# "AN ABERRANT GROUP OF TRILOBITES FROM THE LOWER CAMBRIAN OF SOUTH AUSTRALIA:- SYSTEMATICS, FUNCTIONAL MORPHOLOGY, SEGMENTATION AND GROWTH".

by

K. J. POCOCK, B.Sc.(Hons)

Department of Geology,

University of Adelaide

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## Contents

Text Figures following page

Tables

# SUMMARY

Study of the adult morphology and ontogeny of a new group of trilobites has led to the erection of two new genera, *Emuella* and *Balcorocania*, each with two species, *E. polymera* and *E. dalgarnoi*, and *B. dailyi* and *B. flindersi*, which are considered to constitute a new family, the Emuellidae. The Emuellidae appear to have evolved as successional genera and species with *E. polymera* at the base, *E. dalgarnoi* intermediate between it and *B. flindersi* and the latter leading to *B. dailyi.*

The Emuellidae are considered as structural relics of a basic, very primitive trilobite stock, from which evolved the olenellids in one direction, and at least some redlichiids in another. The family is here included in the suborder Redlichiina (as defined in Harrington et al, 1959), with the proviso that it may become necessary to accord it superfamilial rank, within this suborder, or to consider it as a separate suborder of the Redlichiida.

Studies of the functional morphology of the thorax, have led to a new concept of the cause for the division of the thorax into a prothorax, and long opisthothorax, and of the presence of fusion of segments and macropleurality within the prothorax. The division of the thorax is considered a primitive feature, but initiation of it is held to be mechanical; the macropleural segment is thought to fulfill the roles of stabilization and protection of the long opisthothorax, and fusion of a segment to the macropleural segment is related to a mechanical response to the size of the macropleural spine.

Studies on the segmentation of the Emuellidae have led to the rejection of the hypothesis of asexual budding (Lemche 1957), and have cast doubts on either the validity or the usefulness of the theories of secondary segmentation (Størmer 1941), merocyclism (Raw 1953), and a secondary sexual relationship of the macropleurae (Hupé 1953). An exceptional teratological specimen of *E. polymera* is described and interpreted.

Analysis of the growth of *B. flindersi* has shown that Dyar's Law does not apply in this case and that some cranidial features display allometric growth in the early meraspid period. A change in the growth pattern of the cephalon, from positive allometry to isometry, occurs at meraspid degree 6, which also marks the change in the thoracic segmentation.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University, nor, to the best of my knowledge or belief, does this thesis contain any material previously published or written by another person, except where due reference is made in the text of the thesis.

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This project could not have been undertaken without the permission to use material from two sources: Dr. B. Daily, the original discoverer of the trilobites, kindly lent material from his own collections; Mr. T.A. Barnes, Director of the South Australian Dept. of Mines, authorized the release to the University, of material collected by officers of his department.

## CHAPTER I INTRODUCTION

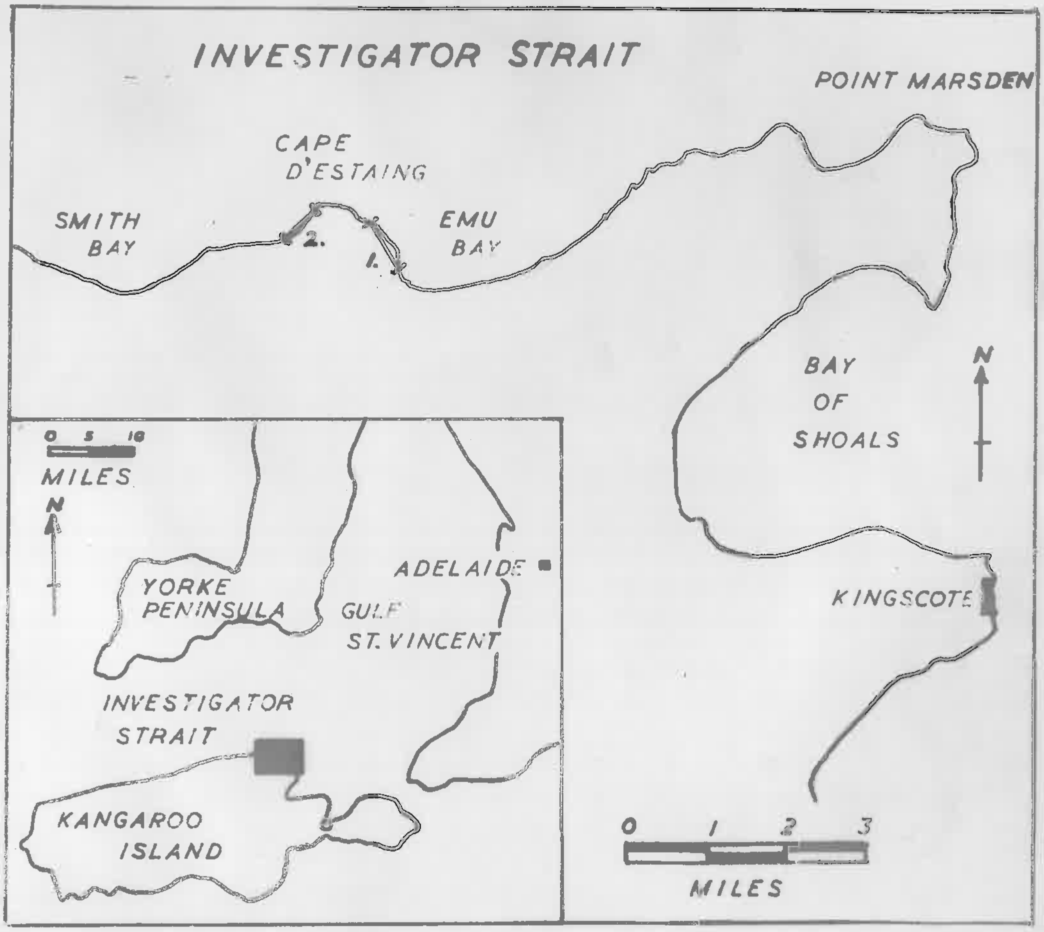
Members of this group of trilobites were first found by Dr. B. Daily of the Geology Department (University of Adelaide), on the west side of Cape D'Estaing, Kangaroo Island, South Australia. This occurrence was first recorded by Daily (1956 p.125). Subsequently the author, whilst working on the eastern side of the Cape, on the Emu Bay section, discovered a second locality (Pocock 1964, p.459). Late in 1961, Messrs. Dalgarno and Johnson of the Geological Survey, S.A. Department of Mines, made a remarkable discovery of a similar trilobite near Oraparinna, in the Flinders Ranges of South Australia. Subsequent work in Kangaroo Island by the author has located a related trilobite, higher in the section than the previous occurrences.

The morphology of these trilobites, all obviously closely related, was realized to be significantly different to any previously described, and the author undertook their description and classification. In addition the large number of larval specimens available, presented the opportunity of tracing the developmental history in some detail.

The presence in the thorax of these trilobites, of a combination of unusual characters, previously found only in very restricted groups of trilobites, provided the means by which numerous hypotheses of segmentation, macropleurality, fusion of segments and division of the thorax could be tested, and also allowed study of the functional morphology of these features.

The large number of specimens available, both larval and adult allowed a variety of statistical methods of analysis of growth and variation to be carried out.

TEXT FIGURE 1



LOCALITY MAP - KANGAROO ISLAND

## CHAPTER II GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

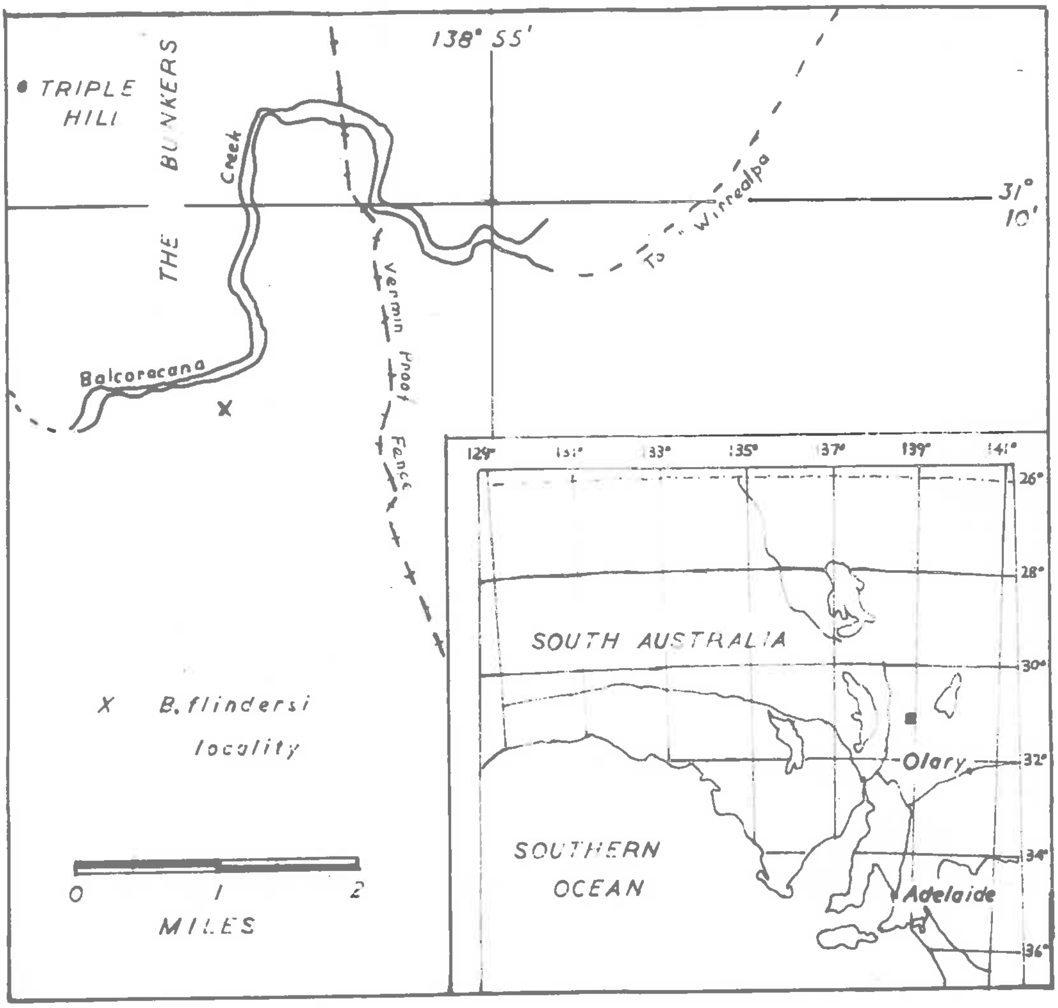
The known occurrences of members of the Emuellidae, are at present restricted to Lower Cambrian rocks of the Adelaide geosyncline. They are, however, widely separated geographically, one locality being known from the eastern portion of the Flinders Ranges, whilst the others are on the north coast of Kangaroo Island, a distance apart of approximately 350 miles.

The Flinders Ranges locality (Text fig. 2) is at Balcorocana (or Ten Mile) Creek near Oraparinna. The trilobites occur in a zone of about 30 feet in the Billy Creek Formation approximately 500 feet above the base (Text fig. ~~3~~2).

The age of the Billy Creek Formation is not known exactly but it is underlain by the Oraparinna Shale, which Walter (1967) on the basis of archaeocyathan studies, dates as middle Lower Cambrian, or the lower Lena stage of U.S.S.R. It is overlain by the Wirrealpa Limestone which contains a fauna which is considered to be lower Middle Cambrian (Daily 1956). The Billy Creek Formation itself is 3300 feet thick and thus the fossiliferous beds occur 2800 feet below the Wirrealpa Limestone, and their probably age is upper Lower Cambrian.

The Kangaroo Island localities are at Cape D'Estaing, approximately 12 miles W. of Kingscote on the northern coast (Text fig. 1). The fossiliferous beds occur in sections on either side of the Cape, outcropping on the wave cut platforms and in cliff sections behind. On the eastern side, the Emu Bay section of Pocock (1964), B. dailyi occurs in a zone approximately 30 feet thick, near the top of the White Point Conglomerate, whilst E. dalgarnoi occurs 250 feet

TEXT FIGURE 2



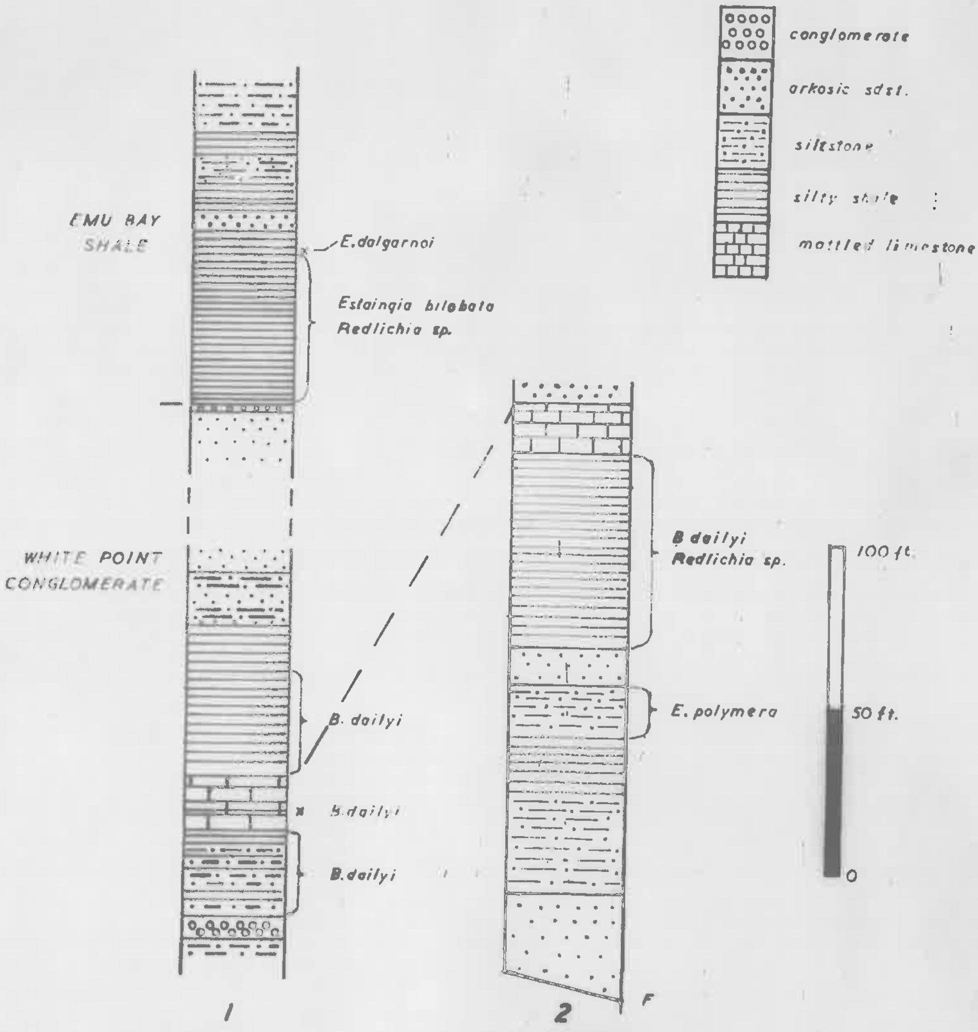
LOCALITY MAP - FLINDERS RANGES

stratigraphically above,in a two foot thick bed immediately above beds containing *Estaingia* and *Redlichia* (Pocock 1964) within the Emu Bay Shale. On the west side of the Cape,in a section which in part can be correlated with the Emu Bay section, *E. polymera* occurs in a thin bed near the base of the sequence, and *B. dailyi* occurs in the overlying 60 feet. Both fossiliferous beds in this case occur in the upper part of the White Point Conglomerate (Text fig.3) At this locality *B. dailyi* is associated with occasional scraps of *Redlichia*.

The age of the White Point Conglomerate and Emu Bay Shale has been discussed by Daily (1956) and Pocock (1964). The evidence is primarily afforded by fossiliferous boulders found in the conglomerate members near the base of the White Point Conglomerate. The boulders, containing Archaeocyatha, are attributed to the middle Lower Cambrian Parara Limestone which outcrops on Yorke Peninsular. Accordingly the lower part of the White Point Conglomerate is post middle Lower Cambrian. Daily (1956, p.125) considers that the Lower-Middle Cambrian boundary falls within the Boxing Bay Formation, which conformably overlies the Emu Bay Shale. Thus the age of the beds in this section containing *B. dailyi* and *E. dalgarnoi* is probably upper Lower Cambrian.

It appears that the Emuellidae as presently known, occur in rocks of probable upper Lower Cambrian age at all localities. At the present time it is not possible to correlate the Flinders Ranges and Kangaroo Island sections, so that the stratigraphic position of *B. flindersi* with respect to the other species is not known. The detailed lithologies and thicknesses of the sections at each locality are given in the accompanying stratigraphic columns (Text fig. 3)

TEXT FIGURE 3



Stratigraphic columns: parts of the stratigraphic successions of Cambrian age of Kangaroo Island.

1. Emu Bay.

2. West of Cape D'Estaing.

## CHAPTER III MODE OF OCCURRENCE

### KANGAROO ISLAND

The stratigraphic distribution and the localities of the three species found on Kangaroo Island have already been given (p.2 - 3; Text figs. 1,2,3). In the section west of Cape D'Estaing, E. polymera occurs in a thin bed of light brown-grey, fine grained silstone, and B. dailyi in a relatively thick sequence of dark grey-brown silstones. In the Emu Bay section east of the Cape, E. polymera has not been found, but B. dailyi occurs in a sequence of rocks of slightly varying character; the basic lithology is always a very fine grained siltstone or silty shale, but varies from very dark and highly micaceous to light brown and calcareous, the latter being interbedded in mottled limestones. E. dalgarnoi, occuring higher in this section, is found in a thinly bedded, dark grey silstone.

In all of the above localities, the trilobites occur largely as disarticulated moults, interspersed with a few complete individuals, on the bedding planes. In the collections of E. polymera and B. dailyi both larval and adult specimens have been found, but in that of E. dalgarnoi, which is very poor, only the adults have been found.

With the exception of the B. dailyi occurrence West of Cape D'Estaing, where occasional fragments of a species of Redlichia have been found, no other fossils are associated with the trilobites.

### FLINDERS RANGES

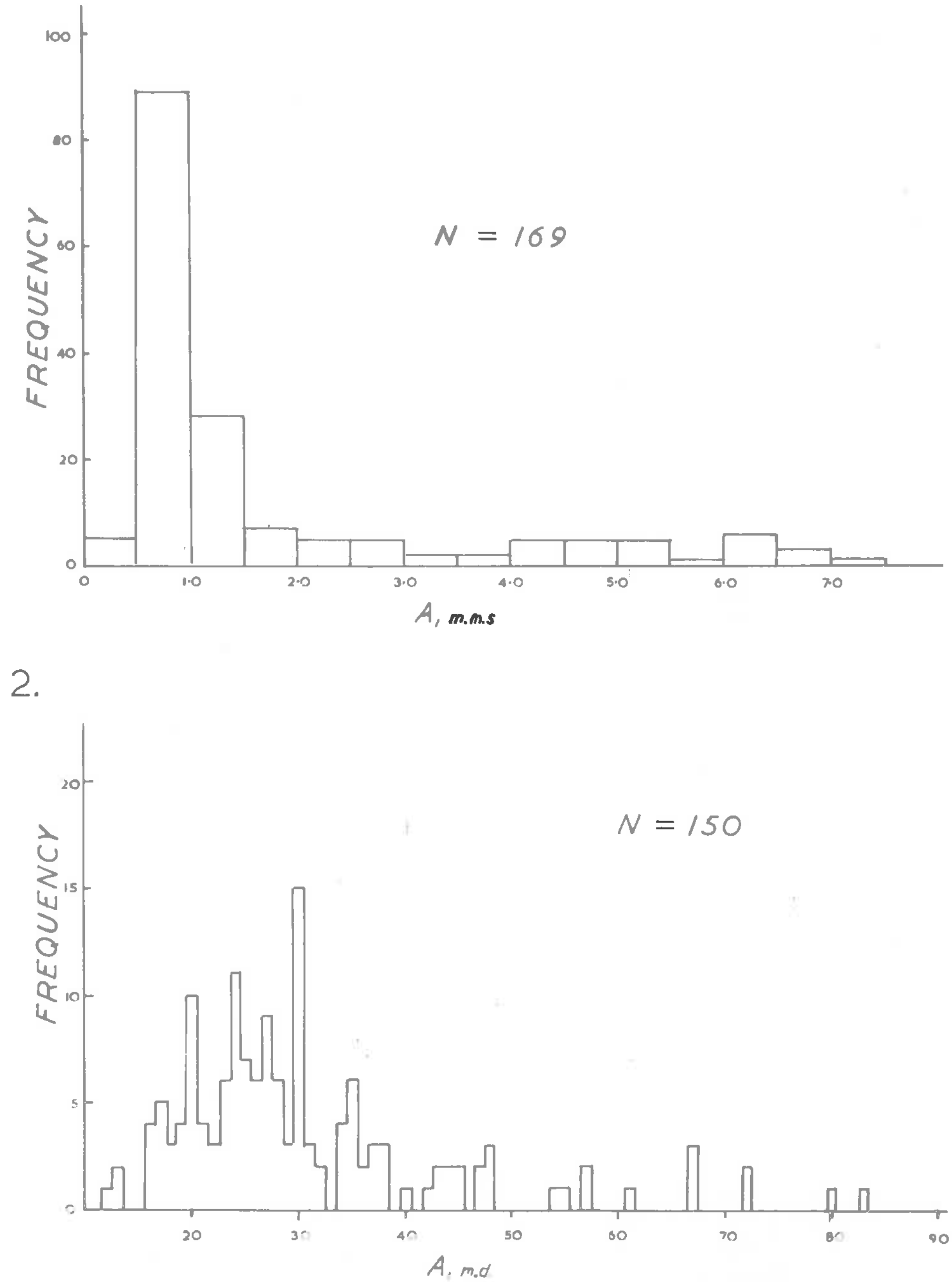
B. flindersi occurs in a sequence of approximately 30 feet of greenish brown tuffaccous shales; for the greater part of this sequence the trilobites are rare, and represented exclusively by moults. However one bed, about 4" thick, near the top of the fossiliferous sequence, is richly fossiliferous, one bedding plane at least being literally covered with complete individuals. Both larval and adult stages are found but whereas the adults are almost entirely represented by complete specimens, the larval stages, especially the very early stages, contain a significant percentage of moults.

The presence of one bedding plane with abundant complete specimens 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 on the bedding plane results from mass mortality, perhaps associated with volcanic activity.

Mass mortality has been invoked many times to explain the characters of some fossil assemblages, and volcanic activity, in particular, has often been suggested as the cause. Brongersma - Sanders (1957) has reviewed this subject and has 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 preponderance of complete exoskeletons, is available. A size frequency distribution of specimens of <u>B. flindersi</u> from the bedding plane has been constructed (Text fig. 4(1)). Examination of the histogram reveals a large number of very small specimens compared to the adults. Craig and Oertel (1966) have constructed theoretical models for various populations, in terms of size and age frequency distributions, by

TEXT FIGURE 4.



Size frequency distribution of *Balcoracania flindersi*:

(1) all individuals (2) larval specimens only

$A_1$ is the cranidial length given in mms. in (1), and in micrometer divisions where 1.00 mms. = 32 divs in (2).

means of a computer program simulating various factors affecting the composition of both living populations and accumulating dead counterparts. They point out (p. 351) that most fossil assemblages differ from the theoretical models, in the absence of large numbers of young individuals. In addition mass mortality will result in a frozen size frequency distribution of a living population, in which small individuals will be very abundant. Thus it can be seen that, the size frequency distribution for B. flindersi approximates that of living population, in the high proportion of young (small) individuals, and most probably represents a case of mass mortality.

## CHAPTER IV METHODS AND TECHNIQUES

Over 800 specimens from the three localities were examined. After preparation each specimen was individually described, photographed and measured. Techniques used are described below, in addition to the methods of reconstruction, illustration and quantitative analysis.

### (a) Collection.

The collections from the Kangaroo Island localities are well controlled stratigraphically, and the later ones were selected with the aim of removing bias as much as possible for later quantitative studies; the material from the original collection was used largely for analysis of morphology. The collection from the Flinders Ranges locality was made simply by removing the fossiliferous bed across the length and depth of the exposure.

### (b) Preparation.

All specimens were prepared by hand, using a sharpened needle under a variable power binocular microscope, mounted on a moveable arm. It was found that the application of limited quantities of water aided in removal of the matrix, and in the splitting of the matrix from the trilobite.

### (c) Measurement.

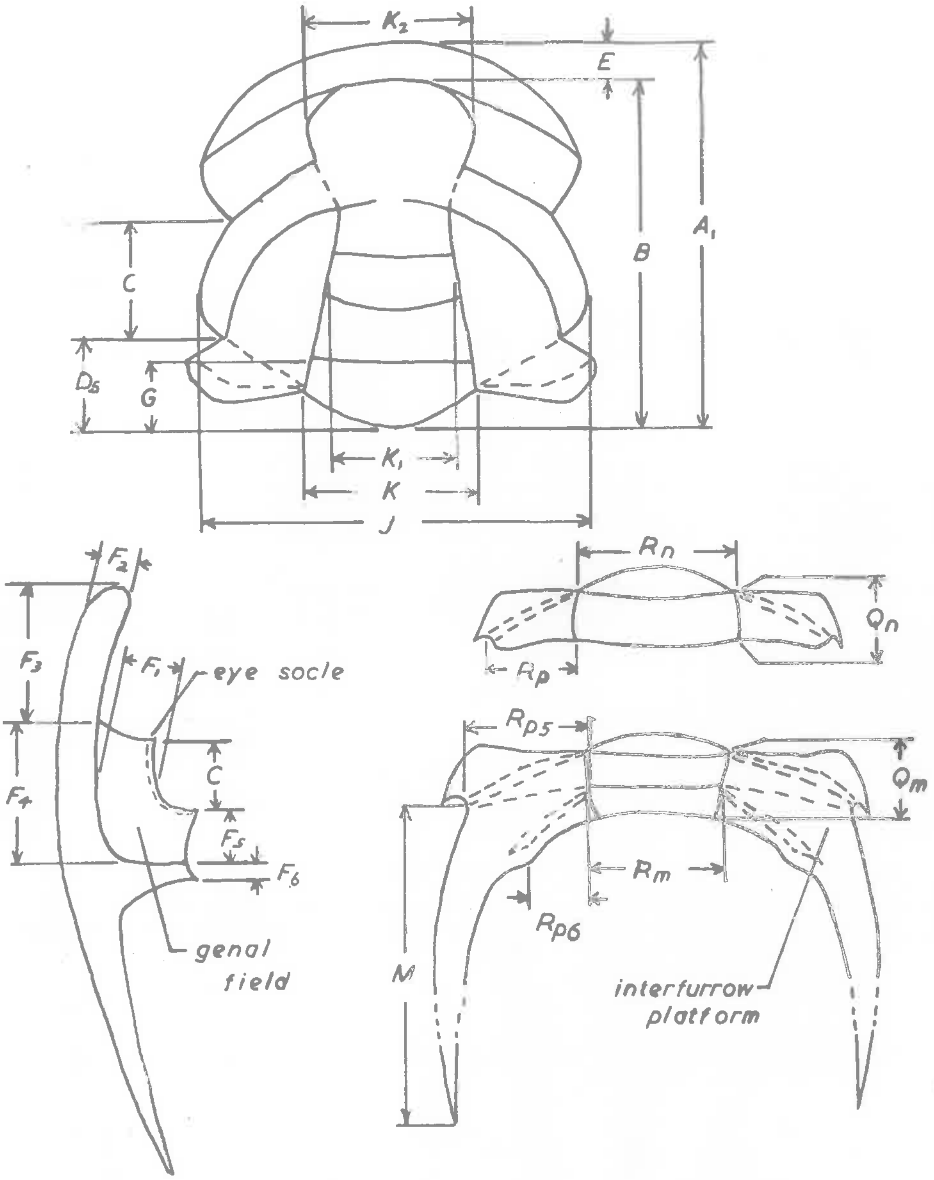
Specimens were measured by means of an ocular micrometer fitted in the binocular microscope; measurements were made at least twice, on different occasions, and the results averaged. As many measurements were made on each specimen as were feasible with regard to completeness; distortion of the specimens was not made a grounds for rejection. The dimensions measured were based largely upon those given by Shaw (1957) but additional dimensions were measured in some cases, particularly for the hypostome and macropleural unit, which were not covered in Shaw's scheme. A list of the dimensions measured is given in Appendix I, and Text figs. 5 and 8 show the dimensions used.

(d) Photography.

The photographing of each specimen was carried out in order to aid in the analysis of variation and distortion, and in reconstruction. All specimens were originally coated with ammonium chloride, but those chosen for illustration were coated with magnesium oxide, the difficulties in using this substance being in this case offset by its greater permanence and its smaller grain size. The specimens were photographed using Adox K.B.14 film in a Leica camera, mounted on a Reprovit stand. It was found that by using different combinations of lenses, numbers of extension tubes and the bellows extension, that satisfactory photographs could be obtained over the complete size range represented by the specimens i.e. from less than 1 mm. to over 10 mms.

(e) Reconstruction and illustration.

Although some degree of distortion and/or flattening is present in all collections, it is found that its range is limited, and that the number of specimens is large enough for an accurate choice to be made for the purposes of reconstruction. Sdzuy (1966) has described methods for obtaining the correct shape from asymmetrically deformed trilobites, but it was found that these



TEXT FIGURE 5

Measurements and additional terminology of the cranidium, librigena, thoracic segment and macropleural unit. The symbols are as defined by Shaw (1957) and as otherwise defined in the text.

methods are most valuable when the degree of distortion is high. When the degree of asymmetrical distortion is relatively low, or a large enough number of specimens are available, the more subjective method is more accurate, as some estimate of flattening can also be made and taken into account. The angles used in the description of the trilobites were measured directly from photographs. As even a small degree of distortion either asymmetrical or symmetrical causes a considerable variation in such angles, specimens with the minimum degree of distortion were chosen for measurement and the measurements averaged. With regard to the angle of the abaxial section of the posterior border, the differences between the species are small, but can be confirmed on a geometrical basis. All measurements are given in the Appendix. Illustration of the reconstructed trilobite is carried out directly from photographs of selected trilobites with the aid of a magnifying light table.

(f) Quantitative analysis.

(1) analysis of variation:- the methods of regression analysis recommended by Shaw (1956) have been followed to a large extent. (2) analysis of distortion:- the ubitiquous distortion of the trilobites in all collections, whether simple flattening, symmetrical or asymmetrical distortion, causes problems in any quantitative analysis carried out on the collections. It has been pointed out that all types of distortion have the nett result of imposing a spurious variability upon the intrinsic variability, which if not separated, will increase the range of the variation (Pocock 1964). In previous statistical work on trilobites either

this effect was ignored or the author selected specimens suitable for measurement. The latter procedure is highly subjective, and not feasible in many cases. It was decided to try and find a more objective basis for selection of specimens used in analysis.

In one collection, the most highly deformed, photographs were taken of every individual. The angle between the original sagittal and transverse directions on each trilobite was then measured directly from the photograph. The collection was then divided into two classes, one in which the difference from 90° for the two axes was equal to or less than 5°, the other in which this difference was greater than 5°. The latter class included specimens in which the difference was up to 18°. Regression analysis were then made on selected variables for the two classes and the significance of the difference between the two sets of coefficients was calculated by means of a modified Students t-test (Simpson, Roe and Lewontin 1960 p.237). The data, methods and results are given in the Appendix ? p.174. and support the hypothesis that the two samples were taken from a single population. It is thus evident that given an adequate number of specimens distortion does not produce a significant increase in the variability, and will not mask a difference, which on statistical grounds may be considered significant. The number of specimens is all important, but will depend to a large extent on the degree of distortion and will vary from sample to sample.

In view of the results of the above test, it was considered that all specimens could be included in the samples used for analysis. However it is possible that in some cases this procedure would be unwise, and it is recommended that for small samples only those showing differences below the 5° level should be used.

(g) Analysis of growth.

The methods used are included in the relevant chapter (Ch. XI).

## CHAPTER V TERMINOLOGY

The terminology used here for the dorsal exoskeleton is largely that recommended in the Treatise of Invertebrate Palaeontology Part O, Trilobita (1959). Several modifications have been adopted for description of the Emuellidae.

The terms anterior pit or fossula have been applied to small depressions occurring in the axial furrow at or near the anterior edges of the glabella (Harrington et al, 1959; p.120). In the Emuellidae depressions occur in these positions, but are related to the junction of the axial furrows and the anterior border furrow; in addition depressions also occur at the junction of the furrows bounding the anterior edge of the eye ridges and the axial furrows. In order to avoid confusion, the former are qualified as "anterior border furrow fossulae" and the latter "eye ridge fossulae". In informal discussion some widely understood informal terms have been used e.g. "posterior limb" for "posterior area of the fixigenae". In larval cephala the term "cheek" is used for the area bounded by palpebral, axial and posterior border furrows, owing to the difficulty in recognizing the limits of the formal divisions of this area, the posterior and palpebral areas of the fixigena.

The terminology of Shaw & Ormiston (1964 p.1001-2) is applied to the librigenae; "genal field" for the area between the border furrow and the eye, and "eye socle" for the portion of the free cheek directly beneath the visual surface of the eye and separated from the genal field by a break in slope.

The hypostome is described as viewed from the ventral side when in situ; the median body will thus be convex. The terminology of the Treatise is again used, but with division of the lateral border into an "anterior lateral border" extending from the anterior wing to the lateral notch, and "lateral border" which is here restricted to that section posterior to the lateral notch. (Text fig. 8).

In the thorax, the sixth segment is macropleural and fused to the fifth; the term "macropleural unit" is used for description of the complex, and "interfurrow platform" for the area between the fifth and sixth pleural furrows (Text fig. 5).

The terminology for ornament, and for convexity and slope is used in the sense of Whittington and Evitt (1953). However, reliance is largely placed upon photographs and reconstructions. In the description all angles are with reference to the sagittal line.

In the larval stages, the widely understood division into protaspid, meraspid and holaspid stages of development is applied. In view of the extremely small number of protaspids available, no division of this stage was adopted. Difficulties arise in the application of the meraspid stage in the Emuellidae. Whittington (1959 p.135) defines the meraspid stage as beginning at "degree '0' with the appearance of the first transverse joint in the exoskeleton separating the cephalon from ... the transitory pygidium" and "the final degree ... is considered to be that in which there is one less than the complete number of freely articulating segments". In the Emuellidae the thorax is divided into a short prothorax and a long opisthothorax. In the view of some authors (Hupe 1953a; 1953c;

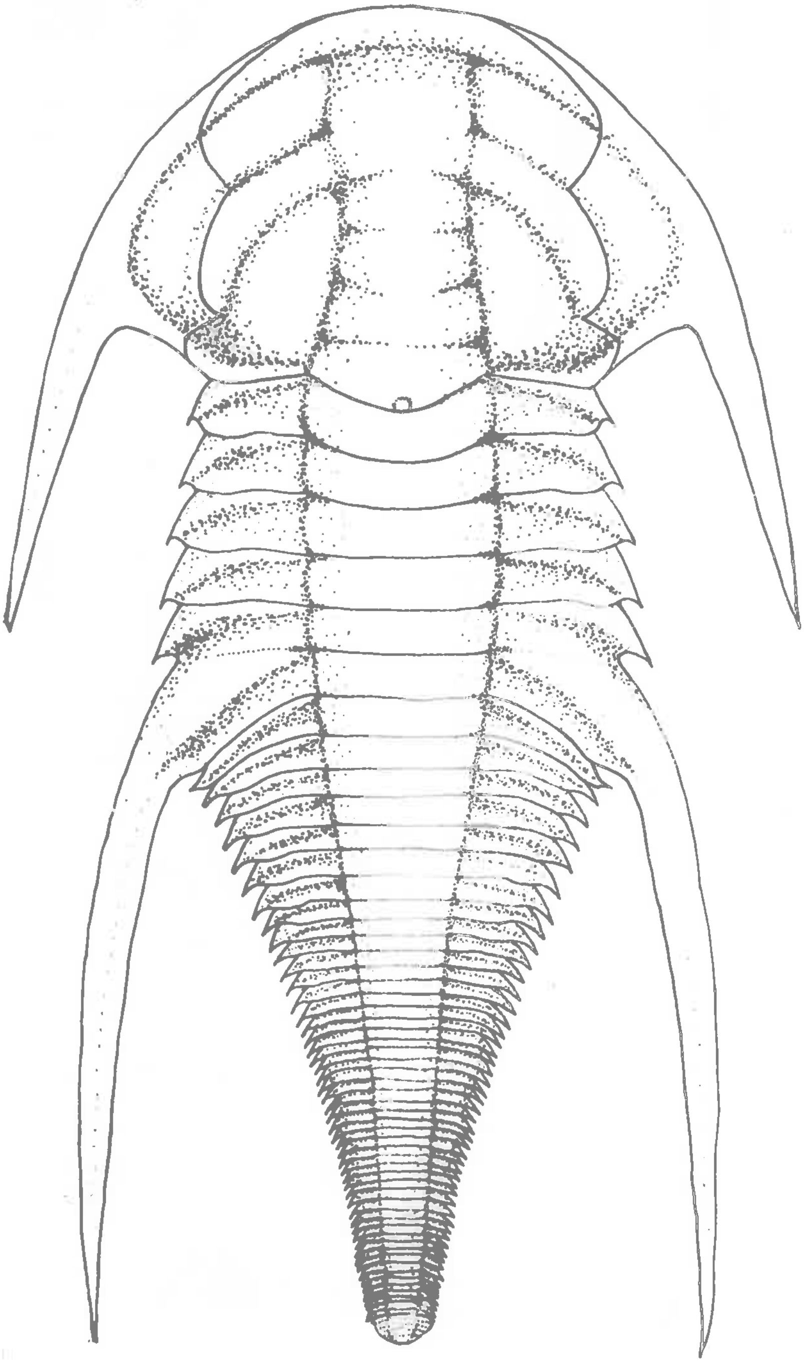
Harrington 1959) the prothorax is homologous with normal thorax of other trilobites and thus the Emuellidae would have only five meraspid degrees, being considered holaspid at the appearance of the sixth segment, still with 50 or so opisthothoracic segments to be released. In addition at degree 6 the cephala of the Emuellidae are still far removed from the holaspid 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 make the use of the term "meraspid period" a little unsuitable for the Emuellidae and for other trilobites with a long opisthothorax. 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 the present in view of the small number of known cases such a division does not seem justified.

## Addendum

The more widely used and understood term "palpebral ridge" is used instead of the term "palpebral rim" of the Treatise terminology.

TEXT FIGURE 6



Reconstruction of the dorsal exoskeleton of the adult of Balcoracania dailyi. The position of the librigena is conjectural. The thorax is shown with the presumed adult number of segments (X 15 ).

## CHAPTER VI SYSTEMATIC DESCRIPTION

The specimens are all deposited on the Palaeontological Collection of the University of Adelaide, South Australia (AUGD).

### FAMILY EMUELLIDAE nov. fam.

Diagnosis:- Medium to large opisthoparian trilobites. Glabella with three pairs of transglabellar furrows in adult; axial furrows converge from occipital ring to anterior glabellar furrow, frontal lobe expanded, rounded laterally; preglabellar field narrow or absent. Eye ridge wide long, directed slightly to posterior of transverse direction; palpebral ridge crescentic. Posterior area of fixigena with fulcrum. Posterior border with section abaxial to fulcrum directed antero-laterally. Anterior section of facial suture diverges from palpebral ridge to border furrow, curves sharply inwards and crosses anterior border diagonally before becoming marginal-ventral; connective suture concave abaxially; rostral plate short (trans.) notched laterally; posterior section of facial suture diverges strongly to posterior; hypostomal suture functional. Hypostome with depressed anterior wing; median body with large subtriangular anterior lobe, subdivided anteriorly by median depression, and small posterior lobe. Librigena with long genal spine.

Thorax with prothorax of six segments, and extremely long opisthothorax of between 48 and 55 segments. Prothorax with sixth segment macropleural and fused to fifth. Macropleural spine long, extends to level of pygidium. Pygidium a minute segmented disc, with entire border.

## GENUS *EMUELLA* nov. gen.

type species: *Emuella polymera* nov. sp:

Plates 1-6, Text figs. 9 (1, 2)

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 ridge relatively short, curved. Posterior border with abaxial section directed antero-laterally at approximately 45°. 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 a known maximum of 58 segments. Strong closely spaced granules on dorsal surfaces.

### *Emuella polymera* nov. sp.

Plates 1-4, Text fig. 9 (1)

Derivation of name:- polymera - for numerous thoracic segments.

Holotype:- AUGD. F 16443 Plate 1, fig. 2.

Selection of holotype:- it was considered essential that a specimen with cephalon and thorax articulated, be chosen. Although the cephalon of the holotype, does not show the diagnostic features as well as some cranidia, it was chosen for the above reason.

Material:- approximately 50 internal and external moulds

Occurrence:- White Point Conglomerate, upper section of formation; on west side of Cape D'Estaing.

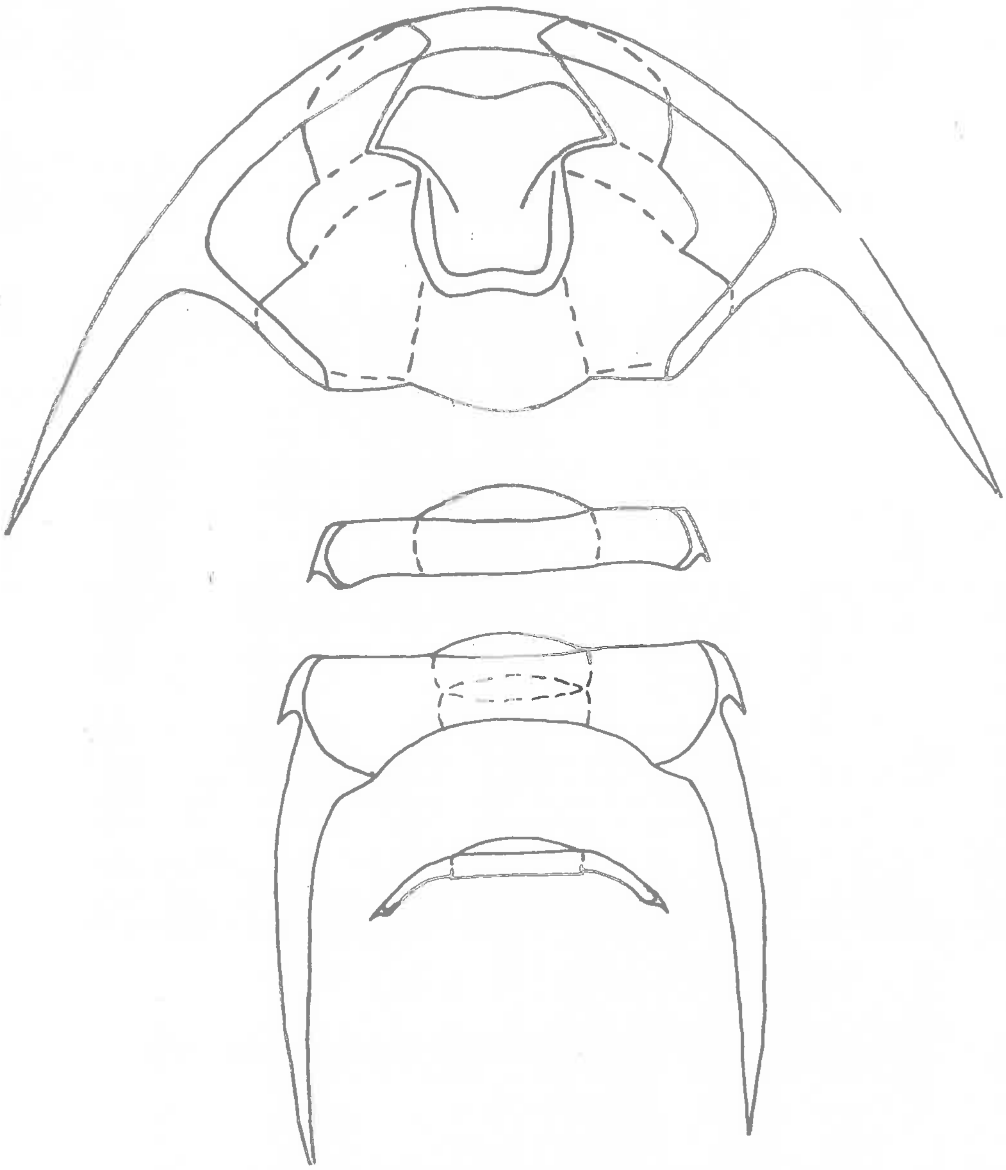
Diagnosis:- Glabellar furrows very shallow, indistinct; posterior and middle furrows transverse. Frontal glabellar lobe only slightly expanded, delineated by deep axial furrows. Anterior cranidial border furrow almost transverse. Palpebral ridge very short, convex exsagittally, highest at mid point, posterior end opposite middle glabellar furrow or lobe. Posterior border raised, constant width, with abaxial section directed antero-laterally at 40°. Anterior section of facial suture diverges at approximately 10°. Thorax with axis wider than half total thoracic width; axial rings of prothorax rise sharply to posterior, sagittally, with 1-4 bearing elongate nodes on posterior margin. Thorax with at least 48 segments.

Description:- Cephalon subtrapezoidal in outline, transversely and sagittally, gently convex. Glabella with three pairs of lateral furrows; axial furrow converge from posterior margin to anterior glabellar furrow, frontal lobe expanded, rounded laterally, straight to slightly curved anteriorly; glabella strongly convex transversely, with slight median ridge extending to anterior glabellar furrow, gently convex sagittally, highest at anterior glabellar lobe, sloping down steeply to anterior border furrow, but with central portion of frontal lobe flat, sloping down more gently to posterior. Occipital furrow narrowest and deepest abaxially (Pl.2, fig.1), curved backwards gently. Glabellar furrows transcurrent, shallow and indistinct; posterior and middle furrows almost transverse, anterior furrow directed slightly forwards (Pl.2, fig.1). Occipital ring approx. one half cranidial width at mid palpebral level, widest sagittally, with posterior edge convex outwards, half sagittal width projecting beyond margin of fixigena. Length (sag.) of glabellar lobes decreases slightly from posterior to anterior, 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, with fossulae present at junction with anterior edge of eye ridge and at junction with border furrow (Pl. 2, fig. 1, 5; Pl. 1, figs. 1, 3). Anterior border medium width, gently convex (sag.). Anterior border furrow almost transverse across cranidium (Pl. 2, fig. 1), moderately deep and narrow abaxially, shallows and broadens abruptly anterior to frontal lobe (Pl. 2,figs. 1,2,5). Eye ridge wide, long, gently convex, transversely and exsagittally, directed to posterior at approximately 20° to transverse line from frontal lobe; anterior furrow indistinct with ridge grading into downsloping anterior lateral sections of cranidium, posterior edge slopes down steeply to furrow continuous with palpebral furrow and aligned adaxially with anterior glabellar furrow (Pl. 2, fig. 2); degree of separation of eye ridge from frontal lobe by axial furrow varies considerably. Palpebral ridge short, less than one quarter glabellar length, anterior end opposite anterior glabellar furrow, posterior end opposite middle glabellar lobe (Pl. 2, fig. 2,5); moderately convex (exsag.) with ends horizontal and mid point highest; slopes up steeply from palpebral furrow with abaxial end convex (Pl. 2,fig. 3); separated indistinctly from eye ridge by change in convexity (Pl. 2,figs. 2,5), in some large specimens by indistinct furrow. Eye ridge appears divided in some large individuals. Palpebral furrow deep, wide, slopes down to posterior. Palpebral area of fixigena slightly convex, horizontal to downsloping posteriorly. Posterior area of fixigena long (exsag.), almost as wide (trans.) as occipital ring, with distinct fulcrum at exsagittal level of posterior end of palpebral furrow. Posterior border narrow, convex; horizontal and directed transversely from axial furrow to fulcrum, abaxial to fulcrum slightly downsloping and directed antero-laterally at approx. 40° to postero-lateral corner of cranidium (Pl. 2,figs. 1-3). Posterior border furrow originates at base of axial furrow, widens abaxially, deep adjacent to border, widens and shallows away from it, overall shape triangular; confluent with posterior end of palpebral furrow (Pl. 1,figs. 1-3; Pl. 2,fig. 5).

Anterior section of facial suture diverges at approximately 10° from palpebral ridge, curves sharply inwards at border furrow, crossing anterior border diagonally to intersect anterior edge opposite junction of axial and border furrows (Pl. 2,figs. 1,5), then marginal-ventral; connective sutures cross doublure, concave abaxially (Pl. 2, fig. 4). Palpebral section of facial suture short, convex abaxially, diverges to posterior at approx. 15°; posterior section relatively long, slightly convex abaxially, diverges at approx. 50° and slopes down to cut posterior border opposite posterior glabellar furrow.

Libtigena (Pl. 2,fig. 4) with long genal spine. Lateral border moderately convex (trans) approx. one third mid palpebral width of librigena. Lateral border furrow distinct, rises steeply to border and slopes up gently to genal field adaxially, curves sharply inwards near base of genal spine, continuous with posterior border furrow, becoming 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



TEXT FIGURE 7

The ventral morphology of the cephalon, a prothoracic segment of the macropleural unit and an opisthothoracic segment; showing the extent of the doublures, and the reconstructed position of the hypostome. (Based upon _E polymera_).

