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# VENTRAL CEPHALIC SUTURES IN CAMBRIAN TRILOBITES

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ABSTRACT. The ventral portions of the cephalic sutures in Cambrian trilobites have seldom been studied and described. This paper attempts to survey the available information, on the basis of both published literature and new observations. The known types of cephalic sutures are defined and their occurrence in trilobites of the different epochs of the Cambrian period is reported. The evolutionary and taxonomic significance of the sutures is briefly discussed.

## INTRODUCTION

MOST of what we know about the cephalic sutures of trilobites had already been discovered by Barrande when, exactly one hundred years ago, he published the first volume of the monumental work *Système Silurien du centre de la Bohème.* Beecher's classification focused attention on the sutures, and the course of these lines, both on the dorsal and ventral sides of the carapace, is generally well known in the post-Cambrian forms. However, in the Cambrian genera and families only the dorsal portions of the cephalic sutures have usually received attention and are discussed in the descriptions of new species, the reason being the difficulty of obtaining specimens where the cephalic doublure is sufficiently well preserved and exposed to reveal the course of the sutures on the ventral side. Hence even recent studies of the sutures of trilobites (Richter, 1932; Stubblefield, 1936) had to rely largely on Barrande's observations for the Cambrian forms.

Preparation of a part of the forthcoming *Treatise on Invertebrate Paleontology* prompted the writer to undertake a survey of the cephalic sutures of Cambrian trilobites, based on both published information and firsthand study of material preserved in the United States National Museum and the writer's own collections. Since the course of the dorsal portions of the sutures is generally well known, the attention was focused on a study of the ventral sutures. Although the results of this investigation have been somewhat disappointing, owing to the exceedingly meager material, they are believed worth publishing, if only to emphasize the need for further research.

## TERMINOLOGY

The terminology here used was introduced by Barrande (1852) and employed with few modifications by Warburg (1925) and Stubblefield (1936). The "facial suture" is understood in Barrande's more comprehensive meaning of the *grande suture,* i. e., it includes the frontal portion that was set off by some authors as a "rostral suture." This distinction, at least in the Cambrian forms (and, in the writer's opinion, also in the later trilobites) is arbitrary and does not fulfill any descriptive or interpretative purpose. The "connective sutures" are a pair of sutures separating the doublure of the free cheeks from the median portion of the doublure (rostrum). The latter, in turn, may be separated from the hypostoma by a "hypostomal suture" or fused with this organ. In other trilobites the paired connective sutures are replaced by a "median suture"; in this case, the hypostomal suture separates the hypostoma from the free cheeks. Median or connective sutures may be lacking, the doublures of the free cheeks being fused into a single piece.

Whenever the meaning of such terms as "wide," "long," etc., might be ambiguous, they are qualified with the abbreviations "tr." (transverse) or "sag." (sagittal) to indicate measurements taken in the transverse or longitudinal directions, respectively.

## THE SUTURES IN CAMBRIAN GENERA AND FAMILIES

For the reasons already mentioned, the following discussion is essentially confined to the ventral sutures. This section reviews the published or new information concerning Cambrian genera and families. The next section attempts to discuss the evolution of the sutures and their taxonomic significance.

*Olenellidae.*—Recent authors (Stubblefield, 1936; Raw, 1937: Störmer, 1942) agree that there is a marginal or submarginal suture separating the dorsal shield from a ventral plate (rostrum) to which the hypostoma is attached. The hypostomal suture is in a state of symphysis in some of the genera. The difficult problem of homologizing the parts of the olenellid cephalon with those of opisthoparian trilobites has been exhaustively discussed in the cited literature.

*Agnostidae.*—As far as anybody has been able to ascertain, the agnostid cephalon lacks sutures and consists of a single piece. Authors, beginning with Barrande (1852) searched in vain for agnostid hypostomas and suspected that these trilobites lacked that organ, at least in calcified form capable of fossilization. This suspicion is confirmed by new observations made by the writer on silicified, enrolled specimens of *Trinodus elspethi* (Raymond) from the Middle Ordovician limestones of Virginia. Tightly enrolled individuals were almost certainly buried alive, since muscle contraction must have been necessary to hold the shields pressed together; at least, it is virtually certain that such specimens do not represent moults. Hence, if the animal had a calcified hypostoma, it should now be present inside the tightly closed box formed by the enrolled shield. Examination of several perfectly silicified individuals, immersed in and filled with xylene, whose refractive index is close to that of quartz and allows a clear view of the space enclosed by the transparent carapace, failed to reveal any trace of the hypostoma, either in place or loose within the enrolled shield.

