THE

ENDOCOPRID DUNG BEETLES

OF

SOUTHERN AFRICA

(COLEOPTERA : SCARABAEIDAE)

BY

ADRIAN LOUIS VICTOR DAVIS B.SC. (HONS.)

THESIS PRESENTED TO RHODES UNIVERSITY
GRAHAMSTOWN

FOR THE DEGREE OF

MASTER OF SCIENCE
DECEMBER, 1977.

INDEX

INTRODUCTION

In January 1788, the first English colonists to reach Australia disembarked with a small breeding herd of cattle (Waterhouse 1974). Together with further introductions, this initial nucleus of bovines had, by 1974, grown to 30 million beasts and formed the basis of a profitable meat and dairy industry.

The arrival of cattle in Australia created serious problems owing to the long term persistence of their dung on the surface. An adult cow is capable of producing an average of 12 dung pads per day (Waterhouse 1974), and during a 12 month period the total dung dropped by a single animal will cover an estimated 5% - 10% of an acre (Bornemissza 1960, Waterhouse 1974). This prevents the growth of grass until the pads have been destroyed by termites (Ferrar & Watson 1970), eroded by the elements (Ferrar 1975) or broken down mechanically (Weir 1971, Ferrar 1975). During the rainy season a rank growth of grass, which is shunned by cattle (Bornemissza 1960, Waterhouse 1974), soon surrounds each pad. This additional reduction in available grazing results in a total loss approaching 20% of an acre per animal per year (Waterhouse 1974). The fresh cow pads accumulating undisturbed on the pastures each day provide ideal breeding sites for certain flies (Ferrar 1973). As a result the numbers of the man-pestering bushfly, *Musca vetustissima* Walker, and the accidentally introduced blood sucking buffalo fly of cattle, *Haematobia irritans exigua* (de Meijere), have increased to pest proportions.

Problems of dung persistence are not encountered in Africa and Asia since during warm, wet periods it is swiftly buried by a large dung beetle fauna which comprises about 1800 species in the Aethiopian zoogeographic region. Australia possesses its own indigenous dung beetle

fauna/.....

fauna of about 250 species but these are adapted to utilising the relatively dry, fibrous pellets voided by the indigenous marsupials. The large, compact, wet droppings of the introduced cattle are comparatively unattractive to most native species (Bornemissza 1960, Waterhouse 1974) and are, at best, utilised only partially (Waterhouse 1974). However, recent observations by Australian workers show that a few native *Onthophagus*, e.g. *O. granulatus*, colonise cow pads in large numbers at certain times of the year. (M.M.H. Wallace *in litt.* to Dr. G.F. Bornemissza February 3rd, 1977).

The absence of a dung and associated fly problem in most other parts of the world was first pointed out, in Australia, by Bornemissza (1960). He proposed that the situation could be rectified by the introduction of a dung beetle fauna which had evolved in parallel with eutherian mammals and their droppings.

The use of dung beetles for fly control has a history stretching back to the turn of the century. In Hawaii, unsuccessful attempts at introduction were made in 1906 and 1908, followed by the successful establishment of three species in 1923 (Waterhouse 1974). Subsequent to later introductions, local cattle farmers reported that the abundance of the horn fly, *Haematobia irritans irritans* (L), was much reduced (Waterhouse 1974). Thus, the decision was taken by the Commonwealth Scientific and Industrial Research Organization (CSIRO) to mount a large scale introduction programme for Australia and, in 1970, a research unit was set up at Pretoria, South Africa.

At this station, beetles for introduction were, and are, selected on various criteria. Chief amongst these are distribution with regard to climate, dung preference, volume of dung buried, overall abundance and whether it is possible to breed the species under laboratory conditions. As Australia is, on average, only 300 - 600 m in altitude and southern

Africa ....

Africa consists for the most part of a plateau lying at 900 - 1500 m, increasing attention has been paid to meteorological data to determine zones of climatic similarity in the two continents. Emphasis has been recently extended beyond Africa in the search for beetles adapted to areas receiving winter rainfall which will be suitable for the cooler southern parts of Australia.

As Australia has had a disastrous history of introductions of flora and fauna with many undesirable results, much care has been taken with the introduction of dung beetles. Only those species which are obligatory dung breeders are selected. As these are adapted both morphologically and biologically to utilisation of dung there is little, if any, danger of their becoming pests themselves.

In order to eliminate the possibility of introducing unwanted members of the fauna associated with dung beetles, especially micro-organisms such as the virus, foot and mouth disease, the introduction is accomplished by sending dung free, surface sterilised eggs. This necessitates the breeding of selected species in the laboratory and the extraction of the eggs from their broods; broods being the moulded portions of dung in which the eggs are laid and the larvae develop. The eggs are consigned to Australia in specially designed containers where they are transferred to artificial or donor broods in quarantine. The latter refers to natural broods from which the egg laid by the parent beetle is removed to be replaced by that of the introduced species. After two generations in quarantine the beetles of the third filial generation are removed to a semi-quarantine "clean room" where mass breeding for release is conducted.

During the period 1970 to 1976, 38 species were transported to Australia, of which 18 have been released in the field and 7 recorded as firmly established.

In order ......

In order to achieve the maximum possible dung removal it is proposed to build up species complexes around these initial introductions so that, as far as possible, there will be beetles active and available to colonise pads dropped at any time of the day or year. It was expected that this approach would necessitate the introduction of representatives from each of the three groups designated by Bornemissza (1969) which were separated on the basis of their breeding (nidification) behaviour. These are:-

1) Paracoprids - Dung beetles which bury dung from immediately beneath the site of deposition. The burrows into which the dung is packed may be excavated vertically or at an angle away from the excrement. This allows a large number of beetles to colonise a single dropping. This method of breeding is exhibited by *Onthophagus, Onitis, Copris* and many other genera which comprise about 87,5% of the species found in the Aethiopian zoogeographic region according to Tribe (1976).

2) Telecoprids - Dung beetles which roll, or butt, portions, or modelled balls of dung some distance from the source before burial takes place. This form of breeding is seen in *Gymnopleurus, Scarabaeus, Sisyphus* and related genera which comprise about 12,2% of the Aethiopian species.

3) Endocoprids - Dung beetles which construct their breeding chambers wholly within dung pads lying on the surface at their site of deposition. The present study has shown this definition to be only partially accurate and the endocoprid habit has therefore been redefined in Chapter 4.2. In the Aethiopian region the endocoprid habit (in which brood balls or brood ovoids are actively modelled) is exhibited by only six species, of which five constitute the genus *Oniticellus (sensu stricto)* (Serville) and the sixth belongs to the monotypic genus *Tragiscus* Klug. These six species comprise the remaining 0,3% of the Aethiopian fauna and all occur in southern Africa.

Unlike ....

Unlike paracoprids and telecoprids, which bury dung at depth for feeding or nidification purposes, endocoprids either do not bury dung or only bury small amounts at superficial levels. (Chapter 7).

This research on endocoprids was conducted to study the possibilities of their use in the Australian dung and fly control project (Chapter 7). Prior to this account almost all literature devoted to *Oniticellus (s. str.)* and *Tragiscus* has been purely taxonomic. The only exceptions dealing with biology, have been publications on *Oniticellus cinctus* by Gardner (1929) and Bornemissza (1969).

The major part of this thesis is concerned with laboratory studies on endocoprid biology and field studies on their ecology. In addition the taxonomy, distribution, evolution and some aspects of their natural history are discussed.

All laboratory work was conducted at the CSIRO Dung Beetle Research Unit based in Pretoria (henceforth referred to as the DBRU) whilst the locations of observations and experimental work conducted in the field are specified in the text.

1. TAXONOMY

Before any ecological study may be conducted it is essential that there is complete comprehension of the taxonomy of the organisms under investigation. This chapter reviews the salient points of the classification of the tribe, Oniticellini, with emphasis on the genera *Oniticellus* (*s. str.*) and *Tragiscus*. All of the species of these two genera studied at the DBRU bred in the endocoprid manner.

All members of the tribe were included in the genus *Onthophagus* Latreille until 1825 when Serville erected the genus *Oniticellus* to separate those species possessing:-

1) a small, but usually visible, escutcheon between the the base of the elytra

and 2) antennae of eight segments.

Subsequently various other genera were described and these are listed by Janssens (1953) as *Drepanocerus* Kirby (1828), *Tragiscus* Klug (1855), *Liatongus* Reitter (1893), *Scaptocnemis* Péringuey (1901), *Tiniocellus* Péringuey (1901), *Helictopleurus* d'Orbigny (1915) (Madagascar only), and *Drepanoplatynus* Boucomont (1920). However, after the description of each new genus, various workers (listed by Janssens) continued to place certain of its species within the genus *Oniticellus*, e.g. Drepanocerus cited as *Oniticellus* by Castelnau (1840), and Sharp (1875); *Liatongus* cited as *Oniticellus* by Felsche (1904) and Paulian (1945); *Tiniocellus* cited as *Oniticellus* by Arrow (1908), and Janssens (1939).

Gillet and Boucomont (1927) considered that *Oniticellus* comprised what has since been divided or redivided into five valid genera; *Liatongus*, *Tiniocellus*, *Tragiscus*, *Oniticellus (s. str.)* and *Euoniticellus* Janssens.

The ....

The genus, *Euoniticellus* Janssens, was erected in 1953 and whilst some recent workers consider this a valid decision (e.g. Ferreira 1972), others (e.g. Halffter and Matthews 1966: 255) have continued to incorporate it as a subgenus of *Oniticellus*. However, differences in the biology of each group which have become apparent during this present study, justify their separation at the generic level. Accordingly, they are treated as separate genera in this thesis.

Oniticellus (*s. str.*) now consists only of those species with a smooth and shiny appearance (Janssens 1953), whose prosterna are produced anteriad into a projection between the anterior legs (Janssens 1953, Ferreira 1966) and whose metacoxae are contiguous (Ferreira 1966).

The members of this genus may be divided into three groups on the basis of morphological and biological criteria (Table 1). Members of each group are found in both the Aethiopian and the Oriental zoogeographic regions. Kraatz (1895), whose decision was followed by d'Orbigny (1916) and Paulian (1945), went a step further and split *Oniticellus* (*s. str.*) into two genera but Janssens (1953) maintained that the progressive reduction of the prosternal projection represents an evolutionary trend and that splitting of the genus is not justified. This prosternal projection is large in group 1, smaller in group 2 and almost non-existent in group 3 (Chapter 8). *Tragiscus* represents a fourth group found only in Africa south of the Sahara (Table 1).

Table 1. ....

TABLE 1. Species list of endocoprid dung beetles

Genus	Group	Species	Continent of distribution
Oniticellus (*s.str.*) (Serville)	1.	*O. egregius* Klug 1855	Africa
		**O. rhadamistus* (Fabricius) 1775	Asia
	2.	*O. planatus* Castelnau 1840	Africa
		O. pseudoplanatus* Balthasar 1964	Africa
		O. cinctus (Fabricius) 1775	Asia
	3.	*O. pictus pictus* (Hausman) 1807	Africa
		**O. pictus orientalis* Janssens 1953	Africa
		O. formosus Chevrolat 1830	Africa
		**O. tessellatus* Harold 1879	Asia
Tragiscus Klug	4.	*T. dimidiatus* Klug 1855	Africa

* Probable endocoprid species which have not been bred at the DBRU and for which no biological references are to be found in the literature.

** Considered a synonym of *O. planatus* in this thesis (1.2.)

1.1. Taxonomy of Group 1. (*O. egregius, O. rhadamistus*)

The two members of this group have well defined characteristics. Since the erection of the genus *Oniticellus* by Serville (1825), no taxonomic confusion has arisen over the species but their generic status has been changed several times (Arrow 1931, Paulian 1945, Balthasar 1963).

Size range:- (Length from the tip of the clypeus to the tip of the pygidium with the head fully deflexed) *O. egregius*:- 9,8 - 15,5 mm (29 specimens measured from the DBRU reference collection).

1.2. ....

1.2. Taxonomy of Group 2. *(O. planatus, O. pseudoplanatus. O. cinctus).*

Since 1825 *O. planatus* has twice been ascribed to other genera (Kraatz 1895, d'Orbigny 1916), whilst *O. cinctus* has had a long history of redescription under other names or placement in other genera (Drury 1837, Harold 1869).

Balthasar (1964) described a third species of the group, *O. pseudoplanatus*, which is extremely close to *O. planatus*. The diagnostic features indicated for this species by Balthasar are:-

1) Smaller size than *O. planatus*.
2) Setal brush along the posterior margin of the elytra poorly developed or absent, usually combined with the absence of depressions from which the larger setae of *O. planatus* arise.
3) Absence of setae on the lateral edge of the sternites.

I believe these features to be of doubtful validity and consider that they merely characterise continuous (or perhaps discontinuous) variation with no discrete population boundary. This opinion is justified on the following grounds.

Size range:- From the data given in Table 2 it can be seen that material of the *O. planatus/pseudoplanatus* species complex in the DBRU reference collection covers a continuous range in length from 6,9 mm to 11,5 mm (measurement from the tip of the clypeus to the tip of the pygidium with the head fully deflexed). Balthasar (1964) implies a discontinuous size range in his material by giving the length of *O. pseudoplanatus* as 7 - 10 mm and that of *O.planatus* as 11 - 13 mm. He does not indicate how he measured his specimens but his upper size limit for *O. planatus* (13 mm) probably represents measurements taken with the head extended.

Balthasar (1964) also stated that the ratio of length:width was different in each species although he did not publish his figures. Despite

a size ......

a size range which would indicate the presence of both species in the material used for Table 2, no consistent difference was detected between the ratios of large or small specimens nor between those of the specimens divided into *O. pseudoplanatus* or *O. planatus* on the basis of Balthasar's characters. (Tables 3 and 4).

Figure 1 demonstrates a direct relationship between length (2) and width (2); measurements which are defined in Table 2. The lack of interruption in this size range provides further evidence that the material used for Table 2 represents a single species.

Setal Brushes

The use of setae as a diagnostic character is not to be recommended as these structures are easily worn away (Chapter 3.1.). However, Janssens (1939, 1940) maintains that the value of such characters is not diminished as they may always be seen in intact specimens or, in their absence, the point of their insertion is always visible.

Unlike the conditions reported by Balthasar (1964), setal brushes were recorded throughout the size range indicated in Table 2 although they were present on only few of the smaller specimens (Tables 2 and 5). The more robust setae of the larger specimens probably persist for longer periods. Nevertheless, even the largest beetles frequently lacked setae (Tables 2 and 5). The strongest setae are found at the lateral end of the brush and are often among the last to be broken off. This could lead to the condition Balthasar (1964) describes for some *O. pseudoplanatus*.

In ....

TABLE 2: Morphometric, biological, and locality data for 100 specimens of the *O. planatus/pseudoplanatus* species complex held in the DBRU reference collection.

Length (1) - Length from the tip of the clypeus to the tip of the pygidium with the head fully deflexed.
Width (1) - Width of the elytra immediately posterior to the protuberances found anteriolaterally.

Length (2) - The distance between the anterior and posterior margins of the prothorax measured mid dorsally.
Width (2) - The distance between the lateral posterior angles of the prothorax.

All measurements were made with callipers. Length (1) was used to facilitate comparison with Balthasar's figures (1964). Length (2) was considered more reliable.

TABLE 2:

*Species	Length(1) mm	Width(1) mm	Ratio(1) Length(1) :Width(1)	Length(2) mm	Width(2) mm	Ratio(2) Length(2) :Width(2)	Sex	*Condition of setal brush	*Condition of setal pits	Sternal setae	Locality
ps	6,9	3,6	1:1,91	3,1	4,4	1:0,70	♂	Absent	Absent	Absent	Pilgrim's Rest,E.Tvl.RSA.
pl	7,2	3,9	1:1,84	3,3	4,8	1:0,69	♂	Inc.	Present	Present	Narok (79 kms NW), Kenya.
ps	7,6	4	1:1,9	3,5	4,8	1:0,73	♂	Absent	Absent	Absent	Durban, Natal, RSA.
ps	7,6	4,2	1:1,8	3,5	4,8	1:0,73	♂	Absent	Absent	Absent	Stutterheim, E.CP, RSA.
pl	7,75	4,2	1:1,84	3,5	4,8	1:0,73	♂	Absent	Present	Absent	Machadodorp, E.Tvl. RSA.
ps	7,8	4,2	1:1,85	3,5	4,8	1:0,73	♂	Absent	Absent	Absent	Machadodorp, E.Tvl. RSA.
ps	7,8	4,3	1:1,81	3,5	4,9	1:0,71	♂	Absent	Absent	Absent	Pilgrim's Rest,E.Tvl.RSA.
pl	7,8	4,4	1:1,77	3,7	5,1	1:0,73	♂	Absent	Present	Absent	Ahero (40 kms S) Kenya.
ps	7,9	4,2	1:1,88	3,6	5,2	1:0,69	♂	Absent	Absent	Absent	Ahero (40 kms S) Kenya.
ps	7,9	4,4	1:1,79	3,6	5,1	1:0,71	♂	Absent	Absent	Absent	Ahero (40 kms S) Kenya.
ps	7,9	4,4	1:1,79	3,75	5,1	1:0,74	♂	Absent	Absent	Absent	Piet Retief, SE.Tvl.RSA.
pl	7,9	4,5	1:1,75	3,6	4,8	1:0,75	♂	Absent	Present	Absent	Uitenhage, E.CP. RSA.
pl	8	4,25	1:1,88	3,5	5	1:0,70	♀	Inc.	Absent	Present	Zeerust, W.Tvl. RSA.
pl	8	4,4	1:1,81	3,6	5,1	1:0,71	♀	PL	Present	Present	Uitenhage, E.CP. RSA.
ps	8	4,5	1:1,77	3,4	4,9	1:0,69	♂	Absent	Absent	Absent	Mt. Sheba, E.Tvl. RSA.
ps	8	4,5	1:1,77	3,2	5,1	1:0,63	♂	Absent	Absent	Absent	Narok (79 kms NW) Kenya.
ps	8	4,6	1:1,73	3,75	5	1:0,75	♂	Absent	Absent	Absent	Piet Retief, SE.Tvl. RSA.
ps	8,1	4,4	1:1,84	3,6	5,1	1:0,71	♂	Absent	Absent	Absent	Nairobi N.P., Kenya.
ps	8,1	4,5	1:1,8	3,4	4,9	1:0,69	♂	Absent	Absent	Absent	Sa Da Bandeira, Angola.
ps	8,1	4,3	1:1,88	3,75	5,25	1:0,71	♂	Absent	Absent	Absent	Amsterdam, SE.Tvl. RSA.
pl	8,2	4,5	1:1,82	3,5	5	1:0,70	♂	Inc.	Present	Present	Pretoria, Tvl. RSA.
ps	8,2	4,5	1:1,82	3,5	5,2	1:0,67	♂	Absent	Absent	Absent	Lolgorien, W. Kenya.

* See notes at foot of Table.

TABLE 2 (continued)

*Species	Length(1) mm	Width(1) mm	Ratio(1) Length(1) :Width(1)	Length(2) mm	Width(2) mm	Ratio(2) Length(2) :Width(2)	Sex	*Condition of setal Brush	*Condition of setal pits	Sternal setae	Locality
ps	8,2	4,5	1:1,82	3,9	5,3	1:0,74	♂	PL	Absent	Absent	Masai Mara G.R. Kenya.
pl	8,2	4,5	1:1,82	3,9	5,1	1:0,76	♂	Inc.	Present	Present	Beira, Mocambique.
pl	8,2	4,6	1:1,78	3,6	5,1	1:0,71	♂	Inc.	Absent	Present	Inyazura, Rhodesia.
ps	8,25	4,7	1:1,8	3,9	5,5	1:0,71	♂	Absent	Absent	Absent	Narok (79 kms NW) Kenya.
pl	8,25	4,75	1:1,73	3,75	5,3	1:0,71	♂	PL	Present	Present	Ahero (40 kms S) Kenya.
pl	8,3	4,7	1:1,76	3,6	5,3	1:0,68	♂	PL	Present	Present	Gorongosa N.P., Mocambique.
ps	8,3	4,7	1:1,76	4	5,5	1:0,73	♂	Absent	Absent	Absent	Port Elizabeth, E.CP.RSA.
ps	8,3	4,75	1:1,74	4	5,5	1:0,73	♀	PL	Absent	Absent	Ditinn, Guinea.
ps	8,4	4,5	1:1,86	3,8	5,2	1:0,73	♀	Absent	Absent	Absent	Durban, Natal, RSA.
pl	8,5	4,5	1:1,88	3,9	5,3	1:0,74	♂	Present	(obscured by setae)	Present	-
pl	8,6	4,5	1:1,91	3,6	5,4	1:0,67	♀	Inc.	Absent	Present	George, E.CP, RSA.
pl	8,6	4,8	1:1,79	3,3	5,5	1:0,60	♂	Absent	Present	Absent	Masai Mara G.R., Kenya.
ps	8,6	4,9	1:1,75	3,8	5,1	1:0,75	♀	Absent	Absent	Absent	Ahero (40 kms S) Kenya.
pl	8,7	4,5	1:1,93	3,7	5,3	1:0,70	♀	Absent	Present	Absent	Masai Mara G.R., Kenya.
ps	8,7	4,8	1:1,81	3,75	5,5	1:0,68	♀	PL	Absent	Absent	Masai Mara G.R., Kenya.
pl	8,7	4,8	1:1,81	3,8	5,6	1:0,68	♂	Inc.	Absent	Present	Kyle G.R., Rhodesia.
pl	8,7	4,75	1:1,83	3,9	5,6	1:0,70	♀	Inc.	Present	Present	Amsterdam, SE.Tvl. RSA.
pl	8,75	4,9	1:1,78	3,8	5,6	1:0,68	♂	Absent	Present	Present	Ahero (40 kms S) Kenya.
pl	8,8	4,8	1:1,83	3,9	5,75	1:0,68	♂	Present	Present	Present	Tzaneen, Tvl. RSA.
pl	8,8	5	1:1,76	4,2	6,1	1:0,69	♂	Present	(obscured by setae)	Present	Pafuri, KNP, NE.Tvl. RSA.
ps	8,9	4,6	1:1,93	3,9	5,4	1:0,72	♀	Absent	Absent	Absent	Penhalonga, Rhodesia.
ps	8,9	4,8	1:1,85	3,9	5,5	1:0,71	♂	Absent	Absent	Absent	Mt. Frere, Transkei, RSA.

TABLE 2 (continued)

* Species	Length(1) mm	Width(1) mm	Ratio(1) Length(1) :Width(1)	Length(2) mm	Width(2) mm	Ratio(2) Length(2) :Width(2)	Sex	* Condition of setal brush	* Condition of setal pits	Sternal setae	Locality
pl	8,9	5	1:1,78	3,9	5,5	1:0,71	♂	Inc.	Present	Present	George, E.CP. RSA.
pl	9	4,8	1:1,87	3,8	5,6	1:0,68	♀	Inc.	Present	Absent	Beira, Mocambique.
pl	9	5	1:1,8	3,9	5,6	1:0,70	♂	Absent	Present	Present	Rustenburg, Tvl. RSA.
pl	9	5	1:1,8	4,1	5,8	1:0,71	♂	Absent	Present	Present	East London, E.CP. RSA.
pl	9	5,1	1:1,76	4	5,9	1:0,68	♂	Absent	Present	Present	Ahero (40 kms S) Kenya.
pl	9	5	1:1,8	4	6	1:0,67	♂	PL	Present	Present	Somkele, Natal, RSA.
ps	9	5	1:1,8	4	5,4	1:0,74	♀	Absent	Absent	Absent	Uitenhage, E.CP. RSA.
pl	9,1	5	1:1,82	4,1	5,9	1:0,69	♂	Inc.	Present	Present	Machadodorp, E.Tvl. RSA.
pl	9,1	5,4	1:1,68	4,2	6	1:0,70	♂	Present	(obscured by setae)	Present	Kisumu, Kenya.
ps	9,2	5	1:1,84	4,1	5,5	1:0,75	♀	PL	Absent	Absent	Ditinn, Guinea.
pl	9,25	5	1:1,85	4,2	6	1:0,70	♀	Absent	Present	Absent	Ditinn, Guinea.
pl	9,25	5,25	1:1,76	4,2	5,9	1:0,71	♀	Present	Present	Present	Masai Mara G.R., Kenya.
pl	9,3	5,3	1:1,75	4,1	5,8	1:0,71	♂	Absent	Present	Present	Amsterdam, SE.Tvl. RSA.
pl	9,3	5,4	1:1,72	4	5,7	1:0,70	♂	Inc.	Present	Present	Lundi, Rhodesia.
ps	9,4	4,9	1:1,91	4,1	5,9	1:0,69	♀	PL	Absent	Absent	Thika, Kenya.
pl	9,4	5,3	1:1,77	4,1	5,8	1:0,71	♂	Inc.	Present	Present	Yankari G.R., Nigeria.
pl	9,4	5,4	1:1,74	4,1	6	1:0,68	♀	Absent	Present	Absent	Masai Mara G.R., Kenya.
ps	9,5	5,2	1:1,82	4,2	5,8	1:0,72	♀	Absent	Absent	Absent	Thika, Kenya.
Pl	9,5	5,6	1:1,69	4,2	6,1	1:0,69	♂	Inc.	Present	Present	Pretoria, Tvl. RSA.
pl	9,6	5,2	1:1,84	4	6	1:0,67	♀	Inc.	Present	-	Beira, Mocambique.
pl	9,6	5,4	1:1,77	4,1	6,1	1:0,67	♀	PL	Present	Present	Ditinn, Guinea.
pl	9,7	5,3	1:1,83	4,2	6,1	1:0,69	♀	Absent	Absent	Present	Inyazura, Rhodesia.
pl	9,6	5,3	1:1,84	4,2	6	1:0,70	♀	Inc.	Absent	Present	Peddie, E.CP. RSA.

