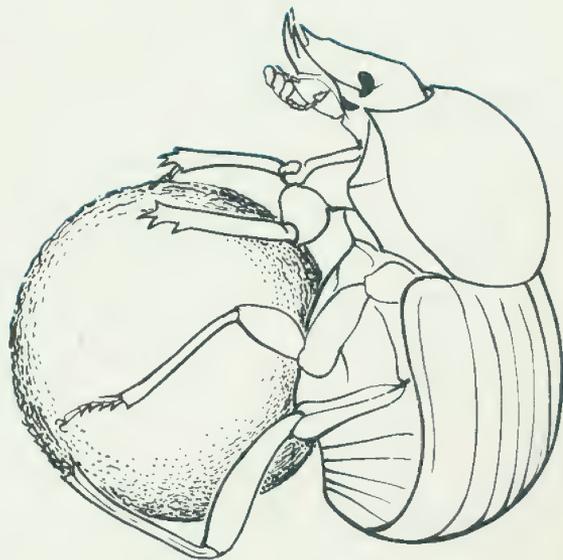
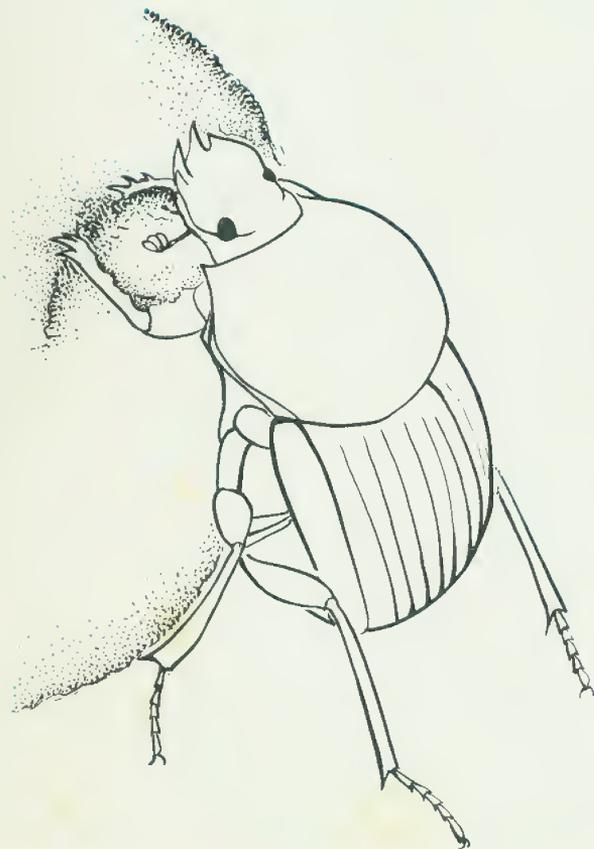


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STUDIES IN THE CORONULIDAE (CIRRIPEDIA):
SHELL MORPHOLOGY, GROWTH, AND FUNCTION, AND THEIR BEARING
ON SUBFAMILY CLASSIFICATION

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ABSTRACT

A new morphological feature of the shell of *Chelonibia caretta* is described. A species *incertae sedis* is compared with *Cylindrolepas darwiniana* Pilsbry, 1916. *Cylindrolepas* may be a junior synonym of *Platylepas* on the basis of this comparison. The shell morphology and probable mode of growth of Coronulidae are described. A new arrangement of genera into subfamilies is proposed. The subfamily Coronulinae Leach, 1812, is emended to include *Coronula*, *Cetopirus*, *Cryptolepas*, and *Platylepas*. The subfamily Xenobalaninae Gruvel, 1903, is emended to include *Xenobalanus*, *Tubicinella*, *Stomatolepas*, and *Stephanolepas*. Chelonibiinae Pilsbry, 1916, and Emersoniinae Ross, 1967, remain unaltered, and Platylepadinae (auct.) is rejected. A possible phylogeny for the family is included.

INTRODUCTION

Monroe and Limpus (1979) identified and listed the barnacle epifauna on turtles in Queensland Waters. Subsequent collection has yielded one other species of uncertain identity, and subsequent examination of specimens of *Chelonibia caretta* has clarified some aspects of shell morphology. Analysis of growth patterns and shell structure has thrown new light on the probable subfamilial relationships.

Specimen numbers prefixed by W refer to the Queensland Museum.

ADDITIONS TO SPECIES DESCRIPTIONS
OF MONROE AND LIMPUS, 1979.

CHELONIBIA CARETTA (SPENGLER, 1790)
(Plate 1, Figs. 1, 2)

MATERIAL EXAMINED

W3654, 15 specimens, North Reef, SE.Q.

Previous authors have remarked on the roughness of the exterior surface of the shell (e.g. Pilsbry 1916, Monroe and Limpus 1979). However, when the outer surface and base of cleaned specimens are examined, the roughness is attributable to infoldings of the outer wall (Plate 1, Fig 2, A). These structures are not present in *Chelonibia testudinaria* (Plate 1, Figs. 3, 4).

?*CYLINDROLEPAS DARWINIANA* PILSBRY, 1916
(Plate 1, Figs. 5-8; Plate 2, Figs. 1, 2)

From host number X9313, *Caretta caretta*, Mon Repos, 2.xi.1972, an empty shell was removed from the area round the base of the tail. In appearance the shell has obvious affinities with *Platylepas*. The midrib structure and the ridges of beading on the outer walls are very similar to those of *P. decorata*.

However the specimen also agrees well with Pilsbry's (1916) description of *Cylindrolepas darwiniana*, but not as well with his figures. These latter are not to the usual high standard of Pilsbry's drawings. It has not been possible to borrow the type of *Cylindrolepas darwiniana*, through no fault of the Academy of Natural Science Philadelphia. Pilsbry's (1916) description is reproduced below for comparison with the plates.

'The barnacle is hexagonal, the carinorostal diameter a little larger than the lateral, of about equal diameter from base to summit; whitish, with fine sculpture of close transverse wrinkles, and on the carina and carinolateral compartments a few low, coarse vertical ribs. The compartments

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when isolated are square. Their summits are beveled and polished, apparently by wear. A median fold or filled sulcus is indicated on the polished summit by a small depression filled with the softer and dull substance of the outer layer; and on some compartments a slight, mesial sulcus is visible externally. The radii are represented by narrow sulci; their edges are distinctly septate. The lower edges of the compartments have about three short, vertical, blunt teeth on each side of a larger median tooth, which bends slightly inward, and is homologous with the prop or midrib in typical forms of *Platylepas*. The sheath is delicately striate transversely, and stops a little short of the basal edges of the compartments. The scuta are in contact with the terga, and together they stretch from end to end of the orifice. Carinorostral diameter, 4 mm; lateral diameter, 3.8 mm, height, 3 mm. Some individuals are slightly larger, greater diameter 5.3 mm.' . . .

'The specimens of *Cylindrolepas* were embedded in a very hard yellowish substance showing but little structure. Dr Thomas Barbour, of the Museum of Comparative Zoology, to whom I applied, concluded that it is the salt-water cured, sun-dried skin of either a loggerhead or green turtle, probably from between the neck and flippers or around the base of the tail.'

The main point of difference between Pilsbry's (1916) description and the photographs of the present specimen is the form and presence of the 'short, vertical, blunt teeth on either side of (the) larger median tooth.' One of these may be seen in Plate 1, Fig. 6, but the ratio of small to large is quite different to that shown in Pilsbry's figure. Nonetheless it is probable that the present material represents specimens of *Cylindrolepas darwiniana* — the first recorded since Pilsbry's description. If this is the case (as only comparison with the types will reveal) then, on shell characters, *Cylindrolepas* should be included in *Platylepas*.

SHELL MORPHOLOGY AND GROWTH WITH A DISCUSSION OF PROBABLE FUNCTION

Shells were cleaned in sodium hypochlorite solution. Histological specimens were decalcified in ethyl-diamine-tetra-acetic acid, stained with

Mallory's collagen stain, Hughesdon's modification (Carleton and Drury, 1957), and mounted in Canada balsam. The plates illustrating many of the morphological features discussed in this section are to be found in Monroe and Limpus (1979) to which much reference is made.

GENERAL REMARKS ON SHELL STRUCTURE

Barnacles of the family Coronulidae are diverse in shape and size. Some of them (subfamily Chelonibiinae) show relatively 'normal' balanomorph external morphology while at the other extreme is *Xenobalanus* with an external morphology reminiscent of the Lepadomorpha.

In common with other Balanomorpha the sheath in coronulids is laid down in zones of growth (Darwin 1854). The transverse striae so produced on the internal surface mark the lines of junction between successive periods of shell deposition — i.e. they mark moults. They are more distinct in some members of the family than others. Darwin (1854) clearly outlines the process of formation of the sheath.

In *Chelonibia testudinaria*, which has a thick outer wall and occupies a conventional balanomorph position on the surface of the host/substrate, the transverse striae are only apparent on the upper one third of the sheath (Fig. 1). In embedded species such as *Stomatolepas* sp. or *Stephanolepas muricata* with frail outer shells the transverse striae are apparent for the full depth of the sheath (Monroe and Limpus, 1979, pl. 2, 3, 6.). The striae may be closely placed as in *Platylepas decorata* (Monroe and Limpus, 1979,

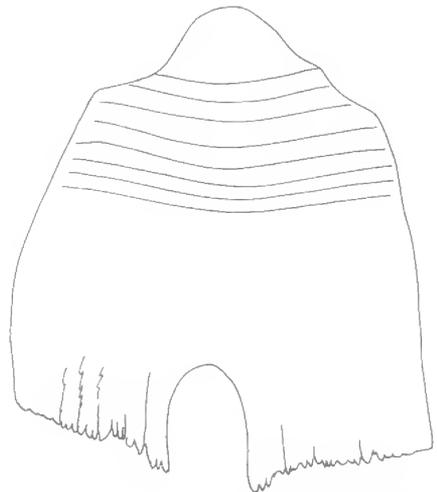


FIG. 1: A portion of the sheath of *Chelonibia testudinaria* showing transverse striae in upper portion.

pl. 4, fig. 8) or more widely as in *Stephanolepas muricata* (Monroe and Limpus, 1979, pl. 2, fig. 3).

It can be inferred from the appearance of transverse striae at different depths on the sheath that moulting in some superficially situated species (such as *C. testudinaria*) becomes less frequent with advancing age. However, in embedded species moulting continues at nearly constant frequency (as judged by the near regular spacing of the striae) throughout life. A corollary of this interpretation of striae spacing is that 'superficial' species remain on the host and continue to deposit shell for some time after their final moult whereas embedded species do not. This point is discussed later.

Pilsbry (1916) interpreted the morphology of coronulid shells as an adaptation to an impact prone situation. The massive shell of *Chelonibia* and the internal buttresses of *Platylepas* and the Coronulinae were seen as strengtheners of the shell. This view was shared by Ross and Newman (1967).

Darwin (1854) and Newman, Zullo, and Wainwright (1965) recognised that the complex wall folding of *Coronula* and *Cryptolepas* and the enclosed papillae of whale skin are a means of improving attachment of the barnacle to the whale. Darwin described and figured the ontogenetic development of this mechanism (Darwin, 1854, p. 15, figs. 4, 10). The latter authors also interpreted the six basal teeth of *Platylepas* as structures which 'lock the barnacle to the surface of the host to which it attaches' (Newman, Zullo, and Wainwright, 1965, p. 172).

Darwin (1854) recognised for *Tubicinella major* the role of the annular ridges as 'necessary to prevent too easy protrusion' of the shell.

It is here proposed that there are two mechanisms operating in the Coronulidae to facilitate attachment to the host — mechanisms adapted to the requirements of attaching to a growing substrate. Both mechanisms are derivations of the growth processes of the barnacle.

On the one hand there is the convoluted wall morphology of *Coronula* and *Cryptolepas*, and on the other hand there is the embedding process of *Tubicinella* spp., *Stomatolepas* spp., and *Stephanolepas muricata* with the concomitant requirement for regular moulting throughout life.

Platylepas spp. show elements of both processes, it being contended here that it is not the basal teeth but the whole shell wall which anchors the barnacle to its host.

One of the requirements for embedding in the

surface layer of an animal host is a means of overcoming the mechanical reaction of the host skin to the downward force of the growing barnacle. The holdfast structures of the established shell provide the necessary anchorage to permit downward growth as well as prevent dislodgement. How the fully embedded species initially gain a purchase to commence their burrowing is not clear from the adult shells available.

CHELONIBIA SPECIES

Chelonibia testudinaria and *C. caretta* are confined to hard areas of the skin of the host — carapace, plastron, and head. *C. testudinaria* attaches superficially and is not overlain by any host tissue. The large number of radial septae with their spiny lower margins (Pl. 1, Fig. 4) do not puncture the host scute but serve to increase the area of contact between the shell and substrate. That is, approximately two thirds (by inspection) of the base becomes effectively calcified and hence more firmly cemented to the substrate.

The forces most likely to dislodge a superficially attached barnacle are lateral — for example from water currents. The form and structure of the shell in *C. testudinaria* are well suited to reduce turbulence and improve adhesion.

When a large specimen of *C. testudinaria* is removed from the host it usually brings with it a portion of the keratinized layer of the scute showing that adhesion of the barnacle to the scute is greater than that of scute to host. However in the case of large (i.e. older) specimens of barnacles the host is probably nearer to moulting and the scutes could be expected to be loose at this time. Being a surface adherent *C. testudinaria* must be shed when host moulting occurs — approximately once a year (Limpus, in Lavery, 1978).

C. caretta has a shell structure and position on the host similar to those of *C. testudinaria*. However there are two differences notable in the context of this discussion: there is a layer of host keratin adherant to the outside of the shell wall which ascends to the level of erosion around the orifice (Monroe and Limpus, 1979, pl. 1, fig. 4), and the outer wall is roughened by longitudinal grooves and ridges (Pl. 1, Fig. 1).

These two features are allied. The longitudinal grooves when seen from their basal ends, appear as infoldings of the outer wall similar in structure to the median suture of *Platylepas* spp. (cf. Pl. 1, Figs. 1, 2 with Monroe and Limpus, 1979, pl. 3, fig. 8; pl. 4, fig. 1) (see below). Examination of the

host scute after removal of *C. caretta* shows that the keratinized layer has been split in two. The lower of these is the layer below the barnacle and is constantly being added to from below by the host epidermis. The upper layer is in keratin which invests the outer wall of the barnacle.

This upper layer is carried up the outer wall by being 'trapped' in the infoldings of the outer wall. *C. caretta* is more firmly attached to the host by virtue of this partial embedding. However since *C. caretta* does not penetrate the scute it will be shed at each host moult.

PLATYLEPAS SPECIES AND ?*CYLINDROLEPAS* DARWINIANA

Platylepas spp. maintain a more secure hold on the host than do *Chelonibia* spp. This is done by penetrating the scutes and soft epidermis of the host and anchoring the shell wall in the dermis and so resisting dislodgement.

The most prominent feature of *Platylepas hexastylus* is the median 'fold', 'sulcus', or 'midrib' or each compartment (Monroe and Limpus, 1979, pl. 4, fig. 3). During growth this structure traps the host scute at its outer end, and aided by the surface sculpture of the shell, carries the layer of scute up and outside the shell (Monroe and Limpus, 1979, pl. 3, fig. 7) in the manner of *Chelonibia caretta* (Monroe and Limpus, 1979, pl. 1, fig. 4). At the same time host scute is carried in between the walls of the fold and trapped. Along the lower edge of the fold, host fibrous connective tissue arising in the dermis is caught. There is no layer of scute below the barnacle. The same trapping of scute and dermis occurs at the compartmental sutures.

Along with the membranous basis the folds hold back the host tissues in a bowl-shaped cavity that allows the body of the barnacle to be partly below the host surface level and the shell to be of lower profile (Monroe, 1979, pl. 6, fig. 9 and pl. 2, fig. 3). The downward force to maintain the cavity may be exerted against the grip on the scutes.

Newman, Zullo, and Wainwright (1965, p. 172) have described the mode of growth of the buttresses of *Platylepas*. 'These are developed by allometric marginal growth increments. Lateral growth is suppressed at the location of each buttress so that it grows only downwards as the rest of the wall grows outwards and downwards'. That is the shell grows in diameter by the twelve lobes of the periphery pushing out into the host and trapping host tissue between themselves as they go. It is clear that the whole wall, and not just

the basal teeth, holds the barnacle so firmly to the host.

When the host moults its scutes, *P. hexastylus* is able to adhere because of its grip on the underlying dermal connective tissue.

Platylepas coriacea is very similar in shell structure to *P. hexastylus*. There is no host tissue on the outer surface of the shell as in *P. hexastylus* and all the anchorage appears to be provided by the nearly horizontal lower edges of the midrib folds. The leathery nature of the skin of the host — the leatherback turtle — may account for the failure of (or lack of necessity for) this species to embed.

P. decorata has midrib folds and props similar to those of the foregoing species but has more elaborate, and efficient, surface sculpture on the parietes to facilitate anchorage (Monroe and Limpus, 1979, pl. 4, fig. 7; pl. 6, fig. 8). Scute tissue becomes engaged in the rows of 'double beads' (cf. Monroe and Limpus, 1979, pl. 4, fig. 7, with pl. 2, fig. 4) and the median fold, while the props penetrate deeply allowing the barnacle to embed almost to its total depth.

?*Cylindrolepis darwiniana* is very like *Platylepas* and would appear, on the basis of the external shell morphology, to attach in a similar manner to *P. decorata*.

STEPHANOLEPAS MURICATA

In this species the simplest development of non-mural holdfast structures is found — blunt 'spines' (Monroe and Limpus, 1979, pl. 2, fig. 1, 2). Their position and structure are intimately associated with the pattern of growth of the shell wall. Once the barnacle has embedded the spines offer a secure mechanical grip on the host.

As outlined above, the outer wall and sheath are deposited in layers (Monroe and Limpus, 1979, pl. 2, fig. 3). In every second layer at both edges of each compartment an outgrowth is formed which curves upwards and reflects slightly back across the outer lamina of the compartment. On the radial side of the compartment these outgrowths are confluent with ridges that cross the radii and engage with the spines of the alar side of the contiguous compartment. These outgrowths become embedded in host connective tissue.

STOMATOLEPAS SPECIES

Stomatolepas spp. are similar to *Stephanolepas muricata*: the walls are thin and frail, and the barnacles are deeply embedded in the host. The outgrowths described in *Stephanolepas* are in *Stomatolepas* species much larger and completely

reflected back across the outer face of the compartments (Monroe and Limpus, 1979, pl. 2, fig. 8). There is also an outgrowth for each layer of the sheath. The projections are confluent with ridges on the radii (Monroe and Limpus, 1979, pl. 2, fig. 7). At the lower (growing) edge of the shell these reflected outgrowths are quite small (Monroe and Limpus, 1979, pl. 2, fig. 8), but successively higher (older) ones are longer with secondary outgrowths (scales) on their upper edges. By mid-height the reflected outgrowths from each side have met in the middle leaving a slight depression (Pl. 2, Fig. 5) which has been interpreted a residual rudimentary midline fold (Pilsbry, 1910).

The implications of this for the classification of the Coronulidae are discussed below. Pl. 2, Fig. 6 shows an histological section (radial) of a decalcified portion of the wall of *Stomatolepas praeagustator*; Pl. 2, Fig. 7 is a similar tangential section. The space x represents the wall, the spaces y the reflected projections and the scales. Ct is host connective tissue and p the periostracum of the barnacle. The space enclosed between the reflected projections and the compartment wall is filled by host connective tissue. Connective tissue is also entwined around the scales, the whole mass forming a complex holdfast structure.

TUBICINELLA CHELONIAE

In this species the holdfast mechanism consists of large upward and outward curving blunt spines whose formation is described in Monroe and Limpus (1979) and Nilsson-Cantell (1932). This species, as does *Stephanolepas muricata* and *Stomatolepas* species, becomes completely embedded in the host.

THE WHALE BARNACLES

Darwin (1854) showed clearly the ontogeny of the holdfast arrangement of the walls of *Coronula diadema*, *C. regina*, and *Cetopirus complanata*. The process is similar to that in *Platylepas* and *Chelonibia caretta* in that it involves trapping of the upper epidermal layer in folds of the shell. It is probable that *Cryptolepas rhachianecti* can be included in this category also.

On the other hand *Tubicinella major* and *Xenobalanus globicipitis*, like *T. chelonie*, *Stomatolepas* spp. and *Stephanolepas muricata*, all 'burrow into' rather than 'grab hold of' the host epidermis. While acknowledging that *Cetopirus*, *Cryptolepas* and some *Platylepas* become covered

to a greater or lesser degree by host epidermis it is not the same process of burrowing as in *Tubicinella*, *Xenobalanus*, *Stomatolepas* and *Stephanolepas*.

HOST REACTION

Chelonibia species do not penetrate the host scutes and so there is no host tissue reaction. However *Tubicinella*, *Stomatolepas*, *Stephanolepas*, and to some extent *Platylepas*, all penetrate the basement membrane below the epidermis and invade the dermis. The host reaction is to lay down a capsule of fibrous connective tissue around the barnacle (Monroe and Limpus, 1978, pl. 2 fig. 1, and Pl. 2, Figs. 3-7). This is very thick and tough in the case of *Tubicinella cheloniae*. As the barnacle expands during growth the capsule becomes very tightly and intimately adherent to the barnacle shell. In the case of *Stomatolepas* spp., because of the action of the reflected projections and scales, the capsule is difficult to remove without damage to the shell and, while present, conceals the true nature of the shell structure (Pl. 2, Fig. 5). In *Platylepas hexastylus* and *P. decorata* the host capsule covers just the basal surface of the barnacle (Pl. 2, Figs. 3-4).

The host tissues are weakest at the interface of the dermal tissue and the capsule — the presumed site of growth of the capsule. It is at this interface that the host tissues yield when barnacles are removed from the host. This allows comparatively easy removal of the barnacle without damage to the host, except in the case of *Stephanolepas muricata*, and some *Platylepas* spp. which are deeply embedded on harder parts of the host. In these cases the host epidermis and scutes tend to grow back over the orifice of the barnacle enclosing it in a narrow-necked sack.

THE GROWTH STRATEGY OF EMBEDDED SPECIES

The remarks of this section are derived from a consideration of embedded species occurring on turtles but outline a growth strategy that probably applies also to embedded species on whales, e.g. *Tubicinella major* and *Xenobalanus globicipitis*.

The nature of the attachment region of the superficially situated *Chelonibia testudinaria* is not especially different from that of any other barnacle having a membranous basis and attaching on a hard surface. The same remark applies to the attachment of *Chelonibia patula* to the surfaces of its hosts — molluscs, xiphosurans,

and Crustacea (and old bones*). Though these barnacles are sloughed at moulting times and require a reproductive strategy to cope with this exigency, while on the host they are able to grow in the normal balanomorph fashion. *Chelonibia caretta* is more intimately attached to the upper stratum of its host, but there is still no necessity for special growth strategies.

The interface between these superficial barnacles and their hosts is, when compared to that of the species considered below, comparatively inert.

When embedded species are considered, i.e. those which penetrate into the dermal layer and are encapsulated by host connective tissue, it becomes apparent that the growth strategy of the normal balanomorph does not suffice. The barnacle would soon be 'grown off' the host by the connective tissue layer with which it is walled off by the host. The problem is analogous to a fish swimming upstream.

The barnacle, having established itself in the host, has to provide for its own increase in size, and also to grow a little faster than would otherwise be required in order to maintain its position against the sloughing process of the host.

Judging by scars on the host's surface it is possible for a barnacle to be completely sloughed

by the connective tissue capsule. In some cases barnacles may be sloughed because they have died and ceased to continue growing against the sloughing process. This is seen in the case of empty barnacle shells found in varying degrees of protrusion from the host.

The extra rate of growth required is expressed as shell height. Consider a barnacle B (Fig. 2a), with a host connective tissue capsule Ct, in host H. Assume that the barnacle is not at present growing but that the host capsule is active in sloughing the barnacle. After a time the barnacles will protrude a little above the host surface (Fig. 2b). Utilizing its purchase on the capsule and the adhesion of that to the host, the barnacle grows downward into the host, maintaining its position on the host, but the body is still at the upper end of the shell, attached by the opercular membrane, and this is projecting above the host surface (Fig. 2c). The barnacle now moults and the body is drawn down the shell, the upper portion of which

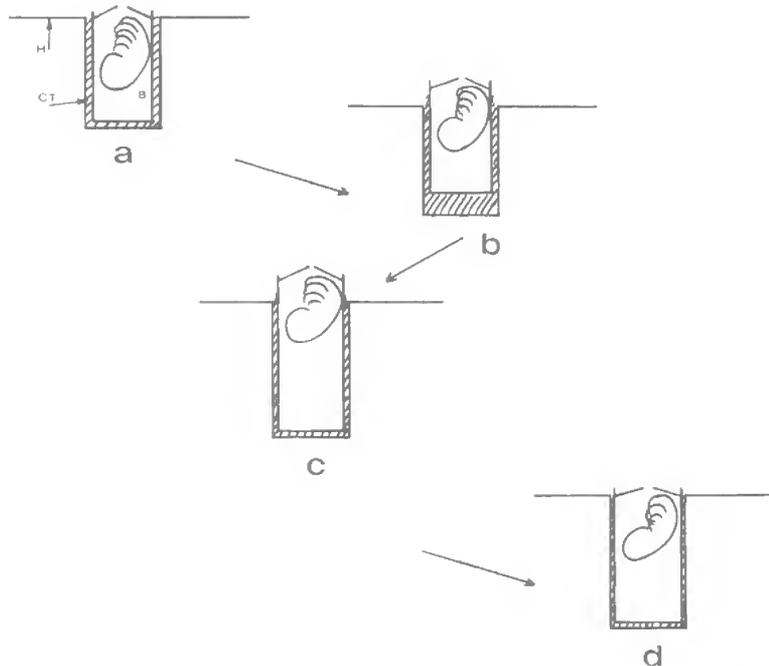


FIG. 2: Schematic drawing of mode of embedding of burrowing coronulidae in turtle hosts: H, host; CT, connective tissue capsule; B, barnacle. For explanation see text.

*Specimen lot W7354, *Chelonibia patula*, 20 individuals, was removed (together with 20 *Balanus trigonus* W7355) from a human femur recovered in 20 m from Moreton Bay near Moreton Is. on July 10th 1977. It may be that *Chelonibia patula* has a substrate preference involving organised calcium matrices.

flakes off along the weakness of the transverse striae in the sheath (Fig. 2d). The connective tissue capsule is degraded round the orifice, probably by the epidermal bacteria of the host. The wounds of *Tubicinella cheloniae* are specially septic.

It can be seen then that although there is a requirement in *Chelonibia* for the orifice to enlarge by erosion in the early period of the barnacle's adult life, facilitated by the weaknesses of the transverse striae and growth of the radii, at maturity this is no longer so. However in the embedded species, continued moulting and growth are required — radial growth maintaining shell diameter, and moulting, with loss of the protruding shell, maintaining the barnacle's position on the host.

DISCUSSION

SUBFAMILY CLASSIFICATION

Definitions and component taxa of three of the four previously accepted subfamilies within the Coronulidae have been given by Newman and Ross (1976) and were used by Monroe and Limpus, 1979. A definition of Platylepadinae was omitted by Newman and Ross, 1976. Zullo (1963) had previously proposed such a subfamily using Pilsbry's (1916) definition of the platylepad series. Newman and Ross's (1976) list of genera within their Platylepadinae is the same as that for Pilsbry's platylepad series and presumably their subfamily would rest upon the same definition.

Further discussion of the authorship of the Platylepadinae will not be undertaken here as morphological information from this study casts doubt upon its integrity as a grouping. The previously accepted subfamilies and their characters are presented in Table 1.

The prime character separating the Platylepadinae from the other subfamilies is the presence or absence of a median sulcus, midrib, or a vestige thereof (Pilsbry, 1916; Zullo, 1963). The

presence of this character has been claimed in *Platylepas*, *Cylindrolepas*, *Stomatolepas*, and *Stephanolepas*. It is certainly present in *Platylepas* (Monroe and Limpus, 1979, pl. 3, fig. 8, pl. 4) are most likely in *Cylindrolepas* (see *Cylindrolepis darwiniana* and Pl. 1, Figs. 5–6). However it is clearly absent from *Stomatolepas* and *Stephanolepas* (Monroe and Limpus, 1979, pl. 2; pl. 3, figs. 1–5). No vestige or precursor of such a structure can be detected. Pilsbry's (1910; 1916) interpretation of the mid compartmental groove in *Stomatolepas* as a rudimentary sulcus is due in his misunderstanding of the mode of growth of the external sculpture. Also he observed shells clothed in connective tissue (as judged by his paratypes) which hinders observation (cf. Pl. 2, Fig. 5 with Monroe and Limpus, 1979, pl. 2, fig. 4). Pilsbry (1916) never saw *Stephanolepas* but inferred from Fischer's (1886) description of smooth mid compartmental areas that it would be similar to *Stomatolepas*.

Similarly a median fold or sulcus is said to be absent in the other subfamilies. However structures very similar in formation and function to the median fold of *Platylepas* can be detected in *Chelonibia caretta* (Pl. 1, Fig. 2).

The Coronulinae are united by the presence of an 'oral hood' (Darwin, 1854, pl. 17, fig. 4a) and the possession of a 'single row of wall tubes formed by infoldings of (the) outer lamina against the sheath' (Newman and Ross, 1976, p. 37).

Much confusion has been brought about by the terms 'infolding' and 'outfolding'. Setting aside the Chelonibiinae and Emersoniinae, which have more recently been included in the Coronulidae, the main division in the Coronulidae, between the Platylepadinae and Coronulinae, has been based chiefly on the type of wall folding. The following paragraphs show that 'in' and 'out' are relative terms that have obscured the similarity between some genera of the Coronulidae.

In *Tubicinella*, tubes (interlaminar pores) are formed by the union of lateral outgrowths from

TABLE 1: THE SUBFAMILIES OF THE CORONULIDAE AND THEIR DISTINGUISHING CHARACTERS (AFTER NEWMAN AND ROSS, 1976, AND ZULLO, 1963).

Subfamily	6 or 8 wall plates	opercular plates weakly articulated	oral hood +/-	tergum reduced	rows of wall tubes	mid-parietal sulcus
Chelonibiinae	6/8	yes	-	+	1	-
Emersoniinae	6	?	?	?	several	-
Platylepadinae	6	yes	-	+	not specified	+
Coronulinae	6	yes	+	+++	1 (wall folds)	-

the outer edges of the interlaminar septa (Darwin 1854). There are no 'infoldings' of the wall in the sense of Newman and Ross (1976). *Xenobalanus* has incomplete interlaminar pores (Pl. 2, Fig. 8) but no 'infoldings' of the outer layer. In *Coronula* and *Cetopirus* such interlaminar pores exist (Darwin 1854) as well as a 'single row of tubes formed by infoldings of the outer lamina against the sheaths' (Newman and Ross, 1976, p. 37). In *Cryptolepas* (which has interlaminar pores (Pilsbry, 1916)) these 'infoldings' produce an incomplete outer wall analogous with that of *Coronula* (Pilsbry, 1916, p. 280, pl. 66).

As shown above *Stomatolepas*, *Stephanolepas*, *Tubicinella* and *Xenobalanus* have no wall folding. What is more, they are all united by other characters: 1, possession of structures arising from the lateral edges of the compartments and forming holdfasts (this is not strictly so in *Tubicinella major* as the annular ridges are formed across the whole of the face of the compartment. The ridges are, however, produced in synchrony with the layers of sheath as are the holdfasts on the other genera included here); 2, the shell is completely embedded in the host, is thin-walled and frail, and grows continually and rapidly (as judged by the relatively wide layers of the sheath) to maintain its position on the host; and 3, the shell is conical; straight sided and only slightly tapering in *Tubicinella*, 'glubulo-conic' (Fischer, 1886) and more strongly tapering in *Stomatolepas* and *Stephanolepas*. Since only three or four sheath layers of *Xenobalanus* are retained at any one time (Pl. 2, Fig. 8) it is difficult to determine if or how the shell tapers, but in general shape it is in conformity with those of the other genera.

Platylepas is said to have an 'infolded' buttress (Pilsbry 1916; Newman, Zullo, and Wainwright, 1965) and this is a convenient way to describe the buttress — especially that of *P. hexastylus* when seen from the exterior, e.g. Monroe and Limpus, 1978, pl. 4, fig. 3. However when seen in basal view, Monroe and Limpus, 1979, pl. 4, fig. 1 the inner edge of the buttress (except in the carina) aligns well with the plane of the intercompartmental sutures (roughly a cylinder), and the lower projection of the buttress — curving in under the lower edge of the sheath — is strongly reminiscent of the structure of *Cetopirus complanata* of which (as *Coronula balaenaris*) Darwin (1854, p. 416) says 'the inner ends of the folded walls . . . descend some little way beneath the basal edge of the sheath, as low, or lower, than the circumference of the shell' (Darwin, 1854, pl. 16, fig. 3). *Platylepas* could be interpreted as a *Coronula* with two

outfoldings in each compartment. Whereas in *Coronula* the space between the two layers of the outfolded outer lamina is narrow and filled by calcareous material, in *Platylepas*, they are wide, though still solidly filled. The 'tubes' in *Coronula*, filled with whale epidermis, are homologous with the narrow space between the walls of the buttress in *Platylepas* in which turtle host tissue is held.

Newman, Zullo and Wainwright (1965, p. 172) recognise that 'in *Platylepas* the regions occupied by the buttresses . . . correspond to the "canals" in the whale barnacles' and that, 'in *Coronula* and *Cryptolepas*, the intervening growth areas (between the canals) . . . could be called buttresses, but they are homologous with the wall proper, rather than the buttresses of *Platylepas*', but they fail to realise the implication of this homology for the classification of the Coronulidae. There has been so much attention focused on the 'in-folding' of buttresses in *Platylepas* and the 'out-folding' to form 'canals' in *Coronula* and *Cryptolepas* that, coupled with a lack of understanding of the function of these structures in *Platylepas*, it has led to the obscuring of the close relationship between these genera. The walls of *Platylepas*, *Coronula*, *Cetopirus*, and *Cryptolepas* are homologous in both structure and function.

On the basis of wall structure then, a second group of genera can be recognised composed of *Coronula*, *Cetopirus*, *Cryptolepas*, *Platylepas* and *Cylindrolepas*.

The remaining genera, *Chelonibia* and *Emersonius*, are at present accommodated in their own subfamilies. *Emersonius cybosyrinx* is a fossil form and is not considered further here. The inclusion of the Chelonibiinae in the Coronulidae is not questioned, and is supported by the presence of involutions in the outer lamina of *Chelonibia caretta* which this study has revealed (Pl. 1, Fig. 1).

The arrangement of subfamilies in the Coronulidae proposed as a result of this study follows.

CORONULINAE LEACH 1812, EMEND.

Wall of 6 plates, exterior lamina of wall folded to produce holdfast structures by trapping host epidermal tissues, attached to surface of host or only shallowly embedded. *Coronula*, *Cetopirus*, *Cryptolepas*, *Platylepas*, *Cylindrolepas*.

XENOBALANINAE GRUVEL, 1903, EMEND.

Walls of 6 plates, holdfast structures produced by outgrowths from edges of compartments in

synchrony with layers of sheath, shell deeply embedded in host. *Xenobalanus*, *Tubicinella*, *Stomatolepas*, *Stephanolepas*.

CHELONIBIINAE PILSBRY, 1916

Chelonibia.

EMERSONIINAE ROSS, 1967

Emersonius.

EVOLUTION

Ross and Newman (1967) proposed a phylogeny for the Coronulidae in which the more generalised 'primitive' chelonibiines exploited the phylogenetically older hosts (Crustacea and molluscs) while the more advanced coronulines were confined to more recent hosts — cetaceans.

The scheme suggests coevolution of the Coronulidae and the major groups of marine vertebrates, the 'higher' subfamilies of barnacles supposedly arising as new host forms became available.

In the light of the above proposed altered subfamily classification it is appropriate to re-examine the probable phylogeny of this family.

Under the proposed classification the Coronulinae are no longer epizooans only of cetaceans but are to be found on phylogenetically 'older' hosts such as turtles. Similarly the Xenobalaninae (which in part takes the place of the Platylepadinae) are no longer confined to the 'middle' range of

hosts but now include species which occur on hosts from turtles to whales (fig. 3).

Ross and Newman (1967, p. 16) maintain that 'the most generalised members of (the Coronulidae) are *Platylepas* and *Chelonibia patula*'. If epizooites are host conservative then *Chelonibia patula* would be a candidate for the position of most generalised coronulid. *Platylepas* however shows all the attributes of the (generally accepted) more advanced *Coronula* (see above).

It is possible to see a relationship between the Chelonibiinae and Coronulinae in the involutions of the exterior wall of *Chelonibia caretta* and the convoluted exterior wall of the coronulines. It is also possible to see a relationship between the Chelonibiinae and Emersoniinae in the well developed radial septae of both groups. However it is not possible to recognise any general morphological affinity of the Xenobalaninae with the above three subfamilies except in the possession of porose walls by some of the xenobalanines and an epizooic habitat.

Figure 4 shows an inferred phylogeny of the Coronulidae based on wall structure and function. The ancestral form is postulated as being similar to *Chelonibia patula*, having porose walls, and radial septae projecting into the cavity of shell. *C. testudinaria* is similar in construction to *C. patula* but has further developed radial septae and the pores in the walls are filled with calcareous matter in the upper parts.

The Emersoniinae are separated from the chelonibiid stock by the formation of intercalary and transverse septae. The Coronulinae arise from the chelonibiid stock somewhat later, there being a strong similarity in the structure and function of the involutions in the outer wall of *C. caretta* and the convoluted wall of the Coronulines. *C. manati* is supposed, on the basis of Pilsbry's 1916 description, to have similar involutions.

Whence the Xenobalaninae arise it is difficult to say. Since they are all burrowing forms they are unlikely to be associated with the 'older' exoskeletal hosts. It is possible that they do not belong in the Coronulidae, but considerations of the anatomy of the soft parts make that improbable.

Darwin (1854) makes note of the 'beaded' nature of the sculpture on the exterior of *Coronula* and *Platylepas*. These beads are synchronous with the layers of the sheath and can be quite elaborate — e.g. in *Cryptolepas rachianecti* (Pilsbry, 1916, pl. 66) and *Cylindrolepas darwiniana* (Pl. 1, Figs. 5, 6). It may be that the Xenobalaninae arose from a stock in which the radial septae were

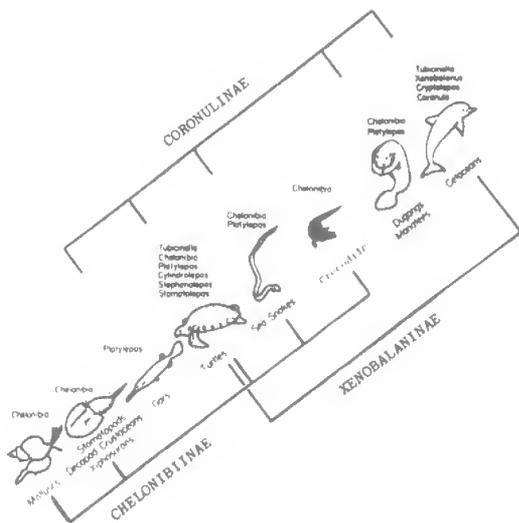


FIG. 3: The relationship between hosts and subfamilies proposed as a result of this study.

suppressed and there was no development of wall convolutions, the development of the holdfast structures taking place by the elaboration of the 'bead' structure at the edges of each compartment. In *Tubicinella major* the annular ridges may be an expression of the growth ridges as seen across the exterior of the compartments in other species — e.g. *Platylepas hexastylus* and ?*Cylindrolepas darwiniana*.

The presence of an oral hood in *Tubicinella major* and *Xenobalanus* in the Xenobalaninae on the one hand and in *Coronula*, *Cetopirus* and *Cryptolepas* in the Coronulinae on the other is an objection to the proposed arrangement of the genera. This structure though, may be developed only in those species occurring on whales as an adaptation to the higher swimming speeds of these hosts.

CONCLUDING REMARKS

The Coronulidae are a very specialized group of barnacles. In the main, they exhibit a high degree of host and site specificity. The principal hosts, turtles and whales, are migratory animals, in some

cases traversing many degrees of latitude in their migrations. The coronulids occurring on these animals can hardly be considered as sessile animals in the sense of the 'normal' barnacle. While it is true that *Lepas* species are to be found only on floating substrates, it can at least for them be pointed out that the substrate moves with nearly the same vagaries as the general body of water around them. Only *Conchoderma virgatum* (Spengler, 1790), an epizooite of epizooites, and *Analesma squalicola* (Love, 1844), share with the coronulids 'active' motion through the water as being normal for the entire population. This fact prompts questions about the breeding biology of the Coronulidae. When are larvae released? Perhaps in synchrony with host aggregations. How long is their pelagic life? The only published information available is for *Chelonibia patula* (Crisp and Costlow, 1963) and that species is found attached to relatively localised hosts — crabs and molluscs.

It was observed during the summer at Mon Repos that newly settled and small *Chelonibia testudinaria* were comparatively abundant (C.

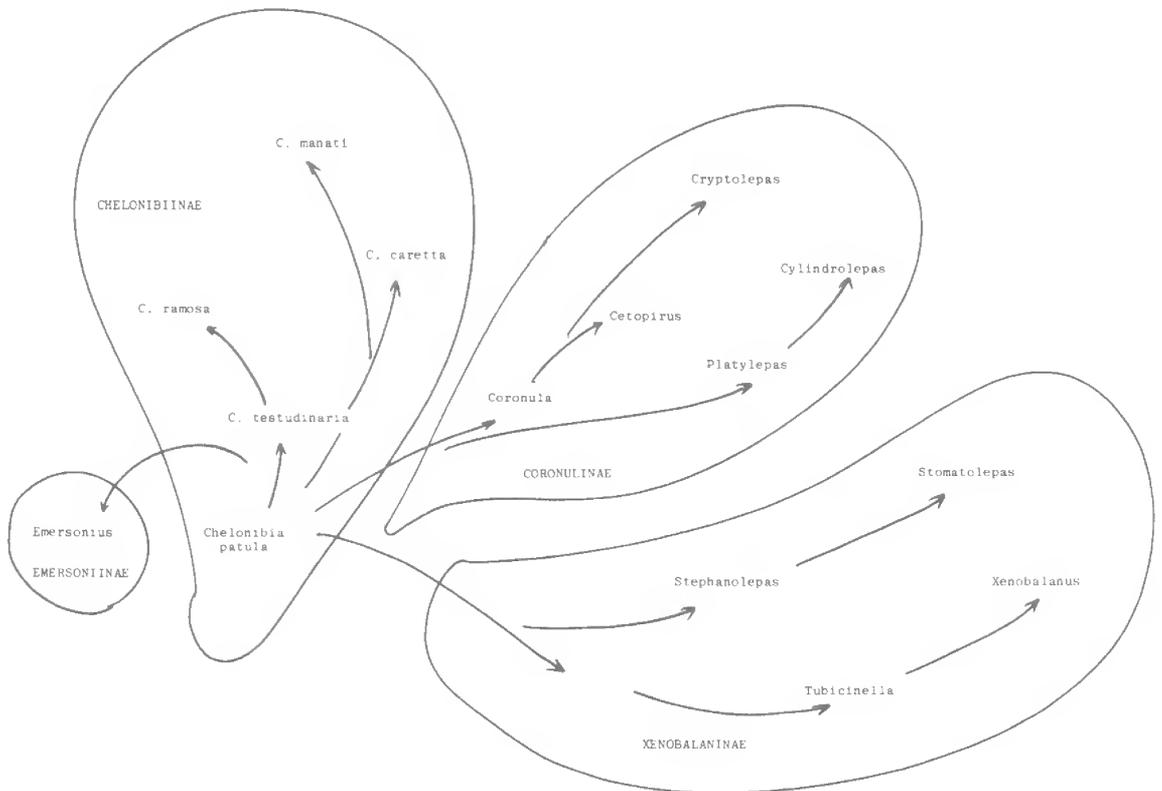


FIG. 4: A possible phylogeny of the barnacles of the family Coronulidae.

Limpus, pers. comm.) which lends some support to the idea that larvae are released during aggregation of the hosts on the breeding grounds.

Some species of coronulid are comparatively rare — e.g. *Stephanolepas muricata* and *Tubicinella cheloniae*. What mechanisms operate to ensure sufficient settlement of larvae is not known. These two species are embedded in firm tissues underlying hard epidermal structures. *T. cheloniae* penetrates the dermal bone of the carapace. Tomlin (1967, not seen, reported in Mitchell and Kozicki, 1975) cites L. Mathews to the effect that an enzyme is secreted by *Tubicinella major* which dissolves skin proteins 'which they then probably consume'. If such a mechanism operates in *T. major* to facilitate embedding (though there is no evidence of reduced feeding ability, as judged by the cirri) a similar one may be present in other Xenobalaninae.

Barnacle cyprids respond positively to specific proteins, arthropodins, but these active substances are not confined to arthropods alone (Crisp 1974). What substance(s) provides the stimulus to settlement of coronulids is not known. The mechanism of site selection on the host is not known though it is possible that turbulence may play some part in defining areas on the host suitable for particular species of barnacles.

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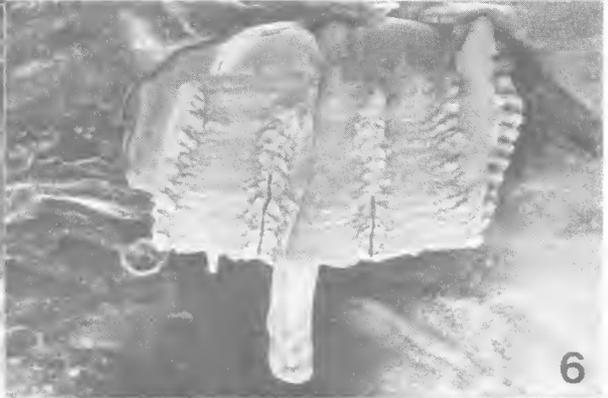
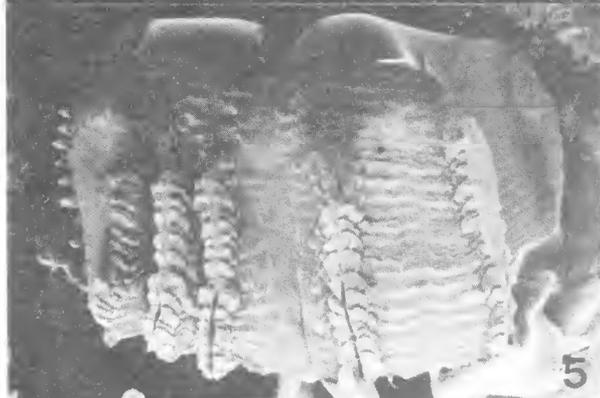
MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE I

FIGS. 1-2: *Chelonibia caretta* (Spengler), W3654; 1, basal edge of exterior of shell showing grooves; 2, peripheral edge of base showing infoldings of outer layer (A).

FIGS. 3-4: *Chelonibia testudinaria* (Linnaeus), W7845; 3, basal edge of exterior of shell; 4, peripheral edge of base.

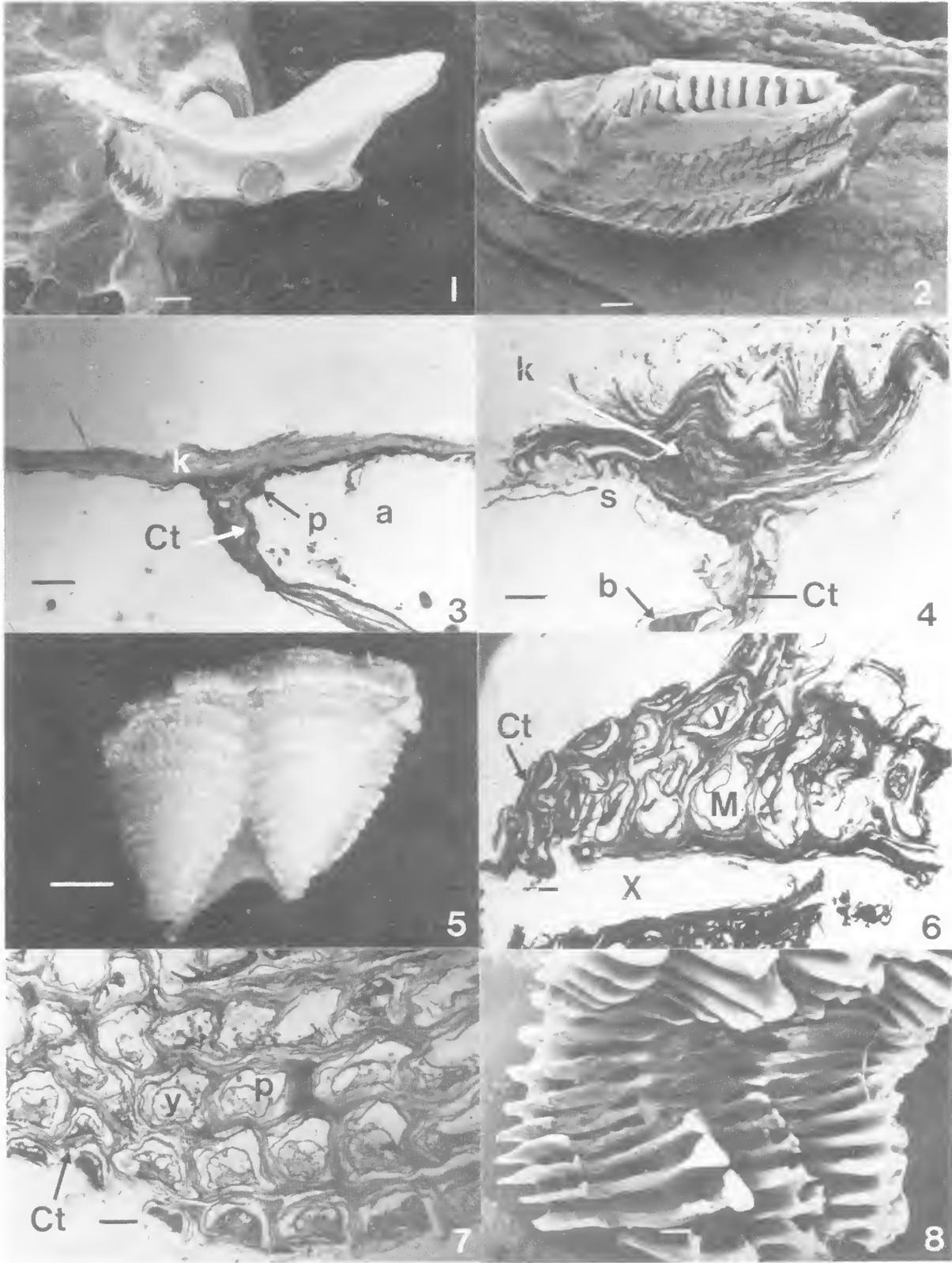
FIGS. 5-8: ?*Cylindrolepas darwiniana*, W7848; 5-6, exterior of compartments; 7, basal view; 8, radial edge of compartment.



MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE 2

- FIGS. 1-2: ?*Cylindrolepas darwiniana* W7848; 1, opercular view of compartment; 2, radial edge of compartment.
- FIG. 3: *Platylepas hexastylos* (Fabricius), W7814; section of decalcified animal showing a, cavity of shell, ct, connective tissue capsule of host, k, keratin layer of host epidermis, p, periostracum of shell.
- FIG. 4: *Platylepas decorata* Darwin, W7811; approximately median radial section of one wall illustrating intimate association of keratin of host, k, with the fine 'beaded' sculpturing on the exterior of the parietes, s, the basal membrane, b, is covered by host connective tissue, ct.
- FIG. 5: *Stomatolepas praegustator* Pilsbry, exterior view of compartment with investing layer of host connective tissue.
- FIG. 6: *Stomatolepas praegustator* Pilsbry, W7815; radial section of decalcified wall, x, reflected projection, y, host connective tissue, ct, and barnacle periostracum, m.
- FIG. 7: *Stomatolepas praegustator* Pilsbry, W7813; tangential section of decalcified wall, symbols as in fig. 6.
- FIG. 8: *Xenobalanus globicipitis* Steenstrup, W7384; exterior view of a compartment showing incomplete fusion of outer lamina.





