BIOGEOGRAPHY OF CARBONIFEROUS ECTOPROCT BRYOZOA

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ABSTRACT. Cryptostomes, principally of the suborders Fenestelloidea and Rhabdomesina, dominated Carboniferous ectoproct bryozoan assemblages. Cystoporates and trepostomes were generally less diverse and less numerous. The bryozoan faunas occurred in eleven geographic regions during the Tournaisian, Viséan, Namurian A, Namurian B and C, Westphalian, and Stephanian. Early Carboniferous bryozoans rapidly evolved from Devonian stocks. Viséan generic assemblages are highly diverse, abundant, and widespread. In contrast, Namurian B and C generic assemblages have low diversity, are sparse, and greatly restricted. Diversification began again in the Westphalian, continued in the Stephanian, and led to the Early Permian ectoproct lineages. Differentiation of assemblages into northern, central, and southern Tethyan faunal regions took place in the late Westphalian. At different times during the Carboniferous, dispersal and exchange of bryozoan genera occurred between faunal regions. Some genera disappeared fom one region and appeared in others, suggesting latitudinal shifts in environmental conditions possibly due to climatic changes.

CARBONIFEROUS bryozoans are an important group of rock-forming fossils which have wide geographical distributions. Many genera have distinctive geographical ranges during different parts of the Carboniferous, and they show patterns of endemism within regions and dispersal between regions during the course of that period. This summary, utilizing published and unpublished data, of these changing relationships suggests that bryozoans when studied in detail, have great potential use in palaeogeographical and biostratigraphical analyses.

Carboniferous bryozoans are dominated by cryptostomes that belong principally to the two suborders Fenestelloidea and Rhabdomesina. For example, during the Viséan, a time when bryozoans were exceptionally abundant in the world faunas, cryptostomes were overwhelmingly abundant and the most important. However, at certain times and at particular sites on the shelf areas, cystoporates, such as *Meekopora*, were the dominant group in the benthic communities. Occasionally trepostomes, such as *Tabulipora*, were the most abundant bryozoans in the community.

At different times during the Carboniferous, bryozoan biogeographical patterns were influenced by numerous geological, climatological, physical, and biological events. These included orogenic activity, cyclic sedimentation, transgressions and regressions, climatic events such as major glaciations, and interaction of species in community associations. All these events greatly modified the adaptive evolutionary trends and dispersals of faunas. Viséan palaeogeography (text-fig. 1) has been reconstructed and climatic belts differentiated using such evidence (see Ramsbottom 1973; Ross 1979).

Time stratigraphic nomenclature of the Carboniferous is presently undergoing re-evaluation because the classic subdivision of the Dinantian (George *et al.* 1976) and Silesian (Ramsbottom *et al.* 1978) have proven difficult to correlate precisely outside north-western Europe. A threefold subdivision in other parts of the world seems to be more readily recognized: Lower Carboniferous corresponding to the Tournaisian through Namurian A, Middle Carboniferous corresponding to Namurian B through the Westphalian, and Upper Carboniferous corresponding to the Stephanian (Ross 1979).

The divisions of the Carboniferous follow that outlined in text-fig. 2. Throughout the discussion, the Western European standard section names are used for brevity, and to provide continuity in comparing faunas from different regions. Correlation of various units in different parts of the world is based on faunal evidence and, for the most part, follows Ross (1979). Distribution patterns are

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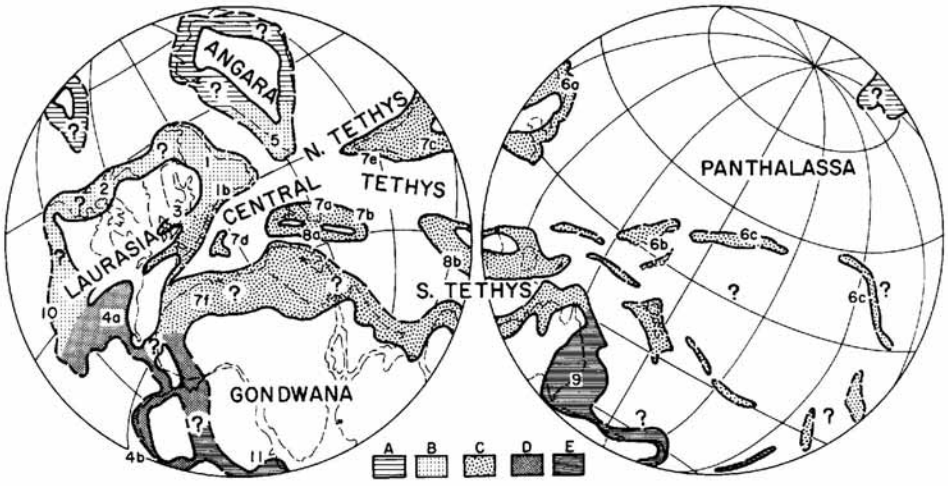
analysed for the Tournaisian, Viséan, Namurian A, Namurian B and C, Westphalian, and Stephanian. These divisions demarcate broad sedimentary, tectonic, and climatic categories and provide a convenient framework for comparing faunas.

The analysis of bryozoan faunas is based on generic distributions (text-figs. 3–12). The systematics of Carboniferous bryozoans at the species level is too inconsistent to attempt analysis at this level. The morphological structures used to separate some species groups appear to have little systematic validity and monographic revisions are necessary. Generic occurrences are classified into eleven regions (text-fig. 1), based on faunal, tectonic, geophysical, and sedimentary interpretations for the different subdivisions of the Carboniferous. Data from some regions for parts of the Carboniferous are lacking due to the incompleteness of the geological record (one such region is region 7b, Kazakhstan, in the later part of the Carboniferous), lack of studies (e.g. region 2, Franklinian seas), or limited availability of literature (e.g. region 7c, China).

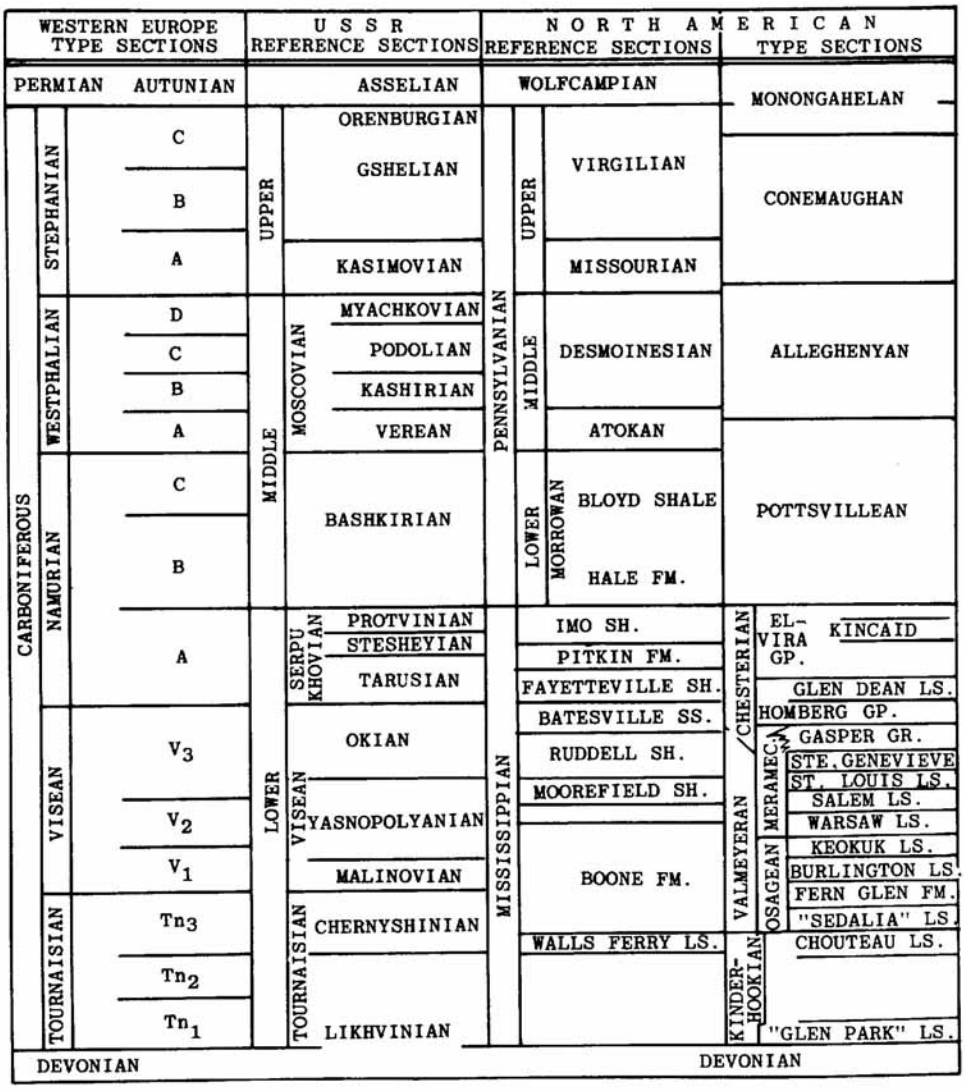
GEOGRAPHICAL DISTRIBUTION OF FAUNAS

Region 1—Russian Platform

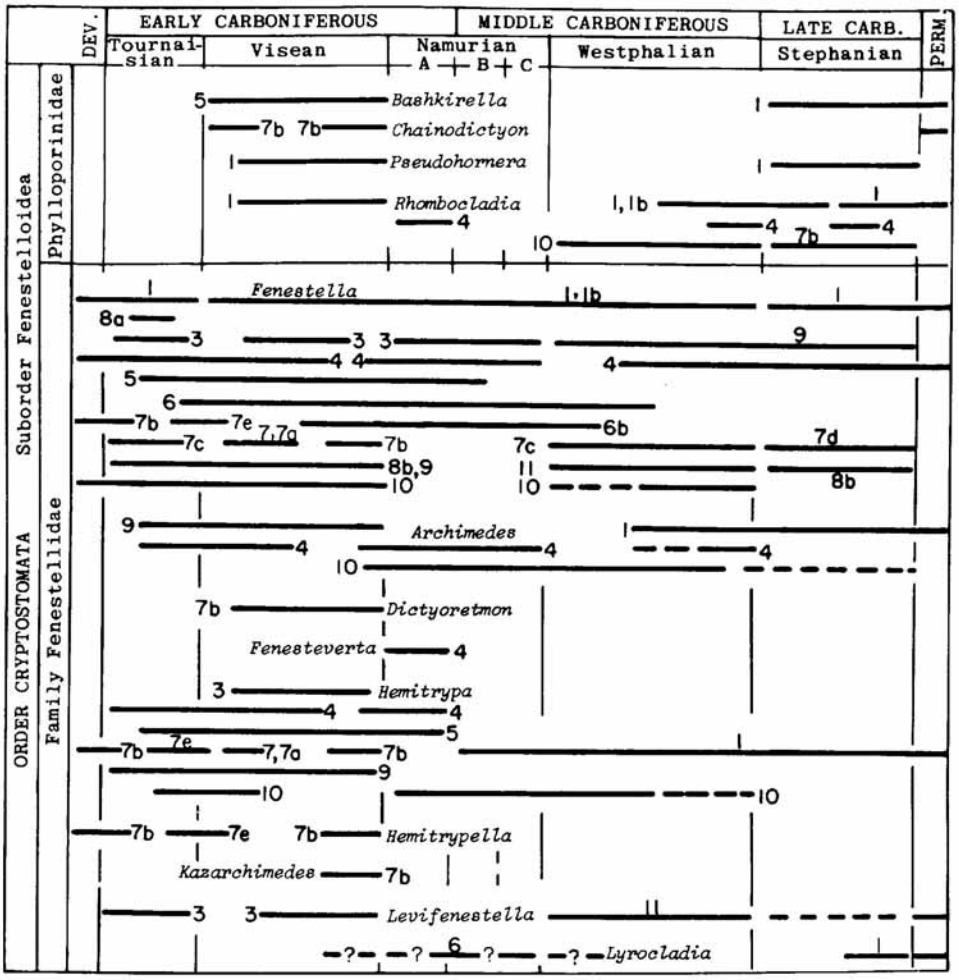
Region 1 includes a number of areas of sedimentation (text-fig. 1). In the east the broad shelf of the Russian Platform includes the Moscow and Voronezh Basins, and in the west it comprises the shallow shelf areas bordering the Uralian seas. The Donetz Basin is another distinctly differentiated area of sedimentation included in this region. (*Text continued on p. 325.*)



