REVIEW OF PERMIAN INVERTEBRATE FAUNAS

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ABSTRACT.—The presently known invertebrate fauna of Permian rocks consists of 1,411 genera and subgenera, 7,359 species, and 892 subspecies. The record is distorted by more complete description of fusulinids and ammonoids than of other groups, by the numbers of reef-dwellers, and by paucity of information on Radiolaria, sponges, and certain other groups. Dominant types of each group are determined and numbers of genera, species, and subspecies in each major taxonomic category are tabulated.

ENVIRONMENTAL conditions during the Permian period were perhaps more variable than they were in any other time of comparable length. The existence of such widely diverse phenomena as glacial climates, evaporite basins, reef systems, starved basins, and geosynclines, and coastal platforms should guarantee a large and varied fauna. The fact that the known invertebrate fauna is not so rich in species as would be expected arises from a number of factors. Well preserved fossils are rare in dolomites, and in coarse clastics. Animals with hard parts do not thrive in evaporite basins and starved basins. Much of the Permian rock of the world is in areas difficult of access, with little population, or with few palaeontologists. Some of these areas are East Greenland, Tasmania, Southern Tunisia, Bolivia, and the semi-arid regions of the United States and Mexico.

The record of Permian invertebrates is a distorted one. Reef-living organisms of West Texas, Sicily, and Russia have received monographic treatment. Fusulinids are easily collected, are stratigraphically useful, so constitute a disproportionate share of described species. Ammonoids are specifically determinable and stratigraphically useful even when decorticated as most mollusks are ; thus a large number of species have been described. A large number of good collecting localities for fossil insects have been found and to that highly diverse class nearly ten percent of described species belong.

The record is distorted by the extensive monographs on the peculiar fauna of Timor and by the recording at length of many brackish-water pelecypod faunas. It is also undoubtedly coloured by the relatively small amount of work on microfossils other than fusulinids and by our failure to discover identifiable remains of such groups as Myriapoda, Scorpionida, Chaetognatha and Ophiuroidea. Radiolaria have been little-studied, few conodonts have been described, and the invertebrate species of shelf environments have not been sufficiently discriminated from the similar species of the Pennsylvanian.

Some years ago the writer published a record of all Permian invertebrates. From that record as brought up-to-date and with the elimination of species from strata more properly assigned to the Pennsylvanian than to the Permian, he derives the following analysis of the invertebrate fauna.

PROTOZOA

Radiolaria—But two genera, each with one species, have been reported. The presence of several genera in the Gaudalupean rocks of Texas and New Mexico is known.

Foraminifera—Intensive study of the fusulinids has resulted in the description of more than twice as many fusulinid species as of all other foraminiferal groups. The fusulinids are, in number of described species,

dominated by *Parafusulina* (75 species), *Pseudoschwagerina* (57 species), *Schwagerina* (182 species), and *Triticites* (76 species). The non-fusulinid Foraminifera are predominantly nodosarians, textularians, and ammodiscids.

PORIFERA

Permian sponges are poorly known. Most of them are reef-dwellers of West Texas and Sicily, or are from the rich fossil collecting ground of Timor. Demospongia and Calcispongea are about equal in numbers. The astonishing total of 43 genera and 71 species are not recognizable or are obviously improperly classified.

COELENTERATA

Anthozoa : Rugose corals predominate. Species of the family Polycoeliidae are most numerous, and lophophyllidids and caniniids are numerous. Tabulate corals are well represented, mainly by favositids. Octocorals are reported by some authors, but the corals are considered rugose by others.

Hydrozoa : Galloway considers that there are no stromatoporoids in Permian rocks. On that basis the 13 genera and 16 species reported are hydractinians.

Scyphozoa : Two genera and 18 species of conulariids have been described. Two species of medusids have been reported, neither of established affinity. Two genera and five species of hyolithids are recorded.

ECHINODERMA

The single reported edrioaster does not belong to that group. The supposed cystoids have been shown to be crinoids.

Blastoidea : Nine families are represented, with Codasteridae most prominent. Orbitremitidae and Pentremitidae are present. All of the described blastoid species are from Timor, excepting 6 from Australia and 4 from Russia.