TABLE 2 (continued)

*Species	Length(1) mm	Width(1) mm	Ratio(1) Length(1) :Width(1)	Length(2) mm	Width(2) mm	Ratio(2) Length(2) :Width(2)	Sex	*Condition of setal brush	*Condition of setal pits	Sternal setae	Locality
ps	9,8	5,4	1:1,81	4,3	6	1:0,72	♀	Absent	Absent	Absent	Stutterheim, E.CP. RSA
pl	9,8	5,5	1:1,78	4,1	6	1:0,68	♀	Present	Present	Present	Peddie, E.CP. RSA.
pl	9,8	5,5	1:1,78	4,3	6,25	1:0,69	♂	Inc.	Present	Present	Bluegumspoort, N.Tvl.RSA
pl	10	5,6	1:1,78	4,2	6	1:0,70	♀	Inc.	Present	Present	Ermelo, Tvl. RSA.
pl	10	5,5	1:1,81	4	6,1	1:0,66	♀	Absent	Present	Absent	Umfolozi G.R.,Natal. RSA
pl	10	5,7	1:1,75	4,5	6,5	1:0,69	♂	Present	Present	Present	Kyle G.R., Rhodesia
pl	10	6	1:1,66	4,4	6,8	1:0,65	♀	Absent	Present	Present	Umfolozi G.R.,Natal, RSA.
pl	10,1	5,5	1:1,83	4,2	6,3	1:0,67	♀	Present	Present	Present	Vredefort, OFS. RSA.
pl	10,1	5,6	1:1,8	4,5	6,2	1:0,73	♀	Inc.	Present	Present	Somkele, Natal, RSA.
pl	10,1	5,7	1:1,77	4,5	6,6	1:0,68	♀	Inc.	Present	Present	Umfolozi G.R.,Natal. RSA.
pl	10,1	5,9	1:1,71	4,6	6,5	1:0,71	♀	Inc.	Present	Present	Port Elizabeth,E.CP.,RSA.
pl	10,2	5,5	1:1,85	4,4	6,4	1:0,69	♀	Inc.	Present	Present	King Williamstown,E.CP.RSA
pl	10,2	5,9	1:1,72	4,2	6,5	1:0,65	♀	Absent	Present	Present	Lothair, SE.Tvl. RSA.
pl	10,25	5,75	1:1,78	4,4	6,6	1:0,67	♀	Inc.	Present	Present	Amsterdam, SE.Tvl. RSA.
pl	10,3	5,8	1:1,77	4,25	6,25	1:0,68	♀	Inc.	(obscured by setae)	Present	Salisbury, Rhodesia.
pl	10,4	5,8	1:1,79	4,5	6,5	1:0,69	♂	Inc.	Present	Present	Mossel Bay,E.CP., RSA.
pl	10,5	5,9	1:1,77	4,3	6,4	1:0,67	♀	Inc.	Present	Absent	Magoebaskloof, N.Tvl.RSA.
pl	10,6	5,9	1:1,79	4,6	6,6	1:0,70	♀	Absent	Present	Present	Salisbury, Rhodesia.
ps	10,6	6	1:1,76	4,5	6,4	1:0,70	♀	PL	Absent	Absent	Bluegumspoort, N.Tvl.RSA.
pl	10,7	6	1:1,78	4,6	6,7	1:0,69	♀	Present	Present	Present	Eshowe, Natal, RSA.
pl	10,9	6	1:1,81	4,5	6,6	1:0,68	♀	Absent	-	Present	Rustenburg, Tvl. RSA.
pl	10,9	6	1:1,81	4,5	6,75	1:0,67	♀	Inc.	Present	Present	Salisbury, Rhodesia.
pl	10,9	6,5	1:1,67	4,8	7	1:0,63	♂	Inc.	Present	Present	Shingwidzi,KNP,NE.Tvl.RSA.

TABLE 2 (continued)

*Species	Length(1) mm	Width(1) mm	Ratio(1) Length(1) :Width(1)	Length(2) mm	Width(2) mm	Ratio(2) Length(2) :Width(2)	Sex	*Condition of setal brush	*Condition of setal pits	Sternal setae	Locality
pl	11	6,2	1:1,77	4,5	6,7	1:0,67	♀	Absent	Present	Present	Bontebok N.P. SW.CP.RSA
pl	11	6,25	1:1,76	4,5	6,5	1:0,69	♀	Absent	Present	Present	Bulawayo, Rhodesia.
pl	11	6,3	1:1,74	4,6	7,1	1:0,65	♀	Present	Present	Present	Gorongosa, Mtn., Mocam.
pl	11,1	6,2	1:1,79	4,6	6,8	1:0,68	♀	Absent	Present	Present	Ermelo, Tvl. RSA.
pl	11,1	6,2	1:1,79	4,3	6,5	1:0,66	♀	Inc.	Present	Present	Plettenburg Bay.E.CP.RSA.
pl	11,1	6,5	1:1,7	4,7	7,4	1:0,64	♀	PL	Present	Present	Wankie N.P., Rhodesia.
pl	11,1	6,25	1:1,77	4,6	7	1:0,66	♀	Absent	Present	Present	Salisbury, Rhodesia.
pl	11,25	6,2	1:1,81	4,6	6,8	1:0,68	♀	Inc.	-	Absent	Punda Milia,KNP,NE.Tvl.RSA
pl	11,4	6,3	1:1,8	4,6	7,3	1:0,63	♀	Absent	Present	Present	Makuti, Rhodesia.
pl	11,5	6,6	1:1,74	4,75	7,1	1:0,67	♀	Inc.	Present	Present	Belfast, E.Tvl. RSA.

* Terminology:

Species - 1) ps :- Those specimens bearing the features designated for *O. pseudoplanatus* by Balthasar (1964)
2) pl :- Those specimens bearing the features for *O. planatus*.

Setal brush - 1) Present :- Fully developed across the width of the posterior dorsal margin of the elytra.
2) PL :- Present but restricted to the lateral parts of the posterior dorsal margin of the elytra (5th - 7th interstrae).
3) Inc.:- Present but thinned out and incomplete through wear. Remnants of the brush still visible on interstriae 1 - 4.

Setal pits - 1) Present :- Present on one or more of interstriae 1 - 4.
2) Absent :- Not detectable on interstriae 1 - 4 but sometimes visible on one or more of interstriae 5 - 7.

TABLE 3:

Mean ratios determined from 100 specimens of the *O. pseudoplanatus/ planatus* species complex used in the compilation of Table 2.

Ratios	Material 9,5 mm or less in overall length	Material 9,6 mm or longer in overall length
length (1) :width (1)	1:1,81	1:1,78
length (2) :width (2)	1:0,71	1:0,68

TABLE 4:

Mean ratios determined from the specimens used in the compilation of Table 2 after division into those possessing the features designated for *O. pseudoplanatus* by Balthasar (1964) and those possessing the features for *O. planatus.*

Ratios	*O.pseudoplanatus*	n	*O. planatus*	n
Length (1) :width (1) all specimens	1:1,82	30	1:1,76	70
Length (2) :width (2) all specimens	1:0,71	30	1:0,69	70
Length (1) :width (2) ♂♂	1:1,82	18	1:1,78	30
Length (1) :width (1) ♀♀	1:1,82	12	1:1,79	40
Length (2) :width (2) ♂♂	1:0,71	18	1:0,70	30
Length (2) :width (2) ♀♀	1:0,72	12	1:0,68	40

FIGURE I : The relationship between * Length (2), width (2) and the presence or absence of setal pits in beetles of the *O. planatus/pseudoplanatus* species complex used in the compilation of Table 2.

Line fitted by regression analysis.

Correlation coefficient (r) = 0,94 which indicates a high positive correlation.

Key to Symbols:-

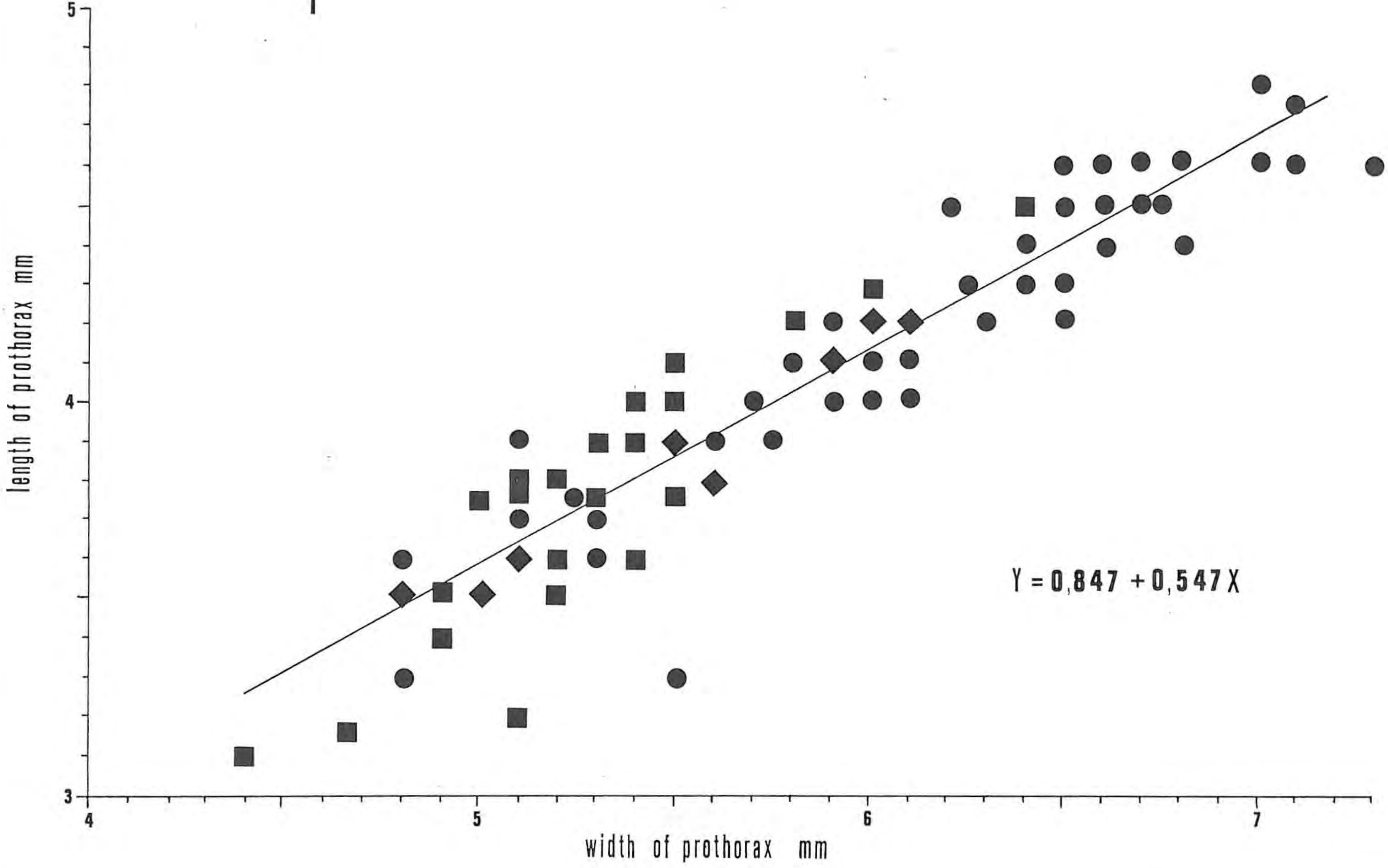
● - Setal pits present on one or more of interstriae one to four

■ - Setal pits absent from interstriae one to four but sometimes present on interstriae five to seven.

◆ - Individuals of similar size, either with pits present or absent.

* See notes at the head of Table 2.

1



5
4
3
length of prothorax mm
4
5
6
7
width of prothorax mm
Y = 0,847 + 0,547 X

In *O. planatus* the setae arise from a variable row of indentations (Balthasar 1964). *O. pseudoplanatus* lacks these structures, although occasionally two to three coarse punctations are seen at the tips of the 6th and 7th interstriae (Balthasar 1964). Tables 2 and 6 demonstrate that well developed indentations are also present on some smaller beetles although they are more typical of larger specimens.

Sternal setae

Sternal setae were absent from most smaller specimens (i.e. 14 out of 17 8 mm in length, or smaller) but not universally so as indicated by Balthasar (1964) (Tables 2 and 7). The tips of small setae could be seen protruding from the lateral edges of the sternites on some small specimens.

Discussion

I stress that the specific characters used by Balthasar (1964) to separate *O. pseudoplanatus* from *O. planatus* can be attributed to reduced development or prominence of the features owing to the small size of the specimens. The differences between these two species are slight compared with the range of variation of the external morphology within some *Copris* species. The magnitude of the ornamentation of the head and prothorax in this genus bears a relationship to the size of the specimen which agrees with similar observations of Dynastinae and *Heliocopris* made by Arrow (1928).

This ....

TABLE 5: Summary of the biological data contained in Table 2 for 100 specimens of the *O. planatus/pseudoplanatus* species complex. The condition of the setal brush in four size divisions is expressed as percentages of the total number of individuals within each division.

TABLE 6: Summary of the biological data contained in Table 2 for 100 specimens of the *O. planatus/pseudoplanatus* species complex. The condition of the setal pits in four size divisions is expressed as percentages of the total number of individuals within each division.

TABLE 7: Summary of the biological data contained in Table 2 for 100 specimens of the *O. planatus/pseudoplanatus* species complex. The condition of the sternal setae in four size divisions is expressed as percentages of the total number of individuals within each division.

5.

		Condition of setal brush				
Length of specimens mm	Mean and standard error mm	Absent	Present only laterally (PL)	Incomplete	Present	n
		Percentage of specimens				
6,9 - 8	7,8 ± 0,22	82	6	12	0	17
8,1 - 9	8,6 ± 0,05	50	18	23	9	34
9,1 - 10	9,6 ± 0,06	37	10	37	16	23
10,1 - 11,5	10,7 ± 0,09	33	7	47	13	26

6.

		Condition of setal pits			
Length of specimens mm	Mean and standard error mm	Absent	Present	?	n
		Percentage of specimens			
6,9 - 8	7,8 ± 0,22	71	29	0	17
8,1 - 9	8,6 ± 0,05	50	44	6	34
9,1 - 10	9,6 ± 0,06	32	63	5	23
10,1 - 11,5	10,7 ± 0,09	3	87	10	26

7.

		Condition of sternal setae			
Length of specimens mm	Mean and standard error mm	Absent	Present	?	n
		Percentage of specimens			
6,9 - 8	7,8 ± 0,22	82	18	0	17
8,1 - 9	8,6 ± 0,05	50	50	0	34
9,1 - 10	9,6 ± 0,06	32	63	5	23
10,1 - 11,5	10,7 ± 0,09	13	87	0	26

This comparison between Coprini and *Oniticellus (s. str.)* was criticised by Cambefort (pers. comm.) on the basis that the features in question, in *Oniticellus (s. str.)* were not a continuous gradation but were either present or absent. However, Arrow (1928) records that there are cases of polymorphism in some *Onthophagus* where "no transitional state seems to exist between the different phases".

The validity of *O. pseudoplanatus* is therefore challenged. Without examining the type specimen (which it is not possible to obtain), it is impossible to pass a definitive judgement, but, on the basis of the published description and material examined, I recommend that *O. pseudoplanatus* should be synonymised with *O. planatus*.

1.3. Taxonomy of Group 3. *(O. pictus pictus, O. pictus orientalis, O. formosus, O. tessellatus).*

Since 1825 *O. tessellatus* has been redescribed once as *O. freyi* by Balthasar (1941) whose determination was followed by Paulian (1945) and was recited by Balthasar (1963). It has not been subject to further confusion probably due to it being the only Asian member of the group. The taxonomy of the African members is, however, still confused by some workers (e.g. Ferreira 1972) despite being correctly interpreted by Janssens (1953). This long history of confusion began with Harold (1869) who synonymised *O. formosus* and *O. pictus*. This decision was followed by Péringuey (1901). D'Orbigny (1916) recognised the validity of the two species but ascribed *O. formosus* to the genus *Liatongus*. Boucomont (1921) again synonymised the two although they were later

reinstated ....

reinstated as valid species (Gillet and Boucomont 1927). Boucomont's 1921 synonymy of *O. formosus* was incorrectly relisted by Ferreira (1972) in distribution lists of *O. pictus*. Previously, Gomes Alves (1950) suggested that the specific differences between *O. pictus* and *O. formosus* were examples of sexual dimorphism, but my examination of other material shows that both males and females possess these supposedly sexually dimorphic characters confirming the observations of Janssens (1953). The synonymy of *O. formosus* with *O. pictus* during the previous century had also formerly led to the redescription of *O. formosus* as *O. parapictus* by Balthasar (1941); the type of *O. formosus* Chevrolat having been lost (Janssens 1953).

In 1953, Janssens separated *O. pictus* into two subspecies; the southern African *O. pictus pictus* and a central African group which he designated *O. pictus orientalis*. *O. pictus pictus* possesses black oval markings in the centre of its femora, whereas those of *O. pictus orientalis* and *O. formosus* are entirely yellow. *O. formosus* may be separated from the subspecies of *O. pictus* by the possession of three weak indentations in the anterior margin of its clypeus as compared with the single indentation of *O. pictus* (Fig. 2). Previously, Janssens (1939) had determined *O. pictus orientalis* as *O. formosus*. He later suggested (1953) that this subspecies was the cause of previous synonymies between the two.

As there is a broad division between the climatic characteristics of the areas occupied by each subspecies the status of this taxon should perhaps be reviewed (chapter 2.4.).

Size range: *O. formosus* :- 7,5 - 11,1 mm (62 specimens measured from the DBRU reference collection).

O. pictus pictus :- 6,3 - 8,7 mm (18 specimens measured from the DBRU reference collection).

1.4. Taxonomy of Group 4 *(T. dimidiatus)*

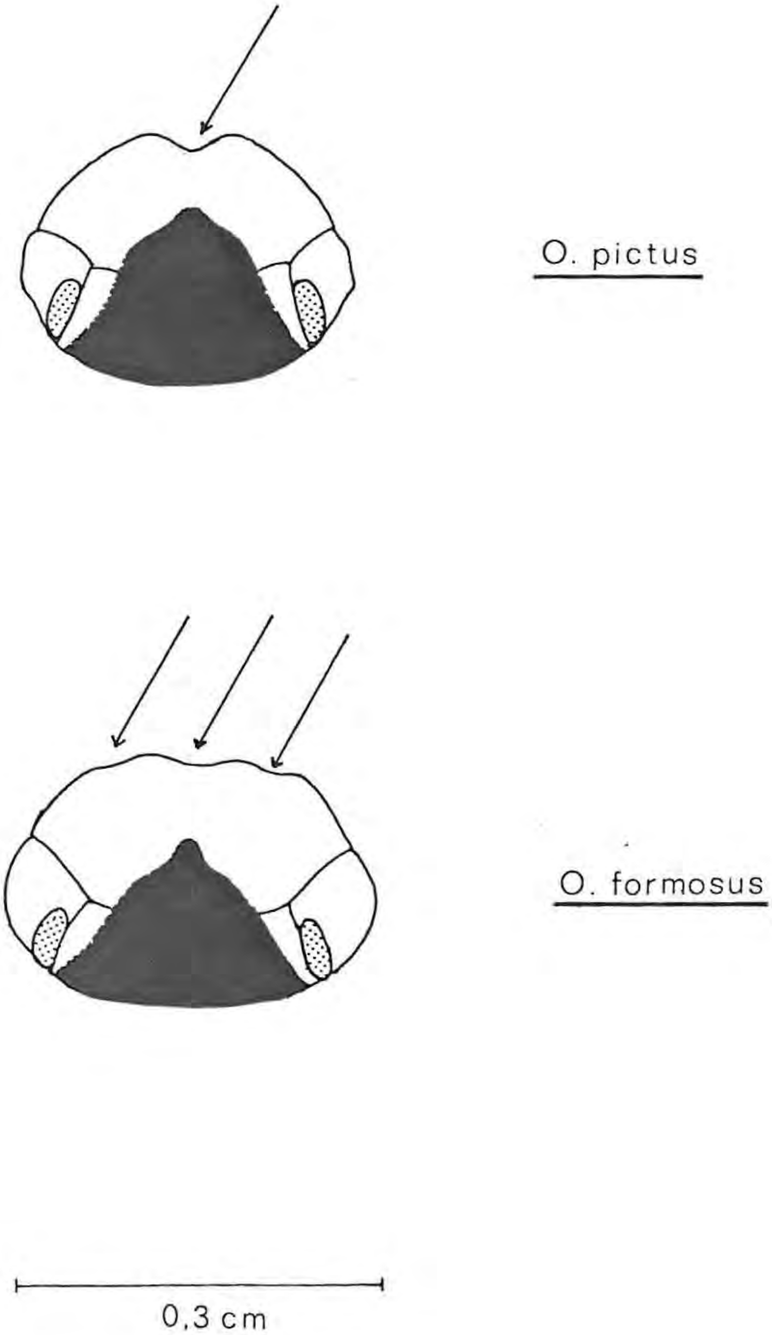
Tragiscus dimidiatus is a very distinctive species. Even so, it has not escaped past assignment to the genus *Oniticellus* (Boucomont 1921, Gillet and Boucomont 1927) or redescription as *Deronitis epphipiatus* (Arrow 1933).

Size range: 13 - 20,2 mm (18 specimens measured from the DBRU reference collection).

In summary, I recognise four African species of *Oniticellus s. str. (O. egregius, O. planatus, O. formosus* and *O. pictus)* and the single species of *Tragiscus (T. dimidiatus)*. These are the five species which are referred to as endocoprids in this thesis, unless specified otherwise (Chapter 8).

Figure 2

Morphological differences between the clypei of *O. pictus* and *O. formosus*.



2. DISTRIBUTION

A discussion of endocoprid distribution in southern Africa is of direct relevance in determining suitable sites for their release in Australia, should introduction be considered desirable.

Their occurence is controlled by a complex of factors and has been strongly influenced by the evolution of nidification behaviour in which the brood chamber is constructed within, or immediately beneath, the dung pad. The interrelationships between the principal factors have been illustrated diagrammatically in Figure 3 and it is suggested that temperature, rainfall and density of the preferred dung type are of primary importance. Latitude and altitude are also important but act only indirectly, chiefly by their effect on temperature. (They have been omitted from Fig. 3 for purposes of simplification). Soil and vegetation types are much less influential and although they limit the distribution of some dung beetle species, e.g. *Catharsius calaharicus* Kolbe, which is restricted to Kalahari sand, and *Copris fidius* (Olivier), which is more common in forest areas, endocoprids are found on a wide variety of soil types ranging from sand to clay, and, in vegetation zones, ranging from grassland to paddocks in forest.

