THE EMUELLIDAE, A NEW FAMILY OF TRILOBITES FROM THE LOWER CAMBRIAN OF SOUTH AUSTRALIA

by K. J. POCOCK

ABSTRACT. Study of the adult morphology and the ontogeny of a new group of trilobites from the Lower Cambrian of South Australia has led to the erection of 2 new genera, *Emuella* and *Balcoracania*, each with 2 species, which are considered to belong to a new family, here named the Emuellidae. The members of this family are characterized by a unique combination of cephalic and thoracic features; the cephalon possesses a complete set of functional sutures of the ptychopariid type, long crescentic eye lobes widely separated from the glabella, and a geniculate posterior border; the thorax is divided into a short prothorax, in which the 6th segment is macropleural and fused to the 5th, and an extremely long opisthothorax containing numerous segments. The family is here included in the suborder Redlichiina.

Study of the ontogeny of two of the species has allowed the cephalic development to be subdivided into stages, which are related, where possible, to meraspid degrees. The fused 5th and 6th segments are released as a unit into the thorax, and the macropleural spine of the 6th has not been observed in the transitory pygidium.

The formation of the opisthothorax results from an abrupt reduction of the space available for the pleurae of segments succeeding the macropleural segment. The macropleural segment serves the role of protection, aids stability, and in the larval stages possibly buoyancy; the fusion of this segment to the preceding assists in control of the former.

The Emuellidae are considered to preserve the structure of possible ancestors of the Olenellina on one hand, and the Redlichiina on the other.

THE trilobites described in this paper were first found by Dr. B. Daily of the Geology Department, University of Adelaide, on the western side of Cape D'Estaing, Kangaroo Island, South Australia (Daily 1956). Subsequently the author discovered a second locality on the eastern side of the Cape (Pocock 1964, p. 459). In 1961, Messrs. Dalgarno and Johnson, of the Geological Survey, South Australian Department of Mines, made a remarkable discovery of a similar trilobite, near Blinman, in the Flinders Ranges, South Australia. Further work by the author has located related trilobites in Kangaroo Island, and extended the known range of occurrence in the Flinders Ranges.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

The known occurrences of members of the group are restricted to Lower Cambrian rocks of the Adelaide Geosyncline. They are, however, widely separated geographically, one locality being in the eastern portion of the Flinders Ranges, and the others on the northern coast of Kangaroo Island, *c.* 350 miles away.

The Kangaroo Island localities are at Cape D'Estaing, approximately 12 miles W. of Kingscote (text-fig. 1). The fossiliferous beds occur in sections on either side of the Cape, outcropping on wave-cut platforms and in cliffs behind. On the eastern side, in the Emu Bay section of Pocock (1964), *Balcoracania dailyi* gen. et sp. nov. occurs in a zone, approximately 30 ft. thick, near the top of the White Point Conglomerate, in association with a species of *Estaingia*, *Hyolithes*, and an unidentified brachiopod; *Emuella dalgarnoi* gen. et sp. nov. occurs 250 ft. stratigraphically above, in a 2-ft. thick bed within the

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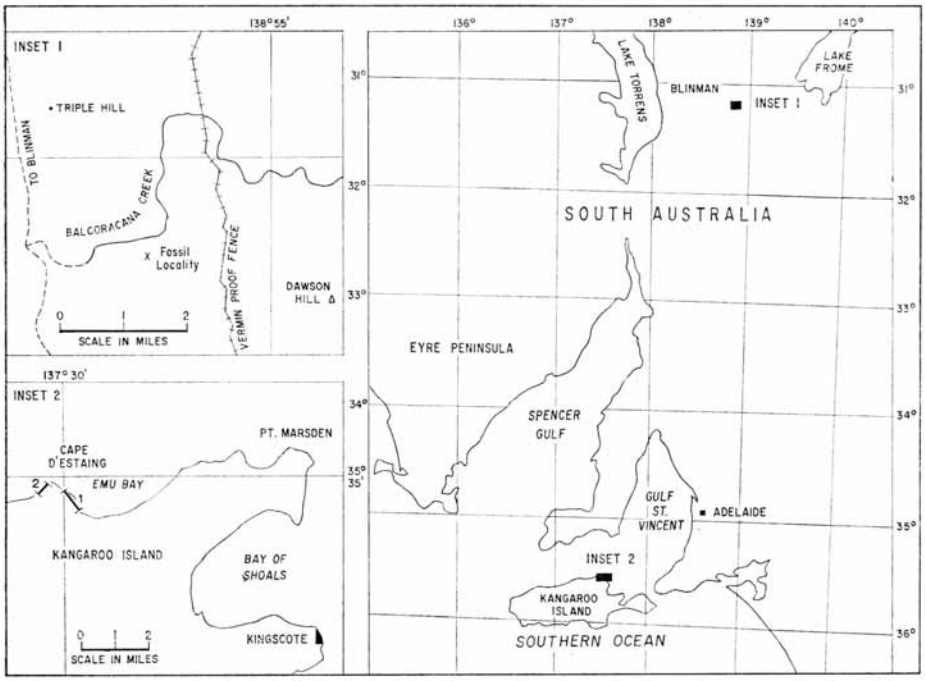
Emu Bay Shale and immediately above beds containing *Estaingia bilobata* Pocock and a species of *Redlichia* (Pocock 1964). On the W. side of the Cape, in a section which can be correlated in part with the Emu Bay section, *Emuella polymera* gen. et sp. nov. occurs in a thin bed near the base of the sequence, and *B. dailyi* occurs in the overlying 60 ft. All the fossiliferous beds at this locality occur in the upper part of the White Point Conglomerate (text-fig. 2).



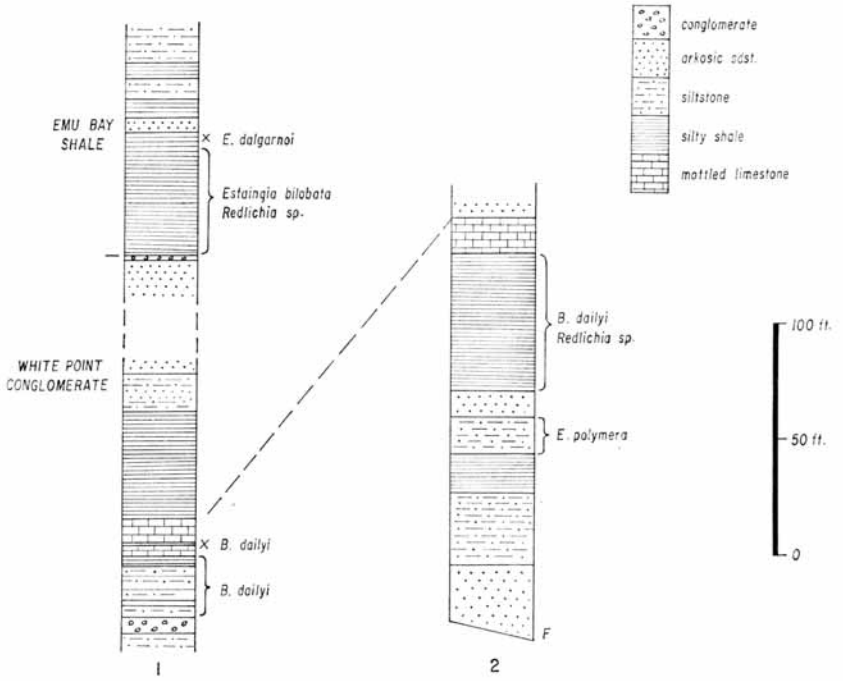
TEXT-FIG. 1. Locality Maps. *Inset* 1, Balcoracana Creek area, Flinders Ranges, South Australia. *Inset* 2, Kangaroo Island, South Australia; 1, Emu Bay section; 2, Cape D'Estaing section.

The Flinders Ranges locality (text-fig. 1) is at Balcoracana Creek, 14 miles ESE. of Blinman. Here *Balcoracania flindersi* gen. et sp. nov. occurs in a 30-ft. thick section of the Billy Creek Formation, approximately 500 ft. above the base.

The White Point Conglomerate and the Emu Bay Shale are considered to be upper Lower Cambrian. The evidence upon which this determination is based was reviewed by Daily (1956) and Pocock (1964).

The Billy Creek Formation is underlain by the Oraparinna Shale of middle Lower Cambrian age (Walter 1967), and overlain by the Wirrealpa Limestone, which Daily (1956) considered lower Middle Cambrian. The Billy Creek Formation at this locality is 3300 ft. thick, and the trilobites occur approximately 2800 ft. below the Wirrealpa Limestone and are thus probably upper Lower Cambrian.

At the present time it is not possible to correlate the Flinders Ranges and Kangaroo Island sections, so the stratigraphic position of *B. flindersi* with respect to the other species is not known.



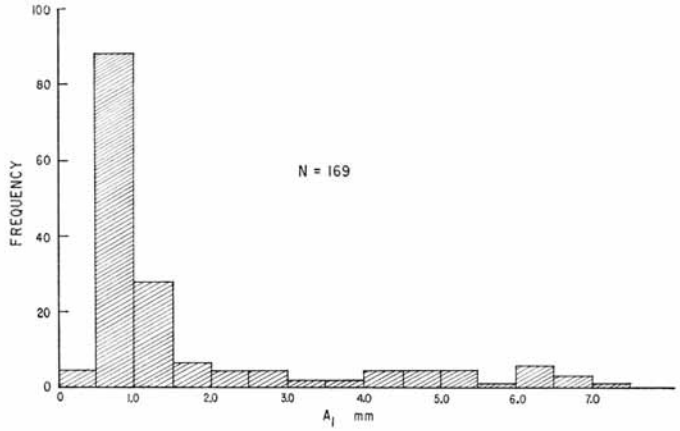
TEXT-FIG. 2. Stratigraphic columns; parts of the stratigraphic successions of Lower Cambrian age of Kangaroo Island, South Australia. 1, Emu Bay section; 2, Cape D'Estaing section.

MODE OF OCCURRENCE

At the Kangaroo Island localities, the trilobites occur on the bedding planes largely as disarticulated moults, interspersed with a few complete individuals. Both larval and adult specimens occur in the collections of *E. polymera* and *B. dailyi*, but only adults of *E. dalgarnoi* have been found. The trilobites occur in fine-grained siltstones or silty shales of slightly varying character.

In the Flinders Ranges, *B. flindersi* occurs in a sequence of greenish-brown tuffaceous shales. Specimens are rare for the greater part of the fossiliferous sequence, and are represented exclusively by moults; however one bed, about 4 in. thick, near the top is richly fossiliferous, one bedding plane being almost covered with complete individuals, both larval and adult. Such an occurrence, in a sequence of sparsely fossiliferous rocks in which only moults are found, combined with the tuffaceous nature of the shale, suggests that the assemblage results from mass mortality, perhaps associated with volcanic activity.

Mass mortality has been invoked many times to explain the nature of some fossil assemblages, and volcanic activity has often been suggested as the cause. Brongersma-Sanders (1957) reviewed this subject, and pointed out the necessity for care in invoking such a phenomenon. In this case, evidence independent of that provided by the presence of tuffaceous material, and the preponderance of complete exoskeletons, is available. The size frequency distribution of the specimens from the bedding plane (text-fig. 3)



TEXT-FIG. 3. Size frequency distribution of *Balcoracania flindersi*. Individuals collected from the Balcoracana Creek locality. A_1 is the cranidial length.

shows a large number of very small specimens compared to the large. Craig and Oertel (1966) constructed theoretical models for various populations, in terms of size and age frequency distributions, and pointed out that most fossil assemblages differ from theoretical models in the absence of large numbers of young (small) individuals. In addition, mass mortality results in a frozen size frequency distribution of a living population, in which small individuals will be very abundant. The size frequency distribution of *B. flindersi* thus approximates that of a living population in the high proportion of small individuals, and the assemblage probably resulted from mass mortality.

METHODS AND TECHNIQUES

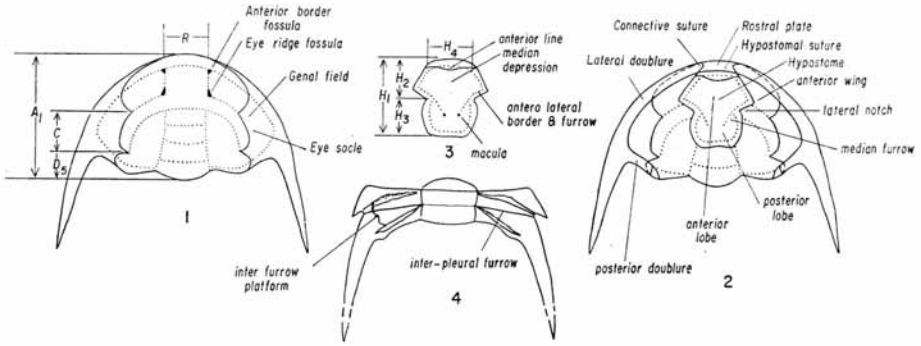
Reconstruction of distorted specimens. Although some degree of distortion and/or flattening is present in all collections, its range is limited and the number of specimens large enough for an accurate reconstruction to be made. Illustrations of reconstructed trilobites, both adult and larval, were made directly from photographs of selected specimens with the aid of a magnifying light table.

Quantitative analysis. A limited statistical analysis of variation has been made using mainly the methods of regression analysis recommended by Shaw (1956). However the parameters for the 'best fit' lines were calculated by the method given by Simpson, Roe, and Lewontin (1960, p. 234).

The measurements on which the analysis is based are given in the Appendix, and the dimensions used are shown in text-fig. 4.

Terminology. The terminology recommended in the *Treatise on invertebrate paleontology*, Part O, *Trilobita* (Harrington *et al.* 1959), is used with some modification, necessitated by the morphology of the trilobites described (text-fig. 4).

The term 'anterior fossulae' has been applied to small depressions in the axial furrows at or near the anterior edges of the glabella (Harrington *et al.* 1959, O120). In the trilobites described below, depressions occur in the axial furrows at their junctions with both the anterior border furrow and the anterior edge of the eye ridge; the term 'anterior furrow fossulae' is applied to the former, and 'eye ridge fossulae' to the latter. In larval forms the informal term 'cheek' is used, owing to the difficulty in distinguishing palpebral and posterior areas in very small specimens; 'cheek furrow' is used to describe



TEXT-FIG. 4. Dimensions measured, terminology, and ventral morphology. 1, Dorsal view of cranidium. 2, Ventral view of cranidium with hypostome in situ. 3, Ventral view of hypostome. 4, Dorsal view of macropleural unit. All diagrams based on specimens of *Balcoracania dailyi*.

a furrow extending onto the cheek from the junction of the axial and glabellar furrows. In the hypostome the terms 'anterior lateral border' and 'border furrow' are applied to the marginal portions between the anterior wing and the lateral notch. The terminology of Shaw and Ormiston (1964) is applied to the librigena. In the thorax, the 6th segment is macropleural and fused to the 5th; the term 'macropleural unit' is applied to this combination and 'interfurrow platform' to the area between the 5th and 6th pleural furrows.

In the systematic description and discussion, all angles are in the horizontal plane, are average values, and are given with reference to the sagittal direction unless otherwise specifically stated.

The widely used terms protaspid, meraspid, and holaspid stages are used. In view of the limited number of protaspides, no division of this stage is applied. Difficulties arise, however, in the application of the meraspid stage. The trilobites described have a short prothorax and an extremely long opisthothorax. Thus in the view of workers who consider the prothorax is homologous to the 'normal' thorax of other trilobites (e.g. Hupé 1953*a*, *c*; Harrington *et al.* 1959), the trilobites described below would have only 5 meraspid degrees, being considered holaspid on the appearance of the 6th (and last) prothoracic segment, with 50 or so articulating opisthothoracic segments still to be released. In addition, at degree 6 the cephalon is still far removed from the adult condition. On the other hand the cephalon does attain the adult condition, except for size, whilst a considerable number of opisthothoracic segments are yet to be released from the transitory pygidium.

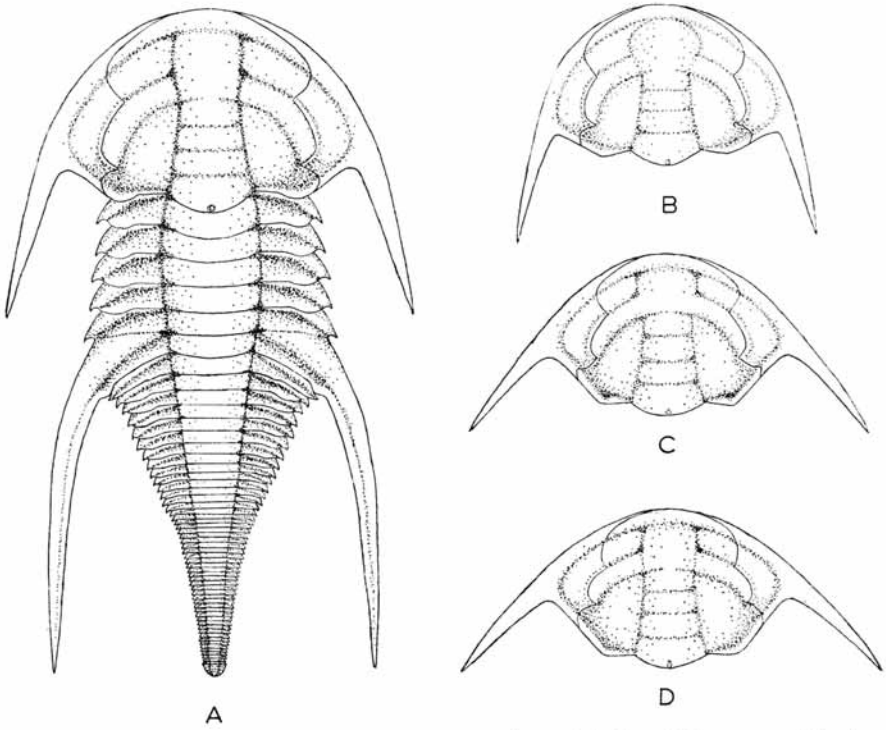
The above considerations illustrate that the usual divisions of the stages of larval development are not always easily applicable. If other cases become known in which cranidial development is completed before thoracic development, a formal division of the meraspid period on this basis may become justified. At present, however, in view of the small number of such cases, such a division does not appear justified.

SYSTEMATIC PALAEONTOLOGY

All specimens are deposited in the Palaeontological Collection of the University of Adelaide, South Australia (AUGD, F series).

Suborder REDLICHIINA Harrington 1959 (*in* Harrington *et al.* 1959)
Family EMUELLIDAE fam. nov.

Diagnosis. Small to medium opisthoparian trilobites. Glabella with 3 transglabellar furrows in adult; axial furrows converge from occipital ring to anterior glabellar furrow;



TEXT-FIG. 5. Reconstruction of adult morphology of members of the Emuellidae. A, complete dorsal exoskeleton of *B. dailyi*; B, cranidium of *B. flindersi*; C, cranidium of *E. dalgarnoi*; D, cranidium of *E. polymera*. Magnification × 10.

frontal lobe expanded, rounded laterally; preglabellar field narrow or absent. Eye ridge wide, long, directed slightly postero-laterally, palpebral lobe crescentic. Posterior area with fulcrum. Posterior border with section abaxial to fulcrum directed antero-laterally. Anterior section of facial suture diverges anteriorly to border furrow, curves sharply inwards and crosses anterior border diagonally, before becoming marginal-ventral; connective suture concave abaxially; rostral plate short (tr.), notched laterally; posterior

section of facial suture divergent; hypostomal suture functional. Hypostome with depressed anterior wings; median body with large subtriangular anterior lobe, subdivided anteriorly by median depression; small posterior lobe. Librigena with long genal spine.

