

UTILITY OF CORALS FOR BIOSTRATIGRAPHIC AND ZOOGEOGRAPHIC ANALYSES OF THE CARBONIFEROUS IN THE CANTABRIAN MOUNTAINS, NORTHERN SPAIN

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Los estudios sistemáticos de los corales del Carbonífero de la Cordillera Cantábrica en el Noroeste de España han avanzado hasta el punto de demostrar que pueden ser bastante útiles para la realización de análisis bioestratigráficos y zoogeográficos. El presente trabajo muestra un análisis de distribución de las faunas basado en 1369 ejemplares asignados a 163 especies pertenecientes a 56 géneros de corales rugosos.

Una zonación bioestratigráfica preliminar basada en distribuciones de taxones a nivel genérico es útil para identificar series o pisos del Carbonífero en el área estudiada. Se han hallado un total de 29 géneros en una sola serie o piso, 25 géneros no aparecen por debajo de una determinada serie o piso y 16 no se encuentran por encima de una determinada serie o piso. Futuros estudios deberían dirigirse hacia la construcción de una escala temporal independiente de los límites de series o pisos.

Tanto la abundancia de corales, como la frecuencia y aparición, la diversidad genérica y específica, la aparición de nuevos géneros, y la diversidad de morfotipos, presentan máximos en los periodos Namuriense A-B, Westfaliense A y Westfaliense D, y mínimos en los periodos Viseense, Namuriense C, Westfaliense B y Cantabriense (Estefaniense A). Debido a que la mayoría de los géneros de corales rugosos tienen su origen fuera del área estudiada, estos máximos y mínimos parecen representar invasiones y retiradas de la fauna de corales que se pueden correlacionar con cambios en los hábitats favorables.

Aunque hay una correlación general de aumento de abundancia y diversidad con la regresión marina a lo largo del Carbonífero superior en el Norte de España, variaciones cíclicas menores en la abundancia y diversidad se relacionan con incrementos en el tamaño del hábitat (ecoespacio) y la diversificación de hábitats. Una migración general de corales de medios de aguas profundas hacia medios generalmente poco profundos a lo largo del Carbonífero es comparable a la tendencia observada en el Carbonífero inferior del «Western Conterminous» de Estados Unidos, y puede estar relacionada con fenómenos mayores de carácter regional.

Comparaciones zoogeográficas con América del Norte y la cuenca del Donetz en la Unión Soviética, por medio del índice de semejanza faunística (SI), sugieren que, durante todo el Carbonífero superior existió una vía de comunicación favorable al flujo genético a lo largo del contacto entre las placas africana, sudamericana y norteamericana, entre España y Norteamérica.

Palabras clave: Bioestratigrafía, Carbonífero, Corales, Cordillera Cantábrica, Zoogeografía.

Systematic studies of Carboniferous corals in the Cantabrian Mountains of northern Spain have progressed to the point where they are quite useful for biostratigraphic and zoogeographic analyses. This report presents a distribution analysis based on 1369 specimens assigned to 163 species representing 56 genera of rugose corals.

A preliminary biostratigraphic zonation based on generic ranges is useful to identify series or stages of the Carboniferous in the area studied. Twenty-nine genera are known only from one series or stage, 25 genera are not known to occur below a par-

ticular series or stage, and 16 genera are not known to occur above a particular series or stage. Future studies should be directed toward construction of a time scale independent of series of stage boundaries.

Coral abundance, frequency of occurrence, generic and specific diversity, influx of new genera, and morphotype diversity, all show maxima in Namurian A-B, Westphalian A, and Westphalian D, and intervening minima in Visean, Namurian C, Westphalian B, and Cantabrian-Stephanian A. Because most of the rugose coral genera originated outside the area studied, these maxima and minima seem to represent invasions and retreats of the coral fauna related with changes in coral habitats. Although there is a general correlation of increased abundance and diversity with regression of the sea through Late Carboniferous time in northern Spain, smaller cyclical variations in abundance and diversity are related to increases in habitat size (ecospace) and habitat diversification. A general migration of corals from deep-water environments to generally shallow water environments through Late Carboniferous time is similar to pattern seen in the Lower Carboniferous of the western conterminous USA and may be related to larger regional events.

Zoogeographic comparisons with North America and the Donetz basin of the USSR by means of similarity index (SI) suggest that a seaway along the juncture of the African, South American, and North American plates provided a communication route for coral gene flow between Spain and North America during the entire Late Carboniferous.

Key words: Biostratigraphy, Carboniferous, Cantabrian Mountains, Rugosa, Zoogeography.

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In recent studies of the stratigraphy and history of the Carboniferous, corals have not been generally regarded as useful as goniatites, conodonts, and foraminifers, which are noted for their geologically rapid dispersal times, widespread distributions, and high rates of evolution. The sessile growth habit of the corals and their inferred sensitivity to depth, salinity, temperature, light transmission, and other environmental factors have elicited scepticism about their use in biostratigraphy. However, recent biostratigraphic studies of Carboniferous corals in North America (Sando and Bamber, 1984) demonstrated empirically that corals are useful as zonal fossils within a province of large areal extent. Moreover, recent global synthesis of provincial distribution of Carboniferous corals (Fedorowski, 1981) suggests that they may provide independent tests for paleocontinental reconstructions by means of similarity comparisons. Because of their sessile benthonic habit, corals may be useful for tracking transgressions and regressions of the sea, using

data on variations in their abundance and diversity. In addition, Bathymetric indexing of corals has been attempted in the Carboniferous of North America (Sando, 1981).

Taxonomic studies of Carboniferous corals in the Cantabrian Mountains of northern Spain (de Groot, 1964; Kullmann, 1966, 1968; Boll, 1983; Rodríguez, 1984a) provide data useful for preliminary biostratigraphic and biogeographic analyses. Some of these data have already been used for preliminary comparisons of the Spanish Carboniferous corals with those of other parts of the world (Rodríguez, 1984b). Herein, we synthesize available data and show how the corals may be useful in future studies of the Carboniferous in Spain.

DATA BASE

This study is based on distribution analysis of 1369 specimens assigned to 163 species representing 56 rugose coral genera from the Carboniferous of the Cantabrian Mountains.

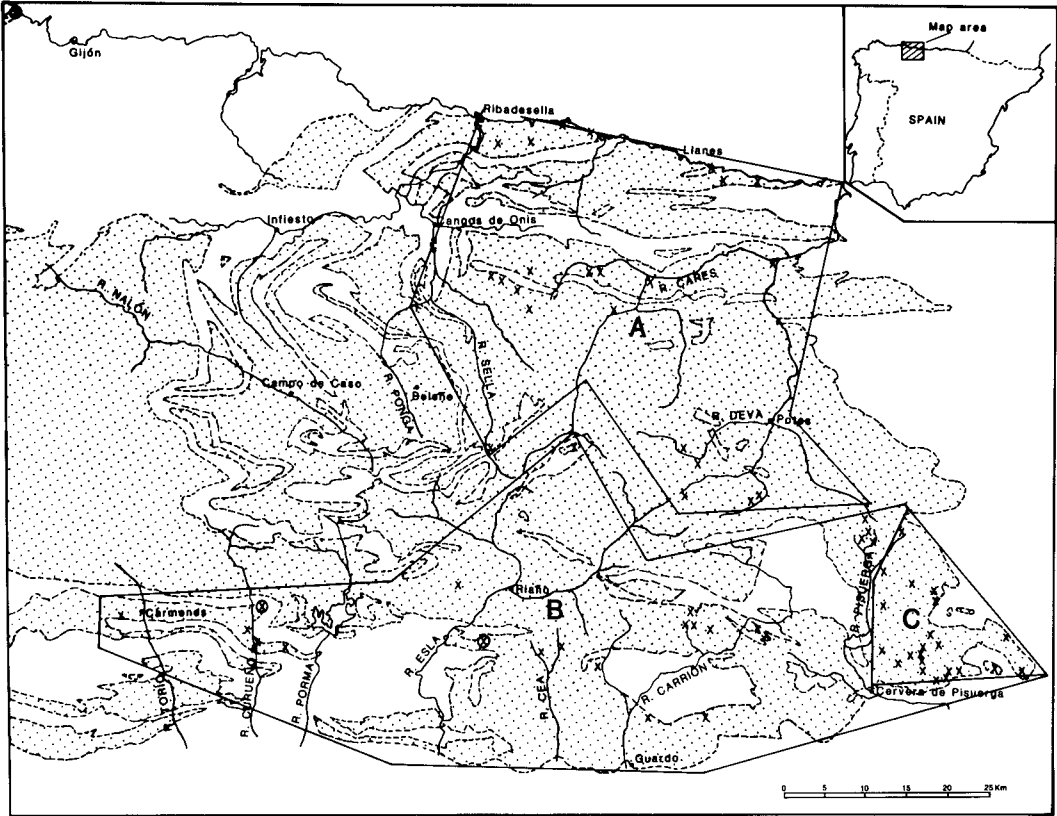


Fig. 1.—Geologic map of a part of the Cantabrian Mountains showing outcrops of Carboniferous rocks (stippled) and areas of Rodríguez (A), Boll (B), and de Groot (C) coral studies. Locations of individual coral localities are indicated by uncircled Xs in the study areas, except for Kullmann localities, which are designated by circled Xs.

The fossils were collected from 71 localities (Fig. 1) and formed the basis for descriptive taxonomy by Kullmann (1966, 1968), de Groot (1964), Boll (1983, 1985) and Rodríguez (1984). Tabulate corals are not represented in the material described and, though present in the study area, were not included in this analysis. Emphasis is placed on genera because species concepts are somewhat controversial; nevertheless, published species concepts were used as a measure of diversity in part of the analysis. Subspecies, varietes, and formae of the authors of the taxonomic papers were considered coordinate with species. Some revision of published generic taxonomy was necessary to make the genera consistent with concepts endorsed by all three of the authors of the present paper. The taxonomic hierarchy is in general agreement with that of Hill (1981). Classification of rugose coral taxa util-

ized in this study is following. The species which are assigned to each genus are placed below it. (See Kullmann, 1966; de Groot, 1964; Boll, 1983, 1985; and Rodríguez, 1984 for descriptions).

