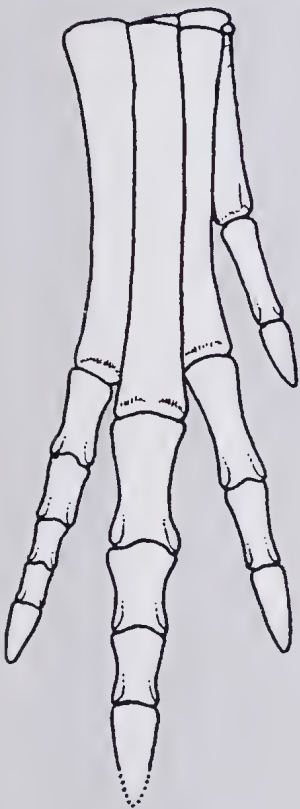


# MEMOIRS

OF THE

# QUEENSLAND MUSEUM



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MEMOIRS

OF THE

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NEW RECORDS OF BOPYRIDAE (CRUSTACEA : ISOPODA : EPICARIDEA)  
FROM QUEENSLAND WATERS

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ABSTRACT

Two species of bopyrids were recovered from commercially caught prawns in Queensland. *Epipenaeon ingens* Nobili 1906, previously recorded from Darwin, was found in four places in Queensland on its type host *Penaeus semisulcatus*, or on *P. merguensis*. On the basis of a high degree of variability in specimens, *E. ingens latifrons* Bourdon 1979 is considered a junior subjective synonym of *E. ingens*. Other members of the genus *Epipenaeon* are listed for comparison.

*Parapenaeon expansus* was found on *Penaeus plebejus* in Moreton Bay, and on *Penaeus* sp. from Karumba.

These constitute new site and host records, for both species.

INTRODUCTION

Parasites of prawns have recently attracted interest as they may be useful as biological markers for prawn sub-populations (Owens 1981, 1983). Bopyrid isopods are among the most obvious parasites carried by Australian prawns. Although several bopyrid species occur in Australian waters only two have been found on commercially valuable prawns. These are *Epipenaeon ingens* Nobili 1906, and *Parapenaeon prox. expansus* Bourdon 1979a, both from 'tiger prawns' taken in the vicinity of Darwin, N.T. (Bourdon 1979b). Recently these bopyrid species were recovered from collections of penaeids made in Queensland waters. This note records where and on what species of hosts they have been found.

Prawns trawled from the Gulf of Carpentaria, Rosslyn Bay, and Maryborough were obtained frozen from fish marketing boards. In Moreton Bay prawns were obtained fresh from trawlers. Parasites were removed and preserved in 70% alcohol. Specimens have been lodged at the Queensland Museum (QM).

EPIPENAEON Nobili 1906

*Epipenaeon ingens* Nobili 1906

*Epipenaeon ingens* Nobili 1906, p. 1099–101 Fig. 1, 1 a–e. Bourdon 1968, p. 327–33, Figs. 145–50.

*Epipenaeon nobili* Nierstrasz and Brender á Brandis 1929, p. 299–302, Figs. 5–9.

*Epipenaeon grande* Nierstrasz and Brender á Brandis 1929, p. 157–58, Fig. 18; 1932, p. 91, Fig. 1.

*Epipenaeon ingens latifrons* Bourdon 1979, p. 429–30, Fig. 4 a–c.

MATERIAL EXAMINED

QM W10438, ♂ + ♀, ex *Penaeus semisulcatus*, Karumba, Gulf of Carpentaria, NW.Q., S.P. Nearhos, 14.vii.79; QM W10445, 15 ♂ + 19 ♀ ex, *P. semisulcatus*, Karumba, S.P. Nearhos, 4.vii.78; QM W10436, ♂ + ♀, ex *P. merguensis*, Karumba, S.P. Nearhos, 14.vii.79; QM W10437, ♂ + ♀, ex *P. merguensis*, Karumba, S.P. Nearhos, 14.vii.79; QM W10439, ♂ + ♀, ex *P. merguensis*, Karumba, S.P. Nearhos, 14.vii.79; QM W10446, 11 ♂ + 22 ♀, ex *P. merguensis*, Karumba, S.P. Nearhos, 17.vii.79; QM W10448, 8 ♀, 2 ♂, ex *P. semisulcatus*, Maryborough, SE.Q., S.P. Nearhos, 10.iv.78; 10 ♂ + 13 ♀, ex *P. merguensis*, Rosslyn Bay ME.Q., S.P. Nearhos 17.vi.78.

OTHER MATERIAL

*E. nobili* ♂ + ♀, ex *P. semisulcatus*, Red Sea, Nierstrasz and Brender á Brandis.

*E. grande* ♀, ex *P. semisulcatus*, Hong Kong, 23.v.1890, Nierstrasz and Brender á Brandis.

*E. ingens latifrons*, 4 ♂ + 4 ♀, ex *P. semisulcatus*, Darwin, Bourdon.

DISTRIBUTION

Mediterranean Sea and the Indo-Pacific region — from Hong Kong in the north to southeast Queensland.

## REMARKS

*E. ingens* was originally described from *Penaeus semisulcatus* from the Red Sea (Nobili 1906). It was redescribed from the same host in the Mediterranean by Bourdon (1968). Bourdon (1979b) synonymized *E. nobili* and *E. grande* with *E. ingens* and described a new subspecies *E. ingens latifrons* from a *Penaeus* sp. for its well developed frontal plate and unusually wide lateral plates.

Examination of 24 specimens from *P. semisulcatus* from the Gulf of Carpentaria and from Maryborough showed that development of frontal plates varied between individuals. The mean ratio of frontal plate length to total length was 0.074 (range 0.03 - 0.10). The types of *E. ingens latifrons* fall within the range. Lateral plates showed similar variation. Specimens from *P. merguensis* from both eastern and northern Queensland have less developed frontal and lateral plates, and in this respect more closely resemble *E. ingens* from the Red and Mediterranean Seas than they do *E. ingens latifrons*. The males from both hosts are very similar and correspond closely to the male described from the Mediterranean, the only *E. ingens* male described.

It appears then, that the development of the frontal and lateral plates vary from individual to individual and from host to host. On this basis we propose that *E. ingens latifrons* be considered a junior subjective synonym of *E. ingens*.

Two other species of *Epipenaeon* also occur on *P. semisulcatus* — *E. elegans* Chopra, 1923 and *E. pestae* Nierstrasz and Brender á Brandis, 1932. The published descriptions of these species are inadequate to clearly separate them from *E. ingens*, considering the highly variable nature of *E. ingens* individuals.

*E. ovalis* Pillai 1954, was recorded from *Parapenaeopsis styliifera* and characterized by having a broader frontal plate and greater development of the pleonal lamellae than *E. ingens*. Both of these features were found to have been variable for specimens of *E. ingens* examined in this study. The type material of *E. ovalis* has been lost and is unavailable for comparative study (Pillai, pers. comm.).

*E. oviformis* Nierstrasz and Brender á Brandis, 1931, described from a *Penaeus* sp. is obviously a juvenile specimen which makes comparison with mature adults impossible. Its status is therefore doubtful.

Of the species described in the genus, at this stage only *E. fissurae* Kensley 1974, seems

definitely separable from *E. ingens*. It can be distinguished by the shape of the antennae, the blunt digitations of the posterior margin of the cephalon and first oostegite, and the knobbed nature of the pleopods.

PARAPENAEON Richardson 1904

*Parapenaeon expansus* Bourdon 1979

*Parapenaeon expansus* Bourdon 1979, 495-8, Figs. 15-8.

## MATERIAL EXAMINED

QM W10440, ♀, QM W10441, ♂ + ♀, QM W10442, 2 ♂, QM W10443, ♀ ex *Penaeus plebejus*, Moreton Bay, SE.Q. S.P. Nearhos, 9.ii.79, 9.ii.79, 12.ii.79 and 1.v.78; QM W10444, ♂ + ♀, ex *P. plebejus*, Moreton Bay, R.J.G. Lester, 23.i.78; QM W10447 ♀ ex *P. plebejus*, Moreton Bay, S.P. Nearhos, 24.iv.78; QM W10451, 6 ♀, ex *Penaeus* sp. Karumbu, Gulf of Carpentaria, NW.Q.S.P. Nearhos, 9.ii.79.

## DISTRIBUTION

Indo-Pacific Oceans from Madagascar to northern Australia and south to Moreton Bay in Queensland.

## REMARKS

Present material of *Parapenaeon expansus* (both males and females) correspond closely to those described by Bourdon (1979a) from the type host *Penaeus teraoi* in Madagascar. This constitutes a new host and distribution record for the species.

## ACKNOWLEDGMENTS

We thank Dr R. Bourdon for his help, advice and the loan of the type material of *E. ingens latifrons* and *P. expansus*. Dr H.E. Gruner, Zoology Museum, East Berlin, kindly loaned specimens of *E. nobili* and Dr T. Wolff, Zoology Museum, Copenhagen loaned the ♀ type specimen of *E. grande*. P.J.F. Davie, Queensland Museum is thanked for his assistance in the preparation of this manuscript.

The study formed part of the Masters Qualifying Thesis for the senior author.

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PITONGA GEN. NOV., A SPIDER (AMAUROBIIDAE : DESINAE) FROM  
NORTHERN AUSTRALIA.

VALERIE TODD DAVIES  
Queensland Museum

ABSTRACT

A 3-clawed spider from the mangroves of the Northern Territory, Australia is described and provisionally placed in the Desinae. It has untoothed tarsal claws and a long inferior claw, a copulatory spur on ♂ tibia II and no serrula.

INTRODUCTION

These spiders were collected by members of the Australian Littoral Society during a survey of the mangrove areas of Northern Australia. The female was found in a crab-hole on the mud, the male walking on the mud and two of the three juveniles collected were in silk cells on the mangrove leaves along the river, the third on mud.

*Pitonga* gen. nov.

Medium sized, 3-clawed spider. Eyes small, in 2 almost straight rows occupying median third of head. Clypeus narrow. Promargin of chelicera with teeth, retromargin without teeth but with a secretory protuberance opposite last promarginal tooth. Labium and maxillae elongate, no serrula. Spinnerets sub-terminal; no colulus. Legs 1423, anterior trochanters un-notched. One long distal trichobothrium on metatarsi, none on tarsi. Male with thick spines on Tibia I and ventral spur-like spine on Tibia II.

'Pitonga' is an aboriginal word meaning mangrove.

*Pitonga woolowa* sp. nov.

Holotype: In crab hole on mud bank, Flying Fox Is., East Alligator River, Northern Territory, W. Houston, 15.vi.81, 1 ♀, QM S1300.

Paratypes: On mud, East Alligator River,

N.T., W. Houston, P. Davie, 23.vi.82, 1 ♂, QM S1301; in silk cells on mangrove (*Avicennia* sp.) leaves, 2 juvs QM S1302. On mud, Point Farewell, East Alligator River, N.T., W. Houston, P. Davie, 18.vi.82, 1 juv., QM S1303.

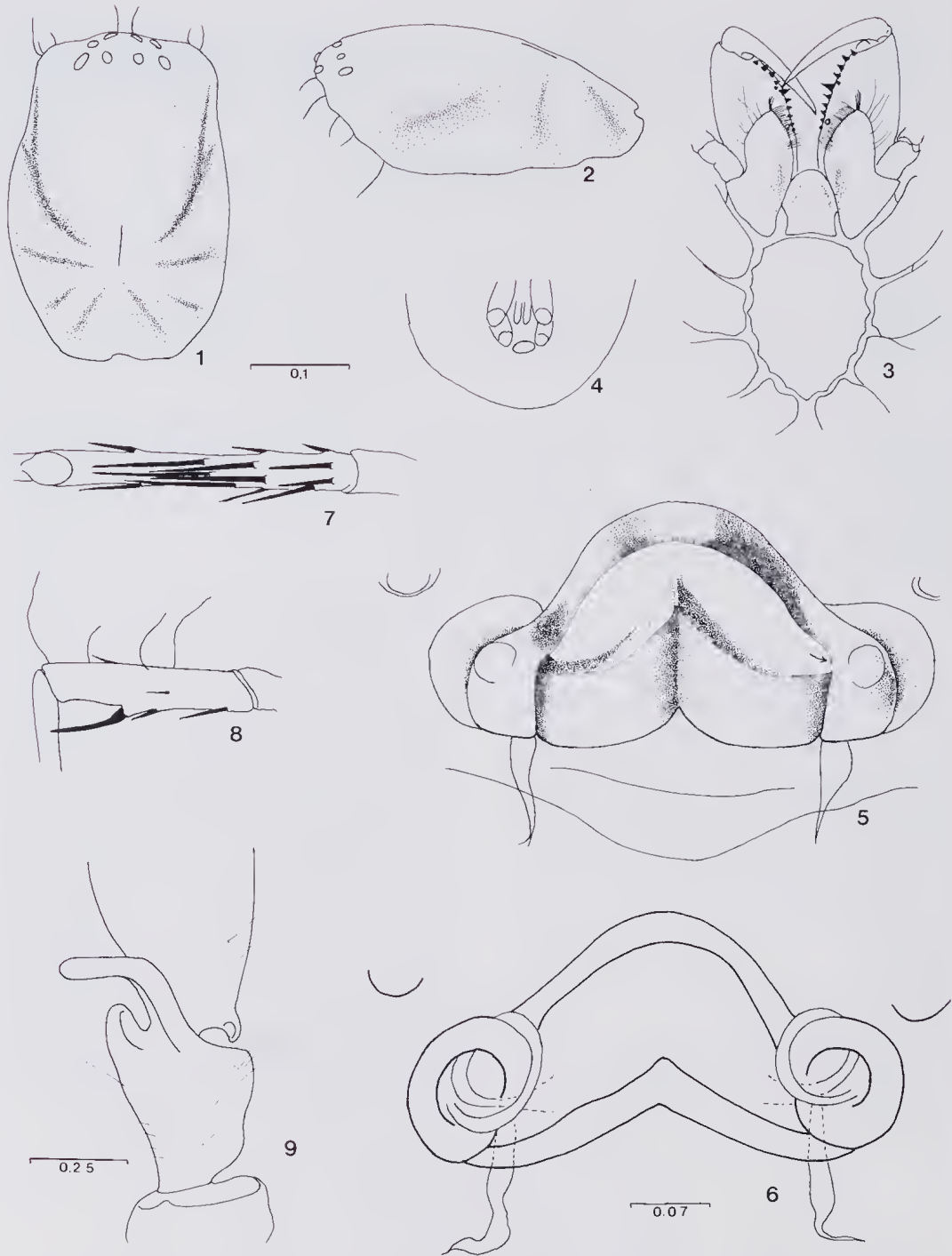
DESCRIPTION OF FEMALE

CL 3.13, CW 2.13, AL 2.87, AW 2.00 (abdomen shrunken).

Colour: The spider is pale and straw-coloured resembling *Clubiona*. Chelicerae, metatarsi and tarsi light brown. Closely adpressed hair on cephalothorax and abdomen, longer hairs on abdomen. Legs hairy, especially laterally on distal segments. Viewed from above anterior row of eyes slightly recurved, posterior row straight; from the front, anterior row straight, the posterior row procurved (Figs. 1, 2). Ratio of eyes AME:ALE:PME:PLE is 9:9:7:10. Clypeus narrower than diameter of AME. Chelicerae large and long (2.0 mm) with boss. Retromargin without teeth, promargin 10 teeth. Small medium tooth opposite 4-5 and retromarginal protuberance opposite the last promarginal tooth between which the tip of the fang rests (Figs. 3, 14). Magnification shows that this boss has regular pores opening on it (Fig. 15). Labium longer than wide 1:0.81. Sternum longer than wide 1:0.71. Spinnerets: small, short and sub-terminal (Fig. 4).

TABLE I: ♀ LEG MEASUREMENTS.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
palp	1.50	0.57	0.69	—	0.94	3.70
I	2.72	1.00	2.50	2.41	0.72	9.35
II	2.13	0.84	1.56	1.81	0.63	6.97
III	1.84	0.84	1.09	1.50	0.53	5.80
IV	2.75	1.00	2.31	2.19	0.63	8.88



FIGS. 1-6: ♀ *Pitonga woolowa* (holotype). 1, cephalothorax, dorsal; 2, cephalothorax, lateral; 3, cephalothorax and mouthparts, ventral; 4, spinnerets; 5, epigynum, external; 6, epigynum, internal.  
 7-9: ♂ *Pitonga woolowa* (paratype). 7, tibia I, ventral; 8, tibia II, retrolateral; 9, I. palp, dorsal.

TABLE II ♂ LEG MEASUREMENTS

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	3.09	1.03	2.97	3.09	0.94	11.12
II	2.41	0.97	1.97	2.25	0.66	8.26
III	2.03	0.94	1.25	1.75	0.53	6.50
IV	3.38	1.06	2.50	2.47	0.75	10.16

Legs 1423 (Table I) tarsi short, about 1/3 metatarsi; hairs plumose (sensu Lehtinen). Posterior trochanters shallowly notched. Tarsus with 3 smooth claws; inferior claw long (Figs. 10, 11). Two stouter hairs lateral to it and cluster of short hairs ventral to it (Fig. 12). Between 2-4 trichobothria in irregular rows on tibiae, one long distal trichobothrium on metatarsi (Fig. 16), none on tarsi. Capsulate tarsal organ (Fig. 17) with pyriform opening.

Notation of Spines: *First leg*: Femur, p 1 distal, d 1.1.1. Tibia, p 1.1.1.1.1(0), v 2.2.2. Metatarsus, p 1.1.1, r 0.1.1, v 2 proximal. *Second leg*: Femur, p 1 distal, d 1.1.1. Tibia, p 0.1.1(0), v 2.1.1. Metatarsus, p 1.0.1., d 0.1.1, r 1.0.1, v 1.2.1(0). *Third leg*: Femur, d 1.1.2. Tibia, p 0.1.1, r 0.1.1, v 2(1).0.0(1). Metatarsus, scattered proximal 5-6, distal whorl 6. *Fourth leg*: Femur, d 1.1.1.1.1.1.0.0. Tibia, r 0.1.0.1, v 2.0.1.0. Metatarsus, scattered proximal 5, distal whorl 5-6.

Epigynum: The fossa has a sclerotized rim which makes it difficult to trace the course of the ducts to the spermathecae (Figs. 5, 6).

There are 4 unbranched abdominal tracheal tubes.

#### DESCRIPTION OF MALE

CL 3.18, CW 2.35, AL 3.13, AW 1.73.

Similar to female in colour, eye ratios, cheliceral teeth and trichobothrial pattern. Legs 1423 (Table II). The prolateral and ventral spines on tibia I (Fig. 7) are enlarged and there is a large ventral spur-like spine on tibia II (Fig. 8) which is presumably used during mating.

Notation of Spines. *First leg*: Femur, p 1 distal, d 1.1.1.1. Tibia, p 2(1).1.1.0(1).1.0, d 1.0.1, r 1(0).1.0(1).1, v 2.2.2.0.0. Metatarsus, p 1.0.1., v 2.2(1).1. *Second leg*: Femur, p 0.0(1).1, d 1.1.1.1. Tibia, p 0.1.0.1(spur), d 0.1.0, r 0.1.0, v 2.1.1. Metatarsus, p 1.1.1, v 2.1.1. *Third leg*: Femur, p 0.1.0, d 1.1.1.0.1, r 0.1.0. Tibia, p 0.1.1, d 0.0.1, r 0.1.1, v 2.0.0. Metatarsus, scattered proximal 6, distal whorl 6. *Fourth leg*: Femur, d

1.1.1.1.0(1).1. Tibia, p 0.1.0.1, v 2.0.1.0. Metatarsus, scattered proximal 6, distal whorl 6. Palp. Embolus thick and spear-shaped, membranous median apophysis (Fig. 13). Small prolateral posterior extension of cymbium. Elaborate tibial apophyses (Fig. 9).

The species name 'woolowa' is an Aboriginal word meaning mud flat.

#### DISCUSSION

It is difficult to decide whether characters in *Pitonga* indicate relationship to a recognised family or are specialized adaptations to the mangrove area in which the spider lives. It seems likely that the long inferior tarsal claw and lack of teeth on any of the claws are adaptations for running on mud.

Lehtinen (1980 : 493) regards the trichobothrial pattern of 2 rows on tibiae, 1 on metatarsi and none on tarsi as the plesiomorphic state; it is found in hypochiloids, haplogynes araneoids and some others. In *Pitonga* the tibial trichobothria are few and irregularly placed. The structure of the trichobothrial base and the ridged (rather than scale-like) cuticle around it, as well as the pyriform aperture of the tarsal organ, suggest amaurobioid rather than araneoid affinities (Lehtinen 1978 : 267, Forster 1980 : 273).

Spination and copulatory spurs on the anterior tibiae of males are common in mygalomorphs and in a few araneids — several other families have metatarsal spurs. A retrolateral tibial apophysis is found in the palp of most ♂ spiders, the main exceptions being most of the araneoid spiders and the lycosids. In *Pitonga* there are 2 apophyses, the second one arises prodorsally and turns retrolaterally. Many amaurobioid spiders have complex tibial apophyses. The absence of a serrula in *Pitonga* is regarded as an apomorphy.

Although *Pitonga* resembles araneoid spiders in trichobothrial pattern and possession of tibial copulatory spurs in the male these characters are regarded as plesiomorphic and thus may not

indicate relationship. The structure of the trichobothrial base and cuticle, the pyriform opening of the tarsal organ and the plumose hairs suggest amaurobioid affinities. Many dictynoids (among the amaurobioids) show a like reduction in tarsal trichobothria. The complex tibial apophysis further supports this view and although there is no colulus the anterior spinnerets are well separated suggesting recent cribellate ancestors.

The hairiness of the legs, the long chelicerae and maxillae, and the coastal locality have influenced the provisional placing of *Pitonga* in the Desinae.

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## PLATE 1

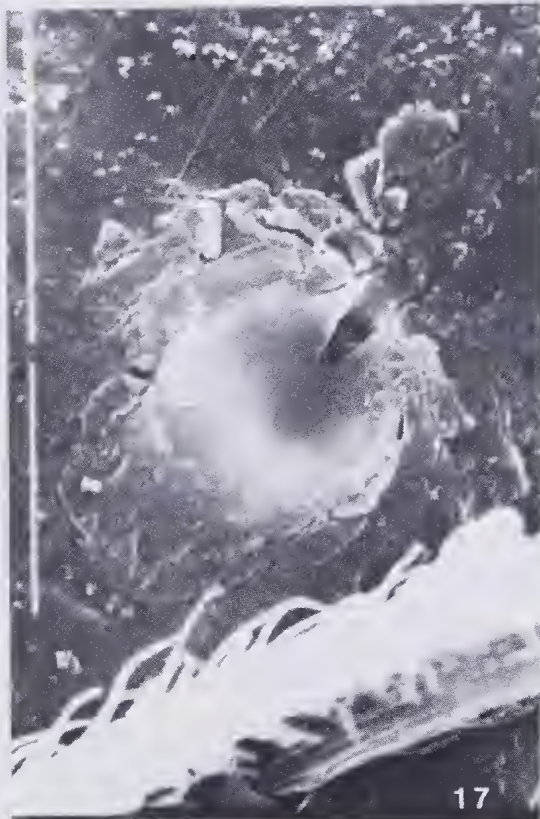
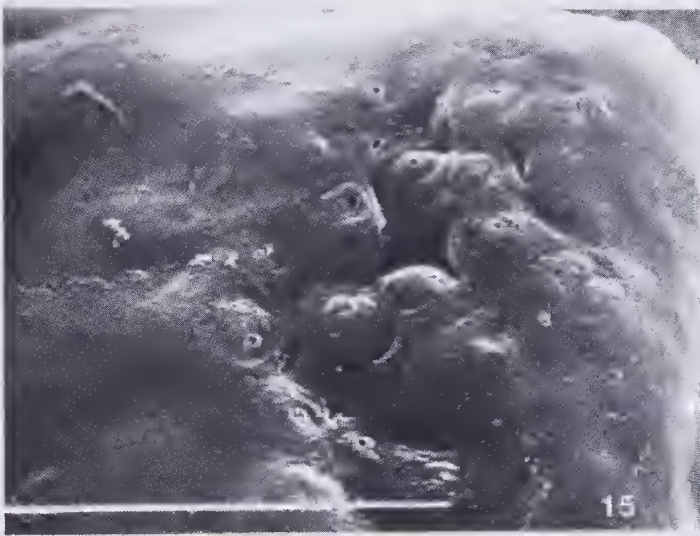
FIGS. 10–13: *Pitonga woolowa*. 10, tarsus IV (QM S1302); 11, tarsus III claws and hairs (holotype), scale line = 71  $\mu\text{m}$ ; 12, same, ventral, scale line = 83.3  $\mu\text{m}$ ; 13,  $\delta$  palp, prolateroventral, scale line = 50  $\mu\text{m}$ .





## PLATE 2

FIGS. 14-17 *Pitonga woolowa*. 14, cheliceral teeth and process (QM S1032), scale line = 50  $\mu$ m; 15, process with pore openings, short scale line = 5  $\mu$ m; 16, trichobothrial base metatarsus III (holotype), short scale line = 12.5  $\mu$ m; 17, tarsal organ tarsus III (holotype), short scale line + 10  $\mu$ m.





REVISION OF THE GENUS *MELITTOBIA* (CHALCIDOIDEA : EULOPHIDAE)  
WITH THE DESCRIPTION OF SEVEN NEW SPECIES.

EDWARD C. DAHMS  
Queensland Museum

ABSTRACT

This taxonomic revision of the genus *Melittobia* contains 2 new combinations, *Tachinobia diopsisiphila* (Risbec), *Cirrospilus (Atoposomoidea) cosmopterygi* (Risbec); a generic diagnosis; the redescription of 7 species, *clavicornis* (Cameron), *acasta* (Walker), *chalybii* Ashmead, *megachilis* (Packard), *hawaiiensis* Perkins, *australica* Girault and *bekiliensis* Risbec; description of 7 new species, *evansi*, *scapata*, *femorata*, *assemi*, *sosui* and one from Argentina not named because of lack of suitable specimens for type selection; synonymies, *strandii* Wolff and Krausse and *Anthophorabia fasciata* Newport become *acasta* (Walker), *japonica* Masi becomes *clavicornis* (Cameron), *sceliphronidis* (Brèthes) becomes *hawaiiensis* Perkins, *Tachinobia gradwelli* Bouček becomes *T. diopsisiphila* (Risbec); *osmia*e Thompson and *hawaiiensis peles* Perkins remain unidentifiable in the absence of types and definitive descriptions; figures and keys are provided to aid in identification of species.

MATERIALS AND METHODS

Specimen Mounting

The methods for mounting *Melittobia* are standards used for other Chalcidoidea involving air dried specimens glued to a card rectangle or cleared in 10% NaOH for mounting on a microscope slide.

Air drying specimens after mounting on a card results in totally collapsed specimens and alteration of subtle colour differences. Added to this is the problem of leaching in ethyl alcohol, e.g. after 12 months in 75% ethyl alcohol some specimens become off-white. Gordh and Hall (1979) reported excellent results using a critical point dryer for specimen preparation of Chalcidoidea before mounting. The procedure involves collecting specimens into 75% ethyl alcohol, slowly dehydrating with alcohol, substitution of liquid CO<sub>2</sub> for absolute alcohol under pressure, raising the temperature until the liquid CO<sub>2</sub> dissolves to gas and finally bleeding off the CO<sub>2</sub> gas. The result with *Melittobia* was beautifully inflated specimens with natural colours which then were mounted on card rectangles. Unfortunately, I have only had access to a critical point dryer for 12 months, therefore most of the specimens at my disposal for this revision were air dried and others were slightly leached because of storage in alcohol. Fortunately some are in very good condition. Notes on specimen preservation are given with the colour notes on each species.

Microscope slide preparations were made for each species depending upon availability of

specimens, e.g. in the case of *M. diopsisiphila* only 2 ♀♀, 1 ♂ exist and no slides were prepared. Wings were first removed from the specimens and placed in Euparal on a microscope slide. The head and body were soaked in 10% NaOH until clear then taken in 15 minute steps through 15% acetic acid, distilled water after which they were dehydrated in ethyl alcohol. When dehydrated they were transferred to a 1:1 mixture of absolute alcohol and Terpeneol and placed under an incandescent bulb until the ethyl alcohol had evaporated. Antennae, heads and bodies were separated and mounted in Euparal. This procedure is discussed more fully by Prinsloo (1980).

Figures

All figures except 1-3 were drawn from cleared, microscope slide-mounted specimens and each has the scale indicated. They were drawn with a camera lucida fitted to a Wild M20 compound microscope and constant magnifications were used for the same part or appendage of all species. Figures 1-3 were drawn from freshly killed, dry-mounted specimens with a camera lucida fitted to a Leitz TS stereomicroscope.

TERMINOLOGY

The terminology used follows that of de V. Graham (1969) except that the body is divided into head, mesosoma (thorax and propodeum) and metasoma (remainder of the abdomen). Figures 1-13 serve to illustrate the general

morphology of *Melittobia* species and the terminology used.

#### HISTORICAL RESUME

The genus *Melittobia* belongs to the chalcidoid family Eulophidae, sub-family Tetrastichinae. Ferrière (1960) grouped it with five other genera of tetrastichine eulophids on the basis of their common possession of a dorsoventrally flattened thorax and large pronotum (*Crataepoides* Zinna, 1955; *Crataepus* Förster, 1878; *Aceratoneuromyia* Girault, 1917; *Pronotalia* Gradwell, 1957; *Crataepiella* Domenichini, 1956). Peck, Bouček and Hoffer (1964) sank two of these — considering *Crataepoides* a junior synonym of *Elachertus* Spinola, 1811 and *Pronotalia* a junior synonym of *Crataepiella*.

Domenichini (1966) divided the Tetrastichinae into two tribes; the Tetrastichini with a genal sulcus and Melittobiini without a genal sulcus. The latter comprised *Melittobia*, *Aceratoneuromyia*, *Crataepus* and *Crataepiella* — the four genera from Ferrière's grouping above. In the same year, Bouček described *Kocourekia* and placed it with genera lacking a genal sulcus. Bouček (1977) described the genus *Tachinobia* and although he made no reference concerning its tribal placement it clearly fits with these genera as the description mentions the lack of a genal sulcus.

None of these treatments take into account many of Girault's genera except *Aceratoneuromyia*. Of the large number of genera described by Girault from Australia, it is not known if any more could be placed in the group lacking a genal sulcus. A revision of Girault's eulophid genera is presently being undertaken by Dr. Bouček. Clarification of this point therefore rests with him.

In summary then, we have six tetrastichine genera, *Aceratoneuromyia*, *Crataepus*, *Crataepiella*, *Kocourekia*, *Melittobia* and *Tachinobia*, grouped on the absence of a genal sulcus. *Crataepus* separates out easily because of the possession of a longitudinal median groove on the mesoscutum and two fore tibial spurs. The six genera show variation in the presence or absence of facial and ocellar lines, and delimitation of the vertex (a groove between the posterior ocelli and the eyes). Facial lines converging from the vertex or ocellar area to the scrobes occur in all except *Kocourekia*. The ocellar area is delimited into an ocellar plate by a groove in *Melittobia* and *Crataepiella*. All genera except *Aceratoneuromyia* have a delimited vertex. Bouček (1977) in his description of *Tachinobia*

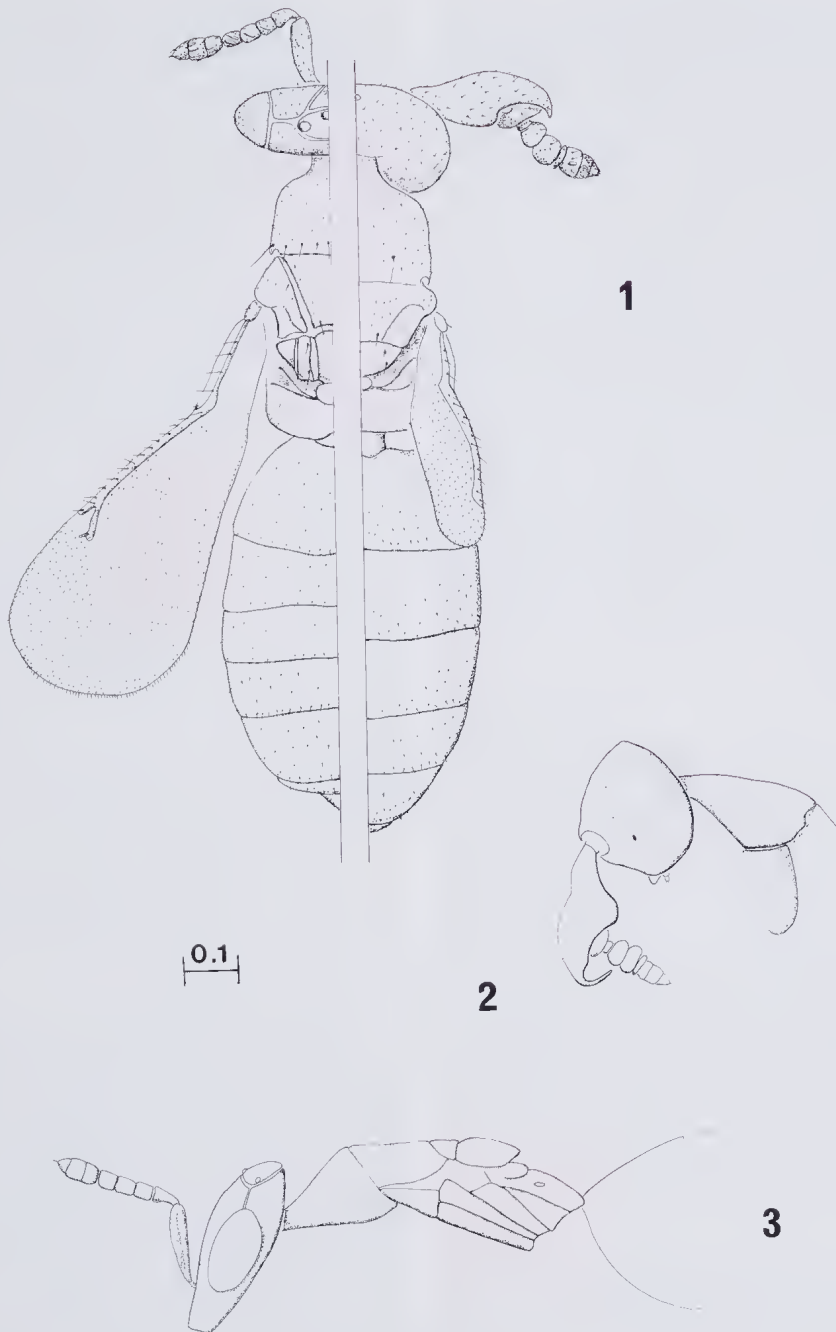
does not mention whether it has a delimited vertex, but his figure of the dorsal aspect of the female's head shows it to be not delimited. In ethyl alcohol preserved specimens of *T. repanda*, the type-species, the vertex is clearly delimited. In facial, ocellar and vertex grooves therefore *Melittobia* most closely resembles *Crataepiella*. The genera also vary in the number of grooves on the scutellum. In *Tachinobia* there are no grooves; *Kocourekia* and *Aceratoneuromyia* have 2 sub-lateral grooves; *Melittobia*, *Crataepus* and *Crataepiella* have 2 sub-lateral and 2 sub-median grooves.

Except for *Kocourekia* all of the genera are known from both sexes. Of these *Melittobia* and *Tachinobia* show pronounced sexual dimorphism with the males greatly modified. Male *Melittobia* are brachypterous with eyes reduced to a single spot whereas male *Tachinobia* are apterous with eyes reduced to several facets. In both, the antennal scapes of the male are greatly enlarged. *Tachinobia* males have a strongly inflated scape with a large clear area ventrally (Fig. 15). The scape of male *Melittobia* is also swollen but with a ventral groove, a cup-shaped depression or hardly grooved at all with a large ventral clear area (Figs 16-19). In the remaining genera, where males are known, they closely resemble the females, are macropterous and have scapes only slightly modified, if at all.

There are other features which separate the genera, e.g., the number of teeth on the mandibles, the degree of flattening of the prothorax, setation and so on. Bouček (1977) gave a tentative key to the Tetrastichinae which separates all six genera very well.

This taxonomic revision arose out of the necessity to establish the identity of a species of *Melittobia* whose biology and behaviour was under study Dahms (1983a). Comparison of my specimens with the type of the single Australian species, *M. australica* Girault, 1912, showed that they were conspecific. However, establishing the validity of Girault's species proved much more difficult as the following account from the literature reveals.

The generic name *Melittobia* Westwood (1847) arose in an atmosphere of confusion because of an argument between Mr G. Newport and Mr. J.O. Westwood over the authorship of this new genus. In 1849 the argument surfaced in the form of a series of letters from the two antagonists to the editors of the *Annals and Magazine of Natural History* published in that journal. The first letter was written by Newport in which he claimed to have been studying the insect since



FIGURES 1-3, *Melittobia australica*. 1 — Dorsal view female and male; 2 — side view male head; 3 — side view female head and mesosoma.

1832 and implied plagiarism by Westwood. However, Newport did not publish a description of the species until 1849 when he called the genus *Anthophorabia* and the species *retusa* after the host *Anthophora retusa* Le Peletier and Serville. His description was preceded by Westwood (1847) in his 'Introduciton to the Classification of Insects' where he mentioned the same species from specimens forwarded to him by Mr Audouin from the nests of *Odynerus*, *Anthophora* and *Osmia*. Westwood also exhibited these specimens in 1847 to the Entomological Society of London and a brief descriptive note appeared with the name *Melittobia audouinii* in that Society's Proceedings for 1847. He later published a more formal description in the *Proceedings of the Linnean Society* in 1849.

Of the two generic names *Melittobia* stands, but neither specific name stands because both had been preceded by Walker who described the species as *acasta* in 1839 and incorrectly assigned it to the genus *Cirrospilus* basing his description on a male that was in fact a female. From all of this, the genus is *Melittobia* Westwood 1847 and the type-species *Cirrospilus acasta* Walker 1939 by synonymy.

Although this confusion was removed fairly early (Smith (1853); Dalla Torre (1898)) further confusion has arisen at the species level. This appears to be related to the relative uniformity of the females. Ferrière (1933) thought it probable that several of the described species were synonyms of *M. acasta* or *M. hawaiiensis*. Examination of females of the various species shows they are difficult to separate and leads one to agree with Ferrière. However, if the greatly modified males are examined, it is clear there are more than two species. Males do not emerge from the host cell or puparium, therefore females are more commonly encountered and their apparent uniformity has led to many misidentifications, not only in collections, but also in the literature, e.g., the name *M. chalybii* Ashmead has been applied to at least 2 species of *Melittobia* from North America, neither of which is the true *M. chalybii*.

Perusal of the literature revealed 13 described species at the start of this revision. In addition there are *M. peloepi* Ashmead, 1892 (published

without a description which means it is a nomen nudum) and *M. hawaiiensis peles* Perkins, 1907. Of the 13 species, 9 are known from both sexes and the remainder from females only. The initial goal was to build up a collection of species based on associated sexes and to use the males to separate species. Decisions were checked against notes on courtship behaviour generously provided by Dr van den Assem from his own work on this aspect of the genus. When the males were suitably sorted, females were checked for reliable morphological differences.

As a result of this study I am recognising 7 of the previously described species *M. clavicornis* (Cameron), *M. acasta* (Walker), *M. chalybii* Ashmead, *M. megachilis* (Packard), *M. australica* Girault, *M. hawaiiensis* Perkins and *M. bekiliensis* Risbec. Two of the three species described by Risbec were incorrectly placed by him in the genus *Melittobia*. *M. cosmopterygi* I have transferred to *Cirrospilus* Westwood and *M. diopsisiphila* to *Tachinobia* Bouček. Four new synonymies occur; *M. japonica* Masi becomes *M. clavicornis* (Cameron), *M. sceliphronidis* (Brèthes) becomes *M. hawaiiensis*, *M. strandi* Wolff and Krausse and *M. fasciata* (Newport) become *M. acasta* (Walker). This leaves *M. osmiae* Thompson and *M. hawaiiensis peles* Perkins neither of which can be placed in the absence of diagnostic descriptions, and I have not been able to locate type-material.

Seven new species are described: *M. scapata*, *M. evansi*, *M. femorata*, *M. digitata* (from North America); *M. assemi* (Seychelles); *M. sosui* (Japan); and a new species from Argentina for which no types can be selected because the specimens are fragmentary.

As a result of ethological work, van den Assem (pers. comms., 1974-81) and van den Assem and Maeta (1978, 1980) divide the genus into species groups: *acasta* group, *hawaiiensis* group and Mahé (*assemi*) group. They regard *M. clavicornis* as the most primitive and keep it separated from these groups. Using morphological grounds the species separate easily on males into the same groups and this is discussed more fully later. For the purposes of the following discussions the species groupings are as follows:

#### ACASTA GROUP

*acasta*  
*evansi* sp. nov.  
*scapata* sp. nov.  
*digitata* sp. nov.  
*femorata* sp. nov.  
*megachilis*  
*chalybii*

#### HAWAIIENSIS GROUP

*hawaiiensis*  
*australica*  
Kauai

#### ASSEMI GROUP

*assemi* sp. nov.  
*sosui* sp. nov.  
*bekiliensis*  
SP. NOV. Argentina



## INTRODUCTORY MORPHOLOGY

Sexual dimorphism in the genus is so extreme that the sexes cannot be associated by morphology alone (Fig. 1). Males are greatly modified and the modifications, involving appendages and body regions, can be related to the restriction of male activity to reproduction, i.e. fighting, courting and mating.

Females are a fairly typical tetrastichine eulophid form with fully developed wings and eyes except in the case of second-form females (see under Polymorphism Dahms, 1983a). They show no gross modifications for courtship and their most marked features are probably related to host seeking in confined spaces and excavation into or out of host enveloping membranes, e.g., enlarged prothorax and dorsoventral flattening of the body. In addition, the head is anteroposteriorly flattened and it articulates with the prothorax close to the vertex which allows the head to fold back almost in the same plane as the body (Fig. 3). The antennae are inserted low on the head and can be pushed forwards when the head is in the flattened position.

Males show a greater range of easily discernible, reliable, morphological features for separation of most species. They are brachypterous, lack compound eyes and are less pigmented than females (Fig. 5). These reductions are related to their not emerging from the host cocoon or puparium. Modifications have taken place to heads, antennae and legs, and these are related to the function of these parts in courtship and fighting. Variations in these modifications are related to specific variations in courtship repertoires.

At the generic level, the male scape is expanded, with a ventral groove or cup and is open distally (Figs 16–19). The groove or cup is used to house the female's antenna during courtship. Covering the distal opening of the scape is a flap-like pedicel which is used in manipulations of the female's antenna. The funicle is four-segmented with specific variation in the relative proportions of the segments (Figs 12, 187, 190, 193, 196, 199, 202, 205, 208, 213, 216, 219). Females have a funicle composed of three relatively uniform segments (Fig. 9).

In frontal aspect (Figs 5, 151–160) the male head is shorter than that of the female (Figs 38–48); the eyes are reduced to single spots, and the ocelli, although present, may be faint. In lateral aspect (Fig. 2) the head is greatly inflated in comparison to that of the female. This can be related to the need for large muscles to carry out

the complicated courtship movements of the enlarged scape and for effective use in combat of the relatively larger mandibles. The prothorax remains large but the remainder of the mesosoma is reduced in correlation with the reduced wings and inability to fly.

Legs play an important part in courtship behaviour. The fore tarsi are used to hold the female by the neck. Fusion of tarsal segments 3 and 4 on the fore leg has occurred in most species, but there is fusion of 2, 3 and 4 in one group and fusion of all segments in another (Figs 20–22). There is a curving of the fused parts of segments 3 and 4 to accommodate the neck of the female. Mid legs are used by all species during all or part of the proceedings and the posterior, ventral surface of the mid femur in all species bears a very long fringe of setae. In some species a long fringe of setae also occurs on the mid trochanter ventrally. These setae appear to be used to brush the female's body during courtship. Their pattern and distribution varies between species (Figs 220–230).

The genitalia of males show very little variation except in size and are of little use taxonomically.

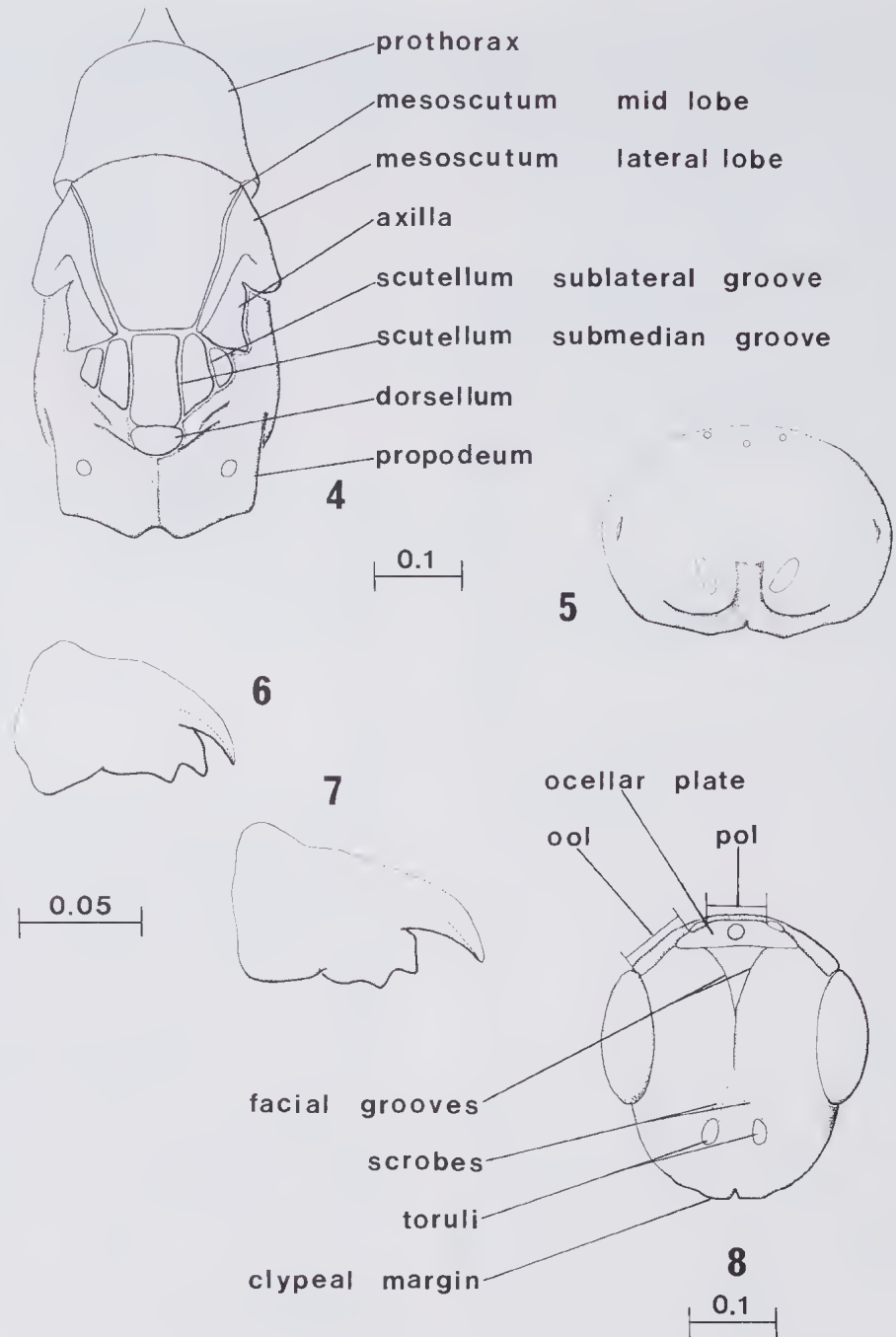
## REVISION

### Introductory Remarks

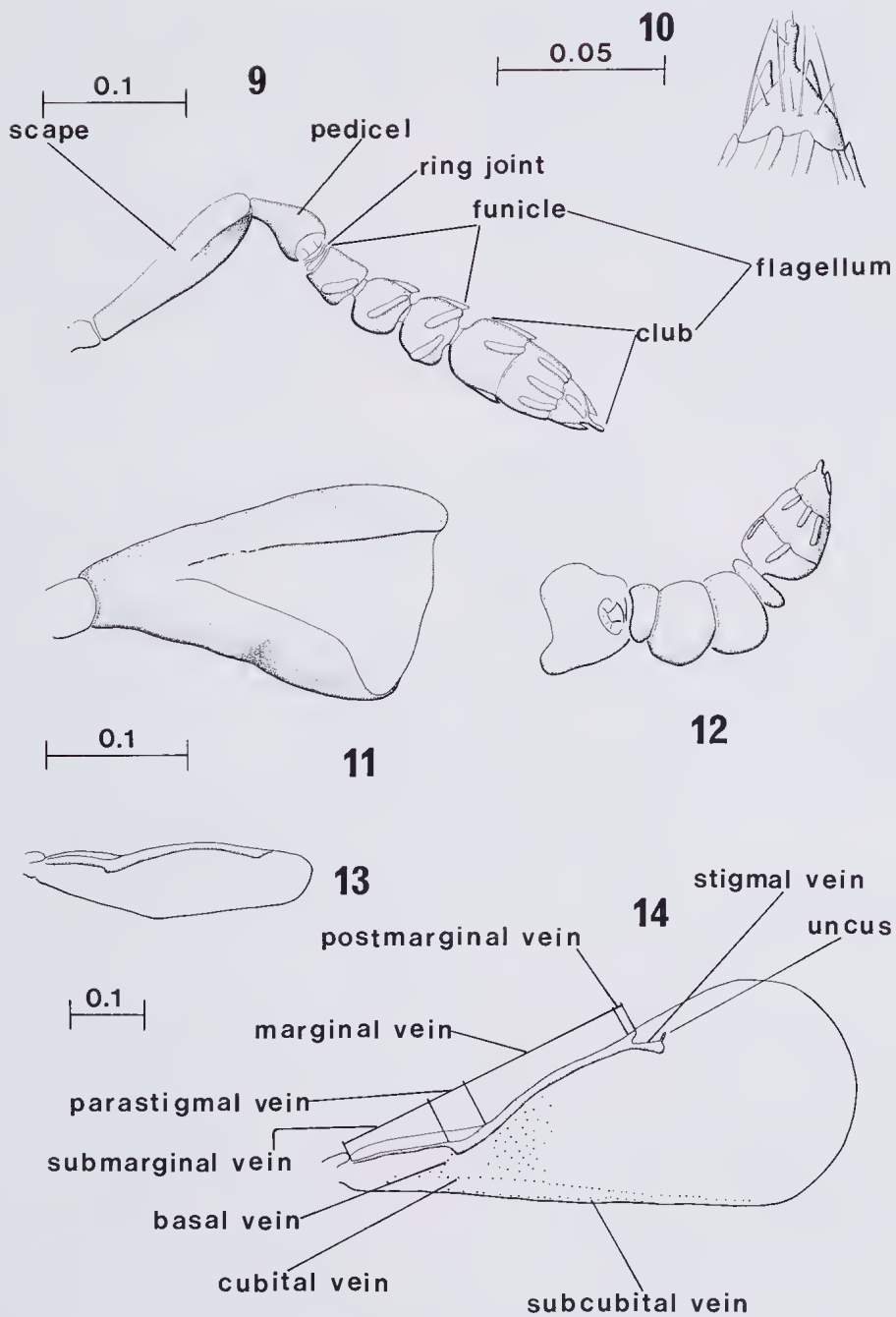
One of the major difficulties in dealing taxonomically with the genus was the apparent uniformity of females. This is mostly due to the gross distortion of the body of females on drying so that differences in the relative proportions of head and mesosoma could not be appreciated. Added to this has been the use by authors of unreliable characters e.g. many aspects of setation. This is again complicated by the description of a few species from the female sex only e.g. *M. megachilis* and *M. japonica*.

As discussed under Introductory Morphology, males show a great range of morphological features for separation of species and by obtaining sexes bred out together it has been possible to separate females of the different species. Distortion of females on drying was overcome by using a critical point dryer (Gordh and Hall, 1979), and several useful proportional features were revealed. In addition colours were preserved without fading, provided the specimens have not been kept for too long in ethyl alcohol. Preparation of microscope slides has allowed appreciation of differences in clypeal margins, antennae, palps, mandibles and wing venation in both sexes.

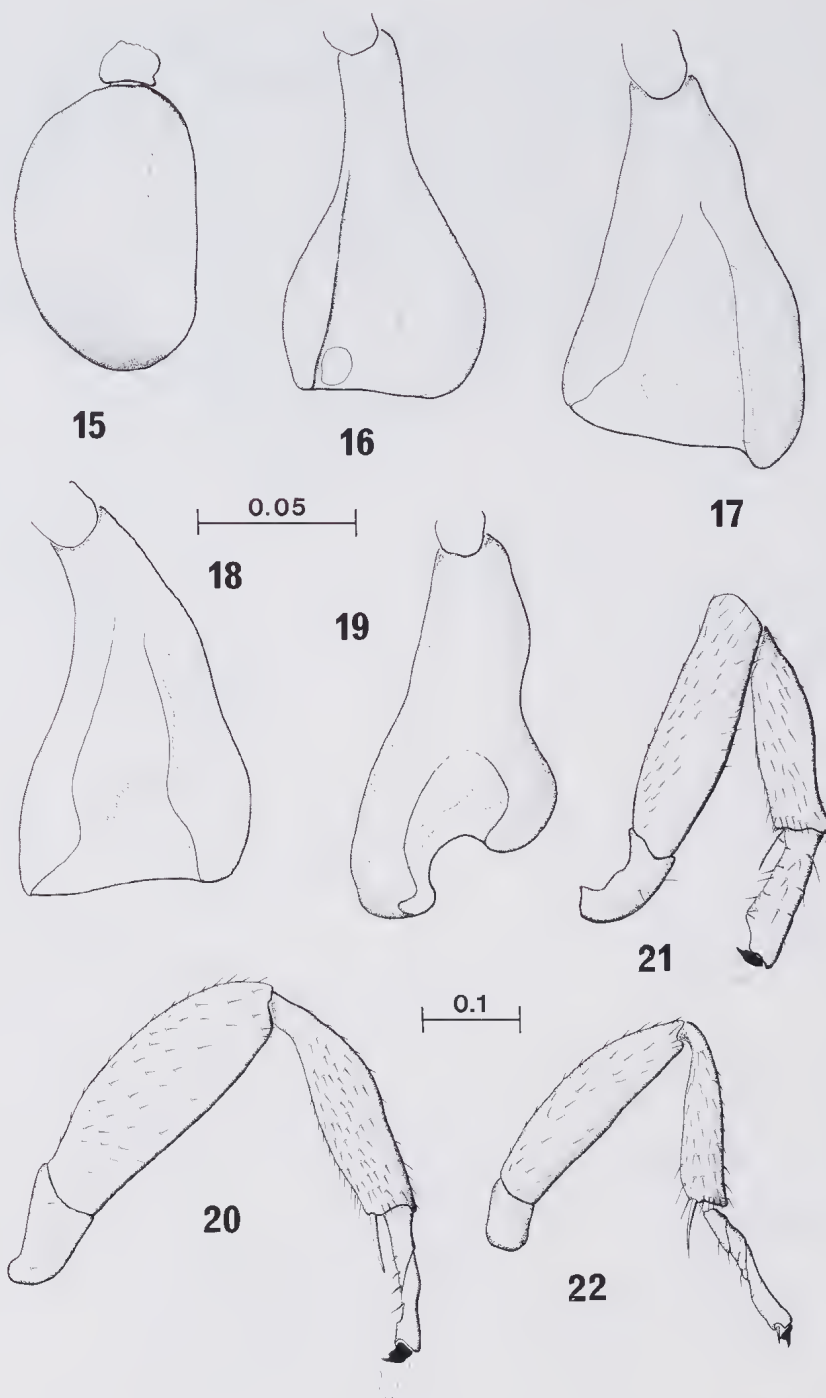
In spite of these techniques, difficulties still exist. Colours vary with the method of



FIGURES 4-8, *Melittobia australica*. 4 — Dorsal female mesosoma; 5 — Frontal aspect, male head; 6 — Female mandible; 7 — Male mandible; 8 — Frontal aspect, female head; POL = posterior ocellar line, OOL = ocellar — ocular line.



FIGURES 9-14, *Melittobia australica*. 9 — Female antenna; 10 — Club segment 3, female antenna; 11 — Male scape; 12 — male pedicel plus flagellum; 13 — Male wing; 14 — Female fore wing.



FIGURES 15-19, Male antennal scapes. 15 — *Tachinobia repanda*; 16 — *Melittobia clavicornis*; 17 — *Melittobia australica*; 18 — *Melittobia assemi* (sp. nov.); 19 — *Melittobia acasta*.

FIGURES 20-22, Male fore legs, *Melittobia* spp. 20 — *assemi* (sp. nov.); 21 — sp. nov. Argentina; 22 — *australica*.

preservation, for example, in older air-dried specimens males tend to become a fairly uniform brown whereas in fresh material subtle infuscations and colour differences occur. Prolonged preservation in alcohol causes leaching of specimens converting dark browns to pale yellows. Hence in this part of species descriptions to follow mention is made of the method of preservation as a reference point for comparison and future descriptions. Although critical point drying has removed the problem of shrinkage there is still a tendency for the heads of females to fold transversely along the line in front of the ocellar plate. This occurs also in some males, which gives a false impression of head shape and proportions. For this reason all L:W proportions were taken from slide mounted specimens. Care was exercised in the preparation of slide material not to over-inflate the specimens during clearing and critical point dried specimens were used as a check that this did not happen. The only L:W proportion not taken from slides is that of the prothorax.

In males, most of the characters that proved useful in separating species have functional significance in courtship. The following features were of use: head shape (frontal and lateral), clypeal margins, mandibles, palps, antennal scapes (plus shape and position of pheromone gland, Dahms (1983b)), relative proportions of funicle segments, distribution of multiporous plate sensilla on the flagellum (MPS formula), presence or absence of a short setal tuft ventrally on the fore trochanters, presence or absence of a very long setal tuft ventrally on the mid trochanters, distribution and differentiation of the long setal fringe ventrally on the mid femora, shape of fore wings, shape of stigmal vein if present. In general, the male mesosoma in dorsal aspect lacks many of the sutures present in the female except for *M. clavicornis* where all are present.

In females, the differences useful for separating species appear to have no functional differences related to courtship except perhaps setation of the eyes and the breadth of separation of the facial grooves (Courtship Dahms, 1983a). The following features were of use: head shape and proportions in frontal aspect, eye setation, degree of convergence of the frontal lines and the distance apart of the upper arms, scrobe length, clypeal margins, mandibles, palps, antennal scape proportions, scape and pedicel colour, number of multiporous plate sensilla per segment of flagellum (MPS formula), position of

subterminal seta on terminal nipple of club segment 3, proportions of nipple, mesosomal proportions and sculpture patterns in dorsal aspect, number of setae on scutellum, wing shape, ratio of submarginal to marginal vein length, and shape of stigmal vein.

Stigmal veins of females show slight variations in each species and the figures 127-139 are of the most common shape. Apart from the usefulness of the nipple on club segment 3 and the setae on this nipple in females, the proportions of the segment itself proved useful. Since the margin between club segment 2 and 3 is undulating, the proportion is worked out on the shortest length and the ratio becomes shortest length to width.

The MPS formula is slightly variable ( $\pm 1$ ) and the figures given in the descriptions represent the maximum counted for 4 antennae in each species. Care should be exercised when counting them as those on the margins of a segment can be easily overlooked and those which wrap around segments (as in female funicular segments) may be counted twice. In all cases descriptions are based upon the type-form only (Polymorphism Dahms, 1983a). Holotype and lectotype selection where possible has been made on the male since, of the sexes, this is the more distinctive.

References given at the start of each description are taxonomic only. Those dealing with biology occur in Dahms (1983a) as do references to recorded hosts. The following abbreviations are used for institutions.

- ANIC: Australian National Insect Collection, C.S.I.R.O., Canberra; Australia.
- BM(NH): British Museum of Natural History, London, England.
- CU, NY: Cornell University, New York, USA.
- DPIQ: Queensland Department of Primary Industries, Brisbane.
- DSIR: Department of Scientific and Industrial Research, Christchurch, New Zealand.
- HDA: Hawaiian Department of Agriculture, Honolulu, Hawaii.
- KU: Kyushu University, Kyushu, Japan.
- MCZ: Museum of Comparative Zoology, Harvard, USA.
- MDA: Museum de La Plata, La Plata, Argentina
- MNHP: Musée National d'Histoire Naturelle, Paris, France.
- NMC: National Museum (Nat. Hist.), Prague, Czechoslovakia.
- QM: Queensland Museum, Brisbane, Australia.

- UCR: University of California, Division of Biological control, Riverside, California, USA.  
 UG: University of Georgia, Athens, Georgia, USA.  
 USNM: United States National Museum, Washington D.C., USA.

#### NEW COMBINATIONS

Two species previously referred to the genus *Melittobia* were found to be misplaced. These are redescribed in their correct genera.

#### GENUS *TACHINOBIA* BOUČEK 1977

Type-species: *Tachinobia repanda* Bouček, 1977 : 27.

*Tachinobia diopsisiphila* (Risbec, 1956)

(Figs 23, 24, 26-31)

*Melittobia diopsisiphila* Risbec, 1956 : 118.

*Tachinobia diopsisiphila* (Risbec). COMB NOV  
*Tachinobia gradwelli* Bouček, 1977 : 28. SYN NOV

This species, only known from females, can be readily separated from the genus *Melittobia* by the following features: head slightly wider than long, vertex almost flat, non-delimited ocellar area, upper facial lines wider than posterior ocelli, shape of clypeus and mandible, pronotum shorter than wide, undifferentiated setae on the mid lobe of mesoscutum, scutellum lacking submedian and sublateral grooves, wings with relatively longer setation and postmarginal vein barely developed or absent.

There is considerable agreement between Risbec's specimens and the description of *T. gradwelli* by Bouček (1977); lower frontal lines separated by twice the diameter of the median ocellus and meeting distinctly below the middle of the eyes, malar space almost equal to mouth breadth, antennal toruli below lower eye margin; setation on dorsal mesosoma more sparse and shorter than *T. repanda*, the type species, fore wings about 2.8 times longer than wide, stigmal vein not much longer than the longest marginal fringe. I have subsequently examined the holotype of *T. gradwelli* and confirmed this synonymy.

Dry and slide mounted specimens of *T. diopsisiphila* clearly show the vertex delimited by a groove passing from the eyes to the ocelli. In his description of the genus *Tachinobia*, Bouček (1977) makes no mention of a groove across the vertex and his figure of the dorsal head of *T. repanda* does not show a groove. Slide mounted material I have made of *T. repanda* do not show

this groove either. However, examination of ethyl alcohol specimens of *T. repanda* clearly show this groove (Fig. 25) and dry specimens of an undescribed species (USNM Collection) also have this groove. This feature should therefore be added to the generic description of *Tachinobia*.

#### MATERIAL EXAMINED

Holotype ♀, '*Tachinobia gradwelli* Bouček (1977)', 'Venezuela, Estado Aragua Turmero 500 mts, xii.1948, H.E. Box', 'Hyper of *Paratheresia claripolopus* (Wulp) ex *Diatraea lineolata* (Walker) in *Zea mays*'.

Four microscope slides containing a total of 24 specimens dry-mounted under coverslips sealed with wax. I have remounted 6 specimens from 2 slides either on cards or in Euparal on the original slides. Details of the labels and remounts are as follows:

- 1) *Melittobia diopsisiphila* Risbec ex dipt. par. de *Diopsis thoracica*, Garoua 12.54, Descamps 213'. (2 ♀♀ cleared and remounted in Euparal on the original slide) (Garoua is in the Cameroon, W. Africa).
- 2) *Melittobia diopsisiphila* Risbec, epip. de *Diopsis thoracica* ex dip. par., Descamps 200, Garoua'. (15 ♀♀ under one coverslip and a fragmentary head under a separate coverslip).
- 3) *Melittobia diopsisiphila* Risbec ex pupa *Pachylopus* sp., Descamps 243, Garoua, 3.54'. (4 ♀♀ remounted; 2 separately on cards, one of which is selected as lectotype, the remaining 2 cleared and mounted in Euparal on the original slide).
- 4) as (3). (7 ♀♀).

There is some disparity between Risbec's published notes and the information on his labels; notably the lack of the name *Steleocerus lepidopus* Becker on his labels and absence of the label name *Pachylopus* in his published account. Neave (1939) lists *Pachylopus* as a genus of Coleoptera which seems doubtful as a host. A few names before *Pachylopus* in Neave is *Pachylopus* a genus of Chloropidae which is more likely to be the true host. *Steleocerus lepidopus* is not mentioned on the labels, but is a chloropid fly. My examination of the series shows 24 specimens plus some cylindrical debris which Risbec may have counted to bring his total to 25. I feel that these 4 slides represent his syntypical series of *T. diopsisiphila* with some error with respect to the chloropid host. From this series a lectotype has been selected and card mounted on a pin. The remaining specimens are on slides and selected as

paralectotypes. Labels have been attached indicating these selections and the specimens reside in the collections of the Musée National d'Histoire Naturelle, Paris.

GENUS *CIRROSPILUS* WESTWOOD, 1832

Type-species: *Cirrospilus elegantissimus* Westwood, 1832

*Cirrospilus* (*Atoposomoidea*) *cosmopterygi* (Risbec)

(Figs 32-37)

*Melittobia cosmopterygi* Risbec, 1951 : 90

*Cirrospilus* (*Atoposomoidea*) *cosmopterygi* (Risbec, 1951) COMB. NOV.

Females of this species are readily separated from the genus *Melittobia* by their colouration, lack of facial grooves, non-delimited ocellar area, non-emarginate clypeus, antennal insertions above lower margins of eyes, 2 segmented funicle, terminal style of club without a terminal seta and with more than 3 subterminal setae, scutellum squarish with only 2 longitudinal grooves, wings with admarginal setae, long marginal fringe and relatively longer discal ciliation on the fore wing.

The black and yellow colouration is typical of *Cirrospilus*. Using Peck, Bouček and Hoffer (1964) the species keys readily to *Cirrospilus* (*Atoposomoidea*). De V. Graham's key (1959) also easily places the species in *Cirrospilus*. Risbec (1951) in his collecting data states that *C. cosmopterygi* was bred from leaf mining lepidopterous larvae; a typical host of *Cirrospilus*. This type of host is not recorded for *Melittobia*.

There has been some difference of opinion as to the status of *Atoposomoidea*, e.g. Delucchi (1958) treats *Atoposomoidea* as a genus. Other workers, e.g. De V. Graham (1959), Bouček (1959) and Kerrich (1969) place it as a sub-genus of *Cirrospilus*. This question is beyond the scope of the present work and it has been decided to follow the direction of Bouček (1959) and leave it as a sub-genus of *Cirrospilus*.

The following redescription has been based upon the syntypical material of Risbec; no other specimens being available. The two females are not cleared and are badly flattened on a microscope slide.

Female: 1.4 mm long; head, antennae brown; mesosoma yellow with black markings (Fig. 33); legs yellow; wings hyaline; metasoma yellow with 2 transverse black bands dividing

metasoma equally into thirds.

Head in frontal aspect (Fig. 32); 0.3 mm wide, length to width about 1:1; vertex collapsed, clearly elevated above eyes, not immargined, not vaulted as in *Zagrammosoma* Schulz; POL approximately equals OOL. Eyes dark, probably red in life, oval, sparsely pilose, closer to vertex than clypeus. Clypeus concave, not emarginate. Antennae (Figs. 34, 36); inserted above level of lower eye margins; scape cylindrical, 3.25 times longer than wide, slightly arched in lateral view; pedicel expanded distally, equal to funicle 1; ring joint compound, of several lamellae; funicle 2-segmented, 1 and 2 cylindrical, equal in length; club 3-segmented, 1 and 2 cylindrical, equal in length, 3 shorter, conical bearing a terminal style with 5 subterminal setae but without a terminal seta. Head lateral and dorsal aspects not visible.

Mesosoma (Fig. 33) in dorsal aspect; pronotum large, slightly wider than long, campanulate; posterior border with four large setae, inner pair closer to one another than to pair at posterior lateral angles. Mesoscutum with clearly defined, sigmoidal parapsidial sutures; mid lobe with 2 pairs of long setae, anterior pair finer and closer together than posterior pair; axillae advanced; scutellum large, wider than long, more angular than in *Melittobia*, posterior margin convex; one pair of sublateral grooves anteriorly in line with posterior parapsidial sutures; 2 pairs of long setae situated on the lateral lobes; 1 pair about mid-way and 1 pair on posterior margin. Dorsellum triangular, apex directed posteriorly, base anteriorly convex. Propodeum appears shallowly inclined, without carinae, length at mid line approximately 1/6 width at posterior lateral angles. Wings hyaline (Fig. 35); fore wings about 2.6 times longer than wide, costal margin almost straight, slightly curved at junction of parastigmal and marginal veins; submarginal 0.27 mm long, postmarginal 0.04 mm long, stigmal 0.06 mm long; submarginal veins with 6 long, erect setae in both specimens; costal cell with 9-10 setae ventrally plus two anterolateral setae dorsally; discal ciliation even, moderately long; 8 long, admarginal setae posteroventrally of marginal vein; marginal fringe long. Hind wing narrow, 0.75 mm long × 0.09 mm wide; apex acute; marginal fringe longer than fore wing marginal fringe;

stigmal vein absent. Lateral aspect not visible.

Metasoma in dorsal aspect, ovoid, 0.69 mm long  $\times$  0.35 mm wide, more acute posteriorly; ovipositor over half length of metasoma, not extruded. Lateral aspect not visible.

Male: Unknown

#### MATERIAL EXAMINED:

One slide bearing 2 ♀♀, 2 pupal cuticles plus one pupa '*Melittobia cosmopterygi* Risbec, Syntypes; Eulophinae, G.B., ex *Cosmopteryx attenuatella*, III .77'.

In his paper, Risbec (1951) gives the locality as M' Bambey, Senegal, and mentions further specimens from *Cosmopteryx* in Niebe. However, he goes on to state that the Niebe material was not in his possession at the time of description. I have been unable to locate the Niebe material and have taken the slide above to include the entire syntypical series. The two specimens on this slide fit Risbec's description of *C. cosmopterygi*. The specimen closest to the Risbec label is selected as the lectotype and the other as the paralectotype. The slide has been labelled accordingly and it is to be found in the collections of the Musée National d'Histoire Naturelle, Paris.

#### GENERIC DIAGNOSIS

##### GENUS *MELITTOBIA* WESTWOOD, 1847

Type-species: *Cirrospilus acasta* Walker, 1839 by synonymy with *Melittobia audouinii* Westwood, 1847

*Melittobia* Westwood, 1847. Type-species, *Melittobia acasta* (Walker, 1839) by synonymy.

*Anthophorabia* Newport, 1849. Type-species, *Anthophorabia retusa* Newport by monotypy.

*Philopison* Cameron, 1908. Type-species, *Philopison clavicornis* Cameron, 1908 by monotypy.

*Sphecophagus* Brèthes, 1910. Type-species, *Sphecophagus sceliphronidis* Brèthes, 1910 by monotypy.

*Sphecophilus* Brèthes, 1910. 311, new name proposed for *Sphecophagus*, Brèthes.

#### Generic Description:

Female: Black to dark brown, shining in most species; moderately setose; 1-1.6 mm long.

Head in frontal aspect (Figs 38-48); variable in shape, about as long as wide with alutaceous sculpturing in most species; vertex elevated above eyes, rounded; facial grooves present, converging ventrally to antennal scrobes, distance between upper arms and degree of convergence variable; antennal scrobes shallow, area between slightly raised; clypeus mostly bilobed, rarely truncate emarginate (Figs 59-69); mandibles (Figs 49-58) tridentate, anterior tooth the largest, acute; palps 1-segmented (Figs 70-81). In lateral aspect (Fig. 3); very narrow, converging ventrally; eyes oval, longer than wide; genae well developed, genal sulci absent. In dorsal aspect ocelli arranged in a shallow triangle positioned on an ocellar plate delimited by grooves; vertex with transverse grooves connecting the ocellar plate to the eyes. Antennae (Figs 82-101); 8 segmented plus 1 compound ring joint, inserted below eyes; toruli closer to one another than to eyes; scape nearly reaching top of eyes, elongate, slightly expanded distally, dorsoventrally flattened, ventrally slightly concave; pedicel pyriform, sub-equal to funicle 1; ring joint thin, compound, of 4 lamellae; flagellum dorsoventrally flattened; funicle 3-segmented, segments sub-equal, about as long as wide, all bear MPS; club 3-segmented, all bearing MPS, segment 2 longest, segment 3 shortest (Figs 102-114), conical with terminal nipple, in some species nearly as long as segment 3; terminal nipple with 2-3 setae shorter than nipple, 1 terminal, the others of variable position from 1/2 way down nipple to base.

Mesosoma in lateral aspect (Fig. 3) relatively flat, prothorax triangular. In dorsal aspect (Figs 1, 4) prothorax large, slightly wider than long, campanulate, posteriorly fringed with relatively long, recurved setae; mesoscutum without a longitudinal median groove, parapsidal sutures well defined; mid lobe contracting posteriorly, posterior margin truncate with 1 large recurved seta at each posterior lateral angle; axillae advanced, acute anteriorly, well defined on mesoscutal and scutellar margins; scutellum transverse, submedian and sublateral grooves present, evenly spaced, inner lobe bearing at least 1 pair (rarely more) of large, recurved setae along outer margin of each submedian groove; dorsellum well defined in non-collapsed specimens, ovoid; propodeum



normally developed, wider than long, not steeply inclined, without a median, longitudinal carina; spiracles freely exposed, round; legs normal, fore and hind coxae the longest, hind coxae the broadest; fore wings (Figs 115–126); normal tetrastichine type, hyaline, discal ciliation evenly scattered, setal lines occur along basal, cubital and subcubital vein positions; submarginal vein shorter than marginal, with 4–6 long setae; postmarginal vein poorly developed; marginal vein fringed with long setae which extend to end of postmarginal vein; remainder of wing around apex to distal subcubital setal line fringed with short setae, the fringe longest on posteroapical margin; stigmal vein short (Figs 127–139), just longer than postmarginal; uncus well developed; hind wings narrow, apex acute; postmarginal and marginal vein not developed; fringed with very long setae from end of marginal vein around apex and along posterior margin. Metasoma elongate, sides sub-parallel, segments of fairly even size; ovipositor not exerted.

Male: Brachypterous, 1.0–1.5 mm long, dark brown to honey yellow in colour.

Head in frontal aspect (Figs 151–160) variable in shape, inflated, wider than long in most species, facial lines absent; clypeus mostly bilobed, rarely truncate emarginate; mandibles tridentate, anterior tooth as in female but much larger (Figs 161–173); palps 1 segmented (Figs 174–184). In lateral aspect (Fig. 2) greatly inflated; eyes reduced to scar-like spots; genal sulcus absent. In dorsal aspect (Fig. 1) ocelli variously reduced; delimiting lines around ocelli and across vertex absent in most species. Antennae (Figs 185–219) greatly modified, 9 segmented, in some a 10th appearing at ring joint (Fig. 202); scape enormously developed, longer than pedicel plus funicle, pyriform to subpyriform, ventrally with either a groove running full length or a distal cup-shaped depression; pedicel produced laterally to form a cap over the distal end of the scape groove or cup; ring segment, compound, thin or in some cases expanded; funicle 4 segmented, with or without plate organs, size and shape of segments variable; club 3-segmented, segments of variable size, terminal segment with a small terminal nipple hardly differentiated in some species; terminal nipple with 2 setae.

Mesosoma of different proportions from female (Fig 1); in lateral aspect flattened, prothorax triangular. In dorsal aspect prothorax large, wider than long, campanulate, posteriorly fringed with relatively long recurved setae, mesoscutum reduced, much wider than long, parapsidal sutures in most species indefinite anteriorly; 1 pair of strong recurved setae on posterior margin; axillae poorly delimited in most species; scutellum in most species without submedian or sublateral grooves, with 4 (rarely more) stiff recurved setae; dorsellum well defined in non-collapsed specimens, more rounded than in female; propodeum well developed, not steeply inclined, smooth, median longitudinal carina absent; spiracles freely exposed, rounded; legs sturdier than in female, fore coxae broad, fore tarsi with at least segments 3 and 4 fused; mid tibiae and in some species mid trochanters ventrally fringed with long setae (Figs 220–230); fore wings reduced (Figs 231–241), of variable width, never longer than mesosoma; marginal vein longer than submarginal; postmarginal and stigmal veins poorly developed; long stiff setae along submarginal and marginal veins, hind wings very reduced, elongate; postmarginal and stigmal veins absent, setation reduced.

Metasoma (Fig. 1) in lateral aspect arched; in dorsal aspect ovoid in life becoming flattened on drying; segments evenly proportioned.

#### Keys for Identification

##### Females

- 1) Facial grooves running separately to scrobes (Figs. 38–45, 48) ..... 2  
 Facial grooves meeting just above middle of eyes then passing as one line to scrobes, upper arm equal to or wider than POL (Figs. 46, 47) ..... 10
- 2) Scape and pedicel dark, concolorous with flagellum (Figs. 83, 84), fore wing with costal margin almost straight (Fig. 116) ..... *acasta* (Walker)  
 Scape and pedicel paler than flagellum, fore wing coastal margin noticeably bent at junction with parastigmal vein ..... 3
- 3) Head broad, length to genal width about 1.1:1 (Figs. 38, 41) ..... 4  
 Head relatively narrow, length to genal width greater than 1.1:1 ..... 5

- 4) Upper arms of facial grooves widely separated, approximately equal to POL, lower arms of facial grooves separated by a distance equal to the diameter of the median ocellus (Fig. 38), clypeal lobes with small lateral undulations (Fig. 59), subterminal seta on antennal nipple situated basally (Fig. 102) ..... *clavicornis* (Cameron)  
Upper and lower arms of facial grooves much closer than above (Fig. 41), clypeal lobes without lateral undulations (Fig. 62), subterminal seta on antennal nipple not basal (Fig. 105)..... *scapata* SP. NOV.
- 5) Eyes densely clothed with long setae (Figs. 44, 48) ..... 6  
Eyes relatively bare, with a few short scattered setae..... 7
- 6) Head and mesosoma densely setose (Fig. 44); clypeal margin bilobed, lobes narrow each with a small, lateral, lobe-like undulation (Fig. 65); nipple on club segment 3 with 1 subterminal seta (Fig. 108) .... *chalybii* Ashmead  
Head and mesosoma not as densely setose (Fig. 48); clypeal margin bilobed, lobes broad, without a small, lateral, lobe-like undulation (Fig. 69); nipple on club segment 3 with 2 subterminal setae (Fig. 114) ..... sp. nov. Argentina
- 7) Terminal seta on postmarginal vein noticeably longer than those on marginal vein (Figs. 129, 131), head sculpture normal, surface shining ..... 8  
Terminal seta on postmarginal vein not noticeably longer than those on marginal vein (Figs. 132, 134), head sculpture fine, surface dull, shagreened ..... 9
- 8) Clypeal margin bilobed each lobe without a lateral, lobe-like undulation (Fig. 61); sculpture pattern on mesoscutum and scutellum very open (Fig. 142); mid lobe of scutellum broad, L:W 1.4:1; MPS formula on flagellum 355:553..... *evansi* SP. NOV.  
Clypeal margin bilobed, each lobe with a lateral, lobe-like undulation (Fig. 63), sculpture pattern on mesoscutum and scutellum mid lobes less open particularly on scutellum (Fig. 144); mid lobe of scutellum narrow, L:W 1.9:1 MPS formula on flagellum 567-653..... *digitata* SP. NOV.
- 9) Scape and pedicel yellow-brown, dorsally dark, reddish-brown (Fig. 90); nipple on club segment 3 long, L:W 4:1, subterminal seta on antennal nipple not basal (Fig. 107) ..... *femorata* SP. NOV.  
Scape and pedicel yellow-brown, not strongly darkened dorsally (Fig. 93); nipple on club segment 3 short, L:W 2.5:1, subterminal seta almost basal (Fig. 109) ..... *Megachilis* (Packard)
- 10) Clypeus bilobed (Fig. 67); upper arms of facial grooves wider than POL (Fig. 47).....11  
Clypeus truncate emarginate (Fig. 68); upper facial grooves as wide as POL (Fig. 46) ... *australica* Girault and *hawaiiensis* Perkins
- 11) Submarginal vein with 5 setae; proximal pair distinctly shorter than rest. *assemi* SP. NOV.  
Submarginal vein with 5 long setae of equal length ..... *sosui* SP. NOV.
- Males
- 1) Scape ventrally with a distal cup-shaped depression (Fig. 19) ..... 8  
Scape ventrally with a longitudinal groove (Figs. 16-17)..... 2
- 2) Head large (Fig. 151) dark brown; scape yellow, distinctly club-shaped (Figs. 185, 186), ventral groove shallow; glandular area large, circular ..... *clavicornis* (Cameron)  
Head and scape concolorous, yellow-brown; not distinctly club-shaped as (Fig. 151), scape groove deep; glandular area not circular .... 3
- 3) Head transversely elliptical, lateral margins broadly rounded (Fig. 158); funicular segmental proportions (Fig. 208), 1 the smallest, narrow, 2+3 the largest, 4 cup-shaped, closely applied to club segment 1; clypeus without lobes..... 4  
Head more or less rectangular (Figs. 159, 160); funicular segmental proportions not as above..... 5
- 4) Flange overhanging scape groove on the side of pedicel attachment with up to 5 setae, only 1 or 2 of which are on the inner margin, 1-2 setae on the proximal floor of groove (Fig. 206)..... *australica* Girault  
Flange overhanging scape groove with more than 5 setae of which most are on the inner margin, flange longer than *australica* or Kauai, 4 setae on the proximal floor of groove (Fig. 209)..... *hawaiiensis* Perkins  
Flange overhanging scape groove with more than 5 setae spread evenly along flange, most of which are on the inner margin, 2 setae on the proximal floor of groove, (Fig. 210) ..... Kauai

- 5) Fore wing apex acute (Fig. 239) ..... 6  
 Fore wing apex rounded (Fig. 241) ..... 7
- 6) Mid femoral fringe sparse (Fig. 228)  
 ..... *assemi* SP. NOV.  
 Mid femoral fringe denser (Fig. 230)  
 ..... *sosui* SP. NOV.
- 7) Mandibles very broad (Fig. 173), projecting well below clypeus when closed; face below toruli with tufts of long, stiff setae (Fig. 160); Maxillary palp broad, distally excavated (Fig. 184); clypeus with 2 broad lobes  
 ..... sp. nov. Argentina  
 Mandibles not projecting well below clypeus when closed; face below toruli without stiff setae, maxillary palp tapered distally as *assemi* (Fig. 182); clypeal margin with narrow lobes as *assemi* (Fig. 159) .. *bekiliensis* Risbec
- 8) Distal scape margin deeply excavated to produce a thumb-like appendage (Figs. 197, 198)..... *digitata* SP. NOV.  
 Distal scape margin not as deeply excavated ..... 9
- 9) Distal scape strongly oblique with a broad excavation overhung by a long setal fringe (Figs. 188, 189)..... *acasta* (Walker)  
 Distal scape not strongly oblique ..... 10
- 10) First funicular segment only slightly wider than segments 2-3 (Figs. 193, 196)..... 11  
 First funicular segment much wider than segments 2-3; the distal ring-joint expanded slightly to give a small segment before funicle 1 (Figs. 202, 205) ..... 12
- 11) Fore wing relatively narrow, L:W 2.6:1; costal cell long, L:W 8:1 (Fig. 233); marginal to submarginal vein length 1.4:1; mid femoral fringe relatively even, longest setae about as wide as femur (Fig. 223); head narrowed above eye spots (Fig. 153) L:W 1:1..... *evansi* SP. NOV.  
 Fore wing relatively broad, L:W 2.4:1; coastal cell shorter, L:W 7.5:1; (Fig. 234) marginal to submarginal vein length 1:1; mid femoral fringe of uneven length, proximal half shorter, just shorter than width of femur, distal half longer, about 1.5 times width of femur (Fig. 222); Head not contracted above eye spots, wider than long, L:W 1:1.3 (Fig. 154)..... *scapata* SP. NOV.
- 12) Fore wing relatively narrow (Fig. 237), L:W 2.9:1, posterior margin almost straight; coastal cell long, L:W 11.7:1; mid femoral fringe uneven, proximal 1/3 shorter than

width of femur, distal 2/3 about as wide as femur (Fig. 226); head densely setose, genae below eye spots contracting to clypeal margin (Fig. 157) ..... *chalybii* Ashmead  
 Fore wing relatively broad, L:W 2.6:1; costal cell short, L:W 7.6:1 (Fig. 236); mid femoral fringe uneven, proximal 1/2 of fringe about as long as width of femur, distal 1/2 of fringe dense, extremely long nearly 2 x width of femur (Fig. 225); head not as densely setose, genal margins below eye spots straight, parallel, not contracting towards clypeus (Fig. 156)..... *femorata* SP. NOV.

## SPECIES DESCRIPTIONS

*Melittobia clavicornis* (Cameron)

(Figs 38, 49, 59, 70, 82, 102, 115, 127, 140, 151, 161, 174, 185, 186, 187, 220 231)

*Philopison clavicornis* Cameron, 1908 : 559.

*Melittobia clavicornis* : Ferrière, 1933 : 103.

*Melittobia japonica* Masi, 1966 : 38, SYN NOV.

*Melittobia japonica* : Iwata and Tachikawa, 1966 : 6.

*Melittobia japonica* : Domenichini, 1966 : 57.

## TYPE SPECIMENS:

I have examined the syntypal series of Cameron which is in the collections of the British Museum (Natural History) London. Details are in the MATERIAL EXAMINED section. I have examined also the syntypal series of *M. japonica* Masi which are in the collections of the Kyushu University, Kyushu Japan. From both these syntypal series I have selected lectotypes. Details occur in the MATERIAL EXAMINED section.

## DISTRIBUTION:

Borneo, Ceylon, Japan (= species 3, van den Assem and Maeta (1978) = Species 1 van den Assem, Bosch and Prooy (1982)).

## DESCRIPTION:

Female: Critical point dried specimens 1.3-1.4 mm long. Head, antennal flagellum, mesosoma, coxae dark brown; trochanters, proximal 2/3 femora, metasoma paler brown; scape, pedicel, remainder of legs yellow-brown.

Head in frontal aspect (Fig. 38) relatively broad, length to genal width 1.1:1; genal-clypeal margin broadly rounded; clypeal margin (Fig. 59) bilobed, each lobe with a small lateral lobe-like undulation; eyes

relatively bare, with a few short scattered setae. Facial grooves remaining separate to meet scrobes well below middle of eyes, upper arms widely separated, maximum distance between arms 3.5 times diameter of median ocellus, greater than POL, converging gradually to scrobes remaining broadly separated but contracting suddenly just before scrobes. Scrobes relatively short, scrobe to eye length 1:3. Mandibles (Fig. 49); anterior tooth long, narrow, 2 and 3 well defined, 2 the more definite. Maxillary palps (Fig. 70) elongate, cylindrical, L:W 5:1. Antennae (Fig. 82); scape L:W 3.7:1; MPS formula on flagellum 354:773; club segment 3 (Fig. 102) shortest length to width 1:2.5; nipple short, broad, L:W 3:1, barely reaching above the MPS; subterminal seta basal.

Mesosoma in dorsal aspect. Setation relatively long. Prothorax wider than long, L:W 1:2. Posterior margin of mesoscutum mid lobe 1.4 times wider than anterior margin of scutellum. Scutellum mid lobe L:W 1.7:1; 1 pair of setae on each submedian lobe, posterior seta almost on hind margin. Sculpture pattern on mid lobes of mesoscutum and scutellum (Fig. 140). Propodeum in dry specimens rectangular, wider than long; posterior margin truncate emarginate; posterolateral angles 90°. Fore wings (Fig. 115); costal margin noticeably angled at junction with parastigmal vein; L:W 2.2:1; marginal to submarginal vein length 1.3:1; marginal to stigmal vein length 3.4:1; submarginal to stigmal vein length 2.7:1; stigmal vein (Fig. 127); terminal seta on postmarginal vein as long as those on marginal vein.

Male: Critical point dried specimens 1.4 mm long. Head, body and legs dark brown, head darkest; scape and legs pale yellow-brown. Head in frontal aspect (Fig. 151) large, slightly wider than long, L:W 1:1.1; vertex depressed medially; lateral margins more or less broadly rounded, slightly contracted below eye spots; clypeal margin bilobed, lobes broad. Mandibles (Fig. 161); anterior tooth of moderate length, relatively close to second, third tooth poorly defined. Maxillary palps (Fig. 174) elongate, cylindrical, slightly curved, L:W 4.8:1. Antennae (Figs. 185-187); scape strongly club-shaped, scape to head length 1:1.8, L:W 1.6:1; ventral surface with a shallow groove, distally truncate not excavated, glandular area large,

circular; funicular segment proportions (Fig. 187) 1 very large, L:W 1:1.8, 2-4 sub-equal, relatively small, about as wide as length of segment 1; MPS formula on flagellum 0122:342.

Mesosoma in dorsal aspect. Prothorax L:W 1:2. Mesoscutum with clearly defined parapsidial sutures; axillae well defined. Scutellum without submedian grooves; sublateral grooves present; 2 pair of large setae present, situated as in female.

Fore trochanters without a ventral tuft of short, stiff setae; tarsal segments 3 + 4 fused. Mid legs (Fig. 220); trochanters without a dense tuft of long, fine setae; femora with a cluster of long, fine setae distally, a few short setae proximally; mid femur L:W 2.7:1; mid tibia relatively short and wide, shape quite distinctive, L:W 2.3:1; mid tarsal joints unfused. Fore wings (Fig. 231) broad, L:W 2.5:1; marginal to submarginal vein length 1.2:1; stigmal vein well developed; costal cell L:W 9:1, costal margin slightly arched.

#### MATERIAL EXAMINED:

BM(NH) 1 ♂ on a card, minus wings; left antennal flagellum separated; dark blue BM 'LECTOTYPE' label, 'Kuching Nov. 07 J.H.', 'This also from *Pison sarawakensis* cocoons', '*Philopison clavicornis* Cameron Type Borneo', 'B.M. TYPE HYM 5.1354'. LECTOTYPE.

1 ♂ glued ventral surface down on a card (only 1 leg attached, and 1 leg glued separately on the card; only 1 fore wing present — torn); blue BM 'PARALECTOTYPE' label, 'Kuching, Nov. 07, J.H. P. Cameron Coll., 1914-100', '*Philopison clavicornis* Cam., Type, Borneo'. PARALECTOTYPE.

1 ♀ glued on a card, intact; blue BM 'PARALECTOTYPE' label, '*Philopison clavicornis* Cam.', 'Kuching J.H.', 'Borneo, J. Hewitt, 1910-380'. PARALECTOTYPE.

2 ♀♀ glued ventral surface down on a card, both incomplete (outer minus metasoma, all wings except 1 hind wing separated in the glue; 1 antenna complete, the other separated, fragmentary : inner complete except for metasoma); blue BM 'PARALECTOTYPES' label, 'Bred from cocoons of *Pison sarawakensis* Kuching, Nov. 07, J.H.' 'This seems to be same as my J.19 is it not?', 'A.B. 2', '*Philopison clavicornis* Cam., Type, Borneo', 'P.

Cameron collection, 1914-110'. PARALECTOTYPES.

1 ♀ on a card buried in glue; blue BM 'PARALECTOTYPE' label, '*Philopison clavicornis*, Cam. Type Borneo', 'P. Cameron Coll. 1914-110'. PARALECTOTYPE.

1 ♀ on a card, intact, blue BM 'PARALECTOTYPE' label, 'Kuching J.H. [this label has July crossed out]', 'P. Cameron Coll. 1914-110'. PARALECTOTYPE.

11 microscope slides with various parts of both sexes as follows:

Slide 1 — 4 coverslips containing a dismembered ♂. '*Melittobia (Philopison) clavicornis*, Cam., ♂', '*Pelopaeus madraspatarum* Borneo, Kuching. (Edinburgh Mus.) J. Hewitt Coll.' PARALECTOTYPE.

Slide 2 — 1 coverslip containing a ♂ head minus mouthparts and antennae. 'Head, ♂, *Melittobia (Philopison) clavicornis*, Cam.', 'Kuching, Borneo Nov. 1907 J. Hewitt 1910-380'. PARALECTOTYPE.

Slide 3 — 3 coverslips containing ♂ antennae and mouthparts. 'Mandibles, Trophi, & Antennae, ♂. *Melittobia (Philopison) clavicornis*, Cam.', 'Kuching, Borneo, Nov. 1907 J. Hewitt 1910-380'. PARALECTOTYPE.

Slide 4 — 1 coverslip containing a ♂ mesosoma + metasoma; minus prothorax, legs, wings and genitalia. 'Meso-Metathorax & Abdomen, ♂ *Melittobia (Philopison) clavicornis*, Cam.', 'Kuching, Borneo Nov. 1907 J. Hewitt 1910-380'. PARALECTOTYPE.

Slide 5 — 1 coverslip containing ♂ wings (2 pairs). 'Wings, ♂. *Melittobia (Philopison) clavicornis*, Cam.', 'Kuching, Borneo Nov. 1907 J. Hewitt 1910-380'. PARALECTOTYPE.

Slide 6 — 1 coverslip containing 1 set of ♂ legs. 'Legs, ♂. *Melittobia (Philopison) clavicornis* Cam.', 'Kuching, Borneo, Nov. 1907 J. Hewitt 1910-380'. PARALECTOTYPE.

Slide 7 — 2 coverslips containing ♂ prothorax and genitalia. 'Prothorax & Genitalia, ♂. *Melittobia (Philopison) clavicornis* Cam.', 'Kuching, Borneo Nov. 1907 J. Hewitt 1910-380'. PARALECTOTYPE.

Slide 8 — 1 large coverslip containing an intact ♀. '♀ *Melittobia (Philopison) clavicornis*, Cam. CO-TYPE', 'Kuching, Borneo J. Hewitt, 1909-182'. PARALECTOTYPE.

LECTOTYPE.

Slide 9 — 4 coverslips containing 1 ♀ head with separated antennae and mouthparts. 'Head, Antennae, Mandibles & Trophi ♀ *Melittobia (Philopison) clavicornis* Cam.', 'Kuching, Borneo J. Hewitt 1909-182'. PARALECTOTYPE.

Slide 10 — 4 coverslips containing 1 ♀ mesosoma (minus legs and wings), metasoma and ovipositor. 'Prothorax, Mesothorax, Metathorax, Propodeum, Abdomen & Ovipositor ♀ *Melittobia (Philopison) clavicornis*, Cam.', 'Kuching, Borneo J. Hewitt 1909-182'. PARALECTOTYPE.

Slide 11 — 2 coverslips containing ♀ wings (2 pairs) and legs (1 set). 'Legs & Wings, ♀ *Melittobia (Philopison) clavicornis* Cam.', 'Kuching, Borneo J. Hewitt 1909-182'. PARALECTOTYPE.

The parts on slides 2-7 all make up a single ♂ and were probably from a single specimen, similarly the parts on slides 9-11 may all be from a single ♀.

USNM 2 ♀♀ intact glued on separate cards on separate pins in Dr. K. Krombein's voucher specimen collection and labelled — 'SRI LANKA : Colombo, 3.x.1977, K.V. Krombein, 10377 A, ex *Paraleptomenes mephitis*'; a pink label, '10377A'.

1 ♀ 1 ♂ on separate pins with above data; ♂ also labelled '*Melittobia clavicornis* (Cam.), det. Z. Bouček, 1978'.

KU 6 points on one pin, 5 each bearing 1 ♀ (upper minus head) and 1 bearing plant material. These are labelled, '*Melittobia japonica* MS., Cotypl, det. L. Masi'. From this syntypal series I have selected the female on the bottom point as the lectotype and marked its point with red. The remaining 4 specimens have been selected as paralectotypes. Labels were applied indicating these selections.

QM 2 microscope slides, 1 with 2 ♀♀ the other with 2 ♂♂ and both labelled, '*Melittobia clavicornis* (Cam.) E. Dahms det. 1981, Chiisageta-gun, Nanango Pref., Japan, Jan. 1977, T. Kitamura ex *Trypoxylon malaisei*'.

In addition to these there is a series of card-mounted specimens each with 1 ♂ 4 ♀♀; 'Chiisagata-gun, Nanango Pref., Japan, Jan. 1977, T. Kitamura ex *Trypoxylon malaisei*', '*Melittobia clavicornis* (Cameron), E. Dahms det. 1981'. These are all critical point dried specimens and one card has been deposited in

each of the following institutions: ANIC, BM(NH), DSIR, KU, MDA, MNHP, NMC, QM, UCR and USNM.

NOTES: The figures of this species were taken from the QM slides of specimens from Japan. The syntypical slides came to hand after figures were assembled.

*Melittobia acasta* (Walker)

(Figs 39, 50, 60, 71, 83, 84, 103, 116, 128, 141, 152, 162, 175, 188, 189, 190, 221, 232)

*Cirrospilus acasta* Walker, 1839 : 328.

*Melittobia audouinii* Westwood, 1840 : 160.

*Melittobia audouinii* : Westwood, 1847 : 18.

*Anthophorabia retusa* Newport, 1849a : 183.

*Melittobia audouinii* : Westwood, 1849a : 295.

*Melittobia audouinii* : Westwood, 1849b : 37.

*Melittobia audouinii* : Westwood, 1849c : 65.

*Anthophorabia retusa* : Westwood, 1849c : 65.

*Anthophorabia retusa* : Newport, 1849b : 513.

*Melittobia audouinii* : Newport, 1849b : 514.

*Melittobia audouinii* : Westwood, 1849d : 39.

*Anthophorabia retusa* : Newport, 1849c : 122.

*Melittobia audouinii* : Newport, 1849c : 122.

*Anthophorabia retusa* : Newport, 1852a : 63.

*Melittobia audouinii* : Newport, 1852a : 65.

*Anthophorabia fasciata* Newport, 1852b : 81  
SYN NOV.

*Anthophorabia fasciata* : Newport, 1853 : 165.

*Melittobia acasta* : Smith, 1853 : 248.

*Melittobia acasta* : Giraud, 1869 : 151, 155.

*Melittobia audouinii* : Ashmead, 1892 : 228.

*Anthophorabia retusa* : Ashmead, 1892 : 228.

*Melittobia acasta* : Dalla Torre, 1898 : 84.

*Melittobia acasta* : Ashmead, 1904 : 348, 380.

*Melittobia acasta* : Schmiedeknecht, 1909 : 466.

*Melittobia acasta* : Morely, 1910 : 57.

*Melittobia acasta* : Waterston, 1917 : 190.

*Melittobia strandi* Wolff and Krausse, 1922 : 16  
SYN NOV.

*Melittobia acasta* : Peck, 1963 : 161.

*Melittobia acasta* : Peck, Bouček and Hoffer, 1964 : 98.

*Melittobia acasta* : Domenichini, 1966 : 56.

*Melittobia acasta* : De Santis, 1957 : 109.

*Melittobia acasta* : De Santis, 1973 : 16.

*Melittobia audouinii* : Bouček, 1977 : 24.

*Melittobia acasta* : Bouček, 1977 : 24.

*Melittobia audouinii* : Gordh, 1979 : 1005.

TYPE SPECIMENS:

I have not seen Walker's type-specimen of *M. acasta* which is in the British Museum (Natural History), London nor have I seen any specimens

of Westwood (*M. audouinii*) and Newport (*Anthophorabia retusa*, *A. fasciata*). The specimens of the last two authors, if they exist, are probably also in the British Museum. My recognition of this species is based upon material identified by Dr Z. Bouček and the exhaustive re-description by Waterston (1917). It is a distinctive species and there can be little doubt of its identity. Newport (1852b) described the species *A. fasciata* provisionally, in the absence of any of the *A. retusa* specimens for comparison, because new specimens to hand showed characters he could not remember in *A. retusa*. However, from the figures in this paper and his 1853 paper, *A. fasciata* is clearly a junior synonym of *M. acasta*.

The type of *M. strandi* Wolff and Krausse (1922) could not be located. From their description and figures this species is clearly a junior synonym of *M. acasta*.

DISTRIBUTION:

England, Europe, Japan (= *M. japonica* of Maeta and Yamane (1974)) (= species 1 of van den Assem and Maeta (1978)), South America, Canada (= *chalybii* of Hobbs and Kronic (1971)) and New Zealand, (= species 2 of van den Assem, Bosh and Prooy (1982)).

DESCRIPTION:

Female: Critical point dried specimens 1.4–1.5 mm long; air dried specimens 1.3–1.5 mm long. Colour air dried specimens: head, scape, pedicel, flagellum, mesosoma, coxae, trochanters, proximal  $\frac{2}{3}$  femora, metasoma dark brown, remainder of legs yellow brown.

Head in frontal aspect (Fig. 39) of moderate width, length to genal width about 1.2:1; genal-clypeal margin not as broadly rounded as *M. clavicornis* clypeal margin (Fig. 60) bilobed, lobes broad; eyes relatively bare, with a few short scattered setae. Facial grooves remaining separate to scrobes, maximum distance between arms not as wide as POL, 2.6 times diameter of median ocellus, converging gradually to meet scrobes well below middle of eyes, lower arms separated by a distance 0.5 times the width of median ocellus. Scrobe to eye length 1:2. Mandibles (Fig. 50); anterior tooth relatively short, narrow, middle tooth more prominent than 3, acute, narrow, third tooth broad not as clearly defined. Maxillary palps (Fig. 71) elongate, cylindrical, slightly widest at middle, of moderate length, L:W 4:1.

Antennae (Fig. 84); scape (Fig. 83) narrow, L:W 3.4:1; MPS formula on flagellum 345:563; club segment 3 (Fig. 103) shortest length to width 1:2; nipple elongate, standing well above MPS, L:W 4.7:1; subterminal seta about mid-way down nipple.

Mesosoma in dorsal aspect. Prothorax L:W 1:1.8. Posterior margin of mesoscutum mid lobe 1.2 times wider than anterior margin of scutellum mid lobe. Scutellum mid lobe L:W 1.7:1; 1 pair of setae on each submedian lobe, posterior setae situated forward of posterior margin by a distance of 1/10th length of submedian lobe. Sculpture pattern on mesoscutum and scutellum mid lobes (Fig. 141). Propodeum wider than long, rectangular, posterior margin transverse, emarginate, posterolateral angles 90°. Fore wings (Fig. 116) relatively long, L:W 2.5:1 costal margin almost straight; marginal to submarginal vein length 1.4:1; stigmal vein (Fig. 128), marginal to stigmal vein length 4.8:1, submarginal to stigmal vein length 3.2:1; terminal seta on post marginal vein as long as those on marginal vein.

Male: Critical point dried specimens 1.4–1.7 mm long. Head, antennae, mesosoma, legs and metasoma medium brown except flagellum infuscated, mesoscutum and axillae very pale; vertex, prothorax, scutellum, coxae, trochanters, proximal 2/3 femora, metasoma lightly infuscated. In air dried specimens the colour becomes a fairly uniform medium to dark brown.

Head in frontal aspect (Fig. 152) vertex broad, almost straight especially in air dried specimens, contracting strongly below eye spots to clypeal margin, L:W 1:1.07; clypeal margin bilobed, lobes broad. Mandibles (Fig. 162) elongate, anterior tooth long, narrow, widely separated from second, second and third teeth broad, 2 the largest. Maxillary palps (Fig. 175) elongate, cylindrical, of medium length, L:W 4:1. Antennae (Figs. 188–190); scape club-shaped, less so than *M. clavicornis*, scape to head length 1.1:1, L:W 2:1; ventral surface distally with a deep, cup-shaped depression, glandular area transversely elongate (Fig. 189); distal scape margin strongly oblique, broadly excavated, excavation overhung by long setae (Fig. 188). Funicular segmental proportions (Fig. 190), 1 the largest, L:W 1:1.3; segments 2–4 small, sub-equal, 2 the smallest, width of 2–4

slightly larger than length of 1; MPS formula 0001:342.

Mesosoma in dorsal aspect. Prothorax L:W 1:1.3. Parapsidal sutures and axillae not as well defined as in *M. clavicornis*. Scutellum without submedian grooves, sublateral grooves faintly defined; 2 pairs of setae positioned as in female. Fore trochanters without a dense tuft of short, stiff setae ventrally; tarsal segments 3 + 4 fused. Mid legs (Fig. 221) trochanters with a dense tuft of long, fine setae ventrally; femoral fringe strongly differentiated, proximal half of femora with fringe of setae shorter than width of femur, distal fringe with long setae, slightly longer than width of femur; mid femur L:W 3.8:1; mid tibia shape distinctive, L:W 3.8:1; mid tarsi without fused segments. Fore wings (Fig. 232) broad, L:W 2.6:1; marginal to submarginal vein length 1.4:1; stigmal vein well developed, broad; costal cell relatively broad, L:W 6.7:1, costal margin strongly arched.

#### MATERIAL EXAMINED:

- BM(NH) 12 ♀♀ 'L.S. Kensington, iii.1948, R.B. Benson, B.M. 1948. 145'; 3 ♀♀ 'England, Hants. Basingstoke, Long Sutton, 4.vi.1948, F.D. Goodliffe', 'Com. Inst. Ent. Coll. No. 11069', 'Pres. by Com. Inst. Ent. B.M. 1948 — 550', 'ex leaf cutter bee'; 1 ♂ 'Basingstoke, Hants., 29.vi.1904, A.H. Hamm', '*Melittobia acasta* Wlk. ♂', '♂ *Melittobia acasta* (Walk.) Det. Z. Bouček 1974', 'Bred from *Odynerus sinuatus*'; 4 ♂♂ 'Cambridge, 1915, Dr G.S. Graham Smith', 'J. Waterston Det. *Melittobia acasta* Walk ♂', 'Bred from *Calliphora*'; 2 ♀♀ 'Haywards Heath, Sussex, v.iii.1919, K.G.B. 1919 — 222', 'Bred from Tachinid puparia ex *A. pyramidea*'.
- USNM 1 ♀, 4 ♂♂ 'ex *Cnidocampa flavescens*' 'Melrose Hills Mass. 9–29', 'Gip. Moth Lab. 13043'; 3 ♂♂ 'ex Tachinid puparium', 'Phila Pa 9–20–24', 'Gip. Moth Lab 11741 J13'.
- QM 2 ♀♀ 1 ♂ on a microscope slide 'Jose C. Paz. Prov. de Bs.As., S/ *Trypoxylon* sp. col. Ibarra Grasso 10/III/1956 ♀ and ♂', '*Melittobia acasta* Det. De Santis'.
- NMC 20 ♀♀ 4 ♂♂ 'Boh. Majdalena, Treboh, v.1963 K. Denes', 'ex pupa *Coroebus undatus* F. (Buprestidae)'; 22 ♀♀ 1 ♂ 'Majdalena Bohemia, v.63, lat. K. Denes', 'ex pupa *Coroebus undatus* F. Buprestidae'; 11 ♀♀ 4 ♂♂ 'Bohemia : Sobeslav, ex *Vespa crabro*,

x.1950, K. Pflieger ed'; 5 ♀♀ 'Italia : Sasso, Furbara, 1948, *Sceliphron destill.*'

In addition critical point dried material as follows:

- 1) 'Lossler, Overijssel Prov., Netherlands, 18.vi.1974, G.A. Bekke, ex pompilid.' 4 ♀♀ 1 ♂ in each of the following institutions: ANIC, BM(NH), DSIR, USNM, MNHP, QM, THAES, UCR, USNM.
- 2) '1 km W. Taitapu New Zealand, 20 March, 1980 R.P. Macfarlane', 'ex nest *Bombus hortorum* nest in box No. C31' 4 ♀♀ 1 ♂ in each of the following institutions: ANIC, BM(NH), DSIR, QM.
- 3) 'Morioka Exp. Stn., Iwate Pref., Japan, 1974, Y. Maeta', 'ex *Osmia imaii*' 4 ♀♀ 1 ♂ in each of the following institutions: ANIC, BM(NH), DSIR, KU, QM, THAES, UCR, USNM.
- 4) 'Lethbridge, Alta, Canada, xi.1974, G.A. Hobbs', 'ex *Megachile relativa*' 4 ♀♀ 1 ♂ in each of the following institutions: ANIC, BM(NH), DSIR, QM, UCR, USNM.

*Melittobia evansi* SP NOV

(Figs 40, 51, 61, 72, 85, 86, 104, 117, 129, 142, 153, 163, 176, 191, 192, 193, 223, 233)

TYPE SPECIMENS:

The types were selected from a laboratory culture maintained at the University of Georgia, Athens, Georgia, U.S.A. which was established from specimens collected at Athens, Georgia, U.S.A., by D.A. Evans, out of nests of *Trypoxylon striatum*. The holotype ♂ (marked H on card-mount) is air dried from alcohol and card mounted with 2 ♂♂ 2 ♀♀ paratypes (USNM). Additional paratypes consist of 15 cards each with 4 ♀♀ and 5 cards each with 1 ♂ 4 ♀♀ critical point dried from alcohol and are deposited in the following institutions USNM BM(NH), QM, UCR, UG. The paratypes are rather pale as a result of leaching in alcohol.

DISTRIBUTION:

Athens, Georgia, U.S.A.; Goshen, N.Y., U.S.A. (= species 3 of van den Assem, Bosch and Prooy (1982)).

DESCRIPTION:

Female: Critical point dried specimens 1.1–1.4 mm long. Colour from air dried material ex alcohol. Head, antennal flagellum,

mesosoma, coxae, proximal 2/3 femora dark brown; metasoma medium brown; scape, pedicel and remainder of legs yellow-brown. Head in frontal aspect (Fig. 40) relatively narrow, length to width of gena about 1.3:1; genae almost parallel, genal-clypeal margin angled rather than broadly rounded; clypeal margin (Fig. 61) bilobed, lobes broad; eyes relatively bare, with a few short, scattered setae. Facial grooves remaining separate to scrobes, maximum distance between arms about 2.2 times diameter of median ocellus; grooves converge gradually to meet scrobes below middle of eyes, minimum distance between grooves 0.5 times the diameter of median ocellus. Scrobe to eye length about 1:2.5. Mandibles (Fig. 51); anterior tooth long, narrow; second and third well defined, second long, narrow. Maxillary palps (Fig. 72) elongate, cylindrical, relatively long, L:W 5:1. Antennae (Figs 85, 86); scape narrow, L:W 4.2:1; MPS formula on flagellum 355:553; club segment 3 (Fig. 104) length to shortest length 1:1.4, nipple broad, L:W 2.5:1, barely projecting above MPS; subterminal seta just below middle of nipple. Mesosoma in dorsal aspect. Prothorax L:W 1:1.4. Posterior margin of mesoscutum mid lobe 1.2 times wider than anterior margin of scutellum mid lobe. Scutellum mid lobe L:W 1.4:1; 1 pair of setae on each submedian lobe of scutellum, posterior setae on posterior margin of lobe. Sculpture pattern on mesoscutum and scutellum mid lobes (Fig. 142), pattern very open. Propodeum wider than long, posterior margin an open V-shape, posterolateral angles obtuse. Fore wings (Fig. 117) L:W 2.4:1; costal margin bent at junction with parastigmal vein; marginal to submarginal vein lengths 1.5:1; 4–5 setae on submarginal vein; stigmal vein (Fig. 129) marginal to stigmal vein length 4.1:1; submarginal to stigmal vein length 2.8:1; terminal seta on postmarginal vein much longer than those on marginal vein.

Male: Air dried specimens ex alcohol 1.4 mm long. Head, antennae, mesosoma, legs pale brown, head darkest, mesoscutum and axillae palest; metasoma dark brown. Head in frontal aspect (Fig. 153), L:W 1:1, vertex rounded, narrower than width below eye spots, genae broadly rounded, not contracted, meeting clypeus in an obtuse angle; clypeal margin bilobed, lobes broad. Mandibles (Fig. 163) long, narrow; anterior



tooth very long; second and third well defined, second the longest. Maxillary palps (Fig. 176) elongate, cylindrical, L:W 4.8:1. Antennae (Figs. 191–193) scape club-shaped, less pronounced than *M. acasta*, scape to head length 1:1.6, L:W 1.7:1; ventrally (Fig. 192) with a distal, deep, cup-shaped depression; glandular area transverse expanding on side opposite pedicel attachment; distal scape broadly excavated, very slightly oblique; funicular segmental proportions (Fig. 193) 1 large, L:W 1:1.6; 2–4 sub-equal, width to length of first 1:1.2; MPS formula 0022:232.

Mesosoma in dorsal aspect. Prothorax L:W 1:1.8. Parapsidal sutures and axillae not as clearly defined as in *M. clavicornis*. Submedian grooves of scutellum absent, sublateral grooves faintly marked; 2 pair of setae positioned as in female. Fore trochanters without a ventral tuft of short, stiff, setae; fore tarsi with segments 3 + 4 fused. Mid legs (Fig. 223); mid trochanters with a dense tuft of long, fine setae; femoral fringe evenly distributed along femur, setae of even length, about as wide as femur, mid femur L:W 3.9:1; mid tibia L:W 3.2:1; mid tarsi without fused segments. Fore wings (Fig. 233) broad, L:W 2.6:1, costal and posterior margin almost parallel; marginal to submarginal vein length 1.4:1; stigmal vein well developed, broad; costal cell narrow, L:W 8:1, costal margin slightly arched.

#### MATERIAL EXAMINED:

Holotype ♂; and paratype ♂♂, ♀♀ from Georgia deposited as in TYPE SPECIMENS section.

USNM 5 ♀♀ 'Goshen, N.Y., 3.22.40, vial 1, R.G. Schmieder', 'Ex *Trypoxylon politum*'; 3 ♀♀ data as above vial 2; 1 ♀♀ 'Goshen, N.Y. 7–27–36, vial 3, R.G. Schmieder', 'Ex *Trypoxylon politum*'. The last specimen is a second form with crumpled wings.

This species is named *evansi* after Dr. D.A. Evans, Kalamazoo College, U.S.A. who brought this species to my attention and has been of help in many other ways.

#### *Melittobia scapata* SP NOV

(Figs 41, 52, 62, 73, 87, 105, 118, 130, 143, 154, 164, 177, 194, 195, 196, 222, 234)

#### TYPE MATERIAL:

Holotype ♂ plus 4 paratype ♀♀ on a single card with the original alcohol labels 'Tompkins Co., N.Y. late Apr., 1974, Suellen Vernoff', 'ex nest *Trypoxylon*', 'CU Lot No. 1040, site C, Nest 88'; 4 ♀♀ 1 ♂ paratypes on a single card with holotype data (USNM); 22 ♀♀ 2 ♂♂ paratypes with holotype data (CU, NY); 2 ♂♂, 3 ♀♀ paratypes on slides (QM) 'New York, U.S.A., 8.May.1971, G. Eichardt, reared nest of mason wasp. Euparal, E.C. Dahms 1980'.

#### DISTRIBUTION:

Tompkins County, New York, U.S.A.

