DEVONIAN IN THE EASTERN HEMISPHERE[1]

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INTRODUCTION

It was the prescient recognition by WILLIAM LONSDALE that corals from the limestones of South Devon were intermediate in type between those then known from the Silurian rocks of the Welsh Borders and those from the Mountain Limestone [Mississippian] that led, in April, 1839, to the founding of the Devonian System by ADAM SEDGWICK and RODERICK MURCHISON (1839a, p. 259, 354; 1839b, p. 121; LONSDALE, 1840, p. 721). This correlation between the marine rocks of Devon and the Old Red Sandstone of Wales, the Welsh Borders, and Scotland WILLIAM BUCKLAND hailed as "undoubtedly the greatest change which had ever been attempted at one time in the classification of British rocks" (GEIKIE, 1875, p. 269). After spending four months of the summer and autumn of 1839 on the Continent, SEDGWICK and MURCHISON were able to recognize the excellent development of the new system along the Rhine valley and Schiefergebirge. In late 1839, MURCHISON proceeded to Russia where, in the Leningrad region, he observed the intercalation of Devonian marine levels within typical Old Red Sandstone sequences. Thus, in an incredibly short time, the new system was recognized and broadly correlated over wide areas of Europe (Fig. 1). Subsequently, knowledge has grown considerably, owing its growth to no small extent to the German school of geologists and paleontologists centered in the several universities that surround the varied Devonian rocks of the Rhenish Schiefergebirge.

This contribution is concerned solely with invertebrates of the Devonian, especially those that have a bearing on broad biogeographical problems. A recent review of Devonian floras was given by EDWARDS (in HALLAM, 1973) and one on Devonian fish by HALSTEAD and TURNER (in HALLAM, 1973). Invertebrates of the Old Red Sandstone facies are similar to those reviewed for the Western Hemisphere by NORRIS (this volume, p. *A*218), and especially various groups of arachnids, scorpions, and early insects add interest to the fauna. But for details on these, and the many groups not discussed here, reference should be made to the appropriate volume of the *Treatise.*

FACIES PATTERNS IN THE EUROPEAN DEVONIAN

The existence of distinct facies regimes in the Devonian, as in other systems, heightens the problems of zonal correlation, paleoecological interpretation, and the recognition of faunal provinces. Because a clarification of these is an essential background to biogeographical analysis, and because in the European Devonian literature several peculiar facies terms are in current usage, a general discussion of facies patterns is an important preliminary to the biogeographical review.

The major facies regimes of continental fluvial facies, nearshore clastic facies, and offshore clear-water facies are known in the European Devonian as the Old Red Sandstone, Rhenish and Hercynian or Bohemian magnafacies (ERBEN, 1964). Some difficulties result from different uses of the last two terms (BROUWER in OSWALD, 1968b, p. 1149), and concern has been expressed that the Rhenish-Hercynian distinction, which is clearly seen in the Lower Devonian of Germany, becomes less clear upward in the succession. The truth is, however, that reef and associated carbonates are almost unknown in the Devonian from the late Frasnian onward; excepting this the distinction remains valid. The accompanying facies transect illustrates the model that has been proposed by SCHMIDT, RABIEN, KREBS, and others to explain the relationships of the facies types (Fig. 2). In some usages the Rhenish facies would include all the neritic environments there marked, in others the reef and associated facies would be included with the Hercynian or Bohemian facies.

It is only the carbonate and basinal facies having a Devonian terminology that need be commented upon here.

For the carbonate complexes KREBS (1974) distinguished the *Schwelm* facies as a bank or biostrome regime in which

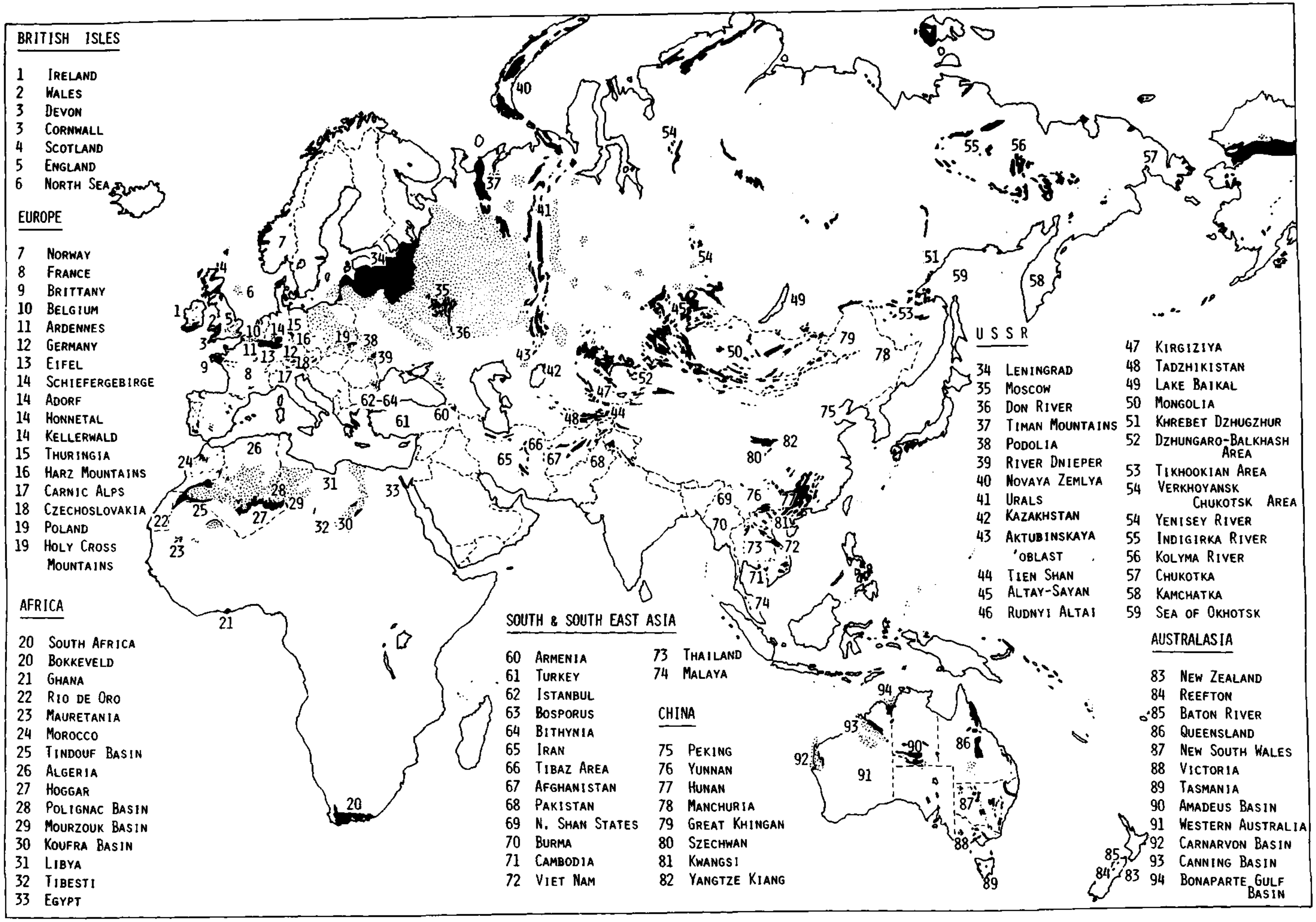


FIG. 1. Main areas of Devonian rocks in the Eastern Hemisphere and localities referred to in the text (House, n). [Outcrops are in black and known subsurface occurrences are stippled.]

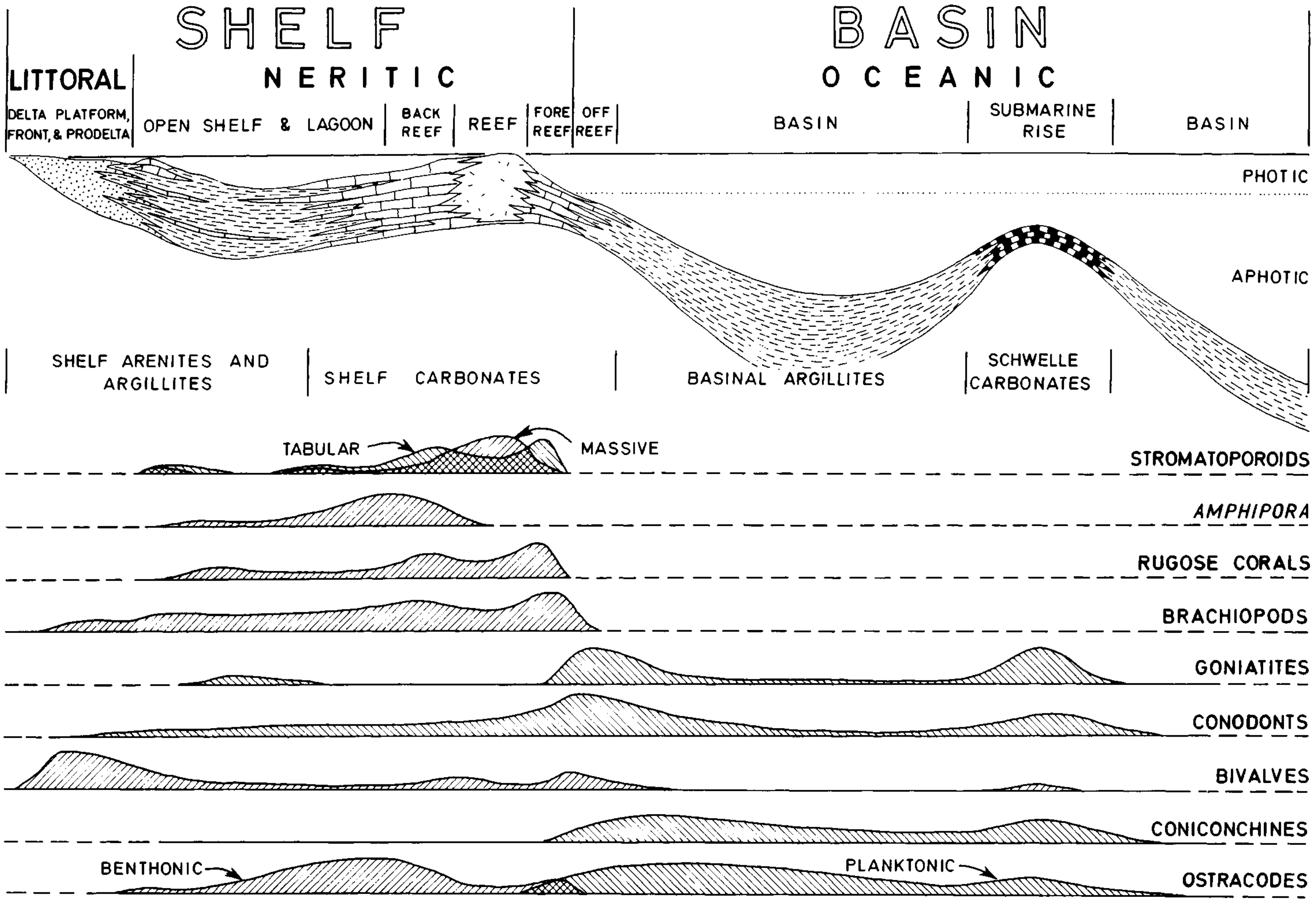


FIG. 2. Distribution of facies types and faunal groups from the Devonian of Europe (after House, 1975b).

the common stromatoporoids and corals lived essentially below the level of strong wave action. This often formed the base on which the true reef, or *Dorp* facies, was developed, usually showing rapid growth of reef organisms, notably stromatoporoids, associated with a subsidence of the platform as a whole. The *Dorp* facies is further subdivided into backreef, reef, and forereef facies. The *Iberg* facies was the final capping phase at the apex of the subsiding reef masses before their final termination (usually in the early and middle Frasnian): by the stage at which this facies was formed, no backreef lagoon existed, and detritus from the capping *Iberg* facies interfingers laterally with basinal argillite within a very short distance.

The basinal argillite areas comprise the *Becken* facies. In the lowest Devonian this is the graptolite shale facies, but with reduction of the graptolites, the nowakiids, and styliolinids, of supposed planktonic habit, characterize the *Styliolinenschiefer* and *Tentaculitenschiefer* of the middle and early Late Devonian. Gradually during the Frasnian these Cricoconarida became extinct or reduced and their place was taken in the planktonic environment by the fingerprint ostracodes of the Entomozoidae characterizing the Late Devonian *Cypridinenschiefer* facies. Tongues of allodapic turbidite limestone from adjacent reefs or crinoid groves project into the lateral *Becken* areas to produce the distinctive *Flinz* facies of alternating limestone and shale units.

The submarine rise or seamount limestones have very much reduced but nearly complete sequences of nautiloid and ammonoid limestones. This is the *Schwelle* facies of pelagic limestones with the distinctive associated lithologies of *Knollenkalk (griotte), Kramenzelstein,* and *Kalkknollenschiefer.*

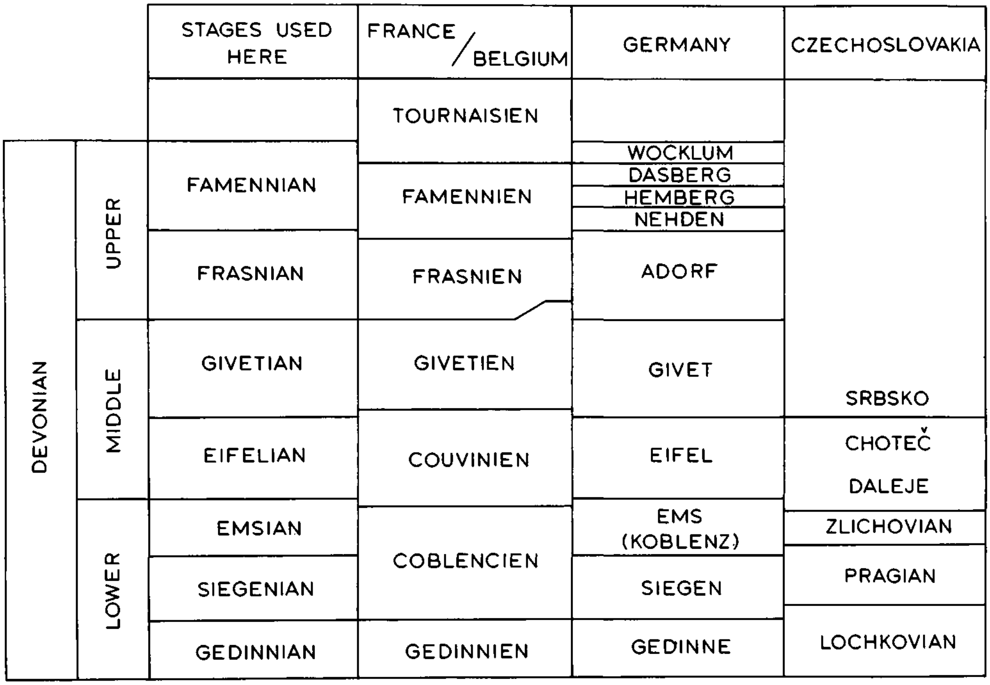
The European Devonian, has a special place in the international development of Devonian studies, and many of the biofacial, biostratigraphic, and biogeographic concepts owe their origin here. It is appropriate that a discussion of the European schemes of zonation and some of the facies concepts should be described as a preliminary to a broader discussion of the biogeography of Devonian rocks of the Eastern Hemisphere.

STAGES AND ZONES OF THE EUROPEAN DEVONIAN

The diversity of facies represented by the European Devonian has resulted in much effort being expended in the establishment of schemes of biostratigraphic zonation as a basis for interpreting these changes. Despite this there remain problems of correlation between the various facies. There is even no agreed consensus for the stage nomenclature and the definition of stages for the European Devonian, although this is currently the concern of the Devonian Subcommittee of the I.U.G.S. Stage or series names in common use are shown in Figure 3. Some notes on usage are required.

STAGES

The Silurian-Devonian boundary stratotype, accepted at the 1972 meeting of the International Geological Congress at Montreal, is within Bed No. 20 of a section at Klonk, near Suchomasty, Czechslovakia, as described by CHLUPÁČ (1972), at the entry of abundant *Monograptus uniformis* (McLAREN, 1972); this is also taken as the Budnanian-Lochkovian boundary in the Czech terminology. This decision brings international stability to the long-continued boundary problem, but pre-1972 literature may well use different boundary definitions. This is particularly so in the British type area for the Silurian and Devonian where the Ludlow Bone Bed, a marker horizon near the original level proposed by MURCHISON (WHITE, 1950; EARP, 1973) may correlate with the base of the Pridolian and of the *M. ultimus* Zone (WESTOLL in HOUSE, ed., 1977), and the new boundary may lie well up in the Downtonian or near the base of the Dittonian. In the classic sections in Podolia in the Ukraine (NIKIFOROVA & PREDTECHENSKIY, 1968; SOKOLOV, 1972) the new boundary falls within the Borschov, and in other regions similar corrections will be needed. The final report of the



		STAGES USED HERE	FRANCE / BELGIUM	GERMANY	CZECHOSLOVAKIA
			TOURNAISIEN		SRBSKO
DEVONIAN	UPPER	FAMENNIAN	FAMENNIEN	WOCKLUM DASBERG HEMBERG NEHDEN	
		FRASNIAN	FRASNIEN	ADORF	
	MIDDLE	GIVETIAN	GIVETIEN	GIVET	
		EIFELIAN	COUVINIEN	EIFEL	CHOTEČ DALEJE
	LOWER	EMSIAN	COBLENCIEN	EMS (KOBLENZ)	ZLICHOVIAN
		SIEGENIAN		SIEGEN	PRAGIAN
		GEDINNIAN	GEDINNIEN	GEDINNE	LOCHKOVIAN

FIG. 3. Stage level terminology used in Europe and that used herein (House, n). (For definitions see text.)

Committee on the Silurian-Devonian boundary (MARTINSSON, ed., 1977) gives an international review of the placing of the boundary.

The type of the Gedinnian Stage is in Belgium and it carries a nearshore clastic-facies fauna that appears to correlate with the Lochkovian; it is to be hoped that the base of the Gedinnian will be so defined as to agree with the system boundary. The base of the Siegenian is taken at the base of the Siegener Schichten of the Rhineland and to correspond approximately to the base of the Schistes de Saint Hubert of the Ardennes; regions again of restricted facies faunas. The major problem here is the placing of the Gedinnian-Siegenian boundary in relation to the Lochkovian-Pragian boundary of Czechoslovakia (PŘIBYL & VANEK, 1968); at present the latter boundary is thought to lie perhaps as high as the middle-upper Siegenian boundary of Germany, but the matter is not resolved. The base of the Emsian in Germany is taken at the base of the Singhofen Beds near the type area (KUTSCHER & SCHMIDT, 1958, p. 57 *et seq.*; ERBEN & ZAGORA in OSWALD, 1968a) and the base of the upper Emsian at the Ems Quartzite. Again there are problems in the correlation of this essentially clastic sequence with the more carbonate-rich rocks of Czechoslovakia. For example, CARLS and others (1972) considered that the Zlichov-Daleje boundary correlates approximately with the lower-upper Emsian boundary, yet others have taken the top of the Zlichov as the top of the Emsian. With such discrepancies, faunal ranges using a "common" stage nomenclature must be treated with the greatest circumspection.

Similar problems surround the Lower-Middle Devonian boundary. The Belgian Couvinian Stage includes the Assise de Bure and equivalents of the Cultrijugatus Schichten; these in Germany are referred to the Emsian, the base of the Eifelian and Middle Devonian being taken in the Eifel at the junction of the Heisdorf and Laucher Schichten. But recently it has become apparent that the latter level may not be the same as that taken in the Schiefergebirge where the *Gracilis*-Grenze (ERBEN, 1962, p. 95) has been used and thought to correspond to the Czech Zlichov-Daleje boundary, a correlation disputed by CARLS and others (1972). The type Givetian (ERRERA, MAMET, & SARTENAER, 1972) in northern France raises less problems since the conodont relations have been established by BULTYNCK (1970). The difficulty here is that the current Couvinian-Givetian boundary seems likely to be younger than the base of the *Cabrieroceras crispiforme* Zone, which has been used to define the junction in the Schiefergebirge, Czechoslovakia (CHLUPÁČ in OSWALD, 1968a, p. 117), North Africa (HOLLARD, 1974), and which has been recognized in North America also (HOUSE, 1962). Only an internationally agreed definition can resolve this problem.

Until very recently, there was considerable agreement on the definition of the Middle-Upper Devonian boundary and on the base of the Belgian type Frasnian, the boundary being drawn at the base of the Assise de Fromelennes (WATERLOT, 1957, p. 199-205) in Belgium and at the base of the *Pharciceras lunulicosta* Zone of Germany (KUTSCHER & SCHMIDT, 1958, p. 309), a level which seems to fall within the conodont *Polygnathus varcus* Zone (HOUSE, 1973a; BENSAID, 1974; BOUCKAERT & STREEL, 1974). Unfortunately, when the primary work on Frasnian conodonts was done on the Adorf type sections (ZIEGLER, 1958, 1962, 1966) the correlation with the goniatite zonation established by WEDEKIND (1913) at that locality was misaligned and it still seems that the 1α limestone of WEDEKIND is placed too high; it is more likely to be represented by the new *Pharciceras*-bearing level described by KULLMAN & ZIEGLER (1970). The result of this error has been that conodont workers have used a boundary higher than the basal *P. lunulicosta* Zone that German geologists have taken as the Middle-Upper Devonian boundary for a considerable time. It seems also to be the reason behind moves in Belgium to redefine the base of the Frasnian at some level near the base of the Assise de Frasnes (HOUSE, 1973a). The lithostratigraphic definition of the base of the Famennian Stage is in southern Belgium at the boundary of the Assise de Matagne and the Assise de Senzeille in the Senzeille railway cutting (SARTENAER, 1970). This seems to be an approximate correlative of the Adorf-Nehden or *Manticoceras-Cheiloceras* Stufen boundary used in Germany. The Belgian boundary seems to lie near the base of the conodont middle *Palmatolepis triangularis* Zone (BOUCKAERT *et al.,* 1972); the German boundary may be near the base of the upper *P. triangularis* Zone (BUGGISCH & CLAUSEN, 1972).

The Devonian-Carboniferous boundary has been defined at the *Wocklumeria-Gattendorfia* Stufen boundary following the Heerlen Conference decision (JONGMANS & GOTHAN, 1937, p. 6) and this was also the recommendation of the Sheffield Conference (GEORGE & WAGNER, 1969, p. xlv). The sections considered particularly important in these discussions are those in the Oberrödinghausen railway cutting in the Hönnetal (SCHINDEWOLF, 1937; VÖHRINGER, 1940; AUSTIN *et al.,* 1970). While there are detailed problems at this level (ALBERTI *et al.,* 1974), the boundary has had the recommendation of the Carboniferous conferences for 40 years and therefore seems the most acceptable, but no recommendation has been made by the Carboniferous Subcommission. Unfortunately, the Belgian and French geologists have not redefined the base of the Tournaisian to correspond with the Heerlen and Sheffield decisions, and their usage has been followed by most Russian authors. It would appear that the basal *Gattendorfia* Stufe agrees approximately with the Tn_{1a}-Tn_{1b} boundary or lies within Tn_{1a} (CONIL & PIRLET, 1970).

These difficulties of definition and usage, and the problems of correlation between the zonal schemes using different groups need to be borne in mind when Devonian literature is read, since quite misleading information on fossil ranges and distribution at particular times can be inferred if the local terminology is misunderstood.

ZONES

Biostratigraphic schemes of zonation have been proposed using a range of invertebrate groups. Again, because these groups tend to be restricted to certain environments, there are substantial problems in the correlation between such schemes. The

	STAGES	STUFEN	AMMONOID ZONES	CONODONT ZONES	OSTRACODE ZONES	
UPPER DEVONIAN	FAMENNIAN	WOCKLUMERIA	*Prionoceras sp.*	*Protognathodus*		UPPER DEVONIAN
			Cymaclymenia euryomphala			
			Wocklumeria sphaeroides	*Spathognathodus costatus*	*Maternella hemisphaerica* and *Maternella dichotoma*	
			Kalloclymenia subarmata			
		CLYMENIA	*Gonioclymenia speciosa*	*Polygnathus styriacus*		
			Gonioclymenia hoevelensis			
		PLATYCLYMENIA	*Platyclymenia annulata*	*Scaphignathus velifer*	*Franklinella intercostata*	
			Prolobites delphinus			
			Pseudoclymenia sandbergeri	*Palmatolepis marginifera*	*Entomozoe(R)serratostriata* *Franklinella intercostata* Interregnum	
		CHEILOCERAS	*Sporadoceras pompeckji*	*Palmatolepis rhomboidea*	*Entomozoe (R) serratostriata* and *Entomozoe (N) nehdensis*	
			Cheiloceras curvispina	*Palmatolepis crepida*	*Ungarella sigmoidale*	
	FRASNIAN	MANTICOCERAS	*Crickites holzapfeli*	*Palmatolepis triangularis*	*Entomozoe (E) variostriata*	
				Palmatolepis gigas	*W. cicatricosa E. barrandi* Interregnum	
			Manticoceras cordatum	*Ancyrognathus triangularis*	*Waldeckella cicatricosa*	
				Polygnathus asymmetricus	*W. cicatricosa E. torleyi* Interregnum	
			Pharciceras lunulicosta	*S. hermanni - P. cristatus*	*Franklinella torleyi*	
MIDDLE	GIVETIAN	MAENIOCERAS	*Maenioceras terebratum*	*Polygnathus varcus*		MIDDLE
			Maenioceras molarium	*Icriodus obliquimarginatus*		
			Cabrieroceras crispiforme	*Polygnathus kokeliana*		
	EIFELIAN	ANARCESTES	*Pinacites jugleri*	*Spathognathodus bidentatus*		
			Anarcestes lateseptatus	*Icriodus corniger*		
LOWER DEVONIAN	EMSIAN	ANETOCERAS	*Sellanarcestes wenkenbachi*	non - latericrescid *Icriodus* - *Polygnathus*	GRAPTOLITE ZONES	LOWER DEVONIAN
			Mimagoniatites zorgensis	*Icriodus bilatericrescens* s.s.- *Sp. steinhornensis* - *Polygnathus*		
	SIEGENIAN		*Anetoceras hunsrueckianum*	*Icriodus h. curvicauda* - *Icriodus huddlei* s.s.	*Monograptus yukonensis* *Monograptus falcarius*	
				Icriodus h. curvicauda - *rectangularis* s.l. *angustoides*	*Monograptus hercynicus*	
	GEDINNIAN			*Ancyrodelloides* - *Ic. pesavis*		
				Icriodus w. postwoschmidti	*Monograptus praehercynicus*	
				Icriodus woschmidti s.s.	*Monograptus uniformis*	

Fig. 4. Zonal schemes for the Devonian using various invertebrate groups. Precise correlation between these should not be inferred (House, n). (For sources see text.)

accompanying table (Fig. 4) is intended to illustrate several of these schemes. Correlation between columns should be regarded as an approximate guide only. In this section reference will be made to some of the more substantial biostratigraphic works that have formed the basis for these zonations.

As for the period up to the close of the Cretaceous, the ammonoid succession has been regarded as giving the Devonian orthochronology, that of the preceding graptolites giving out in the Siegenian where the ammonoids appear. The goniatite and clymenoid zonations result largely from the works of Wedekind (1908, 1913, 1914, 1917) followed by that of Schindewolf (1923, 1937), Schmidt (1921, 1924, 1950), Matern (1931a,b), Clausen (1969, 1971), Bensaid (1974) and others. These mostly concern the German succession. Reviews have been given by House (1962, 1973b) and in the revised *Treatise* Part L, Mollusca 4 (in preparation).

The conodont scheme has developed over the last fifteen or so years, and it now provides the most detailed subdivision available for the Upper Devonian. The major works are by Bischoff & Ziegler (1957), Ziegler (1958, 1962, 1966, 1971), Wittekindt (1965), Krebs & Ziegler (1965), Klapper & Ziegler (1967), Bultynck (1970), and Carls (1969). A general review of the European conodont sequence

	STAGES	STUFEN	TENTACULITED ZONES	W. EUROPE BRACHIOPOD ZONES	USSR BRACHIOPOD ZONES	
UPPER DEVONIAN	FAMENNIAN	*WOCKLUMERIA*			(INCLUDED WITH THE CARBONIFEROUS IN THE U.S.S.R.)	UPPER DEVONIAN
		CLYMENIA		*Ptychomaletaechia letiensis*	*Adolfia talasica*	
		PLATYCLYMENIA			*Leiorhynchus (Zigania) ursus* and *Ptychomaletoechia turanica*	
		CHEILOCERAS		*Pt. dumonti* *Pt. gonthieri* *Pt. omaliusi* *Eoparaphorhynchus lentiformis* etc.	*Zilimia polonica* and *Cyrtospirifer* spp.	
	FRASNIAN	*MANTICOCERAS*	(FOR DETAILED ZONATION SEE LYASHENKO 1965 ETC.)	*Cariorhynchus tumida* *Hypothyridina cuboides* *Cyrtospirifer malaisei* *Cyrtospirifer orbelianus* *Cyrtospirifer tenticulum*	*Hypothyridina cuboides* and *Theodossia anossofi* *Cyrtospirifer* spp. *Mucrospirifer novosibiricus* *Uchtospirifer murchisonianus*	
MIDDLE	GIVETIAN	*MAENIOCERAS*	*Nowakia otomaria*	*Mediospirifer mediotextus* *Stringocephalus burtini* *Undispirifer undiferus*	*Euryspirifer cheehiei* *Stringocephalus burtini* *Bornhardtina langurica*	MIDDLE
	EIFELIAN	*ANARCESTES*	*Nowakia sulcata* *Nowakia holynensis* *Nowakia richteri* *Nowakia cancellata*	*Spinatrypa kelusiana* *Spinacytia ostiolatus* *Euryspirifer intermedius*	*Lazutkinia mamontovensis* *Megastrophia uralensis*	
LOWER DEVONIAN	EMSIAN	*ANETOCERAS*	*Nowakia barrandei* *Nowakia praecursor* *Nowakia zlichovensis*	*Paraspirifer cultrijugatus* *Euryspirifer paradoxus* *Acrospirifer pellico*	*Eospirifer superbus* *Paraspirifer ? gurjevkensis* *Latonotoechia latoma*	LOWER DEVONIAN
	SIEGENIAN		*Nowakia arcuata* — — — — — — — — *Paranowakia intermedia*	*Acrospirifer primaevus*	*Spirigerina supramarginalis* etc.	
	GEDINNIAN		*Paranowakia bohemica* *Tentaculites ornatus*	*Delthyris dumontianus* *Howellella* group	*Howellella* group	

FIG. 4. *(Continued from facing page.)*

is given by Ziegler (1971).

It was not recognized until 1960 that graptoloid graptolites extend up into the Lower Devonian when Lochkovian graptolites were found associated with Rhenish type brachiopods in the Kellerwald (Jaeger, 1965). Notable information has come also from boreholes in Poland (Korejwo & Teller, 1965) and from Thuringia, the Carnic Alps, and other regions. In a review of the Lower Devonian graptolite sequence, Jaeger (1973) recognized the zones indicated on the accompanying table.

For the Cricoconarida (dacryoconarids, "tentaculitids," coniconchines) a detailed zonation using several of the various groups has stemmed from the initial studies by G. P. Lyashenko (1953, 1959) in European Russia. Bouček (1964) followed this scheme for the Prague area and Harz, and Lardeux (1969) for southern Europe and North Africa.

The Late Devonian planktonic ostracodes provide the most useful sequence in the Late Devonian basinal shale facies, and the sequence has been worked out by Rabien (1954, 1956, 1960, 1970), Blumenstengel (1959), and Groos-Uffenorde & Uffenorde (1974).

For the brachiopods the situation is more complex. The zonal schemes given here are taken from Nalivkin, Rzhonsnitskaya, & Markovskiy (1973). But in reality different brachiopod groups have been used for discrimination without always the formal distinction of zones. The most thorough treatment of Devonian brachiopod ranges has been given by Boucot (1975), but since he does not define his stage units there are problems in his collation. Nevertheless, the work of Boucot and his colleagues will be heavily drawn on in the later sections where specific reference to monographic works will be made.

For trilobites, the long continued studies by Rudolf and Emma Richter (especially 1926, 1950, 1952) provide a biostratigraphic foundation, and this work has been continued by Alberti (1968, 1973). Wedekind, using corals, established a series of zones for the German Middle Devonian (Wedekind, 1924-25; Wedekind & Vollbrecht, 1931-32), and Birenheide (1968, 1972) has done much to revise this, but schemes using corals have not found favor internationally.

MAIN AREAS OF DEVONIAN ROCKS

Devonian rocks are widely scattered on all of the continents of the Eastern Hemisphere (Fig. 1), but recorded information varies considerably. The most comprehensive collation for most areas is the *International Symposium on the Devonian System,* edited by D. H. Oswald, published in 1968. For the vast area of Russia there are two volumes of a Silurian-Devonian Boundary Conference (published under the general editorship of D. V. Nalivkin in 1971 and 1973) and the two volumes of the *Devonskaya Sistema* edited by Nalivkin, Rzhonsnitskaya, and Markovskiy (1973). For China the most accessible source is the *Paleogeograficheskiy Atlas Kitaya* (Sokolova, ed., 1962) and a regional stratigraphy (Sokolov, 1960). Australia has been reviewed in a series of Devonian correlation charts (Strusz, 1972; Pickett, 1972; Roberts *et al.,* 1972).

WESTERN AND SOUTHERN EUROPE

The areas of Old Red Sandstone sedimentation comprise Ireland, Wales, Scotland, and Norway. In southeastern England, the North Sea, and probably a subsurface belt passing east to the Baltic States platform, sediments of continental facies are occasionally intercalated by marine tongues. From southwest England and northwestern France, eastward through southern Belgium, the Eifel, Rhenish Schiefergebirge, and Harz Mountains to the Holy Cross Mountains of southern Poland lay the Hercynian (Armorican or Variscan) geosyncline in Devonian times. Farther south the scattered outcrops mostly occur in the Paleozoic massifs strongly affected by late Paleozoic and subsequent tectonism; these mostly indicate marine deposits of geosynclinal type which, with the Hercynian belt, continue eastward into the complex series of outcrops of central Asia and the Himalaya.

SOVIET UNION

From the extensive outcrops of the Main Devonian Field near Leningrad Devonian rocks extend in the subsurface eastward to rise to the surface in the Timan and Ural mountains. Southward they crop out along the tributaries of the Don River south of Moscow and along the Dnieper valley in Podolia. Across the bulk of the Russian platform the deposits are of Middle and Late Devonian age and are represented by continental and evaporite deposits with marine intercalations. In Podolia a marine Lower Devonian sequence follows conformably upward from the Silurian (Kozlowski, 1929; Nikiforova & Predtechenskiy, 1968). A fuller marine sequence is typical for the Devonian in its development from Novaya Zemlya, the Ural and the Timan mountains. The Ural sequences are broadly eugeosynclinal to the east and miogeosynclinal to the west. This belt formed the Uralian geosyncline in Devonian times, and was folded in the late Paleozoic.

Scattered Devonian outcrops stretch from the Tien Shan, through Kazakhstan, the Altay to Baikal and Mongolia to the Khrebet Dzhugzhur, and along the coast of the Sea of Okhotsk. This belt broadly formed the Angaran geosyncline, bounded to the north by the western Siberian plate and by the Siberian platform in the east. This belt, too, was folded by Hercynian movements.

In most of the Devonian the Angaran geosyncline was linked with the southernmost part of the Ural geosyncline, and there appears to have been an almost continuous link with its northern parts via the Altay-Sayan. The central and southern parts of the Central Asian fold belts are affected by the Cimmerian (Carpathian) folding, and the southern parts also by Alpine folding. These areas are often considered extensions of the Tethyan or Mediterranean geosyncline.

Mostly continental Devonian is known in the subsurface between the Urals and the Yenisey River, which forms the western margin of the Siberian platform. The occurrences in the western and southern parts of the platform are also of continental facies. Those of the northern margins are mostly marine and have facies affinities with the Urals. In the Verkhoyansk-Chukotsk region of northeastern Siberia, especially along the Indigirka and Kolyma rivers, marine deposits are widespread, again with Uralian affinities.

CHINA, SOUTH AND SOUTHEAST ASIA

The Devonian outcrops of Russian Kirgiziya and Tadzhikistan pass eastward in tracts that are interpreted as a northerly Mongolian-Manchurian geosyncline (part of the Angaran geosyncline) crossing Mongolia to the Sea of Okhotsk, and passing north of the broad supposed land area of the Peking platform. Another tract passed south of this platform forming the wide outcrops of continental and marine Devonian in eastern China, especially in the ancient provinces of Yunnan and Hunan. Within this tract several circumscribed positive areas seem to have been active throughout the Devonian, such as the Tarim massif with the Kun Lun Shan geosyncline of northern Tibet south of it, and the Tsaidam massif with the Nan Shan geosyncline between it and the Peking platform (which embraced all but the Manchurian part of Inner Mongolia). A complex archipelago is envisaged for southwestern China along and south of the Yangtze Kiang River. Yet farther south is the broad area with isolated outcrops that stretch from the Bosporus coast of Turkey, through Iran, Afghanistan, Pakistan, the Northern Shan States, Viet Nam, Thailand, and Malaya. This last tract is distinctive for the European nature of many of its faunas.

AUSTRALASIA

In New Zealand the Lower Devonian is known in the Reefton and Baton River areas. Devonian rocks are widespread in eastern Australia in a belt from Queensland to Tasmania that formed part of the complex Tasman geosyncline composed of marine, volcanic, and continental deposits. In Central Australia the Amadeus basin has continental deposits. Bordering the margins of the Precambrian platform of Western Australia are the marine deposits forming the three discrete areas of the Carnarvon, Canning (and Lennard Shelf basin and Fitzroy trough), and Bonaparte Gulf basins. In these it is the Upper Devonian that is best developed.

AFRICA

The main development of Devonian rocks is in North Africa in a broad belt from the Tindouf basin and isolated outcrops in Mauritania, Rio de Oro, and northern Morocco eastward to the northern Hoggar, Polignac basin, Mourzouk basin, and Tibesti and Koufra basins at the Libya-Egypt frontier. Broadly, this North African development is of shelf-facies marine Devonian lapping southward onto the African Precambrian shield. The faunal affinities are almost wholly European, but with Appalachian elements in the west.

By contrast, the Bokkeveld development of Lower Devonian marine faunas in South Africa shows typical elements of the Malvinokaffric province discussed with Antarctica and South America in the Western Hemisphere section. The Devonian of Ghana seems to show similar affinities, but with European elements also (ANDERSON *et al.*, 1966).

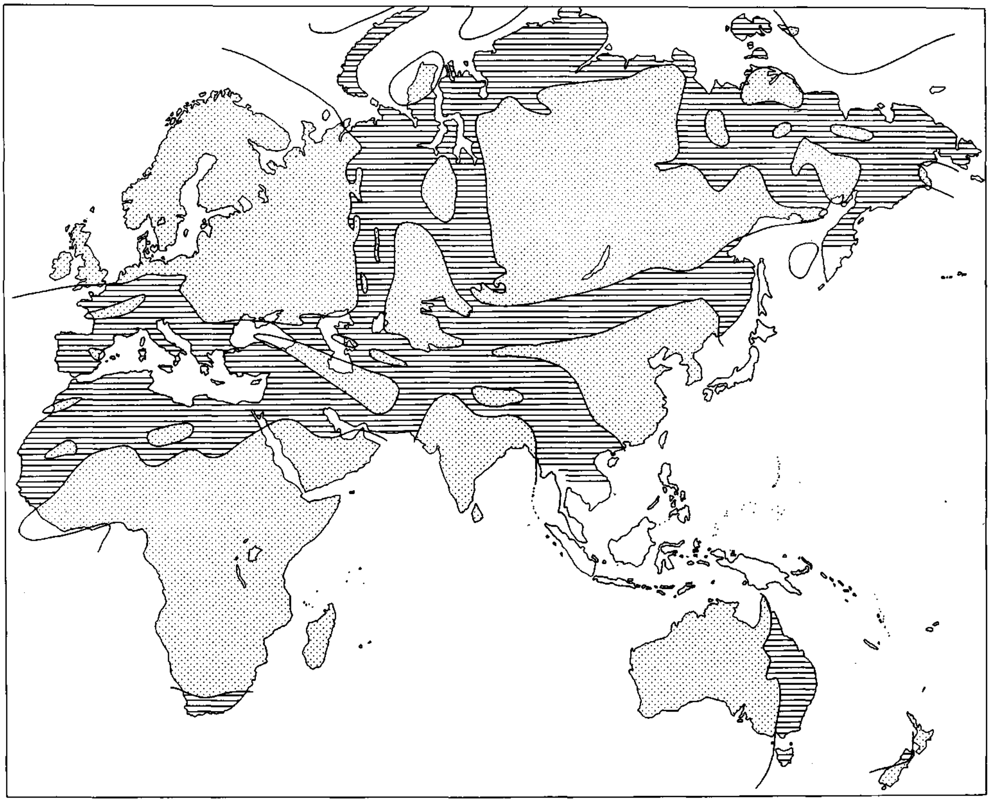


FIG. 5. Paleogeographic map for the Early Devonian (Emsian) of the Eastern Hemisphere (based on Boucot & Johnson, 1973; House, n). [Inferred land areas are stippled and areas of marine rocks are horizontally lined.]

LOWER DEVONIAN FAUNAS

In the Lower Devonian (Fig. 5), faunal provincialism has long been recognized. For the Eastern Hemisphere, and excluding, therefore, the Appalachian province, the division is essentially into an Old World province embracing Europe and North Africa, Asia, Australasia, and western North America, and a Malvinokaffric province embracing South Africa, the Falkland (Malvinas) Islands, South America, and Antarctica (the term Austral province was introduced for the latter by J. M. CLARKE in 1913, but since this could be confused with Australasian faunas, RICHTER (1941) proposed the name *"Malvinocaffrisch"* and it is this in anglicized form that is normally used). Paleomagnetic evidence suggests that the Old World province lay in equatorial and temperate latitudes and that the Malvinokaffric province lay nearer the "southern" pole.

The Old World province is commonly divided into a Rhenish-Bohemian subprovince, comprising Europe excluding the Urals, North Africa, parts of the Near East and, for the late Early Devonian, parts of eastern North America; a Uralian subprovince embracing the Urals and Asiatic Russia and the Angaran geosyncline with elements of the Appalachian province in the latter; a Tasman subprovince recognized in eastern Australia; and a New Zealand subprovince including South Island but with some links *(Reeftonia)* with Southeast Asia (BOUCOT, JOHNSON, & TALENT, 1969; BOUCOT, 1974).

This provincialism is best shown by benthonic organisms, notably brachiopods and corals, and probably reached its acme in the Emsian (BOUCOT, 1975).

EUROPE

In this area there are great faunal contrasts between the Rhenish facies of nearshore clastics with abundant brachiopods and bivalves, the Bohemian facies of calcareous rocks, which carry the richest faunas, and the basinal shales, which preserve graptolites and Cricoconarida. Major problems remain on the detailed correlation between these facies. Space permits only reference to a selection of the many major works on these faunas.

