Art. XVIII.—*Beecher's Classification of Trilobites, after Twenty Years;* by Percy E. Raymond.

In the February and March numbers of this Journal for 1897 appeared the two parts of Professor C. E. Beecher's short paper, on an "Outline of a Natural Classification of the Trilobites." The classification there proposed, modified rather by curtailment than expansion, appeared again in the Eastman edition of Zittel's Textbook of Paleontology in 1900. On this occasion, just twenty years later, it seems fitting to inquire how Beecher's work has stood the test of actual use and I wish also to present what follows as a slight tribute to the memory of my revered teacher. Beecher himself regarded this classification only as an outline, and often expressed the wish that he himself or some other person could find the time to elaborate the classification in the same manner that Professor Schuchert had elaborated his earlier outline scheme for the Brachiopoda.

Professor Beecher's untimely death just seven years after the first part of his "classification" was printed prevented his own return to the subject, and the studies and contributions of other writers on trilobites during these twenty years have dealt usually rather with single species, genera or families than with the subject as a whole. Numerous objections to the scheme proposed by Beecher have appeared, from Pompeckj in 1898 to Swinnerton in 1915, the objections varying in strength from Wood's* sweeping remark that "the only classification of Trilobites which can be adopted is a division into families" to Swinnerton's statement that the majority of new trilobites found since the publication of the classification "fit into it without difficulty and prove that to a large extent it is conceived on a sound basis. A few, however, do not fit in, and have therefore revealed its weakness."†

The most grave criticisms of the classification have been directed against the first of the three orders, the Hypoparia. It will be remembered that Beecher's classification was based upon observations drawn from a review of all that was known of the ontogeny of trilobites. Since the young of practically all primitive trilobites lack eyes on the dorsal side, Beecher grouped all trilobites in which absence of eyes was a primary characteristic, in his first order, Hypoparia. Recent studies and discoveries have led a number of investigators to the conclusion that blindness in the Agnostidæ, Eodiscidæ, Trinucleidæ, Raphiophoridæ and Harpedidæ is secondary and a degenerative, not primitive characteristic. If their position is well taken, then the order should disappear, and the families be distributed in the two orders which remain. A second change

* The Cambridge Natural History, iv, p. 244, 1909.
† Geol. Magazine, Dec. 6, ii, p. 487, 1915.

which has been suggested is the removal of the Calymenidæ from the Proparia to the Opisthoparia. Not of any great importance in itself, such a change reduces an already somewhat small order to such proportions that nearly all the families of trilobites would be grouped in the Opisthoparia and we would truly have arrived at the pass which Woods has deplored. The arguments can probably be best set forth if we take up in order each family whose position in the scheme has been questioned.

Hypoparia.

Agnostidæ.—Beecher included in this family both *Agnostus* and *Microdiscus* (*Eodiscus*), but the remarks which follow exclude the Eodiscidæ. The members of this family were considered by Beecher as the most primitive of trilobites, though he recognized in them certain highly specialized and even degraded characteristics (see his paper, pp. 184–185). He stated that the free cheeks were continuous and ventral in position, and the suture marginal or ventral. He unfortunately furnished no definite proof of these statements, the truth of which has been denied by Jaekel,* Lindström,† and Holm, and questioned by Swinnerton.‡

In his article Beecher states: "In *Agnostus* this feature (the suture) has escaped notice. The examination of extensive series of *Agnostus* in the National Museum and in the Museum of Comparative Zoölogy has proved that under favorable conditions of preservation this genus shows a distinct plate, separated from the cranidium by a suture, and it can be compared only with the free cheeks of other trilobites." Beecher neither mentioned the species in which he saw this plate, nor did he ever figure it.§ Acting on the above hint, however, I

* Zeitschr. Deutsch. Geol. Ges., vol. lxi, p. 387, 1909.

† Kongl. Svenska Vet. Akad. Handl., xxxiv, No. 8, p. 10, 1901.

‡ Geol. Mag., Dec. 6, vol. ii, p. 490, 1915.