#### DESCRIPTION:

Female: Critical point dried specimens 1.6–1.7 mm long. Head, flagellum, mesosoma, coxae, femora dark brown; scape, pedicel, metasoma, remainder of legs medium brown. These specimens have been in alcohol since 1974 and the antennae have leached. The scape and pedicel were probably fairly dark when fresh but not as dark as the flagellum. Head in frontal aspect (Fig. 41) relatively broad, length to genal width 1.1:1; genae broadly rounded, genal-clypeal margin more or less sharply angled; clypeal margin (Fig. 62) bilobed, lobes broad, relatively long; eyes relatively bare, with a few short setae. Facial grooves remaining separate to scrobes, maximum distance between arms 2.1 times diameter of median ocellus; grooves converging sharply to just above middle of eyes then running close and parallel to meet scrobes well below middle of eyes; minimum distance between arms 0.3 times diameter of median ocellus. Scrobe to eye length 1:2.4. Mandibles (Fig. 52) broad, anterior tooth short, narrow, very widely separated from second; second and third broad, equal. Maxillary palps (Fig. 73) elongate, cylindrical, relatively long L:W 4.6:1. Antennae (Fig. 87); scape narrow, L:W 3.4:1; MPS on flagellum 356:673; club segment 3 (Fig. 105) shortest length to width 1:1.8; nipple relatively broad, L:W 2.6:1; subterminal seta just below middle of nipple. Mesosoma in dorsal aspect. Prothorax L:W 1:1.7. Posterior margin of mesoscutum mid lobe 1.6 times wider than anterior margin of scutellum mid lobe. Scutellum mid lobe L:W 2:1; 1 pair of setae on each submedian lobe, posterior setae on posterior margin of lobe. Sculpture pattern on mesoscutum and

scutellum mid lobes (Fig. 143). Propodeum wider than long, posterior margin an open V-shape, posterolateral angles obtuse. Fore wings (Fig. 118) L:W 2.2:1; costal margin bent at junction with parastigmal vein; 5-6 long setae on submarginal vein; marginal to submarginal vein length 1.4:1; stigmal vein (Fig. 130) marginal to stigmal vein length 4.7:1; submarginal to stigmal vein length 3.3:1; terminal seta on postmarginal vein slightly longer than those on marginal vein.

Male: Critical point dried material, 1.4 mm long. Head, body and legs a fairly uniform pale brown; mesosoma lightly infuscated. Head in frontal aspect (Fig. 154) rounded in shape, genae slightly flattened, L:W 1:1.3; clypeal margin bilobed, lobes broad. Mandibles (Fig. 164); anterior tooth long, narrow, widely separated from second; second and third well defined, relatively narrow. Maxillary palps (Fig. 177) elongate, widest basally, L:W 4.5:1. Antennae (Figs 194-196) more or less evenly expanded distally, length to head length 1:1.6, L:W 1.9:1; ventral surface (Fig. 195) with a distal, deep, cup-shaped depression; glandular area transverse, narrow, relatively small; distal end of scape broadly excavated, only slightly oblique; funicular segmental proportions (Fig. 196) segment 1 the largest, L:W 1:1.6; segments 2-4 smaller, sub equal, not much narrower than segment 1; MPS formula of flagellum 0011:122. Mesosoma in dorsal aspect. Prothorax L:W 1:1.4. Parapsidal sutures and axillae not as well defined as in *M. clavicornis*. Submedian grooves of scutellum absent, sublateral grooves poorly defined; 2 pair of large setae positioned as in female. Fore trochanters without a ventral tuft of short, stiff setae; tarsal segments 3 + 4 fused. Mid legs (Fig. 222); trochanters with a dense tuft of long, fine setae; femoral fringe of uneven length, proximal half of fringe short, setae a little shorter than width of femur, distal fringe with longer setae about 1.5 times width of femur; L:W femur 4:1; tibia L:W 3.8:1; mid tarsi without fused segments. Fore wings (Fig. 233) broad, L:W 2.4:1; marginal to submarginal vein length 1:1; stigmal vein well developed; costal cell relatively broad, L:W 7.5:1, costal margin arched.

#### MATERIAL EXAMINED:

Holotype and paratypes as listed in TYPE SPECIMENS section.

This species is named *scapata* to draw attention to the relatively short, narrow scapes in the male.

#### *Melittobia digitata* SP NOV

(Figs 42, 53, 63, 74, 88, 89, 106, 119, 131, 144, 155, 165, 178, 197, 198, 199, 224, 235)

#### TYPE MATERIAL:

Holotype ♂ (indicated by arrow) mounted on a card with 4 ♀ 1 ♂ paratypes '5 mls W. Tallahassee, Florida, U.S.A., J. Trexler, 26.xi.1980, ex *Trypoxylon politum*' (USNM). 15 ♀, 2 ♂ paratypes 'Leon Co. Fla., U.S.A., from culture begun 11.26.1980' in the following institutions: BM(NH), QM, UCR, USNM.

#### DISTRIBUTION:

U.S.A. — Florida, Connecticut, Michigan, Texas, Virginia, Mississippi. (= *chalybii* of Buckell (1928), (= species 4 of van den Assem Bosch and Prooy (1982)).

#### DESCRIPTION:

Female: Critical point dried material. 1.6 mm long. Specimens unleached. Head, antennal flagellum, mesosoma, coxae dark brown; trochanters, proximal 2/3 femora, metasoma lighter brown; scape, pedicel, remainder of legs yellow-brown.

Head in frontal aspect (Fig. 42) relatively narrow, length to genal width 1.4:1; genae long, almost parallel; genal-clypeal margin angled; clypeal margin (Fig. 63) bilobed, lobes broad, each with a small, lateral, lobe-like undulation; eyes relatively bare, with a few, short, scattered setae. Facial grooves separate to scrobes; maximum distance between arms 1.8 times diameter of median ocellus; contracting evenly to meet scrobes below middle of eyes; minimum distance between arms 0.5 times diameter of median ocellus. Scrobe length to eye length 1:1.8. Mandibles (Fig. 53); anterior tooth relatively short, narrow; second and third well defined, second the longest, both relatively acute. Maxillary palps (Fig. 74) elongate, cylindrical, of medium length, L:W 3.8:1. Antennae (Figs 88, 89). Scape narrow, L:W 3.9:1; MPS formula on flagellum 567:653; club segment 3 (Fig. 106) shortest length to width 1:2; nipple relatively broad, L:W 3:1; subterminal seta situated well below half way down nipple.

Mesosoma in dorsal aspect. Prothorax L:W 1:1.2. Posterior margin of mesoscutum mid

lobe 1.3 times wider than anterior margin of scutellum mid lobe. Scutellum mid lobe L:W 1.9:1; 1 pair of setae on each submedian lobe, posterior setae situated on posterior margin of lobe. Sculpture pattern on mesoscutum and scutellum mid lobes (Fig. 144). Propodeum wider than long, posterior margin an open V-shape, posterolateral angles obtuse. Fore wings (Fig. 119) L:W 2.5:1, costal margin bent at junction with parastigmal vein; 4 setae on submarginal vein; marginal to submarginal vein length 1.3:1; stigmal vein (Fig. 131) marginal to stigmal vein length 4.3:1; submarginal to stigmal vein length 3.3:1; terminal seta on postmarginal vein longer than those on marginal vein.

Male: Critical point dried specimens 1.5 mm long. Specimens unbleached. Head, mesoscutum, axillae, scutellum yellow, paler than rest of body; antennae, remainder of mesosoma, legs pale brown; metasomal segments each with a posterior broad, transverse, infuscated band. In air dried specimens the whole insect becomes a medium brown, metasoma black. Head in frontal aspect (Fig. 155) vertex broadly rounded, almost straight in air dried specimens; genal margins relatively straight, contracting slightly to an angular genal-clypeal junction; clypeal margin bilobed, lobes broad, well defined. Mandibles (Fig. 165); anterior tooth of median length, broad, well separated from second; second and third teeth well defined, broad, 3 the broadest. Maxillary palps (Figs 178) elongate, cylindrical, of medium length, L:W 3:1. Antennae (Figs 197–199). Scape club-shaped, length to head length 1:1.5, L:W 1.9:1; ventral surface (Fig. 198) with a distal, cup-shaped depression; glandular area elongate, transverse, narrow; distal club margin very deeply excavated producing a thumb-like projection on the side opposite pedicel attachment. Funicular segmental proportions (Fig. 199) 1 largest, L:W 1:1.7; segments 2–4 sub-equal, 2 the smallest; width of 2–4 approximately equal to length of segment 1; MPS formula on flagellum 021:142. Mesosoma in dorsal aspect. Prothorax L:W 1:1.6. Parapsidal sutures and axillae not as well defined as in *M. clavicornis*. Submedian grooves of scutellum absent, sublateral grooves poorly defined. Fore trochanters without a ventral tuft of short, stiff setae;

fore tarsi with segments 3 + 4 fused. Mid legs (Fig. 224); trochanters with a dense tuft of long, fine setae; femoral fringe of uneven length, proximal 1/3 much shorter than width of femur, medial 1/3 about as wide as femur and distal 1/3 about twice width of femur; L:W femur 4.1:1; tibia L:W 3.4:1; mid tarsi without fused segments; setae on tarsal segments relatively long. Fore wings (Fig. 235) broad, L:W 2.7:1; marginal to submarginal vein length 1.2:1; costal cell narrow, L:W 7.6:1, costal margin slightly arched; stigmal vein well developed.

#### MATERIAL EXAMINED:

Holotype and paratypes as listed in TYPE SPECIMENS section.

USNM 3 ♀♀ 3 ♂♂ 'Connecticut, U.S.A., 6.i.1978, T.M. O'dell', 'ex Lab. culture Tachinid *Blepharipa* sp., U.S. Dep. Agr. & Forest Service'; 3 ♀♀ 1 ♂ 'Gainesville, Fa., 2/17/26', 'ex *Tromotobia rufopectus* on *Argiope* sp.', 'W.A. Murrill coll.'; 2 ♀♀ 1 ♂ 'Norfolk, Va., 5.20.31, L.D. Anderson', 'Reared from larvae and pupae, Sphecoid wasp'; 1 ♀ 4 ♂♂ 'College Station, Brazos Co., Texas, viii.8.1976, Hal Reed'; 40 ♀♀ 9 ♂♂ 'Hillsdale, Michigan, U.S.A., Sept. 1977, B.K. Nübel', 'ex *Megachile* sp. nesting in old *Trypoxylon* nests'; 1 ♂ 'State College, Miss., Ex sphecidae, R.E. Hutchings'.

QM 3 ♀♀ 2 ♂♂ on microscope slides with the Hillsdale data above.

This species has been named *digitata* to draw attention to the deeply excised distal margin of the scape which results in a thumb-like projection on the side opposite the pedicel attachment.

#### *Melittobia femorata* SP NOV

(Figs 43, 54, 64, 75, 90, 91, 107, 120, 132, 145, 156, 166, 179, 200, 201, 202, 225, 236)

#### TYPE MATERIAL:

Holotype ♂ 1 paratype ♀ mounted together 'Jackson and Franklin Counties, North Carolina, U.S.A., C.E. Hinton, 21.vi — 11.viii.1979, ex *Trypoxylon politum*'. (USNM); 44 paratype ♀♀ bearing the same data as holotype in the following institutions: BM(NH), QM, UCR, USNM; 4 ♀♀ 2 paratype ♂♂ on slides bearing the same data as holotype (QM).

## DISTRIBUTION:

North Carolina, U.S.A.

## DESCRIPTION:

Female: Critical point dried specimens 1.5-1.6 mm long. Head, antennal flagellum, mesosoma, coxae, trochanters dark brown; proximal 2/3 femora and metasoma paler brown; remainder of legs, dorsal scape and pedicel rufous brown; ventral scape and pedicel yellow-brown. Sculpture pattern on head relatively fine giving the surface a dull shagreened appearance as in *M. megachilis*. Head in frontal aspect (Fig. 43) relatively narrow, length to genal width 1.3:1; genal-clypeal margin angled; clypeal margin (Fig. 64) bilobed, lobes broad; eyes relatively bare, with only a few short scattered setae. Facial grooves remaining separate to scrobes, maximum width between arms 1.2 times diameter of median ocellus; contracting gradually to meet scrobes below middle of eyes; minimum distance between arms 0.2 times diameter of median ocellus. Scrobe to eye length 1:2.7. Mandibles (Fig. 54); anterior tooth short, very broad, second and third well defined, broad, equal. Maxillary palps (Fig. 75) elongate, cylindrical, relatively long 4.2:1. Antennae (Figs 90, 91); scape narrow, L:W 3.7:1; MPS formula on flagellum 577:763; club segment 3 (Fig. 107) shortest length to width 1:1.8; nipple elongate, L:W 4:1; subterminal seta situated just below middle of nipple.

Mesosoma in dorsal aspect. Prothorax L:W 1:1.5. Posterior margin of mesoscutum mid lobe 1.3 times wider than anterior margin of scutellum. Scutellum mid lobe L:W 1.9:1; 1 pair of setae on each submedian lobe, posterior seta situated on posterior margin of lobe. Mesoscutum and scutellum mid lobe sculpture pattern (Fig. 145). Propodeum with posterior margin truncate emarginate, posterolateral angles 90°. Fore wing (Fig. 120) L:W 2.3:1; costal margin bent at junction with parastigmal vein; 3-5 setae on submarginal vein; marginal to submarginal vein length 1.3:1; stigmal vein (Fig. 132) in some specimens quite distinctive, in others it is not unlike that of *M. scapata* (Fig. 130); marginal to stigmal vein length 5.3:1; submarginal to stigmal vein length 4.0:1; terminal seta on end of postmarginal vein not longer than those on marginal vein.

Male: Critical point dried specimen 1.5 mm long. Head, body and legs rufous brown except for infuscations on distal scape, pedicel, vertex, mesosoma and metasoma. Head in frontal aspect (Fig. 156) vertex broadly rounded, lateral margins flat, parallel, L:W 1:1; clypeal margin bilobed. Mandibles (Fig. 166); anterior tooth long, broad, widely separated from others; second and third teeth well defined, broad, equal. Maxillary palps (Fig. 179) elongate, cylindrical, L:W 4.8:1. Antennae (Figs 200-202); scape gradually expanded from proximal end, distal 1/3 showing a slightly greater expansion; length to head length 1:1.5, L:W 1.8:1; ventral surface with distal, deep, cup-shaped depression; glandular area transverse, broad, expanded at side opposite pedicel attachment; distal end of scape transverse, with a deep, relatively narrow excavation; 5 funicular segments, the first is one of the ring joints expanded and segment 2 is equivalent to segment 1 of other species; funicular segmental proportions 1 small, 2 largest, L:W 1:1.4, segments 3-5 sub-equal with 3 the smallest; width of segments 4-5 to length of segment 2 is 1:1.5; MPS formula on flagellum 00142:432.

Mesosoma in dorsal aspect. Prothorax L:W 1:1.4. Parapsidial sutures and axillae not as well defined as *M. clavicornis*. Scutellum without submedian grooves; sublateral grooves clearly marked; 2 pair of long setae situated as in female. Fore trochanters without a ventral tuft of short, stiff setae; fore tarsi with segments 3 + 4 fused. Mid legs (Fig. 225); trochanters with a ventral tuft of long, fine setae; femoral fringe uneven, proximal fringe about equal to width of femur and extends for approximately half the femur; distal fringe is dense with extremely long setae about 1.75 times width of femur; L:W femur 3.9:1; tibia L:W 3:1; mid tarsi without fused segments. Fore wings (Fig. 236) broad, L:W 2.6:1; marginal to submarginal vein length 1.3:1; costal cell narrow, L:W 7.6:1, costal margin above, straight; stigmal vein well developed.

## MATERIAL EXAMINED:

The specimens listed in TYPE SPECIMENS section.

This species is named *femorata* to draw attention to the extremely long mid femoral setae of the male.

*Melittobia chalybii* Ashmead.

(Figs 44, 55, 65, 76, 92, 108, 121, 133, 146, 157, 167, 180, 203, 204 205, 226, 237)

*Melittobia chalybii* Ashmead, 1892 : 231.

*Melittobia chalybii* : Dalla Torre, 1898 : 85.

*Melittobia chalybii* : Schmiedeknecht, 1909 : 466.

*Melittobia chalybii* : Peck, 1951 : 452.

*Melittobia chalybii* : Burks, 1958 : 67.

*Melittobia chalybii* : Peck, 1963 : 162.

*Melittobia chalybii* : Gordh, 1979 : 1005.

## TYPE MATERIAL:

Ashmead (1892) did not select a primary type and merely said, '... from many specimens of both sexes, reared September 14 from cells of *Chalybion caerubum* Linn. collected in Virginia'. I have selected a lectotype and paralectotypes from his point-mounted, syntypical series in the USNM as follows:

1 ♂ minus right antennae flagellum and left wings 'Bladensb. Va. Sept. 14.91', 'Paratype No. 2135 U.S.N.M.'. LECTOTYPE.

1 ♂ minus left antenna, right antennal flagellum and right wings 'Va.', '♂', 'Allotype No. 2135 U.S.N.M.', '*Melittobia chalybii* Ashm.'. PARALECTOTYPE.

1 ♂ minus both antennal flagella, all wings and part of left mesosoma 'Va.', '♂', 'Paratype No. 2135 U.S.N.M.'. PARALECTOTYPE.

1 ♀ intact 'Bladensb. Va. Sept. 14.91', 'Paratype No. 2135 U.S.N.M.', '*Melittobia chalybii* Ashm.'. PARALECTOTYPE.

1 ♀ intact 'Va.', '♀', 'Paratype No. 2135'. PARALECTOTYPE.

1 ♀ minus right antennal flagellum and all wings 'Va.', '♀', 'Paratype No. 2135 U.S.N.M.'. PARALECTOTYPE.

In addition to the above there is 1 point bearing only some legs from a ♂ syntype labelled 'Va.', '♂', 'Paratype No. 2135 U.S.N.M.'. The USNM labels on these specimens incorrectly indicate that the series contains an allotype and several paratypes. Presumably the specimen with a USNM holotype label no longer exists.

## DISTRIBUTION:

U.S.A. — Virginia and New Jersey.

## DESCRIPTION:

Female: Air dried specimens 1.3–1.5 mm long.

Head, antennal flagellum, mesosoma, coxae,

proximal 2/3 femora dark brown; mesosoma paler; scape, pedicel, remainder of legs yellow brown.

Head in frontal aspect (Fig. 44) extremely setose, relatively broad, length to genal width 1.2:1; genal-clypeal margin broadly rounded; clypeal margin (Fig. 65) bilobed, lobes relatively small, each with a small, lateral, lobe-like undulation; eyes densely clothed in longish setae. Facial grooves remaining separate to scrobes; maximum distance between arms 1.2 times diameter of median ocellus; arms converge gradually to meet scrobes just below middle of eye; minimum distance between arms 0.2 times diameter of median ocellus. Scrobe to eye length 1:1.9. Mandibles (Fig. 55); anterior tooth relatively short, narrow; second and third well defined, 2 the narrowest. Maxillary palps (Fig. 76) elongate, cylindrical, of medium width, L:W 3.4:1. Antennae (Fig. 92); scape narrow, L:W 3.3:1; MPS formula on flagellum 346:663, club segment 3 (Fig. 108) shortest length to width 1:2.6; nipple elongate, L:W 3:1; subterminal seta just below middle of nipple. Mesosoma in dorsal aspect. Prothorax L:W 1:1.4. Posterior margin of mesoscutum mid lobe 1.5 times wider than anterior margin of scutellum mid lobe. Scutellum mid lobe L:W 1.9:1; submedian lobes each with 3–5 setae, sometimes varying between left and right on the same specimen. Mesoscutum and scutellum mid lobes sculpture pattern (Fig. 146). Propodeum posterior margin an open V-shape, posterolateral angles obtuse. Fore wing (Fig. 121) L:W 2.4:1; costal margin not as sharply bent at junction with parastigmal vein as other species (except *M. acasta*); marginal to submarginal vein length 1.5:1; 5–6 long setae on submarginal vein; stigmal vein (Fig. 133); marginal to stigmal vein length 4.6:1; submarginal to stigmal vein length 3.2:1; terminal seta on postmarginal vein as long as setae on marginal vein.

Male: Air dried specimens 1.1 mm long. Head, body, legs uniform golden brown. There are indications that the head may be paler than the rest and that the mesosoma is lightly infuscated, but confirmation requires fresh material.

Head in frontal aspect (Fig. 157) rather globose in slide-mounted specimens, L:W 1:1. In air dried specimens head folds transversely just below ocelli which gives the head a shape more like *M. acasta* (Fig. 152).

Genae contracted well below eye spots; clypeal margin bilobed. Mandibles (Fig. 167) elongate, anterior tooth long, narrow, not widely separated from second; second and third unequal, acute, 2 the longer. Maxillary palps (Fig. 180) elongate cylindrical, of medium length, L:W 3.3:1. Antennae (Figs. 203-205). Scape relatively broad, evenly expanded from proximal end, length to head length 1:1.5; L:W 1.6:1; ventral surface (Fig. 204) with a distal, deep, cup-shaped depression; glandular area geniculate; distal end of scape with a relatively shallow excavation, not as deep as in *M. digitata*; funicular segmental proportions 1 the largest, L:W 1:1.3; segments 2-4 sub-equal, 2 the smallest, width of 2-4 to length of 1 1:1.7; MPS formula on flagellum 021:242.

Mesosoma in dorsal aspect. Prothorax L:W 1:1.3. Parapsidal sutures and axillae not as well defined as in *M. clavicornis*. Scutellum without submedian grooves; sublateral grooves weakly defined; 2-3 pairs of large setae positioned as in female. Fore trochanters with a tuft of short, stiff setae, less dense, but longer than *M. australica*; fore tarsi with segments 3 + 4 fused. Mid legs (Fig. 226); trochanters with a ventral tuft of long, fine setae; femoral fringe uneven, proximal 1/3 shorter than width of femur,

distal 2/3 approximately as long as width of femur; L:W femur 3.7:1; tibia L:W 3.4:1; mid tarsi without fused segments. Fore wing (Fig. 237) broad though relatively elongate, posterior margin relatively straight and parallel to costal margin, L:W 2.9:1; marginal to submarginal vein length 1.6:1; costal cell narrow, L:W 11.7:1, costal margin above not arched; stigmal vein well developed.

#### MATERIAL EXAMINED:

USNM 3 ♀ 3 ♂ syntypes as in TYPE SPECIMENS section. 2 ♀♀ 3 ♂♂ card-mounted 'Marlton, N.J., 3.17.40, vial 6, R.G. Schmieder'; 2 ♂♂ same data but from vial 5.

QM 3 ♀♀ 2 ♂♂ on a microscope slide, same data as above, vial 5.

Over the years the name *M. chalybii* has been applied to more than one species of *Melittobia* from North America. Buckell (1928) applied it to *M. digitata*. Although I have not examined his specimens his figures are quite clear and the scape of *M. digitata* males is very distinctive. However, the most common species confused with *M. chalybii* is *M. australica* from which it is easily distinguished using the following characters:

	<i>chalybii</i>	<i>australiana</i>
Female:		
Scape L:W	3.1:1	2.5:1
Scape & pedicel	yellow brown	infuscated
Clypeal margin	bilobed	truncate
Facial grooves	converge separately to scrobes	converge to meet then pass to scrobes as a single line
Setae on submarginal vein	5-6	4
Setae on each submedian lobe of scutellum	3-4	2
Male:		
Scape	ventral cup	ventral groove
Segment 1 of flagellum	the largest	the smallest
Head shape	Fig. 174	Fig. 175
Clypeal margin	bilobed	without lobes
Mid-leg trochanters	with a dense tuft of long fine setae	without this tuft
Fore-wings L:W	2.9:1	3.7:1
Stigmal vein	well developed	reduced to a swelling on marginal vein

Although *M. chalybii* is the commonest name used in the literature for North American *Melittobia* it was the least common species encountered amongst collections borrowed for this revision or forwarded for identification. In fact the only specimens available were the types and some dried specimens from USNM.

*Melittobia megachilis* (Packard)

(Figs 45, 66, 77, 93, 109, 122, 134, 147)

- Anthophorabia megachilis* Packard, 1864 : 134.  
*Anthophorabia megachilis* : Packard, 1868 : 204.  
*Anthophorabia megachilis* : Packard, 1869 : 206.  
*Pteromalus gerardi* Hickok, 1875 : 131.  
*Anthophorabia megachilis* : Howard, 1885 : 46.  
*Melittobia megachilis* : Cresson, 1887 : 244.  
*Melittobia megachilis* : Ashmead, 1892 : 229.  
*Melittobia megachilis* : Ashmead, 1894 : 26.  
*Melittobia megachilis* : Dalle Torre, 1898 : 85.  
*Chrysocharis aeneus* Brues, (1909) : 161.  
*Melittobia megachilis* : Schmiedeknecht, 1909 : 466.  
*Miotropis megachilis* : Viereck, 1916 : 465.  
*Chrysocharis aeneus* : Girault, 1925 : 3.  
*Melittobia megachilis* : Girault, 1925 : 3.  
*Melittobia megachilis* : Peck, 1951 : 452.  
*Melittobia gerardi* : Burks, 1958 : 67.  
*Melittobia megachilis* : Burks, 1958 : 67.  
*Melittobia megachilis* : Peck, 1963 : 162.  
*Melittobia megachilis* : Gordh, 1979 : 1005.

TYPE SPECIMENS:

Packard's species is represented by a syntypical series of 5 females and a tube of dried larvae. These specimens reside in the collections of MCZ, Harvard. Two of the five females I recovered from amongst the dried larvae and mounted on one card with a paralectotype label. The three remaining females were mounted separately on points as follows:

- 1) A reasonably complete female minus right flagellum and labelled '*Anthophorabia megachilis* Pack. F.W.P.', 'Type 529'. I have removed one fore wing from this specimen and mounted it on a microscope slide.
- 2) A damaged female of which only wings and mesosoma remain mounted upside down in glue and labelled '*megachilis*', 'Type 529'.
- 3) A female without wings labelled '*megachilis*', 'Type 529'. I have cleared and mounted this specimen on the slide with the wing of 1.

From these three I have selected (1) as the lectotype and (2-3) as paralectotypes. All specimens have been labelled accordingly.

I have not examined the types of *Pteromalus gerardi* Hickok and *Chrysocharis aeneus* Brues to confirm these synonymies.

DISTRIBUTION:

The type-locality is Brigport, Vermont, U.S.A.

DESCRIPTION:

Female: Air dried specimens 1.3 mm long; 2 ♀♀ ex larvae 1.5 mm long. Head, antennal flagellum, mesosoma, metasoma dark brown; coxae, femora lighter brown; scape, pedicel, remainder of legs yellow-brown. Sculpture pattern on head relatively fine giving the surface a dull shagreened appearance as in *M. femorata*.

Head in frontal aspect (Fig. 45) relatively narrow, length to genal width 1.4:1; genal margin relatively straight, more or less parallel; clypeal margin (Fig. 66) bilobed; eyes relatively bare, with a few, short, scattered setae. Facial grooves remaining separate to scrobes; greatest width between arms 1.8 times diameter of median ocellus; arms converging gradually to meet scrobes well below middle of eyes; minimum distance between arms 0.2 diameter of median ocellus. Scrobe to eye length 1:2.2 but may be larger because the eyes are folded transversely. Mandibles not visible. Maxillary palps (Fig. 77) elongate, cylindrical, long, L:W 5:1. Antennae (Fig. 93); scape narrow, L:W 3.7:1; MPS formula on flagellum 565:663; club segment 3 (Fig. 109) shortest length to width 1:1.4; nipple relatively short, L:W 2.5:1; subterminal seta almost basal.

Mesosoma in dorsal aspect. Prothorax L:W 1:1.4. Posterior margin of mesoscutum mid lobe 1.5 times wider than anterior margin of scutellum mid lobe. Scutellum mid lobe L:W 1.9:1; 1 pair of setae on each submedian lobe, posterior seta on posterior margin of lobe. Propodeum posterior margin an open V-shape, posterolateral angles obtuse. Mesoscutum and scutellum mid lobe sculpture pattern (Fig. 147). Fore wing (Fig. 122) L:W 2.5:1; marginal to submarginal vein 1.3:1; 4 setae on submarginal vein; marginal to stigmal vein length 5.2:1; submarginal to stigmal vein 4.0:1; terminal seta on postmarginal vein not longer than those on marginal vein.

Male: Unknown.

## MATERIAL EXAMINED:

Only the types of this species were available as in the section TYPE SPECIMENS.

*Melittobia australica* Girault

(Figs 46, 56, 68, 78, 96, 97, 112, 124, 135, 148, 158, 169, 181, 206, 207, 208 227, 238)

*Melittobia australica* : Girault, 1912 : 203.

*Melittobia australica* : Girault, 1913 : 205, 250.

*Melittobia australica* : Girault, 1914 : 8.

*Melittobia australica* : Girault, 1915 : 216, 259.

*Melittobia australica* : Dahms, 1973 : 411.

## TYPE SPECIMENS:

The syntypical series of Girault consists of 7 ♀♀ 2 ♂♂ on a microscope slide '*Melittobia australica* 2 ♀ 2 ♂', 'TYPE Hy/997, A. A. Girault' (QM). There are in DPIQ 5 slides containing numerous specimens of both sexes and all labelled, 'Dep. Ag. & Stk., Qld. CHALCIDIDAE *Melittobia australica* Ex *Pison spinolae* (Hym.) Tambourine 11/12/11 H.T. No. Hy.58', 'Mt. Tambourine S. Queensland Dep. Ag. & S. 11.12.11'. These are all part of the original series bred by Tryon, but have no Girault labels. One of these slides contains 3 females and 1 male therefore fitting Girault's published information for his 'Cotypes' and it would be safe to assume that he saw the remainder of the slides. I am therefore labelling the 5 slides as containing paralectotypes. The QM slide has been relabelled by someone other than Girault and the error in the number of females (2 as opposed to 7) is no doubt one of transliteration. From this series I have selected the intact male as the lectotype and the remaining specimens (7 ♀♀ 1 ♂) as paralectotypes. No locality data occurs on this slide, but the published data read, 'Host, *Pison spinolae* (Hym.) Mt. Tambourine, S. Queensland, Dept. Ag. & S., 11; 12; 11'.

## DISTRIBUTION:

South Africa, Australia, Japan (= species 2 of van den Assem and Maeta (1978)), North America (= *M. chalybii* of Hermann (1971), Evans and Matthews (1976)), Jamaica (= *M. chalybii* of Freemann and Parnell (1973), Freemann (1977)) (= *hawaiiensis* complex of Freeman and Ittyeipe (1976), Jayasingh and Freeman (1980)), (= species 8 of van den Assem, Bosch and Prooy (1982)).

## DESCRIPTION:

Female: Critical point dried specimens 1.1-1.2 mm long. Head, antennal flagellum,

mesosoma, coxae, proximal 2/3 femora dark brown; scape and pedicel barely paler; metasoma paler; remainder of legs pale brown.

Head in frontal aspect (Fig. 46) length to genal width 1.4:1; genal-clypeal margin broadly rounded; clypeal margin (Fig. 68) truncate emarginate; eyes densely covered with long setae. Facial grooves converging to meet just above middle of eyes then passing as a single line to scrobes; maximum width between arms 2.9 times diameter of median ocellus (approximately equals POL). Scrobe to eye length 1:2.8. Mandibles (Fig. 56); anterior tooth long, narrow relatively close to second; second and third tooth well defined, 2 longer and narrower. Maxillary palps (Fig. 78) cylindrical, short, L:W 2.8:1. Antennae (Figs 96, 97); scape broad, L:W 2.5:1; MPS formula on flagellum 445:573; club segment 3 (Fig. 112) shortest length to width 1:1.2; nipple elongate, L:W 4:1; subterminal seta in distal half of nipple.

Mesosoma in dorsal aspect. Prothorax L:W 1:1.5. Posterior margin of mesoscutum mid lobe 1.3 times wider than anterior margin of scutellum mid lobe. Scutellum mid lobe L:W 1.9:1. Mesoscutum and scutellum mid lobe sculpture pattern (Fig. 148). Submedian lobes of scutellum each with 1 pair of setae, posterior seta well forward of posterior margin of lobe. Propodeum posterior margin an open V-shape, posterolateral angles obtuse. Fore wing (Fig. 124) L:W 2.3:1; marginal to submarginal vein length 1.6:1; 4 setae on submarginal vein; stigmal vein (Fig. 135); marginal to stigmal vein length 4.2:1; submarginal to stigmal vein length 2.6:1; terminal seta on postmarginal vein slightly longer than those on marginal vein.

Male: Critical point dried specimens 1.2-1.3 mm long. Entirely honey brown in colour except upper face in an area equivalent to that between the facial grooves in female pale, mesoscutum lightly infuscated, funicle segment 4 plus club strongly infuscated. Head in frontal aspect (Fig. 158) wider than long L:W 1:1.4, transversely elliptical, lateral margins broadly rounded; clypeus deeply impressed, area above impressed clypeus and below toruli with a dense tuft of fine setae (similar to head setation); clypeal margin without lobes, as Fig. 158. Mandibles (Fig. 169); anterior tooth relatively broad and widely separated from second; second and



third well defined, sub-equal, 2 slightly longer. Maxillary palps (Fig. 181) as *M. hawaiiensis*, cylindrical, short and broad, L:W 2.5:1. Antennae (Figs 206–208); scape broad, expanded evenly from proximal end except for a pronounced constriction about mid-way along scape; length to head length 1:1; scape L:W 1.8:1; ventral surface (Fig. 207) with a deep longitudinal groove, proximal end of groove with only one seta; glandular area geniculate, one arm more or less transversely across distal scape, the other along the side of groove opposite pedicel attachment; flange overhanging scape groove on same side as pedicel attachment with up to 5 setae, most of which are not on the margin; distal scape margin more or less transverse, not oblique; funicular segmental proportions (Fig. 208) 1 short the smallest segment; 2 and 3 large, wider than long; 4 short, transverse, cup-shaped, closely applied to club segment 1; MPS formula on flagellum 0000:141.

Mesosoma in dorsal aspect. Prothorax 1:1.5. Parapsidal sutures and axillae reasonably well defined though not as well as in *M. clavicornis*. Submedian grooves of scutellum absent, sublateral grooves faint; 2 pair of setae present, positioned as in female. Fore legs with a dense tuft of short, stiff setae (Dahms 1983b: Plate 4b); tarsal segments 3 + 4 fused. Mid leg (Fig. 227) trochanters without a ventral, dense tuft of long, fine setae; femoral fringe divided into 2 sections, a short proximal tuft on basal 1/4 of femora, a space without setae about equal to 1/4 femoral length followed by a fringe occupying distal 1/2 of femur; setal fringe slightly longer than 1.5 times width of femur; L:W femur 4.3:1; tibia L:W 4.1:1; tarsi without fused segments. Fore wings (Fig. 238) elongate, apex rounded, L:W 3.7:1; marginal to submarginal vein length 1.9:1; stigmal vein reduced to a swelling on end of marginal vein; costal cell narrow L:W 13.5:1; costal margin slightly arched above.

#### MATERIAL EXAMINED:

QM Lectotype and paralectotypes as in TYPE SPECIMENS section; 6 ♀♀ 4 ♂♂ card-mounted 'Brisbane SEQ, E.C. Dahms, Dec. 1979, ex *Sceliphron laetum*'; 2 ♀♀ 2 ♂♂ slide-mounted '*Melittobia australica* Grlt. E. Dahms det. 1980, Brisbane, SEQ, E.C. Dahms, Dec. 1979 ex *Sceliphron laetum*, Uparal E.C.D.'; 27 ♀♀ slide-mounted

'*Melittobia australica* Girault, Bred from cells of *Sceliphron laetum*, 20.1.1918, H. Hacker'; 16 ♀♀ 4 ♂♂ second-form individuals 'Brisbane, January 1981, E.C. Dahms ex laboratory colony on *Sceliphron formosum*'; 17 ♀♀ 4 ♂♂ card-mounted 'Acacia Ridge, Brisbane, SEQ, E. Dahms, 21.1.1979', 'ex *Stenarella victoriae*'; 2 ♀♀ 2 ♂♂ card-mounted, 4 ♀♀ 5 ♂♂ slide-mounted 'Aritagun, Wakayama Pref., Japan, on *Megachile subalbata*, M. Matsuura, iii.1976'; 8 ♀♀ 2 ♂♂ card-mounted, 4 ♀♀ 2 ♂♂ slide-mounted 'Kingston, Jamaica, West Indies, on *Sceliphron assimili*, K. Ittayeipe, v.1975'; 8 ♀♀ 2 ♂♂ card-mounted, 3 ♀♀ 3 ♂♂ slide-mounted 'ex culture maintained at University of Georgia, D.A. Evans, on *Trypoxylon striatum*, v.1975'; 2 ♀♀ 2 ♂♂ on a microscope slide 'Brits., Transvaal, Rep. South Africa on *Sceliphron* sp., R.T. Simon Thomas, xi.1974'.

In addition 4 ♀♀ and 1 ♂ from the following localities are deposited in BM(NH) and USNM.

- 1) 'Brisbane, SEQ, E.C. Dahms, Dec. 1980, ex *Sceliphron laetum*'.
- 2) 'Brisbane, SEQ, E.C. Dahms, January 1981', 'ex laboratory colony on *Sceliphron formosum*, second-forms'.

#### *Melittobia hawaiiensis* Perkins

(Figs 94, 95, 110, 111, 123, 136, 168, 170, 209, 210)

*Melittobia hawaiiensis* : Swezey, 1907 : 125.

*Melittobia hawaiiensis* Perkins, 1907 : 126.

*Melittobia hawaiiensis peles* Perkins, 1907 : 127.

*Sphecophagus sceliphronidis* Brèthes, 1911 : 209.

*Sphecophilus sceliphronidis* : Brèthes, 1911 : 311  
SYN NOV

*Melittobia hawaiiensis* : Masi, 1917 : 226.

*Melittobia hawaiiensis* : Ferrière, 1933 : 103.

*Melittobia hawaiiensis* : Gradwell, 1958 : 277.

*Melittobia peles* : Yoshimoto, 1965 : 683.

*Melittobia hawaiiensis* : Yoshimoto, 1965 : 683.

*Melittobia hawaiiensis* : De Santis, 1973 : 18.

#### TYPE SPECIMENS:

Perkins (1907) did not indicate the location of the type of this species and did not consider it necessary ... 'because the specimens could not be preserved in satisfactory condition for subsequent comparison'. Gradwell (1958) selected a neotype

of this species from a slide containing 11 ♀♀ 1 ♂ in the collections of the British Museum (Nat. Hist.). I have examined this slide and confirmed the separation of *M. hawaiiensis* and *M. australica*. The separation is not easy, but it was aided by fresher material of *M. hawaiiensis* and *M. australica*, in conjunction with the fact that the two will not interbreed (van den Assem pers. comms. 1974–1980). Brèthes (1911) described the species *Sphechophagus sceliphronidis* and in 1911 changed the generic name to *Sphechophilus* believing *Sphechophagus* to be preoccupied. De Santis (1949) transferred this species to the genus *Melittobia*. In 1957 De Santis made *S. sceliphronidis* a junior synonym of *M. acasta*. I have been unable to locate the type of *S. sceliphronidis*, but from Brèthes' figures and description, the species is definitely not *M. acasta* — the scape has a ventral longitudinal groove. The only species it could possibly be, given the present state of knowledge of the world *Melittobia* fauna, are *M. hawaiiensis*, *M. australica* or sp. nov. Argentina. From Brèthes' figures it is clearly not the latter. De Santis (1973) records *M. hawaiiensis* from Argentina but this species is difficult to separate from *M. australica* without slide preparations of the male scape. In the absence of any material of these species from South America and the type of *S. sceliphronidis* I have provisionally placed *M. sceliphronidis* as a junior synonym of *M. hawaiiensis* subject to confirmation.

#### DISTRIBUTION:

South America, Hawaii, New Zealand (= *M. clavicornis* Donovan (1953) and Cowley (1961)) (= species 7 of van den Assem, Bosch and Prooy (1982)), Seychelles, Guam. In the literature there are a great many localities given for this species especially around the Pacific region, e.g. Yoshimoto (1965). Because of the ease of confusion of this species with *M. australica* I have listed only the distribution of specimens I have examined.

#### DESCRIPTION:

Female: In all aspects examined the females of *M. hawaiiensis* and *M. australica* tend to grade into one another e.g. variations in shape of the stigmal vein overlap, the degree of infuscation of the scape and pedicel is variable within each species and overlaps between species and so on. Given the present state of knowledge of the two species I cannot separate them on females.

Male: Again *M. hawaiiensis* and *M. australica* males are very similar in most respects and their variations overlap between species. Only one consistent feature serves to distinguish the species and that is setation on the scape. Compare figures 206, 209 and 210. The flange overhanging the groove of the scape, on the same side as the pedicel is attached, is relatively longer, and has more than 5 setae, most of which are arranged on the edge of the flange; the proximal floor of the groove has more than 2 setae (generally 5 or more) as opposed to 1–2 in *M. australica*. The last mentioned setal arrangement appears very reliable in all specimens of the species that I have examined.

In addition to these species I have specimens of an *hawaiiensis*-type species from Kauai, Hawaii (= species 7/8 of van den Assem et alia (1982)). Again the females appear very similar to *M. hawaiiensis* and *M. australica* except that the nipple on club segment 3 is longer and narrower (Figs 110–112). Males also are very similar except in the setation patterns on the scapes. The flange overhanging the scape groove is relatively short as in *M. australica*, it has more setae than in *M. hawaiiensis* and these setae are distributed along the entire length of the flange, whereas they are more restricted in *M. australica* and *M. hawaiiensis*. The mandibles of males also show some differences (Figs 168–170). However I am rather hesitant to describe the Kauai material as a new species. This whole complex is in need of a detailed morphometric study which could be tied in with ethological work of van den Assem et alia (1982). In the summary of this paper aspects of crossing experiments by van den Assem et alia (1982) with *hawaiiensis* group species and Kauai are discussed.

#### MATERIAL EXAMINED:

BM(NH) Neotype slide with 11 ♀♀ 1 ♂ as figured by Gradwell (1958).

1 ♀ card-mounted 'Mahé '08–9, Seychelles Exp.', 'Percy Sladen Trust Exped., BM 1913–170', '*Melittobia hawaiiensis* Perkins, L. Masi det.'

QM 7 ♀♀ 1 ♂ on a microscope slide '*Melittobia hawaiiensis* Perk., Gahan, ex *Pison argentatum*, Piti, Guam 9–27–36, O.H.S.'; 3 ♀♀ 3 ♂♂ on microscope slides, 4 ♀♀ 2 ♂♂ card-mounted '*Melittobia hawaiiensis* Perkins, ex Lab culture Est. from Te Pirita, Canterbury, New Zealand, Sept. 1974, B.J. Donovan ex *Pison spinolae*, E.C. Dahms

Euparal'; 6 ♀♀ 3 ♂♂ on microscope slides, 1 ♀ 1 ♂ card mounted 'ex lab culture est. from Kilauea, Kauai, Hawaii, 21.xi.1976, S.L. Montgomery and J. Maciolek 100' ex mud nest, E.C. Dahms Euparal'.

*Melittobia assemi* SP NOV

(Figs 67, 79, 125, 137, 149, 159, 171, 182, 211, 212, 213, 228)

TYPE SPECIMENS:

Holotype ♂ 5 ♀ paratypes on the one card 'Anse Bazarca, Mahé Island, Seychelles, ex eumenid species, R.T. Simon Thomas, ii.1976' BM(NH); 2 ♀ paratypes card-mounted, 4 ♀ 2 ♂ paratypes on a slide with data as holotype (QM).

DISTRIBUTION:

Mahé Island, Seychelles (*M. hawaiensis* (in part) of Masi (1917)), Kerala Forest Reserve, India (= species 5 of Assem, Bosh and Prooy (1982))

DESCRIPTION:

Female: Critical point dried specimens 1.3 mm long. Head, flagellum, mesosoma, coxae dark brown; proximal 2/3 femora, metasoma slightly paler; scape, pedicel, remainder of legs pale yellow-brown; upper scape and pedicel lightly infuscated.

Head in frontal aspect as *M. sosui* (Fig. 47) length to genal width 1.3:1; genal-clypeal margin broadly rounded; clypeal margin (Fig. 67) bilobed, lobes small, each sharply separated from a small, lateral, lobe-like undulation. Eyes densely clothed with long setae. Facial grooves converging to meet just above middle of eyes then passing as a single line to scrobes; maximum distance apart of arms greater than POL. Scrobe to eye length 2.6:1. Mandibles as *M. sosui* (Fig. 57) anterior tooth very small, broad; second and third well defined, broad, 3 the broadest. Maxillary palp (Fig. 79) short, broad, L:W 2.5:1. Antennae as *M. sosui* (Figs 100, 101) scape broad, relatively strongly curved, L:W 2.8:1; MPS formula on flagellum 335:263; segment 3 of club as *M. sosui* (Fig. 113) shortest length to width 1:2; nipple relatively long, L:W 3:1; subterminal seta about mid-way down nipple.

Mesosoma in dorsal aspect. Prothorax L:W 1:1.5. Posterior margin of mesoscutum mid lobe 1.1 times wider than anterior margin of

scutellum mid lobe. Scutellum mid lobe L:W 1.9:1; 3-4 setae on each sublateral lobe. Propodeum posterior margin an open V-shape, posterolateral angles obtuse. Fore wing (Fig. 125) L:W 2.4:1; marginal to submarginal vein length 1.5:1; 5 setae on submarginal vein, the proximal 2 about 1/2 length of others; stigmal vein (Fig. 137); marginal to stigmal vein length 3.4:1; submarginal to stigmal vein 3.7:1.

Male: Air dried ex alcohol about 1.3 mm long.

Head, body and legs pale golden brown; antennae also, except funicle 4 and club which are infuscated.

Head in frontal aspect (Fig. 159) broad, vertex broadly rounded, hardly raised, lateral margins broadly rounded contracting slowly below eye spots; genal-clypeal margin broadly rounded; clypeal margin bilobed, lobes long, narrow, clypeus deeply excised between; clypeus deeply impressed, area above impression and below toruli with a dense cluster of long, fine setae. Mandibles (Fig. 171) broad, anterior tooth of medium length, broad, well separated from second; second and third tooth shallowly defined, broad. Maxillary palps (Fig. 182) tapered distally, short, broad, L:W 2.2:1. Antennae (Figs 211-213); scape more or less gradually expanded from proximal end, whole scape curved, concave on outer margin; ventral surface with a deep, longitudinal groove, more open than *M. australica* (Fig. 206), flange over-hanging groove on side of pedicel attachment narrow, without long setae; glandular area geniculate, but distal arm not as transverse as in *M. australica* (Fig. 207); distal scape transverse, not excavated (Figs 211-212); scape length to head length 1.3:1; scape L:W 1.6:1; pedicel tends to be concave on inner margin as in *M. sosui* (Fig. 216); funicular segmental proportions (Fig. 213) 1-3 sub-equal, 4 transverse, cup-shaped, closely applied to segment 1 of club; MPS formula on flagellum 0000:162.

Mesosoma in dorsal aspect. Prothorax L:W 1:1.3. Parapsidial sutures absent, axillae poorly defined. Scutellum without submedian or sublateral grooves; 3-4 pairs of setae on scutellum positioned as in females. Fore trochanters without a ventral, dense tuft of stiff, short setae; tarsi (Fig. 20) with 2 segments, 2 + 3 + 4 fused. Mid legs (Fig. 228); trochanters with 6-12 long, curved, stiff setae; femoral fringe of uneven length,

sparse, proximally absent, followed by a few short setae, then a median fringe of setae not quite long as width of femur, the distal c. 1/4 of fringe consists of short setae, width of femur to length of distal fringe is about 2.5:1; L:W femur 3.6:1; tibia L:W 3.7:1; mid tarsi with 3 segments, segments 1 and 2 with a posterior comb of long thick setae. Fore wing as *M. sosui* (Fig. 239) long, narrow, L:W 4.1:1, apex acute; marginal to submarginal vein length 1.7:1; costal cell narrow, L:W 6:1; stigmal vein reduced to a large swelling at the end of marginal vein.

#### MATERIAL EXAMINED:

Type specimens as in TYPE SPECIMENS section.

QM 1 ♀ 1 ♂ + 1 ♂ head on microscope slides 'Nilambur Kerala State, South India, from H. van den Assem, Feb. 1980, E.C. Dahms Euparal'.

BM(NH) 4 ♀♀ card-mounted 'Percy Sladen Trust expedition, BM 1913-170', 'Mahé '08-9, Seychelles Exp.', '*Melittobia hawaiiensis* Perkins, L. Masi det.'

This species has been named in recognition of Dr van den Assem, Leiden who has been very generous with notes from his ethological studies and with specimens.

#### *Melittobia sosui* SP NOV

(Figs 47, 57, 80, 100, 101, 113, 138, 172, 183, 214, 215, 216, 230, 239, 240)

#### TYPE MATERIAL:

Holotype ♂ 5 ♀ paratypes (one ♀ minus head) card-mounted 'Sosu, Okinawa Isl., Ryuku Arch., Japan, Y. Maeta, 23.xii.1978 ex Eumenid' (KU); 3 ♀ 2 ♂ paratypes on slides with data of holotype (QM).

#### DISTRIBUTION:

Okinawa Isl., Japan (= species 4 of van den Assem and Maeta (1980)) (= species 6 of van den Assem et alia (1982)).

#### DESCRIPTION:

This species is very close to *M. assemi* and the description to follow merely consists of diagnostic differences from *M. assemi*.

Female: Critical point dried specimens 1.3-1.4 mm long. Coloration as in *M. assemi*.

There are some proportional differences between *M. assemi* and *M. sosui* females, but

these are not very significant given the natural variation in *Melittobia* and the polymorphism in the type-forms of *M. sosui* recorded by van den Assem and Maeta (1980). Therefore it would be unwise to rely upon these proportional differences for species separation. As with the *M. hawaiiensis* complex this species group is in need of detailed morphometric analysis.

In females that I have for examination there appear to be three consistent features which are of use:

- 1) Of the 5 setae on the submarginal vein in *M. assemi* the proximal 2 are about 1/2 the length of the remaining 3 whereas in *M. sosui* the 5 are of equal length.
- 2) On each submedian lobe of the scutellum, *M. assemi* has 3-4 setae, occasionally with variation between left and right on the one specimen, whereas in *M. sosui* I observed a consistent 2 on the left lobe and 3 on the right.
- 3) Stigmal veins are different (Figs 137, 138).

Males of the two species are also very similar but there are a few consistently different features:

- 1) The mandibles of *M. sosui* (Fig. 172) are shorter and broader than *M. assemi* (Fig. 171).
- 2) The maxillary palps in *M. sosui* (Fig. 183) are shorter than in *M. assemi* (Fig. 182); L:W 1.4:1 as opposed to 2.2:1 for *M. assemi*.
- 3) The scape of *M. sosui* (Figs 214, 215) is narrower than *M. assemi* (Figs 211, 212); L:W 2:1 as opposed to 1.6:1 for *M. assemi*. In *M. sosui* the flange overhanging the scape groove is broader than in *M. assemi* and bears several long setae (up to 5).
- 4) The mid femoral fringe has more setae and covers a greater length of the femur in *M. sosui* than in *M. assemi* (Figs 228, 230). The shapes of the femora are different; L:W *M. sosui* 3.8:1, *M. assemi* 3.6:1.

#### MATERIAL EXAMINED:

As in TYPE SPECIMENS section.

This species is named *M. sosui* after its type-locality.

*Melittobia bekiliensis* Risbec.

*Melittobia bekiliensis* Risbec, 1952 : 253.

## TYPE MATERIAL:

2 ♀♀ 1 ♂ on minutien pins 'MADAGASCAR, Bekily, REG SUD DE L'ILE', 'MUSEUM PARIS, vi.36, A. SEYRIC', '*Melittobia bekiliensis* Risb', 'Syntype'. From this syntypical series I have selected the male as the lectotype and the females as paralectotypes. They reside in the collections of the Musée National d'Histoire Naturelle, Paris.

## DISTRIBUTION:

Madagascar.

## DESCRIPTION:

Female: Air dried specimens 1.0–1.1 long. Head, pedicel, flagellum, mesosoma dark brown; metasoma slightly paler; scape, legs pale yellow-brown.

These specimens appear to be very similar to females of *M. assemi*. It is difficult to separate them without making slides. This difficulty is increased due to disruption of the thorax by the minutien pin and reliable diagnosis of the female must await fresh material.

Male: Air dried specimen. About 1.2 mm long, specimen curled.

Head in frontal aspect resembling that of *M. assemi* (Fig. 159); not contracting ventrally as strongly as *M. assemi* and the clypeal region is barely impressed; setation below toruli not dense as in *M. assemi*; clypeal margin bilobed, lobes not as long as *M. assemi*. Mandibles not projecting below clypeal margin when closed. Maxillary palps contracting distally as *M. assemi* (Fig. 182). Antennal scapes quite distinctive, expanding evenly from proximal end (no constrictions as in *M. australica* (Fig. 207)), pyriform, not curved as in *assemi* (Fig. 212), dorsal surface smoothly rounded; ventral surface with a deep longitudinal groove, relatively open as in *M. assemi*; flagellum difficult to see; segment 1 very small; 2+3 slightly larger; 4 very wide, asymmetrically cup-shaped, closely applied to club, longest side of 4 nearly covering club segment 1.

Mesosoma in dorsal view. Prothorax wide, triangular, L:W 1:3. Fore legs as in *M. assemi* (Fig. 20). Fore trochanters without a ventral tuft of short, stiff setae; fore tarsi 2 segmented. Mid legs as *M. assemi* except distal setae on femoral fringe are not shorter than those of medial fringe; tarsal segments

appear unfused. Fore wings resemble those of SP NOV Argentina (Fig. 241), apex broadly rounded; stigmal vein well developed.

This is quite a distinctive species in the male. Its scape, maxillary palp and femoral fringe place it with *M. assemi* and *M. sosui*.

Argentina SP NOV

(Figs 48, 58, 69, 81, 98, 99, 114, 126, 139, 150, 160, 173, 184, 217, 218, 219, 229, 241)

## TYPE SPECIMENS:

Material too poor for type selection.

## DISTRIBUTION:

Argentina.

## DESCRIPTION:

Female: Air dried specimens from alcohol 1.1 mm long. Head, mesosoma, antennal flagellum, coxae, proximal 1/3 of femora dark brown; scape, pedicel and remainder of legs yellow-brown; metasoma slightly paler than mesosoma.

Head in frontal aspect (Fig. 48) broad, length to genal width 1.2:1; genal-clypeal margin broadly rounded; clypeal margin (Fig. 69) bilobed, lobes broad, weakly developed; eyes densely covered with long setae. Facial grooves converging separately to scrobes; maximum width between arms 2 times diameter of median ocellus; arms converging gradually to meet scrobes just below middle of eyes; minimum distance between arms 0.25 times diameter of median ocellus. Scrobe to eye length 1:1.9. Mandibles (Fig. 58); anterior and median tooth long, narrow, third shorter and broader. Maxillary palp (Fig. 81) elongate, of medium length, L:W 4:1. Antennae (Figs 98, 99); scape broad, L:W 2.5:1; MPS formula on flagellum 445:463; club segment 3 (Fig. 114) shortest length to width 1:2; nipple relatively long, L:W 3:1; 2 subterminal setae situated in proximal 1/3 of nipple.

Mesosoma in dorsal aspect. Prothorax L:W 1:1.8. Posterior margin of mesoscutum mid lobe equal to width of anterior margin of scutellum mid lobe. Scutellum mid lobe L:W 1.8:1; 1 pair of setae on each submedian lobe, posterior situated on posterior margin of this lobe. Mesoscutum and scutellum mid lobes sculpture pattern (Fig. 150). Fore wing (Fig. 126) L:W 2.2:1; marginal to submarginal vein

length 1.6:1; 4-5 setae on submarginal vein; stigmal vein (Fig. 139); marginal to stigmal vein length 4.8:1; submarginal to stigmal vein length 3.1:1; terminal seta on postmarginal vein no longer than those on the marginal vein.

Male: Air dried specimen from alcohol, metasoma absent, length of head mesosoma 0.5 mm. Head, scape, funicular segments 2-3, legs pale brown; funicular segment 4 club strongly infuscated.

Head in frontal aspect (Fig. 160) broad, more or less rectangular, lateral margins not contracting strongly to clypeus, genae slightly indented below eye spots, L:W almost 1:1; clypeus impressed, area above clypeus and below toruli with a dense tuft of long, thick setae; clypeal margin bilobed, lobes broad, well defined. Mandibles (Fig. 173) very broad, projecting well below clypeus when closed. Maxillary palps (Fig. 184) very distinctive, broad, distally excavated, L:W 1.4:1. Antennae (Figs 217-219); scape relatively evenly expanded from proximal end, distal 1/2 expanding rather suddenly; ventral surface (Fig. 218) with a deep longitudinal groove, more open than *M. australica*; glandular area rather amorphous, extending along groove; scape to head length 1:1.2; scape L:W 1.9:1; distal scape more or less truncate, without an excavation; funicular segments (Fig. 219) transverse, 1 the narrowest; 2 + 3 sub-equal; 4 as wide as 2 and 3, cup-shaped, closely applied to club segment 1; MPS formula on flagellum 0000:131.

Mesosoma in dorsal aspect. Prothorax L:W 1:1.6. Parapsidial sutures and axillae poorly defined. Scutellum without submedian and sublateral grooves. Fore legs (Fig. 21); trochanters without a dense tuft of short, stout setae; tarsal segments fused into 1. Mid legs (Fig. 229); trochanters with a few, curved, short, thick setae; femoral fringe not completely lining femora, basal 1/4 with very short, normal setation, distal 3/4 of even length, slightly longer than width of femur; ventral surface of femur appears grooved to receive tibia; L:W femur 7.2:1; tibia L:W 5.7:1; mid tarsi of 2 segments, 2 + 3 + 4 fused. Fore wing (Fig. 241) relatively broad, L:W 3:1; marginal to submarginal vein length 1.8:1; costal cell narrow L:W 6:1, costal margin above slightly arched; stigmal vein well developed.

#### MATERIAL EXAMINED:

CU, NY ♀♀ fragments card mounted as follows — 3 heads with antennae; 2 heads plus mesosoma and 1 fore wing; 1 complete specimen except for antennae. 1 ♂ head plus mesosoma without wings; several fragmentary females in alcohol 'Ascasubi Argentina, Dec. 1976, R.H. Gonzalez', 'ex *Megachile rotundata*'; 3 ♀♀ 1 ♂ on a microscope slide with above data.

I have not named this species because the specimens are too poor for type-selection.

#### INCERTAE SEDIS

*Melittobia osmia* Thompson

*Melittobia osmia* Thompson, 1878 : 204.

*Melittobia acasta* (?) : Domenichini, 1966 : 56.

#### TYPE SPECIMENS:

Not located.

#### DISTRIBUTION:

Europe.

Domenichini (1966) provisionally placed this species as a junior synonym of *M. acasta*. It may well fit here, but the description is not diagnostic and I could not locate the type. For these reasons it was decided to leave it as a separate species awaiting confirmation.

*Melittobia hawaiiensis peles* Perkins

*Melittobia hawaiiensis peles* Perkins, 1907 : 125.

*Melittobia peles* : Yoshimoto, 1965 : 683.

#### TYPE SPECIMENS:

Not located.

#### DISTRIBUTION:

Oahu, Hawaii.

I have been unable to locate the type of this variety and the brief description by Perkins is insufficient to allow recognition of this taxon.

#### SUMMARY:

Van den Assem and Maeta (1978, 1980) using ethological criteria have divided the genus into *acasta* group, *hawaiiensis* group and Mahé group (= *assemi* group) and have kept *M. clavicornis* separate as the most primitive species. When one looks at the comparative morphology of the males a similar grouping applies using the following characteristics:

	<i>acasta</i>	<i>hawaiiensis</i>	<i>assemi</i>
1) scape:	cup	grooved	grooved
2) gland in scape:	transverse	geniculate	geniculate
3) proportions of funicular segments:	1 largest	1 smallest	all equal
4) funicular seg. 4 cup shaped and closely applied to club 1:	—	+	+
5) presence of plate organs on funicle:	+	—	—
6) mid trochanters with a dense tuft of long fine setae:	+	—	—
7) wings broad:	+	—	—

The grouping on this basis is as follows:

<i>acasta</i> group	<i>hawaiiensis</i> group	<i>assemi</i> group
<i>acasta</i>	<i>hawaiiensis</i>	<i>assemi</i>
<i>evansi</i>	<i>australica</i>	<i>sosui</i>
<i>scapata</i>	Kauai	<i>bekiliensis</i>
<i>femorata</i>		Argentina
<i>digitata</i>		
<i>chalybii</i>		
<i>megachilis</i> (?)		

Of these groups, *hawaiiensis* and *assemi* appear closest. I regard the unifying characters as derived relative to *M. clavicornis* and considering the shared possession of these derived characters, these two groups could confidently be regarded as

monophyletic sister groups. Species within these groups can be sorted on a mixture of derived and relatively primitive features, and this again points to the monophyly of each group. The division is as follows:

	<i>hawaiiensis</i> group	<i>assemi</i> group
1) head	elliptical *	rectangular *
2) mandibles	narrow	broad *
3) funicle segments	1 small 2+3 large *	1-3 sub-equal *
4) mid femoral fringe	long proximally *	short proximally
5) fore trochanters with a dense tuft of short setae	+ *	—
6) mid trochanters with 6-12 long, stiff curved seta	no long setae *	+ *
7) ventral fore trochanters with a dense setae tuft of stiff setae	+ *	—

(\* = characters I regard as derived)

The *hawaiiensis* group has relatively few species which may be a reflection of our state of knowledge of the world fauna. The species *M. hawaiiensis* and *M. australica* is very close morphologically and ethologically, but van den Assem et alia (1982) found that they are reproductively isolated when they tried crossing them. However, they discovered that females of both *M. hawaiiensis* and *M. australica* when crossed with males of Kauai produced fertile female offspring. Reciprocal crosses gave similar results. It appears therefore that male courtship in

*M. hawaiiensis* and *M. australica* is not the same, but there are elements of Kauai male courtship which make them reproductively compatible with either *M. australica* and *M. hawaiiensis* and vice versa. This is a rather interesting situation since both *M. hawaiiensis* and Kauai occur on the islands of Hawaii and given the capability of *Melittobia* to be wind dispersed it is hard to imagine that geographical barriers operate. Given the highly polyphagous nature of *Melittobia* one can argue against ecological isolation. It appears therefore that the

*hawaiiensis* group is a relatively young group in the process of speciation. In contrast the *assemi* group contains more species showing greater morphological diversity. The comparative ethology of *M. assemi* and *M. sosui* only, is known for this group. These two species are very close morphologically and ethologically, (van den Assem and Maeta 1980), which indicates a fairly recent separation. *M. bekiliensis* is close to *M. assemi* on the basis of head and palp shape but its scape and funicle shape I regard as more derived. Sp. nov. Argentina is the most derived species on the basis of mandible and palp shape. The greater number of species in the *assemi* group and their greater morphological diversity suggests that this group is relatively older than the *hawaiiensis* group.

The *acasta* group, however, is less easy to divide phylogenetically. The relatively larger number of species in this group and their morphological and ethological diversity suggests an earlier origin for this group. The characters used for grouping the species are relatively primitive ones (many are shared with *M. clavicornis*) and therefore the group may be paraphyletic rather than monophyletic. Male morphological differences are closely related to the use of appendages and body parts during courtship. Without this knowledge it is difficult to place characters which separate species into a phylogenetic order with any confidence.

Two species, *M. acasta* and *M. digitata* can be grouped on their oblique distal scapc, the excavation of this margin and the transverse, narrow shape of the scape gland. I regard *M. digitata* as the most derived and van den Assem (pers. comms, 1974–1980) regards it to be derived on ethological data also. The reduction in relative size of funicle segment 1 and the size of the scape I regard as derived and unify *M. evansi* and *M. scapata*. Two species, *M. femorata* and *M. chalybii* both possess an extra funicle segment as a result of expansion of one of the ring segment lamellae. Their scape shapes are more similar to one another than to any other species. Figs 203, 204 of *M. chalybii* were from a slide in which the scapes are slightly rolled. In dry specimens the excavation of the scape in *M. chalybii* is of the *M. femorata* type but not so deep. I regard *M. chalybii* as the more derived since the scape gland is geniculate and the mid femoral fringe is more even (the primitive condition appears to be distal fringe much longer than proximal fringe).

The situation however, may not be this simple. Two species, *M. chalybii* and sp. nov. Argentina,

do not entirely fit the species groupings on morphological data. The courtship patterns of these two species are not known, but correlating morphology with known courtship patterns allows some interpretive discussion.

Males of *M. chalybii* have setae on the ventral fore trochanters not unlike those of the *hawaiiensis* group although not as dense, short or stiff and the male scape gland is geniculate although not as well developed as in the *assemi* and *hawaiiensis* groups. However, in scape shape and proportions of the funicular segments (even to the extra, expanded ring segment) *M. chalybii* is extremely similar to *M. femorata* which morphologically is very definitely an *acasta* group species. The long setae on the male mid femora in *M. chalybii* are also of the *acasta* group pattern. If we look at the females of *M. chalybii* we find that they have the *acasta* group narrowly spaced facial grooves, but the eyes are densely setose as in the *hawaiiensis* and *assemi* groups. Thus we find a mixture of morphological features in *M. chalybii* which can be found in all three groups. Sp. nov. Argentina males are easily placed in the *assemi* group on all features except for relatively broad wings. The females differ in that their facial grooves are narrowly spaced as in the *acasta* group.

Turning now to courtship, we find that in *M. australica* (*hawaiiensis* group) the male courtship position involves close application of his mouthparts onto the relatively broad area between the facial grooves of the female, in fact I observed that this area of the female is pushed inwards by the male's mandibles. I have not observed courtship of the *assemi* group species but in *M. assemi* and *M. sosui* the male position as reported by van den Assem and Maeta (1980) and van den Assem et alia (1982) resembles that of the *hawaiiensis* group. From their discussions it is not clear whether the male's mandibles impinge on the area between the facial arms of the female in these two species, but since the area between the facial arms in females of these species is broad there may be some correlation between breadth of this area and male position. If this is so then the courtship position of sp. nov. Argentina is not as in the *hawaiiensis* group but may be more like the *acasta* group where this area in females is relatively narrow. Another factor in both sp. nov. Argentina and *M. bekiliensis* (both *assemi* group) is the relatively broad male wings more like *acasta* group males than males of the *hawaiiensis* group or *M. assemi* and *M. sosui*. Broad male wings and wing vibration by males during courtship are a



correlation in the *acasta* group as are narrow male wings and no wing vibration during courtship by *hawaiiensis* group species as well as the species *M. assemi* and *M. sosui*. Perhaps male wing vibration also occurs during courtship in sp. nov. Argentina and *M. bekiliensis*.

Species where the male scape gland is geniculate involve permanent antennal contact during courtship (*hawaiiensis* group, *M. assemi*, *M. sosui*) which contrasts with permanent contact either through only part of the courtship (*M. acasta*, *M. evansi*) or not at all (*M. digitata*). In *M. chalybii* the geniculate nature of the male scape gland may indicate that permanent antennal contact is more important during courtship in this species than in other *acasta* group species. The presence of the setal tuft on the male ventral fore trochanters in *M. chalybii* indicates that there may be some similarities between male courtship position in *M. chalybii* and the *hawaiiensis* group where these setae rest on the female's mesosoma. However, it may not be entirely so as *M. chalybii* females have narrowly separated facial grooves. The presence of densely setose eyes in females of the *hawaiiensis* and *assemi* groups correlates with a predominance of mid leg action during courtship. *M. chalybii* females have densely setose eyes which perhaps indicates that mid leg action during courtship in this species assumes a more important role than it does in the courtship of other *acasta* group species.

From this speculative evidence there is some suggestion of convergent evolution in courtship behaviour and associated morphology in *Melittobia*. We may therefore be dealing with a polyphyletic group rather than a monophyletic one. Of key importance in understanding this are the courtship patterns of *M. chalybii* and sp. nov. Argentina coupled with a more thorough knowledge of the world fauna. Africa and South America will no doubt yield many more species than are presently known.

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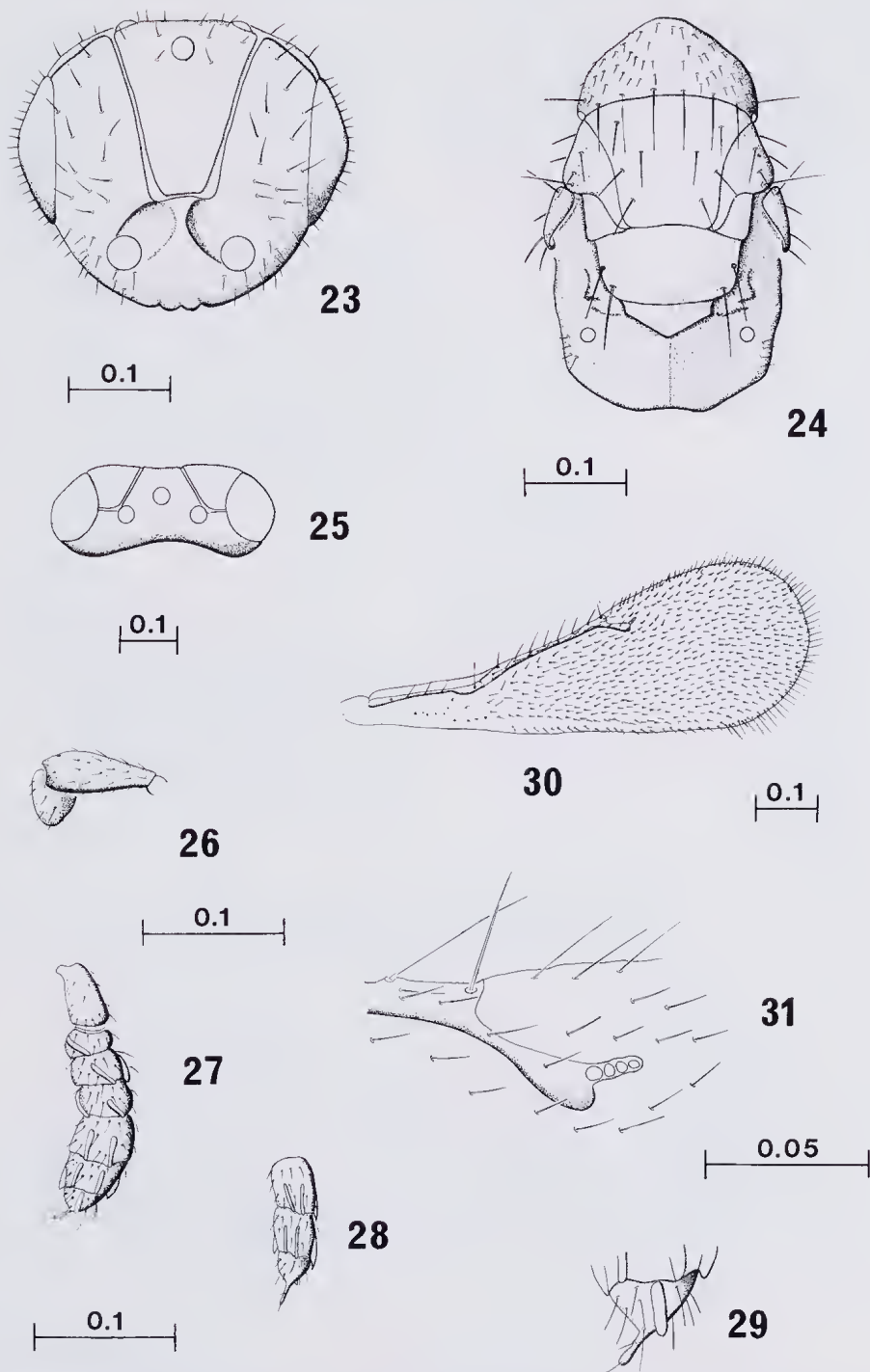
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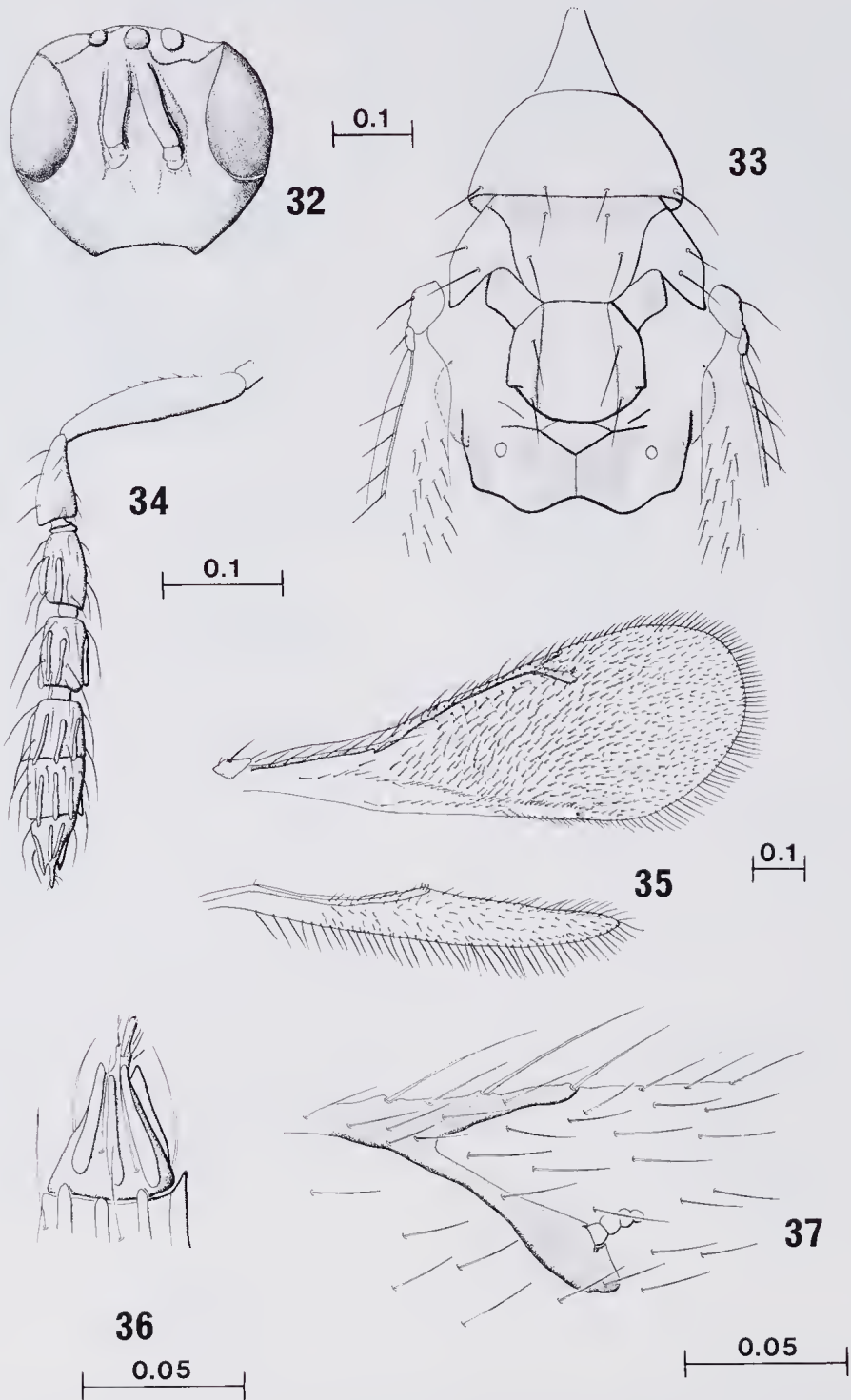
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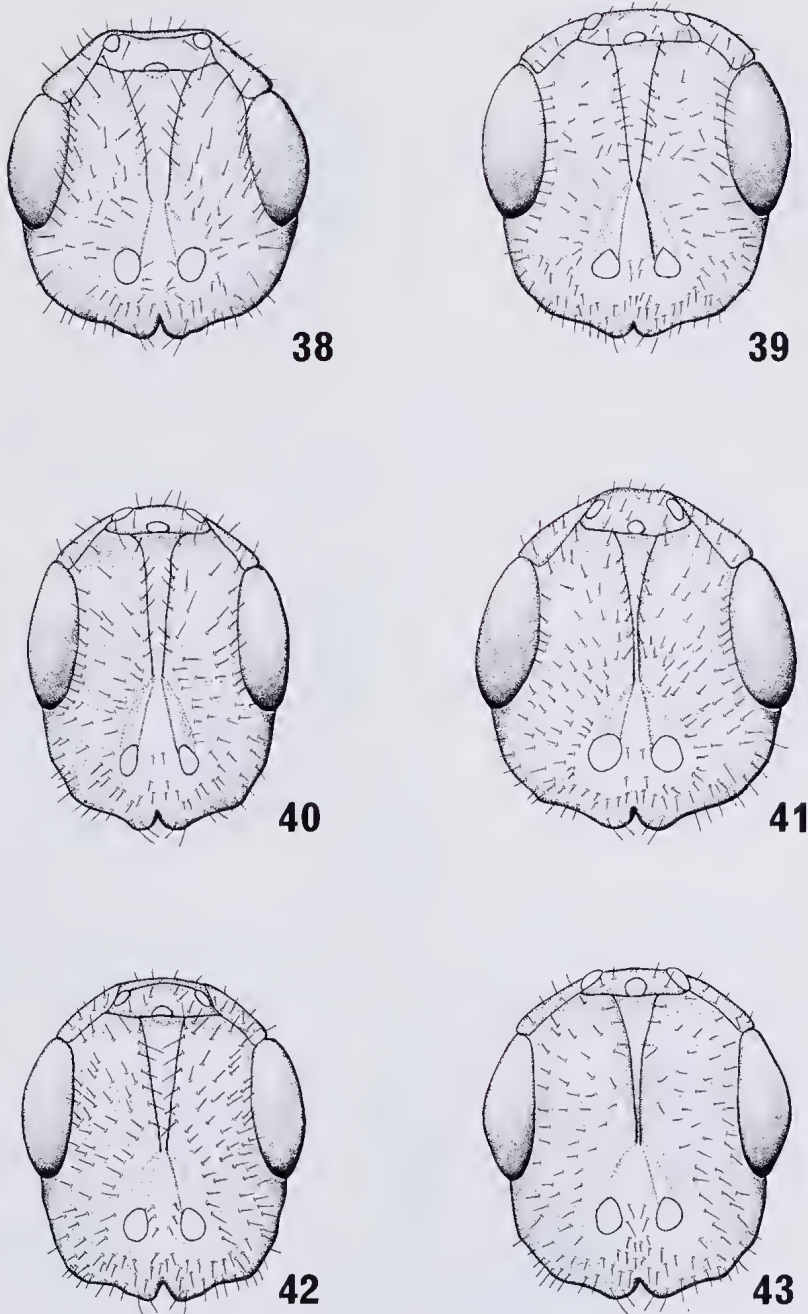
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FIGURES 23, 24, 30-31, *Tachinobia diopsisephila* Female; 23 — Head, frontal aspect; 24 — Mesosoma, dorsal aspect; 26 — Scape and pedicel; 27 — Flagellum, dorsal aspect; 28 — Club, lateral aspect; 29 — Club segment 3; 30 — Fore wing; 31 — Stigmal vein. Fig. 25 — *Tachinobia repanda* female head, dorsal aspect.

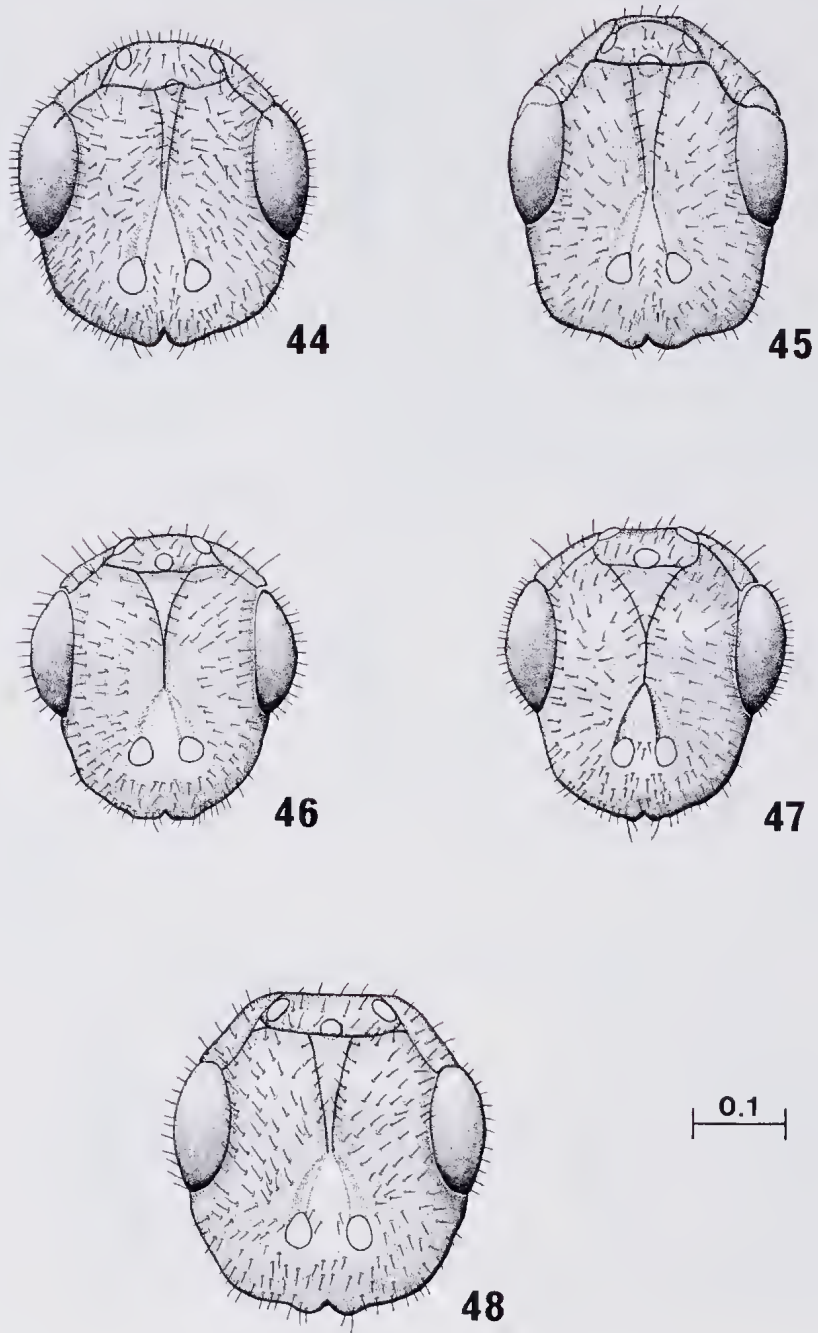


FIGURES 32-37, *Cirrospilus (Atoposomoidea) cosmopterygi* female; 32 — Head, frontal aspect; 33 — Mesosoma, dorsal aspect; 34 — antenna; 35 — wings; 36 — Club segment 3; 37 — Stigmal vein.



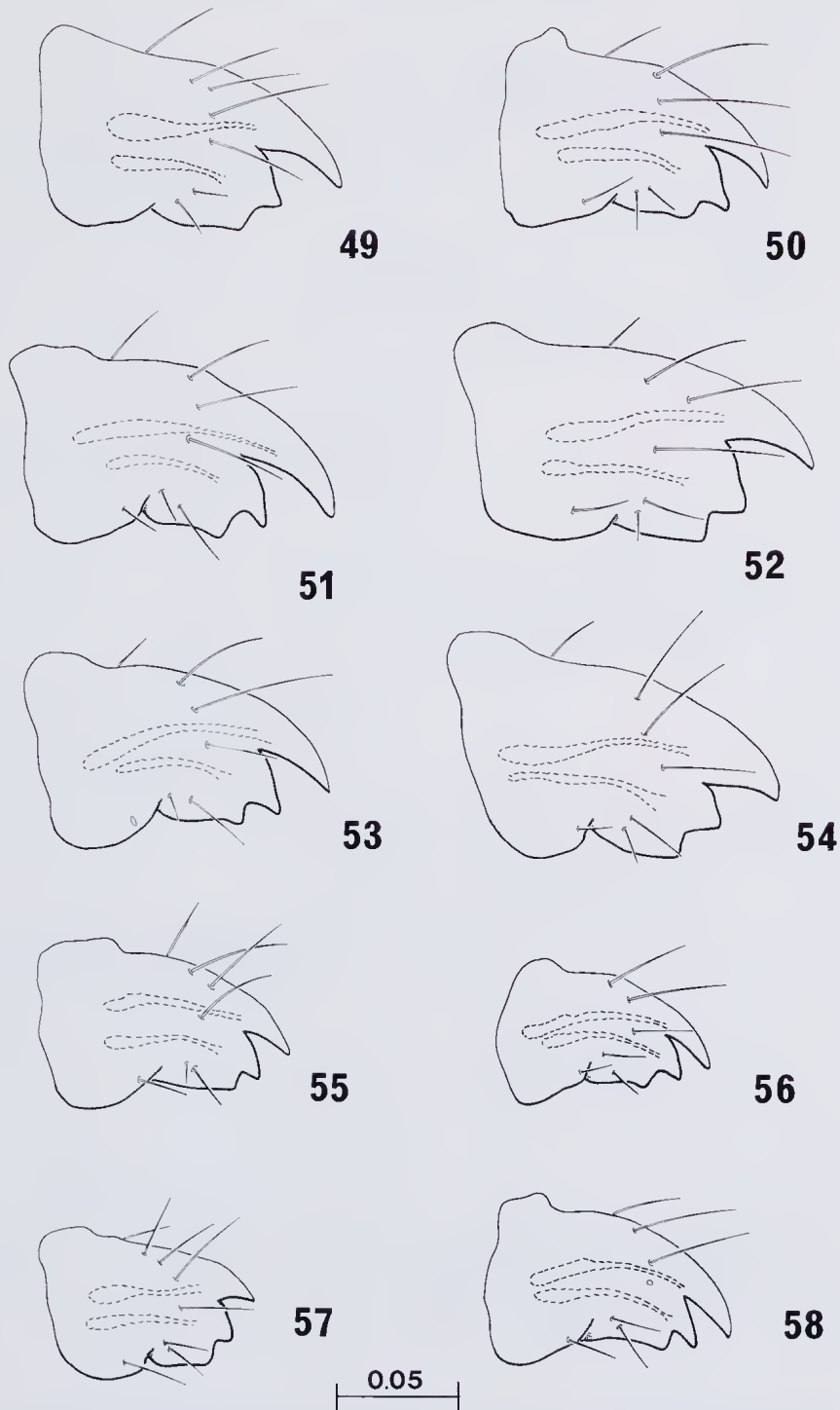
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FIGURES 38-43, Female heads, *Melittobia* spp. 38 — *clavicornis*; 39 — *acasta*; 40 — *evansi*; 41 — *scapata*; 42 — *digitata*; 43 — *femorata*.

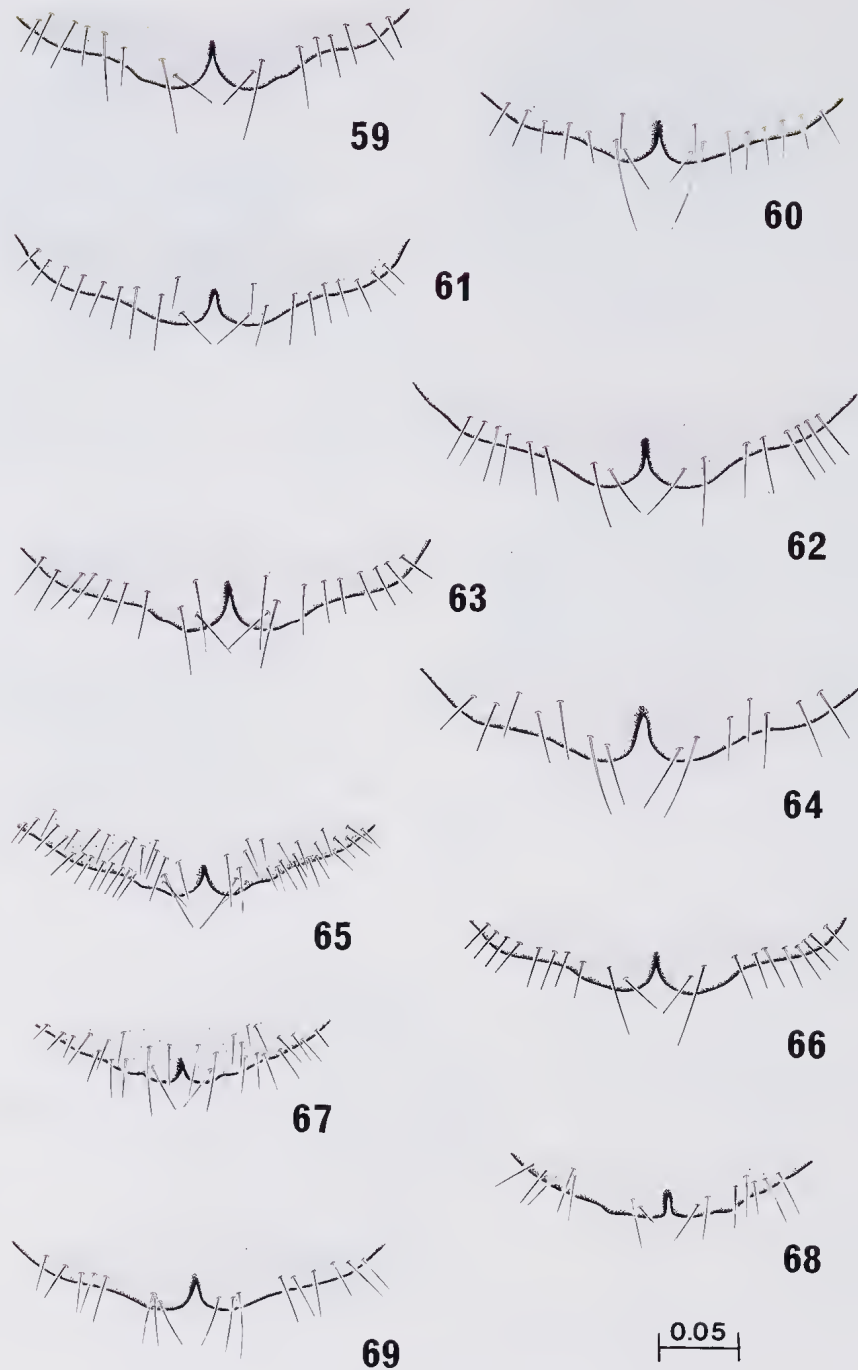


FIGURES 44-48, Female heads, *Melittobia* spp. 44 — *chalybii*; 45 — *megachilis*; 46 — *australica*; 47 — *sosui*; 48 — sp. nov. Argentina.

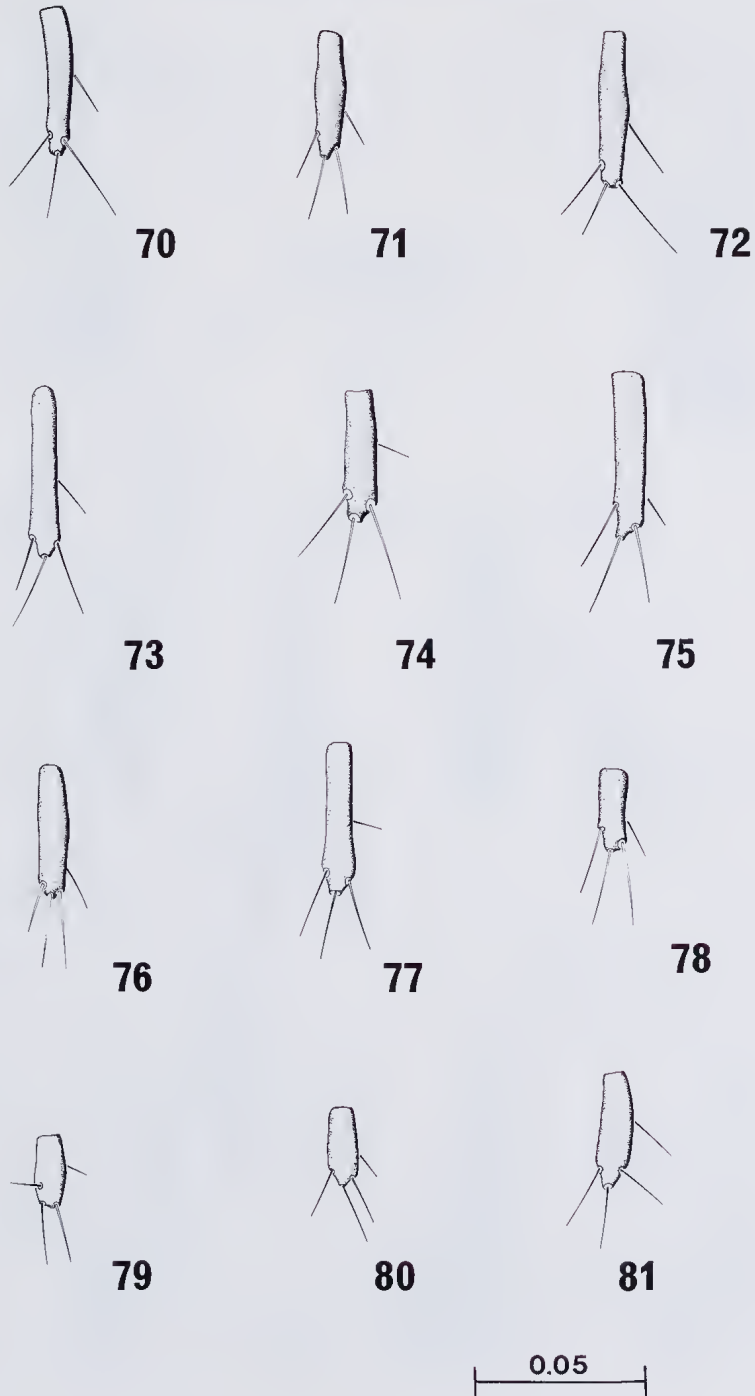




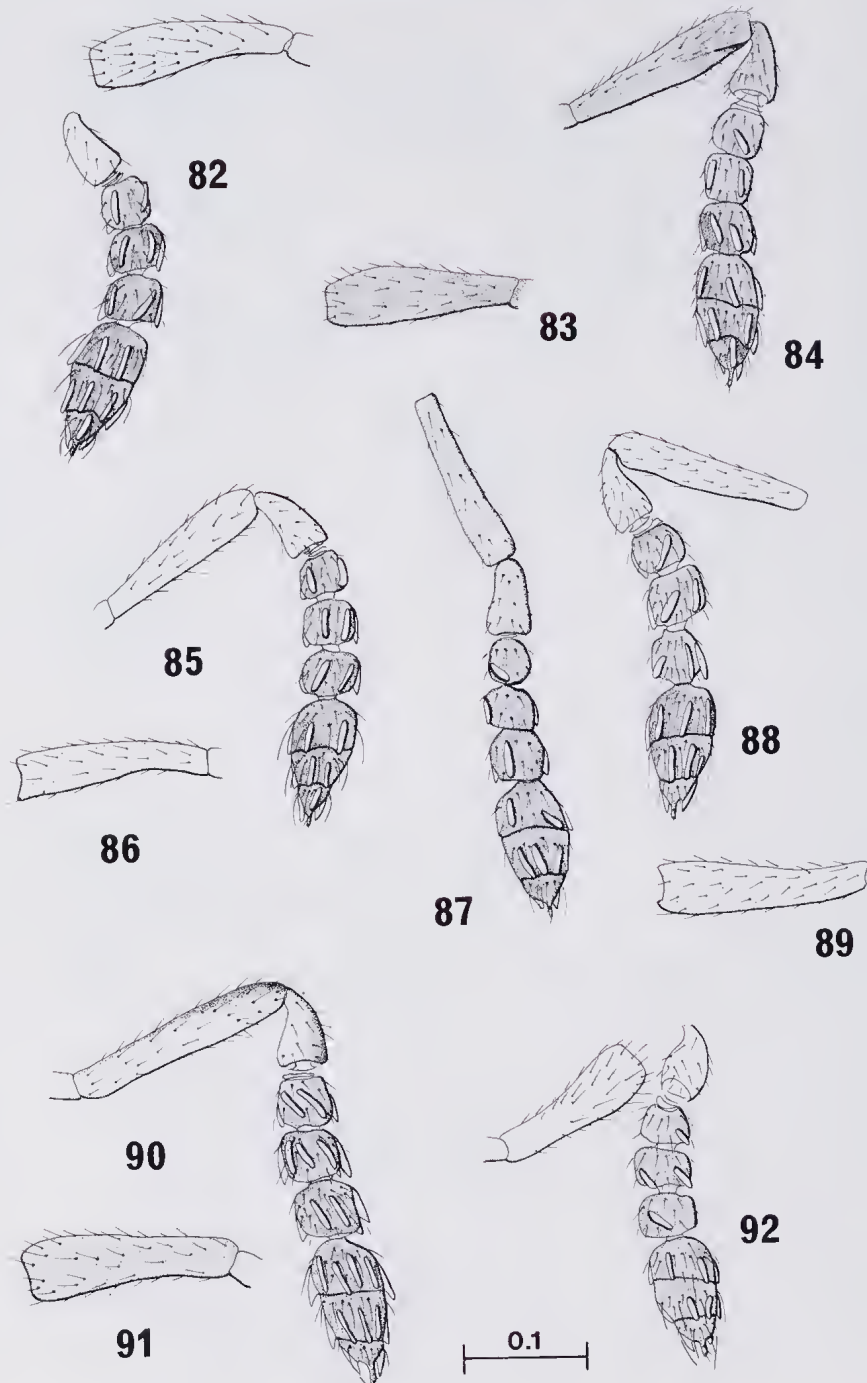
FIGURES 49-58, Female mandibles, *Melittobia* spp. 49 — *clavicornis*; 50 — *acasta*; 51 — *evansi*; 52 — *scapata*; 53 — *digitata*; 54 — *femorata*; 55 — *chalybii*; 56 — *australica*; 57 — *sosui*; 58 — sp. nov. Argentina.



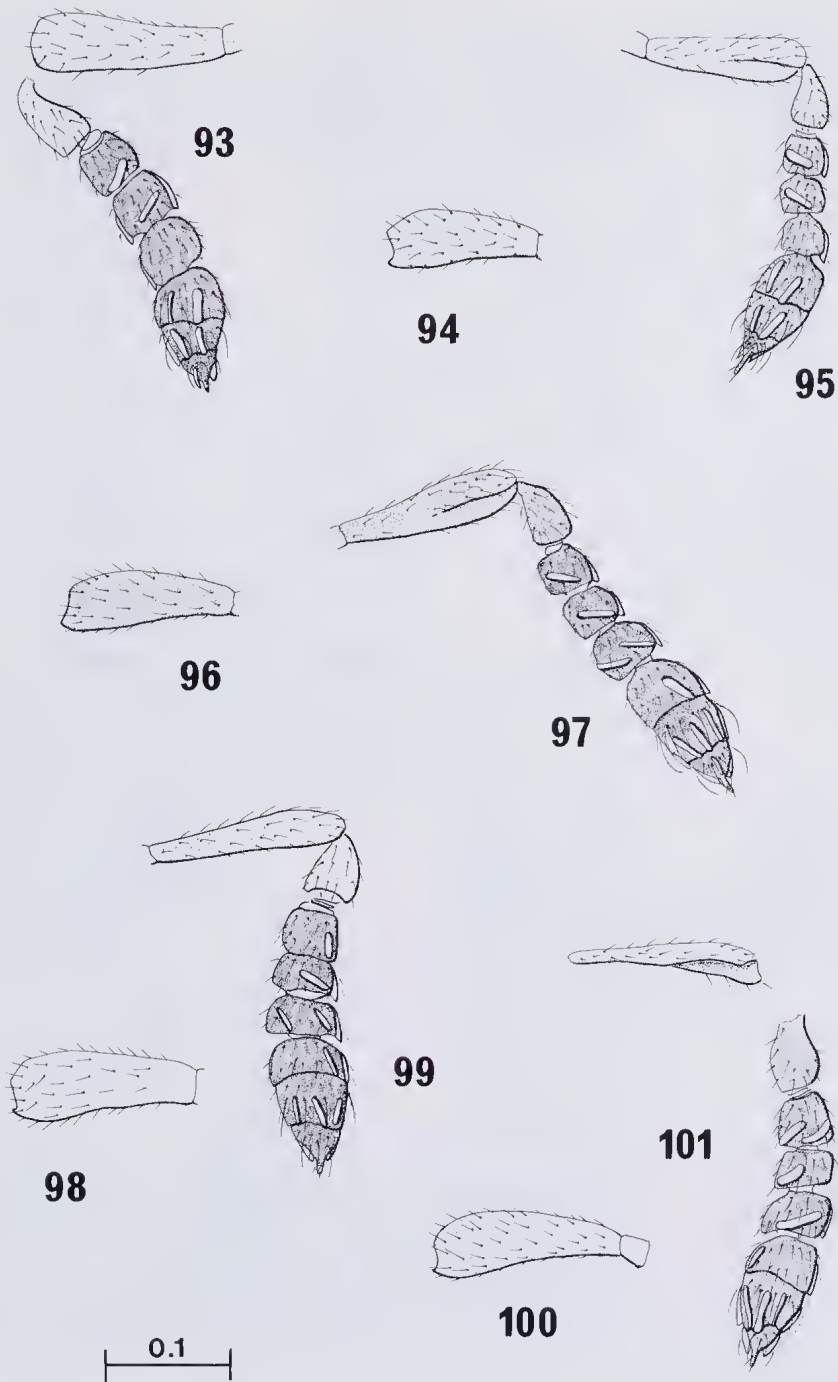
FIGURES 59-69, Female clypeal margins, *Melittobia* spp. 59 — *clavicornis*; 60 — *acasta*; 61 — *evansi*; 62 — *scapata*; 63 — *digitata*; 64 — *femorata*; 65 — *chalybii*; 66 — *megachilis*; 67 — *assemi*; 68 — *australica*; 69 — sp. nov. Argentina.



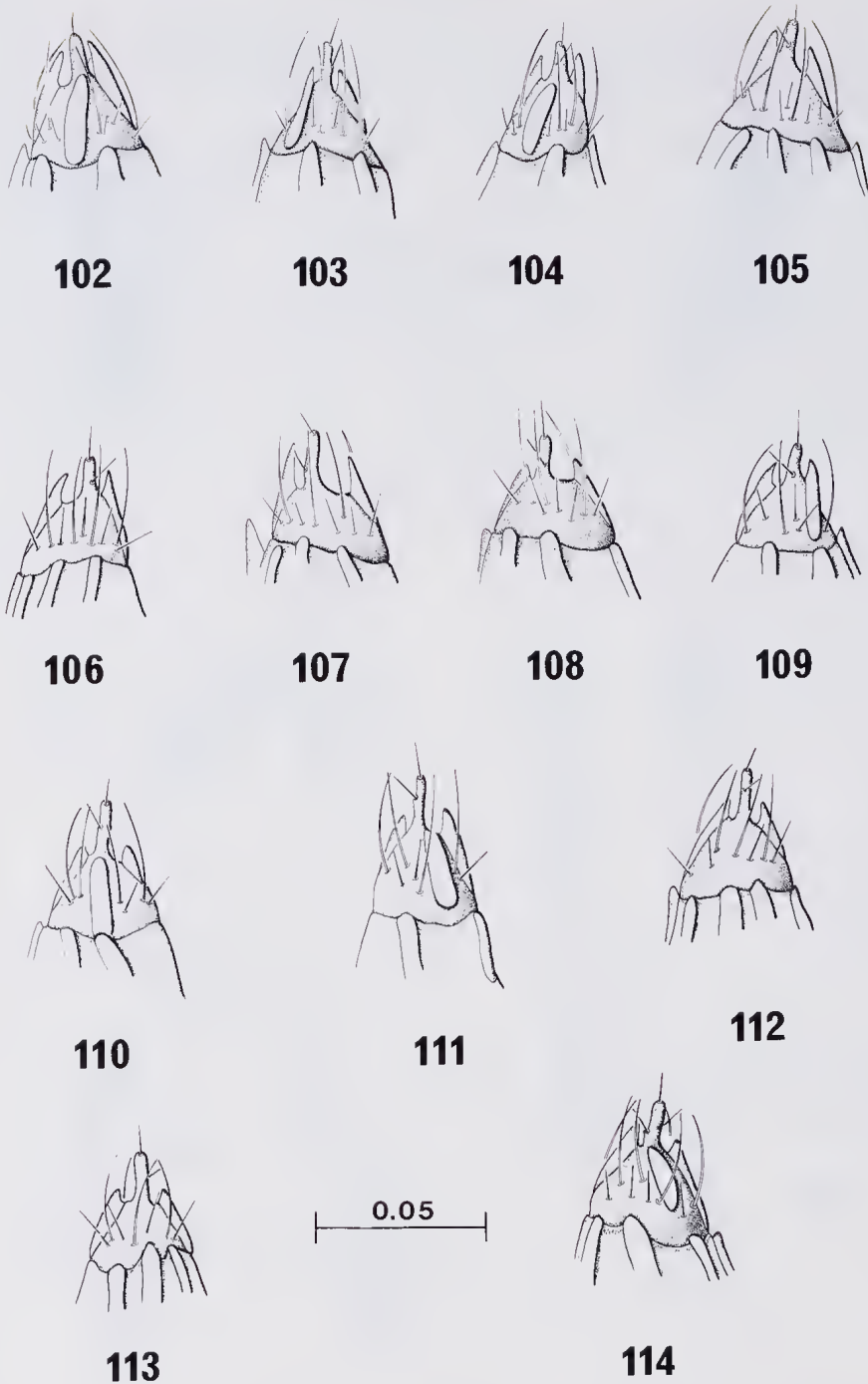
FIGURES 70-81, Female maxillary palps, *Melittobia* spp. 70 — *clavicornis*; 71 — *acasta*; 72 — *evansi*; 73 — *scapata*; 74 — *digitata*; 75 — *femorata*; 76 — *chalybii*; 77 — *megachilis*; 78 — *australica*; 79 — *assemi*; 80 — *sosui*; 81 — sp. nov. Argentina.



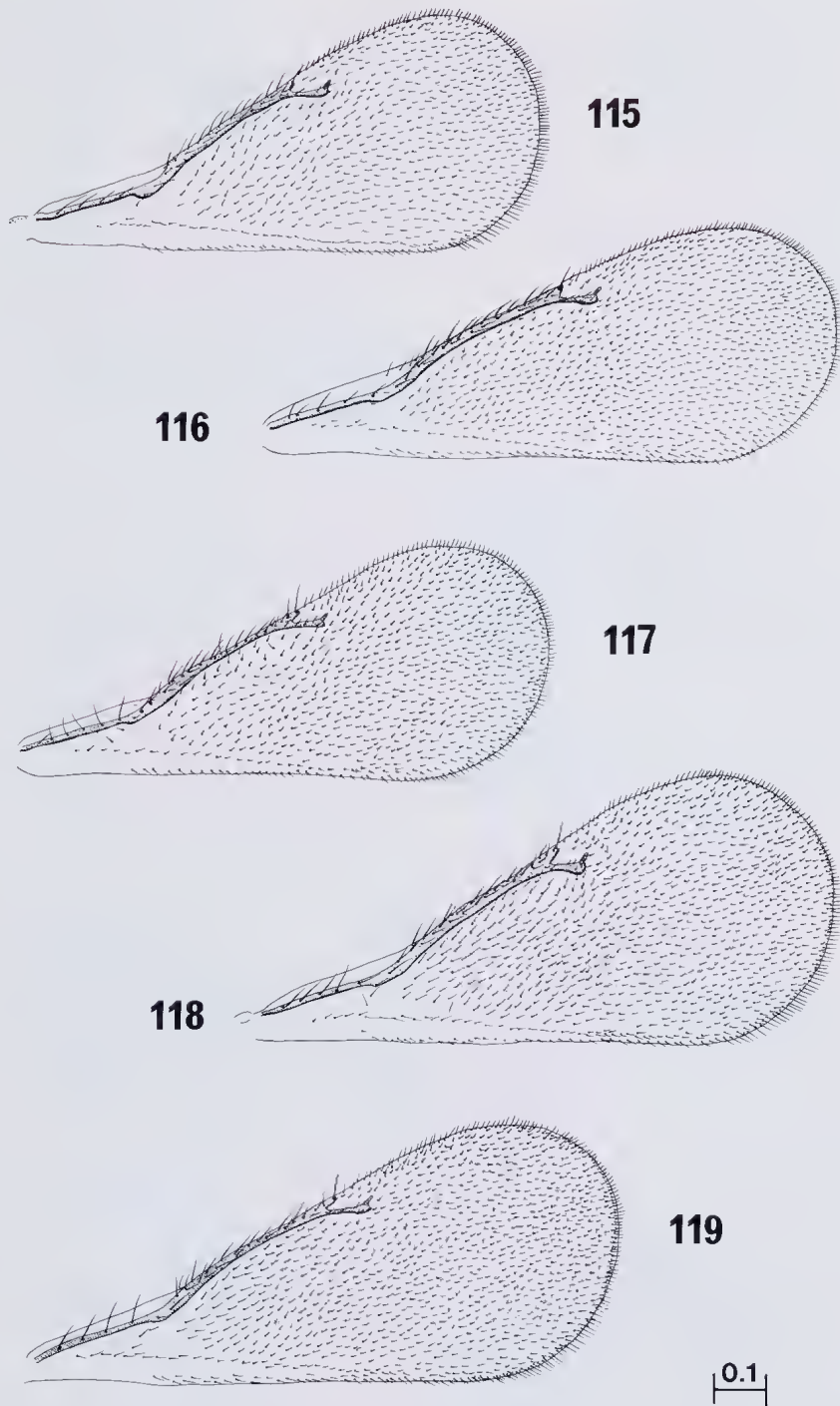
FIGURES 82-92, Female scapes and antennae, *Melittobia* spp. 82 — *clavicornis*; 83 — *acasta*, scape; 84 — *acasta*; 85 — *evansi*; 86 — *evansi* scape; 87 — *scapata*; 88 — *digitata*; 89 — *digitata*, scape; 90 — *femorata*; 91 — *femorata*, scape; 92 — *chalybii*.



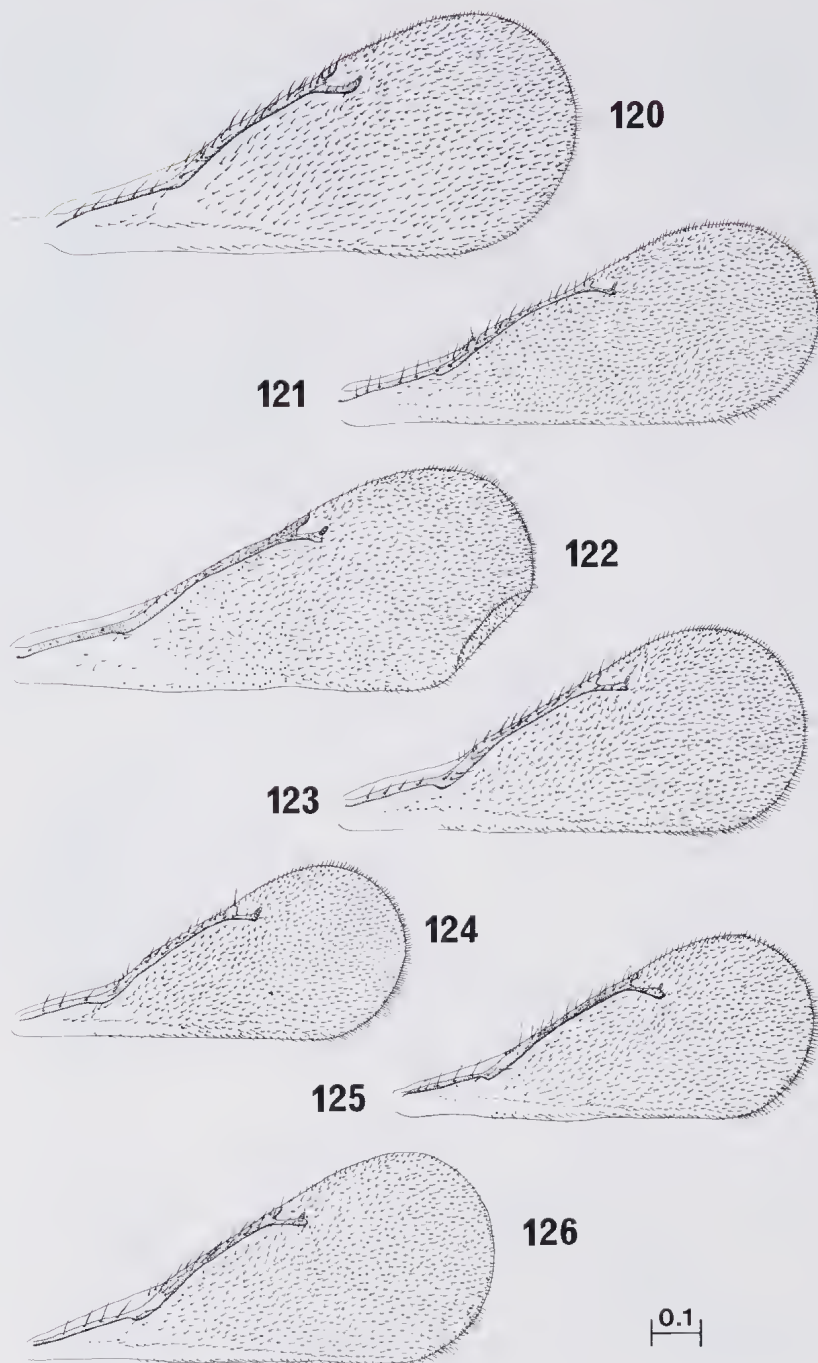
FIGURES 93-101, Female scapes and antennae, *Melittobia* spp. 93 — *megachilis*; 94 — Kauai, scape; 95 — Kauai; 96 — *australica*, scape; 97 — *australica*; 98 — sp. nov. Argentina, scape; 99 — sp. nov. Argentina; 100 — *sosui*, scape; 101 — *sosui*.



FIGURES 102-114, Female antennae, terminal segment, *Melittobia* spp. 102 — *clavicornis*; 103 — *acasta*; 104 — *evansi*; 105 — *scapata*; 106 — *digitata*; 107 — *femorata*; 108 — *chalybii*; 109 — *megachilis*; 110 — *hawaiiensis*; 111 — Kauai; 112 — *australis*; 113 — *sosui*; 114 — sp. nov. Argentina.

