A GENS OF DALMANITID TRILOBITES.

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(Communicated by DR. IDA BROWN.)

With Plates I-II.

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INTRODUCTION.

In the Palæozoic rocks of eastern Australia there is a closely related group or gens of genera and species of trilobites which has heretofore been covered by the single name *Dalmanites meridianus* Etheridge and Mitchell, 1896. The present study shows that this omnibus name has covered forms belonging to the genera *Dalmanites* and *Odontochile.* The group of species concerned includes :

Dalmanites wandongensis, sp. nov.

Odontochile meridianus (Etheridge and Mitchell).

O. loomesi (Mitchell).

O. formosa, sp. nov.

As " *Dalmanites meridianus* " has been relied upon as an index fossil, stratigraphical inaccuracies have resulted from including so wide a range of forms in one species.

In the genera *Dalmanites* and *Odontochile* there are often groups of closely related species which are difficult to differentiate. When describing the dalmanitid genera of North America, Delo (1935, p. 55) noted this feature. The biological inference is that there was a high mutation pressure in these instances, resulting in a group of closely related forms. The genera named are often prolific in numbers of individuals, and this would help in the preservation of a series of forms.

GENERA OF THE GENS.

Dalmanites Barrande, 1852, genotype *Trilobus caudatus* Brünnich, 1781 (see Delo, 1935*b*), groups together typical dalmanitids having an elongate, non-denticulate hypostoma, genal spines, and 11 to 16 pygorachial segments. The genus is restricted to the Silurian in Europe, but continues up into the Lower Devonian in North America. In Australia the range of *Dalmanites* is probably limited to the Silurian, but this cannot be determined with certainty as yet, as there are many unsolved stratigraphical problems relating to the boundary between the Silurian and the Devonian.

The diagnosis of this genus is unusual in that it relies on the hypostoma, which is preserved comparatively rarely, and very seldom *in situ.* It needs to be *in situ* if it is to be actually proved that it belongs to a particular species. The hypostoma is also a " conservative " part of the exoskeleton, varying little from species to species, and sometimes even from genus to genus. The diagnosis of *Dalmanites* is unusual, too, in that it cites no features of the dorsal side of the cephalon, whose morphology provides the chief *fundamenta divisionis* of families, genera and species in the Trilobita. Furthermore, the diagnosis depends on features of the pygidium, which also is generally a conservative part of the exoskeleton, i.e. its variations are usually so small and few that they do not assume taxonomic significance of generic rank. The biological inference from these facts is that while the trilobites of the Dalmanitidæ maintained the general dalmanitid impress, mutations took place in conservative parts of the exoskeleton, viz. the hypostoma and the pygidium. The diagnosis thus selects features which are taxonomically significant but not necessarily biologically important.

Odontochile Hawle and Corda, 1847, genotype *Asaphus hausmanni* Brongniart, varies from *Dalmanites* in having a denticulate hypostoma, and 16 to 22 pygorachial segments. Delo (1940, p. 55) found also that the larger size of *Odontochile* is a helpful guide. *Dalmanites* and *Odontochile* merge into one another, as is illustrated in the gens of *Dalmanites meridianus*. *Odontochile* arose out of *Dalmanites* and is limited to the Lower Devonian. The obvious close relationship of the Australian gens of dalmanitid trilobites now described makes it almost certain that in this case *Odontochile* arose in the Australian area from an Australian *Dalmanites*, and so independent of its genesis in other areas. *Odontochile* may thus consist of groups which have arisen in various parts of the world, and which are closely homologous and isochronous, but actually independent mutations or series of mutations. Evidence is accumulating in support of such a view for a number of fossils. Or to express it another way, because *Odontochile* is found in Australia and North America, it does not necessarily mean that the form originated in one area and migrated to the other. There are records of new mutations in living forms where the same mutation has arisen in different parts of the world at the same time. It would appear that genes have a tendency to alter their constitution in one direction rather than in others, and thus the same mutation may take place in what are apparently the same genes though in different parts of the world. If this is so, then mutations depend on some inherent structural factor as well as perhaps on some external influence (for instance, the influence of X rays on the mutation rate).

R. and E. Richter (1931) have pointed out how *Dalmanitina*, *Dalmanites* and *Odontochile* form a phylogenetic sequence.