THE BIOLOGY OF CEPHALODESMIUS, A GENUS OF DUNG BEETLES
WHICH SYNTHESIZES "DUNG" FROM PLANT MATERIAL
(COLEOPTERA:SCARABAEIDAE:SCARABAEINAE).

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ABSTRACT

The complex and aberrant biology of the endemic, Australian dung beetle genus, *Cephalodesmius*, is described from a detailed study of *C. armiger* and supporting observations on the other two species of the genus, *C. laticollis* and *C. quadridens*. Permanently bonded pairs occupy fixed, subterranean nests in the rainforest floor during their year-long lifespan. Males forage outside the nest for leaves and other plant materials which are processed and cultured by the female into a malleable, dung-like material which is used to construct small brood balls containing larvae. During larval growth the parent beetles cooperate in progressive provisioning of the larval brood balls, a complexity unknown elsewhere in the dung beetles and probably unique in the Coleoptera. Audible stridulation is recorded for the first time in larval Scarabaeidae, and a new mechanism of sound production described in which the tip of the abdomen is rubbed against the underside of the head. Stridulation is interpreted as communication between larva and adult.

The brood nests of *Cephalodesmius* are inhabited by a suite of 8 other insects and mites which enter into a variety of trophic and phoretic relationships with the beetles and these are summarized. The evolutionary significance of the behaviour of *Cephalodesmius* is discussed.

INTRODUCTION

The subfamily Scarabaeinae is a large, diverse and successful group which has earned the common name of 'dung beetles' through their almost universal utilization of animal dung as larval and adult food. Although a few species are known to feed on other diets such as fruits, carrion, feathers and fungi it is generally accepted that dung is the primitive and primary food of the subfamily. The classic observations of J.H. Fabre (1897) were the first to reveal that some dung beetles have complex behaviour patterns by which they manipulate and transport dung to subterranean nests where they rear their immature stages. It is now known that there is a remarkable array of variations on the basic breeding behaviour described by Fabre, that of some species approaching the most intricate known in the Insecta. Halffter and Matthews (1966) give a comprehensive review and analysis of the overall

biology of the world fauna, while Halffter (1977) gives a comparative account of nesting behaviour (nidification) in the subfamily, including possible evolutionary pathways.

The six tribes of Scarabaeinae show a basic behavioural dichotomy into (i) those that bury the dung in preformed burrows at the food source (Onthophagini, Oniticellini, Onitini and Coprini), and (ii) those that form the dung into balls which are transported away and buried at a distance from the source (Scarabaeini and Eurysternini) (Halffter, 1977). The latter group are often termed 'ball-rollers'. All Australian ball-rollers belong to the tribe Scarabaeini and have been comprehensively revised by Matthews (1974) who placed all 16 genera into the primitive, Gondwana subtribe, Canthonina. Matthews notes that 11 genera of the Australian Canthonina, comprising what he terms the 'mentophiline-group', have not been observed to make balls and he suggests they represent an early evolutionary stage before the

acquisition of this ability in the Scarabaeini. He draws attention to the paucity of information on the biology of these 'mentophilines' and suggests such data might throw light on the evolution of behaviour in dung beetles.

One of these mentophilines is *Cephalodesmus* Westwood, an endemic Australian genus with three flightless species restricted to wetter forests of SE Queensland and N.S.W. All three species are common insects where they occur. *Cephalodesmus laticollis* Pascoe and *C. quadridens* Macleay are confined to the northern part of the generic range, while *C. armiger* Westwood is virtually ubiquitous in rainforests and some adjacent sclerophyll forests throughout the range of the genus from the Bunya Mountains south to Wollongong. All three species overlap in the Macpherson Range complex on the N.S.W./Qld border.

Previous observations on the biology of *Cephalodesmus* are fragmentary and somewhat conflicting. Fricke (1967) excavated a burrow near Sydney to find a pair of adult *C. armiger*, a large, oval pellet of what he took to be horse dung, and 5 smaller pellets. He kept the pellets in a container with the adults during which time they consumed part of the 'horse dung' and tended the round pellets. Eventually an adult emerged from one pellet and the others, when opened, contained dead larvae and pupae. Matthews (1974) records his personal observations of *armiger* digging short burrows in captivity, and of both *armiger* and *laticollis* shaping rough balls of dung which they dragged backwards instead of rolling; he also notes an 'extraordinary observation' by G.B. Monteith who reported *C. quadridens* 'in holes filled with pieces of green leaves under logs' at the Bunya Mountains. Finally, a most important early observation, overlooked by other writers but brought to our notice by Dr B.P. Moore, is that of Walker (1905, p. 269) who writes:

'The curious small Coprid, *Cephalodesmus armiger* Westwood, is also somewhat diurnal in its habits. In the Illawarra in April, 1903, I found the females of this beetle busily engaged in filling their burrows under the logs with fresh minced-up leaves of clover and other low-growing plants, presumably as food for the larvae; a habit which recalled to my recollection the proceedings of the still more singular *Lethrus*, which I had observed in Turkey many years ago provisioning its burrow with vine leaves.'

The major inconsistency in these isolated reports is the contrast between the apparently

normal association with dung seen by Fricke and Matthews, and the apparently abnormal association with leaf material noted by Walker and Monteith. Accordingly, a detailed field and laboratory study of the biology of *Cephalodesmus* was carried out during the period 1972-74 in an attempt to resolve this anomaly. The results of this study are presented in this paper. We know now that all the previous observations are indeed correct, except for the certainty that what Fricke saw was not 'horse dung' but plant material mashed by the beetles themselves. *Cephalodesmus* adults do, as noted by Matthews, feed on dung when the opportunity arises but most of their foraging activity goes into gathering leaves and other vegetable material which is mashed and cultured in preformed underground nests into a dung-like substance which forms the larval brood material and much of the adult diet. This remarkable adaptation is quite unique even in an enormous subfamily famous for its behavioural eccentricities. Other striking features of *Cephalodesmus* biology which emerge from this study include: permanent pair-bonding of males and females during a lifetime of almost 12 months; residence in a single burrow during the life of the pair; deposition of eggs in tiny 'egg-balls' which are progressively provisioned with brood material as the larvae inside feed and grow; and phoretic and trophic associations with a large suite of other organisms which share their nests.

Due to the delay in publication of this comprehensive account, certain aspects of our findings have been referred to, with our permission, in other papers dealing with related matters. These include Richards (1973) on phoretic flies, Matthews (1974) with footnotes on use of leaf material, Costa (1975) on phoretic mites, Hammond (1976) on phoretic staphylinids, Matthews (1976) with reference to leaf utilization, but erroneously citing eucalypt leaves, Halffter (1977) who comments on the significance of *Cephalodesmus* to the evolution of nest behaviour in dung beetles, and Edmonds and Halffter (1978) who refer to larval stridulation.

MATERIALS AND METHODS

This study is based on a detailed examination of the biology of *Cephalodesmus armiger*. This was supported by sufficient observations on *C. laticollis* and *C. quadridens* to confirm that all species of the genus have similar behaviour patterns. Studies on *C. armiger* took place in both field and laboratory.

TABLE 1: SUMMARY OF VISITS TO THE *CEPHALODESMIUS ARMIGER* STUDY SITE AT TOOLOOM PLATEAU AND THE COLLECTIONS MADE.

Visit No.	Date	Burrows excavated	Foraging beetles hand-collected	Beetles in pitfall traps since last visit
1	22 Oct. 1972	11	0	No trapping
2	4 Nov. 1972	5	0	No trapping
3	17 Dec. 1972	17	26♂ 0♀	No trapping
4	30 Dec. 1972	32	0	No trapping
5	30 Jan. 1973	9	0	No trapping
6	25 Feb. 1973	20	0	No trapping
7	25 Mar. 1973	12	0	No trapping
8	7 Apr. 1973	11	0	No trapping
9	10 Jun. 1973	21	0	No trapping
10	15 Jul. 1973	11	0	11♂ 5♀
11	5 Aug. 1973	25	0	12♂ 1♀
12	26 Aug. 1973	25	0	13♂ 1♀
13	16 Sept. 1973	9	0	18♂ 4♀
14	30 Sept. 1973	15	0	2♂ 3♀
15	21 Oct. 1973	11	0	6♂ 0♀
16	11 Nov. 1973	12	1♂ 0♀	16♂ 2♀
17	24 Nov. 1973	23	33♂ 1♀	5♂ 1♀
18	8 Dec. 1973	16	31♂ 4♀	1♂ 0♀
19	31 Dec. 1973	18	0	1♂ 0♀
20	19 Jan. 1974	16	0	2♂ 0♀
21	9 Feb. 1974	22	14♂ 20♀	5♂ 5♀
22	28 Feb. 1974	11	80♂ 10♀	1♂ 6♀
23	16 Mar. 1974	21	6♂ 24♀	3♂ 6♀
24	30 Mar. 1974	18	3♂ 11♀	4♂ 4♀
25	27 Apr. 1974	10	4♂ 4♀	4♂ 0♀
26	25 May 1974	11	0	1♂ 1♀
27	14 Jul. 1974	14	0	1♂ 0♀

FIELD STUDIES

The main study site was an area of subtropical rainforest on deep basaltic soil on the Tooloom Plateau in northern New South Wales (28° 29'S, 152° 31'E, Alt. 700 m). The site was chosen for its dense beetle population and its ready accessibility. It was visited 27 times between October 1972 and May 1974 (Table 1). Intervals between visits varied from 2–3 weeks in summer to 4–5 weeks in winter when beetle activity was slight. Each visit usually consisted of an overnight camp by one or both of the authors giving the opportunity for both diurnal and nocturnal observations. During visits one or more of the following activities was undertaken:

(i) **BURROW EXCAVATIONS:** From 10 to 30 burrows were carefully excavated using a flexible probe to follow the shaft from its surface opening to its terminal chamber. The structure of each nest was noted and the contents (beetles, brood mass, brood balls, foraged material, etc.) returned alive to the laboratory for closer study. In all 426 nests were thus excavated (Table 1).

(ii) **OBSERVATIONS AND COLLECTION OF FORAGING ADULTS.** Beetles emerging from their burrows to forage are large enough and slow enough for details of their behaviour to be readily observed with the naked eye. Day and night observations of any foraging activity were made on each visit. Items being carried by beetles were noted or collected for identification and associated phoretic organisms recorded. Samples of foraging beetles were collected into alcohol for sexing and age determination in the laboratory. (Table 1).

(iii) **PITFALL TRAPPING.** To monitor above-ground beetle activity between visits three large formalin-filled pitfall traps (2 gallon buckets) were installed between June 1973 and March 1974 and cleared at each visit. Beetles trapped were counted, aged and sexed (Table 1).

(iv) **BURROW DENSITY ESTIMATION.** On August 26, 1973 an estimate of *armiger* burrow density at the Tooloom study site was made by counting burrow entrances visible in 25 random 1 m² quadrats in each of two 1000 m² plots.

LABORATORY STUDIES

(i) PROCESSING OF CONTENTS OF EXCAVATED NESTS. The following details of nest contents were recorded: number and sex of adult beetles; presence and nature of brood mass and foraged material; number, size and contents (eggs, larvae or pupae) of brood balls; and presence of other organisms. From each batch of nests several females were dissected to ascertain the condition of developing eggs in the ovaries.

(ii) AGEING OF ADULTS. The highly synchronized 12 month life cycle of *Cephalodesmius* means that the whole population is roughly of the same age at a given time. However there is some overlap of two generations in late summer when the new generation is hatching from the nests. At this time samples of hand-collected or pitfall-collected foragers could be divided easily into old and new generation by the excessive wear on the clypeal prongs and tibial teeth of the surviving adults from the old generation.

(iii) ARTIFICIAL NEST STUDIES. To study the behaviour of *Cephalodesmius* inside their burrows pairs of beetles were excavated from field nests and set up in artificial laboratory nests. Initially, 'transect cages' as described by Bornemissza (1971) were experimented with. These are basically a layer of soil held between two sheets of glass. *Cephalodesmius* placed in such containers readily excavated burrows but observation was difficult due to soil adhering to the glass, and constant problems were encountered with maintenance of natural soil moisture. Hence, completely artificial nests were made from Plaster of Paris using plasticine models of the natural burrow configuration as moulds. Fitted with removable glass fronts these were highly successful and the beetles readily adapted to the complete lack of soil. Similar plaster nests have subsequently been used by Klemperer (1979) in studies of geotrupid beetles.

In the late winter of 1973 (July/August) 12 pairs of *Cephalodesmius armiger* and 3 pairs of *C. laticollis* were brought from the field and established in plaster nests; males were marked with paint for ease of recognition. They were regularly supplied with soft leaves (usually clover) and flowers (clover and hibiscus) which they readily carried down to the burrow chamber; some nests were also supplied with dung. These pairs survived in the nests for up to two months during which time they manufactured brood material, formed egg balls and commenced progressive

provisioning of larval balls. Activity was viewed through the glass front which could be temporarily removed to permit photography or inspection of nest contents. All nests eventually died out in the larval stage due to invasions of mites and fungi, and an apparent decline of vigor in the laboratory. The sequence of events observed in the plaster nests is summarized in Fig. 10.

RESULTS

OBSERVATIONS ON *CEPHALODESMIUS ARMIGER*

The annual cycle of activity of this species is indicated by Fig. 1 which gives a summary of burrow types and burrow contents encountered during the regular sampling at the Tooloom study site. The new generation of adults emerges in late summer from subterranean pupal balls in the previous season's nest burrows. These new adults initially form small individual burrows but then gradually pair up until, by the start of winter, virtually the whole population consists of pairs of beetles in larger burrows which they share for the rest of their life. In early spring the beetles start to forage out of their burrow for various items of vegetable detritus which are dragged down to the now-enlarged chamber at the end of the burrow. Foraging soon becomes the sole task of the male while the female remains in the burrow where she manufactures a 'brood mass' from the foraged material. In late September the female starts to construct small 'egg balls' from the brood mass and deposits an egg in each. Larvae hatch inside these tiny balls within a few days and this heralds a long phase of further foraging, brood mass manufacture, and progressive plastering of brood balls which contain ever-growing larvae feeding from within. By mid summer most larvae are full grown and beginning to pupate within the now large balls which are constantly tended by the female. The male by now has ceased foraging and is excluded from the brood chamber of the burrow. Soon after, the new generation emerges by which time the original male and female are usually dead.

Detailed discussion of the various aspects of this life cycle is given under the following headings:

(i) BURROW DENSITY AND POPULATION SIZE. *Cephalodesmius armiger* occurs in a wide range of forest and soil types, and varies considerably in population density and size of individuals from locality to locality. The Tooloom study site was chosen because it was known to have a dense

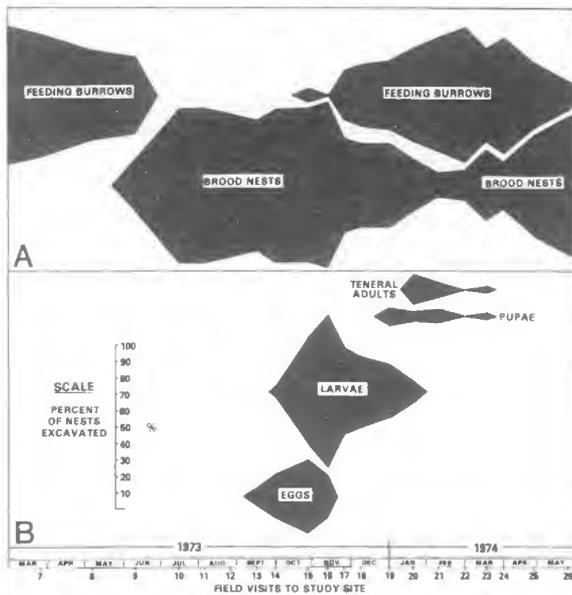


FIG. 1: Seasonal change in frequency of nest type (A) and in presence of life history stages in the burrows (B) of a population of *Cephalodesmius armiger* at Tooloom over a period of 15 months. Widths of the kite diagrams represent the percentage of burrows excavated on each field visit.

population of the largest form of the species known to us. An estimate of beetle density was made in August 1973 based on burrow entrances visible in 25 random 1 m² quadrats in each of two 1000 m² plots. In August the local population consists entirely of paired burrows (see Fig. 1) and hence the number of beetles can be assumed to be twice the number of active burrows. Plot 1 yielded an average of 2.4 burrows/m² (range 0-7) and Plot 2 had an average of 1.2 burrows/m² (range

0-3). Thus the population of this large scarab (12-15 mm length) on the Tooloom Plateau can be estimated at roughly 20 to 50 thousand beetles per hectare. The point to be made from these figures is that this large biomass of beetles is much greater than seems able to survive on mammalian droppings, the normal food source of the subfamily. The Tooloom region has a rather diverse mammal fauna (Calaby, 1966) but the species are mostly small and uncommon; the only species regularly encountered within the study area were the two small macropods, *Thylogale stigmatica* and *T. thetis*, and the two possums, *Pseudocheirus peregrinus* and *Trichosurus caninus*.

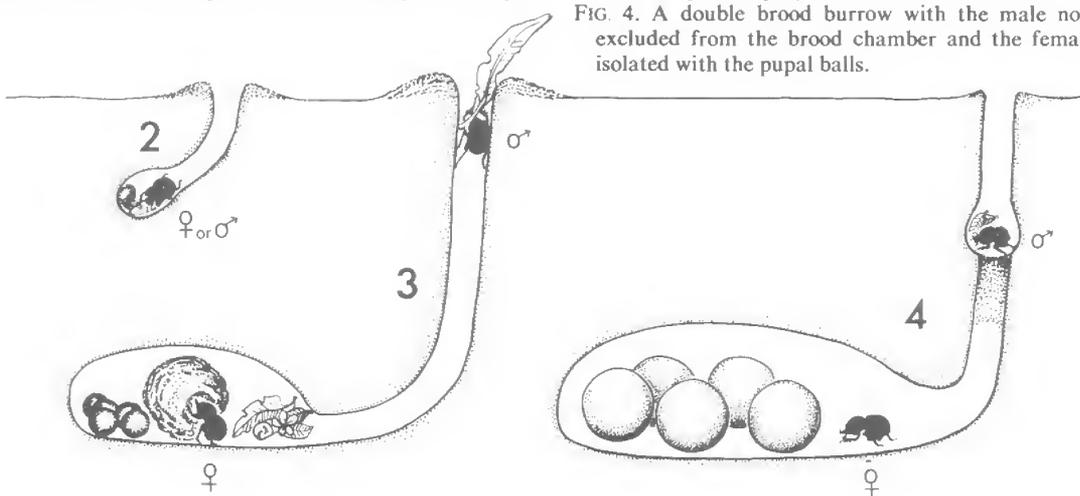
(ii) NEST STRUCTURE AND CONSTRUCTION. *Cephalodesmius* burrows are conspicuous on the forest floor at the study site and appear as vertical shafts with an open, circular entrance 10-12 mm in diameter, usually surrounded by a circular 'pushup' of soil brought to the surface by the beetles. Although the burrow entrances have a rather constant appearance all year round (Plate 2A) their subterranean structure varies seasonally. The main forms encountered are shown in Figs. 2-4.

FIGS 2-4: Types of burrows formed during different stages of the biology of *Cephalodesmius armiger*.

FIG. 2. Short feeding burrows made by newly emerged adults in late summer and occupied by single adults of either sex.

FIG. 3. Brood burrow constructed by a mated pair of adults. Shows the male dragging leaves into the nest and the female attending the brood mass she has manufactured from them. Five small brood balls containing developing larvae are shown at left.

FIG. 4. A double brood burrow with the male now excluded from the brood chamber and the female isolated with the pupal balls.



The simplest type is that made by the newly-emerging adults in late summer. These dig a short, sloping shaft 5–8 cm long which terminates in a small oval chamber not much bigger than the beetle itself (Fig. 2). These are invariably occupied by a single beetle of either sex and may also contain a few leaf fragments. They act as a short-term shelter for new adults before they pair off in autumn. We refer to these burrows as *feeding burrows*. In the field they decline rapidly in abundance by the end of May.

By early winter the great majority of burrows contain two adults, a male and a female, and these we have termed *brood nests*. They differ from feeding burrows in having a vertical entrance shaft, up to 10 cm deep, which turns and runs horizontally for 3–5 cm before opening into a large terminal chamber (Fig. 3). If the ground surface has any gradient the horizontal arm of these burrows invariably runs in the uphill direction. It is not known whether brood nest burrows result from modification of the feeding burrow of one sex after pairing has taken place or are excavated *de novo*. The terminal chamber of brood nests is slowly enlarged during the breeding season as the brood balls and brood mass become larger. It is not known whether one or both sexes are responsible for burrow enlargement, but observations of males scratching their fore tibiae and clypeal prongs against the solid plaster of the artificial nests indicate that the male may be the principal excavator.

In mid to late summer when brood balls are completed and foraging has finished, the male leaves the brood chamber and comes to reside in a small sub-chamber in the vertical shaft just below the ground surface. The remainder of the tunnel leading back to the brood chamber becomes filled with loosely compacted soil which effectively seals off the female beetle and her brood balls, most of which now contain pupae. This stage we have termed the *double brood nest* (Fig. 4). Careful probing is required to detect these double nests as they occur at a time when new season adults are emerging and forming feeding burrows with which double nests could be superficially confused. It is not known which sex causes the shaft blockage in double nests.

(iii) FORAGING BEHAVIOUR (Plates 1A, 1B, 2B, 2C, 2D, 3A, 3B).

Foraging forays outside the burrow form a major part of *Cephalodesmius* activity, especially

during the breeding season. Once the new generation has progressed from the initial feeding burrow phase to the paired brood nest phase it appears that the only reason adults leave the burrow thereafter is in search of food and brood mass material.

Foraging is principally a male activity. Females fend for themselves during the brief feeding burrow stage and during the early stages of the brood nest phase, but once brood mass manufacture starts the female rarely leaves the nest. This is shown by the preponderance of males among beetles intercepted outside the nest by both hand collecting and pitfall trapping during the major foraging period from August to January (Table 1).

Foraging for brood mass material is a daytime activity and takes place during periods of high humidity or direct moisture in the litter layer. Activity starts soon after dawn and continues while environmental moisture persists, usually until about midday. Light rain will stimulate commencement of foraging after it would normally have ceased and it is possible to artificially induce local foraging by sprinkling water on the soil. There is a certain amount of nocturnal foraging but this has some differences which will be discussed later.

Individual foraging sorties have a fairly constant pattern. The beetle emerges from the burrow and walks away from the entrance in a fixed direction with antennae extended and club segments opened wide. After examining several objects the beetle finally chooses one, picks it up with the forelegs, and backs towards the burrow entrance which may be up to a metre distant. Although the entrance may be obscured the beetle maintains an uncannily direct course — obstacles are crossed, not avoided, and a beetle will exert much time and energy in clambering up and over a large leaf rather than change course, e.g. Plate 2D. When the beetle is close to the burrow (within 5 cm) the foraged item is dropped while the beetle turns and walks *forward* towards the entrance. After briefly examining the entrance, apparently to test that it is the correct one, the beetle quickly returns to the foraged item and drags it backwards the remaining distance to the entrance and then down inside. With large items a considerable amount of pulling from inside is required before it is completely in. Rare occasions were noted when a forager tried to enter the wrong burrow and was actively pushed out by the occupant.

The great proportion of items taken into burrows were small leaves or leaf pieces, usually in a partly decayed state (Table 2). However, almost any soft organic matter was acceptable. Small flowers (e.g. *Claoxylon australe*) and fruits (e.g. *Melia azedarach*, *Diploglottis australis*) shed from the canopy trees were highly attractive to the beetles when seasonally available in the litter. *Diploglottis* fruits, although equalling the beetles themselves in size (Plate 2D), were taken into the burrows in large numbers and the soft flesh stripped from the seeds; one burrow (Visit 4) was found to contain 20 stripped seeds; other burrows were found in which multiple germination of the *Diploglottis* seeds had occurred, almost occluding the chamber. Occasionally living plants were attacked: at a steep site on Mt Clunie where litter had been removed by runoff, beetles were seen harvesting soft new shoots from vines on the forest floor. On Visit 23 at Tooloom several dozen beetles were encountered systematically cutting leaves from a newly fallen leafy branch of *Daphnandra micrantha*; individual beetles were seen to make several visits to the same branch, some travelling several metres beyond their normal foraging range to do so. *Daphnandra* is an aromatic plant with powerful alkaloids, and this may have stimulated this mass *Cephalodesmius* activity. The beetles readily took to various human detritus such as watermelon rinds and banana skins, from both of which they efficiently stripped the soft material. Where food material is fragmented before transport back to the burrow, as in the foregoing examples, the beetles use a combination of slashing movements of their saw-toothed fore tibiae and thrusting with their clypeal prongs.

The method used by *Cephalodesmius* to carry the foraged items has been described by Matthews (1974) who notes that it is not similar to that of any known scarabaeine. Objects are grasped by the fore tibiae and held tightly against the head region while the beetle walks backwards on the mid and hind legs. Heavy items, such as *Diploglottis* fruits, are transported by a series of dragging movements; the beetle reaches out as far behind as it can with the hind legs while retaining

a grip on the item with the extended forelegs. After getting purchase with the hindlegs all legs are contracted simultaneously thus dragging the object about a body length; this is then repeated.

Although plant material from the forest floor comprises the great bulk of material taken into the nests it is nevertheless true that animal dung is also occasionally gathered (Plate 3B). Table 2 records that recognizable dung pellets were found in 2.3% of the 426 burrows excavated during the study. Our observations on dung foraging, though sparse, indicate that this is a nocturnal activity and may primarily provide nutrients for adult beetles. At night beetles are often observed sitting at the tops of their burrows with antennae extended. Since most of the rainforest mammals in the study area are nocturnal this behaviour may enable early detection of dung pellets by the beetles. On several occasions pellets were noted lodged across the entrance to beetle burrows, and although too large to be dragged in, the beetle was tearing off portions from inside. When fresh bovine dung was exposed at night great numbers of beetles emerged to carry off portions. Pieces were separated from the main mass by pushing with the head and pulling with the forelegs while the whole beetle rotated; eventually a piece was torn free then dragged away backwards as for other items. No attempt is made to round off the piece after separation from the source. Foraging for plant material was never observed at night.

Artificial nest observations showed that foraging was a spasmodic activity. The male may go several days without foraging then commence a period of prolonged foraging for several hours until the nest chamber is almost filled.

(iv) PREPARATION OF BROOD MATERIAL. The materials dragged into the burrow by the male form the basic ingredients for the female to manufacture a processed, dung-like substance which is used both to make brood balls and as a food supply for adults. Brood mass manufacture starts in early spring (August) when the male begins serious foraging. Foraged items, predominantly leaves, are seized by the female and compressed with her forelegs until a tight mass is

TABLE 2: FORAGED MATERIAL FOUND IN 426 NESTS OF *CEPHALODESMIUS ARMIGER* EXCAVATED DURING STUDY VISITS TO TOOLOOM PLATEAU. FIGURES EXPRESSED AS PERCENTAGES OF TOTAL NESTS.

Empty	Leaves	Fruits	Seeds	Flowers	Leaf shelters of Atteblabidae	Dung
35.6	57.7	1.6	4.9	3.0	1.4	2.3

formed. She constantly attends the mass, shaping squeezing and mashing it with her toothed tibiae and palpating its surface with her mouthparts. New material is compressed into its surface and the faeces of both the male and female are also added. As with all other Scarabaeinae the mandibles of *Cephalodesmius* are membranous and hence no chewing function is available to the female during preparation of the brood mass.

This brood mass grows slowly in size until it reaches three to four times the size of the female herself. By this stage the material has become dark in colour and fungal activity has commenced; almost invariably larvae of the phoretic sphaerocerid fly, *Leptocera myrmecophilia* (Knab and Malloch), are present, tunnelling through the medium. After about two weeks the brood mass reaches a uniform, mushy consistency, still with recognizable fibrous plant material present, but quite malleable. At this stage egg-ball construction may begin.

This final material bears a superficial resemblance to animal dung and Fricke's (1967) mistaken reference to a mass of 'horse-dung' in a burrow of *C. armiger* is quite understandable. That the beetles can prepare the final material entirely from plant matter is shown by the artificial nests which were fed no dung. In the field, new generation beetles start to process leaves into the brood material soon after digging their first feeding burrows and there is generally some brood mass present in the burrows right through the winter when foraging is minimal. This provides adult nutrient during winter but may principally be a mechanism to maintain the fungal flora through the non-breeding season. The mycology of the process needs investigation.

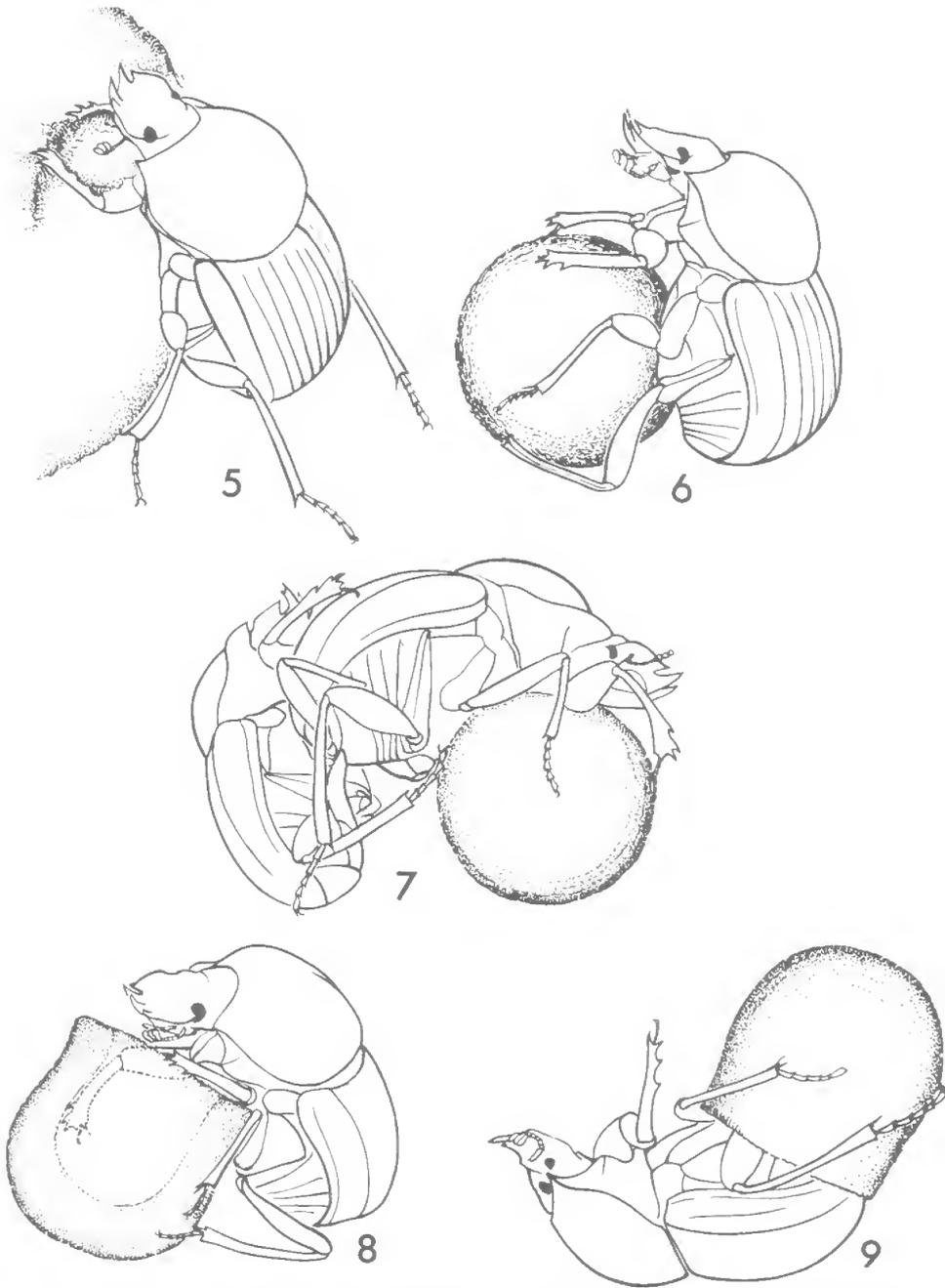
The brood mass apparently provides some nutrient for the adults because the female continuously licks its surface with the spongy lobes of her mentum and maxillae. The male often tries to feed on its surface also but is generally butted away by the female.

(v) EGG BALL CONSTRUCTION AND EGG-LAYING. The female reproductive system of *C. armiger* is normal for the Scarabaeinae in being reduced to a single ovariole on the left side, and the large (2–3 mm long), smooth, oval eggs laid are also normal for the subfamily. Eggs encountered during excavation of nests in the field were each enclosed loosely inside small (5 mm diameter), thin-walled, individual, spherical balls of brood material which we have termed egg balls.

Balls larger than these invariably contained larvae. These field observations posed two problems. Other known ball-rollers do not deposit the egg until sufficient brood material is accumulated for the larva to complete development. But it appeared that *Cephalodesmius* must add more brood material to the brood ball after egg deposition. In other words some degree of progressive provisioning must take place. And secondly, whereas normal ball-rollers have the simple task of depositing an egg in one end of a large ball of brood material, *Cephalodesmius* must possess additional manipulative skills to enable it to enclose its eggs inside fragile, thin-walled spheres of soft material. These problems were clarified by numerous observations on egg laying in the artificial nests.

Egg ball construction is solely a female task and commences once the brood mass has reached the correct state of decomposition. Using the forelegs the female first tears a small chunk from the brood mass (Fig. 5) and begins a long period of manipulation of it lasting up to three hours. Initially this is done in a 'sitting' position where the beetle rests on a tripod formed by the pygidium and the two hind legs (Fig. 6, Plate 2EF). Frequently the beetle topples over due to its activities and continues its manipulations while on its back or side. First the chunk of brood mass is rounded into a sphere using all pairs of legs, then it is turned, probed and licked for a considerable period while all the fibrous material and non-decayed leaf pieces are removed, retaining in the ball only the very fine homogenous substrate. During this phase the male may copulate with the female while she holds the ball (Fig. 7) (see Section vi). Regaining the sitting position, the female begins to hollow out the ball for reception of the egg (Fig. 8). The hollow is enlarged by inserting the forelegs further and further into the cavity, usually holding it steady with one fore tibia on the rim and the other inside pulling outwards to enlarge the cavity or scraping and smoothing the inner surface (Plate 3F). While this is in progress the ball is slowly rotated by the mid-legs giving a 'potter's wheel' effect ensuring uniformity of shape and wall thickness of the finished cup-shaped receptacle. This hollowing process lasts for approximately 30 minutes and the final shaped cup has a slightly flared rim.

Egg laying then takes place. The prepared cup of brood material is nimbly swung between the legs and clamped with its orifice over the abdominal apex and held in position by the mid- and hind-legs (Fig. 9). This lasts for 15–20



FIGS 5-9: Stages in egg-laying by a female *Cephalodesmius armiger*. Redrawn from photographs taken inside an artificial nest.

FIG. 5. The female tears a portion off the mass of cultured brood material.

FIG. 6. She forms it into a smooth sphere while in the 'sitting' position.

FIG. 7. The male approaches and copulates while the female works on the egg ball.

FIG. 8. The female hollows out the ball using the forelegs to form a lipped cup.

FIG. 9. Lying on her back she holds the cup over her abdominal apex and inserts an egg into the hollowed chamber. The opening is then closed and the completed egg ball rounded off.

seconds while an egg is deposited inside. The egg ball is then swung forward and its opening rapidly closed off by the forelegs. An additional 30–60 minutes are then spent in smoothing and rounding the completed egg ball.

Once a female commences egg laying she continues egg ball formation at the rate of approximately one per day until the full complement is reached. In the artificial nests this was between 10 and 12 balls but in field nests the maximum number observed was 7, with the usual number being 4 or 5. No further provisioning of brood material to the first egg balls takes place until the egg laying sequence is complete. Each female has only a single egg laying sequence in its lifetime.

(vi) COPULATION. Observations of copulation in the dung beetles are extremely rare and were reviewed by Halffter and Matthews, 1966. Halffter and Lopez (1977) subsequently studied copulation in *Phanaeus* (Coprini) and reviewed further literature. The great majority mate below ground in association with brood material, the only regular ground surface copulation being recorded in *Phanaeus*. Halffter and Lopez note that, in the Scarabaeini (to which *Cephalodesmius* belongs), mating has always been observed after brood ball construction, an exception being *Megathoposoma* (Wille, 1973).

Copulation was seen on several occasions in *Cephalodesmius armiger* and takes place under two different circumstances. The commonest is in the brood burrow at the time of egg ball construction. This activity appears to act as a behavioural cue for the male to commence copulation, since the male generally mounts the female while she is working on an egg ball (Fig. 7). Union usually lasts only a few minutes and is terminated by the female thrusting the male off. In some artificial nests copulation was noted on several consecutive days each time the female made a new egg ball. This indicates that copulation may be partly ritualized. In some nests no egg ball related copulation was seen.

Copulation also occurs on the ground surface in February–March. This is the period when the new generation is emerging and great numbers of both sexes may be found roaming outside the burrows in the daytime. On Visit 22 ninety foragers were collected at 10 a.m., of which two pairs were in copulation. One pair was an old generation male and a new generation female; the other pair were both new generation individuals. On Visit 23 thirty foragers were collected at 9.30 a.m.

including a new generation pair in copulation. Precisely a year earlier, on Visit 6, a new generation pair dug from a brood burrow were seen to copulate in their storage vial in the laboratory 36 hours after being excavated. These observations suggest that copulation may accompany pair bonding at the time when the new generation is in transition from the individual feeding burrow stage to the paired brood burrow stage in late summer. Such diurnal, above-ground mating unassociated with other breeding behaviour is unrecorded in the Scarabaeini and resembles that described by Halffter and Lopez (1977) for the Coprini genus *Phanaeus*.

(vii) PROGRESSIVE PROVISIONING OF BROOD BALLS. Eggs hatch within a week or so of deposition and the larva feeds on the inner surface of the egg ball as is usual in the Scarabaeini. The thin shell of brood material present in the original egg balls provides larval food for only a short period. Accordingly, additional brood material must be added to the outside of the balls to feed the growing larva inside. This post-eclosion, periodic feeding of progeny by the parents fulfils quite adequately the criteria of 'progressive feeding', a phenomenon usually confined to insects with advanced parental care, such as some Hymenoptera. It is common among ball-roller dung beetles for parents to tend and clean brood balls during larval development inside. But this added complexity in *Cephalodesmius* whereby the parents continue to manufacture brood material and progressively feed it to the developing larvae is unparalleled in the rest of the Scarabaeinae.

During this phase of larval growth inside the brood balls the parent male continues to forage plant material and the female continues to add it to the brood mass. However the process of adding brood material to the brood balls is entirely a female occupation. The male, when not foraging, merely rests immobile in the nest at the bottom of the exit shaft.

External provisioning of the balls does not commence until all egg balls are completed. Thereafter, all brood balls are periodically provisioned in turn so that at any given time all balls in a nest are roughly the same size. In the artificial nests excess balls are abandoned and destroyed during this early period of larval development. This presumably occurs in the field also, as the number of brood balls per nest is at its peak early in the season and then declines slightly later on. The brood material from these terminated balls appears to be returned to the

brood mass or added to other balls as all trace of them soon vanishes.

As the brood balls are enlarged the larvae within feed and grow at a proportionate rate so that the wall of the brood balls always remains at about 2 mm thick. During the later stages of larval development the female spends less time in processing foraged material. Larger larvae seem to be able to handle coarser material and bits of green leaf are often seen in the surface of larger balls. It is possible that some foraged material is added directly to the brood balls at this stage, rather than via culturing in the brood mass. However, brood mass is always present in the nest.

(viii) **LARVAL MORPHOLOGY AND BEHAVIOUR.** Halffter and Matthews (1966) have summarized the remarkable behavioural and morphological adaptations which scarabaeine larvae exhibit for their life inside the spherical cavity of a brood ball. *Cephalodesmius* larvae conform well with all these features, viz. strongly arched body with a humped dorsum and truncate

abdominal apex for gaining purchase on the walls of the feeding cavity; progressive rotation during feeding so that ejected faeces are re-consumed together with new brood material; ability to rapidly seal off perforations in the wall of the brood ball with quick drying larval faeces. They differ from usual dung beetle larvae in being more strongly arched so that their head is almost always in close approximation to the abdominal apex (Fig. 11).

Edmonds and Halffter (1978) give a detailed summary of larval morphology in the Scarabaeinae. They define the subfamily by 26 larval characters and give a key to the 25 genera whose larvae were available to them. *Cephalodesmius* larvae conform with the general subfamily pattern except that they lack the row of 'stridulatory' tubercles on the stipes, the raster on the last abdominal venter, and the transverse row of setae on the labium. They run to couplet 17 in Edmonds and Halffter's Key where they do not fit comfortably with either *Copris* or *Arachnodes*. To enable *Cephalodesmius* to be compared with this

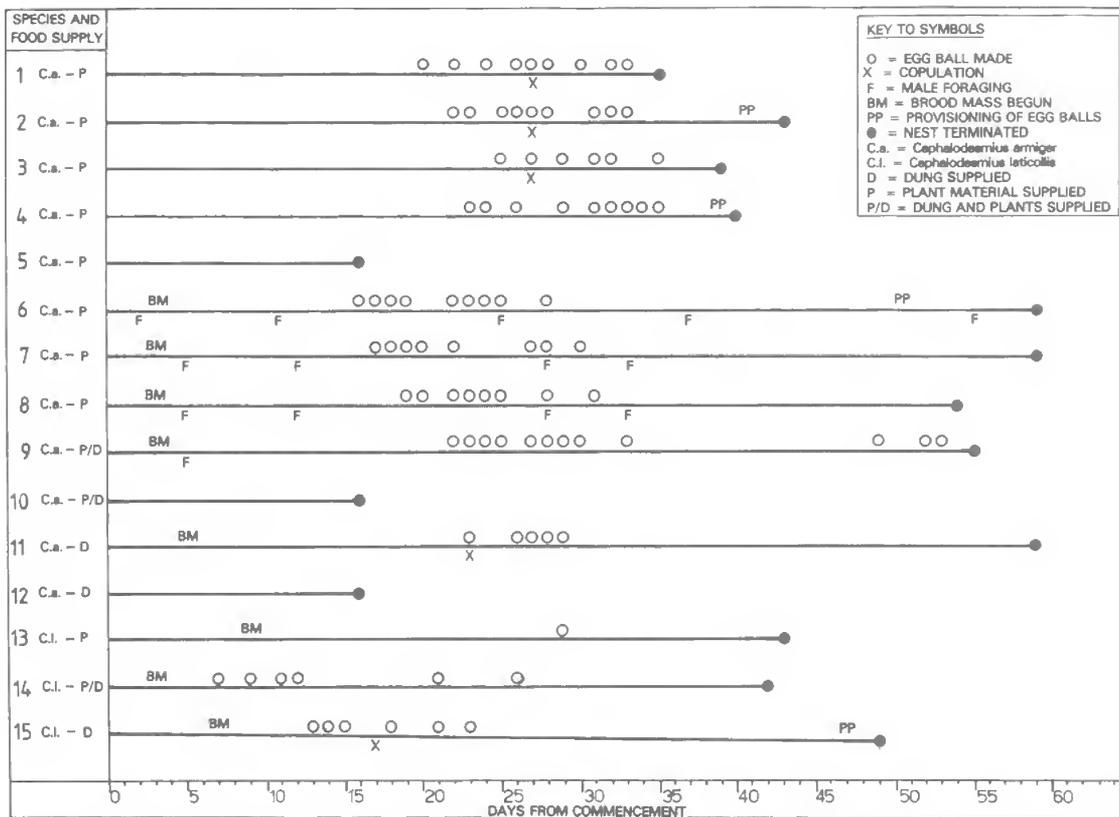


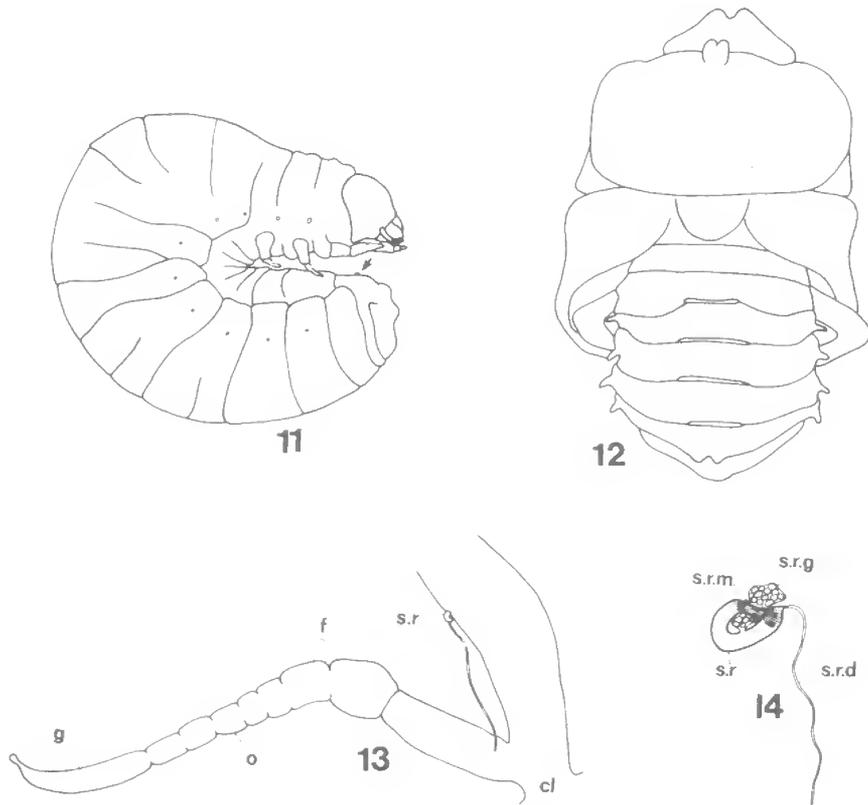
FIG. 10: Sequence of events in artificial plaster nests set up using mated pairs of *Cephalodesmius armiger* or *C. laticollis* dug from field nests.

study a brief description is given using Edmonds and Halffter's format and their paper should be consulted for explanation: (a) Sensory area of third antennomere conical; (b) chaetopariae with 3-4 setae; (c) lateral area of mandibles with two setae; (d) uncus of lacinia with a short, blunt basal tooth; (e) pronotal shields present but lacking produced anterior angles; (f) legs with terminal papillae; (g) third abdominal segment lacking a dorsomedian prominence; (h) last abdominal venter lacking a raster.

Cephalodesmius larvae agree with the genus *Sisyphus* in their lack of stipital tubercles and raster but can be easily separated from this genus and all other dung beetles by the remarkable stridulatory structures described in the following.

On several occasions during our study loud stridulations emanated from late stage larval balls of *Cephalodesmius armiger* after excavation from

field nests. These stridulations occurred when the balls had not been disturbed for some time and the sounds consisted of groups of rapid, short, sharp notes uttered at intervals of several minutes. Halffter and Matthews (1966) note that many scarab larvae of other subfamilies have an apparent stridulatory mechanism between the maxillae and the mandibles. For instance, larvae of the common Brisbane cetoniine, *Diaphonia dorsalis*, have a series of pegs on the anterior margin of the maxillary stipes which rub against a patch of ridges on the posterior margin of the mandible (pers. obs.). But Halffter and Matthews note that actual sound production by larvae has not been recorded in the family. Further, in the subfamily Scarabacinae this stridulatory mechanism is greatly reduced or, as in *Sisyphus*, absent. Such a maxillomandibular stridulatory device is also absent in *Cephalodesmius* but examination



FIGS 11-14: Immature stages and internal anatomy of *Cephalodesmius armiger*.

FIG. 11. Side view of larva removed from a brood ball. The position of the stridulatory structure on the last abdominal sternite is arrowed.

FIG. 12. Dorsal view of pupa, showing supporting processes on prothorax and abdomen.

FIG. 13. Reproductive system of female.

FIG. 14. Detail of the seminal receptacle. Abbreviations: cl., cloaca; f., follicle; g., germarium; h.g., hind gut; o., ovariole; s.r., seminal receptacle; s.r.d., seminal receptacle duct; s.r.gl., seminal receptacle gland; s.r.m., seminal receptacle muscle.

revealed a quite novel stridulation arrangement. It consists of a large, sub-rectangular, well-sclerotised region of the gular part of the head (Plate 3C) which bears about 45 fine transverse ridges (the stridulitrum in the terminology of Ashlock and Lattin 1963) (Plate 3E); against this rubs a small, midline sclerotization of the last abdominal sternum bearing several transverse flanges (the plectrum; Plate 3D, F). This mechanism occurs in all three instars of *Cephalodesmius armiger* as well as in the few larvae of *C. quadridens* and *C. laticollis* available to us. This sort of stridulation, where the two soundproducing components are at opposite ends of the body, and where the animal has to scratch its 'chin' with its 'tail', as it were, is believed to be unique in the insects. Dung beetle larvae, with their head permanently approximating their abdomen, are one of the few animals predisposed to the evolution of such an arrangement.

The functional significance of this stridulation behaviour in *Cephalodesmius* can only be guessed at. It is unlikely that it is of alarm or defense function because it was never heard when nests were being excavated or when balls were being handled. However, the close association between the mother beetle and the larval balls during the process of progressive provisioning suggests that stridulation may be a form of communication between the larva sealed inside the ball and the female. The female has no obvious way of detecting the rate of larval feeding inside the ball, and yet opened balls from excavated nests have remarkably constant thickness of brood material surrounding the feeding larva inside. This suggests that the larva communicates wall thickness to the female; in other words, larval stridulation in *Cephalodesmius* may be just the age-old cry from progeny to parent: 'Bring more food!' No stridulation was observed in adult *Cephalodesmius*.

(ix) PUPATION AND PUPAL MORPHOLOGY.

The growing larval brood balls reach a maximum of 16–18 mm diameter after which provisioning by the parent female ceases and the larva inside soon pupates. At this stage the male stops foraging and becomes sealed off from the nest chamber by a blockage of the entrance shaft. This is the double brood nest stage (see Section ii). The female remains in the inner chamber with the pupal balls.

In the later stages of progressive provisioning of the larval balls their surface is coarse and fibrous because of the incomplete decomposition of the brood material being added. By contrast the shell

of the final pupal balls consists of hard, dark material of very fine texture; the problem of its origin arises. Halffter and Matthews (1966) summarize some observations, especially those of Siyazov (1913) which suggest that the pupal ball shell in some dung beetles may be formed, at least in part, by the faeces of the larva itself. Although our artificial nests did not survive to the pupal stage, and thus direct observations are not available, there is strong evidence that this is also the case in *Cephalodesmius*. Larvae of all ages have the capacity to produce large volumes of liquid faeces which is used to repair accidental holes in the brood ball. The grooming activities of the female parent soon smooth away any external evidence of these repairs. But towards the end of larval growth the amount of larval faeces being ejected from the ball far exceeds that expected in response to accidental ball perforations. For example, if large larval balls dug from field nests are isolated from the female parent for a few hours they become covered with large clots of ejected faeces. On the other hand, if similar balls are confined with the female these clots do not form because they are being continually smoothed over the surface by her. This suggests that when the near-mature larva is consuming the last of the accumulated brood material from the inside surface of the ball it is simultaneously evacuating the undigested residues from its alimentary canal to the exterior of the ball where they are spread by the female and solidify to become the fine-grained, dark material of the pupal shell.

Dung beetle pupae are distinctive in possessing dorsal and/or lateral projections on various of the body segments. These support the pupal body above the inner surface of the pupal ball (Halffter and Matthews, 1966). Edmonds and Halffter (1978) coin the term 'pupal support projections' for these structures and review their distribution among the genera known to them. Pupae of *Cephalodesmius armiger* (Fig. 12) have weak development of pupal support projections and lack the very long, filamentous structures seen in many species; however they possess the full complement of projections which Edmonds and Halffter list as constant in the subfamily as follows: (a) Pteronotal projections — both mesonotum and metanotum bear small, median papillate projections; (b) Lateral tergal projections occur as distinct finger-like lobes on segments 3, 4 and 5 becoming less distinct on segments 6 and 7; (c) Dorsal tergal projections — the median longitudinal fold is weakly developed and replaced functionally by transverse raised folds on most

abdominal terga; (d) Caudal projection takes the form of a thickened tergal area only. In addition to these a prominent, bilobed, pronotal projection is present.