*Eodiscidae.*—No cephalic sutures are known in this family (Rasetti, 1948*a*, 1952*a*). No eodiscid hypostoma has been described; however, the close relationship with *Pagetia* makes it very likely that the Eodiscidae possessed this organ.

*Pagetiidae.*—These trilobites possess small free cheeks, widely separated from each other dorsally and presumably also ventrally, although no direct observation is available on the latter point, as the doublure of the free cheeks could not be studied in any species. The facial sutures on either side are thus apparently unconnected. Öpik (1952) recently described specimens of *Pagetia bootes* with the hypostoma in place. The manner of attachment of this organ has not been ascertained.

*Paradoxididae.*—The doublures of the free cheeks are separated by a wide (tr.) rostrum in all species of *Paradoxides* where these parts of the shield are known. The hypostoma seems to be fused with the rostrum in certain species, e. g., *Paradoxides bohemicus* (Barrande, 1852), a deep furrow marking the position of the fused hypostomal suture. In other species of the same genus (Westergård, 1937) the hypostomal suture seems to be functional.

In *Xystridura saint-smithi* (Chapman), according to Whitehouse (1939), the doublures of the free cheeks are also separated by a wide (tr.) rostrum, and "the hypostome is not permanently attached to the rostrum."

*Redlichiidae.*—Whitehouse (1939), Kobayashi (1944) and Kobayashi and Kato (1951) have shown that *Redlichia* has a wide (tr.) rostrum to which the hypostoma is probably fused. Whitehouse (1939, p. 192, plate 20, fig. 4) states that in *Redlichia idonea* Whitehouse "the hypostome . . . is either fused with the rostrum or tightly attached across the suture." Kobayashi (1944, plate 8, figs. 8, 9) figures a specimen of *Redlichia mansuyi* Resser and Endo where the hypostoma is attached to the rostrum although all the other cephalic parts are separated from each other. There is a depressed (in ventral view) area of the rostrum between the furrow corresponding to the anterior marginal furrow on the cranidium and the anterior margin of the hypostoma. In their paper on the morphology and ontogeny of *Redlichia chinensis* Walcott, the authors (Kobayashi and Kato, 1951) state that "in the present collection no specimen shows the mode of the hypostoma attachment clearly."

*Oryctocephalidae.*—Remarks on the ventral parts of the cephalon of *Oryctocephalus* were published by Saito (1934). Both in *Oryctocephalus orientalis* Saito and *Oryctocephalus* cf. *reynoldsi* Reed, he figured specimens (plate 25, fig. 18; plate 27, fig. 18) showing the free cheeks and hypostoma attached to each other without the remaining cephalic parts. Saito states

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PLATE 1

Fig. 1. *Oryctocephalus walcotti* Resser. Ventral view of free cheeks and attached rostrum and hypostoma, flattened in shale, X4. Specimen no. 96503, U. S. N. M. Middle Cambrian (Spence shale); locality U. S. N. M. 55c, 5 mi. SW of Liberty, Idaho.

Fig. 2. *Fieldaspis furcata* Rasetti. Hypostoma fused with the rostrum, X3. Middle Cambrian (Mt. Whyte formation); Mt. Field, British Columbia.

Fig. 3. *Olenoides curticei* Walcott. Ventral view of cephalon, X2. Restored from specimens preserved in siliceous nodules of the Conasauga formation (upper Middle Cambrian); locality U. S. N. M. 90x, near Center, Alabama.