The brachiopods have generally been used for the subdivision of the nearshore clastic facies. The Gedinnian carries *Quadrifarius, Proschizophoria, Podolella, Mutationella,* and *Cyrtina* as newly appearing forms (BOUCOT, 1960; JOHNSON & BOUCOT in HALLAM, 1973). Near the beginning of the Siegenian appear genera such as *Anoplotheca, Bifida, Meganteris, Multispirifer, Pradoia, Rhenorensselaeria,* and others. The stratigraphically useful spiriferids of the Siegenian and Emsian have been monographed, especially by SOLLE (1953, 1971). Notable studies on Lower Devonian bivalves are by MAILLIEUX (1937) for the Ardennes and BEUSHAUSEN (1895) for the Schiefergebirge. Trilobite faunas include *Acastella* and *Warburgella* in the Gedinnian, and common phacopids, *Treveropyge* and *Burmeisteria* in the Siegenian and Emsian (ALBERTI, 1968; RICHTER & RICHTER, 1954).

The Bohemian facies of Czechoslovakia is best known through the detailed studies of CHLUPÁČ (1957, 1959, 1960, and in OSWALD, 1968a), who gave stratigraphical precision to many of the faunas monographed by BARRANDE. CHLUPÁČ (1972) has also described the faunas around the stratotype for the Silurian-Devonian boundary where the base of the Devonian and of the Lochkovian is characterized by the appearance of *Monograptus uniformis* and *Warburgella rugulosa rugosa*. *Scyphocrinites* is abundant just above and below the boundary. The Lochkovian carries a rich fauna of brachiopods including *Howellella, Plectodonta,* stropheodontids, and spiriferids (HAVLIČEK, 1959), and trilobites such as proetids and scutellids. Merostomes, phyllocarids, bivalves and coral faunas are also richly represented. The overlying Pragian has distinctive brachiopod faunas, including species of *Sieberella, Glossinotoechia, Stegerhynchus, Hysterolites,* and others. The Lower Devonian here has been subdivided by using Cricoconarida (BOUČEK, 1964), and this work has been extended by LARDEUX (1969) to southern Europe and North Africa. In Czechoslovakia (CHLUPÁČ in OSWALD, 1968a, p. 115) the Zlichov-Daleje boundary, marked by the entry of the goniatite *Gyroceratites* and the loss of the bizarre *Caeleceras* and of trilobites, notably *Odontochile,* has been used as the Lower-Middle Devonian boundary, but CARLS and others (1972) have argued that it corresponds rather with the Lower-Upper Emsian boundary of Germany. Representatives of the Bohemian facies also recur in the Harz Mountains (ERBEN, 1953b, 1960).

The basinal shale facies bearing graptolites extends well up into the Lower Devonian (JAEGER, 1965) and *Monograptus hercynicus* also occurs in the late Lochkovian, enabling correlation between the facies as well as internationally where the Lochkovian-Pragian boundary can be identified better than the Gedinnian-Siegenian boundary. In this facies, also, cricoconarids (LARDEUX, 1969) are increasingly important upward in the succession. It is in the Siegenian Hunsrück-Schiefer of this facies that goniatites appear (ERBEN, 1966), particularly *Anetoceras,* and in this unit also is a remarkable pyritic fauna of crinoids, trilobites and other groups revealed in minute detail by X rays (STÜRMER, 1969).

In the Early Devonian of Europe, therefore, three facies regimes carried their own distinctive faunal elements (ERBEN, 1964) and doubtless had independent community evolution. It is this that has led to difficulties in the use internationally of the classical stage divisions adopted here.

Analysis of the faunal communities or assemblages represented in the various facies regimes of the Lower Devonian of Europe has scarcely begun. FUCHS (1971) has made such a study of the upper Siegenian and lower Emsian facies of the Eifel and recognized a seaward sequence of communities dominated by *Mutationella, Trigonorhyn-*

chia-Subcuspidella, Rhenorensselaria, and *Acrospirifer,* followed by a deeper water community of rarer brachiopods, bivalves and orthocones. Boucot (1975) has attempted a preliminary review of communities generally in the Lower Devonian and has drawn attention to the rarity in most of these communities of species or genera of value for time discrimination.

ASIA

Here it is convenient to follow the broad groupings adopted by Nalivkin, Rzhonsnitskaya, & Markovskiy (1973) and Boucot (1975), recognizing the following divisions for convenience: the Uralian region and Arctic Siberia; the Dzhungaro-Balkhash region; the Altay-Sayan area; Mongolia and the Tikhookian area (the Mongolo-Okhotsk region of Boucot); China south of the Peking platform; and the tract of outcrops from Turkey to Southeast Asia. These are in part faunal provinces, in part regionally defined areas.

The Uralian area shows close similarity to Europe and belongs to the Old World province as normally defined. Differences in southern areas, especially southeast Kazakhstan, reflects the terrigenous and volcanic facies there. In the more calcareous facies *Karpinskia* is a characteristic brachiopod, but it also occurs in the Carnic Alps and elsewhere. The Arctic area, including Novaya Zemlya, has widely distributed genera such as *Eoglossinotoechia, Howellella,* and *Hebertoechia,* but the combination of *Phragmostrophia* and *Cortezorthis* also occurs and gives a clear link with Cordilleran faunas (Johnson & Boucot in Hallam, 1973). The goniatite faunas of the Urals and Novaya Zemlya are very close to European groups (Bogoslovskiy, 1969, 1972). Rich coral faunas are present, especially in the upper Lower Devonian reef complexes, but these are mostly of European types with some endemics.

The Dzhungaro-Balkhash area of Kazakhstan is distinctive for the presence in it of brachiopod genera of Appalachian type, such as *Leptocoelia, Rhytistrophia,* and *Meristella* at levels probably correlating with the Siegenian. These occur with a mixture of European and Tasman subprovince types. Links both west and east, via the Angaran geosyncline, are inferred. The Australasian *Maoristrophia* also occurs here.

The Altay-Sayan area is thought to have been in marine contact with the northern Urals and with the Dzhungaro-Balkhash area during much of the Early Devonian. Here, rich faunal sequences in carbonate facies continue upward from the Silurian (Rzhonsnitskaya, 1968). The faunas give good links with the Urals, Podolia, and Czechoslovakia.

In the Mongolia and Tikhookian area Lower Devonian faunas are not well described, but they include *Leptocoelia, Costispirifer,* and *Rhytistrophia* emphasizing links with the Appalachian region. Links to the west are indicated by corals such as *Barrandeophyllum* and *Lindstroemia,* and the crinoid *Kuzbassocrinus.*

Very little is known about the Lower Devonian of China (Hamada in Oswald, 1968a). Early Devonian fish are recorded in Yunnan and other areas, but records of marine fossils are mostly unspecified (Sokolova, 1962). *Hysterolites* and *"Anastrophia"* suggest that the upper Lower Devonian is present in Old World facies. A varied Lower Devonian fauna has recently been described by Mu and others (1974), which includes *Anetoceras, Erbenoceras,* and *Mimagoniatites* mostly of European type. Other faunal elements are also described.

For convenience, the scattered outcrops along the Tethys belt are considered together. The well-known Lower Devonian faunas of Turkish Bithynia (Paeckelmann, 1925; Kullmann, 1973) contain many German genera and species, especially in the Emsian carbonates. In the many Devonian outcrops of Iran, Afghanistan, and Pakistan, Lower Devonian marine faunas are only poorly documented, and the same is true in Burma, Thailand, and Malaya. Noteworthy records are of *Icriodus woschmidti* in the Nowshera Formation of Nowshera, Pakistan (Stauffer in Oswald, 1968a), and Lower Devonian graptolites from Maymyo, Burma, and Thailand (Jaeger, Stein, & Wolfart, 1969). These show that at least locally marine sedimentation continued upward from the Silurian.

AUSTRALASIA

The Tasman geosyncline belt of eastern

Australia has given its name to the Tasman subprovince, a subgroup of the Old World province. Links with Europe are substantial, mainly in Rhenish facies, but also in the carbonate Bohemian type (SAVAGE, 1971). The Early Devonian graptolite faunas of southeastern Australia (JAEGER, 1966, 1970) represent the only graptolite faunas of this age in the southern hemisphere, and they allow close correlation with those of Europe. STRUSZ (1972) has recognized four successive brachiopod faunas for correlation purposes in this area. Fauna I (lower Yeringian) commonly contains *Eospirifer parahentius, Isorthis allani, Lissatrypa lenticulata, Maoristrophia banksi,* and *Boucotia*; Fauna II (upper Yeringian) has the association *Acrospirifer lilydalensis, Cymostrophia stephani,* and *Boucotia*; Fauna III (Tabberabberan) contains *Adolfia, Gypidula vultur,* and *Nadiastrophia*; and Fauna IV (Buchanian), contains common *Buchanathyris, Howittia, Malurostrophia,* and *Spinella.* Fauna I is thought to be Lochkovian, Faunas II and III Pragian, and Fauna IV is thought to range from the latest Pragian to the early Eifelian. Part of Faunas III and IV are referred to the Emsian, and it is then that the Tasman province is particularly well delimitated with genera such as *Reeftonia, Maoristrophia, Nadiastrophia,* and *Notanoplia* (the first two also occur in New Zealand and in Asiatic Russia and Manchuria; BOUCOT, 1975, p. 315). *Australocoelia* gives a single link with the Malvinokaffric province.

By contrast, the coral faunas of this belt, dealt with in many monographs by DOROTHY HILL, include large numbers of endemic elements. The corals and conodonts (PHILIP & PEDDER, 1967) have formed the basis for the recognition of 11 faunas (A-K) of which A-F are referred to the Lower Devonian. The conodont sequence, too, shows differences from that of Europe, a matter emphasized again by TELFORD (1975), who considered the sequence of faunas better related to those of western North America.

The New Zealand subprovince is based on Lower Devonian faunas from Baton River and Reefton, South Island, New Zealand. The Baton River fauna was dated as Upper Siegenian or Lower Coblencian by SHIRLEY (1938), as Gedinnian by BOUCOT, CASTER, IVES, & TALENT (1963), and WRIGHT (in OSWALD, 1968a) has suggested levels from Gedinnian to Emsian may be represented. Forms such as *Fascicostella, Acrospirifer, Cyrtina, Howellella, Mutationella,* and *Hipparionyx* all have a European aspect. The Reefton Beds, on the other hand, seem to be of Emsian age, and *Acrospirifer coxi* in the fauna is sufficiently close to *A. hercyniae* of Germany to suggest early Emsian. Distinctive genera of the fauna are *Reeftonia, Maoristrophia, Tanerhynchia, Pleurothyrella,* and the endemic *Allenetes.* Because it is only this fauna for which any discreteness can be claimed, elevation of the local early Emsian as a subprovince seems excessive, particularly as elements of the fauna are increasingly being recognized in the Orient.

AFRICA

The South African faunas of the Lower Devonian are of Malvinokaffric province type and hence have their affinity with regions discussed in the Devonian of the Western Hemisphere (NORRIS, herein p. A218). The North African Devonian, on the other hand, is clearly of Old World province type.

The Bokkeveld fauna of South Africa (REED, 1925; BOUCOT, CASTER, IVES, & TALENT, 1963) appears to be of early Emsian age. Characteristic brachiopods are *Australospirifer, Australocoelia, Scaphiocoelia,* and *Pleurothyrella.* This fauna has clear links with Antarctica, the Falkland Islands and South America, and slight links *(Australocoelia)* with Australia. Paleomagnetic evidence supports the view that this is a high latitude fauna.

The Accraian Series of Ghana carries a fauna of bivalves, gastropods, and homalonotids (SAUL, BOUCOT, & FINKS, 1963) and rare mutationellid terebratulids (ANDERSON, BOUCOT, & JOHNSON, 1966). Because *Mutationella* has not been recorded from the North African Lower Devonian, but occurs in the Falkland Islands, this has been taken to indicate affinity with the Malvinokaffric province.

The North African Lower Devonian of Morocco and Algeria (HOLLARD & LEGRAND

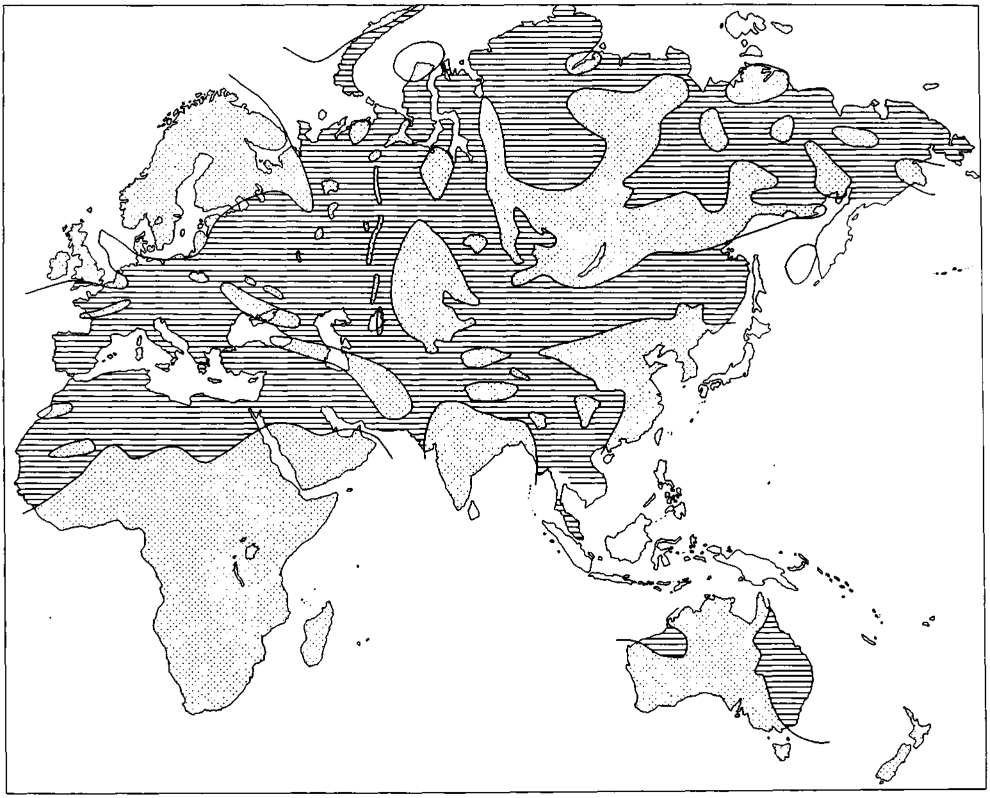


FIG. 6. Paleogeographic map for the Middle Devonian of the Eastern Hemisphere (based on Boucot & Johnson, 1973; House, n). [Inferred land areas are stippled and areas of marine rocks are horizontally lined.]

in OSWALD, 1968a) shows intimate affinity with the classical successions of Germany and Czechoslovakia. But whereas in those areas tectonic complications and poor exposure raise many problems, those of North Africa are superbly exposed along enormous spreads of outcrop. The potential for refined biostratigraphy is immense. Also, facies of both the European Rhenish and Bohemian types occur so that evidence from here has contributed to the correlation between the Czech and German stages.

Monograptus uniformis and the associated Silurian-Devonian boundary faunas and the faunal sequences have been well documented by HOLLARD (1968, 1974), and work by specialists on various groups is in progress, and some on brachiopods (DROT, 1971), cricoconarids (LARDEUX, 1969), and trilobites (ALBERTI, 1969) have appeared. During the Early Devonian, evidence of faunal affinity with North America has not been as well documented as in younger divisions, but OLIVER (1976) has drawn attention to the occurrence of eastern North American coral genera in North Africa.

MIDDLE DEVONIAN FAUNAS

By the Middle Devonian little evidence remains for a Malvinokaffric province in the area considered here (Fig. 6). In many areas, extensive transgressions near the Lower-Middle Devonian boundary, such as the movements across the Russian platform and the Onondaga onlap in North America, led to a general decrease in faunal provincialism, and to a mixing where provinces were adjacent. The distribution of the Old World province is as indicated for the Lower Devonian, but the New Zealand subprovince cannot be recognized. Particularly remarkable, and an indication of the reduction of provincialism by the Givetian, is the almost international distribution, in their appropriate different facies, of the giant *Stringocephalus* and its relatives (Boucot, Johnson, & Struve, 1966) and of *Amphipora* (Duncan in Cloud, 1959), witnessing to the cosmopolitan nature of some elements of the carbonate environment. But isolated areas of reef carbonates, in Europe, the Urals, and other areas are associated with some endemism. The mixing at province boundaries is illustrated by the number of Appalachian province forms occurring in North Africa and Spain, and European elements that are found in eastern North America, and the Appalachian elements that, as in the Lower Devonian, extend westward along the Angaran belt to Kazakhstan.

The Middle Devonian represents one of the chief periods of generic and familial diversification known in the Paleozoic. There appears to be some link between this and the widespread distribution of essentially shallow-water carbonates in areas thought to have been near the tropics, and the early Middle Devonian transgressive movements made these more extensive. But the close of the Middle Devonian saw the loss of many groups, and the brachiopod groups Rhynchotrematidae, Stringocephalidae, Dayiacea, Lyssatripidae, and Palaferellidae appear to have become extinct before the earliest Frasnian (Harland *et al.*, 1967); of trilobite groups, the Calymenina, homalonotids, and cyphaspids are last recorded in the Middle Devonian. The goniatite break is very important, with the loss of all but two or three genera (House, 1973b). The pattern of extinction for several groups is shown in Figure 7.

EUROPE

In the European area the distinction between Rhenish and Hercynian facies is still clear, although the former is much less well developed than in the Lower Devonian. Here for the carbonate facies fundamental work has been done in the establishment of ecologically based faunal assemblages, particularly by Lecompte (1970) and Tsien (1971) for the Ardennes, and by Struve (1963) for the Eifel. These may be briefly summarized, in shallow- to deep-water sequence, as follows (Lecompte's more interpretative terms are given in parentheses): Stromatoporoid *Bankriff* (Turbulent Zone); *Knollen-Blockriff,* and *Rasenriff* with crinoid meadows (Subturbulent Zone); *Rübenriff* (below Turbulent Zone); *Brachiopod-Siedlungen* (Quiescent Zone). The *Knollen-Blockriff* comprises loosely associated cerioid rugose corals and tabulates, the *Rasenriff* fasciculate rugosans and tabulates, and the *Rübenriff* is the zone of horn corals.

In the deeper water Hercynian facies, the basinal argillites are now characterized by styliolinid and nowakiid cricoconarids of supposed planktonic habit and these are abundant in the Tentaculitenschiefer and Styliolinenschiefer units of the Rhenish Schiefergebirge and in equivalent facies in Cornwall and other areas. The pelagic carbonate sequences of the seamounts are rich in goniatites and orthocones, but of types different from those of the Lower Devonian.

In the Middle Devonian brachiopod faunas increased in diversity. The productids entered first apparently in the Eifelian (rather than Emsian; Boucot, 1975), and derivatives are distinctive. Other stocks show distinctive genera; however, definition of a Lower-Middle Devonian boundary using brachiopods is difficult. The *Cultrijugatus Schichten,* here referred to the Lower Devonian, are characterized by species of *Paraspirifer* (Solle, 1971), but the name-giving species occurs in the *Laucher Schichten,* and it is not a diagnostic form. Locally, especially in the Eifel, various brachiopod groups have proved useful in time discrimination, particularly atrypids and reticulariids (Struve, 1966, 1970). One of the most useful genera for the Givetian is *Stringocephalus* and its allies. *Stringocephalus* survived into the earliest Late Devonian as used here, and the extinction corresponded approximately to the Middle-Late Devonian boundary as used here.

Middle Devonian goniatites are characterized by the proliferation of anarcestid and agoniatitid stocks. If Carls and others (1972) are correct in correlating the *Gyroceratites gracilis* boundary (of Erben in Erben, 1962, p. 65) with a level in the Emsian, then it is the occurrence of *Sel-*

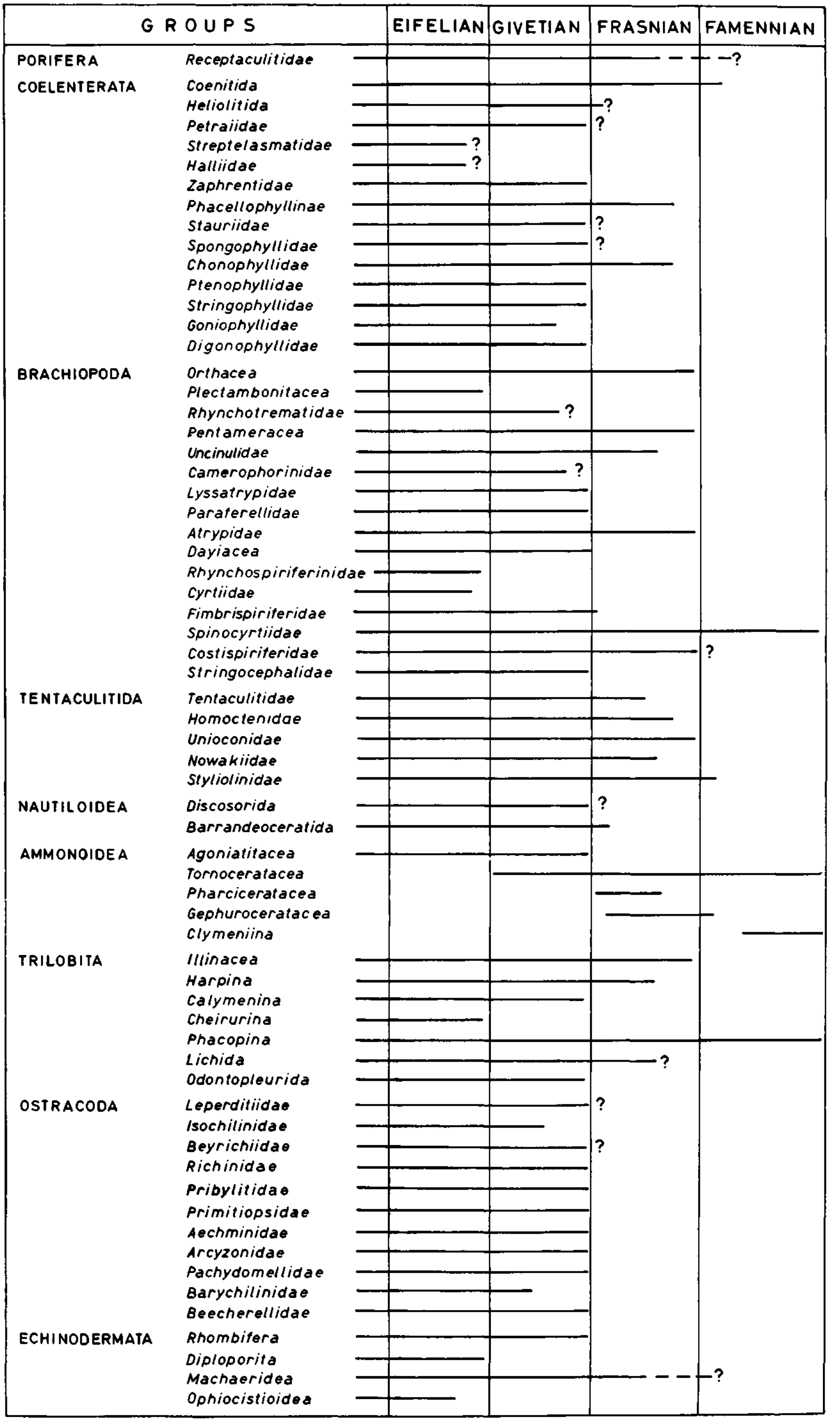


FIG. 7. Pattern of extinctions for selected invertebrate taxa during the Middle and Late Devonian (after House, 1975b).

lanarcestes wenkenbachi (e.g., the *Obere Kondel-Gruppe*) that represents the best fauna taken as terminal Lower Devonian as recommended by SCHMIDT (1926) and widely followed. The upper Eifelian fauna with *Pinacites jugleri* is distinct and quite widely spread in Europe, occurring in the Choteč Limestone in Czechoslovakia. The *Cabrieroceras crispiforme* fauna makes the best marker for the basal Givetian; this occurs in the Kačak Member of the Srbsko Formation of Czechoslovakia, but the relations in Belgium are uncertain because it is not recorded there. The late Givetian is characterized by *Maenioceras, Sobolewia, Agoniatites, Foordites, Holzapfeloceras,* late *Cabrieroceras,* and others. Of these, only *Maenioceras* may just range into the *Pharciceras lunulicosta* Zone, taken here as basal Upper Devonian. Useful as these goniatite faunas are for correlation in deeper water facies, their rarity in near-shore and reef facies raises many problems.

The coral *Calceola* has been used as a guide to the Eifelian, and it is widespread in shale facies of that age but is now known to range both lower and higher. The importance of corals generally in calcareous facies in the Middle Devonian of Europe has been indicated in relation to the recognition of assemblages. It was WEDEKIND who did the primary work in Germany (1924-25) and proved the value of this biostratigraphic tool. His scheme recognized five successive faunas throughout the Middle Devonian. From below upward, these include the *Keriophyllum, Astrophyllum, Digonophyllum, Dohmophyllum, Leptoinophyllum, Stenophyllum, Sparganophyllum,* and *Dialytophyllum* zones. The truth is, however, that subsequent work has shown that the ranges of several of the groups used to define these divisions are not as WEDEKIND supposed, and taxonomic revisions have eliminated many of his names (MIDDLETON, 1959; BIRENHEIDE, 1972).

For trilobites there is a break at the Heisdorf-Lauch boundary marked by the disappearance of forms such as *Basidechenella kayseri, Comura defensor,* and *Acastoides henni posthumus* and the appearance of *Pholonyx philonyx, Schizoproetus onyx,* and *Longiproetus cultrijugati.* In higher Eifelian strata scutellids, harpids, phacopids, and thysanopeltids characterize shallower water facies and proetids and subgenera of *Phacops* characterize the deeper water facies. The Givetian limestone facies is characterized by bizarre spinose trilobites such as *Acanthopyge, Radiolichas,* and *Cheirurus,* in addition to traditional groups.

In the basinal argillite sequences, it is the cricoconarids that are important, and detailed zonations have been established, especially for the Eifelian. The earlier faunas have been studied by ALBERTI (1971), and a general review is given by LARDEUX (1969).

As has already been remarked, there have been attempts to collate faunal information in terms of facies faunas, assemblages, or communities for the carbonate facies of the Middle Devonian, but there has been little systematic collation for other facies (HOUSE, 1975b).

ASIA

Treatment here will follow the pattern adopted earlier for the Lower Devonian. Again, the Uralian faunas show close affinity with Europe, but as before those of the Arctic area differ. The Uralian area, embracing now the Altay-Sayan, has the Eifelian brachiopods *Zdmir* [*Conchidiella*] *pseudobaschkirica, Megastrophia uralensis, Carinatina, Janius,* and other European genera. The Altay-Sayan fauna has a number of endemics. In the Givetian, a similar broad pattern is seen, with common European genera such as *Stringocephalus, Bornhardtina, Uncinulus, Schnurella,* and *Emmanuella,* but in the Altay-Sayan the occasional exotic form *Indospirifer* from the east, and rare endemics such as *Urella* occur (NALIVKIN, RZHONSNITSKAYA, and MARKOVSKIY, 1973). In the Givetian, when substantial general transgression had taken place in the Russian area, there seems to be a decrease in provincialism.

The goniatite sequences of the Urals, and indeed of Russia generally, are not well known (BOGOSLOVSKIY in NALIVKIN, ed., 1973, p. 51), although general correlation with Germany is indicated. Little has been achieved in conodont work or in using cricoconarids (LYASHENKO in OSWALD, 1968b).

Paleogeographic distribution of corals, on the other hand, has been reviewed by Dubatolov & Spasskiy (in Oswald, 1968b) and by Spasskiy and others (in Nalivkin, 1973, p. 220, p. 229). The latter authors recognized three broad time divisions of coral faunas in the Russian Middle Devonian, and listed endemics of particular areas. The wide distribution of European forms is striking, but nevertheless they referred Asiatic faunas to a distinct Uralo-Siberian-Asiatic province with only a separate Mongolian fauna (Mongolo-Okhotsk province).

The Dzhungaro-Balkhash region, with *Euryspirifer, Acrospirifer,* and *Fimbrispirifer* in the Eifelian and *Mucrospirifer* higher continues its Appalachian province aspect. Records of corals such as *Heliophyllum* (Spasskiy and others in Nalivkin, 1973) seem to confirm this, but Oliver (1976) casts doubt on the *Heliophyllum* determination. Several of the brachiopod genera occur again in the Tikhookian and Mongolian area, however, confirming the easterly link in general terms. Corals thought to be distinctive of this area include *Stellatophyllum, Pseudotryplasma, Gurjevskiella,* and *Amurolites,* but with *Iowaphyllum* suggesting an easterly link.

The Chinese Middle Devonian is poorly known. Common European coral genera, including *Calceola,* and brachiopods, including *Stringocephalus,* indicate general links with Europe. Apart from the early work on brachiopods by Grabau (1931-33) and Tien (1938), the work on Yunnan corals by Wang (1948) and the revisions by Hamada (in Oswald, 1968a) seem to be the main sources confirming the general picture. But Spasskiy and others (in Nalivkin, 1973, p. 234) united the corals of this area with those of Australia in a common Sino-Australian realm. Rich faunas of corals, tentaculites, and other fossils have been described by Mu and others (1974).

The Tethyan belt has scattered Middle Devonian faunas that generally are most comparable with those of Europe. From near Istanbul Kullmann (1973) recorded *Latanarcestes noeggerati, Anarcestes lateseptatus,* and *Pinacites jugleri* in successively higher beds following Emsian-Eifelian transitional faunas. The Middle Devonian is poorly known in Iran, but Brice (1970) and Durkoop (1970) have reported a varied fauna of brachiopods and corals from Afghanistan, which have a close link with European and Uralian faunas. Reed (1908) recorded both *Calceola* and *Anarcestes* from northern Burma (Anderson, Boucot, & Johnson, 1969), but good Middle Devonian brachiopod faunas are recorded from Viet Nam and Cambodia, assigned mostly to European species, and including *Calceola* and *Stringocephalus.* There are also records of *Stringocephalus* in Malaya (Gobbett, 1966), and Boucot, Johnson, & Struve (1966) have reviewed the distribution of this genus and its relatives.

AUSTRALASIA

In New Zealand there is no evidence that the Lower Devonian faunal sequence continues into the Middle Devonian. In eastern Australia, however, along the area referred to as the Tasman geosyncline, rocks of this age are well developed. In western Australia, although a Middle Devonian transgressive phase has been reported (Teichert, 1974), little has been described; however, *Stringocephalus* and *Stringophyllum* have been reported from the Canning basin (Pickett, 1972). This section is therefore concerned only with eastern Australia.

The formal biostratigraphic subdivision of Philip & Pedder (1967) has already been noted. In this scheme the Middle Devonian embraces divisions G to K. Most localities are in New South Wales and Queensland and are from discrete outcrops. Fauna G, of *Macgeea touti,* marks the incoming of *Dohmophyllum* and *Stringophyllum,* and Fauna H, of *Taimyrophyllum callosum,* marks the first incoming of *Endophyllum.* The *Xystriphyllum giganteum* fauna (Fauna I) contains the early stringocephalid genus *Bornhardtina,* and the top of this fauna contains conodonts that correlate with the *Polygnathus kockelianus* Zone of Europe. Fauna J (of *Grypophyllum* cf. *G. denckmanni*) and Fauna K (of *"Endophyllum" schlueteri*) have been correlated with the European *Polygnathus varcus* Zone (Klapper, Philip, & Jackson, 1970). Much work remains to be done on the brachiopod faunas, but the general European affinity of the coral faunas is clear. But as HILL (1957) and SPASSKIY and others (in NALIVKIN, 1973) pointed out, and has been emphasized by PEDDER, there is much endemism in the faunas at generic and especially specific level. Thus, the Tasman subprovince continued into the Middle Devonian.

AFRICA

There is no evidence that the faunas of the South African Bokkeveld beds, or that of the overlying Witteberg beds, extend upward into the Middle Devonian. The same is true of the Lower Devonian of Ghana. In North Africa, on the other hand, the Middle Devonian is superbly developed (HOLLARD & LEGRAND in OSWALD, 1968a). The fauna is extremely close to that of Europe, but there is evidence of faunal links with the Appalachian area.

A sequence of goniatite faunas from near the Lower-Middle Devonian boundary has been established by HOLLARD (1974). The levels are characterized, in sequence, by *Sellanarcestes wenkenbachi, Anarcestes lateseptatus lateseptatus,* then *A. lateseptatus plebeius* with *Pinacites jugleri.* The *P. jugleri* faunas HOLLARD referred to the upper Eifelian, as in Germany, and he has disproved the earlier date assigned by SOUGY (1969). A widespread fauna containing *Cabrieroceras crispiforme* is taken to mark the basal Givetian (records of Eifelian *Cabrieroceras* from this area refer to forms best assigned to *Werneroceras*). The detailed affinity of this goniatite sequence with that established in Germany is most striking. The *C. crispiforme* levels seem to correlate exactly with the New York *Werneroceras* Bed.

Among brachiopods, too, typical European forms are well represented (DROT, 1964, 1971), but the coral records of *Heliophyllum* and *Phillipsastrea* are of particular interest (LE MAITRE, 1947, 1952). The former is taken, with otherwise endemic eastern North American forms (OLIVER, 1976), to indicate close links with the Appalachian area. The occurrence of *Phillipsastrea* is interesting, as here and in Spain and England it occurs in the Middle Devonian, but generally in Europe it is an Upper Devonian form (SCRUTTON, 1975).

UPPER DEVONIAN FAUNAS

Approximately at the Middle-Upper Devonian boundary there is widespread evidence of renewed transgression (Fig. 8). In the European area this is represented by the extension of marine sediments well on to cratonic areas (HOUSE, 1975a) and there seems to be a good correlation with the Taghanic onlap of North America (JOHNSON, 1970). Thus, by the middle Frasnian, faunas of the Devonian were probably at their most cosmopolitan. Remarkable changes took place during the late Frasnian. Apparently as a result of continued eustatic rise of sea level, or widespread sea-floor subsidence in shelf areas, there was first a restriction of reef carbonates, then the attenuation of those that remained, and finally this facies almost disappeared. Accompanying this was an associated diminution and extinction of the various specialized reef and associated carbonate organisms. The end of the Frasnian apparently saw the extinction of several groups of brachiopods (Pentameroidea, Atrypoidea, possibly Costispiriferidae, and Orthacea), trilobites (harpids, thysanopeltids, Dalmanitacea, Odontopleuridae, Lichidae), coral and stromatoporoid genera, and almost all groups of Devonian cricoconarids (Uniconidae, Tentaculitidae, Homoctenidae, Nowakiidae) (Fig. 7).

This faunal break between the Frasnian and Famennian is a major Phanerozoic event, and apart from the Permian-Triassic break, is probably the most marked in the Paleozoic as a whole. Documentation is not precise enough to state that all these groups became extinct at the same time, but the main extinctions are clearly late in the Frasnian. Some global cause is required, and MCLAREN (1970) argued, doubtless with tongue in cheek, that a meteorite landing in the Devonian "Pacific" could have set up a tidal wave giving near instantaneous extinction. HOUSE (1975a,b), on the other hand, has pointed out the critical relation between the disappearance of reef carbonates and these extinctions.

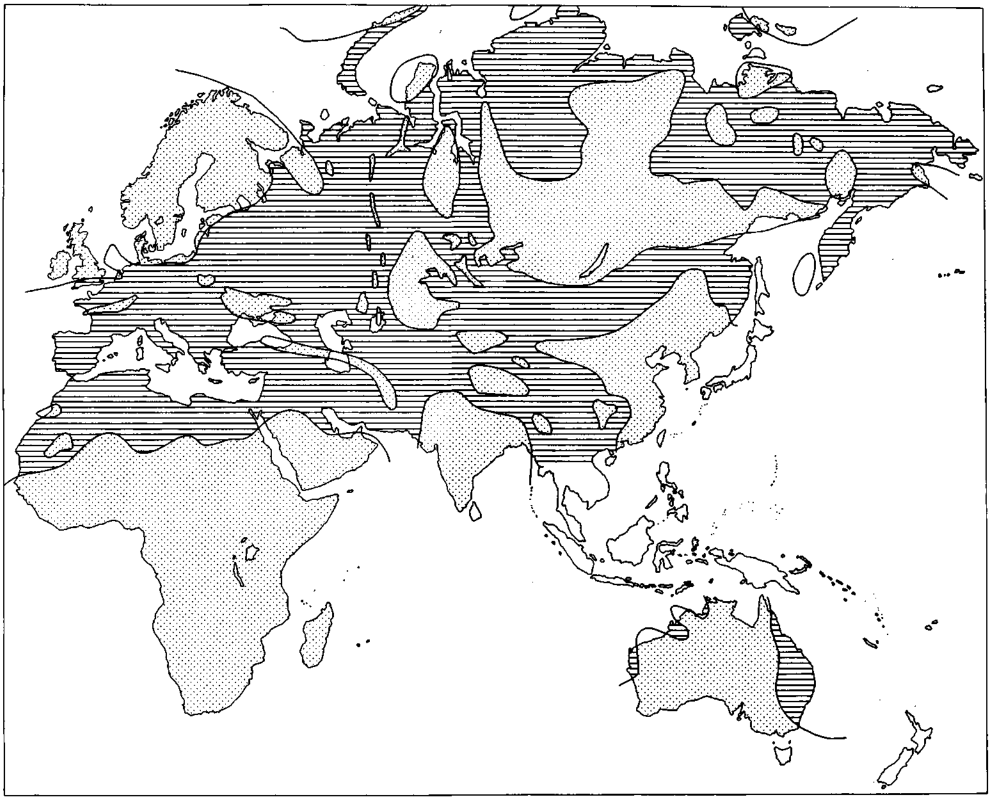


FIG. 8. Paleogeographic map for the Late Devonian (Frasnian) of the Eastern Hemisphere (based on House, 1973; House, n). [Inferred land areas are stippled; areas of marine rocks are horizontally lined.]

Once reefs had gone, not only could their specialized inhabitants not survive, but the removal of any protection that reef carbonates may have provided at platform margins would have rendered vulnerable many other shelf environments.

Faunally, as a result of these events, the Famennian represents a discrete interval terminated by further extinctions (Clymenoidea, Phacopidae) at the close of the stage. The almost complete absence of organodetrital carbonates and associated faunas, the replacement of well-known brachiopod groups by a development of rhynchonellids and spiriferids, the entry and diversity of the clymenoid ammonoids, and in the basinal environment, the replacement of coniconchines by the planktonic ostracodes give a quite different stamp to the Famennian. Some element of provincialism remains, for example, the restriction of well-developed ostracode slate facies to Europe and the Urals, but it is quite diminished in comparison with the Lower and Middle Devonian.

EUROPEAN FRASNIAN

The progressive series of transgressions throughout the Frasnian of Europe resulted in limited preservation of nearshore clastic facies. Better represented are carbonate and reef complexes, basinal argillites, and the reduced successions of seamount *Schwellen*. But these, as has already been indicated, show faunal distinction from those of the Middle Devonian following the extinctions of particularly coral, brachiopod, and trilobite groups near the end of the Givetian. As used here the Frasnian is treated as synonymous, or nearly so, with the Adorfian, named from the reduced goniatite-rich sequence of the northern Schiefergebirge.

The type Frasnian area is in southern Belgium where spectacular knoll-like reef masses are developed in the middle Frasnian, although they appear to have been overwhelmed in the *Palmatolepis gigas* Zone with the onset of the terminal Frasnian transgressions. *Cyrtospirifer,* long considered the main guide to the Upper Devonian, enters in the basal Assise de Fromelennes (LECOMPTE in OSWALD, 1968a) and this explains why the base of the Frasnian was defined at that level in 1952. Other so-called guide fossils include *Hypothyridina cuboides* and *Phillipsastrea hennahi,* but both perhaps have their original types from the Givetian (ORCHARD, 1974; SCRUTTON, 1968). BOUCOT (1975) has indicated a range of brachiopod genera restricted to the Frasnian. The type Frasnian reefs were studied by LECOMPTE (1970 and earlier works) and formed part of the basis for the recognition of depth zonation. This approach has been followed by TSIEN (1971).

Reduced successions of the pelagic carbonates have provided the type sequences for both the goniatite and conodont zonations, which were established at Adorf (now Diemelsee). The distinction of the basal Adorfian goniatite faunas is the occurrence of multilobed pharciceratids such as *Pharciceras* and *Sympharciceras,* also *Epitornoceras, Ponticeras, Probeloceras,* and others unknown in the Middle Devonian. In the middle Fasnian are the typical *Manticoceras* and *Beloceras. Crickites holzapfel* and others characterize the late Frasnian. The pyritic or hematitic fauna of contemporary shales is referred to as the Büdesheimer Schiefer. The goniatite sequence was established mainly by WEDEKIND (1913). The conodont sequence was established by ZIEGLER (1958, 1962), but, as remarked before, certain correlation between the two schemes has not been achieved.

The gradual dominance of fingerprint ostracodes over cricoconarids in the photic zones of the basinal regions took place through the Frasnian, a typical succession being described by KREBS and RABIEN (1964) and this is reproducible in other European areas.

One particularly unusual facies, the two Kellwasserkalk bituminous limestones, were recognized by BUGGISCH (1972) over wide areas of Europe and in North Africa. These carry a remarkable fish fauna and goniatites, orthocones, and even coprolites with conodont assemblages (LANGE, 1968). BUGGISCH considered these units were formed at times of transgression during which large quantities of organic matter were deposited. The deepening in pulses that terminated the various periods of reef development in Belgium were of similar type.

A striking coherence exists in the pattern of Frasnian facies and faunas found in western Europe and North Africa. In the Main Devonian Field near Leningrad, and in the Timan Mountains, widespread shallow-water calcareous environments have rather distinctive brachiopod faunas (LYASHENKO, 1959; NALIVKIN, RZHONSNITSKAYA, & MARKOVSKIY, 1973) and goniatite faunas (BOGOSLOVSKIY, 1969, 1971) that have similarities with Cordilleran types. Also, a cricoconarid sequence, more detailed than elsewhere, has been described (LYASHENKO, 1959). The abundance of fish in interleaving horizons makes this a critical area for correlation into the Old Red Sandstone facies (WESTOLL in HOUSE, 1977).

EUROPEAN FAMENNIAN

The almost complete absence of biohermal carbonates is the most distinctive feature of the Famennian biofacies of Europe. From the Holy Cross Mountains of Poland ROZKOWSKA (1969) has described a sparse fauna of four phillipsastreaid individuals, some endophyllids, one genus of cystiphylloids and the earliest known heterophylloids from the early Famennian, and this is the best European Famennian coral fauna known. The limited stromatoporoid fauna of the Etroeungt (LE MAITRE, 1933) represents the best occurrence of that group. The result is a marked contrast with the earlier Devonian.

In the shallower water, clastic-rich facies brachiopod and bivalve faunas are well developed, the former dominated by rhynchonellids (SARTENAER in OSWALD, 1968b) and spiriferines. SARTENAER recognized in France and Belgium his international *Eoparaphorhynchus* and *Basilicorhynchus* zones of the lower Famennian, but higher faunas are not well discriminated. In northern Europe, this facies intertongues with Old Red Sandstone type terrestrial facies in which fish, plant, and spore remains are common.

