BIOGEOGRAPHY OF PERMIAN ECTOPROCT BRYOZOA

by JUNE R. P. ROSS

ABSTRACT. Earliest Permian (Asselian and early Sakmarian) ectoprocts were widespread, included many lineages of Carboniferous origin, and had a large number of cosmopolitan genera. Marked geographic differences in their generic diversity suggest that physical parameters, such as temperature, were important factors in controlling ectoproct distributions. Late Sakmarian and Artinskian ectoprocts show a number of distribution patterns, as well as the beginning of a clearly defined Tethyan fauna with a number of endemic genera. During the Artinskian, Tethyan genera have greater dispersal so that certain areas, such as Australia and Pakistan, contain a number of Tethyan genera, whereas other areas, such as the Uralian and Franklinian regions, received only a few immigrant Tethyan genera.

By the early part of the Kazanian, ectoprocts are strongly provincial with Tethyan faunas having both high diversity and endemism and non-Tethyan faunas having low diversity. Ectoprocts from Zechstein strata have unusually low diversity, perhaps because of major fluctuations in temperature or salinity, and Australian ectoprocts are also less diverse at this time. Dzhulfian ectoprocts are greatly reduced in generic diversity, geographic distribution, and in total numbers because many lineages become extinct near the middle of the Late Permian. Most ectoprocts of the late Dzhulfian are remnants of Tethyan endemic lineages and only a few genera survive into the earliest Triassic before becoming extinct.

ECTOPROCTS are significant elements in many Permian marine faunas and environments. Cystoporates and cryptostomes are commonly dominant, whereas trepostomes are far less abundant. Text-figs. 1–3 show the Permian range and geographic distributions of ectoproct genera arranged by families. This classification in general closely follows those given by Morozova (1970) and Gorjunova (1975) and has been updated and modified on the basis of additional published and unpublished information on particular genera. Cystoporates, having 25 genera in 6 families, gradually increase in abundance and diversity through the early and middle parts of the Permian and become restricted in distribution in the later part of the Permian. Cryptostomes, having 58 genera in 12 families, developed in a similar pattern to the cystoporates in the Permian. Trepostomes, having 19 genera in 6 families and uncertain family assignment for 2 of these genera, only modestly increased their diversification through the Permian until late Kazanian time when drastic reduction and extinction in numbers of genera occurred. The stratigraphic terminology and correlation of sections in North America, the Russian Platform, and two Tethyan regions (Transcaucasus, and Darvas and Pamir), as used in this paper, are shown in text-fig. 4.

Ectoprocts are among a large number of marine benthic invertebrates that came close to extinction near the end of Permian time. For most invertebrate groups, phylogeny, geographic distribution, and dispersal history are incompletely known or have been only partially examined for the Permian Period. As a result the details of the faunal histories of different invertebrate groups are difficult to relate to each other and to the many physical events which may be deduced from the geologic record. This study summarizes the available data for ectoprocts in terms of their patterns of geographic distribution, their dispersal, and the changes in these patterns during the Permian.