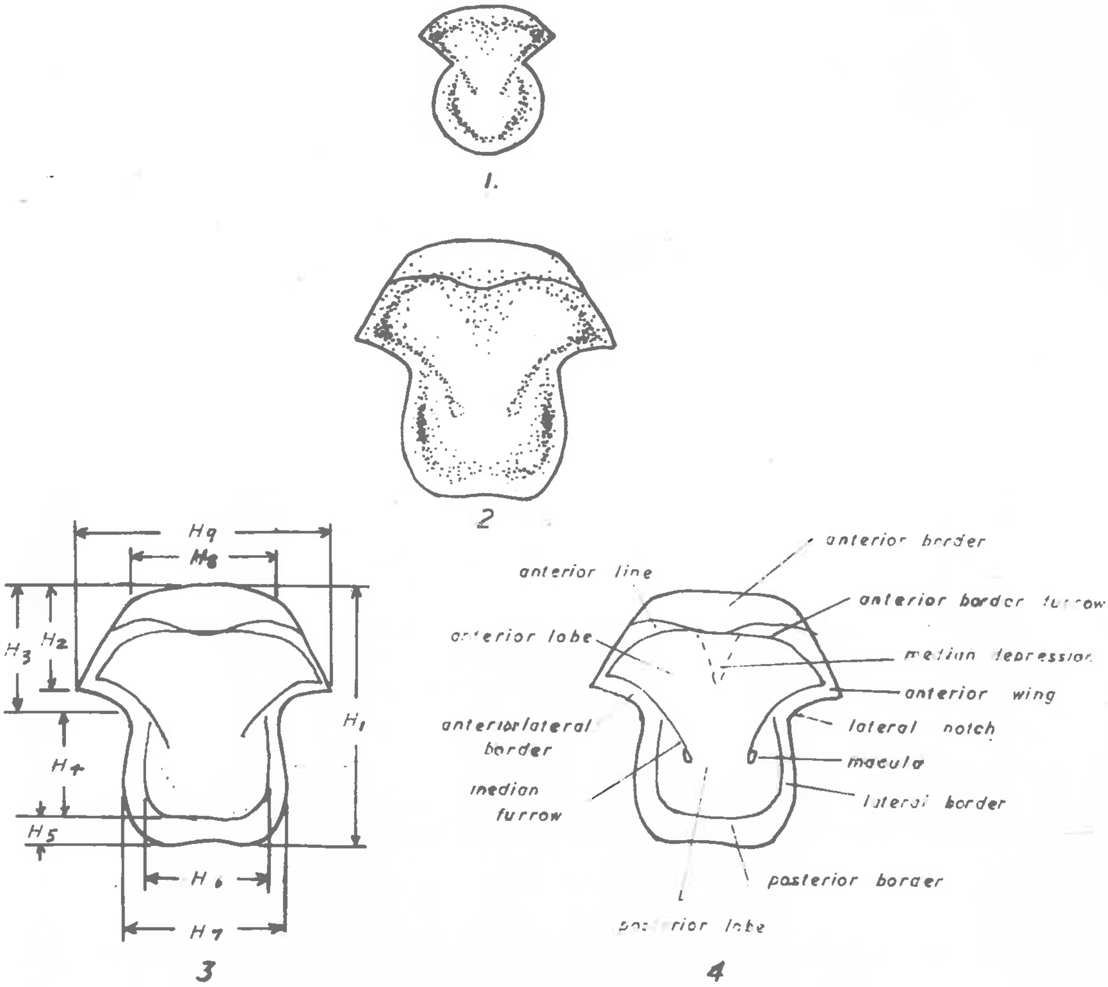
convex upwards at mid width (trans) then forms narrow horizontal to slightly depressed surround below a vertically upturned adaxial edge. Genal spine long, advanced (Pl. 1, figs. 1-3; Text fig. ~~4~~9 (1)), moderately wide at base, tapers slowly and curves inwards towards posterior, subcentral ridge extends to posterior.

Cephalic doublure same width as borders (Pl. 2, fig. 4; Text fig. 7 ). Rostral plate crescentic, length (trans) equal to maximum width of frontal glabellar lobe, notched abaxially (Pl. 4, fig. 5). Doublure of librigena convex ventrally, widens and flattens immediately posterior to connective suture (Pl. 2, fig. 4). Lateral doublure continuous with posterior doublure around base of genal spine. Ventral side of genal spine flat to slightly rounded. Occipital ring with narrow doublure.

Hypostome (Pl. 4, figs. 4,5; Text fig. 8 ) 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 furrow straight, directed obliquely backwards at high angle, not reaching sagittal line (Pl. 4, fig. 5). Posterior section of anterior lobe of median body strongly convex transversely, continuous sagittally with posterior lobe, slopes down anteriorly and divides into symmetrical downsloping ridges directed antero-laterally and separated by concave median depression; abaxially ridges slope steeply down to prominent anterior wings (Pl. 4, fig. 5). Anterior border upsloping from border furrow, trapezoidal in shape with central portion of anterior edge slightly curved forwards along line of hypostomal suture,

TEXT FIGURE 8



Hypostome.

(1) reconstruction of the larval hypostome (X 2 )

(2) reconstruction of the adult hypostome (X 4 )

(3) dimensions measured (defined in Appendix I )

(4) terminology used to describe the adult hypostome

All shown in ventral aspect. No specific or generic differences known.

abaxial sections slope downwards postero-laterally at approx. $50^{\circ}$ in line with antero-lateral edge of anterior wing. Anterior border furrow slightly convex to anterior in central portion, slopes downwards postero-laterally to anterior wing. Anterior lateral border furrow (Pl. 4,fig.5) straight, directed postero-laterally, rising from anterior wing to lateral notch; very narrow anterior lateral border. Median furrow originates at posterior end of anterior lateral furrow (Pl. 4,fig. 4)

Posterior lobe of median body strongly convex transversely, parallel sided to slightly tapering to posterior; posterior lateral corners rounded with prominent boss; slopes down very steeply to lateral border furrow, more gently to posterior. Lateral border furrow originates abaxial to median furrow, deepens to posterior with fossula near posterior end; lateral border slopes up steeply, convex outwards forming shoulder; lateral border and border furrow continuous with posterior border and furrow. Posterior border relatively wide (sag.) horizontal (sag. & trans.); posterior lateral corners rounded; posterior border furrow distinct abaxially, absent sagittally where ridge slopes down from median body across border; small fossulae abaxial to ridge.

Hypostome attatched to rostral plate along hypostomal suture (Pl. 4,fig. 5) extends posteriorly to level of posterior glabellar furrow when in situ.

Ornament of cranidium consists of closely spaced granules with pointed tips covering all dorsal surfaces except furrows (Pl. 2,fig. 2) Cephalic doublure with terrace lines; librigena with long slightly wrinkled, subparallel terrace lines on posterior and most of the lateral doublure; they become less regular and anastomising adjacent to connective suture; pattern of terrace lines on rostral plate unknown. Ventral surface of genal spine covered with longitudinally elongate granules arranged in subparallel rows. Occipital ring bears sagittal, longitudinally elongate tubercle on posterior margin (Pl. 2,fig. 1-2).

Thorax (Pl. 1,figs. 1-2; Pl. 3; Pl. 4,figs. 1-3) with prothorax of six segments, with macropleural sixth fused to fifth, and an opisthothorax of at least 42 segments (Pl. 3,fig. 5). Axis always wider than half total thoracic width, almost parallel sided to fourth segment then tapering evenly to posterior (Pl. 3,figs. 1,5), moderately to gently convex transversely, steep abaxially, rather flat sagittally; axial furrows distinct. Pleurae geniculate, very short (trans.), with pleural spines.

Prothoracic segments 1-4 similar; axial ring narrow (sag.) gently to moderately convex transversely, rising strongly to posterior with small sagittal node on posterior edge (Pl. 3,figs. 1-4); transverse furrow with deep apodemal slit abaxially, widens and shallows adaxially (Pl. 3,figs. 1,2); articulating half ring crescentic three quarters width axial ring sagittally, central portion flat, horizontal, abaxial portions slope down to axial furrow (Pl. 3,figs. 1,2,4). Pleurae strongly geniculate, fulcrum less than half length 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 articulating facet, extreme antero-lateral corner becomes horizontal

(Pl. 3,fig. 2); posterior pleural band narrow, convex even width. Anterior and posterior pleural bands produced into short pleural spine, notched at base; spine of first segment very short, slightly oblique to posterior, situated at midwidth of pleura (Pl. 3,fig. 1); succeeding segments with spines progressively longer, directed more strongly to posterior and situated lower (Pl. 3,fig. 1,4; Pl. 4,fig.3). Pleurae progressively lengthen towards posterior (Pl. 3 fig. 4; Pl. 4, fig. 3). Doublure extends to base of pleural spines.

Macropleural unit consists of fifth and sixth segments; fifth segment similar to preceding segments; axial ring rises steeply to posterior, normal width sagittally; pleurae wider, longer than fourth; pleural furrow more oblique, deeper, slopes up almost vertically to anterior, more gradually to posterior; anterior pleural band widens more rapidly, articulating facet larger, and fulcrum more strongly developed (Pl. 3,figs. 2,3); posterior band even width; line of fusion of pleurae of fifth and sixth sharp with posterior pleural band of fifth, unmodified (Pl. 3,fig. 3) to indistinct (Pl. 3,figs. 2,4); pleural spine longer than preceding, near posterior edge of pleura (Pl. 3,figs. 1-3). Sixth segment macropleural; axial ring normal, posterior edge almost transverse; transverse furrow deep with strong apodemal slits abaxially; shallows sagittally; apodemal slits extend across axial furrow onto pleural field for short distance (Pl. 3,fig.2; Pl. 3,fig. 4); interpleural furrow extends from slit to base of fifth pleural spine; articulating half ring crescentic, two thirds width axial ring, convex transversely; but sometimes with small median longitudinal furrow ~~(Pl. 3,figs. 1,2)~~; pleural furrow originates adaxial and slightly posterior to extremity of apodemal slit (Pl. 4, fig. 3), ~~ventrally forms pronounced ridge at oblique angle to apodemal furrow~~ directed strongly to posterior, widens slightly and deepens to fulcrum then tapers abruptly to form notch and terminates (Pl. 3,fig.3), slopes up vertically to anterior and more gently to posterior; anterior pleural band widens rapidly abaxial to fulcrum, slopes down and out, extreme antero-lateral corner forms horizontal flap fused to fifth segment just adaxial to base of pleural spine (Pl. 3,fig. 1,3); interfurrow platform asymmetrically convex; slopes up gently from fifth pleural furrow, horizontal centrally, and drops almost vertically to posterior; posterior pleural band raised, convex, even width, with distinct notch at base of macropleural spine, just abaxial to fulcrum (Pl. 3,fig. 3); macropleural spine wide, extremely long, tapers gradually and curves inwards to posterior (Pl. 1,fig. 2; Pl. 3,fig. 1), convex to triangular anteriorly becomes flatter to posterior; median ridge extends from posterior edge of interfurrow platform down spine; spine formed by anterior and posterior pleural bands of sixth segment; extends to level of pygidium. Doublure of macropleural unit extends from antero-lateral corner of fifth across base of fifth spine to notch on posterior border of sixth (Pl. 10, fig. 4; Text fig. 7) ?

Opisthothorax:- Axial ring of seventh segment similar in size and morphology to normal prothoracic axial rings (Pl. 3,figs. 1,4); pleurae of seventh blade shaped, curved to posterior following posterior edge of sixth, fulcrum less than one third length (trans) from axial furrow; pleural furrow, wide, deep, diagonal, tapers to point just abaxial to notch of sixth segment; slopes up steeply to anterior, moderately steeply to posterior; anterior pleural band overlapped by posterior band of sixth when articulated (Pl. 3,fig. 1); posterior pleural band convex, raised; pleural spine relatively long, advanced slightly to parallel curve of posterior edge of sixth, curves to posterior; formed by anterior and posterior pleural bands. Succeeding segments with pleurae progressively shorter and more transverse (Pl. 3,fig 1,5); pleural spines long, directed progressively more to posterior and becoming less advanced; fulcrum migrates adaxially and pleurae become more strongly geniculate to posterior (Pl. 3,figs. 1,5; Pl. 4,figs 1-3). At least 42 segments in opisthothorax; most posterior segments extremely narrow (sag.), lack distinct pleural furrows (Pl. 4,fig.2). Doublure of pleura extends to base of pleural spine (Pl. 4,fig. 3). Ornament of thorax consists of granules similar to those of cephalon, distributed evenly and closely spaced on dorsal surfaces.

Pygidium (Pl. 4,fig. 1,2) minute, differentiation from thorax difficult, but appears to contain 4 or 5 segments, with both axial and pleural field furrowed, with furrows directed oblique to posterior abaxially; entire lateral and posterior borders.

### *Emuella dalgarnoi* nov. sp.

Plates 5-6,Text fig. 12 (2)

Derivation of name:- After Mr. R. C. Dalgarno, who discovered the Flinders Ranges locality.

Holotype AUGD. F 164~~60~~59 . Plate 5

Selection of Holotype:- Specimen shows almost complete thorax, articulated to a cephalon which although distorted, displays most of the diagnostic characters.

Material:- Approximately 20 internal and external moulds.

Locality:- Emu Bay Shale, Emu Bay, Kangaroo Island, S.A.

Diagnosis:- Axial furrows converge strongly from posterior edge to occipital furrow, then slightly converging to almost parallel to anterior glabellar furrow. Anterior cranidial border furrow convex outwards. Palpebral ridge relatively short, posterior end opposite posterior glabellar furrow. Posterior border with abaxial section directed antero-laterally at 45°; low, narrow ridge extends from posterior lateral corner of cranidium along line to posterior section of facial suture. Posterior border furrow, with notch abaxial to fulcrum. Anterior section of facial suture diverges at approx. 20°. Thorax with axis approximately half total width. Axial rings of prothorax without nodes. Thorax with 58 segments.

Description:- Glabella with axial furrows converging strongly from posterior edge to occipital furrow, then slightly converging (Pl. 5, fig.1) to almost parallel (Pl. 6, fig.2) to anterior glabellar furrow, frontal lobe slightly expanded, rounded laterally, straight to slightly curved anteriorly sometimes with median depression causing bilobation (Pl. 6, fig. 2,4). Occipital furrow curved slightly backwards, deep, wide abaxially with base, sagittally very narrow, with muscle spots at adaxial ends of wide portion of furrow (Pl. 6, fig.2). Glabellar furrows transglabellar, similar to occipital; posterior furrow slightly convex to posterior, middle transverse, anterior furrow slightly convex to anterior. Occipital ring approximately one half cranidial width at mid palpebral level, even width projecting very little beyond posterior margin of fixigenae. Axial furrow very slightly impressed, deepest at junction with glabellar furrows, anteriorly reaching anterior border furrow (Pl. 6,figs. 1,2). Anterior border furrow convex to anterior. Eye ridge wide directed to posterior at 30° to transverse line, from frontal lobe. Palpebral ridge relatively short less than one third glabellar length, anterior end opposite anterior glabellar lobe, posterior end opposite posterior glabellar furrow, slopes up steeply from palpebral furrow, flat on adaxial side, becoming convex dorsally; slightly convex (exsag.) with highest point towards posterior end (Pl. 6,figs. 1-3); continuous with eye ridge. Palpebral furrow very wide, slopes down to posterior but with small depression opposite mid point of palpebral ridge. Posterior area of fixigenae relatively long (exsag.), two thirds width (trans) occipital ring with fulcrum opposite posterior end of palpebral ridge (Pl. 6,figs. 1,2). Posterior border transverse from axial furrow to fulcrum, widening and rising rapidly; anteriorly drops steeply to border furrow, outer edge concave to posterior (Pl. 6,fig. 3); abaxial to fulcrum border directed antero-laterally at 45°, width constant, upper surface horizontal; to anterior border drops vertically to border furrow, rounded dorsally; narrow ridge, below level of border extends from posterior lateral corner along line of posterior section of facial suture (Pl. 6,figs. 2,3). Posterior border furrow, widens to fulcrum, then with distinct notch (Pl. 6,fig. 2,3), abaxially slopes down slightly and antero-laterally continuous with furrow running along base of sutural ridge (Pl. 6,fig. 4).

Anterior section of facial suture diverges from palpebral ridge at approximately 20°; rostral plate same width as frontal glabellar lobe, notched laterally (Pl. 6, fig. 4). Posterior section of suture relatively long, diverges at 45°; section from palpebral ridge to posterior border straight, then sharply convex abaxially across posterior border (Pl. 6, fig. 2).

Ornament of cranidium pointed granules, closely spaced on glabellar lobes, borders and eye lobes, sparsely distributed on palpebral area of fixigenae and anterior lateral sections of cranidium, absent in all furrows. Paired muscle spots present on abaxial portions of occipital and glabellar furrows (Pl. 6, fig.2). Genal field of librigenae with scattered granules.

Hypostome unknown.

Thorax with axis approx. one half total thoracic width. Maximum number of 52 opisthothoracic segments observed (Pl. 5). Pygidium (Pl. 5) consists of minute furrowed disc, without distinct division into axial and pleural field, with four and five furrows visible, transverse sagittally, abaxially curving obliquely to posterior; entire lateral and posterior borders.

## GENUS *BALCORACANIA* nov. gen.

type species: *Balcoracania dailyi* nov. sp.

Plates 7 - 11; Text figs. 6, 9 (3, 4).

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

*Diagnosis*:- Preglabellar field absent or narrow, downsloping. Palpebral ridge long, crescentic, posterior end opposite posterior half of posterior glabellar lobe or occipital furrow. Posterior border with section abaxial to fulcrum strongly depressed and directed antero-laterally at 60°. Posterior section of facial suture diverges posteriorly at 55° to border furrow, then swings sharply inwards across border. Librigena with genal spine slightly advanced.

Thorax with axis less than half thoracic width. Pleural furrows terminate at base of pleural spine. Macropleural unit without flap between spine of fifth and sixth segment. Fine closely spaced granules on dorsal surfaces. Thorax with 53-61 segments.

### _Balcoracania dailyi_ nov. sp.

Plates 7-10; Text figs. 6, 9 (3).

_Derivation of name_:- After Dr. B. Daily, who first discovered members of this group.

_Holotype_:- AUGD. F.164643 , Plate 7, Fig. 1

_Selection of holotype_:- Specimen is only one known with cephalon articulated with a reasonably complete thorax.

_Locality_:- Upper section of White Point Conglomerate, Kangaroo Island, South Australia.

_Material_:- Approximately 150 internal and external moulds.

_Diagnosis_:- Glabellar furrows distinct only on sides of glabella; frontal glabellar lobe only slightly expanded, indistinct laterally; narrow downsloping preglabellar field; anterior to frontal lobe, anterior border widens, slopes down gradually to border furrow, border furrow abruptly shallows and rises, forming prominent fossula at junction with axial furrow.

_Description_;- Cephalon subsemicircular in outline, transversely and sagittally moderately convex. Cranidium, moderately convex (trans). Axial furrows converge evenly from posterior edge to anterior glabellar furrow, frontal lobe very slightly expanded, slightly rounded laterally, almost straight anteriorly; glabella, strongly convex transversely with weak median ridge extending from posterior to anterior glabellar furrow, gently convex sagittally highest at anterior glabellar lobe, slopes down steeply to preglabellar field, more gently to posterior. Occipital furrow deepest abaxially, curves slightly backwards (Pl. 7, fig. 3). Glabellar furrows transcurrent, distinct abaxially but very shallow and indistinct sagittally (Pl. 7, fig. 5); posterior furrow directed obliquely to posterior abaxially, transverse sagittally (Pl. 7, fig. 1); middle furrow transverse; anterior furrow directed obliquely forwards abaxially. Occipital ring less than half cranidial width at mid-palpebral level, maximum width sagittally, posterior edge convex backwards, posterior half projects beyond margin of fixigenae (Pl. 7, figs. 3,4). Frontal lobe with central portion flat to slightly convex, abaxially convex, occasionally with median depression giving bilobed appearance. Axial furrows slightly impressed below fixigena from posterior edge to eye ridge, rises and becomes indistinct over eye ridge, not impressed on sides of frontal lobe, anteriorly joins anterior border furrow (Pl. 7, fig. 3-5). Deep fossulae at anterior junction of eye ridge and axial furrow (Pl. 7, fig. 5). No distinct preglabellar furrow, narrow preglabellar field slopes down to border furrow (Pl. 7, figs. 3-5). Anterior border medium width, margin convex outwards; abaxially convex, raised, anterior to frontal lobe widens and slopes down flattly to border furrow (Pl. 7, fig.3). Anterior border furrow moderately deep and narrow abaxially, anterior to frontal lobe, abruptly rises, broadens and shallows (Pl. 7, fig.3-5);

fossulaeat junction with axial furrows (Pl. 7, fig. 3,5). Eye ridge wide long. Palpebral ridge wide (trans) long approximately three quarters glabellar length, anterior end opposite anterior glabellar lobe, posterior end opposite occipital furrow or posterior half of posterior glabellar lobe; slopes up flatly from palpebral furrow, becomes progressively higher to posterior, abaxial edge convex upwards and outwards; posterior end high above posterior area of fixigena (Pl. 7, fig. 3-5); separated indistinctly from eye ridge by change in convexity or in some specimens by indistinct longitudinal furrow. Palpebral and eye ridges appear double in some large specimens. Palpebral furrow wide, deepens and slopes down steeply to posterior. Posterior area of fixigena short (exsag.) wider (trans) than occipital ring, depressed, and with strong fulcrum. (Pl. 7, fig. 2); section adaxial to fulcrum horizontal; section abaxial strongly downsloping. Posterior border diverges slightly to posterior from axial furrow to fulcrum, abaxially directed antero-laterally at 50°. Posterior border furrow widens abaxially, deep adjacent to border, shallows away from it, almost straight sided, confluent with posterior end of palpebral furrow (Pl. 7, fig. 2-4).

Anterior section of facial suture diverges at approximately 25° from palpebral ridge (Pl. 7, fig. 1; Pl. 8, figs. 2-4). From point where suture intersects the anterior edge connective sutures cross doublure, sharply convex abaxially (Pl. 8, fig. 4). Rostral suture marginal ventral. Palpebral section of facial suture diverges at approximately 15° to posterior. Posterior section relatively short, diverges at 55°, slopes down steeply to posterior border furrow, then curves sharply inwards across border (Pl. 7, fig. 2-4; Pl. 8, fig. 1); posterior lateral corner of cranidium opposite occipital furrow (Pl. 7, figs 3,4).

Librigena (Pl. 8) with long genal spine, slightly advanced. Lateral border furrow curves sharply inwards near base of genal spine, continuous with posterior border furrow; becomes wider, deeper and downsloping adaxially (Pl. 8, figs. 1,2). Posterior border narrow, convex, high above furrow adaxially, slopes down abaxially to join lateral border (Pl. 8, fig. 2). Genal field slopes up gradually and rather flatly from border furrow, sharply upturned at adaxial edge to form eye socle, moderately convex exsagittally, posterior lateral sections sloping down steeply (Pl. 8, fig. 1).

Cephalic doublure same width as border anteriorly and laterally; posterior fixigenal doublure tapers sharply to point just abaxial to fulcrum (Pl. 7, fig. 2). Rostral plate (Pl. 9, fig. 4) equal in length to maximum width of frontal glabellar lobe (Pl. 7, fig.1). Doublure of librigena moderately to strongly convex (ventrally), widens and flattens preceding connective suture (Pl. 8, fig. 3). Lateral and posterior librigenal doublures continuous (Pl. 8 fig. 1). Ventral side of genal spine slightly rounded to flat.

Hypostome (Plate 9, Text fig. 8) similar in basic morphology to that of E. polymera, but differs from or illustrates more clearly, the following features:- anterior wings very prominent, depressed, wing processes visible in well preserved specimens (Pl. 9, figs. 2,3); position of wing variable resulting in anterior lateral border and furrow being directed postero-laterally (Pl. 9, figs. 4,6) or transversely inwards (Pl. 9, fig. 2,3). Anterior border wide, steeply upsloping, crossed by narrow line in some specimens (Pl. 9, figs. 1,2); line symmetrically concave about sagittal line, abaxially intersecting anterior edge at extremities of hypostomal suture. Median furrow with maculae at posterior ends (Pl. 9, figs. 3,4). Posterior lobe of median body strongly convex (trans), parallel sided (Pl. 9, fig. 2) or slightly tapering to posterior (Pl. 9, figs. 1,5); posterior lateral corner rounded, with prominent boss (Pl. 9, figs. 4,6). Lateral border upsloping with small shoulder at mid length (Pl. 9, fig. 4); border furrow with very deep fossula below shoulder (Pl. 9, fig. 2,4).

Ornament of cranidium consists of fine granules covering all dorsal surfaces; occipital ring with elongate sagittal node on posterior edge (Pl. 7, fig. 4); terrace lines occur on extreme outer edge of anterior and lateral borders (Pl. 7, fig. 4; Pl. 8, fig. 4). Librigena with granules similar to cranidium covering genal field, adaxial portion of lateral border, and dorsal surface of genal spine (Pl. 8, fig. 2,4); abaxial portion of lateral border with wrinkled terrace lines, separated by subparallel rows of elongate granules becoming more numerous towards genal spine (Pl. 8, fig. 4). Lateral and posterior doublure with long regular terrace lines, becoming anastomising adjacent to connective sutures (Pl. 8, figs. 1,3); ventral surface of genal spine with elongate granules arranged in parallel rows. Rostral plate with terrace lines.

Thorax (Pl. 7, fig. 1; Pl. 10, figs. 1-5) similar in basic structure to that of Emuella, but differs from it in the following features;-

Axis narrow, less than half thoracic width, pleurae correspondingly longer (trans) (Pl. 7,fig. 1). Axial furrows slightly converging from first to sixth segment, rapidly converging to about mid length of opisthothorax, then almost parallel to level of pygidium (Pl. 7,fig. 1; Pl. 10,fig. 3). Prothoracic segments with axial rings rising only slightly to posterior, without nodes (Pl. 7, fig. 1); pleurae of segments 1-4 same length (trans); pleural furrow diagonal, tapers abaxial to fulcrum, terminates at base of pleural spine (Pl. 7,fig. 1); pleural spine formed by anterior pleural band above.

Macropleural unit with line of fusion of pleurae generally indistinct, marked by slight furrow to base of fifth pleural spine (Pl. 10, figs. 3,5) or almost completely effaced (Pl. 10,figs. 1,2,4); anterior pleural band of sixth, slopes down to join base of fifth pleural spine without modification (Pl. 10,figs. 4,5)

Thorax contains 53 segments in holaspid.

Pygidium minute, furrowed disc, without distinct division into axial or pleural field, 4 or 5 furrows; entire lateral and posterior borders.

### Balcoracania flindersi nov. sp.
Plate 11-12; Text Fig. 9 (4)

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

Holotype:- AUGD F. 16483 Plate 11, Fig. 4.

Occurrence:- Billy Creek formation, Balcoracana Creek, Flinders Ranges, South Australia.

Diagnosis:- Glabellar furrows deep, distinct, transglabellar; frontal glabellar lobe markedly expanded reaching unmodified anterior border furrow.

Description:- Morphology is very similar to that of B. dailyi but differs in the following:- glabella with deep distinct, transglabellar furrows; posterior furrow curves backwards, middle furrow transverse, anterior furrow convex forwards (Pl. 11, fig. 1,2). Frontal glabellar lobe markedly expanded, rounded anteriorly and laterally, reaches anterior border furrow; no preglabellar field. Anterior border and border furrow unmodified anterior to frontal lobe (Pl. 11, figs. 1-2). Palpebral area of fixigena usually highly inflated, steeply downsloping to posterior.

Thorax (Pl. 11, figs. 1,6) with long opisthothorax with maximum number of 61 segments observed (Pl. 11, fig. 1).

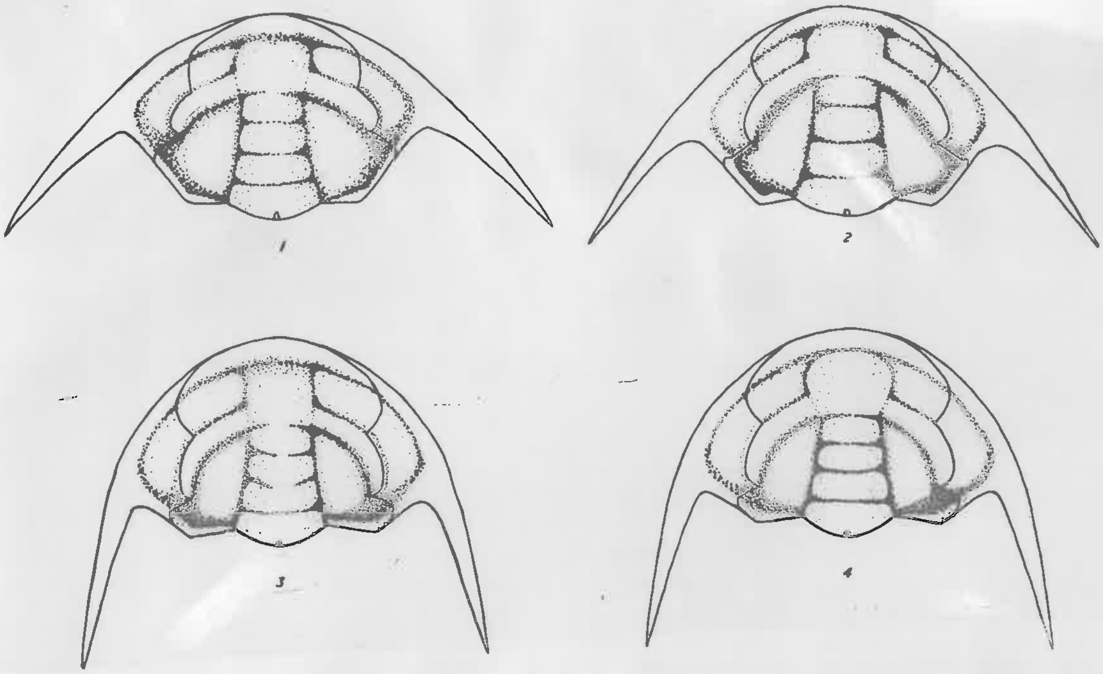
## DISCUSSION

### TAXONOMIC DISCRIMINATION

The differentiation of known members of this group into two genera and four species is based primarily on qualitative considerations, augmented by a statistical analysis of the variation of some characters. A comparison of the morphology of the adults of the four species is presented as Table 1.

The division into the genera Balcoracania and Emuella is based upon the differences in the length and position of the palpebral ridge, the correlated differences of the posterior border and border furrow, and to a lesser extent the proportions and aspects of the structure of the thorax.

TEXT FIGURE 9



Comparison of cephala of the Emuellidae

(1) *E. polymera.*

(2) *E. dalgarnoi.*

(3) *B. dailyi.*

(4) *B. flindersi.*

In the species of Emuella, the palpebral ridge is relatively short with the posterior end varying between the level of the middle and posterior glabellar furrows, the portion of the posterior border abaxial to the fulcrum is directed antero-laterally at 40-45°; the width of the thoracic axis is at least half of the thoracic width, the pleural furrows terminate before the spines and the articulating facet of the sixth prothoracic segment is modified by a horizontal flap attached to the base of the fifth pleural spine.

In Balcoracania the palpebral ridge is long, with its posterior end opposite or just above the level of the occipital furrow, the posterior border furrow widens abaxially and is almost straight sided; the section of the posterior area of the fixigenae abaxial to the fulcrum is strongly depressed, and this section of the border is directed antero-laterally at approximately 55°; the thoracic axis is less than one half the total width, the pleural furrows terminate at the base of the pleural spines; and no flap is present between the fifth and sixth.

The differentiation of the species of Emuella is based on the position and length of the palpebral ridge, the structure of the posterior border and border furrow, and the anterior section of the facial suture. In E. polymera the palpebral ridge is very short with the posterior end opposite the middle glabellar lobe, the distal section of the border furrow and the abaxial section of the border are directed at approximately 40°, and the anterior section of the facial suture diverges at approximately 10°. E. dalgarnoi differs in having a longer palpebral ridge with its posterior end opposite the posterior glabellar furrow, the posterior border furrow with a distinct notch at the fulcrum, the abaxial section of the border directed at 45°, and a more divergent anterior section of the suture; in addition a low ridge runs along the course of the posterior section of the facial suture.

The species of Balcoracania are mainly distinguished on the structure of the frontal glabellar lobe and anterior border furrow, and the lateral glabellar furrows. In B. dailyi the frontal lobe is expanded little laterally, compared with the anterior glabellar lobe, is separated from the anterior border by a narrow, downsloping, preglabellar field, and has distinct anterior border fossulae; the glabellar furrows are shallow and distinct only abaxially. In B. flindersi the frontal lobe is markedly expanded and reaches an unmodified anterior border furrow; the glabellar furrows are distinct both sagittally and abaxially.

## INTRASPECIFIC VARIATION

In all collections some sort of deformation has taken place, increasing and varying the amount and quality of the variation; this factor must be considered when evaluating the intrinsic variation of the collections and thus the species (see p. 10, Appendix IV). The range of variation is approximately the same for the morphological characters or groups of characters for each species. The following groups exhibit a correlated variation:

(a) The convexity of the palpebral area of the fixigena and the depth of the surrounding axial and palpebral furrows. The palpebral area of the fixigena varies from almost flat (trans.) to highly convex; in the former case the furrows are either only slightly impressed or are represented merely by a change in slope, and in the latter case, the axial furrow from the occipital ring to the anterior glabellar furrow and the palpebral furrow are deeply impressed.

(b) The junction of the eye ridge and frontal glabellar lobe; this is probably the most variable of all characters and the most difficult to distinguish between genuine and spurious (deformation effects) variation. The eye ridge varies from being almost completely separated from the frontal lobe by the axial furrow,to joining it without significant interruption. In the former case the axial furrow is deep, but always rises across the ridge i.e. the eye ridge is never completely separated from the glabella.

(c) The frontal glabellar lobe, the preglabellar and the 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 a straight anterior edge to almost circular, being correlated respectively to decreasing convexity of the lobe (sag. and trans.). 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 anterior to the lobe higher above the abaxial sections, and thus with more distinct border fossulae, than those of lower convexity. In B. dailyi,high convexity of the lobe is also associated with a slightly longer (sag.) preglabellar field.

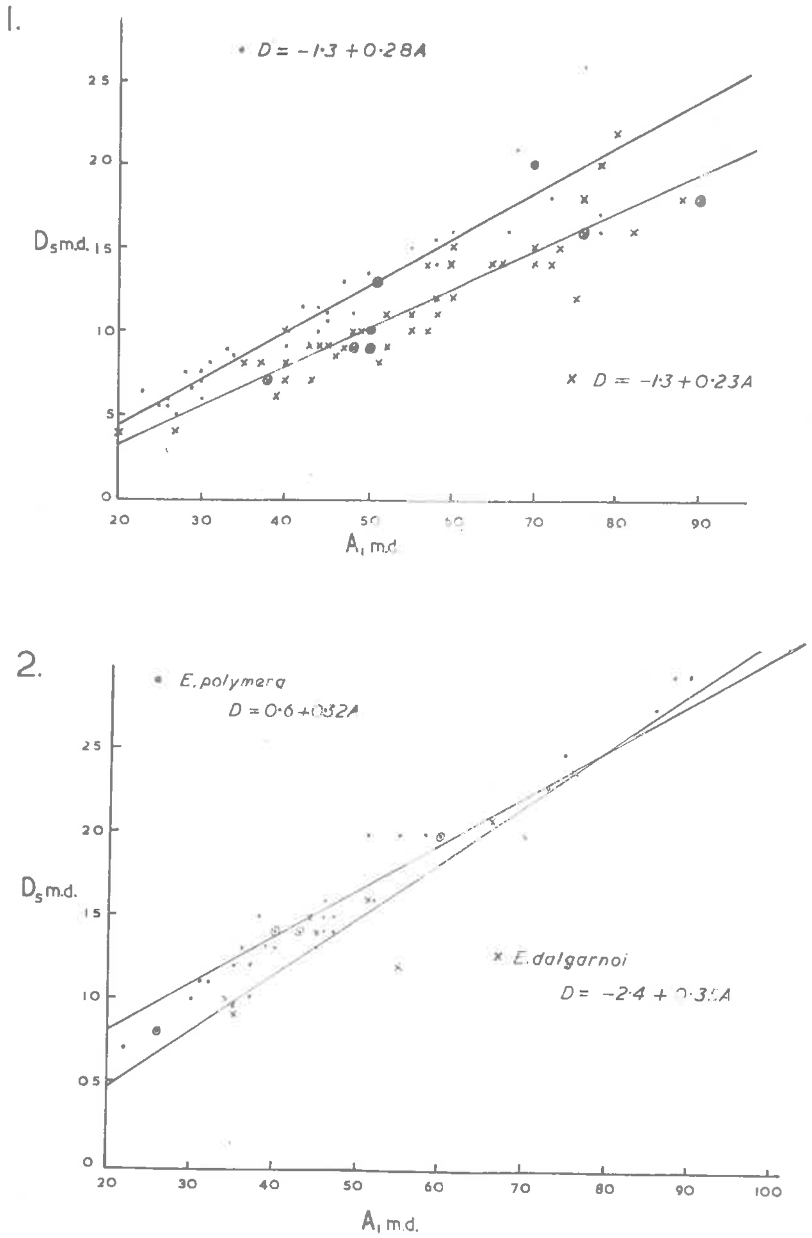
(d) The level of the posterior end of the palpebral ridge; in

Text Figure 10

(1) Comparison of scatter diagrams and best fit lines for selected variables from collections of *B. dailyi* from different localities. The symbol • denotes specimens from the Emu Bay section, the symbol x for those from the section west of Cape D'Estaing.

(2) Comparison of scatter diagrams and best fit lines for the variables $D_5$ the occipital post palpebral length, and A, the cranidial length for the two species of *Emuella*.

Dimensions expressed as micrometer divisions where 1.00 mms. = 12 micrometer divisions. Duplication of points is indicated for the same species (or samples) by a circle, for different species (or samples) by superposition of symbols.



TEXT FIGURE 10.

*Balcoracania* the level varies from the occipital furrow (Pl. 7,fig. 5) to the posterior half of the posterior glabellar lobe (Pl. 7,fig. 3, Pl. 11,fig. 4); in *E. polymera* just below the middle glabellar furrow to mid length of the middle lobe, and in *E. dalgarnoi* just above or below the posterior glabellar furrow. These variations are correlated with changes in the posterior border and border furrow.

(e) The line of fusion of the pleurae of the fifth and sixth prothoracic segments; in ~~*B. dailyi*~~ E. polymera the range of variation includes forms with the posterior pleural band of the fifth still distinct and the line fusion represented by a sharp ridge from the transverse furrow to the base of the fifth pleural spine (Pl. 3,fig. 3), and with an almost completely smooth interfurrow platform with only a short indistinct ridge present (Pl. 3,fig. 4). In the other species the range is much less, variation affecting only the distinctness of the line of fusion on a relatively smooth interfurrow platform (Pl. 10, figs. 4,5)

## QUANTITATIVE DESCRIPTION

Scatter diagrams (Text figs.10-12) were constructed for each of the four species for selected variables and the equations for the "best fit" lines calculated (Table 1). In addition as *B. dailyi* is found at two separate localities a comparison was made of scatter diagrams and "best fit" lines for a pair of variables for samples from each locality (Text fig. 10 (1); Appendix IV (4)). The results support the hypothesis that the two samples came from the same population, despite differences due to different degrees of deformation.

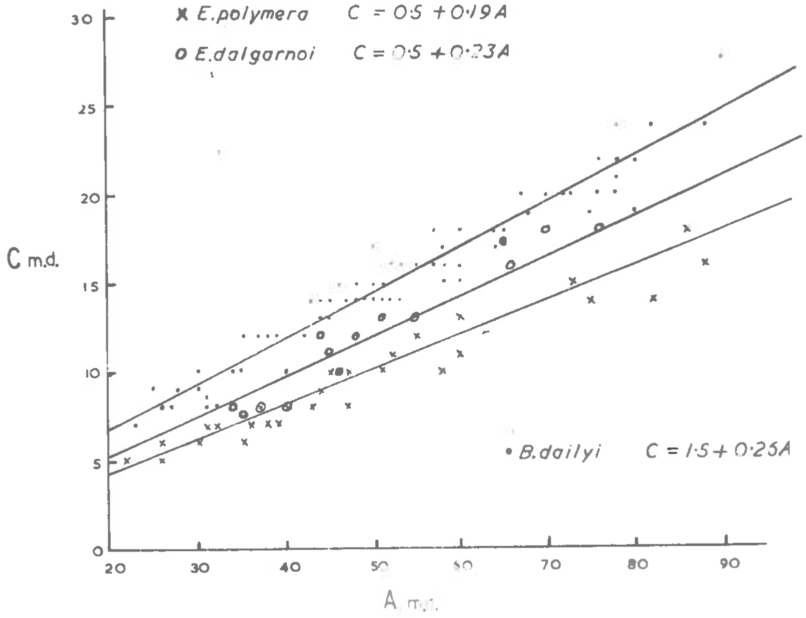
## TEXT FIGURE 11.

(1) Scatter diagrams and best fit lines for adults of *E. polymera*, *E. dalgarnoi* and *B. dailyi*, for $A_1$ the cranidial length plotted against C the palpebral length; (12 micrometer divisions = 1.00 mms)

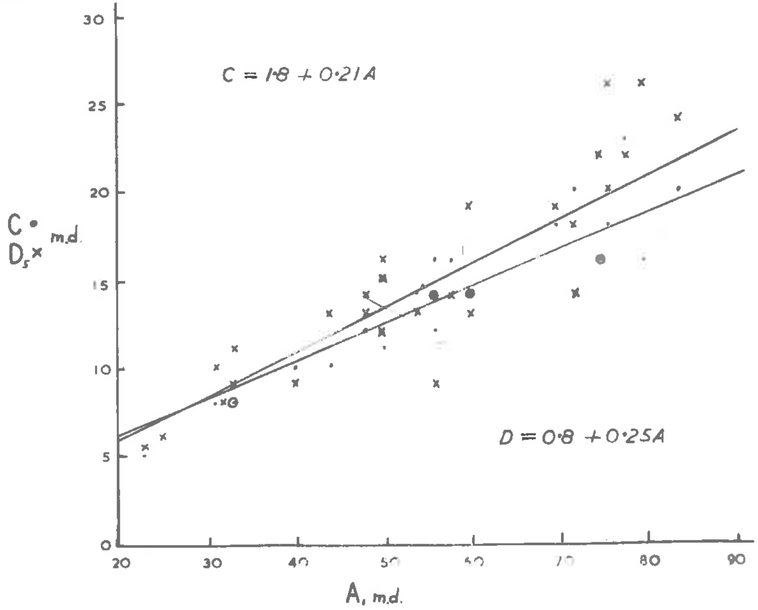
(2) Scatter diagrams and best fit lines for adults of *B. flindersi* for $A_1$ the cranidial length plotted against C the palpebral length, and $D_5$ the occipital post palpebral length; 12 micrometer divisions = 1.00 mms.

TEXT FIGURE II

1.



2.

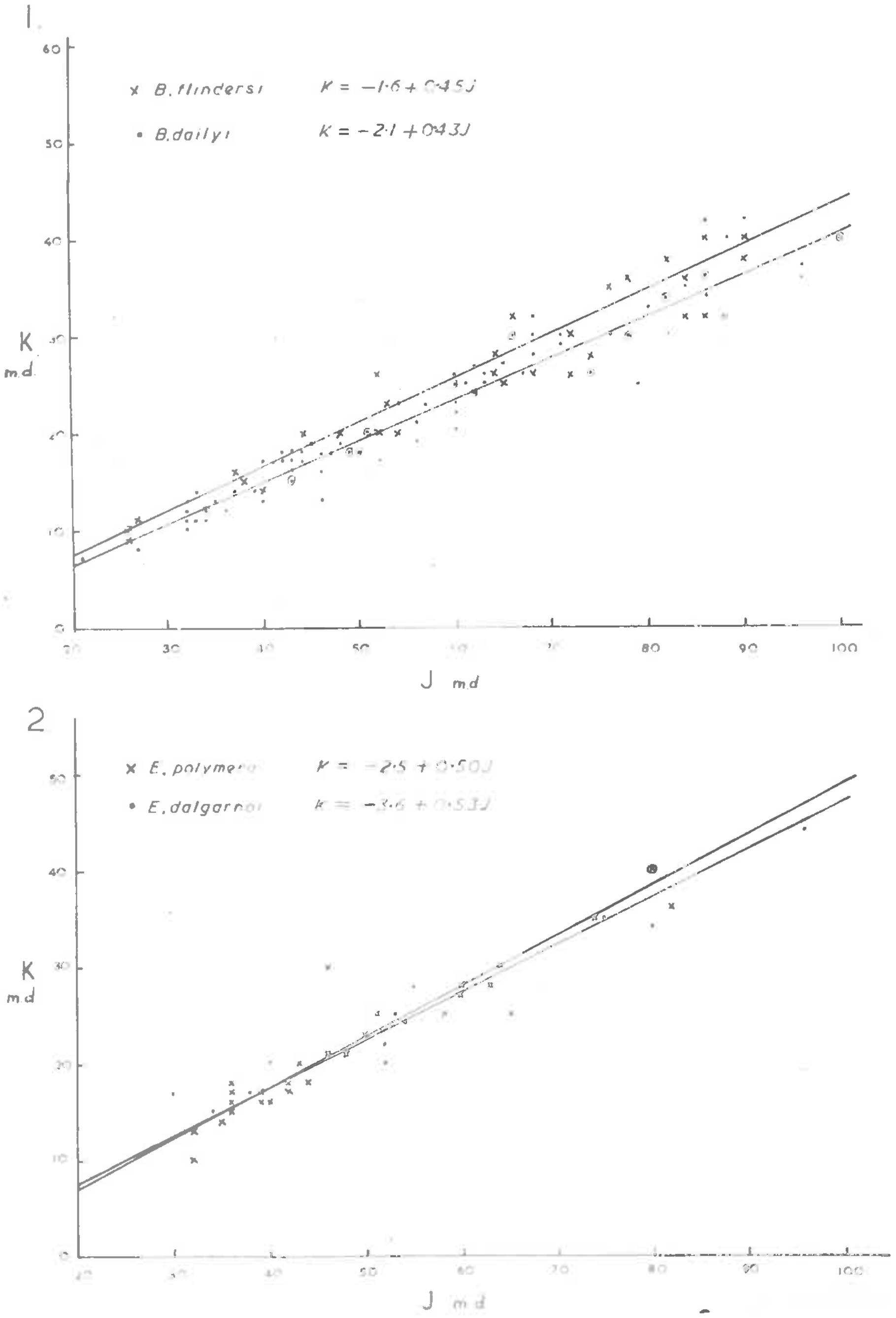


Examination of the scatter diagrams and comparison of the equations of the "best fit" lines for variables, selected on the basis of qualitative work, for the four samples is statistically consistent with either separation into two genera, each with two species, or two species, each with two subspecies. However, it must be remembered that the quantitative analysis can only supplement, not supplant, the qualitative, and it is on the latter grounds that two genera, each with two species, are adopted.

The scatter diagrams and "best fit" lines for cranidial length plotted against occipital post-palpebral length supports the opinion that the position of the posterior end of the palpebral ridge becomes ~~lower~~ more posterior from *E. polymera* to *E. dalgarnoi* to the species of *Balcorocania*. For cranidial length plotted against palpebral length the distribution shows that the palpebral ridge of *B. flindersi* is shorter than might be expected. This is probably due to the anterior end of the palpebral ridge being lower than in the other

The distributions for all variables for *B. flindersi* show a much greater dispersion than those for the other species, and cannot be explained by differences in the deformation of the collections. Its significance is unknown. Comparision of the equations of the best fit lines for all samples, (Table 2) appears to support classification as a separate species, but statistical testing of the significance of the difference was precluded by limitations of time.

TEXT FIGURE 12



Scatter diagrams and best fit lines for J, the mid palpebral cranidial width plotted against K the occipital width. (12 micrometer divisions = 1 mm.)

(1) adults of the species of Balcoracania

(2) adults of the species of Emuella

Comparison of the adult morphology of members of the Emuellidae

TABLE I

| Character | *E. polymera* | *E. dalgarnoi* | *B. dailyi* | *B. flindersi* |
|---|---|---|---|---|
| Palpebral ridge | less than 1/4 glabellar length; post. end opposite middle glabellar lobe; mid point highest. | less than 1/3 glabellar length; post. end opposite post. glabellar furrow, high point towards post. | long, greater than 1/2 glabellar length; post end opposite or just above occipital furrow posterior end highest. | ditto |
| Post. area of fixigenae (ab. to fulcrum) | slightly depressed | slightly depressed | strongly depressed | ditto |
| Posterior border, (ab. to fulcrum) | approx. 40-45° | approx. 45° | approx. 60° | ditto |
| Preglabellar field | absent | absent | narrow (sag), indistinctly differentiated, downsloping | absent |
| Axial furrow (eye ridge to border furrow) | deeply impressed, with fossula at junction with eye ridge | impressed, with fossulae at junction with eye ridge | not impressed, indistinct, with fossula at junction with eye ridge | not impressed, indistinct, fossulae absent |
| Anterior border furrow | fossula at junction with axial furrow, border rises abruptly anterior to frontal glabellar lobe. | ditto | ditto | unmodified, even depth sagitally and abaxially |
| Glabellar furrows | shallow indistinct, almost transverse | wide, deep; anterior furrow convex forwards; post furrow slightly convex backwards | distinct only on sides of glabella | furrows deep, distinct ant. furrow convex ant., post. furrow slightly convex backwards |
| Anterior section of facial suture | diverges at approx. 10° | diverges at approx. 20° | diverges at approx. 25° | ditto |
| Post section of facial suture | diverges strongly | ditto, low sutural ridge present | diverges strongly | ditto |
| Width of thoracic axis | greater than 1/2 total thoracic width | approx. 1/2 total thoracic width | less than 1/2 total thoracic width | ditto |
| Pleural furrow | terminates before pleural spine | ditto | terminates at base of pleural spine | ditto |
| Macropleural unit | horizontal flap joins pleural spine of 5th, to antero-lat. corner of the 6th | ditto | flap between 5 & 6 absent | ditto |
| Ornament of cranidium | large, pointed granules, densely on all dorsal surfaces; occipital node. | closely spaced granules on borders, glabella & eye lobes; widely spaced on palpebral area, absent in furrows; occipital node | fine dense granules on all dorsal surfaces; occipital node | ditto |
| Ornament of thorax | granules on all dorsal surfaces, weak nodes on posterior margins or first four prothoracic segments. | granules on all dorsal surfaces; incipient nodes on first four prothoracic segments | granules on all dorsal surfaces; prothoracic segments without nodes | prothoracic segments without nodes |

# TABLE 2

"Best fit" lines for selected variables by Bartletts method.

(Simpson, Roe & Lewontin, 1960 p.234 ).

| | $A_1 - C$ | $A_1 - D_5$ | $K - J$ |
|---|---|---|---|
| E. polymera | $C = 0.5+0.19A_1$ | $D = 0.6+0.32A_1$ | $K = -2.5+0.50J$ |
| E. dalgarnoi | $C = 0.5+0.23A_1$ | $D = -2.4+0.35A_1$ | $K = -3.6+0.53J$ |
| B. flindersi | $C = 1.8+0.21A_1$ | $D = 0.8+0.25A_1$ | $K = -1.6+0.45J$ |
| B. dailyi | $C = 1.5+0.26A_1$ | | $K = -2.1+0.43J$ |
| (1) locality 1 | | $D = -1.3+0.23A_1$ | |
| (2) locality 2 | | $D = -1.3+0.28A_1$ | |

Calculations for the "best fit" lines are given in Appendix

$A_1$ is the cranidial length, C is the palpebral length, $D_5$ is the occipital post-palpebral length, K is the occipital width, and J the mid palpebral cranidial width.

# ONTOGENY

## INTRODUCTION

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 also well represented numerically, but only a few specimens of E. polymera are known. Consequently it has been found necessary to change the order of description of the ontogenies from that adopted for the descriptions of adult morphology.

## METHODS AND PROCEDURES

The methods and procedures adopted in this study vary slightly depending on the size and the nature of the sample of each species, but are basically similar to those described below for B. flindersi.

All specimens were prepared, measured, photographed and described individually. A reconstruction of an early meraspid cranidium was prepared and compared with that of a holaspid on a modified D'Arcy Thompson diagram (Text fig. 13), using the technique described by Palmer (1957 p. 106). The line of least "distortion" is that of the line of bilateral symmetry and specifically the length of the glabella appears to increase at a rate most nearly proportional to that of absolute size. However the glabellar length is extremely difficult to measure accurately, particularly on small specimens, and the cranidial length ($A_1$) is used as the standard dimension. It is evident that the use of the cranidial length involves some error, as anterior border appears and develops during ontogeny; however it is considered that the practical advantages of accurate measurement on small specimens offsets the theoretical disadvantage. The morphology of each specimen is thus tabulated against cranidial length (in ascending order). Examination of the table and the D'Arcy Thompson grid reveals that several morphological characters underwent progressive change with increase in size. The more prominent of these characters are selected, and the sample subdivided into subclasses as follows:-

(1) the anterior border and border furrow (a) border absent (b) narrow, downsloping without true border furrow (c) narrow, horizontal border anterior to frontal lobe, convex abaxially; distinct border furrow (d) border, convex, raised, even width.