In the deeper water argillite facies only proetids and phacopids remain of trilobite groups. The most remarkable feature is the dominance of planktonic Ostracoda, which often cover bedding planes in the Cypridinenschiefer facies; with them are bivalves, such as *Karadjalia venusta,* which may have been epiplanktonic on floating weed. In shallower silty facies the infaunal *Sanguinolites* is characteristic.

Occurring in the argillites, especially in hematitic or pyritic facies, but more particularly in the seamount or pelagic carbonates, are the rich and varied ammonoid faunas. The goniatite *Cheiloceras* characterizes the earliest Famennian, and then the clymeniids enter, characterizing the later Famennian and showing remarkable diversity until their sudden extinction in the late *Wocklumeria* Stufe. Goniatites such as *Sporadoceras* and *Imitoceras,* and also nautiloids, accompany them; however, for biostratigraphical purposes, it is the conodont sequence established especially by ZIEGLER (1962, 1971) that has international importance and, for the Famennian, this seems well linked to the ammonoid scale.

Much detailed work has been done in Europe on the correlation of beds near the Devonian-Carboniferous boundary (AUSTIN, *et al.,* 1970; VÖHRINGER, 1960; ZIEGLER, SANDBERG, & AUSTIN, 1974). The boundary, in the German (and Heerlen and Sheffield congresses) definition, is marked by the extinction of both clymeniids and phacopids, whereas in the Belgian and Russian definitions the boundary is difficult to diagnose except at low taxonomic levels.

ASIA

For this enormous area the Frasnian and Famennian are here treated together. In the Upper Devonian of Asia the broad geosynclinal tracts recognized earlier in the Devonian remain broadly discrete. These are 1) the Ural belt, including Novaya Zemlya in the north and the Tien Shan and Kazakhstan in the south, 2) the northern Siberian areas of shallow-water sedimentation conveniently termed the Arctic area, 3) the Altay-Sayan area, 4) the Dzhungaro-Balkhash area, linking through the poorly known regions of China and Mongolia to the east, 5) the Tikhookian region of southeast Russia, 6) the Chinese area south of the Peking platform, and 7) the tract of separated and disjunct outcrops from Turkey to Southeast Asia. This grouping (based in part on NALIVKIN, RZHONSNITSKAYA, & MARKOWSKIY, 1973) is here used for discussion.

In the Frasnian and Famennian, the Uralian and Arctic area, comprising the Atlantic region of Russian authors, is essentially of European type. Even the characteristic basinal and seamount facies are known in the Urals. When faunas were most cosmopolitan, in the Frasnian, typical European genera such as *Manticoceras, Hypothyridina, Ladogia, Theodossia,* and *Mucrospirifer* were widely distributed across this broad area. *Ladogioides,* a Cordilleran type, occurs in northeast Siberia. Endemics were rare; among goniatites there is *Tamarites,* probably earliest Frasnian in age. *Manticoceras* of the middle Frasnian is widely distributed (HOUSE, 1973b). The rich coral faunas (DUBATOLOV & SPASSKIY in NALIVKIN, 1973) show less provincialism than earlier in the Devonian and the typical Frasnian genera of Europe are abundant. The apparent uniqueness of the cricoconarid faunas of the Russian platform and Urals in the Frasnian results mainly from the lack of detailed studies elsewhere.

The Uralian and Arctic areas show faunal differences in the Famennian. The former resembles European biofacies and contains a very similar ammonoid sequence (BOGOSLOVSKIY, 1971) and, although only briefly described, the conodont sequence has broad similarities (KHALYMBADZHA & CHERNYSHEVA, 1970), but the brachiopods *Zilimia* and *Dzieduszichia* occur in addition to common European genera. In the Arctic area Famennian ammonoids are very rare, and distinction is given by the occurrence of *Gastrodetoechia* (according to NALIVKIN, RZHONSNITSKAYA, & MARKOWSKIY, 1973, but not recorded by SARTENAER, 1969), a brachiopod common in western North America.

In the Altay-Sayan area, both in the

Frasnian and Famennian, there are close links faunally to the Urals, but faunas of the Kazakhstan area and the Dzhungaro-Balkhash region contain the eastern brachiopod *Yunnanella,* according to NALIVKIN, RZHONSNITSKAYA, & MARKOVSKIY (1973), but SARTENAER (1971) has reassigned most of the specimens on which the genus was recognized. Other evidence of eastern faunal affinity is the record by BOGOSLOVSKIY (1971) of *Sinotites* in the Aktyubinsk district, a genus otherwise known only in the Great Khingan.

The Tikhookian and Mongolian late Devonian faunas include cyrtospiriferids and other brachiopods, many of which are assigned in the literature to New York species. To the south is the remarkable sequence of the Great Khingan (CHANG, 1958). Here the Lower Suhuho Formation, with *Sinospirifer,* atrypids, *Yunnanella,* and *Nayunella* (SARTENAER, 1971), has been referred to the Frasnian. The overlying Upper Suhuho Formation contains a rich goniatite fauna of early Famennian age, including *Cheiloceras, Sporadoceras,* and *Pseudoclymenia,* whereas *Platyclymenia* indicates a middle Famennian age. CHANG (1960) has described the peculiar goniatites *Sinotites* and *Sunites* from here, which are endemic apart from the Aktubinskayan record mentioned above.

The main Upper Devonian records in China are from Yunnan, Kwangsi, Hunan, and Szechwan. The typical Frasnian goniatites *Manticoceras, Beloceras, Eobeloceras,* and *Ponticeras* occur in this area (CHAO, 1956), but there has been considerable doubt as to whether the Famennian is represented at all, a substantial post-Devonian break being thought to be present above the Frasnian. Whether the *Yunnanella*-bearing rocks, which are very widespread (SARTENAER, 1971), are wholly Frasnian is not clear. The earliest Famennian may be present, but atrypids recorded in association with *Yunnanella* suggest that only Frasnian is involved. This is of some importance because the type species of *Cyrtiopsis* is from this region, and in North America this genus has been taken as a Famennian guide. According to the review by SPASSKIY and others (in NALIVKIN, 1973), the Frasnian coral fauna is broadly similar to that of Asia and Australia. The plant *Leptophloeum* is widespread in more terrestrial facies in China, Japan, and also eastern Australia (HAMADA in OSWALD, 1968a). Evidence of late Famennian in southwest China comes from the record of *Cymaclymenia* and *Parawocklumeria* by MU and others (1974).

Upper Devonian rocks are widely exposed in scattered outcrops along the Tethys belt. In Iran, brachiopods of Frasnian age, such as *Ripidiorhynchus* and *Cyphoterorhynchus* are widespread (SARTENAER, 1966), *Cyphoterorhynchus* being found also from Armenia to Pakistan. Early Famennian *Gastrodetoechia* faunas occur, and in the Tabaz area there is a fauna of *Platyclymenia, Sporadoceras,* and *Prionoceras* (WALLISER, 1966). Much richer faunas have been described from Afghanistan by BRICE (1970), including a variety of corals from carbonate horizons. A rich fauna of brachiopods and corals is known from the Northern Shan States (REED, 1908), which includes a record of *Phillipsastrea* and brachiopods seemingly of Frasnian age. Scattered records of Late Devonian in Cambodia, Viet Nam, and Thailand exist. An interesting tie with Europe is the occurrence of the trilobite *Cyrtosymbole (Waribole)* from Malaya (KOBAYASHI & HAMADA, 1966). This is an exotic occurrence of a subgenus abundant in western Europe and eastward to Kazakhstan. So much has still to be learned about these faunas that generalizations are premature. Nevertheless, the affinities with faunas of Europe and the southern Uralian belt seem sufficiently strong to confirm the same provincial assignment given to earlier Devonian faunas.

AUSTRALASIA

The Upper Devonian of Australia (ROBERTS *et al.,* 1972) shows a continued development along the Tasman geosyncline, but additionally spectacular reef development occurs marginal to the Precambrian shield in Western Australia.

In eastern Australia terrestrial facies occur in many areas with European fish genera and *Leptophloeum* and other plant remains of Late Devonian type. Good marine faunas in Queensland include Frasnian corals, cyrtospiriferids and other Frasnian brachiopods and typical European conodonts. McKellar (1970) has established a series of Famennian zones using productoids, some of which have affinities with the western United States as well as with Europe. Other faunas, including *"Cyrtiopsis," Cyrtospirifer,* and *Tenticospirifer,* may be compared with Chinese and European forms. In New South Wales conodonts have enabled correlation with the European zonation in several places (Philip & Jackson, 1971), the faunas ranging through the Frasnian and Famennian. Also known are the Famennian ammonoid genera *Cheiloceras, Genuclymenia, Platyclymenia,* and *Cymaclymenia* (Jenkins, 1968; Pickett, 1960).

The remarkable Frasnian reef sequences of the Canning basin (Playford & Lowry, 1966) and other developments in the Bonaparte Gulf basin and Carnarvon basin are significant for their incredibly close affinity with European faunas. For many goniatites (Glenister, 1958; Petersen, 1975) this is at specific level, as it is for the conodonts (Druce, 1969; Glenister & Klapper, 1966), brachiopods (Veevers, 1959a,b), and phyllocarid crustaceans and other groups (Brunton *et al.,* 1969). *Fitzroyella,* one supposed endemic brachiopod, has since been recorded in Poland (Biernat, 1969). Although indicated in the literature, it would appear that the evidence for the stromatoporoid reef facies extending up into the Famennian in this area is very slight; the Famennian reefs are stromatolitic.

AFRICA

It is only in North Africa that Upper Devonian rocks are preserved and there the faunal agreement with Germany is particularly close. This is well illustrated by the ammonoid sequences (Petter, 1959, 1960), which replicate the standard successions. Goniatite faunas near the Middle-Upper Devonian boundary have been described by Bensaid (1974), who showed that the base of the *Pharciceras lunulicosta* Zone (and *Manticoceras* Stufe) falls within the *Polygnathus varcus* Zone of the conodont zonation, thus solving anomalies in other areas (House, 1973a). The rare endemic form *Petteroceras* is in a fauna mostly conspecific with German forms. This area has also contributed to the correlation of conodont and ammonoid zonations near the Frasnian-Famennian boundary, and Buggisch & Clausen (1972) have demonstrated that the boundary between the *Manticoceras* and *Cheiloceras* Stufen falls at the base of the upper *Palmatolepis triangularis* Zone. Their recognition of the Kellwasser Kalk facies of Germany at the expected levels is another tie.

For other groups also, the congruence with central Europe is apparent. Alberti (1973) recognized only a few new forms of trilobites from the Famennian. For corals, provincialism is mostly lost by the Frasnian, so similarities with eastern North America (Oliver, 1976) are to be expected. North Africa is an area in which much has still to be contributed in detailed biostratigraphy.

DEVONIAN GLOBAL RECONSTRUCTION

Paleomagnetic data allow some approximation to be made on the position of the continents in relation to the magnetic poles and equator in the Devonian. It is assumed that then, as now, the dipole field axis was approximately coincident with the earth's rotational axis. The paleomagnetic evidence cannot give longitude position, and hence positioning of continental masses along lines of latitude is an arbitrary matter and can be changed at will, guided only by the constraints of any geological demands. In the reconstruction given here (Fig. 9), the positioning of the southern continents is that of Briden, Drewry, & Smith (1974), and the same authors in Hughes (1973); the situation is given by them as the same throughout the Devonian. For the northern continents, following the arguments of Roy (1971), the Late Devonian reconstruction brings North America and Europe close together. Russian evidence (Khramov in Oswald, 1968b) would bring Asia perhaps five degrees or so farther south than shown.

It is clear from this reconstruction that

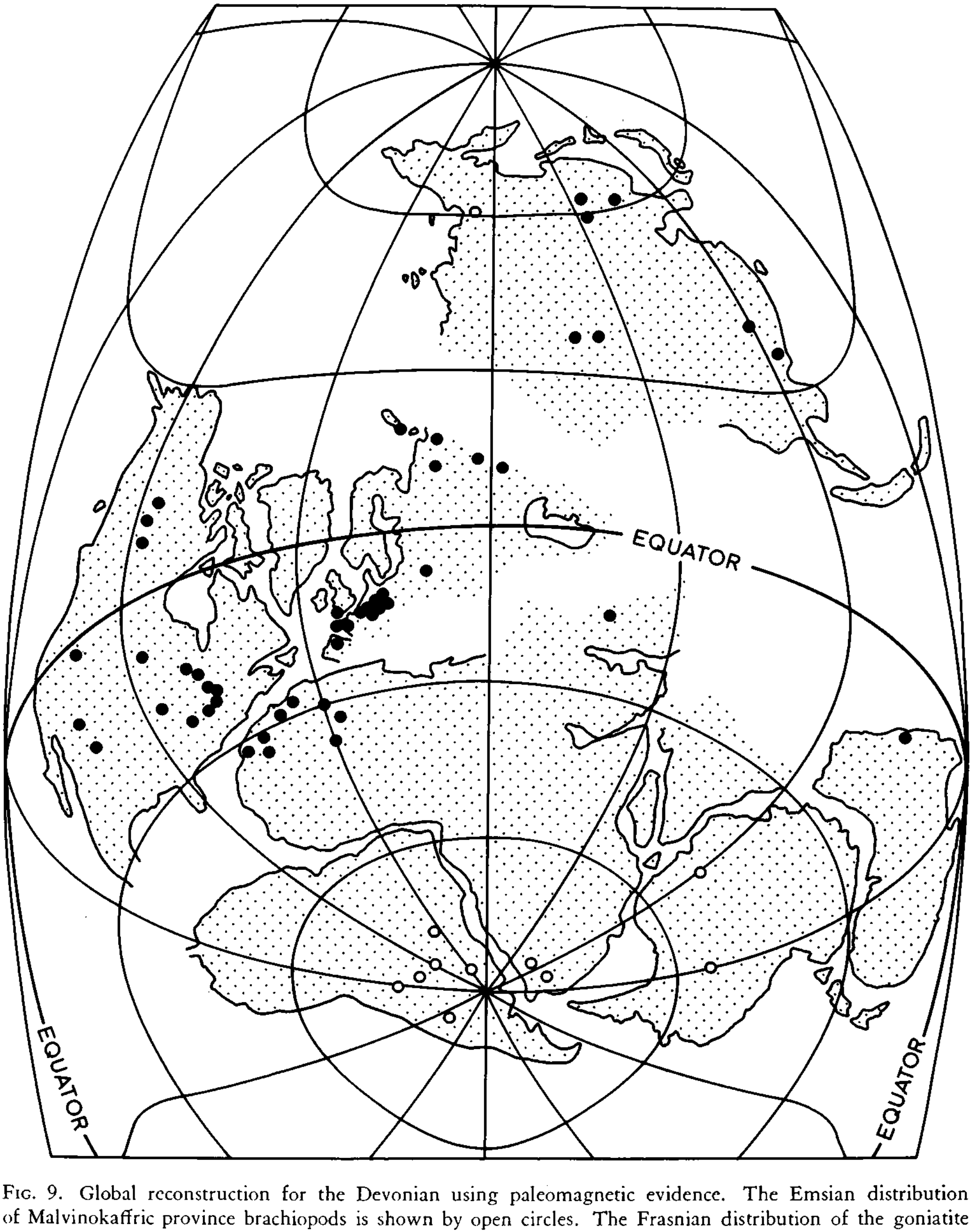


FIG. 9. Global reconstruction for the Devonian using paleomagnetic evidence. The Emsian distribution of Malvinokaffric province brachiopods is shown by open circles. The Frasnian distribution of the goniatite *Manticoceras* is shown by black circles. Note that southeast Asia was probably discrete microplates, the positions of which are uncertain (House, n; for sources see text).

the Malvinokaffric province of the Emsian has essentially a high latitude fauna, and this fact may be the main cause of its uniqueness. Of the divisions of the Old World province, the Rhenish-Bohemian subprovince is clearly tropical (HOUSE, 1975a,b), as is the Uralian subprovince, but the Siberian Arctic faunas, and those of the Angaran and Tethyan belts, are progressively of higher latitude. The break between the Appalachian province and that of the Old World may be explained in two ways.

Firstly, some paleomagnetic reconstructions place North America in a much more southerly position than that given here for the Lower Devonian, when the provincialism was best developed. Secondly, the Caledonian orogeny and mid-Acadian orogeny appear to have interposed an oblique mountain barrier stretching from eastern Greenland and Norway southwestward, between eastern North America and northwest Africa. The latter would have been an effective barrier to migration, although in the Frasnian its effects were mostly lost.

The Appalachian province links with the Mongolian, Tikhookian, and Dzhungaro-Balkhash areas are less readily explained, and the problem looks deceptively easy when only present-day projections are used (as in BOUCOT, 1975, and elsewhere). Cordilleran links with Europe north of the Old Red Sandstone continental area, and with Arctic Siberia, pose fewer problems.

Attempts at global reconstruction using plate tectonic principles have not progressed very far. After the establishment of the Caledonian Mountain belt, the European Hercynian (Armorican, Variscan) geosynclinal belt stretched from Cornwall and Britanny eastward to beyond southern Poland. This has been interpreted as a subduction zone, some authors inferring subduction to the north (BURRETT, 1972; RIDING, 1974), others to the south (ANDERSON, 1975). But the review by KREBS & WACHENDORF (1973) and the various opinions expressed by others, make the placing of any Benioff Zone uncertain, and the possibility of microplate accretion in the southerly belts adds to this uncertainty. RIDING (1974), following many earlier authors, linked the European Hercynian belt with that of the Piedmont and Ouachita belt of eastern North America.

The Ural belt shows some of the characteristics of another subduction belt, but the interpretation of the southern and central Asiatic fold belts in the Devonian is exceedingly difficult, particularly because the northward movement of India through the later Phanerozoic, which is so well documented, may have been associated with microplate accretion. All this will not be resolved until much more detailed paleomagnetic evidence is available.

Using modern-day maps, even more problems relate to the inferred link between Siberia and western North America. CHURKIN (1973) has argued that the Franklinian geosyncline of the Canadian Arctic Islands may have linked with the ancestral Brooks Range belt of Alaska to join the Chukotka geosyncline of northeast Siberia, and he separated this from the Cordilleran geosyncline, which he linked with the Koryak geosyncline of northern Kamchatka. As has been indicated in the preceding pages, there is faunal evidence for some link of this kind, and the proposed paleomagnetic position for Asia seems sufficiently at variance to make it suspect. For the southern continents, the link of the Tasman geosyncline with the Transantarctic Mountain belt in Antarctica has been long attested.

It is clear that in the Devonian shallow seas were widespread over present continental areas (Fig. 5,6,8). The plate tectonic model requires that ocean areas would also have been oceanic in the Devonian, so enormous spreads of seas covered the Devonian globe. It is also clear that ice caps, if they existed, were unlikely to have been large. It would seem, therefore, that a generally much warmer world climate than at present was partly the cause of the enormous diversity of Devonian marine faunas, and was the background for the remarkable development of vascular plants and early vertebrates in the period.

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DEVONIAN IN THE WESTERN HEMISPHERE[1]

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CONTENTS

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INTRODUCTION

The Devonian System was proposed by SEDGWICK and MURCHISON in 1839 for marine rocks in Devon, England, that were the lateral equivalent of the Old Red Sandstone of Scotland and the Welsh Borders (HOUSE, 1964, p. 262). In North America the Devonian System was recognized in 1847 as a result of a visit and the subsequent writings of DE VERNEUIL, whose views were made known by HALL (COOPER *et al.*, 1942, p. 1729). Since 1847, marine and continental Devonian deposits have been recognized in many widespread areas of the Western Hemisphere.

Radiometric evidence on the limits of the Devonian Period on the geological time scale, summarized by FRIEND and HOUSE (1964, p. 233-236), suggests that the base and top of the Devonian should be dated at about 395 and 345 million years, respectively. Using cumulative thicknesses, they estimated the ages of the base of the Middle Devonian at about 370 million years and that of the base of the Upper Devonian at about 358 million years. Accordingly, the approximate durations for the Early, Middle, and Late Devonian are 25, 12 and 13 million years, respectively.

Recent precise radiometric age estimates of the base of the Devonian in eastern North America (BOTTINO & FULLAGAR, 1966) and the top of the Devonian in Victoria, Australia (MCDOUGALL *et al.*, 1966), were 413 ±5 my and 363 ±6 my, respectively.

More recently the International Geochronological Commission (IUGS, 1967) proposed recommendations for a standard global chronostratigraphic (geochronologic) scale in which the averaged datings for the base and top of the Devonian were given as 405 and 350 million years, respectively, with a duration of 55 million years.

Hypothetical Devonian paleolatitudes have been illustrated by JOHNSON (1970c, p. 2088, fig. 6), SMITH *et al.* (1973, fig. 12), and others. JOHNSON showed the equator extending diagonally across North America from near the north end of the Gulf of California in the west to the southern part of James Bay in the east.

Paleogeographic and biogeographic data have been used by numerous workers in reconstructions involving the plate tectonic theory. Various data suggest that the Old and New Worlds were juxtaposed during the Devonian, or nearly so at the beginning of the Devonian (JOHNSON & DASCH, 1972). Regarding the southern continents, the existence of Gondwanaland accounts for the Malvinokaffric distributions in South America, and the Falkland Islands and Antarctica in the Western Hemisphere (JOHNSON & BOUCOT, 1973, p. 95).

The main areas of Devonian rocks in the Western Hemisphere, both in outcrop and the subsurface, are shown in a general way in Figure 1. The distribution of Lower, Middle, and Upper Devonian rocks is shown in Figures 2 to 5. These illustrate the known present distribution for North America and Greenland as generalized facies maps from which more interpretive paleogeographic maps may be drawn if so desired. For South America, where the Devonian sediments consist mainly of clastic rocks and where the geology is known in considerably less detail, the distribution of Lower, Middle, and Upper Devonian is shown on paleogeographic maps. The standard Devonian ammonoid and conodont zones of Europe and North America, along with some other zones and ranges of selected species in Devonian rocks of North America, are shown in Figures 6 and 7.

MAIN AREAS OF DEVONIAN ROCKS

NORTH AMERICA

In North America two main areas of Devonian rocks incompletely surround the Canadian shield on its south, southwest, and north sides (Fig. 1). One is centered in northeastern United States and adjoining eastern Canada, and the other extends southwestward through the Arctic Islands into northern continental Canada and then south-southeastward to north-central United States. These two main areas are separated from one another by a northeast-trending transcontinental arch which extends from New Mexico to Hudson Bay. Thick, but areally restricted remnants of the Cordil-

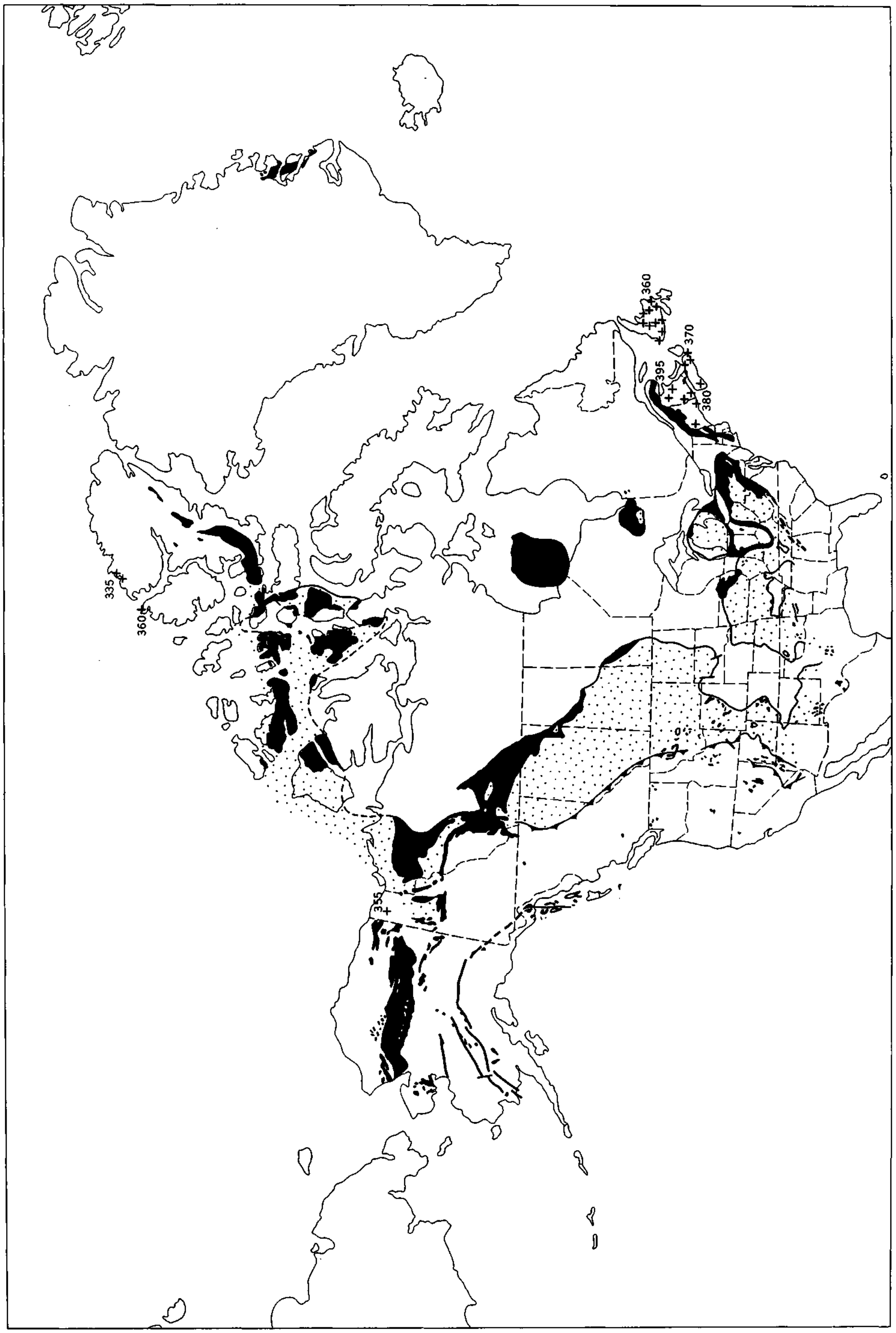


FIG. 1. *(See facing page.)*

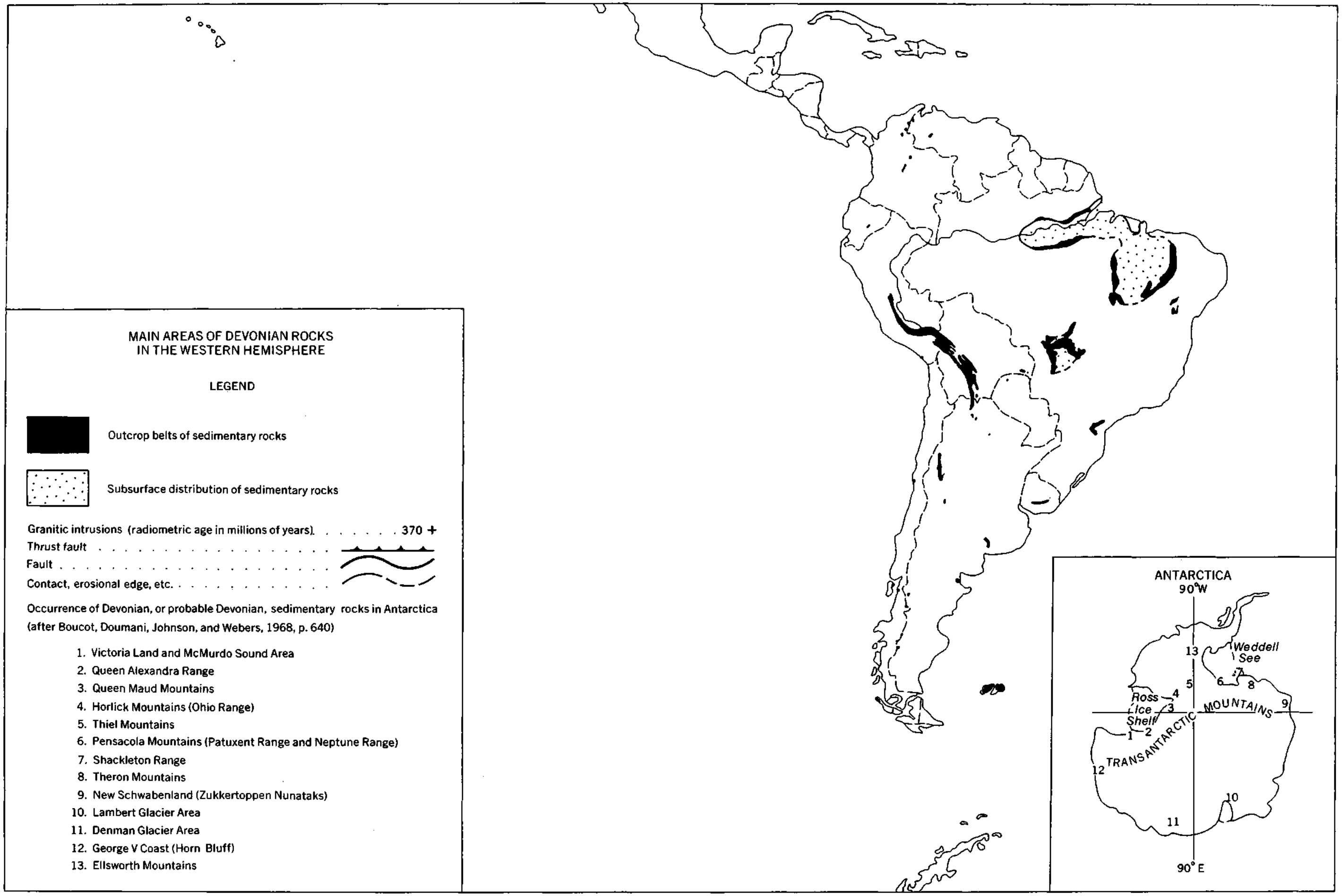


FIG. 1. Main areas of Devonian rocks in the Western Hemisphere (Norris, n).

leran geosyncline are present in the Nevada-Idaho basin of west-central United States.

Devonian rocks are widespread also in Alaska but are incompletely known. The rocks of southeastern Alaska are of eugeosynclinal origin, those in northern Alaska are in a miogeosynclinal belt, and a possible intervening shelf-like environment is suggested for the rocks in the vicinity of the Porcupine and Kuskokwim rivers (Gryc *et al.,* 1968).

Devonian rocks are present also in two intracratonic basins; the Moose River and Hudson Bay in the Hudson platform, which are lithologically and faunally related to the Appalachian sequence of eastern North America (Sanford & Norris, 1975).

GREENLAND

In the folded belt of central East Greenland, bordering the Greenland shield, continental rocks interbedded with volcanic rocks are present in an elongated basin (Fig. 1) where they overlie Caledonian folded formations (Butler, 1961). The sequence is 7,000 to 8,000 meters thick and contains rocks of late Middle (Givetian) and Late Devonian (Frasnian and Famennian) ages dated on rich vertebrate faunas (Allen *et al.,* 1968).

Besides the vertebrates, the arthropod *Estheria* is the only invertebrate found in the East Greenland Devonian succession, and fossil plants, although locally abundant, are generally poorly preserved (Haller, 1971, p. 246). The exceedingly rich vertebrate faunas of East Greenland, summarized by Jarvik (1961, 1963), have attracted considerable interest. Among the large collections of vertebrate remains are forms that are unique to East Greenland and forms showing the transition from fish to tetrapod (e.g., *Ichthyostegalia*).

Devonian continental beds are present also on Spitsbergen (Friend, 1961) and on Bear Island (Holtedahl, 1919) which, along with the Greenland deposits, are interpreted as remnants of the Old Red Sandstone continent (House, 1968b).

SOUTH AMERICA AND FALKLAND ISLANDS

The distribution (Fig. 1) and paleogeography of Devonian rocks of South America and the Falkland Islands (Fig. 2 to 5) have been described by Weeks (1947), Harrington (1962, 1968), and others.

Numerous scattered outcrop belts of Devonian rocks of geosynclinal origin are present in the Andean orogenic belt that borders the entire western margin of the continent, and these occur in Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina, and Chile. Devonian deposits in the pericratonic basins that lie between the Andean folded belt and stable cratonic areas occur in eastern Bolivia, Paraguay, and the Falkland Islands. Large outcrop belts of Devonian rocks are present also in the intercratonic basins, which include the Amazonas basin of northern Brazil, the Parnaíba and São Francisco basins of eastern Brazil, and the Paraná basin of southern Brazil and Uruguay.

A peculiarity of the Devonian of South America is that carbonate rocks are confined to the Andes of the northern part of the continent in the Colombian-Venezuelan frontier area; southward this limy facies gives way to clastic rocks. Caster (1952) has postulated that temperature was probably the critical lime-controlling factor, and that the Devonian sediments of a large part of South America were deposited under a cool regime that inhibited the precipitation of calcium carbonate.

The Devonian sequence of the Falkland Islands has been described by Baker (1923), and summarized by Harrington (1968). Lithologically, this sequence is strikingly similar to that of South Africa, but the Lower Devonian marine faunas are related more closely to those of Brazil. The lower two-thirds of the succession represent shallow-marine deposits, whereas the upper third is of continental, fluviatile origin.

ANTARCTICA

Devonian rocks of Antarctica have been described by Boucot *et al.* (1968). They indicated that Devonian, or probable Devonian, rocks had been recognized from only thirteen scattered localities in ice-free areas around the edge of the continent (Fig. 1). Five of the localities are in or near the Ross Ice Shelf, four are in or near the Filchner Ice Shelf, and the remaining four localities are widely separated in East Antarctica.

The Devonian of Antarctica is part of a succession of sedimentary strata belonging to the Beacon Group. Fish remains, assigned to the Upper or Middle Devonian (Woodward, 1921) have been collected from central Victoria Land. A Lower Devonian marine fauna has been described by Boucot *et al.* (1963) and by Doumani *et al.* (1965) from the Horlick Formation in the Ohio Mountains.

SILURIAN-DEVONIAN BOUNDARY

Most workers throughout the world now agree in placing the Silurian-Devonian boundary at the base of the Gedinnian. This boundary coincides with the base of the *Monograptus uniformis* Zone and is close to the base of the *Icriodus woschmidti* Zone. In shelly successions with corals, brachiopods, and trilobites the boundary is recognizable by the disappearance of pentamerids, *Atrypella, Gracianella,* halysitids, and *Encrinurus,* and by the appearance of terebratulids, *Cyrtina,* and common *Schizophoria* (Berdan *et al.*, 1969).

Recently this boundary was fixed by international agreement on a stratotype at Klonk near Suchomasty, Bohemia, Czechoslovakia. The horizon chosen is immediately below the first occurrence of *Monograptus uniformis,* within bed 20 at Klonk (Chlupáč, 1972, p. 111, 113; McLaren, 1972). The base of the Gedinnian coincides with the base of the Lochkovian (in Nalivkin, 1973, p. 12).

In the standard section of eastern North America the base of the Devonian, defined as the base of the Gedinnian, is located at or near the base of the Helderbergian, which traditionally has been regarded as the lowermost Lower Devonian stage (Berdan *et al.*, 1969).

LOWER DEVONIAN FAUNAS (GEDINNIAN, SIEGENIAN, AND EMSIAN)

EASTERN NORTH AMERICA

The Lower Devonian marine sedimentary sequence of the Appalachian area contains coral, brachiopod, and trilobite faunas of pronounced provincial aspect. Four brachiopod zones, based on rensselariid evolution, were recognized by Boucot and Johnson (1967, 1968) as follows: 1) *Nanothyris* Zone, occurring in the Manlius-Coeymans and Kalkberg-New Scotland intervals (Gedinnian age); 2) *Rensselaeria* Zone, in the Becraft-Port Ewen of the upper Helderbergian and in the Oriskany (Siegenian age); 3) *Etymothyris* Zone; and 4) *Amphigenia* (small form) Zone. The latter two zones occur in the Esopus and Schoharie-Bois Blanc intervals (Emsian age).

Brachiopod assemblage zones were recognized by Boucot and Johnson (1967, 1968) also in those areas where the rensselaeriid zones are poorly represented or absent.

Notable rugose coral assemblages were reported by Oliver (1968) in the Helderberg (Gedinnian and lower Siegenian) and middle Onesquethaw (Emsian). Rugose coral genera occurring in stromatoporoid biostrome facies of the Helderberg include: *Spongyphylloides, Chlamydophyllum,* and *Lyrielasma*; in argillaceous facies: *Cyathophyllum, Enterolasma, Heterophrentis, Siphonophrentis, Lindostroemia,* and *Syringaxon*; and in calcarenite facies, characteristic genera are *Briantelasma, Fletcherina, Nalivkinella, Pseudoblothrophyllum,* and *Aknisophyllum* (Oliver, 1968).

Few corals are known from the lower part of the Onesquethaw (Esopus), but the small assemblage contains the oldest known *"Billingsastraea" (=Asterobillingsa)* (Oliver, 1968, p. 740).

The Schoharie (Emsian) fauna includes the largest and most widespread of the rugose coral assemblages. Some of the more important forms include *Acinophyllum davisi, Acrophyllum oneidaense, Edaphophyllum sulcatum,* and *Kionelasma* (Oliver, 1968, p. 740).

Lower Devonian trilobites in eastern North America also display marked provinciality and their provincial distribution is similar to that of the brachiopods (Ormiston, 1972). Gedinnian endemic genera include *Cordania, Roncellia, Neoprobolium,*

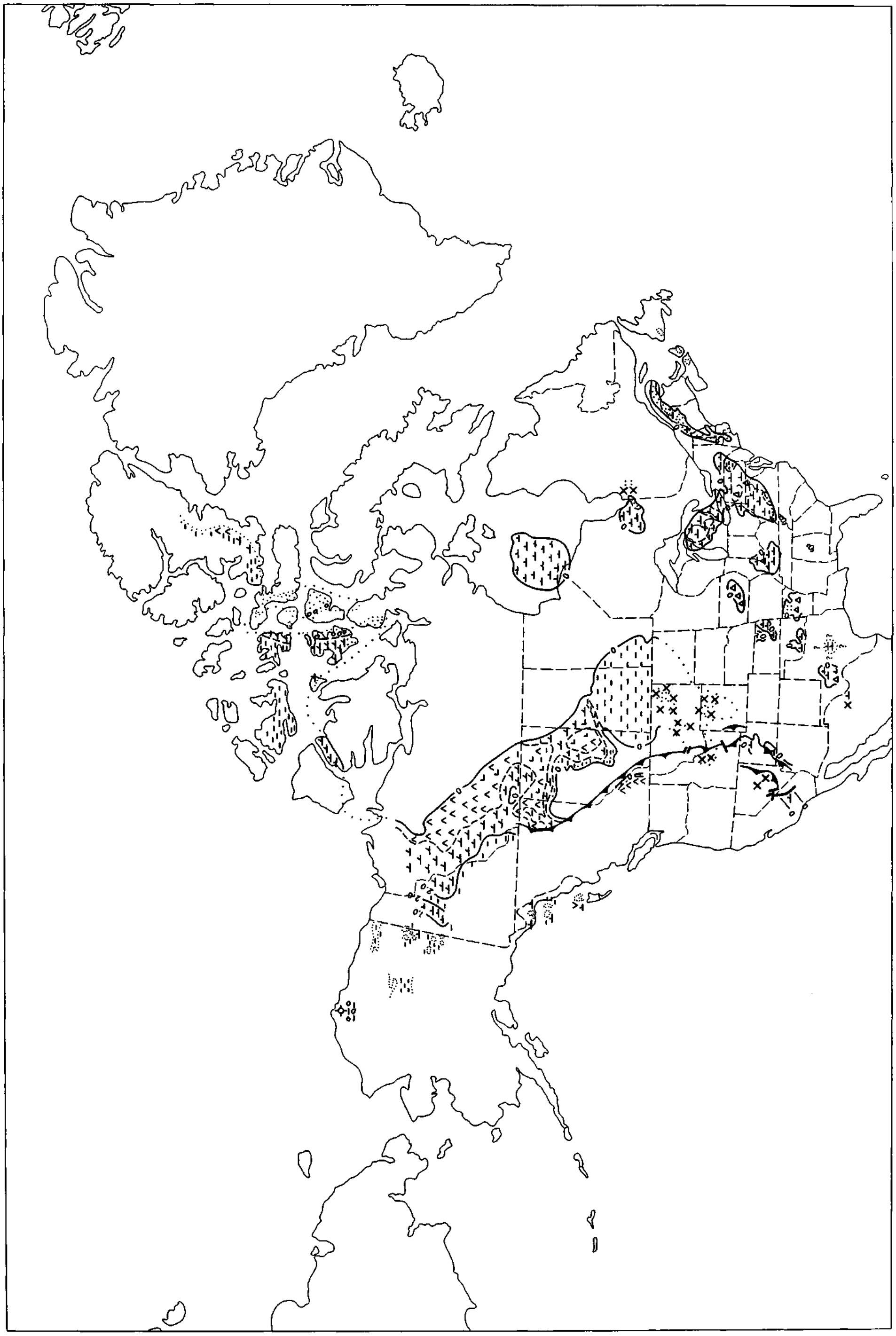


FIG. 2. (See facing page.)

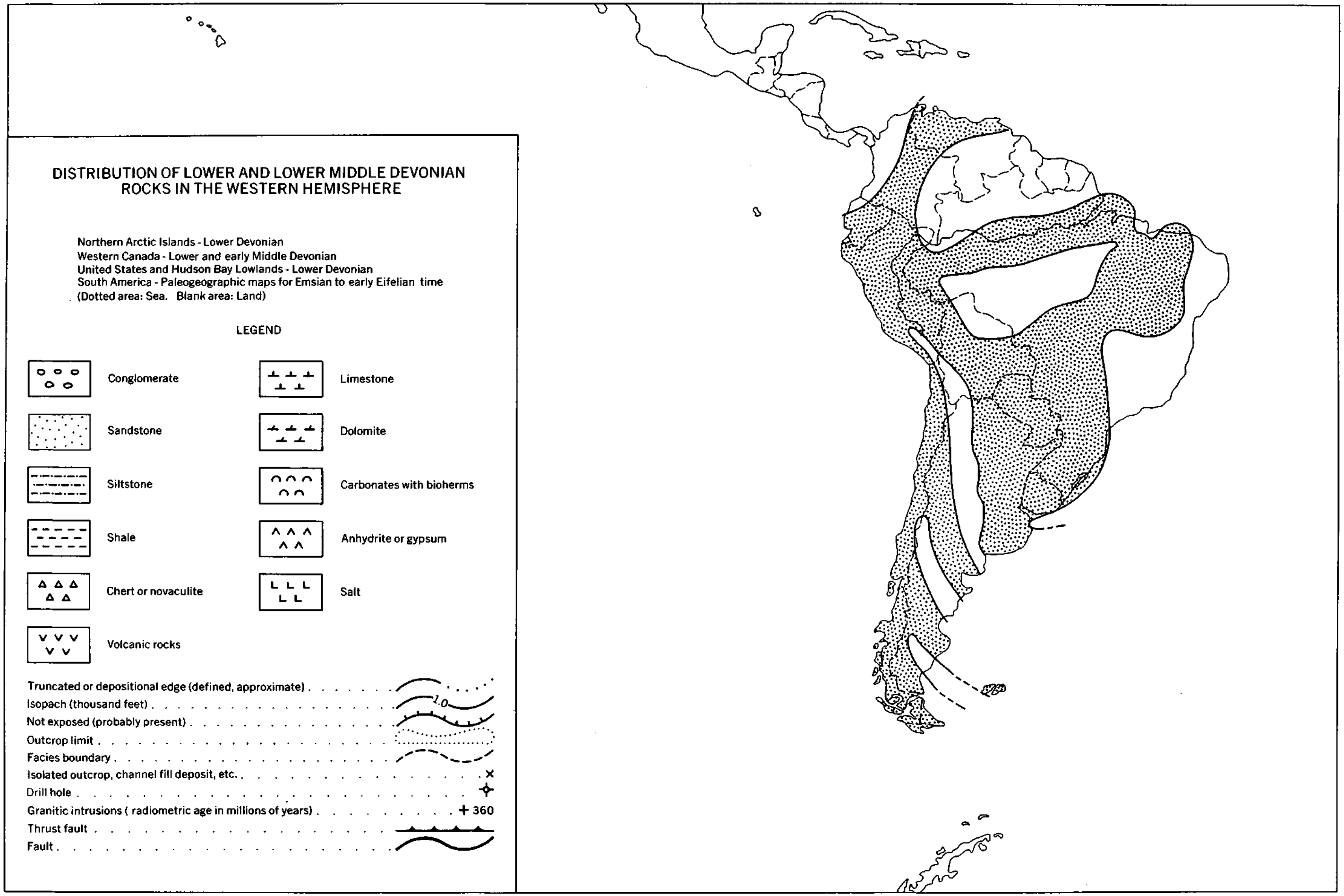


FIG. 2. Distribution of Lower (including some lower Middle) Devonian rocks in the Western Hemisphere (Norris, n).