§ *Agnostidæ.*—In regard to the presence of free cheeks in the Agnostidæ as seen by Beecher, the reason why he "furnished no definite proof of these statements" is as follows: Before he had printed his classification of the Trilobita he and I had gone over the material in the United States National Museum and I distinctly remember that he was especially desirous of seeing Hypoparia. Dr. Walcott had turned over to that museum much material that he had gathered under auspices of the United States Geological Survey and there was considerable material of the genus Agnostus. All of this material Beecher looked over, and among the American species of Agnostus preserved in shales there was one that seemed to show the presence of free cheeks. The evidence at first was not conclusive and he then went over the material again and finally succeeded in finding a free cheek in the form of an imprint lying alone among the heads and tails of Agnostus. The species is now unknown to me. This he showed to me and we agreed that it was actually a free cheek of a species of this genus. In width the free cheek was linear, almost no thicker than a human hair and without a trace of an eye-spot or ornamentation. The reason why he did not figure the specimen was because the Cambrian trilobites were reserved for further study by Walcott, and it was expected that in the course of time the latter would come upon this specimen and figure it in his prospective monograph of Cambrian trilobites.—Charles Schuchert.

have gone over the specimens in the Museum of Comparative Zoölogy, and I find that the facial suture and free cheeks are very well shown on many specimens of *Agnostus nudus*, can be plainly seen on a few specimens of *A. integer** and *A. bibullatus*, and rather imperfectly made out on a number of *A. rex*. Curiously enough, these free cheeks and sutures occur on that portion of the animal which Angelin, Barrande, Jaekel and others have designated the pygidium, a fact which may have caused some investigators to overlook them. The specimens in which these features can be seen are all casts in a very fine-grained shale and are, of course, all from Bohemia. I think the structures can be seen by anyone who has access to a large collection of these species, the only preparation necessary being the flaking off with a fine needle of the cast of the doublure around the margin of the cephalon. Full grown specimens of *Agnostus nudus* are of fair size, and so permit this development. Other species would probably show the features as well under favorable conditions of preservation, but I have looked through our extensive set of Swedish and American specimens without finding any examples showing the sutures. *Agnostus nudus* has one shield evenly convex, and the other with a depressed brim. All authors seem to have considered the evenly convex shield the cephalon, because of the way in which the segments overlap one another. The facial sutures are not marginal, but intra-marginal. They meet in an obtuse angle at the front, and run backward just inside the margin, reminding one much of the course of the pre-ocular portion of the suture in an *Homalonotus*. The sutures keep within the angles, so that the fixed cheeks bear the genal angles, a Proparian characteristic. The sutures in this manner cut off a yoke-shaped area, bounded outside by the facial sutures and inside by a natural edge which follows the outline of the base of the elevated portion of the cranidium (the glabella). Both limbs of the yoke taper backward to a point, and it forms a continuous plate, with no vertical or epistomal sutures. The plate has the position and aspect of a large epistomal plate, but whether called an epistoma or free cheeks, the sutures which separate it from the cranidium must

FIG. 1.

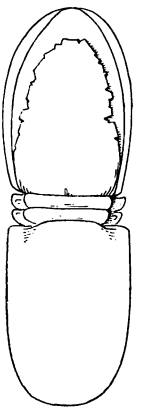

Fig. 1. *Agnostus nudus* (Beyrich). Figure after Barrande, with the sutures and ventral plate added from a specimen in the Museum of Comparative Zoölogy. Enlarged.

* It is shown in one of Barrande's figures of this species, on what he believed to be the pygidium. System Silur. Bohême, I, pl. 49, fig. 5*b*.

on the Beecher hypothesis be interpreted as the facial sutures. Each suture shows a slight outward bend near the anterior end, suggesting the presence of a small eye, but I am not prepared on present evidence to say that eyes were present on the ventral side. Jaekel's* argument that because these trilobites had the power of closing the pygidium against the cephalon, they could not have eyes or facial sutures on the ventral side seems to be absolutely without point.

Swinnerton also cites in favor of his view that the Agnostidæ are degenerate Proparia with fused fixed and free cheeks and obliterated eyes, the fact that Walcott has placed his genus *Mollisonia*† "near the Agnostidæ" (really Eodiscidæ) and in describing it refers to indications of eyes and facial sutures on the dorsal side. I have only the published figures of *Mollisonia* by which to judge of its characteristics, but they seem to justify the rather incomplete descriptions which have been published, and I do not see that any importance can be attached to them in connection with the Agnostidæ. Indeed, it remains to be definitely shown that they are trilobites. The condition of preservation of the specimens indicates a test unlike that of the associated trilobites.