Thorax with prothorax of 6 segments, and extremely long opisthothorax of between 42 and 55 segments. Sixth prothoracic segment macropleural and fused to 5th. Macropleural spine long, extends to level of pygidium. Pygidium a minute segmented disc, with border entire.

Discussion. The Emuellidae bear similarities to certain of the Olenellidae and Redlichiidae. The Emuellidae share with the Olenellidae the division of the thorax, and macropleurality; they differ in the number of segments and the fusion of prothoracic segments, and with regard to cephalic features in the possession of a complete set of functional sutures. The cephalic features are similar to those of some of the families of the Redlichiina, but the latter lack the characteristic thorax of the Emuellidae.

Genus EMUELLA gen. nov.

Type species. Emuella polymera sp. nov.

Plates 106, 107; text-fig. 5 C, D.

Derivation of name. From Emu Bay, Kangaroo Island, South Australia.

Diagnosis. Preglabellar field absent. Anterior border furrow shallows abruptly anterior to frontal glabellar lobe. Palpebral lobe relatively short, curved. Posterior border with section abaxial to fulcrum directed antero-laterally at 45° and slightly depressed. Librigena with advanced genal spine. Thorax with axis more than half thoracic width; pleurae very short. Pleural furrow terminates before pleural spine. Thorax with at least 48, and known maximum of 58 segments. Strong closely spaced granules on dorsal surfaces.

Emuella polymera sp. nov.

Plate 106; Plate 107, figs. 1, 2; text-fig. 5D.

Derivation of name. 'Polymera'—for numerous thoracic segments.

Holotype. AUGD F16643 (Pl. 106, fig. 1). It was considered essential that a specimen with an articu-

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EXPLANATION OF PLATE 106

Figs. 1–7. *Emuella polymera* gen. et sp. nov. White Point Conglomerate, Cape D'Estaing, Kangaroo Island, South Australia. 1, Holotype, F16653, ×10; internal mould of cephalon and thorax; cranidium sagittally compressed, librigenae rotated, macropleural spines incomplete. 2, F16643, ×14; incomplete internal mould of cephalon and thorax; posterior portion of opisthothorax missing. 3, F16645*a*, ×6; incomplete internal mould of cranidium; right posterior area asymmetrically distorted. 4, F16645*b*, ×6; counterpart of fig. 3, showing ornament of cranidium, structure of palpebral lobes. 5, F16648, ×9·5; internal mould of cranidium showing anterior furrow and eye ridge fossulae. 6, F16658, ×20; external mould of hypostome and attached rostral plate; rostral plate incomplete but anterior section of right connective suture can be seen. 7, F16647, ×9; internal mould of librigena showing the long posterior section of the facial suture, the changes in convexity of the genal field, and the widening of the doublure adjacent to the connective suture; the mould of the lateral border is incomplete and collapsed onto that of the doublure.

ated cephalon and thorax be chosen. Although isolated cranidia show some diagnostic features much better, they were not selected for the above reason.

Dimensions of holotype. Length of cranidium 2·8 mm.; palpebral width of cranidium 3·7 mm.; length of prothorax 1·6 mm.; over-all sagittal length of specimen 9·0 mm.

Material. Approximately 50 internal and external moulds, mainly disarticulated.

Occurrence. White Point Conglomerate, upper section of formation; on W. side of Cape D'Estaing, Kangaroo Island, South Australia.

Diagnosis. Axial furrows converge evenly from posterior edge to anterior glabellar furrow; furrows deep, distinct around slightly expanded frontal glabellar lobe. Glabellar furrows shallow, indistinct. Anterior cranidial border furrow almost transverse. Palpebral lobe short, highest at mid point, posterior end opposite middle glabellar furrow or lobe. Posterior border constant width, abaxial section directed antero-laterally at 40°. Posterior border furrow even depth. Anterior section of facial suture diverges anteriorly at 10°. Axial rings of prothorax rise sharply to posterior, with first 4 bearing sagittal, elongate nodes on posterior margin. Thorax with at least 48 segments.

Description. Cephalon subtrapezoidal in outline, gently convex (tr. and sag.). Cranidium gently convex (tr.). Glabella with 3 transglabellar furrows; axial furrows converge evenly from posterior margin to anterior glabellar furrow, diverge and curve around slightly expanded frontal lobe. Preglabellar furrow confluent with anterior border furrow, straight or slightly curved anteriorly. No preglabellar field. Glabella strongly convex (tr.), with slight median ridge extending to anterior glabellar furrow; gently convex (sag.), highest at anterior glabellar lobe, slopes down steeply to anterior border furrow, more gently to posterior. Occipital furrow transverse, or curves slightly to posterior, narrowest and deepest abaxially. Transglabellar furrows shallow and indistinct, posterior and middle furrows almost transverse, anterior furrow curves slightly forwards (Pl. 106, figs. 3, 4). Occipital ring approximately half mid palpebral cranidial width, widest sagitally; posterior edge curves outwards, half sagittal width projecting beyond margins of fixigenae. Length (sag.) of glabellar lobes decreases from posterior to anterior, but frontal lobe longest. Axial furrow slightly to deeply impressed below fixigena from posterior margin to eye ridge, rises and becomes indistinct over eye ridge, deeply impressed from eye ridge to anterior border furrow. Anterior furrow fossulae present at junctions of axial furrows and anterior border furrow (Pl. 106, figs. 3–5). Anterior border medium width, gently convex. Anterior border furrow almost transverse across cranidium (Pl. 106, fig. 3), moderately deep and narrow abaxially, shallows and broadens abruptly, anterior to frontal lobe (Pl. 106, figs. 3–5).

Eye ridge wide, long, gently convex, (tr. and exsag.), directed to posterior at 20° to transverse direction; anteriorly almost grades into gently downsloping frontal area, marked only by indistinct furrow, posteriorly slopes steeply down to distinct furrow continuous with palpebral furrow and aligned abaxially with anterior glabellar furrow (Pl. 106, fig. 4); degree of separation of eye ridge from frontal lobe by axial furrow varies considerably. Palpebral lobe short, less than $\frac{1}{4}$ glabellar length, anterior end opposite anterior glabellar furrow, posterior end opposite middle glabellar lobe (Pl. 106, figs. 3, 4); moderately convex (exsag.), convex upwards with mid point highest; slopes up steeply from palpebral furrow becoming convex (tr.); separated indistinctly from eye ridge by change in convexity (Pl. 106, figs. 4, 5), in some large specimens by indistinct furrow. Palpebral furrow deep, wide, slopes down to posterior. Palpebral area slightly convex (tr.), horizontal to down-sloping posteriorly. Posterior area long (exsag.), almost as wide (tr.) as occipital ring, with distinct fulcrum at opposite posterior end of palpebral furrow. Posterior border narrow, convex, even width; horizontal and transverse from axial furrow to fulcrum; abaxial to fulcrum, slightly downsloping and directed antero-laterally at approximately 40° to postero-lateral corner of cranidium (Pl. 106, figs. 3, 4). Posterior border furrow originates at base of axial furrow, widens abaxially (confluent with posterior end of palpebral furrow); deep adjacent to border, shallows away from it; over-all shape triangular (Pl. 106, figs. 3–5).

Anterior section of facial suture diverges anteriorly at 10°, curves sharply inwards at border furrow, crosses anterior border diagonally to intersect anterior edge opposite junction of axial and border furrows (Pl. 106, figs. 3, 5), then marginal ventral; connective sutures cross doublure, concave abaxially (Pl. 106, fig. 7). Palpebral section of facial suture short, convex abaxially, diverges to posterior at 15°; posterior section relatively long, slightly convex abaxially, diverges to posterior at 50°, and slopes down to cut posterior border opposite posterior glabellar furrow (Pl. 106, figs. 3–5).

Librigena (Pl. 106, fig. 7) with long genal spine. Lateral border moderately convex (tr.), approx. $\frac{1}{3}$ mid-palpebral width of librigena. Lateral border furrow distinct, rises steeply to border and slopes up gently to genal field abaxially; curves sharply inwards near base of genal spine, continuous with posterior border furrow, becomes wider and deeper adaxially. Posterior border narrow, convex, continuous with posterior border of fixigena, slopes down abaxially to join lateral border. Genal field slopes up gradually from border furrows, becomes convex upwards at mid width (tr.), then forms narrow horizontal or slightly depressed surround, below vertically upturned adaxial edge forming eye socle. Genal spine long, advanced (Pl. 106, fig. 2), moderately wide at base, tapers slowly and curves inwards towards posterior; subcentral ridge extends posteriorly.

Cephalic doublure same width as borders. Rostral plate crescentic, length (tr.) equal to maximum width of frontal glabellar lobe, notched abaxially (Pl. 106, fig. 6). Doublure of librigena convex ventrally, widens and flattens immediately posterior to connective suture (Pl. 106, fig. 7); lateral doublure continuous with posterior doublure around base of genal spine. Ventral side of genal spine flat to slightly rounded. Occipital ring with narrow, almost vertical doublure.

Hypostome (Pl. 106, fig. 6; text-fig. 4) with median body subdivided into large subtriangular anterior lobe, and smaller subrectangular posterior lobe. Median body surrounded by furrows and narrow upturned borders; lateral notch towards anterior. Median furrows straight, converge to posterior, not reaching sagittal line. Posterior section of anterior lobe of median body strongly convex (tr.), continuous sagittally with posterior lobe, slopes down anteriorly and divides into 2 down-sloping ridges directed antero-laterally and separated by median concave depression; abaxially ridges slope steeply down to prominent anterior wings. Anterior border slopes up from border furrow, trapezoidal in shape; anterior edge curves slightly forwards along line of hypostomal suture; abaxial section slopes downwards and postero-laterally at 50° to anterior wing. Anterior border furrow slightly convex forwards in central portion, slopes down postero-laterally to anterior wings. Anterior lateral border furrow straight, directed postero-laterally, slopes up from anterior wing to lateral notch; very narrow anterior lateral border. Median furrow originates at posterior end of anterior lateral furrow. Posterior lobe of median body strongly convex (tr.), parallel-sided to slightly tapering posteriorly; postero-lateral corners rounded with prominent bosses; lobe slopes down steeply to lateral border furrows, more gently to posterior border furrow. Lateral border furrow originates abaxial to median furrow, deepens to posterior with fossulae near posterior end; lateral border slopes up steeply from furrow, convex outwards forming shoulder. Posterior border relatively wide (sag.), horizontal (sag. and tr.), posterior lateral corners rounded. Posterior border furrow distinct abaxially, absent sagittally where ridge slopes down from posterior lobe across furrow; small fossulae in furrow abaxial to ridge.

Rostral plate attached along hypostomal suture to median section of anterior border of hypostome; anterior wings free (Pl. 106, fig. 6). Hypostome extends posteriorly to level of posterior glabellar furrow when in situ.

Cranidial ornament of closely spaced granules with pointed tips covers all dorsal surfaces except furrows (Pl. 106, fig. 4). Librigena with long, slightly wrinkled, subparallel terrace lines on posterior and most of lateral doublure; become less regular, and anastomose adjacent to connective suture; pattern of terrace lines on rostral plate unknown. Ventral surface of genal spine with longitudinally

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EXPLANATION OF PLATE 107

Figs. 1, 2. *Emuella polymera* gen. et sp. nov. White Point Conglomerate, Cape D'Estaing, Kangaroo Island, South Australia. 1, F16649, ×5; internal mould of complete prothorax and incomplete opisthothorax, showing articulating half rings and pleural spines of most segments. 2, F16651, ×8; internal mould of left side of macropleural unit and some opisthothoracic segments, showing long pleural spine and almost completely unmodified posterior pleural band of 5th segment.

Figs. 3–6. *Emuella dalgarnoi* gen. et sp. nov. Emu Bay Shale, Emu Bay, Kangaroo Island, South Australia. 3, F16660, ×4·5; almost complete internal mould; right connective suture visible, imprint of hypostome on frontal glabellar lobe. 4, Holotype, F16659, ×8; almost complete internal mould; cephalon slightly compressed sagittally, right librigena rotated clockwise, posterior segments of opisthothorax tilted to anterior. 5, F16661, ×5·5; external mould of cranidium, showing ornament and muscle scars on occipital and glabellar furrows. 6, F16661, ×18; detail of latex mould of specimen in fig. 5; showing posterior border and border furrow, and sutural ridge.

elongate granules in subparallel rows. Occipital ring bears sagittal, longitudinally elongate tubercle on posterior margin (Pl. 106, figs. 3, 4).

Thorax (Pl. 106, figs. 1, 2; Pl. 107, figs. 1, 2) with prothorax of 6 segments, with macropleural 6th fused to 5th, and opisthothorax of at least 42 segments (Pl. 106, fig. 1). Axis more than half total thoracic width, almost parallel sided to 4th segment then tapers evenly to posterior; moderately to gently convex (tr.), steep abaxially, rather flat sagittally; axial furrows distinct. Pleurae geniculate, very short (tr.), with pleural spines.

Prothoracic segments 1–4 similar; axial ring narrow (sag.), gently to moderately convex (tr.), rises from transverse furrow to posterior edge, with small sagittal node on posterior edge; transverse furrow with deep apodemal slit abaxially, widens and shallows abaxially (Pl. 107, figs. 1, 2); articulating half ring crescentic, $\frac{3}{4}$ width axial ring (sag.), central portion flat, horizontal, abaxially slopes down to axial furrows (Pl. 107, figs. 1, 2). Pleura strongly geniculate, fulcrum less than half length (tr.) from axial furrow. Pleural furrow shallow, wide adaxially, tapers diagonally across pleura, terminates before pleural spine; slopes up steeply to anterior pleural band, more gently to posterior band. Anterior pleural band widens to fulcrum, abaxially slopes down and out to form facet; extreme antero-lateral corner becomes horizontal (Pl. 107, fig. 2). Posterior pleural band narrow, convex, even width. Anterior and posterior pleural bands abaxially produced into short pleural spine notched at base; spine of 1st segment very short, slightly oblique to posterior situated at mid width (tr.) of pleura (Pl. 107, fig. 1); succeeding segments with spines progressively longer, directed more strongly backwards and situated more posteriorly (Pl. 106, fig. 2; Pl. 107, fig. 1). Pleurae progressively lengthen towards posterior (Pl. 106, fig. 2; Pl. 107, fig. 2). Doublure extends to base of pleural spine.

Macropleural unit consists of 5th and 6th segments, 5th segment similar to preceding segments; axial ring rises steeply to posterior, normal width sagittally; pleura wider, longer than 4th; pleural furrow more oblique, deeper, slopes up almost vertically to anterior, more gently to posterior; anterior pleural band widens more rapidly, facet larger, and fulcrum more strongly developed (Pl. 107, fig. 2); posterior band even width; pleural spine longer than preceding, near posterior edge of pleura (Pl. 107, figs. 1, 2). Line of fusion of pleurae of 5th and 6th sharp, with posterior pleural band of 5th unmodified (Pl. 107, fig. 2) to indistinct (Pl. 106, fig. 1). 6th segment macropleural; axial ring normal, posterior edge almost transverse; transverse furrow deep with strong apodemal slits abaxially, shallows sagittally; apodemal slit extends onto pleural field for short distance (Pl. 107, fig. 1); interpleural furrow extends from slit to base of 5th pleural spine; articulating half ring crescentic, $\frac{2}{3}$ width axial ring; pleural furrow originates adaxial and slightly posterior to extremity of apodemal slit (Pl. 106, fig. 2), widens slightly and deepens to fulcrum, then tapers abruptly and terminates forming notch (Pl. 107, fig. 2); furrow slopes up vertically to anterior, more gently to posterior; ventrally furrow appears as pronounced ridge at angle to apodeme, directed strongly to posterior; anterior pleural band widens rapidly abaxial to fulcrum, slopes down and out, extreme antero-lateral corner forms horizontal flap fused to 5th just adaxial to base of pleural spine (Pl. 107, fig. 1, 2); interfurrow platform asymmetrically convex (exsag.), slopes up gently from 5th pleural furrow, horizontal centrally, then drops almost vertically to 6th pleural furrow; posterior pleural band raised, convex, even width, with distinct notch at base of macropleural spine, just abaxial to fulcrum (Pl. 107, fig. 2); macropleural spine wide, extremely long, tapers gradually and curves inwards to posterior (Pl. 106, fig. 2; Pl. 107, fig. 1), convex to V-shaped anteriorly, flattens to posterior, median ridge extends from posterior edge of interfurrow platform down spine; spine formed by anterior and posterior pleural bands of 6th segment extends to level of pygidium. Doublure of macropleural unit extends from antero-lateral corner of 5th, across base of 5th spine to notch on posterior border of 6th.

Axial ring of 1st opisthothoracic segment similar in size and morphology to normal prothoracic axial ring (Pl. 107, fig. 1); pleura blade shaped, curved to posterior following posterior edge of 6th segment, fulcrum less than $\frac{1}{3}$ length (tr.) from axial furrow; pleural furrow wide, deep, diagonal, tapers to point just abaxial to notch of 6th; furrow slopes up steeply to anterior, moderately steeply to posterior; anterior pleural band overlapped by posterior band of 6th when articulated (Pl. 107, fig. 1) posterior pleural band convex, raised; pleural spine relatively long, advanced slightly to parallel curve of posterior edge of 6th, curves to posterior; formed by anterior and posterior pleural bands. Succeeding segments with pleurae progressively shorter and more transverse (Pl. 106, fig. 2); pleural spines long, directed progressively more to posterior and becoming less advanced; fulcrum migrates adaxially and pleurae become more strongly geniculate to posterior (Pl. 106, fig. 2; Pl. 107, fig. 1). At least 42

segments in opisthothorax; most posterior segments extremely narrow (sag.), lack distinct pleural furrows (Pl. 107, fig. 1). Doublure of pleurae extends to base of pleural spines.

Thoracic ornament of granules similar to those of cephalon, distributed evenly and closely spaced on dorsal surfaces.

Pygidium unknown.

Emuella dalgarnoi sp. nov.

Plate 107, figs. 3–6; text-fig. 5c.

Derivation of name. After Mr. R. C. Dalgarno, joint discoverer of the Flinders Ranges locality.

Holotype. AUGD F16659 (Pl. 107, fig. 4). Specimen shows almost complete thorax and pygidium articulated to a cephalon, which although slightly distorted, displays most of the diagnostic characters.

Dimensions of holotype. Length of cranidium 3·6 mm.; mid-palpebral width of cranidium 4·8 mm.; length (sag.) of prothorax 2·3 mm.; over-all sagittal length 11·3 mm.

Material. Approximately 20 internal and external moulds; 3 almost complete specimens, 1 well-preserved cranidium, remainder very fragmentary.

Occurrence. Upper part of Emu Bay Shale, Emu Bay, Kangaroo Island, South Australia.

