ONTOGENY OF THE UPPER CAMBRIAN TRILOBITE *LEPTOPLASTUS CRASSICORNIS* (WESTERGAARD) FROM SWEDEN

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ABSTRACT. The development of the dorsal exoskeleton of the trilobite *Leptoplastus crassicornis* (Westergaard) is described from the Upper Cambrian of Andrarum, Scania, Sweden. The cranidium is represented by all stages from protaspis to holaspis, although specimens other than protaspids are disarticulated and precise degrees are unknown; they have therefore been allocated to seven morphological groups. The development of the meraspid librigena, hypostome, and pygidium is also briefly described. The growth of the cranidium is closest to *Peltura scarabeoides* but also shows similarities with *Olenus gibbosus* and *Leptoplastides salteri*. The nature and course of early facial sutures is discussed. Scatter diagrams show growth to be linear and allometric.

AMONGST the reference collections in the Birmingham University Geology Museum are several slabs of black alum-shale material from the 'Olenus Stage' (as labelled) of Andrarum, Scania, Sweden. These are crowded with specimens of the trilobite *Leptoplastus crassicornis* (Westergaard) in all stages of growth, with occasional individuals of *L. norvegicus* (Holtedahl), preserved as internal and external moulds. The specimens are labelled as *Eurycare angustatum* (transferred to *Leptoplastus* by Henningsmoen 1957) but they are considered to belong to *L. crassicornis*, and the association with *L. norvegicus* supports this. Such an assemblage suggests that the material comes from the Subzones *crassicornis* or *ovatus* of the Leptoplastus (2c) Zone (Henningsmoen 1957, chart 2). A continuous series is represented but due to fragmentation of the exoskeleton only the protaspis stages are complete, and consequently the size groups cannot be related to successive degrees.

The numerous specimens were measured using a micrometer eye-piece, but it must be remembered that the measurement of protaspid length in particular (taken when the anterior and posterior margins lie on an approximately horizontal plane) are reduced by the strong curvature of the specimens. The ratios of length and width measurements of cranidium and glabella, when plotted graphically (text-fig. 2), provide a remarkably linear scatter and also demonstrate the allometric growth of these parts. Breaks in the scatters may indicate separation of size groups by instars, but the number of these is small when compared with the number of thoracic segments in the adult and this may be due to the release of two or more segments into the thorax at some instars. It is appreciated that a certain number of young stages of *L. norvegicus* may have been included in the measurements, but such early stages of two closely related species are unlikely to show any significant differences and their possible inclusion is disregarded.

Any size limits imposed to separate the protaspis, meraspis, and holaspis stages would be entirely arbitrary and subjective, but for convenience such limits are employed. The meraspis stage is considered to commence when the posterior transverse ridge of the protaspis is fully developed and a distinct separation of the cranidium and pygidium by a transverse suture is attained. The holaspid condition is based on the evidence of

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a specimen bearing 10 thoracic segments (Pl. 23, fig. 5). As the nature of the suture and free cheeks is not known in detail for early stages the head shield is termed a cephalon up to, and a cranidium after, the meraspid condition is reached. The axis then becomes the glabella, the axial rings and ring furrows become the glabellar lobes and furrows. The descriptions are based mainly in internal moulds, but the external moulds differ insignificantly from them in all important characters.

TABLE 1. Detailed measurements of figured cranidia. Measurements of length of cranidium and glabella include the occipital ring, of width where this is greatest. Eye-lobe measurement is of length.

	Plate	*Fig.*	*No.*	*Length shield*	*Width shield*	*Length axis*	*Width axis*	*No. of segments*
Protaspis	22	1	O6	0·20	0·20	0·19	0·06	5
		2, 3	W10	0·22	0·22	0·20	0·08	5
		4	W77	0·26	0·26	0·21	0·08	6
		5	W80	0·28	0·30	0·26	0·10	6
		6	W77	0·28	0·28	0·22	0·09	6
		7, 8	W61	0·30	0·33	0·26	0·11	7
				Length cranid.	*Width cranid.*	*Length glab.*	*Width glab.*	*Eye-lobe*
Meraspis		9	W62	0·26	0·29	0·22	0·09	(—)
		10	O14	0·27	0·36	0·26	0·11	0·20
		11	W81	0·30	0·41	0·30	0·14	0·20
		12	W47	0·30	0·42	0·30	0·12	0·20
		13	W50	0·32	0·46	0·33	0·13	0·21
		14	W32	0·34	0·48	0·30	0·14	0·22
		15	W2	0·40	0·58	0·36	0·17	0·24
		16	W9	0·42	0·60	0·40	0·19	0·26
		17	W70	0·48	0·74	0·46	0·20	0·28
		18	W40	0·48	0·70	0·46	0·22	0·26
		19	W52	0·58	0·88	0·56	0·24	0·32
		20	W53	0·68	1·20	0·63	0·32	0·40
		21	W44	0·80	1·40	0·74	0·36	0·40
	23	1	O7	0·97	1·80	0·90	0·50	0·46
		2	W55	1·28	2·60	1·16	0·68	0·68 ?
		3	O8	1·40	2·80	1·28	0·72	0·76
		4	O9	1·60	3·20	1·50	0·92	0·88
		5	O2	1·64	(—)	1·46	0·96	0·90
		6	O10	1·76	3·63	1·60	1·16	1·06
Holaspis		7	O3	2·14	(—)	1·84	1·26	1·10
		8	W56	2·48	5·28	2·12	1·40	1·24
		9	W17	2·60	5·92	2·36	1·72	1·40
		10	W21	2·80	6·0	2·56	1·76	1·40
		11	O11	3·20	(—)	2·80	2·0	1·60
		12	W26	5·0	9·0	4·50	3·0	1·40

Terminology. The terminology employed in this paper is a combination of that of Whittington 1957 and 1958 and that of the *Treatise* (Moore, 1959) with the additional use of the term *ring furrow* to denote the transverse furrows of the protaspid cephalic axis. As the nature of the early cephalic segmentation is not yet clear in the olenids, Størmer's (1942) terminology referring to the segmental nature of certain characters (e.g. pre-antennal segment) is not used. Measurements of length are sagittal unless otherwise stated and of width (tr.) where this is greatest, the latter not necessarily comparable. The length of the cranidium includes the occipital ring and length of the pygidium excludes the articulating half-ring. The axial rings and furrows (excluding the occipital furrow) of the protaspis stages are numbered from back to front in accordance with the usual notation for adult trilobites by inference from the development of the respective rings in the meraspid/holaspid periods.