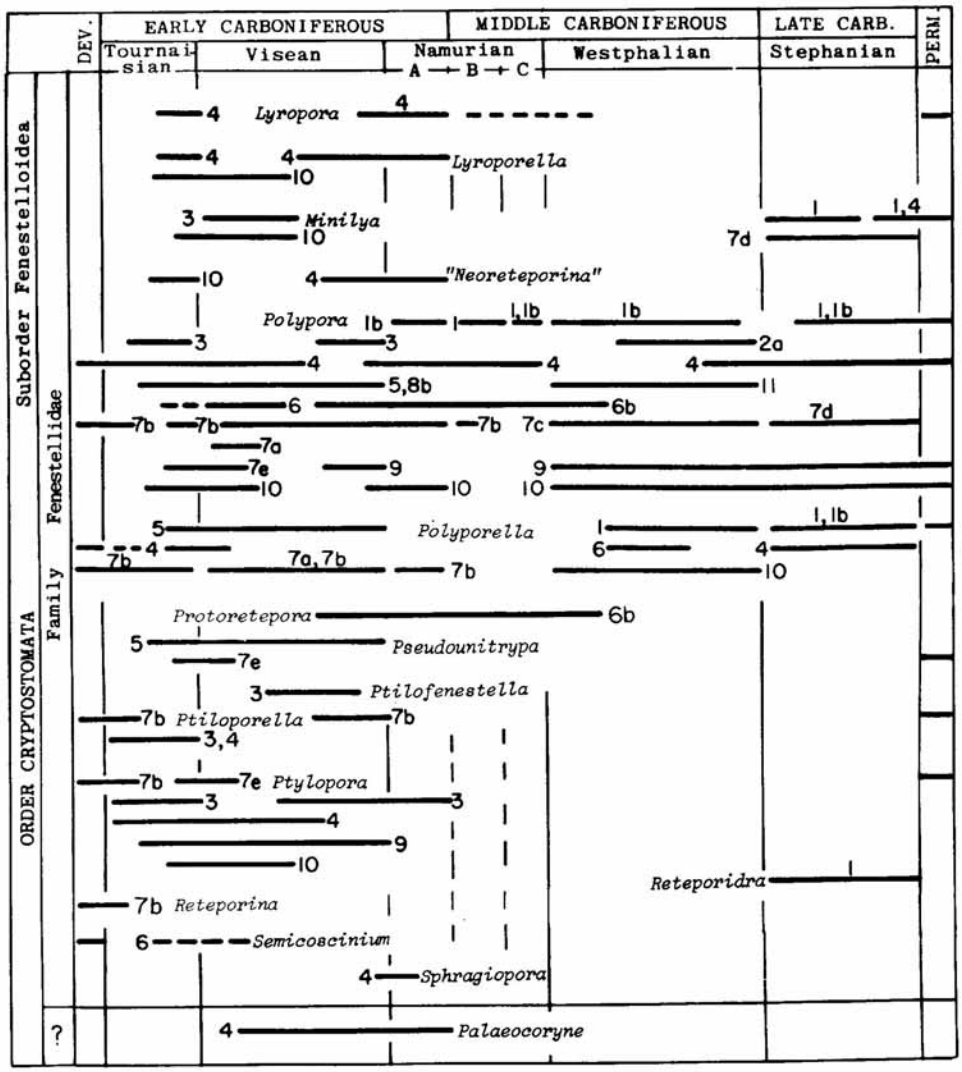
TEXT-FIG. 1. Reconstruction for the Viséan part of the Lower Carboniferous. Relative positions of continental fragments and arcs in Panthalassa are speculative and are shown in relation to the palaeoequator. A—northern cool temperate; B—warm temperate to subtropical; C—Tethyan tropical; D—North American midcontinent and Andean tropical and subtropical; E—southern cool temperate. Geographical regions are: 1, Russian Platform, including Moscow Basin, Voronezh Basin; Uralian shelf; 1b, Donetz Basin; 2, Franklinian shelf and adjacent regions; 3, Northwestern Europe, including Great Britain, Eire, Belgium, Germany, and Poland, and Nova Scotia, Canada; 4, American shelf; 4a, Midcontinent and eastern shelves of U.S. and West Texas; 4b, Andean Sea; 5, Kuznetsk Basin, central Siberia; 6, Northern Tethys; 6a, Khabarovsk and Transbaikal regions; 6b, Japan; 6c, North American Cordillera, western part; 7, Central Tethys; 7a, Uzbekistan and Middle Asia; 7b, Kazakhstan; 7c, China; 7d, Carnic Alps; 7e, Altai; 7f, Morocco; 8, Southern Tethys; 8a, Afghanistan; 8b, Malaya and Thailand; 9, Tasman geosyncline and adjacent shelves; 10, North American Cordillera, eastern part; 11, Patagonian shelf, western Argentina.



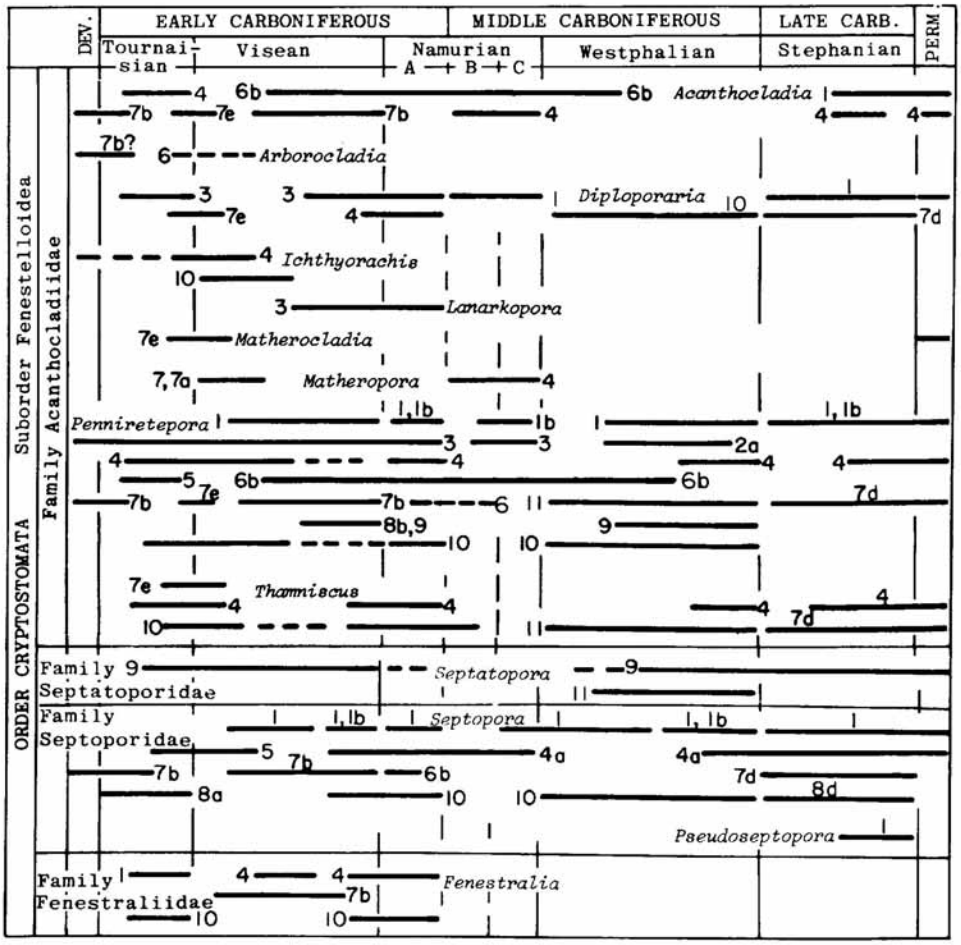
TEXT-FIG. 2. Carboniferous correlation chart comparing stratigraphical divisions in Western European type sections, U.S.S.R. reference sections, and North American reference and type sections.



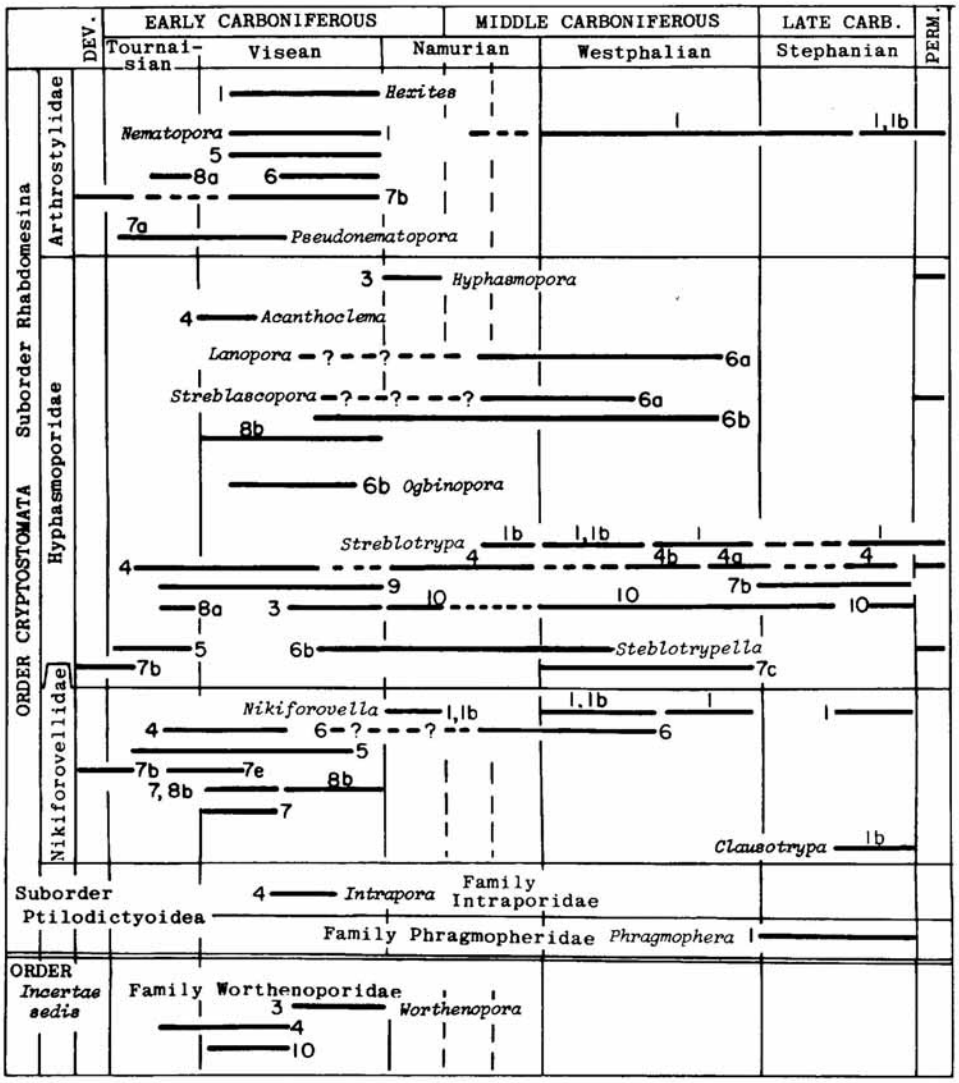
TEXT-FIG. 3. Stratigraphical and geographical ranges of Carboniferous ectoproct bryozoan genera: class Stenolaemata, order Cryptostomata, suborder Fenestelloidea, families Phylloporinidae and Fenestellidae. See Text-fig. 1 for key to numbered geographical regions.