Diagnosis. Axial furrows converge strongly from posterior margin to occipital furrow, slightly converging to almost parallel to anterior glabellar furrow, then shallow around moderately expanded frontal glabellar lobe. Transglabellar furrows wide, shallow, distinct. Anterior cranidial border furrow curves to anterior. Palpebral lobe relatively short, posterior end opposite posterior glabellar furrow. Posterior border widens from axial furrow to fulcrum, directed antero-laterally at 45°; low, narrow ridge extends from posterior lateral corner of cranidium along line of posterior section of facial suture. Posterior border furrow with notch abaxial to fulcrum. Anterior section of facial suture diverges anteriorly at 20°. Axial rings of prothorax without nodes. Thorax with 58 segments.

Discussion. E. dalgarnoi is distinguished from *E. polymera* by the possession of a longer palpebral lobe and consequent differences in the posterior section of the facial suture. The structure of the posterior border and border furrow also differs greatly, with *E. dalgarnoi* having a distinct notch at the fulcrum and a low ridge along the line of the posterior section of the facial suture. The anterior section of the facial suture is noticeably more divergent in *E. dalgarnoi* than in *E. polymera*.

Description. Axial furrows converge strongly from posterior margin to occipital furrow, converge slightly (Pl. 107, fig. 4) to almost parallel (Pl. 107, fig. 5) to anterior glabellar furrow, then diverge and curve around moderately expanded frontal glabellar lobe. Frontal glabellar lobe occasionally with slight anterior median depression resulting in bilobed appearance (Pl. 107, fig. 5). Occipital furrow curves slightly to posterior, moderately deep and wide abaxially, narrows and shallows abruptly sagittally; muscle spots at adaxial ends of broad portion of furrow (Pl. 107, fig. 5). Transglabellar furrows similar to occipital, posterior furrow curves slightly to posterior, middle transverse, anterior furrow curves slightly to anterior (Pl. 107, fig. 5). Occipital ring approximately half mid-palpebral cranidial width, constant width, projects very little beyond posterior margin of fixigena. Axial furrow very slightly impressed, deepest at junction with glabellar furrows, anteriorly reaches anterior border furrow, with small anterior furrow fossula at junction (Pl. 107, fig. 5). Anterior border furrow curves to anterior, shallowest opposite frontal glabellar lobe. Eye ridge wide, directed to posterior at 30° to transverse line. Palpebral lobe relatively short, less than $\frac{1}{3}$ glabellar length, anterior end opposite anterior glabellar lobe, posterior end opposite posterior glabellar furrow; slopes up steeply from palpebral furrow, flat on adaxial side, becomes convex dorsally; slightly convex (exsag.) with highest point towards posterior end (Pl. 107, fig. 3, 5); continuous with eye ridge. Palpebral furrow very wide, slopes down to posterior, but with small fossula alongside mid point of ridge. Posterior area relatively long (exsag.), $\frac{2}{3}$ width (tr.) occipital ring, with fulcrum opposite posterior end of palpebral lobe (Pl. 107, figs. 3, 5). Posterior border transverse from axial furrow to fulcrum, widens and rises rapidly, anteriorly drops steeply to border furrow, outer edge concave to posterior (Pl. 107, fig. 6); abaxial to fulcrum, border directed antero-laterally at 45°, width constant; upper surface horizontal, anteriorly drops

vertically to border furrow. Narrow ridge, below level of posterior border, extends from posterior lateral corner, along line of posterior section of facial suture (Pl. 107, figs. 5, 6). Posterior border furrow widens to fulcrum, then with distinct notch (Pl. 107, figs. 5, 6); abaxially slopes down slightly, continuous with furrow running along base of sutural ridge (Pl. 107, fig. 6).

Anterior section of facial suture diverges anteriorly at approximately 20°; rostral plate same width (tr.) as frontal glabellar lobe, notched laterally (Pl. 107, fig. 3). Posterior section of suture relatively long, diverges to posterior at 45°; section from palpebral ridge to posterior border straight, then sharply convex abaxially across border (Pl. 107, figs. 5, 6).

Cranidial ornament of pointed granules; closely spaced on glabellar lobes, borders, eye lobes; sparsely distributed on palpebral area of fixigena, anterior lateral sections of cranidium; absent in all furrows (Pl. 107, figs. 5, 6). Paired muscle spots present on abaxial portions of occipital and glabellar furrows (Pl. 107, figs. 5). Genal field of librigena with scattered granules.

Hypostome unknown.

Thorax with axis approximately half total thoracic width. Maximum number of 52 opisthothoracic segments observed (Pl. 107, fig. 4). Pygidium (Pl. 107, fig. 4) minute furrowed disc, without distinct division into axial and pleural fields; 4 or 5 furrows, transverse sagittally, curving to posterior abaxially; entire lateral and posterior borders.

Genus BALCORACANIA gen. nov.

Type species. Balcoracania dailyi sp. nov.

Plate 109; text-figs. 5A, B

Derivation of name. After Balcoracana Creek, Flinders Ranges, South Australia.

Diagnosis. Preglabellar field narrow, down-sloping, or absent. Palpebral lobe long, crescentic. Posterior border with section abaxial to fulcrum directed antero-laterally at 60°, and strongly depressed. Librigena with genal spine only slightly advanced. Thorax with axis less than half thoracic width. Pleural furrows terminate at base of pleural spines. Thorax with 53–61 segments. Fine closely spaced granules on dorsal surfaces.

Discussion. The cephala of *Balcoracania* differ from those of *Emuella* in having a longer palpebral lobe and consequently shorter posterior section of the facial suture; the abaxial section of the posterior border is much more strongly depressed and not directed forward as strongly. With regard to the thorax, in *Balcoracania* the axis is narrower than in *Emuella*, and the pleural furrows extend to the base of the spines.

Balcoracania dailyi sp. nov.

Plates 108, 109; text-fig. 5A

Derivation of name. After Dr. B. Daily, who first discovered members of this group.

Holotype. AUGD F16663 (Plate 108, fig. 1). Specimen is only one known with the cephalon articulated to a reasonably complete thorax.

Dimensions of holotype. Length of cranidium 4·7 mm.; mid-palpebral width of cranidium 4·4 mm.; length of prothorax 3·4 mm.; over-all sagittal length of specimen 13·4 mm.

Material. Approximately 150 internal and external mounds, mostly isolated cranidia, librigenae, thoracic segments, and several hypostomes.

Occurrence. Upper section of White Point Conglomerate, W. side of Cape D'Estaing, Kangaroo Island, South Australia.

Diagnosis. Axial furrows converge moderately from posterior margin to middle glabellar furrow, almost parallel to anterior glabellar furrow, then curve indistinctly around slightly expanded frontal

glabellar lobe. Preglabellar furrow indistinct, almost transverse; narrow (sag.) downsloping preglabellar field. Prominent anterior border fossulae. Glabellar furrows distinct only laterally.

Description. Cephalon subsemicircular in outline, moderately convex (tr. and sag.). Cranidium moderately convex (tr.). Axial furrows converge moderately from posterior margin to middle glabellar furrow, almost parallel to anterior glabellar furrow, then curve around very slightly expanded frontal glabellar lobe. Glabella strongly convex (tr.), weak median ridge extends from posterior to anterior glabellar furrows; gently convex (sag.), highest at anterior glabellar lobe, slopes down steeply to preglabellar field, more gently to posterior. Occipital furrow deepest abaxially, curves slightly to posterior (Pl. 108, fig. 2). Transglabellar furrows distinct abaxially, but very shallow and indistinct sagittally (Pl. 108, fig. 5); posterior furrow directed slightly to posterior abaxially, transverse sagittally (Pl. 108, fig. 1); middle furrow transverse; anterior furrow directed slightly to anterior abaxially. Occipital ring less than half mid-palpebral, cranidial width, maximum width sagittally, posterior edge convex to posterior; posterior half of ring projects beyond margin of fixigenae (Pl. 108, figs. 2, 3). Frontal glabellar lobe with central portion flat to slightly convex, occasionally with anterior median depression, giving bilobed appearance. Axial furrow slightly impressed below fixigena from posterior margin to eye ridge, rises and becomes indistinct over eye ridge, not impressed on sides of frontal lobe, anteriorly joins anterior border furrow (Pl. 108, figs. 2, 3, 5). Deep anterior furrow fossulae at junction of axial and anterior border furrows (Pl. 108, fig. 5). Preglabellar furrow very indistinct, almost transverse; narrow (sag.) down-sloping preglabellar field (Pl. 108, figs. 2, 5). Anterior border medium width, margin convex to anterior; abaxially convex, raised, but flattens and widens opposite frontal glabellar lobe (Pl. 108, fig. 2). Anterior border furrow moderately deep and narrow abaxially, rises abruptly, broadens and shallows opposite frontal glabellar lobe (Pl. 108, figs. 2, 5).

Eye ridge wide, long, directed to posterior at 25° to transverse line. Palpebral lobe wide (tr.), long, approximately $\frac{3}{4}$ glabellar length, anterior end opposite anterior glabellar lobe, posterior end opposite occipital furrow or posterior half of posterior glabellar lobe; lobe slopes up flatly from palpebral furrow, abaxial edge convex upwards and outwards; rises to posterior with posterior end high above posterior area (Pl. 108, figs. 3, 5); lobe indistinctly separated from eye ridge by change in convexity or occasionally by indistinct longitudinal furrow. Palpebral furrow wide, deepens and slopes down steeply to posterior. Palpebral area slightly inflated, slopes down to posterior border furrow. Posterior area short (exsag.), wider (tr.) than occipital ring, depressed, with fulcrum opposite posterior end of palpebral lobe (Pl. 108, figs. 2, 4); horizontal from axial furrow to fulcrum, slopes down steeply abaxial to fulcrum. Posterior border directed slightly to posterior from axial furrow to fulcrum, antero-laterally at 50–55° abaxial to fulcrum. Posterior border furrow widens abaxially, deep adjacent to border, shallows away from it; almost straight-sided, confluent abaxially with palpebral furrow (Pl. 108, figs. 3, 4).

Anterior section of facial suture diverges anteriorly at 25°, curves sharply inwards at border furrow, crosses anterior border diagonally; from point where facial suture cuts anterior cranidial edge, connective sutures cross doublure, sharply concave abaxially (Pl. 108, fig. 7). Rostral suture marginal ventral. Palpebral section of facial suture convex abaxially, diverges at 15° to posterior. Posterior

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EXPLANATION OF PLATE 108

Figs. 1–8. *Balcoracania dailyi* gen. et sp. nov. White Point Conglomerate, Cape D'Estaing, Kangaroo Island, South Australia. 1, Holotype, F16663, ×8; external mould of almost complete specimen; macropleural spines incomplete, posterior segments of opisthothorax and pygidium missing. 2, F16665*a*, ×6; internal mould of cranidium showing preglabellar field, fossulae, posterior area; both palpebral lobes incomplete. 3, F16665*b*, ×6; counterpart of specimen in fig. 2; showing palpebral lobes. 4, F16664, ×18; internal mould of portion of cranidium showing posterior area; mould of the abaxial section of posterior border removed to show that of doublure. 5, F16666, ×8; internal mould of cranidium showing anterior border furrow and eye ridge fossulae. 6, F16667, ×9·5; detail of specimen in fig. 8, showing ornament of lateral librigenal doublure. 7, F16669, ×3·5; internal mould of anterior section of librigenal border and doublure, showing the courses of the connective suture and the anterior section of the facial suture, and the ornament. 8, F16667, ×7; internal mould of librigena, with moulds of lateral border and most of posterior border missing, showing lateral and posterior doublures respectively, and convexity of genal field.

section relatively short, diverges to posterior at 55°, slopes down steeply to posterior border furrow, then curves sharply inwards across border (Pl. 108, figs. 3, 8). Posterior lateral corner of cranidium opposite occipital furrow (Pl. 108, figs. 2).

Librigena (Pl. 108, figs. 6–8) with long genal spine, slightly advanced. Lateral border furrow curves sharply inwards near base of genal spine, continuous with posterior border furrow; widens, deepens and slopes down adaxially (Pl. 108, fig. 8). Posterior border narrow, convex, high above furrow adaxially, slopes down abaxially to join lateral border. Genal field slopes up gradually and rather flatly from border furrow, sharply upturned at adaxial edge to form eye socle; moderately convex (exsag.), posterior lateral section slopes down steeply (Pl. 108, fig. 8).

Cephalic doublure same width as border anteriorly and laterally; posterior fixigenal doublure tapers rapidly to point just abaxial to fulcrum (Pl. 108, fig. 4). Rostral plate equal in length (tr.) to maximum width of frontal glabellar lobe. Doublure of librigena moderately to strongly convex, widens and flattens adjacent to connective suture (Pl. 108, fig. 6). Lateral and posterior librigenal doublures continuous (Pl. 108, fig. 8). Ventral side of genal spine slightly rounded to flat.

Hypostome (Pl. 109, figs. 4, 5) similar in basic morphology to that of *E. polymera*, but differs or illustrates more clearly the following features: anterior wings very prominent, depressed; wing processes visible in well preserved specimens (Pl. 109, fig. 4); position of wing results in anterior lateral border and furrow being directed postero-laterally (Pl. 109, fig. 5) or transversely (Pl. 109, fig. 4). Anterior border wide, steeply upsloping, crossed by narrow line in some specimens (Pl. 109, fig. 4); line symmetrically concave about sagittal line, abaxially intersects anterior edges at extremities of hypostomal suture. Median furrow with macula at posterior end (Pl. 109, fig. 5). Posterior lobe of median body strongly convex (tr.), parallel sided (Pl. 109, fig. 4) or tapers slightly to posterior; posterior lateral corner rounded, with prominent boss (Pl. 109, fig. 5). Lateral border up-sloping with small shoulder at mid length (Pl. 109, fig. 5); border furrow with very deep fossula below shoulder.

Cranidial ornament of fine granules covering all dorsal surfaces; occipital ring with elongate sagittal node on posterior edge (Pl. 108, fig. 3); terrace lines on extreme outer edges of anterior and lateral borders (Pl. 108, fig. 3). Librigena with fine granules on genal field, adaxial portion of lateral border, and dorsal surface of genal spine (Pl. 108, fig. 7); abaxial portion of lateral border with wrinkled terrace lines, separated by subparallel rows of elongate granules becoming more numerous towards genal spine (Pl. 108, fig. 7); lateral and posterior doublures with long regular terrace lines, become anastomosing adjacent to connective suture (Pl. 108, figs. 6, 8); ventral surface of genal spine with elongate granules in parallel rows. Rostral plate with terrace lines.

Thoracic axis narrow, less than half thoracic width, pleurae correspondingly long (tr.) (Pl. 108, fig. 1). Axial furrows converge slightly from 1st to 6th segment, rapidly converge to about mid length (sag.) opisthothorax, then almost parallel to level of pygidium (Pl. 108, fig. 1). Axial rings of prothoracic segments rise only slightly to posterior, without nodes (Pl. 108, fig. 1). Pleurae of segments 1–4 equal length (tr.). Pleural furrow diagonal, tapers abaxial to fulcrum, terminates at base of pleural spine (Pl. 108, fig. 1). Pleural spine formed by anterior pleural band only. Anterior pleural band slopes down antero-laterally abaxial to fulcrum to form facet; no modification to antero-lateral corner (Pl. 109, figs. 1, 2). Macropleural unit with line of fusion of pleurae generally indistinct, marked by slight furrow to base of 5th pleural spine (Pl. 109, fig. 3) or almost completely effaced (Pl. 109, fig. 1); anterior pleural band of 6th slopes down to join 5th pleural spine without modification (Pl. 109, fig. 1). Thorax with 53 segments.

Pygidium minute, furrowed, borders entire.

Discussion. B. dailyi is easily distinguished from the species of *Emuella* by the possession of a narrow, down-sloping, preglabellar field, and a long palpebral lobe, the structure of which also differs.

Balcoracania flindersi sp. nov.

Plate 109, figs. 7, 8; text-fig. 5B

Derivation of name. From the Flinders Ranges, South Australia.

Holotype. AUGD F16683 (Pl. 109, fig. 7). Specimen with articulated cephalon and thorax.

Dimensions of holotype. Length of cranidium 3·7 mm.; mid-palpebral width of cranidium 4·5 mm.; length of prothorax 2·7 mm.; over-all sagittal length 10·1 mm.

Material. Approximately 280 replaced tests, internal and external moulds; exoskeletons mainly articulated, but some disarticulated elements.

Occurrence. Lower part of the Billy Creek Formation, Balcoracana Creek, Flinders Ranges, South Australia.

Diagnosis. Axial furrows converge evenly from posterior margin to anterior glabellar furrow, then curve out and around markedly expanded frontal glabellar lobe. No preglabellar field or anterior border fossulae. Transglabellar furrows distinct, deep.

Description. Axial furrows converge evenly from posterior margin to anterior glabellar furrow, then curve out and around markedly expanded frontal glabellar lobe. Occipital furrow, transglabellar furrows deep, distinct; posterior furrow convex to posterior, middle transverse, anterior furrow convex to anterior (Pl. 109, figs. 7, 8). Occipital ring less than half mid-palpebral cranidial width. Frontal glabellar lobe markedly expanded, rounded laterally and anteriorly; reaches anterior border furrow; no preglabellar field; anterior border and border furrow unmodified; no anterior furrow fossulae (Pl. 109, figs. 7, 8). Palpebral lobe long (exsag.), wide (tr.), crescentic; anterior and opposite anterior glabellar lobe, posterior and opposite occipital furrow. Palpebral area usually highly inflated, slopes down steeply to posterior.

Thorax (Pl. 109, figs. 6, 8) with long opisthothorax; maximum number of 61 thoracic segments observed.

Discussion. B. flindersi is primarily distinguished from *B. dailyi* by the morphology of the anterior part of the cranidium, by the degree of expansion of the frontal glabellar lobe, absence of preglabellar field, and anterior furrow fossulae. It is clearly distinguished from the species of *Emuella* by the length of the palpebral lobe and the structure of the posterior area of the fixigena, especially the strong depression of the section abaxial to the fulcrum.

A comparison of the morphology of the adults of the four species is presented in Table 1, and of the adult cephala in text-fig. 5.

Intraspecific variation. In all collections some sort of deformation has taken place, and this factor must be considered in an evaluation of the intrinsic variation of the species. The range of morphological variation is approximately the same for the various characters or groups of characters in each of the species. The following groups exhibit a correlated variation:

EXPLANATION OF PLATE 109

Figs. 1–6. *Balcoracania dailyi* gen. et sp. nov. White Point Conglomerate, Cape D'Estaing, Kangaroo Island, South Australia. 1, F16679, ×10; internal mould of left side of macropleural unit and 1st opisthothoracic segment, showing an articulating facet and pleural spine of 5th segment, and extension of apodemal slit onto interfurrow platform along line of fusion of pleurae. 2, F16678, ×9·5; external mould of portion of thorax showing ornament. 3, F16680, ×10; internal mould of left side of macropleural unit; extent of doublure shown by gap surrounding mould from base of 5th spine to notch on posterior border of 6th segment. 4, F16673, ×8; internal mould of hypostome and detached rostral plate; hypostome with maculae and prominent postero-lateral bosses; rostral plate with notched abaxial ends. 5, F16671, ×10; internal mould of hypostome showing anterior line, depressed anterior wings, and deep fossulae in lateral borders. 6, F16676, ×5; portion of external mould of macropleural unit and 1st opisthothoracic segment, showing articulating half rings, prominent junction of apodeme and pleural furrow, and overlap of posterior pleural band of 6th over anterior pleural band of opisthothoracic segment.