Technique. Photography of specimens of the order of 0·25 mm. across has often proved extremely difficult but some measure of success has been obtained here by the use of a Leitz Wetzlar biological microscope, and the depth of field problem with highly convex specimens has been overcome by using a 35 mm. Leitz objective incorporating an iris diaphragm. All specimens were whitened with ammonium chloride sublimate before photographing but the coarseness of even the finest application obscures some of the very fine ornament and structure of the protaspids.

SYSTEMATIC DESCRIPTION

Family OLENIDAE Burmeister 1843
Subfamily LEPTOPLASTINAE Angelin 1854

Leptoplastus crassicornis (Westergaard 1944)

Plate 22, figs. 1–21; Plate 23, figs. 1–12; Plate 24, figs. 1–20; text-fig. 1.

Material. The specimens are individually numbered on three slabs of rock with white (W) and orange (O) labels and are deposited in the Birmingham University Geology Museum numbered BU 395–7.

Because of the fragmentary nature of the material the descriptions have been included under five separate headings: (*a*) protaspis, (*b*) meraspis/holaspis cranidium, (*c*) librigena, (*d*) hypostome, and (*e*) pygidium. It was found most convenient to divide the series into seven morphological groups, for each of which the size-range, number of specimens measured, and the plate and figure references precede each description. A fuller list of measurements of figured cranidia is given in Table 1.

PROTASPIS

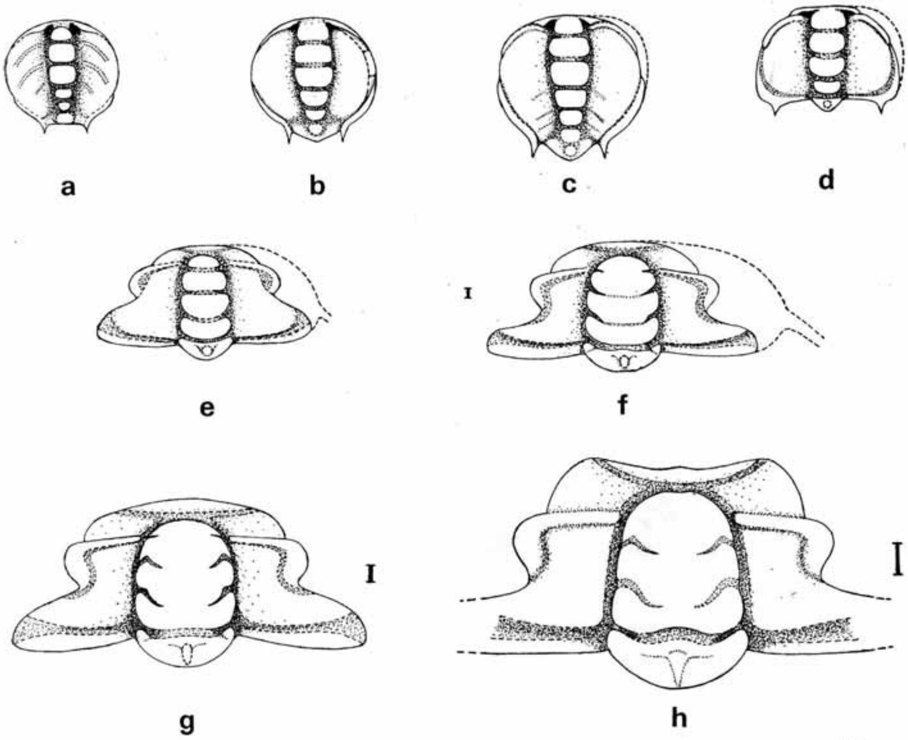
Group 1. Length (entire shield)—0·20–0·25 mm., 6 specimens (Pl. 22, figs. 1–3; text-fig. 1*a*).

The shield is circular in outline, up to 0·26 mm. wide, moderately convex becoming more strongly bent down behind. Axis essentially of 5 rings separated by straight ring furrows with the suggestion of an incipient 6th segment in later stages (Pl. 22, fig. 3).

EXPLANATION OF PLATE 22

Leptoplastus crassicornis (Westergaard). Developmental series of protaspis and early meraspis to show changes in relative dimensions (BU 395, 396). Individual specimen numbers as in Table 1. Fig. 1, ×80; figs. 2, 3, ×70; figs. 4–9, ×65; figs. 10–14, ×50; figs. 15, 16, ×40; figs. 17–19, ×30; figs. 20, 21, ×25.

The axis is slightly constricted behind the 3p ring which is the widest. The frontal lobe is longer than the others and at its antero-lateral corners are a pair of anterior pits which continue laterally into faint furrows, bounded in front by the narrow anterior border. A lateral border extends forwards from a small fine spine (Pl. 22, figs. 2, 3) to the level



TEXT-FIG. 1. Reconstructions of some stages in the development of *Leptoplastus crassicornis* (Westergaard). *a.* W10, ×70; *b.* W80, ×65; *c.* W61, ×65; *d.* W50, ×50; *e.* W53, ×25; *f.* O9, ×12; *g.* W21, ×9; *h.* W26, ×7. Approximate natural sizes are given alongside some figures to show the over-all increase from smallest protaspis to largest holaspis. Suggested positions and shapes of librigenae are given in figs. *b–f*; those in fig. *b* occupy a ventral position, the suture being marginal.

of the 1p axial ring. There are indications on some specimens of several obliquely backwards directed and forwards convex furrows on the pleural regions, but they are very faint.

Group 2. Length (entire shield)—0·26–0·29 mm., 19 specimens (Pl. 22, figs. 4–6; text-fig. 1*b*).

