REVISION OF SILURIAN AND DEVONIAN ALLANICYTIDIIDAE (ANOMALOCYSTITIDA: MITRATA) FROM SOUTHEASTERN AUSTRALIA, TASMANIA AND NEW ZEALAND

MARCELLO RUTA AND PETER A. JELL

Ruta, M. & Jell, P. A. 1999 06 30: Revision of Silurian and Devonian Allanicytidiidae (Anomalocystitida: Mitrata) from southeastern Australia, Tasmania and New Zealand. *Memoirs of the Queensland Museum* **43**(1): 431-451. Brisbane. ISSN 0079-8835.

Additional specimens of the allanicytidiid anomalocystitids *Notocarpos garratti* (Upper Silurian, Victoria), *Tasmanicytidium burretti* (Lower Silurian, Tasmania) and *Allanicytidium flemingi* (Lower Devonian, New Zealand) yield new information, allowing revised diagnoses. *N. garratti* has a system of ridges on the internal surface of C20-C22 and a row of orifice platelets along distal transverse thickening on inside of C1 and C5. Internal ridges on C21 are homologous with similar structures in *Allanicytidium* and *Placocystella*. *T. burretti* has orifice platelets, faint ridges internally on C21, tetramerous rings proximally in the appendage and sculpture on the distal styloid blade. New material of *A. flemingi* shows external sculpture and stereom texture of convex surface, shape of C21 and proximal body excavation. ❐ *Allanicytidiidae, Silurian, Devonian, Victoria, Tasmania, New Zealand.*

Marcello Ruta, Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom; Peter A. Jell, Queensland Museum, P.O. Box 3300, South Brisbane 4101, Australia; *received 20 August 1998.*

Despite extensive discussion on the interrelationships of allanicytidiid anomalocystitids (Caster & Gill, 1967; Philip, 1981; Caster, 1983; Haude, 1995; Ruta & Theron, 1997; Ruta & Jell, 1999a; Ruta, in press), numerous features of several species remain obscure or misinterpreted. All species except for the 2 most basal allanicytidiids, *Protocytidium elliottae* Ruta & Jell, 1999a from the Upper Ordovician of Victoria and *Occultocystis koeneni* Haude, 1995 from the Lower Devonian of Argentina, display very similar plate configurations, especially on the convex surface, making specific recognition difficult. Differences in external sculpture, in body proportions and in shape of individual plates provide diagnostic features (Ruta & Theron, 1997; Ruta, in press).

Newly available material of the allanicytidiids *Notocarpos garratti* Philip, 1981, *Tasmanicytidium burretti* Caster, 1983 and *Allanicytidium flemingi* Caster & Gill, 1967 clarifies poorly understood aspects of their anatomy, permitting revised diagnoses.

SYSTEMATIC PALAEONTOLOGY

Specimens are housed in the Museum of Victoria, Melbourne (prefix NMVP), and Department of Geological Sciences, University of Canterbury, Christchurch (UCM). Most localities are entered on the Museum of Victoria locality register (NMVPL). Terminology, orientation and plate nomenclature follow Ubaghs (1967, 1969) and Ruta (in press), with modifications as in Ruta & Jell (1999a-c). All illustrations are of latex casts from decalcified moulds and whitened with ammonium chloride.

Class STYLOPHORA Gill & Caster, 1960
Order MITRATA Jaekel, 1918
Suborder ANOMALOCYSTITIDA Caster, 1952
Family ALLANICYTIDIIDAE Caster & Gill, 1967

DIAGNOSIS. See Ruta & Jell (1999a).

Notocarpos Philip, 1981

TYPE SPECIES. *Notocarpos garratti* Philip, 1981 from the Ludlow Clonbinane Sandstone Member of the Humevale Formation, central Victoria; by original designation.

DIAGNOSIS (modified from Philip, 1981 and based on the largest available, undeformed specimens). Plate A about as wide as long, with long axis at about 45° to body axis, not in contact with left PLM. Plate B lacking. Plate C as wide as long, with subparallel lateral margins. LOP narrowly wedge-shaped. DLM with poorly developed truncatoconical projection, with process for spine insertion. C1 and C5 about 1.5 times as wide as long. C20 and C22 subrhomboidal, wider than long, with gently sinuous distal margins.

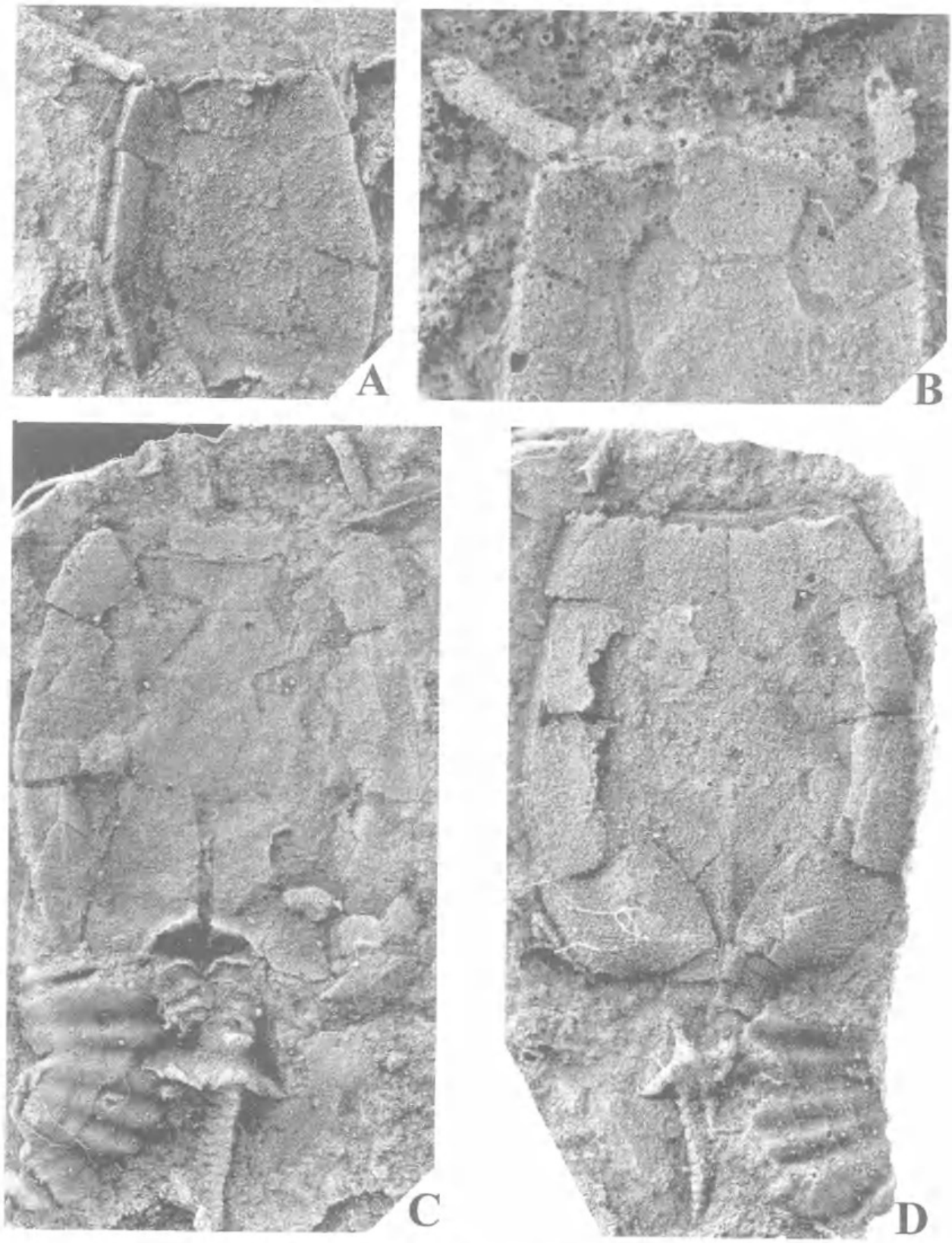


FIG. 1. *Notocarpos garratti* Philip from NMVPL300. A, plano-concave surface of NMVP100452, ×5. B, distal half of plano-concave surface of NMVP100453, ×8. C,D, plano-concave and convex surfaces, respectively, of NMVP100441, ×5.

C21 twice as long as wide, occupying about 40% of width of convex surface, narrowly inserted between C20 and C22, with proximo-lateral margins smoothly concave, with proximal margin about 1/10 plate width, with straight lateral margins parallel to body axis. Spines straight, robust, cigar-shaped, without cutting lateral edges. Transverse ridge ornament on at least some part of A, C, DLM, ILM and PLM. C20 and C22 with same ornament laterally. Riblets and irregularly confluent, short transverse ridges laterally on C11, C13, C15 and C19. C21 without sculpture. Proximal part of appendage of 4 tetramerous rings overlapping each other to a small extent. Proximal styloid blade 1/3 width of distal blade, approximately semicircular, smooth. Distal blade massive, fan-shaped, with straight radiating ridges. Distal part of appendage narrow, truncated abruptly (probably incomplete in all available specimens), presumably not longer than body.

Notocarpos garratti Philip, 1981
(Figs 1-11, 16A)

Notocarpos garratti Philip, 1981: 36, figs 3-6; Caster, 1983: fig. 2C.

MATERIAL. NMVP100459-100460, 22350-22351 from NMVPL299 (= F31 of Williams (1964)) in road cutting south of Bald Hills, c. 3.2km E of Kilmore, Victoria (Ludlow, Dargile Formation); NMVP100440-100445, 100449-100456, 21939-21942, 22349, 22353-22354 from NMVPL300 (= X64 of Williams (1964)) near disused mine on Comet Creek, c. 4.6km SE Clonbinane, Victoria (Ludlow, Clonbinane Sandstone Member, Humevale Formation); NMVP65008-65010, 65022-65028, 65030-65031, 65035-65038, 65040-65042, 65044, 65052-65053 from the type locality, in a cutting on Dry Creek Road, Clonbinane; mid Ludlow, Clonbinane Sandstone Member, Humevale Formation.

DIAGNOSIS. As for genus.

DESCRIPTION. EXTERNAL. (including only new or additional data not in Philip, 1981). MOP broadly trapezoidal, 1.5-2 times as wide as long, with straight distal margin. LOP wedge-shaped, with major axis at c.45° to body axis, narrowly inserted between MOP and DLM, with straight or convex lateral margins, with straight or concave medial margins. C21 much longer than wide, with concave proximo- lateral margins. C11 and C13 shorter than C15 and C19. C15 and C19 same size or larger than C20 and C22. Terrace-like ridges rarely extending across width of marginal plates of plano-concave surface, frequently replaced laterally by short ridges or riblets. Similar pattern on convex suface, except for more numerous riblets and confluent short ridges on lateral 2/3 of C11, C13, C15 and C19. External stereom texture usually compact to coarsely granular, rarely microporous or with vermicular surface pattern.

INTERNAL. C21 and C20 with system of ridges proximally (Figs 9A, 10C, 11). Ridges variable in width, meandering on C21 to form almost bilaterally symmetrical pattern, proximally consisting of straight left and irregularly sinuous right sections normal to proximo-lateral margins of plate running medially to points directly distal to left and right ends of proximal plate margin, distally in sinuous bilaterally symmetrical pattern with 2 lateral and 2 medial lobes. Distally the ridges recurve proximally in thin parallel left and right ridges; proximal ends separated by wide, medial, proximally tapering septum; septum slightly higher than ridges, with almost vertical lateral walls.