Figs. 7, 8. *Balcoracania flindersi* gen. et sp. nov. 7, Holotype, F16683, ×10; internal mould of cephalon and incomplete thorax; cranidium with imprint of hypostome and rostral plate. 8, F16655, ×5; several almost complete specimens on bedding plane.

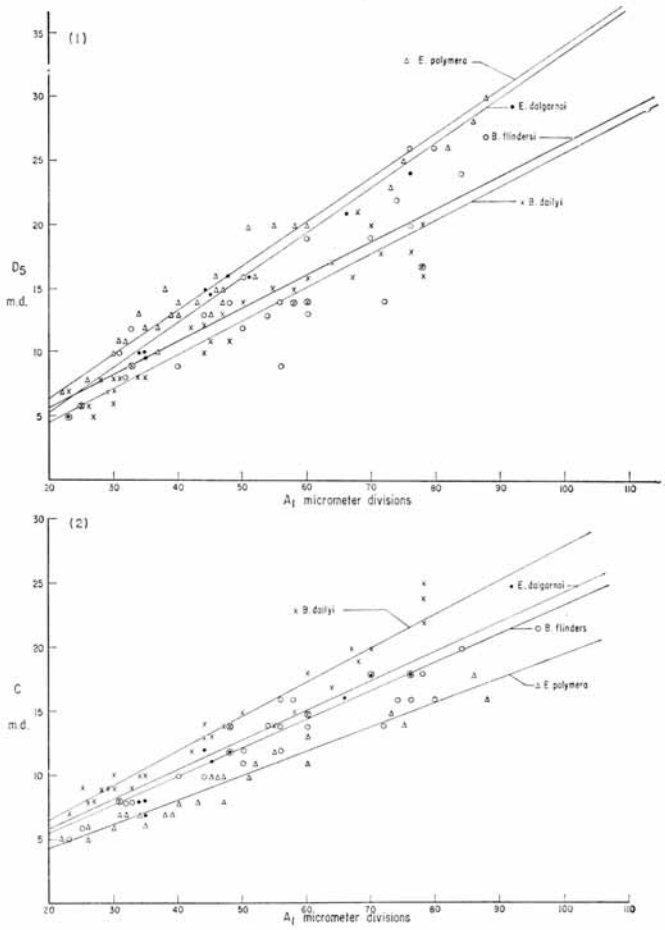
(*a*) Convexity of the palpebral area and the degree of impression of the surrounding axial and palpebral furrows: the palpebral area varies from almost flat (tr.) to highly convex; in the former case the furrows are only slightly impressed or are represented merely by a change in slope; in the latter the surrounding furrows are deeply impressed. However it must be remembered that in *B. flindersi* high convexity of the palpebral area appears to represent the norm.

TABLE 1. Comparison of aspects of the morphology of members of the Emuellidea. The limits of variation for these characters are given in the text.

CHARACTER	*EMUELLA POLYMERA*	*EMUELLA DALGARNOI*	*BALCORACANIA DAILYI*	*BALCORACANIA FLINDERSI*
PALPEBRAL LOBE	SHORT, <1/4 GLABELLAR LENGTH; POST. END OPPOSITE MIDDLE GLABELLAR LOBE; MIDPOINT HIGHEST.	SHORT, > 1/4 AND < 1/3 GLABELLAR LENGTH; POST. END OPPOSITE POST. GLABELLAR FURROW; POST. END HIGHEST.	LONG, > 1/2 GLABELLAR LENGTH; POST. END OPPOSITE OR JUST ABOVE OCCIPITAL FURROW	DITTO
POSTERIOR AREA (ABAXIAL TO FULCRUM)	SLIGHTLY DEPRESSED	DITTO	STRONGLY DEPRESSED	DITTO
POSTERIOR BORDER (ABAXIAL TO FULCRUM)	ANTERO-LATERALLY AT 40°	ANTERO-LATERALLY AT 45°.	ANTERO – LATERALLY AT 50–55°	DITTO
PREGLABELLAR FIELD	ABSENT	DITTO	NARROW (SAG.), INDISTINCT, DOWNSLOPING.	ABSENT
ANT. B FURROW FOSSULAE	PRESENT	DITTO	DITTO	ABSENT
EYE RIDGE FOSSULAE	PRESENT	DITTO	DITTO	ABSENT
ANTERIOR BORDER FURROW	SHALLOWS OPPOSITE FRONTAL GLABELLAR LOBE	DITTO	DITTO	EVEN DEPTH, ABAXIALLY AND SAGITTALLY
TRANSGLABELLAR FURROWS	SHALLOW, INDISTINCT	WIDE, DEEP ABAXIALLY, NARROW, SHALLOW SAGITTALLY	DISTINCT ABAXIALLY, INDISTINCT SAGITTALLY	DEEP, DISTINCT.
ANTERIOR SECTION OF FACIAL SUTURE	DIVERGES AT 10°	DIVERGES AT 20°	DIVERGES AT 25°	DITTO
POSTERIOR SECTION OF FACIAL SUTURE	DIVERGES STRONGLY	DIVERGES STRONGLY, WITH LOW SUTURAL RIDGE	DIVERGES MODERATELY	DITTO
WIDTH ITRU OF THORACIC AXIS	>1/2 TOTAL THORACIC WIDTH	APPROX. 1/2 TOTAL THORACIC WIDTH	< 1/2 TOTAL THORACIC WIDTH	⩽ 1/2 TOTAL THORACIC WIDTH
PLEURAL FURROWS	TERMINATE BEFORE SPINES	DITTO	TERMINATE AT BASE OF SPINES	DITTO
MACROPLEURAL UNIT	ABAXIAL FLAP PRESENT	DITTO	FLAP ABSENT	DITTO
CRANDIAL ORNAMENT	LARGE, POINTED GRANULES, DENSE ON DORSAL SURFACES; OCCIPITAL NODE.	DENSE GRANULES ON BORDERS, GLABELLA, AND EYE LOBES WIDELY SPACED ON PALPEBRAL AREA; ABSENT IN FURROWS, OCCIPITAL NODE	FINE, DENSE GRANULES ON DORSAL SURFACES; OCCIPITAL NODE.	DITTO
PROTHORACIC NODES	PRESENT ON SEGMENTS 1 – 4	DITTO	ABSENT	DITTO
NO. THORACIC SEGMENTS	AT LEAST 48	58	53	61

(*b*) Junction of the eye ridge and frontal glabellar lobe: this appears to be the most variable of all characters and the most difficult to distinguish between genuine and spurious variation. The eye ridge may be almost completely separated from the frontal lobe by the axial furrow, or join it without significant interruption; this appears largely independent of the degree of impression of the axial furrow elsewhere. However, the eye ridge is never completely separated from the glabella.

(*c*) Frontal glabellar lobe, preglabellar and anterior border furrow: the outline and convexity of the frontal glabellar lobe varies considerably in *B. dailyi*, and to a lesser extent in the other species. The outline varies from slightly rounded laterally, with an almost straight anterior edge, to almost circular, being correlated respectively to high and low convexity (sag. and tr.). An important variant is a slightly bilobed outline, resulting from a shallow anterior median depression. In all except *B. flindersi*, forms with high convexity of the frontal lobe have the section of the anterior border furrow opposite the lobe raised with respect to its abaxial sections, and thus have more distinct



TEXT-FIG. 6. Scatter diagrams and 'best fit' lines for adults of the Emuellidae. A_1, the total cranidial length plotted against (1) D_5, the occipital post-palpebral length; (2) C, the palpebral length. All dimensions given in micrometer divisions where 1·00 mm. = 32 micrometer divisions. The symbol ● denotes specimens of *B. dailyi*, × specimens of *B. flindersi*, ○ specimens of *E. polymera*, and △ those of *E. dalgarnoi*.

border fossulae than those forms with low convexity. In *B. dailyi* high convexity of the lobe is also associated with a slightly longer (sag.) preglabellar field.

(*d*) The length and level of the palpebral lobe, and morphology of the posterior limb: although the differences in these morphological characteristics form the primary basis for discrimination of the genera and species, each species has a considerable and occasionally overlapping range.

Quantitative analysis. Limited analysis was undertaken, primarily to provide a quantitative description of the species and additionally to supplement the purely qualitative discrimination of the genera and species.

Qualitative work suggests that the length of the palpebral lobe, and in particular the position of its posterior end, are important for the taxonomic discrimination of the genera and species, although a considerable range of intraspecific variation is observed. Accordingly these characters were selected for analysis, the occipital post-palpebral length (D_5) and the palpebral length (C) being plotted against the cranidial length (A_1) and 'best fit' lines fitted (text-fig. 6); the values for the dimensions are given in the Appendix, and the equations of the 'best fit' lines in Table 2.

TABLE 2. The equations of the 'best fit' lines, calculated by the method (Bartlett's method) given by Simpson, Roe, and Lewontin (1960, p. 234). A_1 is the total cranidial length, C is the palpebral length, and D_5 is the occipital post-palpebral length.

	A_1-D_5	A_1-C
E. polymera	$D_5 = -0{\cdot}4+0{\cdot}34A_1$	$C = 0{\cdot}4+0{\cdot}19A_1$
E. dalgarnoi	$D_5 = -1{\cdot}8+0{\cdot}35A_1$	$C = 1{\cdot}3+0{\cdot}23A_1$
B. flindersi	$D_5 = 0{\cdot}3+0{\cdot}26A_1$	$C = 1{\cdot}1+0{\cdot}22A_1$
B. dailyi	$D_5 = -0{\cdot}7+0{\cdot}26A_1$	$C = 0{\cdot}7+0{\cdot}27A_1$

The plot of occipital post-palpebral length against cranidial length indicates that the two genera can be clearly distinguished quantitatively on the basis of the position of the posterior end of the palpebral lobe. However the parameters obtained for *E. dalgarnoi* are somewhat anomalous, in that the gradient of the 'best fit' line is not significantly different from that of *E. polymera*. The small number of specimens in the sample of *E. dalgarnoi* may be a factor affecting the values of the parameters. The plot of palpebral length against cranidial length, however, shows that the two species can be distinguished quantitatively on the basis of their palpebral lengths. The anomalous values for *Balcoracania flindersi* suggest that the anterior end of the palpebral lobe is lower than in the other species, and this can be verified both qualitatively and quantitatively.

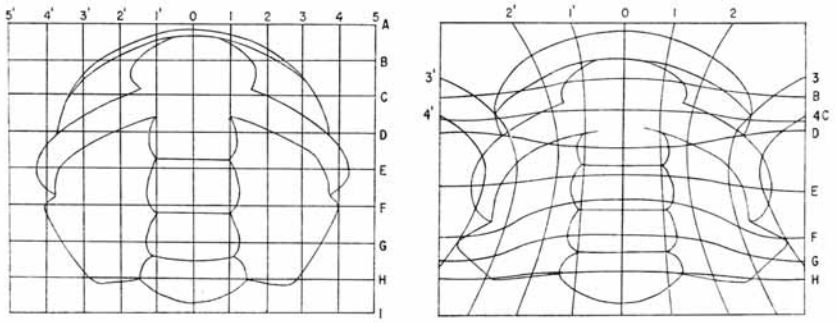
ONTOGENY

Larval stages are known for the species *B. flindersi*, *B. dailyi*, and *E. polymera*. *B. flindersi* is represented by over 150 specimens, and the major features of the ontogeny were elucidated by a study of this material; *B. dailyi* is adequately represented by 30 specimens, but only a few specimens of *E. polymera* are known. The order of description of the ontogenies thus differs from that of the adults.

The methods and procedures adopted vary slightly depending upon the size and nature of the sample, but are basically similar to those described below.

All specimens were prepared, measured, photographed, and described individually. A reconstruction of an early meraspid cranidium was made, and compared with a holaspid cranidium on a modified D'Arcy Thomson diagram (text-fig. 7), using the techniques described by Palmer (1957, p. 106). The line of least 'distortion' is the line of bilateral symmetry, and specifically the length of the glabella increases at a rate most nearly equal to that of absolute size. However the length of the glabella is very difficult to measure accurately on extremely small specimens, and the cranidial length (A_1) is used

instead as the standard dimension. The use of this dimension involves some error, as the anterior border appears and develops during ontogeny; however, it is considered that the practical advantage of accurate measurement offsets the theoretical disadvantages. The morphology of each specimen is then tabulated against cranidial length (in ascending order). Examination of the table and the D'Arcy Thompson grid shows that several characters underwent progressive change with increase in cranidial length; of these, three were selected, the anterior border and border furrow, the palpebral lobe,



TEXT-FIG. 7. Proportional change in dorsal cephalic features of *B. flindersi* during development. Left, Cranidium of Stage II; Right, Holaspid cranidium.

and the anterior section of the facial suture. On the basis of the changes, subclasses were distinguished for each of the three characters, and the size ranges of each subclass noted. Considerable overlap in the range of the subclasses existed, as the characters change at different rates; however, it was found that the sets of data could be combined to give a number of stages of cranidial development, with an acceptable maximum overlap of the cranidial lengths (Tables 3, 6).

The development of the meraspid thorax is incompletely known, and although related, where possible, to stages of cranidial development, is described separately (Tables 4, 7).

The hypostomes present range in length upwards from 0·50 mm., and it is evident that at least the specimens in the lower part of the range have been separated from larval cranidia. Two problems arise: to match the hypostomes with the equivalent cranidia and thus to stages of cranidial development, and to determine an upper size limit, below which the hypostomes may be considered as 'larval'.

Examination of adult specimens of cephala with hypostomes '*in situ*' or close to that position, shows that the posterior edge of the hypostome reaches approximately the level of the posterior glabellar furrow. The sagittal length of the hypostome is thus slightly less than $\frac{3}{4}$ of the cranidial length (A_1), and accordingly an upper limit for the length of larval hypostomes can be fixed. It is unwise, however, to apply this factor to smaller specimens, as it is well known (Whittington 1957, 1959) that the hypostome is proportionately larger in the larval stages than in the adult in some cases. It is therefore necessary to find some dimension of the hypostome which can justifiably be assumed to bear a constant relationship to some dimension of the cranidium, over the

complete ontogeny. In the adult, the hypostome is attached to the posterior edge of the rostral plate, along the line of the hypostomal suture. Thus the length of the posterior edge of the rostal plate is equal to that of the anterior edge of the hypostome, excluding the anterior wings, which are free (text-fig. 4). As it can be assumed that the functional relationship between the rostral plate and hypostome does not change, the relationship between the two dimensions is fixed throughout ontogeny.

The length of the anterior edge of the rostral plate can be measured directly from the cranidium in most cases, as there is a slight change in curvature at the point where the facial suture intersects the anterior edge of the border, and it is from this point that the connective suture originates. The lengths of the anterior and posterior edges of the rostral plate can be taken as identical, within the limits of mensurational error. The length of the articulating section of the anterior edge of the hypostome (H_4) can be measured directly in most cases.

On the above basis, the hypostomes may be matched with a range of cranidia, and thus to a stage of cranidial development (Tables 5, 8).

The resulting descriptions and tabulations are subjective to some extent, owing to (*a*) the gradational nature of the morphological changes; (*b*) the size overlap between morphological subclasses; (*c*) overlap in size between meraspid degrees; and (*d*) method of allotting hypostomes to cranidial stages. However it is considered that, in general, an accurate representation of the ontogeny results.

Ontogeny of Balcoracania flindersi

(*a*) *Development of the cephalon* (Table 3)

Stage I: Cranidial lengths 0·38–0·49 mm. (includes the protopygidium in this stage): protaspides (text-fig. 8 I). Only 3 specimens were found, smaller than the size range for meraspides of degree 0, and only 1 of these was well enough preserved to verify the presence of the protopygidium. However the position of the specimens prevented adequate photography. The specimen is subelliptical in outline, and almost hemispherical, being slightly flat sagittally. It is divided into a large cephalon (or cranidium) and a narrow (sag.) protopygidium by a transverse line. The axis is narrow, flat to slightly depressed, and is defined for the posterior $\frac{3}{4}$ of its length by distinct parallel furrows, and for the remainder by indistinct furrows diverging at 45°. The axis is divided into 5 rings by indistinct transverse furrows, the most anterior furrow being at the point of divergence of the axial furrows. Cheek furrows are present, but indistinct.

The protopygidium is narrow (sag.), approximately $\frac{1}{4}$ the total length (sag.). The axis tapers posteriorly, but is indistinct.

Stage II: Cranidial lengths 0·50–0·64 mm.; meraspid degrees 0–1 (text-fig. 8 II; Pl. 110, figs. 2–4). Numerous specimens falling within this size range have distinct occipital rings and posterior margins, showing them to be meraspid cranidia. Two specimens with attached transitory pygidia, and 1 meraspid degree 1, are included within this range.

The cranidium is subcircular in outline, sagittally subhorizontal, margins steeply down-sloping. The glabella is moderately convex (tr.), $\frac{1}{4}$ the maximum cranidial width; the glabellar and occipital furrows are all distinct and transverse, with an additional indistinct furrow, aligned with the anterior edge of the eye ridge, partially subdividing the frontal lobe (pre-anterior furrow). The axial furrows are parallel from the posterior margin to the anterior furrow or slightly pinched in at the latter, then diverge at about 45° to the anterior edge. The frontal glabellar lobe is thus expanded to the anterior (although partially subdivided). The eye ridge is distinct, directed slightly to the posterior, and steeply down-sloping abaxially. The palpebral lobe is very short, depressed below the level of the cheek and downsloping abaxially; no distinct palpebral furrow; the posterior end of the lobe is opposite the anterior glabellar lobe or middle glabellar furrow. The cheek has a narrow (exsag.) subhorizontal

portion then slopes steeply downwards abaxially and posteriorly. The cheek furrows are short and parallel the eye ridge (Pl. 110, fig. 2). The posterior border is geniculate, with a short transverse section, and a longer section directed antero-laterally at 25–30°, almost to the base of the palpebral lobe. The anterior sections of the facial sutures converge strongly, intersecting the anterior edge at the same places as the axial furrows, the posterior sections are extremely short and diverge at about 30°.

TABLE 3. Larval development of *B. flindersi* based upon stages of development of the cranidium.