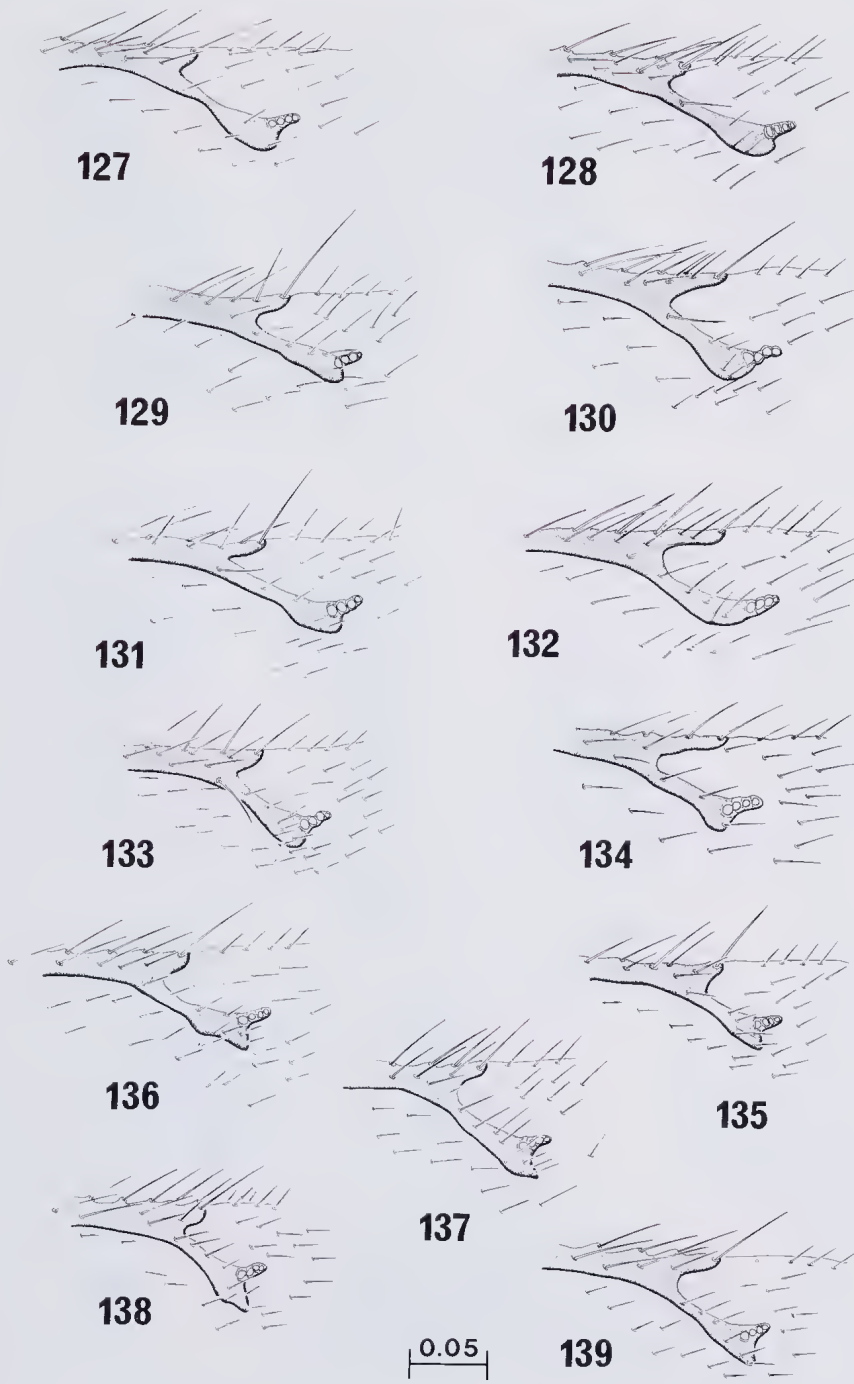


FIGURES 115-119, Female fore wings, *Melittobia* spp. 115 — *clavicornis*; 116 — *acasta*; 117 — *evansi*; 118 — *scapata*; 119 — *digitata*.

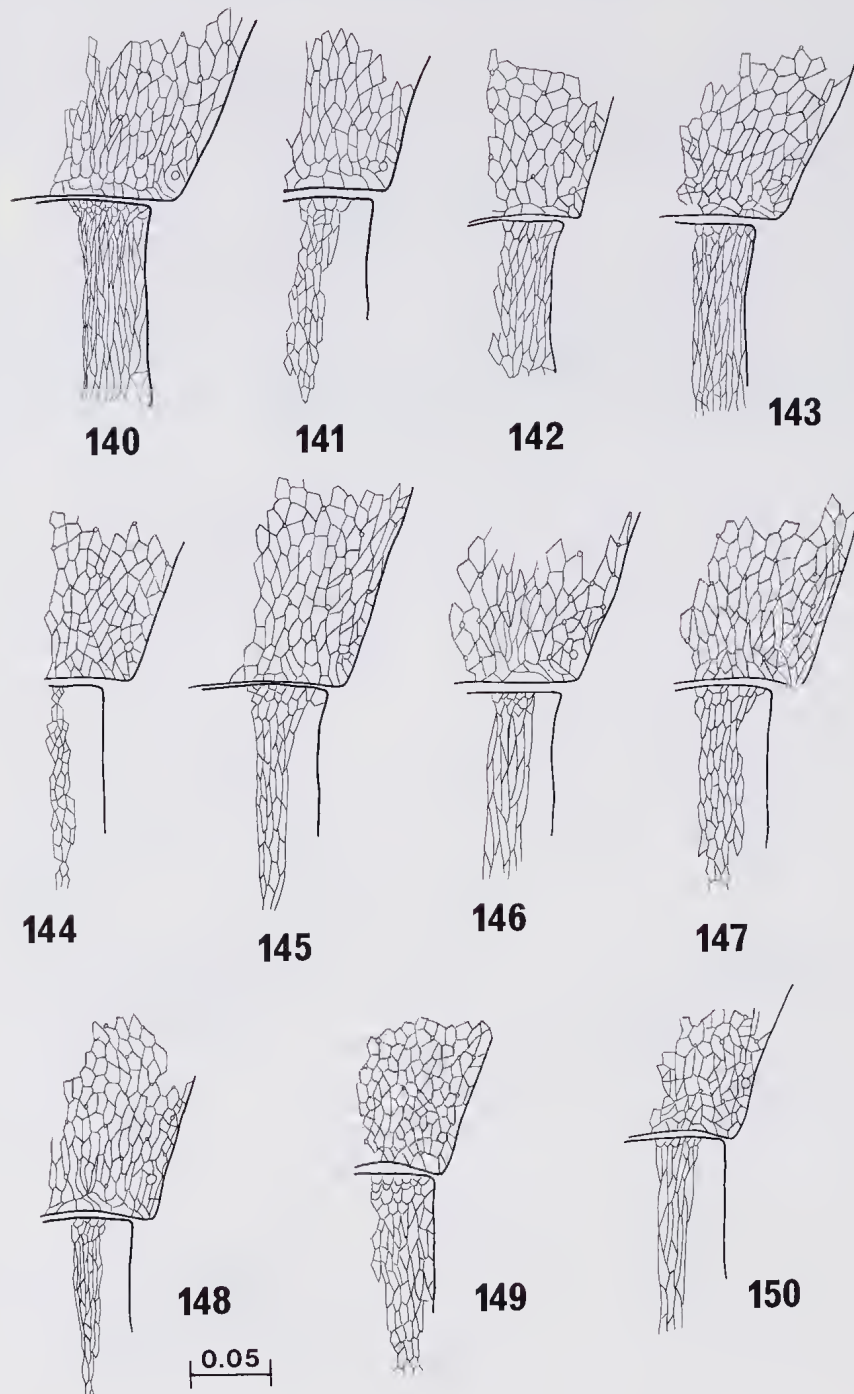


FIGURES 120-126, Female fore wings, *Melittobia* spp. 120 — *femorata*; 121 — *chalybii*; 122 — *megachilis*; 123 — *hawaiiensis*; 124 — *australiana*; 125 — *assemi*; 126 — sp. nov. Argentina.

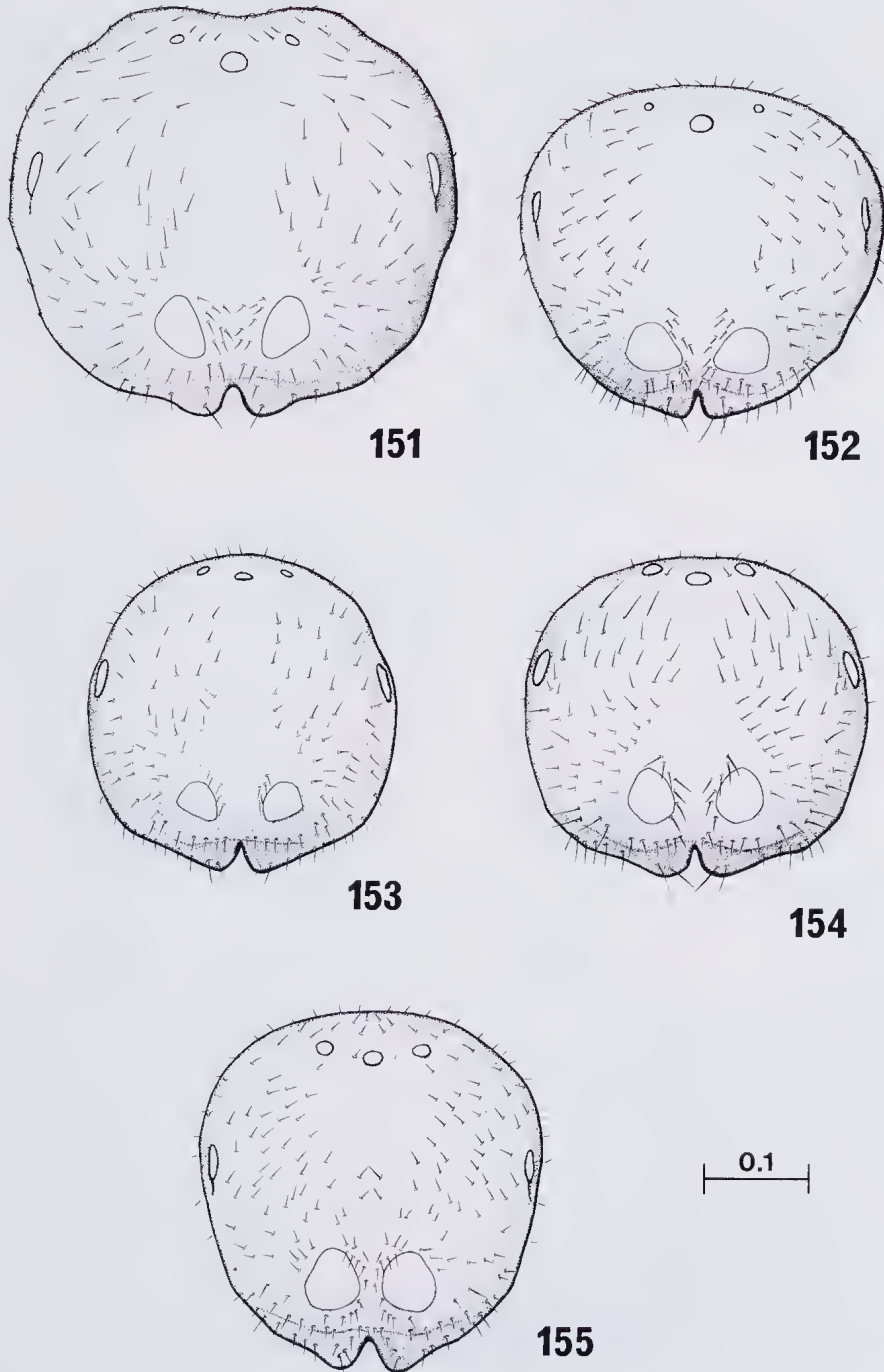




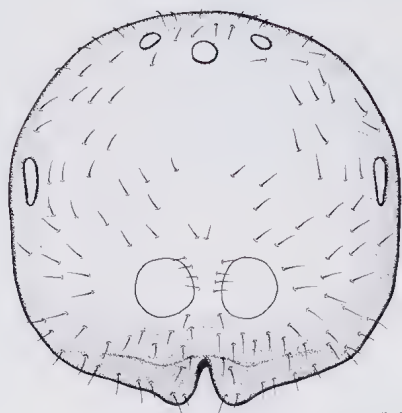
FIGURES 127-139, Female stigmal veins, *Melittobia* spp. 127 — *clavicornis*; 128 — *acasta*; 129 — *evansi*; 130 — *scapata*; 131 — *digitata*; 132 — *femorata*; 133 — *chalybii*; 134 — *megachilis*; 135 — *australica* (paralectotype); 136 — *hawaiiensis*; 137 — *assemi*; 138 — *sosui*; 139 — sp. nov. Argentina.



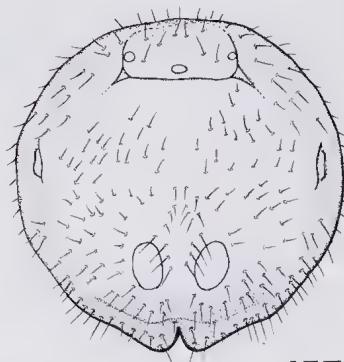
FIGURES 140-150, Female sculpture, mid lobe of mesoscutum, mid lobe of scutellum, *Melittobia* spp. 140 — *clavicornis*; 141 — *acasta*; 142 — *evansi*; 143 — *scapata*; 144 — *digitata*; 145 — *femorata*; 146 — *chalybii*; 147 — *megachilis*; 148 — *australica*; 149 — *assemi*; 150 — sp. nov. Argentina.



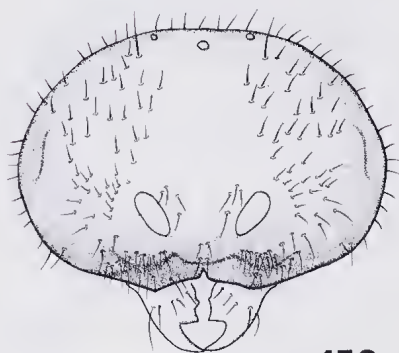
FIGURES 151-155, Male heads, *Melittobia* spp. 151 — *clavicornis*; 152 — *acasta*; 153 — *evansi*; 154 — *scapata*; 155 — *digitata*.



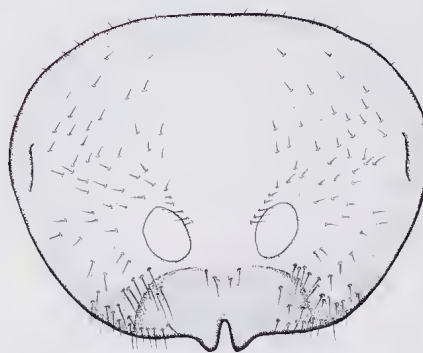
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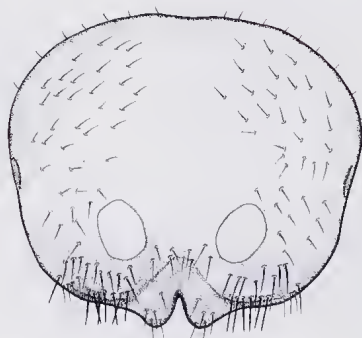
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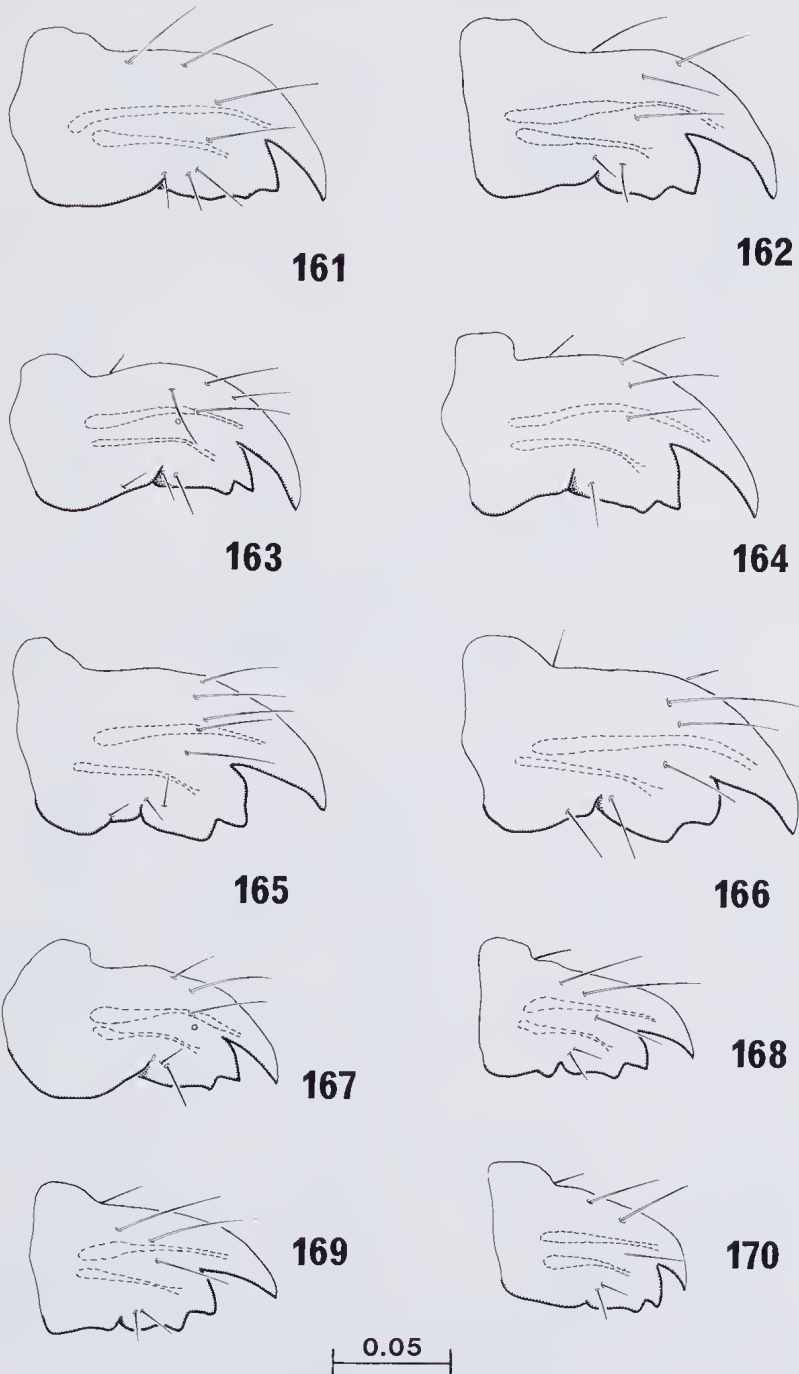
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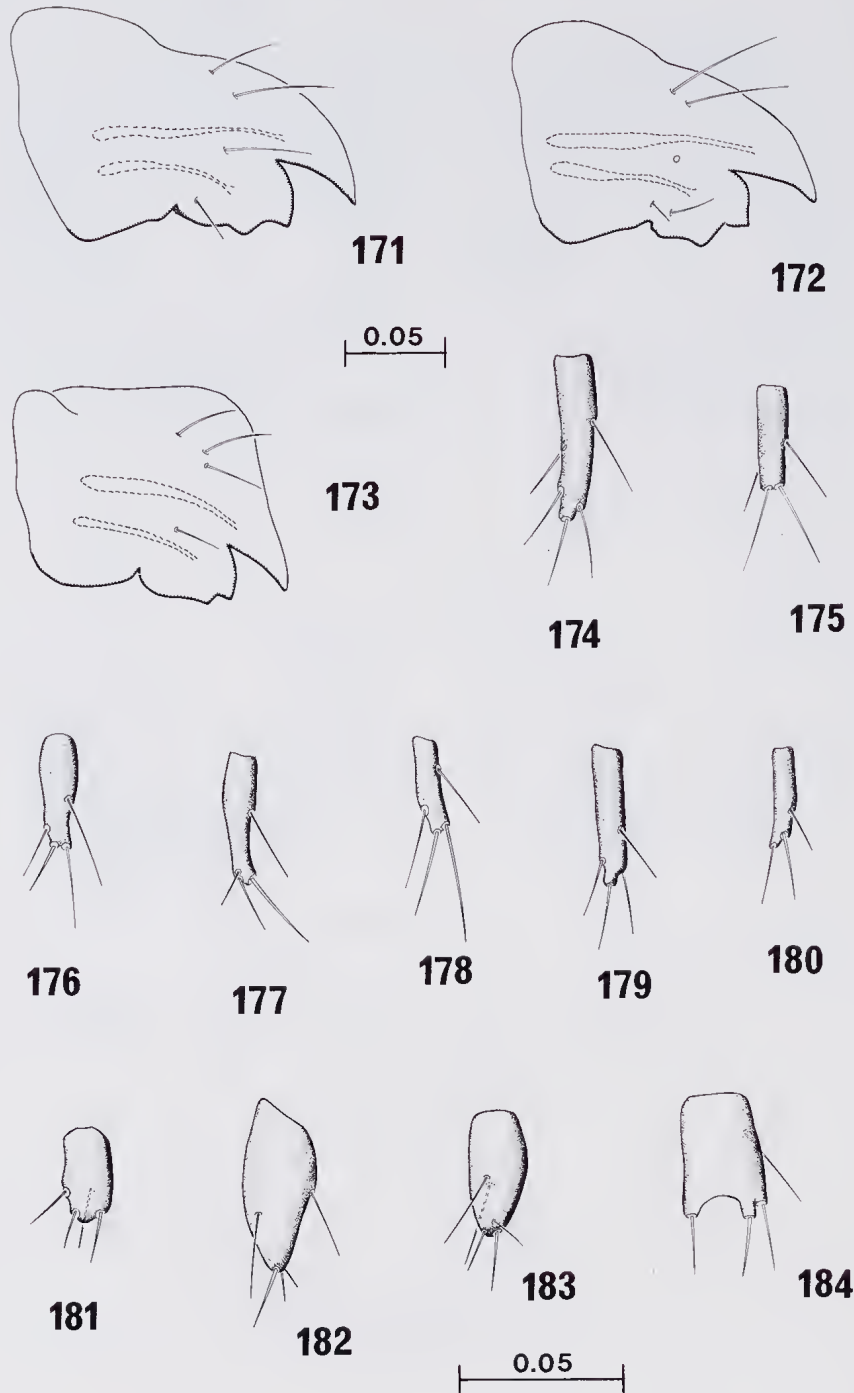
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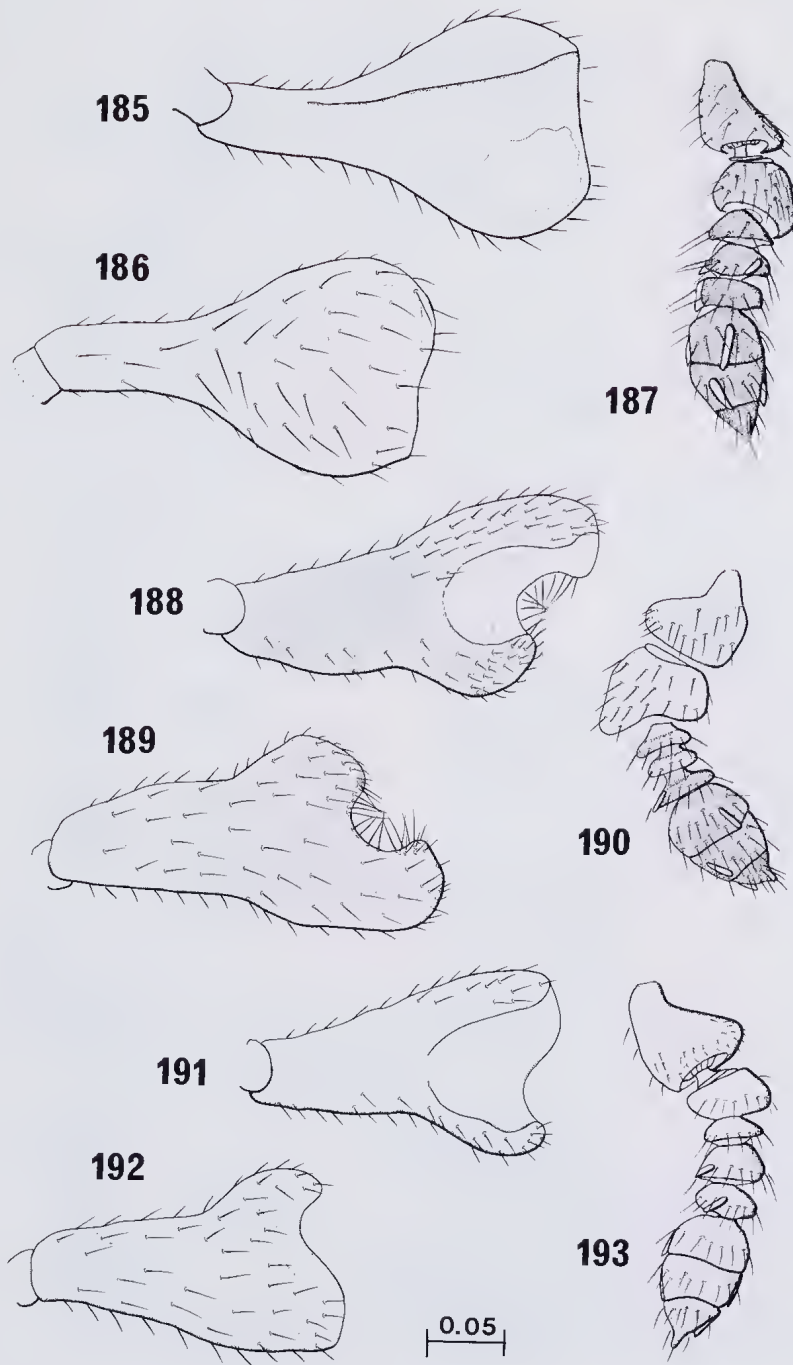
FIGURES 156-160, Male heads, *Melittobia* spp. 156 — *femorata*; 157 — *chalbyii*; 158 — *australica*; 159 — *assemi*; 160 — sp. nov. Argentina.



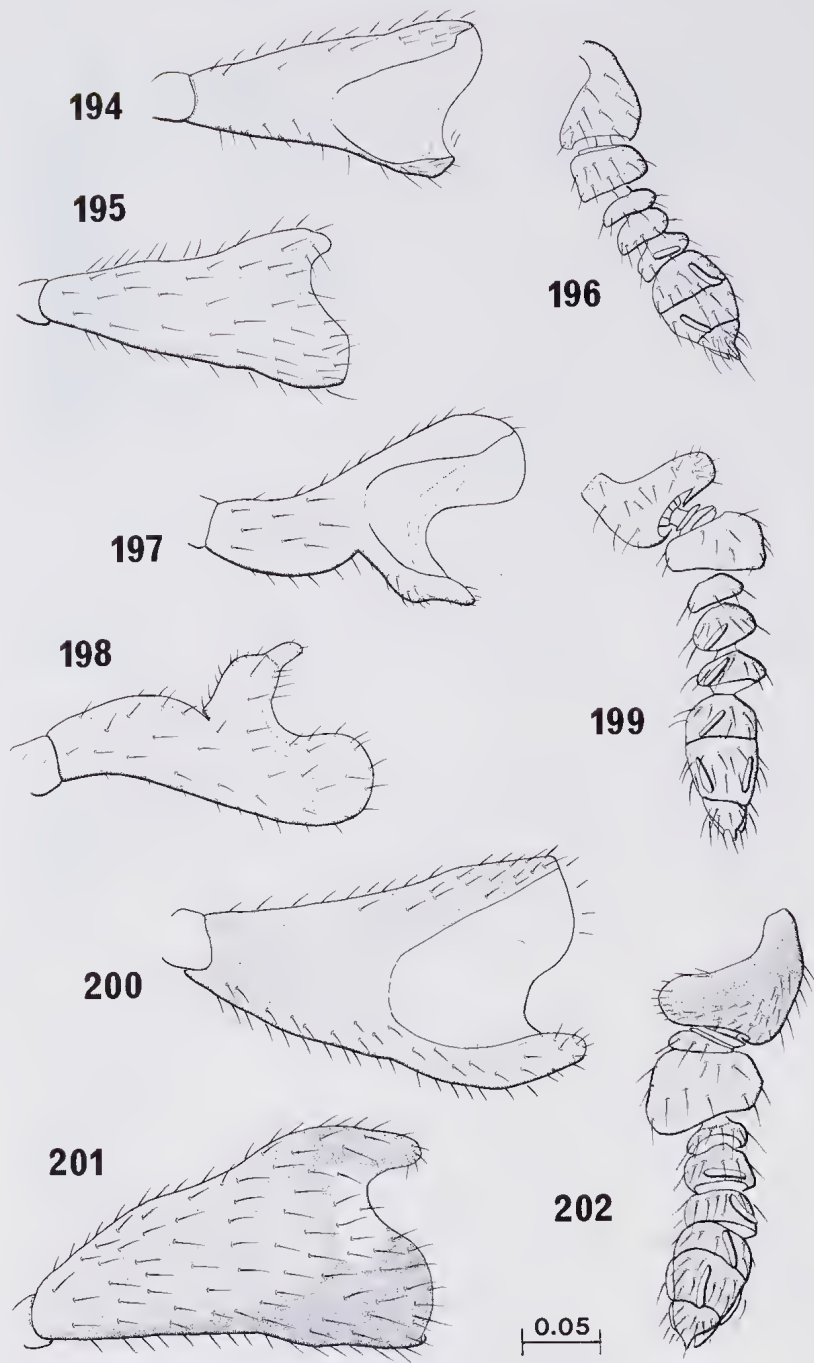
FIGURES 161-170, Male mandibles, *Melittobia* spp. 161 — *clavicornis*; 162 — *acasta*; 163 — *evansi*; 164 — *scapata*; 165 — *digitata*; 166 — *femorata*; 167 — *chalybii*; 168 — *hawaiiensis*; 169 — *australica*; 170 — Kauai.



FIGURES 171-173, Male mandibles, *Melittobia* spp. 171 — *assemi*; 172 — *sosui*; 173 — sp. nov. Argentina.  
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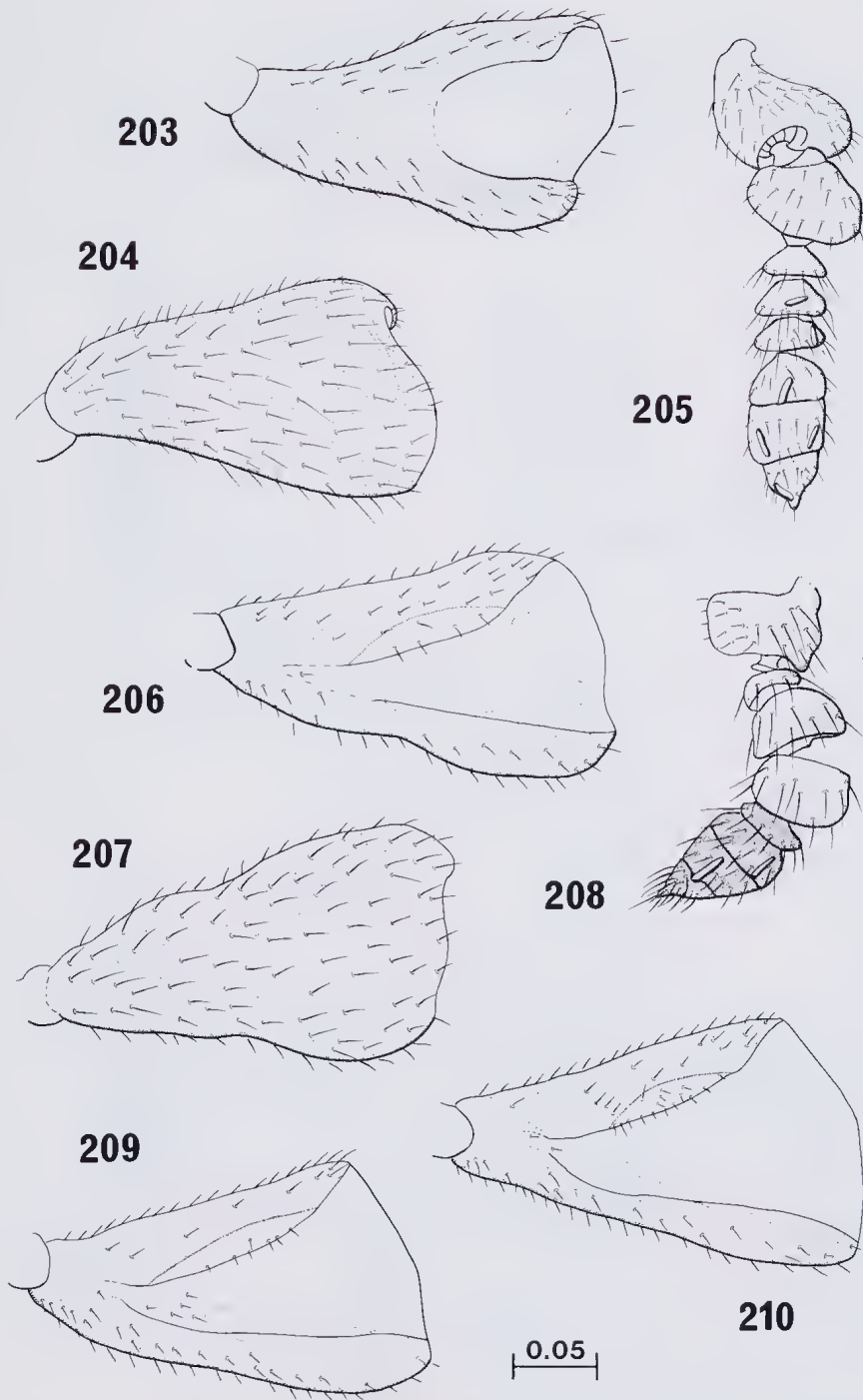


FIGURES 185-193, Male antennae, *Melittobia* spp. 185 — *clavicornis* ventral scape; 186 — *clavicornis* dorsal scape; 187 — *clavicornis* pedicel and flagellum; 188 — *acasta* ventral scape; 189 — *acasta* dorsal scape; 190 — *acasta* pedicel and flagellum; 191 — *evansi* ventral scape; 192 — *evansi* dorsal scape; 193 — *evansi* pedicel and flagellum.

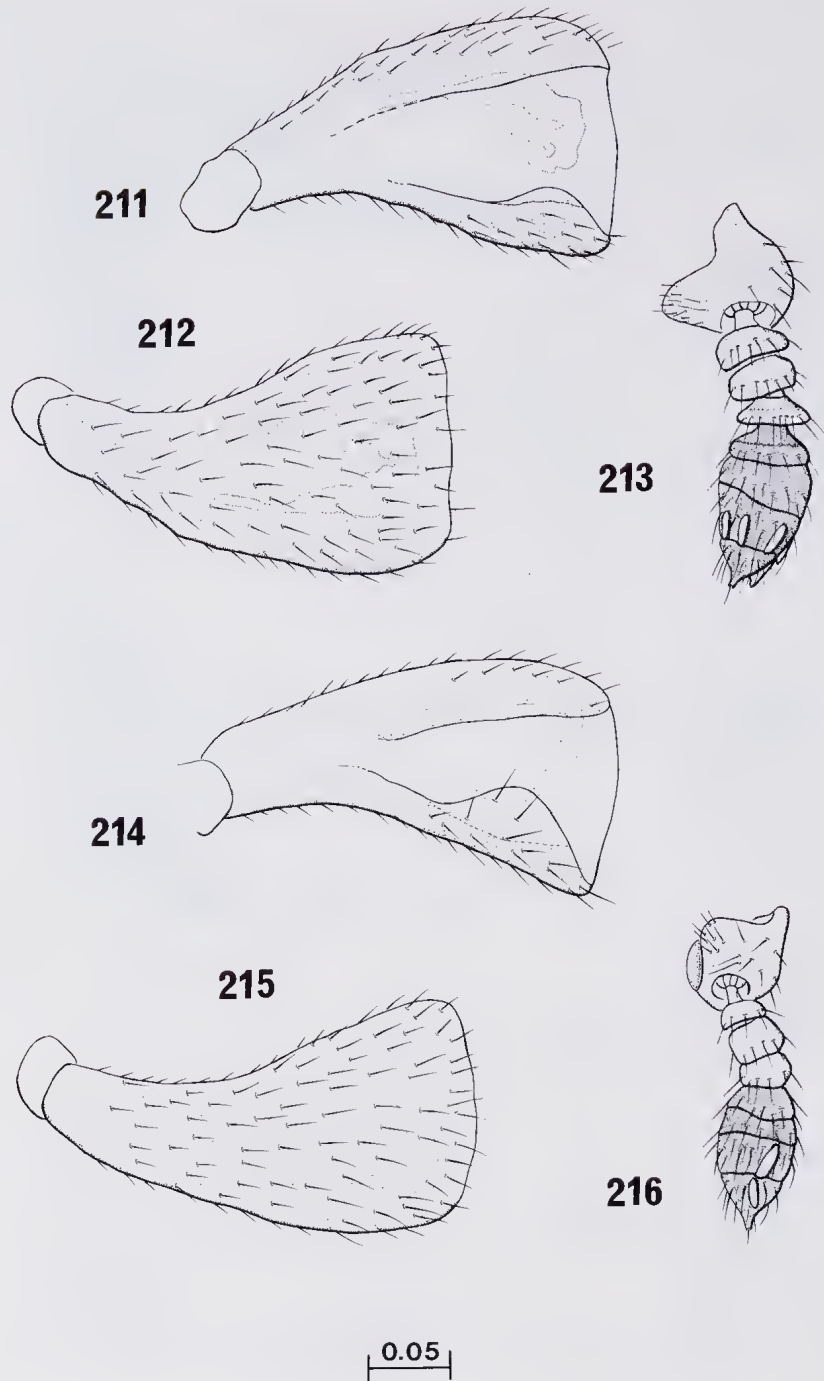


FIGURES 194-202, Male antennae, *Melittobia* spp. 194 — *scapata* ventral scape; 195 — *scapata* dorsal scape; 196 — *scapata* pedicel and flagellum; 197 — *digitata* ventral scape; 198 — *digitata* dorsal scape; 199 — *digitata* pedicel and flagellum; 200 — *femorata* ventral scape; 201 — *femorata* dorsal scape; 202 — *femorata* pedicel and flagellum.

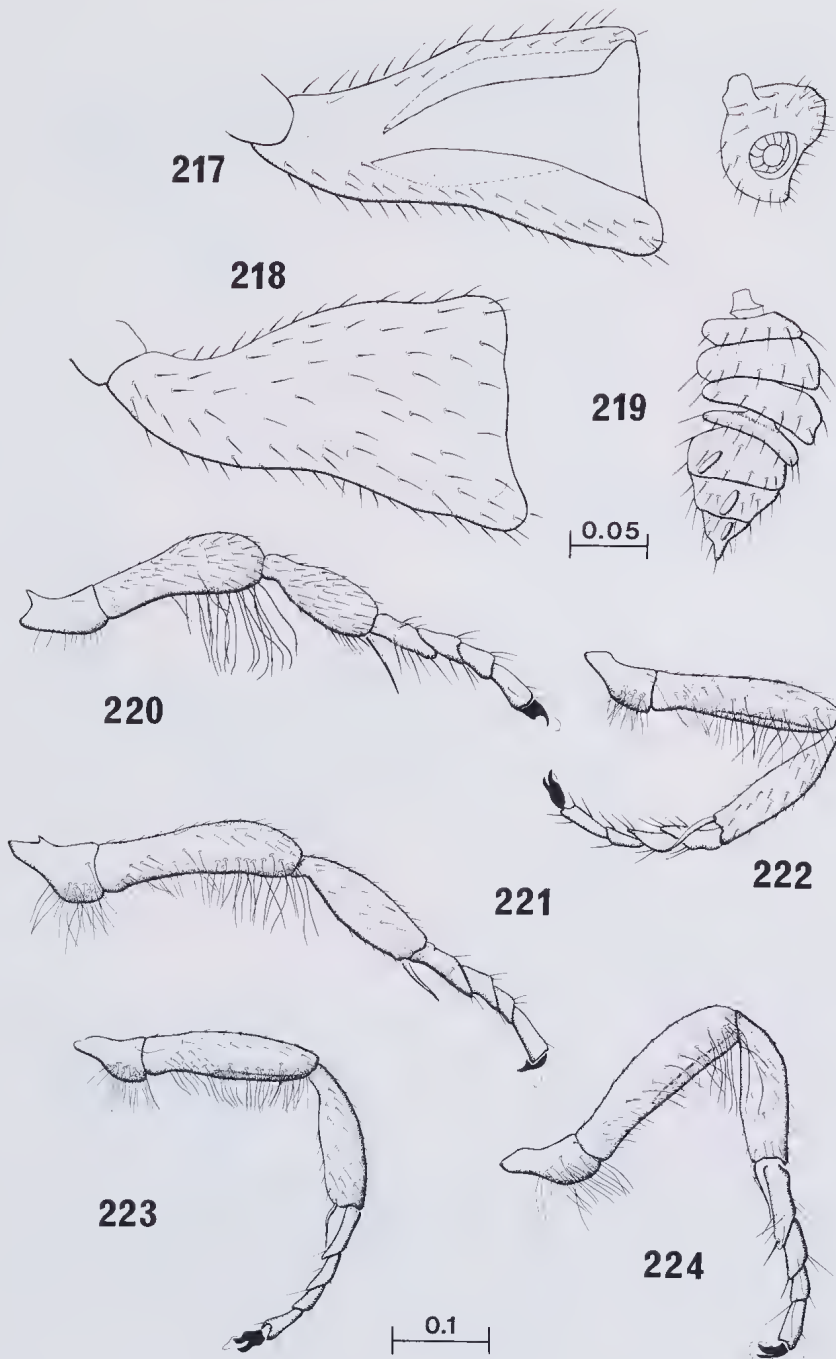




FIGURES 203–210, Male antennae, *Melittobia* spp. 203 — *chalybii* ventral scape; 204 — *chalybii* dorsal scape; 205 — *chalybii* scape and flagellum; 206 — *australica* ventral scape; 207 — *australica* dorsal scape; 208 — *australica* pedicel and flagellum; 209 — *hawaiiensis* ventral scape; 210 — Kauai ventral scape.

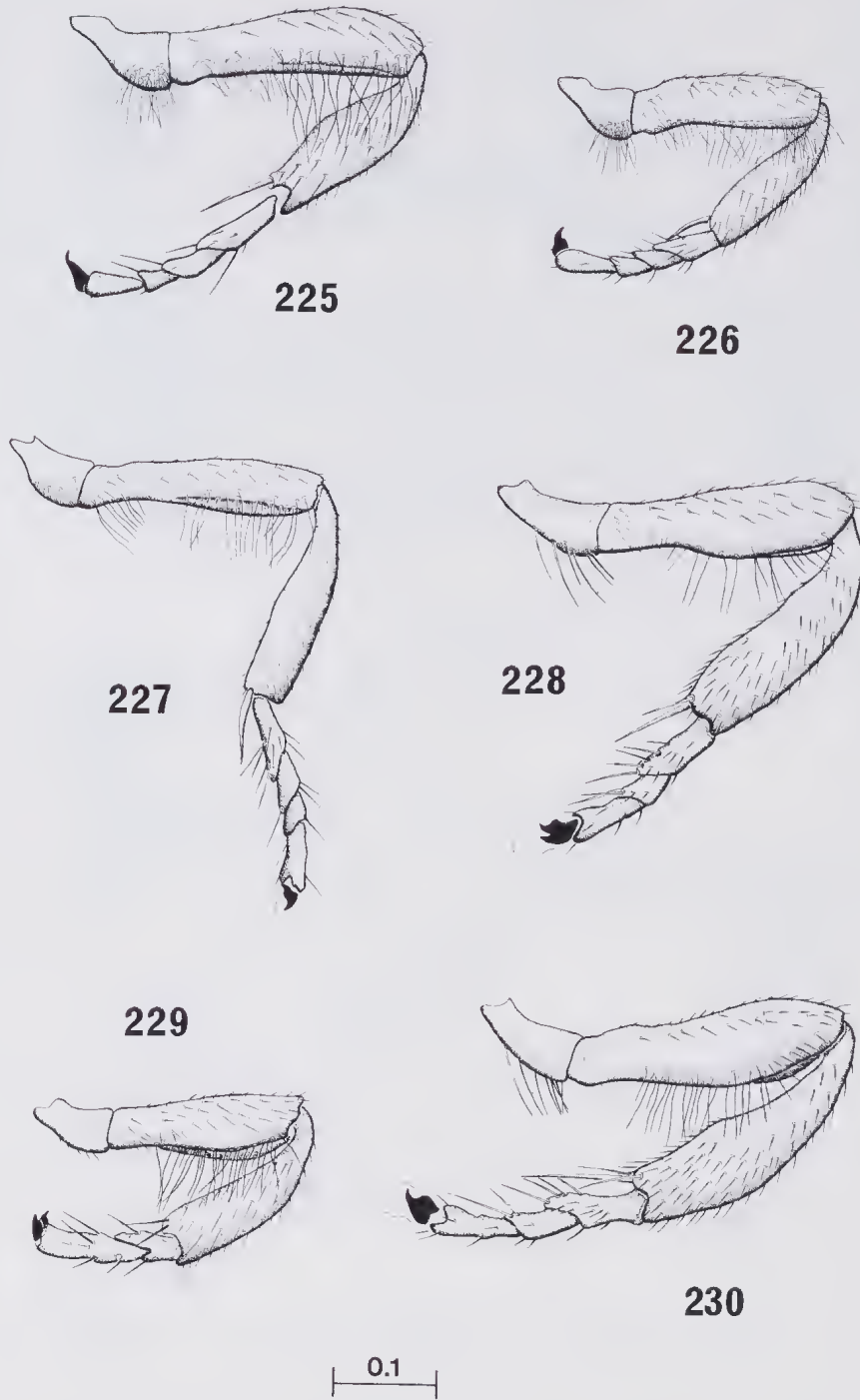


FIGURES 211–216, Male antennae, *Melittobia* spp. 211 — *assemi* ventral scape; 212 — *assemi* dorsal scape; 213 — *assemi* pedicel and flagellum; 214 — *sosui* ventral scape; 215 — *sosui* dorsal scape; 216 — *sosui* pedicel and flagellum.

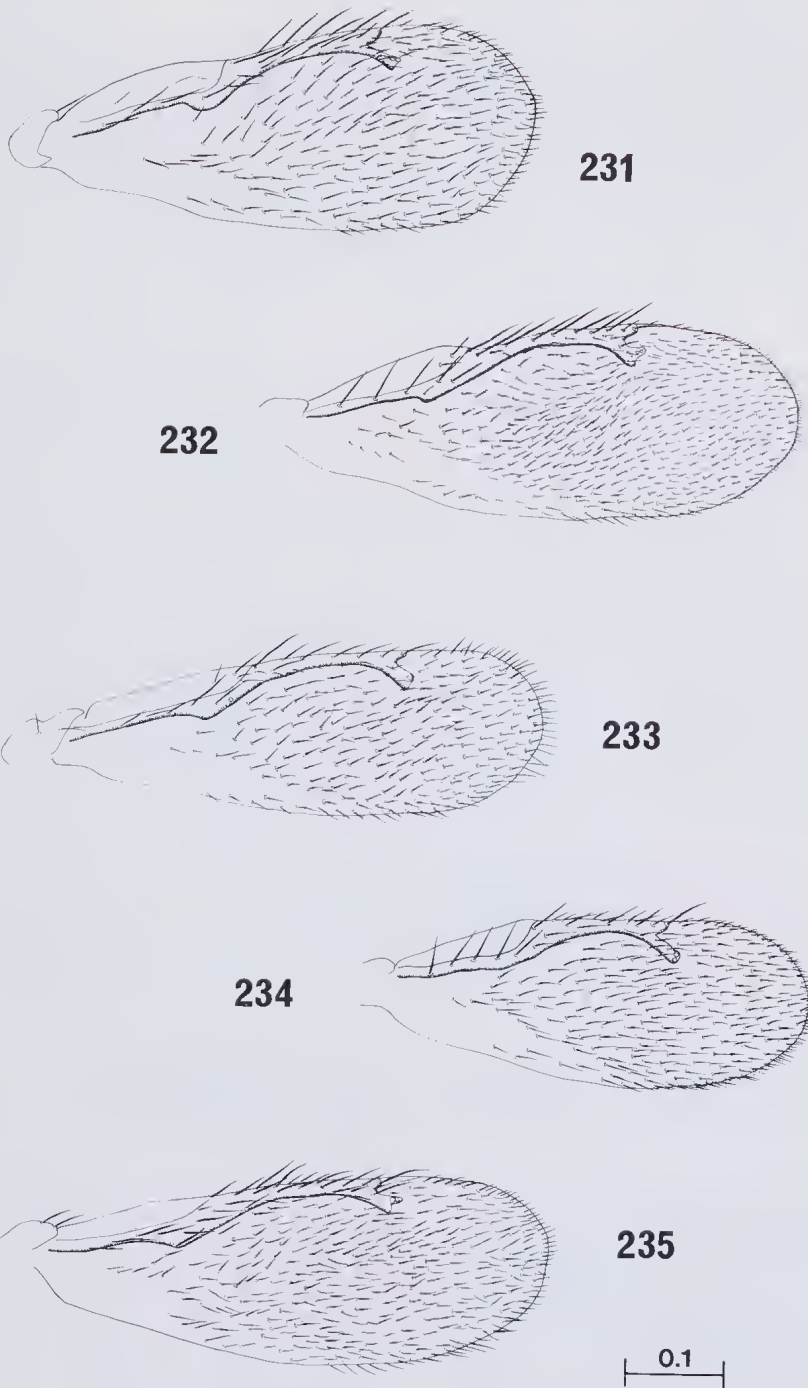


FIGURES 217-219, Male antennae, *Melittobia* spp. 217 — sp. nov. Argentina ventral scape; 218 — sp. nov. Argentina dorsal scape; 219 — sp. nov. Argentina pedicel and flagellum.

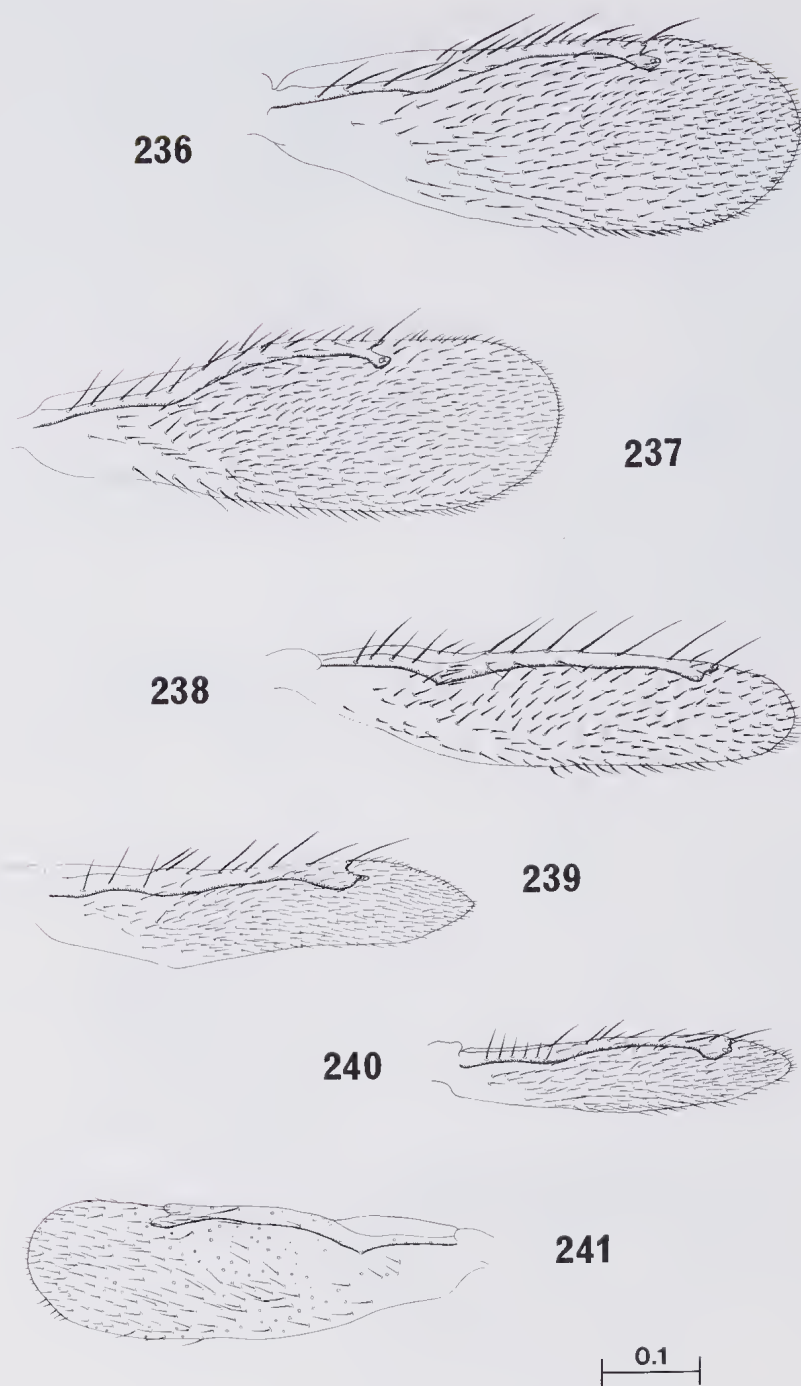
FIGURES 220-224, Male mid legs *Melittobia* spp. 220 — *clavicornis*; 221 — *acasta*; 222 — *scapata*; 223 — *evansi*; 224 — *digitata*.



FIGURES 225-230, Male mid legs, *Melittobia* spp. 225 — *femorata*; 226 — *chalybii*; 227 — *australica*; 228 — *assemi*; 229 — sp. nov. Argentina; 230 — *sosui*.



FIGURES 231-235, Male fore wings, *Melittobia* spp. 231 — *clavicornis*; 232 — *acasta*; 233 — *evansi*; 234 — *scapata*; 235 — *digitata*.



FIGURES 236-241, Male fore wings, *Melittobia* spp. 236 — *femorata*; 237 — *chalybii*; 238 — *australica*; 239 — *sosui* large form; 240 — *sosui* small form; 241 — sp. nov. Argentina.

A REVIEW OF THE BIOLOGY OF SPECIES IN THE THE GENUS *MELITTOBIA*  
(HYMENOPTERA : EULOPHIDAE) WITH INTERPRETATIONS AND ADDITIONS  
USING OBSERVATIONS ON *MELITTOBIA AUSTRALICA*.

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Queensland Museum

ABSTRACT

This paper reviews published accounts of *Melittobia* biology and contains observations on the single Australian species *M. australica*. The species was found to be a highly polyphagous primary ectoparasite attacking the immature stages of nesting Hymenoptera, both solitary and social. It is also hyperparasitic on the immature primary parasites within the primary host's nests, and are reported parasitising the immature stages of hosts belonging to a variety of orders other than Hymenoptera. Females gain access to the host by entering the host cell before it is sealed (delaying oviposition until the host has reached a suitable developmental stage), excavation through the cell wall and enveloping membranes or by oviposition directly through enveloping membranes. Any one species can show this range of behaviour and the female's nutritional condition is important as a factor in deciding which occurs. Females puncture the host with their ovipositors to feed and to subdue an active host but not for oviposition. Males do not feed and are highly aggressive although male aggression seems to vary both within and between species. Courtship is extremely complex and the three basic patterns reported in the literature are summarised and some morphological features are correlated with them. Reproduction is also complex and the importance of parthenogenesis, sib-mating (including mother-son matings), multiple settling by females and sex ratios shifts is discussed. A nutritionally induced polymorphism occurs, as well as sexual dimorphism, and varies with species. The result is type-form and second-form individuals of both sexes which differ morphologically and physiologically. Second-form specimens of both sexes of an *acasta* group species are described and compared with second-form specimens of both sexes of *M. australica*. Dispersal is by flight and evidence suggests that it is wind assisted. The capability of *Melittobia* to use man's transport for dispersal is also discussed. A brief account of the life cycle of *M. australica* is included and compared with published accounts of other species.

INTRODUCTION

Species in the genus *Melittobia* are very efficient organisms. In all stages of their development they show remarkable plasticity of behaviour and adaptability to prevailing conditions. Theoretically, uninseminated females can survive and eventually produce progeny of both sexes even in the absence of preferred hosts. They make very good laboratory animals and their plasticity coupled with arrhenotokous parthenogenesis make them ideal subjects for laboratory investigations into the genetics of speciation and evolution.

Some of the reports on the biology of *Melittobia* species in the literature proved either confusing or inconsistent. Detailed study of the biology of *Melittobia australica* allowed many of the confusing and inconsistent aspects to be

clarified. The following account is therefore a blend of previously published accounts on several species and my recent observations on the single Australian species. The outcome of this review has been of great assistance in understanding phylogeny in the genus and therefore of great assistance in making taxonomic decisions for my revision of the genus (Dahms 1983a)

MATERIALS AND METHODS

Cultures of *Melittobia australica* were maintained in excavated blocks with glass covers in the laboratory without controlled temperature or humidity. Behavioural observations were made with a Leitz TS stereomicroscope with fibre-optics, cold-light illumination. Hosts used for culture of *M. australica* were *Pison* spp., and *Sceliphron* spp. Larvae of the ant genus

*Camponotus* were tried as hosts but proved unsuitable. Although larvae of *Apis mellifera* proved suitable hosts for cultures they suffered high mortality due to mechanical damage during extraction and from not being in a controlled environment.

Investigations into the life history of *M. australica* were carried out using *Sceliphron formosum* prepupae, a supply of which was maintained in the refrigerator without deterioration. In this case the trials were carried out in plastic-stoppered glass vials. A constant temperature room was not available and the colonies were kept in a room with an air conditioner. Under these circumstances the temperatures recorded were 25°C ( $\pm$  5°) and humidity 50% ( $\pm$  5%).

All figures were drawn from cleared microscope slide-mounted specimens and each has the scale indicated. They were drawn with a camera lucida fitted to a Wild M20 compound microscope.

## BIOLOGY

### Hosts

To say that species of *Melittobia* are not host specific is a gross understatement. Waterston's 1917 view of *M. acasta* that it is remarkably polyphagous attacking everything within its limited range of action is more realistic.

In the main, *Melittobia* are primary parasites within the nests of wasps and bees, both solitary and social. Amongst the social species are: *Vespula acadica* (Salden) (H.C. Reed, USA, pers. comm. 1978); *Vespula germanica* (Fabricius) and *Bombus* sp. (R. Macfarlane, New Zealand, pers. comm. 1980); *Polistes exclamans* Viereck (H.C. Reed, USA, pers. comm. 1977); *Bombus pennsylvanicus* (DeGeer) (A.C. Haman, USA, pers. comm. 1977) and *Apis mellifera* Linnaeus (E.H. Erickson, USA, pers. comm. 1978). The last mentioned of course has serious economic implications although van den Assem (pers. comm. 1981) considers that sperm inside the spermathecae of female *Melittobia* do not survive at the relatively high temperatures found inside the hive of *A. mellifera*. *Melittobia* species have reached economic pest status wherever the Alfalfa Leaf-cutter Bee (*Megachile rotundata* (Fabricius)) is cultured (Prof. Thorp, University of California Davis pers. comm. 1981). Four species, *M. acasta* (Walker 1839), *M. chalybii* Ashmead, 1892, *M. japonica* Masi 1966 (= *M. clavicornis* (Cameron 1908)) and *M. megachilis* (Packard 1864) have been recorded in the literature as being

hyperparasitic within nests of Hymenoptera and in the present study *M. australica* Girault, 1912 was found to be hyperparasitic also.

There are published records of *Melittobia* naturally parasitising hosts belonging to orders other than Hymenoptera. Rau (1940) reports breeding *M. chalybii* from the ootheca of the cockroach *Periplaneta americana* (Linnaeus). Howard and Fiske (1911), and Graham-Smith (1916, 1919) have bred *M. acasta* from dipteran puparia. Swezey (1909) discovered *M. hawaiiensis* Perkins, 1907 breeding on the larvae of the bud-moth *Ereunetis flavistriata* Wilson. Howard (1892) reported a species from dipteran puparia within the cells of a mud-dauber's nest and *M. japonica* (= *M. clavicornis*) is noted as utilising similar dipteran hosts by Iwata and Tachikawa (1966). In the present study *M. australica* was bred from dipteran puparia within *Sceliphron* spp. nests.

Laboratory trials by various workers have shown a remarkable range of hosts that *Melittobia* will utilise under these conditions. Balfour-Browne (1922) and Thompson and Parker (1927) found *M. acasta* to be highly polyphagous in the laboratory, even attacking spiders and lepidopteran larvae taken from mud nests. However, the progeny failed to mature and Balfour-Browne felt this may have been due to desiccation of the hosts. These papers contain a very large number of species successfully parasitised from the insect orders Coleoptera, Hymenoptera, Lepidoptera and also from the arachnid order Araneae. Peck (1963) and Burks (1979) provide comprehensive host lists for North American species; Domenichini (1966) has host lists for *M. acasta* and *M. japonica*; (= *M. clavicornis*) and Thompson (1955) listed hosts of *M. acasta*, *M. hawaiiensis* and an unidentified species using Commonwealth Agricultural Bureau records. These lists are extremely long and it is not practical to duplicate them here.

Not all species of Hymenoptera, however, are successful hosts for *Melittobia*. Balfour-Browne (1922) found that *Osmia rufa* (Linnaeus) was rarely attacked in the wild. In the laboratory naked larvae and pupae of *O. rufa* were readily accepted by *M. acasta* females which fed and laid eggs. The eggs often failed to hatch and, if they did hatch, the resulting larvae failed to reach maturity. If he placed *M. acasta* females in a cell with larval *O. rufa* just before the cocoon was spun the *M. acasta* females often became entangled in the outer layers of the cocoon. This did not happen under similar circumstances with



other hosts. Where *M. acasta* females were presented with *O. rufa* pupae inside cocoons they were not attacked and Balfour-Browne suggested that this was due to the toughness of the cocoon. Malyshev (1911) had earlier suggested that some species may escape attack by *Melittobia* as the result of a mechanical barrier related to the type of nesting material used, e.g. those species which use resin for nest construction.

Jayasingh and Freeman (1980) also draw attention to the importance of nest material in host susceptibility to attack by *Melittobia*. They found the resinous nests of *Chalicodoma rufipennis* (Fabricius) to be a total barrier to *Melittobia*. They also found that another factor was direct attack by the mother on *Melittobia* e.g. females of *Pachodynerus nasidens* (Latreille) were observed to crush *Melittobia* females in their mandibles. I have observed parasitic mites which can normally be found on *Sceliphron* spp. larvae acting in competition with *M. australica* larvae and in one case the mite larvae were feeding upon the *M. australica* larvae. From these observations it is clear that *Melittobia* do not have it all their own way.

There are a few indications in the literature that *Melittobia* spp. may be endoparasitic. Girault (1912), at the end of his description of *M. australica* quotes the collector, 'Mr. Tryon informs me that the parasites emerged from the host in its cocoon but not until after it had transformed into the adult, the latter died. A number of parasitic larvae make their way out of each *Pison* and pupate nakedly'. This record I regard as an error based upon an assumption. In all cases I have observed, *M. australica* is very definitely ectoparasitic. Perhaps Mr. Tryon on opening the host cocoon saw prepupal *M. australica* larvae with meconium and assumed that the larvae had emerged from within the host.

Malyshev (1911) states that under certain circumstances *M. acasta* is endoparasitic e.g. when the female oviposits through the cocoon of hymenopteran hosts or through the puparial wall of a dipteran host. Thompson and Parker (1927) found that *M. acasta* would not oviposit in fresh puparia of *Sarcophaga* sp. Oviposition occurs only after the body of the fly has separated from the wall of the puparium creating air spaces. Eggs are placed directly onto the surface of the pupa within. They found the same with some living but slightly desiccated pupae of the ant genus *Camponotus*. Air spaces had developed beneath the cuticle resembling the situation with dipteran

puparia. Maeta and Yamane (1974) reported that one method of oviposition used by *M. japonica* (identification corrected to *M. acasta* by Maeta (1978)) was to oviposit through the wall of cocoons of species belonging to the hymenopteran genera *Osmia*, *Monodontomerus*, *Nematopoides*, *Trypoxylon* and *Chalicodoma*. In all of these situations insertion of the ovipositor through enveloping membranes implies endoparasitism, but the eggs are placed on the surface of the body of the host which means they are in fact ectoparasitic.

In the present investigation *M. australica* was bred from the following hosts:-

- 1) *Pison aureosericeum* Rohwer
- 2) *Pison* spp.
- 3) *Sceliphron laetum* Smith
- 4) *Sceliphron formosum* Smith
- 5) *Megachile* sp.
- 6) *Stenarella victoriae* Cameron
- 7) Dipteran puparia in *Sceliphron* spp. nests
- 8) *Camponotus* sp.
- 9) *Apis mellifera* Linnaeus
- 10) *Anthrax angularis* Thomson

The host given by Girault for the type specimens of *M. australica* was *Pison spinolae* Schuckard. In the above list, 1-6 were naturally infested. *Stenarella victoriae* is an ichneumonid parasite on *Sceliphron* spp. The dipteran puparia in *Sceliphron* nests are thought to be parasites on the provisioned spiders since they are always found in cells fully stocked with dry spiders and without a *Sceliphron* larva. Hosts 8-10 were presented in the laboratory. Larvae of the ant genus *Camponotus* were tried as substitute hosts for laboratory work. Although the *M. australica* progeny developed through to maturity the resulting adults were small and lacked vigor. Honey bee (*Apis mellifera*) larvae were also tried as alternative hosts. They were readily accepted and produced vigorous parasite adults, but proved difficult to extract from the comb without a high percentage of deaths. *Anthrax angularis* was found as a parasite in *Sceliphron* nests. Two larvae were presented to fertilised *M. australica* females and were readily accepted. The resulting progeny were of normal size and vigour. Since *Anthrax angularis* is a natural parasite of *Sceliphron* spp. it is fairly safe to assume that it would be naturally attacked by *M. australica*.

#### Access to the Host

In the literature, workers have put forward several behavioural patterns associated with gaining access to the host as follows:-

- 1) excavation into the host cell and cocoon
- 2) entrance into a host cell before closure
- 3) oviposition through enveloping membranes

#### 1) Excavation

*Melittobia* females have well developed, tridentate mandibles and there are several records in the literature which indicate that they have well developed excavatory powers.

Howard and Fiske (1911) stated that female *M. acasta* in search of a host (sarcophagid puparia in this case) entered damp soil for a distance of several inches. Graham-Smith (1916) however, suggested that the fly puparia buried in the soil were possibly connected to the surface by minute passages sufficiently large to admit *Melittobia*. There may in fact be minute passages left as the sarcophagid larvae dig into the soil and this may not be a case of true excavation by *Melittobia*. More direct evidence was provided earlier by Howard (1892) quoting observations by Giraud. The latter noted that a *M. acasta* female after walking around on the intact cell of the bee *Chalicodoma* sp., stopped and gnawed the membrane until a perforation was made through which she entered the cell. Malyshev (1966) observed that a *M. acasta* female in a host nest moved from one cell through the cell wall into the next cell and through the cocoon to gain access to another host. Graham-Smith (1916) stated that females of *M. acasta* emerged from intact fly puparia through a small hole which one of them excavated. He also noticed that females of *M. acasta* confined in glass tubes with cork stoppers immediately began to excavate a tunnel in the cork stopper. Similarly, Buckell (1928) found females of *M. chalybii* (= *digitata* Dahms 1983a) excavated their way out of glass vials through a 25 mm cork stopper. Torchio (1963) recorded excavation holes in the cell partitions of *Megachile rotundata* (Fabricius) made by *M. chalybii* (which I suspect was *M. acasta*). Cowley (1961) mentioned that *M. clavicornis* (= *M. hawaiiensis* Perkins) will excavate a hole in cocoon walls to gain access to *Pison spinolae* pupae within. Iwata and Tachikawa (1966) observed 1-5 excavation holes each of 0.5 mm made by *M. japonica* (= *M. clavicornis*) females in a series of mud cells of *Auplopus* sp. They also found several incomplete holes whose bottoms were obstructed by sand grains and from this postulated that the excavations were from the outside in. Observations by Maeta and Yamane (1974) on *M. japonica* (= *M. acasta* see Maeta (1978)) led them to conclude that female *Melittobia* have the capacity to excavate holes in

plugs or partitions either of leaf fragments or mud, even if they were fairly thickly constructed.

In this investigation, inseminated female *M. australica* were presented with sealed nests of *Pison* sp. and *Sceliphron* spp. After presentation of the *Pison* nests, *M. australica* females were noted excavating the mud walls. Only one hole was constructed in each cell and several females were observed working at each site. Only one female worked at any one time at the one site with the others taking turns. Graham-Smith (1916) mentioned that *M. acasta* females produce one exit hole in each puparium, rarely two. Also when confined in glass vials he found that only one excavation tunnel was made in each cork stopper and that females worked singly at the excavation. For practical reasons one would expect that the economy in number of holes excavated per cell would be fairly general in the genus, although Iwata and Tachikawa (1966) observed 1-5 per host cell for *M. japonica* (= *M. clavicornis*) as mentioned above.

As soon as the hole in a *Pison* cell was large enough, the female *M. australica* passed through. The next day when the cells were broken open the host cocoon was seen to have a single excavated hole and the parasite females were inside on the body of the host. In the case of the *Sceliphron* spp. nests, excavation was not directly observed, but 24 hours after exposure to inseminated *M. australica* females there were no parasites to be seen. Examination of the host cell walls showed a single excavation in each and on breaking open the cells, I found that the parasite females had penetrated the cocoons to reach the host within by a further single excavation. Under these conditions more than one female had entered each cell. Similarly inseminated *M. australica* females gained access to *Megachile* sp. larvae within a sealed leaf nest lying uncovered on a bench about 2 metres from the release site.

In one instance where plastic stoppered tubes were used for cultures of *M. australica*, I found that adult females were capable of escaping by excavating their way through three sealing flanges on the inserted part of the cap and the rim of the cap where it fitted against the top of the glass tube. They did this in each of the 10 tubes being used.

If presented with *Sceliphron* cocoons outside their mud cells, inseminated *M. australica* females gnawed a hole in the cocoons and oviposition followed feeding. If naked *Sceliphron* prepupae and pupae were presented, oviposition followed feeding without delay. Therefore, as Thompson

and Parker (1927) found with *M. acasta*, the presence and penetration of enveloping membranes are not necessary prerequisites for oviposition in *M. australica*.

## 2) Entrance before the host cell is closed

Several workers have shown that *Melittobia* enter unsealed nests of their hosts and are able to delay oviposition until the host is at a suitable developmental stage.

Schmieder (1933), working with *M. chalybii* reported that female parasites gained access to the larvae of bees and wasps by entering host cells before they were completed. The only evidence to support this in his paper is the fact that examination of a *Trypoxylon* sp. cocoon did not reveal whether or not it contained *Melittobia*. He took this to indicate that the parasite gained access to the host before the cocoon was spun and became enclosed with the host. However, it does not necessarily mean that *M. chalybii* females entered before the nest was closed since they could just as easily have excavated their way into a sealed host cell before the cocoon was spun and then become enclosed with the host. Therefore, this is not conclusive evidence.

Balfour-Browne (1922) noticed *M. acasta* females becoming sealed up in cells being constructed by bees and wasps in elder stems and glass tubes he had provided in his garden. From observation of those in the glass tubes he discovered that their being sealed in the host nests was not accidental. He found that females can delay oviposition for up to 60 days when placed in a cell with an unhatched host egg. The parasite commenced oviposition only when the host reached full-grown larval condition. Feeding by the parasite on the developing host appeared not to affect the latter's development and he had many examples of eggs being pierced by the female's ovipositor for food without affecting development of the host. During his trials he placed up to 15 *M. acasta* females in a cell with a newly hatched *Osmia* sp. larva and allowed them to feed freely on the host for 14 days without apparently affecting the host which completed its development. When he placed *M. acasta* females with older larvae there were no ill effects on the host as long as the parasites were only feeding. He felt quite satisfied that feeding by *M. acasta* females was not necessarily injurious to the host. Malyshev (1966) also mentioned *M. acasta* females entering host cells before they were closed.

Maeta and Yamane (1974) found that, in most *Trypoxylon* sp. cells infested with *M. japonica* (=

*M. acasta* see Maeta (1978)), the closing plugs did not show entrance holes. They concluded that the parasite had gained access to the host cell before it was sealed. When discussing oviposition, they mentioned the capacity of *M. japonica* (= *M. acasta* see Maeta (1978)) females to delay feeding until the host reached a suitable stage for parasitism; in fact they kept females of this species alive for more than 2 months without food.

In this investigation, *M. australica* females were not directly observed entering host cells before they were closed, but there is indirect evidence that this may occur. On numerous occasions *M. australica* females were kept for periods up to 3 weeks without food. At the end of this period, when a suitable host was provided, they fed and subsequently laid fertile eggs. Thus they can survive long periods without ovigenesis being adversely affected. Females accidentally released in the laboratory were later found residing in empty host cells of old *Sceliphron formosum* nests lying on the laboratory bench. When these cells were broken open the parasites showed the usual negative reaction to light which is displayed in the presence of a host. Feeding by *M. australica* females does not affect development of the host e.g. when inseminated females were allowed to feed on prepupal *Sceliphron formosum* larvae for a few days then removed the host successfully passed to pupal and adult stages. Several *Sceliphron formosum* early pupae were supplied each to 10 inseminated *M. australica* females and all hosts continued to develop to full adult colouration in spite of feeding by the parasites and their progeny. Death of the host pupae resulted ultimately due to feeding pressure of the parasites. Therefore, *M. australica* females will enter empty host cells, can delay feeding and oviposition for long periods, and are able to feed on the host larva or pupa without affecting its development.

This capability with its attendant behaviour patterns probably occurs in all species.

## 3) Oviposition directly through enveloping membranes

As mentioned before, Thompson and Parker (1927) found that *M. acasta* oviposits directly through the puparial wall of Diptera and that this takes place only after the fly pupa has separated from the puparial wall. Malyshev (1966) also mentions this. In all cases where I have reared *M. australica* from fly puparia there were no excavation holes in the puparial walls until emergence of the parasite, these being the exit

holes of the progeny. Maeta and Yamane (1974) stated that *M. japonica* (= *M. acasta* see Maeta (1978)) oviposited directly through the cocoon of species of the hymenopteran genera *Osmia*, *Monodontomerus*, *Trypoxylon* and *Chalicodoma*. However, there appears to be some versatility of behaviour here since they also found that in some cases the parasites entered the host cocoons of *Trypoxylon* and *Chalicodoma* before oviposition.

Malyshev (1966) provided an explanation. When a *M. acasta* female's work was finished in one cell of a host's nest she made her way into the next cell with her jaws. If the host cocoon was in close contact with the cell partition the parasite gnawed through both the partition and the cocoon. However, if the cocoon was not in contact with the cell partition and the body of the host was some distance from the cocoon wall the parasite gnawed through the cocoon. Where the cocoon was close fitting he found that the parasite oviposited directly through the cocoon wall. Thus closeness of fit of the cocoon to the host appears to be important, i.e. it is necessary for the tip of the ovipositor to reach the host within and this is substantiated by my observations on *M. australica* outlined below.

For hosts with spacious cocoons this behaviour would not be possible, e.g., it is difficult to imagine *M. australica* ovipositing through the cocoon walls of *Sceliphron* spp. In all cases, whether the *M. australica* females had fed or not, when *Sceliphron* spp. cocoons were provided they were always entered before oviposition.

Although the hosts mentioned above by Maeta and Yamane (1974) are all small with close fitting cocoons, some were found to be entered also and I feel the nutritional condition of the female is important in these cases as well as the closeness of the cocoon to the cell partition. When I presented inseminated unfed females of *M. australica* with *Pison* sp. cocoons, which are close fitting, each was entered by the parasite. On one occasion on breaking open a *Pison* sp. cell collected from the wild I found two *M. australica* females with distended metasomas on the cocoon surface. They were observed to insert their ovipositors through the cocoon wall. The point of insertion was always on the side of the cocoon about 1/2 to 2/3 the way down the wall. The ovipositor was fully inserted followed by a pause of about 3-5 seconds, half withdrawn, reinserted followed by a pause of about 3-5 seconds then fully withdrawn. On one occasion, a female inserted her ovipositor at the upper, anterior end of the cocoon and was

noticed to indulge in partial withdrawals and re-angling the direction of the ovipositor. No pausing occurred and the ovipositor was eventually withdrawn. This end of the cocoon housed the narrow, anterior end of the prepupal larva which from the upper surface of the cocoon was not accessible to the ovipositor of the female. No attempt was made by the females to enter the cocoon. On breaking open the cocoon about 15 eggs were visible on the lateral portions of the prepupal *Pison* larva — none on the anterior portion. It appears therefore that contact of the ovipositor with the host within is necessary before oviposition occurs and that oviposition through enveloping membranes occurs with close fitting cocoons where the parasite female has previously fed. No published records are available on penetration of fly puparia by the female parasite. I have tried *M. australica* on blow fly puparia but without success. Tachinid or sarcophagid puparia were not available. In the case of puparia, the parasite female may feed on the early pupa before it separates from the puparial wall or the pupa within may be close enough to the puparial wall in some areas to allow some body fluids to well out of a puncture site, e.g., Graham-Smith (1919) mentioned that fertilised or unfertilised females of *M. acasta* confined with fly puparia lived for long periods (up to 36 days) and seemed to derive nourishment from fluid exuding from the puparia at ovipositor puncture sites. Van den Assem (pers. comm. 1981) has confirmed this behaviour in all *Melittobia* species in his cultures. However, in some cases, the parasites gnawed their way into fly puparia. He found that in crossing experiments involving the *assemi* group, females gnawed holes in fly puparia and walked on the surface of the pupa within. Van den Assem (1976) found that virgin *M. acasta* females gnawed their way into fly puparia containing males of this species and mated with them.

Migration from one cell to another appears to be nutritionally governed as well. The relatively large eggs (0.3 mm long; females 1.1-1.5 mm long) mean that a female cannot produce her entire egg batch in 1 or 2 days. Oviposition and feeding were observed to be progressive throughout the life of female *M. australica*. It is reasonable to assume, therefore, that competition for food with her progeny may be an important factor in governing the number of eggs per host. On a relatively large host e.g. *Sceliphron* spp. there is probably enough food to support the larvae and the mother for the length of her life. On smaller hosts e.g. *Trypoxylon*, *Osmia*, *Pison*

etc. competition for food with her progeny would necessitate her migration from one cell to another. In this situation, if she has sufficient food for maturation of eggs she may oviposit directly through the enveloping membrane of the host in the next cell. What determines the number of progeny in this case is not known. Perhaps as she approaches the time for nutritional replenishment she might again migrate then penetrate the next cocoon. The whole process of oviposition and nutritional requirements is one deserving close study.

In summary, oviposition behaviour of inseminated *Melittobia* females is very flexible and is dependent upon a number of conditions. If the female parasite encounters a host cell before it is closed, she enters and feeds upon the developing host without affecting its development. She can delay oviposition until the host is at a suitable stage, i.e., the prepupal larva or pupa. If the host is large with a spacious cocoon she can become incorporated within during construction or gnaw in afterwards. She stays with this one host all her life and is assisted in its utilisation by specialised second-form progeny (discussed later). Where the host is small with a close fitting cocoon she can either become incorporated or oviposit through the cocoon wall. Because of the limited food supply on a small host she must seek another to attain her full egg laying potential and moves to another cell. If the cocoon is touching the cell partition and/or she requires additional food she gnaws through the cocoon wall. However, if the cocoon is not in contact with the cell partition and she does not require more food she can continue ovipositing through the enveloping membrane. Where the host cell is sealed she gnaws through the cell wall. If the host has not spun a cocoon she can follow the behaviour patterns above depending upon the size of the host and the closeness of fit of the cocoon. Should she enter a cell and encounter a cocoon, no matter how close fitting she gnaws through it to feed upon the host.

## FUNCTIONS OF THE OVIPOSITOR

Female *Melittobia* use their ovipositors for feeding, to paralyse the host and for egg laying.

### 1) Feeding

When inseminated *M. australica* females were presented with quiescent larvae or pupae, I noticed the ovipositor was fully inserted and within a few seconds, withdrawn. The females moved back and fed on the drop of body fluid

which issued from the host. Old wounds, visible as dark brown spots, were frequently revisited by the females who fed on the congealed body fluids of the host. There appeared to be no favoured spot for puncture of the host's body and on one occasion a female punctured the head capsule of a host larva. Torchio (1963) observed *M. chalybii* (which I feel was probably *M. acasta*) feeding on congealed host body fluids at old puncture sites.

Balfour-Browne (1922) observed this behaviour in *M. acasta* and even the eggs of the hosts were used as a food source. Malyshev (1966) also mentioned the habit of *M. acasta* females feeding on the body fluids of the host oozing from ovipositor penetration points. Schmieder (1933) mentioned this feeding behaviour in *M. chalybii*. Maeta and Yamane (1974) noted dark brown spots on the body of the host and assumed these to be the feeding spots of *M. japonica* (= *M. acasta* see Maeta 1978) females although they did not directly observe this feeding. It was recorded also for *M. japonica* (= *M. clavicornis*) by Iwata and Tachikawa (1966).

This behaviour is no doubt a general one for all species of *Melittobia* and feeding upon the host by the female is recorded amongst other parasitic Hymenoptera. In the case of *Melittobia* it can occur without death of the host and this, together with the female's ability to delay oviposition for long periods is a decided advantage when a host in an early stage of development is encountered.

Doutt (1959) in his review of the biology of parasitic Hymenoptera mentioned this feeding behaviour and that it is well established that feeding on the host body fluids is necessary to obtain protein for ovigenesis. In support he mentioned the work of Flanders (1942, 1953) on *Metaphycus helvolus* (Compere). Over a 3 week period at 80° F and away from its host, ovigenesis ceased in this species. When presented with a host at the end of this period the parasite fed without delay and oviposition began a few days later.

In this investigation, newly emerged, inseminated *M. australica* females when deprived of a host remained as they emerged, i.e., without distended metasomas. When presented with a host pupa after 7 days all females immediately inserted their ovipositors and fed at the puncture sites. Within 24 hours their metasomas were distended and well developed eggs were clearly visible through the intersegmental membranes of the metasoma. They began laying eggs 2-3 days after feeding. It would appear therefore that feeding upon the host is essential for egg maturation in *Melittobia*.

## 2) Preparation of the host

Buckell (1928) presented *M. chalybii* (= *M. digitata*) with active host larvae which became quiescent after 24 hours. He postulated that some paralyzing fluid was injected. Balfour-Browne (1922) found that once an *M. acasta* female had oviposited on a host the latter was doomed even though the eggs were removed before hatching and the adult females removed as well. We have seen before that he found feeding by the adult females did not affect host development. He described a fluid oscillating in the ovipositor as it was being inserted. I have noticed movement in the ovipositor of *M. australica* but consider it more likely to be rotation of the valves of the ovipositor as the female works at insertion. A similar movement was seen during insertion of the ovipositor of *M. australica* for feeding. Balfour-Browne also noticed that the ovipositor was held fully inserted for a period before withdrawal and that the females did not feed at these sites.

When active last instar larvae of *Anthrax angularis* and *Sceliphron* spp. were presented to inseminated *M. australica* females they became very agitated and continually performed twisting and rolling movements. The parasites inserted their ovipositors in spite of the activity and within 24 hours the host larvae were quiescent. In these cases the ovipositor was inserted and held in position for some time before extraction. After withdrawal of the ovipositor the females moved away without attempting to feed at these sites. Once the host larvae were quiescent, the *M. australica* females were noted to insert their ovipositors and feed at the puncture sites after withdrawal.

The minute size of *Melittobia* relative to its hosts makes suppression of an active host seem an impossible task. Beard (1952) working with *Habrobracon hebetor* (Day) found that one part of the venom of this species to 200,000,000 parts of the host's blood was sufficient to cause permanent paralysis. If the levels of potency are similar in *Melittobia*, the task of subduing an active host would not be impossible.

Given the capacity of *Melittobia* to delay oviposition and its ability to feed on the host without affecting the latter's development one wonders whether paralysis of the host is necessary under natural conditions. In all cases where host cells have been broken open and *M. australica* found, the host has been able to produce a cocoon and in some cases development had reached the pupal stage and attained adult colouration before death. Malyshev (1966) suggested that the

stinging by *M. acasta* was for preservation of the host and it may be that under certain circumstances the injection of venom prevents further development of the host. This is an aspect that requires further investigation.

## 4) Oviposition

Last but not least, the ovipositor is used for egg deposition. The ectoparasitic status of the genus has already been discussed. Oviposition therefore, does not involve insertion of the ovipositor into the host. In *M. australica* the tip of the ovipositor was braced against the surface of the host and the metasoma raised releasing the inner ovipositor valves which therefore became arranged at right angles to the metasoma. The relatively large egg appeared to flow down the ovipositor valves onto the host. No particular site on the host appeared to be favoured, but the eggs tended to be deposited in clusters. The surfaces of the eggs were moist, and this coating kept them attached to the host and to each other. This procedure for *M. australica* appears to be fairly standard for the genus.

## HABITS OF THE MALE

In all species for which the male is known he has reduced wings, modified antennae and reduced eyes. His sole function appears to be reproduction. Important aspects of his behaviour are feeding, aggression and courtship.

## 1) Feeding.

Waterston (1917) wrote ... 'The male is at first of a transparent yellowish brown colour, the head sometimes darker but after feeding, the abdomen may be opaque ...' Other workers (Balfour-Browne (1922) with *M. acasta*, Buckell (1928) with *M. chalybii* (= *M. digitata*), Schmieder (1933) with *M. chalybii* and Dahms (1973) with *M. australica*) have not observed males to feed. In most cases when males emerge the host is fully utilised leaving only brothers and sisters as potential food. Male aggression has been mentioned by different workers and Matthews (1975) suggested this aggression may be important for male nutrition as the opponent's body fluids could serve as an additional energy source. As more direct evidence in support he drew attention to the occasional killing by males of virgin female *M. chalybii* (= *M. australica*) presented to them in mating chambers. The male usually tore a hole in the female's metasoma and chewed vigorously on her for several minutes. Graham-Smith (1919) found that in some battles between male *M. acasta* the victor buried his mandibles in the

dorsal part of his adversary's head and continued to bite for several minutes.

I agree with van den Assem, Gijswijt and Nübel (1980) who felt that this suggestion is questionable. Although male aggression has been reported for several species there appears to be some variation in whether an opponent is mutilated or not, i.e., it is apparently not consistent in the genus. Balfour-Browne (1922) observed female mutilation by males in *M. acasta* but felt this was due to experimental conditions. He also noted that male aggression was less prominent where the cell was full of emerging females. In all the years I have been culturing *M. australica* (*M. chalybii* of Matthews (1975)) on only 2 occasions have I noted male aggression causing mutilation of other males and on only one occasion did I observe female mutilation. On these occasions I did not notice males pausing to gnaw on a victim.

The suspicion that males do not feed is substantiated by indirect evidence from my observations with *M. australica*. When males of this species emerge their metasomas are distended, but become increasingly deflated until finally they are very flat. Deflation of the metasoma would result from utilisation of food reserves for spermatogenesis and courtship. That this deflation would be dramatic can be seen from the extremely biased sex ratios recorded in the literature for several *Melittobia* species — 1-13% males. To quantify this — van den Assem, Gijswijt and Nübel (1980) found that the progeny from 29 host puparia each with a single *M. japonica*, (= *M. clavicornis*) female was 1843 individuals of which only 72 were males. The sex ratio of *M. australica* I found to be 3-4% males. If feeding were occurring without being observed then deflation of the metasoma would not have occurred or been so marked. Schmieder (1933) found the males of *M. chalybii* to be short lived. He attributed this to rapid depletion of food reserves resulting from abstinence from food during constant activity, which agrees with my assumption. Male aggression and feeding are topics deserving more detailed investigation.

## 2) Male aggression.

In the genus, males have not only undergone radical modification, e.g. head capsule and antennae, but also have undergone major reductions in non-required organs, e.g., eyes and wings. If males do not feed one would expect a reduction of the mouth parts. However, in all species, the mandibles of males are larger than those of females and each has a well

differentiated, sickle-shaped, anterior tooth. That these mandibles function as weapons in male aggression is reported in many species. Graham-Smith (1919) found that *M. acasta* males were very aggressive and encounters between males resulted in the death of one of the opponents. Only rarely did he find more than one live male in each host puparium. Balfour-Browne (1922) also found *M. acasta* males very aggressive and bouts between males often resulted in death. However, he also noted that in a cell full of emerging females, the males were very busy and paid little attention to each other. Malyshev (1966) found *M. acasta* males to be very aggressive. Hobbs and Krunic (1971) found that some male *M. chalybii* (= *M. acasta*) fought and died before the first females emerged. Often all were dead before the last female emerged. This in addition to the biased sex ratio often meant that late-developing females had no males with which to mate. Buckell (1928) recorded aggression in *M. chalybii* (= *M. digitata*) and he found the males to be extremely pugnacious. They fight until only one is left and, as Graham-Smith (1919) found with *M. acasta*, dead pupae or parts of males were readily attacked. Schmieder (1933) did not observe such fierce fighting between males of *M. chalybii* when confined with or without females. The males, when they met, engaged in a brief excited tussle and then separated. Hermann (1971) did not observe duels between males of *M. chalybii* (= *M. australica*) confined together in gelatin capsules. However, she did find that the first male to emerge touched other male pupae frequently and that these failed to emerge. This same species in Kalamazoo (the *M. chalybii* of Evans and Matthews (1976)) is very aggressive. When I visited Dr. Evans in 1974 I observed battles between these *M. australica* males which frequently resulted in mutilation. The other species kept in culture by Dr. Evans, *M. evansi* (Dahms 1983a), according to him was not as aggressive. Matthews (1975) confirmed that adult male *M. chalybii* (= *M. australica*) in his cultures are highly aggressive and more so than *M. evansi*. In the latter case the first male to emerge systematically decapitates others just prior to emergence from the pupa or immediately after. However, when adult male *M. evansi* met, one adopted an inert or passive posture and the aggressor abandoned it without inflicting injury.

In my cultures of *M. australica* over several years, encounters between males resulted in a brief excited tussle with the males rolling about. After a few seconds the males disengage and go

their separate ways a little faster than usual. I have not observed males paying any attention to male pupae. Males which emerged first walked over the pupal mass palpating it with their antennae and paused only at close-to-emergence females. On two occasions I have noticed male aggression resulting in mutilation of other males and occasionally males confined without females indulged in fatal encounters.

It appears that male aggression is a standard behaviour pattern in the genus and that some species are more aggressive than others. It appears also that male aggression can vary in intensity within a species. Matthews (1975) remarks on *M. evansi* indicate that there may be some variation in the stage at which other males are attacked and his description of males adopting passive postures when encountered by another male is the first record of this type of behaviour in the genus. This aspect of male behaviour would make a very nice study. The implications of male aggression are discussed later under 'Reproduction'.

A peculiar aspect of male aggression is reported for *M. acasta* and *M. chalybii* (= *M. australica*). Balfour-Browne (1922) found that the killing of females by males was not uncommon, but he thought that this was related to experimental conditions. Hermann (1971) found that males of *M. chalybii* (= *M. australica*) eight days or older when placed with a receptive female would grasp her and feed on her. After feeding upon her for a few minutes the males began copulatory behaviour. Such females generally died during courtship or before oviposition. Matthews' (1975) observation on the same species where males chew on a females's metasoma for several minutes has been mentioned under 'Feeding' above. In my colonies of this species male aggression resulting in female mutilation was noticed on only one occasion and several females were affected. I did not observe males pausing to chew or feed upon females which they mutilated. Perhaps Balfour-Browne is correct in assuming male aggression towards females was due to experimental conditions. In the wild, fertilised females disperse fairly soon after mating, but in the laboratory they are kept crowded and confined for several days. With increasing numbers of mated females, presumably with remnants of male odour (see Dahms 1983b), there is an increase in aggression some of which may be directed towards females. Whatever the cause, it appears to be a rare occurrence and is certainly not what one would expect.

### 3) Courtship.

In *Melittobia*, courtship is a lengthy and involved process. Detailed accounts of a few species can be found in Parker and Thompson (1928), Hermann (1971), Hobbs and Kronic (1971), Dahms (1973), van den Assem (1975), Evans and Matthews (1976), van den Assem and Maeta (1978, 1980), and van den Assem, Gijswijt and Nübel (1980), van den Assem, et alia (1982). Van den Assem has been investigating this aspect of behaviour in several species of *Melittobia*. His published work and personal communications over the years have been of immense value in guiding taxonomic decisions in the genus.

Van den Assem's work proves that courtship patterns in the genus show specific characteristics. Within the genus there appear to be three basic patterns (plus another demonstrated only by *M. clavicornis* Cameron 1908). The three basic patterns, *acasta* group, *hawaiiensis* group and *assemi* group, together with that of *M. clavicornis* have been discussed by van den Assem and Maeta (1978, 1980) and van den Assem et alia (1982), but I will briefly outline the situation for the sake of completeness. The reader is referred to Dahms (1983a) for an explanation of the species groups.

In *M. australica* (*hawaiiensis* group) the male stands well forward on the female with his mouthparts depressing her facial triangle just below the ocelli. His scapes, placed over the flagella of the female, lie close to her face. Antennal contact is permanent during courtship and antennation has only one pattern i.e. alternating up and down movements of the flap-like pedicel. The female is held around the neck by the fore tarsi of the male, his mid legs are held forwards with their tarsi alongside the eyes of the female and his hind legs are braced against the wings or hind legs of the female. In *M. acasta* (*acasta* group), males stand with their heads a little further down the face of the female without the close contact of *M. australica*. The flagella of the female fit into cup-shaped depressions of the male scapes which are not pressed against the face of the female. Antennal contact is broken during the antennation sequence which has two consecutive phases: knocking, jerky movements involving the pedicel and at the end of this phase a strong pinch involving the pedicel plus the first funicle segment. Antennal contact is broken after the pinch when the male raises his antennae sideways. The female is held around the neck by the fore tarsi of the male, the mid legs are braced against the thorax of the female and the hind legs are held forwards alongside the thorax of the female.



In these two groups there is an alternation of antennation and leg movements. On the basis of these leg movements, the groups can be called mid leg courters (*hawaiiensis* and *assemi* groups) and hind leg courters (*acasta* group). During antennation, the mid legs of *M. australica* are held laterally and forward with their trembling tarsi alongside the female's eyes. Van den Assem and Maeta (1978) observed that at the start of the display in their 'species 2' (= *M. australica*) the male's middle legs are braced against the female's thorax, but after the first antennation sequence they are brought forward towards the female's head for the mid leg sequence. They do not fully return to the original position after this but are held out trembling and gradually move to the frontal position at the start of the mid leg sequence. From my observations the mid leg sequence involves an upward swing of the mid legs and a return to half way down the female's eyes slightly brushing them. They pause here for a few seconds then are suddenly swung down and backwards and this is accompanied by a strong jerk of the male's body. As with antennation there is no change in the pattern of movements in the mid leg phase until the finale when the male's body undergoes a series of convulsive movements accompanied by up and downward swings of the mid legs beside the female's eyes.

After *M. acasta* males break antennal contact they stretch their fore legs increasing the distance between the heads of the courting couples. At this point the hind legs move forward making swaying movements beside the mesosoma of the female. This sequence is ended by a push against the female's mid legs. The alternation of antennation and leg movements continues for a period, but they begin to overlap at which time there is a change in behaviour pattern. Antennal contact becomes permanent and co-ordination of the hind leg movements change. The hind legs begin to rub up and down on the side of the female's mesosoma. In the finale, the male places his hind legs on the female's wing or metasoma and brings his mid legs forward to stroke the female's eyes with a downward movement. This is done with his antennae stretched downward over the female's face. He then breaks antennal contact, raises his wings at which point the female signals receptivity.

The *assemi* group comprises a new species complex from the Seychelles, India and Japan (van den Assem and Maeta (1980)). Here the courtship pattern resembles that of the *hawaiiensis* group. The male's scape is ventrally grooved and he is a mid leg courter. The male

stands further forward over the female's head so that the distal part of his scapes touch her mouth parts. Antennation involves a quivering motion as in *M. australica* alternating with a pinch using the pedicel. Alternating with antennation van den Assem and Maeta describe the mid leg movements as a very rapid kick involving the synchronous movement of both legs as far forward as his own head. During this movement parts of the female's body are brushed by long bristles on the ventral surface of the femur of the male's mid legs and his tarsi brush the female's pilose eyes. The mid legs return to their initial position except that they are held out laterally from the female's mesosoma. As the sequence proceeds the alternation of antennation and mid leg movements accelerates up to the last quiver which ends in a prolonged pinch. Hereafter the mid leg movements become an asynchronous to and fro rubbing motion which lasts for a few seconds. In the finale, the mid legs are moved synchronously back and forth at which point the female may signal receptivity.

The species which stands alone is *M. japonica* Masi, 1936 (= *M. clavicornis*) and its courtship is reported by van den Assem and Maeta (1978) and van den Assem et alia (1982). Unlike that of the other species, the male scape lacks an obvious groove or cup-shaped depression but has a large clear area distally opposite the attachment of the pedicel. Male courtship position is the same as in *M. acasta* but his scape presses the female's flagellum against her face. Antennation involves a series of knocking movements as in *M. acasta* and alternates with leg movements, but in this species both mid and hind leg movements are prominent. The mid leg movements are rigidly stereotyped involving a rapid flick-like motion towards the female's eyes followed by a pause. At this point the male may raise his antennae sideways and break antennal contact, but this is not always done. The hind leg movements are less stereotyped and involve a walking motion alongside the female's metasoma or folded wings. Leg movements are carried out during antennal raising. There is no finale by the male and the female signals receptivity during the sequence, but always after a mid leg flick.

The courtship pattern in the genus is very complicated and in some species can last up to 30 minutes. I have timed *M. australica* up to 15 minutes.

It is possible to draw some tentative correlations between morphology and courtship patterns in the genus. The following discussion is restricted to those species for which courtship is known and where a species group is mentioned it

includes only *M. australica* and *M. hawaiiensis* (*hawaiiensis* group), *M. assemi* and *M. sosui* (*assemi* group) and *M. acasta*, *M. evansi* and *M. digitata* (*acasta* group). The reader is referred to Dahms (1963a) for figures illustrating morphology.

Broadly spaced facial grooves and densely setose eyes in females correlate with male position (mouth parts impinging on upper face of female) and mid leg courting in the *hawaiiensis* and *assemi* groups. The presence of a dense tuft of stiff setae on the ventral fore trochanters of males of the *hawaiiensis* group seems to indicate some difference in courtship position between males of this group and the *assemi* group where this tuft is absent. Dahms (1983b) discusses the application of this setal tuft by *M. australica* males. Narrowly spaced facial grooves and the sparsity of setae on the eyes of females of the *acasta* group and *M. clavicornis* correlate with the male head not closely applied to the head of the female and the predominance of hind leg action during courtship.

Narrow male fore wings correlates with the absence of male wing vibration during courtship in the *hawaiiensis* and *assemi* groups in contrast to broad male wings and male wing vibration during courtship in the *acasta* group. A grooved ventral scape and a geniculate scape gland in the male correlates with permanent antennal contact during courtship (*hawaiiensis* and *assemi* groups). A cup-shaped depression in the ventral scape and a non-geniculate scape gland in males correlates with antennal contact through only part of courtship (*acasta* group).

Amongst *acasta* group males there is some variation in the size of the scape gland relative to that in *M. acasta*; it is expanded in *M. evansi*, *M. femorata* and *M. chalybii*; similar in *M. digitata*; or reduced in *M. scapata*. Dahms (1983a, b) discusses the possible implications. Also in the *acasta* group there is variation in the size of the first funicle segment in males; large in *M. acasta*, *M. digitata*, *M. femorata* and *M. chalybii* (the last 2 also have an extra expanded ring segment) and relatively small in *M. evansi* and *M. scapata*. At first it was thought that a large first funicular segment in males might correlate with a pinch by the male at the end of each antennal vibration phase, but this does not appear to hold for *M. digitata* where, according to van den Assem et alia (1982), there is no pinch at the end of a series of antennal vibrations.

The mid femoral fringe in males varies between and within species groups. It would be interesting to see if these correlate with variations in male

mid leg movements and/or parts of the female stroked during mid leg action in courtship.

There are a number of puzzling combinations of these correlatable features, e.g. in *M. chalybii* (*acasta* group) the male scape gland is geniculate, his ventral fore trochanters have a setal tuft resembling that of *M. australica* and the female has densely setose eyes (*hawaiiensis* group); the male scape has a ventral cup-shaped depression, his antennal flagellum has a large first funicle segment, his mid legs have an *acasta* group setal fringe, females have narrowly spaced facial grooves and a relatively thin scape in dorsal view (*acasta* group). It appears therefore that we are a long way from understanding species relationships within the genus and further study is required to confirm or rearrange correlations between morphology and courtship. Dahms (1983a) in his summary discusses the matter in greater detail.

## REPRODUCTION

In the parasitic Hymenoptera, several aspects of reproduction are important in understanding evolution: parthenogenesis, sib-mating, biased sex ratios, and sex ratio shifts.

### Parthenogenesis

It is widely accepted that all species of Hymenoptera reproduce parthenogenetically. Gordh (1979) lists three types of parthenogenesis: thelytoky, deuterotoky and arrhenotoky. A few species are thelytokous and the population consists of only females or females plus a few non-functional males. Deuterotokous species are also relatively few in number and unfertilised eggs develop into both sexes. Most species are arrhenotokous, i.e. the population consists of diploid females and haploid males. The latter develop from unfertilised eggs and are therefore impaternal. In this case uniseminated females can and do produce eggs from which only males emerge.

The *Melittobia* species *acasta*, *chalybii* and *digitata* have been shown to be arrhenotokous — Howard and Fiske (1911), Malyshev (1911), Graham-Smith (1919), Balfour-Browne (1922), Buckell (1928) and Schmieder (1933). In the present study, eggs from uniseminated *M. australica* females produced males only, and those from inseminated females resulted in both sexes all of which indicates arrhenotokous parthenogenesis.

### Sib-mating

In the parasitic Hymenoptera, particularly the Chalcidoidea to which *Melittobia* belongs, sib-

mating or close inbreeding appears to be the rule. Hamilton (1967), Askew (1968a) and Crozier (1977) list several biological features which indicate that a species practices close inbreeding:

a) males are apterous or brachypterous and therefore confined to the immediate area of their emergence. Male *Melittobia* are brachypterous and do not leave the host cell or puparium in which they emerge.

b) close inbreeders are gregarious with eggs laid in batches isolated from one another ensuring that males and females from the one mother emerge in spatial and temporal proximity to one another. *Melittobia* are gregarious ectoparasites and their host enveloping membranes (cell walls, cocoons or puparia) ensure isolation of the egg batches.

c) there is a tendency for mating to take place on emergence before dispersal. Female *M. australica* in my colonies would not disperse until after insemination. Dahms (1973) mentioned that unseminated, freshly emerged females of *M. australica* were observed to solicit the attention of males and that it was not uncommon to observe groups of females standing around a male engaged in courtship, palpating him with their antennae. They made no attempt to disperse.

Therefore *Melittobia* fit the biofacies for close inbreeding.

Askew (1968), discussing speciation in the Chalcidoidea, pointed out that the effectiveness of sib-mating as an isolating mechanism is increased by monandry in females, i.e. unreceptivity after an insemination. Gordh and De Bach (1978) found that male polygony and female monandry are common in the Hymenoptera. Female monandry requires extreme economy of sperm utilisation and this has been demonstrated in the arrhenotokous eulophid *Dahlbominus fuscipennis* (Zetterstedt) by Wilkes (1965). He found that from a single mating involving 150 sperm, the female can produce as many off-spring, over 90% of which are females. Out of another batch of 254 eggs which he stained, only 4 contained more than one sperm. Such economy involved the synchronous release of ova and sperm from the storage organs.

In laboratory cultures of *M. australica* I noticed males frequently courting previously inseminated females. Dahms (1973) felt this was due to laboratory conditions where inseminated females could not disperse. In all cases where I have observed male *M. australica* courting previously inseminated females attempts at copulation by the male failed. The normal

situation is that females disperse after insemination which precludes the attempted second mating by a male. This is general for the genus and therefore the species show male polygony and female monandry. However, I have found that *M. australica* females can and do mate a second time apparently when their sperm supply is depleted. Balfour-Browne (1922) considered that *M. acasta* females also are able to mate a second time when their sperm supply is depleted. In both cases the females mate with a son. Under laboratory conditions *Melittobia* exhibit another facet of sib-mating behaviour which appears to be widespread amongst arrhenotokous organisms i.e. virgin females lay only a few eggs which develop into males with which they mate (Hamilton 1967). Howard and Fiske (1911) found that virgin females of *M. acasta* laid 4-5 eggs only and these developed into males. The number of unfertilised eggs laid was equivalent to the number of unfertilised eggs laid if the female had mated. They found also that virgin females lived longer than fertilised females and survived to mate with their sons after which normal egg laying began. Balfour-Browne (1922) observed the same behaviour with virgin *M. acasta*. By removing unfertilised eggs from the hosts as they were laid by unseminated females he was able to more than double the life of the female (up to 202 days) and increase the number of unfertilised eggs laid.

The habit of unseminated females laying only a few eggs has been recorded for *M. chalybii* by Schmieder (1933) and *M. chalybii* (= *M. digitata*) by Buckell (1928). They do not, however, mention whether they mate with their sons. In the present investigation 5 unseminated *M. australica* females were confined singly with a host and produced only one egg each after 5 days. When their sons emerged they mated and normal egg production began. The ability of unseminated females to lay only a few eggs and mate with a son is probably general throughout the genus.

The economy of male production by unseminated females is easy to understand as an adaptation for conservation of food supply that would be depleted by production of superfluous males (Schmieder and Whiting (1946)). In *Melittobia*, mother — son mating has at least two advantages. Where species have a high level of aggression between males, combat may result in total annihilation of males or the surviving males may die before all the females are fertilised. Hobbs and Krunick (1971) found that in *M.*

*chalybii* (= *M. acasta*) all males were often dead before the last of the females became adult, which meant that the last females to emerge had no males with which to mate.

Balfour-Browne (1922) felt that mother-son mating is part of the normal life cycle when a female exhausts her sperm supply. He placed 5 freshly emerged, inseminated *M. acasta* females in separate cells with a host. At the end of 6 to 7 weeks the females had ceased to lay eggs and he noted that the last eggs to be laid produced males only, indicating a depletion of sperm. After providing each female with a male, a second normal egg laying period began. Maeta (1978) has confirmed this with *M. acasta*. In this investigation I noticed egg laying had ceased in a stock colony containing 5 inseminated *M. australica* females on a *S. formosum* host. All of the progeny were in the larval stage. The host was not completely utilised, indicating that egg laying had ceased. The five females were separated and each supplied with a fresh *S. formosum* pre-pupa. Three of the females continued oviposition and produced progeny of both sexes indicating that the original host was probably unsuitable for further oviposition. The two remaining females produced 1 egg each which developed into males with which they mated and normal egg laying followed. It seems, then, that a second mating can occur after sperm depletion. If the host is nutritionally unsuitable for further oviposition, migration within the host nest may occur. Balfour-Browne (1922) with *M. acasta* felt that a female migrates from a cell only when her spermatheca is full. Once a female has completed her first egg laying, she waits for a second mating before migrating. As evidence he noted that in his glass cells the female was often to be seen on the cotton-wool plug after her second mating and that this occurred generally when the host was fully stocked with progeny or fully utilised.

Schmieder's work in 1933 on the polymorphic forms of *M. chalybii* presents a different procedure in host utilisation. The normal or type-form female produces from its first 12-20 eggs rapidly developing second-form females and males which are morphologically and physiologically different from the type-form. Second-form females begin laying eggs immediately after fertilisation and assist the mother in full host utilisation. The procedure adopted in host utilisation may be related to host size. In the case of larger hosts such as *Sceliphron* spp. Schmieder's system operates, and with relatively smaller hosts, e.g. *Pison* spp., migration of females occurs due to competition for food with her progeny. If sperm depletion

occurs in the latter case a female may mate with a son. It is clear that such a close sib-mating situation would ensure maximum host utilisation and maximisation of a female's reproductive capacity. It also means that it is theoretically possible for a virgin female to colonise an area by mating with her son.

From the discussion above and from direct observations on *M. australica*, it is clear that sib-mating is an important part of the normal pattern of reproduction in *Melittobia*. Askew (1968), discussing evolution in the Chalcidoidea, concedes that a small amount of outcrossing occurs which mitigates against any tendency towards inbreeding depression. Crozier (1977) also considered that some outcrossing occurs. He argued that the continued production of males is puzzling if indeed there is no outcrossing. Hamilton (1967) regards male aggression as evidence that some outcrossing occurs in species which exhibit the biofacies of extreme inbreeding and arrhenotoky. He felt that outbreeding was brought about by male migration or multiple settling by females. In *Melittobia*, as males are brachypterous and non-dispersive, multiple settling of females must be the method by which outbreeding occurs. The host to parasite size ratio in *Melittobia*, in some cases, would certainly allow multiple settling and during the years I have been culturing *M. australica* there has been no reluctance by a female to oviposit on a previously parasitised host even in the presence of more than 20 other females. That multiple settling occurs in *Melittobia* can also be inferred from the occurrence of male aggression within the genus. That multiple settling of females is a fairly common event in *Melittobia* can be seen from the high degree of male aggression reported for some species and the enlargement of male mandibles — the weapons used in aggression.

#### Sex ratios

Amongst insects which exhibit extreme inbreeding and arrhenotoky, female biased sex ratios appear to be the norm, i.e., there is extreme economy in the production of males. In *Melittobia* spp. various workers have recorded depressed ratios of 1-13% males and these are made more biased by male aggression. In *M. australica* I have found ratios of 1-4% males. Multiple parasitism has been shown by Wilkes (1966) to result in a shift of sex ratio in the pteromalid wasp *Nasonia vitripennis* Walker, a parasite of house-fly pupae. Increasing the number of females per host resulted in a reduced percentage of female progeny. He postulated three causes for this shift:

- 1) Superparasitism resulted in a greater number of eggs per host and thus the number of eggs per host was in excess of the number of larvae the host could support. He assumed that supernumeraries were eliminated by starvation and that reduced female progeny resulted from stronger male competition. This mechanism has been recorded for a number of hymenopterous species and Wilkes (1966) lists papers covering this subject.
- 2) Detection of previous parasitism.
- 3) Interference from other females on the host.

The last two mentioned result in a higher percentage of unfertilised eggs being laid. Wylie (1965) on reviewing the literature found that females of many hymenopterous species can distinguish between parasitised and unparasitised hosts. There are also cases in the literature where females mark a host that they have parasitised.

In *M. australica* where there is superparasitism, there appears to be a greater production of males but I have not quantified this. If there is a shift in sex ratio then differential larval mortality could be part of the shift since I have observed larval cannibalism on numerous occasions where the host was very crowded. Balfour-Browne (1922) observed similar larval cannibalism in *M. acasta*.

Dr. van den Assem is currently working upon various aspects of sex ratio shifts in parasitic Hymenoptera e.g. Charnow, Hartogh, Los-den, Jones, van den Assem (1981). For this reason I have not pursued this aspect of *Melittobia* biology any further.

Therefore *Melittobia* exhibit the biofacies of extreme inbreeding and arrhenotokous reproduction. Outcrossing due to multiple settling by females appears to be part of the normal pattern of reproduction, and this is clearly indicated by male aggression perhaps coupled with sex ratio shifts in favour of males. The normal sex ratio is strongly female biased and this bias may be increased by male aggression. Males are polygonous and females monandrous, the latter dispersing after insemination. Mother-son mating occurs when the female is uninseminated or if she depletes her sperm supply.

#### POLYMORPHISM

Schmieder (1933) found two forms of each sex in *M. chalybii* which he called the type - (= typical) form and the second-form. The two forms showed marked morphological differences which he described and figured. To summarise

		TABLE 1	
	<i>Type Form</i>		<i>Second Form</i>
male	1) pale		dark reddish-brown
	2) 3 ocelli		ocelli may be absent
	3) eye spot pigmented		eye spot unpigmented
	4) wing normal for male, uncrumpled		wing smaller, uncrumpled
female	1) normal dark colour		paler than type form
	2) wings normal, uncrumpled		wings small, crumpled as they emerged from pupa
	3) cuticle normal, no fusion of sclerites		cuticle thinner, some fusion of sclerites e.g. on abdomen and antennae

He found that in addition to these morphological differences there were '... equally striking differences in their physiological characteristics and in their behaviour'. Courtship behaviour of the male second-form was less regular than in the type-form and he found that when he tried mating males of one form with females of another, the lack of synchrony proved troublesome. Van den Assem (pers. comm. 1981) does not agree with Schmieder's observations on second form male courtship. He has had no difficulty in mating one form male with the other form female. As there seems some doubt about this aspect and since Dr. van den Assem is working on the courtship behaviour of *Melittobia* I have not pursued the matter further.

The physiological differences between females of the two forms in *M. chalybii* are quite pronounced. Females of the second form have larger metasomas in the pupal stage and Schmieder (1933) suggested this was due to eggs developing within the pupa. Egg laying began on the day of emergence after mating in second-form females. He found the life span of second-form females to be shorter than that of the type-form and that they make no effort to disperse, whereas type-form females, after mating make their way out of the host cell and disperse.

Schmieder's investigations led him to conclude that the causal factor was nutritional. The first eggs laid develop rapidly to emerge as second forms and the '... interpolation of an additional

generation of adults in the life history is thus seen to constitute a remarkable biological adaptation which effects a more complete utilisation of the host and, as a corollary, secures the production of the maximum number of offspring from each host ...' The type-form he saw as being morphologically and physiologically the dispersive phase.

Van Lith (1955) found a polymorphism in *M. acasta* in which he mentioned only females which had distended metasomas full of eggs and short, often crumpled, wings. He did not feel there was any connection between the production of these females and nutrition.

Van den Assem and Maeta (1980) recorded male dimorphism in *M. sosui* Dahms 1983a but made no mention of dimorphic females. They did not find any overlap between the two forms of males and felt the causal factor was not nutritional since males of both types emerged from the same host at the same time. Van den Assem (pers. comm. 1981) has informed me that these dimorphic males are actually distinct morphs of the type-form. They are separate from type and second-form males which also occur in this species. This is a rather unusual phenomenon in the genus and is one under study by Dr. van den Assem. Detailed examination of the two morphs of the type-form male shows few differences except in size. In the larger morph the forewings are larger and slightly crumpled (cf. Figs 1 and 2) and the scape is about 1.2 times larger than that of the smaller morph.

I have received for identification some slide-mounted specimens from the U.S. National Museum which are obviously second-form males and females. There is little to use for identification since the dimorphism has affected most of the diagnostic morphological features. Those that appear to be unchanged cause uncertainty, e.g., the mid leg bristle pattern (Fig. 9) and the proportions and shape of the mid tibia of males resemble those of *M. acasta* males whereas the most common scape morphology is that of *M. evansi* (Fig. 11). For the present I have decided to label these specimens as *acasta* group and positive identification must await breeding of second-forms of all species in the *acasta* group. In the following discussion therefore, the features described are compared to those of the *acasta* group rather than to any particular species.

