

COMMONWEALTH OF AUSTRALIA.
DEPARTMENT OF NATIONAL DEVELOPMENT.
BUREAU OF MINERAL RESOURCES, GEOLOGY AND GEOPHYSICS.

BULLETIN No. 42.

THE CAMBRIAN TRILOBITE REDLICHIA: ORGANIZATION AND GENERIC CONCEPT

BY

A. A. ÖPIK.

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Minister : SENATOR THE HON. W. H. SPOONER, M.M.

Secretary : H. G. RAGGATT, C.B.E.

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SUMMARY

The trilobite *Redlichia forresti* (Etheridge), from the lowermost Middle Cambrian Negri Group of Western Australia and the western part of the Northern Territory, occurs in two forms, here interpreted as sexual dimorphism. Males are rare and small; they have strong dorsal and pleural spines and a pygidium comparable with the conventional trilobite pygidium in having a distinctly annulated axis, a continuous elevated border, and a doublure continuous around the ventral margin. Female forms are common and large (100 mm. or longer). Their spines are short and slender, and the pygidium has an unusual structure not previously observed in trilobites: the division into axis and pleurae is indistinct, no border is present, and the doublure is developed only on the flanks, being interrupted in the middle of the posterior end. The absence of a doublure at the posterior end indicates that this part of the body was unprotected by the test and suggests the possibility of a testless "telson" protruding from the rear of the pygidium; the posterior margin of the pygidium is arched. The same pygidial organization is seen in two undescribed Australian species of *Redlichia*. The structure most similar to the "female" pygidium of *Redlichia* seems to be the caudal shield of the Lower Cambrian trilobite *Holmia kjerulfi*.

Short intergenal spines, homologous with the pleural spines, are observed in both sexes of *Redlichia*.

Redlichia has a "normal" short (that is, narrow) rostral shield, not reaching the posterolateral corners of the cephalon. Moults are observed in which the rostral shield and the hypostoma remain fused as a unit. An interlocking system of spines along the frontal marginal furrow of the cranidium and the posterior border of the rostral shield entrapped the soft part of the border, which could be liberated at times of moulting only by the opening of the rostral suture.

Some aspects of the morphogenesis of trilobites are discussed in describing the various parts of the test of *Redlichia*. The similarity of the occipital segment to segments of the thorax ("occipital similarity") and the glabellar lobes and furrows is regarded as an indication that the posterior four segments of the cranidium may have been added to it gradually. The rostral shield is regarded as part of the cephalic doublure, and is, together with the brim and border, not a segment, but a pleural element. The hypostoma is an axial structure of the sternum, not connected with the front of the glabella. The possibility that the hypostoma was formed by the fusion of a pair of appendages, or parts of a pair, is discussed. It is suggested that after the subretroversion of the "prostomium complex and the peristome" that were

without pleurae, the pleurae of the next segments expanded and became fused in front of the glabella, as a brim with a doublure containing the sporadic rostral shield. A similar process of fusion of the last pair of pleurae subsequently created the conventional pygidium. The trilobites are referred to as a class; no current theory has yet completely explained the position of trilobites within the arthropods. The taxonomic position of *Redlichia* and criteria for a taxonomy on the specific level are reviewed.

INTRODUCTION

The main purpose of this paper is to describe the morphology of a single genus of trilobite (*Redlichia*) and to discuss, and settle, the uncertainties of its stratigraphical and geographical distribution. *Redlichia* is the nominate genus of a family and a superfamily ("suborder") and is consequently of paramount taxonomic significance. It is in its general organization related to the olenellids, but differs from them, as do the majority of trilobites, in having well-developed cephalic sutures.

The organization of its pygidium, however, is unique. The genus therefore invites a discussion of various theories concerning the classification, origin, and even progeny of trilobites, and other arthropods as well. The theories are not discussed fully, however, especially those that examine the derivation of ancestors. The only exception is the problem of *Olenellus* as the ancestor of *Limulus*. The main intention here is to view *Olenellus* on its own merits, without attributing to it characters that support the various theories, or interpreting the observed characters as supporting the theories. The structure of rostral shield, hypostoma, and cranidium of *Redlichia* is described and discussed on the basis of the actually preserved material, ignoring discrepancies that may arise when searching for homologies among later arthropods.

Trilobites are, perhaps, the best-known class of Palaeozoic arthropods, but, evidently, no current theory has explained them as yet unambiguously. A synthesis of the theories can be visualized; but still more observations are needed, especially on Cambrian trilobites, to produce it.

This paper was originally prepared in 1950-52; subsequently additions have been made in an attempt to exploit the wealth of new information published on trilobites between 1953 and 1957.

SOURCE OF MATERIAL: AGE AND IDENTIFICATION OF THE SPECIES *REDLICHIA FORRESTI* (Etheridge Jr.).

The specimens of *Redlichia* here described have been selected from the collections of the Bureau of Mineral Resources, Geology and Geophysics, Canberra. The best-preserved material is represented by *Redlichia forresti* (Etheridge Jr.), collected on several occasions by D. M. Traves and myself in northern Australia. The present paper is essentially based on that species.

It now seems that altogether about ten species of *Redlichia* occur in northern Australia. *R. forresti* (Etheridge Jr.), *R. idonea* Whitehouse, and *R. venulosa* (Whitehouse) are already described; the others are now being studied. The occurrence of *R. chinensis* Walcott is recorded by Öpik (1956a, p. 17).

The specimens illustrated by figures 1, 2, and 3, of Plate 1, and all the figures of Plate 2, are conspecific, and are here regarded as *Redlichia forresti* (Etheridge Jr., 1890), for the following reasons:

First, they have all been collected from one and the same formation, at the junction of Brook Creek and Linnekar Creek, a right-hand tributary of the Ord River, East Kimberley Division, Western Australia. Secondly, from the same area and rocks only one species has been found, and from here *R. forresti* was originally described. Thirdly, the available collections from that area in the Bureau of Mineral Resources also contain only one species of *Redlichia*, the cranidia of which correspond to the type specimen of *R. forresti* illustrated by Etheridge. The type itself is not in Australia and could not be examined.¹

Etheridge's type specimen is a cranidium, similar to the specimen figured here on Plate 3, figures 1-4. As the identification of the two published Australian species of *Redlichia* on cranidial characters alone is somewhat inconclusive without a comparison of the types, the above indirect identification of *R. forresti* (only one species in the particular bed of the particular area) is of significance.

The geology of the Ord River area and its *Redlichia*-bearing sequence is described by Matheson & Teehert (1948) and Traves (1955, 1956). *Redlichia forresti* occurs here in the Negri Group, which consists of eight limestone and shale formations that are preserved in several basins. The total thickness is 2,000 feet. The specimens of *Redlichia forresti* here described were collected in the Linnekar Limestone (Traves, 1955), at its type locality and about 750 feet above the base of the group. The Linnekar Limestone is a marine formation between the two gypsum-bearing shale formations that are unfossiliferous. Associated fossils are: a crustacean (*Aluta?*), *Acrotreta*, *Lingulella*, *Biconulites hardmani* (Etheridge), and *Girvanella*.

According to Öpik (1956b, p. 48; 1956c, p. 250), the age of the *Redlichia*-bearing faunas in northern Australia is Middle Cambrian. Elsewhere, in China and Korea, for example, *Redlichia* may also occur in the uppermost Lower Cambrian. In South Australia (Daily, 1956) *Redlichia* occurs in Lower Cambrian and in lower Middle Cambrian. The evidence for a Middle Cambrian age of *Redlichia* in northern Australia is discussed in detail in the next section (p. 10-11).

Two undescribed species (*a* and *b*) of *Redlichia*—both from Gum Ridge, 22 miles east of Tennant Creek, Northern Territory—are illustrated here by their pygidia. The specimens figured on Plate 1, figures 4 and 5, and Text-figure 9, represent one species (*a*); they occur high in the sequence and are younger than *R. forresti*. The other species (*b*) (Plate 1, figure 6) occurs in the basal beds of Gum Ridge. On Plate 3, figures 3-7, a cranidium is illustrated as sp. *c*.

(¹) I saw the type in the British Museum (Natural History) in June, 1957, and am satisfied that the specific identification is correct.

One more species (*d*), illustrated on Plate 6, figures 7 and 8, is found in Queensland in association with *R. idonea*, *R. chinensis*, and *R. venulosa*.

The taxonomic characters of these undescribed species are not discussed here, but as R. & E. Richter (1941b) have suggested that *R. forresti* and *R. idonea* are identical, it is important to maintain that they are distinct species. *R. idonea* has fifteen segments in the thorax, a dorsal spine on the eleventh segment, and, in some specimens, a spine on the fourth segment as well. *R. forresti* has seventeen segments with spines on the twelfth and fourth.

PRESENT STATUS AND AGE OF THE GENUS *REDLICHIA*.

Redlich (1899) established the genus from the Cambrian of the Salt Range of India (now Pakistan), and named it *Hoeferia*, with *H. noettingi* as type. The name *Hoeferia* was preoccupied, and the new name *Redlichia* was proposed by Cossman (1902). King (1941) re-described Redlich's original material, including the types.

The first described species, attributed later to the genus, was *Olenellus? forresti* R. Etheridge Jr. (in Foord, 1890) from Western Australia. Additional species have been described, and more information on the genus has been published, by Mansuy (1912), Walcott (1913), Saito (1934), King (1937, 1941), Endo & Resser (1937), Whitehouse (1939), Lu Yen-Hao (1940; not accessible to me), and Kobayashi (1944). The paper by Kobayashi & Kato (1951), received after the completion of the present one, has not been exploited exhaustively here. A critical review of known species has been made by R. & E. Richter (1941b), who have also described the subgenus *Redlichops* from the Dead Sea area. *Neoredlichia* Saito 1936 may also be a subgenus (see p. 35).

Probably the best known species is *R. idonea* Whitehouse from north-western Queensland. Most of the extra-Australian species have been described from specimens preserved in shale; they are distorted and unsuitable for exact study.

Recent authors mostly regard the family Redlichiidae as a member of the trilobite superfamily Olenellidea Swinnerton (R. & E. Richter, 1941a, p. 33). Richter regarded his superfamily Redlichiidea as a junior synonym of Swinnerton's Olenellidea. *Olenellus* and related genera have no facial sutures, or no anterior branches of the sutures, but have a subcephalic rostral suture extending to the genal angles and cutting off a large rostral shield from the cephalic doublure. *Redlichia* differs from them in having normal facial sutures and a normal rostral shield slightly shorter (or narrower) than the frontal margin of the cranium. Whether the Olenellidae have a sexual dimorphism, as is described here for *Redlichia*, or not, is not yet known, but they warrant some revision. With its externally developed dimorphism *Redlichia* stands at the moment alone amongst trilobites.

Hupé (1952, 1953) revived the superfamily Redlichiidea Richter, as distinct from the Olenellidea. It appears, however, that *Redlichia* and the olenellid *Holmia* should be placed in the same superfamily, as is evident from the similarity of the two genera (see p. 33). However, it may be necessary to remove *Holmia* from the family Olenellidae altogether. Hupé has already established a subfamily Holmiinae. A number of trilobite genera described from Spain and Morocco have been placed in the family Redlichiidae in recent years.

Wilson (1948) has suggested that the Andalusian *Saukianda*-fauna, described by R. & E. Richter (1940) as possibly Upper Cambrian, contains a majority of *Redlichia*-like forms, and that the genus *Perrector* may be a synonym of *Redlichia* itself. They all, however, have large pygidia, which set them apart from the Redlichiidae.

The paramount Andalusian genus *Saukianda* resembles a dikelocephalid, according to Richter. It has a large pygidium, and its only similarity to *Redlichia* is the advanced genal spine. But this is of no significance at all, because such a structure also exists in the Upper Cambrian dikelocephalid genus *Saukiella* Ulrich & Resser 1933, and occasionally in genera of various other families of trilobites, for example Cheiruridae and Lichidae.

No *Redlichia* or Redlichiidae are as yet known from the *Saukianda*-stage of Andalusia. *Saukianda* itself has been placed by Hupé (1952) in a new family, Saukiandidae. The family Redlichiidae, however, may be represented in the Cambrian of the Anti-Atlas by *Neoredlichia* Saito and *Pararedlichia* Hupé. These genera are known only from cranidia, and it is possible that the Korean *Neoredlichia* and the Moroccan species assigned to it are not congeneric. *Neoredlichia* Saito can be regarded as a genus related to *Redlichia*, or even a subgenus of it.

The stratigraphical range of the genus *Redlichia* and its palaeogeographical confinement to southern and south-eastern Asia and Australia are conveniently discussed together.

