

American Journal of Science

APRIL 1940



ON SOME TRINUCLEIDAE DESCRIBED BY JOACHIM BARRANDE

HARRY B. WHITTINGTON.

ABSTRACT. Four species of trinucleids described by Barrande have been restudied. Three are shown to be conspecific and to belong to a genus recently erected in England. The ontogeny of this species is redescrbed and discussed. New information on the fourth species, intermediate between the Dionididae and the Trinucleidae, is given.

I. INTRODUCTION.

II. TERMINOLOGY.

III. ON *ONNIA ORNATUS* (STERNBERG) 1833

- a) Discussion.
- b) Description of the Holaspid Trilobite.
- c) Ontogeny of the Species.

IV. ON *TRINUCLEOIDES REUSSI* (BARRANDE) 1856

- a) Discussion.
- b) Description of the Species.

V. LITERATURE.

I. INTRODUCTION.

AMONG the collections at the Museum of Comparative Zoölogy, Harvard University, is some excellent material of the Trinucleidae described by Joachim Barrande in the first volume and supplement of his 'Système Silurien de la Bohême.' Prof. Percy E. Raymond generously allowed me to borrow some of the material for study. The object of this paper is to redescrbe these Bohemian forms.

In 1929 and 1933 Mr. B. B. Bancroft erected several new genera and many new species of *Cryptolithus* (s. l.) from the upper Ordovician of Shropshire, England. He based these genera and species almost entirely on the pattern features of the pits in the fringe, and they have proved to be valuable zone indices. Dr. L. Størmer (1930) does not accept some of Mr. Bancroft's genera and does not agree that the pattern features of the fringe are reliable as generic characters, but he described

the fringe of many of the Scandinavian trinucleids in great detail. My own stratigraphical work in Wales, and unpublished work by Dr. A. Lamont in Ireland, has tended to uphold the correctness of Mr. Bancroft's views, and it seems important, therefore, that the Trinucleidae should be restudied with special reference to the characters of the fringe. The Bohemian forms redescribed in this paper give in addition information on the ontogeny of one of Mr. Bancroft's genera. The distribution and migration of trilobites in British lower Palaeozoic faunas has recently been discussed by Dr. C. J. Stubblefield (1939), and this present study adds a little that is new to the picture. I hope that the restudy of the American trinucleids will add much more to our knowledge of the distribution and migration of this group.

This work has been done during the tenure of a Commonwealth Fund Fellowship at the Peabody Museum, Yale University. I am very grateful to Prof. Carl O. Dunbar for his continued guidance and assistance. Both he and Professor Raymond have read my manuscript and offered many valuable criticisms.

II. TERMINOLOGY.

The nomenclature used follows Warburg (1925, pp. 2,214) and Størmer (1930). I have followed Raw (1925) and Stubblefield (1926) in using the term "degree" in describing the Meraspid period, but have followed Størmer (1930, p. 59) in regarding degree 6 as the first degree of the Holaspid period. In describing the fringe of *Onnia ornatius* I have found it convenient to use the notation for concentric rows of pits proposed by Bancroft (1929, p. 69):—

"a) Rows situated externally to the girder are denoted by E followed by a numeral. Thus where there are four such rows, say, E₁, E₂, E₃, E₄, E₁ is the row contiguous to the girder, and E₄ the outermost row.

b) Rows situated internally to the girder are denoted by I and a numeral, thus I₁, I₂, I₃, I₁ being contiguous to the girder, and I₃ the innermost row (against the 'cheek')."

III. ON *Onnia Ornatius* (STERNBERG) 1833.

Plates I-III.

a) Discussion.

In 1852 Barrande described four species of the genus '*Trinucleus*', collected from his Stage D. The first, '*T.* *bucklandi*,

has been placed in *Tretaspis seticornis* (Hisinger) by Størmer (1930, p. 55). The other three I regard as conspecific, and place them in the genus *Onnia* Bancroft 1933, adopting the oldest of the specific names. '*Trinucleus*' *ornatus*, as understood by Barrande, came from Stage D_{a3-5} (1852, pp. 68, 626; Barrande gives D_{d3-4}, but the specimens M.C.Z. 2277, labelled by Barrande, are from D_{a5}), and in my material is preserved in black shale, the specimens being flattened but not crushed. '*Trinucleus*' *ultimus* Barrande, from Stage D_{a5}, (1852, pp. 68, 632; 1872, p. 48), is preserved in like manner, but I have very little material. '*Trinucleus*' *goldfussi* Barrande came mainly from Stage D_{a2}, but also from Stage D_{a3-4} (1852, p. 630), and is preserved in a fine grained, buff sandstone, the specimens retaining full convexity. Barrande (1852, pp. 626, 630, 631) comments on the differences between his species. He states that '*T.*' *goldfussi* has an inclined fringe, while that of '*T.*' *ornatus* and '*T.*' *ultimus* is flat; that only in '*T.*' *ornatus* is there a concentric ridge between the two outer rows of the fringe; that '*T.*' *ultimus* has no ornamentation on the glabella or cheek lobes; that the outline of the cephalon of '*T.*' *ornatus* is semi-elliptical, that of '*T.*' *goldfussi* semi-circular; that the cephalon of '*T.*' *goldfussi* is relatively longest; that the lateral margins of the fringe of '*T.*' *ultimus* diverge at 45°, while those of '*T.*' *ornatus* converge backwards. I consider that the fringes all exhibit the same characteristics, and the differences that Barrande points to are accidents of preservation. It may be noted also that in discussing '*T.*' *ultimus* in 1872 (p. 48) Barrande records the finding of young stages, which he says are very like those of '*T.*' *ornatus*.