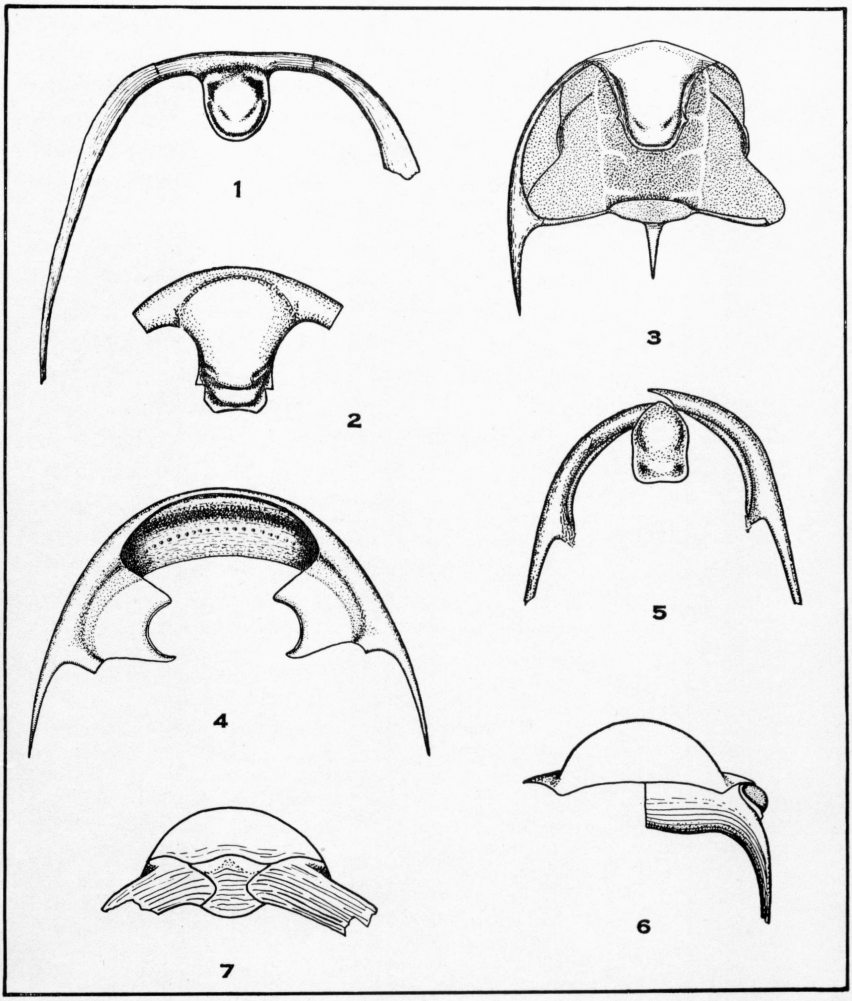
Fig. 4. *Levisella oweni* (Billings). Free cheeks, X3. Restored from specimens in the National Museum of Canada and the writer's collections. Upper Cambrian (Trempealeauian); boulders in Lévis conglomerate, Lévis, Quebec.

Fig. 5. *Bathynotus holopygus* (Hall). Ventral view of free cheeks and attached hypostoma, flattened in shale, X1. Specimen no. 15409, U. S. N. M. Lower Cambrian (Parker shale); Parker's quarry, Georgia, Vermont.

Fig. 6. *Acheilus latus* Rasetti. Anterior view of cephalon, X8. Specimen no. 1226, Laval University. Upper Cambrian (Trempealeauian); boulder in Lévis conglomerate, Lévis, Quebec.

Fig. 7. *Catillicephala impressa* (Rasetti). Antero-ventral view of cephalon, X6, showing the hourglass-shaped rostrum. Upper Cambrian (Dresbachian); boulder in conglomerate, Grosses Roches, Quebec.

PLATE 1



(p. 230) that in *Oryctocephalus orientalis* the free cheeks are "connected ventrally by doublure of anterior border"; and that in *Oryctocephalus* cf. *reynoldsi* (p. 232) the hypostoma is "apparently fused with the doublure of the anterior border." These statements would suggest that the free cheeks, rostrum and hypostoma are fused into a single piece.

The writer examined all the material of *Oryctocephalus* available in the U. S. National Museum. Unfortunately, specimens showing the ventral side of the cephalon are few and not too well preserved. Observations on shields of *O. burgessensis* Resser, *O. reynoldsi* Reed and *O. walcotti* Resser definitely indicate that the hypostoma is fused with the rostrum. This is also shown by a separated hypostoma of *O. primus* Walcott. It is more difficult to ascertain whether there are connective sutures. The specimens figured by Saito, and also a shield of *O. walcotti* figured by Resser (1939, plate 2, fig. 15), show that the free cheeks and rostrum are sometimes preserved in their normal relative positions, although displaced with respect to the cranidium, suggesting that the connective sutures are in a state of complete or partial symphysis. However, the facts may also be interpreted as indicating that the connective sutures were not used in ecdysis like the facial suture. In the above-mentioned specimen of *O. walcotti*, carefully studied and photographed, the connective sutures seem visible, although the possibility that a pair of cracks were produced in the flattening of the shield in the positions of the expected connective sutures is not entirely excluded. A drawing of the free cheeks and hypostoma of this specimen is shown in plate 1, figure 1. The rostrum, if correctly interpreted, is unusually wide (tr.) as it is also observed in the above-mentioned hypostoma of *O. primus*.