Resser, in Endo & Resser (1937, p. 278), writes "It appears that *Redlichia* represents the Olenellidae in the Orient", and gives its age as Lower Cambrian. Howell (1947) regards the Asian *Redlichia* as "a rather late Early Cambrian genus", and the corresponding formations are placed by him also in the Lower Cambrian. The Richters (1941a) suggest for the "*Redlichia*-stage" a position on the Lower Cambrian/Middle Cambrian boundary. They consider that in Korea *Redlichia* occurs above the late Lower Cambrian *Protolenus* (*Lusatiops*) fauna. The "primitiveness" of *Redlichia* is generally interpreted as favouring the Lower Cambrian, with few exceptions (King, 1937). Schindewolf (1955a, 1955b) takes for granted the Lower Cambrian age of the Salt Range *Redlichia* fauna.

R. & E. Richter have contemplated making a palaeogeographical map of the distribution of the *Redlichia* Sea, which they interpret as the initial Tethys. It covers Palestine, Iran, India, the Himalayas, Indo-China, Korea, Manchuria,

Shantung, Hupeh, northern Western Australia, western and central Northern Territory, north-western Queensland, and South Australia. Outside this vast region of the initial Tethys *Redlichia* is unknown. Within it, the Cambrian fossil record, it was assumed, started with the appearance of *Redlichia*, but without associated index forms that could indicate the age of the event and the range of the genus. The age was actually unknown, but all authors were agreed that the choice was between Late Lower Cambrian and early Middle Cambrian time.

It now appears that in South Australia (Daily, 1956) a species of *Redlichia* actually occurs in the Lower Cambrian, but the *Redlichia* faunas of northern Australia (Öpik, 1956a, p. 17; 1956b, p. 48), including *R. chinensis*, are of lower Middle Cambrian age. This is borne out by associated fossils and by the fact that the *Redlichia* faunas everywhere in northern Australia are immediately followed by faunas correlated with the Scandinavian *Ptychagnostus* ("Triplagnostus") *praecurrens* and "*T.*" *gibbus* zones, which are well above the base of the Middle Cambrian. Consequently, the *Redlichia*-bearing beds themselves should be correlated with the greater (lower) part of the *Paradoxides oelandicus* stage of Scandinavia, and are all lower Middle Cambrian in age. In the North American Rocky Mountains, the Middle Cambrian faunas below the Burgess shale should be correlated with the *Redlichia* faunas of northern Australia.

A similar correlation applies to the Himalayas, Korea, and China. The correlation of the Cambrian of the Salt Range and Indo-China is not yet clear, but Lower Cambrian is the lesser probability.

MUSEUM NUMBERS AND SOME DIMENSIONS OF FIGURED SPECIMENS.

CPC⁽¹⁾ 922 (*R. forresti*; Pl. 1, figs. 2, 3; Text-figs. 1, 3):

| | |
|---------------------------------------|-----------------|
| Length of thorax and pygidium | 39 mm. |
| Length of pygidium | 3.5 mm. |
| Width of pygidium | 6.5 mm. (about) |
| Total length (estimated) | 56 mm. |

The cranium is about as long as $5\frac{1}{2}$ anterior segments.

CPC 923 (*R. forresti*; Pl. 1, fig. 1):

| | |
|----------------------------------|--------|
| Length of larger cranium | 21 mm. |
| Width of frontal limb | 21 mm. |

CPC 924 (*R. forresti*; Pl. 2, figs. 2, 3):

| | |
|-----------------------------------|----------|
| Total length as preserved | 12.8 mm. |
| Length of cranium | 4.8 mm. |

The cranium as preserved in the rock is as long as 7 anterior segments but is shortened by slumping.

CPC 925 (*Redlichia* sp. a; Pl. 1, fig. 4):

| | |
|---|----------|
| Length of pygidium | 9 mm. |
| Length without articulation half-ring | 7.5 mm. |
| Width | 15.5 mm. |
| Total length of dorsal shield (estimated) | 150 mm. |

CPC 926 (*Redlichia* sp. a; Pl. 1, fig. 5; Text-fig. 5):

| | |
|---------------------------|-------|
| Width of pygidium | 8 mm. |
|---------------------------|-------|

(¹) C.P.C. = Commonwealth Palaeontological Collection, held in the Bureau of Mineral Resources, Geology and Geophysics, Canberra.

CPC 927 (*Redlichia* sp. b; Pl. 1, fig. 6; Text-fig. 4):

| | |
|----------------------------------|-------|
| Total length of specimen | 6 mm. |
| Length of pygidium | 2 mm. |

CPC 928 (*R. forresti*; Pl. 2, fig. 1; Text-fig. 2):

| | |
|---|-----------|
| Length of preserved portion | 8 mm. |
| Total length of dorsal shield (estimated) | 15-16 mm. |

CPC 930 (*Redlichia* sp. a; Text-fig. 9):

| | |
|----------------------------|---------|
| Length of pygidium | 5.7 mm. |
| Width | 9 mm. |

CPC 2327 (*R. forresti*; Pl. 3, figs. 1-4):

| | |
|-------------------------------|----------|
| Length of cranium | 23.5 mm. |
| Width of frontal limb | 27.5 mm. |
| Width between eyes | 20.5 mm. |

CPC 2328 (*Redlichia* sp. c; Pl. 3, figs. 5-7).

| | |
|-------------------------------|----------|
| Length of cranium | 21.9 mm. |
| Width of frontal limb | 23.2 mm. |
| Width between eyes | 22.5 mm. |

CPC 2329 (*R. idonea*; Pl. 4, figs. 1, 2):

| | |
|--|----------|
| Length of cranium | 13.5 mm. |
| Width of frontal limb | 15.5 mm. |
| Width of rostral shield | 12.3 mm. |
| Length of hypostoma | 6.2 mm. |
| Total length of hypostoma and rostral shield | 8.0 mm. |

CPC 2330 (*R. idonea*; Pl. 5, figs. 1, 2):

| | |
|---------------------------------|-----------------|
| Length of cranium | 11 mm. |
| Width of frontal limb | 11 mm. |
| Width of rostral shield | 9.5 mm. (about) |

CPC 2331 (*R. venulosa*; Pl. 6, figs. 1-3):

| | |
|---|----------|
| Length of cranium | 17.7 mm. |
| Width of frontal limb (estimated) | 17 mm. |

CPC 2332 (*R. idonea*; Pl. 6, figs. 4, 5):

| | |
|---------------------------------------|---------|
| Total length of fragment | 7.8 mm. |
| Width between posterior barbs | 2.7 mm. |

CPC 2333 (*R. cf. idonea*; Pl. 6, fig. 6):

| | |
|--|--------|
| Length of anterior five segments | 12 mm. |
|--|--------|

CPC 2334 (*Redlichia* sp. d; Pl. 6, fig. 7):

| | |
|---------------------------|----------|
| Length of cranium | 16.3 mm. |
|---------------------------|----------|

CPC 2335 (*Redlichia* sp. d; Pl. 6, fig. 8):

| | |
|---------------------------|----------|
| Length of cranium | 14.5 mm. |
|---------------------------|----------|

The largest observed cranium of *R. forresti* (CPC 929, not illustrated) is 32 mm. long; its frontal limb, affected by lateral slumping, is only 29 mm. wide. The total length of the trilobite was about 110 mm. The largest specimen of *R. idonea* is about 180 mm. (7 in.) long (Whitehouse, 1939).

THE DIMORPHISM.

The specimens here attributed to *Redlichia forresti* must be placed in two distinct groups according to the different structure of their pygidia:

Group I. (Pl. 1, figs. 2, 3; Text-figs. 1, 4) has the "usual" *Redlichia* pygidium, slender dorsal spines, and relatively short pleural spines; the posterior pleurae are not extended beyond the pygidium.

Group II. (Pl. 2, figs. 1-3; Text-fig. 2), has a pygidium comparable with the caudal shields of the majority of trilobites, stout axial spines, and relatively long pleural spines. The posterior pleurae are long and extend beyond the pygidium.

The differences and relations between the two groups may be conveniently discussed in two parts: first, the cranidia and the thoraces are compared, to show the taxonomic unity of the two groups; secondly, the structure of the pygidia is described.

The specimens of Group I. (Pl. 1, figs. 2-6; Text—figs. 1, 4) are incompletely preserved. In Plate 1, figure 2, the cranidium is missing except for the narrow posterolateral limbs, which bear short "intergenal" spines. In the right free cheek the anterior part of the subcephalic doublure shows that the rostral shield was slightly shorter (narrower) than the frontal limb of the cranidium. The first segment of the thorax seems to be slightly longer than the next; it has a mark on the axis, interpreted as a node. The axial ring of the fourth segment of the thorax has preserved the base of a slender dorsal spine, which is an important mark for counting the number of segments in less nearly perfect specimens. The twelfth segment of the thorax is accidentally missing in this specimen, but from other, unfigured, specimens (which were unfortunately destroyed by fire in 1953) a long dorsal spine is known to occur on this segment. The anterior pleurae have short spines, which are notched at the base and resemble the advanced genal spines and notch-like genal angles; the posterior pleurae gradually become falcate towards the rear. The posterior pleurae overlap the flanks of the pygidium, but in larger specimens they do not reach its edge. In small specimens the posterior pleurae may extend backward beyond the posterior edge of the pygidium. The thorax has seventeen segments and a final (eighteenth) segment partly attached to the pygidium. According to Kobayashi & Kato (1951), a similar semi-anchylosed segment occurs in *R. chinensis*.

The specimens of Group II. are also damaged. In one of them (Pl. 2, fig. 1) the cephalon and the three anterior segments are missing, but the fourth segment is readily identified by its axial spine, which is stout. The base of a stout spine of the twelfth segment is also preserved. Behind the twelfth segment five more free segments can be counted, and, attached to the pygidium, an eighteenth segment as well (see also Text-fig. 2). The other specimen (Pl. 2, fig. 2) shows the frontal doublure of the free cheek, and here again its shape indicates that the rostral shield was shorter than the anterior cranial limb. The posterolateral limb has the intergenal spine preserved. The axial part of the first segment of the thorax is slightly enlarged; the twelfth segment is overturned and shows the flat ventral side of the dorsal spine. The pleural spines are strong; the anterior ones are slightly advanced, and the posterior become gradually falcate. The posterior pleurae extend slightly beyond the pygidial edge, as in some of the smaller specimens of Group I. Both specimens are small compared with those illustrated on Plate 1, figures 1 and 2.

A slight difference may be detected between the cranidia of Plate 1, figure 1, and Plate 2, figure 2: in the first the posterior end of the palpebral lobe is nearer the glabella than in the small specimen on Plate 2. But it has been observed on numerous specimens of several species of Australian *Redlichia*

that the space between the glabella and the posterior ends of the palpebral lobes becomes narrower with an increase in the general size. Smaller specimens also seem to have stronger spines than large ones. Such characters are of importance only when specimens of similar size are compared.

The following table summarizes the comparison of the two groups:—

| | Description of Characters. | Group I. | Group II. |
|-------------------------|---|----------|-----------|
| Taxonomic characters .. | Number of free segments in thorax .. | 17 | 17 |
| | Semi-attached segments .. | 1 | 1 |
| | Dorsal spine on fourth segment .. | + | + |
| | Dorsal spine on twelfth segment .. | + | + |
| | "Intergenal" spines .. | + | + |
| | Rostral shield shorter than frontal limb .. | + | + |
| | First axial ring enlarged .. | + | + |
| Sex characters .. | Axial spines stout .. | — | + |
| | Axial spines slender .. | + | — |
| | Pleural spines long .. | — | + |
| | Pleural spines short .. | + | — |
| | Size large, average 100 mm. .. | + | — |
| | Size small, average 15 mm. .. | — | + |
| | Posterior pleurae extended beyond pygidium .. | — | + |
| | Posterior pleurae not extended .. | + | — |
| | Occurrence frequent .. | + | — |
| | Occurrence rare .. | — | + |

Group I. most probably represents female, Group II. male, individuals.

Little comment is necessary on the features here designated as of taxonomic significance: the coincidence between the two groups is complete. The number of thoracic segments in previously described specimens of the genus *Redlichia* varies between 14 and 17; the number observed here (17 + 1) is unique. No other species of *Redlichia* has the posterior dorsal spine on the twelfth segment. "Intergenal" spines are occasionally observed, according to Kobayashi & Kato (1951), on larval cranidia of *R. chinensis*, but they are not described from adults of that species or from any stage of other species. In all the above-mentioned features *R. forresti* differs diagnostically from all other known species, and the same features, being common to both groups, unite them in a single species.

There has been no systematic research into the secondary sexual characters of trilobites, although the degree of development of the various spines has occasionally been interpreted as an indication of sexual differences. Observations do exist, however, on the different sizes of the sexes amongst various other arthropods.

The rarity of males (our Group II.) needs some explanation: perhaps there was an original numerical preponderance of females over males, and perhaps different moulting-grounds and extra-seasonal segregation of the sexes are also indicated by the relative rarity of males. It also seems reasonable to suppose that the small males, in spite of their stronger spines, were all too often the victims of the wedding-breakfast.