(x) EMERGENCE AND BEHAVIOUR OF NEW ADULTS. Pupal life is relatively brief, probably of the order of 2–3 weeks. Although direct measurement of pupal period was not possible it can be seen from Fig. 1 that in the field the first teneral adults inside balls occurred only 19 days after the first pupae were encountered. All pupae have emerged by the end of March at Tooloom.

Teneral adults remain inside the pupal balls for a few days while hardening takes place. When they break out of the balls they apparently leave the burrow almost immediately since tenerals were never found free inside the nest chamber. Their exit route is by way of the original entrance burrow since extra exit holes from post-pupal brood chambers were never found. By this stage the original parent female is usually dead and her body was often found in such abandoned nests. The fate of the parent male is uncertain because all trace of him has gone after the exit of the new adults via the secondary chamber he occupied during the double nest phase (Fig. 4).

The new generation adults dig and occupy small individual feeding burrows soon after they emerge from the parent nest. These short, temporary burrows are soon stocked with a few leaves. During this period large numbers of both sexes appear on the ground surface on favourable days (Table 1, Visits 21, 22, 23). While much of this surface activity is undoubtedly concerned with foraging, the incidence of daytime copulation (Section vi) suggests that mate selection also takes place leading to the formation of paired brood nests which rapidly supplant the single feeding burrows.

(xi) OVERWINTERING ADULTS. By the onset of cold weather in April/May almost all burrows are paired brood burrows each containing a new generation male and female (Fig. 1). The terminal chamber is moderately enlarged but usually contains several small leaf pieces and no brood mass. This situation persists through winter.

No daytime foraging was noted in winter but pitfall trapping continues to yield some adults during the coldest months (Table 1). This probably indicates nocturnal foraging by adults for faecal food for themselves; it is significant that these pitfall catches include both sexes. It was a

common observation to find adults at night sitting at the entrances to their burrows with head and extended antennae protruding. Occasional instances were noted where a pademelon (*Thylogale* sp.) dung pellet had been pulled across the entrance to a burrow while the beetle tore away at it from the inside. Since pademelons are entirely nocturnal these observations suggest that the beetles wait at their burrow entrance to sense newly deposited pellets in their vicinity.

Towards the end of winter further enlargement of the terminal chambers takes place, indicated by the appearance of fresh soil pushups at burrow entrances. Then in early August foraging for plant material starts in earnest and soon brood mass manufacture by the female heralds the start of a new reproductive cycle.

(xii) NATURAL ENEMIES. *Cephalodesmius armiger* appears to have few natural enemies despite its large population size. Diurnal foragers would appear to be vulnerable to bird predation, but this was never observed. Foraging adults freeze for several minutes in a rigid, often ungainly, posture when disturbed and this, together with their soil-like colour, affords them considerable cryptic defence.

Few predators enter the underground nests. Of the more than 400 nests excavated active predation was noted on only three occasions. Twice at Tooloom large geoplanid planarian worms were found attacking the nest inhabitants, and once at Lever's Plateau a tenebrionid beetle (*Otrintus cylindricus* Carter) was found with partly consumed adult *Cephalodesmius*. Occasionally nests invaded by fungus were found but it was not clear if the fungal invasion had followed nest death from other causes. The only case of vertebrate excavation of nests was noted at Victoria Park, near Lismore, in December 1974, where a considerable number of nests had been dug up and the adults and larval balls eaten; this is presumed to have been the work of bandicoots (*Perameles* sp. or *Isoodon* sp.).

In late summer and autumn numerous dead adults may be found on the ground surface but this appears to represent natural mortality of the previous year's generation after emergence of their progeny.

A female from Tooloom (Visit 14) dissected for ovary inspection contained numerous encysted nematodes in the body cavity. This suggests that, like many other scarabs, *C. armiger* may act as the intermediate host for a parasitic worm.

(xiii) NEST INQUILINES AND PHORETIC ASSOCIATIONS. The stable, humid environment of *Cephalodesmius* nests and the rich supply of organic material stored therein eminently predisposes them to exploitation by other organisms. During field observations a number of other arthropods were encountered in the nests or on the bodies of the beetles and some were found to have entered into rather intimate associations with their hosts. A more detailed account of the biology of these species and their interaction with *Cephalodesmius* will appear later (Monteith, *in prep.*) but for completeness a brief, annotated list of the more important species is given here. The taxonomy of the mite fauna has already been investigated (Costa, 1975).

ACARINA—MESOSTIGMATA

Family Macrochelidae

Macrocheles tenuirostris Krantz and Filipponi, 1964. A sluggish mite commonly found clinging to adults of *C. armiger*.

Family Laelapidae

Hunteracarus womersleyi Costa, 1975. An active, abundant mite found clinging to the adult beetles and occasionally free in the nest.

ACARINA—ASTIGMATA

Family Anoetidae

Histiostoma sp. A minute, white mite which feeds and proliferates on the outer surface of the brood mass. It has phoretic hypopial stages which attach to the integument of adult *C. armiger*.

Family Acaridae

Caloglyphus sp. This minute white mite with long dorsal hairs built up to considerable numbers among leaf fragments in *C. armiger* nests. Like *Histiostoma* sp., its hypopi were phoretic on the adult beetles.

INSECTA — COLLEMBOLA

Family Entomobryidae

Sinella sp. This springtail was often encountered in numbers in nests of *C. armiger*.

INSECTA — COLEOPTERA

Family Staphylinidae

Anotylus sp. n. This rove beetle habitually bred in the nests of *C. armiger* and its adults and larvae could be found burrowing through the brood mass. Adult *Anotylus* have a phoretic association with the adult scarabs and were often found clinging to the dorsum of

foraging beetles (Plate 1B). This 'kleptoparasitic' relationship is referred to by Hammond (1976).

Oxytelus sp. This species belongs to the same subfamily as *Anotylus* sp. It was taken on several occasions in nests of *Cephalodesmius quadridens*.

INSECTA — DIPTERA

Family Sphaeroceridae

Leptocera myrmecophila (Knab and Malloch) Larvae of this fly were almost invariably found tunnelling through the brood mass of *C. armiger* nests and adults were often found free in the nests. The adults were also strongly phoretic on the adult beetles and were frequently seen riding foragers back to their nests (Plate 2B, 2C, 2D, 3A).

(xiv) OVARIAN CYCLE. The Scarabaeinae show the most extreme ovarian reduction known in the Coleoptera. All 38 species studied to date have only the left ovary present, and this is reduced to a single ovariole (Robertson, 1961; Ritcher and Baker, 1974; Halffter and Lopez, 1977). This was confirmed for *Cephalodesmius laticollis* by Matthews (1974) and that of *Cephalodesmius armiger* is similar (Fig. 13). Its seminal receptacle (Fig. 14) is of the advanced type with the chamber strongly arched and provided with muscles on one side only (Halffter and Matthews, 1966).

Dissection of female beetles collected on each of Visits 4–18 over a period of 12 months showed a pronounced cycle of ovarian activity. No developing egg follicles appear in the ovariole tubes until mid-July, about six weeks before the start of egg-laying in the field. By late August, almost all females have developing follicles. These may number up to 10, which is in contrast to the general tendency in dung beetles for follicle reduction. This appears to accord with the observed pattern of egg production in *Cephalodesmius* where eggs are produced in one-a-day succession for a number of days until egg-laying ceases. By the beginning of December all ovaries are spent.

(xv) RELATIONSHIP WITH MICROFLORA. Halffter and Matthews (1971) have summarized recent studies which indicate that dung beetles have a complex gut flora of saprophytic and cellulose-digesting organisms which aid their utilization of the plant component of their dung food. This aspect of *Cephalodesmius* biology was not investigated in the present study. However

some of our observations indicate that there may be a complex process operating whereby gut-transfer of a fungal organism is effected.

All pupal balls opened during our field sampling were found to have several fungal fruiting bodies projecting from the wall into the pupal chamber. Each fruiting body consisted of a conical base bearing an apical, white spore-body. These delicate fruiting bodies must grow into the interior of the ball after the larva has ceased feeding and has completed the pupal ball by evacuation and solidification of its own faeces (see Section ix). When balls containing hatched, teneral adult beetles were opened, however, these fruiting bodies were invariably missing or truncated. The suspicion that these newly emerged adults had made their first meal of the fungal bodies was confirmed by examining the gut contents of the beetles. It is tempting to speculate that this is a mechanism which enables gut transfer of symbiotic fungus to the new generation of adults. Bearing in mind that these adult beetles later combine their own faeces with the brood mass manufactured from foraged leaves (see Section iv) it is easy to see how this mechanism could effect transfer of the specific fungus used to culture mashed leaves into dung-like brood material. Experimental proof of this apparent transfer process will be of great interest.

NOTES ON OTHER SPECIES OF *CEPHALODESMIUS*

The other two species of *Cephalodesmius* both occur in the same general region where the main studies were carried out. *C. laticollis* is the largest species, reaching 17–19 mm in length, and has a restricted distribution in the red soil rainforests of the Lamington, Tamborine and Springbrook plateaus; Matthews (1974) gives an unconfirmed record for the Dorrigo plateau in New South Wales. *C. quadridens* is the smallest member of the genus, reaching 5–7 mm, and shows sufficient geographic variability that more than one species may be involved (E. Matthews, *pers. comm.*). It is more widespread than *laticollis* and is most abundant in the drier, western part of the generic range. Most rainforest tracts were found to be occupied by two *Cephalodesmius* species and all combinations occurred. At Tamborine, the *laticollis/quadridens* combination occurred at Lamington and Wiangaree *laticollis/armiger* shared the rainforest floor; and *armiger/quadridens* coexisted at Tooloom, Mt Glorious and Bunya Mountains. At no single site were all three species encountered.

During the course of our studies on *C. armiger*

sufficient observations, both in field and laboratory, were made on *laticollis* and *quadridens* to show that they share the same pattern of nest formation and leaf utilization. These are summarized as follows:

(i) *Cephalodesmius laticollis*. This species constructs nests similar to those of *C. armiger* except that the entrance shaft may spiral. The terminal chamber may be as large as a clenched fist. Adults forage in the daytime for both dung and leaves. Dung was found in the nests more often than for *C. armiger*. *C. laticollis* was maintained in artificial nests, but less successfully than for *C. armiger*. However brood mass manufacture and egg ball construction was seen to be similar to that described in *armiger*. In the field, *laticollis* started making egg balls as early as the end of May at Beechmont, much earlier than the Tooloom population of *armiger*. Burrows with full grown larvae were found in October, and empty burrows in December. Thus, there is apparently still only one generation per year, with larval development in winter–spring, rather than spring–summer as in *armiger*. Up to 5 brood balls per nest were found.

(ii) *Cephalodesmius quadridens*. Nests of this small species were excavated at Mt Tamborine, Mt Glorious, Benarkin and the Bunya Mountains. They usually conform to the normal pattern of a vertical shaft and a horizontal, terminal chamber but frequently are under the edge of logs or stones on the ground. None were kept in artificial nests. Though *quadridens* comes commonly to nocturnal, dung-baited pitfall traps all nests examined (over 45) contained only leaf and other plant material. No foraging adults were observed and this may be explained by their small size, or perhaps by nocturnal habits. The life cycle appears shorter than that of the other two species. Egg balls were found in October and teneral adults in December but there is no evidence of more than one generation per year. Up to 9 brood balls per nest have been found. Pupal balls opened at Bunya Mountains in January had fungal fruiting bodies projecting into the chamber as were described for *C. armiger*. An intimate fungal relationship is thus also suggested in *C. quadridens*.

DISCUSSION

As can be seen from the recorded observations both in the field and in laboratory nests, *Cephalodesmius* has a remarkable biology, undoubtedly one of the most complex in the Scarabaeinae. It also exhibits many unique

features found nowhere else in the subfamily. Plant material is used for adult feeding and nidification, with a dung-like substance being formed from it. Pair bonding and residence in a single burrow are longer than recorded for any other dung beetles. Parent to offspring bonds are also stronger, indicated by the novel method of larval stridulation. *Cephalodesmius* is also the only known scarabaeine to exhibit progressive provisioning of the larval food supply.

The use of processed plant material for nidification is unique in the Scarabaeinae, both in the material used and in the manner in which it is converted to a dung-like substance. Most records of dung beetle genera in decomposing vegetable matter cited by Halffter and Matthews (1966) are small species taken in leaf litter samples without any indication that they actually utilize the litter itself. The use of fruits is much better substantiated, with some species such as the Australian *Onthophagus vilis* Harold apparently relying on this sort of medium exclusively for adult and possible larval food (pers. obs.). Even in these species no processing is involved, the decaying fruit merely replaces dung as the food supply.

Permanent pair bonding and residence within a single burrow for the lifetime of the pair are also interesting features of their biology. According to Halffter and Matthews (1966), scarabaeines normally form pair bonds only for the period of nidification, or less. In *Cephalodesmius*, pair bonding extends for almost a year from the short feeding phase until the death of the pair. In the Scarabaeinae the length of burrow occupation by the adults varies. In some (e.g. *Onthophagus*) the female alone is involved in provisioning and stays in the burrow only until egg-laying is complete. In others, such as Halffter's (1977) nidification Groups III and V, females, and sometimes the male also, show brooding behaviour, attending the brood balls for part or all of their development. Again, this brooding period in *Cephalodesmius* is the longest of all Scarabaeinae, with both male and female resident continuously.

Cephalodesmius is the only scarabaeine known to exhibit progressive provisioning of the larval balls. In all other genera, the developing larva is provided with enough food to complete development at the time the egg is laid (Halffter, 1977). This results in a very close bond between the female and the developing larva which she, in fact, never sees or touches. Hence the development of communication via the unusual larval stridulation mechanism, another illustration of the close

relationship of individuals in a *Cephalodesmius* family. This is a truly subsocial relationship, certainly the most complex yet described in the subfamily, and one of the most advanced in the Coleoptera.

The repertoire of manipulative skills in the female *Cephalodesmius* exceeds that of other known scarabaeines. Many of these have no analogous equivalents in normal dung beetles and it must be assumed that many evolutionary steps have led to the intricate mechanisms we see today. These include the procedures of mashing leaf material into brood mass substrate, the process of plastering thin layers of brood material on to the growing brood balls, and, most complex of all, the fashioning of fragile, hollow, egg-ball shells from the brood mass.

So many aspects of *Cephalodesmius* biology are anomalous within the context of known dung beetle behaviour that it is difficult to place the genus into generally accepted evolutionary schemes. The use of leaf material for larval food is not known elsewhere in the Scarabaeinae, but does occur in some Geotrupinae, a subfamily regarded as a primitive relative of the true dung beetles (Ritcher, 1958). Some geotrupines use surface humus or decaying leaves as brood material (Howden, 1955). In particular, the genus *Lethrus* has many parallels with *Cephalodesmius* in that males bring fresh leaves to females in burrows who prepare balls of masticated leaves from them which are used to provision larval cells; the larvae consume the leaf material after it has been invaded by fungal hyphae (Nikolayev, 1966). Now the tribe to which *Cephalodesmius* belongs is generally considered primitive so the question obviously arises as to whether the diet of dung-like, processed leaf material in *Cephalodesmius* is a precursor to true dung feeding in the subfamily. Most evidence, however, indicates that the feeding habits of *Cephalodesmius* should be regarded as specializations on an original coprophagous stock. All the normal modifications of the Scarabaeinae for dung feeding and nidification are present: atrophy of adult mandibles; ability to transport food items, dig nests and prepare spherical brood balls; modification of larval morphology and behaviour for life inside a spherical food source. This seems particularly significant with respect to the adult mouthparts. The Geotrupinae have chewing adult mandibles, and these are used for leaf cutting and mastication in leaf culturing forms such as *Lethrus*, but *Cephalodesmius*, having lost the chewing function, has been forced to develop

alternative mechanisms of leaf harvesting and mastication using its tibiae and clypeal prongs. It is doubtful if this would have come about if *Cephalodesmius* had not developed from a dung feeding ancestor. The occurrence of incipient dung feeding in adult *Cephalodesmius* should probably be interpreted as retention from previously more extensive use of dung in the diet. While it is difficult to conceive that a litter feeder, with its almost limitless food supply, should need to learn to utilize the rare dung pellets as food, it is reasonable to assume that an originally obligate dung feeder might undergo a dietary shift into the more abundant litter but retain facultative use of some dung food, perhaps as a protein source for egg maturation in adults.

The subtribe Canthonina to which *Cephalodesmius* belongs, contains many species which construct multiple brood balls from dung which they transport to underground nests (Halffter, 1977). For the reasons given above we believe that *Cephalodesmius* should be regarded as derived from one of these multiple nest canthonines which initially learned to augment its dung supply by mixing in soft plant material and later became so successful at utilizing this material that it was able to forgo the use of animal dung almost completely.

Halffter (1977), in a discussion of the evolution of nidification in dung beetles, distinguishes six basic groups of nesting patterns and strategies. His Groups I to III are variations on the nesting strategy where food is buried in nests at the food source and his Groups IV to VI cover those that transport food away from its source before digging the nest (the ball-rollers). On the basis of preliminary information on *Cephalodesmius*, Halffter included it, with the taxonomically unrelated subtribe Coprina, in his Group III, which comprises species which make multiple brood balls in a previously excavated gallery and then exhibit parental care. In doing so Halffter dissociates *Cephalodesmius* from the rest of the Scarabaeini which are divided between Group IV (ball-rollers with single ball nests and no parental care) and Group V (ball-rollers with multiple balls and parental care). In this system *Cephalodesmius* is split from its relatives because it does not find food then transport it in search of a nest site as do normal ball-rollers, but rather it builds a nest before actually gathering food. When we consider why this is so it becomes clear that this behavioural anomaly in *Cephalodesmius* is better explained as an unusual Group V pattern than as grounds for transferring it to another

group altogether. The food of normal dung beetles, whether it be dung, carrion or fungi, occurs as discrete masses spatially separated in the environment. The beetles must search actively to find one of these food masses before any brooding behaviour, such as nest excavation, can begin. By contrast, the leaf litter food of *Cephalodesmius* is uniformly and abundantly distributed over the forest floor and thus *Cephalodesmius*, alone among dung beetles, can afford the luxury of dispensing with food searching before brood burrow construction; in fact the brood burrow is made some months before breeding activity starts in the assumption that food will be available when required. It should be noted that when brood foraging commences the ball-roller strategy of transporting food items across the ground surface to the nest site is used. The Coprina of Halffter's Group III bury brood material at the food source. For these reasons, *Cephalodesmius* seems more comfortably accommodated with its taxonomic relatives in Group V of Halffter's evolutionary schema.

Several aspects of *Cephalodesmius* biology merit closer examination than has been possible in the present study. These include the relationship between the beetles and their phoretic associates, the role of fungi in brood material formation, the mechanism of fungal transfer between generations, communication between larvae and adults, the extent and significance of dung feeding by adults, and the relative roles of the sexes in burrow excavation. These intriguing beetles have already proved themselves remarkable, but clearly have many behavioural phenomena yet to be fully understood.

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MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE I.

- A. Foraging male of *Cephalodesmius armiger* carrying a dead leaf backwards towards its burrow.
- B. Foraging male of *C. armiger* with two specimens of a phoretic staphylinid beetle (*Anotylus* sp.) clinging to its dorsum. The staphylinid breeds in the brood mass in burrows of *C. armiger*.

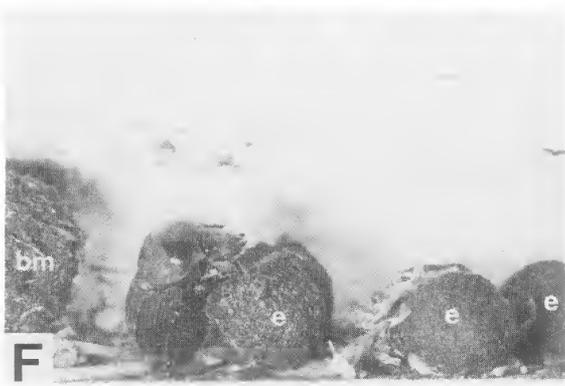
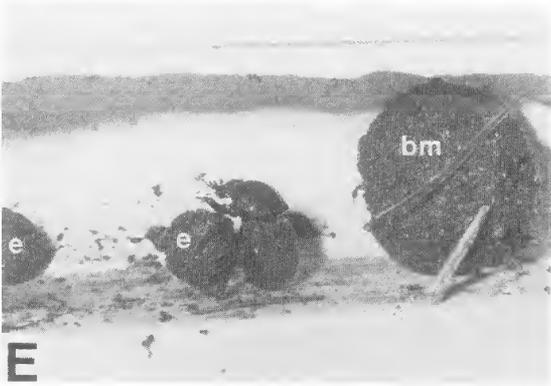
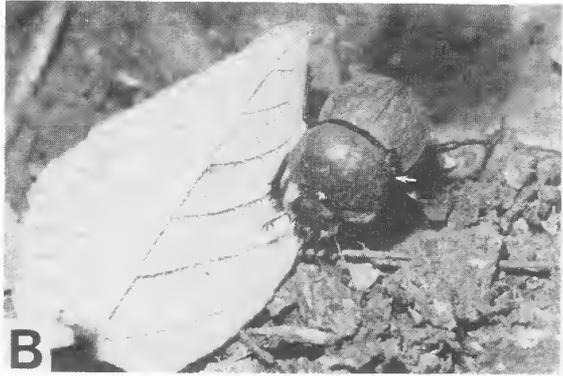


MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE 2.

CEPHALODESMIUS ARMIGER

- A. Typical brood burrow in forest floor showing 'pushup' of soil surrounding entrance.
- B. Foraging male about to drag a green leaf into burrow entrance. Beetle carries a phoretic fly, *Leptocera myrmecophila*, on its prothorax.
- C. Foraging male with phoretic *L. myrmecophila* riding on its back.
- D. Foraging male drags a fallen *Diploglottis* fruit over the edge of a leaf. Two phoretic flies ride on the fruit.
- E. Interior of a plaster artificial nest showing a female beetle shaping a piece of the brood mass (bm) into a sphere which will become an egg ball.
- F. Female beetle hollowing out the inner cavity of a partially finished egg ball (e). Two completed egg balls and the brood mass (bm) are visible.

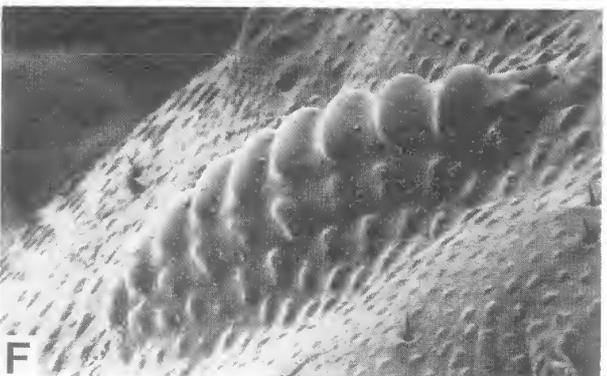
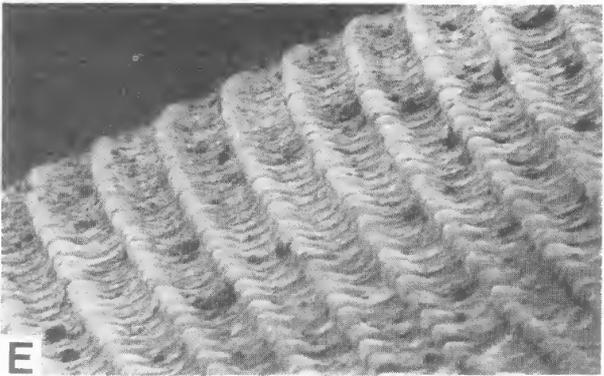
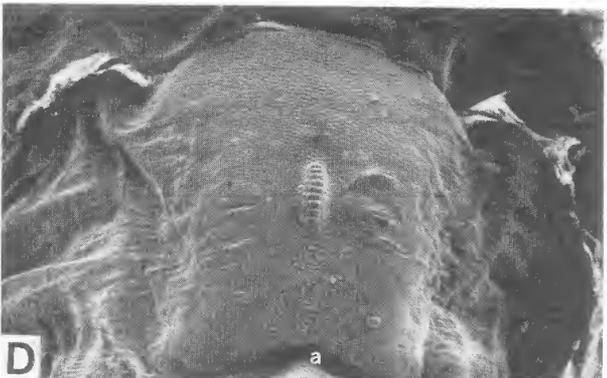
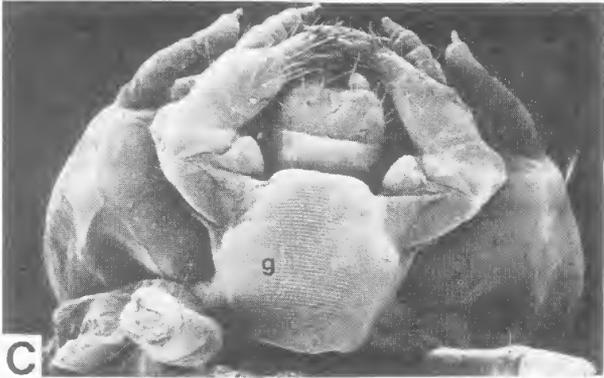


MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE 3.

CEPHALODESMIUS ARMIGER

- A. Foraging male dragging a piece of dead leaf. Phoretic flies, *Leptocera myrmecophila*, ride on the leaf and on the head and thorax of the beetle.
- B. Seven beetles working at night at Tooloom on dingo faeces.
- C. Stereoscan of ventral view of larval head showing area of stridulatory ridges on gula (g).
- D. Stereoscan of last abdominal sternite of larva showing convex stridulatory structure which opposes the gular ridges of the head. Position of the anus (a) is shown.
- E. Detail of gular ridges.
- F. Detail of sternal stridulatory structure.





GEOGARYPUS RHANTUS SP. NOV. (PSEUDOSCORPIONIDA : GARYPIDAE :
GEOGARYPINAЕ); A GENERIC ADDITION TO THE AUSTRALIAN FAUNA.

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ABSTRACT

The pseudoscorpion genus *Geogarypus* is recorded from Australia for the first time. *G. (G.) rhantus* sp. nov. is described from leaf litter collections in the northern part of Cape York Peninsula, Queensland.

INTRODUCTION

The cosmopolitan pseudoscorpionid family Garypidae consists of over a dozen genera. Two subfamilies have been erected to accommodate these genera: the Garypinae and the Geogarypinae (Chamberlin 1930). The Garypinae contains the majority of the genera, only two of which have been recorded from Australia, *Synsphyronus* Chamberlin and *Garypus* L.Koch (Beier 1966). The Geogarypinae is represented by a single genus, *Geogarypus* Chamberlin, which has basically a circum-tropical distribution.

Geogarypus has not hitherto been reported from the Australian continent, even though it seems to be common on islands in the Pacific Ocean and to the north of Australia, including Malaysia, Indonesia and New Guinea (Beier 1957, 1965). Specimens of an undescribed species of this genus were found in leaf litter berlesates from Cape York Peninsula, Queensland. This new species is described in the present paper.

MATERIALS AND METHODS

The specimens were removed from 70% ethanol, treated overnight (15 to 20 hours) with cold 10% potassium hydroxide, washed in distilled water and mounted on microscope slides in Stroyan's modification of Berlese's mountant (Norris and Upton 1974). The chela and chelicera of some specimens were dissected off and mounted separately, the former on cavity slides. This facilitated the inspection of the fine detail of these organs.

All specimens were measured with a micrometer eyepiece on a compound microscope.

Measurements and trichobothrial abbreviations follow those employed by Chamberlin (1931).

All material is lodged in the Queensland Museum.

Genus *Geogarypus* Chamberlin

Geogarypus Chamberlin, 1930: 609. Type species, *Garypus minor* L.Koch, by original designation.

Subgenus *Geogarypus* s.str.

This subgenus may be distinguished from the other subgenera, *Afrogarypus* Beier and *Indogarypus* Beier, by the following combination of characters: absence of dorsal sulcus and internolateral constriction on pedipalpal chela; accessory tooth row present on fixed chelal finger; relatively slender leg segments; trichobothrium *st* of the moveable chelal finger equally spaced between *sb* and *t*.

Geogarypus (Geogarypus) rhantus sp. nov.
(Figs. 1A-F)

MATERIAL EXAMINED

HOLOTYPE: QM S352, ♂, 2.vii.1976, base of Lamond Hill, Iron Range, NE.Q., R.Raven, V.E. Davies.

PARATYPES: QM S652-659, 1 ♂, 3 ♀, 4 tritonymphs, same collection data as holotype. QM S353, S660-667, 5 ♂, 1 ♀, 3 tritonymphs, 27.vii.1976, summit of Lamond Hill, Iron Range, NE.Q., V.E. Davies, R. Raven. QM S351, S647-651, 1 ♂, 2 ♀, 3 tritonymphs, 10-16.xi.1975, Mt Cook (south of Cooktown), NE.Q., R. Raven,

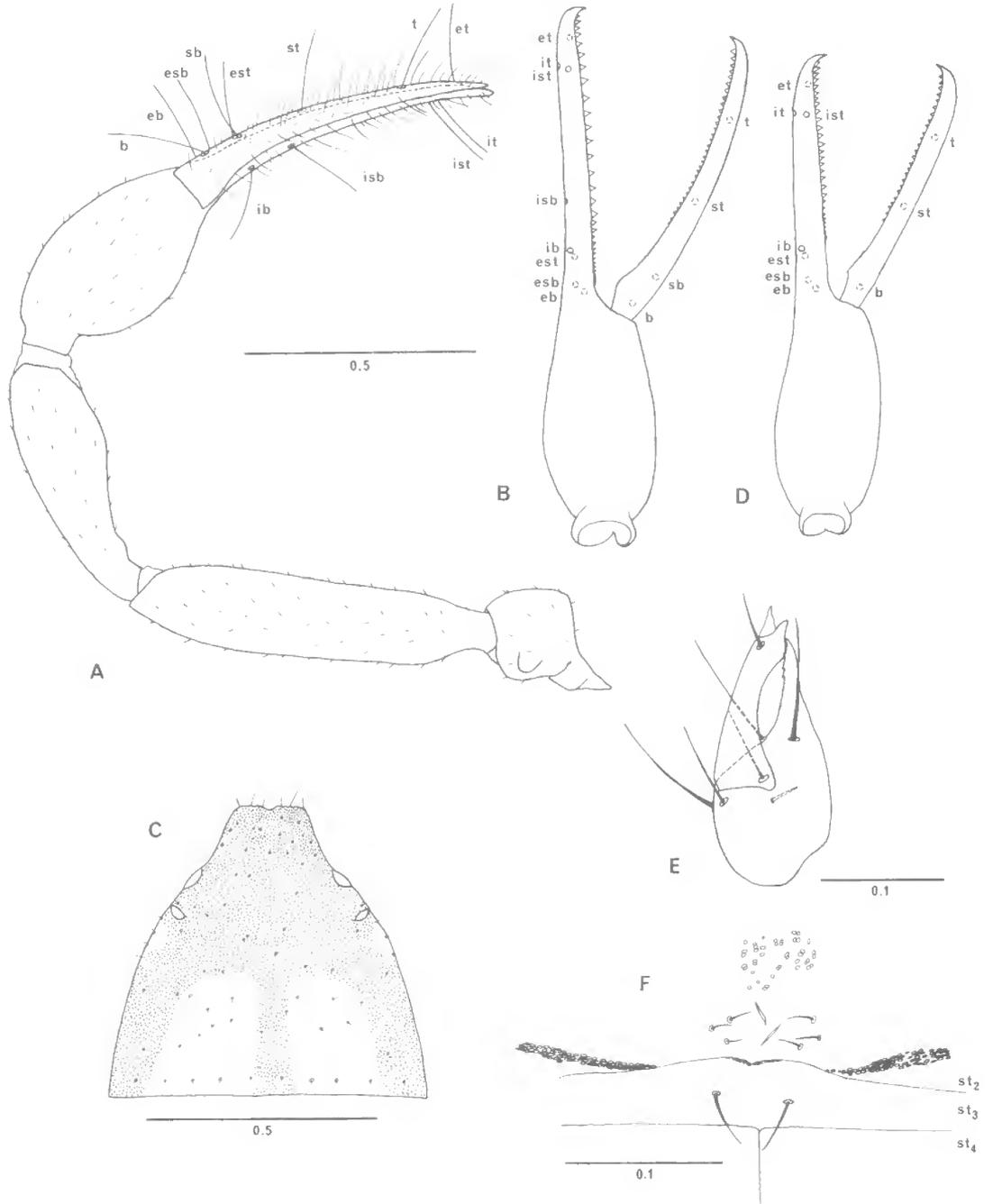


FIG. 1: *Geogarypus (G.) rhantus* sp. nov. A–C, holotype, ♂ S352; A, ventral view of right pedipalp; B, internal lateral view of left pedipalpal chela; C, carapace; D, paratype, tritonymph S656, internal lateral view of left chela; E–F, paratype, ♀ S654; E, left chelicera; F, genitalia. Scale lines in mm.

V.E. Davies. QM S350, 1 ♂, 30.x.-20.xi.1974, Home Rule (near Helenvale), NE.Q., T. Tebble, V.E. Davies, D. Joffe.

DIAGNOSIS

This relatively large geogarypine (femur length 70 to 94 mm) may be distinguished from other members of the genus by carapace mostly brown with small white areas behind eyes and larger white areas laterad of mid-line on posterior half; and chelal trichobothrium *ist* opposite or slightly proximal to *it*.

DESCRIPTION OF ADULTS

Carapace mostly brown with small white areas behind eyes and larger white areas laterad of mid-line on posterior half (Fig. 1C). Pedipalpal coxa brown, trochanter white, femur brown, except for white pedicel, tibia and chela brown. Pedal coxae and trochanter white. Femur I of first pair of legs white; of second pair white distally and proximally, brown medially, all three bands of equal length; of third and fourth pairs white. Femur II, tibia and tarsus I of all legs brown, except for extreme distal end, which is white. Tarsus II of all legs light brown. All terga with brown lateral edges. Terga I and II brown medially; IV to X brown lateromedially; VI to X brown anteromedially; XI brown; the remaining areas white.

Carapace and dorsal side of pedipalpal femur and tibia covered with star-shaped granulations; pedipalpal trochanter, chela and ventral side of femur and tibia covered with lunate ridges, pedal coxae smooth to lightly covered with lunate ridges; all legs rather prominently covered with lunate ridges. Terga reticulate, often coarsely, and sterna smooth to lightly reticulate. Pleural membrane strongly rugose and with sparse setae.

Pedipalpal trochanter 1.43 to 1.53 (♂), 1.40 to 1.48 (♀) times longer than broad. Femur stout, cylindrical, petiolate, slightly concave in the female, 3.59 to 4.73 (♂), 3.63 to 4.54 (♀) times longer than broad. Tibia 2.67 to 3.24 (♂), 2.85 to 3.14 (♀) times longer than broad. Hand ovoid, with pedicel 1.66 to 2.00 (♂), 1.80 to 1.97 (♀) times longer than broad, chela with pedicel 3.39 to 4.07 (♂), 3.67 to 4.13 (♀) times longer than broad. Fingers longer than hand with pedicel, always shorter than femur. Fixed finger with eight trichobothria, moveable finger with four trichobothria (Figs. 1A, B). *it* of fixed finger opposite or slightly distal to *ist*; *isb* closer to *ib* than to *ist*; *ib* opposite *est*; *esb* and *eb* only

approximately two areolar diameters apart. *st* of moveable finger closer to *t* than to *sb*. Fixed finger with 32 to 41 (♂), 21 to 37 (♀) large conical teeth, gradually decreasing in size proximally. Accessory tooth row with 15 to 23 (♂), 12 to 21 (♀) smaller conical teeth. Moveable finger with 18 to 34 (♂), 21 to 37 (♀) retroconical to conical teeth. Nodus ramosus not visible in either finger.

Cheliceral palm with five setae, moveable finger with one seta (Fig. 1E). Flagellum a single blade, 0.02 to 0.03 mm in length. Serrula exterior with 16 to 20 lamellae. Galea simple, slightly curved. Fixed finger with four flattened, retrorse, subapical teeth.

Carapace with four large eyes on small ocular tubercles (Fig. 1C). Anterior pair of eyes slightly larger than posterior pair. Carapace 1.03 to 1.21 (♂), 1.20 to 1.27 (♀) times longer than broad. Hind margin relatively straight, with 7 to 10 (♂), 7 to 11 (♀) setae.

Legs fairly stout. All tarsi segmented, arolium longer than claws.

All setae (except those of fourth coxa of female, which are about 0.14 mm long) small and acicular, about 0.02 mm in length. Setal pattern of male terga I to XI as follows, 7-10:6-9:9-10:8-10:8-11:9-10:8-10:7-10:6-11:4-9:6-10; of female, 7-12:7-12:8-12:10-13:9-12:9-12:7-13:9-12:7-9:4-13. Setal pattern of male sterna I to XI as follows, 0:7-9:12-20:6:9-12:10-14:10-15:10-15:9-14:7-11:0; of female, 0:5-9:0-6:3-9:5-14:13-18:13-17:16-19:11-16:11-12:0. Arranged uniseriately on posterior margin of each segment, except for those associated with genitalia (see below). Coxae of legs I, II, III and IV with 7-9 (♂), 8-13 (♀); 12-16 (♂), 12-19 (♀); 17-29 (♂), 21-33 (♀); and 23-33 (♂), 42-59 (♀) setae, respectively. All spiracles with two setae on anterior guard sclerite, which have not been included in the setae formulae.

Genitalia of male typical of family. Setae of sterna II and III clustered in centre of each segment. Anterior margin of sternum III with generally four, but sometimes three or even two setae on edge of genital operculum. Female with long, tubular, sac-like lateral cribriform plates, arising from a point adjacent to operculum. Median cribriform plates an indefinite cluster (Fig. 1F).

Anus elliptical, subventral, with four setae, anterior pair longer and further apart than posterior pair.

Dimensions (in mm)

When the measurements are expressed as a

fraction, the numerator refers to the length of the character, and the denominator refers to its width. Those in parentheses are the females and follow those of the males.

Body length 1.5–2.0 (2.0–2.3); pedipalps: trochanter .29–.36/.18–.25 (.32–.39/.22–.27), femur .70–.83/.15–.23 (.79–.94/.18–.24), tibia .49–.65/.16–.25 (.58–.67/.18–.24), chela 1.08–1.29/.28–.37 (1.28–1.43/.31–.39), finger length .63–.70 (.73–.80); chelicera .15–.19/.08–.11 (.18–.21/.08–.12), moveable finger length .11–.14 (.11–.15); carapace .58–.68/.64–.82 (.62–.74/.77–.93), cucullus length .12–.20 (.16–.21); leg I: femur I .29–.35/.09–.12 (.31–.38/.10–.13), femur II .16–.21/.08–.11 (.18–.22/.10–.12), tibia .19–.26/.06–.10 (.23–.28/.07–.08), tarsus I .12–.17/.05–.08 (.15–.20/.05–.07), tarsus II .12–.17/.04 (.15–.17/.04–.05); leg IV: femur I .13–.17/.08–.14 (.16–.19/.09–.12), femur II .36–.49/.12–.18 (.47–.57/.14–.19), tibia .26–.36/.07–.10 (.32–.42/.08–.11), tarsus I .17–.21/.05–.07 (.20–.24/.06–.07), tarsus II .15–.20/.04–.05 (.17–.22/.04–.05).

DESCRIPTION OF TRITONYMPHS

Colouration as for adults but much paler.

Pedipalpal trochanter 1.39 to 1.55 times, femur slightly petiolate, 3.21 to 4.45 times, tibia 2.52 to 2.86 times, hand with pedicel 1.73 to 2.08 times, chela with pedicel 3.62 to 4.17 times longer than broad. Fingers slightly longer than hand with pedicel but shorter than femur. Fixed finger with seven trichobothria, moveable finger with three trichobothria (Fig. 1D). *it* of fixed finger opposite *ist*; *ib* and *est* opposite; *esb* slightly distal to *eb*. *st* and *t* of moveable finger slightly closer than *st* and *b*. Fixed finger with 28 to 34 conical teeth, accessory row with 10 to 18 smaller, conical teeth, and moveable finger with 19 to 32 teeth.

Cheliceral palm with five setae, moveable finger with one seta. Flagellum a single blade, 0.02 mm long. Serrula exterior with 15 to 18 lamellae.

Carapace with four eyes (only three on S666), 1.10 to 1.33 times longer than broad. Hind margin with six to seven setae.

Tarsi all segmented, except for S667 which has its left fourth tarsus unsegmented. Arolium longer than claws.

All setae small and acicular. Setal pattern of terga I to XI as follows. 6–8:6–8:6–8:8–9:6–9:7–10:6–9:6–8:6–8:4–7:6; of sterna I to XI, 0:2:2–5:3–7:8–10:8–10:9–12:8–10:6–9:6–8:0.

Coxa of legs I, II, III and IV with 5–9, 7–11, 12–19, and 17–27 setae respectively. All spiracles

with two setae on anterior guard sclerite, which have not been included in the setal formulae. Anus as for adults.

Dimensions (in mm)

Body length 1.6–1.8; pedipalps: trochanter .26–.28/.16–.20, femur .59–.69/.14–.19, tibia .39–.45/.14–.17, chela .94–1.09/.24–.27, moveable finger length .54–.61; chelicera .16–.18/.07–.09; carapace .55–.61/.66–.73, cucullus length .12–.17; leg I: femur I .24–.28/.07–.09, femur II .13–.16/.08–.09, tibia .16–.20/.06–.07, tarsus I .10–.16/.05–.06, tarsus II .13–.15/.04; leg IV: femur I .11–.15/.08–.09, femur II .31–.38/.10–.13, tibia .21–.29/.07–.08, tarsus I .14–.18/.05–.06, tarsus II .13–.17/.04–.06.

ETYMOLOGY

The specific name refers to the star-shaped granulations on the pedipalps and carapace, possibly a generic characteristic (Gr. *rhantos*, sprinkled, spotted).

DISCUSSION

The 15 adults available for study exhibit considerable variation in size, which seems to be correlated with a north-south cline. The larger specimens (pedipalpal femur length: ♂, 0.81 to 0.83; ♀, 0.93 to 0.94) were taken from the southern localities, Mt Cook and Home Rule, while the smaller individuals (including the holotype) (pedipalpal femur length: ♂, 0.70 to 0.74; ♀, 0.79 to 0.84) were taken from Lamond Hill, which is 375 km further NW. This difference is not considered sufficient to warrant the erection of a second species. Further collections are needed to establish the true nature of the possible clinal variation.

G. rhantus is easily distinguished from other members of the genus by the colour pattern of the carapace and by the distribution of the trichobothria. It seems to be most closely allied to *G. elegans* (With) which is known from the Malaysian Peninsula (With 1906).

The new species is the first record of the genus *Geogarypus* from Australia, even though Chamberlin (1930) mentioned that the genus was '... largely Asiatic and Australasian in distribution'. The three garypid genera now known from Australia may be separated by the following key (adapted from Chamberlin 1930);

- 1 Flagellum of one blade; coxae not increasing in width from I to IV (subfamily Geogarypinae).....
.....*Geogarypus*

- Flagellum of more than one blade; coxae increasing in width from I to IV (subfamily Garypinae)2
- 2 (1) Arolium shorter than claws; pedipalpal vestitural setae small and acicular; vitreous pseudoderm absent ...*Garypus*
- Arolium longer than claws; pedipalpal vestitural setae clavate; vitreous pseudoderm present *Synsphyronus*

ACKNOWLEDGMENTS

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THE LOWER JAW OF THE LABYRINTHODONT FAMILY BRACHYOPIDAE

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ABSTRACT

A well preserved labyrinthodont mandible referable to the brachyopid *Brachyops allos* Howie, 1972, has been found in Queensland. Mandibular characteristics not previously reported are the exposure of the articular on the dorsal surface of the retroarticular process, a posterior extension of the angular beneath the retroarticular process, and the presence of relatively few large teeth which curve inwards.

INTRODUCTION

The lower jaw in the brachyopid labyrinthodonts is not well known. *Haddockosaurus bradyi* has the most completely preserved and fully described jaw (Welles, 1947). A labial view of the almost complete jaw of *Bothriceps australis* is figured by Watson (1956). Poorly preserved lower jaws have been assigned to ?*Batrachosuchus* sp. by Watson (1956), *Batrachosuchus concordi* by Chernin (1977), *Blinasaurus henwoodi* by Cosgriff (1969) and *Blinasaurus townrowi* by Cosgriff (1974). Within the superfamily Brachyopoidea Rusconi (1951) has described the lower jaw of *Pelorocephalus* and Bystrow (1938) the lower jaw of *Dvinosaurus*.

In a previous paper (Howie, 1972) I described the skull of a brachyopid labyrinthodont, *Brachyops allos*, from a new locality in the early Triassic Rewan Formation of Queensland. This part of the Rewan Formation is now known as the Arcadia Formation (Jensen, 1975). In a subsequent field trip parts of the left and right mandibles of a brachyopid amphibian were found at the same site as the skull of *Brachyops allos*.

DESCRIPTION

The right mandible QMF10118 consists of the anterior part of the dentary from the symphysis to the anterior border of the adductor fossa, and a small part of the angle of the jaw. The left mandible QMF10119 (Pl.1, Fig.1) lacks a section in the region of the anterior coronoid and most of the angle of the jaw. The missing section in the anterior part of the jaw is probably longer than shown in Fig. 1. The curvature and size of these

lower jaws match the upper jaw of *B. allos* and the teeth of upper and lower jaws are similar in size, shape and number. For these reasons I have referred QMF10118 and QMF10119 to *B. allos*.

Cosgriff (1969) notes that lower jaws of the superfamily Brachyopoidea all have a posterior meckelian foramen and angular-prearticular suture on the ventral surface or very low on the lingual surface. The angular-prearticular suture is mid ventral in *B. allos*, while the posterior meckelian foramen is 2 mm above the ventral

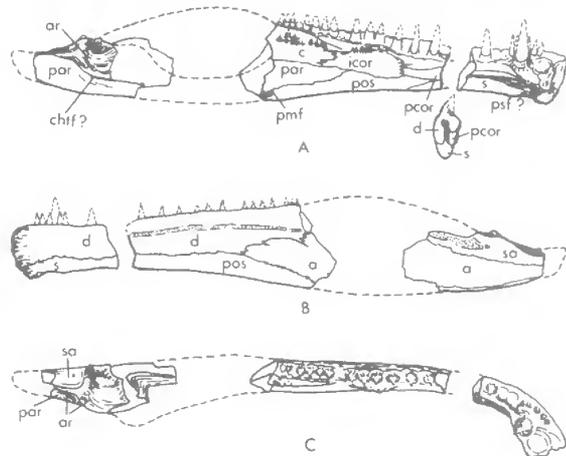


FIG. 1. *Brachyops allos* QMF10119. Reconstruction of left mandible. A, lingual, B, labial, C, dorsal. All x 1. Abbreviations. QMF: Queensland Museum Fossil, UTGD: University of Tasmania Geology Department, a: angular, ar: articular, c: coronoid, d: dentary, icor: intercoronoid, par: prearticular, pcor: precoronoid, pos: postsplenial, psf: postsymphyseal foarmen, s: splenial, sa: surangular.

surface. The jaw is not markedly bowed upwards ventrally as in *Blinasaurus townrowi* Cosgriff (1974) or *Batrachosuchus concordi*, Chernin (1977) but the labial edge of the adductor fossa is bowed dorsally so that the glenoid fossa is set low on the jaw relative to the upper edge of the adductor fossa, a situation found also in *Blinasaurus townrowi*. The jaws are deep in the region of the adductor fossa, but shallow anteriorly with their anterior parts being more rounded in cross section.

The arrangement of the dermal bones of the mandible is typical of that found in other Triassic labyrinthodonts except in the region of the retroarticular process. This is elongate and consists of the prearticular linguallly, and the angular and surangular labially. The most posterior part of the surangular is missing. From above it can be seen that a tongue of the articular extends backwards between the surangular and prearticular — a situation which I found to be present in all brachyopids (see discussion). The dorsal surface of the surangular is not deeply recessed for the depressor mandibulae muscle, and in this the jaw differs from the other brachyopids, especially *Blinasaurus townrowi*.

No well defined chorda tympanica foramen is present, but a break in the bone below the glenoid fossa shows a narrow foramen entering the prearticular and running as a canal below its surface.

LABIAL VIEW. The labial surface of the jaw is ornamented in a ridge-groove pattern which is marked on the angular and surangular, indistinct on the splenial and postsplenial and not present on the dentary except near the symphysis where there is some pitting in the sculpture presumably marking the centre of ossification of the bone. The sensory canal system is represented by an oral sulcus on the surangular and the posterior two thirds of the dentary.

The splenial and postsplenial occupy the lower third of the labial surface. The angular covers less of the labial surface than it does in many labyrinthodonts. Its ventral suture with the prearticular can be seen in a labial view. Posteriorly the angular extends beneath the surangular towards the back of the retroarticular process. The surangular bears a broad section of the oral sulcus below the glenoid.

LINGUAL VIEW. In lingual view the splenial and postsplenial occupy the lower half of the jaw in front of the posterior meckelian foramen. The splenial is separated from the dentary by a groove which is several millimetres deep at the symphysis

but becomes shallow and finally disappears before the splenial meets the postsplenial. An expansion of this groove a centimetre behind the symphysis may be a post-symphyseal foramen. Above the splenial anteriorly is the dentary, while more posteriorly are the three coronoid bones. The precoronoid is small and toothless. The well developed intercoronoid and coronoid project linguallly away from the dentary and both bones bear small labyrinthine teeth. On the posterior border of the coronoid a section of the adductor fossa is preserved.

The anterior part of the prearticular sutures ventrally with the postsplenial and dorsally with the two posterior coronoids. Posteriorly the prearticular occupies the whole of the lingual side of the retroarticular process. The angular is not exposed on the lingual surface.

DENTITION. One symphyseal tusk is present on QMF10118 and one on QMF10119. These are circular in cross section in contrast to the marginal teeth which are elongated across the jaw. In the region of the tusk the marginal teeth are small averaging 2 mm in maximum width at their base. More posteriorly this measurement increases to 4 mm with these larger teeth being found above the pre- and intercoronoids. Above the coronoid the teeth again decrease in size and the most posterior of the teeth preserved are as small as those near the symphyseal tusk. As is usual among the brachyopids the teeth are relatively few in number and many of them are curved inwards. The teeth are attached to the dentary both ventrally and ventrolaterally, a condition which resembles the pleurodont condition often associated with reptiles.

DISCUSSION

The posterodorsal tongue of articular which extends between the surangular and prearticular to the back of the retroarticular process is unusual for Triassic labyrinthodonts but has been seen in the Permian *Trimerorachis* and *Eryops*. The survey below of the other brachyopids shows that this may be present in all of them, presumably as a primitive character retained from Permian ancestors. Watson (1956) labelled the posterior end of the retroarticular process of *Bothriceps australis* as articular and described the retroarticular process as 'made from the articular, covered laterally by the surangular and angular, and mesially by a prearticular...' while in the same paper he describes and illustrates a similar situation in *?Batrachosuchus*. Chernin (1977)

notes that in *Batrachosuchus concordi* the articular extends posteriorly 'to the limit of the retroarticular process', but does not say whether the extension is dorsal, labial, or lingual. No articular has been labelled or described in *Hadrokkosaurus bradyi* by Welles & Estes (1969) while *Blinasaurus henwoodi* was described by Cosgriff (1969) from an internal mould which shows little sutural detail. In April 1980 I examined *Blinasaurus townrowi* material in Hobart and found two specimens in which the articular appears to extend as a posterior tongue between prearticular and surangular. UTGD87805 shows the condition well, while in UTGD85700, although some of the area is covered in plaster, there are indications of a posterior extension of the articular. Illustrations of the lower jaws of members of the brachyopid family Chigutisauridae by Rusconi (1951) show that a posterior extension of the articular may be present but the situation in the family Dvinosauridae cannot be determined from Bystrow's (1938) description. I conclude that this type of retroarticular process is found in the family Brachyopidae but not necessarily throughout the superfamily Brachyopoidea.