*Corynexochidae, Dolichometopidae, Dorypygidae, Zacanthoididae.*—These families are treated as one unit, the dividing lines being to a large extent arbitrary.

The hypostoma and rostrum in place have been observed by the writer in specimens of *Bathyuriscus*, *Kootenia*, *Olenoides*, *Ogygopsis* and other genera. In all instances there is conclusive evidence for the fusion of the hypostoma with the rostrum; the latter separates the doublures of the free cheeks. Fusion of the hypostoma and rostrum is complete in the Dorypygidae, where usually not even a furrow remains to indicate the boundary between the two areas. Good observations were made on shields of *Kootenia dawsoni* (Walcott) from the

*Ogygopsis* shale, and *Olenoides curticei* Walcott from siliceous nodules of the Conasauga formation. Several individuals of *O. curticei* preserve the hypostoma in place and show its anterior outline exactly fitting that of the cranidium. A reconstruction of the ventral appearance of the cephalon of this species is presented in plate 1, figure 3.

In numerous other representatives of the Corynexochidae, Dolichometopidae, Dorypygidae and Zacanthoididae, although the hypostoma was not observed in place, the structure of this organ leaves no doubt as to its manner of attachment. The portion of the shield usually described as the hypostoma includes the fused rostrum, sometimes separated from the main body of the hypostoma by a shallow transverse furrow. The laterally extended "anterior wings" in these families represent the rostrum, in most of the genera sharply truncated by connective sutures perpendicular to the cephalic margin. The typical "corynexochid" hypostoma of *Fieldaspis furcata* Rasetti is shown in plate 1, figure 2. Almost identical or similar hypostomas were observed in species of *Anoria*, *Athabaskia*, *Bathyuriscidella*, *Bathyuriscus*, *Bonnia*, *Corynexochides*, *Corynexochus*, *Dolichometopsis*, *Glossopleura*, *Ptarmigania*, *Ptarmiganoides*, *Zacanthoides*, and other genera. Fusion of the hypostoma and rostrum is the rule in these families. A possible exception is *Amphoton parallela* (Endo and Resser, 1937, plate 38, fig. 12) ; the hypostoma tentatively assigned to the species lacks the strong "anterior wings" and does not suggest direct attachment to the free cheeks. The fact that the hypostomas of other species of the genus (e. g., *Amphoton alia*, Endo and Resser, 1937, plate 38, fig. 16) show the usual corynexochid structure casts doubt on the assignment of the hypostoma in the former case. In *Ogygopsis* the hypostoma and rostrum are sometimes found attached, at other times separated, indicating a line of weakness if not a really functional suture.

*Bathynotus.*—In the Lower Cambrian trilobite *Bathynotus holopygus* (Hall) the doublures of the free cheeks are joined to the hypostoma through a pair of sutures directed obliquely forward and inward (plate 1, fig. 5). Although half a dozen specimens in shale exposed from the ventral side are extant, the writer was unable to ascertain whether or not the free cheeks meet for a short distance on the median line near the anterior margin. In any case it is certain that there is no rostrum, either separate or fused with the hypostoma, a feature that seems to distinguish *Bathynotus* from any other known Lower Cambrian opisthoparian. If the free cheeks meet on the median line, the type of cephalic sutures is essentially the same as in the much later (Upper Cambrian and Ordovician) family Asaphidae. However, partly because the contact of the free cheeks in *Bathynotus* is uncertain, partly because we have reason to believe that the asaphid suture was independently developed, we shall assign *Bathynotus* a special position. The ventral sutures in the closely related Middle Cambrian *Bathynotellus* (Lermontova, 1940) are unknown.

*Conocoryphidae, Ellipsocephalidae, Ptychopariidae.*—For the knowledge of the ventral sutures in these groups we must depend on Barrande's observations. Among the hundreds of species of Lower and Middle Cambrian ptychopariids studied, the writer was unable to locate specimens showing the ventral parts of the cephalic carapace in place.

