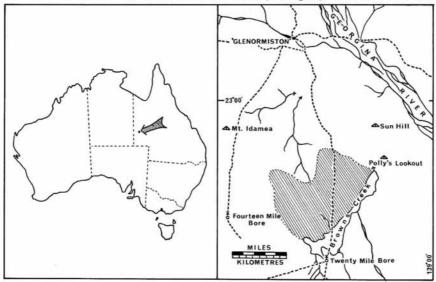
UPPER CAMBRIAN (IDAMEAN) TRILOBITES FROM WESTERN QUEENSLAND, AUSTRALIA

by R. A. HENDERSON

Abstract. This paper reviews new and hitherto poorly understood trilobites from the type section of the early upper Cambrian Idamean Stage on Glenormiston Station, western Queensland. Revisions of local species of Pseudagnostus, Proceratopyge, Eugonocare, Stigmatoa, and Pagodia (Idamea) are given. Two new genera, Aplotaspis (Ceratopygidae) and Prismenaspis (Elviniidae) are established as well as the new species Pseudagnostus curtare, P. margopronus, Proceratopyge cryptica, Aplotaspis mucrora, Aphelaspis australis, Eugonocare whitehousei, E. quadrata, Prismenaspis brownensis, and P. alta. Representatives of Pterocephalia, Yuepingia, and Prochuangia are recorded from Australia for the first time. A biostratigraphic summary for the Idamean Stage and notes of its correlation are given together with discussions of the biomere concept and the significance of the basal Idamean faunal discontinuity.

THE Idamean Stage is the younger of two early upper Cambrian Stages recognized in Australia; both were introduced by Öpik (1963). The preceding Mindyallan Stage is roughly correlative with the *Agnostus pisiformis* Zone of the Swedish upper Cambrian faunal succession while the Idamean Stage approximates to the *Olenus* Zone. Together, the Australian Stages are correlative with the Dresbachian Stage and basal *Elvinia* Zone of the Franconian Stage of the North American Cambrian scale.

Trilobites described here are from some 60 sq km of Georgina Limestone cropping out south of Glenormiston Station Homestead (text-fig. 1). This area has been



TEXT-FIG. 1. Locality map with the area of Georgina Limestone comprising the Browns Creek Section from which the trilobites reported here were collected shaded.

[Palaeontology, Vol. 19, Part 2, 1976, pp. 325-364, pls. 47-51.]

a classic Australian early upper Cambrian trilobite collecting locality and reference area for biostratigraphic subdivision since the reports of Whitehouse (1936, 1939). Öpik (1963, 1967) added a number of new elements to the fauna and offered some revision of Whitehouse's taxa. In addition, he proposed a new biostratigraphic zonation for the early upper Cambrian based on faunas from many scattered outcrop areas in western Queensland among which stratigraphic relationships were poorly known. Öpik's Idamean Stage was a grouping of five zones, three of which were best represented by trilobite faunas collected south of Glenormiston Station Homestead. Hitherto, it has had no designated type section.

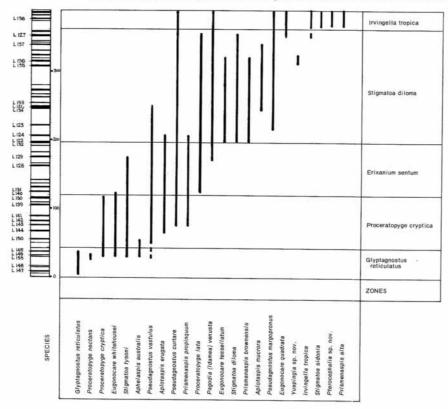
Henderson (in press) has mapped this area in detail and resolved a composite stratigraphy in spite of poor outcrop and structural complexity. The composite succession is here termed the Browns Creek Section. Extensive collections of trilobites have been made from successive limestone horizons for detailed biostratigraphic analysis. Öpik's collections can be integrated into the succession with some accuracy by virtue of their geography, but locality data for Whitehouse's collections are too generalized to allow them to be accurately placed. The revised biostratigraphy of the Browns Creek Section reveals that the entire Idamean faunal succession is represented, passing conformably down into the uppermost zone of the Mindyallan Stage (Henderson, in press). The Browns Creek Section is regarded as the type section for the Idamean Stage.

During the detailed biostratigraphic analysis, it became apparent that some taxonomic revision of the trilobites was needed. The purpose of this report is to describe several new Idamean trilobites and to revise a number of important taxa, mainly established by Whitehouse, which are poorly understood or have been misinterpreted. In addition, it is convenient at this time to give a full listing of the Idamean faunal zonation and to re-examine correlation of the Idamean Stage with biostratigraphic successions recognized elsewhere.

Collections. The study is based on faunas from twenty-seven stratigraphically controlled collection localities. These are designated by numbers, prefixed L, which refer to the Fossil Locality Register of the James Cook University of North Queensland. Complete details of the geography and stratigraphic positions of the localities is given elsewhere (Henderson, in press) and are not repeated here. A summary of their stratigraphic succession is presented in Table 1. Type and figured specimens are listed by numbers prefixed JCF which refer to the Palaeontological Collection of the same institution. Whitehouse's type specimens are curated by the University of Queensland and were consulted in the preparation of this report; specimen numbers pertaining to them are designated by the prefix UQF.

Terminology. Morphological terminology follows that given in Moore (1959) but some terms, especially those applied to agnostids, are from Öpik (1967). The term 'plectral lines' refers to weak, narrow furrows which traverse the frontal area, diverging from the anterior glabellar termination and passing smoothly into confluence with medial terminations of the anterior border furrow. They are characteristic of members of the Ceratopygidae.

TABLE 1. Range chart for Idamean trilobite species described in this report. The column summarizes stratigraphic relationships between collection localities (L140, etc.) for the Browns Creek Section. Limestone horizons are shown as black; intervening horizons are comprised of shale. Thickness scaled in metres.



SYSTEMATIC DESCRIPTIONS

Order MIOMERA Jaekel, 1909
Suborder AGNOSTINA Salter, 1864
Family DIPLAGNOSTIDAE Whitehouse, 1936
Subfamily PSEUDAGNOSTINAE Whitehouse, 1936
Genus PSEUDAGNOSTUS Jaekel, 1909

Remarks. Pseudagnostus is a long-ranging, common late Cambrian genus with considerable potential for interregional correlation. Unfortunately, species groups within it are at present poorly understood due largely to infraspecific variation and uncritical species determinations by many workers. The three species recognized here

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are based on substantial collections from the Browns Creek Section and are stratigraphically restricted. They are closely allied to forms of equivalent age from other regions.

Pseudagnostus vastulus Whitehouse

Plate 47, figs. 10-12

- 1936 Pseudagnostus vastulus Whitehouse, p. 99, pl. 10, figs. 3, 4.
- Pseudagnostus idalis Öpik, p. 153, pl. 62, figs. 8, 9; pl. 63, figs. 1, 3.
 Pseudagnostus idalis Öpik; Hill et al., pl. 12, figs. 1, 2.
- 1971 Pseudagnostus vastulus Whitehouse; Hill et al., pl. 12, figs. 8, 9.

Material. Holotype: UQF 3203, pygidium (figured by Whitehouse, pl. 10, fig. 4). Paratype: UQF 3202, cephalon (figured by Whitehouse, pl. 10, fig. 3). Over twenty-five specimens of each cephala and pygidia, localities L121-122, L124, L128-129, L131, L133-134, L139-144, L150.

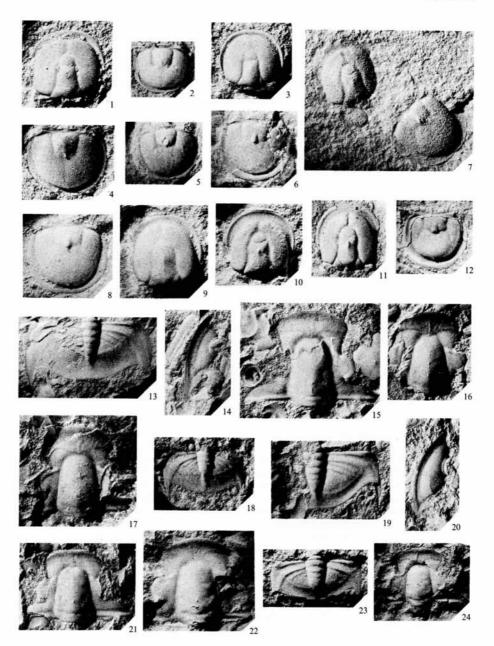
Diagnosis. Pseudagnostus (en grande tenue), with strong, very broad border furrows. Preglabellar median furrow continuous. Glabella with a slight median constriction, posterior rounded to slightly pointed separating well-defined basal lobes. Pygidium with accessory furrows continuous to the border which they typically intersect well anterior to the deuterolobe termination. Pygidial spines small but distinct; located just anterior to the deuterolobe termination. Acrolobes of both cephalon and pygidium faintly constricted and faint, scrobiculate sculpture can often be discriminated on acrolobe flanks of internal moulds.

Dimensions. Cephalic lengths range from 3.0 to 5.1 mm; pygidial lengths from 2.8 to 4.2 mm.

Remarks. P. vastulus Whitehouse is based on material from the type Idamean succession. The two type specimens are associated with Corynexochus plumula Whitehouse on slabs of distinctive limestone that can be confidently assigned to horizons which occur at the base of the zone of Stigmatoa diloma at about the level of localities L121 and L134 (see Table 1). They have been recently refigured in Hill et al. (1971, pl. 12, figs. 8, 9). Unfortunately, the holotype pygidium (UQF 3203) is non-diagnostic because it is only partially exposed. However, the paratype cephalon

EXPLANATION OF PLATE 47

- Figs. 1–5. *Pseudagnostus curtare* sp. nov. 1, JCF 8339, paratype cephalon, L136, ×6. 2, JCF 8309, paratype pygidium, L135, ×6. 3, JCF 8430, paratype cephalon, L138, ×8. 4, JCF 8431, holotype pygidium, L138, ×8. 4, JCF 8431, holotype pygidium,
- L138, ×6. 5, ICF 8314, paratype pygidium, L134, ×6. Figs. 6-9. *Pseudagnostus margopromus* sp. nov. 6, JCF 8316, paratype pygidium, L133, ×6. 7, JCF 8427, disarticulated pygidium and cephalon of one specimen, holotype, L138, ×5. 8, JCF 8428, paratype pygidium, L138, ×6. 9, JCF 8429, paratype cephalon, L138, ×5.
- Figs. 10-12. Pseudagnostus vastulus Whitehouse. 10, JCF 8218, cephalon, L122, ×5. 11, JCF 8304,
- cephalon, L121, ×4. 12, JCF 8454, pygidium, L122, ×6. Figs. 13–18. *Proceratopyge nectans* Whitehouse. 13, JCF 8283, pygidium, ×3. 14, JCF 8441, free cheek, ×4. 15, JCF 8280, cranidium, ×4. 16, JCF 8285, cranidium, ×5. 17, JCF 8284, cranidium, ×4. 18, JCF 8282, pygidium, ×4. All specimens from L149.
- Figs. 19–24. Proceratopyge cryptica sp. nov. 19, JCF 8440, paratype pygidium, L149, ×5. 20, JCF 8295, paratype free check, L149, ×6. 21, JCF 8499, paratype cranidium, L149, ×5. 22, JCF 8290, paratype cranidium, L150, ×5. 23, JCF 8146, paratype pygidium, L155, ×5. 24, JCF 8277, paratype cranidium, L149, ×5.



HENDERSON, Cambrian trilobites

(UQF 3202) and a pygidium from the same slab as, and likely to be conspecific with, the holotype are both conspecific with the abundant material here referred to *P. vastulus*.

P. idalis Öpik (1967) was recorded from the type Idamean succession although the type material is all from other areas. Öpik gave idalis to differ from vastulus in that the accessory furrows extend rearwards beyond the marginal spines. The termination of the accessory furrows is, however, like the strength of the furrows themselves, a variable feature in the material available. A comparison of the type cephala of vastulus and idalis suggests that the latter might be discriminated by the greater width of its border. Border lengths measured at the anterior midline, however, vary from 12% to 16% of the cephalic length on the specimens at my disposal and this difference cannot be regarded as of specific importance.

P. idalis is, therefore, tentatively considered as identical with P. vastulus but conclusive proof of the synonymy must await adequate preparation of the holotype of

P. vastulus.

Pseudagnostus curtare sp. nov.

