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CONTENTS

THE AUSTRALIAN SESARMINAE (CRUSTACEA: BRACHYURA): FIVE SPECIES OF *SESARMA* (*CHIROMANTES*)

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ABSTRACT

Three new species of *Sesarma* (*Chiromantes*) and a new subspecies of *S.* (*C.*) *semperi* are described, and *S.* (*C.*) *livida* is recorded from Australia for the first time. Previous records of *S.* (*C.*) *bidens* are presumed to be based on misidentifications.

An original key to the thirteen known Indo–West Pacific species of this subgenus is presented.

Haswell's 1882 catalogue of the Australian Crustacea lists only four species of *Sesarma* (*S. similis* Hess being a synonym of *S. atrorubens* Hess). Since then the recorded total for Australia has risen to only nine species although as far back as 1917 Tesch recorded 93 for the Indo-Pacific region, and this number has now increased to some 115 species. Because much of the Australian coastline exhibits the required ecological conditions for this essentially tropical estuarine genus it seemed that extensive personal collecting was called for, covering as much of the East Australian coast as is readily accessible. Preliminary study suggests that these collections, augmented by material collected independently by Dr. W. Macnae (see Macnae, 1966) will at least double the Australian records. In the present subgenus three of the five species to be described are new, the others have not previously been recorded from Australia. As this subgenus is not well represented in museums within Australia the present work is based almost entirely on the above-mentioned collections. Most specimens have been deposited in the Queensland Museum, and a series of paratypes sent to the Australian Museum, Sydney.

When collecting, considerable attention was paid to habitat data, and an attempt was made to record the penetration of each species up the estuary in terms of salinity. The salinity varies markedly with the state of the tide, and as

B

the limited time available did not allow more than one reading at most localities, this was recorded as $^0/_{00}$ at an estimated tidal height, and a roughly standardised estimate of salinity at high water was made according to the following table:

State of Tide	Salinity recorded ($^0/_{00}$)			
High water	<5	5–15	15–25	25–35
Half tide	<2	2–10	10–20	20–35
Low water	<1	1– 5	5–15	15–35
Estimated high water salinity	Very low	Low	Moderate	High

This table does not presume to any high degree of accuracy, but is based on a number of readings taken over a range of tidal heights at several localities, mostly on the Burnett River. Although the final estimate can only be approximate it must be more meaningful than a measure of distance from the mouth.

All line drawings were prepared using a camera lucida; those of the male pleopods have been included as much to show the general resemblance between members of this subgenus as to aid in their discrimination. There is an obvious constant facies on which is superimposed variation in such features as orientation of terminal projection, form of extremity of this projection, and relative length and density of bristling (although these latter are subject to intraspecific variation).

Tweedie (1940) commented on the artificiality of the present subgeneric classification of the genus, but while Tesch's (1917) keys remain the basis for students of this genus complete disregard for the subgenera can only make identifications more difficult. Of the four which have been commonly used (*Sesarma* Say, *Holometopus* Milne Edwards, *Parasesarma* de Man, and *Chiromantes* Gistel) the latter does in fact possess the required degree of homogeneity and can be retained on theoretical as well as practical grounds.

Subgenus **Chiromantes** Gistel

Pachysoma de Haan, 1833, p. 5; 1835, p. 33. (Type species: *Grapsus* (*Pachysoma*) *bidens* de Haan.)

[non] *Pachysoma* Macleay, 1821 (Coleoptera).

Chiromantes Gistel, 1848, nom. nov. pro *Pachysoma* de Haan.

Perisesarma de Man, 1895, p. 208. (Rathbun's (1918, p. 284) designation of *S. bidens* (de Haan) as type species is inadmissable as that species was not originally included in this subgenus by de Man. *S.* (*Perisesarma*) *dussumieri* Milne Edwards is here designated type species, and *Perisesarma* becomes a junior subjective synonym of *Chiromantes*).

This subgenus is characterised by the presence of at least two transverse pectinate crests on the upper surface of the chela, the associated development of stridulatory tuberculation on the dactyl of the cheliped, and a distinct epibranchial tooth behind the external orbital angle. Thus defined, the subgenus contains the thirteen Indo–West Pacific species which appear in the key below.

Apart from the addition of four new species, the following nomenclatural alterations have become necessary since the publication of Tesch's (1917) revision. *Sesarma siamensis* Rathbun was shown by Tweedie (1936, pp. 66–7) to be a synonym of *S. fasciatum* Lanchester. This species has been excluded from the present subgenus because the pectinate crests on the chela are more nearly longitudinal than transverse, the dactylar ornamentation is spinose, and the epibranchial tooth is never prominent and often absent. *Sesarma bidens indica* de Man, preoccupied by *Sesarma indica* H. Milne Edwards, has become *Sesarma bidens indiarum* Tweedie, 1940. It is here treated as if it had full specific status.

Alcock (1900, p. 415) inadvisedly united *S. dussumieri, S. haswelli* de Man, and *S. lividum* A. Milne Edwards with *S. bidens*. This move has been adequately criticised by subsequent workers (see de Man 1895, 1903).

It is extremely difficult to differentiate between some of the members of this subgenus, and much reliance has been placed on the detailed conformation of the tuberculation of the dorsal surface of the dactyl of the cheliped. Tweedie (1954) has shown that this functions as a stridulatory organ, and the pectinate crests on the chela are almost certainly for auditory perception. This whole mechanism must be of prime importance to the crabs as a means of intraspecific recognition, as there are no obvious visual recognition features, and coloration is very variable. If the structural configuration of the tubercles reflects the distinctive sounds which must be produced by them, there is surely some justification for using this exhaustively (but not exclusively) in identification. In practice this is the most convenient, often the only, feature for the construction of a key. It is unfortunate that the tuberculation is not fully developed in females, and the following key can not be relied upon unless males are available.

The key is based on information obtained from original descriptions and figures; from de Man's (1888, pp. 175–80) notes on the types of *S. bidens, S. dussumieri, S. guttatum* A. Milne Edwards, and *S. lividum*; from Crosnier's (1965) description of and notes on the type of *S. guttatum*; from photographs of the types of *S. guttatum* and *S. lividum* (attempts to locate the type of *S. haswelli,* reported by Kemp (1918, p. 233) to be housed in the Indian Museum, have not been successful); and from examination of specimens of *S. guttatum, S. indiarum,* and *S. semperi* Bürger in addition to those described below.

4

MEMOIRS OF THE QUEENSLAND MUSEUM

KEY TO THE INDO–WEST PACIFIC SPECIES OF SESARMA (CHIROMANTES)

(Species in bold face are described in this paper; in the case
of other species a reference is given to a recent description.)

1. Distal dactylar tubercle greatly elongate, occupying approximately
    one-quarter the length of the dactyl..........................
    ....*S. onychophora* de Man, 1895.
    Indo-Malaysian Archipelago. (See de Man, 1895, p. 214, pl. 31,
    fig. 39.)

    Distal dactylar tubercle not greatly elongate................... 2

2 (1). Dactylar tubercles 7–9 in number, prominent, subcircular, dome-shaped;
    carapace scattered with small, rounded tufts of hair............. 3

    Dactylar tubercles not prominent, dome-shaped, or if so numbering
    more than 9.. 4

3 (2). Dactylar tubercles 7–8, symmetrical in profile; distal pectinate crest
    with *c.* 20 teeth...............*S. semperi semperi* Bürger, 1894.
    Philippines, Labuan. (See Bürger 1894, p. 630, pl. 21, fig. 1;
    de Man, 1903, p. 542; Tweedie, 1950, pp. 342–3, fig. 1e (male
    pleopod).)

    Dactylar tubercles 8–9, asymmetrical, the proximal slope the longer;
    distal pectinate crest with *c.* 25 teeth.......................
    ....**S. semperi longicristatum** nov.

4 (2). More than 14 distinct dactylar tubercles..................... 5

    Dactylar tubercles 14 or less, or if more than 14, the distal ones very
    low, indistinct, barely discernable............................ 7

5 (4). Dactylar tubercles 16–19, asymmetrical, the proximal slope the longer,
    the distal slope nearly vertically deflexed.....*S. haswelli* de Man, 1887.
    Tropic central Indo-Pacific. (See de Man, 1888, pp. 175–7.)

    Dactylar tubercles symmetrical or nearly so..................... 6

6 (5). Dactylar tubercles 19–26, smaller and more closely arranged on the
    distal third of the dactyl..............*S. eumolpe* de Man, 1895.
    Indo-Malaysian Archipelago. (See de Man, 1895, p. 208, pl. 31,
    fig. 38.)

    Dactylar tubercles 15–16, spaced further apart distally..........
    ....**S. darwinensis** nov.

7 (4). Breadth of penultimate segment of male abdomen *c.* 1·5 times length
    ....*S. dussumieri* A. Milne Edwards, 1853.
    Tropic central Indo-Pacific. (See de Man, 1888, pp. 177–9, pl. 12,
    figs. 8–12.)

Breadth of penultimate segment of male abdomen *c.* twice length 8

8 (7). Fixed finger short, length of cutting edge *c.* 0·37 times length of propodus; dactylar tubercles forming irregular shapes in dorsal view . . . . **S. lividum** A. Milne Edwards, 1869.

Fixed finger longer, length of cutting edge *c.* 0·40 times length of propodus; dactylar tubercles not forming irregular shapes in dorsal view 9

9 (8). Dactylar tubercles low and indistinct, barely discernable on distal half of dactyl, 14 to 16 in all . . . . **S. messa** nov.

All dactylar tubercles distinct 10

10 (9). Dactylar tubercles each with median raised stripe at right angles to axis of dactyl 11

Dactylar tubercles without median stripe 12

11 (10). Dactylar tubercles 10–11, large, symmetrical, subcircular, dome-shaped; median stripe smooth; distal pectinate crest with *c.* 15 teeth . . . . **S. brevicristatum** nov.

Dactylar tubercles 11–13, those on at least the proximal half oval, the longer axis transverse; medium stripe with grooves ("chiton-like"); distal pectinate crest with *c.* 20 teeth . . . . *S. guttatum* A. Milne Edwards, 1869. East Africa. (See Crosnier, 1965, pp. 68–9, figs. 94, 97, 106.)

12 (10). Dactylar tubercles 12–13, oval; male abdomen more than twice as broad as long . . . . *S. bidens* de Haan, 1835. Japan. (See de Haan, 1835, p. 60, pl. 11, fig. 4; pl. 16, fig. 4; Sakai, 1939, p. 688, pl. 79, fig. 1.)

Dactylar tubercles 11–12, subcircular; male abdomen not more than twice as broad as long . . . . *S. indiarum* Tweedie, 1940. Tropic central Indo-Pacific. (See Tesch, 1917, pp. 134–5; Tweedie, 1950, fig. 1f (male pleopod).)

Sesarma (Chiromantes) darwinensis sp. nov.

(Figs. 1A, 2A; pl. 1)

MATERIAL EXAMINED

Holotype: Male (20 mm), Darwin, W. Macnae, Qd Mus. W2442.

Paratype: Male (13 mm), Darwin, W. Macnae (collected with holotype), Qd Mus. W2443.

MATERIAL ILLUSTRATED

Holotype.

DESCRIPTION

CARAPACE: Fronto-orbital width greater than carapace length (*c.* 1·25 times). Lateral margins of carapace only slightly convergent posteriorly, with single epibranchial tooth. Front oblique on either side of broad median emargination, with lateral angles approximately right-angled. Post-frontal lobes distinct, medians only slightly broader than laterals. Carapace hairs arranged sparsely on branchial lines and in sparse, mostly short rows on rest of carapace. Long bristles from median post-frontal lobes meet over frontal furrow. Second branchial line usually arises from first, third variable. Cardiaco-intestinal and lateral portions of gastro-cardiac groove deep.

CHELIPEDS: Upper surface of chela of male with two transverse pectinate crests, the distal one composed of some 15–20 tall teeth; secondary crest smaller but well developed. Outer surface granulate, with some granules tending to coalesce to form an indistinct median longitudinal ridge. Inner surface with scattered granules, some tending to form a transverse ridge dorsally. Immovable finger somewhat flattened on outer surface, with suggestion of ridge ventrally; length of cutting edge 0·40–0·45 times length of propodus.
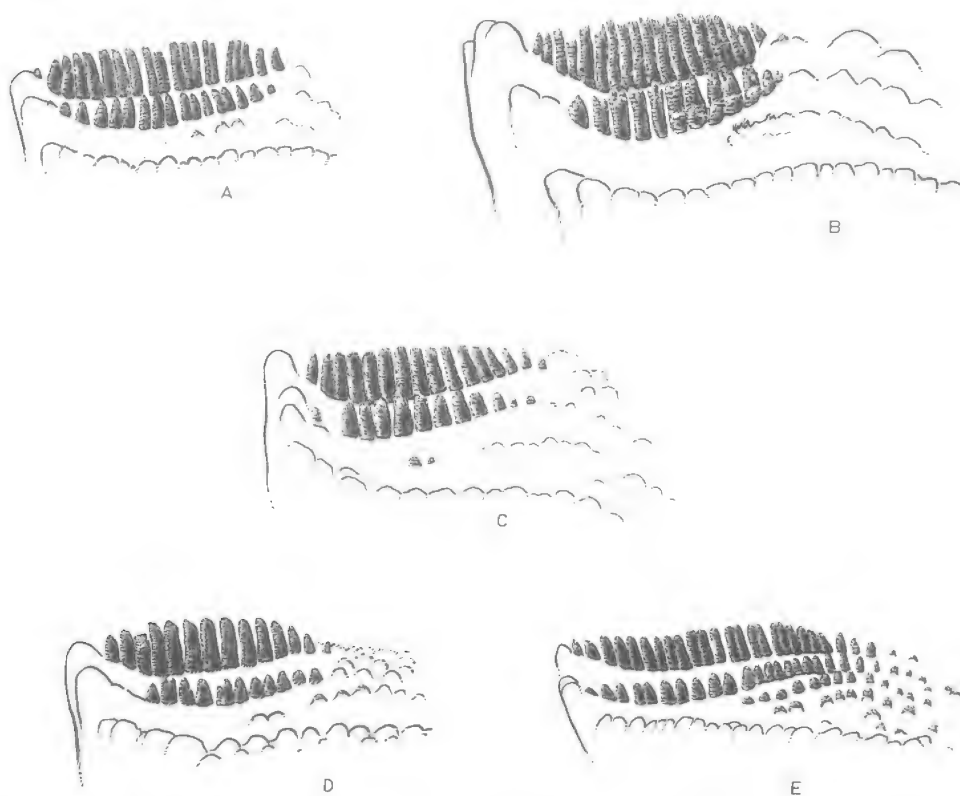

FIG. 1: Postero-dorsal view of pectinate crests on upper surface of chelae of A, *S.* (*C.*) *darwinensis;* B, *S.* (*C.*) *lividum;* C, *S.* (*C.*) *messa;* D, *S.* (*C.*) *brevicristatum;* E, *S.* (*C.*) *semperi longicristatum.*