Barrande states that *Conocoryphe sulzeri, Ellipsocephalus hoffi, Ptychoparia striata,* and *Sao hirsuta* possess a rostrum separated from the doublures of the free cheeks by connective sutures. He figured restorations of the ventral views of the cephala of *Conocoryphe sulzeri* and *Ptychoparia striata* (Barrande, 1852, plate 2b, figs. 24, 26). However, the relative positions of the various parts seem to have been inferred from observation of separate fragments rather than connected cephala, since the only actual individuals figured show only a portion of the hypostoma in place (plate 14, figs. 3, 10) and do not indicate the manner of attachment of this organ. That these trilobites and all their close relatives possess a rostrum seems certain, and also that the hypostoma is never fused with the rostrum. It is even possible that, at least in certain genera, the hypostoma was not directly attached to the rostrum, but separated from it by an uncalcified membrane. This possibility is suggested by the observation that in many ptychopariids there is a considerable distance between the front of the glabella and the anterior marginal furrow where the cephalic doublure apparently terminates. The hypostoma was certainly located under the anterior portion of the glabella, as shown by many crushed specimens where the outline of the hypostoma was impressed on the dorsal shield. There seems to remain an unexplained distance between the posterior margin of the doublure (rostrum) and the anterior margin of the hypostoma, a space that would be occupied by the above-mentioned uncalcified portion of the ventral integument. Further study of better-preserved material is necessary to decide this point. A less likely assumption is that the hypostoma was attached to the doublure by a stalk, as in the olenellid genus *Paedeumias* (Resser and Howell, 1938, plate 9, figs. 6, 7).

*Upper Cambrian trilobites.*—Many of the proposed families of Upper Cambrian trilobites are probably heterogeneous assemblages not representing phylogenetic units. As there is no certainty that all members of such families present the same type of sutures, genera and species where the ventral sutures are known are individually discussed.

In *Dikelocephalus retrorsus*, *D. subplanus*, and other species of the genus described by Ulrich and Resser (1930) specimens are found showing the free cheeks fused through a wide (sag.) doublure, with the hypostoma in place attached to the posterior margin of the doublure. According to the same authors, in other species of the genus (e. g., *D. raaschi* Ulrich and Resser) almost indistinguishable from the preceding in other characters, there is a median suture. Examination of material of these three species in the U. S. National Museum collections confirms Ulrich and Resser's conclusions.

Fused free cheeks were observed and in part reported by the writer (Rasetti, 1944, 1945*a*) in several species of Trempealeauian age from the Levis conglomerate. These are *Hungaia magnifica* (Billings), *Lauzonella planifrons* (Billings), *Levisella brevifrons* Rasetti, *L. oweni* (Billings), *Loganellus macropleurus* Rasetti, and "*Platycolpus*" *capax* (Billings). As a typical example of this type of suture, the free cheeks of *Levisella oweni* are represented in plate 1, figure 4. The writer (Rasetti, 1952*b*) is also describing fused doublures of the free cheeks in *Entomaspis radiatus* Ulrich in Bridge.

A median suture was reported by the writer (Rasetti, 1945*b*) in *Acheilus latus* Rasetti (plate 1, fig. 6). New observations revealed this type of suture also in *Acheilus spinosus* Rasetti, *Leiocoryphe gemma* Clark, and *Stenopilus elongatus* Rasetti. However, careful study failed to show the median suture in complete cephala of *Leiocoryphe transversa* Rasetti and it is possible that the doublures of the free cheeks are fused in this species. Separated free cheeks of *Housia canadensis* (Walcott) from the Goodsir formation (Franconian) of Moose Creek, British Columbia (specimens U.S.N.M. No. 5584) indicate a wide (sag.) doublure terminated by a median suture. This is the earliest occurrence of this type of suture known to the writer.

Presence of a rostrum was reported (Rasetti, 1946) only in *Catillicephala impressa* (=*Cephalocoelia*) from boulders of Dresbachian age. A ventral view of the cephalon of this species is shown in plate 1, figure 7.

This short list includes all the firsthand evidence that the writer was able to collect about the character of the ventral sutures in Upper Cambrian trilobites. However, the search of the relevant literature cannot be considered exhaustive.