Ridge on C20 with first lobe after crossing from C21 V-shaped and apex pointing at co-operculum of C20; second lobe large, club-shaped, with medial arm crossing back to C21, curving latero-distally to surround right proximo-lateral angle of C21, continuing as thinner, straight ridge back on C20; third lobe subtrapezoidal, pointing towards co-operculum, with straight diverging arms; fourth and fifth lobes very weak ridges, finger-like; fifth lobe lateral to co-operculum. Co-operculum of C20 fan-shaped, raised, with slightly thickened margin, with proximal part continuing to proximo-lateral corner of plate as subtriangular, raised structure with almost straight medial margin and broadly concave lateral margin, distally with thick subquadrate body on margin centro-distally; faint, distally concave ridge projecting laterally from co-operculum, almost parallel to proximal arm of fifth lobe, widening and fading laterally.

Orifice platelets overlying transverse thickening on distal interior of C1 and C5, 6-8 in transverse row, rectangular, 1mm wide, 0.75mm long (Figs 5C, 8A).

APPENDAGE. Proximal part of appendage about 1/5 body length, <1/3 body width. Tetramerous rings 4, overlapping each other narrowly, with thickening along distal margins, gently arcuate transversely. Proximal styloid blade smooth, as long as wide, 1/3 distal blade width, slightly broader than and hardly separated from central part of styloid, with roughly semi-circular thick free margin, with convex distal

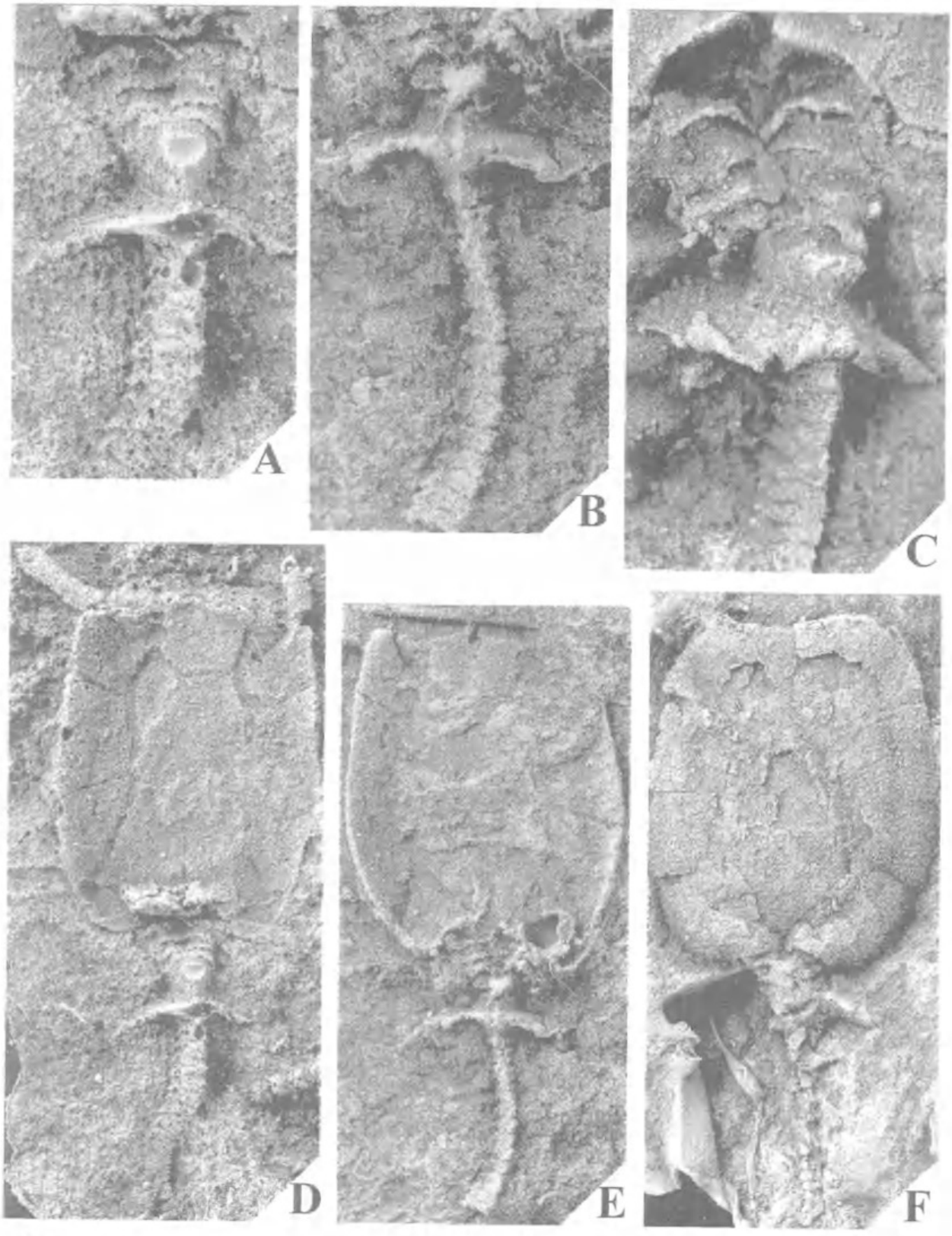


FIG. 2. *Notocarpos garrattii* Philip from NMVPL300. A,D, detail of proximal appendage and plano-concave surface, respectively of NMVP100453, ×10 and ×5, respectively. B,E, detail of proximal appendage and plano-concave surface of NMVP100443, ×8 and ×5, respectively. C, detail of proximal appendage of NMVP100441, ×10. F, convex surface of NMVP100440, ×5.

surface, sometimes exceptionally well-developed and flared (Fig. 10B,D). Distal styloid blade transversely expanded, fan-shaped, slightly recumbent proximally, with sharp free margin, with weak straight radial ridges on proximal and distal surfaces (Fig. 9A,C-D); ridges of proximal surface slightly more robust and wider medially than laterally; ridges of distal surface slightly wider and flatter than on proximal surface; lateral ear-like projections with flat to gently depressed proximal surfaces and semicircular to parabolic margins. Appendage incomplete in most specimens. Ossicles and plates similar to those of *Placocystella africana* in lateral view (Ruta & Theron, 1997); ossicles with slightly more sinuous proximal and distal margins, with apical margin at 45° to horizontal plane, with apex projecting distally, with knobbly sculpture on lateral surfaces. External stereom texture of appendage similar to that of body, sometimes irregular due to coarse, irregular ridges, pustules and shallow pits, especially on tetramerous rings and styloid.

MORPHOGENY. In smallest specimens: length/width ratio of body slightly greater; lateral body margins more convex in proximal 1/3; plate A at least twice as long as wide; MOP as long as wide; proximal and distal margins of DLM and ILM more strongly converging medially; DLM wider than long; angle between lateral and medial margins of C1 and C5 >120°; lateral and medial margins of C1 and C5 sometimes merging into each other along smooth curve; lateral and distal margins of C20 and C22 merging gradually into one another along gently convex curve in plan view, without forming latero-distal angle; C11 and C13 as long as or longer than C15 and C19; C15 and C19 smaller than C20 and C22; proximolateral margins of C21 gently sinuous, diverging at greater angle from longitudinal axis; C21 width/body width slightly higher; C21 length/C1 (C5) length ratio slightly lower; spines more robust, shorter than distal body margin, club-shaped; proximal part of appendage <1/5 as long as body, at least 1/2 as wide distally as proximally; distal styloid blade >1/2 body width; ridges on both surfaces of the body frequently interrupted and replaced by riblets or transversely aligned short ridges; most distal ridges often pustule-like, especially on convex surface.

REMARKS. Although preservation is sometimes poor due to relatively coarse matrix and despite little deformation in some specimens, new material of *Notocarpos* supplements information on external ornament of body plates and styloid. Previously unrecorded features include the rectangular orifice platelets on the inside of C1 and C5 and the system of sinuous ridges on interior proximal 1/2 of convex surface. The latter feature has been documented only in *Allanicytidium* and *Placocystella* among allanicytidiids (Caster & Gill, 1967; Ruta & Theron, 1997). Orifice platelets are known in some Northern Hemisphere anomalocystitids (Jefferies & Lewis, 1978; Kolata & Guensburg, 1979; Kolata & Jollie, 1982; Parsley, 1991).

Tasmanicytidium Caster, 1983

TYPE SPECIES. *Tasmanicytidium burretti* Caster, 1983 from the Lower Silurian Richea Siltstone, Tasmania; by original designation.

DIAGNOSIS. (modified from Caster, 1983). Plate A as long as and c. 1/3 as wide as C; A-C suture straight. LOP-DLM suture strongly concave distally. DLM with latero-distal angles subcylindrical for spine insertion. C20 and C22 with weak transverse keels occupying more than 1/2 of plate width. C21 shield-like, with most proximal part narrowly inserted between C20 and C22, with gently concave proximal margin very narrow. Spines round in cross-section, straight, needle- shaped. Scale-like riblets on lateral 1/2 of PLM and on C11, C13, C15, C19, C20, and C22. C20 and C22 with few, short, transverse terrace-like ridges proximo-laterally.

Tasmanicytidium burretti Caster, 1983 (Figs 12, 16B)

Tasmanicytidium burretti Caster, 1983: 334, figs 2-4.

MATERIAL. NMVP148541 from NMVPL296 near Terry Walshe Road, Tiger Range, on 1:100,000 Wedge Sheet 8112 DN512850, Tasmania; Llandovery, Richea Siltstone (Baillie, 1979).

DIAGNOSIS. As for genus.