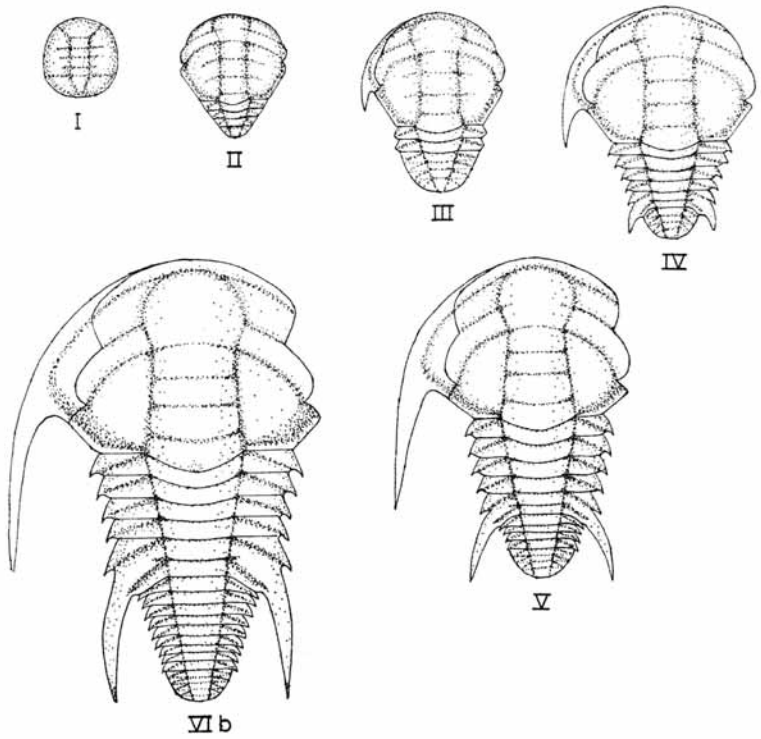
CHARACTER	*STAGE I*	*STAGE II*	*STAGE III*	*STAGE IV*	*STAGE V*	*STAGE VIa*	*STAGE VIb*	*STAGE VIc*
FRONTAL GLABELLAR LOBE	SUB – TRIANGULAR	SIDES ROUNDED SLIGHTLY	SIDES ROUNDED	ROUNDED	UNCHANGED	UNCHANGED	UNCHANGED	UNCHANGED
ANTERIOR BORDER	ABSENT	ABSENT	ABSENT OR MINUTE, DOWN–SLOPING STEEPLY	NARROW, DOWNSLOPING	CONVEX ABAXIALLY, HORIZONTAL SAGITTALLY	UNCHANGED	UNCHANGED OR NARROW, CONVEX, RAISED	CONVEX, RAISED, NARROW TO MEDIUM
ANTERIOR BORDER FURROW	ABSENT	ABSENT	ABSENT	ABSENT	DISTINCT ONLY ABAXIALLY	UNCHANGED	UNCHANGED, OR EVEN DEPTH	EVEN DEPTH
PALPEBRAL LOBE	INDISTINCT, DEPRESSED	DOWNSLOPING ABAXIALLY, BELOW CHEEK LEVEL, 0·17 GLAB. LENGTH	HORIZONTAL, BELOW CHEEK LEVEL; 0·2 GLABELLAR LENGTH	CONVEX, BELOW CHEEK LEVEL; 0·23 GLABELLAR LENGTH	CONVEX, SLIGHTLY BELOW CHEEK LEVEL 0·27 GLABELLAR LENGTH	CONVEX, SAME LEVEL AS CHEEK; 0·30 GLABELLAR LENGTH	UNCHANGED, 0·33 GLABELLAR LENGTH	UNCHANGED
PALPEBRAL FURROW	ABSENT	ABSENT	INDISTINCT	DISTINCT	UNCHANGED	IMPRESSED	UNCHANGED	UNCHANGED
POSTERIOR END OF PALPEBRAL LOBE	OPPOSITE ANT. GLABELLAR FURROW	OPPOSITE ANT. LOBE – POST. FURROW	OPPOSITE MIDDLE FURROW–MIDDLE LOBE	OPPOSITE MIDDLE LOBE–POST. FURROW	OPPOSITE POST. FURROW	UNCHANGED	OPPOSITE POST. FURROW – POST. LOBE	OPPOSITE POST. LOBE–OCCIPITAL FURROW
POSTERIOR BORDER (ABAXIAL TO FULCRUM)	ABSENT	DIVERGES AT 25 – 30°	DIVERGES AT 30 – 35°	DIVERGES AT 35 – 40°	DIVERGES AT 40 – 45°	UNCHANGED	DIVERGES AT 45 – 50°	DIVERGES AT 50 – 55°
POSTERIOR BORDER FURROW	ABSENT	INDISTINCT	DISTINCT, STRONGLY GENICULATE	MODERATELY GENICULATE	WEAKLY GENICULATE WIDENS ABAXIALLY	UNCHANGED	STRAIGHT, WIDENS ABAXIALLY	UNCHANGED
GENAL SPINE	—	—	EXTREMELY SMALL	EXTENDS TO LEVEL OF 1ST OR 2ND SEGMENT	—	—	—	EXTENDS TO LEVEL OF 5TH SEGMENT
ANTERIOR SECTION OF FACIAL SUTURE	?	CONVERGES	CONVERGES	CONVERGES SLIGHTLY	SAGITTAL TO ANTERIOR BORDER FURROW	UNCHANGED OR DIVERGES	DIVERGES SLIGHTLY	DIVERGES MODERATELY
LENGTH OF CRANIDIUM (Ax)	0·38 – 0·49mm. (12 – 15·5mic. divs.)	0·50 – 0·64mm. (16 – 20·5mic. divs.)	0·65 – 0·79mm. (21 – 25·5mic. divs.)	0·80 – 0·94mm. (26 – 30·5mic. divs.)	0·95 – 1·24mm. (31 – 39·5mic. divs.)	1·25 – 1·36mm. (40 – 43·5mic. divs.)	1·37 – 1·49mm. (44 – 47·5mic. divs.)	1·50 – 3·16mm. (48 – 100 mic. divs.)
MERASPID DEGREE	(PROTASPIS)	0 – 1	(1) – 2 – 3	(3) – 4 – 6	7 – 11 – ?	?	?	(6?) – (8 – 53 – (60)

Stage III: Cranidial lengths 0·65–0·79 mm.; meraspid degrees (1), 2 and 3 (text-fig. 8 III; Pl. 110, figs. 5, 6). The axial furrows are deeply impressed, from the posterior edge to the anterior glabellar furrow, faint over the eye ridges, then indistinct on the sides of the frontal lobe. The frontal lobe is rounded laterally, and either reaches the anterior edge, or an extremely narrow, down-sloping anterior border. In the latter case the border and the lobe are separated by a distinct change in slope. The frontal lobe is subdivided by a pre-anterior furrow. The palpebral lobe is short, subhorizontal (tr. and sag.), depressed below cheek level, and with an indistinct palpebral furrow; the posterior end of the lobe is opposite the middle glabellar furrow or just below it. The cheek furrows parallel the eye ridges. The posterior border is horizontal, and separated from the cheek by a distinct border furrow; the border is again strongly geniculate, with the abaxial section directed antero-laterally at 30–35°. The anterior sections of the facial sutures converge strongly, and the posterior sections are very short and diverge at 45°.

The librigena has a small genal spine, which is directed almost sagittally to level of the occipital furrow.

Stage IV: Cranidial lengths 0·80–0·93 mm.; meraspid degrees (3), 4, 6 (text-fig. 8 IV; Pl. 110, figs. 7–9). Axial furrows converge slightly to anterior glabellar furrow, then curve out and around an expanded frontal lobe which is separated from the anterior edge by a narrow down-sloping anterior border. The palpebral lobe is convex (tr. and exsag.), below the level of the cheek, and separated from it by

a distinct palpebral furrow. The posterior end of the lobe is opposite the middle glabellar lobe or posterior furrow. The cheek is wider and flatter than in previous stages; cheek furrows parallel the eye ridge. The posterior border is convex, geniculate, with the abaxial section directed antero-laterally at 35–40°. The librigenal spine reaches the level of the 1st or 2nd thoracic segment.



TEXT-FIG. 8. Development of *B. flindersi*. Roman numerals indicate the stage of cranidial development as described in the text. I, protaspis; II, meraspis, degree 0; III, meraspis, degree 2; IV, meraspis degree 6; V, meraspis, degree 10; VI*b*, meraspis, degree 15. Magnification constant at approximately × 50.

Stage V: Cranidial lengths 0·94–1·24 mm.; meraspid degrees 7–11 (text-fig. 8 v; Pl. 110, figs. 10, 11). The frontal glabellar lobe is rounded, and slopes down to a distinct anterior border furrow. The anterior border is convex abaxially, but narrows and flattens opposite the frontal lobe. The axial and palpebral furrows are deeply impressed and the cheek sometimes shows traces of furrows. One exceptionally well-preserved specimen shows the anterior cheek furrow extending from the middle glabellar furrow to the posterior end of the palpebral lobe, and retains traces of the pre-anterior glabellar furrow. The palpebral lobe is convex (tr. and exsag.), slightly below the level of the cheek, and with its posterior end opposite the posterior glabellar furrow or posterior lobe. The posterior border furrow is deep, weakly geniculate, widens abaxially and becomes confluent with the palpebral furrow. The abaxial section of the posterior border is at 40–45°. The anterior section of the facial suture is directed sagittally to the border furrow, then crosses the border diagonally to cut the anterior

edge opposite the sides of the frontal lobe; the posterior sections are short, diverging, and slightly convex abaxially.

The librigena has a distinct lateral and posterior border and furrow. The genal spine extends to the level of the 4th thoracic segment.

Stage VIa: Cranidial lengths 1·25–1·36 mm.; includes at least meraspid degree 12 (Pl. 110, fig. 12). The length of the frontal glabellar lobe is $\frac{1}{3}$ of the total glabellar length. The palpebral lobe is relatively long, on approximately the same level as the cheek, and with its posterior end opposite the posterior glabellar furrow and lobe. The abaxial section of the posterior border is at 40–45°. The anterior section of the facial suture is directed sagittally or diverges slightly to the anterior border furrow.

Stage VIb: Cranidial lengths 1·37–1·50 mm. (text-fig. 8 VI*b*; Pl. 110, fig. 13). The anterior border is unchanged or becomes convex, with the same width abaxially and sagittally. The posterior end of the palpebral lobe is opposite the posterior glabellar furrow or lobe. The abaxial section of the posterior border is at 45–50°. The anterior section of the facial suture diverges slightly to the anterior border furrow.

Stage IVc: Cranidial lengths 1·50–3·16 mm.; includes meraspides of degrees 18–55 (Pl. 116, figs. 14, 15). The cephala of this group have basically attained the holaspid morphology. With increase in size the anterior border continues to widen and the length of the frontal glabellar lobe decreases in proportion to the total glabellar length. The posterior end of the palpebral lobe is opposite the posterior lobe or occipital furrow, the abaxial section of the border is at 50–55°, and the anterior sections of the facial sutures are divergent.

(*b*) *Development of the thorax* (Table 4)

Degree 0 (2 specimens). The transitory pygidium is triangular in shape, with its maximum width (tr.) at the anterior edge which articulates with the posterior edge of the cranidium between the fulcral points. The axial furrows are shallow and taper to a point on the posterior edge. The pleural field slopes down strongly abaxially, and there is a continuous lateral and posterior margin. The axis is subdivided into 3 or 4 rings in one specimen, and 3 in the other; in both specimens the anterior part of the pleural field is indistinctly furrowed.

Degrees 1–4. The prothoracic segments released from the transitory pygidium possess normal axial and articulating half rings, and geniculate pleurae. At degree 1, the pleural furrows are poorly developed

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EXPLANATION OF PLATE 110

Figs. 1–15. *Balcoracania flindersi* gen. et sp. nov. 1, F16700, ×17; larval hypostome, matched with cranidial, Stage IV. 2, F16687, ×15; cranidium, Stage II, showing cheek furrows. 3, F16688, ×15; meraspis, degree 0, Stage II. 4, F16689, ×15; cranidium, Stage II, showing distinct palpebral lobes. 5, F16690, ×15; cranidium, Stage III, showing distinct cheek furrows. 6, F16691, ×15; meraspis, degree 3, Stage III. 7, F16692, ×15; cranidium, Stage IV, showing narrow down-sloping anterior border. 8, F16693, ×15; crushed and asymmetrically distorted meraspis, degree 6, Stage IV. 9, F16694, ×15; meraspis, degree 6, Stage IV. 10, F16695, ×15; cranidium, stage V, showing distinct cheek furrows. 11, F16696, ×15; incomplete meraspis, degree 11, Stage V. 12, F16697, ×15; cranidium, Stage VI*a*, showing pre-anterior lateral glabellar furrows. 13, F16698, ×15; cranidium, Stage VI *b*. 14, F16699, ×15; meraspis, degree 18, Stage VI*c*; cephalon partly exfoliated, librigenae slightly displaced, portion of opisthothorax and transitory pygidium missing. 15, F16682, ×15; holaspid cranidium, partly exfoliated.

Figs. 16–18. *Emuella polymera* gen. et sp. nov. 16, F16701, ×15; cranidium. 17, F16702, ×15; cranidium showing minute anterior border, anterior position of palpebral lobes. 18, ×3; portion of bedding plane showing F16701–2 in relation to a holaspid cephalon.

Figs. 19–22. *Balcoracania dailyi* gen. et sp. nov. 19, F16703, ×15; cranidium, Stage I. 20, F16704; cranidium, Stage II, showing posterior position of palpebral lobe. 21, F16705, ×15; incomplete cranidium, Stage III, showing distinct development of anterior border and border furrow. 22, F16706, ×15; meraspis, degree 10, Stage IV, showing transitory pygidium with entire margins.

and pleural spines have not been observed; at degrees 2–4, the furrows become more distinct and spines develop. The axial furrows converge evenly to the posterior and are aligned with those of the pygidium; the pleurae are progressively shorter (tr.) to the posterior, and their abaxial ends are aligned with the lateral borders of the pygidium.

The morphology of the transitory pygidium is basically as for degree 0, with very little increase in absolute size. The number of rings on the axis varies from 3 to 4, and the pleural field shows the pleural and interpleural furrows of the two most anterior segments; posteriorly the furrows are indistinct.

TABLE 4. Development of the meraspid thorax and transitory pygidium in *B. flindersi*. A_1, total cranidial length of the articulated cephalon is given in micrometer divisions where 1·00 mm. = 32 divisions.

Meraspid degree	*Cranidial length* (A_1)	*Cephalic stage*	*Segments in transitory pygidium*
0	17	II	3
0	17	II	3–4
1	20	II	4
1	21	III	5
2	23	III	2–3
3	24	III	3–4
3	25	III	2–3
3	26	IV	3
3	26	IV	3
4	26	IV	3
4	27	IV	1
6	28	IV	3
6	29	IV	1–2
6	29	IV	6
6	30	IV	1–2
6	30	IV	4
10	34	V	2
11	38	V	3
18	67	VI*c*	3
18	72	VI*c*	3–4
19	72	VI*c*	3
27	80	VI*c*	3
53	100	VI*c*	3–4

Degree 6 (4 specimens). The prothorax has already attained the characteristic adult morphology; the 5th segment is fused to the macropleural 6th, with the line of fusion visible on the interfurrow platform. The macropleural spine extends to the posterior edge of the transitory pygidium, curving inwards slightly at the posterior end. The axis tapers strongly but evenly to the posterior. The pleurae shorten progressively from the 1st to the 5th segment. The anterior edge of the transitory pygidium articulates with the posterior edge of the 6th between the notches on the posterior border.

Degrees 10–55. The prothorax is as described for degree 6; the opisthothoracic segments are normal. The pleural furrows are generally more distinct towards the anterior, and in the higher degrees do not occur on most of the posterior opisthothoracic segments and the transitory pygidium. The transitory pygidium may have up to 6 distinct axial rings, but generally only the 2 most anterior segments are distinct on the pleural field. The absolute size of the pygidium increases little.

(*c*) *Development of the hypostome* (Table 5)

The hypostome attains the adult morphology when its length (sag.) is approximately 1·45 mm.; from this point onwards the only change is an increase in size. Independent confirmation is given by the fact that the length of the cranidium matched with a hypostome of this size falls within the size range of

Stage VI*c*, the stage in which the cranidium attains the holaspid condition. Changes during ontogeny primarily affect two groups of characters: (*a*) the size and position of the anterior wings; the position is expressed by the ratio of lengths (sag.) from the anterior edge respectively to the level of the anterior wings and to the level of the lateral notch; (*b*) the shape of the posterior lobe of the median body.

The smallest hypostome is matched with cranidia in the upper portion of the size range of Stage III and the lower portion of Stage IV. The posterior lobe of the median body is triangular with the bounding lateral furrows converging to the posterior from the lateral notch. The anterior wings are very small, only slightly depressed, and the ratio of lengths is 1:2, i.e. the wings are towards the anterior end. With increase in size the posterior lobe becomes subrectangular, with a transverse posterior border furrow developing; the anterior wings become more pronounced and depressed, and move progressively to the posterior, the ratio changing to 2:3 (Pl. 110, fig. 1).

TABLE 5. Development of the hypostome in *B. flindersi*. H_1 is the sagittal length of the hypostome, H_4 is the transverse length of the hypostomal suture, R_1 is the transverse length of the rostral suture and A_1 is the total cranidial length; all measurements are expressed in micrometer divisions where 1·00 mm. = 32 divisions. H_4, measured on the hypostome, is approximately equal to R_1, which is measured on the cephalon; thus for any given value of H_4, a range of values for A_1 can be obtained. The hypostome can then be matched to the equivalent stage (or stages).

H_1	H_4 (= R_1)	A_1 *of equivalent cephalon*	*Cephalic stage*
18	15	24–28	III, IV
19	16	28–32	IV, V
26	18	30–34	IV, V
27	18	30–34	IV, V
29	20	34–36	V
32	21	34–38	V
32	22	40–43	VI*a*
35	24	42–43	VI*a*
38	27	45–46	VI*b*
38	28	45–46	VI*b*
42	30	47–57	VI*c*
46	32	55–67	VI*c*

Ontogeny of Balcoracania dailyi

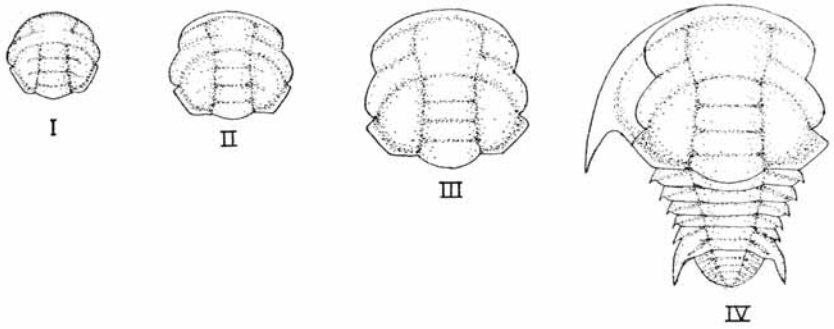
(*a*) *Development of the cephalon* (Table 6; text-fig. 9)

Stage I: Cranidial lengths 0·50–0·70 mm.; all specimens appear to be meraspid cranidia (text-fig. 9 1; Pl. 110, fig. 19).

The cranidium is subcircular in outline with steeply down-sloping margins. The glabella is moderately convex (tr.) and narrow; the glabellar furrows are distinct and transverse. The axial furrows are deep posteriorly, subparallel but pinched in sharply at the anterior glabellar furrow; anteriorly the furrows are faint, diverging around an expanded frontal glabellar lobe. The frontal lobe reaches the anterior edge, and is partially subdivided by short pre-anterior glabellar furrows. The eye ridge is distinct, directly slightly to the posterior, and slopes steeply downwards abaxially. The palpebral lobe is short, depressed below the cheek level, horizontal (sag. and tr.), and is only indistinctly defined by a palpebral furrow; the posterior end of the lobe is opposite the middle glabellar furrow or lobe. The cheek is narrow, steeply down-sloping abaxially and posteriorly, and is subdivided by cheek furrows parallel to the eye ridge. The posterior border is narrow, horizontal or slightly downsloping, and separated from the cheek only by a change in slope. The border is geniculate with short transverse section and a longer section directed antero-laterally at 25–30°. The anterior sections of the facial suture converge strongly to intersect the anterior edge at its junctions with the axial furrows. The posterior sections are extremely short, and curved.