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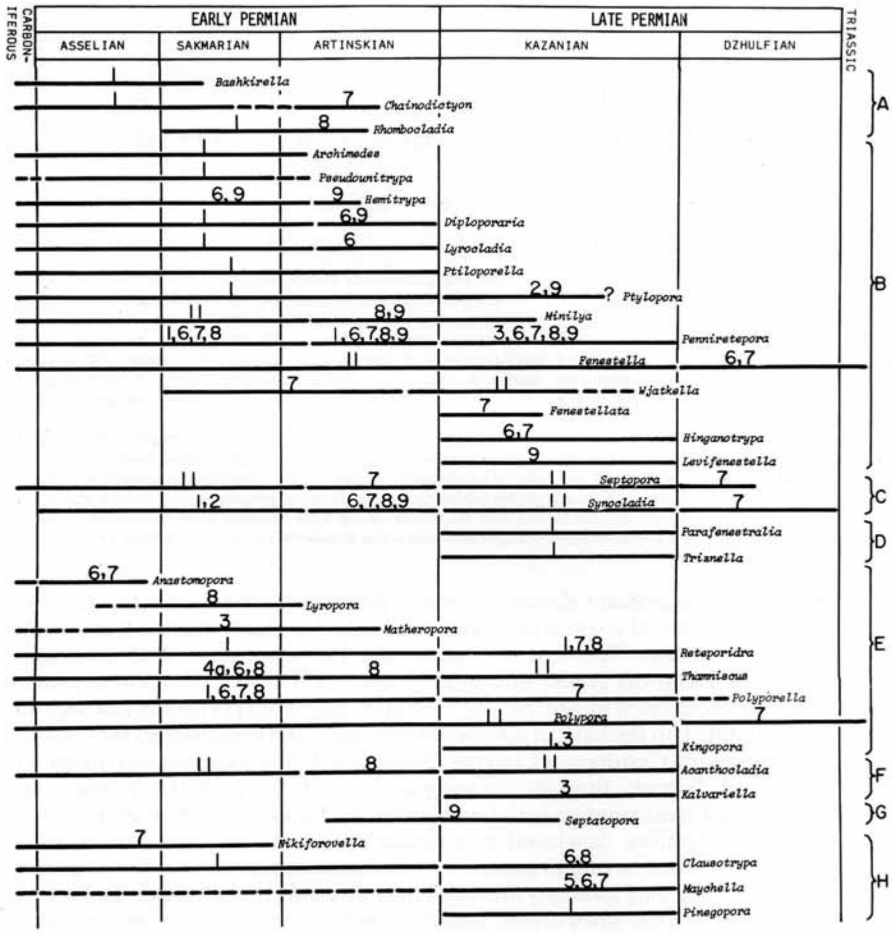
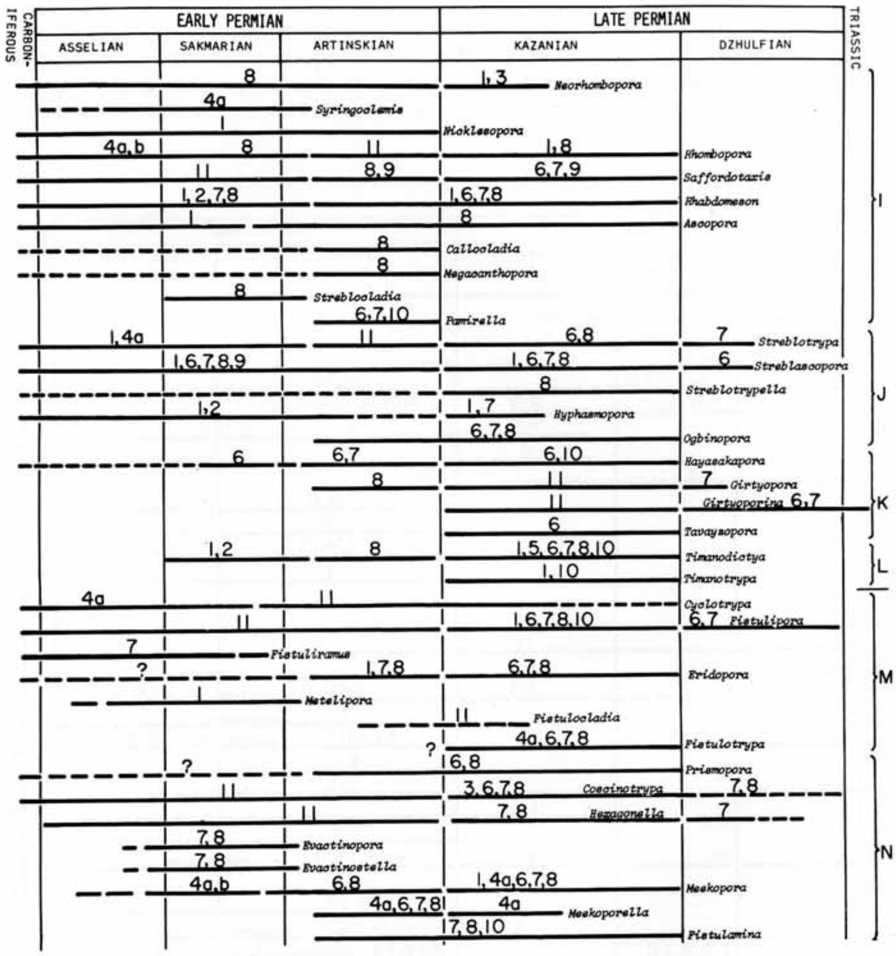
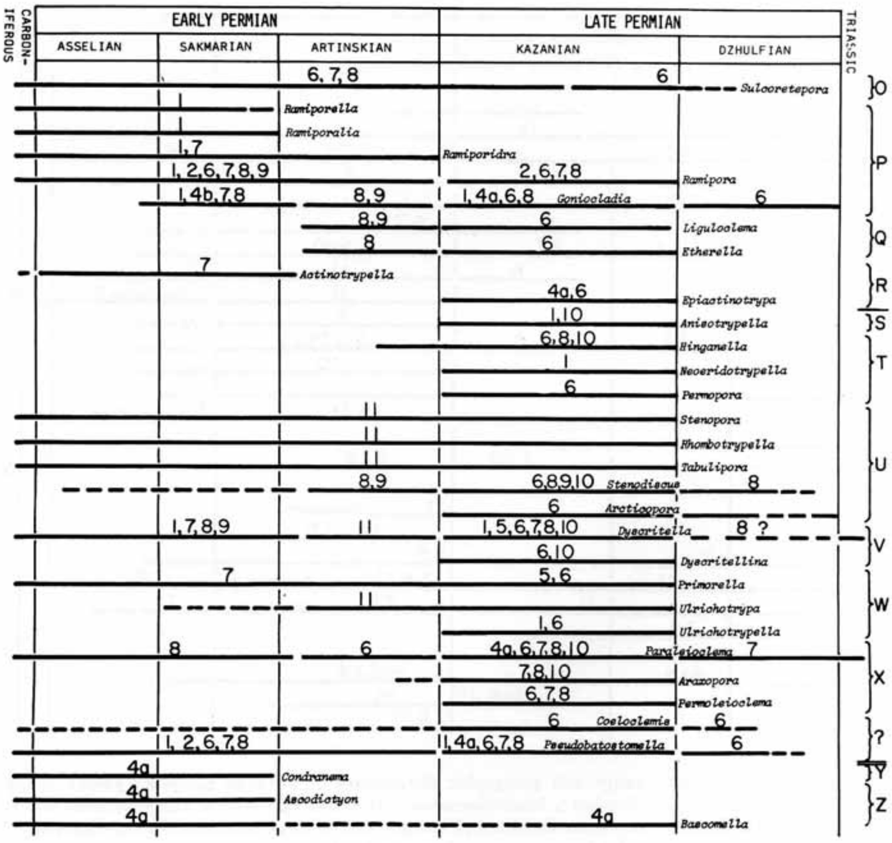


TEXT-FIG. 1. Stratigraphic range and geographical distribution of Permian ectoproct genera; class Stenolaemata, order Cryptostomata: families A, Phylloporinidae, B, Fenestellidae, C, Septoporidae, D, Fenestraliidae, E, Polyporidae, F, Acanthocladiidae, G, Septatoporidae, and H, Nikiforovellidae. Geographical regions are: 1, Russian Platform and Uralian Sea; 2, Franklinian Sea and adjacent shelf; 3, Zechstein Sea; 4, North America, southern part and near-by areas (4a, west Texas and midcontinent; 4b, Andean Sea); 5, parts of northern Siberia and adjacent regions, U.S.S.R.; 6, northern Tethys including the Maritime Territory and Kabarovsk region of U.S.S.R., Japan, and western parts of North American Cordillera; 7, central Tethys including Transcaucasus, Darvas, Pamir, Tibet, Mongolia, and south-west China; 8, southern Tethys including parts of Afghanistan, Salt Range of Pakistan, Western Australia, Malaya, and Thailand; 9, Tasman Geosyncline; 10, North American Cordillera, eastern part; and 11, cosmopolitan distribution. See also text-fig. 5.