DESCRIPTION. EXTERNAL. Largest riblets on convex surface scale-like, closely spaced, with straight to irregular distal margin, confined to C20-C22, about 0.2mm wide; smallest riblets subcircular, sparse, conferring pustulose aspect to distal part of convex surface, about 0.1mm wide (Fig. 12B). Transverse ridges on C20 and C22 faint. Riblets on C15 and C19 never confluent, irregularly spaced, scale-like or sub-rectangular proximally, subcircular to pustulose distally. Riblets on C11 and C13 sparse, small,

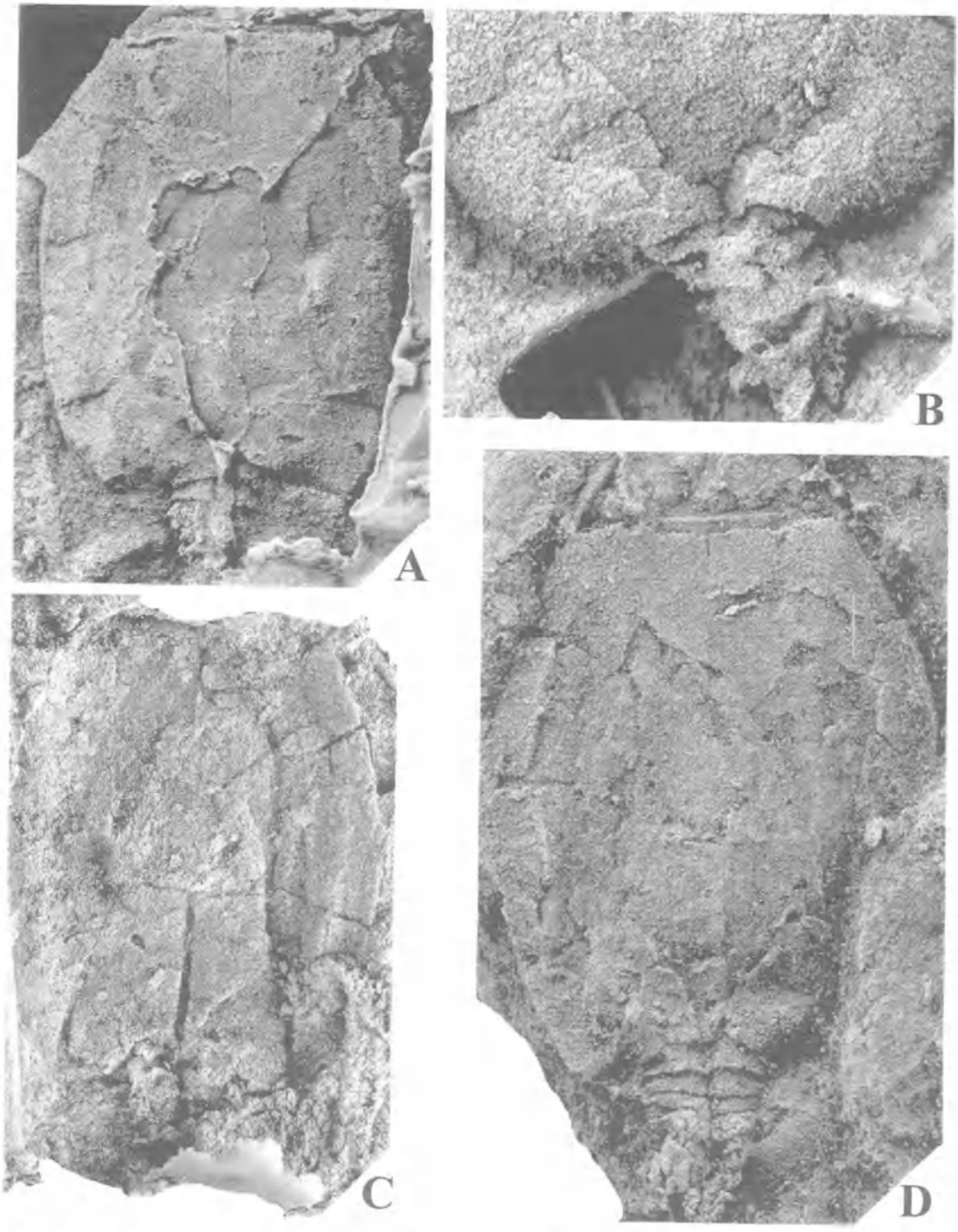


FIG. 3. *Notocarpos garratti* Philip from NMVPL300. A,C, convex and plano-concave surfaces of NMVP100445, ×3. B, proximal convex surface and appendage of NMVP100440, ×10. D, convex surface of NMVP100442, ×4.

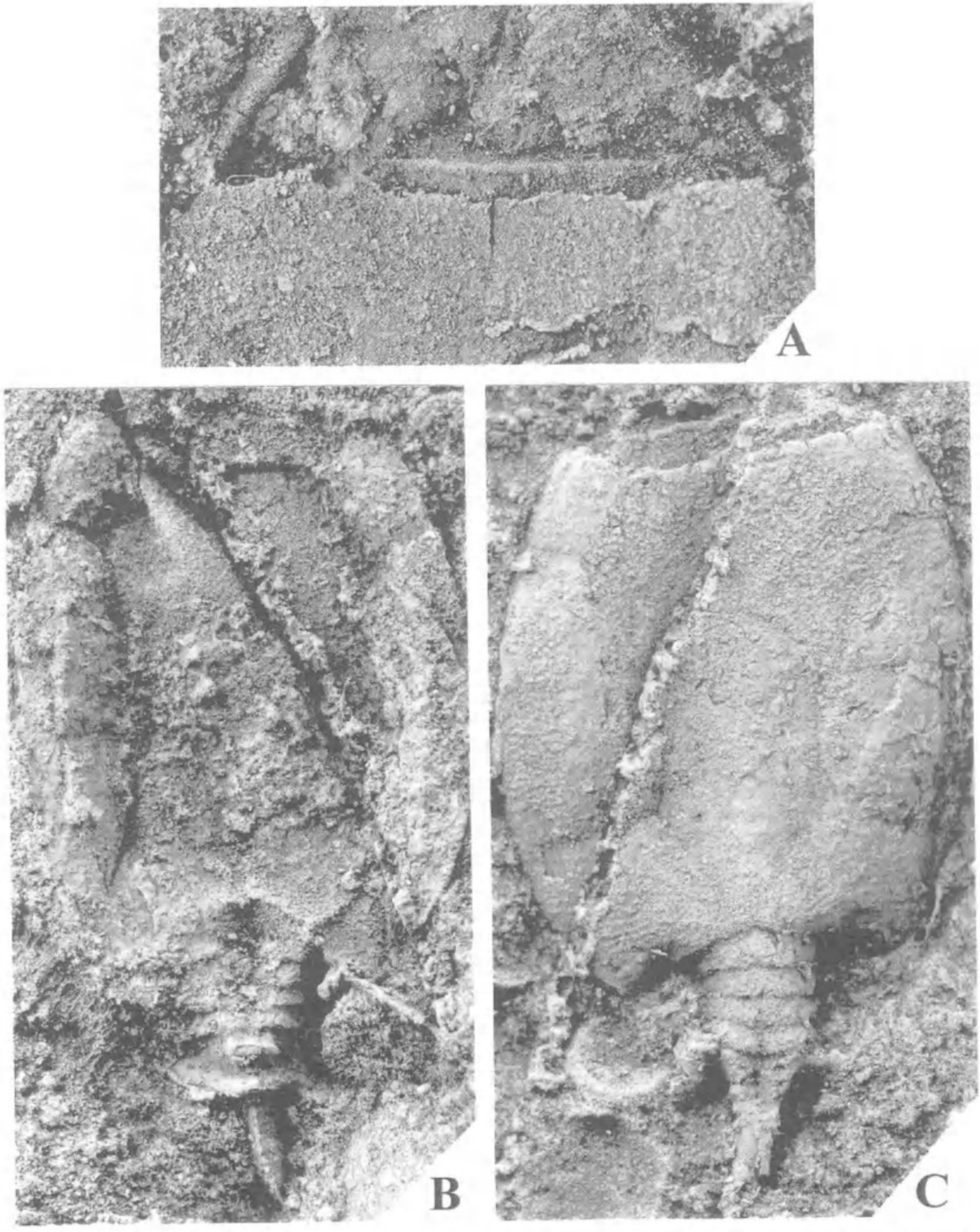


FIG. 4. *Notocarpos garratti* Philip from NMVPL300. A, detail of distal part of convex surface of NMVP100442, ×8. B-C, plano-concave and convex surfaces, respectively of NMVP21939, ×5.

pustulose. Riblets on C21 varying in shape and size proximo-distally, uniformly distributed. C21 with narrow, marginal zone of short, transverse striations. Stereom fabric apparently

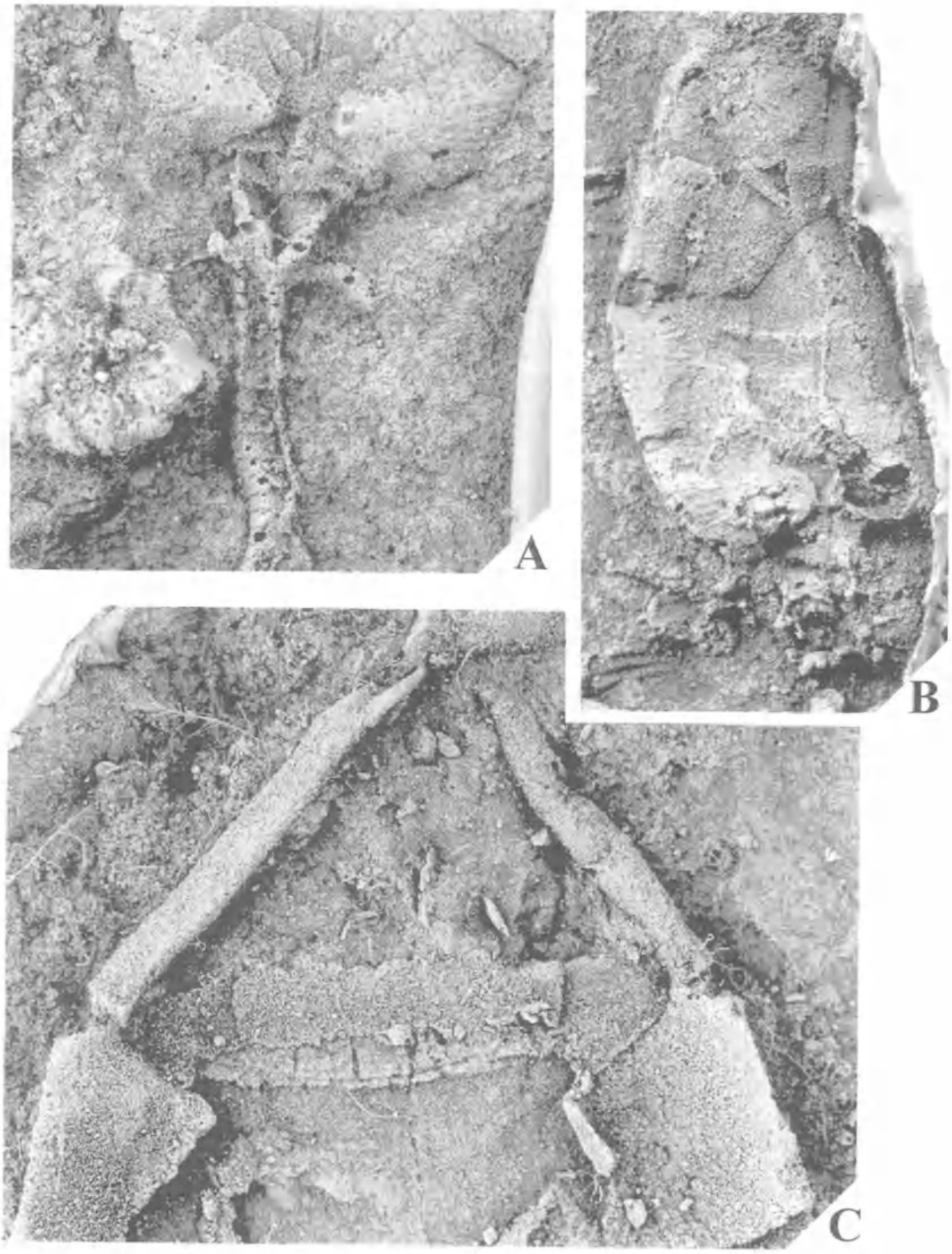


FIG. 5. *Notocarpos garrattı* Philip from NMVPL300. A, proximal part of convex surface and appendage of NMVP100451, ×8. B, convex surface of NMVP100450, ×5. C, distal part of plano-concave surface from interior, with spines and orifice platelets on NMVP100442, ×8.