Here the shield, which may be up to 0·32 mm. wide, shows a 6th axial segment behind the occipital ring representing the single segment of the protopygidium, which is developed as a flat triangular plate of minute size (Pl. 22, fig. 5; text-fig. 1*b*). The axis is still widest, but less constricted, at the 2p ring and is more strongly convex. The anterior lobe reaches almost to the anterior margin and on either side of it the anterior pits and border continue to increase in prominence (Pl. 22, fig. 6). The lateral border is a little wider than before and reaches forwards to opposite the 1p ring furrow. The fixigenal spines are somewhat larger and directed backwards and downwards. From opposite the middle of the occipital ring a change in height of the pleural regions suggests the appearance of an oblique ridge crossing their posterior part, a feature seen better in Group 3 (Pl. 22, fig. 4). The pleural regions are often seen to have a relatively coarse reticulate ornament.

Group 3. Length (entire shield)—0·30–0·32 mm., 5 specimens (Pl. 22, figs. 7, 8; text-fig. 1*c*).

The shield, ranging in width from 0·30 to 0·34 mm., may be thus slightly wider than long and is strongly convex (tr.), being better defined by deep axial furrows than before. The frontal lobe appears to have diminished slightly in relative length and width, while the 2p and 3p rings are of about equal width and 1p and the occipital ring progressively smaller, the abrupt narrowing behind the 3p ring being less marked (Pl. 22, fig. 7). The occipital ring is raised high above the level of the descending protopygidium. Anteriorly a distinct eye-ridge is now seen to trend forwards and outwards from the axial furrow near the 3p ring furrow to the antero-lateral margin where, defined from the anterior border by a shallow furrow, it turns backwards, reaching almost to the level of the 2p ring furrow (text-fig. 1*c*). The anterior pits are very well defined and quite deep. The inflated reticulate pleural regions, still bearing traces of oblique grooves posteriorly, descend evenly outwards all round but are abruptly less convex behind the 1p ring furrow where a shallow oblique groove and faint ridge is developed (Pl. 22, fig. 7). This represents the incipient posterior border and margin of the meraspid cranidium. The lateral border is flange-like, reaches forwards to the level of the 2p axial ring and extends posteriorly into now quite strong spines. The small triangular protopygidium has 2 poorly defined circular segments (Pl. 22, fig. 8). The length of the primary axis (5 segments) is here 0·23 mm. and the cranidial width 0·34 mm. (compare values below for Group 4).

MERASPIS/HOLASPIS CRANIDIUM

Group 4. Length (cranidium)—0·26–0·39 mm., 20 specimens (Pl. 22, figs. 9–14; text-fig. 1*d*).

The width of the cranidium varies in this group from 0·35–0·60 mm., showing quite a considerable individual variation during early growth. The cranidium shows an overall shortening and widening due to the lateral growth of the posterior areas of the fixigenae. The glabella becomes distinctly barrel-shaped by the relative increase in width of the 2p and 3p glabellar lobes, the occipital ring remaining small and becoming triangular in shape with the development in later stages of a small median tubercle or node (Pl. 22,

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EXPLANATION OF PLATE 23

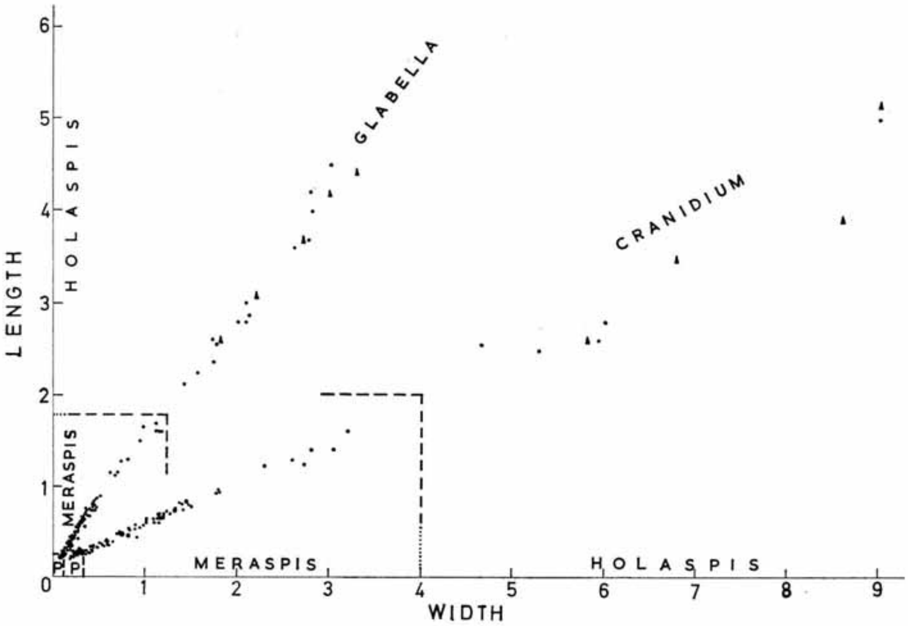
L. crassicornis (Westergaard). Developmental series of late meraspids and of holaspids to show changes in relative dimensions (BU 395, 397). Individual specimen numbers as in Table 1. Fig. 1, ×20; fig. 2, ×16; fig. 3, ×14; figs. 4, 5, ×12; fig. 6, ×11; fig. 7, ×10; figs. 8–11, ×9; fig. 12, ×7.

