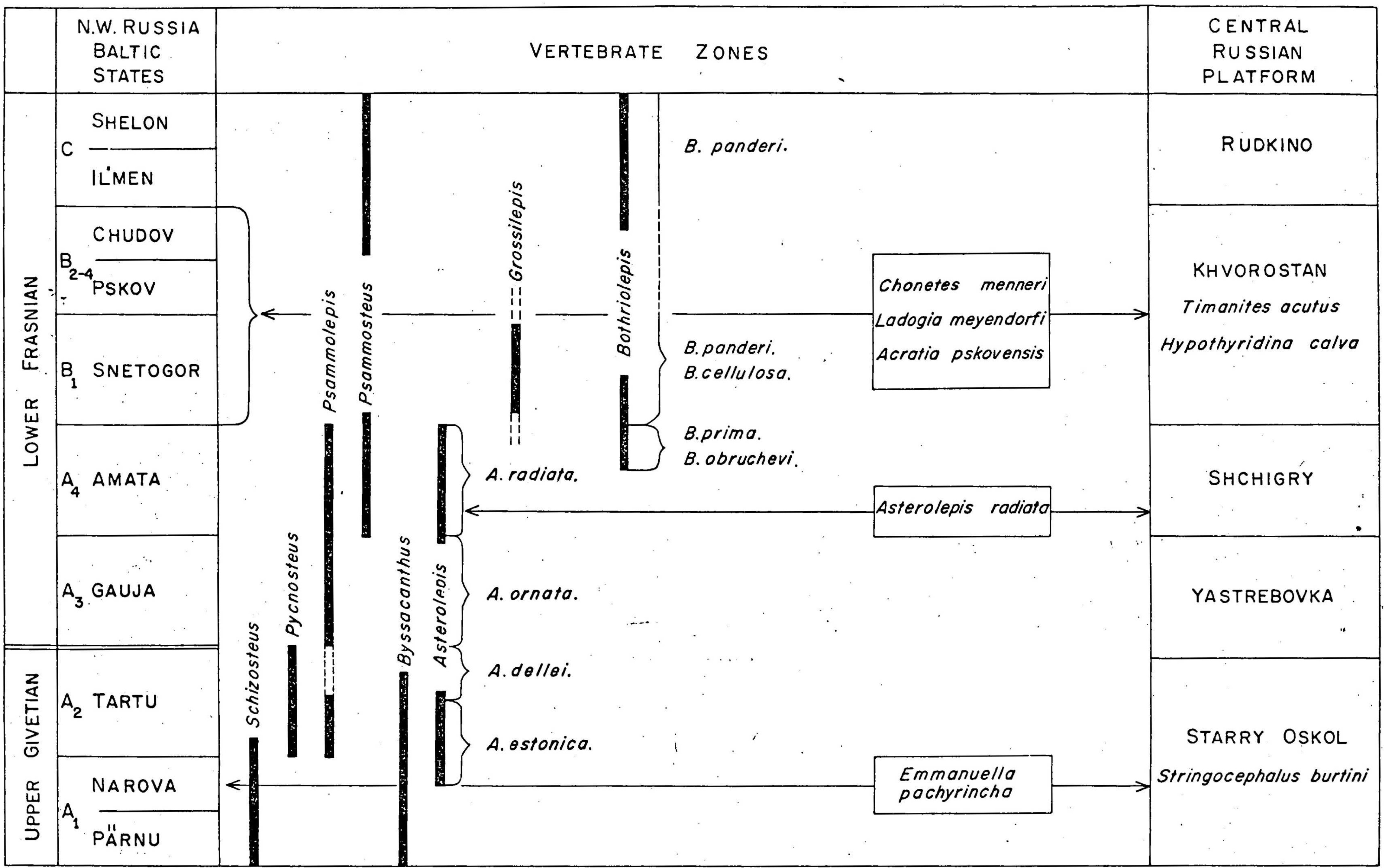

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Fig. 1

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horizon (i.e. within the Asterolepis and Psammolepis Zones) and both the Gauja and Amata horizons included in the basal Frasnian. This is supported by the fact that Asterolepis radiata, which occurs with Bothriolepis in the Amata, is also recorded from the Lower Shchigry Beds in the central region of the Russian Platform (Karatajute - Talimaa, 1963). The Shchigry and underlying Yastrebovka beds lie beneath the early Frasnian Khvorostan, and above the Staryy-Oskol beds, containing Stringocephalus burtini, which according to Boucot et al. (1966, p. 1356) may have persisted into earliest Frasnian time, but in many sequences disappeared before the end of deposition of late Givetian sediments. On this basis the Shchigry and Yastrebovka horizons may be taken to represent the earliest Frasnian and possibly part of the latest Givetian. The absence of Bothriolepis in the Shchigry could indicate correlation with the lower Amata only (Bothriolepis first appears towards the top of A_4) while the Gauja has been included beneath the Amata as the basal Frasnian unit because of the similarity of the vertebrate fauna in these two formations (Obruchev, 1951).

Whether the top of the Givetian lies at the Tartu/Gauja contact or at some level within the Gauja is difficult to determine, but there is now little doubt that the Amata horizon is early Frasnian in age. It follows that, in the Baltic succession at least, Asterolepis crosses the Givetian/Frasnian boundary, whereas Bothriolepis is confined to the Late Devonian.

An equivalent faunal succession occurs in the Upper Old Red Sandstone in Scotland, and both Tarlo (1961, 1964) and Miles (1968) have demonstrated that species at equivalent levels in the two regions are closely comparable. Asterolepis occurs in the Nairn Sandstone, and Bothriolepis first appears in the overlying Edenkillie beds, although Miles (1968, p. 11) has pointed out that at no one locality in Scotland are the two genera known to occur together, as they do in the Amata horizon of the Baltic Province.

No other successions showing the faunal transition from Asterolepis to Bothriolepis are known. In east Greenland the relationship between the Asterolepis horizon in Canning Land and the late Upper Devonian fish-bearing strata from Ymers Island and Gauss Peninsula cannot be determined (Stensiö & Säve - Söderbergh, 1938; Jarvik, 1961), whilst the Spitzbergen species of Asterolepis comes from the Fiskekløfta horizon at the top of the vertebrate succession (Nilsson, 1941; Friend, 1961). A. orcadensis and A. thule from the Orkney and Shetland Islands are not associated with younger antiarch horizons (Watson, 1932), and other Scottish antiarchs (Pterichthyodes, Microbrachius) are also confined to the middle Old Red Sandstone (Eifelian/Givetian) (Westoll, 1951, p. 10).