Genus *Amplexus* Sowerby, 1814

Amplexocarinia wagneri de Groot

A. corrugata (Mather) de Groot

Amplexus stuckenbergi Fomichev of Rodríguez

A. sp. 1 of Rodríguez

A. sp. 2 of Rodríguez

Genus *Kizilia* Degtyarev, 1965

Kizilia transeptata Rodríguez

Genus *Asserculinia* Schouppé Stacul, 1959

Asserculinia berodiensis Rodríguez

Genus *Amplexocarinia* Soshkina, 1928

Amplexocarinia asturica Rodríguez

A. delicata Ross and Ross of Rodríguez

Genus *Cyathaxonia* Michelin, 1847

Cyathaxonia cornu Michelin of Rodríguez

C. cornu var. *cantabrica* de Groot

- C. corisensis* de Groot
C. sp. 1 of de Groot
C. sp. 2 of de Groot
C. degrootae Rodríguez
Cyathocarinia minima Rodríguez
 New genus aff. *Calophyllum* Dana, 1846
Polycoelia cantabrica de Groot
 Genus *Sochkineophyllum* Grabau, 1928
Sochkineophyllum corisense de Groot
 Genus *Tachylasma* Grabau, 1922
Pentaphyllum (Tachylasma) schindewolfi Kullmann
 Genus *Plerophyllum* Hinde, 1890
Plerophyllum (Plerophyllum) tenuiseptatum Kullmann
 Genus *Ufimia* Stuckenberg, 1895
Plerophyllum (Meniscophylloides) simulans Kullmann
P. (Ufimia) inaequale cf. *inaequale* Schindewolf of Kullmann
P. (U.) inaequale cantabricum Kullmann
?P. (U.) alternans de Groot
?Ufimia (?) sp. of Rodríguez
Meniscophyllum sp. of Rodríguez
 Genus *Verbeekiella* Gerth, 1921
?Verbeekiella sp. of Rodríguez
 Genus *Lophocarinophyllum* Grabau, 1922
Lophocarinophyllum karpinskyi Fomichev of Rodríguez
 Genus *Lophophyllidium* Grabau, 1928
Lophophyllidium breimeri de Groot
L. minus de Groot
L. sp. of de Groot
Stereostylus sp. of de Groot
S. (?) sp. ex. gr. newelli (Jeffords) of de Groot
S. cf. lenis Jeffords of Rodríguez
S. adelus Jeffords of Rodríguez
?Stereolasma (?) masiva Rodríguez
 Genus *Hapsiphyllum* Simpson, 1900
?Hapsiphyllum sp. of Rodríguez
 Genus *Allotropiophyllum* Grabau, 1928
?Allotropiophyllum cf. irregulare Fomichev of Rodríguez
?A. sniatkovi Fomichev of Rodríguez
A. sp. of Rodríguez
 Genus *Amplexizaphrentis* Vaughan, 1906
Zaphrentites paralleloides de Groot
Z. clithria de Groot
 Genus *Duplophyllum* Koker, 1924
?Duplophyllum sp. of de Groot
D. minor Rodríguez
D. crassum Rodríguez
D. ercinensis Rodríguez
 Genus *Euryphyllum* Hill, 1937
?E. hispanicum de Groot
 Genus *Bradyphyllum* Grabau, 1928
Bradyphyllum oppositum Fomichev of de Groot
B. (?) sp. 1 of de Groot
B. (?) sp. 2 of de Groot
 Genus *Rotiphyllum* Hudson, 1942
Rotiphyllum exile de Groot
R. aequibile de Groot
R. sp. of Rodríguez
Syringaxon beruinensis Rodríguez
Bradyphyllum oppositum Fomichev of Rodríguez
 Genus *Arachnolasma* Grabau, 1922
?Koninckophyllum histiophylloides de Groot
 Genus *Caninostrotion* Easton, 1943
Caninostrotion variabilis Easton of Boll
C. perejoni Rodríguez
?Bothrophyllum filigranum Boll
 Genus *Corwenia* Smith and Ryder, 1926
Corwenia symmetrica (Dobrolyubova) of de Groot
C. longiseptata (Fomichev) of de Groot, Boll, and Rodríguez
C. cantabrica de Groot
C. barruelensis Boll
 Genus *Neokoninckophyllum* Fomichev, 1939
?Koninckophyllum intermedium (Fomichev) of Boll
K. schizolamellum Boll
?Genus and species indet. 1 of Rodríguez
 Genus *Sestrophyllum* Fomichev, 1953
Sestrophyllum astraeforme Fomichev of Rodríguez
 Genus *Slimoniphyllum* Kato and Mitchell, 1961
Slimoniphyllum (?) of Rodríguez
 Genus *Spirophyllum* Fedorowski, 1970
Koninchophyllum multilamellatum de Groot
K. gentisae de Groot
?K. gentisae forma minor de Groot
 Genus *Asturiphyllum* Rodríguez, 1984
Clisiophyllum sp. 1 of de Groot
C. sp. 2 of de Groot
?Dibunophyllum sp. of de Groot
Asturiphyllum semenoffi Rodríguez
 Genus *Pseudoamygdalophyllum* Rodríguez, 1984
Pseudoamygdalophyllum dobrense Rodríguez
 Genus *Bothrophyllum* Trautschold, 1979
Bothrophyllum pseudoconicum Dobrolyubova of Rodríguez
B. cf. pseudoconicum Dobrolyubova of de Groot
?B. sp. of de Groot
 Genus *Bothroclisia* Fomichev, 1953
Bothrophyllum (Bothroclisia) clisiophylloides Fomichev of Rodríguez
 Genus *Pseudozaphrentoides* Stuckenberg, 1904
P. melendezi Rodríguez
Caninia ornata Fomichev of Boll
C. volgensis Stuckenberg of Boll
?C. minima Rodríguez

- C.* (?) sp. of Rodríguez
Campophyllum? obliquum Fomichev of Rodríguez
- Genus *Fomichevella* Fedorowski, 1975
Caninia loisensis Boll
C. ilazoensis Boll
C. frankenfeldi Boll
C. pandoensis Boll
Skoleckophyllum triseptatum Boll
Fomichevella sotoi Rodríguez
- Genus *Siphonodendron* McCoy, 1849
 ?*Lithostrotion savagei* Boll
Nemistium liebanense Rodríguez
N. (?) sp. of Rodríguez
- Genus *Stylostrotion* Chi, 1935
Lithostrotion reticulatum (Fomichev) of de Groot and Rodríguez
- Genus «*Diphyphyllum*» Lonsdale, 1845
 ?*Diphyphyllum* cf. *multicystatum* Yu of Boll
C. aff. furcatum Thomson of Boll
 ?*Kullmannophyllum triolloense* Boll
- Genus *Tschussovskenia* Dobrolyubova, 1936
 ?*Lithostrotion irregulare* Phillips of Boll
- Genus «*Thysanophyllum*» Nicholson and Thomson, 1876
Stylastraea (Thysanophyllum) trimorpha de Groot
- Genus *Stylastraea* Lonsdale, 1845
Lithostrotion trimorphum de Groot
- Genus *Arachnastraea* Yabe and Hayasaka, 1916
Arachnastraea molli (Stuckenberg) of Boll
A. molli (Stuckenberg) var. *delicata* de Groot
A. molli dilatata de Groot
A. orboensis de Groot
- Genus *Amandophyllum* Heritsch, 1941
 ?*Dibunophyllum bipartitum cantabricum* Boll
 ?*D. bolli* Rodríguez
- Genus *Axophyllum* Milne-Edwards and Haime, 1850
 ?*Carcinophyllum* (?) sp. of de Groot
Axophyllum lonsdaleiforme Salée of Rodríguez
- Genus *Actinocyathus* d'Orbigny, 1849
Lonsdaleia floriformis crassiconus (McCoy) of Boll
- Genus *Semenophyllum* Rodríguez, 1984
 ?*Dorlodotia kionophylloides* Boll
Semenophyllum ilcense Rodríguez
- Genus *Gangamophyllum* Gorsky, 1938
 ?*Gangamophyllum winklerprinsi* Boll
- Genus *Lonsdaleia* McCoy, 1849
Lonsdaleia reutheri Boll
- Genus *Petalaxis* Milne-Edwards and Haime, 1852
Lithostrotionella celadensis de Groot
L. maccoyana Milne-Edwards and Haime) of de Groot
L. maccoyana (Milne-Edwards and Haime) forma *major* de Groot
L. sexangula de Groot
L. monocyclica de Groot
L. orboensis de Groot
L. stylaxis (Trautschold) of Boll
L. (Hillia) wagneri de Groot
L. (H.) perapertuensis de Groot
L. (H.) radians de Groot
L. (H.) intermedia de Groot
L. (H.) santaemariae de Groot
L. (H.) cantabrica de Groot
Petalaxis penduelensis Rodríguez
- Genus *Cystolonsdaleia* Fomichev, 1953
Lonsdaleia portlocki (Stuckenberg) *densiconus* de Groot = *Cystolonsdaleia portlocki* (Stuckenberg) of Rodríguez
- Genus *Ivanovia* Dobrolyubova, 1935
Ivanovia freieslebeni (Stuckenberg) of de Groot
 ?*I. humboldti* (Stuckenberg) of Boll
 ?*I. rhopaloides* Boll
I. podolskiensis Dobrolyubova of Boll and Rodríguez
I. cystiseptata Fomichev of Boll
I. tricyclica Boll
- Genus *Lytvophyllum* Dobrolyubova, 1941
 ?*Dorlodotia schoenembergi* Boll
 ?*D. rosae* Boll
- Genus *Amygdalophylloides* Dobrolyubova and Kabakovich, 1948
Amygdalophylloides ivanovi (Dobrolyubova) of Rodríguez
A. liebanensis Rodríguez
 ?*A. degrootae* Rodríguez = *A. ivanovi* (Dobrolyubova) of de Groot
A. sp. of Rodríguez
- Genus *Axolithophyllum* Fomichev, 1953
Carcinophyllum (Axolithophyllum) quiringi (Weissermel) of de Groot = *Axophyllum quiringi* of Rodríguez
C. (A.) quiringi forma *major* de Groot
 ?*C. (A.) aff. cylindricum* (Dobrolyubova and Kabakovich) of de Groot
Kionophyllum cavum ondulatum Boll
Axolithophyllum hontoriense Rodríguez
- Genus *Kionophyllum* Chi, 1931
Carcinophyllum wagneri de Groot
Kionophyllum cavum dibunum (Chi) of Boll = *K. dibunum* (Chi) of Rodríguez
K. cavum lamellosum Boll
K. agujasense agujasense Boll
K. agujasense variabile Boll
K. grootae Boll
K. extremum Boll
K. flexuosum (Dobrolyubova) of Boll
K. variabile Rodríguez
K. cosgayense Rodríguez
K. sp. of Rodríguez