fig. 11). The 1p to 3p glabellar furrows become gradually shallower, especially medially, while the occipital furrow deepens. The initially curved anterior border becomes distinctly transverse but is still continuous axially with the frontal glabellar lobe. The anterior pits and border furrow combine to form rather large triangular depressions, and the convex anterior border extends laterally beyond the axial furrow to a distance about equal to half the width of the glabella, turning abruptly back so that the eye-ridges become marginal (Pl. 22, fig. 13). The more clearly defined and gently curved eye-ridges extend back to level with the posterior half of the 3p glabellar lobe and show a slight swelling at their posterior (abaxial) end (Pl. 22, figs. 10, 14). The oblique transverse ridge and depression on the pleural regions continue to develop from the protaspis and eventually unite with the lateral border, forming a transverse posterior margin to the cranidium (Pl. 22, fig. 14). The lateral border extends gradually further forwards from the rounded postero-lateral corners of the cranidium, becoming narrower as it does so, to meet but remain distinct from the eye-ridge, and is accompanied by a border furrow continuous with that of the posterior border (Pl. 22, fig. 13). It is clear that a facial suture and free cheek is developed at early stages in this group (see discussion at end), and indeed probably also in Group 3, but no librigenae of such dimensions have been found. As a consequence, the lateral border may now be termed the sutural ridge and the border spines are seen to be of fixigenal origin (i.e. metafixigenal). These latter move relatively outwards to, at most, four-fifths of the distance out from the axial furrow (Pl. 22, fig. 14). The fixigenal areas retain their reticulate pattern to the end of this group, but it is usually lost early in Group 5. These areas commence to inflate individually and the posterior areas to increase gradually in width, the latter also descending rather steeply behind into the posterior border furrow (Pl. 22, fig. 10).

Group 5. Length (cranidium)—0·41–1·00 mm., 53 specimens (Pl. 22, figs. 15–21; Pl. 23, fig. 1; text-fig. 1*e*).

Cranidial width ranges from 0·53 to 1·80 mm. The most important changes in this group affect the glabellar shape and segmentation and the expansion of the posterior fixigenal areas. The glabella continues to expand at the 2p and 3p lobes at first (Pl. 22, figs. 15, 18) but in later stages the 1p lobe and occipital ring take up this change and begin to widen (tr.) so that the sides of the glabella tend to become parallel (Pl. 22, fig. 21). The 2p lobe becomes the longest (sag.) with the 1p and occipital lobes remaining short; the frontal lobe is also reduced. In this group one also sees the first break in continuity of the glabellar furrows, 3p and 2p becoming very indistinct or even disappearing medially (Pl. 23, fig. 1). This is accompanied by an increase in depth of the abaxial parts of the glabellar furrows, 1p and 2p becoming almost notch-like, and by the change in direction of these parts from transverse to inwards and backwards directed. 1p is directed more sharply backwards than 2p (Pl. 22, fig. 20; Pl. 23, fig. 1). The occipital furrow remains continuous and increases in depth, turning forwards abaxially; the median occipital node is very prominent (Pl. 22, figs. 17, 19, 21).

Due to the width increase of the glabella the palpebral areas of the fixigenae become relatively narrower in relation to it than before and become less inflated. The posterior fixigenal areas grow rapidly abaxially and the ratios of cranidial to glabellar width increase, indicating that the growth of these parts does not keep pace. As the fixigenae grow so the sutural ridge is lost, the postero-lateral corners of the cranidium become less well rounded, the posterior margin becomes straighter, and the fixigenal spines are aborted (compare Pl. 22, figs. 15 and 19). The eye-ridges increase in prominence and become more transverse, and the palpebral furrow deepens. The posterior end of the palpebral lobe is at first situated opposite the outer ends of the 2p glabellar furrows but



TEXT-FIG. 2. Scatter diagram showing nature of growth of cranidium and glabella of *Leptoplastus crassicornis* from 116 specimens. Those marked with a triangle are of Norwegian material, measurements being taken directly from the plates of Henningsmoen 1957. Breaks in the scatters might be interpreted as instars, but there is no conclusive evidence which can be used in support of this; no abrupt changes in the morphological development of the cranidium alone are evident. Note relative rates of growth in length and width (allometric) of cranidium and glabella. Measurements in millimetres.

in later stages it extends back to opposite the middle of the 2p glabellar lobe (Pl. 23, fig. 1). The frontal lobe becomes separated from the anterior border of earlier groups by a distinct preglabellar furrow which abaxially defines a true narrow, convex border from a narrow (exsag.) anterior fixigenal area (Pl. 22, fig. 21). The course of the posterior section of the facial suture turns at first slightly outwards behind the palpebral lobe, but in later stages more strongly so, bending back to cut the posterior margin at a distance from the axial furrow of slightly less than the length of the glabella (exc. occipital ring).

Group 6. Length (cranidium)—1·1–1·9 mm., 8 specimens (Pl. 23, figs. 2–5; text-fig. 1*f*).

In this group the cranidium attains, and further develops, the typical adult form and the changes observed are mainly due to size increase. The maximum width of the cranidium in this group is about 3·5 mm. By continued increase in width of the occipital ring and 1p glabellar lobe the glabella soon becomes parallel sided and broadly rounded in front (Pl. 23, fig. 2). The occipital ring may even become slightly wider than the rest of the glabella and has a straighter posterior margin than previously, its abaxial margins turning strongly forwards; the median node becomes somewhat elongate and reduced in prominence. The median parts of 1p and 2p glabellar furrows are gradually lost while the lateral parts become deeper and develop a slight forwards convex curve (Pl. 23, fig. 4). The 3p furrows also continue to get fainter. The eye-ridges are no longer curved but are still directed outwards and slightly backwards. The anterior fixigenal areas and the anterior border increase slowly in length (exsag. and sag. respectively) but a preglabellar area is not yet developed. The posterior margin has become nearly straight, and the convex border widens abaxially along with the border furrow which is now very deep (Pl. 23, figs. 3, 4). The strongly inflated rear parts of the posterior fixigenal areas descend steeply into this border furrow and also into the axial furrow, but the anterior and palpebral areas are much less convex. The by now well-developed palpebral lobes extend back almost to the level of the outer ends of the 1p glabellar furrows (Pl. 23, figs. 2, 4). The course of the facial suture describes a gentle curve from a median marginal position out and back to the front end of the palpebral lobe. Thence, from the back of the palpebral lobe, it turns immediately outwards and runs back in a gentle forwards convex curve (text-fig. 1*f*), bending quite sharply back again to cut the posterior margin at a distance from the axial furrow of a little more than the length of the glabella (excluding occipital ring).