These occurrences of Asterolepis have generally been assigned to the Middle Devonian (Givetian), but it is nevertheless apparent that the validity of biostratigraphic relationships as they occur in the Baltic succession has not been substantiated outside western Europe. This fact is particularly important in relation to the antiarchs, which are widely distributed and therefore potentially valuable as index fossils.

3. Age of *Asterolepis* and *Bothriolepis* in China

There is now good evidence that *Bothriolepis* first appears much earlier in southern China than in Europe, whilst *Asterolepis* may persist well into the Late Devonian. The stratigraphy of these occurrences is considered here in some detail as it is highly relevant both to the biostratigraphic interpretation of vertebrate-bearing Devonian strata in Australia and to our understanding of the general features of antiarch phylogeny.

Bothriolepis was first reported from China by Chi (1940), who described *B. sinensis* from the Lower Tiaomachien Series near Changsha in north-eastern Hunan Province, and on the stratigraphic range of *Bothriolepis* as it was then known, assigned a Late Devonian age to this occurrence. The local stratigraphy has since been studied in detail (P'an, 1958), and it is now established that the fish and plant bed occurs some 125 metres stratigraphically below the Upper Tiaomachien Series (Fig. 2), which contains a fauna including the corals *Calceola* and *Ceriophyllum* and the brachiopod *Leptostrophia maccarthyi* (Hamada, 1967). The Tiaomachien Series is successively overlain by the Chitzechiao Limestone with a Givetian *Stringocephalus burtini* fauna (Tien, 1938), and the Shetienchao Series with *Manticoceras wedekindi* (Sun, 1935) and *Phillipsastrea* and *Sinodisphyllum* (Sun, 1958; Hamada, 1960), of early Frasnian age (Fig. 2). The plants (*Protolepidodendron*) associated with *Bothriolepis* were dated as Middle Devonian by Sze (1946), and Plumstead (1972) has stated that proto-lycopods of this type may occur at least as early as Middle Devonian. The Upper Tiaomachien fauna is given an Eifelian age by Hamada (1967; his Table III, p. 592, erroneously places *B. sinensis* in the Givetian and contradicts his text, p. 591), and the Eifelian age of *B. sinensis* is thus clearly established. This represents the earliest known occurrence of the genus, and compares with the Eifelian appearance of *Gerdalepis* in the Mühlenberg beds of the Rhineland sequence, previously considered to be the earliest reliably-dated antiarch occurrence (Miles, 1967).

igure 2

EUROPEAN & CHINESE STAGES (After Hamada, 1967)	TIAOMACHIEN SECTION [N-E HUNAN PROVINCE] (Chi, 1940; P'an, 1958)	KUTSING-CHANYI REGION [EASTERN YUNNAN PROVINCE] (Wang, 1943 b)	WUTING REGION [YUNNAN PROVINCE] (Wang, 1943 b)	POSHI DISTRICT [S-E YUNNAN] (Wang, 1943 a, b)	LUNGTAN REGION, LOWER YANGTZE VALLEY [KIANGSU PROVINCE] (P'an, 1956)
TOURNAISIAN					KINLING LST. ? — ?
FAMENNIAN (HSIKWANGSHAN)					*Eochoristites, Neospirifer* *Asterolepis, Sinolepis* WUTUNG SERIES
FRASNIAN (SHETIENCHAO)	SHETIENCHAO SERIES *Manticoceras wedekindi*				?~~~? MAOSHAN SANDSTONE
GIVETIAN (TUNGKANGLING)	CHITZECHIAO LIMESTONE *Stringocephalus burtini*	? — ? *Stringocephalus burtini*	? — ? *Martinia*	? — ? *Stringocephalus burtini*	?~~~?
EIFELIAN (YÜKIANG)	UPPER TIAOMACHIEN *Calceola* LOWER TIAOMACHIEN *Bothriolepis sinensis*	*Martinia* *Meristella* *Schluteria* ? — ?	*Bothriolepis – Dianolepis – Wudinolepis* *Calceola, Rostrospirifer*	*Calceola, Bornhardtina* *Bothriolepis* *Protolepidodendron*	
LOWER DEVONIAN	? — ?	LUNGHUASHAN FORMATION (?) *Yunnanolepis, Galeaspis*	?~~~?	*Grypophyllum, Disphyllum* *Yunnanolepis, Galeaspis ?*	

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Fig. 2

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Antiarchs are also known from a number of localities in eastern Yunnan Province. The stratigraphy of these occurrences is inadequately described in the available literature, and some of the so-called "*Bothriolepis*-beds" probably represent the *Yunnanolepis*/*Galeaspis* fauna of possible Early Devonian age (Liu, 1963, 1965). However, *Bothriolepis tungseni* Chang has been described from Middle Devonian strata near Wuting by Chang (1965), where it is associated with the endemic antiarch genera *Wudinolepis* and *Dianolepis* (Fig. 2). Wang (1943 a,b) has described sections from this and other Yunnan fish localities, in which Eifelian corals occur above and below beds containing antiarchs and proto-lycopod plant remains, and it is probable that these occurrences correlate in a broad sense with the Eifelian *Bothriolepis* horizon in Hunan Province. It is noteworthy that there are no authenticated reports of *Bothriolepis* in the Chinese Upper Devonian, although a number of occurrences lack stratigraphic control, and *B. yunnanensis* Liu, for example, may be either Middle or Late Devonian in age (Liu, 1962). Hou & Xian (1964), in describing an early Givetian brachiopod fauna from the Poshi district of Yunnan, state in their English summary that the fauna underlies "*Bothriolepis*-beds of the Lunghuashan Formation". This in itself suggests a late Givetian or Frasnian age for the fish horizon, but since Hamada (1967) places the Lunghuashan Formation in the Lower Devonian, while Wang (1943a) lists the Givetian brachiopod *Bornhardtina* as occurring above the fish horizon in this area, the stratigraphic position and age of this occurrence remains uncertain.

Of equal stratigraphic importance to the early appearance of *Bothriolepis* is the single recorded occurrence of *Asterolepis* in China. P'an (1964) has described the species *A. sinensis* from the upper part of the Wutung Series near Lungtan, in the Lower Yangtze valley, Kiangsu Province. The endemic antiarch genus *Sinolepis* occurs in the same fauna (Liu & P'an, 1958). A Givetian/early Frasnian age has been proposed on the basis of the European stratigraphic range of *Asterolepis* (P'an, 1957; 1964), and Lao & P'an (1959) have also reported Late Devonian plants (Leptophloeum rhombicum and Sublepidodendron mirabile) from a bed two metres below the fish horizon at Nanking.