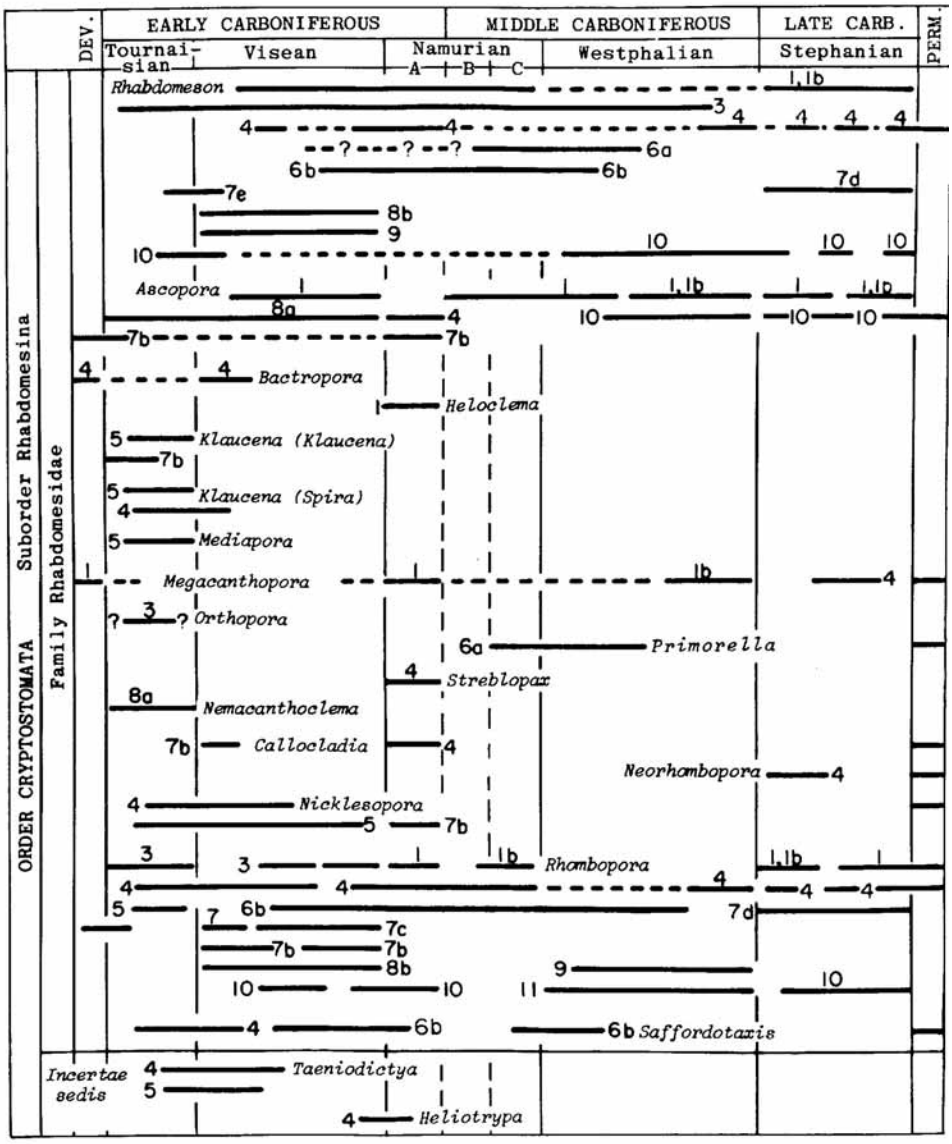
TEXT-FIG. 4. Stratigraphical and geographical ranges of Carboniferous ectoproct bryozoan genera: order Cryptostomata, suborder Fenestelloidea, family Fenestellidae continued from Text-fig. 3. See Text-fig. 1 for key to numbered geographical regions.



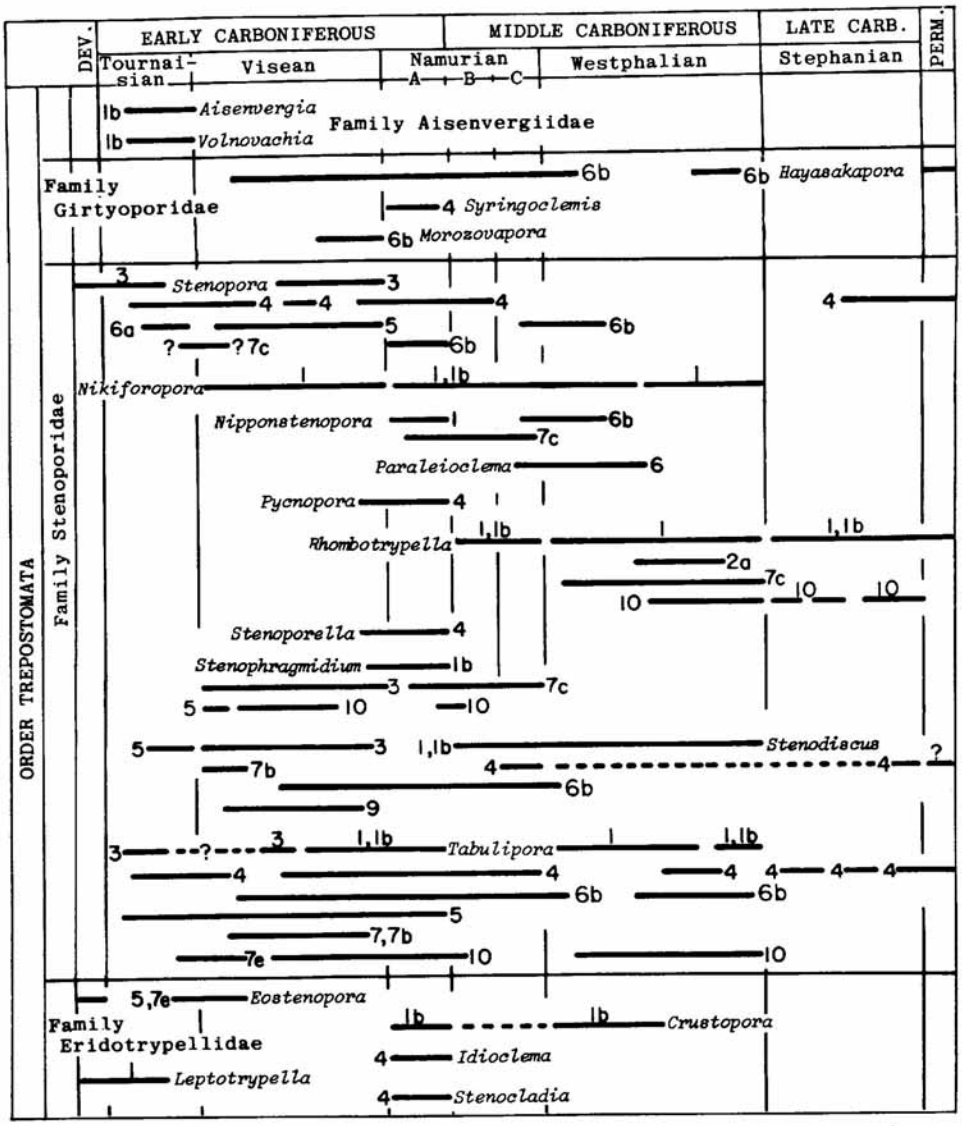
TEXT-FIG. 5. Stratigraphical and geographical ranges of Carboniferous ectoproct bryozoan genera: order Cryptostomata, suborder Fenestelloidea, families Acanthocladiidae, Septatoporidae, Septoporidae, and Fenestraliidae. See Text-fig. 1 for key to numbered geographical regions.



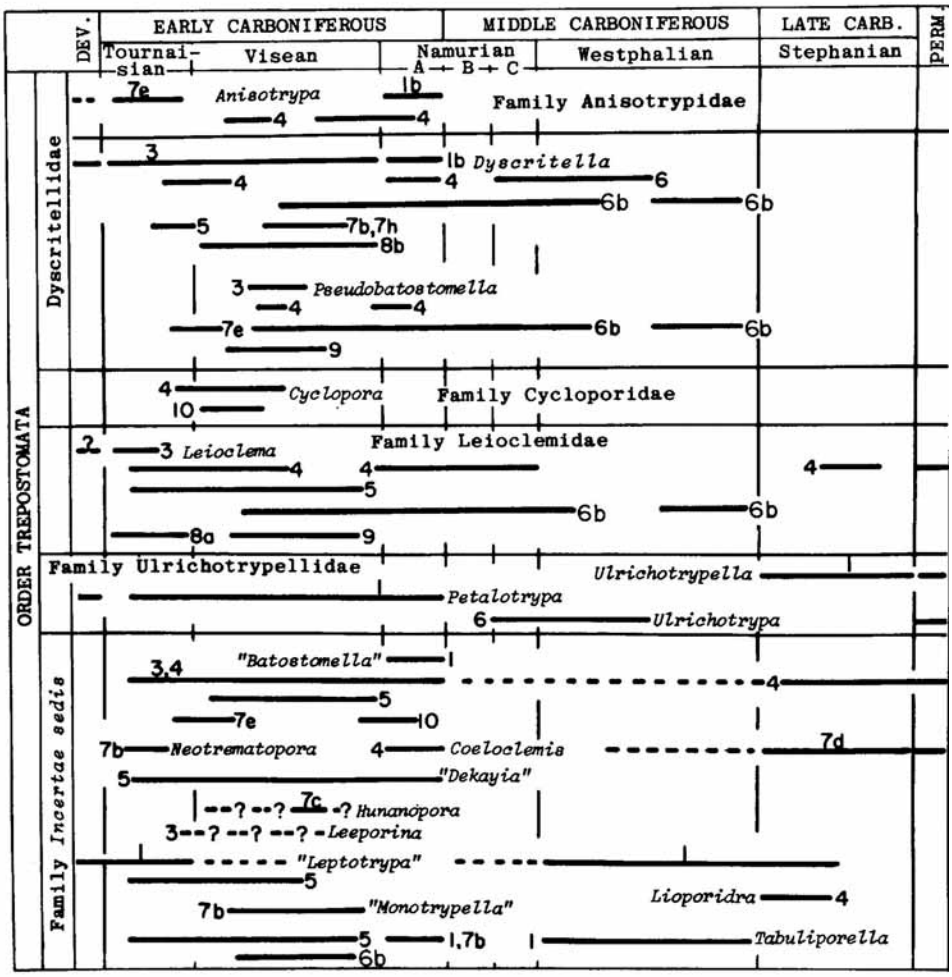
TEXT-FIG. 6. Stratigraphical and geographical ranges of Carboniferous ectoproct bryozoan genera: order Cryptostomata, suborder Rhabdomesina, families Arthrostylidae, Hyphasmoporidae, and Nikiforovellidae; Suborder Ptilodictyoidea, families Intraporidae and Phragmopheridae; order *incertae sedis*, family Worthenoporidae. See Text-fig. 1 for key to numbered geographical regions.