Judging by the size of the cranidium of a specimen which seems to have about 10 thoracic segments (Pl. 23, fig. 5), and that of the smallest available specimen with the full complement of 12 segments (Pl. 23, fig. 7), the holaspid condition is attained when the cranidial length reaches *c.* 2·0 mm. Group 7 is therefore considered to represent the development of the holaspis (adult) stage.

Group 7. Length (cranidium)—2·0 (approx.)–5·0 mm., 14 specimens (Pl. 23, figs. 6–12; text-figs. 1*g*, *h*).

Apart from an over-all size increase of about $2\frac{1}{2}$ times the principal changes concern the glabella. This becomes extremely convex (tr. and sag.), almost semicircular in cross-section, and is raised high above the level of the fixigenae which have been correspondingly reduced in convexity and height. The reduction in over-all convexity of the cranidium continues, and in contrast to the gently arched anterior regions the posterior fixigenae are strongly inflated behind and descend abruptly into the deep and wide posterior border furrow. The glabella continues to widen at the occipital ring and 1p lobes so that the axial furrows become forward convergent. The preglabellar furrow may or may not be confluent with the border furrow, so that a very narrow (sag.) preglabellar area may be present (cf. Pl. 23, figs. 8, 10, and fig. 12). As the glabella widens the glabellar furrows lengthen so that, from occupying only the outer one-fifth of the glabellar width in earlier Groups, they now occupy one-third of the same. 1p and 2p furrows also exhibit a marked sinuosity (Pl. 23, fig. 9) and eventually become quite strongly sigmoidal (Pl. 23, fig. 12), but the 3p furrows remain slightly curved and eventually disappear. As with the glabellar furrows in earlier groups the median part of the occipital furrow tends to weaken (Pl. 23, fig. 8); the median occipital node is more elongate and indistinct. In fig. 12 the glabellar furrows as a whole become much fainter, especially abaxially, and are hardly continuous with the axial furrows. The eye-ridges terminate adaxially opposite the 3p glabellar furrows and are finally almost transverse.

The anterolateral parts of the anterior fixigenal areas tend to grow rather rapidly forwards and downwards, resulting in the anterior border developing a forward concave curve with a slight median expansion. The outer ends of the posterior fixigenae are also strongly bent downwards and invariably hidden, but the posterior sections of the facial suture seem to approach the posterior border at a more acute angle than before.

SUMMARY OF CRANIDIAL DEVELOPMENT

The following summary also acts as a diagnosis for each of the groups described above.

Group 1. Protaspids characterized by 5 axial segments, the absence of palpebral lobes and eye-ridges, and by a lateral border reaching forwards to opposite the occipital furrow.

Group 2. Protaspids with a definite protopygidium of 1 segment, defined by a groove and incipient ridge crossing the posterior part of the pleural regions from the axis to the fixigenal spines. Lateral border reaches forwards to opposite the 1p ring furrow.

Group 3. Late protaspids with a protopygidium of 2 segments, suggestions of eye-ridges extending back to level of 3p axial ring, and a lateral border reaching forwards to level of 2p axial ring.

Group 4. Early meraspids in which the palpebral lobes are defined and the lateral border becomes to sutural ridge by the migration of the suture to the dorsal surface; the ridge reaches forwards the meet the palpebral lobes opposite 2p glabellar furrow. Posterior cephalic border is accentuated and fixigenal spines move out relatively towards the postero-lateral angles of the cranidium. A median occipital tubercle develops.

Group 5. Meraspids showing marked lateral growth of the posterior fixigenal areas and corresponding outwards curve of the suture. Eye-ridges become less curved and less oblique. Glabella widens rapidly at 3p and 2p lobes in early stages and at 1p lobe and occipital ring in later stages, becoming almost parallel sided. Glabellar furrow gradually reduced, the median part of 3p and 2p becoming faint and disappearing. Preglabellar furrow disappears and anterior fixigenal areas develop. Fixigenal spines aborted.

Group 6. Late meraspids in which the glabella becomes parallel-sided and glabellar furrows entirely lateral. Occipital ring slightly wider than glabella, occipital furrow remains deep and continuous. Convexity (tr.) of cranidium as a whole, and of the fixigenae, is reduced except for abaxial regions of posterior areas and their posterior limits. Median part of 1p glabellar furrow obliterated, outer parts of 1p and 2p furrows

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EXPLANATION OF PLATE 24

L. crassicornis (Westergaard). Developmental series of pygidium (figs. 1–7), hypostome (figs. 8–12) and librigena (figs. 13–20). Figs. 1–6, ×25; fig. 7, ×15; figs. 8–12, ×25; figs. 13–16, 18, 19, ×45; figs. 17, 20, ×8. Fig. 1, W64; fig. 2, W42; fig. 3, W30; fig. 4, W65; fig. 5, W22; fig. 6, W46; fig. 7, W36; fig. 8, O18; fig. 9, W1; fig. 10, W67; fig. 11, W13; fig. 12, W29; fig. 13, W59; fig. 14, O19; fig. 15, O22; fig. 16, O17; fig. 17, W42; fig. 18, O16; fig. 19, O27; fig. 20, O28.

become curved and oblique, 3p remaining faint and transverse. Up to 11 thoracic segments present.

Group 7. Holaspids, with very strongly convex and parallel sided to forward narrowing glabella and fainter, strongly sigmoidal 1p and 2p glabellar furrows; 3p furrows may disappear. Preglabellar area may be present. Fixigenae not very convex except abaxial parts of anterior and posterior areas. Eye-ridges almost transverse, palpebral lobes reach back to level with outer ends of 1p glabellar furrows. Anterior border becomes forwards concave. Posterior sections of facial sutures cut posterior border at a more acute angle and more abruptly than before.

LIBRIGENA

There are few complete librigenae preserved but those illustrated show some of the changes which occur (Pl. 24, figs. 13–20).