Phacopina, Kosovopeltis, Homalonotus, Dicranurus, Ceratonurus, Odontochile, Dalmanites, and *Echinolichas.* Siegenian trilobites are less well known. During the Emsian, and continuing into the Eifelian, trilobite provinciality in eastern North America became even more pronounced and is marked by a host of endemic genera including *Odontocephalus, Anchiopsis, Synphoria, Synphoroides, Trypaulites, Phacops, Odontochile, Dalmanites, Corycephalus, Greenops?, Dechenellurus, Terataspis, Echinolichas, Mystrocephala, Crassiproetus,* and *Isoprusia* (Ormiston, 1972, p. 599).

Gedinnian conodonts representative of the *Icriodus (=Pedavis) pesavis* faunas of Nevada are recorded from New York (Klapper *et al.*, 1971, p. 291). Emsian conodont faunas in eastern United States are characterized by the highest occurrence of *Icriodus latericrescens huddlei* and the lowest occurrence of *I. latericrescens robustus* (Klapper *et al.*, 1971, p. 292).

Monograptids are rare in the Lower Devonian of the Appalachian succession (Johnson & Murphy, 1968).

WESTERN NORTH AMERICA

Throughout the Great Basin of Nevada, Utah, and Idaho the Lower Devonian is represented almost wholly by marine carbonate rocks that were deposited on a broad shelf. In the abundantly fossiliferous Lower Devonian strata of Nevada eight distinctive faunal assemblages based on brachiopods have been recognized. These are the *Gypidula pelagica* beds (lower lower Gedinnian), *Quadrithyris* Zone (upper lower Gedinnian), *Spinoplasia* Zone (upper Gedinnian), *Oriskania* beds (lower Siegenian), *Trematospira* Zone (upper Siegenian), *Acrospirifer kobehana* Zone (upper upper Siegenian), *Eurekaspirifer pinyonensis* Zone (lower Emsian), and *Elythyna* beds (upper Emsian) (Johnson, Boucot, & Murphy, 1968; Johnson & Boucot, 1968; Johnson, 1975).

Important forms from the lower *Gypidula pelagica* beds include the lowest *Cyrtina* and *Schizophoria, Icriodus woschmidti,* and monograptids representing the *Monograptus uniformis* Zone (Johnson & Murphy, 1969). The widely distributed index trilobite, *Warburgella rugulosa,* occurs in upper *Gypidula pelagica* beds, above beds with *M. uniformis* (Alberti *et al.*, 1971) and above beds containing *I. woschmidti* (Johnson, Boucot, & Murphy, 1973, p. 11).

Succeeding beds contain two graptolite zones, *Monograptus praehercynicus* and *M. hercynicus* (Johnson & Murphy, 1969); the latter zone is recognized by the presence of *M. hercynicus nevadensis* (Berry, 1967, 1968). *Quadrithyris* Zone brachiopods, *M. hercynicus nevadensis,* and the conodonts *Icriodus pesavis pesavis* and *Spathognathodus johnsoni* are closely associated and treated as one fauna (Johnson & Murphy, 1969, p. 1279).

Monograptus thomasi and *M. yukonensis* occur together and are associated with the conodont *Eognathodus sulcatus* immediately underlying beds of the *Spinoplasia* Zone (Berry & Murphy, 1972; Johnson, 1975). The *Spinoplasia* Zone contains a shelly fauna of Appalachian affinity (Johnson, 1965, p. 374) dated as late Helderbergian (Port Ewen).

An interval above the *Spinoplasia* Zone has been referred to by Johnson (1975) as "beds with *Oriskania,*" but its fauna has not been described.

The succeeding *Trematospira* Zone includes the highest beds in Nevada assignable to the Siegenian. The conodont *Eognathodus sulcatus,* a form that overlaps the lower range of *Monograptus yukonensis* in the Yukon, occurs in the zone.

The *Acrospirifer kobehana* Zone is characterized by many forms that range from underlying to overlying zones and newly introduced elements.

The *Eurekaspirifer pinyonensis* Zone contains a rich megafauna of corals, brachiopods, trilobites, and mollusks, and has yielded the only Lower Devonian goniatites in the western United States (Johnson, 1970b, p. 58).

The *Elythyna* beds contain abundant *E. "undifera"* and are correlated with the upper part of the Sawkill Stage of New York (Johnson, 1970b).

NORTHWESTERN NORTH AMERICA

Lower Devonian strata are distributed widely in the Cordilleran folded belt of northeastern British Columbia, Northwest

Territories, and Alaska. In the Royal Creek section of northern Yukon Territory, the Silurian-Devonian boundary is drawn between beds with *Atrypella* cf. *A. tenuis* and *Gypidula pelagica.* In the Lower Devonian of that area, LENZ (1966, 1968) recognized four brachiopod faunal units and one graptolite zone, and KLAPPER (1969) has outlined the associated conodonts. The four brachiopod faunal units in ascending sequence comprise: *Gypidula* cf. *G. pelagica, Spirigerina, Gypidula* sp. 1-*Davidsoniatrypa* sp., and *Sieberella* cf. *S. weberi-Nymphorhynchia pseudolivonica.*

In the *Gypidula* cf. *G. pelagica* unit the brachiopod genera *Cyrtina* and *Schizophoria* appear at or near the base, and the conodonts *Icriodus woschmidti* and *Ozarkodina remscheidensis* occur together in the unit, an association similar to that known from Nevada.

The *Spirigerina* unit is characterized by *Spirigerina* cf. *S. supramarginalis, Toquimaella kayi,* and *Ogilviella rotunda.* It is correlated with the *Quadrithyris* Zone of Nevada, which JOHNSON (1975) dated as late Lochkovian and correlated with a level near the middle of the type Gedinnian.

An unnamed interval above the *Spirigerina* unit at Royal Creek is characterized by the first appearance of *Eognathodus sulcatus* and the presence of *Icriodus latericrescens* subspecies B, forms which are associated with the *Spinoplazia* Zone of Nevada (KLAPPER, 1969).

The *Gypidula* sp. 1-*Davidsoniatrypa* unit, as emended by LENZ (1968), contains a rich and varied fauna. The principal conodont species in the unit is *Eognathodus sulcatus,* which also occurs in the *Trematospira* Zone of Nevada (KLAPPER, 1969, p. 7). The upper part of the unit is overlapped by the *Monograptus yukonensis* Zone (JACKSON & LENZ, 1963), which also occurs in Alaska (CHURKIN & BRABB, 1965, 1968), in the Canadian Arctic Islands (THORSTEINSSON in BERDAN *et al.,* 1969), and elsewhere.

The *Sieberella* cf. *S. weberi-Nymphorhynchia pseudolivonica* unit succeeds the *Monograptus yukonensis* Zone. The unit contains forms ranging from below, as well as newly appearing species which include the two name bearers as well as *Janius sergaensis, Strophonella?, Cortezorthis* cf. *C. bathurstensis,* and a distinctive echinoderm ossicle with a double axial canal (LENZ, 1968). Associated conodonts include *Polygnathus dehiscens* and *Pandorinellina exigua* dated as early Emsian.

Regionally the *Sieberella* cf. *S. weberi-Nymphorhynchia pseudolivonica* unit correlates with the lower part of the richly fossiliferous carbonate and shale Michelle Formation (NORRIS, 1968a, 1968b; LUDVIGSEN, 1970). Brachiopods in the Michelle include *Cortezorthis* cf. *C. cortezensis, Carinapyga loweryi* and *Schizophoria* cf. *S. nevadensis,* which suggest a correlation with the *Eurekaspirifer pinyonensis* Zone of Nevada of mid-Emsian age (LUDVIGSEN, 1970). Important trilobites in the formation include *Lacunoporaspis norrisi* (most abundant) and *Ricticuloharpes* cf. *R. reticulatus* (ORMISTON, 1971). Conodonts in the Michelle studied by FÅHRAEUS (1971) were assigned to the *Polygnathus dehiscens* fauna. The dacryoconarid fauna of the Michelle was correlated by LUDVIGSEN (1970, 1972) with the *Guerichina strangulata* Zone of late Pragian (early Emsian) age. The ammonoid *Teicherticeras lenzi* described by HOUSE (in HOUSE & PEDDER, 1963) occurs in the lower part of the formation.

Succeeding Lower Devonian faunas in the lower part of the carbonate Ogilvie Formation are correlated also with the *Eurekaspirifer pinyonensis* Zone of Nevada. Two Lower Devonian conodont faunal units were recognized by KLAPPER (in PERRY *et al.,* 1974) in the Ogilvie Formation comprising *Polygnathus perbonus perbonus* and *P. perbonus,* n. subspecies.

Three Lower Devonian graptolite zones and one informal unit were recognized by LENZ and JACKSON (1971) in northwestern Canada. These are, in ascending sequence: *Monograptus uniformis* and *M. hercynicus* zones of Lochkovian age, and beds with *M. thomasi* and the *M. yukonensis* Zone of Pragian age.

NORTHERN NORTH AMERICA (ARCTIC ARCHIPELAGO)

Lower Devonian carbonates and shales are distributed widely in the Franklinian miogeosyncline of the Canadian Arctic Is-

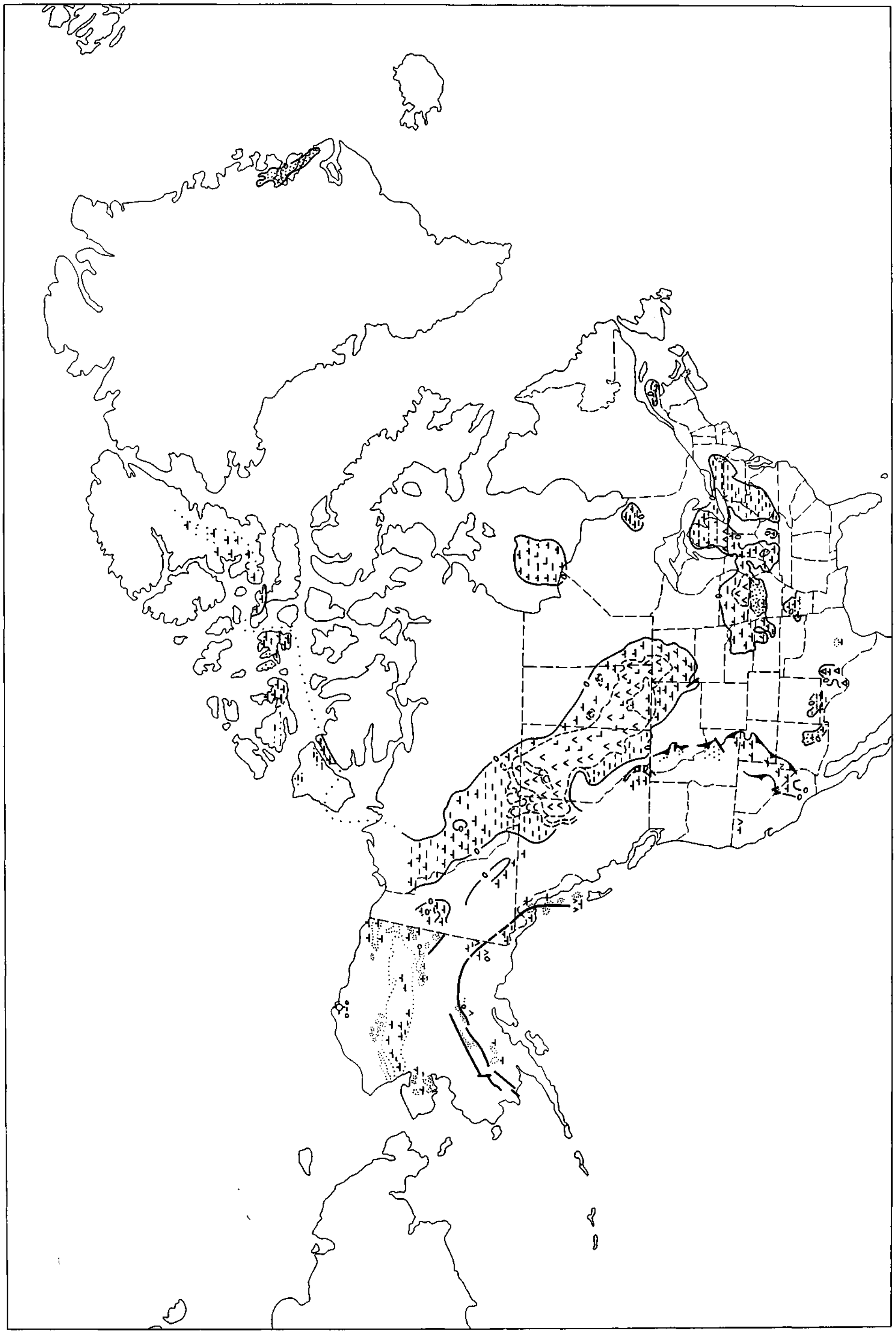


FIG. 3. *(See facing page.)*

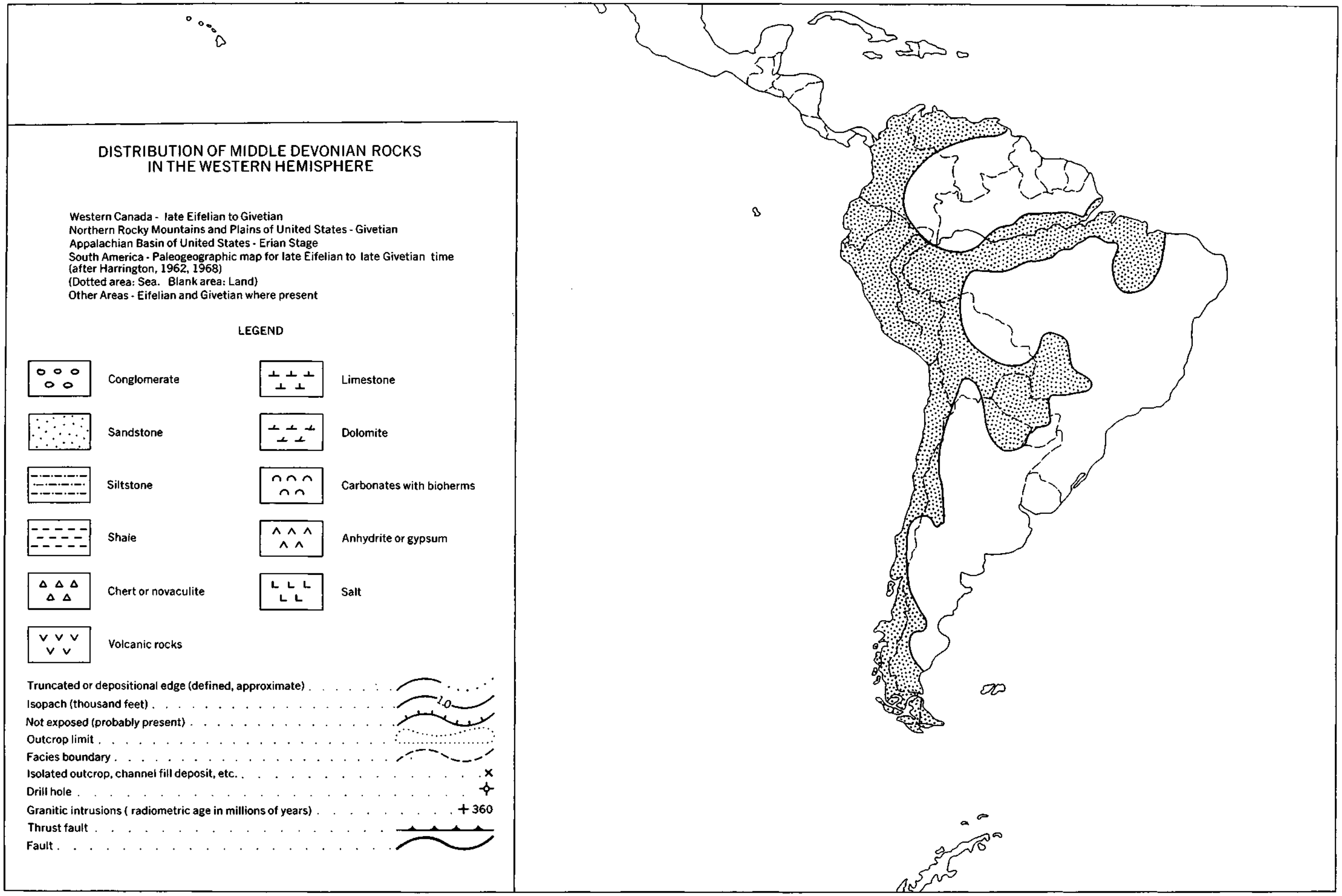


FIG. 3. Distribution of Middle Devonian rocks in the Western Hemisphere (Norris, n).

lands. The graptolite sequence of the Cape Phillips Formation, and partly equivalent Bathurst Island Formation, contain a faunal succession that is continuous across the Silurian-Devonian boundary. Beds containing Pridolian (Late Silurian) monograptids are succeeded by beds containing a succession of monograptids similar to that found in northwestern Canada which include *Monograptus uniformis, Monograptus* of the *M. hercynicus* type, *M.* cf. *M. thomasi,* and *M. yukonensis* (Thorsteinsson in Berdan *et al.,* 1969; Thorsteinsson in McGregor & Uyeno, 1972).

The lower Gedinnian trilobite, *Warburgella rugulosa canadensis,* has been described by Ormiston (1967) from limestones on Baillie Hamilton Island. From Devon Island an equivocal Gedinnian shelly fauna consisting of *Cyrtina, Schizophoria,* and other fossils has been described from the Sutherland River Formation (Boucot *et al.,* 1960; Berdan *et al.,* 1969). From the same island, the brachiopod *Toquimaella kayi* associated with the conodont *Icriodus pesavis pesavis* was reported by Johnson (1967) from the lower part of the Stuart Bay Formation, indicating correlation with the *Quadrithyris* Zone (mid-Gedinnian) of Nevada. From the Stuart Bay Formation on Bathurst Island, Lenz (1973) has described a brachiopod fauna containing species in common with the *Spirigerina* fauna of the Yukon and the coeval *Quadrithyris* Zone of Nevada. Brachiopods of the *Quadrithyris* Zone were recognized by Johnson (1975) also on Prince of Wales and Cornwallis Islands.

From the lower part of the Bathurst Island Formation on Bathurst Island, Uyeno (in McGregor & Uyeno, 1972) reported *Eognathodus sulcatus* and *Ozarkodina remscheidensis* suggesting an early Siegenian age.

The Stuart Bay Formation of Bathurst Island is characterized by *Pandorinellina expansa* and by "two-hole" echinoderm ossicles (McGregor & Uyeno, 1972; Uyeno & Mason, 1975). *Polygnathus dehiscens,* suggesting an early Emsian age, occurs in the lower part of the formation; and *P. perbonus* and other conodonts indicating a middle to late Emsian age occur in the upper part of the formation and in the overlying Eids Formation. A sparse trilobite fauna has been identified by Ormiston (1967) from the Stuart Bay Formation.

A rich brachiopod fauna associated with the conodont *Polygnathus perbonus perbonus* of late Emsian age has been reported by Ormiston (in Klapper, 1969) from the lower part of the Blue Fiord Formation on Devon Island. Brachiopods of probable Emsian age occur also in the Disappointment Bay Formation on Cornwallis and Bathurst Islands (Johnson, 1971b, p. 3268).

Brachiopods described by Brice and Meats (1977) from the lower part of the Blue Fiord Formation on Ellesmere, Devon, and Bathurst Islands are related closely to forms in the *Eurekaspirifer pinyonensis* Zone of Nevada of middle or late Emsian age.

Trilobites of Emsian age described by Ormiston (1967) from the Eids Formation include *Platyscutellum brevicaulis, Cornuproetus tozeri, Harpes* cf. *H. macrocephalus,* and other forms. Elements in this fauna closely resemble forms from Europe and the Urals.

SOUTH AMERICA AND FALKLAND ISLANDS

Two distinct provincial faunal assemblages are known in the Devonian of South America. One, characterizing the Lower Devonian, belongs to the Malvinokaffric realm, a name proposed by Rudolf Richter (1941) and Rudolf and Emma Richter (1942), and derived from Malvinas (Falkland) Islands and the "Kaffric" (South African) Bokkeveld beds. The other, developed in the Lower and Middle Devonian of Venezuela and Colombia, has strong relationships with the Appohimchi subprovince of eastern North America.

The Early Devonian (?early Emsian) Malvinokaffric fauna is characterized by distinctive genera of brachiopods and trilobites unknown in Northern Hemisphere assemblages. Among the brachiopods, *Australospirifer, Australocoelia, Notiochonetes,* and *Scaphiocoelia* are some of the typical representatives. Among the trilobites, *Calmonia, Paracalmonia, Metacryphaeus, Pennaia, Bainella, Tibagya,* and *Probolops* are the most conspicuous. The fauna is characterized also by an abundance of large palaeoneilid and nuculitid bivalves, and by a scarcity of corals, bryozoans, aviculids, pterinids, platyceratids, cephalopods, cystoids, and crinoids (HARRINGTON, 1968, p. 663). In South America, elements of this fauna have been found in the southern two-thirds of the continent; in Peru, Paraguay, Argentina, Paraná basin of Brazil (CLARKE, 1913), Bolivia (WOLFART & VOGES, 1968), and the Falkland Islands (CLARKE, 1913; SHIRLEY, 1964). All of the Lower Devonian (Gedinnian to Emsian) is represented in Bolivia according to WOLFART and VOGES (1968), based on a detailed study of trilobites.

The contemporaneous (?early Emsian) Amazon-Colombian subprovince of the Eastern Americas realm is found in northern South America, mainly in Colombia and Venezuela. The Eastern Americas realm elements have been noted by CASTER (1939), AMOS and BOUCOT (1963), and others. Characteristic brachiopod genera include *Leptocoelia, Megakozlowskiella, Eodevonaria (arcuata)* type, *Prionothyris, Amphigenia, Pentagonia,* and others (BOUCOT, JOHNSON, & TALENT, 1968). The associated corals were studied by SCRUTTON (1973), who concluded that they have strong affinities with the upper Onesquethaw (early Middle Devonian) of eastern North America. The brachiopods, dated by BOWEN (1972) as late Early Devonian, were considered by JOHNSON (in SCRUTTON, 1973) to represent an overlap of late Early and early Middle Devonian forms.

ANTARCTICA

A Malvinokaffric realm faunal assemblage of probable early Emsian age has been described by BOUCOT *et al.* (1963) and DOUMANI *et al.* (1965) from the Horlick Formation in the Ohio Range of Antarctica. Brachiopods are the most abundant fossils and include species of *Pleurothyrella, Australospirifer,* and *Tanerhynchia.* Other forms include the trilobite *Burmeisteria,* and a profusion of bivalves and gastropods that are indistinguishable from South American and South African species.

PROVINCIALISM AND AMMONOID DISTRIBUTION

Silurian shelly faunas, particularly brachiopods, were relatively cosmopolitan, but gave way to moderately provincial faunas during early Gedinnian time. Provinciality became more pronounced in the late Gedinnian when two distinct faunal realms developed, the Eastern Americas and the Old World, each characterized by distinctive brachiopod assemblages (BOUCOT, JOHNSON, & TALENT, 1968). The Appohimchi subprovince of the Eastern Americas realm extended in North America from Gaspé Peninsula to New Mexico. The Cordilleran region of the Old World realm extended from Nevada through the Yukon to the Arctic Archipelago.

During Siegenian time brachiopod provinciality increased and part of Nova Scotia became joined to the Rhenish-Bohemian region of the Old World realm. Western North America remained a part of the Old World realm, except for Nevada, which became an Appalachian enclave (Nevadian subprovince of Eastern Americas realm) in the late Siegenian (BOUCOT, JOHNSON, & TALENT, 1968).

During the early Emsian, marine deposition was more widespread and brachiopod provincialism increased by the addition of the Malvinokaffric realm which, in the Western Hemisphere, covered parts of the southern two-thirds of South America and part of Antarctica. Appohimchi subprovince influence in Nevada ceased as endemic new forms appeared and were joined by brachiopod genera of the Old World realm, the mixture characterizing a Cordilleran region. During the early Emsian, Uralian brachiopod elements from the region bordering the Siberian platform mingled with Cordilleran forms in the northern Yukon and Canadian Arctic, and this mixture is referred to as the Cordilleran-Uralian region of the Old World realm (BOUCOT, JOHNSON, & TALENT, 1968; BOUCOT, 1975).

Beginning approximately in late Emsian or early Eifelian time the Malvinokaffric realm disappeared in Antarctica and remained only in the deeper parts of the basins of southern South America.

Trilobite provincialism in North America

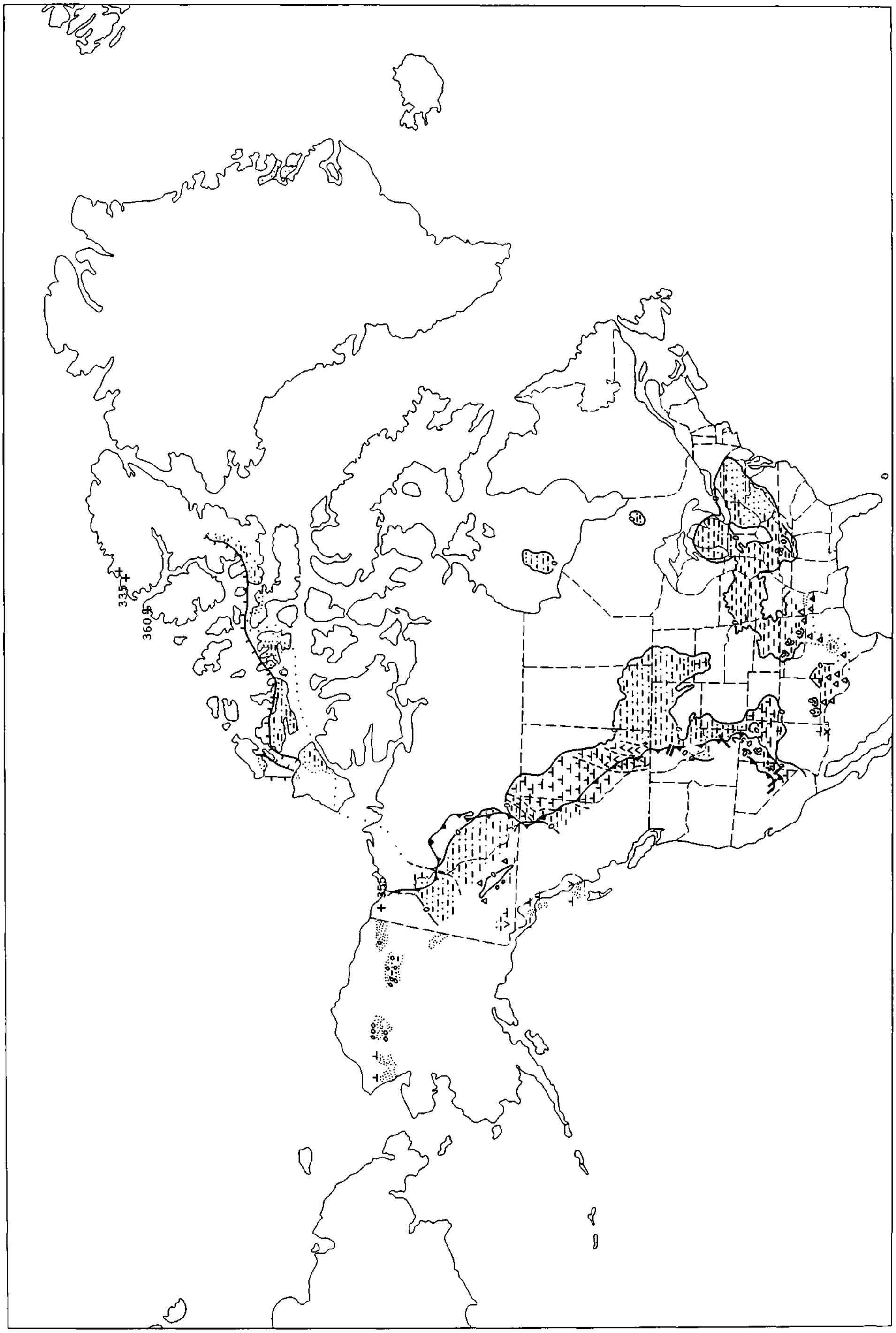


FIG. 4. *(See facing page.)*

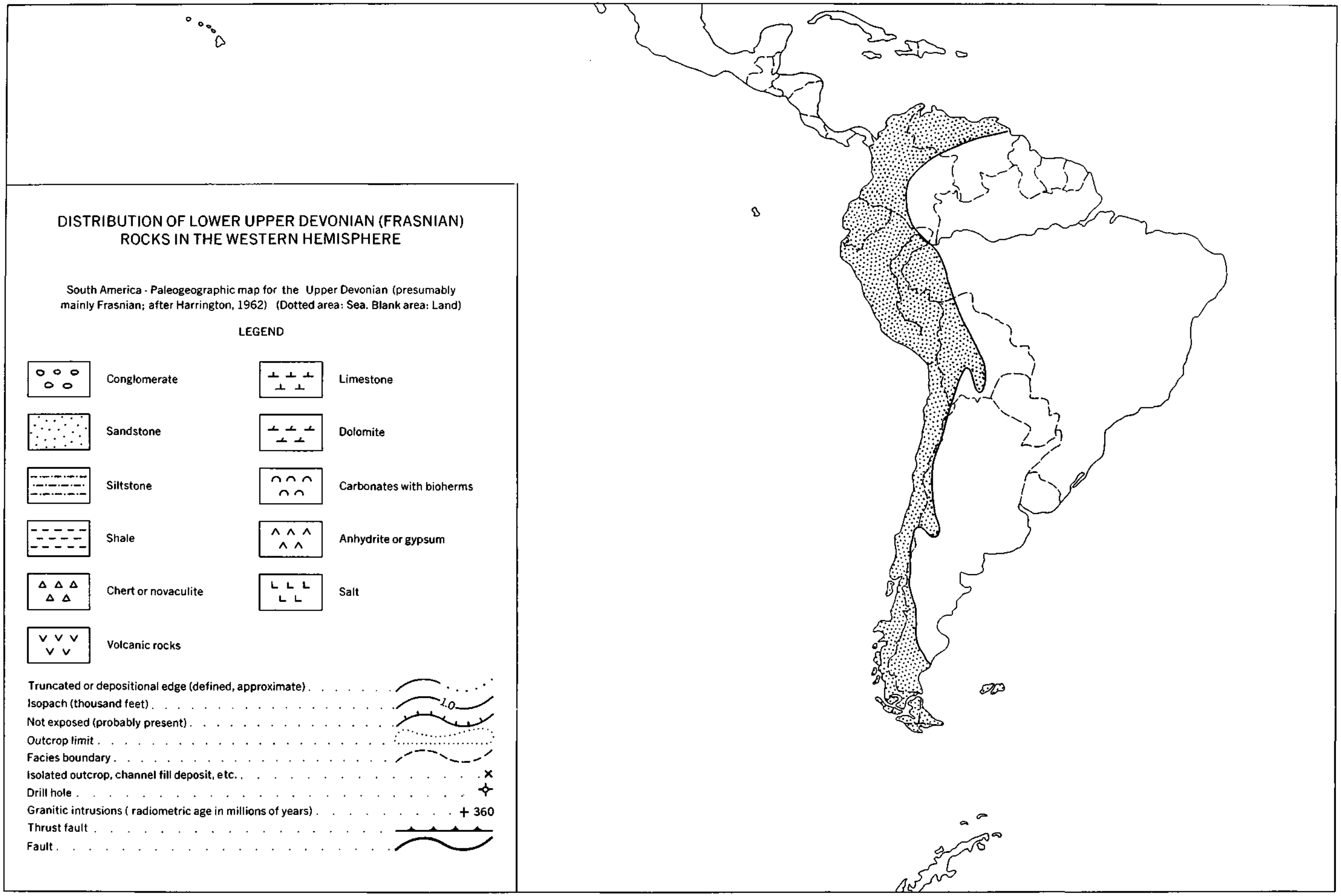


FIG. 4. Distribution of lower Upper Devonian (Frasnian) rocks in the Western Hemisphere (Norris, n).

during the Gedinnian and Siegenian is somewhat similar to that of brachiopods (Ormiston, 1972). During Emsian to Eifelian time provincialism among North American trilobite faunas was most pronounced and at least five biogeographic subdivisions were recognized by Ormiston (1972), comprising the "Appalachian Province," "Old World Province," "Cordilleran Subprovince," "Siberian-Canadian Subprovince," and the "Uralian Subprovince."

In South America, Wolfart and Voges (1968) recognized two major subdivisions of trilobite provincialism in the Malvinokaffric realm, a South American region in the north and a South African-Malvinian-?West Antarctic region in the south. They further recognized two minor subdivisions of the Malvinokaffric realm occurring in the Andean geosyncline and shelf areas, each characterized by distinctive trilobite assemblages.

Goniatites appear in the mid-Siegenian as simple primitive types which diversified rapidly (House, 1967). The richest Lower Devonian ammonoid faunas of the Siegenian and especially the Emsian occur in northern Europe, characterizing the *Mimosphinctes*-Stufe (House, 1964, p. 263). Only a few occurrences are recorded from North America; *Teicherticeras* and *Anetoceras* occur together in Nevada (House, 1962), and *Teicherticeras* (House & Pedder, 1963) and *Anetoceras* (Norris, 1968a) occur separately in the northern Yukon.

MIDDLE DEVONIAN FAUNAS (EIFELIAN AND GIVETIAN)

EASTERN NORTH AMERICA

The Middle Devonian of eastern North America is represented by the Onondaga Limestone, Hamilton Group, Tully Limestone, and their equivalents. Characteristic brachiopods of the Onondaga Limestone and its equivalents include *Coelospira, Levenea, Protoleptostrophia, Amphigenia, "Leptocoelia"* of the *acutiplicata* type, *Longispina, Megakozlowskiella, Elytha, Pentagonia,* and *Centronella* (Boucot, Johnson, & Talent, 1969, p. 25). Within the Onondaga Limestone, the Edgecliff, Moorehouse, and Seneca members have distinct assemblages of rugose corals, and many species range throughout all three members and into the overlying Hamilton Group (Oliver, 1968).

Conodonts in the basal Edgecliff Member of the Onondaga Formation are peculiar to North America, and cannot be dated precisely. The Edgecliff is characterized by a lack of *Polygnathus* and presence of *Icriodus latericrescens robustus* as its only index species (Klapper, 1971, p. 60; Orr, 1971, p. 10). A *Polygnathus costatus patulus-P. linguiformis cooperi* fauna occurs in the Nedrow and lower Moorehouse members of the Onondaga Limestone, associated with the Eifelian ammonoid *Foordites* in the upper part of the Nedrow (Klapper, 1971, p. 60). The succeeding *Polygnathus robusticostatus* fauna is characterized by the name-giver and *P. angusticostatus,* as well as rare occurrences of *P. linguiformis linguiformis* α morphotype and *P. costatus patulus,* which occur in the upper part of the Moorehouse Member. The *P. costatus costatus-P.* aff. *P. trigonicus* fauna occurs in the uppermost bed of the Moorehouse and throughout the Seneca Member of the Onondaga Limestone. The succeeding *P. pseudofoliatus-P.* aff. *P. eiflius* fauna occurs in the *Werneroceras* bed of the Union Springs Member and the Cherry Valley Member of the Marcellus Formation. According to Klapper (1971, p. 60), the conodonts of this fauna indicate correlation with the upper Eifelian and upper Couvinian, rather than with the Givetian as suggested by ammonoid evidence (House, 1962, p. 253-254).

The Givetian in New York embraces roughly the Hamilton Group and Tully Limestone. These sediments form a great clastic wedge filling a geosyncline in eastern New York that thins westward onto the shelf areas of the Midwest where the sequence changes mainly to carbonate rocks. In New York the Hamilton Group has been subdivided into four formations in ascending sequence as follows: Marcellus, Skaneateles, Ludlowville, and Moscow (Cooper, 1933-34). These units are traced westward by means of fossiliferous limestone lenses, the most important of which is the Centerfield Member at the base of the Ludlowville Formation (COOPER & WARTHIN, 1942; COOPER, 1957).

Important brachiopods that range throughout the Hamilton include *Spinocyrtia granulosa, Mucrospirifer mucronatus, Mediospirifer audaculis,* and *Tropidoleptus carinatus.* Brachiopods confined to the Centerfield Limestone at the base of the Ludlowville include *Fimbrispirifer venustus* and *Pentagonia bisulcata. Pustulatia pustulosa* first appears in the Centerfield and ranges upward into rocks of Moscow age. *Spinocyrtia marcyi* appears at the base of the Moscow and ranges upward into beds of Finger Lakes age.

Stringocephalus was reported by COOPER and PHELAN (1966) for the first time in the Midwest from the Miami Bend Formation of Indiana associated with *Subrensselandia* and other megafossils. Conodonts in the Miami Bend are within the zone of *Icriodus latericrescens latericrescens* below the lowest position of *Polygnathus varcus* (ORR, 1969, p. 337), suggesting an early Givetian age.

Much systematic work has been done on the coral assemblages of the Hamilton and Transverse groups but their sequences have not been worked out (OLIVER, 1968, p. 743).

Conodonts of probable early Givetian age, and characterized by the lowest occurrences of *Icriodus latericrescens latericrescens* (below the first appearance in sequence of *Polygnathus varcus*) are known in the Skaneateles Formation of New York and in the lower part of the Traverse Group of Michigan, and elsewhere (KLAPPER *et al.,* 1971, p. 296).

The succeeding *Polygnathus varcus* Zone is characterized in North America by the association of *P. varcus, Icriodus latericrescens latericrescens,* and *Polygnathus linguiformis linguiformis,* which occur in New York in the interval from the Centerfield Limestone (earliest occurrence of *P. varcus*) to the top of the Tully Formation (KLAPPER *et al.,* 1971, p. 297).

In central New York, COOPER and WILLIAMS (1935) divided the Tully into three members: the Tinkers Falls at the base containing abundant *Rhyssochonetes aurora* and *"Stropheodonta" tulliensis*; the Apulia abounding in *Hypothyridina venustula, Schizophoria tulliensis,* and *R. aurora*; and the West Brook, containing a great variety of Hamilton species including crinoids, brachiopods, corals, and numerous mollusks.

Conodonts of the uppermost Middle Devonian *Schmidtognathus hermanni-Polygnathus cristatus* Zone are well developed in a limestone at the base of the New Albany Shale in southern Indiana (KLAPPER *et al.,* 1971, p. 297). Conodonts of this zone have been recognized also in beds in eastern Wisconsin, southern Illinois, Iowa, and elsewhere.

The problem of the boundary between the Middle and Upper Devonian is as yet unresolved. COOPER and OLIVER considered the Tully brachiopods and corals to be Middle Devonian types (COOPER, 1968; OLIVER *et al.,* 1968). HOUSE (1962, p. 256) assigned the Tully to the Upper Devonian (Frasnian), because of the presence, near the top of the formation, of *Pharciceras* and tornoceratids with lingulate lateral lobes. KLAPPER and ZIEGLER (1967) reported that the conodonts in the Tully are confined to the *Polygnathus varcus* Zone of Europe, and dated them as late Givetian.

Many workers in North America place the Middle-Upper Devonian boundary at the base of or within beds carrying the *Pandorinellina insita* fauna, which succeeds the *Schmidtognathus hermanni-Polygnathus cristatus* Zone (KLAPPER *et al.,* 1971, p. 286).

WESTERN NORTH AMERICA

A number of zonal schemes have been proposed by various authors including JOHNSON (1966), JOHNSON and BOUCOT (1968), and others for the Middle Devonian succession of western United States.