Following Bancroft (1929, pp. 72-73, etc.) I regard the characters of the fringe as of the greatest taxonomic value in the Trinucleidae. Størmer (1930, p. 14) does not agree with Bancroft and therefore does not accept his genera erected on this basis. Lamont (1935, p. 320) and more recently Stubblefield (1939, pp. 54-57) have accepted many of the genera and species erected by Bancroft in 1929 and 1933. I have placed the species under discussion in the genus *Onnia* Bancroft for the reasons given below (p. 245). This genus is represented by three species in the highest Caradocian of the East Shropshire and Cross Fell areas (in England, Bancroft 1933, Stubblefield 1939, p. 57). Bancroft (1929, p. 76) notes that the *Onnia* group in England represents an entirely new suite of

Cryptolithus (s.l.) with distinctive fringe characters. The Bohemian forms come from Stage D_{d2-5}, which may be in part older than the British rocks containing *Omnia*, so that the genus affords another example of faunal affinity between the Anglo-Welsh Caradocian and the Ordovician of Bohemia (cf. Stubblefield 1939, p. 52-57). Only in the Bohemian area does it occur in association with *Tretaspis* (Barrande 1852, p. 632). Oehlert (1895, pp. 310-311; 326-327) discusses '*Trinucleus*' *goldfussi* and '*T.*' *ornatus*, and their occurrence in the upper part of the Ordovician of Brittany (i.e. the top of the Gres de May and in the schistes ardoisiers superieures). '*T.*' *goldfussi* is also recorded from Bussaco, Portugal (see Stetson, 1927, p. 91).

b) Description of the Holaspid Trilobite.

Cephalon about twice as wide as long, sub-semicircular in outline, sometimes slightly angulated antero-laterally. Glabella clavate, strongly arched, standing high above cheek lobes. Median and anterior parts ornamented by fine reticulation of sub-oval depressions varying in size. One pair of glabellar furrows, represented by small pits just anterior to the occipital furrow. Occipital furrow shallow, with marked lateral pits extending inwards. Occipital ring swinging forward at its lateral extremities, behind which a pair of strong pits situated on the margin of the cephalon. (Plate III, Fig. 6.) Nuchal spine horizontal, thorn-like. Axial furrows distinct, shallow, with "pseudo-antennary" pits. Arcuate encroachment of glabella into fringe.

Cheeks about as wide as long, with rounded postero-lateral margin, evenly inflated, with shallow posterior marginal furrow. Posterior margin upturned and expanded laterally forming a support for the fringe.

Fringe widening laterally, extending backwards beyond the posterior margin, with long genal spines flexed very slightly outwards. Upper lamella showing the following arrangement of concentric rows of pits:—

E₂ depressed, continuous row of small pits, varying between 25 and 33 on each side; E₁ elevated between concentric ridges, of large pits of equal size. From 18 to 23 pits on each side. I₁ less elevated than E₁, of pits of equal size, continuous, and with concentric ridge internally. From 18 to 25 pits on each side. I₂ of small pits, usually continuous, sometimes 3-4 pits anterior to glabella unite with I₁. About 25 pits on each side.

I_3 of small pits, reaching forward as far as the axial furrow, where it comes off I_2 by division of pits in radial sulci; I_4 always present reaching as far forward as the 4th or 6th pit of I_3 from the axial furrow; I_5 sometimes present around the posterolateral margin of the cheek lobe.

The characters of the upper lamella are those of the *Onnia cobboldi*, *O. gracilis*, *O. superbus* group of Shropshire, England (Bancroft, 1929, pp. 76, 93-94, 1933, p. 2), viz.: E_2 of numerous small pits, and the intercalated pits are similar in size to, and in line with, their neighbours. E_1 and I_1 are of large pits and elevated above E_2 and the inner region of the fringe, although I_1 is less elevated than E_1 , in *O. ornatus* (cf. *O. cobboldi*, Bancroft, 1929, p. 92). Except in front of the glabella these rows are separated by strong concentric and weak radial ridges. I_2 , I_3 , I_4 , form an inner depressed region in which the radial ridges are very strong although the concentric lines are still maintained. On the posterior prolongation of the fringe the pits within E_2 lose regular arrangement and form an irregular network.

Lower lamella of fringe having pits corresponding to upper. Girder wide, rather shallow, lamella flexed upwards from girder internally. Marked concentric ridge between E_1 and E_2 , which unites with the girder as the latter turns outwards at the genal angle and is continuous with the sharp, longitudinal flexure on the lower side of the genal spine. Anteriorly I_1 , I_2 , and I_3 in marked radial sulci. Bancroft (1933, p. 2) states that *Onnia* "differs from the other genera of the sub-family in having the external spine-channel continuous with E_2 ." In *Broeggerolithus* (called *Broeggeria* (Bancroft, 1933, p. 2), pre-occupied, referred to *Broeggerolithus* in Lamont, 1935, p. 320, footnote) E_2 usually fails for a few pits at the genal angle and E_1 becomes external e.g. *B. nicholsoni* (Reed 1910, Pl. xvi, Figs. 3 and 8; 1912, Pl. 18, Fig. 6), *B. broeggeri*, *B. soudleyensis*, *B. globiceps*, *B. longiceps* (Bancroft, 1929, pp. 85, 87, 88, 89). In the species of *Onnia* from Shropshire and *O. ornatus* E_2 does not fail at the genal angle, and this difference between the two groups is presumably that referred to by Bancroft.

Thorax of six segments. Axial ring prominent, convex, a little more than one-fourth the width of the thorax, and decreasing in width posteriorly. Articulating half-ring steeply upturned, about half the width of the axial ring. Appendifers distinct, deep. Marked pits in the axial furrows at posterior