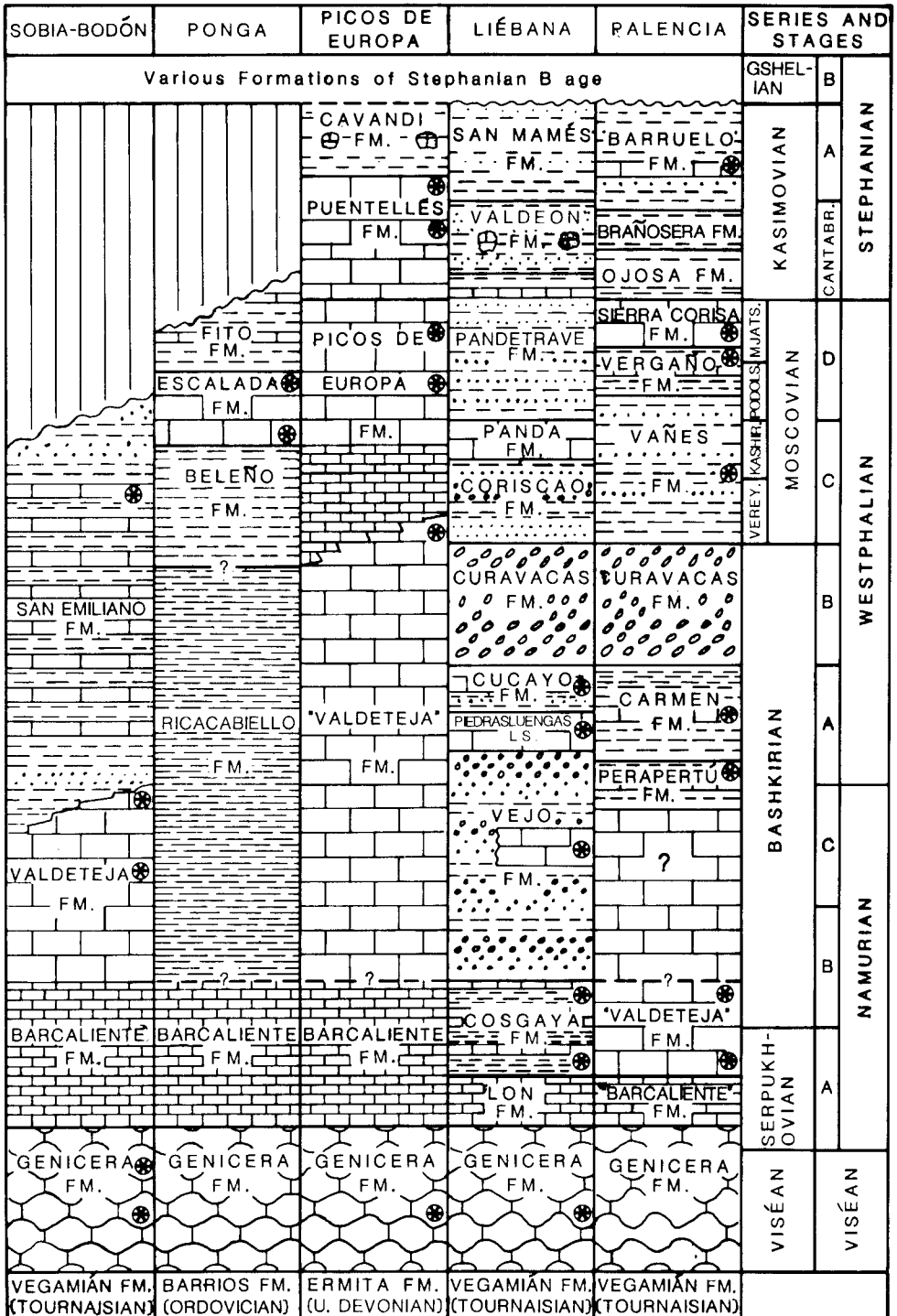


Fig. 2.—Correlation of stratigraphic units in the Cantabrian Mountains. Coral symbols indicate positions of corals collected in this study (corals are also known from some other positions.) Ages of rocks determined mainly by fusulinids; some ages determined by conodonts and goniatites.

- Genus *Lonsdaleoides* Heritsch, 1936
Lonsdaleoides hispanicus de Groot
 Genus *Geyeronaotia* Rodríguez, 1984
Geyeronaotia hispanica Rodríguez
 Genus *Koninckocarinia* Dobrolyubova, 1937
Koninckocarinia concinna de Groot
K. aff. flexuosa Dobrolyubova of Rodríguez
K. (?) sp. of Rodríguez

The stratigraphic setting of the corals (Fig. 2) is taken largely from studies by Martínez-García (1981), Truyols (1983), Sánchez de Posada & Truyols (1983), Martínez-García *et al.* (1983), with some revisions by Rodríguez and Kullman. Ages of the formations were determined mainly by fusulinids and, to a lesser extent, by conodonts and goniatites. Correlations of Carboniferous stages and series follow Fedorowski (1981) in order to utilize his data for biogeographic comparisons.

I

BIOSTRATIGRAPHIC ZONATION

Corals occur in limestones at many levels throughout most of the Carboniferous sequence of the Cantabrian Mountains (Fig. 2). Although corals have not been found in the Tournaisian or in the youngest late Carboniferous, their distribution indicates significant potential for the age determination and correlation of the Carboniferous rocks. Corals are particularly useful for field studies because their visibility permits easy discovery, and most of the genera and some of the species can be identified in the field with a hand lens; in contrast, microfossils are difficult to find and require expensive and time-consuming laboratory preparation for identification and biostratigraphic analysis.

For maximum biochronometric resolution, a coral time scale must first be constructed by determining the ranges of coral taxa with respect to a biostratigraphic framework established on other fossils more useful for worldwide correlation, such as the foraminifera, conodonts, and goniatites (e.g., Sando *et al.* 1969). When this has been done, corals can be used independently, or in conjunction with other fossils, for precise dating and correlation of the rocks (e.g. Sando and Bamber, 1984, and in press).

In the preliminary phase of developing a coral time scale or zonation, the precision of the coral scale can be no better than the precision of the zonal framework based on other fossils. In the Carboniferous of the Cantabrian Mountains, biostratigraphic resolution determined by fusulinids and conodonts is sensitive only to stage-level discrimination. Thus, ranges of coral genera (Fig. 3) can be expressed generally in terms no finer than biostratigraphic stages. However, even this rather crude scale yields data useful for current biostratigraphic work. Twenty-nine genera are known only from one series or stage: *Tachylasma* in the Viséan; *Actinocyathus*, *Amandophyllum*, *Gangamophyllum?*, *Kizilia*, *Lonsdaleia*, *Siphonodendron*, and *Plerophyllum* in Namurian A; *Tschussovskenia?*, in Namurian C; *Asturiphyllum*, *Pseudoamygdalophyllum*, *Stylastraea*, and «*Thysanophyllum*» in Westphalian A; *Slimoniphyllum?* in Westphalian C; *Amplexizaphrentis*, *Arachnolasma?*, *Bothroclisia*, *Bradyphyllum*, *Cystolonsdaleia*, *Euryphyllum*, *Hapsiphyllum?*, *Lonsdaleoides*, new genus aff. *Calophyllum*, and *Sochkineophyllum* in Westphalian D; and *Asserculinia*, *Geyeronaotia*, *Lophocarinophyllum*, *Sestrophyllum*, and *Verbeekella* in Cantabrian-Stephanian A. An additional 25 genera are not known to occur below a particular stratigraphic level: *Cyathaxonia*, *Rotiphyllum*, and *Ufimia* unknown below Viséan; *Axophyllum*, *Caninostroton*, *Lytvophyllum*, and *Semenophyllum* unknown below Namurian A; *Fomichevella* and *Kionophyllum* unknown below Namurian B; *Allotropiophyllum* unknown below Namurian C; *Amplexus*, *Amygdalophylloides*, *Axolithophyllum*, *Duplophyllum*, *Koninckocarinia*, *Petalaxis*, *Pseudozaphrentoides*, *Spirophyllum*, and *Stylostroton* unknown below Westphalian A; *Arachnastraea*, *Corwenia*, *Ivanovia*, *Lophophyllidium*, and *Neokoninckophyllum* unknown below Westphalian C; and *Amplexocarinia* and *Bothrophyllum* unknown below Westphalian D. An additional 16 genera are not known above a particular stratigraphic level: *Lytvophyllum* unknown above Namurian B; *Axophyllum* unknown above Westphalian A; *Caninostroton*, *Fomichevella*, *Pseudozaphrentoides*, *Semenophyllum*, *Spirophyllum*, and *Stylostroton* unknown above Westphalian C; and *Kionophyllum*, *Amigdalophylloides*, *Axolithophyllum*, *Koninckocarinia*, *Petalaxis*, *Arachnastraea*,

CARBONIFEROUS (PART)								SYSTEM	
VISÉAN	NAMURIAN			WESTPHALIAN				CANTABRIAN-STEPHANIAN A	SERIES
	A	B	C	A	B	C	D		STAGE
								<i>Cyathaxonia</i>	
								<i>Rotiphyllum</i>	
								<i>Tachyasma</i>	
								<i>Ufilmia?</i>	
								<i>Actinocyathus</i>	
								<i>Amandophyllum</i>	
								<i>Axophyllum?</i>	
								<i>Caninostrotion</i>	
								<i>"Diphyphyllum"</i>	
								<i>Gangamophyllum?</i>	
								<i>Kizilla</i>	
								<i>Lonsdaleia</i>	
								<i>Lytvophyllum</i>	
								<i>Pterophyllum</i>	
								<i>Semenophyllum</i>	
								<i>Siphonodendron</i>	
								<i>Fomichevelia</i>	
								<i>Klonophyllum</i>	
								<i>Allotropophyllum</i>	
								<i>Tschussovskenia?</i>	
								<i>Amplexus</i>	
								<i>Amygdalophylloides</i>	
								<i>Asturiphyllum</i>	
								<i>Axolithophyllum</i>	
								<i>Duplophyllum</i>	
								<i>Koninckocarinia</i>	
								<i>Petalaxis</i>	
								<i>Pseudoamygdalophyllum</i>	
								<i>Pseudozaphrentoides</i>	
								<i>Splrophyllum</i>	
								<i>Stylastraea</i>	
								<i>Stylostrotion</i>	
								<i>"Thysenophyllum"</i>	
								<i>Arachnastraea</i>	
								<i>Corwenia</i>	
								<i>Ivanovia</i>	
								<i>Lophophyllidium</i>	
								<i>Neokoninckophyllum</i>	
								<i>Silmoniphyllum?</i>	
								<i>Amplexizaphrentis</i>	
								<i>Amplexocarinia</i>	
								<i>Arachnolesma?</i>	
								<i>Bothroclisia</i>	
								<i>Bothrophyllum</i>	
								<i>Bradyphyllum</i>	
								<i>Cystolonsdaleia</i>	
								<i>Euryphyllum?</i>	
								<i>Hapsiphyllum?</i>	
								<i>Lonsdaleoides</i>	
								<i>N. gen. aff. Calophyllum</i>	
								<i>Sochkineophyllum</i>	
								<i>Asserculinia</i>	
								<i>Geyeronautia</i>	
								<i>Lophocarinophyllum</i>	
								<i>Sestrophyllum</i>	
								<i>Verbeekella?</i>	

Fig. 3.—Stratigraphic ranges of coral genera in the Carboniferous of the Cantabrian Mountains.