Dorsal surface of dactyl with 15–16 distinct symmetrical tubercles with their transverse axes much the longer, and with median striated stripe except the more distal ones, which become progressively more dome-shaped. Proximally there is a row of sharp granules on the inner edge of the dorsal surface of the dactyl.
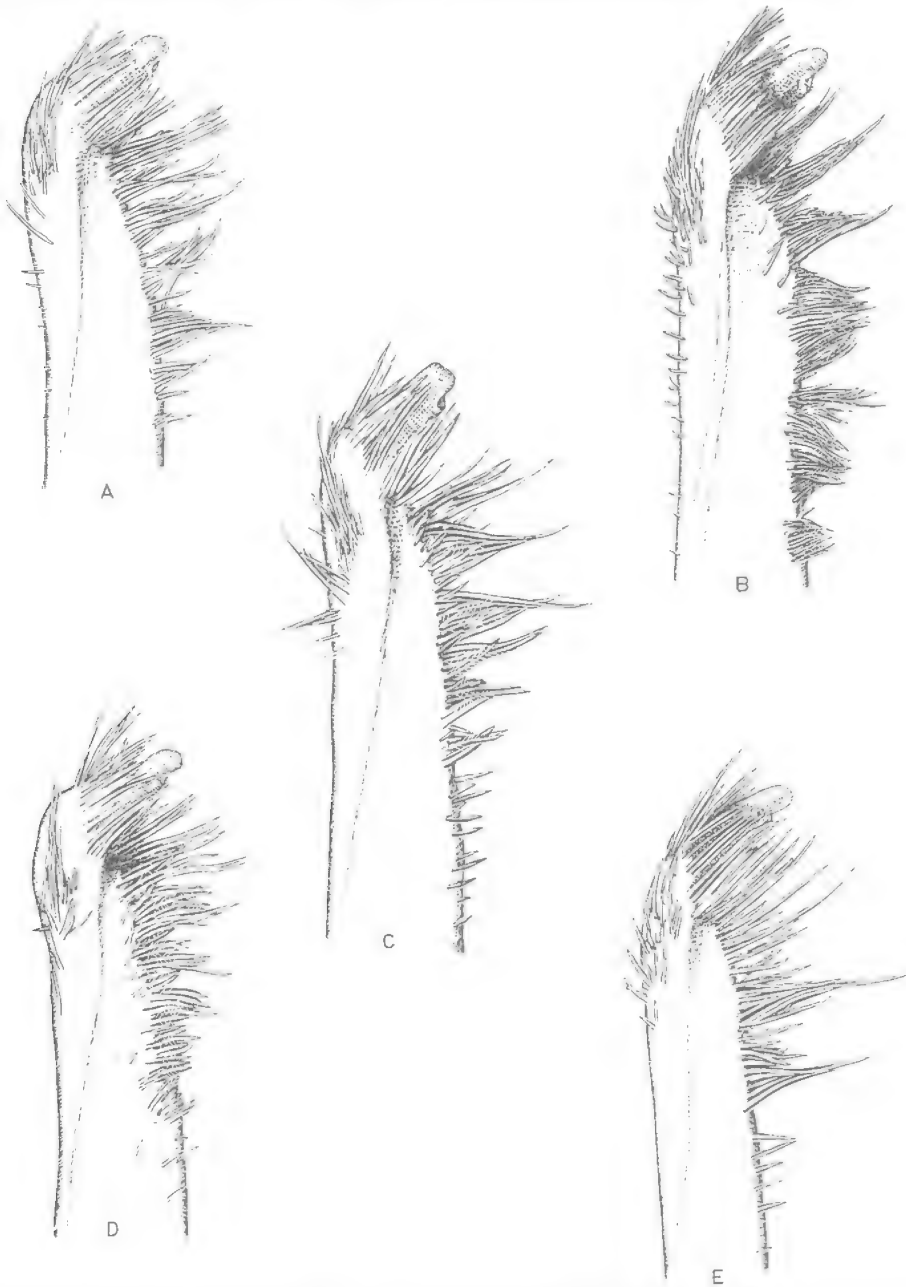

FIG. 2: Right first male pleopods of A, S. (C.) *darwinensis;* B, S. (C.) *lividum;* C, S. (C.) *messa;* D, S. (C.) *brevicristatum;* E, S. (C.) *semperi longicristatum.*

Inner angle of carpus not produced. Dorsal border of merus with small, acute, forwardly directed spine. Ventral border with very prominent, acute, denticulate, subdistal spine.

THIRD AMBULATORY LEG: Twice carapace length. Merus little more than twice as long as broad.

MALE ABDOMEN: Penultimate segment twice as broad as long. Ultimate segment little broader than long.

COLOUR: Alcohol preserved specimens suggest that the original colour was dark mottled carapace, orange chelae, paler legs.

HABITAT

Presumably from mangrove mud-flats.

COMMENTS

This species differs from de Haan's *S. bidens* in having 15–16 dactylar tubercles (as against 12–13), a broader frontal emargination with less markedly projecting front, and the lateral margins of the carapace more nearly subparallel. (Cf. de Haan, 1835, pl. 16, fig. 4; Sakai, 1939, pl. 79, fig. 1.)

S. indiarum Tweedie 1940 differs from the present species in having only 11 subquadrate dactylar tubercles.

S. haswelli de Man has 16–19 dactylar tubercles which are markedly asymmetrical.

Sesarma (Chiromantes) lividum A. Milne Edwards

(Figs. 1B, 2B; pl. 2)

Sesarma lividum Milne Edwards, A., 1869, pp. 25–6; 1873, pp. 303-4, pl. 16, figs. 2, 2a. Brocchi, 1875, p. 83.

Sesarma livida A. Milne Edwards. de Man, 1887a, p. 659; 1887b, pp. 381–2, pl. 17, fig. 1.

Sesarma (Perisesarma) livida A. Milne Edwards. de Man, 1903, p. 539.

Sesarma (Chiromantes) lividum A. Milne Edwards. Rathbun, 1910, p. 329.

Sesarma (Chiromantes) livida A. Milne Edwards. Tesch, 1917, pp. 169-70; 1918, p. 114.

[non] *Sesarma livida* A. Milne Edwards. de Man, 1888, pp. 179-80 (= *S. onychophora* de Man, 1895).

MATERIAL EXAMINED

Seven males (10–26 mm), seven females (15–21 mm), Flying-Fish Pt. road (Innisfail).

MATERIAL ILLUSTRATED

Male (26 mm), Flying-Fish Pt. road, B.C., 29-10-63, Qd Mus. W2444/1.

DESCRIPTION

CARAPACE: Fronto-orbital width greater than carapace length (c. $1 \cdot 2$–$1 \cdot 25$ times). Lateral margins of carapace convergent posteriorly, with single small epibranchial tooth. Front oblique on either side of broad median emargination. Post frontal lobes distinct, medians broader than laterals (c. $1 \cdot 3$ times). Carapace smooth and shining, with hairs along branchial lines and with distinct rows of close-packed hairs on remainder of carapace, particularly anteriorly. Long bristles from median post-frontal lobes meet over the median furrow. Second lateral line arises from, or just short of, first; third variable, usually arises short of carapace margin.

CHELIPEDS: Upper surface of chela of male with two transverse pectinate crests, the primary composed of some 15–17 tall teeth; secondary ridge smaller, but still strongly developed. Outer surface granular, sometimes without median longitudinal row. Inner surface with scattered granules. Immobile finger a little flattened on outer surface, with faintly indicated ventral ridge on some specimens; short, length of cutting edge c. $0 \cdot 36$–$0 \cdot 37$ times length of propodus. Ventral border of chela not concave at base of fixed finger.

Dorsal surface of dactyl with some 11–13 tubercles of which the proximal 7–8 are distinct, but more distal ones become progressively less developed. The shape of the proximal tubercles appears irregular and is somewhat variable, but usually they are resolvable into pairs. The proximal member of each pair is usually subcircular and longitudinally grooved, the distal member is usually smooth, and roughly crescent or comma shaped, with its proximal border concave. The proximal two-thirds of the inner edge of the dorsal surface bears a row of distinct granules.

In the female the chelae are smaller, relatively more elongate, and the peculiar dactylar tuberculation is less distinctly developed although usually still recognisable.

Inner angles of carpus not produced. Dorsal border of merus with small, acute, forwardly directed spinule, sometimes reduced to a right-angled projection. Ventral border with distinct subdistal spine.

THIRD AMBULATORY LEG: Little more than $1 \cdot 75$ times length of carapace. Merus less than twice as long as broad. Length of dactyl c. $0 \cdot 75$ times breadth of merus.

MALE ABDOMEN: Penultimate segment twice as broad as long. Second segment not expanded medially.

COLOUR: Carapace deep purple with few inconspicuous green spots; legs paler purplish. Cheliped with yellow-orange on inner faces of carpus and merus; chelae yellow-orange on base of inner face, darkening distally, orange-brown on outer face.

HABITAT

All specimens were collected on the surface of sandy mud by a small stream running through dense mangrove thicket. When disturbed, the crabs took shelter under rocks, tree trunks, or in shallow burrows. Salinity was high ($31^0/_{00}$ at High Water Neap).

COMMENTS

A comparison of Milne Edwards' (1873) figure of this species with a photograph of his holotype (Paris Museum, male, 26 mm, New Caledonia) reveals many inaccuracies of proportion. To list them here would, in effect, necessitate a repetition of most of the description given above. It is sufficient to say that both the present specimens and the holotype (as far as can be judged from a photograph of the dorsal surface) agree with the above description.

DISTRIBUTION

From New Caledonia (Milne Edwards, 1869, 1873) to Amboina (de Man, 1903), Java (de Man, 1888), and the Gulf of Thailand (Rathbun, 1910).

Not previously from Australia.

Sesarma (Chiromantes) messa sp. nov.

(Figs. 1C, 2C; pl. 3)

Sesarma bidens, de Haan? [sic], Miers, 1884, pp. 246–7.

[?] *Sesarma bidens* (de Haan). Grant and McCulloch, 1906, p. 23. Hedley, 1910, p. 343. Stephenson *et al.,* 1931, pp. 42, 61.

[non] *Sesarma bidens* (de Haan), 1835, p. 60.

> *S. bidens* is generally regarded as being confined to Japanese waters and is not present in existing collections from Australia. The records listed above are undoubtedly based on misidentifications. Miers (1884) mentions that in his specimens the dactylar tuberculation is much less distinctly marked than in *S. bidens* as figured by de Haan, and it is almost certain that they belong to the present species. Subsequent authors have merely listed the name, and their records are included under this species only because this is the most common and widespread of the *S. bidens*-like species on the Queensland coast.

MATERIAL EXAMINED

Holotype: Male (23 mm), Townsville, W. Macnae, Feb. 1962, Qd Mus. W2445.

Paratypes: Male (19 mm), two females (17, 20 mm), Townsville, W. Macnae, Feb. 1962 (collected with holotype), Qd Mus. W2446. Male (21 mm), Townsville, W. Macnae, 4-2-62, Qd Mus. W2447. Male (21 mm), female (ovigerous) (20 mm), Townsville, W. Macnae, 8-2-62, Qd Mus. W2448. Female (21 mm), Townsville, W. Macnae, 3-2-62, Qd Mus. W2449. Four males (26, 24, 17, 16 mm), two females

(17, 15 mm), Townsville, W. Macnae, 27-2-62, Qd Mus. W2450. Male (17 mm), Cape Cleveland (Townsville), D. Fielder, 3-9-63, Aust. Mus. P15348. Male (24 mm), Cairns (airport swamp), W. Macnae, Qd Mus. W2451. Male (20 mm), female (22 mm), between Innisfail and Flying-Fish Pt., W. Macnae, 13-3-62, Aust. Mus. P15349. Three males (19, 18, 14 mm), two females (17, 10 mm), one mile towards Innisfail from Flying-Fish Pt., B.C., 29-10-63, Qd Mus. W2452. Two females (24, 20 mm), Pannikin I., Moreton Bay, W. Stephenson, 12-8-58, Qd Mus. W2453. Male (24 mm), Brisbane R. mouth, B.C., Nov. 1964, Qd Mus. W2454. Male (19 mm), Cawarral Ck., Rockhampton, N. Milward, 17-12-65, Qd Mus. W2455.

MATERIAL ILLUSTRATED

Holotype.

DESCRIPTION

CARAPACE: Fronto-orbital width greater than carapace length ($c.$ $1 \cdot 2$ times). Lateral margins of carapace with single epibranchial tooth, slightly concave, subparallel except for projecting external orbital angles and epibranchial teeth. Front with rounded lobes on either side of broad, shallow median emargination. Frontal margin usually distinctly concave laterally, adjacent to blunt lateral angles. Post-frontal lobes distinct, medians broader than laterals ($c.$ $1 \cdot 3$–$1 \cdot 4$ times). Carapace smooth and shining, somewhat wrinkled and punctate posteriorly, with hairs along branchial lines and forming distinct rows of close-packed, long hairs on rest of carapace, particularly anteriorly. Long bristles from median post-frontal lobes meet over the median furrow. Second lateral line arises from, or just short of, first; third variable, usually arises short of carapace margin.

CHELIPED: Upper surface of chela of male with two transverse pectinate crests, the distal one composed of some 14–19 broad teeth; secondary crest smaller but still well developed. Sometimes a row of horny granules is present proximal to the secondary crest. Outer surface granular, sometimes with a suggestion of a median longitudinal row. Inner surface with scattered granules. Immovable finger a little flattened on outer surface with faintly indicated ventral ridge; length of cutting edge $c.$ $0 \cdot 40$–$0 \cdot 45$ times length of propodus. Ventral border of chela concave at base of immovable finger.

Dorsal surface of dactyl with some 14–16 very low, subcircular tubercles of which the proximal 5–8 are distinct, but the more distal ones become progressively almost indiscernable. On the proximal two-thirds of the inner edge of the dorsal surface there is a row of sharp, distinct granules which are often more obvious than the tubercles.

In the female the chelae are smaller, relatively more elongate, but essentially similar in tuberculation to those of the male.

Inner angle of carpus not produced. Dorsal border of merus with small, acute, forwardly directed spinule, sometimes reduced to a right-angled projection. Ventral border with distinct subdistal spine.

THIRD AMBULATORY LEG: Twice carapace length. Merus twice as long as broad, length of dactyl approximately equal to breadth of merus. (In one specimen the dactyl was only 0·75 times the breadth of the merus.)

MALE ABDOMEN: Penultimate segment almost twice as broad as long. Second segment expanded medially so that its median length is approximately twice its lateral length.

COLOUR: Carapace and legs sometimes olive-grey, more usually black to deep violet or reddish-brown, with variable proportion of greenish mottling. Chelae reddish-brown.

HABITAT

At approximately H.W.N. in estuaries and sheltered bays in mangrove thicket near water of moderate salinity (minimum $16^0/_{00}$ at half flood tide).

COMMENTS

Although recorded localities for specimens on hand range from Moreton Bay north only to Cairns, Macnae (1966, p. 79, as undescribed *Sesarma*) reports that this species is abundant from Thursday I. to Port Curtis.

This species differs from *S. bidens* in having lower, much less distinct dactylar tubercles and more nearly parallel carapace margins. The male abdomen of this species differs from *S. bidens* (see de Haan 1835, pl. 16, fig. 4) and other members of this subgenus here described, in that the second segment is much longer in the mid-line than it is laterally. The specific name was formed from the initial letters of "Medially Expanded Second Segment of Abdomen".

Sesarma (Chiromantes) brevicristatum sp. nov.

(Figs. 1D, 2D; pl. 4)

MATERIAL EXAMINED

Holotype: Male (21 mm), Halifax–Lucinda road, W. Macnae, 20-3-62, Qd Mus. W2456.

Paratypes: Female (ovigerous) (17 mm), two indet. (14, 13 mm), Halifax–Lucinda road, W. Macnae, 20-3-62 (collected with holotype), Qd Mus. W2457. Two males (20, 18 mm), Townsville, and Innisfail–Flying-Fish Pt. road, W. Macnae, 13-3-62, Aust. Mus. P15347. Five males (20, 18, 16, 14, 11 mm), female (17 mm), 1 mile towards Innisfail from Flying-Fish Pt., B.C., 29-10-63, Qd Mus. W2459.

MATERIAL ILLUSTRATED

Holotype.

DESCRIPTION

CARAPACE: Fronto-orbital width greater than carapace length (*c*. 1·2 times). Lateral margins of carapace behind the single epibranchial tooth concave, subparallel. Front only slightly sinuous, oblique on either side of broad, shallow median emargination, with lateral angles acute. Median post-frontal lobes distinct, only slightly broader than laterals. Carapace hairs arranged sparsely on branchial lines, and in mostly short rows on anterior half of carapace. Long bristles from the median post-frontal lobes meet over the frontal furrow. Second branchial line arises from first, third arises short of lateral margin.

CHELIPEDS: Upper surface of chela of male with two transverse pectinate crests, the primary short, composed of some 15 (13–19) tall teeth, much larger than the secondary crest which may have as few as 6 (to 14) low horny granules. Outer surface granular, with variably indistinct median longitudinal ridge. Inner surface with scattered granules. Immovable finger flattened on outer surface, with slight ridge ventrally; length of cutting edge *c*. 0·4 times length of propodus.