TEXT-FIG. 2. Stratigraphic range and geographic distribution of Permian ectoproct genera; order Cryptostomata (continued): families I, Rhabdomesidae, J, Hyphasmoporidae, K, Girtyoporidae, and L, Timanodictyidae. Order Cystoporata: families M, Fistuliporidae, N, Hexagonellidae. See text-figs. 1 and 5 for key to numbered geographical regions.

Information from this group of organisms should contribute to a more thorough understanding of late Palaeozoic biogeographical relationships and may have important implications concerning the time, and the nature, of changes in marine connections between different areas. It may help in elucidating changes in characteristics of ocean currents, and changes in local and world climates and in temperature gradients.



TEXT-FIG. 3. Stratigraphic range and geographical distribution of Permian ectoproct genera; order Cystoporata (continued): families O, Sulcoreteporidae, P, Goniocladiidae, Q, Etherellidae, and R, Actinotrypidae. Order Trepostomata: families S, Anisotrypidae, T, Eridotrypellidae, U, Stenoporidae, V, Dyscritellidae, W, Ulrichotrypellidae, X, Araxoporidae, and (?) *Incertae sedis*. Class Gymnolaemata, order Ctenostomata: families Y, Vinellidae and Z, Ascodictyidae. See text-figs. 1 and 5 for key to numbered geographical regions.

PALAEOGEOGRAPHIC DISTRIBUTION

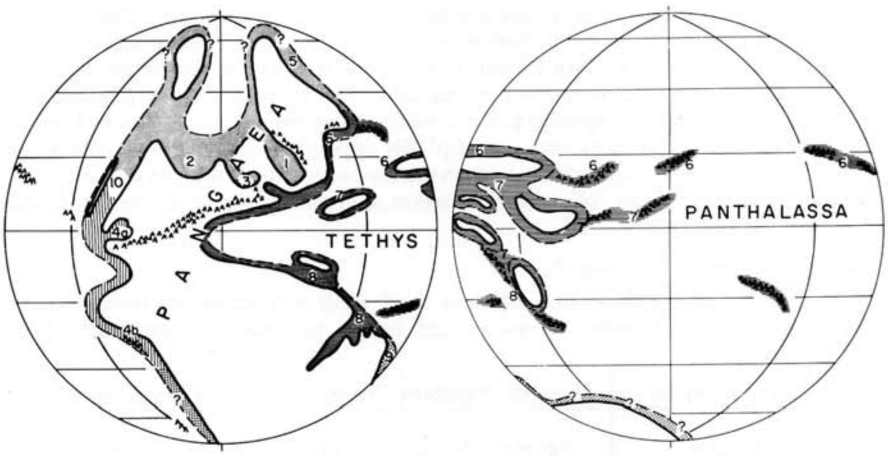
Information on phyletic evolution and biogeographic patterns for Permian ectoprocts, as with other invertebrate groups, is far more complete for certain regions of the world and particular rock sequences than for others. In some areas large gaps exist in our knowledge of the composition of ectoproct faunas. Extensive faunas are known from the Russian Platform, Ural Mountain region, Transcaucasus, Pamir and Darvas region, Maritime Territory of the U.S.S.R., Kabarovsk, and Far East regions of the U.S.S.R. Newly described faunas are available from China, Tibet, Japan, Thailand, and Malaya. Described ectoproct faunas from western and eastern Australian basins provide considerable data, as do early studies on faunas from Timor. Only sketchy information is available from the Salt Range, Pakistan, and adjoining areas of India and Kashmir, and also for the Carnic Alps. In the mid 1960s ectoprocts from the German Zechstein strata were re-examined and some information for England and north-east Greenland and Spitsbergen is available. Permian faunas of North America and South America remain very incompletely studied. These various faunas are assigned to ten palaeogeographic regions in reconstructing the ectoproct distributional patterns (text-fig. 5). The following discussion summarizes major ectoproct faunal features of these regions.

Russian Platform and Uralian Sea

On the Russian Platform and adjacent shelf areas rich ectoproct faunas were a continuation of Carboniferous faunas and extend up into the later part of the

TEXT-FIG. 4. Permian correlation chart comparing stratigraphic nomenclature in North America, Russian Platform, and two Tethyan regions (Transcaucasus, and Darvas and Pamir).

Kazanian (Nikiforova 1939; Trizna 1950; Shulga-Nesterenko 1952; Trizna and Klautsan 1961; and Morozova 1970). In the Asselian and Sakmarian fenestrate cryptostomes of the families Fenestellidae and Polyporidae were dominent members of the hydractinoid reefs and adjacent shelf biota. In addition, the cryptostomes *Ascopora*, *Nicklesopora*, *Streblotrypa*, *Acanthocladia*, and *Timanodictya*, the stenoporid trepostome *Rhombotrypella*, and the cystoporates, *Hexagonella*, *Fistulipora*, and *Ramipora*, were also part of this rich fauna. Although only sixteen genera are listed for the Sakmarian of this region, the fauna is rich and diverse in species.