A zonal sequence based on brachiopods proposed by JOHNSON and BOUCOT (1968, p. 69) for the Middle Devonian of central Nevada includes the following in ascending sequence: the *Leptathyris circula* Zone with cricoconarids identified by BOUČEK including *Nowakia otomari, Variatellina pseudogeinitziana,* and *Striatostyliolina striata*; the *Warrenella kirki* Zone with *Cabrieroceras* cf. *C. crispiforme* in the lower faunule; beds with *Warrenella franklini* associated with *Leiorhynchus castanea, Parastringocephalus, Subrensselandia, Mimatrypa* cf. *M. insquamosa,* and *Schizophoria mc-*

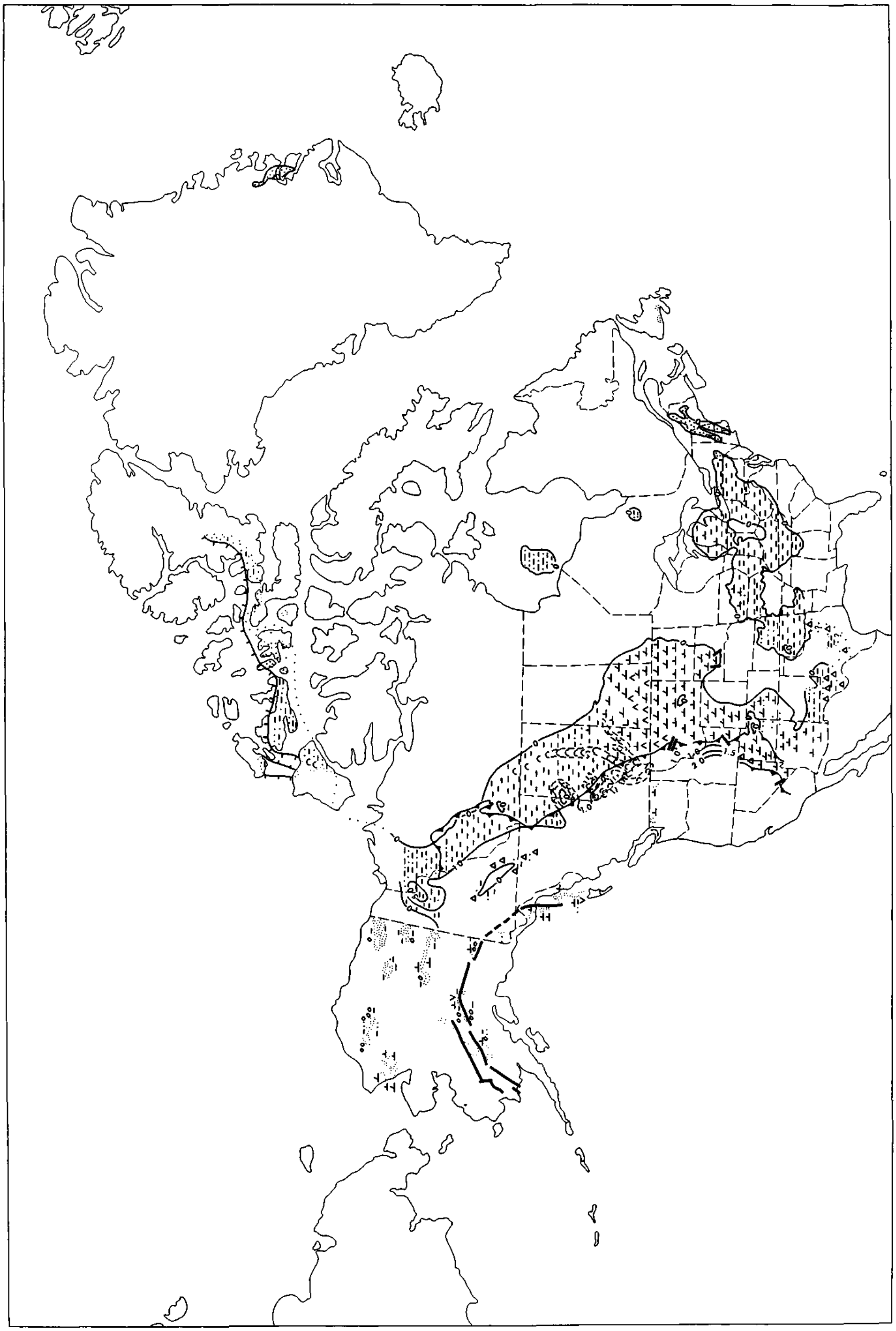


FIG. 5. *(See facing page.)*

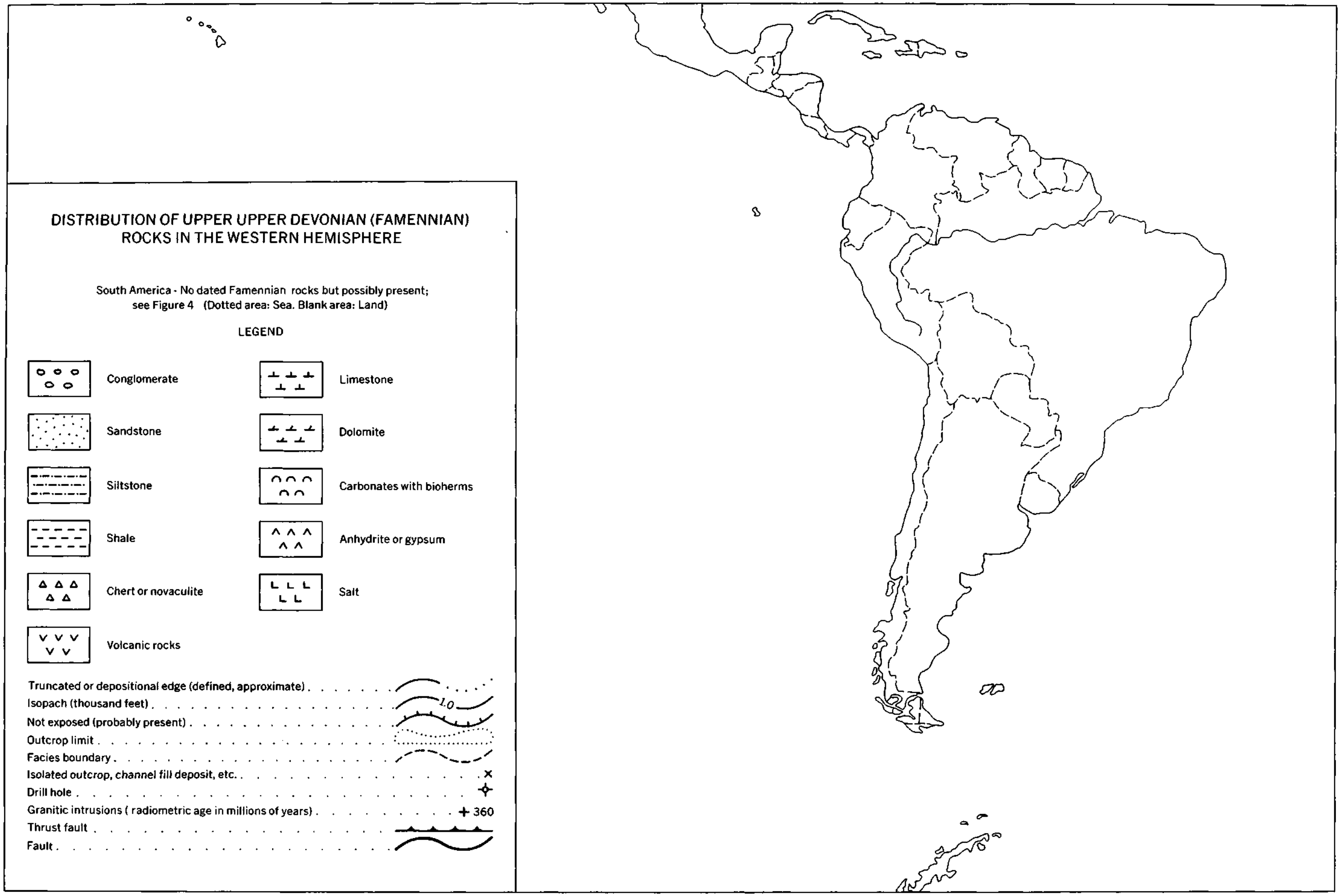


FIG. 5. Distribution of upper Upper Devonian (Famennian) rocks in the Western Hemisphere (Norris, n).

farlani; and *Warrenella occidentalis* Zone containing *Schmidtognathus hermanni-Polygnathus cristatus* Zone conodonts identified by KLAPPER, indicating a late Givetian age.

The two brachiopod faunal units above the *Warrenella kirki* Zone were later subdivided by JOHNSON (1970c, p. 2089) into three units comprising, in ascending sequence, the *Leiorhynchus castanea* Zone, the *Rhyssochonetes aurora* fauna, and the *Leiorhynchus hippocastanea* Zone.

The *Leptathyris circula* Zone with its basal *Pentamerella* Subzone contains a large brachiopod fauna described by JOHNSON (1966, 1970a). An interval containing abundant two-hole echinoderm ossicles occurs at the base of the zone in some sections of Nevada (JOHNSON, 1971a, p. 304). Conodonts in the zone are assignable to the upper Eifelian *Polygnathus kockelianus* Zone.

The succeeding lower *Warrenella kirki* Subzone, as restricted by JOHNSON (1971a), is characterized by *Spinulicosta muirwoodi, Leptathyris index,* and the goniatite mentioned above.

The upper *Warrenella kirki* Subzone contains a less diversified fauna and is characterized by a great abundance of *W. kirki kirki* and *Leiorhynchus miram alpha* (JOHNSON, 1971a, p. 304-305).

The *Leiorhynchus castanea* Zone of Nevada is characterized by *Parastringocephalus* cf. *P. dorsalis, Subrensselandia nolani, Warrenella* cf. *W. franklini, Polygnathus varcus,* and other fossils (JOHNSON, 1969; 1970c, p. 2087). It was dated by JOHNSON as pre-Taghanic Givetian.

The succeeding *Rhyssochonetes aurora* fauna includes *R. aurora solex, Leiorhynchus* sp. aff. *L. mesacostale,* and *Polygnathus varcus.* It is correlated with the Lower Taghanic of New York (JOHNSON, 1970c, p. 2087).

The *Leiorhynchus hippocastanea* Zone contains *Warrenella occidentalis, Hadrorhynchia sandersoni,* abundant *Emanuella* cf. *E. meristoides,* and a conodont fauna of the *Schmidtognathus hermanni-Polygnathus cristatus* Zone. This is the highest brachiopod fauna of Middle Devonian aspect in Nevada and it is correlated with the Middle Taghanic of New York (JOHNSON, 1970c).

NORTHWESTERN NORTH AMERICA

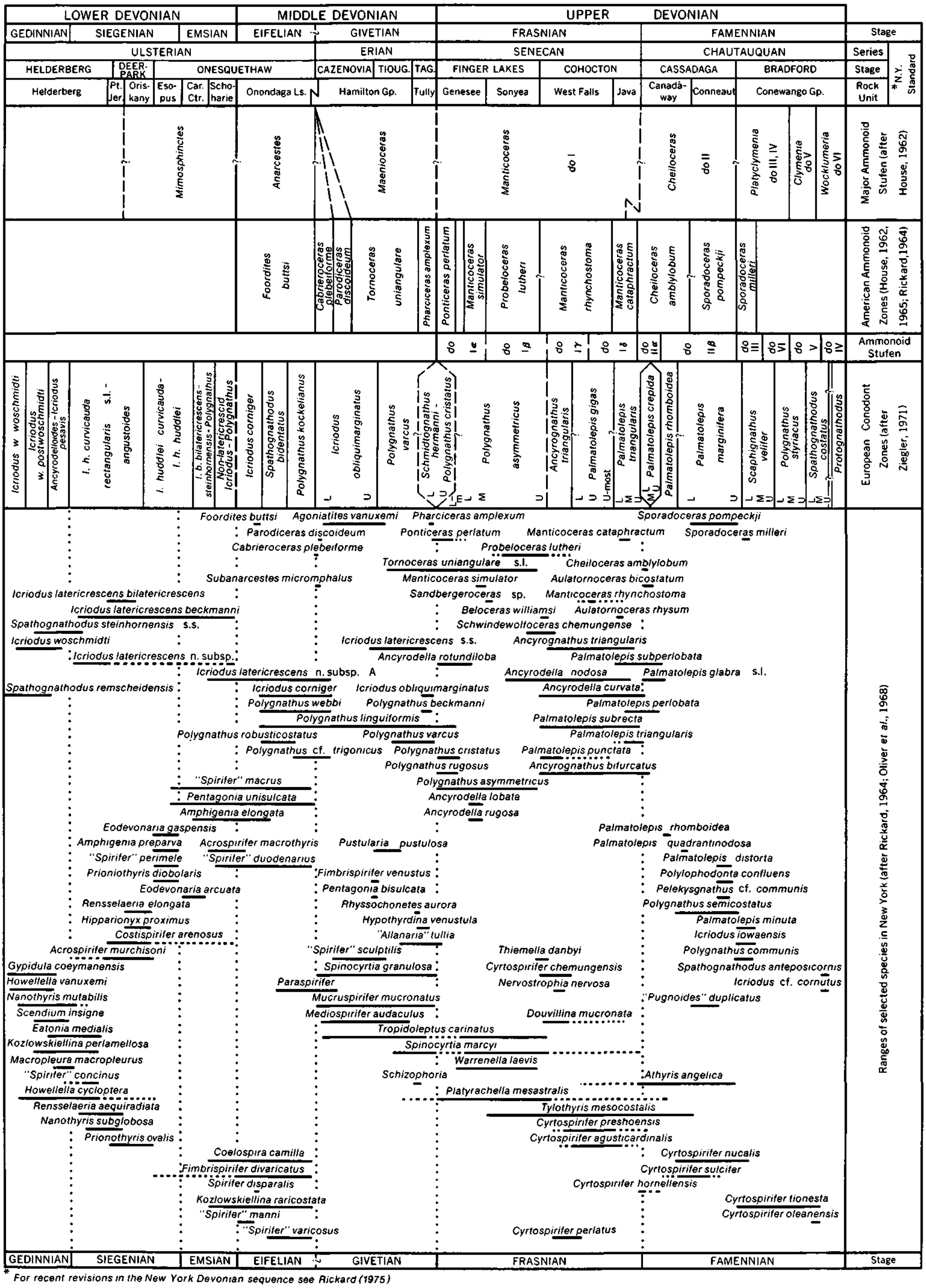
Faunal assemblages of late Early Devonian (Emsian) to late Middle Devonian (Eifelian) age that are widespread in the northern Yukon comprise, in ascending sequence: *Moelleritia canadensis, Gasterocoma? bicaula, "Schuchertella" adoceta,* and *Radiastraea verrilli.*

The very large and distinctive ostracode, *Moelleritia canadensis* (COPELAND, 1962), is generally the only megafossil found in dolomitic rocks in the upper half of the Gossage Formation and upper part of the Bear Rock Formation in northern Yukon Territory and adjacent District of Mackenzie. Although formerly dated as Eifelian, conodonts recovered from the Bear Rock Formation (UYENO & MASON, 1975, p. 720) suggest that *M. canadensis* probably is confined to beds of late Emsian to early Eifelian age.

Echinoderm ossicles with double and crosslike axial canals, named *Gasterocoma? bicaula* by JOHNSON & LANE (1969), occur in a variety of facies in beds immediately above *M. canadensis,* but also overlap this form. In Nevada, *G.? bicaula* occurs at the base of the *Leptathyris circula* Zone of Eifelian age. In northern Yukon the acme zone of these ossicles is above *M. canadensis,* but they range down to the *Sieberella-Nymphorhynchia pseudolivonica* unit of mid- or early Emsian age, and range upward into beds of early Eifelian age.

In succeeding beds two widely distributed, richly fossiliferous associations that occur typically in the Hume Formation of the central Mackenzie River region are present. These are characterized by *"Schuchertella" adoceta* and *Radiastraea verrilli* (approximately equivalent to *"Carinatina" dysmorphostrota* and *"Spinulicosta" stainbrooki* zones, respectively). These faunal assemblages have been listed and commented upon by CRICKMAY (1966), CALDWELL (1971), LENZ and PEDDER (1972), PEDDER (1975), and others.

The *"Schuchertella" adoceta* Zone contains many brachiopods that extend into overlying zones, but the corals *"Microcyclus" multiradiatus, Radiastraea trochomisca, R. verrilli,* and *Taimyrophyllum*



* For recent revisions in the New York Devonian sequence see Rickard (1975)

FIG. 6. Main Devonian faunal zones, and ranges of selected species in New York (Norris, n).

triadorum are diagnostic of the zone (Pedder, 1975, p. 572). Conodonts in the zone suggest an Eifelian, probably early Eifelian, age (Uyeno in Lenz & Pedder, 1972), and Eifelian goniatites have been recorded by House and Pedder (1963) in the stratigraphically lower Funeral Formation.

The *"Carinatina" dysmorphostrota* Zone contains a rich fauna including *Spinatrypa borealis, S. andersonensis, S. coriacea*; and the corals *Radiastraea tapetiformis, Taimyrophyllum stirps, Aphroidophyllum howelli, A. meeki,* and *Mackenziephyllum insolitum* (Pedder, 1975, p. 572). Conodonts identified by Uyeno (in Lenz & Pedder, 1972) from the zone indicate an Eifelian age.

Upper Middle Devonian (Givetian) zones, or "hemerae," recognized by Crickmay (1966) in western Canada comprise: *Desquamatia (Variatrypa) arctica, Stringocephalus glaphyrus, S. chasmognathus, S. aleskanus, S. axius, Leiorhynchus hippocastanea, Emanuella vernilis,* and *Desquamatia (Independatrypa) independensis.*

An alternative zonal scheme proposed by Pedder (1975) for Givetian strata of the central Mackenzie valley area is as follows, in ascending sequence: *Leiorhynchus castanea, Ectorensselandia laevis, Stringocephalus aleskanus, Leiorhynchus hippocastanea* and *Grypophyllum mackenziense.*

Desquamatia (V.) arctica occurs in the Elm Point of Manitoba, lower Methy of Alberta and Saskatchewan, lower Pine Point of the Great Slave Lake area, upper Hume and lower Hare Indian of the Mackenzie area, and is present also in the Hudson platform and Michigan. Conodonts associated with *D. (V.) arctica* in Manitoba (Uyeno in Norris & Uyeno, 1972) and in the Hudson platform (Uyeno in Sanford & Norris, 1975) are dated as late Eifelian and probably younger.

Stringocephalus, a guide fossil for the Givetian, is widely distributed in western North America (Boucot, Johnson & Struve, 1966, p. 1358, fig. 2) and was discovered recently in Indiana of the midcontinent area (Cooper & Phelan, 1966). *Stringocephalus* and the closely related genus *Geranocephalus* are extremely variable forms and some of the named species are difficult to differentiate and correlate precisely. The earliest forms in western Canada appear in the Winnipegosis, Methy, and Pine Point formations and include *Stringocephalus glaphyrus* and *S. sapiens.* The *Stringocephalus* and associated mollusks in the Miami Bend Formation of Indiana are closely related to forms in the Winnipegosis Formation of Manitoba. Some of the later stringocephalids include *Stringocephalus asteius* and *S. alaskanus,* which occur in the Ramparts Limestone of the Mackenzie region.

The *Leiorhynchus hippocastanea* Zone occurs in post-*Stringocephalus* beds below the reefs of the Ramparts Formation of the Mackenzie valley. Diagnostic brachiopods include *Schizophoria mcfarlani, Stelckia galearius, Hadrorhynchia sandersoni, "Atrypa" percrassa, Warrenella occidentalis timetea,* and other forms (Pedder, 1975, p. 574).

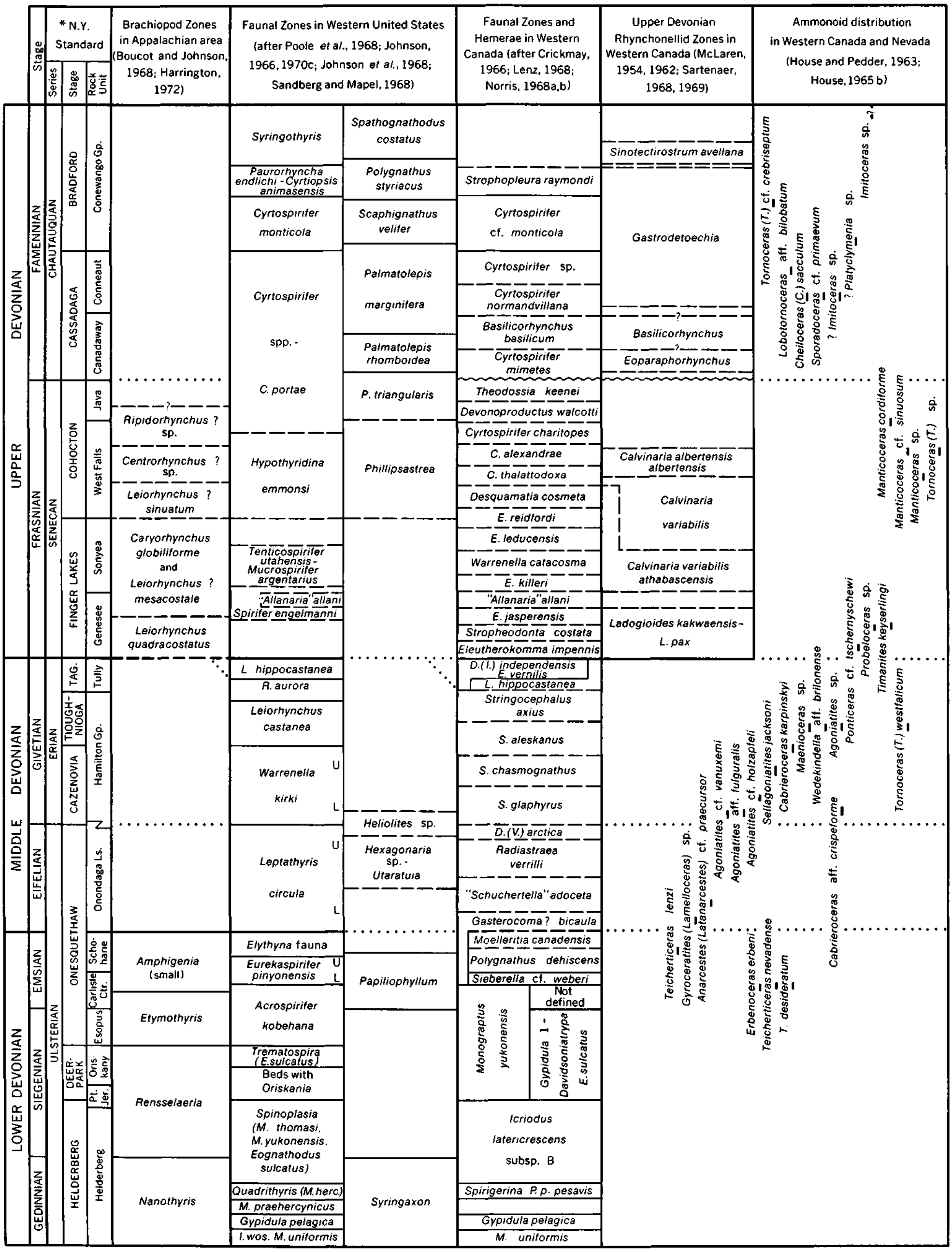
The *Grypophyllum mackenziense* Zone occurs in the upper reefal part of the Ramparts Limestone and is approximately equivalent to the *Emanuella vernilis* Zone of the Slave Point Formation of the Great Slave Lake area and the *Desquamatia (I.) independensis* Zone of the Swan Hills Formation of northern Alberta. Conodonts of the *Schmidtognathus hermanni-Polygnathus cristatus* Zone of late Givetian age occur with both the *Leiorhynchus hippocastanea* and *G. mackenziense* faunas.

NORTHERN NORTH AMERICA

The Middle Devonian Series in the Canadian Arctic is represented by marine clastic carbonate rocks, including some remarkably persistent formations.

The upper two-thirds of the poorly fossiliferous, clastic Eids Formation of Bathurst Island contains the *Icriodus corniger-I. curvirostratus-I. introlevatus* assemblage and *Polygnathus linguiformis linguiformis,* which Uyeno (in McGregor & Uyeno, 1972) considered to be of mid-Couvinian age.

The Blue Fiord Formation contains abundant megafossils of which stromatoporoids, corals, brachiopods and trilobites are important elements. The upper range of the "two-hole" echinoderm ossicle, *Gasterocoma? bicaula,* extends into the lower part of the formation on Bathurst Island (McGregor & Uyeno, 1972, table 1). Brachio-



* For recent revisions in the New York Devonian sequence see Rickard (1975)

FIG. 7. Some Devonian faunal zones of Appalachian area, western United States, and western Canada, and ammonoid distribution in Devonian rocks of western Canada and Nevada (Norris, n).

pods from the middle and upper parts of the formation were correlated by BRICE and MEATS (1977) with the Nevada zones of *Leptathyris circula* (Eifelian) and lower part of *Warrenella kirki* (late Eifelian or Givetian), respectively. ORMISTON (1967) has indicated that the Blue Fiord trilobite fauna is highly diverse. Species that are identical with Eifelian forms from Europe include *Harpes macrocephalus, Astycorphe cimelia, Leonaspis elliptica,* and *Otarion belanops.* About half of the Blue Fiord trilobites are dechenellids, including *Dechenella (D.) mclareni, D. (D.) tesca, Deltadechenella bathurstensis,* and many others. Associated corals, according to Ormiston (1967), consist entirely of genera present in beds of Eifelian age in Germany. Conodonts recorded by Uyeno (in McGregor & Uyeno, 1972) include a form close to *Icriodus corniger* and *Eognathodus bipennatus,* indicating an Eifelian age.

The succeeding Bird Fiord Formation has a relatively restricted fauna. Corals are generally rare; brachiopods include *"Camarotoechia princeps," Emanuella,* and abundant *Atrypa*; trilobites are very restricted, comprising only five genera of which four are rare. The presence of *Ancyropyge manitobensis* is the best evidence furnished by trilobites for the Givetian age of the greater part of the Bird Fiord Formation. In Manitoba this form occurs in the Winnipegosis Formation with *Stringocephalus.*

Brachiopods of the Bird Fiord Formation recently studied by Brice and Meats (1977) were correlated with the upper *Warrenella kirki* Subzone (early Givetian) of Nevada.

Conodonts recovered by Uyeno (in McGregor & Uyeno, 1972) from the lower part of the Bird Fiord Formation of Bathurst Island are nondiagnostic. However, *Icriodus* cf. *I. obliquimarginatus* occurs in the upper part of the formation, a form commonly associated with *Polygnathus varcus,* and indicating a Givetian age.

On Melville Island, in a shale-sandstone facies, the Givetian brachiopod *Leiorhynchus castanea* was found, indicating marine connection with the mainland of western Canada. *Stringocephalus* has not been found in the Canadian Arctic, presumably because of provincialism and unfavorable facies during this interval.

PROVINCIALISM AND AMMONOID DISTRIBUTION

During the Eifelian and most of the Givetian, excluding the Taghanic Stage, the contrast between the brachiopod faunas of the Eastern Americas and Old World realms continued to be pronounced (Johnson & Boucot, 1973). The Malvinokaffric realm seas had retreated from Antarctica and remained only in the deeper parts of the troughs of southern South America. The Cordilleran region of the Old World realm in western North America extended from southeastern California to the Northwest Territories (Johnson & Boucot, 1973). Throughout most of Middle Devonian time the Eastern Americas realm in eastern North America and northern South America continued to bear a distinctly endemic fauna.

Pronounced trilobite provinciality continued from the Emsian into the Eifelian and, in western North America, exhibited even greater provinciality than the contemporaneous brachiopods (Ormiston, 1972). A decrease in trilobite provinciality occurred in the Givetian, which is marked by the southward migration of *Ancyropyge* from the Arctic Islands into the Northwest Territories, Manitoba, Nevada, and Michigan. This increasing trend towards cosmopolitanism is marked also by the appearance of *Scutellum* in the Appalachian area, and the wide distribution of *Dechenella* in western Canada and the Great Basin (Ormiston, 1972).

Ammonoid dispersion increased in the middle Devonian, especially during the Givetian. Eifelian ammonoids recorded from North America include *Gyroceratites (Lamelloceras)* and *Anarcestes* from the Northwest Territories (House & Pedder, 1963). *Foordites* from the New York Onondaga Limestone and from Virginia (House, 1962), and *Foordites* and *Cabrieroceras* from the Columbus Limestone of Ohio (Sweet & Miller, 1956). House (1964, p. 265) pointed out that a distinctive feature of North American Eifelian ammonoid faunas is the apparent absence of *Anarcestes* of the *A. lateseptatus* group and *Pinacites,* genera which in Europe characterize the lower and upper Eifelian, respectively.

Givetian ammonoid faunas in North America are much more widespread and begin with the entry of *Cabrieroceras plebeiforme* (House, 1964). From the Northwest Territories *Wedekindella, Maenioceras,* *Agoniatites, Tornoceras,* and *Cabrieroceras* are recorded (House & Pedder, 1963; House, 1964), all of which are closely related to European forms. Of interest is the apparent absence of Middle Devonian goniatites from the more southerly Rocky Mountains and the platform areas of the Plains.

The Givetian goniatites which occur in the New York-Pennsylvania embayment do not show typical European features (House, 1964, p. 265). From this area *Tornoceras (Tornoceras), Agoniatites,* and other forms are known from the Cherry Valley Limestone, but typical genera (e.g., *Maenioceras, Wedekindella, Sobolewia*) are lacking. From farther south in Virginia, however, *Sobolewia* and *Maenioceras,* which resemble a mid-Givetian fauna from Devon are recorded (House, 1962). From this distribution House (1964) suggested that there was trans-Arctic contact between Europe, Russia, and western Canada, and perhaps trans-Atlantic contact between Europe and Virginia. During the same time little connection was made across the shelf areas over much of northern United States and southern Canada.

The first goniatite from the Devonian of South America was described recently by Leanza (1968). It was named *Tornoceras baldisi* and was collected from the Chavela Formation outcropping in San Juan Province of Argentina. Leanza (1968) dated the new species as Late Devonian but, according to W. W. Nassichuk (pers. commun., October, 1973), the suture line of the new form closely resembles that of *Tornoceras uniangulare aldense* (House, 1965a), which occurs in the Middle Devonian (Givetian) Alden Marcasite of New York State.

UPPER DEVONIAN FAUNAS (FRASNIAN AND FAMENNIAN)

EASTERN NORTH AMERICA

The Upper Devonian of the New York standard section is subdivided into the Senecan Series (Frasnian) with the Finger Lakes and Cohocton stages, and the Chautauquan Series (Famennian) embracing the Cassadaga and Bradford stages. The rocks of this interval are almost entirely clastic and make up more than two-thirds of the volume of sedimentary rocks in the Appalachian basin (Rickard, 1964). The position of the base of the Upper Devonian is not agreed upon but generally it is taken at the base of the Geneseo Shale.

Conodonts and ammonoids are the principal fossils used for correlating the New York Upper Devonian with Europe. Conodonts of the upper part of the *Schmidtognathus hermanni-Polygnathus cristatus* Zone occur at the base of the Genesee Group. The presence of the *Pandorinellina insita* has not been demonstrated in New York (Rickard, 1975). Conodonts of the lowermost *Mesotaxis asymmetrica* Zone occur in the Lodi Limestone. The lower *M. asymmetrica* Zone begins in the lower Penn Yan Shale where *Ancyrodella rotundiloba* first appears. The base of the middle *M. asymmetrica* Zone appears in the upper West River Shale where it is marked by *Palmatolepis punctata.* Conodonts of the upper *M. asymmetrica* Zone occur in the lower Rhinestreet Shale; and the *"Ancyrognathus" triangularis* Zone occurs in the middle and upper parts of the Rhinestreet. Upper *Palmatolepis triangularis* Zone conodonts occur in the upper Hanover and Dunkirk shales (Rickard, 1975, p. 9).

Ammonoid zones in rocks of the lower Upper Devonian (Senecan Series) comprise in ascending sequences: *Epitornoceras peracutum, Ponticeras perlatum, Manticoceras styliophillum, Sandbergeroceras syngonum, Probeloceras lutheri, P. strix, Manticoceras rhynchostoma,* and *Crickites* cf. *C. holzapfeli* (House & Kirchgasser in Rickard, 1975). *Probeloceras strix* is a new zone described by Kirchgasser (1975) that occurs in the upper Cashaqua and lower Rhinestreet shales of New York.

Well-known brachiopods in rocks of the Finger Lakes Stage include: *Mucrospirifer posterus,* limited to the Genesee Group; *Warrenella laevis* and *Spinocyrtia marcyi,* ranging throughout the stage; and *Tylothyris mesocostalis,* appearing in the Sonyea Group and ranging into higher beds.

The brachiopod genus *Cyrtospirifer* first appears in the lower part of the West Falls

Group with *C. chemungensis* and *C. perlatus* as important species; and *C. angusticardinalis* and *C. preshoensis* make their appearance in the upper part of the group.

The Frasnian-Famennian boundary in Belgium traditionally has been placed at the base of the Assise de Senseille, which appears to correspond to a level slightly below the base of the *Cheiloceras*-Stufe (House in Rickard, 1975). Opinions differ on the position of the *Manticoceras*-*Cheiloceras* boundary relative to the conodont zonation. In New York this boundary is placed at or near the base of the Upper *triangularis* Zone (Rickard, 1975). House (1967, 1973) recorded that *Crickites*, indicative of the upper *Manticoceras*-Stufe, occurs 30 feet below the top of the Hanover Shale, and Klapper *et al.* (1971) referred the upper Hanover to the upper *triangularis* Zone.

Ammonoids and conodonts are rarer in the upper Upper Devonian (Chautauquan Series) and correlation with the Famennian of Europe becomes increasingly more difficult.

Conodont zones represented in rocks of the Cassadaga Stage include the upper *Palmatolepis triangularis*, *P. crepida*, *P. rhomboidea*, and *P. marginifera*, but the precise limits of the zones are unknown (Rickard, 1975).

The ammonoid *Cheiloceras amblylobum*, associated with conodonts of the *Palmatolepis crepida* Zone, occurs in the Gowanda Shale. The youngest ammonoid zone, *Sporadoceras milleri*, present in Pennsylvania, occurs in the lower part of the Bradford Stage which correlates with part of Zone *do*III of Europe (Oliver *et al.*, 1968, p. 1033).

Scattered conodonts indicate that succeeding rocks of the Bradford Stage may include equivalents of the European ammonoid Zones *do*IV to *do*VI (Oliver *et al.*, 1968, p. 1035).

Brachiopods in rocks of the Bradford Stage include *Cyrtospirifer tionesta* that ranges throughout the stage; and *C. oleanensis* and *"Camarotoechia" allegania* that appear in the upper part of the stage.

WESTERN NORTH AMERICA

Various megafaunal zonal schemes have been proposed for the abundantly fossiliferous Frasnian rocks of western Canada by a number of workers including Crickmay (1966), Maurin and Raasch (1972), McLaren (1954, 1962), Raasch in Dooge (1966), Warren and Stelck (1950), and others. Frasnian rhynchonellid brachiopods studied by McLaren (1954, 1962) are useful zonal fossils, especially for the lower three-quarters of the Frasnian succession. McLaren's zones are listed on Figure 7, as well as an alternative zonal scheme proposed by Crickmay (1966).

The *Eleutherokomma impennis* to *E. killeri* zones occur typically in the Waterways (Beaverhill Lake) Formation of northern Alberta. Elements of these zones are recognized in Manitoba, Saskatchewan, the Alberta Rocky Mountains, and elsewhere.

Conodonts in the Waterways Formation studied by Uyeno (1974) comprise the *Pandorinellina insita* fauna, and Lower and Middle *Mesotaxis asymmetrica* zones which correlate with the lower *Manticoceras*-Stufe of Europe.

The genus *Ladogioides*, commonly associated with *Eleutherokomma impennis* and *Platyterorhynchus russelli*, is also a valuable zone marker for the base of the Frasnian succession in northern Alberta, northeastern British Columbia, and the southern Northwest Territories.

McLaren's (1962) *Calvinaria variabilis athabascensis* Zone is not contiguous with the *Ladogioides* Zone, but is restricted to the Maligne and lower Perdrix formations in the Alberta Rockies and the Cooking Lake Formation of central Alberta.

The *Calvinaria variabilis insculpta* Zone of McLaren (1962) occurs in the upper Perdrix Formation and its equivalents in the Alberta Rocky Mountains, and in the Duvernay Formation of the central Alberta subsurface. *Leiorhynchus* (=*Caryorhynchus* of some authors) *carya* commonly is associated with the zone fossil and represents the last occurrence of the genus in the area. *Eleutherokomma* disappears late in the *C. variabilis insculpta* Zone, within the *"Desquamatia" cosmeta* Zone of Crickmay (1966). *Cyrtospirifer* first appears in the lower part of the *C. variabilis insculpta* Zone, within the *E. reidfordi* Zone of Crickmay (1966), suggesting a correlation with the lower part of the Cohocton Stage of

New York of mid-Frasnian age.

The *Calvinaria albertensis albertensis* Zone of McLaren (1962) is represented in the lower and middle Mount Hawk Formation and its equivalents in the Alberta Rocky Mountains and in the Ireton Formation of the Alberta subsurface.

In the upper Frasnian succession, Crickmay's (1966) zones of *Cyrtospirifer charitopes, Devonoproductus walcotti,* and *Theodossia keenei* are represented. The lower two zones occur typically in the Redknife Formation and the upper zone occurs in the Kakisa Formation of the Trout River outcrop area described by Belyea and McLaren (1962). The fauna of the *T. keenei* Zone is separated from overlying faunas by a profound break that is remarkably widespread throughout western and northern Canada. This break at the end of the Frasnian is marked by the disappearance of numerous corals, stromatoporoids, stropheodontids, pentamerids, and atrypids.

Fossiliferous Frasnian rocks of western United States are less abundant and less continuous than those in western Canada. Various tentative megafaunal zones have been proposed by Poole *et al.* (1968), Johnson (1970c), Baars (1972), and others. Brachiopod zones used by Poole *et al.* (1968) in southwestern United States are listed on Figure 7.

Six brachiopod zones were recognized by Crickmay (1966) within Famennian rocks of western Canada comprising in ascending sequence: *Cyrtospirifer mimetes, Basilicorhynchus basilicum, Cyrtospirifer normandvillana, C.* sp., *C.* cf. *C. monticola,* and *Strophopleura raymondi.* Another zonal scheme based on rhynchonellids and proposed by Sartenaer (1968, 1969) for the same interval is as follows: zones of *Eoparaphorhynchus, Basilicorhynchus, Gastrodetoechia,* and *Sinotectirostrum avellana.*

The *Eoparaphorhynchus* Zone is restricted to the lower part of the lower Famennian and is represented in the Trout River and Sassenach formations, and in the upper part of the Winterburn Group. The zone is represented by *E. maclareni* in the Mackenzie River area and Alaska; by *E. lentiformis* in the area east and north of Jasper in the Rocky Mountains; and by *E. walcotti* in Nevada and Utah.

The succeeding *Basilicorhynchus* Zone is restricted to the upper part of the lower Famennian and occurs in the Tetcho Formation, in the lower part of the Wabamun Group, and in the upper Sassenach and lower Palliser formations.

The *Gastrodetoechia* Zone extends from the middle Famennian to the lower part of the upper Famennian. The zone is present in the Rocky Mountains and Northwest Territories of Canada, and in Idaho, Montana and Utah of the United States. The zone contains a large brachiopod fauna, as well as ammonoids described by House (in House & Pedder, 1963), which include species of *Cheiloceras, Tornoceras* and *Platyclymenia.*

The *Sinotectirostrum avellana* Zone occurs in the upper part of the upper Famennian and is known only in the North Nahanni and Root Rivers areas of the Northwest Territories and from wells in northeastern British Columbia. The zone corresponds to Hume's (1922) *Athyris angelica* Zone.

Famennian brachiopod assemblages recognized by Poole *et al.* (1968) in southwestern United States comprise in ascending sequence: *Cyrtospirifer* spp.-*C. portae, C. monticola, Paurorhyncha endlichi-Cyrtiopsis animasensis,* and *Syringothyris* spp.

NORTHERN NORTH AMERICA

Upper Devonian rocks in the eastern Arctic Islands are predominantly clastic strata of nonmarine origin. Marine Frasnian rocks, however, have been reported from scattered localities in the western Arctic Islands, notably Banks, Melville, and Prince Patrick islands. On Banks Island the early Frasnian is indicated by the presence of *Ladogioides pax, Eleutherokomma* cf. *E. impennis,* and *"Allanaria" allani*; and the mid-Frasnian by *Cyrtospirifer thalattodoxa* and *Calvinaria albertensis.* A rich fauna of middle to late Frasnian age occurs in reefs on northeastern Banks Island and includes *Hexagonaria, Phillipsastrea, Theodossia,* and others (Klovan & Embry, 1971).

Marine Famennian megafossils of the Canadian Arctic Islands have been summarized by McLaren (in Kerr, McGregor & McLaren, 1965). They occur in the upper part of the Griper Bay Formation on Bathurst, Cameron, Byam Martin, and Melville islands. Brachiopods of this assemblage represent a single fauna and include *Acanthatia* sp., *Basilicorhynchus* sp., *Ptychomaletoechia?* sp., and possibly *Cyrtospirifer* sp. Conodonts associated with the brachiopods on Byam Martin Island include *Palmatolepis perlobata* and *Icriodus costatus.* The former ranges from the upper *Palmatolepis triangularis* Zone through the lower *"Spathognathodus" costatus* Zone (McGregor & Uyeno, 1972).

SOUTH AMERICA

In Late Devonian time the sea withdrew from most of the extra-Andean regions of South America, but seems to have persisted in the Andean belt. The upper barren parts of the Devonian clastic successions in western Venezuela, southern Peru, central Bolivia, and western Argentina may belong in the Upper Devonian (Harrington, 1962, p. 1786). Recently, Cousminer (1964, p. 33-35) reported lower Upper Devonian palynomorphs from the upper part of the Devonian succession of Bolivia. Sparsely fossiliferous rocks present also in the Parnaíba basin of Brazil are probably of early Frasnian age (Harrington, 1968, p. 662). A few authors, notably Maack (1964), have argued that South America was glaciated during the Late Devonian. Maack (1964, p. 291, 292) cited as evidence widespread Upper Devonian tillites present in northeastern Brazil and northwestern Argentina.

PROVINCIALISM AND AMMONOID DISTRIBUTION

Beginning in late Eifelian time, routes for faunal migration were reestablished between the midcontinent area and western North America via the Williston basin, as indicated by an intermingling of Eastern Americas and Old World shelly elements in Indiana, Michigan, northern Ontario, and northern Manitoba. The separation between the Old World and Eastern Americas realms apparently was breached completely by onlap of epicontinental seas during the Taghanic (Johnson, 1970c), resulting in a single cosmopolitan brachiopod fauna in the marine areas of North America and elsewhere during the Frasnian (Johnson & Boucot, 1973). Important widespread brachiopod genera of this fauna include *Calvinaria, Cariniferella, Devonoproductus, Douvillina, Eleutherokomma, Hypothyridina, Nervostrophia, "Spirifer"* of the *orestes*-type, *Tenticospirifer,* and *Theodossia* (Johnson & Boucot, 1973, p. 94).

The tubular stromatoporoid *Amphipora* abundant in western North America and the Old World reached the midcontinent and Appalachian areas during this interval (Duncan in Cloud, 1959, p. 948, fig. 12); and similar evidence showing intermingling of coral genera was cited by Oliver (1975).

In contrast to the cosmopolitanism shown by Frasnian brachiopods, trilobites are very scarce at this time; *Scutellum* and a few phacopids only are known in western North America (Ormiston, 1972, p. 602). The radiation in the cyrtosymbolinids that took place in Europe did not reach North America because of the shutting-off of the migration route from Europe to North America by a continental clastic wedge which was deposited across northern Alaska and the Arctic Islands during the Frasnian and Famennian (Ormiston, 1972, p. 602).

At the end of Frasnian time a number of important invertebrate groups became extinct, including the brachiopod taxa Atrypoidea, Pentameroidea, Stropheodontidae, Delthyridae, and Meristellinae. Among the trilobites, the harpids and thysanopeltids disappeared in the Late Devonian, probably in late Frasnian time (House, 1967).

The principal brachiopod genera that survived the extinction at the end of the Frasnian and continued into the Famennian include: *Attribonium, Aulacella* or *Rhipidomella, "Chonetes"* or *Retichonetes, Crurithyris, Cupularostrum* or *Ptychomaletoechia, Cyrtina, Cyrtospirifer, Productella, Schizophoria,* and *Steinhagella* (Johnson & Boucot, 1973). Along with these survivors the Famennian brachiopod fauna comprises principally new rhynchonellid, productid, athyridid and spiriferid genera, some of which are widely distributed (Sartenaer, 1969), indicating continued cosmopolitanism (Johnson & Boucot, 1973).