The angular of *Brachyops allos* extends to the back of the retroarticular process on the labial side. This is seen also in *Hadrokkosaurus bradyi*, *Blinasaurus henwoodi*, *B. townrowi*, ?*Batrachosuchus* sp. and *Batrachosuchus concordi*, but not in the Chigutisauridae or *Dvinosaurus*.

This description of *B. allos* and subsequent discussion leads to an expansion of previous definitions of the type of mandible found in the family Brachyopidae. The mandible differs from that in other labyrinthodonts in possessing the following combination of characters: retroarticular process elongate, posterior meckelian foramen and angular-prearticular suture on ventral surface or very low on lingual surface, articular exposed on the dorsal surface of the retroarticular process between surangular and prearticular, angular extending posteriorly far along the undersurface of the retroarticular

process, dentition characterised by a relatively few large teeth which are curved inwards.

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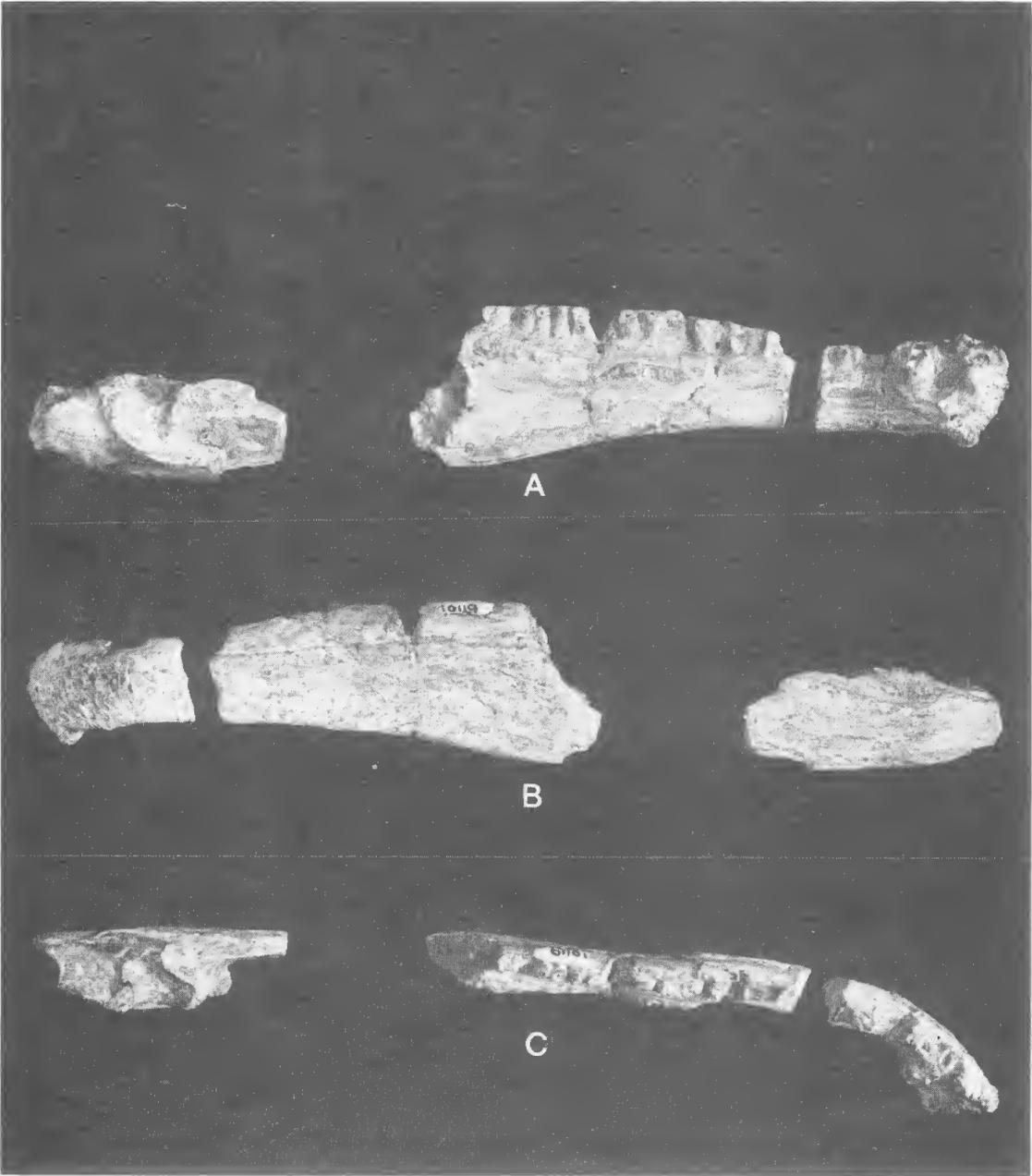
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MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE 1.

BRACHYOPS ALLOS QMF10119.

Left mandible. A, lingual, B, labial, C, dorsal. All x 1.





FROG AND REPTILE TYPE SPECIMENS IN THE QUEENSLAND MUSEUM,
WITH A CHECKLIST OF FROGS AND REPTILES IN QUEENSLAND

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ABSTRACT

Types of 16 species of frogs and 34 species of reptiles added to the Queensland Museum collection since 1971 are listed, together with new information of *Micropechis crucifer* and other De Vis type specimens. A checklist of frogs and reptiles known to occur in Queensland is also presented.

Since the publication of the first list of Queensland frog and reptile type specimens (Covacevich, 1971) there have been many additions to the collections, and several changes in type status and names. In addition the holotype of one species (*Hyla luteiventris* Ogilby, 1907), which was presumed lost from the Queensland Museum in 1971, has been located in the Australian Museum (Cogger, 1979a, p. 174).

Type specimens, descriptions of which have been published prior to the end of June, 1980, are listed by family in alphabetical order under the name by which they were first described, with relevant collection data. An asterisk beside a date indicates that it could be of collection, donation, receipt, or registration. All other dates are of collection.

LIST OF FROG AND REPTILE TYPE
SPECIMENS DEPOSITED IN THE QUEENSLAND
MUSEUM SINCE 1971

AMPHIBIA

MYOBATRACHIDAE

Kyarranus kundagungan Ingram and Corben,
1975 *Mem. Qd Mus.* 17(2): 335–9, pl. 42.

HOLOTYPE: J23944; ♀, Mistake Mountains (800 m), 83 km SW Brisbane, SE.Q., coll. C.J. Corben, A.K. Smyth, 3.i.1974.

PARATYPES: J23945; Mistake Mountains, SE.Q., coll. C.J. Corben, A.K. Smyth, 3.i.1974. J23946; Teviot Falls, SE.Q., coll. G.J. Ingram, 3.i.1974. J22677–81; Cunningham's Gap, coll. G.J. Ingram, C.J. Corben, 26.vi.1973.

Ranidella bilingua Martin, Tyler and Davies,
1980

Copeia, 1980 (1): 93–9.

PARATYPES: J31538; Dead Horse Spring, 1.5 km NE of Lake Argyle Village, NW.W.A., coll. M. Davies, A.A. Martin, M.J. Tyler, 19.ii.1977. J31537; Mitchell Plateau, NW.W.A., coll. M. Davies, A.A. Martin, M.J. Tyler, W.E. Duellman, 27.i.1978.

Ranidella deserticola Liem and Ingram, 1977

Vic. Nat. 94(6): 255–8.

HOLOTYPE: J22654; ♂, Charleville, SW.Q., coll. D.S. Liem, 13.ii.1971.

PARATYPES: J22655; Charleville, SW.Q., coll. D.S. Liem, 13.ii.1971. J25000–2; 42 km E. of Thargomindah, SW.Q., coll. G.J. Ingram, C.J. Corben, 26.xii.1974. J27237; Polygammon Creek on Middleton-Hamilton Hotel Road, SW.Q., coll. C. Corben, A. Smyth, G. Roberts, 27.x.1975. J28925; 130 km E. of Birdsville, SW.Q., coll. R.J. McKay, 1.ix.1976. J31601–3; Thargomindah, SW.Q., coll. R. Raven, 8.xi.1976.

Rheobatrachus silus Liem, 1973

Mem. Qd Mus. 16(3): 467–9, pl. 30.

HOLOTYPE: J22489; ♂, Kondalilla, 3 km SW. Montville (500 m), SE.Q., coll. D.S. Liem, 2.vi.1972.

PARATYPES: J22490–5; Kondalilla, 3 km SW. Montville, SE.Q., coll. D.S. Liem, 30.vi.1972. J22496; as for J22490–5, coll. D.S. Liem, 2.vi.1972. J22497 as for J22490–5, coll. D.S. Liem, 17.v.1972.

Taudactylus eungellensis Liem and Hosmer, 1973

Mem. Qd Mus. 16(3): 445–8.

HOLOTYPE: J22433; ♂, see Table 1.

PARATYPES: J22434–7, J22442–9; Finch Hatton Gorge, 60 km W. of Mackay, ME.Q., coll. D. Liem, 19.v.1972. J22438–41; see Table 1. There are discrepancies in the collection data given for some of these specimens in the Liem field data book, the Queensland Museum register (for which data was supplied verbally by Dr Liem), and the type description. These are set out in Table 1.

Taudactylus liemi Ingram, 1980

Mem. Qd Mus. 20(1): 111–9, pl. 1.

HOLOTYPE: J32625; ♀, Crediton, ME.Q., coll. J. Covacevich, P. Filewood, R. Monroe, 15–22.iv.1975.

PARATYPES: J31515–8; Dalrymple Heights, ME.Q., coll. G. Czechura, 3.vii.1974. J32618–24, J32626–33, J32660–8, J32694; Crediton, ME.Q., coll. J. Covacevich, P. Filewood, R. Monroe, 15–22.iv.1975. J34420; 18 km N. Dalrymple Heights, ME.Q., coll. G.J. Ingram, 7.xii.1978.

Taudactylus rheophilus Liem and Hosmer, 1973

Mem. Qd Mus. 16(3): 450–4, pl. 29.

HOLOTYPE: J22418; ♀, SW slope Mt. Lewis (1200 m), NE.Q., coll. W. Hosmer 29.iv.1972.

PARATYPES: J22419–20, J22426–7, J22429–30; as for holotype. J22421–5, J22428, J22431–2; SW slope, Mt. Lewis (1200 m), coll. W. Hosmer and D. Liem, 27.v.1972.

REMARKS.

Liem and Hosmer (1973) list the date of collection for the holotype as 26.xii.1971. The Liem field data book corresponds with the type description, but not with the Queensland Museum register (29.iv.1972).

PELODRYADIDAE

Cyclorana verrucosus Tyler and Martin, 1977

Rec. S. Aust. Mus. 17(15): 267–9.

HOLOTYPE: J18105; ♀, 18 km W. of Dalby, SE.Q., coll. I.R. Straughan, 8.ii.1964.

PARATYPES: J12274; Brookstead via Pittsworth SE.Q., coll. I.R. Straughan, 17.ii.1964. J18104, J18107; Waratah Station via Cunnumulla, SW.Q., coll. A.K. Lee, 19.i.62. J18108; 21 km E. of Dalby, SE.Q., coll. A.K. Lee, 16.xi.1963. J18109, J18112; Warrawee, near Petrie, SE.Q., coll. I.R. Straughan, 10.ii.1964. J18111; 18 km W. of Dalby, SE.Q., coll. I.R. Straughan, 8.ii.1964. J18114, J18115; Warrawee, near Petrie, SE.Q., coll. I.R. Straughan, 8.i.1964. J18116; 21 km E. of Dalby, SE.Q., coll. I.R. Straughan, 16.xi.1963. J18117; Warrawee, near Petrie, SE.Q., 9.ii.1964.

Litoria cooloolensis Liem, 1974

Mem. Qd Mus. 17(1): 169–74, pl. 5.

HOLOTYPE: J22646; ♂, Lake Coolamera, Cooloola, SE.Q., coll. D.S. Liem, 27.ix.1972.

PARATYPES: J22647–51; Lake Coolamera, Cooloola, SE.Q., coll. D.S. Liem, 27.ix. 1972.

TABLE 1: COLLECTION DATA FOR THE HOLOTYPE AND FOUR PARATYPES OF *T. EUNGELLENSIS* IN THE LIEM FIELD DATA BOOK (D.S.L.), QUEENSLAND MUSEUM REGISTER, AND THE TYPE DESCRIPTION (LIEM AND HOSMER, 1973). ALL SPECIMENS COLLECTED BY D. LIEM.

J register numbers	Collection localities and dates		
	Liem field data book	Queensland Museum register	Liem and Hosmer (1973)
J22433 (DSL 6060)	(pencil) Eungella; (pencil) 24.xi.1971 (ink) Finch Hatton Gorge (ink) 19.v.1972	Finch Hatton Gorge, 19.v.1972 60 km W. of Mackay	Eungella, 75 km 24.xi.1971 W. of Mackay, 900 m
J22438–9 (DSL 4819, 4820)	1 m E. Eungella 19.xii.1971	Eungella, 75 km 19.xii.1971 W. of Mackay	Finch Hatton 24.xi.1971 Gorge, 60 km W. of Mackay
J22440 (DSL 4821)	1 m E. Eungella 24.xi.1971	Eungella, 75 km 24.xi.1971 W. of Mackay	Eungella, 75 km 19.xii.1971 W. of Mackay
J22441 (DSL 6043)	1 m E. Eungella, 18.v.1972 2000'	Eungella, 75 km 24.xi.1971 W. of Mackay	Eungella, 75 km 19.xii.1971 W. of Mackay

Litoria longirostris Tyler and Davies, 1977
Copeia 1977 (4): 620–3.

HOLOTYPE: J26930; ♂, Upper Rocky River, McIllwraith Range, NE.Q., coll. P.S. Lavarack, B. Gray, R.J. Grimes, 26.ix.1975.

PARATYPES: J26931–2; Upper Rocky River, McIllwraith Range, NE.Q., coll. P.S. Lavarack, B. Gray, R.J. Grimes, 26.ix.1975.

Litoria lorica Davies and McDonald, 1979
Trans. R. Soc. S. Aust. 103(7): 169–76.

HOLOTYPE: J36090; ♂, Alexandra Creek near Thornton Peak, NE.Q., coll. J.W. Winter, R.G. Atherton, 10.xii.1976.

PARATYPES: J36091–2; as for holotype. J 36093; Alexandra Creek near Thornton Peak, NE.Q., coll. J.W. Winter, R.G. Atherton, 11.xii.1976.

Litoria nyakalensis Liem, 1974

Mem. Qd Mus. 17(1): 157–60, pl. 4.

HOLOTYPE: J22624; ♂, Henrietta Creek, Palmerston National Park (800 m), NE.Q., coll. D.S. Liem, 17.x.1972.

PARATYPES: J22625–8; as for holotype. J22629–30; Beatrice Creek, Palmerston National Park, NE.Q., coll. D.S. Liem, 29.xi.1971.

Litoria olongburensis Liem and Ingram, 1977 *Vic. Nat.* 94(6): 258–62.

HOLOTYPE: J22652; ♀, Coomboo Lake, Fraser Island, SE.Q., coll. R. Shine, 10.i.1972.

PARATYPES: J22954–5; 3 km from Pt. Lookout on Dunwich Road, North Stradbroke Island, SE.Q., coll. C.J. Corben, G.J. Ingram, 10.iii.1973. J27480; Teewah Creek, Cooloola, SE.Q., C. Corben, A. Smyth, 29.xii.1973. J27493; coll. Teewah Creek, Cooloola, SE.Q., coll. G.J. Ingram, G. Czechura, 30.xii.1973. J27500; Teewah Creek, Cooloola, SE.Q., C. Corben, A. Smyth, -.xi.1973. J28229; Bribie Island, SE.Q., coll. D. Barry, 30.xi.1976. J28230–1; Teewah Creek, Cooloola, SE.Q., coll. G. Ingram, R. Raven, 13.vii.1973.

Litoria rheocolus Liem, 1974

Mem. Qd Mus. 17(1): 152–7, pl.3.

HOLOTYPE: J22631, ♂, Kuranda, 50 km W. Cairns, NE.Q., coll. D.S. Liem, 21.v.1972.

PARATYPES: J22632–4; Kuranda, 50 km W. Cairns, NE.Q., coll. D.S. Liem, 21.v.1972. J22635–9; Bloomfield Road, 50 km SE. Cooktown, NE.Q., coll. D.S. Liem, 14.x.1972. J22640–5; Cape Tribulation, 100 km N. Cairns, NE.Q., coll. D.S. Liem, 11.x.1972. Collection data for J22645 in the Liem field data book and the

type description is Shipton's Flat, 14.x.1972. Tyler and Davies (1978, p. 35) emend the name to *Litoria rheocola*.

MICROHYLIDAE

Cophixalus concinnus Tyler, 1979

Copeia 1979 (1): 118–21.

HOLOTYPE: J30743; ♀, Thornton Peak (1250 m), NE.Q., coll. J. Winter, 15.xi.1973.

PARATYPES: J30744, J30746; as for holotype. J30745; Thornton Peak (1250 m), NE.Q., coll. J. Winter, 12.xi.1973.

Cophixalus saxatilis Zweifel and Parker, 1977

Amer. Mus. Novit. 2614: 1–10.

PARATYPE: J27150; ♂, Black Mountain, via Cooktown NE.Q., coll. C.J. Corben, G.J. Ingram, A. Smyth, 18.xi.1975.

REPTILIA

GEKKONIDAE

Cyrtodactylus galgajuga Ingram, 1978

Vic. Nat. 95(3): 142–6.

HOLOTYPE: J29474; near Black Mtn. (15° 40'–145° 14') Trevethan Ra., 22 km S of Cooktown, NE.Q., coll. G.J. Ingram and D. Miller, 1.i.1977.

Gehyra catenata Low, 1979

Vic. Nat. 96: 190–6.

HOLOTYPE: J15633; ♂, Batheston Station, ME.Q., (22° 26' 148° 47'), coll. J. Covacevich and T.P. Tebble, 12.ix.1968.

PARATYPES: J11532; 23 km S of Barcaldine, SC.Q., coll. A. Bartholomai, 21.v.1963*. J11541–3; 37 km S of Blackall, SC.Q., coll. A. Bartholomai, 21.v.1963*. J11544; 44 km S of Barcaldine, SC.Q., coll. A. Bartholomai, 21.v.1963*. J11776–7; 8 km N of Mitchell, SC.Q., coll. C.J. Limpus 30.x.1962*. J13003–5; 160 km N of Clermont, ME.Q., coll. A. Bartholomai and T.P. Tebble, 9.vi.1964*. J24945; 15 km SSW. of Barmount, ME.Q., coll. T. Low, 11.xii.1974. J28793–5; 16 km E of Barcaldine, SC.Q., coll. T. Low, 6–10.vii.1976. J28839–40; 30 km E of Barcaldine, SC.Q., coll. T. Low, 6–10.vii.1976. J30257–9; 30 km E of Barcaldine, SC.Q., coll. T. Low, -.vii.1976. J30263–4; hwy 1, 125 km S of Mackay, ME.Q., coll. T. Low, 3.xi.1977.

Localities for nine paratypes given in the type description differ from those in the register. Most differences are minor ones of distance but for J28839–40 and J30257–9 there are major anomalies (e.g. 30 km E of Barcaldine vs 15 km SSW of Barmount).

Phyllurus caudiannulatus Covacevich, 1975
Mem. Qd Mus. 17(2): 297–300, fig. 4 pls 36–40.
 HOLOTYPE: J15619; ♂, Bulburin S.F., via Many Peaks, ME.Q., coll. J. Covacevich, T.P. Tebble, 3.ix.1968.
 PARATYPES: J22286–7; Granite Ck. Bulburin S.F. via Many Peaks, ME.Q., coll. G.B. and S.R. Monteith, 1.iv.1972. J24132; Forest Station, 700 m, Bulburin S.F., via Many Peaks, ME.Q., coll. S.R. Monteith, 29.iv.1974. J25411; Eungella National Park, via Mackay, ME.Q., coll. K. McDonald, -xi.1975.

Phyllurus salebrosus Covacevich, 1975
Mem. Qd Mus. 17(2): 300–2, fig. 4, pls 36–40.
 HOLOTYPE: J8142; ♂, Monto, SE.Q., coll. G. O'Connor, 28.viii.1951*.
 PARATYPES: J2879; Roma, SC.Q., coll. H. Hare, -iii.1915*. J4474; Coongoola, Colosseum, ME.Q., coll. W.H. Edwards, -.1926* J4897; Coomoboolaroo Station, via Duaringa, ME.Q., coll. C.A. Barnard, 11.vi.1929*. J5390; Goodnight Scrub, Wallaville, SE.Q., coll. B.A. Shaw, 1.viii.1932*. J6198; Goodnight Scrub, Wallaville, SE.Q., coll. S. Bow, 26.v.1937*. J6382; roof of cave, Cracow Creek, Cracow, ME.Q., coll. T.B. Rigby, -ii.1938*. J8377; Injune, ME.Q., coll. E. Sellens, 29.viii.1952* J9770; Lowmead, ME.Q., coll. 9.iv.1957*. J22288; Bulburin S.F., via Many Peaks, ME.Q., coll. G.B. and S.R. Monteith, 1.iv.1972.

Collectors and dates not included in original description. J4474 is from Coongoola, Colosseum, ME.Q., not Coongoola, near Cunnamulla, SC.Q., as indicated in the original description.

PYGOPODIDAE

Aprasia parapulchella Kluge, 1974
Misc. Publ. Mus. Zool. Univ. Mich. 147: 53–5, 189.
 PARATYPE: J22308; Coppins Crossing, 5.25 km WN.W. Canberra along Molonglo R., A.C.T., coll. A.G. Kluge, R.E. Barwick, R. Jenkins, 20.xii.1971.

Aprasia pseudopulchella Kluge, 1974
Misc. Publ. Mus. Zool. Univ. Mich. 147: 56–7, 189.
 PARATYPE: J9761; between Sevenhill and Clare, S.S.A., coll. B.B. Lowery, 13.vi.1957*.

Delma borea Kluge, 1974
Misc. Publ. Mus. Zool. Univ. Mich. 147: 81–2, 192.
 PARATYPES: J2261–2; Port Darwin, N.T., coll.

G.F. Hill, 20.ii.1915*. J21775; Mt. Erskine, W.A., coll. L. Marshall, 23.vi.1971.

Delma plebeia De Vis, 1888
Proc. Linn. Soc. N.S.W. 2: 825–6.
 LECTOTYPE: J254; restricted type locality Brisbane, SE.Q. See Covacevich, 1971, p. 55 and Kluge, 1974, p. 121.
 PARALECTOTYPES: J12768–70; Brisbane or Gympie, SE.Q. See Covacevich, 1971, p. 55.

Delma tincta De Vis, 1888
Proc. Linn. Soc. N.S.W. 2: 824–5.
 LECTOTYPE: J241; restricted type locality Normanton, NW.Q. See Covacevich 1971, p. 55 and Kluge, 1974, p. 123.

Delma torquata Kluge, 1974
Misc. Publ. Mus. Zool. Univ. Mich. 147: 125–7, 196.
 HOLOTYPE: J14365, Upper Brookfield, SE.Q., coll. E.J. Nielsen, 7.xi.1967.
 PARATYPES: J5683; Crow's Nest, SE.Q., coll. A. MacDiarmid, 14.ix.1934*. J9285; Pomona, SE.Q., coll. L. Brockhurst, 27.viii.1956*. J21220; Kenmore, SE.Q., coll. T. Low, 8.vi.1971*.

SCINCIDAE

Anomalopus pluto Ingram, 1977
Vic. Nat. 94: 52–3.
 HOLOTYPE: J26261; McDonald Crossing, Cockatoo Ck., 115 km S of Bamaga, Cape York, coll. L. Webb, G. Monteith, and G. Ingram, 14.vii.1975.

Carlia amax Storr, 1975
Rec. W.A. Mus., 1974, 3(2): 160–2.
 PARATYPES: J2246; Port Darwin, N.T., coll. G.F. Hill, 16.v.1915*. J23971–2 (formerly WAM R23199–200); Pine Ck., N.T., coll. G.M. Storr, 12.ix.1964.

Carlia dogare Covacevich and Ingram, 1975
Vic. Nat. 92: 21–2, pl.1b.
 HOLOTYPE: J20557; 5–6 km N mouth of McIvor R., NE.Q., 15° 8' 145° 15' coll. C. Tanner, J. Covacevich, T. Tebble, 20.xi.1970.
 PARATYPES: J20436–42, J20444–6; Lizard Is., NE.Q., coll. J. Covacevich, 9–13.xii.1970. J20451–55; Watson's Bay, Lizard Is., NE.Q., coll. J. Covacevich, 8–12.xii.1970. J20507, J20545–6, J20548; nr mouth of McIvor R. NE.Q., coll. J. Covacevich, T. Tebble, C. Tanner, 18.xi.1970. J20556, J20558–J20563; 5–6 km N of mouth of McIvor Rd., NE.Q., coll. J. Covacevich, C. Tanner, T. Tebble, 20.xi.1970. J20617–9; near

mouth McIvor R., NE.Q., coll. J. Covacevich, T. Tebble, 18.xi.1970. J20621-6; 8 km N of mouth of McIvor R., NE.Q., coll. J. Covacevich, T. Tebble, 19.xi.1970. J20652; 3.5 km N of mouth of McIvor R., NE.Q., coll. J. Covacevich, T. Tebble, C. Tanner, 17.xi.1970. J20749-50; Cape Flattery, NE.Q., coll. C. Tanner, no date.

Carlia gracilis Storr, 1975

Rec. W.A. Mus., 1974, 3(2): 158-9.

PARATYPES: J23975-6 (formerly WAM R23529-30); Casuarina Beach, 12.5 km NNE of Darwin, N.T., coll. G.M. Storr, A.M. Douglas, 18.ix.1964.

Carlia jarnoldae Covacevich and Ingram, 1975

Vic. Nat. 92: 19-21, pl. 1a

HOLOTYPE: J20739; Wakooka Outstation, Starcke Station, NE.Q., 14° 33' 144° 33', coll. J. Covacevich, C. Tanner, and T. Tebble, 27.xi.1970. PARATYPES: J7782, J7784; Stannary Hills, near Herberton, NE.Q., coll. T.L. Bancroft, no date. J14031-3; as for J7782. J17820; Isabella Falls, 32 km N.W. of Cooktown, NE.Q., coll. J. Covacevich and T. Tebble, 4.x.1969. J17821; 16 km N.W. of Cooktown, NE.Q., coll. J. Covacevich and T. Tebble, 7.x.1969. J18036-7; Chillagoe area, NE.Q., coll. J. Wertz, 4.xii.1969. J19407-8, J19411; Mt. Molloy, NE.Q., coll. F. Little, no date. J20513; Melville Range, Cape Melville, NE.Q., coll. J. Covacevich, T. Tebble, C. Tanner, 30.xi.1970. J20543; Wakooka Outstation, Cape Melville, NE.Q., coll. J. Covacevich, T. Tebble, C. Tanner, 30.xi.1970. J20738; Wakooka Outstation, Cape Melville, NE.Q., coll. J. Covacevich, T. Tebble, C. Tanner, 27.xi.1970. J20760-1, J20765; 3.2 km from Wakooka on C. Melville road, NE.Q., coll. J. Covacevich, T. Tebble, C. Tanner, 26.xi.1970. J23443-6, J23448, J23464; 5-6 km W of Rokeby homestead, via Coen, NE.Q., coll. C. Tanner, J. Covacevich, 30.v.1973. J23453, J23455; foothills Mt. Fraser, via Mt. Molloy, NE.Q., coll. C. Tanner, J. Covacevich, 12.v.1973.

Carlia johnstonei johnstonei Storr, 1975

Rec. W.A. Mus. 1974, 3(2): 162-5.

PARATYPES: J23977-8 (formerly WAM R44268-9); Mitchell Plateau, W.A., 14° 53' 125° 49', coll. W.H. Butler, 4.viii.1973.

Carlia prava Covacevich and Ingram, 1975

Vic. Nat. 92: 22, pl. 1c.

HOLOTYPE: J14101; ♂, Magnificent Ck., Kowanyama (Mitchell River Mission), 15° 18' 141° 44', coll. P. Graf, 19.x.1965*.

PARATYPES: J14094-7, J14099, J14100, J14102-3, Magnificent Ck., Kowanyama (Mitchell River Mission), 15° 18' 141° 44', coll. P. Graf, 18.x.-4.xi.1965*.

Carlia rimula Ingram and Covacevich, 1980
'Contemporary Cape York Peninsula'

Roy. Soc. Qd 1979 Symposium Proceedings, 46-7.

HOLOTYPE: J24602; Second Claudie River Crossing, Iron Range Road, via Coen, NE.Q. (12° 44' 143° 13'), coll. G.J. Ingram, 1.x.1974.

PARATYPES: J24603-7; as for holotype. J26299; 13 km S of Coen, coll. G.J. Ingram, 18.vii.1975. J26280-3; 5 km along Lankelly Ck. from Coen, coll. G.J. Ingram, 16.vii.1975. J31810; 7 km N of Pascoe R. mouth, NE.Q., coll. G.J. Ingram, 23.xi.1977. J31812; 5 km N Pascoe R. mouth, NE.Q., coll. G.J. Ingram, 21.xi.1977. J34476-7; Buthen Buthen, Nesbit R., NE.Q., coll. G.V. Czechura, -.viii.1978.

Carlia rufilatus Storr, 1975

Rec. W.A. Mus. 1974, 3(2): 157.

PARATYPES: J2619-20; Darwin, N.T., coll. G.F. Hill, ?17.xi.1915*. J7789; Darwin, N.T., coll. G.F. Hill, 1948*. J23973-4 (formerly WAM R23123-4); 37 km SE. of Kununurra, W.A., coll. G.M. Storr, A.M. Douglas, coll. 8.ix.1964.

Carlia scirtetis Ingram and Covacevich, 1980
'Contemporary Cape York Peninsula'

Roy. Soc. Qd 1979 Symposium Proceedings, 46-7

PARATYPES: J21369-70; Black Mountain, Black Trevethan Range, approx. 20 km S of Cooktown, NE.Q., coll. F. Parker, C. Tanner, 22.ii.1971. J25160; Black Mountain, Black Trevethan Range, coll. D. Joffe and J. Covacevich, 5.xi.1974. J25935; Black Mountain, Black Trevethan Range, coll. J. Covacevich, no date.

Cryptoblepharus carnabyi Storr, 1976

Rec. W.A. Mus. 4(1): 60-1.

PARATYPES: J30924-5 (formerly WAM R18263, R18267); Hamelin Pool, W.A., coll. —, 19.ii.1962. J30926 (formerly WAM R39031); S end of Bellefin Prong, E. coast of Carrarang Station, W.A., coll. A. Baynes, 24.viii.1970. J30927 (formerly WAM R42368); Dirk Hartog Is., W.A., coll. —, -.ix.1972.

Cryptoblepharus fuhni Covacevich and Ingram, 1978.

Mem. Qd Mus. 18(2): 151-4, fig. 1.

HOLOTYPE: J20566; Melville Ra., Cape Melville

NE.Q. (14° 16' 144° 30'), coll. J. Covacevich, C. Tanner, T. Tebble, 30.xi.1970.

PARATYPES: J20515-6, J20567-71; as for holotype.

Ctenotus hebetior Storr, 1978

Rec. W.A. Mus. 6(3): 328-30.

HOLOTYPE: J28374; 5 km NW. Fermoy, C.Q., 23° 09' 143° 00', coll. G. Harold, M. Peterson, 8.xi.1976.

Ctenotus lateralis Storr, 1978

Rec. W.A. Mus. 6(3): 323-5, pl. 1.

HOLOTYPE: J28372; 14 km N.Mt. Isa NW.Q., 20° 37' 139° 32', coll. G. Harold, M. Peterson, 20.xi.1976.

Ctenotus pulchellus Storr, 1978

Rec. W.A. Mus. 6(3): 326-8, pl. 2.

HOLOTYPE: J28375; 72 km NN.E. Mt. Isa, NW.Q., 20° 19' 139° 47', coll. G. Harold, M. Peterson, 21.xi.1976.

Ctenotus quinkan Ingram, 1979

J. Herp. 13(3): 280-1.

HOLOTYPE: J28353; 30.4 km SW Laura (15° 42' 144° 36'), NE.Q., coll. G.J. Ingram, D. Miller, G.J. Roberts, 5.i.1977.

Ctenotus rawlinsoni Ingram, 1979

J. Herp. 13(3): 279-80.

HOLOTYPE: J32398; 36 km N. Hopevale Community (15° 7' 145° 15'), coll. G.J. Ingram, 14.vii.1976.

PARATYPES: J32397, J32401-2, J32409; as for holotype. J32397, coll. G. Tracey.

Ctenotus striaticeps Storr, 1978

Rec. W.A. Mus. 6(3): 330-1, pl. 4.

HOLOTYPE: J28373; 72 km NN.E. Mt. Isa, NW.Q., 20° 19' 139° 47', coll. G. Harold, M. Peterson, 21.xi.1976.

Lampropholis tetradactyla Greer and Kluge, 1980

Occ. Pap. Mus. Zool. Univ. Mich. 196: 2-12.

HOLOTYPE: J29853; vicinity of Smoko Ck. at Kennedy Kirrama Road, Kirrama S.F., NE.Q., coll. A. and P. Greer, 8.vi.1976.

PARATYPES: J24814; Sugar Cane Ck., approx. 7 km due W of South Mission Beach, coll. G. Monteith, 4.ix.1974. J28183-6; Paluma, near Townsville, NE.Q., coll. D. Taplin, no date.

Lerista ameles Greer, 1979

Rec. Aust. Mus. 32(10): 383-6.

HOLOTYPE: J30004; 19.7 km W junction Kennedy and Gulf Highways along Gulf Highway, NE.Q., coll. A.E. Greer, 22.vi.1977.

Lygosoma devisii Boulenger, 1890

Proc. Zool. Soc. Lond. 1890: 79.

HOLOTYPE: J234.

This specimen is also the holotype of *Heteropus lateralis* De Vis, 1885 because *L. devisii* is a replacement name for *H. lateralis*. See Covacevich, 1971, p. 56 for collection data.

Lygosoma waitei Zietz, 1920

Rec. S. Aust. Mus. 1(3): 211.

LECTOTYPE: J248.

PARALECTOTYPES: J13719-22.

These specimens are also the types of *Heteropus vertebralis* De Vis 1888, because *L. waitei* is a replacement name for *H. vertebralis*. See Covacevich, 1971, p. 57 for collection data.

Menetia maini Storr, 1976

Rec. West. Aust. Mus. 4(2): 198-9.

PARATYPE: J28377 (formerly WAM R20346); Derby, NW. W.A., coll. P. Slater, -.xi.1961.

Menetia surda Storr, 1976

Rec. West. Aust. Mus. 4(2): 196-8.

PARATYPE: J28376 (formerly WAM R48203); 20 km NN.W. of Tenindewa, W.A., no date.

Menetia timlowi Ingram, 1977

Vic. Nat. 94: 185-6.

HOLOTYPE: J24940; Barmount, 80 km NW of Marlborough, ME.Q., coll. T. Low, 12.xii.1974.

PARATYPES: J24448; Magnetic Is., NE.Q., coll. T. Low, -.vii.1974. J26147; 7 km N of Chinchilla, SE.Q., coll. G. Czechura, G. Ingram, W. Gaynor, 28.viii.1975.

Menetia zynja Ingram, 1977

Vic. Nat. 94: 186-7.

HOLOTYPE: J24454; Mt. Unbunmaroo, 90 km NW of Boulia, W.Q. (22° 32' 140° 18'), coll. A. Elliot, 30.vi.1974.

REMARKS: Rankin (1979, p. 495-6) has placed *M. zynja* in the synonymy of *Menetia maini* Storr, 1976. Label attached to specimen gives 'Black Mountain' as its locality. Black Mountain and Mt. Unbunmaroo are the same locality.

Sphenomorphus amplus Covacevich and McDonald, 1980

Mem. Qd Mus. 20(1): 97–8.

HOLOTYPE: J26054; Finch Hatton Ck., Eungella National Park, ME.Q., coll. K.R. McDonald, 7.ii.1975.

PARATYPES: J31647; Eungella Hotel Grounds, ME.Q., coll. K.R. McDonald, P. Wilson, 10.i.1976. J31648; Broken R., Eungella N.P., ME.Q., coll. K.R. McDonald, J. Miller, 14.i.1976. J31649; Wishing Pool, Eungella N.P., coll. V.R.J. Hansen, K.R. McDonald, 7.i.1976. J31650–2; Finch Hatton Gorge, Eungella N.P., coll. V.R.J. Hansen, K.R. McDonald, 15.i.1976. J31653; Finch Hatton Gorge, coll. V.R.J. Hansen, 2.ix.1975. J31654; Finch Hatton Gorge, coll. V.R.J. Hansen, 13.viii.1975 (description 13.ix.1975). J31655; Finch Hatton Gorge, coll. K.R. McDonald, V.R.J. Hansen, 15.i.1976. J31656; Finch Hatton Gorge, coll. K.R. McDonald, J. James, 17.iii.1975. J31657; Finch Hatton Gorge, coll. V.R.J. Hansen, 25.iii.1975. J31658; Finch Hatton Gorge, coll. K.R. McDonald, V.R.J. Hansen, 17.ii.1975. J31659; Finch Hatton Gorge, coll. K.R. McDonald, V.R.J. Hansen, 15.i.1976. J31660; Finch Hatton Gorge, coll. V.R.J. Hansen, 21.vii.1975. J31661–73; Finch Hatton Gorge, coll. K.R. McDonald, V.R.J. Hansen, 5.i.1976. J32784–5; Brandy Ck., Conway State Forest, via Proserpine, ME.Q., coll. J. Covacevich, R. Monroe, P. Filewood, 22–29.iv.1975 (description 19–22.iv.1975). J33980, J33983; Finch Hatton Gorge, coll. R. Monroe, J. Covacevich, P. Filewood, 7–14.iv.1975. J33984; Finch Hatton Gorge, coll. V.R.J. Hansen, 8.iv.1975. J33985, J34022–3, J34026–9, J34034–5, J34061, J34084; Finch Hatton Gorge, coll. J. Covacevich, R. Monroe, P. Filewood, 7–14.iv.1975.

Sphenomorphus fuscicaudis Greer, 1979

Rec. Aust. Mus. 32(9): 373–83.

HOLOTYPE: J25218; top of Mt. Finnigan (3700'), Mt. Finnigan N.P., NE.Q., coll. J. Covacevich, K. McDonald, 9.xi.1974.

PARATYPES: J15807; Crystal Cascades, nr. Cairns, NE.Q., coll. J.M. Wertz, 1968. J22666; Big Tableland (approx. 2300'), approx. 20 km SE Cooktown, NE.Q., coll. C. Tanner, J. Covacevich, 3.i.1972. J25220; just W of Obree Point, E of Home Rule, NE.Q., coll. K. McDonald, J. Covacevich, 17.xi.1974; J25221; near 'The Granites' via Home Rule, NE.Q., coll. K. McDonald, J. Covacevich, 17.xi.1974. J25135; Mt. Finnigan N.P. (2600'), NE.Q., coll. K.

McDonald, J. Covacevich, 10.xi.1974. J25142, J25144–5; slopes of Mt. Hartley, NE.Q., coll. T. Tebble, V. Davies, J. Covacevich, 30.x.1974. J25273; Mt. Hartley, NE.Q., coll. V. Davies, D. Joffe, J. Covacevich, 6.xi.1974. J25288; nr. Home Rule, on track to 'The Granites', NE.Q., coll. K. McDonald, J. Covacevich, 11.xi.1974. J29074–5; 'A' road, Danbulla S.F., 17° 7' 145° 38' (720 m), NE.Q., coll. C. Limpus, 4.ix.1974. J29706; Lake Eacham N.P., NE.Q., coll. D.J. Duncan, 19.ix.1974. J29077; Lake Eacham N.P., coll. K. McDonald, D.J. Duncan, 21.ix.1974.

Sphenomorphus luteilateralis Covacevich and McDonald, 1980

Mem. Qd Mus. 20(1): 96–7.

HOLOTYPE: J31685; Eungella National Park (21° 03' 148° 35'), ME.Q., coll. K.R. McDonald, D. Vlasak, 9.i.1976.

PARATYPES: J31674–J31684, J31686, J31690–J31697; as for holotype. J31687–8; as for holotype, coll. J. James, K. McDonald, 15.iii.1975. J31689; as for J31687, 14.iii.1975.

NEW INFORMATION ON DE VIS TYPE SPECIMENS

Hyla irrorata De Vis, 1885

Proc. Roy. Soc. Qd 1: 128–9.

(=*Litoria caerulea* (Shaw) after Covacevich, 1974).

NEOTYPE: J9255; Dalby, SE.Q., donor Northern Downs News.

REMARKS:

Both Fry (1912) and Copland (1962) presumed the types of *H. irrorata* were lost. Copland (1962) designated J9255 the neotype of *H. irrorata*. Covacevich (1971) located eleven possible type specimens of *H. irrorata*. Subsequently, Covacevich (1974) has shown that the 'syntypes' could not be type specimens but that they were identified as *H. irrorata* by De Vis.

Calyptopymnus verecundus De Vis, 1905

Ann. Qd Mus. 6: 46–7, pl. 15.

HOLOTYPE: J462; see Covacevich, 1971, p. 60 for original data.

Moody (1977, p. 759–60) has recently examined and redescribed the holotype of *C. verecundus*. He has reassigned it to *Cordylus cordylus* Cuvier and restricted the type locality of *C. verecundus* to 'the Cape region of South Africa'.

Micropechis crucifer De Vis, 1905
Ann. Qd Mus. 6: 52.

HOLOTYPE: J197; see Covacevich 1971, p. 64 for data.

In attempting to resolve the question of the identity of *Micropechis crucifer*, knowing that two other De Vis type specimens from the 'Solomon Is' and the 'Darling Downs' — *Calyptoprymnus verecundus* and *Tropidechis dunensis* (after Moody, 1977 and Cogger, 1966) — were in fact African species, we sent photographs of the holotype of *M. crucifer* to Dr. Donald Broadley of Umtali Museum, Rhodesia. He suggested (*in litt.* 7th July, 1977) that, from the photographs, *M. crucifer* most closely resembled *Elaps lacteus* (Linnaeus), a South African snake.

Covacevich (1971) has noted measurements and scale counts given by De Vis fit those of J197 (the holotype of *M. crucifer*) reasonably well. The subcaudals of J197 are described by De Vis as being divided. They are single. In *Elaps lacteus* these scales are single. Descriptions of *Elaps lacteus* by Boulenger (1896) and Fitzsimmons (1962) and of *Micropechis crucifer* De Vis, 1905 are compared in Table 2.

In the light of Dr. Broadley's suggestion, and from these data, we suggest that *Micropechis crucifer* De Vis is a junior subjective synonym of *Elaps lacteus* (Linnaeus).

CHECKLIST OF QUEENSLAND SPECIES
 OF FROGS AND REPTILES

The following list of 90 species of frogs and 336 species of reptiles recorded from Queensland prior to June, 1980 has been prepared in response to many enquiries about species present and their authors. The family classifications of Savage (1973) for frogs and Smith, Smith, and Sawin (1977) for snakes have been followed.

This list is based essentially on Queensland Museum records and on the work of Cogger (1979b). Some exceptions to this are based on more recent literature (e.g. Ingram, 1980 for *Taudactylus* and Covacevich and McDonald, 1980 for *Sphenomorphus amplus* and *S. luteilateralis*). Others, inclusions in or exclusions from the list, are based on new, but as yet unpublished information (e.g. Czechura, Ingram and Liem for *Nyctimystes dayi* and Menzies and Ingram for *Litoria genimaculata*).

AMPHIBIA

ANURA

MYOBATRACHIDAE

Adelotus Ogilby 1907

A. brevis (Günther 1863)

TABLE 2: A COMPARISON OF *ELAPS LACTEUS* and *MICROPECHIS CRUCIFER*.

Characters	<i>Elaps lacteus</i>		<i>Micropechis crucifer</i> De Vis 1905
	Boulenger, 1896	Fitzsimmons, 1962	
midbody scales	15	15	15
ventrals	160–209	(♂♂) 160–190 (♀♀) 184–209	185
anal	divided	divided	divided
subcaudals	26–42	(♂♂) 34–41 (♀♀) 25–33	29
preocular	1	1	1
postocular	1	1	1
upper labials	6 3 and 4 enter orbit	6 3 and 4 enter orbit	6 3 and 4 enter orbit
lower labials	first 3 in contact with chin shields	first 3 in contact with anterior sublinguals	first 3 in contact with chin shields

- Assa* Tyler 1972
A. darlingtoni (Loveridge 1933)
- Kyarranus* Moore 1958
K. kundagungan Ingram & Corben 1975
K. loveridgei (Parker 1940)
- Lechriodus* Boulenger 1882
L. fletcheri (Boulenger 1890)
- Limnodynastes* Fitzinger 1843
L. convexiusculus (Macleay 1877)
L. fletcheri Boulenger 1888
L. peronii (Duméril & Bibron 1841)
L. salmini Steindachner 1867
L. tasmaniensis Günther 1858
- Mixophyes* Günther 1864
M. balbus Straughan 1968
M. fasciolatus Günther 1864
M. iteratus Straughan 1968
M. schevilli Loveridge 1933
- Neobatrachus* Peters 1863
N. centralis (Parker 1940)
N. sudelli (Lamb 1911)
- Notaden* Günther 1873
N. bennetti Günther 1873
N. melanoscaphus Hosmer 1962
N. nichollsi Parker 1940
- Platyplectrum* Günther 1863
P. dumerilii (Peters 1863)
P. ornatus (Gray 1842)
P. terraereginae (Fry 1915)
- Pseudophyrne* Fitzinger 1843
P. coriacea Keferstein 1868
P. major Parker 1940
- Ranidella* Girard 1853
R. deserticola Liem & Ingram 1977
R. parinsignifera (Main 1957)
R. remota Tyler & Parker 1974
R. signifera (Girard 1853)
R. tinnula (Straughan & Main 1966)
- Rheobatrachus* Liem 1973
R. silus Liem 1973
- Taudactylus* Straughan & Lee 1966
T. acutirostris (Andersson 1916)
T. diurnus Straughan & Lee 1966
T. eungellensis Liem & Hosmer 1973
T. liemi Ingram 1980
T. rheophilus Liem & Hosmer 1973
- Uperoleia* Gray 1841
U. laevigata Keferstein 1867
U. marmorata Gray 1841
U. rugosa (Andersson 1916)
- PELODRYADIDAE
- Cyclorana* Steindachner 1867
C. alboguttatus Günther 1867
C. australis (Gray 1842)
- C. brevipes* (Peters 1871)
C. cultripes Parker 1940
C. dahlii (Boulenger 1895)
C. novaehollandiae Steindachner 1867
C. platycephalus (Günther 1873)
C. verrucosus Tyler & Martin 1977
- Litoria* Tschudi 1838
L. bicolor (Gray 1842)
L. barringtonensis (Copland 1957)
L. brevipalmata Tyler, Martin & Watson 1972
L. caerulea (Shaw 1790)
L. chloris (Boulenger 1893)
L. cooloolensis Liem 1974
L. dentata (Keferstein 1868)
L. dorsalis Macleay 1878
L. fallax (Peters 1880)
L. freycineti Tschudi 1839
L. genimaculata (Horst 1883)
L. glandulosa Tyler & Anstis 1975
L. gracilentata (Peters 1870)
L. inermis (Peters 1867)
L. infrafronata (Günther 1867)
L. latopalmata Günther 1867
L. lesueurii (Duméril & Bibron 1841)
L. longirostris Tyler & Davies 1978
L. lorica Davies & McDonald 1979
L. nannotis (Andersson 1916)
L. nasuta (Gray 1842)
L. nigrofrenata (Günther 1867)
L. nyakalensis Liem 1974
L. olongburensis Liem & Ingram 1977
L. peronii (Tschudi 1838)
L. rheocola Liem 1974
L. rothi (De Vis 1885)
L. rubella (Gray 1842)
L. tornieri (Nieden 1923)
L. tyleri Martin, Watson, Gartside, Littlejohn & Loftus-Hills 1979
L. verreauxii (Duméril 1853)
L. wotjulumensis (Copland 1957)
- Nyctimystes* Stejneger 1916
N. dayi (Günther 1897)
- MICROHYLIDAE
- Cophixalus* Boettger 1892
C. concinnus Tyler & Davies 1979
C. exiguus Zweifel & Parker 1969
C. neglectus Zweifel 1962
C. ornatus (Fry 1912)
C. saxatilis Zweifel & Parker 1977
- Sphenophryne* Peters & Doria 1878
S. fryi Zweifel 1962
S. gracilipes (Fry 1912)
S. pluvialis Zweifel 1965
S. robusta (Fry 1912)

RANIDAE

- Rana* Linnaeus 1758
R. daemeli Steindachner 1868

BUFONIDAE

- Bufo* Laurenti 1768
B. marinus (Linnaeus 1758)

REPTILES

CROCODYLIA

CROCODYLIDAE

- Crocodylus* Laurenti 1768
C. johnsoni Krefft 1873
C. porosus Schneider 1801

TESTUDINES

CHELONIIDAE

- Caretta* Rafinesque 1814
C. caretta (Linnaeus 1758)
Chelonia Latreille 1801
C. depressa Garman 1880
C. mydas (Linnaeus 1758)
Eretmochelys Fitzinger 1843
E. imbricata (Linnaeus 1766)
Lepidochelys Fitzinger 1843
L. olivacea (Eschscholtz 1829)

DERMOCHELYIDAE

- Dermochelys* Blainville 1816
D. coriacea (Linnaeus 1766)

CHELIDAE

- Chelodina* Fitzinger 1826
C. expansa Gray 1857
C. longicollis (Shaw 1802)
C. novaeguineae Boulenger 1888
C. rugosa Ogilby 1890
Elseya Gray 1867
E. dentata (Gray 1863)
E. latisternum Gray 1867
Emydura Bonaparte 1836
E. krefftii (Gray 1871)
E. macquarii (Gray 1831)
E. signata Ahl 1931
E. subglobosa (Krefft 1876)

GEKKONIDAE

- Carphodactylus* Günther 1897
C. laevis Günther 1897
Crenodactylus Dixon & Kluge 1964
C. ocellatus (Gray 1845)
Cyrtodactylus Gray 1827
C. galgajuga Ingram 1978
C. louisianensis (De Vis 1892)
C. pelagicus (Girard 1857)

Diplodactylus Gray 1832

- D. byrnei* Lucas & Frost 1896
D. ciliaris Boulenger 1885
D. conspicillatus Lucas & Frost 1897
D. elderi Stirling & Zietz 1898
D. steindachneri Boulenger 1885
D. stenodactylus Boulenger 1896
D. taeniatus (Lönnerberg & Andersson 1913)

D. taenicaudus De Vis 1886

D. tessellatus (Günther 1875)

D. vittatus Gray 1832

D. williamsi Kluge 1963

Gehyra Gray 1834

- G. australis* Gray 1845
G. baliola (Duméril 1851)
G. catenata Low 1979
G. oceanica (Lesson 1830)
G. punctata (Fry 1914)
G. variegata (Duméril & Bibron 1836)

Hemidactylus Oken 1817

H. frenatus Duméril & Bibron 1836

Heteronotia Wermuth 1965

H. binoei (Gray 1845)

Lepidodactylus Fitzinger 1843

- L. lugubris* (Duméril & Bibron 1836)
L. pumilus (Boulenger 1885)

Lucasium Wermuth 1965

L. damaeum Lucas & Frost 1895

Nephrurus Günther 1876

- N. asper* Günther 1876
N. levis De Vis 1886

Oedura Gray 1842

- O. castelnaui* Thomassin 1889
O. coggeri Bustard 1966
O. lesueurii (Duméril & Bibron 1836)
O. marmorata Gray 1842
O. ocellata Boulenger 1885
O. rhombifer Gray 1845
O. robusta Boulenger 1885
O. tryoni De Vis 1885

Phyllurus Schinz 1822

- P. caudiannulatus* Covacevich 1975
P. cornutus (Ogilby 1892)
P. salebrosus Covacevich 1975