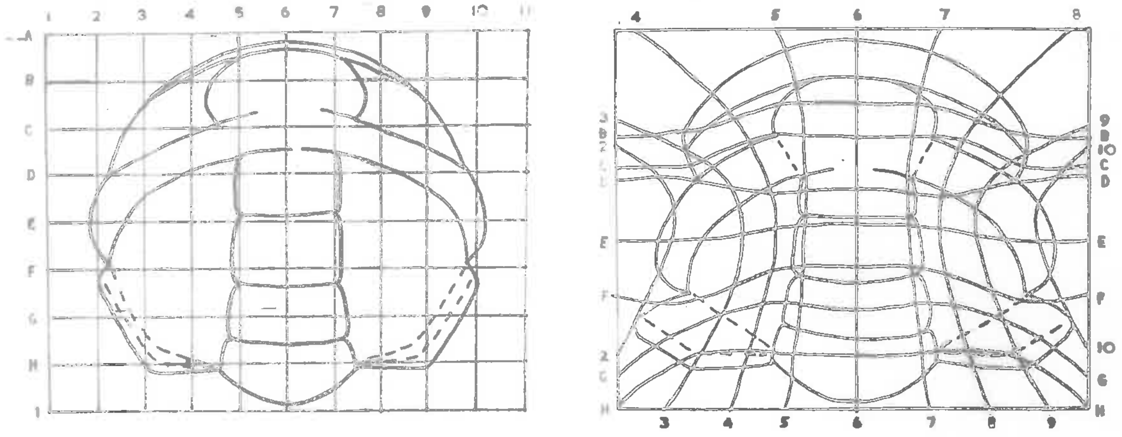
(2) position of the posterior end of the palpebral ridge (a) anterior furrow (b) anterior lobe - middle furrow (c) middle lobe (d) posterior furrow (e) posterior lobe - occipital furrow

(3) anterior sections of the facial sutures (a) converging (b) sagittal (c) diverging.

The size ranges of each subclass were then noted; considerable overlap of the ranges of subclasses exists, and the changes in different characters develop at different sizes. However it is found that the sets of data can be combined to give a number of stages of cranidial development, with an acceptable maximum overlap of the equivalent size ranges (Table 3).

The development of the meraspid thorax is incompletely known, and although related where possible, to stages of cranidial

# TEXT FIGURE 13



1. 2.

Proportional change in the dorsal cephalic features of B. flindersi during development.

1. Cranidium of Stage II, meraspid degree 0.

2. Holaspid cranidium.

Intersections of vertical and horizontal lines are at the same morphological positions on both drawings.

development, is described separately (Tables 4,7).

The hypostomes present range in length upwards from 0.50mms, and it is evident that at least the specimens in the lower part of the range, have been separated from larval (meraspid) cranidia. Two problems arise; to fix an upper size limit below which the hypostomes may be said to be "larval"; and the match these hypostomes with their equivalent cranidia and so to stages of cranidial development.

Examination of adult specimens of cephala, with hypostomes in or close to the articulated position, shows that the posterior edge of the hypostome reaches approximately the level of the posterior glabellar furrow. The length of the hypostome in the adult is thus slightly less than three quarters of the cranidial length ($A_1$), and accordingly an upper limit for the hypostomal length can be fixed. It is unwise however, to apply this factor for smaller hypostomes, 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 (i.e. allometric growth between hypostome and cranidium takes place in the larval stages). It is therefore necessary to find some dimension of the hypostome, which can justifiably be assumed to bear a constant relation to a 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 rostral plate is equal to that of the anterior edge of the hypostome, excluding the anterior wings which are free (Text fig. 7). As it can be assumed that the functional relationship between the rostral plate and hypostome has not changed, 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; 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 can also be measured directly in most cases.

On the above basis, the hypostomes may be matched with a range of cranidia,and 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 overlaps between morphological subclasses (c) the overlap between meraspid degrees (d) the method of determining equivalence between hypostome and cranidium. However it is considered that, in general, an accurate representation of the ontogeny results.

## THE ONTOGENY OF BALCORACANIA FLINDERSI.

The collection of B. flindersi contains approximately 180 larval specimens ranging in size from 0.5 mm upwards. The preservation is by replacement of the tests by a relatively thick calcite sheet, which is easily fractured, collapsed or distorted. However sufficient detail is preserved to elucidate the main ontogenetic changes, and approximately 140 specimens were described and measured.

Most of these specimens are cranidia, only 24 having the thorax attached, and of these only half are complete enough, or well preserved enough, to ascertain the meraspid degree with any certainty.

DEVELOPMENT OF THE CEPHALON (Table 3)

Stage I - cranidial lengths 0.38 - 0.49 mms. (includes the protopygidium in this stage); protaspis. Text fig. 14 (1), Plate 13, fig. 1 . Only three specimens were found smaller than the cranidial size range of meraspids of degree 0, and of these only one (Pl. 13, fig. 1 ) is well enough preserved to verify the presence of the protopygidium. This specimen is subelliptical in outline, subhorizontal centrally, and slopes down steeply marginally. It is divided into a large cephalon (or cranidium) and a narrow (sag.) crescentic protopygidium, by a transverse ridge (posterior border of the cephalon). The axis is narrow, less than one third width of the cephalon, flat to slightly depressed, and is defined for the posterior three quarters of it's length by distinct parallel furrows, and for its anterior one quarter by indistinct furrows diverging at 45° to the anterior edge of the cephalon. The axis is divided into five rings by indistinct transverse furrows, the most anterior furrow being at the point of divergence of the axial furrows. The pleural regions are incompletely subdivided extending a short distance abaxially from the junctions of the axial and transverse glabellar furrows. The most anterior furrow is very indistinct, but probably represents the posterior margin of the eye ridge. A palpebral ridge is not visible. A short section of the antero-lateral edge is straight and this may possibly represent the anterior section of the facial suture.

The protopygidium is small, approximately one quarter total sagittal length of the protaspis. The axis tapers posteriorly and does not appear to reach the posterior edge. No furrows could be distinguished on the pleural regions.

Stage II - cranidial lengths 0.50 - 0.64 mms; meraspid degrees 0-1; Text fig. 14 (II), Plate 13 figs.2-4. Numerous specimens falling within this size range have a distinct occipital ring and posterior border, showing them to be meraspid cranidia. Two specimens with attached transitory pygidia and one meraspid of degree 1 are included within this size range.

The cranidium is subcircular in outline, centrally subhorizontal, steeply downsloping marginally. The glabella is moderately convex transversely and approximately one quarter the mid palpebral cranidial width; anterior, middle, posterior and occipital furrows are all distinct, and transverse; an indistinct fifth furrow, anterior to the normal anterior furrow, aligned with the anterior edge of the eye ridge, is visible in some well preserved specimens (Plate 13, fig. 4 ). The axial furrows are slightly impressed and deepen at the junctions with the glabellar furrows; from the posterior edge to the anterior furrow they are parallel or slightly pinched in at the latter, become very faint at the junctions of the eye ridges and frontal lobe, then diverge at approximately 45° to the anterior edge. The glabellar lobes are subequal in size; except the frontal lobe which is approximately one quarter the total glabellar length and is expanded to the anterior. The eye ridge is distinct, directed slightly to the posterior from the posterior section of the frontal lobe (the area between the anterior and pre-anterior glabellar furrows), and steeply downsloping abaxially. The palpebral ridge is very short, depressed below the level of the cheek, downsloping abaxially, and not separated from the cheek by a distinct palpebral furrow; the posterior end is opposite the anterior glabellar lobe or the middle glabellar furrow. The cheek has a narrow (exsag.) subhorizontal portion then slopes steeply downwards abaxially, and posteriorly. It is subdivided by forrows parallel to the eye ridge and extending a short distance abaxially from the junctions of the axial and glabellar furrows (Pl. 13 fig. 3 ). The posterior border is narrow and downsloping, and separated from the cheek by an indistinct furrow (posterior border furrow). The border is geniculate, with a short transverse section and a longer section directed antero-laterally at approx. 65° (to the transverse line) almost to the base of the palpebral ridge. The anterior section of the facial suture converges strongly, intersecting the anterior edge at its junction with the axial furrow; the posterior section is extremely short and diverges at approximately 30° to the sagittal line.

<u>Stage III</u> - cranidial lengths 0.65-0.79 mms; meraspid degrees (1), 2,3 Text fig. 14 III, Plate 13 figs.5, 6 . The axial furrows are deeply impressed, and deepest at the junctions with the glabellar furrow, from the posterior edge to the anterior furrow, indistinct on the sides of the frontal glabellar lobe, and very faint to absent at the junction of the eye ridge and frontal lobe. The frontal lobe is rounded laterally, long sagittally being approximately two fifths total glabellar length; it reaches the anterior edge in some members of

this stage, in others an extremely narrow, downsloping anterior border is differentiated from it by a distinct change in slope; the frontal lobe is subdivided by a pre-anterior furrow, aligned with the anterior edge of the eye ridge. The palpebral ridge is short, subhorizontal (sag. & trans.), depressed below the level of the cheek and separated from it by an indistinct palpebral furrow; the posterior end is opposite the middle glabellar furrow or the anterior portion of the middle glabellar lobe. The cheek is subdivided by furrows parallel to the eye ridge, extending a short distance abaxially from the junctions of the axial and glabellar furrow. The posterior border is horizontal, separated from the cheek by a distinct border furrow; the border is strongly geniculate, with short transverse section and long antero-lateral section directed at about 60° to transverse line. The anterior section of the facial suture converges strongly; posterior section is very short and diverges at approximately 45°.

Librigena with small genal spine directed almost sagittally to level of posterior edge of the cranidium.

<u>Stage IV</u> - cranidial lengths 0.80 - 0.93 mms. meraspid degree (3), 4,6; Text fig. 14 (IV), Plate 13 figs. 7-9. Glabella with sides tapering slightly forwards to anterior glabellar furrow; frontal lobe rounded not reaching anterior edge, but with narrow downsloping anterior border separated from it by a distinct change in slope. Palpebral ridge is convex (sag. & trans), below the level of the cheek and separated from it by a distinct palpebral furrow; relatively short, with posterior end opposite the middle glabellar lobe or the posterior glabellar furrow. The cheek is wider and flatter than in previous

stages, and slopes down less steeply to the palpebral furrow. The cheek is subdivided by furrows parallel to the eye ridge extending from the junction of the axial and glabellar furrows. One exceptionally well preserved specimen shows the anterior furrow extending from the middle glabellar furrow to the posterior end of the palpebral ridge. The posterior border is convex (exsag.), geniculate, with abaxial portion directed at 50-55° to the transverse direction. Librigena with genal spine directed almost sagittally to level of the first or second thoracic segment.

Stage V - cranidial lengths 0.94 - 1.24 mms; meraspid degrees 7-11. Text fig. 14 (V), Plate 13, figs. 10-11. Frontal glabellar lobe slightly less than one third total glabellar length, rounded, sloping down anteriorly to distinct anterior border furrow. Anterior border convex abaxially, narrows and flattens anterior to the frontal lobe. The axial and palpebral furrows are deeply impressed, resulting in a highly inflated cheek which sometimes retains slight traces of the furrows. The palpebral ridge is convex, slightly below the level of the cheek; the posterior end is opposite the posterior glabella furrow. The posterior border furrow is deep, weakly geniculate, widening abaxially and becoming confluent with the palpebral furrow. The abaxial section of the posterior border is directed antero-laterally at 45-50° to the transverse direction. The anterior section of the facial suture is directed sagittally to the anterior border furrow, then diagonally crosses the border to intersect the anterior edge opposite the sides of the frontal lobe; the posterior section is short, diverging, slightly convex abaxially.

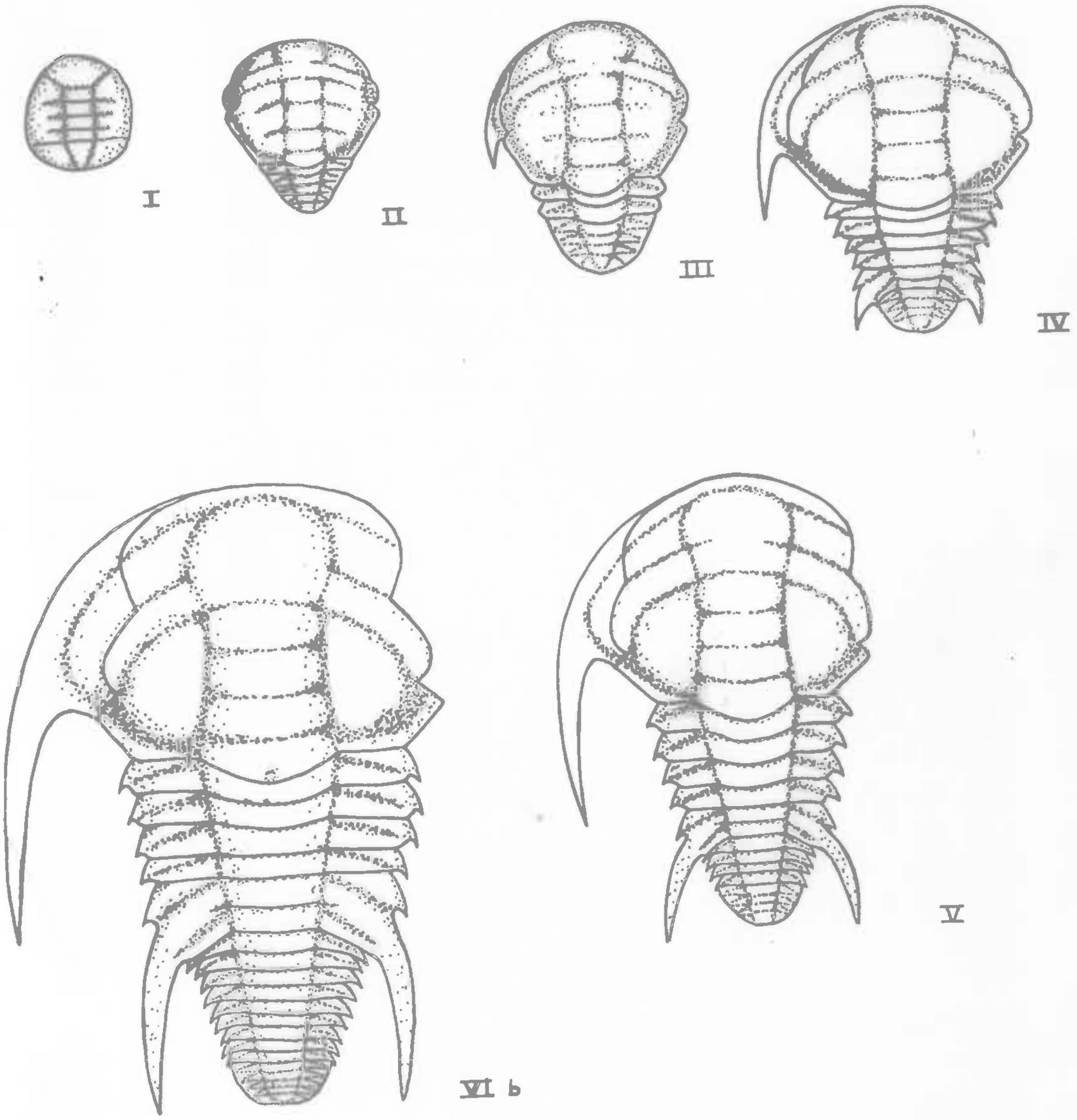
The librigena has distinct lateral and posterior borders and border furrows. The genal spine extends to the level of the fourth thoracic segment.

Stage VI a - cranidial lengths 1.25 - 1.36 mms; includes at least meraspid degree 12; Plate 13, fig. 12. ~~Text fig. 14.~~ The frontal glabellar lobe is approximately one third the total glabellar length. The palpebral ridge is relatively long, on approximately the same level as the cheek, and with the posterior end opposite the posterior glabellar furrow. The cheek is moderately inflated and smooth. The posterior border furrow is almost straight, widening and sloping down abaxially. The abaxial section of the posterior border is directed antero-laterally at 45-50°. The anterior section of the facial suture is directed sagitally or diverges slightly to the anterior border furrow.

Stage VI b - cranidial lengths 1.37 - 1.50 mms; Plate 13, figs. 13 ; Text fig. 14 (VIb). The frontal glabellar lobe slopes down to the anterior border furrow. The anterior border is unchanged, or becomes convex, with the width equal abaxially and sigittally. The posterior end of the palpebral furrow is opposite the posterior glabellar furrow or the posterior lobe. The anterior section of the facial suture diverges slightly to the anterior border furrow. The posterior glabellar furrow is slightly convex to the posterior, the anterior furrow to the anterior, and the pre-anterior furrow is restricted to the abaxial portions of the glabella.

Stage VI c - cranidial lengths 1.50 - 3.16 mms; includes meraspids of degrees 18 to 55. The cephala of this group have attained basically

TEXT FIGURE 14.



Development of B. flindersi. The magnification is held constant at X30. Roman numerals indicate the stage of cranidial development as described in the text.

| | | | |
|---|---|---|---|
| I | Protaspid | II | Meraspid degree 0 |
| III | Meraspid degree 2 | IV | Meraspid degree 6 |
| V | Meraspid degree 10 | VIb | Meraspid degree 15 |

Development of the meraspid cephalon in B. flindersi

TABLE 3.

| Feature | Stage I | Stage II | Stage III | Stage IV | Stage V | Stage VIa | Stage VIb | Stage VIc |
|---|---|---|---|---|---|---|---|---|
| Frontal glabellar lobe | subtriangular; $\frac{1}{4}$ B | slightly rounded laterally; approx. $\frac{1}{4}$ B | rounded laterally; 2/5 B | rounded; approx. $\frac{1}{3}$ B | unchanged; slightly less than $\frac{1}{3}$ B | unchanged; approx. $\frac{1}{3}$ B | unchanged | unchanged; between $\frac{1}{4}$-$\frac{1}{3}$ B. |
| Anterior border | absent | absent | absent or minute, downsloping steeply | narrow, downsloping | convex laterally, horizontal sagittally | unchanged | convex, raised narrow or unchanged | convex, raised, narrow to medium |
| Anterior border furrow | absent | absent | absent | absent | distinct laterally, indistinct sag. | unchanged | even depth or unchanged | even depth |
| Palpebral ridge | indistinct, depressed | downsloping abaxially, below cheek level; 0.17 B | horizontal below cheek level; 0.2 B | convex, below cheek level; 0.23 B | convex slightly below cheek level; 0.27 B | convex, same level as cheek; 0.30 B | unchanged; 0.33 B | unchanged |
| Palpebral furrow | absent | absent | indistinct | distinct | slightly impressed | impressed | unchanged | unchanged |
| | anterior glabellar furrow | anterior lobe - middle furrow | middle furrow - middle lobe | middle lobe posterior furrow | posterior furrow | unchanged | post.furrow - post.lobe | posterior lobe - occipital furrow |
| Posterior border (ab.to fulcrum) | absent | approx.65° to transverse line | approx. 60° to transverse line | approx. 55° to transverse line | approx. 50-45° transverse line | unchanged | 35-40° to transverse line | unchanged |
| Posterior border furrow | absent | indistinct, | distinct, strongly geniculate | moderate geniculate | weakly geniculate, widening abaxially | unchanged | straight, widens abaxially | unchanged |
| Anterior section of facial suture | ? | converging | converging | slightly converging | directed sagittally to ant. border furrow | unchanged or slightly diverging | slightly diverging | diverging |
| Genal spine | | ? | extremely small | extends to level of 1st or 2nd thoracic segment | - | - | - | extends to level of 5th prothoracic segment |
| Length of cranidium | 0.38-0.49 mms. (includes protopygidium) | 0.50-0.64 mms. 16-20.5 m.d. | 0.65-0.79 mms. 21-25.5 m.d. | 0.80-0.94 mms. 26 - 30.5 | 0.94-1.24 mms. (31-39.5 mic.div.) | 1.25-1.36 mms. (40-43.5 mic. div.) | 1.37-1.49 mms. (44-47.5.m.d.) | 1.50-3.16 mms. (48 - 100 m.d.) |
| Meraspis degree | Protaspis | 0 - 1 | (1-)2 - 3 | (3-) 4 - 6 | 7 - 11 | | | 16? - 18 - 53 |

the holaspid condition. The anterior border continues to widen, and the sagittal length of the frontal glabellar lobe decreased proportionately; a progressive change which continues in the holaspid development. The palpebral ridge is above the level of the cheek, and the posterior end is opposite the posterior end of the posterior glabellar lobe or the occipital furrow. The abaxial section of the posterior border is directed antero-laterally at 35-40° to the transverse direction. The frontal lobe is undivided. The anterior section of the facial suture is divergent.

## DEVELOPMENT OF THE THORAX (Table 4, Text fig. 14)

Specimens of meraspids are available from degree 0 to the holaspid period, with the degrees 1-6 well represented.

Degree 0. (2 specimens). Thoracic segments have not yet been released from the transitory pygidium, which however is freely articulating with the posterior edge of the cranidium. The transitory pygidium is triangular, with its maximum width at the anterior edge, tapering posteriorly to a point. The anterior edge is equal in width and articulated with the section between the fulcral points of the cranidium i.e. it articulates with the occipital ring and the transversely directed sections of the posterior cranidial border. The axis is defined by shallow axial furrows, and tapers backwards, to a point on the posterior edge. The pleural field slopes down strongly abaxially, and has a continuous lateral and posterior edge (probably with very narrow doublure). The axis is subdivided into 3 or 4 rings in one specimen and 3 in the other; the pleural field is indistinctly divided in its anterior portion.

The length of the transitory pygidium is slightly less than half cranidial length.

Degree 1. (1 specimen). Text fig. 14 (II). The thoracic segment released from the pygidium possesses a normal axial and articulating half ring, and geniculate pleura; the pleural furrow is directed transversely and is poorly developed; pleural spines were not observed and do not appear to have developed at this stage. The axial furrows of the segment converge slightly to the posterior and are aligned with those of the pygidium. The morphology of the transitory pygidium is basically the same as above (Degree 0). In this specimen the axis of the pygidium is divided into four axial rings, and the pleural field shows the pleural and interpleural furrows of the anterior two segments.

Degree 3. (2 specimens). The three thoracic segments are similar, decreasing in size (sag. & trans) to the posterior, with the pleural furrows becoming more distinct and short pleural spines developing, to the anterior. The axial furrows converge evenly to the posterior and are aligned with those of the pygidium; the pleurae progressively shorten to the posterior,and the line of their abaxial edges is aligned with the direction of the pygidial border. The pygidial border is even.

The transitory pygidium has its axis divided into three or four axial rings, and the pleural field shows the furrows of the anterior two segments distinctly, and of the posterior segments indistinctly.

The ratio of lengths of prothorax: transitory pygidium is approximately 1 : 1.

Degree 4. (2 specimens). Both specimens show the axis of the pygidium with three distinct rings and the pleural field with only the anterior two pleura differentiated. The ratio of length prothorax: length opisthothorax is now approximately 3 : 2. The pygidium shows a smooth continuous lateral border.

Degree 6. (3 specimens). Text fig. 14 (IV). The complete prothorax has been released from the transitory pygidium and has already attained its characteristic morphology. The fifth segment is already fused to the sixth which is macropleural, the line of fusion being visible on the inter-furrow platform. The macropleural spine is rather broad at its base, and extends to the posterior edge of the pygidium or slightly beyond it.

The transitory pygidium articulates with the section of the sixth segment between the notches on the posterior border. The axis is divided into two or three distinct axial rings. The length is less than that of previous degrees and the ratio of prothoracic length: transitory pygidial length is 2.5-3 : 1.

Degrees 10-11. (2 specimens). The prothorax is as above; the opisthothoracic segments possess functional axial and articulating half rings, geniculate pleura with pleural furrows and short pleural spines. The articulation between the prothorax and opisthothorax is as in the adult. The transitory pygidium retains the morphology of that of degree 6,but is slightly longer. The axis of the pygidium is divided into two or three rings and the pleural field shows several furrows.

## TABLE 4.

Development of thorax during ontogeny of B. flindersi

| Meraspid Degree | Cranidial Stage | Segments in transitory pygidium | Cranidial Length $A_1$ |
|---|---|---|---|
| 0 | II | 3 | 17 |
| 0 | II | 3-4 | 17 |
| 1 | II | 4 | 20 |
| 1 | III | 5 | 21 |
| 2 | III | 2-3 | 23 |
| 3 | III | 3-4 | 24 |
| 3 | III | 2-3 | 25 |
| 3 | IV | 3 | 26 |
| 3 | IV | 3 | 26 |
| 4 | IV | 3 | 26 |
| 4 | IV | 1 | 27 |
| 6 | IV | 3 | 28 |
| 6 | IV | 1-2 | 29 |
| 6 | IV | 6 | 29 |
| 6 | IV | 1-2 | 30 |
| 6 | IV | 4 | 30 |
| 10 | V | 2 ? | 34 |
| 11 | V | 3 | 38 |
| 18 | VIc | 3 | 67 |
| 18 | VIc | 3-4 | 72 |
| 19 | VIc | 3 | 72 |
| 27 | VIc | ? | 80 |
| 53 | VIc | 3-4 | 100 |

The cranidial stage of development is the equivalent for the cranidial length $A_1$ of the specimen. $A_1$ given in micrometer divisions where 32 mic. div. = 1.00 mms.

The ratio of length prothorax: length opisthothorax; length pygidium is approximately 2.5 : 1 : 1.

Degree 18-19. The axis of the transitory pygidium is divided into three or four rings whilst the pleural field shows two .The absolute length of the pygidium remains almost constant whilst the ratio of lengths is now approximately 5 : 5 : 1.

Degree 27-55. The length of the opisthothorax increases greatly, to become greater than that of the prothorax and pygidium combined.

### DEVELOPMENT OF THE HYPOSTOME (Table 5)

The hypostome reaches the adult condition when it attains a length (sag.) of approximately 1.45 mms; from this point onwards it does not undergo any change in morphology other than isometric increase in size. An 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, i.e. the stage in which the cranidium has attained the holaspid condition. Changes during ontogeny primarily affect two groups of characters (a) the size and relative position of the anterior wings; the position is given by the ratio of the lengths (on the sagittal line) 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 (Text fig. 11 ? (1)) is matched with cranidia with lengths falling in the upper portion of the size range of Stage III, and the portion of that of Stage IV. The posterior lobe of the median body is triangular, with the bounding lateral furrows converging posteriorly from the lateral notch. The anterior border is slightly crescentic upsloping and very narrow; the anterior wings are very small, only slightly depressed and the ratio giving relative position is 1 : 2 i.e. wings towards the anterior end.

One specimen is matched with cranidia falling within the size ranges of the upper part of Stage IV and the lower part of Stage V. It is proportions and morphology are unchanged from the slightly smaller specimen.

Four hypostomesare known equivalent to cranidia of Stage V. With increase in size there is a progressive movement towards the posterior of the anterior wings,which also become longer and more strongly depressed; the ratio changes from 1 : 2 to 8 : 13 (0.500-0.61). The lateral furrows bounding the posterior lobe converge less rapidly, and small posterior furrow develops.

Three specimens are known matched with cranidia of Stage VIa, and three with cranidia of Stage VIb. There is a continuation of the trends already observed,with the ratio changing from 8 : 13 - 2 : 3 (0.61 - 0.67) and with the continued development of a straight posterior edge of the posterior lobe.

Three specimens are matched with cranidia of Stage VIc. The hypostomes have attained the adult condition with strongly depressed anterior wings only slightly in advance of the lateral notch,and a subquadrangular posterior lobe of the median body with the lateral border furrows parallel or slightly converging posteriorly, a straight posterior border and border furrow and rounded posterior lateral corners.

# TABLE 5.

Hypostomes of *B. flindersi*.

| $H_1$ | $H_8$ | $A_1$ of equivalent cranidium | | Cranidial Stage | |
|---|---|---|---|---|---|
| | | estimated | calculated | estimated | calculated |
| 18 | 15 | 24-28 | 24 | III or IV | III |
| 19 | 16 | 28-32 | 25 | IV or V | III |
| 26 | 18 | 30-34 | 34 | IV or V | V |
| 27 | 18 | 30-34 | 36 | IV or V | V |
| 29 | 20 | 34-36 | 39 | V | V |
| 32 | 21 | 34-38 | 43 | V | VIa |
| 32 | 22 | 40-43 | 43 | VIa | VIa |
| 35 | 24 | 42-43 | 47 | VIa | VIb |
| 35 | 24 | 42-43 | 47 | VIa | VIb |
| 38 | 27 | 45-46 | 51 | VIb | VIc |
| 38 | 28 | 45-47 | 51 | VIb | VIc |
| 42 | 30 | 48-57 | 56 | VIc | VIc |
| 46 | 32 | 55-67 | 61 | VIc | VIc |
| 56 | 35 | 67-72 | 74 | VIc | VIc |
| 85 | 64 | 80- | 113 | VIc | VIc |

$H_1$ is the length of the hypostome, $H_8$ is the length of the hypostomal suture (measured from the hypostome), $A_1$ is the cranidial length: all dimensions given in micrometer divisions. The dimensions of the equivalent cranidium are (1) estimated,by matching $H_8$ with the length of the rostral plate (measured on the cranidium (2) calculated,by the presumed relation $A_1 = \frac{4}{3}$ H. (32 mic.div. = 1.00 mms.)

## THE ONTOGENY OF "BALCORACANIA DAILYI

The collections of *B. dailyi* include approximately 30 larval specimens, of which approximately half have retained at least part of the thorax. The preservation is by means of external and internal moulds which allow considerable detail to be observed; however specimens from both collections are rather strongly distorted and this introduces difficulties, particularly in the larger specimens.

CEPHALIC DEVELOPMENT (Table 6).

Stage I.- cranidial lengths 0.50 - 0.70 mms. (18-22.5 mic. div.). Text fig. 15 I, Plate 13, fig. 18 ; All specimens found in this size range appear to be meraspid cranidia.

The cranidium is subcircular in outline, subhorizontal centrally, steeply downsloping marginally. The glabella is moderately convex and extremely narrow; the glabellar furrows are distinct and transverse. The axial furrows are impressed, and deepen at junctions with the glabellar furrows; they are subparallel, but pinched in sharply at the anterior glabellar furrow; anteriorly the axial furrows are very faint, diverging and downsloping around the frontal lobe to the anterior edge. The frontal lobe is approximately one third the total glabellar length. The eye ridge is distinct, directed slightly to the posterior from the frontal lobe, and sloping steeply downwards abaxially. The palpebral ridge is relatively short, depressed below the cheek level, horizontal (sag. & trans.) or slightly tilted downwards abaxially, and is only indistinctly separated from the cheek by a palpebral furrow; the posterior end is opposite the middle glabellar lobe. The cheek is narrow (trans.) and slopes steeply downwards abaxially to the palpebral ridge and posteriorly to the posterior border furrow. It is subdivided by furrows parallel to the eye ridge, and extending a short distance abaxially from the junctions of the axial and glabellar furrows.

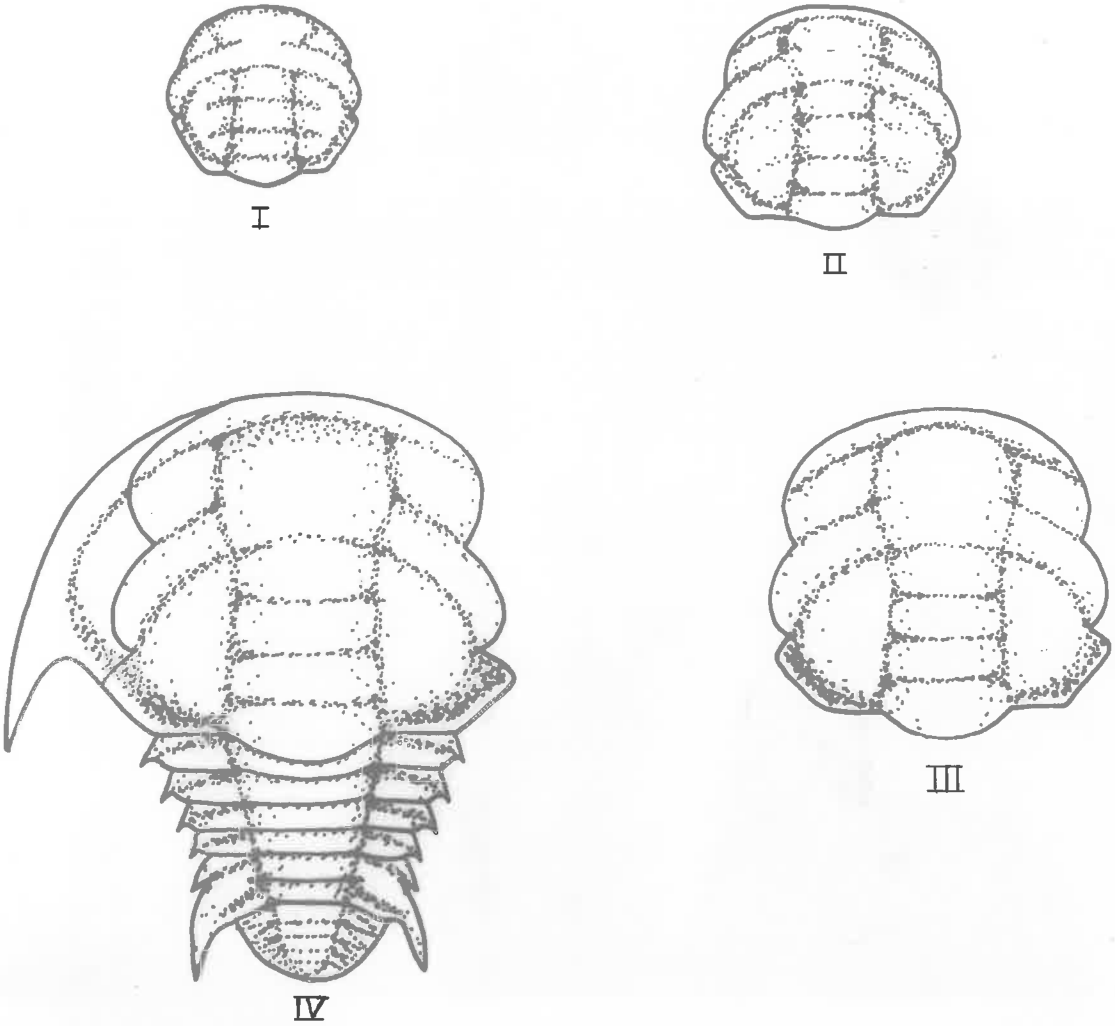
The posterior border is narrow and slightly downsloping or horizontal, and is separated from the cheek only by the change in slope. The border is geniculate with a short transverse section, and a longer section directed antero-laterally at 65° (to transverse line) to base of palpebral ridge. The anterior section of the facial suture converges strongly to intersect the anterior edge at its junction with the axial furrow. The posterior section is extremely short and curved.

Stage II - cranidial length 0.72 - 0.92 mms. (23 - 29.5 mic.div.) Text fig. 15 II, Plate 13, fig. 19. The axial furrows converge evenly from the posterior edge to the anterior glabellar furrow, but are not "pinched in" at this point; the frontal glabellar lobe is expanded, slightly rounded laterally, and not reaching the anterior edge, but with a narrow downsloping anterior border, separated by a distinct change in slope. The palpebral ridge is convex transversely and exsag., below the level of the cheek and separated from it by a distinct palpebral furrow; relatively long (one quarter glabellar length) with posterior end opposite the posterior portion of the middle glabellar lobe or the posterior glabellar furrow. The cheek is wider and slopes down less steeply to the palpebral ridge and posterior border. The posterior border is narrow, convex, and slightly raised, and the posterior border furrow is distinct. The abaxial portion of the posterior border is directed antero-laterally at between 50-55° to the transverse line. The anterior sections of the facial sutures is directed sagittally for a short distance before curving inwards to intersect the anterior edge opposite the side of the frontal glabellar lobe. The posterior section is short, diverging, and slightly convex abaxially.

Stage III - cranidial lengths 0.94-1.14 mms., (30-37.5 mic. div.) Text fig. 15 III, Plate 13, fig. 20 . The frontal lobe is rounded laterally, shorter, approx. one quarter glabellar length, and slopes down anteriorly to the anterior border furrow. The anterior border is narrow, slightly convex and raised abaxially, horizontal to slightly downsloping anterior to the frontal glabellar lobe. The anterior border furrow is distinct abaxially, shallows and becomes indistinct anterior to the frontal lobe. The palpebral ridge is convex (sag. and trans.), on the same level as the cheek, and separated from it by an impressed palpebral furrow; the posterior end is opposite the posterior glabellar furrow. The cheek is slightly inflated and slopes down posteriorly to the posterior border and border furrow. The abaxial section of the posterior border is directed anterolaterally at between 45 and 50°; the posterior border furrow is weakly geniculate. The anterior section of the facial suture diverges slightly to the anterior border furrow, then curves diagonally inwards to anterior edge across the border.

Stage IV - cranidial lengths 1.16 - 1.48 mms. (37-47.5 mic. div.) Text fig. 15 IV, Plate 13 , fig. 21 . Meraspid degrees 6 - 13. Specimens falling within this size range include both cranidia, and cephala with attached thoraces and transitory pygidia, of degrees 6 to 13. No meraspids of a degree less than 6 have been found with

TEXT FIGURE 15



Development of *B. dailyi*. Magnification held constant at X40.

Numerals indicate the stage of cranidial development

Stage IV shows meraspid of degree 6.

**Balcoracania dailyi** - Cephalic development

TABLE 6.

| Feature | Stage I | Stage II | Stage III | Stage IV | Stage V |
|---|---|---|---|---|---|
| Frontal glabellar lobe | subtriangular; approx. $\frac{1}{3}$ glabellar length | slightly rounded laterally; $\frac{1}{3}$ glabellar length | founded laterally; $\frac{1}{4}$ glabellar length | unchanged; $\frac{1}{4}$ glabellar length | unchanged |
| Anterior border | absent | narrow, downsloping steeply | convex abaxially, horiz.sl. downsloping ant. to frontal lobe | border convex, slightly raised | unchanged |
| Anterior border furrow | absent | indistinct or absent | indistinct sagittally, distinct abaxially | distinct, but with border pits | unchanged |
| Frontal area | absent | absent | absent | minute | very narrow |
| Palpebral ridge | below cheek level; horiz. downsl. ab.; $\frac{1}{4}$ glabellar length | below cheek level, convex (sag. & trans); $\frac{1}{4}$ glabellar length | on same level as cheek, convex between $\frac{1}{4}$ - $\frac{1}{3}$ glabellar length | above level of cheek convex $\frac{1}{3}$ glabellar length | unchanged |
| Palpebral furrow | absent to indistinct | distinct | distinct, impressed | unchanged | unchanged |
|  | middle glabellar lobe | post middle glabellar lobe or post glabellar furrow | post. glabellar furrow | post glabellar furrow post glabellar lobe | post glabellar lobe - occipital furrow |
| Post. border (ab. to fulcrum) | approx. 60° to transverse line | approx. 50 - 55° to transverse line | approx. 45 - 50° | approx. 40° | unchanged |
| Post. border furrow | indistinct | distinct, mod. geniculate | weakly geniculate | straight, widening abaxially | unchanged |
| Anterior section of facial suture | converges slightly | short sagittally directed section | slightly diverging | diverging | unchanged |
| Genal spine | - | - | - | minute, reaches post border to level of 1 - 2 thoracic seq. | lengthens rapidly to adult condition |
| Cranidial length $(A_1)$ | 0.50 - 0.70 mms.<br>16 - 22.5 m.d. | 0.72 - 0.92 mms.<br>23 - 29.5 m.d. | 0.94 - 1.14 mms.<br>30 - 36.5 m.d. | 1.16 - 1.48 mms.<br>37 - 47.5 m.d. | 1.50 - 2.90 mms.<br>48 - 93 m.d. |
| Meraspid degree |  |  |  | 6 - 10 | - 12 - 39 - |

the thorax attached.

The frontal glabellar lobe is rounded, and reaches the anterior border furrow. The anterior border is narrow and convex sagittally and exsagittally. The anterior border furrow is deep abaxially, but shallows abruptly anterior to the frontal lobe, with small pits present at its junction with the axial furrows. A minute, downsloping preglabellar field is present, but is not distinctly separated from the frontal lobe. The palpebral ridge is above the level of the cheek, relatively long, one third glabellar length, and its posterior end is opposite the posterior glabellar furrow or lobe. The posterior border is directed at approximately 40° anterolaterally, abaxial to the fulcrum. The posterior border furrow is straight, widening and sloping down abaxially. The anterior section of the facial suture diverges at 10° to the border furrow.

The free cheek is narrow (transversely), the genal spine is very short, extending gradually through this size range from the level of the posterior border to that of the first or second thoracic segment.

Stage V - cranidial lengths 1.50 - 2.90 mms., (48 - 93 mic. div.) meraspid degrees 13 - 47. The cephala of this group have attained basically the holaspid condition. The anterior border, and the preglabellar field continue to widen, and the sagittal length of the frontal glabellar lobe decreases proportionately; a change which continues in the holaspid development. The fossulae at the junction of the anterior border furrow and axial furrows, deepen. The posterior end of the palpebral ridge is opposite the posterior end of the posterior glabellar lobe or the occipital furrow. The abaxial section of the posterior border is directed anterolaterally at 30-35° to the transverse direction.

DEVELOPMENT OF MERASPID THORAX. Table 7.

No meraspis of a degree less than six, i.e. with prothorax free, is known from this species. The holaspis has a prothorax of six segments and an opisthothorax of 47 segments.

Degree 6. (4 specimens). The prothorax has already attained all the morphological features characteristic of the adult; the fifth segment is fused to the macropleural sixth, with the line of fusion visible on the interfurrow platform. The macropleural spine extends to the posterior edge of the transitory pygidium or slightly beyond it, and curves inwards slightly at the posterior end. The axis tapers strongly but evenly, from the anterior edge of the prothorax to the posterior edge of the transitory pygidium. The prothoracic pleurae shorten (trans.) progressively to the fifth segment. The transitory pygidium is triangular in shape, with its maximum width at the anterior edge, and tapering symmetrically to the posterior. The anterior edge is equal in width and articulated to the section of the macropleural sixth segment between the notches on the posterior border. The axis is moderately convex and is outlined by slightly impressed axial furrows; it tapers and slopes down to the posterior edge. The pleural field slopes down steeply abaxially and has a smooth and continuous lateral and posterior margins. The axis is subdivided into a number of rings by transverse furrows, generally distinct anteriorly and becoming narrower and less distinct to the posterior. The pleural field is less clearly segmented, and only one or two segments can be distinguished in the anterior section; towards the posterior, segments become so small that it is not possible to distinguish between pleural and interpleural furrows. Three of the four specimens found of this degree exhibited three or four axial rings and one or two complete pleura; however one specimen showed six distinct and at least one indistinct, axial rings, and three distinct pleura; the two most anterior segments appear to be semi-ankylosed.

The prothorax is slightly more than twice the length of the transitory pygidium.

Degree 10. (3 specimens). The prothorax is normally developed with the macropleural spine extending just beyond the posterior edge of the transitory pygidium. The four segments of the opisthothorax possess functional axial and articulating half rings, geniculate pleura with pleural furrows and short pleural spines. The articulation between the sixth and seventh segment is as in the adult. The transitory pygidium retains the morphology and approximate size of that of degree 6. The number of axial rings present varies from 3 to 5, and the number of distinct pleura from 1 to 2, on the three specimens examined.

The transitory pygidium and opisthothorax are of approximately equal length, but together are shorter than the prothorax.

Degrees 11 - 14. The ratio of the lengths - prothorax : opisthothorax : transitory pygidium changes from 2 : 1 : 1 at degree 11 to 3 : 2 : 1 at degree 14 with the absolute length of the transitory pygidium remaining almost constant. The transitory pygidium of a degree 11 specimen shows five distinct axial rings, that of two degree 12 specimens, five, and,

## TABLE 7.

Development of the thorax of *B. dailyi* during ontogeny.

| Meraspid degree | Cranidial Stage | Segments in the transitory pygidium | Cranidial Length |
|---|---|---|---|
| 6 | IV | 3 | 38 |
| 6 | IV | 4 + | 40 |
| 6 | IV | 4 | 40 |
| 6 | IV | 3 | 44 |
| 10 | IV | 4 - 5 | 45 |
| 10 | V | 3 | 48 |
| 12 | V | 5 | 48 |
| 13 | V | 4 + | 46 |
| 13 | V | 5 | 48 |
| 14 | V | 4 + | 50 |
| 17 | V | 3 | 54 |
| 21 | V | 3 - 4 | 53 |
| 22 | V | 9 | 61 |
| 24 | V | 4 + | 75 |
| 28 | V | 6 - 8 | 75 |
| 35 ? | V | 4 | 115 |
| 39 | V | 6 | 107 |

Cranidial length given in micrometer divisions where 32 mic.div. = 1.00mms.

four distinct and 2-3 indistinct, axial rings, and of one degree 13 specimen,four distinct and 2-3 indistinct axial rings.

Degrees 21 - 22. (2 specimens). The transitory pygidia show 3 or 4 axial rings for one specimen and nine distinct axial rings for the other. The anterior three segments of the latter are completely individualized and appear to be only semi-ankylosed both to each other and to the remainder of the pygidium. The opisthothorax is now longer than the prothorax; the length of the transitory pygidium relatively constant, in comparison with earlier degrees, but is 40% greater in the specimen showing nine rings than that showing only 3 or 4.

Degrees 24 and 28. The opisthothorax is now considerably longer than the prothorax. The transitory pygidium of degree 24 has 4 distinct and 1-2 indistinct axial rings, and that of degree 28 has 6 to 8.

Holaspid. The opisthothorax contains 47 and the pygidium between four and six segments.

DEVELOPMENT OF HYPOSTOME. Table 8.

The changes taking place in the larval development are similar to those in *B. flindersi* i.e. the position and size of the anterior wings and the shape of the posterior lobe of the median body are affected.

The smallest hypostome found is matched with cranidia with lengths - size ranges falling in Stage I. The ratio expressing relative position of the anterior wings is 2 : 5 and the posterior lobe is V-shaped.

Two specimens are matched with cranidia of Stage II, and show a slight increase in the length of the anterior wings and slight shift towards the posterior, with a ratio of 5 : 12.

Several specimens fall within the size ranges of Stages III and IV. The anterior wings are relatively further to the posterior, indicated by a range from 5 : 12 to 1 : 2. The posterior lobe of the median body is still triangular, but slightly rounded.

Specimens larger than the last group are matched with cranidia of Stage V i.e. the holaspis condition. The anterior wings are prominent, posterior in position, the median body slightly tapering or parallel sided.

### ONTOGENY OF EMUELLA POLYMERA. (Plate 13, figs 16, 17. ) ?

Only ten specimens of E. polymera are known which are considered to be larval stages, and of these only two retain the meraspid thorax. In view of this it is neither possible or adviseable to formally divide the development into stages as was done with the species of Balcoracania.

The smallest specimen found, had a sagittal length of 0.40 mms. and appears to be a badly preserved protaspis; the axis is clearly defined and there is a narrow downsloping protopygidium, but other details are obscure. At a cranidial length of approximately 0.67 mm., a narrow downsloping anterior border appears in front of the frontal glabellar lobe, the palpebral ridge is below the cheek level and extends posteriorly to the level of the middle glabellar lobe, the anterior section of the facial suture has a very short sagittally directed section; this cranidial size corresponds to meraspid degree 1. An exceptionally well preserved specimen (Pl. fig. ) shows ? a pre-anterior glabellar furrow, and subdivision of the cheek area

# TABLE 8.

Development of Hypostome of *B. dailyi*.

| $H_1$ | $H_8$ | $A_1$ of equivalent cranidium | | cranidial stage | |
|---|---|---|---|---|---|
| | | estimated | calc. | estimated | calc. |
| 20.5 | 12 | 19 - 21 | 27 | I | II |
| 22 | 16 | 23 - 25 | 29 | II | II |
| 25 | 18 | 25 - 28 | 33 | II | III |
| 25 | 20 | 28 - 35 | 33 | II & III | III |
| 28 | 20 | 28 - 35 | 37 | II & III | IV |
| 33 | 22 | 35 - 38 | 44 | III & IV | IV |
| 39 | 28 | 44 - 47 | 52 | IV | V |
| 42 | 29 | 48 - 50 | 56 | V | V |
| 45 | 29 | 48 - 50 | 60 | V | V |
| 53 | 39 | 69 - | 71 | V | V |
| 56 | 43 | | 74 | V | V |

$A_1$ given in micrometer divisions where 32 mic.div. = 1.00 mms.

by furrows. At approximately 0.80 mms. the anterior border has become horizontal abaxially, the palpebral ridge 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 - 1.40 mms. the anterior border becomes horizontal to slightly convex, the border furrow develops fossulae, the palpebral ridge extends just beyond the level of the middle glabellar furrow, and the anterior section of the facial suture becomes slightly divergent. The meraspis degree 7 is included in this range. At approx. 1.7 mms. the cranidium exhibits the holaspid morphology.

No hypostomes are known, which ~~are~~ could be considered to be larval.

## DISCUSSION

The studies of the ontogenetic development of the three species represented by larval stages, reinforce the basis of the taxonomic discriminations made on 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 all undergo similar types of changes during their ontogeny, but the individual changes occur at different rates for each species. Thus the cranidia (cephala) 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 to other features.

The size at which the cephalon attains the holaspid condition differs in the genera. In *E. polymera* it is reached with a cranidial size of approximately 1.7 mms.; in *B. flindersi* and *B. dailyi* at approximately 1.5 mms.

The development of the thorax is extremely similar in all species. It follows the general pattern of thoracic development for trilobites (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. In addition a size frequency diagram of cranidial length has a polymodal distribution with only four distinct peaks over the range for cranidial lengths of meraspid degrees 0 to 6 (Text fig 4(2)). It is thus evident that the fifth and sixth segments develop in the transitory pygidium together, and are released into the thorax as a unit. At degree 6, the sixth 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. The length of the pleura of the seventh segment is limited by the necessity for articulation with the modified posterior margin of the sixth; and in fact the segment bears exactly the same relationship to the sixth at meraspis degree 7, as it does in the holaspis. In turn succeeding segments are modified.

In all species the length of 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 (Table 4 & 7). Also the length of the cranidium varies considerably for a given degree and considerable overlap between cranidial sizes may be present between successive degrees. For example in B. flindersi, five specimens of degree 6 are known, two with two segments, one each with three; four and six; the length of the transitory pygidium ranges between 0.15-0.21mms for the specimens with lower numbers of segments, and is 0.30 mms for the specimen with six; three specimens are known of degree 3 with a cranidial length range which overlaps that of 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 meraspids of degree 6 or more, specimens occur (see above) with considerably more segments in the transitory pygidium than the average number for the equivalent degree. In these cases the most anterior two or three segments appear to be fully formed and only semi-ankylosed to the transitory pygidium (Pl. 13 fig. 22 ). It thus seems probable that in the development of the opisthothorax more than one segment may be released during some moults.