The ammonoid genus *Manticoceras,*

guide fossil for the Frasnian, is more widely distributed than any other, but is absent from South America (House, 1964). Ties between North America and Europe are indicated by occurrences of early Frasnian forms in several places. *Timanites* is recorded from Alberta, and *Koenenites* is known from Michigan (Miller, 1938). *Pharciceras* is the European guide genus of the lower Frasnian, and it, or its close allies, occur in the upper Tully Limestone of New York (House, 1962, 1968a). The most widespread distribution of *Manticoceras* apparently occurred in the middle Frasnian, where the genus is known from the Northwest Territories, Alberta, Ontario, including the Hudson Bay Lowlands (Miller, 1938, p. 115, 116), Michigan, Iowa, Utah, New Mexico, Missouri, Ohio, Virginia, and especially New York. These occurrences form a link with those along the northern Siberian coast (House, 1964, p. 266). The richest North American Frasnian goniatite faunas occur in New York where a succession of species closely allied to those of Europe may be recognized.

In North America, *Cheiloceras* is known from New York (House, 1962) and western Canada (House & Pedder, 1963), and is apparently almost as widespread as *Manticoceras* geographically, but is sparser numerically (House, 1964). This sparseness marks the beginning of geopraphical restriction of later Devonian ammonoid faunas.

Clymeniids entered with the faunas of the *Platyclymenia*-Stufe, a fauna well known from Europe and North Africa. In North America representatives of this fauna occur in the Three Forks Shale of Montana and include *Tornoceras, Platyclymenia, Rectoclymenia,* and *Raymondiceras* (House, 1964). The latter genus is recorded also from New Mexico (Miller & Collinson, 1951). Of interest is the apparent absence of this fauna from eastern North America, except for *Sporadoceras milleri* from Pennsylvania, which may occur at this level (House, 1962, p. 263).

The goniatites and clymeniids of the uppermost Famennian, including the *Clymenia* and *Wocklumeria* zones known in England, Germany, France, North Africa, and elsewhere, are sparingly represented in North America and the traces found are equivocal. *Cyrtoclymenia* and *Cymaclymenia* are known from Ohio, and *Cyrtoclymenia* from New Mexico (House, 1962), and also from Alaska (Sable & Dutro, 1961). None of the North American occurrences can be dated certainly as latest Famennian, and all may well be mid-Famennian in age (House, 1954, p. 268).

DEVONIAN CONTINENTAL DEPOSITS AND ASSOCIATED INVERTEBRATE FAUNAS

Nonmarine Devonian rocks occur in several well-known areas in the Western Hemisphere, the main areas being in the Appalachians of the eastern United States and Canada, in Arctic Canada, and in eastern Greenland; these are commonly referred to as "Old Red Sandstone" basins of deposition. Devonian continental beds also are represented possibly around the edges of the cratonic basins of South America and Antarctica where clastic sequences are largely barren or sparsely fossiliferous and difficult to date. Smaller, thinner, and more isolated occurrences are known also in the southern part of the Hudson Bay Lowlands (Sanford & Norris, 1975), in Montana and Wyoming (Sandberg, 1961), in Arizona (Teichert & Schopf, 1958), in the Rocky Mountains of Alberta (Aitken, 1966), and elsewhere. Many of these deposits contain abundant plant and fish remains but lack identifiable invertebrate fossils.

Invertebrate fossils in Devonian continental beds are generally scanty in variety and numbers. A few of the more important forms include the brachiopod genus *Lingula,* several mollusks (e.g., *Amnigenia*), leperditiid ostracodes, the euryptids *Pterygotus* and *Eurypterus,* ceratiocarid crustaceans, and the arthropod *Estheria.*

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CARBONIFEROUS[1]

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CONTENTS

INTRODUCTION

The name Carboniferous was introduced by Conybeare and Phillips (1822) for the English succession that included the Old Red Sandstone, Mountain Limestone, Millstone Grit, and Coal Measures. Later Sedgwick and Murchison (1839) removed the Old Red Sandstone from the Carboniferous to establish the Devonian System. In 1841 Murchison established the Permian System in the Province of Perm, Russia, as overlying the Carboniferous. Since then the lower and upper boundaries of the Carboniferous with adjacent systems have presented problems. The Old Red Sandstone (Devonian) of Devonshire is mainly nonmarine, is structurally deformed, and lacks diagnostic fossils of worldwide biostratigraphic value. The overlying Permian (Magnesian Limestone) in England also has few abundant fossils and the Russian Carboniferous and Permian sections are far away and have different faunal and floral assemblages than the Carboniferous and Permian of England. Furthermore, Murchison's original definition of the Permian System left some doubt concerning the placement of beds above the Moscovian Stage and below the Artinskian Stage, beds having marine faunas that are not present in the predominantly nonmarine sections in northwestern Europe.

The recognition of lateral changes in facies in the upper part of the Devonian from continental beds in Devonshire into marine strata bearing marine faunas in the lower Rhine valley led to the acceptance of locating a succession in marine strata that could serve as a type section to define the Devonian-Carboniferous boundary. Although the Rhine valley sections contain a variety of cephalopods and conodonts, faunas of the carbonate facies are poorly represented. The Belgium succession includes bioherms and reefs in this interval, and after considerable study the lower boundary was agreed upon by the first *Congrès de stratigraphie et de géologie du Carbonifère,* Heerlen, 1927, as the base of the Tournaisian Stage in Belgium. At the second Heerlen congress (1935) the base was reassigned as the first appearance of a zonal guide fossil, the ammonoid *Gattendorfia subinvoluta,* a useful index fossil in the German strati-

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graphic section, which was thought to be equivalent to the Etroeungt beds at the base of the Tournaisian Stage. Later study has demonstrated that the lower beds in the type sections of the Tournaisian include strata older than the zone of *Gattendorfia subinvoluta* and span nearly the entire latest Devonian zone of *Wocklumeria*. The Subcommission on Carboniferous Stratigraphy at the Seventh *Congrès International de stratigraphie et de géologie du Carbonifère* (1971) adopted several working agreements that attempted to resolve this boundary problem. These in effect are as follows:

1. The base of the *Gattendorfia subinvoluta* Zone will continue to serve as the accepted base of the Carboniferous.
2. Because the geographic distribution of the zone name-bearer is restricted, the evolution (first appearance) of the conodont *Siphonodella sulcata* from its Devonian ancestor (which occurs at the same stratigraphic position as the appearance of *G. subinvoluta* in the German succession) will be used on a worldwide basis as the base of the Carboniferous.
3. The designation of a stratotype will be postponed until a search has been made for a suitable, continuous, marine stratigraphic succession, preferably in the region of the original chronostratigraphic units (stages).
4. The boundary of the lowest Carboniferous stage is to be modified to correspond with the lower boundary of the system.

The upper boundary of the Carboniferous has been placed at several positions although there are at least six major recognizable, worldwide, marine, faunal biostratigraphic zones between the top of the Moscovian Stage and the base of the Artinskian Stage. Presently most European and North American biostratigraphers follow the recommendations of the All Soviet Committee on the Carboniferous-Permian boundary (1952) in placing the top of the Carboniferous at the top of the Gshelian Stage. In the past the Carboniferous-Permian boundary has been placed as high as the top of the Sakmarian Stage (or base of the Artinskian Stage) or lower at the top of the Asselian Stage or even within the Asselian. Some biostratigraphers have continued to use the term Permo-Carboniferous for the interval between the Gshelian and Artinskian. Thus, the Autunian Series of Europe and the lower part of the Dunkardian Series and the Wolfcampian Series and even the lowest parts of the Leonardian Series in North America at times have been correlated with the Carboniferous or "Permo-Carboniferous" based on these various boundary positions. The top of the Carboniferous has only infrequently been placed below the top of the Gshelian Stage in the Soviet Union.

Subdivisions.—Three different schemes of subdivision of Carboniferous rocks are extensively used (Fig. 1): the western European classic sections with subdivision into Lower and Upper parts; the southern Urals, Russian platform, and greater Donetz basin sections with subdivision into Lower, Middle, and Upper parts; and the central North American sections recognizing the Mississippian and Pennsylvanian as independent systems. Other sets of subdivisions proposed for various eastern Asia and Gondwana regions probably are equally useful. Correlations between different Carboniferous biogeographic realms and regions are still incomplete and Figure 1 indicates a generally accepted correlation of the three sets of series and stages.

In northwestern Europe the Carboniferous System is divided into two subsystems, the Dinantian below and Silesian above. The Dinantian takes its name from the Dinant area of Belgium where type sections for the mainly carbonate series, Tournaisian (MORTELMANS, 1969) and Visean, are located (GEORGE, 1969). The Silesian takes its name from the coal basins of the Silesian region of Poland. Three series are recognized: the Namurian (at the base), Westphalian, and Stephanian, and the successions are largely nonmarine or paralic with a few marine bands (transgressions) and a number of deeply weathered, flinty underclays (seatearths). In practice the Namurian (HUDSON, 1945; RAMSBOTTOM, 1969) and most of the Westphalian marine bands are correlated with the British succession which has a slightly more complete fauna than the type succession on the European continent (Fig. 1). The Westphalian (CALVER, 1969) is subdivided into four stages (A, B, C, and

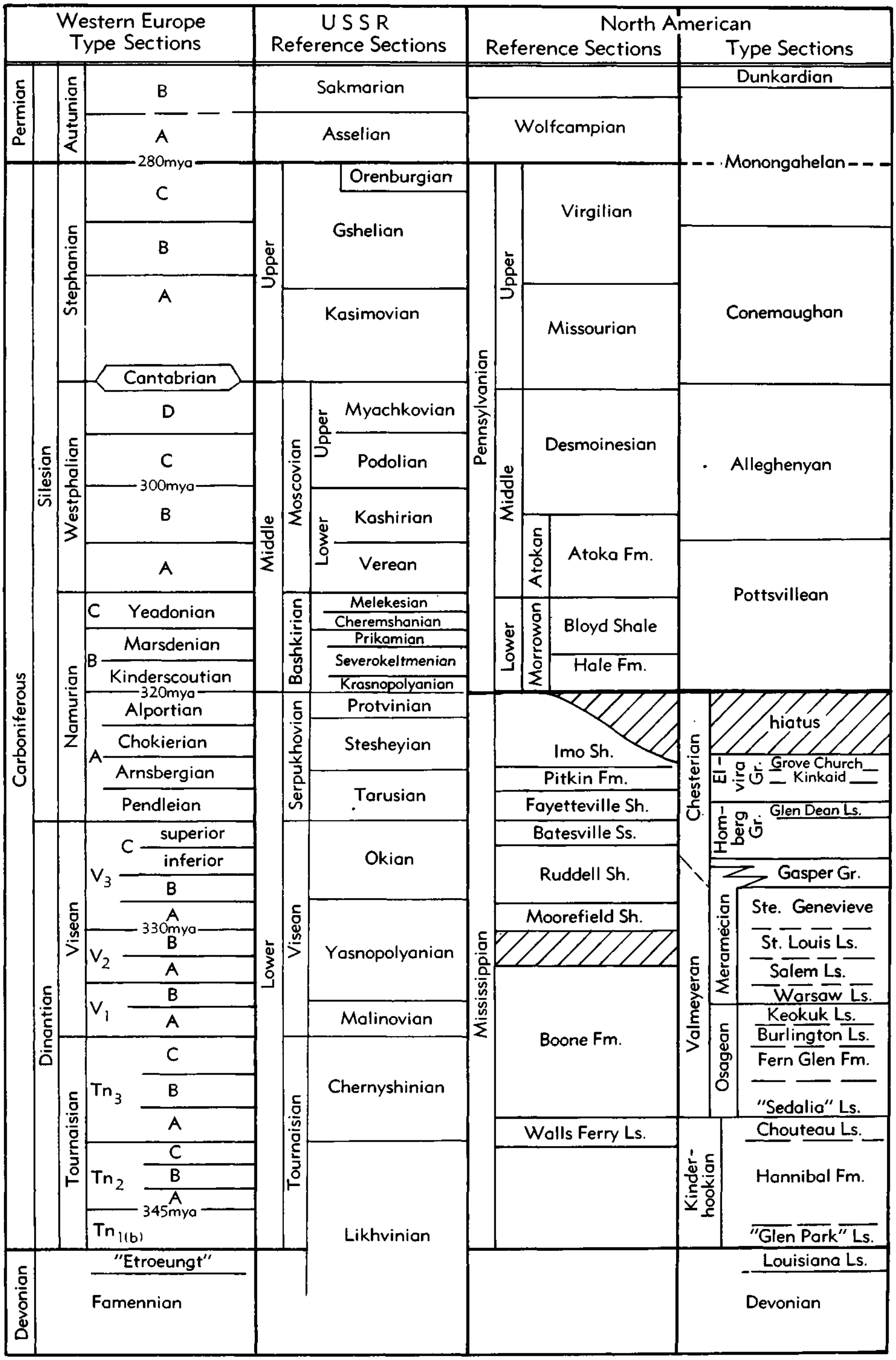

FIG. 1. Comparison of Carboniferous stratigraphic terminology in western Europe, European USSR and North America, and correlation of boundaries. Biostratigraphic zone fossils for ammonoids, foraminiferids, brachiopods, corals, and megaflora indicate approximate relationship between zonations based on different

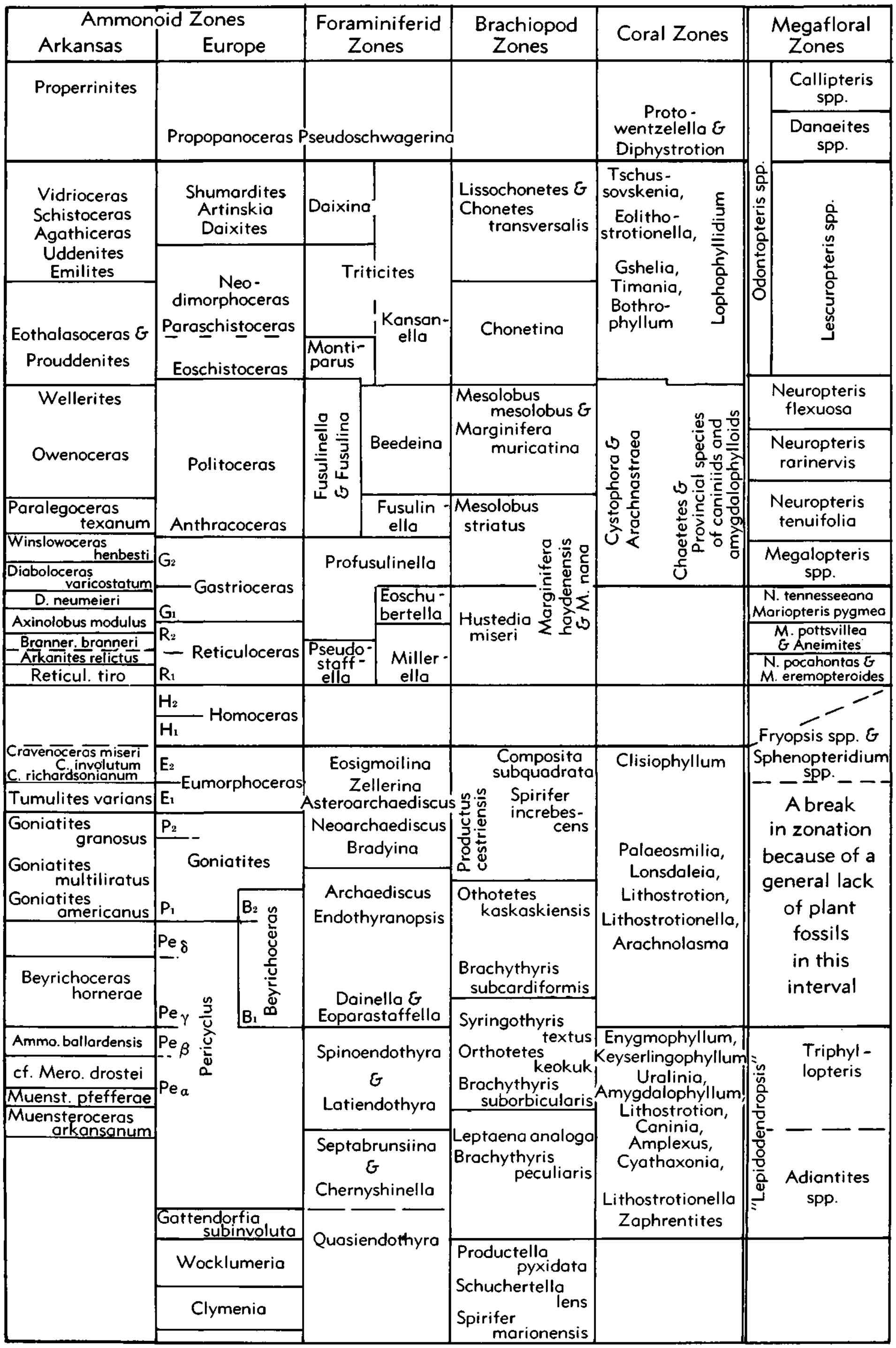

FIG. 1. (*Continued from facing page.*)

groups. See Figure 7 for ranges of stratigraphically important genera of conodonts. The megafloral zones are for the Euramerian floral region (modified from Read & Mamay, 1964).

D) by three marine bands and some differences in floral content. The Stephanian has no marine bands in its type area where it is subdivided into three stages (A, B, and C) based on floral differences. The Upper Westphalian and Lower Stephanian were separated by the International Subcommission on Carboniferous Stratigraphy (1967) by using Tonstein 60 as the boundary in the Saar-Lorraine area. A floral succession that either spans Late Westphalian-Early Stephanian time or fills a gap between them has been found in northern Spain and named the Cantabrian Stage (WAGNER, 1969). At present the type section of the Stephanian lies in the coal basin of St. Étienne in Loire and passes transitionally upward into beds having fossil floras of Autunian (Early Permian) appearance (LIABEUF & ALPERN, 1969). Correlations of the Westphalian and Stephanian are based mainly on the distribution of plant leaves, stems, and spores and become complicated by ecological differences in floras between basins of approximately the same age, but in different environmental settings (i.e., elevation, rainfall) (BOUROZ, 1969; DE MAISTRE, 1969).

The North American succession of strata equivalent to the Carboniferous is separated into two local systems, the Mississippian below and the Pennsylvanian above. The Mississippian System, named for a sequence of predominantly limestone, sandstone and shale exposed along the Mississippi valley in Missouri, Illinois, and Iowa, is based on the "Mississippi Group" (WINCHELL, 1869), between the Devonian and the "Coal Measures." The "Coal Measures" were renamed the Pennsylvania Series (WILLIAMS, 1891) for exposures in Pennsylvania. Both system names gained wide usage in North American textbooks early in this century. The type Mississippian strata (Fig. 1) have a clastic and limestone portion at their base (WELLER *et al.,* 1948), the Kinderhookian Series (the original definition included some latest Devonian beds), which represents a shallow-water facies with reworked faunas in part. The mainly carbonate succession is divided into the Osagian Series, which is mainly middle and late Tournaisian, and the Meramecian Series, which includes all except latest Visean equivalents. These two carbonate series are locally dominated by echinoderm faunas that, in general, are not a typical lithofacies and this has made correlation outside the type region difficult. The upper part of the carbonate sequence grades laterally into the basal part of the Chesterian Series. The Chesterian has fifteen or so sequences of transgressive and regressive sediments that are terminated by a major regional unconformity.

The type Pennsylvanian (BRANSON, 1962) is in southwestern Pennsylvania in strata that are predominantly nonmarine with a few marine beds. Because of uncertaintly in correlating the strata of the type area with marine and paralic strata in much of the rest of North America, a set of standard reference sections was established in the southern Midcontinent region (in Arkansas, Missouri, Oklahoma, Kansas, and Iowa) (MOORE *et al.,* 1944). These reference sections form the basis for five standard series, in ascending order: Morrowan, Atokan, Desmoinesian, Missourian, and Virgilian. The lower two, Morrowan and Atokan, are located near the southern edge of the Early Pennsylvanian North American craton and are geosynclinal sequences deposited at a time of active tectonic deformation of the main part of the geosyncline to the south (GORDON, 1974). The type section of the Desmoinesian was deposited to the north in Iowa, well on the North American craton, as were the Missourian and Virgilian series in Missouri and Kansas. These higher three series include evidence of numerous transgressions and regressions and complications of repeated cyclothems (WANLESS, 1969). On the cratonic shelf, low tectonic arches and shallow basins (Illinois, Michigan, and Forest City basins) caused sedimentary units to thin and disappear or thicken and change facies (WANLESS, 1969). These standard sections are marine and paralic and are separated from areas to the southwest by block-faulted uplifts and basins and from areas west of the Southern Rockies by the transcontinental arch.

The third set of sections that are used as references for the Carboniferous are those on the Russian platform (DALMATSKAYA *et al.,* 1961), southern Urals, and greater Donetz basin (AYZENVERG, 1969). In these sections the Tournaisian and Visean strata and faunas are similar to those in the Belgian type area and no major correlation problems are apparent. The "Namurian" on the Russian platform, which equates to only the lower part of the Namurian of the Belgium section, was renamed the Serpukhovian Stage by EYNOR in 1970. The Tournaisian, Visean, and Serpukhovian stages are included by Soviet biostratigraphers in their Lower Carboniferous.

A major unconformity separates these Lower Carboniferous units from higher Carboniferous units on the Russian platform (BARKHATOVA *et al.*, 1970); however, the sections near the margins of the geosynclines (Southern Urals) and sedimentary troughs (Donetz basin) have a succession, called the Bashkirian Stage, which marks the base of the Middle Carboniferous. The Bashkirian is overlain by the Moscovian Stage, which covers most of the Russian platform and forms the upper part of the Middle Carboniferous. The Upper Carboniferous, Kasmovian and Gshelian stages, is present on much of the Russian platform where it is overlain by the Asselian Stage (Lower Permian).

As revised in 1974, the Lower Carboniferous of the Russian platform is correlated with the North American Mississippian; the Middle Carboniferous is correlated with the Morrowan, Atokan, and Desmoinesian; and the Upper Carboniferous with the Missourian and Virgilian. Most marine Carboniferous sequences on cratonic shelves and in geosynclines are adaptable to this three-fold subdivision. In the succeeding discussions in this paper, Lower, Middle, and Upper Carboniferous will be used as outlined above.

The Carboniferous histories of Australia, peninsular India, South America east of the Andes, and Antarctica are generally similar, although not as closely similar as their Permian and Triassic histories.

Two regions of deposition were present in Australia during the Carboniferous: an eastern region along the Tasman geosyncline, which was divided into a number of structurally delimited basins; and a western region which included the Carnarvon, Canning and Bonaparte Gulf basins. In the eastern region seven faunal zones are recognizable in the Lower Carboniferous succession (HILL, 1957; CAMPBELL & MCKELLAR, 1969; CAMPBELL *et al.,* 1969; ROBERTS, 1975), based primarily on coral and brachiopod ranges. Above these seven faunal zones, one brachiopod zone is recognized in Middle Carboniferous strata and another zone is identified in what are probably Upper Carboniferous strata. These two highest zones are interbedded with rocks having the *Rhacopteris* flora.

The zonation in the eastern region is not applicable to the western basins where different brachiopod zones and conodont zones are used for the Lower Carboniferous succession. Middle and Upper Carboniferous strata in the western region are poorly fossiliferous and pass upward without much depositional change into beds of probably Early Permian age bearing *Eurydesma.*

The eastern Australian Lower Carboniferous includes conglomerate and sandstone beds at its base and a succession of shale with a few limestone beds. The Middle and Upper Carboniferous are mainly clastic rocks and volcanics and include conglomerates, tuffs, flows, tillites, diamictite with a few limestones and marine and nonmarine shales. The Tournaisian and early Visean corals show similarity to those of southeastern Asia, but later Visean and early Namurian corals show considerable endemism (HILL, 1948, 1957, 1973; CAMPBELL & MCKELLAR, 1969). This has been interpreted as a gradual change from warm or temperate marine conditions to cooler conditions before the end of the Early Carboniferous. The two marine zones within the predominantly clastic and volcanic beds of Middle and Late Carboniferous age having interbedded tillites and glacial marine beds represent possible times of climatic warming in an otherwise cold interval. The Early Permian *Eurydesma* fauna is closely associated with glacial deposits and is considered to be a cold-water assemblage.

In eastern South America, in Brazil, Argentina, Paraguay, and Uruguay, Lower Carboniferous, and possibly Middle Carboniferous, strata are separated from Upper Carboniferous and Permian strata by a major regional unconformity that forms the sub-Gondwana surface (CASTER, 1952). The relationship between the Lower and Middle Carboniferous of Argentina suggests that a hiatus of some magnitude exists between them. The Lower Carboniferous marine faunas are mainly conulariids, brachiopods, and bivalves (Amos & Sabattini, 1969) and are not completely studied. The Middle Carboniferous faunas contain brachiopods, bryozoans, and trilobites, which are similar to Australian faunas of this age. These faunas also include the cephalopods *Anthracoceras* and *Eoasianites,* which are similar to those of the Desmoinesian of North America. Strata of probable Late Carboniferous age in Argentina have plants that may be Stephanian and locally marine faunas of brachiopods, such as *Cancrinella, Crurithyris, Tornquistia, Spirifer,* and *Alispirifer.* The lateral relationships of these Argentinian faunas to nearby glacial deposits remain unanswered; however, *Eoasianites* and other faunas and floras of probable late Middle Carboniferous age are known from beds within the Tubarão glacial beds in Brazil and Uruguay. The coals of the Paraná basin in Brazil are in interglacial deposits that lie between glacial beds and are probably Carboniferous in age rather than Permian; however, the upper part of the tillite succession may be Early Permian in age if the occurrence of *Eurydesma* is a reliable guide.

In the Cape region of South Africa, the Lower Dwyka Shale contains a sparse flora similar to the *Rhacopteris* flora in Middle or Upper Carboniferous strata of eastern Australia. Most of the overlying tillite of the Dwyka is probably Late Carboniferous in age. The *Eurydesma* fauna occurs in mudstone and shale above the tillites of the Dwyka and is considered to be of Early Permian age.

The Carboniferous in other Gondwanan continents or continental fragments is poorly understood. In Madagascar the Carboniferous, if present, seems to be represented by a thin tillite, and in the Falkland Islands, the succession is remarkably similar to that in South America and South Africa. The Lower? Carboniferous contains plant fossils and is overlain by tillites and clastic beds interbedded with marine units of probable Middle and Late Carboniferous age. In Antarctica, Devonian strata having fish remains are unconformably overlain by tillite and coal-bearing sandstone that are considered to be Permian based on the presence of *Glossopteris* without non-Gondwanan plants.

BIOSTRATIGRAPHIC AND BIOGEOGRAPHIC ANALYSIS

The Carboniferous Period, estimated to extend from 345 mya to 280 mya (Francis & Woodland, 1964), had a duration of 65 my, which approximates the length of each of the four other long geologic periods, the Cambrian, Ordovician, Cretaceous, and Tertiary. During this long interval of time, distributions of marine invertebrate faunas were strongly influenced by changes in climate; in seaways, their interconnections, and sea levels; in the relative position of land areas; and in tectonic, orogenic, and epeirogenic changes. The details of how these physical changes modified the Carboniferous physical environment are much less thoroughly known that is the actual distribution of most of the fossil groups representing part of the biological environment. At present the mechanisms of the dispersals of faunas between different realms and regions during the Carboniferous are not well understood and require much more study. These dispersals appear to reflect the different threshhold levels of each faunal group to dispersal filters that accompanied changes in paleogeographic climate and environments during the period. This was a period of widespread crustal deformation as well as sea-level and climatic fluctuations, even unconformities on the more stable parts of continental masses are commonly irregular in duration and extent. Later crustal movements have partially obscured Carboniferous tectonic settings. In addition, Carboniferous biostratigraphers started only in the late 1960's to reconsider distributions of pre-Mesozoic faunas and floras in the context of plate tectonic models.

The biogeographic distribution of many invertebrates during the Carboniferous Period (Eynor *et al.,* 1973; Ross, 1973) is marked by times of widespread dispersals of nearly cosmopolitan faunas but this is contrasted at other times by well-developed provincialism with many endemic genera and families. These distributional patterns have been studied for Protozoa (Foraminiferida), Coelenterata (Rugosa), Brachiopoda (Articulata), Mollusca (Cephalopoda), and Arthropoda (Insecta). Although many questions remain unanswered, a general pattern for marine invertebrates shows increasing provincialism after the Visean. Provincialism was particularly strong by the beginning of the Middle Carboniferous followed by some decrease in the levels of provincialism near the end of Middle Carboniferous (Ross, 1970).

During parts of the Carboniferous, strongly differentiated provincial faunas result in a number of biostratigraphic problems. Within individual biogeographic realms (or regions) correlation is based largely on successful and abundant endemic faunas. Therefore, correlation from one biogeographic realm (or region) to the next is generally more difficult and less certain than within a particular realm because distinctive genera and families may have considerably different stratigraphic and geographic ranges in different realms. At several times during the Carboniferous, incomplete faunal interchange between provinces took place and resulted in the introduction of new lineages into another province and often the extinction, at least within several provinces, of another lineage, presumably by ecologic replacement. The biogeographic distribution of other invertebrate groups is less thoroughly studied, but available data suggest that they also may have a similar pattern. Terrestrial insect distributions are closely comparable to those recorded for plant fossils.

The biostratigraphic distribution of Carboniferous fossils is well known for a number of groups that are extensively used as zonal index fossils. In marine carbonate strata protozoans (Foraminiferida), corals (Rugosa), and brachiopods are commonly abundant and are widely used for correlation because of their rapid evolution or distinctive morphological features or both. Shaly marine sequences may have large numbers of mollusks (Cephalopoda) which, because of their rapid evolution, are valuable guide fossils. Conodonts occur in most Carboniferous marine strata and have been particularly thoroughly studied from Lower Carboniferous strata.

FORAMINIFERS

This group of microfossils is widely used in correlating marine strata, particularly the calcareous foraminifers that are commonly abundant in limestone. A large proportion of the foraminifers used in interregional correlation are nearly cosmopolitan and are the basis for a worldwide correlation scheme (Fig. 2, 3), although numerous species and genera have endemic distributions.

In summarizing the Lower Carboniferous foraminiferal zonation, data were compiled from the publications of Rauzer-Chernousova (1948), Reytlinger (1960, 1962, 1963, 1969), Lipina (1963, 1964, 1965, 1970, 1973) Mamet (1962, 1968), Mamet and Skipp (1971), Sando, Mamet, and Dutro (1969), Conil (1964), Conil and Lys (1968), and Conil, Paproth, and Lys (1968). In the lower Tournaisian (Zones 6 and 7) the earliest Carboniferous foraminiferal zone is identified as Zone 6, which is characterized in Eurasia by an abundance of Quasiendothyridae, which are absent in most of North America. Also present in both regions are species of *Septaglomospiranella, Latiendothyra,* and *Earlandia.* This fauna is not diverse and a number of the species are endemic. The next younger Tournaisian foraminiferal zone (Zone 7) has nearly uniform faunas in Eurasia and North America. It is characterized by many genera of the Tournayellidae. Especially abundant are individuals of *Septaglomospiranella* and *Palaeospiroplectammina,* and the first appearance of *Tuberendothyra* of the Endothyridae.

The upper part of the Tournaisian has two zones, the lower, Zone 8, contains the first appearance of *Spinoseptatournayella* and *Spinoendothyra* and an abundance of *Tuberendothyra.* The upper zone, Zone 9, is characterized by an abundance of *Tuberendothyra,* as well as *Spinoendothyra,* and shows a continued increase in faunal diversity. Some genera, which are common to abundant in Eurasia, such as *Brunsia, Urbanella, Glomospiranella,* and others, are rare or lacking in North America.

Zone 10 is of earliest Visean age. The important faunal elements in North America are *Tournayella, Eoforschia* of the group

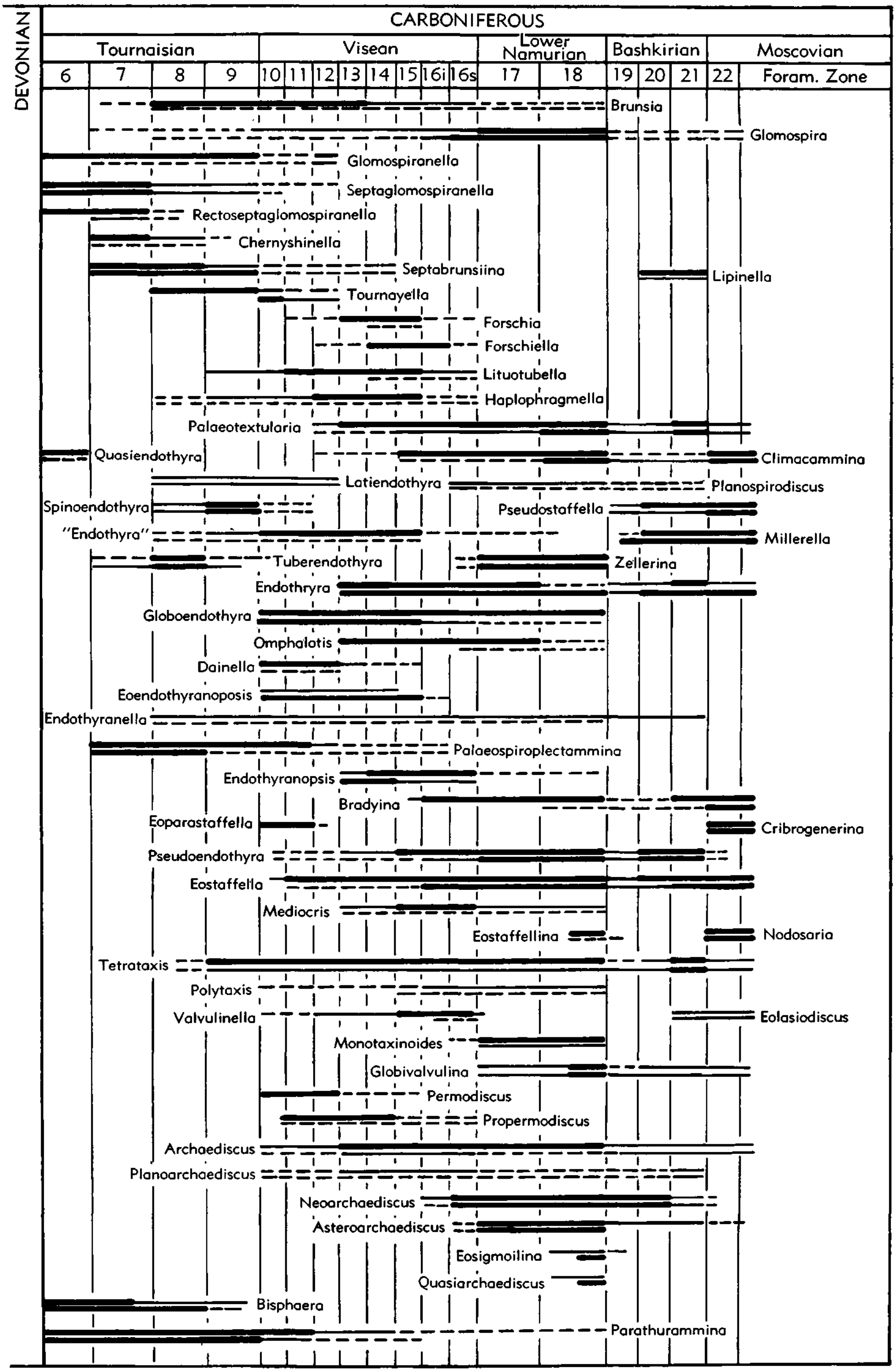

FIG. 2. Stratigraphic range of important genera of Foraminiferida in the Lower and part of Middle Carboniferous. The upper line indicates the range in Europe and the lower line the range in North

E. moelleri, Spinoendothyra (sparse), *Calcisphaera, Pachysphaerica, Tetrataxis, Globoendothyra baileyi, Eoendothyranopsis, Propermodiscus, Archaediscus* of the group *A. kerstovnikovi,* and *Planoarchaediscus.* In Eurasia *Brunsia, Endothyra* of the group *E. prisca, Latiendothyra, Dainella, Eoparastaffella,* primitive *Eostaffella, Permodiscus, Urbanella,* and *Lituotubella* are common but are unreported or sparse in North America.

Zone 11 is late early Visean in age. The important genera in North America are *Tournayella, Eoforschia, Eoforschia* of the group *E. moelleri, Endothyra* of the group *E. prisca, Globoendothyra,* and *Eoendothyranopsis* of the group *E. spiroides, Tetrataxis, Archaediscus* of the group *A. krestovnikovi* and *Planoarchaediscus.* In Eurasia *Forschia* (first appearance), *Lituotubella, Eotextularia, Latiendothyra, Dainella, Eoparastaffella, Polytaxis, Valvulinella* (rare), *Permodiscus,* and *Archaediscus* of the group *A. moelleri* are important parts of this fauna but are sparse or unreported in North America.

Zone 12 is of early middle Visean age. Characteristic genera of Zone 12 in North America are *Tournayella, Eoforschia* of the group *E. moelleri, Palaeotextularia* of the group *P. consobrina, Globoendothyra, Eoendothyranopsis* of the group *E. spiroides, Tetrataxis, Propermodiscus, Archaediscus* of the group *A. krestovnikovi,* and *Planoarchaediscus.* In Eurasia, diagnostic faunal constituents are: *Forschia, Forschiella* (first appearance), *Lituotubella, Haplophragmella, Eotextularia, Cribrostomum, Climacammina* of the group *C. prisca, Endothyra* of the group *E. prisca, Dainella, Eostaffella, Vissariotaxis* (first appearance), *Permodiscus* and *Archaediscus* of the group *A. chernoussovensis* (first appearance).

Late middle Visean (Zone 13) foraminifers include: *Eoforschia, Paleotextularia* of the group *P. consobrina, Climacammina* of the group *C. prisca, Globoendothyra, Eoendothyranopsis, Tetrataxis, Propermodiscus, Archaediscus* of the group *A. krestovnikovi, Archaediscus* of the group *A. moelleri, Archaediscus* of the group *A. chernoussovensis* and *Planoarchaediscus,* and the following first appear: *Endothyra* of the group *E. bowmani, Globoendothyra* of the group *G. tomiliensis, Eoendothyranopsis* of the group *E. rarus,* and *Endothyranopsis* of the group *Endothyranopsis compressus.* In Eurasia, important genera include *Forschia, Lituotubella, Haplophragmella, Cribrostomum, Climacammina* of the group *C. prisca, Endothyra* of the group *E. prisca, Dainel'a, Eostaffella, Valvulinella, Vissariotaxis, Omphalotis, Endostaffella, Endothyra* of the group *E. pauciseptata, Janischewskina,* and *Mediocris* make their first appearance.

Early late Visean foraminifers (Zone 14) in North America are found in the uppermost part of the St. Louis Limestone and the lowermost part of the Ste. Genevieve Limestone and include most of the faunal elements listed under Zone 13 with the addition of *Cribrostomum, Eoendothyranopsis utahensis, Eoendothyranopsis macrus, Mikhailovella,* and *Cribrospira.* Rare specimens of *Forschia* and *Lituotubella* are recognized in the northernmost Cordillera. In Eurasia also the faunas of Zones 13 and 14 are very similar.

Middle upper Visean (Ste. Genevieve in part) (Zone 15) in North America is characterized by abundant *Palaeotextularia* of the group *P. consobrina, Cribrostomum, Endothyra* of the group *E. bowmani, Globoendothyra, Eoendothyranopsis utahensis, Tetrataxis* and the first appearance of *Climacammina* of the group *C. prisca, Palaeotextularia* of the group *P. longiseptata, Climacammina* of the group *C. patula,* and *Endothyranopsis crassus.* In Eurasia, *Forschia, Forshiella, Haplophragmella, Endothyra* of the group *E. prisca, Endothyranopsis compressus, Pseudoendothyra, Eostaffella, Mediocris, Valvulinella, Vissariotaxis, Archaediscus* of several groups, and *Planoarchaediscus karreri* are important.

Late Visean Zone 16i (early Chesterian) is characterized by common to abundant *Cornuspira, Palaeotextularia* of the group *P. consobrina, Climacammina* of the group *C.*

FIG. 2. *(Continued from facing page.)*
America (mainly western part). [Thick lines indicate abundant, thin lines common, and dashed lines rare or questionable occurrences. Numbered foraminiferal zones and data from Mamet & Skipp (1971); Ross, n.]

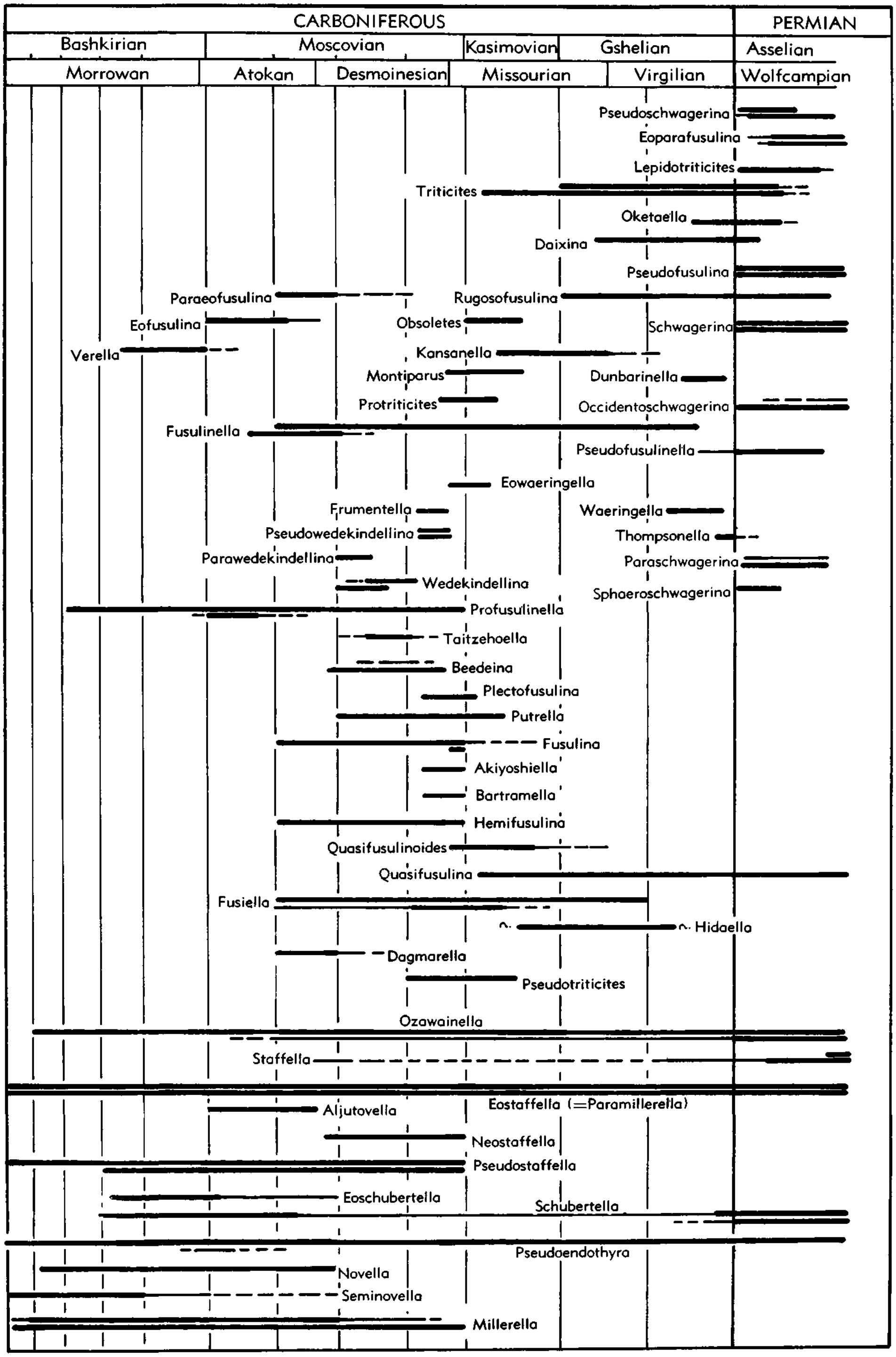

FIG. 3. Range of Middle and Late Carboniferous fusulinacean genera in Arctic-Eurasian province (upper line) and in North American Midcontinent province (lower line) (data from Ayzenverg and others, 1969;

prisca, Palaeotextularia of the group *P. longiseptata, Climacammina* of the group *C. patula, Endothyra bowmani, Endothyranopsis crassus, Globoendothyra globulus, Pseudoendothyra, Eostaffella (= Paramillerella), Tetrataxis, Archaediscus* of the group *A. krestovnikovi, Archaediscus* of the group *A. moelleri, Archaediscus* of the group *A. chernoussovensis,* and *Stacheia. Archaediscus* of the group *A. latispiralis* and *Neoarchaediscus* appear for the first time. The Eurasian fauna is similar but differs in retaining *Forschia* (sparse,), *Forschiella* (sparse), *Lituotubella* (sparse), *Haplophragmella, Cribrostomum, Endothyra* of the group *E. prisca, Globoendothyra, Omphalotis, Cribrospira, Bradyina,* and *Mediocris* as important elements.