The diagnostic features are unusual in *Odontochile* as they are in *Dalmanites*. In a mobile animal the anterior end is naturally more specialized, as it is nearest the sources of stimuli which guide its movements. The great amount of specialization in the anterior end (cephalization) readily provides a basis for classification, and that is why from the Arthropoda to the Mammalia cephalic structures possess both biological significance and taxonomic usefulness. The diagnoses of *Dalmanites* and *Odontochile* provide an exception to this general rule. Probably the addition of extra segments in the pygidium of *Odontochile* was not a development of much biological moment. It appears to be part of the general enlargement of the animal, and the advantages (as far as we can see) simply those of larger size and weight. The denticulate hypostoma of *Odontochile* probably gave more area for muscle attachment, and new angles of muscle action. However, the supersedence of *Dalmanites* by *Odontochile* must surely mean that the new structures were of some biological advantage. But we are limited by not being able to discover what changes there were in the soft parts of the animals concerned.

Some Species of the Gens.

Dalmanites wandongensis sp. nov.

Plate 1, figs. 1–4.

Phacops (*Odontochile*) *caudatus* McCoy, 1876, pp. 13–15, Pl. XXII, figs. 1-7; Pl. XXIII, figs. 7, 8, 9–10.

Type Material.

Holotype, consisting of the internal cast (steinkern) of a pygidium in bluish-grey, very fine-grained sandstone from " Wandong, near Kilmore ", i.e. the Geological Survey of Victoria fossil locality Bb 18 on Broadhurst's Creek. The specimen was presented to the University of Melbourne Dept. of Geology by Mr. F. H. McK. Grant on 24.6.31, and is now Reg. No. 1946 in that department.

Two paratypes, consisting of counterparts of an almost complete cephalon inferred to belong to the same species, preserved in mottled greyish very fine-grained sandstone from " Wandong, Victoria ", probably the same locality as the holotype. The specimens are Reg. Nos. 420A and 420B of the Department of Geology Museum, University of Melbourne. The counterparts are an internal cast or steinkern, and an external mould.

Description of Holotype.

About 27 mm. wide at anterior end, and 25 mm. long without terminal point, i.e. as actually preserved. The rachis is 6 mm. wide anteriorly, and 2 mm. wide posteriorly just before it is rounded off. There are ten pleural segments, the elevated portion of each being divided throughout its length by a median furrow. The anterior ribs are slightly deflected backwards, and this deflection is strongly increased about two-thirds of the distance to the margin. The amount of general deflection increases with each rib until the most posterior one is almost parallel with the median longitudinal axis of the pygidium.

Fourteen pygorachial segments can be counted. They are flattened and rounded at their ends in the anterior part of the pygidium where the segments are fully developed. The margin is entire. The perimeter of the pygidium describes a more or less equilateral triangle. The terminal spine is incomplete, but its morphology can be seen in McCoy's Plate XXIII, figs. 9–10. On the right side of the pygidium the doublure is shown ; it is 2 mm. wide.

Description of Paratypes.

Cephalon sub-triangular in outline, the margin tending to form a point in front of the glabella. Cephalon tumid, rising about half a centimetre above the plane of the margin. Width 4 cm. and length 2 cm. The glabella is tumid but the eyes rise even higher than it. The axial furrows, if produced as far as the longitudinal median axis of the trilobite, make an angle of about 22°. The first (most anterior) pair of glabellar furrows are oblique, and make an angle of about 70° with the median longitudinal axis. The second and third pairs of furrows are transverse, narrow, and deep ; neither reach the axial furrows. The neck furrow reaches the axial furrow, but the third and second glabellar furrows respectively have their outer ends progressively further away from the axial furrows.

The posterior margin of the cephalon makes an angle of about 60° with its lateral margin. The general spines are wide, and probably long (judging by the convergence observed on the part preserved, and McCoy's Plate XXIII, fig. 7).

The eyes are large and very elevated (Pl. 1, figs. 3–4). Anteriorly, they reach the end of the first glabellar furrow, and posteriorly they almost reach the neck furrow. The visual area is almost vertical, being directed slightly upwards and outwards. The visual area measures half a centimetre high by $1\frac{3}{4}$ cm. wide.