The smallest fragment (Pl. 24, fig. 13), very doubtfully a free cheek, measures 0·36 mm. long and 0·10 mm. wide. The outer margin is entire but the ?sutural margin is probably not preserved in its original form. It may belong to an early meraspid stage as Plate 1, fig. 10. The ?genal spine is short and postero-lateral. During subsequent development (Pl. 24, figs. 14–18) the librigena becomes wider than long and increases strongly in convexity in the ocular region as the librigenal spine migrates forwards from a postero-lateral (Pl. 24, fig. 14) to lateral (Pl. 24, fig. 17) position. The adult genal spine is very long and robust, developing a strong outwards convex curve with a slightly reflexed tip. The lateral border and furrow do not appear until quite a late stage.

Due to imperfect preservation of the sutural margin in most cases it is almost impossible to assign the illustrated librigenae to respective cranidia, but from comparison of relative sizes it appears that Plate 24, fig. 14 might belong to a late Group 4 meraspid, Plate 24, figs. 15–18 to stages in Group 5, and Plate 24, figs. 19–20 to a late holaspid (e.g. Pl. 23, fig. 11).

HYPOSTOME

A few stages in the development of the hypostome are shown on Plate 24, figs. 8–12, taken from quite a large number of specimens. Few changes in relative dimensions occur, changes being mainly due to accentuation of the features present in the early forms. The smallest hypostome (Pl. 24, fig. 8) is about 1·28 mm. long and wide with a weakly convex middle body (strongest posteriorly) and narrow, convex borders. At a length of 0·33 mm. (Pl. 24, fig. 9) the middle body has increased in posterior convexity and is well raised above the now wider posterior border. The lateral border furrows are pit-like anteriorly and the anterior wings very small. By the time a length of 0·60 mm. is reached (Pl. 24, figs. 10, 11) its maximum width (ant.) is 0·56 mm. and the lateral borders are strongly constricted and ridge-like at one-third of their length from the front. The middle body has its highest point posteriorly at a single median apex. The posterior border is more broadly curved behind and descends almost immediately from the border furrow. The largest hypostome (Pl. 24, fig. 12) is 1·12 mm. long and wide (ant.). It differs from the earlier stages in having a very shallow anterior border furrow, deep and pit-like lateral border furrows at the constriction, and in the shape of the middle body. This latter rises very high above the posterior border, is somewhat truncated behind, and has a double apex at its postero-lateral corners. A narrow convex rim runs around the margin of both lateral and posterior borders.

PYGIDIUM

The pygidia (Pl. 24, figs. 1–7) are considerably less common than cranidia and no advanced meraspid pygidia have been seen. The figures show most of the changes which occur during growth. It is impossible to accurately assign any but the smallest pygidia to respective cranidial sizes.

The smallest meraspid pygidium (Pl. 24, fig. 1) is 0·32 mm. wide and 0·16 mm. long with semicircular outline. The narrow axis has 2 distinct rings and an indication of a third, the pleural regions have 2 pairs of straight, oblique pleural furrows. At the lateral margin is a narrow convex rim leading into the first of 3 pairs of fine marginal spines which increase in length adaxially. The pygidium is moderately convex sagittally.

During subsequent development (Pl. 24, figs. 2–7) the pygidium is seen to develop 4 axial rings and a rounded terminal piece ((Pl. 24, figs. 4 and 7), 4 pairs of oblique pleural furrows, and 4 pairs of marginal spines. The axis increases in width at the expense of the pleurae from a quarter to a half or more (Pl. 24, figs. 2 and 7) of the total width and the median axial tubercles of the transitory pygidium are lost on the adult; the early segments are tuberculate and pass forward into the thorax, but the later true pygidial segments are smooth. The adult pygidial pleurae are relatively both shorter (exsag.) and narrower (tr.) than the early segments and the marginal spines smaller. Of the latter, all but the 4th pair, which remain long and fine, are short and triangular in the adult. An over-all change in shape from semicircular to triangular is seen and the sagittal convexity of early stages is completely lost, the adult pygidial pleural lobes being flat (in contrast to the strongly convex axis).

DISCUSSION

The development of *L. crassicornis* is similar in some respects to that of *Olenus gibbosus* (Strand 1927). The protaspid axis differs principally in the shape, size, and late-stage segmentation of the frontal lobe and in that it is widest anteriorly. The transverse suture and ridge between the cephalon and protopygidium/transitory pygidium is developed at an earlier stage and the fixigenal spines are longer. The protaspis is also somewhat larger throughout development in *O. gibbosus*. In meraspid stages the sutural ridge and fixigenal spine are retained longer, but the two species agree in the possession of a straight anterior cranidial border.

Early protaspid development of *L. crassicornis* is most like that of *Peltura scarabeoides* (Whittington 1958), especially in intermediate stages (Group 2 here), but the meraspid axial development is closer perhaps to that of *Leptoplastides salteri* (Raw 1925).

Regarding the nature and course of the facial sutures, the interpretation of Whittington (1958, pp. 203–4) for *P. scarabeoides* may be equally applied in this case. The facial suture is not clearly developed on the present material of *L. crassicornis* until early meraspid stages, but the presence and nature of the sutural ridge is identical in both species. The abrupt anterior termination of the lateral border (= sutural ridge of larger specimens) seen in Plate 22, figs. 7, 8 and in its interpretation, text-fig. 1*c*, suggests that the facial suture, after running alongside the eye-ridge, crosses the border on to the ventral surface (?doublure). As growth proceeds its course is extended backwards to cut the border postero-laterally, and is accompanied by the loss of the metafixigenal spine. It is clear that the metafixigenal spine, which may be (as here) essentially transient, has previously been too freely equated with the fixigenal spines of adult olenids such as *Saltaspis* and *Nericiaspis*. From such an assumption *L. crassicorne* could easily be referred to the proparian condition during early meraspid development, but subsequent development shows that the final condition is opisthoparian. It is unfortunate that there are no well-preserved early meraspid librigenae (excluding the doubtful specimen in Pl. 24, fig. 13) from which one might determine the origin of the librigenal spine. It is possible, as suggested by Palmer (1958) for *Crassifimbra walcotti*, that the librigenae of protaspids may be represented at first by an entirely ventral plate, the suture thus being marginal (see text-fig. 1*b*). In later protaspids and early meraspids (text-fig. 1*c–e*) the librigena and facial suture become dorsal and the point where the posterior section cuts the border migrates slowly backwards outside the sutural ridge, which thus becomes a structure separate from the true marginal border.