Latest Visean foraminifers (Zone 16s) in North America are similar to those of the preceding zone (Zone 16i) but include, in addition, the first appearance of *Zellerina* and *Asteroarchaediscus* (very scarce). *Glomospira, Planospirodiscus,* and *Neoarchaedicus* become abundant faunal elements. In Eurasia, the fauna is much the same, but primitive ancestral *Loeblichia?* appears. This is the highest zone having *Lituotubella* (very sparse), *Haplophragmella* (sparse), *Cribrostomum, Globoendothyra* of the group *G. tomiliensis, Endothyranopsis compressus* (sparse), *Janischewskina, Valvulinella, Howchinia, Propermodiscus,* and *Planoarchaediscus* and marks the top of the Visean.

The lowest Namurian foraminifers (Zone 17) occur in the Glen Dean Limestone (Chesterian Series) in North American and include abundant coiled unichambered calcareous Foraminiferida, such as *Pseudoglomospira, Trepeilopsis,* and *Palaeotextularia* of the group *P. consobrina. Climacammina* of the group *C. prisca, Palaeotextularia* of the group *P. longiseptata, Climacammina* of the group *C. patula, Endothyra* of the group *E. bowmani, Pseudoendothyra, Eostaffella, Tetrataxis, Archaediscus* of the group *A. krestovnikovi, Archaediscus* of the group *A. chernoussovensis, Archaediscus* of the group *A. latispiralis, Neoarchaediscus, Earlandia, Calcisphaera* of the group *C. laevis, Stacheia, and Tuberitina* remain important faunal elements. To these are added *Monotaxinoides, Vissariotaxis,* primitive *"Globivalvulina," Mediocris* (very rare), and abundant specimens of *Asteroarchaediscus.* The Eurasian fauna is similar, differing largely in being more abundant and in possessing a few elements such as *Bradyina* and *Loeblichia,* which have not been observed in faunas of this age in North America.

Foraminifers in upper Lower Namurian strata (upper part of the Chesterian) (Zones 18-19) in North America contain most of the faunal elements of Zone 17 and also include the first appearances of highly evolved *Bradyina, Pseudoendothyra* of the group *P. kremenskensis, Eostaffellina, "Globivalvulina"* of the group *G. parva, Eosigmoilina,* and *Quasiarchaediscus.* In these zones Eurasian faunas have a few elements, such as *Loeblichia,* which have not been reported from North America. In the Donetz basin and in many other parts of Eurasia, Namurian foraminifers of the *Homoceras* Zone (Zone 19) are characterized by the transitional archaediscid-miliolid *Quasiarchaediscus-Eosigmoilina?* fauna. Although beds of this age are missing in the type Mississippian section, this foraminiferal fauna is reported from the North American Cordillera (MAMET, SKIPP, SANDO, & MAPEL, 1971).

Foraminiferal zones in the Morrowan of the North America Midcontinent region and the Bashkirian of the Donetz basin (Fig. 3) are particularly diverse and differ in faunal composition. The Morrowan is dominated by *Millerella, Eoschubertella,* and trilayered *Globivalvulina,* and the Bashkirian has abundant *Bradyina, Archaediscus, Asteroarchaediscus, Neoarchaediscus, Pseudoendothyra, Eostaffella, Novella* (primitive), *Pseudostaffella, Schubertella, Seminovella, Verella, Eofusulina, Ozawainella,* and *Profusulinella.* The early Bashkirian in the Donetz basin and southern Ural Mountains can be divided on the basis of fusulinaceans

FIG. 3. *(Continued from facing page.)*

Rauzer-Chernousova and others, 1951; Ross, 1967, 1970, 1973; Rozovskaya, 1950, 1969; Thompson, 1948, 1966, 1967; Ross, n). [Thick lines indicate abundant, thin lines common, and dashed lines rare or questionable occurrences.]

into a lower zone having the first appearance of *Pseudostaffella, Seminovella,* and *Millerella,* and a higher zone having the first appearance of *Novella* and *Ozawainella.* The late Bashkirian is characterized by a lowest zone having the first appearance of *Profusulinella,* a middle zone having the first appearance of *Schubertella* and *Verella,* and a highest zone having the first appearance of *Parastaffella.* In addition, species groups of *Palaeotextularia, Climacammina, Endothyra, Bradyina, Pseudoendothyra, Eostaffella (=Paramillerella), Tetrataxis, Eolasiodiscus,* and *Neoarchaediscus* and the first appearance of *Lipinella* are important zonal fossils among the other foraminiferids in the Bashkirian. In the Midcontinent region of North America the Morrowan Series is the time equivalent of most or all of the Bashkirian. The middle part of the type Morrowan has *Millerella* as the dominant foraminifer and in other areas higher parts of this stratigraphic interval have in addition *Eoschubertella* and *Pseudostaffella* (THOMPSON, 1948).

Above the Morrowan and its equivalents, foraminiferal correlations are based largely on members of the superfamily Fusulinacea (THOMPSON, 1948, 1966, 1967; RAUZER-CHERNOUSOVA *et al.,* 1951, 1954, ROZOVSKAYA, 1950, 1969; ROSS, 1967, 1970, 1973). A few long-ranging genera of smaller foraminifers appear near the base of the Moscovian and Atokan-Desmoinesian sequences, such as *Nodosaria* and *Cribrogenerina,* but these and their late Carboniferous descendants have not been studied in as much detail as the earlier Carboniferous genera. Although the Midcontinent North American and Arctic-Eurasian fusulinid faunas show general similarities during the remainder of the Carboniferous, the range of many genera differs between the two regions, and a number of endemic genera are reported (Fig. 3) in both regions.

Atokan fusulinids are characterized in North America by *Profusulinella* in the lower part, which evolved with little overlapping range into *Fusulinella* in the upper part to provide a twofold division into a zone of *Profusulinella* and a zone of *Fusulinella.* Several long-ranging genera such as *Millerella, Eostaffella (=Paramillerella), Parastaffella, Pseudostaffella,* and *Eoschubertella* persist from the Morrowan in the Midcontinent North American sections into the Atokan. One lineage of *Fusulinella* evolved through several transitional species into *Beedeina* near the base of the Desmoinesian Series and formed the beginning of the zone of *Beedeina,* which characterizes most of the Desmoinesian strata. *Fusulinella, Eoschubertella,* and *Pseudostaffella* continue into the zone of *Beedeina* but are usually rare above the lower third of the zone. *Wedekindellina* first appears slightly above the base of the zone. In the northern Cordilleran region *Akiyoshiella, Pseudowedekindellina, Eowaeringella,* and *Bartramella* appear in the assemblage. The highest species of *Beedeina* occur near the top of the Desmoinesian Series.

The Atokan-Desmoinesian interval is correlated with the Moscovian Stage in Eurasia and the Arctic. The lower part of the Moscovian contains a fusulinacean assemblage that includes most of the Bashkirian genera, except *Verella,* and the first appearance of *Aljutovella, Hemifusulina,* and *Eofusulina.* The upper part of the Moscovian has the additional genera *Fusulinella, Fusulina, Ozawainella, Fusiella, Wedekindellina, Putrella,* and *Protriticites.*

Except for the lowest part of the Missourian Series, the later part of the Pennsylvanian in North America is characterized by the zone of *Triticites.* The oldest Missourian assemblage includes *Fusulina* (of the Russian-platform type; it is not a *Beedeina*), and associated *Oketaella, Schubertella,* and *Eowaeringella.*

The succeeding zone of *Triticites* includes most of the Missourian and Virgilian series and has the first appearance of *Triticites, Iowanella,* and *Kansanella* in the Midcontinent region. Of these, *Triticites* is long ranging and continues into overlying zones in the Permian. Within the zone *Waeringella* and *Dunbarinella* appear briefly. The top of the zone of *Triticites* is usually placed below the first occurrence of *Schwagerina* or *Pseudofusulina.*

In Eurasia and the Arctic, the zone of *Triticites* in its lower part includes forms ancestral to *Triticites* that have subsequently been given generic status, *Protriticites, Obsoletes, Montiparus,* as well as *Fusulinella, Quasifusulina,* and the last of *Quasifu-*

sulinoides. *Triticites* is advanced but relatively unspecialized when it first appears in the middle part of the zone and early in its history it gives rise to *Daixina* and *Jigulites* and finally to primitive *Pseudofusulina* near the top of the zone (Reytlinger, 1969). In the Soviet Union, a number of fusulinacean paleontologists include the overlying zone of *"Schwagerina"* (i.e., Asselian Stage) in the Carboniferous, whereas most other paleontologists and biostratigraphers place the Asselian in the basal part of the Permian. The Asselian, as a biostratigraphic unit, is correlated with the lower part of the North American Wolfcampian Series (Neal Ranch Formation), which is considered lowest Permian by most North American paleontologists.

The biogeographic distribution of Carboniferous Foraminiferida has been discussed by Eynor and others (1973), Lipina (1973), Lipina and Reytlinger (1970), Mamet and Skipp (1971), Ross (1967, 1973), and Thompson (1967).

The epeirogenic sea of the North American craton had an impoverished foraminiferal fauna compared to the seas in the miogeosynclines and on the edges of the craton. The fauna on the craton is less diverse and is characterized by accumulations of monogeneric and even monospecific assemblages and there are fewer individuals. The least diverse and most endemic foraminiferal faunas in North America are in the upper Mississippi valley and Midcontinent regions and this leads to difficulties in extending biozones of the type sections of the Mississippian to the Cordilleran region. The distribution of different families of Foraminiferida is affected by the environments of this epeirogenic sea. Cornuspiridae and Fischerinidae? are evenly distributed in North America, Tournayellidae are mainly restricted to the Cordillera, Forschiidae are rare in the Midcontinent, and Palaeotextulariidae are common in the Visean of the Cordillera but scarce in rocks older than Namurian in the Midcontinent. Endothyridae are widespread in North America and the variety of species makes them stratigraphically useful in the Midcontinent.

Early Carboniferous foraminiferal assemblages of Eurasia and North America show some latitudinal differences but there is no evidence of exclusive provincialism. The most complete assemblages are in miogeosynclines and on shelf margins in the Urals, Donetz, Turkey, North Africa, western Europe, Iran, Vietnam, and Australia, and form a Tethyan realm. The foraminiferal faunas in northern Siberia, Kuznetzk, Japan, and the Cordilleran and Appalachian geosynclines differ from the Tethyan populations in having a much greater percentage of Endothyridae, a sparsity of Forschiidae, Bradyinidae, and Palaeotextulariidae, and a lower species diversity.

Inverse relations exist between the importance of planispirally coiled *Eoendothyranopsis* and of *Eostaffella* and *Pseudoendothyra;* in the European Visean *Eostaffella* and *Pseudoendothyra* are abundant and *Eoendothyranopsis* is scarce whereas in North America the Visean *Eoendothyranopsis* is abundant and *Eostaffella* is sparse. Exchanges of fauna between the two realms were widespread during most of the Early Carboniferous and the North American fauna, despite impoverishment in many elements, always has counterparts in Eurasian faunas.

Middle and Late Carboniferous members of the superfamily Fusulinacea are widely distributed, commonly abundant, and evolved rapidly. Figure 3 shows the stratigraphic and geographic distribution of genera belonging to the five Carboniferous families of fusulinaceans. In the Eurasian-Arctic province many more genera and a more complex zonal sequence of genera in these families arose than in the Midcontinent-Andean province (Ross, 1967). Infrequent and incomplete faunal exchange through a filter region between faunal provinces, such as occurred early in Morrowan time and again early in Atokan time, established the initial fusulinacean stock that produced successive provincial lineages characterizing the zones of *Millerella, Profusulinella, Fusulinella,* and *Beedeina* in the Midcontinent-Andean province.

A nearly independent evolutionary history of the Eurasian-Arctic and Midcontinent-Andean faunal provinces is indicated by the different stratigraphic ranges of *Profusulinella, Fusulinella, Beedeina,* and *Fusulina* in the two provinces. In the Eurasian-Arctic province *Fusulinella* and *Fusulina* appear at about the same time and persist, along with their ancestor, *Profusulinella,* until near the end of the Moscovian. In the Midcontinent province a phylogenetic sequence from *Profusulinella* to *Fusulinella* to *Beedeina* shows little stratigraphic overlap between these three genera. *Fusulina* appears briefly in the basal part of the Missourian (Midcontinent-Andean province) only after the extinction of *Beedeina.* The few genera of Fusulinidae that are nearly cosmopolitan, such as *Pseudostaffella, Fusulinella, Wedekindellina,* and *Beedeina,* have different species complexes in the different provinces during the Middle Carboniferous. Near the end of the Middle Carboniferous, a few genera, such as *Fusiella,* which is typical of the late Moscovian of the Eurasian-Arctic province, and *Bartramella* appear abruptly in the Desmoinesian in the Midcontinent-Andean province.

In both provinces many lineages of Middle Carboniferous foraminiferids became extinct at about the end of Desmoinesian or Moscovian time and relatively few genera survived into the Late Carboniferous. Most surviving lineages were modified sufficiently to be given new generic names. In the Eurasian-Arctic province rapid evolution produced a sequence of early schwagerinid genera: *Protriticites, Montiparus, Obsoletes,* and finally *Triticites. Triticites* is the only genus of this sequence that successfully invaded the Midcontinent province. However, the Midcontinent genera, *Iowanella* and *Kansanella,* are probably derived from the Eurasian-Arctic genus *Montiparus* and not directly from *Triticites.* In Eurasian-Arctic faunas *Fusulinella* persisted in a distinctive facies and gave rise to *Pseudofusulinella* near the end of Late Carboniferous time. *Eowaeringella* appears to be restricted to North America and ranges from the Middle Carboniferous into the Upper Carboniferous; it gave rise to the Virgilian *Waeringella* of the Midcontinent province and possibly gave rise to *Thompsonella.* During the later part of the Late Carboniferous in the European part of the Eurasian-Arctic province *Triticites* evolved into several diverse lineages with several subgenera, such as *Jigulites* and *Rauserites,* and the genera *Pseudofusulina, Rugosofusulina,* and *Daixina.* Some of these are restricted to the Eurasian-Arctic province and, at times, to only certain of its subprovinces. Within the Midcontinent-Andean province species of *Triticites* form several distinctive lineages.

In comparison with the Early and Middle Carboniferous, during Late Carboniferous both the Eurasian-Arctic and Midcontinent-Andean provinces had less diversity. Major morphological changes occurred in only the earliest part and again in the later part of the Late Carboniferous and seem to coincide with increased dispersal.

The patterns of distribution and dispersal and intervals of endemic evolution of Foraminiferida during the Carboniferous (Ross, 1970) are similar to those that have been demonstrated for rugose corals (Hill, 1957, 1973) and ammonoids (Ruzhentsev, 1966; Gordon, 1970). As with many questions of biogeography, it is difficult to establish causal factors for these similar histories; however, some speculations are possible. Lipina and Reytlinger (1970) suggested that the faunal differences between the European and Siberian subprovinces of their Eurasian foraminiferal province coincide with the change from tropical to extra-tropical floral zones and their interpretation is supported by the decrease in foraminiferal diversity and lack of forms having massive shells. Early and Middle Carboniferous paleofloral regions (Meyen, 1970) of the Euramerican region extending from south-central Asia across Europe into North America have woods lacking annual rings (indicative of tropical climate) and those in the Angaran region have woods with annual rings (indicative of extra-tropical climates).

CORALS

Although Carboniferous coral occurrences (Fig. 1, 4) are considered to be closely related to biofacies, they have been widely used for establishing stratigraphic correlations. Where corals are abundant and several biofacies are represented, correlations within a province are usually consistent with those based on other fossil groups. Corals apparently did disperse slowly and relatively infrequently between some provinces after the Visean and this limits their effective use in younger Carboniferous strata.

Lower Carboniferous coral faunas in North America, Eurasia, and Australia are sufficiently distinct from one another that Hill (1948, 1957, 1973) considered each of these areas a separate zoogeographic region. The Eurasian region includes four major subdivisions: 1) a western European province including part of the maritime provinces of eastern Canada and northwestern Africa, 2) an eastern European province, 3) a Chinese-Japanese province, and 4) a southcentral Asian province, which with additional study may be further subdivided (Hill, 1973).

During earliest Carboniferous time (Tournaisian) the North American zoogeographic region was subdivided by the transcontinental arch that partially separated coral faunas of the stable broad Mississippi valley epicontinental shelf from the faunas of the Cordilleran geosyncline and its marginal shelf. According to Hill (1973), a number of solitary coral genera of the Mississippi valley shelf appear to be related to ceratoid genera of the western European province. In addition, several North American endemic lineages developed (e.g., *Clinophyllum* and *Neozaphrentis*) and some genera continued from Late Devonian time (e.g., *Microcyclus* and *Hadrophyllum*). The North American Cordilleran coral faunas include a number of genera in common with those of the Mississippi valley shelf, such as *Cyathaxonia* and *Homalophyllites,* but also include several eastern European genera such as *Keyserlingophyllum, Enygmophyllum,* and *Uralinia?* which suggest a shallow marine connection with the Uralian geosyncline. *Zaphrentites, Amplexus,* and *Vesiculophyllum* are also present in this fauna.

Within the Eurasian region, Hill (1973) recognized considerable provincialism. The western European province (including a portion of northwestern Africa) has great diversity and includes an impressive assemblage of corals characterized by *Cravenia, Allotropiophyllum, Amplexocarinia, Amplexus, Caninia, Caninophyllum, Cyathoclisia, Koninckophyllum, Cryptophyllum, Cyathaxonia, Lonsdaleia, Menophyllum, Sychnoelasma, Palaeosmilia, Rotiphyllum, Siphonophyllia, Thysanophyllum, Zaphrentis,* and a number of tabulate corals (Hill, 1948). The eastern European corals of the Russian platform (and the margins of that platform) contain different species assemblages that were used by Vasilyuk *et al.* (1970) to identify three subprovinces: one in the north in the region of Novaya Zemlya, another in the Moscow basin, and a third in southern Ural-Donbas (or south-shelf edge). In these subprovinces the tabulate corals *Syringopora, Tetraporinus, Roemeripora, Michelinia, Emmonsia,* and *Gorskyites* are important and *Caninia, Caninophyllum, Uralinia, Siphonophyllia* and other caninioid genera are present. Farther east the Kazakhstan Tournaisian coral faunas are small in number of species and genera and include a Chinese element, *Cystophrentis,* suggesting connections to the east. The Kuznetzk basin faunas include *Cyathoclisia* and possible ancestors of the Visean *Arachnolasma* and *Yuanophyllum* of China. Late Tournaisian coral faunas became more widely dispersed in the east European-Asian provinces, and of these *Uralinia, Keyserlingophyllum,* and *Enygmophyllum* are particularly widespread and

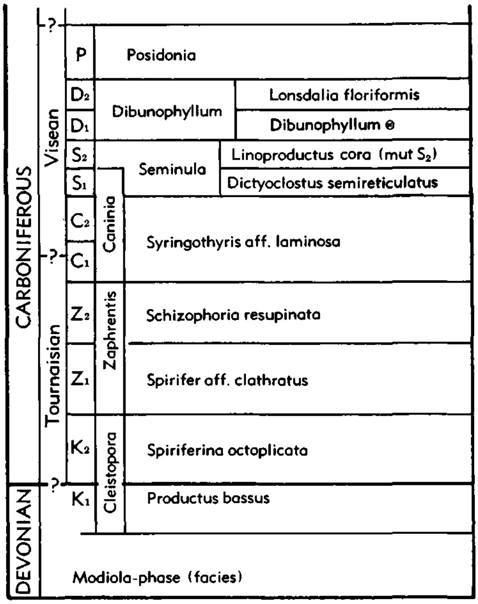

Fig. 4. Coral and brachiopod zonation of the Lower Carboniferous of the Avon section of southern England (Vaughan, 1905, 1915) and approximate correlation with the boundaries of the Tournaisian and Visean stages of Belgium (modified from Vaughan, 1915; George, 1969).

characteristic and were dispersed as far as the western Cordilleran province of North America. The southern Ural, Kazakhstan, and Kuznetzk areas have a number of distinctive genera, such as *Bifossularia*, indicating dispersal of some genera was still partially restricted. Kazakhstan had several endemic species or subspecies and Kuznetzk, in addition to endemic species, had several endemic genera, such as *Kuzbasophyllum, Adamanophyllum,* and *Tachyphyllum* (DOBROLYUBOVA, *et al.*, 1966). The appearance of *Chia* and *Tetraporinus* in the Donetz basin at this time suggests faunal dispersals along an east-west seaway (or shelf margin) with parts of China. Along the northwestern edge of the Angaran craton IVANOVSKIY (1967) reported a small coral fauna including *Amplexus, Campophyllum, Tachyphyllum?,* and *Trochophyllum* and on the northeastern edge of the Angaran craton the Tournaisian coral fauna includes *Uralinia, Keyserlingophyllum, Amplexus, Caninia, Caninophyllum, Rotiphyllum, Sychnoelasma,* and *Trochophyllum.*

HILL (1973) recognized a Chinese province in which *Cystophrentis* and *Pseudouralinia* are common together with the widely distributed genera *Caninia* and *Zaphrentites.* In Japan a Tournaisian sequence includes three assemblage zones: *Amygdalophyllum* and *Lithostrotionella* at the base; next, *Amplexus* and *Syringopora*; and *Sugiyamaella* near the Tournaisian-Visean boundary.

Thus far, relatively few coral localities are reported from the Tournaisian of the Australian biogeographic region. The earliest occurrences (which may prove to be latest Devonian) include *Lithostrotion, Amygdalophyllum, Naoides* (endemic), *Michelinia, Yavorskia,* and *Syringopora.* Another locality has *Cladochonus* and *Bibucia* (endemic) and a higher locality has *Amygdalophyllum* and *Merlewoodia* (endemic).

Visean corals were also divided into three zoogeographical regions by HILL (1973): North American region, eastern Australian region, and Eurasian region. The Eurasian region includes the maritime provinces of Canada and Bonaparte basin (northwestern Australia) in addition to much of northwestern Africa. Visean coral faunas are more diverse than those of the Tournaisian and include a number of new introductions and newly evolved genera.

In the Cordilleran province of North America a large representation of species of *Lithostrotionella* is associated with *Lithostrotion, Thysanophyllum, Sciophyllum, Diphyphyllum,* and *?Dorlodotia.* In addition, *Ekvasophyllum, Faberophyllum, Liardiphyllum,* and *Zaphriphyllum,* along with a number of nondissepimented genera, occur in the northern part of the North American Cordilleran and also in the Taymyr geosyncline north of the Angaran shield. The epicontinental shelf of central North America contained a less diverse fauna than the Cordilleran region and includes at least one genus, *Palaeosmilia,* of Eurasian affinities.

On the basis of Visean corals, the Eurasian faunal region is divisible into a number of provinces and subprovinces. The western European province (including Nova Scotia and northwestern Africa) has a diverse fauna with the characteristic genera *Allotropiophyllum, Amplexus, Caninia, Carruthersella, Cravenia, Cyathaxonia, Dibunophyllum, Koninckophyllum, Lithostrotion, Lonsdaleia, Orionastrea, Zaphrentites,* and *Palaeosmilia,* but lacks *Lithostrotionella, Ekvasophyllum, Faberophyllum, Liardiphyllum, Zaphriphyllum,* and *Gangamophyllum.* The Nova Scotian Visean coral fauna includes the distinctly Eurasian genera *Lonsdaleia* and *Dibunophyllum.* The eastern and southeastern European Visean province includes most of the genera of the western province and, in addition, has some distinctive genera, such as *Gangamophyllum, Turbinatocaninia,* and *Paralithostrotion,* as well as a few genera, such as *Eolithostrotionella* and *Melanophyllum,* that suggest connections with parts of central and eastern Asia. The Donetz basin fauna is largely western European in its affinities but does carry representatives from the proto-Tethys geosynclinal margin, such as *Neoclisiophyllum* and *Arachnolasma* of Chinese affinities, *Amygdalophyllum* with Australian affinities, and a number of endemic genera.

Farther south in Turkey, Iran, and southern Soviet Union, Visean corals include a mixture of eastern European and Chinese genera, including *Kueichouphyllum* and

Kueichowpora, and in Ferghana the fauna appears to be a combination of various genera from western European, eastern European, central and eastern Asian, and Australian faunas. In the Visean, other areas in central Asia also include mixtures of genera from western or eastern European or Chinese faunas but with endemic species, as in Pamir and Kazakhstan. In the Kuznetzk basin, endemism is more marked and is indicated by the genera *Kuzbasophyllum, Adamanophyllum,* and *Bifossularia.* Also present is the North American *Faberophyllum.* In the eastern part of the Taymyr area (VASILYUK *et al.*, 1970) the mainly Eurasian genus *Lithostrotion* occurs with Chinese tabulate and North American rugose genera.

The Chinese coral province of the Visean has a distinctive mixture of western European, North American, and more or less endemic southeast Asian genera. Subprovinces are apparent. In Hunan, YU (1934, 1937) recognized two assemblages, the *Thysanophyllum* and *Yuanophyllum* assemblage zones, based on endemic species. In the lower zone *Kueichouphyllum, Bothrophyllum, Caninia, Dibunophyllum, Kwangsiphyllum,* and *Lithostrotion* are common and in the higher zone *Cyathaxonia, Rotiphyllum, Zaphrentites, Zaphrentoides, Heterocaninia, Dibunophyllum, Clisiophyllum, Koninckophyllum, Arachnolasma, Ekvasophyllum, Caninostrotion, Lithostrotionella, Lithostrotion,* and *Aulina* form the dominant part of the assemblage. The upper part of the Hunan Visean succession has reduced diversity and *Lonsdaleia* and *Arachnastrea* appear in this province for the first time.

In Sinkiang and Kansu, Visean coral faunas include *Siphonophyllia, Palaeosmilia, Kueichouphyllum, Yuanophyllum, Arachnolasma, Gangamophyllum,* and others with important endemic species and many endemic species of more widespread genera. Elements of this fauna have been traced into Yunnan, Tibet (YANG & WU, 1964), Nepal (FLÜGEL, 1966), and farther along the proto-Tethys. Much of this coral fauna is traceable along the western margin of the South China-Indochina craton (FONTAINE, 1961; SMITH, 1948) and into the Bonaparte Gulf basin of northwestern Australia.

In Japan, Visean corals form a separate subprovince of the Chinese province and are further divisible into an inner and outer zone based on sedimentary environmental features as well as faunal composition. The outer zone of dark limestone facies includes many genera typical of the main part of the Chinese province but also includes *Pseudodorlodotia, Sciophyllum, Setamainella,* and *Tschussovskenia;* this assemblage may extend into the lower part of the Namurian. The inner zone is largely a reef and slope facies and contains *Nagatophyllum, Echigophyllum, Taisyakuphyllum, Pseudopavona,* and *Akiyosiphyllum.* In this inner zone the fauna ranges from upper Visean into Middle Carboniferous and becomes increasingly endemic.

Eastern Australia forms a separate Visean coral region and has *Lithostrotion, Michelinia, Caninophyllum, Amygdalophyllum, Nothaphrophyllum* (endemic), *Symplectophyllum* (endemic), *Merlewoodia* (endemic), *Orionastraea, Palaeacis, Aphrophylloides, Heterophyllia, Syringopora,* and *Aphrophyllum.* Although many endemic species and several endemic genera are important constituents of this fauna, the lower endemic Tournaisian genera, such as *Bibucia* and *Naoides,* are not found in Visean faunas, and only the endemic *Merlewoodia* appears as a holdover among the Visean assemblages.

Lower Namurian coral faunas are much less widely distributed than either Tournaisian or Visean faunas and usually are a continuation of upper Visean assemblages that are reduced in diversity and numbers. The central North American region contains coral faunas having *Palaeosmilia, Kinkaidia, Caninostrotion, Koninckophyllum,* and a few other genera, all with distinctive endemic species (EASTON, 1945). The Namurian fauna of the western Cordillera of North America has *Caninia, Zaphrentites, Lithostrotionella, Syringoporella?, Hayasakaia?,* and *Siphonophyllia?* (SANDO, 1965; ROWETT, 1969) most of which have endemic species but are predominantly descended from faunas of the Chinese Visean province.

The Eurasian region is still clearly distinguished during the Namurian and is composed of faunal provinces that are related to their Visean predecessors. About a dozen genera range from the Visean into the Namurian of western Europe (HILL, 1973) although species (and individuals) are much less numerous. These genera are *Aulina, Aulophyllum, Carcinophyllum, Clisiophyllum, Dibunophyllum, Koninckophyllum, Lithostrotion, Lonsdaleia, Zaphrentites, Carruthersella, Palaeacis,* and *Palaeosmilia?.* The Donetz basin continues to have a dominantly western European fauna with a few Chinese genera. The eastern European province has *Arachnolasma, Gangamophyllum, Kazachiphyllum, Melanophyllum, Nervophyllum,* and *Paralithostrotion,* in addition to most of the western European genera.

In central Asia, Kazakhstan, and Pamir, the Namurian corals are closely similar to those reported from the eastern European province. The Chinese province carries a continuation of its Visean coral faunas and Namurian coral assemblages are difficult to distinguish from Visean ones. Corals have not been reported from the Namurian strata of Kuznetzk and Australia.

Late Namurian (or Bashkirian) coral faunas are relatively poorly known probably because rocks of this age with a coral-bearing carbonate facies are not extensively exposed. In the Donetz basin and southern Ural regions a continuation of earlier genera, such as *Lithostrotion, Orionastraea,* and *Corwenia,* is accompanied by the appearance of *Eolithostrotionella, Cystophora,* and *Donophyllum.* Endemic complexes of species of caniniid-clisiophyllid corals, in which the axial structures are poorly developed or lack a clearly defined pattern, are common and include species of *Lophophyllum, Neokoninckophyllum, Yuanophylloides, Caninia, Campophyllum, Yakovleviella,* and others, including the endemic genus *Sestrophyllum.* The Chinese genus *Arachnolasma* is present, and in the Donetz basin *Cyathaxonia, Lophophyllidium, Zaphrentites, Allotropiophyllum,* and the endemic *Parastereophrentis, Kumpanophyllum,* and *Cystilophophyllum* have been recorded. In the southern Urals, the endemic *Lytvophyllum* is present at this time. Bashkirian coral faunas from Japan are rare, not widely distributed, and include *Diphyphyllum, Thysanophyllum, Lithostrotionella, Nagatophyllum,* and *Chaetetes.* A *Cyathaxonia*-bearing fauna has been reported from the Atokan of the United States and may be of late Bashkirian age.

Near the western end of the proto-Tethys in northwestern Spain, DE GROOT (1963) reported endemic species of *Lithostrotionella, Dibunophyllum, Clisiophyllum, Koninckophyllum, Pseudozaphrentoides, Koninckocarinia,* and *Carcinophyllum.* Other Bashkirian (or Morrowan) coral faunas are poorly known, but apparently are present in the marine part of the proto-Tethyan geosyncline in Tien Shan along the southern edge of the Angaran craton. In North America, Morrowan corals are widely distributed but are not well known.

Moscovian (Atokan-Desmoinesian) corals are more widely distributed than Bashkirian corals, but have not been thoroughly studied. Most of western Europe had nonmarine deposition during most of this time (Westphalian) but in the eastern European province along the edges of the Russian platform *Cystophora* and *Arachnastraea* are common and *Koninckocarinia, Carniaphyllum, Caninophyllum, Bothrophyllum,* and *Timania* may be present in various localities in the Ural, Donetz basin, Tien Shan, and Kazakhstan regions. The first species of *Durhamina* has been reported from the northern Urals (MINATO & KATO, 1965a). Farther east, the Middle Carboniferous of China contains *Kionophyllum* and *Gshelia.* However, these faunas are poorly known and are apparently not abundant or common. The earliest waagenophyllid, *Huangia,* occurred in China during the Moscovian (MINATO & KATO, 1965b). In Japan the inner zone assemblages with *Nagatophyllum* apparently range from strata of late Visean age upward into strata of Namurian age and probably into strata as young as Moscovian age. In northwestern Spain, DE GROOT (1963) recorded endemic species of *Koninckophyllum, Carcinophyllum, Lithostrotion, Corwenia, Arachnastraea,* and *Lithostrotionella* from Moscovian strata. In North America a number of genera and species were endemic to central North America during the Pennsylvanian including the middle Pennsylvanian (Atokan-Desmoinesian) genera *Empodesma, Stereocorpha, Lophotichium, Barytichisma, Acaciapora,* and *Cumminsia;* endemic species of *Dibunophyllum* and *Neokoninckophyllum;* and also the highest occurrence of

Chaetetes in the North American region.

During Moscovian time (Hill, 1957), a distinctive coral province extended at least from Spitsbergen along the Russian platform and western side of the Ural geosyncline across southern Europe to northwestern Spain. In southeastern Asia several genera, such as *Gshelia, Cyctophora,* and *Arachnastraea,* suggest a separate province at this time.

Post-Moscovian—pre-Permian (i.e., Late Pennsylvanian) coral faunas have not been widely studied and apparently are not common. The eastern European province has a continuation of dominant Moscovian genera, such as *Timania, Gshelia, Bothrophyllum, Caninophyllum, Eolithostrotionella, Tschussovskenia,* and *Protolonsdaleiastraea. Kionophyllum* and *Amandophyllum* spread to the Carnic Alps during latest Carboniferous time. Also, in very Late Pennsylvanian time in southwestern North America *Durhamina, Stereostylus,* and *Leonardophyllum* formed the beginnings of several endemic lineages that extended into Early Permian time. *Lophophyllidium, Syringopora, Aulopora,* and *"Caninia"* also are recorded from the Upper Pennsylvanian at several localities in central North America. Limited knowledge of post-Moscovian (post-Desmoinesian)—pre-Permian corals of the Carboniferous does suggest well-developed provincial and regional faunas. These faunas included new families and genera that led to an increasing diversity marking the beginning of the Permian; however, the details are not presently known.

BRACHIOPODS

Near the end of the Devonian many of the major brachiopod superfamilies and families either became extinct or were greatly reduced in importance. These include the strophomenaceans, punctate and impunctate orthids, pentamerids, atrypaceans, dayiaceans, and early terebratulids (Rudwick, 1970). The surviving rhynchonellids, spiriferids, and strophomenids (particularly those with tubular spines or shell cementation) evolved rapidly to give the Lower Carboniferous brachiopods high taxonomic diversity (Fig. 5), and they were adapted to a wide range of environmental habitats. Other strophomenids, such as chonetaceans, davidsoniaceans, and strophalosiaceans, spiriferids, atrypids, rhynchonellids, and the few surviving terebratulids also underwent significant taxonomic expansions. In the Early Carboniferous several major families of spiriferids evolved (Ivanova, 1972): Spiriferidae and Syringothyrididae (both of which may have first evolved in the Late Devonian), and Brachythyrididae, Choristitidae, Paeckelmanellidae, Davidsoninidae, and Spiriferellinidae. Several Carboniferous subfamilies have short stratigraphic ranges. The subfamily Spiriferinae appears to range no higher than the upper part of the Visean. Although present earlier, Neospiriferinae were common in the Middle and Late Carboniferous and gave rise to the Trigonotretinae during the Late Carboniferous. The family Davidsoninidae appeared in the Visean and became extinct by the end of the Namurian (Ivanova, 1972). Rapid evolution and short stratigraphic ranges of species of the family Choristitidae are useful in subdividing the Middle Carboniferous in Eurasia (Khalymbadzha & Tikhvinskiy, 1967).

During the Tournaisian and Visean, spiriferids were widespread and most groups were cosmopolitan. Beginning in the Namurian their distributions became increasingly more restricted as endemic species and then endemic genera replaced the older more cosmopolitan species and genera. Middle Carboniferous spiriferids are less well known but are commonly abundant and diverse in regions of marine epicontinental deposition (Khalymbadzha & Tikhvinskiy, 1967). However, the number of cosmopolitan species and genera was considerably less than in the Early Carboniferous. The data available for spiriferid distributions in the Late Carboniferous are less complete than for the other parts of the Carboniferous, but a renewed diversification in the Early Permian suggests increasing geographic dispersal during the Late Carboniferous.

The general history of the evolution and geographic distribution of productoid brachiopods (Muir-Wood & Cooper, 1960) is similar to that of the spiriferids. Most Early Carboniferous diversity in the productoids was in lineages that first appeared in the Late Devonian. Tournaisian and Visean

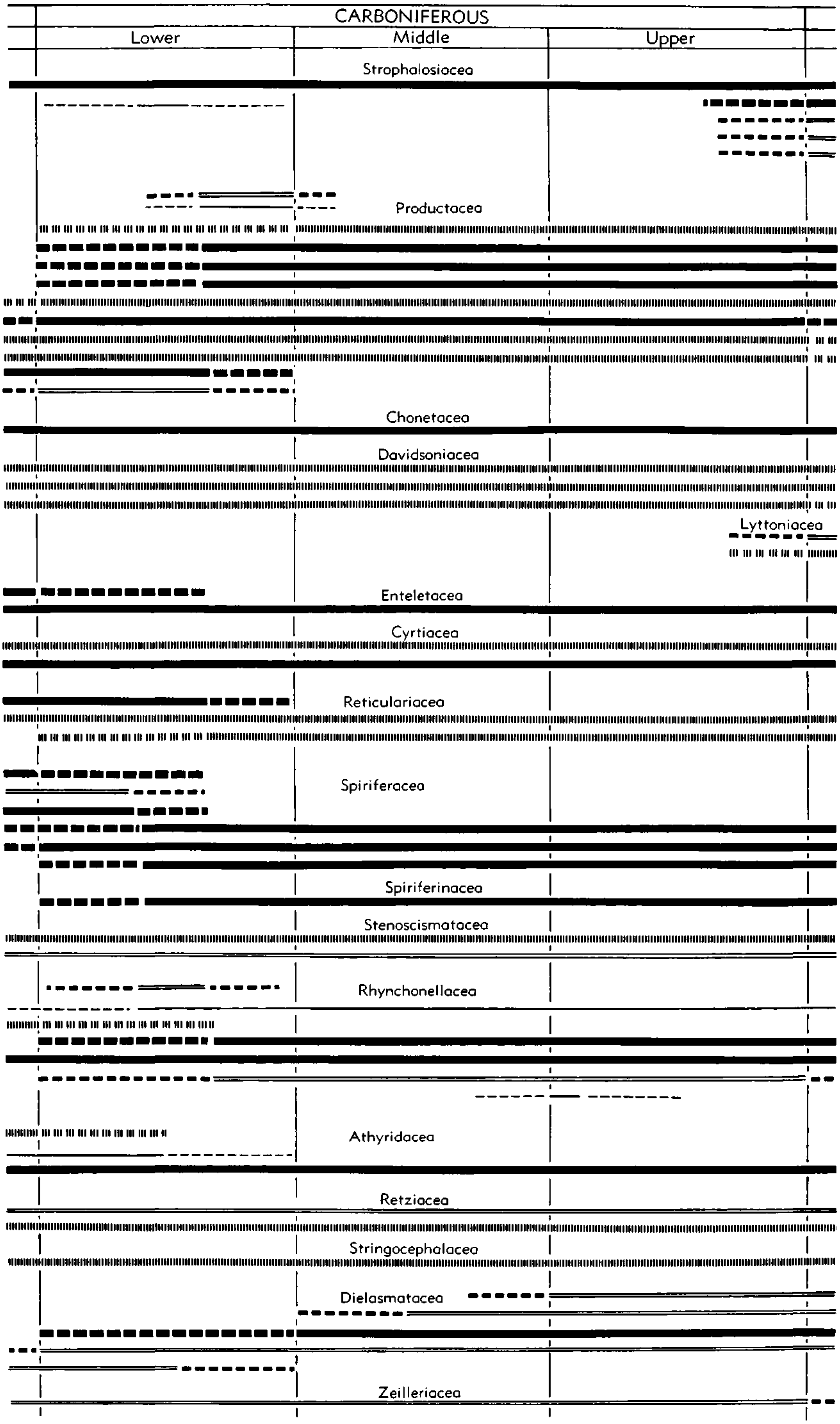

FIG. 5. Stratigraphic ranges of superfamilies and families of brachiopods in the Carboniferous. Dashed lines indicate the limits of uncertainty of the stratigraphic range of each family. The number of genera

productoids evolved into diverse and widespread groups that contained many cosmopolitan elements as well as a number of endemic and locally important genera (e.g., the four genera of the Gigantoproductidae). During the later part of the Early Carboniferous a number of genera and subfamilies became extinct (Sinuatellidae, Productellidae).

Middle Carboniferous productoids had less cosmopolitan distributions. Most Carboniferous genera of the Linoproductidae, except *Striatifera,* had endemic distributions and only near the end of the period or in the Early Permian did this family become widely dispersed. This distributional pattern is also apparent in the Buxtoniidae, Dictyoclostidae, and Echinoconchidae. Several families had subfamilies or genera with disjunct distributions during the Carboniferous: during the Visean the family Strophalosiidae had only one genus in Europe and two in North America; and during the Late Carboniferous the subfamily Echinosteginae had two endemic stocks, one in North America, and other in the Ural region, that gave rise to major lineages that subsequently dispersed in the Early Permian. Several of the surviving Devonian lineages, such as the Leioproductidae, Productininae, Overtonidae, and Productidae, evolved a number of endemic genera in addition to a few cosmopolitan genera in the Lower Carboniferous. The reduction in productoid generic diversity near the beginning of the Middle Carboniferous was followed by a gradual increase in diversity again near the end of Middle Carboniferous time, and it continued through the late Carboniferous into the Early Permian.