TABLE 6. Larval development of *B. dailyi* based upon stages of development of the cranidium.

CHARACTER	*STAGE I*	*STAGE II*	*STAGE III*	*STAGE IV*	*STAGE V*
FRONTAL GLABELLAR LOBE	SUB-TRIANGULAR	SLIGHTLY ROUNDED ABAXIALLY	ROUNDED ABAXIALLY	UNCHANGED	UNCHANGED
ANTERIOR BORDER	ABSENT	NARROW, DOWNSLOPING STEEPLY	CONVEX ABAXIALLY, HORIZONTAL TO SLIGHTLY DOWNSLOPING SAGITTALLY	BORDER CONVEX, SLIGHTLY RAISED	UNCHANGED
ANTERIOR BORDER FURROW	ABSENT	INDISTINCT OR ABSENT	INDISTINCT SAGITTALLY, DISTINCT ABAXIALLY	DISTINCT, WITH BORDER FURROW FOSSULAE	UNCHANGED
PREGLABELLAR FIELD	ABSENT	ABSENT	ABSENT	MINUTE	NARROW, DOWNSLOPING
PALPEBRAL LOBE	BELOW CHEEK LEVEL, DOWNSLOPING ABAXIALLY, 1/4 GLABELLAR LENGTH	BELOW CHEEK LEVEL, CONVEX (SAG. AND TR.) 1/4 GLABELLAR LENGTH	SAME LEVEL AS CHEEK, CONVEX, BETWEEN >1/4 & <1/3 GLABELLAR LENGTH	ABOVE CHEEK LEVEL, CONVEX, 1/3 GLABELLAR LENGTH	UNCHANGED
PALPEBRAL FURROW	ABSENT TO INDISTINCT	DISTINCT	DISTINCT, IMPRESSED	UNCHANGED	UNCHANGED
POSTERIOR END OF PALPEBRAL LOBE	OPPOSITE MIDDLE GLABELLAR LOBE	OPPOSITE MIDDLE LOBE-POSTERIOR FURROW	OPPOSITE POSTERIOR FURROW	OPPOSITE POSTERIOR FURROW-POSTERIOR LOBE	OPPOSITE POSTERIOR LOBE-OCCIPITAL FURROW
POSTERIOR BORDER (ABAXIAL TO FULCRUM)	DIVERGES AT 30°	DIVERGES AT 35–40°	DIVERGES AT 40–45°	DIVERGES AT APPROX. 50°	DIVERGES AT 50–55°
POSTERIOR BORDER FURROW	INDISTINCT	DISTINCT, MODERATELY GENICULATE	WEAKLY GENICULATE	STRAIGHT, WIDENS ABAXIALLY	UNCHANGED
ANTERIOR SECTION OF FACIAL SUTURE	CONVERGES SLIGHTLY	SHORT SECTION DIRECTED SAGITTALLY	DIVERGES SLIGHTLY	DIVERGES MODERATELY	UNCHANGED
GENAL SPINE	–	–	–	MINUTE, EXTENDS TO LEVEL OF POSTERIOR BORDER OF 1ST.–2ND. SEGMENT	LENGTHENS RAPIDLY TO ATTAIN ADULT CONDITION
LENGTH OF CRANIDIUM (A)	0·50–0·70mm. (16–22·5 mic. divs.)	0·72–0·92mm. (23–29·5 mic. divs.)	0·94–1·14mm. (30–36·5 mic. divs.)	1·15–1·48mm. (37–47·5 mic. divs.)	1·50–2·90mm. (48–93 mic. divs.)
MERASPID DEGREE	–	–	–	6–10	(11)–12–39–(52)



TEXT-FIG. 9. Development of *B. dailyi*. Numerals indicate stages of cranidial development as described in the text. I, II, and III, meraspid cranidia; IV, meraspis, degree 6. Magnification constant at approximately ×50.

Stage II: Cranidial lengths 0·72–0·93 mm. (text-fig. 9 II; Pl. 110, fig. 20). The axial furrows converge evenly from the posterior edge to the anterior glabellar furrow, then diverge around an expanded and rounded frontal glabellar lobe. The frontal lobe is separated from the anterior edge by a narrow downsloping anterior border. The palpebral lobe is convex (tr. and exsag.), below the cheek level, but distinctly defined by a palpebral furrow; the lobe is relatively long (¼ glabellar length) with the posterior edge opposite the posterior glabellar furrow or just anterior to it. The cheek is wider (tr.) than in Stage I, less steeply down-sloping; the cheek furrows are indistinct. The posterior border is narrow, convex, and the border furrow is distinct. The abaxial portion of the border is directed antero-laterally

at 35–40°. The anterior sections of the facial suture are directed sagittally for a short distance before curving inwards; the posterior sections are short, diverging and slightly convex abaxially.

Stage III: Cranidial lengths 0·94–1·14 mm. (text-fig. 9 III; Pl. 110, fig. 21). The frontal glabellar lobe is rounded laterally, and slopes down to an anterior border furrow. The anterior border is narrow, slightly raised and convex abaxially, horizontal to slightly down-sloping opposite the frontal lobe. The anterior border furrow is distinct abaxially, shallow and indistinct opposite the frontal lobe. The palpebral lobe is convex (tr. and exsag.), on the same level as the cheek, and defined by a distinct palpebral furrow; the posterior end is opposite the posterior glabellar furrow. The abaxial section of the posterior border is directed antero-laterally at 40–45°; the posterior border furrow is slightly curved. The anterior sections of the facial suture diverge slightly to the border furrow.

Stage IV: Cranidial lengths 1·16–1·48 mm.; specimens falling within this size range include both cranidia and cephala with attached thoraces and pygidia, of degrees 6–13 (text-fig. 9 IV; Pl. 110, fig. 22).

The frontal glabellar lobe is rounded. The anterior border is narrow and convex, both abaxially and sagittally; the border furrow is deep abaxially, but shallows abruptly opposite the frontal lobe, with small anterior furrow fossulae. A minute, down-sloping preglabellar field is present, but not distinctly separated from the frontal lobe. The palpebral lobe is above the cheek level, about $\frac{1}{3}$ of glabellar length, with its posterior end opposite the posterior glabellar furrow or lobe. The abaxial section of the posterior border is directed antero-laterally at 50°. The posterior border furrow is almost straight, widening abaxially and sloping downwards abaxially. The anterior section of the facial suture diverges at 10° to the border furrow.

The librigena is narrow (tr.) with the genal spine very short, extending through the size range from the level of the posterior border to that of the 1st or 2nd thoracic segment.

TABLE 7. Development of the meraspid thorax and transitory pygidium in *B. dailyi*. A_1, total cranidial length of the articulated cephalon is given in micrometer divisions where 1·00 mm. = 32 divisions.

Meraspid degree	*Cranidial length* (A_1)	*Cephalic stage*	*Segments in transitory pygidium*
6	38	IV	3
6	40	IV	4–5
6	40	IV	4
6	44	IV	3
10	45	IV	4–5
10	48	V	3
12	48	V	5
13	46	V	4–5
13	48	V	5
14	50	V	4–5
17	54	V	3
21	53	V	3–4
22	61	V	9
24	75	V	4–5
28	75	V	7–8
35	115	V	4
39	107	V	6

(*b*) *Development of the thorax* (Table 7)

No meraspis of a degree less than 6 is known from this species. The development from this degree is basically the same as in *B. flindersi*, but a greater variation in the number of segments in the transitory pygidium is observed, both within a degree and between degrees. Three specimens of degree 6 show 3 or 4 axial rings, and 1 or 2 complete sets of pleurae on the pygidium, but another specimen shows 6 distinct, and at least 1 indistinct axial rings, and 3 distinct sets of pleurae; the 2 most anterior segments appear fully formed, but their abaxial ends are continuous with the lateral border of the pygidium.

1 specimen of degree 21 possesses a pygidium with 9 distinct axial rings; the anterior 3 segments are completely formed, and appear to be only semi-ankylosed to each other and the rest of the pygidium. In this specimen the pygidium is 40% longer than in others with a normal complement of segments.

(*c*) *Development of the hypostome* (Table 8)

The changes taking place during the development are similar to those in *B. flindersi*. The smallest hypostome is matched with a cranidium of Stage I, and the smallest with the holaspid morphology with a cranidium larger than those of Stage IV.

TABLE 8. Development of the hypostome in *B. dailyi*. Explanation as for the table 5.

H_1	H_4 (= R_1)	A_1 *of equivalent cephalon*	*Cephalic stage*
20·5	12	19–21	I
22	16	23–25	II
25	18	25–28	II
25	20	28–35	II, III
28	20	28–35	II, III
33	22	35–38	III, IV
39	28	44–47	IV
42	29	48–50	IV
45	29	48–50	IV
53	39	69–	IV

Ontogeny of Emuella polymera (Plate 110, figs. 16–18)

Only 10 specimens of this species are known which are considered larval, and of these, only 2 retain the meraspid thorax. Accordingly the development is not divided into stages, as with the species of *Balcoracania*.

The smallest specimen found had a sagittal length of 0·40 mm., and appears to be a protaspis; however it is badly preserved and details are obscure. At a cranidial length of about 0·67 mm., a narrow down-sloping border appears in front of the frontal glabellar lobe, the palpebral lobe is below cheek level and extends posteriorly to the level of the middle glabellar lobe, and the anterior section of the facial suture has a very short sagittally directed section; one specimen of this size (Pl. 110, fig. 16) shows a pre-anterior glabellar furrow, and cheek furrows. This cranidial size corresponds to meraspid degree 1. At about 0·88 mm., the anterior border has become horizontal abaxially, the palpebral lobe extends to the level of the middle glabellar furrow, and the frontal lobe is outlined by deep axial furrows. A well preserved specimen shows that the cheeks are still furrowed. With further increase in size from 1·00 to 1·40 mm., the anterior border becomes horizontal to slightly convex, the border furrow develops fossulae, the palpebral lobe extends just beyond the middle glabellar furrow, and the anterior sections of the facial suture become slightly divergent. A meraspid degree 7 is included in this range. At approximately 1·7 mm., the cranidium exhibits the holaspid morphology.

No hypostomes which could be considered larval are known.

Discussion

The studies of the ontogenetic development of the three species reinforces the basis of the taxonomic discriminations made on the adult morphology; in particular, the species of *Balcoracania*, which are morphologically very close in the adult, can be clearly discriminated by their ontogenetic development.

The cephala of the three species undergo similar types of changes during their ontogeny, but the individual changes occur at different rates in each species. Thus the cranidia exhibit different combinations of characters at a given age (measured against cranidial length). In addition other features which are characteristic of the adult of the

species appear or are attained at some stage during the ontogeny. In *E. polymera* the characteristic relative length and position of the palpebral lobe is attained at an extremely early stage. In contrast, the preglabellar field which characterizes *B. dailyi* develops rather late compared with other features.

The size at which the cephalon attains the holaspid morphology differs in the genera. In *E. polymera* it is reached at a cranidial length of 1·7 mm., in the species of *Balcoracania* at 1·5 mm.

The development of the thorax is extremely similar in all species. It follows the general pattern outlined by Whittington (1957, 1959), with two important modifications; the release of the macropleural unit, and the change from prothoracic to opisthothoracic segments. With regard to the macropleural unit, it is significant that in *B. flindersi* where numbers are sufficient for all stages of early meraspid development to be represented, no meraspis of degree 5 has been discovered. It is evident that the 5th and 6th segments develop together in the transitory pygidium, and are released into the thorax as a unit. At degree 6, the 6th segment is already macropleural, and the spine reaches the level of the posterior edge of the transitory pygidium. However no trace of the macropleural spine has been found in transitory pygidia of degrees 0–4, indicating that the spine develops very rapidly, ostensibly during the period of the moult at which the macropleural unit is released into the thorax.

After the release of the macropleural unit into the thorax, there occurs a change in the size of the segments released, and the opisthothorax develops.

In all species the length of the transitory pygidium and the number of segments, as indicated by the number of furrows on the axis, vary both within an individual degree and between degrees (Tables 4, 7). Also the length of the cranidium varies considerably for a given degree, and considerable overlap may occur between successive degrees; 3 specimens are known of degree 3 with a range of cranidial lengths which overlaps that for specimens of degrees 4 and 6. It thus appears that segments may be added to the transitory pygidium during individual degrees, implying the occurrence of more than one moult within a degree. In addition, in meraspides of degree 6 or more, specimens occur with considerably more segments in the transitory pygidium than the average. In these cases the most anterior 2 or 3 segments appear to be fully formed, and only semi-ankylosed to the pygidium. It thus seems probable that in the development of the opisthothorax, more than one segment may occasionally be released during some moults.

Comparison of the rates of cephalic and thoracic development raise some points of interest. At degree 6 the cranidium has a length of 0·88 mm. in *B. flindersi*, but 1·25 mm. in *B. dailyi*; the cranidial development is thus further advanced in *B. dailyi* at this stage of thoracic development. In both species, however, the cranidium attains the holaspid condition at a cranidial length of 1·50 mm.; in *B. flindersi* this stage is reached at degree 16, and in *B. dailyi* at degree 13. The larval development of the thorax is thus far from complete and significantly lags behind that of the cranidium.

FUNCTIONAL MORPHOLOGY

The characters of the thorax of the Emuellidae are analysed on a basis of function, both in the adult trilobite and during development, and an attempt is made to seek causes framed in terms of adaptation.

Division of the thorax. The division of the thorax into a prothorax, characterized by a constant number of segments with normal pleurae, and an opisthothorax with a variable number of segments with pleurae clearly reduced in size, was previously only known in the Olenellidae (Hupé 1953*a*, *b*, *c*, 1955; Harrington *et al.* 1959).

In the Olenellidae the number of prothoracic segments varies from 11 in *Neltneria*, to 17 in *Fallotaspis* and *Nevadia*. The number of opisthothoracic segments differs more widely, from 2 to 30, but in general is low.

The division of the thorax has been considered to be a primitive character and to be lost in more advanced trilobites (Hupé 1953*a*, *b*; Harrington *in* Harrington *et al.* 1959). The number of segments in the opisthothorax has also been equated to the degree of 'primitiveness', those with many segments being considered the least evolved. In addition, the prothorax has been considered homologous to the thorax of normal trilobites, because of the fixity of the number of segments, and the opisthothorax as homologous with the pygidium. In most of the Olenellidae in which the prothorax is relatively long and multisegmented, and the opisthothorax short and with only a few segments, the homology may seem justified. However in *Paedeumias robsonensis* (Burling), in which the opisthothorax is as long as the prothorax and contains more than twice the number of segments, it appears difficult to justify its homology with the normal pygidium. It is even more difficult in the case of the Emuellidae where the opisthothorax is twice the length of the prothorax, and has between 48 and 55 segments; in addition the prothorax contains only 6 segments. It is considered that such a homology is inaccurate, or at least misleading.

In attempting to explain the phenomenon on the basis of functional morphology, three questions must be faced; why does the change occur, at what point does it take place, and what causes the eventual termination of segmentation? An attempt is made to answer these questions with reference to the Emuellidae, and to test the validity of the resulting hypothesis by comparison with the Olenellidae.

In the prothorax of the Emuellidae, the posterior edges of the first 4 normal segments are directed transversely, but those of the 6th segment are directed postero-laterally, from the axial furrow to the notch at the base of the macropleural spine. If the 7th segment is to articulate in the normal fashion with the posterior edge of the 6th, its pleurae must necessarily be reduced in length, as the axial ring can only have normal taper. It is considered that in this case, it is the abrupt space reduction, consequent upon the change in direction of the posterior border of the macropleural segment, which initiates the change in the nature of the segments released from the transitory pygidium.

In the adult, the segments of the opisthothorax form a perfectly graded series between the posterior border of the 6th segment and the anterior pygidial border (text-fig. 5A). In the ontogeny of the Emuellidae, meraspid degree 6 shows the transitory pygidium articulating with the posterior border of the 6th, in the same relative position and manner as does the 7th segment in the adult, and displaying a perfect gradation with the prothorax (text-fig. 8). In succeeding meraspid degrees, the absolute size of the transitory pygidium increases only very slightly, whilst that of the 6th segment increases more rapidly, and the opisthothorax remains perfectly graded with respect to both. Thus the release of segments from the transitory pygidium ceases when the ratio of the lengths (tr.) of the posterior border of the 6th and the anterior pygidial border becomes constant. It is notable in this connection that in the ontogeny of the Emuellidae, the

cephalon attains the holaspid condition whilst segments are still being released into the opisthothorax.

In the Olenellidae, only *Neltneria* has the last prothoracic segment macropleural, and it is notable that the number of prothoracic segments is less than in other members of the family. In *Neltneria* the posterior edges of the pleurae of the 11th segment have only very short transversely directed sections before the spine curves to the posterior; thus the space available for pleurae of succeeding segments is reduced. In addition the mechanics of articulation necessitate a progressive inclination of the pleurae to the posterior, with the last opisthothoracic segment having its pleurae wrapped around the sides of the pygidium. In the Olenellinae and *Fallotaspis*, it is the 3rd prothoracic segment which is macropleural. The posterior edge of the macropleural segment is transverse for most of its length, thus it does not cause an abrupt decrease in the space available for succeeding segments. However it does reduce the space, and causes the pleurae of succeeding segments to be progressively inclined to the posterior, and it appears to be this factor which finally causes a change in the nature of the segments released. As this is a more gradual process than in the Emuellidae, a greater number of prothoracic segments are released. In the Olenellidae which possess an opisthothorax, but not macropleural spines, e.g. *Elliptocephala*, *Nevadia*, the segments have pleurae progressively inclined to the posterior, and possessing long pleural spines. In those without division of the thorax, e.g. *Holmia*, the pleurae are again inclined progressively to the posterior, but do not possess long pleural spines; consequently space reduction does not reach a critical point.

It is thus considered that the division of the thorax can be explained as a response to a space reduction, either abrupt or gradual, which necessitates a change in the nature of the segments, in order to maintain the ability to articulate freely. It may be significant however, that the phenomenon has only been observed in Lower Cambrian trilobites. Possibly only primitive trilobites had this ability, or that more advanced ones solved similar problems in a less dramatic fashion.

Macropleurality. This feature occurs in many Cambrian and post-Cambrian families. In the Cambrian it is widespread, with most genera of some families exhibiting this feature; these include the Olenellidae, Neoredlichiidae, Bathynotidae, Paradoxididae, Zancanthoididae, and Dolichometopidae. In post-Cambrian families, such as the Shumardiidae, Asaphidae, Remopleurididae and Cyclopygidae, expression of the feature is usually confined to a single genus.