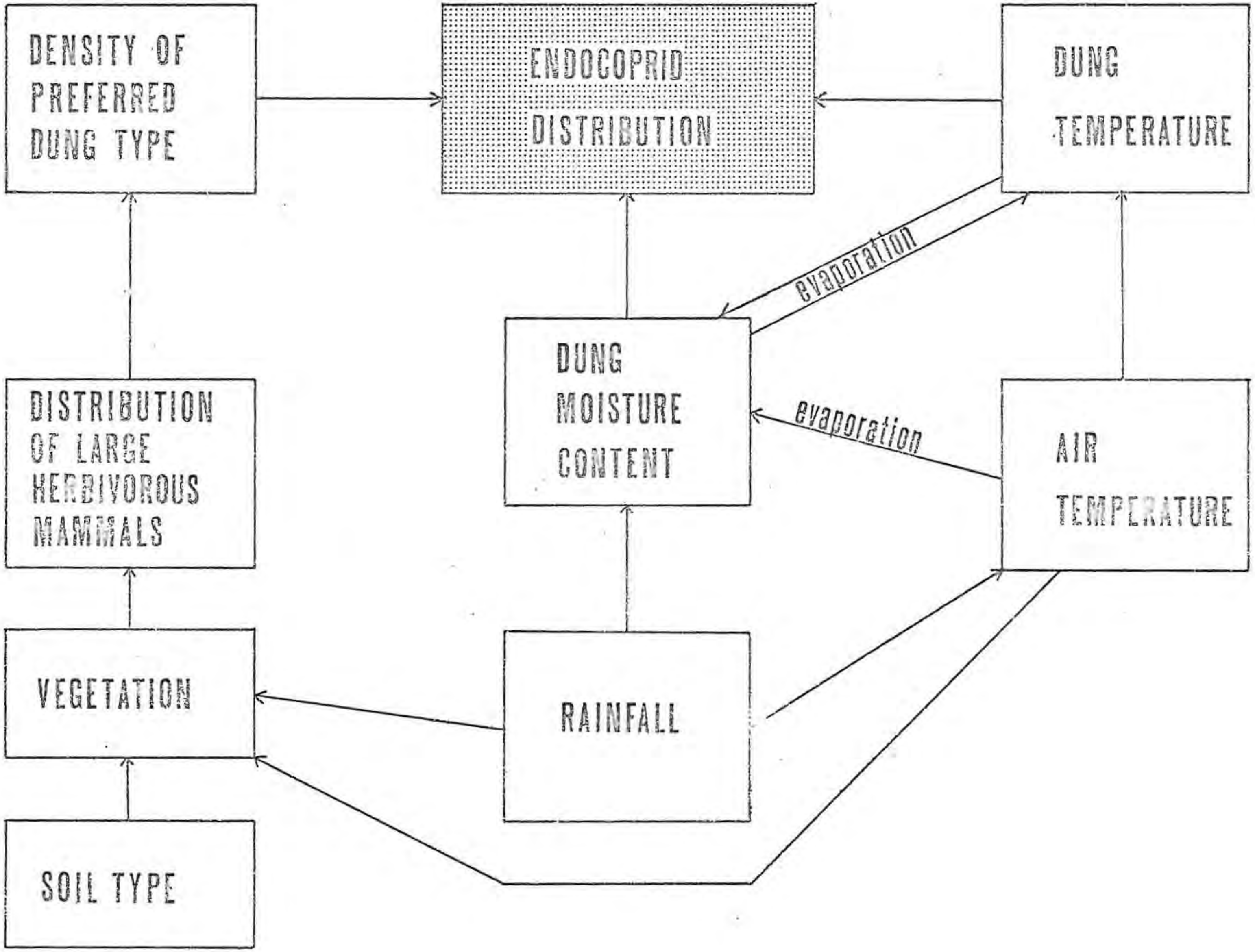
Many of the conclusions reached in this chapter are based on observations and, in the absence of supporting experimental data, must be seen as tentative.

2.1. Temperature

The proximity of endocoprid brood chambers to the surface has imposed greater restrictions on their distribution in relation to temperature than is exhibited by paracoprid and telecoprid beetles.

In ....

Figure 3: Diagram showing the principal factors controlling endocoprid distribution.



In addition, it is apparent from observations that minimum temperatures influence the distribution of most endocoprids more strongly than maximum temperatures.

Table 8 shows the relationship between maximum and minimum temperatures recorded at various levels above and below the soil surface near Brits (25^{0} 35'S 27^{0} 49'E) on July 17th, 1974. It can be seen that the minimum temperature is experienced at "grass roots" level (an inexact term in use at the Weather Bureau, Pretoria, referring to a height of 2,5 cm above the soil surface).

The extremes of temperature recorded in fresh cow pads are even greater than those of the surrounding air (Landin 1961), therefore, endocoprids, which spend pratically their whole lives actually in, or immediately beneath dung pads, will be subjected to the greatest possible thermal extremes at any given locality. This probably explains their observed restriction to the tropics and warm mid latitudes where winters are sufficiently warm for their continued activity. Credence is added to this by observations of dung at Irene Research Station (near Pretoria) where fresh pads were partially frozen during winter 1972. No endocoprids were found under these conditions. These extreme fluctuations in temperature are probably never experienced by paracoprids and telecoprids owing to their habit of overwintering in the soil where they are insulated by the overlying earth. Winter dormancy may explain why they have been able to colonise colder areas than endocoprids.

Figure 4 shows the localities from which reference material was collected by members of the DBRU between July, 1970 and March, 1977. It has been included for purposes of comparison with Figures 5 to 14.

Table 8 ....

TABLE 8: Temperature data from Brits recorded on the 17th July, 1974. (Information supplied by the Weather Bureau, Pretoria).

	Depth BELOW the soil surface		Height ABOVE the soil surface	
	30 cm	10 cm	2,5 cm	30 cm
Max. °C (14h00)	13,6	17,5	-	22,7
Min. °C (08h00)	12,5	7,7	-6,0	-2,3
Range °C	0,9	9,8	-	20,4

Figures 5 and 6 show the distribution of three species of endocoprid in relation to the frequency and duration of frost. It can be seen that at the limits of their range endocoprids occur in comparatively cold areas, but observations suggest that relative abundance is low, e.g. *O. formosus* in the northern Cape and western Transvaal; *O. planatus* in the eastern Orange Free State.

Figures 7 and 8 show the distribution of three species of endocoprid in relation to altitude. That of *O. pictus pictus* probably shows the effects of maximum temperature in that it is restricted to progressively higher altitudes in its more northerly distribution.

Figures 9 and 10 show the distribution of three species of endocoprid in relation to isotherms representing mean annual temperature.

Figures ....

Figures 11, 12 and 13 show the distribution of the same three species plotted against isolines of "effective temperature" (E.T.). E.T. used in this context, (the same term has a different conceptual basis where it is used in other scientific disciplines), is a concept originated by Bailey (1960) and developed from the idea of summer as the biologically most significant period of the year. He points out that, at any given locality, the annual cycle of biological activity commences and ceases at approximately the same temperature. This temperature delimits the summer period and is considered as representing the E.T.

Bailey (1960) arrived at a numerical interpretation of the concept by selecting limits to the polar and tropical regions delineated by the climatic classification of Köppen (1931). The polar isoline of E.T. was taken to be 10°C which represented the mean temperature of the warmest month of the year whilst the tropical limit was set at 18°C which was equivalent to that of the coldest month of the year. Thus, at the polar limit, mean temperatures do not theoretically rise above the value of the E.T. on any day of the year, whereas at the tropical limit, temperatures are at or above the E.T. for the full 365 days. From these limits Bailey (1960) derived an equation for calculating the E.T. which denotes that the value of each isoline is determined from the relationship between mean annual temperature (T) and the annual temperature range between the coldest and warmest months. (AR). This equation is:-

$$\text{E.T.} = \frac{8(T) + 14(AR)}{AR + 8} \quad {}^{\circ}\text{C}$$

By virtue of its derivation, the magnitude of the E.T. implicates the duration of the summer period (Table 9) which decreases with increasing latitude and altitude.

Table 9 ....

TABLE 9: The relationship between the value of the effective temperature and the duration of the period (Td) during which temperatures are theoretically at or above the E.T. (after Stuckenberg 1969).

E.T. °C	Td	Climate Classification
18° and above	365	Tropical
17°	282	Warm mid Latitudes
16°	254	
15°	214	
14°	183	
13°	151	Cool mid Latitudes
12°	111	

The chief failing of the concept, which Bailey (1960) freely admits, is the fact that biological response to atmospheric factors is not direct and uniform but is modified by the effects of photoperiod, soil temperatures, rainfall patterns or characteristics of the animals themselves such as diapause. It is, however, directly applicable to endocoprid distribution since no dormancy has been detected, rainfall patterns do not influence occurrence and, as pointed out above, their restriction to dung pads subjects them directly to surface temperature fluctuations.

Whilst the numerical expression of E.T. is highly artificial, the distribution of snakes and frogs in southern Africa was shown by Stuckenberg (1969) to bear a close relationship to isolines of E.T.

Similarly ....

Similarly, it is clear that the distributional patterns of endocoprids exhibit a closer correlation to E.T. than to isotherms of mean annual temperature. It is significant to note that the distribution of *O. formosus* is largely limited to the 15^{O}C isoline where the theoretical duration of the summer is 214 days. In the laboratory, *O. formosus* bred continuously

lived for only 142 days (Table 22). Allowing for the probable increase in longevity of non breeding beetles, they would only just be able to survive the winter in areas with an E.T. of 15^{O}C. *O. planatus*, which colonises much cooler areas, lives for considerably longer periods.

2.2. Rainfall

Whereas most dung beetles are dependent on rainfall to initiate activity (chapter 5.1.), endocoprids are probably influenced by rain only in relation to its effects on pad moisture (Fig. 3) as they are apparently much less influenced by ambient soil moisture than paracoprids and telecoprids (Bornemissza 1969). This independence from soil moisutre content may explain why they are found within a similar rainfall range at all altitudes unlike other dung beetles which tend to occupy a progressively more restricted rainfall range with increasing altitude.

As both *O. planatus* and *O. pictus pictus* tend to be less abundant in areas where the annual rainfall is lower than 500 mm (Figs. 11 and 13), neither species is found in hot, dry areas nor in the winter rainfall area of the south western Cape where summers are hot and dry. Observations of *O. planatus* suggest that it has a limited tolerance of dry conditions. Thus it is possible that the rapidity of pad desiccation is the reason for this exclusion as it does occur in hot, but wet and humid areas, e.g. Beira (19^{O} 50'S 34^{O} 51'E).

In ....

In southern Africa, *O. formosus* is not found in extremely wet areas irrespective of temperature, and its distribution appears to be limited at the 1000 mm isohyet (Fig. 12). Observations indicate that *O. formosus* larvae have an especially low resistance to moist conditions at the prepupal stage. The wet, southern coastline of Natal may therefore act as a barrier against the spread of this species further south since, with respect to rainfall and temperature, the drier coastal parts of the eastern Cape would appear to be suitable for *O. formosus* but it has never been collected from there.

O. egregius may be the only species of *Oniticellus* (*s. str.*) which lacks the independence of rainfall patterns shown by other African endocoprids. Like most paracoprids and telecoprids it possibly relies on precipitation to trigger emergence from its broods. (chapter 4.6.)

2.3. Availability of Preferred Dung Type

Distribution studies suggest that a viable population of endocoprids may only be maintained where there is a sufficient density of large, intact, dung masses, i.e. those of the larger herbivores (bovines, equines, elephants and rhinoceri). Pellets are rarely colonised and there are only three records of endocoprids collected from the dung of antelope or other smaller mammals (Table 10). Larval desiccation would probably prevent successful breeding in such droppings.

Endocoprids are absent from most of the arid central and western regions of South Africa, where, at one time, there were dense concentrations of buck but the density of the large indigenous mammals was very low. This absence cannot be explained purely in terms of low precipita-

tion......

tion since whilst present day distribution of bovine domestic stock is also of very low density, *O. formosus* has been recorded from the northern margins of this arid region on two separate occasions. At the driest of these two localities, 17 km SW of Vanzylsrus (26° 55'S 21° 55'E - 200 mm rain per annum), the cattle population is probably permanent due to the availability of borehole water from the Kuruman River bed. This indicates that at the drier end of its range the presence of *O. formosus* may be directly limited by the density of suitable dung.

Endocoprids may be divided into two groups on the basis of dung preference. Those found abundantly in afibrous dung (cow, buffalo, etc.) are widespread throughout Africa south of the Sahara (*O. formosus, O. pictus, O. planatus*). The second group sharing a preference for coarse fibred dung (elephant, rhinoceros, etc.) are mostly restricted to game reserves and a few areas where these indigenous animals still survive (*O. egregius, T. dimidiatus*). *O. egregius* is also found in a few areas far removed from game reserves where horses occur in sufficient numbers to maintain a viable population, e.g. Pretoria area. However, at De Wildt (near Pretoria), *O. egregius* has, on three occasions, been recorded from cow dung whilst a fourth pad contained two *O. egregius* brood balls. This species is usually found breeding only in coarse fibred dung and these records probably resulted from a paucity of horse dung at the time of observation.

In addition to Africa, endocoprids are found commonly in much of the warmer southern regions of Asia including India, China, S.E. Asia and the East Indies. In common with Africa, eutherian mammals dropping copious amounts of dung have had a long evolutionary history in Asia.

Figure 4: The Southern African localities from which reference material was collected by members of the DBRU between July, 1970 and March, 1977 (inclusive).

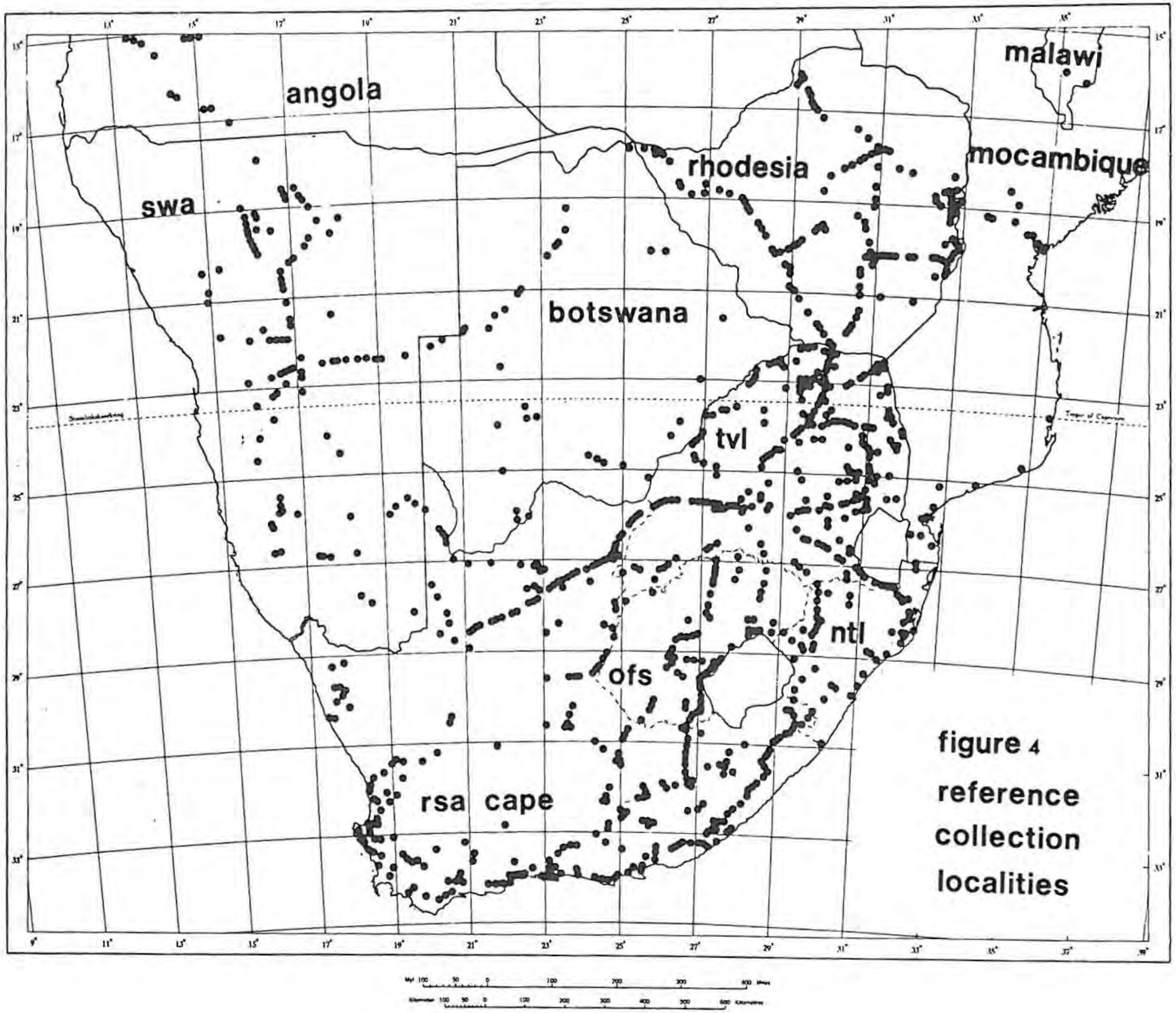


Figure 5: The distribution of *O. planatus* in relation to the duration and frequency of the frost period in South Africa. (Information on the frost isolines taken from The Development Atlas, Dept, of Planning 1965),

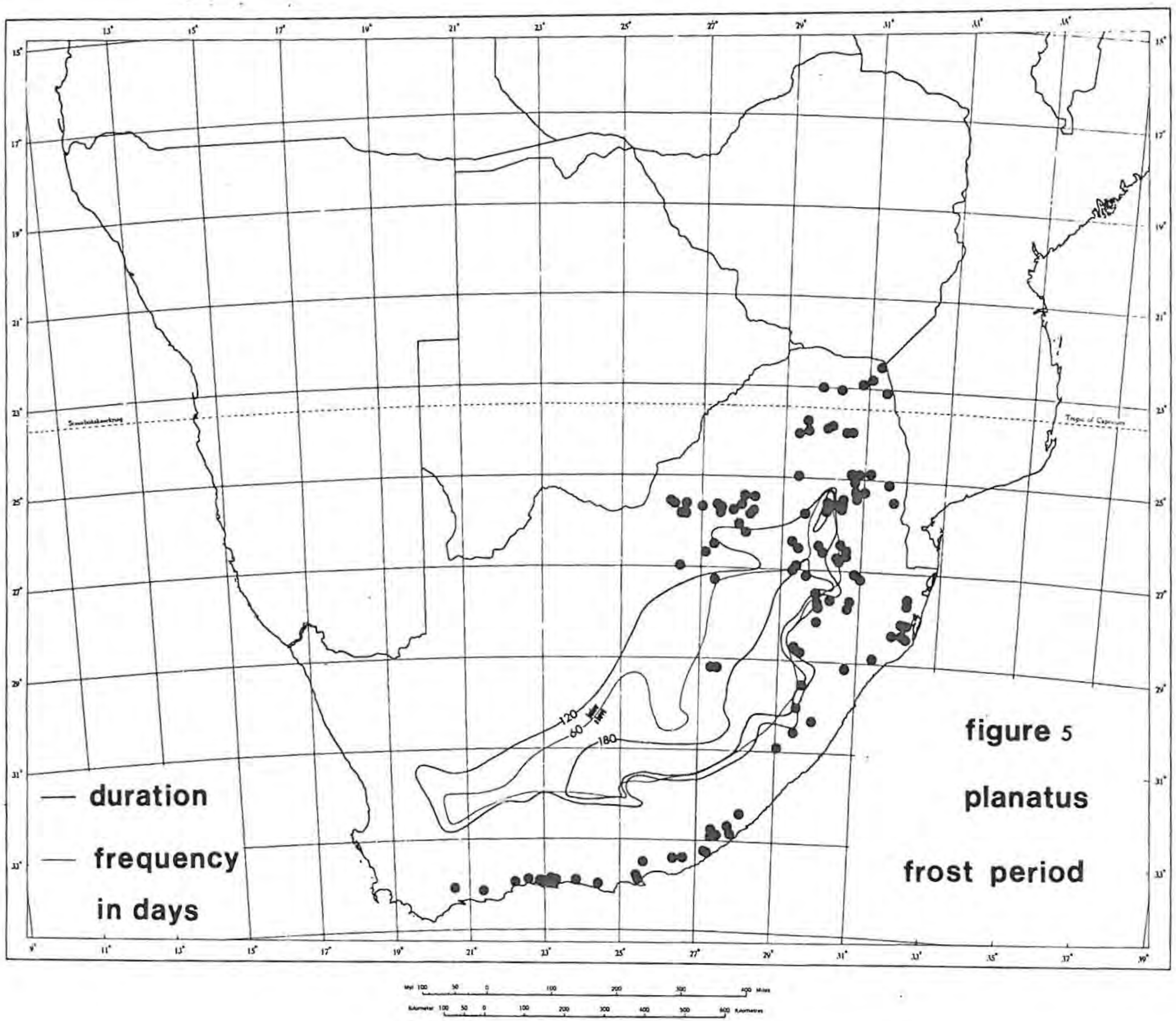


Figure 6: The distribution of *O. formosus* and *O. pictus pictus* in relation to the duration and frequency of the frost period in South Africa.

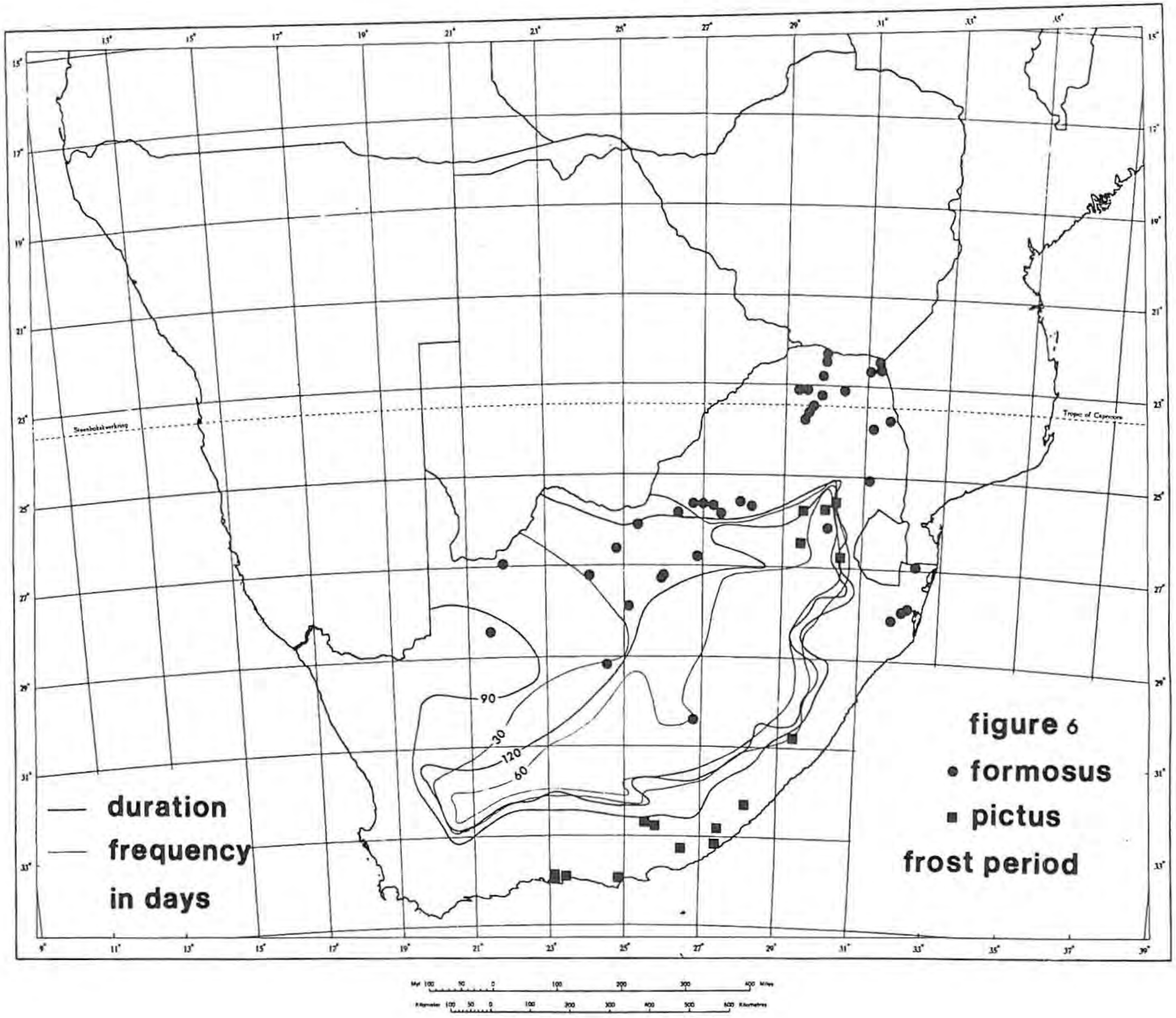


Figure 7: The distribution of *O. planatus* in relation to altitude in Southern Africa.