Crinoidea : The Permian crinoid fauna includes flexible crinoids of the Order Sagenacrinoidea, with the genus *Calycocrinus* accounting for half the known species. Inadunates are most numerous, with abundant allagecrinids, codiacrinids, and erisocrinids. The peculiar and sadly misnamed genus *Calceolispongia* has 21 species. Camerates are rare, with but 11 genera and 36 species. Nearly two-thirds of all known Permian crinoid species are from Timor.

Echinoidea : All described forms are regular echinoids. Most of the named species are known only by spines.

Asteroidea : Three species have been described, all from New South Wales.

Holothuroidea : The group is known from a few recorded plates and spicules.

BRYOZOA

A small number of ctenostomate bryozoans are known. Of the more than a hundred species of cyclostomate forms, about half are fistuliporids. The genus *Stenopora* is the dominant genus of the Trepostomata, with 37 of the 52 species. Cryptostomate bryozoans are overwhelmingly predominant, with more than two-thirds of the species ; fenestellids provide more than half the cryptostomes, and acanthocladiids are numerous.

BRACHIOPODA

Atremata : Represented by 9 species of "*Lingula*".

Neotremata : Relatively few species, most of them orbiculoids and discinids.

Protremata : The Permian fauna is rich. There is a great variety of orthothetids, of chonetids, and of *Enteletes* and its relatives. Large numbers of leptodids, of richthofenids and of productids adapted for the reef environment have been described. Fifty-four productid genera and 556 species have been made known to date.

Telotremata : The dominant family is the spiriferids with 31 genera and 341 species. Dielasmatids, athyrids, camarotoechiids, and spiriferinids are numerous.

MOLLUSCA

Lamellibranchiata : Permian forms are quite varied. The Taxodonta are predominantly nuculids, species of *Parallelodon*, and anthracosiids. The Dysodonta contain the abundant pectinoids, represented by 249 species of such genera as *Aviculopecten*, *Pseudomonotis* and *Streblochondria*. Mytilids and other families of the order are rather sparse. The Preheterodonta are mainly species of *Schizodus* and *Pleurophorus*. The Heterodonta of the Permian consist of species

of the Astartidae, of the Myalinidae, of *Allorisma*. of *Conocardium*, and of numerous thick-shelled brackish-water species.

Gastropoda : Classification of Permian gastropods is as yet unsatisfactory. Most characteristic are the euomphalids. Pleurotomariids and bellerophontids are most numerous and there are many species of neritopsids, murchisoniids, loxonematids, and subulitids.

Amphineura : Three genera and 8 species have been reported, but many of these are of doubtful validity.

Scaphopoda : Scaphopods are locally abundant. Four genera and 15 species are known.

CEPHALOPODA

Nautiloidea : Eighteen genera and 68 species of orthoceratites have been recorded. Coiled nautiloids are fairly abundant and there has been what seems to be excessive generic discrimination. Fifty-four genera and 183 species have been described. Nautiloid mandibles have been recorded from the Kaibab of the Grand Canyon region.

Ammonoidea : Permian rocks at many places are rich in specimens of ammonoids and palaeontologists have made them well known. The Goniatitina are overwhelmingly predominant with 39 genera and 311 species. Most numerous are popanoceratids and gastrioceratids, but a total of 12 families is represented. The Prolecanitidea are represented by 3 families with 10 genera and 104 species. The Ceratitina are prophetic of Triassic forms and contain 10 Permian genera and 30 species of xenodiscids and otoceratids.

Belemnitoidea—A single genus and species of belemnites has been described from Permian rocks of East Greenland.

ARTHROPODA

Trilobita : All species are proetids and the lack of variety in the group has led palaeontologists to divide the known forms into an excessive number of genera and species. Fifteen genera, 75 species, and 8 subspecies have been described.

CRUSTACEA

Cirripedia : Three genera and three species of barnacles have been reported, all of doubtful validity.

Branchiopoda : The Conchostraca of the Permian are known from 14 genera and 70 species. One species of the Notostraca is known.

Malacostraca : Phyllocarids, syncarids, peracarids, and eucarids have been reported.

Ostracoda : Permian ostracods have been assigned to 12 families and to 61 genera. The genus *Bairdia* has 54 described Permian species. The family Kirkbyidae contains the greatest number of genera (14), but has only 50 species.