Pseudothecadactylus Brongersma 1936

P. australis (Günther 1877)

Rhynchoedura Günther 1867

R. ornata Günther 1867

Underwoodisaurus Wermuth 1965

- U. milii* (Bory 1825)
U. sphyrrurus (Ogilby 1892)

PYGOPODIDAE

- Delma* Gray 1831
D. borea Kluge 1974

D. inornata Kluge 1974

D. nasuta Kluge 1974

D. plebeia De Vis 1888

D. tincta De Vis 1888

D. torquata Kluge 1974

Lialis Gray 1835

L. burtonis Gray 1835

Pygopus Merrem 1820

P. lepidopodus (Lacépède 1804)

P. nigriceps (Fischer 1882)

P. orientalis (Günther 1876)

AGAMIDAE

Amphibolurus Wagler 1830

A. barbatus (Cuvier 1829)

A. caudicinctus (Günther 1875)

A. fordi Storr 1965

A. isolepis (Fischer 1881)

A. muricatus (Shaw 1790)

A. nobbi Witten 1972

A. nuchalis (De Vis 1885)

A. pictus Peters 1866

A. vitticeps Ahl 1926

Chelosania Gray 1845

C. brunnea Gray 1845

Chlamydosaurus Gray 1825

C. kingii Gray 1825

Diporiphora Gray 1842

D. australis (Steindachner 1867)

D. bilineata Gray 1842

D. lalliae Storr 1974

D. magna Storr 1974

D. winneckeii Lucas & Frost 1896

Gonocephalus Kaup 1825

G. boydii (Macleay 1884)

G. spinipes (Duméril 1851)

Lophognathus Gray 1842

L. gilberti Gray 1842

L. longirostris Boulenger 1883

L. temporalis (Günther 1867)

Moloch Gray 1841

M. horridus Gray 1841

Physignathus Cuvier 1829

P. lesueurii (Gray 1831)

Tympanocryptis Peters 1863

T. cephalo Günther 1867

T. intima Mitchell 1948

T. lineata Peters 1863

T. tetraporophora Lucas & Frost 1895

VARANIDAE

Varanus Merrem 1820

V. acanthurus Boulenger 1885

V. brevicauda Boulenger 1898

V. eremius Lucas & Frost 1895

V. giganteus (Gray 1845)

V. gilleni Lucas & Frost 1895

V. glebopalma Mitchell 1955

V. gouldii (Gray 1838)

V. indicus (Daudin 1802)

V. mertensi Glauert 1951

V. prasinus (Schlegel 1844)

V. semiremex Peters 1869

V. spenceri Lucas & Frost 1903

V. storri Mertens 1966

V. timorensis (Gray 1831)

V. tristis (Schlegel 1839)

V. varius (Shaw 1790)

SCINCIDAE

Anomalopus Duméril 1851

A. frontalis (De Vis 1888)

A. lentiginosus (De Vis 1888)

A. ophioscincus (Boulenger 1887)

A. pluto Ingram 1977

A. reticulatus (Günther 1873)

A. truncatus (Peters 1876)

A. verreauxii Duméril 1851

Carlia Gray 1845

C. amax Storr 1975

C. bicarinata (Macleay 1877)

C. coensis (Mitchell 1953)

C. dogare Covacevich & Ingram 1975

C. foliorum De Vis 1885

C. jarnoldae Covacevich & Ingram 1975

C. longipes Macleay 1877

C. munda (De Vis 1885)

C. mundivensis (Broom 1898)

C. novaeguineae (Meyer 1874)

C. pectoralis (De Vis 1885)

C. rhomboidalis (Peters 1869)

C. rimula Ingram & Covacevich 1980

C. schmeltzii (Peters 1867)

C. scirtetis Ingram & Covacevich 1980

C. tetradactyla (O'Shaughnessy 1879)

C. vivax (De Vis 1885)

Cryptoblepharus Wiegmann 1834

C. carnabyi Storr 1976

C. fuhni Covacevich & Ingram 1978

C. litoralis (Mertens 1958)

C. plagioccephalus (Cocteau 1836)

C. virgatus (Garman 1901)

Ctenotus Storr 1964

C. alacer Storr 1970

C. brooksi (Loveridge 1933)

C. decaneurus Storr 1970

C. essingtonii (Gray 1842)

C. hebetior Storr 1978

C. inornatus (Gray 1845)

C. joanae Storr 1970

C. lateralis Storr 1978

C. leae (Boulenger 1887)

- C. leonhardii* (Sternfeld 1919)
C. pantherinus (Peters 1866)
C. pulchellus Storr 1978
C. quinkan Ingram 1979
C. rawlinsoni Ingram 1979
C. regius Storr 1971
C. robustus Storr 1971
C. schevilli (Loveridge 1933)
C. schomburgkii (Peters 1863)
C. spaldingi (Macleay 1877)
C. strauchii (Boulenger 1887)
C. striaticeps Storr 1978
C. taeniolatus (Shaw 1790)
C. uber Storr 1969
- Egernia* Gray 1839
E. cunninghami (Gray 1832)
E. frerei Günther 1897
E. hosmeri Kinghorn 1955
E. inornata Rosén 1905
E. major (Gray 1845)
E. modesta Storr 1968
E. rugosa De Vis 1888
E. saxatilis Cogger 1960
E. slateri Storr 1968
E. stokesii (Gray 1845)
E. striolata (Peters 1870)
E. whitei (Lacépède 1804)
- Emoia* Gray 1845
E. atrocostata (Lesson 1830)
E. cyanogaster (Lesson 1830)
- Eremiascincus* Greer 1979
E. fasciolatus (Günther 1867)
E. richardsoni (Gray 1845)
- Eugongylus* Fitzinger 1843
E. rufescens (Shaw 1802)
- Lampropholis* Fitzinger 1843
L. challengerii (Boulenger 1887)
L. delicata (De Vis 1888)
L. guichenoti (Duméril & Bibron 1839)
L. tetradactyla Kluge & Greer 1979
- Leiopisma* Duméril & Bibron 1839
L. platynota (Peters 1881)
- Lerista* Bell 1833
L. allanae (Longman 1937)
L. ameles Greer 1979
L. bipes (Fischer 1882)
L. fragilis (Günther 1876)
L. karlschmidti (Marx & Hosmer 1959)
L. labialis Storr 1972
L. muelleri (Fischer 1881)
L. orientalis (De Vis 1888)
L. punctatovittata (Günther 1867)
L. stylis (Mitchell 1955)
L. wilkinsi (Parker 1926)
- Menetia* Gray 1845
M. greyi Gray 1845
M. maini Storr 1976
M. timlowi Ingram 1977
- Morethia* Gray 1845
M. adelaidensis (Peters 1874)
M. boulengeri (Ogilby 1890)
M. taeniopleura (Peters 1874)
- Nannoscincus* Günther 1872
N. graciloides (Lönnerberg & Andersson 1913)
- Notoscincus* Fuhn 1969
N. ornatus (Broom 1896)
- Omolepida* Gray 1845
O. branchialis (Günther 1867)
- Proablepharus* Fuhn 1969
P. kinghorni (Copland 1947)
P. tenuis (Broom 1896)
- Saiphos* Gray 1831
S. equalis (Gray 1825)
- Sphenomorphus* Fitzinger 1843
S. amplus Covacevich & McDonald 1980
S. brachysomus Lönnerberg & Andersson 1915
S. crassicaudus (Duméril 1851)
S. fuscicaudis Greer 1979
S. luteilateralis Covacevich & McDonald 1980
S. mjobergi (Lönnerberg & Andersson 1915)
S. murrayi (Boulenger 1887)
S. nigricaudis (Macleay 1877)
S. ornatum (Macleay 1877)
S. pardalis (Macleay 1877)
S. punctulatus (Peters 1871)
S. quoyii (Duméril & Bibron 1839)
S. scutirostrum (Peters 1873)
S. tenuis (Gray 1831)
S. tigrinum (De Vis 1888)
- Tiliqua* Gray 1825
T. gerrardii (Gray 1845)
T. multifasciata Sternfeld 1919
T. occipitalis (Peters 1863)
T. rugosa (Gray 1827)
T. scincoides (Shaw 1790)
- Tropidophorus* Duméril & Bibron 1839
T. queenslandiae De Vis 1890
- TYPHLOPIDAE**
Rhamphotyphlops Fitzinger 1843
R. affinis (Boulenger 1889)
R. australis (Gray 1845)
R. bituberculatus (Peters 1863)
R. broomi (Boulenger 1898)
R. diversus (Waite 1894)

R. endoterus (Waite 1918)
R. grypus (Waite 1918)
R. leucoproctus (Boulenger 1889)
R. ligatus (Peters 1879)
R. nigrescens (Gray 1845)
R. polygrammicus (Schlegel 1839)
R. proximus (Waite 1893)
R. unguirostris (Peters 1867)
R. weidii (Peters 1867)

SERPENTES

BOIDAE

Aspidites Peters 1876
A. melanocephalus (Krefft 1864)
A. ramsayi (Macleay 1882)
Chondropython Meyer 1875
C. viridis (Schlegel 1872)
Liasis Gray 1842
L. albertsii Peters & Doria 1878
L. childreni Gray 1842
L. mackloti Duméril & Bibron 1844
L. olivaceus Gray 1842
Python Daudin 1803
P. amethystinus (Schneider 1801)
P. spilotes (Lacépède 1804)

ACROCHORDIDAE

Acrochordus Hornstedt 1787
A. arafurae McDowell 1979
A. granulatus (Schneider 1799)

COLUBRIDAE

Amphiesma Duméril, Bibron & Duméril, 1854
A. mairii (Gray 1841)
Boiga Fitzinger 1826
B. irregularis (Merrem 1802)
Cerberus Cuvier 1829
C. rhynchops (Schneider 1799)
Dendrelaphis Boulenger 1890
D. calligaster (Günther 1867)
D. punctulatus (Gray 1827)
Enhydris Sonnini & Latreille 1802
E. polylepis (Fischer 1886)
Fordonia Gray 1842
F. leucobalia (Schlegel 1837)
Myron Gray 1849
M. richardsonii Gray 1849
Stegonotus Duméril, Bibron & Duméril 1854
S. cucullatus (Duméril, Bibron & Duméril 1854)
S. parvus (Meyer 1875)

ELAPIDAE

Laticauda Laurenti 1768
L. colubrina (Schneider 1799)

HYDROPHIIDAE

Acalyptophis Boulenger 1896
A. peronii (Duméril 1853)

Acanthophis Daudin 1803
A. antarcticus (Shaw 1794)
A. pyrrhus Boulenger 1898
Aipysurus Lacépède 1804
A. duboisii Bavay 1869
A. eydouxii (Gray 1849)
A. laevis Lacépède 1804
Astrotia Fischer 1856
A. stokesii (Gray 1846)
Cacophis Günther 1863
C. harriettae Krefft 1896
C. krefftii Günther 1863
C. squamulosus (Duméril, Bibron & Duméril 1854)
Cryptophis Worrell 1961
C. nigrescens (Günther 1862)
Demansia Gray 1842
D. atra (Macleay 1885)
D. olivacea (Gray 1842)
D. psammophis (Schlegel 1837)
D. torquata Günther 1862
Denisonia Krefft 1869
D. devisii Waite & Longman 1920
D. maculata (Steindachner 1867)
D. punctata Boulenger 1896
Emydocephalus Krefft 1869
E. annulatus Krefft 1869
Enhydrina Gray 1849
E. schistosa (Daudin 1803)
Ephalophis Smith 1931
E. greyi Smith 1931
E. mertoni (Roux 1910)
Furina Duméril, Bibron & Duméril 1854
F. diadema (Schlegel 1837)
Glyphodon Günther 1858
G. barnardi Kinghorn 1939
G. dunmali Worrell 1955
G. tristis Günther 1858
Hemiaspis Fitzinger 1861
H. daemeli (Günther 1876)
H. signata (Jan 1859)
Hoplocephalus Wagler 1830
H. bitorquatus (Jan 1859)
H. stephensii (Krefft 1869)
Hydrelaps Boulenger 1896
H. darwiniensis Boulenger 1896
Hydrophis Latreille 1802
H. caeruleascens (Shaw 1802)
H. elegans (Gray 1842)
H. gracilis (Shaw 1802)
H. kingi Boulenger 1896
H. major (Shaw 1802)
H. melanosoma Günther 1864
H. obscurus Daudin 1803
H. ornatus (Gray 1842)
H. pacificus Boulenger 1896

- Lapemis* Gray 1834
L. hardwickii Gray 1834
- Notechis* Boulenger 1896
N. scutatus (Peters 1862)
- Oxyuranus* Kinghorn 1923
O. microlepidotus (McCoy 1879)
O. scutellatus (Peters 1867)
- Pelamis* Daudin 1803
P. platurus (Linnaeus 1766)
- Pseudechis* Wagler 1830
P. australis (Gray 1842)
P. colletti Boulenger 1902
P. guttatus De Vis 1885
P. porphyriacus (Shaw 1794)
- Pseudonaja* Günther 1858
P. guttata (Parker 1926)
P. ingrami Boulenger 1908
P. modesta (Günther 1872)
P. nuchalis Günther 1858
P. textilis (Duméril, Bibron, & Duméril 1854)
- Simoselaps* Jan 1859
S. australis Krefft 1864
S. fasciolatus (Günther 1872)
S. incinctus Storr 1967
S. semifasciata (Günther 1863)
S. warro (De Vis 1885)
S. woodjonesi (Thomson 1934)
- Suta* Worrell 1961
S. suta (Peters 1863)
- Tropidechis* Günther 1863
T. carinatus (Krefft 1863)
- Unechis* Worrell 1961
U. carpentariae (Macleay 1887)
U. dwyeri (Worrell 1956)
U. nigrostriata (Krefft 1864)
- Vermicella* Günther 1858
V. annulata (Gray 1841)
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A NEW SPECIES OF SCINCID LIZARD OF THE GENUS *LEIOLOPISMA*
(SCINCIDAE:LYGOSOMINAE) FROM SOUTHEASTERN QUEENSLAND AND
NORTHEASTERN NEW SOUTH WALES

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and

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ABSTRACT

Leiolopisma zia sp. nov. is an egg laying skink found only in rainforest and antarctic beech forests of northeast New South Wales and southeast Queensland.

INTRODUCTION

Lizards of the genus *Leiolopisma* (*sensu* Greer 1974) are a major component of the cool and cold temperate reptile faunas of Australia (Rawlinson, 1975). Until recently, only one species, *L. platynota*, was known to occur as far north as northeastern New South Wales and southeastern Queensland (Cogger, 1979, p.580). Another species, here described as *L. zia* sp. nov., has been collected in this area.

Abbreviations used in text: SVL — snout-vent length; TL — tail length; HW — head width; AG — distance between the axilla and groin; FL — length of fore limb; HL — length of hind limb. Numbers prefixed by J are specimens housed in the Queensland Museum and by R, in the Australian Museum.

Ratios are expressed as percentages and measurements are in millimetres.

Leiolopisma zia sp. nov.

Fig. 1.

HOLOTYPE: J 30563, adult male, Mt. Superbus State Forest, SE Queensland, (28° 13S, 152° 26E) collected by R. Sadlier on 1-2 Jan, 1978.

PARATYPES: Qld.: J26025, Cunningham's Gap; J 30213, 30555-62, Mt. Superbus State Forest; N.S.W.: J 27787-8, 27793, Tweed Lookout, Wiangarie State Forest; J 27855-8, Brindle Crk., Wiangarie; R 49178, 74709-18, Rainforest end of Softwood Rd., Styx River State Forest; R 54619, Marengo State Forest.

DIAGNOSIS: *L. zia* can be distinguished from all other *Leiolopisma* by the following combination of characteristics: rainforest dwelling, egg-laying skink with small limbs (FL/SVL 17-22; HL/SVL

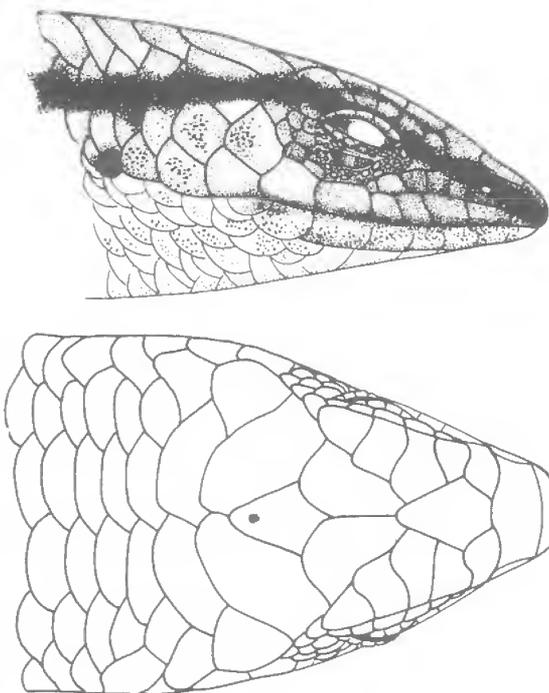


FIG. 1. *Leiolopisma zia*

Above. Lateral view of head.
Below. Dorsal view of head.

23–29), divided frontoparietal, a high number of supraciliaries (usually 7 or 8), a low number of midbody scale rows (22–26) a very low number of lamellae under the fourth toe (14–17), a dark vertical midrostral dash, and in life with bright yellow from chest to vent.

DISTRIBUTION: Rainforests, including antarctic beech forests, of northeastern New South Wales and southeastern Queensland, from Cunningham's Gap in the north to Styx River State Forest in the south (Fig. 2).

DESCRIPTION OF HOLOTYPE: SVL 58.0, TL 92.0, TL/SVL 157, AG 34.0, AG/SVL 59.0, HW 7.4, HW/SVL 13.0, FL 11.0, FL/SVL 19.0, HL 14.5, HL/SVL 25.0. No supranasals or postnasal scales. Rostral and frontonasal in broad contact.

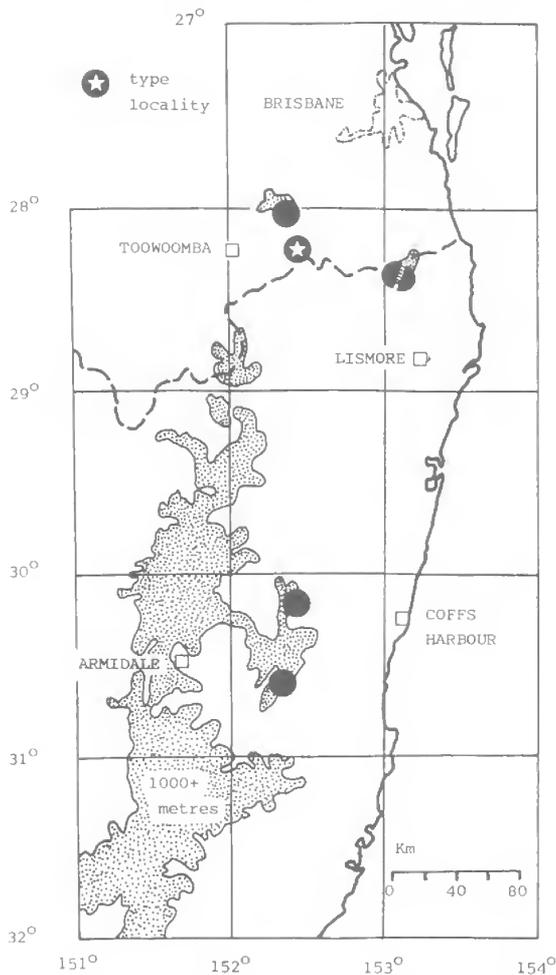


FIG. 2. Distribution of *Leiopisma zia*

Frontal and frontonasal in narrow contact. Prefrontals large, fail to meet, contact the frontonasal, anterior and posterior loreals, first supraciliary, first supraocular and frontal. Anterior and posterior loreals large, former smaller than latter. Frontoparietals divided. Interparietal separate, large, about three-quarters size of a frontoparietal. Parietals large, contact along midline. One very enlarged pair of nuchals followed by a series of smaller pairs. Four supraoculars, the second largest. Seven supraciliaries. Ten upper ciliaries and 13 lower ciliaries on right eye, sixth and seventh upper ciliaries project outwards. Lower eyelid moveable with a large transparent palpebral disc bordered above by the lower ciliaries but otherwise surrounded by small granular scales. Length of palpebral disc 1.0. Length of eye 2.3. Seven upper labials, fourth and fifth below eye. Ear opening obvious, tympanum sunken. Height of external ear opening 1.2. No ear lobules. Eight preanal scales, central pair enlarged. Subdigital lamellae black, undivided and rough, 15 under fourth toe. Palmar tubercles black, flattened asymmetrically with apical point directed distally. Midbody scales in 24 rows. Number of scales from chin to cloaca 62. Dorsal and lateral scales smooth with 3–5 striations. Ventral scales smooth.

COLOUR IN PRESERVATIVE: Dorsally brown with light brown and black fleckings; a light brown dorsolateral line edged in black, breaking up at base of tail. Upper lateral surface of body and head, dark brown grading into a pale lower lateral surface flecked with black. A black midrostral dash. Ventrally white, with black spots from chin to neck; palms and subdigital lamellae black.

DESCRIPTION OF PARATYPES: As for holotype except as follows: SVL 33–59 (N = 29, mean = 42.0). TL 38–80 (N = 7, mean = 62.5). TL/SVL 114–153 (N = 7, mean 133.3). HW 4–7 (N = 27, mean = 6.0). HW/SVL 10–13 (N = 27, mean = 12). AG 20–39 (N = 29, mean = 30.7). AG/SVL 56–66 (N = 29, mean 60.8). FL 6–11 (N = 29, mean 10.3). FL/SVL 17–22 (N = 29, mean = 19.1). HL 8–15 (N = 29, mean = 13.1). HL/SVL 23–29 (N = 29, mean 25.9). Supraciliaries (left and right sides counted) 6–9 (N = 58, mean = 7.5). Midbody scale rows 22–26 (N = 29, mean = 24.0). Number of scales from chin to cloaca 51–63 (N = 27, mean 57.0). Number of scales under fourth toe 14–17 (N = 27, mean = 15.6).

COLOUR IN LIFE: Dorsally dark to light brown with neck and head becoming increasingly bronzed towards the snout; distal half of the tail increasingly suffused with red-brown towards the tip. On the snout is a dark mid-rostral vertical dash. A dark dorsolateral line sharply margined above, begins at the rostral and breaks up behind the hind limb. Laterally, dark brown above becoming lighter below. Ventrally, bright yellow from chest to vent, sharply fading to off-white at base of tail; distal part of tail suffused with red-brown; chin, throat and neck speckled with black.

HABITAT: *L. zia* is found in moist areas in rainforests, including antarctic beech (*Nothofagus moorei*) forests. Specimens are abundant in both clearings and undisturbed areas.

FIELD NOTES.

All specimens taken at the Softwood Road, Styx River State Forest, N.S.W., on the 19 November, 1977 were under flat rocks. No active specimens were seen, presumably because of cool conditions. Species of skink synchronsympatric with *L. zia* were *Lampropholis* cf. *L. challengerii* which

forages in clearings, on tracks and wherever sunlight penetrates to the ground; *Sphenomorphus murrayi* inhabiting burrow systems in and under rotting logs; and *Sphenomorphus* cf. *S. tympanum* inhabiting fallen rotting timber mazes at the forest's edge.

An examination of gut contents of *L. zia* revealed the remains of insects and an oligochaete earth worm.

REPRODUCTION

Table 1 is a summary of available reproduction data. *L. zia* is an egg-laying skink. The females carry and presumably also deposit between 3 and 6 eggs (mean 5.2), by early January. In males, the testes are well developed in mid-November and mid-December but are much reduced in size by mid-March. Mating was not observed, but the condition of the testes suggests that insemination possibly occurs in spring (October to November) and/or soon after egg deposition in mid-summer. The latter strategy seems more likely and implies that females store sperm through the winter, as has been reported for *L. coventryi* (Rawlinson,

TABLE 1: SUMMARY OF REPRODUCTIVE DATA FOR *LEIOLOPISMA ZIA*.

Collection date	Males	Females
(seasonally ranked)	reproductive condition	reproductive condition
19 Nov 1977 (Softwood Road)	all with well developed testes R74710 R74712 R74714 R74715	all with well developed eggs in oviducts. oviducts L R 3 3 R74709 2 3 R74711 3 3 R74713
13 Dec 1977 (Softwood Road)	with well developed testes, R74717	R74716 laid 3 eggs in captivity between 24.xii.1977 and 31.xii.1977 (see below for oviposition details), R74718 an immature subadult.
3 Jan 1975 (Softwood Road)		no oviduct eggs, oviducts large, convoluted but not noticeably distended. R49178
12 March 1976 (Marengo State Forest)	testes much reduced in size. R54619	

1975). This species also occurs in high rainfall cool temperate forests.

One captive female deposited 3 eggs in a shallow depression under a small mat of live moss in a vivarium between 24 and 31 December, 1977. She had scooped out the 25 mm deep x 50 mm long x 25 mm wide depression by pushing the moist (but not wet) soil sideways and upwards with legs and tail so that the depression was surrounded by a mound. The eggs were not covered with soil, but the nest was hidden from above by the mat of moss. Two of the three parchment shelled eggs were stuck together. On 11 February 1978 all three were measured: two live eggs, length both 11.4 mm, diameter 7.0 and 6.9 mm; one preserved egg (undissected), length 10.7 mm, diameter 6.5 mm. The live eggs did not hatch and when dissected on 16 March 1978, they contained the remains of well formed lizards with scales.

Two further females collected on 20 December, 1978 were housed in separate containers. Between 24 and 27 December, 1978, one of them deposited six eggs into an excavated burrow under bark and covered them with soil. Between 28 December, 1978 and 2 January, 1979, the other female deposited five eggs in almost identical fashion. On 18 January, 1979, four of all the eggs had

collapsed. The remaining seven were measured and they had an average length of 9.9 mm, and an average diameter of 8.4 mm. None of these hatched and only one was found to contain a well developed embryo.

ACKNOWLEDGMENTS

H. Cogger, J. Coventry, J. Covacevich, G. Czechura, J. Ehmann, P. Hardy, A. Greer, S. Sands and G.M. Storr assisted in the preparation of the paper. The support of the C.S.I.R.O. Science and Industry Endowment Fund is also gratefully acknowledged.

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FIVE NEW SPECIES OF SKINKS (GENUS *LAMPROPHOLIS*)
FROM QUEENSLAND AND NEW SOUTH WALES.

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and
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ABSTRACT

Lampropholis basiliscus sp. nov. and *L. czechurai* sp. nov. are from the rainforests of northeastern and mid-eastern Queensland; *L. mirabilis* sp. nov. is a rock-dweller in northeastern Queensland; *L. amicula* sp. nov. is found in heath and open forest in southeastern Queensland; and *L. caligula* sp. nov. from mid-eastern New South Wales has not been collected in recent times.

INTRODUCTION

Four of the five species described here can be easily placed in the two subgroups of *Lampropholis* defined by Greer and Kluge (1980). *L. mirabilis* and *L. amicula* are members of the *L. delicata* complex, and *L. czechurai* and *L. basiliscus* are members of the *L. challengerii* complex. *L. caligula* may be an aberrant member of the *L. delicata* complex. The genus *Lampropholis* was recently resurrected and redefined by Greer (1974).

Abbreviations used in the text are: SVL — snout to vent length; HW — head width; FL — length of fore-limb; HL — length of hind-limb; TL — length of tail. Measurements are given in millimeters and all ratios are expressed as percentages. Register numbers prefixed by J are housed in the Queensland Museum, by R in the Australian Museum and by D in the National Museum of Victoria.

LAMPROPHOLIS MIRABILIS sp. nov.

Figs. 1, 6.

HOLOTYPE. J24439, Magnetic Island, northeastern Queensland (19° 08'S, 146° 50'E), collected by T. Low, July, 1974.

PARATYPES. Magnetic Island (J4404, 24339, 24416, 24424, 24435, 24437-8, 24440-1, 24528, R9453-7); Mt. Cleveland, Cape Cleveland (J27615, J32555, R95434-51); Mt. Elliot (J24340).

DIAGNOSIS. A large, long legged, chocolate and white speckled, rock-dwelling *Lampropholis* distinguished from all members of this genus by its high number of midbody scale rows (29-33) and its high number of lamellae under the fourth toe (27-32).

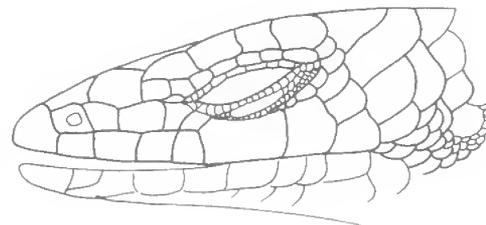
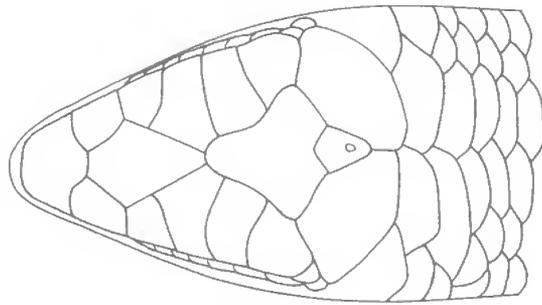


FIG. 1. Holotype (J24439), *L. mirabilis*
A. Dorsal view of head
B. Lateral view of head

DESCRIPTION. SVL: 27–51 (N=13, mean 40.9); HW/SVL: 13–16 (N=11, mean 14.2); FL/SVL: 28–34 (N=12, mean 32.0); HL/SVL: 45–51 (N=12, mean 47.7); TL/SVL: 151–165 (N=4, mean = 159). Four supraoculars. Supraciliaries 7 (counted on both sides), rarely 8 (N=24, mean 7.1). Upper labials 7, 5th below eye. A pair of enlarged nuchals contacting the parietals. Palpebral disc small. Ear aperture about equal to palpebral disc in size. No ear lobules. Midbody scale rows 29–33 (N=12, mean 30.9). Mid-dorsal scales smooth with 3–4 striations. Number of scales from chin shields to cloaca 58–64 (N=12, mean 60.3). Lamellae under fourth toe 27–32 (N=12, mean 28.7), smooth.

On upper parts of body the ground colour is olive, flecked with chocolate and white spots or blotches. Laterally, the colour and pattern is similar but the chocolate markings may coalesce to form barring. Head bronze. Underparts immaculate.

DISTRIBUTION: Known only from granite rocks on Magnetic Island, Cape Cleveland and Mt. Elliot, northeastern Queensland.

ETYMOLOGY: From the Latin *mirabilis*, wonderful.

REMARKS: Covacevich and Ingram (1978) have commented on the adaptations to saxatiline habitats of six species of skinks (including this species as *L. sp. nov.*). Like other rock-dwelling skinks *L. mirabilis* has longer legs, a higher number of toe lamellae and midbody scale rows, and dark colouring with white flecking, when compared to its congeners.

LAMPROPHOLIS CZECHURAI sp. nov.

Figs. 2, 6.

HOLOTYPE: J34402 Charmillin Creek, via Ravenshoe, northeastern Queensland (17° 43'S, 145° 31'E), collected by G.V. Czechura, 28th August, 1978.

PARATYPES: Home Rule, near Shipton's Flat (J25227); Mt. Lewis (J27072–3); 5.1 km N of road around Tinaroo Lake via Forestry Road B (R89757); The Crater, Atherton Tableland (J12148–50); Mt. Fischer, via Millaa Millaa (J31201, 31204–6); Charmillin Creek, via Ravenshoe (J34403, 34405–7, R94472–81).

DIAGNOSIS: A small, dark, rainforest inhabiting *Lampropholis* distinguished from members of this genus other than *L. basiliscus* and *L. tetradactyla*, by the presence of four nuchal scales contacting the parietals. It is easily distinguished from *L. tetradactyla* in having 5 toes instead of 4. *L. czechurai* may be distinguished from *L. basiliscus* by its very concave canthus rostralis and pointed snout, and in colour and pattern of breeding male (side of head and body black speckled with white vs a dark stripe from nostril through eye and continuing backwards above forelimb to varying distances along the body). *L. challengerii* usually has two nuchals contacting the parietals but in some specimens it may be higher; *L. czechurai* may be distinguished from these by its smaller size (maximum SVL 34 vs 58) and lower number of toe lamellae (15–19 vs 22–28).

DESCRIPTION: SVL: 20–34 (N=12, mean 29); HW/SVL: 13–16 (N=12, mean 14.5); FL/SVL: 21–27 (N=12, mean 23.2); HL/SVL: 27–35 (N=12, mean 31.3); TL/SVL: 104–131 (N=5, mean 117.3). Four supraoculars. Supraciliaries 7, rarely 6 or 8 (N=32, mean 7). Upper labials 6, 4th below eye. Two pairs of nuchals contacting the parietals. Palpebral disc small. Ear aperture about half the size of the palpebral disc. No ear lobules. Midbody scale rows 22–24 (N=12, mean

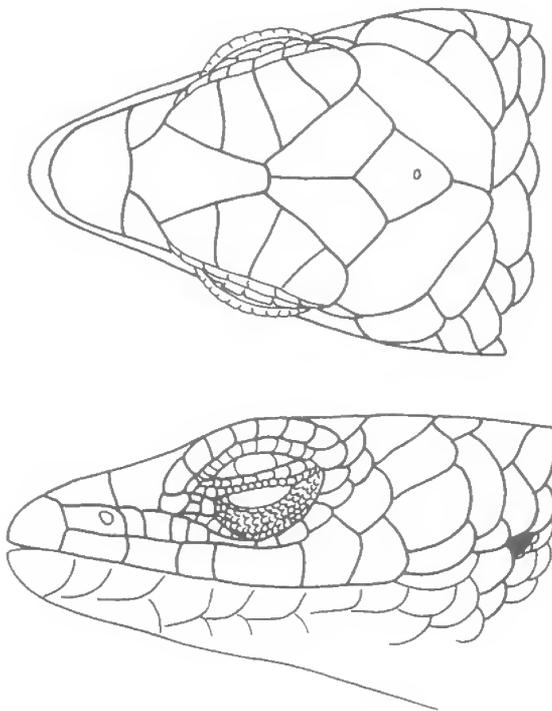


FIG. 2. Holotype (J34402), *L. czechurai*
A. Dorsal view of head
B. Lateral view of head

22-8). Mid-dorsal scales smooth with 3-4 striations. Number of scales from chin shields to cloaca 46-56 (N=10, mean 49.9). Lamellae under fourth toe 15-19 (N=12, mean 16.2), medially grooved.

On upper parts of body, the ground colour is fawn to dark reddish brown with dark and light speckling or dashes, sometimes coalescing into wavy lines. Laterally as above but in breeding males the side of the neck and head jet black with some lighter speckling; sides of the body dark heavily dotted in black with lighter speckling. There is a distinct light spot at the posterior base of the thigh. In some specimens there is light dorsolateral line edged in black. Ventrally cream with sporadic brown speckles.

DISTRIBUTION: Shipton's Flat, 30 km S of Cooktown, in the north to Charmillin Creek at the southern end of the Atherton Tableland in the south.

ETYMOLOGY: Named for Mr Gregory Czechura, Queensland Museum.

REMARKS: The closest relative of *L. czechurai* appears to be *L. tetradactyla*. These species are similar in head shape, in having a low number of toe lamellae and in the number of nuchals contacting the parietals (for details of *L. tetradactyla*, see Greer & Kluge, 1980).

Greer and Kluge (1980) listed four characters shared by *L. basiliscus* and *L. tetradactyla* and not shared with other members of the *L. challengerii* complex. *L. czechurai* exhibits these same four characters.

LAMPROPHOLIS BASILISCUS sp. nov.

Figs. 3, 7.

HOLOTYPE. J34409 Charmillin Creek, via Ravenshoe northeastern Queensland (17° 43'S, 145° 31'E), collected by G.V. Czechura, 28th August, 1978.

PARATYPES. Northeastern Queensland: Mt. Webb (J32354); Big Tableland (R26833); Mt. Hedley (J25265); Mt. Hartley (J24848); Gap Creek, 12 Mile Scrub (J25301, 27258); Track between Granite Creek and Cedar Bay (J25204); Home Rule (J24918, 25137-8, 25229, 25257, 25289, 25308, R26783); Shipton's Flat (J17902-3, 27135, 27141); 13 km S of Helenvale (J24648) Thornton Peak (R56563-4, 56571, 56573, 56589, 57129, 59329, 87080-1), 1.5 km E of Barron River Bridge via Kennedy Highway (R87071-2); 10.4 km N of Kennedy Highway via

Black Mountain Road (R87078-9); Kuranda (R67048-67058); Danbulla State Forest, via Atherton (R87066-70); Tinaroo Dam (J12145); 1.8 km S of Yungaburra (R63891-2); 2.2 km S of Yungaburra (R63871-5); near Cairns (R57766); 6.9 km S of Atherton (R87082-6); Crater, Atherton Tableland (J12146-7, 12158-9); (R18300); Bartle Frere (J30810); The Boulders, Babinda (R87075-7); Innisfail (J17435, R16167); Flying Fish Point (J25450); South Johnstone (R16334); Charmillin Creek, via Ravenshoe (J34408); 18.2 km S of Kennedy Highway at Ravenshoe via Tully Falls Road (R87073-4); Tully Falls (J11161); 13.5 km W junction to Mission Beach South via Tully - Mission Beach Road (R87061-4); just E of Stony Creek Bridge on Tully - Mission Beach Road (R87065); Mission Beach (J30811); Herbert Gorge (J25022-7, 25029-45, 25047-59, 25061); Kirrama Range, 13 km NW of Cardwell (R60507-8); Smoko Creek at Kirrama State Forest Road, W of Kennedy (R87057-9); 13 km W of Bruce Highway via Kirrama State Forest Road (R87060); Cardwell (J25825-75); Hinchinbrook Island (J26330-2, J26375-6); 3.4 km SE of Wallaman National Park (R87052); 5.8 km ESE of Wallaman National Park (R87053-6); Paluma Dam (R87051); Paluma (J29668).

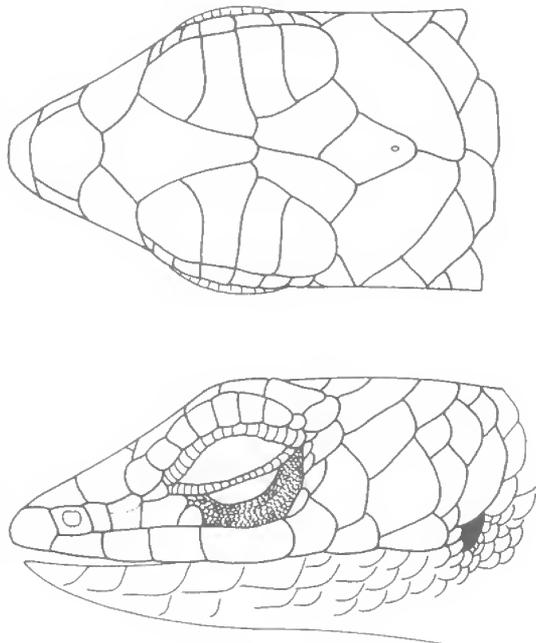


FIG. 3. Holotype (J34409), *L. basiliscus*
A. Dorsal view of head
B. Lateral view of head

Mid-eastern Queensland: Box Creek, Mt. Dryandra (R47868); Brandy Creek (J32758, 32760, 32766-71, 32780-3, 32794); 7.4 km E of junction of road to Mandalay via Airlie Beach - Shute Harbour Road (R87096); 9.2 km W of Cathu State Forest Office (R87087-87095); St. Helen's Gap, 3.7 km N of Mt. Charlton (R87097-103); Finch Hatton (J32602, 32605, J34000-6, 34036, 34038-40, 34042, 34047, 34062, 34066, 34069, 34092-3, 34095-100).

DIAGNOSIS. A large rainforest dwelling *Lampropholis* distinguished from members of this genus other than *L. tetradactyla* and *L. czechurai*, in having more than two nuchals contacting the parietals. It is easily distinguished from *L. tetradactyla* by having 5 fingers and for differences from *L. czechurai*, see the diagnosis of that species. Further distinguished from *L. challengerii* by its higher number of supraciliaries (usually 7 vs 6).

DESCRIPTION. SVL: 18-47 (N=100, mean 36.3); HW/SVL: 11-16 (N=82, mean 14.0); FL/SVL: 21-33 (N=88, mean 29.1); HL/SVL: 31-27 (N=86, mean 39.0); TL/SVL: 124-180 (N=16, mean 152.9). Four supraoculars. Supraciliaries 7, rarely 5 or 8, and uncommonly 6 (N=199, mean 6.9). Upper labials 6, 4th below eye. Nuchals contacting the parietals 3 or 4, rarely 2, 5 or 6 (N=100, mean 3.6). Palpebral disc small. Ear aperture about equal to palpebral disc in size. No ear lobules. Midbody scale rows 21-28 (N=96, mean 23.8). Mid-dorsal scales smooth with 2-4 striations. Number of scales from chin shields to cloaca 44-59 (N=83, mean 50.7). Lamellae under fourth toe 16-25 (N=95, mean 20.9), medially grooved.

On upper parts of body and head the ground colour is fawn to reddish brown with or without light and dark speckling. Upper lateral surface darker than lower lateral surface; the former often with a dark stripe beginning at nostril, continuing through eye, and going backwards for varying distances past forelimb. There is a distinct light spot at the posterior base of the thigh. In some specimens there is a light dorsolateral line edged darkly. Ventrally, cream with or without brown speckling (see Fig. 4 in Greer and Kluge, 1980).

DISTRIBUTION. Mt. Webb, 50 km N of Cooktown to the Paluma Range, near Townsville; also 290 km south of this area, from Proserpine to Eungella, via Mackay. This disjunct distribu-

tion conforms with the occurrence of major 'blocks' of rainforest.

ETYMOLOGY. From the Latin *Basiliscus*, a lizard.

REMARKS. Greer and Kluge (1980) discussed *L. basiliscus* under the name 'northern challengerii'.

L. basiliscus occurs in two widely separated 'blocks' of rainforest. Specimens from the southern 'block' (the Clarke Range, via Mackay) differ slightly from those from the northern rainforests from the Paluma Range to Mt. Webb. Southern specimens show a tendency to be slightly smaller and 'stubbier', and to have slightly lower midbody and toe lamellae counts than northern specimens. There are, however, 'overlaps' for these features in the two populations. In addition colour, pattern, and other scale counts for them are very similar, suggesting clinal rather than specific or subspecific differences.

LAMPROPHOLIS AMICULA sp. nov.

Figs. 4, 6.

HOLOTYPE. J24333, 3 km E. of Lake Coolamerra, Cooloola, southeastern Queensland (26°

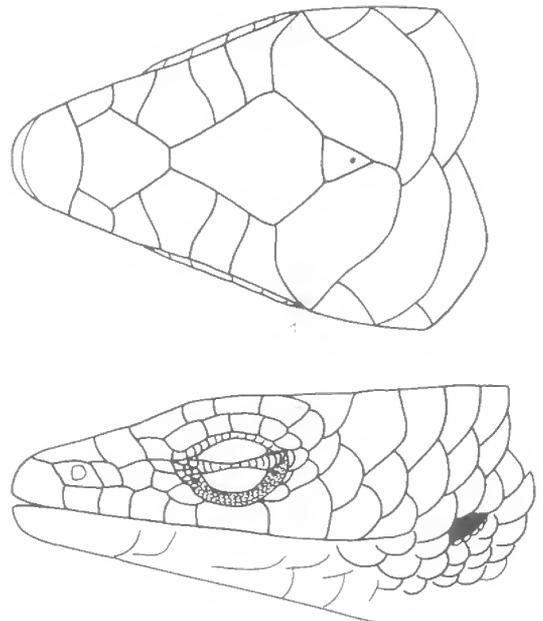


FIG. 4. Holotype (J24333), *L. amicula*
A. Dorsal view of head
B. Lateral view of head

02'S, 153° 05'E) collected by G.J. Ingram on 6th August, 1973.

PARATYPES. Burnett Range, via Tansey (J31308); 3 km E of Lake Coolamera, Cooloola (J24332); 1.6 km E of Lake Coolamera, Cooloola (J24496); Cooloola (J32519); Boroumba Dam, Conondale Range (D49367); near junction of Booloumba and Tragedy Creeks, Conondale Range (J24497); Gherulla Creek, Conondale Range (J30828); Marlaybrook, Bunya Mountains (J27523); Cunningham's Gap (J22729); Mt. Coot-tha (J37177-8, 37287-9); Daisy Hill State Forest (D49366, J34330-1); Upper Emu Creek, Mt. Superbus (J32090); 10.6 km SW of the Cambronn Bridge — Kenilworth road via Tragedy Creek Road, Kenilworth State Forest (R76126); junction Yabba Road and Jimna Range Road, Jimna Range (R76127-8).

DIAGNOSIS. A little, small limbed *Lampropholis* distinguished from all other members of this genus (except *L. caligula*) by its 5 supraciliaries. Further distinguishable from *L. caligula* by its higher number of supraoculars (4 vs 3) and upper labials (7 vs 6).

DESCRIPTION. SVL: 22-34 (N=19, mean 29.4); HW/SVL: 11-15 (N=19, mean 12.8); FL/SVL: 16-23 (N=14, mean 20.9); HL/SVL: 25-31 (N=14, mean 28.6); TL/SVL: 121-157 (N=8, mean 124.1). Four supraoculars. Supraciliaries 5, very rarely 6 (N=37, mean 5.0). Upper labials 7, 5th below eye. Two nuchals contacting the parietals. Palpebral disc small. Ear aperture about half the size of palpebral disc. No ear lobules. Midbody scale rows 19-23 (N=21, mean 21.4). Mid-dorsal scales smooth with 3-4 striations. Number of scales from chin shields to cloaca 50-60 (N=14, mean 53.7). Lamellae under fourth toe 17-21 (N=19, mean 18.9).

Colour drab, with a pattern resembling *Lampropholis delicata*. Dorsal surface of head brown. Dorsal surface of neck, trunk and tail darker brown. Dorsolateral scales on neck, trunk and anterior section of tail with a light yellow upper half and black lower half giving the impression of a light dorsolateral stripe bordered below by black. This 'stripe' extends from the eye onto the tail where it breaks up. Upper lateral surface from eye to anterior section of tail black. Lower lateral surface light grey with flecks of black and brown. Ventral surface light grey with some scattered black flecks especially under the tail. Dorsal and lateral surface of legs and arms black. Palms and subdigital lamellae black.

DISTRIBUTION. Southeastern Queensland from the Burnett Range in the north, to Daisy Hill, 13 km S of Brisbane in the south and west to the Great Dividing Range.

ETYMOLOGY. From the Latin *amicula*, a friend.

REMARKS. *L. amicula* occurs in open forest and heath. It resembles *L. delicata* and is often mistaken for a juvenile of that species, but it can be easily distinguished by its lower number of supraciliaries (5 vs 7).

LAMPROPHOLIS CALIGULA sp. nov.

Figs. 5, 6.

HOLOTYPE. R13313 Pol Blue, Barrington Tops, mid-eastern New South Wales (31° 59'S, 151° 30'E) collected by W. Barnes and party.

PARATYPES. Barrington Tops (R8758); Pol Blue, Barrington Tops (R13314, 94993); Tubrabucca, Barrington Tops (R13329, 94994, J38704).

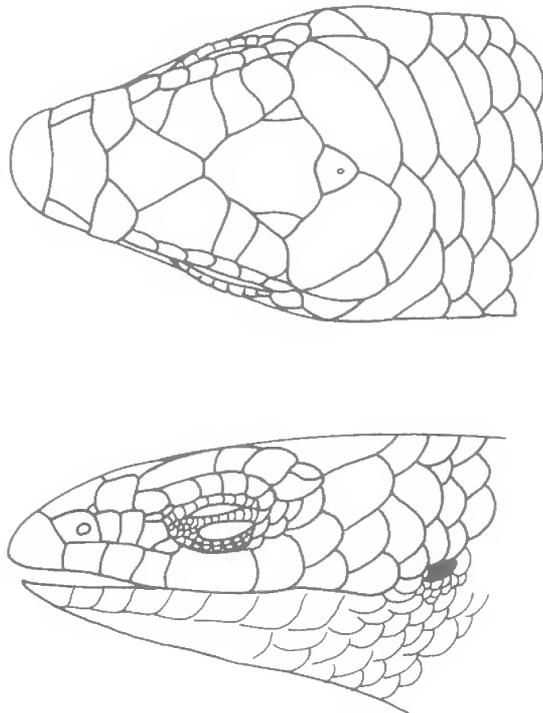


FIG. 5. Holotype (R13313), *L. caligula*
A. Dorsal view of head
B. Lateral view of head

DIAGNOSIS. A large, drab *Lampropholis* distinguished from all other members of this genus by its 5 supraciliaries and 3 supraoculars. Further distinguished from *L. amricula* by its low number of upper labials (5 vs 7).

DESCRIPTION: SVL: 35–48 (N=7, mean 40.1); HW/SVL 11–12 (N=7, mean 11.7); FL/SVL: 17–19 (N=7, mean 18.1); HL/SVL 27–30 (N=7, mean 28.6); TL/SVL: 109–133 (N=3, mean 119.7). Supraoculars (counted on both sides) 3, rarely 4 (N=19, mean 3.1). Supraciliaries 5, rarely 6 (N=14, mean 5.1). Upper labials 6, rarely 7 (N=7, mean 6.1), 4th (rarely 5th) below eye. Two nuchals contacting the parietals. Palpebral disc small. Ear aperture about half the size of palpebral disc. No ear lobules. Midbody scale rows 19–23 (N=7, mean 21.0). Mid-dorsal scales smooth with 3–4 striations. Number of scales from chin shields to cloaca 60–67 (N=7,

mean 63.4). Lamellae under fourth toe 17–22 (N=7, mean 19.6), smooth.

Colour drab with a pattern resembling *L. delicata* and *L. amricula*. Upper parts brown. Laterally black on upper half of surface becoming grey with flecks of black or brown on the lower surface. Sides of tail with 2–3 black stripes. Ventrally grey.

DISTRIBUTION: Known only from the Barrington Tops area in mid-eastern New South Wales.

ETYMOLOGY: From the Latin *caligula*, a small military boot.

REMARKS: *L. caligula* is unusual when compared to the other species of this genus. While appearing similar to *L. delicata* in colour pattern it has 6 upper labials like the *L. challengeri* complex. However it differs from both in usually having less than four supraoculars.

ACKNOWLEDGMENTS

We thank Ms Jeanette Covacevich, Ms Susan Sands, Mr G. Czechura, Mr J. Coventry, Mr E. Wixted and Dr A. Greer for their help with the work for this paper. Many of the specimens of *L. basiliscus* and *L. czechurai* used in these descriptions were collected on field trips funded by the Australian Biological Resources Study.

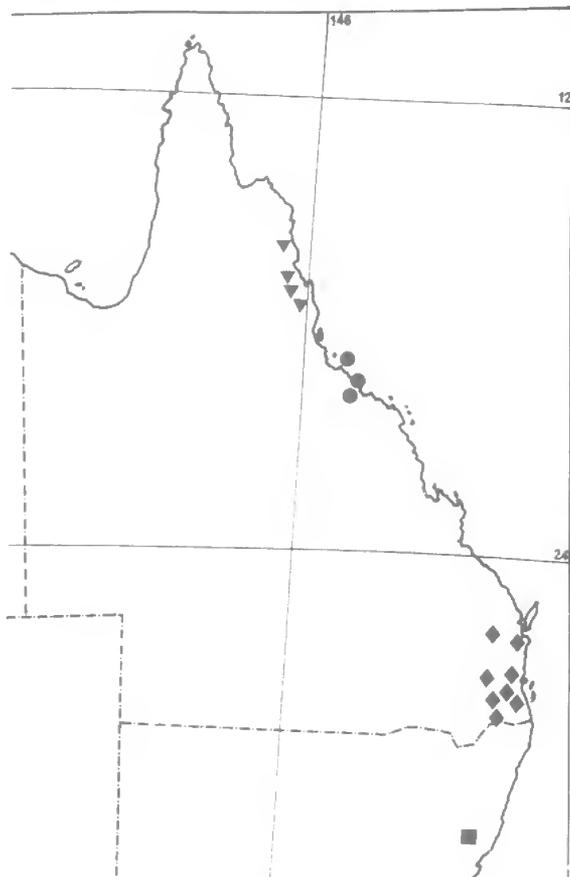


FIG. 6. Distribution of *Lampropholis mirabilis* ●, *L. czechurai* ▼, *L. amricula* ◆, *L. caligula* ■.