Summarizing what has been said about the Agnostidæ, it may be stated that interpreting trilobites in the generally accepted way these trilobites do possess facial sutures, that the sutures and free cheeks are ventral in position, and the position of the free cheeks is such that these trilobites, had they been of progressive stock, would have given rise to Proparian descendents. Since the free cheeks are not visible from the dorsal side they can not be placed in the Proparia, and Beecher's order Hypoparia is justified, even if this family only is to be included in it.

Eodiscidæ.— The discovery by Walcott of two species of Eodiscids with free cheeks and eyes seems to me a remarkable confirmation of the correctness of the position to which Beecher referred this family. *Pagetia*‡ is an undoubted Eodiscid and has eyes very far from the glabella, i. e., near the margin, and the facial sutures are short and have a typical Proparian course. Now this is exactly what one would expect in the case of a trilobite in which the eyes had just migrated over the lateral margins and is in entire harmony with all Beecher's ideas. If *Pagetia* were the oldest known genus of the Eodiscidæ, one might argue with some plausibility that the other eodiscids were degenerate from such a state of development. The opposite is, however, true. The great development of the Eodisci-

* Op. cit., p. 388.
† Smithsonian Miscl. Coll., vol. lvii, p. 195, pl. 24, fig. 3, 1912.
‡ Ibid., vol. lxiv, No. 5, p. 408, pl. 67, 1916.

dæ was in the Lower Cambrian, and the specimens bearing the eyes are from the Middle Cambrian. Not only that, but these species are highly specialized eodiscids, as is shown by the reduction to two thoracic segments, the practical obliteration of furrows on the pleural lobes of the pygidium, and the great axial spines, especially in *Pagetia bootes*.

The discovery of a genus with two species which bear eyes very close to the lateral margins seems to be a confirmation of the previous supposition that the Eodiscidæ have ventral free cheeks. Since the great majority, including the most primitive of the genera and species of this family, do not show free cheeks on the dorsal surface and so come within the limits of the Hypoparia as defined by Beecher, it seems to me that the family should remain in that order. Like the Agnostidæ, the Eodiscidæ appear to have Proparian tendencies.

Shumardidæ.—These little trilobites are still too much of a puzzle to be discussed at any length, and the ultimate disposition of the family has no particular bearing upon the question at hand.

Harpedidæ.—Of this family I have no personal knowledge, but as its principal characteristics are even more primitive than those of the Trinucleidæ and as the organization of its cephalon is so closely parallel to that of the latter group, I do not yet see any particular reason to remove the family from the position in which Beecher placed it.

I have the paper by Richter mentioned by Swinnerton, and though I have the greatest respect for the work of Dr. and Frau Richter, still Middle Devonian species of Harpes can not be considered as exactly the ones to study in getting at the primitive characteristics of this group. There seems no *à priori* reason why simple or aggregate eyes should not develop on trilobites absolutely independently of the compound eye, and the presence of such eyes in a Silurian or Devonian trilobite whose ancestors were more nearly blind does not seem any proof at all that they are remnants of fully developed compound eyes.

Trinucleidæ.—It is in connection with this family that the principal objection against the order Hypoparia has been raised. The present opinion of a number of paleontologists, best summarized by Swinnerton, is that the Trinucleidæ are degenerate descendents of trilobites with eyes, that the free and fixed cheeks are coalesced with the obliteration of the suture, and that the ocelli on the cheeks represent the degenerate remains of compound eyes. These paleontologists believe that the facial suture of McCoy is the real facial suture and either deny the presence or question the morphology of the facial suture of Barrande. This idea is of course not new, but has been given especial

impetus of late years by the reference by Lake of *Orometopus** to the Trinucleidæ. (Using Trinucleidæ in a broad sense, as including the Raphiophoridæ.)

The question of the facial suture may be taken up first. Reed is the latest writer on the Trinucleidæ, and his excellent series† of papers have added much that was new about the family. Dr. Reed seems, however, to have changed his mind about the sutures several times in the course of preparation of the papers, a thing for which anyone who has studied this puzzling family can readily forgive him. On page 170 of the concluding article he states:—"No satisfactory evidence of such sutures [across the cheeks and apart from the marginal suture round the fringe] in young or adult has been produced, and McCoy's figures and description of their presence in his genus *Tretaspis* are not supported by the specimens which he used." Yet on the final page he concludes that the fixed and free cheeks are fused and the eyes degenerate. He does not anywhere deny the reality of the marginal suture, but offers two possible explanations of it, the second of which he adopts. Firstly, the ventral plate may represent a second underturned segment of the ancestral annelid, or secondly, the marginal suture may represent a secondary facial suture to assist in moulting and compensate for the one lost by fusion.