TEXT-FIG. 5. Palaeogeographic reconstruction for the early part of the Late Permian. Numbers refer to the following regions: 1, Russian Platform and Uralian Sea; 2, Franklinian Sea and adjacent shelf; 3, Zechstein Sea; 4, North America, southern part (4a), and Andean Sea (4b); 5, parts of northern Siberia and adjacent regions, U.S.S.R.; 6, northern Tethys including the Maritime Territory and Kabarovsk region of U.S.S.R., Japan, and western parts of North American Cordillera; 7, central Tethys including Transcaucasus, Darvas, Pamir, Tibet, Mongolia, and south-west China; 8, southern Tethys including parts of Afghanistan, Salt Range of Pakistan, Western Australia, Malaya, and Thailand; 9, Tasman Geosyncline; and 10, North American Cordillera, eastern part.

During Early Artinskian (Irginian) time, generic diversity remained high and ectoprocts were abundant in reef limestones and bedded limestone shelf facies (Trizna and Klautsan 1961). Only a few Sakmarian species persisted into the Artinskian so that the majority of species are new. The greatest number of new species belong to *Fenestella* and *Polypora*. *Rhombotrypella*, *Penniretepora*, *Clausotrypa*, and *Hexagonella* also flourished. However, *Timanodictya*, *Reteporidra*, *Lyrocladia*, *Ascopora*, and *Nicklesopora* were less abundant than they were in the Sakmarian. Goniocladiids, such as *Goniocladia*, became a significant part of the fauna in the early and middle part of Artinskian time and new genera, such as *Ptylopora* and *Ptiloporella*, first appear in Early Artinskian time.

During Middle Artinskian (Sarginian) time, generic diversity continued to be high and the greatly varied lithofacies of reef and intrareef environments were highly suited for ectoprocts. About half of the species are new and the remainder continue from Sakmarian or early Artinskian ectoproct faunas. The trepostomes *Pseudobatostomella* and *Stenopora*, the fistuliporid cystoporate *Eridopora*, and some rhabdomesid cryptostomes are significant parts of these ectoproct assemblages. Species of *Fenestella* and *Polypora* remained important in the fauna.

Before the end of Artinskian time, generic diversity decreased markedly in ectoprocts, apparently as a result of changes in the Uralian Geosyncline and on the Russian Platform due to tectonic movements (Nalivkin 1973). *Fenestella, Polypora, Rhombotrypella, Pseudobatostomella*, and *Streblotrypa* have new species assemblages and are well represented. *Paraleioclema* and *Tabulipora* are additions to the assemblages. Both *Clausotrypa* and *Hexagonella*, however, disappear before the end of the Artinskian.

In Kazanian time (Morozova 1970) the generic diversity gradient for ectoprocts increases from the southern part of the Uralian Sea north and westward towards the Arkhangel region. Eleven genera are present in the southern part of the Uralian Sea in the region of Tatarian A.S.S.R., whereas in the north, twenty-six genera are present. Genera that are well represented in all parts of this Uralian Sea include the trepostomes *Pseudobatostomella, Dyscritella, Rhombotrypella*, and *Tabulipora*, and the cryptostomes *Wjatkella, Fenestella, Streblascopora, Pinegopora, Parafenestralia*, and *Triznella*. In the northern region these genera are joined by six other genera, the trepostomes *Ulrichotrypella* and *Anisotrypella*, the cystoporates *Goniocladia* and *Meekopora*, and the cryptostomes *Timanotrypa* and *Girtyoporina*. No ectoprocts are reported in younger units of the Late Permian on the Russian Platform and adjacent regions.

Franklinian Sea, Barents Shelf, and adjacent shelves

Although not well known, ectoprocts from this region, which stretches from Novaya Zemlya to Spitsbergen, Greenland, and the Canadian Arctic Islands, have affinities with faunas of the Russian Platform and Uralian Sea. In north-east Greenland, Sakmarian strata contain the trepostomes *Rhombotrypella, Stenopora*, and *Tabulipora* and the cryptostomes *Polypora, Fenestella*, and *Timanodictya* (Ross and Ross 1962). A sparse Early Permian fauna from Novaya Zemlya has *Pseudobatostomella*?, *Fenestella, Ramipora*, and *Hyphasmopora* (Nikiforova 1936). From Spitsbergen, an Upper Permian fauna of probable Kazanian age has *Fenestella, Polypora, Ptylopora, Septopora, Stenopora, Tabulipora*, and *Ramipora* (Nikiforova 1936; Malecki 1968).

Zechstein Sea (Late Permian) of England, Germany, Poland, and southern Baltic region

In western Europe, fenestrate cryptostomes dominate the Late Permian faunas but have low generic diversity. In this region the polyporid *Kingopora* and *Fenestella* have a wide distribution and the fauna may also include the cryptostomes *Thamniscus, Acanthocladia, Penniretepora*, and *Synocladia*, the trepostome *Stenopora*, and the hexagonellid cystoporate *Coscinotrypa* (Dreyer 1961).

North America, southern part

Faunas from this region are poorly known but assemblages have been described from the midcontinent region of the United States (Moore and Dudley 1944) and Texas (Girty 1908; Morozova 1966, 1970). In the midcontinent region (Nebraska, Kansas, Oklahoma) cryptostomes are abundant in strata of Wolfcampian age and include *Fenestella, Polypora, Septopora, Thamniscus, Streblotrypa, Rhombopora,* and *Syringoclemis.* The Wolfcampian of Nebraska contains the fistuliporid cystoporate *Cyclotrypa* and in Kansas the hexagonellid cystoporate *Meekopora.* These cystoporates are present also in the Leonardian with *Meekoporella* and *Fistulipora* and all four genera extend into the early Guadalupian (Wordian). In the Guadalupian the cystoporates *Goniocladia* and *Epiactinotrypa* also appear. Early Guadalupian cryptostomes are characterized by increased diversity with *Acanthocladia, Fenestella, Polypora, Thamniscus, Girtyopora,* and *Girtyoporina.* The trepostomes are *Pseudobatostomella*?, *Stenopora,* and *Paraleioclema*? Younger Guadalupian (Capitanian) faunas contain the cystoporates *Fistulipora* and *Goniocladia,* the cryptostomes *Acanthocladia, Fenestella,* and *Girtyoporina,* and the trepostome *Paraleioclema.*

Andean Sea

Two Early Permian (Wolfcampian) faunas in southern Peru contain the cystoporates *Goniocladia* and *Meekopora,* the cryptostomes *Acanthocladia, Fenestella, Polypora, Septopora,* and *Rhombopora* (Chronic 1953).