Dorsal surface of dactyl with 10–11 symmetrical tubercles, the first small, the third the largest, then gradually decreasing in size distally. These tubercles are very prominent, broadly oval or subcircular with a smooth raised stripe at right-angles to the axis of the dactyl. Proximally there is a row of granules on the inner edge of the dorsal surface of the dactyl.

In females and smaller males the proximal pectinate crest may be replaced by a row of granules, the dactylar tubercles are less prominent but still very distinct.

Inner angle of carpus not produced. Dorsal border of merus with small acute forwardly directed spine. Ventral border with very prominent, acute, denticulate subdistal spine.

THIRD AMBULATORY LEG: Approximately twice carapace length. Merus little more than twice as long as broad.

MALE ABDOMEN: Penultimate segment twice as broad as long, as long as ultimate segment.

COLOUR: Dark purplish with pale green mottling, the relative areas of each colour varying from almost entirely purple to almost entirely green. Cheliped with carpus pale yellowish or darker red, chela usually bright orange in large males, sometimes nearly black with variable green mottling.

HABITAT

In burrows and under logs on sandy mud occasionally on tree trunks to a height of 8 ft, in tall, open mangrove thicket well back from the stream at M.T.L., but covered at H.W.N. Salinity high. Also collected from base of hard, grassed, earth bank on Johnstone R.; salinity low to very low.

COMMENTS

Recorded localities for specimens on hand range only from Townsville to Innisfail, but Macnae (1966, p. 79, as *Sesarma* cf. *guttata*) reports that this species is common from Thursday I. to Port Curtis.

This species differs from *S. bidens* and from *S. indiarum* in having a less pronouncedly bilobate front and a raised median stripe on each dactylar tubercle. The dactylar tubercles are fewer and more circular than in *S. bidens,* more prominent than in *S. indiarum.* From other species of this subgenus it is readily distinguished by the above key.

The specific name owes its origin to the distal pectinate crest of the chela, which is characteristically rather short and high.

Sesarma (Chiromantes) semperi longicristatum ssp. nov.

(Figs. 1E, 2E; pl. 5)

MATERIAL EXAMINED

Holotype: Male (20 mm), Rose Bay, Townsville, J. Jackson and B.C., 22-10-63, Qd Mus. W2460.

Paratypes: Two males (14·5, 10 mm), two females (ovigerous) (15, 14 mm), female (12 mm), Thompson's Pt., Rockhampton, B.C., Dec. 1961, Qd Mus. W2461. Five males (19, 15, 13, 13, 13 mm), two females (13, 12·5 mm), Burnett Hds., Bundaberg, B.C., Dec. 1961, Qd Mus. W2462. Male (12 mm), Boyne R., Gladstone, B.C., 12-12-61, Aust. Mus. P15346. Female (ovigerous) (20 mm), Townsville, W. Macnae, 8-2-62, Qd Mus. W2463. Four males (19, 14, 13·5, 12 mm), two females (ovigerous) (19, 14·5 mm), female (15 mm), Port Alma, Rockhampton, B.C., 6-12-61, Qd Mus. W2464. Male (18 mm), Townsville, W. Macnae, 14-2-62, Qd Mus. W2465. Male (17 mm), Sandgate, Brisbane R., Aust. Mus. P7915.

MATERIAL ILLUSTRATED

Holotype.

DESCRIPTION

CARAPACE: Fronto-orbital width greater than carapace length (*c.* 1·25 times). Lateral margins of carapace subparallel, convex behind single very acute epibranchial tooth. Lateral margin of external orbital angle only slightly convex. Front on either side of broad shallow median emargination almost straight, oblique, with lateral angles obtuse or right-angled. Post-frontal lobes not prominent. Median lobes broader than laterals (*c.* 1·3 times). Carapace with hairs arranged sparsely on branchial lines; remainder of carapace with small tufts of sparse hairs. This tufting is a useful character for the rapid field identification of both sexes. Second and third branchial lines arise short of carapace margin.

CHELIPEDS: Upper surface of chela of male with two long, low, transverse pectinate crests, the primary row composed of some 25 teeth, the secondary of some 24. One or two subsidiary rows of horny granules are common proximal to the secondary crest. Outer surface granular, with indistinct median longitudinal ridge. Inner surface with scattered granules. Outer surface of immovable finger flattened, with slight longitudinal ridge ventrally; length of cutting edge $c.$ $0 \cdot 4$ times length of propodus.

Dorsal surface of dactyl with 7–9 tubercles, the first the smallest, the third the largest, gradually decreasing in size distally. The tubercles are asymmetrical, the proximal slope the longer. Proximally there is a row of granules on the inner edge of the dorsal surface of the dactyl. In females and smaller males the tubercles are lower, more asymmetrical, the pectinate crests much reduced.

Inner angle of carpus not produced. Dorsal border of merus with small, acute, forwardly directed spine. Ventral border with long, acute, denticulate subdistal spine.

THIRD AMBULATORY LEG: A little more than twice carapace length, less than twice fronto-orbital width. Merus $c.$ twice as long as broad.

MALE ABDOMEN: Penultimate segment twice as broad as long, with sides subparallel proximally, abruptly converging to ultimate segment in distal third. Ultimate segment as long as penultimate, length $c.$ $0 \cdot 8$ times breadth.

COLOUR: Carapace dark or mottled, chelae pale orange to yellowish.

HABITAT

Under stones, among grass, or burrowing in soft mud at H.W.N. in areas of moderate to high salinity.

COMMENTS

Although recorded localities for specimens on hand range from Moreton Bay north only to Townsville, Macnae (1966, p. 79, as *Sesarma* cf. *semperi*) reports that this species is common from Thursday I. to Port Curtis.

S. semperi is very close to *S. brevicristatum*, differing from that species most obviously in—

(1) The tuberculation of the dactyl of the cheliped.

(2) The length of the pectinate crests on the chela.

(3) The distinctive patches of disarrayed pubescence on the carapace.

(4) The arrangement of the branchial lines.

(5) The much less prominent post-frontal lobes.

(6) The more obtuse lateral angles of the front.

Specimens of *S. semperi semperi* Bürger obtained from the National Museum of Singapore agreed well with Bürger's (1896) figure (pl. 21, fig. 1a, b, c), but differed in having the margin of the carapace less convergent posteriorly, the penultimate segment of the male abdomen subparallel in the proximal two-thirds rather than converging, and the teeth in the cutting edge of the dactyl more distinct. The presence of the small, distinctive tufts of hair on the carapace of these specimens agreed well with those of the Australian subspecies and were a major factor in deciding that their relationship was subspecific.

S. semperi longicristatum differs from typical *S. semperi* in the following particulars:—

(1) There are 8–9 asymmetrical dactylar tubercles (7–8 symmetrical tubercles in *semperi semperi*).

(2) The antero-lateral margins of the mesogastric region are less distinct.

(3) The median post-frontal lobes are lower and less abruptly marked anteriorly than in *S. semperi* s.s.

(4) The pectinate crests of the chela are longer, some 25 teeth being present in the distal row, and one or two granular, spinous or even pectinate rows are usually present between the proximal crest and the proximal edge of the propodus. In *S. semperi* s.s. there are *c.* 20 teeth in the distal crest and at the most only a short row of granules proximal to the proximal crest.

The specific name emphasises one of the more easily recognisable distinctions between this and the preceding species.

DISCUSSION

The species of this subgenus form a well knit group, their discrimination has always been difficult and their relationships subject to a variety of interpretations (e.g., see Alcock, 1900; de Man, 1895, 1903). The addition of three new species and one subspecies does not simplify the situation and at first glance it would seem that, in the absence of established sympatry, it might be possible to reduce a number of these species to subspecific status. The factors opposing such a step are twofold.

Firstly, it was commonly found that a single mangrove swamp contained populations of *S. lividum, S. messa, S. brevicristatum* and *S. semperi longicristatum*. The differences between these four are slight, residing principally in the details of configuration of the dactylar tubercles, but these differences are constant and all four indubitably represent distinct species. These four thus provide a rough standard degree of difference between species within the subgenus, and this standard is not overstretched by retaining the existing nominate species as full species.

Secondly, because of the large number of similarities that are shared by all taxa, and the small number of differences, it is difficult to limit any attempt at grouping or to confine any group within the framework of a polytypic species.

Speculation on how such a large group of so closely similar species could have arisen is probably futile without more detailed biogeographic information. Tweedie (1950) has commented on the restricted distribution of this genus as a whole, and it seems possible that limited means of dispersal, the scattering of mangrove swamps suitable for habitation, and the specialised behavioural isolating mechanism which is presumed to be provided by the auditory signalling device of the chelar dactyl could all combine to permit the establishment of genetically discrete populations with such rapidity that there has been no noticeable divergence of other characters.

Within Australia the subgenus appears to have a restricted habitat, being found only on tidal mud flats among mangroves, rarely extending for any distance up estuaries.

ACKNOWLEDGEMENTS

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PLATE 1

Sesarma (Chiromantes) darwinensis.
Holotype. Scale in mm.

PLATE 1

PLATE 2

Sesarma (Chiromantes) lividum.
Scale in mm.

Plate 3

Sesarma (Chiromantes) messa.
Holotype.   Scale in mm.

PLATE 4

Sesarma (Chiromantes) brevicristatum.
Holotype.   Scale in mm.

PLATE 5

Sesarma (Chiromantes) semperi longicristatum.
Holotype.   Scale in mm.

TROPOSODON, A NEW GENUS OF FOSSIL MACROPODINAE (MARSUPIALIA)

Alan Bartholomai
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ABSTRACT

A new genus, *Troposodon,* is proposed for *Sthenurus minor* Owen, 1877, and *Halmaturus vinceus* De Vis, 1895, is placed in synonymy with *T. minor.* The stratigraphic position of the holotype of *T. minor* is in doubt, but referred material from the Darling Downs in the collections of the Queensland Museum has been derived from both the Pleistocene fluviatile deposits and the Chinchilla Sand of ?Pliocene age.

The taxonomy of many of the fossil macropodids has, as indicated by Ride (1964), been confused by the uncertainty of generic limits, poorly studied subjective synonymy and species limits, and generally unknown temporal relations between named species. This is particularly true of many of the fossil marsupials from the Darling Downs area of south-eastern Queensland.

Considerable revisionary work has been conducted on several genera in these Pleistocene and probable Pliocene deposits, clarifying their taxonomy and stratigraphic position, but the generic positions of the majority of the fossil macropodids revised and described by De Vis (1895) are still unsatisfactory. Bartholomai (1966) has redescribed many of the type specimens of these, and selected lectotypes for those species for which holotypes were not designated, thereby enabling more detailed taxonomic studies to be undertaken.

In the present case this work has proven, as suggested by Stirton (1963) and Tedford (1966), that *Halmaturus vinceus* De Vis is synonymous with *Sthenurus minor* Owen. However, this species cannot be placed in *Sthenurus* Owen, as redefined by Bartholomai (1966) or Tedford (1966), nor can it be referred to any other described macropodid genus. A new genus, *Troposodon,* is therefore proposed for the species.

Specimens referrable to *T. minor* are reasonably common in the Upper Cainozoic deposits of Queensland, and sufficient material is present in the collections of the Queensland Museum to evaluate size and morphological variation. No specific differences are considered to exist between the sample from the Pleistocene fluviatile deposits and that from the Chinchilla Sand.

The author expresses his appreciation to Dr. R. W. George, of the Western Australian Museum, for the loan of recent macropodid specimens for comparison, and to Miss Jocelyn A. Tommerup, Biometrician, Queensland Department of Primary Industries, for discussion on the statistics involved in the present study.

All figures throughout are natural size and all measurements are in millimetres. A copy of the data treated statistically in this publication has been lodged in the library of the Queensland Museum.

<div align="center">

Family MACROPODIDAE

Subfamily MACROPODINAE

Genus **Troposodon** nov.

</div>

TYPE SPECIES: *Sthenurus minor* Owen, 1877.

DIAGNOSIS: The characters of this genus are those of the type species until any other species is described.

DISCUSSION: Owen (1877) originally referred *Troposodon minor* to the genus *Sthenurus* Owen. However, as Stirton (1963) has indicated, the discussion was confusing because Owen thought that *Sthenurus* and the genus *Protemnodon* Owen were closely related. In addition, he mistook the upper teeth in *Protemnodon* for those of *Sthenurus* and consequently referred maxillary specimens of *Sthenurus* to *Protemnodon*. In fact, reference of the species to *Protemnodon* rather than *Sthenurus* would have been more appropriate.

Lydekker (1887) transferred the species to the genus *Macropus* Shaw, employing the combination *M. minor* (Owen). While he realised this name was preoccupied by *M. minor* Shaw, 1800, he did not reject and replace it. Owen's species, however, does not belong with *Macropus*.

As in the genus *Sthenurus,* the molar teeth in *Troposodon* are ornamented by low folds and tubercles of enamel. But, apart from this feature, and their general macropodine bilophodont condition, the molars in *Sthenurus* are dissimilar structurally. In particular, the lophids and lophs are more rectilinear in that genus, while in the lower molars the talonid basin is centrally elevated. In the uppers, the median valley is centrally and labially elevated. The structure of P_2 and P_3 in *Sthenurus* is also markedly unlike that in *Troposodon,* in possessing lingual and postero-labial crests.

Among the recent macropodines, somewhat similar premolar structure to that in *Troposodon* is seen within the genus *Lagostrophus* Thomas. The small Banded Hare-Wallaby, *L. fasciatus,* possesses lower deciduous and permanent premolars which are only slightly less L-shaped than in *T. minor*. However, the lower molars, while occasionally ornamented anterior to the protolophid by folds of enamel, differ considerably in the structure of the forelink. This generally turns abruptly lingually before reaching the anterior cingulum, and unites with a rather strong ridge from the metaconid in the trigonid basin. The upper premolars are similar to those in *T. minor,* but while

the upper molars possess a fold of enamel below the crest of the metaloph, they are otherwise dissimilar. In particular, there is a strong anterior ridge from the paracone to the anterior cingulum, and strong ridges descend posteriorly and anteriorly from the paracone and metacone respectively, across the labial extremity of the median valley. The palate in *L. fasciatus* is markedly incomplete posteriorly. Raven and Gregory (1946) attribute the peculiarities in *L. fasciatus* to a reversal to life in the thickets.

Troposodon minor (Owen, 1877)

(Figures 1–4)

Sthenurus minor Owen, 1877, pp. 352-361, pl. 37, figs. 1-3, pl. 38, figs. 1-4.

Macropus minor (Owen); Lydekker, 1887, pp. 218-219.

[non] *Macropus minor* Shaw, 1800, p. 513, pl. 116.

Halmaturus vinceus De Vis, 1895, pp. 100-102, pl. 16, figs. 12-15.

Halmaturus minor (Owen); De Vis, 1895, p. 118, pl. 18, figs. 1-2.

Macropus minor (Owen); Simpson, 1930, p. 72.

Macropus vinceus (De Vis); Simpson, 1930, p. 73.

"Halmaturus" vinceus De Vis; Bartholomai, 1966, pp. 120-121, pl. 17, figs. 4-6.

MATERIAL: F3394, cast of holotype of *Sthenurus minor* Owen, B.M.(N.H.) No. 48409, partial palate with left $P^3 - M^3$, M^4 erupting, right $P^2 - M^3$, M^4 erupting, P^3 exposed by fenestration, juvenile (figd. Owen, 1877, pl. 37, figs. 1-3, pl. 38, figs. 1-4, Talbragar country, Co. Bligh, N.S.W., age Upper Cainozoic (?Pleistocene).

F3577, lectotype of *"Halmaturus" vinceus* De Vis (figd. Bartholomai, 1966, pl. 17, figs. 4-6).