The first of these suppositions can not in our present state of ignorance of the ancestor of the trilobites be profitably discussed. It may be remarked however, that if Bernard was right in considering the oculiferous segment of the ancestral annelid to have been the first, then another ancestor for *Trinucleus* than for the remainder of the trilobites would be called for. The second point, however, needs further consideration.

If, as Reed claims, the marginal suture is secondary after complete fusion of the primary sutures, then this splitting must have taken place after the animal had become fully adapted to that mode of life which led to the obliteration of the true sutures. In other words, the fringe must have been fully developed before the splitting took place. Now whatever the primary functions of the perforations of the fringe, the numerous invaginations certainly greatly strengthen the brim and reduce rather than enhance the chances that it would split. Moreover, if the whole fringe were merely the doublure of the free cheeks, as would be necessary in his interpretation, why is the pattern of the lower side unlike the upper? The fact that the patterns are unlike certainly argues for the independent origin of the lower plate. Among Opisthoparian

* British Cambrian Trilobites, Palaeontogr. Soc., vol. lxi, p. 46, pl. 4, figs. 6–10, 1907.

† Geol. Mag. Dec. 5, vol. ix, pp. 346 and 385, 1912; Dec. 6, vol. i. p. 349, 1914: Dec. 6, vol. iii, pp. 118 and 169, 1916.

trilobites there are two types of head structure: one in which the facial sutures are confluent around the frontal margin, and the free cheeks do not meet but are separated by an epistoma: another in which the free cheeks meet in a vertical suture and an epistoma is apparently absent. Now the first condition is very much more common than the second, and where the second condition is best shown, in the Asaphidæ, there is considerable evidence that proves that the epistoma is present, but that the epistomal sutures are obliterated and that the vertical suture is secondary. If, then, *Trinucleus* is a degenerate Opisthoparian, the plate in front of the hypostoma must be the epistoma, and the chances are that the part of the marginal suture directly at the front is a part of the true facial suture. If that be the case then the facial suture is not entirely obliterated, and we ought in the thousands and thousands of specimens which have been examined, to find at least one or two which show traces of the remainder of the facial suture or of the epistomal sutures. In no case among the Opisthoparian or Proparian trilobites where the cheeks are fused have the sutures become entirely obliterated.

It is probably permissible to say, without being accused of sectional pride, that the North American specimens of "*Trinucleus*" are more numerous and better preserved than those of any other region. We do not find the abundant entire specimens such as occur in Bohemia, but in our specimens the test is well preserved and the specimens are not flattened. And anyone who collects in our rocks readily becomes convinced that the ventral plate of "*Trinucleus*" is readily separable from the cranidium. One of these plates, naturally separated, when viewed from the inside, shows the first two rows of "hour-glass structures" broken across at the constriction, but the posterior rows of pits were not deep enough to connect across, so that they show from the inside as hemisphæric mounds. The angles of this ventral plate carry the genal spines, and where the cranidium is found without the ventral plate, the angles are smoothly rounded, showing that the suture becomes dorsal in position at least at those points. The fact that this ventral plate is entirely separable along well-defined sutures, and that it bears the genal spines, seems rather conclusive evidence that it is a primarily independent plate, and that the suture is not secondary. Reed has suggested a comparison with *Limulus*, but in that genus the crack extends only around the front and sides of the cephalothorax, does not extend to the angles, and does not cut off a separate plate. If the marginal suture in the Trinucleidæ were a similar makeshift cracking, there seems no reason why it should not be similarly incomplete. The marginal suture of *Trinucleus*

seems homologous with the ventral suture of *Agnostus*, and that, not being at an edge, can not well be explained as a secondary splitting.

There remains to be discussed the question of *Orometopus*. Why should it be included in the Trinucleidæ? It is so unlike any of the Trinucleids that the burden of proof that it belongs to that family should be upon those who have placed it there, but its present placing has been accepted with such avidity that it is necessary to make some comments. Lake says of *Orometopus** :—"The clavate glabella, the horizontal grooved pleuræ, and the broad triangular tail, are characters which it shares with those genera [Trinucleus and Ampyx], and which differentiate it from other families."