Parts of northern Siberia and adjacent regions, U.S.S.R.

A late Permian fauna from the Kolyma and Omolon massifs and adjacent regions includes an abundance of cryptostomes, such as *Fenestella, Wjatkella, Maychella, Polypora, Synocladia,* and *Timanodictya,* the cystoporate *Fistulipora,* and the trepostomes *Dyscritella* and *Primorella* (Nekhoroshev 1935, 1959; Morozova 1970).

Northern Tethyan Sea

This region includes Japan, the Maritime Territory of the U.S.S.R., Kabarovsk region, and possibly parts of the north-eastern Siberian region of the U.S.S.R. In Japan, ectoproct faunas are abundant in a number of depositional basins and range through most of the Permian (Sakagami 1970). Asselian and Sakmarian ectoprocts (Zone of *Pseudoschwagerina*) include the cystoporates *Sulcoretepora, Fistulipora,* and *Coscinotrypa,* the trepostomes *Pseudobatostomella, Stenopora,* and *Tabulipora,* and a great many cryptostomes, such as *Anastomopora, Fenestella, Penniretepora, Polypora, Thamniscus, Hayasakapora,* and *Streblascopora.* Artinskian ectoprocts (Zone of *Parafusulina*) include *Fistulipora, Pseudobatostomella, Stenopora, Fenestella, Penniretepora, Hayasakapora,* and *Streblascopora,* which range up from the zone below, and hexagonellid cystoporates *Meekopora, Meekoporella,* and *Prismopora,* which show considerable diversity. In the Zone of *Neoschwagerina* (Early Guadalupian as correlated by Ross and Nassichuk 1970), many genera range up from the Zone of *Parafusulina* and additional genera include the hexagonellid *Fistulamina,* the cryptostomes *Saffordotaxis* and *Septopora,* and the trepostome *Ulrichotrypella.* In the Japanese succession the youngest ectoprocts occur in the Zone of *Yabeina–Lepidolina* (Late Guadalupian to Early Dzhulfian) and include many cystoporates, such as

Coscinotrypa, *Fistulipora*, *Goniocladia*, *Meekopora*, *Prismopora*, *Ramipora*, and *Sulcoretepora*. Cryptostomes are represented by *Clausotrypa*, *Rhabdomeson*, *Septopora*, and *Synocladia* and trepostomes remain sparse.

In the Maritime Territory and Kabarovsk region of the U.S.S.R., Permian strata are structurally complex and have an abundant ectoproct fauna (Nikitina, Kiseleva, and Burago 1970). The Early Permian part of these faunas is poorly known. Strata of Kazanian age contain *Coscinotrypa*, *Fenestella*, *Polypora*, *Dyscritella*, *Paraleioclema*, and *Permoleioclema* and, from the upper part of the Zone of *Yabeina*, Morozova (1970) lists thirty genera, eighteen of which occurred in both the Maritime Territory and Kabarovsk region. Both areas contain the cystoporates *Fistulamina* and *Fistulipora*, the trepostomes *Dyscritella*, *Hinganella*, *Ulrichotrypella*, *Stenodiscus*?, *Tabulipora*, *Paraleioclema*, and abundant cryptostomes, such as *Clausotrypa*, *Fenestella*, *Polypora*, *Septopora*, *Girtyoporina*, *Girtyopora*, *Rhabdomeson*, *Streblascopora*, and *Maychella*.

Central Tethyan Sea

This region includes the Transcaucasus, Darvas, Pamir, part of Afghanistan, Tibet, Mongolia, and south-west China.

In the Transcaucasus region, cryptostomes dominate the Late Permian fauna (Morozova 1970). The ectoprocts in the Gnishikian (Early Guadalupian) include the cryptostomes *Fenestella*, *Polypora*, *Septopora*, *Rhabdomeson*, *Streblascopora*, and *Ogbinopora*, the cystoporates *Fistulipora*, *Cyclotrypa*, *Hexagonella*, and *Sulcoretepora*, and the trepostomes *Paraleioclema* and *Araxopora*. In the Kachikian (later Guadalupian) only the trepostome *Araxopora* is reported. The Dzhulfian has the cryptostomes *Polypora*, *Septopora*, *Synocladia*, *Streblotrypa*, and *Girtyoporina*, and the cystoporate *Fistulipora*.

In the Darvas and Pamir region ectoproct faunas range from Asselian into Pamirian strata (Gorjunova 1975). In the Early Permian ectoprocts are abundant, whereas Late Permian ectoprocts are sparse. In south-west Darvas, Asselian and Sakmarian ectoprocts include the cystoporates, *Actinotrypella*, *Fistulipora*, *Goniocladia*, *Ramiporida*, and *Sulcoretepora*, the trepostomes *Rhombotrypella* and *Primorella*, and the cryptostomes *Rhabdomeson* and *Streblascopora*. Artinskian ectoprocts are less diverse and include the cystoporates *Cyclotrypa*, *Eridopora*, *Fistulipora*, and *Hexagonella*. Sakmarian deposits in south-east Pamir have biostromes of the cryptostome *Nikiforovella*. Artinskian deposits have a more diverse fauna including the cystoporates *Fistulamina* and *Ramiporidra*, the trepostomes *Dyscritella* and *Rhombotrypella*, and abundant cryptostomes *Pamirella* and *Streblascopora*.