Ivanovia, and *Neokoninckophyllum* unknown above Westphalian D.

Many of these genera have longer strati-

graphic ranges in other parts of the world. This should not deter their use for biostratigraphy in the area studied because the

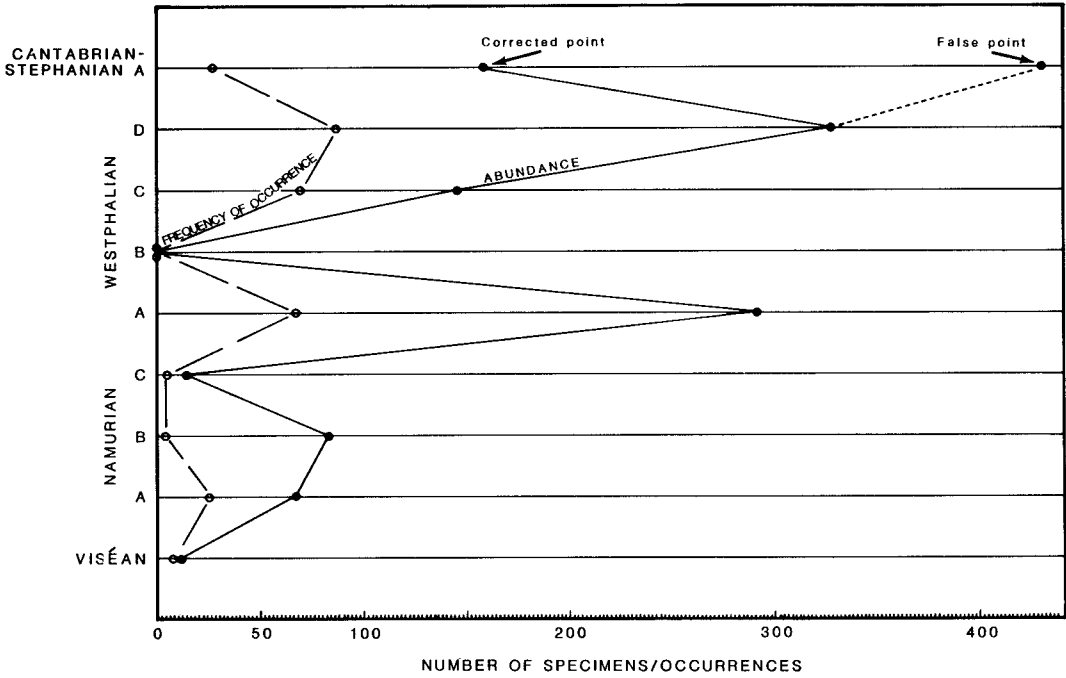


Fig. 4.—Temporal variation in abundance (number of specimens) and frequency of occurrence (number of localities) of coral genera in the Carboniferous of the Cantabrian Mountains.

amount of data available and the size of the area studied are large enough to insure a high probability that the ranges are locally valid. Of course, any zonation is only a working hypothesis that must be constantly tested whenever opportunities for testing against other scales are presented.

Future biostratigraphic work on the Carboniferous corals of the Cantabrian Mountains should be directed toward construction of a finer resolution coral time scale independent of series and stage boundaries. This can be accomplished by careful documentation of generic and specific ranges within many stratigraphic sections correlated by means of independent biostratigraphic and lithostratigraphic datum planes. Joint sampling programs would be very helpful in this work. Boundaries of zoogeographic provinces or subprovinces, determined by means of similarity analysis (e.g., Sando et al. 1975, 1977), are useful for evaluating the effective areal application of the coral zonation.

SIGNIFICANCE OF TEMPORAL VARIATIONS IN CORAL ABUNDANCE AND DIVERSITY CHRONOLOGY OF ABUNDANCE, FREQUENCY, AND DIVERSITY

Interesting patterns become evident when data on coral abundance, frequency of occurrence, generic and specific diversity, influx of new genera, and morphotype diversity are analyzed in terms of successive time periods in the Carboniferous of the Cantabrian Mountains. A simple graph of abundance (Fig. 4) shows successive peaks in Namurian B, Westphalian A, and Westphalian D, with intervening minima in the Viséan, Namurian C, Westphalian B, and Cantabrian-Stephanian A. Abundance data for the Cantabrian-Stephanian A were adjusted by eliminating data from one locality, where an excessive number of specimens of one species were collected because of easy access to the locality. Note that each successive peak is higher than the previous one and that the Westphalian peaks

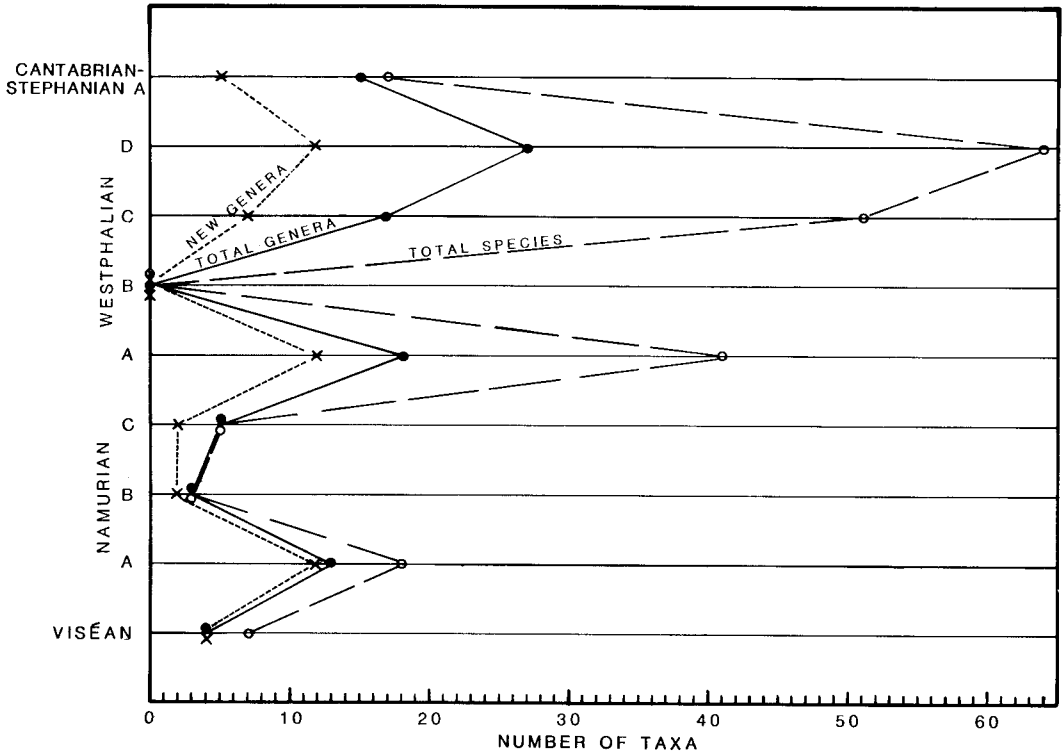


Fig. 5.—Temporal variation in generic diversity (number of genera), specific diversity (number of species), and new genera (number of genera new to the area) in corals from the Carboniferous of the Cantabrian Mountains.

are much higher than the Namurian one. The graph of frequency of occurrence (Fig. 4) follows nearly the same pattern as that for abundance, but the Namurian peak is in Namurian A.

Graphs of specific and generic diversity (Fig. 5) show patterns very similar to those of abundance and frequency of occurrence. Here again we see three successive peaks in Namurian A, Westphalian A, and Westphalian D and intervening minima in the Viséan, Namurian B, Westphalian B, and Cantabrian-Stephanian A. The peaks are again progressively higher in successive time periods. A graph of the appearance of genera new to the area (Fig. 5) also follows essentially the same pattern, but the peaks maintain constant values in successive time periods.

Graphs of temporal variations in the diversity of four coral morphotypes (Fig. 6) show significant deviations from the patterns derived from the data described above. Simple

solitary corals (without dissepiments) show a peak diversity in the Viséan instead of the Namurian, but then peak again in Westphalian A and D, coincident with other data. Dissepimented solitary corals show diversity peaks in Namurian A, Westphalian A, and Westphalian D, similar to other data. Fasciculate (branching) colonial corals show diversity peaks in Namurian A, Westphalian A, and Westphalian D, also similar to the peaks of other data. Massive colonial corals, on the other hand, show a peak in Namurian A, equivalent peaks in Namurian C and Westphalian A, and then a peak in Westphalian C. In spite of these deviations, there is a general shift toward higher peaks in successive time periods of all morphotypes except the dissepimented solitary corals, which have their greatest diversity in Westphalian A.