One juvenile palate, 5 juvenile maxillae, 4 adult maxillae, 24 juvenile mandibular rami, 24 adult mandibular rami and 5 isolated teeth from the following localities in the eastern Darling Downs: King Creek, Clifton; King Creek, bridge on Pratten road at M.R. 873335 Clifton 1 ml. map; King Creek, between Nobby and Pilton near M.R. 039454 Clifton 1 ml. map; King Creek; Gowrie; ? Gowrie; Condamine River, Macalister, 2 mls downstream from "Armour"; Condamine River, near "Armour" homestead, Macalister; Dalby; Ravensthorpe, Pilton; "Sharrow" (Harrow, Cambooya); Pirrinuan, Jimbour Creek, near Dalby; and from the eastern Darling Downs (particular localities unspecified). An adult palate, 5 adult maxillae, 11 juvenile mandibular rami, 19 adult mandibular rami and 2 isolated teeth derived from the following localities in the western Darling Downs: Condamine River, 50 yards east of Chinchilla Rifle Range, Rifle Range No. 78, Par. Chinchilla; Condamine River, Chinchilla, at M.R. 363677 Chinchilla 4 ml. map; Condamine River, bend in Por. 150, Par. Chinchilla; Middle Gully System, Chinchilla Rifle Range, Chinchilla; Chinchilla; 70 feet deep in well at Warra; and from the western Darling Downs (particular localities unspecified).

An adult mandibular ramus from Por. 117, Par. Binjour, near Gayndah, S.E.Q.

C

DIAGNOSIS: Moderately large; palate entire; P^3 subrectangular to subtrianglar in basal outline, with well defined lingual and posterolingual basins and cingula. Upper molars and molariform deciduous premolar low crowned, with much reduced forelink; shelf-like areas present, posterior to loph crests, ornamented by subsidiary ridges and tubercles in $M^1 - M^3$, and occasionally in M^4. Mandible with moderately elongate, deep symphysis, flanged ventrally to below P_3; geniohyal pit moderately deep; ramus moderately deeply grooved laterally to below anterior molars. I_1 small, oval in section. P_2 and P_3 with longitudinal crests markedly L-shaped; lower molars with low crowns, well developed anterior and posterior cingula; shelf-like areas present anterior to lophid crests, variably ornamented by subsidiary ridges and tubercles in $M_1 - M_3$, and occasionally in M_4.
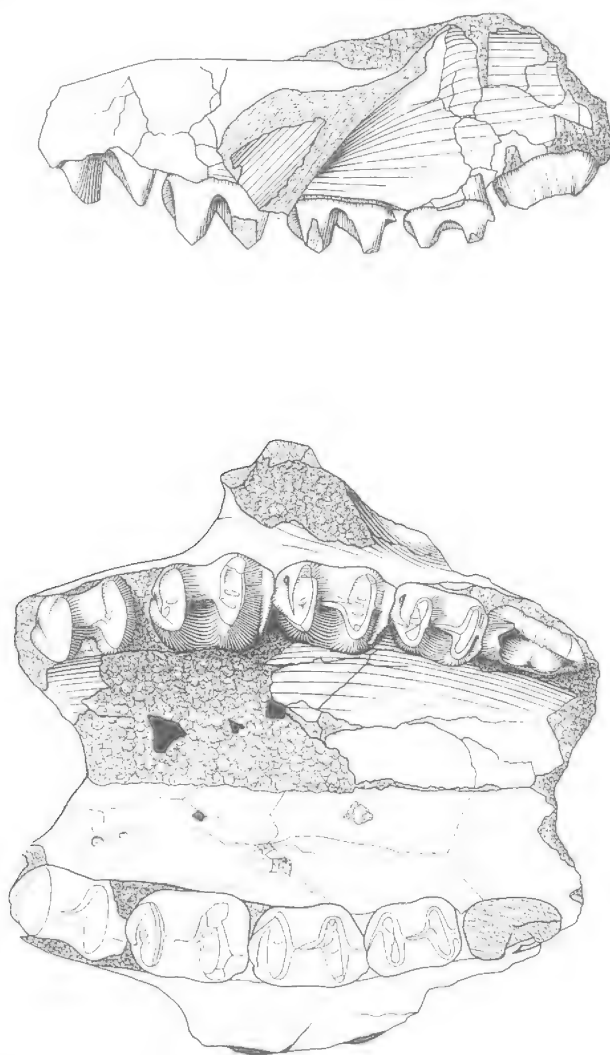

FIG. 1: *Troposodon minor* (Owen). Lateral and occlusal views of incomplete palate; F3576, Gowrie, S.E.Q.

DESCRIPTION: Skull known only from fragmentary maxillary specimens. Palate entire posteriorly, pierced by several, small, post-palatine foramina; infra-orbital canal moderately short, opening $17 \cdot 0 - 19 \cdot 0$ antero-ventral to orbital rim; zygomatic process relatively short.

I^{1-3} unknown.

P^2 known only in extremely worn state; subtriangular in basal outline, broken posteriorly; longitudinal crest low, slightly concave labially; two low, broad, vertical ridges reach crest between paracone and metacone. Lingual cingulum low, worn, uniting with crown base below paracone; lingual basin shallow, broader posteriorly.

DP^3 molariform, subrectangular in basal outline, unconstricted across median valley, being variably laterally swollen at lingual extremity of valley; lophs low, bowed anteriorly; metaloph broader than protoloph. Anterior cingulum low, broad, short, with only slight indication of presence of forelink labiad to axis of crown. Midlink moderately strong, passing posteriorly to near midpoint of metaloph; slight, ornamented, shelf-like area present posterior to protoloph crest, between paracone and midlink; median valley narrowly U-shaped in labial moiety, broadly so in lingual portion. Ridge from hypocone strong, descending posteriorly to near postero-labial base of crown, flaring posteriorly above axis of crown; ridge from metacone weaker, descending postero-lingually to median part of ridge from hypocone, forming margin to shelf-like area below metaloph crest; area ornamented by low, variable ridges and tubercles. Basally, with slight lingual stylar cusp variably developed below protocone.

P^3 subtriangular to subrectangular in basal outline, being generally broader posteriorly than anteriorly; longitudinal crest low, slightly concave labially, but varying to almost straight; apex of paracone about one-quarter distance along crown from anterior point; up to five sets of extremely variable, but generally weak vertical labial and lingual ridges transect crest with production of reduced cuspules. Hypocone moderately high, being almost as high as metacone, united to metacone by high, strong, labial ridge. Posterior ridge from metacone curves lingually at base of crown to below hypocone, forming low, moderately narrow, short posterior cingulum; small posterior fossette developed between cingulum and ridge connecting posterior cusps. Anterior ridge from hypocone descends sharply to form moderately low lingual cingulum to below paracone; connected to it by low vertical ridge; lingual cingulum somewhat sinuous in lingual view, being highest opposite centre of longitudinal crest; cingulum and longitudinal crest normally converging anteriorly, but cingulum often variably expanded laterally towards anterior extremity, resulting in near parallel crests. Lingual basin shallow, subtriangular to subrectangular in shape, variably traversed by low, broad ridges. Labial base of crown slightly but variably tumescent; poorly defined stylar cusp developed at anterior extremity.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, usually very slightly constricted across median valley; lophs low, bowed anteriorly; metaloph slightly broader than protoloph in M^1, but generally narrower in M^2 and M^3, and particularly so in M^4. Anterior cingulum low, broad, ascending labially; forelink reduced, occasionally absent,

positioned labiad to axis of crown when present; labial margin of cingulum variably united to paracone by slight vertical ridge; occasionally, variable, slight accessory links parallel forelink in labial moiety of anterior cingular shelf. Lingual margin of median valley sometimes variably swollen laterally. Moderatey strong ridge descends postero-labially from protocone, then turns posteriorly across median valley as generally moderately low midlink to unite with extremely short ridge from near midpoint of protoloph; weaker ridge from paracone descends postero-lingually to midlink limiting shelf-like area below protoloph crest; shelf-like area variably ornamented by subsidiary ridges and tubercles in $M^1 - M^3$, and occasionally so in M^4. Median valley broadly U-shaped. Strong ridge curves postero-labially from hypocone to near postero-labial base of crown, generally flaring posteriorly above axis of crown; weaker ridge descends postero-lingually from metacone towards ridge from hypocone, limiting shelf-like area below metaloph crest; shelf-like area variably ornamented by subsidiary ridge and tubercles in $M^1 - M^3$, and occasionally so in M^4. Base of protoloph below protocone usually with variable stylar cusp; weak posterior cingulum occasionally present in posterior molars.
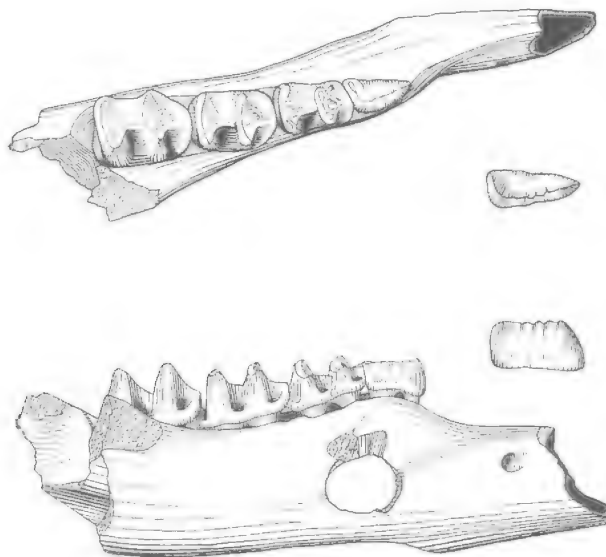

Fig. 2: *Troposodon minor* (Owen). Occlusal and lateral views of juvenile mandibular ramus, with unerupted P_3 exposed by fenestration; F3581, Gowrie, S.E.Q.

Mandible moderately deep, relatively thick; symphysis set at approximately $12°$ to base of mandible, not ankylosed, comparatively short, deep posteriorly, but relatively shallow anteriorly; flanged postero-ventrally resulting in distinct ventral extension of basal margin below P_3; geniohyal pit moderately deep, relatively high, anterior to

posterior symphysial limit. Diastema comparatively short, with crest acute; ventral margin of ramus sharply rounded between symphysis and diagastric ridge. Mental foramen comparatively small, oval, close to diastemal crest and about half-way between anterior of P_3 and limit of ramus; accessory foramen occasionally developed half-way between $M_2 - M_3$ and ventral margin of ramus. Ramus with deep lateral groove from between mental foramen and diastemal crest to below anterior root of M_2. Diagastric process very weak, separated from base of angle by very shallow post-diagastric sulcus, bounded above by shallow diagastric fossa; this fossa separated above from shallow depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, with well defined angle, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process above large mandibular foramen. Masseteric crest raised to about level of alveolar margin; masseteric foramen moderately large, with deep masseteric fossa. Angle of mandible, condyle and bulk of coronoid process not preserved.

I_1 imperfectly preserved; small, oval in transverse section, much higher than wide, enamelled both labially and lingually.

P_2 robust, moderately elongate, subtriangular in basal outline. Longitudinal crest abruptly curving postero-lingually, giving crest a marked L-shaped appearance; crest transected by three variable sets of vertical labial and lingual ridges, with production of cuspules at crest. Base of crown usually swollen lingually.

DP_3 molariform, slightly constricted across talonid basin, with lophids moderately low, slightly convex posteriorly. Hypolophid much broader than protolophid. Trigonid basin broad, its length being less than distance between lophids. Forelink moderately high, strong, descending slightly antero-lingually from protoconid to near midpoint of moderately low anterior cingulum; relatively strong ridge descends antero-labially from metaconid to unite with forelink, with production of shelf-like area below protolophid crest; second ridge occasionally present descending from metaconid to lingual extremity of anterior cingulum; shallow fossette formed in labial moiety of trigonid basin. Midlink moderately high, strong, descending from hypoconid across talonid basin to near midpoint of protolophid. Talonid basin labially and lingually broadly U-shaped, but occasionally with low labial fold; slight ridge descends antero-labially from entoconid towards midlink, with production of shelf-like area below hypolophid crest; this ridge occasionally passes into talonid, parallelling midlink. Weak ridge descends posteriorly from entoconid to unite with lingual extremity of short, broad, well defined posterior cingulum.

P_3 elongate, robust, subtriangular in basal outline, with longitudinal crest abruptly curving postero-lingually giving the crest a marked L-shaped appearance; crest normally transected by three moderately coarse sets of vertical labial and lingual ridges, and posteriorly by a set of very weak ridges; cuspules produced along crest. Lingual base of crown variably swollen.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline; lophids low with hypolophid broader than protolophid in M_1, almost equal in M_2 and M_3, and narrower in M_4. Trigonid basin relatively broad, moderately long, its length almost equalling distance
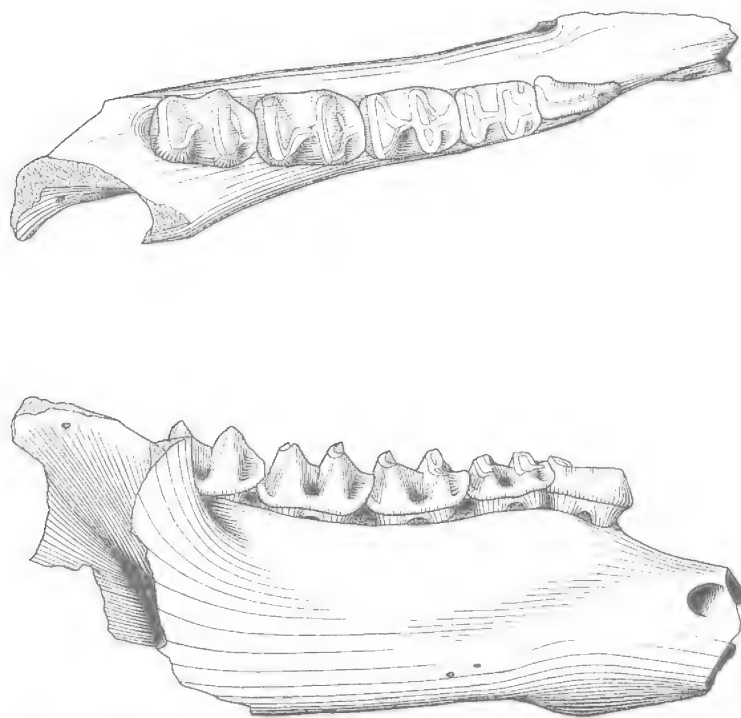
FIG. 3: *Troposodon minor* (Owen). Occlusal and lateral views of adult mandibular ramus; F655, Gowrie, S.E.Q.

between lophids. Forelink relatively high, strong, descending antero-lingually from protoconid then anteriorly to near midpoint of moderately high anterior cingulum; forelink occasionally ornamented by subsidiary ridging; antero-labial fossette formed in trigonid basin. Moderately strong accessory ridge descends antero-labially from metaconid to forelink, with production of shelf-like area ornamented by variable subsidiary ridges and tubercles. Strong ridge descends antero-lingually from hypoconid, then anteriorly above talonid basin as strong, moderately high midlink; this unites with short ridge from near centre of protolophid; talonid basin broadly U-shaped labially and lingually, occasionally with low fold at labial margin. Moderately strong accessory ridge descends antero-labially from entoconid towards midlink, with production of shelf-like area below hypolophid crest; shelf-like area ornamented by variable subsidiary ridges and tubercles in M_1 and M_2, usually absent in M_3 and M_4. Slight variable ridge descends posteriorly from entoconid to unite with broad, well defined posterior cingulum.

DISCUSSION: The holotype of *Troposodon minor* was originally forwarded to the British Museum (Natural History) by the Reverend W. B. Clarke in 1877, and was recorded by Owen (1877) and Lydekker (1887) as having been derived from a rocky

alluvial deposit in the shaft of a gold lead in the County of Phillip, New South Wales. Ride and Mahoney (pers. comm.) have indicated that this locality is incorrect, Clarke having initially misinformed Owen regarding the type locality. Clarke (1878, p. 209) has corrected the locality to "Talbragar country", in a footnote relating to information received from a Mr. Lowe. Doubt still exists as to whether the specimen was from Pleistocene alluvial deposits or whether it was derived from possibly older deposits in a gold lead, so that its exact position within the Upper Cainozoic remains problematical.