However, the Wutung flora was originally dated as Early Carboniferous by Gothan & Sze (1933), and more recently Sze (1956) has described a Lepidodendropsis, and Ho (1959) has listed a brachiopod assemblage including species of Neospirifer and Eochoristites from the same locality near Lungtan, both of which support an Early Carboniferous age. Although Ho gives no details of the stratigraphic relationship between the fish and brachiopod horizons in the Lungtan section they would appear to be closely associated, as the fish bed itself lies only 100 metres stratigraphically below the late Tournaisian Kinling Limestone (P'an, 1956). The sequence is apparently conformable and this occurrence must therefore be accepted as good evidence that the upper stratigraphic range of Asterolepis in China is higher than in Europe, and may even extend into the late Famennian.

4. Age of *Bothriolepis* in North America

In North America *Bothriolepis* is known from Ellesmere Island in Arctic Canada (Kiaer, 1915), the Appalachian region of Canada and the United States (Newberry, 1889; Eastman, 1899), and the southwest United States (Denison, 1951). The Arctic and Appalachian occurrences have not been dated on marine invertebrates but evidently extend well into the Late Devonian. In the northeastern United States the species *B. minor* Newberry and *B. nitida* (Leidy) have been recorded from various horizons, probably including Famennian strata, but neither species has been adequately described, and Denison (1951) has noted the possibility that *B. nitida* may be identical with *B. coloradensis* from the western United States. The well-known *B. canadensis* Whiteaves from the Escuminac Formation in Quebec is considered by Stensiö (1948) to be early Frasnian in age, but it is only in the western United States that *Bothriolepis* can be accurately dated on marine invertebrates.

Denison (1951) described the species *B. darbiensis* from the Darby Formation in west central Wyoming and reviewed the occurrence of *B. coloradensis* Eastman in the Elbert Formation of southwest Colorado, the Parting Member of the Chaffee Formation in central Colorado, and the Temple Butte Formation in northwest Arizona. Sandberg & Mapel (1967) also report *Bothriolepis* plates from the Souris River and Maywood Formations in Dakota and Montana, and Poole et al. (1967) note occurrences in the Bluebell Dolomite in Utah. In addition *Bothriolepis* has recently been found in Nevada (T.G. Morgan, pers. comm.).

Sandberg & Mapel (1967) and Poole et al. (1967) consider the fish-bearing strata to be of Frasnian age, but J.G. Johnson (1970) suggests that they should more correctly be referred to the Taghanic Stage, which includes part of both Givetian and Frasnian. He correlates the fish horizon with the *Leiorhynchus hippocastanea* brachiopod fauna which belongs to the *Schmidtognathus hermanni*/*Polygnathus cristatus* conodont Zone, which according to Ziegler (1971) spans the Middle/Late Devonian boundary. In Nevada *Bothriolepis* occurs with

Leiorhynchus and about 5 metres above a horizon yielding *hermanni-cristatus* Zone conodonts (T.G. Morgan, pers. comm.).

Asterolepis has also been reported from North America. Eastman (1907) identified the genus in material from the Chapman Sandstone in Maine, but Gross (1931, p. 59) has expressed doubt about the correctness of this identification. Denison (1968) has figured an asterolepid nuchal plate from the Middle Devonian of Idaho which he compares with the European genus *Pterichthyodes*, but the precise age of these beds is unknown.

Figure 3

EUROPEAN MARINE STAGES	CHINA	AUSTRALIA	NORTH AMERICA	EAST GREENLAND	SCOTLAND	BALTIC PROVINCE	GERMANY
TOURNAISIAN	?			?			
FAMENNIAN	*Asterolepis* *Sinolepis*	?	?	*Remigolepis* *Bothriolepis*	(? *Remigolepis*) ↑	↑	
FRASNIAN	?	*Remigolepis* *Bothriolepis* *Hillsaspis*	*Bothriolepis*	?	*Bothriolepis* (*Grossilepis*) *Asterolepis*	*Bothriolepis* (*Grossilepis*) *Asterolepis*	*Lepadolepis*
GIVETIAN	?	?	? ? *Pterichthyodes*	*Asterolepis*	*Asterolepis* *Pterichthyodes* *Microbrachius*	*Asterolepis* *Byssacanthus*	*Grossaspis* ↑
EIFELIAN	*Bothriolepis* *Dianolepis* *Wudinolepis*						*Gerdalepis*
EMSIAN	*Yunnanolepis*	? *Pterichthyodes*					
SIEGENIAN	?						

Fig. 3

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5. Australian Middle-Late Devonian placoderms

It is now possible to reassess the biostratigraphy of Bothriolepis and associated genera in Australia interms of the stratigraphic occurrence of antiarchs in other regions (see Figure 3). Locality information for the assemblages discussed below is given in Tomlinson's (1968) review of Australian Late Devonian fishes, and relevant stratigraphy for Upper Devonian occurrences in New South Wales is summarised in Conolly (1965).

Bothriolepis is the best-known and most widespread Australian form, being reported from southeast, central and northwest Australia. The various occurrences are still largely undescribed, however, and with the assignment of Bothriolepis gippslandiensis Hills from Victoria to the new genus Hillsaspis (Stensiö, 1969, p.508), there is no currently named Australian species of the genus. Asterolepis is apparently much less common than Bothriolepis, and both the reported occurrences (McCoy, 1876; Hills, 1958; see also Hill et al., 1967) are based on probably erroneous identifications. However, fragmentary remains which may be tentatively ascribed to Asterolepis occur with Bothriolepis in material now under study from the Knobby Sandstone in the northeast Canning Basin (Veevers et al., 1967).

In eastern Australia Bothriolepis is associated with the genera Remigolepis, Phyllolepis, and Groenlandaspis, suggesting strong faunal affinities with the Late Devonian of eastern Greenland (Hills, 1958). It must be emphasized, however, that there is little detailed knowledge of faunal composition or of any differentiation into a faunal succession even at generic level, and consequently only general biostratigraphic conclusions can be reached at this stage. New evidence tends, if anything, to confuse the issue further, as the age of associated invertebrates and consideration of Chinese antiarch occurrences suggest earlier dates for the fish faunas, in apparent contradiction to the late Famennian age indicated by the presence of Remigolepis, Phyllolepis, and Groenlandaspis. There are, however, reasonable theoretical arguments, although as yet no substantial evidence, that these three genera may appear earlier in Australia than in Europe.