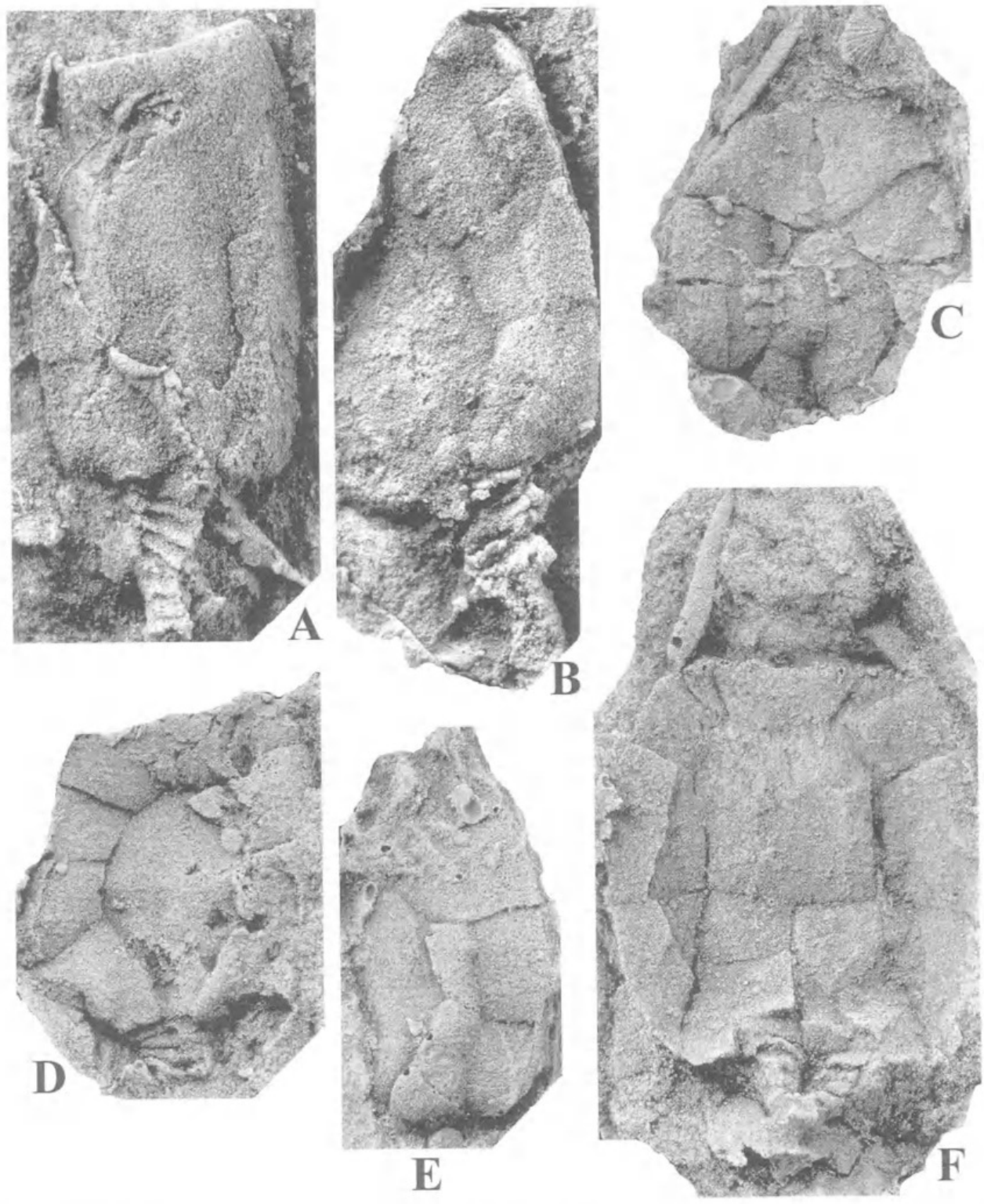
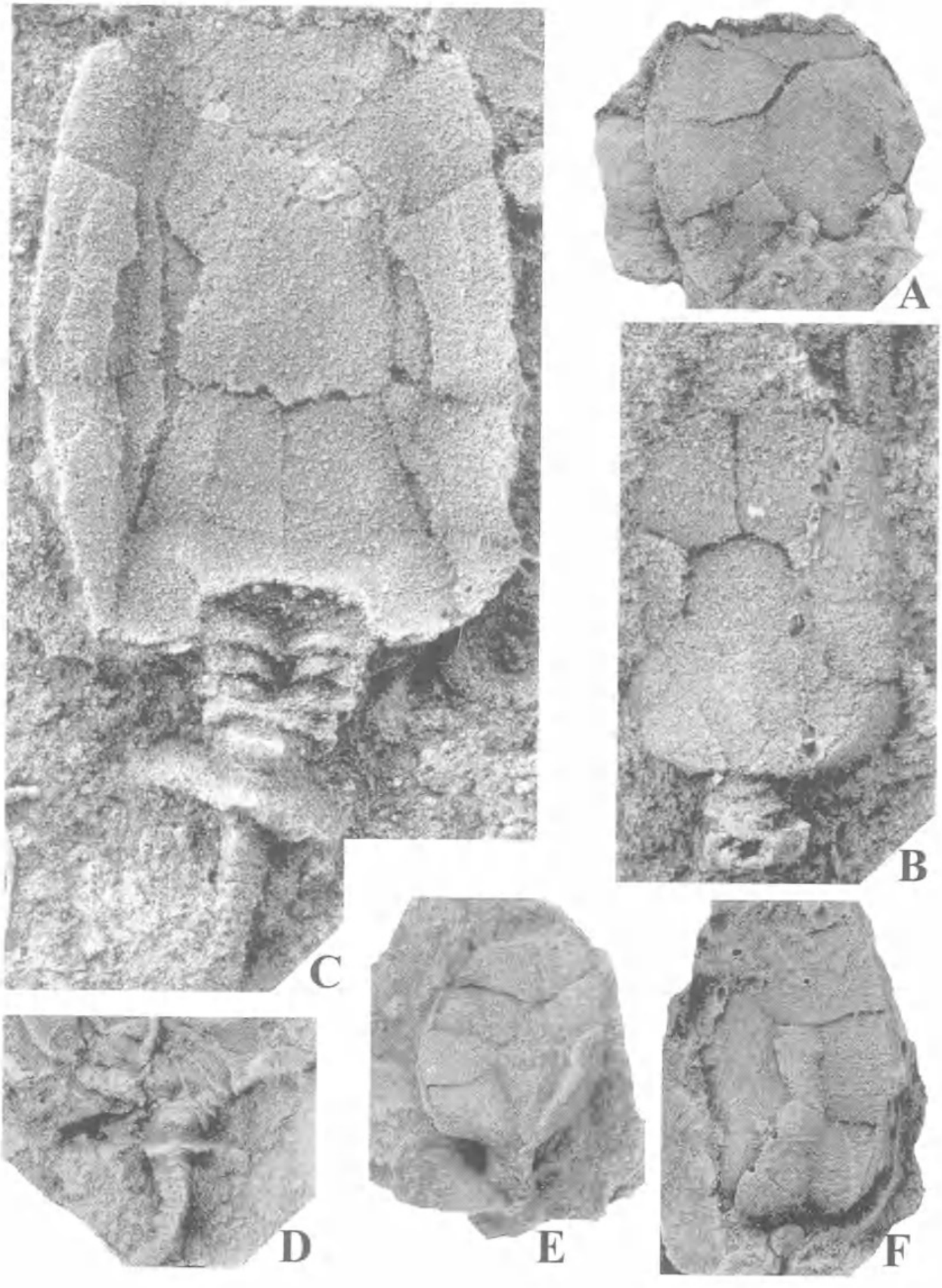


FIG. 6. *Notocarpos garratti* Philip. A, convex surface of NMVP100459. B, partial convex surface of NMVP100460. C, partial (distal) convex surface of NMVP65040. D, convex surface of NMVP65027. E, partial convex surface of NMVP65037. F, plano-concave surface of NMVP65031. A-B from NMVPL299, ×5. C-F from G23, ×3.


A
B
C
D
E
F

microporous to compact. Stereom centrally on C1 and C5 of irregular, subcircular shallow pits separated by weak trabeculae, proximally compact or minutely porous, distally vermicular, with irregularly sinuous, thick bifurcating trabeculae separated by shallow, narrow furrows and often flanked by short thickenings of variable shape and size.

INTERNAL. C5 and C13 with laterally displaced, subhemispherical thickenings. C21 with subcentral straight ridge on proximal half surrounded by poorly defined, sinuous ridges as in *Allanicytidium* and *Notocarpos*. Distal margin of C1 and C5 with transverse row of 5-6 central subquadrate orifice plates, 0.3-0.5mm wide, bordered proximally by smaller, rectangular platelets. Orifice plates and inside of convex surface with compact to microporous stereom.

APPENDAGE. Tetramerous ring plates of convex side arcuate in cross-section, with thin ridge running close to the thickened distal margins. Styloid with large distal blade; blade with concentric, externally convex, closely spaced ridges on proximal (Fig. 12A) and distal surfaces (Fig. 12B), arranged in sectors delimited by radial furrows running on distal surface from insertion of blade on styloid to blade margin, and corresponding to radial ridges with zig-zag course on proximal surface; concentric ridges alternating on both sides of zig-zag ridges and radial furrows, with degree of curvature increasing in more apical sectors (i.e. sectors which are closer to midpoint of blade margin).

REMARKS. The new specimen adds information on orifice plates, tetramerous rings of appendage, shape and ornament of styloid blade, external body sculpture and inside of convex surface. The specimen is slightly deformed, but the convex surface is fully articulated. Comparison with the holotype permits an approximate estimate of body outline and general proportions. The elongate-ovoid or vasiform body (Caster, 1983) is almost certainly a genuine feature, although it may be slightly exaggerated in Caster's reconstruction.

Allanicytidium Caster & Gill, 1967

TYPE SPECIES. *Allanicytidium flemingi* Caster & Gill, 1967 from the Lower Devonian Reefton Group, New Zealand; by original designation.

DIAGNOSIS. (modified from Caster & Gill, 1967). Body subquadrate to ovoid, with broad margined re-entrant for insertion of appendage. A and C longer than wide, almost mirror images of each other. DLM with latero-distal angles projected into subconical processes for spine insertion. C1 and C5 thickened internally along distal margin, with sinuous proximo-lateral margins. C11 and C13 approximately equal in size to C1 and C5, with broadly concave medial margins and irregular proximal margins. C15 and C19 2/3 size of C11 and C13, each with sinuous proximal margin. C20 and C22 larger than C15 and C19, as wide as long. C21 with concave proximo-lateral margins interrupted by marked expansion in proximal half, with straight subparallel lateral margins. Closely spaced, polygonal to scale-like riblets on lateral marginal plates of plano-concave surface, near lateral margins of A and C and along most of the lateral margins of PLM. Proximal styloid blade semicircular, with thick, radial ridges on its distal surface. Distal styloid blade much wider than tall. Ossicles with lateral vertical grooves and poorly developed, nodose apices.

Allanicytidium flemingi Caster & Gill, 1967
(Figs 13-15, 16C)

Allanicytidium flemingi Caster & Gill, 1967: S564, figs 360, 361; Caster, 1983: figs 1, 2A.