De Vis (1895) separated much of the Queensland material from *T. minor,* and described a new species, *Halmaturus vinceus,* for these specimens. He failed to designate a holotype, and Bartholomai (1966) selected F3577 as lectotype of *"H." vinceus.* Of the specimens referred by De Vis (1895) to *H. minor,* only the juvenile maxilla containing $M^1 - M^3$, with P^3 ready to erupt has been recognised. As with the lectotype of *"H." vinceus,* this is morphologically identical with the holotype of *T. minor.* One of the mandibular specimens referred by Lydekker (1887) to *Macropus minor,* B. M. (Nat. Hist.) No. 50063a, from Gowrie, S.E.Q., a cast of which, F3401, is present in the Queensland Museum collections, is identical with other specimens here referred.
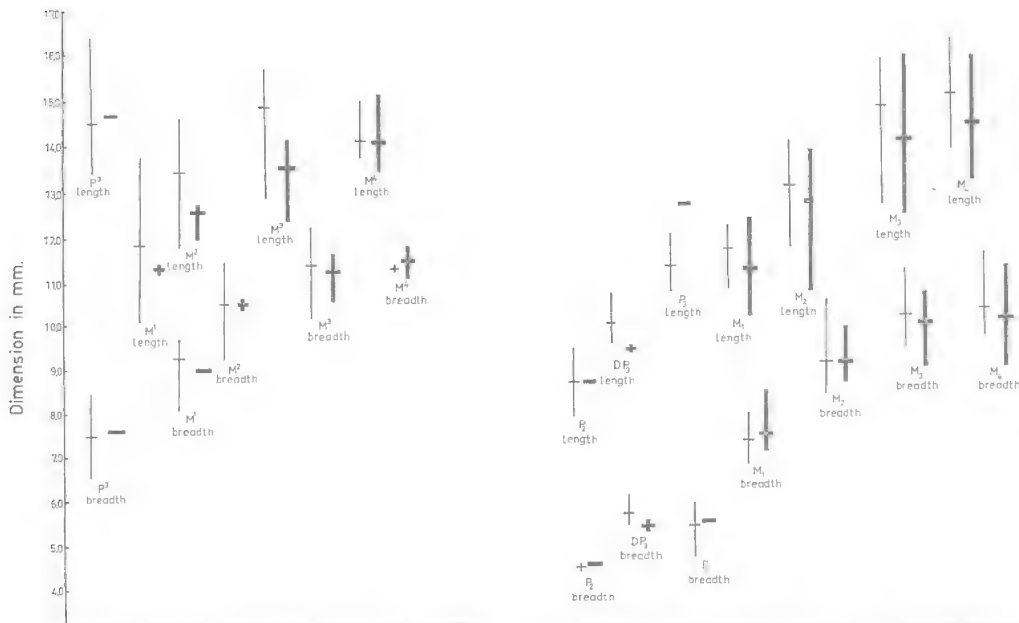

FIG. 4: *Troposodon minor* (Owen). Observed ranges and means for lengths and breadths of cheek teeth for eastern and western Darling Downs samples; vertical lines represent observed ranges, horizontal bars represent position of means, light lines represent eastern Darling Downs sample and heavy lines are for western Darling Downs sample.

TABLE 1

COMPARISON OF MEANS OF SAMPLES OF *Troposodon minor* (OWEN), FROM THE EASTERN AND WESTERN DARLING DOWNS DEPOSITS

Character	Eastern Darling Downs Sample				Western Darling Downs Sample				Comparison of Means	
	N	X̄	OR	s	N	X̄	OR	s	t	P
P² length	1	11·60	—	—						
width metaloph	—	—	—							
DP³ length	3	10·83	10·7–11·0	—						
width protoloph	2	7·75	7·7–7·8	—						
P³ length	12	14·45	13·3–16·4	0·9501	1	14·70	—	—	0·16	0·5
width metaloph	11	7·51	6·6–8·5	0·6533	1	7·60	—	—	0·12	0·5
M¹ length	14	11·83	10·1–13·8	0·8905	3	11·33	11·2–11·4	—	0·48	0·5
width protoloph	11	9·27	8·0–9·8	0·5728	1	9·00			0·45	0·5
M² length	14	13·44	11·8–14·7	0·9866	4	12·45	11·9–12·7	0·4282	1·91	0·1–0·05
width protoloph	14	10·49	9·2–11·5	0·7809	4	10·43	10·4–10·5	0·0503	0·15	0·5
M³ length	11	14·90	12·8–15·9	0·9899	6	13·52	12·3–14·2	1·6795	3·03	0·01
width protoloph	11	11·36	10·2–12·3	0·7461	6	11·17	10·6–11·6	0·3503	0·58	0·5
M⁴ length	11	14·23	13·7–15·1	0·7578	6	14·13	13·5–15·3	0·6595	0·36	0·5
width protoloph	2	11·30	11·2–11·4	0·1415	6	11·53	11·1–11·8	0·2875	0·45	0·5
P₂ length	4	8·73	7·9–9·6	0·7363	1	8·70	—		0·04	0·5
width posteriorly	4	4·63	4·5–4·7	0·0872	1	4·70	—		0·23	0·5
DP₃ length	8	10·15	9·6–10·8	0·4472	2	9·50	9·4–9·6	0·1415	0·34	0·5
width protolophid	7	5·76	5·5–6·2	0·2636	2	5·50	5·4–5·6	0·1415	1·09	0·5–0·1
P₃ length	11	11·35	10·8–12·1	0·3561	1	12·70	—		3·63	0·01
width posteriorly	11	5·53	4·7–6·0	0·3839	1	5·60	—		0·17	0·5
M₁ length	23	11·83	10·8–12·4	0·3980	7	11·27	10·3–12·5	0·8750	2·41	0·05–0·01
width protolophid	20	7·44	6·8–8·1	0·3575	6	7·57	7·1–8·6	0·5502	1·22	0·5–0·1
M₂ length	27	13·22	11·8–14·3	0·5787	16	12·73	10·8–14·0	0·8994	2·18	0·05–0·01
width protolophid	25	9·18	8·5–10·7	0·4707	15	9·20	8·7–10·0	0·4192	0·02	0·5
M₃ length	30	14·98	12·8–16·0	0·8399	16	14·24	12·6–16·0	0·7806	3·66	0·01
width protolophid	27	10·23	9·5–11·4	0·5208	13	10·09	9·1–10·8	0·4132	0·85	0·5–0·1
M₄ length	21	15·35	14·0–16·5	0·6852	13	14·57	13·3–16·0	0·7949	3·03	0·01
width protolophid	20	10·48	9·8–11·7	0·5310	11	10·17	9·1–11·4	0·6182	0·27	0·5

With the exception of one mandibular ramus, specimens now referred to *T. minor* in the Queensland Museum collections are from localities within both the Pleistocene fluviatile deposits and the Chinchilla Sand of possible Pliocene age. Species differences generally exist within genera in the eastern and western Darling Downs deposits, as shown by Woods (1958, 1960) and Bartholcmai (1962, 1963). However, in the case of *T. minor,* no constant morphological differences could be found to justify separation of the specimens within the two samples. Structurally, the lower molars in specimens from the Chinchilla Sand tend to have a better defined accessory ridge in the trigonid basin from the metaconid to the forelink, but this is by no means constant. Table 1 illustrates some apparent differences in the comparison of means of the samples from

TABLE 2

COEFFICIENTS OF VARIATION FOR COMBINED EASTERN AND WESTERN DARLING DOWNS SAMPLES OF *Tropsodon minor* (OWEN)

Character	F. 3394, cast of holotype		N	OR	$\overline{X}$	s	V
	right	left					
P² length	—	—	1	—	11·60	—	—
width metaloph	—	—	—	—	—	—	—
DP³ length	11·0	—	3	10·7–11·0	10·83	0·1530	1·41
width protoloph	—	—	2	7·7– 7·8	7·75	0·0708	0·91
P³ length	13·8	13·7	13	13·3–16·4	14·55	0·9107	6·26
width metaloph	—	6·6	12	6·6– 8·5	7·60	0·6164	8·11
M¹ length	11·9	11·9	17	10·1–13·8	11·74	0·8389	7·15
width protoloph	—	8·8	12	8·0– 9·8	9·17	0·5416	5·91
M² length	13·5	13·8	18	11·8–14·7	13·22	0·9747	7·19
width protoloph	9·2	9·9	18	9·2–11·5	10·48	0·6839	6·53
M³ length	15·9	15·8	17	12·3–15·9	14·42	1·1418	7·91
width protoloph	10·8	11·1	17	10·2–12·3	11·29	0·6290	5·57
M⁴ length	—	—	9	13·5–15·3	14·40	0·6892	4·79
width protoloph	—	—	8	11·1–11·8	11·48	0·2713	2·36
P₂ length	—	—	5	7·9– 9·6	8·72	0·6471	7·42
width posteriorly	—	—	5	4·5– 4·7	4·64	0·0894	1·93
DP₃ length	—	—	10	9·4–10·8	10·02	0·4826	4·82
width protolophid	—	—	9	5·4– 6·2	5·70	0·8216	2·60
P₃ length	—	—	12	10·8–12·7	11·47	0·5157	4·50
width posteriorly	—	—	12	4·7– 6·0	5·56	0·3655	6·57
M₁ length	—	—	30	10·3–12·5	11·70	0·5792	4·95
width protolophid	—	—	26	6·8– 8·6	7·49	0·3934	5·25
M₂ length	—	—	43	10·8–14·3	12·80	0·8287	6·47
width protolophid	—	—	40	8·5–10·7	9·20	0·4557	4·95
M₃ length	—	—	46	12·6–16·0	14·16	0·7507	5·30
width protolophid	—	—	40	9·1–11·4	10·18	0·4810	4·72
M₄ length	—	—	34	13·3–16·5	15·05	0·8479	5·63
width protolophid	—	—	31	9·1–11·7	10·36	0·5964	5·76

the eastern and western Darling Downs deposits by Student's test. These indicate significance in the lengths of M^3, P_3, M_3, and M_4 at the 1% level, and approach significance in the lengths of M_1 and M_2, at the 5% level. This is graphically illustrated in figure 4. Length of tooth is a character affected by attrition, particularly in adult specimens, and as the proportion of adult specimens is greater in the western Darling Downs sample, it is not believed that separation on this basis, at the specific level, is warranted at this time.

The summaries of measurements in Table 2 for combined samples of maxillary and mandibular teeth indicate only slight to moderate variation, as expressed by the coefficient of variation and are not inconsistant with the values of V suggested by Simpson *et al.* (1960) for dimensions in teeth in a single fossil species from differing stratigraphic levels. Many of the extremely small values for V are related to the small samples analysed. The coefficient of variation for length of tooth is often larger than that for breadth, particularly in those samples with a small number of variants. This again is influenced not only by initial size differences, but also by the reduction of the anterior and posterior cingula by attrition between adjacent teeth.

Two isolated left lower premolars, F4402 and F4436, suggest the presence of material distinct from *T. minor* in the Chinchilla Sand. Only F4402 has specific locality information, namely Warra, S.E.Q. F4436 is unworn and possesses extremely well-defined vertical ridges transecting the longitudinal crest. The teeth are considerably larger than the corresponding teeth in *T. minor,* but the evidence is too meagre to draw any definite conclusions at this time.

As with the majority of the Australian Upper Cainozoic marsupials, mandibular remains of *T. minor* have never been found associated with maxillae. Occlusion is, however, satisfactory and because of the similarity in ornamentation of the upper and lower molars, no doubt exists as to the correctness of their present association. As yet, post-cranial remains of *T. minor* are unknown.

In *T. minor,* the permanent premolars usually enter the tooth row after the emplacement of the third molars and are generally in use during the eruption of M^4 and M_4. However, F4445 illustrates the condition where M_4 is in place in advance of P_3. In both the holotype palate and the palate F3576, the left P^3 is erupted before the right permanent upper premolar.

It appears that the tooth structure in *T. minor* indicates a secondary reversal from grazing macropodines to a semi-browsing habit, although it is unlikely that such reversal was in any way as complete as that in *Sthenurus* or *Procoptodon* Owen.

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A NEW INTERPRETATION OF *AUSTROPELOR*, A SUPPOSED JURASSIC LABYRINTHODONT AMPHIBIAN FROM QUEENSLAND

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Austropelor wadleyi has been something of an enigma to palaeontologists ever since it was named by Longman in 1941. This species, based upon a single fragment of bone found in the Marburg Sandstone of Queensland, was described as a portion of the skull of a labyrinthodont amphibian of Jurassic age. These determinations by Longman of its taxonomic relationships and geologic age would seem to be mutually incompatible, for the reason that all evidence elsewhere in the world indicates the labyrinthodonts to have become extinct at the close of Triassic time. Therefore, if *Austropelor wadleyi* is a Jurassic labyrinthodont, the fossil is of extraordinary significance as being the only record of the persistence of this group of tetrapods beyond the upper limits of the Triassic.

Is the fossil sufficiently complete and of such preservation as to allow its unequivocal identification as a labyrinthodont? Are the sediments in which it was found definitely of Jurassic age?

Romer, in 1947, expressed doubts on both scores. "Neither the nature of the specimen nor the age of the formation appear to be too well established" (Romer, 1947, p. 344). Whitehouse, in 1955, indicated that the specimen could be accepted as a labyrinthodont, for which reason he regarded the Marburg Sandstone as of Triassic age. "Recently F. Broili and J. Schroeder, German authorities on the group, examined the specimen and expressed themselves satisfied with it as a labyrinthodont" (Whitehouse, 1955, p. 56). Since 1955 various ideas have been put forward as to the age of the Marburg Sandstone, with the unquestioned acceptance of *Austropelor* as a labyrinthodont.

It is the purpose of this paper to review the fossil as carefully as possible, in an attempt to throw additional light on the problem of its taxonomic position and perhaps of its age.

At this place I wish to express my appreciation to Mr. Jack T. Woods, Director, and Mr. Alan Bartholomai, Research Curator (Geology), of the Queensland Museum, for the opportunity to prepare further and study the type of *Austropelor*

wadleyi. It was my good fortune to be able to examine *Austropelor* at the Queensland Museum, and to visit its type locality at Lowood[1] in company with Messrs. Woods and Bartholomai. Subsequently Mr. Woods very kindly brought the specimen to New York, on the occasion of a visit he made to the United States, in order that it might receive additional preparation, ably executed by Mr. Gilbert Stucker of The American Museum of Natural History. And here I have been able to study the fossil in detail and at some leisure.

The photographs that illustrate the type of *Austropelor wadleyi* in this paper were made by Mr. Chester Tarka, and the drawing was made by Mr. Michael Insinna, of the Department of Vertebrate Palaeontology of The American Museum of Natural History.

A RECONSIDERATION OF THE TYPE OF *Austropelor wadleyi*

This fossil, Queensland Museum No. F2628, consists, as Longman pointed out, of three conjoined pieces, the combined length of which is slightly less than 100 mm. On one side the bone is heavily rugose, this rugosity characterized by longitudinal striations and ridges. On the other side the bone is smooth. Along one edge of the bone, between its rugose and smooth sides, is a series of closely set alveoli of comparatively small size, transversely broad as compared with their longitudinal dimensions. There are some 18 alveoli, none of which contains teeth, but all of which are shallow, their basins being filled with cancellous bone. On the rugose side there is a sharp edge running along the borders of the alveoli, and below this edge at a distance of about 8 mm is a very heavy longitudinal ridge. On the smooth side the bone is convex beyond the margins of the alveoli, this convexity merging into a slight longitudinal concavity that occupies the length of the bone near the margin opposite the alveoli. This margin of the bone is rounded, and marks the juncture, opposite the alveoli, between the rugose and smooth sides of the bone. It is a natural border, and shows little breakage.

The form of the bone, its heavy rugosities on one side, and the closely set, transversely broadened alveoli, filled with cancellous bony tissue, are typically labyrinthodont. No other tetrapod jaw would seem to fulfill these characters. The possibility that the fragment might be a portion of a crocodilian jaw was, for instance, considered. But the rugosities are too heavy for a crocodilian jaw of this size, and the alveoli do not accord with what might be expected in a crocodilian bone. For in the crocodilians, and in the archosaurians in general, the alveoli are round or even longitudinally extended, and they are open, not filled by cancellous bone. In short, the form and structure of the alveoli in *Austropelor wadleyi* are of the type that is characteristic for the implantation of labyrinthine teeth.