The characteristics which ally *Orometopus* with the Trinucleidæ and Raphiophoridæ are all to be found in the thorax and pygidium, and the result of the experience of all students of trilobites has been to learn that the thorax and pygidium seldom show characteristics of family rank. Within the same family the thorax and pygidium are often highly variable, and the thoraces and pygidia of some species in totally unrelated families are quite similar. The broadly rounded form, flat segments and wide short pygidium of *Orometopus* make it look like a trinucleid or ampycid, but those families share with *Harpes* and many of the Olenidæ the form of the thoracic segments, and the pygidium is olenid in outline.

Orometopus differs from the Trinucleidæ in the possession of compound eyes and large free cheeks on the dorsal side, in lacking a specialized glabella which enlarges forward, in possessing more than 6 thoracic segments, and especially in the form of the hypostoma, which is nearly square in *Orometopus* with a straight posterior border and nearly circular with a median tongue-shaped posterior projection in "*Trinucleus*." The similarities consist merely in the form of the thoracic segments and pygidium, and are of too little importance to outweigh the evidence of the other characteristics of the animals.

Orometopus can, I think, be quite definitely eliminated as a possible ancestor of the Trinucleidæ. From Barrande's work many stages in the development of "*Trinucleus*" are known. Although the protaspis has not been seen, specimens without thoracic segments and only 1^{mm} long have been figured. The striking thing about the young "*Trinucleus*" is that the pygidium is nearly or quite as large as the cephalon. This is very unusual in the young of trilobites, and if we can trust the young as pointing toward the ancestral line, some isopygous group like the Agnostidæ or Eodiscidæ is indicated, rather

* Op. cit., p. 44.

than such a form as *Orometopus*. In fact, the row of pustules on the border of some species of *Eodiscus* foreshadows to some extent the Trinucleid fringe. The ontogeny of such a species as *Cryptolithus ornatus* (Sternberg) shows that in the youngest stages now known the cephalon of *Cryptolithus* has a narrow brim without pits, that at the same time as the development of the first thoracic segment a single row of pits is present, and with increasing growth the brim widens with successive rows of pits. It is interesting to note that the cephalon of the oldest of the Trinucleids, *Trinucleus reussi* Barrande, shows in the adult a form corresponding to the second stage in the development of *Cryptolithus ornatus*, having but a single well developed row of pits on its narrow brim, and showing the same large side lobes on the glabella. This form I propose to make the type of a separate genus, *Trinucleoides*.

To summarize for the Trinucleidæ then, it may be said:—firstly, that there is no positive evidence that the free and fixed cheeks are fused, Reed having definitely shown that the suture of McCoy is not a facial suture.

Secondly, the ventral plate is an easily separable and independent plate, bounded by sutures which on Beecher's conception of the morphology of the head would be the facial sutures.

Thirdly, *Orometopus* does not in itself present any very strong evidence that it is the ancestor of the Trinucleidæ.

Fourthly, the ontogeny of the Trinucleids points to an isopygous ancestor with ventral free cheeks, of the same type as Eodiscidæ or Agnostidæ.

Until some stronger evidence of the degeneracy of the Trinucleids from an Opisthoparian ancestor is adduced, I think the family may safely be left in the Hypoparia.

Raphiophoridæ.—Professor Swinnerton is entirely correct when he states that the Raphiophoridæ "are presumably placed in the Hypoparia because of their evident relationship to the Trinucleidæ." It is no part of the function of a "natural" classification to force apart evidently related families merely to be consistent with the definitions. The more natural a classification is, the more impossible it is to frame definitions which are rigid. The word "generally" must be freely used or understood. That the highest families of one order should parallel the lowest of a more advanced order is to be expected, and may be construed as furnishing a proof of the success of a classification, rather than as militating against it.

The Raphiophoridæ furnish one point of considerable interest in connection with this discussion. It is generally accepted that the epistoma and the free cheeks are parts of the same

segment, but it is possible to think of them as belonging to different segments, in which case the ventral plate of the Agnostidæ and Trinucleidæ might be thought of as simply an epistoma and not as undifferentiated free cheeks and epistoma. Free specimens of *Lonchodomas portlocki* (Barrande) show on the ventral side of the head a yoke-shaped plate like that of *Agnostus nudus*, but instead of being confined to the ventral side, it laps over the margins up onto the dorsal side, being separated from the cranidium by a suture which has the course of the ordinary facial suture. The absence of eyes makes the analogy with the ventral plate of Agnostus the more complete, and there can be no doubt that in this case the ventral plate has encroached upon the dorsal side, and there can also be no doubt that the plate represents the undifferentiated free cheeks and epistoma.