MATERIAL. NMVP27474 (plaster replica of holotype NZGS38/370203) and UCM440 from Rainy Creek near Reefton, Westland, South Island, New Zealand in the Emsian, Reefton Group.

DIAGNOSIS. As for genus.

DESCRIPTION. EXTERNAL (Figs 13, 14A). Riblet size (0.1-0.5mm wide), shape and distribution variable on different plates and on the same plate of convex surface. Riblets closer together on lateral 1/2 of marginal plates. Largest riblets on lateral 1/2 of C15, C19, C20 and C22, crescent-shaped, rectangular or irregularly polygonal, in irregular transverse rows, often resulting in vermicular surface, as opposed to

FIG. 7. *Notocarpos garratti* Philip. A, convex surface of NMVP65028. B, convex surface of NMVP22354. C, plano-concave surface of NMVP21941. D, proximal appendage of NMVP65053. E, convex surface of NMVP65035. F, convex surface of NMVP65037. A, D-F from G23, all ×3. B-C, from NMVPL300, ×8 and ×6, respectively.

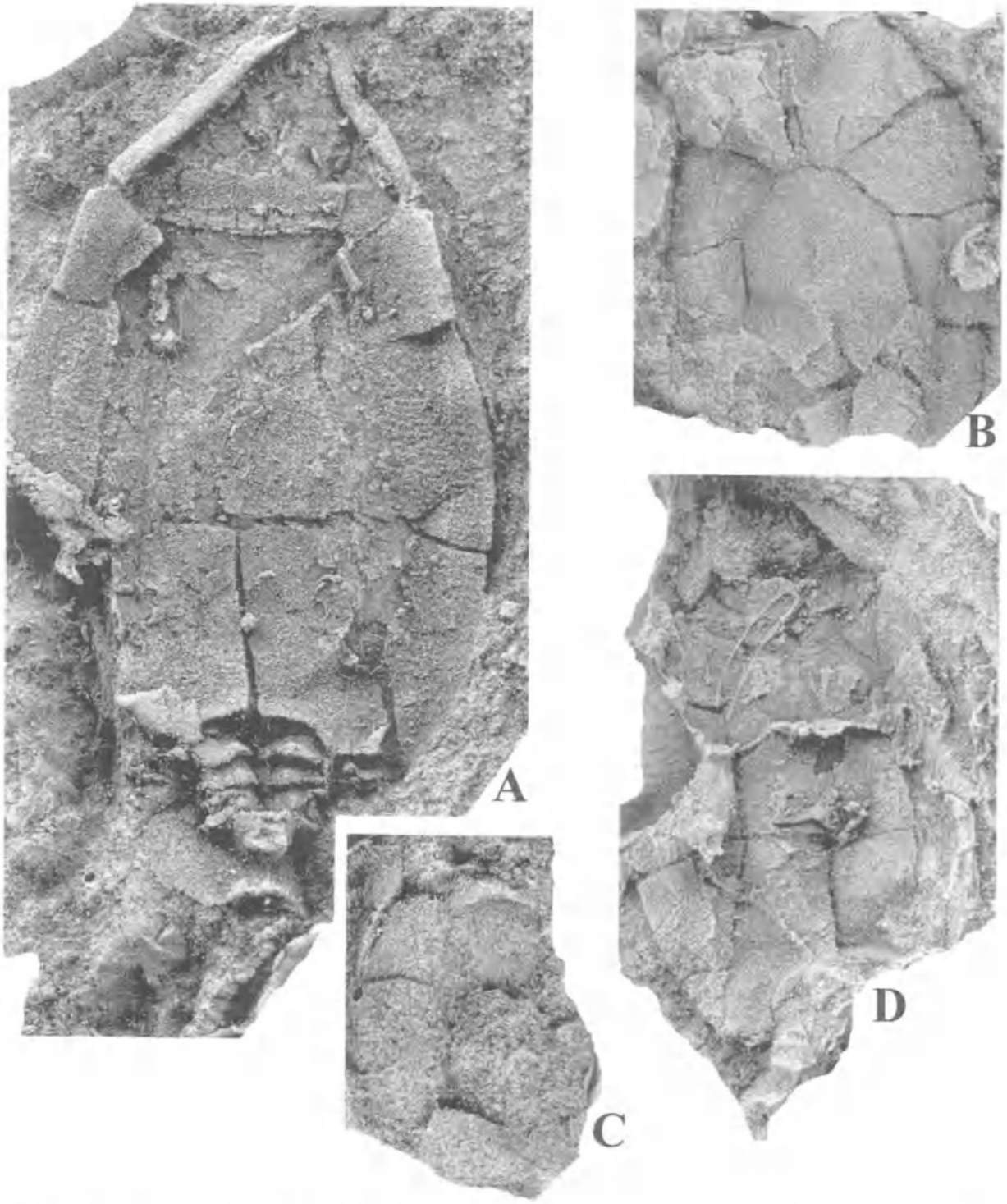


FIG. 8. *Notocarpos garratti* Philip. A, exterior view of plano-concave surface of NMVP100442 from NMVPL300, ×4. B, convex surface of NMVP65042. C, partial convex surface of NMVP65025. D, partial plano-concave surface of NMVP65044. B-D, from G23, ×3.

tuberculate or scaly elsewhere. Smallest riblets distally and proximo-medially on C20 and C22 and on proximal 1/2 of C21, generally scale-like to broadly rounded, slightly wider than long, with poorly defined margins, sometimes reduced to small pustules without distal slope. Riblets on C21 less pronounced than those on lateral 1/2 of marginal plates, with more regular, convex distal

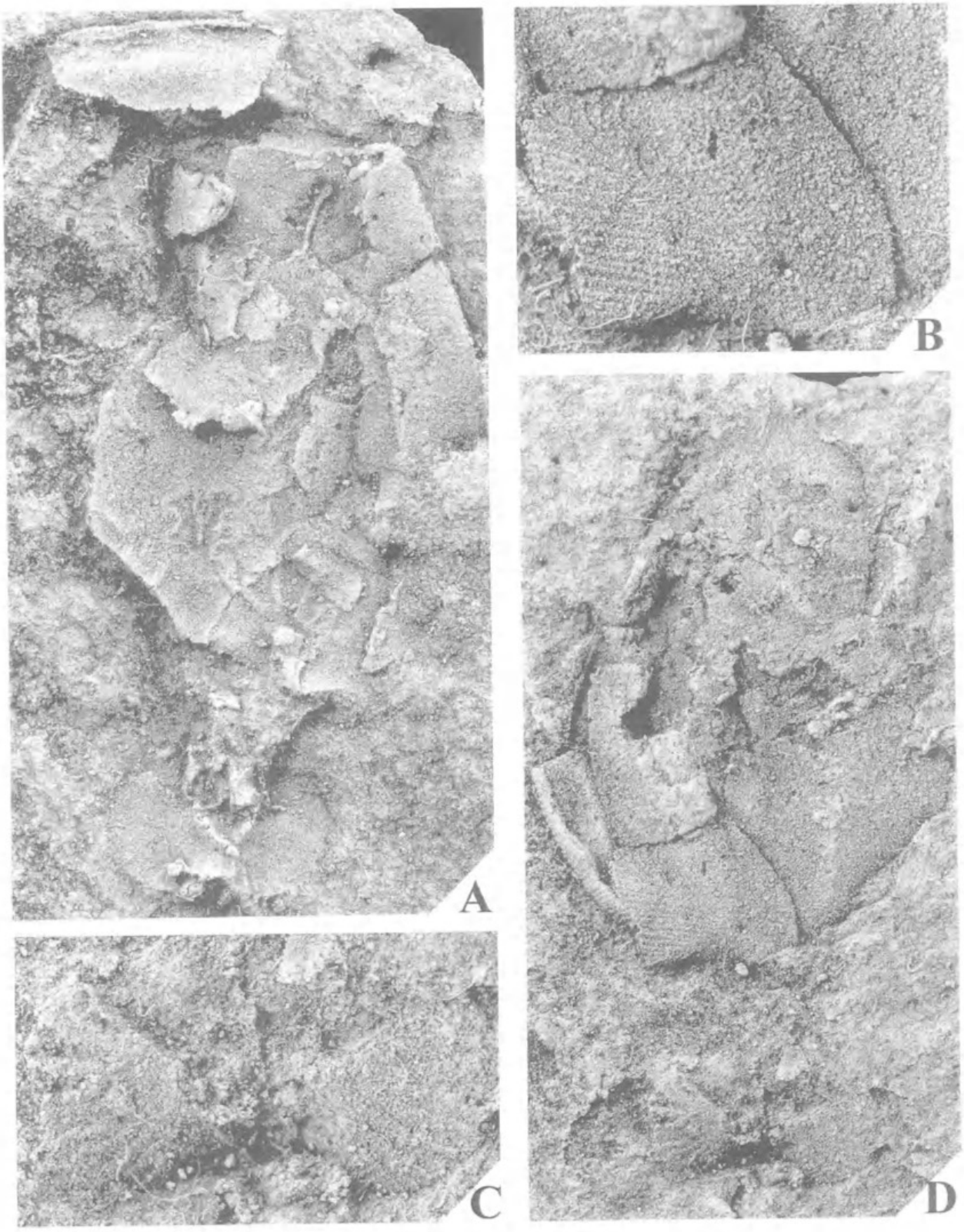


FIG. 9. *Notocarpos garratti* Philip, NMVP100444 from NMVPL300. A, inside of convex surface with system of ridges on C20 and C21 and disrupted co-operculum on C20, ×4. B, detail of C20 from D, ×8. C, detail of styloid from A, ×8. D, partial convex surface, ×4.