Plate 47, figs. 1-5

1936 Pseudagnostus cf. cyclopyge (Tullberg); Whitehouse, p. 100, pl. 10, fig. 8. 21960 Pseudagnostus communis (Hall and Whitfield); Bell and Ellinwood pars, pl. 51, figs. 10, 16–18.

Material. Holotype: JCF 8431, L138; cephalon. Paratypes: JCF 8178, JCF 8189, L128; JCF 8332, JCF 8339, L136; JCF 8430, L138; JCF 8188, L139; cephala. JCF 8374, L127; JCF 8177, JCF 8190, L128; JCF 8314, L134; JCF 8309, L135; JCF 8333–8334, L136; pygidia. Additional specimens, L121, L133–134, L137, L143.

Diagnosis. Partially effaced Pseudagnostus characterized by a narrow glabella and narrow cephalic and pygidial borders. Pygidium short, with a length/breadth ratio of less than 0·8; it has weak accessory furrows and small spines located well forward of the deuterolobe termination.

Description. Cephalon wider than long, not strongly arched and somewhat effaced. Preglabellar median furrow weak but continuous. Glabella narrow for the genus, tapered slightly anteriorly, pointed at its posterior termination and with a straight transverse furrow. Glabellar node weak, elongate and medial in position. Border narrow with a distinct furrow and rim of approximately equal widths.

Pygidium well arched and unusually short with a length/breadth ratio of less than 0.8. Acrolobes slightly constricted. Traces of two axial rings anterior of a strong transverse furrow which is deflected posteriorly by a strong, elongate axial node. The furrow is only slightly anterior of the axis midpoint. Vestiges of a third axial ring show as two low swellings which head the lines of notulae showing on internal moulds. Anterior portion of axial furrows strong, slightly convergent, terminating in distinct pits at their intersection with the transverse furrow. Posterior axial furrows obscure. Accessory furrows weak; on some specimens they meet the border opposite the spines while on others they cannot be traced to the border. Border narrow for the genus with a broad furrow and a weak, narrow rim. A pair of weak spines are present, located well forward of the deuterolobe termination.

Dimensions. Holotype pygidium is 3·2 mm in length. Cephalic lengths range from 2·6 to 5·0 mm; pygidial lengths from 2·7 to 3·6 mm.

Remarks. The unusually short pygidium with the transverse axial furrow positioned almost half-way along the axis and the distinct pits at the termination of the anterior portion of the axial furrows set this species apart from others. P. cyclopygeformis (Sun 1924, p. 26, pl. 2, fig. 1a-h) appears to be related. Its cephalic characteristics closely resemble those of curtare but its pygidium has a length/breadth ratio of 0·9 or greater and thus is distinctly longer than that of the present species. P. curtare may well be represented among the range of forms referred to P. communis (Hall and Whitfield) by Bell and Ellinwood (1960). Specimens they figure in pl. 51, figs. 10, 16–18 appear to be indistinguishable from this Australian species.

Pseudagnostus margopronus sp. nov.

Plate 47, figs. 6-9

Material. Holotype: JCF 8427, L138; cephalon and pygidium from a single specimen. Paratypes: JCF 8429, L138; cephalon. JCF 8364, JCF 8369, L127; JCF 8316, L133; JCF 8428, L138; pygidia. Additional specimens, L121, L123, L136.

Diagnosis. Partially effaced *Pseudagnostus* with general morphology in common with the *communis* species group but characterized by shelf-like cephalic and pygidial borders which lack or have very poorly developed border furrows.

Description. Cephalon well domed, approximately as wide as long, slightly effaced but axial furrows distinct. Preglabellar median furrow continuous. Glabella with a slight median constriction, a distinct frontal lobe, and a pointed posterior extremity which clearly separates the basal lobes. Glabellar node elongate, just anterior of glabellar centre. Acrolobe faintly scrobiculate on some internal moulds. Border broad, shelf-like, border furrow lacking or very poorly developed.

Pygidium distinctly wider than long, well domed. Acrolobes slightly constricted; anterior portions of the axial furrows clear and converging slightly posteriorly. Two vestigial anterior axial lobes distinguishable, terminated by a transverse furrow of variable strength which is deflected posteriorly by an elongate axial node. Third ring of axial lobe vestigially represented by a pair of low swellings and these are followed on internal moulds by rows of notulae. Posterior axial furrows obscure, weakly convex laterally; posterior axial segment narrow. Accessory furrows generally clear, obliquely angled to reach the border well forward of the axis termination. A small terminal node can be distinguished. Border broad, shelf-like, lacking a border furrow or almost so. Marginal spines minute, located just anterior to the deuterolobe termination.

Dimensions. Holotype cephalon length is 3.9 mm; holotype pygidial length 4.0 mm. Cephalic lengths range from 3.9 to 4.3 mm; pygidial lengths from 3.0 to 4.0 mm.

Remarks. P. margopronus resembles P. vastulus Whitehouse but is somewhat effaced in comparison to this species and lacks its characteristic border furrow. In most characters P. margopronus resembles members of the P. communis species group listed by Palmer (1968, p. 30) but the shelf-like nature of its cephalic and pygidial

borders, which at best have very faint border furrows, allows discrimination. P. sentosus Grant (1965, p. 108, pl. 9, figs. 2, 3, 5) also appears to be allied but the same distinction applies.

> Family GLYPTAGNOSTIDAE Whitehouse, 1936 Genus GLYPTAGNOSTUS Whitehouse, 1936 Glyptagnostus reticulatus (Angelin)

Material. Twelve cranidia and ten pygidia; localities L145, L147-149, L155.

Remarks. Glyptagnostus reticulatus has been thoroughly described by Palmer (1962) and Öpik (1961a, 1963); a full synonymy was compiled by Palmer (1968), the only subsequent addition being that of Jago (1974). It has a world-wide distribution and is thus a most important species for intercontinental correlation. Palmer (1962) has documented an evolutionary sequence involving two subspecies of reticulatus discriminated by the length of the terminal bulb of the pygidial axis which is significantly longer in younger populations. It is worth recording that the few pygidia from the Browns Creek Section appear to confirm this trend.

> Order PTYCHOPARIIDA Swinnerton, 1915 Suborder PTYCHOPARIINA Richter, 1933 Family CERATOPYGIDAE Linnarsson, 1869 Genus PROCERATOPYGE Wallerius, 1895

- 1895 Proceratopyge Wallerius, p. 56. 21935 Kogenium Kobayashi, p. 273.
- ?1935
- 1937 Lopnorites Troedsson, p. 34.

Type species. Proceratopyge conifrons Wallerius.

Diagnosis. Ceratopygidae with the cephalon comprising about one-third of the total exoskeleton length. Glabella with subparallel sides or tapering anteriorly; surrounded by clearly defined axial furrows and possessing poorly defined lateral glabellar furrows. Thorax comprising nine segments. Pygidial spines subtended from the first segment.

Remarks. A wide range of morphological variation is shown among the some twentytwo nominate species of Proceratopyge but useful subgeneric groupings are not as yet apparent. Troedsson (1937) introduced Lopnorites, type species L. rectispinatus Troedsson, to include species distinguished from *Proceratopyge* (s.s.) by possessing eye ridges. Westergaard (1947), however, described eye ridges from the type species of Proceratopyge, P. conifrons, thus eliminating the original basis for Lopnorites. Later Kobayashi and Ichikawa (1955) recognized Lopnorites as a subgeneric category set apart from Proceratopyge (s.s.) in possessing a subparallel-sided glabella. Öpik (1963) considered that Lopnorites might be best characterized by the number of axial rings of the pygidium. Accordingly, species with six or more axial rings may be grouped in *Lopnorites* while those with less than six may be referred to *Procera*topyge (s.s.). However, glabella shape and the number of axial rings are but two of a number of characters which vary among species of Proceratopyge and division on either of these criteria does not result in the grouping of closely allied species. Further, intraspecific variation in the Australian species *P. lata* embraces the characteristics of both *Proceratopyge* and *Lopnorites* in terms of either glabella shape (see Pl. 48, figs. 8, 10) or the number of axial rings (Pl. 48, figs. 9, 11). *Lopnorites* is here regarded as a valueless taxon best treated as synonymous with *Proceratopyge*.

Kogenium Kobayashi, based on K. rotundum Kobayashi (1935, p. 274, pl. 17, figs. 6-9) is of uncertain status. As noted by Öpik (1963, p. 97), pygidia of K. rotundum cannot be distinguished from those of Proceratopyge but cranidia appear to have been mismatched and apparently represent a stock of trilobites unrelated to the Ceratopygidae. Cranidia of different morphology were subsequently assigned to K. rotundum by Kobayashi (1962, p. 120) but these closely resemble cranidia of Aplotaspis gen. nov. established herein. K. rotundum is based on pygidial characters (Kobayashi 1962, p. 119). The same is therefore true for Kogenium which is best regarded as a tentative synonym of Proceratopyge.

Proceratopyge ranges as low as the zone of Lejopyge laevigata in Sweden (Westergaard 1947), the zone of Agnostus pisiformis in Kazakhstan (Ivshin and Pokrovskaya 1968), and the zone of Blackwelderia and Drepanura in southern China (Jegorova et al. reported in Kobayashi 1971) but the available evidence suggests it to range no lower than the zone of G. reticularis in Alaska (Palmer 1968) and Australia. In Australia its range extends upwards to the base of the local zone of Irvingella tropica and it is a characteristic element of the Idamean Stage being represented at almost

every locality in the Browns Creek Section.

Two of the Australian species recognized by Whitehouse (1939) must now be discarded. The holotype of *P. rutellum* figured by Whitehouse (1939, pl. 25, fig. 9) cannot be located but appears to represent *Aplotaspis erugata* (Whitehouse) in the poor definition of the glabella from the exceedingly narrow fixed cheeks and the near absence of lateral glabellar furrows. A paratype cranidium, UQF 3389, figured by Whitehouse (1939, pl. 25, fig. 10) is identical with *A. erugata*. The two species are here regarded as synonymous. *P. polita* Whitehouse (1939, p. 251, pl. 25, fig. 14) does not belong in *Proceratopyge*. It is known only from a cranidium which superficially resembles that of *Proceratopyge* but which lacks the characteristic glabellar tubercle. In its observable characteristics *P. polita* resembles *Mapania*, cephala of which are distinguished from *Proceratopyge* primarily by lacking a glabellar node (Öpik 1961*b*, p. 166). Other trilobites from near Polly's Lookout, the type locality of *P. polita*, indicate a pre-Idamean age (Henderson, in press).

Proceratopyge nectans Whitehouse

Plate 47, figs. 13-18

1939 Proceratopyge nectans Whitehouse, p. 249, pl. 25, fig. 8a, non fig. 8b.

Material. Holotype: UQF 3386, cranidium, 16 miles south of Glenormiston Homestead (figured by Whitehouse, pl. 25, fig. 8a). Thirty cranidia, twenty-five pygidia, five free cheeks, and numerous fragments, 1.149

Diagnosis. Cranidium with a gently tapering glabella showing indistinct lateral glabellar furrows; posterior borders narrow and strap-like. Frontal area elongate for the genus, about one-third of the cranidial length. It is gently concave and possesses

distinct plectral lines. Pygidium and free cheeks with unusually broad borders. Axial lobe of pygidium with four or five axial rings.

Description. Frontal area gently concave, about one-third of the cranidial length. Anterior border broad, gently upturned and with an arcuate anterior margin. Border furrow distinct, confluent with diverging plectral lines which extend from the glabellar termination to the border furrow. Glabella gently tapering, lateral glabellar furrows lacking or obscure. Palpebral lobes short, about 35% of the glabellar length and terminating posteriorly opposite the glabellar node. Eye ridges distinct. Posterior cranidial limbs narrow, strap-like. Free cheek with a broad border and a narrow, elongate genal spine. Pygidial border flattened and exceptionally broad, its span being approximately equal to the length of the pleural field. Axis narrow, tapering and extending on to the border; axial rings are poorly defined and number four or rarely five. Pygidial spines elongate.

Dimensions. Cranidial lengths range from 2·1 to 8·8 mm; lengths of pygidial axes from 3·2 to 5·6 mm.

Remarks. The pygidium figured as *P. nectans* by Whitehouse (1939, pl. 25, fig. 8b) has a narrow border and belongs to *P. cryptica* sp. nov. which is contemporary with nectans in the lower portion of its range. *P. nectans* is a distinctive species of Proceratopyge, characterized by the very broad borders of its pygidium and free cheeks. Cranidia have elongate frontal areas which in general allow separation from cranidia of *P. cryptica* sp. nov. (see text-fig. 2) which are otherwise very similar. This difference is statistically significant; the statistic 'z' evaluating differences in slope of the regressions given in text-fig. 2 is 3-97 (see Imbrie 1956, p. 235).