There are about 486 lenses in the eye, made up of 27 rows in the middle with 12 lenses each, and on each side of that, 10 rows with numbers gradually descending from 11 to 4 lenses per row. Thus there are 47 rows of lenses present. This description is made from the right eye, which is the better preserved, and which is present also in the counterpart. The external mould of the eye shows that the lenses were most strongly convex on their outer surfaces, while the internal cast shows that on their inner surfaces the lenses were also convex, though not so strongly. Each lens must therefore have been quite bulbous, and possessed of at least some of the properties of a " bull's eye " lens.

The external mould shows that the surface of the cephalon possessed a fine granular type of " ornament ".

Comment.

McCoy (Pl. XXII, fig. 3) figured a hypostome which is non-denticulate, thus providing further evidence that the genus is *Dalmanites.* The specimens figured by McCoy were housed in the National Museum, Melbourne, but some of them cannot now be located, including the cephalon (Pl. XXII, fig. 1). The number of segments cannot be counted on the pygidia available, except the specimen figured in Pl. XXII, fig. 6, but this is exceptionally wide and may well be a variant of the species as *O. loomesi* is of *O. meridianus.* All McCoy's specimens come from the same locality as the holotype.

Odontochile meridianus (Etheridge and Mitchell.)

Hausmannia meridianus Etheridge and Mitchell, 1896, pp. 504–509, Plate XXXVIII, figs. 1–8 ; Plate XL, fig. 1.

Dalmanites meridianus Mitchell, 1919, pp. 443–446, Plate XV, figs. 3–4 ; Plate XVI, figs. 6–7.

Type Specimens.

Etheridge and Mitchell did not name a holotype when they described their species in 1896, but in 1919, when Mitchell was describing the closely allied *O. loomesi,* he included in his plate XV a photograph (a drawing was published with the original description) of a complete specimen which he referred to as " the original type specimen of *Hausmannia meridianus* ". It is the obvious choice, and so this specimen may be regarded as the holotype and the other specimens figured in the original paper as paratypes. Mitchell figured three more pygidia belonging to *O. meridianus* in his 1919 paper (Pl. XV, fig. 4, and Pl. XVI, figs. 6, 7) and these may be regarded as hypotypes.

Generic Position.

Originally described as *Hausmannia,* the above species was later referred to *Dalmanites* by Mitchell (1919), but is now referred to *Odontochile* because the holotype has 17 pygorachial segments, and the form therefore falls within this genus by definition (more than 16 pygorachial segments). A hypotype figured by Mitchell (1919, Pl. XVI, fig. 6) shows 18 pygorachial segments.

Etheridge and Mitchell (1896, Pl. XXXVIII, fig. 8) figured a damaged hypostome, to which reference was not made in the text. In size and proportions it corresponds fairly closely to hypostomes of species of *Odontochile* in Victoria, but no denticles (such as are characteristic of that genus) can be seen in Etheridge and Mitchell's drawing.

Odontochile loomesi (Mitchell).

Pl. 1, figs. 5–6.

Dalmanites (*Hausmannia*) *loomesi* Mitchell, 1919, pp. 441–449, Plate XV, figs. 1–2; Plate XVI, figs. 3–5.

Type Specimens.

Mitchell did not name any types and so all his figured specimens must be regarded as syntypes. The first specimen figured (Pl. XV, fig. 1) is a complete carapace, and the description is largely based on it. This therefore is selected as a holotype and becomes the lectoholotype. The other specimens figured are lectoparatypes. Through the courtesy of Mr. H. O. Fletcher, palæontologist, Australian Museum, Sydney, I have been able to examine the lectoholotype, and rephotograph it (Pl. I, figs. 5–6).

Generic Position.

This species is referred to *Odontochile* because the lectoholotype possesses 16 pygorachial segments, and the lectoparatypes possess about 20 and 16 respectively. Describing the pygidium, Mitchell says: "Axis consists of 16 to 20 rings (dependent on the state of maturity)." The form therefore belongs to *Odontochile* by definition. In discussing pygidial segmentation, Mitchell (p. 445) mentions that Silurian forms do not have more than 16 segments, then states that his species has up to 20, but claims nevertheless that his species "shows transition towards the pygidial segmentation of the Devonian species". He seems to have thought that Reed's (1905) definition of 12 to 16 segments for Silurian species referred to the number of pygopleural segments, whereas it refers to the number of pygorachial segments.