In south-west Darvas the lower part of the Upper Permian has no recorded ectoprocts and, in the upper part of the Upper Permian, only the cystoporate *Fistulipora* is thus far reported. In central Pamir Late Permian ectoprocts include the cystoporates *Eridopora* and *Fistulipora* and the cryptostome *Ogbinopora*. In south-east Pamir the cystoporate *Hexagonella* and the trepostome *Araxopora* are reported from the Murgabian.

In central eastern China, in the Yangshin Series, the Lower Permian Chihsia Limestone has the cosmopolitan genera *Fenestella*, *Polypora*, *Septopora*, and *Fistulipora* (Loo 1958). The first three of these genera, as well as *Acanthocladia*, *Dyscritella*, and *Stenopora*, occur also in the Upper Permian Maokou Limestone in the

Yangshin Series. The succeeding Loping Series contains *Fistulipora*, *Polypora*, *Septopora*, *Penniretepora*, *Synocladia*, *Pseudobatostomella*, and *Paraleioclema*. The Jisu Honguer Limestone of Inner Mongolia has a fauna which is similar to that of the Maokou Limestone. However, the fauna also contains the cryptostomes *Streblascopora*, *Maychella*, *Rhabdomeson*, *Girtyopora*, and *Girtyoporina*, the cystoporates *Fistulamina* and *Hexagonella*, and the trepostomes *Tabulipora* and *Paraleioclema* (Grabau 1931; Morozova 1970).

Southern Tethyan Sea

This region includes central eastern Afghanistan, the Salt Range of Pakistan, Thailand, Malaya, Western Australia, and Timor.

In central eastern Afghanistan, ectoprocts are abundant in Sakmarian to Kazanian strata (Termier and Termier 1971). Sakmarian and Artinskian faunas have many polyporids and fenestellids, such as *Polypora* (*Pustulopora*), *Polypora* (*Paucipora*), *Fenestella*, and *Minilya*. Other cryptostomes are *Rhabdomeson*, *Rhombopora*, *Saffordotaxis*, and *Septopora*. The cystoporates include *Cyclotrypa*, *Goniocladia*, *Meekopora*, and *Sulcoretepora*. The relatively sparse trepostomes include *Dyscritella*, *Rhombotrypella*, and *Tabulipora*. Several genera, including *Rhombotrypella* and the abovementioned four cystoporates, extend up into the Kubergandinian. The cryptostomes *Ascopora*, *Streblascopora*, *Septopora*, and *Acanthocladia* also appear in the Kubergandinian. In the Murgabian, *Tabulipora* reappears and the cystoporates include *Coscinotrypa*, *Goniocladia*, and *Hexagonella*, and the cryptostomes are *Streblascopora*, *Rhabdomeson*, *Thamniscus*, and *Reteporidra*.

In the Salt Range of Pakistan, Early Permian (Artinskian) ectoproct faunal assemblages have the cystoporates *Fistulipora* and *Hexagonella*, the trepostomes *Stenodiscus* and *Stenopora*, and the cryptostomes *Fenestella*, *Polypora*, *Acanthocladia*, *Thamniscus*, *Rhombopora*, and *Girtyopora*; not a markedly diverse fauna. In the Late Permian the two cystoporates, *Fistulipora* and *Hexagonella*, are joined by *Goniocladia* and the cryptostomes *Polypora*, *Synocladia*, and *Rhombopora* (Waagen and Pichl 1885; Waagen and Wentzel 1886).

In Thailand Late Sakmarian to Late Artinskian ectoproct faunas have many cystoporates, including *Fistulipora*, *Coscinotrypa*, *Goniocladia*, *Hexagonella*, *Liguloclema*, *Sulcoretepora*, and *Ramipora*, many cryptostomes, including *Acanthocladia*, *Fenestella*, *Polypora*, *Thamniscus*, *Penniretepora*, *Rhabdomeson*, *Ascopora*, *Streblascopora*, *Streblotrypa*?, *Rhombopora*, *Ogbinopora*, and *Timanodictya*?, and the trepostomes *Dyscritella* and *Leioclema*? (Sakagami 1970, 1976). Malaya has a distinctive Guadalupian fauna having *Clausotrypa*, *Araxopora*, *Pseudobatostomella*, *Paraleioclema*, and *Fenestella* (Sakagami 1970, 1976).

In the western part of Australia the Fitzroy trough of the Canning Basin and the Carnarvon Basin (Crockford 1951, 1957; Ross 1963) have Sakmarian ectoproct assemblages containing the cystoporates *Evactinostella*, *Fistulipora*, and *Hexagonella*, the cryptostomes *Streblascopora*, *Fenestella*, *Lyropora*, and *Polypora*, and the trepostomes *Dyscritella*, *Stenopora*, and *Paraleioclema*. Artinskian faunas show much greater diversity with the addition of the cystoporates *Prismopora*, *Eridopora*, *Etherella*, *Goniocladia*, *Liguloclema*, *Fistulamina*, *Evactinopora*, and *Ramipora*, and the cryptostomes *Acanthocladia*, *Septopora*, *Synocladia*, *Minilya*, *Saffordotaxis*, *Rhabdomeson*, *Megacanthopora*?, *Callocladia*?, *Rhombocladia*, *Streblotrypa*, and *Streblocladia*. In the Bonaparte Gulf Basin, strata of probable early Late Permian age contain a sparse fauna of *Fistulipora*, *Ramipora*, *Streblotrypa*, and *Rhombopora*. In the Fitzroy trough, Upper Permian strata of Tatarian age have an ectoproct assemblage with *Dyscritella* and *Stenodiscus*.