Female: Larger than type-forms, 1.7-2.1 mm long. Colour brown except flagellum which is infuscated. Head in frontal aspect quite broad and more rounded than in type-forms. Eyes relatively smaller. Ocelli variously

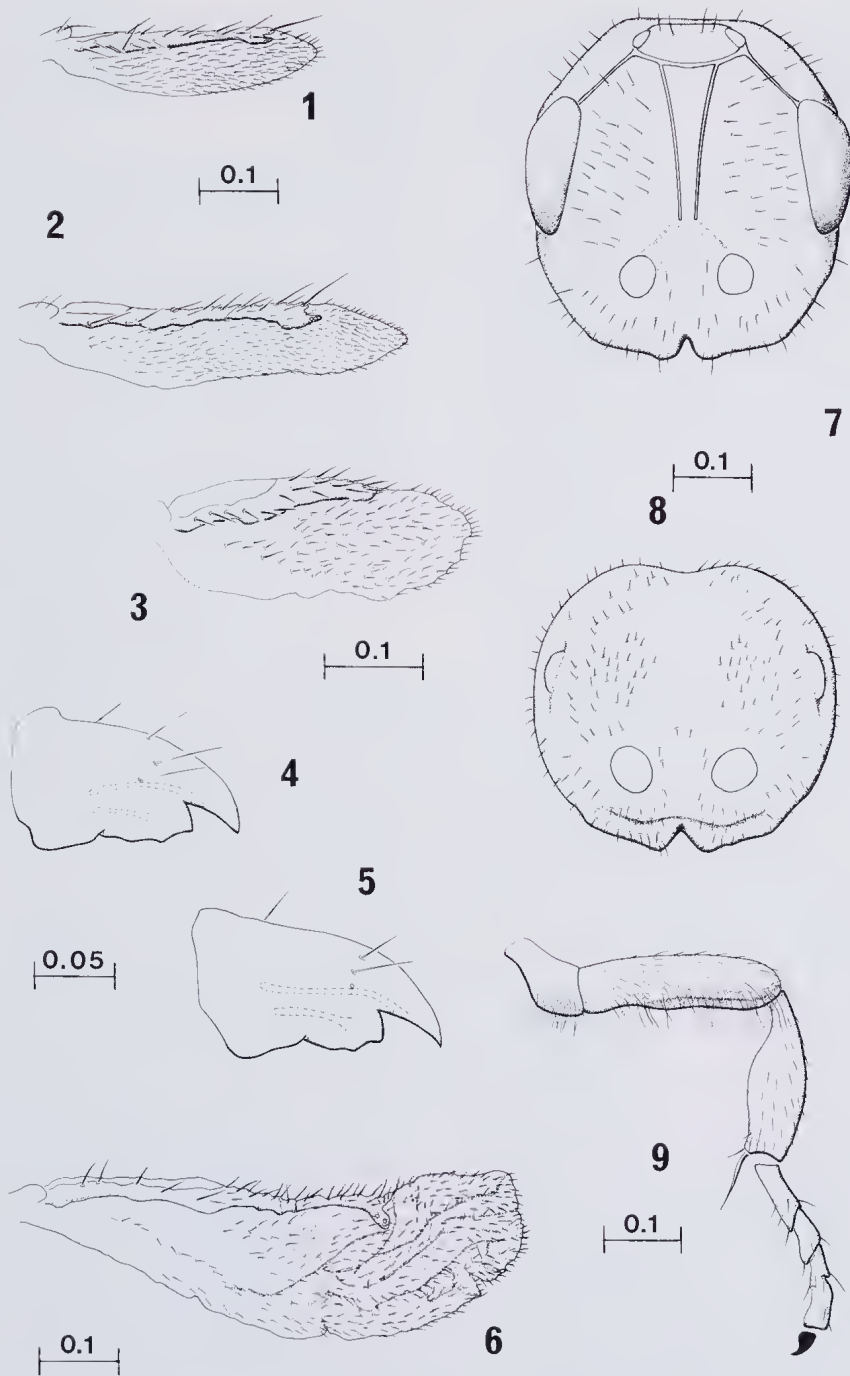
reduced as follows: 2 normal posterior ocelli with either a very small or absent median ocellus; normal right, posterior ocellus and with median ocellus; or small right ocellus only. Scrobes shorter than type-forms. Mandibles (Fig. 4) more like those of the male. Antennae variable (Figs 13-15) even between right and left on the same specimen; scapes of variable shape with some showing expansion similar in form but not size to those of some males; flagellum showing fusion of segments in some specimens e.g. fusion of funicle 2 and funicle 3 is the commonest, but fusion of funicle 3 and club 1 also occurred and in some, the delimitation of club segments is imperfect; plate organs in some specimens are modified to peg-like structures (Fig. 16). In lateral aspect the head appears to be more inflated than in type-forms.

Mesosoma in dorsal aspect (Fig. 10) appears broader and shorter than in type-forms; setal fringe on posterior margin of prothorax shorter; sutures on mesonotum less distinct than type-form particularly those delimiting the axillae; position of setae on scutellum variable even from right to left on the one specimen e.g. normal position as in type forms or with anterior setae moved close to posterior setae; propodeum much broader and shorter than type-form, more angular in shape resembling the propodeum of the male. Legs similar to those of type-forms. Wings reduced (Fig. 6), crumpled, remaining as they emerge from the pupa; postmarginal and stigmal veins poorly developed, the stigmal in some specimens closely resembling that in type-form male wings. Lateral aspect not visible.

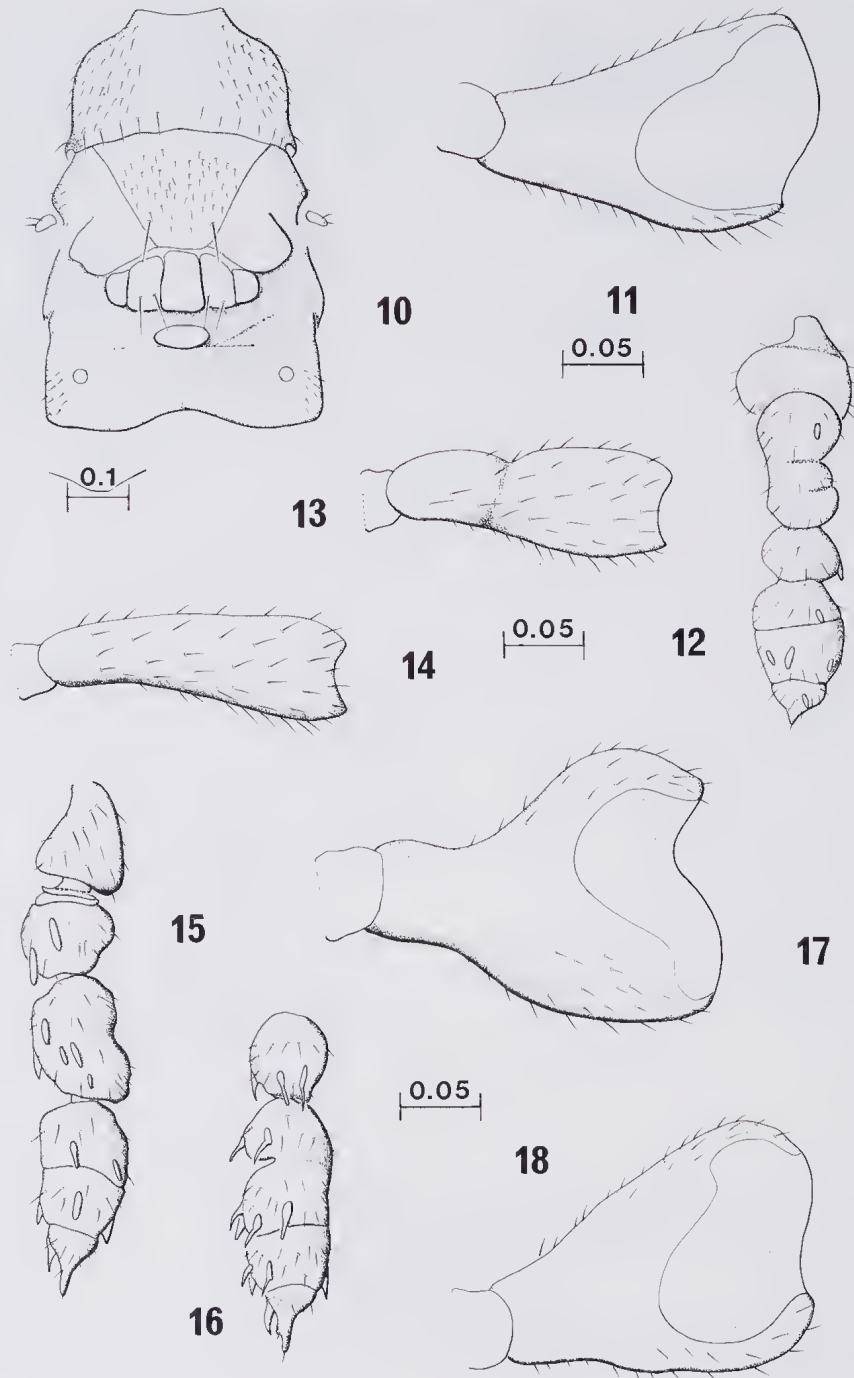
Metasoma in dorsal aspect much larger than that of pre-feeding type-form females.

Male: 1.6-1.8 mm long. Colour light brown.

Head in frontal aspect (Fig. 8) rounded, not contracted ventrally as in some type-forms. Mandibles (Fig. 5) not unlike those of the female second-form. Eyes are much larger than those of the type-forms. Ocelli variously developed as follows: median ocellus reduced or absent, posterior ocelli normal; only the right, posterior ocellus developed, the others absent; or all ocelli absent. Antennae (Figs 11, 12, 17, 18) variable, the predominant scape morphology is as in Fig. 11, but there is variation even between left and right on the same specimen (Figs 17, 18), scape glands vary



FIGURES 1, 2 — *Melittobia assemi* (sp. nov.) male fore wings.  
 FIGURES 3-9, *Melittobia acasta* group second-form male and female; 3 — Male fore wing; 4 — Female mandible;  
 5 — Male mandible; 6 — Female fore wing; 7 — Frontal aspect, female head; 8 — Frontal aspect, male head; 9 —  
 Male mid leg.



FIGURES 10-18, *Melittobia acasta* group second-form male and female. 10 — Dorsal female thorax; 11 — Male scape; 12 — Male flagellum; 13,14 — Female scapes; 15,16 — Female flagella; 17,18 — Male scapes from the same specimen.



in shape and development even between right and left on the same specimen funicular segments all fairly uniform in size unlike those of type-form *M. acasta* group where segment 1 is enlarged; flagellum showing different degrees of segmental fusion even between right and left on the same specimen as follows: funicle segments 1 and 2; 1, 2 and 3; 2 and 3; 4 plus club segment 1; and in some the delimitation of club segments is imperfect; plate organs appear to be reduced. Lateral aspect not visible.

Mesosoma in dorsal aspect similar to the type-forms. Legs not greatly modified; mid leg (Fig. 9) similar to that of *M. acasta*, some specimens showing fusion of tarsal segments 3 and 4; in some specimens tarsal segments 3 and 4 of hind legs are also fused. Wings (Fig. 3) not much reduced in size, stigmal vein absent in most specimens, poorly developed in others.

Metasoma of normal proportions.

#### Material Examined:

14 ♀♀, 2 ♂♂, on microscope slides labelled 20 mi. South Washington D.C. December 1974 *Trypoxylon* sp. nest Col Gordh; 8 ♀♀, 8 ♂♂ on microscope slides, data as before but collected 10 January, 1975; 10 ♀♀, 6 ♂♂ on microscope slides labelled, Augusta West Virginia February 1975 ex *Trypoxylon* nest Col. A. Menke. These are in the collections of the U.S. National Museum, Washington, D.C.

A polymorphism without the marked morphological differences of *M. chalybii* and the *M. acasta* group discussed above occurs in *M. australica*. In my trials where up to 20 *M. australica* larvae per host were bred on *Sceliphron formosum* prepupae, second-form progeny resulted. Trials were not carried out to determine the upper limit of parasite to host larvae for second-form production. Males of *M. australica* second-form were larger than the type-form but otherwise appeared morphologically similar to the latter. Second-form females were larger than the type-form with reduced eyes, shortened wings and enlarged metasomas. In neither sex was there any evidence of fusion of tarsal or antennal segments and the scapes of both forms were normal. The shortened wings of the second-form females were not crumpled, but fully expanded without any alteration of venation.

Second-form *M. australica* females differ behaviourally and physiologically from type-form females. They are ready to lay eggs immediately

after insemination, i.e. on the day of emergence. Type-form, inseminated females begin laying 4-5 days after being placed on a host. Second-form females make no attempt to disperse from the breeding chamber, but remain on or under the host and show a negative reaction to light typical of laying, type-form females with a host. Type-form females, after insemination, make their way to the top of breeding jars and show a positive reaction to light, e.g. if released they move in a direct line towards windows.

Some of the features of second-form *M. acasta* group females are similar to those in type-form males. In comparison to type-form females, the head is shorter, broader and more inflated and the eyes are relatively smaller. The mandibles more closely resemble those of a male; the scapes are expanded and some resemble the sorts of expansions found in male scapes (Fig. 13); the mesosoma, particularly the propodeum, is shorter and broader as in males; and in some cases the stigmal vein in the crumpled wings resembles that in males.

It is interesting that the *M. acasta* group females on hand show modifications resembling those from which the present male morphology appears to have arisen and that these modifications are nutritionally induced, at least in part. Males tend to emerge first e.g. Buckell (1928) found that *M. chalybii* (= *M. digitata*) males emerge after 21 days and females after 37 days. Schmieder (1933) found that the first progeny to emerge in *M. chalybii* were second-form individuals. Differential development of the sexes is no doubt related to their dispersive and non-dispersive roles, and in the male subsequent modifications plus embellishments would be related to the restriction of their role to combat, courtship and copulation.

In addition, the second-form males of the *acasta* group on hand show quite an amount of variation in both head and scape morphology, e.g. Figs 17, 18 are right and left scapes of the same specimen. This is in contrast to males of the *hawaiiensis* group. I have not seen polymorphic forms of the *assemi* group. From our knowledge of species at the moment the *acasta* group contains the greatest number of species (7), the *hawaiiensis* group contains 2 and the *assemi* group contains 4. Perhaps this apparently greater diversity of species in the *acasta* group is related in part to the variability found amongst second-form *acasta* group males. However, this is speculative since the world fauna is not properly known and the full implications of polymorphic forms in *Melittobia* require much more study.

LIFE HISTORY OF *M. AUSTRALICA*.

No particular part of the host was favoured for oviposition and eggs were laid in clusters generally in the intersegmental grooves of prepupae. Eggs are large relative to the female's metasoma; 0.38 mm long by 0.1 mm wide. The length of the metasoma of inseminated, unfed females is 0.6 mm. Eggs are elongate, slightly curved with broadly rounded ends, one end being slightly wider than the other. They fit the hymenopteriform type of Clausen (1962). They are white and translucent with a thin, smooth chorion. The surface appears moist and coated with a substance that makes them loosely adhere to each other and to the host.

Larvae hatched in 3-4 days and the newly hatched larvae fitted the hymenopteriform type of Clausen (1962), i.e., white, translucent, visibly segmented grub unadorned by obvious spines, setae etc. The head and mouth parts are relatively small. The eggs, larvae and larval head of *M. australica* resembles the figures of *M. acasta* (Balfour-Browne 1922). As feeding proceeds waste material can be seen accumulating within the larva. No attempt was made to determine the number of larval moults, but Balfour-Browne (1922) recorded 2 larval moults plus the larva to pupal moult in *M. acasta*. After 7-9 days, larvae were fully grown and measured 1.6 mm long by 0.5 mm wide. They were distended and smooth without obvious segmentation. When feeding finished, the larvae rolled from the host remains and voided waste material as faecal pellets resembling strings of beads. One day later they pupated. At this stage it was easy to distinguish the sexes because of the enlarged scape and absence of eyes in the male. The pupal stage lasted 3-4 days and the total life cycle was therefore 14-18 days. In the case of second-form progeny, the life cycle duration was 12-13 days. The above figures were obtained from rearings at 25-30°C.

The average total production from 10 type-form females, each on a separate *S. formosum* prepupa was 370 females and 7 males. The percentage males varied between 1 and 4% in newly emerged adults.

The literature reports a wide range for life cycle duration. Balfour-Browne (1922) obtained a time of 17-23 days for *M. acasta* at an unspecified temperature which compares with 25-29 days (second-form) and 37-47 days (type-form) recorded by van Lith (1955) for the same species at 18-19°C. Buckell (1928) found that male *M. chalybii* (= *M. digitata*) took a total of 21 days

compared to 37 days for females but did not specify any rearing temperatures. Schmieder (1933) bred *M. chalybii* at 19-25°C and recorded a life cycle length of 90 days for type-form individuals and 14 days for second-form individuals. It appears therefore that some standardisation of rearing temperatures is required before results can be compared. Even so, the result of 90 days for *M. chalybii* type-form individuals obtained by Schmieder (1933) seems excessively long in comparison with other figures. My results with *M. australica* show very little difference in life cycle time between type and second-form individuals.

## DISPERSAL

There are two aspects to dispersal, natural and man assisted. The latter is important since the plastic behaviour exhibited by *Melittobia* has allowed it to avail itself of man's travelling facilities.

Males do not disperse, but die in the host cell or puparium in which they emerge. Inseminated type-form females escape from the host cell or puparium either by excavation or through entrance holes made by the mother. From this point on workers provide a variable story.

Graham-Smith (1916, 1919) observed that female *M. acasta* can fly for a considerable distance. Malyshev (1911) in contrast, found that *M. acasta* females could fly only a few millimetres. Balfour-Browne (1922) observed that female *M. acasta* fly only 25 mm or so at a time and for the most part do not use their wings. He suggested they might disperse by phoresy, but there is no evidence to support this. Buckell (1928) did not observe *M. chalybii* (= *M. digitata*) flying, but noted they hop like fleas when disturbed and concluded that although they were winged they were flightless, relying on their legs for dispersal. Krombein (1967) found that *M. chalybii* females do not fly frequently but rely on walking. Van den Assem (pers. comm. 1981) considers that flying in *Melittobia* spp. is partially a matter of temperature. At higher temperatures or in direct sunlight *Melittobia* females will fly away, but at temperatures less than 20°C they will not.

Evidence in the literature seems to suggest that the dispersal power of female *Melittobia* is limited, but my observations and some recent work by Freeman (1977) and Freeman and Parnell (1973) indicate that this is not so. When I released inseminated *M. australica* females in the laboratory they dispersed initially by hopping and

running. Later they flew. They were noted to be capable of flying 3 metres towards a closed window where they accumulated. Within 5 minutes there were no females left in a 1 metre radius of the release area. This area had been cleared prior to release to avoid females hiding or being unobserved. When the window was opened the females flew outside. I suggest that all emerging fertilised female *Melittobia* have functional wings used for dispersal. This dispersal is no doubt assisted by air currents.

Freeman and Parnell (1973), investigating the mortality of *Sceliphron assimile* Dahlbom caused by *M. chalybii* (= *australica*) in Jamaica, found that the parasite accounts for 76% of developmental mortality in the host. Moreover, where *Sceliphron* forms large breeding populations the parasite kills a higher proportion of them. Freeman (1977) found some variations in the percentage mortality expected on the basis of a linear density-dependent relationship and that these were often partly due to the effects of the prevailing easterly or south-easterly winds carrying *Melittobia* across Jamaica. Each host cell can yield up to 300 alate *Melittobia* which means that large numbers of females can be released into the air from host nests. Freeman (1977) argued that the further inland or westward a host cell might be the greater its chances of being found by a flying *Melittobia* since there would be an increasing number up-wind of host nests producing *Melittobia*. Conversely, nests near the sea shore or towards the east would have less chance of being found. He concluded there is circumstantial evidence that the higher percentages of *Melittobia* parasitism observed away from the shore and to the west were caused by dispersal of the parasite by the wind.

Further circumstantial evidence exists to support long range dispersal. Using figures provided by Freeman (1977) it is seen that each host cell can produce up to 300 alate females. At 10 high-density sites the host had 3499 cells with 3458 eggs laid of which 1430 were killed by *Melittobia*. The maximum yield from these cells is nearly 500,000 alate female *Melittobia*. Dispersal would be necessary just to find enough hosts and if it did not occur one could probably expect a higher percentage developmental mortality by *Melittobia* than the 41.4% recorded by Freeman and Parnell (1973) in areas of host density. Since *Melittobia* are delicate insects one would expect passive wind dispersal to result in high mortality. The production of large numbers of alate females could offset the risk factors in wind dispersal.

Man's ability to travel on a global scale has provided *Melittobia* with an added means of dispersal. Several features of its biology allow it to take advantage of man's travelling facilities.

- 1) *Melittobia* are highly polyphagous. One could reasonably expect to find mud nesting Hymenoptera and cockroach oothecae associated with ships and packing crates. In the past, hygiene on sailing ships was probably not of a high standard and some fly puparia were no doubt present. On long journeys more hosts could be taken on board at port stops. All of the above hosts are recorded for *Melittobia*.
- 2) Females are able to delay feeding and oviposition for several weeks until a host is at a suitable stage for oviposition or until a suitable host is located. Modern, rapid transport reduces the risk for *Melittobia* and packing crates provide the necessary hosts rather than air craft e.g. the North American *Sceliphron caementarium* (Drury) is spreading rapidly through the Pacific region and in July 1979 was intercepted at Alice Springs, Australia in packing crates from North America (Naumann 1980 unpublished report). In December 1980 this species was collected from Eight Mile Plains near Brisbane from nests in a dwelling.
- 3) *Melittobia* females have the capacity to be very efficient founder organisms. It is theoretically possible for an unseminated female to begin a new population by laying a few unfertilised eggs. These develop into males with whom she then mates. This aspect has been discussed more fully under 'Reproduction'.

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AN INTERPRETATION OF THE STRUCTURE AND FUNCTION OF THE  
ANTENNAL SENSE ORGANS OF *MELITTOBIA AUSTRALICA* (HYMENOPTERA :  
EULOPHIDAE) WITH THE DISCOVERY OF A LARGE DERMAL GLAND IN THE  
MALE SCAPE.

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ABSTRACT

The importance of the antennae during courtship behaviour of *Melittobia* species prompted an investigation into the histology of the enlarged male scape using the single Australian species *Melittobia australica*. The application of the male scape during courtship suggests a possible chemical communication between the antennae of the two sexes. Histological and SEM work reveal the presence of a large dermal gland in the male scape. SEM work and chemical applications reveal the presence of long thin unfluted setae, tapering fluted setae, multiporous plate sensilla and short basiconic capitate pegs on the antennae of both sexes (the short basiconic capitate pegs are absent in most males). Together with behavioural observations these are used to suggest the possible structure and function of the antennal sense organs and the most likely receptor for the male scape pheromone.

MALE SCAPE

Amongst the parasitic Hymenoptera, male antennation is a common component of precopulatory behaviour and it reaches a high expression in *Melittobia* (Gordh and DeBach (1978)). The enlargement of the male scape and its application discussed by Dahms (1983b) suggest that it has a function in stimulating the female's antennae. In males of all species cleared in 10% NaOH the scapes show a clear delimited zone (Pl. 1a, *M. australica*). In *M. australica* the surface appears to have a cellular pattern at higher magnifications. Since all internal tissue is removed in this process, the clear delimited zones must be cuticular which suggests mechanical stimulation of the female's flagellum. However, freshly killed *M. australica* males used for AgNO<sub>3</sub> staining to test for touch chemoreceptors when examined after 30 minutes in Toluene were found to be not completely cleared. In the scapes of these males could be seen a cellular-like zone occupying the same area as the clear delimited zone in NaOH cleared specimens. (Pl. 1a) is a lateral view of the side opposite pedicel attachment and (Pl. 1b) is an end view of the same side. This cellular-like zone was absent in specimens fully cleared in Toluene indicating that it was internal tissue. Serial sectioning of male *M. australica* scapes clearly shows large dermal

glands which follow the clear delimited zone in NaOH cleared specimens (Pl. 3b, c; 4a). The sections also show that the inner cuticular lining on the scape groove is much thinner than the outer cuticle and that there are cuticular infoldings along the length of the gland. These cuticular infoldings form the limits of the clear zone in NaOH cleared specimens.

To prepare them for SEM examination, males were treated with 10% NaOH until cleared to remove any glandular secretions which might obscure the cuticular surface of the gland. They were then dehydrated in alcohol and finally treated with Toluene to remove any wax which might obscure cuticular pores. Males were air dried and mounted upside down on stubs in preparation for gold coating. It was noticed that after removal from Toluene and air drying the flexible intersegmental cuticular areas became white while the thicker cuticular sclerites remained yellow-brown. The lining of the scape groove became white indicating that it was flexible thin cuticle, which would explain the cuticular infoldings around the gland for support. SEM photomicrographs (Pl. 2b, c; 3a) show the cuticular surface over the gland to be well differentiated and perforated by numerous pores. At higher magnifications the cuticular surface over the gland shows a somewhat reticulate

appearance. Noirot and Queenedey (1974) mention cuticular specialisations in Heteroptera, Blattodea and butterflies associated with dermal glands and that these serve as evaporative areas ensuring rapid evaporation of secretions. The cuticular area over the scape gland in *M. australica* fits this pattern.

The shape, size and position of the scape gland varies with species and provides a very useful taxonomic tool. I refer the reader to my taxonomic revision of the genus (Dahms 1983a) for a fuller discussion together with figures and a discussion of species groups.

Van den Assem et alia (1982: 458) raise a rather interesting point. They found that males with their antennae removed do court females and induce receptivity. From this they concluded that stimuli which might arise from them are by no means necessary. The data they present are from mutilation experiments with *M. acasta* (Walker) and it is not clear from their account if they carried out similar trials with all species at their disposal. If we look at the male scape gland in *M. acasta* it is not as extensive as in the *hawaiiensis* and *assemi* groups. The cuticle over the scape gland in *M. acasta* as shown by Van den Assem et alia (1982, Pl. 1) does not appear to have an evaporative function as it does in *M. australica* (Pl. 2c, 3a). Perhaps the scape gland does not have the importance in the *acasta* group that it has in the *hawaiiensis* and *assemi* groups. It is interesting to note also that antennal contact is permanent throughout courtship in the *hawaiiensis* and *assemi* groups but only through part of the cycle in *M. acasta* and *M. evansi* Dahms (1983a) but not in *M. digitata* Dahms (1983a). There may be some variation in the importance of permanent antennal contact in some members of the *acasta* group (not studied by Van den Assem et alia (1982)) which seem to have relatively expanded scape glands eg. *M. femorata* Dahms (1983a) and *M. chabylii* Ashmead. In the latter the scape gland is geniculate as in the *hawaiiensis* and *assemi* groups although that of *M. chabylii* is not as extensive.

Goodpasture (1975) observed pores in the modified scapes of the torymid chalcidoid wasps *Monodontomerus montivagus* Ashmead and *M. clementi* Grissell which were applied to the tip of the female flagellum during the climax phase of courtship. He concluded that the male scapes might be the source of chemical communication as a behavioural cue and further suggested that the pores indicated either a chemical sensory function or pheromone elaboration sites. From

my studies on *M. australica* I suggest that they are probably the latter. Antennation during courtship is a common phenomenon in Chalcidoidea and is often accompanied by antennal modifications. Pheromone glands in male antennae may also be a common occurrence. Houston (1975) has found antennal modifications containing dermal glands in several Australian species of the bee genus *Hylaeus*. Antennal modifications containing glands may be more widespread in the Hymenoptera than current knowledge indicates.

#### ANTENNAL SENSE ORGANS

During the course of a biological study on *M. australica* Dahms (1983b) it was decided to investigate the sense organs on the antennae since the latter play an important part in precopulatory behaviour. The following discussion is based on SEM work, behavioural observations and a few chemical applications. It does not have the benefit of histological or electro-physiological data, therefore the structures and functions of the sense organs are suggested rather than conclusively proven.

Males of all species of *Melittobia* have their compound eyes reduced to a single ocellus-like spot. Picard (1922) examined *M. acasta* males histologically and found that the reduced eyes lacked the normal structural elements of even an ocellus. The optic ganglia were also reduced relative to the female. He related this reduction, together with shortened wings and relatively reduced pigmentation, to the male's restriction to the host cell or puparium in which they emerge. This reduction in functional elements in the eyes of males is no doubt general in the genus.

The sole function of the male is related to reproduction. Van den Assem and Putters (1980) found that sound production is not involved in the courtship of *Melittobia*. Presumably males rely on chemical and tactile stimuli for locating females and for precopulatory behaviour. Chemical information appears to play an important role in the behaviour of both sexes. The size of the complex gland in the male scape and the role of this segment during precopulatory behaviour suggests that the female receives a considerable chemical input during antennation. Behavioural observations (mentioned under 'Long thin unfluted setae' below) indicate that the sexes are chemically different and there are easily discernible behaviour patterns depending on the sex encountered by individuals of both sexes. Females have additional occasions in which olfactory reception could be important e.g. host



location and feeding. The antennae of both sexes have setae whose structure suggests tactile receptivity.

SEM examination of the antennae of males and females of *M. australica* revealed the presence of the following sensory structures:-

- 1) long thin unfluted setae
- 2) tapering fluted setae
- 3) multiporous plate sensilla
- 4) short basiconic capitate pegs

1) Long thin unfluted setae (Pl. 5b,)

These are readily distinguished by the absence of both a basal socket and fluting. They are only present on the club of both sexes especially at the tip of the terminal segment.

Lack of a socketed base suggests they are not tactile in function. A possible contact chemoreceptive function is suggested by their concentration at the tips of the antennae, particularly noticeable in males, and by behavioural observations.

A male can instantly distinguish between the sexes by tapping another individual with the tips of his antennae. His behaviour varies dramatically according to the sex encountered; another male induces aggression, a female is mounted.

Females can also distinguish between the sexes. Virgin female *M. australica* when confined without males stand around with their mandibles open. When provided with a dead male pupa they immediately become active and begin searching behaviour. When another female is encountered they stop, palpate the encountered female with the tips of the antennae then resume searching behaviour. When the dead male pupa was encountered and palpated, searching behaviour ceased. The females stood around the pupa continually palpating it with the tips of their antennae. Some of the females opened their mandibles. In cultures, similar reactions occurred and it was not uncommon to see groups of females standing around a male engaged in courtship, palpating him with the tips of their antennae. Mandibular opening was also observed in these groups of virgin females and it suggests that mandibular glands could be the source of a female odour. Gordh and DeBach (1978) mentioned that mandibular involvement in courtship appears to be an adaptation in some Chalcidoidea; also studies showed that olfaction could be used for mate attraction. They suggested that the gland-like ducts in the mandibles of chalcidoids may indicate exocrine glands. The mandibles of both sexes in *Melittobia* have two

such gland-like ducts. During courtship in *M. australica*, mandibular opening by females occurs towards the end of the sequence which brings them into close proximity with the flagellum of the male.

Female behaviour on a host also suggests a contact chemoreceptive function for these sensilla. A fertilised female uses her ovipositor to puncture the host then feeds on the droplet of host body fluid that wells forth. After withdrawal of the ovipositor the female moves backwards palpating the surface of the host with the tips of her antennae until the droplet is encountered. At this point feeding begins. Female *M. australica* revisit old puncture sites to feed upon congealed host body fluids which they relocate by palpation with the tips of their antennae.

SEM examination of the tip of these setae does not reveal the typical pores of contact chemoreceptor sensillae. Following the procedures of Slifer, Prestage and Beams (1957) very good results were obtained using AgNO<sub>3</sub>. After 60 minutes, the AgNO<sub>3</sub> had penetrated the tips of these setae (Pl. 5a). The penetration was more rapid in males than in females which is probably related to the setae being of larger diameter in the males. These tests, behavioural observations and location of these setae suggest therefore that they are touch chemoreceptors.

In the female, touch chemoreceptors on the terminal antennal segments would also be of use in host identification. Female *M. australica* walk over a host nest palpating it with their antennae. Once it has been identified and entered these sensillae may be of use in detecting the presence of enveloping membranes, e.g. cocoons. They may also help differentiate hosts e.g. oviposition behaviour differs between hymenopteran and some dipteran hosts. Should a *Melittobia* female enter a host cell when the host is immature these sensillae would allow her to distinguish between the host and its provisioned food. The relative amount of food provision and its state of preservation may be of use in distinguishing if the host had failed or its stage of development. On the other hand these sensillae may be used directly to ascertain the age of the host. No information is available on whether there are chemical differences between the different stages of a host, but since the hymenopteran hosts I have observed accumulate waste internally and pass it out just before pupation as meconium, the relative amount of internally accumulated waste or the presence of meconium may be an important sensory signal for oviposition in *Melittobia*.

Finally these sensilla may be useful in detecting the suitability of a host i.e. whether the host is diseased.

## 2) Tapering fluted setae (Pl. 5b, ii)

These arise from a socketed base and show a slightly whorled fluting on the surface (Pl. 6d). They do not take up AgNO<sub>3</sub> stain. The fluting provides rigidity allowing the setae to resist bending thus transferring maximum movement to the socketed bases. In the male they are present on all antennal segments with marked differentiation. On the proximal segments of the flagellum they are long and numerous, but are reduced in length and number towards the terminal club segment (Pl. 6a). On the other segments of the antenna they are also relatively shorter and are fairly evenly distributed except for their absence on the lining of the scape groove and for a relatively denser arrangement of shortish setae on the upper surface of the lateral expansion of the pedicel. In the female they are present on all segments of the antenna and have a fairly even distribution (slightly fewer on the club) without any size differentiation. In general, they are shorter and finer than in the male and they are shorter and finer than the long thick non-fluted setae on the clubs of both sexes.

Because of the fluting and socketed base I assume they are touch receptors. Their general uniformity in size and shape in the female indicates they have no specific function, just providing generalised tactile information, e.g. they would be of assistance in estimating the size of the hole the female excavates in the host cell. In this way the female would be able to estimate if the excavation is wide enough and when penetration has been effected. Female *M. australica* when excavating in a *Sceliphron formosum* nest were noted to insert their antennae periodically and touch the walls of the excavation with the sides of the flagellum. Differentiation of these sensilla on the male flagellum suggests a specific function. When a male encounters a female he mounts her first then searches for her head with his antennae. When he mounts a female he orientates longitudinally on her and taps his flagella either side of the female's extremity like a pair of cupped hands thus engaging the long setae on the proximal flagellar segments. When the female's posterior metasoma is touched the male turns 180° and repeats the procedure at the head then scoops her antennae into his scape groove. Where the female's head is touched no turning occurs. This may not be the

only sensory input e.g. if the female produces a female scent from mandibular glands then orientation on the female could also involve olfactory information via his multiporous plate sensilla.

Before passing on to the other sensilla, mention should be made of two clusters of differentiated, socketed, fluted setae occurring on leg segments in the male. In *M. australica* and *M. hawaiiensis* males the ventral surfaces of the fore-trochanters bear a dense tuft of thick, short, socketed setae with whorled fluting (Pl. 4b). In males of all other known species except *M. chalybii* where they are not as well developed the fore-trochanters have a few fine, undifferentiated, scattered setae ventrally. During courtship of *M. australica* and *M. hawaiiensis* these setae press firmly down on the pronotum of the female. In all other species for which courtship is known, the position of the male is such that the fore trochanters are not in contact with the female. It is difficult to suggest the use that these serve, but since modifications in male *Melittobia* morphology are closely linked to some aspect of courtship there must be some important sensory input via these setae. Perhaps they are useful in positioning the male for courtship.

Another group of differentiated, fluted setae with socketed bases occur on the posterior ventral surfaces of the mid femora of males of all species and ventrally on the mid trochanters of all species except *M. australica* and *M. hawaiiensis*. Those of *M. australica* are definitely socketed with shallow, unwhorled fluting (Pl. 4c). These setae in all species are much longer than the general body setation and there is some differentiation amongst them. The mid legs are used by the males of all species during courtship and in *M. australica* these setae were noted to brush the 'shoulder' junction of the pro- and mesonotum of the female. The pattern of distribution and the degree of differentiation amongst these setae varies with the species Dahms (1983a). It would be interesting to see if these variations are related to specific differences in male mid leg movements and/or the parts of the females brushed. Their function in the male may be to signal contact with that part of the female to be stroked and their input to the female would most likely be tactile also via her undifferentiated general body setation. Females do show differentiated long setae on the posterior pronotum, the mid-lobe of the mesoscutum and the scutellum, but these are not in a position to be stimulated by the differentiated mid leg setae of the male.

3) Multiporous plate sensilla (plate organs) (Pl. 5b, iii).

These are raised sensilla which appear as pale areas on dry and slide-mounted antennae of most Hymenoptera. In *Melittobia* they are elongate ( $0.009 \times 0.003$  mm) on female club segments of *M. australica* and are present on all flagellar segments in both sexes except for males of the *M. hawaiiensis* and *M. assemi* groups where they are restricted to the club segments only. On the funicle segments they tend to be orientated transversely and in general they are fewer in number than on the middle club segment. On the club segments they tend to be longitudinal in arrangement and the transverse arrangement on the funicle segments may be related to the smaller number per segment. Distribution on each segment is uniform, i.e. there is no accumulation on any one side. The pattern of distribution along the antenna seems to vary with species and there is a small amount of intraspecific variation.

Multiporous plate sensillae have been assigned various functions, e.g. mechanoreceptors (Merlin 1941), auditory receptors (Ruland, 1888), air pressure receptors (McIndoo 1914, 1922), photoreceptors (Booth, 1963) and so on. More recent work indicates an olfactory function. The reaction of *M. australica* multiporous plate sensilla to ethyl acetate (discussed later) certainly indicates a reaction to chemicals.

Studies by Slifer, Prestage and Beams (1959) showed that some of the peg sensilla on the flagellum of grasshoppers had numerous fine pores in their cuticular walls and these could be demonstrated by soaking the antenna in 0.5% methylene blue. Sections revealed fine nerve fibres running to each pore. Further work has shown these to be olfactory receptors. Electrophysiological work by Lacher and Schneider (1963) and Lacher (1964) has shown that the multiporous plate sensilla on honey bee (*Apis mellifera*) antennae are olfactory. Slifer and Sekhon (1961) demonstrated fine pores in the cuticle of these, but not the fine fibrils. Slifer (1969) felt that further examination will probably reveal fine fibrils passing to these pores. Multiporous plate sensilla in aphids examined by Slifer, Sekhon and Lees (1964) differ in structure from those of the honey bee partly in the possession of an inner and outer cuticular layer. Dendrites pass singly or in groups through pores in the inner cuticular layer and enter a fluid filled chamber between the two cuticular layers in which they branch repeatedly. The fluid filled chamber has some importance in interpreting results obtained when I treated *M. australica*

females with ethyl acetate (discussed later). The outer cuticular layer of aphid multiporous plate sensilla are penetrated by numerous fine pores each supplied with fine fibrils. It could not be determined if these fine fibrils were connected to the dendrites, but Slifer, Sekhon and Lees (1964) felt this was probably the case. Freshly moulted specimens admitted crystal violet dye through these pores. The presence of fine filaments terminating in the pores plus the staining via these pores were taken to indicate an olfactory function for aphid multiporous plate sensilla.

Slifer (1969) examined the sense organs on the antennae of the pteromalid wasp *Nasonia vitripennis* (Walker). When treated with 0.5% crystal violet dye the stain rapidly entered the multiporous plate sensillum and examination showed the presence of numerous fine pores in the surface. In cross section these multiporous plate sensilla were seen to have an inner membrane similar to the multiporous plate sensilla of aphids. The inner cuticle lies just above two shelf-like invaginations of the cuticle. She noticed a large group of dendrites just below the proximal end of the inner membrane and presumed that these passed through the inner membrane, as in the aphid, and sent filaments into the pores in the outer surface.

The multiporous plate sensilla of *M. australica* resemble those of *Nasonia vitripennis* in overall shape and appearance. In cleared specimens, two longitudinal cuticular invaginations can be seen on either side of the multiporous plate sensilla as in *N. vitripennis*. I have not carried out histological investigation of the *M. australica* multiporous plate sensilla to confirm the presence of an inner membrane but am fairly certain there is one. Attempts to demonstrate pores in the outer wall using 0.5% crystal violet solution as used by Slifer (1960, 1969) were not successful even in freshly moulted specimens and SEM investigations did not reveal pores either. Slifer, Sekhon and Lees (1964) found that the plate organs of aphids showed crystal violet penetration when fixed four hours after the final moult but no penetration at 24 hours and 48 hours after final moult. They suggested that the minute pores in the older specimens might be rimmed with a waxy or hydrophobic material which prevents entry of the dye. Locke (1964) when discussing the formation of the insect cuticle states that the secretion of the endocuticle and the secretion of wax can occur concurrently and extend through the intermoult period. Therefore, it is possible that wax secretions constrict the pores after moulting. Pl. 8a-c show

the thin walled basiconic pegs of the grasshoppers *Atractomorpha similis* (Bolivar) freshly moulted and *Valanga irregularis* (Walker) several hours after moulting. The difference between the two is thought to be a result of wax encroachment. Gold coating would further fill the fine pores and obscure them in older specimens.

The normal method used for preparing *M. australica* for SEM examination involved killing by immersion in 75% ethyl alcohol before gold coating. When freshly moulted specimens were killed using ethyl acetate vapour before gold coating the result showed multiporous plate sensilla with a crumb-like surface which at higher magnifications look like exudations from pores in the surface (Pl. 6b-d). It can be seen that the surface of the antenna lacks the usual crazed appearance of older antennae and this is thought to be because the wax layer was absent or very thin. Older specimens when killed with ethyl acetate showed multiporous plate sensilla with a blistered appearance and distribution of the blisters matched distribution of the exudations in freshly moulted specimens (Pl. 6d). It is thought that the exudations arise from the fluid filled space between the outer and inner membranes of the multiporous plate sensilla and that this is in response to fairly high ethyl acetate concentration being an attempt to protect the sensitive nerve ending from a pungent vapour. The analogy is to the mammalian nasal mucosa which produces copious mucus in response to pungent vapours.

Barlin and Vinson (1981) investigated the multiporous plate sensilla on the antennae of several species of Chalcidoidea. In some cases they also found that the presence of pores in the outer plate was shown by exudations. Their investigations revealed two types of multiporous plate sensilla; Type 1 - present in both sexes and possessing a thin outer cuticle with numerous pores; Type 2 - present in females only and possessing a thick outer cuticle with fewer pores. Both types were found in all species studied except three i.e. not all species were found to have Type 2 multiporous plate sensilla. In *M. australica*, the females appear to have only Type 1. However, my work on *M. australica* antennal sense organs was carried out some time before the appearance of the paper by Barlin and Vinson and time does not permit a more thorough investigation of this aspect. I have not investigated the multiporous plate sensilla on the male antennae.

The similarity of the multiporous plate sensillae of *M. australica* to those of *Nasonia vitripennis*, the presence of pores on the outer surface in

conjunction with the results of Slifer et alia on other receptors having porous surfaces and the results of Barlin and Vinson with various chalcidoids suggest strongly that the multiporous plate sensilla of *M. australica* are olfactory in function. From their reaction to ethyl acetate they are probably very sensitive.

Before discussing their function we should look at the short basiconic capitate pegs as these appear also to be olfactory in function.

4) Short basiconic capitate pegs (Pl. 5b, iv).

These organs are absent from the antennae of males of most species but are present on the funicle and club of females where they predominate on the dorsal or outer surface. They arise from a circular, shallow, relatively broad depression in the cuticle. Thereafter the peg tapers into stalk which terminates in a spherical knob, the whole resembling a champagne cork. They occur sub-marginally on the distal portions of the segments and are directed towards the distal tip of the antenna.

These were not recorded on the antennae of *Nasonia vitripennis* by Slifer (1969) but were found subsequently in this species and another pteromalid wasp *Peridesmia discus* (Walker) by Miller (1972). Weseloh (1972) found them on the antennae of the encyrtid wasp *Cheiloneurus noxius* Compere. Neither gave any details of their ultrastructure but Miller (1972) assumed they were not touch receptors because of their sheltered location. Slifer, Prestage and Beams (1957, 1959) suggest that basiconic capitate pegs may function in olfaction if they are thin walled or in the perception of irritant substances if they are thick walled.

When females of *M. australica* were killed by immersion in 75% ethyl alcohol, SEM examination showed no details other than a crazed surface thought to be wax (Pl. 7a). Freshly moulted females killed with ethyl acetate vapours showed weeping from slits or rows of pores arranged along the longitudinal axis of its capitate tip or caput. In Pl. 7b-d these slits or rows of pores can be seen quite clearly. The distal tip of the caput was devoid of exudations and resembled a tonsure. Around the base of the peg were exudations resembling those of the multiporous plate sensilla.

If one is to accept the reasoning put forward earlier to explain the exudations from multiporous plate sensillae then the internal structure and the function of the short basiconic capitate pegs may be the same as the multiporous plate sensilla. They are undoubtedly olfactory in function. Therefore there are two

morphologically different olfactory sensilla on the antennae of all females and some males.

Schneider and Steinbrecht (1968) when discussing insect olfactory sensilla indicated there are two physiological types of olfactory cells — odour specialists and odour generalists. The former respond to biologically important odours, e.g. sex attractants, warning or specific food odours. Both types may be found in the one sensillum and this has been demonstrated in the multiporous sensilla of the honey bee *Apis mellifera*.

In *Melittobia*, evidence suggests specific and sexually different chemical signals. The sources are the male scape gland and circumstantial evidence indicates mandibular glands in both sexes. These would suggest the presence of odour specialist, olfactory cells. Electro-physiological work would be required to identify the presence and location of these cells but some speculation is possible.

In the males of most species the antennae lack short basiconic capitate pegs. In females these are located mostly on the upper surface of the antennae which is the surface applied to the inner lining of the male scape groove or cup containing the dermal gland. The short basiconic capitate pegs therefore might contain odour specialist olfactory cells for perception of a male pheromone. Females are able to detect males from a distance, e.g. when a male is placed in with a group of inactive virgin females the latter immediately become active and move fairly directly towards the male. Hermann (1971) mentions male calling in *M. chalybii* (= *M. australica*). It was noticed in my colonies of *M. australica* that males walk about with their scapes raised laterally and flagellar segments extended so that the tip of the scape groove was open. They also stand around in this pose. It could be that they are exposing their scape gland to attract females. The rearing jars are much larger than the host cell or puparium and it is difficult to imagine the need for such a system in the confines of a host cocoon or puparium.

The distribution of multiporous plate sensilla varies in males. In the *hawaiiensis* and *assemi* groups they occur on the club segments only, but in the *acasta* group they occur on all flagellar segments. During courtship *M. australica* females were noticed to open their mandibles. Initially I thought this to be the signal for the female's readiness to copulate thus inducing the male's finale. However, van den Assem does not agree (Pers. comm. 1980). Mention has been made

previously of virgin females without males standing with open mandibles. When provided with a dead male pupa females located it and again stood with open mandibles. It was argued that mandibular glands may be the source of female scent and if this is so then opening mandibles during courtship probably means some chemical input by the female. If virgin females call by mandibular glands then the only olfactory receptors in most males are the plate organs and these would contain the odour specialist olfactory cells. During courtship of species in the *hawaiiensis* and *assemi* groups the male position is such that his clubs are in close proximity to the female's mandibles when open. In these groups only male club segments bear plate organs. During courtship of the *acasta* group the male does not stand so far forward and his funicular segments would be in contact with her open mandibles. This is thought to have some bearing on retention of plate organs on the funicle as well as the club segments in the *acasta* group males.

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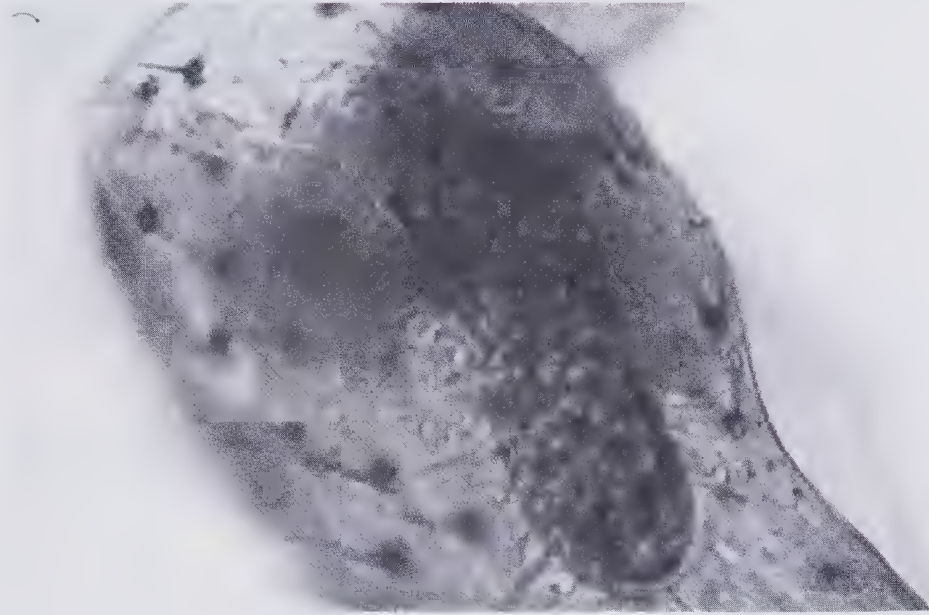
## PLATE 1

*Melittobia australica* male scape, AgNO<sub>3</sub> stain, Euparal slide  
mount, × 900

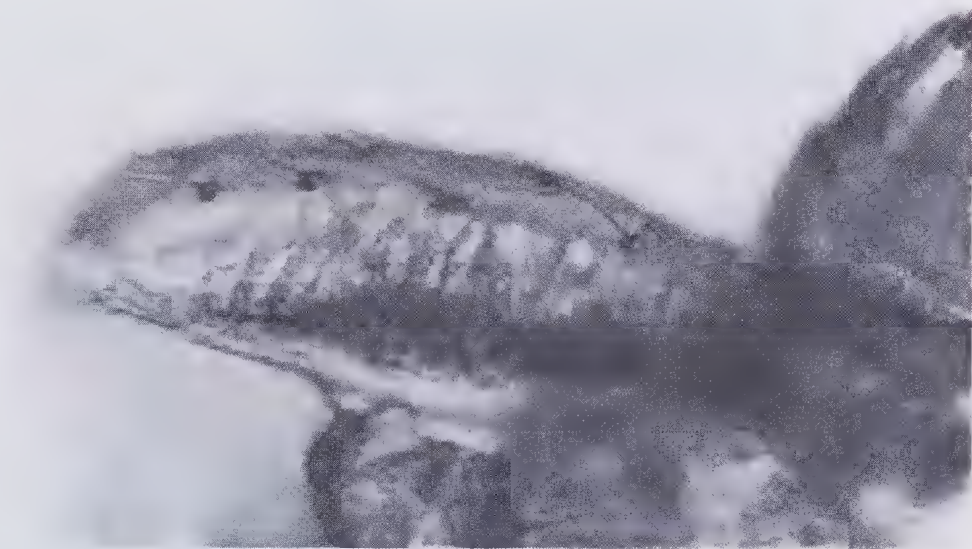
- a) Lateral view.
- b) Ventral view.



# Plate 1



**a**



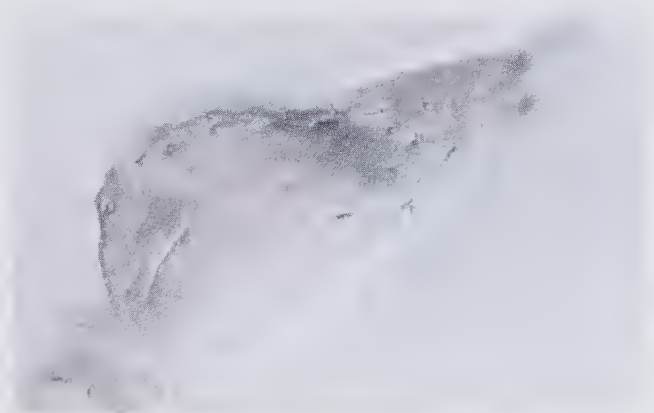
**b**

## PLATE 2

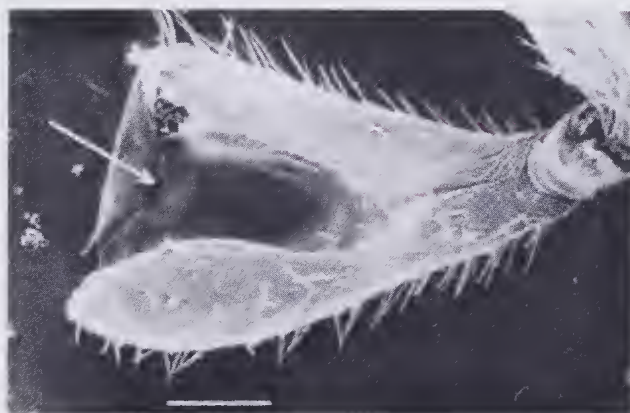
*Melittobia australica* male scape.

- a) Dorsal view, NaOH cleared, Euparal slide mount, × 340.
- b) Ventral view, showing transverse arm of gland, SEM, × 340.
- c) Cuticular surface over gland, SEM, × 2,000.

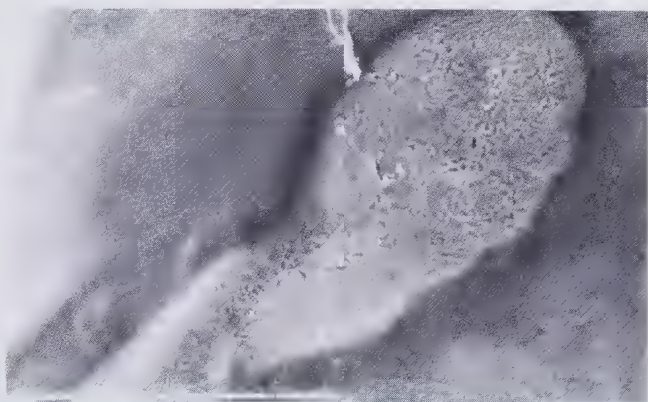
# Plate 2



**a**



**b**



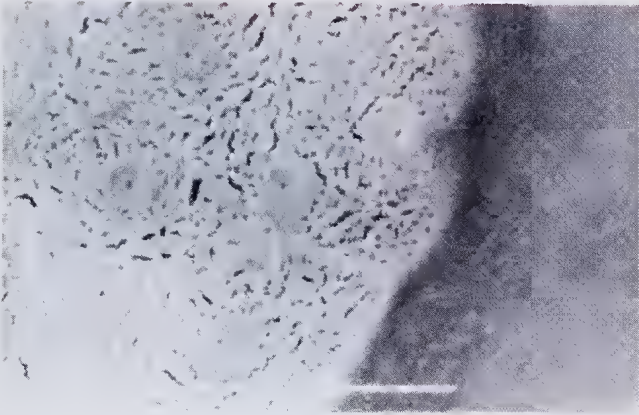
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## PLATE 3

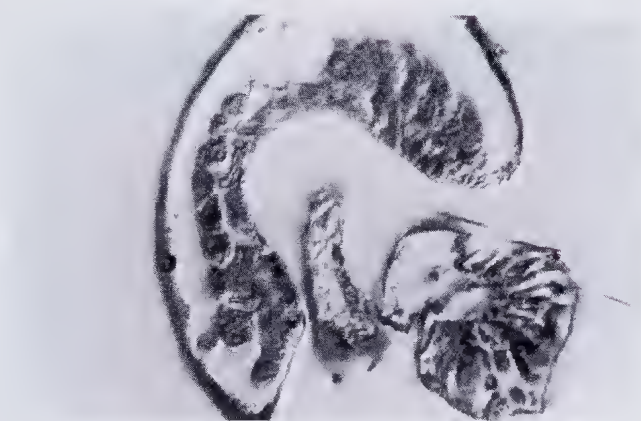
*Melittobia australica* male scape.

- a) Cuticular surface over gland showing pores, SEM, × 5,200.
- b) TS male scape just proximal of scape attachment — section through transverse arm of gland, Euparal slide mount, × 650.
- c) TS more proximal region of scape-section through longitudinal area of gland, Euparal slide mount, × 700.

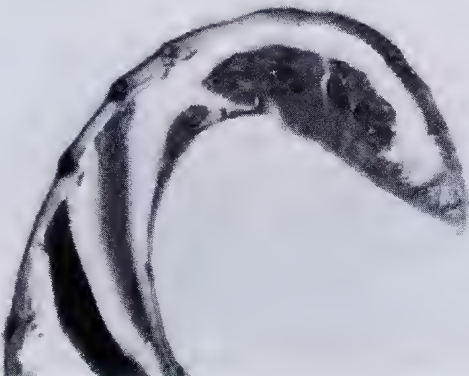
**Plate 3**



**a**



**b**



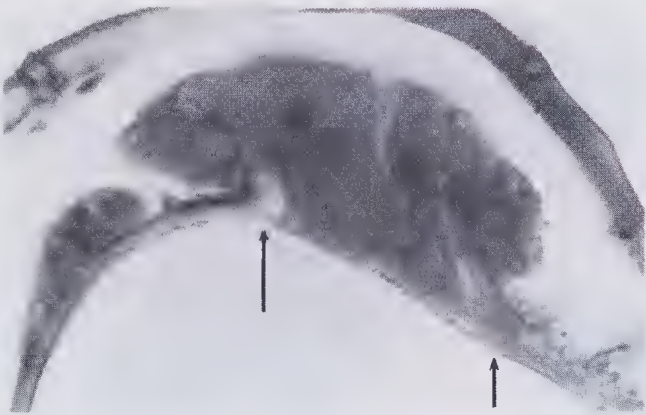
**c**

## PLATE 4

*Melittobia australica* male scape and setae on legs.

- a) TS longitudinal area of scape showing cuticular invaginations to support gland, Euparal slide mount,  $\times 2,000$ .
- b) Dense setal tuft on ventral fore-trochanters, SEM,  $\times 1,000$ .
- c) Seta in mid-femoral fringe, SEM,  $\times 4,000$ .

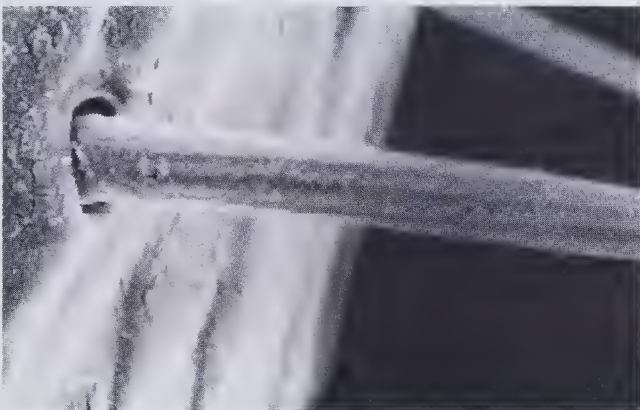
**Plate 4**



**a**



**b**



**c**

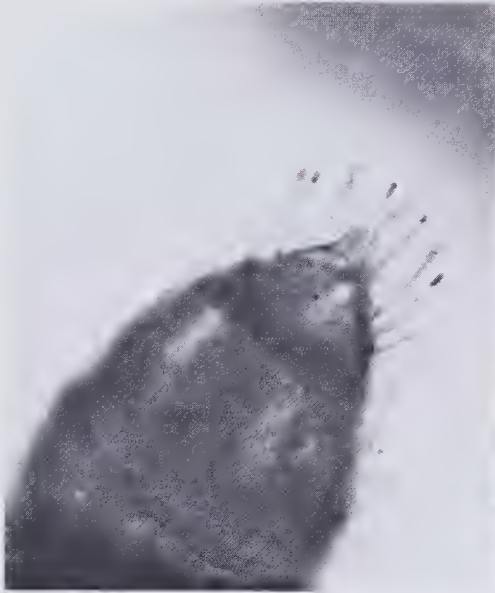
## PLATE 5

*Melittobia australica* male, female antennae.

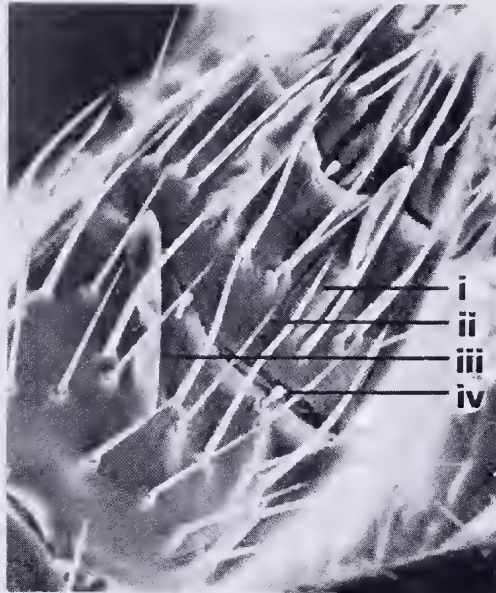
- a) Male club, AgNO<sub>3</sub> stain, Euparal slide mount.
- b) Female club, SEM, × 900.
  - i) long thin unfluted setae.
  - ii) tapering fluted seta.
  - iii) multiporous plate sensillum.
  - iv) short basiconic capitate peg.
- c) Male club, segments 2 and 3, SEM, × 2,000.
- d) Male tapering fluted setae, SEM, × 2,800.



# Plate 5



**a**



**b**



**c**



**d**

## PLATE 6

*Melittobia australica* male flagellum and female sensillae.

- a) Male flagellum, SEM,  $\times 600$ .
- b) Distal female club after exposure to ethyl acetate, SEM,  $\times 1,300$ .
- c) Multiporous plate sensillum of freshly moulted female after exposure to ethyl acetate, SEM,  $\times 10,000$ .
- d) Multiporous plate sensillum of older female after exposure to ethyl acetate, SEM,  $\times 5,500$ .

# Plate 6



**a**



**b**



**c**



**d**

## PLATE 7

*Melittobia australica* female short basiconic capitate pegs.

- a) Older female killed by immersion in ethyl alcohol, SEM,  $\times 13,000$ .
- b-d) Freshly moulted female after exposure to ethyl acetate, SEM, (b  $\times 10,000$ ; c  $\times 18,000$ ; d  $\times 13,000$ ).

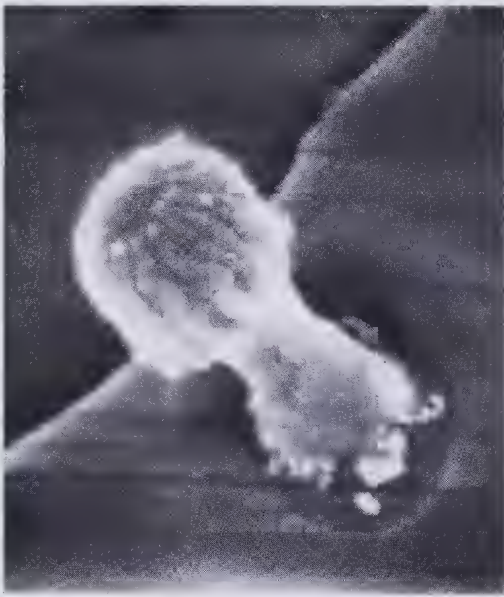
# Plate 7



**a**



**b**



**c**



**d**

## PLATE 8

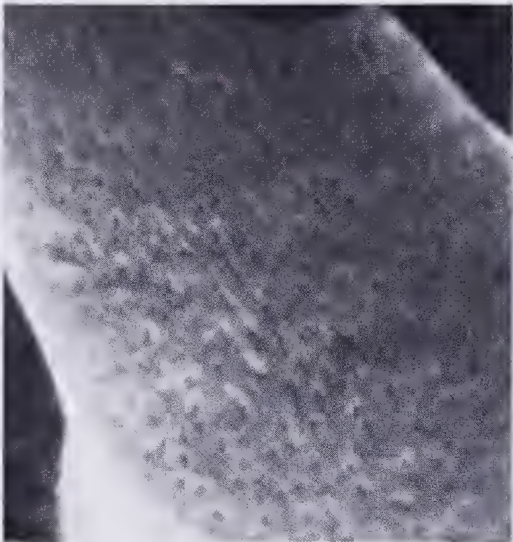
Grasshoper basiconic pegs.

- a) Freshly moulted *Atractomorpha similis*, SEM,  $\times$  6,000.
- b) Freshly moulted *Atractomorpha similis*, SEM,  $\times$  21,000.
- c) Several hours after moulting *Valanga irregularis*, SEM,  $\times$  7,500.

**Plate 8**



**a**



**b**



**c**





A NEW SPECIES OF *APTENOCANTHON* MATTHEWS FROM NORTH QUEENSLAND. (COLEOPTERA : SCARABAEIDAE : SCARABAEINAE)

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ABSTRACT

*Aptenocanthon monteithi* sp. nov. is described from the Atherton Tableland area in northern Queensland. The nearest relatives are from mountains in eastern New South Wales.

INTRODUCTION

The dung beetle genus *Aptenocanthon* was erected by Matthews (1974) for the species *A. hopsoni* Carter (formerly *Panelus* and a second new species, *A. rossi*. Both species were known only from wet, high altitude localities in central New South Wales, Barrington Tops and Mt Wilson respectively. Both species were poorly known, but *A. hopsoni* has since been taken in numbers at Barrington Tops, from altitudes of 500 m to 1400 m, in both dung baited pitfall traps and sieved litter (T.A. Weir, pers. comm.), and *A. rossi* has been recorded at Mt Irvine at 750 m at dung baited pitfall traps (Williams and Williams 1982).

It is thus with some interest that a new species was taken recently on top of the Bellenden-Ker Range in north Queensland, 1900 km north of the previous records for the genus. The specimens were taken by an expedition, organized jointly by the Queensland Museum and the Earthwatch Organization, to study the change in insect fauna with altitude on Mt Bellenden-Ker, a locality noted for relict and other interesting species in both the botanical and insect world. Subsequently, further specimens of the same species were taken on mountain areas on the Atherton Tableland proper, namely the Mt Fisher and Mt Haig areas, 45 km S.W. and 40 km N.W. from the original Bellenden-Ker locality respectively.

Genus *Aptenocanthon* Matthews

*Aptenocanthon* Matthews 1974, *Aust. J. Zool.*, *Supp. Ser.* No 24, pp. 93–97. Type species *Panelus hopsoni* Carter, 1936.

*Aptenocanthon monteithi* sp. nov. (Figs. 1 and 2)

Holotype: Queensland Museum T8592 ♂, Bellenden-Ker Range, N. Qld., Summit TV Stn.,

1560 m, 25–31.x.1981, Earthwatch/Qld. Museum, QM Berleseate No. 372, 17.16S, 145.51E, Rainforest. Sieved litter.

Allotype: Queensland Museum T8593 ♀, Bellenden-Ker Range, N. Qld., Summit TV Stn., 1560 m, 25–31.x.1981, Earthwatch/Qld. Museum, Pitfall trap in rainforest.

Paratypes (34): Bellenden-Ker Range, Summit TV Stn., 1560 m, 17.x–5.xi.1981, Earthwatch/Qld. Museum (5 ♂♂, 4 ♀♀), same data 1–7.xi.1981, (1 ♂), same data 25–31.x.1981 (3 ♂♂). Mt Bartle Frere, 0.5 km north of South Peak, 1500 m, 6–8.xi.1981, Earthwatch/Qld. Museum, (4 ♂♂); Mt Bartle Frere, NW/Centre Peak ridge, 1400–1500 m, 7–8.xi.1981, Earthwatch/Qld. Museum, (3 ♂♂). Mt Fisher, 7 km SW Millaa Millaa, N. Qld., 1050–1100 m, 27–29. IV. 1982, Monteith, Yeates and Cook, (1 ♂, 1 ♀), 26 km up Tinaroo Ck Rd., via Mareeba, N. Qld. 11.xi.1982, Morgan, Brown and Storey, (1 ♀), same data 10–30.xi.1982, (2 ♀♀), same data 1–23.xii.1982, (1 ♀), same data 23.xii.1982–12.i.1983, (2 ♀♀), same data 12–28.i.1983, (1 ♀), same data 28.i–16.ii.1983, (1 ♀). (Paratypes placed in Queensland Museum, ANIC Canberra, South Australian Museum, Queensland D.P.I., Coll. R.I. Storey, Mareeba, H.F. Howden, Ottawa, A. Walford-Huggins, Julatten, P. Allsopp, Toowoomba, G. Williams, Taree).

Total length 3.3–4.1 mm. colour black, legs reddish brown antennae yellow brown.

Male

*Head:* Clypeal teeth small, close together, U-shaped between, rest of margin feebly sinuate to genal angles which are angulate, margin very feebly beaded. Surface nitid, densely punctuate with moderate simple punctures, effaced along edge of clypeus, glabrous. Dorsal part of eyes small, about 4 facet rows wide, separated by

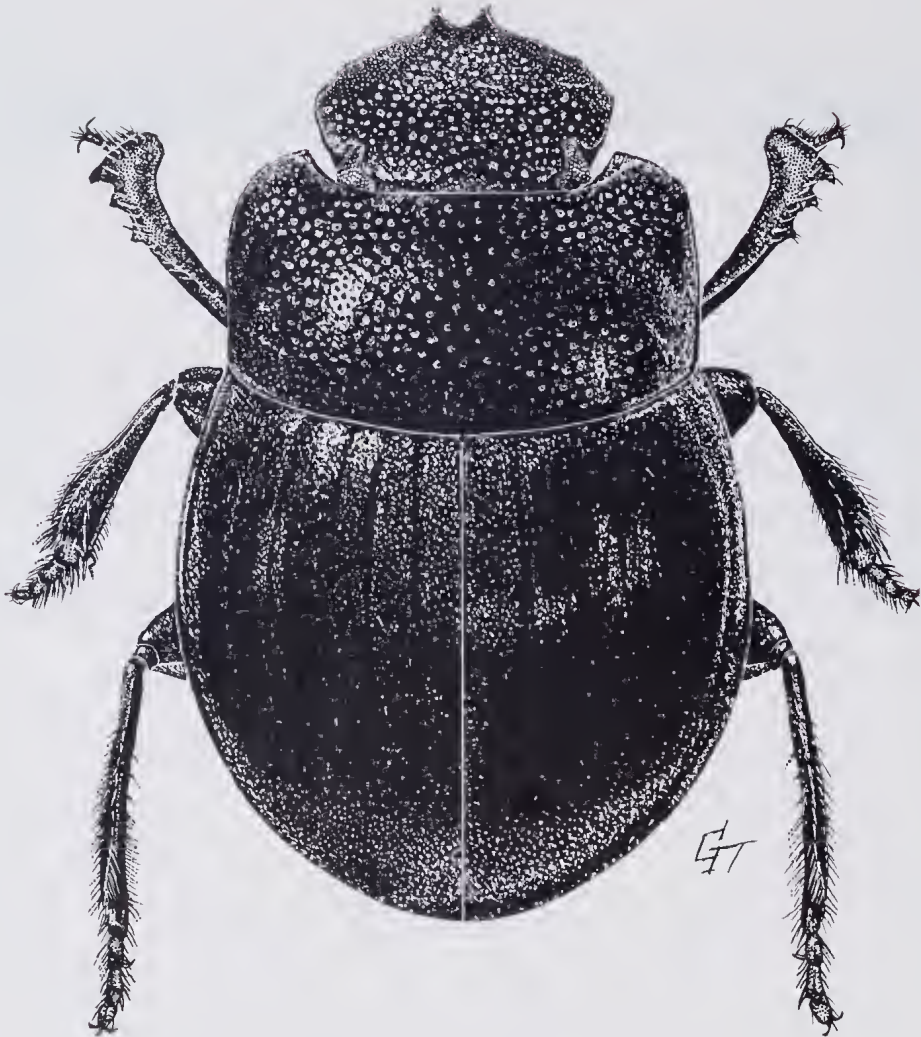


FIGURE 1: *Aptenocanthon monteithi* sp. nov., male paratype.

about 8-10 eye widths, canthus incomplete. *Pronotum*: Anterior angles quadrate, feebly projecting, lateral angles very obtuse, rounded, posterior angles obtuse. Pronotal surface smooth, nitid, punctate with moderate simple punctures which are effaced along lateral margin and posterior angles, reduced in centre of disk, glabrous. Lateral edge rounded to deflexed portion, finely margined. *Elytra*: Striae on disk effaced, almost undetectable, impunctate, intervals feebly convex, very finely punctate, surface feebly shagreened, glabrous. Surface deflexed outside 7th stria, forming pseudepipleura about 2/3 length of elytra, the

edge beaded with a slightly raised nitid area between it and the 7th stria, with two fine striae between edge of pseudepipleura and the feebly sinuate epipleura. *Hind Wing*: Entirely absent. *Sterna*: Mesosternum with a few large superficial umbilical punctures on edges. Median lobe of metasternum nitid, impunctate, lateral lobes with numerous large, shallow umbilical punctures. *Legs*: Fore tibia with inner edge broadly concave, outer edge with three short teeth on apical 1/3, distal edge straight, transverse, with inner apical angle produced into a broad inwardly projecting truncate lobe, tibial spur short, triangular. Middle and hind legs unmodified. *Abdomen*: Pygidium

strongly convex, smooth nitid, scattered very fine punctures, glabrous. Each sternite with several large punctures near ends, in a shallow depression which is deepest on 6th. Aedeagus with parameres asymmetrical, as in Fig. 2.

#### Female

Fore tibia with inner apical angle not produced into a truncate lobe, tibial spur and teeth on outer edge slightly larger. Abdominal sternites expanded. Otherwise similar to male.

#### COMMENTS

The specimens from the Bellenden-Ker Range were all taken above 1400 m in a habitat described by Tracey and Webb (1975) as simple Microphyll Vine-Fern Forest grading into thicket at the absolute summit. It was not taken at lower altitudes at this locality even though sites at 5, 100, 500 and 1054 m were collected intensively. However, the two additional localities are at lower altitudes, in the vicinity of 1000 m. Individuals were taken in pitfall traps, dung baited traps and in sieved litter.

The species is named for Dr G.B. Monteith who was involved with the organizing of the Earthwatch expedition and has contributed much to the knowledge of Australian Scarabaeinae.

The following adaptations of Matthews (1974) key should aid in separating the three species:

- 1) Pygidium with a strong transverse basal groove; elytral striae distinct, with prominent punctures on intervals; central N.S.W. .... 2  
Pygidium without a basal groove; elytral striae almost obsolete, intervals very finely punctate; north Queensland  
..... *monteithi* sp. nov.
- 2) Elytral intervals flat, glabrous; lateral elytral carina sharply defined basally; outer edge of epipleura strongly sinuate .... *hopsoni* Carter  
Elytral intervals convex, densely setose; lateral elytral carina feeble, broadly rounded; epipleura normal.... *rossi* Matthews

#### DISCUSSION

Some problems were encountered in placing *monteithi* within the genus *Aptenocanthon*. Specimens of both *A. hopsoni* and *A. rossi* were available for comparison. It agrees with these species in size and general appearance, secondary sexual characters, shape of mentum and labial palps, size of eyes and flightless condition. Differences include shape of the lateral edge of the pronotum, shape of pseudopipleura, nine as

opposed to eight elytral striae, and lack of pygidial sculpturing. It is this author's opinion that grouping the three species in one genus is more useful than creating a new genus as they are closer to each other than to related genera. The lack of basal pygidial groove in *monteithi* is interesting, as it is a feature of *Aptenocanthon* and related genera — the Australian *Tesserodon* Hope and the New Caledonian *Onthobium* Reiche, though in the Australasian *Ignambia* Heller and New Zealand *Saphobius* Sharp it is lacking. The Australian genus *Lepanus* Balthasar is similar in having variable pygidial sculpturing and is more heterogeneous than *Aptenocanthon* as envisaged here.

Australian dung beetles of the tribe Scarabaeini all fall within the subtribe Canthonina, which though found almost worldwide has a basically southern distribution, being best represented in the neotropical region. Australian species make up 14% of the world species diversity (Matthews, 1974). Australian Canthonina can be further divided into two groups — those with simple claws and pseudopipleura and those with dentate or subdentate claws and without pseudopipleura. *Aptenocanthon* falls within the first group, usually referred to as the mentophilines. Matthews (1974) considered this the most primitive of the two groups, both structurally and in behaviour, with ball-rolling being unknown in the group.

The mentophiline group shows a basic Gondwanan distribution, with genera in Australia, New Zealand and New Caledonia. The genus *Ignambia* also occurs in New Guinea, as well as Australia and New Caledonia (Howden, 1981). Scarabaeinae as a whole occur in warm temperate to tropical climates. Some genera in Australia are southern (*Aulacopris* White and *Cephalodesmius* Westwood) and others such as *Tesserodon* and *Ignambia* are essentially tropical. *Amphistomus* Landsberge has a complex of species along the eastern and northern coasts. The situation in *Aptenocanthon*, with such widely separated flightless mountain top species is unique in Australian Scarabaeini, though a flightless species of *Aulacopris* is now known to occur in north Queensland and will be described in a subsequent paper. This distribution in flightless species of insects with southern genera being found on north Queensland mountain tops has been recorded in other families: *Hackeriella* (Peloridiidae) and *Kumaressa* (Aradidae) in Hemiptera and *Lissapterus* (Lucanidae) in Coleoptera. Recent

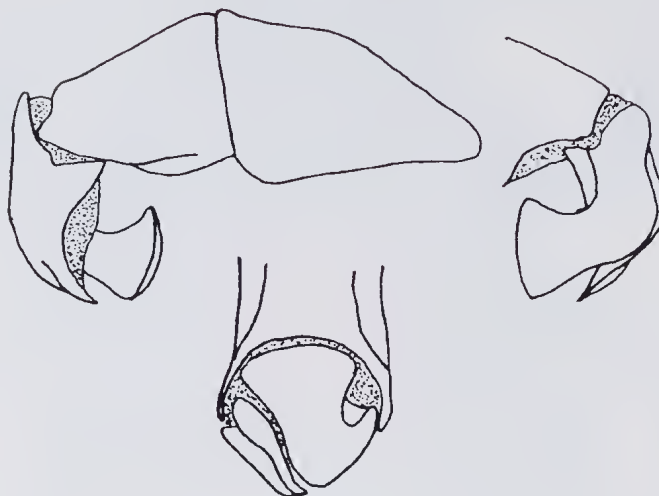


FIGURE 2: Aedeagus, *A. monteithi* sp. nov.

publications by Monteith (1980) and Kikkawa et al. (1981) have given summaries of the phenomenon and its importance to studies in Australian biogeography.

The discovery of *A. monteithi* gives further support to the view that high mountain tops in north Queensland, and the Bellenden-Ker range in particular, are major refugia for wet area plants and insects in Australia.

#### ACKNOWLEDGMENTS

The author wishes to thank Mr Geoff Thompson of the Queensland Museum for the drawing in Figure 1, Dr Geoff Monteith, Queensland Museum and Mr Tom Weir of CSIRO, Canberra for helpful comments on the manuscript and Mr G. Williams of Taree for the loan of specimens. The Earthwatch Organization rates thanks for their assistance in funding of the field work involved.

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SPAWNING OF THE AUSTRALIAN LUNGFISH, *NEOCERATODUS FORSTERI*  
(KREFFT) IN THE BRISBANE RIVER AND IN ENOGGERA RESERVOIR,  
QUEENSLAND.

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ABSTRACT

The Australian lungfish, *Neoceratodus forsteri* (Krefft) breeds annually between mid-August and December. The onset of oviposition is not related to rainfall, temperature, pH or dissolved O<sub>2</sub> content of the water in which they live. Lungfish begin to spawn when daylength has been increasing for 6–11 weeks, provided that suitable weeds are growing, and the rate of flow of the water may also have an effect on the site chosen for spawning.

INTRODUCTION

Caldwell (1884) was the first to report finding eggs of the Australian lungfish, *Neoceratodus forsteri* (Krefft), in the Burnett River, 14 years after Krefft (1870) had described the adult fish from the Mary River. Semon, who studied the development of *N. forsteri* (1893), found eggs in shallow water amongst weeds in the Boyne River, a tributary of the Burnett (1899:96). Eggs are deposited among growing water weeds or on the sides and bottom of submerged logs (Illidge 1892). Plants important for egg laying in the Burnett River are *Hydrilla verticillata*, *Vallisneria spiralis* and *Nitella* sp. (Bancroft 1911). Spawn has also been found on the roots of the water hyacinth, *Eichornia crassipes*, in Enoggera Reservoir, Brisbane (Bleakly, per. comm., 1969), from "weeds" in a tributary of the Burnett River (Grigg 1965) and on the submerged roots of *Callistemon saligna* growing beside the Brisbane River (Kelly, per. comm., 1977). Spencer (1925) states that eggs are laid separately amongst vegetation, but not attached to it, and that they finally lie on the mud.

There is only one published report on the breeding behaviour of *N. forsteri* in the wild (Grigg 1965). The breeding season has been recorded as August-October in Enoggera Reservoir (Bleakly, cited by Grigg 1965), September in the Boyne River (Semon 1899), August-November in Enoggera Reservoir (Kemp 1977), September-October (Spencer 1926), November-December (Illidge 1893), August-October in the Burnett River (Bancroft 1911 and 1928) and August in a tributary of the Burnett

River (Grigg 1965). Factors which influence spawning are not known.

This work was undertaken to determine the times and places of spawning of *N. forsteri* in a river and a lake environment in southeast Queensland, and to discover any possible environmental regulation of breeding. In this respect the Australian lungfish was compared with the African and South American species, *Protopterus annectens* (Owen), *Protopterus aethiopicus* Heckel and *Lepidosiren paradoxa* Fitzinger.

MATERIALS AND METHODS

Information on breeding, stages of eggs collected and weeds used for oviposition were recorded from Enoggera Reservoir from 1971–1973 and from the Brisbane River from 1978–1981. Rainfall data for these years was obtained from the Bureau of Meteorology in Brisbane, Queensland.

Information on hours of daylight was obtained from the records of the Department of Mapping and Surveying, Brisbane, Queensland.

Observations were made during the period July 1979 to November 1979 at two breeding sites in the Brisbane River: one was a bed of *Vallisneria spiralis* and the other, submerged roots of *Callistemon saligna* 1 km downstream. Temperature and dissolved oxygen were measured in the field between 11 am and 1 pm. Water samples were taken to measure pH in the laboratory. Eggs were collected from weeds or roots in the area from which the samples were taken. Plants were identified from Aston's (1973)

description. Further observations on temperature and dissolved oxygen in relation to spawning were made during the period May 1980 to January 1981.

Eggs were kept in insulated containers and assessed for their stage of development in the laboratory, 1–2 hours after collection. The onset of oviposition was determined by subtracting the age of the oldest eggs found from the date of collections, e.g. minus 1 day if the oldest eggs were cleavage stages or minus 6 days if the oldest were neurulae of stage 18. Ages were based on times of development of eggs maintained in the laboratory at 18–22°C, temperatures comparable to those of the river at the time of collection (Kemp 1981).

## RESULTS

### Breeding Behaviour

i) Plants in the breeding areas and their potential as oviposition sites. A list of plants in the lake and river breeding areas is given in Table 1, with observations on the use made of the weeds for spawning. The weeds were present at all times except for *Eichornia crassipes*, *Hydrilla verticillata* and *Potamogeton javanicus*, all of which die off in winter.

Weeds used consistently for spawning are *E. crassipes* (in river and lake), *Vallisneria spiralis* and submerged roots of *Callistemon saligna* (river only). Fewer eggs were found on *H. verticillata*, *Potamogeton perfoliatus* or *Nitella* sp. Use of *Ceratophyllum* sp. or filamentous algae was incidental and occurred only when these weeds grew amongst *C. saligna* and *V. spiralis* (*Ceratophyllum*) or coated the *C. saligna* roots (algae).

TABLE 1: UTILISATION OF WEEDS FOR SPAWNING IN ENOGGERA RESERVOIR AND IN THE BRISBANE RIVER.

Species of Weed	Lake	River
<i>Eichornia crassipes</i>	*	*
<i>Hydrilla verticillata</i>	?	*
<i>Vallisneria spiralis</i>	-	*
<i>Callistemon saligna</i> (submerged roots)	-	*
<i>Nitella</i> sp.	-	*
<i>Potamogeton crispus</i>	-	©
<i>Potamogeton perfoliatus</i>	-	*
<i>Potamogeton javanicus</i> **	©	-
<i>Ceratophyllum</i> sp.***	©	*
<i>Nymphoides indica</i>	©	©
<i>Nymphaea capensis</i>	©	-
<i>Nymphaea flava</i>	©	©
<i>Ludwigia peploides</i>	-	©
<i>Brachiaria mutica</i>	©	-
<i>Rumex bidens</i>	©	-

Sedge	-	©
Filamentous algae***	-	*
<hr/>		
* used for spawning		
© not used		
- weed has not been found		
? weed too deep to sample		
** breeding behaviour observed but no eggs found		
*** growing with or on <i>C. saligna</i> roots or <i>V. spiralis</i> plants		

ii) Oviposition in the lake. Eggs were always found attached to the roots or submerged floats of *E. crassipes*. Eggs have not been found on or among any other weeds in this locality, or lying free at the bottom of the lake, as measured by dredging samples or by diving. *H. verticillata*, used by fish in the Burnett River for spawning (Bancroft 1911 and 1928), also occurs in the lake but it was too deep to be easily sampled.

During the breeding season of *N. forsteri*, air breathing is frequent, and is accompanied by a distinct loud burp, made in the air with the lips clear of the water. During two periods of observation groups of fish appeared to be responding to each other. On the first occasion, one fish in the centre of a group 'sounded', then a fish to one side, then a fish to the other side, then the central fish, and finally one ahead of the first fish. On the second occasion one fish after another breathed air, in no particular order, along a weed bank about 20 m in length. The fish were spaced at 2–4 m intervals, and several minutes elapsed between each breath. During the period of observation (2 hours during the day), individual fish breathed at regular intervals of about 20 minutes. Pairs of fish also perform circling movements at the surface of the water close to weed banks.

Fish manoeuvre into the root mass of *E. crassipes* to spawn, and may lay eggs deep within the mass of roots as well as on the edges. Oviposition was observed once at 11 am in the lake. The female turns on her side when laying eggs and the male, entwined around her, fertilises the eggs as they emerge. Eggs less than 3 hours old (uncleaved, or in stage 1 or 2) were often found during daytime collecting trips.

Eggs laid at one time are found in a circumscribed area of the roots, for example all at the top. It is possible to distinguish individual clutches by their different ages, i.e. a set of late neurulae compared with a set of early cleavage stages. Eggs are laid over areas of 1–5 sq.m, on the roots and occasionally on partly submerged floats of the hyacinth, in varying positions from near the surface to a depth of one metre. They are

attached quite firmly by the outer jelly layer which is sticky when first laid. Eggs were usually placed singly, or occasionally in pairs.

Fish performing frequent air breathing and circling movements have been observed in beds of *Potamogeton javanicus* in the lake, but eggs have not been found on this weed despite extensive searches. Adult lungfish have also been seen at night in para grass, *Brachiaria mutica*, which grows thickly in shallow water beside the shore, but again no eggs have been collected from this plant.

iii) Oviposition in the Brisbane River. Eggs are laid on the submerged roots of *Callistemon saligna*, with or without a covering of filamentous algae, in beds of *Vallisneria spiralis*, mixed stands of *V. spiralis* and *Hydrilla verticillata*, or on the upper parts of the alga *Nitella* sp. which also grows with *V. spiralis*. Eggs have also been found on fronds of *Ceratophyllum* sp. growing amongst *C. saligna* roots, and on *E. crassipes*.

Eggs were not found on sedge or on *Ludwigia peploides* which occur in shallow water near consistently used *V. spiralis* beds, nor on the *H. verticillata* growing in deep water nearby. Also fish did not appear to lay on *V. spiralis* growing in a substrate of fine black mud, but used weeds rooted in fine sand or gravel. In 1980 and 1981, logging operations upstream resulted in a deposit of silt throughout the *V. spiralis* bed, and although this was fine, it was not as fine as the mud and the fish continued to lay eggs.

*Nymphoides indica*, *Nymphaea flava* and isolated fronds of *Ceratophyllum* are also ignored by the fish, as is *Potamogeton crispus* which occurs in deeper or faster flowing water.

Eggs may be found close to the surface to a depth of 1.5 m. They occur on leaves or on the partly exposed upper roots of *V. spiralis*, sometimes partly buried in the substrate, and on any part of the *C. saligna* root mass, on or under the mat of filamentous algae if this is present. Sometimes the eggs are laid so high on the root mass that a drop in the water level after laying leaves the eggs exposed.

During 1980 *E. crassipes* was plentiful in the river and the fish used it for spawning. In one area they seemed to prefer it to *C. saligna* nearby laying eggs exclusively on the water hyacinth when it grew sufficiently dense (Fig. 1), and in another locality they used both. River fish often laid eggs in clusters of 4-14 eggs (i.e. close together but not touching) on *E. crassipes*.

In localities containing *V. spiralis* or *C. saligna*, different clutches of eggs could not usually be distinguished. Eggs of various ages appeared to be randomly distributed.

On one occasion only, in 1978, eggs were found lying free on the bottom of the river, in shallow, weed free areas amongst the *V. spiralis* plants. Many of these eggs were dead and all were exposed to sunlight and to higher temperatures than the eggs which were hidden in the *V. spiralis* leaves. The weed free areas did not look like nests and no adults were in attendance.

#### Other Observations

Both the lake and the river have a permanent inflow of water. Enoggera Reservoir is situated on a creek fed by springs in the D'Aiguilar Ranges to the west of Brisbane. Although the creek is reduced in times of drought, it is permanent. Water levels in the Brisbane River fluctuate because it supplies water for Brisbane, but the flow is continuous.

In both lake and in river, fish lay eggs in areas with a slow or moderate current of water, free of floating debris. Eggs are not found in still water, even if suitable weeds are available.

Fish do not guard the eggs in any of the spawning localities.

Suitable weeds for spawning are always present in the river. This was not always the case in the lake as *E. crassipes* dies off in winter. In 1973, as there was a mild winter and the weeds did not die off, so suitable weeds were present throughout the year.

#### The timing of oviposition

Data on the duration of breeding by fish in the lake and in the river (calculated from the age of the oldest eggs found and the last date on which new laid eggs were collected) are shown in Figure 1. Changes in hours of daylight and the daily rainfall are included.

In the lake, breeding began in mid-September in 1971 and in early September in 1972. In 1973 oviposition began early in August, lasted for about one week and began again in early October (Fig. 1). In 1971 and 1972 breeding had been in progress for some time when the first eggs were collected, as a proportion of the eggs collected were in late stages of development (over 10 days old) in contrast to the first collection of 1973 when almost all the eggs found were at stage 11 (less than 2.5 days old) or younger. At the first part of the spawning season of 1973 progressed the high proportion of young eggs gave way to peaks of older embryos and finally to collections consisting entirely of larvae close to hatching. This progression is not always so obvious. Most collections from the lake show a proportion of older eggs, unlike collections from the river.

In the river, the breeding season started earlier and lasted longer, normally from mid to late August until November (Fig. 1). *V. spiralis* beds were used for spawning a little earlier than *C. saligna* roots in 1979 and at much the same time in 1980. The *V. spiralis* beds were discovered in the middle of the 1978 season, some time after breeding had begun. Oviposition is continuous in the *V. spiralis* beds throughout the breeding season, but not on the *C. saligna* roots where breaks may occur. In 1978 a small number of eggs appeared very late, in December, on *V. spiralis* plants (Fig. 1). In every collection from the river, even late in the season, a proportion of young eggs was present.

#### *Leading Stimulus for Oviposition*

The start of oviposition did not appear to be related to rainfall. In the lake during the 1971 and 1972, oviposition began after a dry winter, but before heavy rains. In 1973, spawning followed a heavy rainfall in the previous month, stopped after 2 dry months and started again during a month of moderate rainfall (Fig. 1).

On the river, rainfall was generally lower than on the lake, and oviposition began in mid or late August or early September in each year in both breeding areas (Fig. 1). In 1979, in the *V. spiralis* beds, there was a lag of two months between a peak of heavy rainfall and production of eggs. In 1980 heavy rain fell in May, very little in June, July or August and eggs were not found until the end of August (Fig. 1). In 1981, the start of spawning followed a dry month and came to an end before much rain fell.

In the *C. saligna* area, a peak of rain followed the start of oviposition in 1978, and preceded spawning by 3 and 4 months respectively in 1979 and 1980 (Fig. 1). This area was destroyed by logging operations before the start of the 1981 season.

Eggs less than 3 days old were found following rain within the preceding 3 days in 6 out of 15 collections that yielded new laid eggs in the lake. In the river 6 out of 24 and 3 out of 21 collections contained newly laid eggs in *C. saligna* and *V. spiralis* beds respectively. The rainfalls which did precede the finding of newly laid eggs were usually light, less than 25 mm. In both areas the heaviest rains occurred in January and February, when the fish do not spawn.

In every year, in both areas, *N. forsteri* begins to breed at a time of increasing daylength, in nine out of ten cases within 10 weeks after the shortest day and once in the lake after 11 weeks (Fig. 1).

#### *Other conditions in the Brisbane River at the time of spawning.*

The numbers of eggs found and the physical conditions at the time of collection on successive dates in two different localities in the Brisbane River in 1979 and 1980 are given in Fig. 2.

Temperatures are moderate initially and fairly steady but influenced by cold water from Somerset Dam higher up the river, released at irregular intervals in response to requirements in Brisbane. There was no marked rise until mid-October.

pH remains steady and slightly alkaline. Dissolved oxygen levels fluctuated, low at first and then higher, and were normally reasonably high during the day in the weed beds, probably because of photosynthesis by water plants. Levels of dissolved oxygen fell in November when water temperatures in the weed beds where the fish spawned were consistently over 24°C.

A large number of eggs were laid in the *V. spiralis* area in August 1979, at the same time as the level of dissolved oxygen rose, and fewer eggs were found in late September when the level of dissolved oxygen fell. There was a second rise in the number of eggs collected and in the level of dissolved oxygen before egg laying stopped in mid-November when levels of oxygen were low. A similar but less exact correspondence between number of eggs collected and levels of dissolved oxygen was found in the *C. saligna* area in 1979. Conversely, in 1980, oviposition began when levels of dissolved oxygen were falling in both areas, and reached a peak as the level of dissolved oxygen continued to fall.

#### DISCUSSION

Lungfish in the lake have been observed to spawn by day, and recently laid eggs are frequently found late in the morning in the river and the lake. This suggests that lungfish spawn during the day in these localities. This conflicts with the observation of Grigg (1965) who observed courtship behaviour in the evening and found eggs the following morning. Differences in timing are probably not important and more information may show that the time of oviposition is variable in both areas.

The significance of increased air breathing is also hard to assess. Normally this occurs rarely (Bancroft 1918 and Longman 1926). Possibly oxygen requirements are higher in the breeding season, or perhaps the sound made represents a "mating call" as Kesteven states (1944: 221). Johnels and Svensson (1955: 158) mention that "a



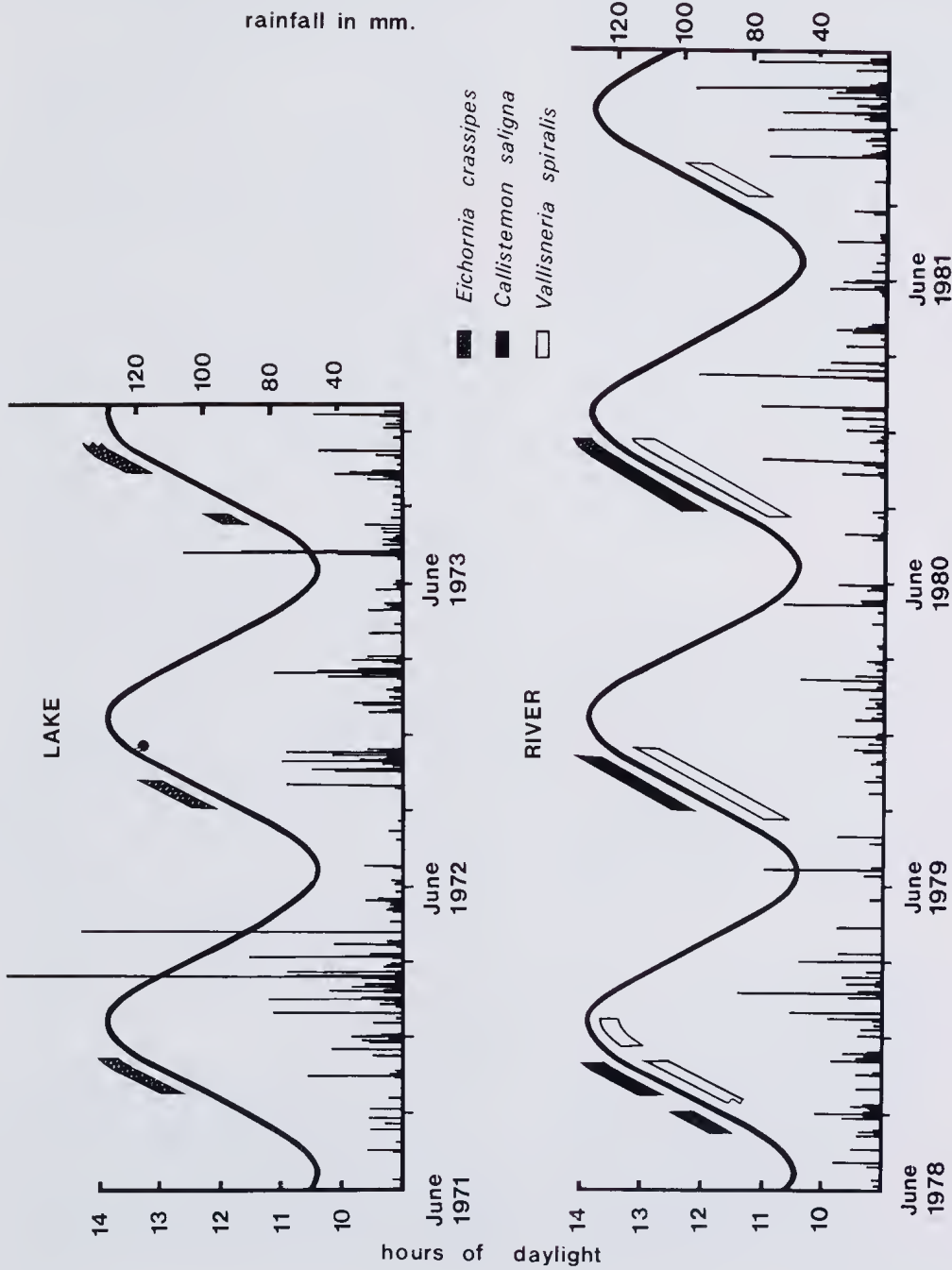


FIGURE 1. Hours of daylight, daily rainfall and duration of oviposition in Enoggera Reservoir (1971-73) and the Brisbane River (1978-1981). The first day of each third month is marked; rainfalls of less than 3 mm are not included; the start of oviposition is calculated by subtracting the age of the oldest eggs found from the date of collection, and the end from the last day on which new laid eggs were found.

substantial shrieking sound, which is very audible in the swamps" can occasionally be heard when *Protopterus annectens* breathes air, but they do not associate this sound with breeding behaviour. *Lepidosiren paradoxa* is supposed to be able to make a cry like a cat (Natterer, cited by Kerr 1900). Circling movements at the surface are presumably part of courtship, as eggs are actually laid when the fish are entwined. This has also been observed when lungfish have spawned in captivity (Hegedus 1970 and Moreno 1968).

*N. forsteri* does not build a nest, unlike the South American lungfish, *L. paradoxa* (Kerr 1900) or the African lungfish, *P. annectens* (Budgett 1901 and Johnels and Svensson 1955) and *P. aethiopicus* (Greenwood 1958). Also, unlike the males of other species of lungfish (Kerr 1900, Budgett 1901 and Johnels and Svensson 1955), *N. forsteri* does not appear to care for its young. There is little similarity in the breeding behaviour of the Australian lungfish and that of African or South American species except perhaps the laying of separate clutches of eggs in one place (Johnels and Svensson 1955). Whether this suggests that male *N. forsteri* have territories for oviposition which are visited by successive females for spawning, as appears to be the case in *P. annectens*, or whether it is fortuitous, remains to be seen.

Suitable weeds are available all the year round in the Brisbane River, but they occur seasonally in the lake, and this may affect the time of spawning in the latter area. In 1973 in the lake weed was available during the winter and early spring and in this year spawning first occurred in August and again in early October. Also, availability of suitable weed for oviposition for a long time may determine the length of the breeding season in the river. Presence of suitable weed is known to affect the timing of spawning in goldfish, *Carassius auratus* Linnaeus (Stacey, Cook and Peter 1979a).

Lungfish are specific in their choice of weeds for oviposition. In the lake, eggs are laid on *Eichornia crassipes* roots, and perhaps also on *Potamogeton javanicus* and para grass. In the river, eggs were found attached to submerged roots of *Callistemon saligna* or *Eichornia crassipes*, to *Vallisneria spiralis*, *Potamogeton perfoliatus*, *Nitella* sp. and *Hydrilla verticillata* plants, occasionally to *Ceratophyllum* associated with *C. saligna* or *V. spiralis*, and also on filamentous algae covering the *C. saligna* roots. Some weeds, like *Potamogeton crispus*, are not used for spawning, perhaps because they only

occur in fast flowing water. Weeds which do not form dense banks, e.g. *Nymphaea capensis* and *N. flava*, *Nymphoides indica*, *Ludwigia peploides* and *Rumex bidens*, which all have submerged stems, are likewise not used for egg laying. Some of the results reported here are in agreement with those of Semon (1893 and 1899), Bancroft (1911, 1918 and 1928) and Illidge (1893).

*P. aethiopicus* and *P. annectens* lay large numbers of eggs, several thousand in one season, in their nests (Budgett 1901, Greenwood 1958 and Johnels and Svensson 1955). This does not appear to be the case with *N. forsteri*, which produces hundreds of eggs at the most in the wild. In captivity, numbers of 200 and 500-600 eggs laid at one time have been reported (Hegedus 1970 and Moreno 1968).

Substrate and current may also be important in the choice of a spawning area. Eggs are found on weeds growing in areas with a slow or moderate current of fresh water, where there is a substrate of fine sand or gravel. Such areas provide a suitable micro-environment for the larva when it hatches i.e. a place to hide in dense cover, with readily available food. There is also an adequate level of dissolved oxygen maintained by plants which are carrying out photosynthesis. Eggs of other species of lungfish are laid in stagnant water with low oxygen tension (Greenwood 1958) and it appears to be necessary for the adult to agitate the water (Budgett 1901 and Greenwood 1958), or otherwise oxygenate it (Kerr 1900).

Eggs laid loose on the river bed were found once only, at the height of the spawning season. This is regarded as an abnormal feature, the result perhaps of crowding in the weed bed. The eggs may even have been washed into the exposed pools where they were found, after original deposition in the weed bed. Observations reported by Macleay (1884) at second hand that lungfish pair, scoop out an indentation in the mud, spawn there and remain together nearby have not been confirmed. Also, contrary to Spencer's (1925) results, eggs were found to be firmly attached to weeds in most cases and sometimes quite difficult to remove.

Successive collections of young eggs in the breeding areas followed by periods without newly laid eggs or without any eggs at all must reflect either individual fish becoming ready to breed or the same female spawning several times. The number of old eggs in lake collections is probably a result of delayed hatching in eggs from this source (Kemp 1981).

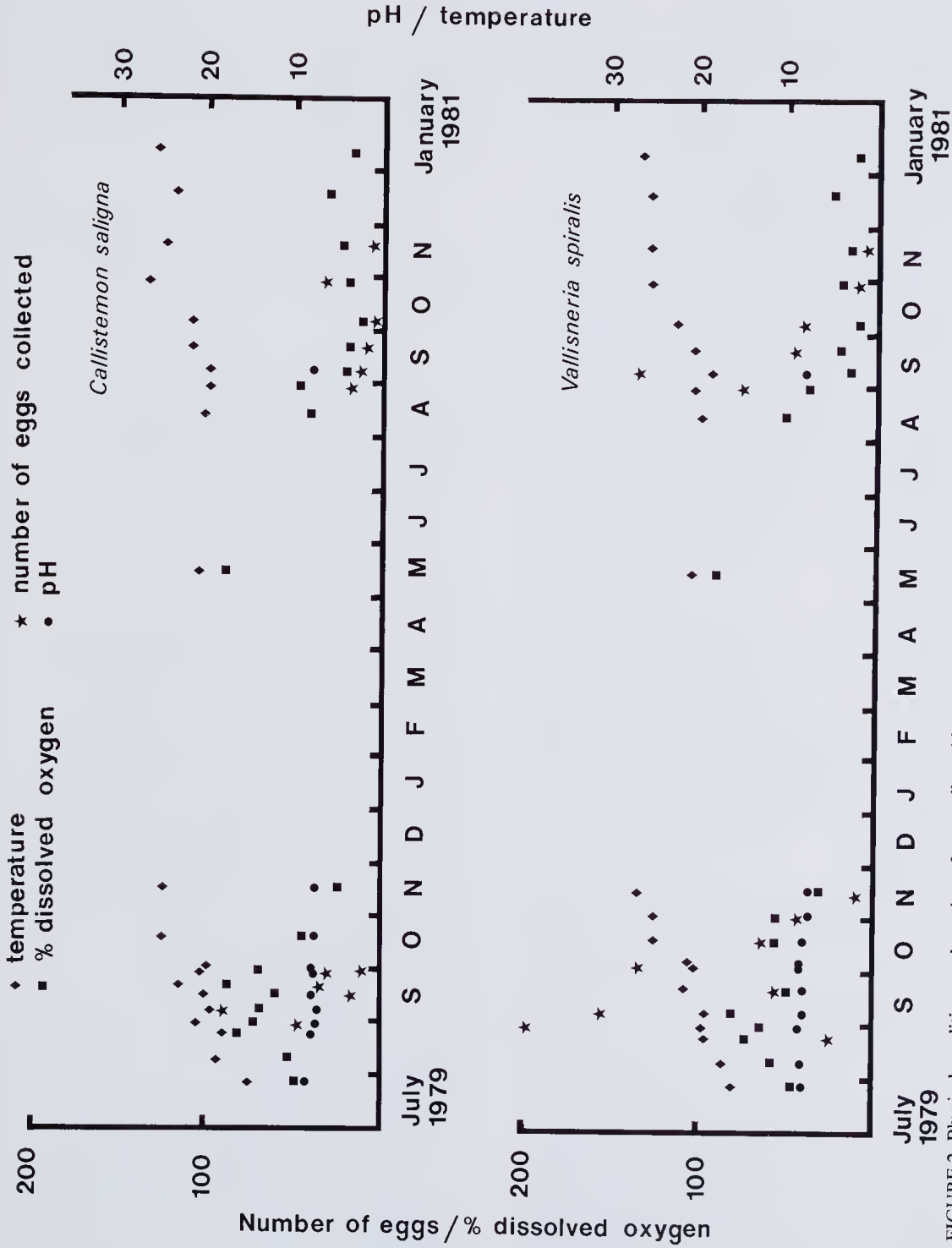


FIGURE 2. Physical conditions and number of eggs collected in 1979 and 1980 in two areas of the Brisbane River.

Differences in spawning times between the lake and the river are probably related to the availability of suitable weeds. As the season of 1973 showed, if weed is present spawning may occur in the lake as early as August, as it does in the river. Differences in breeding times between the lake, the river and more northerly river systems may arise for similar reasons.

Attempts to relate dissolved oxygen content of the water, temperature, pH and water level were inconclusive, but none of these factors appeared to act as a trigger for spawning. In one season, in the river, there was an apparent correlation between oviposition and a raised oxygen content in the water. However, in the following year, spawning occurred while oxygen content in the water was falling. Water levels fluctuated but did not appear to be related to spawning. Temperatures remain the same level in the months preceding spawning and in the early part of the breeding season, and pH stays the same throughout. There are no sudden changes of pH or temperature to correspond with the beginning of spawning, unlike the situation with certain other fish, e.g. *Carassius auratus* where temperature is involved in the stimulus for spawning (Stacey, Cook and Peter 1979a) and *Carassius klungingeri* (Lake 1967).

Breeding in the Australian lungfish appears to be associated with a rising photoperiod and with the presence of suitable aquatic weeds. Oviposition in the river and in the lake begins when the daylength has been increasing for up to 11 weeks, if suitable weeds are present. A similar situation has been reported in other fish (Stacey, Cook and Peter 1979a and b, Urasaki 1973 and Pike 1973).

Rainfall sufficient to flood the environment of the lungfish does not usually occur in the months before they spawn, and the fish lay eggs irrespective of rain. This differs from the behaviour of other fish, e.g. *Cyprinus carpio* (Pike 1973), or *Protopterus annectens* and *Lepidosiren paradoxa* which spawn when the dried out swamps where they aestivate are flooded (Kerr 1900 and Johnels and Svensson 1955) or *Protopterus aethiopicus* which breeds after rain (Greenwood 1958). Spawning in response to flood and a minimum temperature is an adaptive characteristic of some Australian freshwater fish e.g. the golden perch *Plectroplites ambiguus*, the silver perch *Bidyanus bidyanus* and the Murray cod *Maccullochella macquariensis*, all of which live in the Murray-Darling River system which often dries out to

become chains of water holes (Lake 1967). However, a response to flood is not to be expected in a species living in Enoggera Reservoir or the Brisbane River both of which have a permanent inflow of water. Most features of the oviposition of *N. forsteri* appear to be related to the particular environment.

#### ACKNOWLEDGMENTS

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A BIOGEOGRAPHICALLY SIGNIFICANT NEW SPECIES OF *LEIOLOPISMA*  
(SCINCIDAE) FROM NORTH EASTERN QUEENSLAND

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ABSTRACT

The rock-dwelling skink *Leiolopisma jigurru* sp. nov. is described from the summit of Mt Bartle Frere, on southern Cape York Peninsula, northeastern Queensland. The combinations of 30 mid-body scales and paired fronto-parietals distinguishes this species from all but one of its Australian congeners. Colour, pattern, and 4th toe lamellae count distinguish it from *L. entrecasteauxii*.

Zoogeographic studies of the vertebrates of Cape York Peninsula have focussed on the New Guinea influence and on the high proportion of endemic species in the area. The discovery of a species of *Leiolopisma* at 1620 m in tropical Queensland and separated from its congeners by a gap of 1500 km highlights a new aspect of the zoogeography of vertebrates of the Cape — 'temperate' taxa occurring as relicts in the tropics. The distribution of *Leiolopisma* species is paralleled in several other, mainly invertebrate, taxa.

*L. jigurru* sp. nov. shares many morphological features with other skinks confined to rock 'islands'.

The species is 'rare' but its habitat is well protected.

INTRODUCTION

In October — November 1981, curators from the Queensland Museum and 'Earthwatch' volunteers undertook an altitudinal survey of invertebrates of the Bellenden Ker Range, on southern Cape York Peninsula, northeastern Australia. (See definitions of Cape York Peninsula by Covacevich and Ingram 1980, and Covacevich et al. 1982). This range, the second highest in Australia, supports dense rainforest and has not been methodically surveyed before. During this survey, it was possible to collect frogs and reptiles on Mt Bartle Frere, the highest and most southern peak of the range. Amongst the material collected and now located in the Queensland Museum are two new species of skinks belonging to the genera *Lampropholis* and *Leiolopisma*. The *Lampropholis* sp. nov. occurs widely in the rainforests of the Bellenden Ker Range and is, along with other members of this genus, the subject of revision of Mr Mark Schuster of the University of New England.

Greer (1974, 1979) has discussed the relationships of the skinks, including those in the genera *Leiolopisma* and *Lampropholis*. He has shown that *Leiolopisma* spp. have alpha palates (with the inner edges of the palatal rami diverging posteriorly along the smooth curve) while

*Lampropholis* spp. have beta palates (with the rami having a large recurving process anteriorly). Such a major difference; Greer's (1974) diagnoses of the genera; Cogger's (1979) additional diagnostic feature of narrowly separated nasals for *Leiolopisma* vs widely separated nasals for *Lampropholis*; and the fact that *Leiolopisma* spp. are generally viviparous (Rawlinson 1976) while *Lampropholis* spp. lay eggs communally (Ingram, pers. comm.) suggest that assigning skinks to these two genera would be a simple task. Such is not the case however.

The palate in small skinks cannot be examined easily and there is considerable overlap in the characters used by Greer and Cogger to distinguish these genera. Further, Ingram and Ehmann (1981) have recently described an egg-laying species of *Leiolopisma*, *L. zia*, from southeastern Queensland and northeastern New South Wales. Examination of the karyotypes of most currently recognised species of *Leiolopisma* (including *L. jigurru*), *Lampropholis*, and most other genera in the *Eugongylus* group sheds no further light on the problem of separating *Leiolopisma* from *Lampropholis*. All species of *Leiolopisma* examined have 30 chromosomes and are very similar karyotypically. The only variation is in pairs 6–9 which is also a

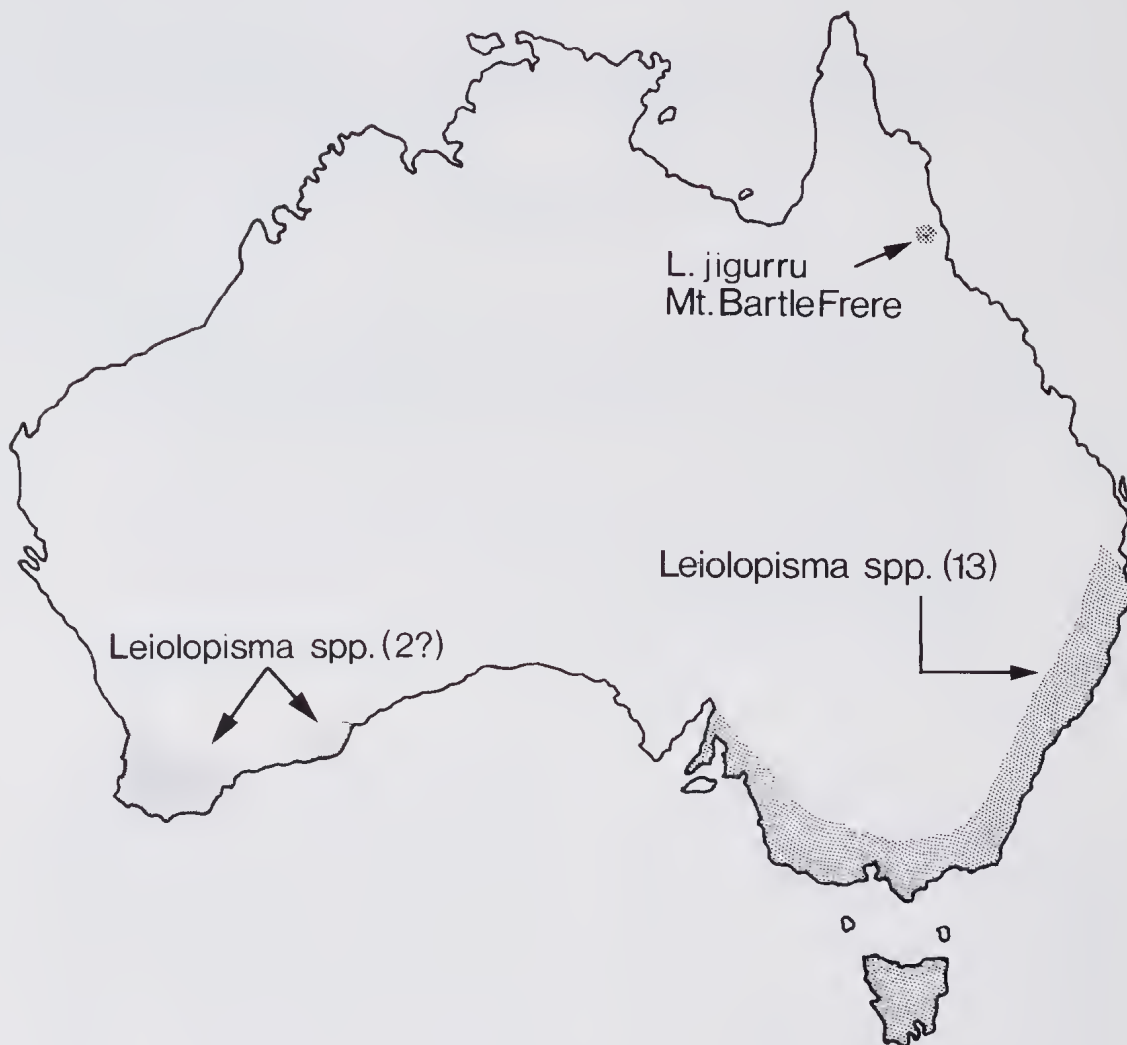


FIGURE 1: Occurrence of *Leiolopisma* species in Australia.

characteristic of *Lampropholis* spp. (S. Donellan, pers. comm.).