Rare specimens allied to, but specifically distinct from, *P. nectans* occur higher in the Idamean succession but the species are as yet incompletely known and unnamed. The cranidium described by Öpik (1963, p. 99, pl. 5, fig. 5A, text-fig. 37) as *P. cf. chuhsiensis* Lu from the zone of *I. tropica* is such a form and shows the characteristic elongate frontal area. Pygidia have a broad border like *P. nectans. P. chuhsiensis* Lu (1956a, p. 280, pl. 1, figs. 1–6) may indeed be allied to these forms as Öpik suggested.

It is evident that two species groups are represented among Australian *Proceratopyge*, one comprised of *P. nectans* and its offshoots and the other the partial lineage of *P. cryptica* sp. nov. and *P. lata* Whitehouse.

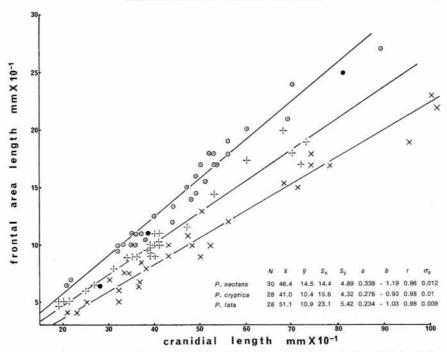
Proceratopyge cryptica sp. nov.

Plate 47, figs. 19-24; Plate 48, figs. 1-3

1939 Proceratopyge nectans Whitehouse pars, pl. 25, fig. 8b.1968 Proceratopyge cf. P. chuhsiensis Lu; Palmer, p. 55, pl. 10.

Material. Holotype: JCF 8278, L149; cranidium. Paratypes: JCF 8200, JCF 8269, L130; JCF 8151, L142; JCF 8195, JCF 8277, JCF 8439, L149; JCF 8290-8292, JCF 8294, JCF 8442, L150; cranidia. JCF 8275, JCF 8440, L149; JCF 8293, L150; JCF 8146, L155; pygidia. JCF 8295, L149; free cheek. Additional specimens, L130, L141-142, L144-145, L149-150.

Diagnosis. Frontal area a little more than a quarter of the cranidial length, with a gently upturned border and distinct plectral lines. Glabella gently tapering with weak, variable glabellar furrows. Palpebral lobes short and the posterior cranidial



TEXT-FIG. 2. Reduced major axis regressions of frontal area length plotted against cranidial length for Idamean species of *Proceratopyge*. The following standard symbols are employed in the tabulated statistics: N—number of specimens; \bar{x} —mean of x; \bar{y} —mean of y; Sx—standard deviation of x; Sy—standard deviation of y; a—growth ratio; b—initial growth index; r—correlation coefficient; σ_a —standard error of slope.

limbs narrow and strap-like. Free cheeks with narrow borders. Pygidium twice as wide as long, with five or six axial rings.

Description. Frontal area a little over a quarter of the cranidial length, very gently concave and with an arcuate margin. Anterior border gently upturned, narrow; border furrow distinct, confluent with divergent plectral lines which extend from the glabellar termination. Glabella gently tapering, lateral glabellar furrows variably developed but commonly two pairs are distinguishable, the posterior pair invariably with their strongest indentation sagittally orientated. Eye ridges are discernible. Palpebral lobes short, little more than a third of the glabellar length and terminating posteriorly opposite the glabellar node. Posterior limbs narrow, strap-like. Free cheeks with a narrow border and a long genal spine. Pygidium about twice as wide as long with the maximum span of the concave border less than half the length of the pleural fields. Axis strong, tapering, with five or six rings and a pointed terminus. Lateral spines long and narrow.

Dimensions. Holotype cranidium is 7.2 mm in length. Cranidial lengths range from 1.9 to 7.2 mm; lengths of pygidial axes from 1.6 to 4.5 mm.

Remarks. P. cryptica shows a striking resemblance to the Alaskan species described as P. cf. chuhsiensis Lu by Palmer (1968). The only distinction is in the relative length of the frontal area, the two larger Alaskan specimens plotting at the extreme edge of variation in P. cryptica (text-fig. 2). This difference is regarded as intraspecific and the two species united. P. chuhsiensis Lu (1956a, p. 280, pl. 1, figs. 1-6) although established on poorly preserved material appears to be distinct as its palpebral lobes measure about half the glabellar length. P. cryptica is allied to P. liaotungensis Kobayashi and Ichikawa (1955). The cephalic characteristics of the Manchurian species are not well documented but the glabella appears to be more squat than that of P. cryptica. Pygidia of the two species are indistinguishable.

Proceratopyge lata Whitehouse

Plate 48, figs. 4-11

1939 Proceratopyge lata Whitehouse, p. 248, pl. 25, figs. 12, 13.
 1963 Proceratopyge lata Whitehouse; Öpik, p. 98, pl. 4, figs. 9, 10; pl. 5, figs. CC, EF, GF.

1971 Proceratopyge lata Whitehouse; Hill et al., pl. 8, figs. 2, 3.

Material. Holotype: UQF 3391, a cranidium, 5 miles north of Twenty Mile Bore, Glenormiston (figured by Whitehouse, pl. 25, fig. 12). Thirty-five cranidia, nineteen pygidia, six free cheeks, localities L121-124, L127, L129, L134-137.

Diagnosis. Proceratopyge closely allied to P. cryptica sp. nov. but differing in the nature of the anterior border of the cranidium which is less than 25% of the cranidial length and is sharply upturned to the anterior margin. Pygidium with five or six axial rings.

Description. Frontal area short, less than 25% of the cranidial length. Anterior border distinct, confluent with plectral lines which diverge from the glabellar termination. Anterior portion of the border sharply upturned to a flattened anterior margin. Glabella gently tapering with variably developed lateral glabellar furrows. On some specimens three pairs can be distinguished while on others, even from the same locality, only a single pair is discernible. The posterior pair have their strongest

EXPLANATION OF PLATE 48

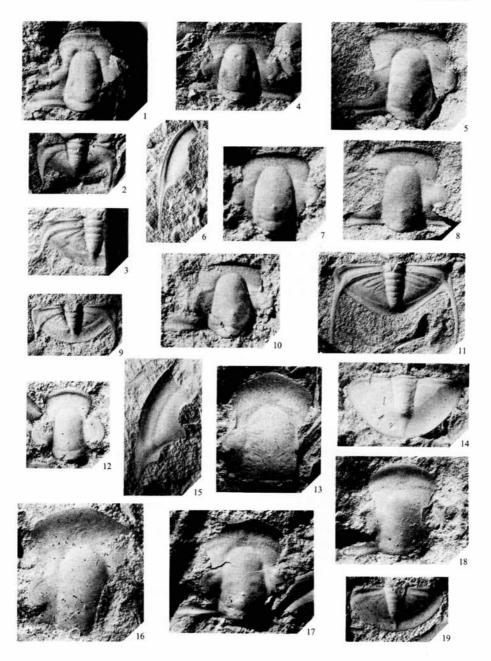
Figs. 1-3. Proceratopyge cryptica sp. nov. 1, JCF 8278, holotype cranidium, L149, ×3. 2, JCF 8293, paratype pygidium, L150, ×5. 3, JCF 8275, paratype pygidium, L149, ×4.

Figs. 4-11. Proceratopyge lata Whitehouse. 4, JCF 8287, cranidium, L129, ×6. 5, JCF 8258, cranidium, L122, ×4. 6, JCF 8448, free cheek, L136, ×3. 7, JCF 8435, cranidium, L137, ×8. 8, JCF 8446, cranidium, L136, ×4. 9, JCF 8267, pygidium, L122, ×6. 10, JCF 8452, cranidium, L137, ×8. 11, JCF 8329, pygidium, L136, ×3.

Fig. 12. Yuepingia sp. nov. JCF 8353, cranidium, L136, ×6.

Figs. 13–14. Aplotaspis mucrora gen. et sp. nov. 13, JCF 8234, paratype cranidium, L121, \times 3. 14, JCF 8232, holotype pygidium, L121, \times 2.

Figs. 15-19. Aplotaspis erugata (Whitehouse). 15, JCF 8250, free cheek, L130, × 4. 16, JCF 8254, cranidium, L144, ×5. 17, JCF 8247, cranidium, L130, ×5. 18, JCF 8257, cranidium, L139, ×5. 19, JCF 8471, pygidium, L130, ×4.



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indentation sagittally oriented. Palpebral lobes very short, 25–30% of the glabellar length, typically terminating just anterior of the glabellar node. Free cheek with a narrow border, a strong border furrow and a long, slender, pleated genal spine. Pygidium twice as wide as long with a distinct, narrow, concave border. Axis strong, tapering with five to seven rings. Lateral spines delicate and elongate, nearly as long as the pygidium is wide.

Dimensions. Cranidial lengths range from 2·1 to 10·1 mm; lengths of pygidial axes from 2·1 to 6·0 mm.

Remarks. P. lata is a variable species even among material from a single locality. It also shows systematic morphological change in time. Cranidia from lower horizons in general have less steeply upturned zones of the anterior border, are less flattened along their anterior margins, and their frontal areas are a little more elongate (compare early specimens illustrated in Pl. 48, figs. 4, 5 with late specimens illustrated in figs. 7, 8, 10).

P. lata is closely allied to P. cryptica and the two species probably comprise a bioseries. Their ranges abut in the Browns Creek Section, but an evolutionary transition is not recorded, and an abrupt change in cranidial morphology occurs where their ranges meet. The two species are discriminated on the relative lengths of their frontal areas as shown in text-fig. 2. Discrimination of the slopes of the calculated regression lines is statistically valid with the statistic 'z' having the value of 3·26 (see Imbrie 1956, p. 235). The stronger reflection of the anterior border, the more flattened anterior margin, and the slightly shorter palpebral lobes of the cranidia of P. lata also serve to distinguish it from P. cryptica. Pygidia of the two species cannot be separated with confidence, especially when specimens from low in the range of P. lata are involved (see Pl. 48, figs. 2, 3, 9).

Genus YUEPINGIA Lu, 1956b Yuepingia sp. nov.

Plate 48, fig. 12

Material. JCF 8335-8336, JCF 8353; cranidia; locality L136.

Description. Cranidium with a gently tapering glabella which lacks lateral glabellar furrows and bears a small posterior glabellar tubercle. Occipital furrow distinct and narrow; occipital lobe flattened. Fixed cheeks comprised almost entirely of large, subhorizontal, semicircular palpebral lobes which measure a little over half the glabellar length and which are located opposite the glabellar midpoint. Weak palpebral furrows can be distinguished. Frontal area about 40% of the glabellar length; border furrow very faint passing into confluence with equally faint plectral lines which diverge from the anterior glabellar termination. The border is initially flattened and slightly declined but is gently turned up into a narrow lip at the periphery.

Dimensions. Cranidial lengths range from 2.7 to 3.8 mm.

Remarks. Hitherto Yuepingia has been known only from the southwestern Chinese type species niobiformis Lu (1956b, p. 378, pl. 1, figs. 6-13) and Y. glabra Palmer (1968, p. 56, pl. 13, figs. 9, 12-16) from Alaska. The Australian cranidia shows good agreement with these species in major characteristics but differs in possessing a slightly

more elongate frontal area with a more distinct border lip and in the more posterior position of the palpebral lobes. It clearly represents a new species but formal naming must wait the collection and description of further material.

Genus APLOTASPIS nov.

Type species. Aplotaspis erugata (Whitehouse)

Diagnosis. Partially effaced Ceratopygidae lacking pygidial spines. Glabella tapering anteriorly, with poorly defined axial furrows. Lateral glabellar furrows lacking or indistinct. Frontal area elongate, measuring almost half the glabellar length, and comprised largely of the anterior border. Palpebral lobes short, about a quarter of the glabellar length. Thorax comprises eight segments. Pygidium and free cheeks with well-defined, broad, concave borders.