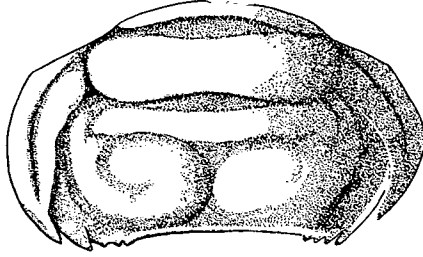


Fig. 1.—*R. forresti* (Eth. Jr), female pygidium (specimen Pl. 1, figs. 2, 3; greatly enlarged).

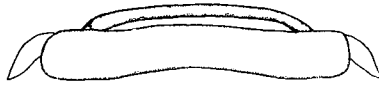
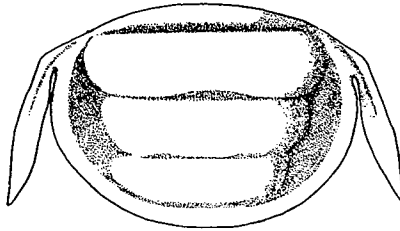


Fig. 2.—*R. forresti* (Eth. Jr), male pygidium (specimen Pl. 2, fig. 1; greatly enlarged).

THE DIMORPHIC PYGIDIA.

GROUP I.

Pygidia of Group I. of *R. forresti* (Pl. 1, figs. 2, 3; Text-figs. 1, 4) are small, about 1/15 or 1/16 of the total length of the trilobite. They are strongly vaulted and are bilobed by a longitudinal median depression. The flanks are narrow and depressed, and the rear has an abrupt edge and no border. The posterior margin (Text-fig. 9) is arched upwards. Two axial annulations and a slight indication of a third annulation are present, and two distinct pleurae and about two pairs of short spines form the pleural border. The pygidium is slightly asymmetrical (Text-fig. 1) but to a lesser degree than that of *R. chinensis* (Saito, 1934, Pl. 26, fig. 10). The doublure is developed only on the flanks—as the doublure of the distal ends of the pleurae. The posterior margin is a clean-cut edge: the test is not folded and duplicated under the dorsal shield, and thus the pygidial doublure of Group I. of *R. forresti* is incomplete, being discontinuous in the middle.

The same condition of the pygidial doublure is seen in two undescribed Australian species of *Redlichia*. The first (*Redlichia* sp. *a*) is shown in Plate 1, figures 4 and 5, and Text-figures 5 and 9. Plate 1, figure 4, represents a steinkern in which the absence of a doublure can be seen where the margin is damaged. The second specimen (Pl. 1, fig. 5), an external mould, has the steinkern of the left doublure completely preserved. The exterior of a pygidium is shown in Text-figure 9.

The second undescribed species (*Redlichia* sp. *b*; Pl. 1, fig. 6) is represented by a specimen compressed in shale whose posterior margin is also a clean-cut edge; its lateral doublure is reconstructed in Text-figure 4.

It may be understood from Kobayashi & Kato (1951, p. 125) that an interrupted doublure seems to occur in *R. chinensis* also. The authors mention the doublure of the anterior pleurae of the pygidium; but they state that "the ventral side of the pygidium behind this segment is as yet unknown, but may be covered by the doublure widely, because it is seen in . . . *Wanneria walcottana*". To observe the doublure the outer test must be peeled off. Without a doublure the outer test adheres to the rock as seen in the material described by Kobayashi & Kato. I conclude that the test has not peeled off because there is no doublure present.

If compared with all known trilobites—all of which have the doublure continuous around the pygidium—the posterior caudal margin of Group I. of *Redlichia* can be described as being open and unprotected by the test. Perhaps it was open for a "telson" that did not have a rigid test. If a test had been present, it must have been either rigidly connected with the pygidial edge or articulated with it, and in the latter case there would be an axial articulation doublure on the pygidial margin. The bilobation of the pygidium suggests that the problematical telson may have been biramous.

Alternatively the unprotected part of the body may have been the whole of the anal segment, including the telson; now the anal segment should have pleurae, and the posterior pygidial pleurae are indicated by a pair of tiny spines. They are covered by the lateral doublure. Consequently, a telson is the greater possibility.

The structure of the pygidia of Group I. may also be described from another point of view: the posterior doublureless end of the pygidium is the real axial termination, whereby *Redlichia* differs from all other trilobites, in which the post-axial terminal margin is formed by fusion of the posterior pleurae along the mid-line to close the pleural platform.

GROUP II.

The pygidia of Group II. (Pl. 2, figs. 1-3; Text-fig. 2) are also small, about 1/17 of the total length of the trilobite. As explained above, the pygidium of the more complete of the two specimens (Pl. 2, figs. 2, 3) is shortened by slumping, and the description refers to the second specimen, in which the pygidium is undistorted. It has two distinct annulations of the axis and one indistinct, terminal, annulation. The raised border is continuous around the free edge. Attached to the anterior corners is a pair of free pleurae or spines, whose doublure is not connected with that of the pygidium: the first segment is semi-anchylosed. The margin is nearly vertical, and its free edge is folded under to form a continuous, normal, doublure. There is no gap in the doublure, and no need to postulate the existence of a "telson".

The ventral side of this sort of pygidium is not completely exposed in the available material, and details of the structure of the doublure must remain unknown for the time being. While discussing the present paper, Dr. O. P. Singleton drew my attention to the short note by Stubblefield (1942) on a collection of *Redlichia* from the Ord River region, the type area of *R. forresti*. It is hoped that the question of the ventral side of pygidia of Group II. will be answered when the results of study of this material are published.

The two kinds of pygidia cannot be interpreted as different ontogenetic stages, because pygidia of Group I. (females) of *R. forresti* as small as, and even smaller than, those of Group II. (male) have been found.

TWO SPECIES VERSUS SEXUAL DIMORPHISM.

Imperfect material, for example material consisting only of two sorts of pygidia, could be exploited to establish two distinct species and genera of trilobites, and to assign them to different families. Even now, with reasonably complete material in hand, the possibility of a taxonomic division should be discussed, and the reasons of preference for a dimorphism within a single species amplified.

When Text-figures 1 and 2 are compared, it is apparent that the anterior part of the two pygidia is similar, but that striking differences appear in the posterior part, behind the first segment with its wing-like free pleurae. These differences in the morphology of *R. forresti* may be viewed from another standpoint than sexual dimorphism: they may be conceived as an evolutionary change—a saltation—and the beginning of an altogether new lineage.

As the two forms are contemporaneous, it is difficult to tell immediately which of them is the parental form. Moreover, it is not known whether a similar dimorphism occurs in other species of *Redlichia*; the “female” form of pygidium is known in other species in various countries, so that, if the dimorphism represents a saltation, the “male” form may be the new Australian design.

This last assumption, if correct, implies one more complication in the history of trilobites: the “normal” trilobite pygidium, with complete doublure, is polyphyletic, because it was already in existence in a number of different genera before *Redlichia*, for example ptychopariids, ellipsocephalids, and eodiscids. So perhaps the opposite is correct: the pygidium with closed doublure is the fundamental design, whereas the open caudal shield is a subsequent development in the redlichoid, or even a variation within the olenelloid, stock. Now a closed shield can be derived from an open one by fusion of the posterior pleurae behind the axis, but the specialization is not likely to be reversible.

It may be concluded that the open pygidium of *Redlichia* is an ancestral and primitive character, well behind its time even at the close of the Lower Cambrian; and this conclusion remains valid in the case of a single dimorphic species.

The explanation of the dimorphism of *Redlichia* as regular ontogenetic stages is rejected; and although a number of observations and considerations support the concept of sex dimorphism, the possibility of an evolutionary saltation remains real. Whether it consisted only in a sudden development of sexual dimorphism, whether a new, externally dimorphic, species arose, or whether the course of evolution was towards a new species with the “male” pygidium, is still obscure. Study of the ontogeny of *Redlichia* and of the morphology of species other than *R. forresti* may answer the question: Does the dimorphism of *R. forresti* represent the unique case of preserved palaeontological evidence for co-existing abrupt saltations of taxonomic significance?

The taxonomic significance of the co-existence of two different pygidial designs in forms otherwise morphologically identical deserves further comment: if the two forms are specifically distinct, they are not of the same genus or even the same family, and, indeed a subdivision of trilobites into two sections—(1) *Redlichia* with open pygidium and (2) *Redlichia* with normal pygidium *plus* all other trilobites—would be reasonable. The other interpretation—a single species unique in the development of such a dimorphism and regarded

as a separate division against all other trilobites—is equally admissible taxonomically. However, if no pygidia were known, but only cranidia and thoraces, there would be evidence for only one species of an ordinary genus of trilobites.

Admittedly, many species and even genera of trilobites are based on differences of pygidial structure: the genera *Albertella* and *Zacanthoides* or *Fieldaspis*, “*Atabaskia*, *Ptarmigania*, *Dolichometopsis*, *Stephenaspis*, and possibly several others” (Rasetti, 1951, p. 159), are distinguished by pygidia less strikingly different than the two forms of *R. forresti*, and could be used as examples of how to split the latter into two units. The two pygidial designs of *Redlichia*, however, permit an explanation that does not automatically involve taxonomic consequences, and this explanation is: a single dimorphic species.

The preferred interpretation may be merely a reflexion of my personal attitude, and an attempt to avoid the taxonomic complications outlined above; nevertheless, it is a convenient and adequate presentation and arrangement of the observed facts and is chosen because I consider that the morphology of the *Redlichia* pygidium is too unusual and distinctive for the current criteria of trilobite taxonomy to be applied.

COMPARISON WITH OTHER *REDLICHIAE* AND RELATED TRILOBITES.

The pygidia of the numerous Asian species of *Redlichia* are inadequately described, but no male forms can be recognized in the figured material. The clearest illustration is that of *R. chinensis* published by Saito (1934, Pl. 26, fig. 10), which corresponds to pygidia of Group I. and may be regarded as a female. A similar reconstruction is given by Kobayashi & Kato (1951) for the same species. A re-examination of material from Asia should also yield pygidia of Group II., and a confirmation of the dimorphism of the genus *Redlichia*.

A re-examination of the actual material of the olenellids also seems worth while, as *Olenellus* itself, *Callavia crosbyi* Walcott (1910, Pl. 20, fig. 8), and *Wanneria? pennapyge* Raw (1936) all have more-or-less bilobed pygidia, externally comparable with the female *Redlichia*, although it is not the bilobation, of course, but the structure of the doublure, that is significant. But *Redlichia* cannot serve in forecasting the structure of the pygidia of the Olenellidae. For example, the bilobed pygidium of *Wanneria walcottana* (Wanner), in Wanner (1901, Pl. 32, fig. 4), is “normal”, with a wide continuous doublure.

The female pygidium of *Redlichia* is externally nearly identical with the pygidium of *Holmia kjerulfi* (Linnarsson). Indeed, if a pygidium of *Holmia* were found in northern Australia it would most probably be determined as a

Redlichia. The similarity of Text-figure 1 to the pygidium of *Holmia* in Walcott (loc. cit., Pl. 27, fig. 7) and Holm (1887, Pl. 15, figs. 15, 16) is obvious. In both specimens the lateral, pleural, test has peeled off and the doublure is visible, but the test in the middle is preserved as it generally is in *Redlichia*.

A female *Redlichia* retaining its open pygidium during the whole of its life may be considered as being an "adult larva", and the particular structure of its pygidium may be regarded as primitive and inherited from the "ancestral annelid". The open pygidium represents also a deviation from the scheme of caudalization as visualized by Swinnerton (1915, 1923). According to this scheme, the initial pygidium is formed by fusion of the test of the anal segment or telson with that of the segment in front of it. In the open pygidium, however, segments in front of the telson are fused and the telson itself remains free. Thus, a "shield" is formed that can be interpreted as an imperfect pygidium or as a "macropleural fusion" within the thorax.

The ontogeny of *Redlichia* is neither well enough known nor well enough preserved to trace the development of the pygidium in detail, but studies on other trilobites may indicate the possible course of development. Thus, in the paradoxidid *Xystridura* from the Middle Cambrian of northern Australia, the posterior pleurae of the "transitory pygidium" of the early meraspis stages are not fused: the axis itself is the termination without any evidence of a doublure. The final pygidium is formed in the later meraspid stages, when the fusion of the pleurae is complete and the continuous pleural platform established.

Ontogenetically the "open" pygidium precedes the "normal" pygidium in *Xystridura*, and a similar succession may be present phylogenetically in *Redlichia*. Consequently, caudalization and the formation of the conventional trilobite pygidium are late events in the evolution of the trilobite class and postdate cephalization.

The study of the organization and ontogeny of *Xystridura* is not yet concluded and is, moreover, delayed, and it is hoped that the foregoing observations may prompt other students of trilobites to check the neglected history of the pygidial doublure in early Cambrian forms. Later trilobites are less promising, as more of the early development took place *in ovo*.

According to Schindewolf (1955a), *Redlichia noettingi* (the type species) has no rostral suture and therefore no rostral shield: the cranial doublure remains attached. If this is correct it is evidence that the Australian forms differ taxonomically from the Salt-Range species. The hypostoma of *R. noettingi* is attached to the doublure, but, contrary to Schindewolf's interpretation, this may be interpreted not as a primary absence of a suture but as a secondary anchylosis.