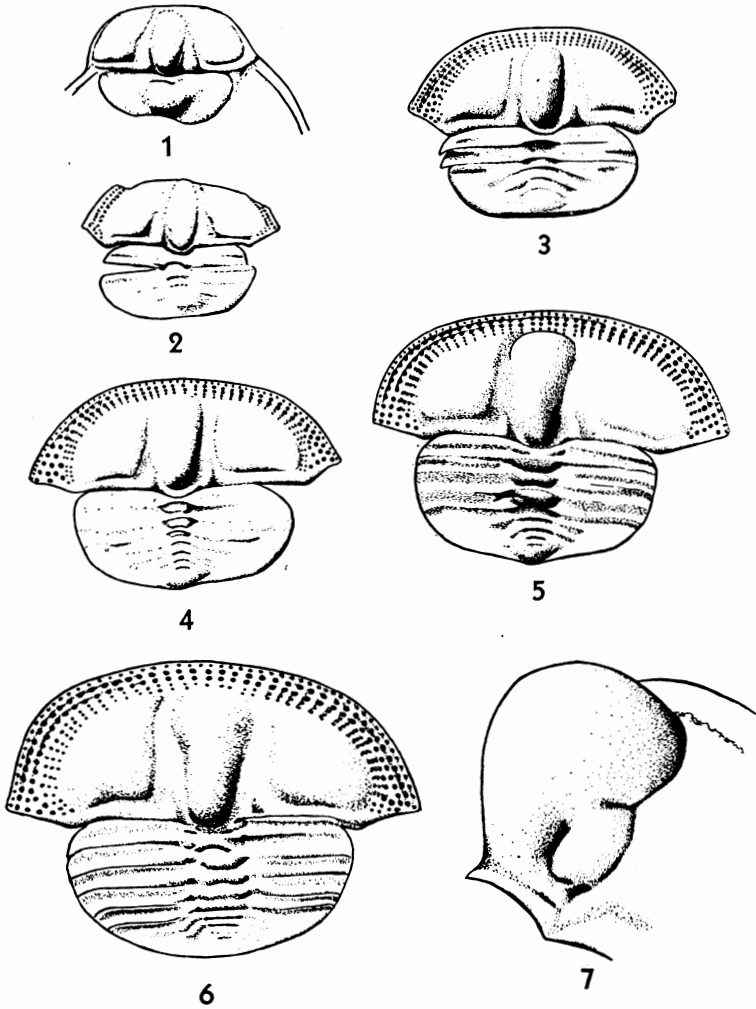


PLATE I.

Onnia and *Trinucleoides*

Figs. 1-6 drawings of Meraspid degrees of *Onnia ornatus* (Sternberg) 1833. Fig. 1, degree 0, from M. C. Z. 2275a (see Pl. II, Fig. 1.), x23. Fig. 2, degree 1, from M. C. Z. 2260a (see Pl. II, Fig. 3.), x11. Fig. 3, degree 2, from M. C. Z. 2277a (see Pl. II, Fig. 5.), x13. Fig. 4, degree 3, from M. C. Z. 2277b (see Pl. II, Fig. 6.), x11. Fig. 5, degree 4, from M. C. Z. 2277c (see Pl. III, Fig. 1.), x11. Fig. 6, degree 5, from M. C. Z. 2277d (see Pl. III, Fig. 3.), x11.

Fig. 7 drawing of glabella of *Trinucleoides reussi* (Barrande) 1856 in postero-lateral view, from M. C. Z. 1969b, x8.

edge of axial ring. Articulating furrow deep. Pleurae flat; pleural furrows narrow at axial furrow, widening rapidly laterally. Pleural extremities blunt.

Pygidium about three times as wide as long, sub-triangular, postero-lateral margin vertical anteriorly, changing to moderately steep posteriorly. Rachis narrow, bounded by shallow axial furrows, narrowing rapidly posteriorly. First two segments well-marked, the first very strong, appendifers distinct, deep; posteriorly segmentation only faintly indicated. Pleurae corresponding to first segment very distinct, to second faint, others scarcely indicated. Postero-lateral margin with terrace lines.

Material—Labelled '*Trinucleus ornatus*':—M. C. Z. 2221, 2240, 2247 from Trubin, Stage D_{a3}; M. C. Z. 2219, 2271, from Czernin, Stage D_{a3}; M. C. Z. 2235, 1777 from Welki Chuckly, Stage D_{a4}; M. C. Z. 1778 from Winice, near Beraun, Stage D_{a4}; M. C. Z. 2218 from Zahorzan, Stage D_{a4}. Labelled '*Trinucleus goldfussi*':—M. C. Z. 2179, 2180, 2197 from Mt. Drabow, Wesela (M. C. Z. 2179 and 2180 labelled by J. Barrande) Stage D_{a2}; M. C. Z. 2194 from near Beraun, Stage D_{a2}; M. C. Z. 2205 from Wesela, Stage D_{a2}; M. C. Z. 1782 from Brdatka, Stage D_{a2}. Labelled '*Trinucleus ultimus*' M. C. Z. 2291 from Leiskow, Stage D_{a5}.

c) Ontogeny of the Species.

Meraspid Period.

Degree 0.

Plate I, Fig. 1, Plate II, Figs. 1-2.

Cephalon transverse, posterior margin arching back behind glabella and laterally curving forward, the genal angles being situated quite far forwards. Glabella narrow, clavate, very strongly arched, standing high above the cheek lobes, descending very steeply posteriorly to the occipital furrow. Axial furrows well-marked; at about one-third the length of the glabella opening into the large triangular fields which flank the posterior portion of the glabella. Laterally these fields are bounded by the alar furrows, which run obliquely from the axial to the posterior marginal furrows. The alae are large, convex, triangular, and are not crossed by the occipital furrow. They are clearly separated from the glabella by the lateral depressions in the occipital furrow, and the shallow furrows which run forward from these depressions to unite with the axial furrows. Occipital furrow distinct, curving backwards and nar-

rowing behind the glabella, and laterally opening into the rather wide, marked depressions.

Cheek lobes quite strongly inflated, postero-lateral margins rounded. Posterior marginal furrows distinct, running directly outwards from the alar furrows and curving forwards postero-laterally. Posterior border wide, evenly convex.

Fringe narrow, flat, no pits discernible on the specimens which can definitely be assigned to degree 0. One specimen (Plate II, Fig. 2) apparently without thoracic segments, has the pygidium displaced sideways and rotated relative to the cephalon, and shows one row of pits on the lateral portion of the fringe, with two extra pits at the genal angle. The dimensions of this individual are intermediate between those given for degree 0 and degree 1 (see table), the width of the cephalon being 1.8 mm., the length .6 mm. Posterior edge of the fringe a convex ridge continuous with the posterior border of the cephalon. Genal angles advanced, with a long, broad, gently curving genal spine.

PLATE II.

Onnia ornatus (Sternberg) 1833.

Figs. 1-7 untouched photographs of Meraspid degrees. Fig. 1, degree 0. M. C. Z. 2275a, x20. Fig. 2, degree 0. M. C. Z. 2275b, x20. Fig. 3, degree 1. M. C. Z. 2260a, x20. Fig. 4, degree 2. M. C. Z. 2274a, x20. Fig. 5, degree 2. M. C. Z. 2277a, x15. Fig. 6, degree 3. M. C. Z. 2277b, x15. Fig. 7, degree 3. M. C. Z. 2274d, x15.

PLATE III.

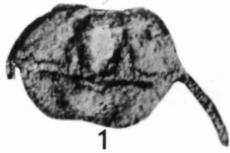
Onnia ornatus (Sternberg) 1833.