Several features of considerable interest arise when the rates of cephalic and thoracic development are compared. In B. flindersi the maximum size for the protaspis is indicated by the presence of a meraspid of degree 0 with a total length of 0.75 mms. The general range for protaspids is 0.25 - 1.00 mm. (Whittington 1957, 1959). ~~This seems to indicate that development of the thorax in this species is started considerably earlier than is usual.~~ By the time that meraspis degree 6 has been reached, the cranidium has a length of approximately 1.25 mms. in B. dailyi, but only 0.88 mms. in B. flindersi. The cranidial development is accordingly further advanced in B. dailyi at this degree of thoracic development. In both species however the cranidium attains the holaspid condition at a cranidial length of 1.50 mms; in B. flindersi this stage is reached at meraspid degree 16, and in B. dailyi at degree 13. The development of the thorax is thus far from complete and lags behind that of the cranidium.

# CHAPTER VII TAXONOMIC POSITION OF THE GROUP

## INTRODUCTION

The genera Emuella and Balcoracania possess a combination of unusual morphological features that set them apart from other groups of trilobites; the cephalon with a complete set of functional sutures, expanded frontal glabellar lobe, long crescentic eye lobes and geniculate posterior border; the hypostome with subdivision of the anterior lobe of the median body; the thorax with prothorax and opisthothorax, macropleurality, fusion of segments, great number of segments and minute pygidium.

Many trilobites of more than a few groups are similar in some respects; some indeed possess a combination of some of these characters, however no genus or group of trilobites possess the combination of cephalic and thoracic features which characterize the two genera. Accordingly it is proposed that the genera Emuella and Balcoracania should be combined in a separate taxon and that the taxon be of familial rank. The genus Emuella is chosen as the nominate genus and the family thus named Emuellidae.

The relation of the Emuellidae to other taxa is important and can only be judged on the basis of morphological similarity. Some of the diagnostic characters of the family are found only in Cambrian trilobites, others in both Cambrian and post-Cambrian trilobites. When considering the taxonomic position of the family, similarities in Cambrian, and in particular, Lower Cambrian trilobites are accorded more weight than those in post Cambrian groups.

The Emuellidae are characterized by a combination of diagnostic characters of cephalon, thorax and pygidium. This imposes certain conditions on the type of comparisons which can validly be made. In particular it is considered that the presence of a large pygidium (cf. cephalon) invalidates comparisons based on the cephalon alone, and this is used as a premise for the detailed comparisons of the cephalon which follow.

The taxonomic position of the Emuellidae is assessed with regard both to features of adult morphology and of ontogenetic development. The most recent complete classifications of trilobites is that given in the Treatise of Palaeontology Part O, Trilobita. Whilst it is understood that many authors have subsequently disagreed with sections of the classification, it remains the standard at this stage. Accordingly in reviewing the taxonomic position of the Emuellidae, the framework provided by the Treatise is used, as are the categories used in comparison with this group. This procedure does not imply the author's acceptance of the entire or any given part of the classification given in the Treatise.

## COMPARISONS OF ADULT MORPHOLOGY

### (a) Thorax and pygidium.

The division into pro- and opisthothorax is definitely known only in some members of the Lower Cambrian Olenellidae. In addition most of the Olenellidae also possess one or more macropleural segments.

The Olenellinae have a prothorax with fourteen segments with the third macropleural, an opisthothorax with a variable number of segments and a minute pygidium. Most genera have between two and five segments in the opisthothorax, but species of Paedeumias possess many more, with P. robsonensis (Burling) with an opisthothorax as long as the prothorax and containing 29 segments. The Fallotaspidinae have a 17 segment prothorax with the third macropleural, a few opisthothoracic segments and a minute furrowed pygidium. Oth subfamilies, Callaviiae, Neltneriinae, Nevadiinae and Elliptocephaliinae have between eleven and seventeen prothoracic segments, up to eleven opisthothoracic segments and minute pygidia, but lack macropleural segments. The remaining subfamilies lack the thoracic division but have large numbers of segments in the cases of Holmiinae and Wanneriinae, and a small number with two macropleural segments in the aberrant Olenelloidiinae.

Macropleurality is widespread in genera of many families, besides the Olenellidae, both Cambrian and post Cambrian. Cambrian families with genera exhibiting this feature include the Neoredlichiidae, Bathynotidae, Paradoxididae, Zacanthoididae (Albertella), Despujolsiidae and Dolichometopidae (Anoria); post-Cambrian families include Shumardiidae (Shumardia), Asaphidae (Promegalaspides), Remopleurididae (Hypodicrantus), ~~Housiidae (Housia)~~ and Cyclopygidae (Pricyclopyge). The presence of macropleural segments in genera of so many unrelated families casts grave doubts on its taxonomic value, unless used in combination with other thoracic features.

The lower to middle Cambrian family Bathynotidae deserves special comment. One of its two known genera, Bathynotellus is the only previously recorded trilobite with fusion of segments into a unit within the thorax; a feature which it combines with macropleurality of one of these segments. The other genus, *Bathynotus* combines macropleurality with a change in the nature of its post macropleural segments which resembles the division into pro- and opistho-thorax.

In *Bathynotus* the thorax has thirteen segments with the eleventh macropleural and the pleuræ of the twelfth and thirteenth reduced; the pygidium is large, and semicircular, with two axial divisions (Text fig. 16(5)). *Bathynotellus* has a thorax with thirteen segments, but with the posterior ones fused into a unit which has three axial rings and a macropleural spine; the pygidium is again rather large, with five axial divisions, and articulates with the macropleural unit in a way similar to that between macropleural unit and transitory pygidium of a meraspis degree 6 of the Emuellidae (Text fig. 16(6)). The two genera appear to be very closely related as the macropleural segment and two reduced segments of *Bathynotus* appear to be homologous with the segments of the macropleural unit in *Bathynotellus*.

It is suggested that the postmacropleural segments in *Bathynotus* are simply normal thoracic segments modified by the presence of a posteriorly directed macropleural spine and the proximity of the pygidium, and that fusion of the three segments in *Bathynotellus* represents a further response to this problem. Accordingly they cannot be homologized with a true opisthothorax which results from a change in the primary nature of segmentation, and is always associated with a small pygidium. Thus the similarity with the Emuellidae is confined strictly to the macropleural segment and its fusion to other segments, and this appears to result from a similar response to a similar functional relationship. However such similarities whatever their

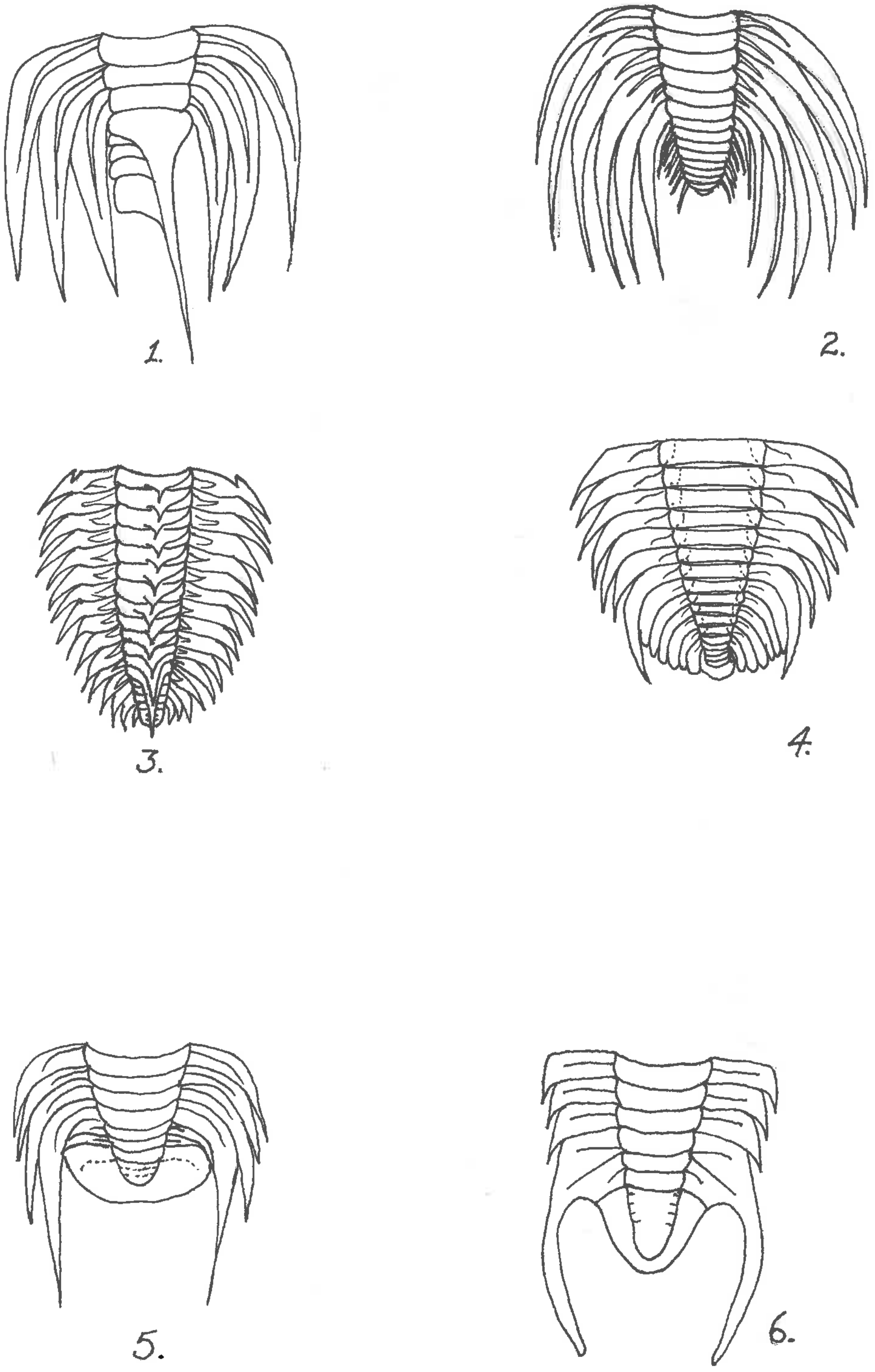
Text Figure 16

Comparison of the posterior sections of the thorax, and the pygidium in related genera.

1. *Olenellus thompsoni*.
2. *Nevadia weeksi*.
3. *Holmia kjerulfi*.
4. *Neltneria jaqueti*.
5. *Bathynotus holopyga*.
6. *Bathynotellus germolaeri*

(All diagrams modified from Harrington et al., 1959).

TEXT FIGURE 16



cause may be, add some weight to any comparison between the two families.

(b) Cephalon.

In the cephalon of the Emuellidae, the combination of sutural pattern, structure of the eye lobes and of the posterior limb form the essential diagnostic feature; the shape of the glabella, for reasons given below, is of lesser importance in most cases.

The sutural pattern consists of functional, rostral, connective, hypostomal and facial sutures. The facial sutures are of the opisthoparian type with the anterior section diverging to the border furrow then swinging diagonally inwards across the border before becoming marginal; the posterior section is also divergent; the connective sutures are concave abaxially, and with the rostral and hypostomal sutures isolate a short (trans.) rostral plate. This is the cephalic type, based on sutural pattern known as "pytchoparid", in the terminology of Rasetti (1952) and Harrington (1959) and is considered to be the primitive type from which all others are secondarily derived (Harrington 1959 p.68, 158). Many taxa have members with this cephalic type and those with Cambrian representatives include the Redlichiacea, Elliptocephalacea, Paradoxididae and Ptychoparidae.

The eye lobe of the Emuellidae consists of wide (exsag.), continuous eye and palpebral ridges extending in a crescent from the frontal glabellar lobe, and with the palpebral sections widely separated from the glabella. Genera of many families possess similar eye lobes with Cambrian groups including members of the Dolerolenidae, Ellipsocephalidae, Protolenidae, Bathynotidae and Ptychopariidae bearing the greatest resemblance. Many families of the Ptychopariina are also similar but are not considered because of the structure of the thorax or pygidium.

The glabella of the Emuellidae tapers anteriorly to the anterior glabellar furrow, but has a variably expanded frontal lobe. The ontogeny of members of the Emuellidae, together with the presence of variants with the frontal lobe bilobed, suggests that this feature may be due to arrested development i.e. the persistence of a larval characteristic into the adult. Thus the glabella of the family is thought to bear more relationship to those of the Olenellidae, where the same situation may exist, and to regularly tapering forms such as displayed by the Redlichiidae, Dolerolenidae, Bathynotidae and some Ellipsociphalidae, Protolenidae and Ptychopariidae.

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

The overall morphology of the cephalon is most similar to that of some members of the families 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 subfamily Antagminae of the Ptychopariidae are probably the closest. In addition because of their special resemblance with the thorax of the Emuellidae, cephalic features of the Olenellidae and Bathynotidae are discussed.

Dolerolenus has an evenly tapering glabella, wide eye ridges which however are rather faint, and crescentic palpebral ridges which terminate away from and opposite the posterior glabellar furrow. The anterior section of the facial suture diverges, then cuts inwards across the anterior border, but this is not as marked as in the Emuellidae. The posterior section of the facial suture diverges very strongly giving a very long posterior limb with a transversely directed posterior border, thus differing markedly from the geniculate border of the Emuellidae; the genal spine is also much shorter and not advanced.

*Bergeroniellus* and *Estaingia* resemble the Emuellidae in the structure and position of the eye lobes and to some extent the course of the facial sutures. The subgenera *B. (Bergeroniaspis)* Suvorova and *B. (Olekmaspis)* Suvorova are the closest. The glabella of *Estaingia* is slightly constricted in the region of the middle and anterior glabellar lobes and 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 have long genal spines with that of *B. (Olekmaspis)* being slightly advanced. However they differ from the Emuellidae by the presence of wide preglabellar fields, and transverse posterior borders and border furrows. *Protolenus* is very similar to *Estaingia* except for a narrower preglabellar field and evenly tapering glabella, and so shares most of the above dissimilarities.

Of the early ptychopariids, the Antagminae bear most resemblance. *Eoptychoparia*, *Poulsenia* and *Proliostracus* have tapering glabellas and similar eye lobes. *Poulsenia* in particular has only a very 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 suture appear to cut diagonally across the border and vary from slightly divergent (Eoptychoparia) to rather strongly converging (Poulsenia). In all genera of this subfamily the posterior border furrow is transverse, and the posterior border is straight and directed slightly posterior to the transverse direction; the posterior section of the facial suture varies in degrees of divergence and outward curvature. The posterior limb of the Antagminae thus is in sharp contrast to that of the Emuellidae.

In the Olenellidae the major differences are associated with a different sutural pattern; the facial sutures are absent, being replaced by a perrostral suture; the hypostomal suture may or may not be functional. The eye lobes are directed strongly backwards and the palpebral ridges are close to or touching the glabella at their posterior end. The shape of the glabella differs considerably; it may taper evenly (Fallotaspis, Nevadia), expand forwards (Olenellus, Fremontia) or taper forwards but with an expanded frontal lobe (Fremontella, Bristolia, Paedeumias). The posterior border is generally straight and transverse with long genal spines at the posterior lateral corners; the spines are advanced in some genera (Fremontella, Bristolia).

The Bathynotidae also differ from the Emuellidae in the sutural pattern; the hypostomal suture is fused and the rostral suture reduced to a point from which the connective sutures diverge backwards. The glabella tapers forward evenly and although the position of the eye lobes is similar to that of the Emuellidae, the eye ridge is very faint. The genal spine is produced posteriorly to an enormous extent, being longer than the thorax and pygidium combined.

## COMPARISON OF DEVELOPMENTAL HISTORY

It has been stated (Whittington 1957, p.462) that "the nature of the developmental history and the morphology of the protaspis ... offer additional criteria for judging relationship between families and larger groups". On this basis the larval development of the Emuellidae is compared with those known from families which appear to be related on the basis of holaspid morphology i.e. the Olenellidae, Redlichiidae, Doleroleridae, Protolenidae, Paradoxididae and Ptychopariidae.

The ontogeny of the Emuellidae has been fully described elsewhere, but to summarize, the protaspis has an axis with four furrows which extend onto the pleural region; the frontal glabellar lobe is subtriangular, expanding outwards and downwards to the anterior edge; changes taking place during the meraspid development involve gradual loss of the furrows on pleural regions, the reduction in the size of the frontal glabellar lobe and the concomitant development of the anterior border, the lengthening of the palpebral ridge, and the change in direction of the anterior section of the suture.

In the Olenellidae, protaspids have not yet been recognized (Whittington 1959). However the meraspid development is broadly known from the investigations on *Olenellus gilberti* Meek and *Paedeumias clarki* Resser by Palmer (1957) and the reinvestigation of *Elliptocephala* and *Paedeumias* by Whittington (1957). In the earliest degrees (Whittington 1957, figs. 2 & 3) the frontal glabellar lobe is rounded and separated from the anterior border by a distinct preglabellar field; the eye lobes are thick and long, curving from the frontal lobe almost to the intergenal furrow and in most cases rather widely separated from the sagittal line; the lateral border terminates outside and at the base of the eye lobe and the postero-lateral corner is produced into a large intergenal spine; procranidial spines may be present, and in *O. gilberti* and *P. clarki* the pleural regions are subdivided by furrows extending from the glabella furrows (Palmer 1957, fig. 6 Pl. 19, No. 1). With increase in size the furrows on the pleural areas disappear, the eye lobe curves inwards at the posterior end and the fixigenal (or intergenal) spines diminish and the genal spines increase in length. The development of the thorax is not fully known, but appears normal, except for the presence of macropleural spines.

The ontogeny of *Redlichia chinensis* Walcott has been investigated by Kobayashi and Kato (1951). The nature of the material appears to allow interpretations other than those of the authors; however some important features can be clearly seen. The smallest protaspis (Kobayashi and Kato 1951 Pl. 1 fig. 1) has an axis which extends from the anterior to almost the posterior edge, tapering to the posterior and subdivided by a median furrow or series of medial depressions. A meraspid of degree 0, with a transitory pygidium with three segments, (op cit Pl. 1 fig. 4) clearly shows a circular frontal glabellar lobe, long crescentic eye lobe extending backwards, a very narrow frontal area of the fixigena banded by the eye ridge and a convergent anterior section of the suture, and subdivision of the pleural field by transverse furrows extending from glabellar to palpebral furrows; the first segment of the transitory pygidium is macropleural.

In later meraspid degrees the subdivision of the pleural field is lost, the eye ridge rotates to the posterior, and the posterior end of the palpebral ridge moves inwards towards the glabella with the consequent development of a long highly divergent posterior section of the suture, the anterior section of the suture becomes increasingly divergent, and the expanded frontal glabellar lobe is reduced so that the glabella is tapering regularly to the anterior.

The ontogeny of the Dolerolenidae is not well known, but Kobayashi and Kato (1951 Text fig. 1) illustrate several protaspids redrawn from Bornemann (1891, Pl. 20, fig. 1, 2 & 6). These appear to have an expanded frontal glabellar lobe probably reaching the anterior edge, an antero-lateral eye and palpebral ridge depressed below cheek level, and subdivision of the pleural field. Unfortunately Bornemann's paper was not available to the author.

The ontogeny of the Paradoxididae is known from Paradoxides pinus (Westergård 1936, Stormer 1942, Whittington 1957, 1959) and P. rugulosus (Růžička 1943). The earliest protaspis has a regularly expanding glabella, with the frontal lobe reaching the anterior edge and with a median depression along most of its length; the eye ridges are long and thin, directed slightly posterolaterally from the frontal glabellar lobe, the palpebral ridge is long extending to the level of the occipital furrow; the posterior lateral corner is produced into fixigenal spines. In slightly later protaspids a long narrow librigena with a small genal spine is deduced to be present; the anterior section of the suture is sagittally directed and the posterior section of the suture is absent; the median glabellar furrow becomes restricted to the anterior glabellar lobes, and the protopygidium has the first segment macropleural. During meraspid development, the frontal glabellar lobe, initially bilobed, becomes rounded anteriorly and separated from the anterior border by a preglabellar field; the anterior section of the suture becomes increasingly divergent and a posterior section develops as the palpebral ridge becomes separated from the posterior border; the fixigenal spines diminish in size and finally disappear, whilst the genal spine lengthens. In the thorax, the 1st and 2nd segments which were both strongly macropleural in early meraspid degrees of *P. pinus*, undergo relative changes in the length of the spines, the first becoming reduced almost to normal, the second reducing more slowly and remaining slightly macropleural in the adult.

In the Protolenidae, larval stages of *Lermontovia dževanovskii* Suvorova and several species of *Bergeroniellus* and *Bergeronaspis* have been illustrated by Suvorova (1956); all of these appear to be meraspid cranidia. In the smallest cranidia (generally less than 1mm. long), the frontal glabellar lobe is bilobed and reaches a distinct anterior border furrow, the eye and palpebral ridges are long and crescentic, the anterior section of the suture is directed sagittally, and in some of the species the posterior lateral corner is produced into a fixigenal spine. With increase in size the frontal lobe becomes rounded and reduced in size, a preglabellar field develops, the anterior section of the suture becomes divergent and the fixigenal spine rapidly disappears. One specimen of *Bergeroniaspis subornata* (Suvorova 1956, Pl. XI fig.3) appears to be very similar to the earliest meraspid cranidia of the Emuellidae, with the frontal lobe expanding anteriorly and reaching a narrow downsloping anterior border and appearing not to be bilobed. Most of the species of both Bergeroniellus and Bergeroniaspis differ from previously described groups in the possession of four pairs of lateral glabellar furrows, the most anterior pair being aligned with the anterior edge of the eye ridges.

The ontogeny of members of the Ptychopariidae is not known, but may be comparable to that of the solenopleurid Sao, originally described by Barrande (1852) and revised by Růžička (1943) and Whittington (1957, 1959). Whittington (1959 p.132) gives the following description of the earliest protaspis of Sao; "... the cephalic axis divided into five rings decreasing in length posteriorly and the protopygidial axis short and low. Pleural regions are faintly divided at the posterior margin of the cephalon. Eye lobes are close to the margin of the cephalon, eye ridges curve in to the axial furrow just behind anterior pits, and a sutural ridge is adjacent to the extremity of the frontal glabellar lobe. Librigenae are narrow, posteriorly extended into short librigenal spines and defined by sutures running a short distance inside anterior and lateral cephalic margins...". Protaspids of other lower Cambrian ptychoparids appear to be similar although in some, fixigenal spines may occur e.g. Olenus (Størmer 1942; Whittington 1957). Post-protaspis development of the cranidium in Sao involves reduction of the size of the frontal glabellar lobe, inward and backward migration of the eye lobe and associated changes in the facial sutures; and loss of the sutural ridge and anterior pits.

## CONCLUSIONS

It has been emphasized that it is the combination of cephalic and thoracic characters that distinguish the Emuellidae as a separate taxon. It is axiomatic that in assessing the relationship of the family to other trilobites, the same basis will apply.

The relationship of the Olenellidae and the Emuellidae is shown by the similarities of the thorax; macropleurality and division of the thorax. The latter is of considerable importance as in contrast to the Bathynotidae, it results in both cases from an inability to stabilize the structure and composition of the thorax. The opisthothorax of the Emuellidae indicates that it is in an earlier developmental stage than that of the Olenellidae; the number of segments is greater and the variation between species is greater than in the Olenellidae where the number is small, except in *Paedeumias*, and in some subfamilies stabilization of the thorax has been attained. The small number of prothoracic segments in the Emuellidae is accorded less weight as it is believed that this is primarily determined in this case by the position of the macropleural segment. Ontogenetic studies do not support the hypothesis that the prothorax is homologous to the normal thorax and the opisthothorax to the pygidium, at least in this case. The structure of the cephalon also suggests that the Olenellidae are more advanced. The chief differences are related to the metaparian (fused) and perrostral sutures which are now thought to be secondarily derived from the ptychoparid sutural type which is displayed by the Emuellidae (Hupé 1953(a); Harrington 1959).

The Emuellidae are thus regarded as structural relics of the ancestors of the Olenellidae. 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 sub-order Olenellina. Of the other groups showing similarities, three belong to the Order Redlichiida, and one to the order Ptychopariida.

Of the four groups, the Antagminae and the Bathynotidae exhibit the least similarities to the cephalon of the Emuellidae. In the Antagminae the eye lobes are shorter and thinner than in the other groups, and the facial sutures show only a general resemblance to those of the Emuellidae; the Bathynotidae also have much thinner eye lobes, and a more distinct relationship to the Emuellidae is indicated by the sutural pattern which differs by fusion of the hypostome, and loss of the rostral plate. The Antagminae possess a relatively long thorax and small pygidium, but no other point of similarity to that of the Emuellidae; the thorax of the Bathynotidae is very similar in several respects, but this is thought to be largely the result of convergence. Accordingly it is suggested that the Emuellidae be placed in the Order Redlichiida rather than Ptychopariida and be included in the suborder Redlichiina.

Within the suborder the position is unclear. The Dolerolenidae and the Protolenidae bear approximately the same degree of resemblance 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 (<u>Bergeroniellus</u>, <u>Estaingia</u>) transitional between the Ellipsocephalacea and the Paradoxidacea (Öpik 1963; Pocock 1964).

The comparison of the ontogenies of the families regarded as related to the Emuellidae on the basis of the holaspid morphology, appears to affirm the degrees of relationship deduced on that basis, but fails to definitely indicate a solution to the problems which arose. It is considered that the protaspid and early meraspid periods are most important, as in the later meraspid development differences inevitably arise as the holaspid condition is being attained.

Of the families considered, it appears that the protaspids of the ptychopariids are furtherest from those of the Emuellidae. In Sao the possession of sutural ridges and anterior pits, and the absence of bilobation of the glabella and subdivision of the pleural field are considered more important than the similarity of the position of the eye lobes and other features. On the assumption of a basic similarity between the protaspids of Sao and the Antagminae, an assumption by no means certain, comparison of the protaspids appears to confirm the more distant relation of the Antagminae to the Emuellidae.

The remaining families are all members of the Order Redlichiida and thus some similarity is to be expected. In all families there is a similar reduction in the size of the frontal glabellar lobe, and the development of an anterior border and preglabellar field; in some the frontal lobe remains expanded relative to the rest of the glabellar as in the Emuellidae (Paradoxididae, Olenellidae), in others the glabella tapers forward evenly (Redlichiidae, Dolerolenidae); the presence of a preglabellar field in the meraspids of all groups is not considered a major difference, as it $_s$ initial development can be seen in B. dailyi. The most important remaining characters of the protaspids and early meraspids are subdivision of the pleural field, bilobation of the glabella and presence of fixigenal (or intergenal) spines. The Emuellidae have distinct furrows, possible bilobation of the frontal lobe, but lack fixigenal spines in all known species. The Redlichiidae have distinct furrows, definite bilobation, but appear to lack spines. The Dolerolenidae represented only by protaspids appear to possess only the furrows. The Paradoxididae lack furrows, but have spines and bilobation. The Olenellidae represented only by meraspids, have furrows and spines and possibly lack the bilobed axis. The Protolenidae known only from meraspid cranidia in Bergeroniellus and associated species, lack furrows, but have a bilobed glabella and some species possess fixigenal spines. Protaspids of Strenuella gripi Kautsky (1945), a related protolenid, have a bilobed axis and fixigenal spines but apparently lack the furrows (Whittington 1947 p.426-427). It is thus apparent all families bear some relationship to each other, but it is difficult to decide to which group the Emuellidae bear the closest relationship. The dangers of using any of these characters as a taxonomic basis while protaspids and meraspids of the families are incompletely known, is exemplified by the presence of fixigenal spines in meraspids of some species of Bergeroniellus and their absence in others.

It is accordingly considered that the position of the Emuellidae within the Sub-order Redlichiina is reasonably based, its superfamilial position is best left open for the present. It is also conceived that in the future, with additional information available the Emuellidae may be better placed in a separate sub-order.

## CHAPTER VIII EVOLUTION OF THE FAMILY EMUELLIDAE

### INTRAFAMILIAL RELATIONSHIPS

In order to form a clear picture of the evolutionary relationships of the genera and species within the family,it is necessary to combine the knowledge of adult morphology and ontogenetic development,with that available of the vertical distribution of the members.

On the basis of adult morphology it is clear that E.dalgarnoi is intermediate between E. polymera and the Balcoracania species; the palpebral ridge, the posterior border and furrow, the facial sutures and the relative dimensions of the thoracic axis and pleurae, in E. dalgarnoi all lie between the limits for these structures observed in the E. polymera,and B. dailyi and B. flindersi However it is not possible to determine in which direction evolution has proceeded on this basis alone, and it is here that knowledge of the ontogenies is invaluable. In all known ontogenies in the family,in the earliest stages the palpebral ridge is short and anterior, lengthening and moving to the posterior during development with correlated changes taking place in the posterior border and border furrow; similarly the anterior section of the facial suture changes from converging to diverging, and in B. dailyi the preglabellar field develops very late in ontogeny. It would therefore seem that E. polymera with it's short, high palpebral ridge and only slightly diverging suture is the most primitive or earliest member of the family, and that B. flindersi is the immediate ancestor of B. dailyi. Evolution would thus proceed from E. polymera to E. dalgarnoi to B. flinderia to B. dailyi.

The stratigraphic occurrence of the trilobites suggests the possibility of either chrono-species or chrono-subspecies. Evidence has been presented earlier to uphold the contention that the differences between the trilobites are sufficient to warrant separation on a specific level. Thus it appears that for example *E. polymera* and *E. dalgarnoi* are probably chronospecies.

This scheme is not in complete accord with the stratigraphic evidence (Text fig. 3) but it must be remembered that the sections are incomplete, that full ranges of species are not known, and that vital sections are not available. In the section west of Cape D'Estaing, *E. polymera* is succeeded immediately above by *B. dailyi*, but *E. dalgarnoi* has not been found; in the Emu Bay section *E. polymera* has not been found and *B. dailyi* is succeeded after a considerable stratigraphic interval by *E. dalgarnoi*. In the latter section the beds below those containing *B. dailyi*, in which it might be expected that *E. polymera* be found, are covered by beach deposits. The two Kangaroo Island sections can be correlated at least in part, so the overall picture is that of *E. polymera* at the base, immediately succeeded by *B. dailyi*, then after an interval of time by *E. dalgarnoi*. It must also be remembered that the lithologies of the sediments in which each of the species occurs, differ slightly, so that appearance is not necessarily controlled by the evolutionary changes. The occurrence of *B.flindersi* is so far limited to the Flinders Ranges, and the section cannot be matched with those of Kangaroo Island.

## EVOLUTIONARY POSITION OF THE EMUELLIDAE

Evidence has been given for the placement of the Emuellidae within the suborder Redlichiina, but with the proviso that it might be necessary later to make a separate suborder to contain them (see p. 85 ). In the possession of a ptychopariid sutural pattern, thick, long eye lobes, expanded frontal glabellar lobes, and long thorax combining macropleurality with division of thorax, the Emuellidae appear to be very primitive, and must be placed near the base of the evolution of the Redlichiida. It has long been suggested that the Olenellina have evolved from a redlichiid type trilobite with a ptychopariid sutural pattern (Hupé 1953; Harrington 1959). The Emuellidae possess such a cephalon and in addition combine with it thoracic features which are shared only by some of the Olenellina, i.e. a long multisegmented thorax, macropleurality and division of the thorax. Although the known members of the Emuellidae are far too high in the Lower Cambrian to be direct ancestors, they exhibit all the features which one might expect of them, and are regarded as preserving the structure of the ancestors to the Olenellina. The Olenelliina may therefore have evolved from an emuellid type ancestor by migration of the sutures and eventual loss and by reduction of the opisthothorax and it's loss in some members. It is thought also that other members of the Redlichiida have evolved from a similar ancestor, by loss of the opisthothorax, retention of the basic sutural pattern, reduction of the frontal glabellar lobe and development of the preglabellar field. In the Bathynotina a further step has been taken by migration of the sutures (in the opposite direction to the Olenellina), and the eventual loss of the rostral plate. The proposed evolution of the Emuellidae provides interesting examples of mosaic evolution

(Simpson 1944), i.e. the more of less independent evolution of the thorax and the cephalon in the various descendent groups.

It is interesting to note that in the ontogenies known of members of the Redlichiina, the changes taking place in the early meraspid stages are strikingly similar to the complete ontogeny of the Emuellidae, whilst the later stages in, for example, *Bergeroniellus* and *Redlichia* involve reduction of the frontal glabellar lobe and development of a preglabellar field. The latter has already been noted to take place very late in the ontogeny of *B. dailyi*, regarded as the most evolved of the Emuellidae.

## CHAPTER IX FUNCTIONAL MORPHOLOGY

### INTRODUCTION

The characters of the thorax of the Emuellidae are analysed on the basis of function, both in the adult trilobite and during the development. An attempt is made to seek causes framed in terms of adaptation, however it is realized that this may not be the underlying cause in some cases.

The occurrence of division of the thorax, macropleurality and fusion of the segments in other groups of trilobites is covered more fully in the chapter dealing with the taxonomic position and evolution of the group, and is clearly summarized in this chapter.

### DIVISION OF THE THORAX

The division of the thorax into a pro-thorax, 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 Lower Cambrian Olenellidae (Hupé 1953 a,b,c, 1955; Harrington et al1959).

In the Olenellidae the number of prothoracic segments differs between genera but not species; it is 17 in Fallotaspis and Nevadia, 16 in Callavia, 15 in Wanneria, 14 in members of the Olenellinae, 13 in Elliptocephala and 11 in Neltneria; the number of opisthothacic segments differs more widely both between genera and in the one genus; it is 4 in Fallotaspis, 11 in Nevadia, 2 in Callavia and Wanneria, varies between 2 and 30 in the Ollenellinae, 5 in Elliptocephala, and 6 in Neltneria.

The division of the thorax is considered by most authors

(Hupé ~~1953~~, 1953a, 1953b, Harrington 1959) to be a primitive character inherited from a worm like ancestor, and lost in more specialized trilobites. The number of segments in the opisthothorax has also been equated to degree of "primitiveness", those with many segments being considered the least evolved. In addition the prothorax has been considered as homologous with 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 the prothorax is long and multisegmented, and the opisthothorax short and with only a few segments and the homology would seem to be justified. However in <u>Paedumias robsonensis</u> (Burling) the opisthothorax is as long as the prothorax and contains more than twice the number of segments, and it appears difficult to justify the homology of the opisthothorax with the pygidium of the normal trilobite. It is even more difficult in the case of the Emuellidae where the opisthothorax is twice as long as the prothorax and has between 48 and 55 segments, and in addition the prothorax contains only six segments. It is thus considered that such a homology is inaccurate or at the least misleading.

An explanation of the division of the thorax has apparently never been attempted on the basis of functional morphology; in attempting to do so, it appears that it must be accepted that some trilobites have the ability to abruptly change the type of segment released from transitory pygidium, and such an ability may be considered to be "primitive", whilst other more "advanced" trilobites do not possess it. The problems then arise as to why this change occurs, at what point it takes place, and what causes the release of segments to cease eventually. It is proposed to attempt to answer these questions with reference to the Emuellidae, and to test the resulting hypothesis by reference to the Olenellidae.

In the Emuellidae the prothorax consists of six segments with the sixth macropleural and fused to the fifth, an opisthothorax of between 48 and 55 segments, which is approximately twice as long as the prothorax, a minute segmented pygidium. The posterior edges of the normal prothoracic segments are directed transversely, but that of the sixth is directed postero-laterally at a considerable angle from the axial furrow to the notch at the base of the macropleural spine. The mechanics of articulation thus enforce a maximum length of the seventh segment (first opistho~~racic~~-thoracic segment), equal to the length between the notches on the posterior border of the sixth; the axis of the seventh can show only normal taper, so the length of the pleurae of this segment is accordingly considerably reduced. The lengths of the pleurae in succeeding segments thus also are reduced. It is apparent that in this case it is the space reduction consequent upon the direction of the posterior border of the macropleural segment, together with the necessity of articulation, which initiated the change in the nature of the segments released from the transitory pygidium.

In the adult the segments of the opisthothoracix form a perfectly graded series between the posterior border of the sixth segment & the pygidium; the axis tapers gradually in series with that of the prothorax, and the pleurae with that of the seventh segment. In the ontogeny of the Emuellidae, the meraspid degree 6, shows the transitory pygidium articulating with the posterior border of the sixth, in the same relative position and manner as does the seventh segment in the adult, ~~and displaying a perfect gradation with the prothorax to the posterior.~~ In succeeding meraspid degrees the absolute size of the transitory pygidium remains approximately constant whilst that of the sixth segment increases, and the opisthothorax remains perfectly graded with respect to them. Thus in the adult, the number of opisthothoracic segments is determined by the relative lengths (trans.) of the posterior border of the sixth segment and the anterior border of the pygidium, and the gradation of segments between them i.e. release of segments from the transitory pygidium ceases when a perfectly graded condition is attained. It is notable, in this connection, that in the ontogeny of the Emuellidae, the cephalon attains the holaspid condition a considerable period of time before the thorax i.e. 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 segments in the prothorax is less than in other members of the family. In *Neltneria* (Text fig. 16 (~~4~~3)) the posterior edge of the eleventh pleura has only a very short transverse section before the spine curves to the posterior; thus the space available for the pleurae of succeeding segments is reduced compared with previous segments. In addition the mechanics of articulation necessitate a progressive direction of the pleurae to the posterior, with the last segment having it pleurae wrapped around the sides of the pygidium. In the Olenellidae with prothoracic macropleural segments (the Olenellinae, *Fallotaspis*) it is the third segment which is macropleural and it's posterior edge is transverse for most of it's length; thus it does not significantly reduce the space available for succeeding segments. In these genera, however, the structure of the macropleural third segment may cause the pleurae of the succeeding segments to be progressively directed to the posterior, and it appears that it is this factor which finally forces a change in the nature of segments released (Text fig. 16 (1)). As this is a more gradual process than the sudden space reduction in the Emuellidae, a greater number of prothoracic and smaller number of opisthothoracic segments are released. In the Olenellidae which possess an opisthothorax but not macropleural spines (*Elliptocephala*, *Nevadia*, Text fig. 16 (2)), the segments have pleurae progressively directed to the posterior and possessing long pleural spines. In those without division of the thorax (*Holmia*, no. Text fig. 16 (3)), the pleurae are once again progressively directed to the posterior but do not possess long pleural spines; consequently space reduction does not reach a critical point.

## MACROPLEURALITY

In the Emuellidae the last segment of the prothorax is macropleural. The spine is formed by both anterior and posterior pleural bands of the sixth segment; it tapers gradually to the posterior, curving inwards slightly, and extending to 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 fifth segment, to which the sixth is fused, to the notch on the posterior border of the sixth; the spine is thus hollow, almost flat on top and 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 the succeeding degrees the length of the spine increases to maintain the same position relative to the transitory pygidium.

In view of the high correlation between the lengths of the macropleural spine and opisthothorax and pygidium at all ontogenetic stages, it is considered that the macropleural 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 apposed to the bottom rather than the delicate pleural spines of the opisthothorax.

Hupé (1950, 1953c) has suggested that the macropleural segments are the genital segments containing the gonopores. The basis for this suggestion is that as the trilobites are primitive, they were near the original condition where gonads and gonopores were metameric, and would be localized on segments of particularly primitive character. He considers that the macropleural segments are the most primitive because of their narrow axis, and then compares the position of the macropleural segment in the trilobites with the position of the gonopores in the Insecta, Myriapoda, Crustacea and Chelicerata (Hupé 1950, Fig. 78), concluding that the opisthogoneate and progoneate tendencies of the "Antennulata" existed in trilobites of the Lower Cambrian.

There appears to be no concrete 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; it is assumed, therefore, the gonopore will be located on the ventral side, and one might expect to find some modification of the ventral morphology. However in the Emuellidae the doublure of the macropleural segment is strictly comparable in structure and position to that of the normal prothoracic segments; the segment differs mainly in the relative development of the spine. It must therefore be assumed that the gonopores are carried in the soft ventral integument and there seems 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 in pairs on most if not all thoracic segments (Raymond 1920, and others), appears the more reasonable.

Hupé's contention that the macropleural segments in Lower Cambrian trilobites have two preferred positions, one early in segmentation and one late appears to have some validity. The Olenellinae are characterized by having the third segment macropleural in a long prothorax, the Emuellidae and *Neltneria* the last macropleural. Other related families display a similar division, but two at least (*Olenelloides* and *Bathyuriscidella*) possess two macropleural segments more or less symmetrically placed within the thorax. Even allowing a genital function for the macropleural segments,it is considered that comparison with advanced groups of arthropods, all with a fixed number of segments, does not appear to be valid. The significance of the apparent division is not known.

In all genera whose adult 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 suddenly develops at the time of release from the transitory pygidium (Emuellidae). The time at which this occurs depends upon the relative position of the segment in the thorax; however in an appreciable percentage the segment is released very early in the meraspid development. In no known case does the macropleural segment develop after release from the transitory pygidium. This implies that the macropleural segments have some adaptive significance in the larval stages,either apart from or together with a possible underlying sexual function or that sexually maturity is very precocious in the trilobites. Hupé (1953 c, p.116) whilst allowing possible adaptive function with regard to a pelagic life, considers their presence would be almost universal if this were the case; he accordingly considers that sexual maturity is precocious. He considers that an assumed change from allometric to isometric growth during the early meraspid period marks the onset of sexual maturity (1953 c, p.121). However this alleged change is based on little data, is unsupported by statistical testing and is not necessarily indicative of maturity. Therefore it is considered that the first alternative, that of an adaptive significance in the larval stages is the more likely possibility. Indeed Hupé's reasons for rejecting this possibility apply equally well if not better to the ~~equation~~ interpretation of the macropleural segments as genital i.e. lack of universality.

In the Emuellidae the function of stabilization and protection both in larval and adult forms seems highly probable. In *Paradoxides pinus* (Whittington 1957, 1959; Westergård 1936) the first and second segments are both strongly macropleural when they first appear; during meraspid development the spines of both regress, the first more rapidly than the second, so that at degree 15 (Whittington 1957, fig. 5E) the first is normal while the second is still strongly macropleural and in the holaspid the second is now only very weakly macropleural. The same sort of phenomenon occurs in both 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 in the larval stages the macropleural spines have a similar adaptive function.

The retention of the macropleural spines in most adults raises several problems. In the Emuellidae the spines retain the adaptive significance which they had in the larval stages despite a presumed change of mode of life. However this is less obviously so in the great majority of cases. The spines may retain some function of protection or stabilization in some cases, but in others they occur in genera belonging to families in which the other members appear perfectly adapted to their habitat and mode of life e.g. *Octinellus* in the Illaenidae. The question thus arises as to whether the adaptive function of the macropleural segments in the larval stages are secondary or not; and if so what is the primary function. In this context Hupé's suggestion cannot be dismissed entirely.

Raw (1953) has suggested that the presence of macropleural segments is related to merocyclism inherited from a polychaete ancestor, and that it occurs most frequently in primitive forms, but is lost when the segments become graded. Macropleurality undoubtedly occurs most commonly amongst Lower Cambrian forms e.g. the Olenellidae but even in these groups it is difficult to match macropleurae with cycles of segmentation. Raw (1953 p.94) cites *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) has attempted to apply Raw's concepts to *Olenellus* and *Paedeumias*, but has found it necessary to combine them with Stormer's theory of secondary segmentation in order to fit merocycles. The presence (quoted above) of contiguous macropleural segments in the larval stage *Paradoxides pinus* and other genera, appears to offer insurmountable difficulties to Raw's concept. In post Cambrian trilobites the sporadic occurrence of macropleural segments in many positions affords another difficulty. In *Acidaspis*, Hupé (1950) lists seven species with five different positions of the macropleural spine; *Albertella* may have the spine either on the third or fourth segment. Manton's studies on the functional morphology are interesting in this context, in that she concludes that body form is largely determined by locomotory habits. (Manton 1952, 1960, 1964)

It is therefore considered that the concept of merocyclism cannot adequately explain either occurrence or position of macropleural segments.

## FUSION OF THORACIC SEGMENTS

The Emuellidae have the macropleural sixth segment of the prothorax fused with the fifth. A search of the literature has revealed only one other genus, Bathynotellus which shows a similar fusion of segments within the thorax, and in addition one of the segments involved is also 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 fifth prothoracic segment appears to be simply a device to increase the muscular control of the long macropleural spine, and so aid in support and stability. The apodemal slit of the sixth is very strongly developed and the fusion of the fifth allows it to extend abaxially onto the interfurrow platform. In addition it allows the elongated apodemal slit to abut against the abaxial end of the sixth pleural furrow, so that ventrally it forms a transverse apodeme with an accessary ridge joining it anteriorly. This provides both a much greater area for muscle placement and a more efficient one. On the pleural field the development of the horizontal flap between the anterior lateral corner of the sixth and the pleural spine of the of the fifth, appears to be a strengthening device.

In *Bathynotellus* the thorax has ten segments followed by a unit which has three axial rings and a macropleural spine and which articulates with a large pygidium (Text fig. 16(6)). In order to understand the situation in *Bathynotellus* it is necessary to look to the other member of the family, the genus *Bathynotus*.

*Bathynotus* has a thorax of 13 segments with the eleventh macropleural and the twelve and thirteenth segments with considerably reduced pleurae (Text fig. 16 (5)). The macropleural spine is directed posteriorly and in combination with a large pygidium reduces the space available for the development of the pleurae of the two posterior segments. It has already been pointed out (p. 93 ) that such a space reduction has resulted in the development of an opisthothorax in the Emuellidae and Olenellidae. The large pygidium in the Bathynotidae suggests that they were more advanced than the other two groups, and had stabilized the number of segments in the thorax. It is evident therefore that they solved the problem in a different way, that is by the fusion of the two posterior segments to the macropleural eleventh; the eleventh, twelfth and thirteenth segments in *Bathynotus* being homologous with the macropleural unit of *Bathynotellus*.

# CHAPTER X SEGMENTATION

## INTRODUCTION

Study of the Emuellidae, in particular of their ontogenies, has provided evidence of a new feature in the segmentation, and support for some features already established in other groups. The observations on the release of the fifth and sixth segments from the transitory pygidium as a unit, provides for the first time, evidence for the release of fused segments into the thorax. Observations also support the existence of more than one moult within each degree, and the release of more than one segment from the transitory pygidium during a single moult, features already established for other groups (Whittington 1957, 1959). More important, however, is the fact that the knowledge of the ontogeny of the Emuellidae, combined with their unusual morphology, has provided the means, in some cases for the first time, of testing several theories of segmentation, both of thorax and cephalon. In particular the theories of secondary segmentation of the thorax (Størmer 1941; Hessler 1962), merocyclism (Raw 1953) and asexual reproduction (Lemche 1957) are examined. In addition a unique teratological specimen, with disruption of thoracic segmentation, is described in detail.

## THEORIES OF THORACIC AND PYGIDIAL SEGMENTATION

### (a) Primary or secondary segmentation?

The nature of the segmentation of the thorax has been a subject of much debate since Størmer (1941) suggested that the thoracic segments, in particular the pleurae, were not coincident with the somites. He concluded that the pleural furrows were in fact the somitic boundaries and the pleurae consisted of the fused portions of successive somites i.e. the segmentation is secondary. For various reasons this view has been rejected by the majority of workers (Ross 1951a, b; Hupé 1953c; Raw 1953; Whittington and Evitt 1954; Whittington 1956, 1957). However, largely on the basis of studies of carboniferous trilobites, it has recently been defended by Hessler (1962).

Hessler found that (1) in adult pygidia, the pleural furrows are more prominent than the interpleural furrows and are consistently well developed throughout, and the interpleural furrows are absent posteriorly becoming pronounced only anteriorly (2) in larval (transitory) pygidia the pleural furrows are nearly always clearly marked and the interpleural furrows may be entirely absent (3) developmental anomalies, presumed to be somitic in nature, are bounded by pleural furrows. On this evidence, and on the basis of the well substantiated formation of somites at the anterior border of the hindmost somite in the pygidium (Whittington 1957, 1959), he considered that the pleural furrows are the true boundaries between somites and that the strengthening anteriorly of the interpleural furrows reflects "the gradual development of the functional units which when released from the transitory pygidium will become thoracic pleurae" (Hessler 1962 p.1306).

There is no "a priori" reason why the fact, that in some trilobites the pleural furrows are more prominent on the posterior regions of the pygidium, should be interpreted as indicating that they represent the boundaries of the original somites; an equally valid conclusion is that they are related to an essential feature of the somite and not the division between somites. In the latter respect studies on the alimentary system of segments appear to favour this point of view (Öpik 1961). The somites are fused in the pygidium and the segments are released into the thorax at its anterior edge: it is to be expected that the eventual lines of division (the interpleural furrows) will become more prominent to the anterior, but it cannot be said that they must necessarily be present immediately on production. Hessler (1962 p.1307) admits that some pygidia bear both pleural and interpleural furrows on all somites of the pygidium and that the condition is common, but considers that no information is offered as to which furrow defines the somite. When this evidence is combined with that of the morphology of the normal thoracic segment, the inference is strongly that the interpleural furrows are exactly what they appear to be, i.e. the boundary of the original somite. It is clear that Hessler's contention, even accepting his interpretation of the pleural furrow, can be sustained only if the pleural furrow is the usual furrow to appear first. In this connection the older and more primitive trilobites are of far greater importance than the younger and more advanced ones, in which practically any condition may be secondary.

In the Emuellidae, a Lower Cambrian family, it is the pleural furrow, not the interpleural furrow which becomes less pronounced, and finally absent, to the posterior. The gradual loss of the pleural furrow occurs in the opisthothorax (Pl. 5; 4, figs.1,2) In transitory pygidia, pleural furrows are found only on the anterior segments of early meraspid specimens; in late meraspid transitory pygidia and adult pygidia they are completely absent. One late meraspid specimen (Pl. 4, figs 1,2) shows the transitory pygidium with seven segments and a terminal piece; the axial furrows are faint and the furrows indicating segments are continuous on the axial and pleural fields.

The contention that the abnormalities observed on the pygidia of specimens of Griffithides wilsoni Walter (Hessler 1962, p. 1308; pl. 176, figs. 1, 2 & 4) are bounded by pleural furrows, appears to be highly subjective.

Størmer (1941) also considered that the segmentation of the axis is secondary, at least in part. On the basis of the attachment of the longitudinal muscles to apodemes in the transverse furrow, this furrow is considered to be the primary intersomitic boundary. In this hypothesis Størmer has received more general support (Hupé 1953c and others). However, acceptance of limited secondary segmentation of the axis in no way directly supports a secondary nature for the pleurae. In the Emuellidae, the fifth and sixth segments are fused; the line of fusion of the pleurae is generally plainly visible (Pl. 3, figs. 1-4); the apodemal slit of the sixth transverse furrow extends onto the pleural field along the posterior edge of the line of fusion (Pl. 3, figs. 2 & 4), whilst the abaxial end of the pleural furrow is posterior to the apodeme. This appears to confirm that the anterior edge of the pleurae is closely connected with the transverse furrow considered to be the primary intersomite boundary of the axial part of the segment.