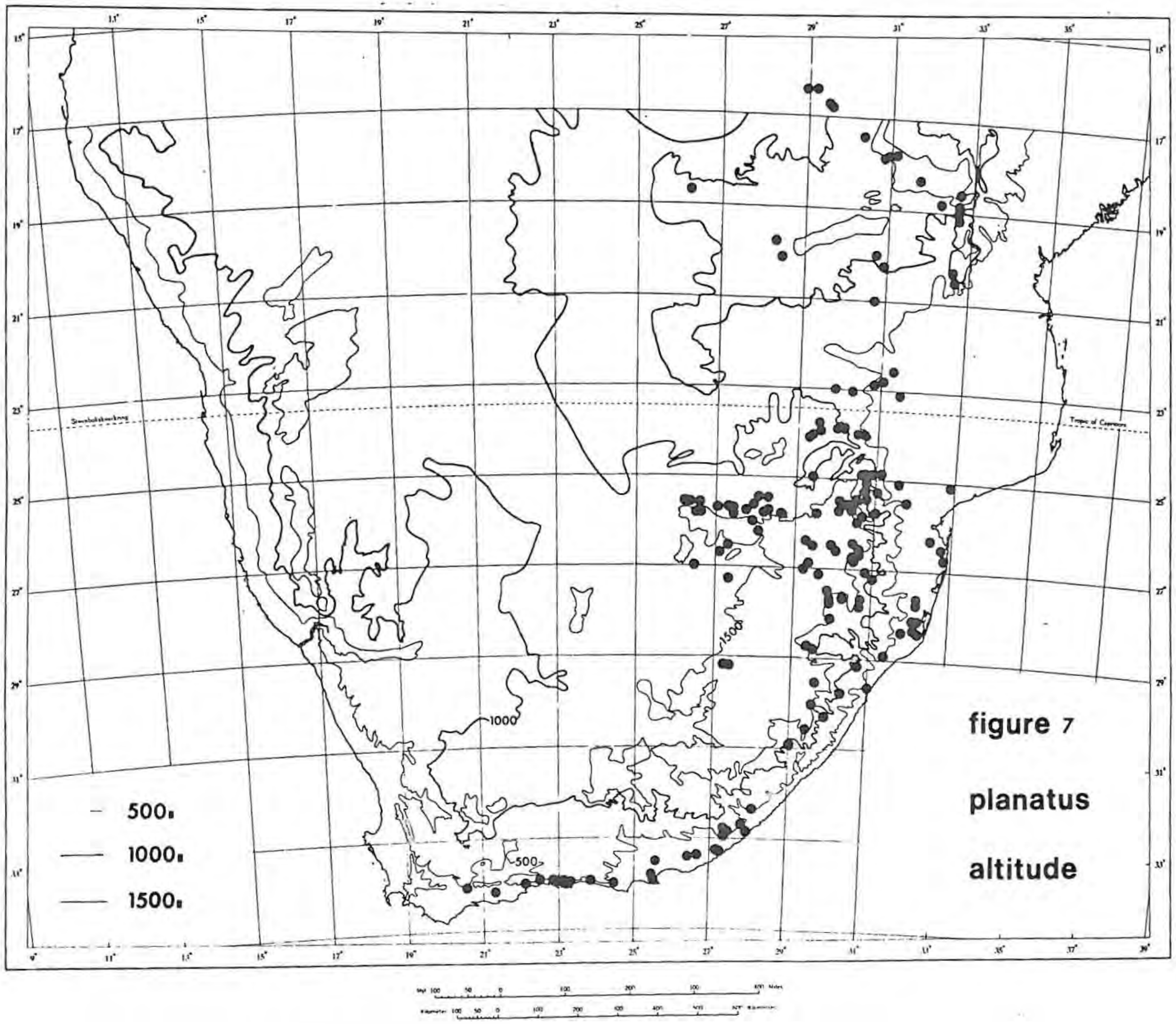


Figure 8: The distribution of *O. formosus* and *O. pictus pictus* in relation to altitude in Southern Africa.

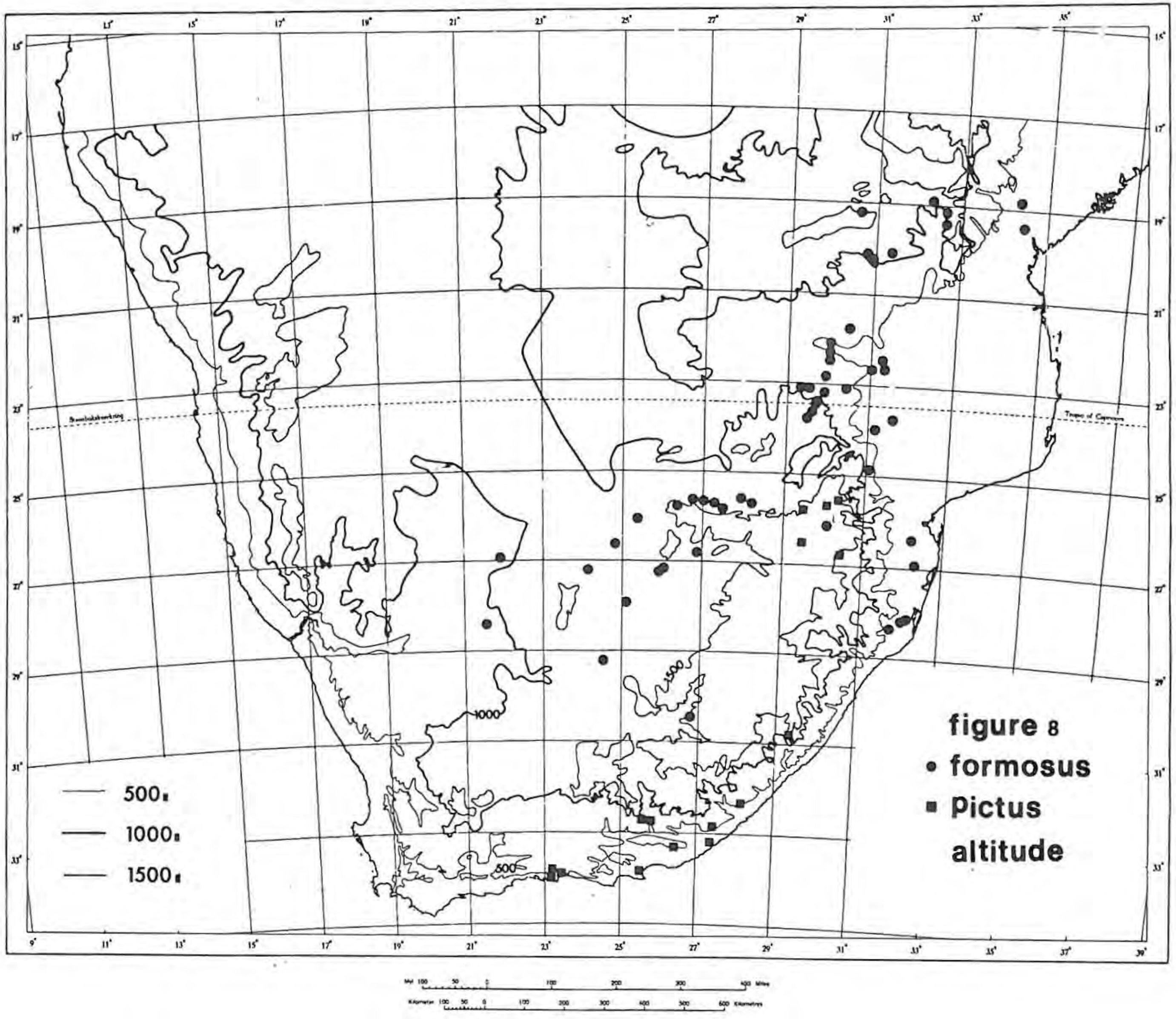


Figure 9: The distribution of *O. planatus* in relation to the 15°C and 17,5°C isotherms representing mean annual temperature in Southern Africa.

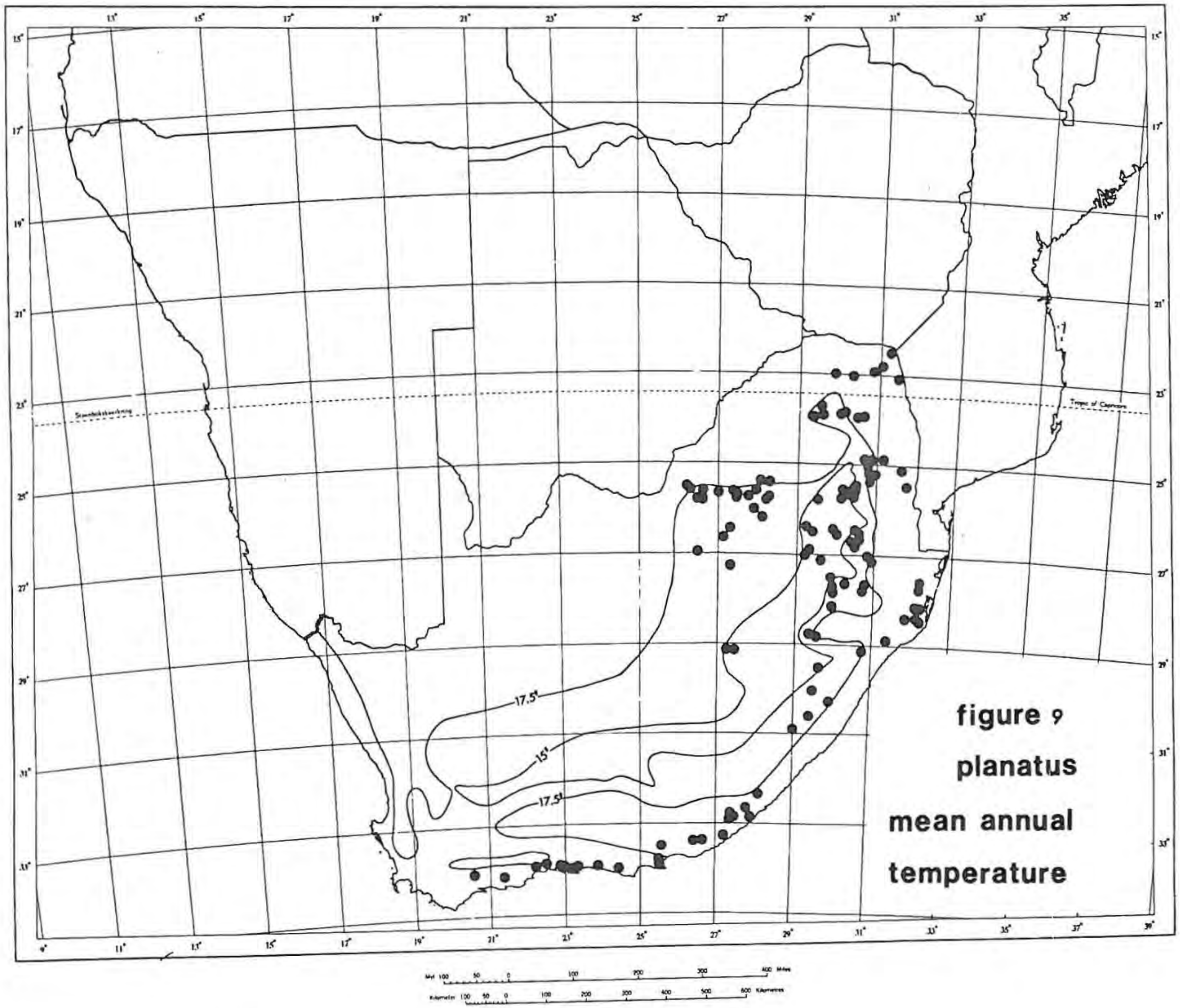


Figure 10: The distribution of *O. formosus* and *O. pictus pictus* in relation to the 15°C and 17,5°C isotherms representing mean annual temperature in Southern Africa.

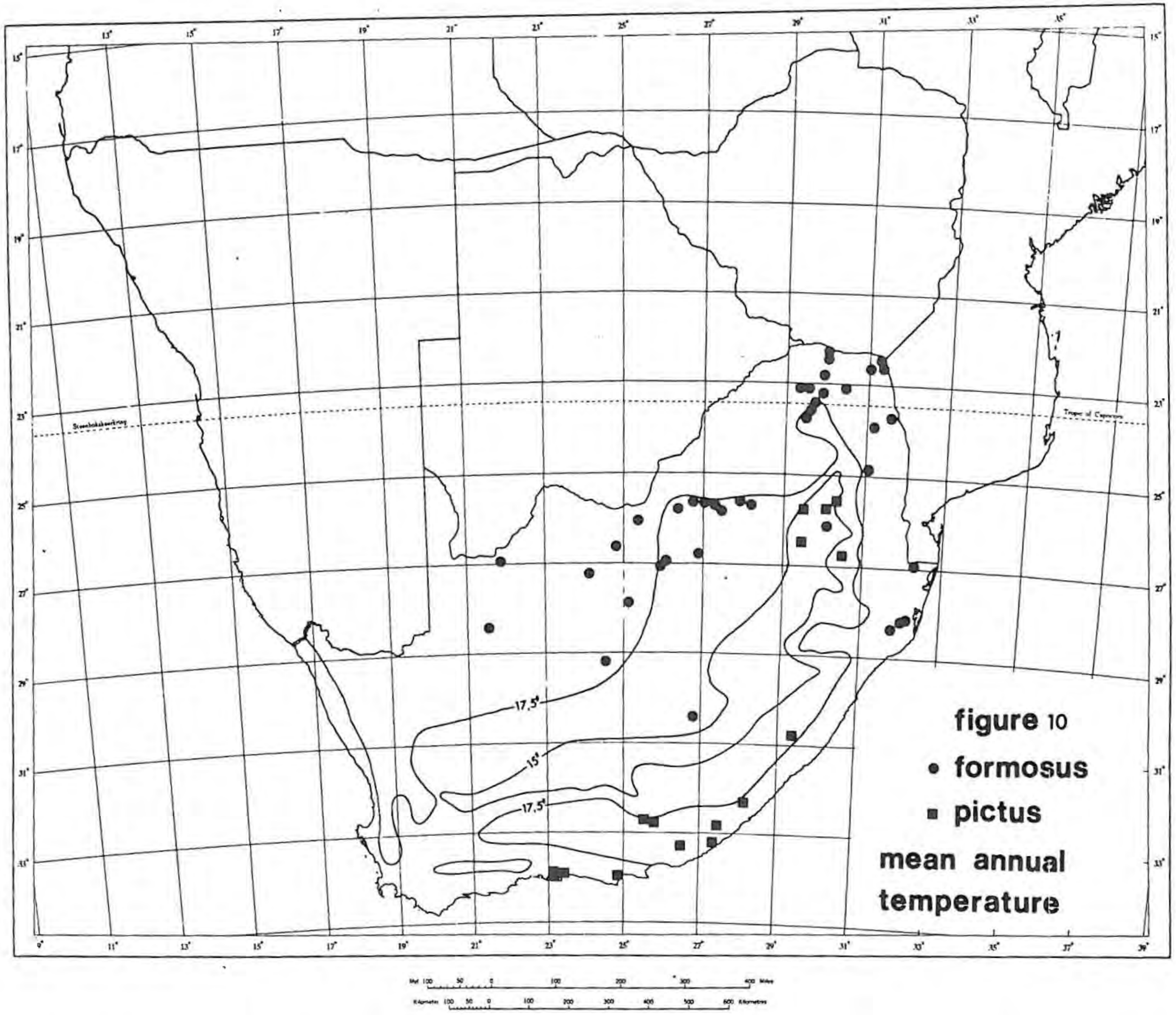


Figure 11: The distribution of *O. planatus* in relation to the 14°C and 15°C isolines of effective temperature (explanation in text) and the 500 mm isohyet (rainfall) in Southern Africa.

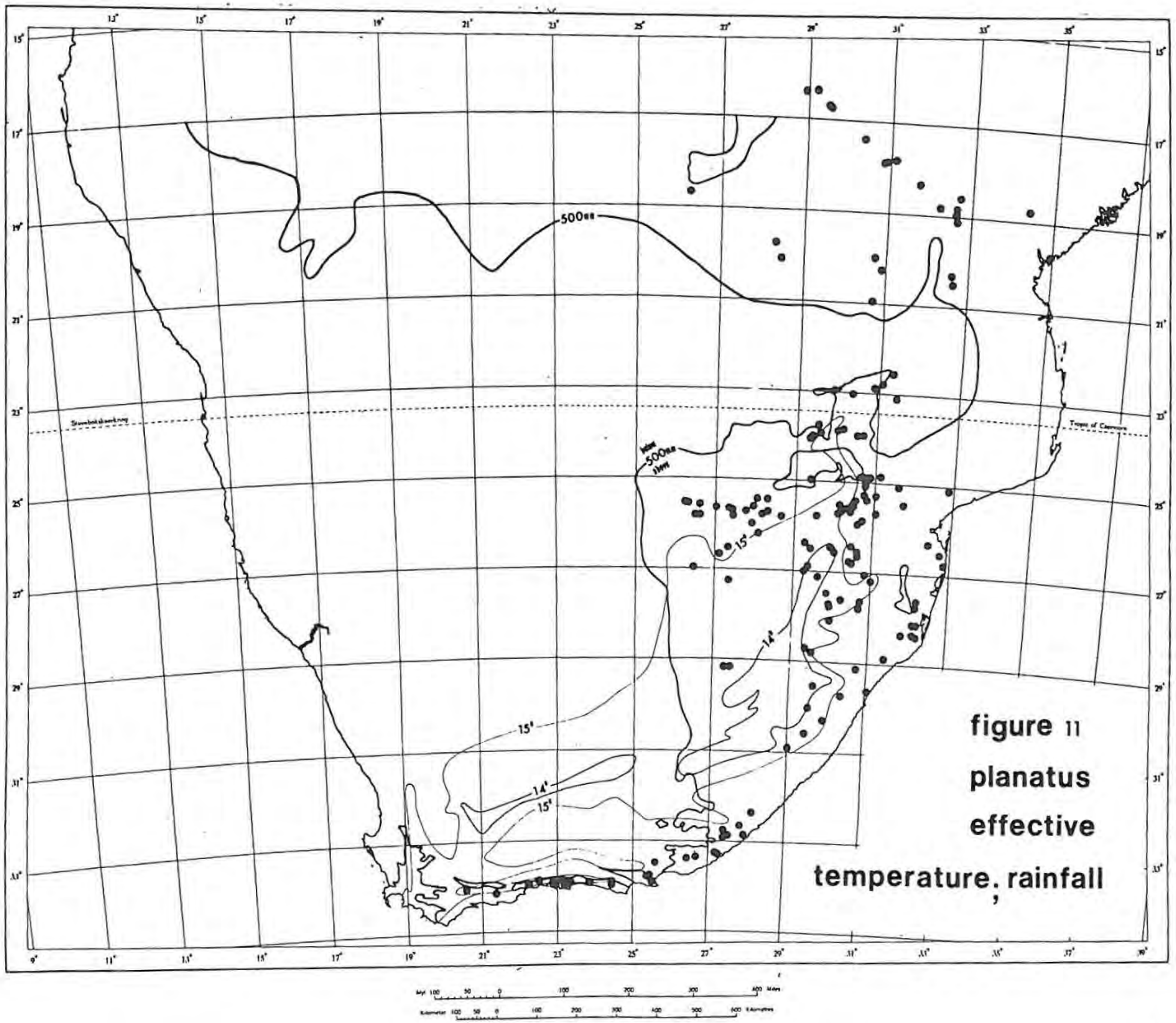


Figure 12: The distribution of *O. formosus* in relation to the isoline of effective temperature and the 200 mm and 1000 mm isohyets in Southern Africa.

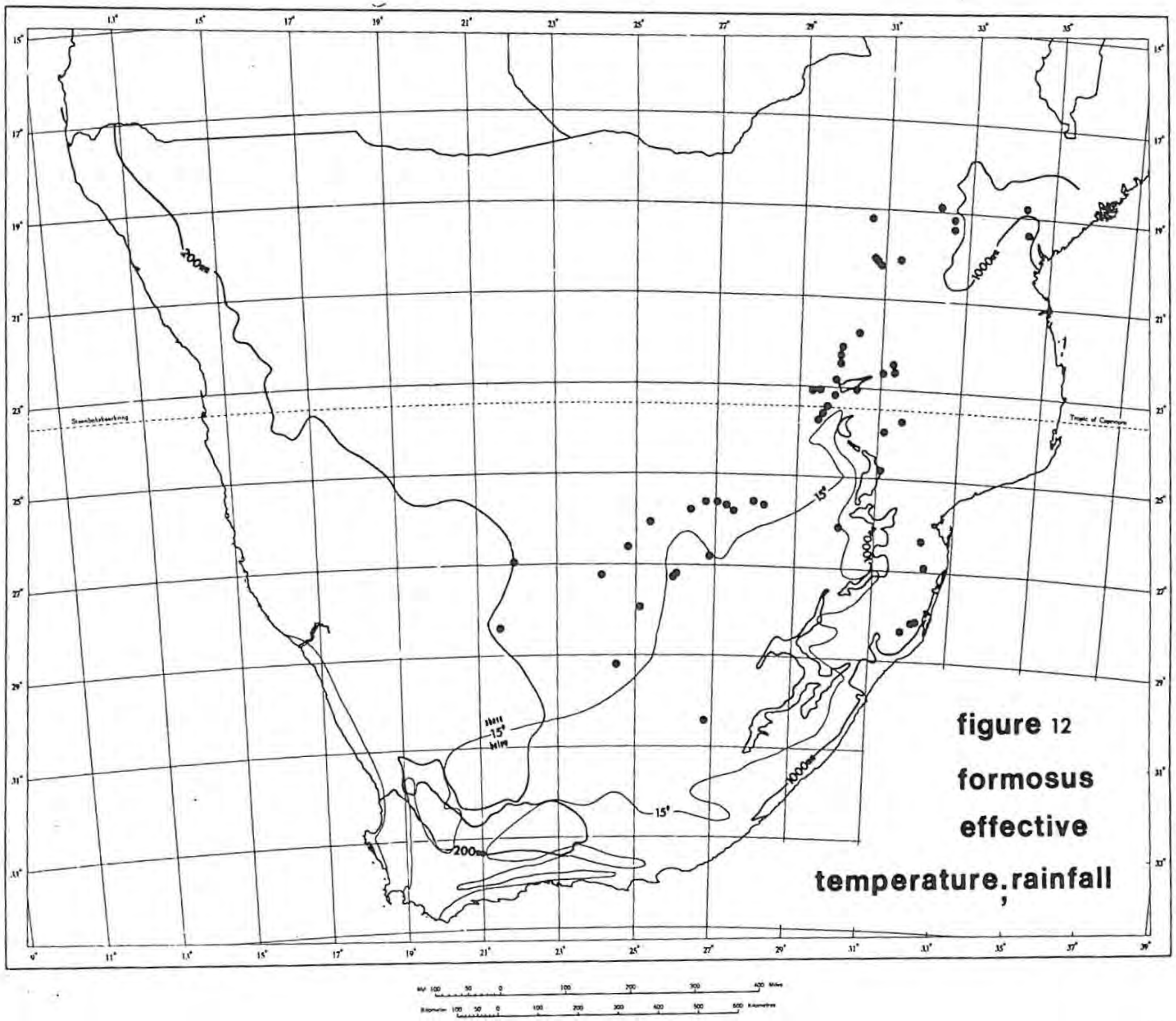


Figure 13: The distribution of *O. pictus pictus* in relation to the 14°C, 15°C and 16°C isolines of effective temperature and the 500 mm isohyet in Southern Africa.