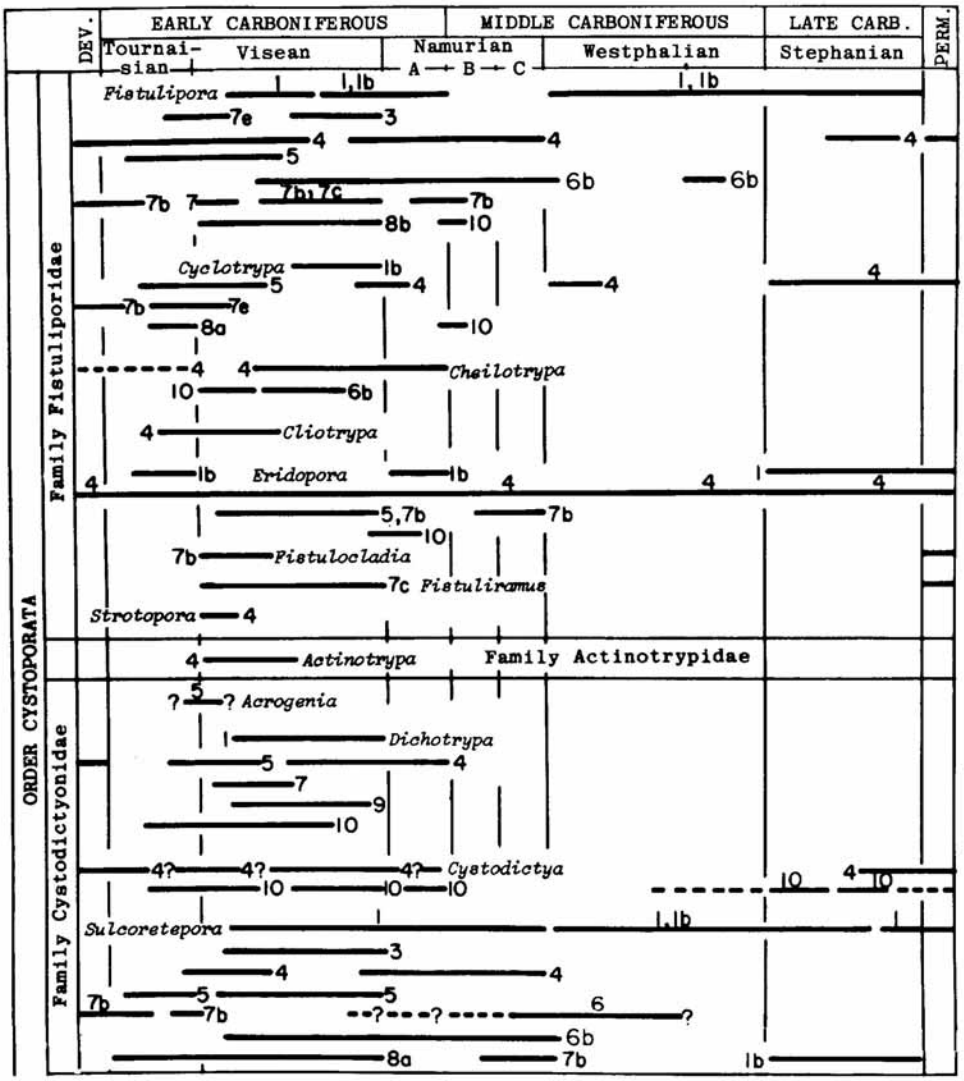
TEXT-FIG. 7. Stratigraphical and geographical ranges of Carboniferous ectoproct bryozoan genera: order Cryptostomata, suborder Rhabdomesina, family Rhabdomesidae; suborder and families *incertae sedis*, *Taenodictya* and *Heliotrypa*. See Text-fig. 1 for key to numbered geographical regions.



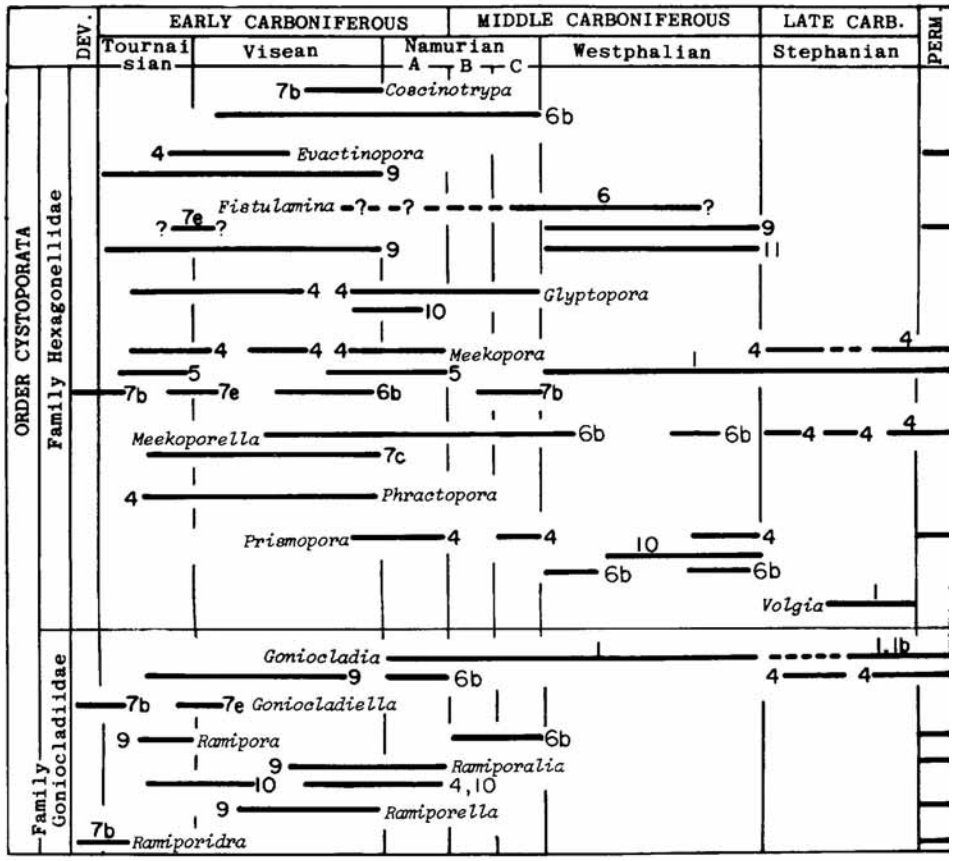
TEXT-FIG. 8. Stratigraphical and geographical ranges of Carboniferous ectoproct bryozoan genera: order Trepostomata, families Aisenvergiidae, Girtyoporidae, Stenoporidae, and Eridotrypellidae. See Text-fig. 1 for key to numbered geographical regions.



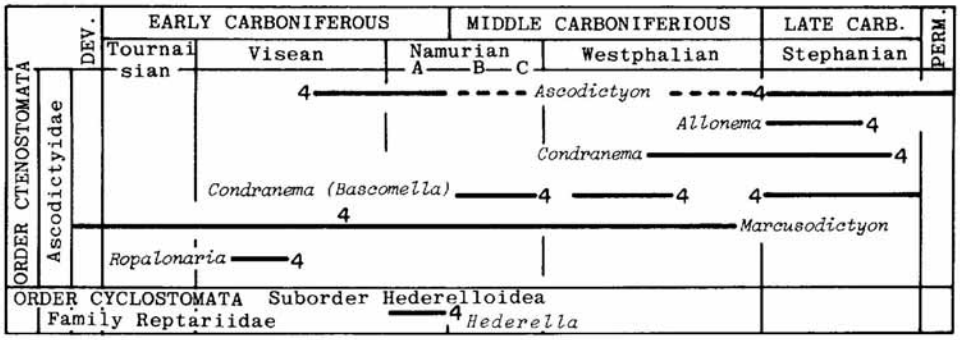
TEXT-FIG. 9. Stratigraphical and geographical ranges of Carboniferous ectoproct bryozoan genera: order Trepostomata, families Dyscritellidae, Cycloporidae, Leioclemidae, Ulrichotrypellidae, and families *incertae sedis*. See Text-fig. 1 for key to numbered geographical regions.



TEXT-FIG. 10. Stratigraphical and geographical ranges of Carboniferous ectoproct bryozoan genera: order Cystoporata, families Fistuliporidae and Cystodictyonidae. See Text-fig. 1 for key to numbered geographical regions.



TEXT-FIG. 11. Stratigraphical and geographical ranges of Carboniferous ectoproct bryozoan genera: order Cystoporata, families Hexagonellidae and Goniocladiidae. See Text-fig. 1 for key to numbered geographical regions.



TEXT-FIG. 12. Stratigraphical and geographical ranges of Carboniferous ectoproct bryozoan genera: class Gymnolaemata, order Ctenostomata, family Ascodictyidae; class Stenolaemata, order Cyclostomata, family Reptariidae. See Text-fig. 1 for key to numbered geographical regions.

In most parts of the platform, the bryozoan distribution (text-figs. 3–12) in the biota is closely linked with differences in ecological conditions (Shulga-Nesterenko 1955; Ivanova 1958). On the Russian Platform, the Carboniferous consists of characteristically shallow shelf sediments with comparatively thin-bedded units deposited far from clastic sources, and with sedimentary conditions similar to much of the Carboniferous of the midcontinental shelf of the United States, e.g. Kansas. Generally bryozoan species occur at specific horizons in certain facies and they do not have continuous vertical ranges. As a consequence, genera and species appear to have migrated in synchrony with transgressions and regressions. This gives rise to at least two types of patterns in the occurrence of genera. One pattern in which genera with adaptive plasticity evolved into different species groups that reappear vertically in the time-rock sequence, and the other in which a genus appears for a short interval and is then absent. In deposits of the Russian Platform and in those of the Uralian seas, fenestrate colonies of the Fenestellidae are dominant. In deposits of the deeper parts of the shelf at considerable distances from the shore, massive colonies of *Meekopora* occur, together with numerous branching colonies of *Ascopora* and *Archimedes*.

On the Russian Platform in the lower part of the Lower Carboniferous (Tournaisian), bryozoans are rare. In the Chernyshinian, a fauna predominantly of brachiopods has only a few bryozoans that are represented by the four genera *Fenestella*, *Fenestralia*, '*Leptotrypa*', and *Leptotrypella* (Astrova 1978; Lavrentjeva 1970, 1974; Morozova 1963). However, the assemblages are characterized principally by various species of *Fenestella*. This genus has several distinctive lineages which are extensively developed in the Carboniferous of the Russian Platform (Morozova 1974; Shulga-Nesterenko 1951).

The maximum development of Lower Carboniferous bryozoans occurs in Viséan strata (particularly in the upper part of the Yasnopolyanian) and in the Namurian A (particularly in the Stesheyian). The similarity of species in the upper part of the Yasnopolyanian in the Moscow and Voronezh Basins suggests connection of these basins at that time (Shulga-Nesterenko 1955). The Viséan bryozoan fauna consists of at least fifteen genera in ten families. They are *Pseudohornera*, *Rhombocladia*, *Fenestella*, *Septopora*, *Pennirétepora*, *Hexites*, *Nematopora*, *Rhabdomeson*, *Ascopora*, *Pseudobatostomella*, *Nikiforopora*, *Tabuliporella*, *Fistulipora*, *Dichotrypa*, and *Sulcoretepora*. The distinctive arthrostylid *Hexites* is found only on the Russian Platform, together with *Sulcoretepora* and very thin, thread-like colonies of the arthrostylid *Nematopora* (Astrova 1973; Dunaeva 1973*a*; Morozova 1955; Shishova 1952; Shulga-Nesterenko 1955).

In Namurian A strata, the diverse fauna of fifteen genera in ten families includes several genera found in the Viséan, namely *Fenestella*, *Septopora*, *Rhabdomeson*, *Tabuliporella*, *Fistulipora* and *Sulcoretepora* (Dunaeva 1973*a*, 1973*b*; Gorjunova and Kruchinina 1975; Shishova 1952; Shulga-Nesterenko 1955). Additional genera appearing for the first time in this region are the cryptostomes *Polypora*, *Nikiforovella*, and *Heloclema*, the trepostomes *Nippostenopora*, *Tabulipora*, '*Batostomella*', and *Petalotrypa*, and the cystoporate *Goniocladia*.

In the lower part of the Middle Carboniferous (Namurian B and C), although the number of genera is slightly reduced, a great many families are represented. The cryptostomes include *Fenestella*, *Polypora*, *Diploporaria*, *Rhabdomeson*, *Ascopora;* the trepostomes *Nikiforopora*, *Rhombotrypella* and *Stenodiscus;* and the cystoporates *Sulcoretepora* and *Goniocladia* (Dunaeva 1973*a*; Gorjunova and Kruchinina 1975; Trizna 1961).