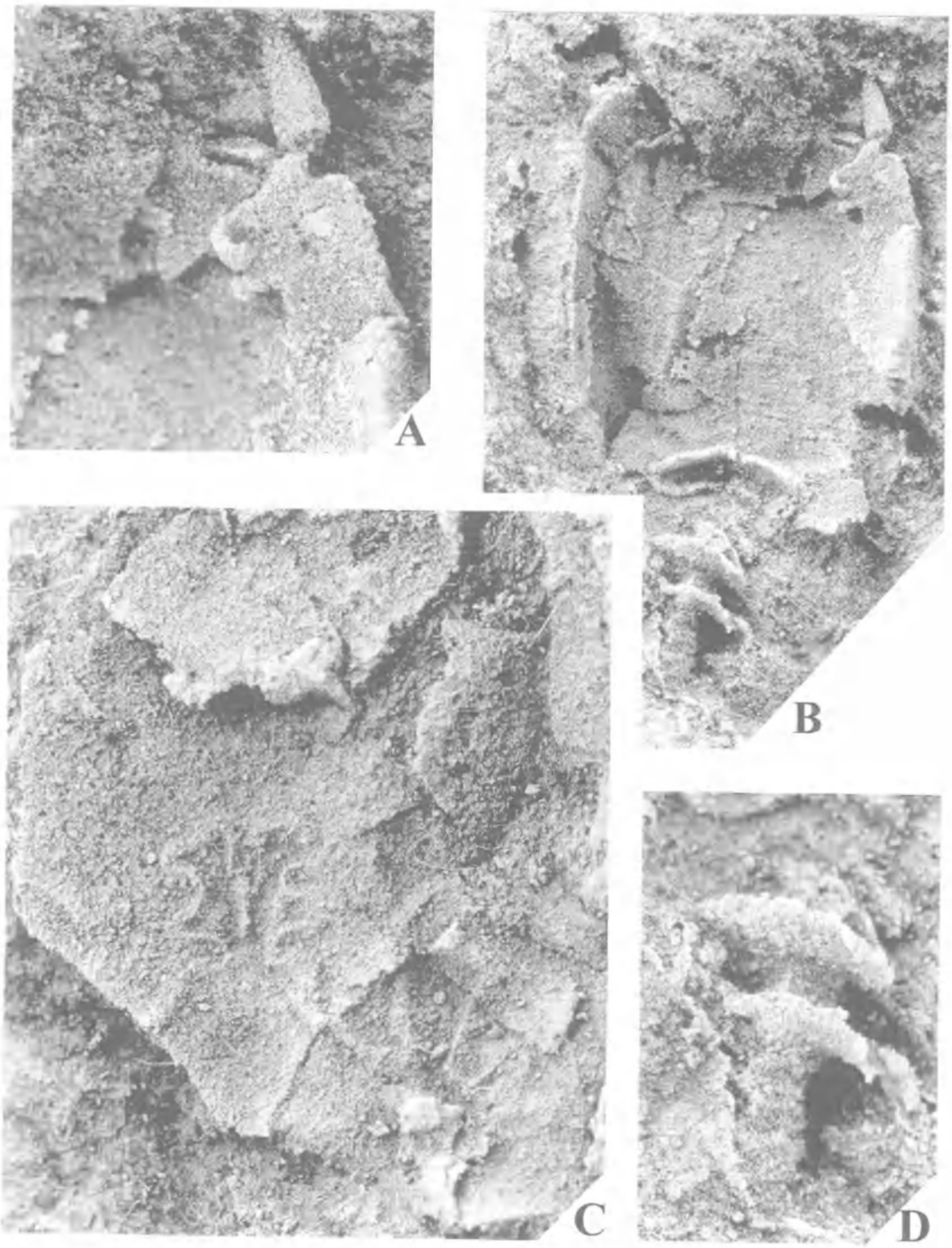


FIG. 10. *Notocarpos garratti* Philip. A-B, D, inside of plano-concave surface (B) with detail of laterodistal corner (A) showing articulation of spine and proximal appendage (D) of NMVP100463 from NMVPL299, ×10, ×5 and ×10, respectively. C, inside of C20 and C21 of NMVP100444 from NMVPL300, ×8.

margins, 1.5 times wider than long. Riblets on marginal plates 1.5-3 times as wide as long, with sharp, straight to crescentic, rarely polygonal distal margins.

INTERNAL (Figs 14B-C, 15A). Internal surface of lateral marginal plates finely granular, of small irregular pores and furrows. Deeper portions of stereom sponge-like to coarsely perforate, especially on C21. Peripheral bands, corresponding to external bands, of fibrillar stereom composed of parallel striations perpendicular to plate margins and intercalated with transversely elongate to subcircular pores. Bands divided into lateral part and medial part by thin ridge reaching maximum thickness along distal margins of marginal plates and latero-distal margins of C21; medial part 2-3 times as wide as lateral part. Portion of band running along distal angle of C21 1.5 times wider than elsewhere, with coarse stereom, without radial pattern of trabeculae in proximal 1/2, with fine, closely spaced, short trabeculae forming a fringe in distal 1/2 (Fig. 14B-C). Subelliptical, proximo-distally elongate, subcentral thickenings on lateral marginal plates of convex surface, with slightly raised margins. Thickening stereom compact peripherally, porose to sponge-like centrally.

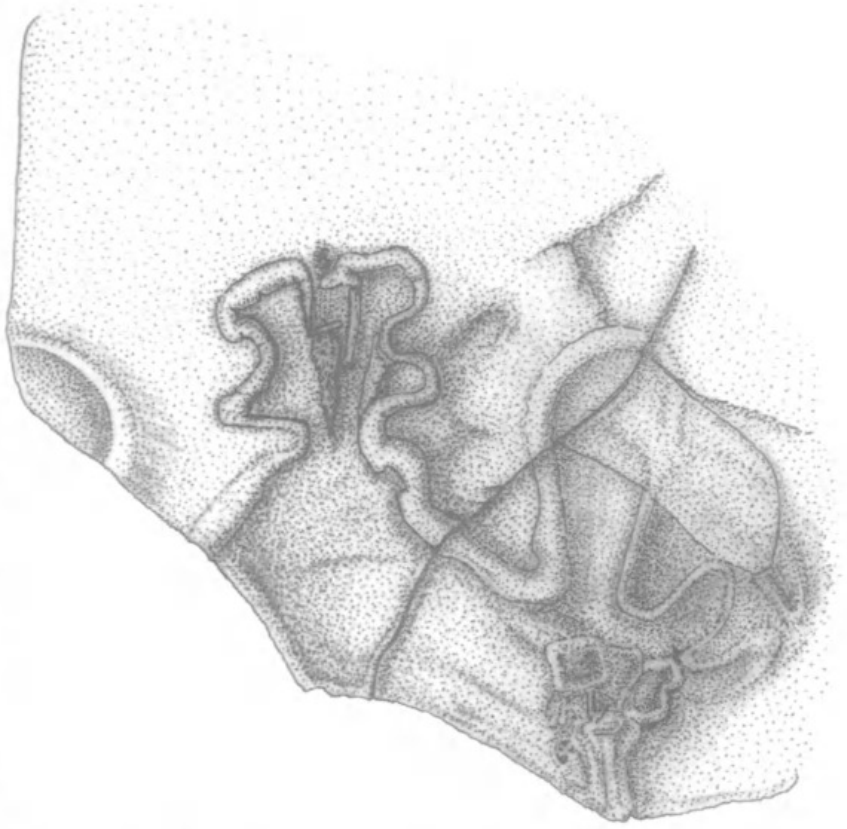


FIG. 11. Camera lucida drawing of system of ridges on internal surface of C20 and C21 in *Notocarpos garratti* Philip, based on NMVP100444.

Stereom (Figs 13-14). External skeleton of microporous stereom without surface pattern. Surface of largest riblets coarsely granular to compact, with minute pores in smallest ones. Stereom near plate margins of larger pores of more irregular shape than those on central part of plates. Plate margins bordered by band 0.2-1mm wide, generally without riblets and with stereom of fine, closely spaced, straight parallel trabeculae and subcircular irregularly distributed pores. Changes of stereom structure through plate thickness visible if skeletal surface is eroded or broken. Stereom of deeper parts of skeleton generally coarser than surface stereom, labyrinthine, of short irregular thin branching trabeculae delimiting irregular pores. Deeper stereom at level of peripheral bands composed of sinuous, branching trabeculae delimited by irregular furrows, replaced by granular fabric immediately adjacent to margins.

Proximal body excavation. Proximal margins of PM crescent-shaped, with medial 1/2 slightly raised above subhorizontal projections (Fig. 15A). Apophyses subvertical, c. 1/2 as wide as each PM, subtriangular, with 1/3 of external surface closer to proximal margins of PM almost flat, remainder gently convex, with lateral ends turning abruptly towards convex surface and continuing into bases of apophyseal horns. Left horn missing. Right horn of uniform width, slightly distal to apophysis, subhorizontal, flat in cross-section, with free margins gently convex externally and only slightly diverging latero-medially (Fig. 15B). Medial end of right horn truncated abruptly without signs of breakage, therefore presumably complete, straight, oblique to longitudinal axis, reaching point at c. 2/3 of apophysis width in latero-medial direction. Space between internal margin of right horn and apophysis transversely

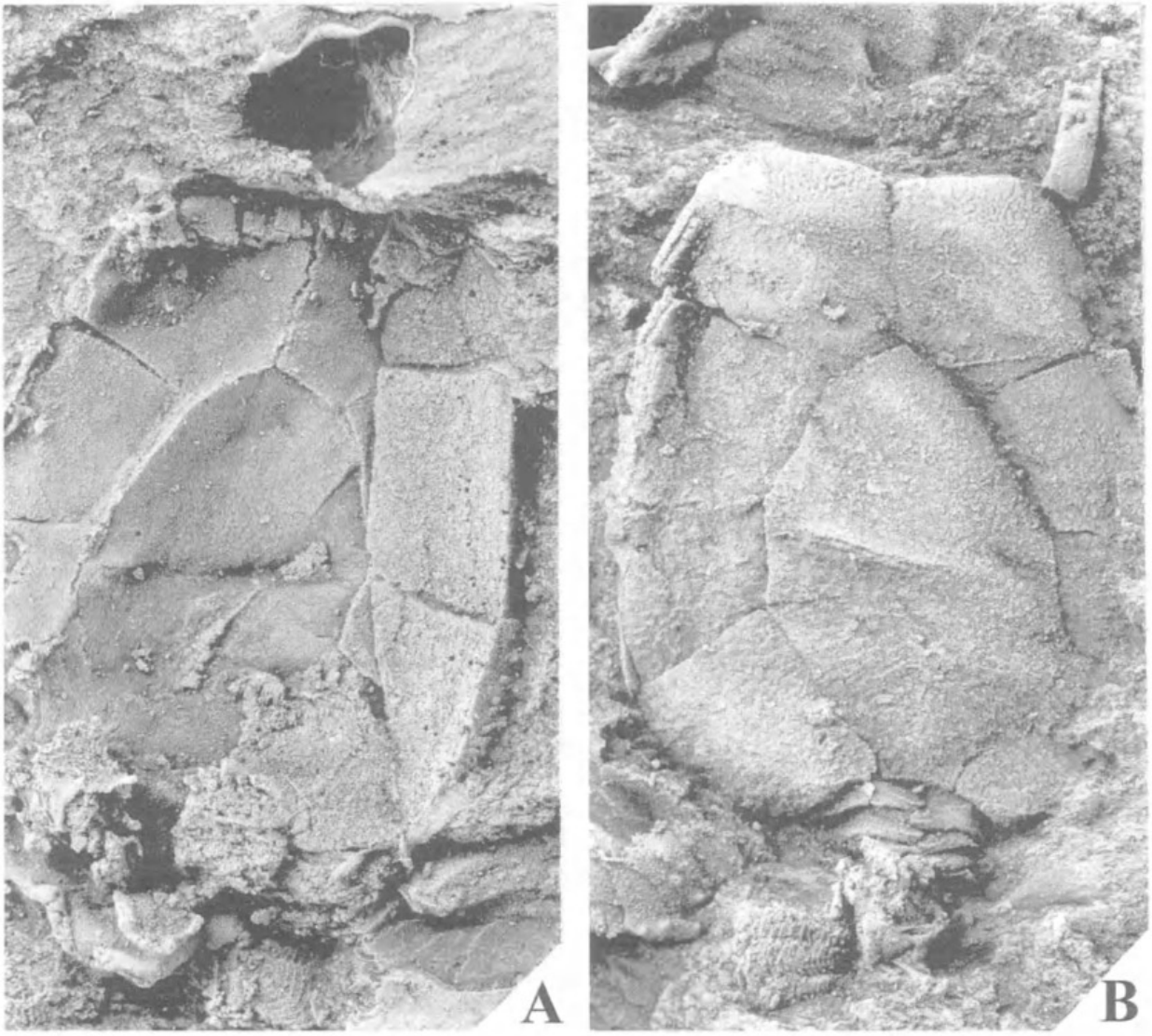


FIG. 12. *Tasmanicytidium burretti* Caster, incomplete plano-concave surface, external (B) and partially disrupted internal side (A) of convex surface, broken left spine, body sculpture, tetramerous rings and styloid with external ornament on distal blade. NMVP148541 from NMVPL296, ×6.

elongate, tapering slightly latero-medially and bent gently towards plano-concave surface.