Description. Cephalon opisthoparian, semicircular. Glabella inflated, arched in the sagittal plane, passing smoothly into the flattened cheeks and the frontal area; axial furrows indistinct. Frontal area very long, almost half the glabellar length, concave and rising anteriorly. The border furrow lies just anterior to the glabellar termination and is interrupted by a broad plectrum. Facial sutures divergent, initially straight but later passing into the curvature of the anterior margin. Glabellar furrows lacking or almost so; a small posterior glabellar node is present. A narrow occipital lobe is just discernible, divided from the glabella by a very weak occipital furrow. Fixed cheeks about half the glabellar width, largely comprised of slightly raised, strongly curved palpebral lobes which are located just anterior of the glabellar midpoint and are a little over a quarter of the glabellar length. Palpebral furrows distinct. A weak eye ridge slopes forward to the glabella which it joins some distance before the glabellar termination. Posterior limbs narrow, elongate, strap-like. Free cheek initially convex but sloping out to a very broad, concave border; its anterior termination is pointed and there is a short genal spine. Thorax of eight segments, each with distinct axial furrows and pleurae which are sharply turned downwards towards the periphery and have broad, distinct pleural grooves. Pygidium semicircular with the axis weakly convex, tapering posteriorly; up to five poorly defined axial rings can be differentiated. Pleural fields dropping gently to a broad, flattened border and reflected at their leading edges into a lip which terminates distally in distinct articulating facets. Three very faint, narrow pleural ribs may be distinguished.

Remarks. Whitehouse (1939, p. 239) incorrectly interpreted erugata as possessing a narrow frontal area and referred the species to Charchaqia Troedsson as a result. In fact the single specimen available to Whitehouse is misleading in that its frontal area is not fully exposed. The true cranidial morphology of erugata described here show it to represent a new genus, Aplotaspis nov., for which it is designated the type species

Aplotaspis belongs to the Ceratopygidae Linnarsson, other members of which have a large frontal area, a glabella with subparallel sides, poorly defined glabellar furrows, a post-central glabellar node and a semicircular pygidium with a tapering axis, weak pleural ribs, and a well-defined border. The number of thoracic segments lies within the range shown by the Ceratopygidae. Its closest relative is Yuepingia Lu (1956b,

p. 377) recently reviewed by Palmer (1968, p. 56). Aplotaspis is, however, readily discriminated by its much shorter palpebral lobes, much larger frontal area, and its very clear pygidial border.

Among previously described taxa the unclassified Alaskan pygidium of Franconian age listed by Palmer (1968, p. 103, pl. 13, fig. 10) resembles Aplotaspis as does the unclassified pygidium from the Irvingella tropica Zone listed in Öpik (1963, p. 100, pl. 5, fig. BB). Cranidia assigned to the type species of Kogenium Kobayashi, K. rotundum, by Kobayashi (1962, p. 120) appear to be indistinguishable from Aplotaspis. However, K. rotundum was established by Kobayashi (1935, p. 274, pl. 17, figs. 6-9) for pygidia of Proceratopyge morphology and mismatched cranidia which are unrelated to the Ceratopygidae. Kogenium is not, therefore, a senior synonym of Aplotaspis.

Aplotaspis erugata (Whitehouse)

Plate 48, figs. 15-19; Plate 49, figs. 1-4

- 1939 Charchaqia erugata Whitehouse, p. 239, pl. 25, figs. 6, 7a.
- 1939 Proceratopyge rutellum Whitehouse, pl. 25, figs. ?9, 10.
- 1971 Charchaqia erugata Whitehouse; Hill et al., pl. 6, fig. 7.

Material. Holotype: UQF 3369, a whole specimen about 4 miles north of Twenty Mile Bore, Glenormiston (figured by Whitehouse, pl. 25, figs. 6, 7a). Twenty-five of each cranidia and pygidia, localities L122, L124, L128–130, L139–141, L143–144.

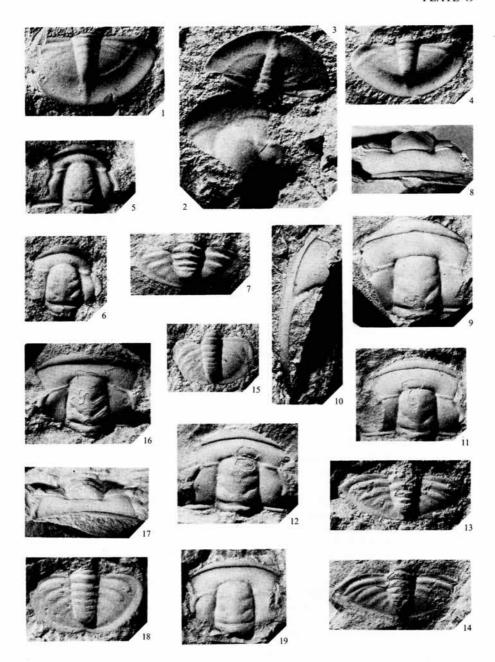
Diagnosis. Aplotaspis with the anterior margin of cranidia uniformly arched or indistinctly pointed. Span of the pygidial border distinctly shorter than the anterior width of the pleural fields.

Dimensions. Cranidial lengths range from 3.0 to 7.4 mm; pygidial lengths from 2.0 to 4.5 mm.

Remarks. A. erugata is a common species in the upper P. cryptica Zone and in the Erixanium sentum Zone and is somewhat variable in its definitive characters. The width of the pygidial border is variable (Pl. 48, fig. 19; Pl. 49, figs. 1, 3, 4) but is never as broad as that of A. mucrora. Likewise the anterior cranidial margin may be evenly arched (Pl. 48, fig. 18) or slightly pointed (Pl. 48, fig. 16) but never displays the straight limbs and clear point of A. mucrora.

EXPLANATION OF PLATE 49

- Figs. 1-4. Aplotaspis erugata (Whitehouse). 1, JCF 8253, pygidium, L144, ×5. 2, JCF 8248, cranidium, L130, ×5. 3, JCF 8249, pygidium, L130, ×5. 4, JCF 8252, pygidium, L144, ×5. Figs. 5-7. Aphelaspis australis sp. nov. 5, JCF 8126, holotype cranidium, ×5. 6, JCF 8127, paratype
- cranidium, ×6. 7, JCF 8131a, paratype pygidium, ×4. All specimens from L155.
- Figs. 8-14. Eugonocare quadrata sp. nov. 8-9, JCF 8410, paratype cranidium, L138, ×2. 10, JCF 8357, paratype free cheek, L127, ×2·5. 11, JCF 8417, paratype cranidium, L138, ×2. 12, JCF 8415, paratype cranidium, L138, ×3. 13, JCF 8361, paratype pygidium, L127, ×4. 14, latex peel from JCF 8414, holotype pygidium, L138, ×3.
- Figs. 15-19. Eugonocare whitehousei sp. nov. 15, JCF 8157, paratype pygidium, L144, ×4. 16-17, JCF 8262, paratype cranidium, L130, ×2. 18, JCF 8159, holotype pygidium, L149, ×3. 19, JCF 8161, paratype cranidium, L149, ×2.5.



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Aplotaspis mucrora sp. nov.

Plate 48, figs. 13-14

?1939 Eugonocare tessellatum Whitehouse pars, pl. 23, fig. 16.

Material. Holotype: JCF 8232, L121; pygidium. Paratypes: JCF 8234-8235, L121; JCF 8236-8237, L136; cranidia. JCF 8231, JCF 8233, JCF 8203, L121; JCF 8311, L133; pygidia.

Diagnosis. Aplotaspis with the anterior margin of cranidium distinctly pointed. Span of the pygidial border measuring about the same as the anterior width of the pleural fields.

Dimensions. Holotype cranidium is 9.4 mm in length. Cranidial lengths range from 6.3 to 9.4 mm; pygidial lengths from 4.1 to 9.4 mm.

Remarks. A. mucrora is an uncommon species in the zone of Stigmatoa diloma. The pygidium figured by Whitehouse (1939, pl. 23, fig. 16) and referred to Eugonocare tessellatum Whitehouse, now numbered UQF 3366 in the University of Queensland collections, appears to belong to this species.

Family PTEROCEPHALIIDAE Kobayashi, 1935 Subfamily APHELASPIDINAE Palmer, 1960 Genus APHELASPIS Resser, 1935

Aphelaspis is a characteristic early upper Cambrian North American genus commonly employed as a zonal index (see Palmer 1965b, p. 5). Records of it from other areas are, however, rare; they include western Antarctica (Webers 1972), southern China (Jegorova et al. reported in Kobayashi 1971), Kazakhstan (Ivshin 1956), northern Siberia (Rosova 1968; Pokrovskaya 1961), and Australia (Thomas and Singleton 1956).

Aphelaspis australis sp. nov.

Plate 49, figs. 5-7

Material. Holotype: JCF 8126, L155; cranidium. Paratypes: JCF 8132, L149; JCF 8127-8130, L155; cranidia. JCF 8443, L150; JCF 8131, L155; pygidia.

Diagnosis. Aphelaspis characterized by a short frontal area measuring about 40% of the glabellar length, elongate palpebral lobes, and a pygidium which is twice as long as wide

Description. Cranidium with the glabella curved sagittally, distinctly tapering, bluntly rounded anteriorly, and with two pairs of weak, posteriorly directed lateral glabellar furrows. Occipital furrow well marked, occipital lobe narrow with a small median tubercle. Frontal area about 40% of the glabellar length, unequally divided by a strong border furrow into a broader, convex, downsloping preglabellar field and a narrower, convex border. Fixed cheeks a little wider than half the maximum glabellar width, convex and rising slightly to the long, gently curved palpebral lobes, which are positioned a little anterior to the glabellar midpoint. Narrow eye ridges and palpebral furrows are well marked. The posterior limbs are short, narrow, and with strong furrows. Pygidium semicircular in outline, about twice as wide as long. Axis strong, gently tapering to a blunt terminus and with five rings. Pleural fields with three pairs

of broad, rounded ribs on which interpleural grooves can just be recognized. The border is well marked, narrow, and flattened.

Dimensions. Holotype cranidium is 4.5 mm in length. Cranidial lengths range from 3.1 to 7.3 mm; pygidial lengths from 3.0 to 3.4 mm.

Remarks. The nearest match for A. australis is with A. brachyphasis Palmer (1962, p. 33, pl. 4, figs. 1–19) and A. subditus Palmer (1962, p. 35, pl. 4, figs. 20–22, 25) but it is set apart from these and other species of Aphelaspis by its short frontal area and semicircular pygidium with a narrow, flattened border.

Genus EUGONOCARE Whitehouse, 1939

1939 Eugonocare Whitehouse, p. 224.

1967 Eugonocare Öpik, p. 202.

Type species. Eugonocare tessellatum Whitehouse 1939,

Diagnosis. Aphelaspidinae characterized by a subquadrate cranidium in which the interocular width clearly exceeds the cranidial length. Free cheeks with a long, slender genal spine. Pygidium lacking spines.

Description. Aphelaspidinae with a squat, subquadrate cranidium such that the interocular width clearly exceeds the cranidial length. Glabella gently tapering to subquadrate with an abruptly rounded anterior termination and two pairs of well-marked posteriorly directed lateral glabellar furrows. A third pair of lateral glabellar furrows is just discernible near the anterior glabellar termination. Occipital lobe clearly demarcated, possessing a small occipital node. Palpebral lobes set opposite the glabellar midpoint and measure about one-third its length. Fixed cheeks weakly convex, subhorizontal, and broad; about 65% of the glabellar width measured on the same line. Eye ridges distinct, joining the glabella near its termination. Preglabellar field convex with a delicate, venulose ornamentation, downsloping to a well-developed border furrow. Anterior border convex, narrow, sharply reflected into the border furrow. Free cheeks with venulose ornament, a very long, slender genal spine, and a well-developed border furrow. Most of the border is convex but there is a distinct zone of concavity adjacent to the margin.

Pygidium transversely subovate; axis strongly arched, gently tapering, reaching almost to the border and with five or six well-marked rings. Pleural areas weakly convex, with three or four broad, weak ribs bearing distinct pleural grooves. Border narrow, flattened, lacking spines.

Remarks. Öpik (1967) regarded Eugonocare as a probable junior synonym of Proaulacopleura Kobayashi (1936, p. 93) which is based on P. buttsi Kobayashi. Recent reports by Palmer (1962, 1965b) show, however, that P. buttsi is best referred to Aphelaspis. Cranidia of Eugonocare are set apart from A. buttsi and other species of Aphelaspis by their squat, subquadrate shape with the interocular width distinctly exceeding the cranidial length. In Aphelaspis these two measurements are subequal. The cranidia of some species of Olenaspella, for example O. regularis Palmer (1962, p. 38, pl. 5, figs. 1–3), are inseparable from Eugonocare but this genus is set apart by virtue of its pygidial spines. Whitehouse's concept of Eugonocare is now known to have been partially in error because most of the pygidia and the single free cheek which he figured as representa-

tive of the genus were misidentified.