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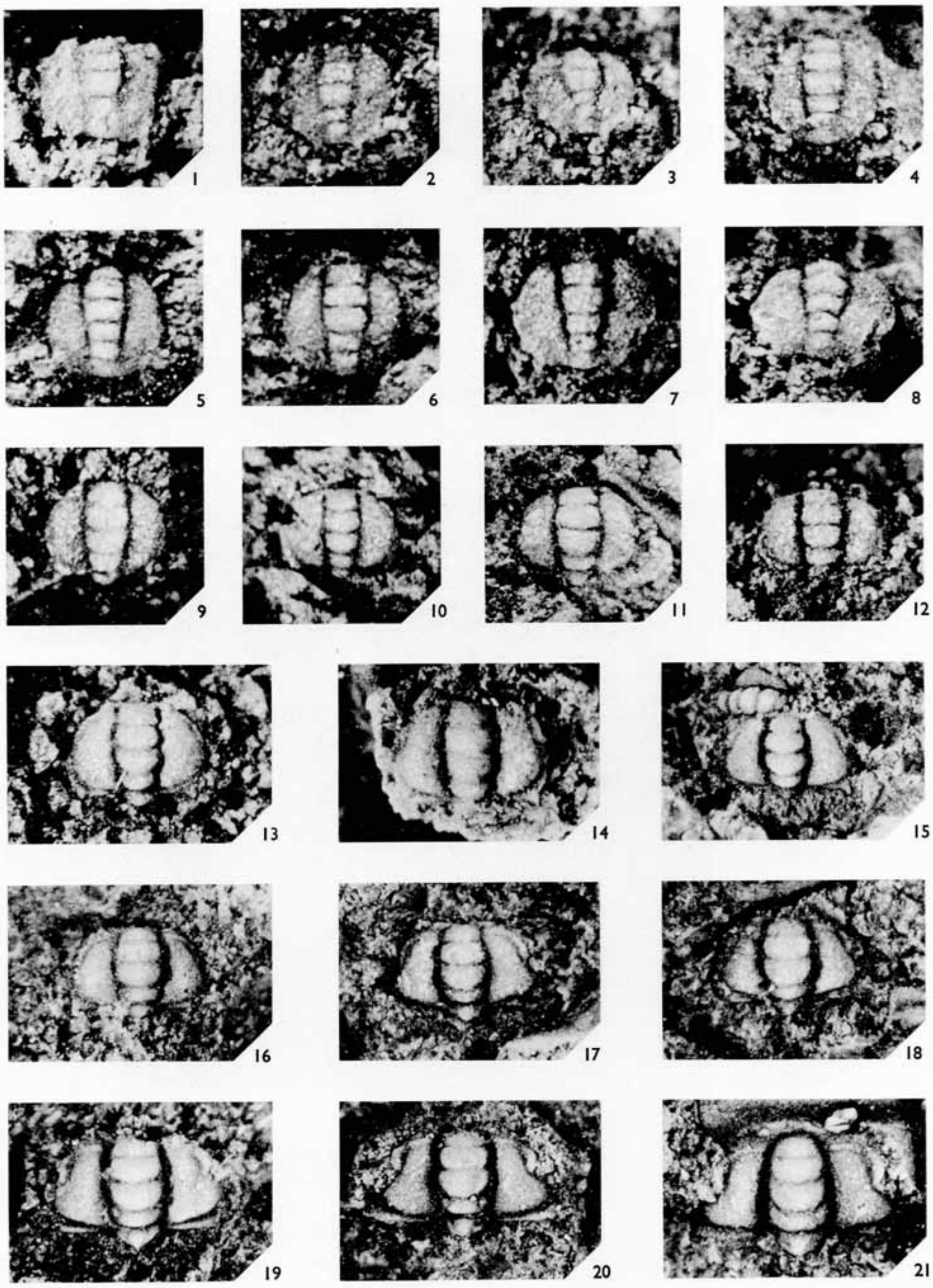