The Bartle Frere skink described here has an alpha palate, a characteristic of *Leiolopisma*. It also has the widely separated nasals of *Lampropholis*. The degree of separation of the nasals in *Leiolopisma* as presently defined apparently varies considerably (e.g. *L. zia*, narrow vs *L. trilineata*, wide, but not as wide as in the species described here). No data on breeding biology for this new species are available because only a handful of specimens are known.

In the light of this information it is reasonable to assign the Bartle Frere species to *Leiolopisma*.

*Leiolopisma jigurru* sp. nov.  
(Pls 1a, b; 2a, b; 3)

#### MATERIAL EXAMINED

Holotype: QM J40040, ♀, near summit of South Peak of Mt Bartle Frere, NE.Q., 1620 m, on granite boulders; J. Covacevich, R. McKay, D. Marshall; 7-8 Nov., 1981.

Paratypes: AM R95553, Mt Bartle Frere, 1524 m, 23 Jan., 1977; J39494-99, Northwest Peak of Mt Bartle Frere, 1440 m, under exfoliated granite, 7-8 Nov., 1981; J39492-3 as for holotype.



## DIAGNOSIS

A mid-body scale count of 30 and paired frontoparietal scales distinguishes *Leiopisma jigurru* from other Australian species of *Leiopisma* except *L. entrecasteauxii* (Dumeril and Bibron). *L. entrecasteauxii* has a lower lamellae under the 4th toe count (16–22) than *L. jigurru* (26–29) and lacks the distinctive dark brown to black, and white to cream colour pattern of *L. jigurru*.

Ten New Zealand species of *Leiopisma* have the combination of 30 mid-body scale rows and paired frontoparietals, but only 3 species also have a 4th toe subdigital lamellae count which overlaps with that of *L. jigurru*. These are *L. infrapunctatum* (Boulenger), *L. nigriplantare* (Peters), and *L. lineocellatum* (Dumeril and Dumeril). Colour and pattern quickly distinguish *L. jigurru* from these species. See Pl. 1a–b, 2a–b and Hardy (1977, figs 27, 30–32, 33).

## DESCRIPTION OF HOLOTYPE

Snout-vent length 68.9 mm, tail 126.3 mm; T/SVL% 183.3; tip of snout – forelimb/axilla – groin = 22.2/37.0 (.59); head width 7.5 mm.

Head slender. Rostral broad, in contact with the nasals and frontonasal. Frontonasal broader than long, bordered by two large prefrontals which do not meet. Frontal twice as long as broad, narrow posteriorly, and equal in length to the frontoparietals and parietal together. Frontal in contact with first and second supraocular. Supraoculars 4, the second largest and the fourth smallest. Seven supraciliaries. Two frontoparietals, which are distinct from and larger than interparietal. Seven supralabials, 5th largest and, with sixth, contacting eye. Lower eyelid scaly with a large oval palpebral disc. Ear opening large, nearly round, with a deeply set tympanum, and without auricular lobules.

Mid-body scales 30. Mid-dorsal scales slightly larger than ventral and lateral scales, and lightly striated. Limbs and digits long. Twenty-six lamellae under 4th toe.

Colour (in life): Basically brown and black dorsally and cream ventrally, with a metallic sheen. See Pl. 1a, b. and 2a, b for distinctive pattern.

## VARIATION IN THE PARATYPES

SVL 34.5 – 67.2, Tail 63.5 – 115.5 (part of the tail of J39495 has been lost), tip of snout – forelimb/axilla – groin .54 – .88, head width 4.5 – 8.2, T/SVL 135 – 189%. There is little variation.

Lamellae under the fourth toe, 27–29. In six paratypes there are 8 supraciliaries. One specimen (J39492) has an extruded columnar hemipenis.

## DISTRIBUTION AND HABITAT

*Leiopisma jigurru* is known from only one locality – Mt. Bartle Frere, on southern Cape York Peninsula, NE.Q. It is found amongst granite boulders which occur as large ‘fields’ surrounded by dense rainforest near the mountain summit. Specimens were collected at 1440 m, 1524 m, and 1620 m. The type locality is cool to cold throughout the year and is frequently covered in mist. Climatic data are not recorded on Mt Bartle Frere but average annual rainfall (1974–1980) on the adjoining peak, Mt Bellenden Ker (1560 m), is 7736 mm. In early November, 1981 when all but one of the skins in the type series were collected, daily temperatures ranged from 7° – 20°C.

## ETYMOLOGY

‘Jigurru’ is both the Mamu and the Ngajan name for this lizard, according to Molly Ramond and George Watson, the last people to speak these languages well. Their people lived in the rainforest country at the headwaters of the Mulgrave and Russell Rivers on the slopes of the Bellenden Ker Range and their territories overlapped in the high mountains such as Bartle Frere. ‘For more than ten thousand years they lived in harmony ... with their environment. One hundred years ago many of them were shot and poisoned ...’ (Dixon, 1972).

## DISCUSSION

Biogeographic studies of the herpetofauna of Cape York Peninsula have focussed on Pleistocene New Guinea migrations and on the high proportion of taxa endemic to the area (e.g. Keast 1959; Storr 1964; Tyler 1972; Covacevich and Ingram 1980; Kikkawa et al. 1981; Covacevich et al. 1982). The discovery of *Leiopisma jigurru* on the ‘temperate’ summit of Mt. Bartle Frere on southern Cape York Peninsula in tropical Queensland highlights another aspect of its biogeography.

Several taxa whose present distribution is concentrated in the southern, temperate zones of Australia, are known to have relict representatives in cool, montane habitats in the tropics. This pattern has been observed for certain landsnails (Ohdner 1917) and plants and insects (Monteith 1980, Storey 1983) but has not

been previously recorded for vertebrates. Spiders (Gradungulidae, Migidae) and the marsupial *Antechinus stuartii* also have similar distributions. (V. Davies, S. Van Dyck, pers. comm.). The occurrence of *Leiolopisma* spp. is of special interest because, with the discovery of *L. jigurru*, it is a parallel of the southeastern Australia — montane northeastern Queensland — New Caledonia — New Zealand occurrence noted for some insects and plants (Monteith, 1980).

Forty-two species of *Leiolopisma* are now recognised. They occur in Tasmania, Lord Howe Island, mainland southeastern and southwestern Australia; New Zealand and the Chatham Islands; New Caledonia and the Loyalty Islands; and Mauritius (Greer 1979). The present 'stronghold' for the genus is temperate southeastern Australia — New Zealand (Hardy 1977). The Australian distribution of members of this genus is shown in Fig. 1. There is a gap of some 1500 km between the Mt Bartle Frere population of *L. jigurru* and the other two species occurring in Queensland, *L. platynota* (Peters) and *L. zia* Ingram and Ehmann, both of which occur in Queensland only at high altitudes in the extreme southeast of the state. *L. platynota* has a fairly broad coastal distribution from southeastern Queensland to northeastern Victoria (Cogger 1979). *L. zia*, on the other hand, is restricted to high altitude (above 1000 m) rainforests and Antarctic Beech (*Nothofagus*) forests of southeastern Queensland and northeastern New South Wales (Ingram and Ehmann 1981).

Greer (1974) has suggested a southern, Tasmanian/southeastern Australian, centre of diversity for *Leiolopisma*. Hardy (1977) revised New Zealand species of the genus and suggested a northern, New Guinean, centre of diversity. The discovery of the temperate relict species, *Leiolopisma jigurru*, in tropical Queensland may be used to support either hypothesis.

*L. jigurru*, is an agile and fast-moving posturing heliotherm like other lygosomine skinks endemic to isolated rocky areas. It is a typical rock dweller in being flattened dorsoventrally, large in relation to its congeners, and in having long digits and limbs and a highly achromatic pattern (Covacevich and Ingram 1980).

Frog and reptile species have been described as 'rare' for conservation purposes if they are known from 20 or less museum specimens or from five or less localities (Covacevich, et al. 1982). *L. jigurru*, qualifies as a 'rare' species on

both counts, but is well protected. The type locality and other potential habitats on the Bellenden Ker Range lie in State Forest and National Park.

#### ACKNOWLEDGMENTS

'Earthwatch' is a private, American-based, non-profit organization which makes available volunteer workers to assist research programmes involving field expeditions. Without the support of 'Earthwatch', *L. jigurru* would not have been collected. Dr G. Monteith led the expedition and made the trip to Bartle Frere possible.

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## PLATE 1

a,b *Leiopisma jigurru* sp. nov. from the summit of Mt Bartle Frere, NE.Q., showing highly achromatic pattern, dorsoventral flattening, and long digits.



## PLATE 2

- a Close-up lateral view of *L. jigurru* sp. nov. showing ear opening, eye detail and colour pattern.
- b Dorsal view of head scales of *L. jigurru* sp. nov.



a



b

## PLATE 3

Mist-covered granite boulders near the summit of Mt. Bartle Frere,  
type locality of the temperate relict, *L. jigurru* sp. nov.







DINOSAUR TRACKWAYS IN THE WINTON FORMATION (MID-CRETACEOUS)  
OF QUEENSLAND

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ABSTRACT

Dinosaur trackways have been discovered at several closely-grouped sites in mid-Cretaceous sediments of the Winton Formation, central W. Queensland. At one of these sites about 209 m<sup>2</sup> of bedding plane was exposed to reveal trackways of more than 150 bipedal dinosaurs. One of these trackways is very much larger than any of the others; it is attributed to a large theropod dinosaur (carnosaur) and is identified as cf. *Tyrannosauropus*. The remaining trackways are referred to two new ichnotaxa — *Wintonopus latomorum* and *Skartopus australis* — which are attributed to ornithopods and coelurosaurs (respectively). The sizes of the track-makers are estimated by means of allometric equations derived from osteological data; the speeds of the track-makers are estimated by using the mathematical relationships of size, speed and gait that have been determined for living tetrapods. The carnosaur is estimated to have been about 2.6 m high at the hip, and to have been walking at a speed of about 7 km/h. The ornithopod track-makers ranged from 14 to 158 cm in height at the hip; these animals were using a fast running gait equivalent to cantering or galloping in mammals, and their mean speed is estimated at 16 km/h. The coelurosaur track-makers ranged from 13 to 22 cm in height at the hip; these too were using a fast running gait, and their mean speed is estimated to have been 12 km/h. The trackways of the ornithopods and coelurosaurs are interpreted as those of animals caught up in a stampede — which was presumably triggered by the approach of the carnosaur. It is suggested that relative stride length (i.e. stride length relative to height at the hip) is the best available criterion for appraising the locomotor performances of dinosaurian track-makers. By this criterion the performances of the Winton ornithopods and coelurosaurs are outstandingly good. There is an indication that these animals were running at or near their maximum speeds — with relative stride lengths in the range 3.9 to 5.0. If the most highly adapted of cursorial dinosaurs (the ornithomimids or 'ostrich dinosaurs') attained such figures for relative stride length their speeds would have been up to about 60 km/h.

INTRODUCTION

In June 1976 Mr Ron McKenzie showed us some well-preserved dinosaur footprints that he had collected from a site about 120 km SW of Winton, central west Queensland. The footprint site, which was later named Seymour Quarry, was in sediments of the Winton Formation (mid-Cretaceous) and its existence was known to many residents in the Winton area. In 1971 a small field party including Dr R.H. Tedford (American Museum of Natural History) and Dr A. Bartholomai (Queensland Museum) paid a brief visit to the site; this party established that the footprint horizon extended to a second site some 100 metres away (Knowles 1980). This second

site, which was later named Lark Quarry, subsequently proved to be of very great interest.

The footprints at these localities attracted our attention because of their abundance, their excellent preservation and their remarkably small size (by dinosaurian standards). In 1976 we carried out preliminary excavations at both sites, and in the following year a large labour-force of volunteers co-operated in a major excavation at Lark Quarry. This excavation revealed several thousands of footprints representing the trackways of well over 100 bipedal dinosaurs -- many of them apparently no bigger than chickens. In preliminary accounts the Lark Quarry trackways have been interpreted as

evidence of a dinosaur stampede (Thulborn and Wade 1979, Wade 1979). If this interpretation is correct it may carry important implications for current understanding of dinosaur biology. The present work has three aims: 1) to provide a systematic account of the trackways at Lark Quarry and its surroundings; 2) to offer some interpretations regarding the sizes, speeds and behaviour of the track-makers; 3) to justify those interpretations and to consider their implications for the understanding of dinosaur biology.

#### LOCALITIES

The footprints described in this paper were found at three localities on Mt Cameron property, SW of the town of Winton in central west Queensland. About 95 km SW of Winton the road to Jundah and Stonehenge runs along the crest of a west-facing scarp (the Tully Range) which is formed by sediments of the Winton Formation capped by duricrust. The localities are close to the foot of the scarp, alongside a track leading NW to Cork Station. The maximum distance between any two of the localities is about 200 m (see map, Fig. 1).

*Seymour Quarry.* A deep hillside cutting alongside the track to Cork Station. The site is identified as an opal mine on the Brighton Downs sheet of the BMR 1:250,000 series of geological maps (sheet SF/54-15; map reference 23°01'S, 142°24'W). Footprints occur as natural casts below a thin bed of red arkosic sandstone that outcrops at the foot of the hill. This friable sandstone overlies a weathered mudstone, and its lower surface is infiltrated by dark brown ironstone which prevents the footprints from crumbling on exposure. Traces of plant rootlets are preserved along with the footprints, while these themselves are very well preserved and may even show indications of skin texture (see p. 422, Pl. 1). The footprints are attributed to small bipedal dinosaurs of two types (coelurosaur and ornithomimid), and they appear to represent continuations of trackways at another site to the SW (Lark Quarry). This first site is named for Mr Glen Seymour, its discoverer and former manager of Cork Station.

*Lark Quarry* (Pl. 3). A large excavation revealing more than 200 m<sup>2</sup> of a single bedding plane. This site is located to the SW of Seymour Quarry, and has been the subject of preliminary descriptions (Thulborn and Wade 1979, Wade 1979). The Lark Quarry bedding plane carries well over 3000 footprints, representing the trackways of at least 150 bipedal dinosaurs. The

trackways are almost entirely unidirectional: one track-maker was headed to the SW, whereas all the others were headed to the NE (in the direction of the present Seymour Quarry). The footprints occur as natural moulds in a bed of laminated claystone which varies between 6 and 12 cm in thickness. The footprint itself will be referred to as a mould, and the filling of the footprint as a cast, in conformity with standard ichnological usage. The claystone is generally bright pink in colour (though individual laminae range from pink through red to purple), and its upper surface appears to be stained dark red-brown by ironstone infiltration. This 'surface stain' is in fact an extremely thin adhesion from the base of the overlying sandstone. Below the claystone is a thick bed of arkosic sandstone; this is buff in colour and finely cross-bedded. Similar sandstone/claystone couplets occur above and below the trackway horizon. The next claystone bed below the trackway horizon also bears footprints in the form of natural moulds, though these are uncommon and seem to have no preferred orientation. The footprint horizon at Seymour Quarry seems to be an extension of the main trackway surface at Lark Quarry; it is possible to trace the footprint horizon through intermediate outcrops, though there is a complete break of about 30 metres caused by a creek bed. Moreover there is a uniform dip to the NW of about 4°, and by taking direct line of sight along the Lark Quarry bedding plane this will be found to coincide with the footprint horizon at Seymour Quarry. It may be mentioned that the reverse procedure (extrapolating the dip of the beds at Seymour Quarry) was used to locate the Lark Quarry trackways in the first instance (Knowles 1980). At both sites the footprints are similar in diversity, in abundance, in morphology and in their singular orientation. Lark Quarry has been designated an Environmental Park by the National Parks and Wildlife Service, Queensland, and is now roofed for its protection. The site is named for Mr Malcolm Lark, of Miles, who played a leading role in its excavation.

*New Quarry.* One of a series of small hillside exposures scattered from 100 to about 120 m due S of Lark Quarry. At the New Quarry site the trackway of a single bipedal dinosaur was measured *in situ*. In its preservation this trackway is identical to those at Lark Quarry. There is a major erosional gap between New Quarry and Lark Quarry, but at both sites the footprints occur at equivalent levels in similar sequences of sandstone/claystone couplets. Moreover at both

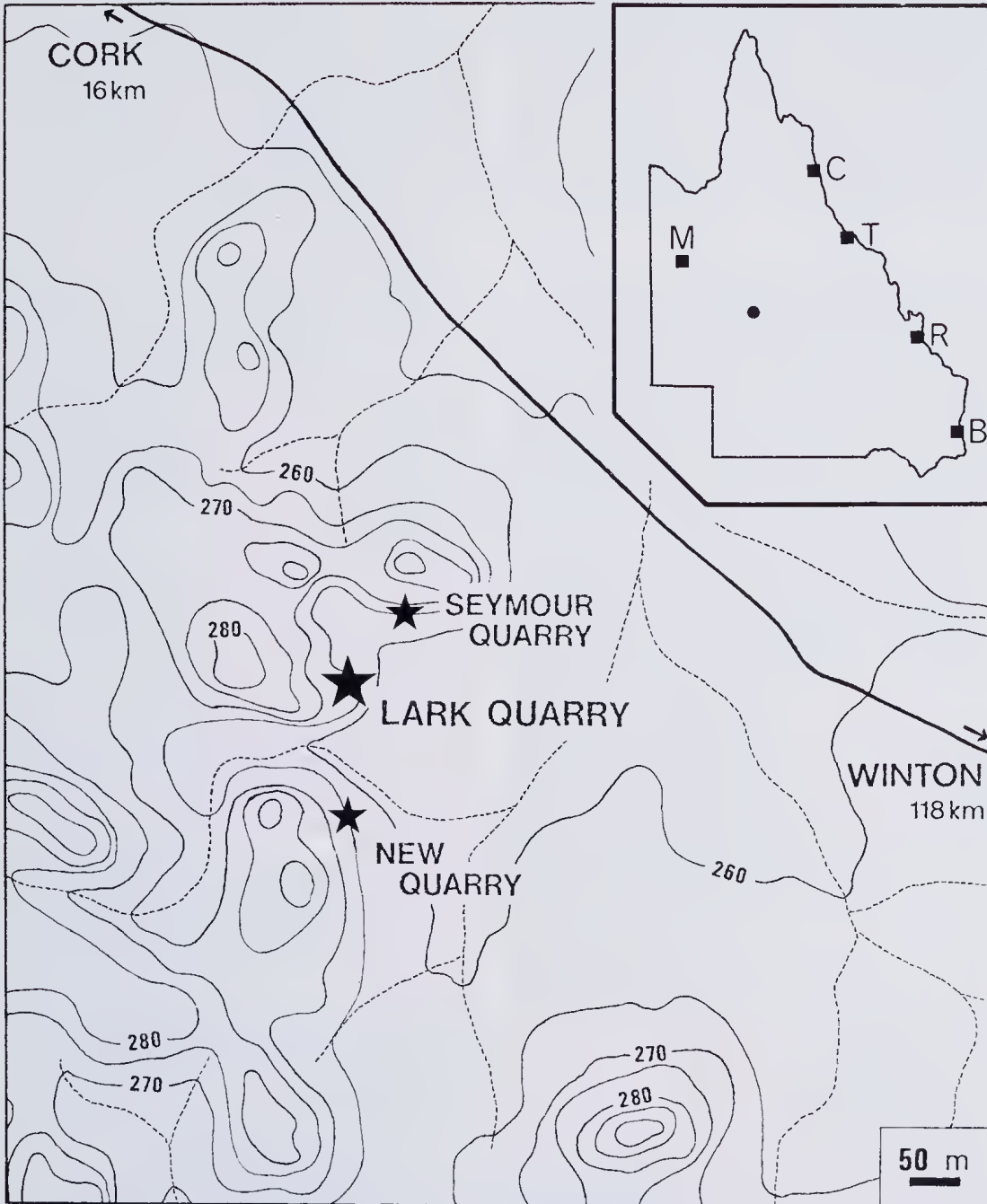


FIGURE 1. Map showing location of footprint sites. Contours are at 5 m intervals, and dashed lines indicate dry creek-beds. Inset map shows location of quarry in Queensland. B, Brisbane; C, Cairns; M, Mt. Isa; R, Rockhampton; T, Townsville.

sites there is a marked change in sediment type about 5 or 6 m above the footprints — the appearance of a yellowish arkose containing scattered plant fragments. The evidence is not conclusive, but it suggests that the New Quarry trackway is at about the same stratigraphic level as the Lark Quarry trackways. Footprints also occur in the next claystone layer below the New Quarry trackway; at this lower level the claystone is thoroughly trampled and churned up by deep footprints without preferred orientation.

## METHODS

### EXCAVATION AND COLLECTION OF FOOTPRINTS

At Seymour Quarry the footprint horizon was reached by digging through the overburden of soil and weathered rock. The thin sandstone layer bearing the footprints (natural casts) proved rather fragile; most footprints collected from this site are on small slabs or are in the form of detached casts (see Pl. 1). One large slab (QM F12266) is approximately 95 by 40 cm and carries casts of at least 28 footprints — representing about 19 trackways.

At Lark Quarry the footprints were exposed by breaking up and removing a thick overburden of sandstone. Fortunately the sandstone was well jointed (as is the footprint surface — see Pl. 4), and it could be removed in blocks once these had been levered out with crowbars and jack-hammer. About 60 tons of overburden was removed, exposing an area of more than 209 m<sup>2</sup>. It was then necessary to clean the footprints (natural moulds) by removing the sandstone that filled them. This sandstone filling was soft enough to be broken up with an awl. At the bottom of each footprint mould the colour of the sandstone filling changed from orange-red to bright yellow-green — a useful guide to ensuring that the footprints were fully excavated. More than 3300 footprints were exposed and cleaned in this way. A portion of the footprint bed was removed from the eroded NE margin of the site and was transferred to the Queensland Museum (QM F10321). In addition several individual footprints were collected — including holotypes of the new ichnotaxa described below.

### FIBREGLASS REPLICAS

After the Lark Quarry bedding plane had been exposed, and its footprints were thoroughly excavated, it was swept free of dust and rock debris; large parts of the bedding plane were then coated with liquid latex, which was reinforced with a cloth backing. Once it had set, the latex was stripped off in the form of large 'peels'

(Wade 1979). These latex 'peels' were later used as a basis for moulding a fibreglass replica of the bedding plane and its footprints. The entire area shown in Fig. 3 was included in this replica. Individual footprints were also replicated (see, for example, Pl. 5, Fig. A). These high-fidelity replicas are much lighter and more durable than plaster casts; they enabled us to undertake a long-term study of the Lark Quarry footprints, even though our total expenditure of time at the site was no more than a few weeks.

### ILLUSTRATIONS

The Lark Quarry bedding plane is almost horizontal, and its footprints are under natural low-angle lighting for only a few minutes after dawn and before dusk. Even at these times of day it may be difficult to obtain worthwhile photographs because the direction and intensity of lighting cannot be adjusted. We obtained few good quality photographs of individual footprints *in situ*. Most of our illustrations (Pl. 5 to 16) show fibreglass replicas of the footprints — though some do show original material (including type specimens; see plate captions).

Most of the area exposed at Lark Quarry was marked out with a grid of chalk lines, and each quadrat was photographed from a height of 1 metre (with the camera mounted on a rigid iron frame). The resulting photographs were then assembled into an accurate and detailed photomosaic — a representative portion of which is reproduced as Pl. 4. The same photographs were later used in drawing up a chart to show the distribution of footprints at Lark Quarry (Pl. 17).

### DESCRIPTIONS

There are no universally accepted methods for describing footprints and trackways (Sarjeant 1975, Leonardi 1979a), and it is necessary to define the measurements and statistics we employ. All linear measurements are expressed in centimetres.

*Footprint length* (abbreviation FL) — the maximum footprint dimension measured along, or parallel to, the axis of the longest digit (see Figs. 2A, B).

*Footprint width* (FW) — the maximum footprint dimension measured at a right angle to footprint length (Figs. 2A, B).

The ratio *footprint width / footprint length* (ratio FW/FL) is used to express footprint proportions.

We discovered that FL and FW were quite variable within each trackway, so that neither of these measurements could be regarded as a completely reliable indicator of the track-maker's

size. Consequently we calculated an *index of footprint size* (SI) for each footprint:

$$SI = (FL \times FW)^{0.5}$$

This index was found to be remarkably consistent within each trackway, and it seems to be a useful guide to the relative sizes of two or more track-makers. The index is expressed in centimetres.

*Interdigital angles* (expressing divarication of digits) are commonly cited in descriptions of vertebrate footprints, but they are difficult to measure consistently (see Sarjeant 1975) and are often so variable that they are of questionable value (see comments of Welles 1971). We have not attempted to compile detailed measurements of interdigital angles, and they will be mentioned only as approximate averages.

*Pace length* (PL) — the distance between corresponding points in two successive footprints (left and right, or right and left; see Fig. 2C).

*Stride length* (SL) — the distance between corresponding points in two successive prints of a single foot (see Fig. 2C).

With measurements of two successive paces (PL<sup>a</sup> and PL<sup>b</sup>), and of the stride (SL) that they encompass, it is possible to calculate *pace angulation* (ANG) as follows:

$$\cos \text{ANG} = \frac{(PL^a)^2 + (PL^b)^2 - (SL)^2}{2 \times (PL^a) \times (PL^b)}$$

The more nearly pace angulation approaches to 180° the narrower is the trackway and the less obvious is the zig-zag arrangement of its footprints (see Fig. 2C).

The ratios *pace length / footprint length* (PL/FL) and *stride length / footprint length* (SL/FL) are often used in definitions of ichnotaxa (see, for example, Lull 1953, Haubold 1971) and are also provided here. These ratios tend to increase as a track-maker accelerates, and they can therefore give a useful indication of a track-maker's gait. In calculating these ratios FL was taken to be the mean for the two footprints defining each pace or stride.

To calculate means and other statistics it was usually necessary to reduce sample sizes (N) by excluding data from damaged or badly distorted footprints.

## DESCRIPTIONS

At first glance the dinosaur trackways at Lark Quarry present a rather confusing picture (Pl. 4). However, it soon becomes apparent that the trackways can be sorted into several natural groups on the basis of size, orientation, preservation and footprint shape. Five such groupings may be recognized.

A. Remnants of a few trackways made by fairly large bipedal dinosaurs. These remnants comprise scattered footprints which are very poorly preserved and have no preferred orientation. The footprints appear to have been tridactyl, with rather short, thick and bluntly-rounded toes, and they are tentatively attributed to ornithopod dinosaurs. They seem to have been formed, then eroded and filled with water-laid sediment, well before the substrate was exposed to the air and the other footprints were formed at Lark Quarry. It was not possible to obtain any accurate measurements, and these remnants of old trackways will not be considered further.

B. A single trackway of a medium-size bipedal dinosaur (B in Fig. 3). This trackway extends across the southern part of Lark Quarry from WSW to ENE, and is attributed to an ornithopod dinosaur. The tridactyl footprints have relatively short, broad and well-rounded digits (see example *a* in Fig. 4) and are referred to the same ichnotaxon as the many small footprints in group *D* (below). However, this trackway is much larger than any of those in group *D*, and it was certainly formed at an earlier date: some of its footprints were deeply impressed in soft waterlogged mud and others (in lower-lying areas) were partly destroyed by scouring. This trackway seems to have been formed at about the time the substrate was draining free of surface water and was becoming exposed to the air.

C. A single trackway of an exceptionally large bipedal dinosaur (C in Fig. 3). This trackway extends across the northern part of Lark Quarry from NE to SW, and is attributed to a carnosaur — a large representative of the Theropoda. The footprints are very obvious basin-like structures (Pl. 5, Fig. B), and some of them show clear traces of three tapering or V-shaped digits (Fig. 4).

D. Numerous trackways of small to medium-sized bipedal dinosaurs; extending from SW to NE (Fig. 3, Pl. 4). The footprints are well preserved and each of them comprises three fairly short, thick and bluntly rounded digits. These trackways are attributed to ornithopod dinosaurs, and their footprints may be found superimposed upon those of the carnosaur (*C*, above) and upon those of coelurosaurs (*E*, below).

E. Numerous trackways of small (and sometimes very small) bipedal dinosaurs; extending from SW to NE (Fig. 3, Pl. 4). Each of these trackways comprises footprints with three fairly long, narrow and sharply-pointed digits. The trackways are attributed to coelurosaurs (small dinosaurs of the suborder Theropoda), and

their footprints may be found superimposed upon those of the carnosaur (*C*) and upon those of the ornithopods (group *D*).

Footprints in the latter three groups are equally well preserved, and all of them seem to have been formed at about the same time. These footprints were formed after the muddy substrate had been exposed long enough to have attained a firm plastic consistency. From the evidence of superimposed footprints it is clear that the carnosaur traversed the Lark Quarry area before some, at least, of the ornithopods and coelurosaurs did so.

The trackways attributed to ornithopods (group *D*) and coelurosaurs (group *E*) extend in a single direction, and among them it is common to find trackways coinciding, intersecting at low angles, or weaving together inextricably (Pl. 4 and 14). Moreover in some places the trackways of small, and even medium-size, individuals quite simply disappear: apparently these smaller dinosaurs were so light that their feet failed to break through the firmer patches of surface sediment. These discontinuities are especially noticeable among the coelurosaur trackways (group *E*); the coelurosaur track-makers seem to have had relatively large feet (by comparison with the ornithopod track-makers), and their widely-spread and probably rather springy toes seem to have functioned as analogues of snow-shoes. Many of the track-makers, both ornithopods and coelurosaurs, seem to have been roughly similar in size (the majority having hip height estimated at less than 50 cm), and the footprints in any one trackway are not always consistent in their shape or spacing. This combination of factors makes it difficult to trace any single trackway, with confidence, for more than a few strides. Consequently our descriptions and analyses are based, in the main, on relatively short sections of trackways. For the ornithopod dinosaurs (group *D*) we examined 57 sections of trackways; on average each of these comprises 3 strides (a sequence of 5 footprints). The longest section of ornithopod trackway studied here comprises 17 strides (a sequence of 19 footprints). For the coelurosaurs (group *E*) we examined 34 sections of trackways; here the average number of strides per section of trackway is between 3 and 4 (between 5 and 6 footprints). The longest section of coelurosaur trackway studied here comprises 22 strides (a sequence of 24 footprints). The difference in sample size (57 ornithopod trackways as opposed to 34 coelurosaur trackways) does not indicate that ornithopods

were more abundant than coelurosaurs. On the contrary, the ornithopod track-makers were probably outnumbered by the coelurosaur track-makers (see p. 443). The sample sizes differ for two reasons. First, the coelurosaur trackways are affected by so many discontinuities that it is difficult to find sequences of more than a few paces. Second, the coelurosaur footprints show much less variation in size and shape than do the ornithopod footprints: coincident or intersecting trackways of ornithopods could usually be separated through differences in footprint size or footprint shape, but coincident or intersecting trackways of coelurosaurs were usually inextricable.

The trackways of the carnosaur, the ornithopods and the coelurosaurs are described in turn. But before proceeding to these descriptions it will be useful to consider the circumstances under which the trackways were formed. It is important to determine these circumstances because some of them (e.g. the consistency of the substrate) have a direct bearing on footprint morphology, while others (e.g. the physical geography) are pertinent to the behaviour of the track-makers.

The Winton Formation is a series of continental sediments that reaches a thickness of more than 1000 feet in the area around Winton (Casey 1966). The sediments are mainly sandstones, siltstones and mudstones, though there are some intraformational conglomerates and coal seams. Fragments of fossil wood are common, but other well preserved fossils are rare; these include angiosperm leaves, conifers, freshwater bivalves, lungfish toothplates and fragmentary remains of sauropod dinosaurs (Senior, Mond and Harrison 1978, Coombs and Molnar 1981). The Winton Formation is mid-Cretaceous in age (probably uppermost Albian to Cenomanian), and the conditions under which its sediments accumulated were well summarized by Senior et al. (1978, p. 15): 'Terrestrial-fluviatile, paludal, lacustrine. Low relief, wide river flats, local development of short lived lakes and swamps.'

The sediments at and around Lark Quarry are of lacustrine and fluviatile origin. At the time the dinosaur trackways were formed the Lark Quarry site seems to have represented part of a major drainage channel; it was most probably part of a platform lying on point bar deposits, a sand-spit, that had built out into a lake which deepened to the SW (see Fig. 25A). The Lark Quarry bedding plane now dips NW at 4°, but it originally had a



run-off to the SW — as is indicated by the orientation of drag marks and prod-marks produced by floating vegetation (Pl. 4). At times of flood the lake would have spread over a wide area (including all three footprint localities) to deposit sand followed by muddy sediments. In the intervening periods the lake would have receded to become little more than a remnant water-hole surrounded by newly-exposed mud. It was during such a period that the trackways seem to have been formed.

The mud began to compact under water, and before it was fully exposed a single dinosaur traversed the southern part of the future Lark Quarry site from WSW to ENE. In this trackway (B) some footprints were formed as the animal crossed slightly elevated and newly-exposed patches of very soft sediment; the other footprints were formed in lower-lying areas of mud which were still covered by water. These lower-lying footprints were subsequently scoured and eroded as the remaining surface water drained off to the SW. At the future site of Lark Quarry the recently-laid sand and overlying mud were penetrated by narrow, vertical and unbranched tubes that probably mark the escape of buried arthropods (Pl. 2, Fig. B). Traces of similar escape burrows may be found at the Seymour Quarry site, along with horizontal and oblique tubular structures that seem to represent plant rootlets of various sizes (Pl. 1, Figs. A, B). The presence of plant rootlets might indicate that the mud was exposed sufficiently long for terrestrial vegetation to take hold. After the mud had been exposed for some time it was traversed by a single carnosaur and by numerous ornithopods and coelurosaurs (trackway groups C, D and E above). The mud was exposed long enough to achieve a firm plastic consistency, but not long enough for desiccation cracks to appear. The period of exposure would certainly have been a matter of hours, if not of days or weeks. Evidently the mud was not waterlogged at the time it was traversed by the dinosaurs: none of the thousands of footprints collapsed or slumped after withdrawal of the track-maker's foot. Nor does the mud seem to have been very tenacious, for there are very few instances in which it adhered to a track-maker's foot. In one of these (footprint No. 8 in Fig. 4) the mud adhering to the underside of a single toe was drawn up into a longitudinal crest; in another (Pl. 8, Fig. C) mud adhered to one toe in the form of a 'cusp' or 'bubble-like' structure. However, we suspect that in many cases the imprints of one or more digits have been narrowed by suction created during

withdrawal of the track-maker's foot. Overall it seems that the mud may have had the consistency of potter's clay at the time it was traversed by the dinosaurs.

### CARNOSAUR TRACKWAY

Ichnogenus cf. *Tyrannosauropus* Haubold 1971

Eleven footprints at Lark Quarry are far bigger than any others, and form a single trackway extending from NE to SW (Figs 3 and 4, Pls 4 to 6). This trackway is attributed to a carnosaur — a large bipedal predator of the dinosaur suborder Theropoda (order Saurischia).

It was not feasible to collect any of the carnosaur footprints, for to do so it would have been necessary to destroy many other trackways. In any case, the footprints do not show sufficient detail to warrant their assignment to any new or existing ichnospecies. Measurements of the carnosaur trackway were taken directly from the bedding plane at Lark Quarry and were checked on fibreglass replicas (QM F10322) at the Queensland Museum.

#### DESCRIPTION.

The trackway comprises deep, basin-like and rather 'messy' footprints, often with poorly defined margins. Evidently the track-maker's feet plunged right through the muddy surface layer and churned up the underlying sandy sediment. In most cases the impact of the foot caused sediment to bulge up between the toes and behind the foot to leave a prominent raised rim to the footprint (Pl. 5, Fig. B). The sandy sediment in the floor of the footprint is usually raised into a series of irregular ripples. Two of the carnosaur footprints have been illustrated elsewhere (Thulborn and Wade 1979, fig. 2), and two more examples are shown here (Pls 5 and 6). The following description is a generalized one, based on information from all better-preserved footprints in the trackway.

Each footprint is tridactyl, with clear imprints of digits 2, 3 and 4, but with no trace of the hallux (digit 1). The three digits are relatively short, emerging from a large basin-like depression representing a 'sole' or 'pad' to the foot; in footprint No. 3, for example, the length of digit 3, as a free entity, represents only about 41% of total footprint length (Pl. 5, Fig. A). The digits are usually quite sharply defined, but often there is no clear outline to the back of the foot, making it difficult to obtain a measurement of total footprint length (see, for example, Pl. 5). All the better-preserved footprints are slightly narrower

than long, with footprint width equivalent to some 85–90% of footprint length. The digits are broad and straight, and taper sharply to V-shaped tips. In none of the footprints are there traces of digital swellings or nodes that might indicate the phalangeal formula. Digits 2 and 4 are distinctly shorter than digit 3, and are roughly mirror-images — being almost complementary in shape, size and angle of divergence from digit 3. In one of the best-preserved footprints (No. 3; Pl. 5, Fig. A) the interdigital angles are about 33° (2–3) and 30° (3–4).

Mean measurements of footprint size, pace length and stride length are as follows (each with standard deviation and coefficient of variation):

Mean FL: 51.4 ± 6.5 cm (CV 13%; N 7)

Mean FW: 46.1 ± 4.0 cm (CV 9%; N 10)

Mean PL: 166.6 ± 26.5 cm (CV 16%; N 10)

Mean SL: 330.6 ± 37.4 cm (CV 11%; N 9)

Mean ratio FW/FL: 0.88 ± 0.05 (CV 6%; N 7).

The near-symmetrical footprints are arranged with slight positive rotation (i.e. they point not only forwards, but slightly inwards). They form a narrow trackway, with mean pace angulation calculated at 170°47' (SD 9°26'; CV 5.5% N 9). The trackway has a slightly sinuous course from NE to SW. From the spacing and orientation of the first few footprints we suspect that the animal actually approached the present Lark Quarry site from the NNE; the orientation of the last (11th) footprint indicates that the animal made an abrupt right-hand turn and moved off to the NW (see Fig. 3). There is no trace of a tail drag.

Some of the footprints show additional details of interest. Footprint No. 7, for example, consists of little more than shallow imprints of the three digits (Pl. 6), and seems to have been formed on a relatively resistant patch of sediment. In this footprint there is evidence that the tips of the digits extend forwards, beneath the surface of the sediment, as conical tunnels about 4 cm in length. These tunnels appear to be marks of long, robust and sharply-pointed claws. Traces of similar claws occur in several other footprints of the carnosaur. In footprint No. 8 the central digit (3) is unusually broad and contains a longitudinal crest of mudstone in the midline (Fig. 4; see also Thulborn and Wade 1979, fig. 1B). This crest was presumably formed by mud adhering to the underside of the middle toe as the animal's foot was lifted from the substrate; other prints from the same foot do not show this feature. Fig. 4 illustrates variation in shape of the carnosaur's footprints.

#### STATUS AND AFFINITIES.

The occurrence of a carnosaur trackway at Lark Quarry is not unduly surprising. Carnosaurs seem to have had an almost world-wide distribution during the Cretaceous period, with their footprints having been reported as far afield as Spitzbergen (Edwards et al. 1978) and Western Australia (Colbert and Merrilees 1968). No skeletal remains of carnosaur are recorded from Queensland, though footprints of large theropod dinosaurs are well known in the Jurassic rocks of the state (Ball 1933, 1934a, 1934b, 1946; Anonymous 1951, 1952a, 1952b; Staines 1954; Bartholomai 1966). For the sake of convenience we may distinguish two major groupings of carnosaur footprints in general: those with relatively long and slender toes, and those with comparatively short and thick toes. Examples of these two groupings are, respectively, *Megalosauropus* and *Tyrannosauropus* (see Haubold 1971 and references cited therein). The former are probably footprints of smaller and more gracile carnosaur, such as *Allosaurus* and *Megalosaurus*, while the latter probably represent bigger and more robust forms like *Tyrannosaurus*. The footprints of the Lark Quarry animal have rather short thick toes, and they appear to be closer in appearance to *Tyrannosauropus* than to any other form of carnosaur footprint so far described. The Lark Quarry footprints resemble *Tyrannosauropus* in general shape and proportions (mean ratio FW/FL of 0.88 as opposed to approximately 0.86 in *Tyrannosauropus*), but they differ in the following respects: in size (FL up to 80 cm in *Tyrannosauropus*), in pace angulation (170° as opposed to approximately 150°), and in the ratio SL/FL (6.4 as opposed to 5.0). On the basis of these similarities and differences we recommend that the Lark Quarry footprints should be referred to as cf *Tyrannosauropus*. This identification does not imply that the theropod dinosaur *Tyrannosaurus* was responsible for the Lark Quarry trackway; the track-maker can be identified no more precisely than 'carnosaur'.

It must be mentioned here that footprints of carnosaur have often been confused with those of ornithopod dinosaurs (bipedal herbivores of the suborder Ornithopoda, order Ornithischia). The source of this confusion is partly historical: the first footprints to be attributed to a particular genus of dinosaur — the ornithopod *Iguanodon* — happened to be large tridactyl examples from the Lower Cretaceous of Europe. Subsequently, there grew a common tendency for any large tridactyl footprints to be ascribed to *Iguanodon*.

or to some similar ornithopod dinosaur (see comments by Beckles 1862, Charig and Newman 1962, Sarjeant 1974). Such confusion has, in fact, occurred over footprints from the Australian Cretaceous: large tridactyl prints from the Broome Sandstone (Lower Cretaceous) of Western Australia were attributed to iguanodonts by McWhae et al. (1958), but were later identified as those of theropod dinosaurs (Colbert and Merrilees 1968). Iguanodontids and some theropods both produced large tridactyl footprints which may, in some circumstances, be difficult to distinguish — particularly if preservation is poor. It has been suggested to us (by Dr D.B. Norman, pers. comm.) that some doubt may attach to the footprints of the Lark Quarry animal, and that these might actually be footprints of an iguanodontid ornithopod. However, several distinctive features of the footprints lead us to conclude that they are almost certainly those of a carnosaur. First, the footprints are slightly longer than broad, whereas those of ornithopods are commonly broader than long (see, for example, Langston 1960, Currie and Sarjeant 1979, and the many ornithopod footprints described below). Next, the three digits have an almost symmetrical arrangement; in many ornithopod footprints digit 2 is more widely spaced from digit 3 than is digit 4 (see same examples). Third, the Lark Quarry footprints have traces of a large pointed claw on each toe; the ungual phalanges of the larger ornithopods were blunter, and sometimes rather hoof-like, structures. Finally, the central digit (3) is V-shaped in outline; in ornithopod footprints digit 3 tends to have roughly parallel margins that curve round to form a U-shaped extremity. These basic distinctions seem to confirm that the large trackway at Lark Quarry is that of a carnosaur (see Fig. 4).

#### ORNITHOPOD TRACKWAYS

Ichnogenus *Wintonopus* ichnogen. nov.

Type and only ichnospecies *W. latomorum* ichnosp. nov.

HOLOTYPE: single right footprint, preserved as natural mould; QM F10319 (Pl. 7, Fig. A).

REFERRED MATERIAL: QM F10320 (single left footprint, as natural mould; Pl. 11, Fig. A); QM F10321 (rock slab with footprints and trackways as natural moulds); QM F12264 (single right footprint, as natural cast; Pl. 1, Figs. A, B); QM F10322 (fibreglass replicas of footprints and trackways preserved as natural moulds; Pl. 8 to

10; Pl. 11, Figs. B, C, D; Pl. 13, Fig. C; Pl. 14, Fig. A; Pl. 16, Figs. B, C).

LOCALITIES: Lark Quarry (QM F10319, QM F10320, QM F10321, QM F10322); Seymour Quarry (QM F12264). See Fig. 1 for location of quarries.

HORIZON: interbedded sandstones and mudstones about the middle of the Winton Formation; early Upper Cretaceous (Cenomanian).

ETYMOLOGY: Ichnogenus name derived from the name Winton and the Greek *pous* (foot); ichnospecies name (from Latin *latomus*, stonemason) as tribute to the many volunteers who worked at the Lark Quarry excavation.

DIAGNOSIS (ichnogenus and ichnospecies): narrow trackway of small to medium-size digitigrade biped, with pace angulation about 160°. Footprint size index (SI) usually between 3.2 and 11.1 cm, but occasionally as high as 26.6 cm. No imprints of hand or tail. Footprints tridactyl (digits 2, 3 and 4), slightly broader than long (ratio FW/FL about 1.15), showing distinct positive rotation. Digits broad, with rounded or bluntly angular tips, without indications of phalangeal pads. Digit 3 longest, with sub-parallel sides. Digit 4 shorter and slightly narrower than digit 3, extended as blunt posterior salient. Digits 3 and 4 close together, parallel or only slightly divergent. Digit 2 shortest, and widely separated from digit 3 (with interdigital angle often about 60°). Imprints of digits 2 and 3 sometimes completely separated. Posterior margin of foot convex forwards. Ratio PL/FL usually between 8.0 and 13.5, rarely as low as 4.0 or as high as 15.0; ratio SL/FL usually between 16.0 and 24.0, rarely as low as 8.0 or as high as 27.0.

DESCRIPTION. The holotype is a sharply defined footprint, probably formed by the foot penetrating and leaving the substrate with minimal disturbance (Pl. 7, Fig. A). Few of the footprints referred to *Wintonopus latomorum* are identical to the holotype: the majority have less complete imprints of the digits, and many appear to have been disfigured by withdrawal of the track-maker's foot from the sediment. Nevertheless all these disfigured and less complete examples can be interpreted as variants of the footprint pattern exemplified by the holotype (see Fig. 5). Variation in shape of the footprints is described first; thereafter we describe variation in size, proportions and spacing of the footprints.

All the footprints are tridactyl. They are often several centimetres deep, yet none of them shows any trace of digit 1. If this digit was present in the

track-maker's foot it must have been quite short and non-supportive, so that it failed to touch down even when the three weight-bearing digits sank quite deeply into the mud. Digit 1 was probably no longer than it is in ornithopods such as the Lower Cretaceous *Hypsilophodon* (Fig. 6B). The imprint of digit 4 extends farther back than the imprints of digits 2 and 3, giving the impression of a distinct salient or 'spur' at the posterolateral corner of the footprint. This 'spur' is unlikely to indicate the presence of a functional digit 5 (which is vestigial in even the earliest ornithopod dinosaurs) and probably reflects that the distal end of metatarsal 4 was located well to the rear of the foot, in standard ornithopod fashion (see, for example, the foot of *Fabrosaurus* — Thulborn 1972, fig. 12B).

Nearly all the footprints are asymmetrical, with a strongly divergent digit 2, so that isolated examples are readily identified as left or right. This method of identification has been verified in at least 60 *Wintonopus* trackways. Only a few footprints (in otherwise typical trackways) show any close approach to a symmetrical arrangement of the three digits. These near-symmetrical prints could have been produced in any of several ways: by some degree of spreading and/or closure of digits in the foot; by partial flexion of the divergent digit 2; by rotation of the foot around the long axis of digit 3 (so that digit 2 was carried laterally and slightly underneath digit 3); by the foot meeting the substrate at an unusual oblique angle (with the long axis of digit 3 directed forwards, downwards and slightly outwards).

The imprints of the digits are usually quite short and relatively broad. In most footprints the three digits are about equally broad (as, for example, in the holotype), but in a few cases digit 3 is much broader than digits 2 and 4 (e.g. Pl. 9, Fig. D; Pl. 10, Fig. D). In these examples digit 3 seems to have borne most of the track-maker's weight, while the flanking digits splayed out to form smaller and shallower imprints. A very similar effect was described by Sternberg (1932) in an ornithopod footprint (*Gypsichnites pacensis*) from the Lower Cretaceous of British Columbia. Digit 3 is longest, and in the least-disfigured footprints digits 2 and 4 extend about equally far forwards. The imprint of digit 3 is often straight, but sometimes shows very slight curvature (convex laterally; e.g. Pl. 11, Fig. A; Pl. 15, Fig. B). The hindmost margins of digits 2 and 3 lie on a line approximately normal to the long axis of digit 3, whereas digit 4 extends well behind this line to form the posterior salient or 'spur'. In

consequence the posterior margin of the footprint (or the line connecting the hindmost points of the three digital imprints) is arched forwards. In some footprints, such as the holotype, the three digital imprints are joined together posteriorly, and the arched rear margin is continuous. Evidently these footprints were formed by the foot sinking into the mud up to, or beyond, the distal end of the metatarsus. In many other examples the foot did not sink so deeply, so that the three digital imprints are partly or completely separated and there is no continuous rear margin to the footprint (e.g. Figs 5D, E, F; Pl. 8, fig. B). The imprint of digit 2 is often completely separated from that of digit 3, whereas the imprints of digits 3 and 4 are usually joined together (e.g. Pl. 8, Figs A, B, D). This difference probably indicates that digit 2 diverged from digit 3 higher up the metatarsus than did digit 4 (see foot skeletons of ornithopods, Fig. 6). There are no certain indications of phalangeal pads in any of the footprints. The tips of the digital imprints are generally well-rounded in outline — except where they have been extended forwards as scrape-marks (see below) — but are sometimes a little sharper in the smallest footprints (Pl. 11). Interdigital webbing is limited in extent; the holotype shows traces of a small web between digits 3 and 4, and less certain traces of another between digits 2 and 3.

*Wintonopus* material from Seymour Quarry comprises natural casts reinforced by superficial infiltration of ironstone. The surfaces of the casts are wrinkled and finely tuberculate, and somewhat reminiscent of reptilian skin texture (Pl. 1). However, it is not certain that these specimens do show preservation of skin texture: an apparently identical texture is found on footprint casts attributed to the coelurosaurs and on some areas of seemingly undisturbed sediment, and it may be no more than a by-product of ironstone formation.

Practically every *Wintonopus* footprint at Lark Quarry seems to have been disfigured to some extent as the track-maker's foot was withdrawn from the mud. Basically, each foot sank quite deeply into the mud, and as it was lifted clear at the end of the stride the tips of one or more digits tended to drag and scrape through the rim of the newly-formed footprint. So, in many cases, there are scrape-marks extending forwards from one or more of the digital imprints. Digit 3 was longest in the foot and, for that reason, tended to produce a scrape-mark most frequently (e.g. Pl. 8, Fig. A). Digit 4 was intermediate in length between digits 2

and 3, and was next most likely to produce a scrape-mark, whereas digit 2 was shortest (parallel to the long axis of digit 3) and rarely did so (e.g. Pl. 10, Fig. D). In most cases the scrape-marks are fairly short, but in a few examples they are longer than the digital imprints (Pl. 8, Fig. A, and Pl. 10, Fig. D). The scrape-marks are not straightforward extensions of the digital imprints, but veer away from them at a distinct angle. Sections of trackways show that each foot was planted into the mud with slight positive rotation (i.e. with the toes pointing forwards and inwards). But as the foot was lifted from the mud it evidently turned to face directly ahead, so that the tips of the toes swept forwards and slightly outwards. In other words the foot was placed in the mud at one angle and was withdrawn at a different angle, and it is for this reason that the digital imprints have a different orientation from their scrape-marks. In some footprints this effect is so marked that the tip of digit 3 appears to be forked or Y-shaped (e.g. Pl. 8, Fig. D, and, to a lesser extent, in the holotype). In such examples the medial branch of the fork was formed when the digit was placed into the mud, and the lateral branch is a scrape-mark produced when the digit was withdrawn in a different direction. An exactly comparable type of scrape-mark was illustrated by Sarjeant (1970, Fig. 5e) in an ornithopod footprint (? *Satapliasaurus* cf. *S. dsoceniidzei*) from the Middle Jurassic of Yorkshire, England.

Clear examples of backwardly-directed scrape-marks are less common. Again, the longest digit (3) seems to have produced a scrape-mark most frequently whereas the shortest digit (2) rarely produced one. These scrape-marks are also aligned at a slight angle to the long axes of the digital imprints (e.g. Pl. 8, Fig. B), confirming that the tips of the digits swung laterally as the foot was lifted from the substrate.

The development of these scrape-marks (whether forwards or backwards) is best understood in relation to the sequence of events during the track-maker's stride cycle (Fig. 7). At the start of this cycle the forwardly-extended foot would have been planted into the sediment with slight positive rotation (Stage 1 in Fig. 7). The initial footprint would have been quite shallow. At mid-stride the track-maker's centre of gravity would have passed forwards above the foot, which would then have sunk deeper into the substrate (Stage 2 in Fig. 7). In many instances the foot also slipped backwards a little, so that the front margins of the footprint are distinctly

'stepped' or 'terraced' (see, for example, Pl. 8, Figs. A, B; Pl. 9, Fig. D). Shortly thereafter the foot began to rotate (so that the long axis of digit 3 was directed straight ahead), and the rear part of the foot started to lift clear of the substrate. Sometimes the toes continued to slip backwards as they were lifted from the footprint: in these cases the toe-tips incised deep slots in the floor of the footprint (Stage 3A in Fig. 7) or even breached the rear wall of the footprint to leave backwardly-directed scrape-marks (Stage 3B). More commonly there was limited back-slip of the toes (Stages 1 to 2) and the toes-tips dragged through the front wall of the footprint to produce forwardly-directed scrape marks (Stage 3C).

*Wintonopus* footprints are typically broader than long, even though many examples have their total length exaggerated by scrape-marks. In some cases the track-maker's foot was planted into the mud at a steep angle, to leave relatively short and stubby imprints of the toes (e.g. Pl. 8, Fig. B). In other cases the foot seems to have lost its purchase in the muddy substrate, and the toes slithered back to form deep scratches that exaggerate the total length of the footprint (e.g. Pl. 9, Fig. B). In still other cases only the distal parts of the toes entered the mud, and then skidded backwards to produce a footprint consisting of little more than three long scratch-marks (e.g. Pl. 10, Fig. A). A few footprints consist of three puncture-marks apparently formed by the toes entering and leaving the mud almost vertically (e.g. Pl. 15, Fig. C).

Measurements of footprints, paces and strides were taken from parts of 57 different trackways of *Wintonopus* (see 'Methods' for descriptions of measurements). Fifty-six of these trackways are on the Lark Quarry bedding plane; the other section of trackway is at a different site — New Quarry. The 56 trackway sections at Lark Quarry comprise 284 footprints, representing 228 paces and 172 strides. This sample provides the following mean figures for dimensions of footprints, paces and strides:

#### Overall means

Mean FL:  $6.71 \pm 3.39$  cm (CV 51%; N 200)

Mean FW:  $7.58 \pm 4.51$  cm (CV 60%; N 214)

Mean PL:  $68.3 \pm 32.2$  cm (CV 47%; N 215)

Mean SL:  $131.7 \pm 63.4$  cm (CV 48%; N 162)

The high coefficients of variation reflect considerable ranges in size. Nearly all the trackways are those of small animals, with footprint lengths between 2 cm and 16 cm, and stride lengths in the range 49–271 cm; but the size

distribution, as a whole, is attenuated by the presence of a single very large trackway with footprints up to 33 cm long and stride lengths reaching 345 cm (trackway 'B' in Fig. 3; see Figs 8 and 10).

The index of footprint size, the pace angulation and various ratios were calculated from the basic measurements listed above (see 'Methods'); they have the following means:

*Overall means*

Mean SI:  $7.20 \pm 3.93$  (CV 55%; N 173)

Mean ANG:  $161^{\circ}24' \pm 11^{\circ}20'$  (CV 7% N 145)

Mean ratio FW/FL:  $1.15 \pm 0.25$  (CV 22%; N 173)

\*Mean ratio PL/FL:  $10.18 \pm 2.00$  (CV 20%; N 120)

\*Mean ratio SL/FL:  $19.84 \pm 3.69$  (CV 19%; N 88)

(\* FL is mean for two footprints defining each pace or stride)

Footprint proportions (FW/FL) and pace angulation appear to show relatively little variation, and are probably good diagnostic characters; that is, *Wintonopus* trackways are characterized by being narrow, and fairly straight, and by having footprints that are usually broader than long.

There is a strong positive correlation between any two measurements of size in the *Wintonopus* trackways and footprints; for example:

variables	product moment correlation coefficients	
	untransformed data	log transformed data
FL : FW (N 174)	0.87	0.89
*FL : PL (N 112)	0.86	0.87
*FL : SL (N 79)	0.87	0.89
*FW : SL (N 89)	0.89	0.93
*SI : SL (N 59)	0.90	0.92

(\*mean for two footprints defining each pace or stride)

The correlations between stride length and footprint dimensions (FL, FW or SI) are worthy of note. It is only to be expected that bigger animals would take bigger strides, but stride length varies according to the gait and speed of an animal — and not simply to its size alone. The impressive correlations between foot size and stride length imply that the *Wintonopus* track-makers at Lark Quarry were all using a similar

gait; in a random sample of dinosaur trackways one might expect to find a somewhat looser correlation between stride length and footprint dimensions.

The correlation between footprint size (SI) and footprint proportions (ratio FW/FL) is much poorer: 0.22, with untransformed data, N 172. So, too, is that between footprint length and pace angulation (0.23, with untransformed data, N 73). These poor correlations seem to confirm our observation that footprint proportions and pace angulation tend to remain fairly constant throughout the entire size range of *Wintonopus* trackways (see further discussion below).

All the preceding estimates and statistics are based on pooled data from the *Wintonopus* trackways (i.e. on every available example of the 284 footprints and their paces and strides). If the data are grouped, and mean figures are taken for each of the 56 trackways studied, there emerges a somewhat similar pattern of size distribution and correlations (see Figs 9 and 10). Means based on the grouped data may be summarized as follows:

*Means per trackway*

Mean FL:  $6.64 \pm 3.07$  cm (CV 46%; N 56)

Mean FW:  $7.55 \pm 4.36$  cm (CV 58%; N 56)

Mean PL:  $67.1 \pm 30.6$  cm (CV 46%; N 55)

Mean SL:  $128.0 \pm 59.6$  cm (CV 47%; N 52)

Mean SI:  $7.05 \pm 3.58$  cm (CV 51%; N 56)

Mean ANG:  $162^{\circ}47' \pm 8^{\circ}46'$  (CV 5%; N 51)

Mean ratio FW/FL:  $1.14 \pm 0.19$  (CV 18%; N 56)

Mean ratio PL/FL:  $10.18 \pm 1.97$  (CV 19%; N 49)

Mean ratio SL/FL:  $19.75 \pm 3.50$  (CV 18%; N 44)

Most coefficients of variation remain very high. An analysis of variance (see Sokal and Rohlf 1969, p. 204 *et seq.*) will reveal how much of this variation lies within the *Wintonopus* trackways:

variable	variation within trackways (%)	variation among trackways (%)
FL	15.1	84.9
FW	6.0	94.0
PL	7.5	92.5
SL	2.4	97.6
SI	0.8	99.2
ratio FW/FL	52.1	47.9
ANG	77.9	22.1

Evidently footprint dimensions, pace length and stride length remain fairly constant within the *Wintonopus* trackways. Footprint length is

somewhat more variable than footprint width within the trackways, but the index of footprint size is virtually constant. (Footprint length is more variable than footprint width because it is more strongly affected by the angle at which the foot enters and leaves the substrate, and by the development of scrape-marks; see Fig. 5). Stride length appears to be remarkably consistent within trackways, though pace length is more variable. Footprint proportions (ratio FW/FL) and pace angulation appear to vary more within trackways than they do between trackways; but these two features show little overall variation in the first place — so they may still be regarded as good diagnostic characters. In general, most of the variation in footprint dimensions, paces and strides can be attributed to the difference in size between one trackway and another.

**STATUS AND AFFINITIES.** The footprints referred to *Wintonopus latomorum* vary a good deal in size and in appearance, yet they all show some at least of the following diagnostic characters: a widely spaced or divergent digit 2, a backwardly-projecting 'spur' behind digit 4, a forwardly-arched rear margin, and a width that equals or exceeds footprint length. Where the footprints can be connected into trackways they are arranged with distinct positive rotation, and the trackways are always narrow and rather straight (with pace angulation about  $160^\circ$ ). Moreover, footprint dimensions are strongly correlated one with another, and with stride length. In short, all the footprints may be regarded as those of animals sharing one distinctive pattern of foot structure (see Fig. 6C) and using the same gait. For these reasons it seems justifiable to assemble all these footprints in a single ichnospecies. Differences in shape between one footprint and another appear to be no more than circumstantial (see preceding descriptions and Fig. 5). According to recent recommendations for the nomenclature of trace fossils (see Article 40 in Basan 1979) it might be legitimate to define several ichnospecies of *Wintonopus* on the basis of footprint shape alone — e.g. a 'scratchy-toed' species, a 'stubby-toed' species, and so on. In the present circumstances, where footprint shape varies within a single trackway, such a measure would be rather confusing. Moreover there is no clear evidence that *Wintonopus* footprints of different morphology were 'produced in different phases of behavior' on the part of the track-maker (as Basan's Article 40 seems to require). In addition it may be noted that the range of variation in

*Wintonopus* is no greater than that in some existing ichnotaxa — e.g. the ichnogenus *Anomoepus* (as defined by Lull 1953), and the ichnospecies *Grallator variabilis* and *G. olonensis* (as defined by de Lapparent and Montenat 1967).

The makers of the *Wintonopus* trackways were almost certainly dinosaurs of the suborder Ornithopoda (bipedal herbivores of the order Ornithischia). Ornithopods had a world-wide distribution during the Mesozoic era: their skeletal remains and their footprints have been reported from every continent except Antarctica. The following features of *Wintonopus latomorum* seem to be characteristic of very many ornithopod footprints: the footprint is tridactyl, and its width rivals or exceeds its length; the digital imprints are relatively short, thick and blunt (indicating the presence of 'hoof-like' unguals rather than sharp claws); the space between digits 2 and 3 is distinctly greater than that between digits 3 and 4; the outer margins of digits 2 and 4 diverge only slightly from the longitudinal axis of digit 3, so that the footprint has sub-parallel sides; there are sometimes traces of small interdigital webs. In all these features *W. latomorum* resembles other footprints attributed to ornithopod dinosaurs — e.g. *Amblydactylus* ichnospp. from the Lower Cretaceous of Canada (Sternberg 1932, Currie and Sarjeant 1979); unnamed types from the Late Jurassic/Early Cretaceous of Mexico (Ferrusquia-Villafranca et al. 1979); footprints of *Iguanodon*, from the Lower Cretaceous of Europe (Beckles 1862, Dollo 1906). However, the footprints described here are distinctly smaller than many others attributed to ornithopod dinosaurs (see Table 1). Of the 57 *Wintonopus* trackways examined in this study only two have mean SI greater than 12 cm (actually 12.7 cm and 26.6 cm); among other footprints attributed to ornithopods only those of *Anomoepus* ichnospp. are commonly found to be so small. Aside from this *Wintonopus* differs from most other ornithopod footprints in one other respect — in the absence (or weak development) of an imprint representing a 'sole' or 'heel' to the foot. The rear margin of the footprint is concave (arched forwards) rather than convex (arched backwards) and presumably corresponds to the natural arch formed by the distal ends of the metatarsals. This distinctive footprint shape seems to indicate that the *Wintonopus* track-makers were thoroughly digitigrade, whether they were walking or running (see later discussion of speeds and gaits). These differences in size and shape are sufficient to

distinguish *Wintonopus* from most other tracks attributed to ornithopod dinosaurs. *Anomoepus* ichnospp. are comparable in size to *Wintonopus*, but are distinguished by narrower and more acutely pointed digits with obvious phalangeal nodes (see Lull 1953). In addition most examples of *Anomoepus* have the ratio PL/FL much lower than it is in *Wintonopus* (Fig. 11).

However, two types of footprint described by de Lapparent and Montenat (1967) from the Rhaeto-Liassic of Vendée (W France) bear some definite resemblances to *Wintonopus*. One of these types, *Anatopus palmatus*, was also attributed to an ornithopod dinosaur but is, unfortunately, represented by only three isolated footprints. In all three cases footprint size index is about 9.0 cm — well within the range described for *Wintonopus*; the ratio FW/FL is about 1.14

— practically identical to the mean for *Wintonopus* (1.15). *Anatopus* appears to resemble *Wintonopus* not only in size, shape and arrangement of the three digits, but also in possessing what seem to be anterolaterally directed scrape-marks at the tips of digits 3 and 4 (see de Lapparent and Montenat 1967, fig. 16, but note the different identification of digits). Nevertheless *Anatopus* certainly differs from *Wintonopus* in that the digits are relatively narrow and show distinct outlines of phalangeal pads. Moreover, de Lapparent and Montenat identified traces of very extensive interdigital webbing in the type specimen of *Anatopus*. A second type of footprint, *Saltopoides igalensis*, was attributed to a theropod dinosaur but is, once again, rather similar to *Wintonopus* (see de Lapparent and Montenat 1967, Fig. 15).

TABLE 1: A COMPARISON OF SIZE AMONG FOOTPRINTS ATTRIBUTED TO ORNITHOPOD DINOSAURS.

mean index of footprint size (cm)			
68.5	'Ornithopoda', Jurassic of Brazil (Leonardi 1980)	17.5	?cf <i>Satapliasaurus</i> , M Jurassic of England (Sarjeant 1970)
61.4	<i>Amblydactylus gethingi</i> , L Cretaceous of Canada (Sternberg 1932)	15.7	<i>Irenichnites gracilis</i> , L Cretaceous of Canada (Sternberg 1932)
51.3	<i>Iguanodon</i> , L Cretaceous of Portugal (Antunes 1976)	15.6	<i>Sauropus barrattii</i>
46.3	<i>Irenesauripus acutus</i> , L Cretaceous of Canada (Sternberg 1932)	15.0	<i>Anomoepus crassus</i>
28.6	<i>Gypsichnites pacensis</i> , L Cretaceous of Canada (Sternberg 1932)	10.7	<i>Anomoepus isodactylus</i>
24.7	'Ornithopod morphotypes', Jurassic/Cretaceous of Mexico (Ferrusquia-Villafranca <i>et al.</i> 1978)	9.2	<i>Anomoepus intermedius</i>
23.5	<i>Satapliasaurus</i> cf <i>S. dsocenidzei</i> , M Jurassic of England (Sarjeant 1970)	9.0	<i>Anatopus palmatus</i> , Rhaeto-Liassic of France (de Lapparent and Montenat 1967)
18.5	<i>Satapliasaurus dsocenidzei</i> , L Cretaceous of Georgia, USSR (Gabouniya 1951)	8.7	<i>Anomoepus curvatus</i> , Triassic of Connecticut (Lull 1953)
18.3	<i>Amblydactylus kortmeyeri</i> , L Cretaceous of Canada (Currie and Sarjeant 1979)	7.7	<i>Anomoepus scambus</i> , Triassic of Connecticut (Lull 1953)
17.6	<i>Iguanodon</i> , U Jurassic of England (Delair and Brown 1974)	7.2	<i>Wintonopus latomorum</i>
		6.2	<i>Anomoepus gracillimus</i> , Triassic of Connecticut (Lull 1953)
		5.4	<i>Anomoepus minimus</i> , Triassic of Connecticut (Lull 1953)

Triassic of Connecticut (Lull 1953)

*Saltopoides* has a footprint size index about 13.4 cm, but the footprints differ from those of *Wintonopus* in being distinctly longer than wide (FW/FL ratio about 0.75). In addition the lateral and medial margins of the footprints are divergent (rather than parallel as in *Wintonopus*), and there is no very marked positive rotation of the footprints. *Saltopoides* also differs in showing

faint indications of phalangeal pads, but in two other respects it is very like *Wintonopus* — in having high values for pace angulation (almost 180°) and for the ratio PL/FL (11.1). In summary, *Wintonopus* is similar to both *Anatopus* and *Saltopoides* in some features, but in neither case is there an exact correspondence in footprint morphology.



## COELUROSAUR TRACKWAYS

Ichnogenus *Skartopus* ichnogen. nov.

Type and only ichnospecies *S. australis* ichnosp. nov.

HOLOTYPE: single left footprint, preserved as natural mould; QM F10330 (Pl. 7, Figs. B, C).

REFERRED MATERIAL: QM F10321 (rock slab with footprints and trackways as natural moulds); QM F12265 (single right footprint, as natural cast; Pl. 1, Figs. C, D); QM F10322 (fibreglass replicas of footprints and trackways preserved as natural moulds; Pl. 10, Figs B, D; Pl. 12; Pl. 13, Figs A, B; Pl. 14; Pl. 15, Fig. A; Pl. 16).

LOCALITIES: Lark Quarry (QM F10330, QM F10321, QM F10322); Seymour Quarry (QM F12265). See Fig. 1 for location of quarries.

HORIZON: interbedded sandstones and mudstones about the middle of the Winton Formation; early Upper Cretaceous (Cenomanian).

ETYMOLOGY: Ichnogenus name derived from Greek *skartes* (nimble) and *pous* (foot); ichnospecies name refers to southern (Australian) provenance.

DIAGNOSIS (ichnogenus and ichnospecies): trackway of small digitigrade biped, with pace angulation about 150°. Footprint size index (SI) between 2.9 and 5.7 cm. No imprints of hand or tail. Footprints tridactyl (digits 2, 3 and 4), slightly longer than broad (ratio FW/FL about 0.95) showing distinct positive rotation. Digit imprints narrow, straight and sharply pointed, without indications of phalangeal pads. Digit 3 longest; digits 2 and 4 about equal in length, and almost equally divergent from digit 3 (both interdigital angles between 25° and 30°). Imprint of digit 4 extends slightly farther back than imprint of digit 2, but does not form a posterior salient or 'spur'. Traces of small interdigital webs sometimes present. Posterior margin of footprint is an oblique line (posterolateral to anteromedial), either straight or arched forwards. In some examples there is an imprint of the metapodium: this is sub-rectangular in outline and roughly equivalent in length to digit 3. Ratio PL/FL usually between 5.5 and 8.5, rarely as low as 5.2 or as high as 9.1; ratio SL/FL usually between 11.0 and 16.0, rarely as low as 10.6 or as high as 17.3.

DESCRIPTION: The holotype is a well-defined footprint, impressed in the substrate with minimal disturbance. In general the footprints identified as *Skartopus* show much less variation

in shape than do those referred to *Wintonopus*. Once again, however, all the variations that do exist may be interpreted as circumstantial modifications of the footprint pattern shown by the holotype. Variation in footprint shape is described first; thereafter we describe variation in size, proportions and spacing of the footprints.

All footprints referred to *Skartopus* are tridactyl, with clear traces of digits 2, 3 and 4. The footprints sometimes reach a depth of 2 cm, or more, but none of them shows any certain trace of the hallux (digit 1). If the hallux was present in the track-maker's foot it must have been relatively short and without a major supportive role; presumably it extended no farther than the line of the metatarso-phalangeal contacts in digits 2, 3 and 4 (see Figs 6D-F). Where the three digits are deeply impressed, as in the holotype, it may be seen that their rear ends do not fall on a straight line. Digits 2 and 4 extend slightly farther back than digit 3, to form a curve (convex forwards) that presumably reflects the natural arch formed by the distal ends of the metatarsals.

*Skartopus* footprints are almost bilaterally symmetrical. It is sometimes difficult to identify isolated examples as left or right, but the following features are often useful guides: the space between digits 2 and 3 is slightly greater than that between 3 and 4; digit 2 is slightly more divergent than digit 4; scratch-marks, often present at the tips of the digit imprints, extends forwards and laterally. All these features are well shown in the holotype (Pl. 7, Figs B, C). Where the footprints can be connected into sections of trackway they are easily identified as left and right on account of their positive rotation (see Pl. 14, Fig. B).

The imprints of the digits are straight, and relatively long and narrow (by comparison with those of *Wintonopus*). In all cases the three digit imprints are about equally broad. Digits 2 and 4 are roughly equal in length, and digit 3 is longer. In nearly all examples the tips of the digit imprints are quite sharply pointed. The interdigital angles are small, and in some footprints digits 3 and 4 are sub-parallel (e.g. the holotype). There are no definite indications of phalangeal pads in any of the footprints. The holotype shows traces of small interdigital webs, as do several other footprints in the referred material (e.g. Pl. 12, Fig. D). *Skartopus* material from Seymour Quarry comprises natural casts with a finely wrinkled ironstone surface; it is not certain if this wrinkling is a representation of original skin texture (see Pl. 1 and p. 422).

Variation in footprint shape is less marked in *Skartopus* than in *Wintonopus*. Divarication of the digits is slightly more pronounced in some footprints than in others, but in all cases the digits form a near-symmetrical pattern. In most *Skartopus* footprints the digits terminate in sharp scratch-marks; apparently similar marks have been illustrated (though not described as such) in coelurosaur footprints from the mid-Cretaceous of Israel (Avnimelech 1966, pl. 7, fig. 2). Variation in the shape of *Skartopus* footprints is most easily explained by reference to events during the track-maker's stride cycle (Fig. 12). At the start of this cycle the forwardly-extended foot would have been planted on the sediment, and there would have been a very shallow initial footprint, or no footprint at all (Stage 1 in Fig. 12). At mid-stride the track-maker's centre of gravity passed forwards above the foot, which in some cases sank into the substrate (Stage 2A in Fig. 12). Later, as the rear part of the foot started to lift clear of the sediment, the claws pressed down and slightly backwards to produce sharp outlines to the tips of the digital imprints (Stage 3A in Fig. 12). At this point the toes sometimes started to slip backwards, their claws incising grooves in the floor of the footprint (Stage 4A in Fig. 12). This sequence of events produced sharp-toed tridactyl footprints such as the holotype (Pl. 7, Figs. B, C), some of which are secondarily deepened by backwardly-directed scratch-marks (e.g. Pl. 12, Figs. C, D; Pl. 13, Fig. A). However, in many other cases the foot did *not* sink into the substrate at mid-stride (Stage 2B in Fig. 12). To judge from the number of discontinuities (or 'missing' footprints) in *Skartopus* trackways this seems to have been a very frequent occurrence. There are at least two obvious reasons why the feet of *Skartopus* track-makers did not always leave recognizable footprints. First, the track-makers seem to have been remarkably small, and presumably light, dinosaurs (see Fig. 15). Second, it appears that coelurosaurs have bigger feet (relative to hip height) than many other bipedal dinosaurs (see later discussion concerning sizes of track-makers). It seems, then, as if the *Skartopus* track-makers may have been lightweight dinosaurs with large spreading feet that acted as analogues of snow-shoes. Even if the entire foot did not sink into the substrate the tips of the toes sometimes left imprints as the track-maker 'kicked off' at the end of its stride (Stage 3B in Fig. 12). The toes then slithered back through the mud to leave a series of curved parallel scratches (Stages 4B and 5B in Fig. 12). In some cases only

one or two of the toes left such traces (e.g. Pl. 16, Fig. A).

A few *Skartopus* footprints are noteworthy in that they appear to include an imprint of the metapodium (e.g. Pl. 12, Figs A, B; Pl. 13, Fig. B). In these examples the imprint of the metapodium is a large sub-rectangular depression behind the three digit imprints. The metapodium imprint is no wider than the maximum spread of the digits, and it is roughly as long as the imprint of digit 3; it is widest at the rear, where it is broadly rounded in outline (convex backwards). Footprints with such traces of the metapodium are uncommon, and most of them occur singly and at random in the *Skartopus* trackways. However, one short section of trackway (a sequence of 3 paces) is composed entirely of such footprints (Pl. 14, Fig. B).

Measurements of footprints, paces and strides were taken from parts of 34 trackways of *Skartopus australis* (see 'Methods' for description of the measurements). All 34 trackways are on the Lark Quarry bedding plane, and they comprise a total of 191 footprints (representing 157 paces and 123 strides). This sample provides the following mean figures for measurements of footprints, paces and strides:

#### Overall means

Mean FL:  $4.46 \pm 0.70$  cm (CV 16%; N 131)  
 Mean FW:  $4.10 \pm 0.56$  cm (CV 14%; N 158)  
 Mean PL:  $32.1 \pm 4.0$  cm (CV 12%; N 151)  
 Mean SL:  $61.7 \pm 7.8$  cm (CV 13%; N 122)

The coefficients of variation are considerably lower than those for equivalent measurements in *Wintonopus* — in consequence of the much smaller size range in *Skartopus*. The index of footprint size, the pace angulation, and standard ratios were calculated from the basic measurements listed above (see 'Methods'); they have the following means:

#### Overall means

Mean SI:  $4.29 \pm 0.52$  cm (CV 12%; N 126)  
 Mean ANG:  $152^{\circ}38' \pm 11^{\circ}44'$  (CV 8%; N 112)  
 Mean ratio FW/FL:  $0.94 \pm 0.16$  (CV 17%; N 126)  
 \*Mean ratio PL/FL:  $7.27 \pm 1.33$  (CV 18%; N 97)  
 \*Mean ratio SL/FL:  $14.03 \pm 2.26$  (CV 16%; N 85)

(\* FL is mean for two footprints defining each pace or stride)

Pace angulation appears to show relatively little variation, and is probably a good diagnostic character. In general terms pace angulation is about 10° greater in *Wintonopus* than in *Skartopus* — so that trackways of the latter tend to be slightly broader and to have a more obvious zig-zag arrangement of the footprints. In addition the footprints of *Skartopus* are commonly longer than broad whereas the reverse is true in *Wintonopus*.

There is generally a poor correlation between any two measurements of size in the *Skartopus* material; for example:

variables	product moment correlation coefficients	
	untransformed data	log transformed data
FL : FW (N 131)	0.36	0.34
*FL : PL (N 70)	0.04	0.16
*FL : SL (N 64)	0.07	0.07
*FW : SL (N 88)	0.23	0.20
*SI : SL (N 57)	0.15	0.10

(\*mean for two footprints defining each pace or stride)

The correlations are not improved by transformation of the data. These poor correlations may be attributed, once again, to the limited size range of the footprints and trackways (see further discussion below). The correlation between footprint size index (SI) and footprint proportions (ratio FW/FL) is also poor (-0.19, with untransformed data; N 126), as is that between footprint length and pace angulation (-0.18, with untransformed data; N 61). The significance of these poor correlations will be examined later (p. 430).

A somewhat similar pattern of size distribution and correlations emerges if the data are grouped and mean figures are taken for each of the 34 *Skartopus* trackways (see Figs 14 and 15). Means derived from the grouped data may be summarized as follows:

#### Means per trackway

- Mean FL: 4.46 ± 0.50 cm (CV 11%; N 34)
- Mean FW: 4.14 ± 0.49 cm (CV 12%; N 34)
- Mean PL: 32.0 ± 2.6 cm (CV 8%; N 34)
- Mean SL: 61.8 ± 4.8 cm (CV 8%; N 34)
- Mean SI: 4.28 ± 0.43 cm (CV 10%; N 34)
- Mean ANG: 153°37' ± 9°35' (CV 6%; N 34)
- Mean ratio FW/FL: 0.94 ± 0.12 (CV 13%; N 34)
- Mean ratio PL/FL: 7.19 ± 1.08 (CV 15%; N 29)
- Mean ratio SL/FL: 13.73 ± 1.73 (CV 13%; N 32)

Analysis of variance (below) reveals that there is as much, or more, variation within trackways as there is among trackways:

variable	variation within trackways (%)	variation among trackways (%)
FL	57.9	42.1
FW	46.2	53.8
PL	79.9	20.1
SL	50.6	49.4
SI	52.1	47.9
ratio FW/FL	74.5	25.5
ANG	49.9	50.1

However, all these characters show little overall variation in the first place (see coefficients of variation) — so that most, if not all, of them may still be regarded as of diagnostic value.

**STATUS AND AFFINITIES.** The footprints designated *Skartopus australis* do not vary a great deal in size or in shape. They consistently show the following distinctive features: a near-symmetrical arrangement of three long, relatively narrow and sharply pointed digits, a forwardly arched rear margin (except where there is an imprint of the metapodium), and a length that equals or exceeds footprint width. Where the footprints can be connected into trackways they are found to be disposed with distinct positive rotation; the trackways are moderately broad, with pace angulation about 150°. By comparison the trackways of *Wintonopus* appear to be narrower, with pace angulation about 160°. Variation in shape of the *Skartopus* footprints appears to be circumstantial — the occasional appearance, in otherwise normal trackways, of footprints represented only by scratches or of footprints including a trace of the metapodium. The scratch-like footprints were probably formed when the track-maker's foot slipped backwards across the surface of the muddy substrate (Stages 2B to 5B in Fig. 12); footprints with a trace of the metapodium were presumably formed when the track-maker inadvertently came down 'flat-footed', or perhaps when the foot sank deeply in the mud. (Note, however, that one short section of trackway consists entirely of footprints with traces of the metapodium (Pl. 14, Fig. B). This sequence of footprints could be fortuitous, or it could derive from any of several factors — e.g. a pathological condition of the track-maker, or an accumulation of mud on the animal's feet.)

There is limited variation in size of the *Skartopus* footprints, paces and strides. The biggest footprint is less than twice the size of the

smallest (in terms of SI); by contrast the biggest example of *Wintonopus* is nearly 12 times the size of the smallest. The coefficients of variation indicate that dimensions of footprints, paces and strides vary much less in *Skartopus* than they do in *Wintonopus* — yet the correlation between any two of these dimensions is in most cases very much poorer in *Skartopus* (compare Figs 10 and 15). These poor correlations do not necessarily indicate that the *Skartopus* material is a heterogeneous assortment of footprints and trackways: rather, they reflect the very limited range in size. For comparative purposes the entire sample of *Skartopus* tracks might be regarded as equivalent to a small size class selected from the *Wintonopus* sample. A very similar relationship between two ichnotaxa has been well illustrated by de Lapparent and Monténat (1967, fig. 8). In other words the *Skartopus* footprints and trackways are all roughly similar in their dimensions, so that there is as much (or more) variation within a trackway as there is between one trackway and the others (see analysis of variance). In addition it must be noted that the *Skartopus* footprints and trackways are, on the whole, much smaller than the *Wintonopus* footprints and trackways — yet both have been measured within the same limits of error. Small measurement errors would be of negligible importance in the large *Wintonopus* tracks, but they would certainly tend to blur correlations in the absolutely smaller *Skartopus* tracks. Overall the *Skartopus* footprints are quite consistent in

size, shape, and their spacing within trackways; for these reasons it seems justifiable to assemble them in a single ichnospecies. The range of variation seen in this assemblage is no greater than that in several other ichnospecies attributed to coelurosaurs (e.g. *Grallator olonensis* and *G. variabilis*, de Lapparent and Monténat 1967).

The *Skartopus* footprints were very probably made by coelurosaurs — small representatives of the dinosaur suborder Theropoda. Skeletal remains and footprints of theropods have been recorded from every continent except Antarctica; theropod body fossils have not yet been reported from Queensland, though their footprints are well known in the state (for references see p. 420). In their size and general appearance the *Skartopus* footprints are comparable with those attributed elsewhere to coelurosaurs (see review by Haubold, 1971). The examples listed in Table 2 will illustrate the basic agreement in size. All these examples (including *Skartopus*) share the following similarities: the imprints of digits 2, 3 and 4 are rather narrow and quite sharply pointed; the digits diverge (usually) at low angles, and often have a near-symmetrical arrangement. However, *Skartopus* differs from nearly all other trackways attributed to coelurosaurs in having exceptionally high values for the ratios PL/FL and SL/FL (Fig. 16). *Skartopus* is also distinctive in its footprint morphology. It differs from *Columbosauripus* ichnospp. in the lesser divarication of the digits; in addition the digital

TABLE 2: A COMPARISON OF SIZE AMONG FOOTPRINTS ATTRIBUTED TO SMALL THEROPOD DINOSAURS.

mean index of footprint size (cm)		7.5	<i>Anchisauripus hitchcocki</i> , Triassic of Connecticut (Lull 1953)
24.3	<i>Anchisauripus minusculus</i> , Triassic of Connecticut (Lull 1953)	5.8	<i>Otouphepus magnificus</i> , Triassic of Connecticut (Lull 1953)
14.1	<i>Grallator formosus</i> , Triassic of Connecticut (Lull 1953)	4.3	<i>Skartopus australis</i>
12.2	<i>Columbosauripus</i> (2 ichnospp.), Cretaceous of Canada and Algeria (both ichnospp. illustrated by Haubold 1971, q.v.)	3.8	<i>Plesiornis pilulatus</i> , Triassic of Connecticut (Lull 1953)
10.2	<i>Coelurosaurichnus</i> (5 ichnospp.), Triassic of Europe (all ichnospp. illustrated by Haubold 1971, q.v.)	3.7	<i>Wildeichnus navesi</i> , Jurassic of Argentina (Casamiquela 1964)
8.1	<i>Grallator</i> cf. <i>G. variabilis</i> , Triassic of Algeria (Bassoullet 1971)	3.4	<i>Grallator gracilis</i> , Triassic of Connecticut (Lull 1953)
		2.5	<i>Stenonyx lateralis</i> , Triassic of Connecticut (Lull 1953)
		0.4	<i>Coelurosaurichnus</i> ichnospp., Triassic of England (Wills and Sarjeant 1970)

imprints of *Columbosauripus* tend to be broader than those of *Skartopus*, and digit 4 is often considerably longer than digit 2 (see Haubold 1971, fig. 47). *Coelurosaurichnus* ichnospp. are distinguished from *Skartopus* by very distinct imprints of claws and phalangeal pads, by the common preponderance of digit 4 over digit 2, and (in many cases) by having digit 3 noticeably broader than the flanking digits. In a few instances, however, *Coelurosaurichnus* does resemble *Skartopus* in having the rear margin of the footprint arched to the front. Similarly *Grallator* ichnospp. differ from *Skartopus* in possessing well developed phalangeal pads, traces of acuminate claws and, very often, a pronounced 'spur' formed by the backwards extension of digit 4 (see Lull 1953). *Stenonyx* may be distinguished from *Skartopus* by the same features and, in some instances, by the presence of a hallux imprint. *Wildeichnus* appears to differ in possessing a prominent 'spur' behind digit 3 and in showing a clear imprint of the hallux. To summarize, *Skartopus* is similar in basic morphology to other coelurosaur footprints, but it may be distinguished from these through differences in divarication and relative lengths of the digits, through lacking imprints of phalangeal pads or of acuminate claws, through the absence of a posterior 'spur', through the absence of a hallux imprint, through the relative straightness of the digits, and through its high values for the ratios PL/FL and SL/FL.

## DISCUSSION

### SIZES AND SPEEDS OF TRACK-MAKERS

From studies of locomotion in living terrestrial vertebrates Alexander (1976) determined the following relationship between stride length ( $\lambda$ , in metres), height at the hip ( $h$ , also in metres) and speed ( $u$ , in metres per second):

$$(1) \quad \lambda/h \cong 2.3 (u^2/gh)^{0.3}$$

In this equation  $\lambda$  represents our measurement for stride length (SL), and  $g$  is a constant — the acceleration of free fall; the ratio  $\lambda/h$  is termed 'relative stride length' (Alexander 1976). Alexander indicated that this relationship seems to hold true, at least in general terms, for large and small animals, both bipeds and quadrupeds, at gaits from slow walk to fast run. In addition he observed that the relationship does not seem to be seriously affected by variation in the consistency of the substrate. With additional data from fast-moving African ungulates Alexander, Langman

and Jayes (1977) refined expression (1) to give:

$$(2) \quad \lambda/h \cong 1.8(u^2/gh)^{0.39}$$

These authors concluded that expression (2) is best applied to animals that are cantering or galloping, whereas expression (1) is appropriate for animals using slower gaits. In mammals the change from a walking gait to a trotting gait occurs when  $\lambda/h$  is approximately 2.0 (Alexander 1976); the change from trotting to galloping follows when  $\lambda/h$  has increased to about 2.9. This latter figure is derived from two generalizations presented by Alexander (1977). The first of these is that mammals tend to shift from a trotting or racking gait to a galloping or cantering gait when the quantity  $\hat{u}$  reaches a value of about 1.5. The quantity  $\hat{u}$ , or 'dimensionless speed', was defined by Alexander as follows:

$$(3) \quad \hat{u} = u(gh)^{0.5}$$

where  $h$  is expressed in metres and  $u$  is in m/s. The second generalization, which seems to apply to a wide variety of animals through a wide range of speeds, is that

$$(4) \quad \lambda/h \cong 2.3\hat{u}^{0.6}$$

where  $\lambda/h$  represents mean relative stride length. From these generalizations it may be assumed that the shift from trotting to galloping occurs when

$$(5) \quad \begin{aligned} \lambda/h &\cong 2.3 (1.5)^{0.6} \\ \lambda/h &\cong 2.9 \end{aligned}$$

Consequently it is possible to identify the gaits of dinosaurian track-makers on the basis of relative stride length, as follows:

*walk*:  $\lambda/h < 2.0$ ; locomotor performance equivalent to walking in mammals.

*trot*:  $\lambda/h = 2.0$  to  $2.9$ ; locomotor performance equivalent to trotting or racking in mammals.

*run*:  $\lambda/h > 2.9$ ; locomotor performance equivalent to cantering, galloping or sprinting in mammals.

To estimate the speeds of certain dinosaurs Alexander (1976) transformed expression (1) to give:

$$(6) \quad u \cong 0.25g^{0.5}\lambda^{1.67}h^{-1.17}$$

This equation was then applied to data from dinosaur trackways, where  $\lambda$  could be measured directly (Alexander's  $\lambda =$  SL of our descriptions) and where  $h$  might be estimated from the size of the footprints. This method has since been applied to more than 50 dinosaur trackways, including a sample of those at Lark Quarry (Russell and Béland 1976; Tucker and Burchette 1977; Coombs 1978; Thulborn and Wade 1979;

Farlow 1981; Kool 1981; Thulborn 1981, 1982). Table 3 presents a summary of the speeds so far estimated in this way.

Figures listed in Table 3 for the Lark Quarry dinosaurs are preliminary estimates, and they will be revised in the present work. Our discussion will focus on the problem of estimating  $h$  on the basis of footprint dimensions. It is desirable that  $h$  should be estimated with reasonable care, because an underestimate will generate an overestimate of the track-maker's speed; conversely an overestimate of  $h$  will generate an underestimate of speed. In some instances the hindlimb length of a dinosaurian track-maker has been estimated from the evidence of pace length or stride length (e.g. Avnimelech 1966); an estimate of this type is of questionable value, simply because pace length and stride length vary according to the gait and speed of the track-maker (Lull 1953, p. 146). In other cases hindlimb length has been estimated on

the basis of footprint dimensions; for example, Avnimelech (1966, p. 5) suggested that in the footprints of bipedal dinosaurs the length of digit 3 represented about 18% of hindlimb length. Elsewhere Alexander suggested (1976) that  $h$  could be calculated as approximately four times footprint length for a variety of dinosaurian track-makers, both bipeds and quadrupeds, and this suggestion has been rather widely accepted (see all sources cited in Table 3). However, Coombs (1978) expressed some reservations about this generalization, and Alexander (1976) did mention that footprint length could represent anything between  $0.23h$  and  $0.28h$  in the bipedal dinosaurs that he examined. In discussing the sizes and speeds of the Lark Quarry track-makers we will investigate some other methods for estimating  $h$ .

In comparing the sizes, weights and speeds of various dinosaurs Coombs (1978, Table 2) drew a

TABLE 3: SUMMARY OF SIZES AND SPEEDS PREVIOUSLY ESTIMATED FOR DINOSAURIAN TRACK-MAKERS.

ichnotaxa or track-makers	(N)	$h$ (m)	$u$ (m/s)	$u$ (km/h)	$\lambda/h$	gait	source
Bipedal dinosaurs	(6)	0.6–2.1	1.2–3.6	4.3–13.0	1.2–2.5	walk (4) trot (2)	Alexander 1976
Sauropods	(2)	1.5–3.0	1.0–1.1	3.6–4.0	0.8–1.1	walk	
Ornithomimid	(1)	1.2	1.8	6.4	1.5 <sup>e</sup>	walk	Russell and Béland 1976
<sup>a</sup> Giant ornithopod	(1)	3.4	7.5	27.1	2.7 <sup>c</sup>	trot	
<sup>a</sup> Giant ornithopod	(1)	3.4	2.4	8.5	1.3	walk	Thulborn 1981
? <i>Anchisauripus</i>	(2)	0.4–0.6 <sup>e</sup>	1.3–2.2 <sup>x</sup>	4.5–7.9	1.3–1.4 <sup>c</sup>	walk	Tucker and Burchette 1977
Carnosaur	(1)	2.6	2.3	8.2	1.4	walk	Thulborn and Wade 1979
Ornithopods	(10)	<1.0	4.3 <sup>m</sup>	15.5 <sup>m</sup>	>2.0	trot/run	(Lark Quarry)
Coelurosaurs	(10)	<1.0	3.6 <sup>m</sup>	13.0 <sup>m</sup>	>2.0		
<i>Gypsichnites pacensis</i>	(1)	1.2	2.0	7.2 <sup>x</sup>	1.8	walk	
<i>Irenesauripus</i> spp.	(3)	1.5–2.1	1.4–2.7	5.0–9.7 <sup>x</sup>	1.2–1.6	walk	
<i>Irenichnites gracilis</i>	(1)	0.6	2.8	10.1 <sup>x</sup>	2.3	trot	Kool 1981
<i>Amblydactylus kortmeyeri</i>	(1)	0.5	1.1	4.0	1.5	walk	
<i>Tetrapodosaurus borealis</i>	(1)	1.4	0.9	3.2 <sup>x</sup>	0.9	walk	
<sup>f</sup> Theropods	(3)	1.2–1.5 <sup>e</sup>	8.3–11.9	29.9–42.8	3.7–4.9	run	
<sup>s</sup> Theropods	(3)	1.5–1.8 <sup>e</sup>	1.8–2.5	6.4–8.9	1.5–1.8	walk	Farlow 1981
Theropods	(15)	1.5 <sup>mc</sup>	4.2 <sup>m</sup>	15.2 <sup>m</sup>	2.3 <sup>m</sup>	trot	

a: two interpretations of single trackway.

f: three fastest of Farlow's 15 track-makers.

s: three slowest of Farlow's 15 track-makers.

e: figures estimated from published data.

m: mean.

x: Coombs (1978) provides different speed estimates, apparently through computational error (Farlow 1981).

distinction between 'height at hips' (as had been estimated by Colbert 1962) and 'standard [or skeletal] hindlimb length' (the sum of the lengths of femur, tibia and metatarsal 3). He indicated that there was sometimes a considerable difference between these two dimensions — particularly among large dinosaurs. In addition a rather similar distinction has been made between skeletal hindlimb length ( $h$ ) and 'height of the hindlimb' ( $H$ ) — the latter being defined as 'the

combined lengths of femur, tibia and longest metatarsal, plus an increment of 9% to account for ankle bones and for soft tissues at knee, ankle and sole' (Thulborn, 1982, p. 228). For present purposes these various dimensions are assumed to be roughly equivalent, on the grounds that they are likely to be of great significance only in large dinosaurs. Our estimates of  $h$  for the Lark Quarry track-makers (Tables 4 and 5) are based on osteometric data and may be regarded as

TABLE 4: ESTIMATES OF SIZE, SPEED AND RELATIVE STRIDE LENGTH FOR 57 *WINTONOPUS* TRACK-MAKERS.

	estimated $h$	estimated speed		estimated $\lambda/h$
	(cm)	(m/s)	(km/h)	
1.	13.7	2.8–3.5 (3.1)	10.0–12.5 (11.2)	3.6–4.2 (3.9)
2.	16.8	3.3–4.0 (3.6)	11.9–14.3 (12.9)	3.8–4.3 (4.0)
3.	16.3	(3.5)	(12.6)	(4.0)
4.	16.8	3.0–3.3 (3.1)	10.6–11.8 (11.3)	3.5–3.8 (3.6)
5.	18.9	2.9–3.3 (3.1)	10.5–11.9 (11.2)	3.3–3.6 (3.4)
6.	18.6	(3.2)	(11.6)	(3.5)
7.	18.4	3.4–3.9 (3.7)	12.1–14.0 (13.5)	3.7–4.1 (4.0)
8.	19.7	3.0–3.1 (3.0)	10.6–11.3 (11.0)	3.3–3.4 (3.3)
9.	20.1	3.8–4.4 (4.1)	13.7–15.8 (14.7)	3.9–4.4 (4.2)
10.	18.4	3.1–3.8 (3.4)	11.2–13.8 (12.4)	3.5–4.1 (3.8)
11.	20.4	3.8–4.2 (4.0)	13.6–15.2 (14.4)	3.9–4.2 (4.1)
12.	23.7	2.6–3.2 (2.9)	9.4–11.5 (10.5)	2.7–3.2 (3.0)
13.	27.1	4.0–4.5 (4.3)	14.5–16.1 (15.5)	3.7–4.0 (3.8)
14.	25.5	4.4–4.9 (4.6)	15.8–17.6 (16.7)	4.0–4.4 (4.2)
15.	29.1	4.5–5.0 (4.7)	16.1–18.0 (17.0)	3.9–4.2 (4.0)
16.	22.0	3.7–4.3 (3.9)	13.2–15.3 (14.0)	3.7–4.1 (3.9)
17.	29.6	(4.1)	(14.6)	(3.5)
18.	32.6	4.8–5.2 (5.0)	17.3–18.5 (17.9)	3.9–4.1 (4.0)
19.	27.4	4.3–5.0 (4.7)	15.3–17.8 (16.8)	3.8–4.3 (4.1)
20.	29.7	4.1–5.4 (4.6)	14.7–19.3 (16.5)	3.6–4.4 (3.9)
21.	29.2	(6.3)	(22.7)	(5.0)
22.	26.4	4.3–4.4 (4.3)	15.6–15.8 (15.6)	(3.9)
23.	30.7	3.8–4.3 (4.1)	13.7–15.6 (14.6)	3.3–3.7 (3.5)
24.	33.2	(3.5)	12.5–12.7 (12.6)	(3.0)
25.	34.7	4.1–4.9 (4.6)	14.6–17.8 (16.4)	3.3–3.9 (3.7)
26.	30.1	3.5–4.7 (4.2)	12.7–16.9 (15.2)	3.2–4.0 (3.7)
27.	33.6	(4.1)	(14.8)	(3.4)
28.	31.0	3.7–3.9 (3.8)	13.3–14.1 (13.7)	3.3–3.4 (3.3)
29.	34.2	3.8–5.0 (4.3)	13.7–18.0 (15.5)	3.2–4.0 (3.5)
30.	29.5	(4.3)	(15.5)	(3.7)
31.	32.4	4.3–4.5 (4.4)	15.6–16.2 (15.8)	3.6–3.7 (3.6)
32.	38.8	3.9–5.0 (4.5)	14.0–18.0 (16.2)	3.1–3.8 (3.5)
33.	29.2	3.2–3.4 (3.3)	11.6–12.3 (11.9)	3.0–3.1 (3.1)
34.	33.4	3.7–4.6 (4.1)	13.3–16.5 (14.9)	3.2–3.7 (3.4)
35.	33.7	(3.9)	(14.0)	(3.3)
36.	28.1	3.8–5.5 (4.9)	13.8–19.8 (17.7)	3.5–4.6 (4.2)

37.	45.6	5.8-6.3 (6.1)	20.9-22.7 (21.9)	4.0-4.2 (4.1)
38.	44.6	(5.7)	(20.4)	(3.9)
39.	37.1	(4.2)	(15.2)	(3.4)
40.	38.1	4.2-4.8 (4.5)	15.0-17.3 (16.2)	3.3-3.7 (3.5)
41.	35.8	3.2-4.9 (4.0)	11.4-17.7 (14.4)	2.7-3.8 (3.3)
42.	39.6	3.4-4.5 (3.9)	12.3-16.0 (14.0)	2.8-3.4 (3.1)
43.	49.3	5.6-6.5 (6.0)	20.0-23.2 (21.6)	3.7-4.2 (3.9)
44.	41.8	2.5-3.3 (3.1)	9.2-12.0 (11.0)	2.2-2.7 (2.5)
*45.	47.4	(1.1)	(4.0)	(1.5)
46.	49.4	(7.8)	(28.2)	(4.9)
47.	58.7	(4.0)	(14.4)	(2.7)
48.	61.5	6.0-7.6 (6.8)	21.8-27.3 (24.4)	3.6-4.3 (4.0)
49.	53.6	6.1-6.6 (6.4)	22.1-23.7 (22.9)	3.9-4.1 (4.0)
50.	54.9	5.0-7.0 (5.7)	18.0-25.0 (20.4)	3.3-4.2 (3.6)
51.	52.0	5.4-5.7 (5.5)	19.4-20.5 (19.9)	3.6-3.7 (3.6)
52.	60.3	6.1-6.5 (6.3)	22.1-23.4 (22.8)	3.7-3.9 (3.8)
53.	53.9	8.2-8.3 (8.2)	29.4-29.9 (29.7)	(4.9)
54.	61.9	(5.1)	(18.5)	(3.2)
55.	54.7	5.0-6.3 (5.7)	18.2-22.6 (20.7)	3.3-3.9 (3.7)
56.	70.0	5.4-7.0 (6.3)	19.6-25.1 (22.6)	3.2-3.9 (3.6)
57.	158.4	4.6-5.0 (4.8)	16.7-18.1 (17.2)	2.1-2.2 (2.1)
Means		4.3-4.8 (4.6)	15.4-17.4 (16.4)	3.5-3.9 (3.7)

\*New Quarry trackway.

For each track-maker we show the range and the mean (in parentheses) of speed and relative stride length. A single figure (in parentheses) indicates that only one stride could be measured, or that there was little or no variation in stride length. Figures for the New Quarry track-maker (No. 45) were excluded from calculations of overall means.

equivalent to skeletal hindlimb length. If these estimates were increased by 9% (to provide estimates of  $H$ , or 'height of the hindlimb') the mean increment for the ornithopod track-makers would be 3.1 cm; for the coelurosaur track-makers the mean increment would be 1.5 cm. These small increases in estimated body size would not affect the general conclusions that we draw regarding the speeds and gaits of the track-makers.

#### CARNOSAUR TRACKWAY

In the trackway of the Lark Quarry carnosaur footprint length ranges from 41 cm (estimated) to 64 cm; mean footprint length is 51.4 cm. With the assumptions used by Alexander (1976)  $h$  could be estimated to lie in the range 1.64 to 2.56 cm — with the mean estimate at 2.06 m. However, it seems legitimate to base our estimate of  $h$  on the best-preserved and most complete footprint; this particular footprint (number 3 in the trackway) is 64 cm long, providing estimated  $h$  of 2.56 m. The footprint has a well-defined rear margin, and its length is not exaggerated by scrape-marks; other footprints in the carnosaur trackway appear to have less complete impressions of the rear part of

the foot, and they would probably generate underestimates of  $h$  (and, in consequence, overestimates of the carnosaur's speed).

There are at least two other ways to estimate  $h$  for the Lark Quarry carnosaur. First it is possible to compare the sizes of carnosaur footprints to the sizes of carnosaur skeletons. Footprints attributed to tyrannosaurs are reported to reach a maximum length of about 80 cm (Haubold 1971), while the largest well-known tyrannosaur, *Tyrannosaurus rex*, has a skeletal hip height about 3.17 m (representing the sum of the lengths of femur, tibia and longest metatarsal). With the admittedly untestable assumption that the largest known footprints were made by animals about the size of *Tyrannosaurus*, skeletal hip height could be predicted as 3.96 times footprint length. In the case of the Lark Quarry carnosaur this method would indicate a skeletal hip height of about 2.54 m.

Next it is possible to make use of the fact that metatarsus length (MT) is strongly correlated with skeletal hip height in carnosaur — see Fig. 17, where the least squares regression line represents the following allometric equation:

$$(7) h \cong 4.15MT + 28.52 \text{ cm}$$



(In this equation all measurements are expressed in cm; Bartlett's three-group method (see Sokal and Rohlf 1969, p. 483) yields a virtually identical equation). To apply equation (7) in the case of the Lark Quarry carnosaur it is first necessary to estimate MT on the basis of footprint size. It should be possible to make such an estimate with a fair degree of accuracy because in many bipedal dinosaurs MT is roughly equivalent to the summed lengths of phalanges in digit 3 ( $\Sigma P$ ; see Figs 6 and 18, and various illustrations given by Coombs 1978); moreover, in a digitigrade animal

such as a dinosaur total footprint length (FL) should be slightly greater than  $\Sigma P$  (Fig. 18). In carnosaur MT seems to be a little greater than  $\Sigma P$  (see Russell 1970, Table 1, for data on Canadian carnosaur), but would probably have been less than FL (which comprised  $\Sigma P$ , claw sheath, joint capsules and, possibly, a 'heel' region supported by the distal part of the metatarsus). Evidently MT would have been somewhat less than total footprint length. For practical purposes we will assume that MT is roughly equivalent to footprint size index (SI) — which is also less than FL

TABLE 5: ESTIMATES OF SIZE, SPEED AND RELATIVE STRIDE LENGTH FOR 34 *SKARTOPUS* TRACK-MAKERS.

	estimated h (cm)	estimated speed (m/s)	estimated speed (km/h)	estimated $\lambda/h$
1.	13.3	3.0-4.2 (3.7)	10.8-15.1 (13.3)	3.8-5.0 (4.5)
2.	13.3	3.8-4.4 (4.2)	13.6-15.9 (15.0)	4.6-5.2 (4.9)
3.	14.4	2.8-3.3 (3.1)	10.2-12.0 (11.2)	3.6-4.0 (3.8)
4.	14.5	3.2-3.9 (3.5)	11.4-14.0 (12.6)	3.9-4.5 (4.2)
5.	14.8	3.5-4.1 (3.8)	12.5-14.7 (13.6)	4.1-4.7 (4.4)
6.	14.9	2.8-3.4 (3.0)	10.2-12.2 (10.8)	3.5-4.0 (3.7)
7.	15.0	2.9-3.3 (3.1)	10.6-11.9 (11.2)	3.6-3.9 (3.8)
8.	15.1	3.4-3.6 (3.5)	12.1-13.0 (12.5)	4.0-4.2 (4.1)
9.	15.2	3.1-3.8 (3.4)	11.3-13.8 (12.3)	3.8-4.4 (4.0)
10.	15.3	2.8-3.5 (3.0)	10.1-12.5 (10.9)	3.4-4.1 (3.7)
11.	15.5	3.3-3.4 (3.3)	11.8-12.3 (12.1)	3.9-4.0 (3.9)
*12.	15.5	3.4-3.6 (3.4)	12.1-12.8 (12.4)	3.9-4.1 (4.0)
13.	15.5	3.6-4.1 (3.9)	12.8-14.9 (14.0)	4.1-4.6 (4.4)
14.	15.6	3.4-3.8 (3.6)	12.2-13.5 (13.0)	4.0-4.3 (4.2)
15.	16.2	3.6-3.9 (3.7)	12.9-13.9 (13.3)	4.1-4.3 (4.2)
16.	16.3	2.8-3.2 (3.0)	10.2-11.4 (10.6)	3.4-3.7 (3.5)
17.	16.4	3.1-3.3 (3.2)	11.3-11.8 (11.6)	3.7-3.8 (3.7)
18.	16.6	3.3-3.5 (3.4)	11.9-12.4 (12.1)	3.8-3.9 (3.8)
19.	16.6	(3.2)	(11.4)	(3.7)
20.	17.2	2.5-3.7 (3.1)	8.8-13.3 (11.3)	3.0-4.1 (3.6)
21.	17.7	2.8-3.9 (3.3)	9.9-13.9 (12.0)	3.2-3.8 (3.7)
22.	17.9	3.1-3.9 (3.3)	11.0-14.1 (12.0)	3.5-4.2 (3.7)
23.	17.9	2.5-3.1 (2.8)	9.0-11.3 (10.1)	3.0-3.5 (3.2)
24.	18.2	2.3-3.2 (2.6)	8.3-11.6 (9.5)	2.8-3.6 (3.1)
25.	18.2	2.2-2.8 (2.5)	8.0-10.2 (9.1)	2.7-3.2 (3.0)
26.	18.3	(3.2)	(11.7)	(3.6)
27.	18.5	2.6-2.8 (2.7)	9.4-10.1 (9.7)	3.0-3.2 (3.1)
28.	19.3	2.9-3.5 (3.2)	10.4-12.6 (11.4)	3.2-3.7 (3.5)
29.	19.3	2.5-2.6 (2.5)	8.9-9.3 (9.1)	2.9-3.0 (2.9)
30.	19.6	2.7-2.9 (2.8)	9.8-10.5 (10.1)	3.1-3.2 (3.1)
31.	19.9	3.2-3.7 (3.5)	11.7-13.2 (12.6)	3.5-3.8 (3.7)
32.	20.1	2.6-3.0 (2.8)	9.2-10.7 (10.1)	2.9-3.2 (3.1)
33.	21.6	2.5-3.1 (2.9)	9.1-11.3 (10.3)	2.8-3.3 (3.1)
34.	21.9	2.7-3.4 (3.0)	9.6-12.2 (10.6)	2.9-3.5 (3.1)
Means		3.0-3.5 (3.2)	10.7-12.5 (11.6)	3.5-3.9 (3.7)

For each track-maker we show the range and the mean (in parentheses) of speed and relative stride length. A single figure (in parentheses) indicates that only one stride could be measured, or that there was little or no variation in stride length.

\* Trackway No. 12 was made by an animal with consistent 'flat-footed' gait (see Plate 14, fig. B). The length of each footprint is exaggerated by an imprint of the metatarsus, and to estimate the animal's size and speed our measurements of total footprint length were reduced by 50%.

because the footprint is longer than wide. The best-preserved carnosaur footprint at Lark Quarry has SI of 57.69 cm; by substituting this figure for MT in equation (7) we can estimate skeletal hip height to have been about 2.68 m.

These various estimates are in close agreement, and they indicate that the Lark Quarry carnosaur was between 2.54 and 2.68 metres in height at the hip. The mean figure, which we will use for estimating the animal's speed, is 2.59 m. Apparently the animal was about the same size as one specimen of the Canadian carnosaur *Albertosaurus libratus* (National Museum of Canada, No. 2120, with  $h$  about 2.63 m; Lambe 1917); it would have been intermediate in size between specimens of *Daspletosaurus torosus* ( $h$  2.40 m, estimated from data of Russell 1970) and *Tyrannosaurus rex* ( $h$  about 3.17 m; Osborn 1917).

The strides of the Lark Quarry carnosaur range in length from 2.82 m to 3.74 m (mean 3.31 m). Consequently relative stride length ( $\lambda/h$ ) is estimated to range from 1.09 to 1.44 (mean 1.28). In every stride  $\lambda/h$  is well below 2.0, which indicates that the animal was using a walking gait (Alexander 1976) and that its speed is most appropriately estimated with equation (6). The carnosaur's progress may be plotted in some detail, as follows:

stride	speed		$\lambda/h$
	(m/s)	(km/h)	
1	2.34	8.43	1.44
2	2.13	7.65	1.36
3	2.35	8.47	1.44
4	2.34	8.43	1.44
5	1.76	6.32	1.21
6	1.67	6.03	1.18
7	1.74	6.26	1.20
8	1.54	5.54	1.12
9	1.47	5.28	1.09
means	1.93	6.93	1.28

The animal took a slightly weaving course (Fig. 3), during which it showed a definite tendency to decelerate (i.e. to shorten its strides). Its first four strides are relatively long and are defined by very deep footprints; the animal then switched quite abruptly to a series of shorter strides (Nos. 5-9, Fig. 22A) and its footprints became noticeably shallower. The last two strides are the shortest and were taken as the animal made a sharp turn to its right.

#### ORNITHOPOD TRACKWAYS

In our preliminary account of Lark Quarry (1979) the makers of the ornithopod trackways

(*Wintonopus*) were estimated to range from the size of bantams to the size of ostriches; their mean speed was calculated to be about 4.31 m/s (15.52 km/h). These preliminary estimates of size and speed were derived from a small sample (parts of 10 trackways) with the methods described by Alexander (1976).

In the 57 trackways studied here mean footprint length ranges from 2.40 cm to 22.75 cm (mean 6.68 cm); by excluding the earlier-formed trackway of the exceptionally large animal (No. 57 in Table 4) the range of means for footprint length is reduced to 2.40 — 10.86 cm (with overall mean 6.39 cm). Alexander assumed (1976) that height at the hip ( $h$ ) could be estimated as approximately four times footprint length for a variety of dinosaurian track-makers; if we apply this assumption to the *Wintonopus* data the track-makers are estimated to have had  $h$  ranging between 9.60 and 43.44 cm (mean 25.58 cm), with the single large individual at 91.0 cm. However, Alexander indicated that footprint length (FL) could represent anything between  $0.23h$  and  $0.28h$  in the bipedal dinosaurs that he studied (1976), and it seems worthwhile to investigate an alternative method for estimating  $h$ .

Analysis of variance (p. 424) revealed considerable variation in footprint length within the *Wintonopus* trackways. Within a single trackway there may occur foreshortened ('stubby-toed') prints, normal prints and attenuated toe scratches from a single foot (Figs 5L and 7, Pl. 10D). Consequently mean footprint length for a trackway may not be a satisfactory indicator of the track-maker's size — because the mean will be affected by the relative frequencies of foreshortened and attenuated footprints. Fortunately footprint size index (SI) seems to be a reliable guide to the relative sizes of two or more track-makers: the index differs from one trackway to the next, but is virtually constant within any one trackway. Footprint size index is usually a little greater than footprint length in *Wintonopus* (because the footprints are usually broader than long), and it has the following range: 2.89 to 12.69 cm (mean 6.74 cm), with the single large individual at 26.59 cm. Two observations make it possible to estimate  $h$  on the basis of SI: first, in the foot skeletons of many ornithopods the summed lengths of phalanges in digit 3 ( $\Sigma P$ ) is roughly equal to the length of metatarsal 3 (MT; see Figs 6A, C); and, second, there exists a strong correlation between MT and skeletal hip height in ornithopods (see Fig. 19). So, to calculate  $h$  for the *Wintonopus* track-makers there seems to be only one prerequisite —

an estimate of MT (or of  $\Sigma P$ ) derived from SI. By dinosaurian standards the *Wintonopus* track-makers seem to have been fairly small animals, so that absolute differences between FL and  $\Sigma P$  (and hence MT) are likely to have been small. For the sake of convenience we will assume that SI is roughly equal to MT. It may be noted that SI is usually a little greater than FL, because the *Wintonopus* footprints are normally a little broader than long. Consequently our estimates of  $h$  (based on SI) will tend to be slightly greater than similar estimates based on FL. This difference will, on the whole, have a conservative effect — in the sense that the sizes of track-makers may overestimated, and their speeds may be underestimated.