Eugonocare is a characteristic element of Idamean faunas in north-western Queensland and is abundantly represented in collections from the Browns Creek Section. It has also been recorded from Victoria, Australia (Thomas and Singleton 1956) and doubtfully from western Antarctica (Webers 1972). The Kazakhstan species O. evansiformis Ivshin (1962, p. 70, pl. 4, figs. 11-18; text-fig. 17) is known from cranidia alone and may well represent Eugonocare. It occurs with Irvingella and is, therefore, probably younger than American Olenaspella which are restricted to pre-Dunderbergia zones of the Dresbachian Stage (Palmer 1965b) whereas Irvingella is a characteristic member of the American Elvinia Zone assemblage. As noted by Öpik (1963, p. 88), Eugonocare(?) sp. recorded by Lu (1956b) from Kueichou, China is more likely to be a representative of Stigmatoa Öpik.

The three species recognized here are closely allied and are discriminated essentially

on pygidial shape (text-fig. 3).

Eugonocare tessellatum Whitehouse

Plate 50, figs. 1-5

1939 Eugonocare tessellatum Whitehouse, p. 226, pl. 23, figs. 15, 17 (non figs. 16, 18); pl. 25, fig. 7b.

Material. Holotype: cephalon UQF 3370a, b from c. 4½ miles north of Twenty Mile Bore, Glenormiston (figured by Whitehouse, pl. 23, fig. 15; pl. 25, fig. 7b). Fifteen cranidia, ten pygidia, eight free cheeks; localities L121-122, L132-136.

Diagnosis. Anterior cranidial border narrow, convex. Pygidium of moderate width (text-fig. 3) with five axial rings and pleural grooves which are not strongly oblique, reaching almost to the axial furrows.

Dimensions. Cranidial lengths range from 6.5 to 12.0 mm; pygidial lengths from 4.7 to 8.8 mm.

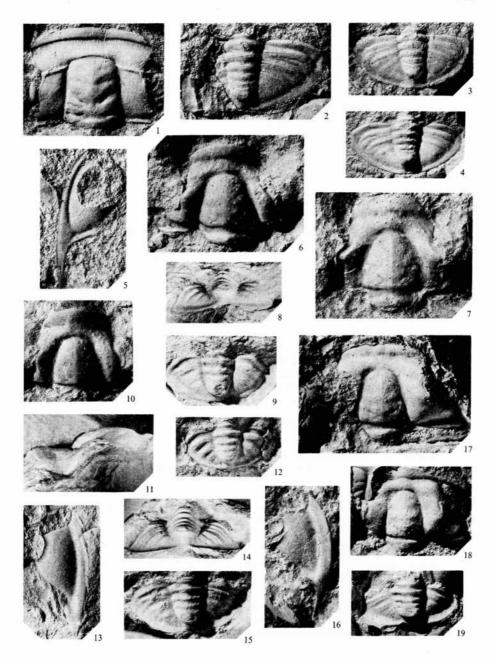
Remarks. The free cheek figured by Whitehouse (1939, pl. 23, fig. 18) cannot be located in the University of Queensland collections. It appears to be from a Pagodia (Idamea). Likewise the pygidium (UQF 3366) figured in plate 23, fig. 16 was misidentified and probably represents Aplotaspis mucrora sp. nov. The second figured pygidium (UQF 3365a, pl. 23, fig. 17) is only a fragment but appears to have been correctly identified.

EXPLANATION OF PLATE 50

Figs. 1-5. *Eugonocare tessellatum* Whitehouse. 1, JCF 8259, cranidium, L132, ×3. 2, JCF 8317, pygidium, L136, ×2·5. 3, JCF 8260, pygidium, L132, ×3. 4, JCF 8271, pygidium, L122, ×3. 5, JCF 8350, free cheek, L136, ×4.

Figs. 6-13. *Prismenaspis propinquum* (Whitehouse). 6, JCF 8265, cranidium, L130, ×4. 7, JCF 8244, cranidium, L139, ×3. 8-9, JCF 8264, pygidium, L130, ×3. 10-11, JCF 8263, L130, ×3. 12, JCF 8246, pygidium, L139, ×3. 13, JCF 8445, free cheek, L139, ×3.

Figs. 14-19. Prismenaspis brownensis gen. et sp. nov. 14-15, JCF 8299, holotype pygidium, L121, ×2. 16, JCF 8306, paratype free cheek, L121, ×3. 17, JCF 8307, paratype cranidium, L135, ×1·5. 18, JCF 8345, paratype cranidium, L136, ×2·5. 19, JCF 8300, paratype pygidium, L121, ×2.



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The cranidial characteristics of E. tessellatum as redefined in this report are inseparable from those of the stratigraphically lower species E. whitehousei sp. nov. and the two species are differentiated by their pygidia. Since the holotype of E. tessellatum is a cranidium, a difficult situation arises. The cranidium is associated in the same slab with A. erugata (Whitehouse) but the range of that species overlaps those of both E. tessellatum and E. whitehousei. However, the type locality of E. tessellatum is given by Whitehouse as $4\frac{1}{2}$ miles north of Twenty Mile Bore, Glenormiston where mapping suggests that strata predating the range of E. tessellatum are lacking (Henderson, in press). This conclusion is substantiated by other taxa among the collections which Whitehouse recorded from the type locality and it can be assumed that the holotype cephalon is contemporary with pygidia on which the species is now recognized.

Eugonocare whitehousei sp. nov.

Plate 49, figs. 15-19

Material. Holotype: JCF 8159, L149; pygidium. Paratypes: JCF 8262, L130; JCF 8154, L139; JCF 8168, L140; JCF 8158, L144; JCF 8161, L149; cranidia. JCF 8199, JCF 8266, JCF 8270, L130; JCF 8175, L131; JCF 8155-8157, L144; JCF 8160, L149; pygidia. Additional specimens, L141-143, L145, L150.

Diagnosis. Glabella distinctly tapering, anterior border narrow, convex. Pygidium elongate for the genus (text-fig. 3), with pleural grooves which are not oblique and reach to the axial furrows.

Dimensions. Holotype pygidium is 7.0 mm in length. Cranidial lengths range from 6.0 to 12.0 mm; pygidial lengths from 2.5 to 9.1 mm.

Remarks. Cranidia of E. whitehousei are indistinguishable from those of the type species, E. tessellatum. Thus the immature cranidia referred to in Öpik (1967, p. 203, pl. 8, fig. 2) as E. tessellatum could belong to either species. Pygidia exceeding 5·0 mm in length are however readily distinguishable by shape (text-fig. 3) but smaller pygidia are subject to confusion due to crossing of the growth trends.

Eugonocare quadrata sp. nov.

Plate 49, figs. 8-14

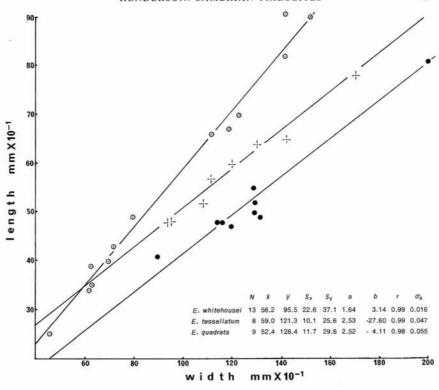
Material. Holotype: JCF 8414, mould of pygidium, L138. Paratypes: JCF 8358, JCF 8365, JCF 8376-8377, JCF 8383-8385, L127; JCF 8371, JCF 8409-8410, JCF 8412-8413, JCF 8415, JCF 8417, L138; cranidia. JCF 8359-8362, L127; JCF 8408, L138; pygidia. JCF 8357, JCF 8381-8382, L127; JCF 8411, L138; free cheeks.

Diagnosis. Glabella subquadrate, barely tapering. Anterior border broad for the genus, convex near the border furrow but flattened or slightly concave adjacent to the anterior margin. Pygidium short (text-fig. 3) with five axial rings and oblique pleural grooves which do not reach to the axial furrows.

Dimensions. Holotype pygidium is 5.7 mm in length. Cranidial lengths range from 4.1 to 15.5 mm; pygidial lengths from 4.1 to 8.2 mm.

Remarks. A well-preserved free cheek illustrated in Plate 49, fig. 10 shows the long, delicate genal spine characteristic of the genus. Pygidial characteristics serve best to distinguish *E. quadrata* from the two species which precede it in north-western Queensland but its cranidial characteristics are also unique.





TEXT-FIG. 3. Reduced major axis regressions of pygidial width plotted against pygidial length for Idamean species of *Eugonocare*. Symbols for tabulated statistics are as for text-fig. 2.

Subfamily PTEROCEPHALIINAE Kobayashi, 1935 Genus PTEROCEPHALIA Roemer, 1849 *Pterocephalia* sp. nov.

Plate 51, fig. 10

Material. JCF 8418, JCF 8426, L138; fragmentary cranidia.

Description. Cranidia effaced for the genus. Glabella gradually tapering and gently convex with a distinct axial crest. It has barely discernible lateral glabellar furrows between which some four, very poorly defined, glabellar lobes can be distinguished. Occipital lobe and furrow poorly defined. Posterior limb elongate with a narrow furrow. Fixed cheeks narrow, sloping gently upward; palpebral lobe short and positioned opposite the glabellar midpoint. Frontal area gently concave and lacking a border furrow. It has the overlapping, terraced ornament and strongly curved anterior margin characteristic of the genus.

Dimensions. Cranidial lengths range from 20.5 to 23.0 mm.

Remarks. The effaced character of this species and its lack of a distinguishable border furrow appear to separate it from other described Pterocephalia.

Family ELVINIIDAE Kobayashi, 1935 Genus PRISMENASPIS nov.

Type species. Prismenaspis propinquum (Whitehouse)

Diagnosis. Cranidium pustulose, tumid; glabella with four pairs of lateral glabellar furrows. Frontal area elongate and containing a broad border furrow. Internal moulds of the preglabellar field show a distinctive coarse punctation. Free cheeks with a short, stout spine. Pygidium possesses strong axial rings and inflated pleural fields with strong, broad ribs.

Description. Cranidium large, pustulose, with strong axial and preglabellar furrows. Glabella tumid, sagittally arched, tapering forward with four pairs of very weak lateral glabellar furrows; glabellar lobes decline in size anteriorly. Occipital lobe and furrow strong; prominant occipital node. Fixed cheeks tumid, inclined upward, about half the posterior glabellar width. Palpebral lobes short, about 30% of the glabellar length, set a little anterior to the glabellar midpoint. Palpebral rim well developed and wide for the family. Eye ridges narrow, distinct, sloping obliquely forward, and joining to the first glabellar furrow. Facial sutures anterior to the eye subparallel. Frontal area relatively broad, comprised of a weakly convex preglabellar field set at an angle to a weakly convex border of approximately equal width. The border furrow is clear, but not sharply defined. Preglabellar field with a distinctive, coarsely punctate ornament on internal moulds. Posterior limbs elongate, triangular with furrows expanding laterally. Free cheek with a projecting pointed tip, a short, stout spine, and a broad, weakly convex border.

Pygidium tumid, semicircular in outline. Axis broad slightly tapering, with four strong rings; terminus broadly rounded, vertically truncate, and reaching almost to the periphery. Pleurae narrow, inflated and downsloping, bearing up to four broad ribs each with a pleural groove. Border narrow and weakly convex or broad and flattened. Border furrow lacking.

EXPLANATION OF PLATE 51

Figs. 1-4. Prismenaspis alta gen. et sp. nov. 1-2, JCF 8420, paratype cranidium, ×2-5. 3, JCF 8419, holo-

type cranidium, ×2·5. 4, JCF 8421, paratype pygidium, ×3. All specimens from L138. Figs. 5-7. Stigmatoa diloma Öpik. 5, JCF 8349, cranidium, ×4. 6, JCF 8348, cranidium, ×4. 7, JCF 8328,

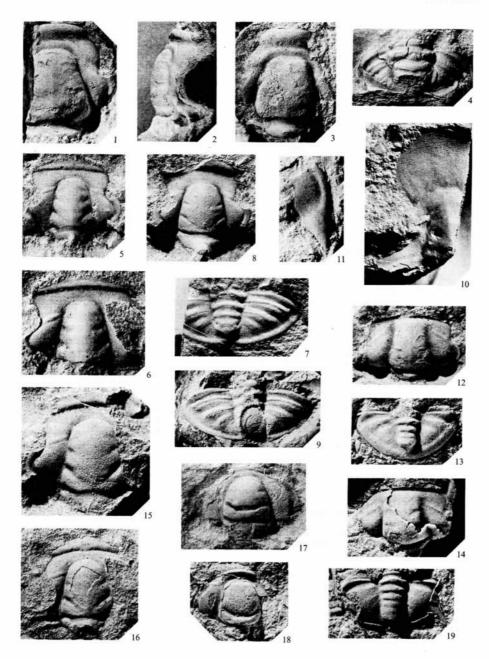
pygidium, ×2.5. All specimens from L136. Figs. 8-9. Stigmatoa tysoni Öpik. 8, JCF 8453, cranidium, L143, ×4. 9, JCF 8279, pygidium, L149, ×2·5. Fig. 10. Pterocephalia sp. nov. JCF 8418, cranidium, L138, ×2.