In the Emuellidae the last segment of the prothorax is macropleural. The spine, which is formed by both anterior and posterior pleural bands, tapers gradually to the posterior, curving inwards slightly, and extending to the level of the posterior edge of the pygidium or just beyond it. The doublure of the segment extends from the base of the pleural spine of the 5th, to which the 6th is fused, to the notch on the posterior border of the 6th. The spine is thus hollow, almost flat on top, slightly V-shaped to rounded below.

In the ontogeny of the Emuellidae, the spine appears abruptly at meraspid degree 6, without having previously appeared in the transitory pygidia of earlier degrees. The general form is the same as in the adult, with the spine extending to the level of the posterior edge of the transitory pygidium. In succeeding degrees, the length of the spine increases to maintain the same relative position.

In view of the high correlation between the lengths of the macropleural spine, and the opisthothorax and pygidium at all ontogenetic stages, it is considered that the spine serves both to stabilize and protect the opisthothorax. In a rest position on the sea floor, the flattish base of the spine would be opposed to the bottom, rather than the delicate pleural spines.

Hupé (1950, 1953*c*) suggested that the macropleural segment is the genital segment containing the gonopores on the basis that as the trilobites themselves are primitive, they are near the original condition where gonads and gonopores are metameric, and would be localized on segments of particularly primitive character. Hupé considered that the macropleural segments are the most primitive because of their narrow axis, and then compared the position of the macropleural segments in trilobites with the position of the gonopore in the Insecta, Myriapoda, Crustacea, and Chelicerata (Hupé 1950, fig. 7*a*), concluding that the opisthogoneate and progoneate tendencies of the 'Atennulata' existed in trilobites in the Lower Cambrian.

There is little evidence that the macropleural segments are the most primitive; in fact in any one trilobite it is the macropleural segment which, by definition, is the most specialized. There is no evidence of a structure on the dorsal surface of the macropleural segment which could be interpreted as a gonopore; thus if the gonopore is located on the ventral side, some modification of the ventral morphology might be expected. However, in the Emuellidae, the doublure of the segment is strictly comparable in structure and position to that of normal prothoracic segments. If it is assumed that the gonopores were carried in the soft ventral integument, there seems to be no reason why the macropleural segment alone should carry them. The suggestion, based on comparison with a hypothetical annelid ancestor, that the gonopores will occur on most, if not all thoracic segments (Raymond 1920, and others), appears the more reasonable.

The contention by Hupé (1953*b*) that macropleural segments in Lower Cambrian trilobites have two preferred positions, one anterior and one posterior, appears to have greater validity. The Olenellidae are characterized by having the 3rd prothoracic segment macropleural, the Emuellidae and *Neltneria* the last. Other related families display a similar division, but at least 2 genera (*Olenelloides* and *Bathyuriscidella*) possess 2 macropleural segments, more or less symmetrically placed in the thorax. The significance of the apparent division is not known.

In all genera whose adults possess macropleural segments, and whose ontogeny is known, the macropleural segment either appears in the transitory pygidium and is released at the appropriate meraspid degree (Olenellidae, *Shumardia*), or develops suddenly at the time of release from the transitory pygidium. In no known case does the macropleural segment develop after release into the thorax. This implies that the segments have some adaptive significance in the larval stages or that sexual maturity is very precocious. Hupé (1953*c*, p. 116), whilst allowing a possible secondary adaptive function connected with pelagic life, considered that the presence of such segments would be almost universal if this were the case; he accordingly considered sexual maturity to be precocious, and that a presumed change from allometric to isometric growth during the early meraspid period marked this change (1953*b*, p. 121). However, this alleged change is based on little data, is unsupported by statistical testing, and in any event is not necessarily indicative of sexual maturity. Therefore it is considered that the first alternative, that of adaptation to a pelagic existence is the more likely possibility.

Indeed Hupé's reasons, i.e. lack of universality, for rejecting this as the primary cause, apply equally well to the interpretation of the macropleural segments as genital.

In *Paradoxides* (Westergard 1936, Whittington 1957, 1959) the 1st and 2nd segments are both strongly macropleural when they first appear, but regress during meraspid development, the 1st more rapidly than the 2nd, so that at degree 15 (Whittington 1957, fig. 5*b*) only the 2nd is macropleural. In the adult, the 2nd segment is only weakly macropleural. The same sort of phenomenon occurs in both the Olenellidae and Redlichiidae, and may be comparable to the regression, during the same period, of the fixigenal and intergenal spines of the Olenellidae and Paradoxididae. Whittington (1957, p. 450) has attributed to the latter a role of support and buoyancy in a supposed pelagic life. It is reasonable to suggest that the macropleural spines had a similar adaptive function. In the Emuellidae it seems probable that the spines also served a protective function, a role which continued into the adult stages. However, the retention of the macropleural spines in adults of most genera raises several problems. The spines may retain a function of stabilization or protection in some cases, but in others they occur in genera belonging to families in which the other members appear well adapted to their habitat and mode of life, e.g. *Octinellus* in the Illaenidae. The question thus arises as to whether the adaptive function is secondary or not. In this context Hupé's suggestion as to the primary function cannot be dismissed.

Raw (1953) suggested that the presence of macropleural spines is related to merocyclism inherited from a polychaete ancestor, occurring most frequently in primitive forms and becoming lost when the segments achieve a graded condition. Macropleurality undoubtedly occurs most commonly amongst Lower Cambrian forms, but even here it is difficult to match macropleurae with cycles of segmentation. Raw (1953, p. 94) cited *Olenelloides armatus* (Peach) as an example where one macropleural segment alternates with two normal segments. This genus is generally regarded as aberrant, but even here it is necessary to consider the cephalic spines as representing macropleurae. Palmer (1957, p. 111) attempted to apply merocyclism to *Olenellus* and *Paedeumias*, but found it necessary to combine it with the hypothesis of secondary segmentation (Størmer 1941) in order to fit merocycles. The presence of contiguous macropleural segments in the larval stages of *Paradoxides* and other genera casts grave doubts on Raw's concept. In post-Cambrian trilobites the sporadic occurrence of macropleural segments in more than one position affords another difficulty; in *Acidaspis*, Hupé (1950) listed seven species with five different positions of the macropleural segment.

Manton's studies on the functional morphology of modern arthropods are interesting in the above context, since she concludes that body form is largely determined by locomotory habits (Manton 1952, 1960, 1964).

Fusion of thoracic segments. The Emuellidae have the 5th and 6th segments of the prothorax fused together. Only one other genus, *Bathynotellus*, shows a similar fusion of segments within the thorax, and in addition one of the segments involved is macropleural. However, it is believed that there is a different functional basis for the fusion in the two cases.

In the Emuellidae the fusion of the otherwise normal 5th segment to the 6th appears to be simply a device to increase the muscular control over the long macropleural spine, and so aid in support and stability. The apodemal slit of the 6th is very strongly de-

veloped, and the fusion of the 5th allows its abaxial extension onto the inter-furrow platform. It also allows the elongated apodemal slit to abut against the adaxial end of the 6th pleural furrow, so that ventrally it forms a large transverse apodeme buttressed by an accessory ridge. On the pleural field, the development of a horizontal flap between the anterior lateral corner of the 6th and the pleural spine of the 5th (*E. polymera*) appears to be a strengthening device.

In *Bathynotellus*, the thorax has 13 segments, but the posterior ones are fused into a unit which has 3 axial rings and a macropleural spine; the pygidium is large, and its articulation with the macropleural unit is similar to that between the macropleural unit and transitory pygidium of meraspid degree 6 of the Emuellidae. In order to understand the situation in *Bathynotellus*, it is necessary to consider the allied genus *Bathynotus*.

Bathynotus has a thorax of 13 segments, with the 11th macropleural, the posterior 2 with considerably reduced pleurae, and a large pygidium. The macropleural spine is directed posteriorly, and in combination with the pygidium reduces the space available for the development of the pleurae of the two segments between them. It has been suggested above that a similar space reduction has resulted in the development of an opisthothorax in the Emuellidae and Olenellidae. However, the large pygidium in the Bathynotidae suggests that they were more advanced than the other two groups, and had stabilized the number of thoracic segments. The reduced segments thus cannot perhaps be homologized with a true opisthothorax, which is always associated with a small pygidium. It is evident that the problem was solved in a different way, by fusion of the two posterior segments to the macropleural 11th. Thus the 11th, 12th, and 13th segments in *Bathynotus* are homologous with the macropleural unit of *Bathynotellus*.

TAXONOMIC POSITION

The genera *Emuella* and *Balcoracania* possess a unique combination of cephalic and thoracic morphology that sets them apart from other groups of trilobites, and it is proposed that they should be placed in a separate taxon of familial rank, the Emuellidae.

The relation of the Emuellidae to other taxa can only be judged on morphological similarity. Some of the diagnostic characters of the family are found only in Cambrian trilobites, others occur in both Cambrian and post-Cambrian trilobites. However, when assessing the taxonomic position of the family, similarities in Cambrian and particularly Lower Cambrian trilobites are accorded most weight.

The combination of diagnostic characters of cephalon, thorax, and pygidium in the Emuellidae imposes certain conditions on the type of comparison which can validly be made. In particular, it is considered that the presence of a large pygidium largely invalidates comparisons based on the cephalon alone, and this is used as a premise for detailed comparisons of the cephala which follow.

The taxonomic position is assessed with regard both to features of adult morphology, and of ontogenetic development.

Comparisons of adult morphology

(*a*) *Thorax and pygidium*. The division of the thorax is known, apart from the Emuellidae, in some members of the Olenellidae. The occurrence and nature of the division in this family has already been discussed, but in general the genera are usually

characterized by a long prothorax (11–17 segments), and a short opisthothorax, the exception in the latter case being *Paedeumias robsonensis* (Burling), which has at least 29 opisthothoracic segments.

The occurrence of macropleurality has also been discussed. The presence of such segments in genera of so many obviously unrelated families casts grave doubts on the taxonomic value of this character, unless used in association with other thoracic features. In this context, the combination of macropleurality and thoracic division in some members of the Olenellidae is particularly important.

The Bathynotidae also show a combination of thoracic features similar to the Emuellidae, particularly *Bathynotellus*, in which fusion of segments is combined with macropleurality. However, it has been suggested above that the similarities are largely the result of convergence, and additionally the presence of a large pygidium in *Bathynotellus* precludes a close relationship.

(*b*) *Cephalon*. In the cephalon of the Emuellidae, the combination of sutural pattern, structure of the eye lobes, and of the posterior limb, constitute the essential diagnostic features; the glabellar shape is of lesser importance.

The sutural pattern consists of functional rostral, connective, hypostomal, and facial sutures. The cephalon is of the 'ptychopariid' type in the terminology of Rasetti (1952), and is considered to be the primitive type from which all others are secondarily derived (Harrington *in* Harrington *et al.* 1959, pp. 68, 158). Many taxa have members of this type, and those with Cambrian representatives include the Redlichiacea, Ellipsocephalacea, Paradoxididae, and Ptychopariidae.

The eye lobes consist of wide, essentially continuous eye ridges and palpebral lobes, extending in crescents from the frontal glabellar lobe, with the palpebral sections widely separated from the glabella. Genera of many families possess similar eye lobes, with the Cambrian groups Dolerolenidae, Ellipsocephalidae, Protolenidae, Bathynotidae and Ptychopariidae bearing the greatest resemblance.

The geniculate posterior limb of the Emuellidae appears to have no parallel in any other Cambrian family.

The glabella tapers forward to the anterior glabellar furrow, but has a variably expanded frontal glabellar lobe. The ontogeny of the members of the Emuellidae, together with the presence of variants with a bilobed frontal glabellar lobe, suggests that this shape may be due to the persistence of a larval characteristic into the adult. Thus the presence of an expanded frontal lobe in other genera does not necessarily mean a close relationship; conversely a regularly tapering glabella need not indicate a distant relationship.

The over-all morphology of the cephalon is most similar to some members of the Dolerolenidae, Protolenidae, and Ptychopariidae. Of these, the genera *Dolerolenus*, *Bergeroniellus*, and *Estaingia* of the so-called protolenoids, *Protolenus* of the undoubted Protolenidae, and members of the Antagminae, are probably the closest. In addition some of the Olenellidae are discussed, because of special similarities in the thorax to the Emuellidae.

Dolerolenus differs from the Emuellidae in the possession of an evenly tapering glabella, the faintness of the eye ridges, and the length of the posterior limb which is also transversely directed; the genal spine is also much shorter and not advanced.

Bergeroniellus and *Estaingia* resemble the group in the structure and position of the eye lobes, with the subgenera *B.* (*Bergeroniaspis*) and *B.* (*Olekmaspis*) being the closest. The glabella of *Estaingia* approaches the shape of that of *Balcoracania dailyi* in particular. The shape of the glabella of *Bergeroniellus* varies slightly, but is generally slightly tapering to the anterior. Both genera differ from the Emuellidae in the presence of wide preglabellar fields and transverse posterior limbs. *Protolenus* is similar to *Estaingia* except for a narrower preglabellar field and evenly tapering glabella, and so shares most of the above dissimilarities.

Of the Antagminae, *Eoptychoparia*, *Poulsenia*, and *Proliostracus* have a tapering glabella, and eye lobes similar to the Emuellidae. *Poulsenia*, in particular, has only a short preglabellar field, and the frontal lobe bears a similar relationship to the anterior border furrow, as does *B. dailyi*. The anterior sections of the facial sutures cut diagonally across the border, and vary from slightly divergent (*Eoptychoparia*), to rather strongly converging (*Poulsenia*). In all genera the posterior limb is in marked contrast to that of the Emuellidae.

In the Olenellidae the major differences are associated with the sutural pattern, the eye lobes and the posterior border.

(*c*) *Conclusions.* The strong similarities in the thorax of the Olenellidae and the Emuellidae suggest a close relationship, but the indications are that the latter are probably the more primitive group. The structure of the cephalon also suggests that the Olenellidae are the more advanced, as the 'olenellid' sutural pattern is now thought to have been secondarily derived from the 'ptychopariid' type, which is displayed by the Emuellidae (Hupé 1953*a*, Harrington *in* Harrington *et al.* 1959). Together these features suggest that an 'emuellid' stock may have given rise to the olenellid branch. This, however, does not settle the question of their placement within the existing taxonomic framework, for the very presence of the characters which suggest this relationship precludes the placement of the Emuellidae within the suborder Olenellina.

The other groups which show similarities to the Emuellidae belong to suborder Redlichiina (Dolerolenidae, Protolenidae), suborder Bathynotina (Bathynotidae), and suborder Ptychopariina (Antagminae). Of these, the Bathynotidae and the Antagminae exhibit the least similarities to the Emuellidae. Accordingly it is suggested that the family be placed in the suborder Redlichiina.

Within the suborder the position is not clear. The Dolerolenidae and the Protolenidae bear approximately the same degree of over-all similarity to the Emuellidae, but are placed in different superfamilies (Poulsen *in* Harrington *et al.* 1959), the Dolerolenidae in the Redlichiacea, and the Protolenidae in the Ellipsocephalacea. In addition the Dolerolenidae are thought to be transitional between the two superfamilies (Sdzuy 1959), and the protolenoids (*Bergeroniellus*, *Estaingia*) transitional between the Ellipsocephalacea and the Paradoxidacea (Öpik 1961, Pocock 1964).

Comparisons of developmental history

Whittington (1957, p. 462) stated that 'the nature of the developmental history and the morphology of the protaspis . . . offer additional criteria for judging relationships between families and larger groups'. The ontogenies of the Emuellidae are compared with those known from groups which, on the basis of holaspid morphology, appear

to be related: the Olenellidae, Redlichiidae, Dolerolenidae, Protolenidae, and Ptychopariidae.

Protaspides have not yet been recognized in the Olenellidae, but the meraspid development is broadly known from the investigations of Whittington (1957, 1959) and Palmer (1957). The ontogeny of *Redlichia chinensis* (Walcott) has been studied by Kobayashi and Kato (1951); at least one protaspis and several meraspides are described. The ontogeny of the Dolerolenidae is not well known but Kobayashi and Kato (1951, text-fig. 1) illustrated several protaspides of *Dolerolenus*, redrawn from Bornemann (1891). In the Protolenidae, Suvorova (1956) described larval stages of *Lermontovia* and *Bergeroniellus*; all specimens appear to be meraspid cranidia. Protaspides of *Strenuella*, a related protolenid, have been described by Kautsky (1945). Amongst the Ptychopariidae, the ontogeny of *Sao* is well known (Whittington 1957).

A comparison of the ontogenies of the families listed above with those of the Emuellidae, appears to affirm the degree of relationship deduced from the holaspid morphology, but fails to solve the problems which arise. Of the families considered, the protaspides and early meraspides (considered to be of greatest diagnostic value) of the Ptychopariidae are furthest from those of the Emuellidae. The remaining families are all members of the Order Redlichiida, and thus some similarity is to be expected.

In these families there is a similar reduction of the size of the frontal glabellar lobe, but to varying and generally greater degrees than in the Emuellidae, and a similar development of the anterior border and preglabellar field. The presence of a preglabellar field in the meraspides of all groups is not considered a major difference, as in the Emuellidae its initial development can be seen in *B. dailyi*. The most important remaining characters of the protaspides and early meraspides are the cheek furrows, bilobation of the frontal glabellar lobe, and the fixigenal spines. The Emuellidae have distinct cheek furrows, occasional bilobation, but lack fixigenal spines; the Redlichiidae have distinct furrows, definite bilobation, but also appear to ack spines; the Dolerolenidae, although very incompletely known, appear to possess only the cheek furrow; the Olenellidae have furrows and spines, but apparently lack the bilobation; the Protolenidae lack cheek furrows, but are bilobed, and some, but not all, species have fixigenal spines. It is thus apparent that all families bear some relationship to each other, but the degree of relationship is difficult to determine.

It is accordingly considered that the placement of the Emuellidae in the suborder Redlichiina is reasonably based, but its superfamilial position is best left open for the present.

EVOLUTION

Intrafamilial relationships. On the basis of adult morphology, *E. dalgarnoi* is intermediate between *E. polymera* and the species of *Balcoracania*; the morphology of the palpebral lobe, the posterior limb and the facial sutures, all lie between the limits for these structures in the other species. However, with so few species and incomplete stratigraphic information, further speculation is unwise.

Evolutionary position of the Emuellidae. In the possession of a ptychopariid sutural pattern, thick long eye lobes, expanded frontal glabellar lobe, long thorax combining

macropleurality and division, and a diminutive pygidium, the Emuellidae appear to be very primitive, and must be placed near the origin of redlichiid evolution.

It has been suggested that the Olenellina have evolved from a redlichiid-like trilobite with a ptychopariid sutural pattern (Hupé 1953*a*, Harrington *in* Harrington *et al.* 1959). The Emuellidae possess such a cephalon, and combine with it thoracic features which are shared only with some of the Olenellina, i.e. long, multisegmented thorax, division into pro- and opisthothorax, and macropleurality. Although the known members of the Emuellidae occur far too high in the Cambrian to be direct ancestors, they exhibit all the features which might be expected of such an ancestor. Thus, the Olenellina may have evolved from an 'emuellid'-type ancestor by migration and eventual loss of the facial sutures, and by reduction of the opisthothorax. Other members of the Redlichiida may have evolved from a similar ancestral stock by loss of the opisthothorax, retention of the basic sutural pattern, reduction of the frontal glabellar lobe, and development of the preglabellar field. The loss of the opisthothorax is foreshadowed in some of the Olenellina, and the development of the preglabellar field in *B. dailyi*. It is interesting to note that the changes taking place in the early meraspid stages of members of the Redlichiina are strikingly similar to the complete ontogeny of the Emuellidae.