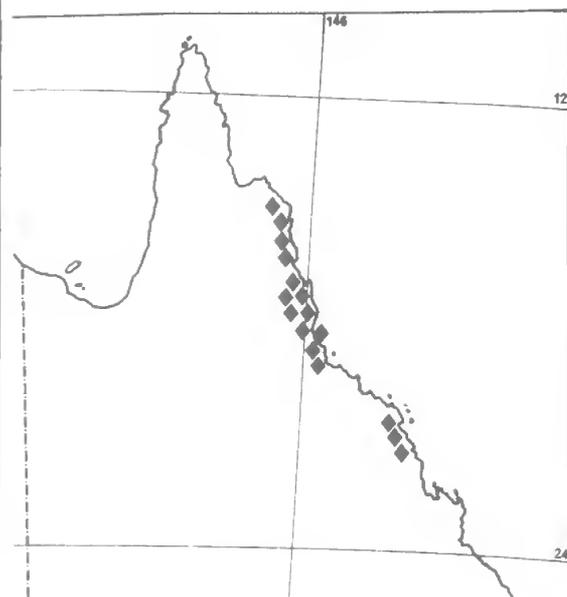


FIG. 7. Distribution of *Lampropholis basiliscus*

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MUTTABURRASAUROUS, A NEW IGUANODONTID
(ORNITHISCHIA: ORNITHOPODA) DINOSAUR
FROM THE LOWER CRETACEOUS OF QUEENSLAND

ALAN BARTHOLOMAI
and
R.E. MOLNAR
Queensland Museum

ABSTRACT

A partial skeleton of an iguanodontid ornithopod has been recovered from the Mackunda Fm. (Albian) on the Thomson River near Muttaborra, central Queensland. This material is referred to *Muttaborrasaurus langdoni*, gen. et sp. nov. This new iguanodontid is characterized by an inflated, hollow muzzle; maxillary teeth lacking any central carina; a low, broad skull; anterior caudal centra with ventral excavations; four metatarsals, and; an apparent articulation of the fibula with the astragalus.

INTRODUCTION

Dinosaur remains are uncommon in Australian deposits. Of those discovered, by far the greatest number have been from Queensland. Excluding footprints, widely known in Queensland and elsewhere, the majority of records involving actual bone remains are from the freshwater and shallow marine sediments of the Great Artesian Basin, which cover much of the state. Described remains have been of partial skeletons and isolated bones and in recent years, field investigations in the freshwater sediments of the Winton Formation have yielded fragmentary skeletons of sauropods. Some of this work was undertaken independently by the Queensland Museum, while part was in conjunction with the American Museum of Natural History.

Among earlier collected material the most completely known species, described by Longman (1926, 1927), is the sauropod *Rhoetosaurus brownei* from the freshwater Injune Creek Beds of Middle Jurassic age on "Taloona" Station. Recent investigations of the site confirmed the presence of additional material which was apparently *in situ*. Study of these remains, still lacking cranial material, will add considerably to knowledge of this animal.

Dinosaur bones have also been recorded from the Wilgunya Sub-Group (especially the Toolebuc Limestone) of Lower Cretaceous (Albian) age,

associated with a rich, shallow water, marine invertebrate fauna and a broad suite of marine vertebrates including fish and marine reptiles. The only described dinosaur material is another large sauropod, *Austrosaurus mckillopi* Longman (1933) recovered from 'Clutha' Station, near Maxwellton, central Queensland. The material comprises a series of dorsal vertebrae and part of a rib. An isolated, partial cervical vertebra (QM F6142) from a very large sauropod is also known from the Wilgunya Sub-Group.

Other described remains from Australia are based on even less material than *Austrosaurus*. Seeley (1891) recorded the presence of *Agrosaurus macgillivrayi* from isolated bones from unrecorded sediments, probably of Triassic age, from the coast of North Queensland. A series of opalized specimens from the Cretaceous sediments at Lightning Ridge, northern New South Wales was described by Huene (1932). These comprised a theropod tooth, a theropod caudal vertebra *Walgettosuchus woodwardi*, a femur described as *Fulgurotherium australe* and a theropod metacarpal described as *Rapator ornitholestoides*. These have recently been reviewed by Molnar (1980), who also reported hypsilophodontid material from the Ridge. Recently isolated theropod and hypsilophodontid material has also been discovered on the Victorian coast, near Cape Paterson and Cape Otway.

The material considered in the present study represents the most completely known dinosaur yet discovered from Australia. Its location was brought to the notice of the Queensland Museum in 1963 by a grazier, Mr D. Langdon, of Muttaborra, central Queensland. The specimen was exposed within a cattle holding area on the banks of the Thomson River, near Muttaborra. Unfortunately, it had been somewhat scattered by stock over the years and some had been collected by local residents before recovery could be organized. However, recognizing the importance of the find, residents returned much of the removed material and it is believed that no major elements originally preserved now remain in private hands. The discovery was previously recorded by Bartholomai (1966) and Hill, Playford and Woods (1968).

Preparation and reassociation of the parts of the specimen have been achieved with considerable difficulty, using a combination of mechanical and acetic acid techniques and jig-saw puzzle approach. Although limited further detail will be forthcoming with continued preparation, the authors believe that further delay in its description is unwarranted.

The assistance of the Myer Foundation in awarding a Travel Grant to the senior author, in part to enable comparative studies to be undertaken in England and France, is gratefully acknowledged. Mr M. Tanimoto drew our attention to published photographs of *Probactrosaurus*, for which we are grateful.

We would also like to thank Margaret Oakden for her restoration, and Dianne Ashwell for typing the drafts of the ms.

Order ORNITHISCHIA Seeley
Suborder ORNITHOPODA Marsh
Family Iguanodontidae Cope
Genus *Muttaborrasaurus* nov.

TYPE SPECIES: *Muttaborrasaurus langdoni* nov.

DIAGNOSIS: Large iguanodontid with nasal region of snout inflated; maxillary teeth with multiple low ridges but lacking central carina; postorbital region of skull broad and low; quadrate inclined posteriorly; lateral process present on frontal; dorsal centra keeled; anterior caudal centra with ventral pits; four metatarsals present. A differential diagnosis will be presented with the comparison with other ornithopods.

ETYMOLOGY: Derived from Muttaborra, the name of the township in central Queensland near the type locality, and *sauros*, Latin, used in the sense of reptile or saurian.

SPECIES: *Muttaborrasaurus langdoni* nov.

TYPE SPECIMEN:

Queensland Museum F6140, a nearly complete skeleton, lacking most of the tail. This material includes the phalanges previously numbered F6095 (figured in Hill, Playford and Woods, 1968).

LOCALITY: The banks of the Rock Hole, Thomson River, on "Rosebery Downs" Station, approximately 4½ km southeast of Muttaborra, central Queensland, at M.R. 242175 Muttaborra 4-mile series (approximately M.R. 245165 on the Muttaborra 1:250000 series).

HORIZON: Mackunda Fm.

AGE: Albian (Vine and Day, 1965).

ETYMOLOGY: The specific name honours Mr. D. Langdon, of Muttaborra, who discovered the specimen, and reported it to the Queensland Museum.

DIAGNOSIS: As only a single species is attributed to this genus, the specific diagnosis necessarily cannot be separated from that of the genus.

The bones were partially exposed by weathering in a calcareous mudstone concretion (or series of concretions) which had been exposed on the surface being harder than the containing sediment. Nearby concretionary structures contained a rich suite of shallow water marine pelecypods, gastropods and rare ammonites.

It is clear that the holotype and the invertebrates were recovered from the Mackunda Formation, within the Manuka Sub-Group, regarded by Vine *et al.* (1967) and Vine and Day (1965) as being of Lower Cretaceous (Albian) age. The dinosaur thus adds to the known fossil record of the Tambo Faunal Division. Vine and Day (1965) regard the argillaceous and arenaceous sediments of the Mackunda Formation as having been deposited in marine and paralic environments. Because of the close association of the dinosaur remains with non-abraded shallow-water marine molluscs, it is believed that the specimen was preserved some distance from the Albian shoreline, away from the influence of heavy wave action. It is assumed that the carcass floated out to sea, sank and was interred within the marine muds.

DESCRIPTION

THE SKULL

The skull is preserved in a slightly distorted and crushed condition. Some shedding and bone loss has occurred, particularly posterodorsally, anteriorly and on the right side. Only the posterior portions of the mandibles are known. However, most major external bone elements are represented, particularly from the left side. Matrix masks much of the ventral surface, although elements are occasionally seen in section along fortuitous cracks. The skull is illustrated in its existing state in Plate 1, and Fig. 1 while Fig. 2 shows the reconstructed skull.

Several notable features of the skull stand out. The postorbital region of the skull is low and broad, even accounting for its incompleteness dorsally. In height this region is slightly over half its maximum breadth. The anterior portion of the snout as preserved is greatly inflated into an apparently hollow bulla, giving the skull a unique

appearance unlike that of any other described form. This structure will be described in greater detail with the discussion of the nasal and premaxillary bones. The foramen magnum is not circular or elliptical in form, but has the peculiar appearance of being in form like a large semicircle joined to a small one of about half its radius (Fig. 1). The bar posteriorly bounding the infratemporal fenestra is remarkable for its anteroposterior breadth.

SUPRAOCCIPITAL. The supraoccipital forms most of the dorsal roof of the foramen magnum. It is mainly known from its external, posterior aspect, the surface of which is inclined very slightly anteriorly. The ventral one-third is weakly concave transversely, while the dorsal two-thirds bears a strong, narrow, median ridge separating deep, lateral concavities for *M. spinalis capitis*. The surface immediately below the ridge is transversely concave and carries a deep, narrow groove leading to a small foramen on each side of the midline. The bone is extended laterally into

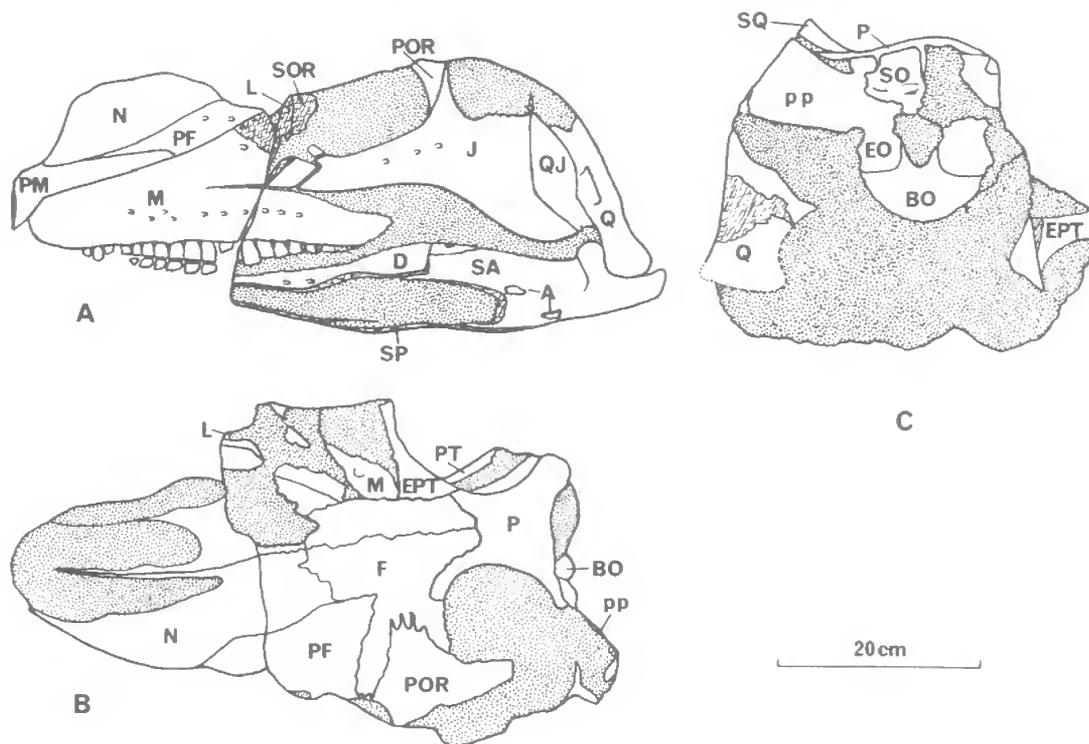


FIG. 1. The skull and jaws of *Muttaborrasaurus langdoni* (QM F6140) as preserved. A, lateral view; B, dorsal view; C, posterior view. Abbrev.: A, angular; BO, basioccipital; D, dentary; EO, exoccipital; EPT, ectopterygoid; F, frontal; J, jugal; L, lacrimal; M, maxilla; N, nasal; P, parietal; PF, prefrontal; PM, premaxilla; POR, postorbital; pp, paroccipital process; PT, pterygoid; Q, quadrate; QJ, quadratojugal; SA, surangular; SO, supraoccipital; SOR, supraorbital; SQ, squamosal. The stipple represents matrix, and the hatching broken surfaces.

leaf-shaped borders. The superior rim of the foramen magnum is broadly concave transversely and is angled obliquely anterodorsally. A weak, median, ventral process is present extending into the foramen magnum.

Sutural relationships with the exoccipital-opisthotic are difficult to interpret but traces suggest the limits to the bones. Relationships of the supraoccipital and proötic are largely obscured.

Near the ventrolateral border with the paroccipital process, a shallow transverse groove leads to the centre of the posterior surface and is defined dorsally by a very small, posteriorly directed process.

EXOCCIPITAL AND OPISTHOTIC. Sutural relationships between the exoccipital and opisthotic are difficult to interpret. They combine to make up the bulk of the lateral and dorsolateral margins of the foramen magnum and ascend as a stout pillar from the upper limit of the occipital condyle to obliquely meet the supraoccipital. A short posteromedial process forms the dorsolateral

margin of the foramen magnum. The surface is deeply concave and the bones continue posterolaterally into a broad, flaring, paroccipital process. A shallow depression is present immediately lateral to the margin of the foramen magnum. Dorsally, a stout buttress from the paroccipital process supports the parietal and laterally this process supports the squamosal. Posteriorly the paroccipital process is gently convex dorsoventrally but is planar anteriorly. Lateral aspects of the cranial base are only partly visible. A large foramen, presumably for the hypoglossal n., is present anterolaterally in the ascending pillar close to the basioccipital.

BASIOCCIPITAL. The basioccipital forms the occipital condyle and the ventral and ventrolateral margins of the foramen magnum. The condyle is well developed, rounded and produced ventrally as well as posteriorly. Other surfaces are masked by matrix.

PROÖTIC AND BASISPHENOID. The proötic is partially exposed on the right side, sufficient to observe part of its articulation with the parietal

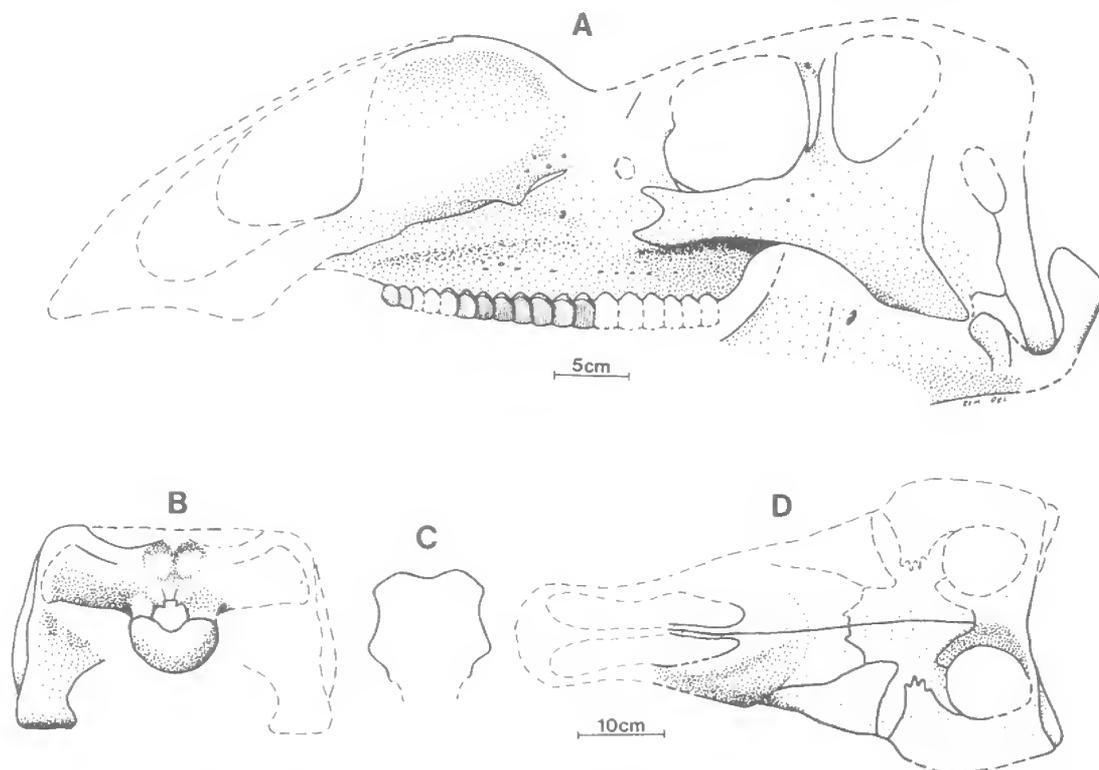


FIG. 2. Reconstruction of the skull of *Muttaborrasaurus langdoni* (QM F6140). A, lateral view; B, posterior view; C, cross-section through nasal bulla just behind posterior extremity of nares; D, dorsal view. Reconstructed portions dashed, right side of skull based on left, cranial roof region based on those portions of the roofing elements preserved, and anterior portion of snout reconstructed by analogy with *Iguanodon mantelli*.

but insufficient for description. The basisphenoid is masked by matrix.

PARASPHENOID. This bone is largely covered by matrix. A fortuitous break across the skull exposes in section what probably is the parasphenoid. It appears as a small, anteriorly directed process, V-shaped in section, with the dorsal arms slightly directed mesially and containing a very deep, dorsal concavity (PL. 2, B). A very deep, extremely thin flange of bone extends ventrally at the mid-line. This flange is deeper in this section than the main body of the bone.

LATEROSPHEOID. The laterosphenoid is too poorly exposed for description.

ORBITOSPHEOID. If preserved, the orbitosphenoid is still masked by matrix.

PREMAXILLA. The premaxilla is incomplete anteriorly and dorsally and little remains of the edentulous portion. It was relatively large and was expanded anteriorly both transversely and dorsoventrally. Posteriorly, it is produced into a relatively short, thin, flat process between the maxilla and nasal. Dorsomesially, the premaxilla is concave and floors the nasal passage. It is sharply excavated ventromesially with a sharply crested, free ventrolateral border produced to about the same level as, or slightly dorsal to, the anterior margin of the maxillary dentition. Remnants remain of the median dorsal process contributing to the anterior and dorsal aspects of the naris. The ventrolateral margin remaining is rugose, suggesting the presence of a horny sheath.

MAXILLA. The maxilla is known both laterally and in section but mesial aspects are masked by matrix. The bone is elongate and anteriorly is dorsoventrally shallow but is much deeper posteriorly. The lateral margin is longitudinally shallowly concave anteriorly, near planar above the mid-cheek area and markedly concave below the orbit. A series of foramina are present, irregularly placed anteriorly but becoming more regular in a single series posteriorly, slightly above the mid-line of this part of the bone. All are directed posteriorly and probably transmitted nerves and blood vessels to the cheeks (cf. Galton, 1973a).

The maxilla bears a minimum of 18 functional, socketed teeth. Anterior to the first tooth, is an edentulous section extending a short distance to butt against the ventrolaterally directed expansion of the premaxilla. Internally, the ventral part of the bone is a robust, longitudinally orientated rod with the convexity directed slightly dorsomesially. The lateral margin above the foramina is

relatively thin and the foramina appear to open into a broad, transversely concave, channel-like shelf.

Immediately above the main body of the maxilla, the bone is flexed along a longitudinal axis, the angular relationship being emphasized by dorsoventral crushing. A tongue-like extension of the maxilla joins the anterodorsal surface of the jugal. Dorsally, the maxilla broadly contacts the nasal and anterodorsally it contacts the premaxilla. Posterodorsally, it appears excluded from contact with the prefrontal but contacts the lacrymal posteriorly and posterodorsally. In this area it surrounds the posteroventral, ventral and anteroventral margins of the small antorbital fenestra. The dorsal part of the maxilla is sharply concave anteriorly and slightly sinuous across its greatest height.

NASAL. The nasal is a relatively thin bone, widely expanded dorsally into a bizarre, bulbous structure which, allowing for slight dorsoventral crushing of the skull, was higher than the cranial roof. Loss of bone has occurred anterodorsally and the nasal opening was apparently relatively large, ovate and directed dorsoanterolaterally. Contact with the premaxilla is short laterally, and posteriorly it joins the prefrontal and frontal. The bulk of the ventral contact is with the maxilla, although minor contact with the lacrymal is present posteriorly. The bulbous expansion is longitudinally sinuous laterally. In a dorsoventral section, it is shallowly concave laterally. A series of small foramina are present posteroventrally. The anterior and dorsal edges contribute to the dorsomesial and lateral borders of the naris.

LACRYMAL. The lacrymal is not well preserved on either side. Sufficient remains to indicate that it was a relatively small but comparatively thick bone wedged between the maxilla, jugal, prefrontal and supraorbital. The lacrymal forms part of the anterior margin of the orbit and contributes to the anterodorsal, dorsal and posterodorsal margins of the antorbital fenestra. The lacrymal duct is directed through the dorsal body of the bone.

PREFRONTAL. The prefrontal is a large bone positioned between the frontal, nasal, lacrymal and supraorbital. Its anteroventral margin is truncate, giving a broad contact with the posteroventral margin of the nasal, while its posterior margins expand and contribute to the skull roof and the bulk of the anterodorsal orbital margin. It widely excludes the frontal from much of the orbital margin. The dorsal surface is flattened.

SUPRAORBITAL. The supraorbital is incomplete posteriorly. Shedding and fracturing have largely obscured its surface features. It is a small element at the anterodorsal orbital margin and making wide contact with the prefrontal and lacrimal. Posteriorly it probably paralleled the dorsal orbital margin.

POSTORBITAL. This is a triradiate element, sharp edged and forming the posterodorsal and part of the posterior orbital margins and the anterolateral portion of the upper temporal bar. The bone is damaged dorsally and posteriorly but it was flattened dorsally. The posterior process tapers away from the body of the bone, while the ventral process is elongate and tapers along the anterior surface of the ascending process of the jugal. A circular depression, with rugose posterior and dorsal rim, containing a foramen is present towards the top of the ventral process. Contact mesially is with the parietal and frontal and anteriorly with the frontal, which it excludes from major contribution to the dorsal orbital margin.

PTERYGOID. The pterygoid is largely masked by matrix and only the broad right alar process for the quadrate is exposed.

ECTOPTYERYGOID. The ectopterygoid is exposed only on the right side and from above. It has been somewhat damaged by fracturing. The main portion consists of a stout bar, subtriangular in section, which continues mesially into a widely expanded plate, the expansion being greatest posteroventrally. The anterior surface of the bar contacts the mesial portion of the posterior surface of the maxilla, while the bar is slightly expanded laterally near its junction with the jugal. The mesial flared section is subtriangular with the apex directed dorsally and with the bone thinning anteriorly and posteriorly. It broadly contacts the pterygoid.

PALATINE AND VOMER. These bones are masked by matrix but a portion of a bone interpreted as palatine is visible from above in the right orbital area.

FRONTAL. The frontal is a large, elongate bone contributing minimally to the dorsal orbital margin and forming a large proportion of the dorsal skull roof. Considerable shedding has occurred but sutures may still be interpreted. The frontal is nearly planar anteroposteriorly and transversely, contributing to the rather flat skull roof.

PARIETAL. The parietal has suffered shedding dorsally and along the occipital crest. It is a large element in dorsal aspect, extending anterior the

supratemporal fenestrae. The bone contributes to the anterodorsal and mesial margins of the supratemporal fenestra, and contacts the frontal. From above the surface is flattened on its lateral portion but mesially it is weakly crested between the supratemporal fenestrae. A strong occipital crest is also formed posteriorly where it extends above and well posterior to the supraoccipital plane. Transversely, the dorsal margin of the occipital crest is strongly convex. Lateral margins of the crest are supported by stout buttresses from the paroccipital processes. Posteroventrally, the bone contacts the squamosal and laterally contacts the laterosphenoid, supraoccipital and postorbital within the supratemporal vacuity.

JUGAL. The jugal is a large bone contributing to the ventral moiety of the infratemporal fenestra and to the posteroventral margin of the skull. Its ventral margin is concave. The outer orbital margin is gently rounded and a shelf of the jugal extends mesially to contribute to the floor of the orbit. In this area, the jugal has an anterior process whose external surface is relatively straight and shallow, penetrated by a series of small foramina below the orbit. Its anterior margin is markedly indented to accommodate the two posterior projections of the maxilla and the lacrimal. A narrow, curved rod extends dorsally forming the posteroventral orbital rim, and passes behind the postorbital process. The rod thus contributes the bulk of the anterior rim of the infratemporal fenestra. A second, flattened but broader and thinner process extends dorsally as the posterior margin to this fenestra. A broad, flat, thin plate extends posteroventrally toward the quadrate, overlying the quadratojugal. Externally, the jugal is gently convex longitudinally and transversely.

SQUAMOSAL. Very little of the squamosal is preserved; all that remains is the posteroventral area. This extends mesially in contact with the parietal and is supported laterally by the paroccipital process.

QUADRATOJUGAL. This is a relatively thin, small, sheet-like plate positioned between the jugal and the quadrate. Posterodorsally, the quadrate appears to overlie the quadratojugal but ventrally, the quadrate is partially overlapped. A relatively large fenestra is present at the junction of the quadrate and quadratojugal. The bone does not extend ventrally as far as the jugal. It is broadly convex longitudinally and transversely, with a spine (now broken) at its ventral extremity.

Due to the relatively great anteroposterior length of the quadratojugal, the posterior bar of

the infratemporal fenestra presents an unusually broad appearance in lateral view.

QUADRATE. The quadrate is a large, robust bone forming the posteroventral corner of the skull and bearing the articulating condyle for the lower jaw. The condyle is rounded anteroposteriorly and very gently convex transversely. It is expanded to a greater extent than the body of the bone immediately dorsal to it, this expansion being conspicuously greater mesially. The anterior surface above the condyle is gently concave transversely and longitudinally, whereas the posterior surface is strongly convex transversely and concave longitudinally. Sharp angles are produced where the surfaces meet anteromesially and anterolaterally. Above the condyle, the bone twists slightly. Dorsally, the quadrate is expanded anteriorly and probably contributes to the posterior wall the infratemporal channel. It is channelled anteriorly, near the quadratojugal by a fenestra to which it contributes the posterior, dorsal and ventral margins. In section, the dorsal part of the bone was broadly U-shaped, with the arms extending mesially.

A peculiarity of the quadrate is its orientation. The ventral articular end of the quadrate is located posterior to the dorsal portion of this element, so that the posterior surface slopes down and back. Although the dorsal extremity of the quadrate is not preserved, the position of the paroccipital process indicates that it was not placed posterior, or even directly above, the ventral articular end.

DENTARY. The dentary is incomplete anteriorly and ventrally. Below the middle of the tooth row, the mesial and lateral parts of the dentary are approximately parallel but posteriorly, they diverge considerably.

Laterally, the dentary, as preserved, is longitudinally concave. Although lacking, it is likely the anterior portion was longitudinally convex laterally. Inner surfaces of the dentary are correspondingly convex posteriorly and presumably concave anteriorly, probably giving the lower jaw a gently sinusoidal aspect in ventral view. The greater posterior thickness of the jaw is achieved external to the tooth row. Transversely, the lateral surface is gently convex anteriorly and strongly convex posteriorly, but the mesial surface has much less convexity.

The lower limits and external expression of the Meckelian canal are not preserved, although a portion of the splenial margin is present. Massive expansion of the canal occurs anterior and ventral to the coronoid process into an adductor fossa

which increases in depth and width posteriorly. Several foramina occur along the lateral surface of the dentary, presumably for nerves and blood supply to the cheeks. The dentary is overlapped by the splenial but the relationship with the coronoid is unknown on the mesial surface. Laterally, the dentary overlaps the surangular and is overlapped by the coronoid.

SPLENIAL. The splenial is a very thin bone applied mesially to the ramus and is gently concave longitudinally and convex transversely. Its ventral extent is unknown.

ANGULAR. Only fragments of the angular remain. These suggest a relatively thin bone which tapers posteriorly where it overlaps a considerable portion of the surangular.

SURANGULAR. This is a relatively large bone, the extreme dorsal and the mesial aspects of which are still masked by matrix. It is laterally thin but much thicker posteroventrally. Longitudinally, the lateral surface is gently convex, except in the area immediately anterolateral to the articulation where a very strongly defined, and dorsolaterally projecting, rounded boss is present. Ventrally, it is gently longitudinally concave. A very large foramen is present anteriorly near the coronoid junction. Dorsally the surangular butts against the coronoid.

PREARTICULAR. This is visible ventrally and posteromesially. It is a flattened, thin bone which tapers posteriorly and thins anteriorly. Posteriorly, it becomes transversely convex and overlaps the articular.

ARTICULAR. The articular is somewhat masked by the quadrate, but appears triangular in dorsal aspect with the base anterior. The vertex is formed by a high, triangular dorsomesial expansion thickened posteriorly, that forms the retroarticular process. Anterior to this is the concavity for the quadrate articulation. The articular is overlapped laterally and ventrally by the bones anterior to it.

CORONOID. Still masked dorsally by matrix, the coronoid is a large element present as a dorsal extension of the ramus under the jugal. Its internal extent is unknown.

TEETH

Only maxillary teeth are exposed; the dentary teeth are present but are deeply masked by matrix. Anterior maxillary teeth are much smaller than those in the middle of the series and size of posterior teeth appears reduced compared with those in the mid-cheek area. The maxillary teeth are arranged in a single row.

MAXILLARY TEETH (Plate 2). The crowns of the teeth are laterally compressed and are wider than the roots whose extent and shape are unknown. The lateral surfaces of the crowns (and apparently the mesial side of dentary crowns) are covered by thin enamel. This is finely and evenly ornamented with vertical ridges and grooves with up to 13 ridges visible in teeth in the midmaxillary area. Considerable variation in numbers of ridges is evident however and anterior maxillary teeth have only 7 ridges. In unworn maxillary teeth, the secant occlusal surface is nearly straight but is angled obliquely posteriorly, with serrations corresponding with the position of the vertical ridges at the distal edge.

Wear with the dentary teeth maintains a sharp, enamelled lateral margin to the maxillary teeth and the tooth row rapidly assumes a straight, continuous cutting edge along the length of the skull. Mesially, the occlusal surface of the crowns assumes an inclined, concave wear facet.

The teeth curve slightly mesially. Posterolaterally, the crown is deeply, vertically grooved and it appears that this groove, like the lateral surface, is enamelled. Crowns are closely pressed together along their anterior and posterior margins. Mesially, each tooth slopes obliquely from the occlusal surface and near the socket, the crowns are very wide, the transverse dimension being even greater than the length of the crown. Fracturing

of the skull reveals that replacement appears to have been alternate.

THE VERTEBRAL COLUMN AND RIBS

Because of disassociation it is unclear whether the vertebrae represented comprise the total number present during life. It appears likely that most presacral centra are present but judging from comparison with related forms, some posterior dorsal vertebrae are probably lacking. Remains of sacral vertebrae are present but shedding has been extensive in this region and insufficient exists for description. Caudal vertebrae are known from only a small series, presumably from the area immediately posterior to the sacrum. Distal caudal vertebrae are unrepresented and were probably lost before preservation.

The presacral series comprises 9 cervicals and a minimum of 15 dorsals. From attachment scars on the ilium, the number of sacral vertebrae appears to have been six. Neural arches throughout are poorly preserved.

ATLAS. This consists of an intercentrum, an odontoid process and two neural arches and is illustrated in Fig. 3. Largest of these components is the intercentrum, a subrescentic bone with a large, shallow, anterior depression for the occipital condyle. Obliquely inclined, this depression has a sharply rounded edge ventrally. Two surfaces are

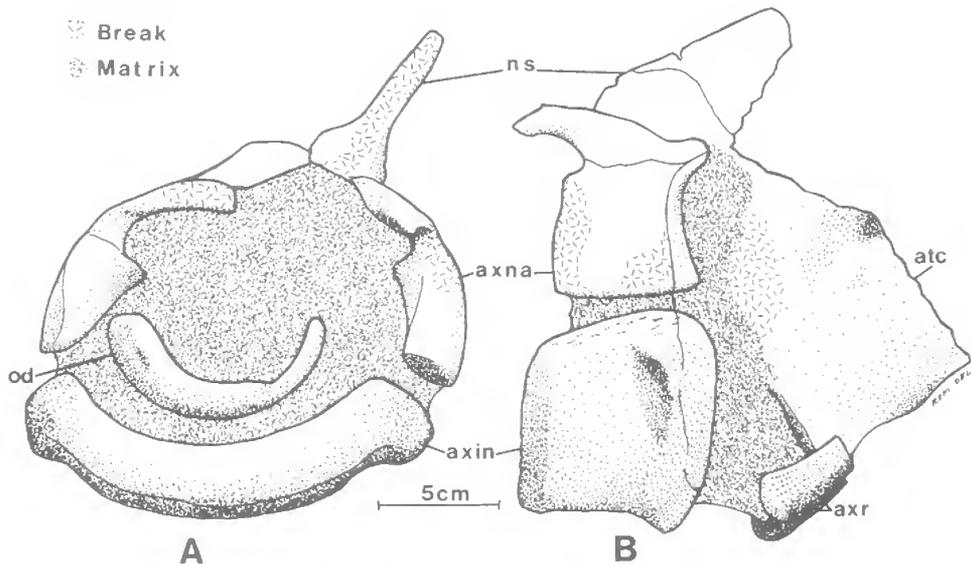


FIG. 3. Atlas-axis complex of *Muttaborrasaurus langdoni* (QM F6140) as preserved. A, anterior view; B, lateral view. Abbrev.: atc, atlantal centrum; axin, axial intercentrum; axna, axial neural arch; axr, axial ribs; ns, neural spine; od, odontoid process. The axial ribs and atlantal centrum are broken posteriorly, and have been rotated backwards and clockwise relative to the axis.

present laterally, directed dorsolaterally and slightly anteriorly for the neural arches. Ventrally, the surface is near planar anteroposteriorly, medially abruptly curving ventrally at the posterior margin, forming a distinct edge with the posterior surface. Posteriorly, the surface mesial to the rib facet is gently concave transversely and strongly convex dorsoventrally. The rib facet is broadly rounded.

The odontoid process is near planar anteriorly. The anterior crescentic area is flattened and slightly inclined, with a slight median depression for the occipital condyle.

The neural arches are irregular bones, separated from one another dorsally. Two articulating surfaces are present ventrally. The larger, directed anteroposteriorly and curving posteromedially is for the intercentrum, while the other faces anteromedially and forms a continuation of the intercentral articulation for the occipital condyle. Externally, the neural arches are broadly convex dorsoventrally, although a short, stout process is directed posterolaterally. Anteriorly, the area of the prezygopophysis is thin and flared, with two lobes, the inner of which is the more robust. The postzygopophysis is weakly defined, directed posteromedially. A strong concavity is present between this and the short posterolateral process.

The atlantal rib is small, laterally flattened and ovate in section. The head is slightly expanded with an obliquely inclined concave surface for articulation, broadly convex in lateral view.

AXIS. The axis is incomplete, being known only from the anterior moiety. The centrum is near planar anteriorly except for a shallow medial depression at the ventral margin. If an intercentrum was present, it must have been extremely small. The neural arch is well developed with a strong, laterally compressed neural spine, incomplete posteriorly. Anteriorly, the spine is slightly thickened. Prezygopophyses are transversely convex and the atlantal postzygopophyses articulated around their lateral surfaces. The suture between neural arch and centrum is indistinct.

A small fragment of the rib of the axis tapers rapidly posteriorly, suggesting it was very short. It is subtriangular to subovate in section and was probably single headed.

CERVICAL VERTEBRAE 3 TO 9 AND RIBS. All cervical vertebrae have opisthocelous centra, although by cervical 9, the degree of concavity and convexity of the centrum has been considerably reduced. All have articulating ends that are

broader than they are deep. The centrum of cervical 3 is ventrolaterally compressed resulting in production of a ventral crest which is broader posteriorly than anteriorly. The other cervical centra all have a well developed ventral keel.

The neuro-central suture is clearly above the parapophysis in all cervicals back to cervical vertebrae 8 and 9 where it straddles the suture. The parapophysis is comparatively small in cervical 3 but in posterior cervicals, it is considerably expanded. Diapophyses are poorly exposed and in most vertebrae have been lost along with the bulk of the neural arches. However in mid-cervical vertebrae they are robust, extending well out from the arch. Anterior cervicals have the parapophysis extended laterally and directed dorsolaterally. A broad ridge is developed laterally on all centra by dorsolateral compression of the centrum, giving the centrum a cruciate cross-section.

Prezygopophyses and postzygopophyses are robust and, in mid-cervical vertebrae, extend anteriorly and posteriorly to positions about one-third the length of the centra on either side. In cervical 6, a strong ridge is present running from the middle of the dorsomesial surface of the postzygopophysis towards the neural spine. This becomes weaker in more anterior vertebrae and is virtually lacking by cervical 5. A weak neural spine is present on cervical 5, becoming slightly stronger posteriorly. In anterior cervicals, the prezygopophysis appears continuous laterally with the margin of the centrum, but in posterior cervicals, the zygopophyses are separated from the central margins by excavated areas.

Cervical ribs are well preserved but are known only from the mid-cervical area. Heads are bifid, widely separated by a deep, lateral excavation which continues obliquely posterodorsally, and supported below by a continuation of the lateral ridge from the capitulum. The tuberculum is more robust than the capitulum and has a concave articulation. The rib of cervical 5 extends posteriorly to above the middle of cervical 7. The body of the rib is subtriangular in section, with the apex directed mesially.

DORSAL VERTEBRAE AND RIBS (Fig. 4). All centra of dorsal vertebrae are amphiplatyan to mildly amphicoelous. It is likely that the series preserved is incomplete and exact determination after dorsal vertebra 9 is uncertain. Length of the centrum remains reasonably constant back to the mid-dorsal region where a slight decrease in length is seen. More posteriorly, centra appear to be increasing in length. Width of dorsal vertebrae

decreases from dorsal 1 to 6 then increases until width again exceeds length (Table 1).

In the first dorsal vertebra the centrum is laterally compressed, producing a ventral keel which is thicker and deeper anteriorly than posteriorly. The degree of compression decreases posteriorly so that the ventral part becomes progressively rounded.

The neural arches are poorly preserved although some anterior and mid-dorsal representation is present. The level of the diapophysis drops sharply from dorsal 1 to 3. Succeeding dorsals maintain the diapophyses at about the level of that on dorsal 3, at least to the mid-dorsal region. Anterior dorsal vertebrae have large prezygopophyses set widely apart but mid-dorsal examples are smaller and closer together. The articular surfaces of the prezygopophyses preserved are all inclined from the horizontal at a low angle of about 30°.

The angle between the transverse process and the vertical gradually widens posteriorly, from about 60° in dorsal 2 to about 75° in the mid-dorsal region. The first neural spines are thin, but they become thicker posteriorly. The posterior edge is much wider than the anterior. Spines appear to increase in height posteriorly but are not excessively developed.

Dorsal ribs are known only from sections, some

TABLE 1
VERTEBRAL MEASUREMENTS (CM)

<i>Vertebra</i>	<i>Length</i>	<i>Maximum Central Breadth</i>
Cervical 3	12.2	12.9
Cervical 5	13.6	13.2*
Cervical 6	12.2	12.8*
Cervical 7	11.6	14.9
Cervical 8	10.4	15.8
Dorsal 1	9.0	15.5
Dorsal a (anterior)	11.0	—
Dorsal b (anterior)	12.1	12.9
Dorsal c (mid)	11.3	11.3
Dorsal d (mid)	11.9	—
Dorsal e (posterior)	10.0	14.0
Caudal a	8.5	11.0
Caudal b	7.8	10.8
Caudal c	10.2	—

Exact position of lettered vertebrae not determined, sequence indicated by the sequence of lettering. Dorsal b follows dorsal a directly, as does dorsal d, dorsal c.

*Breadth estimated by doubling distance from midline to edge of centrum.

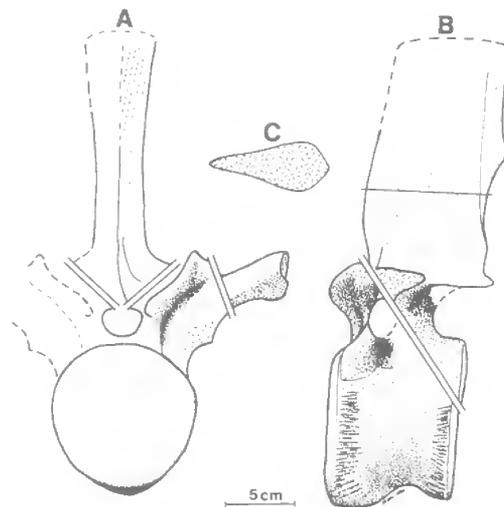


FIG. 4. Composite of two dorsal vertebrae of *Muttaborrasaurus langdoni* (QM F6140). Centrum and prezygopophysis of an anterior dorsal combined with arch and spine of a posterior dorsal. Unprepared posterior dorsals indicate that the central form is very similar between the anterior and posterior dorsals, but that the prezygopophyses are more nearly horizontal in the posterior dorsals. A, anterior view; B, lateral view; C, cross-section through spine at horizontal plane indicated in B.

preserved in correct position. Anterior and mid-dorsal ribs are double-headed and all are strongly curved close to their articulation. Distally, they are anteroposteriorly expanded and are flatter mesially than laterally, and this is still evident by dorsal vertebra 9. The capitulum is borne on the proximal end of the rib, while the tuberculum is on a more dorsolaterally placed step and faces dorsomesially. Anterior ribs have the capitulum and tuberculum widely separated.

SACRAL VERTEBRAE. Because of shedding, little can be said about sacral vertebrae other than that at least part of the series was fused. From interpretation of articulations on the ilium, it appears that 6 sacral vertebrae were present.

The single sacral (or dorso-sacral) centrum that has been completely freed from the matrix is deeply constricted, with amphiplatyan central articular surfaces. The (presumably) anterior articular surface has deep, radial grooves peripherally, some extending as much as two-thirds of the distance to the centre, but most rather shorter. The posterior surface bears irregular depressions, but nothing comparable to the grooves. The floor of the neural canal is deeply excavated, but is not yet entirely cleared so that the total depth of the excavation is not known.

At the base of the pedicles, anteriorly, on each side there opens a large, U-shaped foramen running posteroventrally into the centrum.

CAUDAL VERTEBRAE. Very weathered caudal vertebrae are present and have been determined as being from the area immediately posterior to the sacrum. None have preserved a neural arch and all have suffered some degree of shedding. Measurements, mostly estimated, are listed in Table 1. Centra appear to be amphicoelous or amphiplatyan and become lower and thinner progressively back along the series. All have a somewhat squared appearance with lateral surfaces merging with ventral around sharply rounded ventrolateral borders. Mid-ventrally, there is a deep pit in anterior caudals which is not due to crushing. The ventral margin slopes abruptly posteriorly in this area and a somewhat sharper slope defines the articulation for large chevrons, none of which has been preserved.

OSSIFIED TENDONS. Ossified tendons are present in the collection but preparation has not revealed any *in situ*. They appear to have been up to 0.5 cm in diameter.

THE PECTORAL GIRDLE

SCAPULA. Scapulae are preserved on both sides

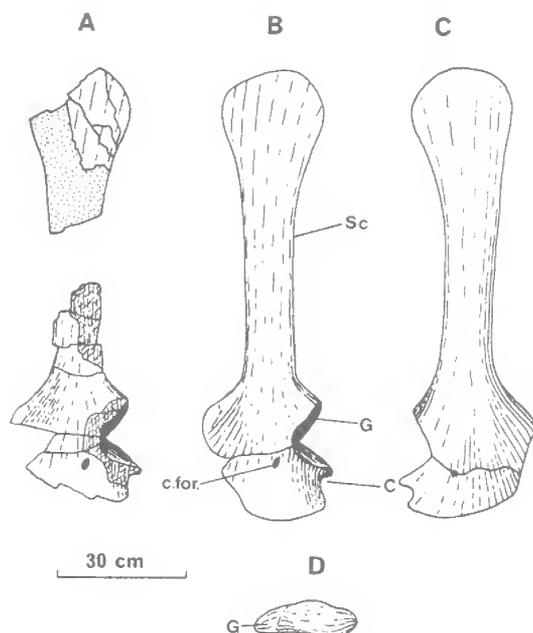


FIG. 5. Left scapulocoracoid of *Muttaburrasaurus langdoni* (QM F6140). A, lateral view as preserved; B, lateral view reconstructed; C, medial view reconstructed; D, glenoid aspect reconstructed. Abbrev.: C, coracoid; c.for., coracoid foramen; G, glenoid; Sc, scapula. Hatched areas represent broken surfaces.

but that on the right is better represented. Contact between the proximal and distal extremities is not preserved. The scapula is illustrated in Fig. 5.

The bone is apparently long and slender but is much more robust proximally. The distal end is expanded and the shaft is gently curved, conforming with the shape of the rib cage. From the mid-shaft area the dorsal border is nearly straight, but ascends abruptly anteriorly at the coracoid contact. A well-defined facet is present for the coracoid. Externally, the proximal end is broadly convex but internally the surface is concave. Ventrally, it is expanded into a posteroventral extension, comprising the bulk of the glenoid cavity. Both the glenoid cavity and the articulation for the coracoid are rugose. The anterior edge of the scapular blade is thin and rounded as is the posterior edge, continuing slightly onto the dorsal surface. The dorsal edge is thicker.

CORACOID. Coracoids are known from fragments from both sides and the element is figured in Fig. 5. The bone is apparently small, short and deep. It is thick along the scapular facet, while the distal portion become much thinner. Externally the bone

is shallowly concave over the dorsal two-thirds and convex towards the ventral border. It is broadly sigmoid internally and externally along the scapular articulation and the coracoid contributes slightly less to the glenoid cavity than does the scapula. The articulation is sigmoid, ovate and rugose. The coracoid foramen is complete and opens internally in a broad notch along the articular margin. Ventrally, the margin is sharply concave anterior to the glenoid cavity limit.

STERNUM

Sternal bones have not been located with certainty, although fragments may represent these elements.

THE FORE-LIMB

HUMERUS. The humerus is incompletely represented from the left side. As with other limb bones, shedding and bone loss have occurred particularly in the mid-shaft region and have proceeded to the extent of excluding contact between proximal and distal parts. This is shown in Fig. 6, while measurements are listed in Table 2.

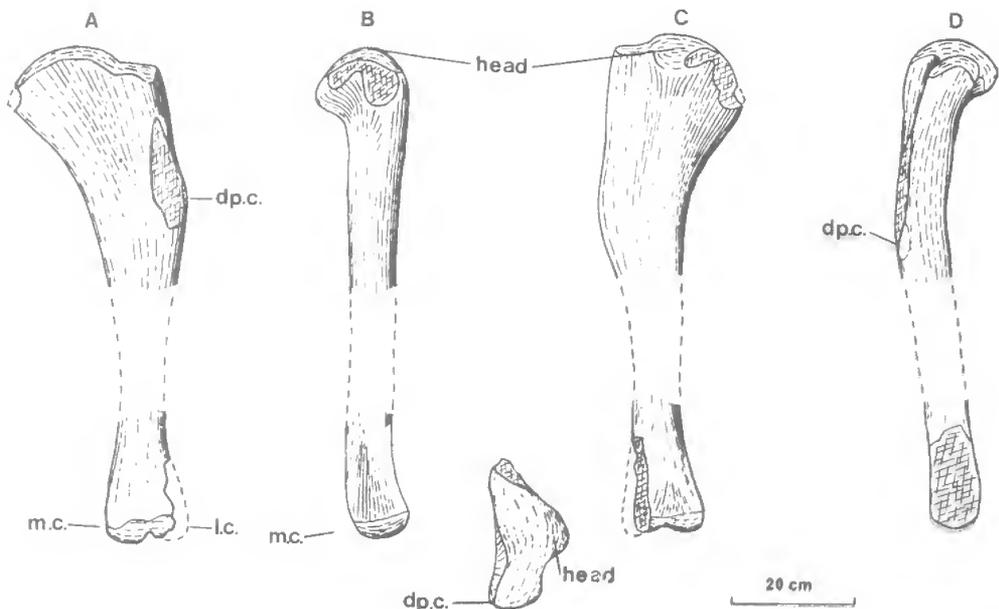


FIG. 6. Left humerus of *Muttaburrasaurus langdoni* (QM F6140). A, anterior view; B, medial view; C, posterior view; D, lateral view; E, proximal view. Abbrev.: dp.c., deltopectoral crest; l.c., lateral condyle; m.c., medial condyle. Hatched areas represent broken surfaces.

TABLE 2

MEASUREMENTS OF GIRDLE AND LONG BONES (CM)

Element	Length	Proximal width	Distal width
Scapula, lt.	—	27.7*	—
Coracoid, lt.	—	26.1*	—
Radius, lt.	—	10.5	8.7
Ulna, lt.	—	14.4	10.2
Femur, rt.	101.5	34.4	34.0
Tibia, rt.**	96.2	—	—
Fibula, rt.	—	19.7	11.6

*at glenoid border

**with calcaneum + astragalus

The humerus is elongate being the longest element of the fore-limb. It exhibits a sigmoidal flexure in lateral view, the proximal end being more posteriorly positioned than the distal end. Proximally, the head is expanded transversely and posteriorly. Towards the centre of the shaft, the posterior surface is broadly convex whereas the anterior surface is nearly flat, these being joined by rounded margins. The medullary cavity is extensive, at least in the mid-shaft region. The proximal moiety of the bone is strongly curved medially, with the head positioned internal to the plane of the distal moiety. The head is subspherical, positioned approximately in the centre of the proximal surface, supported by a strong buttress arising abruptly from the posterior surface of the shaft. Greater and lesser tuberosities are well developed. The proximal surface, particularly of the head, is rugose. Below the head, the anterior surface is broadly concave, particularly towards the weakly-developed deltopectoral crest which extends well down the length of the shaft. The crest progressively thickens distally toward the apex and its margin is rounded.

Distally, the humerus is robust and heavy, being more expanded transversely than anteroposteriorly. Both the radial and mesial condyles are defined

and are separated by a deep, wide concavity for the olecranal process. The mesial condyle is produced more distally than the radial condyle but the latter slopes anterolaterally from the posterior surface while the former has a mesial surface which is rounded but near vertical. The posterior surface of the distal end is slightly concave and the articulation is rugose. The supinator ridge is moderately well developed.

ULNA. Only the left ulna is preserved and a mid-shaft fracture has minimal contact. Measurements are provided in Table 2 while the bone is illustrated in Fig. 7. The ulna is somewhat longer and considerably heavier than the radius but is shorter than the humerus. It is more expanded proximally than distally. Part of the olecranal process is lacking but the process was apparently not extensive. The articulating surface is shallowly concave and moderately narrow. Anteriorly, the surface of the shaft and the head are shallowly concave to accommodate the radius, while mesially the shaft is flattened.

The ulna is slightly expanded distally and shows moderate anterior concavity. Posteriorly, the bone is correspondingly convex. The long axis of the distal expansion is inclined to that of the proximal expansion at an angle of 60°. The articulating surface is rugose and is broadly convex in both directions. Towards the centre, the shaft narrows and is subtriangular in section with a small medullary cavity.

