

PRESIDENTIAL ADDRESS

STUDIES ON TRILOBITES IN LAST THREE DECADES*

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Among fossils ancient extinct organisms bear particular importance for palaeontologists because such fossils are monopolistic objects of their study. Trilobites are typical of this category. SHIRAKI'S find of Ordovician trilobites near Mt. Taipaik (大白山) in Korea drove me in 1926 to this mountainous region for fossil hunting. In those days the Trilobita belonged to the Crustacea and comprised 20 families or so, but now there are about 150 families which constitute an independent class of the Arthropoda. It is indeed a great advancement. Because I was fortunately able to participate in this progress, I wish to outline the results of this epoch in morphology, taxonomy and descriptive work.

It was in summer, 1932, that Dr. STØRMER and I were invited by Prof. RAYMOND to his home. It was a memorable evening for me, because it was about the *Wendepunkt* in Trilobitology. Needless to say, the late Prof. RAYMOND was the well known successor of Prof. BEECHER in this science, who had thoroughly proven the crustacean nature of trilobites in 1920 and developed BEECHER'S tripartation of the Trilobita. Therefore I visited him at Harvard to discuss the trilobite classification.

At that time Dr. STØRMER was engaged

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in trilobite morphology. In a preliminary report (1933) he pointed out the analogy and homology of the trilobitan appendages with those of the crustaceans and arachnoids respectively, emphasizing that the trilobite has only one segment of the propodite and the characteristic gill-blades on the expodite which are quite different from crustacean setae. It took much more time to reconstruct the appendages of Trentonian *Ceraurus pleurexanthemus* out of serial sections of its rolled specimens. His *Studies on Trilobite Morphology, Parts 1 to 3* were successively published in 1939, 42, and 51 through which it was determined that trilobites have the appendages of same pattern as those of the Trilobitoidea and they are closely related to the Chelicerata. As a result the taxonomic position of the Trilobita was promoted as below.

Phylum Arthropoda
Subphylum Trilobitomorpha STØRMER, 1944
Class Trilobitoidea STØRMER, 1959
Class Trilobita WALCH
Subphylum Chelicerata
Subphylum Pycnogonida

It is interesting to note that the crest of *Palaeontologia Sinica* is a tail of a trilobite called *Drepanura* which has long been known among the Chinese by the name of bat-stone (CHANG, 1921). About 250 years ago LYWYD (1698) described Trinuclei. The first Linnean

species was *Entomolithus paradoxus*, 1745, but it was a composite species, γ form of which was *Agnostus pisiformis* (LINNÉ), 1757. The term, *Trilobites*, was proposed by WALCH in 1771 and 5 genera were distinguished by BRONGNIART in 1822. Subsequently trilobites had been classified by DALMAN, EMMRICH, MILNE-EDWARDS, BURMEISTER, HAWLE and CORDA, BARRANDE, SALTER and others in various manners before BEECHER proposed his *Natural Classification of Trilobita* in 1897. The last one was different from the preceding ones in that it was founded on recapitulation theory.

From ontogenetical point of view BEECHER laid special stress on eyes and facial sutures. His classification received wide acceptance, although its validity was questioned by POMPECKJ immediately, a year after the proposal. REED also noted that part of blindness is the result of aphotic adaptation, although he agreed that many blind trilobites are primitive. Later the Hypoparia were ignored by SWINNERTON (1915). While POULSEN reported the proparian suture in the early larval stage of *Peltura scaraboeoides* (1923), RICHTER (1932) considered the Proparia to be more primitive than the Opisthoparia.

In 1935 I pointed out the *polyphyletism of the Proparia* as well as the Hypoparia by the fact that Cambrian proparians or hypoparians reveal little relationship not only among themselves, but also to later proparians or hypoparians. Therefore I had to conclude that BEECHER'S three orders are not natural groups.

Although the facial suture is one of the most important criteria, the natural classification must be founded on *combination of evolutionary characters*. Each biocharacter developed in one or more

trends, two of which happened to be even opposed. A trilobite group developed along the trend of a character slowly, but the development was quicker in another group. Thus the evolution of trilobites is complicated. For the natural classification not only morphological and ontogenetical evidences, but also specio-temporal distribution must be brought into consideration because the *parallelism of the trilobite evolution* among palaeogeographic provinces cannot be overlooked.