In Figure 7, smoothed curves are plotted from the graphed coral data and compared to curves depicting temporal variations in six en-

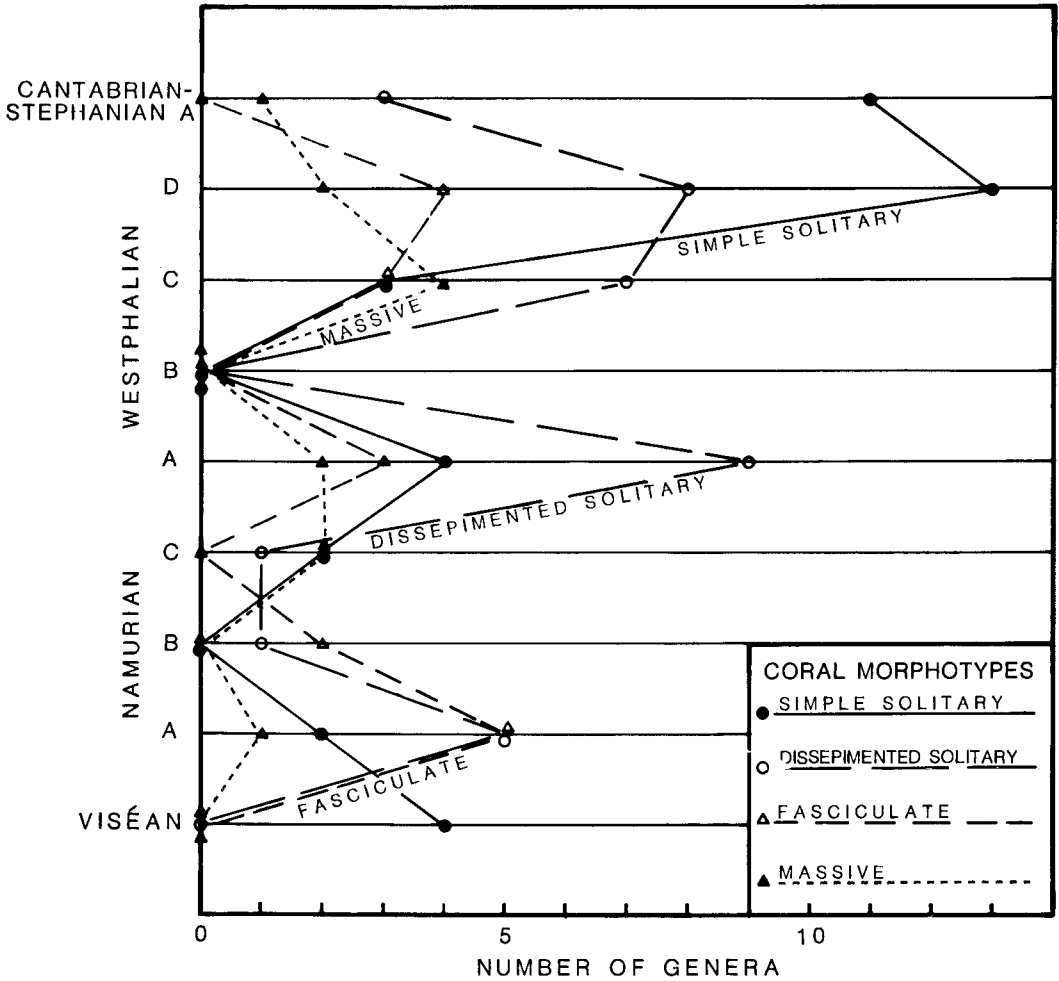
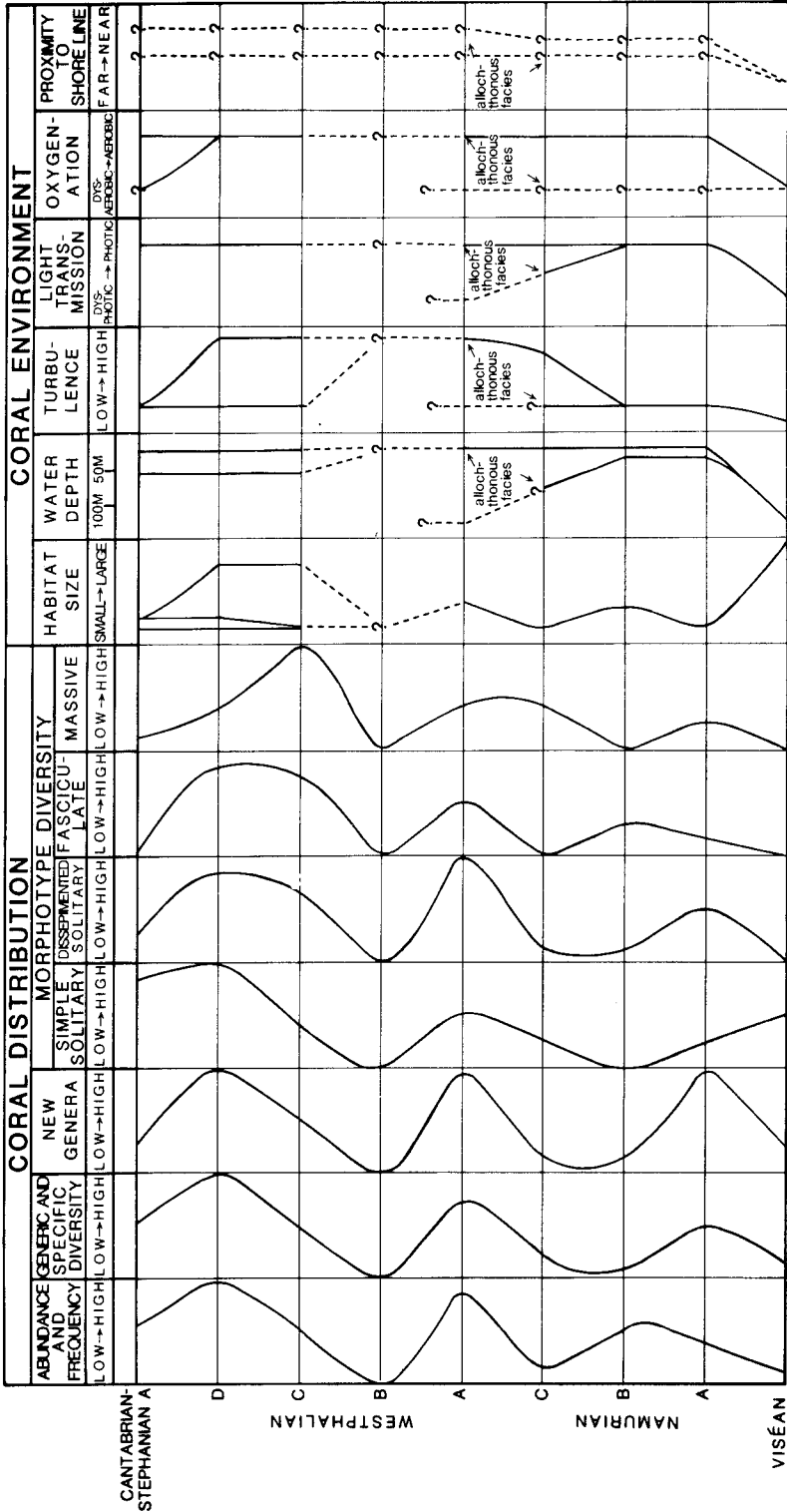


Fig. 6.—Temporal variation in morphotype diversity (number of genera) in corals from the Carboniferous of the Cantabrian Mountains.

Environmental parameters derived by analysis of the grain size, colour, bedding thickness, chert content, areal distribution, flora, and fauna of carbonate rocks from which the corals were collected. The biota of all coralliferous habitats indicates normal marine salinities. Habitat size was estimated from the known areal distribution of the coralliferous rocks. Water depth was estimated mainly from the occurrence of red, green, and blue green algae, using the criteria of Sando (1981); abundance of conodonts (deep water), shelly benthos (shallow water), goniatites (deep water), and fusulinids (shallow water)

were used as accessory depth criteria. Turbulence was estimated mainly from grain size, bedding thickness, and nature of the cement in coarser grained rocks (spar versus mud). Light transmission (photic versus dysphotic) was estimated from the occurrence of algal types (see above). Oxygenation (aerobic versus dysaerobic) was estimated from various lithic and biotic parameters. Proximity to shoreline is a parameter that was not readily estimable on available data, but the presence of coal in associated rocks in some time periods, and the general tenor of other parameters, were used where possible.



ECOLOGIC HISTORY OF CORAL FAUNA

Comparison of the data on coral distribution with environmental parameters (Fig. 7) permits a historical analysis of the development of the coral fauna. The Viséan habitat (Genicera or Alba Formation) was a large area of deep, quiet, dysphotic, dysaerobic water located far from shore. The coral fauna, exclusively simple solitary forms, was characterized by low generic and specific diversity and low abundance and frequency of occurrence.

Namurian A marked the first appearance of shallow-water environments, characterized by small areas of nearshore marine habitats less than 50 m deep having low turbulence and good light transmission. Two shallow-water habitats appeared at this time, one characterized by probable dysaerobic conditions (Cosgaya Formation) and the other by aerobic conditions (Valdeteja Formation). Coral abundance and frequency increased, and the influx of new genera into the area caused a peak in generic and specific diversity. The diversity of the simple solitary forms declined, but complex solitary and colonial corals entered the area for the first time and dominated the available ecospace. Thus, the first expansion of the coral fauna was associated with the appearance of shallow-water habitats characterized by good aeration and light transmission, and restriction of the size of the ecospace.

Namurian B was characterized by a continuation of the coral environments of Namurian A (Cosgaya and Valdeteja Formations), but the size of the ecospace expanded slightly. Coral abundance and frequency was high in Namurian B, but generic and specific diversity declined, coincident with a decline in the influx of new genera. The coral fauna was composed exclusively of complex solitary and fasciculate forms. The restricted diversity of the coral fauna may be related to the presence of non-coralliferous terrigenous facies (Ricacabiello Formation) and turbidite facies (Vejo Formation) in the area.

Namurian C was marked by a continuation of a shallow-water coralline environment (Valdeteja Formation) and the presence of a probably deeper environment represented only by large limestone blocks in a turbidite facies (Vejo Formation). Habitat size was probably slightly diminished. Coral abundance and frequency, generic and specific diversity, and number of new genera are all quite low. Fasciculate corals are absent, complex solitary corals increased slightly in abundance, and massive corals reappeared. The continued diminution of the coral fauna was probably related to similar factors that operated during Namurian B.

In Westphalian A, corals are rare in the Carmen, Perapertu, and Cucayo Formations, representing a deep-water environment, but are common in allochthonous debris flows and megabreccias formed in shallow-water. Corals are also common in shallow-water sediments of the Piedrasluengas Formation. Westphalian A was marked by a significant areal expansion of the shallow-water habitat. Coral abundance and frequency, generic and specific diversity, and the influx of new genera all show peak levels during this time. The peaks for abundance and frequency and generic and specific diversity are all higher than the first peaks observed in Namurian A-B, whereas the peak for new genera is about the same as the Namurian A peak. All coral morphotypes show high diversities. This expansion of the coral fauna was related to expansion and diversification of favorable shallow-water habitats and concurrent diminution of turbidite production.

No corals were found in strata dated as Westphalian B, which are characterized by continental conglomerates (Curavacas Formation), marine shale (Ricacabiello Formation), interbedded marine shale and limestone (San Emiliano Formation), and shallow-water limestone (Valdeteja Formation). Actually, corals may be present in the Valdeteja and San Emiliano Formations at this time, but may not be recognized because of difficulties in dating these rocks. However, the reality of the diminution of the coral fauna is supported by the predominance of facies representing environments unfavorable for coral growth. This period coincides with the Paleozoic tectonic phase.

←
 Fig. 7.—Correlation of temporal variations in coral distribution with temporal variations in coral environment in the Carboniferous of the Cantabrian Mountains. See text for explanation.

Westphalian C (upper San Emiliano, uppermost Valdeteja, and lower Escalada Formations) and Westphalian D (upper Escalada, Picos de Europa, Vergaño, and Sierra Corisa Formations) were characterized by a great expansion and diversification of shallow-water coralline environments and a corresponding renaissance of the coral fauna, which reached its greatest peak in Westphalian D.