Figure 19A shows the relationship between MT and skeletal hip height in a sample of 32 ornithopod skeletons (with MT ranging from 6.3 to 38.1 cm); the least squares regression line represents the following allometric equation:

$$(8) \quad h \cong 3.76MT^{1.16}$$

where both  $h$  and MT are expressed in centimetres. By substituting SI for MT in this equation we estimate that the Lark Quarry ornithopods ranged in skeletal hip height from 12.86 to 71.57 cm (mean 34.41 cm), with the solitary large individual at 168.81 cm. However, the regression equation for cursorial ornithopods (with femur shorter than tibia) is slightly different from that for graviportal ornithopods (with femur longer than tibia); for cursorial ornithopods the equation is:

$$(9) \quad h \cong 3.97MT^{1.08}$$

while for graviportal ornithopods it is:

$$(10) \quad h \cong 5.06MT^{1.07}$$

The two regression lines, which are shown in Fig. 19B, have similar slopes but different intercepts. In general terms equation (10) provides estimates of  $h$  about 20 to 25% greater than those derived with equation (9). The Lark Quarry ornithopods seem to have been small animals, judging from the size of their footprints, and this might indicate that equation (9), based on data from cursorial ornithopods, should be used to estimate  $h$ . It must be admitted, however, that the exact identity of the *Wintonopus* track-makers is unknown — beyond that fact that they seem to have been ornithopods of some sort. For this reason we have obtained three estimates of  $h$  for each track-maker (by substituting SI for MT in each of the preceding equations), and we will use the mean figure in calculating the speed of each animal. These mean values for  $h$  range from 13.70 to

69.98 cm (overall mean 34.82 cm), excluding the single large animal with  $h$  estimated to be 158.59 cm.

Of the 57 *Wintonopus* trackways examined here only one appears to have been made by an animal more than 1 metre high at the hip. Forty-six of the track-makers (81%) are estimated to have  $h$  less than 50 cm, and 24 of them (42%)  $h$  less than 30 cm. In all cases Alexander's assumptions (1976) would provide smaller estimates of  $h$ .

In terms of general body size the Lark Quarry animals may be compared with cursorial ornithopods of the families Fabrosauridae, Hypsilophodontidae and Heterodontosauridae (see skeletal reconstructions or flesh restorations given by Galton 1974, Thulborn 1972, Santa Luca et al. 1974); they might also be compared with juvenile specimens of some bigger graviportal ornithopods (e.g. the juvenile hadrosaurs described by Horner and Makela 1979) and with the juvenile psittacosaur recently described by Coombs (1980a, 1982). From the evidence of trackways it does not seem possible to decide with certainty whether the Lark Quarry ornithopods were small cursorial forms ranging up to adult status, or whether they were juveniles of some bigger graviportal ornithopod. Neither of these possibilities can be dismissed entirely: two types of small ornithopod, resembling hypsilophodontids, are reported from the Cretaceous of Victoria (Flannery and Rich 1981), and a large ornithopod with  $h$  about 2.44 m was recently described from the Lower Cretaceous of Queensland (*Muttaborrasaurus*, Bartholomai and Molnar 1981). In either case it would still seem reasonable to regard the smallest (at least) of the Lark Quarry track-makers as juvenile animals. It has sometimes been supposed that juvenile dinosaurs were rare (Richmond 1965, Leonardi 1981), but Horner and Makela (1979) found that more than 80% of dinosaur specimens collected from the Two Medicine Formation (Upper Cretaceous) of Montana could be identified as juveniles or subadults. It seems that juvenile dinosaurs may have been quite common, at least in some localities.

The curve illustrating size frequency distribution for the *Wintonopus* track-makers is distinctly skewed and is similar to the type of curve derived by Boucot (1953) from 'life assemblages' of fossils (see Fig. 21A). The curve might be interpreted in any of several ways. First it could simply be regarded as a survivorship curve for a population of small cursorial ornithopods. According to this interpretation the

animals would normally have grown to achieve  $h$  of about 30 cm (peak of curve); thereafter the mortality rate would have reached its maximum (steepest part of curve), with fewer and fewer animals surviving to reach greater and greater size (by virtue of the indeterminate growth prevailing among reptiles). This interpretation assumes, of course, that the sample of 57 track-makers is truly representative of the dinosaur population from which it was drawn; it also assumes the existence and constancy of some strong correlation between size and age. Secondly it is possible to interpret Fig. 21A as a survivorship curve based on a sample drawn from a population of big graviportal ornithopods (with assumptions as above). In this case it would appear that there was a high rate of mortality among juveniles or subadults once these had attained  $h$  of about 40 cm. The adults, presumably with  $h$  of 1.5 metres or more, would then have been comparatively rare and relatively long-lived. Next there is the possibility that our sample of 57 track-makers is not a representative one: it could comprise animals from two or more species, or there could be serious under-representation of bigger animals in a single species. (It seems scarcely possible that smaller animals could be under-represented). There is no obvious reason to assume that the *Wintonopus* trackways were produced by two or more different types of dinosaur: none of the frequency distributions is strongly bimodal (Figs 8 and 9), there are impressive correlations between any two dimensions of the footprints and trackways (Fig. 10), and all the footprints can be interpreted as those of animals sharing one distinctive pattern of foot structure (Fig. 6C) and using the same gait (Fig. 11). We cannot discount entirely the possibility that our sample of 57 *Wintonopus* trackways might be heterogeneous (in which case we could deduce nothing about the population structure and possible affinities of the track-makers), but this possibility does seem rather unlikely: it supposes the co-existence of two or more dinosaurian species, each of which is represented by juveniles or is characteristically of small size, and each of which produced *Wintonopus*-like trackways. The final possibility is that bigger animals did exist, but that they are under-represented in our sample. Under-representation of bigger animals could not be regarded as an effect of sampling: trackways of large animals are not common at Lark Quarry, and we ensured that our sample contained data from the largest and second-largest examples of *Wintonopus*. Consequently this final possibility must imply that large and small animals were

segregated, either fortuitously or through some deliberate strategy on the part of the potential track-makers. Of all these possible interpretations the simplest would certainly seem to be the first — that the sample of 57 trackways is representative of a dinosaur population in which animals rarely grew to hip heights estimated at greater than 70 cm. Finally there is some evidence of three size classes in the *Wintonopus* sample (note the three clumps of data points in Fig. 10). In terms of estimated hip height these three size classes have approximate limits of 13 to 20 cm, 25 to 40 cm, and 50 to 60 cm. There is no way to investigate the possibility that these size groupings might be equivalent to age classes.

From our estimates of  $h$  it is calculated that the mean value of  $\lambda/h$  per trackway ranges from 2.69 to 5.03 (overall mean 3.69); these figures exclude values for the solitary large animal ( $\lambda/h$  2.10), and for the New Quarry track-maker. It seems that all the *Wintonopus* track-makers at Lark Quarry were using a gait faster than a walk ( $\lambda/h$  greater than 2.0). Two individuals were apparently moving at a trot or a slow run (with mean  $\lambda/h$  at 2.1 and 2.7), whereas all the others (96%) were using a fast running gait equivalent to a mammalian gallop (with  $\lambda/h$  at 3.0 or greater).

The 56 ornithopod track-makers at Lark Quarry all have  $\lambda/h$  estimated to be greater than 2.0, so that their speeds are most appropriately estimated by means of equation (2) re-written as:

$$(11) \quad u \equiv [gh(\lambda/1.8h)^{2.56}]^{0.5}$$

In this equation  $\lambda$  and  $h$  are expressed in metres and  $u$  is in metres per second. Mean speed per trackway is estimated to range from 2.92 m/s (10.52 km/h) to 8.24 m/s (29.66 km/h), with the overall mean for 55 animals (excluding solitary large individual) at 4.48 m/s (16.12 km/h). The one exceptionally large animal has an estimated mean speed of 4.78 m/s (17.22 km/h). The minimum speed estimated for any of these track-makers, on the basis of its single shortest stride, is 2.22 m/s (8.00 km/h); the maximum speed estimated for any of the track-makers, on the basis of its single longest stride, is 8.30 m/s (29.88 km/h).

The single *Wintonopus* trackway at New Quarry has mean SI of 8.91 cm; for this track-maker  $h$  is estimated to have been 47.4 cm, indicating  $\lambda/h$  of about 1.54. The New Quarry animal was not associated with those at Lark Quarry, and it seems to have been using a different gait (walking rather than running). Its speed, which is best calculated with equation (6), is estimated to have been 1.11 m/s (3.98 km/h).

Even if its speed is estimated, inappropriately, with equation (11) the New Quarry animal would still seem to have been moving more slowly than any of the Lark Quarry track-makers (i.e. at 1.76 m/s, or 6.34 km/h).

The estimated sizes, speeds and relative stride lengths of all 57 *Wintonopus* track-makers are summarized in Table 4. The animals seem to have maintained fairly constant speeds, and in most cases mean stride length for the second half of the trackway differs only slightly from mean stride length for the first half (see Fig. 23A). On average the difference between these two means is an increase of 1.3%. An analysis of stride lengths in the longest section of ornithopod trackway (No. 41 in Table 4, comprising 17 strides) reveals no consistent trend towards acceleration (lengthening of strides) or deceleration (shortening of strides). Mean stride length for the second half of this trackway is 6.8% less than mean stride length for the first half. Short sections of this trackway (Fig. 22B) might give the impression of a strong tendency to lengthen or shorten the strides, yet the track-maker seems, overall, to have maintained a reasonably consistent stride length ( $116.82 \pm 11.13$  cm; CV 9.5%).

To summarize, the *Wintonopus* trackways at Lark Quarry seem to have been made by small ornithopod dinosaurs, mostly less than 60 cm in height at the hip. All these dinosaurs seem to have been using a fast running gait, with  $\lambda/h$  in most cases between 3.2 and 4.1. For the majority speeds are estimated between 3.4 m/s (12.2 km/h) and 5.6 m/s (20.2 km/h), and there is no clear evidence that the animals were accelerating or decelerating.

#### COELUROSAUR TRACKWAYS

In our preliminary study of Lark Quarry (1979) we estimated that the makers of the coelurosaur trackways (*Skartopus*) had a size range equivalent to that between bantams and half-grown emus; their mean speed was estimated to have been about 3.62 m/s (13.04 km/h). These preliminary estimates of size and speed were obtained by applying Alexander's method (1976) to parts of 10 trackways.

With Alexander's working assumption (1976) that footprint length (FL) represents about  $0.25h$  it may be estimated that the 34 trackways studied here were made by animals ranging from 14.5 to 22.5 cm in height at the hip (overall mean 17.8 cm). But again, as with the ornithopod track-makers, it may be worthwhile to investigate another method for estimating  $h$ .

Analysis of variance (p. 429) reveals that FL is highly variable within and among the *Skartopus* trackways; so, too, are footprint width (FW) and footprint size index (SI). Consequently there seems to be little advantage in selecting SI, rather than FL or FW, as an indicator to the relative sizes of the track-makers. None of these variables appears to be a very reliable guide to the relative sizes of the track-makers, but this fact is not particularly important because all these animals seem to have been much the same size anyway. Our estimates of size and speed for the track-makers will be based on mean FL per trackway. It might not be appropriate to base these estimates on mean SI (as was done for the ornithopod trackways) because this is usually less than actual footprint length — on account of the footprints usually being longer than broad. This preference for FL, rather than SI, will have a conservative effect — in that estimates of  $h$  will tend to be increased and estimates of speed will tend to be decreased. In the 34 trackways studied here mean FL ranges from 3.62 to 5.62 cm, with the overall mean at  $4.46 \pm 0.50$  cm.

In a variety of coelurosaurs MT (the length of metatarsal 3) is strongly correlated with skeletal hip height; this relationship illustrated in Fig. 20, where the least squares regression line represents the following allometric equation:

$$(12) \quad h \cong 3.06MT^{1.14}$$

Both MT and  $h$  are expressed in centimetres. To estimate  $h$  for the Lark Quarry coelurosaurs we will substitute FL for MT in this equation, on the assumption that these two dimensions were roughly equal. This assumption is reasonable because both dimensions were probably a little greater than  $\Sigma P$  (summed lengths of phalanges in digit 3). The slight preponderance of FL over  $\Sigma P$  is apparent from Fig. 18; from various illustrations of coelurosaur foot skeletons it appears that MT is also a little greater than  $\Sigma P$  — in a ratio about 11:10 (see Figs 6D, E, and references given in caption to Fig. 20).

By substituting FL for MT in equation (12) we estimate that the Lark Quarry coelurosaurs ranged from 13.27 cm to 21.93 cm in height at the hip (with mean for the 34 animals at  $16.92 \pm 2.23$  cm). These estimates are slightly smaller than those obtained with Alexander's assumption that  $h$  is approximately four times FL; for the smallest track-maker the two estimates differ by 12 mm, and for the largest they differ by 6 mm. These differences are unlikely to be of great significance, especially since Alexander's work (1976) indicates that  $h$  could represent anything

from about 3.6FL to about 4.3FL in the various bipedal dinosaurs that he studied. Moreover these differences will not affect the general conclusions that we draw regarding the gaits and speeds of the track-makers (see Table 6, where our estimates for  $h$  are increased by about 40 to 50%).

From these estimates it seems that the *Skartopus* track-makers were somewhat smaller than the familiar coelurosaurs *Coelophysis* ( $h$  from 33.7 to 55.9 cm in 13 specimens listed by Colbert 1964), *Ornitholestes* ( $h$  about 48.3 cm, Osborn 1917) and *Podokesaurus* ( $h$  25.5 cm, Talbot 1911). The only well known coelurosaur of comparable size would seem to be *Compsognathus*, with  $h$  as little as 21.1 cm (for holotype, estimated from measurements given by Ostrom 1978). However, the *Skartopus* footprints do agree in size with many other footprints attributed to coelurosaurs (see Table 2).

The size frequency distribution for the *Skartopus* track-makers is distinctly skewed (Fig. 21B) and is open to the several interpretations that were considered earlier for the *Wintonopus* track-makers. The possible interpretations may be summarized as follows:

1. The 34 *Skartopus* track-makers represent a coelurosaur population in which individual animals grew to a maximum hip height estimated at 22 cm. This interpretation assumes that the sample of 34 track-makers is truly representative of the population from which it was drawn (i.e. that it includes both juveniles and adults), and that there existed a strong unvarying correlation between size and age.

2. The 34 track-makers are juveniles of some type of theropod dinosaur that grew to greater size — though the bigger individuals are not represented at Lark Quarry. This implies that large and small animals were segregated, either by chance or through their behaviour.

3. The sample of 34 trackways is heterogeneous. This assumes that two or more types of small (or juvenile) dinosaurs made identical trackways at a single site, and that they did so at approximately the same time.

All these possible interpretations involve untestable assumptions, but the first of them would seem to be the simplest. In any case it is noteworthy that the *Skartopus* track-makers must have been remarkably small animals by dinosaurian standards. Even if it is assumed that the track-makers were exceptionally long-legged animals resembling ornithomimids (or 'ostrich dinosaurs') it may be estimated that the largest of

them was less than 32 cm in height at the hip (see Table 6 and further discussion below).

With our estimates of  $h$  the mean value of  $\lambda/h$  per *Skartopus* trackway is found to range from 2.90 to 4.94, with the overall mean at 3.71. In only three trackways is minimum  $\lambda/h$  (based on the shortest stride) estimated to be less than 2.9, and in no case does it fall below 2.7. Evidently all 34 track-makers were using a fast running gait. These figures for  $\lambda/h$  indicate that the speeds of the track-makers are most appropriately estimated by means of equation (11). Mean speed per trackway is estimated to range from 2.53 m/s (9.09 km/h) to 4.16 m/s (14.98 km/h), with the overall mean at 3.22 m/s (11.58 km/h). The minimum speed estimated for any of the track-makers, on the basis of its single shortest stride, is 2.23 m/s (8.03 km/h); the maximum speed estimated for any of the track-makers, on the basis of the single longest stride, is 4.42 m/s (15.91 km/h).

Table 5 presents a summary of estimated size, speed and relative stride length for each of the 34 track-makers. There is no clear indication that the animals were either accelerating or decelerating. In most cases mean stride length for the second half of a trackway differs only slightly from mean stride length for the first half (Fig. 23B). On average this difference between the two means is a decrease of about 2.1%. From Fig. 23B it appears that the majority of track-makers showed a slight reduction in stride length during their progress. However, this tendency to shorten the strides is neither consistent nor well-marked, and it is probably of little significance. By way of illustration Fig. 22C shows an analysis of the longest section of coelurosaur trackway (No. 20 in Table 5, comprising 22 strides): in the latter half of this trackway mean stride length is 2.5% less than mean stride length in the first half, but there is no consistent trend towards progressive shortening of the strides. Short sections of the trackway could give the impression of a strong trend to shortening or lengthening the strides, yet the track-maker seems, overall, to have maintained a fairly consistent stride length ( $61.77 \pm 5.40$  cm; CV 8.7%).

In summary, the *Skartopus* trackways seem to have been produced by small coelurosaurs, all of which are estimated to have been less than 22 cm high at the hip. All of these animals seem to have been using a fast running gait; estimates of  $\lambda/h$  are in most instances greater than 2.9, though a few trackways include short strides indicating occasional lapses of  $\lambda/h$  as low as 2.7. Mean

TABLE 6: ESTIMATES OF SIZE, SPEED AND RELATIVE STRIDE LENGTH FOR 34 *SKARTOPUS* TRACK-MAKERS — WITH THE ASSUMPTION THAT THESE WERE ANIMALS RESEMBLING ORNITHOMIMIDS. RANGES AND MEANS OF ESTIMATES SHOWN AS IN TABLE 5.

	h (cm)	speed (m/s)	speed (km/h)	$\lambda/h$
1.	19.5	2.2-3.1 (2.8)	8.0-11.1 (9.9)	2.6-3.4 (3.1)
2.	19.6	2.8-3.3 (3.1)	10.1-11.8 (11.1)	3.1-3.5 (3.4)
3.	20.9	2.1-2.5 (2.3)	7.6-8.9 (8.4)	2.4-2.8 (2.6)
4.	21.1	2.4-2.9 (2.6)	8.5-10.4 (9.4)	2.7-3.1 (2.9)
5.	21.5	2.6-3.0 (2.8)	9.4-10.9 (10.2)	2.8-3.2 (3.0)
6.	21.6	2.1-2.5 (2.3)	7.6-9.1 (8.1)	2.4-2.8 (2.5)
7.	21.7	2.2-2.5 (2.3)	7.9-8.9 (8.3)	2.5-2.7 (2.6)
8.	21.9	2.5-2.7 (2.6)	9.0-9.7 (9.4)	2.7-2.9 (2.8)
9.	22.0	2.3-2.9 (2.6)	8.4-10.3 (9.2)	2.6-3.0 (2.8)
10.	22.1	2.1-2.6 (2.3)	7.5-9.3 (8.2)	2.4-2.8 (2.5)
11.	22.4	2.5-2.6 (2.5)	8.9-9.2 (9.1)	2.7-2.8 (2.7)
*12.	22.4	2.5-2.8 (2.6)	9.0-9.6 (9.3)	2.7-2.9 (2.8)
13.	22.4	2.7-3.1 (2.9)	9.6-11.2 (10.5)	2.9-3.2 (3.1)
14.	22.6	2.6-2.8 (2.7)	9.2-10.2 (9.8)	2.8-3.0 (2.9)
15.	23.2	2.7-2.9 (2.8)	9.7-10.5 (10.0)	2.8-3.0 (2.9)
16.	23.4	2.1-2.4 (2.2)	7.7-8.5 (8.0)	2.4-2.6 (2.4)
17.	23.5	2.4-2.5 (2.4)	8.5-8.9 (8.7)	(2.6)
18.	23.8	2.5-2.6 (2.5)	9.0-9.4 (9.1)	(2.7)
19.	23.8	(2.4)	(8.6)	(2.6)
20.	24.6	1.9-2.8 (2.4)	6.7-10.0 (8.5)	2.1-2.8 (2.5)
21.	25.3	2.1-2.9 (2.5)	7.5-10.6 (9.1)	2.3-2.9 (2.6)
22.	25.4	2.3-3.0 (2.5)	8.4-10.7 (9.1)	2.4-2.9 (2.6)
23.	25.4	1.9-2.4 (2.1)	6.8-8.5 (7.7)	2.1-2.5 (2.3)
24.	25.8	1.7-2.4 (2.0)	6.3-8.8 (7.2)	1.9-2.5 (2.2)
25.	25.9	1.7-2.1 (1.9)	6.1-7.7 (6.9)	1.9-2.3 (2.1)
26.	26.0	(2.5)	(8.9)	(2.5)
27.	26.2	2.0-2.1 (2.0)	7.2-7.7 (7.4)	2.1-2.3 (2.2)
28.	27.2	2.2-2.7 (2.4)	7.9-9.6 (8.7)	2.3-2.6 (2.5)
29.	27.3	1.9-2.0 (1.9)	6.8-7.1 (6.9)	2.0-2.1 (2.0)
30.	27.6	2.1-2.2 (2.2)	7.5-8.0 (7.8)	2.2-2.3 (2.2)
31.	27.9	2.5-2.8 (2.7)	8.9-10.1 (9.7)	2.5-2.7 (2.6)
32.	28.2	2.0-2.3 (2.1)	7.1-8.2 (7.7)	2.1-2.3 (2.2)
33.	30.1	1.9-2.4 (2.2)	7.0-8.7 (8.0)	2.0-2.4 (2.2)
34.	30.5	2.1-2.6 (2.3)	7.4-9.4 (8.2)	2.1-2.5 (2.2)
Means		2.3-2.6 (2.4)	8.1-9.5 (8.7)	2.4-2.7 (2.5)

estimated speeds of the track-makers are generally in the range 2.82 m/s to 3.61 m/s (10.16 to 13.00 km/h), and there is no clear indication that the animals were either accelerating or decelerating.

The preceding estimates of size and speed depend on the assumption that the Lark Quarry track-makers had hindlimb proportions similar to those in 'typical' coelurosaurs such as *Coelophysis*, *Compsognathus* and *Ornitholestes*. However, one group of small to medium-sized theropod dinosaurs — the ornithomimids or 'ostrich dinosaurs' — is characterized by unusual hindlimb proportions: these animals have exceptionally long hindlimbs terminating in relatively short toes. For the sake of completeness

we will examine the possibility that *Skartopus* trackways might have been made by animals resembling ornithomimids.

From published measurements of ornithomimid skeletons (Russell 1972 — *Ornithomimus*, *Struthiomimus*, *Dromiceiomimus*; Osmólska et al. 1972 — *Gallimimus*) it appears that MT represents something between 1.45 and 1.72 times  $\Sigma P$  (the mean figure derived from 9 specimens being 1.57). Since FL was probably a little greater than  $\Sigma P$  (see Fig. 18) we may assume, for the sake of convenience, that MT was equivalent to about 1.5FL. From the same osteometric data it seems that there is a strong positive correlation between MT and skeletal hip height ( $r = 0.997$ ,  $N = 9$ ); the latter may be

predicted by means of the following allometric equation:

$$(13) \quad h \cong 3.49MT^{1.02}$$

where  $h$  and  $MT$  are expressed in centimetres. If the Lark Quarry coelurosaurs resembled ornithomimids in limb proportions their skeletal hip heights might, then, be estimated as follows:

$$(14) \quad h \cong 3.49(1.5FL)^{1.02}$$

This method provides estimates of  $h$  ranging from 20.44 to 31.96 cm (with overall mean of 25.27 cm). Consequently estimates of mean  $\lambda/h$  per trackway would range from 1.96 to 2.88 (with overall mean 2.49). In only two of the 34 cases would the estimate for mean  $\lambda/h$  be less than 2.0 (actually 1.99 and 1.96). These figures would indicate that all the *Skartopus* track-makers were trotting or running (or, in two cases, were at least on the point of breaking into a trot). Estimates of mean speed per trackway, obtained with equation (11), range from 1.85 m/s to 2.97 m/s (6.67 km/h to 10.69 km/h), with the overall mean at 2.33 m/s (8.40 km/h). These particular estimates of size, speed and relative stride length are summarized in Table 6.

It seems difficult to escape the conclusion that *Skartopus* trackways are those of running dinosaurs — even with the assumption that these might have been exceptionally long-legged dinosaurs resembling ornithomimids. There are at least two good reasons for believing that the track-makers were not ornithomimids. First there is simply the matter of size: the *Skartopus* footprints are much smaller than the foot skeleton in any specimen of ornithomimid dinosaur so far described. In the smallest of the complete foot skeletons listed by Osmólska et al. (1972, p. 131)  $\Sigma P$  is 12.8 cm. One smaller example is listed by these authors, but it lacks the penultimate phalanx in digit 3; for this specimen we estimate  $\Sigma P$  to have been about 9.0 cm. In the ornithomimids described by Russell (1972)  $\Sigma P$  ranges from 21.5 cm to more than 25.5 cm. Footprints attributed to ornithomimids, or to unknown but presumably similar dinosaurs, have  $FL$  from about 10 cm (*Hoplichnus shingi*, Welles 1971) to about 28 cm (*Ornithomimipus angustus*, Sternberg 1926). By comparison the largest figure for mean  $FL$  in any of the *Skartopus* trackways is 5.62 cm. In the second place there seem to be no certainly-identified skeletal remains of ornithomimids from the Gondwana continents. A few bones (dorsal vertebrae and a phalanx) from the Lameta Formation of India were described by von Huene and Matley (1933) as *Ornithomimoides mobilis* and *O. barasimlensis*,

but Osmólska et al. regarded the material as 'systematically insufficient' (1972, p. 104). Russell (1972) considered the two species to be *nomina vana*. Molnar (1980), examining these and other records, concluded that there was no evidence suggesting that ornithomimids existed on the southern continents. In summary, the *Skartopus* footprints seem rather too small to be those of ornithomimids, and there is little evidence to suggest that such dinosaurs existed in the southern continents. Consequently we may assume the Lark Quarry trackways to have been made by some other type of theropod dinosaur — which presumably had 'typical' limb proportions.

#### A DINOSAUR STAMPEDE?

The most distinctive features of the Lark Quarry trackway site are: (1) that the dinosaurian track-makers were very numerous; (2) that nearly all these track-makers seem to have been small by dinosaurian standards; (3) that trackways of the two main types (*Wintonopus* and *Skartopus*) are in some places coincident, superimposed or interwoven; (4) that all the trackways (except that of the carnosaur) head in a single direction; and (5) that all the track-makers (except the carnosaur) seem to have been running. This combination of features appears to be unique, and it previously led us to interpret the Lark Quarry trackways as the result of a dinosaurian stampede (Thulborn and Wade 1979). The evidence underlying this interpretation may now be examined in more detail.

The Lark Quarry bedding plane carries one of the densest accumulations of dinosaur footprints yet reported (see Table 7). In our preliminary description of the site we estimated that these footprints represented the trackways of at least 130 dinosaurs (excluding the carnosaur), with coelurosaurs (= *Skartopus* trackways) outnumbering ornithopods (= *Wintonopus* trackways) in a ratio about 55:45. It proved impossible to assign every footprint at Lark Quarry to a particular trackway, and so our estimate for the number of track-makers must be checked in some other way. In a 1 metre wide transect at a right angle to the direction of the trackways (between points X-X in Fig. 3) we counted a total of 350 footprints. In practically all cases mean pace length for a track-maker (whether ornithopod or coelurosaur) is less than 1 metre — which means that nearly every animal crossing the line of the transect should have left at least one footprint in the metre-wide strip. Consequently the *maximum* number of animals that crossed the transect could be estimated at



350. However, mean pace length for *Wintonopus* is 68 cm (i.e. about 1½ footprints per metre), and for *Skartopus* it is 32 cm (i.e. about 3 footprints per metre). By assuming that ornithopods and coelurosaurs were present in equal numbers we can estimate the number of animals to have crossed the transect as:

$$\frac{350}{(3 \times 0.5) + (1.5 \times 0.5)} = 156 \text{ animals}$$

This very rough estimate must be regarded as an absolute minimum. We suspect that coelurosaurs outnumbered ornithopods, but it is impossible to make allowance for this without identifying every footprint and assigning to it a particular trackway. This proved an impossible task (for reasons described earlier; see p. 418). Moreover it is certain that many smaller animals (both coelurosaurs and ornithopods) crossed our transect without leaving recognizable footprints: these animals would have been so light that their broad-spreading and rather springy feet simply failed to break through the surface of the sediment. This seems to have happened very commonly, to judge from the number of discontinuities or 'gaps' in the trackways at Lark Quarry. The area of bedding plane exposed at Lark Quarry is delimited partly by erosion and partly by undisturbed overburden (mainly to S and SW, see Pl. 3). Within this area the footprints are fairly evenly distributed (Pl. 4), and it seems almost certain that more of them could be revealed by extending the quarry to the SSW. Our estimate of 156 animals may well represent a fraction of the number of dinosaurs that traversed Lark Quarry and its environs.

Trackways are certainly abundant, but this fact alone does not support the hypothesis of a dinosaur stampede. However, this fact does assume some significance when one considers that all the trackways may have been formed simultaneously by animals running in a single direction.

There are several reasons for believing that all the *Wintonopus* and *Skartopus* trackways at Lark Quarry were formed at, or about, the same time (excepting the single unusually large example of *Wintonopus*). First, all these trackways are very similar in preservation; there is no evidence (such as scouring or erosion) to indicate that some tracks are much older than others. Second, all the trackways are impressed to about the same depth — evidently in sediment of uniform consistency. If the trackways had accumulated over a lengthy period one might expect to find evidence of a

change in the consistency of the substrate (i.e. some tracks more deeply impressed than others). Finally there is the evidence of superimposed footprints; these are quite common, and in all cases the later-formed print is similar in its depth and state of preservation to the earlier-formed one. These similarities are apparent even where three or more animals have trodden the same spot (see Pl. 13, Fig. C; Pl. 16, Figs B, C). Ornithopod footprints (*Wintonopus*) may be found superimposed on footprints of other ornithopods or of coelurosaurs (*Skartopus*), and the same is true for the coelurosaur footprints. Footprints of both types may be found superimposed upon those of the carnosaur. From the evidence of superimposed footprints it may be deduced (a) that the carnosaur traversed the area before some (at least) of the ornithopods and coelurosaurs did so; (b) that some ornithopods preceded some coelurosaurs; and (c) that some coelurosaurs preceded some ornithopods. But from the evidence as a whole it is possible to reach a more general conclusion: that both ornithopods and coelurosaurs traversed the Lark Quarry site at (or about) the same time, and that they did so *after* the passage of the solitary carnosaur. This is exactly the chronological sequence to be expected if the approach of the carnosaur had triggered a stampede of the ornithopods and coelurosaurs. Of course there is no absolute proof that the Lark Quarry trackways were formed in exactly this sequence, but it is difficult to imagine any other when one considers that all the ornithopod and coelurosaur track-makers were running in a single direction.

Perhaps the most striking feature of the Lark Quarry site is that all the animals responsible for *Wintonopus* and *Skartopus* trackways were headed in a single direction — about 55° E of true N, and in almost direct opposition to the course taken by the solitary carnosaur (see Pl. 4). None of these abundant ornithopod and coelurosaur trackways deviates more than a few degrees from a single compass bearing, and in this respect the Lark Quarry site appears to be unique. Dinosaur tracks uncovered at other prolific localities are randomly oriented (e.g. see de Lapparent and Montenat 1967, Tucker and Burchette 1977) or show some less obvious tendency to sub-parallel alignment (e.g. see Avnimelech 1966, Ostrom 1972). And at sites where sub-parallel trackways do predominate these often represent a 'two-way traffic' — with some trackways diametrically opposed to others (e.g. Avnimelech 1966, pl. VIII; Ostrom 1972, fig. 4). By contrast the Lark

TABLE 7: COMPARISON OF STATISTICS FOR VARIOUS TRACKWAY SITES.

site	age	area(m <sup>2</sup> )	number of footprints	number of trackways	source
Ain-Sefra, Algeria:	Triassic	1	12	?	Bassoullet 1971
St Laurent de Treves, France:	L Jurassic	25	24	?	Thaler 1962
Bendrick Rock, S Wales:	U Triassic	25	400	?	Tucker and Burchette 1977
Rocky Hill, Connecticut:	Rhaetic	930	1000+	?	Ostrom 1972
Swanage, S England:	U Jurassic	47 <sup>c</sup>	46	3	Charig and Newman 1962
Kerman area, Iran:	Jurassic	5	8	76 <sup>c</sup>	de Lapparent and Davoudzadeh 1972
Tocantins River, Brazil:	Jurassic — Cretaceous	6–8000	47+	6	Leonardi 1980
Beth Zayit, Israel:	Cenomanian	400	200+	?10	Avnimelech 1966
F6 Ranch, Texas:	Aptian — Albian	?	76	15	Farlow 1981
Serrote do Letreiro, Brazil:	Triassic	'spacious'	?	17	Leonardi 1979
Mt Tom, Massachusetts:	Rhaetic	800	137	28+	Ostrom 1972
Lark Quarry, Queensland:	Cenomanian	209	3300+	130+	Thulborn and Wade 1979

(<sup>c</sup> — estimated figures.)

Quarry trackways are more nearly parallel and (excepting the carnosaur trackway) entirely unidirectional. The coincidence of so many trackways certainly implies that some external factor controlled the behaviour of the track-makers (cf. Ostrom 1972). At the time the trackways were formed the Lark Quarry site appears to have been part of a broad drainage channel, and it is conceivable that the track-makers might have been funnelled along a common route by physical barriers such as levees or steep banks. However, there is no direct evidence of such barriers, and it may be recalled that remnants of a few randomly oriented trackways do occur at the site. These scattered and eroded remnants of trackways testify that some medium-sized bipedal dinosaurs (probably ornithopods) traversed the area before the carnosaur made its appearance, and that they did so randomly — that is, seemingly without the control of physical barriers. Apparently the behaviour of the *Wintonopus* and *Skartopus* track-makers was influenced by some factor that had not previously affected the movements of dinosaurs across the same area. Next, it is obvious that the Lark Quarry site cannot have been part of some established route along which dinosaurs were accustomed to move in either direction. Nor is it possible to believe that the dinosaurian track-makers could have adhered with absolute fidelity to a system of 'one-way' routes. One general conclusion seems inescapable: that the singular

orientation of trackways at Lark Quarry must reflect some unusual behaviour on the part of the track-makers.

There can be little doubt that all the *Wintonopus* and *Skartopus* trackways at Lark Quarry were made by running animals. In most cases relative stride length is estimated to have been well over 2.9 — apparently indicative of a fast running gait equivalent to a mammalian gallop or sprint. In the few remaining cases relative stride length is estimated to have been between 2.0 and 2.9 — indicative of a gait equivalent to mammalian trotting. Our estimates of relative stride length (and hence of speed) depend in turn upon estimates of hindlimb height. The piling of estimate upon estimate may, indeed, have introduced and multiplied some errors, but these are unlikely to be of very great significance for our general conclusions. For example, in the case of the *Wintonopus* track-makers our estimates of hindlimb height are consistently greater than those that would be obtained by straightforward application of Alexander's method (1976). Consequently relative stride length (and speed) may, if anything, be underestimated for these animals. Our estimates of hindlimb height for the *Skartopus* track-makers are slightly smaller than those that would be obtained with Alexander's method; but even if our estimates are increased by as much as 40 or 50% it still appears that these dinosaurs would have been running (compare Tables 5 and 6). In

any event, it is not necessary to estimate hindlimb height in order to demonstrate that the *Wintonopus* and *Skartopus* track-makers had an exceptionally long-striding gait: this is fully apparent from simple ratios of SL/FL and PL/FL (see Figs 11 and 16). Once again it appears that the Lark Quarry dinosaurs were indulging in unusual behaviour, for reports of trackways attributed to running dinosaurs are otherwise very few (see Farlow 1981, Thulborn 1982). Here it is worth recalling that the single *Wintonopus* trackway at another site (New Quarry) is that of a walking animal.

In summary, the Lark Quarry site has revealed a most unusual assemblage of dinosaur trackways, and to account for their origin it seems legitimate to postulate some exceptional pattern of behaviour on the part of the track-makers. The findings of this study seem to confirm, or even strengthen, our earlier interpretation of the trackways as evidence of a dinosaur stampede. Indeed, it is not easy to propose (let alone justify) an alternative interpretation. This difficulty arises for two reasons: (1) because all the *Wintonopus* and *Skartopus* trackways are unidirectional, and (2) because all these trackways seem to have been made by running dinosaurs. It seems very unlikely that this assemblage of trackways could represent a series of events — i.e. the passage, at intervals, of individual animals or of small groups. Any such series of events would have involved the most remarkable coincidences: at different times various dinosaurs would have traversed the same area, but always in exactly the same direction, and always at a run. Consequently one is forced to conclude that the Lark Quarry trackways represent a *single* event — a conclusion supported by the uniform preservation of the trackways. We submit that a group of more than 150 animals running in one direction must constitute a stampede or some similar event. Several experienced stockmen have examined the Lark Quarry trackways; all of them agreed that the trackways could well have resulted from a stampede, though on two occasions we were offered an alternative explanation (as a joke) — that the track-makers were being 'herded' or 'driven'.

There arise some intriguing questions. First, what caused the stampede? Only one piece of fossil evidence seems to hint at a plausible answer — the trackway of the single carnosaur. It is quite conceivable that a gathering of ornithopods and coelurosaurs, drinking or foraging round a water-hole, might have been startled by the approach of

a large predatory dinosaur. We have reservations about reading too much significance into the evidence of a single dinosaur trackway, but the only alternative is to admit that the unusual behaviour of the *Wintonopus* and *Skartopus* track-makers is inexplicable. A second question arises: why did the ornithopods and coelurosaurs run to the NE if this was the very direction from which the carnosaur had approached them? Here we can only offer speculations. The ornithopods and coelurosaurs had reached the water-hole, to the SW of the present Lark Quarry site, by some unknown and presumably preferred or 'normal' route. One might have expected these animals to have made their escape by such a route. The fact that some, at least, did not do so seems to imply that their preferred route had been blocked — perhaps by the manoeuvres of the carnosaur, which certainly made a sharp right turn. In making this turn to its right the carnosaur would simultaneously have opened up a new escape route — to the NE, and along the broad drainage channel that extended over the present Lark Quarry site towards Seymour Quarry. This reconstruction of events (Fig. 25) accords with all available evidence and seems to be fairly parsimonious. The motives of the carnosaur remain unknown; it may simply have been approaching the water-hole to drink, or it may have been hunting — perhaps attempting to corral its prey on the point extending SW into the water-hole. If the animal were hunting it is possible to speculate a little further. First, it seems likely that this large predator would have selected its prey from among the ornithopods; the coelurosaurs, insofar as they are known from their trackways, would seem to have been rather small game. Next it is conceivable that the carnosaur may not have been hunting alone: it might possibly have been assisted by another carnosaur (or perhaps even more than one) strategically placed to forestall the escaping ornithopods and coelurosaurs. This is no more than a speculation, but it might help to account for the remarkably close grouping of the ornithopods and coelurosaurs — especially since their progress over the Lark Quarry site seems not to have been constrained by physical barriers. These suggestions are not inconsistent with previous speculations on the hunting behaviour of large theropod dinosaurs (Farlow 1976).

Whatever the carnosaur's manoeuvres or intentions may have been, a number of *Wintonopus* and *Skartopus* track-makers did run to the NE, across the present Lark Quarry and

Seymour Quarry sites. In doing so these animals seem to have traversed an area that they had not trodden before (or, at least, not in the immediate past). Their trackways at Lark Quarry are strictly unidirectional, and none of them seems to have been made by a walking animal. Evidently these ornithopods and coelurosaurs were not following some well-trodden path, and they may in fact have been moving across an area that was formerly unattractive to them. It is not difficult to imagine in what sense the Lark Quarry area might have been unattractive to small bipedal dinosaurs: it was covered by a layer of soft mud, into which the animals might (and certainly did) sink to a depth of several centimetres. This would have been of little consequence to a very large animal such as the carnosaur; as this animal traversed the area its feet plunged right through the mud to rest on the firmer sandy sediments below. But it is conceivable that the small coelurosaurs (mean hip height about 17 cm) and ornithopods (mean hip height about 35 cm) ran some risk of becoming bogged. If these small dinosaurs were crossing an unattractive or even dangerous area, it is reasonable to suppose that they were doing so under some quite unusual and compelling circumstances.

Our reconstruction of the events at and around Lark Quarry is illustrated in Fig. 25. This reconstruction takes into account all the peculiarities of the Lark Quarry trackways, and we have found no evidence that conflicts with it. A central assumption of this reconstruction is that the behaviour of the carnosaur was responsible, at least in some measure, for the unusual behaviour of the ornithopods and coelurosaurs. This assumption naturally implies that very little time would have elapsed between the formation of the carnosaur's trackway and the formation of the ornithopod and coelurosaur trackways. The uniform preservation of all these trackways seems to indicate that they were formed at *about* the same time ... but there is no certain way to discover if the carnosaur preceded the ornithopods and coelurosaurs by a matter of minutes or by a matter of hours. However there is one suggestive clue, provided by ornithopod and coelurosaur footprints superimposed on those of the carnosaur. In their preservation these superimposed prints are identical to those elsewhere, yet they were formed in thin streaks and pockets of mud remaining in the floor of the carnosaur's prints. The fact that these remnant patches of mud had not dried out, despite their thinness, suggests that little time elapsed (or that drying was very slow). If the intervening period

were to be estimated in terms of hours, rather than minutes, we could no longer maintain our suggestion that the carnosaur's behaviour prompted the stampede of ornithopods and coelurosaurs. Even so, it would remain clear that a stampede (or some similar event) did occur — though its cause would be unknown.

The minimum distance travelled by the stampeding ornithopods and coelurosaurs is more than 95 metres — from the SW end of Lark Quarry to the NE end of Seymour Quarry. From the speed estimates presented earlier it may be calculated that most of the ornithopods and coelurosaurs covered this distance in less than 30 seconds; at their minimum speeds the slowest ornithopod and the slowest coelurosaur would have done so in 38 seconds and 45 seconds respectively. There is no indication of either the start or the end of the stampede.

Finally, it might be objected that our use of the term 'stampede' is inappropriate because the animals involved seem to have been moving at rather low speeds (mean 16 km/h for ornithopods, and mean 12 km/h for coelurosaurs). In a present-day stampede, comprising ungulate mammals, one might expect to find animals moving several times faster than the dinosaurs at Lark Quarry. However, such comparisons of absolute speeds are of limited significance — simply because the dinosaurs that traversed Lark Quarry were, on the whole, much smaller than living ungulates. To measure and compare the locomotor performances of different-sized animals it is necessary to select criteria that will reduce or eliminate the effects of size-differences. Such criteria will be examined below.

#### IMPLICATIONS FOR THE UNDERSTANDING OF DINOSAUR BIOLOGY

It has sometimes been supposed that juvenile dinosaurs were rare (Richmond 1965, Leonardi 1981), and that small (but adult) dinosaurs were equally rare or 'unknown' (Bakker 1972). However, there have recently been reports of juvenile dinosaurs, some no bigger than rats or pigeons, and even embryonic dinosaurs (see Bonaparte and Vince 1979, Kitching 1979, Coombs 1980a, 1982, Carpenter 1982, among others). The Lark Quarry trackways provide striking confirmation that small dinosaurs — whether adults or juveniles, or both — may have been abundant in some localities. This fact should certainly have some bearing on the debate over thermoregulation in dinosaurs, though at this

point we cannot pursue so large and complicated a subject (see Thomas and Olson 1981 for a comprehensive review).

It seems impossible to distinguish with certainty between trackways made by small (but adult) dinosaurs and those made by juveniles. Consequently it is fruitless to use ichnological data in speculating about the reproductive strategies and population dynamics of dinosaurs. These aspects of dinosaur biology should more properly be investigated on the basis of body fossils — where it might prove possible to determine relationships between age, sexual maturity and body size. Nevertheless we have outlined some possibilities regarding population structure of the *Wintonopus* and *Skartopus* track-makers (Fig. 21). It must be emphasized that these are only possibilities, for we cannot agree entirely with the assumption that footprints of different sizes were made by animals of different ages (Leonardi 1981). Such an assumption is valid only if growth proceeded at a constant rate through the lives of the track-makers. Moreover the assumption would seem to be particularly suspect where there is a limited range in size of footprints (e.g. *Skartopus*, where the largest footprint is less than twice the size of the smallest). Even so, it may be legitimate to identify very small footprints as those of juveniles in cases where there is a very great range in footprint size (e.g. *Wintonopus*, where the largest footprint is nearly 12 times the size of the smallest).

Ostrom (1972) compiled data on dinosaur trackways in order to examine the possibility that some dinosaurs might have been gregarious. At various sites he found trackways grouped in near-parallel arrangement, and he concluded that several different kinds of dinosaurs may well have been gregarious in habit. Ostrom's conclusion is supported, incidentally, by the identification of dinosaurian adaptations for intra-specific combat, display and vocalization (Galton 1970, Hopson 1975, Molnar 1977, Weishampel 1981). The trackways at Lark Quarry provide strong evidence of gregarious behaviour, for they seem to have resulted (with the exception of the carnosaur trackway) from the movement of a single large group of dinosaurs. This group seems, however, to have been heterogeneous and, perhaps, rather disorganized. The trackways of coelurosaurs (*Skartopus*) and ornithopods (*Wintonopus*) are thoroughly intermingled, and there is no clear indication that the two types of dinosaur were segregated. This could indicate that these coelurosaurs and ornithopods were in the habit of moving together as a 'mixed herd', as

was suggested by Krassilov (1980). In this case one might envisage the coelurosaurs as opportunists — ready to seize insects and other small animals as they were flushed from vegetation by an ornithopod herd moving through its feeding grounds. Alternatively the trackways at Lark Quarry could have resulted from accidental mingling of an ornithopod herd with one or more foraging parties of coelurosaurs. Even so it would be reasonable to regard both the ornithopods and the coelurosaurs as gregarious, for it seems unlikely that so many individuals could have gathered independently and at random in the vicinity of the Lark Quarry site. Nevertheless it is just conceivable that all the Lark Quarry track-makers were normally solitary animals: they might have been attracted to the Lark Quarry water-hole during a period of drought. However, we have found no desiccation cracks or other evidence of drought, and it may be recalled that all the trackways seem to have been formed in moist sediment. Moreover, the much-trampled claystone layer at New Quarry seems to confirm that the Lark Quarry area was quite commonly frequented by large numbers of dinosaurs.

Several studies of dinosaur trackways have employed Alexander's method (1976) to estimate the speeds of the track-makers (Russell and Béland 1976, Tucker and Burchette 1977, Coombs 1978, Thulborn and Wade 1979, Kool 1981, Farlow 1981, Thulborn 1981, 1982). These studies have made it possible to compare the speeds of various dinosaurs under various circumstances (e.g. see Russell and Béland 1976), or to compare the speeds of dinosaurs to those recorded for mammals and ground-dwelling birds (e.g. see Farlow 1981). Such comparisons of absolute speeds are certainly interesting, but they often give a poor indication of relative locomotor performances. A mammalian analogy will make this clear: if a horse, a dog and a mouse all move at 6 km/h, the horse will be walking, the dog will be trotting, and the mouse will literally be galloping (Heglund et al. 1974). Absolute speed is identical for all three animals, but their locomotor performances are obviously very different. Exactly similar relationships between size, speed and gait would have prevailed in dinosaurs, despite Kool's generalization (1981) that different-sized animals, including dinosaurs, 'all walk at roughly the same speed'

To evaluate and compare the locomotor performances of dinosaurs it is desirable to adopt some criterion that will reduce or eliminate the effect of differences in body size. In comparing

the locomotor performances of fishes it is common practice to express burst speeds in terms of body lengths per second, and by analogy the speeds of dinosaurian track-makers might conveniently be expressed in terms of  $h/s$  (a 'size-related' speed, where  $h$  is height at the hip). Table 8 presents examples of such 'size-related' speeds, compared to absolute speeds, for a variety of dinosaurian track-makers. Evidently dinosaurs with similar absolute speeds may have very different 'size-related' speeds, and *vice versa*. In terms of such 'size-related' speed the locomotor performances of the Lark Quarry ornithopods and coelurosaurs are outstanding, although in terms of absolute speed these animals seem to have been moving rather slowly. However, such 'size-related' speed is no more useful for comparing locomotor performances than is absolute speed. The following (hypothetical) example, where three different-sized animals are moving at the same 'size-related' speed, will make this clear:

$h$ (m)	'size-related'		relative		gait
	speed ( $h/s$ )	absolute speed (m/s)	stride length ( $\lambda/h$ )		
0.5	3.0	1.5	1.8		walk
1.5	3.0	4.5	2.5		trot
3.0	3.0	9.0	3.1		run

Evidently the effects of size-differences are undiminished, because large animals need to attain faster gaits and higher absolute speeds in order to match the 'size-related' speeds of small animals.

Heglund, Taylor and McMahon (1974) proposed that 'speed at the trot-gallop transition point is a "physiologically similar speed" for animals of different size'. We may extend this proposition to identify two points at which animals of different sizes would attain 'physiologically similar' speeds: the walk-trot transition, and the trot-run transition. At such points different-size animals will have different absolute speeds (and different 'size-related' speeds), but their locomotor performances may be regarded as equivalent. These two points may be defined in terms of relative stride length ( $\lambda/h$  about 2.0 and 2.9 respectively). They may also be defined in terms of Froude number ( $u^2/gh$ ; see Alexander 1976), or in terms of 'dimensionless speed'  $u(gh)^{0.5}$ ; see Alexander 1977). It is probably most convenient to compare locomotor performances in terms of  $\lambda/h$ , because estimates of this ratio have been cited in previous studies of speed in dinosaurian track-makers. From the

estimates of  $\lambda/h$  presented here (Tables 4, 5 and 8) it is clear that the locomotor performances of the Lark Quarry ornithopods and coelurosaurs were superior (and often far superior) to those of most other dinosaurian track-makers. Estimates of Froude number and of 'dimensionless speed' (equivalent to the square root of Froude number) point to the same conclusion.

Relative stride length would seem to be a useful and fairly realistic basis on which to evaluate and compare the locomotor performances of different-size animals. But even on this basis an element of bias will emerge because there probably exists a negative correlation between body size and maximum  $\lambda/h$ ; this seems to be the case among some living mammals (see data presented by Alexander et al. 1977), and it is reasonable to suppose that a similar relationship between size and gait prevailed among dinosaurs. Consequently straightforward comparisons of  $\lambda/h$  might in some cases be a little misleading; for example, two dinosaurian track-makers with  $\lambda/h$  estimated at 2.0 could scarcely be regarded as maintaining equivalent performances if one of them were a large dinosaur moving at maximum speed and the other were a small dinosaur capable of accelerating to greater speeds. Unfortunately there is no way to eliminate this bias, because there is insufficient evidence (either from living animals or from dinosaur trackways) to determine the regression of maximum  $\lambda/h$  on body size (represented by  $h$  or by body mass). All that may be said, in general terms, is that small dinosaurs probably attained higher values for maximum  $\lambda/h$  than did large dinosaurs. Indeed, it has been maintained (Thulborn 1982) that giant dinosaurs were unable to extend  $\lambda/h$  beyond 2.0 and were physically incapable of running. Nevertheless comparisons of  $\lambda/h$  would seem, for the present at least, to give the best indication of relative locomotor performances among dinosaurs. And on this basis the performances of the Lark Quarry ornithopods and coelurosaurs appear to be exceptional.

If the ornithopods and coelurosaurs at Lark Quarry were caught up in a stampede, or some similar event, one might expect these animals to have been running at or near their maximum speeds. And if this were the case it might be possible to determine a relationship between body size ( $h$ ) and maximum running speed. Such a relationship might then be used to gain some idea of the maximum speeds of dinosaurs in general. Fig. 24A is a plot of estimated mean speed against estimated hip height for ornithopods and coelurosaurs at Lark Quarry. In this diagram it is

TABLE 8: A COMPARISON OF THE LOCOMOTOR PERFORMANCES OF VARIOUS DINOSAURIAN TRACK-MAKERS.

## A. LARGE THEROPODS

ichnotaxon or track-maker	h (m)	absolute speed (m/s) (km/h)		relative stride length ( $\lambda/h$ )	size-related speed (h/s)	Froude number ( $u^2/gh$ )	dimensionless speed ( $u(gh)^{-0.5}$ )	source
* <i>Megalosaurus insignis</i> :	1.5	2.4	8.6	1.7	1.6	0.38	0.62	de Lapparent and Zbyszewski 1957
<i>Irenesauripus mcleani</i> :	1.7	0.7	2.4	0.8	0.4	0.03	0.17	Sternberg 1932
* <i>Megalosaurus</i> :	1.8	2.2	8.0	1.6	1.3	0.29	0.54	de Lapparent and Zbyszewski 1957
* <i>Irenesauripus acutus</i> :	2.2	2.5	8.9	1.6	1.1	0.28	0.53	Sternberg 1932
* <i>Irenesauripus occidentalis</i> :	2.3	0.9	3.3	0.9	0.4	0.04	0.19	Sternberg 1932
cf <i>Tyrannosauropus</i> :	2.6	1.9	6.9	1.3	0.7	0.15	0.38	this paper
* <i>Tyrannosauropus petersoni</i> :	3.6	2.7	9.6	1.4	0.7	0.20	0.45	Haubold 1971

## B. SMALL AND MEDIUM-SIZED THEROPODS

* <i>Grallator gracilis</i> :	0.17	0.8	2.9	1.7	4.8	0.41	0.64	Lull 1953
* <i>Plesiornis pilulatus</i> :	0.20	0.9	3.3	1.8	4.7	0.43	0.66	Lull 1953
* <i>Grallator cursorius</i> :	0.32	2.4	8.7	2.3	7.5	1.86	1.36	Lull 1953
* <i>Hopiüchnus shingi</i> : <sup>a</sup>	0.55	13.1	47.2	7.0	23.8	31.99	5.66	Welles 1971
* <i>Hopiüchnus shingi</i> : <sup>b</sup>	1.00	8.2	29.5	3.8	8.2	6.86	2.62	
* <i>Anchisauripus sillimani</i> :	0.69	0.5	1.9	0.9	0.8	0.04	0.20	Lull 1953
* <i>Grallator formosus</i> :	0.82	1.6	5.8	1.6	2.0	0.33	0.57	Lull 1953
* <i>Saltopoides igalensis</i> :	0.83	8.4	30.1	4.2	10.1	8.70	2.95	de Lapparent and Montenat 1967
* <i>Anchisauripus exsertus</i> :	1.07	2.1	7.7	1.8	2.0	0.43	0.66	Lull 1953
* <i>Dilophosauripus williamsi</i> :	1.37	1.3	4.8	1.3	1.0	0.13	0.37	Welles 1971
* <i>Ornithomimipus angustus</i> :	1.56	1.3	4.8	1.2	0.9	0.12	0.34	Sternberg 1926
<sup>c</sup> Theropod Q94/98:	1.16	12.1	43.6	4.9	10.4	12.94	3.60	Farlow 1981
	1.46	10.1	36.4	3.9	6.9	7.16	2.68	
<sup>c</sup> Theropod BLV/A3:	1.48	9.4	33.8	3.7	6.4	6.12	2.47	Farlow 1981
	1.85	7.9	28.3	3.0	4.3	3.42	1.85	
<sup>c</sup> Theropod 86/0-82:	1.52	11.9	42.8	4.3	7.8	9.55	3.09	Farlow 1981
	1.90	10.0	35.9	3.5	5.4	5.34	2.31	
<i>Skartopus</i> Nr 25:	0.18	2.2	8.0	2.7	12.1	2.73	1.65	this paper <sup>d</sup>
<i>Skartopus</i> (mean):	0.17	3.2	11.6	3.7	18.8	6.18	2.49	
<i>Skartopus</i> Nr 2:	0.13	4.4	15.9	4.9	33.1	14.92	3.86	

## C. ORNITHOPODS

* <i>Anomoepus minimus</i> :	0.28	0.3	1.2	0.9	1.2	0.04	0.20	Lull 1953
<i>Amblydactylus kortmeyeri</i> :	0.64	0.8	2.8	1.1	1.2	0.10	0.31	Currie and Sarjeant 1979

* <i>Anomoepus crassus</i> :	0.84	0.6	2.3	0.9	0.7	0.05	0.22	Lull 1953
* <i>Sauropus barrattii</i> :	0.88	1.9	6.7	1.7	2.1	0.40	0.63	Lull 1953
<i>Irenichnites gracilis</i> :	0.89	1.6	5.9	1.6	1.9	0.31	0.56	Sternberg 1932
* <i>Satapliasaurus</i>								
<i>dsoceniidzei</i> :	1.08	1.0	3.5	1.1	0.9	0.08	0.30	Gabouniya 1951
* <i>Gypsichnites pacensis</i> :	1.74	1.3	4.8	1.2	0.8	0.10	0.32	Sternberg 1932
<sup>c</sup> Ornithopod:	3.44	7.6	27.2	2.7	2.2	1.70	1.30	Brown 1938
	3.44	2.4	8.6	1.3	0.7	0.17	0.41	
<i>Wintonopus</i> Nr 44:	0.42	2.5	9.2	2.2	6.0	1.53	1.24	
<i>Wintonopus</i> (mean):	0.35	4.6	16.5	3.7	13.3	6.26	2.50	this paper <sup>d</sup>
<i>Wintonopus</i> Nr 21:	0.29	6.3	22.7	5.0	21.7	14.03	3.75	
<i>Wintonopus</i> (New								
Quarry):	0.47	1.1	4.0	1.5	2.3	0.26	0.51	this paper

In most cases  $h$  is estimated by methods introduced in this paper.

\*stride length estimated from published data (e.g. pace length or ratio of pace length: footprint length).

<sup>a</sup>with  $h$  estimated as for an ornithomimid; equation (14).

<sup>b</sup>with  $h$  estimated by Welles (1971).

<sup>c</sup>first estimate of  $h$  represents four times footprint length, after Farlow (1981); second estimate is the mean of two, calculated as for a carnosaur and as for a coelurosaur (equations (7) and (12) respectively).

<sup>d</sup>all track-makers at Lark Quarry. First estimate represents the worst-performing track-maker (in terms of  $\lambda/h$ ), and the third estimate represents the best-performing track-maker. Track-makers are listed by number in Tables 4 (*Wintonopus*) and 5 (*Skartopus*).

<sup>e</sup>two interpretations of single trackway (Russell and Béland 1976; Thulborn 1981), both with  $h$  estimated as four times footprint length.

immediately obvious that the trend (or first principal axis) of the distribution is roughly parallel to the regression lines defining size/speed relationships at the walk-trot transition ( $\lambda/h$  2.0) and the trot-run transition ( $\lambda/h$  2.9). This parallelism is not an artefact generated by our methods for estimating size and speed (note size/speed relationship for the New Quarry ornithopod); nor does it appear to be fortuitous. Instead it demonstrates very clearly that most animals at Lark Quarry were running and, moreover, that animals of different sizes were maintaining equivalent locomotor performances (in terms of  $\lambda/h$ ). Mean  $\lambda/h$  for the ornithopod track-makers is estimated to be 3.69; for the coelurosaur track-makers it is estimated to be 3.71. Fig. 24B is similar to Fig. 24A, except that it illustrates the relationship between estimated maximum speed and estimated hip height. In this diagram the line drawn through the distribution is not derived from our data: it is a line defining the theoretical regression of speed on size ( $h$ ) when  $\lambda/h$  is at a value of 3.93. (The figure of 3.93 was selected on the basis of our findings: among the ornithopod track-makers the mean figure for maximum  $\lambda/h$  per trackway is 3.94, and among the coelurosaur it is 3.92). Evidently the actual relationship between size and speed conforms quite closely to the theoretical relationship at this

particular value for  $\lambda/h$ . In other words most of the Lark Quarry track-makers seem to have been running at a 'physiologically similar [or standard] speed' — even though the track-makers were of various sizes and had different absolute speeds. It seems quite probable that the 'physiologically similar' speed shared by the Lark Quarry dinosaurs did represent maximum or near-maximum speed. If this were not so one might reasonably expect that small animals would have matched the absolute speeds of larger ones. Further, it is difficult to conceive of any circumstances that might have led different-sized dinosaurs to run at a 'physiologically similar' speed less than maximum speed. From the evidence presented in Fig. 24 we may deduce that small bipedal dinosaurs, with  $h$  up to about 60 cm, could attain maximum  $\lambda/h$  of at least 3.93. In our preliminary account of the Lark Quarry site (Thulborn and Wade 1979) we attempted to account for the 'rather low' absolute speeds of the track-makers by suggesting that the animals might have been fatigued, or that they might have been retarded by sinking deeply into the muddy substrate. However, we have found no evidence that the track-makers were decelerating to any marked degree, and Alexander pointed out (1976) that relationships between body size, speed and stride length did not seem to be seriously affected



by the consistency of the substrate. Even so, it may be more accurate to re-phrase our general conclusion as follows: that the Lark Quarry animals were running at maximum or near-maximum speed *under the conditions that then prevailed*. We cannot determine to what extent those prevailing conditions might have affected the locomotor performances of the Lark Quarry dinosaurs.

If small bipedal dinosaurs were capable of attaining maximum  $\lambda/h$  about 3.93 we may estimate the maximum speeds of these animals by substituting  $3.93h$  for  $\lambda$  in equation (2). This equation may then be re-written as follows:

$$(15) \quad u \cong [gh (3.93h / 1.8h)^{2.564}]^{0.5}$$

and simplified to give:

$$(16) \quad u \cong (72.22h)^{0.5}$$

where  $h$  is in metres and  $u$  is solved in metres per second. This equation may be applied equally well to trackway data (with  $h$  estimated from footprint dimensions) or to osteometric data (with  $h$  measured directly). The maximum estimate of  $\lambda/h$  for any of the Lark Quarry track-makers is 5.03 (for a *Wintonopus* track-maker, No. 21 in Table 4). If this figure (rather than 3.93) represents maximum  $\lambda/h$  for small bipedal dinosaurs we may estimate their maximum speeds by substituting it for  $\lambda$  in equation (2). The equation may then be re-written and simplified to give:

$$(17) \quad u \cong (136h)^{0.5}$$

However, the assumption behind this equation is that nearly all track-makers at Lark Quarry would have been running at somewhat less than their maximum possible speeds. Consequently it seems reasonable to qualify our conclusions as follows: the Lark Quarry track-makers seem to have attained maximum  $\lambda/h$  of at least 3.93 and, in some instances, as high as 5.03. If these conclusions do have more general application it should be possible to predict maximum running speed for any small bipedal dinosaur ( $h < 70$  cm) that is known from a skeleton or a trackway: its maximum speed would probably lie between the two estimates to be obtained with equations (16) and (17). It might also be legitimate to make use of these equations in estimating maximum speeds for some medium-size bipedal dinosaurs (with  $h$  up to 1.5 or 2 m), but it is certainly not appropriate to do so for very large bipeds or quadrupeds. This is because a dinosaur moving with  $\lambda/h$  as high as 3.93 must incorporate an unsupported interval in each stride, and the

ability to use unsupported intervals is generally restricted to animals with body mass less than 500–800 kg (see discussions by Coombs 1978, Thulborn 1982). Many large bipedal dinosaurs were certainly above this critical weight limit, as were nearly all of the quadrupedal forms (see, for example, the body weights estimated for dinosaurs by Colbert 1962). Coombs indicated (1978) that the best mammalian runners had optimum body mass of about 50 kg — but not over 500 kg or below 5 kg — and it seems likely that dinosaurs would have been under similar physical constraints. In addition it is possible that the maximum speeds of quadrupedal dinosaurs were restricted by structural peculiarities of the limbs and their girdles (see Thulborn 1982). Even so, it may be legitimate to apply equations (16) and (17) in the case of some quite large bipedal dinosaurs that seem to have been very lightly constructed. Notable among these are the ornithomimids or ‘ostrich dinosaurs’; these animals possess striking cursorial adaptations and are commonly supposed to have been the swiftest of all dinosaurs (Russell 1972, Coombs 1978). One example of the ornithomimid *Dromiceiomimus* has skeletal hip height of 1.22 metres and is estimated to have had a live body weight of about 154 kg (Russell and Béland 1976); with equation (16) the maximum speed of this animal may be estimated at 9.31 m/s (33.5 km/h). Among the ornithomimids described by Osmólska et al. (1972) the largest example (*Gallimimus*) has skeletal hip height of 1.94 metres; this dinosaur’s maximum speed may be estimated at 11.82 m/s (42.6 km/h). These speeds (c. 35–45 km/h) could conceivably be the highest attained by any of the dinosaurs. However, it is certainly possible that the ornithomimids were able to extend relative stride length beyond 3.93 — particularly in view of their cursorial adaptations. Russell and Béland (1976) used Alexander’s method (1976) to consider the hypothetical example of an ornithomimid ( $h$  about 1.22 metres) running at 80 km/h; at this speed the animal’s stride length would have been about 8.6 metres, indicating  $\lambda/h$  about 7.05. It is difficult to imagine that any dinosaur could have extended stride length to such a degree. Among living mammals such a high figure for  $\lambda/h$  is achieved only by the most highly adapted of quadrupeds — which are able to employ stride-lengthening techniques unavailable to bipeds (e.g. scapular rotation and flexion/extension of the vertebral column). An example may help to make this clear. At a speed of 10 m/s (36 km/h) a

human sprinter with hip height about 95 cm will have relative stride length in the region of 4.6 — as estimated with equation (2). To attain  $\lambda/h$  of 7.0 a human athlete must perform a leap. We suspect that similar constraints apply to raites, though we have been unable to find suitable data on these animals. By comparison it is unlikely that a bipedal dinosaur could have maintained a running gait with  $\lambda/h$  as high as 7.05, even though the ornithomimids may have reached maximum values of  $\lambda/h$  somewhat higher than 3.93. If the largest ornithomimid mentioned above (*Gallimimus*, with  $h$  of 1.94 metres) had been capable of achieving maximum  $\lambda/h$  of 5.0 its maximum speed would have been about 16 m/s (58 km/h) — as estimated by means of equation (17).

The general conclusion to be drawn from the Lark Quarry trackways is that small bipedal dinosaurs ( $h < 70$  cm) attained maximum  $\lambda/h$  of at least 3.93, and possibly as high as 5.03. These same figures for maximum  $\lambda/h$  might also apply to somewhat larger bipedal dinosaurs, providing that these had live body weights less than 500–800 kg. Larger and heavier dinosaurs, both bipeds and quadrupeds, probably attained lower figures for maximum  $\lambda/h$  — simply because they would have been too heavy to have made use of unsupported intervals. If the most highly adapted of dinosaurian cursors — the ornithomimids — did have maximum  $\lambda/h$  of about 3.93 their maximum speeds might have been about 35–45 km/h. Even if ornithomimids were capable of attaining  $\lambda/h$  as high as 5.03 their maximum speeds might still have been no greater than about 60 km/h. These estimates fall rather short of the maximum possible speeds attributed to ornithomimids on the basis of anatomical comparisons (70–80 km/h, or even more; see Russell 1972).

Are these general conclusions supported or contradicted by evidence from other dinosaur trackways? Trackways attributed to running dinosaurs appear to be uncommon, but we will examine those few examples that have come to our attention. In describing a short section of ornithopod trackway from the Cretaceous of Colorado, Brown (1938) mentioned that each footprint measured 34 inches (c. 86 cm) in width and length, and that the track-maker had 'stepped' a distance of 15 feet (c. 4.6 metres).

Brown did not suggest that this trackway had been made by a running dinosaur: instead he accounted for the remarkably long stride by suggesting that the track-maker was a gigantic creature nearly twice the height of *Tyrannosaurus* in its classic standing pose (i.e. 35 feet as opposed to 18 feet). By using Alexander's methods (1976) to determine speed and hip height Russell and Béland (1976) estimated that this trackway had been made by a very large animal ( $h$  about 3.44 metres) running at a speed of 7.54 m/s (27.1 km/h). Russell and Béland estimated that the Colorado ornithopod had weighed about 11 tonnes, and from their figures it may be calculated that  $\lambda/h$  was in the region of 2.7. These estimates have, at best, an indirect bearing on our general conclusions: if a giant dinosaur was capable of running at 27 km/h one might reasonably expect the much smaller dinosaurs at Lark Quarry to have matched, or even surpassed, such a speed. However, it may be recalled that the best available measure for comparing locomotor performances seems to be relative stride length ( $\lambda/h$ ), rather than absolute speed. Moreover there is a suspicion that Brown may have misinterpreted the Colorado trackway, and that the dinosaur responsible for it was actually walking ( $\lambda/h$  1.34) at a speed no greater than 8.5 km/h (see Thulborn 1981).

In *Saltopoides igalensis*, the trackway of a bipedal dinosaur from the Rhaeto-Liassic of France, de Lapparent and Montenat (1967) found the ratio PL/FL to be as high as 11/1 (see Fig. 16). These authors considered that the track-maker was most probably a long-legged coelurosaur; they gave a figure of 15.5 cm for footprint length, and from their diagram of the trackway (1967, fig. 15B) we estimate stride length to have been about 344 cm. The *Saltopoides* footprints are rather large by coelurosaurian standards (see Table 2), and they could quite possibly have been made by a medium-size theropod closer in appearance to carnosaurs. Alternatively the track-maker might have been a rather large coelurosaur with 'typical' hindlimb proportions, or a coelurosaur with hindlimb proportions resembling those of ornithomimids. By considering all these possibilities we may obtain several estimates of size and speed for the track-maker:

assumed status of track-maker	$h$ (m)	$\lambda/h$	estimated speed		equations used	
			(m/s)	(km/h)	( $h$ )	(speed)
'typical' coelurosaur	0.70	4.9	9.45	34.0	(12)	(11)
carnosaur-like	0.93	3.7	7.57	27.3	(7)	(11)
ornithomimid-like	0.85	4.0	8.10	29.2	(14)	(11)

In each case  $\lambda/h$  is found to be greater than 2.0, so that speed is most appropriately estimated with equation (11). These estimates of speed and relative stride length are in fair agreement with the conclusions we have drawn from the Lark Quarry trackways, and they might be taken to indicate that the *Saltopoides* track-maker was running at or near its maximum speed. It is noteworthy that all three estimates of  $\lambda/h$  are below 5.0.

From the Kayenta Formation of Arizona (Early Jurassic or Late Triassic) came a sequence of three dinosaur footprints described by Welles (1971) as *Hopiichnus shingi*. The maker of this

trackway was evidently a long-striding bipedal dinosaur: footprint length was about 10 cm whereas pace length was found to be 191 cm. Welles commented that pace length was 'tremendous' in relation to the size of the footprints (compare data in Fig. 16), but he did not suggest that the track-maker had been running. He considered, instead, that the track-maker had been an exceptionally long-limbed animal (perhaps an ornithomimid) with  $h$  about 1 metre. Dr Welles also informs us (pers. comm.) that the morphology of the footprints seems to indicate a walking gait rather than a running gait. We may consider several estimates of size and speed for the *Hopiichnus* track-maker:

assumed status of track-maker	$h$ (m)	$\lambda/h$	estimated speed		equations used	
			(m/s)	(km/h)	( $h$ )	(speed)
'typical' coelurosaur	0.42	9.0	16.03	57.7	(12)	(11)
ornithomimid-like	0.55	7.0	13.10	47.2	(14)	(11)
ornithomimid-like	1.00	3.8	8.18	29.5	-	(11)
ornithomimid-like	1.00	3.8	7.32	26.4	-	(6)

In the last two cases  $h$  is the estimate by Welles (1971); and in one of these speed is estimated by means of equation (6), which is appropriate for walking animals, even though  $\lambda/h$  is greater than 2.0. It seems impossible to draw any firm conclusions from these estimates of size, speed and relative stride length. For the animal to have been walking (with  $\lambda/h$  less than 2.0) it would need to have been at least 1.9 metres high at the hip; this improbably high figure is equivalent to 19 times footprint length. It may be recalled that Alexander (1976) found  $h$  to be approximately 4 times footprint length among bipedal dinosaurs; and even on the assumption that the track-maker could have been an ornithomimid-like dinosaur we estimate  $h$  to have been less than 6 times footprint length (see the second of the cases listed above). If we adopt Welles's estimate for  $h$  (equivalent to 10 times footprint length) the *Hopiichnus* track-maker is found to be similar to the Lark Quarry track-makers in terms of size/speed relationship ( $\lambda/h$  3.82 as opposed to mean of 3.93). This close correspondence in relative stride length might indicate that the *Hopiichnus* track-maker was running at or near its maximum speed — if it were indeed an extremely long-limbed dinosaur. Estimates of  $h$  obtained with equations (12) and (14) are equivalent to 4.2 and 5.5 times footprint length (see the first two cases listed above), but these indicate that  $\lambda/h$  was as high as 7.0 or 9.0. It is difficult to imagine that any bipedal dinosaur could have attained such values for relative stride

length. In summary, we are unable to offer any satisfactory interpretation of the *Hopiichnus* trackway. If the track-maker had hindlimb proportions resembling those in any known dinosaur it must have been progressing in a series of phenomenal leaps. If the track-maker had been using a running gait ( $\lambda/h$  from 2.9 up to about 5.0) it must have had hindlimbs about twice as long as those of an ornithomimid with comparable foot length. And if the track-maker had been walking ( $\lambda/h$  less than 2.0) it must have had hindlimbs about 3 times as long as those of an ornithomimid with comparable foot length. There is no indication that the animal might have been swimming, and only touching down occasionally with its feet (cf. theropod trackways described by Coombs 1980b).

Alexander's methods (1976) have recently been applied by Farlow (1981) to a series of 15 dinosaur trackways in the Cretaceous of Texas. Three of these trackways seem to have been made by fast-running animals, with  $\lambda/h$  in the range 3.7 to 4.9 and speeds estimated from 30 to 43 km/h. Once again it is noteworthy that estimates of  $\lambda/h$  are less than 5.0. Farlow identified the Texas track-makers as theropod dinosaurs, and from the size of their footprints they might be envisaged either as exceptionally large coelurosaurs or as small to medium-size carnosaurs. Consequently it is possible to compare several estimates of size and speed for these track-makers:

assumed status of track-maker	$h$ (m)	$\lambda/h$	estimated speed		equations used	
			(m/s)	(km/h)	( $h$ )	(speed)
*Q94/98:						
theropod	1.16	*4.9	*11.9	*42.8	-	(6)
theropod	1.16	*4.9	*12.1	43.6	-	(11)
coelurosaur-like	1.42	4.0	10.3	37.0	(12)	(11)
carnosaur-like	1.49	3.8	9.9	35.7	(7)	(11)
*BLV/A3:						
theropod	1.48	*3.7	*8.3	*29.9	-	(6)
theropod	1.48	*3.7	*9.4	33.8	-	(11)
coelurosaur-like	1.87	2.9	7.7	28.0	(12)	(11)
carnosaur-like	1.82	3.0	8.0	28.6	(7)	(11)
*86/0-82:						
theropod	1.52	*4.3	*11.1	*39.9	-	(6)
theropod	1.52	*4.3	*11.9	42.8	-	(11)
coelurosaur-like	1.93	3.4	9.8	35.4	(12)	(11)
carnosaur-like	1.86	3.5	10.1	36.4	(7)	(11)

(\*trackway identification numbers and estimates taken from Farlow, 1981)

None of these estimates seems to be in serious conflict with our general conclusions. If  $h$  is estimated as 4 times footprint length only one of the track-makers (Q94/98) is found to have attained  $\lambda/h$  very much greater than 3.93. If  $h$  is estimated with the methods introduced in this paper it appears that this same track-maker would have rivalled the Lark Quarry dinosaurs in its locomotor performance ( $\lambda/h$  3.8 to 4.0).

To summarize, we have found no certain evidence that any bipedal dinosaur greatly surpassed the locomotor performances of the Lark Quarry dinosaurs. The Colorado ornithopod (Brown 1938) may have been walking with  $\lambda/h$  about 1.34 (Thulborn 1981); even if the track-maker had been trotting or running (Russell and Béland 1976)  $\lambda/h$  would have been no greater than 2.7. The *Saltopoides* track-maker (de Lapparent and Monténot 1967) seems certainly to have been running, with mean  $\lambda/h$  of 4.2 (based on three estimates for  $h$ ). If this track-maker had resembled carnosaurs or ornithomimids in body build it would appear to have matched the locomotor performances of the Lark Quarry animals, having  $\lambda/h$  in the range 3.7 to 4.0. But if the *Saltopoides* track-maker is envisaged as an exceptionally large coelurosaur with 'typical' hindlimb proportions its locomotor performance ( $\lambda/h$  4.9) is matched by only a few of the Lark Quarry dinosaurs. The *Hopiichnus* trackway (Welles 1971) presents intractable problems of interpretation. If this track-maker resembled any known dinosaur in hindlimb proportions its locomotor performance must have been phenomenal:  $\lambda/h$  would have been at least 7.0, and possibly 9.0 or higher. It is difficult to believe that any bipedal animal could sustain a running gait with such figures for  $\lambda/h$ . But if the

*Hopiichnus* track-maker had achieved this feat it would be necessary to abandon, or at least modify, the conclusions we have drawn from the Lark Quarry trackways. In this case further problems would arise. If the *Hopiichnus* track-maker and the Lark Quarry track-makers were running at or near maximum speed we might be forced to question Alexander's findings (1976, 1977) on the relationships of size, speed and gait in living tetrapods. Alternatively we must suppose that the Lark Quarry dinosaurs were very severely retarded by sinking into the muddy substrate (with the effect of reducing  $\lambda/h$  from at least 7.0 to 4.0 or less). If the Lark Quarry track-makers had been running well below their maximum possible speeds (but were not seriously retarded by the muddy substrate) another question will emerge: what circumstances caused these animals to run at a 'physiologically similar speed' ( $\lambda/h \cong 3.93$ ) a good deal less than maximum speed? We cannot find a satisfactory answer. Next it might be surmised that the *Hopiichnus* track-maker had been travelling with  $\lambda/h$  no greater than 5.0 (the maximum estimate from any trackway considered here); in this case the track-maker must be envisaged as an animal with hindlimbs very much longer (relative to foot length) than those in any known dinosaur. Evidently all these interpretations of the *Hopiichnus* trackway present difficulties; for the present we must regard the significance of this trackway as uncertain or equivocal. Finally we estimate that the three fastest of the Texas theropods (Farlow 1981) were travelling with  $\lambda/h$  between 2.9 and 4.0. These theropods, whether coelurosaurs or carnosaurs, seem to have maintained locomotor performances equivalent or inferior to those of the Lark Quarry dinosaurs.

## CONCLUSIONS

The most reliable guide to the size of a dinosaurian track-maker is probably footprint size index (SI) — rather than footprint length (FL) or any similar dimension. This conclusion is based on analysis of variance in a sample of 57 *Wintonopus* trackways, and it remains to be tested elsewhere. The *Skartopus* trackways cannot be used to test this conclusion because they do not show sufficient variation in size.

In bipedal dinosaurs the anatomy and posture of the foot were such that metatarsus length (MT) can be estimated on the basis of footprint dimensions (Fig. 18). Such an estimate of MT can then be used to predict skeletal hip height ( $h$ ) because these two dimensions are strongly correlated in each major group of bipedal dinosaurs. We provide allometric equations to predict  $h$  in the following groups of dinosaurs: coelurosaurs (with 'typical' hindlimb proportions), ornithomimids, carnosaurs, ornithopods in general, cursorial ornithopods, and graviportal ornithopods. These equations were used to obtain the following estimates of  $h$  for dinosaurian track-makers at the Lark Quarry site: about 2.6 m for the single carnosaur (trackway identified as cf. *Tyrannosauropus*); from 14 cm to 70 cm for the numerous ornithopods (trackways identified as *Wintonopus latomorum* ichnogen. et ichnosp. nov.), but with one large individual at about 1.6 m; from 13 to 22 cm for the numerous coelurosaurs (trackways identified as *Skartopus australis* ichnogen. et ichnosp. nov.).

The carnosaur traversed the Lark Quarry area from NE to SW, and a mixed group of ornithopods and coelurosaurs subsequently crossed the same area in the opposite direction. This mixed group comprised at least 150 animals. The gaits of these (and other) dinosaurian track-makers must be defined arbitrarily: this is because bipedal dinosaurs had the same sequence of limb movements at all speeds (and because the sequence of limb movements is unknown in quadrupedal dinosaurs). We define three dinosaurian gaits on the basis of relative stride length ( $\lambda/h$ ): a walking gait ( $\lambda/h < 2.0$ ), a trotting gait ( $\lambda/h$  between 2.0 and 2.9), and a running gait ( $\lambda/h > 2.9$ ). These may be regarded as 'physiologically similar' to the walking, trotting and running gaits of mammals (see Heglund et al. 1974, Alexander 1977). On this basis it is determined that the carnosaurian track-maker was walking ( $\lambda/h$  1.3) whereas the ornithopods and coelurosaurs were using a fast running gait

equivalent to cantering or galloping in mammals (mean  $\lambda/h$  about 3.7). An ornithopod track-maker at a second site (New Quarry) was found to have been walking ( $\lambda/h$  1.5).

The relationships between size ( $h$ ), speed and gait in living tetrapods (see Alexander 1976, 1977; Alexander et al. 1977) were used to estimate the speeds of the track-makers. It is estimated that the carnosaur was walking at a speed of about 7 km/h; for a sample of 56 ornithopods mean speed is estimated to have been about 16 km/h, and for a sample of 34 coelurosaurs it is estimated to have been about 12 km/h. For the single ornithopod at New Quarry estimated speed is 4 km/h.

The findings of this study support our preliminary interpretation of the Lark Quarry trackways — that the ornithopods and coelurosaurs were caught up in a stampede, which may have been generated by the approach of the carnosaur (Thulborn and Wade 1979, Wade 1979). We can find no evidence that conflicts with this interpretation. Indeed, it is difficult to imagine any other circumstances that might account for a mixed group of 150 dinosaurs running in a single direction. Moreover there is some indication that the ornithopods and coelurosaurs were running at or near their maximum speeds (under the conditions that prevailed): different-sized individuals were moving at different absolute speeds, but they seem to have maintained a 'physiologically similar speed' measured in terms of relative stride length ( $\lambda/h \cong 3.7$ ). It is difficult to believe that so many animals could have maintained and shared a 'physiologically similar speed' other than maximum speed.

To measure and compare the locomotor performances of dinosaurian track-makers it is desirable to adopt some criterion that will eliminate (or at least reduce) the effects of differences in body size. Direct comparisons of absolute speed are of little value because they are biased in favour of larger animals; comparisons of a 'size-related' speed ( $h/s$ , analogous to body lengths per second in studies of fish locomotion) are equally biased in favour of small animals. Of the criteria that are available for appraising locomotor performance the most suitable would seem to be relative stride length ( $\lambda/h$ ), Froude number (see Alexander 1976), and 'dimensionless speed' (see Alexander 1977). In terms of these criteria the locomotor performances of the Lark Quarry ornithopods and coelurosaurs are outstandingly good; their performances are better (and usually far better) than those of most other dinosaurian track-makers.

The ornithopods and coelurosaurs at Lark Quarry attained maximum  $\lambda/h$  of at least 3.9, and possibly as high as 5.0. This latter figure might represent the maximum limit of relative stride length for any bipedal dinosaur: it is difficult to imagine that any bipedal animal could extend  $\lambda/h$  much beyond 5.0, and we have found no certain evidence of any dinosaur having done so. If the most highly adapted of dinosaurian cursors — the ornithomimids — attained  $\lambda/h$  of 5.0 their maximum speeds might have been about 60 km/h.

Finally it is clear that small dinosaurs, whether juveniles or adults (or both), may have been abundant in some localities. It may not be legitimate to identify small footprints as those of juvenile dinosaurs, because dinosaurian rates of growth are unknown and may not have been constant. For this reason it is probably fruitless to investigate dinosaurian demography on the basis of ichnological data.

#### ACKNOWLEDGMENTS

Many residents in and around Winton took an active interest in the work at Lark Quarry and made generous offers of material assistance: in particular we thank Peter Knowles ('Namarva'), Eric and Marjorie Bryce ('Colston'), Roslyn and Bob Blackett ('Amelia Downs'), Arthur and Roslyn Wallace ('Cork'), and Ron McKenzie (Winton). Among the many persons who played roles in the discovery and excavation of the trackways we extend particular thanks to Malcolm Lark, Barbara Molnar, Duncan McPhee, students from the University of New South Wales and the University of Queensland, members of the 6th Battalion, Royal Australian Regiment, and local friends too numerous to list. Our work relied heavily on support from members of the Queensland Museum staff, especially Alan Bartholomai, Errol Beutel, Don Dale, Yvonne Evans, Ralph Molnar, Howard Plowman, Andrew Rozefelds and Terry Tebble. Most photographs are the work of Alan Easton, and Fig. 1 is based on an aerial survey commissioned by the Queensland National Parks and Wildlife Service. Dave Norman (London), Philip Currie (Alberta), Jim Farlow (Michigan) and Sam Welles (California) offered useful comments and information about dinosaur tracks elsewhere in the world. One of the authors (R.A.T.) received continuing financial support from the Australian Research Grants Committee.

In June 1982 Lark Quarry and a surrounding area (about 374 hectares) were designated an Environmental Park under the joint trusteeship

of the Winton Shire Council and the Queensland Museum. This end was achieved through the goodwill and co-operation of Roslyn and Bob Blackett ('Amelia Downs'), members of the Winton Shire Council, and officers of the Queensland National Parks and Wildlife Service (especially Alan Chenoweth and Warren Oxnam). The Winton Shire Council has constructed an access road to the trackway site, which is now furnished with a permanent walkway and a protective roof (designed by Duncan McPhee, who also worked on site during excavations). Neville Agnew (Conservator, Queensland Museum) is undertaking a long-term study to monitor and retard any deterioration of the trackway surface.

To all these individuals and organizations we express our sincere thanks.

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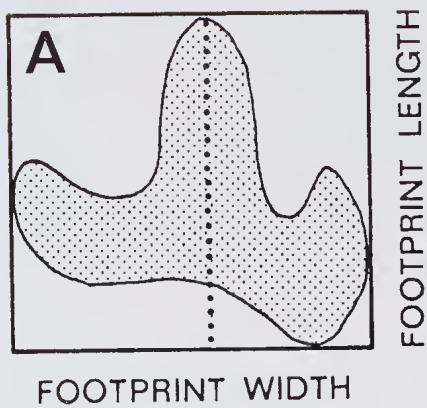
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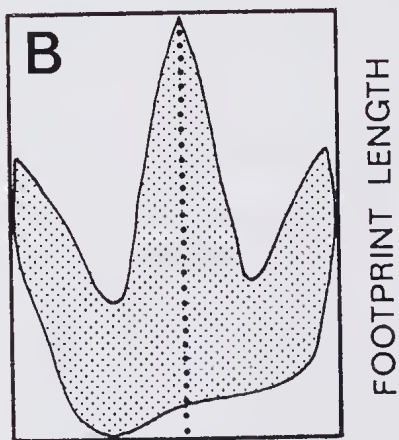
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FOOTPRINT WIDTH



FOOTPRINT WIDTH

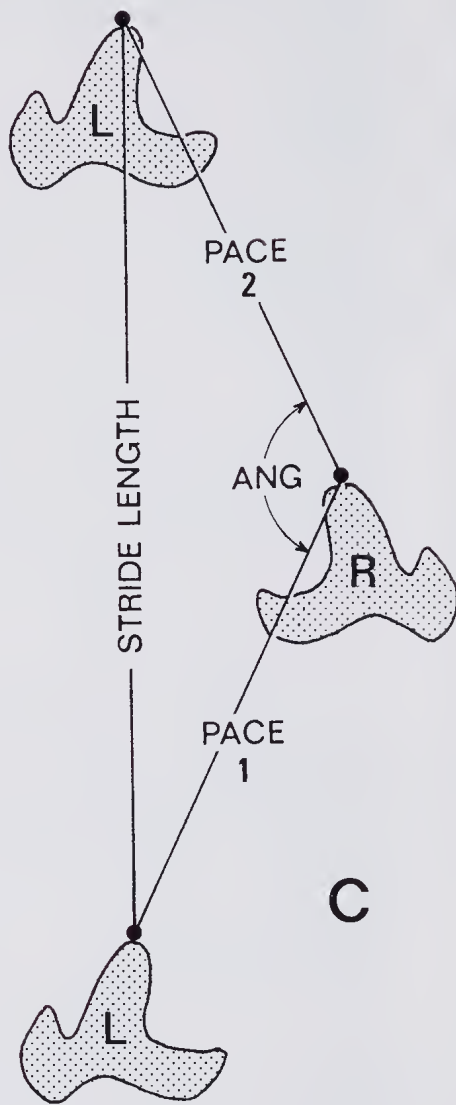


FIGURE 2. Diagrams to illustrate measurements of footprints and trackways. A, outline of ornithopod footprint showing footprint length measured along or parallel to the axis of digit 3 (dotted line); footprint width is measured at a right angle to footprint length. B, outline of coelurosaur footprint showing corresponding measurements of length and width. C, short section of ornithopod trackway showing measurements of two successive paces and a single stride. Pace angulation (ANG) is calculated from the lengths of the paces and the stride (see 'Methods').

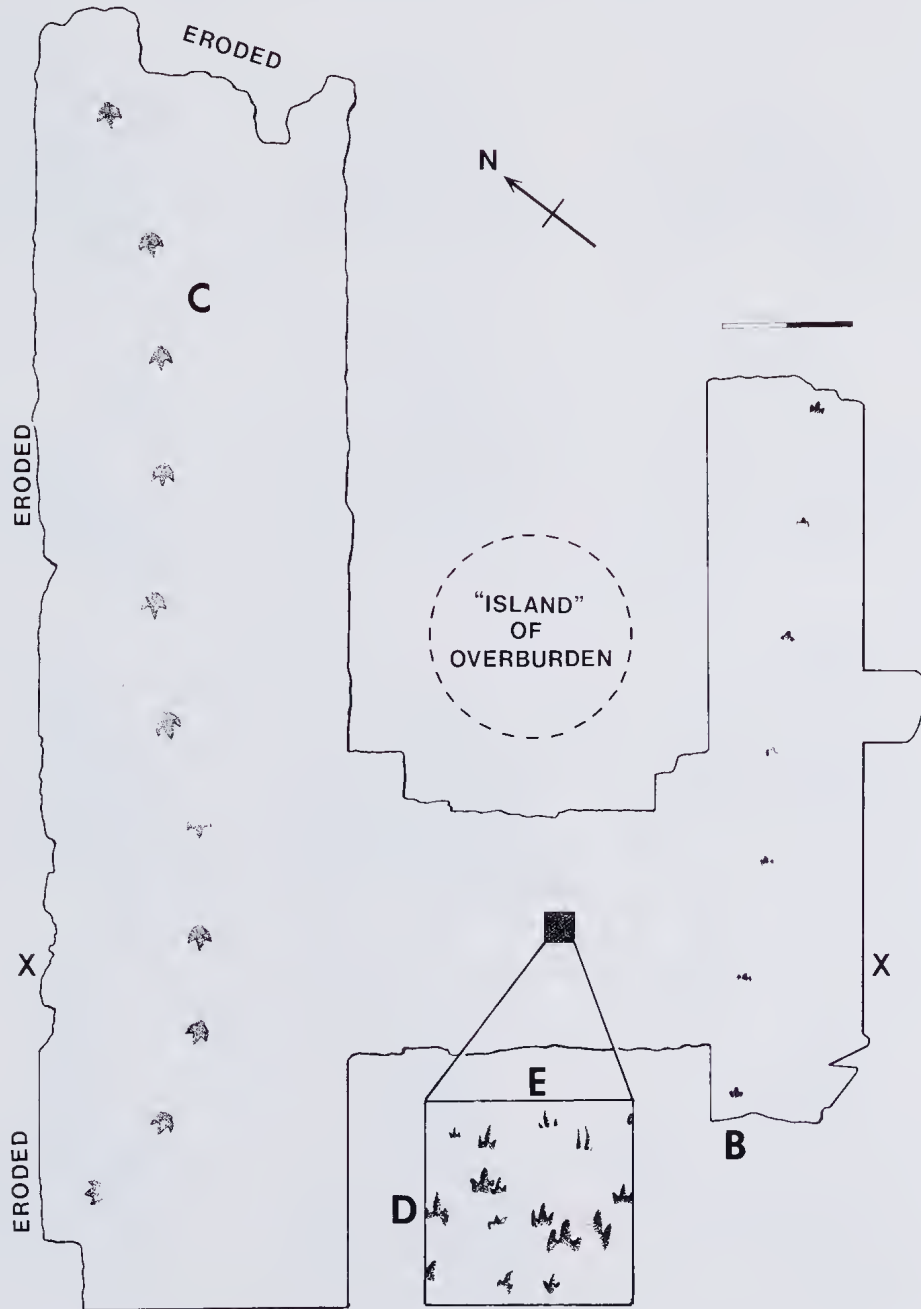


FIGURE 3. Outline chart of the study area at Lark Quarry. Scale bar indicates 2 m. Trackway of the solitary carnosaur is shown at left (C), and partly eroded trackway of an exceptionally large ornithopod is shown at right (B). A representative portion of the bedding plane is enlarged (bottom centre) to illustrate the abundance and orientation of small footprints attributed to ornithopods (D) and coelurosaurs (E). Trackways are identified by corresponding letters in descriptions (p. 417). The number of track-makers was estimated by counting footprints in a metre-wide transect between the points marked X. The area shown in outline was photographed (see Pl. 4), replicated in fibreglass and studied in detail. Adjoining areas of bedding plane (mainly to S and SW) were exposed during excavations but were not studied in detail. An outlier or 'island' of overburden was left undisturbed in the area indicated.

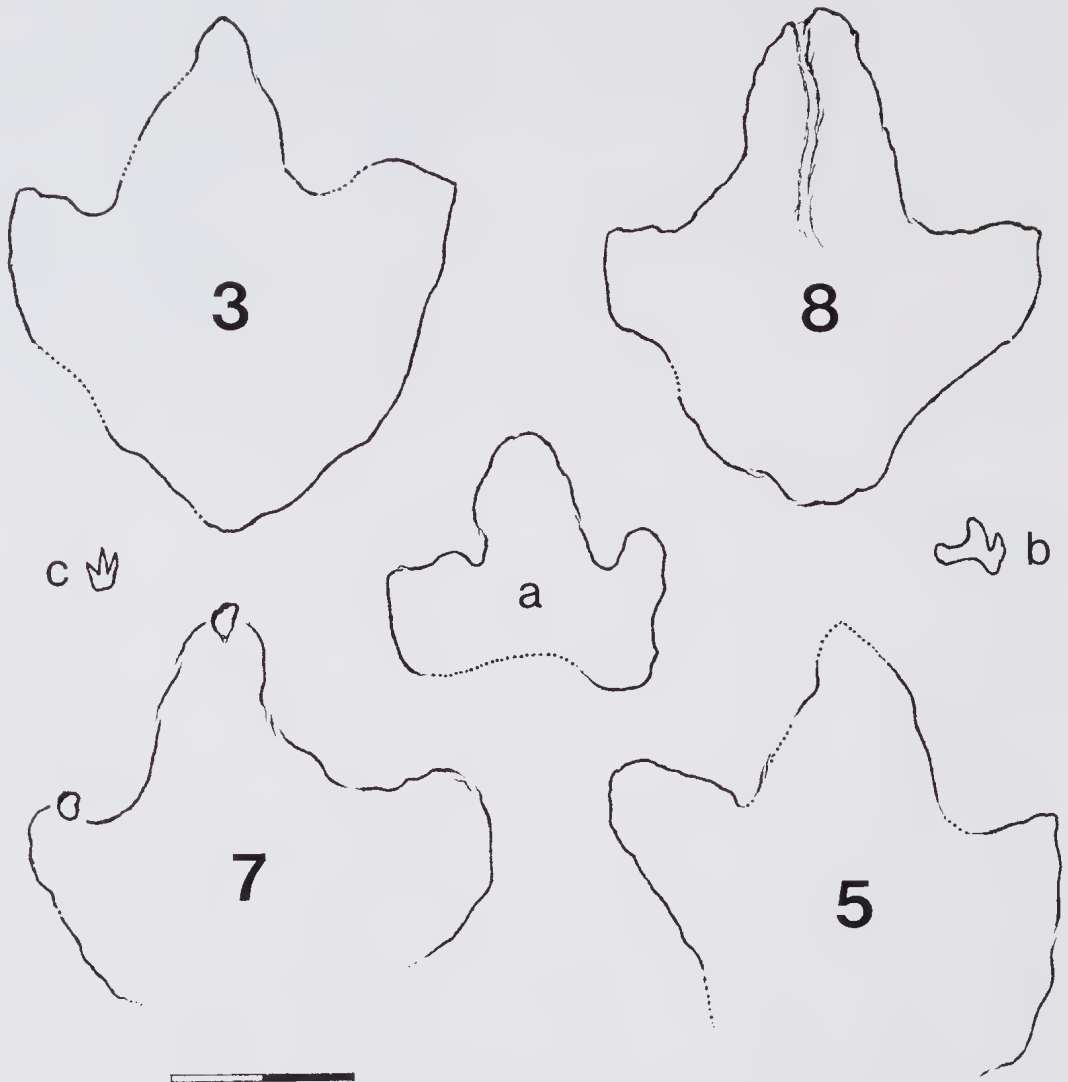


FIGURE 4. Variation in size and shape of the footprints at Lark Quarry. Scale bar indicates 20 cm. The four large footprints are from the trackway of the carnosaur (cf. *Tyrannosauropus*) and are identified by their number in the sequence 1-11. Footprint 7 shows traces of large pointed claws (see also Pl. 6); footprint 8 shows a longitudinal crest formed by mud adhering to the underside of the track-maker's middle toe. *a*, the largest ornithopod footprint (*Wintonopus*) found at Lark Quarry. *b*, an 'average' ornithopod footprint (*Wintonopus*) at Lark Quarry, based on mean dimensions in 284 examples. *c*, an 'average' coelurosaur footprint (*Skartopus*) at Lark Quarry, based on mean dimensions in 191 examples.

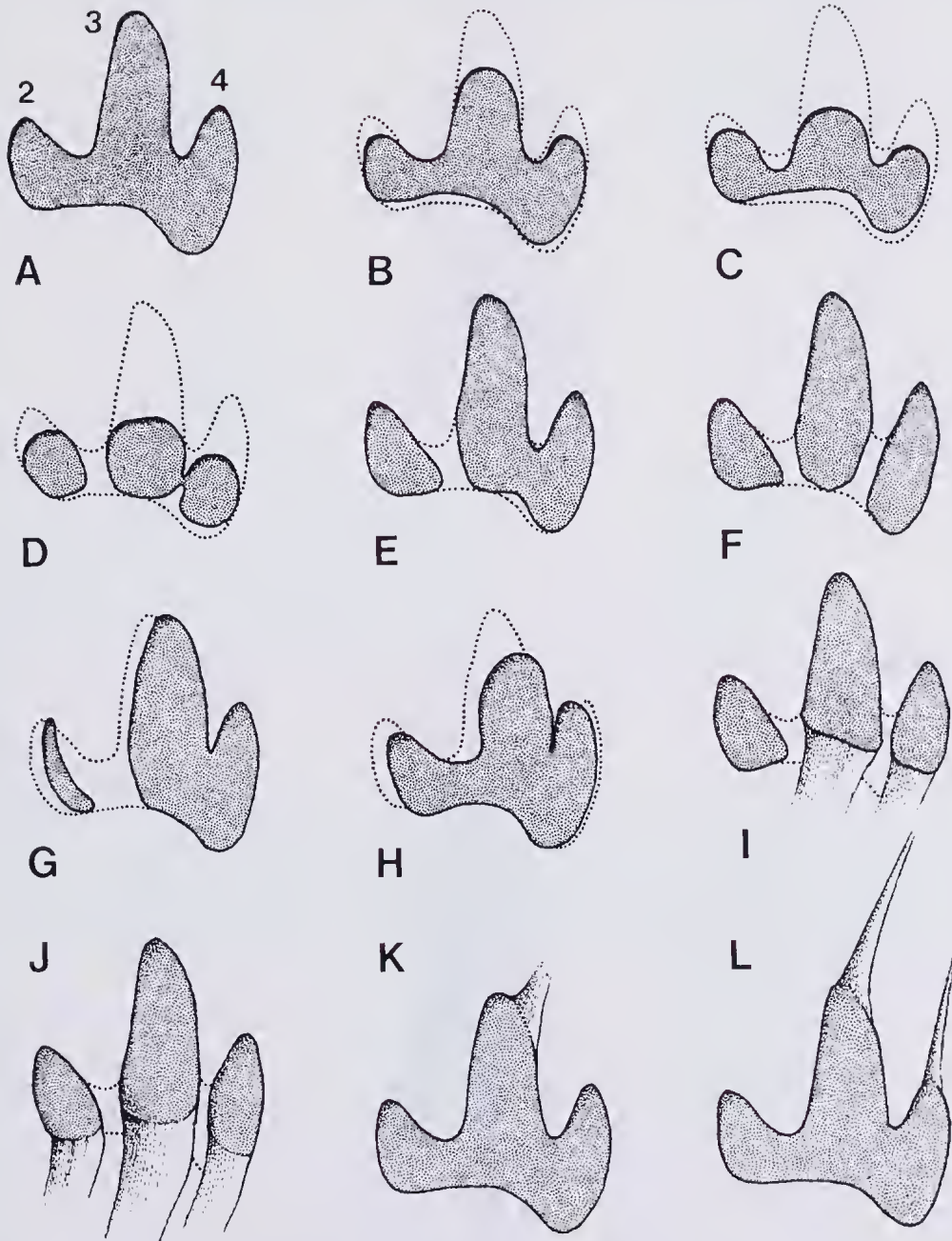


FIGURE 5. Diagrams to illustrate variation in shape of ornithopod footprints (*Wintonopus*) at Lark Quarry. A, complete and undistorted imprint of a right foot; all other diagrams illustrate variation on this basic footprint shape. Examples B, C and D are fore-shortened or 'stubby-toed' footprints formed by the toes entering and leaving the sediment at a steep angle. In example D the toes entered the sediment vertically but did not sink to the level of the interdigital web between digits 2 and 3. In examples E and F the foot has not sunk deeply enough to leave traces of one or both of the interdigital webs. In examples G and H footprint width is reduced because the foot entered and left the sediment obliquely — with the track-maker's weight carried mainly on the outer two digits. Examples I and J show backwardly directed scrape-marks; examples K and L show scrape-marks directed anterolaterally.

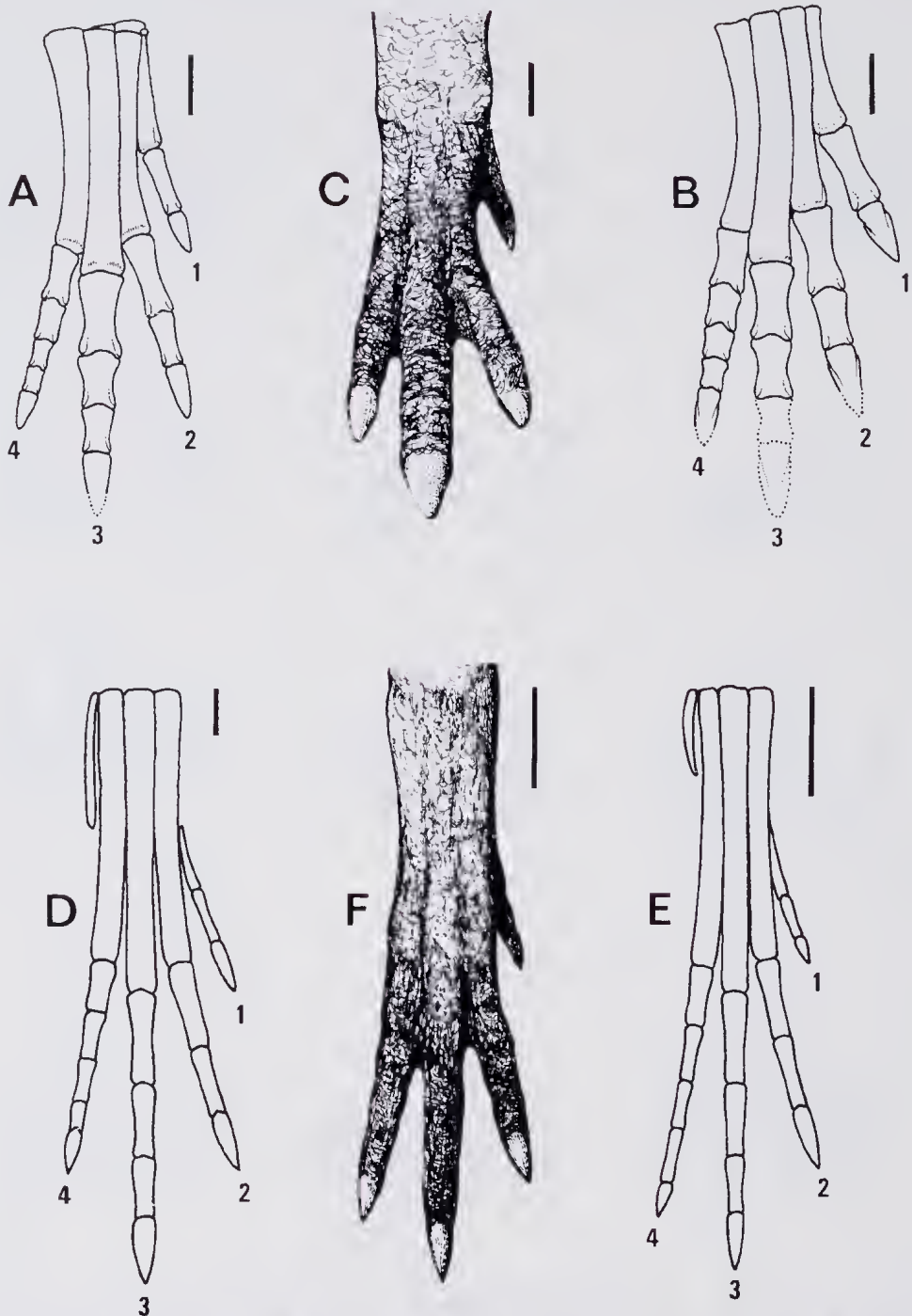


FIGURE 6. Foot structure in small bipedal dinosaurs. In all cases the right foot is shown in anterior view and the scale bar indicates 2 cm. A, foot skeleton in the Upper Jurassic ornithopod *Nanosaurus*; B, foot skeleton in the Lower Cretaceous ornithopod *Hypsilophodon*; C, attempted restoration of foot structure in the *Wintonopus* track-maker (based on mean dimensions in 284 footprints); D, foot skeleton in the Triassic coelurosaur *Coelophysis*; E, foot skeleton in the Upper Jurassic coelurosaur *Compsognathus*; F, attempted restoration of foot structure in the *Skartopus* track-maker (based on mean dimensions in 191 footprints). A and B after Galton and Jensen (1973); D and E after Ostrom (1978).

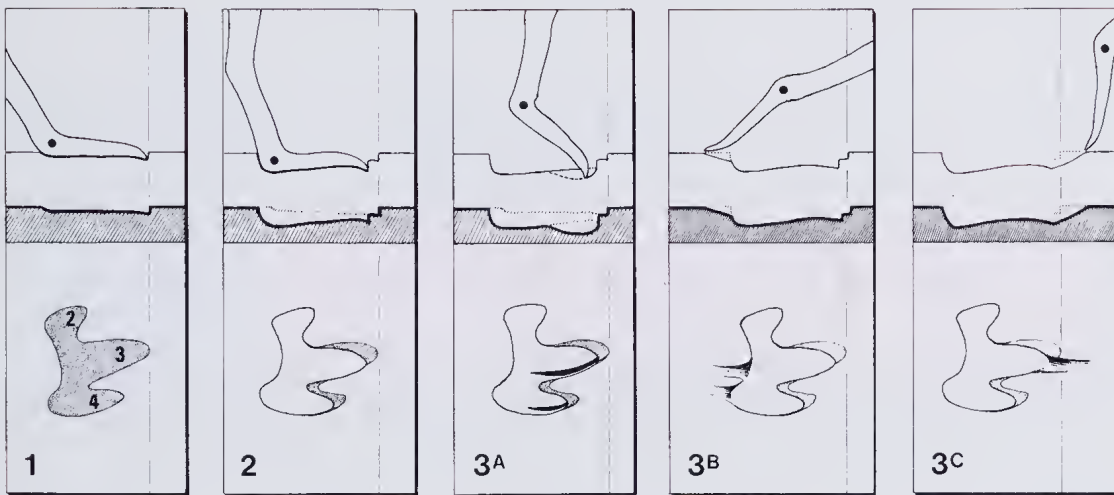


FIGURE 7. Morphological features of ornithopod footprints (*Wintonopus*) related to events during the track-maker's stride cycle. Each diagram shows position of foot (at top, with distal end of metatarsus indicated by a spot), longitudinal section of corresponding footprint (at middle), and corresponding plan view of right footprint (at bottom). Stage 1: start of stride, with forwardly extended foot; initial footprint (shaded) is shallow and shows positive rotation. Stage 2: as the track-maker moves forwards the foot sinks deeper, rotates to face directly ahead, and slips backwards a little (unshaded footprint). Stage 3A: as foot starts to lift from the substrate the toes continue to slip backwards, incising slots in the floor of the footprint. Stage 3B (following Stage 2, or via Stage 3A): toes slip back far enough to breach rear wall of footprint, producing backwardly-directed scrape-marks. Stage 3C (following Stage 2): toes do not slip backwards but drag through front wall of footprint to produce forwardly-directed scrape-marks.

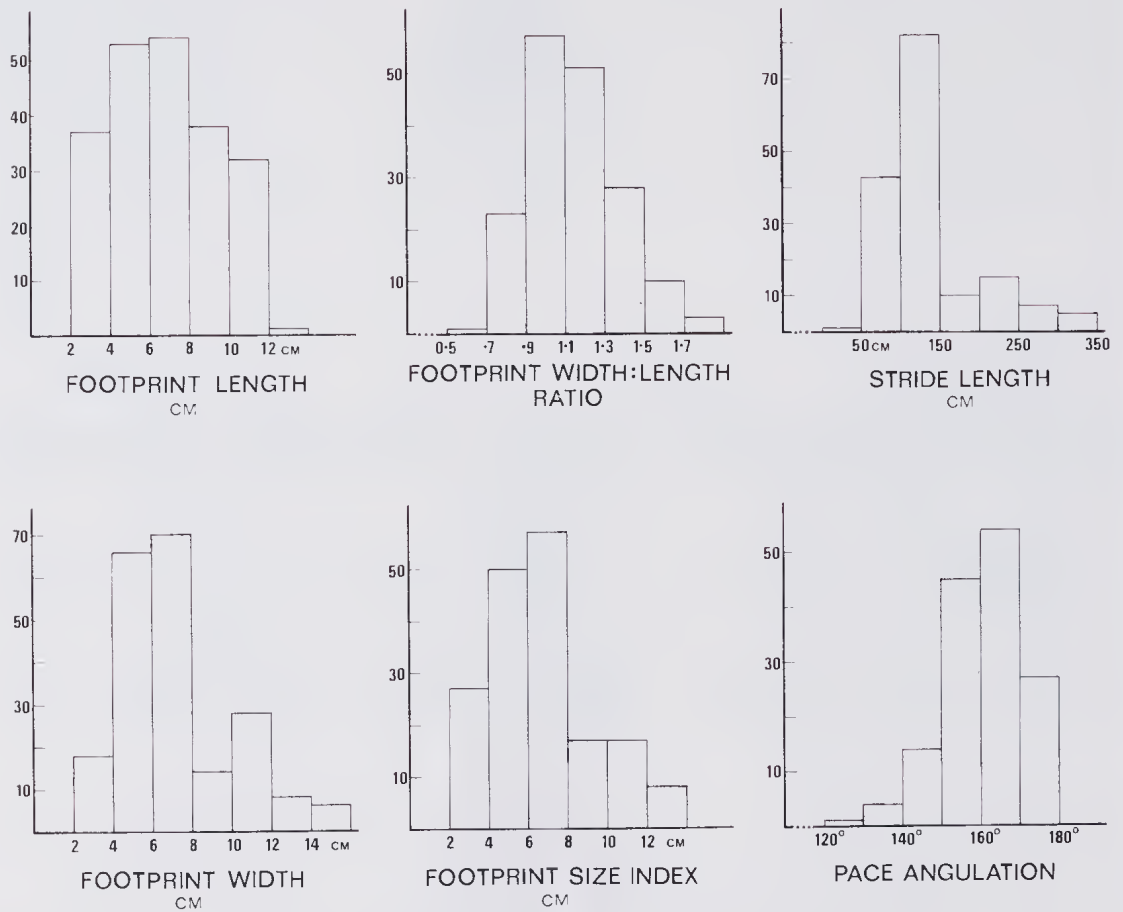


FIGURE 8. Frequency distributions based on pooled data from *Wintonopus* (ornithopod) trackways at Lark Quarry. All modal classes drawn to uniform height, and vertical scales are absolute frequencies. Diagrams for footprint length, footprint width and footprint size index exclude data from single exceptionally large trackway (No. 57 in Table 4; see also Fig. 9).