Before discussing these problems in detail, it should first be mentioned that the isotopic age of 362 ± 6 m.y. (McDougall et al., 1966) for the Taggerty fish fauna of eastern Victoria (Hills, 1929; 1931) can no longer be maintained on palaeontological evidence to correspond to the Devonian-Carboniferous boundary; the conclusions reached below suggest that this age more probably approximates the Middle-Late Devonian boundary. This contention is supported by two similar isotopic ages for rocks in eastern Queensland (the Retreat Granite and Mount Morgan Tonalite) which intrude Givetian and/or are unconformably overlain by Upper Devonian sediments (Webb & McDougall, 1968; p. 318, 330), and is in agreement with the Middle - Late Devonian absolute age proposed by Friend & House (1964). There is however more recent evidence to the contrary (Francis, 1971) and further data are required to clarify the point.

Palaeontological evidence relating to the age of Australian fish faunas may now be considered in detail under the following headings:-

(a) Age of associated invertebrate faunas.

In her review of Australian Late Devonian fishes, Tomlinson (1968, p.212) concluded, largely on an assessment of the age of the Late Devonian Cyrtospirifer fauna in New South Wales, that late Frasnian was the earliest likely age for the appearance of Bothriolepis in Australian sequences.

More recently, however, Roberts et al. (1972) have listed an invertebrate assemblage from the Merimbula Formation in eastern New South Wales which contains, in addition to Cyrtospirifer spp., the brachiopods Ladjia cf. L. saltica Veevers, an early Frasnian zone fossil from the Canning Basin, and Cyphoterorhynchus, which occurs in the Frasnian of the Carnarvon Basin. Furthermore, of the three Cyrtospirifer species originally determined by Mackay (1964) from Mount Lambie, C. gneudnaensis Glenister also occurs in the Carnarvon Basin Frasnian, C. inermis (Hall) extends right through the Upper Devonian of the Catskill Delta sequence in the eastern United States, and only

C. oleanensis Greiner is apparently restricted to the Late Devonian and Early Mississippian (Greiner, 1957). The recent discovery of abundant Atrypa associated with Cyrtospirifer near Marulan, New South Wales, is further evidence of a Frasnian age for the assemblage (P.H. Creaser, pers. comm.).

The fish and brachiopod horizons appear to be closely associated. South of Braidwood, New South Wales, fishplates occur about 300 metres stratigraphically above the Cyrtospirifer zone (N.E.A. Johnson, 1964) whilst at Wellington in the Catombal Group they have been found above and within, and near Cargo within and below, the brachiopod horizon. Bothriolepis is definitely known to occur in these horizons at Mount Canoblas (Hills, 1932) and at Krawaree (Johnson, 1964). At the latter locality it is associated probably with Phyllolepis and possibly with Remigolepis.

(b) Stratigraphic significance of Bothriolepis.

A species of Bothriolepis is now known to occur in the Gogo Formation of the Canning Basin (Miles, 1971b), which is dated on conodonts as basal Frasnian (to 1α) in age (Seddon, 1970), and may extend down into the Givetian (E.C. Druce, pers. comm.). Confirmation that the New South Wales Cyrtospirifer fauna is also early Frasnian would indicate a similar first appearance in the southeast Australian sequence, suggesting that, as in Europe, Bothriolepis is restricted to the Late Devonian.

However, Chang (1965) has commented on the close similarity between the bothriolepid genera Hillsaspis from Victoria and Dianolepis from the Eifelian of southern China, and recent studies have shown a possible relationship between B. kwangtungensis from the Middle Devonian of central southern China and a new Bothriolepis species from the Knobby Sandstone in north western Australia. A further indication of Chinese affinity is the occurrence of antiarchs (cf. Pterichthyodes) in the Early Devonian fauna from Taemas, New South Wales (Hills, 1958, p. 88), together with new forms showing both antiarchan and arthrodiran affinities. In view of the existence of primitive antiarchs in the Chinese Lower and Middle Devonian, and the Eifelian appearance of *Bothriolepis* in southern China, it is evident that the tacitly-assumed restriction of *Bothriolepis* to the Frasnian/Famennian part of the Australian sequence may require revision.

The upper limit of *Bothriolepis* in Australia is notknown, but in the absence of contrary evidence, its association with *Remigolepis* and *Phyllolepis* may be taken to indicate that it extends well into the Famennian, as it does in Europe.

(c) The stratigraphic significance of *Remigolepis*.

The antiarch *Remigolepis* was first described by Stensiö (1931) from the Upper Devonian of East Greenland, where it occupies a zone above the arthrodire *Phyllolepis* and beneath *Groenlandaspis*. Hills (1932) first noted its Australian occurrence, and it has recently been reported from Scotland (Miles, 1968).

From published accounts and an examination of original and more recent collections it now appears that *Remigolepis* is definitely known in Australia only from the Hervey Group in central NSW New South Wales. It may also occur south of Braidwood, New South Wales (Johnson, 1964), but this requires checking. Its Victorian occurrence (Hills, 1932, p. 853) is doubtfully based on an isolated mixilateral plate with *Remigolepis*-like overlap areas, which probably belongs to *Bothriolepis*.

Numerous fish horizons occur throughout the Hervey Group, but they are poorly known. *Remigolepis* occurs in the lowermost Mandagery Sandstone and equivalents in the Nangar Subgroup of Conolly's (1965) Central Province, where it is associated with *Bothriolepis* and *Phyllolepis*. Conolly equates the basal Beargamil Subgroup of the Central Province with the *Cyrtospirifer* horizons in the Lambie and Catombal Groups of the Eastern Province, and if this is accepted, the *Remigolepis*/*Bothriolepis* assemblage would broadly correlate with the fish horizons within and above the *Cyrtospirifer*-Zone. Taking into account the possible early Frasnian age of the *Cyrtospirifer*-fauna, it follows that on present interpretations of New South Wales Upper Devonian stratigraphy, *Remigolepis*, like *Bothriolepis*, makes its first appearance in the Frasnian.