Cantabrian-Stephanian A was a time of marked reduction of habitat size. Nearshore shallow-water habitats were available (Puentellés and Barruelo Formations), but were dominated by factors, such as poorer oxygenation and greater supply of terrigenous sediment, unfavorable to corals. All the coral distribution parameters declined accordingly. This period coincides with the Leonian and Asturian tectonic phases.

ANALYSIS

Very few of the Carboniferous coral genera in the Cantabrian Mountains originated certainly in that area; only four of the 56 genera recognized in the total fauna are endemic. Thus, the variations in abundance and diversity probably represent invasions and retreats of the coral fauna rather than simple evolutionary responses within a closed system.

The overall pattern of deposition from Viséan to Stephanian time in the Cantabrian Mountains is one of gradual progressive regression (Sánchez de la Torre and others, 1983). The general response of the corals to this pattern is an increase in abundance and diversity. This correlation of an increase in abundance and diversity with regression fits the model proposed by Kauffman (1977) to explain variations in evolutionary rates of Cretaceous benthonic organisms. However, cyclical variation in Carboniferous coral abundance and diversity within this general pattern are not related in a simple way to regressive movements of the sea in the Cantabrian Mountains. Expansions of the coral fauna appear to be related to increases in habitat size and spatial heterogeneity within the general pattern of regression. This suggests that a simple correlation of diversity with increased environmental stress due to reduced ecospace (Kauffman, 1977) may be modified in a setting where variations in diversity depend mainly on faunal invasions and retreats.

Another interesting trend observed for the Spanish Carboniferous coral fauna is its first appearance in a deep-water environment in the Viséan and its migration to generally shallow-water environments later in Carboniferous time. A similar pattern was described by Sando (1981) in the Mississippian (Lower Carboniferous) of the Western Interior Province of the conterminous USA, where corals first appeared in deep water in the lower Tournaisian and then migrated to generally shallow-water environments during the upper Tournaisian, Viséan, and lower Namurian. The development of the western interior USA fauna also seems to have been characterized by a generally progressive increase in diversity and abundance, but a detailed analysis of these factors has not been made. If similar patterns could be established for Carboniferous coral faunas in other parts of the world, they might form the basis for a general correlation with world-wide tectonic and depositional events in the Carboniferous.

II ZOOGEOGRAPHIC RELATIONS WITH NORTH AMERICA

Previous analyses of the zoogeographic affinities of the Carboniferous rugose corals of northern Spain stressed strong similarities with coeval faunas in North Africa, western Europe, Yugoslavia, the Donets and Moscow basins and Middle Asia of the USSR, China, and Japan (Fedorowski, 1977, 1981; Rodríguez, 1984a, b). Fedorowski used qualitative techniques to define coral provinces and sub-provinces in the Carboniferous of the world. The Spanish corals were included in Fedorowski's (1981) Western European Province during the Viséan and Serpukhovian (Namurian A) and were placed in his gigantic Mediterranean Province during the Bashkirian (Namurian (B-C and Westphalian A-B), Moscovian (Westphalian C-D), and Kasimovian (Cantabrian-Stephanian A-B). Fedorowski's (1977) earlier paleogeographic maps showed good connections between Spain and North America, but his later (1981) maps suggested that such close connections were unlikely. Rodríguez (1984b) made a preliminary analysis of a part of the Carboniferous coral fauna from the Cantabrian Mountains and used endemism and similarity indices of Sando et al.

TABLE I.—Distribution of rugose coral genera in North America, northern Spain, and Donets basin during the Serpukhovian.

E = endemic genus. ? = uncertain identification.

Genera	NORTH AMERICA				Northern Spain	Donets basin
	Pacific Coast	Western interior	South-eastern	Maritime		
<i>Actinocyathus</i>		X	X		X	X
<i>Adamanophyllum</i>						X
<i>Amandophyllum</i>					X	
<i>Amplexizaphrentis</i>		X	X	X		X
<i>Amplexus</i>		X	X			X
<i>Aulina</i>						X
<i>Axophyllum</i>					X	X
<i>Barytichisma</i>		X				
<i>Bothrophyllum</i>						X
<i>Caninia</i>				X		
<i>Caninostrotion</i>			X		X	
<i>Claviphyllum</i>						X
<i>Clisiophyllum</i>				?		?
<i>Corwenia</i>				X		
<i>Dibunophyllum</i>	X			X		X
« <i>Diphyphyllum</i> »				X	X	X
<i>Gangamophyllum</i>					?	X
<i>Hexaphyllia</i>	X					
<i>Kinkaidia</i>			E			
<i>Kizilia</i>					X	
<i>Koninckophyllum</i>			X	X		
<i>Lithostrotion</i>	X					X
<i>Lonsdaleia</i>			X	X	X	
<i>Lophophyllidium</i>			X			
<i>Lytvophyllum</i>					?	X
<i>Neokoninckophyllum</i>						X
<i>Nervophyllum</i>						X
<i>Palaeosmilla</i>						X
<i>Palastraea</i>			X			
<i>Petalaxis</i>		?				
<i>Pterophyllum</i>					X	
<i>Pseudozaphrentoides</i>						X
<i>Rozkowskia</i>						X
<i>Semenophyllum</i>					E	
<i>Siphonodendron</i>	X			X	X	X
<i>Siphonophyllia</i>	X	X	X			
<i>Spirophyllum</i>						X
« <i>Thysanophyllum</i> »				X		
<i>Turbinatocania</i>		?	?			
<i>Ufimia</i>						X

(1977) to augment qualitative comparisons with other areas. Although Rodríguez stressed the obvious communications with other parts of Fedorowski's Mediterranean Province he also suggested that North American inf-

luences were important during the Viséan and Serpukhovian.

Consistent taxonomic concepts are vital to any meaningful analysis of zoogeographic relationships. In practice, this means that work-

ers malting the analysis should be intimately familiar with the taxa of all regions studied. Accordingly, one of the aims of the present study was to examine critically the relationships of the Spanish faunas to North American faunas. Previous lack of useful data on the distribution of coral genera in the Pennsylvanian of North America was a deterrent to meaningful analysis. Compilations of such data by Sando (1984, and unpublished) provided a good basis for consistent analysis.

The present study utilizes endemism (EI) and similarity (SI) indices (Sando et al. 1975, 1977) to quantify relationships of the Spanish Carboniferous rugose corals with those of North America. Time intervals used in the comparison are the ones used by Fedorowski (1981), so that inferred paleogeographic relationships can be compared using the paleogeographic maps constructed by Fedorowski. Quantitative similarity comparisons are also made with the Donets basin coral faunas in order to have a base line for evaluating similarities with North American faunas. Fedorowski's (1981) taxonomic characterization of the Donets basin faunas, with minor emendations, was used to provide data for this analysis.

CHRONOLOGY OF ENDEMISM AND SIMILARITY

Viséan.—The Spanish Viséan coral fauna is so impoverished, probably because of its deep-water habitat, that comparisons with other regions are virtually impossible. Only four genera (*Cyathaxonia*, *Rotiphyllum*, *Tachylasma*, *Ufimia?*) are known, and all are cosmopolitan (EI-O), making similarity indices meaningless. All but *Tachylasma* are known from the Viséan in North America (Western Interior Province), where they are interpreted to have occurred predominantly in deep water (more than 100 m, see Sando, 1981). The Spanish Viséan corals seem to have been part of a widespread, freely circulating deep-water fauna.

Serpukhovian (Namurian A).—The distribution of North American corals in the Serpukhovian (Table I) is given in terms of provinces established by Sando et al. (1975, 1977). Corals of this age are so poorly known from the Alaskan Province that this area was omitted from the analysis. The Maritime Province in

Nova Scotia was included in the Western European Province by Fedorowski (1981) because of its strong relationships with the faunas of Great Britain and France.

Rugose coral faunas of the Pacific Coast, Western Interior, and Maritime Provinces of North America were cosmopolitan during the Serpukhovian (EI-0), but the fauna of the Southeastern Province was characterized by high edemism (EI-18). The Spanish fauna was only moderately endemic (EI-8).

Similarity analysis indicates poor gene flow between Spain and all the North American provinces during the Serpukhovian. The Pacific Coast (SI-13) and Western Interior (SI-11) Provinces show the lowest similarity, whereas the Southeastern (SI-26) and Maritime (SI-27) Provinces have higher similarities. For comparison, the Donets basin fauna shows moderate similarity (SI-37).

Bashkirian.—Bashkirian rugose coral faunas are too poorly known from Canada and Alaska for reliable comparison with the Spanish fauna. In the conterminous USA, data on generic compositions of the faunas are limited and have not been analyzed by zoogeographic provinces like those proposed for the Lower Carboniferous. For convenience, comparisons (Table II) are made in terms of three operational areas: the western interior region (Montana, North Dakota, South Dakota, Idaho, Wyoming, Nevada, Utah, Colorado, Arizona, New Mexico, and California), the midcontinent region (Texas, Oklahoma, Arkansas, Kansas, Nebraska, Iowa, Missouri, and Indiana), and the eastern region (Michigan, Illinois, Ohio, Kentucky, West Virginia, and Pennsylvania). Information on the western interior region is based on data from Sando (1984 and 1985), whereas information on the midcontinent and eastern regions was compiled almost entirely from published descriptions of nominal species. No faunal lists were used in the analysis.

Rugose corals are so rare in the eastern region of the USA during the Bashkirian, because of the paucity of favorable marine habitats, that no meaningful comparisons can be made with the Spanish fauna. The cosmopolitan genus *Lophophyllidium* may be the only genus known from this area, but even its occurrence is of uncertain age.

The midcontinent fauna was highly endem-

TABLA II.—Distribution of rugose coral genera in North America, northern Spain, and Donets basin during the Bashkirian.

E = endemic genus. ? = uncertain identification or occurrence.