Schindewolf takes for granted the Lower Cambrian age of the *Redlichia*-beds and concludes that, because of this age, a secondary anchylosis of cranium, rostral shield, and hypostoma, is improbable. But I believe that such an anchylosis may occur in some individuals of a species—and may have been a temporary condition in the life of a single individual.

If the anchylosis were complete and permanent, the inwardly-directed spines (Text-fig. 6) on the edge of the rostral shield (or cranidial doublure in the case of *R. noetlingi*) would create the moulting dilemma: burst or die.

THE PROBLEM OF THE TRILOBITE TELSON.

It is suggested on page 16 that in the female *Redlichia* the hind part of the body may have extended beyond the caudal shield to form a "telson" unprotected by the test. As long as its existence is still in question, and the absence of the test is not proven by direct evidence, it is better, perhaps, to call this structure a "telsonic extension" from its topological position.

A spine may have been present here, either (1) articulated with the anal segment or (2) attached to the anal segment as a part of it. An articulation such as occurs between the tergites was not necessarily present with an unprotected telson. The articulation "doublure" of the anal segment is necessary only when the next following segment has a test and an articulation half-ring extending under the "doublure".

The caudal rami described by Walcott (1918) in *Neolenus* (= *Olenoides*) *serratus* have been interpreted as modified posterior appendages. If so, their position is pre-telsonic. But they are observed in combination with a pygidium that has a normal, continuous, doublure, and therefore direct comparison with *Redlichia* is not possible.

The combination of telson and caudal rami occurs in living Crustacea and may also have existed in some trilobites. Of course, *O. serratus* has only rami (or "cerci" in the terminology of Størmer, 1944) and no morphological telson, although the terminus of the pygidial axis, placed behind the anus, might be termed "telsonic".

In several trilobite genera of different super-families the terminus of the pygidial axis is extended into an immovable spine; examples are *Pagetia* Walcott, *Eochuangia* Kobayashi 1934, and the latter's probable synonym *Ataktaspis* Lochman 1944. This spine is a dorsal structure extending above the doublure, which is not involved. The immobility has here only a relative meaning: the segments of the pygidium are fused, but the presence of a furrow dividing the annulations indicates an undeveloped articulation of the somites

involved. Hence the spine is an extension of the terminal segment, which, in turn, is "potentially" articulated with the penultimate somite. It seems that, for terminal axial spines of the type represented in *Pagetia* and *Eochuangia*, the term "telsonic spine" is applicable.

The foregoing description of telsonic structure seems to coincide with that of the "telson spine" in Cambrian Merostomata (Raasch, 1939).

Another type of terminal axial spine is developed in several post-Cambrian trilobites, for example in the Dalmanitidae and Asaphidae. The dorsal side of their spines seems to be the extension of the axis, but the ventral side, usually flattened, is an extension of the pygidial doublure. Obviously pleural as well as axial elements are involved here. The caudal spine of the asaphid *Thysanopyge* Kayser (Ordovician, Argentina) has serrate lateral edges; this serration may correspond to an obliterated segmentation. Moreover, the older dalmanitids, and some of the older asaphids, have no caudal spines at all. For such structures, polyphyletic in origin, and composed of more than one element, the term "caudal spine" seems to be more appropriate than "telsonic spine", which has a restricted significance.

The problems of trilobite axial spines and of the origin of the telson of the Xiphosura have been linked together by Størmer (1944). He works with the homology of the rudimentary post-telsonic segments of *Limulus* and the "rudimentary" ("anemic", "atrophic", "reduced") post-thorax of olenellids. This homology is, however, disputable, because the olenellid post-thorax is not "rudimentary" in the same sense as the "post-telsonic" segments of *Limulus*.

The history of the idea began in 1910, when Walcott wrote (p. 246): "The telson of *Olenellus* is not considered to be a true pygidium. It resembles the telson of *Limulus*, but this resemblance does not necessarily indicate that *Olenellus* was the ancestor of *Limulus*; its origin does, however, indicate the manner in which the telson of *Limulus* may have originated". And the "manner of origin" of the telson of *Olenellus* is outlined by Walcott as follows (p. 245): "*Olenellus* stage: fourteen fully developed segments, a large third segment, and the fifteenth segment a strong terminal telson; posterior rudimentary segments and true pygidium of the *Paedeumias* stage absorbed or the rudimentary segments and pygidium have disappeared and the large median spine of *Paedeumias* has become the telson of *Olenellus*".

This concept has become obsolete since the restudy of *Olenellus* and *Mesonacis* by Resser & Howell (1938), which showed that *Olenellus* is only an imperfectly preserved "*Mesonacis*", in which the pygidium and the thoracic segments posterior to the spine are accidentally missing. The dorsal spine is not an isolated "telson", but an axial spine of the fifteenth segment. Consequently the term "rudimentary", applied to the posterior segments of *Paedeumias* and "*Mesonacis*", has lost its meaning also. Once it was logical, because the posterior segments in the concept of Walcott were regarded as phylogenetically

outlived and disappearing. But now, when no disappearance is observable, the term "rudimentary" can only mean "decreasing in size in the caudal direction", and the appearance of a specialized flexible opisthothorax.

Størmer (*loc. cit.*, pp. 114-116) follows Ivanov in considering the possibility that the dorsal spine of the primitive Olenellida is homologous with the telson of *Limulus*. According to Ivanov, rudimentary segments posterior to the telson exist in *Limulus*. These rudimentary segments are supposed to be homologous with the "rudimentary" segments of *Olenellus* behind the dorsal spine. But *Olenellus* has no rudimentary segments, and, moreover, the primitiveness of *Olenellus* is itself a highly disputable concept. It would seem that the "manner of origin" is applicable to *Limulus*, but not to trilobites, and there is no indication that *Olenellus* was the ancestor of *Limulus*.

THE OCCIPITAL SEGMENT AND "OCCIPITAL SIMILARITY".

The similarity of the occipital segment to the segments of the thorax nearest to it has been considered by trilobite students ever since Barrande. For brevity, it is here referred to as "occipital similarity".

Occipital similarity is important in theories concerned with the character of the segmentation, and in the problem of the number of segments and appendages in the original head of trilobite ancestors.

Occipital similarity may be interpreted as an indication that the occipital segment is not an original somite of the head, but a later acquisition. It can also be dismissed as an accidental similarity, and the occipital segment regarded as an original integral part of the head. Two diverse theories of the formation of the trilobite head depend on these assumptions. The first assumption suggests that the trilobite head was formed gradually, by subsequent addition (cephalization) of somites of the thorax to the head that had only a small number of "original" segments. The second assumption implies the possibility of a more-or-less simultaneous coalescence of a fixed number of somites constituting the cephalon. Assuming a fixed number of segments one should also assume that these segments were in some respects similar ("cephalic") among themselves, and different from the remaining segments of the body.

Consequently the interpretation of the position of the trilobite class within arthropods depends to some extent on the interpretation of occipital similarity. For example, if the occipital segment is an element of the thorax and not of the original head, there would be one or more segments less in the head, and *Redlichia* would appear to be nearer to crustaceans than to arachnomorphs, including *Limulus*.

The structure of the posterolateral limbs (fixigenes) of *Redlichia* is explained in Text-figure 3. In *R. forresti* short "intergenal" spines are present and, by reason of the notch at their base, have an advanced position similar to the advanced position of the genal spines and of the pleural spines of the anterior segments of the thorax. In other species "fixigenal" or "intergenal" spines are not observed, except in larvae of *R. chinensis*, according to Kobayashi & Kato (1951).

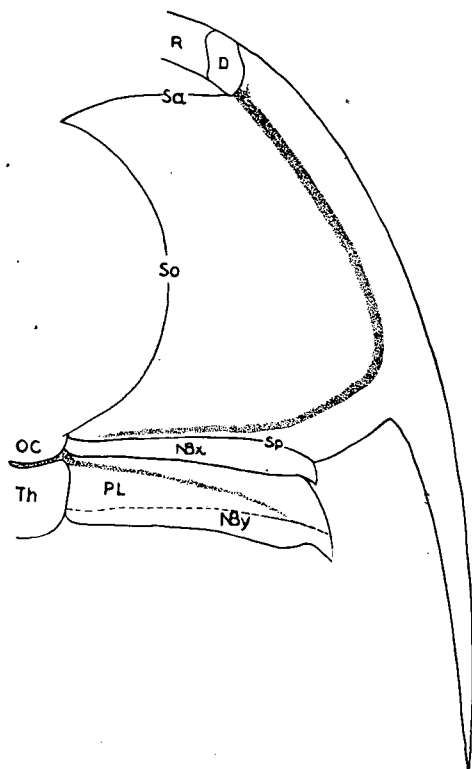


Fig. 3.—*R. forresti* (Eth. Jr), cheek and first thoracic segment (specimen Pl. 1, fig. 2; diagrammatic). D.—anterior end of doublure of cheek; NBx.—posterior portion of occipital pleura; NBy.—posterior portion of pleura of first thoracic segment; OC.—occipital ring; PL.—pleura; R.—rostral shield; Sa.—anterior branch of facial suture; So.—ocular section of facial suture; Sp.—posterior branch of facial suture (between R and D is subcephalic branch of facial suture); Th.—axial ring of first thoracic segment.

The structure of the posterolateral limbs repeats precisely that of the posterior portion of the thoracic segments. Doubtless the posterolateral limbs represent this posterior half of the occipital pleurae, and the "intergenal" spine is a pleural terminal spine. A similar structure is also present in *Zacanthoides*.

This is a conservative view defended by Richter, and it can be traced back to Barrande. It is based on the morphological evidence provided by occipital similarity. Raw (1953), however, claims that "this likeness is attributable to

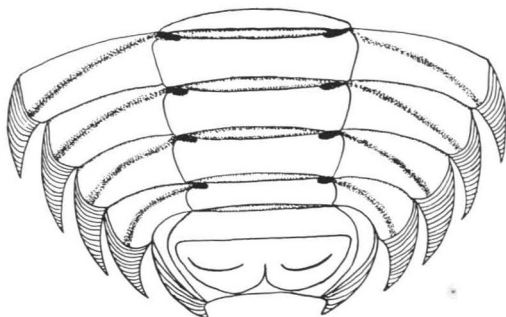


Fig. 4.—*Redlichia* sp. *b*, female, showing extent of pleural doublure (specimen Pl. 1, fig. 6; diagrammatic). Median posterior edge of pygidium has no doublure.

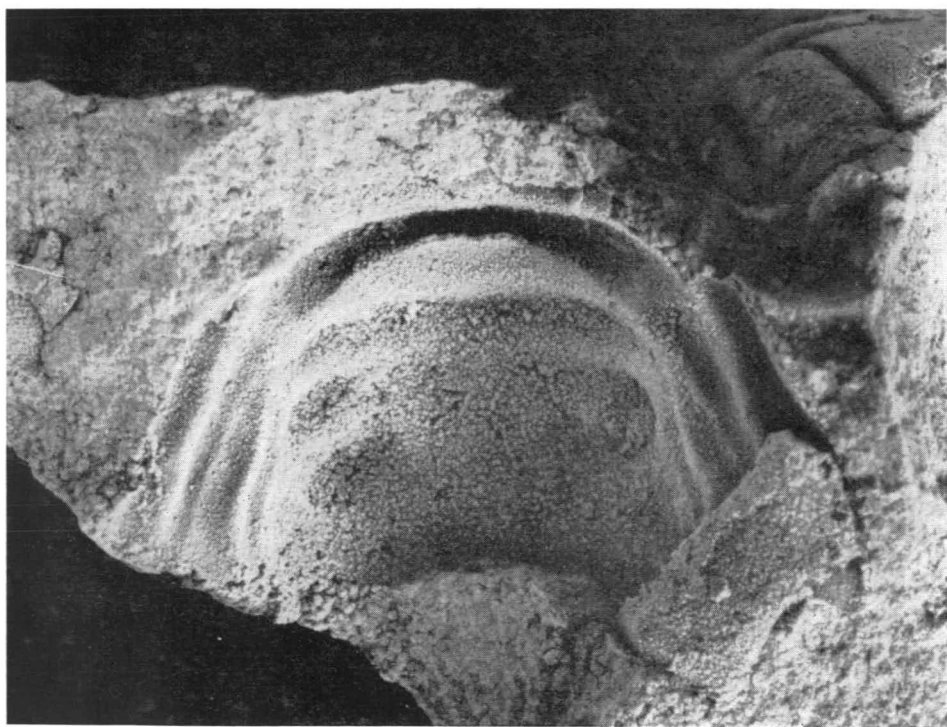


Fig. 5.—*Redlichia* sp. *a*, female pygidium, showing the three pairs of muscle attachments, steinkern of doublure, and marginal spine (specimen Pl. 1, fig. 5).