It is considered that the evidence afforded by the Emuellidae and close examination of the inherent assumptions, substantially weaken the hypothesis of secondary nature of the thoracic pleurae.

(b) Asexual reproduction by budding.

The hypothesis that trilobites reproduced asexually by budding from the thorax,was first proposed by Lemche (1957). Whilst some of the evidence on which Lemche based his theory could be refuted on the basis of previous work, until now it has not been possible to critically test the hypothesis on all points. The Emuellidae provide the means to do this. Although Lemche's hypothesis has not gained acceptance amongst specialists in the group, it has recently been accepted without serious examination by at least one non-trilobite specialist concerned with problems of arthropodan evolution (Sharov 1965).

Lemche's suggestion was prompted by the presence of an opisthothorax in the Olenellidae. For the following reasons he suggested that asexual budding was taking place at the time of fossilization in some specimens (1) such segments occur only in fully grown specimens (2) in Olenellus vermontanus Hall (redrawn from Walcott 1910) the width (trans.) of the axial rings of the anterior segments of the opisthothorax is greater than that of the posterior prothoracic segments (3) the median spine of O. vermontanus (Lemche's fig. 1) could develop into the spine at "the usual terminal position of the animal" (Lemche 1957, p.801) (4) the decrease in the size of the pleural lobes of the opisthothorax.

On this basis, Lemche suggested that the Olenellidae with 2-6 segments in the opisthothorax represent animals with incomplete rudiments of new individuals in the process of development, and that the specimen of Paedeumias robsonensis (Burling 1916) with at least 29 opisthothoracic segments, represents an animal with several such rudiments in varying stages of development. Lemche (p.801) noted that no "rudiment" of the head has ever been found intercalated between segments and suggested that the head would develop suddenly after release, as a broad rudiment, specimens of Wanneria walcottana (Walcott) with short broad cephala being cited as possible examples.

Some of these points may be examined without reference to the Emuellidae. The axial spine of O. vermontanus occurs on the first opisthothoracic segment, as figured by Walcott (1910) not on the last prothoracic segment as claimed by Lemche; accordingly the postulated homology is falsely based. Examination of Walcott's plates of W. walcottana (Walcott 1910, Pl. 30 ) suggests that the dimensions of the cited cephela are due to the effects of compression along the axial line

The Emuellidae with an extremely long opisthothorax afford an excellent means by which some of Lemche's other points may be tested. Of prime importance is the presence of meraspids, with transitory pygidia attached and with the opisthothorax at varying stages of development (Text fig. 14, 15). All meraspids, and indeed all adults, have an opisthothorax in which the segments are perfectly graded between the prothorax and pygidium. In view of the explanation given for P. robsonensis, particular attention was directed to every fifth and sixth segments in the opisthothorax. If the hypothesis was soundly based, one would expect that these segments would show signs of fusion and macropleurality. However, no evidence of this nature was seen in these, or in any other, opisthothoracic segments.

In the light of close examination of the proposed evidence and that provided by the Emuellidae, it would appear that Lemche's hypothesis of asexual reproduction in trilobites possessing an opisthothorax is not tenable. Evidence for an alternative explanation of this feature based on the grounds of functional morphology is given elsewhere in this thesis (p.93-95)

(c) Merocyclism

Raw (1953 p.93) proposed the term merocyclism for the presence of a periodicity of segment type in polynoid polychaets which he compares with trilobites, and suggested that such periodicity occurred in trilobites with the regular alternation of macrosomites with normal somites. This may be expressed (Raw 1953 p.93; Palmer 1957 p.122) as an alternation of macropleural and normal segments. The evidence of a regular alternation in trilobites, and in particular Lower Cambrian trilobites has been considered with regard to the functional morphology of the macropleural segments of the Emuellidae (p. 100 )

In the Emuellidae only the sixth segment is macropleural, and there is no suggestion of a regular occurrence in either pro- or opisthothorax.

TERATOLOGY

One specimen of E. polymera (plate 4,figs.1,2;text fig.17) shows abnormalities in the opisthothorax related to the disruption of the normal mode of segmentation. Teratological specimens of trilobites involving thoracic segments have long been known (Westergård 1936; Resser 1939; Ross 1951) but in all cases the malformations consist of abnormal fusion of a segment, or exceptionally two segments to either the cephalon or pygidium. The specimen of E. polymera thus provides the first known example involving segments within the thorax.

The specimen shows a distinct fracture running from the left side of the glabella to the macropleural unit; this fracture appears to be definitely post-mortal. However symmetrically placed lines, representing breaks in the normal convexity of the axial rings, extend from the second opisthothoracic segment to the eighth on the right side of the axis, and to the sixteenth on the left side. The line on the right side appears to be simply a furrow and does not involve any of the segments in the disrupted area, however the line of the left side involves all the segments within this area; terminating at the posterior end of the last disrupted segment, it is also associated with depression of the portions of the axial rings abaxial to it. In the light of these considerations it is considered probable that the left hand "fracture" on the opisthothorax occurred during the life of the trilobite. An explanation of the disruption on the segmentation, on this basis, follows a more detailed description of the specimen.

The axial ring of the ninth segment of the opisthothorax is of normal width at the axial furrows, but tapers adaxially and

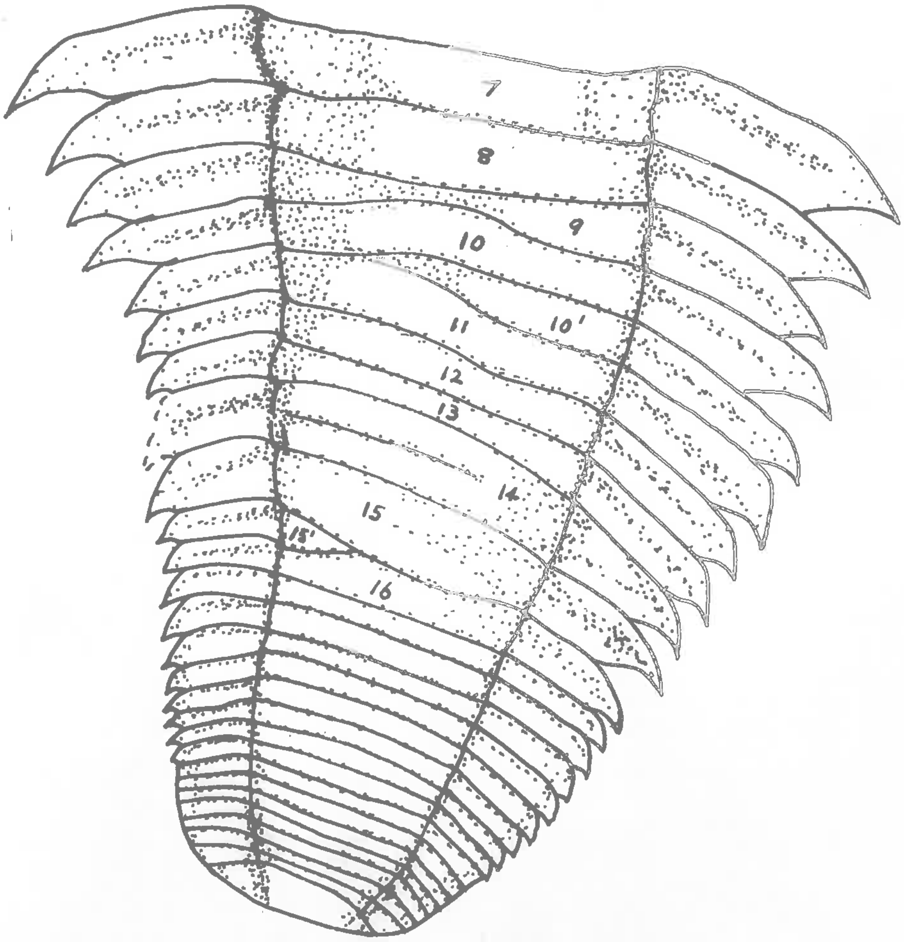
and is very narrow sagittally; on the right hand side the axial ring appears normal abaxially but this section tapers to a point before the sagittal line; the remainder of the axial ring is depressed to the level of the transverse furrow; the segment has normal pleurae on both sides. The tenth segment has its axial ring curving backwards on the left side, with the section abaxial to the fracture depressed to the same level as the ninth. On the left side a normal transverse furrow separates the tenth and eleventh segments; on the right side a half segment is interposed between them. The axial ring of the half segment has portion of an axial ring on the normal level; this section tapers to a point on the sagittal line, then a depressed section reaches to the line of fracture before disappearing; the pleura is normally developed on the right side. The axial ring of the eleventh segment curves to the posterior around the half segment on the right side; abaxial to the "fracture", the ring is depressed as before. The twelfth and thirteenth segments are almost normal, but curve slightly to the posterior from left to right; the left side abaxial portions of the rings are only slightly depressed. The fracture is very near the axial furrow as it crosses the fourteenth and thus only a very narrow strip of the ring is depressed. On the left hand side of the fourteenth, the axial ring is subdivided by a deep transverse furrow which extends from the axial furrow to slightly past the sagittal line before dying out. The pleurae on both sides on this segment are wider than usual, but with only one pleural furrow. This appears to indicate that it is a case of partial subdivision of one segment, rather than incomplete fusion of two. However the details of the morphology of the pleurae are not clear and either interpretation may be held. The fifteenth segment is very wide and the ring is divided by a furrow on the right side; the furrow is wide abaxially and tapers to a point on the axial line. The pleural portions of this segment are extremely wide, with the left side appearing to have one strong, diagonal pleural furrow, but the right side possibly being more complex. Following the fifteenth another half segment occurs, this time on the left side. The ring of the sixteenth segment is accordingly modified to curve around the half segment,but also tapers to the right so that the posterior edge is straight. It is followed by eight normal opisthothoracic segments and a pygidium with seven segments and a terminal piece.

The overall picture of the disruption of normal segmentation is thus basically that of depression of the sections of the axial rings abaxial to the "fracture", the sagittal reduction of the width of the 9th, the occurrence of a half segment on the right side,the complex character of both fourteenth and fifteenth segments, and the occurrence of a further half segment on the opposite side.

The disruption of normal segmentation appears to be the result of injury to the trilobite which may have resulted in the "fracture" lines noted on opisthothorax. The exact time of injury cannot be determined, but it could not be later than the time of release of the ninth opisthothoracic segment i.e. meraspid degree 15. As depression of sections of the axial rings abaxial to the fracture line occurs in segments down to the sixteenth, it is suggested that the injury affected not only the released thoracic segments but also the left side of the transitory pygidium. The pygidium of the specimen contained seven segments on death (several degrees later) so it is not inconceivable that the transitory pygidium contained a similar number of segments and that the left abaxial portions of them were affected.

The initial disruption to segmentation resulted in abnormalities to the left sides of the ninth and tenth, and release of the first half segment on the right side, probably due to the injury on the left side preventing the formation of firstly normal segments, then a complete segment. The eleventh segment is similarly affected but its abnormal condition appears to be mainly the result of accommodation of the half segment. The net result is the skewing of the axis of the opisthothorax to the left. A degree of balance is finally achieved by the release of another half segment, on the left side, between the fifteenth and sixteenth segments, allowing the succeeding segment to have a normal posterior edge. The position of the half segment is below the area affected by injury, the "fracture" running into the axial furrow at the fourteenth; thus "balance" was achieved only after the release of the injured segments. The half segment is immediately preceded by two complex segments which may represent previous attempts to balance the segmentation.

The nature of articulation between segments in the disrupted area cannot be determined it seems possible that the half segments were fused to the following segments; in view of the release



TEXT FIGURE 17

Posterior portion of the opisthothorax, and the pygidium, of a teratological specimen of E. polymera. Numbers refer to the equivalent segments of opisthothorax only.

of the macropleural unit as a whole, they were probably released together from the transitory pygidium.

The presence of eight normal opisthothoracic segments posterior to the last abnormal one, as well as the number of segments in the disrupted zone, necessitated the continued existence of the animal for a significant period of time after the disruption to segmentation. This implies that the animal was able to carry out its essential life functions for at least this period of time. However it's failure to reach the adult number of segments may indicate that the injury finally resulted in its death.

## CEPHALON

In the past century many palaeontologists and zoologists have expressed opinions concerning the nature of the segmentation of the arthropod head, and in particular of the trilobite cephalon. The trilobites are conceded to be the most primitive class of arthropods and thus the original segmentation of the cephalon is extremely important in any hypothesis concerning the nature of the arthropod head. Manton (1960) concluded that the arthropod head contained an unsegmented acron, one, two or three pre-oral, and four post-oral segments. However it must be remembered that recent work, notably Tiegs and Manton (1958) and Manton (1952, 1960, 1964) has strongly suggested that a polyphyletic origin of the arthropods, rather than a monophyletic one previously considered (Snodgrass 1938), is probable. Manton (1964) has showed on the basis of mandibular mechanisms of modern arthropods, that one line almost certainly separate from the others, consisted of the Trilobita and Chelicerata supporting Størmer's contention that these groups were considerably removed from the Crustacea (Størmer 1944).

Harrington (1959 p.0153) lists twelve palaeontologists who have speculated upon the composition of the trilobite cephalon, and comments that ten different opinions were held. It is beyond the scope of this thesis to review all the hypotheses, particularly in view of their wide disparity. It is proposed only to consider the recent accounts, most of which give references to the earlier works, of Størmer (1942, 1944, 1951); Raw (1953); Hupé (1953a,c,1960); Palmer (1957) and Whittington (1957). In addition particular attention is given to those questions on which the Emuellidae may provide new evidence; the number of primary segments in the cephalon, and the significance of the furrows on the pleural regions of some larval trilobites.

(a) Number of segments in the cephalon.

Whittington (1957) from a study of the ontogenies of many trilobites, has summed up the evidence which is provided by the protaspid and early meraspid stages. The glabella is usually divided by furrows into five rings with the anterior ring longest and often subdivided; the eye ridge, when present, reaches the axial furrow opposite the anterior ring and may be associated with an anterior pit; the pleural regions are subdivided by the posterior cephalic border which may be subparallel with the eye ridge; diagonal furrows occur on the pleural regions extending abaxially from the ring furrows. This evidence in combination with knowledge of the trilobite appendages leads Whittington to suggest that the protaspid glabella has "five cephalic segments, and perhaps add that the greater length of the anterior ring, and presence in some examples of subdivision, may argue that at least part of the sixth segment is included",(Whittington, p.449). He also acknowledges the difficulties in determining how many segments may make up the hypostome, doublure and frontal area, and so rejects Størmer's view (1942 p.96) of the anaprotaspid period as "comprising only primary segments, axis with five segments".

Hupé (1953 c ) considers that in most trilobite protaspids, the facts favour three primary post-oral segments, with a fourth and most posterior segment, the occipital, being added later as a result of teloblastic segmentation; thus the frequent resemblance of the occipital with thoracic segments is explained. In this he agrees with Öpik (1958) who has presented evidence of striking similarity of the occipital and thoracic segments in some trilobites ("occipital similarity"). With regard to the anterior segments, Hupé considers the development of Paradoxides pinus Holm (Westergård 1936) to be typical ; in the late protaspis the frontal lobe, till then undivided, becomes subdivided by a furrow into two equal segments. He considers that these two segments are genetically similar to the posterior four, and thus considers the glabella to have six segments.

In the adult trilobite Hupé (1953a p.273) on the basis of observations on the glabellar segmentation and divisions of the eye ridges in many Lower Cambrian Redlichiida, has described two segments (x and pnt) and infers a third in front of the segment bearing the ocular lobes. Thus he recognizes up to eight segments incorporated in the adult cephalon.

Størmer (1941) recognized four post oral segments, the leg segments, an antennal segment, comprising the frontal glabellar lobe, eye and palpebral ridges, and a complex pre-antennular segment which axially includes the preglabellar field, rostrum and possibly the hypostome and the anterior part of the frontal glabellar lobe. The occipital segment incorporates the pleural spines of the first thoracic segment in its pleural areas.

Raw (1925, 1953) also suggests six segments, but strenuously disagrees with Størmer on their nature, particularly of the pleural regions. Raw bases his view of the concept of merocyclism, applied in particular to the spines of larval cephala; he thus claims the first, third, fourth and the sixth are macrosomites, but with the third and fourth fusing to form his "parial" spine. In addition the anterior two segments, axially comprising the rostral plate and the hypostome have been secondarily subretroverted. Raw's view on the nature of the cephalic spines have been opposed by many authors (e.g. Whittington 1959; Størmer 1942; Stubblefield 1936); it is thus doubtful if his concept of merocyclism is valid.

Palmer (1957) combines the concept of merocyclism with the theory of secondary segmentation (Størmer 1942 p.124-132) to indicate that the olenellid cephalon may be composed of a minimum number of eight primary dorsal segments. His suggestion is that macrosomites, indicated by macropleurality, alternate regularly with two normal somites in the cephalon and anterior portion of the thorax. The observational basis for this suggestion is that the macropleural segment including the ocular lobes and frontal glabellar lobe,is separated by two normal segments from the macropleural segment including the pre-occipital segment and the intergenal spines. However the latter segment is separated from the next macropleural segment by the occipital and two thoracic segments, and if the merocyclism is to hold it is necessary to invoke Størmer's theory. Thus "the occipital ring and the pleural tips of the first thoracic segment are parts of the first primary segment behind the pre-occipital. In like manner the axial part of the first and second thoracic segments and the pleural tips of the second and third thoracic segments are respectively parts of the second and third primary segments behind the pre-occipital" (Palmer p.122); that is the macropleural spine belongs to the second axial ring of the thorax, and the merocyclic condition is fulfilled. As the most anterior primary segment is considered to be the one from which the genal spines develop, and is thus macropleural,it must necessarily be separated from the segment including the ocular lobes by two normal segments on the basis of the presumed merocyclism. Accordingly a minimum number of eight primary segments is obtained.

In the earliest meraspids of the Emuellidae the axis is divided into occipital, posterior, middle, anterior and frontal glabellar lobes. Thus five segments are indicated; however the frontal lobe is expanded and in later specimens in which the eye ridge is well defined,an extra furrow aligned with the anterior edge of the eye ridge,is seen to subdivide it. Accordingly a minimum number of six primary segments is indicated, but the undivided section of the frontal lobe is still relatively large and may contain more than one segment. In this respect it is interesting to note that during ontogeny of the Emuellidae, and of other groups, the expanded frontal lobe initially reaches the anterior edge and later is reduced in size and retreats posteriorly; the development of the anterior border, border furrow and preglabellar field if present, is in this sense secondary and the assumption that one or all of these areas represent primary segments probably is not justified. With regard to the eye ridges, unlike those described by Hupé (1953a), they appear to be undivided throughout the ontogeny, but appear double in very large adults. It is considered that in this case, the division is unrelated to primary segmentation.

In the early stages of the ontogeny of the Emuellidae, fixigenal spines such as those observed in the olenellids, apparently do not occur. It is therefore not possible to relate Raw's theory of merocyclism to the Emuellidae. Størmer's theory of secondary segmentation and Palmer's adaption of it are discussed in the next section.

(b) Furrows on the pleural areas of larval trilobites.

In determining the course and position of the pleurae of the primary segments, the nature of these furrows is all important. Raw (1953) and Whittington (1957) consider that the joints between thoracic segments and between the cephalon and thorax, are along the primary segments i.e. interpleural, and therefore consider that the pleural furrows, intergenal and posterior border furrow and the cheek furrows are homologous and intrasegmental. Raw in particular has pointed out the diagonal course of these furrows and has associated it with the musculature, although as Hessler (1962) has pointed out is difficult to conceive the function of such muscles. The homology of the posterior border furrow and pleural furrows also fits well with the ideas of Opik (1958) and Hupé (1953c) on "occipital similarity", although Raw (1953) has claimed that this similarity is due to identical functional requirements. A corollary of the intrasegmental view is as Whittington (1957 p. 453) has pointed out, that the intergenal spine in the olenellids and the fixigenal spine in Paradoxides cannot be the distal part of the pre-occipital segment as claimed by Palmer (1957) and by Hupé (1953a,c).

Størmer (1941) bases his theory of secondary segmentation on the belief that the cheek furrows are intersegmentary, homologizing them with the intergenal (posterior border furrow) and pleural furrows; this view necessitates a secondary, mechanical origin of the joint between the cephalon and thorax, cutting across the primary segments, and a similar view of the joints between thoracic pleurae. The intergenal spine is considered to be the distal part of the pre-occipital segment, and the pleurae of the occipital segment include the pleural spines of the first thoracic segment.

It is evident that both theories depend upon interpretations of the nature of the cheek furrows; both homologize cheek furrows, intergenal or posterior border furrow, and pleural furrows. Størmer considers the cheek furrows intersegmentary, therefore the others must also be of this nature; Whittington and others consider the pleural furrows are intrasegmentary and thus all others will also be of this nature. It is considered that proponents of both theories err, in their common assumption of the homology between these furrows. There is no "a priori" reason why this should be so, and evidence will be presented in this regard.

In the Emuellidae it has already been noted that the theory of secondary segmentation as applied to the thoracic pleurae is considered unlikely. In the earliest meraspids of the Emuellidae cheek furrows are present, extending abaxially from the junctions of the axial furrows and the posterior and middle glabellar furrows; no furrow is known to be present extending from the junction of the axial and occipital furrows. The cheek furrows are always parallel to the furrows bounding the eye ridge; as the course of the ridge becomes more oblique during ontogeny so the cheek furrows become diagonal. In the protaspis the furrows are indistinct,but appear to be at right angles to the axis and parallel to the posterior cephalic boundary. In one meraspid specimen the anterior cheek furrow appears to terminate at the base of the palpebral ridge. For these reasons it is believed that in the Emuellidae the furrows bounding the eye ridges, anteriorly and posteriorly, the cheek furrows and the posterior cephalic boundary are homologous and intersegmentary, bounding the primary somites; the diagonal course of the cheek furrows being due to the posterior movement and lengthening of the palpebral ridges during ontogeny. In addition Hupé (1953cfig.52) shows a protaspis of <u>Liostracus</u>, originally figured by Warburg (1925), on which he considers the cheek furrows are parallel to the cephalo-pygidial joint and are therefore intersegmentary; on this specimen, Hupé also shows cheek furrows which extend abaxially from the axial furrow at mid width of the glabellar lobes, and which he considers to be intra-segmentary. In larval specimens of *Redlichia chinensis* (Kobayashi and Kato 1951, Pl. 1 fig.4) the cheek furrows are very distinct and are at right angles to the axis and parallel to the posterior cephalic boundary.

The question as to the nature of the intergenal furrow (Olenellidae) or posterior border furrow (other groups) is crucial, for it is Størmer's assumption of the homology of this furrow with the cheek furrows which necessitates an assumption of secondary segmentation of the pleural regions; on the other hand it is the presumed homology of this furrow with pleural furrows which leads Whittington and others to consider the cheek furrows as intra-segmental.

In the earliest meraspids of the Emuellidae the posterior border furrow is represented only by a break in slope and it is only later that a definite furrow develops. However, even from the earliest stages the "furrow" does not leave the junction of the occipital and axial furrows but originates at the base of the axial furrow. It is considered that an homology between this furrow and the cheek furrows cannot be sustained in this case. In a specimen of *Redlichia chinensis* (Kobayashi and Kato 1951, Pl. 1 fig.4) a cheek furrow does occur at the junction of the axial and occipital furrows; although no border furrow has developed at this stage it seem unlikely that this cheek furrow can be considered as intrasegmentary. The case of the intergenal furrow in the Olenellidae appears more complex. Palmer's specimens (1957, pl. 19) support his claim for its intersegmentary origin, but it is a different structure to the posterior border furrow in the adult, which develops much later.

It is considered therefore that the cheek furrows are intersegmentary, and that at least in some groups the posterior border furrow develops later, and must be considered as intrasegmentary, as are also the pleural furrows. Størmer's theory of secondary segmentation of the pleurae is accordingly held to be unlikely.

Palmer's ingenious combination of merocyclism and secondary segmentation to determine the number of primary dorsal segments in the olenellid cephalon is thus unlikely on the grounds that secondary segmentation of the pleurae appears to be unlikely, and that merocyclism if it exists, is not regular enough to be used in prediction.

## CONCLUSIONS

A review of the theories of segmentation in the light of fresh evidence from the study of the Emuellidae has led to several important conclusions.

Lemche's theory of asexual budding of trilobites can be rejected outright, for the basis on which it stood is found to be false. It is found that in some groups at least the posterior border furrow is not homologous to the cheek furrows in larval specimens, and it is therefore unnecessary to invoke secondary segmentation of the pleural regions to explain the primary segmentation of the cephalon. The cheek furrows are considered to be intersegmentary and the posterior border furrow and pleural furrows, intrasegmentary. The primary cephalon of the Emuellidae consists of at least six segments with the possibility of subdivision or a multiple nature of the most anterior segment. No evidence for a teloblastic origin of the most posterior cephalic segment exists in the Emuellidae, but the possibility cannot be rejected. Evidence from the ontogeny suggests that secondary segmentation is unlikely.

# CHAPTER XI ANALYSIS OF GROWTH

## INTRODUCTION

The use of modern statistical methods in the study of trilobites is relatively recent, Kaufmann (1933) appearing to have been the earliest. This was probably due to the complex nature of most trilobite samples, and their generally small (numerically) size. The impetus for recent studies of this nature is twofold; firstly Shaw's (1956) recognition that the only valid quantitative method of describing most samples is regression analysis, and secondly the recovery of large numbers of trilobites of all growth stages by the methods of acid digestion. Shaw (1956, 1959) however was primarily concerned with the description of variation, rather than growth. In recent years, various statistical methods have been employed in growth studies on trilobites by Gaines (1951), Palmer (1957, 1958, 1962), Bright (1959) and Hunt (1967). The collections of the Emuellidae, although not as large as those used in the above studies, allows two aspects of growth to be studied (a) the mode and rate of growth (b) allometric growth.

## MODE AND RATE OF GROWTH

In order to carry out studies on growth it is necessary to be able to recognize age groups within the sample. Simpson, Roe and Lewontin (1960, p.385) state that "given a sample that is known or may reasonably be assumed to be homogenous except in age, age groups may be recognized by biological or by statistical methods or by a combination of both". In trilobite samples it may be assumed that some samples satisfy the above conditions, providing a large enough number of specimens of all or at least some developmental stages are present.

Two biological methods of recognizing age groups may be available in trilobite samples, however both involve assumptions which are known to be unwarranted in some cases. The first involves the recognition of morphologically distinct stages which do not intergrade, and which are assumed to be the result of successive moults (i.e. successive instars). However Hunt (1967) points out that there is no assurance that a single morphotype includes only one instar, and although study of the ontogeny of the Emuellidae has allowed the recognition of stages of cranidial development, all the changes are gradual and each stage contains more than one meraspid degree. The second method depends on the presence of meraspids of known degree, each free thoracic segment being considered as the result of a single moult. In this case it is known (Whittington 1957, 1959; this thesis p. 67 ) that in some trilobites this is not the case; more than one segment may be released during a single moult, and conversely more than one moult may occur within a single meraspid degree.

Simpson,Roe and Lewontin (1960 p.385) also state that "the appropriate statistical method is obtaining frequency distributions for characters that change with age ... the most obvious and generally the most useful characters are linear dimensions involved in growth". In addition, under certain conditions scatter diagrams of pairs of selected dimensions may also indicate age groups. If the variation of the selected dimension or dimensions within an instar is less than the average increase in those dimensions between instars,grouping of points on the scatter diagrams and distinct peaks on the frequency distributions, representing instars will occur. If however the converse is true, the grouping in the scatter diagrams will be submerged and the distribution, distinctness, and even number of peaks on the size frequency distribution may be modified.

In both methods it is necessary to choose linear dimensions so that effects of possible allometric growth are excluded as far as possible. Palmer (1957 p.110) states that "it is necessary to find out which linear dimensions increased at a rate most nearly proportional to increases in actual size." The most convenient method of making such a choice is by visual comparison of an early larval stage and a holaspid on a D'Arcy Thompson grid (Palmer 1957 text fig. 11 ). In the case of the Emuellidae, the cranidial length is chosen, for reasons already stated (p. 42 ).

According to Dyar's law (Thompson 1942 p.165), the linear dimensions of successive arthropod instars increase at a constant geometric rate. Assuming this law to apply to trilobites, Palmer (1957, 1962) has calculated a growth factor, actually the geometric growth increment, that is a measure of the percentage increase in size of the linear dimensions of successive instars. On this basis Palmer (1957) calculated such a growth factor for two olenellid trilobites in three different ways involving biological and statistical methods of recognizing instars. An attempt to repeat the procedure for a non-olenellid failed, because it was not possible to recognize instars (Palmer 1958). A similar attempt (Palmer 1962) met with qualified success. Palmer recognized morphological groups which he considered to represent successive instars, and constructed size frequency histograms for each group. However examination of this histogram (1962,text fig. 1) shows that one group is distinctly bimodal (metaprotaspid stage IV) and that complete overlap existed between some groups. Palmer, recognizing the overlap, combined such groups and calculated a growth factor, which on other grounds he later discarded. It appears that in this case the assumptions involved in the recognition of instar groupings were unjustified.

Hunt (1967) working on large numbers of an agnostid species was able to recognize nine instars in the ontogeny, on the basis of grouping in scatter diagrams of selected dimensions. Calculation of the geometric growth increment for successive instars showed that, with exception of the eighth and ninth instars, growth conformed well with Dyar's law. A slowing of growth between the last two instars was attributed to the attainment of sexual maturity. In addition the average for the geometric growth increment was near that expected for the trilobite to double its weight between successive instars (Przibram 1931, Kesling 1953).

In the Emuellidae, in particular B. flindersi, numerous specimens representing most ontogenetic stages are available. Although a great majority of these are cranidia, specimens with the thorax attached are sufficiently common to provide some control. Stages of cephalic development based on morphology have been recognized, but it is known that each includes more than one meraspid degree, and all morphological changes are gradual. It is thus necessary to calculate geometric growth by the use of specimens in which the meraspid degree is known. It is possible to calculate this for the successive instars represented by the meraspid degrees 0 to 6, and for two other sets at higher degrees; in addition the average geometric increment is calculated for several periods of growth by use of the formula $AK = A_1$ , $AK^2 = A_2$ etc. where A, $A_1$ and $A_2$ etc. represent the cranidial lengths of successive instars, and K the geometric growth increment. These procedures have several disadvantages. Only small numbers of specimens are known for degrees 0-6, and thus the value A which is available, may differ from the mean A of that instar, as it is known the A varies quite considerably within each instar. It is also known that the values for A of successive meraspid degrees may overlap, and that in the Emuellidae each free thoracic segment does not necessarily indicate a single moult. In spite of these objections it is considered that the results obtained have a general validity.

A purely statistical method of recognizing instars is also employed. A size frequency distribution of cranidial lengths of *B. flindersi* was constructed (Text fig. 4 (2)). It is obvious from examination that only the first stages are represented sufficiently to have any validity. When combined with the knowledge of dimensions of meraspids of known degree, it is evident that the first peak represents a late protaspid instar and the polymodal block with peaks at 17, 20, 24, 27 and 30 micrometer divisions represents the instars from degrees 0 to 6. However, even allowing for the release of the macropleural unit during one moult, the number of peaks does not agree with the presumed number of instars. It is considered that the absence of one peak is probably due to a combination of relatively small number of specimens and overlap of ranges of the dimension for successive instars. Some valuable information, however, may still be obtained; the last peak is very strong and suggests a value of 30 mic. div. as the best value for degree 6, rather than the average of 29 mic. div. calculated from 5 specimens of this degree.

The results (Table 9) appear to show a significant decrease in the geometric growth increment during ontogeny. The average increment for degrees 0 to 6 is 1.12 (average of individual values of successive instars and calculated average of 0-6); the calculated average increment between degrees 6 and 19 is 1.07, and between degrees 19 and 53 is 1.01. It is evident that Dyar's law does not apply to the growth of B. flindersi, except perhaps between degrees 0 & 6, a significant decrease being evident from degree 19 onwards. It is perhaps significant that it is approximately at this degree that the cephalon attains the holaspid condition.

Simpson Roe and Lewontin (1960 p. 392-396) have developed methods for estimating $K_g$, the geometric rate of change, and changes of $K_g$ over the size range. The relation

$$Kg_1 = \frac{\log_e Y_1 - \log_e Y_0}{t_1 - t_0}$$

and so on is used in calculating the latter. The values for the instars (meraspid degrees) of B. flindersi are given in Table 9. A significant decrease is evident, although the trend is not regular. The lack of regularity in the decrease is perhaps the result of too few specimens.

Insufficient specimens are available to carry out similar

## TABLE 9.

Geometric growth increments K and geometric rate of increase $K_G$ for meraspids of known degree; dimensions of cranidial lengths $A_1$ in mic. divs., and are the average of all individuals for a given degree. (*B. flindersi*); 32 mic. div. = 1.00 mms.

| Degree | $A_1$ | $\log_e A_1$ | K | | $K_G$ |
|---|---|---|---|---|---|
| 0 | 17 | 2.8332 | 0-1 | 1.20 | 0.19 |
| 1 | 20.5 | 3.0204 | 1-2 | 1.15 | 0.09 |
| 2 | 23 | 3.1135 | 2-3 | 1.10 | 0.12 |
| 3 | 25.3 | 3.2308 | 3-4 | 1.05 | 0.03 |
| 4 | 26.5 | 3.2581 | 4-5 | 1.13 | 0.10 |
| 6 | 30 | 3.3534 | 6-10 | 1.03 | |
| 10 | 34 | 3.5264 | 10-11 | 1.12 | 0.11 |
| 11 | 38 | 3.6376 | 11-18 | 1.08 | |
| 18 | 69.5 | 4.2413 | 18-19 | 1.04 | 0.04 |
| 19 | 72 | 4.27867 | 19-27 | 1.01 | |
| 27 | 80 | | 27-53 | 1.01 | |
| 53 | 101 | | 6-19 | 1.07 | |
| | | | 19-53 | 1.01 | |

estimates for the other species.

## ALLOMETRIC GROWTH

The concept of allometric growth is now firmly established in palaeontology, and has been applied in studies on both vertebrates (e.g. Kurten 1954; Robb 1953), and invertebrates (e.g. Kermack 1954; Burma 1948). Allometry and its relations to ontogeny and phylogeny has recently been the subject of a review by Gould (1966). However, to the author's knowledge, allometric studies have not been directly applied to trilobites, although some authors have implied the presence of allometric growth factors.

Shaw (1956 p.1214) stated that "it is possible that when complete ontogenetic series, including protaspids, are analysed, some evidence for the existence of allometric growth may appear, but to date no such data have been obtained". Bright (1959) in a biometrical study of *Elrathia kingii* (Meek), has shown by use of ratios a "decrease in the length of the cranidium relative to the pygidium as total length increases" (p.93), but has not specifically analysed the data in terms of allometric growth. Palmer (1957) in the description of the ontogeny of two olenellids has shown that for some characters, curvilinear growth is exhibited in the earliest meraspid stages, but that even in rapidly changing characters, rectilinear growth is displayed after the first few instars (1957, p.110). For the regressions of the distance between the intergenal spines, and their lengths, against glabellar length Palmer has calculated separate "best fit" lines for the upper and lower parts of the distributions. However the data are not analysed beyond this stage.

## TABLE 10.

Selected larval specimens of *B. flindersi*.

| Cranidial length (A) | Palpebral length (C) |
|---|---|
| 17 | 2 |
| 20 | 2.5 |
| 23 | 4.5 |
| 25 | 5 |
| 25 | 6 |
| 26 | 6 |
| 26 | 6 |
| 27 | 6 |
| 27 | 7 |
| 28 | 8 |
| 29 | 8 |
| 30 | 10 |
| 34 | 11 |
| 34 | 12 |
| 38 | 12 |
| 42 | 12 |
| 45 | 15 |
| 57 | 16 |
| 67 | 21 |
| 72 | 20 |
| 72 | 18 |
| 80 | 21.5 |
| 100 | 30 |

Dimensions in micrometer divisions where 1.00 mm. = 32 m.d.

In the Emuellidae, examination of the D'Arcy Thompson diagram (Text fig. 13 ) suggests that the palpebral ridge and the anterior border grow allometrically with respect to overall size, particularly in the early meraspid stages. The length of the palpebral ridge can generally be measured with accuracy, but the width of the anterior border is extremely difficult to measure accurately, particularly in very small specimens; accordingly the former character is used in the analysis of allometric growth. The analysis is only carried out on the larval stages of B. flindersi, which are more numerous and better preserved than in the other species.

METHODS OF ANALYSIS

Simpson, Roe and Lewontin (1960 p.406-7) point out that the simple allometric equation $Y = bX^{\alpha}$ is derived from a consideration of the relative growth of two dimensions over time, and that this relationship between dimensions should be termed "allometry of growth". In order to determine the parameters of "allometry of growth", measurements must be taken on a single specimen at a series of ages or periods in its growth; this procedure is rarely possible in palaeontology. However, in some fossils distinct growth stages can be recognized, and it is possible to use the dimensions of different individuals at different growth stages. Thus the parameters calculated from this sort of data describe the allometry of growth of an "average" individual of the species. In most fossil samples the dimensions are measured on a number of individuals of varying sizes whose ages or stage of growth are not accurately known; there is no guarantee that the larger individual is older or vice versa. Parameters calculated

## TABLE 11.

Dimensions of a sample of 103 individuals of the meraspid stage of B. flindersi.

| Class Range of Cranidial length | Number | Cranidial Length ($A_1$) | Palpebral Length (C) |
|---|---|---|---|
| 15 - 19.5 | 10 | 17.8 | 2.8 |
| 20 - 24.5 | 14 | 22.5 | 4.6 |
| 25 - 29.5 | 23 | 26.7 | 5.1 |
| 30 - 34.5 | 21 | 30.7 | 7.8 |
| 35 - 39.5 | 13 | 36.3 | 9.7 |
| 40 - 44.5 | 6 | 42.5 | 11.8 |
| 45 - 49.5 | 5 | 46.2 | 13.4 |
| 50 - 54.5 | 1 | 54.0 | 16.0 |
| 55 - 59.5 | 3 | 56.3 | 17.0 |
| 60 - 64.5 | 1 | 62.0 | 17.4 |
| 65 - 69.5 | 2 | 67.0 | 18.5 |
| 70 - 74.5 | 2 | 72.0 | 20.0 |
| 75 - 79.5 | 1 | 76.0 | 20.5 |
| 80 - 84.5 | 1 | 80.0 | 21.5 |

Arranged by 5 micrometer divisions (0.16 mms.) class range increments of cranidial length. Dimensions of cranidial length $A_1$, and palpebral length C, in mic. divisions; logarithms to the base 10 of A & C.

## TABLE 12.

Deviations from simple allometry; data from meraspids of known degree; dimensions in mic. divs. are the average for specimens of a given degree.

| Instar | $\alpha$ |
|---|---|
| 0 - 1 | 1.95 |
| 1 - 2 | 3.60 |
| 2 - 3 | 2.38 |
| 3 - 4 | 1.49 |
| 4 - 6 | 2.32 |

from this type of data describe "allometry of size" rather than of growth. However the simple allometric equation frequently applies to such data as it is not assumed that all individuals grow at the same rate, but only that the relative growth rates of the dimensions are much the same for all individuals measured.

In the collection of larval specimens of B. flindersi there occur both isolated cranidia and meraspid cranidia of known degree. It is therefore possible to calculate the parameters of allometry of growth of an "average" B. flindersi by using only those specimens of known degree (Table 10). The small number of specimens available probably affect the significance of the results to some degree. The parameters for allometry of size are calculated from the measurements of the two dimensions for all larval specimens (Table 11).

In both cases the dimensions (cranidial length $A_1$, and palpebral length C) are plotted on rectangular co-ordinate graph paper to give scatter diagrams. The power function $Y = bX^{\alpha}$ may be expressed logarithmically as $\log Y = \log b + \alpha \log X$; accordingly the dimensions are converted to their natural log. equivalents, replotted, and the "best fit" line calculated by Bartlett's method (Simpson, Roe & Lewontin, 1961 p.232-237). The parameters of this line when reconverted to their exponential form are those of the simple allometric equation.

In order to test for deviations from simple allometry different methods must be used for the two sets of data. In the case of "allometry of growth", for each growth period $\alpha$ is estimated by the relation

$$\alpha_1 = \frac{\log_e Y_2 - \log_e Y_1}{\log_e X_2 - \log_e X_1},$$

and so on. The values for $\propto$ for each period are then graphed (Simpson, Roe & Lewontin 1961, p.409-410). The best method for observing deviations from simple size allometry is that suggested by Richards and Kavanaugh (1945). From the "best fit" line for simple allometry the theoretical value of $\log_e Y$ is calculated for each value of $\log_e X$. The deviations of the actual values from the theoretical values are then tabulated and plotted on a scatter diagram against the corresponding values of $\log_e X$.

## RESULTS AND INTERPRETATIONS

(a) Allometry of growth.

Examination of the scatter diagrams (Text fig. 18) clearly shows both deviation from isometric growth, and from simple allometric growth. The distribution may be divided into a lower group with log A equal to or less than 1.48 ($A_1$ = 30 mic. div.) and an upper group with log A greater than 1.48. The two groups may be treated separately and best fit lines and allometric growth parameters are calculated for both. For the lower group the equation is

$$\log C = -3.26 + 2.86 \log A$$

or converted to its exponential form $C = .006A^{2.86}$

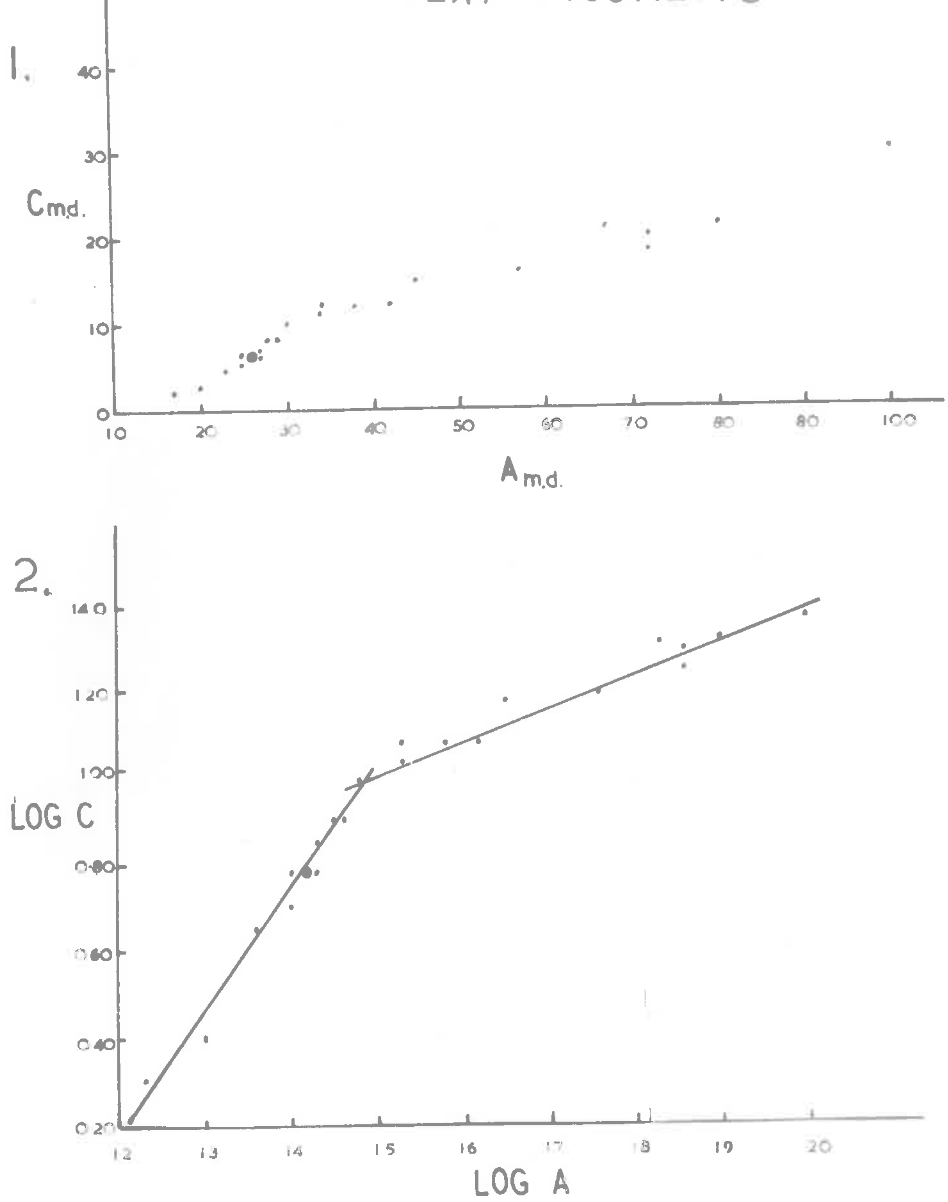
The value of $\propto$ , the allometric constant, is clearly significantly different from unity (isometric growth), and establishes that within this size range, the palpebral ridge grows allometrically with respect to the cranidial length. For the upper group the equation is

$$\log C = -0.17 + 0.79 \log A$$

or $$C = 0.68A^{0.79}$$

The value of $\propto$ in this case is much nearer to unity, and as it's

TEXT FIGURE 18



Larval specimens of B. flindersi of known meraspid degree.

(1) Growth curves of palpebral length C relative to cranidial length $A_1$, with dimensions expressed as micrometer divisions where 1.00 mm = 32 m.d. Data from Table

(2) Relative growth curves of the palpebral length C plotted logarithmically against the logarithm of cranidial length. Data from Table . Best fit lines for simple allometry plotted. Grouped data given in Table

estimation is based on an extremely small number of measurements, may not differ significantly from unity, i.e. within this size range the dimensions may be growing isometrically with respect to each other.

A value of 1.48 for log A is equivalent to a cranidial length (A) of 30 mic. div. or 0.94 mms. This value is extremely significant as it is at this cranidial length (average) that meraspid degree 6,is attained, i.e. all prothoracic segments have been released from the transitory pygidium. Thus the attainment of meraspid degree 6 marks significant changes in the growth pattern of the cranidium as well as those of the thorax.

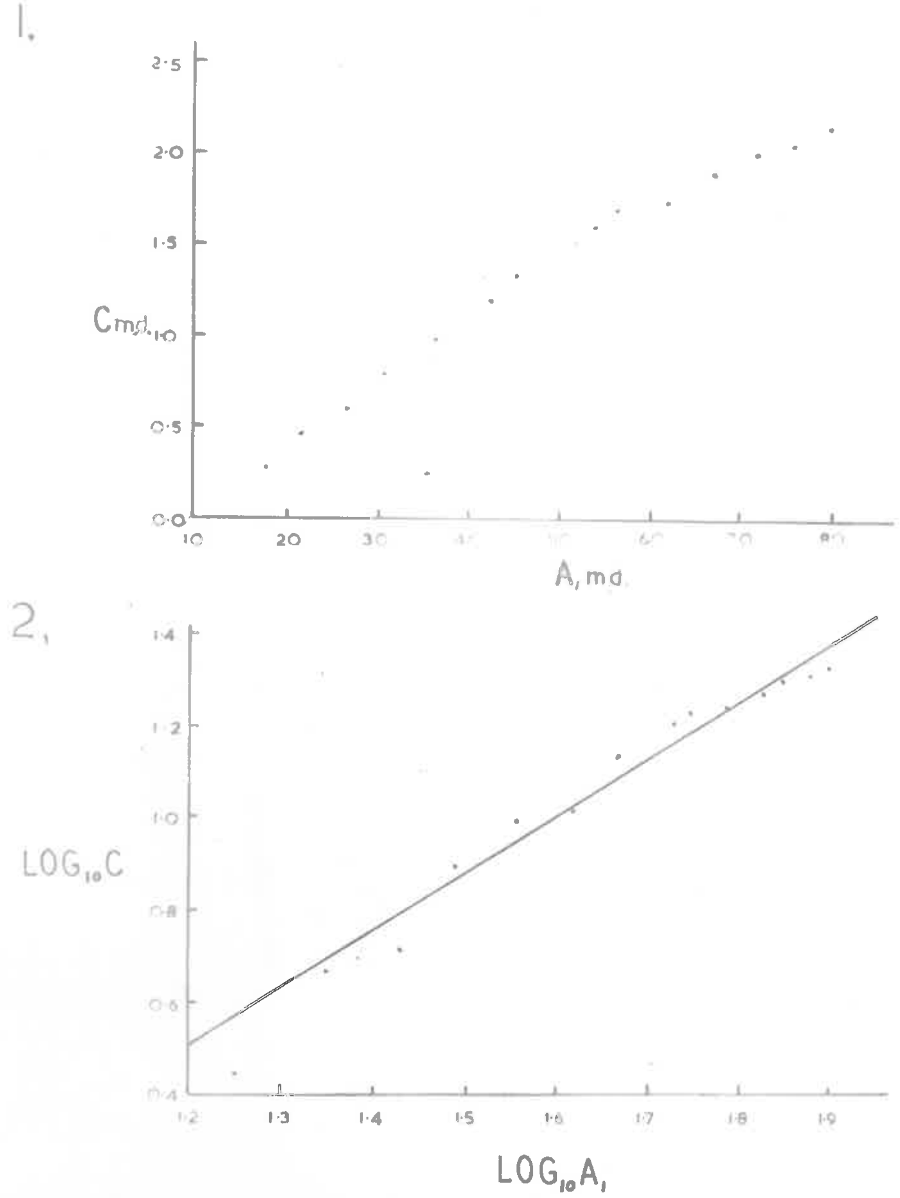
Examination of the scatter diagram (Text fig. 18) also suggests that deviations from simple allometry occur within this group. The results are given in Table 12 and the deviations plotted (Text fig. 20 (1)). Although the average value for the group is 2.86, the individual values for each growth period vary from 1.50 to 3.60. It is considered that some of this "deviation" may be the result of estimation based on small numbers of specimens, but that it does constitute a real phenomen.

(b) Allometry of size.

The scatter diagrams (Text fig. 19) show that the distinct division into two parts shown in the other data is masked in this case. This is probably due to the variability and to the effects of grouping of the original data. However it is evident that the distribution is not entirely described by assuming rectilinear relationships. The "best fit" line for the data is

$$\log C = -0.80 + 1.25 \log A_1$$

TEXT FIGURE 19



Larval specimens of B. flindersi.

(1) Growth curve of palpebral length against cranidial length; dimensions given as micrometer divisions where 1.00 mm = 32 m.d.

(2) Relative growth curve of palpebral length plotted logarithmically against the logarithm of cranidial length. Best fit line for simple allometry plotted for complete data.