The remainder of the Middle and Upper Carboniferous bryozoan faunas show increased diversity with time (Gorjunova 1975; Gorjunova and Kruchinina 1975; Shishova 1950, 1952, 1957; Shulga-Nesterenko 1955, 1958; Trizna 1961; Viskova 1961). In the Westphalian, the faunas have at least twenty-two genera in thirteen families. In the Kashirian Substage, bryozoans are present occasionally in large numbers, and this includes the characteristic *Nematopora*. The majority range up in the sequence from lower horizons, e.g. *Rhombocladia*, *Fenestella*, *Polypora*, *Septopora*, *Pennniretepora*, *Nematopora*, *Nikiforovella*, *Rhabdomeson*, *Ascopora*, *Nikiforopora*, *Stenodiscus*, *Tabulipora*, *Rhombotrypella*, *Tabuliporella*, '*Leptotrypa*', *Fistulipora*, *Sulcoretepora*, and *Goniocladia*. New genera in the faunas are *Archimedes*, *Polyporella*, *Streblotrypa*, *Ramiporella*, and the wide ranging *Meekopora*.

In the Stephanian, the bryozoan faunas show continued diversification and include at least thirty-three genera in fifteen families. Bryozoans are well represented in the lower part of the Kasimovian Stage and are exceptionally rich and variable in the lower part of the Gshelian. More than half the genera range up from the Westphalian or lower horizons, e.g. *Rhombocladia*, *Pseudohornera*, *Fenestella*, *Polypora*, *Septopora*, *Pennniretepora*, *Diploporaria*, *Archimedes*, *Rhabdomeson*, *Ascopora*, *Nikiforovella*, *Nematopora*, *Rhombopora*, *Streblotrypa*, *Tabulipora*, *Rhombotrypella*, *Fistulipora*, *Sulcoretepora* and *Goniocladia*. New occurrences in this stage are *Pseudoseptopora*, *Reteporidra*, *Minilya*, *Lyrocladia*, *Bashkirella*, *Acanthocladia*, *Ramiporidra*, *Volgia*, *Eridopora*, *Ulrichotrypella*, *Phragmophera*, *Nicklesopora*, and *Primorella*.

In the Donetz Basin (region 1b), the Tournaisian bryozoan fauna is slightly more varied than that on the Russian Platform. The fauna comprises the distinctive trepostomes *Aisenvergia* and *Volnovachia*, as well as *Fenestella*, '*Leptotrypa*', *Eridopora*, and *Megacanthopora* (Astrova 1978; Dunaeva 1973*c*, 1973*d*; Nikiforova 1927*a*, 1933*a*). The Viséan bryozoan fauna is limited in generic diversity and comprises only *Fenestella*, *Tabulipora*, *Nikiforopora*, *Fistulipora*, and *Cyclotrypa*. In the Namurian A, a marked increase in the diversity of the fauna results from the influx of ten additional genera, together with the genera noted above, except for *Cyclotrypa*. The additional genera are *Polypora*, *Septopora*, *Pennniretepora*, *Nikiforovella*, *Megacanthopora*, *Anisotrypa*, *Tabulipora*, *Nikiforopora*, *Stenophragmidium*, *Dyscritella*, *Crustopora*, *Fistulipora*, and *Eridopora*.

In the Namurian B and C, the bryozoan fauna is much reduced, paralleling changes in the faunas in the Russian Platform. The fauna comprises *Fenestella*, *Polypora*, *Pennniretepora*, *Streblotrypa*, *Rhombopora*, *Nikiforopora*, *Rhombotrypella*, and *Stenodiscus*. This Donetz Basin Namurian B and C fauna has a closer generic similarity to faunas of the Russian Platform than at other times during the Carboniferous.

In the Westphalian, although there is increased diversity in the fauna, it is not as great as in the Russian Platform faunas. Most genera range up from lower horizons—*Fenestella*, *Polypora*, *Pennniretepora*, *Septopora*, *Nikiforovella*, *Nikiforopora*, *Crustopora*, *Megacanthopora*, *Stenodiscus* and *Fistulipora*. Additional genera are *Rhombocladia*, *Ascopora*, *Streblotrypa*, and *Sulcoretepora*.

In the Stephanian, the rich bryozoan fauna is not as diverse as that of the Russian Platform. New genera are *Polyporella*, *Clausotrypa*, *Rhabdomeson*, *Goniocladia*, and *Nematopora*. Genera ranging up from lower horizons are *Fenestella*, *Polypora*, *Pennniretepora*, *Rhombotrypella*, *Ascopora*, *Rhombopora*, *Streblotrypa*, and *Tabulipora*.

Region 2—Franklinian Shelf

There was an extensive shelf area bordering the Franklinian seas (text-fig. 1). Although bryozoans are known from this region, the fauna is not documented except for Westphalian assemblages in eastern Greenland. The two cryptostomes *Polypora* and *Pennirетepora*, and the trepostome *Rhombotrypella* are recorded (Ross and Ross 1962) (text-figs. 4, 5, 8).

Region 3—Northwest Europe and Nova Scotia

In the Carboniferous shelf area extending as a tongue of the ocean from region 1 and now encompassing part of north-western Europe (Great Britain, Ireland, Belgium, Germany, and Poland) and also Nova Scotia (text-fig. 1), a distinctive series of bryozoan assemblages occur (text-figs. 3–12). Generic distribution data are drawn from Bell (1929), Bojkowski (1966), Davies and Wilson (1972), Demanet (1938), Graham (1975), Kaisin (1942), Kelley (1967), Lee (1912), Miller (1961*a*, 1961*b*, 1962*a*, 1962*b*, 1963), Mitchell (1971), Nekhoroshev (1932), Olaloye (1974), Owen (1966, 1969, 1973), Shepard-Thorn (1963), Tavener-Smith (1965*a*, 1965*b*, 1973, 1974), and Wilson (1961). Fenestrate and pinnate colonies dominate almost all the assemblages, and the distinctive genus *Rhabdomeson* is closely associated with marine bands intercalated in the coal depositional cycles. Many of these assemblages have limited generic diversity, particularly those with *Rhabdomeson*, and appear to be part of brackish water biota.

In the Tournaisian, only cryptostomes of the families Fenestellidae, Acanthocladiidae, and Rhabdomesidae are reported. The genera are *Fenestella*, *Levifenestella*, *Polypora*, *Ptiloporella*, *Ptylopora*, *Diploporaria*, *Pennirетepora*, *Rhabdomeson*, *Rhombopora*, and *Orthopora*.

In the Viséan, a marked increase in generic diversity is found in the Scottish area where trepostomes flourished. Other areas of this region still had primarily fenestelloid and rhabdomesine representatives. The fauna comprises distinctive cryptostome assemblages with *Fenestella*, *Levifenestella*, *Hemitrypa*, *Minilya*, *Polypora*, *Ptilofenestella*, *Ptylopora*, *Diploporaria*, *Pennirетepora*, *Septopora*, *Streblotrypa*, *Rhabdomeson*, *Rhombopora*; the trepostomes *Stenopora*, *Tabulipora*, *Stenodiscus*, *Stenophragmidium*, *Dyscritella*; the custoporate *Fistulipora*; and a genus of uncertain assignment *Worthenopora*.

In the Namurian A, the bryozoan faunas have several cryptostomes of which *Rhabdomeson* is widespread in the eastern part of this region and *Pennirетepora* is abundant in the western part. Other genera are *Fenestella*, *Ptylopora*, *Diploporaria*, *Lanarkopora*, *Stenodiscus*, *Tabulipora*, and '*Batostomella*'.

In the Namurian B and C, the bryozoan faunas are very sparse and are represented by *Fenestella*, *Pennirетepora*, and *Rhabdomeson*. The latter is widespread in the western part of the region. In the Westphalian, only *Rhabdomeson* is reported and is widespread in the western part of the region.

Region 4—American Shelf

In region 4a, the midcontinent and eastern shelves of the United States and west Texas (text-fig. 1) (see Gordon 1974, for the distribution of seas), the Carboniferous sediments have prolific bryozoan faunas in a number of stratigraphic units, even at the beginning of the Carboniferous. The species commonly have a restricted distribution being confined to a particular shelf area bordering one of the several basins. Most of the genera are widespread. Generic distribution data are drawn from Bassler (1941), Blake (1973, 1976), Chronic (1953), Condra (1903), Condra and Elias (1944*a*, 1944*b*, 1944*c*), Conkin and Fuson (1970), Deiss (1927), Duncan (1969), Easton (1943), Elias (1956, 1957, 1970), Gautier (1970), Haas (1946), Hernon (1935), Horowitz (1968, 1977), Huffman (1970, 1971), Koenig (1958), Lane (1973), McFarlan (1942), McKinney (1968, 1969, 1971, 1972, 1977), Moore (1929, 1930, 1964), Moore and Dudley (1944), Nickles and Bassler (1900), Nitecki and McKinney (1975), Payton (1966), Perkins, Perry and Hattin (1962), Perry and Hattin (1958), Perry and Horowitz (1963), Perry and Rodriquez (1960), Peterson, Hoare, and Sturgeon (1974), Richards (1959), Sayre (1930), Tischler (1963), Ulrich (1888), Utgaard and Perry (1960), and Warthin (1930).

In the Osagean (Tournaisian), cryptostome genera are dominant with both fenestelloids and

rhabdomesines. The fenestelloids comprise *Fenestella*, *Archimedes*, *Hemitrypa*, *Lyropora*, *Lyroporella*, *Polypora*, *Polyporella*, *Ptylopora*, *Ptiloporella*, *Pennireteporα*, *Thamniscus*, and *Taenodictya*. The rhabdomesines are *Acanthoclema*, *Streblotrypa*, *Streblotrypella*, *Klaucena* (*Spira*), *Nicklesopora*, *Rhombopora*, and *Saffordotaxis*. In addition there are several cystoporates—*Fistulipora*, *Sulcoretepora*, *Coscinotrypa*, *Evactinopora*, *Glyptopora*, *Meekopora*, and *Phractopora*, and the trepostomes *Leioclema*, *Tabulipora*, and '*Batostomella*'.

The Viséan bryozoans have slightly greater generic diversity and cryptostomes are overwhelmingly dominant. The fenestellid *Archimedes* is very abundant in some units. The faunas comprise the cryptostomes *Fenestella*, *Archimedes*, *Hemitrypa*, *Lyropora*, *Lyroporella*, *Polypora*, *Polyporella*, *Ptylopora*, *Reteporina*, *Sphragiopora*, *Diploporaria*, *Septopora*, *Fenestralia*, *Intrapora*, *Taenodictya*, *Rhabdomeson*, *Rhombopora*, *Bactropora*, and *Heliotrypa*; the cystoporates *Fistulipora*, *Actinotrypa*, *Sulcoretepora*, *Glyptopora*, *Meekopora*, *Phractopora*, and *Prismopora*; the trepostomes *Tabulipora*, *Cyclopora*, *Leioclema*, *Anisotrypa*, and the distinctive genus *Worthenopora*.

In Namurian A, bryozoan assemblages are prolific and they have high generic diversity. *Archimedes* is very abundant in many assemblages. *Tabulipora* also is very abundant and dominant in specific biota. The fenestelloid cryptostomes include *Rhombocladia*, *Fenestella*, *Archimedes*, *Fenesteverta*, *Lyropora*, *Lyroporella*, *Polypora*, *Reteporina*, *Pennireteporα*, *Thamniscus*, and *Septopora*. Rhabdomesine cryptostomes are *Streblotrypa*, *Streblotrypella*, *Rhabdomeson*, *Ascopora*, *Callocladia*, *Streblopax*, and *Rhombopora*. The cystoporates are represented by four families, and include *Fistulipora*, *Cheilotrypa*, *Eridopora*, *Dichotrypa*, *Sulcoretepora*, *Glyptopora*, *Meekopora*, *Prismopora*, and *Ramiporalia*. The trepostomes have several stenoporids, such as *Stenopora*, *Stenoporella*, *Pycnopora*, and *Tabulipora*, as well as several other genera including *Anisotrypa*, *Stenocladia*, *Idioclema*, *Syringoclemis*, *Dyscritella*, *Coeloclemis*, and '*Batostomella*'.