Genera	NORTH AMERICA				
	Eastern USA	Midcontinent	Western interior	Northern Spain	Donets basin
<i>Allotropiophyllum</i>				?	
<i>Amandophyllum</i>		X	X		X
<i>Amplexus</i>		X	X	X	
<i>Amplexizaphrentis</i>		X	X		X
<i>Amplexocarinia</i>			X		X
<i>Amygdalophylloides</i>				X	
<i>Asturiphyllum</i>				E	
<i>Axolithophyllum</i>				X	X
<i>Axophyllum</i>				X	
<i>Barytichisma</i>		X	X		X
<i>Bradyphyllum</i>		?	X		X
<i>Bothrophyllum</i>			X		X
<i>Crataniophyllum</i>			E		
<i>Cumminsia</i>		E			
<i>Cyathaxonia</i>				X	?
<i>Cystophora</i>					X
<i>Duplophyllum</i>				?	
<i>Fomichevella</i>				X	
<i>Heintzella</i>			X		
<i>Kionophyllum</i>			?	X	
<i>Koninckocarinia</i>				X	
<i>Koninckophyllum</i>		?			
<i>Leonardophyllum</i>		E			
<i>Lophamplexus</i>		X			
<i>Lophophyllidium</i>	?	X	X		X
<i>Lophotichium</i>		E			
<i>Lytvophyllum</i>				?	X
<i>Neokoninckophyllum</i>		X	X		X
<i>Orygmophyllum</i>					X
<i>Petalaxis</i>		X	X	X	
<i>Pseudoamygdalophyllum</i>				E	
<i>Pseudozaphrentoides</i>		X	X	X	X
<i>Rotiphyllum</i>		?		X	X
<i>Rozkowskia</i>					X
<i>Sestrophyllum</i>					X
<i>Sochkineophyllum</i>		X			
<i>Spirophyllum</i>				X	X
<i>Stereocorypha</i>		E			
<i>Stylastraea</i>				X	
<i>Stylostrotion</i>				X	
« <i>Thysanophyllum</i> »				X	
<i>Tschussovskenia</i>				?	
<i>Yuanophylloides</i>					X

ic (EI-24) in contrast to the low endemism of the western interior fauna (EI-7) during the Bashkirian. The coeval Spanish fauna was moderately endemic (EI-9).

Low similarity indices between Spain and the midcontinent area (SI-21) and the western interior region (SI-23) indicate poor communication between the two areas. Similarity in-

TABLA III.—Distribution of rugose coral genera in North America, northern Spain, and the Donets basin during the Moscovian.

E = endemic genus. ? = uncertain identification.

Genera	NORTH AMERICA				
	Eastern USA	Midcontinent	Western interior	Northern Spain	Donets basin
<i>Allotropiophyllum</i>				?	
<i>Amandophyllum</i>		X	X		X
<i>Amplexizaphrentis</i>			X	X	X
<i>Amplexocarinia</i>				X	
<i>Amplexus</i>			X	X	
<i>Amygdalophylloides</i>				X	
<i>Arachnolasma</i>				X	
<i>Axolithophyllum</i>				X	X
<i>Barytichisma</i>			X		X
<i>Bradyphyllum</i>			X	X	X
<i>Bothroclisia</i>				X	
<i>Bothrophyllum</i>			X	X	X
<i>Caninostrotion</i>				?	
<i>Corwenia</i>				X	
<i>Cyathaxonia</i>				X	X
<i>Cystolonsdaleia</i>				X	X
<i>Duplophyllum</i>				X	
<i>Euryphyllum</i>				?	
<i>Fomichevella</i>				X	
<i>Gymmophyllum</i>		E			
<i>Hapsiphyllum</i>				?	
<i>Ivanovia</i>				X	X
<i>Kionophyllum</i>				X	
<i>Koninckocarinia</i>				X	
<i>Lophamplexus</i>		X	X		
<i>Lophophyllidium</i>		X	X	X	X
<i>Lonsdaleoides</i>				X	
<i>Neokoninckophyllum</i>			X	X	X
<i>Petalaxis</i>				X	X
<i>Orygmophyllum</i>					X
<i>Pseudozaphrentoides</i>			X	X	X
<i>Rotiphyllum</i>				X	X
<i>Semenophyllum</i>				E?	
<i>Sestrophyllum</i>					X
<i>Slimoniphyllum</i>				?	
<i>Sochkineophyllum</i>				X	
<i>Spirophyllum</i>				X	
<i>Stylostrotion</i>				X	X
<i>Ufimia</i>				?	

dices are even lower than for the Serpukhovian. The relationship between Spain and the Donets basin (SI-30) is only slightly better than that for North America, indicating only slightly higher gene flow.

Moscovian (Westphalian C-D).—Canada and Alaska are excluded from the similarity analy-

sis (Table III) because of poor knowledge of their rugose coral faunas. No genera are recorded from the eastern USA at this time because of unfavorable, predominantly nonmarine habitats.

Endemism indices indicate a cosmopolitan fauna in the western interior region (EI-0) and

TABLE IV.—Distribution of rugose coral genera in North America, northern Spain, and Donets basin during the Kasimovian.
E = endemic genus. ? = uncertain identification.

Genera	NORTH AMERICA				
	Eastern USA	Midcontinent	Western interior	Northern Spain	Donets basin
<i>Allotropiophyllum</i>				X	
<i>Amandophyllum</i>		X	X		
<i>Amplexizaphrentis</i>		X			
<i>Amplexocarinia</i>				X	
<i>Amplexus</i>			X	X	X
<i>Asserculinia</i>				X	
<i>Asturiphyllum</i>		X			
<i>Axolithophyllum</i>	?	X			X
<i>Bothrophyllum</i>				X	X
<i>Bradyphyllum</i>			X		
<i>Corwenia</i>		X		X	
<i>Cyathaxonia</i>				X	X
<i>Duplophyllum</i>				X	
<i>Geyronaotia</i>				E	
<i>Ivanovia</i>					X
<i>Kionophyllum</i>		X	?		
<i>Lophamplexus</i>		X	X		
<i>Lophocarinophyllum</i>				X	
<i>Lophophyllidium</i>	X	X	X	X	X
<i>Neokoninckophyllum</i>		X	X		X
<i>Orygmophyllum</i>					X
<i>Paraheritschioides</i>			E		
<i>Pseudozaphrentoides</i>		X	X		X
<i>Rotiphyllum</i>				X	X
<i>Sestrophyllum</i>				X	X
<i>Tachylasma</i>					X
<i>Ufimia</i>				?	
<i>Verbeekiella</i>				?	

a highly endemic one in the midcontinent region (EI-25). The endemism of the midcontinent coral fauna is exaggerated because of the low total number of genera known (one endemic genus in a total of four genera), the Spanish fauna was characterized by low endemism (EI-3).

The similarity of the Spanish fauna to the midcontinent fauna is low (SI-8), but similarity to the western interior fauna is moderate (SI-38). Similarity between the Spanish fauna and that of the Donets basin (SI-55) is high, indicating good gene flow.

Kasimovian (Cantabrian-Stephanian A).—Canada and Alaska are again excluded from the analysis (Table IV) because of poor knowledge of their faunas. Endemism indices show cosmopolitan faunas in the eastern and mid-

continent regions (EI-0). The western interior faunas shows moderate endemism (EI-11), whereas the Spanish fauna shows low endemism (EI-7).

Similarity indices comparing the Spanish fauna with those of the eastern USA (SI-18), midcontinent region (SI-16), and western interior (SI-17) are all low, indicating restricted communication between Spain and North America. Similarity to the Donets fauna is moderate (SI-44).

INTERPRETATION

Fedorowski (1977, 1981) presented two different paleogeographic models to explain the relationships between coral faunas in various parts of the world during the Carboniferous.

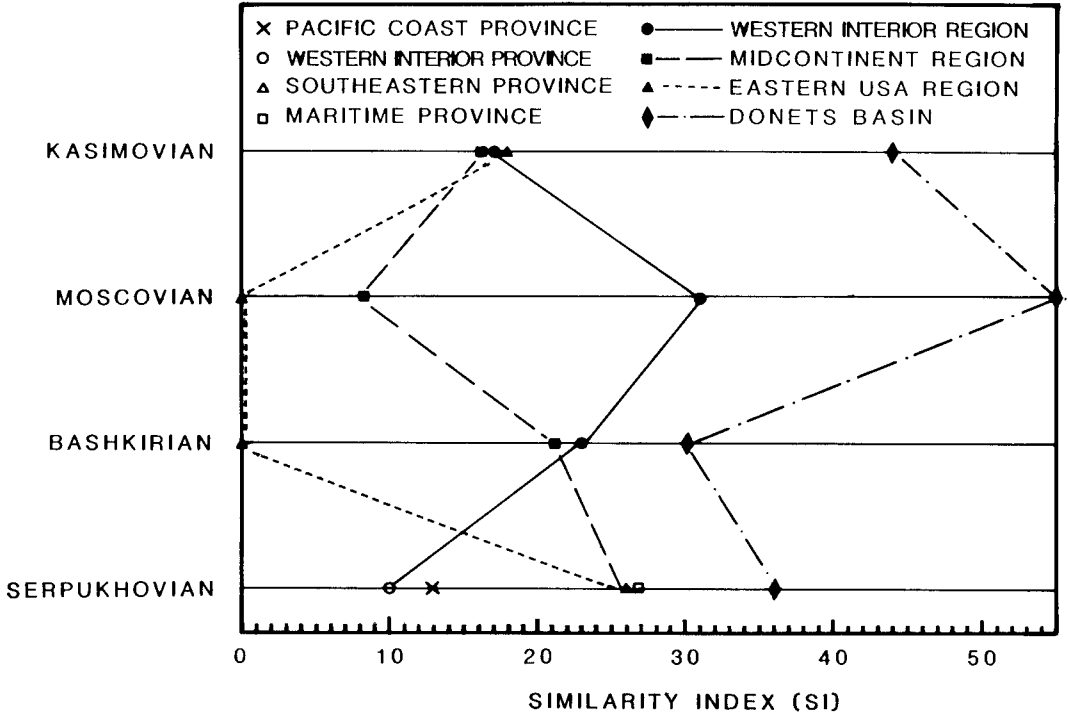


Fig. 8.—Temporal variation in similarity indices of Spanish Upper Carboniferous rugose coral faunas in comparison with coeval North American and Donets basin faunas.