## TABLE 13.

Cranidial length and palpebral length in mic. divisions from Table 11 taken as natural logs.

| $A_1$ | C | $\log_e A_1$ | $\log_e C$ | Calc. $\log_e C$ | Deviation calc.-obs. |
|---|---|---|---|---|---|
| 17.8 | 2.8 | 2.8792 | 1.0296 | 2.943 | 1.91 |
| 22.5 | 4.6 | 3.1135 | 1.5261 | 3.131 | 1.61 |
| 26.7 | 5.1 | 3.2847 | 1.6292 | 3.268 | 1.54 |
| 30.7 | 7.8 | 3.4243 | 2.0541 | 3.330 | 1.28 |
| 36.3 | 9.8 | 3.5918 | 2.2824 | 3.514 | 1.23 |
| 42.5 | 11.8 | 3.7257 | 2.3462 | 3.705 | 1.35 |
| 46.2 | 13.4 | 3.8330 | 2.5953 | 3.707 | 1.11 |
| 54 | 16.0 | 3.9890 | 2.7003 | 3.830 | 1.13 |
| 56.3 | 17.0 | 4.0307 | 2.8332 | 3.863 | 1.03 |
| 62 | 17.4 | 4.1271 | 2.8565 | 3.941 | 1.09 |
| 67 | 18.5 | 4.2047 | 2.9178 | 3.994 | 1.07 |
| 72 | 20.0 | 4.2767 | 2.9958 | 4.064 | 1.07 |
| 76 | 20.5 | 4.3307 | 3.0204 | 4.104 | 1.08 |
| 80 | 21.5 | 4.3820 | 3.0681 | 4.144 | 1.08 |

"Best fit" line for simple allometry from Calculation.IV (a)

$\log C_1 = -0.80 + 1.25 \log A_1$.

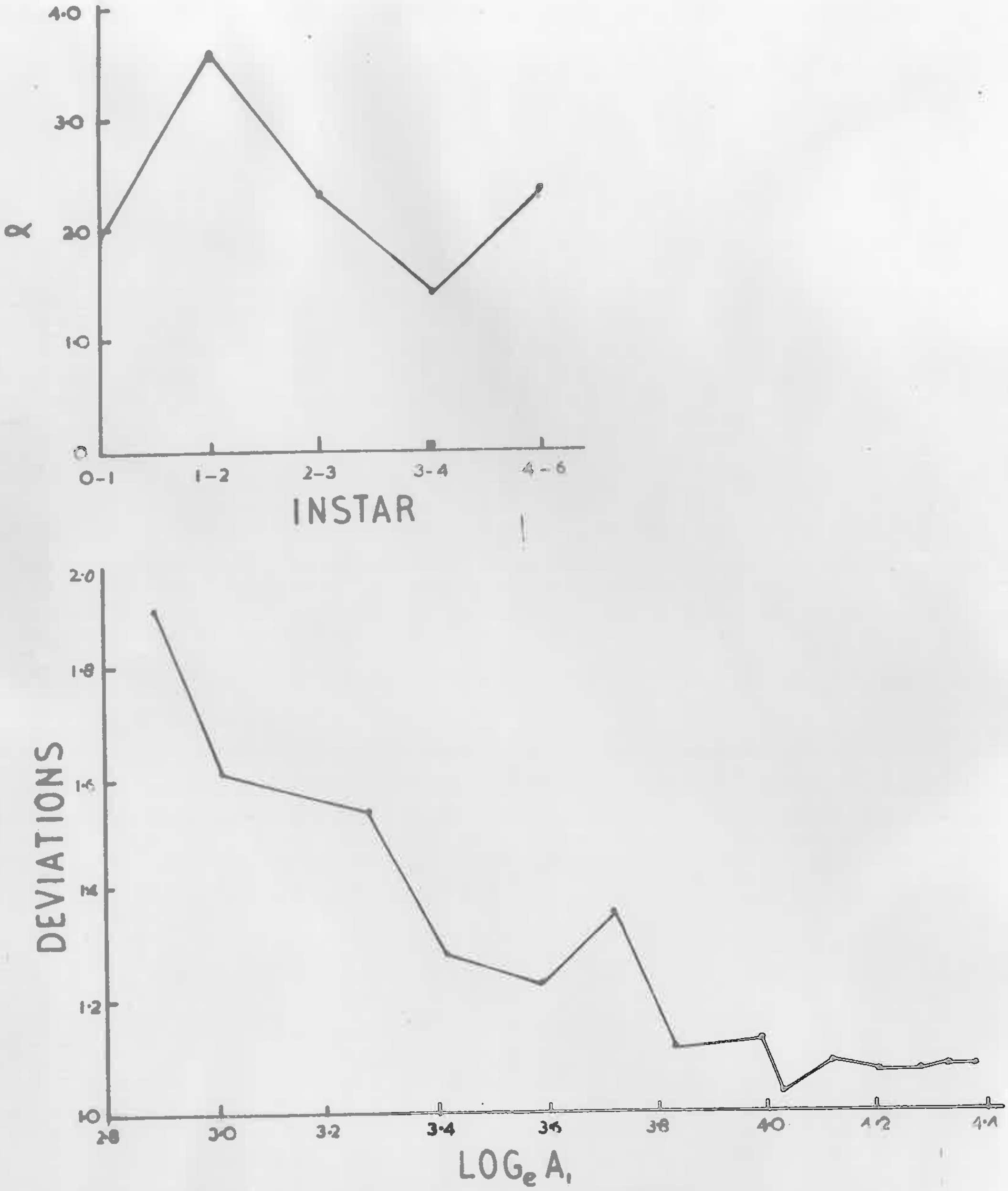
The value of 1.25 for $\alpha$ differs significantly from unity in this case, indicating allometric growth of the palpebral ridge with respect to the cranidial length. The deviations from simple size allometry are tabulated (Table 13) and plotted (Text fig. 20 (2)). It is evident that there is a distinct trend towards decrease in the amount of deviation with increase of cranidial length. The deviation is very high for the smallest specimens decreases rapidly and becomes almost constant for the largest specimens. This accords reasonably well with the estimates developed from the other data, indicating considerable deviation in the early meraspid stages, and perhaps isometric growth, without much deviation, in the later stages.

All calculations of the parameter estimates are given in Appendix V .

### (c) Comparison of results

The results obtained for allometry of growth, based on data from meraspids of known degree only, are far more precise, than those obtained for allometry of size, based on data from all larval specimens. However, the studies on allometry of size indicate that, at least in this case, allometric growth, and even deviations from simple allometry can be detected by analysis of this type of data.

# TEXT FIGURE 20



(1) Changes in $\alpha_1$ the coefficient of allometry, from one instar to another; growth of palpebral length relative to cranidial length of meraspids of known degree of *B. flindersi*.

(2) Deviations from simple allometry for palpebral length relative to cranidial length for larval specimens of *B. flindersi*; on the abcissa the natural logarithmic values of cranidial length; on the ordinate the deviations between observed palpebral lengths and the values predicted by the best fit line relating the logarithm of the cranidial length to the logarithm of the palpebral length.

## CHAPTER XII CONCLUSIONS

The more important results and conclusions of the study of this group of trilobites have been presented throughout the text. In view of the wide range of studies from which they have been drawn, it is thought useful to bring them together.

### SYSTEMATICS

Analysis of the morphology of the adults leads to the conclusion that they should be divided into two genera *Emuella* n.g. and *Balcorocania* n.g., and that each genus should have two species; the species of *Emuella* being named *polymera* and *dalgarnoi* whilst those of *Balcorocania*, *dailyi* and *flindersi*

A combination of cephalic and thoracic features serves to define the group. In the cephalon they possess a ptychopariid sutural pattern, long thick crescentic eye lobes, a glabella with three transglabellar furrows, tapering anteriorly to the anterior glabellar furrow then with an expanded frontal glabellar lobe which generally reaches the border furrow, and a posterior border with a distinct fulcrum and its abaxial section directed antero-laterally. The thorax has a prothorax of six segments with the sixth macropleural and fused to the fifth, and an extremely long opisthothorax of up to 55 segments, followed by a minute segmented pygidium.

The genera are separated primarily on the length and position of the palpebral ridge, *Emuella* with a short ridge located anteriorly and *Balcorocania* with a long ridge extending to the posterior. Associated with the length of the ridge is the direction of the abaxial section of the posterior border and the structure of the border furrows. Species are separated on details of the above characters, and otherssuch as presence or absence of apreglabellar field in Balcorocania.

All the species show variation of similar style and range. An important variant noted in all species,both in adult and larval specimens,is the bilobation of the frontal glabellar lobe.

ONTOGENY

The ontogenies of the members of the group reinforce the taxonomic discriminations made of the basis of adult morphology. Of the four species, ontogenies of three are known in reasonable detail and are basically similar.

The protaspid period is not well represented in any species, but appears to have a narrow axis with five rings, with anterior ring longest and expanding to the anterior edge; furrows extend onto the cheek regions from the ring furrows; the posterior cephalic border is transverse, parallel to the cheek furrows and separates the cephalon from a small crescentic protopygidium. In the meraspid development three sets of characters undergo progressive change; the palpebral ridge originally anterior and very short, lengthens and becomes more posterior and correlated changes occur in the posterior border and border furrow; the frontal glabellar lobe becomes rounded and an anterior border and border furrow develop in front of it; the anterior sections of the facial suture changes direction from convergent to divergent. The combination of these changes is used as a basis for dividing cephalic development into stages correlated with cranidial size (length). The changes take place at different rates in the species,so that at a given size they will exhibit different combinations of the characters.

In the meraspid period the cheek furrows gradually disappear, but remain parallel to the eye ridge as it swings from a transverse to postero-lateral direction. An additional glabellar furrow aligned with the anterior edge of the eye ridge is present up until the late meraspid period.

The development of the thorax differs from the normal (as described by Whittington 1959,for example) in that the macropleural spine of the sixth segment is not developed until after release of the sixth from the transitory pygidium,and then extends to the level of the pygidium throughout ontogeny; that the fifth and sixth segments fused in the adult, are released from the transitory pygidium in this condition i.e. there is no meraspid of degree 5; that there is a perfect gradation from the macropleural segment to the posterior edge of the pygidium throughout the development of the opisthothorax.

It was found that a size overlap occurred between successive meraspid degrees, that more than one segment may be released from the transitory pygidium during a single moult, and conversely that more than one moult may occur for a given degree. The absolute size of the transitory pygidium showed very little increase from start to finish of the meraspid period.

A matching of the development of thorax to that of the cephalon revealed that in all species the cephalon attained the holaspid condition (except for size) a considerable period of time before the thorax attained the holaspid number of segments.

The development of the hypostome showed a progressive movement to the posterior of the anterior wings, and a change in shape of the posterior lobe of the median body, from triangular to sub-rectangular.

## TAXONOMY

The genera *Emuella* and *Balcoracania* are characterized by the combination of unusual characters of the cephalon and thorax. Whilst many groups of trilobites are similar with respect to either cephalic or thoracic characters, none combine similarities of both. Accordingly *Emuella* and *Balcoracania* are combined as a separate taxon, which has at least familial rank. The genus *Emuella* is chosen as the nominate genus and the family is thus called the Emuellidae.

The combination of cephalic and thoracic characters is also used as the basis for assessing the taxonomic position of the Emuellidae. The thorax of the Emuellidae is most similar to that of the Olenellidae, both groups exhibiting division of the thorax and macropleurality. The Bathynotidae are also similar with one genus with a macropleural segment, and the two following segments with reduced pleurae, and the other genus with a macropleural segment showing fusion with other thoracic segments. However where as the similarities with the Olenellidae, with respect to division of the thorax, are considered to arise from the same reason, the inability of a primitive trilobite to stabilize the composition of the thorax in certain circumstances, the similarities with the Bathynotidae are considered to be largely convergent.

The groups which exhibit similarities to the cephalon of the Emuellidae all belong to the Suborder Redlichiina; within this group the Dolerolinidae, and some members of the Protolenidae, principally the so-called protolenoids, bear approximately the same degree of resemblance. However these groups are not only placed in separate superfamilies but are regarded by some authors (Sdzuy 1959; Öpik 1961a; Pocock 1964) to be transitional between superfamilies.

When a combination of cephalic and thoracic characters is considered, the Olenellidae, with a similar thorax, differ by lack of the ptychopariid sutural pattern and the other groups, with a similar cephalon, resemble the Emuellidae only in the relatively large number of segments in the thorax.

Comparison of the ontogenies of the families regarded as related on the basis of adult morphology appears to affirm the degree of relationship deduced on this basis, but fails to indicate a solution to any of the problems which arose.

On the basis of adult morphology and ontogeny the Emuellidae is at the present considered best placed within the Suborder Redlichiina. It is considered that at some later date it may be separated as a separate suborder or at least accorded superfamilial rank.

## EVOLUTION

Studies on the adult morphology and ontogeny of the Emuellidae combined with the stratigraphic evidence support a pattern of successional species (and genera); the sequence being *E. polymera* to *E. dalgarnoi* to *B. flindersi* to *B. dailyi*. At the present however the stratigraphic ranges of the species are not fully known.

It has been suggested that olenellids evolved from a "redlichid" ancestor possessing a ptychoparid sutural pattern (Hupé 1953a; Harrington 1959). The Emuellidae combine these cephalic features with possession of a long multi-segmented thorax, macropleurality and division of the thorax, a combination of thoracic features shared only by some of the Olenellidae. Although the Emuellidae are too high in the Lower Cambrian to be the ancestors to the Olenellidae they are considered to have preserved their structure, i.e. are structural relics of the ancestors of the Olenellidae. The Olenellidae are thus considered to have evolved from an "emuellid" type ancestor by migration and eventual loss of the facial suture, but preserving in most cases the essential features of the thorax.

Members of the Redlichiina on the other hand have probably evolved from the same stock by preservation of the sutural pattern, reduction of the frontal glabellar lobe, development of the preglabellar field, and loss of the opisthothorax; the latter also occurring in some of the more advanced members of the Olenellina.

The Bathynotina have advanced a further step by migration of the sutures leading to the loss of the rostral plate; whether the bathynotids evolved directly from the emuellid stock or from a basic redlichid stock is a matter for conjecture. The ontogenies of these various groups appear to support an evolutionary scheme with the emuellid stock at the base.

## FUNCTIONAL MORPHOLOGY

### (a) Division of the thorax.

This feature of the thorax is examined for the first time on a mechanical basis. It is considered that inability to stabilize the composition of the thorax is a primitive character, but initiation of the division is mechanical, being due to a reduction at some stage in the space available for the development of the pleurae of succeeding segments, considering the mechanics of articulation. Such a reduction may be sudden, due to a macropleural segment e.g. Emuellidae, Neltnerinae, or gradual, due to a progressive inclination of pleurae toward the posterior which reaches a critical point of space reduction, e.g. Olenellidae, Fallotaspidae. The length of the opisthothorax of the Emuellidae is controlled by the relative widths of the first opisthothorax segment and the pygidium, and the attainment of a graded condition of the opisthothorax. This appears to be supported by perfect gradation within the opisthothorax throughout ontogeny, and the fact that the cephalon attains the holaspid condition before segmentation ceases, i.e. before the conditions stated above have been fulfilled.

The suggestion that the prothorax is homologous to the normal thorax of the trilobites, and the opisthothorax is homologous to the pygidium, while perhaps having some validity in several cases, is an inaccurate expression or interpretation of the phenomen when applied to the Emuellidae.

(b) Macropleurality

The fact that the macropleural spine extends to the base of the pygidium from its initial appearance to the holaspid condition, strongly suggests that it serves to balance and protect the opisthothorax. Hupé's suggestion (1950) that macropleurae have a secondary sexual meaning, representing the segments carrying the gonopores, is considered unlikely. However the functional explanation given above may not necessarily explain the primary causes of the appearance of the macropleurae, even in the Emuellidae, and in this regard Raw's concept of merocyclism may possibly have some validity.

### (c) Fusion of segments

This feature which is found in only one other trilobite Bathynotellus, is considered to be due to the necessity of having strong muscles controlling movements on the long macropleural spine. The fusion of the two segments allows the apodemal slit to be extended onto the pleural field and to abut against the adaxial end of the pleural furrow, thus providing a larger area for muscle attachment. The fusion of segments in Bathynotellus appears to result from an entirely different cause, i.e. is convergent.

## SEGMENTATION

### (a) Primary and secondary segmentation

In the light of evidence from the adult morphology and ontogeny of the thorax in the Emuellidae, and the suggested homology of the cheek furrows with the posterior cephalic border in larval stages, Størmer's theory of secondary segmentation of the pleural regions, is considered unnecessary and unlikely. Hessler's defence of this theory is based on highly developed carboniferous trilobites, and the feature on which he bases the defence is probably secondary.

### (b) Asexual reproduction.

Lemche's hypothesis of asexual budding, based on the presence of an opisthothorax in some trilobites is rejected, both on the grounds of detailed examination of portion of his evidence, and in the light of that provided by study of the Emuellidae.

### (c) Merocyclism.

The concept of merocyclism as defined by Raw (1953) may have some validity when applied to some Lower Cambrian trilobites. However it does not appear to explain the distribution of macropleural segments in some Lower Cambrian and in all post Cambrian trilobites, or to be regular enough to be used in determinations of the number of primary cephalic segments (Palmer 1957).

### (d) Primary segmentation of the cephalon.

The protaspids and early meraspids of the Emuellidae show an extra anterior glabellar furrow aligned with the anterior edge of the eye ridge, suggesting at least six primary dorsal segments in the cephalon. The cheek furrows of these stages are considered to be intersegmentary and homologous with the furrows bounding the eye ridge, and the joints between the cephalon and thorax, and the thoracic segments. The posterior border furrow, which develops as such in the middle meraspid period is considered intrasegmentary and homologous to the pleural furrows.

## (3) Teratology.

A teratological specimen with disruption of segmentation for portion of the opisthothorax is described; it is concluded that the disruption was due to an injury to a larval specimen at or not later than meraspid degree 15, in which the transitory pygidium contained at least eight segments; the injury affecting the left hand side of the latter segments as well as the thoracic segments.

### (f) Analysis of growth.

Two aspects of growth are studied in B. flindersi, the rate of growth and allometric growth.

Study of the larval specimens allows the calculation of the geometric growth increment and the geometric rate of increase for successive meraspid degrees; the results strongly suggest that Dyar's Law does not hold in this case, there being a significant decrease in the increment after about the 19th meraspid degree, and a decrease in the geometric rate of increase.

The simple allometric equation is applied to two samples of larval specimens, one to allow estimation of the parameters for allometry of growth of the "average" B. flindersi, the other to allow estimation for allometry of size.

Allometric growth of the length of the palpebral ridge with respect to the cranidial length during the early meraspid degrees, is demonstrated. The data for allometry of growth shows a distinct change in the growth pattern of the cranidium at meraspid degree 6; below this a value of $\alpha$ of 2.79 indicates allometric growth, above this it is probable that isometric growth occurred. Deviations from simple allometry, both of size and growth occur.

## APPENDIX I

The dimensions of the exoskeleton which have been measured on members of the Emuellidae are listed below, and shown on Text Figures 4 & 7. Most of these dimensions have been previously defined and standardized by Shaw (1957). However, in the case of the librigenae, thorax and hypostome, additional measurements are necessary, and these are listed below. Not all of the listed dimensions have been utilized in the analysis, and the measurements are therefore not listed in either the Tables or the Appendices.

(a) Cranidium

Total cranidial length ($A_1$)
Total glabellar length ($B_1$)
Sagittal width of the cranidial border (E)
Sagittal width of the occipital lobe (G)
Exsagittal palpebral length (C)
Occipital post-palpebral distance ($D_5$)
Palpebral cranidial width (J)
Transverse occipital length (K)
Palpebral glabellar width ($K_1$)
Maximum glabellar width ($K_2$)

(b) Librigena

Exsagittal ~~cranidial~~ length (C)
Palpebral width of the genal field ($F_1$)
Lateral border width ($F_2$)
Length of the anterior portion of the librigenal doublure ($F_3$)
Genal field length ($F_4$)

Length of the posterior portion of the genal field ($F_5$)

Posterior border width ($F_6$)

(c) <u>Thoracic segment</u>

Transverse length of axial lobe ($R_n$)

Axial sagittal width of axial ring ($Q_n$)

Transverse pleural length ($R_p$)

(d) <u>Macropleural unit</u>

Transverse length of the macropleural unit ($R_m$)

Axial sagittal width of the macropleural unit ($Q_m$)

Transverse pleural length ($R_{p_8}$)

Distance to point of geniculation of the pleurae ($R_{p_6}$)

Length of the genal spine (M)

(e) <u>Hypostome</u>

Hypostomal length ($H_1$)

Distance (sag.) to anterior wing ($H_2$)

Distance to lateral notch ($H_3$)

Length of posterior lobe of the median body ($H_4$)

Length of the posterior border ($H_5$)

Maximum width of the posterior lobe of the median body ($H_6$)

Maximum width of posterior section of the hypostome ($H_7$)

Length (transverse) of the hypostomal suture ($H_8$)

Distance between the anterior wings (maximum width of anterior section of hypostome) ($H_9$)

(f) Thorax

Axial length of the prothorax ($Q_{pt}$)

Axial length of the opisthothorax ($Q_{ot}$)

Axial length of the transitory pygidium ($Q_{tp}$)

Total axial length of the thorax and the pygidium ($Q_t$)

## APPENDIX II

(1) Measurements of selected dimensions of larval specimens of the Emuellidae. Only those dimensions used or mentioned in the text are given. All measurements given as micrometer dimensions where 1.00 mms. = 32 divisions.

| $A_1$ | C | $D_5$ | J | K | $K_2$(R) | $Q_1$ | $Q_m$ | $R_1$ | $R_m$ | $Q_{pt}$ | $Q_{ot}$ | $Q_{tp}$ | $Q_t$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 12 | | | 12 | | | | | | | | | | |
| 13 | | | 13 | | | | | | | | | | |
| 13 | | | 13 | | | | | | | | | | |
| 16 | | | 15 | | | | | | | | | | |
| 16 | 2 | | 16 | 4 | 7 | | | | | | | | |
| 16 | 3? | | 18 | 5 | 10 | | | | | | | | |
| 17 | | | 21 | | | 1 | | 5 | | | | 8 | 8 |
| 17 | 2 | | 19 | 5 | | 2 | | 5 | | | | 7 | 7 |
| 17 | | | 16 | 5 | 7 | | | | | | | | |
| 17 | 3 | 7 | 18 | 5 | | | | | | | | | |
| 18 | 3 | 8 | 22 | 6 | | | | | | | | | |
| 18 | 3 | 7 | 21 | 6 | 10 | | | | | | | | |
| 18 | | | 18 | 6 | 9 | | | | | | | | |
| 18 | 3 | 6 | 19 | 7 | 10 | | | | | | | | |
| 19 | 2 | 12 | 19 | 6 | 12 | | | | | | | | |
| 19 | 3 | 9 | 21 | 6 | 10 | | | | | | | | |
| 19 | 3.5 | 9 | 18 | 6 | | | | | | | | | |
| 19 | | | 20 | 7 | 9 | | | | | | | | |
| 20 | 2.5 | 9 | 22 | | | 2 | | 6 | | 2 | | 8 | 10 |
| 20 | 4 | 8 | 20 | 6 | 9 | | | | | | | | |
| 20 | 5 | 8 | 21 | 6 | 11 | | | | | | | | |
| 20 | | | 17 | 6 | 12 | | | | | | | | |
| 20 | 3 | 7 | 21 | 6 | 10 | | | | | | | | |
| 20 | | | 20 | 5 | 8 | | | | | | | | |
| 20 | | | | 7 | 11 | | | | | | | | |
| 20 | | | 21 | 5 | | | | | | | | | |
| 20 | | | | 5 | | | | | | | | | |
| 21 | 4 | 7.5 | 22 | 7 | | | | | | | | | |
| 21 | | | 21 | 6 | 10 | | | | | | | | |
| 21 | 5 | 7 | 21 | 7 | 9 | | | | | | | | |
| 21 | 4 | 6? | 23 | 6 | 12 | 2 | | | | | | | |
| 21 | 3 | 9 | | | | 2 | | 7 | | 2 | | 8 | 10 |
| 22 | 5 | 7 | 24 | 7 | 9 | | | | | | | | |
| 22 | 4 | 7 | 23 | 6 | 12 | | | | | | | | |
| 22 | | | 25 | 7 | 13 | | | | | | | | |
| 23 | | | 23 | | | | | | | | | | |
| 23 | | | 25 | 8 | 14 | | | | | | | | |

| $A_1$ | C | $D_5$ | J | K | $K_2(R)$ | $Q_1$ | $Q_m$ | $R_1$ | $R_m$ | $Q_{pt}$ | $Q_{ot}$ | $Q_{tp}$ | $Q_t$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 23 | 5 | 8 | 24 | 10 | 12 | | | | | | | | |
| 23 | 6 | 8 | 22 | 6 | | | | | | | | | |
| 23 | | | 27 | 7 | 12 | | | | | | | | |
| 23 | 5 | 8 | 26 | 8 | 14 | | | | | | | | |
| 23 | | | 25 | 8 | 12 | | | | | | | | |
| 24 | | | | | | 2.5 | | | 5 | 6.5 | | 8.5 | 15 |
| 24 | | | 25 | 7 | 10 | | | | | | | | |
| 24 | 6 | 9 | 24 | 7 | 13 | | | | | | | | |
| 24 | 4 | 12 | 30 | | 15 | | | | | | | | |
| 24 | 6 | 7 | 25 | 8 | 14 | | | | | | | | |
| 24 | 5 | 8 | 28 | 9 | 12 | | | | | | | | |
| 24 | 5 | 8 | 26 | 7 | | | | | | | | | |
| 24 | 5 | 6 | 23 | 7 | | | | | | | | | |
| 24 | 5 | 7 | 24 | 7 | | | | | | | | | |
| 25 | 5 | 6 | 25 | 8 | | | | | | 6 | | 7 | 13 |
| 25 | 6 | 8 | 30 | 10 | 15 | | | | | 9 | | 6 | 15 |
| 25 | 5 | 10 | 24 | 8 | 12 | | | | | | | | |
| 25 | 5 | 8 | 28 | 9 | 15 | | | | | | | | |
| 25 | 5? | 13? | 28 | 8 | 13 | | | | | | | | |
| 25 | 5 | 8 | 25 | 7 | 12 | | | | | | | | |
| 26 | 6 | 11 | 31 | 10 | 15 | | | 9 | | 10 | | | |
| 26 | 6 | 9 | 28 | 9 | 13 | | | | | 7 | | 5 | 12 |
| 26 | | | 31 | 10 | 15 | | | | | | | | |
| 26 | 6 | 10 | 31 | 10 | 13 | | | | | | | | |
| 26 | 6 | 8 | 26 | 9 | 12 | | | | | | | | |
| 26 | 8 | 8 | 30 | 9 | 14 | | | | | | | | |
| 27 | 6 | 9 | 28 | 9 | | 2 | | | | 11 | | 5? | 16 |
| 27 | 7 | 10 | 31 | 9 | 15 | 2.5 | | 8 | 5 | 13 | | 5 | 18 |
| 27 | 6 | 10 | 29 | 10 | 13 | | | | | | | | |
| 27 | 6 | 9 | 28 | 9 | 13 | | | | | | | | |
| 27 | 7 | 8 | 31 | 10 | 17 | | | | | | | | |
| 27 | 6 | 8 | 28 | 9 | 15 | | | | | | | | |
| 27 | 6 | 13 | 30 | 9 | 15 | | | | | | | | |
| 27 | 7 | 12 | 29 | 10 | 14 | | | | | | | | |
| 27 | 6 | 9 | | | | | | | | 7 | | 8 | 15 |
| 28 | | | 30 | 9 | | | | | | | | | |
| 28 | 9 | 18 | 30 | 9 | 14 | | | | | | | | |
| 28 | 6 | 10 | 25 | 8 | 12 | | | | | | | | |
| 28 | 8 | 9 | 30 | 12 | 16 | 3 | | 13 | 6 | 15 | | 5 | 20 |
| 28 | 7 | 8 | | | | 3 | 10 | 4.5 | 7 | 14 | | 10 | 24 |
| 30 | 10 | 8 | 36 | 11 | | 3 | 5 | 11 | 7 | 15 | | 8? | 23? |
| 30 | 8 | 9 | 32 | 10 | 16 | | | | | | | | |
| 30 | 6 | 15 | 35 | 9 | 16 | | | | | | | | |
| 30 | 7 | 7 | 32 | 10 | 18 | | | | | | | | |
| 30 | 8 | 10 | 30 | 10 | 17 | | | | | | | | |
| 30 | 7 | 10 | 34 | 11 | 16 | | | | | | | | |
| 30 | 11 | 9 | 37 | 10 | 16 | | | | | | | | |

| $A_1$ | C | $D_5$ | J | K | $K_2$(R) | $Q_1$ | $Q_m$ | $R_1$ | $R_m$ | $Q_{pt}$ | $Q_{ot}$ | $Q_{tp}$ | $Q_t$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 30 | 8 | 8 | 30 | 9 | 16 | | | | | | | | |
| 30 | 7 | 12 | 35 | 10 | 16 | | | | | | | | |
| 30 | 8 | 10 | 33 | 10 | 17 | | | | | | | | |
| 30 | 8 | 13 | 35 | 9 | 16 | | | | | | | | |
| 31 | 7 | 10 | | | | | | | | 13 | 1 | 6 | 20 |
| 31 | | | 34 | 11 | 18 | | | | | | | | |
| 31 | 8 | 10 | 33 | 11 | 16 | | | | | | | | |
| 31 | 8 | 8 | 31 | 8 | 19 | | | | | | | | |
| 32 | 7 | 9 | 33 | 11 | 17 | | | | | | | | |
| 32 | 7 | 14 | 34 | 12 | 17 | | | | | | | | |
| 34 | 9 | 11 | 36 | 11 | 17 | | | | | | | | |
| 34 | 9 | | 40 | 12 | 21 | | | | | | | | |
| 34 | 11 | 8 | | | | 3 | 5 | 13 | 8 | 18 | | 5? | 23 |
| 34 | 12 | 10 | 45 | 15 | | | | | | 20 | 8 | 7 | 35 |
| 35 | | | 37 | 13 | 21 | | | | | | | | |
| 35 | 9 | | 36 | 11 | 20 | | | | | | | | |
| 35 | 10 | 10 | 36 | 12 | - | | | | | | | | |
| 35 | 8 | 10 | 37 | 12 | 21 | | | | | | | | |
| 35 | 9 | 10.5 | 39 | 13 | 20 | | | | | | | | |
| 36 | 12 | 11 | 45 | 15 | - | | | | | | | | |
| 36 | 11 | 11 | 42 | 13 | 20 | | | | | | | | |
| 37 | 10 | 15 | 42 | 15 | 21 | | | | | | | | |
| 38 | 12 | 12 | 49 | 16 | 15 | 4 | 6 | 15 | 10 | 20 | 9 | 7 | 36 |
| 38 | | | 40 | 13 | 21 | | | | | | | | |
| 38 | 10 | 13 | 40 | 13 | 22 | | | | | | | | |
| 40 | 11 | 24 | 44 | 15 | 22 | | | | | | | | |
| 42 | 12 | 12 | 45 | 17 | 25 | 4 | 7 | 18 | 11 | 25 | 10+ | | |
| 43 | 11 | 11 | 45 | 16 | 22 | | | | | | | | |
| 43 | 13 | 13 | 45 | 16 | 24 | | | | | | | | |
| 44 | 14 | | 48 | 17 | 26 | | | | | | | | |
| 44 | 12 | 12 | 40 | 13 | 20 | | | | | | | | |
| 45 | 11 | 26 | 52 | 18 | 28 | | | | | | | | |
| 45 | 15 | 12 | 54 | 18 | 29 | 5 | | 19 | | | | | |
| 45 | 13 | 11 | 56 | 21 | 29 | | | | | | | | |
| 47 | 14 | 16 | 56 | 20 | 28 | | | | | | | | |
| 47 | 14 | 14 | 52 | 18 | 29 | | | | | | | | |
| 48 | 15 | | 60 | 19 | 30 | | | | | | | | |
| 48 | | | 53 | 17 | 24 | | | | | | | | |
| 54 | 16 | 13 | 61 | 21 | 30 | | | | | | | | |
| 55 | 18 | 20 | 64 | 25 | 32 | | | | | | | | |
| 57 | 18 | 17 | 55 | 21 | 26 | | | | | | | | |
| 57 | 16 | 15 | | | | 6 | 12 | 22 | 19 | 33 | 32 | + | |
| 67 | 16 | 19 | 83 | 29 | 32 | | | | | | | | |
| 67 | 21 | 15 | 80 | 32 | 40 | 11 | 12 | 32 | 22 | | | | |
| 72 | 20 | 16 | 91 | 32 | 39 | 8 | 13 | 34 | 21 | 38 | 40 | 8 | 86 |
| 72 | 18 | 15 | 83 | 40 | - | 10 | 13 | 37 | 25 | 52 | 44 | 9 | 105 |
| 80 | 19 | | 88 | 35 | 48 | 11 | 16 | 35 | 27 | 1 | | | |
| 101 | 30 | | | | | 16 | 23 | 59 | 37 | 74 | 124 | 8 | 206 |

(2) Measurements of larval specimens of <u>B. dailyi</u>.

| $A_1$ | C | J | K | $K_2$ | $Q_1$ | $Q_m$ | $R_1$ | $R_m$ | $Q_{pt}$ | $Q_{ot}$ | $Q_{tp}$ | $Q_{tot}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 18 | 2 | 19 | 5 | 8 | | | | | | | | |
| 19 | 5 | 23 | 7 | 13 | | | | | | | | |
| 20 | 3 | 21 | 6 | 10 | | | | | | | | |
| 21 | | 23 | 7 | 12 | | | | | | | | |
| 23 | | 21 | 7 | 14 | | | | | | | | |
| 23 | 6 | - | 10 | 15 | | | | | | | | |
| 25 | 5 | 26 | 8 | 18 | | | | | | | | |
| 25 | | 30 | 7 | 18 | | | | | | | | |
| 27 | 5 | 29 | 8 | 18 | | | | | | | | |
| 28 | | 28 | 9 | 18 | | | | | | | | |
| 35 | 10 | 43 | 15 | 22 | | | | | | | | |
| 35 | 11 | 36 | 13 | 18 | | | | | | | | |
| 36 | 12 | 41 | 12 | 20 | | | | | | | | |
| 38 | | 48 | 19 | 22 | | | | | | | | |
| 38 | | 39 | | 24 | - | - | 15 | 9 | 18 | - | 11 | 29 |
| 40 | | | | | | | 15 | 8 | 22 | - | 10 | 32 |
| 40 | | 39 | 10 | - | 3 | 5 | 15 | 8 | 20 | - | 9 | 29 |
| 41 | | | | 24 | | | | | | | | |
| 43 | 13 | | 13 | 25 | | | | | | | | |
| 44 | | | | 28 | 4 | 6 | 17 | 10 | 25 | - | 10 | 35 |
| 45 | | 46 | 19 | 26 | 4 | 6 | 17 | 10 | 25 | 10 | 10 | 45 |
| 46 | 15 | 55 | 23 | | | | | | | | | |
| 46 | 13 | 48 | 16 | 30 | | | | | | | | |
| 46 | | | | | | | 23 | 15 | 27 | 16 | 11 | 54 |
| 48 | | | | 28 | | | | | | | | |
| 48 | 16 | 55 | 20 | 33 | | | | | | | | |
| 48 | 19 | 56 | 21 | 30+ | | | | | | | | |
| 48 | 11+ | 51 | 21 | 30+ | 6 | - | 20 | 13 | 23 | 11 | 11 | 45 |
| 48 | | | | | 4 | - | 24 | 13 | 27 | 21 | 8 | 56 |
| 50 | 20 | 60? | 20 | - | 5 | - | 20 | 12 | 30 | 20 | 10 | 60 |
| 53 | 15? | 52 | 21 | - | 8 | 11 | 21 | 16 | 40 | 38 | 8 | 86 |
| 54 | 16 | 67 | 27 | 38 | 7 | 10 | 26 | 18 | 32 | 25 | 8 | 65 |
| 61 | | 80 | | | 8 | 13 | 32 | 21 | 42 | 37 | 61 | 90 |
| 61 | 19 | 61 | 27 | - | | | | | | | | |
| 67 | 27 | 74 | 24 | - | | | | | | | | |
| 69 | 27 | 80 | 32 | 35 | | | | | | | | |
| 69 | 26 | 83 | 34 | 40 | | | | | | | | |
| 72 | 26 | 88 | 40 | - | | | | | | | | |
| 75 | 26 | 80 | 26 | | 8 | 13 | 27 | 19 | 45 | 50 | 10 | 105 |
| 75 | 25 | 98 | 40 | | | | 40 | 30 | 55 | 76 | 8 | 139 |
| 75 | 24 | 99 | 40 | 40 | | | | | | | | |
| 93 | 26 | 104 | 45 | | | | | | | | | |
| 93 | | 112 | 45 | | 13 | 24 | 53 | 40 | 77 | 97 | 5 | 176 |
| 107 | 32 | 119 | 56 | 48 | 13 | 24 | 53 | 40 | 80 | 137 | 13 | 230 |
| 115 | 35 | 98 | 48 | | 1 | | 48 | 35 | 85 | 123 | 9 | 217 |

(3) Measurements of larval specimens of *E. polymera*

| A | C | J | K | $K_2$ |
|---|---|---|---|---|
| 12.8 | - | 14 | 3 | - |
| 17 | 4 | 22 | 6 | - |
| 22 | 5 | 24 | 7 | 9 |
| 26 | 4 | 26 | 8 | 13 |
| 27 | 5 | 25 | 11 | 10 |
| 29 | 6 | 30 | 10 | 14 |
| 30 | 5 | 31 | 9 | 16 |
| 32 | 5 | 40 | 11 | - |
| 32 | 6 | 28 | 8 | - |
| 43 | 6 | 48 | 16 | 21 |
| 45 | - | - | - | - |
| 57 | 13 | 80 | 27 | - |

# APPENDIX III

Measurements of selected dimensions of adult specimens of the Emuellidae. Only those dimensions are given which are used in calculation or referred to in the text. All measurements given as micrometer divisions where 1 mm. = 12 divisions.

(1) Adults of *E. polymera*

| $A_1$ | C | $D_5$ | J | K | $K_2$ |
|---|---|---|---|---|---|
| 16 | 2 | 6 | 18 | 6 | 8 |
| 22 | 5 | 7 | 32 | 10 | |
| 26 | 6 | 8 | 32 | 13 | 14 |
| 26 | 5 | 8 | 34 | 14 | 12 |
| 30 | 6 | 10 | 36 | 16 | 15 |
| 31 | 7 | 11 | 36 | 15 | 15 |
| 32 | 7 | 11 | 43 | 17 | 18 |
| 34 | 7 | 13 | 36 | 18 | 14 |
| 37 | 8 | 10 | 43 | 20 | 18 |
| 35 | 6 | 12 | 42 | 18 | 18 |
| 37 | 8 | 12 | 39 | 17 | |
| 38 | 7 | 15 | 36 | 17 | 15 |
| 39 | 7 | 13 | 39 | 16 | 15 |
| 40 | 8 | 14 | 50 | 23 | 20 |
| 40 | 8 | 13 | | | |
| 43 | 8 | 14 | 40 | 16 | |
| 43 | 9 | 14 | 44 | 18 | 18 |
| 45 | 10 | 13 | 51 | 25 | 24 |
| 46 | 10 | 15 | 46 | 21 | 21 |
| 46 | 10 | 16 | 48 | 21 | 20 |
| 47 | 10 | 15 | | | |
| 47 | 8 | 14 | 60 | 28 | 25 |
| 51 | 10 | 20 | 46 | 30 | 25 |
| 52 | 11 | 16 | | | |
| 55 | 12 | 20 | 60 | 27 | 23 |
| 58 | 10 | 20 | 58 | 25 | 24 |
| 60 | 13 | 20 | 63 | 28 | 25 |
| 60 | 11 | 20 | 60 | 25 | |
| 73 | 15 | 23 | 64 | 30 | |
| 75 | 14 | 25 | 74 | 35 | 32 |
| 82 | 14 | 26 | 82 | 36 | 36 |
| 86 | 18 | 28 | 80 | 40 | 32 |
| 88 | 16 | 30 | 80 | 40 | 40 |
| 102 | 20 | 32 | 128 | 60 | 54 |
| 90 | 12 | 30 | 80 | 40 | 40 |

(2) Adults of *E. dalgarnoi*.

| $A_1$ | C | $D_5$ | J | K | $K_2$ |
|---|---|---|---|---|---|
| 35 | 7.5 | 9 | 34 | 15 | |
| 35 | 7.5 | 9.5 | 38 | 17 | 16 |
| 45 | 11 | 14 | 52 | 22 | - |
| 44 | 12 | 15 | 53 | 25 | 24 |
| 48 | 12 | 16 | 54 | 24 | 26 |
| 51 | 13 | 16 | 55 | 28 | 23 |
| 55 | 13 | 12 | - | 28 | |
| 66 | 16 | 21 | 75 | 35 | 30 |
| 70 | 18 | 20 | 80 | 34 | 36 |
| 76 | 18 | 24 | 88 | 50 | 48 |
| 106 | 22 | 38 | 96 | 44 | 48 |
| 34 | 8 | 10 | 40 | 20 | 20 |

(3) Adults of *B. flindersi*.

| $A_1$ | C | $D_5$ | J | K | $K_2$ |
|---|---|---|---|---|---|
| 23 | 5 | 5.5 | 27 | 11 | 12 |
| 25 | 6 | 6 | 26 | 9 | 7 |
| 31 | 8 | 10 | 34 | 12 | 17 |
| 32 | 8 | 8 | 37 | 16 | 15 |
| 33 | 8 | 9 | 38 | 15 | 16 |
| 33 | 8 | 12 | 40 | 14 | 15 |
| 40 | 10 | 9 | 48 | 20 | 20 |
| 44 | 10 | 13 | 52 | 22 | 22 |
| 44 | - | - | 52 | 20 | 24 |
| 48 | 12 | 14 | 44 | 20 | - |
| 48 | 14 | 13 | 54 | 20 | 20 |
| 50 | 11 | 12 | 53 | 23 | 23 |
| 50 | - | - | 62 | 24 | 26 |
| 50 | 12 | 16 | 52 | 26 | 26 |
| 54 | 14 | 13 | 66 | 32 | 34 |
| 56 | 16 | 14 | 72 | 26 | 26 |
| 56 | 14 | 9 | 64 | 26 | 28 |
| 56 | 12 | 14 | 64 | 28 | 30 |
| 58 | 16 | 14 | 64 | 28 | 30 |
| 60 | 14 | 19 | 74 | 28 | 30 |
| 60 | 15 | 15 | 65 | 25 | 30 |
| 60 | 14 | 14 | 68 | 26 | 28 |
| 60 | 14 | 19 | 64 | 28 | 30 |
| 60 | 14 | 13 | 72 | 30 | 32 |
| 70 | 18 | 19 | 94 | 40 | 44 |
| 72 | 14 | 14 | 76 | 36 | 36 |
| 72 | 20 | 18 | 86 | 32 | 34 |
| 72 | | | 78 | 36 | 36 |
| 74 | 16 | 22 | 110 | 40 | 40 |
| 76 | 18 | 26 | 90 | 40 | 40 |

| $A_1$ | C | $D_5$ | J | K | $K_2$ |
|---|---|---|---|---|---|
| 76 | 16 | 20 | 82 | 38 | 38 |
| 78 | 18 | 17 | 86 | 40 | 38 |
| 80 | 16 | 26 | 94 | 40 | 44 |
| 80 | - | - | 84 | 36 | 38 |
| 84 | 20 | 24 | 84 | 32 | 38 |

(4) Measurements of adults of *B. dailyi* - Cape D'Estaing sample

| $A_1$ | C | $D_5$ | J | K | $K_2$ | $\alpha$ |
|---|---|---|---|---|---|---|
| 19 | - | | 26 | 10 | 10 | |
| 20 | 7 | 4 | 26 | 10 | 11 | 7.5 |
| 27 | 8 | 4 | 35 | 13 | 14 | 7.5 |
| 31 | 8.5 | 8? | 32 | 13 | 14 | 5 |
| 31 | 11 | 7 | 52 | 20 | 20 | 4 |
| 33 | - | - | 33 | 14 | 14 | |
| 35 | 12 | 8 | 42 | 17 | 17 | 7 |
| 37 | 12 | 8 | 30 | 17 | 17 | 6 |
| 38 | 12 | 7 | 40 | 13 | 12 | 2 |
| 38 | 12 | 7 | 38 | 15 | 16 | 0 |
| 39 | 12 | 6 | 43 | 16 | 17 | $9^{\circ}$ |
| 39 | 12 | 9 | 43 | 17 | 16 | 5 |
| 40 | 12 | 7 | 43 | 15 | 17 | $5^{\circ}$ |
| 40 | 12 | 8 | 49 | 18 | 18 | 3 |
| 40 | 10 | 10 | 40 | 17 | 15 | 4 |
| 43 | 14 | 9 | 60 | 23 | 23 | 0 |
| 43 | 14 | 7 | 60 | 25 | 25 | 7 |
| 44 | 12 | 9 | 43 | 18 | 18 | 7 x 2 |
| 45 | 14 | 9 | 45 | 19 | 17 | $1.5^{\circ}$ |
| 46 | 15 | 8.5 | 46 | 18 | 22 | 5 |
| 47 | 14 | 9 | 47 | 18 | 18 | 9 |
| 48 | 14 | 9 | 67 | 26 | 25 | 3 |
| 48 | 15 | 9 | 50 | 18 | 18 | $4^{\circ}$ |
| 48 | 14 | 10 | 48 | 19 | 20 | $6^{\circ}$ |
| 49 | 14 | 10 | 49 | 18 | 17 | 0 |
| 50 | 17 | 10 | 60 | 26 | 26 | 5 |
| 50 | 15 | 10 | 71 | 29 | 27 | 5 |
| 50 | 14 | 9 | 66 | 30 | 30 | 5 |
| 50 | 15 | 9 | 50 | 21 | 20 | 5 |
| 51 | 12 | 13 | 43 | 18 | 20 | $0^{\circ}$ |
| 51 | 15 | 13 | 51 | 20 | 21 | $3^{\circ}$ |
| 51 | 14 | 8 | 51 | 20 | 20 | 4 |
| 52 | 14 | 9 | - | - | - | 5 |
| 55 | 16 | 11 | 65 | 27 | 27 | 5 |
| 55 | 14 | 10 | 60 | 25 | 25 | $12^{\circ}$ |

| $A_1$ | C | $D_5$ | J | K | $K_2$ | $\propto$ |
|---|---|---|---|---|---|---|
| 52 | 16 | 11 | 66 | 30 | 30 | 10° |
| 53 | 16 | 14 | 56 | 19 | 22 | 1 |
| 55 | 16 | - | | | | 5° |
| 57 | 18 | 10 | 78 | 30 | 27 | 1.5° |
| 57 | 16 | 14 | 57 | 23 | 20 | 4.5° |
| 58 | 16 | 12 | 62 | 27 | 27 | 6° |
| 58 | 17 | 11 | 60 | 20 | 22 | 4° |
| 60 | 14 | 14 | 68 | 30 | 25 | 12° |
| 60 | - | - | 61 | 25 | 24 | 10° |
| 60 | 16 | 15 | 65 | - | - | 1° |
| 60 | 14 | 12 | 60 | 22 | 20 | 4° |
| 64 | - | - | 90 | 40 | 45 | 4° |
| 65 | 18 | 14 | - | 35 | 30 | 6° |
| 66 | 18 | 14 | 68 | 28 | 28 | 1° |
| 70 | 20 | 14 | 72 | 30 | 25 | 5.5 |
| 70 | 20 | 15 | 76 | 30 | 32 | 6° |
| 72 | 20 | 14 | 100 | 40 | 45 | 2° |
| 73 | 20 | 15 | 100 | 40 | 32 | 5 |
| 75 | 19 | 12 | 96 | 37 | 40 | 5 |
| 76 | 20 | 16 | 86 | 34 | 32 | 4° |
| 76 | 22 | 18 | 82 | 34 | 30 | 4° |
| 76 | 22 | 16 | 86 | 42 | 36 | 5 |
| 78 | 21 | 20 | 90 | 38 | 30 | 3° |
| 80 | 19 | - | 80 | 33 | 30 | 5 |
| 80 | 22 | 22 | 84 | 35 | 33 | 12° |
| 82 | 24 | 16 | 108 | 48 | 44 | 5 |
| 88 | 24 | 18 | 86 | 36 | 36 | 5 |
| 90 | 28 | 18 | 90 | 38 | 34 | 1½° |
| 90 | 28 | 18 | 96 | 36 | 34 | 4° |

(5) Measurements of adults of *B. dailyi* - Emu Bay sample

| | | | | | | |
|---|---|---|---|---|---|---|
| 18 | 6 | 3 | 21 | 7 | 9 | 5 |
| 23 | 7 | 6.5 | 27 | 8 | 10 | 5 |
| 25 | 9 | 5.5 | 32 | 10 | 12 | 5 |
| 26 | 8 | 6 | 32 | 11 | 14 | 5 |
| 27 | 8 | 5 | 33 | 11 | 13 | 5 |
| 28 | 9 | 7.5 | 32 | 10 | 12 | 5 |
| 29 | 9 | 6.5 | 36 | 12 | 14 | 5 |
| 30 | 10 | 6 | 37 | 14 | 15 | 5 |
| 30 | 9 | 7.5 | 39 | 14 | 14 | 5° |
| 30 | 10 | 7 | 34 | 12 | 14 | 5° |
| 31 | 8 | 8 | 34 | 11 | 13 | 5° |
| 31 | - | - | 34 | 12 | 13 | 5° |
| 33 | 9 | 8.5 | 41 | 17 | 15 | |
| 34 | 10 | 8 | 43 | 15 | 16 | |
| 35 | 10 | 8 | 44 | 18 | 18 | |

| $A_1$ | C | $D_5$ | J | K | $K_2$ | $\propto$ |
|---|---|---|---|---|---|---|
| 40 | 10 | 9 | 46 | 16 | 20 | |
| 42 | 12 | 12 | 46 | 13 | 17 | |
| 44 | 13 | 11.5 | 54 | 23 | 22 | 5° |
| 44 | 14 | 10 | 50 | 18 | 21 | |
| 45 | 13 | 11 | | 20 | 20 | |
| 45 | 9 | 10.5 | 44 | 17 | 19 | |
| 47 | 14 | 13 | 56 | 21 | 22 | 5 |
| 48 | 14 | 11 | 52 | 17 | | 5 |
| 50 | 15 | 13.5 | 64 | 26 | 22 | |
| 55 | 14 | 15 | - | 22 | 23 | 5° |
| 58 | 15 | 15.5 | 63 | 25 | 23 | |
| 58 | 15 | 14 | 63 | 26 | 26 | |
| 60 | 15 | 14 | 62 | 24 | 23 | 5 |
| 60 | 18 | 16 | 79 | 25 | 25 | 5 |
| 64 | 17 | 16.5 | 68 | 32 | 30 | 5 |
| 64 | 18 | - | 74 | 26 | 34 | |
| 65 | - | - | 74 | 25 | 28 | |
| 67 | 20 | 16 | 86 | 36 | 35 | |
| 68 | 19 | 21 | 71 | 30 | 33 | 5 |
| 70 | 20 | 20 | 78 | 30 | 30 | 5 |
| 70 | 20 | 20 | 88 | 40 | 38 | 5 |
| 72 | 20 | 18 | 88 | 32 | 28 | 5 |
| 76 | 20 | 18 | 88 | 32 | 34 | |
| 76 | 20 | 26 | - | 40 | 36 | 5 |
| 78 | 22 | 17 | 82 | 34 | 34 | 5 |
| 78 | 24 | 16 | 88 | 32 | - | 5 |
| 90 | - | - | 90 | 42 | 42 | 5 |

## APPENDIX IV

Calculations of "best fit" lines. Dimensions in mic. div.