In Namurian B and the early part of Namurian C, the seas were very much reduced in area on the midcontinent and eastern shelves and bryozoan faunas are sparse, having only ten genera. They comprise the cryptostomes *Fenestella*, *Polypora*, *Matheropora*, *Septopora*, *Rhombopora*, and *Streblotrypa*; the cystoporates *Cyclotrypa* and *Sulcoretepora*; and the trepostomes *Stenopora* and *Tabulipora*.

Westphalian sediments contain more varied bryozoan assemblages with eighteen genera in ten families. Cystoporates are as numerous as cryptostomes in some assemblages. The faunas include the cryptostomes *Rhombocladia*, *Fenestella*, *Polypora*, *Acanthocladia*, *Matheropora*, *Thamniscus*, *Pennireteporα*, *Rhabdomeson*, *Rhombopora*; the cystoporates *Fistulipora*, *Cyclotrypa*, *Sulcoretepora*, *Coscinotrypa*, and *Prismopora*; and the trepostomes *Anisotrypa*, *Stenopora*, and *Tabulipora*.

In the Stephanian, the momentum of increasing generic diversity was maintained and the bryozoan assemblages comprise twenty-three genera in thirteen families. Many of the genera in the Westphalian range into the Stephanian. The rhabdomesine *Rhombopora* is widespread. Cryptostomes and cystoporates are still the characteristic representatives. The cryptostomes include *Rhombocladia*, *Fenestella*, *Polypora*, *Septopora*, *Acanthocladia*, *Pennireteporα*, *Thamniscus*, *Rhabdomeson*, *Megacanthopora*, *Rhombopora*, and *Streblotrypa*. The cystoporates comprise *Fistulipora*, *Cyclotrypa*, *Eridopora*, *Cystodictya*, *Sulcoretepora*, *Meekopora*, *Meekoporella*, and *Goniocladia*. The trepostomes are represented by *Stenopora*, *Tabulipora*, *Leioclema*, and '*Batostomella*'.

In region 4b (Andean Sea) to the south-west of region 4a (midcontinent and eastern shelves of the United States and west Texas), the faunas are poorly documented. Two cryptostome genera, *Fenestella* and *Streblotrypa*, are reported from Westphalian (Desmoinesian) rocks in Peru (Chronic 1953).

Region 5—Kuznetsk Basin

This region encompasses the area of the Kuznetsk Basin (Kuzbass) and central Siberia. Faunal studies include monographs by Nekhoroshev (1926, 1956), Nikiforova (1933*b*), and Trizna (1958). These bryozoan faunas have been more extensively documented than those from other regions to the east. Only Lower Carboniferous assemblages are reported from Tournaisian to

Lower Namurian sediments. Because some of the units are probably Upper Devonian, the faunal lists of the early literature may also include bryozoans of that age. The fauna from the lowest Abyshchevski unit has been excluded from the present considerations because it is probably Upper Devonian.

As in Region 4a, the Tournaisian has a high diversity of about twenty two genera in eleven families. Cryptostomes have the greatest generic representation and include *Fenestella*, *Hemitrypa*, *Polypora*, *Pseudounitrypa*, *Pennniretepora*, *Streblotrypella*, *Klaucena* (*Klaucena*), *Klaucena* (*Spira*), *Mediapora*, *Nicklesopora*, *Rhombopora*, and *Nikiforovella*. There are only three cystoporates, *Fistulipora*, *Sulcoretepora*, and *Meekopora*, and six trepostomes, *Stenopora*?, *Stenodiscus*, *Tabulipora*, *Leioclema*, '*Dekayia*', and *Tabuliporella*.

In strata of Viséan age, a comparably diverse set of bryozoan assemblages occurs, although the number of cryptostome genera is slightly reduced. Genera found in both stages are *Fenestella*, *Hemitrypa*, *Polypora*, *Pseudounitrypa*, *Nicklesopora*, *Nikiforovella*, *Fistulipora*, *Sulcoretepora*, *Stenopora*, *Stenodiscus*, *Tabulipora*, *Leioclema*, *Tabuliporella*, and '*Dekayia*'. New additions in the Viséan are *Bashkirella*, *Nematopora*, *Eridopora*, and *Petalotrypa*. In sediments considered Viséan–Namurian, the bryozoan assemblage consists of *Fenestella*, *Hemitrypa*, *Meekopora*, *Stenopora*?, *Tabulipora*, and '*Dekayia*'.

Region 6—Northern Tethys

The region, which in the later part of the Carboniferous is gradually identifiable as the Northern Tethys, includes a number of different tectonic blocks extending over a wide area (Khabarovsk region, Japan, and western North American Cordillera). The broad Transbaikal region also is included, although Lower Carboniferous bryozoan faunas of this region are also closely allied to the Central Tethys region. The limited information of faunas in this region allows only an incomplete listing of the genera which range through Viséan to Westphalian strata. Distribution data are drawn from Duncan (1950), Popeko (1977), Romantchuk (1975), Sakagami (1970). Sakagami and Sugimura (1978, 1979), Sugimura (1972), and Sugimura and Ota (1971).

From the Khabarovsk province (region 6a), a diverse fauna of probable Middle Carboniferous age was reported. A more precise age determination is not available at this time. The bryozoans comprise the cryptostomes *Fenestella*, *Lyrocladia*, *Pennniretepora*, *Lanopora*, *Streblascopora*, *Rhabdomeson*, and *Nikiforovella*, the cystoporates *Sulcoretepora* and *Fistulamina*, and the trepostomes *Tabulipora*, *Paraleioclema*, *Dyscritella*, *Ulrichotrypa*, and *Primorella*.

From Japan (region 6b), highly diverse Lower and Middle Carboniferous faunas are found. The detailed study of bryozoan assemblages from this region provides more complete information than for many other regions. The Viséan faunas have at least eighteen genera in eleven families. The cryptostomes are represented by *Fenestella*, *Polypora*, *Protoretepora*, *Acanthocladia*, *Pennniretepora*, *Streblascopora*, *Streblotrypella*, *Rhabdomeson*, *Rhombopora*, and *Nematopora*. The cystoporates are *Fistulipora*, *Cheilotrypa*, *Sulcoretepora*, *Meekopora*, and *Meekoporella*. The trepostomes include two distinctive girtyoporids, *Hayasakapora* and *Morozovapora*, as well as *Stenodiscus*, *Dyscritella*, and *Pseudobatostomella*.

Faunas in the *Millerella* Zone with *Profusulinella* of uppermost Namurian to lowest Westphalian age, comprise *Fenestella*, *Polypora*, *Protoretepora*, *Acanthocladia*, *Pennniretepora*, *Septopora*, *Streblascopora*, *Streblotrypella*, *Saffordotaxis*, *Fistulipora*, *Hayasakapora*, *Stenopora*, *Nipponostenopora*, *Leioclema*?, and *Pseudobatostomella*.

Bryozoans from the *Profusulinella* Zone at the base of the Westphalian have *Fenestella*, *Polypora*, *Protoretepora*, *Pennniretepora*, *Streblascopora*, *Streblotrypella*, *Rhabdomeson*, *Rhombopora*, *Fistulipora*, *Cheilotrypa*, *Sulcoretepora*, *Prismopora*, and *Stenopora*.

Bryozoan faunas from the western North American Cordillera (region 6c) have not been documented except for a few localities. Reports refer to the occurrence of bryozoans but no identifications are available. From the Brooks Range, Alaska, Mississippian bryozoans are fairly well represented but they are not particularly diversified. They are recorded from several horizons. The Viséan assemblages comprise the cryptostomes *Fenestella*, *Hemitrypa*, *Polypora*, *Pennniretepora*, and

Fenestralia; the cystoporates *Cystodictya* and *Dichotrypa*; and an unidentified large ramose stenoporid. A bryozoan assemblage from Viséan–Namurian A strata has *Hemitrypa*, other fenestellids, *Fistulipora*?, *Cystodictya*, and stenoporids.

Region 7—Central Tethys

Region 7 encompasses various shelf regions which are now widely dispersed. It includes Kazakhstan, Uzbekistan, Karatau, Tien Shan, Bet Pak Dala, Altai, China, Tibet, Carnic Alps, and Morocco. Differentiation of these faunas into the Central Tethys occurred in the later part of the Carboniferous. The southern Siberian assemblages are almost all Lower Carboniferous. Those of China are Lower and Middle Carboniferous, Moroccan genera are Lower Carboniferous, and those of the Carnic Alps are Upper Carboniferous.

From region 7a (Uzbekistan, Karatau, Bet Pak Dala, and Tien Shan) several Lower Carboniferous bryozoan assemblages are known. Nikiforova (1927*b*, 1933*b*, *in* Nekhoroshev 1956) identified abundant bryozoans in the upper half of the Tournaisian and lower part of the Viséan from Karatau and Tien Shan. The assemblages comprise the genera *Fenestella*, *Hemitrypa*, *Ptylopora*, *Reteporina*, *Polypora*, *Reteporidra*, *Thamniscus*(?), *Penniretepora*, *Septopora*, *Arborocladia*, *Rhombopora*, *Nikiforovella*, *Streblotrypa*, *Streblotrypella*, *Nematopora*, *Fistulipora*, *Sulcoretepora*, *Dichotrypa*, *Gonicocladia*, *Petalotrypa*, '*Batostomella*', *Leioclema*, *Stenopora*, *Tabulipora*, and *Tabuliporella*. Viséan bryozoan assemblages from Median Tien Shan and north-east Uzbekistan comprise the cryptostomes *Fenestella*, *Hemitrypa*, *Polypora*, *Polyporella*, *Matheropora*, *Pseudonematopora*, *Rhombopora*, and *Nikiforovella*, and the cystoporates *Fistulipora* and *Dichotrypa* (Balakin 1969, 1975). From the Lower Viséan strata of the Chatkal region a most abundant and diverse fauna with forty-one genera in fourteen families is indicated. Only *Fenestella*, *Hemitrypa*, and *Polypora* are recorded (Balakin 1972).

From region 7b (Kazakhstan), diverse bryozoan faunas occur in the Upper Devonian and Lower and Middle Carboniferous. Some of the bryozoans attributed to the earliest Carboniferous may be Late Devonian in age, because of changes in the position of the boundary between the two systems since publication of bryozoan studies in the 1950s. In the Tournaisian, the assemblages contain *Fenestella*, *Hemitrypa*, *Hemitrypella*, *Polypora*, *Polyporella*, *Ptiloporella*, *Ptylopora*, *Reteporina*, *Acanthocladia*, *Arborocladia*?, *Penniretepora*, *Septopora*, *Nematopora*, *Streblotrypella*, *Ascopora*, *Rhombopora*, *Nikiforovella*, *Fistulipora*, *Cyclotrypa*, *Sulcoretepora*, *Goniocladiella*, *Ramiporidra*, *Meekopora*, and *Neotrematopora* (Nekhoroshev 1953; Gorjunova 1975). *Fenestella*, *Klaucena*, and *Rhombopora* are identified as characterizing Lower Tournaisian rocks and *Fenestella* (*Rectifenestella*), *Polypora*, *Fistulocladia*, and *Sulcoretepora* as common in the Upper Tournaisian strata (Plamenskaja 1979).

In the early Viséan, fenestellids and polyporids are numerous and diverse. *Stenodiscus*, *Callocladia*, and *Chainodictyon* appear for the first time (Plamenskaja 1979). In the middle Viséan, *Fistulipora* and *Septopora* predominate and *Dyscritella* appears for the first time. In the later Viséan, *Tabulipora* is widespread (Plamenskaja 1979). Additional genera recorded from the Viséan are *Fenestella*, *Dictyoretmon*, *Hemitrypa*, *Hemitrypella*, *Kazarchimedes*, *Ptiloporella*, *Acanthocladia*, *Penniretepora*, *Fenestralia*, *Nematopora*, *Rhombopora*, *Nikiforovella*, *Eridopora*, '*Monotrypella*', and *Pseudobatostomella* (Astrova 1973; Nekhoroshev 1953; Plamenskaja 1964).