REMARKS. Caster & Gill (1967) gave a succinct but comprehensive description of *Allanicytidium* based on an almost complete external mould of the plano-concave surface and internal mould of the convex surface of a single individual (see also Caster, 1983). Replicas of type material in the Museum of Victoria include the partial external mould of the convex surface of the holotype, illustrated here for the first time together with a second specimen. Both individuals provide data on external sculpture and changes in stereom fabric of the interior of the convex surface, the shape of C21 (especially its proximal 1/4) and the morphology of the proximal body excavation. Knowledge of other skeletal features (e.g. MOP; internal side of plano-concave surface; ornament of distal styloid blade and distal ossicles) is still not available.

SUMMARY AND CONCLUSIONS

Configuration of the convex surface of the 3 allanicytidiids discussed herein (Fig. 16A-C) are compared to that of *Placocystella africana* (Fig. 16D). Although similar to *Allanicytidium flemingi*, the Lower Devonian *Australocystis langei* Caster, 1956 from Brazil is omitted from the following discussion because of the incomplete preservation of its convex surface

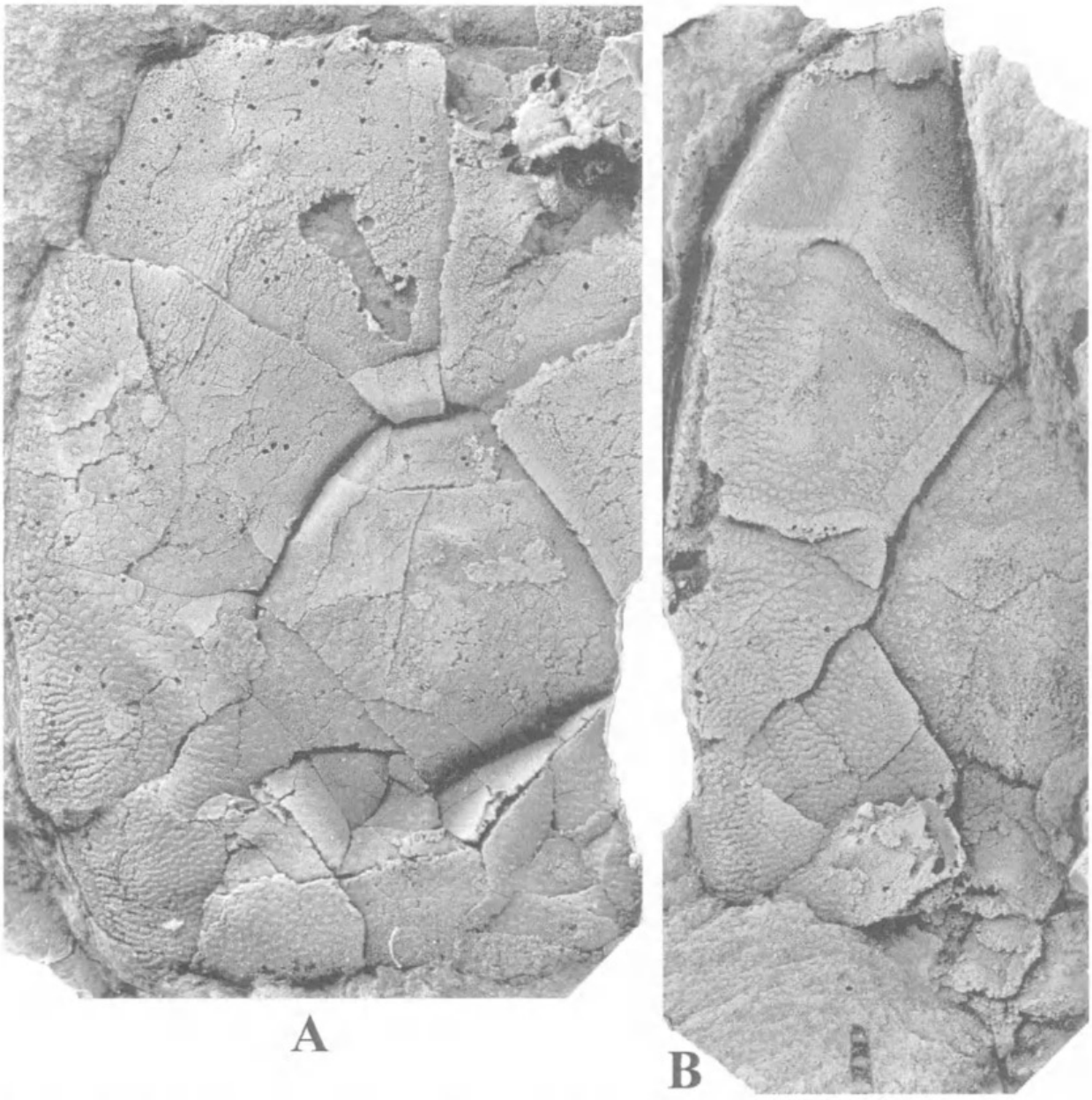


FIG. 13. *Allanicytidium flemingi* Caster & Gill, from Rainy Creek near Reefton, NZ. A, partial convex surface and body sculpture of UCM440, ×5. B, partial convex surface of NMVP27474 (replica of holotype NZGS 38/370203), ×5.

(Ruta & Theron, 1997; Ruta, in press). The proximal neck-like region in C21 in *Allani- cytidium* and *Placocystella* suggests that these taxa are closer to each other than either is to *Tasmanicytidium* or *Notocarpos* (Ruta & Theron, 1997; Ruta, in press). In *Tasmanicytidium*, the neck is not developed, but a short subtrapezoidal region between the proximo-medial angles of C20 and C22 indicates where the neck developed in more derived allanicytidiids. In passing from *Tasmanicytidium* through *Placocystella* to *Allanicytidium*, the C20/C21 and C21/C22 sutures became progressively more tortuous, resulting in development of lateral angular projections, poorly developed and close to the proximal margin of C21 in *Placocystella*, prominent and displaced halfway along the length of the neck in *Allanicytidium*.

External sculpture in *Notocarpos* has transitional features between those of certain anomalocystitids from the Northern Hemisphere (e.g. *Placocystites forbesianus* de Koninck,

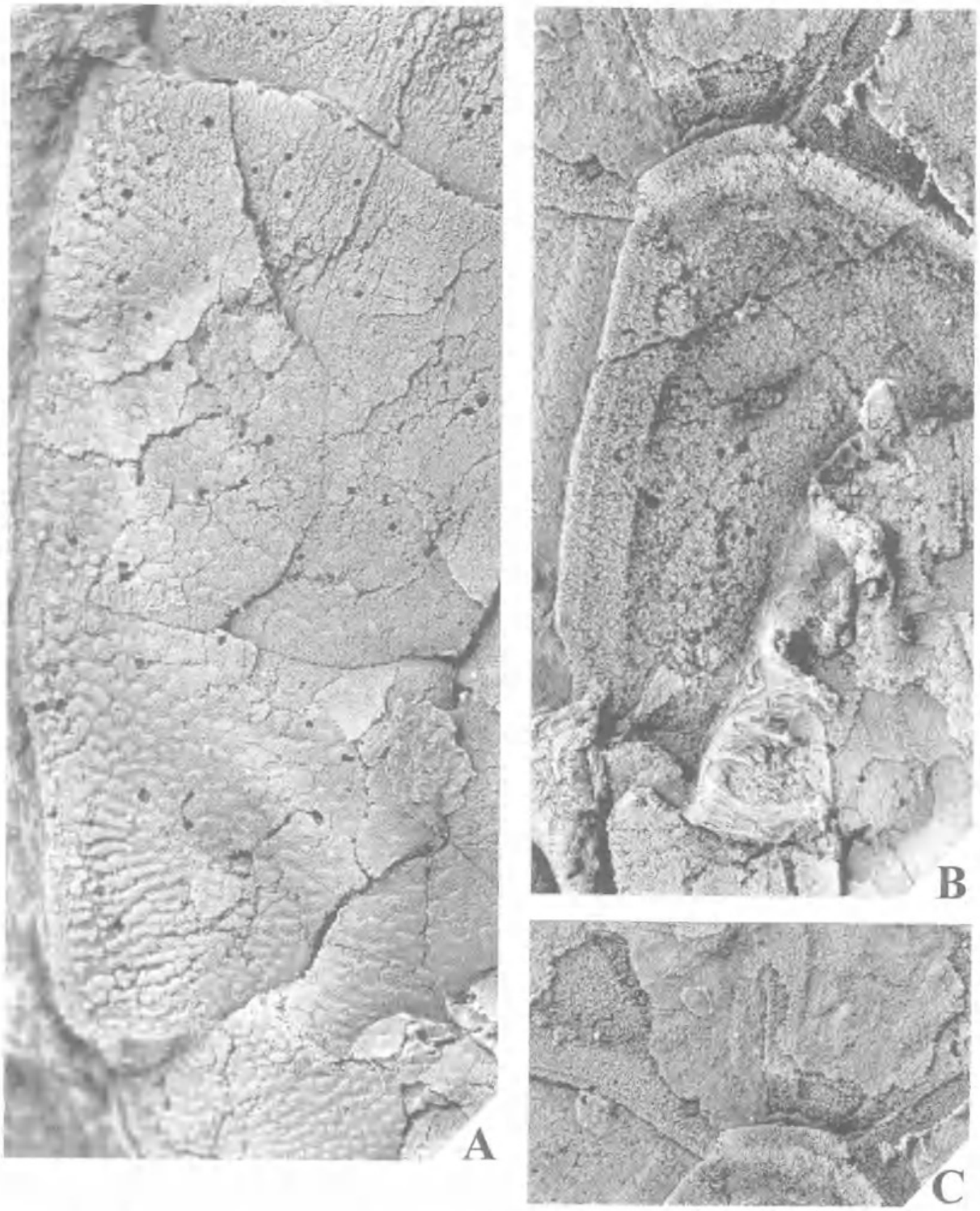


FIG. 14. *Allanicytidium flemingi* Caster & Gill, UCM440, from Rainy Creek near Reefton, NZ. A, detail of sculpture and stereom fabric of convex surface, ×10. B,C, inside of distal part of C21, showing peripheral band, ×10 and ×8, respectively.

1869; Jefferies & Lewis, 1978) and those of more derived allanicytidiids. In the light of Jefferies' (1984) reconstruction of ontogenetic changes in *Placocystites*, Ruta & Theron (1997) and Ruta (in press) invoked paedomorphosis to explain the sculpture pattern of the allanicytidiids.