This evidence supports the earlier suggestion by Tomlinson (1968, p.213) that *Remigolepis* may have appeared earlier in Australia than in the type area of east Greenland. Alternatively the base of the *Remigolepis* series in Greenland may be somewhat older than previously assessed, and this point should be clarified when the stratigraphic relationships of *Remigolepis* in Scotland have been elucidated, as its presence suggests that the Scottish sequence should encompass any time gap between the Baltic and Greenland successions (Fig. 3). It should be noted, however, that from a phylogenetic point of view, an early Australian appearance of *Remigolepis* is not unreasonable. Although Stensiö (1931, 1948) has classified the genus in a separate order because it lacks a distal joint in the pectoral fin, Gross (1965) has pointed out that in its other characters *Remigolepis* conforms closely to the Asterolepididae. He concludes, on the basis of pectoral fin abnormalities in *Asterolepis* suggestive of the fin structure in *Remigolepis*, that the absence of the distal joint is secondary, and that *Remigolepis* is derived from asterolepid stock. If this is accepted, the apparent hiatus in European sequences between the upper range of *Asterolepis* and the first appearance of *Remigolepis* cannot reflect a continuous phylogenetic lineage, and both younger *Asterolepis* (as indicated in China) and older *Remigolepis* occurrences might reasonably be expected.

(d) The stratigraphic significance of *Phyllolepis*.

The highly specialized arthrodire *Phyllolepis* is characteristic of the youngest vertebrate horizons in the Devonian of Europe. In Scotland it occurs only 50 metres below the base of the Carboniferous (Westoll, 1951) and in northwest Russia, Latvia, and Belgium it is restricted to the Famennian (Vasiliauskas, 1963; Tarlo, 1964; Miles, 1968). In Greenland it occupies a stratigraphic position beneath the zone of *Remigolepis* (Jarvik, 1961). Fragmentary remains of *Phyllolepis* also occur in North America and Antarctica, but it is not known in China. In all these areas it is commonly associated with *Bothriolepis*, and in the Greenland sequence it also occurs with *Remigolepis* in the basal beds of the "*Remigolepis* series."

In Australia the characteristic *Phyllolepis* ornamentation was first recognised in the Mansfield region of Victoria by Hills (1931) and subsequently reported in the Hervey Group in New South Wales (Hills, 1936). It has also been reported from Krawaree, New South Wales (Johnson, 1964), and the Dulcie Range in the Northern Territory (Hills, 1959).

More recently however, a possibly Middle Devonian vertebrate assemblage, which includes the new genus *Wuttagoonaspis* with phyllolepid-type ornamentation, has been discovered in the Mulga Downs Group in western New South Wales (Fletcher, 1964; Ritchie, 1973). The ornament of *Wuttagoonaspis* demonstrates that caution must be exercised in ascribing fragmentary remains to *Phyllolepis*, although it has now been confirmed that *Phyllolepis* does in fact occur in the Mansfield sequence in Victoria (Professor J.W. Warren, pers. comm.), and the Jemalong Range in New South Wales (M.W. Bell, pers. comm.).

An interesting point regarding the stratigraphic range of *Phyllolepis* is raised by the apparent absence of heterostracan agnathans in the Australian Devonian. It has long been recognized that *Phyllolepis* is adaptively similar in body form to the psammosteid heterostracans which were prolific in European vertebrate faunas during the Givetian and Frasnian. The appearance of *Phyllolepis* immediately after the psammosteids disappear at the top of the Frasnian (Tarlo, 1964; Miles, 1968) suggests convergent specialization in the phyllolepid lineage to replace the adaptively similar psammosteids.

Although the arthrodiran affinities of *Phyllolepis* are well established (Stensiö, 1934; 1936), its ancestry is obscure, and Miles (1971a) has suggested that *Wuttagoonaspis* could be a related form, although Ritchie (1973) considers the latter to have petalichthyid rather than phyllolepid affinities. Whether or not such a relationship is confirmed, the presence of psammosteids in the Upper Devonian of Australia has yet to be demonstrated (although according to

Tarlo (1964) they may occur in Antarctica), and the earlier appearance of *Phyllolepis* or related forms in Australian sequences is therefore a distinct possibility.

(e) The stratigraphic significance of *Groenlandaspis*.

The arthrodire *Groenlandaspis* was originally described by Heintz (1930) and Stensiö (1934, 1939) from East Greenland, where it occupies the uppermost vertebrate horizon, above the zones of *Bothriolepis* and *Remigolepis*. Westoll (1951) has suggested that its age may be Early Carboniferous.

In Australia fragmentary remains of the genus were first reported by Rade (1964) from the Mulga Downs Group of western New South Wales. The presence of this or a closely related form has now been confirmed in both the Mulga Downs and Hervey Groups (A. Ritchie, pers. comm.). The stratigraphic implications of this are not clear, as in other respects the Mulga Downs and Hervey Group faunas are quite distinct, but again it can be argued that a more extended stratigraphic range than is indicated by the Greenland sequence is not unlikely.

Groenlandaspis, although poorly known, is generally considered to be a somewhat specialized dolichothoracid arthrodire. The Dolichothoraci reached their acme in the Emsian/Eifelian but were then rapidly replaced by other groups (Miles, 1969), and apart from a reported *Phlyctaenaspis* in the Frasnian of the eastern United States (Denison, 1950), *Groenlandaspis* is the only Late Devonian representative of the suborder. Nevertheless its affinities and stratigraphic occurrence show that the fossil record of this group is incomplete, and recent discoveries of abundant dolichothoracids in the Upper Devonian of Antarctica confirm that until the stratigraphic significance of other Late Devonian dolichothoracids is determined, *Groenlandaspis* cannot be utilized as a reliable indicator of the latest Devonian in Australian successions.

6. Conclusions

The evidence as it stands indicates that detailed European correlations based on placoderms cannot be assumed to apply to extra-European continental successions. The following facts, however, seem to be established:-

a) In northwestern Australia, the Baltic and Leningrad regions of Russia, and Nevada in the western United States, associated marine assemblages (including conodonts) show that *Bothriolepis* first appears at least as early as late Givetian or early Frasnian.

b) On similar evidence the youngest species of *Asterolepis* reported from the Baltic succession is early Frasnian in age.

c) In China, invertebrate evidence indicates that *Bothriolepis* first appears in the Eifelian, and that *Asterolepis* may persist well into the Famennian.

d) In Australia the antiarchs *Bothriolepis* and *Remigolepis* and the arthrodires *Phyllolepis* and *Groenlandaspis* apparently lack the temporal significance that they show in the European Late Devonian. Associated invertebrates suggest that *Remigolepis*, *Phyllolepis* and *Groenlandaspis* may appear earlier than in Europe, and on Chinese evidence the same may apply to Australian species of *Bothriolepis*.