Longman identified the fragment as the portion of a right maxilla, from that part of the skull in the vicinity of the narial opening. "On the median border of the upper surface the contours are disrupted for two-thirds of the length where the fragment was broken off from the cranial roof. The remaining third presents a smooth surface which apparently represents the narial opening" (Longman, 1941, p. 30). If such is the case, then this fragment represents a very large skull indeed, because the entire smooth or inner portion of the bone, a natural surface, shows little antero-posterior curvature, and thus would indicate a nasal opening of enormous size—much larger proportionately than is characteristic of other labyrinthodonts. Furthermore, the bone is too narrow to be from the border of the palatal vacuity (which is large in these animals) and in addition there is lacking a secondary row of teeth that would be expected from such a location. Longman thought that the longitudinal ridges on the bone were a part of the system of mucous canals, so typical of labyrinthodonts.

It is here maintained that Longman was mistaken in his morphological identification of the bone. The fossil is not part of a skull, but a portion of a left mandibular ramus. The rugose surface of the bone does not show any indications of a mucous canal system, as Longman thought; rather these rugosities are of the irregular type characteristic for the external surface of a labyrinthodont mandible, as may be seen by comparison with other labyrinthodont lower jaws. The single row of alveoli, bordered internally by a robustly convex region, forming the upper portion of the internal or lingual surface of the mandible, also is typical for a labyrinthodont lower jaw. Indeed, the cross-section of the bone can be matched to a considerable degree by cross-sections in other labyrinthodont rami.

This new identification of the type of *Austropelor wadleyi* as the segment of a left mandibular ramus rather than a portion of a maxilla, as originally determined by Longman, in no way affects the assignment of the fossil to the Labyrinthodontia. Moreover, it confirms the opinion of Broili and Schroeder, as cited by Whitehouse, as to the general zoologic relationships of the specimen. The larger taxonomic implications of the fossil thus remain unchanged.

The Possible Taxonomic Relationships of *Austropelor*

Where is *Austropelor wadleyi* to be placed within the Labyrinthodontia? This question is not easily answered, because the type specimen is so very incomplete that it has few features on which to base any detailed comparisons.

The genus *Austropelor* is not included in Case's study of the Stegocephalia of 1946. In Romer's monograph of 1947 on the Labyrinthodontia it is mentioned in two places as a very problematical form. Von Huene places it, under the name of *"Australopelor"*, within the Metoposauridae in his volume on the lower tetrapods, published in 1956. In the very comprehensive compendium on the lower tetrapods, published in 1964 under the editorship of Orlov, Shishkin proposes that *Austropelor*

is a questionable synonym of *Paracyclotosaurus,* which, of course, brings it within
the Cyclotosauridae. In accordance with this conclusion the Cyclotosauridae are
shown in a table, on page 65 of the above-mentioned volume, as extending from the
beginning of the Middle Triassic through the Lower Jurassic. Other authors who
have had occasion to consider *Austropelor* have done so without going into the
problem of its exact relationships.

In view of the trends of a labyrinthodont evolution, it seems overwhelmingly
probable that *Austropelor* is a stereospondyl. Within the Stereospondyli it would
furthermore seem that, tenuous though the evidence may be, the best clues as to
the relationships of *Austropelor* are to be found in the relationship of the size of
the teeth to the mandibular ramus, and in the cross section of the ramus. In these
respects it shows some resemblances to *Eupelor,* for example. In both of these

TABLE 1

COMPARISON OF MEASUREMENTS OF MANDIBULAR RAMI

Species	Depth (mm)	Breadth (mm)	Alveoli per 50 mm	Ratio, breadth/ depth	Alveoli to jaw depth
Austropelor wadleyi QM No. F2628	33·5*	22·0*	9	60	6/33·5
Paracyclotosaurus davidi AMNH No. 8252 (cast) ..	48·0*	44·5*	9	93	8/48
Eupelor fraasi AMNH No. 2994	43·5	24·5	7	56	6/43·5

* Anterior part of ramus.

genera the depth of the mandibular ramus is appreciably greater than its breadth,
the measurements in *Eupelor* being taken at a point not far behind the symphysis.
In *Paracyclotosaurus* the breadth of the ramus nearly equals its depth in this same
portion of the jaw, and this relationship of jaw depth to breadth in its anterior
portion is seen in *Parotosaurus,* as recently figured by Welles and Cosgriff (1965).
In these latter two genera the depth of the jaw anteriorly is about equal to the
space occupied by eight teeth, whereas in *Austropelor* and *Eupelor* the comparable
depth of the jaw is equivalent to the space occupied by six teeth. In other words,
the teeth of *Austropelor* and *Eupelor* are relatively somewhat larger than they are
in *Paracyclosaurus* and *Parotosaurus.*

On the basis of this evidence it is here maintained that *Austropelor* certainly is not to be considered as another species of *Paracyclotosaurus,* nor is it very likely a member of the Capitosauridae. It seems more probably a brachyopid labyrinthodont, and possibly a metoposaur, as indicated by von Huene in 1956.

Two other Australian labyrinthodonts should be considered in the light of any possible taxonomic connections they might have with the fossil now being discussed, especially since they are both brachyopids. These are *Bothriceps australis* and *Platyceps wilkinsoni.*

The first of these two forms is based upon a small skull, in which much of the bone is eroded away, with a closely conjoined lower jaw. The specimen was collected many years ago, and its geologic horizon and locality are unknown. Because of the small size of the specimen, *Bothriceps* is not readily comparable with *Austropelor.* Of course, this might be a juvenile individual, but the skull has the appearance of a fully developed animal, which makes it seem unlikely as a close relative of *Austropelor.* Moreover, lack of stratigraphic and locality records for this specimen makes it almost valueless in this connection.

The type of *Platyceps,* a larval animal, with gill arches preserved, is from the Narrabeen Formation of early Triassic age. Because of its nature and age, it cannot be compared with *Austropelor.*

THE GEOLOGIC AGE OF *Austropelor*

The crucial problem as to the age of *Austropelor wadleyi* must now be faced. Does this fossil represent a persistence of the labyrinthodonts (and if so, the only known record) into Jurassic time?

The type fossil was found in a block of Marburg Sandstone, in the bed of the Brisbane River, about one mile south-east of Lowood Railway Station. Although the rock containing the fossil was not in place, there can be no doubt as to its identity as of the Marburg Sandstone. The river bed at this locality is filled with such blocks which have fallen down from banks and cliffs, composed of the Marburg Sandstone bordering the river.

The age of the Marburg Sandstone has been variously interpreted. This sandstone, of varying composition, and strongly cross-bedded, rests on sandstones of the Bundamba Group, and is overlain by the Walloon Coal Measures. In the type description of *Austropelor wadleyi* a section on the age of the "bone-bearing sandstone at Lowood", written by Dr. F. W. Whitehouse, indicates all three of the rock groups referred to by him as *series*—Bundamba, Marburg and Walloon—to be of Jurassic age. "Sufficient it is to say that these three series (Bundamba, Marburg and Walloon) are Jurassic in age and that the Marburg Series which has this bone bed may be placed tentatively about the middle of the period" (Whitehouse in Longman, 1941, p. 32).

As mentioned above, Whitehouse, in 1955, revised this opinion and placed the Marburg Sandstone definitely within the Upper Triassic because of the presence in it of a labyrinthodont amphibian. Hills, in his brief review of Australian fossil vertebrates published in 1958, mentioned *Austropelor* as among the Jurassic tetrapods of this continent.

It is now generally maintained that the Bundamba Group is of Upper Triassic age, while the Walloon Coal Measures are to be placed within the Lower Jurassic (see Cameron et al., 1960). Where then is the intervening Marburg Sandstone to be placed? De Jersey, in the above publication, was rather noncommittal. "However, the general similarity of the microfloras [of the Marburg and Walloon] suggests that there is no major time break between the two formations. Consequently, on the basis of the Lower Jurassic age suggested below for the Walloon Coal Measures, the Marburg Sandstone would be either late Triassic or early Jurassic" (de Jersey, in Cameron *et al.,* 1960, p. 291). This same author has, however, more recently come to the conclusion that, upon the basis of paleobotanical evidence as well as upon the established conformable relationships above and disconformable relationships below it, the Marburg Sandstone should be closely associated with the overlying Jurassic Walloon Coal Measures rather than with the underlying Triassic Bundamba Group.

" . . . the occurrence of *Classopollis* down to the lowest known outcrop of the formation at Lowood is strong evidence for placing the whole of the Marburg Sandstone in the Jurassic. The Jurassic age of the formation is further indicated by the presence of forms . . . which are known from Jurassic sediments elsewhere, but have not been found in the Triassic."

"This microfloral evidence of a Jurassic age is in conflict with the conclusions of Whitehouse (1955) who suggested an Upper Triassic age for the formation . . . based on the occurrence of a jaw fragment of a Labyrinthodont in the Marburg Sandstone . . . Whitehouse considered that the absence of Labyrinthodonts from the post-Triassic sediments elsewhere indicated that the Marburg Sandstone could not be younger than Upper Triassic. In the writer's opinion, greater reliance should be placed on the microfloral evidence of a Jurassic age than that of this isolated bone fragment, and the possibility must be considered that the jaw fragment in question, if correctly identified, may be a re-worked fossil from underlying Triassic sediments" (de Jersey, 1963, p. 14).

These conclusions have been recently strengthened, as the present writer is informed by Mr. Woods, by palynological studies as yet unpublished. There seems indeed little reason on the basis of the abundant evidence now at hand to question the Jurassic age of the Marburg Sandstone.

In view of the undoubted taxonomic position of *Austropelor wadleyi* within the Labyrinthodontia, and the almost certain position of the Marburg Sandstone within the Jurassic sequence in Queensland, serious consideration must therefore be given

to the suggestion by de Jersey (which has been made by other authorities as well) that the fossil is a re-worked specimen from underlying Triassic sediments. This solution of the problem is hereby proposed, even though it involves certain difficulties. For instance, in a letter to the present writer Mr. Woods has stated that "I would expect remané material to have to be mineralized more extensively to survive any considerable transport during the deposition of such sands." Yet in spite of this qualification, the occurrence of the single type specimen of *Austropelor wadleyi* as a re-worked fossil seems the most logical explanation for its presence in the Marburg Sandstone. Such an interpretation is in accordance with all present records of labyrinthodont stratigraphic relationships. There will have to be more definite evidence than is afforded by the single specimen of *Austropelor wadleyi* to justify the extension of the labyrinthodont amphibians into Jurassic sediments.

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PLATE 6

FIG. 1: *Austropelor wadleyi* Longman. Holotype, Queensland Museum No. F. 2628. Portion of a left mandibular ramus, occlusal view, natural size. This view shows the well-defined, shallow alveoli, not clearly visible prior to recent preparation of the specimen.

FIG. 2: *Austropelor wadleyi* Longman. Holotype, Queensland Museum No. F. 2628. Portion of a left mandibular ramus, external lateral view, natural size. This view shows the characteristic rugosities on the external surface of the dentary.

FIG. 3: Comparison of cross sections of the left mandibular ramus at a short distance behind the symphysis in three labyrinthodont amphibians. A. *Paracyclotosaurus davidi,* a capitosaur; B. *Austropelor wadleyi;* C. *Eupelor fraasi,* a metoposaur. All natural size.
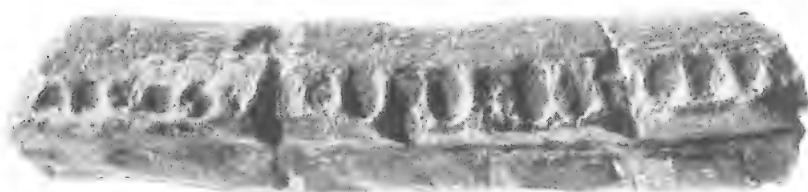
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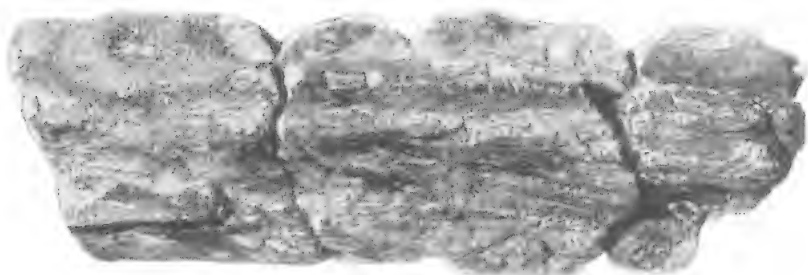
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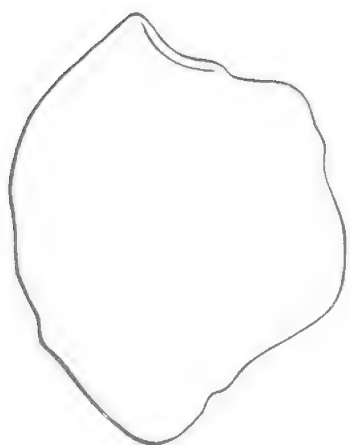
3A   3B   3C

THE SUBSPECIES OF THE FIG PARROT, *OPOPSITTA DIOPHTHALMA*

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SUMMARY

The Fig Parrot (*Opopsitta diophthalma* Hombron and Jacquinot) occurs in New Guinea and the adjacent islands and north-eastern Australia as far south as northern New South Wales. In this revision nine subspecies have been recognized following examinations of specimens of all of the described races. The subspecies *O. d. festetichi* and *O. d. coccineifrons* have been provisionally accepted pending the acquisition of more material, but *O. d. boweri* and *O. d. tweedi* have been dismissed. The recognition of *O. coxeni* as a distinct species has been rejected.

The Fig Parrot, *Opopsitta diophthalma* (Hombron and Jacquinot), is a polytypic species widely distributed throughout the New Guinea area and along the coast of north-eastern Australia as far south as northern New South Wales. A number of subspecies have been described from various parts of its range. The aim of the work reported in this paper was the determination of the status of these subspecies.

In 1964, with assistance from the Frank M. Chapman Memorial Fund, the author visited New York and examined the specimens of *Opopsitta diophthalma* in the collections of the American Museum of Natural History (AMNH). Upon returning to Australia, he examined the skins in the Australian Museum (AM), Sydney and the National Museum of Victoria which also houses the H. L. White Collection (HLW). Specimens from the Queensland Museum (QM) were forwarded on loan.

It was found that pests had caused such severe damage to the type material of *O. d. marshalli* that it was useless for determining the status of the race. As no other material had been collected, the author, under a further grant from the Frank M. Chapman Memorial Fund, led an expedition to Iron Range, Cape York Peninsula in January 1966 for the purpose of collecting new material near the type locality of *marshalli*. An examination of the six specimens collected made it clear that *marshalli* was a valid race. Consequently (Forshaw, 1966) a submission was placed before the International Commission of Zoological Nomenclature requesting that the holotype of *O. d. marshalli* be set aside and one of the recently collected specimens (QM. O.10691) be designated the neotype.

Skins that were unsexed or had inadequate locality data were not used. All differences in plumage were noted, but wing measurements were taken only from adult specimens.

SPECIMENS EXAMINED:—Four males, three females, Misol: one female, one imm. male, Kafau, West Irian: one imm. male, Kapaur, West Irian: one male, one female, north-west New Guinea (=West Irian): two males, Waigeu Island: two males, one female, two imm. males, one imm. female, Kubor Range, New Guinea: one male, Miku Bay, N.G.: one male, Sinibang, N.G.: one male, Ramu River, N.G.: one male, Holnicote Bay, N.G.: one female, Kamusi R., N.G.: one male, Brown R., N.G.: one male, one female, Angabunga R., N.G.: three males, two females, Upper Aroa R., N.G.: five males, three females, one imm. male, Aru Is.: one male, Fly R., N.G.: five males, four females, Fergusson I., N.G.: eight males, seven females, Sudest (=Tagula) I., N.G.: three males, three females, Iron Range, north Queensland: one male, Tolga, N.Q.: two males, one female, Barron R., N.Q.: three males, one female, Cedar Bay, N.Q.: two females, Rockingham Bay, N.Q.: six males, three females, three imm. males, two imm. females, Cairns, N.Q.: three females, Lake Eacham, N.Q.: one male, five females, Cardwell, N.Q.: two females, Russell R., N.Q.: two females, Queensland: one female, Brisbane, Q.: four males, one female, Richmond R., New South Wales: two males, Tweed R., N.S.W.: one male, south-east Queensland.