CEPHALOPODS

Carboniferous cephalopods were a diverse, rapidly evolving, free swimming, benthonic group that forms one of the important series of stratigraphic index fossils for the period. As with several other groups of Carboniferous fossils, the cephalopods of Europe and central and southwestern United States are known in considerably more detail than in many other parts of the world because of the availability of collections of specimens and more detailed study. Many species and genera are believed to have lived within particular depth intervals and, as a consequence, if a cephalopod assemblage was derived from the overlying water column, deeper water sediments commonly contain a greater diversity than shallower water sediments. On the other hand, many empty shells floated and were carried by currents hundreds, perhaps thousands, of kilometers beyond the biogeographic areas occupied by living specimens, as presently happens to shells of recent *Nautilus.* Thus, a number of cephalopod fossil assemblages, particularly those having an unusually large number of species and genera, is believed not to be living assemblages, but postmortem collections of drifted shells concentrated at shorelines.

Carboniferous cephalopods include the remnants of the subclass Actinoceratoidea, which had a long history in the early and middle Paleozoic, the long-ranging subclass Nautiloidea, and the rapidly diversifying subclass Ammonoidea. Only a few genera of the subclass Actinoceratoidea have been reported from Carboniferous strata (TEICHERT *et al.,* 1964): *Mstikhinoceras* from the Visean of the Russian platform, *Carbactinoceras* and *Aploceras* from Visean strata in western Europe, and *Rayonnoceras,* which is longer ranging and more widespread in both North America and Europe.

In the subclass Nautiloidea three orders occur in the Carboniferous: Orthocerida, Oncocerida, and Nautilida. The Orthocerida includes a smaller superfamily, Orthocerataceae, having long-ranging genera that are mainly European and North American in distribution and a larger superfamily, Pseudorthoceratacea. This latter superfamily includes *Pseudocyrtoceras, Cyrtothoracoceras,* five closely related genera, *Pseudactinoceras, Bergoceras, Campyloceras, Eusthenoceras,* and *Paraloxoceras,* which are known only

FIG. 5. *(Continued from facing page.)*
in each family is shown by the type of line; less than three (single fine line), three to six (double fine lines), seven to twelve (broken thick line), and more than twelve (solid thick line). (Data from Rudwick, 1970; Ross, n.)

from the Tournaisian and Visean of western Europe, and *Euloxoceras* from the upper Mississippian and Pennsylvanian of central North America. The remaining seven pseudorthoceratid genera are widespread and apparently cosmopolitan. The order Oncocerida has three Lower Carboniferous genera of which *Argocheilus* is known only from China and the other two from North America and Europe.

The order Nautilida has nine families in the Carboniferous, six of which contain a number of genera that appear to be widespread in Europe and North America in Lower Carboniferous strata; for example, in the family Koninckioceratidae, *Millkoninckioceras, Endololobus, Knightoceras, Planetoceras,* and *Temnocheilus;* in the family Trigonocerataceae, *Aphelaeceras, Maccoyoceras, Rineceras, Stroboceras, Thrincoceras,* and *Vestinautilus;* in the family Solenochilidae, *Acanthonautilus;* in the family Liroceratidae, *Liroceras;* and the family Ephippioceratidae, *Ephippioceras.* A few of these genera are recorded elsewhere also, such as *Liroceras* and *Ephippioceras.* Among the nine nautilid families, many other genera are known from Lower Carboniferous strata from limited geographical areas, for example, *Tylonautilus, Duerleyoceras, Lophoceras, Subvestinautilus, Trigonoceras, Discitoceras, Epistroboceras, Leuroceras, Lispoceras, Mesochasmoceras, Pararineceras, Subclymenia, Diorugoceras, Phacoceras, Epidomatoceras,* and *Bistrialites* are known from Europe (mostly western Europe), and *Edaphoceras, Tylodiscoceras, Chouteauoceras,* and *Diodoceras* are known only from central and eastern North America.

Middle and Upper Carboniferous genera of the family Tainoceratidae are widely distributed in North America and Europe, except for *Gzheloceras* from the Urals. In the family Grypoceratidae most genera are nearly cosmopolitan, such as *Domatoceras, Stenopoceras,* and *Titanoceras,* and in the family Solenochilidae *Solenochilus* is also cosmopolitan. A few Pennsylvanian genera seem restricted to North America, including *Coelogasteroceras, Condraoceras* (which appears also in the Permian of Europe), and *Megaglossoceras.* A few additional distributions are of interest largely because they indicate the incompleteness of these records. *Valhallites* has been reported only from Siberia and Arkansas, and *Phacoceras* is known not only from the Lower Carboniferous of Europe but also from the Lower Permian of Australia.

The subclass Ammonoidea is widely, and commonly abundantly, distributed in Carboniferous strata and appears to be generally more cosmopolitan than the Actinoceratoidea and Nautiloidea (MILLER & FURNISH, 1957). The evolution and biostratigraphic zonation of Carboniferous ammonoids have been extensively studied in Europe and North America because of the usefulness of this group as stratigraphic index fossils. Based on these studies, ammonoids from the rest of the world have been compared and analyzed and assigned to biostratigraphic units. RUZHENTSEV (1966) recognized nine major biostratigraphic assemblages (Fig. 6) using the stratigraphic ranges of 158 ammonoid genera.

Few recent studies have considered the geographical distributions of Carboniferous Ammonoidea in detail. Data available for Tournaisian and Visean goniatites (BISAT, 1924; DRAHOVZAL, 1972; HODSON & RAMSBOTTOM, 1973) indicate that seven assemblage zones were widely distributed. The oldest of these Carboniferous goniatite faunas appears at the edges of the Hercynian belt in Europe, Kazakhstan, and North Africa, and commonly occurs in strata that rest without hiatus on highest Devonian strata. The succeeding five zones are identified mostly on the basis of ranges of genera of Goniatitidae that are widely distributed in the northern hemisphere, but they are poorly known from the southern hemisphere except Australia where two of the assemblage zones are recorded. Based on wide geographic distribution, these five sets of late Tournaisian and Visean assemblage zones are considered to be cosmopolitan. The highest Visean assemblage zone is likewise widely distributed but the species show provincial distributions.

Provincialism becomes characteristic of ammonoids for the remainder of the Lower and Middle Carboniferous. For example, about half of the Ural faunas are made up of members of the Prolecanitidae, Agathiceratidae, Pronoritidae, Delepinoceratidae, and Ferganoceratidae; forms that are absent in

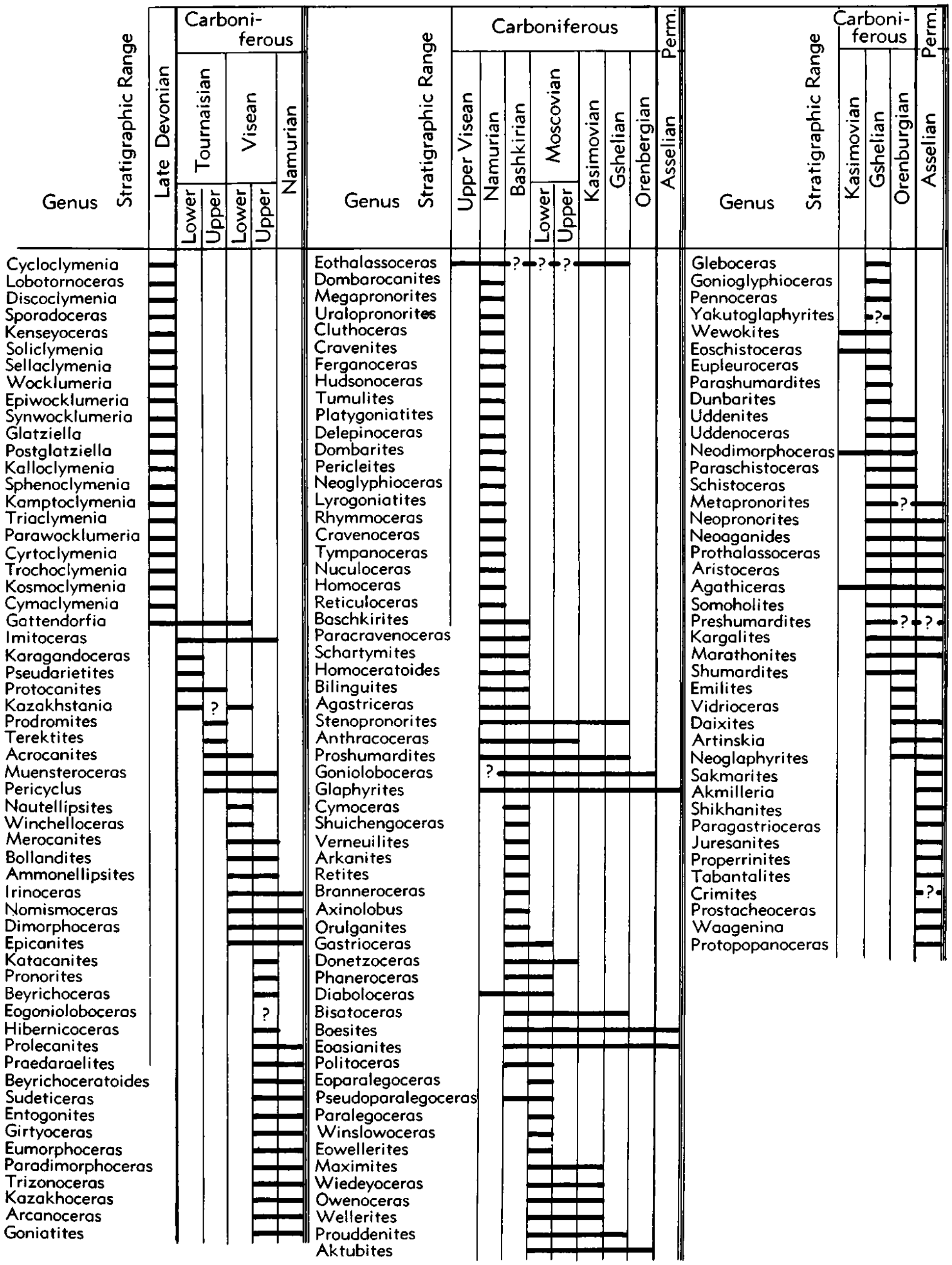

FIG. 6. Ranges of ammonoid genera in the Upper Devonian, Carboniferous, and Lower Permian. (Data from Ruzhentsev, 1960, 1966; Ross, n.)

northwestern Europe. Namurian and early Westphalian ammonoid distributions are characterized by a number of provincial faunas in which generic ranges extend irregularly upward in the succession (RAMSBOTTOM, 1971); some lineages became extinct or evolved into new but endemic genera. Goniatitids persisted in North Africa

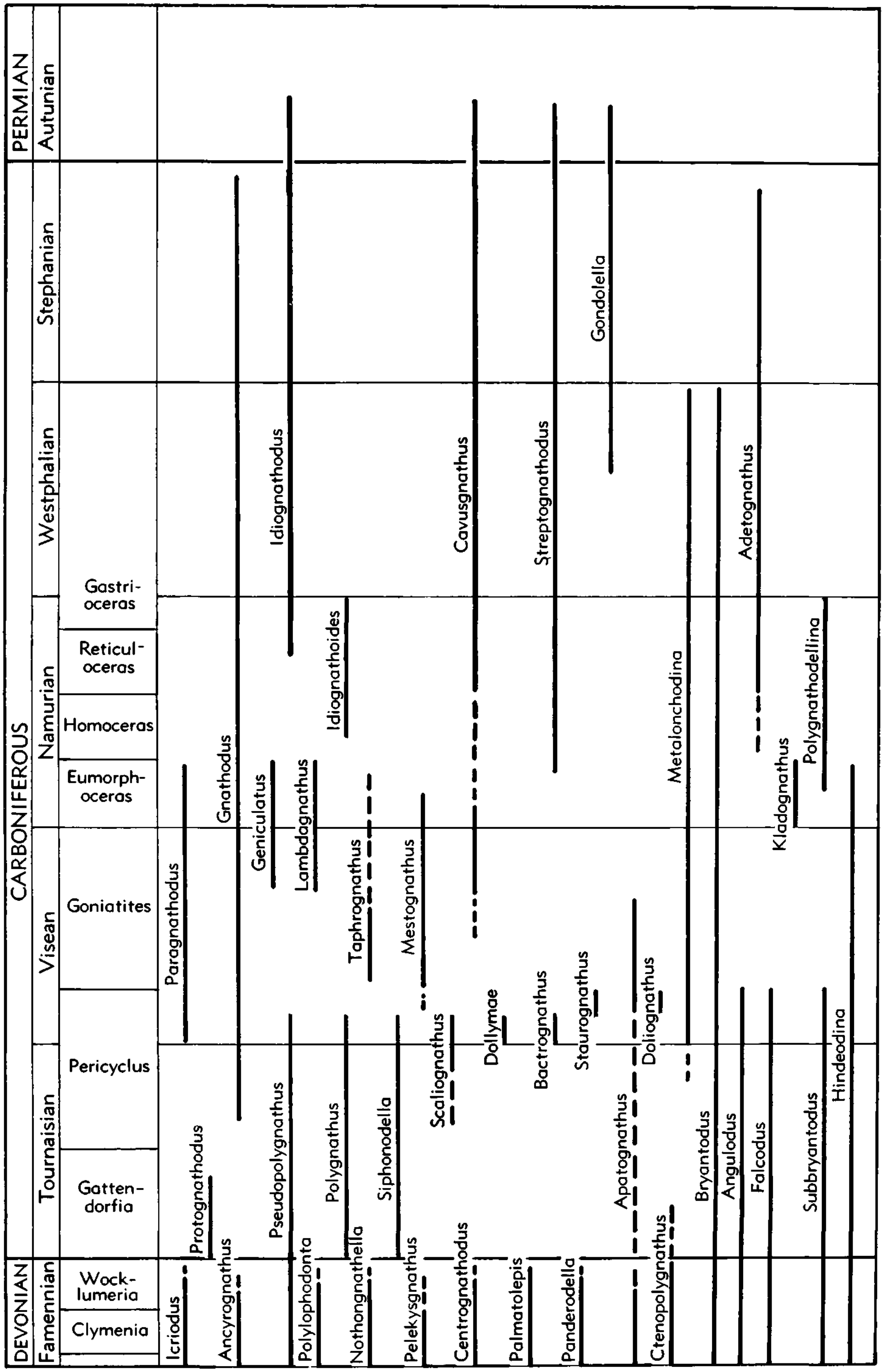

FIG. 7. Stratigraphic range of important genera of conodonts in the Carboniferous. Several genera that

and Arkansas well into the Namurian to give rise to *Proshumardites,* and in the Ural region *Dunbarites* and *Platygoniatites* persisted into the Namurian, whereas in northwestern Europe the only goniatitids to survive are in the base of the Namurian. Although the genus *Cravenoceras* (Zone E_1) is widespread and cosmopolitan, its species tend to be endemic to several provinces. *Eumorphoceras* and *Delepinoceras* are widespread but their contribution to various faunas varies considerably and *Cravenoceratoides* (Zones E_{2b} and E_{2c}) is a common northwestern European genus that has also been recorded from Spain, the Sahara, and central Asia.

At the top of Zone E_2 and in Zone H, goniatite zonal index faunas are lacking in North America, but they are common in northwestern Europe, North Africa, and possibly in the eastern Urals; the zonal genus *Homoceras* has been reported from as far east as the Tien Shan Mountains. Pronoritids are commonly associated with these occurrences except in northwestern Europe.

Reticuloceras is common in the Ural Mountains, Donetz basin, and to the south along the proto-Tethyan geosyncline where it is associated with *Proshumardites* and pronoritids, but *Reticuloceras* is rare in North America where *Syngastrioceras* and *Cymoceras* dominate. In northwestern Europe the goniatite fauna is less diverse and restricted. Later *Reticuloceras* stocks in northwest Europe and North America appear to have had independent histories.

Gastrioceras, Branneroceras, and *Syngastrioceras* form the typical assemblage of Zone G_1 and are nearly cosmopolitan except for northwestern Europe where *Gastrioceras* occurs without the other two typical genera. In succeeding strata with Zone G_2, northwestern European goniatites represent a relict fauna with the exception of *Politoceras,* which was introduced from North America. In North America the Middle Carboniferous is an interval of increasingly diverse goniatite faunas, and a number of genera, such as *Bisatoceras, Gonioloboceras, Gonioglyphioceras, Wiedeyoceras, Dunbarites, Vidrioceras, Paralegoceras, Diabloceras, Winslowoceras,* and *Owenoceras,* are endemic.

Late Carboniferous ammonoids appear to be more cosmopolitan in distribution than those of the Middle Carboniferous. *Dunbarites* was still endemic to south-central North America as were *Eupleuroceras* and *Vidrioceras,* and in the Ural Mountains *Gleboceras* was endemic.

Tournaisian and Visean seas covered a larger proportion of continental platforms than did Namurian and later seas (RAMSBOTTOM, 1971). The most varied cephalopod faunas are in the proto-Tethyan region which was connected at various times to these epicontinental seas. When ammonoid distributions are plotted on reconstructed Carboniferous paleogeographic maps, they occur between Carboniferous latitudes 60°N and 50°S.

CONODONTS

The use of discrete conodont elements in establishing a detailed biostratigraphic zonation for the Devonian and Lower Carboniferous has provided a tool for accurately dating many marine strata that have relatively few other fossils (Fig. 7). Little biological information is available about the organism which bore the conodont elements. Assemblages containing different types of conodont elements are not commonly preserved, so the custom of referring to each type of element as a different form taxon is a useful biostratigraphic expedient. Although many of the conodont guide fossils have an uneven geographic and stratigraphic distribution (RHODES & AUSTIN, 1971), they form a widely used biostratigraphic scheme. The British Tournaisian and Visean are divided into 14 zones based on conodont succession and the comparable sections in North America are divided into 13 zones and in Germany into eight zones.

In North America and in many other

FIG. 7. *(Continued from facing page.)*
range through the Carboniferous, such as *Spathognathodus,* and have species with distinctive stratigraphic ranges, are not shown. (Data from Rhodes and Austin, 1971; Collinson, Rexroad, & Thompson, 1971; Lane, Merrill, Straka, & Webster, 1971; Meischner, 1970; Ross, n.)

parts of the world (Sandberg *et al.*, 1972), *Siphonodella* has an important succession of species that permits subdivision of the lower part of the Lower Carboniferous. These are succeeded in the upper part of the Lower Carboniferous by a number of species of *Spathognathodus, Polygnathus, Bactrognathus, Taphrognathus, Apatognathus,* and *Cavusgnathus,* which have distinctive stratigraphic ranges.

In England the Lower Carboniferous conodont succession is characterized by a large number of short-ranging species of spathognathodids and pseudopolygnathids. *Siphonodella,* a distinctive genus for the Tournaisian elsewhere, is very rare in England. *Gnathodus* has many short-ranging species in Visean and lower Namurian strata. *Idiognathodus* first appears at about the same horizon as the cephalopod *Reticuloceras* and different species of *Idiognathodus* are distinctive in the upper part of the Namurian. *Gnathodus* becomes increasingly rare in this interval and finally disappears. Westphalian conodont faunas lack *Gnathodus* and are dominated by species of *Idiognathodus.*

In North America, Mississippian conodont zonation has been well studied in the upper Mississippi valley and adjacent areas (Collinson, Rexroad, & Thompson, 1971) and 16 named conodont zones and several subzones are recognized (Fig. 7). The Kinderhookian Series has six zones based on stratigraphic ranges of species of *Siphonodella, Gnathodus,* and *Protognathodus.* The Osagean Series is subdivided using ranges of species of *Bactrognathus, Doliognathus, Gnathodus, Pseudopolygnathus, Polygnathus,* and *Taphognathus.* The base of the Chesterian Series falls within one of these zones. Species of *Kladognathus* appear in the upper part of the Chesterian and the highest zone in the Mississippi valley region has the first appearance of *Streptognathodus.* The top of the type Mississippian System is marked by a major hiatus; however, at least part of the missing interval is represented by strata in Nevada where a higher conodont zone, *Gnathodus girtyi simplex* Zone, is assigned to the Mississippian.

Studies in North American Pennsylvanian conodont zonation have concentrated on the lower part of the succession, particularly the Morrowan Series (Lane *et al.*, 1971). Four Morrowan zones are recognized based on ranges of species of *Spathognathodus, Idiognathoides,* and *Gnathodus.* In the Midcontinent area, *Idiognathoides* dominates the Morrowan conodont faunas. Several species of *Gondolella* are restricted to the Desmoinesian, Missourian or Virgilian series and a species of *Gnathodus* occurs in the Desmoinesian. *Idiognathodus* and *Streptognathodus* are important in late Carboniferous conodont faunas of the Midcontinent region.

In the central Appalachian Mountains, Pennsylvanian lineages of *Gnathodus* start in the lower part of the Pottsvillean Series and have not been found above the middle part of the Conemaughan Series. Specimens of *Idiognathodus* are the most abundant conodont in the Pottsvillean and Alleghenyan Series but *Streptognathodus* dominates the Conemaughan Series.

In the southwestern part of the Cordilleran miogeosyncline, the first appearance of species of *Streptognathodus* and *Idiognathoides* is in strata of early Morrowan age. A number of species appear in both the Cordillera and the Midcontinent areas but they seem to have different regional stratigraphic ranges and apparently reflect intermittent connection between the two regions.

The Carboniferous succession in Germany is divisible into 14 conodont zones and subzones (Meischner, 1970). Tournaisian strata are divided into five conodont zones based on ranges of species of *Protognathodus, Pseudopolygnathus, Polygnathus,* and *Siphonodella.* Five zones are recognized in Visean strata based on ranges of species of *Scaliognathus, Gnathodus,* and *Paragnathodus,* some of which range upward into the lower part of the Namurian. From strata of the *Homoceras* Zone and higher Namurian and Lower Westphalian, species of *Gnathodus* dominate the conodont faunas. The first appearance of *Idiognathodus* is in the middle part of the *Gastrioceras* Zone at the base of the Westphalian, a stratigraphic position that suggests *Idiognathodus* occurs higher in Germany than in England or North America.

Studies of the biogeographic distribution of conodonts (Druce, 1973) have come about only since the completion of detailed stratigraphic analyses from a number of different regions. Several Carboniferous genera are apparently geographically restricted to certain regions. The late Tournaisian genera *Bactrognathus* and *Staurognathus* are found only in the Midcontinent and southwestern regions of the United States and other reported occurrences are questionable. *Cavusgnathus* occurs in the Visean of North America, England, Scotland, and Germany, but is rare or lacking in other parts of Europe (Druce, 1973); however, this genus may be closely associated with nearshore deposits (Lane *et al.*, 1971) and these distributions may reflect inadequate sampling. Other Tournaisian or Visean genera with restricted distributions include *Clydagnathus* (Western Australia and southern England), *Doliognathus* and *Dollymae* (Europe and central North America), *Mestognathus* (Nova Scotia, Australia, and Europe), and *Taphrognathus* (North America, British Isles, and Australia). Among the Middle and Late Carboniferous conodonts, *Gondolella* was restricted to central North America but became widespread during the Permian Period.

Most other important zonal index genera are cosmopolitan in distribution including *Gnathodus, Idiognathodus, Spathognathus,* and *Siphonodella.* Several genera have patchy distributions but are reported from many different parts of the world; these include *Idiognathoides, Scaphignathus,* and *Streptognathodus.* Conodont distributions in the Carboniferous are not particularly provincial and many of the patterns of distribution may be the result of inadequate sampling of all of the biofacies for each zone (Druce, 1973). Most conodont studies have concentrated on Lower Carboniferous (Tournaisian, Visean, and lower Namurian) strata where other faunas generally also suggest cosmopolitan distributions. At present there is insufficient knowledge of Middle and Upper Carboniferous conodonts to evaluate their geographic distributions.

INSECTS

Insect fossils from the base of the Westphalian through the remainder of the Carboniferous have the potential of being extremely useful as index fossils (Fig. 8, 9). They show considerably greater taxonomic diversity and more rapid evolution than do the fossil flora with which they are commonly associated. Many insects have stratigraphic ranges that are closely similar in North America and Europe and relatively few have strongly endemic distributions.

Although relatively few of the 17 orders of Insecta of the Carboniferous have been studied in terms of their world paleogeography, several analyses have examined the evidence from one or two orders in a more limited geographic framework. The early Insecta of the eastern Canadian (Maritime provinces) Carboniferous have a pronounced number of European elements (Durden, 1967, 1969) as do the plant fossils (Bell, 1938). Some European elements appear farther to the southwest and some American elements appear to the east in Wales and France, suggesting a transitional belt of provincial differentiation and a lack of major physical barriers. Blattoid (cockroach-like) insects appear in lower or middle Namurian strata of central Europe and upper Namurian of western Europe and eastern Canada. By early Westphalian time, the insect assemblage, characterized by blattoids, dispersed into central eastern North America (Pennsylvania and Maryland) and two parallel bands of geographically distinct assemblages (but with overlapping boundaries) are recognized. By middle Westphalian time, additional assemblages are recognized and have distributions that also form subparallel geographic bands from central North America into western Europe. During the later part of Westphalian time several earlier assemblages were reduced in size but the assemblage from the southern part of western Europe expanded markedly over a much larger area. Several assemblages were missing during this time, but because they (or their descendants) reappear in younger strata, Durden (1974) assumed that they were displaced geographically outside present collecting localities.

The early Stephanian of Europe was complicated by the Asturian orogenic phase, which disrupted many of the Westphalian depositional patterns and caused major changes in insect distributions and also in

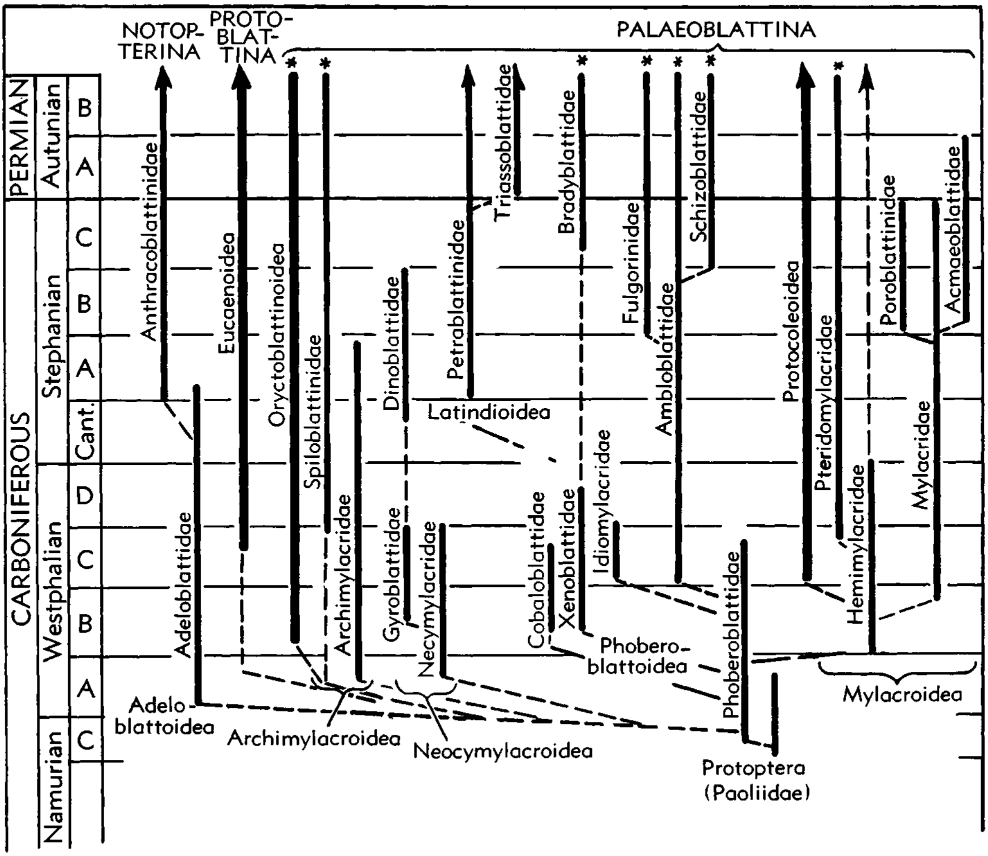

FIG. 8. Ranges of families, superfamilies, and suborders of early blattoid-like insects and phylogenetic relations. Lineages marked with an asterisk became extinct during the Permian. Lineages with arrows have given rise to recent descendants. (Data from Durden, 1969; Ross, n.)

plant distributions (de Maistre, 1970). Southwest European insect assemblages of this age are found as far west as Pennsylvania associated with the remnants of an earlier north-central (Mazonian) North American assemblage. Many of the non-blattoid insect assemblages of the Stephanian include a significant percentage of new groups that have no known immediate ancestors suggesting dispersal from earlier isolated provinces that are not known at present. During the Stephanian an eastern North American (Ottweilerian) assemblage developed and expanded westward into Missouri and eastward into the Saar basin. During middle Stephanian time (Missourian-early Virgilian) the southwest European (Iberian) assemblage occurred in Portugal, southern Pennsylvania, Missouri, and possibly in Brazil. Just to the north of the Iberian assemblage the Ottweilerian assemblage continued to be widespread, reaching from eastern Germany to Pennsylvania and, as mixed faunas, as far west as central Colorado. In Kansas, the beginnings of two assemblages are seen, the Zavjalovian and the Elmoan, which are mixed with Ottweilerian genera. The Elmoan assemblage has many new genera and these are presumed to have dispersed into Kansas at this time from an unknown area to the northwest.

During late Stephanian to early Autunian time the Ottweileran insect assemblage extended from Wettin, Germany, through Pennsylvania into Colorado. At Wettin this assemblage also included forms similar to those reported from strata of about the same age in the Kuznetzk basin, Siberia. The

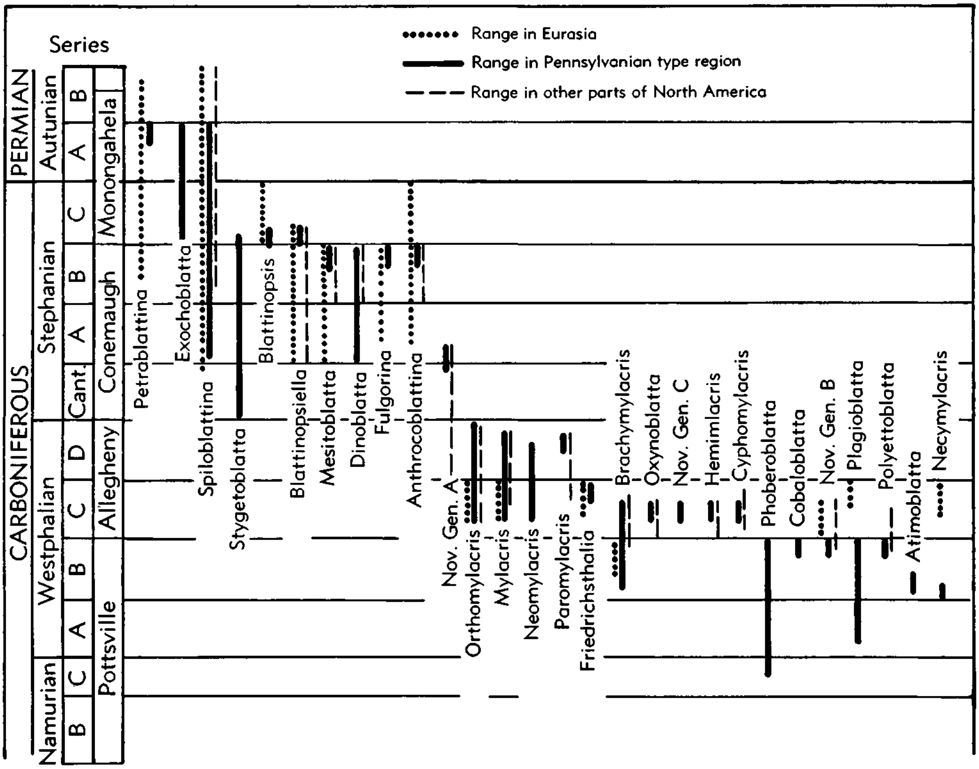

FIG. 9. Ranges of blattoid-like insect genera having multiple occurrences in Eurasia, Pennsylvania (type region), and other parts of North America. (Data from Durden, 1969; Ross, n.)

Iberian assemblage occurred to the south in Texas at this time.

The late Virgilian and Wolfcampian distribution of blattoid-like insects showed a continuation of the Iberian assemblage in Texas. The Lebachian assemblage, a new, rich and varied assemblage, is known mainly from this interval in Germany and West Virginia, with a few representatives in Texas and Kansas. In Colorado parts of this assemblage are mixed with genera of Ottweilerian and Zavjalovian affinities in a predominantly Elmoan fauna. DURDEN (1974) was able to trace many of these groups through the Early Permian and showed that most of the three Early Permian assemblages had their origins during the Late Carboniferous.

BIOGEOGRAPHIC INTERPRETATION

Three general trends appear from the foregoing analyses of the distributions of Carboniferous invertebrate faunas; one has evolutionary implications and the other two have climatic fluctuation and climatic zonation implications. Faunas of Tournaisian and Visean times were relatively widespread; many were nearly cosmopolitan and the remainder had low levels of provincialism. These were also times of widespread, shallow, warm-water carbonate deposition, particularly on continental platforms. As a great percentage of the area of these platforms was submerged, world sea level was apparently relatively high and the marine connections between adjacent platforms were well established. After the Visean, Carboniferous faunas became increasingly provincial with several times of infrequent to frequent dispersal between marine prov-

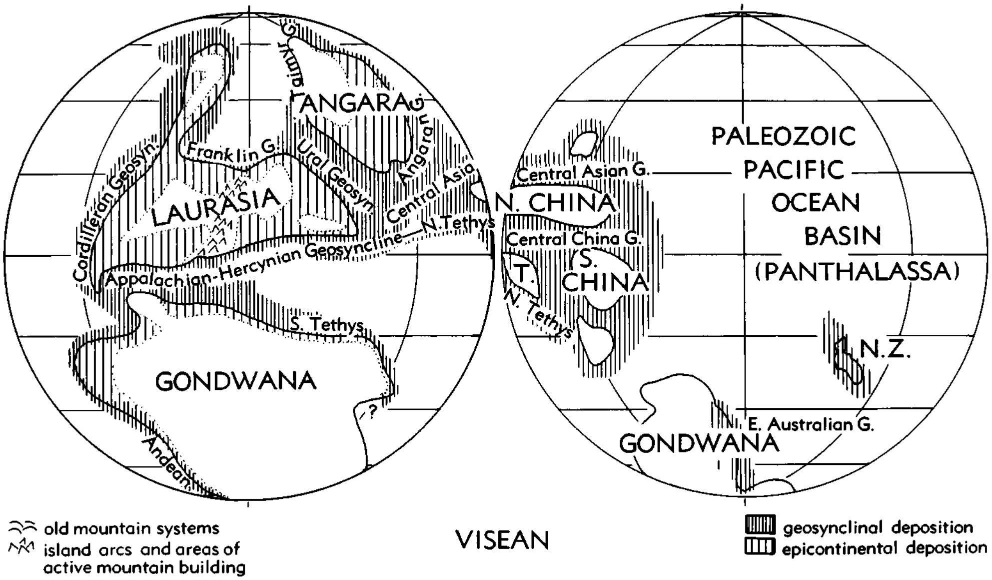

FIG. 10. Reconstruction of Carboniferous paleogeography during an interval of relatively high sea level: middle Early Carboniferous (Visean) (Ross, n). [Explanation: N.Z., New Zealand; T., Tarim stable block.]

inces until the end of the Carboniferous.

The later part of the Early Carboniferous was the beginning of Hercynian mountain building and saw an increase in volcanic activity in parts of Europe and western Siberia. These events are also associated with the beginning of cyclic sedimentation, the reduction in warm-water carbonate deposition, and probably the initiation of glaciation in parts of the Gondwana continent in conjunction with general lowering of world temperatures. During the later part of the Early Carboniferous the average sea level declined and reached a minimum level before the beginning of the Middle Carboniferous. Most of the continental shelves were extensively exposed to erosion at this time (EYNOR *et al.,* 1965). Dark shale, sandstone and limestone are typical deposits and marine connections between regions were mainly by seaways through those geosynclines that had not been disrupted by orogenic activities. Much of the Hercynian orogeny was well advanced by this time and, during the later part of the Early Carboniferous and Middle and Late Carboniferous, this fold belt prevented direct marine connection between western North America and southeastern Europe.

During Middle Carboniferous time, sea level gradually rose accompanied by a series of transgressions and regressions, reaching a comparatively high level during the Desmoinesian when seas covered much of the continental platforms. As world sea level started to fall again near the end of the Middle Carboniferous a number of changes started to take place in marine invertebrate faunas. Many of those faunal groups that had held dominant positions in Middle Carboniferous communities became gradually less important and a number of transitional forms appeared which evolved into new genera, and also new families, in the early part of the Late Carboniferous. The end of the Middle Carboniferous is marked by a reduction in world sea level of almost the same magnitude, but of shorter duration, as that at the end of the Early Carboniferous. A number of previously important genera and families of the Early and Middle Carboniferous did not survive into the Late Carboniferous.

During the Late Carboniferous the new lineages of marine invertebrate faunas evolved into numerous genera and families and gradually formed a large variety of communities. The faunas and communities

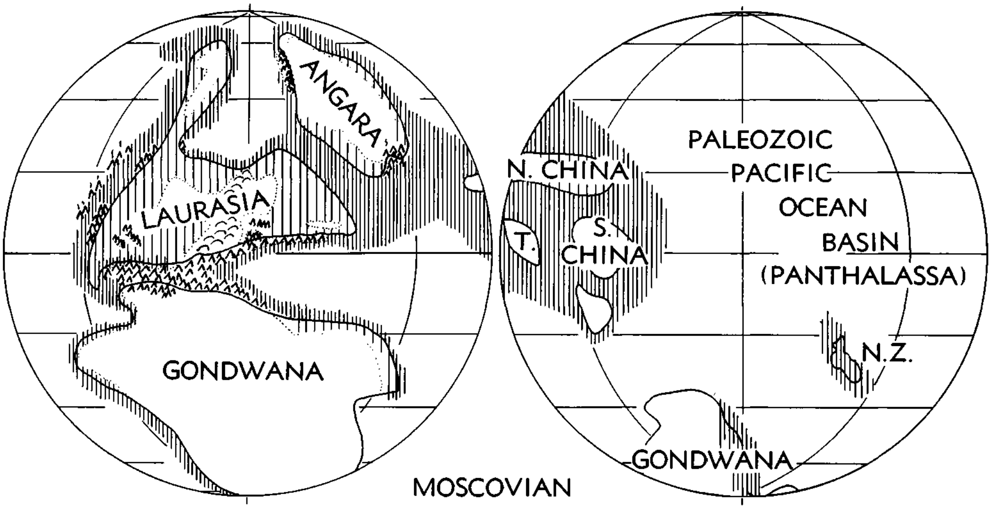

FIG. 11. Reconstruction of Carboniferous paleogeography during an interval of relatively high sea level: late Middle Carboniferous (Moscovian) (Ross, n). [See Fig. 10 for explanation of abbreviations and symbols.]

were not highly specialized, suggesting that they were adapted to fluctuating climatic conditions. Although cyclic sedimentation continued through the Late Carboniferous, local variations in the sedimentary cycles became more pronounced and, in general, the volume of clastic material became greater. This suggests orogenic activity had reached a level that significantly altered local climatic patterns and related erosional rates and that interglacial intervals were warmer, dryer, and probably of longer duration. The faunal changes at the end of the Carboniferous and the beginning of the Permian, while significant, were concurrent with specialization of existing Late Carboniferous families into an increasingly complex set of Permian communities and increased dispersals between faunal provinces.

Climatic zonation in the Carboniferous was first recognized in the distribution of Carboniferous plants, which may exhibit seasonal growth features such as growth rings. Carboniferous floras (MEYEN, 1972) became differentiated into at least two regions near the beginning of the Namurian, i.e., the Euramerian and Angaran regions, characterized largely by different ecological associations of lepidophytes. The Euramerian flora was tropical but it has not been established yet that the Angaran woods were extra-tropical at this time. Middle Carboniferous floras of the Euramerian and Angaran regions show substantial differences in composition and woods from the Angaran region consistently have annual rings. Early and Middle Carboniferous floras from Gondwana are poorly known and fossil wood data are not available for comparison.

Late Carboniferous plants form four paleofloral regions, Euramerian, Cathaysian, Angaran, and Gondwanan (JONGMANS, 1936; HALLE, 1937). The Euramerian and Cathaysian floral regions differ mainly in the presence of large numbers of endemic genera. These two floras are diverse, generally lack annual rings and are considered tropical. The Angaran flora had a few Euramerian elements but endemic genera were dominant by the end of the Late Carboniferous. This flora had annual growth rings and is considered extratropical. The Gondwanan flora is poorly known from strata older than Late Carboniferous; however, by Late Carboniferous time it was widespread and remarkably uniform in species composition. This early Gondwanan flora is associated with tillites and possibly was contemporaneous with glaciation. The flora was deciduous and had annual rings, a relatively low number of genera and species and is considered to be extra-tropical. The Gondwanan flora was isolated from other floras at this time, having few, if any, genera and species in common with the Euramerian, Cathaysian, or Angaran floras.

Some marine invertebrate evidence also suggests well-developed climatic zonation during the Carboniferous. A tropical foraminiferid faunal belt is identified for the Early and Middle Carboniferous based on greater species diversity and dominance of calcareous taxa (MAMET & SKIPP, 1970). The position of this tropical belt corresponds closely to the position of tropical climates as suggested from plant data. Away from this tropical belt foraminiferids gradually become less diverse and arenaceous taxa become dominant. The margins of the Angaran continent and the Gondwanan continent are identifiable by these two changes (YUFEREV, 1969). Also, ammonoid distributions appear to be restricted to a band about 50° to 60° on either side of a Carboniferous paleoequator (RAMSBOTTOM, 1971).

Two paleogeographic maps, one of Visean time (Fig. 10) and the other of Moscovian times of major marine transgressions onto the cratonic platforms. During Visean time, marine connections existed in an east-west direction near the paleoequator from western North America to eastern Asia and this apparently accounts for the nearly cosmopolitan nature of the equatorial marine faunas. By Moscovian time, the Hercynian orogeny had closed off these east-west marine connections along the paleoequator and dispersal of tropical marine faunas between different provinces became more difficult because these organisms had to pass through extratropical areas in order to disperse into other provinces. These generalized maps leave many details to be explained; for example, the Middle Carboniferous marine faunas of one tectonic belt in the western Cordillera of North America are probably tropical whereas faunas in the adjacent tectonic belt are probably nontropical, suggesting a more complicated history of geographic displacement than indicated by these maps. Of particular concern is the need for additional criteria and evidence that would establish the relative positions during the Carboniferous of the cratonic blocks that presently form southern and southeastern Asia.

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