The need for comprehensive taxonomic studies of extra-European Devonian vertebrate faunas is clearly evident, and there is little doubt that current concepts on the spacial and temporal distribution of the Placodermi as a whole will require extensive revision when Australian and Chinese faunas are adequately described. It is to be hoped that this will lead not only to a workable vertebrate biostratigraphy for Devonian continental deposits throughout the world, but also toward an understanding of the phylogenetic and palaeogeographic implications of Devonian fish distributions.

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7. References

ARONOVA, S.M., et al., 1967: Devonian of the Russian Platform. **1**, 379-96 in Oswald, D.H. (1967) which see.

BOUCOT, A.J., JOHNSON, J.G. & STRUVE, W. 1966: *Stringocephalus*, Ontogeny and Distribution - J. Paleontol. **40** 1349-64.

CHANG, K.J. 1965: New Antiarchs from the Middle Devonian of Yunnan - Vertebr. Palasiatica **9** 1-14.

CHI, Y.S. 1940: On the discovery of *Bothriolepis* in the Devonian of central Hunan - Bull. geol. soc. China **20**(1) 57-71.

CONOLLY, J.R. 1965: The stratigraphy of the Hervey Group in central New South Wales - J. Proc. R. Soc. NSW **98** 37-84.

DENISON, R.H., 1950: A new arthrodire from the New York State Devonian - Amer. J. Sci., **248** 565-80.

------------- 1951: Late Devonian freshwater fishes from the western United States - Fieldiana, Geol. **11** 221-61.

DENISON, R.H. 1968: Middle Devonian fishes from the Lemhi Range of Idaho Ibid. 16 269-88.

EASTMAN, C.R. 1899: Upper Devonian fish fauna of Delaware Country, N.Y. - 17th ann. Rept. N.Y. State Geol. 1897 317-27.

__________ 1907: Devonic fishes of the New York formations - Mem. N.Y. State Mus., 10 1-235.

EICHWALD, E.I. von, 1840: Die Thier- und Pflanzenreste des alten rothen Sandsteins und Bergkalks im Novgorodschen Gouvernment. - Bull. Acad. Sci. St. Petersburgh, 7, 78-91.

FLETCHER, H.O. 1964: New linguloid shells from Lower Ordovician and Middle Palaeozoic rocks of New South Wales - Rec. Aust. Mus. 26(10) 283-94.

FRANCIS, E.H., 1971: British basalts. Item 360 in The Phanerozoic Time-scale - a supplement. - Special Publication of the Geological Society No. 5, London. 73-4.

FRIEND, P.F. 1961: The Devonian stratigraphy of north and central Vestspitzbergen - Proc. Yorks. geol. Soc. 33 77-118.

______ & HOUSE, M.R. 1964: The Devonian Period in The Phanerozoic Time-scale. - geol. Soc. London, supplement to quarterly journal 120S, 233-6.

GOTHAN, W. & SZE, H.C. 1933: Ueber die Palaeozoische Flora der Provinz Kiangsu - Mem. nat. Res. Inst. Geol. 13, Acad. Sin.

GREINER, H. 1957: "*Spirifer disjunctus*": its evolution and paleoecology in the Catskill Delta - Peabody Mus. nat. Hist. Yale Uni. Bull 11 1-71.

GROSS, W. 1931: *Asterolepis ornata* Eichw. und das Antiarchi - problem - Palaeontogr. 75 1-62.

________ 1933: Die Fische des baltischen Devons. - Palaeontogr. 79(A), 1-74.

________ 1940: Acanthodier und Placodermen aus den *Heterostius* - Schichten Estlands und Lettlands. - Tartu Uelik., Lood. Selts. Aruand. 46, 12-98.

GROSS, W. 1941: Die *Bothriolepis* - arten der *Cellulosa* - Mergel Lettlands. - K. svenska. Vetensk Akad. Handl. (3) 19, 1-79.

________ 1942: Die Fischfauna des baltischen Devons. - Korresp Bl. Naturf Ver. Riga, 64, 373-436.

__________ 1950: Die paläeontologische und stratigraphische Bedeutung der Wirbeltierfaunen des Old Reds und der marinen altpaläozoischen Schichten - Abh. dt. Akad. Wiss. Berl. Math. - Nat. Kl. 1949 1-130.

__________ 1965: Uber die Placodermen - Gattungen *Asterolepis* und *Tiaraspis* aus dem Devon Belgiens und einen fraglichen *Tiaraspis* - Rest aus dem Devon Spitzbergens - Bull. Inst. R. Soc. nat. Belg. 41 1-19.

HAMADA, T. 1960: The Middle Palaeozoic Formations in China and Korea II Northwest and South China. - Japan. J. Geol. Geogr. 31 219-39.

__________ 1967: Devonian of East Asia. 1 583-98 in Oswald, D.H. (1967) which see.

HEINTZ, A. 1930: Oberdevonische Fishreste aus Ost - Groenland. - Skr. Svalbard. Ishavet. 30 31-46.

HILL, D., et. al. (Editors) 1967: Devonian fossils of Queensland - Qd Palaeontogr. Soc. Brisbane.

HILLS, E.S., 1929: The geology and palaeontography of the Cathedral Range and Blue Hills in northwestern Gippsland. - Proc. R. Soc. Victoria 41, 176-201.

__________ 1931: The Upper Devonian fishes of Victoria, Australia, and their bearing on the stratigraphy of the state. - geol. Mag., 68 206-31.

__________ 1932: Upper Devonian fishes from New South Wales. - Quart. J. geol. Soc. 88 850-8.

__________ 1936: Records and descriptions of some Australian Devonian fishes - Proc. R. Soc. Victoria 48 (N.S.) 161-71.

__________ 1958: A brief review of Australian fossil vertebrates. in Westoll, T.S. (Editor), Studies on Fossil Vertebrates. London, Athlone Press.

__________ 1959: Record of *Bothriolepis* and *Phyllolepis* (Upper Devonian) from the Northern Territory of Australia. - J. R. Soc. N.S.W. 92 174-5.

HO, H.L. 1959: Some new materials of Lower Carboniferous fossils from Lungtan of Nanking with a discussion of the age of the Wutung Series - Acta. Palaeontol. Sin. **7** 319-28 (in Chinese with English summary).