SYSTEMATICS

Opopsitta diophthalma diophthalma (Hombron and Jacquinot)

Psittacula diophthalma Hombron and Jacquinot, 1841, Ann. Sci. nat., Zool. (2) **16**: 318. (southern coast of New Guinea = Triton Bay.)

RANGE: West Irian, including the western islands, and western New Guinea as far east as Astrolabe Bay in the north and Etna Bay in the south.

PLUMAGE: Some variation was evident in the specimens examined. Adult males had the forehead, crown, lores and cheeks varying from bright scarlet to deep red, and on the hind-crown there was a variable band of orange-yellow. On the lower cheeks under the red there was a band of mauve-blue and above and in front of the eye a patch of bright sky blue; the innermost wing-coverts were bright orange-red. Adult females and immatures had the lower cheeks buff-brown instead of red, and below the red line extending underneath the eye there were some pale blue feathers, which became more conspicuous towards the sides of the head.

Gyldenstolpe (1955) examined an adult female from the Vogelkop, West Irian, and reported that below the red line underneath the eye there was no blue colouration, this part being dusky white. Specimens from Misol Island and the north of West Irian examined in this study did possess the blue colouration.

SIZE: The wing length of seven males was $80·7 - 91·3$ mm ($86·6$ mm.) and of five females was $80·5 - 85·7$ mm ($82·8$ mm.).

Opopsitta diophthalma festetichi (Madarasz)

Cyclopsittacus festetichi Madarasz, 1902, Term-Tud. Füz. **25**: 350. (East coast of Bougainville, Solomon Islands, error = Astrolabe Bay, northern Territory of New Guinea.)

RANGE: The Astrolabe Bay area, New Guinea; limits unknown.

PLUMAGE: The original description of *festetichi* stated that it resembled *diophthalma,* but the green of the general body plumage was darker.

Peters (1937) and Mayr (1941) synonymized this race with *diophthalma,* but Gyldenstolpe (1955) advocated its acceptance and referred to it 10 specimens collected by him near Nondugl in the Wahgi Valley. He compared these specimens with a single female from the Vogelkop and found that they were easily distinguishable by their markedly darker green plumage. Furthermore, the females had darker red on their foreheads and the yellow bands on the crowns were more prominent and more orange-yellow in colour. Attention was also drawn to their possession of a blue line under the eye but, as reported above, this is also present in *diophthalma.*

Two males (CSIRO 2178 and 2306) and one female (CSIRO 2125) from the Kubor Range were examined and compared with two males (AMNH 618919 and 618929) and one female (AMNH 618913) of the nominate race. The green of the upper parts was darker in the Kubor birds, but there was virtually no difference in the colour of the underparts. In the males the orange-yellow bands on the crowns were definitely wider and more pronounced than in any of the typical birds, while in the female it was comparable with those of the typical males. Another conspicuous difference noted was that the innermost wing-coverts were a much darker and deeper red. All of these plumage differences were also present in three immature birds, but no immature *diophthalma* were available for direct comparison.

SIZE: The wing length of two males from the Kubor Range was $92 \cdot 0 - 99 \cdot 0$ mm ($95 \cdot 5$ mm) and for one female was $92 \cdot 0$ mm. These agree with $96 \cdot 0 - 99 \cdot 0$ mm ($97 \cdot 6$ mm) for three males and $93 \cdot 0 - 98 \cdot 0$ mm ($94 \cdot 7$ mm) for four females collected by Gyldenstolpe. The larger size, coupled with apparent plumage differences, supports the provisional retention of *festetichi* as advocated by Gyldenstolpe.

Opopsitta diophthalma coccineifrons (Sharpe)

Cyclopsittacus coccineifrons Sharpe, 1882, J. Linn. Soc. (Zool.) **16**: 318. (Astrolabe Mountains New Guinea.)

RANGE: South-eastern New Guinea.

PLUMAGE: The original description stated that this race was distinguished from *diophthalma* by having the front of the face, lores, and cheeks dull red not scarlet.

Rothschild and Hartert (1901) and Peters (1937) declared that *coccineifrons* was a doubtful race. Mathews (1927) accepted it, but Mayr (1941) placed it in synonymy with *diophthalma*. Ogilvie-Grant (1915) said that it was easily separable as a subspecies because in the male the red on the forehead and cheeks was "of a rather dull crimson-scarlet instead of bright scarlet" and the yellow band across the crown was distinctly wider.

In the specimens examined there was considerable variation in the red of the cheeks and forehead, but the wide yellow band on the crown was a constant character. The red on the innermost wing-coverts was darker than in the males of *diophthalma*.

The differences between this race and *festetichi* were not striking and one male (AMNH 618937) from the Huon Gulf area appeared to be intermediate in both plumage and size. The specimens of *coccineifrons* tended to show lighter green on both the upper and under surfaces and lighter, brighter red on the forehead, cheeks, and innermost wing-coverts. However, individual variation detracted from the consistency of these differences. It is possible that an examination of a larger series of specimens from eastern New Guinea may result in the synonymizing of *festetichi* with *coccineifrons*, but for the present it seems advisable to accept both races.

SIZE: The wing length for nine males was $82 \cdot 8 - 92 \cdot 1$ mm ($87 \cdot 0$ mm) and for four females was $82 \cdot 3 - 88 \cdot 3$ mm ($85 \cdot 3$ mm). Only two males (AMNH 618937 and 618947) exceeded $89 \cdot 0$ mm, the remainder being decidely smaller than the average for *festetichi*.

Opopsitta diophthalma aruensis (Schlegel)

Psittacula diophthalma aruensis Schlegel, 1874, Mus. Pays-Bas, 3, Psittaci revue, p. 33. (Aru Islands.)

RANGE: The Aru Islands and southern New Guinea between the Mimika and Fly Rivers.

PLUMAGE: A complete absence of red from the facial markings of adult females and immatures at once distinguishes this race. The forehead and crown are bright blue with buff-brown bases to the feathers becoming noticeably paler towards the lores and periophthalmic region; the lores and cheeks are buff-brown, bordered below by mauve-blue bands extending to and becoming paler on the chin. The adult male differs from the male of *coccineifrons* by having the blue patch above the eye more greenish in colour and restricted in extent, by having the mauve-blue bands under the cheeks continue through to the chin, and by having the yellow band on the crown very much reduced or even absent altogether. In the specimens examined the green of the upper surface in both sexes was noticeably lighter and more yellowish than in *coccineifrons*.

SIZE: The wing length for six males was $82 \cdot 2 - 86 \cdot 9$ mm ($84 \cdot 9$ mm) and for three females was $80 \cdot 0 - 84 \cdot 7$ mm ($81 \cdot 6$ mm).

Opopsitta diophthalma virago (Hartert)

Cyclopsittacus virago Hartert, 1895, Novit. Zool. **2**: 61. (Fergusson Island.)

RANGE: Fergusson and Goodenough Islands in the D'Entrecasteaux Group, New Guinea.

PLUMAGE: The adult male of *virago* is distinguished from that of *aruensis* by the absence of the blue patch from in front of and above the eye, by the replacement of the mauve-blue bands below the cheeks by a bright blue spot on either side of the neck, and by the paler red on the crown and face. The adult female has the periophthalmic region green instead of blue as in *aruensis,* has a well-defined bright red spot on the middle of the forehead, has the cheeks green with a few pale blue and buff markings, and lacks the mauve-blue bands under the cheeks. No immature specimens of this race were examined.

SIZE: The wing length for five males was $81 \cdot 3 - 85 \cdot 7$ mm ($83 \cdot 8$ mm) and for four females was $81 \cdot 5 - 84 \cdot 1$ mm ($83 \cdot 0$ mm). It was noted that the maximum lengths were in the types (AMNH 618961 ♂ and 618962 ♀).

Opopsitta diophthalma inseparabilis (Hartert)

Cyclopsittacus inseparabilis Hartert, 1898, Bull. Brit. orn. Cl. **8**: 9. (Sudest Island.)

RANGE: Tagula (= Sudest) Island in the Louisiade Archipelago, New Guinea.

PLUMAGE: This distinct insular subspecies (see Hartert, 1899, pl. 4) resembles the female of *virago* and is one of the two races characterized by the almost complete absence of sexual dimorphism. Both sexes have the entire head, except the forehead and forepart of the crown, bright green as on the underparts; the forehead is bright red bordered behind on the forepart of the crown by bright blue.

In the specimens examined the females appeared to have less red on the forehead, while in both sexes the green of the general body plumage was duller and slightly more yellowish than that of either *virago* or *aruensis*. No immature specimens were examined.

SIZE: The wing length for eight males was $78 \cdot 5 - 88 \cdot 8$ mm ($83 \cdot 4$ mm) and for seven females was $79 \cdot 5 - 86 \cdot 4$ mm ($84 \cdot 2$ mm).

Opopsitta diophthalma marshalli Iredale

Opopsitta marshalli Iredale, 1946, Emu **46**: 1, pl. 1. (Great Divide Range behind Lockhart River, Cape York Peninsula.)

RANGE: Cape York Peninsula, Queensland.

PLUMAGE: Direct comparisons between specimens of *marshalli*, the northernmost of the Australian subspecies, and *aruensis* showed that, although the two races were very similar, constant differences did exist. In the adult male the blue patch in front of the

eye was deeper and darker than in *aruensis* and had no greenish tinge. Variation in the intensity of the red colouration of the face was evident in the three males examined. The darkest red in *marshalli* (CSIRO 690) agreed with the palest in *aruensis* (AMNH 618951), while the palest in *marshalli* (CSIRO 692) approached the orange-red colouration found in the males of *virago*. There was also variation in the blue on the outer edges of the wing primaries, but in all specimens it appeared to be darker than in *aruensis*. The yellow band on the crown was conspicuous in one individual (CSIRO 692), present in another (CSIRO 690), and faintly indicated in the third (CSIRO 688). Variation in this characteristic was also found in *aruensis,* but in no specimen was it as prominent as in the first specimen of *marshalli* (CSIRO 692).

Comparison of adult females showed that in *marshalli* the feathers on the forepart of the crown were tipped with bright violet-blue as against pale sky blue in *aruensis*. One of the specimens examined (CSIRO 691) had two reddish feathers on either side of the upper mandible above the lores, similar markings to those shown in Iredale's drawing of the immature male. The females also showed the darker blue on the wing primaries. No immature specimens were collected.

Mayr (1947) compared Iredale's description and drawing of *marshalli* with a series of *aruensis* and declared that he could not find a single difference. He stated that absolute identity could not be established until the Cape York specimens were compared directly with specimens of *aruensis* but, until a valid distinction was found, *marshalli* would have to be considered a synonym of *aruensis*. Doubts have always existed concerning the status of this race and many authors have followed Mayr's decision. It must be pointed out that the colours of the heads in Iredale's drawing are not a true representation of the colours of *marshalli,* and indeed the blue on the crown of the female appears to be closer to that found in *aruensis*. Direct comparisons between the two races have brought out distinctions and shown *marshalli* to be a valid subspecies.

SIZE: The wing length for three males was $83 \cdot 5 - 86 \cdot 7$ mm ($84 \cdot 5$ mm) and for three females was $79 \cdot 0 - 85 \cdot 6$ mm ($82 \cdot 7$ mm).

Opopsitta diophthalma macleayana (Ramsay)

Cyclopsitta macleayana Ramsay, 1874, Sydney Morning Herald, 5 Nov., 1874. (Scrubs on the coast range, near Cardwell, Rockingham Bay, Queensland.)

Opopsitta diophthalma boweri Mathews, 1915, Aust. avian Rec. **2** (7): 127. (Barron River, North Queensland.)

RANGE: Coastal areas of northern Queensland.

PLUMAGE: The adult male of this race has only the centre of the forehead and the lower cheeks red, the remainder of the facial area being blue, darker on the sides of the forehead, paler and more greenish around the eyes. The adult females and immatures have the lower cheeks buff-brown with bluish markings.

In the specimens examined the mauve-blue bands below the cheeks were slightly narrower than in *aruensis*. Furthermore the green of the general body plumage of the females was duller and more yellowish than that of the males and resembled that of both sexes of *inseparabilis*.

In the original description of *O. d. boweri* Mathews stated that it differed from *leadbeateri* (= *macleayana*) by "being less conspicuously marked, the red on the face and forehead not so bright, the yellow on the sides of the body not so pronounced." Mathews (1927) later synonymized this race with *leadbeateri* (= *macleayana*), which he regarded as a separate species. Peters (1937) did likewise but retained *macleayana* as a subspecies of *O. diophthalma*.

As well as the type (AMNH 618990) of *boweri* another male (AMNH 618991) and a female (AMNH 618992) from the type locality were examined. Slight differences in the red on the face and forehead and the yellow on the flanks were not constant and were counterbalanced by the individual variation present in the specimens of *macleayana*. Therefore *boweri* must be synonymized with *macleayana*.

SIZE: The wing length for 13 males was $83 \cdot 2 - 89 \cdot 7$ mm ($86 \cdot 7$ mm) and for 17 females was $79 \cdot 1 - 89 \cdot 0$ mm ($85 \cdot 3$ mm). For *boweri* the wing length for two males was $86 \cdot 9 - 87 \cdot 7$ mm ($87 \cdot 3$ mm) and for one female was $87 \cdot 0$ mm; these measurements were within the range for *macleayana*.

Opopsitta diophthalma coxeni (Gould)

Cyclopsitta coxeni Gould, 1867, Proc. zool. Soc. Lond. **1867**: 182. (" . . . scrub on the east coast", i.e. near Brisbane, Queensland.)

Opopsitta coxeni tweedi Mathews, 1917, Aust. avian Rec. **3**: 128. (Tweed River, New South Wales.)

RANGE: The coastal regions of southern Queensland and northern New South Wales from Maryborough in the north to the Macleay River in the south.

PLUMAGE: A very distinct isolate, *coxeni* is the southernmost of all the races of *O. diophthalma* and is the second subspecies lacking notable sexual dimorphism. Both sexes have the crown green with a few blue feathers on the centre of the forehead; the cheeks are orange-red bordered below by a variable mauve-blue band.

In the specimens examined the adult males had some reddish feathers on the lores and surrounding the blue on the forehead. They also had slightly brighter and more extensive red cheeks and deeper blue primaries. The green of the general body plumage of both sexes was dull yellowish-green, similar to that of the females of *macleayana*.

Mathews did not give any distinguishing features for the race *tweedi*. In the original descritpion he merely stated that it was based on the specimen described and figured in his *Birds of Australia* (1917). Subsequently (1927) he synonymized it with *coxeni,* which was treated as a distinct species.

As well as the type (AMNH 618998) of *tweedi,* another male (HLW 199) from the Tweed River was examined, but no differences distinguishing them from *coxeni* could be found. This race must be synonymized with *coxeni.*

SIZE: The wing length for seven males was $92 \cdot 8 - 96 \cdot 6$ mm ($94 \cdot 6$ mm) and for four females was $92 \cdot 2 - 93 \cdot 7$ mm ($92 \cdot 8$ mm). The wing length for 2 males of *tweedi* was $95 \cdot 0 - 96 \cdot 2$ mm ($95 \cdot 6$ mm); this measurement was within the range for *coxeni.* These measurements showed that *coxeni* is decidely larger than the other Australian subspecies and approaches *festetichi* in size.

DISCUSSION

In the New Guinea area there are two well-differentiated subspecies of *O. diophthalma* (*virago* and *inseparabilis*) and another (*aruensis*) which inhabits southern New Guinea as well as the Aru Islands. The existence of what appears to be a distinct population in northern New Guinea is a feature of the distribution pattern of the remaining races. The status of this race is uncertain, but it has been assigned to *festetichi.* A darker plumage colouration and larger size distinguish it from the nominate race. On the other hand, differences from *coccineifrons,* the eastern race, are not striking and, if more material were examined, could prove to be inconsistent. An indication of this is the fact that one of the specimens examined appeared to be intermediate in both plumage and size.

In the Huon Peninsula – Astrolabe Bay region of New Guinea the Ramu and Markham Rivers and their tributaries penetrate the mountain ranges by means of deep valleys which tend to separate one massif from another. Such a terrain could disrupt the distribution of a species and provide physical barriers favourable to the establishment of morphologically distinct populations. It is desirable that more material from this region be examined and compared directly with the types of *festetichi* and *coccineifrons.* In my opinion this could result in the synonymizing of these two races, but it seems doubtful that they in turn could be synonymized with *diophthalma* as has been done by Mayr (1941).