Figs. 11-14. Pagodia (Idamea) venusta Whitehouse. 11, JCF 8394, free cheek, ×3. 12, JCF 8392, cranidium, ×2.5. 13, JCF 8407, pygidium, ×4. 14, JCF 8473, cranidium, ×4. All specimens from L138.

Figs. 15-16. Stigmatoa sidonia Öpik. 15, JCF 8391, cranidium, ×4. 16, JCF 8390, cranidium, ×4. Both specimens from L138.

Figs. 17–18. Irvingella tropica Öpik. 17, JCF 8388, cranidium, ×2·5. 18, JCF 8389, cranidium, ×2·5. Both specimens from L138.

Fig. 19. Prochuangia sp. JCF 8366, pygidium, L127, ×3.



HENDERSON, Cambrian trilobites

Remarks. Prismenapsis is most closely allied to the imperfectly known genus Protemnites Whitehouse (1939, p. 209) which itself requires some comment and clarification. It is based on a single species, P. elegans Whitehouse (1939, p. 210, pl. 22, fig. 12a, b, non fig. 13), known from two cranidia on a chert slab. Whitehouse refers to two pygidia on the same slab in his description, but the figured pygidium (UQF 3331) is from a separate slab and represents Pagodia, presumably P. (Idamea) superstes Whitehouse which occurs at the same locality. The two unfigured pygidia are probably conspecific with the associated cranidia. They have a strongly arched axis with four well-marked rings, flattened pleural fields with four, low, rounded ridges each of which bears a weak pleural groove and what appears to be a wide, flat border.

The age of *Protemnites* is in doubt. It is recorded by Whitehouse as from 'beds at the base of a hill immediately west of Tyson's bore on Glenormiston' in association with Idamea superstes Whitehouse, Aspidagnostus parmatus Whitehouse, Pseudagnostus nuperus Whitehouse, and 'Elathriella' plebeia Whitehouse. Most of these species are poorly defined and none are known from other localities. Current data suggest that the ranges of Idamea and Aspidagnostus do not overlap, indicating that the collection is probably of mixed age. The Protemnites slab contains cranidia referable to either Hypagnostus or Kormagnostus, genera known to range no higher

than the Australian Mindyallan Stage and its equivalent elsewhere.

Prismenapsis is distinguished from Protemnites by possessing an additional pair of lateral glabellar furrows and by the weak impression of all four pairs of furrows. It is further distinguished by the obliquity of its eye ridges and by the inflated pleural regions of its pygidium. In all other features, including details of cranidial ornamentation, Prismenapsis and Protemnites are alike. Both are best referred to the family Elviniidae in the sense of Palmer (1965b, p. 32) and are here considered to be allied to the characteristic North American genus Dunderbergia. Prismenaspis differs from Dunderbergia in its broader, less convex anterior border and less sharply defined anterior border furrow.

Three post-Idamean north Siberian genera, Ketyna, Mansiella, and Nyaya established by Rosova (1963, 1968) appear to be affiliated with Prismenaspis. All three have pygidial morphology of the Prismenaspis style but their cranidia possess fewer than four glabellar furrows and appear to have distinctly less elongate posterior limbs.

Prismenaspis propinguum (Whitehouse)

Plate 50, figs. 6-13

1936 Eugonocare propinquum Whitehouse pars, p. 227; pl. 23, fig. 19, non fig. 20.

Material. Holotype: pygidium, UQF 3392, 5 miles north of Twenty Mile Bore, Glenormiston (figured by Whitehouse, pl. 23, fig. 19). Twenty-one cranidia, ten pygidia, and four free cheeks; localities L122, L124, L128-130, L139-140, L143.

Diagnosis. Cranidium inflated with a strongly arched glabella and fixed cheeks. Like that of P. brownensis but the preglabellar field is fractionally longer and the angle made by the preglabellar field and the anterior border is more distinct. Anterior border inclined upwards with respect to the glabella and with the anterior margin strongly arched as viewed from the front. Pygidium with an axis which is about the same width as the pleural fields. Pleural grooves weak, barely distinguishable on some specimens. Border narrow, weakly convex.

Dimensions. Cranidial lengths range from 7.5 to 12.5 mm; pygidial lengths from 4.4 to 7.8 mm.

Remarks. Whitehouse mistakenly associated pygidia of *P. propinquum* with cranidia of *Eugonocare* believing that the pygidial characteristics were sufficient to discriminate the new species, *propinquum*. He designated his figured pygidium (now numbered UQF 3392) as the holotype. The paratype cephalon is missing from the University of Queensland collections but evidently represents either *E. tessellatum* Whitehouse or *E. whitehousei* sp. nov.

Prismenaspis brownensis sp. nov.

Plate 50, figs. 14-19

Material. Holotype: JCF 8299, L121; pygidium. Paratypes: JCF 8201, JCF 8239, L122; JCF 8307, JCF 8354, JCF 8356, L135; JCF 8342-8346, L136; cranidia. JCF 8300, L121; JCF 8355, L135; JCF 8338, L136; pygidia. JCF 8306, L121; free cheek. Additional specimens, L122-123, L133.

Diagnosis. Cranidium inflated with strongly arched glabella and fixed cheeks. Anterior border not inclined upward with respect to the glabella. Anterior border and the preglabellar field meet in less of an angle and the anterior margin is less strongly arched as viewed from the front than in *P. propinquum*. Pygidium with an axis which is about the same width as the pleural fields. Pleural ribs broad and weak with distinct pleural grooves. Border flat and broad.

Dimensions. Holotype pygidium is $8\cdot2$ mm in length. Cranidial lengths range from $5\cdot8$ to $19\cdot2$ mm; pygidial lengths from $7\cdot2$ to $8\cdot2$ mm.

Remarks. Cranidia of both *P. brownensis* and *propinquum* are variable in a similar fashion. The axial furrows may be nearly straight or distinctly curved and the glabellar may be truncated or with a rounded anterior termination. In both species the preglabellar field can be a little longer than the anterior border or vice versa, and in both there is variation in the angular relationship of the preglabellar field and the anterior border. Some individual variants among cranidia cannot be referred to either species with confidence and it is the nature of the pygidium which allows clear specific discrimination.

These two species are closely related and may comprise a local bioseries. The collection at L122 is from a stratigraphic horizon when their ranges abut. Here cephala resemble *brownensis*, but two fragmentary pygidia are of the *propinquum* style with one having a broader border than typical of that species. These specimens could represent a fragment of an intermediate population but are too few in number to give an adequate indication. For the time being both species are listed from this locality.

Prismenaspis alta sp. nov.

Plate 51, figs. 1-4

Material. Holotype: JCF 8419, L138; cranidium. Paratypes: JCF 8420–8425, L138; cranidia. JCF 8421, L138; pygidium.

Diagnosis. Cephalon effaced for the genus with the glabella not strongly arched either

sagittally or transversely and the fixed cheeks weakly convex and inclined slightly upward. Frontal area short for the genus and the preglabellar field is distinctly shorter than the border with which it makes but a slight angle. Pygidium with an axis which is distinctly broader than the pleural fields, weak pleural ribs and a rather broad, flat border.

Dimensions. Holotype cranidium is 14.2 mm in length; cranidial lengths range from 11.5 to 15.5 mm; the single pygidium is approximately 6.0 mm in length.

Remarks. Cranidia which represent *P. alta* are distinctive. The length of the frontal area in *P. alta* is 28%–30% of the glabellar length, and the preglabellar field is distinctly shorter than the anterior border. In *P. brownensis* and *P. propinquum* the frontal area is never less than 35% of the glabellar length and the preglabellar field and border are of approximately equal lengths. In addition, cranidia of *P. alta* are effaced and less inflated compared to those of the other two species. The pygidium of *P. alta* resembles that of *P. brownensis* in the nature of the pleural ribs and border but is readily distinguished by its broad axis.

Genus IRVINGELLA Ulrich and Resser, 1924 Irvingella tropica Öpik

Plate 51, figs. 17-18

1963 Irvingella tropica Öpik, p. 96, pl. 4, figs. 5-8; text-fig. 36.

Material. Four cranidia, L138; one doubtful cranidium, L127.

Diagnosis. Irvingella with a frontal area some 20% of the glabellar length, comprised of a narrow, convex border and a slightly longer preglabellar field which are separated by a distinct border furrow. Glabella broad, tapering gently forward, with a rounded anterior termination. Fixed cheeks some 60% of basal glabellar width; palpebral lobes gently and evenly curved.

Dimensions. Cranidial lengths range from 7-1 to 9-5 mm.

Remarks. I. tropica is allied to I. angustilimbatus Kobayashi which was redescribed by Palmer (1968, p. 46, pl. 6, figs. 17-18, 21-23) and is characterized by its distinctly tapering glabella. Indeed, a single cranidium described by Palmer as an extreme variant of I. angustilimbatus was regarded by him as indistinguishable from I. tropica. Among American Irvingella, only angustilimbatus has a well-developed cranidial border and it is the oldest of the American species (Palmer 1968).

Hitherto *Irvingella* has been recorded from a single locality in Australia, near Mistake Bore, Chatsworth Station 180 km to the north-east of the Browns Creek Section (Öpik 1963).

Family EULOMATIDAE Kobayashi, 1955 Genus STIGMATOA Öpik, 1963

1963 Stigmatoa Öpik, p. 87.

Type species. Stigmatoa diloma Öpik.

Diagnosis. Glabella uniformly tapering with three pairs of straight lateral glabellar furrows which progressively increase in length and strength posteriorly. Occipital

lobe well defined and bearing a stout, elongate spine. The preglabellar field is steeply declined to a well-defined border and border furrow which bears 20–30 regularly spaced pits. Fixed cheeks strongly convex, terminating in large palpebral lobes set opposite the glabellar midpoint. Eye ridges clear, anteriorly directed; anterior facial sutures divergent. Pygidium twice as wide as long with a smoothly curved posterior margin. Border narrow, convex; border furrow poorly defined. Axis tumid with four rings and the convex pleural fields each bear four broad ribs with weak interpleural grooves.

Remarks. Öpik established the genus on cranidial characteristics; the single pygidium he figured as S. diloma (Öpik 1963, text-fig. 32) is unrelated and of undetermined affinities. Pygidia of two species figured here are almost identical and of little use in species discrimination. In spite of abundant cranidial material in the collections reported here, no free cheeks have been identified.

Stigmatoa has recently been reported from northern Victoria Land, Antarctica by Shergold et al. (1976). It also appears in faunal lists given for the Cambrian succession of Altay, U.S.S.R. by Poletaeva and Romanenko (1970) but this record must be treated with caution as the associated assemblage is of middle Cambrian age.

Stigmatoa diloma Öpik

Plate 51, figs. 5-7

1963 Stigmatoa diloma Öpik, p. 89, pl. 4, fig. 2; text-fig. 31; non text-fig. 32.

Material. Twelve cranidia and three pygidia; localities L121-122, L127, L136.

Diagnosis. Glabella elongate, length of frontal area less than one-third that of the glabella. Interocular span about one-third of the glabellar width measured on the same line. Anterior border slightly concave adjacent to the anterior margin. Preglabellar field with venulose ornament.

Dimensions. Cranidial lengths range from 5.5 to 11.0 mm; pygidial lengths from 7.5 to 8.4 mm.

Remarks. The pygidium of S. diloma is indistinguishable from that of S. tysoni in spite of substantial differences in cranidial morphology between the two species. The slight, anterior concavity of the anterior border is a consistent feature of the cranidia examined and can be taken as a reliable characteristic for the discrimination of S. diloma from S. sidonia.

Stigmatoa sidonia Öpik

Plate 51, figs. 15-16

1963 Stigmatoa sidonia Öpik, p. 91; pl. 4, fig. 1; text-fig. 34.

Material. Five fragmentary cranidia, L138.