Figs. 1-7 untouched photographs of Meraspid degrees and the Holaspid. Fig. 1, degree 4. M. C. Z. 2277c, x10. Fig. 2, degree 4. M. C. Z. 2271a, x10. Fig. 3, degree 5. M. C. Z. 2277d, x10. Fig. 4, the Holaspid. M. C. Z. 2240a, x2. Fig. 5, lower lamella of fringe of Holaspid. M. C. Z. 2221a, x2. Fig. 6, cephalon of Holaspid. M. C. Z. 2218a, x2. Fig. 7, cephalon of Holaspid, in lateral view. Labelled '*Trinucleus goldfussi*.' M. C. Z. 1782a, x2.

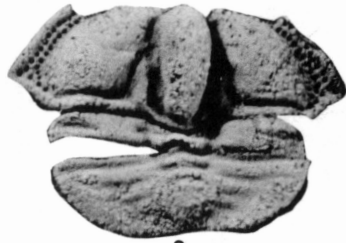
PLATE IV.

Trinucleoides reussi (Barrande) 1856.

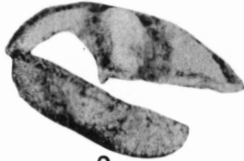
Figs. 1-8 untouched photographs of the Holaspid trilobite. Fig. 1, rubber mould from external cast of portion of cranidium. M. C. Z. 1979b, x5. Fig. 2, rubber mould of part of lower lamella of fringe and part of genal spine. M. C. Z. 1979a (see Fig. 4), x5. Fig. 3, rubber mould from internal cast of portion of cephalon and thorax, showing position of spine on glabella. M. C. Z. 1978a, x5. Fig. 4, internal cast of nearly complete Holaspid. M. C. Z. 1979a, x2. Fig. 5, internal cast of nearly complete Holaspid. M. C. Z. 1974a, x5. Fig. 6, anterior view of external cast of anterior part of fringe, broken longitudinally and showing correspondence of pits on upper and lower lamellae. M. C. Z. 1969a, x5. Fig. 7, rubber mould of ventral surface of hypostome. M. C. Z. 1973a, x5. Fig. 8, ditto. M. C. Z. 1973b, x5.



1



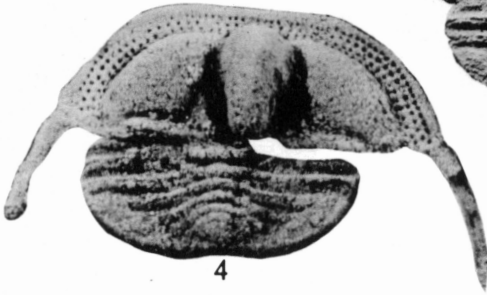
3



2



5



4



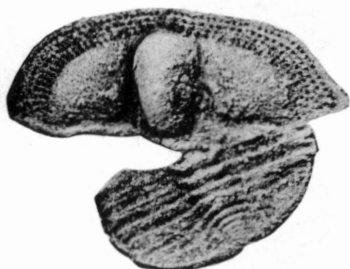
6



7



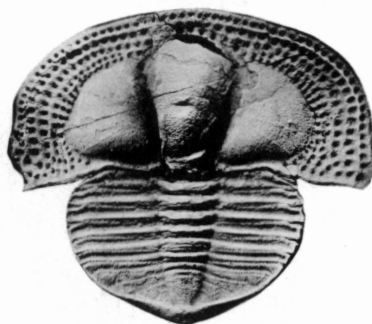
1



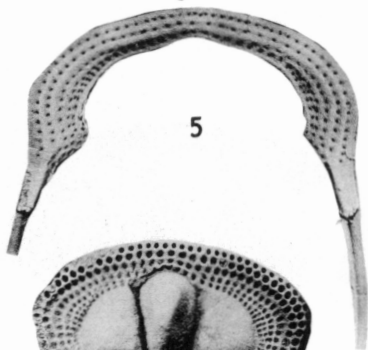
2



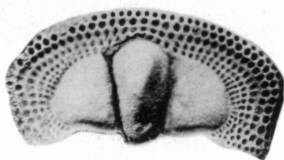
3



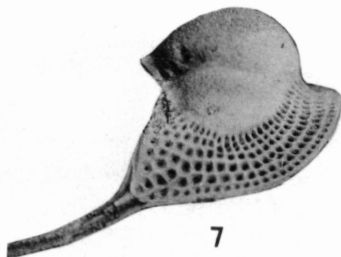
4



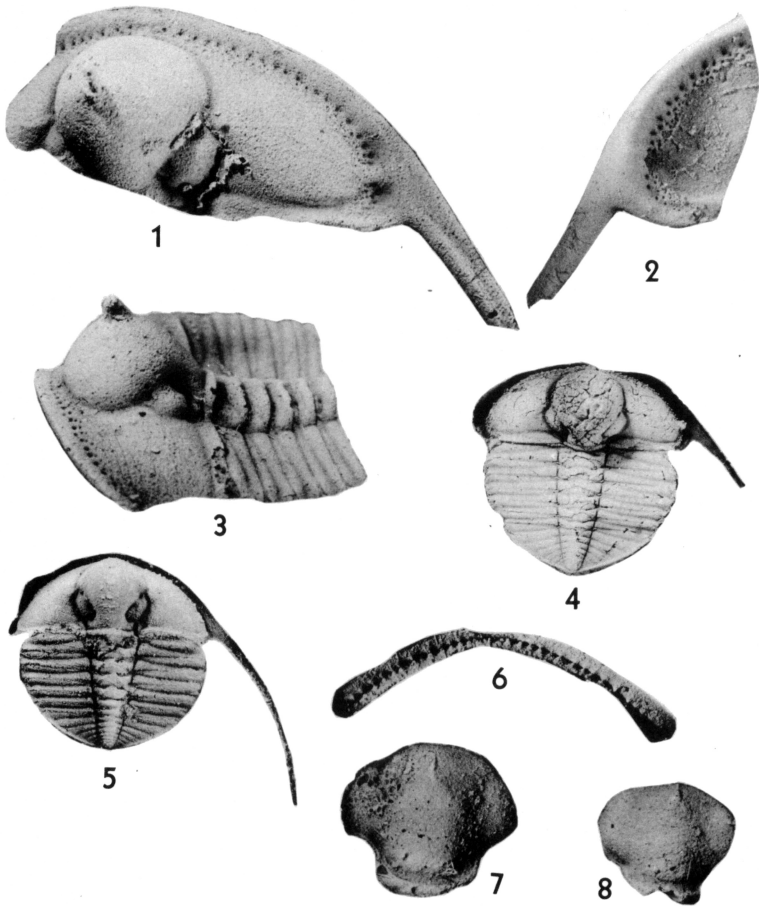
5



6



7



Transitory pygidium transverse, sub-semicircular in outline, anterior margin curving axially to conform with the curve of the occipital ring of the cephalon, rounded antero-lateral margins. Width considerably less than greatest width of cephalon. Lack of definition between axis and pleurae. First axial ring narrow, distinct, laterally and posteriorly to which is a strongly convex area, highest axially, delimited by broad, shallow furrows running from the anterior margin obliquely to meet at the flat axial area of the posterior border. Outside the shallow furrows the postero-lateral areas of the transitory pygidium are very gently convex.