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APPENDIX

Measurements of selected dimensions of adult specimens of the Emuellidae. All measurements are given as micrometer divisions where 1·00 mm. = 12 divisions.

1. *Emuella polymera*

A_1	C	D_5	A_1	C	D_5
16	2	6	45	10	13
22	5	7	46	10	15
26	6	8	46	10	16
26	5	8	47	10	15
30	6	10	47	8	14
31	7	11	51	10	20
32	7	11	52	11	16
34	7	13	55	12	20
35	6	12	58	10	20
37	8	10	60	13	20
37	8	12	60	11	20
38	7	15	73	15	23
39	7	13	75	14	25
40	8	14	82	14	26
40	8	13	86	18	28
43	8	14	88	16	30
43	9	14			

2. *Emuella dalgarnoi*

A_1	C	D_5	A_1	C	D_5
34	8	10	51	13	16
35	7	9	66	16	21
35	8	10	70	18	20
44	12	15	76	18	24
45	11	14	106	22	38
48	12	16			

3. *Balcoracania flindersi*

A_1	C	D_5	A_1	C	D_5
23	5	5	58	16	14
25	6	6	60	14	19
31	8	10	60	15	15
32	8	8	60	14	14
33	8	9	60	14	19
33	8	12	60	14	13
40	10	9	70	18	19
44	10	13	72	14	14
48	12	14	72	20	18
48	14	13	74	16	22
50	11	12	76	18	26
50	12	16	76	16	20
54	14	13	78	18	17
56	16	14	80	16	26
56	14	9	84	20	24
56	12	14			

4. *Balcoracania dailyi*

A_1	C	D_5	A_1	C	D_5
23	7	7	47	14	13
25	9	6	48	14	11
26	8	6	50	15	14
27	8	5	55	14	15
28	9	8	58	15	15
29	9	7	58	15	14
30	10	7	60	15	14
30	9	8	60	18	16
30	10	6	64	17	17
31	8	8	67	20	16
33	9	9	68	19	21
34	10	8	70	20	20
35	10	8	70	20	20
42	12	12	72	20	18
44	13	12	76	20	18
44	14	10	78	24	16
45	13	11	78	22	17
			78	25	20

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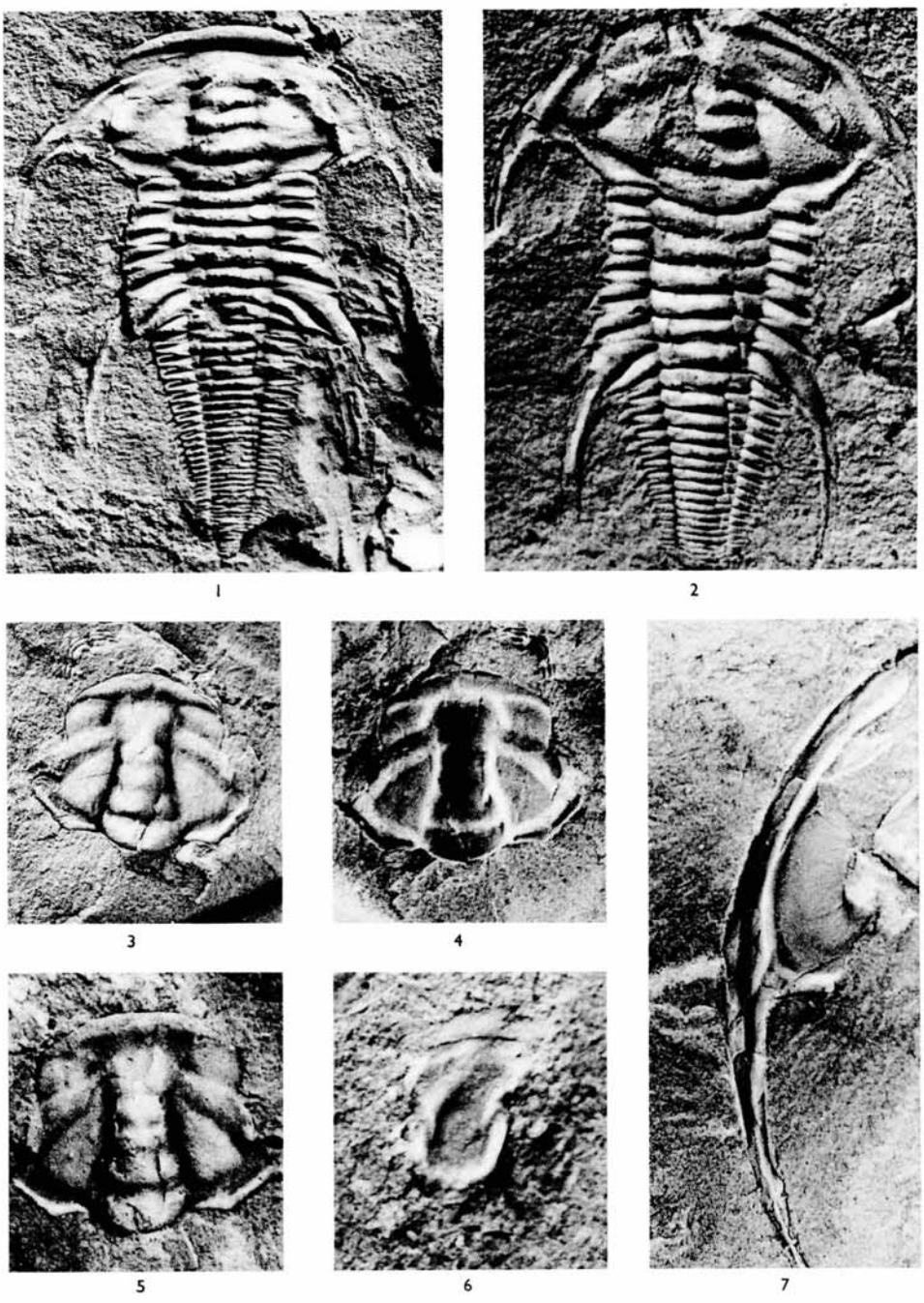

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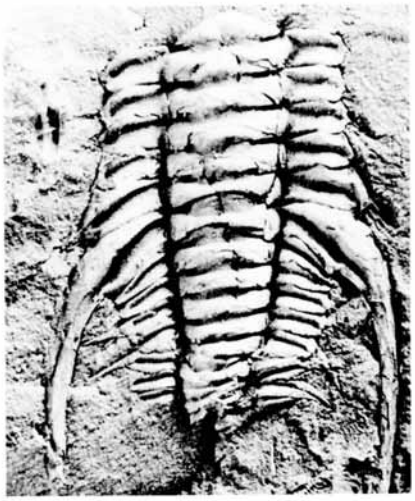

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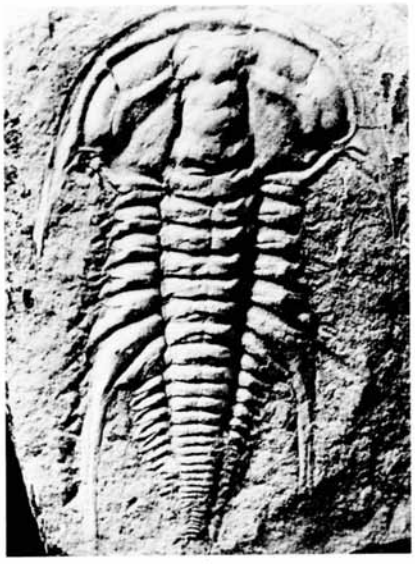

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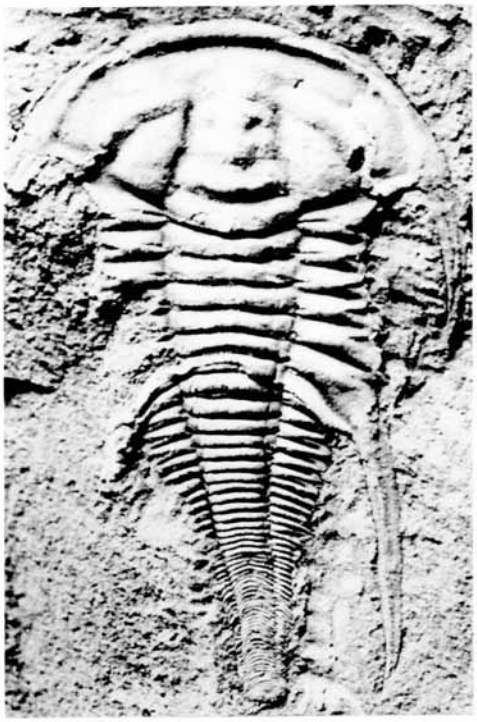

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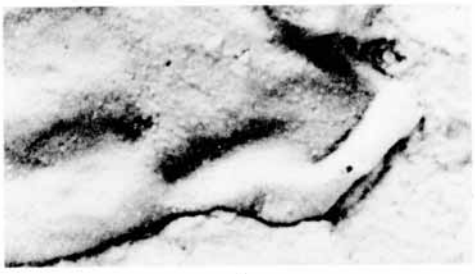

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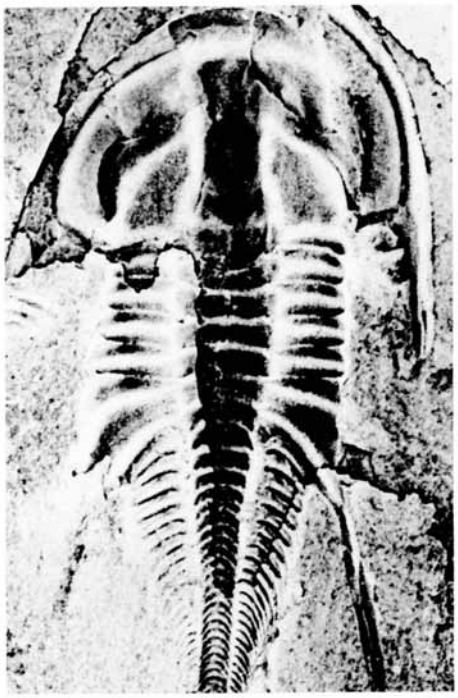

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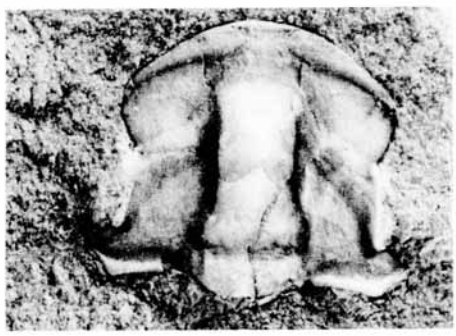

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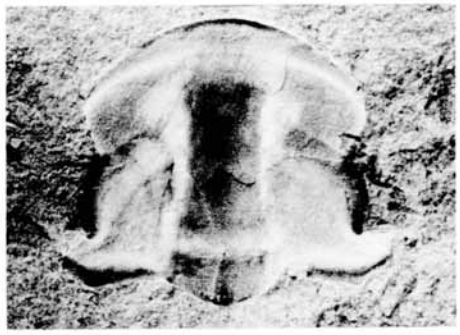

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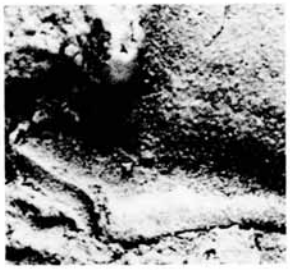

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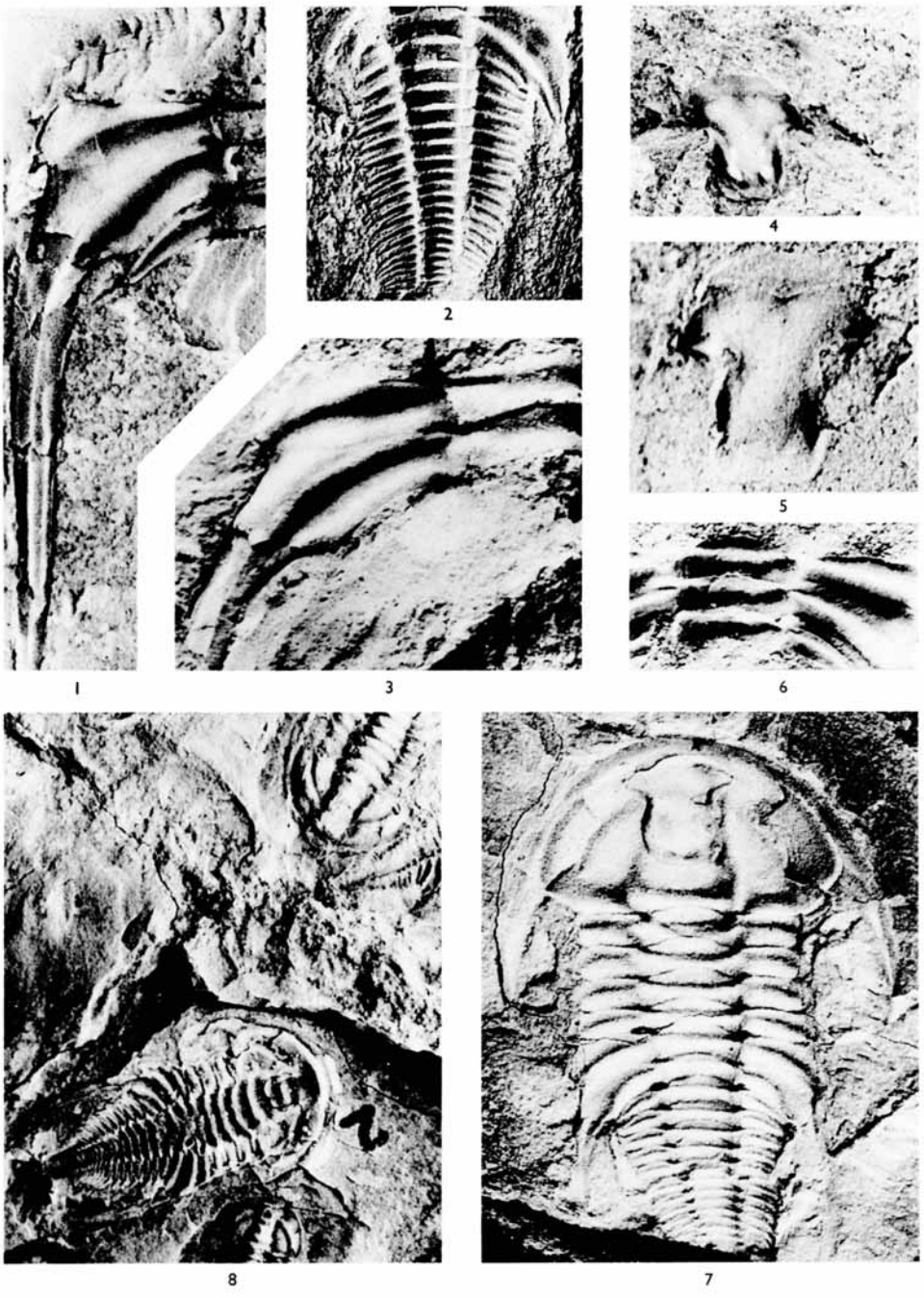

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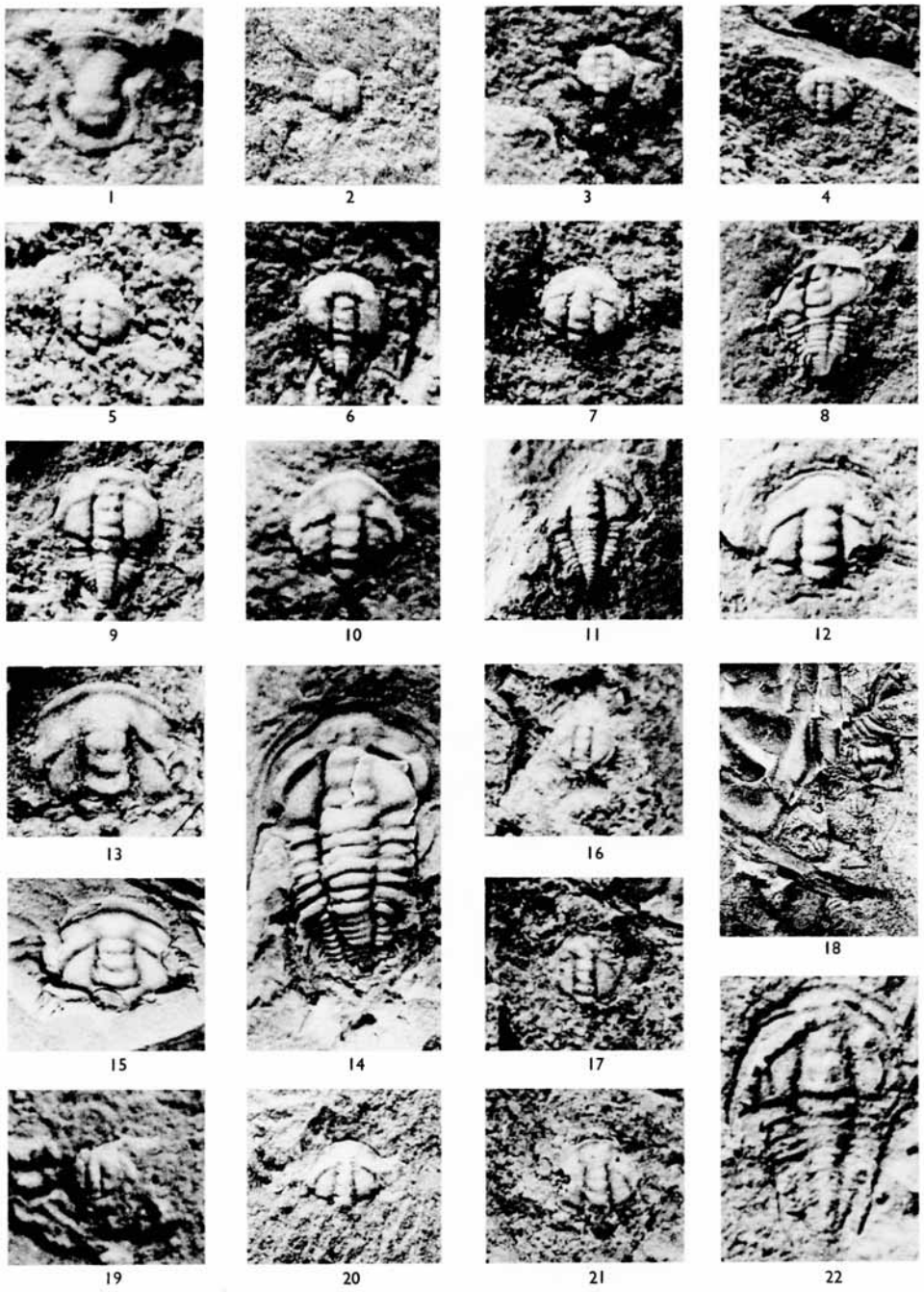

POCOCK, Lower Cambrian Emuellidae