Diagnosis. Cranidial characteristics identical to *S. diloma* except that the anterior border is convex right to the anterior margin and the venulose ornament appears to be lacking from the preglabellar field.

Dimensions. Cranidial lengths range from 6.5 to 9.3 mm.

Remarks. S. sidonia is probably derived from S. diloma which it so closely resembles.

Specimens from the present collection like Öpik's single specimen, are associated with *I. tropica* and lie stratigraphically above *S. diloma*. The range of *I. tropica*, however, appears to extend a little below that of *S. sidonia* as at L127 a poor specimen which probably represents *I. tropica* is associated with *S. diloma*.

Stigmatoa tysoni Öpik

Plate 51, figs. 8-9

1963 Stigmatoa tysoni Öpik, p. 92, pl. 4, fig. 3.

Material. Three fragmentary cranidia and one pygidium; localities L130, L143, L145, L149.

Diagnosis. Glabella squat, length of frontal area more than one-third of glabellar length. Preglabellar field lacking venulose ornament. Fixed cheeks narrow; interocular span about half the width of the glabella measured on the same line. Anterior border convex right to the anterior margin.

Dimensions. Cranidial lengths range from 6.7 to 7.4 mm; the single pygidium is 6.5 mm in length.

Remarks. The occipital spine shows well on JCF 8453 and is bent posteriorly with the distal portion orientated parallel to the glabellar crest. S. tysoni is allied to Stigmatoa sp. recorded by Shergold et al. (1976) from northern Victoria Land, Antarctica.

Family KAOLINSHANIIDAE Kobayashi, 1935 Genus Prochuangia Kobayashi, 1935 *Prochuangia* sp.

Plate 51, fig. 19

Material. JCF 8366, JCF 8469, L127; pygidia.

Description. Pygidium semicircular with an inflated axis tapering gently, reaching almost to the posterior margin and bearing six rings. Pleural fields convex, lacking ribs, with their anterior margins raised into prominent ridges. A pair of strong, diverging spines originate from the midpoints of pleural margins. Shell surface with well-developed pustules on both the pleural fields and the axis.

Dimensions. The two pygidia range from 1.7 to 6.0 mm in axial length.

Remarks. The figured specimen is an internal mould and does not show the pustulose ornamentation of the shell surface. The specimens are indistinguishable from *Prochuangia granulosa* Lu (1956b, p. 376, pl. 1, fig. 5), which is known from a single pygidium from the Yüping district, eastern Kueichou Province, China. They may well be conspecific with the Chinese species but, bearing in mind the specific provinciality of Australian Idamean polymerid taxa, it would be premature to record them so until cranidia are known.

Family LEIOSTEGIIDAE Bradley, 1925 Subfamily PAGODIINAE Kobayashi, 1935 Genus PAGODIA Walcott, 1905 Subgenus IDAMEA Whitehouse, 1939

The status of Pagodia (Idamea) has been exhaustively treated by Öpik (1967) who also substantially clarified its morphology. As discussed below, P. (I.) baccata Öpik and the type species P. (I.) venusta Whitehouse are the only two species constituting the subgenus and they may themselves prove to be synonymous.

Pagodia (Idamea) venusta Whitehouse

Plate 51, figs. 11-14

1939 Idamea venusta Whitehouse, p. 232, pl. 24, figs. 4–5, non pl. 24, fig. 6.
 1967 Pagodia (Idamea) venusta Whitehouse; Öpik, p. 260, pl. 18, fig. 6a-c; text-fig. 88.

1967 Pagodia (Idamea) extricans Öpik, p. 261, pl. 18, figs. 4, 5.

Material, Twenty-six cranidia, twenty-one pygidia, and twelve free cheeks; localities L121-122, L127, L138.

Diagnosis. P. (Idamea) possessing non-granulose or weakly granulose cranidial and pygidial surfaces.

Description. Cranidium distinctly wider than long with broad, convex fixed cheeks measuring from 60 to 75% of the glabellar width. Glabella tapering gently forward, often with slight constriction anterior to the midpoint, truncate against the border furrow. Four pairs of weak lateral glabellar furrows; the first are located adjacent to the eye ridges and the last extend a little closer to the glabellar midline than the others with each of the pair enclosing a distinct median bulge. Palpebral lobes gently curved, posterior in position, margined by quite strong palpebral furrows and measuring almost half the glabellar length. Eye ridges distinct and forward sloping. Anterior border a narrow, steeply upturned lip separated from the glabella by a deep, narrow border furrow. Its anterior margin bears delicate, subparallel terrace lines. Occipital lobe, furrow, and node well developed. Posterior limbs strongly furrowed, barely extending beyond the palpebral lobes. Free cheek rather tumid with a strongly convex border passing into confluence with a broad-based, squat, convex genal spine.

Pygidium semicircular with well-developed, widely spaced articulating facets and a broad, convex border. Axis strongly arched, gently tapering with four or five rings. Pleural fields weakly convex with three or four broad, weak ribs.

Test surfaces of both pygidia and cranidia may be smooth except for fine puncta or bear small, scattered granules.

Dimensions. Cranidial lengths range from 3.5 to 8.5 mm; pygidial lengths from 2.9 to 6.0 mm.

Remarks. P. (I.) venusta was established from silicified material and another silicified cranidium was later referred to the species by Öpik. As noted by Öpik (1967, p. 259) the single pygidium referred to P. (I.) venusta by Whitehouse is unrelated. The cranidial proportions of P. (I.) extricans Öpik are identical with those of venusta which is given by Öpik as distinguished by its impunctate test and lack of external eye ridges. P. (I.) extricans was, however, described from shelly material and these distinctions are almost certainly due to differing modes of preservation. Only a single

species of nongranulose or weakly granulose *P.* (*Idamea*) can be discriminated in the Browns Creek Section; the lower part of its range overlaps with that of *Corynexochus plumula* and is consistent with the association of *venusta* and *C. plumula* reported by Öpik from Mount Idamea 20 km to the north-west. The single locality from which *extricans* is known corresponds to a horizon at the base of the range of the comparable species in the Browns Creek Section (see Henderson, in press). The ages of *P.* (*I.*) *venusta* and *extricans* are, therefore, not widely discrepant as Öpik thought and they lie within the lower portion of the range of a single comparable species collected in this project. *P.* (*I.*) *venusta* and *P.* (*I.*) *extricans* are here regarded as synonymous and identical with the material described here.

P. (I.) baccata Öpik (1967, p. 262, pl. 17, figs. 1–8; pl. 18, figs. 1–3; text-fig. 89) is given as distinguished from P. (I.) venusta by its granulose surface ornament, but may prove to be an extreme variant of P. (I.) venusta. The material available includes a number of specimens which show incipient granulation (see Pl. 51, fig. 14) and which otherwise encompass in their variation the morphology of P. (I.) baccata. Only a single specimen shows a granulation as strong as the types of baccata but a precise discrimination of this species from venusta is not at present clear.

BIOSTRATIGRAPHY

Henderson (in press) has recognized five assemblage zones in the Browns Creek Section of the Idamean Stage, each being named for its characteristic species. Ranges of those species discussed in the systematic descriptions are illustrated in Table 2. The full zonal assemblages, including four species recorded from other areas by Öpik (1963, 1967), are listed below.

Glyptagnostus reticulatus Zone

Aspidagnostus strictus Öpik, Innitagnostus inexpectans (Kobayashi), Peratagnostus nobilis Öpik, Glyptagnostus reticulatus (Angelin), ?Pseudagnostus vastulus Whitehouse, Olemus ogilviei Öpik, Proceratopyge nectans Whitehouse, Aphelaspis australis sp. nov., and Blountia (Mindycrusta) advena Öpik.

Proceratopyge cryptica Zone

Peratagnostus nobilis Öpik, Pseudagnostus vastulus Whitehouse, P. curtare sp. nov., Corynexochus plumula Whitehouse, Proceratopyge cryptica sp. nov., Aplotaspis erugata (Whitehouse), Aphelaspis australis sp. nov., Eugonocare whitehousei sp. nov., Stigmatoa tysoni Öpik, and Prismenaspis propinquum (Whitehouse).

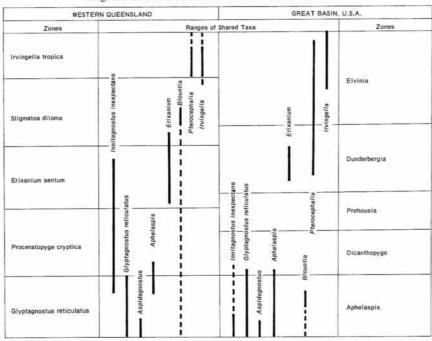
Erixanium sentum Zone

Peratagnostus nobilis Öpik, Innitagnostus inexpectans (Kobayashi), Pseudagnostus vastulus Whitehouse, P. curtare sp. nov., Corynexochus plumula Whitehouse, Proceratopyge lata Whitehouse, Aplotaspis erugata (Whitehouse), Eugonocare tessellatum Whitehouse, Erixanium sentum Öpik, Stigmatoa tysoni Öpik, Prismenaspis propinquum (Whitehouse), and Pagodia (Idamea) baccata Öpik.

Stigmatoa diloma Zone

Peratagnostus nobilis Öpik, Pseudagnostus vastulus Whitehouse, P. curtare sp. nov., P. margopronus sp. nov., Corynexochus plumula Whitehouse, Proceratopyge lata Whitehouse, Aplotaspis mucrora sp. nov., Yuepingia sp. nov., Eugonocare tessellatum Whitehouse, E. quadrata sp. nov., Blountia (?Mindycrusta) georginae Öpik, Asilluchus nanus Öpik, Erixanium strabum Öpik, E. alienum Öpik, Stigmatoa diloma Öpik, Prismenaspis brownensis sp. nov., Prochuangia sp. nov., and Pagodia (Idamea) venusta Whitehouse.

TABLE 2. Chart showing the ranges of taxa shared between the Pterocephaliid Biomere and the Idamean Stage and the best match of zonations for these two divisions.



Irvingella tropica Zone

Agnostotes inconstans Öpik, Pseudagnostus curtare sp. nov., P. margopronus sp. nov., Olenus delicatus Öpik, Proceratopyge lata Whitehouse, Eugonocare quadrata sp. nov., Pterocephalia sp. nov., Stigmatoa sidonia Öpik, Prismenaspis alta sp. nov., Irvingella tropica Öpik, Pagodia (Idamea) venusta Whitehouse, and Hercantyx rudis Öpik.

NOTES ON IDAMEAN CORRELATIVES

Glyptagnostus reticulatus, characteristic of the lowest zone of the Idamean Stage, and Irvingella, characteristic of the highest, are widely distributed taxa on a global basis and provide a means of reasonably accurate correlation of the Idamean Stage with biostratigraphic units recognized in many other regions. Only five Idamean genera, Eugonocare Whitehouse, Asilluchus Öpik, Hercantyx Öpik, Aplotaspis gen. nov., and Prismenaspis gen. nov. are presently unknown outside Australia; many of the others are useful in correlation.

North America

The most complete and thoroughly documented Idamean equivalent in North America comprises the Pterocephaliid Biomere of the Great Basin region described by Palmer (1965b). The biomere lies within the familiar Dresbachian and Franconian Stage divisions established in the upper Mississippi Valley region and widely employed in North America. The boundary between the two stages is generally taken at the base of the *Elvinia* Zone which is the uppermost of five zones recognized in the biomere. While the utility of the biomere as a biostratigraphic concept may be disputed, the zonation recognized by Palmer has been established beyond doubt and can be successfully applied to Cambrian successions throughout North America with the exception of the restricted province of Baltic aspect located on south-eastern Newfoundland, Cape Breton Island, and eastern New England (see North 1971). *G. reticulatus* occurs at the base of the biomere sequence and *Irvingella* towards the top. Prominent faunal discontinuities mark its boundaries, similar to that at the base of the Idamean Stage. Ranges of common genera, with the exception of *Pseudagnostus* which ranges well beyond the limits of the Idamean Stage and its equivalents, and the best match of the Pterocephaliid Biomere zonation with that of the Idamean Stage is presented in Table 2.

In terms of evolutionary aspect, the Pterocephaliid and Idamean faunas show striking similarities in spite of possessing dissimilar taxonomic complements. In both, some species groups can be identified which undoubtedly comprise segments of individual bioseries. Among Idamean faunas there are series of Eugonocare (three species), Stigmatoa (three species), Prismenaspis (three species), Aplotaspis (two species), and Proceratopyge (two species). Similar trends in quite different genera, involving up to five species are reported from Great Basin sequences by Palmer

(1965b).