FIG. 2.

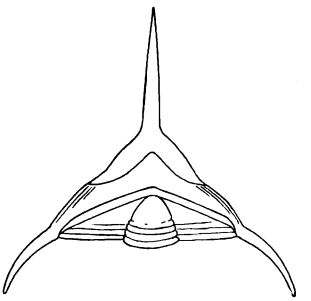

FIG. 2. *Lonchodomas portlocki* (Barrande). Figure, somewhat restored, of an enrolled specimen in the Museum of Comparative Zoology to show the continuous ventral plate of the cephalon. Enlarged.

All the families of the Hypoparia have now been reviewed and it hardly seems that there is strong evidence at the present time for removing any of the families from that order. Within the order there seems to be a tendency in two directions, in the Agnostidæ and Eodiscidæ toward the Proparia, and in the Trinucleidæ and Raphiophoridæ toward the Opisthoparia. That the Eodiscidæ should in the Middle Cambrian have produced a true Proparian, *Pagetia*, and that on the other hand the Opisthoparian Trinucleids should apparently hark back to another branch of the same stock, shows that we can not dispense with the order and relegate its families to the Opisthoparia and Proparia. The attempt to show that the Agnostidæ, Trinucleidæ and Harpedidæ are degenerate Proparia and Opisthoparia seems to fall from lack of evidence, while the evidence for their primitive position seems to increase with new discoveries.

Opisthoparia.

Mesonacidæ.—The suggestions of Swinnerton in regard to this family and his proposed order Protoparia are certainly exceedingly interesting and attractive, and offer the only logical explanation so far put forward for the condition seen in the Mesonacidæ. Unfortunately, to accept Swinnerton's explanation involves a belief in the polyphyletic origin of the trilobites, which hardly seems probable, in view of the compactness of the group.

There can be no doubt, in spite of statements to the contrary, that a fair proportion of specimens of Mesonacids show distinct traces of facial sutures, particularly of the part behind the eyes. This posterior portion of the sutures is well shown in Walcott's* figures of *Elliptocephala asaphoides* (pl. 24), *Mesonacis vermontana* (pl. 26), *Callavia bröggeri* (pl. 27), and *Callavia callavei* (pl. 42,—this shows anterior portion of sutures also). The fact that specimens often show the facial suture on one half of the cephalon and not on the other, and that the anterior portion may show on a specimen which shows no trace of the posterior portion, would seem to indicate that these sutures are vestigial and not rudimentary and in a state of symphysis and not synthesis (see Swinnerton, p. 492).

When Swinnerton states that the young Mesonacids do not show facial sutures, and that in the youngest known specimens the eyes are fully developed and on the dorsal surface, he is correct, for there is here an anomaly among trilobites. While the eyes come in at the margin and move (relatively) backward through the growth of the free cheeks during development there is no suggestion that they were ever ventral or came over the margin. The facial sutures are much more in evidence in the adult than in the young. If the Mesonacids could be considered as highly specialized trilobites occupying a terminal position in their particular line of development, we might explain this as a case of "earlier inheritance," but all the evidence of the thorax and pygidium seems to point to the primitive state of development in the Mesonacidæ.† From a study of the young stages in the development of Elliptocephala and other genera of the family it is possible to develop a theory of

* Smithsonian Miscl. Coll., vol. liii, No. 6, 1910.

† The supposed possession by *Olenellus* of a telson in place of a pygidium has been used as an argument that the Mesonacidæ are specialized trilobites. Personally, I do not believe that the spine seen at the termination of *Olenellus* is a pygidium, or takes the place of the pygidium, but that this spine is the normal spine seen on the 15th segment of all species of Mesonacis and Paedeumias. In other words Paedeumias seems to me to be a complete specimen of Olenellus. This belief is of long standing, as may be seen by my wording of the definition of Olenellus in the "Eastman-Zittel" textbook, and has just received an interesting confirmation in the discovery by Walcott that *Olenellus gilberti* is a *Mesonacis* (Smithsonian Miscl. Coll., vol. iv, p. 406, pl. 45, fig. 3).

the secondary origin of the free cheeks on a plan quite different from that set forth by Professor Beecher.