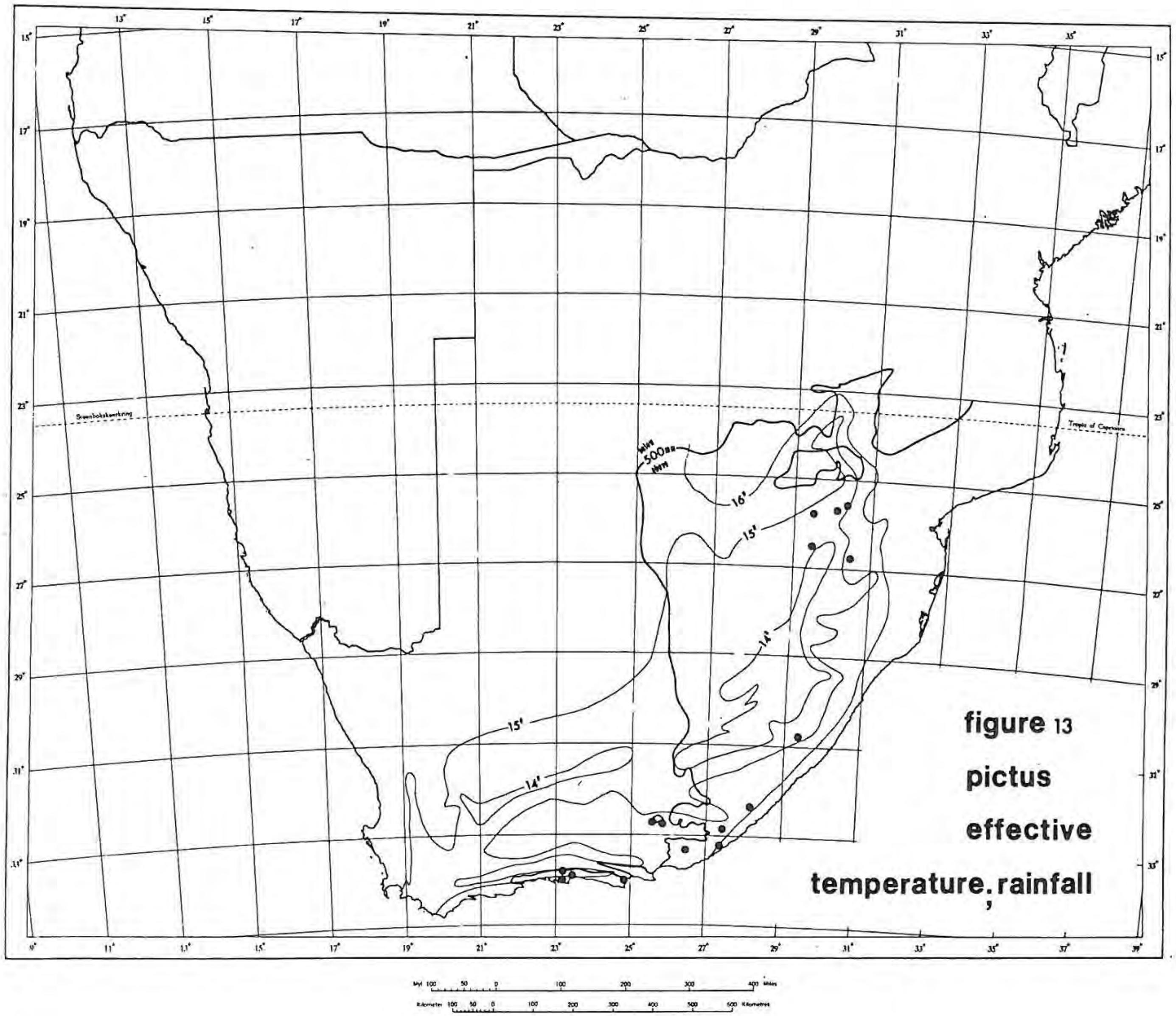
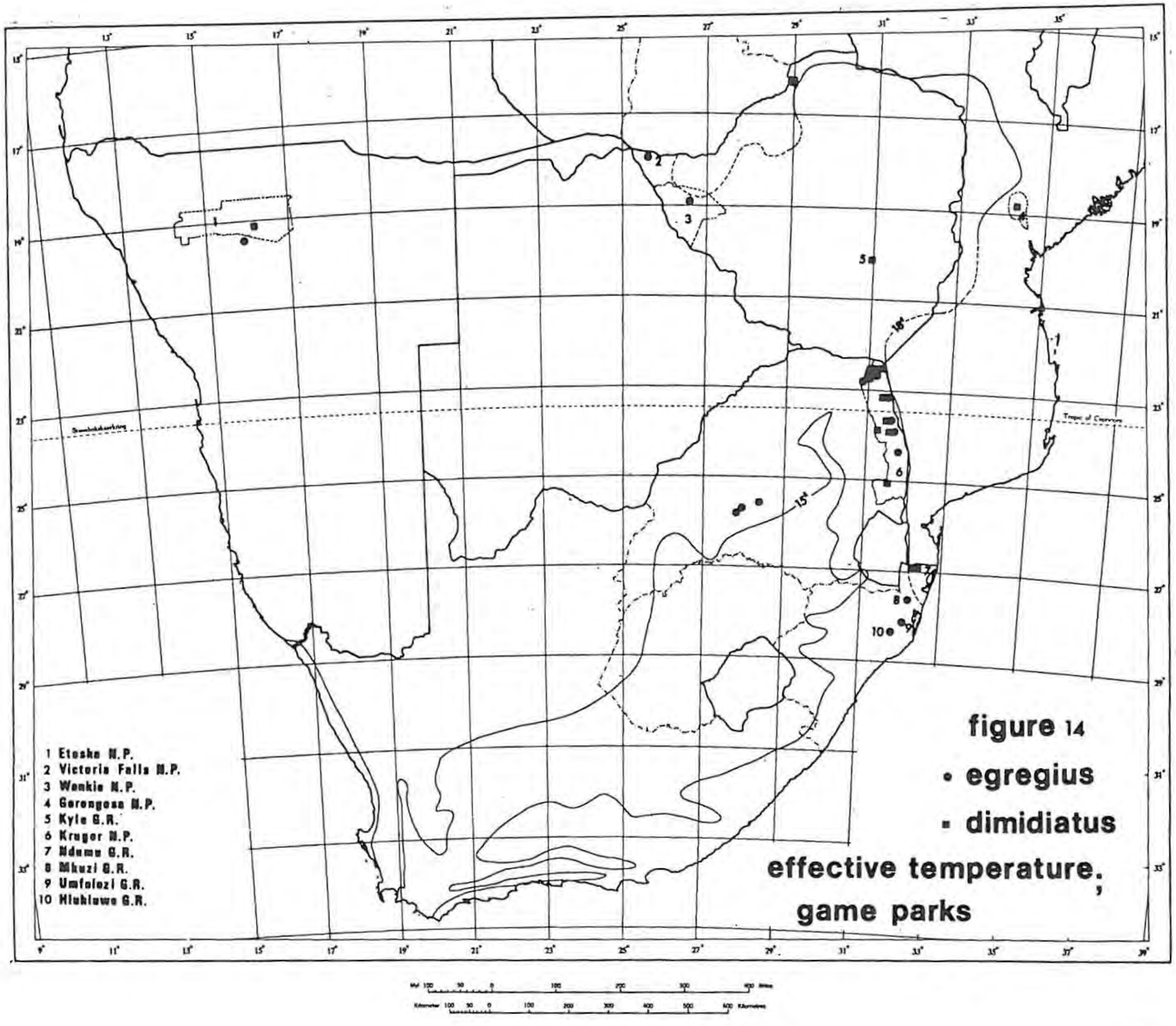


Figure 14: The distribution of *O. egregius* and *T. dimidiatus* in relation to national parks, game reserves and the 15^0C and 18^0C isolines of effective temperature in Southern Africa.



In Australia, mammals dropping suitably sized pads are only recent introductions and no endocoprids have been found there. Also, apart from *Eurysternus magnus* Laporte (Chapter 8), none are found in America where the only animal dropping large pads which is not a recent introduction, the American bison, migrated onto the continent via the cold north.

2.4. Distribution of the subspecies of *O. pictus*

The two subspecies of *O. pictus* are separated by a distance of 1600 km between the most northerly record of the one (*O. pictus pictus*) and the most southerly of the other (*O. pictus orientalis*) (Table 10). The altitudes of the most northerly localities from which *O. pictus pictus* is represented in the DBRU reference collection range between 1077 m and 1870 m (56 km E of Machadodorp to Belfast). At the one locality for which altitude data are available for *O. pictus orientalis* it occupies lower, hotter country (925 m - Bitshumbi - 0° 40'S 29° 25'E). On the same latitude as Belfast (25° 40'S) only *O. formosus* is found below 1075 m.

The geographical isolation of the subspecies in areas of widely differing climate suggests the possibility that they may deserve specific status. This question might be resolved through interbreeding experiments.

TABLE 10 ....

TABLE 10: Summary of the distribution of five endocoprid species in southern Africa (figs. 7 - 14) based on the DBRU reference collection with notes on the overall geographic range of each species.

A.

SPECIES	R A N G E S					*DUNG PREFERENCE	OVERALL GEOGRAPHICAL RANGE
	LATITUDE	E.T. °C	MEAN ANNUAL temp. °C.	RAINFALL mm p/a	ALTITUDE m		
O. egregius	15-21°S	15,8-16,4	20,1-22,2	457-670	973-1274	Elephant Rhinoceros Horse Cow(4) Donkey(2) Buffalo(1)	Eastern Africa from Natal to Somalia including Ethiopia, Kenya, Tanzania, E.Zaire, Mocambique and Botswana. Southern African distribution fig. 14.
	21-26°S	15,9-17,4	19,1-22,9	ca450-700	300-1216		
	26-31°S	17,6	22,7	650-900	91-230		
	15-29°S	15,8-17,6	19,1-22,9	ca450-900	91-1274		
O. planatus	15-21°S	15,2-18,4	17,2-25,5	600-1520	7-1776	Cow, Elephant, Buffalo Rhinoceros (3) Horse(2) Human/Cow mixture(1)	Much of the moister regions of Africa south of the Sahara including Guinea (Conakry), Nigeria, Congo (Brazzaville), Central African Empire, Ethiopia, Kenya, Tanzania, Uganda, Rwanda, Burundi, Angola, Southern African distribution fig. 11.
	21-26°S	13,5-17,7	12,6-25,2	ca450-1600	15-1870		
	26-31°S	14,3-17,6	14,8-22,7	630-1200	5-1780		
	31-33°S	15,2-15,6	17,1-18,3	618- 750	375-838		
	33-35°S	14,7-16,3	15,5-18,7	360- 860	110-570		
	15-35°S	13,5-18,4	12,6-25,2	360-1600	5-1870		

* Numbers in parenthesis indicate the number of observations made by the members of the DBRU when this number is smaller than five.

B.

SPECIES	RANGES					* DUNG PREFERENCE	OVERALL GEOGRAPHICAL RANGE
	LATITUDE	E.T. °C	MEAN ANNUAL temp. °C	RAINFALL mm p/a	ALTITUDE m		
O. pictus pictus	21-26°S	13,5-14,5	12,6-15,5	735-900	1077-1870	Cow Horse(1) Buck(1)	Fig. 13.
	26-31°S	14,0-15,4	13,9-17,9	754-ca900	914-1733		
	31-33°S	15,0-15,6	16,9-18,3	560-618	375-1077		
	33-35°S	14,9-15,5	16,1-17,3	576-800	58-570		
	25-35°S	13,5-15,6	12,6-18,3	560-900	58-1870		
** *O. pictus orientalis*	0-9°S	17,9	23,7	934	925	-	E.Zaire, Rwanda, Burundi and possibly N.Zambia
O. formosus	15-21°S	15,6-18,4	18,3-25,5	600-1000	58-1446	Cow, Elephant Horse(1) Buffalo(1) Donkey(1) Waterbuck (1), Fringe eared oryx (1), Human/Cow mixture(1)	Much of the warmer and, especially the drier regions of Africa south of the Sahara including Senegal, Nigeria, Kenya, Tanzania, Angola, and possibly Guinea (Bissau). Southern African distribution: Fig. 12
	21-26°S	14,2-17,7	14,6-25,2	325-ca775	150-1717		
	26-31°S	14,8-17,6	16,2-22,7	200-900	91-1335		
	15-30°S	14,2-18,4	16,2-25,5	200-1000	58-1717		
T. dimidiatus.	16-21°S	16,6-18,4	20,6-25,5	457-1000	58-1274	Elephant Rhinoceros (1)	Eastern Africa from Natal to Uganda including Kenya and E.Zaire. Southern African distribution: Fig. 14.
	21-26°S	16,6-17,7	21,7-25,5	ca450-590	300-462		
	26-31°S	-	-	-	-		
	15-27°S	16,6-18,4	20,6-25,5	ca450-1000	58-1274		

**Information on *O. pictus orientalis*, a subspecies from east central Africa has been included for purposes of comparison with *O. pictus pictus*. Temperature and rainfall data has been drawn from Rwindi (1040 m) which is 40 km south of the type locality of *O. pictus orientalis* (Bitshumbi, which is alternatively spelt, Vitshumbi).

3. METHODS

As Bornemissza (1969) suggested that endocoprids might be of extensive use in Australia for combatting dung breeding flies, the basic purpose of the present study was to determine whether they would, in fact, be beneficial in this respect and to study the feasibility of their introduction into Australia (Chapter 7).

Methods employed in the field were developed primarily to show the ecological relationships between endocoprids, dung and activity by other dung beetles. Since the results of these investigations indicated that any relationships between endocoprids and dung breeding flies would probably be somewhat tenuous, no further research was carried out in this direction.

In the laboratory, methods were developed for breeding endocoprids under artificial conditions and for providing the largest numbers of eggs within the shortest possible time. These methods were restricted to the simplest possible procedures with a view towards facilitating handling of the group should introduction to Australia be considered desirable. These, and additional methods employed in the laboratory provided much data on the life histories and biology of available endocoprid species.

3.1. Field Studies

Field Monitoring at De Wildt (Chapter 5)

In addition to the purposes outlined above, field monitoring was conducted to determine how annual activity patterns and fluctuations in the relative abundance of endocoprids are directly and indirectly influenced by the endocoprid habit.

The site ......

The site chosen for this exercise was a field of indigenous grassland near De Wildt (22 km WNW of Pretoria) where three species of endocoprid occur sympatrically *(O. planatus, O. formosus* and *O. egregius)* De Wildt, with a mean, annual, surface temperature of approximately 18,7°C, stands at approximately 1300 m and receives an average, annual rainfall of 700 mm which falls mostly between October and April.

Once a month, dung dropped by pasture and/or hay fed cattle was collected at Rietondale Experimental Farm (Pretoria) to provide standard pads for sampling. The differences between individual pads were expiated by adding a little water and mixing the dung to an homogenous consistency which was maintained at an approximately standard value throughout the experimental period (ca 78% water content by weight).

In the middle of each calendar month, this dung was transported to De Wildt where, between 09h00 and 12h00, 60 pads were set out in five lines of 12 per line. These dung pads of about 1,75 litres each were dispensed from standard measuring containers and deposited at approximately 4 m intervals along each line. The distance between lines was about 14 m. Each pad was moulded into a semi-spherical shape. Relocation and identification was facilitated by the use of bright red numbered stakes which were placed alongside. Cows were present in the field, but their interference with monitoring pads was minimal.

For the first two days, and during subsequent collections, a visual estimate was made of percentage dung removal from all pads. This could not be measured accurately as pads could not be disturbed prior to their scheduled date of retrieval.

The 60 pads were divided into four sub-samples of 15 pads each and their remains, after dung beetle activity, were collected, three per row, on the third, seventh, fourteenth and twenty-first days after setting. The timing of the collections was determined after preliminary observations of endocoprid behaviour. When a pad was sampled, note was taken of the position of any endocoprid brood chambers and the species of endocoprid present therein. After the recording of data, pads were scooped up with a trowel, together with any loose underlying soil, and placed in a polythene bag with the respective numbered stake. The samples were returned to the laboratory in Pretoria where any brood balls present were removed, counted, their diameters measured, note taken as to whether the contained larvae were alive or dead, and, if alive, general stage of larval development recorded (i.e. egg, first or second instar larvae). The remnants of the pads, if dry, were then broken up and sieved to separate the beetles. If wet, they were broken up in a large container of water to isolate the beetles by flotation. Usually a large amount of other floating material would rise to the surface. This was strained off and sorted manually on a tray.

Extracted endocoprid beetles were identified, sexed and counted. Once they could no longer interfere with the current monitoring they were released at the De Wildt monitoring site. Note (species, sex and number) was also taken of any beetles other than endocoprids, found in the pads but these data were unacceptable as a quantitative record owing to the number of specimens (paracoprids) which remained in their burrows under the dung during sampling.

In mid April 1975, a burst dam inundated the field and forced the discontinuation of monitoring.

Field monitoring to detect freshly emerged beetles (Chapter 5.5)

Subsequent to the abandonment of monitoring, a method was discovered of differentiating freshly emerged from older endocoprids. As this enabled determination of whether fluctuations in endocoprid numbers were due to physical factors or, at least partially due to influx of freshly emerged beetles, monitoring was recommenced at De Wildt in February 1976 when the flood waters had subsided and the ground surface was no longer saturated.

In the genus *Oniticellus* (*s.str.*), the posterior, dorsal margin of the elytra bears a row of relatively elongate setae. In young specimens these are complete but with increasing wear, as the beetle ages, they are gradually broken off until in the most worn specimens they are absent. The amount of wear was divided into three stages, as follows:-

(1) Setae more or less intact - young/recently emerged beetles.
(2) Setae thinned out but still present as tufts etc. } older
(3) Less than five setae of the original complement remaining.} beetles

Under laboratory conditions it was shown that within approximately four weeks the amount of wear exhibited by beetles of the same age could be at either stage two or three. Therefore this method is not valid as an indication of gross age structure of endocoprid populations.

To detect freshly emerged beetles the same procedure as described for field monitoring was again utilised except that commencement was at the beginning of each calendar month and only 30 pads were employed. These were distributed in two rows of 15. Collections were made in two samples of 15 pads, (eight and seven per row). During the warmer months (February to

April)......

April) collections were made on the third and seventh days. During the cooler months (May to June) the collections were made on the seventh and fourteenth days whilst during the coldest month (July) pads were retrieved on the fourteenth and twenty-first days. The pattern of collections was designed after evaluation of the results of the first monitoring exercise. Collections were timed to coincide with peak presence of endocoprids in the monitoring pads. The recording of data was as for field monitoring but, in addition, the state of setal wear was noted for each endocoprid recovered. This second monitoring exercise was discontinued in August 1976 owing to the small numbers of endocoprids which were being attracted.

3.2. Laboratory studies

Life history studies (Chapter 4).

Endocoprids breed by excavating chambers in, or immediately beneath, dung pads in which modelled balls of dung are constructed. The larvae develop within these brood balls. (Chapter 4).

Life history studies of *O. formosus* and *O. planatus* were made in plastic containers (32,5 x 21,5 x 16 cm). Five to ten centimeters of loose soil was placed in each and fresh pads of 1,5 - 2 litres of cow dung were placed at one end. Pairs of beetles were introduced to each pad (termed setting). After 3 - 7 days a small pad (approx. 0,2 litres) was placed at the opposite end of each container to attract the endocoprids as they emerged from the large pads. These small pads were checked for emerged endocoprids every 3 - 4 days and replaced with fresh dung. When a male emerged it was placed with food in a small pot until the exit of the female from the large pad.

Once ....

Once the female had left, the large pad was checked for the position of the brood chamber, the number of contained broods was counted and the stage of larval development recorded. If the larvae had died the approximate stage at which death had occurred was determined from the size of the larval cavity. The length of the breeding cycle was taken from the time of setting until the time of female emergence (or emergence of the filials). As laboratory breeding did not usually commence until the pad was an average of 6 - 8 days old, seven days were subtracted from each total in Tables 17 to 19 for a more accurate assessment of the length of the breeding cycle.

At times, some of the filial beetles emerged with or before the parent female. In this case the same procedure as above was followed and the parent was separated from the filials by inspection of setal wear.

A similar procedure was used for cultures of *O. egregius* and *T. dimidiatus* except that larger containers were used (44 x 35 x 20cm) and pairs of beetles were placed on 3 - 4 litres of white rhinoceros dung obtained from Pretoria Zoo. After the emergence of the female, the parent pairs of all species were immediately reintroduced to a fresh pad. This procedure was continued until the death of the female.

"Induced" brood ball production (Chapter 4)

If, instead of waiting for the female endocoprid to emerge of its own accord, it was removed from a pad after a short period and introduced to another, it could be induced to lay more eggs in its lifetime than it would under natural conditions. This would be useful for producing large numbers of eggs within a short period for an introduction programme.

The ....

The setting procedure was the same as that described for life history studies except that the large pads were changed every two weeks in the case of *O. pictus*, *O. formosus* and *O. planatus*, every week in the case of *O. egregius* and every three weeks for *T. dimidiatus*. The broods were then counted and removed to other containers for artificial culturing. The parent beetles were reset. This procedure was continued until the death of the female.

Culturing endocoprid brood balls under artificial conditions.

Brood balls removed from dung pads were surrounded with slightly moist peat moss in closed plastic containers (25 x 17,5 x 8 cm or 20,5 x 10 x 6 cm). This partially reproduced the conditions encountered in the well aerated, endocoprid brood chambers.

Under natural conditions the brood balls are tightly packed within the chamber and moisture is slowly lost to the dry exterior. However, it was not advisable to crowd the broods under artificial conditions as a saturated atmosphere (indicated by condensation) could easily be created, especially by slightly overmoistening the peat. Such conditions resulted in the larvae broaching the brood ball walls forming large holes which were plugged by the extrusion of larval gut contents. This aggravated the effects of saturation by causing balls to congeal together and led to high larval mortality. This has never been observed in nature. At the end of the feeding period the gut contents are voided prior to pupation. Insufficient rapidity in the drying of broods at this stage of development was invariably fatal. It was found that a single layer of broods, each separated by a space of at least 1 cm filled with peat moss, gave the highest percentage survival rates. Emerged beetles were collected from the surface of the peat moss during the early afternoon. It was not necessary to water the broods of most species except, perhaps, those of *O. egregius* which were watered on occasion. (Chapter 4.6.).

Investigations of the method of brood ball construction by female endocoprids.

As most endocoprid activity takes place within the pad, observation of brood ball construction has proved difficult. The stages were therefore determined by disturbing breeding females. Brood balls are initially small and are elaborated to the finished size by the addition of dung to their exterior. This was demonstrated by disturbing endocoprid females at various intervals after setting in order to measure the diameters of the brood balls with callipers.

Experiment to determine whether variability in soil and dung moisture contents results in differences in the positioning of the brood chamber in *O. planatus*. (Chapter 4.2).

In the field, brood chambers of *O. planatus* are more often found in the soil immediately beneath dung pads. In the laboratory they are usually lodged in the pad. It was thought that chamber position might be controlled by differences in the moisture contents of dung and earth and this was tested in the laboratory.

Sixteen plastic containers (32,5 x 21,5 x 16 cm) were filled to a depth of 7 cm with a dry, measured mixture of one part sand to two parts river loam. The containers were divided into four sets of four, each given a different treatment and the earth firmly tamped down. These treatments were as follows:-

1) Left dry
2) 250 ml water added = 4% water content by volume
3) 500 ml water added = 9% water content by volume
4) 750 ml water added = 12% water content by volume

(2 to 4 - soil mixed by hand to an homogenous consistency.)

Cow dung was collected at Rietondale Experimental Farm and treated in four different ways. Five 1,5 litre pads were then measured out from the dung of each consistency by use of standard measuring containers. Each pad was weighed and one from each treatment was placed on each soil type to give the total of 16 different soil/dung combinations. The fifth pad of each dung moisture consistency was dried out and reweighed to determine percentage moisture content by weight. The percentage moisture contents by weight and treatments used for each of the four dung consistencies were as follows:

1) Percentage water content = 72% - Dryer than natural dung obtained by pressing freshly dropped manure between absorbent material for 24 hours.
2) Percentage water content = 75% - Naturally dropped dung.
3) Percentage water content = 82%) Water added. Dung and water mixed to
4) Percentage water content = 86%) an homogenous consistency.

Single pairs of *O. planatus* were placed in each container and left for two weeks. After the 14 days had elapsed, a record was made of the position of the brood chamber and the number and size of the brood balls in each. Each dung pad was also carefully scraped to remove adhering soil grains and then weighed.

Changes in the internal organs of brooding female *O. planatus* studied by dissection. (Chapter 4. 5)

During the larval development of most endocoprids, the female beetle tends the brood balls (termed brooding). As the pad quickly dries out and feeding is probably not possible, dissections of female *O.planatus* were conducted to investigate the gut contents and the state of other internal organs during brooding.

Twenty-five pairs of recently emerged *O.planatus* were set utilising the same method described for life history studies. After 14 days had elapsed, five pairs of beetles were removed and the females dissected. Further dissections were conducted at weekly intervals thereafter (i.e. three, four and five weeks after setting). Females which had emerged from the pads between five and six weeks after being set were placed in small containers with fresh dung and dissected nine days later.

During dissections, four different observations were made:

(i) State of the gut (full, partially full or empty)
(ii) Colour of the fat body (white or yellow)
(iii) Colour of the fluid in the haemacoel (colourless or yellow)
(iv) State of the ovary (differentiated into follicles, degenerating or undifferentiated).

The ovary was dissected out and stored with the beetle in 10% Formalin.

4. BREEDING BIOLOGY AND LIFE CYCLE

Much of the biology and behaviour exhibited in breeding activity by endocoprids is related to the fact that the brood chambers are positioned at, or close, to the surface of the earth. This has resulted in the restriction of breeding space whilst the mode and speed of brood construction has been influenced by physical factors and the likelihood of rapid desiccation. The speed and style of larval development has been unaffected by nidification behaviour and is similar to that of many other dung beetles, especially various *Onthophagus* species bred at the DBRU.

4.1. Reifungsfrass Period (Maturation Feeding)

Studies of various Scarabaeinae have shown that a period of feeding (on dung) is necessary in all freshly emerged adults before they attain sexual maturity. This has been termed the reifungsfrass period by German workers (Halffter and Matthews 1966 : 87). In the species of the European *Gymnopleurus* and *Sisyphus* studied by Prasse (1957a), this period has a duration of 3 - 3½ months. In species from the hot temperate regions of South Africa, the feeding period is often short, e.g. three days in *Onitis alexis* Klug, although it is of longer duration in more specialised species: 7 - 21 days in southern African *Sisyphus* (Paschalidis 1974 : 88) and approximately 21 days in *Kheper nigroaeneus* (Boheman) (Tribe 1976 : 87). Differences between the European and South African fauna are thought to be due to specialisation rather than temperature although there is no experimental evidence.

In *O. planatus*, the only endocoprid species for which the reifungsfrass period has been accurately determined, 9 - 11 days of

feeding ....

feeding was required (at a mean temperature of 25^{o}C) before females commenced laying eggs. As *O. planatus* colonises fresh pads, this feeding period does not affect potential brood production in the species because intact pads usually become suitable for breeding only after about seven days.

4.2. Brood Chambers

Endocoprid breeding commences with the excavation of a cavity (termed the brood chamber) in which the brood balls of most species are later constructed from dung shreds. Bornemissza (1969) defined this form of nidification as being confined to breeding inside dung pads. However, only three African species of endocoprid have been observed to conform to this definition (*O. formosus, O. pictus* and *T. dimidiatus*). The other two African species (*O. planatus, O. egregius*) are capable of constructing their brood chambers in a pit excavated from the soil immediately beneath the dung. In *O. planatus*, chambers situated in this position are most usually observed in the field whereas, in the laboratory, they are more often in the pad.

The literature suggests that *O. cinctus*, an Asian endocoprid, has similar habits to *O. planatus*, since although the definition of endocoprid nidification, formulated by Bornemissza (1969), was derived from this same Asian species bred in the laboratory, in Australia, Gardner (1929) had already recorded *O. cinctus* brood balls occurring immediately beneath dung pads in India.

In many months of breeding *O. egregius*, only four observations, from a total of 117, were made of brood chambers which had not been constructed in a shallow pit under the dung. In three of these cases the chamber was partially in the pad and partially in the soil. On the other occasion

the........

the base of the chamber was at ground level. It is not uncommon to find *O. planatus* chambers also positioned partially in the dung and partially in the soil.

These observations call for extension of the scope of the definition of an endocoprid breeder. Thus, I define the endocoprid method of nidification as constituting the construction of the brood chamber within or immediately beneath the pad. In the latter position the base of the pad usually forms the roof of the chamber, although, on rare occasions, some species may construct a short (not more than 2,5 cm) tunnel between chamber and pad. This has only been observed in the laboratory.