Not all ectoproct faunas described from Timor (Bassler 1929) are assignable to stratigraphically identified units. Those faunas which are placed stratigraphically include faunas of Early Permian and Late Permian ages. The Bitauni Beds (Artinskian) have a sparse fauna comprised of the cystoporate *Fistulipora*, the cryptostomes *Fenestella*, *Rhombopora*, and *Streblascopora*, and the trepostomes *Hinganella* and *Ulrichotrypa*. In the Basleo Beds (early Late Permian) cystoporates became more abundant and include *Eridopora*, *Fistulotrypa*, *Fistulipora*, *Goniocladia*, and *Hexagonella* and occur with the trepostome *Hinganella* and the cryptostomes *Streblascopora* and *Fenestella*. The overlying Amarassi Beds have a sparse fauna consisting of *Clausotrypa*, *Fenestella*, *Fistulipora*, and *Stenopora*. Younger strata, of probable Late Kazanian age, contain the two cryptostomes *Streblotrypella* and *Rhabdomeson*.

Tasman Geosyncline (eastern Australia)

Permian ectoproct faunas in the northern part of the Tasman Geosyncline have a pattern of diversity similar to that of Western Australia. Sakmarian faunas of the Bowen Basin and Springsure Shelf, Queensland (Wass 1969), are sparse and contain *Fenestella* and *Polypora*. In Artinskian faunas, cystoporates and cryptostomes are more abundant and include *Liguloclema*, *Goniocladia*, *Fistulipora*, *Ramipora*, *Diploporaria*, *Penniretepora*, *Polypora*, *Minilya*, *Saffordotaxis*, *Rhombopora*, and *Streblascopora*. The trepostomes are *Dyscritella*, *Stenodiscus*, and *Stenopora*. The Late Permian (Kazanian) fauna has the cryptostomes *Fenestella*, *Polypora*, *Septatopora*, *Levifenestella*, *Penniretepora*, *Ptylopora*, and *Saffordotaxis*, and the trepostomes *Paraleioclema*?, *Stenodiscus*, and *Stenopora*.

In the southern part of the Tasman Geosyncline (Sydney Basin of New South Wales), the Early Permian (Sakmarian) faunas are restricted and include only *Dyscritella* and *Stenopora*. In slightly younger (Artinskian) strata species diversity increases markedly, particularly in the genus *Stenopora*. Also, additional genera are found in this part of the sequence and include *Fenestella*, *Minilya*, *Polypora*, *Rhombopora*, and *Pseudobatostomella*? Strata of the same age in Tasmania also show great species diversity in *Stenopora* and, in addition, also contain *Stenodiscus* and *Hemitrypa*?

North American Cordilleran Geosyncline and adjacent shelf

A published abstract on the Guadalupian faunas from this region (Gilmour and Snyder 1976) indicates that the generic composition of assemblages from north-eastern Washington, north-eastern Nevada, and central Wyoming has similarities with the faunas of the Russian Platform, Maritime Territory of the U.S.S.R., and Japan. *Fenestella*, *Polypora*, *Timanotrypa*, *Fistulipora*, *Anisotrypella Paraleioclema*, and *Stenodiscus* occur in all three regions. Other genera such as *Wjaktella*, *Girtyopora*, *Girtyoporina*, *Hayasakapora*, *Pamirella*, *Timanodictya*, *Cyclotrypa*, *Hinganella*, *Stenopora, Araxopora, Rhombotrypella*, and *Ulrichotrypa* are also present only in parts of the North American Cordillera. This generic grouping suggests a mixing of Tethyan and non-Tethyan elements.

Africa

Permian ectoprocts occur in scattered localities in Africa, including Egypt and Tunisia, but little faunal data are published. Fenestellid fragments and the trepostome *Dyscritella* were found in the lower part of the Dwyka Tillite in Namibia (South West Africa) (Wass 1972). Associated bivalves indicate a Kazanian age for these beds.

SUMMARY OF DISTRIBUTIONS

Many cystoporate genera during much of the Early Permian are widespread, particularly among the fistuliporids (*Fistulipora, Cyclotrypa*), the hexagonellids (*Hexagonella, Coscinotrypa, Meekopora*), and the goniocladiids (*Goniocladia, Ramipora*). During the early part of the Late Permian (Kazanian), some of these (*Cyclotrypa, Goniocladia, Meekopora*, and *Ramipora*) continue to have a widespread distribution. Other cystoporates, such as the hexagonellids *Evactinopora, Evactinostella, Fistulamina, Prismopora*, and the sulcoreteporid *Sulcoretepora*, form a distinctive part of many Early Permian Tethyan faunas. In Late Permian Tethyan assemblages the fistuliporid *Fistulotrypa*, the hexagonellids *Fistulamina* and *Prismopora*, and the sulcoreteporid *Sulcoretepora* are common.

Trepostomes also are generally either cosmopolitan or Tethyan. *Stenopora, Rhombotrypella, Tabulipora*, and possibly *Pseudobatostomella* are cosmopolitan genera that range through the Early and into the Late Permian. Genera restricted to Tethyan regions include *Paraleioclema* in the Early and Late Permian and *Araxopora, Arcticopora, Dyscritellina, Permocleioclema, Permopora*, and *Primorella* in the Late Permian. A number of genera, such as *Dyscritella*, are widely distributed in the Uralian and Tethyan regions early in the Permian, but become distinctive members of the Tethyan region by Late Permian.