RADIUS. Only the left radius is preserved and, although nearly complete, has minimal contact in the mid-shaft area. Its measurements are presented in Table 2 and it is shown in Fig. 7. It is the smallest and shortest bone of the fore-arm. Its distal end is somewhat expanded with an approximately semicircular articulation. The shaft is not greatly constricted. In section, it is subelliptical towards the mid-shaft region with the long axis directed anteroposteriorly, the section becoming more circular proximally.

The articulation of the elbow was located *in situ*.

CARPALS. The bones of the wrist are preserved

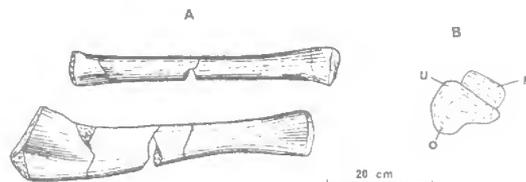


FIG. 7. Antebrachial elements of *Muttaburrasaurus langdoni* (QM F6140). A, lateral view; B, proximal view. Abbrev.: o. olecranon; R, radius; U, ulna. Hatched areas represent broken surfaces.

only on the left side. Because of partial disassociation they are difficult to interpret and it is uncertain whether all elements present have been preserved. Six elements only are discernable.

Only a fragment of the radiale is preserved, this closely adpressed to the lateral margin of the intermedium.

The intermedium viewed anteriorly (and allowing for slight loss posterodorsally) was semi-circular in shape with a truncated anterodorsal corner. Remains of a large distal carpal element exist below the intermedium.

The ulnare is cushion-shaped with a smooth, concave proximal surface forming the chief contact with the ulna. The posterior surface is concave. It appears to slightly over-ride the margin of the intermedium, with which it articulates. Remains of a small carpal element, possibly C5, are present lateral to the ulnare.

A further large distal carpal element is present below the ulnare. All carpals are well ossified with clear articular relationships.

METACARPALS. Only two metacarpals from the left forefoot are known and these have been interpreted as metacarpals IV and V. Measurements are listed in Table 3.

Metacarpal IV is short and stout and is constricted mesially, with moderately expanded articular ends. The proximal articulation is slightly concave transversely and slightly convex dorsoventrally. Distally, the articulation is more strongly convex. In section, the shaft is subcircular.

Metacarpal V is similar in shape to metacarpal IV but is slightly shorter and slightly less robust.

PHALANGES. Again, well preserved phalanges are only known from the left manus, associated with the metacarpals interpreted as IV and V and are illustrated in Plate 2 with measurements listed in Table 3. Digit IV has at least three phalanges present while digit V has four. Additional fragmentary, isolated phalanges are present but cannot be assigned with certainty.

The proximal phalanx of digit IV is robust and short. The dorsal rim of the proximal articulation is weakly convex whereas the articulation is dorsoventrally weakly concave. The mesial extension of the distal articulation is produced to a greater extent than the lateral. The dorsal rim is deeply concave while the articulation is dorsoventrally convex. Ventrally, the bone is somewhat flattened while it is somewhat convex dorsally. The second phalanx is considerably smaller. Dorsally, it is weakly convex proximally and concave distally. Only part of the proximal articulation of the third phalanx of digit IV is preserved.

The proximal phalanx of digit V is slightly shorter than that of digit IV and appears to have been less robust. The second phalanx is slightly longer than its counterpart in digit IV. The third phalanx is short and reduces in width rapidly towards its distal end. A very small, sub-circular nugget of bone is preserved as a continuation of this digit which is interpreted as the terminal phalanx of digit V.

An isolated fragmentary element, interpreted as the ungual phalanx possibly from digit II, is very large, robust and tapers anteriorly.

An incomplete element from which there has been much shedding, seems to represent a manual spike comparable to that of *Iguanodon*. The flattened element tapers strongly from a slightly convex basal articular surface, apparently toward an apex now missing. If this is properly interpreted as a manual spike, it was larger with respect to the metacarpals than in *Iguanodon*.

THE PELVIC GIRDLE

ILIUM. The right ilium is almost complete but only weathered fragments of the left are preserved. Although incomplete, the anterior process accounts for about two-fifths of the total ilial length (Fig. 8). Measurements for the ilium appear in Table 2. The shallow process is directed ventrally and laterally apparently to clear the ribs. The dorsal surface is inflated medially from above

TABLE 3
MEASUREMENTS OF MANUAL AND PEDAL ELEMENTS
(CM)

Element	Length	Proximal width	Distal width
Metacarpal IV	8.7	5.6	5.1
Metacarpal V	7.7	—	5.3
Phalanx IV, 1	4.4	4.6	—
Phalanx IV, 2	2.6	4.0	—
Phalanx V, 1	4.0	4.7	—
Phalanx V, 2	2.9	3.6	—
Phalanx V, 3	2.2	2.2	—
Metatarsal I	—	7.7	—
Metatarsal II	45.9	11.2	11.8
Metatarsal III	—	10.9	14.0
Phalanx II, 1	11.1	12.7	—
Phalanx II, 2	10.5	9.8	—
Phalanx III, 1	—	14.4	—
Phalanx III, 2	11.7	12.8	—
Phalanx IV, 1	16.1	11.5	—

the centre of the acetabulum, anteriorly to near the limit of the anterior process and is reasonably strongly sinuate in outline from above and broadly convex laterally.

The bone is deepest and thickest above the anterior portion of the acetabulum. A slight lateral expansion of the dorsal border is present above the level of the anterior acetabulum extending anteriorly to above the level of the preacetabular notch. Generally, the ilium is thin. Dorsoventrally, the lateral surface is weakly concave from above the preacetabular notch anteriorly along the anterior process. Internally, the body of the ilium is more strongly concave, with the development of a strong, tuberculate ridge above the articular facets for the sacrum. This ridge exists along the bulk of the length of the ilium from above the base of the anterior and postacetabular processes, extending about midway between the dorsal margin and the acetabulum in the main body of the ilium. Articular facets for the sacral vertebrae are poorly defined but are present between the pre- and postacetabular notches.

The postacetabular process is slightly incomplete. It appears that the mesial shelf developed

towards the base may disappear before reaching the posterior extremity. Length of the process from the ischial tuberosity is about one-quarter the ilial length as preserved. The preacetabular notch is moderately wide. The pubic peduncle is long and deflected. Within the acetabulum, the inner surface of the pubic peduncle is moderately expanded laterally and ventrally from above providing a moderately concave roof for the head of the femur. The acetabular broader is well defined anteriorly but less well defined posteriorly. The ischial peduncle swells rapidly posteriorly and laterally forming a strongly concave tuberosity for the articulation of the ischium. In its contribution to the acetabulum, it has a rugose articular surface. Anteriorly the medial margin of the ilial acetabulum is prolonged ventrally to partially wall the acetabulum medially. The postacetabular notch is virtually absent being represented only by a weak, broad concavity.

PUBIS. Parts of the pubis are known from both sides. The bone shown in Fig. 8 and measurements appear in Table 2. Although contact is poor, little of the prepubic process is believed missing. It is elongate and deep. The blade is thin and slightly

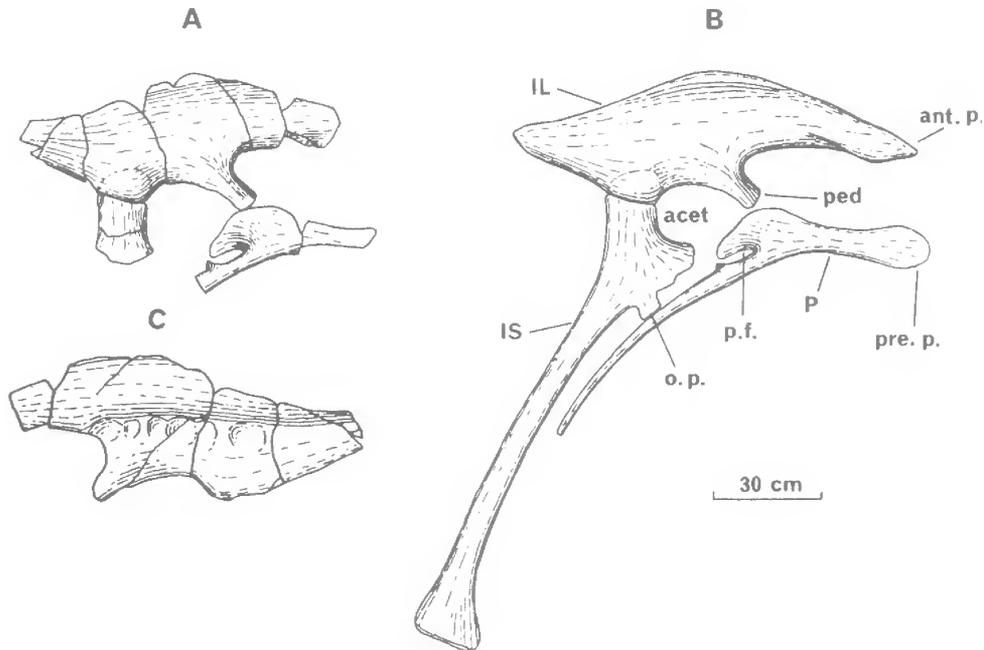


FIG. 8. Right pelvis of *Muttaburrasaurus langdoni* (QM F6140). A, lateral view of pelvic elements as preserved; B, lateral view of pelvis reconstructed; C, ilium in medial view. Pubis in A represents portions preserved of both right and left pubes. Abbrev.: acet, acetabulum; ant.p., anterior process; IL, ilium; IS, ischium; o.p., obturator process; P, pubis; ped, pubic peduncle; p.f., pubic foramen; pre.p., prepubic process.

expanded distally, producing a marked dorsal concavity behind the anterior margin. The dorsal margin is thicker than the ventral which appears to be subacute. The process is slightly sigmoidal in dorsal view.

The main body of the pubis is thicker, especially dorsally. A subtriangular facet is present dorsally which articulates with the pubic peduncle of the ilium. The acetabular border is anteroposteriorly concave, moderately broad and shallowly concave transversely. Again the medial margin rises to form a medial wall for the acetabulum, especially anteriorly. The acetabular border is approximately ovate in shape, extending posteroventrally as a moderately extensive process. The process dorsally bounds a large pubic foramen. The postpubis borders the foramen ventrally and has a short projection of bone which incompletely encloses the foramen posteriorly. The postpubis is very slender but largely missing.

ISCHIUM. Each ischium is represented by the proximal ends only (Fig. 8). The proximal end has a broad, deeply curving proximal border forming a part of the ventral and posterior acetabular boundaries. The articular surface for the ilium is expanded laterally and is posteriorly convex and anteriorly concave transversely and slightly concave anteroposteriorly. The surface is rugose. The articulation is complete with the ischial

peduncle of the ilium. Below the ilial branch, the ischium becomes narrow and plate-like. The pubic branch and the obturator process are lacking.

THE HINDLIMB

FEMUR. The femur is reasonably well known from both sides of the body but in each, shedding has occurred in the mid-shaft region. Fig. 9 illustrates the extent of this as well as a reconstruction.

The femur is the longest and most robust bone in the hindlimb. Measurements are provided in Table 2. The shaft is strongly curved in the parasagittal plane. The head is clearly defined, set nearly at right angles to the shaft. It is robust, sub-spherical with the dorsal surface rugose, and with the neck compressed anteroposteriorly. A shallow, well-defined groove extends on the posterior surface from the head towards the body of the shaft.

The greater trochanter is massive, widely expanded anteroposteriorly and gently convex proximally, produced to about the same level as the plane of the head. The dorsal surface between the head and the greater trochanter is shallowly concave. The lesser trochanter is a large structure originating from the anterolateral border of the shaft and produced proximally to about the same level as the great trochanter, separated from it by

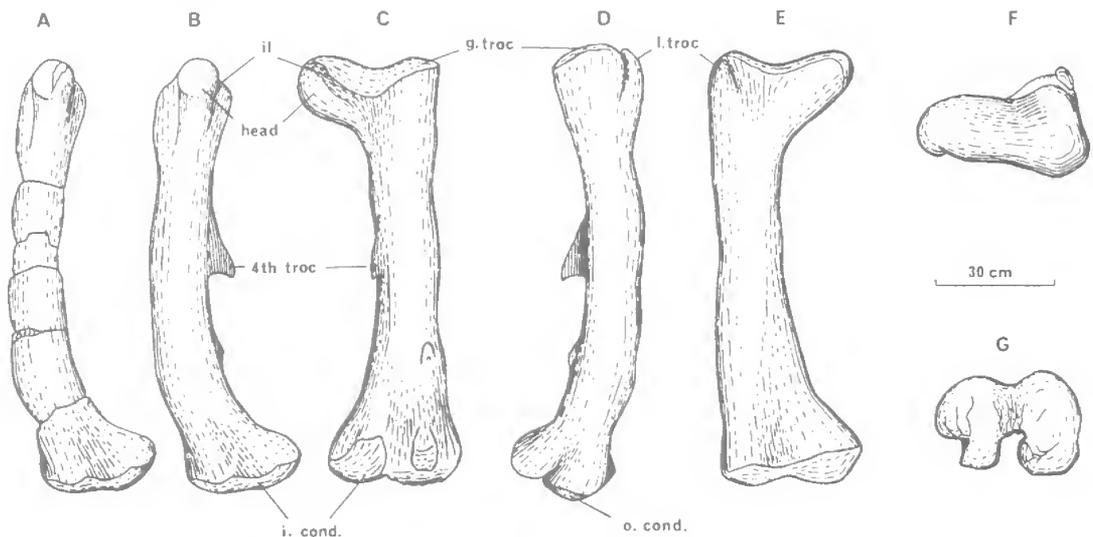


FIG. 9. Right femur of *Muttaburrasaurus langdoni* (QM F6140). A, F and G, femur as preserved, others reconstructed. A and B, medial view; C, posterior view; D, lateral view; E, anterior view; F, proximal view; G, distal view. Abbrev.: g.troc, greater trochanter; i.cond., medial condyle; il, fossa for ischial peduncle; l.troc., lesser trochanter; o.cond., lateral condyle; 4th troc, fourth trochanter.

a deep, narrow cleft. It is placed anterolateral to the greater trochanter. The anterolateral border of the shaft is subangular in the proximal one-third owing to a ridge from the lesser trochanter base which continues to curve across the anterior face of the shaft. This divides two flattened surfaces almost at right angles to one another. Posteriorly the shaft is longitudinally concave. The base of a large fourth trochanter is present posteromesially. An isolated fourth trochanter shows this structure to have been pendant in its free extent.

Distally, the shaft terminates in well-developed inner and outer condyles, separated by a deep, intercondylar groove. The inner condyle is more robust than the outer and its articular surface is more extensive. The interior, dorsal border of the inner condyle shows coarse striations. The intercondylar groove has a deep, narrow extension into the body of the inner condyle, approximately opposite a shallow concavity on the mesial surface. A deep cleft bounds the outer condyle posterolaterally. Strong ridges ascend the body of the shaft posteriorly from the inner and outer condyles giving the shaft a concave popliteal surface. The lateral ridge is expanded at a position about one-third the length of the femur from the distal end into a lateral supracondylar tuberosity with a shallow pit directed posteriorly. Distally the anterior surface of the shaft is broadly concave

longitudinally to form a shallow anterior intercondylar sulcus then markedly swollen opposite the lateral supracondylar tuberosity. The distal articulating surface is extremely rugose.

TIBIA. Tibiae are preserved on both sides but the right is more complete. In each, shedding has occurred in the mid-shaft region. The right tibia is illustrated in Fig. 10 together with a reconstruction. The bone is robust and slightly shorter than the femur. Its proximal extremity is heavier than the distal and is expanded both laterally and anteroposteriorly, the latter expansion being the greater. This expansion occurs on the mesial portion of the head and produces a robust inner condyle, separated by a deep, narrow popliteal notch from a strong outer condyle. The proximal articular surface is rugose and convex with the inner condyle contributing considerably more than the outer to its area, but both extend posteriorly to about the same extent. Anterolaterally, a broad cnemial crest is present which extends somewhat diagonally well down the length of the shaft.

Posterior to the crest is a gently concave surface for the inner surface of the fibula. The anteromesial margin of the shaft in this area is broadly convex transversely. The extension of the cnemial crest passes internally to merge with the base of the inner malleolus. Towards the middle of the body of the shaft, expansion occurs laterally

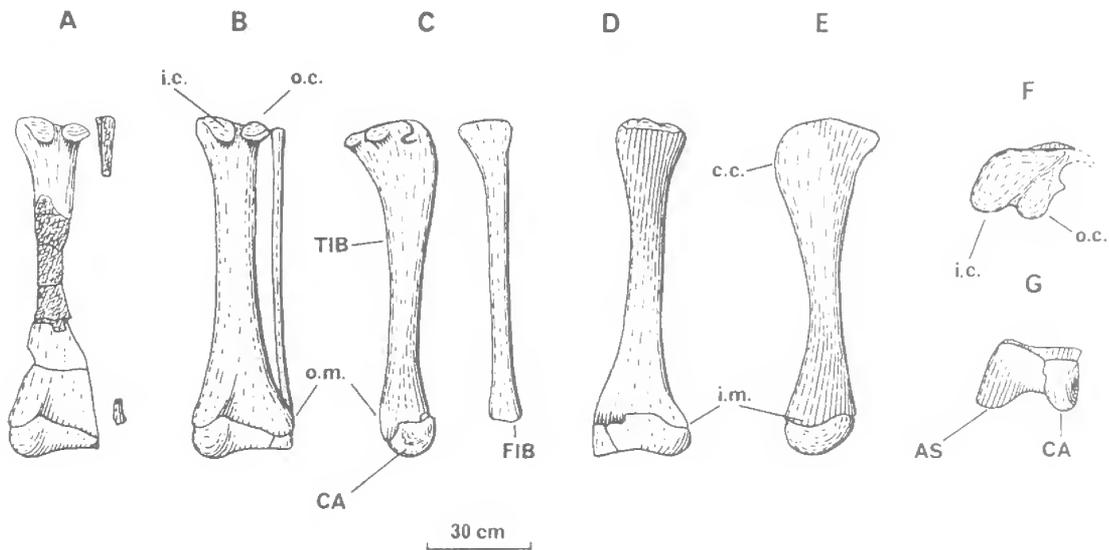


FIG. 10. Right crus and proximal tarsus of *Muttaburrasaurus langdoni* (QM F6140). A, F, and G, material as preserved, others reconstructed. A and B, posterior view; C, lateral view; D, anterior view; E, medial view; F, proximal view; G, distal view. Abbrev.: AS, astragalus; CA, calcaneum; c.c., tibial crest; FIB, fibula; i.c., inner condyle; i.m., inner malleolus; o.c., outer condyle; o.m., lateral malleolus; TIB, Tibia.

with resultant rotation of the greatest breadth of the bone, this continuing to the distal end. The anterior surface distally is nearly flat, with a shallow anterolateral depression for the distal end of the fibula. The concavity between the distal malleoli continues for only a short distance along the shaft. The articulation for the astragalus and calcaneum is broadly and deeply concave transversely and convex anteroposteriorly. A strong ridge ascends from the highest point along the posterior border.

FIBULA. The proximal portions of both fibulae and the distal extremity of the right fibula are represented. The extent of the bone preserved is indicated, reversed, in Fig. 10, together with a reconstruction. The bone was long and slender, and measurements appear in Table 2. On the right side the distal portion of the tibia retains its articulation with the astragalus and calcaneum, and the distal portion of the fibula may also be articulated here. The position of the latter shows that the fibula must have been slightly shorter than the tibia.

The proximal end of the fibula is expanded anteroposteriorly, the posterior expansion being the greater, with a broadly convex outer margin and a shallowly concave inner margin closely juxtaposed with the head of the tibia. The proximal articular surface is gently convex transversely and rugose. The anteroposterior breadth of the bone continues greater than the transverse below the head, but towards the middle

of its length the shaft becomes subtriangular in section.

Distally, the extremity is incomplete but robust. Anterolaterally it is produced into a low, rounded process. A medial break and the position of the astragalus articular surface for the fibula indicate that it must have curved anteriorly around the tibia to articulate mesially with a dorsolaterally placed surface of the astragalus.

ASTRAGALUS. The astragalus is the largest bone of the tarsus. It has been preserved on both sides, fused with the calcaneum and closely adhering to the tibia. It is illustrated in Fig. 10 showing its greater mesial than lateral depth. Distally, the articulation is strongly convex anteroposteriorly and concave transversely. A low broad process is present at the posterior proximal border opposite a strong ridge on the tibia. Anteriorly, a low ascending process forms a junction with the tibia, is broadly convex transversely but laterally a strong, but low process is present bearing the dorsolaterally facing articulation for the fibula (Fig. 11).

The distal articulating surface is coarsely rugose. The proximal articulation is concave anteroposteriorly. When in articulation, the astragalus is much more exposed anteriorly than posteriorly.

CALCANEUM. Both calcanea are preserved but that on the left side is more complete. The bone is illustrated in Fig. 10 and is closely associated with the tibia and fused with the astragalus. Anteriorly,

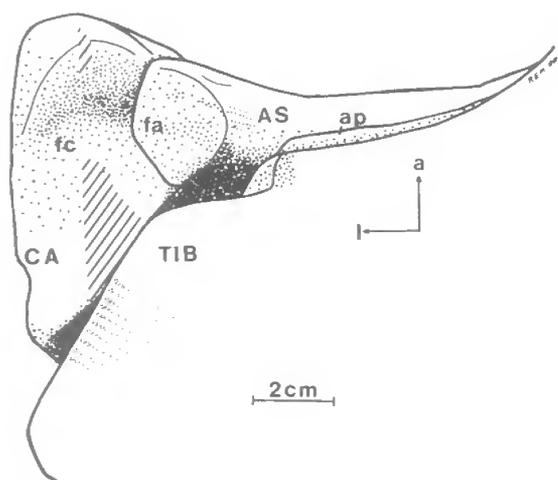


FIG. 11. Dorsal view of left proximal tarsus in articulation with tibia, of *Muttaburrasaurus langdoni* (QM F6140) showing the fibular facet of the astragalus. Abbrev.: a, anterior; ap, ascending process of the astragalus; AS, astragalus; CA, calcaneum; fa, fibular facet of astragalus; fc, fibular facet of calcaneum; l, lateral; TIB, anterior face of tibia. Diagonal lines represent broken surfaces.

the border of the calcaneum is approximately as deep as the posterior border. In anterior view, it is less exposed than the astragalus. The proximal surface is transversely and anteroposteriorly concave. The exposed articulation for the fibula is strongly concave anteroposteriorly and transversely is strongly concave to accommodate the posterolateral margin of the tibia, this being separated from the tibial articulation by a sharp, strong ridge. The distal articulation is rugose, broadly convex anteroposteriorly and weakly convex transversely.

DISTAL TARSAL I. Only a small fragment, possibly representing this element, has been located, closely adhering to distal tarsal II from the right side but it is too fragmentary to warrant description.

DISTAL TARSAL II. This element is known from both sides (Fig. 12). On the left side it is preserved somewhat displaced above metatarsal II and part of metatarsal III. It is a relatively thin bone, subhexagonal in proximal view and with an anteroposteriorly convex articulating surface. Transversely, this surface is slightly concave while the inner border is deeper than the outer. It articulates proximally with the astragalus. The distal articulating surface is slightly concave and is marked by a low, broad ridge running transversely from the lateral aspect towards the centre of the surface. Measurements are provided in Table 3.

METATARSALS. No metatarsal is preserved completely. Fragmentary remains are known from both sides but the left foot is more completely

preserved. This is illustrated in Fig. 12 together with a reconstruction and measurements are provided in Table 3.

Proximal and distal ends of metatarsals II–IV are known for the left foot but all bones have been broken in the mid-shaft region. Only metatarsal IV has its length confirmed by fitted fragments but shape of the shaft in this and other metatarsals has been modified by shedding. Metatarsal IV appears to have been a long, relatively slender bone, the longest of the metatarsal series. Its proximal end, although incomplete, is rugose and is expanded both anteroposteriorly and transversely but the former is the greater. The articulation is nearly flat. In the shaft area, an anteromesial angle is present. Distally, the bone is slightly angled laterally. The head is expanded in both mesial and lateral moieties with the articulation rugose, transversely broad and deep, strongly convex anteroposteriorly and weakly concave transversely.

Metatarsal III is the heaviest element. Its proximal articulation is flattened and rugose but a narrow, deep notch is present about mid-way along its lateral rim. The head is slightly incomplete but is much more expanded anteroposteriorly than transversely. The transverse expansion is greater anteriorly and posteriorly than above the centre of the shaft, giving the head a waisted appearance in proximal view. Anteriorly, the head somewhat overhangs the shaft, this being more pronounced at the anterolateral border. The shaft is very angular anteromesially and considerably less angular anterolaterally. The

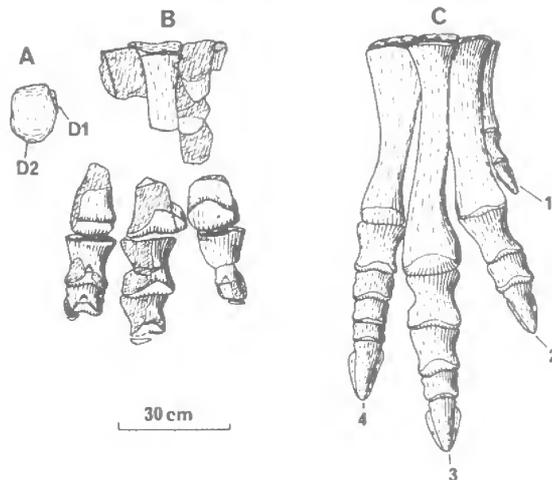


FIG. 12. Right pes of *Muttaborrasaurus langdoni* (QM F6140). A, the distal tarsals preserved; B, pes as preserved; C, pes reconstructed. Abbrev.: D1, distal tarsal 1; D2, distal tarsal 2.

anterior surface is flattened towards the proximal end. Distally, the bone is considerably expanded, this being greater transversely than anteroposteriorly. Deep depressions are present laterally and mesially. The articulation is rugose, broadly convex anteroposteriorly and shallowly concave transversely.

Metatarsal II is moderately robust. Its proximal articulation is partly masked by tarsal II but is rugose and apparently flat. It is expanded more strongly anteroposteriorly than transversely. The shaft appears more angular anterolaterally but shedding has occurred anteromesially. Distally, the bone is expanded but the anteroposterior expansion here remains greater than the transverse. The lateral portion of the distal articulation appears much stronger than the mesial, directing the articulation slightly inwards. The head is rugose, broadly convex anteroposteriorly and shallowly concave transversely.

There is no indication of metatarsal V, and if present it was excluded from the foot. The right metatarsus is less complete than the left, the distal ends of three metatarsals and the proximal ends of two being represented. One of these proximal ends however (*vide* Table 3) is considerably smaller than any of those of the left metatarsals, and of different form. It is thus interpreted as the proximal end of metatarsal I. The proximal articular surface is subtriangular in proximal aspect and strongly convex anteroposteriorly. It is slightly rugose. Little of the shaft is preserved but indicates that the cross-section was basically in the form of a thin isosceles triangle with the base directed anteriorly.

PHALANGES. Some phalanges from both feet are preserved but those from the left side are more complete. Extent of preservation is indicated in Fig. 12 and measurements are presented in Table 3. The reconstruction includes elements which are not represented at all. Only proximal elements of digits II–IV are known.

The proximal element of digit II is the longest in the foot. Its proximal articulation is considerably expanded and obliquely subovate, the outline being generally rounded except ventrally where a reasonable concavity is present. The articulation is slightly concave. The mesial surface of the shaft is convex while the lateral surface is flattened. Distally, the articulation is expanded. Deep depressions are present laterally and mesially, flanked by heavy, rounded ridges around the margins of the articular surface. No other phalanges are preserved on digit II.

The proximal phalanx of digit III is moderately

elongate and is more robust than that of digit II. The proximal articular surface is similar to that in digit II but is slightly less concave ventrally and its oval outline is not oblique. The mesial moiety of the distal articulation is slightly more extensive than the lateral. Deep mesial and lateral depressions are present bounded by strong, rounded ridges limiting the articular surface. The second phalanx of digit III is short compared with the first (Table 3). Proximally, the dorsal and ventral borders are expanded into lips which fit around the articulation of the first phalanx. The lateral borders of the expanded proximal articulation are hollowed with the mesial moiety larger than the lateral. The distal articulation is concavoconvex to fit the third phalanx. Depressions are present mesially and laterally at the distal end of the shaft. Only the dorsal and ventral lips of the third phalanx are preserved.

In digit IV, the proximal phalanx is robust and short; shorter than those in digits II and III (Table 3). The articulating surface of the proximal end is concave and subovate, being flattened ventrally and more vertical mesially than laterally. Its distal articulation is approximately symmetrical like that in the corresponding bone of digit III, but the lateral moiety slopes outwards slightly more than the mesial. The lateral and mesial depressions are, however, less well defined. The second phalanx is relatively short (Table 3). It is like the corresponding bone of digit III, but is more vertical mesially than laterally. Lateral and mesial depressions near the distal articulation are comparatively shallow.

COMPARISON

INTRODUCTION

Recently much work has appeared on the non-hadrosaurian ornithopods. Galton has studied *Camptosaurus* (1980), *Dryosaurus* (1977a), *Hypsilophodon* (1974a), *Parksosaurus* (1973b), *Thescelosaurus* (1974b), *Valdosaurus* (1977b), *Vectisaurus* (1976) and the fabrosaurids (1978). He has not had the field to himself: Dodson (1980) is studying *Camptosaurus* and *Tenontosaurus*, Norman is working on *Iguanodon*, Rozhdstvenskii (1966) has described *Probactrosaurus*, Santa Luca (1980) has described *Heterodontosaurus*, Thulborn both fabrosaurids (1970a, 1970b, 1971, 1972, 1974) and hypsilophodontids (1973), and Taquet *Ouranosaurus* (1976). Hadrosaurs as well have had their share of work: Ostrom (1961), Rozhdstvenskii (1965, 1968) and Dodson (1975).

We can do no better than to quote Dodson (1980): 'Suddenly ornithopods have become a very-well studied group.'

Galton (1972) redefined the families of non-hadrosaurian ornithopods, later (1978) refining his definition of the Fabrosauridae. Basically Galton considered the Iguanodontidae as a grade of large, graviportal, non-hadrosaurian ornithopods (see also, Galton, 1974b). Dodson (1980) has pointed out the unsatisfactory nature of this definition and implicitly presented a new definition exemplified with *Camptosaurus*. Dodson's definition, restricted to the postcranial anatomy, comprised the following features:

- (1) scapular blade constricted with strong flare at coracoid articulation;
- (2) prominent acromion with clavicular facet;
- (3) coracoid short with respect to scapular length;
- (4) coracoid subquadrate in form, with abrupt craniodistal angle;
- (5) coracoid foramen near the scapular articular surface, opening mesially at the scapulocoracoid articulation;
- (6) humerus relatively short and narrow;
- (7) deltopectoral crest weak, giving a proximal to distal taper to the humerus;
- (8) radius distally compact and rounded;
- (9) carpus compact and heavily ossified;
- (10) carpal articular relationships well defined;
- (11) three proximal and five distal carpals present;
- (12) ilium massive, with straight dorsal margin;
- (13) moderate medial reflection of postacetabular ventral margin of ilium;
- (14) prepubis deep and flat, postpubis stout and decurved;
- (15) ischial shaft rounded and decurved with distal expansion;
- (16) femur curved with prominent lesser trochanter;
- (17) well-defined anterior intercondylar sulcus on femur;
- (18) pes short and stocky, metatarsus and digits broad.

This is almost a description of *Muttaburrasaurus*.

Galton (1977a) illustrates variations found in skeletal elements of *Hypsilophodon foxii*. Some of Dobson's criteria (e.g. constriction of the scapular blade, subquadrate form of coracoid) here seem to occur as individual variations. Such variation however is difficult of interpretation. Some modern tetrapods, *Trichosurus vulpecula* (brush-tail possum) and *Trichosurus caninus* (bobuck) among mammals and *Amphibolurus nuchalis* and *Amphibolurus reticulatus* as well as *Ctenotis robustus* and *Ctenotis arcanus* (Czechura, pers. comm., 1980) among reptiles, would be virtually impossible to distinguish from skeletal material alone. Such osteological differences as exist would be interpreted as individual variations were these species known only from fossil material. Furthermore there is no suggestion that *Camptosaurus* exhibits the variation reported in *Hypsilophodon*, and thus we shall adopt here Dodson's (1980) criteria.

COMPARISON

The close agreement of *Muttaburrasaurus* with *Camptosaurus* in the features given by Dodson (basic agreement in fifteen of eighteen features, the remaining features being not determinable from the incomplete material of *Muttaburrasaurus*) implies that *Muttaburrasaurus* is an iguanodontid. Thus this section will include a brief comparison of *Muttaburrasaurus* with the other ornithopod families, but a more extensive comparison with the other well known iguanodontid genera.

In addition to being much larger and later than any known fabrosaurids, *M. langdoni* differs from the Fabrosauridae (Galton, 1978) in having: inset maxillary and dentary toothrows; a continuous, homodont dentition; well-defined occlusal wear surfaces on the maxillary dentition; ilium without lateral supra-acetabular flange; robust limb bones; and femur with massive greater trochanter. It differs from the Heterodontosauridae in lacking caniniform teeth and in having a well-developed anterior process to the pubis. (Galton, 1972). It differs from the Hypsilophodontidae in having a continuous wear facet on the maxillary teeth in one plane (Galton, 1972). It differs from the Hadrosauridae in lacking a dental battery of multiple tooth rows, but having only a single row each of maxillary and dentary teeth; having a reduced number of cervical vertebrae; and lacking a well-developed antitrochanter on the ilium (Lull & Wright, 1942).

Muttaburrasaurus langdoni shares the following characteristics with the iguanodontids, specifically with *Camptosaurus*:

- (1) scapular blade constricted with strong flare at coracoid articulation;
- (2) prominent acromion;
- (3) coracoid short with respect to scapula;
- (4) coracoid foramen near articular surface for scapula, opening mesially at the scapulocoracoid articulation;
- (5) humerus relatively narrow;
- (6) deltopectoral crest weak;
- (7) radius distally compact and rounded;
- (8) carpus compact and heavily ossified;
- (9) carpal articular relationships well-defined;
- (10) ilium massive;
- (11) medial postacetabular ventral margin of ilium reflected;
- (12) prepubis flat and deep;
- (13) femur curved with prominent lesser trochanter;
- (14) well-defined anterior intercondylar sulcus on femur;
- (15) pes short and stocky, metatarsus and digits broad.

Muttaburrasaurus is clearly referable to the Iguanodontidae on postcranial characteristics. *M. langdoni* shows some specific similarities to *Camptosaurus* which it does not share with the other well-known genera of iguanodontids (*Iguanodon*, *Ouranosaurus*, *Probactrosaurus*, and *Vectisaurus*). These include the possession of a skull that is low and broad, especially in the postorbital region, and a pes with four metatarsals (although there is no indication that the pes of *M. langdoni* was tetradactyl).

Muttaburrasaurus however shows clear distinction from each of the well known iguanodontid genera. It may be distinguished from the species of *Iguanodon* by:

- (1) presence of the inflated nasals,
- (2) much more extensive quadratojugal,
- (3) presence of the surangular boss,
- (4) postorbital region of skull low and broad,
- (5) maxillary teeth lacking carina,
- (6) caudal centra strongly excavated ventrally, and
- (7) femoral shaft more strongly curved.

It may be distinguished from *Ouranosaurus nigeriensis* by:

- (1) presence of the inflated nasals, but
- (2) absence of the low domes of the posterior portion of the nasals,
- (3) presence of the surangular boss,
- (4) maxillary teeth lacking carina,
- (5) dorsal vertebrae with low to moderately, but not extremely, elevated spines,
- (6) carpals not fused,
- (7) anterior process of pubis less deep,
- (8) femoral shaft curved,
- (9) lesser trochanter placed nearly anterior to greater, and
- (10) pes with four metatarsals.

It may be distinguished from *Camptosaurus* by:

- (1) presence of the inflated nasals,
- (2) maxillary teeth lacking carina,
- (3) radius and ulna more slender,
- (4) metatarsal II (and hence presumably the other metatarsals) more slender,
- (5) astragalus fused with calcaneum, and
- (6) low ascending process present on astragalus.

It may be distinguished from *Vectisaurus valdensis* by:

- (1) posterior dorsal vertebrae with less elevated neural spines,
- (2) dorsal neural spines not cleft posteromedially,
- (3) posterior faces of dorsal centra only slightly concave, and
- (4) indication of six, rather than five, sacral vertebrae.

It may be distinguished from *Probactrosaurus* spp. by:

- (1) broad post-infratemporal bar,
- (2) postorbital region of skull low and broad,
- (3) anterior portion of maxilla shallow, and
- (4) longer preacetabular process on ilium, and
- (5) femoral shaft more strongly curved.

Photographs of a mounted skeleton of *Probactrosaurus gobiensis* in Rozhdestvenskii (1973) and Saito (1979) aided our understanding of its differences from *Muttaburrasaurus*.

There are other characteristics that also distinguish *Muttaburrasaurus* from the (well-

known) iguanodontids. Except for *Camptosaurus*, none have the posteriorly sloping quadrate, nor do the others have contact between the fibula and astragalus (not included in the differential diagnosis because this is an inferred rather than observed character state). Thus it is clear that *Muttaburrasaurus* is as different from the known genera of iguanodontids as each is from the others, and is probably more distinct from most of them than *Iguanodon* is from *Probaetrosaurus*. It is also clear that its greatest similarity is to *Camptosaurus*, known from western North America and western Europe (Galton, 1980).

One other form to which *Muttaburrasaurus* must be compared, if only because of the apparent similarity in maxillary tooth form, is *Mochlodon*. *Mochlodon* Seeley 1881 is almost unanimously considered a subjective synonym of *Rhabdodon*

Matheron 1869 (de Lapparent & Lavocat, 1955; Romer, 1966; Steel, 1969; Olshevsky, 1978). The name *Rhabdodon* is preoccupied by Fleischmann, 1831, and hence we use the junior subjective synonym *Mochlodon*. The humerus of *Mochlodon* shows a well-developed deltopectoral crest (de Lapparent, 1947, pl. 4, fig. 9) and the lesser trochanter is less prominent (Matheron, 1869, pl. 5). Thus we feel that *Mochlodon* does not meet Dodson's criteria for an iguanodontid. *Muttaburrasaurus* clearly differs from *Mochlodon* in having strongly keeled dorsal centra, a nasal bulla, and a much higher number of maxillary teeth (18 in *Muttaburrasaurus*, 9 in *Mochlodon*). Even the crowns, although clearly similar, differ. A central carina is present on at least some maxillary crowns of *Mochlodon* (Nopcsa, 1904, pl. 2, fig. 1), and the number of

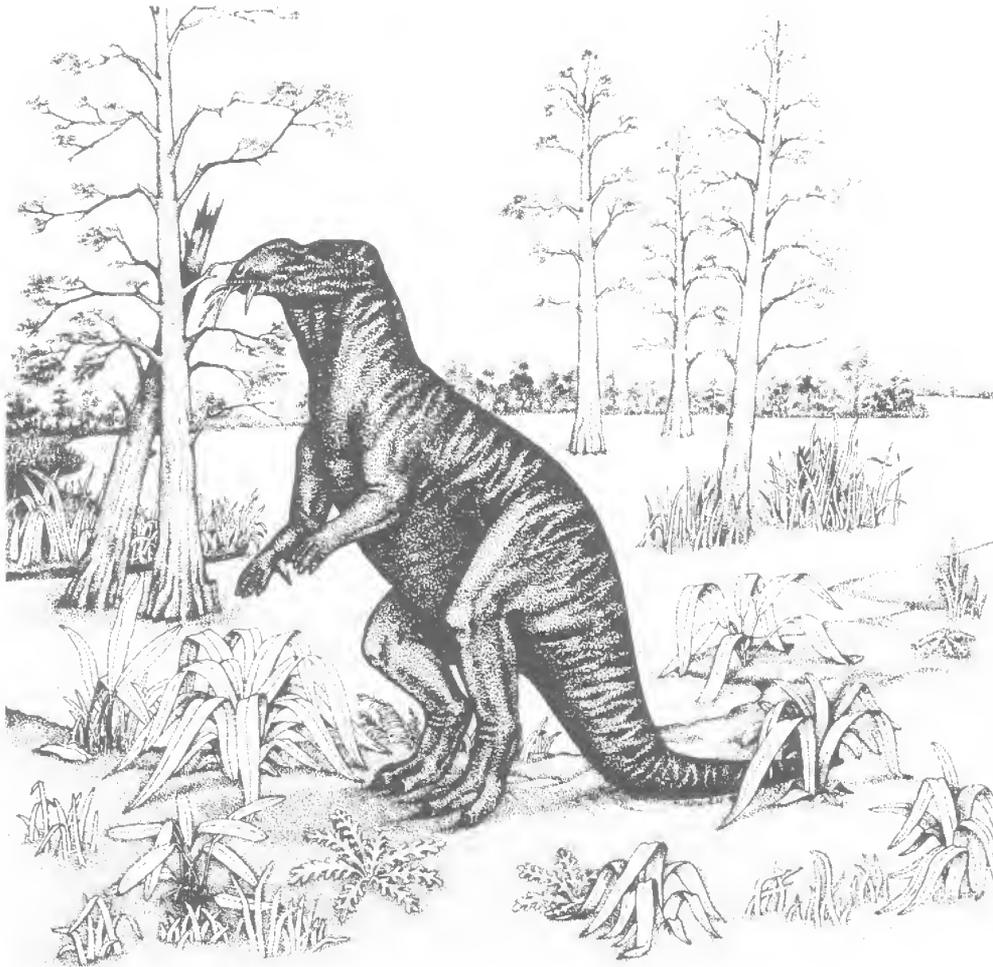


FIG. 13. Reconstruction of *Muttaburrasaurus langdoni*.

low ridges can be higher in *Mochlodon* (17 are visible on a tooth figured by Nopcsa, 1902, Taf. 2, Fig. 1). Thus one must take care in assessing relationships among ornithopods from tooth form, as has recently been stressed by Rozhdestvenskii (1977). Furthermore the radius, ulna and fibula of *Mochlodon* are much more massive than in *Muttaborrasaurus*, and the femur is curved in the transverse rather than the parasagittal plane (de Lapparent, 1947). Thus we feel that no close relationship is indicated.

DISCUSSION

The Iguanodontidae are known from Europe, Asia, North America, Africa and now Australia (Fig. 14), from the Tithonian to the Santonian (*Craspedodon*). They were obviously widespread, only South America not yet having yielded recognizable skeletal material. Even here there is evidence from footprints, *Camptosaurichnus* and *Iguanodonichnus* (Casamiquela and Fasola, 1968) from the Valanginian or Berriasian of Colchagua, Chile and *Sousaichnium* (Leonardi, 1976) from the Jurassic of Goias, Brazil, that iguanodontids were present. *Muttaborrasaurus* substantiates Colbert's (1973) comments on the distribution of iguanodontids into Australia.

Muttaborrasaurus is a moderately large iguanodontid, about 7 m long and 3 m high at the hips (Fig. 13). It is also one of the later iguanodontids (Table 4), and no subsequent iguanodontids are represented by specimens nearly as complete, although the contemporaneous

Probactrosaurus is represented by reasonably complete material (Rozhdestvenskii, 1966). *Muttaborrasaurus* and *Ouranosaurus* suggest a tendency towards elaboration of the cranial skeleton in later iguanodontids, although the number of specimens is still too few to elucidate this trend. There is no indication however that *Muttaborrasaurus* was on the line toward hadrosaurs, as *Ouranosaurus* (Taquet, 1975) and *Probactrosaurus* seem to have been. Thus whatever the selective advantage of the nasal bulla of *Muttaborrasaurus*, it was presumably a parallel development to the cranial structures of the hadrosaurs.

Unlike the condition of *Camptosaurus*, *Iguanodon* and the hadrosaurs, all of the maxillary (and presumably dentary) crowns are erupted to the same degree, as if the entire dentition were replaced *en masse* rather than piecemeal. Thus there appears a single wear surface over the whole tooth row, edged with enamel laterally in the maxillary dentition, and mesially in the dentary teeth. The occlusal plane, allowing for the distortion by mesial flexion of the toothrows, appears to have been almost vertical. The plane is also straight anteroposteriorly. Ergo the dentition appears to have functioned as a pair of shears, comparable to the dentition of the ceratopsians (Ostrom, 1964). Further work on this aspect of the anatomy of *Muttaborrasaurus* must await complete exposure of the skull, but we cannot help pointing out that the unusually broad post-infratemporal bar of *Muttaborrasaurus*



FIG. 14. Geographic distribution of iguanodontids. Solid circles indicate localities yielding iguanodontid skeletal remains: the taxa represented are those given in Table 4 plus the unstudied iguanodontid from Romania reported by Jurcsák and Popa (1978). The solid triangles represent iguanodontid tracks from regions where skeletal material has not been reported, tracks found on other continents (e.g. Asia, Europe) are not included. The open circle indicates a second iguanodontid locality near Hughenden in the Allaru Mudstone (specimen not collected). Map for the Lower Cretaceous, but Upper Jurassic and Upper Cretaceous localities included.

reflects increased volume of the adductor chamber and allows increased area of attachment for an expanded adductor mass. We can only speculate about the feeding habits, but perhaps this ornithopod was partially carnivorous.

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TABLE 4
THE DISTRIBUTION OF IGUANODONTIDS

Stage	Queensland	S. Africa	W. Africa	N. Africa	Mongolia	Iberian Peninsula	W. Europe	W. North America
Campanian								
Santonian							<i>Craspedodon lonzeensis</i>	
Coniacian								
Turonian								
Cenomanian							<i>Craspedodon hilli</i> & <i>Eucercosaurus tanyspondylus</i> *	
Albian	<i>Muttaborrasaurus langdoni</i>				<i>Probactrosaurus alashanicus</i> & <i>Probactrosaurus gobiensis</i>			
Aptian		<i>Ouranosaurus nigeriensis</i>		<i>Ouranosaurus?</i> sp. #			<i>Iguanodon mantelli</i>	<i>Camptosaurus depressus</i>
Neocomian					<i>Iguanodon orientalis</i>	<i>Iguanodon mantelli</i>	<i>Iguanodon bernissartensis</i> ** <i>Iguanodon fittoni</i> , <i>Iguanodon hollingtonensis</i> , <i>Iguanodon mantelli</i> & <i>Vectisaurus valdensis</i>	<i>Iguanodon ottingeri</i>
Tithonian							<i>Iguanodon hoggii</i>	
Kimmeridgian						<i>Camptosaurus</i> sp.	<i>Camptosaurus prestwichii</i>	<i>Camptosaurus dispar</i> ***
Oxfordian								

* Includes *Syngonosaurus macromerus*

** Also reported from this area and time are: *Iguanodon atherfieldensis*, *I. dawsoni*, *I. gracilis* and *I. seelyi*

*** Includes *Camptosaurus amplius*, *C. browni*, *C. medius* and *C. nanus*

cf. P. Taquet (1976), originally reported as *I. mantelli*

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MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE I

The skull of *Muttaborrasaurus langdoni* (QM F6140). The scales are in cm.

- A. Lateral view of skull supported by a block of plasticene.
- B. Posterior view.
- C. Dorsal view.

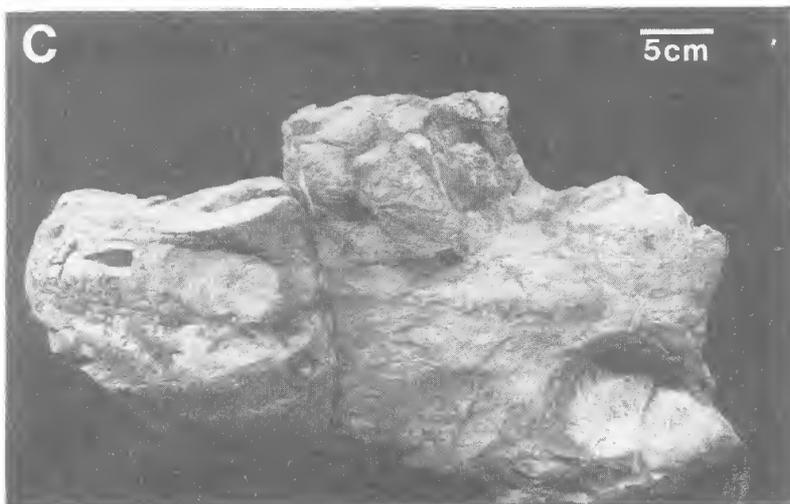
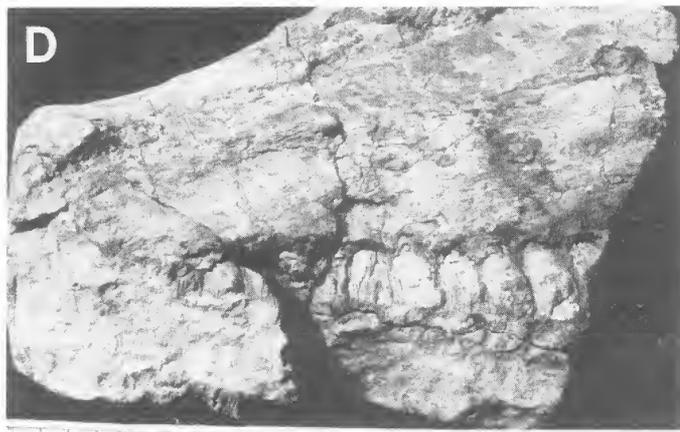


PLATE 2

The maxillary dentition and parasphenoid of *Muttaborrasaurus langdoni* (QM F6140). The scales are in cm.

- A. Break through skull (visible in Plate 1A just above the supporting plasticene) showing maxillary teeth of the right side (t) in section.
- B. The same break showing maxillary teeth of the left side (t) and parasphenoid (p) in section.
- C. The anteriormost maxillary crown on the left side (at lower left).
- D. The left maxillary dentition in lateral view.





SAUROPODA (REPTILIA, SAURISCHIA) FROM THE
CRETACEOUS OF QUEENSLAND

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ABSTRACT

Five new specimens of Sauropoda have been collected from the Upper Cretaceous Winton Fm. in Queensland, Australia. Among the elements preserved are incomplete pectoral and pelvic girdles, fore- and hindlimb bones, metacarpals, and caudal vertebrae. Because of the fragmentary nature of the specimens, comparison to other sauropods is difficult, but the Winton sauropod appears to be a relatively primitive member of the suborder. There are few similarities to the Australian sauropod *Rhoetosaurus* and the specimens are tentatively identified as *Austrosaurus* sp.

INTRODUCTION

In 1959, following the discovery of one bone by a station hand, Dr Alan Bartholomai collected several fragmentary dinosaur elements from Cretaceous sediments on Alni Station, northwest of Winton in Queensland. Four additional specimens are subsequently collected from the adjoining Elderslie and Lovelle Downs Stations by Dr Mary Wade of the Queensland Museum. All five specimens are referable to the Sauropoda, a group previously recorded from one Jurassic (Longman, 1926, 1927) and one Cretaceous specimen (Longman, 1933) in Australia. Sauropod elements, usually isolated, have also been found in the Lower Cretaceous near Hughenden (F6142, L349, and probably F2470), and at Chorregon, southeast of Winton (F10916), in Queensland, and probably at Lightning Ridge, New South Wales (F10230, a cast). Because of the general paucity of dinosaur remains in Australia, the five new specimens from Winton are deemed worthy of description despite their incomplete condition.

ACKNOWLEDGMENTS

We wish to thank Drs Alan Bartholomai and Mary Wade for offering us these specimens for

study, and especially for their patience during the preparation of this paper. Thanks are also extended to Mr Mick Elliott, Mr Mike Elliott, Mr David Casey, members of the Watts family, and other personnel of Alni, Elderslie, and Lovelle Downs Stations for their enlightened cooperation and assistance in securing the specimens described below. Dr John S. McIntosh kindly gave us his opinions on sauropod taxonomy and aided our understanding of North American and European sauropods.

MATERIAL

Specimen F3390: Proximal and distal ends of humerus, proximal and distal ends of femur, proximal ends of three metacarpals; from Alni Station, about 1 km south of Alni homestead, 50 km northwest of Winton, Queensland (22° 11'S, 142° 28'E).