The manner in which the pad is attacked may reflect the relative ability of each endocoprid species to withstand desiccation and may be utilised to control or reduce the speed of water loss around the brood chamber. In *O. planatus*, which has been observed to require moister conditions than *O. formosus*, dung burrowing results in a series of distinct branching and anastimosing tunnels. Whatever the pad moisture content, *O. planatus* brood balls are always tightly packed within the brood chamber which has a smooth, well defined wall and a single entrance hole. Dung burrowing, by *O. formosus*, is characterised by shredding, i.e. the undigested, fibrous material is loosened and separated which allows air to permeate the spaces and so increases the speed of desiccation. In the field, *O. formosus* brood chambers were usually sited towards the centre of the pad and little shredding was noted around the walls but, in the slower drying laboratory pads, the chambers tended to be sited superficially and a large portion of the pad edge was often shredded to form part of the brood chamber wall. Brood balls were sometimes pushed to the surface of these shreds so that they were in direct contact with the air. Therefore, in prolonged, wet conditions this

species .....

species is possibly able to actively modify the rate of desiccation by utilising shredding to increase pad moisture loss. This would be an advantage for this dry adapted species whose tolerance of wet conditions is low.

In addition to pad moisture content, the siting of the brood chamber is probably influenced by other microclimatic factors in the dung, e.g. temperature. A laboratory experiment conducted on brood chamber position in *O. planatus* (Chapter 3.2.), to show the effects of different dung and soil moisture contents, gave inconclusive results. Sixteen combinations of moisture content were utilised from abnormally dry to very wet. The resulting brood chambers were mostly confined to the dung indicating that moisture alone plays a minor role in influencing chamber position. Therefore, as *O. planatus* chambers are more often in the soil in the field, radiant heat from the sun and its effects on dung temperature might be a factor more likely responsible for the differences recorded in laboratory and field positions. It is possible that radiant heat might act in conjunction with its effects on pad moisture content, especially as there is probably greater insulation against heat and loss of moisture beneath the pad. Further tests need to be conducted on this aspect.

As a final comment on the factors influencing brood chamber position, the siting of those of *O. egregius* may be dictated by physical requirements in the mode of brood construction, especially in the production of a clay shell around each brood "ovoid". (Chapter 4.3).

The numbers of brood chambers per pad was usually low and probably reflected restricted space for chamber construction. Observations, at De Wildt, showed that a single cow pad often supported only one brood chamber. The incidence of two chambers was much less common whilst the occurrence of three and four was each noted on two occasions only. In all De Wildt monitoring pads with two brood chambers, *O. formosus* was breeding in the pad and *O. planatus* in the soil. This behaviour would tend to reduce pressure for breeding space in the pad, and, many other observations made of multiple chambers involved these two species in a similar relationship with a maximum of two chambers actually in a pad. The only occasion on which more than two chambers have been observed in a cow pad,occurred near Pietersburg (23^{0} 56'S 29^{0} 29'E), where a large pad was found to house four small *O. formosus* chambers containing a combined total of 15 brood balls.

The abundance of endocoprid dung beetles is generally low over their entire range. A total of one to four per pad (total number of *O. formosus* and *O. planatus*) or one to three per pad (total number of each sex of both species) was most usual at De Wildt (Figs. 15 - 21). In 80% of the samples of 15 pads, collected during field monitoring, less than 50% of the pads of each sample contained endocoprids. (Table 11).

However, the abundance of endocoprids was sometimes relatively high, at De Wildt, but whilst results show that 11,2% of the pads colonised during the breeding season contained more that one female endocoprid, only 1,6% of these pads contained more than one brood chamber. (Fig. 17 and Table 12).

TABLE 11 ......

TABLE 11: Showing the number of pads from each De Wildt, monitoring sample (15 pads) which contained endocoprids.

Number of pads in each 15 pad sample containing endocoprids.	No. of 15 pad samples	% of the total number of 15 pad samples taken.
0	7	10
1	16	22
2	8	11
3	5	7
4	4	5
5	7	10
6	4	7
7	9	12
over 7	12	16
TOTAL	72	100

TABLE 12 Number of endocoprid brood chambers per pad in De Wildt monitoring pads.

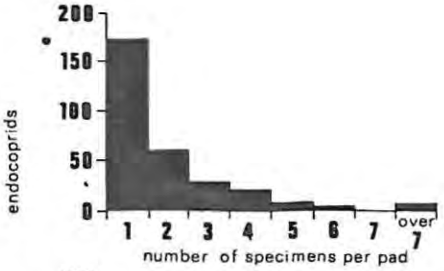
No. of Brood chambers per pad.	No. of pads with brood chambers	% of Total..
1	67	93
2	4	6
3	1	1
Total	72	100

FIGURES 15 to 21

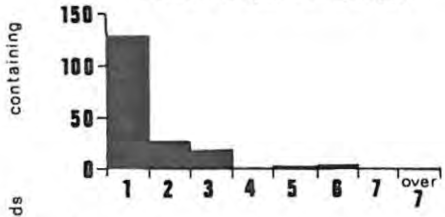
Numbers of adult endocoprids collected from individual monitoring pads at De Wildt. Of a total of 1080 pads set, only 305 were colonised by endocoprids. Of the remaining 775, 23 were removed by children prior to sampling.

FIGURE 15	Total number of endocoprids per pad (*O. planatus* and *O. formosus* males and females).
FIGURE 16	Total number of male endocoprids per pad (*O. planatus* and *O. formosus*).
FIGURE 17	Total number of female endocoprids per pad *O. planatus* and *O. formosus*).
FIGURE 18	Total number of *O. formosus* per pad (males and females).
FIGURE 19	Total number of *O. planatus* per pad (males and females).
FIGURE 20	Number of *O. formosus* females per pad.
FIGURE 21.	Number of *O. planatus* females per pad.

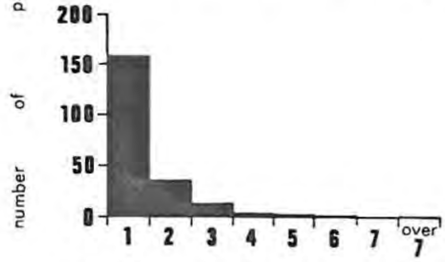
15



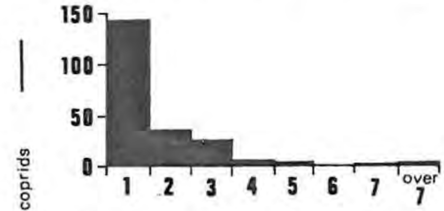
16



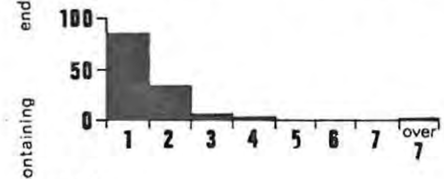
17



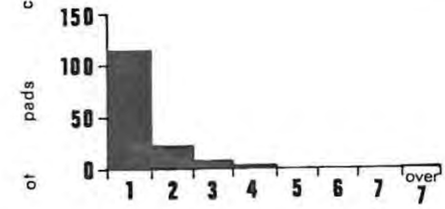
18



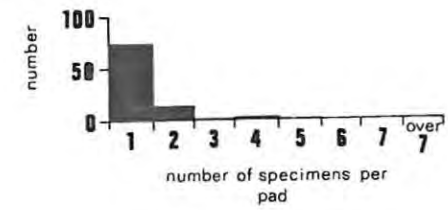
19



20



21



It is less likely that the low incidence of more than one chamber per pad can be explained in terms of the immaturity of the extra females in the remaining 9,6% of the pads since maturation feeding and commencement of breeding in *O. planatus* was accomplished in the same pad, although this was admittedly under laboratory conditions. A more feasible explanation might be furnished by the observation that, at De Wildt, breeding had occurred where three *O. formosus* females occupied the same pad on only two occasions. In each case, only one brood chamber was constructed and each contained only a single brood ball. On this evidence it might be tentatively suggested that, in cow pads, competition for breeding space between three or more (and perhaps, sometimes, even two) females of the same endocoprid species might inhibit each other's breeding activity. If correct, and this can probably be tested by simple field experiments, this will have a significant effect on adult numbers and the group's usefulness in the Australian dung control project. (Chapter 7).

4.3. Manner of Brood Construction

Two main divisions are exhibited in endocoprid brood construction. The method utilised by *O. egregius* allows it to commence breeding in relatively fresh dung (approximately four days old). Examination of the procedure employed suggests it has been modified only slightly from that utilised by *Euoniticellus* and *Onthophagus* (Chapter 8). The other endocoprid species, whose breeding is largely restricted to dung pads, commence breeding only in much drier dung (approximately seven days old). This has strongly influenced the methods utilised for constructing brood balls although it appears that these methods, at least in *O. planatus*, may have evolved from the *O. egregius* style of construction (Chapter 8). Usually more than one brood ball is constructed in each chamber.

In *O. egregius* ....

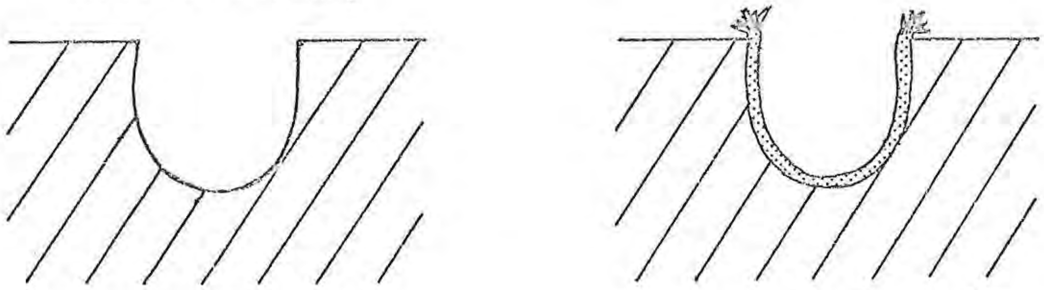
In *O. egregius*, brood construction (Fig. 22) commences with the excavation of a depression in the soil, approximately 2 cm deep by 1,5 cm in diameter. This is lined with dung transported from the overlying pad and is progressively thickened by the internal application of further dung to form the wall of the future brood ovoid. The female lays in the rudimentary egg chamber, and it appears that by pushing its legs outwards, it levers the prothorax against the opposite wall so wedging itself firmly in position to provide a stable base from which to compress the dung between its flattened head and the side of the depression. It is unknown whether the legs play an active part in the packing of the wall. This procedure has a dual effect. In increasing the density of the wall, much of the contained moisture with its suspension of small particles, is squeezed to the surface of the egg chamber. This provides moisture for the support of the egg and food with a fine grained matrix easily utilisable by a small larva. The egg chamber is comparatively large and the egg is laid on end at its base. The top of the brood ovoid is then sealed. The fibres which protrude from the rim of the fully lined depression probably aid closure. This forms a brood in which the base and sides of the wall are of uniform thickness (Fig. 22e). It is probable that the earth adhering to the outside of the compressed walls is tamped down to form the fine grained, hard, clay shell which constitutes the final stage of brood production in *O. egregius*. Brood ovoids are completed one at a time. In this way the brood chamber is extended in size with each successive brood. The chamber is lined with dung and a little loose fibre often lies between the broods.

Figure 22:

Manner of brood ovoid construction in *O. egregius*.

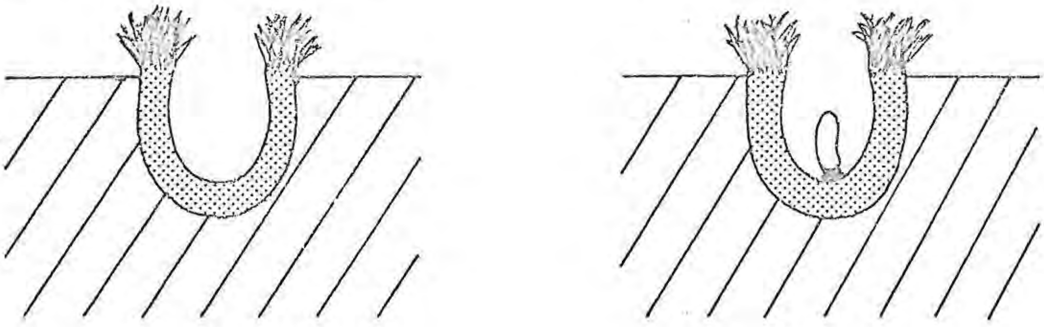
a) Pit excavated in the earth beneath dung

b) Pit lined with dung



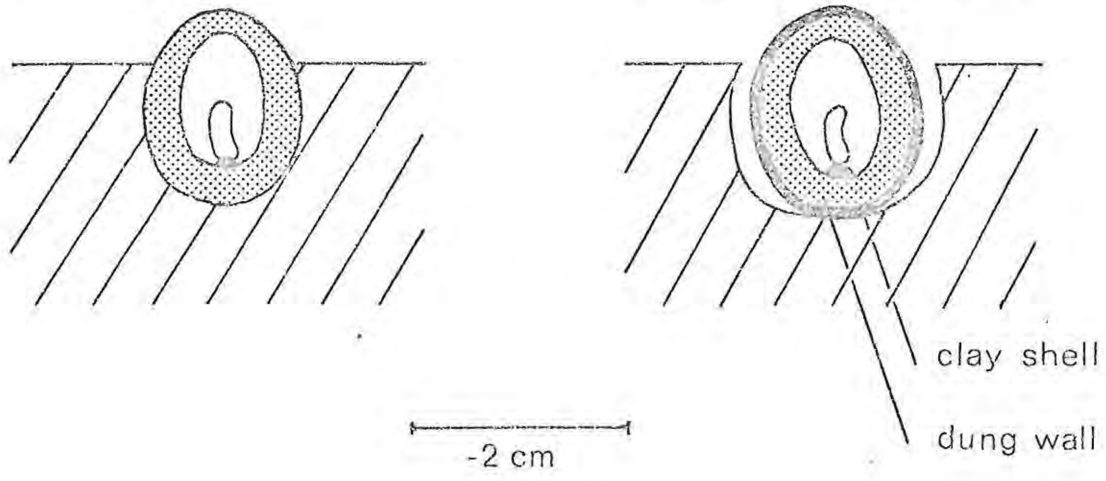
c) Dung lining thickened

d) Egg laid



e) Brood sealed

f) Clay shell constructed



Several observations have been made of the male and female together in the egg chamber and it is possible that mating takes place there, but co-operation between the sexes in actual brood construction has not been observed in any endocoprid.

In *O. planatus* (Fig. 23), if the chamber is constructed in the pad, a small area is shredded to commence brood production. If constructed in the soil, dung shreds are removed from the pad to fill the small excavation. The female burrows into the centre of these shreds and commences pressing the dung outwards in a manner similar to *O. egregius*. The portion of the brood ball wall which forms the lower sector of the future egg chamber (Fig. 23c), is compressed against the base of the brood chamber or previously constructed balls, but it is not clear whether, or not, more dung is added internally to increase the thickness of this wall. The egg is laid on end at the base of the egg chamber, and the ball is sealed and rounded off. Whether all loose particles (Fig. 23e) are removed from the outside or incorporated in the ball is unknown. This initial brood ball is left and another is commenced. Later when egg laying is complete, further dung is added to the outer wall of each ball (termed elaboration), increasing its diameter by about 2 mm (Table 13). Chambers continue to be increased in size only with each successive brood.

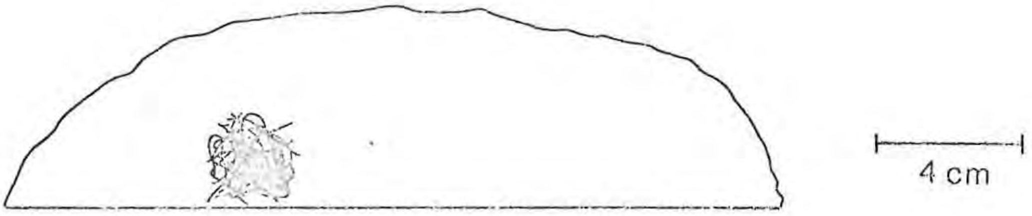
This method of brood production apparently contrasts with that described by Bornemissza (1969) for the Asian endocoprid, *O. cinctus*, where the egg was laid first and the ball built around it. However, this could be construed as referring to the "cup" stage of brood construction in *O. planatus*. (Fig. 23d).

No ....

Figure 23:

Manner of brood ball construction by *O. planatus*.

a) Brood chamber excavated by shredding dung

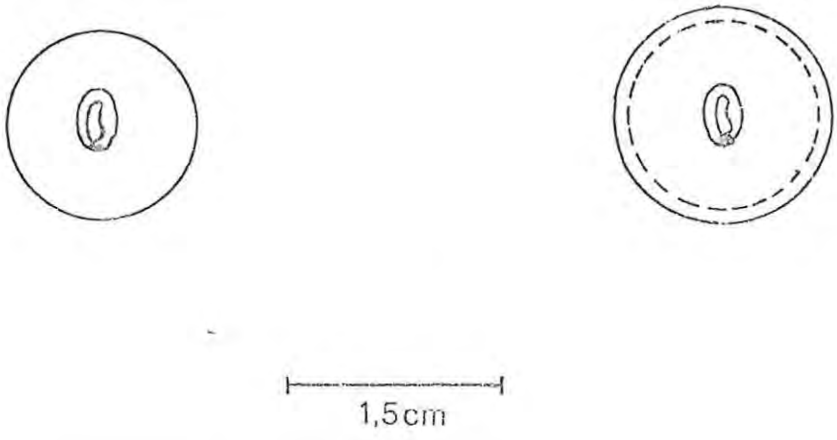


b) Female makes pit in shreds

c) Lower portion of pit compressed against base of brood chamber

d) Egg laid (= "Cup Stage")

e) Ball sealed



f) Walls smoothed

g) Ball elaborated by addition of dung after termination of egg laying

No observations have been made of the early stage of brood construction by *O. formosus* and *T. dimidiatus* but the initial brood balls of each are considerably smaller than those of *O. planatus* relative to the size of their completed broods. Like those of *O. planatus* they are elaborated with drier dung, once egg laying has terminated, so that about 5 mm is added to the diameter of each ball (Table 13).

TABLE 13

Elaboration (increase in the diameter of initial brood balls by application of further dung) (Fig. 23g) in two species of endocoprids.

SPECIES	INITIAL SIZE (cm)		FINISHED SIZE (cm)		Mean increase in diameter (cm)	n
	Mean	Range	Mean	Range		
O.planatus	3-7 days after setting		8-12 days after setting		0,23	34
	1,13	1,04 - 1,28	1,36	1,25 - 1,5		
O.formosus	7 days after setting		13 days after setting		0,46	53
	0,89	0,75 - 1,1	1,35	1,03 - 1,6		

In the soil, excess moisture, derived from the compression of fresh dung by breeding female Scarabaeinae, is probably absorbed into the burrow or chamber walls. In dung pads, the absence of a well developed moisture gradient, immediately beyond the boundaries of the chambers, may explain why all African endocoprids, except *O. egregius*, breed in older pads when the process of desiccation is well advanced.

In ....

In these older pads, the moisture content only remains suitable for endocoprid brood production over short periods so that the emphasis is on rapidity in egg laying. This is exemplified by *O. formosus* and *T. dimidiatus* where economy in time and labour, during egg laying, is achieved by merely enclosing each egg in a small, compact, brood ball which is perfectly adequate for short term protection. Further dung, to bring each ball up to finished size, is only added after egg laying has terminated which suggests that elaboration does not require such moist dung and, therefore, does not interfere with egg laying. The addition of dung results in the spherical broods, characteristic of most endocoprid species, in which the egg chamber is central and equally well protected against desiccation on all sides.

At least one field observation suggests that elaboration of the initial broods is essential for larval survival. Near Pietersburg, two out of eleven *O. formosus* broods recovered from a single chamber, remained small and unelaborated. Both contained dead larvae.

4.4. Life Cycle

After the initial maturation feeding, the newly emerged female mates and commences constructing brood balls of dung as described in the previous sections.

The single egg laid in each brood ball hatches within approximately four days, (n = 12) in *O. planatus* (at 31,3^{o}C), and then passes through three larval instars (Fig. 24). As the young larva feeds, utilising its well sclerotised chewing mouthparts to cut particles of dung from the egg chamber wall, it enlarges the cavity to accommodate its increased size. The dorsal hump, containing a diverticulum of the gut,

FIGURE 24

Generalised life cycle of an endocoprid dung beetle.

a) Brood ball with egg

b) 1st instar larva

c) 2nd instar larva

d) 3rd instar larva

e) prepupa

f) pupa

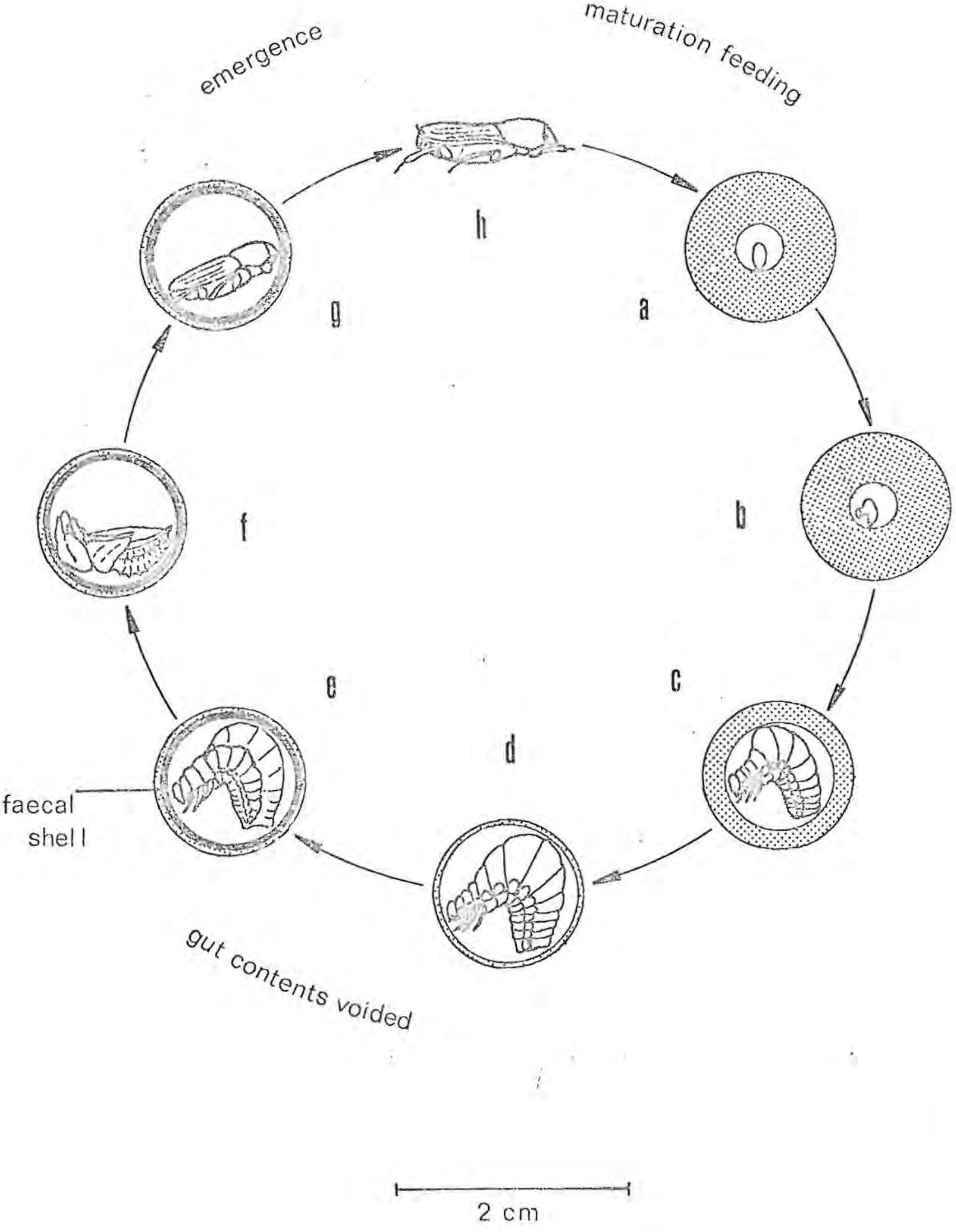
g) Sclerotising teneral adult

h) Adult flies to dung

Brood balls drawn in transverse section.

See text for explanation.

24



emergence
maturation feeding
h
g
a
f
b
e
c
d
faecal shell
gut contents voided
2 cm

Is typical of scarabaeine larvae and, used in conjunction with the truncated, pygidial segment, aids movement within the ball and allows the larva to wedge itself in position during feeding (Fig. 24d). The larva quickly increases in size and soon reaches the third larval instar which is the longest in duration. In *O. planatus*, larval development takes from 11 to 13 days (mean, 11,8 days; n = 6), at a mean tempterature of 31°C. The parent females of most endocoprid species remain in the brood chambers tending the brood balls until, at least, the end of the third larval instar. (Chapter 4.5.).