HOU, H.F. & XIAN, S.Y. 1964: Brachiopod fauna of the Nanpanjiang Limestone of Eastern Yunnan and its geological age. Ibid. **12** 411-26 (in Chinese with English Summary).

HOUSE, M.R., 1973: Delimitation of the Frasnian. Acta Geol. Pol. **23**, 1-14.

JARVIK, E. 1961: Devonian vertebrates. *in* Raasch, G.O. (Editor), Geology of the Arctic. University of Toronto Press.

JOHNSON, J.G. 1970: Taghanic onlap and the end of North American Devonian provinciality - geol. Soc. America Bull. **81** 2077-105.

JOHNSON, N.E.A. 1964: The geology of the Krawaree area, New South Wales - M.Sc. Thesis, Australian National University. (unpubl.)

KARATAJUTE - TALIMAA, V.N. 1958: Asterolepids of the Devonian of SSSR and their stratigraphic distribution - Akad. nauk. SSSR paleontol. Inst. Moscow 1958, 1-18 (In Russian).

__________________ 1963: Genus *Asterolepis* from the Devonian of the Russian Platform *in* Grigelis, A. & Karatajute-Talimaa, V. (Editors) The data of Geology of the Lithuania. Vilnius. (In Russian with Lithuanian and English summaries).

KIAER, J.A. 1915: Upper Devonian fish remains from Ellesmere Land, with remarks on *Drepanaspis*. Rep. 2nd Norweg. Arct. Exped. Fram. **33** 1-56.

LAHUSEN, J. 1880: Zur Kenntniss der Gattung *Bothriolepis* - Eich. Zap. vseross. miner. Obschch., (2) **15**, 125-38.

LAO, H. & P'AN, P. 1959: Discovery of *Leptophloeum rhombicum* from the Wutung Series in the vicinity of Nanking and its stratigraphic significance - Geol. Review. **19**(7) (in Chinese).

LIASHENKO, A.I. & LIASHENKO, G.P. 1967: Correlation of Devonian deposits of the Russian Platform and the western slope of the Urals. 2, 511-24 in Oswald D.H. (1967) which see.

LIU, T.S. & P'AN KIANG, 1958: Devonian fishes from the Wutung Series near Nanking, China. - Palaeontol. Sinica 141 (N.S. C15) 1-41.

LIU, Y.H. 1962: A new species of Bothriolepis from Yunnan - Vertebr. palasiat. 6 80-5 (in Chinese with English summary).

________ 1963: On the Antiarchi from Chutsing. Yunnan - Ibid. 7 39-46. (In Chinese and English).

________ 1965: New Devonian agnathans of Yunnan. - Ibid 9 125-40. (In Chinese and English).

MACKAY, R.M. 1964: Lepidophloios and Cyrtospirifer from the Lambie Group at Mount Lambie, NSW. - J. Proc. R. Soc. NSW 97 83-9.

McCOY, F. 1876: Asterolepis ornata (Eichwald) var. australis (McCoy) - Prodromus of the Palaeontology of Victoria. Dec. iv 19, 20. Melbourne, G. Skinner. London, Trubner & Co.

McDOUGALL, I. et al., 1966: Isotopic age determinations on Upper Devonian rocks from Victoria, Australia: a revised estimate for the age of the Devonian-Carboniferous boundary. - Bull. geol. Soc. Amer. 77, 1075-88.

MILES, R.S. 1967: Class Placodermi in Harland W.B. et. al. (Editors). The Fossil Record. - Geol. Soc. London.

__________ 1968: The Old Red Sandstone antiarchs of Scotland. Family Bothriolepididae. - Palaeontog. Soc. (Monogr.) 122 1-130.

__________ 1969: Features of placoderm diversification and the evolution of the arthrodire feeding mechanism - Trans. R. Soc. Edinb. 68 123-70.

__________ 1971a: Palaeozoic Fishes, by J.A. Moy-Thomas (2nd ed. revised by R.S. Miles) London. Chapman and Hall.

__________ 1971b: Paleozoic fish. McGraw-Hill Yearbook of Sci. & Tech. 1971 312-14.

NEWBERRY, J.S. 1889: The Palaeozoic fishes of North America - Monogr. U.S. Geol. Surv. 16 1-340.

NILSSON, T. 1941: The Downtonian and Devonian vertebrates of Spitzbergen 7. Order Antiarchi - Skr. Svalbard. Ishavet. 82 1-54.

OBRUCHEV, D.V. 1951: On the boundary of the Middle and Upper Devonian in the Main Field - Dokl. Akad. Nauk. SSSR 78 981-4 (in Russian).

____________ 1958: On the biostratigraphy of the Lower and Middle Palaeozoic ichthyofaunas of the USSR - Sov. Geol. 11 40-53 (in Russian with English Summary).

____________ 1964: Class Placodermi in Fundamentals of Palaeontology, 11, 1-522 (ed. D.V. Obruchev) Moscow. (English translation, 1967, Israel program for scientific translations).

OSWALD, D.H. (Editor) 1967: International Symposium on the Devonian System, Calgary 1967. 2 vols. Alberta Society of Petroleum Geologists, Calgary.

P'AN, K. 1956: On the Palaeozoic stratigraphy of the Nanking Hills - Sci. Sin. 4 543-60.

________ 1957: The correlation and age of the Wutung Series of the lower Yangtze valley, and with a special discussion of the first discovery of Asterolepis in China. - Acta Geol. Sin. 37 457-73 (in Chinese with English summary).

________ 1958: On the age of the Tiaomachien Series of Hunan - Ibid 38 135-44. (In Chinese with English summary).

________ 1964: Some Devonian and Carboniferous fishes from south China - Acta. Paleontol. Sin. 12 139-83 (in Chinese with English summary).

PANDER, C.H. 1846: Page 292 in KEYSERLING, A., 1846, Wissenschaftliche Beobachtungen auf einer Reise in das Petschora-Land. St. Petersberg.

PLUMSTEAD, E.P. 1972: Three thousand million years of plant life in Africa - Alex L. du Toit mem. lect. 11. Geol. soc. S. Afr. 1-72.

POOLE, F.G. et al. 1967: Devonian of the southwestern United States. 1, 879-912 in Oswald D.H. (1967) which see.

RADE, J. 1964: Upper Devonian fish from the Mt Jack area New South Wales, Australia - J. Paleontol. 38 929-31.