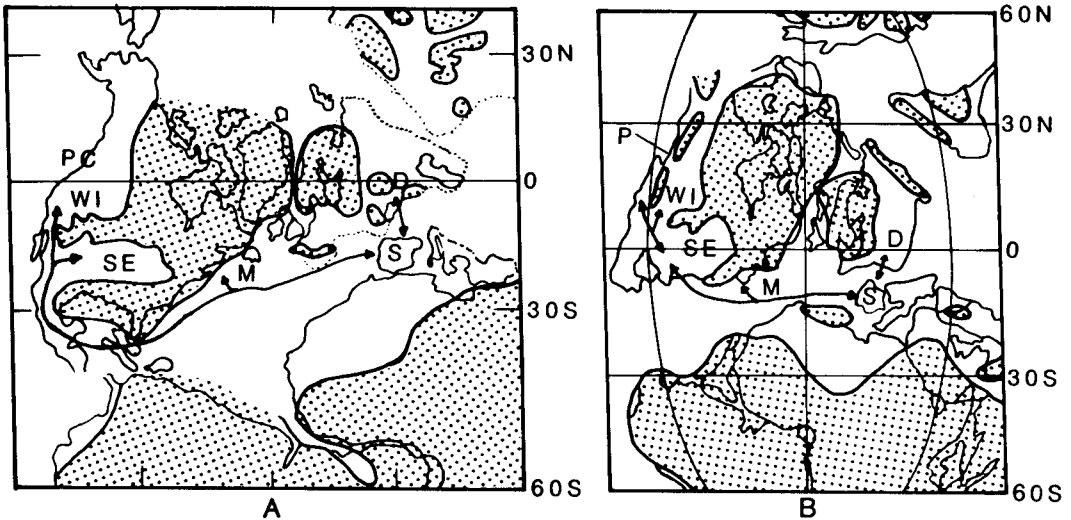


Fig. 9.—Serpukhovian paleogeography modified from Fedorowski (1977, fig. 3) (A) and (1981, fig. 2) (B), showing locations of coral habitats in Spain (S), Donets basin (D), and the Pacific Coast (PC), Western interior (WI), Southeastern (SE), and Maritime (M) Provinces of North America (Sando *et al.* 1977). Main communication routes of coral gene flow shown by arrows. Land areas stippled.

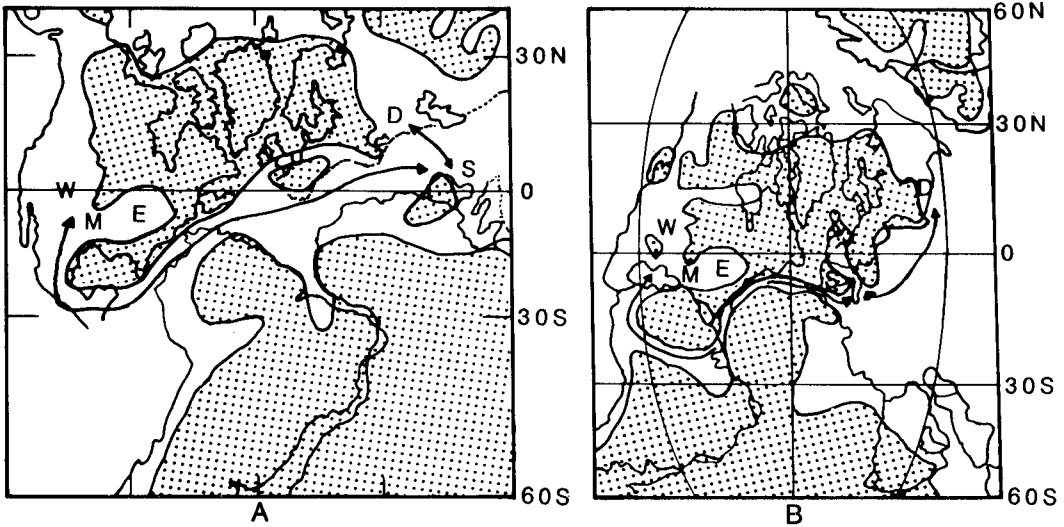


Fig. 10.—Bashkirian paleogeography modified from Fedorowski (1977, fig. 4) (A) and (1981, fig. 3) (B), showing locations coral habitats in Spain (S), Donets basin (D), and the eastern (E) midcontinent (M), and western interior (W) regions of the USA. Symbols the same as for Figure 9.

In his 1977 paper, Fedorowski based his model on plate tectonic reconstructions of Smith and others (1973), whereas in 1981, he revised his model on the basis of plate tectonic reconstructions of Scotese *et al* (1979). In the latter paper, Fedorowski (1981, p. 88) was forced to propose some revisions of the plate tectonic model because qualitative similarity comparisons of the coral faunas were not compatible with the model.

A comparison of the variation in similarity indices (Fig. 8) of the Spanish faunas with North American and Donets basin faunas provides a means of testing quantitatively Fedorowski's (1977, 1981) paleogeographic models for the Serpukhovian, Bashkirian, Moscovian, and Kasimovian time intervals (Figs. 9-12). We revised Fedorowski's maps for North America during these time intervals to show the maximum extent of marine sedimentation, based on McKee *et al.* (1975). The basic premise in this analysis is that similarities between faunas of different zoogeographic regions generally vary inversely with the migration-route distances between these regions (Sando *et al.* 1977).

Serpukhovian similarity indices suggest little choice between the two paleogeographic models (Fig. 9) for this stage. The higher similarity with the Donets basin (Fig. 8) suggests

closer proximity between Spain and that area than between Spain and North America. Progressively lower North American similarity indices suggest progressively longer migration routes to Spain for the Maritime, Southeastern, Pacific Coast, and Western Interior Provinces, respectively. Similarity indices for the Southeastern Province and Maritime Province favour the paleogeography shown in Figure 9B.

Bashkirian similarity indices (Fig. 8) again favour a closer proximity of Spain to the Donets basin, which is reflected on both paleogeographic models (Fig. 10). The reduction in Donets basin SI from the Serpukhovian is reflected in both models but is better explained by Figure 10B. Fedorowski's revision of the plate tectonic reconstruction of Scotese *et al.* (1979), postulating a connection between Spain and North America along the juncture of the African, South American, and North American plates, is strongly supported by similarity indices for the midcontinent and western interior regions. Zero similarity between Spain and the eastern region of the USA is a function of inhospitable, predominantly nonmarine habitats in the eastern region. The model of Figure 10B is preferred over that of Figure 10A because of its shorter migration route distance to the USA, if Fedorowski's re-

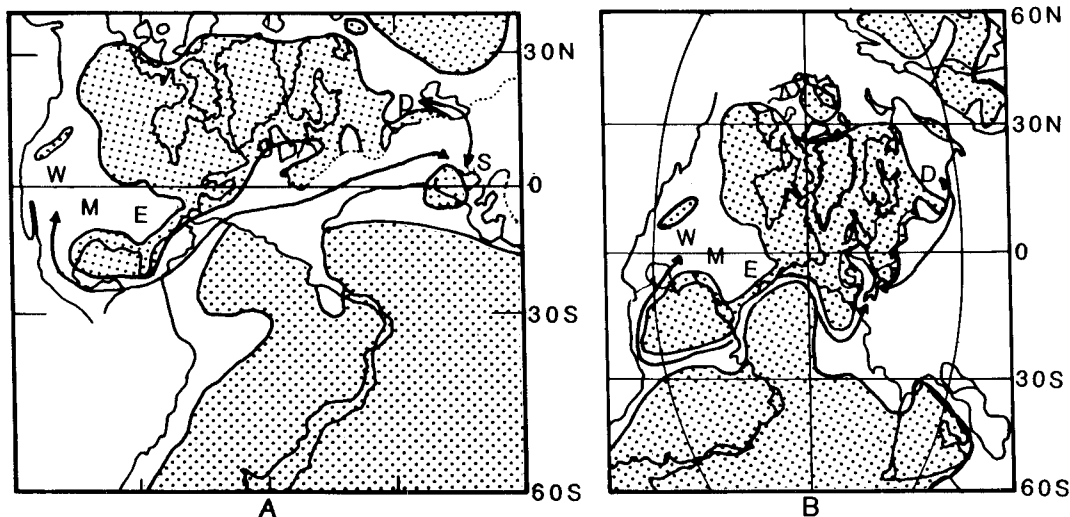


Fig. 11.—Moscovian paleogeography modified from Fedorowski (1977, fig. 5) (A) and (1981, fig. 4) (B). See Figure 10 for explanation of symbols.

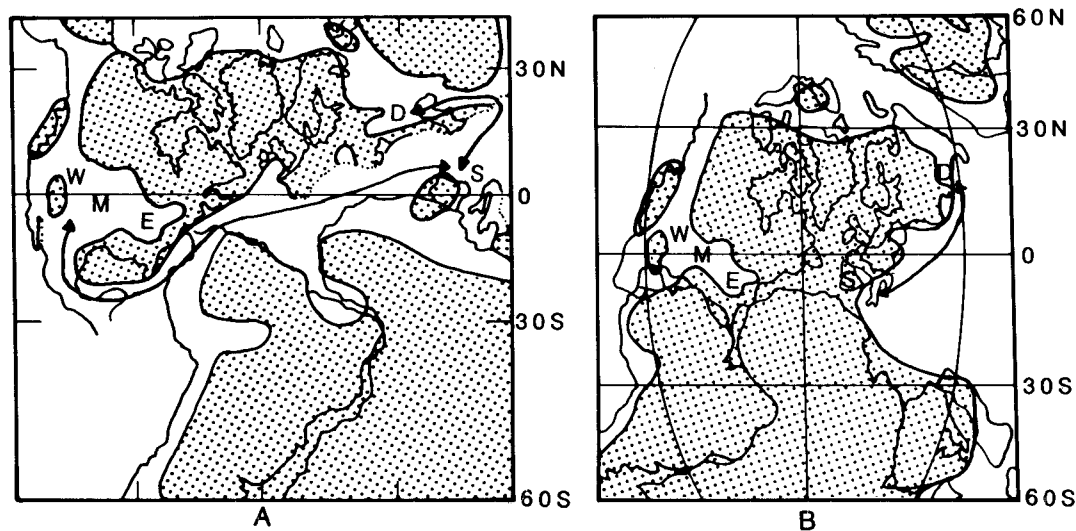


Fig. 12.—Kasimovian paleogeography modified from Fedorowski (1977, fig. 6) (A) and (1981, fig. 5) (B). See Figure 10 for explanation of symbols.

vision is accepted. Any record of this postulated seaway may have been lost by subsequent subduction.

Moscovian similarity indices (Fig. 8) show maxima for the Donets basin and the western interior region, a minimum for the midcontinent region, and zero for the eastern region. The eastern region index is again a function

of inhospitable habitats. The Donets basin and western interior maxima (higher than Bashkirian) are not explained by either models (Fig. 11), nor is the lower index for the midcontinent region. Factors such as favourable currents may have altered the simple correlation of similarity with migration route distance. The model depicted in Figure 11B

again seems more reasonable, if Fedorowski's postulated connection between the plates is accepted.

Kasimovian indices (Fig. 8) again suggest a closer proximity of Spain to the Donets basin than to North America. However, North American similarities support the model shown in Figure 12A, which provides a connection between Spain and North America,

rather than Figure 12B, which does not. Fedorowski (1981, p. 141) discussed this problem and pointed out that a continental barrier might explain the presence of undescribed endemic genera in North America but would not explain the common occurrences of geyrophyllids and sestrophyllids on both sides of the barrier during this time. Similarity analysis favours a connection.

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