Furthermore it was concluded that at least four groups of trilobites had already appeared in the early Cambrian period. Therefore their Pre-Cambrian divergence is pre-palaeontological. The *four palaeontological stocks* were the Agnostida, Redlichida (or Mesonacida), Corynexochida and Ptychoparida which formed the four primary orders in my classification in 1935. The secondary orders are later groups which appeared so sporadically that their origin is obscure.

Subsequently in 1936 the invalidity of the Proparia was vindicated by the discovery of a proparian off-shoot of the Olenidae in the Lower Ordovician of Argentina. In the same year STUBBLEFIELD discussed cephalic sutures in great detail and concluded that the proparian condition might be regarded as arrested development. WHITEHOUSE (1936, 39) on the other hand recognized 7 Cambrian stocks of trilobites. In applying JAEKEL'S terms (1909), he combined his Agnostida and Eodiscida into the Miomera and the remaining five into the Polymera. Then, RESSER (1938) segregated his Agnostida out of the Trilobita inclusive of eodiscids. On the contrary, I monographed the agnostids (1939) and eodiscids (1944) with the result it was concluded that

the two constitute my Agnostida which represent the most specialized distinctive order of the Trilobita.

After the rejection of the tripartation, STØRMER (1948) applied BEECHER'S orders to his classification, beside Protoparia which was a homonym of SWINNERTON'S (1915). He took the olenellid anaprotaspid for the incipient form, but recently WHITTINGTON (1957) pointed out that the smallest olenellid larvae so far known are meraspid cephalae, instead of protaspids. BEECHER'S orders were accepted still later in some text-books (MOORE, LALICKER and FISCHER, 1952; SHROCK and TWENHOFEL, 1953). Naturally closer studies were made on cephalic sutures by many students. RASETTI (1952) distinguished 7 types of sutures among early Cambrian trilobites to which two later Cambrian types were added. More types are known at present, but at the same time it has been ascertained that the same suture type occurs in the three polymeric orders.

About 30 years ago the classification of Cambrian trilobites was so ambiguous that even specialists arranged them in the alphabetical order by generic names. Especially, little was known of intergeneric relationship among those

of Asia or the Pacific province. This was the reason why I made a special study on Cambrian genera and families. Though very tentative, in 1935 I classified the Cambrian trilobites into 34 families which were grouped into the above 4 primary orders in addition to the Dikelocephalida.

Lately the interfamily relationship was examined by HENNINGSMOEN (1951) with special reference to the outline of the glabella and its furrows, although the relation of the glabella to the major cephalic configuration, I think, would be no less an important criterion. He obtained 12 superfamilies, two-thirds of which were derivatives from the Conocoryphacea. Then, HUPÉ (1953, 55) combined the Eodiscoidea and Agnostoidea into the Miomera and the other 24 superfamilies into the Polymera. In the latest classification elaborated by HARRINGTON et al. (1959) the comprehensive Polymera or Conocoryphacean derivatives are divided into several orders and suborders. In seeing this scheme in *Treatise on Invertebrate Paleontology* I was rather astonished to find that the result agrees with mine so well in the fundamental frame as seen below.

Treatise, 1959.	Author, 1935.
Agnostida KOBAYASHI.....	Agnostida
Redlichida RICHTER	Mesonacida (or Redlichida)
Corynexochida KOBAYASHI	Corynexochida
Ptychopariida SWINNERTON	Ptychoparida
Ptychopariina RICHTER	(Ptychoparida)
Asaphina SALTER	Dikelocephalida (from Ptychoparida, 1936)
Illaenina JAANUSSON	Proetacea (from Ptychoparida)
Harpina WHITTINGTON	Harpacea (ditto.)
Trinucleina SWINNERTON	Trinucleacea (ditto.)
Phacopida SALTER.....	(Phacopacea)
Phacopina STRUVE.....	Phacopacea (unknown origin)
Cheirurina HARRINGTON and LEANZA	{Cheiruridae (ditto.) Encrinuridae (ditto.)

Calymenina SWINNERTON	Calymenacea (from Ptychoparida)
Lichida MOORE	Lichadea (from Mesonacida or Zacanthoidae?)
Odontopleurida WHITTINGTON	Odontopleuridae (ditto.)