The study of the young specimens of Mesonacids figured by Ford,* Beecher, and Walcott indicates that the cephalon of these trilobites is made up of six similar segments each consisting of an axial and pair of pleural portions. The axial portions are ranged one behind the other in a straight line, while the pleuræ are bent abruptly backward so that the anterior ones closely envelop and crowd those behind. The effect of this crowding has been to eliminate the greater part of the pleuræ of the last segments, though these three segments combined produced one pair of spines which project beyond the posterior border. The first two segments of the cephalon are more or less coalesced, and their pleuræ also unite to produce

FIG. 3.

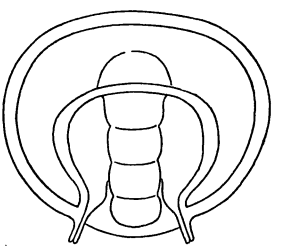

FIG. 3. *Elliptocephala asaphoides* Emmons. A very young specimen, representing one of the earliest stages known in the development of a Mesonacid. After Walcott. Much enlarged.

a pair of free spines. In the smallest specimens known these spines are very close together (Walcott, loc. cit. pl. 25, figs. 1, 2) or may even be coalesced (pl. 25, fig. 22). On further growth. there is a spreading out along the posterior margin, as is shown by the fact that the spines move outward. The spines of the first two segments separate, so that the spines of the first segment move to the genal angles, or in some cases, even around to the front of the cephalon (Walcott, loc. cit. pl. 36, fig. 14; pl. 7, figs. 9-11); the spines of the second segment move outward to form the intergenal spines, or where the 3 pairs of spines remain, the genal spines; and the inner spines of the young are either suppressed or, in exceptional cases, become intergenal spines. If then, we think of the dorsal surface of the head of these trilobites as consisting of 6 united segments, the first act in forming the head was the sharp bending back of all the pleuræ to form an oval head

* This Journal (3), vol. xiii, p. 265, 1877; vol. xv, p. 129, 1878; vol. xxii, p. 250, 1831.

shield, and then by secondary growth of interstitial tissue at the back, the pleuræ were again forced around into nearly their original position, but as the pleuræ of the third, fourth, and fifth segments had been largely obliterated in the turning backward, the new cheeks were composed principally of the pleuræ of the first and second segments. Unless one believes with Lindström that the Mesonacidæ were blind, it follows that even in these young forms the inner edges of the pleuræ of the first (dorsal) segment carried the visual surface of the eye, and the pleuræ of the second segment formed the palpebral lobes.

In order to facilitate moulting there should have been some sort of a suture in the Mesonacidæ, and seemingly there was a ventral suture, at least in the young, very similar to the suture in the Agnostidæ. Walcott has figured several specimens in which the hypostoma is attached to a narrow "doublure", and one remarkable specimen from Pennsylvania in which the hypostoma attached to a narrow "doublure" has swung back so that it presents its ventral face to the observer on the same block with and still attached to the head shield. This doublure is analogous to the ventral plate of *Agnostus*, and that the suture along which it separated was not marginal is shown by the fact that the plate is attached at the intergenal and not at the genal spines. If this plate is not accidentally separated, then it is an epistoma, and constitutes the seventh and anterior segment which made up the head of the trilobite, the hypostoma being its appendage.

It would be easy to conceive that, to facilitate the removal of the covering of the eye in moulting, dorsal facial sutures should be secondarily developed. Beginning at the front of the eye and running back to the posterior margin of the head, there was a natural line of weakness, because it was the line of division between the original first and second segments of the dorsal side. And it is known that the posterior portion of the suture does follow this line, as, when present, it comes out at the intergenal spine. Forward from the front of the eye, the course of the facial suture had no natural line to follow, but in most cases seems to be guided by the outline of the hypostoma, hence the outward curve. Following this line of reasoning it would follow that the lines which are seen on the heads of Mesonacids are rudimentary sutures, and that Swinnerton was right in regarding the ancestral trilobite as being without free cheeks. And, further, it is conceivable that in the process of evolution, the free cheeks crowded upon the epistoma so as to greatly reduce its size, or even force it out entirely.