Degree 1.

Plate I, Fig. 2, Plate II, Fig. 3.

Cephalon less transverse, genal angles less far advanced. Glabella very similar, descending less steeply to the occipital furrow. Axial furrows with distinct "pseudo-antennary" pits. Triangular fields lateral to posterior part of the glabella now narrower, exhibiting the same subdivision. The alae distinct, narrower, not crossed by the occipital furrow, separated from the glabella by the lateral depressions in the occipital furrow, and the shallow furrows running anteriorly from these depressions. Occipital furrow distinct, the increased convexity of the occipital ring and furrow reducing the slope of the glabella down to the occipital furrow.

Cheek lobes similar, less well-rounded postero-lateral margins. Posterior marginal furrows and posterior border similar, the less advanced position of the genal angles reducing the postero-lateral curve of the border.

Fringe slightly wider, upper lamella only known. Two complete rows of pits (cf. Raymond, 1917, p. 204, who states that there is only one row), in radial and concentric arrangement. Anteriorly radial arrangement dominates, the radii being flexed somewhat outwards. Laterally concentric arrangement dominant, with concentric ridge between rows. Three or four additional pits at the postero-lateral margins of the cheek lobes. About 23 pits in each row on each side.

Thorax with one segment. Axial ring convex, narrow axially and widening laterally, descending steeply to the articulating furrow. Axial furrows shallow, with shallow articulating-joint pits posteriorly. Pleurae convex, with a short, shallow furrow laterally.

Transitory pygidium sub-semicircular in outline, anterior border straight. Axial region distinct, first three segments visible, the third being ill-defined. Appendifers on second segment. Posteriorly axial region convex, not divided from pleural lobes. First three pleurae visible. Postero-lateral regions of transitory pygidium convex, posterior axial portion flattened.

Degree 2.

Plate I, Fig. 3, Plate II, Figs. 4-5.

Cephalon sub-semicircular in outline, genal angle somewhat in advance of posterior border.

Glabella as in degree 1. Axial furrows a little deeper. Triangular fields lateral to the posterior part of the glabella reduced in width, with the same sub-divisions. Alae narrow, convex, crescentic in outline, not crossed by occipital furrow, separated from glabella as before.

Cheek lobes as in degree 1.

Fringe considerably wider, rather broad margin. Upper lamella taking on the characteristics of adult. Three complete rows of pits, a fourth nearly complete, and laterally a few pits of a fifth row. The outer row of small pits, the next two of fewer, larger pits, the fourth row small pits. Radial arrangement strong anteriorly, concentric arrangement weak, few pits of the fourth row missing in front of the glabella. Radii flexed outwards anteriorly, and occasionally an intercalated pit in front. Laterally concentric arrangement dominates, strong concentric ridges separate the first and second, and second and third rows. Within the third row the arrangement is strongly radial, the pits of the fourth and fifth rows being in radial sulci. First row with 25-27 pits on each side, second, third and fourth with about 24, fifth row extending forward to about the ninth pit of the fourth row from the axial furrow. Lower lamella unknown. Genal spines broad, curved, long, extending backwards beyond the pygidium.

Thorax of two segments. Axial ring very convex, about half the width of the pleurae. Pleurae with pleural furrows deep, extending from axial furrows to border and broadening laterally.

Transitory pygidium with depressed semi-circular outline. Rachis with three distinct segments, not clearly bounded posteriorly, forming part of a broad, very convex area, flanked by a depressed central and gently convex lateral area of the pleural

lobes. This general contour of the dorsal surface of the transitory pygidium, independent of the division of the axial furrows, is very pronounced in degree 0 (see p. 247), and is still very evident in degree 2. Three pleurae, corresponding to the segments on the rachis.

Degree 3.

Plate I, Fig. 4, Plate II, Figs. 6-7.

Cephalon semi-circular in outline, genal angles in advance of posterior border. Cheek lobes reticulated (Plate II, Fig. 7).

Glabella clavate, now proportionately wider in front. Axial furrows deeper, with "pseudo-antennary" pits; the alae now very much reduced in length, the depression separating them from the glabella much shallower, broad alar furrows in line with the axial furrows.

Fringe slightly wider. Upper lamella with similar features to that of degree 2, but the fourth row, I_2 , is now well developed, separated from I_1 in the lateral region by a concentric ridge. I_3 of small pits, reaching forward to the axial furrow, and laterally in strong radial arrangement with I_2 . I_4 present in two specimens as very small pits, reaching forward to the ninth pit of I_3 from the axial furrow. E_1 having a tendency to be elevated laterally. Lower lamella not known.

Thorax of three segments, very similar to the adult form, appendifers and articulating-joint pits distinct.

Transitory pygidium with rachis more clearly defined, but still forming, with the axial areas of the pleurae, a sub-triangular convex area. Three, sometimes four, axial segments, with corresponding pleurae, visible.

Degree 4.

Plate I, Fig. 5, Plate III, Figs. 1-2.

Cephalon having very much the form of the adult. Axial furrows widen posteriorly into short alar furrows, the alae being still further reduced, not crossed by the occipital furrow, and separated from the glabella by the deep lateral depressions in the occipital furrow, which connect with the axial furrows. Reticulated ornament on the glabella and cheek lobes.

Fringe with upper lamella showing rows E_1 , E_2 , I_1 — I_4 in arrangement and number corresponding with the adult, although E_1 and I_1 are not so elevated. I_5 cannot be distinguished, but there are some additional pits at the postero-

lateral margins of the cheek lobes. Lower lamella with weak girder situated as in the adult, and concentric ridge between E_2 and E_1 . Genal spines broad, long, reaching back beyond the pygidium. No genal prolongation of the fringe.