It is obvious that palaeontology depends on palaeontography which depends in turn on fossils. Silicified material is a favourite of palaeontologists as it can yield by observations a great deal of unexpected data especially on the ventral morphology and ontogeny. During my stay at the U. S. National Museum I saw some beautiful brachiopods extracted by Dr. COOPER. In 1935 he sent me a photograph of silicified trinucleid which he had found in Virginia. Next year free trilobites from the Upper Ordovician of Percé, Quebec were illustrated in a paper by COOPER and KINDLE. This line of investigation was greatly improved in the United States. One cannot but admire a free carapace with a hypostoma, especially of a larval form.

Although I do not intend to go into details of descriptive works at this time, they were developed in various trends in these 30 years. Namely, many ancient type specimens in Norway, Bohemia and other countries were precisely restudied; the Olenidae, Odontopleuridae and other selected families thoroughly revised; large faunas in Britain, Sweden, Esthonia, Rheinland, South France and other classical areas monographed; and innumerable new trilobites described from Palaeozoic areas which had previously been little or not well investigated.

Much we owe to POULSEN and TROEDSON for the knowledge of the rich Arctic faunas. Some 30 species of trilobites had been known from the Andine province before 1935 when I described the *Kainella* faunule of Prairie

Catamarca, but according to HARRINGTON and LEANZA (1957) the Ordovician of Argentina comprises at present more than 130 species. Likewise, only about 35 species were known from the Cambrian of Siberia before the *Atlas of the leading forms of fossil faunas in USSR*, Vol. 1, Cambrian (1940) in which LERMONTOVA took part. Since 1950, however, new genera proposed for Cambrian trilobites from Siberia and Central Asia have numbered some 70 in total. It is predicted that described trilobites from Australasia are only a small part of those which really existed (ÖPIK et al. 1957).

A monumental work was published by WALCOTT as early as in 1913 for the *Cambrian faunas of China*. Trilobites of Eastern Asia were further amplified by MANSUY, REED, YABE, SUN, SAITO, SHENG, WANG, ENDO, RESSER and others and recently by HSÜ, LU, CHANG, CHIEN, CHU, HSIANG, YI and others. In Japan trilobites are uncommon but *Coronoccephalus* and a few others were described by HAMADA, IGO, OKUBO and others. It is a remarkable fact that the Asia-Pacific faunas contain quite distinct genera and families, the Eoasidaspidae by POLETAYEVA for example.

Here the trilobitology is reviewed in connection with geology. BENSON'S discovery of Cambrian trilobites in New Zealand (1956) is crucially important for the reason that Ordovician has been the oldest dated rock among the Pacific islands. Similarly, BURAVAS' find of trilobites at Tarutau, Southwest Thailand is invaluable in that the isle is the southernmost Cambrian locality of

Eurasia and at the same time these are the oldest fossils in the Burmese-Malayan geosyncline (1957).

A copious Lower Cambrian fauna was described from the Anti-Atlas by HUPÉ (1952). It is interesting to see in the type section of Amouslek that *Neoredlichia* occurs in the midst of the olenelloid zones. In Australia on the contrary *Redlichia* is said to be earliest Middle Cambrian except in South Australia where it occurs in the Lower Cambrian (ÖPIK et al. 1957). Prior to this, SAITO (1933) suggested that the *Redlichia* stage in North Korea is lowest Middle Cambrian since it is underlain by the *Protolenus* bed with disconformity. SAITO'S species was, however, later eliminated from *Protolenus*, s. str. In South China on the other hand it was clarified that various protolenoids evolved parallel to redlichids.

It is certain that the redlichids migrated from Eastern Asia to North Africa in the Olenellian epoch through the Himalayan trough. Probably Atlantic *Bailiella* took the same path, because it is reported from South France, Kashmir, Tonkin-Yunnan border, Korea, North China and Central Siberia. It is more certain that the Dorypygidae entered into Northern Europe from Eastern Asia through Central Asia (IVSHIN, 1953), because the family is well represented in Kazakstan and West Siberia. It is understandable that *Centropleura* could migrate from the Atlantic province to New Siberia and Central Siberia, but how *Centropleura* reached Australia from Asia remains a puzzle.