"Best fit" lines calculated by the method given by Simpson, Roe & Lewontin (1960 p.234). (12 mic. div. = 1.00 mms.)

CALCULATION 1 (a) Adults of *E. polymera*. $A_1$ the cranidial length, against C the palpebral length and $D_5$ the occipital mid palpebral length.

| | $A_1$ | C | $D_5$ | |
|---|---|---|---|---|
| | 22 | 5 | 7 | |
| | 26 | 6 | 8 | |
| | 26 | 5 | 8 | |
| Group 1. | 30 | 6 | 10 | $_1\bar{A}_1 = 31.3$ |
| | 31 | 7 | 11 | |
| 10 individuals | 32 | 7 | 11 | $_1\bar{C} = 6.4$ |
| | 35 | 6 | 12 | |
| | 36 | 7 | 13 | $_1\bar{D}_5 = 10.7$ |
| | 37 | 8 | 12 | |
| | 38 | 7 | 15 | |
| | 39 | 7 | 13 | |
| | 40 | 8 | 14 | |
| | 40 | 8 | 13 | |
| | 43 | 8 | 14 | |
| | 43 | 9 | 14 | |
| Group 2. | 45 | 10 | 13 | |
| | 46 | 10 | 15 | |
| 11 individuals | 46 | 10 | 15 | |
| | 47 | 10 | 15 | |
| | 47 | 8 | 14 | |
| | 51 | 10 | 20 | |
| | 52 | 11 | 16 | |
| | 55 | 12 | 20 | |
| | 58 | 10 | 20 | |
| Group 3. | 60 | 13 | 20 | $_3\bar{A}_1 = 68.9$ |
| | 60 | 11 | 20 | |
| 10 individuals | 73 | 15 | 23 | $_3\bar{C} = 13.4$ |
| | 75 | 14 | 25 | |
| | 82 | 14 | 26 | $_3\bar{D}_5 = 22.8$ |
| | 86 | 18 | 28 | |
| | 88 | 16 | 30 | |

$\bar{A}_1 = 48.0$ $\quad {}_1\bar{A}_1 = 31.3$ $\quad {}_3\bar{A}_1 = 68.9$

$\bar{C} = 9.6$ $\quad {}_1\bar{C} = 6.4$ $\quad {}_3\bar{C} = 13.4$

$\bar{D}_5 = 16.0$ $\quad {}_1\bar{D}_5 = 10.7$ $\quad {}_3\bar{D}_5 = 22.8$

(1) $$B = \frac{{}_3\bar{C} - {}_1\bar{C}}{{}_3\bar{A}_1 - {}_1\bar{A}_1} = \frac{13.4 - 6.4}{68.9 - 31.3} = 0.19$$

$$A = \bar{C} - B\ \bar{A}_1 = 9.6 - (0.19)\ (48.0) = 0.5$$

The equation of Bartletts "best fit" line is then

$$\underline{C = 0.5 + 0.19\ A_1}$$

(2) $$B = \frac{{}_3\bar{D}_5 - {}_1\bar{D}_5}{{}_3\bar{A}_1 - {}_1\bar{A}_1} = \frac{22.8 - 10.7}{68.9 - 31.3} = 0.32$$

$$A = \bar{D}_5 - \bar{B}.\ \bar{A}_1 = 16.0 - 0.32.48.0 = 0.6$$

The equation of Bartletts "best fit" line is then

$$\underline{\bar{D}_5 = 0.6 + 0.32\ \bar{A}_1}$$

<u>CALCULATION 1 (b)</u> Adults of <u>E. polymera</u>. J mid palpebral cranidial width against K the occipital width

| | J | K | |
|---|---|---|---|
| | 32 | 10 | |
| | 32 | 13 | |
| | 35 | 14 | |
| Group 1 | 36 | 15 | $\bar{J}_1 = 36.1$ |
| | 36 | 16 | |
| 10 individuals | 36 | 17 | $\bar{K}_1 = 15.2$ |
| | 36 | 18 | |
| | 39 | 16 | |
| | 39 | 17 | |
| | 40 | 16 | |

| | J | K | |
|---|---|---|---|
| Group 2<br>10 individuals | 42 | 17 | |
| | 42 | 18 | |
| | 43 | 20 | |
| | 44 | 18 | |
| | 46 | 21 | |
| | 46 | 30 | |
| | 48 | 21 | |
| | 50 | 23 | |
| | 51 | 25 | |
| | 58 | 25 | |
| Group 3<br>10 individuals | 60 | 27 | $\bar{J}_3 = 71.0$<br>$\bar{K}_3 = 32.7$ |
| | 60 | 28 | |
| | 63 | 28 | |
| | 64 | 30 | |
| | 65 | 25 | |
| | 74 | 35 | |
| | 80 | 40 | |
| | 80 | 40 | |
| | 82 | 36 | |
| | 82 | 38 | |

$\bar{J} = 51.4$ $\bar{J}_1 = 36.1$ $\bar{J}_3 = 71.0$

$\bar{K} = 23.2$ $\bar{K}_1 = 15.2$ $\bar{K}_3 = 32.7$

$$B = \frac{\bar{K}_3 - \bar{K}_1}{\bar{J}_3 - \bar{J}_1} = \frac{32.7 - 15.2}{71.0 - 36.1} = 0.50$$

$A = \bar{K} - B\bar{J} = 23.2 - 0.50.51.4 = -2.5$

The equation of Bartletts "best fit" line is then

$$K = -2.5 + 0.50\,J$$

CALCULATION 2. Adults of *E. dalgarnoi*

(a) $A_1$ cranidial length, against C palpebral length and $D_5$ occipital post palpebral length; J midpalpebral width against K occipital width.

| | $A_1$ | C | $D_5$ | |
|---|---|---|---|---|
| Group 1 | 34 | 8 | 10 | $_1\bar{A}_1 = 37.0$ |
| | 35 | 7.5 | 9 | $_1\bar{C} = 8.8$ |
| 4 individuals | 35 | 7.5 | 9.5 | $_1\bar{D}_5 = 10.9$ |
| | 44 | 12 | 15 | |
| | 45 | 11 | 14 | |
| Group 2 | 48 | 12 | 16 | |
| | 51 | 13 | 16 | |
| 4 individuals | 55 | 13 | 12 | |
| | 66 | 16 | 21 | $_3\bar{A}_1 = 79.3$ |
| Group 3 | 70 | 18 | 20 | |
| | 76 | 18 | 24 | $_3\bar{C} = 18.5$ |
| 4 individuals | 106 | 22 | 38 | |
| | | | | $_3\bar{D}_5 = 25.8$ |

$\bar{A}_1 = 55.3$ $\quad$ $_1\bar{A}_1 = 37.0$ $\quad$ $_3\bar{A}_1 = 79.3$

$\bar{C} = 13.2$ $\quad$ $_1\bar{C} = 8.8$ $\quad$ $_3\bar{C} = 18.5$

$\bar{D}_5 = 17.0$ $\quad$ $_1\bar{D}_5 = 10.9$ $\quad$ $_3\bar{D}_5 = 25.8$

(1) $$B = \frac{_3\bar{C} - {}_1\bar{C}}{_3\bar{A}_1 - {}_1\bar{A}_1} = \frac{18.5 - 8.8}{79.3 - 37.0} = 0.23$$

$A = \bar{C} - B\,\bar{A}_1 = 13.2 - 0.23.55.3 = 0.5$

The equation of Bartletts "Best fit" line is

$$\underline{C = 0.5 + 0.23A_1}$$

(2) $$B = \frac{_3\bar{D}_5 - {}_1\bar{D}_5}{_3\bar{A}_1 - {}_1\bar{A}_1} = \frac{25.8 - 10.9}{79.3 - 37.0} = 0.35$$

$B = \bar{D}_5 - B\,\bar{A}_1 = 17.0 - 0.35.55.3 = -2.4$

The equation of Bartletts "best fit" line is

$$\underline{D_5 = -2.4 + 0.35\,A_1}$$

(b)

| | J | K | |
|---|---|---|---|
| | 34 | 15 | |
| Group 1 | 38 | 17 | ${}_1\bar{J} = 41.0$ |
| 4 individuals | 40 | 20 | |
| | 50 | 22 | ${}_1\bar{K} = 18.5$ |
| Group 2 | 53 | 25 | |
| 3 individuals | 54 | 24 | |
| | 55 | 28 | |
| | 75 | 35 | |
| Group 3 | 80 | 34 | ${}_3\bar{J} = 84.8$ |
| 4 individuals | 88 | 50 | |
| | 90 | 44 | ${}_3\bar{K} = 41.8$ |

$$\bar{J} = 60.5 \qquad {}_1\bar{J} = 41.0 \qquad {}_3\bar{J} = 84.8$$

$$\bar{K} = 28.5 \qquad {}_1\bar{K} = 18.5 \qquad {}_3\bar{K} = 41.8$$

$$B = \frac{{}_3\bar{K} - {}_1\bar{K}}{{}_3\bar{J} - {}_1\bar{J}} = \frac{41.8 - 18.5}{84.8 - 11.0} = 0.53$$

$$A = \bar{K} - B\,\bar{J} = 28.5 - 0.53.60.5 = -3.6$$

The equation of Bartletts "best fit" line is

$$\underline{K = -3.6 + 0.53J}$$

CALCULATION 3. Adults of *B. flindersi* :- variables as above

(a)

| | $A_1$ | C | $D_5$ | |
|---|---|---|---|---|
| | 23 | 5 | 5.5 | |
| | 25 | 6 | 6 | |
| Group 1 | 31 | 8 | 10 | ${}_1\bar{A}_1 = 35.7$ |
| | 32 | 8 | 8 | |
| 10 individuals | 33 | 8 | 9 | ${}_1\bar{C} = 8.9$ |
| | 33 | 8 | 12 | |
| | 40 | 10 | 9 | ${}_1\bar{D}_5 = 9.9$ |
| | 44 | 10 | 13 | |
| | 46 | 12 | 14 | |
| | 48 | 14 | 13 | |

| | $A_1$ | C | $D_5$ | |
|---|---|---|---|---|
| | 50 | 11 | 12 | |
| | 50 | 12 | 16 | |
| | 54 | 14 | 13 | |
| Group 2 | 56 | 12 | 14 | |
| | 56 | 14 | 9 | |
| 10 individuals | 56 | 16 | 14 | |
| | 58 | 16 | 14 | |
| | 60 | 14 | 19 | |
| | 60 | 15 | 15 | |
| | 60 | 14 | 19 | |
| | 60 | 14 | 13 | |
| | 60 | 14 | 14 | |
| | 70 | 18 | 19 | $_3\bar{A}_1 = 71.8$ |
| Group 3 | 72 | 14 | 14 | |
| | 72 | 20 | 18 | $_3\bar{C} = 16.4$ |
| 10 individuals | 74 | 16 | 22 | |
| | 76 | 18 | 26 | $_3\bar{D}_5 = 18.9$ |
| | 76 | 16 | 20 | |
| | 78 | 18 | 17 | |
| | 80 | 16 | 26 | |

$\bar{A}_1 = 54.5$ $\quad {}_1\bar{A}_1 = 35.7$ $\quad {}_3\bar{A}_1 = 71.8$

$\bar{C} = 13.3$ $\quad {}_1\bar{C} = 8.9$ $\quad {}_3\bar{C} = 16.4$

$\bar{D}_5 = 14.4$ $\quad {}_1\bar{D}_5 = 9.9$ $\quad {}_3\bar{D}_5 = 18.9$

(1) $$B = \frac{{}_3\bar{C} - {}_1\bar{C}}{{}_3\bar{A}_1 - {}_1\bar{A}_1} = \frac{16.4 - 8.9}{71.8 - 35.7} = 0.21$$

$$A = \bar{C} - B\,\bar{A}_1 = 13.3 - 0.21.54.5 = 1.8$$

The equation of the "best fit" line is

$$\underline{C = 1.8 + 0.21\,A_1}$$

(2) $$B = \frac{{}_3\bar{D}_5 - {}_1\bar{D}_5}{{}_3\bar{A}_1 - {}_1\bar{A}_1} = \frac{18.9 - 9.9}{71.8 - 35.7} = 0.25$$

$$A = \bar{D}_5 - B\,\bar{A}_1 = 14.4 - 0.25.54.5 = 0.8$$

The equation of the "best fit" line is

$$\underline{D_5 = 0.8 + 0.25A_1}$$

(b)

| | J | K | |
|---|---|---|---|
| | 26 | 9 | |
| | 27 | 11 | |
| | 34 | 12 | |
| Group 1 | 37 | 16 | ${}_1\overline{J} = 39.8$ |
| | 38 | 15 | |
| 10 individuals | 40 | 14 | ${}_1\overline{K} = 16.3$ |
| | 44 | 20 | |
| | 48 | 20 | |
| | 52 | 20 | |
| | 52 | 26 | |
| | 53 | 23 | |
| | 54 | 20 | |
| | 64 | 26 | |
| Group 2 | 64 | 28 | |
| | 64 | 28 | |
| 9 individuals | 66 | 32 | |
| | 68 | 26 | |
| | 72 | 26 | |
| | 72 | 30 | |
| | 74 | 28 | |
| | 76 | 35 | |
| | 78 | 36 | |
| Group 3 | 82 | 38 | ${}_3\overline{J} = 83.4$ |
| | 84 | 32 | |
| 10 individuals | 84 | 36 | ${}_3\overline{K} = 35.7$ |
| | 86 | 32 | |
| | 86 | 40 | |
| | 90 | 40 | |
| | 94 | 40 | |

$\overline{J} = 62.4$ ${}_1\overline{J} = 39.8$ ${}_3\overline{J} = 83.4$

$\overline{K} = 26.2$ ${}_1\overline{K} = 16.3$ ${}_3\overline{K} = 35.7$

$$B = \frac{{}_3\overline{K}_1 - {}_1\overline{K}}{{}_3\overline{J} - {}_1\overline{J}} = \frac{35.7 - 16.3}{83.4 - 39.8} = 0.45$$

$$A = \overline{K} - B\,\overline{J} = 26.2 - 0.45.62.4 = -1.6$$

The equation of the "best fit" line is

$$K = -1.6 + 0.45\,J$$

CALCULATION 4 Adults of *B. flindersi*

(a) Variables $A_1$ & $C_1$

|  | $A_1$ | C |  |
|---|---|---|---|
| Group 1<br>23 individuals | 20 | 7 | $_1\bar{A}_1 = 33.0$<br>$_1\bar{C} = 10.0$ |
|  | 23 | 7 |  |
|  | 25 | 9 |  |
|  | 26 | 8 |  |
|  | 27 | 8 |  |
|  | 28 | 9 |  |
|  | 29 | 9 |  |
|  | 30 | 9 |  |
|  | 30 | 10 |  |
|  | 31 | 8 |  |
|  | 31 | 9 |  |
|  | 32 | 8 |  |
|  | 34 | 10 |  |
|  | 35 | 10 |  |
|  | 35 | 12 |  |
|  | 37 | 12 |  |
|  | 38 | 12 |  |
|  | 39 | 12 |  |
|  | 40 | 10 |  |
|  | 40 | 12 |  |
|  | 42 | 12 |  |
|  | 43 | 14 |  |
|  | 44 | 13 |  |
| Group 2<br>22 individuals | 44 | 14 |  |
|  | 45 | 13 |  |
|  | 45 | 14 |  |
|  | 46 | 15 |  |
|  | 47 | 14 |  |
|  | 48 | 14 |  |
|  | 48 | 15 |  |
|  | 49 | 14 |  |
|  | 50 | 14 |  |
|  | 50 | 15 |  |
|  | 50 | 17 |  |
|  | 51 | 14 |  |
|  | 51 | 15 |  |
|  | 52 | 14 |  |
|  | 52 | 16 |  |
|  | 53 | 16 |  |
|  | 55 | 16 |  |
|  | 57 | 16 |  |

|  | $A_1$ | $C$ |  |
|---|---|---|---|
|  | 57 | 18 |  |
|  | 58 | 15 |  |
|  | 58 | 16 |  |
|  | 58 | 17 |  |
|  | 60 | 15 |  |
|  | 60 | 16 |  |
|  | 60 | 18 |  |
|  | 64 | 17 |  |
|  | 64 | 18 |  |
|  | 65 | 18 |  |
|  | 67 | 20 |  |
|  | 68 | 19 |  |
|  | 70 | 20 |  |
|  | 72 | 20 |  |
| Group 3 | 73 | 20 | ${}_3\bar{A}_1 = 73.1$ |
|  | 75 | 19 |  |
| 23 individuals | 76 | 20 | ${}_3\bar{C} = 20.3$ |
|  | 76 | 22 |  |
|  | 78 | 20 |  |
|  | 78 | 21 |  |
|  | 78 | 22 |  |
|  | 78 | 24 |  |
|  | 80 | 19 |  |
|  | 80 | 22 |  |
|  | 82 | 24 |  |
|  | 88 | 24 |  |
|  | 90 | 28 |  |

$\bar{A}_1 = 52.4$ $\quad {}_1\bar{A}_1 = 33.0$ $\quad {}_3\bar{A}_1 = 73.1$

$\bar{C} = 15.1$ $\quad {}_1\bar{C} = 10.0$ $\quad {}_3\bar{C} = 20.3$

$$B = \frac{{}_3\bar{C} - {}_1\bar{C}}{{}_3\bar{A}_1 - {}_1\bar{A}_1} = \frac{20.3 - 10.0}{73.1 - 33.0} = 0.26$$

$$A = \bar{C} - B\,\bar{A}_1 = 15.1 - 0.26.52.4 = 1.5$$

The equation of the best fit line is

$$\underline{C = 1.5 + 0.26\,A_1}$$

(b) Variables J & K

| | J | K | |
|---|---|---|---|
| Group 1<br>31 individuals | 21 | 7 | $_1\bar{J}$ = 36.1<br>$_1\bar{K}$ = 13.7 |
| | 26 | 10 | |
| | 26 | 10 | |
| | 27 | 8 | |
| | 30 | 17 | |
| | 32 | 10 | |
| | 32 | 11 | |
| | 32 | 12 | |
| | 32 | 13 | |
| | 33 | 11 | |
| | 33 | 14 | |
| | 34 | 11 | |
| | 34 | 12 | |
| | 34 | 12 | |
| | 35 | 13 | |
| | 36 | 12 | |
| | 37 | 14 | |
| | 38 | 15 | |
| | 39 | 14 | |
| | 40 | 13 | |
| | 40 | 17 | |
| | 41 | 17 | |
| | 42 | 17 | |
| | 42 | 18 | |
| | 43 | 18 | |
| | 43 | 17 | |
| | 43 | 16 | |
| | 43 | 15 | |
| | 43 | 15 | |
| | 43 | 17 | |
| | 44 | 18 | |
| Group 2<br>31 individuals | 45 | 19 | |
| | 46 | 13 | |
| | 46 | 16 | |
| | 46 | 18 | |
| | 47 | 18 | |
| | 49 | 18 | |
| | 49 | 18 | |
| | 50 | 18 | |
| | 50 | 18 | |
| | 51 | 20 | |
| | 51 | 20 | |
| | 52 | 17 | |
| | 52 | 20 | |
| | 54 | 23 | |

|  | J | K |  |
|---|---|---|---|
|  | 56 | 19 |  |
|  | 56 | 21 |  |
|  | 57 | 22 |  |
|  | 60 | 20 |  |
|  | 60 | 22 |  |
|  | 60 | 23 |  |
|  | 60 | 25 |  |
|  | 60 | 25 |  |
|  | 60 | 26 |  |
|  | 61 | 25 |  |
|  | 62 | 24 |  |
|  | 62 | 27 |  |
|  | 63 | 28 |  |
|  | 63 | 26 |  |
|  | 64 | 26 |  |
|  | 65 | 27 |  |
|  | 66 | 30 |  |
|  | 66 | 30 |  |
|  | 68 | 28 |  |
|  | 68 | 30 |  |
|  | 68 | 32 |  |
|  | 71 | 29 |  |
|  | 71 | 30 |  |
|  | 72 | 30 |  |
|  | 74 | 26 |  |
|  | 74 | 26 |  |
| Group 3 | 76 | 30 | $_3\overline{J}$ = 31.8 |
|  | 78 | 30 |  |
| 31 individuals | 78 | 30 | $_3\overline{K}$ = 33.2 |
|  | 79 | 25 |  |
|  | 80 | 33 |  |
|  | 83 | 30 |  |
|  | 83 | 34 |  |
|  | 83 | 34 |  |
|  | 84 | 35 |  |
|  | 86 | 34 |  |
|  | 86 | 36 |  |
|  | 86 | 36 |  |
|  | 86 | 42 |  |
|  | 88 | 32 |  |
|  | 88 | 32 |  |
|  | 88 | 40 |  |
|  | 90 | 40 |  |
|  | 90 | 42 |  |
|  | 96 | 36 |  |
|  | 96 | 37 |  |
|  | 100 | 40 |  |
|  | 100 | 40 |  |

$\overline{J} = 57.8 \qquad {}_1\overline{J} = 36.1 \qquad {}_3\overline{J} = 81.8$

$\overline{K} = 22.8 \qquad {}_1\overline{K} = 13.7 \qquad {}_3\overline{K} = 33.2$

$$B = \frac{{}_3\overline{K} - {}_1\overline{K}}{{}_3\overline{J} - {}_1\overline{J}} = \frac{33.2 - 13.7}{81.8 - 36.1} = 0.43$$

$$A = \overline{K} - \overline{J}.B = 22.8 - 0.43.57.8 = -2.1$$

The equation of the "best fit line is

$$\underline{K = -2.1 + 0.43\ J}$$

(c) Adults of <u>B. dailyi</u> - variables $A_1$ & $D_5$

(i) Emu Bay Collection

| | $A_1$ | $D_5$ | |
|---|---|---|---|
| Group 1<br>12 individuals | 23 | 6.5 | ${}_1\overline{A}_1 = 28.8$<br>${}_1\overline{D}_5 = 6.8$ |
| | 25 | 5.5 | |
| | 26 | 6 | |
| | 27 | 5 | |
| | 28 | 7.5 | |
| | 29 | 6.5 | |
| | 30 | 7 | |
| | 30 | 7.5 | |
| | 30 | 6 | |
| | 31 | 8 | |
| | 33 | 8.5 | |
| | 34 | 8 | |
| Group 2<br>12 individuals | 35 | 8 | ${}_2\overline{A}_1 = 48.8$<br>${}_2\overline{D}_5 = 12.4$ |
| | 42 | 12 | |
| | 44 | 11.5 | |
| | 44 | 10 | |
| | 45 | 11 | |
| | 47 | 13 | |
| | 48 | 11 | |
| | 50 | 13.5 | |
| | 55 | 15 | |
| | 58 | 14 | |
| | 58 | 15.5 | |
| | 60 | 14 | |
| Group 3<br>12 individuals | 60 | 16 | ${}_3\overline{A}_1 = 71.4$<br>${}_3\overline{D}_5 = 18.7$ |
| | 64 | 16.5 | |
| | 67 | 16 | |
| | 68 | 21 | |
| | 70 | 20 | |

| $A_1$ | $D_5$ |
|---|---|
| 70 | 20 |
| 72 | 18 |
| 76 | 18 |
| 76 | 26 |
| 78 | 16 |
| 78 | 17 |
| 78 | 20 |

$\bar{A}_1 = 49.7 \qquad {}_1\bar{A}_1 = 28.8 \qquad {}_3\bar{A}_1 = 71.4$

$\bar{D}_5 = 12.6 \qquad {}_1\bar{D}_5 = 6.8 \qquad {}_3\bar{D}_5 = 18.7$

$$B = \frac{{}_3\bar{D}_5 - {}_1\bar{D}_5}{{}_3\bar{A}_1 - {}_1\bar{A}_1} = \frac{18.7 - 6.8}{71.4 - 28.8} = 0.28$$

$$A = \bar{D}_5 - B.\ \bar{A}_1 = 12.6 - 0.28.49.7 = -1.3$$

The equation of the "best fit" line is

$$\underline{\bar{D}_5 = -1.3 + 0.28\ A_1}$$

(ii) Cape D'Estaing Collection

| | $A_1$ | $D_5$ | |
|---|---|---|---|
| Group 1<br>19 individuals | 20 | 4 | ${}_1\bar{A}_1$ = 38.6<br>${}_1\bar{D}_5$ = 7.7 |
| | 27 | 4 | |
| | 31 | 8 | |
| | 35 | 8 | |
| | 37 | 8 | |
| | 38 | 8 | |
| | 38 | 7 | |
| | 38 | 7 | |
| | 39 | 6 | |
| | 39 | 9 | |
| | 40 | 7 | |
| | 40 | 8 | |
| | 40 | 10 | |
| | 43 | 9 | |
| | 43 | 7 | |
| | 45 | 9 | |
| | 46 | 8.5 | |
| | 47 | 9 | |
| | 48 | 9 | |

| | $A_1$ | $D_5$ | |
|---|---|---|---|
| | 48 | 9 | |
| | 48 | 10 | |
| | 49 | 10 | |
| | 50 | 10 | |
| | 50 | 10 | |
| | 50 | 9 | |
| | 50 | 9 | |
| | 51 | 13 | |
| | 51 | 13 | |
| Group 2 | 51 | 8 | $_2\overline{A}_1 = 52.8$ |
| | 52 | 9 | |
| 20 individuals | 52 | 11 | $_2\overline{D}_5 = 10.9$ |
| | 53 | 14 | |
| | 55 | 11 | |
| | 55 | 10 | |
| | 57 | 10 | |
| | 57 | 14 | |
| | 58 | 12 | |
| | 58 | 11 | |
| | 60 | 14 | |
| | 60 | 15 | |
| | 60 | 12 | |
| | 65 | 14 | |
| | 66 | 14 | |
| | 70 | 14 | |
| | 70 | 15 | |
| | 72 | 14 | |
| | 73 | 15 | |
| Group 3 | 75 | 12 | $_3\overline{A}_1 = 75.5$ |
| | 76 | 16 | |
| 19 individuals | 76 | 18 | $_3\overline{D}_5 = 16.1$ |
| | 76 | 16 | |
| | 78 | 21 | |
| | 80 | 22 | |
| | 82 | 16 | |
| | 88 | 18 | |
| | 88 | 18 | |
| | 90 | 18 | |
| | 90 | 18 | |

$\overline{A}_1 = 55.6$ $\quad$ $_1\overline{A}_1 = 38.6$ $\quad$ $_3\overline{A}_1 = 75.5$

$\overline{D}_5 = 11.5$ $\quad$ $_1\overline{D}_5 = 7.76$ $\quad$ $_3\overline{D}_5 = 16.1$

$$B = \frac{{}_3\bar{D}_5 - {}_1\bar{D}_5}{{}_3\bar{A}_1 - {}_1\bar{A}_1} = \frac{16.1 - 7.7}{75.5 - 38.6} = 0.23$$

$$A = \bar{D}_5 - B.\bar{A}_1 = 11.5 - 0.23.55.6 = -1.3$$

The equation of the "best fit" line is

$$\underline{D_5 = -1.3 + 0.23A_1}$$

(iii) Test of significance of the difference between the values of B calculated for the above samples (Simpson, Roe and Lewontin 1960 p.237)

| | (1) <u>Emu Bay</u> | (2) <u>Cape D'Estaing</u> |
|---|---|---|
| $(X-\bar{X})(Y-\bar{Y})$ | 245.8 | 513.2 |
| $(Y-\bar{Y})^2$ | 159.9 | 245.2 |
| | $N = 36$ | $N_1 = 58$ |

(1) Emu Bay

$$\therefore SY^2 = \frac{159.9}{33} = 4.9$$

$$SXY = \frac{245.8}{33} = 7.5$$

(2) Cape D'Estaing

$$SY^2 = \frac{245.2}{55} = 4.5$$

$$SXY = \frac{513.3}{55} = 9.3$$

(1) Emu Bay

$$\begin{aligned} SB^2 &= SY^2 - 2BSXY + B^2SY^2 \\ &= 4.9-2.0.28.7.5 + 0.08.4.9 \\ &= 4.9-4.2+0.4 \\ &= 1.1 \end{aligned}$$

(2) Cape D'Estaing

$$\begin{aligned} SB_1^{\ 2} &= SY^2-2BS_{xy}+B^2S_y^{\ 2} \\ &= 4.5-2.023.9.3+0.05.4.5 \\ &= 4.5-4.3+0.2 \\ &= 0.4 \end{aligned}$$

$$t = \frac{(X_3-X_1-X_3^{\ 1}+X_1^{\ 1})(B-B_1)}{\frac{2S_b^{\ 2}}{K} + \frac{2S_b^{\ 2}}{K}} = \frac{(5.7)(0.05)}{0.18 + 0.04}$$

$$= 0.62$$

t has $N_1 + N - 6 = 88$ degrees of freedom

thus values of t within the limits ± 0.62 occur between 40 & 50% of the time

i.e. - the two samples are from the same population

<u>CALCULATION 5.</u> <u>*B. dailyi*</u> best fit lines for $A_1$ & C of two samples from the locality west of Cape D'Estaing (a) is equal to or less than $5^{\circ}$, (b) is greater than $5^{\circ}$.

(a)

| | $A_1$ | C | |
|---|---|---|---|
| | 38 | 12 | |
| | 38 | 12 | |
| | 40 | 12 | |
| | 40 | 10 | |
| Group 1 | 43 | 14 | ${}_1\bar{A}_1 = 43.4$ |
| | 46 | 15 | |
| 9 individuals | 48 | 14 | ${}_1\bar{C} = 13.7$ |
| | 48 | 15 | |
| | 50 | 15 | |
| | 50 | 17 | |
| | 51 | 14 | |
| | 51 | 15 | |
| Group 2 | 53 | 16 | ${}_2\bar{A}_1 = 54.2$ |
| | 55 | 16 | |
| 9 individuals | 55 | 18 | ${}_2\bar{C} = 16.1$ |
| | 57 | 16 | |
| | 58 | 16 | |
| | 58 | 17 | |
| | 60 | 16 | |
| | 66 | 18 | |
| | 70 | 20 | |
| Group 3 | 72 | 20 | ${}_3\bar{A}_1 = 74.6$ |
| | 73 | 20 | |
| 9 individuals | 76 | 20 | ${}_3\bar{C} = 20.9$ |
| | 76 | 22 | |
| | 88 | 24 | |
| | 90 | 28 | |

$\bar{A} = 57.4$ ${}_1\bar{A}_1 = 43.4$ ${}_3\bar{A}_1 = 74.6$

$\bar{C} = 16.7$ ${}_1\bar{C} = 13.2$ ${}_3\bar{C} = 20.9$

$$B = \frac{{}_3\bar{C} - {}_1\bar{C}}{{}_3\bar{A}_1 - {}_1\bar{A}_1} = \frac{20.9 - 13.2}{74.6 - 43.4} = \frac{7.7}{31.2} = 0.25$$

$$A = \bar{C} - B\,\bar{A}_1 = 16.7 - 0.25.57.4 = 2.3$$

The equation of the "best fit" line is

$$C = 2.3 + 0.25\,A_1$$

(b)

| | A | C | |
|---|---|---|---|
| | 20 | 7 | |
| | 22 | 8 | |
| | 35 | 12 | |
| Group 1 | 37 | 12 | ${}_1\bar{A}_1 = 34.4$ |
| | 39 | 12 | |
| 8 individuals | 39 | 12 | ${}_1\bar{C} = 11.1$ |
| | 40 | 12 | |
| | 43 | 14 | |
| | 47 | 14 | |
| | 48 | 14 | |
| | 49 | 14 | |
| Group 2 | 51 | 16 | ${}_2\bar{A}_1 = 50.6$ |
| | 52 | 14 | |
| 7 individuals | 52 | 16 | ${}_2\bar{C} = 14.6$ |
| | 55 | 14 | |
| | 60 | 14 | |
| | 65 | 18 | |
| | 70 | 20 | |
| Group 3 | 75 | 19 | ${}_3\bar{A}_1 = 73.0$ |
| | 76 | 22 | |
| 8 individuals | 78 | 21 | ${}_3\bar{C} = 19.4$ |
| | 80 | 19 | |
| | 80 | 22 | |

$$\bar{A}_1 = 52.7 \qquad {}_1\bar{A}_1 = 34.4 \qquad {}_3\bar{A}_1 = 73.0$$

$$\bar{C} = 15.0 \qquad {}_1\bar{C} = 11.1 \qquad {}_3\bar{C} = 19.4$$

$$B = \frac{{}_3\bar{C} - {}_1\bar{C}}{{}_3\bar{A}_1 - {}_1\bar{A}_1} = \frac{19.4 - 11.1}{73.0 - 34.4} = \frac{8.3}{38.6} = 0.22$$

$$A = \bar{C} - B\,\bar{A}_1 = 15.0 - 0.22.52.7 = 3.4$$

The equation of the "best fit" line is

$$\underline{C = 3.4 + 0.22\,A_1}$$

(c) To test the significance of the differences of B calculated for the above samples

| (1) $<5^o$ | (2) $>5^o$ |
|---|---|
| $B = 0.25$ | $B^1 = 0.22$ |
| $\overline{X}_3 - \overline{X}_1 = 33.1$ | $\overline{X}_3{}^1 - \overline{X}_1{}^1 = 38.6$ |
| $(Y-\overline{Y})^2 = 132.8$ | $(Y-\overline{Y})^2 = 93.0$ |
| $(Y-\overline{Y})(X-\overline{X}) = 322.1$ | $(X-\overline{X})(Y-\overline{Y}) = 252.3$ |
| $N = 27$ | $N^1 = 23$ |
| $K = 9$ | $K^1 = 8$ |
| $\therefore S_y{}^2 = \frac{132.8}{24} = 5.53$ | $S_y{}^2 = \frac{93.0}{20} = 4.65$ |
| $S_{xy} = \frac{322.1}{24} = 13.42$ | $S_{xy} = \frac{252.3}{20} = 12.62$ |
| $S_B{}^2 = S_y{}^2 - 2BS_{xy} + B^2S_y{}^2$ | $S_{B^1}{}^2 = 4.65 - 5.55 + 0.23$ |
| $= 5.53 - 6.71 + 0.35$ | $= - 0.67$ |
| $= -0.83$ | |

$$t = \frac{(31.2 - 38.6)(0.25-0.22)}{\frac{2.083}{9} + \frac{2.0.67}{8}} = \frac{-7.4.0.03}{0.18+0.17} = \frac{.22}{.59}$$

$$= 0.37$$

$t$ has $N + N^1 - 6 = 27+23-6 = 44$ degrees of freedom

values of $t$ falling within $\pm$ 0.37 occur between 20 & 30% of the time.

i.e.- the difference between the two samples is not significant.

## APPENDIX V

(a) Calculation:- estimation of allometric equation parameters from data of Table 13.

| | log A | log C | |
|---|---|---|---|
| Group 1<br>5 classes | 1.2504 | 0.4393 | |
| | 1.3522 | 0.6637 | |
| | 1.4265 | 0.7059 | $\bar{A}_1 = 1.41$ |
| | 1.4871 | 0.8932 | |
| | 1.5599 | 0.9895 | $\bar{C}_1 = 0.74$ |
| Group 2<br>4 Classes | 1.6284 | 1.0730 | |
| | 1.6646 | 1.1271 | |
| | 1.7324 | 1.2041 | |
| | 1.7505 | 1.2305 | |
| Group 3<br>5 classes | 1.7924 | 1.2406 | |
| | 1.8261 | 1.2672 | $\bar{A}_3 = 1.85$ |
| | 1.8513 | 1.3010 | |
| | 1.8808 | 1.3118 | $\bar{C}_3 = 1.29$ |
| | 1.9031 | 1.3324 | |

$$\bar{A} = 1.65$$

$$\bar{C} = 1.06$$

$$B = \frac{\bar{C}_3 - \bar{C}_1}{\bar{A}_3 - \bar{A}_1} = \frac{1.29 - 0.74}{1.85 - 1.41} = 1.25$$

$$A = \bar{C} - B\,\bar{X} = 1.06 - (1.25.1.65)$$

$$= -1.80$$

Best fit line $\log C = -1.80 + 1.25 \log A$

$$\therefore \quad C = 0.16A^{1.25}$$

where $\alpha$, the allometric constant is 1.25

(b) Calculation - best fit lines for simple allometry by Bartletts method

(i) cranidial lengths equal to or less than 30 mic.div.(log A= 1.48)

(ii) " " greater than 30 mic.div.

(i)

|  | $\log A_1$ | $\log C_1$ |  |
|---|---|---|---|
| Group 1<br>4 individuals | 1.23 | 0.30 | ${}_1\bar{A}_1 = 1.32$ |
|  | 1.30 | 0.40 |  |
|  | 1.36 | 0.65 | $\bar{C}_1 = 0.51$ |
|  | 1.40 | 0.70 |  |
| Group 2<br>4 individuals | 1.40 | 0.78 |  |
|  | 1.42 | 0.78 |  |
|  | 1.42 | 0.78 |  |
|  | 1.43 | 0.78 |  |
| Group 3<br>4 individuals | 1.43 | 0.85 | ${}_3\bar{A}_1 = 1.46$ |
|  | 1.45 | 0.90 |  |
|  | 1.46 | 0.90 | $\bar{C}_3 = 0.91$ |
|  | 1.48 | 1.00 |  |

$$\bar{A}_1 = 1.40 \qquad \bar{C} = 0.74$$

$$B = \frac{\bar{C}_3 - \bar{C}_1}{{}_3\bar{A}_1 - {}_1\bar{A}_1} = \frac{0.91 - 0.51}{1.46 - 1.32} = \frac{0.40}{0.14} = 2.86$$

$$A = \bar{C} - B\,{}_1\bar{A} = 0.74 - (2.86 . 1.40)$$

$$= 0.74 - 4.00$$

$$= -3.26$$

$\therefore$ the best fit line for simple allometry is

$$\log C = -3.26 + 2.86 \log A.$$

$$\text{or } C = A^{2.86}$$

(ii)

| | log $A_1$ | log C | |
|---|---|---|---|
| Group 1<br>4 individuals | 1.53 | 1.04 | $_1\bar{A}_1 = 1.57$ |
| | 1.53 | 1.08 | |
| | 1.58 | 1.08 | $\bar{C}_1 = 1.07$ |
| | 1.62 | 1.08 | |
| Group 2<br>3 individuals | 1.65 | 1.18 | |
| | 1.76 | 1.20 | |
| | 1.83 | 1.32 | |
| Group 3<br>4 individuals | 1.86 | 1.30 | $_1\bar{A}_3 = 1.91$ |
| | 1.86 | 1.26 | |
| | 1.90 | 1.33 | $C_3 = 1.34$ |
| | 2.00 | 1.48 | |

$$\bar{A} = 1.73 \qquad \bar{C} = 1.21$$

$$B = \frac{\bar{C}_3 - \bar{C}_1}{_1\bar{A}_3 - {_1\bar{A}_1}} = \frac{1.34 - 1.07}{1.91 - 1.57} = \frac{0.27}{0.34} = 0.79$$

$$A = \bar{C} - B\,\bar{A}_1 = 1.21 - 0.79.1.73 = 1.20 - 1.37$$

$$= -0.17$$

∴ the best fit line for simple allometry is

$$\log C = -0.17 + 0.79 \log A$$

or $\underline{C = 0.68\ A^{0.79}}$

(c) Calculation - deviations from simple allometry; data from meraspids of known degree; dimensions are the average for specimens of that degree

| Instar | A | C | $\log_e A$ | $\log_e C$ |
|---|---|---|---|---|
| 0 | 17 | 2 | 2.8332 | 0.6932 |
| 1 | 20.5 | 2.8 | 3.0204 | 1.0578 |
| 2 | 23 | 45 | 3.1345 | 1.5041 |
| 3 | 25 | 5.5 | 3.2189 | 1.70488 |
| 4 | 26.5 | 6 | 3.2772 | 1.7918 |
| 6 | 30 | 8 | 3.4012 | 2.0794 |

for the entire period the best fit curve of simple allometry is

$$A = .006\ C^{2.86}$$

for each period   is estimated from

$$\alpha_1 = \frac{\log_e C_2 - \log_e C_1}{\log_e {}_1A_2 - \log_e {}_1A_1}$$

| Instar | | $\alpha$ |
|---|---|---|
| 0 - 1 | $\frac{.3646}{1.1672}$ | 1.95 |
| 1 - 2 | $\frac{.4463}{.1241}$ | 3.60 |
| 2 - 3 | $\frac{.2008}{.0844}$ | 2.38 |
| 3 - 4 | $\frac{.0869}{.0583}$ | 1.49 |
| 4 - 6 | $\frac{.2876}{.1240}$ | 2.32 |

## Appendix VI

Measurements of the angle which the abaxial portion of the posterior border subtends to the sagittal direction. Measurement given only for specimens on which both sides may be measured, and with a difference between the sides not exceeding 10°. (see p. 10 and Table 1)

| E. polymera | | E. dalgarnoi | | B. dailyi | | B flindersi | |
|---|---|---|---|---|---|---|---|
| L.S. | R.S. | L.S. | R.S. | L.S. | R.S. | L.S. | R.S. |
| 30 | 30 | 45 | 55 | 60 | 60 | 60 | 60 |
| 45 | 42 | 42 | 40 | 45 | 50 | 56 | 55 |
| 35 | 35 | 53 | 45 | 60 | 55 | 58 | 60 |
| 41 | 38 | 45 | 45 | 62 | 58 | 60 | 60 |
| 40 | 45 | 48 | 44 | 50 | 53 | 60 | 61 |
| 52 | 44 | 44 | 40 | 56 | 56 | 70 | 66 |
| 43 | 43 | | | 60 | 60 | 55 | 66 |
| 47 | 38 | | | 50 | 60 | 61 | 62 |
| 34 | 40 | | | 65 | 70 | | |
| 44 | 45 | | | 70 | 63 | | |
| 44 | 43 | | | 65 | 60 | | |
| 36 | 40 | | | | | | |

## REFERENCES

BARRANDE, JOACHIM,

1852 Systeme Silurun du centre de la Boheme: 1.e.Partic, Crustaces, Trilobites: v.1, 935 p., 51 pl. (Prague and Paris).

BORNEMANN, J.G.

1891 Die Versteinerungun des Cambrischen Schichtensystems der Insel Sardinien Abt. 2. Nova Acta der Leop. - Carol. Deutsch Akad. der Naturforscher, v.56, No. 3, p.427-528, pls. 19-28.

BRIGHT, R.C.

1959 A paleoecologic and biometric study of the Middle Cambrian trilobite *Elrathia kingii* (Meek).J.Paleont., v.33, No.1, p. 83-98, pls. 17-18.

BRONGERSMA - SANDERS, M.

1957 Mass mortality in the sea p.941-1010 in "Treatise on marine ecology and palaeoecology" ed. Hedgpeth, J.W. Mem. Geol. Soc. Amer., No.67, vol.1,

BURMA, B.H.

1948 Studies in Quantitative Palaeontology: I. Some Aspects of the Theory and Practice of Quantitative Invertebrate Paleontology: Jour., Paleont., v.22, p.725-761, 23 Text figures.

BURLING, L.D.

1916 Paedumias and the Mesonacidae, with descriptions of a new species having at least 44 segments, from the Lower Cambrian of British Columbia., Ottawa Naturalist, v.30, p.53-58, 1 pl.

CRAIG, G.Y. AND OERTEL, G.

1966 Deterministic models of living and fossil populations of animals. Quant. J. Geol. Soc. London v.122, p.315-355.

DAILY, B.

1956 The Cambrian in South Australia; in El sistema Cambrico, su palaeogeografi y el problema su base. 20th. Int. geol. Congr., Mexico, v.2, p.91-147.

GOULD, S.J.

1966 Allometry and size in ontogeny and phylogeny. Biol. Rev., v.41, p.587-640.

HARRINGTON, H.J. et al.,

1959 Treatise on Invertebrate Paleontology, (O), Arthropoda, I. Lawrence, Kansas. 560 p.

HESSLER, R.

1962 Secondary segmentation in the thorax of trilobites. J.Paleont., v.36, No.6, p.1305-1312.

HUPÉ, P.

1950 A propos des segments macro-pleuraux des trilobites. Bull. Soc. Géol. France, ser.5, v.20, p.191-193

1953a Contribution á l'étude du Cambrien inferieur et du Précambrien III de l'Anti-Atlas morocain. Service géol. Maroc (Rabat), Notes et Mém., No.103, 402p. 24 pl.

1953b Quelque remarques sur la croissance et la segmentation des trilobites. Bull. Soc. Géol. France, Bull ser.6., v.3, p.3-11.

1953c Classification des trilobites. Ann. Paléont. (Paris). v.39, p.61-168 (1-110)

HUPÉ, P.

1955 Classification des trilobites. Ibid., v.41, p.91-325(111-345).

1960 Reflexions sur quelque traité de la structure cephalique chez les larves de trilobites. Bull. Soc. Géol. France, ser. 7, v.1, No.7, p.745-758.

HUNT, A.S.

1967 Growth, variation and instar development of an agnostid. J. Paleont., v.41, No.1, p.203-208, Pl.22.

KAUFMANN, R.

1933 Variatiationsstatistische Untersuchungen uber die "Artabwandlung" and "Artumbildung" in der Oberkambrischen Trilobitengattung *Olenus* Dalm. Abh. Geol. - Pal. Inst. Greigswald., v.10, p.1-54.

KAUTSKY, F.

1945 Die Unterkambrische Fauna von Aistjakk in Lappland. Geol. Foren.i Stockholm. Forhandl., v.67 No.441, p.129-211

KESLING, R.V.

1952 Doubling in size of ostracod carapaces in each moult stage. J. Paleont., v.26, No.5, p.772-780.

KERMACK, K.A.

1954 A biometrical study of *Micraster coranguinum* and *M. (Isomicraster) senonensis.* Phil. Trans. Roy. Soc. ser.B, v.237, p.375-428, Pl.24-26.

KOBAYASHI, T. AND KATO, F.

1951 On the ontogeny and ventral morphology of *Redlichia chinensis,* with description of *Alutella nakmurai* new gen. and sp..J. Fac. Sci. Imp. Univ. Tokyo, sec.2, v.9, No.3, p.355-493, pl.1-9.

KURTEN, B.

1954 Observations on allometry in mammalian denstitions; its interpretation and evolutionary significance. Acta zool. Fenn., v.85, p.1-13.

LEMCHE, H.

1957 Supposed asexual reproduction in trilobites. Nature, London, v.180 p.801-2.

MANTON, S.M.

1952 The evolution of arthropodan locomotory mechanisms, Part 2, General introduction to the locomotory mechanisms of the Arthropoda. J. Linn. Soc. (Zool.), v.42, p.93-117.

1960 Concerning head development in the arthropods. Biol. Rev., v.35, p.265-282.

1964 Mandibular mechanisms and the evolution of arthropods. Phil. Trans. Roy. Soc., ser.B, v.247, p.1-183, Pl.1.

ÖPIK, A.A.

1958 The Cambrian trilobite Redlichia; organisation and generic concept. Bull. Bur. Min. Resour. Aust., No.42.

1961a The geology and palaeontology of the headwaters of the Burke River, Queensland. Ibid., No.53.

1961b Alimentary caeca of agnostids and other trilobites. Palaeontology, v.3, p.410-38, Pl.68-70

PALMER, A.R.

1957 Ontogenetic development of twoolenellid trilobites. J. Paleont., v.31, No.1, p.105-128, Pl.19

1958 Morphology and ontogeny of a Lower Cambrian pytchopariod trilobite from Nevada. J. Paleont. v.32, No.1, p.154-170.

PALMER, A.R.

1962 Comparative ontogeny of some opisthoparian, gonatoparian, and proparian, Upper Cambrian trilobites. J. Paleont., v.36, No.1, p.87-96.

POCOCK, K.J.

1964 *Estaingia*, a new trilobite genus from the Lower Cambrian of South Australia. Palaeontology, v.7, pt.3, p.458-471, Pls.75-76.

PRZIBRAM, H.

1931 Connecting laws of animal morphology. Four lectures held at the University of London, March, 1929. Univ. London Press, 62p.

RASETTI, F.

1952 Ventral cephalic sutures in Cambrian trilobites. Am. J. Sci., v.250, p.885-898.

RAW, F.

1953 The external morphology of trilobites. J. Paleont., v.27, No.1, p.82-129.

RAYMOND, P.E.

1920 The appendages, anatomy and relationships of trilobites. Mem. Conn. Acad. Arts & Sci., No.7, 169 p.

RESSER, C.E.

1939 The Spence Shale and its fauna. Smithsonian Misc. Coll., v.97, No.12, p.1-29.

ROBB, R.C.

1935 A study of mutations in evolution. I. Evolution in the equine skull. II. Ontogeny in the equine skull. J. Genet., v.31, p.39-52.

ROSS, R.J.

1951a Ontogenies of three Garden City (early Ordovician) trilobites. J. Paleont. v.25, p.578-586, pl.81-84

1951b Stratigraphy of the Garden City formation in north eastern Utah, and its trilobite faunas. Bull. Peabody Mus. Nat. Hist., No.6, 161p., 36 pl. (New Haven).

RICHARDS, O.W. AND KAVANAUGH, A.J.

1945 The analysis of growing form. p.180-230 in "Essays on growth and form" ed. Le Gros Clark. W.E., and Medawar, P.E., Oxford, Clarendon Press.

RŮŽIČKA, R.

1943 Příspěvek k ontogenii českých Paradoxidu a rodu Sao. Věstník Král. České Spol. Nauk, tř. Mat- Přir, p.1-42, pl.1-5.

SDZUY, K.

1959 Die unterkambrische Trilobiten - Familie Dolerolenidae. Senckenbergiana Leth., v.40, p.389-407

1966 An improved method of analysing distortion in fossils Palaeontology v.9, pt.1, p.125-134

SHAROV, A.G.

1965 Origin and main stages of the evolution of arthropods. Zool. Zh. SSSR. Part I, v.44, No.6, p.803-17; Part II, v.44 No.7, p.963-79. (in Russian)

SHAW, A.B.

1956 Quantitative trilobite studies. I - The statistical description of trilobites. J. Paleont., v.30, No.5, p.1209-1224.

1957 Quantitative trilobite studies. II: Measurement of the dorsal shield of non agnostidean trilobites. J. Paleont., v.31, No.1, p.193-207.

SHAW, A.B.

1959 Quantitative trilobite studies. III. *Proliostracus strenuelliformis* Poulsen 1932. J. Paleont., v.33, No.3, p.474-487.

SHAW, F.C. AND ORMISTON, A.

1964 The eye socle of trilobites. J. Paleont., v.38, No.5, p.1001-1002.

SIMPSON, G.G.

1944 Tempo and Mode in Evolution. Columbia University Press, New York. 237 p.

SIMPSON, G.G., ROE, A, AND LEWONTIN, R.C.

1960 Quantitative Zoology. New York. 440p.

SNODGRASS, R.E.

1938 Evolution of the Annelida, Onychophora, and Arthropoda. Smithsonian Misc. Coll., v.97, No.6, 159p.

STORMER, L.

1941 (1942) Studies in trilobite morphology. II. The larval development, the segmentation and sutures, and their bearing on trilobite classification. Norsk. geol. Tiddsskr., v.21, p.49-164. 2 pl.