Data on Alaskan faunas presented by Palmer (1968) are of interest because some taxa are shared with Australia but are unknown elsewhere in North America. These include *Proceratopyge cryptica* sp. nov. with *Peratagnostus* (Franconian-1 fauna of Palmer) and *Corynexochus plumula* Whitehouse (Dresbachian-2 fauna of Palmer). The Franconian-1 fauna, judging from the Australian ranges of the shared taxa, is probably of Dresbachian age and best regarded as correlative with a horizon within the *Prehousia-Dicanthopyge* zonal interval. Alaskan *Yuepingia* are associated with taxa which post-date the Idamean and its correlatives.

Scandinavia

The upper Cambrian faunal succession for Norway has been summarized by Henningsmoen (1958) and that for Sweden by Westergaard (1947). Biostratigraphic schemes for the two countries are very similar. Few genera are shared with Australia but the cosmopolitan species *G. reticulatus* makes its appearance at the base of the Scandinavian *Olenus* Zone and this horizon is correlative with the base of the Idamean. The association of *Olenus* with *G. reticulatus* in Australia supports this contention. *Proceratopyge* in Scandinavia ranges below *G. reticulatus* into the *Agnostus pisiformis* Zone considered by Öpik (1967) as correlative with the Mindyallan Stage.

The Scandinavian correlative of the upper Idamean is uncertain. G. reticulatus is restricted to the basal three of six Olenid subzones in Sweden and the upper limit of Proceratopyge is within the lower portion of the succeeding Parabolina-Orusia Zone. Irvingella is known from Sweden but its horizon is uncertain and tentatively placed at the base of the Peltura-Sphaerophthalmus-Ctenopyge Zone, three zones

and fourteen subzones above the incoming of *G. reticulatus* and immediately below the first appearance of *Lotagnostus*. The inferred position of the Swedish *Irvingella* seems anomalously high and synchroneity between the *Peltura-Sphaerophthalmus-Ctenopyge* Zone and the upper Idamean unlikely. This contention is supported by the association of *Olenus delicatus* Öpik with *I. tropica* in western Queensland (Öpik 1963).

Siberia

Ivshin and Pokrovskaya (1968) proposed a twofold stage subdivision for the upper Cambrian in Siberia. The Tuorian Stage, the older of the two, is based on a succession on the Lena River in the Tuora-Sis area of the north-western Siberian Platform. Three zones are recognized in the Tuorian and the highest of these is a correlative of the lower Idamean. It is characterized by *G. reticulatus* and shares *Aphelaspis*, *Aspidagnostus*, and *Innitagnostus inexpectans* (Kobayashi) with Australia. The Australian species *Erixanium sentum* Öpik is restricted to the upper portion of the zone and apparently occurs with *G. reticulatus* suggesting that the Siberian teilzones for these species do not exactly match their Australian counterparts. The anomalous *Crepicephalus borealis* Lermontova also listed from the upper Tuorian has been reinterpreted by Palmer (1965b, p. 64) as representative of a new aphelaspid genus allied to *Eugonocare* Whitehouse and *Olenaspella* Wilson.

The Shidertinian Stage is based on a section from the Olenta River adjacent to Kujanda, Kazakhstan and is subdivided into four zones. The lowest of these contains *Irvingella* and is correlative with the upper Idamean. Early Shidertinian horizons in the Tuora-Sis area, succeeding the type Tuorian contain the Australian species *Agnostotes inconstans* Öpik and *Proceratopyge lata* Whitehouse in addition to *Irvingella*.

Upper Cambrian zonations and faunas throughout Siberia have recently been reviewed by Rosova (1968). Areas with Idamean correlatives show diverse faunas. Some, including those just discussed and faunas from the northern Anabarsk Rise adjacent to the Olyenyok River, the Chopko River district of the Norilsk Region, and the Altai Mountains have a cosmopolitan flavour with such taxa as *G. reticulatus*, *Irvingella*, *Olenus*, *Olenaspella*, *Proceratopyge*, and *Aphelaspis*. Others, however, such as the faunas of the Igarsk Region studied in considerable detail by Rosova, the Kureysk Region, north-western Salair, and Shoriya are almost exclusively endemic in their generic aspect.

Northern China and Korea

The Idamean Stage appears to be an approximate correlative of the Paishan 'Stage' which was first introduced by Endo as a formation for a thin interval of limestone in a substantial late Cambrian section at Paichiashan, Liaotung Peninsula, northern China. Fossils were described from the formation by Endo and Resser (1937). The name Paishan has subsequently been widely used by Kobayashi and others to denote a *de facto* stage division. It is regarded as partially correlative with the Changshan 'Stage' introduced by Sun as a lithostratigraphic unit of shales recognized in the east Hopei district, northern China. A small late Cambrian fauna was described from it by Sun (1924) and it too has been subsequently employed as a *de facto* stage division.

According to Kobayashi (1967, p. 389) the Changshan 'Stage' is equal to the Paishan 'Stage' and succeeding Daizan 'Stage' of the Paichiashan section.

Paishan faunas are widely distributed in northern China and Korea (Kobayashi 1966a, b) and differ markedly from those of the preceding Kushan 'Stage'. Kobayashi (1967, p. 410) records that none of the approximately forty genera of polymerid trilobites known from the Kushan survived the 'Stage'. Paishan elements shared with the Idamean Stage are Prochuangia, Irvingella, Pseudagnostus, and Proceratopyge. An association of G. reticulatus with Olenus is known from South Korea (Kobayashi 1962), but its position relative to the reference 'stage' divisions remains to be established.

Southern China

Literature relating to early upper Cambrian trilobites from the Yangtze Basin and adjacent areas is summarized in Kobayashi (1967). No comprehensive local biostratigraphic scheme is as yet available. The succession from the Hunan-Kueichow border area recorded by Jegorova et al. (see Kobayashi 1971, pp. 176-177) is in part an Idamean correlative. Collections from the three localities highest in the succession jointly contain Aphelaspis, Prochuangia, Proceratopyge, and G. reticulatus. They appear to represent the equivalent of the lower Idamean. The reported association of G. reticulatus with G. stolidotus at one stratigraphically lower locality and of Yuepingia with Drepanura and Blackwelderia at another conflict with range data for these taxa from other regions and needs confirmation.

A small fauna recorded from the highest Cambrian unit of the Yüping region of eastern Kueichow by Lu (1956b) contains Pseudagnostus, Prochuangia, Yuepingia, and probably Stigmatoa. It is an upper Idamean correlative.

A fauna of Idamean age is recorded from the Ellsworth Mountains, western Antarctica by Webers (1972). Aphelaspis, Eugonocare, Pseudagnostus, and a new, unnamed genus compared to Onchopeltis and possibly identical with Prismenaspis gen. nov. are elements affiliated with the Australian fauna reported here.

Trilobites from northern Victoria Land first reported by Laird et al. (1972) and described by Shergold et al. (1976) are also of Idamean age. They include Prochuangia, Stigmatoa, Irvingella, and probably Aphelaspis.

STATUS OF THE BIOMERE CONCEPT

The Biomere was introduced by Palmer (1965a) as a new type of biostratigraphic unit characterized by a space/time plexus of fossils with a common evolutionary fabric, discriminated from preceding and succeeding biomeres by a sharp faunal discontinuity. The type example is the Pterocephaliid Biomere, based on polymerid trilobite faunas from the U.S.A. which have been thoroughly described from the Great Basin region by Palmer (1962, 1965b) and which are fairly well known from several other regions. The feature which sets the biomere apart from other units employed in biostratigraphy is that its boundaries are diachronous. Palmer thus envisages biomeres as spatial entities separated by a geographic boundary which migrated with time. With evolution continuing unabated in each subjacent biomere,

the actual record of the faunal discontinuities separating them will be represented by different taxa at different geographic locales as determined by the spatial movement of the discontinuities in time.

The Idamean Stage is clearly an Australian counterpart of the Pterocephaliid Biomere. It shows an internal evolutionary continuity and has a striking faunal break at its base as already noted by Öpik (1966). Of thirty-four genera of polymerid trilobites known from the preceding upper zone of the Mindyallan Stage, only *Blountia* continued into the Idamean. Agnostids fared slightly better; of five Idamean genera known, three are holdovers from the Mindyallan Stage. Post-Idamean faunas are yet to be documented from Australia and the nature of the upper Idamean boundary is therefore unknown.

Öpik's designation of the Idamean as a stage is supported here and it is thus

pertinent to discuss the status of the biomere concept.

The essential biomere characteristic of diachronous boundaries has been argued by Palmer (1965a, b) for the faunal discontinuity between the Pterocephaliid Biomere and the preceding Crepicephalid Biomere. In the McGill section, Nevada and the Cedar Bluff Section, Alabama three taxa, G. r. angelini (Resser), A. buttsi (Kobayashi), and Olenaspella separata Palmer are represented at the base of the Aphelaspis Zone which is the basal zone of the Pterocephalid Biomere. In all other known sections, the earliest Aphelaspis Zone taxa can be matched with forms occurring a little higher in the McGill and Cedar Bluff sections. The data can be explained in one of three ways: the faunal discontinuity is synchronous in all sections and the species teilzones are diachronous; the discontinuity in all but the McGill and Cedar Bluff sections constitutes a paraconformity; or the species teilzones are synchronous and the discontinuity diachronous. A more substantial indication of the geographic distribution of sections of the McGill and Cedar Bluff type is required before a reliable choice can be made. Palmer cites the biostratigraphy of the McGill section as compared to that of the Snake Range section 50 miles to the south-east as confirmation of the diachronous nature of the faunal discontinuity. The upper two zones of the Crepicephalid Biomere are the Cedaria Zone (lower) and Crepicephalus Zone (upper). At McGill the discontinuity lies between the Cedaria Zone and the basal angelinibuttsi-separata faunule of the Aphelaspis Zone, while at Snake Range it lies between the Crepicephalus Zone and a higher faunule of the Aphelaspis Zone. These data are interpreted by Palmer as evidence of the faunal boundary migrating with a southeasterly component in time. However, such an explanation seems unlikely because the same faunal boundary which migrated 50 miles between these sections so as to allow the complete elimination of the Crepicephalus Zone from the McGill section moved much more rapidly over a substantial portion of the U.S.A. as demonstrated by widely scattered sections with the full succession of Cedaria, Crepicephalis, and Aphelaspis zones.

It can be argued, as has Palmer (1972), that faunal replacement of the Pterocephaliid and Idamean type cannot be synchronous as it is not evolutionary in nature. Thus the replacing elements must have existed elsewhere in prior time. But this is the situation for almost all traditional biostratigraphic units be they zones, stages, series, periods, or eras. The number of biostratigraphic boundaries recognized by a point in an evolutionary continuum are completely overshadowed by the number recognized

on the basis of a sudden faunal change. Even for a boundary recognized in an evolutionary continuum, some measure of space/time ambiguity remains unless the populations concerned are panmictic. It must be concluded that the logical basis of the biomere concept is faulty, and there is little advantage in employing the term in preference to traditional names for biostratigraphic units.

SIGNIFICANCE OF THE BASAL IDAMEAN FAUNAL DISCONTINUITY

The basal Idamean faunal discontinuity is a striking local extinction event and is correlative with similar phases of extinction in China and the U.S.A. It is tempting to consider it as a world-wide event as did Öpik (1966), with an extraterrestrial cause. Siberian data, however, conflict with such a view as they show no evidence of a faunal discontinuity at that time; indeed Ivshin and Pokrovskaya (1968) note a faunal discontinuity at the division between their Tuorian and Shidertinian Stages, a horizon approximately correlative with the base of the Irvingella tropica Zone in Australia and the Elvinia Zone in the U.S.A. Much of the Siberian fauna remains to be described and the basal Idamean discontinuity may be still obscured for this reason. It is worth recalling that at the time of introduction of the Dresbachian and Franconian Stages in North America, the basal Pterocephaliid discontinuity was not recognized as a convenient position for a stage boundary.

In both Australia and the U.S.A. the faunal discontinuity lies between the teilzones of G. stolidotus Öpik and G. reticulatus (Angelin), both of which are apparently cosmopolitan taxa. Further, the bioseries of G. r. angelini (Resser) and G. r. reticulatus appears to be represented in Australia as well and may also prove to be cosmopolitan. The existence of this striking extinction event and a potential independent means of establishing its space/time distribution is deserving of attention among palaeontologists. It may provide a unique opportunity to examine the phenomenon of extinction which is the least well understood major feature in the history of life.

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