Odontochile formosa sp. nov.

Plate II, figs. 1–2.

Type Material.

A cast of a complete carapace constitutes the holotype (Univ. of Melbourne, Dept. of Geol., Reg. No. 882, presented by Mr. W. McCormack). It is preserved in bluish grey, very fine grained sandstone, which is very compact, so much so that the original calcareous material is preserved in some of the fossils, which is unusual in the Silurian and Devonian rocks of Victoria.

Locality.

The holotype was collected from a Country Roads Board quarry, 1⅞ miles 20° W. of S. from Kinglake West (Tommy's Hut) Post Office. It is near the headquarters of Scrubby Creek, and the military map reference is Kinglake sheet 247,847.

Etymology.

The trivial name is derived from the Latin *formosus*, "beautiful in form", a reference to the elegant proportions and well-developed structures of the species.

Whole Carapace.

The carapace is large, being about 16 cm. long and 9 cm. wide. The general outline is ovoid. Cephalon with large eyes and very long genal spines. Pygidium large and mucronate. Whole carapace covered with fine granulation. The carapace has been compressed dorso-ventrally, the greatest displacement taking place in the cephalon.

Cephalon.

Sub-triangular in outline. A flat border 3 to 4 mm. wide is shown on the left side of the cephalon, but as the frontal margin is not preserved, it cannot be proved whether this border extended right round the cephalon or not. As preserved, the cephalon is 3·2 cm. long and 9 cm. wide, a ratio of length to width of about 1 : 2·8.

The glabella is approximately 3·8 cm. wide anteriorly and 2 cm. wide posteriorly. There is a central longitudinal furrow in the frontal lobe, believed to be due to compression of a tumid carapace. The axial furrows, if produced as far as the median longitudinal axis of the trilobite, make an angle of about 50°. The first (most anterior) glabellar furrows make an angle of about 140°. The second and third furrows are more or less transverse, and reach the axial furrows. The free cheeks are moderately tumid for this genus. The marginal furrow and neck furrow make an angle of about 50° (left side of cephalon measured).

The eyes are large, reaching from the first furrow to the third. A line joining the ends of the left eye measures 1·5 cm. The facets are small, circular and closely packed, there being 12 or more (the preservation is not good) in the central rows, and less towards the ends. There are of the order of 40 rows.

The genal spines are long and strong. On the right side of the holotype an almost complete genal spine is preserved, but it is turned under somewhat by compression. As preserved, it measures about a centimetre wide where it leaves the cephalon proper, and reaches as far as the eighth segment of the thorax, where it is broken off, the width there being 2 mm.

Thorax.

The thorax consists of eleven segments, and is approximately 6 cm. long and 9 cm. wide, a ratio of 1 : 1·5. The greatest width of the axis is 2·5 cm., a ratio of axis to thorax of 1 : 3·6, and of axis to pleuron of 1 : 1·3. Each pleuron is divided by a narrow median furrow for practically its whole length. The outer ends of the pleura are deflected ventrally, and terminate in pleural spines.

Pygidium.

The pygidium has 18 pygorachial segments plus the rounded terminus. There are 12 pygopleural segments. The right half of the pygidium is partially obscured by the matrix, but judging by the left half the pygidium must be 9 cm. wide. The length (without the terminal spine) is about 6·5 cm., a ratio of width to length of 1 : 1·4. The mucro is broken, but was 1 cm. wide where it joined the rest of the pygidium. It appears to be narrowing rapidly.

The greatest width of the rachis is 1·7 cm. (i.e. about one-fifth of the width of the pygidium), and the smallest 0·5 cm. The rachis tapers gradually and ends before reaching the terminal spine. The posterior margins of the pygorachial segments nearer the thorax arch in the middle in an anterior direction. Like the thoracic axial segments, the anterior pygorachial segments have short furrows towards their ends. The posterior pygorachial segments become mere rings without specialized structure.

The anterior pygopleural segments are gently curved posteriorly. This curvature increases until the last segment is actually parallel to the longitudinal axis of the trilobite. A narrow median furrow is present in all the pygopleural segments. Each furrow commences at the rachis and terminates abruptly just before reaching the margin of the pygidium, which is fused into a continuous line. Where the pygidium is broken away a little, a well-developed doublure (of the order of ½ cm.) can be seen.