Thorax of four segments.

Transitory pygidium sub-triangular in outline, margin steep laterally, less steep posteriorly. Rachis distinctly outlined having four segments anteriorly, posterior part faintly segmented. Four pleurae visible, pleural lobes bordered by narrow, elevated ridge.

Degree 5.

Plate I, Fig. 6, Plate III, Fig. 3.

Cephalon exhibiting most of the adult characters. The alae are present, much as in degree 4, not crossed by the occipital furrow. Cheek lobes with reticulate ornament.

Fringe shows few pits of I_5 postero-laterally. No genal prolongation.

Thorax of five segments. Appendifers deep, distinct. Each segment shows deep pits at the posterior ends of the axial furrows—the pits associated with the articulating joint.

Transitory pygidium very much as degree 4, with four distinct axial and pleural segments.

Material—All labelled '*Trinucleus ornatus*': Degree 0—M. C. Z. 2275 from Czernin, Stage D_{a3} ; Degree 1—M. C. Z. 2260 from Czernin and Trubska, Stage D_{a3} ; Degree 2—M. C. Z. 2274 from Czernin, Stage D_{a3} ; Degree 3—M. C. Z. 2268 from Toczniak, Stage D_{a3} ; Degree 4—M. C. Z. 2271 from Czernin, Stage D_{a3} ; Degree 5—M. C. Z. 2266 from Toczniak, Stage D. Degrees 2-5—M. C. Z. 2277 from Trubin, Stage D_{a5} , labelled by Barrande.

Discussion.

The material of *Onnia ornatus* described above offers no information on the development of the dorsal shield of the trilobite during the Protaspid Period, but through the Mera-spid and Holaspid Periods it increases in length by some 28 times, and the width of the cephalon, which in degree 0 is rather less than twice the length of the trilobite, becomes in the Holaspid only slightly greater than the length. This change is accompanied by progressive growth of the cephalon and the formation of new post-cephalic segments, which latter

show an increase of greater relative length than breadth (cf. Stubblefield, 1926, p. 362). When the full number, six, of segments is acquired, *O. ornatus* is certainly less than one-third, and probably about one-sixth, of the length to which it will attain.

a) Growth of the Cephalon.

Throughout the Meraspid and Holaspid Periods the cephalon continues to form something like 55 per cent of the length of the trilobite (see Table I). The dimensions also show that the cephalon has a tendency to become progressively somewhat less transverse, which feature is common to the known ontogenies of the trinucleids.

The alae of *Onnia ornatus* were noted by Barrande (1852, pp. 265-266) as elongate prominences on each side of the base of the glabella which persisted through each degree of development, but disappeared in the adult. His illustrations (1852, Pl. 30, Figs. 41-50) show this, the alae at degree 5 being very much reduced. The largest individuals of the Holapsid Period show no distinct alae, and they are absorbed into the glabella during this period. Through the successive degrees in size the occipital ring becomes progressively more inflated, and also swings forward at its lateral extremities with the development of a pair of deep pits on the cephalic margin. These pits, noted by Reed (1914, p. 353, in discussing a tretaspid referred to by him as '*Trinucleus seticornis*'), are probably associated with the articulating joint between the cephalon and the first segment of the thorax. With the increasing convexity and swinging forward of the lateral extremities of the occipital ring, the small alae lose their convexity and become indistinguishable from the posterior part of the glabella. The occipital furrow becomes stronger, the lateral depressions more pronounced, and the glabellar furrows appear first as shallow circular pits, and gradually become more distinct.

The changes in the alae in the ontogenies of *Reedolithus carinatus* (Angelin) and *Tretaspis seticornis* (Hisinger) have been discussed by Størmer (1930, pp. 34-39, 61-67). In neither of these genera are the alae so distinctly separated from the glabella during development as in *Onnia ornatus*. The alae of *O. ornatus* seem to be much more closely comparable to those of *Cryptolithus* (s.s.) (Beecher, 1895, p. 309, Pl. III, Figs. 1-2) and to *Reuscholithus* (Banerft, 1929, p. 84, Fig. 4)—if we

interpret Bancroft's figures as showing alae. The alae in *T. seticornis* are absorbed into the glabella at a much earlier stage than in *O. ornatus*. Størmer (1930, p. 37) in discussing *R. carinatus* notes that the alae are not crossed by the occipital furrow, and seem to be connected with the occipital ring. This seems to be true also of *O. ornatus*.

Lateral eye tubercles are not known among the adult of *Cryptolithus* (s.l.). They are, however, present in the young stages of *Cryptolithus* (s.s.) (Beecher, 1895, p. 308, Pl. III, Figs. 1-2) and *Reuscholithus* (Bancroft, 1929, p. 84, Fig. 4). In *O. ornatus* they may be present in degrees 0 and 1, but the preservation of my material is such that I can make no decision on this point.

The fringe undergoes a progressive modification. At degree 0 it is probably without pits (cf. Barrande, 1852, p. 265), although one specimen (see p. 247) suggests that large individuals of degree 0 may have one row. Pits were not recognized in the earliest degrees of *Reedolithus carinatus* (Størmer, 1930, p. 34) or *Tretaspis seticornis* (op. cit., p. 61). Addition of rows, from the interior edge, is rapid, and by degree 4 the fringe is very similar to the adult form. The genal angles are situated rather far forward in degree 0, though not as far as in *Reuscholithus* (Bancroft, 1929, p. 84, Fig. 4). By degree 4 they are approximately in line with the posterior border, but the genal prolongation of the fringe seen in the larger adults takes place during the Holoaspid Period.

b) Growth of the Thorax and the Pygidium.

The table of dimensions shows that the thorax occupies an increasing proportion of the length of the trilobite, from zero to more or less than one-quarter in the largest whole shields. The transitory pygidium, which in degree 0 has a length approaching that of one-half of the whole trilobite, shows a steadily decreasing proportion down to the smallest Holoaspid, where it is less than one-sixth of the total. In the largest Holoaspids it is more nearly one-fifth. Thus the thorax grows at the expense of the pygidium (cf. Raymond, 1920, pp. 134-137, Stubblefield, 1926, p. 368).