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the muscular connection and movement between the two" (the thorax and the cephalon). Such a possibility is not observable, but the likeness is. Ontogenetically the cephalon antedates the segments of the thorax, and one may assume that, for mechanical reasons, the pre-existing structure of the occipital segment was reflected in the subsequent somites of the thorax and even of the pygidium. This "reflected" occipital similarity, if accepted as an analogy only, may serve to dismiss the axial ball-and-socket similarity, of course; but the similarity of the notched pleural terminations and the advanced intergenal spines of *Redlichia* (Text-fig. 3), has nothing to do with the mechanics of articulation. In most species of *Redlichia*, and in most trilobites, the intergenal spines disappear in adults, but the articulation remains unchanged. Thus, occipital similarity is a vanishing homology independent of mechanics and suggests that the occipital segment is a late acquisition of the cephalon. In some trilobites occipital similarity is observable also in the preoccipital segment, and even beyond it, as for example in *Cybele*. It can be said that in many trilobites occipital similarity is preserved in the posterior four glabellar lobes, but decreases markedly toward the front (see Öpik, 1937).

Palmer (1957), in describing the morphogenesis of *Olenellus*, has shown beyond doubt that the intergenal spine is connected with the preoccipital glabellar lobe. More, however, can be seen in his photographs (Pl. 19, figs. 2, 6, 11, 15; Text-figs. Ia, IIc, IIIc). The posterior border of the occipital segments is continuous with the border of the intergenal spine, as, on the ventral side, is the occipital doublure. The continuity is maintained in a manner suggesting that the pleural spine of the occipital segment is also contained in the intergenal spine. Consequently, the pleural spine of the neck segment need not be placed in the pleural tips of the next following segment of the thorax. The occipital segment remains a complete unit, as described in *Redlichia*.

The intergenal spine of *Olenellus* is a compound structure within which the pleura of the preoccipital somite remains dominant during all subsequent instars, but without obliterating the connexion with the occipital segment. This suggests that the preoccipital segment is macropleural ("mono-macropleural") and that the intergenal spine is a fusion of two or more pleurae. The "intergenal spinules" may indicate that pleural spines of all four post-ocular segments are completely represented in a secondary "poly-macropleural" structure in the head of *Olenellus*.

Indeed, segments of trilobites do merge to form compound macropleural units. Daily (1956, p. 132) states that in a Lower Cambrian trilobite from South Australia "the fifth and sixth thoracic segments are fused and macropleural". Öpik (1937, pp. 127, 129) has also suggested that in *Holmia kjerulfi* the occipital ring is "double" and contains the elements of two fused segments in its axial lobe.

CONCEPT OF THE GENUS *REDLICHIA*.

The type species of *Redlichia*, *Hoeferia noetlingi* Redlich 1899, is inadequately known, and though it provides a diagnosis of the genus, a more complete concept has to be based on other, better known species.

Some additional observations on details of the structure of the test, which are obscure on Asian material but discernible in tectonically undistorted Australian specimens, may be discussed before the generic concept of *Redlichia* is considered.

The head of *Redlichia* is well known from a number of species. The long tapering glabella, the large eyes with their extremities close to the dorsal furrow, the neck furrow shallow in the middle, and the advanced genal spines, are regarded as being olenelloid and primitive. The well-developed facial sutures, missing in the olenelloids, delineate a cranidium separate from the free cheeks. In the olenelloids, however, the head is a unit on its own and a cranidium is not differentiated—perhaps because of loss of sutures by their ancestors.

The cranidium has a wide frontal limb which is as wide as the cranidium between the posterior ends of the sutures.

The head is moderately convex, and is evenly sloping. The eyes are not elevated, and remain below the level of the glabella. Besides the neck furrow three pairs of lateral glabellar furrows are present, but the two anterior pairs are usually weak.

The occipital furrows and the posterior glabellar furrows are of similar structure: they are deep on the flanks, and each pair is connected in the middle by a shallow depression (Pl. 6, fig. 1; Text-fig. 8) crossing the glabella. The connecting furrows are homologous with the articulation furrows of the thorax, and are an illustration of occipital similarity. The connecting furrows are widened in the middle and show a "floor" that can be interpreted as rudiments of the posterior part of the articulation half-rings and the furrows separating the half-rings from the corresponding axial lobes. Thus, vestiges of an obsolete articulation are preserved in the glabellar furrows of *Redlichia*.

The cephalic dorsal furrows are deep at their junction with the glabellar furrows and shallow in contact with the glabellar lobes. In non-flattened specimens even a confluence of the two posterior glabellar lobes with the fixed cheek is evident (Pl. 3, figs. 1-4). In Plate 3, figure 2, however, the depressed dorsal furrow separates the glabellar lobe from the fixed cheek on one side, but on the other side the depression is only slightly indicated and the "confluence" is nearly complete. In a single specimen it is an irregularity; within a species a certain variability of the furrows and glabellar lobes is thus indicated. It is also noted that the test is thickest in the furrows and that exfoliated cranidia usually

have the furrows clearly indicated. In flattened specimens the furrows become accentuated and a former confluence of lobes on the surface cannot be definitely recognized.

The importance of flattening and exfoliation can be assessed from comparison of the specimens Plate 1, figure 1 (*R. forresti*, flattened), Plate 3, figure 1 (*R. forresti*, not flattened), and Plate 3, figures 5-7 (*Redlichia* sp. c, exfoliated only). The latter shows only indications of the two anterior pairs of glabellar furrows on the steinkern; consequently those furrows were not visible on the surface of the test. A confluence of the palpebral lobe with the frontal lobe was probably present. The dorsal furrows are nearly of even depth. The species (*Redlichia* sp. c) is clearly different from *R. forresti*, and the difference is accentuated by the greater curvature of the palpebral lobes and by proportions.

If this cranidium were flattened in shale, the manifestation of its dorsal and glabellar furrows would be the same as in the flattened specimen of *R. forresti* (Pl. 1, fig. 1), and a specific discrimination would be less reliable. The dorsal furrows in *R. forresti* (Pl. 3, figs. 1-4), as seen in the non-flattened specimen, have an up-and-down course, different from the specimen of *Redlichia* sp. c (Pl. 3, figs. 5-7). This course is levelled out by compression in the flattened specimen, consequently flattening and exfoliation render the cranidia unreliable for diagnosing: specimens of different species may seem to be identical, and a single species may be split when results of mechanical deformation are mistaken for organic structures. This is all common knowledge that should be applied in the taxonomy of *Redlichia* as well.

R. forresti (pl. 3, figs. 1-4) has a slightly carinate glabella owing to a median spine-shaped elevation extending from the second to the first glabellar lobe. It is definitely not a spine, being only an elevation of the test; but it may represent the vestige of a spine homologous with the other axial spines, and, perhaps, with the true axial spine of the frontal lobe of the glabella of *Olenellus hermani* Kindle & Tasch (1948). It may even be the result of coalescence of vestiges of several glabellar spines. The vestige of the glabellar spine, the larger first segment of the thorax with its node, and the two other axial spines, show a fair merocyclism (Raw, 1953) of distribution.

The rostral shield is quite different from that of the olenellids. Instead of the crescentic piece reaching nearly to the genal angles, suggested by Whitehouse (1939, p. 192), it does not extend into the doublure of the cheeks at all. From Text-figure 3, and Plate 2, figures 2 and 4, it is evident that the subcephalic extensions of the facial sutures cut the doublure beneath the wings of the frontal limb of the cranidium, and that the wings themselves overlap the doublure of the cheeks, and therefore the rostral shield is definitely narrower than the

frontal limb. Schindewolf (1955a) has observed a similar structure in *R. noettingi*. Isolated rostral shields of *R. forresti*, *R. idonea*, and other, undescribed, species have an even, clean-cut frontal edge, and isolated cranidia show a similar edge along the frontal margin. Moults of *R. idonea* are observed (Pl. 4) in which the hypostoma and the rostral shield form a fused unit resting in situ, whereas the cranidium is pushed aside. The front of the cranidium and the rostral shield in the same moult reveal clean-cut edges corresponding to the rostral suture. Thus the rostral suture, sub-marginal to the cranidial front, exists in *Redlichia* as well as in the olenellids. A nearly complete rostral shield of *R. mansuyi*? Resser & Endo has been illustrated by Kobayashi (1944, Pl. 8, fig. 9), where the true course of the subcephalic part of the facial suture is shown (left side). It is the same as in *R. idonea* (Pl. 4, fig. 2). The rostral shield of *Redlichia* can be best compared with *Paradoxides*, e.g. *P. pinus* Westergaard (1936, Pl. 6, fig. 15).

On the ventral surface, the posterior border of the rostral shield of *Redlichia* is densely stitched with a row of pits (Pl. 5; Pl. 6, fig. 5), which corresponds to inwardly directed spines. On the dorsal surface, along the internal surface of the frontal marginal furrow, another row of spines is present, which on the outer surface is usually reflected as a row of pits with a "plug" in the centre. The points of the spines of the dorsal test seem to have each a socket to accommodate the points of the opposing spines of the rostral shield: the rostral shield is then interlocked with the cranidium. Obviously, the soft part of the head enclosed between the shields was perforated by a corresponding row of lacunae (Text-fig. 6).

The stitched rostral shield is also known in some Olenellidae, e.g. in *Wanneria* (Walcott, 19, 10, Pl. 10, fig. 6) and in several other Cambrian and Ordovician trilobites. A similar organization occurs in *Xystridura*. The facial sutures of *Redlichia* would normally be adequate for moulting, but the trap of the interlocking spines makes an extra provision for successful moulting necessary—in this case the rostral suture which cuts off the trapping piece altogether.

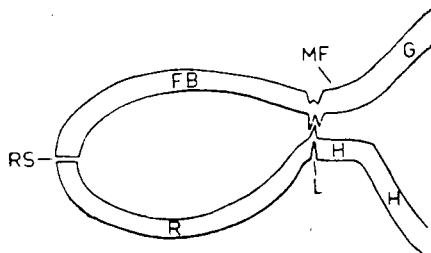


Fig. 6.—*Redlichia*, vertical section through frontal border (diagrammatic; greatly enlarged). FB.—frontal border of cranidium; G.—glabella; H.—hypostoma; L.—interlocking spines and lacunae of soft parts; MF.—marginal furrow; R.—rostral shield; RS.—rostral suture.

An unusual interpretation of the subcephalic structure of *Redlichia chinensis* has been put forward by Kobayashi & Kato (1951, p. 124). It seems that the structure described there as "the so-called hypostoma support or attachment or rostral plate of some authors" is the expanded frontal part of the hypostoma with its lateral wings, an integral part of the hypostoma, and is "fused with the doublure", i.e. with the rostral shield. And the "median doublure" in the terminology of the authors is the rostral shield itself.

The term "rostral shield" designates that part of the cephalic doublure that becomes a unit of the test when cut by sutures. "Rostrum" has been used in the literature for this piece interpreted as an axial element, and a segment. No evidence has been observed in support of an axial nature of the rostral shield. Morphologically it is pleural doublure, the ventral part of the border, similar to the border of the pygidium. In all trilobites the sutures are confined to the pleural lobe; the axial lobe is not involved, and no reason exists for assuming that the sporadic subcephalic sutures ever cut the axial lobe. Using Raw's terminology, in the prot-arthropod the prostomium and the persistome (axial elements without pleurae) were subretroverted. After this had happened the pleurae of the third segment (the foremost segment with pleurae) became medially fused to form a "brim". The doublure of that brim became the potential rostral shield. The fusion of the hypostoma and the rostral shield (doublure) is no evidence for the axial nature of the rostral shield. All axial parts of the tergum are surrounded by pleurae.

The hypostoma of *Redlichia* has two pairs of posterolateral curved spines or barbs. Amongst the Olenellidae *Holmia* has a quite similar hypostoma. The general structure of the hypostoma of *Redlichia* is that of any other trilobite; it has wings, a marginal furrow, a border with a doublure, an anterior (central) lobe and a posterior lobe. Maculae are present also. All the interpretations of the nature of the trilobite hypostoma are also applicable to the hypostoma of *Redlichia*.

Raw (1953), p. 115) follows the most popular view in regarding the hypostoma as the test of the subretroverted "prostomium complex", i.e. a tergite in a secondary ventral position with its front and rear exchanged. Raw rejects the Richters' interpretation of the hypostoma as the sternite of the second (in Raw's enumeration) glabellar lobe. In Richters' interpretation the front and the rear of the hypostoma are in the normal position. No definite evidence favours the tergite nor the sternite interpretation, except for the requirements of the theories, and the possible homology with the labrum.