Comparison.

The new species simulates closely *Odontochile dunbari* Delo from the Devonian of Missouri (Bailey limestone). *O. dunbari* has the same number of both pygorachial and pygopleural segments as *O. formosa* ; it has a similar deflection of the pygopleural segments, and a similar furrowing ; the pygorachial segments have a similar arching of the posterior edge ; and finally, the two species are of similar proportions. The cephalon and thorax of *O. dunbari* are unknown (see Delo, 1940, p. 56).

Determination of Dalmanitids.

In members of the Dalmanitidæ, the number of pygorachial segments is important both for generic and specific determinations. But the number of segments that can be counted varies with the maturity of the animal, and so it is very important to have a mature specimen on which to base a determination. Delo has pointed out that size is a helpful guide in making generic determinations, and it is also a specific character. Here again there is variation with stage of growth. It is therefore important in determining any of these forms to be sure that the trilobite is a mature specimen, otherwise the determination can be misleading. It is desirable to have a range of specimens in hand before a new species is described, and there is uncertainty, in my opinion, in describing a new species from a solitary pygidium as has been done.

The genus *Dalmanites* grades into the genus *Odontochile*, and difficulty can attach to their separation. However, most difficulties disappear if mature specimens are chosen, and then the criteria set out in the diagnoses of the genera objectively applied.

Character of Gens.

The fact that for over 50 years so many species belonging to two genera have been given the one name indicates the solidarity of the gens. The forms are very much alike and constitute a closely related genetic sequence. The species described in this paper are apparently only some of a number belonging to the gens. Material seen from Tasmania, Victoria and New South Wales suggests the presence of other species. The gens is characterized by large eyes set high in the exoskeleton so as to rise well above the glabella. As far as it has been worked out, the genealogical relationships appear to be as follows :

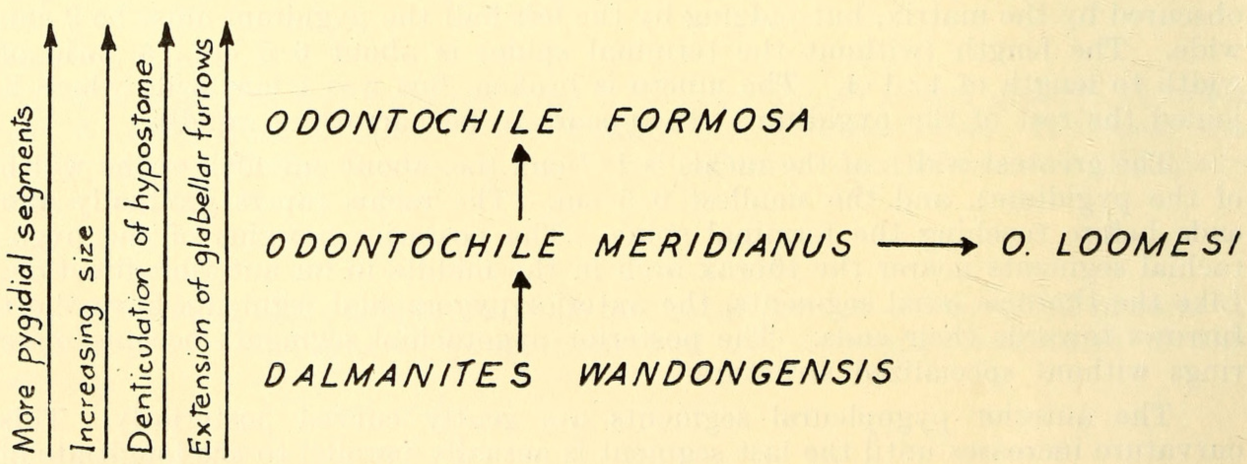

Fig. 1.

O. loomesi is very closely related to *O. meridianus*, but its different proportions from the other members of the gens shows that it is a branch away from the main line of development.

The signs of maturation in these trilobites are larger size, more advanced development of the posterior segments of the exoskeleton, greater tumidity, deeper impression of glabellar furrows, and in general a better development of the animal's exoskeletal structures. It is interesting to note that these same factors operate in the evolution of the gens. The only new structure in the sequence is the generic one of denticles on the hypostome—a minor specialization of an already existing part.