Stubblefield (1936, p. 367) in discussing *Shumardia pusilla*, states that "The formative zone [i.e. the zone from which segments originate], which apparently produced the thoracic segments, also produced the pygidial segments, and is still active when the true pygidium exists as such, for a new segment is

added in the moult between degree 6 and the Holaspid Period by the fission of the pre-existing terminal segment of the shield." In *Onnia ornatus* the smallest individuals that I have of degree 6, over 7 mm. in length, have the first segment of the pygidium indicated by the pleural furrows only, behind which the pleural lobes are smooth. In the larger individuals (see Pl. III, Fig. 4) the first segment is defined by the rib furrows, which are especially clear laterally, disappearing near the rachis, and two further segments are defined by the rib furrows. This evidence suggests the continued activity of the formative zone in *O. ornatus* during the early part of degree 6. The rachis, however, in the smaller individuals of degree 6 shows some 9 segments, while in the largest specimens only three segments can be seen. This may be a later degenerative development, such as that suggested by Raw (1925, p. 247), in considering *Leptoplastus salteri*.

The transitory pygidium of degree 0 has a median strongly convex area, separated from the lateral gently convex areas by oblique shallow furrows (see p. 247). This general form persists, with diminishing relief, until degree 4. The rachis develops within the central convex area, and the lateral boundaries of the convex region have no relation to the axial furrows. This relief is most marked in the posterior half of the transitory pygidium, and disappears gradually anteriorly, so that the first segment assumes the form of the last thoracic segment before it is released to become a freely articulating segment.

IV. ON *Trinucleoides reussi* (BARRANDE) 1856.

Plate I, Fig. 7, and Plate IV.

a) Discussion.

The genus *Trinucleoides* was proposed in 1917 by Raymond (p. 204) for '*Trinucleus*' *reussi* Barrande, and has since been discussed by Raymond (1925, p. 19), Stetson (1927, p. 98) and Størmer (1930, p. 13). No other species of the genus is known. Raymond (1925, p. 19) stated that *Trinucleoides* has "only one row of large pits"; Stetson (1927, p. 98) regarded it as having "two concentric rows of very small pits"; and Størmer (1930, p. 15) described it as having "2-3 rows of concentrically arranged small pits." The arrangement of the pits in the material available to me (see p. 258) is somewhat different from the statements quoted. Consequently I do not think that the comparison of the arrangement of the pits in the fringe of Meraspid degree 1 of *Tretaspis seticornis* with

that of *Trinucleoides reussi*, made by Størmer (1930, p. 13), can be upheld. Raymond (1917, p. 204) compares the lateral lobes of the glabella of *T. reussi* with the alae of *Onnia ornatus*. However, the lateral lobes of the former are anterior to the occipital furrow, while the alae of *O. ornatus* seem to be connected with the occipital ring and are never crossed by the occipital furrow (see p. 254, and Pl. I, Fig. 7).

Størmer remarks that "It is difficult to decide if the form [*Trinucleoides reussi*] has to be placed among the Trinucleidae or the Dionididae." (1930, p. 13.) The cephalon resembles *Dionide* in the lateral lobes and the spine of the glabella, the lines on the cheek lobes, the form of, and the position of the marginal suture on, the fringe, and the hypostome. The thorax and pygidium recall the Trinucleidae but are not distinctive.

Trinucleoides reussi comes from the lowest part of stage D, and is the earliest trinucleid known from these rocks. Raymond (1917, p. 204) has described it as "the oldest of the Trinucleids," but the unusual form *Trinucleus nordenskiöldi* Bulman (1931, pp. 85-87, Plate XI, Figs. 2-3) from the Upper Llanvirnian of Peru is probably as old, or older.

b) Description of the Species.

Cephalon sub-semicircular in outline, genal angles slightly in advance of the posterior margin. Glabella sub-conical, slightly longer than wide, very strongly convex. Without median tubercule, but with stout spine arising from highest point, directed vertically in the axial plane, and somewhat anteriorly in lateral view. Størmer (1930, p. 85) has suggested that this spine was used for balance while swimming. Sub-oval, gently convex lateral lobes, steeply tilted, flanking the median part of the glabella posteriorly. First pair of glabellar furrows elongated pits directed postero-medially and defining the antero-lateral edge of the lateral lobes. Second pair of glabellar furrows deep, arising on the glabella just within the axial furrows, curving in a crescentic arc to bound the lateral lobes postero-laterally; connected at the inner ends by shallow furrows with the first glabellar furrows, which thus delimit the lateral lobes (see Pl. I, Fig. 7).

Occipital furrow distinct, shallow, with shallow lateral depressions, which depressions are connected by a very shallow furrow with the outer ends of the second glabellar furrows.

Occipital ring straight, immediately behind the lateral extremities a pair of pits may be distinguished.

Axial furrows distinct, shallow; "pseudo-antennary" pits not observed; swinging out around the lateral lobes of the glabella, and at the posterior edge of these lobes a deep, elongate depression is developed in the axial furrows. Pre-glabellar furrow narrow, distinct, forming a regular curve with the axial furrows.

TABLE II.
Dimensions in millimetres of Holarpid Individuals of
Trinucleoides reussi.

Length of trilobite	9.7	12.6	14.5	
Length of cephalon	4.2	5.3	6.0	6.9
Width of cephalon	c10.2	15.2	16.2	16.5
Length of glabella	3.5	3.9	4.9	4.5
Width of glabella	3.8	4.9	5.5	5.9
Length of thorax	3.9	c5.0	5.7	
Width of thorax	9.5	11.7	13.6	
Length of pygidium	2.0	2.4	3.3	
Width of pygidium	6.5	9.4	10.4	
Specimen number	M.C.Z.	M.C.Z.	M.C.Z.	M.C.Z.
	1975a	1975b	1979a	1970a
Figure number			Pl. IV,	
			Fig. 4	

Cheek lobes sub-triangular in outline. Postero-laterally to the lateral lobes of the glabella flat, then curving steeply down to the margins. Several specimens show a faint ridge on the cheek lobe, which takes a curving course from a point opposite the anterior edge of the lateral lobe of the glabella to the anterior edge of the radial ridge which crosses the fringe. A second sub-parallel ridge seems to branch off and run to the posterior edge of this radial ridge. (Pl. IV, Fig. 1.) The lines on the cheek lobe of *Dionide formosa* (Barrande, 1852, Pl. 42, Fig. 24) are perhaps comparable.