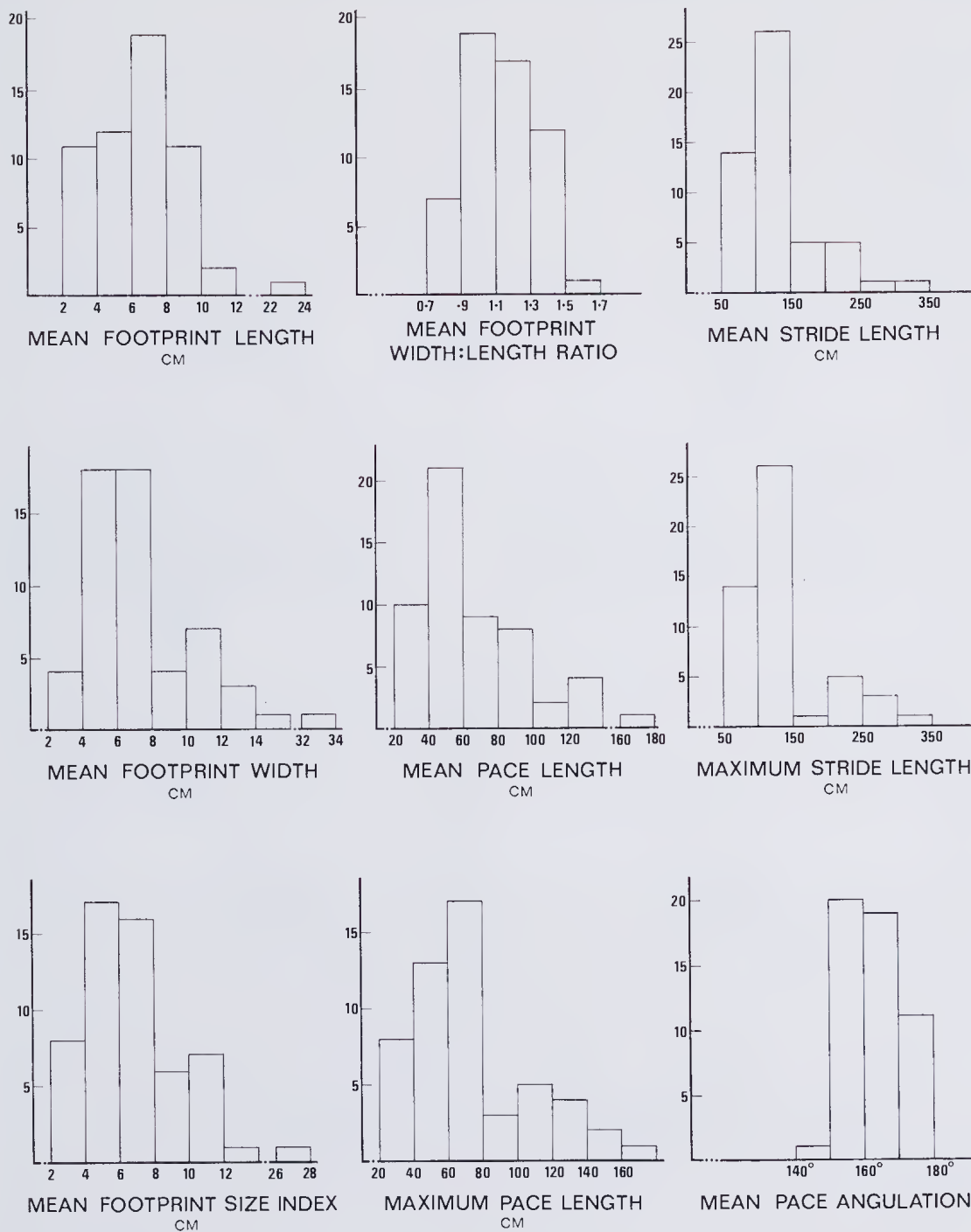


FIGURE 9. Frequency distributions based on grouped data from *Wintonopus* (ornithopod) trackways at Lark Quarry. All modal classes drawn to uniform height, and vertical scales are absolute frequencies.

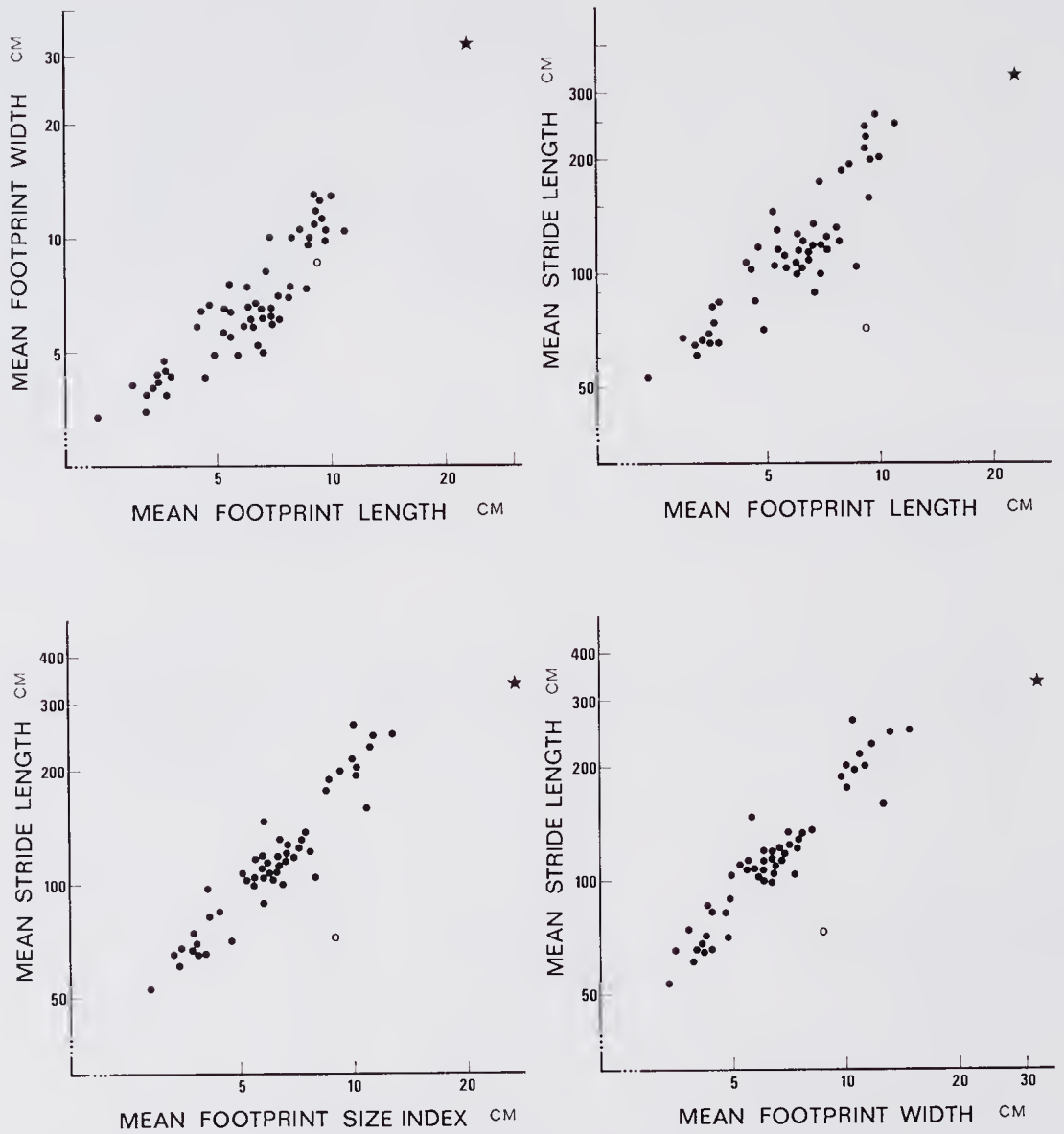


FIGURE 10. Scatter diagrams based on grouped data from *Wintonopus* (ornithopod) trackways. In all cases both axes have logarithmic scales. Note that the New Quarry track-maker (open circle) resembles Lark Quarry track-makers (solid circles) in footprint proportions, but is distinguished by its relatively short stride. The same is true (but less obviously so) for the single exceptionally large track-maker at Lark Quarry (star).

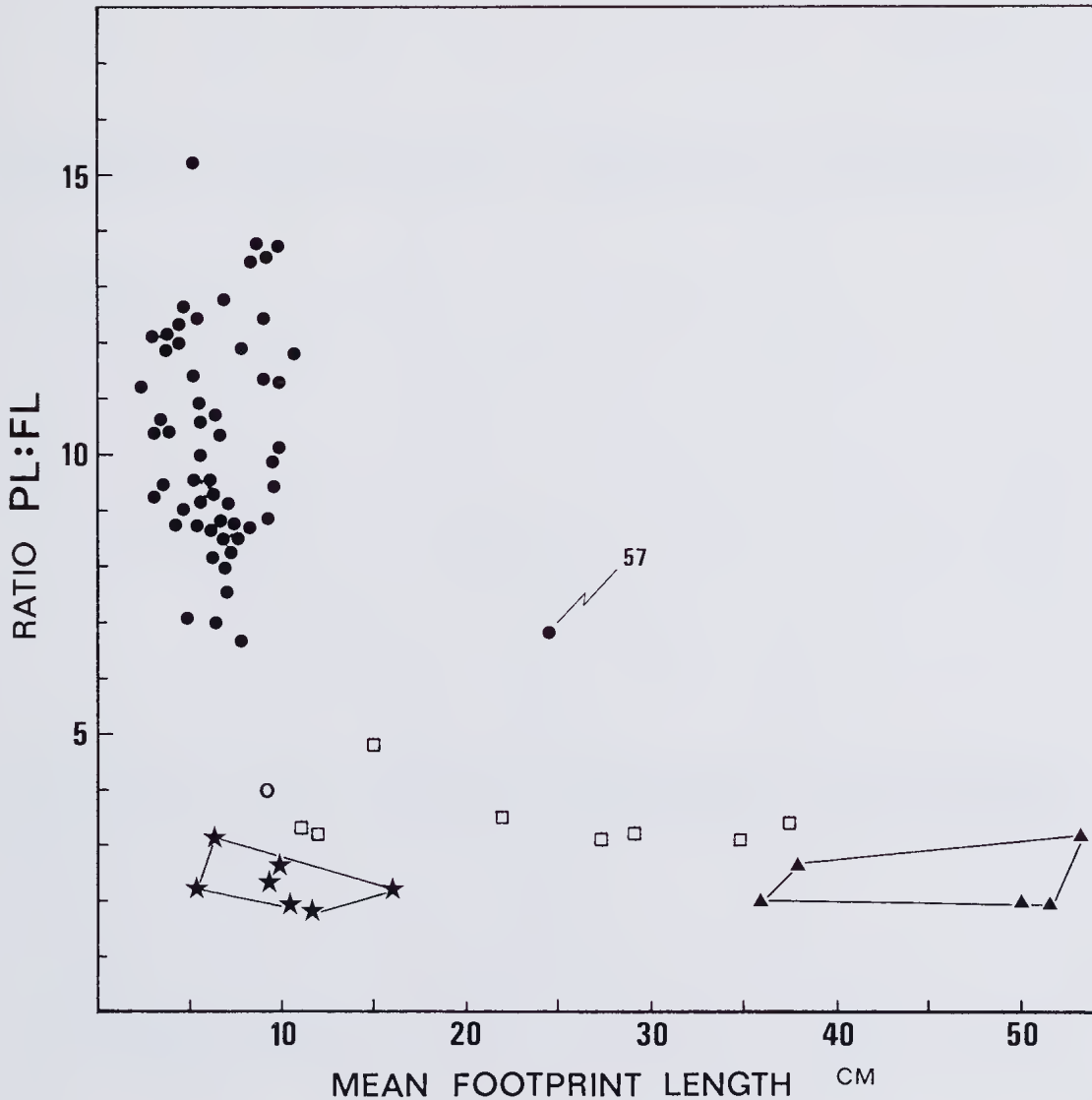


FIGURE 11. Scatter diagram to illustrate relationship between pace length and footprint length in trackways attributed to ornithopod dinosaurs. Solid circles — *Wintonopus* (at Lark Quarry; No. 57 is the single large trackway formed at slightly earlier date); open circle — *Wintonopus* (at New Quarry); stars — *Anomoepus*; triangles — *Irenesauripus*; open squares — various trackways including *Amblydactylus*, *Gypsichnites* and *Sauropus*. Incorporating data from Sternberg 1932, Lull 1953, Currie and Sarjeant 1979.

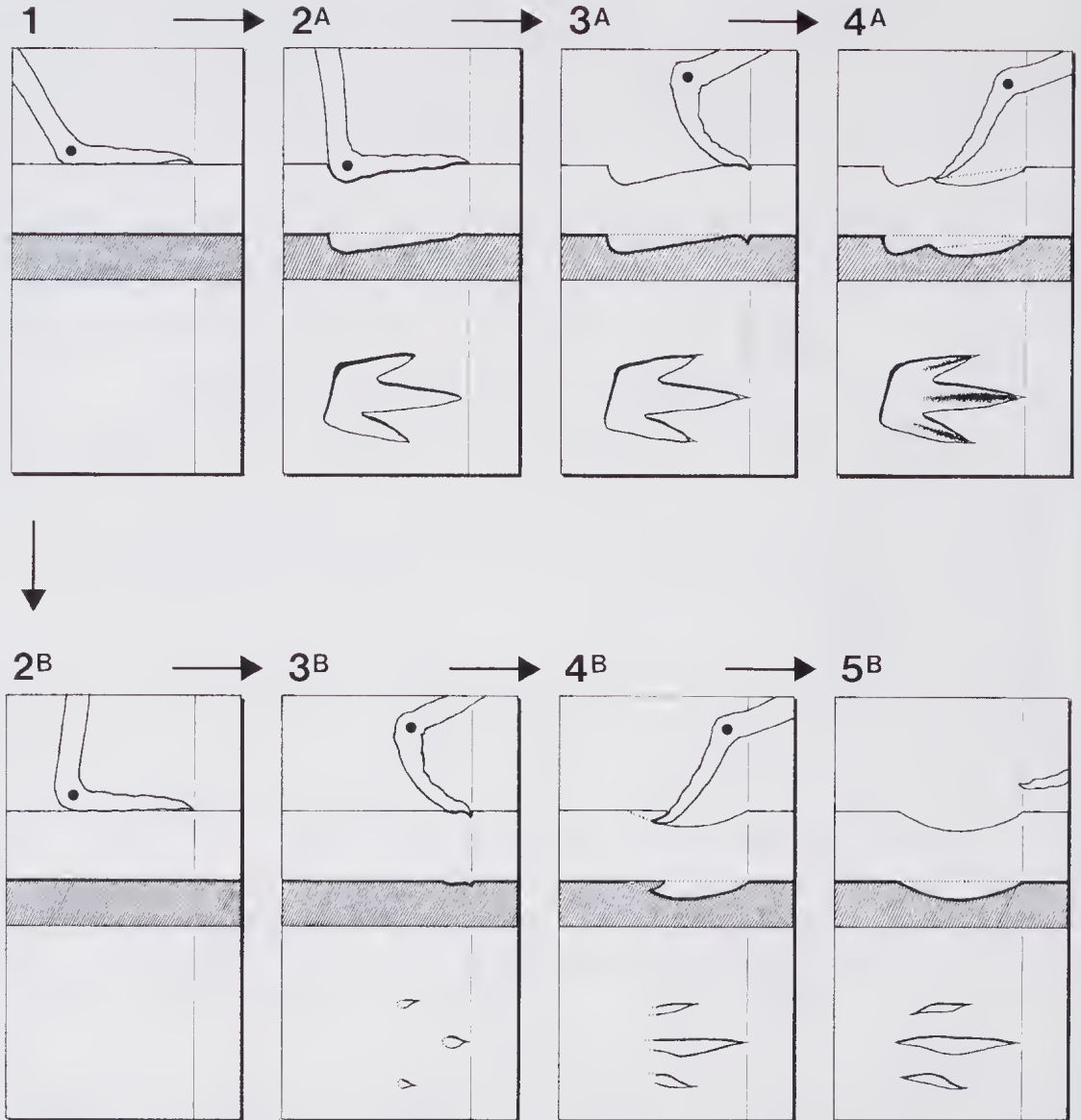


FIGURE 12. Morphological features of coelurosaur footprints (*Skartopus*) related to events during the track-maker's stride cycle. Each diagram shows position of foot (at top, with distal end of metatarsus indicated by a spot), longitudinal section of corresponding footprint (at middle), and corresponding plan view of footprint. Stage 1: start of stride, with forwardly extended foot; initially there is no footprint, or a very shallow one. Stage 2A: as the track-maker moves forwards the foot sinks deeper. Stage 3A: the foot lifts from the substrate, leaving sharp imprints of the claws. Stage 4A (frequently follows Stage 3A): the toes slip backwards, incising slots in the floor of the footprint. The sequence of Stages 2B to 5B is equivalent to the sequence 2A to 4A, but the foot does not sink into the substrate; the only traces are scratches produced by the toes slipping backwards.

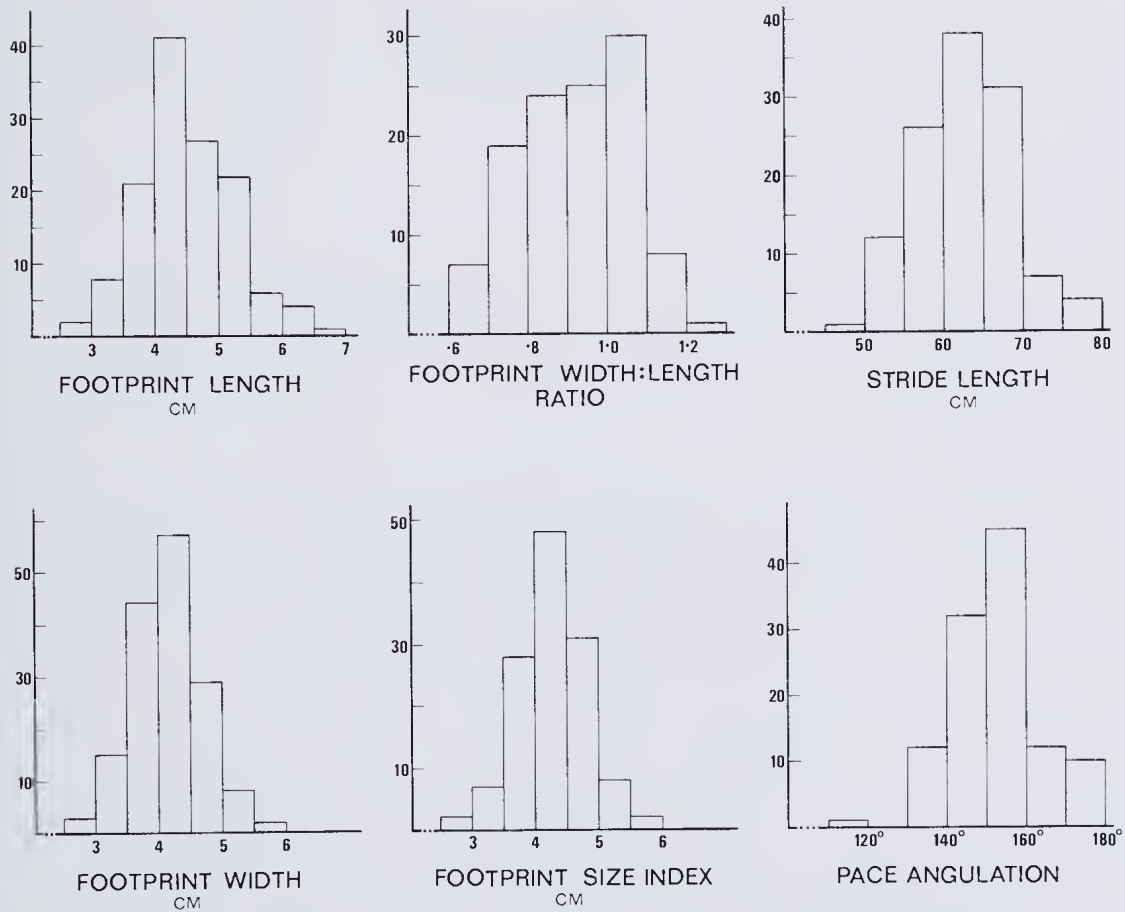


FIGURE 13. Frequency distributions based on pooled data from *Skartopus* (coelurosaur) trackways at Lark Quarry. All modal classes drawn to uniform height, and vertical scales are absolute frequencies.

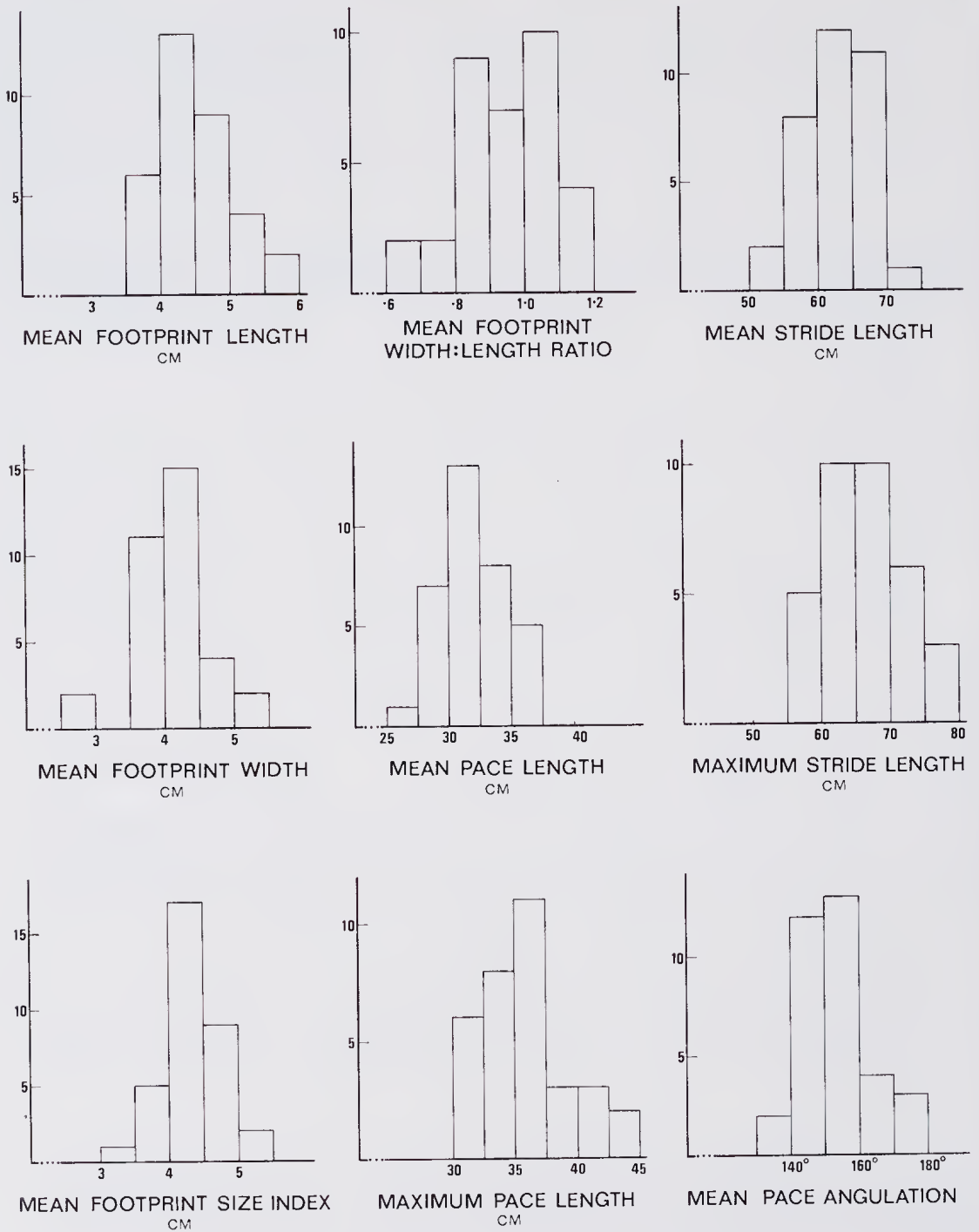


FIGURE 14. Frequency distributions based on grouped data from *Skartopus* (coelurosaur) trackways at Lark Quarry. All modal classes drawn to uniform height, and vertical scales are absolute frequencies.

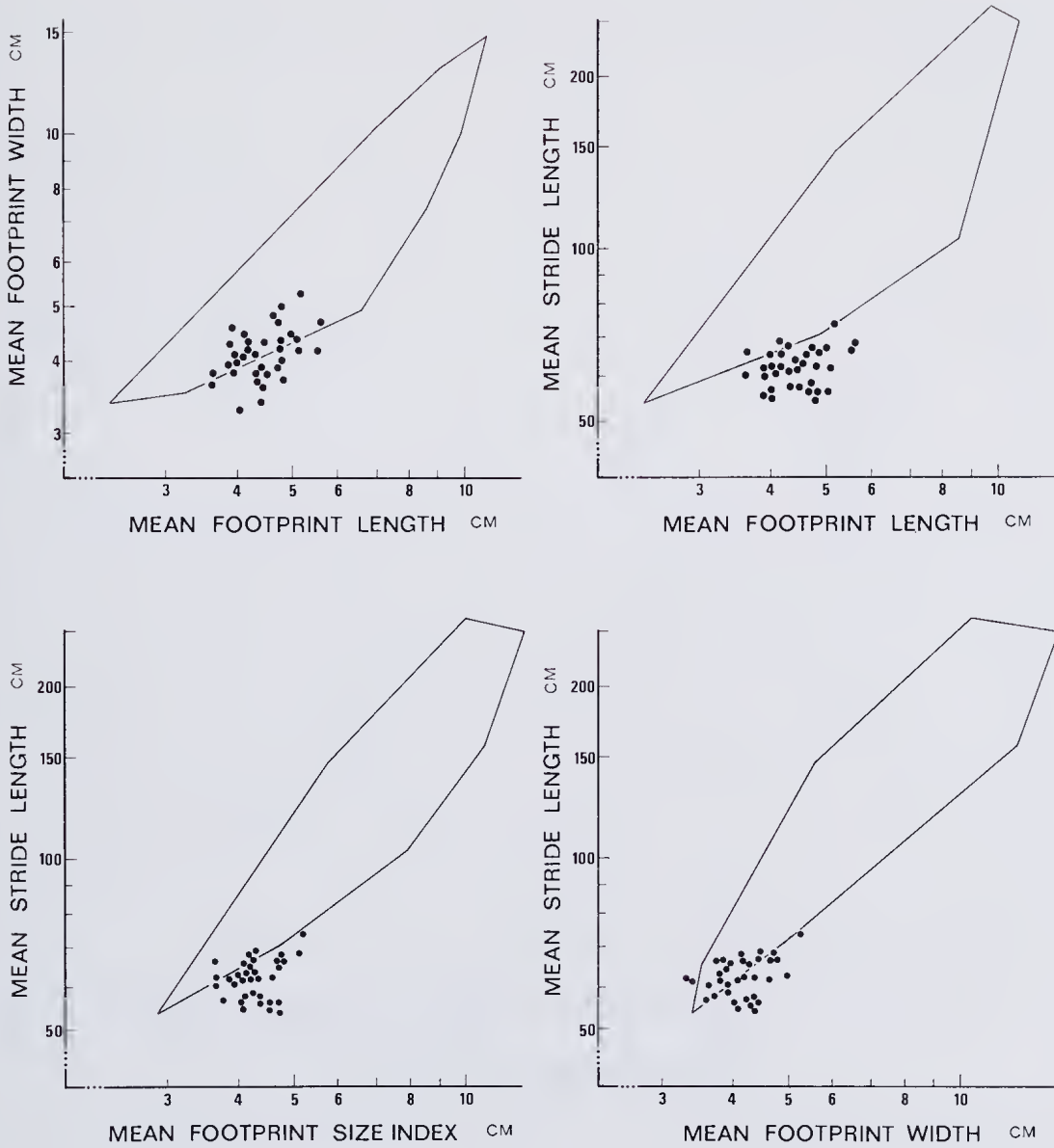


FIGURE 15. Scatter diagrams based on grouped data from *Skartopus* (coelurosaur) trackways at Lark Quarry. In all cases both axes have logarithmic scales. Polygons define distributions for *Wintonopus* (ornithopod) trackways at the same site.

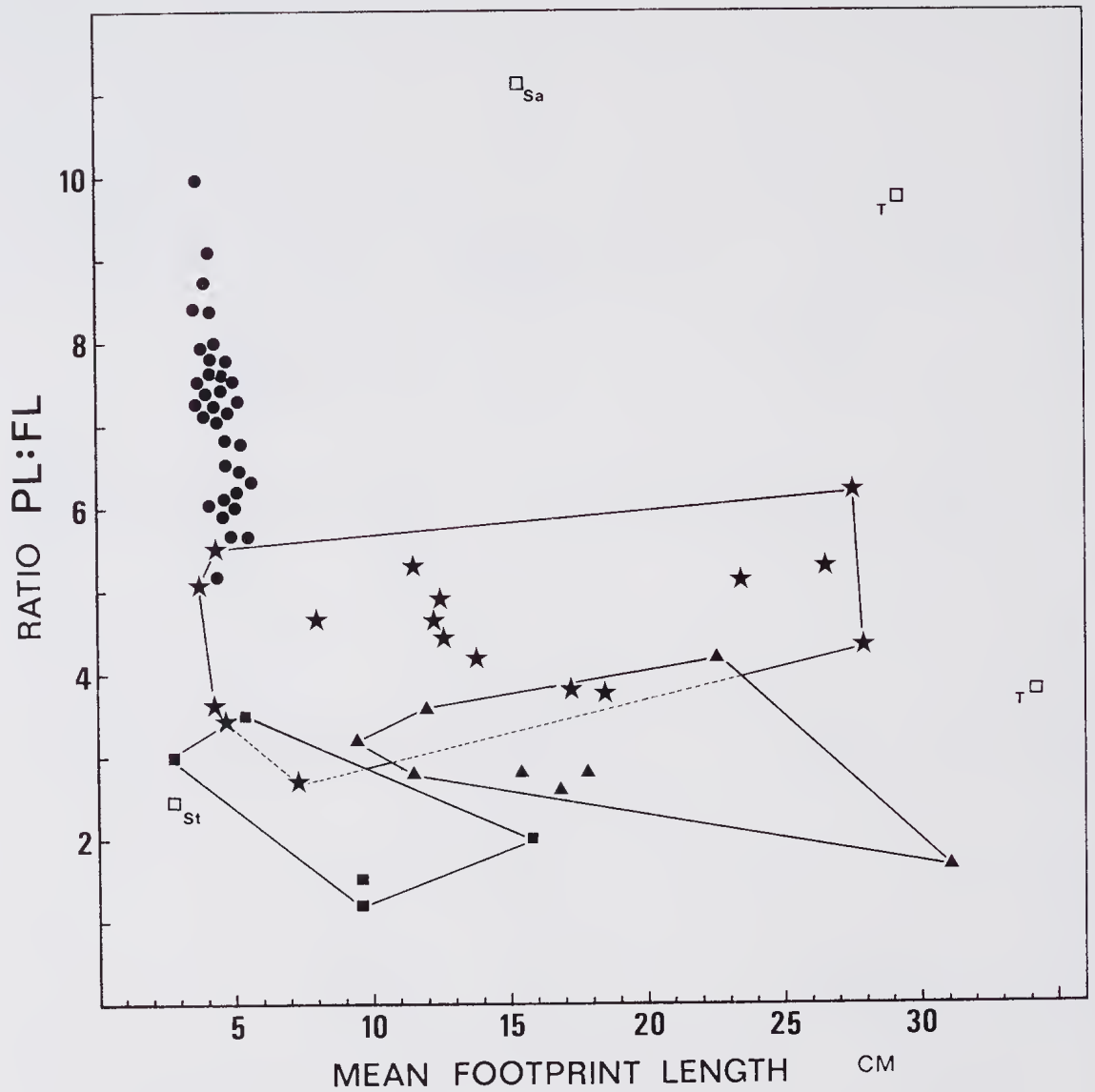


FIGURE 16. Scatter diagram to illustrate relationship between pace length and footprint length in trackways attributed to small and medium-sized theropod dinosaurs. Solid circles — *Skartopus* (at Lark Quarry); stars — *Gallator*; triangles — *Anchisauripus*; solid squares — *Plesiornis*; Sa — *Saltopoides*; St — *Stenonyx*; T — unidentified theropods. Incorporating data from Lull 1953, de Lapparent and Monténat 1967, Bassoulet 1971, Tucker and Burchette 1977, Farlow 1981 (two smallest of 15 unidentified theropods).



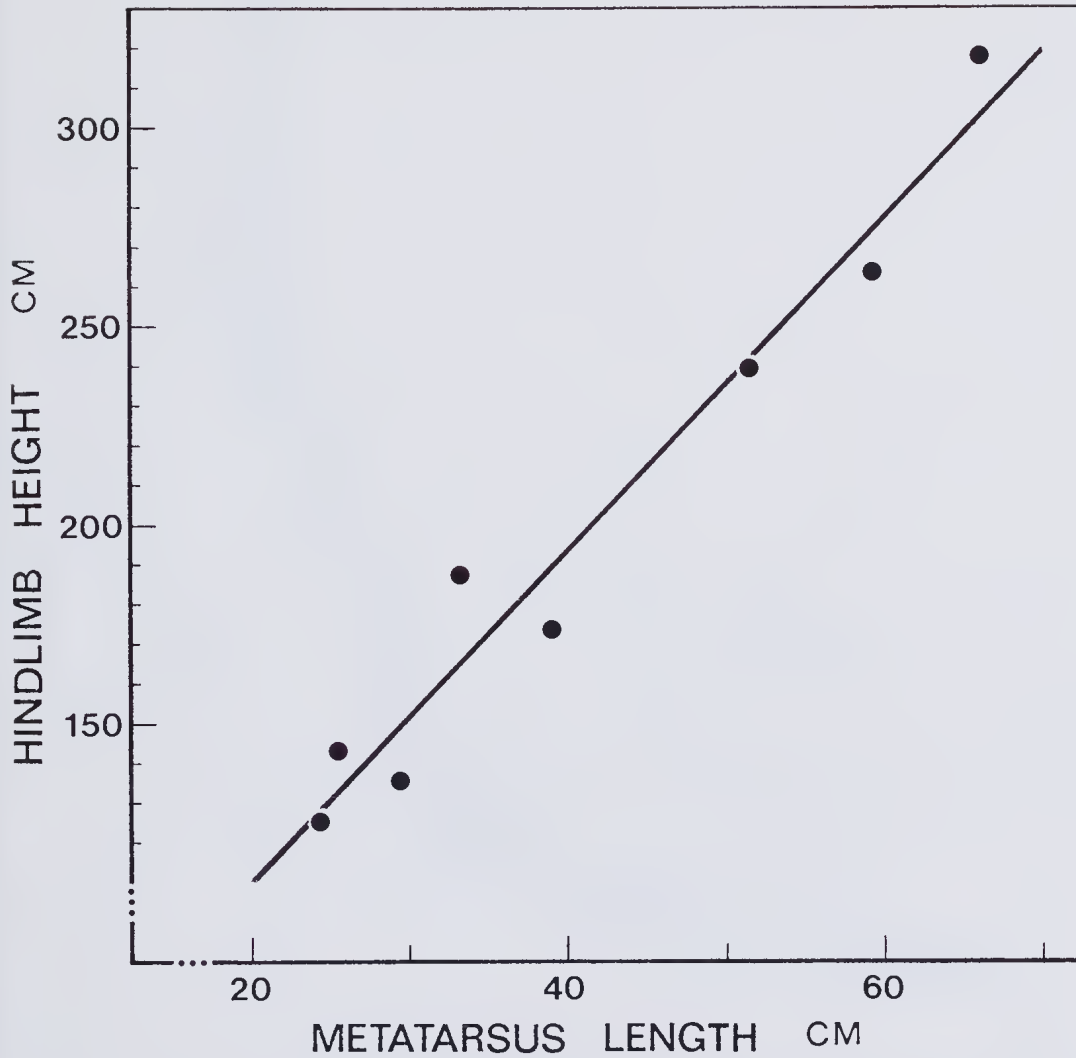


FIGURE 17. Relationship between hindlimb height and metatarsus length in large theropod dinosaurs. Product-moment correlation coefficient ( $r = 0.979$ ) is not improved by transformation of data. Least squares regression line represents equation (7) in text. Based on data from Lambe 1917 (*Gorgosaurus*), Osborn 1917 (*Tyrannosaurus*), Gilmore 1920 (*Allosaurus*, *Ceratosaurus*), von Huene 1932 (*Megalosaurus*), Welles 1954 (*Dilophosaurus*), Russell 1970 (*Daspletosaurus*).

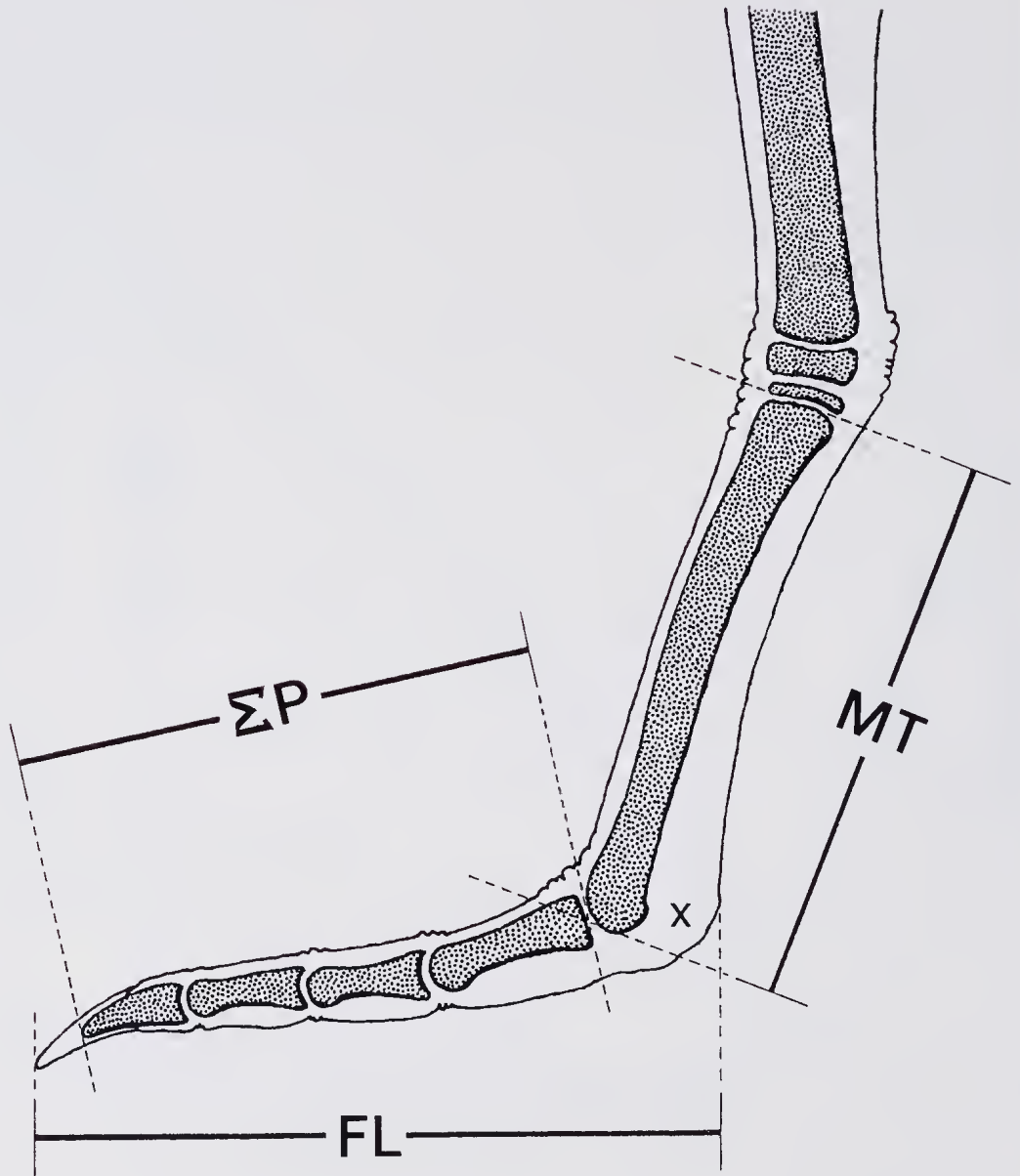


FIGURE 18. Diagrammatic comparison of dimensions in the foot of a bipedal dinosaur. The diagram represents a vertical section along digit 3, with bones stippled and other tissues in outline.  $\Sigma P$  represents the sum of the lengths of phalanges in digit 3. FL (footprint length) comprises  $\Sigma P$  together with claw sheath, joint capsules, base of the metatarsus and (perhaps) a fleshy 'heel' at point X. MT (length of metatarsus) is often about the same length as  $\Sigma P$ .

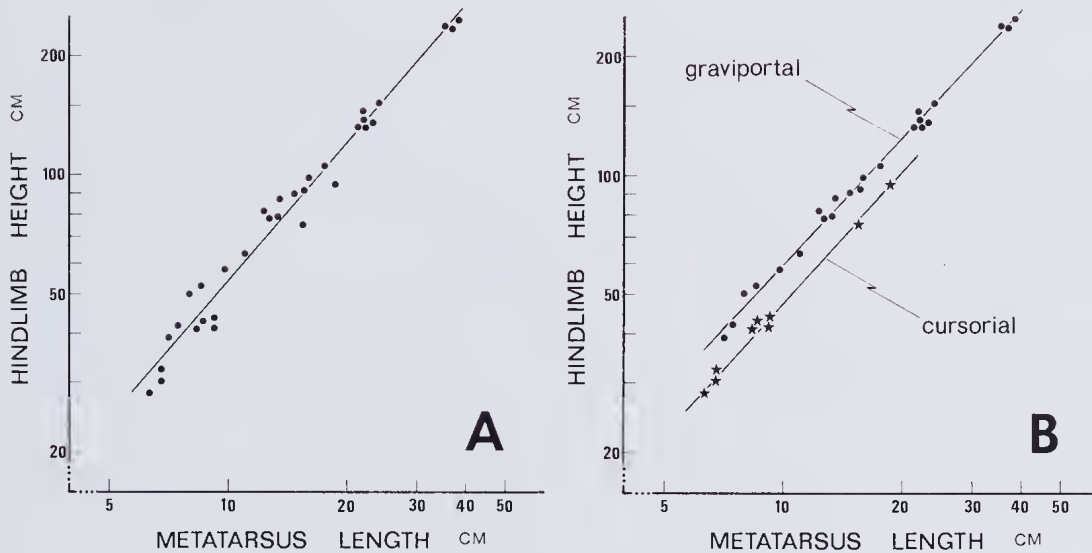


FIGURE 19. Relationship between hindlimb height and metatarsus length in ornithopod dinosaurs. Logarithmic scale on both axes. A, heterogeneous sample of 32 ornithopod dinosaurs;  $r = 0.988$ ; least squares regression line represents equation (8) in text. B, same data, but with graviportal ornithopods (23 specimens) separated from cursorial ornithopods (9 specimens); for graviportal ornithopods  $r = 0.997$  and least squares regression line represents equation (10) in text; for cursorial ornithopods  $r = 0.997$  and least squares regression line represents equation (9) in text. Based on data from Gilmore 1915 (*Thescelosaurus*) and 1924 (*Stegoceras*), Parks 1920 (*Kritosaurus*), Osborn 1924 (*Protiguanodon*, *Psittacosaurus*), Hooley 1925 (*Iguanodon*), Lull and Wright 1942 (*Anatosaurus*, *Corythosaurus*), Thulborn 1972 (*Fabrosaurus*), Galton 1974 (*Hypsilophodon*, *Dryosaurus*, *Parksosaurus*), Galton and Jensen 1973 (*Nanosaurus*), Santa Luca et al. 1974 (*Heterodontosaurus*), Dodson 1980 (*Camptosaurus*, *Tenontosaurus*).

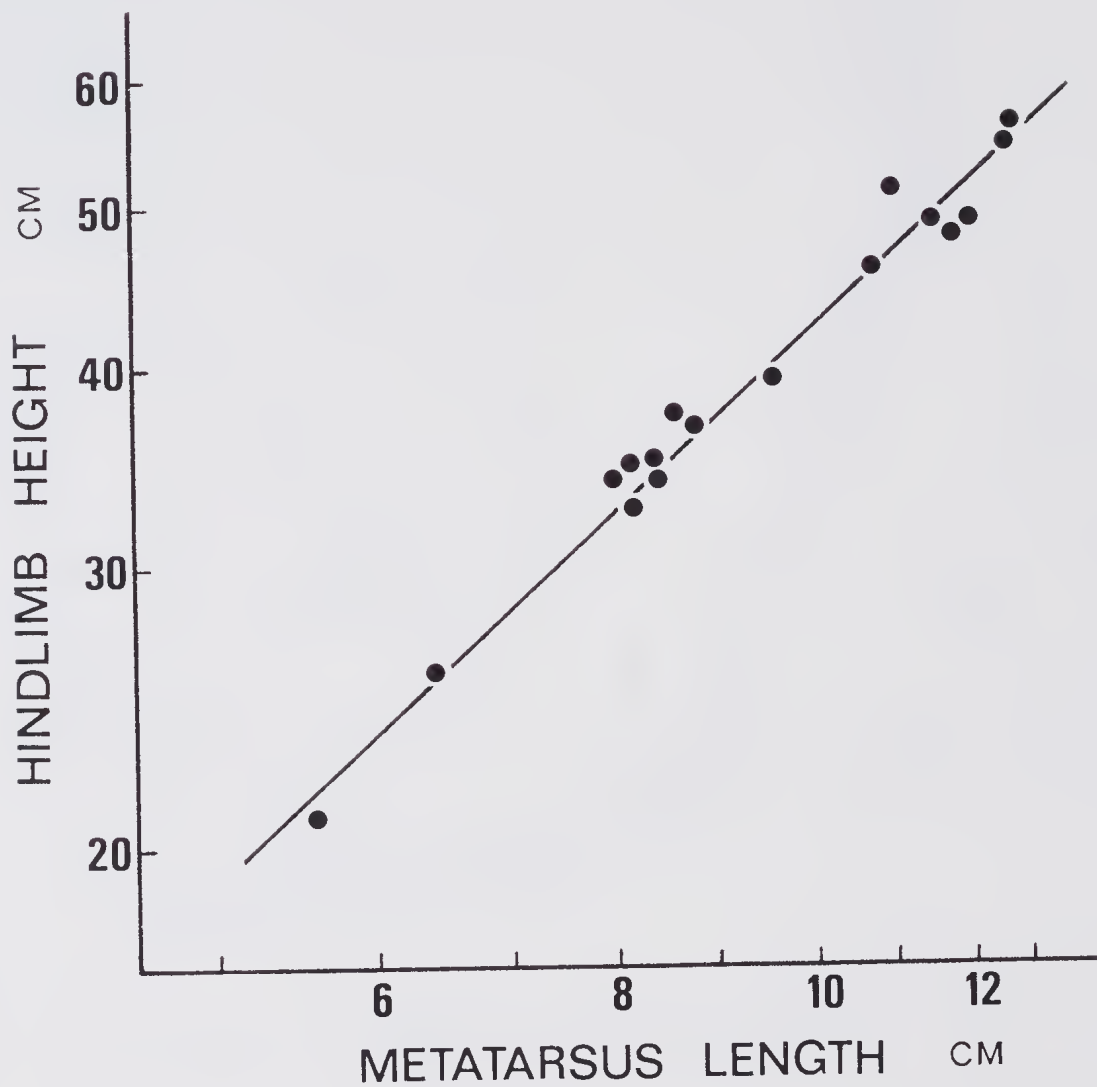


FIGURE 20. Relationship between hindlimb height and metatarsus length in coelurosaurs. Logarithmic scale on both axes;  $r = 0.989$ , and least squares regression line represents equation (12) in text. Based on data from Talbot 1911 (*Podokesaurus*), Osborn 1917 (*Ornitholestes*), Colbert 1964 (*Coelophysis*), Ostrom 1978 (*Compsognathus*).

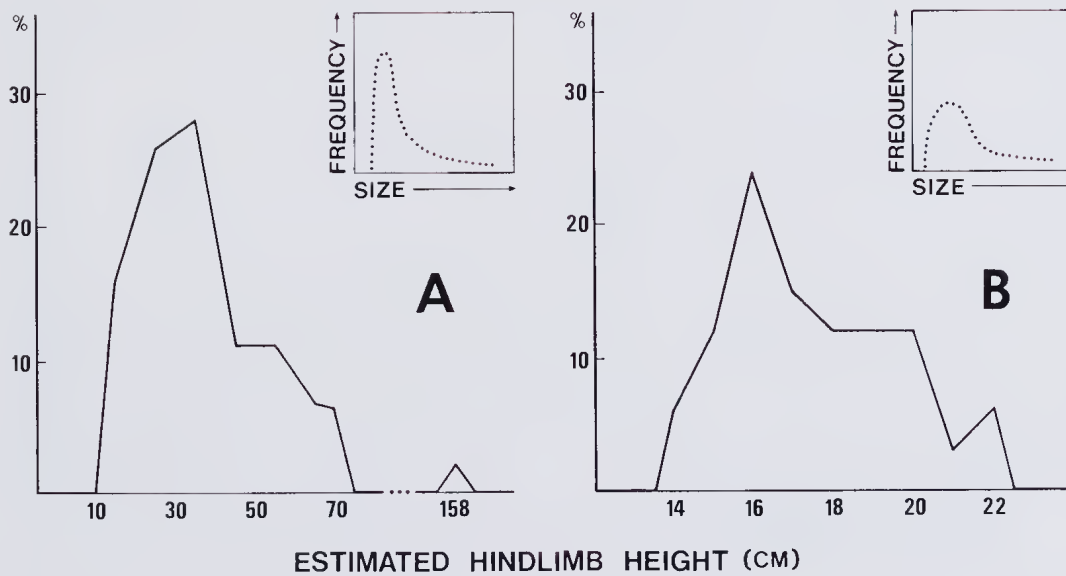


FIGURE 21. Comparison of size-frequency curves for (A) *Wintonopus* track-makers and (B) *Skartopus* track-makers at Lark Quarry. Vertical scale is percentage frequency. Insets show examples of similar curves for populations with different mortality rates and different initial population sizes (adapted from Boucot 1953).

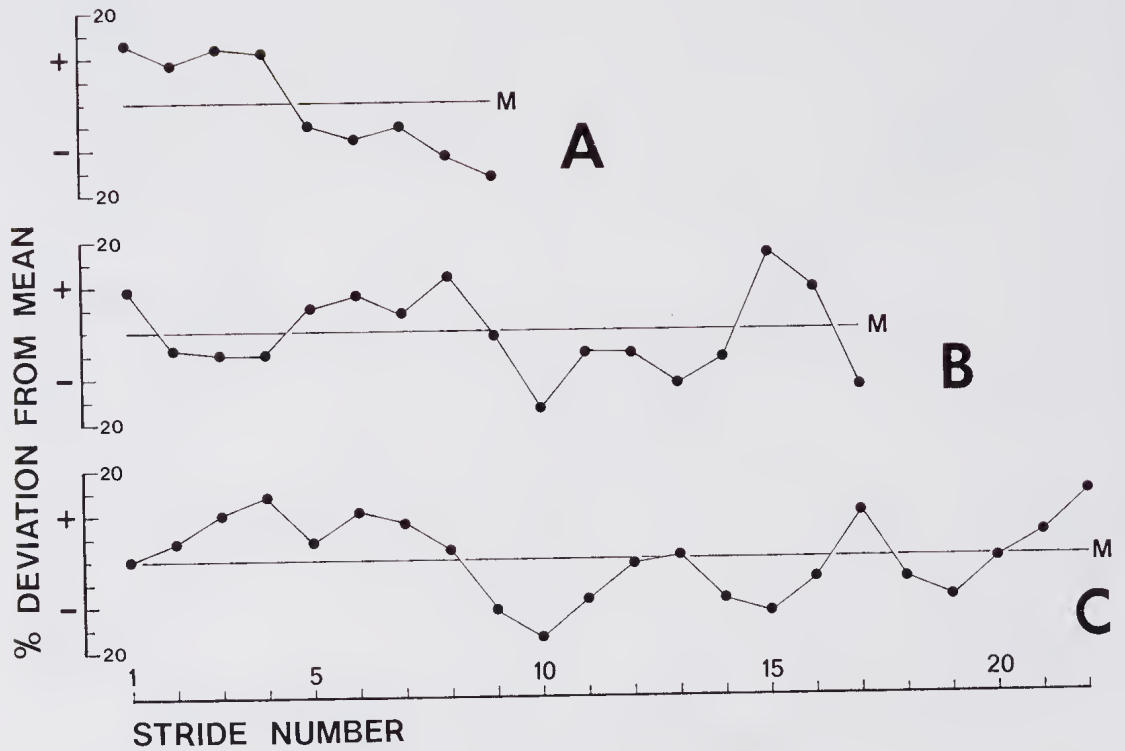


FIGURE 22. Variation in stride length for three track-makers at Lark Quarry. A, carnosaur trackway (cf. *Tyrannosauropus*) comprising 9 strides. B, ornithopod trackway (*Wintonopus*) comprising 17 strides. C, coelurosaur trackway (*Skartopus*) comprising 22 strides. In each case the scale at left indicates percentage deviation from mean stride length (horizontal line, M).

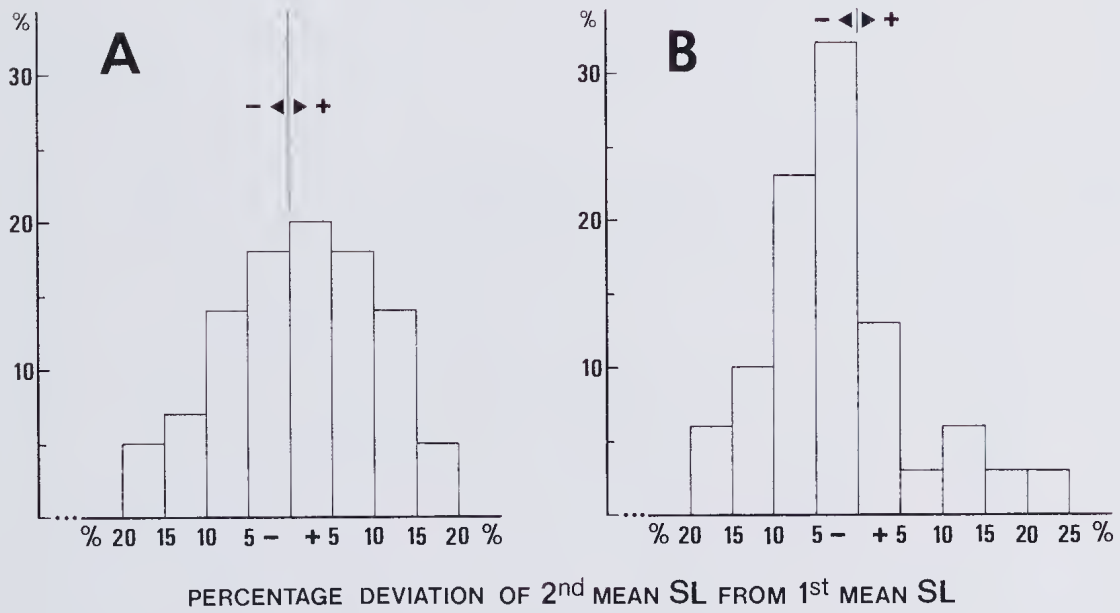


FIGURE 23. Consistency of stride length for (A) 56 *Wintonopus* track-makers and (B) 34 *Skartopus* track-makers at Lark Quarry. Horizontal scale indicates percentage deviation (+/-) of mean stride length for second half of trackway (2nd mean SL) from mean stride length for first half of trackway (1st mean SL). Trackways showing no deviation are shared equally between + (0-5%) and -(0.5%) classes. Vertical scale is percentage frequency.

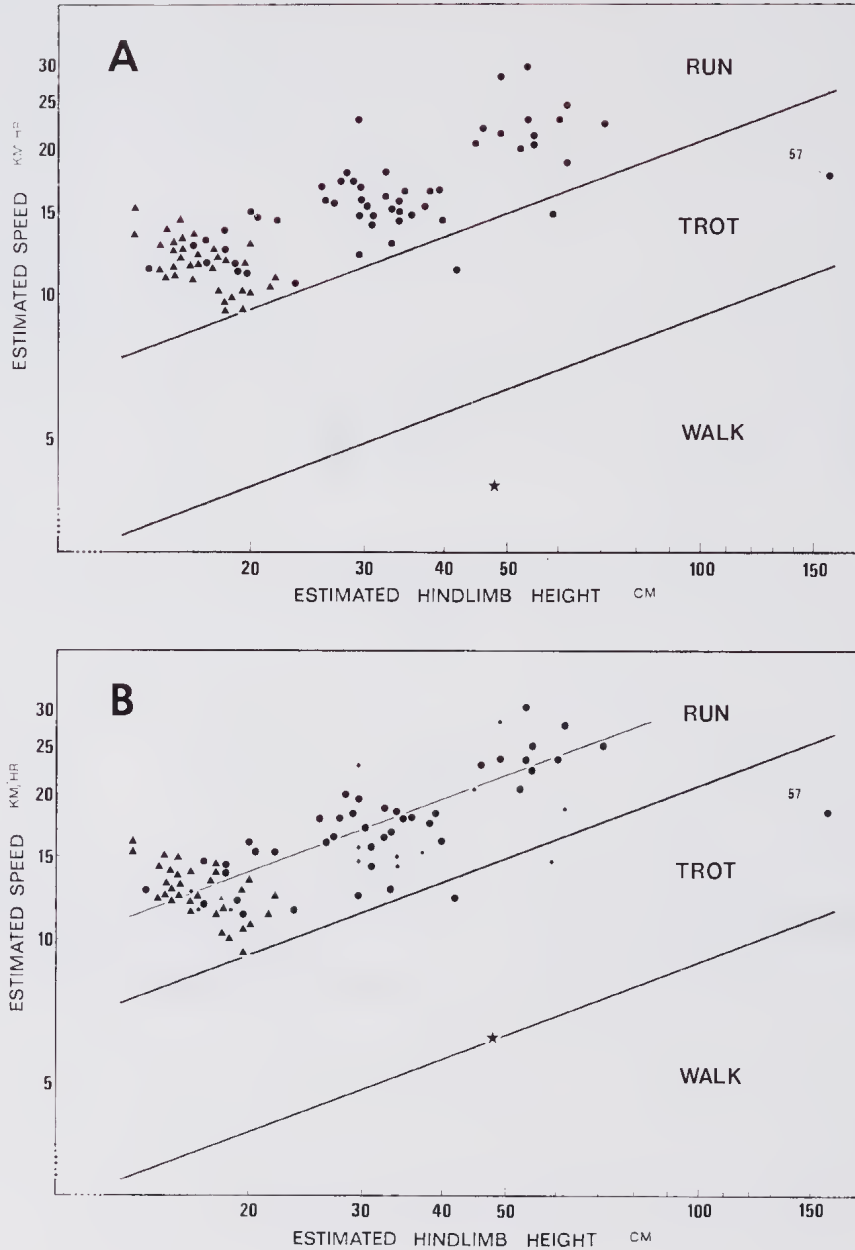


FIGURE 24. A, relationship between estimated mean speed and estimated hindlimb height for *Wintonopus* track-makers (solid circles) and *Skartopus* track-makers (triangles) at Lark Quarry. For the single *Wintonopus* track-maker at New Quarry (star) speed is estimated with equation (6) in text. Logarithmic scale on both axes. Lines defining gaits correspond to size/speed relationships when  $\lambda/h$  is 2.0 (walk-trot transition) and 2.9 (trot-run transition). B, relationship between estimated hindlimb height and estimated maximum speed (based on single longest stride per trackway). Small symbols indicate that maximum speed is also mean speed (i.e. all strides in trackway are equal in length, or only a single stride could be measured). Speed for the New Quarry track-maker (star) is maximum possible estimate, derived (perhaps inappropriately) with equation (11) in text. Line drawn through distribution indicates the theoretical regression of speed on hindlimb height when  $\lambda/h$  is 3.93.



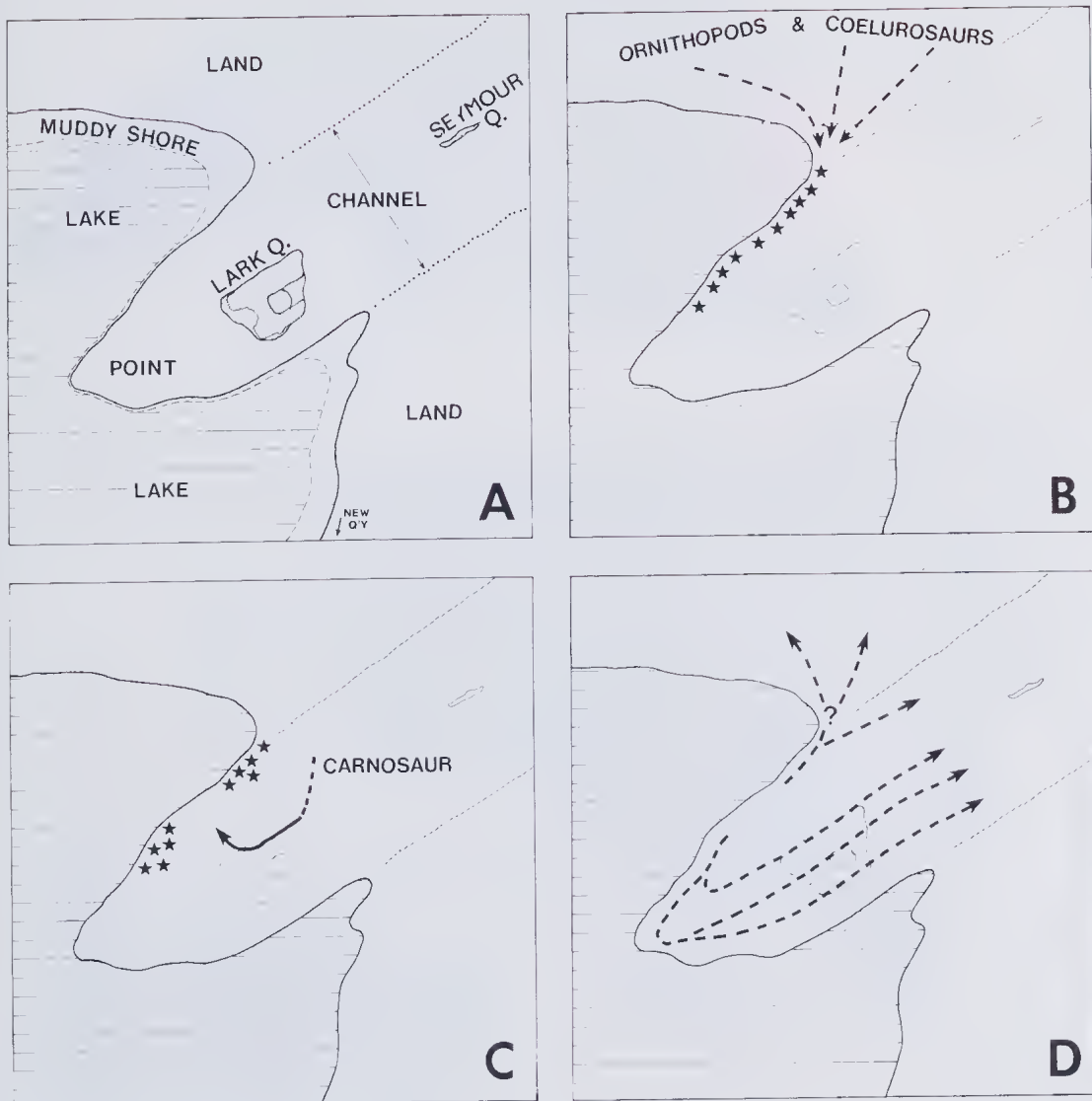


FIGURE 25. Reconstruction of geographic features and events leading to formation of the Lark Quarry trackways. A, outline reconstruction of geographic features at the time the trackways were formed. Sites of Lark Quarry and Seymour Quarry are superimposed. B, ornithopods and coelurosaurs congregate to drink or to forage in the area marked by stars (possibly also further to SW). C, carnosaur traverses future site of Lark Quarry from NE to SW; it turns sharp right to approach the ornithopods and coelurosaurs, which begin to disperse. D, ornithopods and coelurosaurs take fright and stampede, presumably on account of carnosaur's subsequent behaviour (unknown); some may escape via their entry route (?), but at least 150 are driven round the point to the SW and can only escape by running to the NE — across the future sites of Lark Quarry and Seymour Quarry.

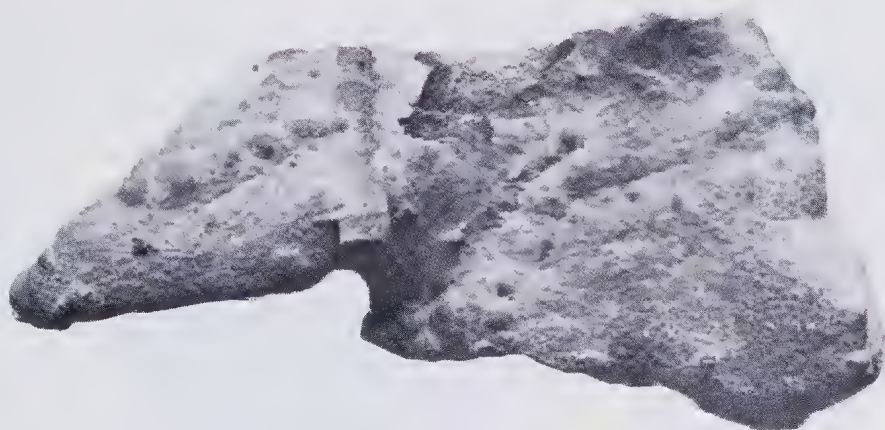
## PLATE I

*Wintonopus latomorum* ichnogen. et ichnosp. nov.,  
and *Skartopus australis* ichnogen. et ichnosp. nov.

Referred specimens, preserved as natural casts at Seymour Quarry.  
All  $\times 1.0$ .

FIGURES A-B: *Wintonopus latomorum*; right footprint in posterior (A) and inferior (B) views. The specimen is a natural cast detached from overlying sandstone. Distal parts of all three digits are broken away; so too is the inferior part of digit 3 (which in Fig. B reveals sandstone filling and ironstone cortex). Adherent tubular structures are plant rootlets and/or burrows of invertebrates. Fine tubercles and wrinkles may represent skin texture. In Fig. B note concave posterior margin (uppermost). (QM F12264).

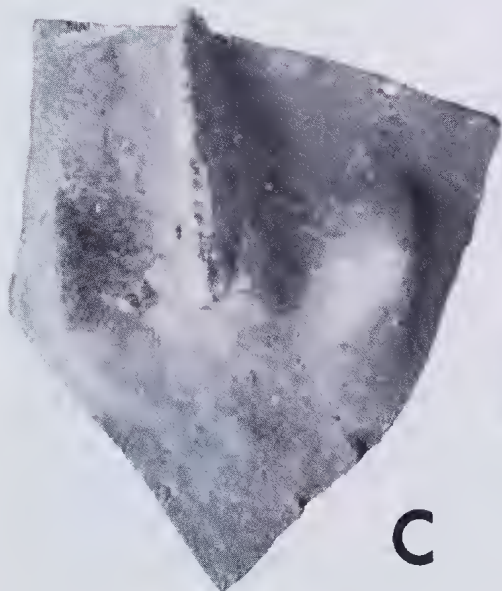
FIGURES C-D: *Skartopus australis*; right footprint in inferior (C) and anterior (D) views. A-natural cast still attached to a small portion of overlying sandstone. (QM F12265).



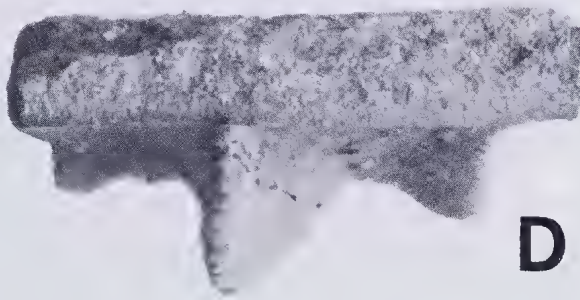
**A**



**B**



**C**



**D**

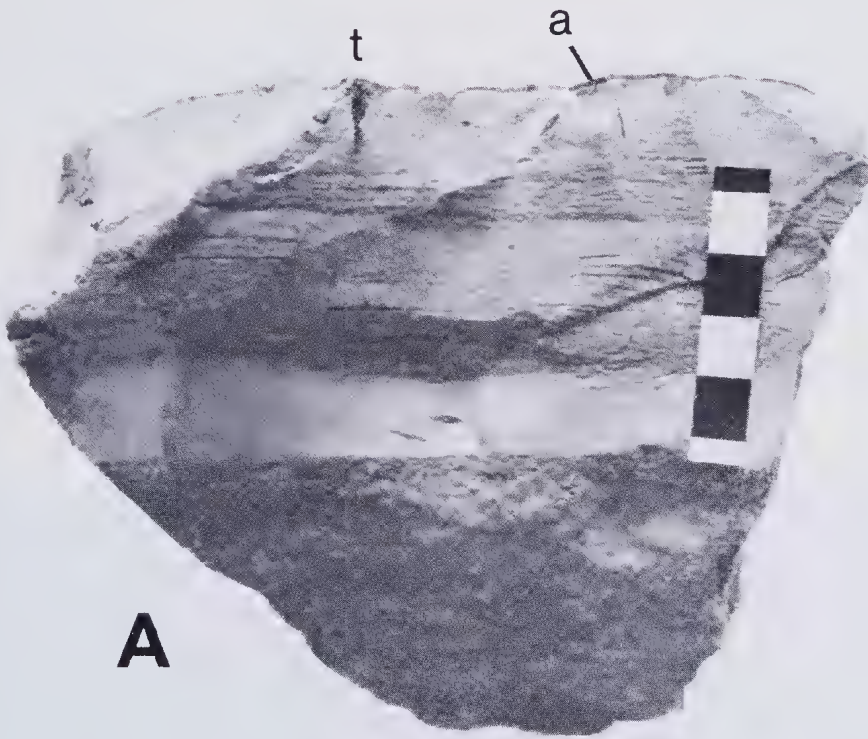
## PLATE 2

Sediments at Lark Quarry.

FIGURE A: Freshly-broken hand-specimen showing finely laminated claystone in which dinosaur footprints occur as natural moulds. Dark-coloured sediment below the level of the scale-bar (marked in cm) is part of the underlying sandstone.

FIGURE B: Natural section (joint face) through laminated claystone and the underlying sandstone bed. Scale bar marked in cm. Colour contrast between claystone and sandstone is slightly masked by iron-staining (especially at upper left). The three slot-like cavities (across centre) are pick-marks.

Abbreviations: *a*, thin ferruginous adhesion from overlying sandstone; *f*, dinosaur footprint, still filled with overlying sandstone; *t*, tubular structures (possibly escape burrows of arthropods).



**A**



**B**

## PLATE 3

Lark Quarry, viewed from the NW. Carnosaur footprints (cf. *Tyrannosauropus* ) are visible in front of kneeling figure at centre. The site is now roofed for its protection.



## PLATE 4

Portion of Lark Quarry bedding plane to show abundance, relative sizes and orientation of dinosaur footprints. All footprints are natural moulds, and lighting is from the lower left. Area shown is near the W corner of the quarry (see Fig. 3 in text) and is approximately 2.8 by 3.8 m. The sequence of three large footprints (numbered 6 to 8) is from the trackway of a carnosaur that travelled to the SW (towards bottom of page). The numerous small footprints (350+) are attributed to coelurosaurs and small ornithopods, all of which travelled in the opposite direction.





## PLATE 5

Carnosaur footprints, cf. *Tyrannosauropus*.

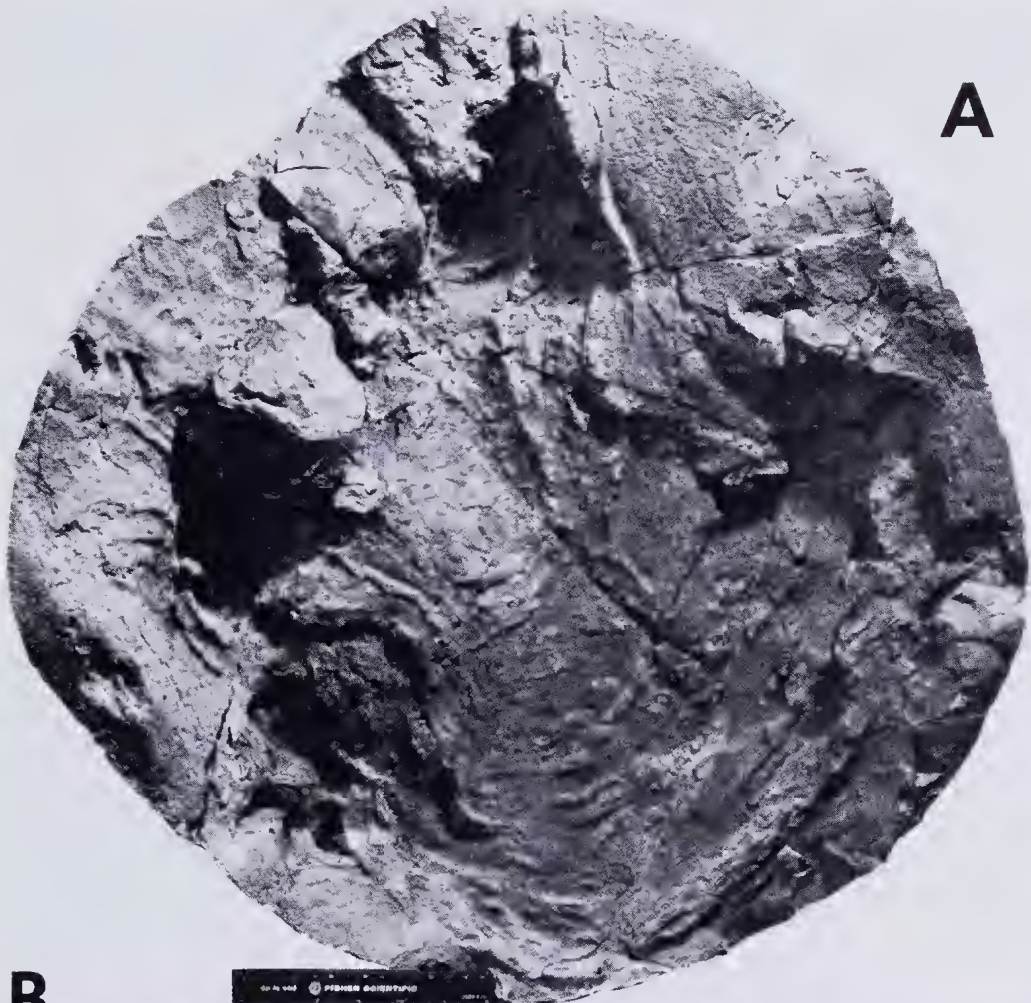
FIGURE A: Single left footprint preserved as natural mould,  $\times 0.22$ .

Photographed from fibreglass replica (QM F10322/I), lighting from N. This is footprint number 3 in the carnosaur trackway (11 prints) at Lark Quarry. Note ripples of sandy sediment in the floor of the print, and surrounding footprints of small dinosaurs.

FIGURE B: Portion of Lark Quarry bedding plane (NW margin)

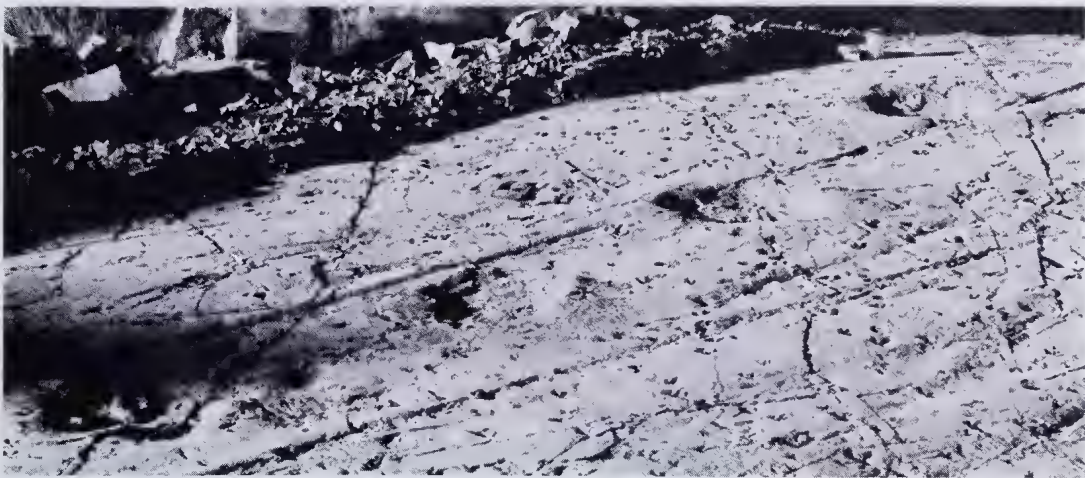
showing first four footprints in carnosaur trackway. Photographed obliquely under natural low-angle illumination.

Scale indicated by stride of the carnosaur (3.31 m or approximately 11 feet). The animal moved from NE (top right) to SW (lower left); note the upwelling of sediment around each footprint, and the numerous footprints of small dinosaurs that moved in the opposite direction.



**A**

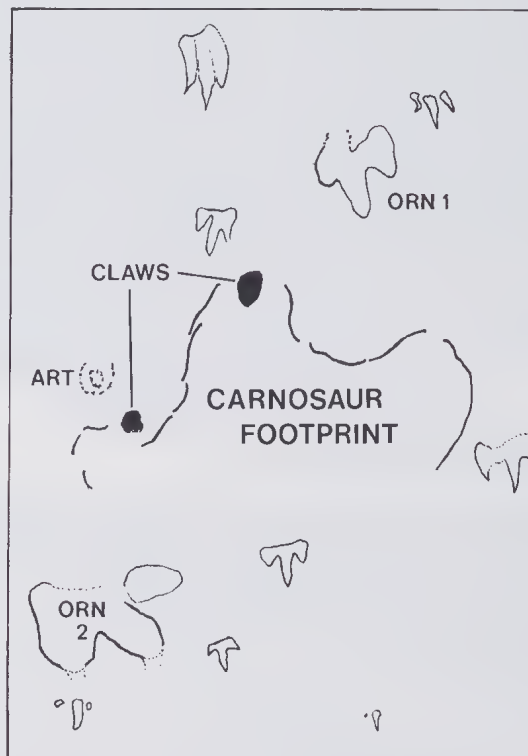
**B**



## PLATE 6

Carnosaur footprint, cf. *Tyrannosauropus*.

Single left footprint preserved as natural mould,  $\times 0.25$ . Photographed from fibreglass replica (QM F10322/II), with lighting from NW. This is footprint number 7 in the trackway at Lark Quarry. In diagrammatic key (below): ART, artefact (a pick-mark); ORN 1, ornithopod footprint still filled with sandstone; ORN 2, ornithopod footprint with scrape-marks extending forwards from digits 3 and 4. All other footprints appear to be those of coelurosaurs.

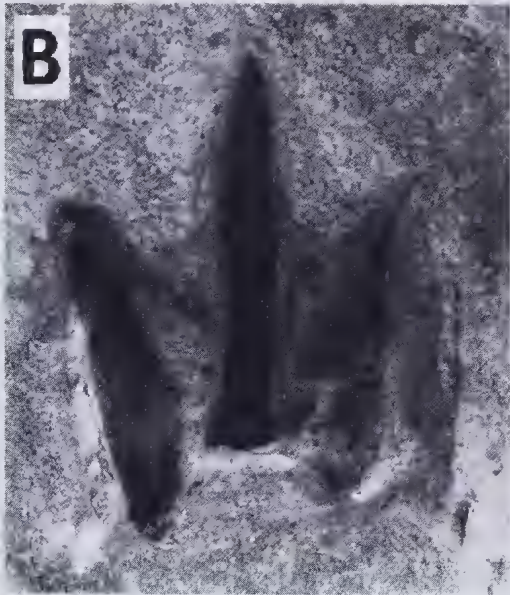




## PLATE 7

*Wintonopus latomorum* ichnogen. et ichnosp. nov.  
and *Skartopus australis* ichnogen. et ichnosp. nov.

- FIGURE A: *Wintonopus latomorum*, holotype (QM F10319). A right footprint preserved as natural mould,  $\times 1$ . Lighting from NE. Attributed to an ornithopod dinosaur.
- FIGURES B and C: *Skartopus australis*, holotype (QM F10330). A right footprint preserved as natural mould,  $\times 1$ . In Fig. B lighting is diffuse, from above; in Fig. C lighting is from E. Attributed to a small theropod dinosaur (coelurosaur).



## PLATE 8

*Wintonopus latomorum* ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry, and all photographed from fibreglass replicas.

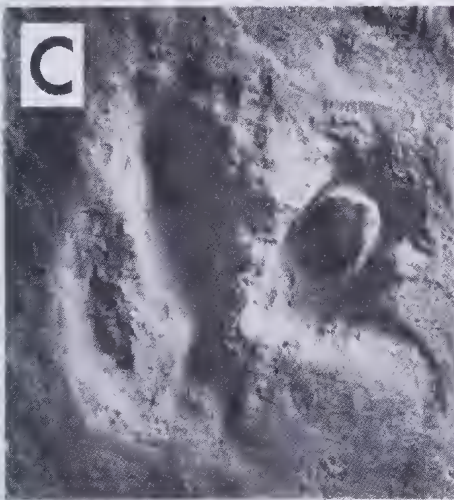
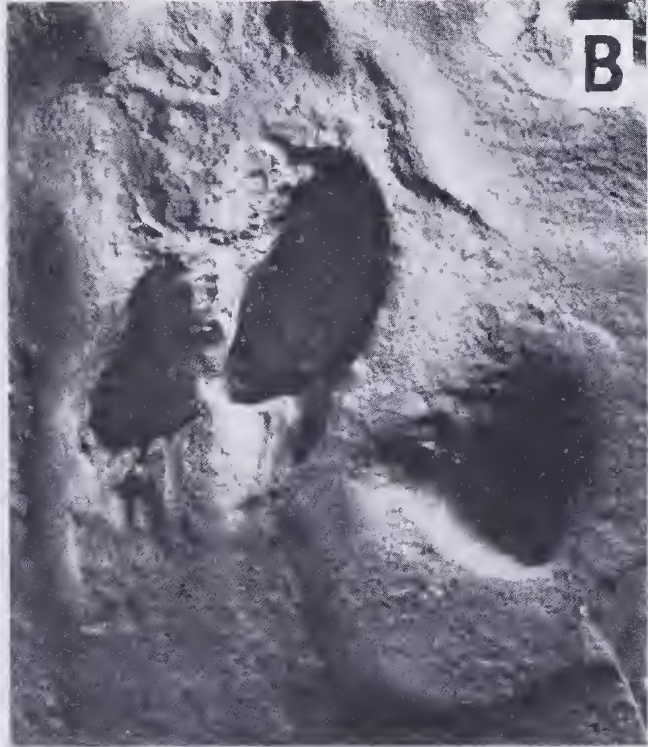
FIGURE A: Right footprint,  $\times 0.5$ . Lighting from E. Showing pronounced anterolateral scrape-mark from digit 3, and a shorter scrape-mark from digit 4. No trace of interdigital web between digits 2 and 3. (QM F10322/II).

FIGURE B: Left footprint,  $\times 0.5$ . Lighting from NE. Footprint foreshortened by toes entering and leaving sediment at steep angle. Interdigital web is clearly imprinted between digits 3 and 4, faintly imprinted between digits 2 and 3. Note backwardly-directed scrape-marks from digits 3 and 4. (QM F10322/II).

FIGURE C: Left footprint,  $\times 0.5$ . Lighting from NE. Digit 2 contains raised 'cusp' formed by sediment adhering to underside of track-maker's toe. Footprint has poorly defined outline because it was badly damaged during excavation. (QM F10322/B).

FIGURE D: Left footprint,  $\times 0.5$ . Lighting from SE. Anterolateral scrape-mark produces forked or Y-shaped outline to digit 3. Interdigital web is clearly imprinted between digits 3 and 4, absent between digits 2 and 3. (QM F10322/II).





## PLATE 9

*Wintonopus latomorum* ichnogen. et ichnosp. nov.

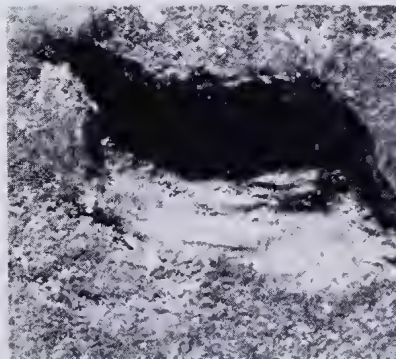
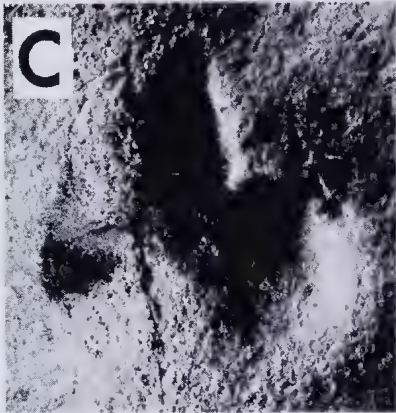
Referred specimens, all preserved as natural moulds at Lark Quarry, and all photographed from fibreglass replicas.

FIGURE A: Left footprint,  $\times 1$ . Lighting from E. Shallow imprint with digit 2 exceptionally broad, and digit 4 represented by a furrow. Probably formed with the track-maker's body weight carried mainly on the two inner toes. (QM F10322/B).

FIGURE B: ?Right footprint,  $\times 0.75$ . Lighting from E. Showing backwardly-directed scrape-marks from all three digits. (QM F10322/A).

FIGURE C: Right footprint,  $\times 1$ . Lighting from NW. From the smallest trackway referred to *W. latomorum*. Note the distinct 'spur' behind digit 4, and the faint indication of an anterolateral scrape-mark from digit 3. (QM F10322/B).

FIGURE D: Right footprint,  $\times 0.75$ . Lighting from N. From the second-largest trackway referred to *W. latomorum*. (QM F10322/1).



## PLATE 10

*Wintonopus latomorum* ichnogen. et ichnosp. nov.,  
and *Skartopus australis* ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry,  
and all photographed from fibreglass replicas.

FIGURE A: *Wintonopus latomorum*; left footprint,  $\times 0.75$ . Lighting  
from NW. With all three digits represented by furrows, and with  
distinct trace of interdigital web between digits 3 and 4. There  
may also be a very faint imprint of the metapodium. (QM  
F10322/A).

FIGURE B: *Skartopus australis*; ?right footprint,  $\times 0.66$ . Lighting  
from W. Characteristically divergent digits, but one of them (?)  
unusually exaggerated in width. Presumably formed with track-  
maker's body weight carried mainly on the two inner toes. (QM  
F10322/B).

FIGURE C: *Wintonopus latomorum*; two right footprints,  $\times 1$ .  
Lighting from NE. The slightly larger print (below) is fore-  
shortened by toes entering the sediment at a very steep angle. As  
toes were withdrawn the central one scraped the sediment  
forwards — so that it folded over to conceal digit 4 of a smaller  
and earlier-formed print. (QM F10322/II).

FIGURE D: *Wintonopus latomorum*; left footprint,  $\times 0.33$ . Lighting  
from E. Showing exceptionally broad imprint of digit 3, and  
forwardly directed scrape-marks from all three digits. The scrape-  
mark from digit 3 is extremely long and is deflected slightly as it  
runs through the earlier-formed footprint of a coelurosaur  
(*Skartopus australis*). (QM F10322/II).



## PLATE 11

*Wintonopus latomorum* ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry.

FIGURE A: Left footprint,  $\times 1$ . Lighting from NE. Note deeply imprinted interdigital webs, and distinct curvature of digit 3. Photographed from rock slab (QM F10320).

FIGURE B: ?Left footprint,  $\times 1$ . Lighting from N. Extremely fore-shortened on account of toes entering and leaving sediment at a very steep angle. Trace of posterior 'spur' at left (behind digit ?4) seems to confirm identification as left footprint. Fibreglass replica (QM F10322/II).

FIGURE C: ?Left footprint,  $\times 1$ . Lighting from SE. Three small pits seem to indicate brief touch-down of toe-tips after they had been withdrawn from the footprint. Location of these pits indicates that the foot was shifted forwards and slightly to the right, and that it was rotated around the axis of digit 3. Fibreglass replica (QM F10322/II).

FIGURE D: Three left footprints (representing three track-makers),  $\times 1$ . Lighting from W. All three examples show characteristic 'spur' behind digit 4. Uppermost example is very fore-shortened, with shallow imprint of digit 2; imprints of digits 3 and 4 are amalgamated. Lowermost example (bisected by joint) shows Y-shaped tip to digit 3. Fibreglass replica (QM F10322).



## PLATE 12

*Skartopus australis* ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry, and all photographed from fibreglass replicas.

FIGURES A and B: Single right footprint,  $\times 1$ . In A lighting is from the NE, in B lighting is from the E. Showing full imprint of the metapodium. Note sharply pointed tips of digits (QM F10322/I).

FIGURE C: ?Right footprint,  $\times 1$ . Lighting from NE. Somewhat fore-shortened, and with deeply incised scratches formed by backwards sweep of the track-maker's foot. (QM F10322/B).

FIGURE D: Right footprint,  $\times 1$ . Lighting from E. Characteristic symmetrical arrangement of narrow and sharply pointed digits. Showing faint imprint of metapodium, traces of interdigital webs, and scratch-marks behind digits. (QM F10322/II).



**A**



**B**



**C**



**D**



## PLATE 13

*Wintonopus latomorum* ichnogen. et ichnosp. nov.,  
and *Skartopus australis* ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry,  
and all photographed from fibreglass replicas.

FIGURE A: *Skartopus australis*; ?left footprint,  $\times 0.66$ . Lighting  
from SW. Showing deeply incised scratch in the floor of each  
digit imprint. (QM F10322/B).

FIGURE B: *Skartopus australis*; ?left footprint,  $\times 0.5$ . Lighting from  
N. Much fore-shortened example with imprint of metapodium.  
Fore-shortening accounts for apparently unusual thickness and  
bluntness of digit imprints (QM F10322/B).

FIGURE C: An amalgam of at least four footprints,  $\times 0.66$ . Lighting  
from NW. Two outer digits of a left ornithopod footprint  
(*Wintonopus latomorum*) are visible at left, with a forwardly  
directed scrape-mark from digit 3. Note that all footprints are  
similar in depth, in state of preservation, and in orientation. (QM  
F10322).



## PLATE 14

*Wintonopus latomorum* ichnogen. et ichnosp. nov.,  
and *Skartopus australis* ichnogen. et ichnosp. nov.

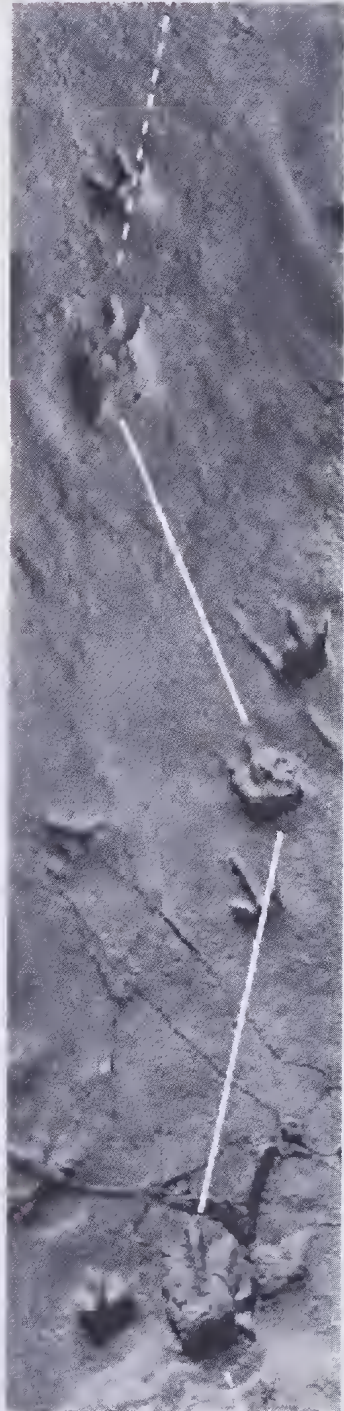
Referred specimens, all preserved as natural moulds at Lark Quarry, and all photographed from fibreglass replicas.

FIGURE A: Group of three footprints (representing three animals),  $\times 0.66$ . Lighting from SW. At top is a right footprint referred to *Wintonopus latomorum*; this shows exaggerated imprint of digit 2, and was presumably formed with track-maker's body weight carried mainly on the inner side of the foot. At centre is a footprint comprising three long scratches — probably from the left foot of a *Wintonopus* track-maker. Spacing of the three scratches would correspond to spacing of three digits in a left footprint of *Wintonopus* type. At bottom left is a ?right footprint referred to *Skartopus australis*. (QM F10322/B).

FIGURE B: Portion of Lark Quarry bedding plane,  $\times 0.175$ . Lighting from S. Three footprints connected by lines are referred to *Skartopus australis* and form part of a single trackway. All three footprints (and two others not shown) have traces of the metapodium. Despite its 'flat-footed' gait this animal seems to have kept pace with other track-makers at Lark Quarry (see estimates of speed in Table 5). (QM F10322/B).



**A**



**B**

## PLATE 15

*Wintonopus latomorum* ichnogen. et ichnosp. nov.,  
and *Skartopus australis* ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry.

FIGURE A: *Skartopus australis*; ?right footprint,  $\times 1$ . Lighting from W. Note sharply pointed digits. Fibreglass replica (QM F10322/II).

FIGURE B: *Wintonopus latomorum*; left footprint,  $\times 0.5$ . Lighting from NE. Showing characteristic proportions and spacing of the digits; note very slight curvature of digit 3. The outer side of the track-maker's foot (digit 4) was much more deeply impressed than the inner side (digit 2). Photographed from rock slab (QM F10320).

FIGURE C: A mixture of at least three footprints (representing at least three animals),  $\times 1$ . Lighting from N. Apparently one example of *Wintonopus latomorum* is superimposed obliquely on another. The line of three puncture-like marks (top left) is a smaller and extremely fore-shortened footprint — formed by the track-maker's toes entering the sediment vertically. Photographed from rock slab (QM F10320).



**A**



**B**



**C**

## PLATE 16

*Wintonopus latomorum* ichnogen. et ichnosp. nov.,  
and *Skartopus australis* ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry, and all photographed from fibreglass replicas.

FIGURE A: *Skartopus australis*; left footprint,  $\times 0.66$ . Lighting from SE. All three digits represented by scratches; note characteristic divergence of the digits (QM F10322/B).

FIGURE B: A group of between 6 and 8 footprints,  $\times 0.5$ . Lighting from W. At lower left is an example of *Wintonopus latomorum* (somewhat damaged during excavation); at top right is a second example showing characteristic Y-shaped tip to digit 3. This second example has largely obliterated an earlier-formed footprint (to right), and is in turn partly distorted by a later-formed print (to left). At centre is a little-distorted example of *Skartopus australis*. Towards bottom right is a complete amalgam of at least two unidentifiable footprints (QM F10322/B).

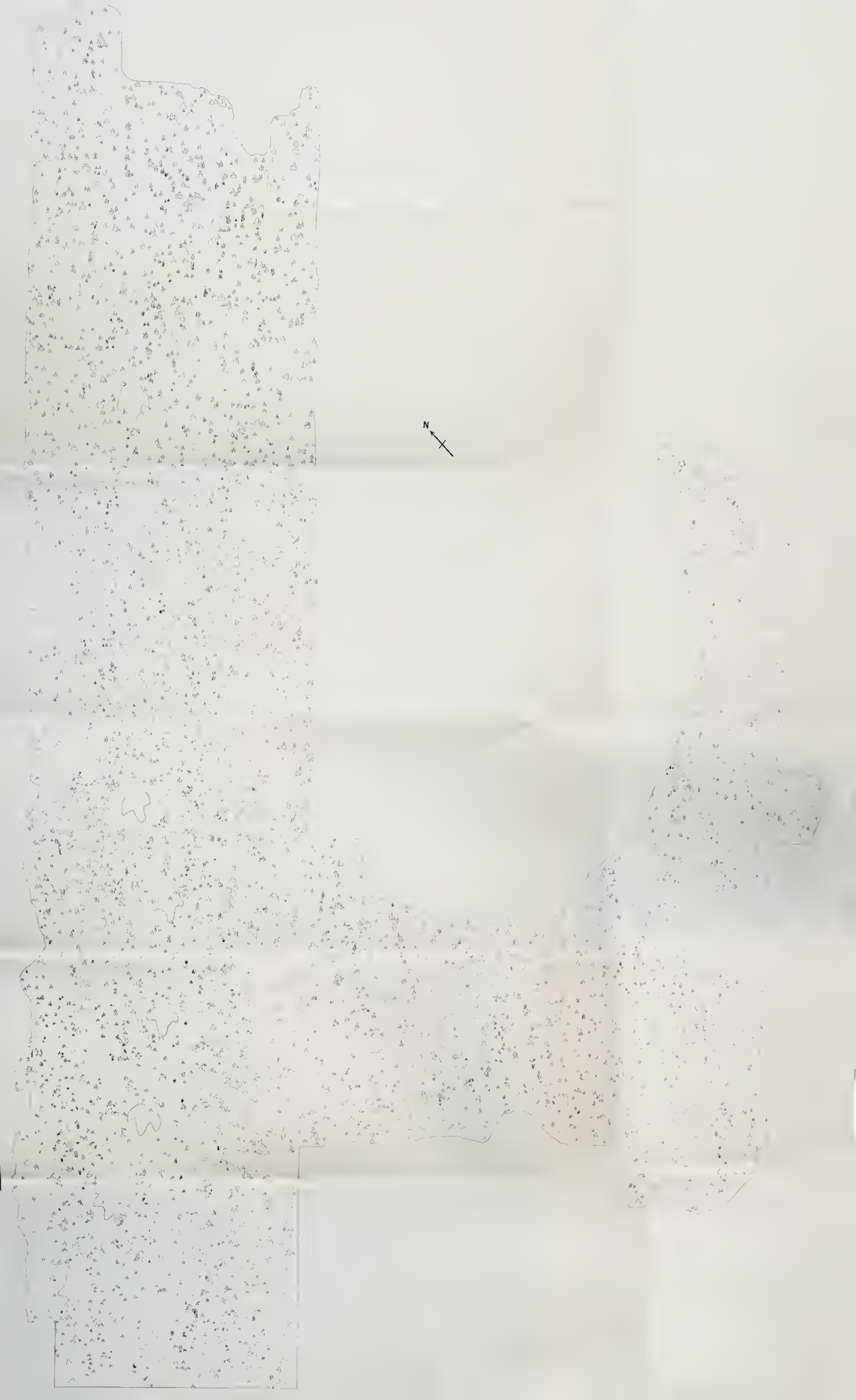
FIGURE C: Three footprints (representing three animals),  $\times 1$ . Lighting from W. A footprint at lower right (?*Skartopus*) is extended into anterior scrape-marks which partly disrupt two earlier-formed footprints. At lower left is a very characteristic example of *Wintonopus latomorum* (left footprint); at upper right is a smaller example (?right footprint). (QM F10322/A).





## PLATE 17

Plan of footprints at Lark Quarry. Arrow indicates north.









THE THORNTON PEAK MELOMYS, *MELOMYS HADROURUS* (RODENTIA :  
MURIDAE): A NEW RAINFOREST SPECIES FROM NORTHEASTERN  
QUEENSLAND, AUSTRALIA.

J.W. WINTER  
Queensland National Parks and Wildlife Service  
Townsville

ABSTRACT

*Melomys hadrourus* is described from six specimens collected from Thornton Peak and the McDowall Range, northeastern Queensland. It is a large species within the size range of described *Melomys* such as *M. levipes* and *M. leucogaster*. The well developed white-tipped tail and the robust skull, as demonstrated by the thickness of I<sup>1</sup>, suggest affinities with *Uromys*, but in general body size it is distinctly smaller than *Uromys porculus*, the smallest *Uromys*. *M. hadrourus* is considered an upland relict species with no vicariants. All four collection localities are in rainforest in the upland (> 300 m) zone of the Thornton Peak massif, isolated from other upland areas of the Daintree and Bloomfield valleys.

INTRODUCTION

Rainforest in Australia occurs as a series of discontinuous blocks throughout coastal eastern Australia (Webb and Tracey 1981). Within tropical Australia the most extensive area of rainforest is in the Townsville to Cooktown region. This region is of particular interest to the zoogeographer because of the relatively high number of endemic species and of a faunal affinity with New Guinea (*vide* Kikkawa, Monteith and Ingram 1981 for a recent review). The region is geomorphologically diverse and, although extensive collections of mammals have been made from the region (*vide* Lumholtz 1889, Cairn and Grant 1890, Tate 1952, Taylor and Horner 1973), some areas remained unworked by mammalogists. The upland area of the Thornton Peak massif, isolated by the Daintree and Bloomfield valleys (Fig. 1) was one such area. Thus the opportunity of helicopter transport to the summit of Thornton Peak, offered by the Commonwealth Forestry and Timber Bureau (now CSIRO, Division of Forest Research), Atherton, was accepted. The circumstances of the visit and the subsequent capture of a new species of rodent have been given elsewhere (Winter 1978). This newly discovered species is described here.

SYSTEMATICS

*Melomys hadrourus* sp. nov.

HOLOTYPE: Queensland Museum JM504 adult female, skin and torso in spirit, skull extracted,

collected 16 November 1973, by J.W. Winter.

TYPE LOCALITY: Thornton Peak summit area at altitude 1220 m, latitude 16°09'30''S, longitude 145°21'45''E (Mossman sheet, 1:100,000 series R631, grid reference CC250126), northeastern Queensland, Australia (Fig. 1).

PARATYPES: From Thornton Peak type locality Queensland Museum JM3837 adult female (Watts and Aslin 1981, Pl. 2), skin and torso in spirit, skull extracted, collected 5 June 1974, by J.W. Winter; from southern face of Thornton Peak at altitude 640 m, latitude 16°10'30''S, longitude 145°21'45''E (Mossman CC250108) Australian Museum M12520 adult female, skin in spirit, skull extracted, collected between 3 and 13 November 1975, by H. Posamentier; from southern face of Thornton Peak at altitude 1020 m, latitude 16°10'15''S, longitude 145°22'00''E (Mossman CC252115), Australian Museum M12521 subadult male, skin and torso in spirit, skull extracted, collected 13 November 1975, by H. Posamentier; from McDowall Range crest, northeastern Queensland, at altitude 520 m, latitude 16°06'20''S, longitude 145°20'00''E (Mossman CC218190), Queensland Museum JM2173 subadult male, puppet skin and extracted skull, with torso in spirit, colour photograph (Anon. 1977), and subadult male (escaped), both collected 20 October 1976, by J.W. Winter and R.G. Atherton.

DIAGNOSIS:

A large *Melomys* with head-body length to 180 mm, condylobasal length to 42.7 mm

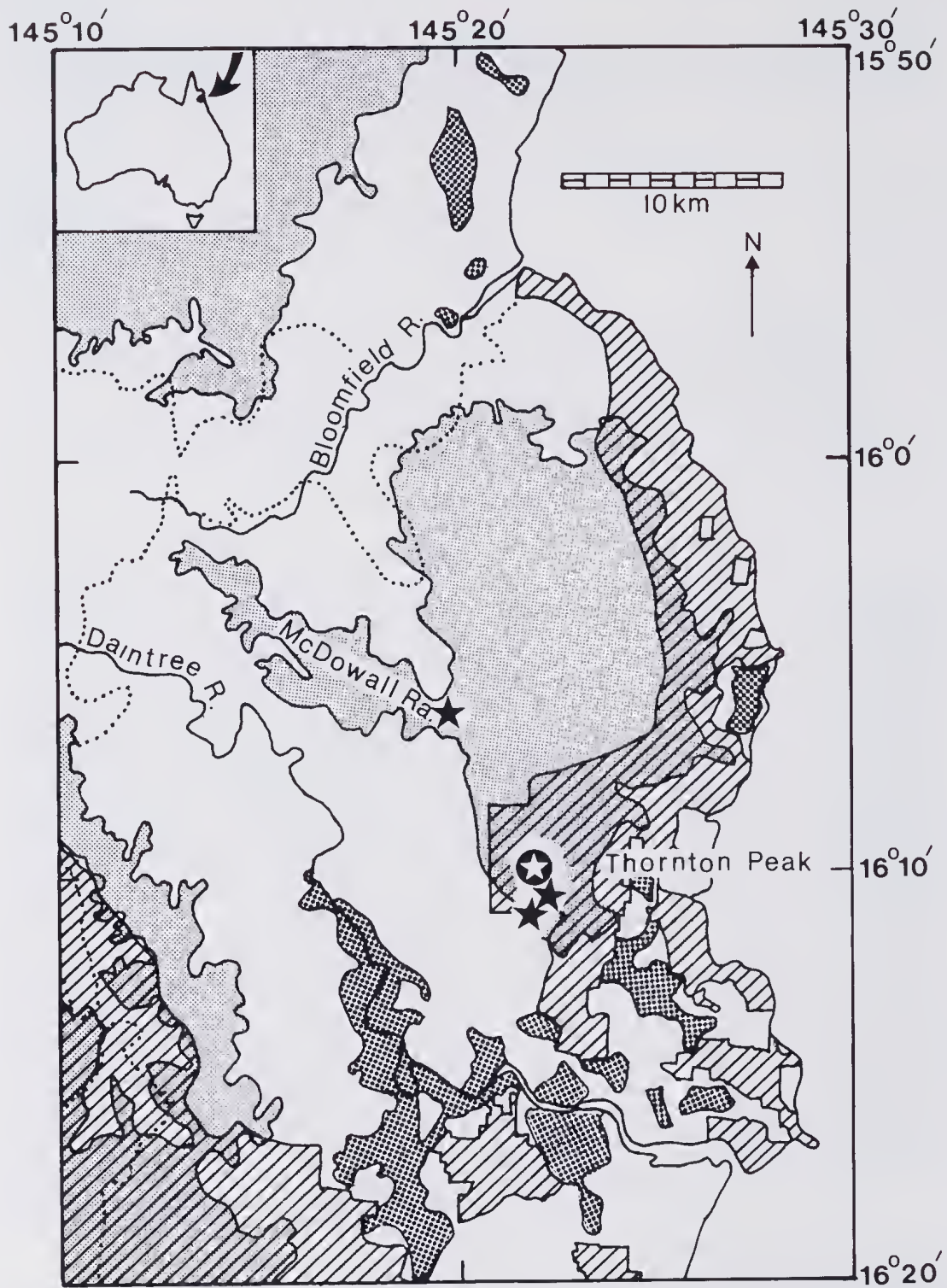


FIGURE 1. Map of the Thornton Peak and adjacent uplands above 300 m (light stippling) in altitude, showing type locality (circled star) and other capture localities (solid stars) of *Melomys hadrourus*, cleared land (heavy stippling), and national park (cross hatching).



(occipitonasal length to 45.3 mm); tail longer than the head-body length, relatively thick ( $\geq 4.7$  mm diameter at the base), apical quarter white, scales non-abutting and subtending one hair per scale. Distinguished from *Uromys* by smaller size (condylobasal length  $< 43$  mm, occipitonasal length  $< 46$  mm) and from juvenile *U. caudimaculatus* by shorter pes length ( $< 39$  mm). Distinguished from other large *Melomys* by the thicker tail; from *M. leucogaster* group by the longer rostrum (nasal length: condylobasal length  $< 1: 2.45$ ); from *M. levipes* group by greater thickness of I' ( $\geq 2.3$  mm) and tail longer than the head-body length. Distinguished from other Australian *Melomys* by greater size (head-body length  $> 165$  mm, pes s.u.  $> 35$  mm, occipitonasal length  $> 44$  mm) and by the thicker tail with only one hair per scale.

#### DESCRIPTION:

Pelage generally soft and guard hairs not prominent, colour light fawn becoming lighter ventrally, no prominent markings other than a white patch on the throat and sternum. A detailed description of the holotype follows (colour names after Ridgway 1912): dorsally median fur is 15–18 mm long in lumbar region to c. 14 mm between ears and 4–5 mm on nasals, basal two thirds of fur Pale Mouse Gray with apical third Cinnamon-buff on back, Ochraceous Orange between ears and Tawny to Light Buff on nasals giving it a slightly grizzled appearance; terete guard hairs 20–24 mm long on back and c. 15 mm on nasals with basal one third Pale Mouse Gray and apical two thirds Tawny tending to a colourless tip of up to 2 mm; laterally mid-body fur grades to Ochraceous Buff on apical third and Pale Mouse Gray on basal two thirds, on side of face below eye it is Warm Buff for apical third and Pale Mouse Gray for basal two thirds, and in region of mysticeal vibrissae fur Light Buff apically with basal two thirds White; guard hairs greatly reduced in number, but otherwise as dorsally, ventrally fur 8–9 mm long on abdomen with basal half Pallid Mouse Gray median quarter Fawn Colour and apical quarter Light Buff, from mid-thoracic region to chin fur is White throughout its length, width of white patch 10–15 mm with constriction at level of fore-legs.

Ears: Prominent and rounded, skin Fuscous, sparsely covered with Tawny to colourless hairs c. 1 mm long.

Vibrissae: Approximately 30 mysticeal vibrissae on each side and up to 73 mm long, from Mars Brown basally through Tawny medially to colourless apically in varying proportions; three

supraorbital vibrissae on right side (none on left) up to 15 mm long, colour as for mysticeal vibrissae; one postorbital on each side 21–23 mm long, colour as for mysticeal vibrissae; submentals numerous and up to 6 mm long, colourless; ulnar carpals 4 each side and up to 12 mm long, colourless.

Manus: Skin Cream-Buffer in preserved specimen and sparsely covered dorsally with colourless hairs c. 2 mm long, except for mid-dorsal line in which median section of hair is partially Tawny; for foot pads see Pl. 1.

Pes: Skin Cream-Buffer in preserved specimen and sparsely covered dorsally with colourless hairs c. 2 mm long, except for line of hairs outward of mid-dorsal line in which median section of hair partially Tawny; for foot pads see Pl. 1.

Tail: Longer than head-body (Table 1), diameter at base c. 5 mm, scales round and reduced (not abutting) with slight sculpturing and subtending one hair each (Pl. 1), length of scale hair 1.5 scales on basal portion and less than 0.5 on apical portion; colour of scales Tawny dorsally for basal three quarters, slightly paler ventrally especially at base, apical quarter pure white dorsally and ventrally (Pl. 1), hairs Tawny to colourless. The general impression is of a large thick tail more reminiscent of that of a juvenile *Uromys caudimaculatus caudimaculatus* than of a typical *Melomys*. (vide Pl. 3).

Skull: Characteristic of genus but generally larger and more robust, particularly incisors (Table 2, Pl. 2); crown pattern of cheek teeth characteristic of genus (Pl. 2), alveolar pattern M<sup>1</sup>, M<sup>2</sup>, M<sup>3</sup>: 4,4,3 (= pattern D of Knox 1976), anterior face of incisors orange.

Mammary formula 0-2=4, vagina perforate, teats small and not lactating.

#### VARIATION OF PARATYPES:

Pelage of paratypes similar to that of holotype including ventrally a patch of fur, white to base, from chin to the mid-thoracic region; tail of JM2173 and M12521 with white tip of c. 28 mm (25 + c. 3 mm which withered away — vide photograph of this specimen in Anon. 1977) and 52 mm respectively; JM3837's tail (complete on capture) and that of individual in Pl. 3 also had extensive white tips; apical third of M12520's tail missing on capture; measurements of external features and skulls given in Tables 1 and 2; mammary formula of JM3837 0-2=4, not known for M12520.

A subadult male captured at the McDowall Range locality, and which subsequently escaped, is illustrated in Pl. 3.

## ETYMOLOGY:

The specific name is derived from the Greek, *hadros* (well-developed, bulky, stout, large, strong and great) and *oura* (tail), and refers to the well-developed tail of *M. hadrourus*, which is its most characteristic external feature.

## TAXONOMIC POSITION

## COMPARATIVE MATERIAL EXAMINED:

*Melomys levipes shawmayeri* Rümmler 1935, type, British Museum (Natural History), London (BM) No. 35.12.20.2 (field No. S.M. 368 in Tate 1951), specimen and photographs; *Melomys levipes lanosus* Thomas 1922, type, BM 22.2.2.26 (not 22.2.22.26 as given in Tate 1951), specimen and photographs; *Melomys levipes levipes* (Thomas 1897), cotype, BM 97.8.7.72, specimen and photographs; *Melomys levipes rattoides* Thomas 1922, type BM 22.2.2.25, specimen and photographs; *Melomys levipes naso* (Thomas 1911), type, BM 11.11.11.54, specimen and photographs; *Uromys sapientis* Thomas 1902, type BM 2.5.1.4, specimen and photographs; *Uromys porculus* Thomas 1904, type BM 89.4.3.8. *Uromys caudimaculatus aruensis* Gray 1873, Museo Civico di Storia Naturale, Genoa (MSNG) No. 3605a and type, No. 3248 (skull missing), specimens only; *Melomys levipes levipes* (Thomas 1897), cotype, MSNG 3600a, specimen only; *Melomys leucogaster leucogaster* (Jentink 1909), American Museum of Natural History (AMNH) No. 105723, specimen and photographs; *Melomys leucogaster latipes* Tate and Archbold 1935, type AMNH 104273, photograph only. *Melomys levipes lorentzii* (Jentink 1909), type, Rijksmuseum van Natuurlijke Historie, Leiden (RNHL) No. 25494 (Field No. 132), photograph only; *Melomys leucogaster leucogaster* (Jentink 1909), type, RNHL 25493 (Field No. 119), photographs only.

Specimens of *Uromys caudimaculatus* (Kreff 1867), *Melomys cervinipes* (Gould 1852), *Melomys capensis* Tate 1952, and *Melomys burtoni* (Ramsay 1887) were on hand from field collections in northeastern Queensland by the author, and *Melomys rubicola* Thomas 1924 from field collections on Bramble Cay by C.J. Limpus (pers. comm.).

Measurements used for comparative purposes in Figs. 2 and 4 were those given in Tate (1951) unless otherwise stated.

## GENERIC POSITION:

*Melomys hadrourus* belongs to the mosaic-tailed rats lacking a distinct prehensile tail, within

the *Uromys* group of genera of Tate (1951). This group consists of relatively small rats within the genus *Melomys* Thomas 1922 and much larger rats of the genera *Uromys* Peters 1867 and *Solomys* Thomas 1922. Tate (1951) included *Solomys* as one of several subgenera of *Uromys*, but Laurie and Hill (1954) accorded it full generic rank (type species *Uromys sapientis* Thomas 1922). *M. hadrourus* lies at the top of the size range of the described *Melomys* as indicated by its skull size (Fig. 2). The skull is generally more heavily built than in other *Melomys*, although *M. levipes naso* is similar. The depth of I', is generally greater than in other *Melomys* the only overlap being with *M. l. leucogaster* (AMNH No. 105723) (Fig. 3). The tail is distinctly thicker than in all other *Melomys* examined and is similar to that of juvenile *Uromys caudimaculatus caudimaculatus* and the juvenile male *Uromys caudimaculatus aruensis* Gray 1873 (type, MSNG No. 3248). Nevertheless *M. hadrourus* is distinctly smaller than *Uromys porculus* Thomas 1904 (the smallest *Uromys*) as is shown by skull size (Fig. 2) and I' depth (Fig. 3). (*Uromys porculus* Thomas 1904, is still retained in the genus *Melomys* by Laurie and Hill (1954), but I agree with Tate's (1951) decision to include it within *Uromys*. My agreement with Tate is based on skull size of *porculus* which fits into the *Uromys* group rather than the *Melomys* group (Fig. 2)). Although *Solomys* has relatively inflated bullae as in *Melomys*, its larger body size and V-shaped rear margin to the palate (Laurie and Hill 1954) distinguish it from *Melomys*.