At this point it should be mentioned that R. Richter (1932) and Stubblefield (1936) refer to unpublished observations by Resser of Lower Cambrian trilobites possessing a type of suture not listed above, consisting of facial sutures extending onto the doublure and not connected by a marginal (rostral) suture. All the genera of Lower Cambrian trilobites in the U. S. National Museum having been examined, the writer can state with certainty that such sutures do not exist among them, unless the above description applies to the sutures of the Pagetiidae, which, however, almost certainly were not the object of Resser's remarks. Resser's unpublished, erroneous observations led R. Richter to uphold the theory that the facial sutures form one unit with the connective sutures, and that the marginal (rostral) suture represents a later development. One of the results of the present study is the accumulation of extremely strong evidence against this view and in favor of Barrande's conception of the *grande suture* as a unit. Among the hundreds of genera of Cambrian opisthoparian trilobites examined by the writer in the course of his studies, very few (e. g., *Catillicephala*), and none of these Lower or Middle Cambrian, show the connective suture as the natural continuation of the dorsal portion of the facial suture. Usually the *grande suture* does not form any angle at the points where it is joined by the connective sutures (if any), so that examination of the cranidium does not enable one to establish whether or not there are connective sutures, or, if their presence is known, to determine their location. This statement applies regardless of the position of the frontal portion of the *grande suture*, whether marginal, dorsal-intramarginal, or ventral-intramarginal. Setting off a portion of this suture as a "rostral suture" appears both arbitrary and useless.

## EVOLUTION OF THE CEPHALIC SUTURES

Let us first review the types of ventral cephalic sutures observed in Cambrian trilobites in the order of their appearance.

In the Early Cambrian we observe a number of different types of ventral cephalic sutures, which we designate by a characteristic genus or family. These are: (1) the olenellid type, which might be further subdivided depending on whether or not the hypostoma is fused with the rostrum; (2) the agnostid type, i. e., lack of all sutures and probably of a hypostoma; (3) the eodiscid type, similar to the preceding except for the probable presence of the hypostoma; (4) the pagetiid type; (5) the corynexochid type, i. e., doublures of the free cheeks separated by the rostrum which is fused with the hypostoma; (6) the ptychopariid type, differing from the preceding in the lack of fusion of the hypostoma with the rostrum; (7) the bathynotid type.

In the Medial Cambrian all these types of sutures are presumably still represented by the respective groups, with the exception of the Olenellidae. No new types of sutures are known to have arisen through this epoch.

In the Late Cambrian, the Eodiscidae and Pagetiidae with their respective types of sutures become extinct. The agnostids persist through this epoch and the succeeding Ordovician period. Trilobites with corynexochid sutures become exceedingly rare. The only case known to the writer where the shape of the hypostoma definitely indicates fusion with the rostrum is *Hemirhodon* (Rasetti, 1946, 1948*b*) of late Medial Cambrian and early Late Cambrian age. Most of the Upper Cambrian opisthoparian trilobites seem to possess ptychopariid sutures, although this statement would at present be difficult to substantiate with actual observations. However, it is made highly plausible both by the obvious ptychopariid affinities of a great number of Upper Cambrian genera, and by the fact that this type of suture is of usual occurrence in the post-Cambrian families (Calymenidae, Otarionidae, Dimeropygidae, Proetidae) of almost certain ptychopariid descent.

Two new types of sutures are first known with certainty among medial and late Upper Cambrian (Franconian and Trempealeauian) trilobites, although in view of the small number of genera where the ventral sutures are known, we cannot exclude that these types had appeared earlier. In either of these cases the rostrum has been eliminated, the free cheeks meeting on the median line where they may be separated by a median suture (8, asaphid type) or fused together (9, levisellid type). The hypostoma remains separated from the doublure of the free cheeks by a functional hypostomal suture. The former type of suture is well known in the Ordovician Asaphidae, the latter in the early Ordovician genera *Nileus* and *Symphysurus*. Fusion of the doublures of the free cheeks also occurs in the "hypoparian" families and in the proparian family Phacopidae.

The affinities and systematic position of the Olenellidae, and in particular the important and difficult question whether they gave rise to opisthoparian forms, were exhaustively discussed by several authors (Stubblefield, 1936; Raw, 1937; Störmer, 1942), and the writer, having no new facts or viewpoints to present, leaves this group out of consideration. Furthermore, since he is satisfied that the eodiscids and the agnostids left no descendants, the following discussion is confined to the significance of the ventral cephalic sutures for the phylogeny and taxonomy of the opisthoparian trilobites (which include the post-Cambrian "hypoparian" families).