In Namurian A strata, the bryozoans *Fenestella* (*Laxifenestella*), *Nicklesopora*, *Eridopora*, *Fistuliramus*, *Meekopora*, and *Tabuliporella* are common. In Namurian B and C strata, *Fenestella* (*Fabifenestella*), *Fenestella* (*Alternifenestella*), *Sulcoretepora*, and *Coscinotrypa* are recorded (Plamenskaja 1979). In undifferentiated Namurian rocks, *Polypora*, *Polyporella*, *Ascopora*, and *Fistulipora* are present (Nekhoroshev 1953).

In region 7c (China), scant data are available on the faunas mainly due to the lack of availability of the literature. From Tournaisian rocks in Western Guishou, *Fenestella*, *Anisotrypa*, and *Stenophragmidium* are reported. In the Viséan, there are three genera, *Rhombopora*, *Fistulipora*, and *Fistuliramus*. Namurian strata have *Stenophragmidium* and *Nipponostenopora*. Rocks of Westphalian age have *Fenestella*, *Polypora*, *Streblotrypa*, and *Rhombotrypella*. Overlying strata of

probable Lower Permian (Asselian) age have *Polypora*, *Septopora*, and *Meekopora* (Lu *et al.* 1978). *Meekopora* is reported from the Lower Carboniferous of Tibet (Yang and Hsia 1975).

From region 7d (Carnic Alps), Stephanian assemblages which are extensively silicified have limited generic diversity. The bryozoans that have been recorded (Ceretti 1963, 1964, 1967; Johnsen 1906; Kodsi 1967) are *Rhombocladia*, abundant *Fenestella*, *Polypora*, *Minilya*, *Thamniscus*, *Diploporaria*, *Pennirетepora*, *Rhabdomeson*, *Streblotrypa*, *Rhombopora*, and abundant *Sulcoretepora*.

From region 7e (Rudny Altai), Lower Carboniferous faunas have numerous bryozoans (Nekhoroshev 1956). In the Upper Tournaisian, the bryozoans comprise *Fenestella*, *Hemitrypa*, *Hemitrypella*, *Polypora*, *Pseudounitrypa*, *Ptylopora*, *Diploporaria*, *Pennirетepora*, *Rhabdomeson*, *Rhombopora*, *Fistulipora*, *Cyclotrypa*, *Sulcoretepora*, *Meekopora*, *Crustopora*, *Tabulipora*, *Pseudobatostomella*, and '*Batostomella*'. Viséan assemblages contain *Fenestella*, *Hemitrypa*, *Polypora*, *Pseudounitrypa*, *Ptylopora*, *Reteporidra*, *Acanthocladia*, *Matherocladia*, *Pennirетepora*, *Thamniscus*, *Streblotrypa*, *Ascopora*, *Rhombopora*, *Nikiforovella*, *Fistulipora*, *Dichotrypa*, *Sulcoretepora*, *Goniocladiella*, *Ramiporella*, and *Tabulipora*. From Namurian strata, a less diverse assemblage is found, with *Fenestella*, *Polypora*, *Reteporidra*, *Streblotrypa*, *Rhabdomeson*, *Rhombopora*, *Fistulipora*, *Fistulamina*, *Sulcoretepora*, *Goniocladia*, and *Tabulipora*.

From region 7f (Morocco), Viséan strata have *Archimedes* (Nekhoroshev 1929) and *Dyscritella* and *Tabulipora* (Termier and Termier 1950).

Region 8—Southern Tethys

This region contains deposits of the seaways of the southern Tethys, and includes bryozoan-bearing sediments now found in Afghanistan, Malaya, and Thailand.

In Afghanistan (region 8a), Tournaisian bryozoan assemblages (Termier and Termier 1971) comprise *Fenestella*, *Septopora*, *Nematopora*, *Nemacanthopora*, *Streblotrypa*, *Cyclotrypa*, *Sulcoretepora*, and *Leioclema*. In strata of Tournaisian–Viséan age, the bryozoans *Ascopora* and *Sulcoretepora* occur.

In Thailand and Malaya (region 8b) (Sakagami 1967, 1970, 1971*a*, 1971*b*, 1972), Upper Tournaisian–Lower Viséan bryozoans comprise *Fenestella* and *Polypora*. More diverse faunas of Viséan age contain *Fenestella*, *Polypora*, *Pennirетepora*, *Streblascopora*, *Rhabdomeson*, *Rhombopora*, *Nikiforovella*, *Fistulipora*, and *Dyscritella*. An Upper Carboniferous occurrence of probable Stephanian age has *Fenestella* and *Septopora*.

Region 9—Tasman Geosynclinal Shelf

This region on the western shelf of the Tasman geosyncline contains deposits with bryozoan assemblages in a number of basins that extend from northern Queensland to New South Wales and Tasmania. Distribution data are summarized from Campbell (1961), Campbell and Engel (1963), Campbell and McKellar (1969), Campbell and McKelvey (1972), Crockford (1947, 1949, 1951), Engel (1975), Fleming (1969, 1972), and Roberts (1963). Fenestelloids are the dominant bryozoans, and the distinctive fenestelloid *Septatopora* ranges from the Upper Tournaisian to near the top of the Viséan, reappears in the lower Westphalian, and extends into the top of the Stephanian. Tournaisian bryozoan assemblages comprise *Fenestella*, *Ptylopora*, *Septatopora*, *Streblotrypa*, *Fistulamina*, *Evactinopora*, *Ramipora*, and *Goniocladia*. An assemblage of Middle Tournaisian to Lower Viséan age has *Archimedes*, *Hemitrypa*, *Streblotrypa*, *Fistulipora*, *Fistulamina*, and *Evactinopora*. In the Viséan, there is greater diversity in the assemblages which comprise *Fenestella*, *Archimedes*, *Hemitrypa*, *Polypora*, *Ptylopora*, *Pennirетepora*, *Septatopora*, *Rhabdomeson*, *Streblotrypa*, *Fistulipora*, *Dichotrypa*, *Fistulamina*, *Goniocladia*, *Evactinopora*, *Ramiporalia*, *Ramiporella*, *Stenodiscus*, and *Leioclema*.

In the Westphalian, the fenestelloids are widespread and include *Fenestella*, *Polypora*, *Pennirетepora*, and *Septatopora*. *Rhombopora* and *Fistulamina* are also present. Stephanian rocks have the fenestelloids *Fenestella*, *Polypora*, and *Septatopora*.

Region 10—North American Cordillera

The broad shelf areas of the eastern part of the North American Cordillera are included in this region (see Gordon 1974, and Ross 1979, for distribution of seaways). Faunal development in this region contrasts strongly with the faunas of region 4. Distribution data are drawn from Burkle (1960), Condra and Elias (1944*a*), DeVoto (1965), Fritz (1963), Gordon (1974), Gordon and Duncan (1961, 1970), Hotz and Wilden (1964), Lane (1962), Malone and Perry (1965), Perry and Gutschick (1959), and Webster and Lane (1967).

In the Tournaisian, the bryozoan assemblages contain principally cryptostomes and cystoporates with *Fenestella*, *Polypora*, and *Cystodictya* being widely distributed. Other genera are the cryptostomes '*Neoreteporina*', *Ptylopora*, *Pennniretepora*, '*Ichthyorachis*', and *Fenestralia*, and the cystoporates *Cheilotrypa*, *Dichotrypa*, and *Ramiporalia*. *Hemitrypa*, *Polypora*, *Thamniscus*, and *Rhabdomeson* occur in either uppermost Tournaisian or lowest Viséan strata.

Viséan bryozoan assemblages increase in diversity and have distinctive cryptostome and cystoporate assemblages. The cryptostomes include the fenestelloids *Fenestella*, *Archimedes*, *Hemitrypa*, *Minilya*, *Lyroporella*, *Polypora*, *Ptylopora*, *Pennniretepora*, '*Ichthyorachis*', and *Fenestralia*, and the cystoporates comprise *Cystodictya*, *Dichotrypa*, *Cheilotrypa*, and *Ramiporalia*. Two other genera, the trepostome *Cyclopora* and *Worthenopora*, are reported.

In Namurian strata, documented bryozoan assemblages have less generic diversity than those of the Viséan. In Namurian A, five cryptostomes (*Fenestella*, *Archimedes*, *Polypora*, *Pennniretepora*, and *Thamniscus*), two cystoporates (*Cystodictya* and *Ramiporalia*) and the trepostome *Tabulipora* are recorded. A similar grouping of genera is reported from the Namurian B, except that *Thamniscus* is absent, and *Cyclotrypa*, *Tabulipora*, and *Stenophragmidium* are present.

In Westphalian strata, more diverse bryozoan assemblages are found. The fenestelloids are represented by *Rhombocladia*, *Fenestella*, *Archimedes*, *Polypora*, *Polyporella*, *Diploporaria*, *Pennniretepora*, and *Septopora*. The rhabdomesines comprise *Rhabdomeson*, *Ascopora*, *Rhombopora*, and *Streblotrypa*. Only one cystoporate, the distinctive *Prismopora*, and two trepostomes, *Tabulipora* and the characteristic *Rhombotrypella*, are present.

Region 11—Patagonian Shelf

In this region on the northern shelf of the Patagonia Basin, Westphalian bryozoans are recorded from Argentina (Barbosa 1971; Sabattina 1972). The faunas, as in region 9, are dominated by fenestelloids—*Fenestella*, *Levifenestella*, *Polypora*, *Pennniretepora*, *Thamniscus*, and *Septatopora*. *Rhombopora* and *Fistulamina* also are present.

BIOGEOGRAPHICAL PATTERNS

Tournaisian

Groups well-represented generically are the Fenestellidae, Acanthocladiidae, Rhabdomesidae, Fistuliporidae, Hexagonellidae, and Goniocladiidae (text-figs. 3–5, 7, 10, 11). Many genera had widespread distributions, although some endemism was present in certain families and groups. The Russian Platform and the Donetz Basin were for the most part not colonized by bryozoans.

In region 4a, midcontinent and eastern shelf areas of the United States, there were a large number of endemic as well as many cosmopolitan genera. Several genera were distinctive of the region, such as *Lyropora*, *Lyroporella* (also present in the eastern part of the North American Cordillera), *Ichthyorachis*, *Worthenopora*, *Cyclopora*, *Cliotrypa*, *Glyptopora*, and *Phractopora*. Genera such as *Hemitrypa*, *Ptylopora*, *Pennniretepora*, *Polypora*, *Nikiforovella*, *Rhabdomeson*, *Rhombopora*, *Tabulipora*, *Leioclema*, *Fistulipora*, and *Meekopora* had a wide distribution in tropical and subtropical regions of the Tournaisian (text-figs. 3–11). Other genera, including *Thamniscus*, *Streblotrypella*, *Klaucena* (*Klaucena*), *Stenopora*, and *Cyclotrypa*, having tropical to subtropical distribution in the Tournaisian were as common or as widespread as those mentioned above. Several genera, such as *Hemitrypa*, *Ptylopora*, *Streblotrypa*, and *Evactinopora* found in Tournaisian tropical

and subtropical latitudes (regions 4, 5, and 7) were present also in the southern cool temperate latitudes of the Tournaisian of the western shelf area of the Tasman geosyncline. This distribution suggests that oceanic circulation patterns supplied warm waters from the tropical regions to ameliorate these normally cool waters. Also in the tropical regions, these genera probably occurred in the deeper shelf waters where temperatures were lower. During Tournaisian time, certain genera, including *Hemitrypella*, *Acanthocladia*, *Septopora*, and *Ascopora*, were typical of tropical waters. The only cool temperate Tournaisian fauna included *Septatopora*, *Goniocladia*, and possibly *Fistulamina*, from the western Tasman geosynclinal shelf.