Therefore, on the basis of general body size which is within the range described for *Melomys*, I have placed *M. hadrourus* in that genus. Other features such as the well-developed tail and thick I', indicate affinities with *Uromys*; the configuration of the tail in particular is aberrant for *Melomys*. These features may well become significant in determining the generic status of *M. hadrourus* should the two genera at some future time be distinguished on anything other than size.

## SPECIFIC POSITION:

*Melomys hadrourus* is similar in size to the larger New Guinean forms within the *M. levipes* and *M. leucogaster* groups (Fig. 2). It differs from the members of the *M. leucogaster* group by having a distinctly longer rostrum, as shown by the ratio of the nasal length to condylobasal length of the skull (Fig. 4), and by the skull longer relative to its breadth (Fig. 2).

Five of the subspecies of *M. levipes* recognised by Tate (1951) are close to *M. hadrourus* in size,

viz *M. l. rattoides*, *M. l. naso*, *M. l. lanosus*, *M. l. shawmayeri*, and *M. l. lorentzii* (*M. l. levipes* with a condylobasal length of 37.0 mm and zygomatic width of 19.4 mm, cotype, BM 97.8.7.72 is not one of the larger members of the *M. levipes* group (Fig. 2)). All five subspecies have slender tails typical of the genus *Melomys*, and all have tails shorter than the head-body length, in contrast to the thick tail of *M. hadrourus* which is longer than the head-body length. The depth of I<sup>1</sup> in *M. hadrourus* is significantly greater than in these five large *M. levipes* subspecies (Fig. 3). In the photograph of the skull of *M. l. lorentzii* (RNHL 25494) the posterior margin of the palate is obscured by remnants of the soft palate, but in the other four subspecies the margin lies forward of the posterior end of the molar row, whereas in *M. hadrourus* it lies well behind (Pl. 2).

*Melomys hadrourus* has one hair per tail scale as do *Melomys leucogaster*, *M. levipes naso*, and *M. levipes levipes*, but differs from these respectively by having a longer rostrum, a longer thicker tail, and a larger body size. *Melomys levipes rattoides*, *M. l. shawmayeri*, *M. l. lanosus* all have three hairs per tail scale, as does *M. l. lorentzii* except for one specimen (Tate 1951). *Melomys levipes lorentzii* has a mammary formula of 0-1 = 2 (Zeigler 1972) in contrast to the 0-2 = 4 which is typical for the genus and *M. hadrourus*.

*Melomys hadrourus* differs from other Australian *Melomys*, which are placed into the *M. cervinipes* (including *capensis* and *rubicola*) and *M. lutillus* (= *burtoni* vide Knox 1978) groups by Tate (1951), by being distinctly larger (Fig. 2) and by having only one hair per tail scale in contrast to the three in the other two groups.

Baverstock, Watts and Hogarth (1977) examined the chromosomes of the paratype (JM3837) (their specimen no. IMVS 181F) of *Melomys hadrourus*. The karyotype had a diploid number of 48, which is the standard number for the Australian species they examined in the *M. cervinipes* and *M. burtoni* complexes. The karyotype differed from *M. ?littoralis* (= *burtoni* vide Knox 1978) by two fixed rearrangements (pairs 2 and 4) and from *M. cervinipes* by three fixed rearrangements (pairs 1, 2 and 4) (Baverstock et al. 1977). From their chromosomal work on the Australian *Melomys*, Baverstock, Watts, Adams and Gelder (1980) concluded that three karyotypic forms occurred in Australia; *M. burtoni*, *M. cervinipes* (including *capensis*), and the Thornton Peak melomys (*M. hadrourus*).

The alveolar pattern (type D) of *Melomys hadrourus* is the same as that of *M. cervinipes* (including *rubicola*) and *M. rufescens* (Alston 1877) but differs from that of the *M. burtoni* group (Knox 1976).

It is concluded, therefore, that *Melomys hadrourus* is a valid species, quite distinct from other described *Melomys*.

#### HABITAT AND DISTRIBUTION

All specimens of *Melomys hadrourus* were caught in rainforest on the Mareeba Granite of the Thornton Peak massif. The type locality, where JM504 and JM3837 were caught within 100 m of each other, was within 200 m of the head of a gully, with numerous boulders, on the western face of Thornton Peak, and which was one of the northernmost tributaries of Hilda Creek. The gully originated at a fern-covered saddle (*Glyeichenia* sp.) at the northwestern end of the summit valley. The vegetation (Pl. 4) was simple microphyll vine-fern thicket (Tracey 1982) with a canopy height of 6-12 m. Thin wiry lianes and tree ferns were common, with *Lacospadix* palms abundant in the understorey. Ground cover was sparse leaf litter with scattered ferns and tree seedlings between boulders and fallen logs. Mosses and lichens were abundant from the ground layer through to the canopy. The summit area of Thornton Peak is wet with a rainfall likely to be similar to that of the summit of Bellenden Ker, 130 km to the southeast, which has an annual average of 8529 mm recorded over a six year period (Tracey 1982). Even in the dry season months of April to October the summit is enveloped in cloud much of the time.

JM2173 and a subadult male, which subsequently escaped, were caught on the crest of the McDowall Range within 100 m of the road in simple notophyll vine forest (Tracey 1982). Canopy height was 20-25 m and tree diameters mainly in the 40-50 cm range with a few up to 70 cm. There was a straddled understorey and a scattered shrub layer which consisted mainly of *Calamus* clumps without the climbing tendrils. *Lacospadix* palms and tree ferns were scarce, woody lianes moderately common, but wiry lianes absent. Ground cover was sparse and leaf litter and bare soil with sparse tree seedlings and very sparse ferns. This site is below the cloud line that generally envelopes the summit of Thornton Peak, and mosses and lichens were relatively sparse. Rainfall is less than for the summit region, and the locality comes between the 2500 and 3750 mm isohyets (Tracey 1982). M12520 was caught in mesophyll vine forest and M12521 in simple

mesophyll vine forest — simple notophyll vine forest at sites 39 and 40 respectively (Broadbent and Clark 1976) on a steep southerly ridge immediately to the west of the main branch of Hilda Creek.

JM504 and JM3837 were captured in aluminium Elliott traps (33 × 9 × 9 cm) (Pl. 4) set on the ground and baited with sweet-potato in linseed oil. Both McDowall Range animals were caught in cage traps (one aluminium and one wire with slightly larger dimensions than for the above) set on the ground and baited with rolled oats plus aniseed oil and sweet-potato in linseed oil respectively. Both the Australian Museum animals were caught in snap traps (one a Conibear) set on the ground; the bait was either peanut butter compound or aniseed oil (Broadbent and Clark 1976). Table 5 in Broadbent and Clark (1976) lists 5 '*Melomys* "levipes" group' as being captured at site 39. There was some confusion over the identity of *M. hadrourus* with *M. cervinipes* at the time. In fact only one specimen of *M. hadrourus* (M12520) was kept from this site and one adult male, probably attributable to *M. hadrourus*, was discarded because of damage received on capture.

All four localities at which *M. hadrourus* has been captured are in the upland (> 300 m) zone of the Thornton Peak massif. The area of this upland zone (measured as a flat surface from the 1:100 000 vegetation map, Tracey and Webb 1975) is approximately 24,780 ha and 96 per cent is rainforest. The Thornton Peak upland zone is isolated from other upland zones to the southwest and northwest by the Daintree and Bloomfield valleys respectively, and the latter, with open forest vegetation, also acts as an ecological barrier (Fig. 1).

Thornton Peak itself (altitude 1374 m) and the eastern fall of the massif are national park (Fig. 1). Approximately 5620 ha (22.7%) of the upland zone is within the national park, the remainder is within timber reserve. The relative isolation and rugged terrain of the area have, to date, protected the upland zone from major forestry, mining and agricultural developments. The clearing of rainforest that has taken place in the area has been restricted to the lowlands (Fig. 1).

#### HABITS

All specimens of *M. hadrourus* were caught in traps set on the ground, but like *M. cervinipes* and *Uromys caudimaculatus* it is probably scansorial. The stomach of M12521 was filled with a creamy coloured endosperm of a nut. Adult

female JM3837 was captured 5 June 1974 and kept alive in captivity until 2 February 1975. She did not give birth to young. Adult female JM504, captured 16 November 1973, had a perforate vagina and small teats that were not lactating (contents of uteri unknown). The breeding condition of adult female M12520 was not recorded. The three males (JM2173, M12521 and the escaped individual) were all subadults with testes abdominal and captured in October and November. Subadult male, JM2173, when handled, gave squeaks similar to that of *M. cervinipes* but deeper in pitch, and not a *Uromys*-like growl.

At the type locality *M. hadrourus* was recorded as living sympatrically with three other rodents; *M. cervinipes* (Gould 1852), *Rattus fuscipes* (Waterhouse 1839) and *Rattus leucopus* (Gray 1867). At the McDowall Range locality, in addition to these three species, *Uromys caudimaculatus* was also recorded.

#### DISCUSSION

*Melomys hadrourus* represents a third phylogenetic line of *Melomys* in Australia with clear differences from the *M. burtoni* and *M. cervinipes/capensis* species groups both in karyotype and in morphology (larger size, well-developed tail, on hair/tail scale). On size alone its closest affinities would seem to be the New Guinean species groups, *M. leucogaster* and *M. levipes*. At one stage it was thought that *M. hadrourus* was closely allied to *M. levipes* (Baverstock et al. 1977) and therefore a vicariant with New Guinean affinity (Kikkawa et al. 1981). *Melomys hadrourus*, however, has certain affinities with *Uromys*, namely the general configuration of the tail and the more robust skull, particularly in the thickness of 1'. It also has other clear differences from *M. leucogaster* (longer rostrum) and *M. levipes* (tail longer than head-body length, one hair per tail scale in contrast to the three in four of the large subspecies, palate margin posterior to tooth row).

It is suggested here that *M. hadrourus*, although included with the genus *Melomys* on size, is an aberrant form for the genus. Whether these differences warrant removing *M. hadrourus* from *Melomys* as a third genus, or alternatively using it to synonymise *Melomys* and *Uromys*, requires an extensive review of the mosaic-tailed rats, beyond the scope of this paper. For the present, it is judged to be sufficiently different from other described species for it to be treated as a species without vicariants.

This being the case, *M. hadrourus* belongs to the group of species, endemic to the Townsville to Cooktown region, and considered to be relicts of a wet- and cool-adapted fauna which may have originated in Australia from a common pre-Pleistocene stock of Australia and New Guinea; mammalian representatives of this group are *Antechinus godmani* (Thomas 1923), *Pseudocheirus herbertensis* (Collett 1884), *Pseudocheirus lemuroides* (Collett 1884) and *Hypsiprymnodon moschatus* Ramsay 1876 (Kikkawa et al. 1981). Their survival has been dependent on the continuous existence of rainforest refugia, of which the uplands of the Thornton Peak massif is one example (Webb and Tracey 1981).

#### ACKNOWLEDGMENTS

I wish to thank the Commonwealth Forestry Timber Bureau (now CSIRO Division of Forest Research), Atherton, for making available the helicopter transport which enabled me to make the first visit to the summit of Thornton Peak, and to those people who subsequently helped in the search for further specimens of the Thornton Peak melomys — Rob Atherton, Louise Atherton, Cherie Daniel, Curly Matthew, Dan Norris, Ian Shield, Mark Weaver, David Winter and Margaret Winter. I also wish to thank Mr H. Posamentier, the Australian Museum, for making available to me the specimens of *M. hadrourus* that he captured, and Dr P.D. Dwyer, University of Queensland, for the skull of *Uromys anak*. Ms E.J. Knox and Mr J.A. Mahoney very kindly read early drafts of the manuscript and made many useful suggestions for its improvement. Photographs in Pl. 1 and 2 were supplied by the Department of Primary Industries, Photographic Department, and Hans and Judy Beste took the photographs used in Pl. 3. Finally I wish to thank the staff of the British Museum (Natural History), London, and Museo Civico di Storia Naturale, Genoa, the Rijksmuseum van Natuurlijke Historie, Leiden, the American Museum of Natural History, the Australian Museum, and the Queensland Museum for their help in examining their collections and in supplying photographs.

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TABLE 1: EXTERNAL BODY MEASUREMENTS, WEIGHTS AND HAIRS PER TAIL SCALE OF *MELOMYS HADROURUS*.  
\*MEASUREMENTS TAKEN BY H. POSAMENTIER.

	Holotype		Paratypes		Escaped	
Museum no.	JM504	JM3837	JM2173	M12520*	M12521*	
Status	Adult ♀	Adult ♀	S-Adult ♂	Adult ♀	S-Adult ♂	S-Adult ♂
Weight (g)	149	164	125	162	149	152
Head-body length (mm)	180	177	174	171	173	184
Tail-vent length (mm)	196	-	184	-	188	197
Pes s.u. (mm)	38	37	38	38	38	37
Ear (to notch) (mm)	24	23	25	24.5	23.5	23
Tail diameter at base (mm)	5.1	5.2	4.7	5.6	5.1	-
Tail scale rows/cm	12.5	13	11	12	13.5	-
Hairs/tail scale	1	1	1	1	1	-

TABLE 2: SKULL MEASUREMENTS (IN MM) OF *MELOMYS HADROURUS*. DEFINITION OF MEASUREMENTS AS GIVEN BY, — TAYLOR AND HORNER (1973),<sup>2</sup> — MAHONEY (1972), OR<sup>3</sup>— CORBET (1964). 1' THICKNESS MEASURED PARALLEL TO HORIZONTAL PLANE FROM POSTERIOR POINT OF EMERGENCE FROM PREMAXILLA.

	Holotype		Paratypes		
	JM504	JM3837	M12520	M12521	JM2173
<sup>1</sup> Occipitonasal length	45.3	44.2	44.6	44.2	44.7
<sup>1</sup> Condylbasal length	42.2	42.7	41.2	41.2	42.0
<sup>1</sup> Basal length	39.5	40.1	38.8	38.4	39.0
<sup>1</sup> Zygomatic width	22.6	22.5	21.5	21.4	22.2
<sup>1</sup> Interorbital width	7.1	6.8	6.9	7.0	7.2
<sup>2</sup> Width of rostrum	7.1	6.7	6.7	6.8	7.0
<sup>2</sup> Nasal length	17.8	17.4	17.4	17.2	17.7
<sup>2</sup> Maximum width across paired nasals	5.0	5.4	4.9	5.1	5.0
<sup>2</sup> Maximum width across paired parietals	16.6	15.8	16.5	16.9	16.0
<sup>1</sup> Mastoid width	16.0	16.1	15.7	15.8	16.2
<sup>2</sup> Interparietal length	6.1	5.7	6.0	6.6	5.1
<sup>1</sup> Interparietal width	11.6	11.2	11.6	11.2	11.8
Zygomatic plate minimum width	5.2	5.8	5.4	5.2	5.6
<sup>1</sup> Palatal length	25.2	25.2	24.9	24.7	24.9
<sup>3</sup> Diastema length	13.2	13.6	13.9	13.6	13.2
<sup>1</sup> Anterior palatal foramen length	6.6	6.5	6.0	5.8	6.4
<sup>1</sup> Anterior palatal foramina width	2.5	2.8	2.5	2.6	2.7
<sup>2</sup> Palate width between anterointernal roots of M <sup>1</sup>	4.9	4.8	4.8	4.2	4.7
<sup>2</sup> Palate width between anterior roots of M <sup>3</sup>	5.3	5.2	5.4	5.2	5.7
<sup>1</sup> Bulla length	4.9	4.9	5.0	5.1	5.0
<sup>1</sup> M <sup>1-3</sup> length (crowns)	7.3	7.6	7.3	7.2	7.1
<sup>1</sup> M <sup>1-3</sup> length (alveoli)	8.1	8.2	8.3	7.8	8.0
M <sup>1</sup> length x width (crowns)	3.4x2.3	3.8x2.1	3.6x2.2	3.4x2.3	3.3x2.3
M <sup>2</sup> length x width (crowns)	2.7x2.1	2.5x2.0	2.8x2.2	2.8x2.1	2.6x2.3
M <sup>3</sup> length x width (crowns)	1.6x1.6	1.6x1.5	1.7x1.6	1.7x1.6	1.5x1.6
1' thickness	2.5	2.5	2.3	2.3	2.4
<sup>2</sup> Length of mandibular ramus from tip of incisor	31.1	32.3	30.5	30.0	30.8
<sup>2</sup> Height of condyle above ventral surface of mandibular ramus	11.5	11.6	12.0	11.5	12.0
M <sub>1-3</sub> length (crowns)	7.5	7.4	7.6	7.8	7.1
M <sub>1-3</sub> length (alveoli)	7.8	8.3	7.7	8.1	7.9
M <sub>1</sub> length x width (crowns)	3.2x2.2	3.3x1.9	3.1x2.1	3.1x2.0	3.1x2.1
M <sub>2</sub> length x width (crowns)	2.5x2.1	2.2x1.7	2.6x2.1	2.7x2.1	2.5x2.1
M <sub>3</sub> length x width (crowns)	1.9x1.7	1.9x1.4	1.8x1.6	1.8x1.6	2.0x1.6

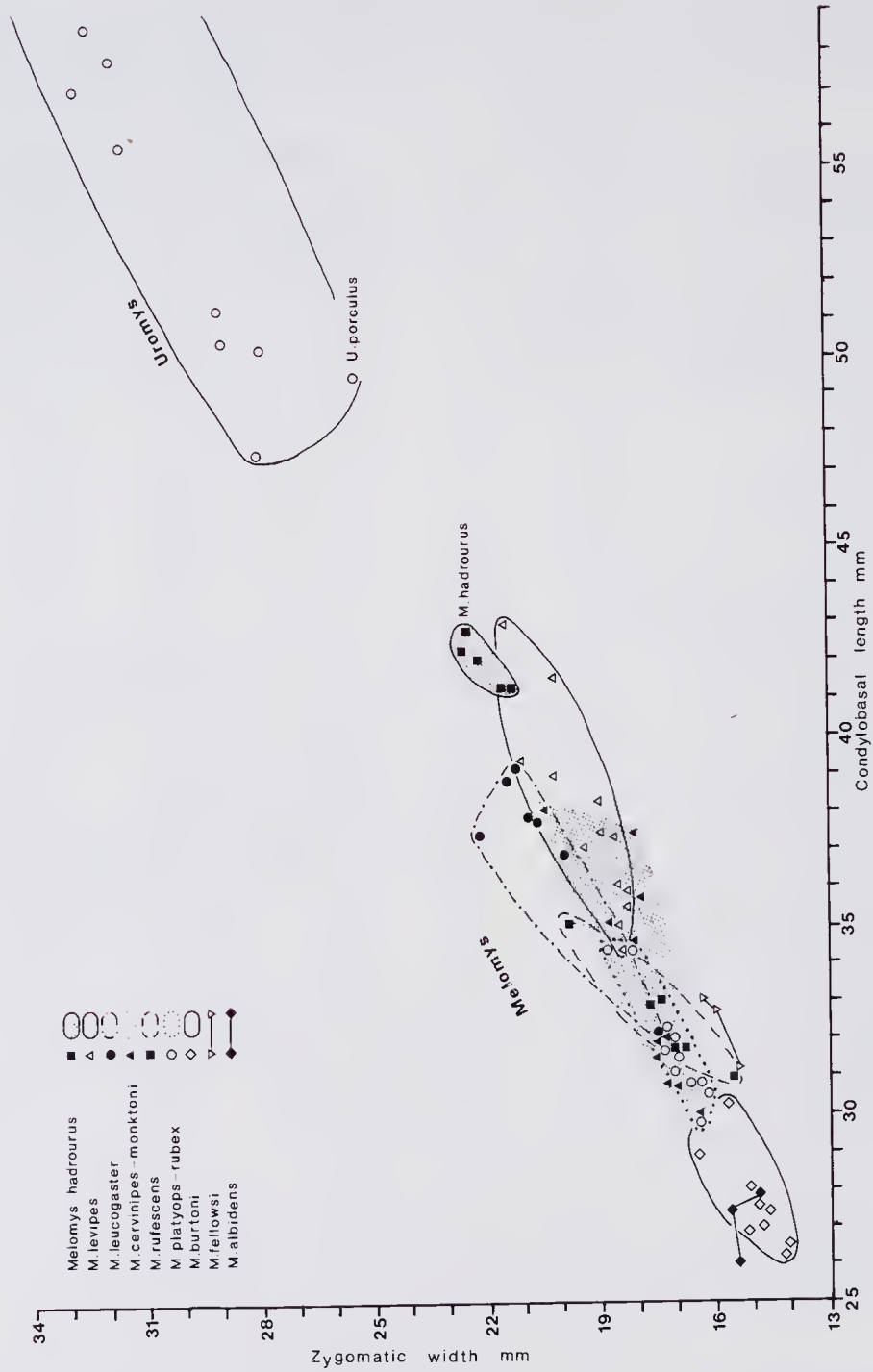


FIGURE 2. The relationship between condylobasal length and zygomatic width in *Uromys*, *Melomys hadrourus* and other *Melomys* species groups.



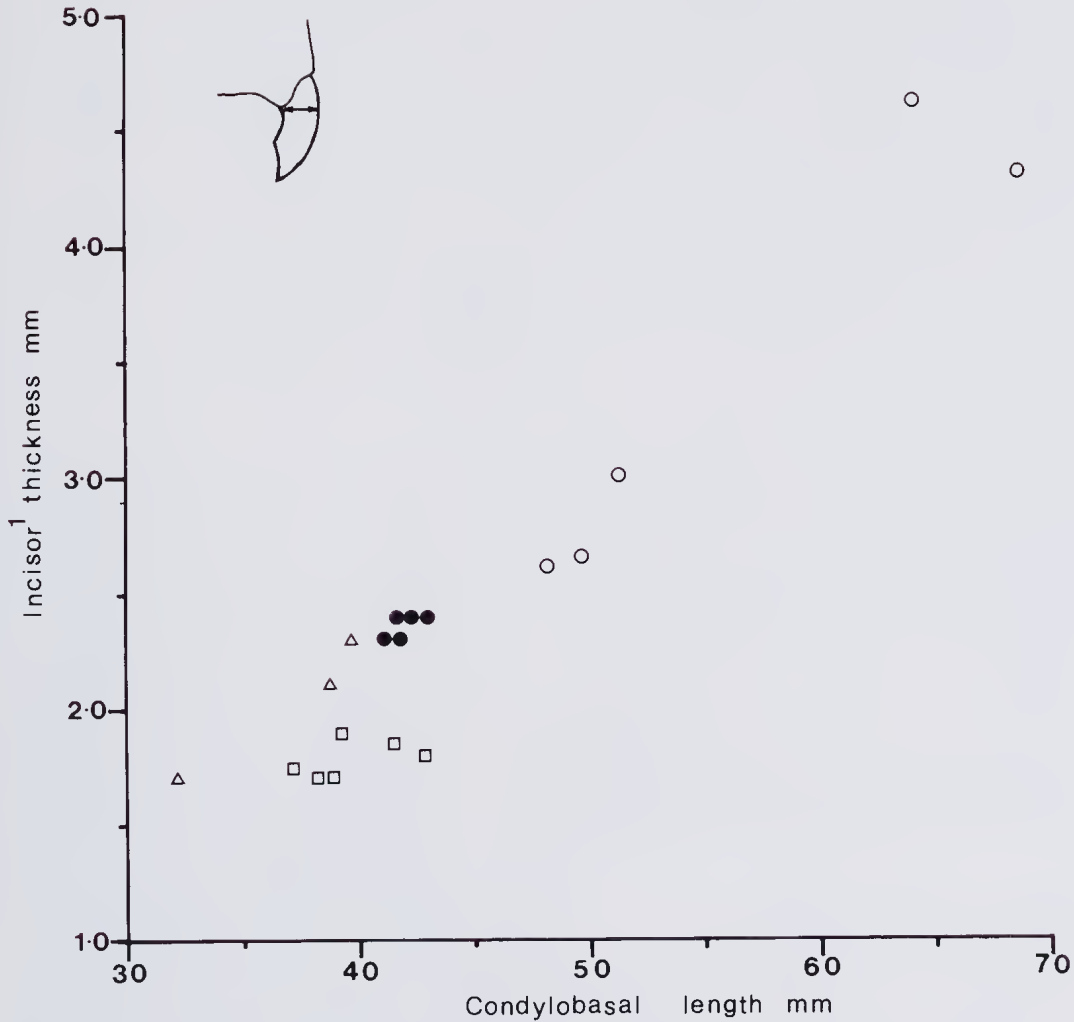


FIGURE 3. The relationship between condylobasal length and incisor<sup>1</sup> thickness in *Melomys hadrourus* (●), *M. leucogaster* (△), *M. levipes* (□), and *Uromys* spp. (○). <sup>1</sup> measurements: *M. leucogaster latipes* AMNH 104273 (1.7'), *M. leucogaster* RNHL 25493 (2.1') *M. l. leucogaster* AMNH 105723 (2.3), *M. levipes lanosus* BM 22.2.2.26 (1.7\*), *M. levipes shawmayeri* BM 35.12.20.2 (1.7\*), *M. l. levipes* BM 97.8.7.72 (1.75\*), *M. l. levipes rattooides* BM 22.2.2.25 (1.8\*), *M. levipes naso* BM 11.11.11.54 (1.85\*), *M. levipes lorentzii* RNHL 25494 (1.9'), *Uromys caudimaculatus caudimaculatus* juv. QM JM3839 (2.6), *U.c. caudimaculatus* adult QM No. JM3840 (4.6), *U. porculus* BM 89.4.3.8 (2.65\*), *U. sapientis* BM 2.5.1.4 (3.0\*), *U. anak* QM JM3838 (4.3). Measurements supplied by P.D. Jenkins, BM (\*); C. Smeenk, RNHL (+); C. Smeenk, RHNL (+); M.A. Lawrence, AMNH (').

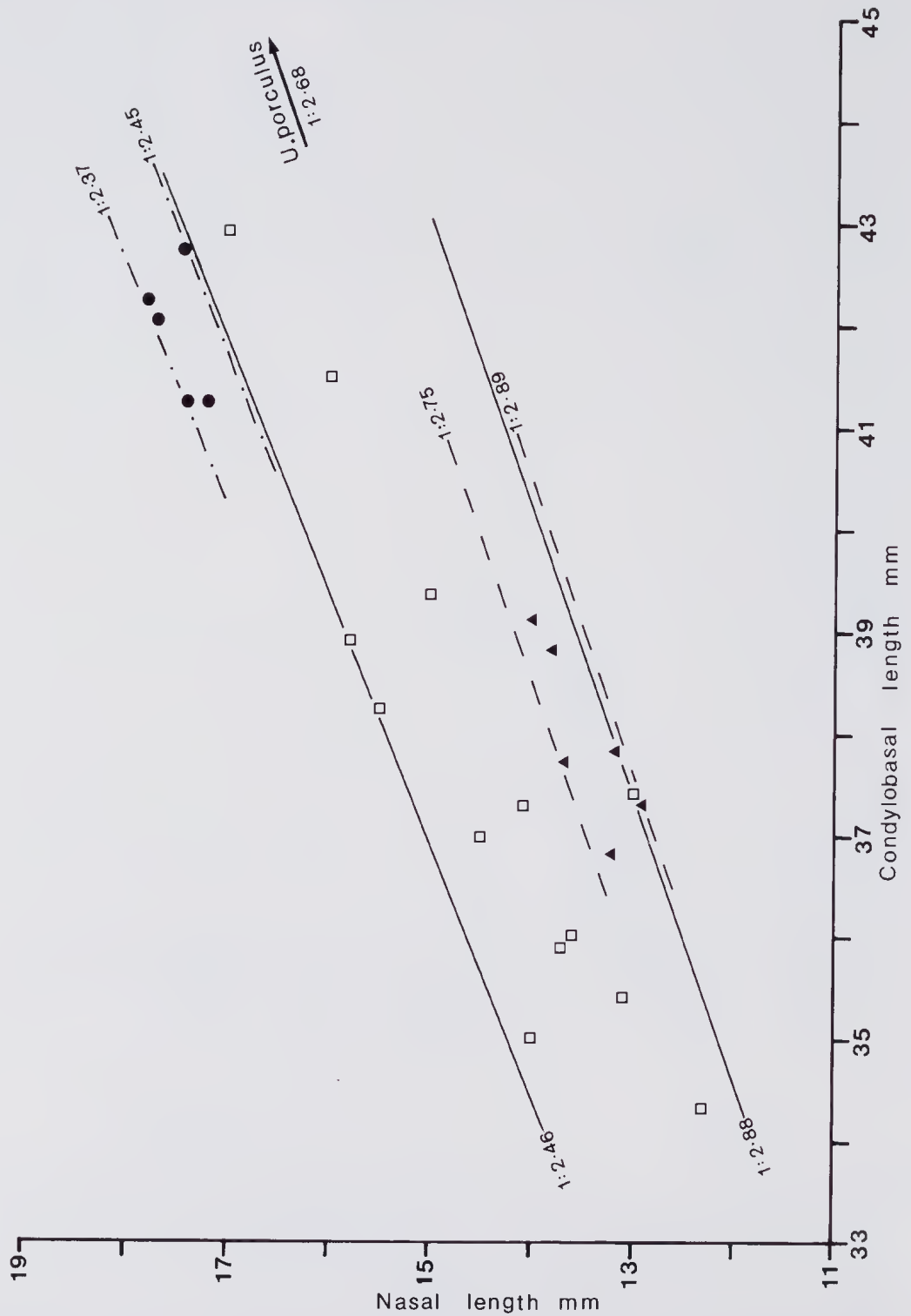
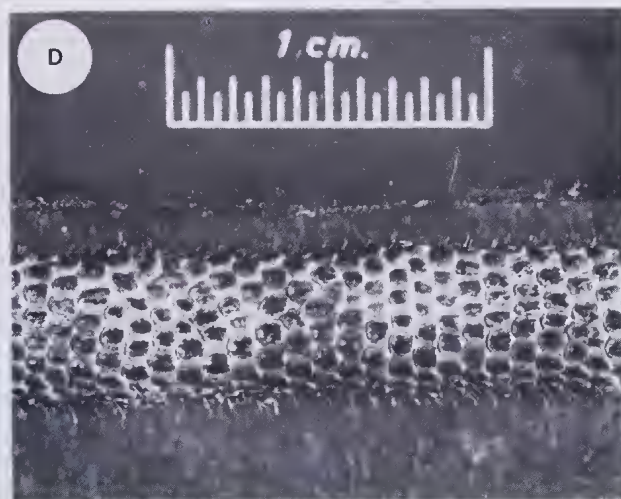
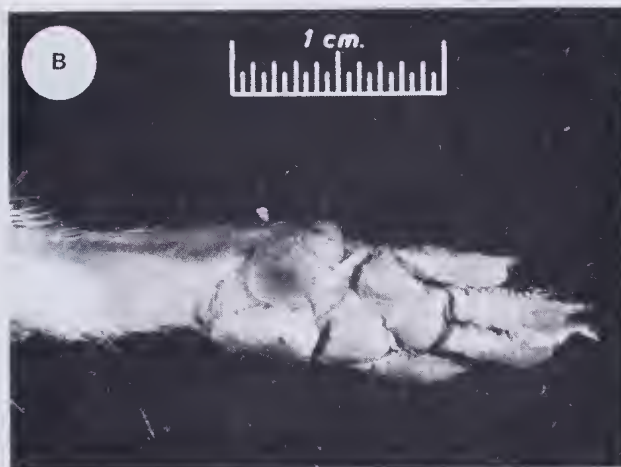


FIGURE 4. The relationship between nasal length and condylobasal length expressed as a ratio, in *Melomys hadrourus* (o), *M. levipes* (□), and *M. leucogaster* (△). The upper and lower limits of the ratio are shown.



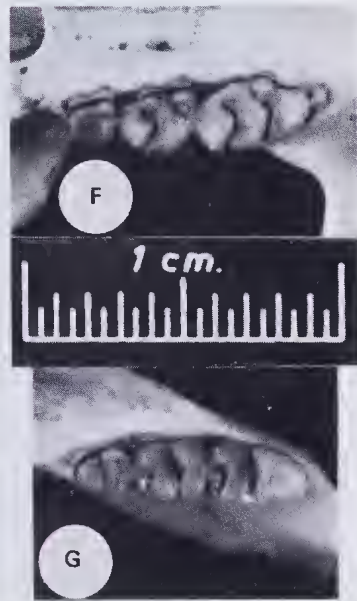
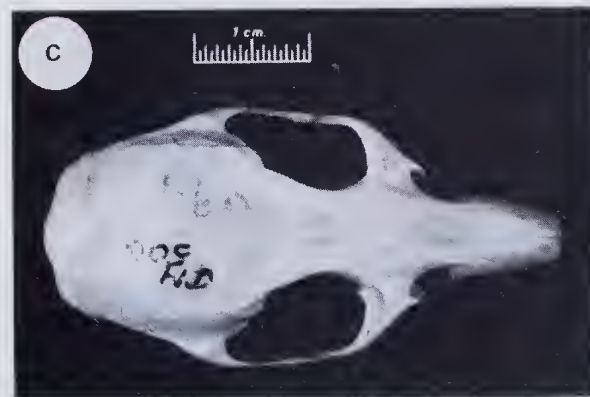
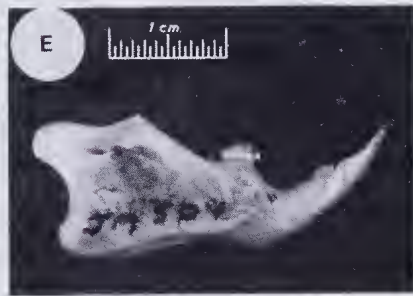
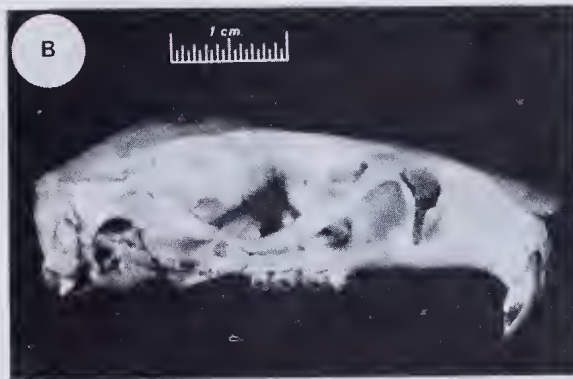
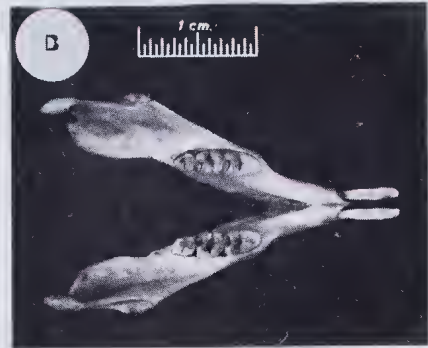
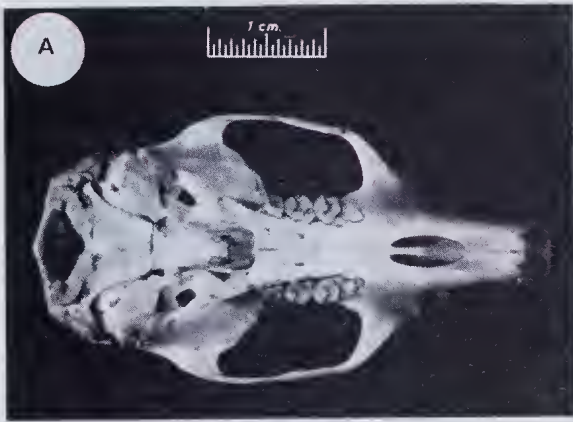
## PLATE 1

External features of *Melomys hadrourus* (QM JM504, holotype) from Thornton Peak, N.E. Queensland. A: pes, B: manus, C: tail, D: tail detail about one third from the base.



## PLATE 2

Skull features of *Melomys hadrourus* (QM JM504, holotype) from Thornton Peak, N.E. Queensland. A-E: cranium and mandible, F: upper left molars, G: lower left molars.



## PLATE 3

Subadult male of *Melomys hadrourus* from the McDowall Range,  
N.E. Queensland. The animal subsequently escaped.





## PLATE 4

Type locality of *Melomys hadrourus*. Simple microphyll vine-fern thicket, Thornton Peak, N.E. Queensland.





## THE MT. INGLIS CACHE: A NEW PERSPECTIVE ON ABORIGINAL MATERIAL CULTURE IN THE CENTRAL HIGHLANDS OF QUEENSLAND.

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### ABSTRACT

This paper describes a cache of Aboriginal material recovered from 'Mt. Inglis' Station in the Central Highlands of Queensland. The cache includes bones, skins and lithic materials. Rockshelter caches, particularly of organic items provide evidence for a range of Aboriginal material culture, activities and practices which were never ethnographically described. The Mt. Inglis cache of ceremonial and decorative items was probably hidden for later re-use during the final phase of traditional Aboriginal culture in the region.

### INTRODUCTION

In 1901 Archibald Meston, then Protector of Aborigines for southern Queensland, visited the upper Maranoa River in the Central Queensland Highlands 'to obtain some ethnological specimens said to exist in sandstone caves' (Meston 1901). Meston well appreciated the importance of these finds, and a mere 40 years after the first European occupation of the area, he states —

In the caves and rockshelters of our mountain ranges there are still hundreds of specimens specially valuable to ethnology, and the value is incalculable when we regard them as among the last available memorials of a primitive race rapidly vanishing from the face of the earth (Meston 1901).

This was the first published account of a cache of Aboriginal material culture from shelters in the Queensland Central Highlands, and remains one of the few.

In 1975, such an Aboriginal cache was discovered on "Mt. Inglis" Station, northeast of Carnarvon Gorge (latitude 24°46'S, longitude 148°18'E). The find became known to local residents, but fortunately much of the material was left *in situ*. The Archaeology Branch, D.A.I.A. was notified of the find, and in accordance with the Aboriginal Relics Protection Act of 1967-76, it was decided to recover the cache to prevent its unauthorised removal. In January 1976, I removed the cache, assisted by Jeff Pratt (then Aboriginal Relics Ranger for Central Queensland).

### DESCRIPTION

The material was located in a small shelter on the southern slope of a rocky hillside, overlooking a black-soil flat (Pl. 1). The surrounding vegetation comprised an open woodland of ironbark (*Eucalyptus melanophloia*), round-leaved box (*E. populnea*), bloodwood (*E. terminalis*), and yellowjack, with an *Acacia* understory. Water was available at a permanent spring some 300 metres to the north.

The shelter faced north and measured 6 by 4.5 metres with a maximum dripline height of 1.5 metres. The cache was positioned on a small ledge in the roof, 50 cm back from the entrance and facing east. The ledge measured 70 by 30 cm and was 92 cm above the shelter floor. The cave was an obvious one, but to a casual observer it was 'obviously empty' as the shelf was not visible from the entrance.

Originally the cache had been concealed with three sandstone blocks (25 cm maximum dimension) placed at the front of the ledge. These had been shifted and at the time of the removal sections of marsupial skin and twine were hanging down from the ledge. The material had already been removed several times for inspection after its initial discovery, and had suffered some damage because of this. On the shelter floor beneath the ledge, lay a deposit of red ochre, necklace reels, lengths of twine, skin and feathers. As part of the recovery procedure, this area of the floor deposit was sifted through to a depth of 3 cm. The poor condition of the organic items recovered from the shelter floor would indicate that deterioration

here was rapid. All the material found on the floor had probably fallen from the ledge recently.

A photographic record was kept as each item was removed, described, numbered, then double-sealed in polythene bags. Foam chips were placed between the bags and the exterior bag partially inflated. No noticeable damage occurred to the material during transit to Brisbane, and it is now held in the collections of the Queensland Museum (S181/1-88).

The cache comprised 29 items as well as 26 incomplete lengths of twine (S181/6,10,14,27,28,31,35,26,37,41,42,46,47,49) and 8 fragments of skin (S181/7,10,13,14,17,26). The more complete items are described below in the order of registration by the Queensland Museum.

(S181/1): A juan knife comprising a large, silcrete blade of trigonal cross-section and backed by steep, bi-directional retouch along the thick back. The distal end tapers to a point, whereas the proximal end has a haft of Whiptail wallaby (*Macropus parryi*) skin which extends for 3.5 cm. The skin is attached by a black resin which has red ochre embedded in it. This classic juan knife (Mulvaney and Joyce 1965, p. 190) is 15.5 cm in length, 4.4 cm wide and 2.5 cm thick.

(S181/2): A small, sandstone grindstone measuring 10.3 by 7.4 by 2.0 cm. Both major facets exhibit grinding and smoothing, the obverse side being slightly convex and the reverse slightly concave. A thick coating of red ochre on both ground surfaces shows that the grindstone was used as a palette.

(S181/3): A water-rolled, quartzite pebble measuring 7.8 by 7.2 by 3.1 cm. It has red ochre and kaolinite adhering to the flat, reverse side and probably functioned as an upper grinding stone.

(S181/4): A lump of kaolinite measuring 7.0 by 5.7 by 6.0 cm. It appears to have been used as a source of white pigment, and has abraded areas and striations. Six holes 8 mm in diameter and 10 mm deep, and 10 smaller holes 2 mm in diameter have also been drilled into the material.

(S181/5): A cylindrical mass of compressed, emu feathers which has been consolidated with red ochre grease and unidentified adhesives (Pl. 2a). Tests undertaken by the Pathology Division (Qld. Health Dept.), have shown that human blood was not the adhesive used. The remnants of a skin wrapping have the fur side out. The original feather mass has now disintegrated into two sections, the largest of which measures 25 by 11 by 7 cm and the smaller 13 by 7 by 4 cm. Three smaller wads of emu feathers and red ochre wash (S181/8,9,30), are almost certainly fragments of the same original item.

A section of long-bone can be seen embedded in the largest feather mass, while on one side three cylindrical objects tightly wrapped in possum fur twine, with a dense red ochre coating are partially revealed. On the upper side of this mass there are the negative impressions of two similar objects. Another impression can be seen on the second largest feather mass. It is 13 cm in length and 1 cm in diameter.

(S181/12): A length of necklace comprising 13 small reels of cut reed sections which have an outside diameter of 4.5 mm and vary in length from 4 to 6 mm. Eleven reels are threaded on 2-ply bark fibre 2 mm in diameter. The twine and reels have been coloured with red ochre (Pl. 2b). A further 31 reels of the same necklace (S181/25) were recovered from the shelter floor.

(S181/15): A lump of prepared red ochre which has fragmented into 2 sections. Each measures 3 by 3 by 1.5 cm.

(S181/16): A small section of string bag measuring 3 by 2 cm. The fabric is of 2-ply, bark fibre twine of variable diameter, which is woven in the knotted netting technique. The bag has a mesh size of 1.5 by 1.1 cm and is probably a fragment of S181/34.

(S181/18): A bag made from Brush-tailed possum (*Trichosurus vulpecula*) skin which has the fur facing inwards (Pl. 2c). The bag was originally cylindrical in shape with a circular base sewn across the centre, with sinew threaded through pierced holes, and measures 22 cm in length and 9 cm in diameter. The top of the bag is made from the rear portion of the animal and is open with 3 small pierced holes around the periphery for a draw string. Two holes where the limbs have been detached, the cloaca and the remains of the pouch, can still be seen.

When removed the bag contained 34 artefacts of opaline chert (S181/55-88; Fig. 2; Table 1) and a lump of yellow ochre measuring 3.8 by 3.5 by 2.3 cm. The ochre has an ovate depression in one face.

(S181/19): A pouch of Whiptail wallaby (*M. parryi*) skin. The fur faces inwards but most of the fur has been removed (Pl. 2d). Traces of red ochre occur on the interior and exterior. The pouch measures 21 by 14 by 5 cm and contains an emu feather head-dress, a bone point and a small long-bone shaft.

The head-dress has been manufactured by attaching the emu feathers to a stem of 7 lengths of bark fibre, which have been tightly bound transversely with a strand of bark fibre. A small tassel of bark fibre with a large knot at one end originates from the top of the fibre stem. The

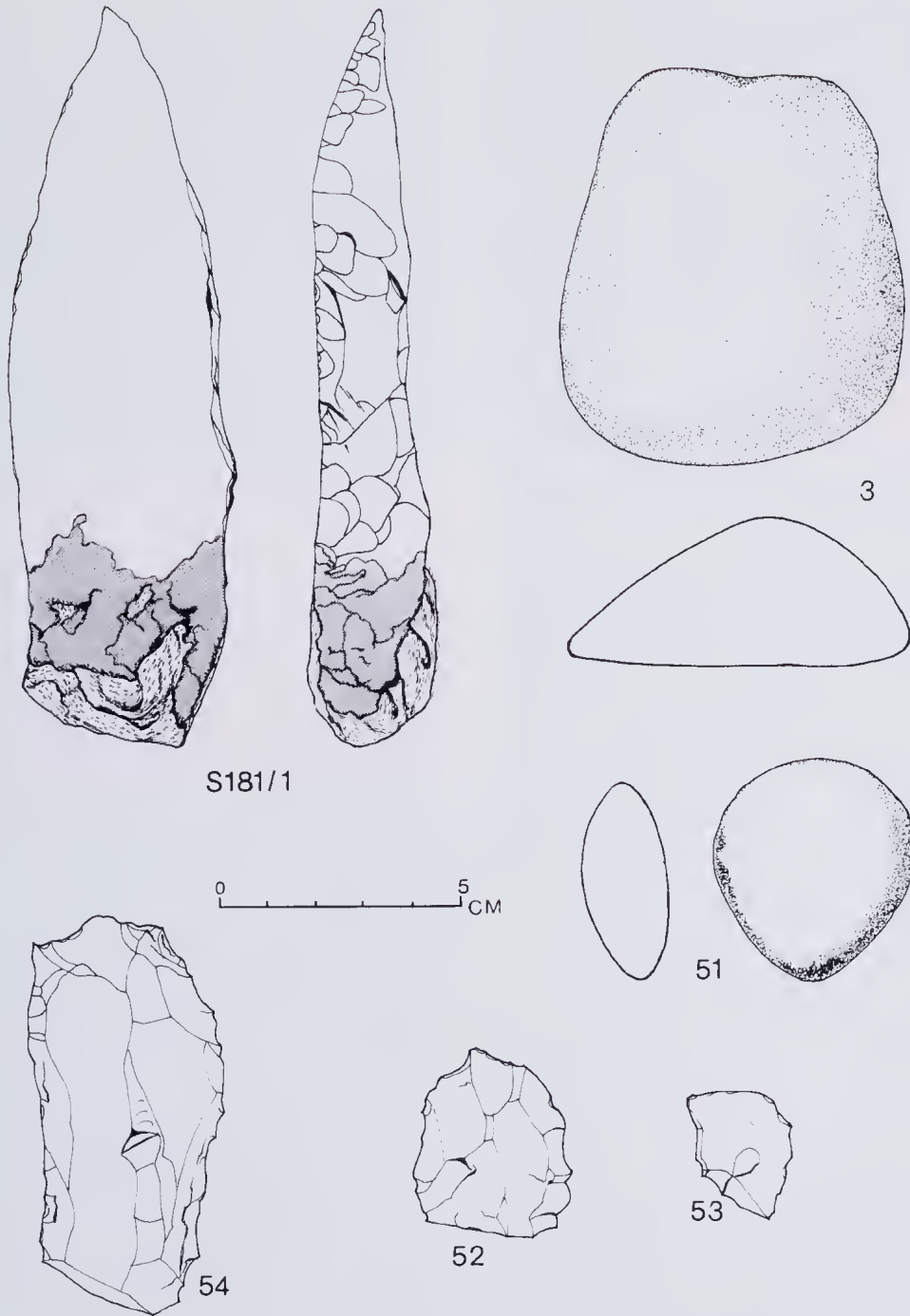


FIGURE 1. S181/1 hafted juan knife; 3 water-rolled quartzite pebble; 54 large silcrete scraper. 52 silcrete flake; 53 opaline chert flake; 51 amorphous quartz pebble.

stem is 0.7 mm in diameter. Its length was not determined as the item was not removed from the pouch.

The bone point (S181/20) is made from the proximal end of a juvenile macropod fibula. The point is polished as well as ground. It is 17 cm in length.

The long-bone shaft (S181/21) is from a bird of pelican or broilga size. It has been snapped at both ends and has traces of red ochre adhering. The shaft is 12 cm in length and 0.6 cm in diameter.

(S181/22): A section of Brush-tailed possum (*T. vulpecula*) skin. It has the fur facing out and the anterior has been coloured with red ochre wash. The base of the tail has been reversed, plugged with skin, fur and sinew, then tightly bound. This 'plug' measures 1.4 cm in length and 0.4 cm in diameter. The inverted testes are evident on the inner surface near the tail plug. The skin measures 34 by 6 by 5 cm.

(S181/23): An elongate parcel wrapped in Brush-tailed possum skin (*T. vulpecula*) with the fur facing outwards (Pl. 2e). The parcel contains a red-ochred mass of emu feathers and at least 8 strands of 2-ply, fur twine (3 mm diameter). A section of the skin wrapping has been bound with sinew. The parcel measures 29 by 10 by 5 cm.

(S181/24): A dried cloaca of a large macropod which has been compressed to form a circular pendant (Pl. 2f). Cloacal hairs form a fringe around the periphery of the disc. A hole has been pierced near the edge and threaded with a length of sinew which has been knotted at one end. The disc has a maximum diameter of 51 mm and is 4 mm in thickness.

(S181/25): Thirty-one necklace reels of cut reed sections recovered from the shelter floor. These are part of the same necklace as S181/12.

(S181/28d): A wad of Brush-tailed possum fur (*T. vulpecula*) which measures 5 by 2 by 0.5 cm.

(S181/29): A fragment of string bag manufactured from bark fibre and coloured with red ochre. It measures 10 by 7 cm. The fabric is compacted so that the original mesh size is no longer visible but it is of the loop and single twist weave (See Davidson 1933, p. 262; Roth 1901, pl. 17). The string is 1.5 mm in diameter. The remains of the original opening are still visible. This is 2.5 cm in diameter and has a draw string 0.9 mm in diameter.

(S181/32): A close-meshed armband which is woven in the loop and single twist technique. The fabric is of 2-ply, fur twine 1.5 mm in diameter and coated with red ochre (Pl. 2g). Remnants of the finishing off weave are still evident at the top

and bottom of the band which is 14 cm in width, 11 cm in expanded diameter and has a circumference of about 30 cm.

(S181/33): A head-net which is woven in the knotted netting technique. The fabric is of 2-ply, bark fibre twine which is 1 mm in diameter and coloured with red ochre (Pl. 2h).

The net is bell-shaped and is 15 cm in diameter at the open end and 9 cm in depth. The body of the head-net is woven from a circular ring at the top which is 2 cm in diameter. The fabric has a mesh size of 5 mm.

(S181/34): The remains of a string bag which measures 42 by 29 cm (Pl. 3a). It is manufactured in the knotted netting technique with a mesh size of 2 cm. The fabric is of 2-ply, bark fibre twine which is 1.5 mm in diameter. A small portion of the neck remains.

A piece of macropod skin adheres to the bag (probably due to insect activity). This measures 16 by 9.5 cm.

(S181/38): A cylindrical roll of budgeroo bark (*Lysicarpus angustifolius*) which measures 28 cm in length and 8 cm in diameter (Pl. 3b). The roll contains four bundles of 'pins' bound up with bark fibre, and a packing of dry grass. One of the bundles was removed for examination and was found to contain 20 sticks, each about 9 cm in length, 3-4 mm in diameter and tapering to a point at one end. At the other, blunt end, some of the sticks are split and down and feathers of the sulphur-crested cockatoo have been inserted. These splits have then been bound up with bark fibre strands or fur twine. Other sticks remain undecorated.

The bark cylinder has been loosely bound with 2-ply, bark-fibre twine (2.5 mm diameter) which encircles the cylinder four times.

(S181/39): A quid comprising a continuous strand of coarse bark fibre. It measures 4.3 by 2.5 by 1.5 cm and appears to have been chewed.

(S181/40): A quid of bark fibre measuring 5.5 by 2.0 by 0.5 cm. It appears to have been chewed and small indented tooth marks are visible.

(S181/43): A section of tibia shaft from a small macropod of pademelon size. The shaft has been snapped at both ends and measures 6.4 cm in length and 0.9 cm in diameter. This item was recovered from the shelter floor beneath the cache shelf. It may therefore, have been deposited by a natural predator.

(S181/44): A belt made from a single strand of 2-ply, bark fibre twine (1.5-2.0 mm diameter) arranged in three parallel loops, then transversely bound with 2-ply, fur twine which is 1-2 mm diameter (Pl. 3c). Each end of the bark fibre



strand terminates in a small loop around the composite inner core of the belt.

The belt is 6 mm in diameter and 82 cm in length.

(S181/45): Four parallel lengths of ochred, 2-ply, bark fibre twine which have been knotted together at each end (Pl. 3d). The 'tassle' is 18 cm in length and each length of twine is 4 mm in diameter. The knots measure 2.7 by 1.7 cm.

(S181/48): Four parallel lengths of ochred, 2-ply, bark fibre twine of which only one remains complete. The lengths are knotted together at both ends. The 'tassle' is 18 cm in length and each length of twine is 3 mm in diameter.

(S181/50): A parcel wrapped in Rock wallaby (*Petrogale penicillata*) skin with the fur facing inwards (Pl. 3e). At one end the skin has been folded in on itself, while the other has been sewn up with 2-ply, bark fibre strand.

The parcel measures 35 cm in length, 13 cm in width and 8 cm in depth. It contains 1045 gram of finely powdered, red ochre and has been bound with 2-ply, bark fibre twine around the mid-section. This twine is of variable diameter and has been knotted once.

(S181/51): A water-rolled pebble of pink, amorphous quartz measuring 4.5 by 4.0 by 1.9 cm (Fig. 1).

(S181/52): A flake of fine-grained, white silcrete measuring 4.2 by 3.5 by 1.0 cm (Fig. 1).

(S181/53): A flake of opaline chert measuring 2.9 by 2 by 0.5 cm (Fig. 1).

(S181/54): A unifacially retouched scraper of fine-grained, white silcrete. It measures 8.5 by 4.0 by 1.5 cm and has two worked edges of 63° and 72° respectively (Fig. 1).

(S181/55-88): Thirty-four stone artefacts of opaline chert found in the possum skin bag (S181/18). Details of these are given in Table 1 and Fig. 2.

TABLE I. Attributes of thirty-four opaline chert artefacts found in the possum skin bag. (Queensland reference numbers S181/55-88).

S181	Description	Dimensions (cm)			Edge Damage	Edge Angle
		length,	width,	thickness		
55	Utilised flake	2.5	2.1	.5	Bifacial utilisation Unifacial utilisation	52° 69°
56	Utilised flake	2.1	1.5	.4		
57	Utilised flake	2.0	1.2	.3	Bifacial utilisation Bifacial utilisation	34° 30°
58	Tula adze slug with adhering resin	1.7	.6	.4	Step fractured retouch	48°
59	Utilised flake	3.0	1.7	.5	Unifacial utilisation	46°
60	Utilised flake	2.7	1.7	.5	Bifacial utilisation	24°
61	Utilised flake	1.7	0.6	.3	Unifacial utilisation	30°
62	Tula adze slug with adhering resin	2.1	.6	.3	Step fractured retouch	56°
63	Utilised flake	2.5	1.9	.4	Bifacial utilisation Bifacial utilisation	52° 41°
64	Utilised flake	2.1	1.1	.2	Bifacial utilisation	32°
65	Utilised flake	2.0	1.7	.2	Bifacial utilisation	35°
66	Tula adze slug with adhering resin	1.5	.6	.3	Step fractured retouch	56°
67	Utilised flake	2.5	2.1	.4	Bifacial utilisation Bifacial utilisation Unifacial utilisation	45° 52° 69°
68	Unused fragment	1.9	1.3	.5		
69	Utilised flake	1.9	1.6	.4	Unifacial utilisation	42°
70	Utilised flake	3.0	2.1	.6	Bifacial utilisation Unifacial utilisation	36° 62°
71	Utilised flake	2.6	1.2	.4	Unifacial utilisation	54°
72	Utilised flake	2.7	1.5	.3	Bifacial utilisation Bifacial utilisation	30° 28°

73	Utilised flake with resin adhering	3.1	1.4	.5	Bifacial utilisation	45°
74	Utilised flake.	2.1	2.1	.5	Unifacial utilisation	50°
75	Utilised flake	1.8	1.1	.3	Unifacial utilisation	35°
76	Utilised flake	1.7	1.0	.3	Bifacial utilisation	32°
77	Utilised flake	2.9	2.8	.9	Bifacial utilisation	50°
					Bifacial utilisation	50°
78	Utilised flake	2.5	1.9	.7	Bifacial utilisation	15°
79	Utilised flake	2.5	2.1	.6	Bifacial utilisation	32°
80	Utilised flake	2.0	1.7	.4	Bifacial utilisation	39°
					Unifacial utilisation	45°
81	Utilised blade	4.3	1.5	.8	Unifacial utilisation	61°
					Bifacial utilisation	42°
82	Utilised flake	2.3	2.1	.8	Bifacial utilisation	65°
					Bifacial utilisation	25°
83	Utilised flake	2.7	1.9	.2	Bifacial utilisation	30°
					Bifacial utilisation	28°
84	Utilised flake	1.6	1.6	.2	Bifacial utilisation	36°
					Bifacial utilisation	42°
85	Utilised flake	2.9	1.9	.7	Bifacial utilisation	32°
86	Utilised flake	3.4	2.3	1.3	Unifacial utilisation	32°
87	Utilised flake	2.5	1.6	.6	Unifacial utilisation	30°-57°
88	Unused fragment	2.1	1.4	.2		

## DISCUSSION

### *Ethnographic context*

Mt. Inglis is located within the boundary of the Kanaloo linguistic group which occupied the headwaters of the Comet River, from below Rolleston to the Carnarvon Range (Oates and Oates 1970; Quinnell 1976, p. 14). The demographic history of this population is briefly described by Josephson (1887), who states that around 1860, when Europeans first settled the area, 'the tribe' numbered 500 persons. By 1869 this was reduced to 300 and by April 1879 the numbers had fallen to 200.

More detailed information on Aboriginal groups within the area is provided by Priddle (n.d.), who lived in Rolleston. People camped near Rolleston still went on 'walk-about' and carried out 'tribal' ceremonies until about 1920. During walk-about the Rolleston group went to a series of swamps 32 km to the south. They did not go to Lake Nuga Nuga owned by the Moolayamber group — the Bemburraburra (Goddard 1940/41, p. 368), nor did they go to Fifteen Mile Swamp on 'Consuelo' Station owned by the 'Carnarvon tribe' (Priddle n.d., p. 6-7). On this evidence, it is possible to sketch in the territorial boundaries of local, land-owning Aboriginal groups, or patriclans. Mt. Inglis

occurs within, or immediately adjacent to the territory of the group which utilised Carnarvon Gorge — possibly the Goon-garee (Winterbotham 1958, p. 219).

Ethnographic details on the material culture, social organisation and ceremonies of Aborigines in the upper Comet region are sparse (see Josephson 1887, p. 96-7; Winterbotham 1958). However, the range of material culture in general use throughout the Central Queensland Highlands can be partially reconstructed by synthesizing several sources of information (see Morwood 1979, p.49-80). These sources include the reports and collections of early observers (e.g. Ahern 1887; Landsborough 1862; Mitchell 1848) and the work of salvage ethnographers (e.g. Curr 1887; Donovan 1976; Howitt 1904; Kelly 1935). The recorded material culture included hand-thrown spears, clubs, boomerangs, softwood shields, axes, bags, baskets, containers, hunting and fishing nets, bone and stone tools, bark paintings, bullroarers, message sticks, bone points, pubic aprons, possum skin rugs, necklaces, pendants, head-dresses, bracelets, burial cylinders, huts, burial platforms and wells. In common with other areas of Australia, the majority of observations and collections are biased towards the hunting and fighting

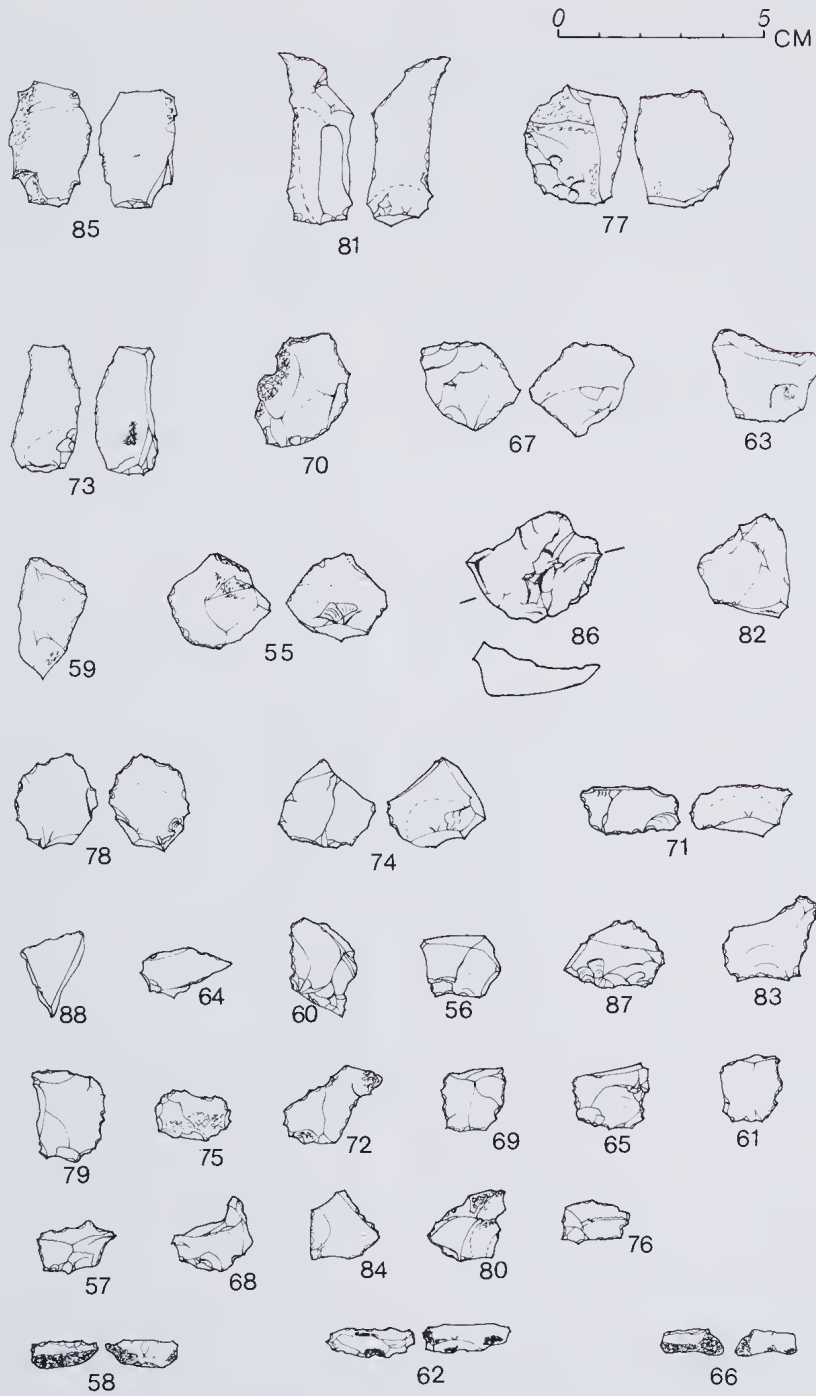


FIGURE 2. Thirty-four opaline chert artefacts found in the possum skin bag (S181/18) and described in Table 1.

implements of men (see McBryde 1978, p. 185). The list can be extended by including surviving field evidence (e.g. dams, stone arrangements, scarred trees, stone tool scatters), but this field evidence is usually biased towards the larger and less perishable elements of the culture, and often comprises the by-products rather than the end-products of manufacturing activities. Stenciled objects in the numerous rock art sites of the Central Highlands provide further evidence of Aboriginal material (e.g. Beaton and Walsh 1977). However, stencil art also tends to be biased towards men's equipment (Morwood 1979, p. 347). The range of goods recovered from Mt. Inglis and other rockshelter caches provides a complementary perspective to the more traditional sources of evidence on the material culture of this region.

#### *Stone tools*

There are no ethnographic observations of stone tool use in the region, but the Mt. Inglis assemblage compares well with the most recent assemblages recovered from archaeological excavations (e.g. Beaton 1977; Morwood 1979; Mulvaney and Joyce 1965). Most notably, blade technology is evident although the majority of tools are amorphous flakes. The last 2000 years of Central Highland stone tool use are characterised by an increase in the frequency of tula adze slugs (Morwood 1979, p. 227), and these are also well represented in the Mt. Inglis collection (S181/58, 62, 66). Similarly, juan knives are distinctive implements occurring only in the most recent industries of the area — the oldest specimen recovered is less than 600 years in age (Mulvaney and Joyce 1965, p. 192).

The principal difference between Mt. Inglis stone artefacts and excavated assemblages in the area, are the high proportion with retouch or use-wear, the small size of the specimens in the possum skin bag (S181/18), and the preservation of hafting medium on the tula adze slugs and the juan knife. Other hafted juan knives are known (e.g. Tindale 1957, p. 28; Mulvaney and Joyce 1965, p. 190), but the Mt. Inglis specimen (S181/1) appears to be the largest specimen yet recorded, as well as the only hafted example remaining in an Australian collection.

The function of the amorphous quartz pebble (S181/51) is uncertain, although similar pebbles have been found in other caches. For instance, the Keegan collection includes several quartz and quartzite pebbles. All have clear indications of percussive use, and several have vegetable mastic adhering. The cultural context of the Mt. Inglis

example and three recorded from a shelter in Moolayamber Gorge (Queensland Museum Reg. QE 3171), would suggest that some specimens were also of ceremonial use. Spencer (1922, p. 105) described one such ceremonial stone collected from the adjacent Springsure area. This was carried about wrapped in possum skin and was not allowed to be seen by women or uninitiated men. Ethnographic observations throughout Queensland also state that quartz pebbles were often used as 'magic stones' for a variety of purposes, including the healing of the sick (e.g. Hamlyn-Harris 1915, p. 6).

Both the small grindstone (S181/2) and the quartzite pebble (S181/3) have adhering red ochre, testifying to their use in the preparation of pigment for art or decoration. This conclusion is supported by their association in the cache with red, yellow and white pigment.

#### *Containers*

Bags, baskets, etc. are poorly represented in Australian museum collections, and the Mt. Inglis examples add considerably to the range previously described for the region. All of the woven material is of 2-ply string. Occasionally, 3-ply is found in Central Highland caches but is rare (Peter Keegan, pers. comm.). The dilly-bags (S181/16,29,34) are all manufactured from plant fibre, most probably from the kurrajong (*Brachychiton populneum*) or from reeds, as recorded ethnographically (Donovan 1976, p. 112; Josephson 1887, p. 96; MacGlashan 1887, p. 19; Sheridan and Bay 1887, p. 252). Both the knotted netting and the loop and single twist (see Davidson 1933, p. 258) were used in the manufacture of the bags. The same techniques were employed for a range of woven items in this region including the Mt. Inglis head-net (knotted netting), the armband (loop and single twist) and a hunting net (knotted netting) recovered from a cave near Springsure and now in the Queensland Museum collections (QE 3167).

The only previous reference to the use of skin containers is by Donovan (1976, p. 112) who states that bags for carrying infants on the upper Nogoa River were made from kangaroo skin rubbed with wood ash. Each end was tied with sinew or fibre and a handle attached. The skin wallets and wrappers from Mt. Inglis (S181/5,18,19,23,50) are not unique however, as similar items are known from other caches. For instance, the Keegan collection includes an inverted, possum skin bag very similar to the Mt. Inglis example (S181/18). It has the leg openings closed by sinews. The mouth of this bag has a

'stopper' comprising a tassel of emu feathers, and it contains about a dozen stone flakes of varying materials, some of which have adhering resin. Containers made from the belly section of a goanna skin are also known, one end being finely stitched up and the other fitted with a string handle (Peter Keegan, pers. comm.).

The use of bark for manufacturing shallow dishes, buckets and cylindrical burial cylinders is ethnographically described (e.g. Josephson 1887, p. 96; Lethbridge 1885), so the use of this material for 'wallets' (S181/38) is not surprising. Skin and bark containers are not specifically mentioned by early observers, but the Mt. Inglis examples are very similar in type and content to those reported elsewhere. In Central Australia, for instance, Spencer and Gillen (1938, p. 611) described examples made from skin, or from small slabs of bark tied round with string. These contained emu feathers, tendon, stone tools, lumps of ochre, pendants, nose-bones, armllets, necklets and charms.

The function of the emu feather mass (S181/5,8,9,30) is uncertain. It is clearly not a kadaitcha shoe as described by Porter (1961, p. 50) in the Aramac region, but may have functioned to protect and conceal the length of bone and other objects contained within it (cf. Spencer 1922, p. 107, 120). The latter are very similar in appearance to several objects found in the Moolayamber cache (QE3171), as well as to the Mandu-kuya amulets described by Roth (1903, p. 37) for N.W. Queensland.

#### *Adornments*

Several of the cached adornments have specific ethnographic references. Necklaces of stong grass or reed stems cut into lengths (cf. S181/12,25), were said to have been common in the region (e.g. Sheridan and Bay 1887, p. 252). Decorative loops or reed beads also occur on one of the string bags held in the Keegan collection.

Ochre and kaolinite (S181/4,5,18,50) were used for decoration of the body, implements and rockshelter walls (e.g. Josephson 1887, p. 96-7). In fact, the practice of coating implements with ochre may be one factor in the excellent preservation of cached organic items in this region. Under normal conditions such material would be subject to attack by insects, fungi, bacteria and other micro-organisms and would deteriorate rapidly. The fact that the Mt. Inglis cache was saturated with red ochre suggested that the ochre could have played a role in preservation. X-ray fluorescence spectroscopy was undertaken on a sample of the cached ochre

by Dr John Kleeman (Geology Dept., U.N.E.). This demonstrated the presence of significant concentrations of copper, zinc and lead, as well as traces of mercury. The results are detailed in Appendix 1. Such heavy metal ions are bio-toxins and are active constituents in many insecticides and fungicides (Mr Peter Gregg, Microbiology Dept., U.N.E. pers. comm.; A/Prof John Brown, Botany Dept., U.N.E. pers. comm.). In the concentrations present they could have inhibited, if not prevented, biological damage to organic material.

The feathers of the emu, white cockatoo and other birds were used for personal adornment. In 1847, for instance, Mitchell (1848, p. 160) saw Aborigines coloured with ochre, and with white cockatoo feathers in their hair and beards. The use of feathered 'pins' as found in the roll of budgeroo bark (S181/58) was not recorded for the Central Highlands, although similar examples also occur in the Keegan collection. Roth (1897, p. 108) describes their use in North West Queensland thus —

Feather-tufts or "aigrettes" are formed with various birds feathers tied on a small sprig, which is stuck indiscriminately here and there into the hair: among birds so utilised are the emu, eagle-hawk, pelican, turkey, crow, etc. These feather-tufts are very generally used in times of rejoicing, at corroboree: they may sometimes be stuck into the waist-belt either at its side or back, or may be fixed under the armllets.

Given this documented association between the use of feather-tufts, armllets and belts, it is significant that all of these items also occurred in the Mt. Inglis cache.

The hair net (S181/32), armllet (S181/32), and belt (S181/44), are identified on the basis of their similarity to those described by Roth (1897, p. 109) in northwest Queensland, as well as on general characteristics and size: their use was not recorded in the Central Highlands. Roth states that the hair-net was a sort of netted cap used to prevent the hair dangling in the eyes. It had a circular ring at the top from which the body of the net was woven from flax fibre string, then coated thickly with red ochre grease. When manufactured by men, the body was woven using the simple loop weave. Another type was made by the women using the knotted netting technique, as used for the Mt. Inglis example.

Many different items were used as pendants in the Central Highlands, including shells, eagle-claws, and even 'a copy of last year's Nautical

Almanac' (Middleton and Noble 1887, p. 90; Mitchell 1848, p. 358). The use of a dried, compressed macropod cloaca as a pendant (S181/24), however, was never noted in this region or elsewhere.

The bone point (S181/20) and bird-bone tube (S181/21) contained in the skin pouch, can be matched both in the ethnographic and archaeological records. Beaton (1977, p. 122) found bone points during excavations at Cathedral Cave in Carnarvon Gorge, and suggested that they were utilitarian items used for piercing skins. Porter (1961, p. 50) described the ceremonial use of bone points near Aramac in Central Queensland for inducing sickness and death. He states that the ceremonial user wore appropriate make-up as well as kadaitcha shoes fashioned from emu feathers and held together with gum and dried blood (cf. Roth 1897, p. 152).

A decorative function is also possible, as it is known that Central Highland initiation ceremonies included piercing of the nasal septum of the novices (e.g. Josephson 1887, p. 97; Looker, et al. 1887, p. 273). The Mt. Inglis bone artefacts are indeed very similar to the nose-pins described by Roth (1897, p. 110) in northwest and Petrie (1904, p. 20) in southeast Queensland. These could be a sharp pointed bone of a turkey, pelican, kangaroo or emu. Other objects such as grass or reeds could also be used.

The cultural context of many cached examples suggests a decorative or ceremonial role. For instance, one bone point was illegally removed from the Goat Rock site on the upper Warrego River where it was associated with a bark, burial cylinder (Fred Cameron, pers. comm.). Another was found with 3 human skeletons and ceremonial items in Moolayamber Gorge (QE3171). The fact that the Mt. Inglis bone point and tube occurred in a pouch, with a presumed emu feather head-dress, strongly suggests that they were of decorative function.

#### *The function of Central Highlands caches*

Central Highland caches add significantly to the range of Aboriginal material culture known from the region, but just as important is the evidence that they provide for economic and social/ceremonial practices. Two types of caching behaviour were ethnographically described in the region —

- 1) The temporary storage of useful, valued items.
- 2) The permanent disposal of burial cylinders.

Examples of temporary storage include the hanging of large, hunting nets in trees or on platforms (Donovan 1976, p. 121; Landsborough 1862, p. 101; Mitchell 1848, p. 303, 367). While exploring the upper Maranoa River, Mitchell also found a club and a shield stored on a platform (British Museum of Mankind Reg. 48/2-2/1 and 48/2-2/2). Two hardwood clubs and a hunting net (QE 3617-9), found in a shelter on the Staircase Range (Springsure area), may have been deposited in this way. Elsewhere, the practice of leaving grindstones as 'appliances' at campsites where they were re-used, has been described (e.g. Gould 1977, p. 173; Peterson 1968, p. 568). Grindstones have been found on the floors of many Central Highland rockshelters where they appear to have been deliberately left as 'appliances' (e.g. the Art Gallery, Cathedral Cave). The disposition of functional ground implements (axes, mullers) recovered in archaeological excavations, suggests that many were originally placed against shelter walls for later retrieval. In fact, caching of implements appears to have been a major depositional mechanism for ground stone artefacts in shelters (Morwood 1979, p. 219-20). Other items found cached near occupation sites include stone knives, cores and wooden implements (pers. obs.; G. Walsh, pers. comm.). There are also widespread reports from other areas, of the caching of sacred items which were periodically removed for ceremonial use (e.g. Spencer and Gillen 1912, p. 208). Archaeological excavations have shown that the (presumed) temporary caching of implements has a long history — one huge silcrete core positioned against the rear wall of Native Well 1 is approximately 6000 years old (Morwood 1979, p. 203).

The permanent caching of burial cylinders was also described by early European observers. Depending on the status of the deceased several different means of disposing of the dead were used in the Central Highlands including cremation (Looker, et al. 1887, p. 273) and burial (Lethbridge 1885). Sometimes final disposal of the remains was delayed for considerable periods (two or three years), during which time they were carried tightly bound up in a sheet of bark (see Robins and Walsh 1979). The common method for finally disposing of such burial cylinders was to drop them into a pipe of a hollow tree (Muirhead and Lowe 1887, p. 27; Looker, et al. 1887, p. 273). However, the fact that many burial cylinders have been found cached in Highland shelters and crevices, suggests that this was an

alternate means (e.g. Gaukrodger 1924; Goddard 1940/41).

It is significant that many caches of material culture have been found in direct association with human remains. The earliest report of this association was by A.S. MacLellan (1901), who wrote of Aboriginal art and burials at 'the Tombs' rockshelter on the upper Maranoa River

—  
 Many a skeleton I saw in the caves there, and hand and foot imprints and other impressions on the walls and roofs of the caves; and fishing nets made out of fibre or bark. These caves served as a vault for this wild race.

More recent finds include a sewn marsupial skin blanket, a bone point, and "a witch-doctor's skin-bag" associated with a painted burial cylinder at Goat Rock, on the upper Warrego River (QE 6422; Morwood 1979). Another cache found in Moolayamber Gorge comprised a bone point, three amorphous quartz pebbles (with percussion marks and adhering ochre), nine amulets tightly wrapped in ochred possum-fur string, and a small steel blade. This material was found in association with 3 human skeletons and it is now in the collections of the Queensland Museum (QE 3171). The mortuary context of these caches suggest that they were unlikely to be merely temporary storage of valued items, but were intended as 'grave goods'. Looker, et al. (1887, p. 273) reports that when deceased persons were cremated, their belongings were burnt also, so similar principles of disposal may have applied for other burial practices. However, the 'burials' associated with mortuary caches are often of children, who were too young to have used the material in life (Peter Keegan, pers. comm.). Obviously mortuary practices in the Central Highlands were far more complex and variable than those ethnographically observed. The cultural context (rock art, occupation deposits), content of caches, and age structure of associated human remains could provide valuable evidence for these undocumented activities if properly researched.

Unfortunately, the potential of this source of cultural data has never been realised as most burials and caches of material culture were, and continue to be, desecrated and dispersed without proper study. Research and management priorities for this region must include detailed recording of *in situ* cached material, plus documentation and description of finds already in private and public collections. Some of the ethical

problems in dealing with mortuary evidence have already been discussed by Robins and Walsh (1979).

### CONCLUSIONS

There is no evidence that the Mt. Inglis cache was ever associated with human remains. This collection of ceremonial/decorative items is, therefore, unlikely to have been a permanent, mortuary cache, but was probably hidden for later re-use.

The age of the material is unknown but such 'de facto' refuse (see Schiffer 1973, p. 60) most probably relates to the terminal phase of Aboriginal occupation. On the evidence of Priddle (n.d., p. 34), elements of traditional life in this region continued until 1920, and this provides the most recent possible date for the material. A similar cache from Moolayamber Gorge contained a metal knife with a resin haft, indicating a post-European contact date — i.e. later than 1840 for this region. The Mt. Inglis material can, therefore, be compared and contrasted with ethnographic observations of the contact period. Clearly this material provides evidence for a range of material culture and activities, many of which were never documented.

Such cached material also provides a timely reminder to researchers. Most of the evidence for 'recent' Aboriginal culture in the Central Highlands is based on superficial and biased ethnographic accounts and collections. There is therefore, a tendency to equate the simplicity of surviving evidence with a simplicity of life-style and material culture (cf. White 1977). It is a sobering thought that for a minimum of 19,000 years (see Mulvaney and Joyce 1965), successful Aboriginal occupation of the Highlands depended on a finely-honed economic and ideological adaptation. This was based on non-material, esoteric knowledge about a wide range of resources, yet both the ideological and organic components of Aboriginal culture are beyond the usual scope of archaeological investigation.

### ACKNOWLEDGMENTS

The Mt. Inglis material was removed and researched under the auspices of the Archaeology Branch, D.A.I.A. I wish to thank Kate Sutcliffe and Jeff Pratt for organising logistic support. Richard Robins and Michael Quinnell (Queensland Museum) and Peter Keegan (Roma resident) gave considerable assistance while the following people also provided expertise on various aspects of the work — Dr John Kleeman

(X-Ray fluorescence spectroscopy), A/Professor John Brown (biocides), Dr Hans Brunner (hair identification), Dr Michael Archer and Steve Van Dyke (faunal identification), Dr Neville Stevens (geological advice), Kathy Morwood (draughting), Alan Easton (photography) and Wendy Chappell (typing).

Appendix 1 — Results of X-ray fluorescence spectroscopy of red ochre.

Dr John Kleeman, Geology Dept., U.N.E.

Item S181/50 of the Mt. Inglis cache contained 1045 grams of finely powdered, red ochre. Three grams of this was removed and prepared as a pressed sample mount. The basis of the technique used to test for heavy metal ions is fully described in Norrish and Chappel (1967). The following results were obtained —

Cu	45 ± 4 ppm
Zn	79 ± 6 ppm
Pb	66 ± 5 ppm
Hg	1-3 ppm (semi-quantitative)
As	not detected at K <sub>α</sub> or K <sub>β</sub> location, say less than 20 ppm
Cd	not detected at K <sub>α</sub> location, say less than 10 ppm

Note that the lower limits of detection for As and Cd are not well known as we do not analyse them routinely. Subject to a (perhaps) imprecise "less than" figure, they are not present in the sample.

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## PLATE I

Context of the Mt. Inglis cache.

Top — general view of Mt. Inglis shelter (central background).

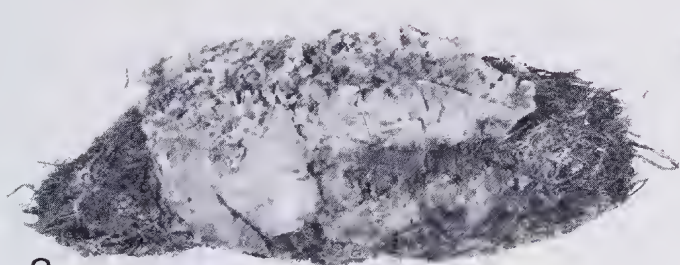
Middle — general view of site during cache removal.

Bottom — cache after removal of three concealing sandstone blocks.



## PLATE 2

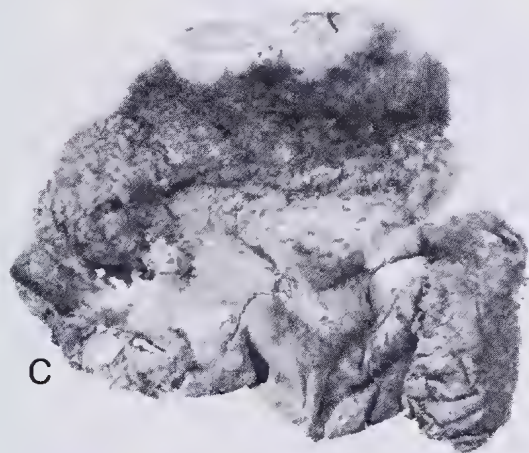
Items from the Mt. Inglis cache. a consolidated emu feather mass and skin wrapping (S181/5); b length of necklace (S181/12); c possum skin bag and ball of yellow ochre (S181/18); d pouch of Whiptail wallaby skin containing bone tube, bone point and emu feather head-dress (S181/19); e possum skin parcel containing emu feathers and fur twine (S181/23); f pendant made from dried cloaca of a large macropod (S181/24); g fur twine armband (S181/32); h bark-fibre head-net (S181/33). Photos courtesy Queensland Museum.



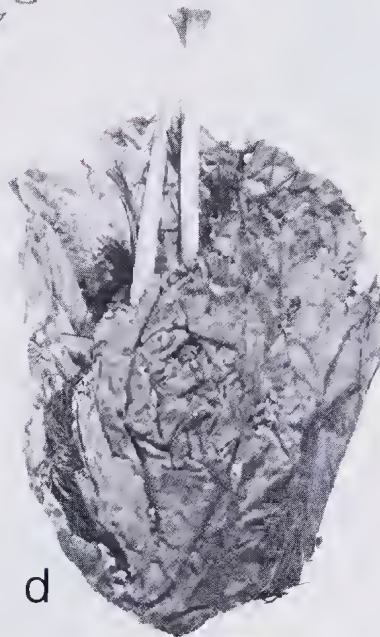
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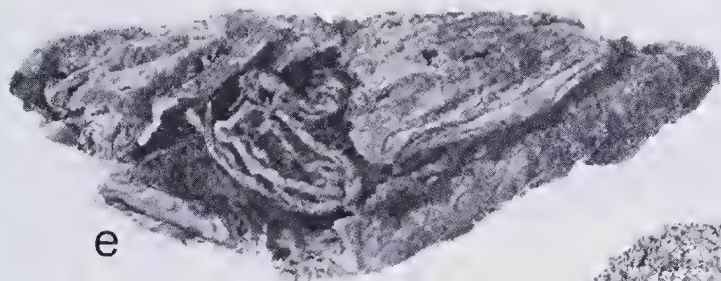
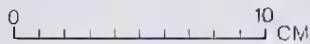
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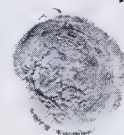
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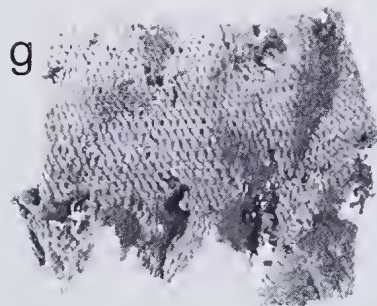
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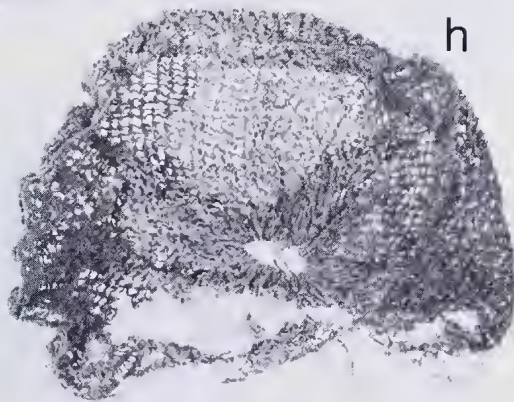
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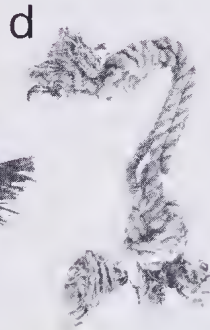
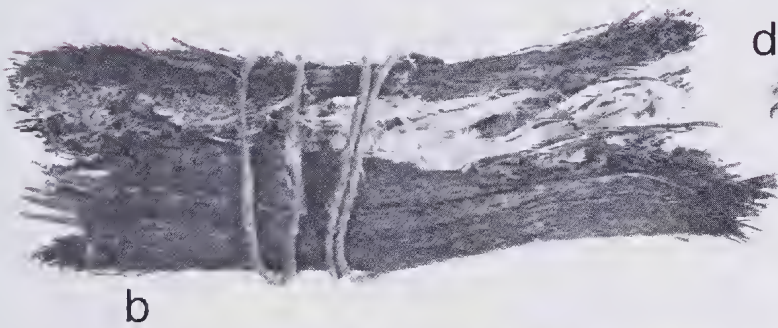
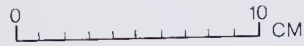
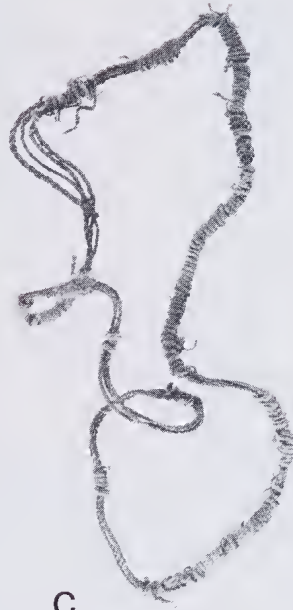
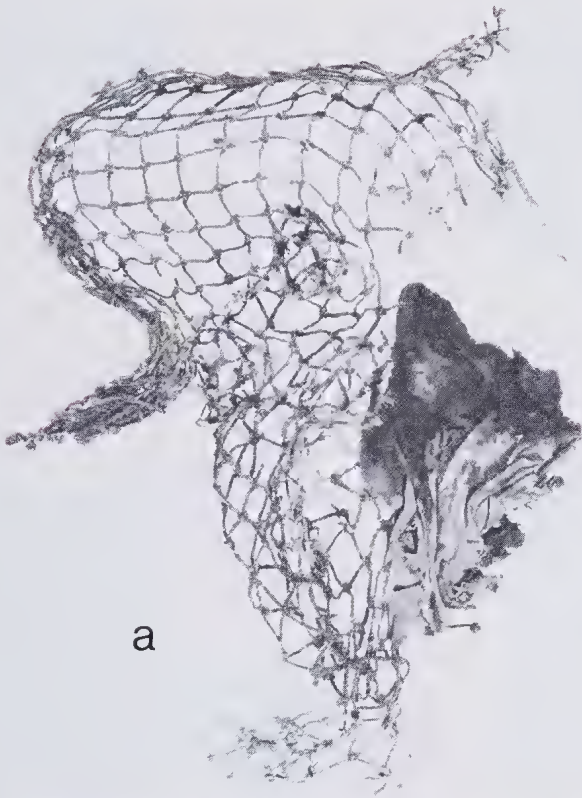
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## PLATE 3

Items from the Mt. Inglis cache. a remains of string bag (S181/34); b roll of budgeroo bark containing feathered 'pins' (S181/38); c waist-belt of fur and bark-fibre twine (S181/44); d tassle of bark-fibre twine (S181/45); e parcel of Rock wallaby skin containing powdered red ochre (S181/50). Photos courtesy Queensland Museum.







## INCISED STONES FROM GLENORMISTON STATION, S.W. QUEENSLAND

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### ABSTRACT

This paper describes an Aboriginal cache of incised stones and an associated myth. The stones, incised designs, and story are then discussed in the light of other evidence for Aboriginal culture in S.W. Queensland.

### INTRODUCTION

Many years ago Charlie Trotman, an elderly Aborigine from Glenormiston Station showed Jim Newman (widely known as 'Old Kookaburra') an Aboriginal cache in a small rockhole near Lake Wonditti, northeast of Glenormiston homestead, S.W. Queensland (Lat. 22°55'S, Long 138°48'E). The cache comprised natural stones which were said by the local Arraringa people to be a stone boomerang, knife, healing stone, and kadaitcha shoe. A solitary mulga tree adjacent to the rockhole was said to have been a spear.

The cache site is close to a tailing yard and over the years the material was removed several times for examination by musterers camped nearby. As a result the stone knife had disappeared and Mr Newman, who is of Kalkadoon descent, feared for the safety of the remaining items. In 1977, he contacted one of the authors (M.G.) and asked for the items to be removed to a place of safe-keeping. They are now in the collection of the Queensland Museum (Reg. No. S362/1-3). This paper is written with the consent and co-operation of Mr Newman.

The associated mythology of the material concerns a Kalkadoon man who had been promised a wife by the local people, and who travelled down to Lake Wonditti for this purpose. Finding nobody there he threw his equipment into the rockhole and vanished. The story is best told as explained by Jim Newman to Kate Sutcliffe (Archaeology Branch, D.A.I.A.) during a taped interview.

'A man had been around here cooking and got friendly with this dark old fella and he tell me a story then. The black fella call it religion. You see it is a religion to them. He showed me these things — stone boomerangs, stone knife,

what they cut the kidneys out with, and a healing stone, what they heal the wound up with. You got to put it in the fire like a soldering iron. You put the stone in the fire then you put it on the wound and heal it up and its as good as new again.

So I want to get to the bottom, to get the full story how he got there to leave no feathers there. Well he said he come across from here between Cloncurry and the Georgina. According to this old fella telling the story, telling it to me, he had to go and pick up his little wife what the black fella gave him in black fella law. He had to go and get his wife. When he go there, there was no one there at this one little lake-waterhole. It's a lovely big lake fresh water, but it was milky, the colour was milky.

So, I'm baking bread one afternoon and this old fella said to me, "I'll show you devil directly". I wasn't interested about the devil at all, I went about cooking my bread. So at last I gave up.

Not very far away from where our camp was, he had a little shallow cave with all these stones in it — the boomerang, the kadaitcha shoe, like these T..... It was all red stone.

Well I said, "How he get there then?" He couldn't find this girl, nobody there, tribe's gone. So, well he pulls his boots off. Threw them into this cave — stone knife, and the boomerang and this healing stone. In they go. He stuck his spear in the ground alongside the cave. And he told me that from the spear this little mulga tree grow. And there's no mulga around the placc within 40 mile around in the area. All the rest of the trees are whitewood, bloodwood, coolibah, gum.

And I said "What happened to him then?", I said. Well, he said he just went like this

“choo!”. He said, he went straight up into the cloud. Well I said “He must be still up there then. How could he disappear into the cloud, a Kalkadoon black fella and leave all his gear behind.” He said “choo!” like somebody give him a bump and away he went.

Well, that’s the end of that old story. It was handed down to one another. They handed it down to me and now I’m giving it to you on tape’.

#### DESCRIPTION

The Glenormiston cache comprised three limestone fragments of unusual shape. Each has a natural surface staining/patina of red colouration. Almost certainly the material is derived from an exposure of Georgina limestone which outcrops immediately south of Glenormiston Station (Dr. Neville Stevens; pers. comm.).

The ‘*boomerang*’ is an elongate, arc-shaped fragment measuring 48.0 cm in length, 11.0 cm in width and 4.2 cm in thickness. At one end sinuous lines, a circle, and a bird track have been incised to a depth of approximately 0.2 mm (Fig. 1a). The incised motifs are of the same colour as the unmodified limestone surface.

The ‘*kadaitcha shoe*’ is a weathered fragment 23.5 cm in length, 11.0 cm in width and 4.9 cm in thickness. Fine bedding lines 2 mm apart occur at right angles to the long axis, while the upper surface has an irregular topography of ridges and grooves formed by solution grooving. A pattern of shallowly incised concentric circles and connecting lines occurs on the upper surface (Fig. 1b). The lower surface is slightly convex in cross-section and bears a finely incised figure of an Aboriginal warrior with shield, spear, spear-thrower, head-dress, and body decoration (Fig. 1c). All of the incised designs on the fragment are shallow and approximately 0.1 mm in depth and thickness. The incised designs are similar in colouration to the remainder of the fragment, and accurate discernment requires oblique lighting. It is apparent that the incised designs are of some antiquity as more recent scratches of similar depth are white in colour.

The ‘*healing stone*’ is water-rolled and roughly spherical in shape. It has a maximum diameter of 6.9 cm and exhibits bruising and patina loss in one area. However, the white colouration of this suggests that it is probably modern damage.

#### DISCUSSION

McCarthy (1976, p. 66) notes that Aboriginal incised stones have been found in New South Wales and Queensland ‘but they are very rare’. The Glenormiston examples are significant not only because such artefacts are uncommon, but also because the associated mythology is known. ‘Old Kookaburra’ (pers. comm.) states that he knows of a similar cache located between Glenormiston and Tobbomoree (N.T.) Stations, so the find is not unique. For example, Stubbs (1974, p. 86) illustrates a fine-grained, igneous rock with an incised, linear pattern which was found on Glenormiston Station. An incised pebble was also recovered from a rock hollow at a rock engraving site near Mt. Isa (pers. knowledge). Designs on this pebble include a grid, a dot series, a concentric circle, and a 5-tiered chevron (see Armstrong n.d., p. 58). Unfortunately, the ceremonial context and function of such items is unknown.

The incised motifs are of particular interest as they probably relate to the associated mythology. Those on the stone ‘boomerang’ and the upper surface of the ‘kadaitcha shoe’ can be closely matched in motif emphasis and composition with designs found on other items of material culture from the area — e.g. boomerangs, *tjurunga*. Kelly (1968, p. 565) for instance, describes concentric circles and a sinuous line incised on a *tjurunga* of an elder of the Mulligan river *woma* snake totem. Circles, concentric circles, spirals, sinuous lines, and bird tracks are also widely used in the numerous rock art assemblages of western Queensland (Elkin 1949/50; Morwood 1979). Typically, there is a high proportion of non-figurative designs and many of these are shared with assemblages of central Australian art (cf. Edwards 1965, 1966; Mountford 1960; Mountford and Edwards 1963).

The incised figure on the ‘kadaitcha shoe’ (Fig. 1c) is very different from other figurative motifs known from the area. Normally the figurative component of western Queensland Aboriginal art would fall into Maynard’s ‘Simple Figurative’ category. (Maynard 1976). It is crudely naturalistic, rigid, standardised, and comprises simplified silhouettes of humans and animals. Humans are usually male and depicted from the front with splayed legs and exaggerated penises. Anatomical detail is minimal and the figures lack facial features and body contours.

By contrast the Glenormiston incised figure is depicted in twisted perspective and conveys a

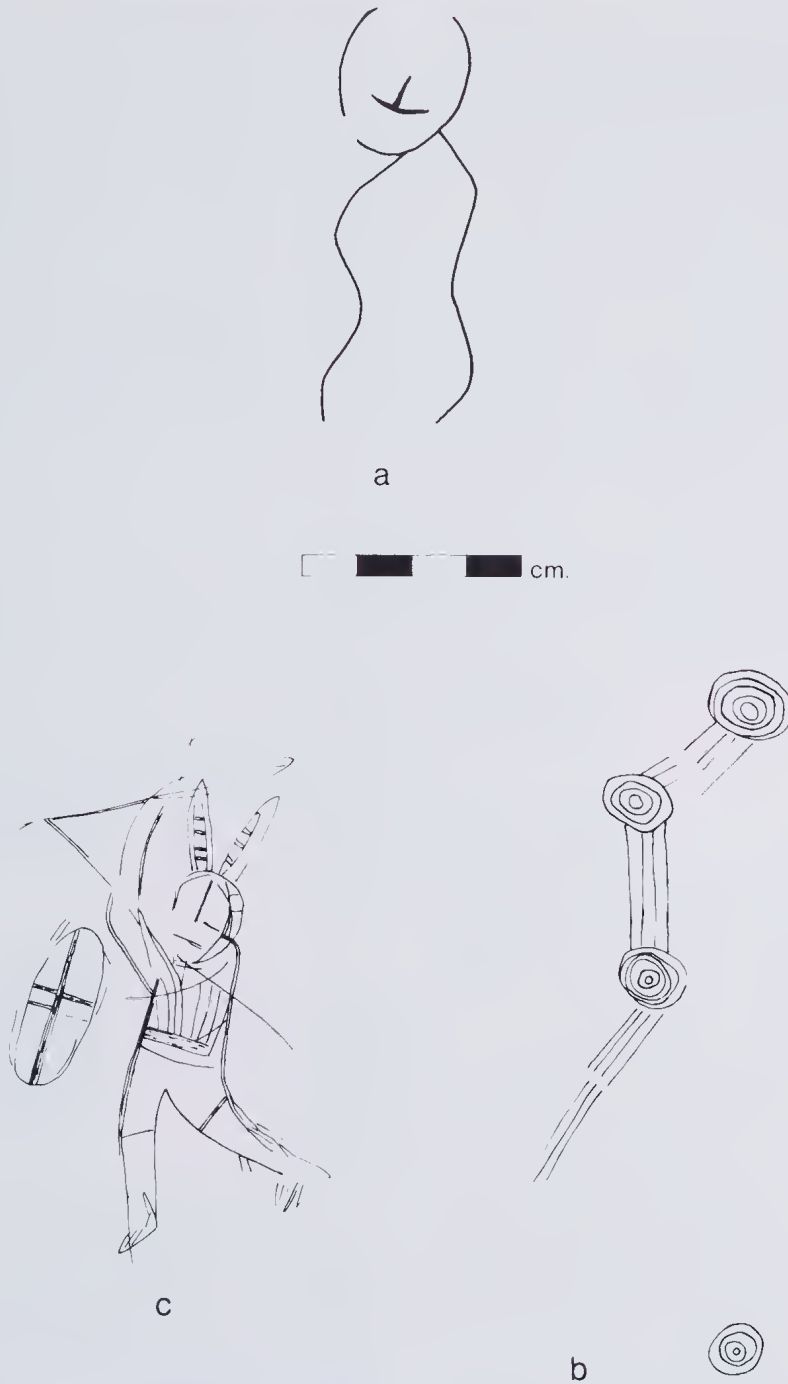


FIGURE 1. Designs incised on items from the Glenormiston cache

- a) Track-line-circle composition on the 'boomerang'.
- b) Line-circle composition on the upper surface of the 'kadaitcha shoe'.
- c) Figure of an Aboriginal warrior on the lower surface of the 'kadaitcha shoe'.

sense of movement. The amount of detail shown and the fact that the principal outlines of the body were carefully incised several times suggests that the task was not undertaken casually but was of some importance. Facial features and body contours are shown, while body decoration and associated weapons are accurately depicted — the figure advances clutching a decorated shield with the right arm poised to propel a spear from a spear-thrower. Although the associated story concerns a Kalkadoon man, it is interesting that the spear-thrower illustrated is of the flattened, leaf-shaped type used on the upper Mulligan and upper Georgina Rivers and along the Toko Range (i.e. local). It is quite different from the linear lath type used by the Kalkadoon in the Boulia, Leichhardt-Selwyn and Cloncurry districts (Roth 1897, pp. 148-9 and Fig. 372). Body decoration includes a head-dress (possibly feathers or ceremonial items), a series of vertical lines down the chest (probably body paintings) a belt (?), and horizontal lines across the thighs. The figure appears to be wearing kadaitcha (?) boots as described in the associated myth. In the attention to detail, style and depiction of movement this incised human figure differs markedly from the basic naturalism characteristic of western Queensland figurative art.

The associated mythology also has several features of interest. It includes a covert explanation for the unexpected absence of the wife. In the story the hero arrives to collect his wife but finds her absent. The colour of Lake Wonditti, is then described as 'milky'. This had seminal connotations and suggests that the wife may have absconded with another man.

The Glenormiston myth also differs in an important detail from other myths recorded in this region. The mythology of the Nappamerrie engraving site on Cooper Creek, provides an interesting contrast, as this appears to be the only rock art site in southwest Queensland for which details of the associated mythology have been recorded. These engravings comprise concentric arcs, upright lines, and circles, and refer to a 'murra murra' myth of the dog cult-totem of the Yanruwanto tribe (Elkin 1949/50).

'The petroglyphs are said to have been made by two "dog women", Widjini and Kilki mura (heroines), who camped at the spot and used to sit under the two big ti-trees nearby. A third slab was similarly and distinctly marked. My informant said it represented *poa*, a grass seed. The concentric arcs represented the falling of

the grass seed on a heap under the grinding stones.' (Elkin 1949/50, p. 141).

The Nappamerrie myth ends with the two heroines travelling up-stream to a spot called Malgera where they can still be seen as white stone. This type of transformation and residence at a specific locality is characteristic of the murra, or 'western' myths found throughout the Australian arid zone (See Allen 1972, p. 112). In northeast South Australia and southwest Queensland, murra myths were associated with patrilineal cult-totems, together with a philosophy of localised totem centres and clans (Elkin 1933, p. 138). Although not stated in Elkin's account, Malgera would certainly have served as a ceremonial centre of the local dog totem (cf. Spencer and Gillen 1912, pp. 96-7). The out-come of the myth associated with the Glenormiston incised stones differs in an important detail: the hero did not remain at a specific locality but left the earth and disappeared into a cloud. This trait is far more characteristic of Aboriginal mythology in SE. Australia with matrilineal, 'social' totemism and non-localised clans (Elkin 1933, p. 138).

To conclude, the Glenormiston material adds significantly to the little information available on the cultural and mythological context of Aboriginal art in southwest Queensland. Aspects of the cache also extend the range of material culture, art and mythology of the region beyond that previously recorded.

#### ACKNOWLEDGMENTS

This paper could not have been written without the considerable assistance of Mr Jim Newman of Mt. Isa. We also wish to thank Dr Neville Stevens (Mineralogy Dept., Queensland University) for his geological identifications, Dr Nicolas Peterson (A.N.U.) for his anthropological advice, and Wendy Chappel for typing.

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## TWO ABORIGINAL SHELTERS IN SOUTHWESTERN QUEENSLAND

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### ABSTRACT

Two dome-shaped shelters made of Gidgee (*Acacia cambagei*) by Aborigines, post-European contact, have been found in southwestern Queensland. Shelter 1 is in good condition. From this the general sequence of construction can be established.

Shelter 2 is similar, but in poor condition. Such shelters are important and should be preserved.

### INTRODUCTION

Few aboriginal shelters can be seen in areas of Queensland where Aborigines no longer make or use such shelters. Despite their ephemeral appearance and the short term usage envisaged by their builders, some shelters can still be found in remote parts of southwestern Queensland where the dry climate and isolation have retarded processes of decay and destruction. Age, frail construction, and general lack of protective measures afforded these structures makes detailed description of them necessary if data about site location, site use, dwelling construction and Aboriginal history is to be recorded and preserved.

Two previously unrecorded shelters were examined by one of us (E.D.) in mid 1982 in the Birdsville area. These are reported here. Further information is held in the Queensland Museum, and the Archaeology Branch Department of Aboriginal and Islanders Advancement.

### THE SITE

The shelters are situated approximately 85 m apart, 100 m up a gentle slope from a seasonal drainage line which, during floods, forms part of the Diamantina River Channels. The general area is treeless, lightly grassed, 'undulating stony downs' (Dawson 1974). Stands of Gidgee (*Acacia cambagei*) grow along the drainage line. The nearest permanent water to the site is at Nerathella Waterhole, 3.5 km to the north. No artefacts were observed near either shelter.

### SHELTER 1 (Pl. 1, Fig. 1)

The shelter lies on a small mound. It was based on four forked interlocking branches (Fig. 1, a, b,

c, d), presumably from the nearby *Acacia cambagei* stand.

The frame of the dome-shaped shelter was formed by burying the stout ends of four forked branches (Fig. 1, a, b, c, d) in the ground. Three of these branches are long, and curved. These (Fig. 1 a, c, d) interlocked. A 'ridge pole' (Fig. 1e) was placed from the remaining structural branch which is short, straight and stout, (Fig. 1b) to rest near the top of the 'dome' formed by the interlocking branches. (Fig. 1 a, c, d). The stoutest of the main supports has a maximum diameter of 16 cm. Diameter of the most slender structural branch is 7 cm. The basic frame was overlaid with curved branches (of diameters varying between 3 cm and 15 cm). The butt ends of these non-structural branches were also buried in the earth. The entrance (Fig. 1) faces east. All branches used were cut by metal axes (Pl. 3c). This shelter is in good condition generally, although some of the small, lighter, lateral 'wall liners' have collapsed and now lie at random round the base. Charcoal fragments indicating the former fire place, lie 4.5 m from the shelter entrance.

### SHELTER 2 (Pl. 2b)

This is very similar to shelter 1, but is less well preserved. Only one main structural support branch and the 'ridge pole' are still upright. All the curved 'wall' timbers have collapsed and lie within 4 m of the standing support branch. A fireplace consisting of charcoal and baked clay was located 8.0 metres from the former entrance.

### DISCUSSION

There are no known station records, published accounts, or archival material on these shelters.

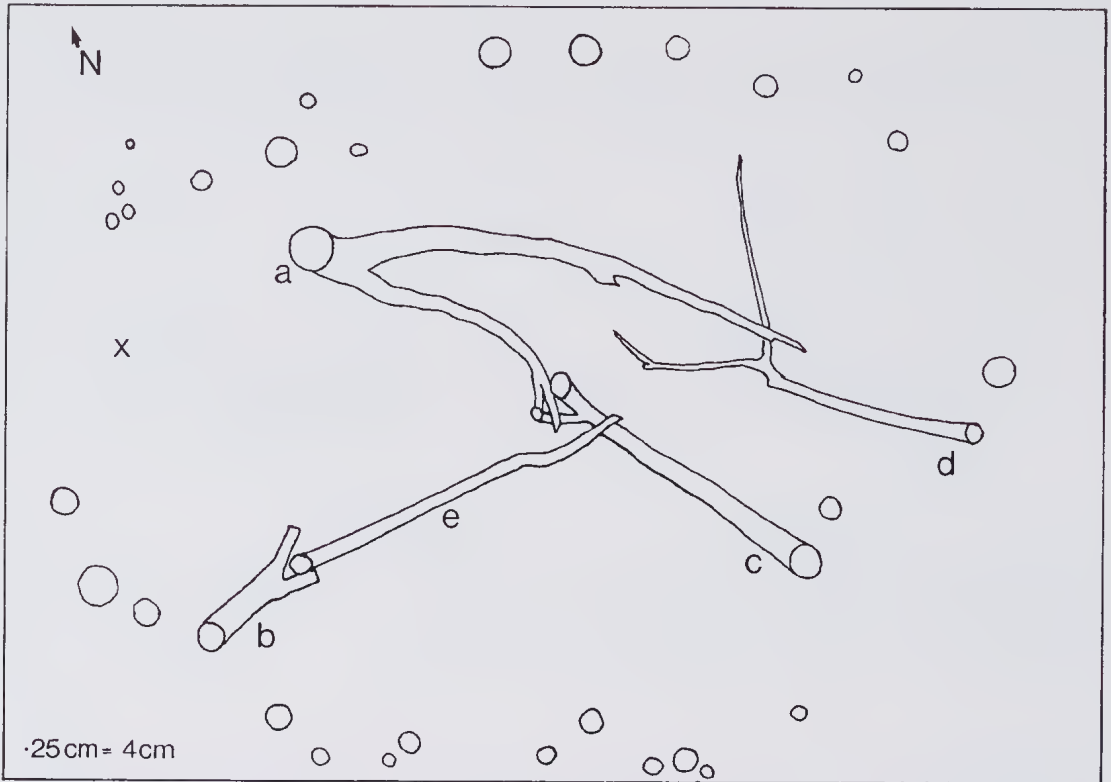


FIGURE 1. Plan of shelter 1 showing position and size of structural and other branches. Main structural branches are drawn in full. Position of embedded ends of other branches are indicated by open circles. Entrance (X).

Metal axe cuts (Pl. 3c) on all timbers indicate that the shelters were constructed after European settlement (i.e. at least since the 1870's). Local opinion suggests the shelters were probably constructed at a temporary camp site by shepherds when floods restricted movement (J. Evans, pers. comm.).

Shelters such as these are important for two reasons: Firstly, they may be seen as historical documents of recent Aboriginal occupation for which few written records exist (e.g. Duncan-Kemp 1933, 1964; Robins 1981). As tangible evocative evidence of Aboriginal occupation they may become a focal point for folk sentiment. Secondly, they offer archaeological evidence for such factors as technology, site location, campsite size and seasonality. Such evidence may assist in the formulation of models of Aboriginal settlement and subsistence. Although this evidence may not be able to be applied in the form of direct analogy to prehistoric archaeological evidence it may help explain anomalies observed in the archaeological record in other areas.

#### ACKNOWLEDGMENTS

Jim Evans of Durrie Station and Genevieve and Ashley Daley of Mt. Leonard provided information on the shelters and on early history of the area. One plant specimen was identified by the Government Botanist. Jeanette Covacevich (Queensland Museum) assisted in preparing the manuscript. Plates were prepared with the assistance of Maureen Kelly and David Bligh (Queensland Museum).

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## PLATE 1

Aboriginal shelters near Birdsville, SE.Q.

- a) Shelter 1 and Shelter 2, 85 m apart in undulating, stony downs.
- b) Shelter 1 showing size and general appearance.



## PLATE 2

General appearance of the shelters.

- a) Shelter 1
- b) Shelter 2



## PLATE 3

## Detail of Shelter 1

- a) Entrance
- b) Structural detail near the entrance. One of the main structural branches (Fig. 1b) and the 'ridge pole' (Fig. 1e) can be seen slightly to the right of centre.
- c) Metal axe cut Gidgee (*Acacia cambagei*) ends.



WILLIAM ALEXANDER MCDOUGALL  
1905-1982



The death occurred on 7th January 1982 of the retired Government Entomologist for Queensland and noted authority on native Muridae, Dr William Alexander McDougall. Mac had served as an Entomologist and Zoologist in the Queensland Department of Primary Industries for 45 years and after his retirement in 1971 was made an Associate of the Queensland Museum in which capacity he continued to work in Australian native rats especially *Melomys*.

Mac's zoological career commenced in 1926 when he was appointed to the Bureau of Sugar Stations at that time a branch of the Department of Agriculture and Stock (now Primary Industries). He trained as an entomologist under Professor Goddard in the Zoology Department of the University of Queensland and subsequently served at Meringa 1928-32 and Mackay 1932-49. Whilst at Mackay he undertook research on the range of insect problems in sugar cane including major work on wireworms which earned him the degree of MSc in 1934. However, following a period of study on rats at the University of Sydney his main interest became an investigation of the biology, ecology and control of the canefield rat (*Rattus conatus* Gould). For this

work he was awarded the degree of DSc in 1949 and acknowledged as the Australian authority on rodent ecology and control. Some of his early rat studies had also involved collaborative work with medical researchers on the control of Weil's Disease in canefield workers.

In 1949 he transferred from the Sugar Bureau to take charge of the Entomology Section within the Science Branch of the Department. During the next 22 years he was to make totally different but equally important contributions in entomology and zoology. He recruited and guided the work of a group of entomologists and zoologists who were to make agricultural entomology and native fauna research into the vigorous disciplines they are today in Queensland. He exercised a very personal style of leadership and all of his staff were actively encouraged to seek further training with the result that their record for higher degrees and scientific publications was outstanding. It was due in part to the high standards of experimentation he demanded but also to his superb skills as a scientific editor.

Parts of his Departmental duties involved service on interstate committees. He was often controversial but the minutes of these committees carry frequent evidence of the salutary effect of his comment. Most important would have been his contributions Australia-wide as a foundation member of the Committee of Commonwealth and State Entomologists. Within Queensland he was a member of the Agricultural Requirements Board from its inception in 1952. This Board carried the responsibility of regulating the use of pesticides within Queensland and he instituted and followed a rigid ethical code in the approval of insecticides.

Towards the end of his career Mac was able to expand his interest in vertebrate zoology by the formation of a zoology group within Entomology to work on native fauna. This group became the Fauna Branch of the Department of Primary Industries at his retirement and subsequently merged with National Parks to form the independent National Parks and Wildlife Service of Queensland. This provided him personally with the opportunity to develop his original interest in the Muridae, and after retirement he undertook a reorganisation of the Queensland Museum reference collection based on newly available chromosome and skeletal studies by members of his previous staff.

Mac was very much a Queenslander. He was born in Ipswich but raised in Goondiwindi although he returned to Ipswich for his secondary education as a boarder at the Ipswich Grammar



School. He excelled at sport and in his final year was a member of every school sporting team and captain of all but one. Later at the University of Queensland as a student of King's College his sporting prowess was again apparent with the award of the blues for cricket and football. In North Queensland he was similarly successful at inter-city cricket and tennis.

His personal interests were mainly his family, the staff who worked for him and their families, and sport, latterly as a spectator, but he participated in a wide range of community activities. To Mrs McDougall, their daughters and grandchildren we express our appreciation of Mac as a friend and mentor and of his contributions to his chosen discipline.

**N.W. HEATHER.**





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