Posterior marginal furrow shallow, swinging sharply forward for a short distance from the axial furrows, then curving gently back behind the flat areas of the cheek lobes, and running directly outwards. Posterior border thus rather wide and flat axially, somewhat narrower, flexed upwards laterally.

An unusual feature of the specimens preserved as internal moulds is that the conical glabella is frequently fractured at the position of the hypostome, which is thus preserved as an

external cast (Pl. IV, Figs. 7-8). This hypostome is described and figured by Barrande, and has been compared by Størmer (1930, p. 13) with that of *Dionide*.

Fringe unique in form for the family, consisting of a narrow, almost flat upper lamella, the lower lamella being a distorted 'U' in cross-section, directed downward and backward from the margin of the cephalon, then turning steeply upwards and outwards, and bent back flat anteriorly to unite with the upper lamella in a marginal suture, which is thus on the upper surface of the fringe close to the anterior edge (Pl. IV, Fig. 1). Postero-laterally the marginal suture swings inward diagonally across the fringe, and curves on to the posterior border of the cephalon, which it cuts (Pl. IV, Fig. 1). The lower lamella and the long, broad genal spines thus become a continuous structure. The fringe is pitted on the inner edges. There is a sharp change of slope between that of the cheek lobes and the flat upper lamella of the fringe, and at this change of slope there is one row of large pits, irregularly spaced in concentric arrangement. In between and just within this row are a number of small pits in quite irregular arrangement, most numerous laterally, rare or absent anteriorly. Correspondingly arranged pits on the lower lamella (Pl. IV, Fig. 6). Laterally, a short distance ahead of the genal angle, and within the marginal suture, the pitted portion of the fringe is crossed by a rather wide, raised radial ridge, which interrupts the pitting (Pl. IV, Fig. 1). One specimen shows the structure of the lower lamella in this region (Pl. IV, Fig. 2). Lower lamella showing terrace lines.

Thorax with six segments which decrease in length and width posteriorly. Axial ring convex, about one-fourth the width of the thorax; articulating furrows distinct, shallow; appendifers deep, small. Articulating half-ring elevated, almost as wide as axial ring. Axial furrows distinct, pits associated with articulating joints not prominent. Pleurae flat, bent down at extremities, pleural furrows distinct, shallow.

Pygidium sub-triangular in outline, about three times as wide as long. Rachis bounded by distinct shallow axial furrows, decreasing in breadth posteriorly; first three segments distinctly developed, appendifers shallow, posteriorly faintly segmented or smooth. First pleurae with pleural furrows, the next three or four being seen, but without furrows. Narrow elevated border and steep margin to pygidium posteriorly and laterally.

Material—M. C. Z., 1973, 1974, 1975, 1979 from Wosek, Stage D₀₁; M. C. Z. 1979, labelled by Barrande; M. C. Z. 1969, 1970, 1972, 1978.

V. LITERATURE.

- Bancroft, B. B.: 'Some New Species of *Cryptolithus*, (s. l.), from the Upper Ordovician.' Mem. Proc. Manchester Lit. Phil. Soc., Vol. 73, pp. 67-98, 1929.
- : 'Correlation Tables of the Stages Costonian-Onnian in England and Wales.' Privately published, 1933.
- Barrande, J.: 'Système Silurien de la Bohême.' Prague and Paris. Vol. I, 1852.
- : Ibid. Vol. I, Supplement, 1872.
- Beecher, C. E.: 'Structure and Appendages of *Trinucleus*.' This Journal, Vol. 49, pp. 307-311, 1895.
- Bulman, O. M. B.: 'South American Graptolites, with special reference to the Nordenskiöld Collection.' Ark. f. Zool. K. Svenska Vetensk.-Akad., Stockholm, Band 22A, No. 3, pp. 1-111, 1931.
- Lamont, A.: 'The Drummuck Group, Girvan; a Stratigraphical Revision, with Descriptions of New Fossils from the Lower Part of the Group.' Trans. Geol. Soc. Glasgow, Vol. xix, pp. 288-334, 1935.
- Oehlert, D.-P.: 'Sur les *Trinucleus* de l'Ouest de la France.' Bull. Soc. Geol. France, series 3, Vol. xxiii, pp. 299-336, 1895.
- Raw, F.: 'The Development of *Leptoplastus salteri* and other Trilobites.' Quart. Jour. Geol. Soc. London, Vol. lxxxi, pp. 223-324, 1925.
- Raymond, P. E.: 'Beecher's Classification of Trilobites, after Twenty Years.' This Journal, Vol. 43, pp. 196-210, 1917.
- : 'The Appendages, Anatomy, and Relationships of Trilobites.' Conn. Acad. Arts and Sciences, Vol. vii, 1920.
- : 'Some Trilobites of the Lower Middle Ordovician of Eastern North America.' Bull. Mus. Comp. Zool. Harvard, Vol. lxxvii, No. 1, pp. 1-180, 1925.
- Reed, F. R. C.: 'New Fossils from the Dufton Shales.' Geol. Mag., Dec. V, Vol. vii, 1910.
- : 'Notes on the genus *Trinucleus*.' Part I. Geol. Mag., Dec. V, Vol. ix, pp. 346-353 and 385-394, 1912.
- : 'Ditto, part III. Geol. Mag., Dec. VI., Vol. i, pp. 349-359, 1914.
- Stetson, H. C.: 'The Distribution and Relationships of the Trinucleidae.' Bull. Mus. Comp. Zool. Harvard, Vol. lxxviii, No. 2, pp. 87-104, 1927.
- Størmer, L.: 'Scandinavian Trinucleidae, with special reference to Norwegian Species and Varieties.' Skrift. Norske Vidensk. Akad. Oslo. I Math. Nat. Kl. No. 4, 1930.
- Stubblefield, C. J.: 'Notes on the Development of a Trilobite, *Shumardia pusilla* (Sars.)' Jour. Linn. Soc. London—Zool., Vol. 36, pp. 345-372, 1926.
- : 'Some Aspects of the Distribution and Migration of Trilobites in the British Lower Palaeozoic Faunas.' Geol. Mag., Vol. lxxvi, pp. 49-72, 1939.
- Warburg, Elsa: 'The Trilobites of the *Leptaena* Limestone in Dalarne.' Bull. Geol. Inst. Univ. Upsala, Vol. xvii, 1925.