Gill (1949) has summarized the reasons that support the tergite nature of the hypostoma. He is right in concluding that the hypostoma is an axial structure and that it has no pleural elements involved. Consequently, the absence of pleurae in the "prostomium complex" of Raw is considered also. The axial nature of the hypostoma is, however, not yet the evidence that it is the subretroverted extension of the axis and that the frontal lobe of the glabella is continuous with the anterior border of the hypostoma. The frontal "brim" with its doublure is "pleurae" that separate the hypostoma from the front of the glabella. The assumption that the frontal doublure (rostral shield) is a segment and, consequently, axis is a requirement of the particular theory and has no morphological support, other than as the next link in the chain of assumptions, e.g. that a part of the axis was transformed into pleurae. It seems also unlikely that pleural elements of the brim and doublure have divided the axis in two parts before the subretroversion and disrupted its continuity. It is, however, probable that the axial hypostoma is a sternite that postdates the subretroversion and the formation of the brim with its doublure and sporadic rostral shield.

A third interpretation—a modification of the sternite hypothesis—is possible: the hypostoma was formed by the fusion of a pair of cranial appendages. They could be the appendages of the fifth glabellar lobe (Raw's second) that are believed to be missing in the trilobite head altogether, or parts of the appendages of the antennular segment (the sixth counting from the rear; AI in Öpik, 1937), with the "anterior pits" as the appendiferi. The anterior pits are the pair of apodemes that also support the wing extremities of the hypostoma. The antennae(-ulae) in trilobites are uniramous and may not represent complete appendages. Raw (1955, pp. 735, 736, 748) thinks that the missing appendages "became reduced, and enclosed in an extension of the alimentary canal". The reduction happened "under cover of the labrum, which as the hypostoma is well developed". Thus, either the missing appendages are preserved as vestiges in the proventricle under its test (hypostoma), or the hypostoma, being itself the test of the proventricle, represents the modified appendages.

The appendiferi of the segments of the thorax of *Redlichia* are normal, developed as dorsal pits or internal elevations at the anterior angles of the axial rings (compare *Ceraurus aculeatus*, or *Reraspis*, in Öpik, 1937). In the thorax of *Redlichia* (Pl. 1, fig. 6), they are clearly visible. In the pygidium of a female *Redlichia* (Pl. 1, fig. 5; Text-fig. 5), however, three pairs of large oval swellings on the flanks of the axis represent the appendiferi. This is in contrast to other trilobites, where the structure of the appendiferi is uniform in pygidium, thorax, and neck segment, and, usually, in the posterior segment of the glabella. The pygidial appendiferi of *Redlichia* may be compared with those of *Phalacroma glandiforme* (Angelin) in Westergaard (1946, Pl. 16, fig. 2).

The external ornament of *Redlichia* consists of lines, granulation arranged in lines, and faint scattered granulation. Some species are nearly smooth, however, and in the ornamented forms the ornament is not persistent over the whole test. For example, *R. forresti* seems to have a nearly smooth test, whereas *R. idonea* is lineate with a fingerprint pattern on the glabella. It is observable that the presence of the ornament depends on the state of preservation, and its absence in specimens of one locality, or in some specimens of another locality, is no sure indication that these tests were originally smooth. The neck spine, here regarded as an "ornament", consists only of a small marginal point and is mostly absent altogether. Its specific value is small: for example, in *R. idonea* some specimens have such a spine, but most have none.

"Facial lines" (Pl. 4, fig. 2; Pl. 5; Pl. 6, figs. 1, 7), which run along the anterior branches of the sutures on the frontal limb (brim), may or may not be present in specimens of a single species. This instability is the reason why these lines are regarded here as ornament. Whitehouse (1939) has observed the lines in "*Mesodema*" *venulosa*. The lines are straight and slightly elevated and terminate in the marginal furrow, which is shallow at the terminations. On both sides of the termination, however, a shallow pit is present. Comparable lines occur on the pleurae on both sides of the pleural furrow (Pl. 6, figs. 4-6). The lines on the pleurae and the facial lines may represent vestiges of similar organs. The facial lines, consequently, may indicate the position of pleural elements within the otherwise fused cephalon.

The facial lines commonly start at the suture near to the palpebral lobe, as seen in illustrations of "*Mesodema*", and are not connected with that lobe. The suture, in such cases, cuts the facial line and the pleura it represents (Pl. 6, fig. 1).

All sufficiently well-preserved specimens of *R. idonea*, and two specimens of *R. chinensis* collected at Yelvertoft (Queensland), show the facial lines. In some specimens of *Redlichia* (Pl. 5, fig. 1), however, the facial lines start near the frontal end of the palpebral lobe, as stated by Whitehouse to be the case in "*Mesodema*", and are not cut by the suture. A published example is *R. carinata* Mansuy (1912). A specimen of *R. noetlingi* illustrated in Schindewolf (1955b, Pl. 6, fig. 5) shows a similar facial line.

The two posterior glabellar lobes may be clearly separated from the fixed cheek by the dorsal furrow, or may exhibit various degrees of confluence with that cheek.

The doublure of the thoracic segments is normal as in other trilobites. It is relatively short, with an asymmetrical shallow sinus, the deepest point of which lies behind the middle, just at the external end of the pleural furrow.

It is ornamented, or perhaps fortified, by faint irregular terraced lines running only approximately parallel to the inner edge of the doublure.

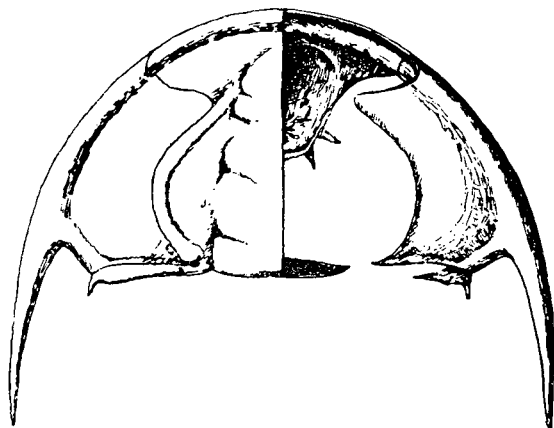


Fig. 7.—*R. forresti* (Eth. Jr), reconstruction of head. Right half of cranidium removed to show position of hypostoma, course of sutures, and posterior doublures. Clean-cut edge of front represents rostral suture. Relationship and function of pits and spines along marginal furrow and posterior border of rostral shield explained in Text-figure 6. Doublure of neck-ring (articulation half-ring) and doublure of posterolateral limb left in situ; latter cut off by posterior branch of facial suture. Note small size of hypostoma. Details of internal face of hypostoma unknown; possibly connected with cranidium by a protuberance in front of anterior glabellar furrow. Such connexion not shown in reconstruction.

The concept of the genus *Redlichia* can be summarized as follows:—

Olenelloid trilobite, but with normal (non-olenelloid) complete facial suture, a rostral suture, and a normal rostral shield shorter than the frontal limb of the cranidium. Glabella long and tapering forward. Glabellar furrows shallow; the posterior one may cross the glabella. Occipital furrow also shallow, with slightly deeper appendiferi at its ends. Palpebral lobes long, with their extremities, in adult specimens, almost reaching the dorsal furrows. Eye-lines absent in adults. Free cheeks wide with advanced genal spines and acute genal angles. Posterolateral limbs repeating the structure of the posterior half of the thoracic pleurae and, in some species, also with advanced "intergenal" (pleural) spines. A short marginal occipital spine present in some species.

Thorax of 14 to 17, perhaps 18, segments, gradually decreasing in width in the caudal direction. Pleurae with terminal spines, advanced on the anterior, and falcate on the posterior, somites. Dorsal axial spines often on the fourth, and regularly on the eleventh or twelfth, segment. No differentiation into pro-thorax and post-thorax is evident.

Pygidium small (about 1/15 to 1/17 of the total length of the trilobite), of perhaps three segments. Sexual dimorphism reflected in the occurrence of two different designs of the pygidia. Female pygidium with narrow depressed flanks and arched posterior margin; axis reaching

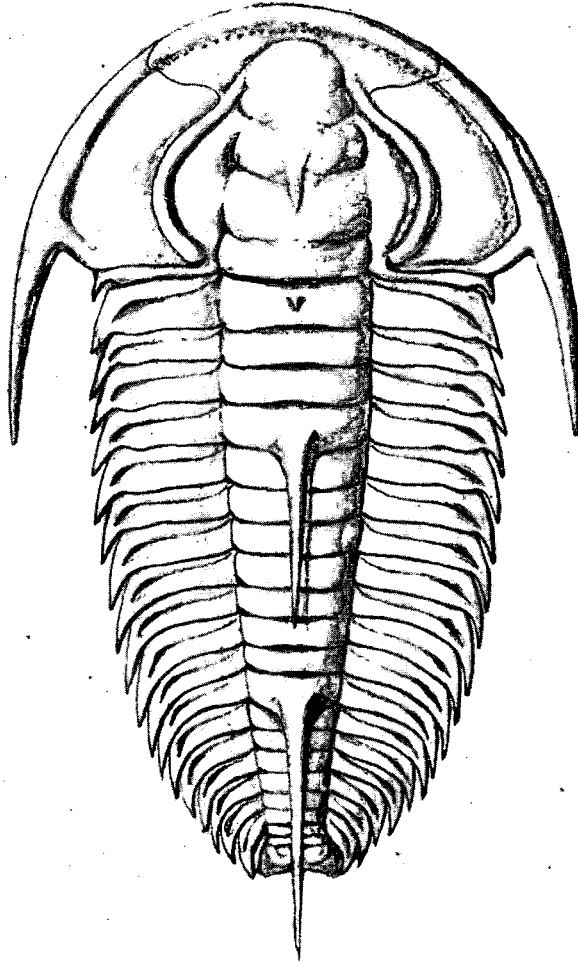


Fig. 8.—*R. forresti* (Eth. Jr), reconstruction based on specimens Plate 1, figure 2, and Plate 3, figures 1-4. Postulated telson omitted. Dorsal spines perhaps not so strong at their bases as shown here. First ten pleurae slightly flattened.

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posterior margin, and doublure not developed in centre. Male pygidium with continuous elevated border, wide annulated axis, normal continuous doublure.

Hypostoma olenelloid in shape, with two pairs of lateral spines, is fused to the rostral shield. Posterior border of the rostral shield with a row of inwardly directed spines, corresponding to similar spines in the frontal marginal furrow.

The relationship of *Redlichia* with other genera of olenelloid trilobites is significant. No particular genus can be named with which *Redlichia* can be compared in most of its characters. The "redlichoid" features seem rather to be distributed unevenly among various Olenellidae; or, perhaps, *Redlichia* is composed of various characters of diverse olenelloid forms. Thus the pygidium, of the female form of *Redlichia* is nearly identical with the caudal shield of *Holmia kjerulfi* (Linnarsson); so is the hypostoma. The posterolateral limbs may be compared with those of *Holmia*, or better perhaps with the extra-olenellan *Zacanthoides*. *Callavia* and *Holmia* have a comparable number of thoracic segments. The development of the dorsal spines recalls *Olenellus*. The glabella is best compared with *Nevadia*, *Nevadella*, and *Callavia burri* Walcott. *Redlichia* has a spinose border of the rostral shield in common not only with *Wanneria*, but also with the paradoxidid *Xystridura* and several other unrelated trilobites. The completeness, though not the exact course, of the facial suture and the size of the rostral shield lead *Redlichia* out of the cluster of olenellids towards *Paradoxides* and the majority of the Opisthoparia.

As it occurs in the lower Middle Cambrian, and in the upper Lower Cambrian, *Redlichia* obviously cannot be the ancestor of the more ancient Olenellidae or the contemporaneous Paradoxididae and Zacanthoididae. But amongst all the trilobites mentioned above *Redlichia* has preserved the greatest number of ancestral characters and is therefore the most primordial or primitive of them. *Redlichia* is the nearest to the roots from which the other, more specialized, olenellids originated.

SOME ASPECTS OF THE TAXONOMY OF *REDLICHIA*.

A satisfactory taxonomy of the species of *Redlichia* is difficult owing to the imperfect preservation of most of the material. The species as yet described may include some synonyms, and some material regarded as a single species may be composite. Thus, the Yelvertoft material is mostly regarded as *R. idonea* Whitehouse. However, within this assemblage specimens of similar size and similar proportions may differ one from one another in several characters. Some cranidia have a neck spine that is missing in others. The curvature of the sutures and the arrangement of the spines of the thorax show variations. The ornament varies in pattern and intensity and may even be nearly absent. The possibility exists that specimens attributed to *R. idonea* may belong to several closely related forms.

Saito (1934) grouped the Korean species of *Redlichia* according to the angle formed by the sagittal line and the anterior branch of the facial suture of the cephalon. Depending on the species (or group of species), this angle varies from 20 to 90 degrees and is a good criterion. The angle depends on two factors: (1) the width of the frontal limb: the wider it is the larger is the angle (this is the main factor); and (2) the length of the frontal limb and frontal part of the glabella: the longer these are the smaller will be the angle.

Another arrangement can be based on the ratio of the width of the frontal limb (measured between the frontal ends of the cephalic sutures) to the total length of the cranidium. The accuracy of the ratio is, however, influenced, within certain small limits, by the mode of preservation. Flattened cranidia show a slightly higher figure than less compressed ones. The ratio tends to increase with increasing size of the specimens.