In this way of thinking of the trilobite head, the anterior segment was not oculiferous, the eyes would never have been ven-

tral in position, and there is no reason why in development they should travel backward. This seems the greatest argument against Swinnerton's view, for in practically all trilobites except the Mesonacidæ, the eyes appear first at the margin and do travel backward. Beecher's theory seems to explain all trilobites except the Mesonacidæ, while Professor Swinnerton's applies to the Mesonacidæ principally, and unless it can be shown that the Trilobita are polyphyletic, it seems better to adhere to Beecher's idea, and await an explanation of the Mesonacidæ which is in accordance with our notions of other trilobites.*

As a matter of fact, if Swinnerton's suggestion of the Protoparia were logically carried out, it would affect the present classification but slightly. He would probably remove the Raphiophoridæ to the Opisthoparia, but the remaining Hypoparia would become Protoparia and the Mesonacidæ would replace the Raphiophoridæ as the highest of the Protoparia. It is not at all a consequence of his definition of the Protoparia that the Agnostidæ and Trinucleidæ should be considered degenerate animals, On the contrary, as they possess a large ventral plate (epistoma) and no visible free cheeks, the traces of eyes which they possess may well be considered rudimentary instead of vestigial, and when, as in *Pagetia* among the Eodiscidæ, eyes become fully developed, facial sutures and free cheeks are formed. At first sight, this method of the formation of the free cheeks would seem to apply only to the Opisthoparia, but in the secondary forward movement of the pleural portions of the head, as evidenced by the forward migration of the spines, is seen a modus by which the posterior portion of the facial suture may be brought to terminate in front of the genal angle, and so produce the Proparia.†

I have thus developed Swinnerton's scheme at greater length than did its proposer in order to show how attractive it is, and how well it explains conditions which obtain in the Mesonacidæ, and at the same time, how little change its adoption would make in our present classification. Little is known of the morphology of the head of the trilobite, and it is entirely possible that the free cheeks may be a part of the epistomal segment in one group of them, and a part of the first dorsal segment in others. The problem is well worth keeping in mind in future investigations. Until more is known, however, it seems as though the Mesonacidæ were in as secure a place

* Beecher pointed out that the actual protaspis of *Elliptocephala* is not yet known, and when discovered it may prove to be eyeless, and in conformity with other young of Cambrian trilobites.

† See in this connection Dr. Clarke's figures of *Proboloides cuspidatus* from the Devonian at Ponta Grossa, Brazil. Monographias do Serviço Geologico e Mineralogico do Brazil, 1, 1913, pl. 7.

near the base of the Opisthoparian pyramid as high in the Hypoparia (Protoparia).

Proparia.

Calymenidæ.—When I was preparing the revision of the families of trilobites for the second edition of the "Eastman-Zittel" Textbook I was at first inclined to follow the suggestion of Pompeckj* and others and place this family near the Olenidæ in the Opisthoparia, but after considerable study of the evidence for and against, left the family where Beecher placed it. I remember, as a student, asking Beecher why this family was placed in the Proparia rather than in the Opisthoparia. He replied that while as a group, the post-ocular portions of the facial sutures cut the genal angles, in *Pharostoma*, one of the geologically older and presumably primitive genera, (also so considered by Pompeckj) the genal spines were borne by the fixed cheeks and the free cheeks were decidedly Proparian. This seems a proper reason, and if this Proparian family can be derived from an Olenid stock, so much the better for our general knowledge of trilobites. In addition to the statement in regard to the condition of the cheeks in *Pharostoma*, it may be mentioned that the cheeks in the earlier stages of the development of the common *Calymene senaria* of the American Trenton are also distinctly Proparian, so that the parallelism of the adult with *Triarthrus* in this matter is a secondary affair.

With this I shall close my remarks on the objections which have been raised to the Beecher classification. I think that Professor Swinnerton has sufficiently shown the very inadequate basis of Gürich's classification, and the same remarks with which an eminent investigator has dismissed Professor Jaekel's suggested classification of the reptiles may be applied to the result of his endeavors in behalf of the trilobites. To discuss at the present time Professor Swinnerton's proposed sub-orders and families would not be appropriate. The samples which Dr. Walcott has recently been giving us of his wonderful store of Cambrian trilobites indicate clearly the futility of proceeding to the refinements of classification until that fauna is quite fully described.

Museum of Comparative Zoölogy,
Harvard University,
Cambridge, Mass.

* Ueber Calymmene Brongniart, Neues Jahrb., vol. i, 1898, p. 187.