The overwhelming majority of Lower and Middle Cambrian opisthoparians possessed a rostrum (the only known exception is *Bathynotus*) either fused with the hypostoma (corynexochid type) or separated from it (ptychopariid type). There are no direct observations of the ventral sutures in Lower Cambrian ptychopariids, but by analogy with the Middle Cambrian forms we may safely assume that they had the same type of suture. We have yet no evidence to decide whether these types of sutures were independently inherited from Precambrian ancestors, or developed one from the other, and, if so, which was the primitive one. In certain families, presence or absence of a hypostomal suture does not seem to possess much significance (Olenellidae, *Paradoxides*). However, no example of fusion is known in the ptychopariids, where a functional hypostomal suture, or even an uncalcified membrane, seems to be a constant characteristic.

The asaphid and levisellid types appear much later and almost certainly derive from one or both of the previous types—more probably from the ptychopariid type, as both asaphid and levisellid sutures always include a functional hypostomal suture. This agrees with the fact that most of the above-mentioned Upper Cambrian genera showing levisellid or asaphid sutures appear on other grounds as descendants of the ptychopariid stock (which seems true of the overwhelming majority of the known Upper Cambrian genera). An alternative hypothesis is that *Bathynotus* represents the ancestral stock of trilobites with asaphid sutures, since it already lacked a rostrum; but it is an unlikely assumption as we know no intermediate forms connecting *Bathynotus* with the Asaphidae. The derivation of the asaphid and levisellid types of sutures from the ptychopariid type is easy to imagine, the connective sutures approaching each other until they merge into a median suture, or becoming fused either before or after coalescing into a single suture.

Among the post-Cambrian opisthoparian trilobites, the ptychopariid type of suture is the most common, followed by the asaphid and levisellid types in order of frequency. Fusion of the hypostoma with the rostrum seems unknown. It should be noted that the ptychopariid type of suture also occurs in those families (Illaenidae, Scutellidae) which, from the general appearance, have been considered (Richter, 1932) as descendants of the corynexochid stock. The lack of fusion of the hypostoma with the rostrum may be an indication against this assumed ancestry, when coupled with the fact that corynexochid trilobites seem almost entirely to disappear with the end of the Middle Cambrian and we are unable to connect them with the above-mentioned families. Unfortunately, we are at present unable to trace the Cambrian ancestry of many other post-Cambrian families, e. g., the Lichadidae, Odontopleuridae, and the proparian Cheiruridae, Encrinuridae and Phacopidae.

To assess the value of the ventral cephalic sutures for the phylogeny and taxonomy of the Cambrian genera, it will be necessary to know the types of sutures in a much greater number of forms. It does not seem plausible to expect that a phylogenetic classification of the Cambrian trilobites will be based on this character alone, or, for that matter, on any other single feature. The more we know about Cambrian trilobites, the stronger the conviction that there are no clear-cut characters of the exoskeleton that can be used for major subdivisions. A rational classification can emerge only from observing gradual changes of species and genera in space and time and establishing lines of descent. What we already know indicates that the task will be made difficult by widespread parallelism and convergence. It is possible that knowledge of the ventral sutures may furnish the clue for separating superficially similar but distantly related phylogenetic series.

It is hoped that this brief survey of the little we know about the ventral sutures in Cambrian trilobites will stimulate much-needed new observations. The following points are especially suggested to the attention of paleontologists: (1) observation of the ventral integument in Lower and Middle Cambrian ptychopariids, to establish the manner of attachment of the hypostoma to the rostrum; (2) study of the earliest appearance of the asaphid and levisellid types of sutures; (3) observation of the change in types of cephalic sutures in fairly well established phylogenetic series, to determine in what directions sutures have evolved, e. g., whether changes consisted in fusion of pre-existing sutures or appearance of new ones.

Both fossils in shale and limestone can be valuable in supplying this information. When collecting trilobites from shales where entire shields are not uncommon, attention should be paid to specimens exposed from the ventral side (unfortunately neglected by most collectors), which may preserve the hypostoma in place. Free cheeks separated from the cranidium but still attached to each other may furnish evidence for the levisellid type of suture. Cephala in limestone preserving the free cheeks should be carefully prepared to show the anterior doublure. Even isolated free cheeks, when the doublure is carefully exposed, may prove whether or not it extended to the midline, indicating absence or presence of the rostrum. Studies of this type will add far more to our knowledge of these organisms than the descriptions of endless new species, especially when based on insignificant differences from already known forms.