Once feeding has been completed, the mature, third instar larva extrudes its gut contents over the wall of the larval cavity, and, taking on a wrinkled, yellow appearance, enters the dormant prepupal stage which, in *O. planatus*, lasts approximately 1 day (n = 6). The gut contents dry out to form a hard, faecal shell. The pupa is equipped with dorsal projections which prevent direct contact with the moist, brood ball wall and, in *O. planatus*, this stage lasts six days at 31,3°C (n = 11). The teneral adult does not break through the brood ball wall immediately but remains dormant whilst completing sclerotisation which takes approximately 2 - 3 days in *O. planatus*. Sclerotisation commences during the late pupal stage. All immature stages of *O. planatus* were bred at a constant mean temperature of 30,5 - 32°C (range 26,5 - 34°C) in thermostatically controlled rooms subjected to 24 hr artificial lighting. Under these conditions brood balls were constructed at a rate of 3 - 4 per day.

New adults emerge by eroding the thinnest part of the brood ball wall using their clypei and prothoracic legs. In *O. egregius*, which is the only endocoprid species whose broods possess a readily discernible orientation, this is at any point on the circumference

immediately/......

immediately beneath the apex. It is unknown whether any particular orientation is exhibited by the spherical broods of the other species but those of *O. formosus* often dry to a very hard consistency and emergence is aided by the presence of a thin spot in the brood ball wall. This spot only becomes detectable during the third larval instar and may represent the last feeding centre. The head of the pupa is always to be found behind this spot. One observation of the edges of the emergence hole of an *O. formosus* brood being soft and moist, after the recent emergence of a new adult, may indicate additional aids employed during emergence by this species. The brood balls of another dry adapted species *T. dimidiatus*, also show the same feature whereas, in *O. planatus*, thin spots, if present, are poorly developed.

The timing of dung beetle emergence correlates with the period of flight activity exhibited by each species. The crepuscular flying *Onitis*, *O. crenatus* Reiche and *O. alexis* Klug, usually emerge at dusk but the genera *Oniticellus (s. str.)* and *Tragiscus* are strictly diurnal and emergence of new adults occurs during late morning to early afternoon apparently when temperatures have risen above a critical value (approx. 27°C in the laboratory for *O. formosus*). In blacked out constant temperature rooms subjected to 24 hr artificial lighting, *O. planatus* were recorded as having emerged at various times of the day from 09h30 to 16h00.

In the laboratory, pairs of *O. planatus* were bred in constant temperature rooms at 25°C, 28°C and 32°C. These temperatures fluctuated from 25°C to 34°C. No breeding was recorded at a mean constant temperature of 20°C. Table 14 shows the increase in duration of the development period (from the egg to the freshly emerged adult) with decrease in mean temperature. This varied from 24 - 28 days at 27,5°C - 28°C (mean 26,5 days, n = 31) to 21 - 27 days at 31,5°C - 32°C (mean, 23,8 days ; n = 40).

Optimum ....

TABLE 14:

The relationship between temperature and the duration of development (from the egg to the freshly emerged adult) in *O. planatus*.

Mean temp. °C	Duration of development in days		n
	Mean	Range	
27,5	27,5	27 - 28	8
27,6	27	27	1
27,8	26,5	25 - 28	16
28,1	25	24 - 26	5
29,8	22	22	3
30,9	22,5	21 - 24	12
31,3	21,5	21 - 22	2
31,5	23,3	21 - 24	16
31,6	23,8	22 - 26	31
31,8	25,5	24 - 27	5

Optimum temperatures for development were shown to be between 29,8°C and 31,3°C (21,5 - 22,5 days).

Under laboratory conditions, dung pads dried out slowly owing to the absence of radiant heat from the sun, the restriction of air flow and limited drainage. Many of the broods constructed in these pads died before development was complete and, as Paschalidis (1974 :110) showed that prolonged exposure to excessively moist conditions, "over 12%", killed the immature stages of *Sisyphus*, it is thought that the same factor may have been responsible for the death of endocoprid larvae. The percentage mortality in laboratory life histories is shown in Table 15.

TABLE 15:

Percentage mortality of the immature stages of *Oniticellus (s.str.)* species in laboratory life histories recorded at the time of parental emergence from the brood chamber after brooding.

SPECIES	% larval mortality in laboratory life histories	n	Total number of immature stages
O. planatus	85	852	1000
O. formosus	73	535	732
T. dimidiatus	22	13	60

Table 16 shows that the most vulnerable stage during the larval development of *O. planatus* and *O. formosus* is the point of transition between larva and pupa. Since the larval gut contents are voided at the end of the feeding period it is thought that the major, contributory factor towards mortality at this stage was the slow rate of desiccation of these voided gut contents. The greatest larval mortality in *T. dimidiatus* was at the egg to first instar larval stage.

(Table 16) ....

(Table 16). Excepting a small peak in mortality at the same stage in *O. planatus*, larval death during other stages was minimal in all endocoprids. It is not known whether excess moisture was the direct cause of death or whether it merely promoted conditions suitable for pathogenic organisms.

TABLE 16:

Observed mortality of the immature stages of *Onticellus (s.str.)* species in the laboratory (expressed as percentages of total mortality).

	Percentage died as					
SPECIES	eggs/1st instar larvae	2nd instar larvae	3rd instar larvae/prepupae	pupae	teneral adults	n
O. planatus	8	1	88	3	0	852
O. formosus	1	0,5	96	2	0,5	535
T. dimidiatus	85	0	15	0	0	13

4.5. "Brooding" behaviour (Brutpflege)

The females of certain genera of the subfamily Scarabaeinae remain in attendance in their brood chambers during larval development. As "parental care" in dung beetles is indirect and less complex than the intensive larval supervision (brood care) exhibited by some other groups of insects this behaviour is termed "brooding".

Brooding has been previously reported from only the Coprini and the Scarabaeini but, during this study members of a third tribe, the Oniticellini have also been shown to exhibit similar behaviour. In the Coprini, various American (e.g. Lindquist 1935) and European (e.g. von Lengerken 1954) workers, have recorded brooding in a number of Copris species of the northern hemisphere and in the genus *Synapsis* (Halffter and Matthews 1966: 165). In the Aethiopian zoogeographic region brooding has been demonstrated in various *Copris* studied at the DBRU, e.g. *C. fidius* and *C. fallaciosus* Gillet, and in two *Heliocopris* species, *(H. japetus* Klug and *H. hamadryas* (Fabricius)), investigated by Klemperer and Boulton (1976).

In the Scarabaeini, brooding was reported to be exhibited by three South American species of *Canthon* (Judulien 1899) but this observation has not been confirmed (Halffter and Matthews 1966: 166). However, Tribe (1976) gave a detailed description of brooding behaviour in *Kheper nigroaeneus* (Boheman) an African member of the tribe.

In the Oniticellini, most members of the genera, *Oniticellus (s.str.) (O. planatus, O. formosus* and *O. pictus pictus*) and *Tragiscus (T. dimidiatus)* occurring in southern Africa, have been found to exhibit brooding. The only exception is *O. egregius* which abandons its broods soon after egg laying has terminated. The occurrence of brooding behaviour in three tribes whose phyletic lineage is held to be so widely divergent (Halffter and Matthews 1966: 198), would suggest its independent evolution in each group.

The duration of both larval development and brooding activity is dependent on temperature. The increasing duration of the brooding period with decrease in mean temperature is shown in Tables 17, 18 and 19 for three species of endocoprid studied at the DBRU.

The stages ....

TABLE 17:

Duration of the breeding and brooding period with decreasing mean temperature in *O. planatus*. Numbers represent the period between the approximate time of commencement of breeding and the emergence of the parent female (or emergence of the filials) from the brood chamber. Seven days have been subtracted from the original data to allow for the mean duration of the pre-breeding period.

For example, at a mean temperature range of 27°C - 26°C, brooding females were recorded as having left the brood chamber after a mean period of 37 days when the progeny had died at the 3rd larval instar/ prepupal stage, after 39 days when the progeny had reached the teneral adult stage and after 40 days if they emerged with the first filials. The mean duration of the breeding and brooding period in each column relates to the most advanced immature stage in each brood chamber. The overall percentage breakdown of stages of development at the time of parental emergence from the brood chamber has been recorded in Table 20 for *O. planatus*, *O. formosus* and *T. dimidiatus*.

Mean Temp. range °C	Most advanced immature stage of progeny recorded at the time of emergence of the brooding female from the brood chamber				Range of duration of breeding and brooding period (in days)	n
	3rd instar larva/ prepupa dead	pupa	Teneral adult	Filial adults (parent emerged with filials or filials emerged before parent)		
	Mean duration of breeding and brooding period (in days)					
29-28	29	-	-	-	27-30	2
28-27	35	-	-	-	32-42	12
27-26	37	-	39	40	(29)33-42	18
26-25	37	-	-	45	31-47	4
25-24	38	-	-	34	31-42	9
24-23	41	-	53	49	38-53	7
23-22	-	-	-	-	-	0
22-21	-	51	53	-	47-56	8

TABLE 18 ....

TABLE 18:

Duration of the breeding and brooding period with decreasing mean temperature in *O. formosus*. Numbers represent the period between the approximate time of commencement of breeding and the emergence of the parent female (or emergence of the filials). Seven days have been subtracted from the original data to allow for the mean duration of the pre-breeding period. The mean duration of the breeding and brooding period in each column relates to the most advanced immature stage in each brood chamber. An example to aid interpretation of Tables 17 to 19 is given in the legend of Table 17.

Mean Temp. range °C	Most advanced immature stage of progeny recorded at the time of emergence of the brooding female from the brood chamber				Range of duration of breeding brooding period (in days)	n
	3rd instar larva/ prepupa dead	pupa	Teneral adult	Filial adults (parent emerged with filials or filials emerged before parent)		
	Mean duration of breeding and brooding period (in days)					
29–28	–	–	–	–	–	0
28–27	38	35	36	–	32–42	8
27–26	40	37	39	38	34–42	8
26–25	45	–	–	–	23–45	3
25–24	37	37	–	43	28–45	5
24–23	44	43	–	–	28–49	6
23–22	–	52	–	–	50–53	1
22–21	–	50	–	–	36–64	2

TABLE 19 ....

TABLE 19:

Duration of breeding and brooding period with decreasing mean temperature in *T. dimidiatus*. Numbers represent the period between the approximate time of commencement of breeding and the emergence of the parent female. Seven days have been subtracted from the original data to allow for the mean duration of the pre-breeding period. The mean duration of the breeding and brooding period in each column relates to the most advanced immature stage in each brood chamber. An example to aid interpretation of Tables 17 to 19 is given in the legend of Table 17.

Mean Temp. range °C	Most advanced immature stage of progeny recorded at the time of emergence of the brooding female from the brood chamber				Range of duration of breeding and brooding period (in days)	n
	egg dead	1st instar larva dead	3rd instar larva	Pupa		
	Mean duration of breeding and brooding period (in days)					
25-24	12	-	-	-	8-18	2
24-23	15	-	40	46	12-46	5
23-22	-	18	48	-	16-48	2
22-21	30	-	-	-	28-32	1

The........

The stages of larval development, reached at the time of parental departure from the brood chambers, may reflect relative viability of the final immature stages of these three species. In *O. planatus*, the parent remained in the chamber until, or even after, the emergence of the first filial adults in almost half of the recorded cases, whereas, in *O. formosus*, over half of the progeny were only at the pupal stage when the parent departed. In *T. dimidiatus*, the majority of the larvae had only reached late third instar before the departure of the parental females. (Table 20). In this latter species, if the larvae died whilst young, the parent beetle abandoned the chamber (Table 19).

TABLE 20: Stage of development of the immature stages of three species of endocoprid at the time of parental departure from the brood chamber after brooding. Figures expressed as percentages of the total number of immature stages.

	Percentage at the							
SPECIES	Egg 1st instar larval stage.	2nd instar larval stage	3rd instar larval stage	Pre-pupal stage	pupal stage	Teneral adult stage	% of Emerged filials	n
O. planatus	0	0,7	0	2	31,1	20,3	45,9	148
O. formosus	0	0	2	8,6	55,9	27,9	5,6	197
T. dimidiatus	0	0	92	0	8	0	0	47

Table 21 ....

Table 21 shows that in *O. planatus*, the pattern of emergence differs according to temperature since above 23°C filial emergence was generally with or before that of the parent whereas below 22°C parental emergence occurred whilst the majority of offspring were at the pupal stage.

TABLE 21:

The timing of emergence from the brood chamber, after brooding by *O. planatus* females at different temperature ranges.

Numbers expressed as percentages of the total number of immature stages.

Mean Temp. range °C	Immature stage of progeny when parent emerged			n
	% at the pupal stage	% at the Teneral adult stage	% of filial adults (filials emerged with or before parent.)	
29-23	22	34	44	100
22-21	68	32	0	25

As the males of endocoprid species do not assist in brooding they usually spent less time in each laboratory pad than the females (Tables 17, 18 and 22). The duration of colonisation by males was however, relatively prolonged and was probably influenced by the slow rate of pad desiccation in the absence of radiant heat from the sun. Similarly, as brooding activity is not exhibited by *O. egregius*, both sexes usually departed from the pad after only 8 - 13 days.

TABLE 22 ....

TABLE 22:

Duration of pad colonisation by the males of *O. planatus* and *O. formosus* in laboratory life histories.

	Duration of pad colonisation (days)	
	O. planatus	*O. formosus*
mean	26	30
range	11 - 58	11 - 49
n	71	31

Halffter and Matthews (1966: 243) state that adult Scarabaeinae feed on "more or less fresh dung". Therefore, as endocoprids spend most of the brooding cycle in dry dung, female *O. planatus* bred under laboratory conditions (at a mean temperature of 26°C) were removed from their chambers at various stages during brooding and dissected to inspect the condition of the gut, the fat body and the ovary. These dissections showed that physiological changes occurred during each brooding cycle which were probably connected with the inability to feed. As in *O. planatus*, the abdominal ventriculus of the mid gut of females usually remained full to partially full throughout brooding, it was not possible to determine whether feeding or the absorption of nutriment through the gut wall was continued, but, the advancement of pad desiccation, physiological changes to the ovary and reports of brooding species from other tribes would suggest that little, if any, feeding probably occurred. In the Coprini, Von Lengerken (1954: 347) and previous workers noted that *Copris hispanus* (L) was never observed to feed during brooding, whilst Rommel (1961)

reported ......

reported that the gut of the same species remained completely empty. However, Tribe (1976: 121) recorded that brooding females of *Kheper nigroaeneus* (Scarabaeini) do continue feeding during each cycle, "though at a much reduced rate". As their guts were completely collapsed at the end of the brooding cycle (Tribe 1976: 127), this feeding was probably minimal.

In female *O. planatus* and *O. formosus* the fat body is a well developed, diffuse structure with its numerous lobules tightly packed into the haemacoel. Prior to maturation of the ovary in teneral beetles, the developing fat body was seen to be bright yellow, but during the development of follicles, and especially after breeding, it became off-white, rarely pale yellow. The disappearance of this yellow coloration from the fat bodies coincided with the appearance of a pale yellow colour in the most mature follicles in the proximal part of the ovary.

The female reproductive system of insects usually consists of paired ovaries each of which is typically composed of a series of ovarioles opening into a common duct. In many species of Scarabaeinae, and probably universally throughout the subfamily (Halffter and Matthews 1966: 197), there is extreme reduction in the ovarian apparatus. Only the left ovary remains and this is itself reduced to only one ovariole. In *O. planatus*, this single ovariole contains a mean range of 6 - 9 follicles developing in linear series.

During the breeding and brooding cycle a sequence of changes was observed in the ovaries of laboratory bred *O. planatus*. Two weeks after the beetles had been set (and approximately one week after the commencement of breeding) the ovary remained fully differentiated into follicles (Fig. 25a), although further development was probably suspended

with ......

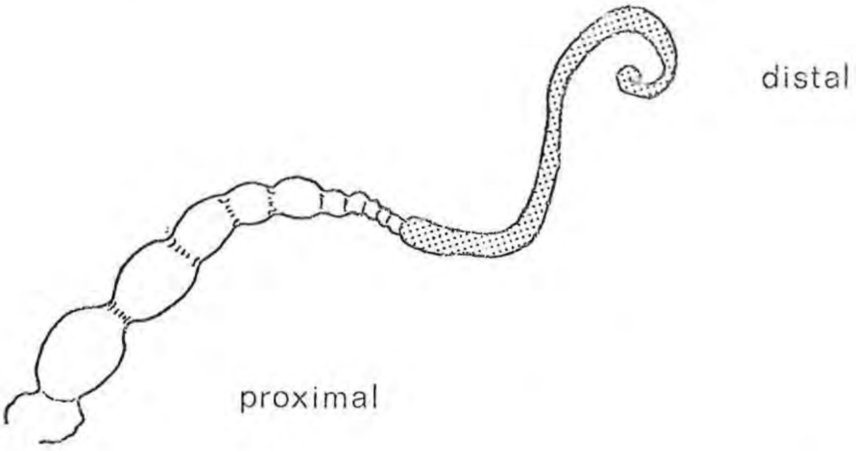
with the termination of egg laying. After three weeks the ovaries showed signs of degeneration apparently beginning at the distal end. The number of follicles visible decreased from a mean range of 6 - 9, to only 4 - 7 (Fig. 25b). Follicular outlines were less distinct and the fluid of the haemacoel had often assumed a pale to bright yellow coloration. After four weeks the ovaries had completely regressed. No follicles were visible and the ovarioles appeared as narrow tubes (Fig. 25c). Similar observations were made after five weeks and before six weeks had elapsed, from the date of setting, the remaining females had emerged from the brood chambers. Before further breeding could occur, these parent females had to engage in a period of feeding. In *O. planatus*, ovarian recovery from brooding was rapid and within nine days of introduction to a small fresh pad they had already laid 4 - 5 eggs. Recovery from brooding in other genera may take much longer and in *Kheper nigroaeneus* 3 - 5 weeks was necessary for ovarian recovery (Tribe 1976:128).

Resorption of oocytes is usually associated with starvation and examples are seen in the Orthoptera, Heteroptera, Diptera, Hymenoptera and other Coleoptera (Chapman 1969: 295). Starvation is almost certainly the reason for degeneration of the follicles in *O. planatus*. Periodic resorption of the oocytes during extended periods of brooding explains why full egg laying potential is never realised in the field nor if laboratory bred endocoprids are allowed to emerge voluntarily from breeding pads (Table 24).

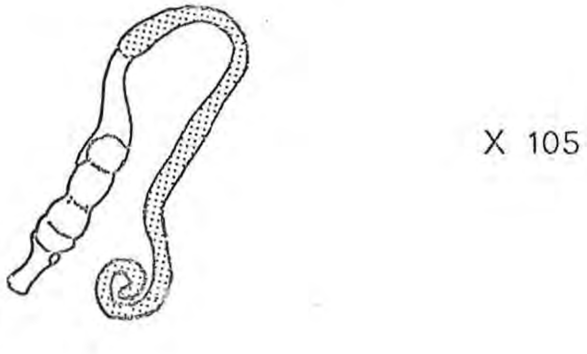
FIGURE 25:

Stages in the degeneration of the ovary of *O. planatus* during brooding.

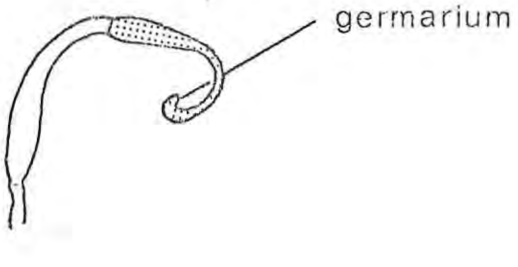
a) Fully differented after the termination of egg laying (two weeks after setting).



b) Degenerating (three weeks after setting).



c) Fully regressed (four and five weeks after setting)



As no adult endocoprid has mouthparts capable of utilising solid food, a point is reached when dung becomes unavailable for feeding because of desiccation (Halffter and Matthews 1966: 23). The lowest percentage moisture content at which feeding can occur in endocoprids is unknown but presumably the drier the dung the greater the time and energy required to obtain adequate nutriment. As the brooding endocoprids can apparently breed only in drier pads, and the breeding behaviour is geared to rapid egg and brood production, it would be necessary and advantageous that the feeding and breeding periods be divorced. Sufficient storage space for the necessary predigested food products to fuel yolk provision (vitellogenesis) and egg production in the absence of feeding, might be provided by the extensively developed fat bodies of endocoprids. The colour changes seen in this diffuse organ during egg laying certainly provides circumstantial evidence that it might be involved in this stage of the breeding cycle. Indeed, it has long been known that proteins and lipids are transferred from the cells of the fat body (trophocytes) to the oocytes during the early stages of oogenesis in meroistic ovarioles (Chapman 1969: 290).

However, the development of the fat body is not unique to endocoprids since dissections of females of *Euoniticellus intermedius* (Reiche), *Liatongus militaris* (Castelnau), *Onthophagus quadrinodosus* Fahraeus and *O. gazella* Fabricius, showed that the fat bodies of these species were also well developed. It is possible that the presence of a well developed fat body is general in the tribes Oniticellini and Onthophagini. Therefore it is probable that it was already present in a well developed state in the ancestors of the endocoprid dung beetles and

that ....

that with the evolution of the endocoprid mode of nidification the importance of its role in the breeding cycle merely increased. Its retention in the other extant genera, which breed mostly in fresh dung, suggests it either has additional functions or that it performs similar functions for different reasons.

The functions served by the presence of parental females in the brood chambers of Coprini and Scarabaeini "has not been satisfactorily determined" (Halffter and Matthews 1966: 165). The same is true of endocoprids. Halffter and Matthews (1966:155) stated that one obvious visible effect of removing female *Copris* was "the consequent growth of moulds on the surface of the brood ovoids". This fungus was cleaned off when they were returned to the female (Von Lengerken 1954:343, Halffter and Matthews 1966:165). Portions of the brood balls of *O. planatus* which protruded from the peat moss in which the larvae were reared artificially also quickly grew a thick coating of mould.

In *Copris*, throughout the brooding cycle the female could be seen moving over the broods patting them with the fore legs and apparently tasting the surface (Halffter and Matthews 1966:165). Removal of the female seemed to lower the chances of survival (Halffter and Matthews 1966:165), but the effect of removing endocoprid females could not be determined owing to the multiplicity of other factors contributing to larval mortality in the laboratory.

In conclusion, although there is little direct evidence to show how brooding behaviour might enhance larval survival its occurence in three separate tribes would indicate that it is advantageous.

4.6. ....

4.6. Overwintering

Tribe (1976:118) maintained that the envelopment of brood ovoids or brood balls within clay shells was restricted to species which overwintered as larvae or whose broods were buried shallowly. Since desiccation resistance appears to be one of the functions of the clay shell, Tribe's statement apparently implies that he considers the clay coated broods a protection against the dry winters of the Transvaal. Although recent observations (Aschenborn, per.comm.) show that *Copris elphenor* Klug, is an exception, since it constructs clay coated broods, but overwinters as adults, many other species do follow Tribe's ruling. *O. egregius* might also conform to this rule since although none of its clay invested broods have been found in the field during the southern African winter, neither have adult *O. egregius* been found active between May and October, unlike the adults of the brooding endocoprids (Chapter 5.1.).

The emergence of most endocoprid species is independent of rainfall patterns but *O. egregius* broods kept in the laboratory during winter apparently required moisture to induce adult emergence which might suggest some form of obligatory larval dormancy. In spring, these broods were divided into two groups, only one of which was watered initially. After a few days filial adults began to emerge but none emerged from the other half of the broods until they too were watered.

Overwintering by the southern African species of the brooding genera may be divided into two main behavioural groups. Whilst the broods of all known brooding species are naked in the early stages of larval development, those of many Coprini only remain so up until the second (or perhaps, in *Copris fallaciosus*, the third) larval instar when a clay shell is constructed. Most of these species overwinter as larvae,

e.g. ......

e.g. *C. fallaciosus* (Aschenborn, pers.comm.), *Heliocopris hamadryas* and *H. japetus* (Klemperer and Boulton 1976). The clay coated broods of *C. elphenor* (above) are an exception in that the filials emerge in autumn and overwinter as adults.

The brooding endocoprids and Scarabaeini constitute the second main behavioural group. Their broods remain perpetually naked but, like *C. elphenor*, they also overwinter as adults. None, either in the field or in the laboratory, has been observed in a state of larval dormancy. However, whilst *Kheper nigroaeneus* (Scarabaeini) exhibited an obligatory, winter aestivation as adults in the soil (Tribe 1976: 119) endocoprid activity was continuous throughout the year (Chapter 5.1.). In heated laboratories endocoprids continued breeding during winter. Cooler temperatures merely led to a slower rate of development (Table 14) whilst breeding ceased where temperatures were too low. The effects of suddenly decreasing the temperature during the breeding cycle was not tested but *O. formosus* was found brooding as late as May 2nd (1972) near Stella (26° 32'S 24° 50'E). *O. planatus* subjected to cool winter temperatures became immobile but resumed activity once they were exposed to warmer temperatures.

4.7. Fecundity and Longevity

The procedure utilised for the first life histories conducted in the laboratory was to replace the dung pad every two weeks. Later when brooding activity had been discovered, the pads were left until the breeding female emerged of her own accord (Chapter 3.2). Whilst the differences in handling did not significantly affect the average length

of ....

of the life history (Table 23), it did influence the overall number of brood balls constructed within that lifetime. Table 24 shows that endocoprid females changed every two weeks, laid more eggs than those left undisturbed until they voluntarily departed from the brood chamber.