In *R. noettingi* (the type species), this ratio is about 1.0, which means that the cranidium is as wide as it is long. *R. nobilis* Walcott, *R. forresti*, *R. idonea* (1.0-1.1), *R. mansuyi* Resser & Endo, and *R. murakamii* R. & E., belong to the same group. Most probably, *R. carinata* Mansuy (1912) should also be included here.

Hupé (1952) has placed *R. carinata* and *R. mansuyi* (with a query) in his new genus *Pararedlichia*. Consequently, he regards the two species as congeneric. *R. mansuyi*, however, is well preserved and is beyond doubt a genuine *Redlichia*, close to the type species. *R. carinata* is represented by distorted cranidia only; it is, however, a *Redlichia* with long posterolateral limbs and a facial line and may be related to *R. idonea* and *R. murakamii*. *Pararedlichia* (*P. pulchella* Hupé) is known only from cranidial fragments. It may be a redlichiid with a short triangular posterolateral limb and therefore generically distinct.

R. chinensis has a ratio of about 1.4 and represents a group of forms with a visibly very wide frontal limb. *R. manchuriensis* Resser & Endo and *R. longispina* Kobayashi have a slightly narrower frontal limb.

R. coreanica Saito, with a ratio of about 0.7, has a visibly narrow frontal limb. Otherwise it corresponds to the generic concept.

R. cf. walcotti Saito (1934) has a ratio of about 1.2 and is intermediate between *noettingi* and *chinensis*. It differs by its plump glabella from all other species. Its free cheek showing the advanced spine and the long posterolateral limb is typical. The specimen is probably shortened longitudinally, and hence the apparent curvature of the palpebral lobes is increased and the glabella appears to be "shorter and wider". Hupé (1952) renamed this specimen *Latiredlichia saitoi* Hupé n.gen., n.sp. and selected it as the type of his new family, Latiredlichiidae. They are synonyms of *Redlichia* and Redlichiidae.

R. walcotti Mansuy (1912) is known from a number of cranidia, which may not be all conspecific; figures 4c and 4d, Plate III., in Mansuy represent a genus different from *Redlichia*. Hupé selected, however, Mansuy's figure 4g to illustrate his new genus *Saukiandops* with *R. walcotti* as type species. The

material allows no definite diagnosis in relation to *Redlichia*. It includes two cranidia on one slab, and a type has not been selected. *Saukiandops* is a latiredlichiid according to Hupé. It may be, indeed, very near to *Pseudosaukianda lata* Hupé, whose redlichiid relationship is doubtful. *Pseudosaukianda* and *Longianda* seem to have a bathyuriscid organization, but they differ from other bathyuriscids in their greater number of thoracic segments.

Hupé (1952, p. 203), in discussing the similarity of *Longianda* to the Corynexochidae (bathyuriscids), regards it as homoeomorphism, because *Longianda* has fifteen segments in the thorax and resembles *Redlichia*, whereas the bathyuriscids have eleven or less. The number of segments in the thorax is, however, irrelevant, because the bathyuriscids have large pygidia retaining several segments that can be interpreted as parts of the thorax of earlier and less "caudalized" forms. *Longianda* and *Pseudosaukianda* are multisegmented bathyuriscids and their affinity with *Redlichia* is remote.

Of course, *Redlichia* itself may be excluded now from the rest of the superfamily Redlichioidea (in Hupé's sense) and transferred to the Olenelloidea. Even then, *Longianda* and *Pseudosaukianda* cannot be left with the "Redlichioidea without *Redlichia*". Polymerid trilobites cannot be classified by the number of segments of the thorax, when other morphological features are ignored and dismissed as homoeomorphism. On the contrary, similarity of the number of segments and multisegmentation, which occur in genera of diverse trilobite stocks, are better examples of homoeomorphism. Swinnerton (1915, p. 495) writes: "the use of the number of free segments and the size of the pygidium as the definite characters of orders or sub-orders results in the bringing together of forms which belong to quite different lines of descent". One should remember that the suborders of Swinnerton became superfamilies subsequently.

Neoredlichia Saito (*R. nakamurai* Saito) is well enough preserved to see that it is not a genuine *Redlichia*: the frontal limb is very narrow, the postero-lateral limb is short, and the genal spine is in the normal position, not advanced, and slightly deflected. It may be a subgenus of *Redlichia*, or a separate redlichiid genus, or may represent another family, the Neoredlichidae Hupé. The scarcity of material makes the Neoredlichidae a "forecast" term to be proven by further research.

Mesodema venulosa Whitehouse (1939) is doubtless a redlichiid trilobite. The only described specimen is an external mould of an imperfect cranidium. It is laterally and symmetrically compressed. It differs from *R. nobilis*, or *noetlingi*, or *idonea* by the palpebral lobes' arising directly from the frontal lobe of the glabella, and the continuity of the second glabellar lobe with "post-ocular portions of the fixed cheeks". The "continuity of the lobes" or the confluence of the glabellar lobes with the fixed cheek is, I think, variable within a species and may be of no generic value. Lateral compression may have accentuated the confluence of lobes in the type specimen of *Mesodema venulosa* as well. *Redlichia* sp. d (Pl. 6, fig. 8), also from Yelvertoft, shows the confluence of the palpebral lobe with the frontal lobe of the glabella, but lacks all the other

characters of a *Mesodema*. This specimen differs from *R. idonea* by the greater distance of the palpebral lobe from the neck-ring. Another specimen of the same species (Pl. 6, fig. 7) shows a *Mesodema*-like "facial line", but a confluence of lobes is not apparent.

It has been indicated above that the dorsal furrows of the cranium are better developed inside the test, as seen in exfoliated specimens; compressed specimens show the furrows more clearly than uncompressed ones. *R. forresti* (Pl. 1, fig. 1) is flattened, but its test is preserved. Its dorsal furrows are still visible. The uncompressed cranium of the same species (Pl. 3, figs. 1-4) shows the continuity of the second glabellar lobe with the "post-ocular portions of the fixed cheeks", although to a lesser degree than does the external mould of *Mesodema* illustrated by the Whitehouse.

"Facial lines" (see above, p. 31) cannot serve to separate *Mesodema* from *Redlichia*.

It seems that *Mesodema venulosa* is a *Redlichia* related to *R. idonea* and *R. forresti*. *Redlichia venulosa* (Whitehouse) differs from *R. idonea* in having a venulose ornament, a deeper occipital furrow, a pointed edge of the occipital lobe, and a more slender glabella (Pl. 6, figs. 1-3).

The specimen (Pl. 6, fig. 1) attributed here to *R. venulosa* (Whitehouse) differs from the type specimen by the absence of confluence of the lobes. But it is exfoliated to an extent that renders it impossible to detect the original structure. The foreshortened photographs (Pl. 6, figs. 2, 3) taken at the same angle as the illustration by Whitehouse (1939, Pl. 19, fig. 1) reveal a similarity in proportions to the type of *venulosa*. Our specimen, however, is not laterally compressed and therefore appears to be plumper.

CONCLUSION.

This paper deals with the anatomy of Australian *Redlichiae*. The taxonomy is reserved for the future. Some of the illustrated specimens already may suggest new specific, or even generic, names, although a conservative approach seems to be more warranted at the present state of knowledge. Unfortunately some of the specimens illustrated here were destroyed by a fire and cannot be selected as holotypes.

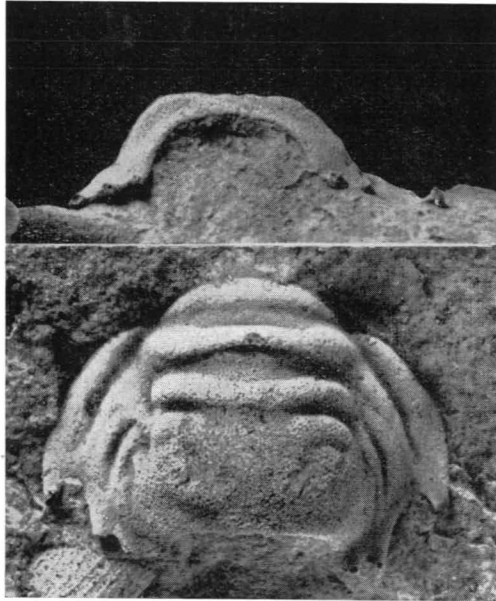


Fig. 9.—*Redlichia* sp. *a*, pygidium, Gum Ridge Formation, Northern Territory, x4.—Rubber cast representing external surface of test. Rear view (above) shows arched opening. Specimen (as usual) asymmetrical: four spines on left and three on right flank. A “spur” extends from left anterior pleura over upper part of next pleura and joins axis. Transverse furrow of second segment widened and showing articulation half-ring. (CPC 930.)

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PLATE 1.

All are female specimens (except figure 1) according to pygidial structure.

1. *Redlichia forresti* (Etheridge, Jr.), two cranidia in calcareous shale, Negri Group, junction of Linnekar Creek and Brook Creek, Western Australia, x 2. Posterolateral limbs missing; their structure apparent from Plate 2, figure 4, and Text-figure 3. CPC 923.
2. *Redlichia forresti*, locality and bed as in figure 1, x 2. Twelfth segment with dorsal spine missing; base of dorsal spine on fourth segment preserved. Cranidium has preserved posterolateral limbs only; structure of cranidium evident from figure 1. CPC 922.
3. Same specimen as figure 2, x 4. Dorsolateral view of posterior segments and pygidium.
4. *Redlichia* sp. *a*, Gum Ridge Formation, east of Tennant Creek, Northern Territory, x 4. Internal mould of pygidium, with no doublure in middle. CPC 925.
5. *Redlichia* sp. *a*, locality and bed as in figure 4, x 6. External mould of another pygidium with lateral doublure preserved. CPC 926.
6. *Redlichia* sp. *b*, lower part of Gum Ridge Formation, east of Tennant Creek, Northern Territory, x 6. Posterior segments and pygidium, compressed in shale, show doublure exposed on right. No doublure at rear of pygidium. CPC 927.



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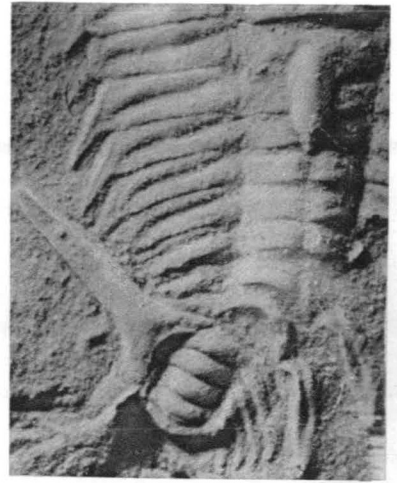
PLATE 2.

Redlichia forresti (Etheridge, Jr.), Negri Group, junction of Linnekar Creek and Brook Creek, Western Australia. All are male specimens (except figure 4) according to pygidial structure.

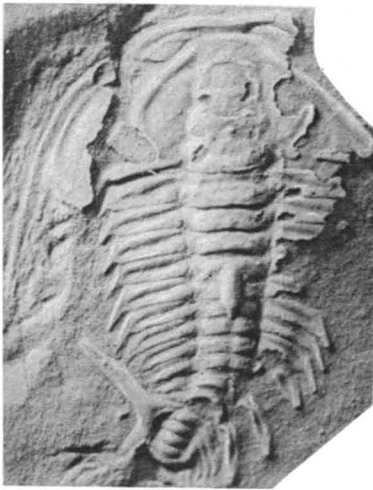
1. Pygidium and posterior segments, x 10. Bases of dorsal spines on fourth and twelfth segments are preserved. See also Text-figure 2. CPC 928.
2. Nearly complete specimen, longitudinally distorted by slumping, x 5. Twelfth segment (with dorsal spine) overturned. Frontal part of cranidium and posterolateral limb with intergenal spine preserved. CPC 924.
3. Same specimen as figure 2, but much enlarged, to show distortion (shortening) of pygidium.
4. Same specimen as Plate 1, figure 2, much enlarged, to show course of suture, anterior portion of doublure of free cheek, and posterolateral limb of cranidium with advanced intergenal (=pleural) spine and its doublure, which is cut by posterior branch of facial suture. See also Text-figure 3.



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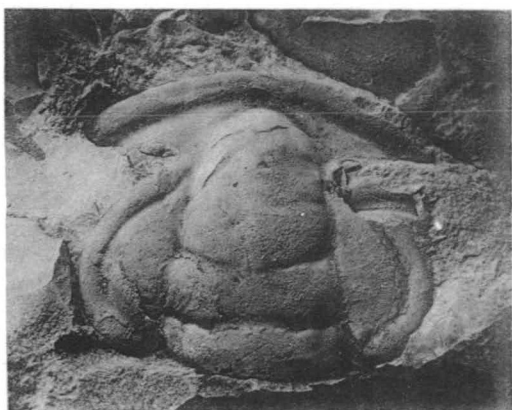
PLATE 3.

Two cranidia of similar age are illustrated.