Myriapoda : Only two forms have been reported from Permian rocks.

Insecta : Nineteen orders of insects are known in Permian rocks. Cockroaches account for a quarter of the species. The Hemiptera are the most varied group with 77 genera and 188 species. The last of the Palaeodictyoptera, of the Megasecoptera, of the Protohemiptera (numerous, 45 genera and 66 species), and of the Caloneurodea occur. The Protoperlaria (13 genera and 18 species) and the Protelytroptera (10 genera and 16 species) are exclusively Permian. The first dragonflies, may flies, stone flies, book lice, bugs, cicadas, thrips, lacewing flies, scorpion flies, and beetles occur in the Permian. The curious extinct order Glosselytrodea has one representative.

Chelicerata : No arachnid is certainly known in Permian rocks. The Merostomata are represented by 4 genera and 6 species of xiphosurans and by 3 genera and 5 species of eurypterids.

ANNELIDA

Remains of 22 species assigned to the Annelida have been reported, nearly all of tubicolous worms.

A tabulation of the presently known fauna is given here. That only 7579 species have been described is remarkable. The slow growth of further knowledge of the fauna is illustrated by the fact that only one new Permian invertebrate species has been found in England since 1861. On the basis of present interpretation of the scope of a species, it is predicted that it will be many years before the number of species reaches ten thousand.

TABULATION OF DESCRIBED PERMIAN INVERTEBRATE SPECIES

	Families	Genera	Species	Sub-species
FORAMINIFERA				
fusulinids	3	55	655	95
other	15	68	256	94
Total	18	123	811	99
PORIFERA				
DEMOSPONGIA	8	23	43	3
CALCISPONGIA	5	13	40	0
HYALOSPONGIA	1	1	1	0
incertae sedis	..	26	45	5
Total	14	63	129	8
COELENTERATA				
ANTHOZOA				
Octocoralla	1	1	2	0
Zoantharia	..	..	..	..
Rugosa	12	78	385	35
Tabulata	3	25	83	1
incertae sedis	..	6	11	0
HYDROZOA	..	13	16	0
HYOLITHIDA	..	2	5	0
CONULARIDA	..	2	18	0
medusoids	..	1	2	0
Total	..	128	522	36
ECHINODERMA				
PELMATOZOA				
Blastoidea	9	23	49	23
Crinoidea	..	..	..	..
Inadunata	17	77	245	32
Flexibilia	3	12	42	12
Camerata	4	11	36	2
ELEUTHEROZOA				
Asteroidea	..	2	3	0
Echinoidea	..	4	20	0
Holothuroidea	..	5	8	0
Total	..	134	393	69
BRYOZOA				
CTENOSTOMATA	3	5	8	0
CYCLOSTOMATA	3	16	111	7
TREPOSTOMATA	3	6	52	8
CRYPTOSTOMATA	6	33	377	74
Total	15	60	548	89

	Families	Genera	Species	Sub-species
BRACHIOPODA				
ATREMATA	1	1	9	0
NEOTREMATA	2	5	13	0
PROTREMATA	8	117	1002	215
TELOTREMATA	9	86	933	237
Total	20	209	1957	452
MOLLUSCA				
LAMELLIBRANCHIATA				
Taxodonta	7	25	232	8
Dysodonta	6	38	372	10
Preheterodonta	2	10	94	2
Heterodonta	8	33	272	27
Subtotal ..	23	106	970	47
GASTROPODA	11	62	522	17
AMPHINEURA	1	3	8	0
SCAPHOPODA	2	4	15	0
CEPHALOPODA				
Nautiloidea	11	74	250	2
Ammonoidea	17	63	311	36
Belemnoidea	1	1	1	0
Subtotal ..	29	138	562	38
Total	66	313	2077	102
ARTHROPODA				
TRILOBITA	1	15	75	8
CRUSTACEA				
Cirripedia	1	3	3	0
Branchiopoda	..	14	71	0
Malacostraca	..	15	22	0
Ostracoda	12	61	233	10
Total	..	93	329	10
INSECTA	..	355	705	19
CHELICERATA	6	7	11	0
Total	..	470	1120	37
ANNELIDA	..	10	22	0
Grand Total ..	..	1510	7559	892