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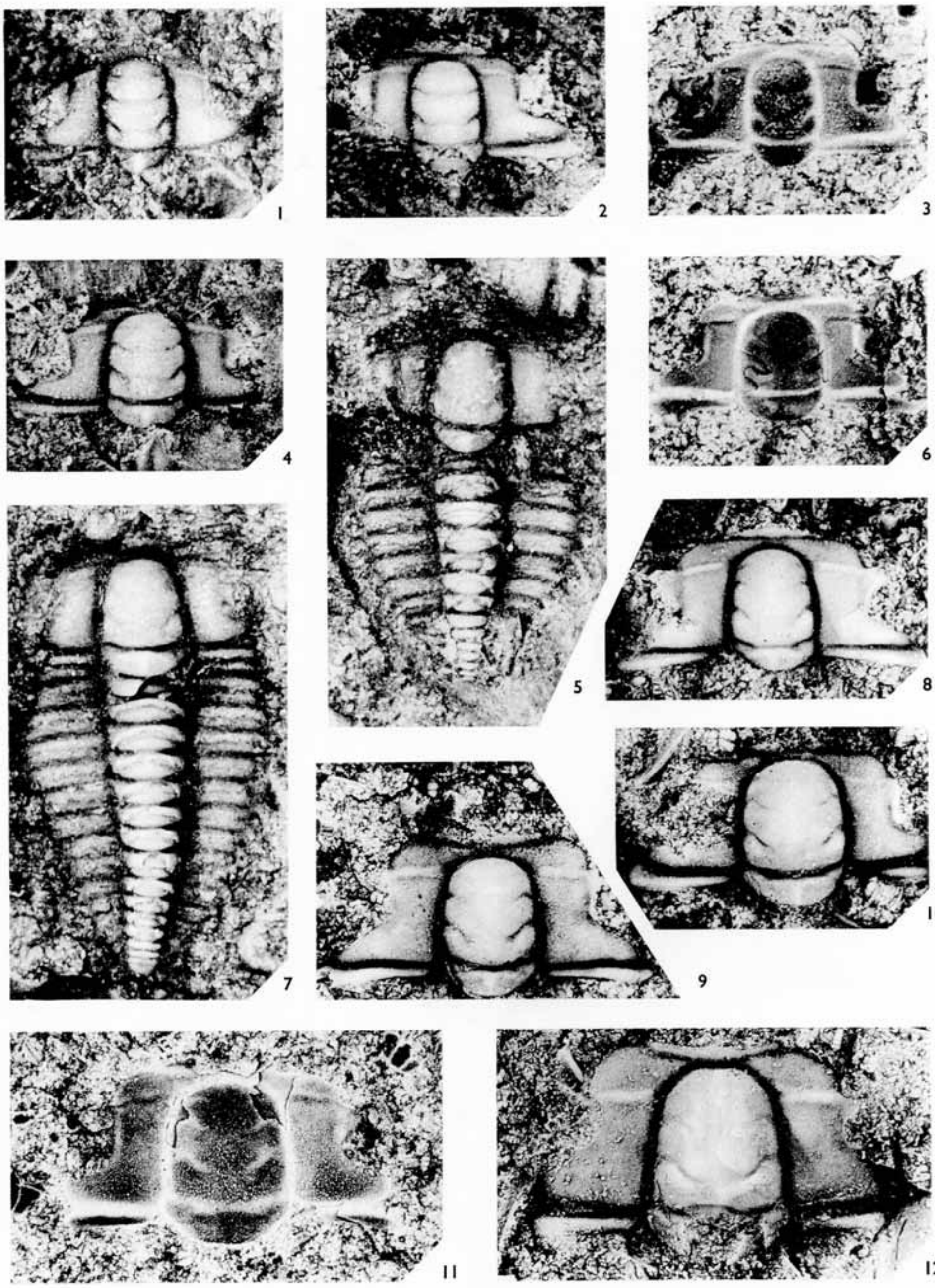

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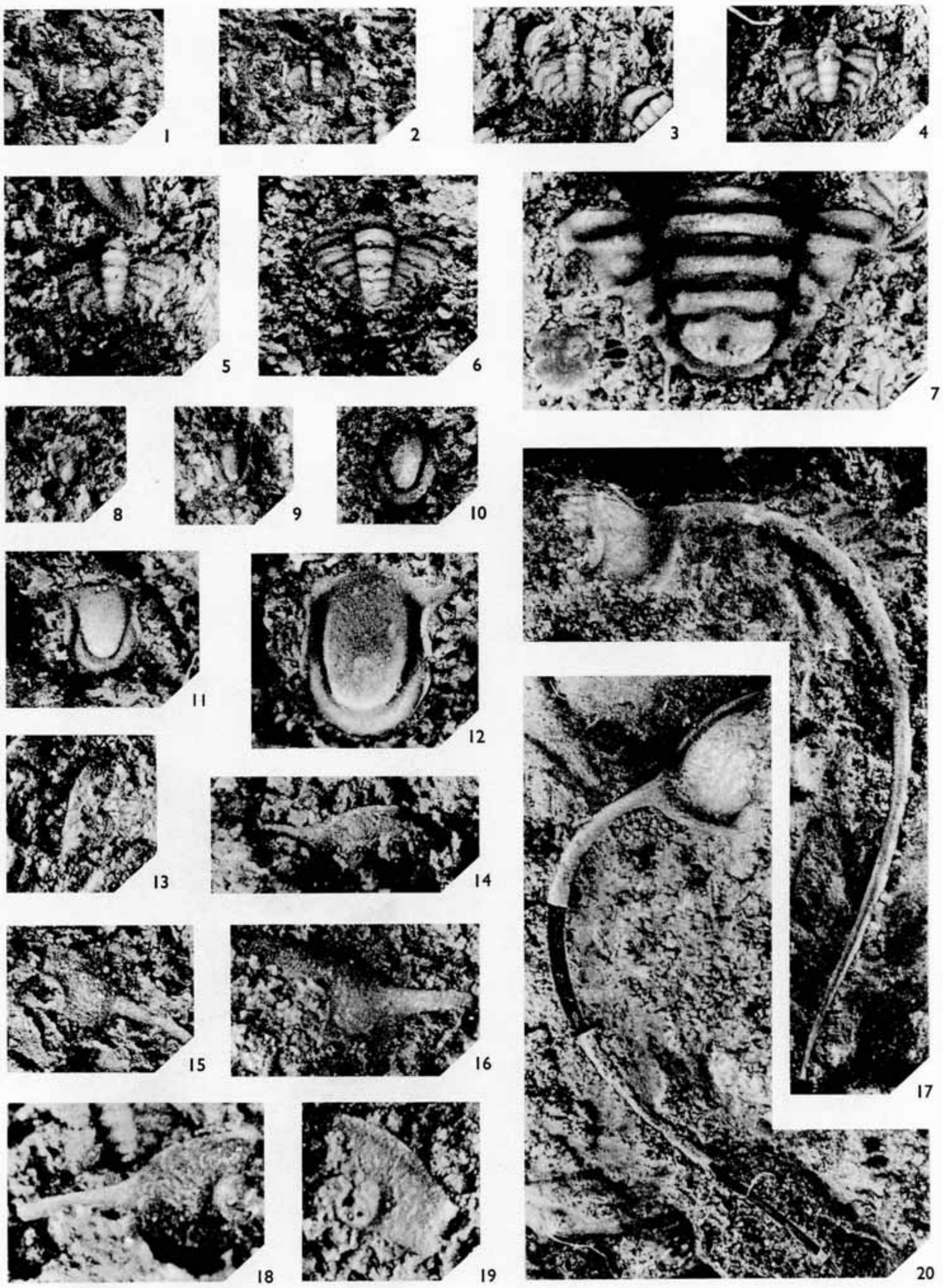

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