1944 On the relationships and phylogeny of fossil and recent Arachnomorpha. Skr. norske Vidensk Akad., No.5 p.1-158.

SUVOROVA, N.P.

Cambrian trilobites from the eastern Siberian Platform, Part 1. Protolenidae. Trud. Inst. paleont. Akad. nauk S.S.S.R., No.63, p.1-158, 12 pl.

THOMPSON, D'ARCY,

1917 Growth and Form. Cambridge University Press.

TIEGS, O. AND MANTON, S.M.

1958 The evolution of the Arthropoda. Biol. Rev., v.33, No.3, p.255-337.

WALCOTT, C.D.

1910 Cambrian geology and palaeontology, No.6, Olenellus and other genera of the Mesonacidae. Smithsonian Misc. Coll., v.53, No.6, p.231-422, pl.23-44.

~~1916 Cambrian geology and palaeontology III, No. , Cambrian trilobites. Ibid., v.~~

WALTER , M.R.

1967 Archaeocyaths and the biostratigraphy of the Lower Cambrian Hawker Group, South Australia. J. geol. Soc. Aust., v.14, pt.1, p.139-152, pl.7-8.

WARBURG, E.

1925 The trilobites of the Leptaena limestone in Dalarne with a discussion of the zoological position and the classification of trilobita. Geol. Inst. Univ. Uppsala, Bull., v.17, 446p., 11 pl.

WESTERGÅRD, A.H.

1936 Paradoxides oelandicus beds of Oland. Sverig. Geol. Undersok, ser. C., No.394, p.1-66, pl.1-12.

WHITTINGTON, H.B.

1957 The ontogeny of trilobites. Biol. Rev., v.32, p.421-469.

1959 Ontogeny of Trilobita, in Harrington, H.J. et al, Treatise on Invertebrate Paleontology, Part O, Arthropoda I, ed. R.C. Moore., Lawrence, Kansas. p.127-145

WHITTINGTON, H.B. AND EVITT, W.R.

1953 Silicified Middle Ordovician trilobites. Mem. geol. Soc. Amer., 59, 137p., 33 pl.

## EXPLANATION OF PLATE 1.

### "Emuella polymera"

Fig.1. AUGD F16442 Internal mould of the cephalon and incomplete thorax. The cephalon is asymmetrically distorted, but shows the right side librigena in almost the normal position. (x 11)

Fig.2. AUGD F16443 Holotype. Internal mould of an incomplete cephalon and thorax. Although portions of the glabella and left side of the cephalon are missing, the diagnostic features of the species (e.g. short palpebral ridge) are clearly shown. The prothorax is complete, but the posterior portion of the opisthothorax is missing. (x 13)

Fig.3. AUGD F16444 Internal mould of cranidium and portions of the librigenae. The librigenae are slightly displaced in the clockwise direction. (x14)

# PLATE I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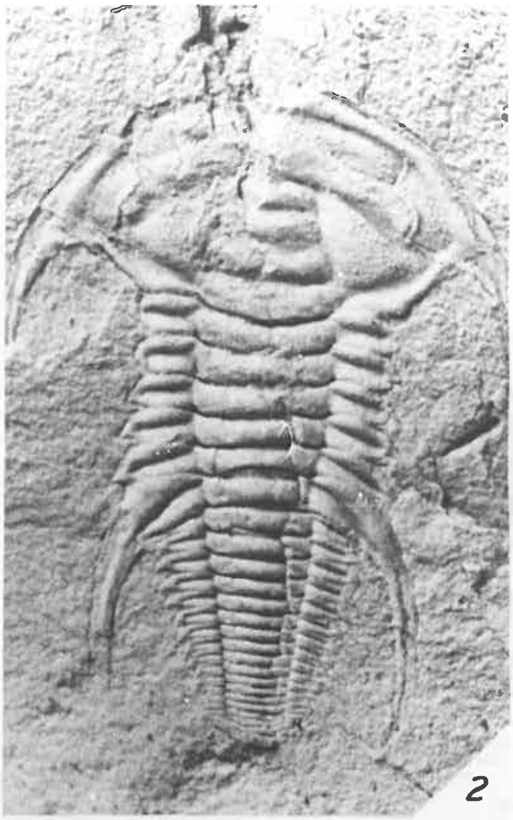
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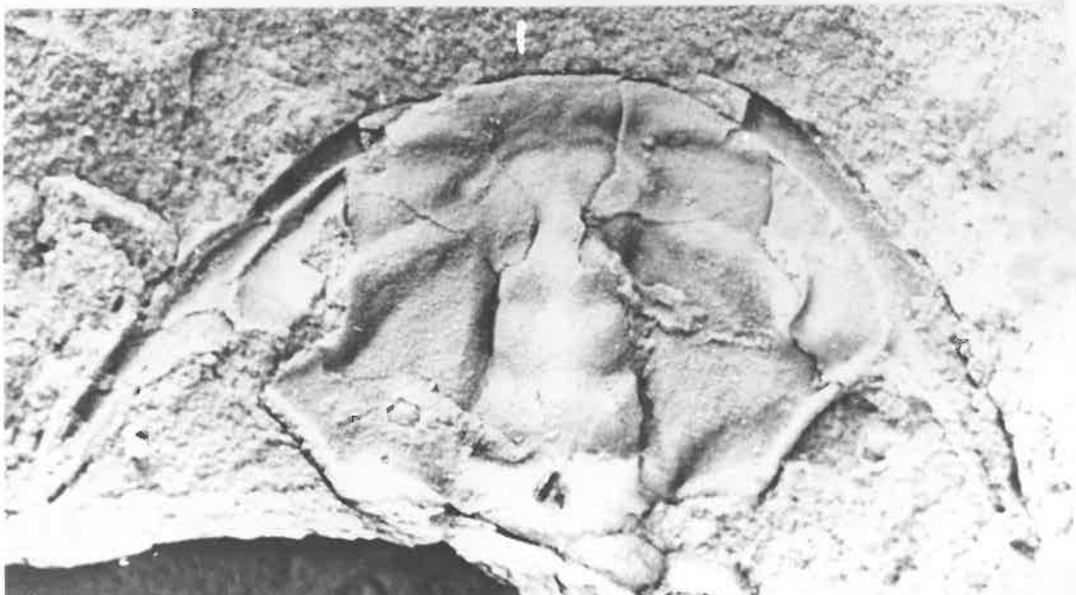
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# EXPLANATION OF PLATE 2.

## "Emuella polymera"

Fig.1. AUGD F16445 Incomplete mould of the ventral side of a cranidium; left side palpebral ridge and distal portionn of posterior area of fixigena missing; shows typical course of anterior section of facial suture, shape and structure of glabella, eye and palpebral ridge. The course of the abaxial section of the left side posterior border and border furrow indicates some asymmetrical distortion. (x 12)

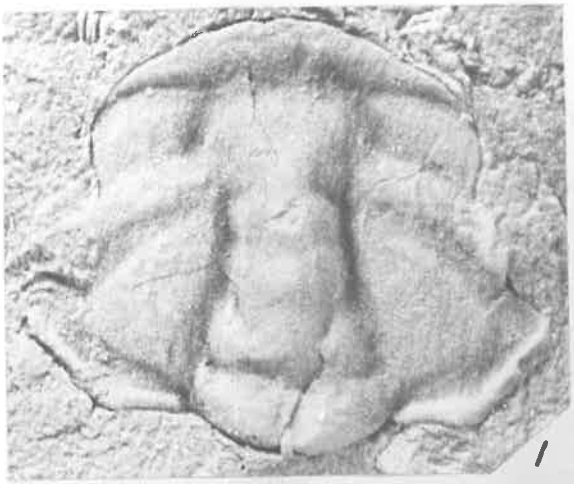
Fig.2. Counterpart of Fig.1; external mould, showing ornament of cranidium. (x 12)

Fig.3. AUGD F16446 Incomplete internal mould of a cranidium, showing the elevation and shape of the palpebral ridges, and morphology of the posterior border and border furrow. (x 20)

Fig.4. AUGD F16447 Mould of the ventral of a librigena; showing the long posterior section of the facial suture, the change of convexity of the genal field, and the widening of the doublure adjacent to the connective suture. (x 13)

Fig.5. AUGD F16448 Internal mould of a cranidium; showing the anterior border furrow and eye ridge fossulae. (x 15)

# PLATE 2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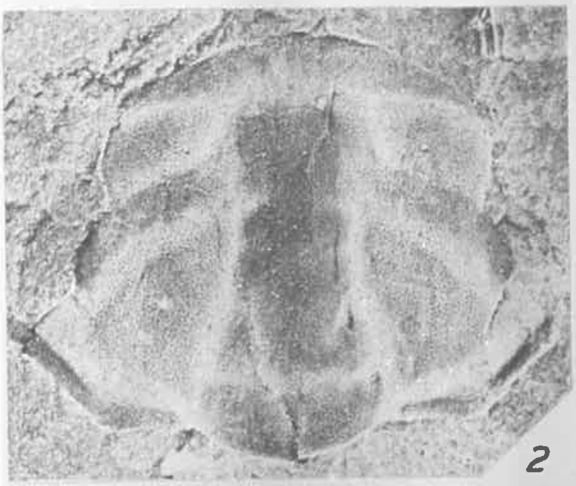
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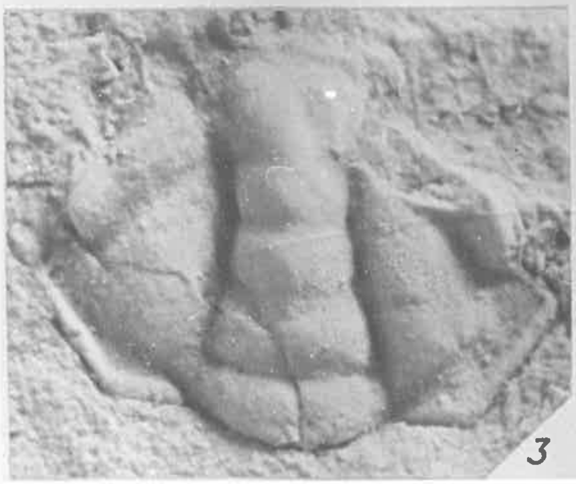
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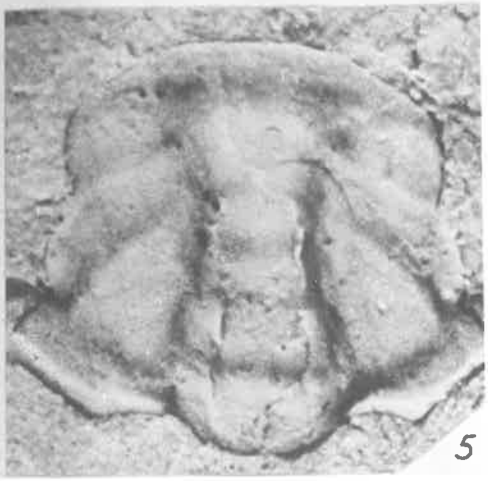
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# EXPLANATION OF PLATE 3.

## "Emuella polymera"

Fig.1. AUGDF16449 Mould of the ventral side of a complete prothorax and incomplete opisthothorax; showing moulds of the articulating half rings of most segments; the nature of the pleural spines on both prothoracic and opisthothoracic segments. Several of the opisthothoracic segments are displaced relative to each other. (x 5)

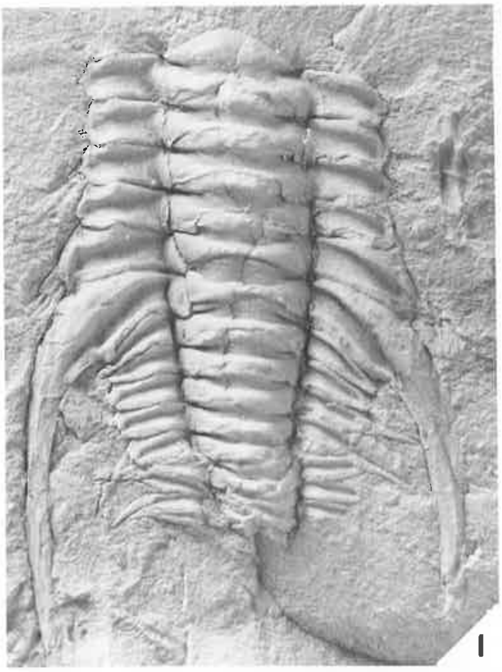
Fig.2. AUGDF16450 Mould of the ventral side of the 4th prothoracic segment, the macropleural unit and the first opisthothoracic segment; showing the deep apodemal slits of the 4,5 & 6th segments; and incomplete effacement of the line of fusion of the pleurae of the 5 & 6th segments. (x 8)

Fig.3. AUGDF16451 Mould of the ventral side of the left side of a macropleural unit and some opisthothoracic segments; showing the long pleural spine of the 5th, the practically unmodified line of fusion of the pleural regions of the 5 & 6th, the horizontal flap joining the abaxial corner of the 6th to the base of the 6th pleural spine, and the structure of the 6th pleural furrow and posterior border, with a fulcrum, and the notch advancing the macropleural spine. (x 8)

Fig.4. AUGDF16452 Mould of the ventral side of a complete prothorax and several opisthothoracic segments (the posterior ones displaced); showing the slight nodes on the raised posterior sagittal margin of the axial rings of the prothoracic segments 1 - 4 and possibly 5. (x 10)

Fig.5. AUGD F16453 Incomplete mould of the ventral side of the cephalon, and thorax; the cephalon is sagittally compressed, (x 11).

# PLATE 3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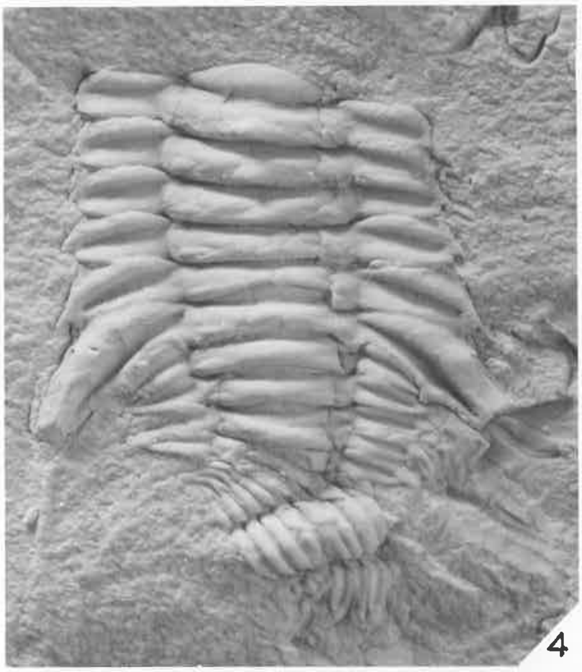
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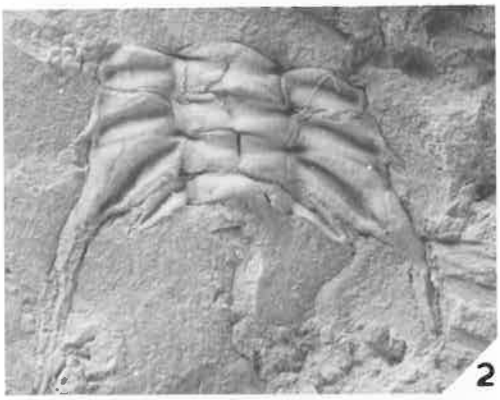
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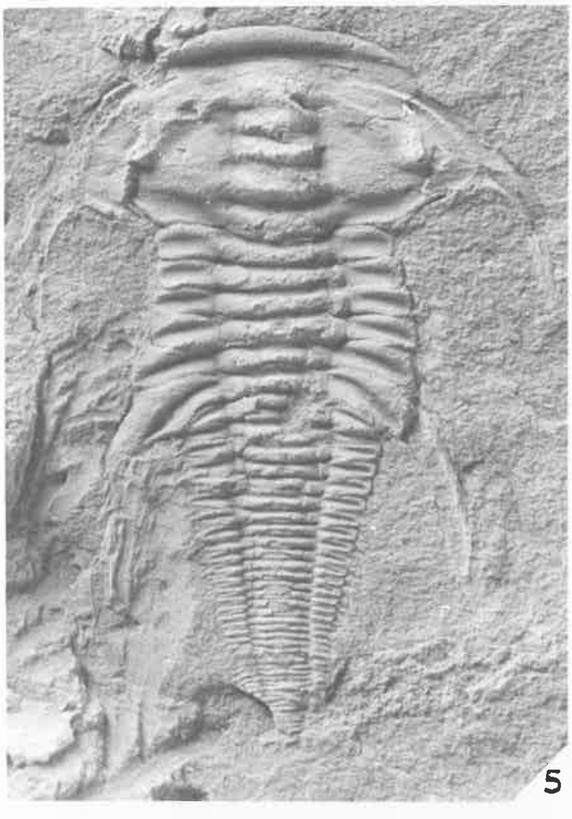
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## EXPLANATION OF PLATE 4

### "*Emuella polymera*

Fig.1. AUGD.F16454. Internal mould of an almost complete specimen, with a teratological opisthothorax. (X18)

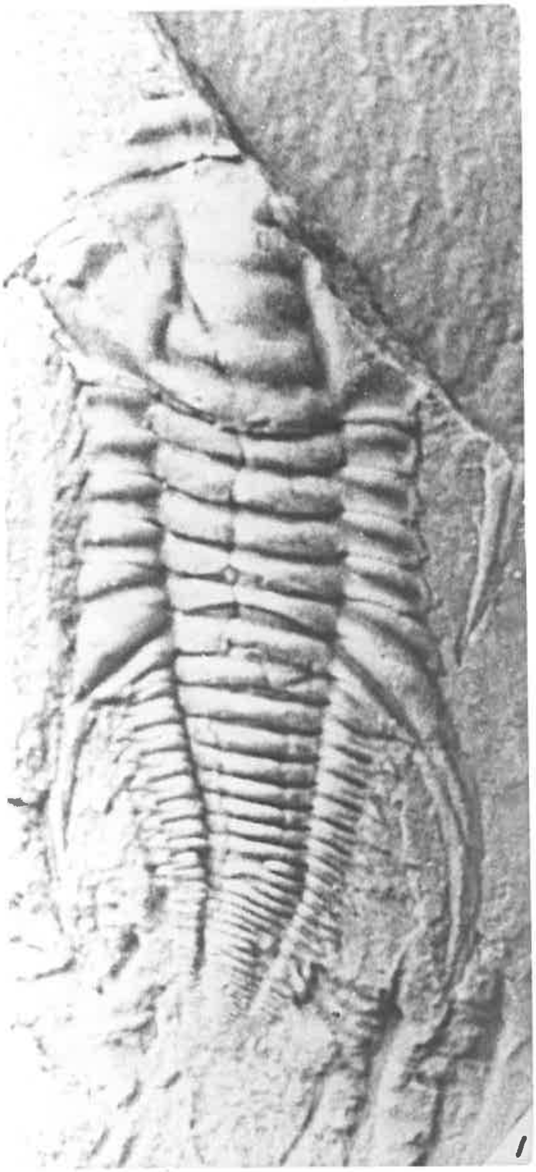
Fig.2. AUGD.F16454. Detail of figure 1, showing the disrupted segmentation of the posterior portion of the opisthothorax, and the pygidium. (X28)

Fig.3. AUGD.F16456. Internal mould of the complete prothorax, and anterior portion of the opisthothorax. The doublure of the opisthothoracic pleural spines is well shown on the left side. (X8)

Fig.4. AUGD.F16457. External mould of the hypostome. (X12)

Fig.5. AUGD.F16458. External mould of the hypostome and attached rostral plate (r.p.); rostral plate showing abaxial notches. Compare with Plate 4, fig.4. (X24)

# PLATE 4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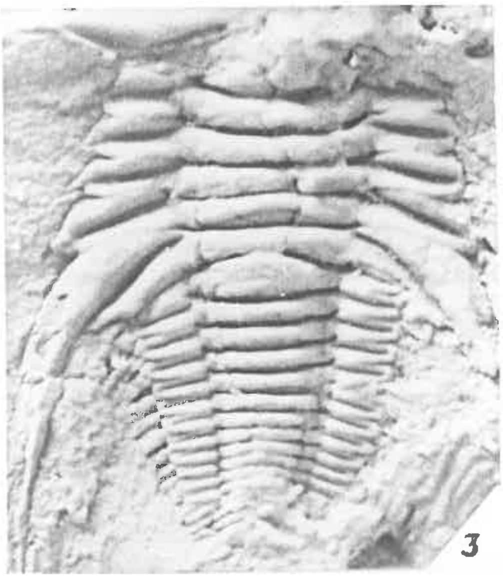
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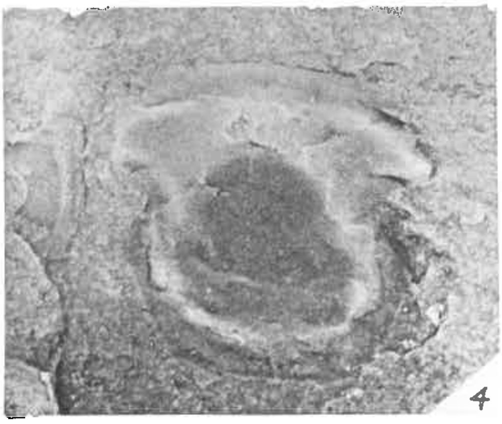
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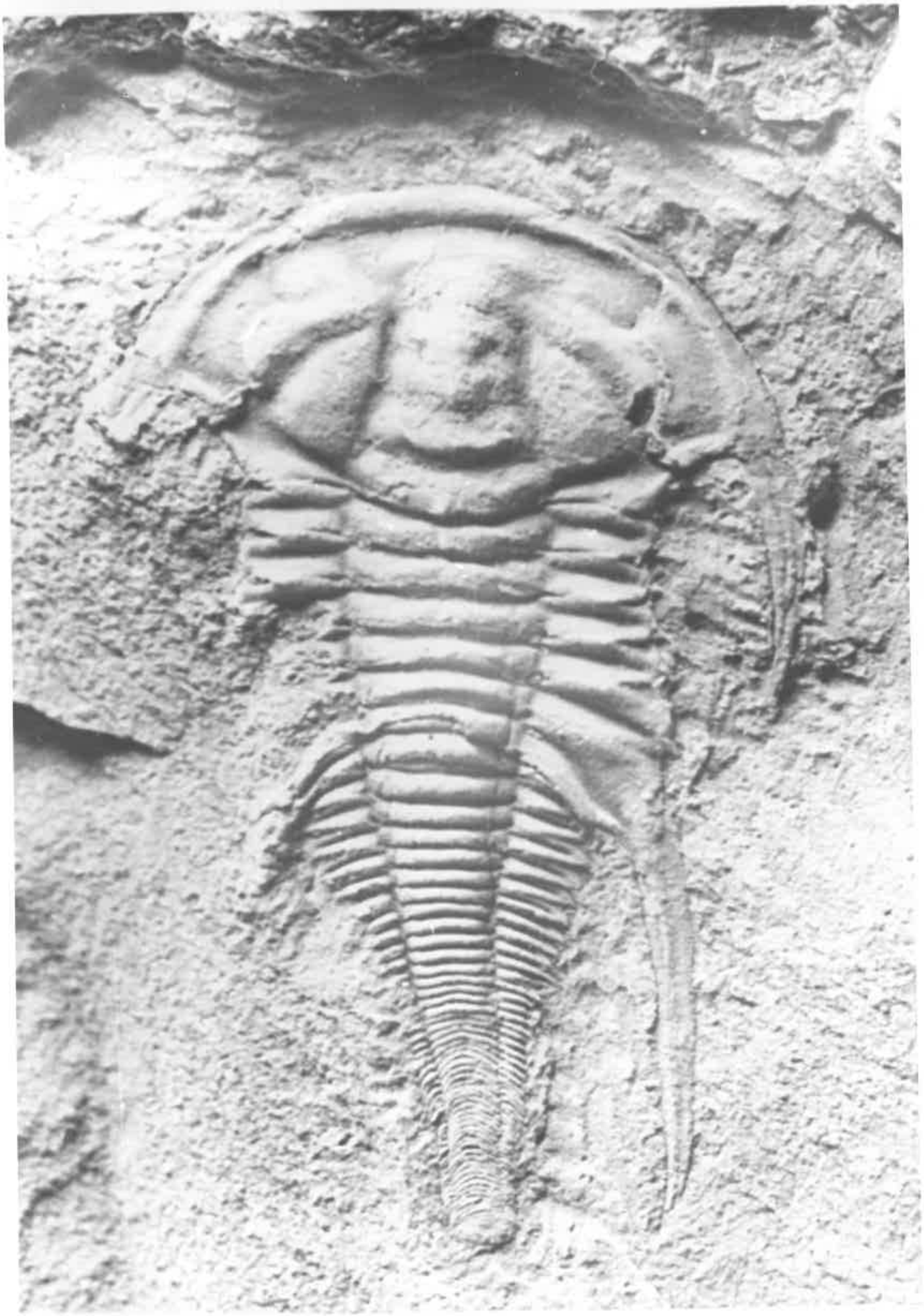
# EXPLANATION OF PLATE 5.

## "*Emuella dalgarnoi*"

AUGD.F16459. Holotype. Internal mould of an almost complete specimen. The cephalon is compressed sagittally, and the right librigenae has rotated in a clockwise direction. The posterior segments of the opisthothorax have tilted anteriorly so that the axial rings appear to be convex to the anterior. (× 14)

PLATE 5



# EXPLANATION OF PLATE 6

## "Emuella dalgarnoi"

Fig.1. AUGD.F16460. Internal mould of an almost complete specimen. The rostral plate is visible beneath the anterior border and an imprint of an apparently overturned hypostome occurs on the frontal glabellar lobe. The genal spines of the librigenae have been pushed towards the axis. (X 6)

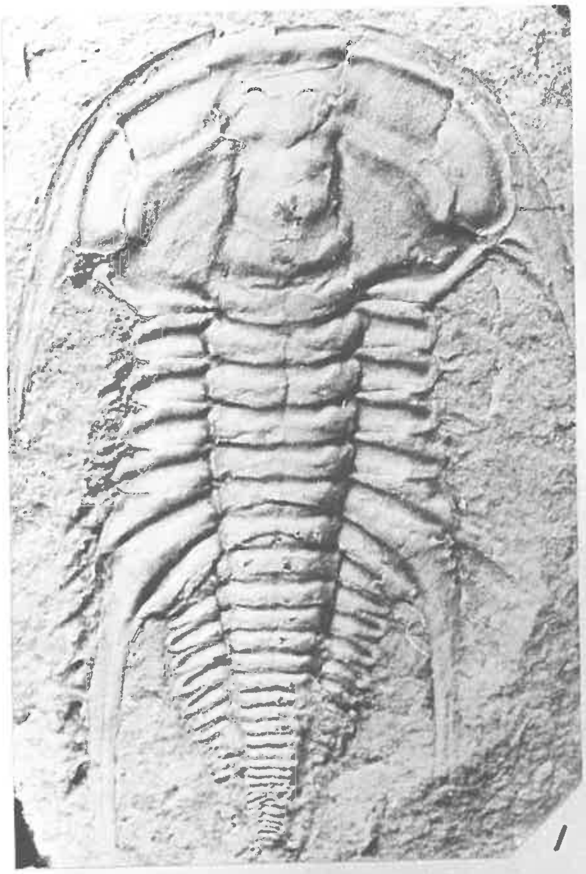
Fig.2. AUGD.F16461. External mould of a sagittally compressed cranidium; showing the cranidial ornament, and muscle scars on the glabellar and occipital furrows. (X 8)

Fig.3. AUGD.F16461. Detail of latex mould of the specimen in Fig.2. The structure of the posterior border and border furrow, and the sutural ridge is well displayed. (X 18)

Fig.4. AUGD.F16460. Detail of fig.1:- L.d. marks the external mould of the librigenal doublure; r.p. the mould of the rostral plate. The course of the connective suture is well shown. (X 11)

Fig.5. AUGD.F16462. External mould of an almost complete specimen with the librigenae almost in situ. (X 6)

PLATE 6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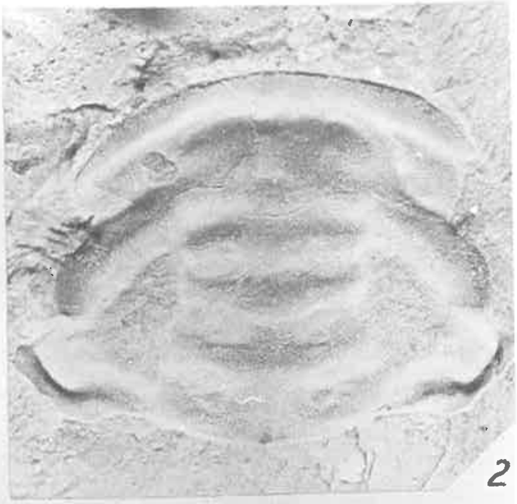
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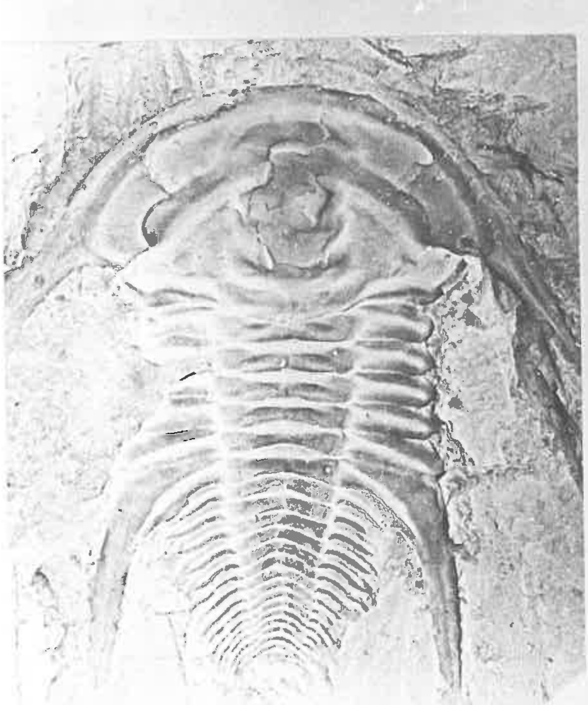
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## EXPLANATION OF PLATE 7

## "Balcoracania dailyi"

Fig.1. AUGD.F16463. External mould of an almost complete specimen (X 8) Holotype.

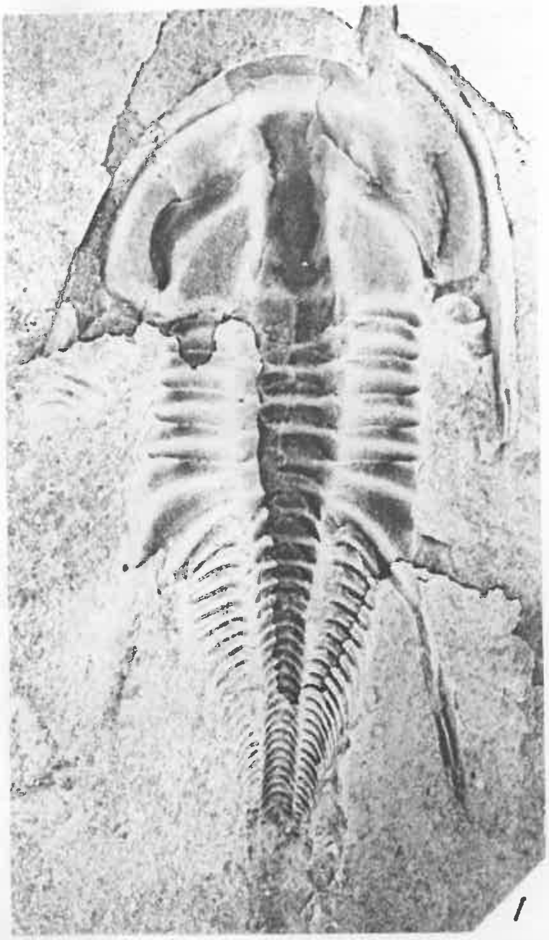
Fig.2. AUGD.F16464. Internal mould of portion of a cranidium showing the structure of the posterior border and border furrow. The mould of the abaxial portion of the posterior border has been removed to show the doublure. (p.d.) (X 20)

Fig.3. AUGD.F16465. Internal mould of a cranidium showing the preglabellar field and associated structures, and the posterior border and border furrow; both palpebral ridges are incomplete. (X 8)

Fig.4. AUGD.F16465. Counterpart of specimen in Fig.3., with the palpebral ridges well shown. (X 8)

Fig.5. AUGD.F16466. Internal mould of a cranidium showing a marked development of the anterior border and eye ridge fossulae. (X 13)

# PLATE 7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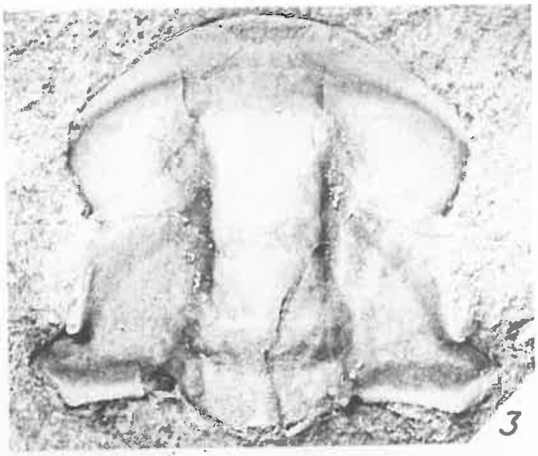
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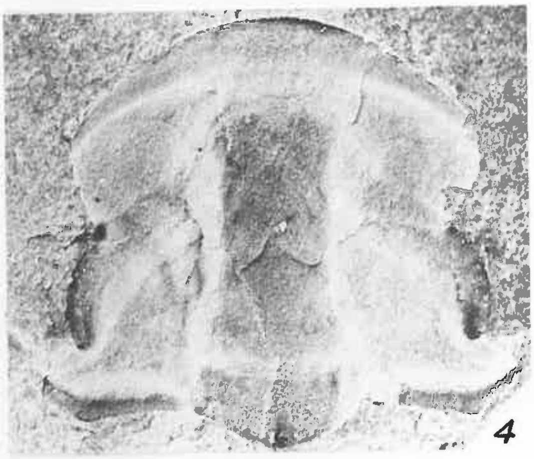
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## EXPLANATION OF PLATE 8.

"Balcoracania dailyi"

Fig.1. AUGD.F16467. Mould of ventral side of librigenae; with impressions of moulds of lateral border and portion of the posterior border missing, revealing those of the lateral and posterior doublures. The specimen shows well the vertically upturned edge forming the eye socle, the downsloping nature of the adaxial posterior portion of the genal field; and the rounded lateral doublure. (x 10)

Fig.2. AUGD.F.16468. Mould of the dorsal side of the genal field, posterior and lateral borders and the genal spine, showing the ornament and the course of the anterior section of the facial suture. (x 10)

Fig.3. AUGD.F16467. Detail of Fig.1. showing the shape of the connective suture and the ornament of the ventral side of the lateral doublure. (x 12)

Fig.4. AUGD.F16469. Section of a mould of the dorsal side of the anterior lateral librigenal doublure, and the internal mould of that portion anterior to the anterior section of facial suture; showing the trace of the anterior section of the facial suture, the connective suture and the mould of the ornament of the dorsal side of the lateral border. (x 14)

# PLATE 8


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## EXPLANATION OF PLATE 9.

### "*Balcoracania dailyi*"

Fig.1. AUGD.F16470. Internal mould of a hypostome. (X10)

Fig.2. AUGD.F16471. Internal mould of a hypostome, showing the anterior line, depressed anterior wings possibly with wing processes, and the deep fossulae in the lateral border furrows. (X10)

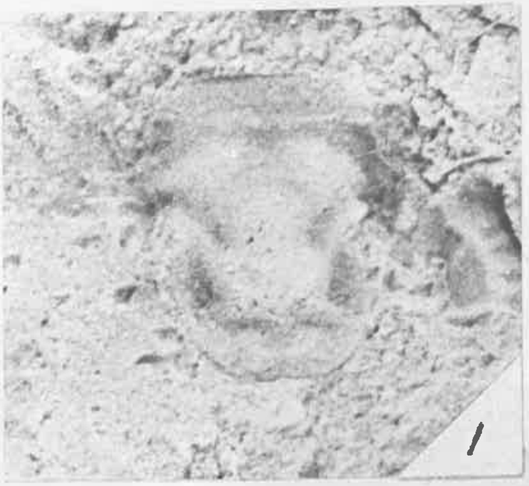
Fig.3. AUGD.F16472. External mould of a hypostome showing the pronounced median depression, and the anterior wing. (X12)

Fig.4. AUGD.F16473. Internal mould of a hypostome showing possible maculae, and strong bosses at the posterior lateral corners of the posterior lobe of the median body. (X13)

Fig.5. AUGD.F16474. External mould of a hypostome showing the anterior line, anterior border furrow and median depression. (X12)

Fig.6. AUGD.F16475. External mould of a hypostome. (X12)

# PLATE 9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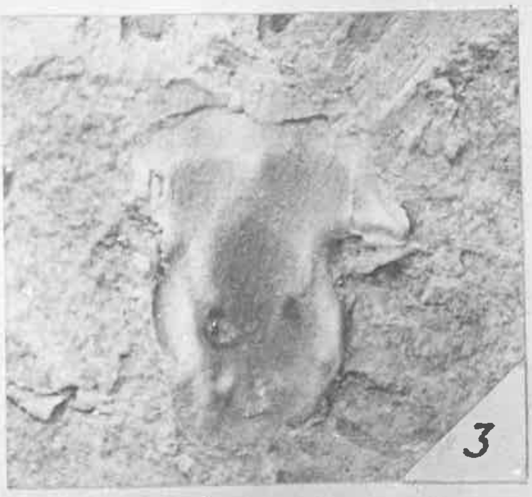
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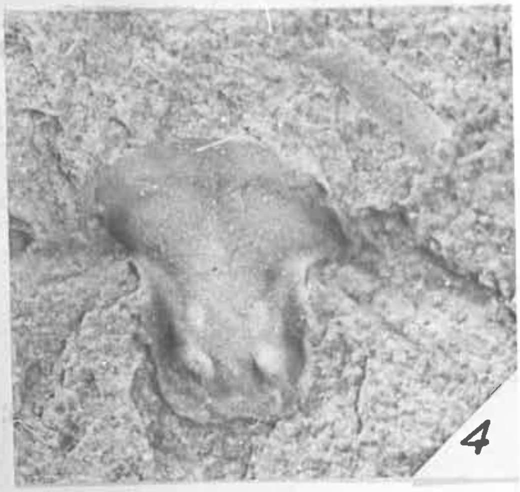
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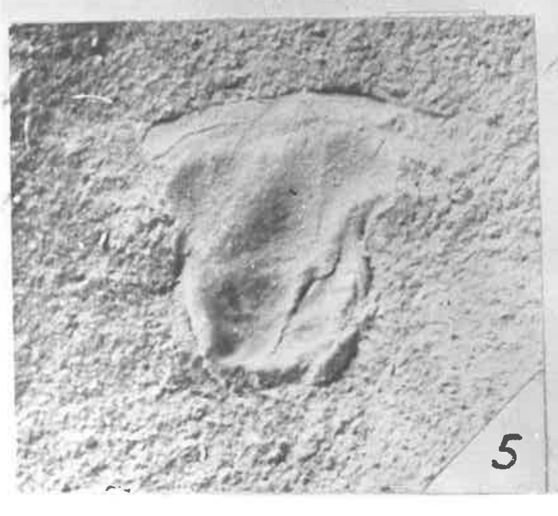
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# EXPLANATION OF PLATE 10

## "Balcoracania dailyi"

Fig.1. AUGD.F16476. External mould of the macropleural unit, and the 1st opisthothoracic segment; showing the articulating half rings of the 5th, 6th & 7th, and the overlap of the posterior band of the 6th on anterior band of the 7th. (X 5)

Fig.2. AUGD.F16477. External mould of an incomplete macropleural segment and several opisthothoracic segments, showing the ornament. (X 14)

Fig.3. AUGD.F16478. External mould of an incomplete thorax, showing the taper of the opisthothoracic axis. (X 12)

Fig.4. AUGD.F16479. Internal mould of the left side of the macropleural unit and the 1st opisthothoracic segment; showing the articulating facet and pleural spine of the fifth, the extension of the transverse furrow of the 6th onto the pleural field, and the extent of the doublure (shown by the gap surrounding portions of the mould). (X 14)

Fig.5. AUGD.F16480. Internal mould of the left side of a macropleural unit. (X 10)

# PLATE 10


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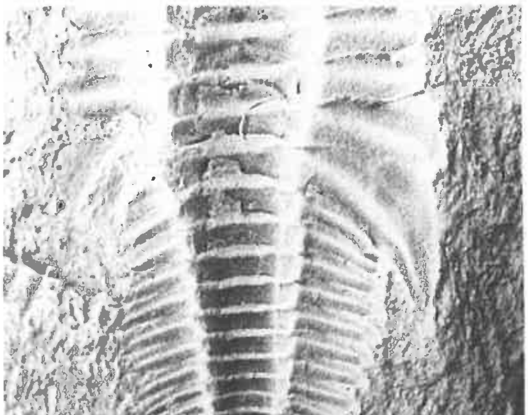
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## EXPLANATION OF PLATE 11

## "Balcoracania flindersi"

Fig.1. AUGD.F16481. Exfoliated cast of an almost complete specimen. The prothorax is disrupted the second segment having been overridden by the posterior ones. The opisthothorax contains 55 segments. (X12)

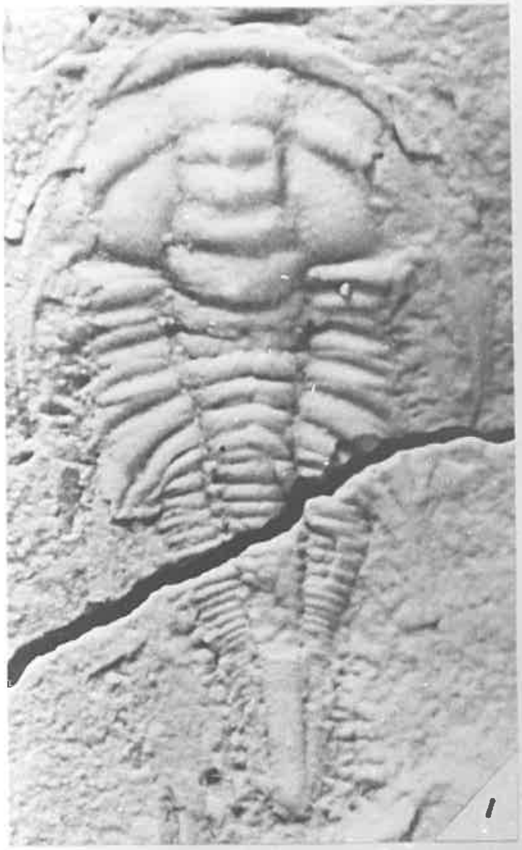
Fig.2. AUGD.F16482. Partly exfoliated cast of a cranidium. (X13)

Fig.3. AUGD.F16483. Detail of specimen of fig.4, showing imprint of the librigenal doublure (l.d.), the rostral plate (r.p.) and the hypostome (hy.) on the internal mould of the cephalon. (X12)

Fig.4. AUGD.F16483. Holotype. Internal mould showing cephalon with imprints of the hypostome and rostral plate, and with right side librigena in situ. The prothorax is complete and shows the extent of the articulating half rings. (X8)

Fig.5. AUGD.F16484. Internal mould of the posterior portion of the opisthothorax and pygidium. (X16)

PLATE II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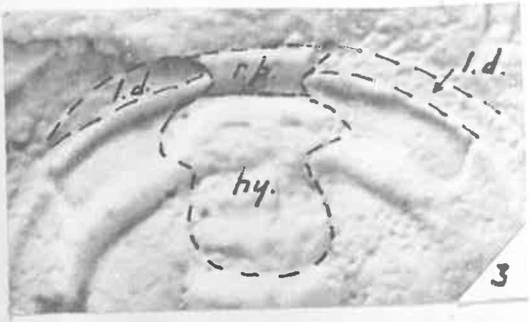

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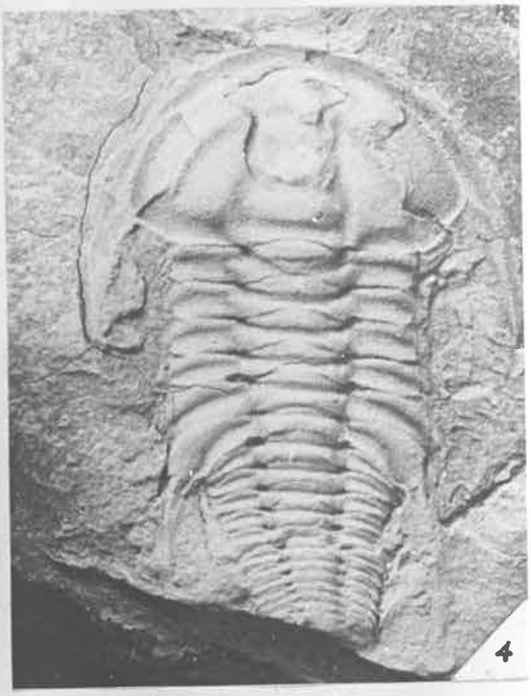
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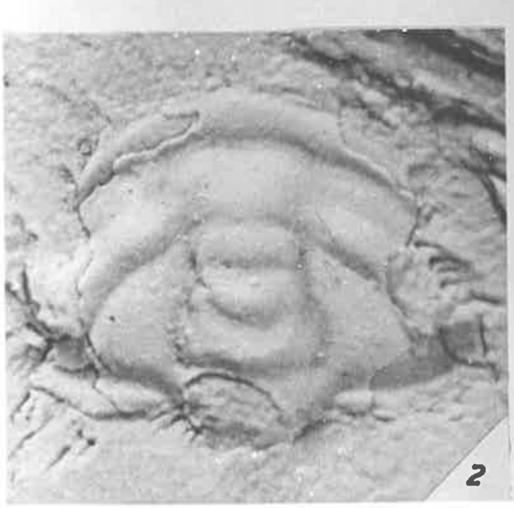
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# EXPLANATION OF PLATE 12

## "*Balcorocania flindersi*

AUGD.F16485. Typical mode of occurrence of *Balcorocania flindersi* from the Flinders Ranges locality (Text fig.2)

# PLATE 12

## EXPLANATION OF PLATE 13

All figures except Figure 15 shown at a magnification of X 15.

Fig.1. AUGD.F16486. *B. flindersi*. Stage I. Protaspis.

Fig.2. AUGD.F16487. *B. flindersi*. Stage II. Cranidium showing faint furrows on the cheeks.

Fig.3. AUGD.F16488. *B. flindersi*. Stage II, meraspid degree 0. Transitory pygidium with 3 segments indicated.

Fig.4. AUGD.F16489. *B. flindersi*. Stage II. Cranidium showing expanded frontal lobe, downsloping steeply to the anterior edge, the short palpebral ridge and curving posterior border.

Fig.5. AUGD.F16490. *B. flindersi*. Stage III. Cranidium clearly showing the furrows on the cheeks.

Fig.6. AUGD.F16491. *B. flindersi*. Stage III, meraspid degree 3. Transitory pygidium with 2 or 3 segments indicated; cranddium with a minute downsloping anterior border.

## EXPLANATION OF PLATE 13

Fig.7. AUGD.F16492. *B. flindersi*. Stage IV. Cranidium showing traces on a glabellar furrow subdividing the frontal glabellar lobe.

Fig.8. AUGD.F16493. *B. flindersi*. Stage IV, meraspid degree 6. Cranidium crushed and asymmetrically distorted; transitory pygidium showing the entire border, and with 4 to 6 segments indicated on the axis.

Fig.9. AUGD.F16494. *B. flindersi*. Stage IV, meraspid degree 6. Cranidium with the frontal glabellar lobe slightly crushed; transitory pygidium with 4 segments indicated.

Fig.10. AUGD.F16495. *B. flindersi*. Stage V. Cranidium clearly showing anterior border and border furrow, subdivision of the frontal glabellar lobe by a fifth pair of glabellar furrows, and furrows subdividing the cheeks (palpebral areas of the fixiginae).

Fig.11. AUGD.F16496. *B. flindersi*. Stage V, meraspid degree 11.

## EXPLANATION OF PLATE 13

Fig.12. AUGD.F16497. *B. flindersi*. Stage VIa. Cranidium with distinct furrows subdividing the frontal glabellar lobe.

Fig.13. AUGD.F16498. *B. flindersi*. Stage VI6. Incomplete cranidium showing the anterior border and border furrow, and the slightly diverging anterior of the facial suture.

Fig.14. AUGD.F16499. *B. flindersi*. Stage VIc, meraspid degree 18. Anterior border of the cranidium disrupted by the doublures of the librigінae.

Fig.15. AUGD.F16500. *B. flindersi*. Larval hypostome showing the tapering posterior lobe of the median body, and the anterior position of the anterior wings. The hypostome is matched to a cranidium of Stage VIc. (X 177)

Fig.16. AUGD.F16501. *E. polymera*. Cranidium showing traces of furrows on the pleural fields, the short high palpebral ridge, and the curving posterior border and border furrow.

# EXPLANATION OF PLATE 13

Fig.17. AUGD.F16502. E. polymera. Cranidium showing anterior position of the palpebral ridge.

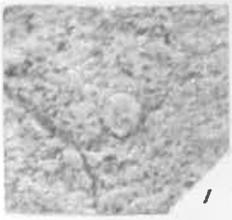
Fig.18. AUGD.F16503. B. dailyi. Stage I. Cranidium showing shape of the glabella, and faint furrows on the cheeks.

Fig.19. AUGD.F16504. B. dailyi. Stage II. Cranidium showing minute downsloping anterior border, and anterior section of the facial suture with a short sagittally directed portion.

Fig.20. AUGD.F16505. B. dailyi. Stage III. Cranidium showing sagittally directed anterior section of the facial suture.

Fig.21. AUGD.F16506. B. dailyi. Stage IV, meraspid degree 10. Internal mould. Cranidium disrupted by the librigenal doublures; transitory pygidium showing an entire border and with at least 6 segments indicated on tha axis and pleural field.

Fig.22. AUGD.F16507. B. dailyi. Posterior section of the opisthothorax and the transitory pygidium of a specimen of Stage V. The transitory pygidium is estimated to contain 9 segments, the anterior two being semi-ankylosed.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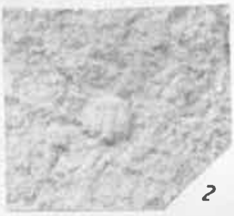
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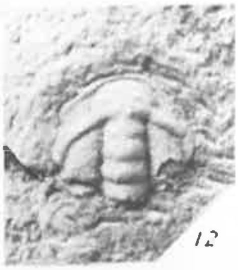
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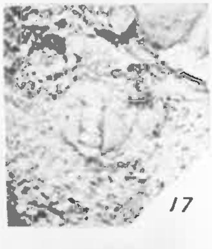
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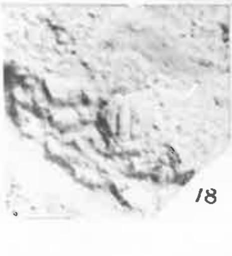
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