RITCHIE, A. 1973: Wuttagoonaspis gen. nov., an unusual arthrodire from the Devonian of western New South Wales, Australia. - Palaeontogr. 143(A), 58-72.

ROBERTS, J. et al. 1972: Correlation of the Upper Devonian Rocks of Australia - J. geol. Soc. Aust. 18 467-90.

ROHON, J.V., 1900: Die devonischen Fische von Timan in Russland. - Prag. Böhm. Ges. Wiss. Sitz. ber.

RZHONSNITSKAYA, M.A. 1967: Devonian of the U.S.S.R. 1, 331-48. in Oswald, D.H. (1967) which see.

SANDBERG, C.A. & MAPEL W.J. 1967: Devonian of the northern Rocky Mountains and plains. 1, 843-78 in Oswald, D.H. (1967) which see.

SEDDON, G. 1970: Frasnian conodonts from the Sadler Ridge - Bugle Gap area, Canning Basin, Western Australia - J. geol. Soc. Aust. 16 723-53.

STENSIÖ, E.A. 1931: Upper Devonian vertebrates from East Greenland, collected by the Danish Greenland expedition in 1929 and 1930. - Medd. Grønland 96 1-212.

__________ 1934: On the Placodermi of the Upper Devonian of East Greenland. 1. Phyllolepida and Arthrodira - Ibid. 97 1-58.

__________ 1936: On the Placodermi of the Upper Devonian of East Greenland. Supplement to part 1. - Ibid. 97 1-52.

__________ 1939: On the Placodermi of the Upper Devonian of East Greenland. 2nd Supplement to part 1 - Ibid. 97 1-33.

__________ 1948: On the Placodermi of the Upper Devonian of East Greenland. 2. Antiarchi: Subfamily Bothriolepinae. With an attempt at a revision of the previously described species of that family - Ibid 139 1-622.

STENSIÖ, E.A. 1969: Elasmobranchiomorphi: Placodermata: Arthrodires. *in* Piveteau, J. (Editor) Traité de Paleontologie *4*(2) 71-692.

STENSIÖ, E.A. & SÄVE-SÖDERBERGH, G. 1938: Middle Devonian vertebrates from Canning Land and Wegener Peninsula (East Greenland) Pt 1. Placodermi, Ichthyodorulites - Medd. Grønland *96* 1-38.

SUN, Y.C. 1935: On the occurrence of the *Manticoceras* fauna in central Hunan. - Bull. geol. Soc. China **14** 249-52.

________ 1958: The Upper Devonian coral faunas of Hunan - Palaeontol. Sin. *8* (N.S.B.).

SZE, H.C. 1946: On the age of the *Protolepidodendron* and *Bothriolepis* - bearing Formation in southwestern China - Bull. geol. Soc. China **24** 211-5.

________ 1956: On some specimens of *Lepidodendropsis hirmeri* Lutz from the Wutung Series of the province Kiangsu. - Acta. Palaeontol. Sin. *4*(1) 52-7 (In Chinese with English summary).

TARLO, L.B.H. 1961: Psammosteids from the Middle and Upper Devonian of Scotland - Q. J. geol. Soc. Lond. **117** 193-213.

________ 1964: Psammosteiformes (Agnatha). A review with descriptions of new material from the Lower Devonian of Poland. 1. General part - Palaeontol. Pol. **13** 1-135.

TIEN, C.C. 1938: Devonian Brachiopoda of Hunan - Palaeontol. Sin. *4* (N.S.B.) 1-192.

TOMLINSON, J.G. 1968: A new record of *Bothriolepis* in the Northern Territory of Australia - Bur. Miner. Resour. Aust. Bull. **80** 191-224.

TRAQUAIR, R.H. 1895: The extinct vertebrate animals of the Moray Firth area. *in* Harvie Brown J.A. & Buckley T.E. A vertebrate fauna of the Moray Basin. London, Cambridge and Glasgow.

VASILIAUSKAS, V. 1963: Phyllolepis tolli sp. nov. and some questions of the stratigraphy of the Famennian deposits in the Baltic area. in Grigelis, A. & Karatajute - Talimaa, V. (Editors). The data of geology of the Lithuania. Vilnius (In Russian with Lithuanian and English summaries).

VEEVERS, J.J., et. al. 1967: Sandstone of probable Lower Carboniferous age in the north-eastern Canning Basin, W.A. - Aust. J. Sci. 29(9) 330-1.

WANG, H.C. 1943a: The Middle Devonian Rugose corals of Eastern Yunnan - Sci. Rec. 1 555-61.

________ 1943b: The stratigraphic position of the Devonian fish-bearing series (Bothriolepis bed) of Eastern Yunnan. Ibid 1 562-64.

WATSON, D.M.S. 1932: On three new species of fish from the Old Red Sandstone of Orkney and Shetland - Summary of Progress for 1931, Mem. geol. Surv. 157-63.

WEBB, A.W. & McDOUGALL, I. 1968: The geochronology of the igneous rocks of eastern Queensland. - J. geol. Soc. Aust. 15, 313-46.

WESTOLL, T.S. 1951: The vertebrate bearing strata of Scotland - Int. Geol. Congr. 1948, 18(2) 5-20.

ZIEGLER, W. 1971: European Devonian conodont stratigraphy. in Sweet, W.C. & Bergström, S.M. (Editors): Symposium on Conodont Biostratigraphy. - geol. Soc. Amer. Mem. 127, 227-84.

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CAPTIONS FOR FIGURES 1-3

Figure 1: Correlation of the Baltic vertebrate succession with the Russian Platform marine sequence.

Stratigraphic ranges of psammosteid and antiarch genera and species of *Asterolepis* and *Bothriolepis* are shown on the left. Species on which correlations are based are shown in boxes on the right.

References to Figure 1 in text-p. 3.

Position of Figure 1 in Manuscript-p. 4.

Figure 2: Stratigraphic occurrence of antiarchs in Southern China.

References to Figure 2 in text-pp. 7, 8.

Position of Figure 2 in Manuscript-p. 7.

Figure 3: Stratigraphic occurrence of antiarchs in different regions. For completeness 15 of the 17 genera listed by Stensiö (1969, p. 669) are included, although stratigraphic details on many of these are uncertain. Both *Cypholepis* Gross and *Taeniolepis* Gross (Obruchev, 1964, p. 163, 165) are doubtful genera and have been excluded.

References to Figure 3 in text-p. 12.

Position of Figure 3 in manuscript-p.11.