Cryptostomes have different patterns of distribution compared to cystoporates and trepostomes and, because they are more abundant and more widely distributed, they are a more useful group for delineating faunal regions. The fenestellids *Fenestella* and *Penniretepora* and the polyporid *Polypora* appear to be cosmopolitan from the Asselian through the Kazanian. The septoporid *Septopora* is cosmopolitan during the Sakmarian, appears to be restricted to the Tethyan Seas during the Artinskian, and is cosmopolitan again during the Kazanian. The septoporid *Synocladia* first appears in the Franklinian Sea and gradually becomes cosmopolitan by the Early Kazanian. The Uralian Sea region has the distinctive fenestellid genera *Ptylopora* and *Ptiloporella* during the Early Permian and *Parafenestralia* and *Triznella* in the Late Permian. Some cryptostomes display a bipolar distribution in the Early Permian, such as the septoporid *Synocladia* and the fenestellid *Diploporaria*, both of which occur in the Uralian Sea and the Tasman Geosyncline. Several genera, such as the timanodictyid *Timanodictya* and the rhabdomesid *Ascopora*, dispersed from the Uralian Sea into the Tethyan Seas during the Early Permian. Other genera, such as the nikiforovellid

Clausotrypa, are in the Uralian Sea in the Early Permian and in the Tethyan Seas by the Late Permian. However, other genera appear restricted to the Tethyan Seas during the Permian, such as the fenestellid *Hinganotrypa*, the polyporid *Lyropora*, the nikiforovellid *Nikiforovella*, the rhabdomesid *Pamirella*, the girtyoporids *Hayasakapora* and *Tavayzopora*, and the hyphasmoporid *Ogbinopora*.

CONCLUSIONS

The world distribution of Permian ectoproct genera and families shows that the faunas of the Tethyan region are the most diverse and that many genera are restricted to that region. This suggests that Tethyan ectoproct faunal assemblages most likely inhabited warm, probably tropical, water when viewed in conjunction with associated faunas. In the early part of the Early Permian (Asselian, Early Sakmarian), the Uralian and Tethyan Seas had a large number of genera in common suggesting that these two seas were interconnected and their respective temperature or environmental conditions were similar, but not identical. At about this time, the ectoproct assemblages in southwestern Africa, India, Pakistan, and Australia were much reduced in number of genera and families and are associated with glacial deposits. This indicates that these ectoprocts are adapted to cool water, and the low diversity in associated faunas tends to confirm this interpretation.

In the middle and later parts of the Early Permian, a number of changes take place in ectoproct distributions which become progressively more pronounced before the end of the Early Permian. The Tethyan ectoprocts become increasingly more diverse and much of the generic evolution appears centred in one or more parts of that large region. New genera appear in the Uralian Sea, but relatively few disperse into the Tethyan region, so that most of the genera and species lineages become endemic to the Uralian and Franklinian Seas along the north margins of the European and North American continents. By the end of the Early Permian, the Uralian Sea reached an unusual set of environmental conditions that greatly reduced its marine fauna to a few groups, including some ectoprocts, which apparently were adapted to fairly wide ranges in salinity and temperatures. This is suggested by the presence of evaporites, limited associated faunas, and interstratified nonmarine beds. Direct marine connections between the Uralian Sea and the Tethys were probably terminated in the middle part of the Early Permian. The Pakistan and Australian ectoprocts also become increasingly diverse during the middle and later parts of the Early Permian suggesting a rapid warming of those seas. Ectoprocts in these two areas are closely related to each other and to other, more normal, Tethyan assemblages. Although a number of typical Tethyan fossil groups, such as fusulinaceans, some corals, brachiopods, and cephalopods, are not well represented, there are enough similarities to suggest that a southern Tethyan fauna existed which included the portion of the fauna that was able to adapt or disperse in slightly cooler water. The similarity of some of these marginal southern Tethyan faunas to those of the Early Artinskian of the Uralian Sea further suggests that the Uralian Sea was cooler than the typical Tethys. The Tethys during the middle and later parts of the Early Permian appears to have been a broad region (text-fig. 5) and the distribution of Permian ectoprocts suggests that the present-day configuration of the Tethyan faunal belt is the result of three or more tropical to subtropical subregions that have been structurally displaced against one another in post-Palaeozoic time (Monger and Ross 1971; Ross 1976).

In the early part of the Late Permian ectoprocts continued to have much the same geographical distribution patterns that were apparent by the end of the Early Permian. The Uralian, Franklinian, and Zechstein Seas contain a generally similar ectoproct fauna which is relatively low in diversity and associated with other faunas also having low diversity. Pakistan, India, and Australia also have lower ectoproct diversities at this time suggesting that in non-Tethyan regions, this was a time of increased extinctions, possibly because of ecological stress. The Tethyan ectoproct faunas continue to be highly diverse and apparently evolved nearly independently of other regions. A few of these Tethyan forms were able to disperse into other regions, as in the south-western United States, during this time, but a Tethyan faunal assemblage is clearly recognizable in contrast to one or more non-Tethyan assemblages.

The ectoproct distribution in the latest part of the Permian presents a number of difficulties for interpretation. For the most part, these ectoprocts are poorly known on a world-wide basis and this fact may be significant in itself. A number of genera persist in the Tethyan region, nearly all of which are continuations of earlier Tethyan endemic genera, and a few of these even extend into earliest Triassic strata. However, most of the Permian lineages became extinct either before, or early in, the latest Permian (Dzhulfian) and no completely acceptable explanation for this part of their evolutionary history has been made. In nearly all non-Tethyan regions latest Permian faunas in general are scarce and poorly known and this suggests abnormal marine environmental conditions were operating world-wide to reduce the faunas. Although mutual dependence on complex and obligatory community structure may be a possible factor, it seems more likely that rates of change in environmental conditions exceeded the abilities of the organisms to adapt.

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JUNE R. P. ROSS

Department of Biology
Western Washington University
Bellingham, Washington 98225
U.S.A.

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