The glabellar furrows are of considerable phylogenetic significance, and their development in the gens is consequently of some interest and importance. In *D. wandongensis* the glabellar furrows do not reach the axial furrow. In the younger specimens of *O. formosa* (Pl. II, fig. 2), they reach nearer the axial furrow than they do in *D. wandongensis*, but still they do not reach it. In well-matured specimens of *O. formosa* like the holotype, however, the glabellar furrows do reach the axial furrow, although the part nearer the axial furrow is comparatively shallow. Nevertheless the glabellar furrows do definitely conjoin with the axial furrows. Thus in the life history of the individual *O. formosa*, the trend found in the gens as a whole is exemplified.

Stratigraphical Considerations.

The genus *Dalmanites* was believed to be restricted to the Silurian until Delo found that in North America (though as far as is known not elsewhere in the world), there is a slight overlap into the Devonian. He has described forms from the Helderbergian. *Odontochile*, as far as is known, is restricted to the Devonian.

Odontochile formosa comes from beds which have been referred to the Lower Devonian. *Odontochile meridianus* and *O. loomesi*, on the other hand, come from beds which have been described by Dr. Ida Brown (1941) as Silurian in age. The range of *Odontochile* is therefore greater than formerly believed (as was the case with *Dalmanites*), or some revision of the age determination of the beds concerned is indicated. The beds with *Odontochile* also contain the genera *Pleurodictyum* (*vide* Hill, 1943, pp. 58–59) and *Dicranurus* (Gill, 1948), which are restricted to the Devonian elsewhere.

It should be noted that *Odontochile meridianus* and *O. loomesi* are not so well advanced in development as *O. formosa*, from which it may be inferred that they are older in age. A similar position was noted with *Dicranurus* (Gill, 1948).

Chapman (1914, p. 219) referred the beds on Broadhurst's Creek at Wandong to the Melbournian Series, but later (1915, p. 161, footnote) referred them to low down in the Yeringian or passage beds, making mention specifically of the presence of " *Dalmanites meridianus* ". It was the presence of this fossil which influenced the reference of these beds to the Yeringian Series by the present writer in 1940 (p. 254). *Dalmanites* is a Silurian genus, but extends up into the Devonian (Helderbergian) in North America. *Dalmanites wandongensis* therefore does not determine the age of the beds at Broadhurst's Creek, Wandong. More palæontological work will have to be done before their place in the stratigraphic sequence can be established.

" *Dalmanites meridianus* " has been recorded from Killara (Gill, 1938, p. 170 ; 1939, p. 142). This is a species of *Odontochile*, but a determination is not attempted because the material in hand is not good enough for description. The same applies to specimens from Whittlesea (Chapman in Jutson, 1908), where the species also is an *Odontochile* (determined from F. S. Colliver Collection, No. 2784). Similarly, specimens from Tasmania (Etheridge, 1897) must await the collection of further material to effect their elucidation. The large number of pygorachial segments, a feature specially noted by Etheridge, again indicates the genus as being *Odontochile*.

Acknowledgements.

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Explanation of Plates.

Plate I.

Fig. 1.—*Dalmanites wandongensis*, sp. nov., internal cast of cephalon, *paratype*. Natural size.

Fig. 2.—*D. wandongensis*, sp. nov., internal cast of pygidium, *holotype*. Natural size.

Fig. 3.—*D. wandongensis*, sp. nov., eye of internal cast, ×4. *Paratype*.

Fig. 4.—*D. wandongensis*, sp. nov., eye of external mould, ×4. *Paratype*.

Fig. 5.—*Odontochile loomesi* (Mitchell), internal cast of complete carapace, *lectoholotype*.

Fig. 6.—*O. loomesi* (Mitchell), internal cast of eye, ×6. *Lectoholotype*.

Plate II.

Fig. 1.—*Odontochile formosa*, sp. nov., internal cast of complete carapace, *holotype*. Natural size.

Fig. 2.—*O. formosa*, sp. nov., internal cast of cephalon of young specimen from Davies' Quarry, on the western branch of Stony Creek, about a mile north of Kinglake West State School (same locality as *Dicranurus kinglakensis*), *hypotype*. Natural size. Note that the second and third glabellar furrows fail to reach the axial furrows, as they do on the mature specimen. Univ. of Melbourne, Dept. of Geology, Reg. No. 1947.