Specimen F6737: Nine caudal vertebrae, one partial neural arch, three partial dorsal vertebrae, partial scapula, proximal ends of ischium, rib pieces; from Lovelle Downs Station, about 3 km east-southeast of Lovelle Downs homestead, 50 km northwest of Winton, Queensland (22° 09'S, 142° 34'E).

Specimen F7291: One metacarpal, distal end of ?ulna, distal end of femur; from Lovelle Downs

Station, about 2 km east of Lovelle Downs homestead, 50 km northwest of Winton, Queensland (22° 09'S, 142° 33'E).

Specimen F7292: 18 caudal vertebrae, one ?carpal, two partial ulnae, two partial radii, two partial humeri, partial scapular blade, fragment of ?ilium, four metacarpals, rib pieces; from Elderslie Station, in triangle paddock near the woolshed, ½ km southwest of Top Horse Bore, about 4 km north-northeast of Elderslie homestead, 50 km northwest of Winton, Queensland (22° 15'S, 142° 29'E).

Specimen F7880: Coracoid (?), femoral head; from Elderslie Station, 2 km north of Top Horse Bore, about 6 km north-northeast of Elderslie homestead, 50 km northwest of Winton, Queensland (22° 13'S, 142° 29'E).

STRATIGRAPHY

All specimens are from the Winton Fm. (of Whitehouse, 1954; see also Vine and Day, 1955) of middle Cretaceous, late Albian to early Cenomanian age (Dettmann, 1973). The bones were collected from the surface and probably represent a lag concentrate formed by deflation. The material probably comes from high within the Winton Fm. Associated fossils include silicified conifer wood, unionids, and lungfish. All specimen numbers refer to the Queensland Museum collections.

DESCRIPTION

DORSAL VERTEBRAE: The anterior portions of the centra of three dorsal vertebrae are preserved in specimen F6737. Two of these are too poorly preserved to warrant description, while the other represents approximately the anterior third of the centrum. The anterior central face is distinctly convex, and the centrum itself depressed (about 20 cm wide by 15 cm deep). The anterior walls of small but deep pleurocoels are present. The extent of the pleurocoels is difficult to trace, but must have reached nearly the midline. As far as can be determined the pleurocoels were simple medially closed tubes with no sign of any expanded chambers as are often found among sauropods. The remainder of the centrum is filled with small chambers apparently entirely closed off from each other, as well as from the pleurocoels, by bony lamellae. This vertebra almost exactly matches an unfigured dorsal from the holotype of *Austrosaurus mckillopi* in the general form and proportions of the central face and anterior wall of the pleurocoel.

CAUDAL VERTEBRAE (Plate 1): Specimens F6737 and F7292 contain a total of 27 caudal centra plus a fragmentary neural arch. Three middle caudals in specimen F7292 are poorly preserved and provide few details worthy of note (Plate I:D,E,K). Maximum transverse diameters of these centra exceed the length, and there is a slight but distinct dorsoventral compression. Neither these, nor any of the other caudal vertebrae have pleurocoels. The two largest centra in specimen F6737, possibly adjacent elements and derived from caudals five through twelve, are nearly circular in face view and are relatively short, maximum length being about half the maximum (Plate I:A). The expanded, platycoelous articular ends are slightly offset such that the anterior end is higher than the posterior. The larger of these two centra retains the base of a massive, anteroposteriorly compressed diapophysis that arises from the juncture of the broken neural arch and the centrum. Chevron facets are not visible on either of these centra, and there are no diapophyseal struts and buttresses such as are found on anterior caudals of some sauropods. The next centrum of F6737, from near the middle of the tail, has less expanded articular ends than the preceding vertebrae, and its maximum diameter is only slightly greater than its length (Plate I:B). A small, blunt diapophysis arises from the upper third of the centrum and slants obliquely backward and slightly upward. Bases of an anteriorly positioned neural arch occupy about half the length of this centrum (Plate I:B2). Broad, blunt chevron facets face downwards and backwards at the posterior margin of the centrum. Length and transverse diameter are subequal on the next more posterior vertebrae of F6737 (Plate I:C), which was separated from the centrum previously described by two or three missing elements. Broken bases of the diapophyses arise about one-third of the centrum's height below the neural arch and near midlength. Neural arch bases are positioned toward the anterior end of the centrum, and chevron facets are not preserved.

The next four vertebrae of specimen F6737 are from the distal half of the tail (Plate I:G,H,I,J). All are platycoelous to amphiplatyan but with centrally placed concavities in the faces, and are nearly circular in end view. All four of these centra are about the same length, but maximum diameter decreases regularly through the series. In section the bottom of each centrum is formed by a broad, flat surface. Neural arch bases are uniformly set toward the anterior end of the

centra, and diapophyses are absent. Blunt chevron facets protrude from the posterior margin of each centrum, but there is only a faint suggestion of corresponding facets anteriorly (Plate I:1).

A series of twelve small caudals in specimen F7292 comes from the distal third of the tail (Plate I:L through Y). The most anterior of the set comes from about the same point along the tail as the smallest caudal in specimen F6737. All twelve distal caudals have lengths greater than their maximum transverse diameter. Expanded articular ends are platycoelous to amphiplatyan on the more anterior caudals of this series, becoming biconvex on the distal centra (although always retaining a central concavity). Chevron facets, barely projecting off the central articular surface are visible on several centra of this series, and diapophyses are absent from all, as would be expected in distal caudals. Neural arches sit toward the anterior end of each centrum, being centred about one-third of the way back, shifting further back on the more distal vertebrae. Two nearly complete neural arches on vertebrae near the middle of this series are low (neural spines not developed) and simple in structure (Plate I:Q,S). In section the bottoms of the centra show a broad, flat surface.

A fragmentary neural arch in specimen F6737 is probably derived from an anterior caudal but cannot be fitted to any of the centra described above (Plate I:F). A single prezygapophysis on this fragment is a simple massive projection devoid of supporting struts and laminae and its anteroposteriorly elongate articular surface is flat. The neural arch wall is entirely filled with spongy bone with no sign of a pleurocoel.

SCAPULA (Plate II:D,E, Plate III:A,B): A fragmentary scapular body in specimen F6737 preserves much of the glenoid and the coracoid articulation (Plate II:D,E). The thickened glenoid region has a concave articular surface whose transverse and longitudinal dimensions are about equal. A narrower but longer coracoid articulation meets the glenoid at an angle of 115°. The 'spine' of the scapular body runs forward perpendicularly to the posterior margin, at an angle of about 40° to the coracoid articular surface. The posterior margin at about this point is produced back into a shallow 'shelf', which in section forms an acute angle unlike the rounded section of the posterior margin closer to the glenoid. This 'shelf' is the presumptive attachment of the serratus ventralis or biceps brachii. In general form, so far as can be determined from such an incomplete specimen, the body of the scapula resembles most closely

that of *Laplatasaurus araukanicus* (von Huene, 1929).

A flattened fragment in specimen F7292 is a broken scapular blade (Plate III:A,B). The piece is 60 cm long by 24 cm wide with a slightly concave medial surface and a low, longitudinal ridge along the outer surface. This elongate ridge is offset towards what is regarded as the anterior edge of the blade.

CORACOID (Plate II:A,B,C): Specimen F7880 includes an approximately equidimensional element identified as a coracoid. The element shows an open coracoid notch rather than a closed foramen (Plate II:A). Although there is considerable breakage around the notch, at one point unbroken bone surface can be traced from within the notch onto the outside, scapular articular surface. A massive and rather long, narrow, convex scapular articulation and a short, broad, concave glenoid region are present. Specimen F7292 contains a possible second coracoid (Plate II:B,C). The fragment is shallowly concave on one surface, convex on the opposite. A massive thick region protruding from one edge probably represents the base of the glenoid. The actual articular surface of the glenoid as well as all of the scapular contact region is missing.

HUMERUS (Plate III:C,D,E,I,J): A very fine proximal end of a humerus together with a detached distal end, probably of the same bone, are included in specimen F3390. The proximal end is strongly compressed anteroposteriorly forming a wide, gently convex extensor surface and a broad, shallowly concave flexor surface (Plate III:I). A well delineated, roughly oval head lies near mid-width of the proximal end and extends back onto the extensor surface (Plate III:J). The head is better defined, has a smoother articular surface, and extends somewhat farther onto the extensor surface than is typical among sauropods. Subequal medial and lateral processes slope away from the head, both processes ending in fairly sharp shoulders where they meet the shaft. Most adult sauropod humeri have a more rounded, less angular proximal end. Only the most proximal end of the delto-pectoral crest is preserved as indicated by the thickened lateral margin of the shaft.

The broken distal end of a humerus in specimen F3390 may be part of the same bone as the preceding piece (Plate III:D,E). At least half the ulnar condyle as well as the median posterior region of the radial condyle are missing. As with the humeral head, the distal articulations are more clearly defined on this specimen and have smoother articular surfaces than is typical of

sauro pods. Viewed laterally the ulnar condyle has an almost circular curve with little flattening at the distal end. Both ulnar and radial condyles wrap well up onto the flexor surface. As preserved, the distal humeral fragment is about 38 cm long, the proximal fragment about 21 cm long. Assuming the humerus was massive and short as in *Apatosaurus* would give an estimated original length of about 80 cm. Assuming a long slender humerus as in *Brachiosaurus* would give an original length of up to 120 cm. The Queensland material is fairly similar to *Cetiosaurus* (see discussion below), and restoring the humerus after this genus gives an estimated original length of about 90 cm, short for a sauropod.

A rather battered humerus in specimen F7292 includes most of the shaft but is missing both articular ends (Plate III:C). Proximally this specimen is broad, with a wide, shallow flexor surface bounded by a thin delto-pectoral crest. Distally the bone narrows and thickens to an oval cross section. In most sauropods the humerus remains wider and more anteroposteriorly compressed toward the distal end. The degree of tapering in the Queensland specimen is somewhat unusual, but is matched by the humerus of *Dinodocus mackesoni* (Woodward, 1908). As preserved the humerus of specimen F7292 is about 90 cm long with a maximum width of 38 cm. The original length of the humerus is estimated at 110 to 120 cm, a moderate size for a sauropod.

A badly shattered proximal end of a humerus in specimen F7212 adds little additional information. As in specimen F3390, the medial process meets the shaft at a fairly sharp angle, but the head in specimen F7292 is not as well defined because of post mortem damage. Distally the shaft of this fragment appears to be more compressed than that of F7292, but again this may be a matter of poor preservation.

ULNA (Plate IV:A,B,C): Specimen F7292 includes shafts of two ulnae, one of which retains the distal articular surface intact and the proximal end as a detached fragment. Proximally there is a broad, flat anterior surface and a posterior ridge that rises to a low, rugose olecranal process, so that sections through the proximal end are irregularly triangular with the widest surface facing the radius and the most obtuse corner formed by the olecranal process (Plate IV:A,B). Sections through the distal region of the ulna are crudely circular. The distal articular surface is rugose and irregularly shaped, but is roughly circular when viewed end-on. The alae that embrace the radius are greatly prolonged distally,

extending down about 80 per cent of the length of the ulna. In other sauropods the alae rarely extend more than 60 per cent of the ulnar length. As preserved, the longer shaft piece is 67 cm long exclusive of the isolated proximal end (which is 24 cm long). The original length of the ulna is estimated at about 95 cm.

RADIUS (Plate IV:D,E): There are two almost complete radii in specimen F7292. Most of the radial shaft is roughly circular in section, with a somewhat flattened surface facing the ulna. Distally the radius is anteroposteriorly compressed, with the distal articular surface at an angle of about 70° to the long axis of the shaft. The radius is more massive than usual among sauropods, with a more marked distal expansion. The proportions are matched by those of several titanosaurid radii. The proximal end seems also compressed, but much of it has been lost from both radii. The more complete radius, which retains fragments of the proximal articular surface, measures 80 cm in length (Plate IV:D).

ISCHIUM (Plate III:F,G,H): The proximal end of a right ischium in specimen F6737 preserves both articular surfaces and part of the acetabulum, but is lacking all of the blade (Plate III:F,G,H). The massive iliac articulation is slightly convex and in face view forms a half-moon shaped surface whose flat margin is directed laterally. A more elongate, less massive pubic articulation is shorter and straighter than in most Sauropoda. The pubic and iliac articular surfaces are set at an angle of about 65° to each other, a rather low value for sauropods. Along the margin of the acetabulum the ischium thins down to an almost blade-like edge, much of which has been broken off.

FEMUR (Plate V:A,B,E through J): Specimen F3390 includes proximal and distal ends of a femur that is missing the intervening shaft, the two femoral pieces being among the best of the Winton material (Plate V:A,B,G,H). The femoral head is elevated well above the level of the greater trochanter and is displaced medially so as to project well into the acetabulum. As is typical of sauropods, the head blends into the laterally positioned trochanters with no intervening groove or furrow. In anterior view the femoral head looks bulbous and rounded, but a proximal view reveals strong anteroposterior compression that echoes a similar compression of the shaft, at least some of which is due to post-mortem crushing (Plate V:A). There is a slight hip or bulge along the lateral edge of the shaft a little distal to the greater

trochanter, and a similar bulge along the medial edge further distal. These two hips give the proximal third of the femur a weakly sinuous curvature in anterior view (Plate V:B). The bulge along the medial edge of the femur is associated with a low, ridge-like fourth trochanter. The femoral shaft is anteroposteriorly compressed, but is not very broad, and consequently gives the impression of being a long, slender element.

A second isolated femoral head in specimen F7880, twice as large as that of F3390, is less compressed and more nearly spherical in proximal view. It somewhat resembles the femoral head of *Amphicoelias* (Osborn and Mook, 1921, fig. 125).

Articular surfaces of the distal femoral piece in specimen F3390 wrap well up onto both anterior and posterior surfaces of the distal femoral shaft. Viewed laterally these condyles form almost a semicircle with a slight flattening of the distalmost surface. A deep furrow separates a longer medial condyle from a broader lateral condyle slightly inset posteriorly from the lateral margin of the shaft. As in many other sauropods the medial condyle shifts toward the center of the femoral shaft as it curves up the flexor surface. As preserved, the combined femoral head and proximal shaft piece of specimen F3390 are about 56 cm long; the distal femoral piece is about 31 cm long giving a minimum femoral length of over 85 cm. Assuming that the femur of the Winton sauropod was proportioned similarly to that of *Cetiosaurus* would imply a missing shaft segment amounting to approximately one-third the total femoral length, giving an estimated original length of about 127 cm, a moderate size for a sauropod. The distal femoral piece of specimen F7291 is very similar in form to that of specimen F3390 and about 20 per cent larger (Plate V:I,J).

MESOPODIAL (Plate VI:R,S): A flat, block-like bone in specimen F7292 is tentatively identified as a carpal. In face view the element is roughly circular with one flattened margin (Plate VI:S). Maximum diameter is a little less than twice the thickness of this element. In size and general conformation this bone resembles a 'probable carpal' of *Camarasaurus grandis* (Ostrom and McIntosh, 1966, pl. 79, figs. 1-5).

METAPODIALS (Plate VI:A through Q): Specimen F3390 contains proximal ends of three metacarpals I, II(?), and III (Plate VI:L through Q). Metacarpal I is by a slight margin the largest of the three. Its articular end is bounded anteromedially by a long convex border, anteriorly by a short straight edge, posteriorly by a longer

straight segment, and laterally by a shallow concave surface which receives mc II. The element doubtfully identified as mc II is the smallest metacarpal of F3390. Its articular surface is bounded by a short, convex anterior (?) margin and longer medial and lateral edges. There is a blunt projection anterolaterally that presumably contacted mc III. With its characteristic triangular shape in proximal view (Plate VI:P), mc III is the most readily identified of these three bones. The anterior border of its articular surface is shorter than the subequal medial and lateral edges. In anterior or medial view all metacarpals show gently convex articular ends.

Specimen F7292 includes four metacarpals. Mc I is represented by the proximal end which has the characteristic flat, oval articular surface with a flattened, downturned border facing mc II (Plate VI:J,K). Two fragments tentatively identified as mc II are missing the middle region of the shaft (Plate VI:F,G,H). The damaged proximal articulation is irregularly triangular in outline. An almost complete mc III has a slightly damaged proximal end that still retains the typical triangular shape (Plate VI:I). This element is about 42 cm in length, very large even for a sauropod. The final metacarpal of specimen F7291 is missing some of the proximal end, but the damaged upper shaft is roughly triangular suggesting that this element is another mc III (Plate VI:A,B,C). As preserved, this bone is about 41 cm in length.

Specimen F7291 contains a single, almost complete metacarpal I that measures about 37 cm in length (Plate VI:D,E). The proximal articular face has a shape almost identical to that of mc I of specimen F7292.

In proximal view the metacarpals of specimen F3390 are quite different in form from those of specimens F7291 and F7292. There is little likelihood that any of these specimens are misidentified metatarsals, so that either there are two sauropods represented, or the metacarpal form altered with growth (metacarpals of specimen F3390 are about one-half the size of those of specimen F7292). Some of the sauropod material from near Hughenden is quite distinct from that from Winton, and suggests that there were at least two different sauropods during the Cretaceous in Queensland.

OTHER FRAGMENTS (Plate VI): Several bones among the specimens described here are difficult to identify positively because of their fragmentary, shattered condition. Several of these elements are in specimen F7291, including the distal articular

surface of a long bone that is roughly circular in end view and is tentatively identified as the distal end of an ulna. A badly crushed end of a large bone (Plate V:C,D) included in this specimen may be the proximal end of an ulna, but is too incomplete for confident identification. Another massive fragment in specimen F7292 may well be part of the anterior portion of an ilium, but again the specimen is too fragmentary for certain identification (Plate II:F,G).

Both specimens F7292 and F6737 include fragments of ribs. Those of specimen F7292 measure in section about 5 by 8 cm, while those of specimen F6737 are distinctly thinner, measuring 2 by 5 cm.

DISCUSSION

Although the Winton specimens described herein are clearly sauropod, their fragmentary condition is a severe barrier to determining more intimate relationships to other genera. Moreover, it is generally agreed that no satisfactory system of sauropod taxonomy has yet been devised, and that sauropod nomenclature at the generic and specific level is in great need of extensive review and revision (e.g. Ostrom, 1970). Family group names follow Romer (1956) as a descriptive convenience, not because Romer's taxonomic system is preferable. It is not clear how many taxa are represented by the five specimens from Queensland. There is certainly a considerable size difference between the relatively small individual represented by specimen F3390, and the considerably larger animal of specimen F7292. Moreover there are the differences in metacarpal and rib form previously described: these differences however are insufficient to confidently indicate the presence of more than one taxon. Thus for this discussion all of the Winton material is grouped together and is considered a single species. The groups considered here are ranked in increasing similarity to the Winton sauropod, except that the two previously described Australian sauropods (*Rhoetosaurus* and *Austrosaurus*) are discussed last.

DIPLODOCINAE AND APATOSAURINAE: *Diplodocus* is one of the best known sauropods (Osborn, 1899; Hatcher, 1901; Holland, 1906; Gilmore, 1932), but other Diplodocinae, particularly *Barosaurus* and *Amphicoelias*, are only poorly known (Lull, 1919; Janensch, 1929, 1935, 1961; Osborn and Mook, 1921). *Apatosaurus* (= *Brontosaurus*) is another thoroughly studied genus that is close morphologically to *Diplodocus* (Hatcher, 1902; Riggs, 1903; Osborn, 1905;

Holland, 1915; Gilmore, 1936; Berman and McIntosh, 1978), and in fact probably does not warrant separation into its own subfamily. These genera are among the most advanced of the sauropods. They differ from the Winton sauropod in having the following features: 1) pleurocoels in anterior caudals; 2) tall and generally complex caudal transverse processes and caudal ribs; 3) more strongly expanded articular faces on caudal centra; 4) neural arches at approximately mid-length of caudal centra; 5) moderately procoelous anterior caudals (but not as strongly procoelous as in the Titanosaurinae); and, 6) large pleurocoels in the dorsals. Additionally, *Barosaurus*, *Diplodocus* and *Apatosaurus* have massive femora with poorly defined heads at most slightly elevated above the level of the proximal trochanters, not at all like the elevated head of the femur in specimen F3390. In *Amphicoelias* the femoral head is well above the level of the trochanters, the head is subspherical and the femoral shaft nearly circular in section, a possibly unique configuration among sauropods (Osborn and Mook, 1921). Specimen F7880 also has an isolated femoral head of subspherical shape. *Amphicoelias* however differs from the Winton sauropod in having amphicoelous dorsals with small pleurocoels, more gracile ulnae with shorter radial alae, and in lacking the 'shelf' along the posterior margin of the scapula. In spite of a few similarities, the Winton sauropod cannot be considered a member of the Diplodocinae or Apatosaurinae.

The Chinese *Mamenchisaurus* (Young, 1954, 1958, Young and Chao, 1972) is considered here in view of the similarity of its chevrons to those of *Diplodocus* (Berman and McIntosh, 1978). It shows no close resemblance to the Queensland material and differs in the following points: 1) less marked development of the humeral head; 2) radius with less constriction at midshaft, and less dilation of the distal end; 3) femur with less marked elevation of the head above the level of the proximal trochanters (although bulges of the lateral and medial margins are present as in the Winton sauropod); and, 4) proximal caudals markedly procoelous. Thus *Mamenchisaurus* shows no special similarity to the Winton sauropod material.

TITANOSAURINAE: As used by Romer (1956) this large subfamily includes most Cretaceous sauropods as well as many sauropod taxa from Gondwanaland, including *Titanosaurus*, *Antarctosaurus* and *Laplatasaurus* (Lydekker, 1893; Huene, 1927, 1929, 1932; von Huene and Matley,

1933). Although some species are similar to the Winton sauropod in scapular form, especially the posterior marginal 'shelf', and in having a robust radius, titanosaurs differ in having strongly procoelous anterior caudals. Amphiplatyan centra are present by the middle third of the tail in many titanosaurs, but because the anterior caudals of the Winton sauropod are clearly not procoelous, the subfamily Titanosaurinae is dismissed from further consideration. This decision is contingent on having correctly estimated the position in the caudal series of the isolated caudal centra of specimen F6737 in particular, but their size relative to the other caudals and the dorsal pieces lends confidence to this determination. Other differences include a usually less well-marked humeral head (although *Antarctosaurus brasiliensis* Arid and Vizotto, 1971, has a proximal humerus of very similar form), shorter radial alae of the ulnae, and femoral head less clearly elevated above the trochanters.

EUHELOPODINAE: Two genera considered to belong to this group by Romer (1956). *Euhelopus* (Wiman, 1929) and *Tienshanosaurus* (Young, 1937), have a 'shelf' along the posteroventral scapular margin similar to that in the Winton sauropod. This is, however, the only obvious similarity. Both genera differ from the Queensland material in having an angle of 90° or more between the ilial and public articular surfaces of the ischium, and in lacking the marked elevation of the femoral head above the level of the proximal trochanters. In addition the humerus of *Euhelopus* (Young, 1935) shows less development of the head than in the Winton sauropod.

CAMARASAURINAE: As defined by Romer (1956), this subfamily contains only *Camarasaurus*, a genus represented by one of the most complete sauropod skeletons ever found (Gilmore, 1952; Riggs, 1901; Osborn, 1906; Gregory, 1919; Osborn and Mook, 1921; Lull, 1930). Borsuk-Bialynicka (1977) considered *Opisthocoelicaudia* to be a second genus referable to the Camarasaurinae. *Camarasaurus* anterior caudals are amphicoelous or platycoelous, and the general contour of centra from comparable regions of the tail is similar to the Queensland specimens. *Camarasaurus* also has simple transverse processes on caudals, and bifid chevron facets that are more prominent at the posterior than the anterior end of caudal centra. The arches of the seventh through fifteenth caudals of *Camarasaurus* are shifted anteriorly as in the Winton sauropod. *Camarasaurus* has only a slight lateral bulge of the femoral shaft just distal to the

greater trochanter. The medial edge of most *Camarasaurus* femora are smoothly convex, no bulge in the region of the fourth trochanter as found in the Winton specimens. Other differences in *Camarasaurus* femora include a head that is only slightly elevated above the level of the trochanters, and a shaft that is very broad distally. These differences could result from the larger size of *Camarasaurus* relative to specimen F3390. The humerus of specimen F3390 has a better defined head that extends farther onto the extensor surface than the head of a *Camarasaurus* humerus. An angle of about 110° between the iliac and pubic articulations of a *Camarasaurus* ischium, compared with about 65° in the Winton sauropod, is a more convincing point of distinction, and the dorsals of *Camarasaurus* show cavernous pleurocoels quite unlike those of the fragmentary dorsals of the Winton sauropod.

Opisthocoelicaudia differs from the Winton sauropod in having: 1) extensive pleurocoels in the posterior dorsals; 2) anterior caudals (to the fifteenth) that are markedly opisthocoelous; 3) a more robust humerus, with less prominent head; 4) more robust radius, ulna and metacarpus; and 5) a femur generally similar to that of *Camarasaurus*. The posterior dorsals are similar to those of the Winton sauropod in being strongly opisthocoelous with depressed centra. Such isolated points of similarity do not suggest any close relationship of the Winton sauropod with the camarasaurines.

BRACHIOSAURINAE AND CETIOSAURINAE: Differences between these two subfamilies include: 1) deep pleurocoels in anterior dorsals of Brachiosaurinae, solid centra in Cetiosaurinae; 2) very long neck in Brachiosaurinae, moderate in Cetiosaurinae; and 3) forelimb as long or longer than hindlimb in Brachiosaurinae, hindlimb longer than forelimb in Cetiosaurinae. In most skeletal elements and morphologic features where comparisons can be made to the Winton sauropod, the subfamilies Cetiosaurinae and Brachiosaurinae are essentially identical. The only well known genus of the Brachiosaurinae is *Brachiosaurus* itself (Riggs, 1904; Janensch, 1936, 1950). *Pleurocoelus* and *Bothriospondylus* are represented by relatively poor material while *Pelorosaurus* is known almost entirely from isolated elements. The very long metacarpals of the Winton sauropod are suggestive of the Brachiosaurinae, but the two fragmentary humeri among the Queensland material are rather short for a *Brachiosaurus*-like genus, and the angular proximal end of the humerus in specimen F3390

is quite unlike the rounded adult proximal humerus of *Brachiosaurus*. Femora of *Brachiosaurus* have a marked lateral bulge just distad to the greater trochanter, but the posterior dorsals of *Brachiosaurus* (and other brachiosaurs) show more extensive pleurocoels than those of the Winton sauropod suggesting that it is unlikely to be a brachiosaurine.

No genus of the Cetiosaurinae is represented by a really good specimen, but some comparisons are possible with *Cetiosaurus* itself as well as with *Haplocanthosaurus*. *Cetiosaurus* femora are similar to those of the Winton sauropod in degree of elevation of the head above the level of the greater trochanter and in having both a lateral bulge of the shaft just distal to the greater trochanter, and a medial bulge in the region of the fourth trochanter (Phillips, 1871; de Lapparent, 1955). A *Cetiosaurus* coracoid figured by Lapparent (1955, Pl. IV) is close in form to that of the Winton sauropod. *Cetiosaurus* is also similar in having neural arches set towards the anterior margin of caudal centra and in having prominent, bifid chevron facets only at the posterior end of caudal centra (Phillips, 1871, Fig. 45). An angle of about 80° between the pubic and ilial articulations of a *Cetiosaurus* ischium (Reynolds, 1939) is close to the 65° of that of the Winton specimen.

In *Haplocanthosaurus* (Riggs, 1904; Hatcher, 1903) the femoral head is more elevated above the level of the proximal trochanters than in the Winton specimens. *Haplocanthosaurus* also differs in the following features: 1) medial edge of the femur without a bulge in the region of the fourth trochanter; 2) neural arches at midlength of caudal centra; 3) angle between ilial and public articulations of ischium about 95°; and 4) dorsals with more extensive pleurocoel development.

All genera included in the subfamilies Cetiosaurinae and Brachiosaurinae are similar to the Winton sauropod in the following respects: 1) no pleurocoels in caudal centra; 2) caudals platycoelous to amphiplatyan; 3) chevron facets not confluent; 4) chevron facets larger at posterior end of centrum than at anterior end; 5) femoral head elevated above level of proximal trochanters; 6) lateral bulge of shaft just distal to the greater trochanter of femur; and 7) angle between ilial and pubic articulations of ischium less than in 'advanced' sauropods (e.g. *Apatosaurus*, *Diplodocus*, and *Camarasaurus*), but brachiosaurs differ in dorsal pleurocoel form: both brachiosaurs and cetiosaurs lack the robust radius of the Winton sauropod. Among the sauropod groups

recognised by Romer (1956), the Cetiosaurinae includes genera that are most similar to the Queensland material described herein.

RHOETOSAURUS: *Rhoetosaurus brownei*, known from a single specimen from the Jurassic of Queensland (Longman, 1926, 1927) has been classified as a cetiosaurine (Romer, 1956), and is similar to the Winton sauropod in most of the features noted in the preceding section. Linear dimensions of the *Rhoetosaurus* specimen are 40–50% larger than elements of specimen F3390, but are only slightly larger than the individual represented by specimen F7292. The massive femur of *Rhoetosaurus* has a poorly defined head only slightly elevated above the greater trochanter, and there is no outward bulge of the femoral shaft just below the trochanter. The dorsals of *Rhoetosaurus* have large pleurocoels, but there are no caudal pleurocoels. The anterior chevron facets are probably confluent, and the chevrons wedge equally between posterior and anterior faces of adjacent caudal centra. There are no signs of struts or buttresses associated with the diapophyses of the caudals, and the neural arch is centrally placed on the centra. The caudals are generally similar in form to those of the Winton sauropod, but the dorsals are clearly different. Because of the incomplete condition of the *Rhoetosaurus* type and the new Queensland specimens, no other comparisons are possible.

AUSTROSAURUS: *Austrosaurus mckillopi* from the Lower Cretaceous (Allaru mudstone, Albian) of north central Queensland is known only from the type specimen, a series of six fragmentary dorsal vertebrae (Longman, 1933). These vertebrae are deeply opisthocelous with relatively small pleurocoels and an extensive, cancellous internal structure that is distinctive (Longman, 1933), and matched in the Winton sauropod dorsal pieces. *Austrosaurus* is not readily placed in a group with the other sauropod genera, and consequently it has been classified in the Cetiosauridae (Longman, 1933), the Brachiosauridae (Romer, 1966), and as Sauropoda, *incertae sedis* (Romer, 1956), the last assignment being the most realistic if not the most satisfactory. Dorsal vertebral pieces of the Winton sauropod (specimen F6737) match in form and internal structure those of *A. mckillopi*, although there is a possibility that the centra of the Winton sauropod were less strongly constricted than those of *Austrosaurus*. Thus tentative reference of the Winton sauropod material to *Austrosaurus* sp. is warranted.

SUMMARY AND CONCLUSIONS

Cretaceous sauropod remains from Queensland, Australia, described herein, have the following significant features: 1) no struts and buttresses supporting diapophyses of caudal vertebrae; 2) no pleurocoels within caudal centra; 3) neural arches set toward anterior end of caudal centra; 4) likely 'open' chevrons articulating intervertebrally; 5) chevron facets at posterior end of centra larger than at anterior end; 6) angle of about 65° between pubic and iliac articular surfaces of ischium; 7) a notch rather than a foramen in the coracoid; 8) joint surfaces of long bones smoother and better defined than is typical of sauropods; 9) humerus tapers greatly distal to delto-pectoral crest, shaft section not greatly compressed; 10) femoral head elevated above level of proximal trochanters; 11) metacarpals exceptionally large, both relative to other limb elements and absolutely, compared to other sauropods; 12) exceptionally long radial alae of ulnae; 13) small dorsal pleurocoels; 14) cancellous internal structure in dorsal centra, similar to that found in *Austrosaurus mckillopi*; and 15) a well-developed 'shelf', along the posteroventral margin of the scapula. The new material has few similarities to the Australian Jurassic sauropod *Rhoetosaurus*, but (partially perhaps for want of homologous elements) cannot be distinguished from the Australian Cretaceous sauropod, *Austrosaurus*. Distinct similarities to *Austrosaurus* are found in the structure of the dorsals. We regard the present material as inadequate for proper definition of a new taxon, and the specimens are here classified as *Austrosaurus* sp. and considered most likely to belong to the Cetiosaurinae (*sensu* Romer, 1956) among currently defined sauropod groups.

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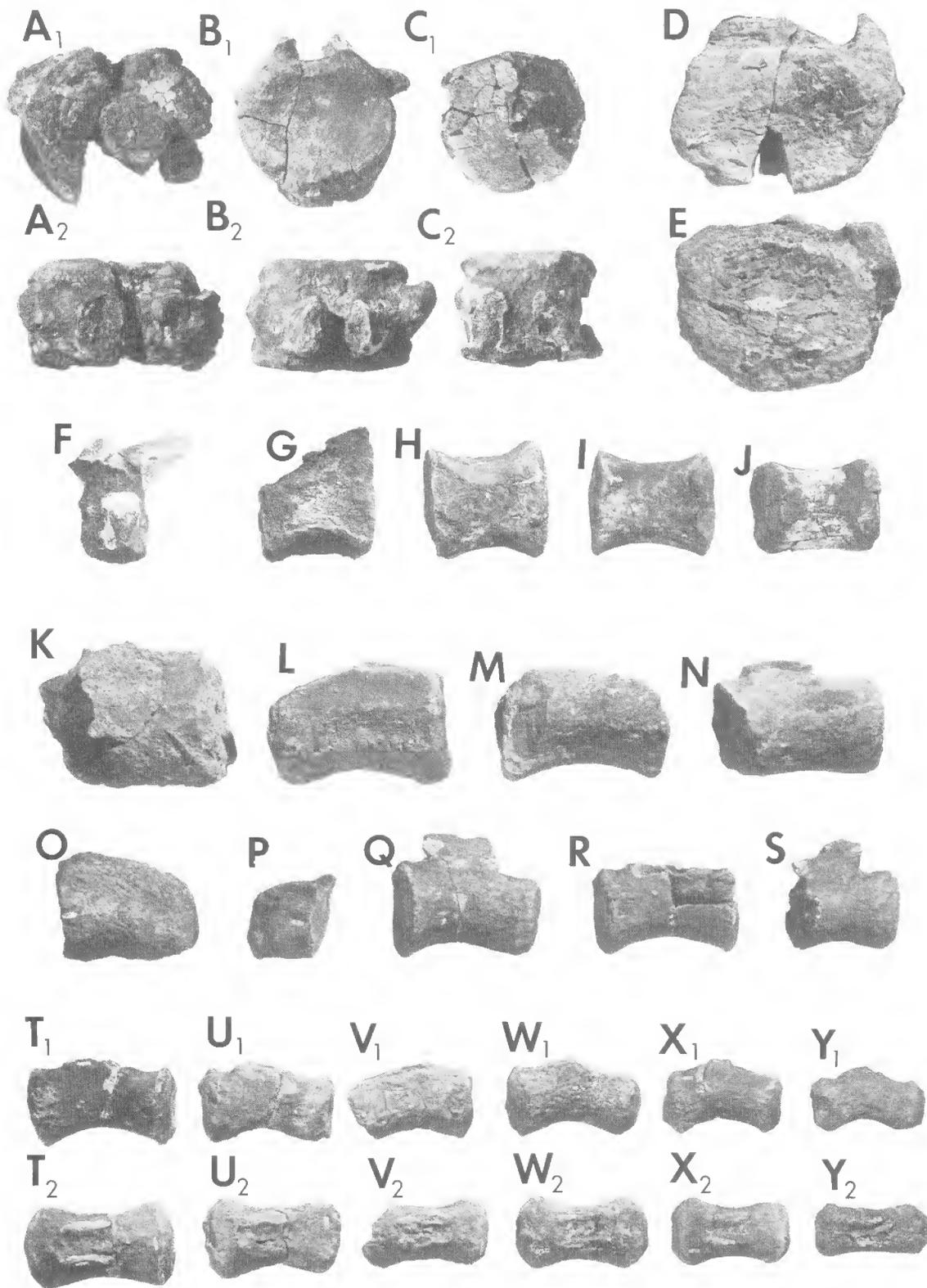
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MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE I

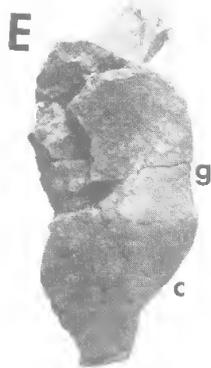
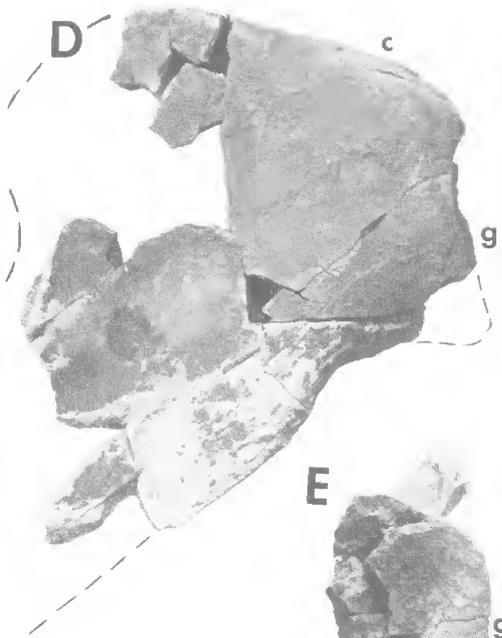
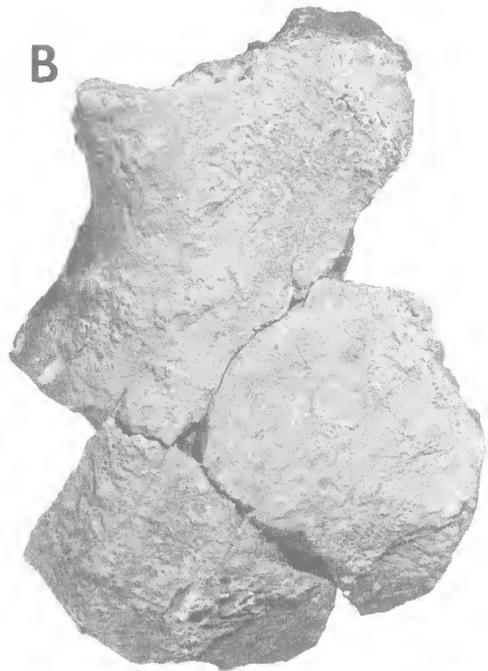
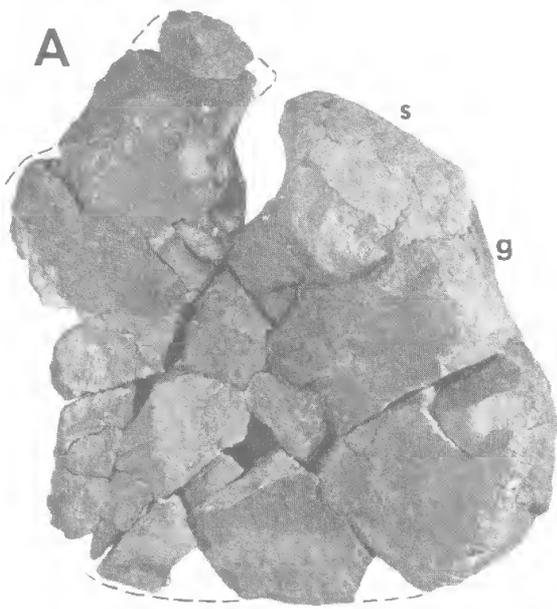
Caudal vertebrae. A₁ through C₁, F6737, anterior caudals, anterior views; A₂ through C₂, same vertebrae in dorsal view; D and E, F7292, middle caudals, anterior views; F, F6737, fragment of a neural arch with one prezygapophysis; G through J, F6737, distal caudals, ventral views; K through S, F7292, middle to distal caudals, lateral views; T₁ through Y₁, F7292, distal caudals, lateral views; T₂ through Y₂, same vertebrae as preceding in dorsal views. Approximately one-sixth natural size.



MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE II

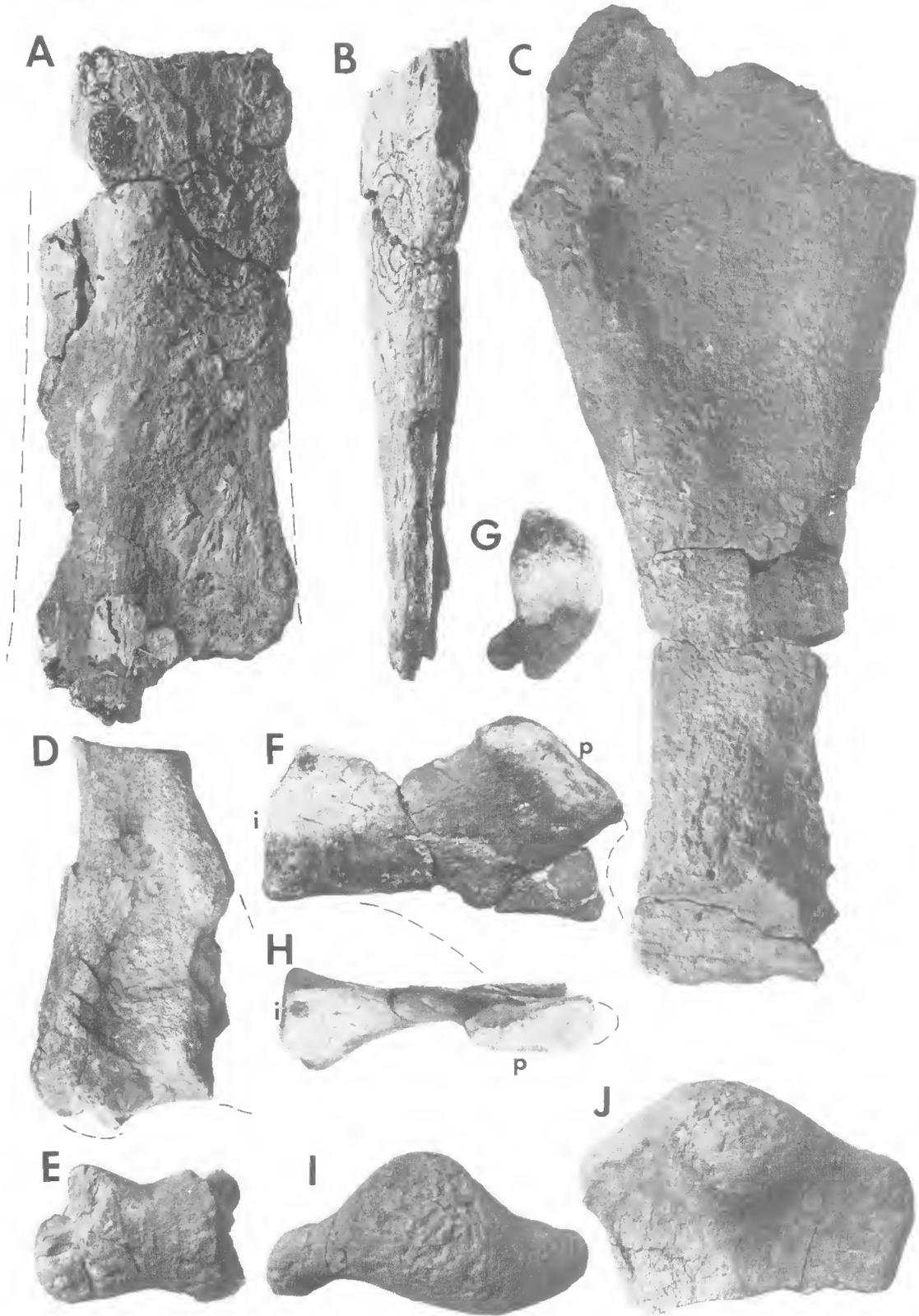
Girdle elements. A, F7880, left coracoid, medial view, g : glenoid, and s : scapular surface; B and C, F7292, ?coracoid, medial and edge views; D and E, F6737, left scapular fragment, medial view and view of glenoid, c : coracoidal, and g : glenoid surface; F and G, F7291, uncertain fragment, possible coracoid or fragment of ilium.
Approximately one-sixth natural size.



MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE III

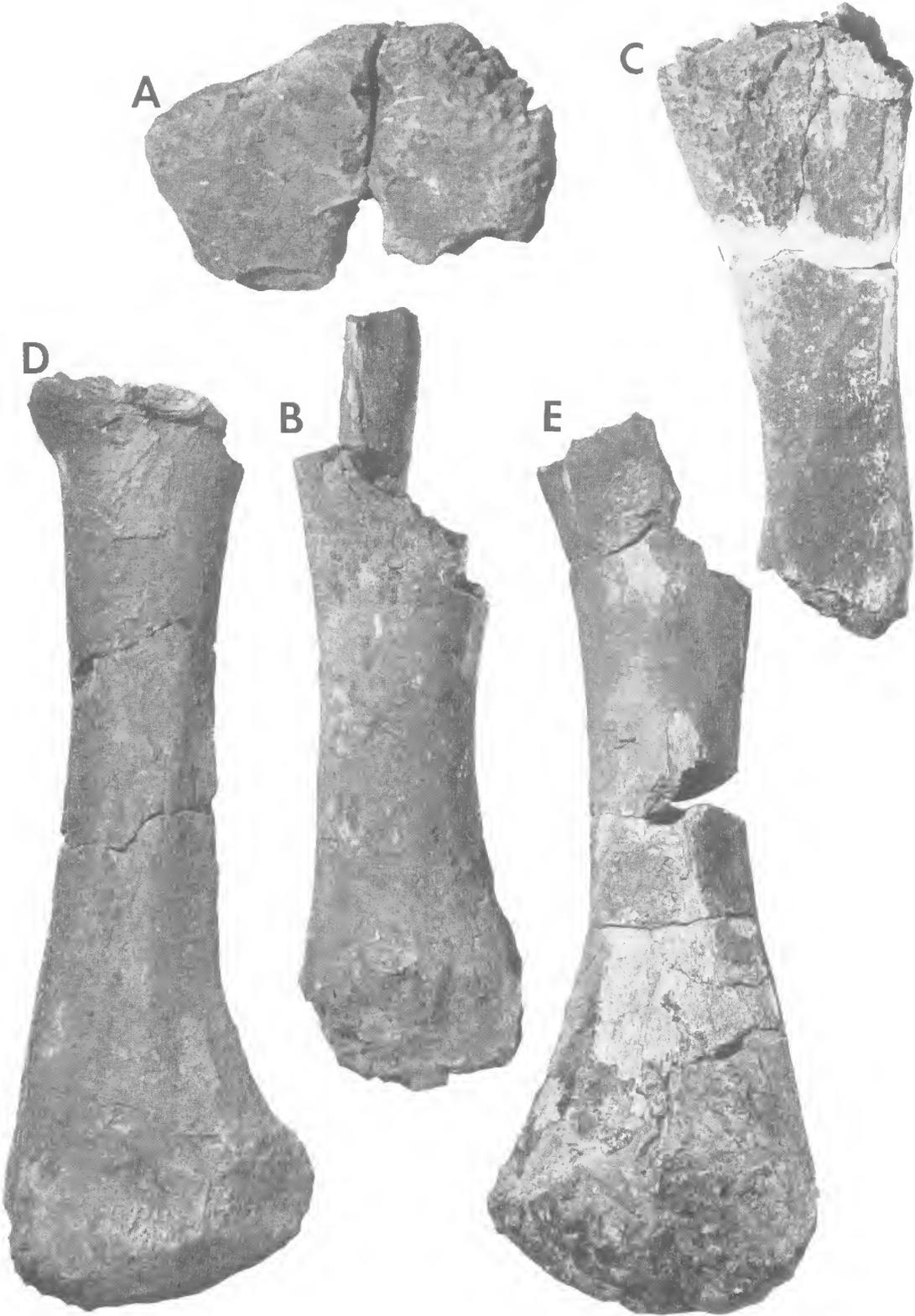
Girdle and limb elements. A and B, F7292, scapular blade, lateral and edge views; C, F7292, left humerus, flexor surface; D and E, F3390, distal end of left? humerus, views of extensor surface and articular end; F, G, and H, F6737, fragmentary left ischium, lateral and anterior views, and view of iliac articular surface; I and J, F3390, proximal end of right humerus, views of proximal end and extensor surface, i : ilial and p : pubic articular surfaces. Approximately one-sixth natural size.



MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE IV

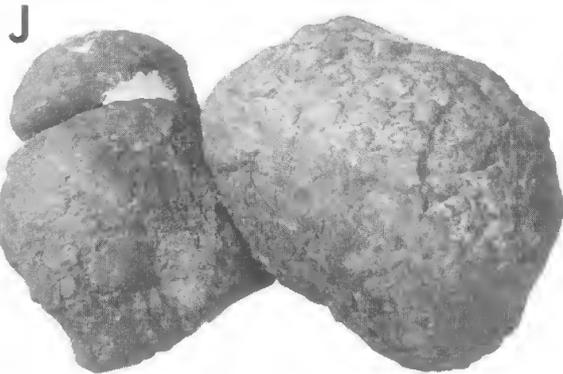
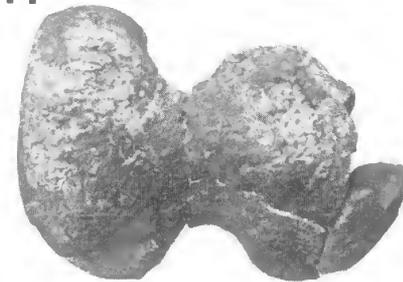
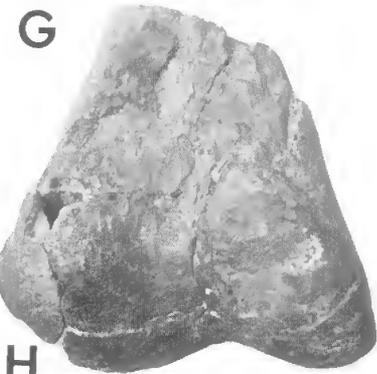
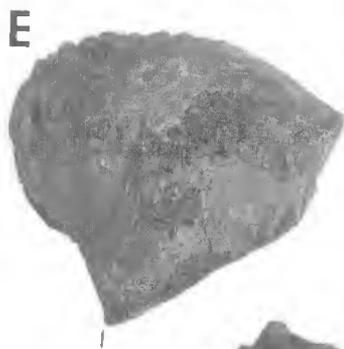
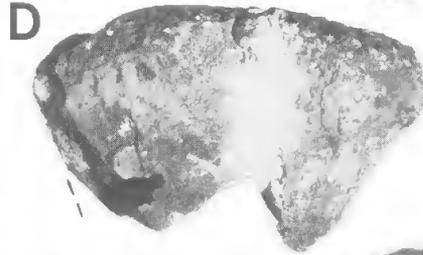
Forelimb elements, all from specimen F7292. A, proximal end of an ulna, anterior view; B, distal end of an ulna, anterior view; C, shaft of an ulna, anterior view; D and E, two radii, lateral views. Approximately one-sixth natural size.



MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE V

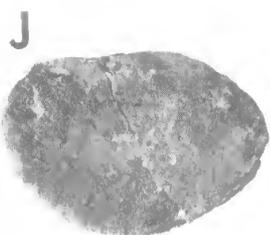
Primarily hindlimb elements. A and B, F3390, proximal end of a femur, proximal and anterior views; C and D, F7291, uncertain fragment, possibly the proximal end of an ulna; E and F, F7880, head of a femur; G and H, F3390, distal end of a femur, posterior and distal views; I and J, F7291, broken distal end of a femur, anterior and distal views. Approximately one-sixth natural size.



MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE VI

Meso- and metapodials. A, B, and C, F7292, metacarpal III, anterior, lateral, and proximal views; D and E, F7291, metacarpal I, anterior and proximal views; F and G, F7292, proximal half of metacarpal II, anterior and proximal views; H, F7292, distal half of a metacarpal, probably the same metacarpal II as the preceding, anterior view; I, F7292, metacarpal III, anterior view; J and K, F7292, proximal end of metacarpal II, proximal and ?lateral views; L through Q, F3390, metacarpals I, II, and III, proximal and ?anterior views; R and S, F7292, uncertain element, possibly a carpal, two views. Approximately one-sixth natural size.







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