As discussed elsewhere (1949), it is remarkable that the occurrence of *Glyptagnostus reticulatus* in four continents indicates the oldest world instant in the geological age. Because

Olenus, *Hedinaspis* and *Glyptagnostus* occur in Korea all in dark carbonaceous limestones along the axis of the Yokusen geosyncline, I suggested that their wide Eurasiatic dispersal was made possible with the aid of oceanic currents comparable to the Sargass sea of today (1943-44). It was emphasized further that the axial zone of the Appalachian geosyncline was the route of migration from the Atlantic to the Cordilleran or the Andean province (1957). WILSON (1957) noted also the cosmopolitan Olenidae in dark argillaceous geosynclinal sediments and jointly with LOCKMAN, he (1958) elucidated the evolution and distribution of the Cambrian trilobites in North America, in classifying their habitats into the cratonic, intermediate and extracratonic realms.

Incidentally, it is noteworthy that *Asaphopsis*, *Taihungshania*, *Synhomalonus*, *Coronocephalus*, *Crotalocephalus*, *Thysanopeltella*, *Dechenella* and some other genera provide undeniable evidence for sea connection from Eastern Asia to Europe or Australasia in the Ordovician, Gotlandian or Devonian period.

Now I recollect RAYMOND'S address on *Pre-Cambrian Life* (1935) in which he spoke of the diversity of naked pelagic animals in the late Pre-Cambrian period and their armouring at the transition to the Cambrian due to their benthonic adaptation on shallow bottom and the superiority in struggle for existence which took place by over-population. This interpretation applies to trilobites as well as other animals. Fossil records in the transitional epoch are still meager, but medusae and annelids were lately discovered in South Australia far below the archaeocyathid limestone (GLASSNER, 1959). In my opinion the

Proterozoic glaciations causing changes of hydrosphere not only in areal extension but also in variation of environments, most probably favoured this important step in the development of aquatic life. It is also remembered that the Neo-Cryptozoic eon is comparable with the whole Phanerozoic eon in time length (1944-45).

At all events four primary stocks of trilobites appeared in the early Cambrian epoch among which the shortest survivors were the Redlichida, probably followed by the Corynexochida and then by the Agnostida. It is, however, an important problem, whether the Corynexochida really disappeared before the Ordovician period, because the order flourished most in the insufficiently explored Asio-Pacific province and because the phylogenetic position of the Damesellidae, Leiostegiidae and Komaspiidae remains unsolved. The origin of cheirurids, phacopids, odontopleurids and lichids is still unknown. In view of the resemblance of the Eoacidaspidae to the Corynexochida, however, I think future researches in the Asio-Pacific province may throw light on the derivation of certain secondary stocks from the primary.

The rise and fall of trilobite families took place on the largest scale during the late Cambrian and early Ordovician epochs. All of the Cambrian families died out by the end of the Ordovician period, while some forerunners of the post-Cambrian families appeared already in the latter part of the Cambrian period. The evolution of trilobites is so highly complicated that it can hardly be unified by any theory. However, the rule of effacement, that is, that effacement advances from the distal to the proximal part of a shield (1939), applies not only to the Miomera, but

also to the Polymera. Rules on hypertrophy of the axial lobe and caudalization of post-cephalic segments also meet with few exception. In the future, combination of such rules will make it possible to decipher the tangled history of evolution.

I shall close my speech with a few words of reference to some new compilations. GRABAU and SHIMER'S *Index Fossils of North America* was completely revised and reillustrated by SHIMER and SHROCK (1944). Publications of this kind were compiled for the Cambrian of U. S. S. R. by VOLOGDIN (1940), for the Palaeozoic of Western Siberia by KHALFIN (1955) and for Fossil Invertebrates of China by Academia Sinica (1957). These two Soviet publications contain many new genera and species by LERMONTOVA and others. STØRMER (1949) and HUPÉ (1953) presented a chapter on Trilobita respectively in GRASSÉ'S *Traité de Zoologie* Tom. 6 (1949) and PIVETEAU'S *Traité de Paléontologie* Tom. 3 (1953). HUPÉ'S *Classification des Trilobites* (1953, 55) and HARRINGTON and others' Trilobita in MOORE'S *Treatise* (1959) give the most comprehensive information on the class but for Asiatic genera it is hoped more supplementary information will be gathered to complete our knowledge.

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Three Trilobite Families
At RAYMOND's Garden, Aug. 4th, 1932.

From the left side.

Dr. Leif STØRMER, Miss RAYMOND, Mrs. STØRMER, Mrs. RAYMOND,
Mrs. KOBAYASHI, Prof. Percy E. RAYMOND and the Author.