Viséan

Families well represented in the Viséan were the Fenestellidae, Acanthocladiidae, Arthrostylidae, Hyphasmoporidae, Nikiforovellidae, Rhabdomesidae, Stenoporidae, Dyscritellidae, Fistuliporidae, Cystodictyonidae, Hexagonellidae, and Goniocladiidae. Greater generic diversity and more widespread distribution of the genera than in the Tournaisian show that the Viséan was a very favourable time for colonization and growth of cryptostome and cystoporate bryozoans.

In the tropical to subtropical Viséan deposits of the Russian Platform, Kazakhstan shelf and Kuznetsk Basin, distinctive phylloporinid lineages are represented by *Bashkirella*, *Chainodictyon*, *Pseudohornera*, and *Rhombocladia*. The genus *Fenestella* is cosmopolitan in Viséan faunas. *Archimedes* has a disjunct pattern, similar to that in the Tournaisian, occurring in the northern tropical midcontinent and eastern shelf areas of the United States and in the southern temperate region on the western shelf of the Tasman geosyncline. In the Late Viséan, this genus appears in the eastern part of the North American Cordillera.

In tropical and subtropical areas during the Viséan, widespread genera, which were commonly also abundant, comprise *Hemitrypa*, *Polypora*, *Polyporella*, *Diploporaria*, *Pennirepora*, *Nematopora*, *Nikiforovella*, *Rhombopora*, *Tabulipora*, *Dyscritella*, *Fistulipora*, *Sulcoretepora*, and *Cyclotrypa*, *Cheilotrypa*, *Sulcoretepora*, and *Meekopora*. The genus *Septopora* had mainly a subtropical distribution but was occasionally tropical. Several genera show a tropical and subtropical distribution and also occur in the southern cool temperate region; they include *Ptylopora*, *Streblotrypa*, *Rhabdomeson*, *Stenodiscus*, *Pseudobatostomella*, *Leioclema*, *Dichotrypa*, and *Fistulamina*. On the other hand, *Hemitrypella*, *Acanthocladia*, *Streblascopora*, and *Coscinotrypa* were tropical. Genera that were tropical and subtropical but were either not as widespread and/or not as abundant are *Pseudounitrypa*, *Thamniscus*, *Fenestralia*, *Worthenopora*, *Stenopora*, *Eridopora*, and *Cystodictya*. *Stenophragmidium* was subtropical. *Septatopora*, *Goniocladia*, and *Ramiporella* were the only southern cool temperate genera.

Namurian A

In Namurian A time, a marked reduction in the number of ectoproct genera occurred, and they were not as widely distributed as in the Viséan. Genera, such as *Hemitrypa*, *Polypora*, *Ptylopora*, *Nikiforovella*, *Streblotrypa*, *Rhombopora*, *Dyscritella*, *Fistulipora*, and *Eridopora*, were less widely dispersed (text-figs. 3, 4, 6, 7, 10). Namurian phylloporinids have been recorded only from region 4a (midcontinent and eastern shelf areas of the U.S.). *Fenestella*, although widespread, is not reported from a number of regions including the central and southern Tethys. In comparison with the Tournaisian and Viséan bryozoan distribution patterns, genera were more widespread in subtropical areas and less widespread in the tropics during Namurian A time. Genera having a tropical distribution were primarily located in the midcontinent and eastern shelves of the United States (region 4a), and include *Streblascopora*, *Nicklesopora*, *Stenodiscus*, *Idioclema*, *Stenocladia*, *Cheilotrypa*, *Dichotrypa*, *Coscinotrypa*, and *Prismopora*. Genera that were widespread in the tropical and subtropical seaways include *Polypora*, *Pennirepora*, *Septopora*, *Rhabdomeson*, *Rhombopora*, *Diploporaria*, *Sulcoretepora*, *Meekopora*, *Fistulipora*, and *Dyscritella*. Several genera, *Ascopora*, *Stenopora*, *Anisotrypa*, and *Goniocladia*, had a tropical to subtropical distribution but were not as widespread and/or as abundant as those noted above. The genera *Archimedes*, *Thamniscus*, *Fenestralia*, *Streblotrypa*, *Cystodictya*, and *Glyptopora* were confined to the tropical to subtropical

regions of the midcontinent and eastern shelves in the United States and to the eastern part of the North American Cordillera, and this distribution emphasizes the more provincial occurrence of bryozoan genera in Namurian A rocks. The trepostomes *Stenophragmidium* and *Tabulipora* had mainly a subtropical distribution, but they also overlapped into tropical areas. Subtropical genera were *Hyphasmopora*, *Ptylopora*, *Eridopora*, and *Ramiporalia*.

Disjunct distributions between tropical to subtropical and southern cool temperate waters were no longer present during Namurian A time. A cooling trend had apparently reduced temperatures in the southern latitudes as well as lowered the over-all water temperatures of all oceans.

In comparison to Viséan bryozoan genera, some Namurian A genera, such as *Cheilotrypa* and *Dichotrypa*, show that there was a latitudinal shift from subtropical to tropical conditions, and this parallels the cooling trend that pushed genera into tropical areas where waters were cooler. This could indicate that the subtropics were too cool for these genera in Namurian A time.

Namurian B and C

Bryozoan assemblages were very much reduced in generic diversity and the genera less widespread, occurring in a limited number of regions. Shelves and basins on the Russian Platform, midcontinent and eastern parts of the United States, the northern Tethys, and possibly the central Tethys shared a number of genera (*Fenestella*, *Polypora*, *Sulcoretepora*, and *Tabulipora*), however, these represented continuation of lineages that were previously present in these regions in Namurian A time. Some genera are found in the Donetz Basin or north-western Europe, e.g. *Rhabdomeson*, *Tabulipora*, and *Pennireteporа*, as well as in most of the regions noted above. Shelves and basins on the Russian Platform, mid-continent and eastern parts of the United States, and the northern Tethys were apparently refugia for many genera, as well as the sites for the evolution of new lineages. On the Russian Platform *Hemitrypa* became established for the first time but was no longer present in the assemblages on the midcontinent and eastern shelves of the United States. The earliest occurrence of the distinctive genus *Rhombotrypella* is also of Namurian B/C age on the Russian Platform. *Ascopora*, *Nikiforopora*, and *Stenodiscus* were elements of the isolated Russian Platform faunas.

On the shelves of the midcontinent and eastern parts of the United States, genera such as *Archimedes*, *Stenopora*, *Streblotrypa*, *Glyptopora*, and *Prismopora* survived. *Archimedes* also dispersed into the eastern part of the North American Cordillera. In the northern Tethys, a group of genera (*Streblascopora*, *Streblotrypella*, *Saffordotaxis*, *Nikiforovella*, *Primorella*, *Hayasakapora*, *Dyscritella*, *Pseudobatostomella*, *Ulrichotrypa*, *Coscinotrypa*, *Meekoporella*, and *Ramipora*) became endemic lineages and formed the nucleus for the evolution of a Tethyan fauna.

Westphalian

Bryozoans during this stage showed a resurgence in generic diversity and they were widespread. *Fenestella* had a cosmopolitan distribution, similar to that during the Viséan. *Polypora*, *Pennireteporа*, *Rhombopora*, *Prismopora*, and *Rhombotrypella* were also cosmopolitan. Dispersal of *Rhombotrypella* from the Russian Platform apparently took place via a northern route through the Franklinian seas to the eastern part of the North American Cordillera. It doesn't occur in the midcontinent and eastern part of the United States until the Early Permian. *Rhombocladia*, *Archimedes*, *Septopora*, *Streblotrypa*, and *Tabulipora* extended throughout the Russian Platform, the shelves of the midcontinent and eastern United States, and the eastern part of the North American Cordillera. During this time *Hemitrypa* occurred only on the Russian Platform and the eastern part of the North American Cordillera and *Ascopora* only in the Donetz Basin and eastern part of the North American Cordillera. The Tethyan fauna contained *Streblascopora*, *Streblotrypella*, *Nikiforovella* (this genus was present also on the Russian Platform and in the Donetz Basin), *Primorella*, *Saffordotaxis*, *Hayasakapora*, *Stenopora*, *Nipponstenopora*, *Dyscritella*, *Pseudobatostomella*, *Leioclema*, and *Ulrichotrypa*. The distinctive genus *Septatopora* was distributed in the cool temperate regions of both the Tasman geosynclinal shelf and the North Patagonian shelf during the Westphalian. Certain genera, such as *Nematopora*, *Nikiforopora*, *Stenodiscus*, *Crustopora*, and

Ramiporella, appear to have been restricted to the Russian Platform. Exchange of some genera between the Russian Platform and the northern Tethys is suggested by the occurrence in both regions of *Nikiforovella*, *Fistulipora*, *Sulcoretepora*, and *Meekopora*.

Stephanian

Generic diversity increased, particularly during the latter half of this stage. Genera, such as *Rhombocladia*, *Fenestella*, *Polypora*, *Pennniretepora*, *Septopora*, *Streblotrypa*, *Rhabdomeson*, and *Rhombopora*, had a cosmopolitan distribution. Three centres of high diversity, the Russian Platform, Donetz Basin, and the eastern part of the North American Cordillera, contained several genera that gave rise to lineages in the Permian. On the Russian Platform these genera were *Bashkirella*, *Hemitrypa*, *Nematopora*, and *Ulrichotrypella*. On the midcontinent and eastern shelves of the United States these genera were *Megacanthopora*, *Stenopora*, *Stenodiscus*, *Tabulipora*, *Leioclema*, *Fistulipora*, *Cyclotrypa*, *Eridopora*, and *Meekoporella*. The distinctive genera *Archimedes*, *Rhombotrypella*, and *Ascopora* occurred in the Russian Platform, Donetz Basin, and the eastern part of the North American Cordillera. They represent genera which gave rise to extensive lineages in the Permian. Features of the Tethyan bryozoan faunas for this time interval lack adequate documentation and are not decipherable.

SUMMARY

Bryozoan faunas in the early Carboniferous were the culmination of Devonian bryozoan faunas and they were gradually replaced by Middle and Late Carboniferous faunas which, in turn, were largely the progenitors of Early Permian bryozoan faunas. Distribution patterns of Carboniferous bryozoans show widespread dispersal of many genera, particularly during the Viséan. In several regions, such as the shelves of the midcontinent and eastern United States, endemism was a distinctive feature. Generic diversity fluctuated markedly during the Carboniferous in various faunas and at different times. The Viséan, for example, was a time of high diversity, whereas the Namurian B and C were times of greatly reduced diversity of bryozoan genera throughout the world. Westphalian bryozoans showed a resurgence of diversity and became increasingly widespread so that several genera were almost cosmopolitan. The distribution patterns at that time suggest that the Franklinian seas were warmer and no longer were a barrier to the dispersal of many bryozoans. By Stephanian time the major lineages of the bryozoans which form the dominant parts of the Early Permian faunas were well established. Generic diversity continued to increase during Stephanian time, particularly in the tropical and subtropical shelves on the opposite sides of Pangaea.

Diversity fluctuated not only regionally at different times, but also as changes in local ecological conditions, in particular in shelf and basinal areas. These shifts in ecological conditions were most readily exemplified in coal basins, such as in regions 1 and 3, where marked sedimentological differences in successive horizons and associated changes in bryozoan assemblages can be readily traced. These ecological associations are characterized by particular genera.

On a broader scale, the bryozoan faunas characterized geographical regions. These faunas dispersed from one region to another as transgressions, climatic patterns, and tectonic events modified the different seaways. As a result, many different paths of faunal dispersal are encountered. As the Carboniferous period progressed, some faunas dispersed from the Russian Platform to the eastern part of the North American and Tethyan regions. Other faunas from the midcontinent and eastern parts of the United States dispersed to the eastern part of the North American Cordillera and the Russian Platform. Still others dispersed from the eastern part of the North American Cordillera to the midcontinent and eastern parts of the United States.

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