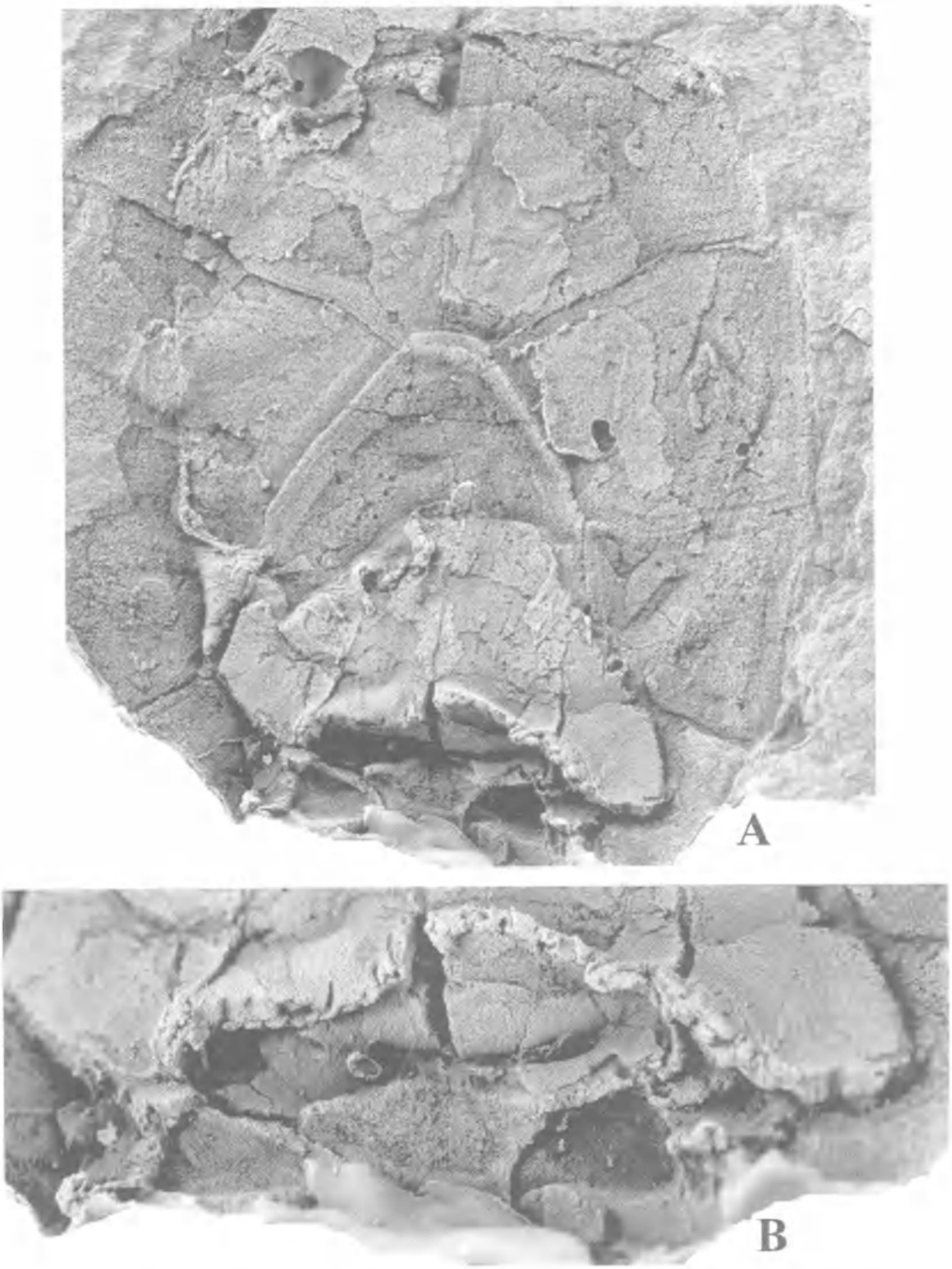


FIG. 15. *Allanicytidium flemingi* Caster & Gill, UCM440, from Rainy Creek near Reefton, NZ. A, inside of convex surface showing stereom fabric and peripheral bands, ×5. B, proximal body excavation with apophyseal horns, ×10.

Paedomorphic changes in allanicytidiid evolution are suggested by the smallest specimens of *Notocarpos* with sculpture of short ridges or riblets. The strongly diverging proximo-lateral margins of C21 in young *Notocarpos* are reminiscent of those of more derived allanicytidiids (e.g. *Tasmanicytidium* and *Placocystella*). It is possible that paedomorphic changes occurred repeatedly in the allanicytidiid clade and affected various structures (ornament; plates) differently.

Few changes affected the general plating pattern of the body (Ruta & Jell, 1999a). These involve relative proportions of MOP, LOP, A and C plates, on the plano-concave surface, and outline of C21, on the convex surface. A detailed analysis of character changes is provided by Ruta (in press).

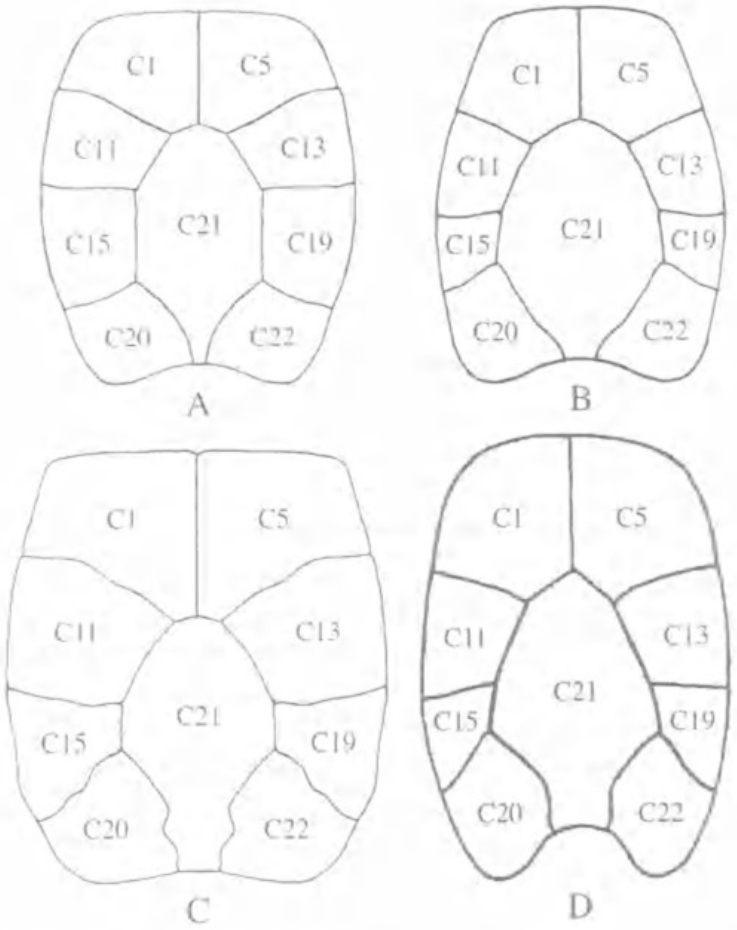


FIG. 16. Reconstruction of plating pattern of convex surface in *Notocarpos garratti* Philip (A), *Tasmanicytidium hurretti* Caster (B), *Allanicytidium flemingi* Caster & Gill (C) and *Placocystella africana* (Reed) (D). Drawings not to scale.

ACKNOWLEDGEMENTS

David Holloway, Museum of Victoria, Melbourne and David MacKinnon, University of Canterbury, Christchurch lent material in their care. Steve Eckardt provided access to his collection. Andrew Milner, Birkbeck College, University of London offered suggestions to improve the text. We thank referees Chris Paul and Reimund Haude for useful suggestions but assume responsibility for the above ourselves. M. R. thanks the Museum of Victoria, Melbourne and the Queensland Museum, Brisbane for hospitality and for providing access to facilities.

LITERATURE CITED

BAILLIE, P.W. 1979. Stratigraphic relationships of Late Ordovician to Early Devonian rocks in the Huntley Quadrangle, south-western Tasmania. Papers and Proceedings of the Royal Society of Tasmania 113: 5-13.

CASTER, K.E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoid Echinodermata. Bulletins of American Paleontology 34: 1-47.

1956. A Devonian placocystoid echinoderm from Paraná, Brazil. Paleontologia do Paraná (Centennial Volume): 137-148.

1983. A new Silurian carpoid echinoderm from Tasmania and a revision of the Allanicytidiidae. Alcheringa 7: 321-335.

CASTER, K.E. & GILL, E.D. 1967. Family Allanicytidiidae, new family. Pp. 561-564. In Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas Press: New York).

GILL, E.D. & CASTER, K.E. 1960. Carpoid echinoderms from the Silurian and Devonian of Australia. Bulletins of American Paleontology 41: 5-71.

HAUDE, R. 1995. Echinodermen aus dem Unter-Devon der argentinischen Präkordillere. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 197: 37-86.

JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. Paläontologische Zeitschrift 3: 1-128.

JEFFERIES, R.P.S. 1984. Locomotion, shape, ornament and external ontogeny in some mitrate calcichordates. Journal of Vertebrate Paleontology 4: 292-319.

JEFFERIES, R.P.S. & LEWIS, D.N. 1978. The English Silurian fossil *Placocystites forbesianus* and the ancestry of the vertebrates. Philosophical Transactions of the Royal Society of London, Series B 282: 205-323.

KOLATA, D.R. & GUENSBURG, T.E. 1979. *Diamphidiocystis*, a new mitrate carpoid from the Cincinnatian (Upper Ordovician) Maquoketa Group in southern Illinois. Journal of Paleontology 53: 1121-1135.

KOLATA, D.R. & JOLLIE, M. 1982. Anomalocystitid mitrates (Stylophora, Echinodermata) from the Champlainian (Middle Ordovician) Guttenberg Formation of the Upper Mississippi Valley region. Journal of Paleontology 56: 531-565.

KONINCK, M.L. De 1869. Sur quelques échinodermes remarquables des terrains paléozoiques. Bulletin de l'Academie Royale des Sciences Belgique 28: 544-552.

PARSLEY, R.L. 1991. Review of selected North American mitrate stylophorans (Homalozoa: Echinodermata). Bulletins of American Paleontology 100: 5-57.

PHILIP, G.M. 1981. *Notocarpos garratti* gen. et sp. nov., a new Silurian mitrate carpoid from Victoria. Alcheringa 5: 29-38.

RUTA, M. (in press). A cladistic analysis of the anomalocystitid mitrates. The Zoological Journal of the Linnean Society.

RUTA, M. & JELL, P.A. 1999a. *Protocytidium* gen. nov., a new anomalocystitid mitrate from the Victorian latest Ordovician and evolution of the Allanicytidiidae. Memoirs of the Queensland Museum 43: 353-376.

1999b. *Adoketocarpus* gen. nov., a mitrate from the Ludlovian Kilmore Siltstone and Lochkovian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 377-398.

1999c. Two new anomalocystitid mitrates from the Lower Devonian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 399-422.

RUTA, M. & THERON, J.N. 1997. Two Devonian mitrates from South Africa. Palaeontology 40: 201-243.

UBAGHS, G. 1967. Stylophora. Pp. 496-565. In Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas: New York).

1969. Les échinodermes carpoides de l'Ordovicien inférieur de la Montagne Noire (France). Cahiers de Paléontologie (Editions du Centre National de la Recherche Scientifique: Paris) 1-112.

WILLIAMS, G.E. 1964. The geology of the Kinglake district, central Victoria. Proceedings of the Royal Society of Victoria 77: 273-328.