## REFERENCES

Barrande, Joachim, 1852. Système Silurien du centre de la Bohème, Prague and Paris.

Endo, Riuji, and Resser, C. E., 1937. The Sinian and Cambrian formations and fossils of southern Manchoukuo, Mukden.

Kobayashi, Teiichi, 1944. The Cambrian formations of the middle Yangtze valley and some trilobites contained therein: Japanese Jour. Geology and Geography, vol. 19, pp. 89-105.

———, and Kato, Fujio, 1951. On the ontology and ventral morphology of *Redlichia chinensis* with description of *Alutella nakamurai,* new gen. and sp.: Tokyo Imp. Univ., Fac. Sci. Jour., sec. 2, vol. 8, pp. 99-143.

Lermontova, E. V., 1940. Arthropoda: *In* Vologdin, Atlas of the leading forms of the fossil faunas of the U. S. S. R., vol. 1, Cambrian, pp. 112-193 (in Russian), Leningrad, Moscow.

Öpik, A. A., 1952. The hypostoma of *Pagetia*: Jour. Paleontology, vol. 26, pp. 272-274.

Rasetti, Franco, 1944. Upper Cambrian trilobites from the Lévis conglomerate: Jour. Paleontology, vol. 18, pp. 229-258.

———, 1945*a*. New Upper Cambrian trilobites from the Lévis conglomerate: Jour. Paleontology, vol. 19, pp. 462-478.

———, 1945*b*. Description supplémentaire de trois genres de trilobites cambriens: Naturaliste Canadien, vol. 72, pp. 117-124.

———, 1946. Early Upper Cambrian trilobites from western Gaspé: Jour. Paleontology, vol. 20, pp. 442-462.

———, 1948*a*. Lower Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidea): Jour. Paleontology, vol. 22, pp. 1-24.

———, 1948*b*. Middle Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidea): Jour. Paleontology, vol. 22, pp. 319-339.

———, 1951. Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains: Smithsonian Misc. Coll., vol. 116, no. 5, pp. 1-277.

———, 1952*a*. Revision of the North American trilobites of the family Eodiscidae: Jour. Paleontology, vol. 26, pp. 434-451.

———, 1952*b*. Cephalic sutures in the Upper Cambrian trilobite *Entomaspis*: Jour. Paleontology, vol. 26, pp. 797-802.

Raw, Frank, 1937. Systematic position of the Olenellidae (Mesonacidae): Jour. Paleontology, vol. 11, pp. 575-597.

Resser, C. E., 1939. The Spence shale and its fauna: Smithsonian Misc. Coll., vol. 97, no. 12, pp. 1-29.

———, and Howell, B. F., 1938. Lower Cambrian *Olenellus* zone of the Appalachians: Geol. Soc. America Bull., vol 49, pp. 195-248.

Richter, Rudolph, 1932. Crustacea: Handwörterbuch der Naturw., 2d ed., pp. 840-863, Jena.

Saito, Kazuo, 1934. Older Cambrian trilobita and Conchostraca from Northwestern Korea: Japanese Jour. Geology and Geography, vol. 11, pp. 211-237.

Störmer, Leif, 1942. Studies on trilobite morphology. Part II: The larval development, the segmentation and the sutures, and their bearing on trilobite classification: Norsk geol. tidsskr., vol. 21, pp. 49-164.

Stubblefield, C. J., 1936. Cephalic sutures and their bearing on current classifications of trilobites: Biol. Rev., vol. 11, pp. 407-440.

Ulrich, E. O., and Resser, C. E., 1930. The Cambrian of the upper Mississippi valley. Part I, Trilobita; Dikelocephalinae and Osceolinae: Milwaukee Public Mus. Bull., vol. 12, pp. 1-122.

Warburg, Elsa, 1925. The trilobites of the *Leptaena* limestone in Dalarne: Upsala Univ., Geol. Inst., Bull., vol. 17, pp. 1-446.

Westergård, A. H., 1937. *Paradoxides oelandicus* beds of Öland: Sveriges geol. undersökning, ser. C, no. 394, Årsbok 30, no. 1, pp. 1-66.

Whitehouse, F. W., 1939. The Cambrian faunas of northwestern Australia. Part 3: the polymerid trilobites: Queensland Mus. Mem., vol. 2, pp. 179-282.

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