Prior to the discovery of *marshalli* on Cape York Peninsula, the relationship between the Australian races of *O. diophthalma* and those from New Guinea does not seem to have been fully appreciated. Rothschild and Hartert (1901) recognised similarities in plumage between the females of *macleayana* and *virago* and, to a lesser degree, between the males of *macleayana* and those of both *virago* and *aruensis.* They treated *macleayana* as a race of *O. diophthalma* but, because of its large size and the almost entirely blue foreheads in both sexes, *coxeni* was considered to be a distinct species. Mathews (1927 and 1946) retained all of the New Guinea forms as races of *O. diophthalma* but gave specific status to *leadbeateri* ($=$ *macleayana*) and *coxeni.*

When commenting on the discovery of *marshalli,* Mayr (1947) remarked that it was to be expected that a population of this species would be found on Cape York, in the distributional gap betweeen the areas inhabited by the New Guinea races and *macleayana*

from northern Queensland. In fact, *marshalli* is exactly what Mayr had suggested it should be—a population connecting the Australian races with those from New Guinea.

Keast (1961) cited *O. diophthalma* in Australia as an example of the speciation process acting on isolated populations. The isolates are confined to the three major tracts of rain forest along the north-eastern coast. As stated by Keast (*loc. cit.*) *coxeni* and *macleayana* are approaching the degree of differentiation typical of species, whereas *marshalli* is probably a recent immigrant. Similar degrees in variation are shown by the insular forms in New Guinea. The race *inseparabilis* inhabits the island farthest away from the mainland and shows nearly as much difference from *coccineifrons* as does *coxeni* from *marshalli* and *aruensis*. The female of *virago* resembles both sexes of *inseparabilis,* while both sexes of *coxeni* show affinities with the male of *macleayana.* In other words the path of migration or colonization is indicated by the areas in which intermediate forms occur. It is true that size differences are shown by *coxeni* and not by *inseparabilis,* but in my opinion these do not warrant the former being singled out as the only race having acquired specific differentiation.

CONCLUSIONS

Specimens of all of the subspecies of the Fig Parrot, *Opopsitta diophthalma,* have been examined and the plumage and size differences noted. Characteristics separating *marshalli* from *aruensis* have been fully described. The races *boweri* and *tweedi* have been synonymized with *macleayana* and *coxeni* respectively, while *festetichi* and *coccineifrons,* hitherto generally synonymized with *diophthalma,* have been accepted pending the acquisition of more material and its subsequent comparison with the types.

It has been shown that both well-differentiated and poorly-differentiated races are found in this species. The former occur as isolates in the New Guinea area as well as in north-eastern Australia. Comparison has been made between the affinities of *coxeni* and *inseparabilis* with the nominate race as indicated by the distribution of intermediate forms. The recognition of *coxeni* as a distinct species has been rejected.

ACKNOWLEDGEMENTS

Dr. D. Amadon of the American Museum of Natural History, and Messrs. J. H. Calaby, W. B. Hitchcock, and B. V. Fennessy of this Division read the manuscript and offered useful criticisms.

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OBLICARINA, A NEW PERMIAN BIVALVE GENUS

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ABSTRACT

A new genus, *Oblicarina,* is erected for the bivalve *Chaenomya ? carinata* Etheridge, 1892, from middle Permian beds of Queensland. It is distinguished from *Chaenomya* Meek, 1865, and from allied Australian species placed in *Vacunella* Waterhouse by its pronounced posterior umbonal ridge and prosocline obliquity. The Lower Permian species *Mytilomorpha translata* Reed, 1932, from the Agglomeratic Slate of Kashmir, is referred to the same genus.

In 1892 Etheridge named and described *Chaenomya ? carinata* from middle Permian beds of Banana Creek, Dawson River, Queensland. The species is distinguished from *Chaenomya* Meek 1865 by its ornament of finer pustules, strong posterior umbonal ridge, smaller posterior gape, apparently smaller pallial sinus, and different protractor-retractor complex. It is closer to other Australian species that have been referred to *Chaenomya,* and are now placed in *Vacunella* Waterhouse 1965a, but is distinguished by its prosocline outline, the strength of its posterior umbonal ridge, and possibly by the anterior retractor and protractor complex and shallower pallial sinus. These criteria are considered to be of more than specific rank and to warrant the erection of a new genus.

An allied species is present in the Permian beds of Kashmir.

Genus **Oblicarina** nov.

Type Species: *Chaenomya ? carinata* Etheridge 1892.

Diagnosis: Highly prosocline moderately to well inflated shell, with incurved anterior umbones and pronounced posterior umbonal ridges. Posterior dorsal face flat or concave. Posterior dorsal gape narrow. Shallow sulcus on flank of shell. Ornament of wrinkles, low concentric costae, and fine pustules (5 to 8 per mm). Hinge short, edentulous, thickened. Anterior adductor subquadrate, placed at the anterior ventral extremity, adjoined by short protractor to a small rounded anterior retractor. Posterior muscle scars and pallial sinus not known for certain, but adductor possibly large, sinus possibly very shallow. By analogy with other species it is probable that the ligament is partly external and opisthodetic, supported by nymphs, partly internal.

D

DISCUSSION: The new genus is most closely allied to a group of Australian Permian bivalves which includes *Allorisma curvatum* Morris, 1845, *Pholadomya* (*Homomya*) *audax* Dana, 1847, *P.* (*Homomya*) *glendonensis* Dana, 1849, *Panopea* (*Mya*) *plicata acuta* Etheridge Sr., 1872, in part, pl. 21, fig. 3, not fig 3a (see Waterhouse, 1965b), *Sanguinolites etheridgei* de Koninck, 1877, *S. mitchelli* de Koninck, 1877, and *Chaenomya ? bowenensis* Etheridge Jr., 1892. *Allorisma curvatum* (see pl. 1, figs. 1, 4) was made the type of a new genus *Vacunella* by Waterhouse (1965a), and the remaining species are congeneric.
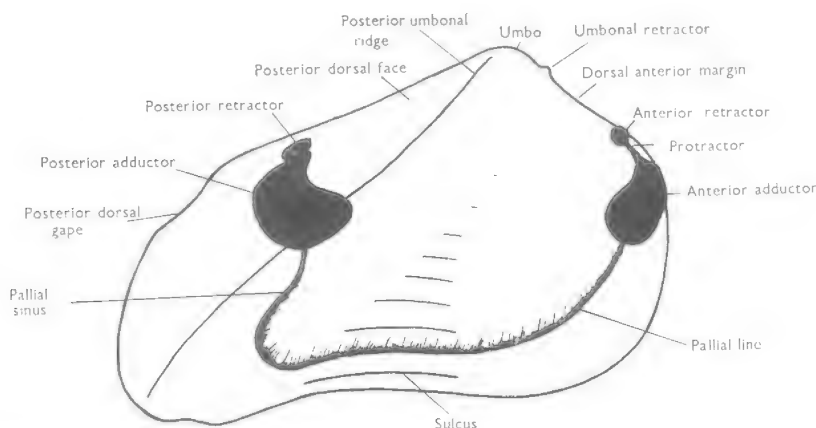
FIG. 1: Internal mould of generalised right valve of *Vacunella–Oblicarina* to show various morphological features. Based on Waterhouse (1965a, fig. 1, p. 369), with nomenclature of anterior musculature emended from Runnegar (1965).

The narrow posterior gape, ornament and edentulous hinge of these species are much the same as in the new genus. Some of the Australian species of *Vacunella* are moderately prosocline, and a few New Zealand allies have a weakly convex posterior umbonal ridge, but none are as oblique as *O. carinata* or have such a pronounced posterior umbonal ridge and flat or concave posterior dorsal face. The anterior retractor lies further from the adductor in *Vacunella,* and the protractor "isthmus" between the two is therefore longer (fig. 2a). Also the pallial sinus is possibly shallower in *O. carinata* (cf. fig. 2a with 2e), though this is not certain.

The type species of *Chaenomya, C. leavenworthensis* (Meek and Hayden, 1859), is less inflated than *O. carinata,* with parallel ventral and dorsal margins, and no posterior umbonal ridge. The posterior gape is huge, and the pustules coarse (2 or 3 per mm) and aligned radially. The anterior adductor scar lies close to the dorsal margin, and adjoins a rounded pedal scar, with no isthmus. The pallial sinus is high, but not very deep (fig. 2c).
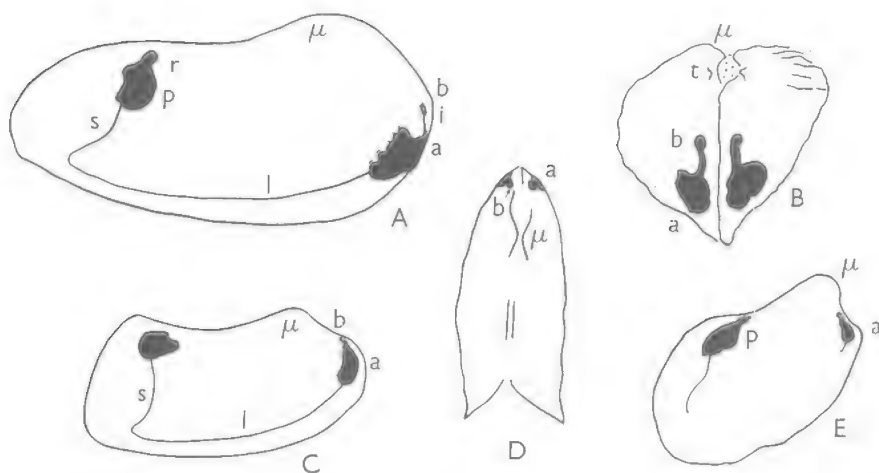
FIG. 2: Muscle scars in *Vacunella, Chaenomya* and *Oblicarina.* All specimens half natural size.

A,B, *Vacunella curvata* (Morris), lateral aspect of right valve, and anterior view based chiefly on F197, Australian Museum (from Maitland), with details added of the umbonal retractors from F30077, and posterior adductor and pallial sinus from specimens such as F8136, Australian Museum (from Wollongong).

C,D, *Chaenomya leavenworthensis* (Meek and Hayden), lateral aspect of right valve and dorsal aspect, sketched from photographs of the original type, USNM 1019a, Smithsonian Institution, with the posterior adductor rather suppositious, and the posterior retractor not clear on the photographs.

E, *Oblicarina carinata* (Etheridge), lateral aspect of right valve, pallial line and posterior adductor not certain.

a = anterior adductor;	p = posterior adductor;
b = anterior retractor;	r = posterior retractor;
i = "protractor isthmus between	s = pallial sinus;
adductor and protractor;	t = umbonal retractor;
l = pallial line;	μ = umbo.

TERMINOLOGY: The parts of the shell are named as in Waterhouse (1965a), except for the adoption of the suggestion of Runnegar (1965) that the moderately prominent rounded muscle scar behind the anterior adductor and well in front of the umbo be termed the anterior retractor, and that any scars between this and the adductor be referred to the protractors. In some species and genera there are no such scars, indicating that the protractors were possibly attached to the adductor muscle and not to the shell. Runnegar's proposals seem to be consistent with the muscle pattern outlined for the Palaeotaxodonts *Yoldia* and *Acila* by Heath (1937, pl. 10, fig. 1; pl. 5, fig. 39), though some species of *Nuculopsis* (*fide* Driscoll, 1964) have a pattern that suggests the arrangement shown in Waterhouse (1965a). According to Johnstone (1900, pl. 1, fig. 3; pl. 2, fig. 10) the anterior retractor of *Cardium* lies in front of or below the protractor.

Oblicarina carinata (Ethridge Jr.)

(Fig. 2E; pl. 1, figs. 2, 3.)

Chaenomya ? carinata Etheridge, 1892, p. 279, pl. 43, figs. 5, 6.

HOLOTYPE: F1218, Queensland Museum, Brisbane; the sole specimen figured and described by Etheridge (1892) from Banana Creek, from beds now assigned to the Flat Top Formation on information supplied by courtesy of Dr. J. F. Dear, Geological Survey of Queensland, to Mr. J. T. Woods.

DIMENSIONS (mm)

Length	Height	Width	Hinge length	Hinge thickening width	Distance of umbo from anterior margin	Width of gape
51	44·5	40·5	34	10·5	9·5	7

DESCRIPTION: Short, high, prosocline, well inflated, umbones anteriorly placed, incurved, orthogyrous, anterior ventral margin recessed, but not necessarily with a lunule as reported by Etheridge. Ventral margin well rounded in outline, diverging posteriorly from the hinge at 30°. Shallow sulcus lying on the flank of the shell below umbo, inclined posteriorly from hinge at 70°. Posterior umbonal ridge sinuous in outline, extending to posterior ventral extremity, inclined from hinge at 50°. Posterior dorsal face high and concave, with a low groove just inside the umbonal ridge on the left but not the right valve. Regular concentric wrinkles cover the first formed part of the shell, fading posteriorly on the posterior dorsal face, and feebly developed around the posterior ventral margin. Traces of fine costae (2 per mm) also present, and about 5 to 7 pustules per mm, not aligned radially or in any other well defined pattern. Anterior muscle scars as for genus. Posterior adductor possibly indicated by large rhomboid slightly raised area on the mould close to hinge, and suggestions of a possible pallial line on the left valve indicate a short very shallow pallial sinus (transposed onto the right valve in fig. 2e).

Oblicarina translata (Reed)

Mytilomorpha translata Reed, 1932, p. 61, pl. 8, figs. 9, 9a, 10, 10a.

LECTOTYPE: The specimen figured by Reed (1932, pl. 8, fig. 10, 10a) is designated lectotype. F15552, Geological Survey of India, Calcutta.

DISCUSSION: This species from the Agglomeratic Slate of Kashmir is more elongated and less inflated than *O. carinata* but otherwise agrees in its prosocline outline, bluntly carinate posterior umbonal ridge, and narrow posterior gape. About 7 or 8 pustules per mm are visible on one of the specimens (Reed, 1932, pl. 8, fig. 9).

The hinge, well displayed on the lectotype, bulges slightly just below the umbo of each valve.

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I wish to thank Mr. J. T. Woods, Director of the Queensland Museum, Brisbane, for kindly lending the type specimen of *Chaenomya* ? *carinata* Etheridge, for facilitating publication of the present note, and for providing information on locality and age. Mr. M. V. A. Shastry, and Mr. S. C. Shah, Chief Palaeontologist and Palaeontologist respectively, at the Geological Survey of India, kindly made facilities available for examining *Mytilomorpha translata* Reed at the Geological Survey of India, Calcutta. Drs. A. Lee McAlester and Copeland MacLintock of the Peabody Museum, Yale University, and Dr. Erle G. Kauffman of the Smithsonian Institution loaned specimens of the type species of *Chaenomya,* and photographs of their types.
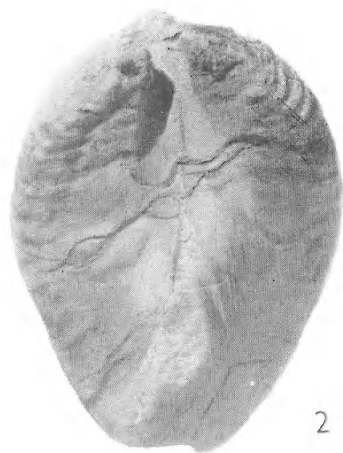
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PLATE 7

FIGS. 1, 4: *Vacunella curvata* (Morris), dorsal and oblique lateral views for comparison with *Oblicarina*. Note absence of well defined posterior umbonal ridge, and the more or less rounded nature of the posterior dorsal face. Specimens kept at the Australian Museum, Sydney—F51563, locality not certain, possibly Wollongong (Fig. 1) and F197 from Maitland Group, Maitland (Fig. 4). Natural size.

FIGS. 2, 3: *Oblicarina carinata* (Etheridge), dorsal and lateral views of the holotype F1218, Queensland Museum, Brisbane. Natural size.

1

2

3

4

CONTENTS