- 1-4. *Redlichia forresti* (Etheridge, Jr.), cranidium in hard grey smelly lutitic limestone, junction of Linnekar Creek and Brook Creek, Western Australia, x 1.8 (about). Test intact. Different views illustrate "up-and-down" course of dorsal furrows and "confluence of lobes" developed to a different degree on right and left sides of specimen. CPC 2327.
- 5-7. *Redlichia* sp. c., cranidium in hard splintery chert, probably from Gum Ridge, east of Tennant Creek, Northern Territory, x 2 (about). Test completely dissolved. CPC 2328.



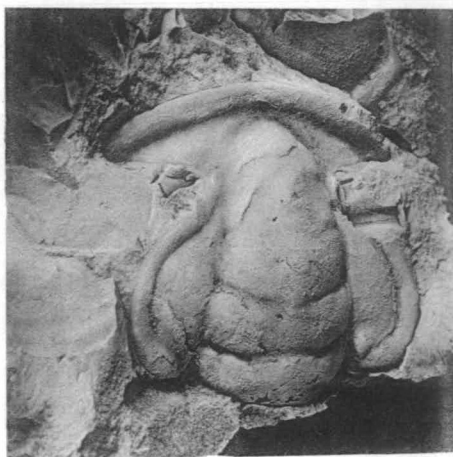
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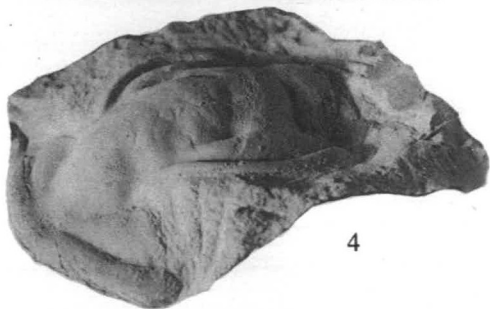
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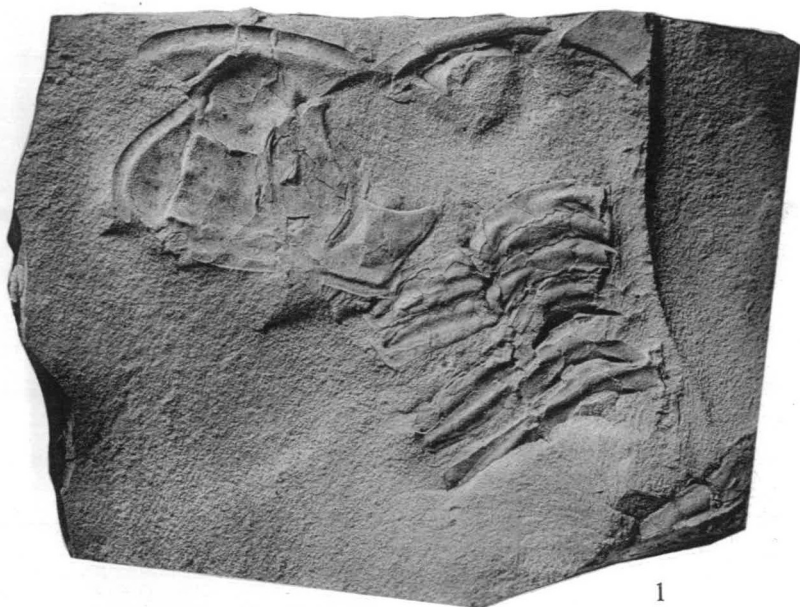
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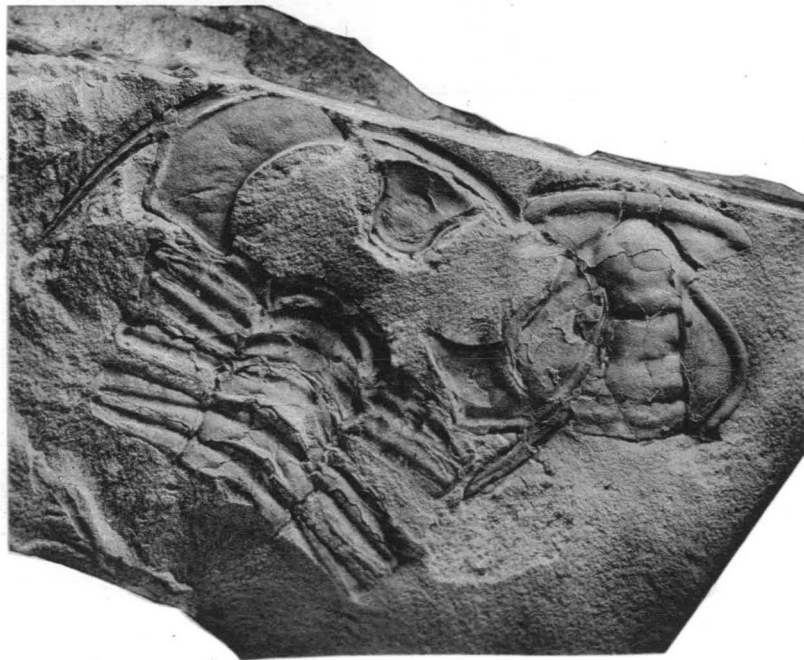
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PLATE 4.

Redlichia idonea Whitehouse, exuvia in hard white siliceous shale, Yelvertoft Bed, Hall's Memorial, Barkly Highway, Queensland, x 2. No test preserved. Hypostoma/rostral-shield unit and free cheeks nearly in original position; cranidium thrown sideways and on top of right cheek; three segments overturned, as is apparent from comparison of figures 1 and 2. Note facial lines on wings of frontal limb and lines on pleurae.
CPC 2329.



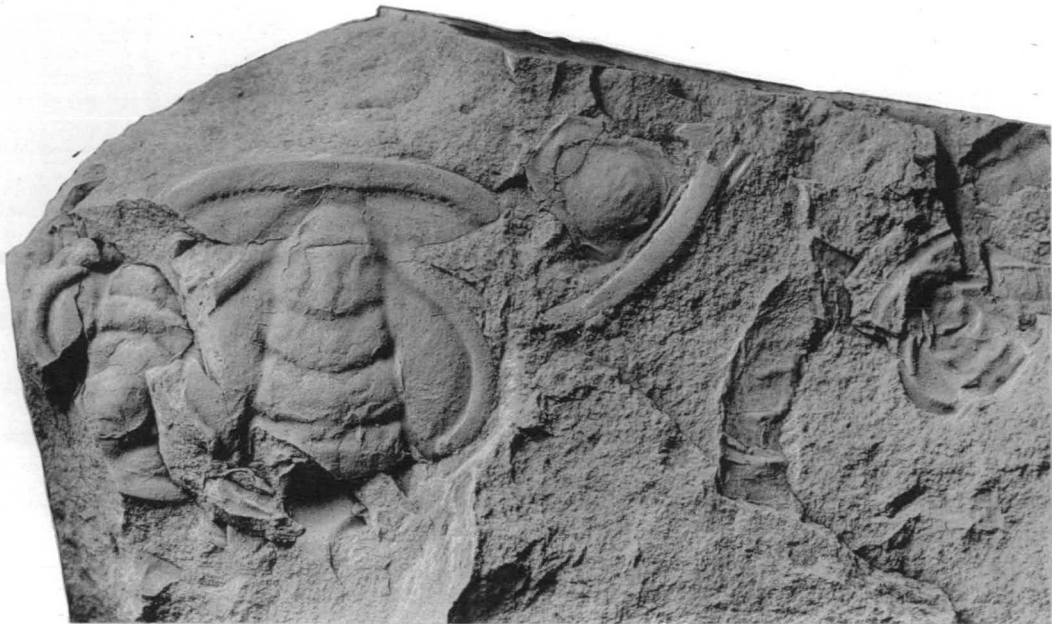
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PLATE 5.

Redlichia idonea Whitehouse, soft siliceous shale, Yelvertoft Bed, Hall's Memorial, Barkly Highway, Queensland, x 4. Cranidium and hypostoma/rostral-shield unit, probably fragments of a single individual. Note pits and spines in frontal furrow and along posterior edge of rostral shield. Frontal winged part of hypostoma, connected to rostral shield, is corrugated. CPC 2330.



1

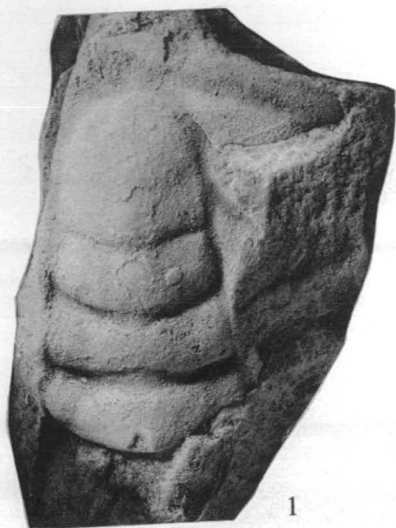


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PLATE 6.

All specimens from Yelvertoft Bed, Hall's Memorial, Barkly Highway, Queensland.

- 1-3. *Redlichia venulosa* (Whitehouse), cranidium in hard chert. Figure 1, x 3 (about). Figures 2 and 3, two differently foreshortened photographs taken to facilitate comparison with similarly foreshortened photograph of type specimen in Whitehouse (1939, Pl. 19, fig. 1). CPC 2331.
- 4, 5. *Redlichia idonea* Whitehouse, hypostoma/rostral-shield unit in hard siliceous shale. Figure 4, x 4. Note pits (corresponding to spines) along inner border of rostral shield and lines on fragments of pleurae. Frontal winged part of hypostoma is bent. CPC 2332.
6. *Redlichia* cf. *idonea*, portion of thorax, x 2. Note lines on pleurae. Segment with axial spine is eleventh segment. CPC 2333.
7. *Redlichia* sp. *d*, cranidium in hard siliceous shale, x 2. Note facial line, tubercle on edge of neck-ring, distance of posterior end of palpebral lobe from neck-ring, and lack of "confluence of lobes". CPC 2334.
8. *Redlichia* sp. *d*, cranidium in hard siliceous shale, x 2. Note absence of facial line. Confluence of anterior end of palpebral lobe and frontal lobe of glabella indicated but intercepted by an accidental depression. CPC 2335



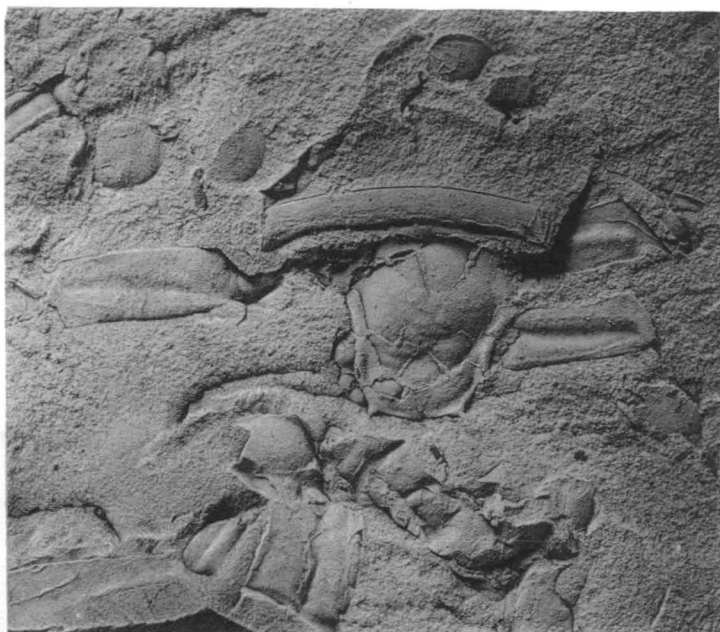
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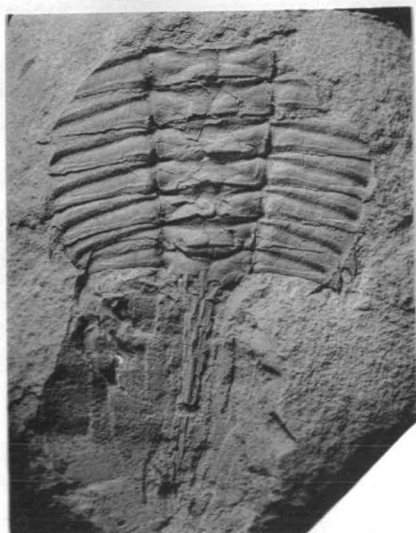
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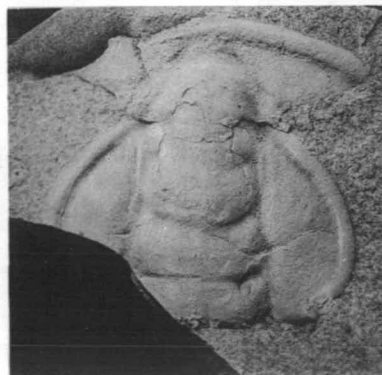
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