The number of brood balls constructed in any one brood chamber depends on the length of the period during which pad moisture conditions are suitable for egg laying. In the laboratory this period is much longer than in the field, owing to the slower rate of desiccation. The mean number of broods (13,5) in laboratory chambers (Table 25) therefore far exceeded the number found in the field where a range of 1 - 12, with a mean of only five per chamber, was recorded for *O. planatus* and *O. formosus* in De Wildt monitoring pads with less than 20% of their bulk removed by other dung beetles. As these chambers may have been disturbed before egg laying had terminated, these figures may be artificially low. During field trips, principally in the Pietersburg and Messina (22^{0} 20'S 30^{0} 03'E) areas, an average of seven broods per chamber was recorded for *O. formosus*. In nature, the maximum ever found in a single brood chamber of this species was 17.

In the laboratory, the average number of broods per chamber varied with the age of the beetle. In studies of *O. planatus* and *O. formosus* the greatest number was constructed in the third chamber produced after the commencement of breeding by a newly emerged female and was followed by a sharp decline in both species (Tables 26 and 27). The low average number of brood balls in chamber two of *O. formosus* (Table 27) reflects low fertility and premature death of many specimens, possibly due to disease.

Table 23 ....

TABLE 23: Longevity of endocoprid species in laboratory life histories.

	*LLH		*IBLH		LLH	IBLH
	O. formosus	*O. planatus*	*O. formosus*	*O. planatus*	*T.dimidiatus*	*O. egregius*
Range (days)	41-262	55-389	71-174	139-324	139-212	44-165
Mean (days)	142	223	121	235	177	98

* Terminology:

LLH :- Laboratory life histories in which the female was allowed to remain in the brood chamber until it emerged voluntarily.

IBLH :- "Induced breeding" life histories in which the female was introduced to a fresh pad every 14 days.

TABLE 24 : Total number of broods produced by endocoprid species during their life histories conducted in the laboratory.

	*LLH		*IBLH		LLH	IBLH
	O. formosus	*O. planatus*	*O. formosus*	*O. planatus*	*T. dimidiatus*	*O. egregius*
Range	40-83	11-97	6 -142	46-160	16-22	23-133
Mean	59	52	70 **(93)	144	19	65

** Mean after deletion of the total number of broods produced during two short lived life histories.

TABLE 25 : Numbers of broods constructed per brood chamber by endocoprid species during laboratory life histories.

	*LLH		*IBLH		LLH	IBLH
	O. formosus	*O. planatus*	*O. formosus*	*O. planatus*	*T. dimidiatus*	*O. egregius*
Range	1-28	2-32	1-26	1-22	3-7	1-16
Mean	13,5	13,5	10,4	9,4	5,8	7,5

* See notes at foot of Table 22.

TABLE 26: Mean number of brood balls constructed in each successive brood chamber during the laboratory life histories (*LLH) of *O. planatus*, i.e. from the commencement of breeding by newly emerged females until their deaths.

Brood chamber number:-	Commencement of breeding	1	2	3	4	5	6	7	8	Death of beetles
Total number of brood balls		367	366	339	164	40	37	12	5	
Total number of chambers		32	25	19	16	9	9	5	1	
Mean number of brood balls per chamber		11,8	14,6	17,8	10,3	4,4	4,1	2,4	5	

TABLE 27: Mean number of brood balls constructed in each successive brood chamber during the laboratory life histories (*LLH) of *O. formosus*, i.e. from the commencement of breeding by newly emerged females until their deaths.

Brood chamber number:-	Commencement of breeding	1	2	3	4	5	6	7	Death of beetles
Total number of brood balls		358	172	193	79	33	7	1	
Total number of chambers		29	26	12	8	4	1	1	
Mean number of brood balls per chamber		12,3	6,6	16,1	9,9	8,3	7	1	

*LLH :- See notes at foot of Table 22.

4.8. Summary

Upon emergence from their broods, endocoprids engage in a short feeding period before attaining sexual maturity. The females then commence to excavate a chamber within or immediately beneath a dung pad in which the brood balls, or brood ovoids, are constructed. The most specialised manner of construction is exhibited by the most desiccation tolerant species. The degree of desiccation resistance may also be reflected by characteristics of dung burrowing activity, brood chamber position and the development of thin spots in the brood ball walls to aid emergence.

The restricted space available for breeding sites within or under dung pads probably limits the numbers of endocoprids able to breed in a single pad. This may therefore affect the size of the population which is usually composed of low numbers of individuals. Breeding by most endocoprid species, (excluding *O. egregius*), commences only in older pads (seven days or older) which is probably related to requirements of dung consistency. As this leaves only a short period of suitable moisture conditions for breeding, a specialised manner of brood construction has developed which enables the maximum possible numbers of eggs to be laid within the time available. As feeding may not be possible during breeding activity, the rapid rate of egg laying may be supported by nutriment drawn from the extensively developed fat body. Females of most endocoprid species tend their naked broods during larval development, but the clay coated broods of *O. egregius* are abandoned soon after construction. The ovary of *O. planatus* is resorbed during brooding probably to prevent starvation. The functions served by brooding are not clear.

The ....

The brooding species remain active as adults throughout winter but *O. egregius* may exhibit an obligatory dormancy during the dry season. All species are diurnal flyers.

In the laboratory it was shown that if female endocoprids are introduced to a fresh pad every 14 days, total brood production during the life history of the brooding species is much greater than if they are allowed to remain in the pad until they emerge voluntarily. Longevity is unaffected by the numbers of eggs laid. Laboratory brood production is greater than that observed in the field, probably due to the slower rate of pad desiccation in the laboratory. Large numbers of broods were constructed in the first three chambers produced by newly emerged females followed by a sharp decline. High larval mortality was experienced in the laboratory which possibly resulted from excessively moist conditions.

5. ECOLOGY

The relationships between endocoprids, other dung beetles, and climatic factors, were determined from monthly trappings conducted at De Wildt (near Pretoria) (Chapter 3.1.). Most dung beetle activity, excluding that of the brooding endocoprids, was shown to be initiated by rainfall whilst all dung burial activity was directly related to temperature and the rate of pad desiccation. Whilst endocoprids require largely intact pads for a high rate of breeding success, the burial of dung by paracoprids and telecoprids deprived the endocoprids of their breeding sites. All references to dung burial refer to activity by paracoprid and telecoprid dung beetles. Endocoprids either do not bury dung or bury only small amounts at superficial levels (Chapter 7). All results from De Wildt refer to the endocoprid species, *O. formosus* and *O. planatus*. *O. egregius* was also present but was attracted to the monitoring pads of cow dung on only four occasions owing to its preference for coarse fibred dung (Chapter 2.3.).

5.1. Annual cycle of dung beetle activity

Most paracoprid and telecoprid dung beetles exhibit a seasonal pattern of activity. This is reflected by monthly means of percentage dung removal at De Wildt which show that the greatest dung burial was effected during the hot, wet summer, least in the cool dry winter (Fig.28).

Figures 28 and 32 demonstrate that at De Wildt, which is characteristic of the warmer regions of the world, most paracoprids and telecoprids emerge only in response to rainfall, as long as temperatures are adequate. Beetle activity and high percentage dung removal then continue as long as there is regular precipitation and temperatures remain favourable. (Figs. 28 and 32 - December 1973 to March 1974). At De Wildt,

the ....

the decline of the summer paracoprid and telecoprid fauna in March is marked by decreasing dung burial (Fig 28), whilst the mass emergence of the autumn active *Onitis caffer* Boheman is responsible for the increased burial activity during the following two months. With the end of the rainy season and, in the Transvaal, the onset of cooler temperatures, paracoprid and telecoprid beetle activity gradually declines and finally ceases, resulting in the minimal dung burial recorded at De Wildt during June to September 1974 (Fig. 28). During winter most paracoprids and telecoprids remain dormant in the soil (Halffter and Matthews 1966:88) either as adults or as third instar larvae in a state of diapause.

Paracoprids and telecoprids occurring in warmer regions with distinct wet and dry seasons also exhibit seasonal activity. Observations show that under dry conditions dung beetles are only able to excavate shallow depressions or superficial burrows which is probably due to the cementing of the soil grains. By way of contrast, endocoprid dung beetle activity is continuous throughout the year (Fig. 33), probably since they spend their whole lives within or immediately under dung pads where they are supported by the pad moisture content. They are, therefore, independent of rainfall patterns and none, except, perhaps, *O. egregius*, exhibit dormancy (Chapter 4.6.).

5.2. Daily flight activity

The large paracoprid beetles which are responsible for the majority of the dung burial at De Wildt (Table 28) are all crepusular flyers, whereas the species of *Sisyphus*, which are responsible for shredding dung pads, and the endocoprid genera, only exhibit diurnal flight activity. It appears that the arrival of most endocoprids at dung pads is later than that of most paracoprids and telecoprids.

Depending on the temperature, flight activity by endocoprids may be initiated at any time from late morning to early afternoon. Field observations showed that most diurnal beetles only exhibited flight activity when the sun was shining. If the light intensity and radiant heat was reduced by clouds covering the sun, beetles ceased flying within minutes. Low numbers of endocoprids were recovered from monitoring pads during rainy weather.

TABLE 28 :

The species of large paracoprid dung beetles responsible for the majority of the cow dung burial recorded at De Wildt.

Summer active (October - April)	*Onitis alexis* Klug *O. viridulus* Boheman *O. uncinatus* Klug *Copris elphenor* Klug *Catharsius tricornutus* Degeer *Heliocopris hamadryas* (Fabricius)
Autumn active (April - June)	*Onitis caffer* Boheman

5.3. Pad colonisation

Pad colonisation and the duration endocoprid dung beetles remain in or under the dung is dependent on the rate of pad desiccation. Whilst Landin (1961) records various factors as influencing the rate of pad desiccation in Sweden (temperature, precipitation, dew, humidity, wind speed, soil drainage and, in cow dung, crust formation), at De Wildt, temperature, precipitation and activity by paracoprid and telecoprid dung beetles (percentage dung removal and degree of shredding) were apparently the most important elements affecting the rate of desiccation.

Table ....

Table 29 shows that, during the hot summer, paracoprids and telecoprids colonised cow pads within the first day and maximum dung removal was effected after about three days (mean daily temperature at De Wildt in January is approximately 23,7°C) as long as mean daily temperatures remained sufficiently high (ca 23°C). When temperatures decreased, it was apparent that whilst the timing of arrival was scarcely affected (determined by the appearance of excavated earth beside pads which indicated burrow construction by paracoprids), the rate of dung removal declined until, in early winter, burial activity continued for over 14 days (Table 29) (mean daily temperature at De Wildt during May is approximately 15,4°C). During rainy periods, observations suggest that dung burial was suspended. The resulting lower temperatures extended the duration of dung removal and apparently affected the amount buried (Figs 28, 32 and Table 29, February to May 1975).

In contrast to paracoprid and telecoprid activity, both the timing of endocoprid arrival and the duration of pad colonisation showed seasonal variation which was probably associated with the rate of dung desiccation (Figs 26 and 27). Figure 26 shows that arrival by endocoprids was within the first three days during December 1974, because high percentage dung removal and high mid summer temperatures led to rapid pad desiccation. In the absence of rainfall, the duration of their sojourn was brief (Fig 27 - December 1974) and few dung beetles were recovered from seven day old pads. During autumn and winter, the amount and rate of dung burial was much reduced due to the decline in temperature and reduction in the numbers of paracoprids and telecoprids remaining active. This resulted in a slower rate of desiccation so that peak arrival of endocoprids was much later whilst duration of pad colonisation was much longer (Figs 26 and 27). Rainy weather also extended the duration of colonisation (Fig 27 - early 1975).

TABLE 29 .....

TABLE 29 :

Cumulative percentage rate of dung removal from De Wildt monitoring pads by paracoprid and telecoprid dung beetles. The one, two and three day, plus the one and two week dung removal percentages have been expressed as a percentage of the mean estimated removal after three weeks.

		Cumulative percentage rate of dung removal by paracoprids and telecoprids						Actual 3 week % dung removal	Approx. mean night min. air temp.	
	Months	1 day	2 day	3 day	1 week	2 weeks	3 weeks		at 30 cm	at 2,5 cm
1973	Dec./Jan.	58	77	82	94	96	100	89	16,7	10,9
1974	Jan./Feb.	65	77	87	104	95	100	90	17,8	11,7
	Feb./Mar.	30	57	65	96	101	100	88	16,8	10,6
	Mar./Apr.	29	74	75	118	95	100	48	14,2	9,5
	Apr./May	11	24	38	87	94	100	65	11,0	7,0
	May./June	0	0	3	44	78	100	74	3,4	0,1
	June/July	0	0	0	0	54	100	17	2,3	-1,5
	July/Aug.	0	0	0	0	0	100	35	1,4	-2,2
	Aug./Sep.	0	0	0	0	0	100	0	3,3	-0,7
	Sep./Oct.	0	0	0	0	0	100	0	10,0	5,8
	Oct./Nov.	8	22	44	65	77	100	39	12,9	8,5
	Nov./Dec.	35	63	66	76	140	100	60	15,4	11,1
1974	Dec./Jan.	24	55	68	78	103	100	46	16,2	9,7
1975	Jan./Feb.	19	39	58	99	102	100	45	16,9	10,9
	Feb./Mar.	18	40	58	90	116	100	16	16,4	11,0
	Mar./April	0	34	38	66	97	100	28	13,7	10,2
	Apr./May	*–	–	24	64	111	100	18	8,9	5,8
	May/June	–	–	0	28	65	100	15	3,8	0,9

*– :- No records made

FIGURE 26

The relationship between monthly peak, occurrence of endocoprid numbers in 15 pad monitoring samples (X) and the time of the year,which implies late arrival at winter pads and early arrival at summer pads. Samples of four or less have not been considered which accounts for the lack of data for the months of Jan./Feb. 1974 and Mar./April 1975.

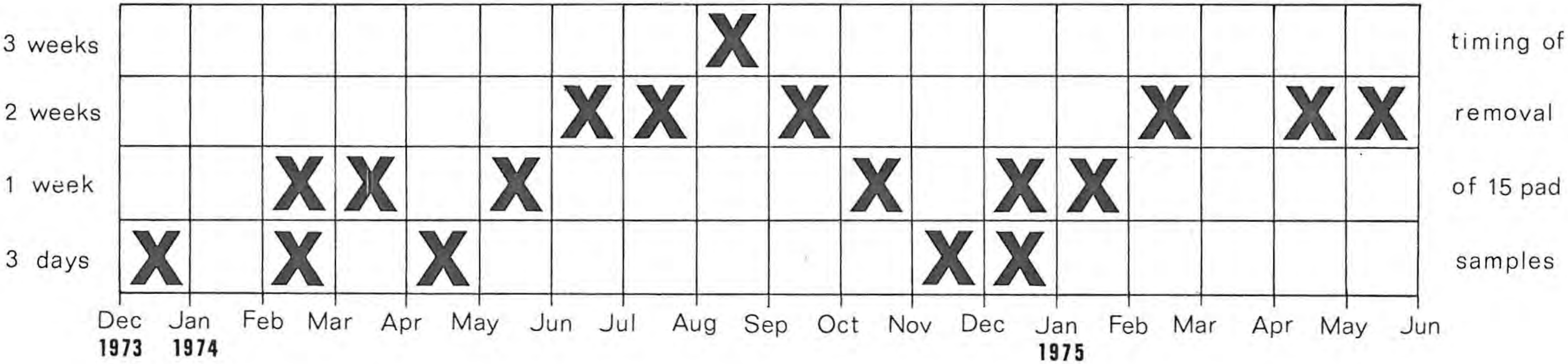


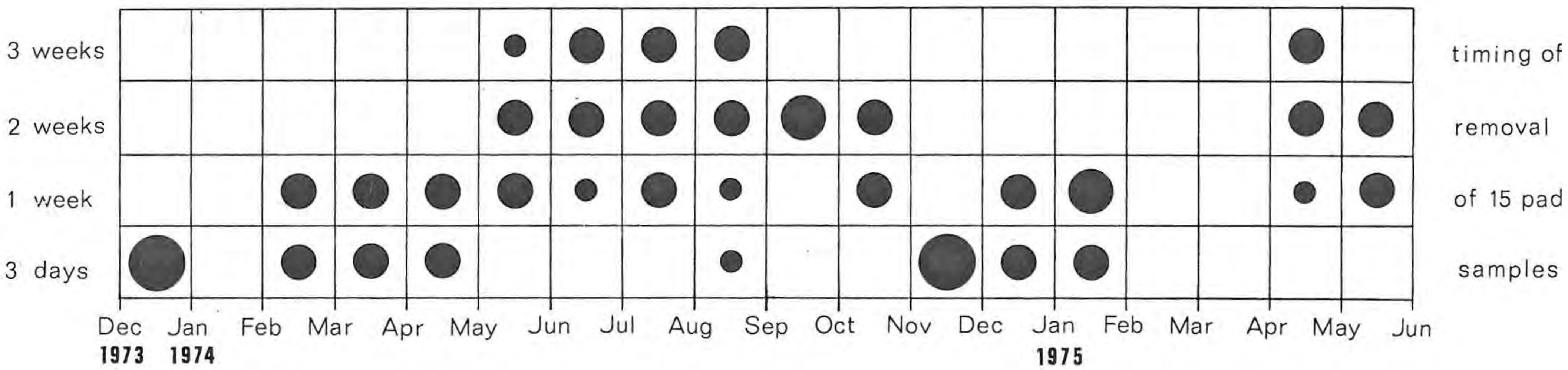
FIGURE 27 The percentage of the total numbers of endocoprid beetles, captured during each month of monitoring at De Wildt, occurring in each 15-pad sample. This figure indicates the duration of dung pad colonisation by the majority of the endocoprid species collected each month. Samples containing five or less beetles have not been considered, which accounts for the lack of data for the months of Jan./Feb. 1974, Feb./Mar. and Mar./Apr. 1975.

● :- 6 - 25% of the total number of endocoprids recovered during one months monitoring

● :- 26 - 50% of the total number of endocoprids recovered during one months monitoring

● :- 51 - 75% of the total number of endocoprids recovered during one months monitoring

● :- 76 -100% of the total number of endocoprids recovered during one months monitoring



5.4. Endocoprid breeding

Endocoprids are opportunists breeding whenever temperatures are sufficiently high and dung removal by paracoprids and telecoprids, sufficiently low (Figs. 28, 29, 30 and 31). Tables 30 and 31 show that the decline in the numbers of endocoprids present in De Wildt monitoring pads and the decrease in endocoprid breeding activity are directly related to increasing percentage dung removal by paracoprids and telecoprids. Greatest breeding success was achieved in pads with less than 20% of their volume removed. There was a sharp drop in successful brood chamber construction above 20% but further decline followed a comparatively shallow gradient. Therefore greatest breeding success at De Wildt occurred before the first rains in spring when temperatures were rising and dung removal by all beetles was at a minimum. (Figs 28 and 29).

TABLE 30 :

The decrease in the percentage of De Wildt monitoring pads containing endocoprid beetles (O. *planatus* and O. *formosus*) relative to increasing percentage dung removal by paracoprid and telecoprid dung beetles.

% Dung removal by paracoprids and telecoprids	% of pads containing endocoprids	Total number of pads
0 - 20	39	565
21 - 40	26	94
41 - 60	28	74
61 - 80	19	144
81 - 100	5	180

TABLE 31 ....

TABLE 31 : Endocoprid brood production in two and three week old De Wildt monitoring pads showing decreasing breeding success with increasing percentage dung removal by paracoprid and telecoprid dung beetles.

% Dung removal	Number of available pads after 2 and 3 weeks during breeding period (Aug. - May)	Total Number of Brood chambers constructed in 2 and 3 week old pads	Total Number of Brood balls in 2 and 3 week old pads	Mean Number of Brood chambers per available 2 and 3 week old pads	Mean Number of Brood Balls per available 2 and 3 week old pads	Mean Number of brood balls per chamber
0-20	129	56	272	0,43	2,10	4,86
21-40	42	7	24	0,16	0,57	3,43
41-60	28	3	13	0,10	0,46	4,33
61-80	64	6	28	0,09	0,43	4,67
81-100	93	2	2	0,02	0,02	1

FIGURE 28 Estimated percentage dung removal (by paracoprids and telecoprids) from 15 monitoring pads after three weeks exposure to dung beetle activity.

FIGURE 29 Number of endocoprid brood balls (*O. formosus* and *O. planatus*) recovered from the 60 pads of each monitoring exercise.

FIGURE 30 Number of endocoprid brood chambers (*O. formosus* and *O. planatus*) constructed in the 60 pads of each monitoring exercise.

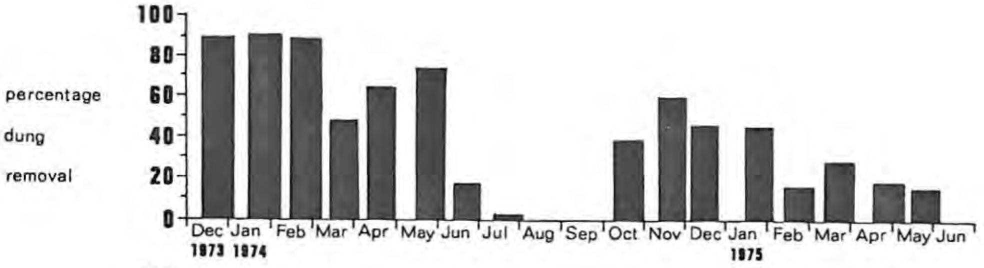
FIGURE 31 Approximate mean, minimum, night temperature during each three week monitoring period. ▨ at 30 cm ▦ at 2,5 cm (Temperature data recorded at Hartbeespoort Agricultural station, Brits (near De Wildt).

FIGURE 32 Total monthly rainfall recorded at Hartbeespoort Agricultural station, Brits (near De Wildt) from December 1973 until June 1975).

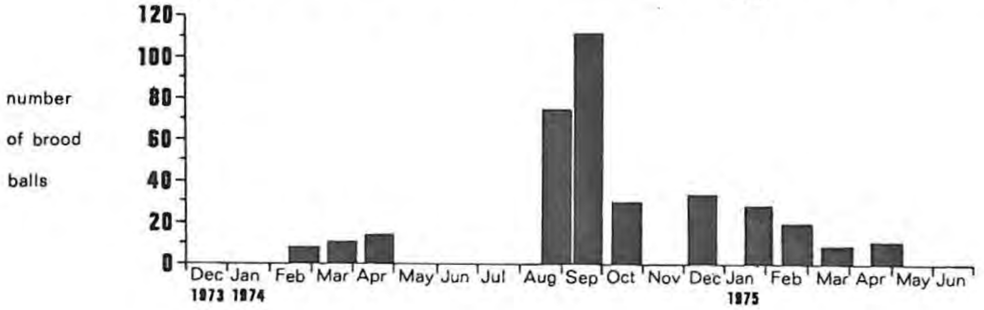
FIGURE 33 Total number of endocoprid beetles (*O. formosus* and *O. planatus*) recovered from the 60 pads of each monitoring exercise.

FIGURE 34 Number of pads (out of 60) colonised by endocoprid beetles during each monitoring exercise.

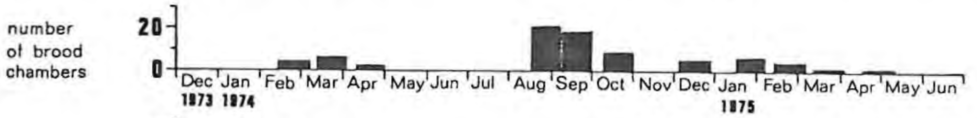
28



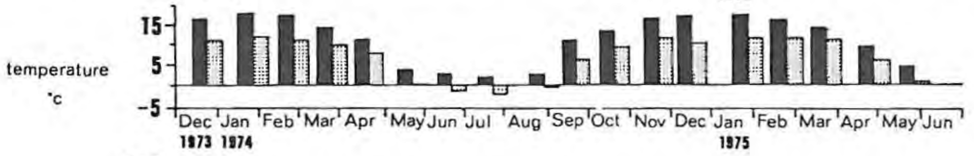
29



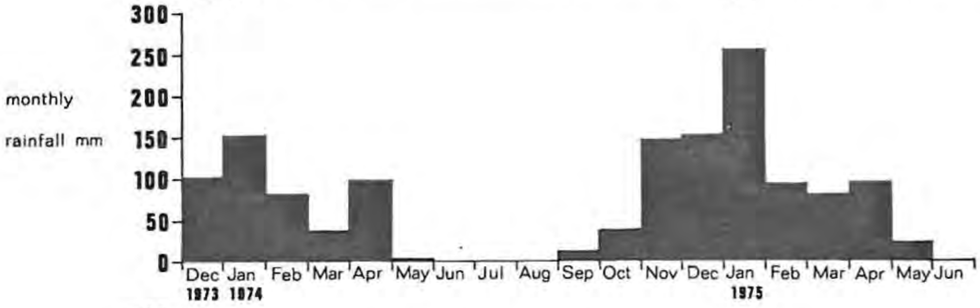
30



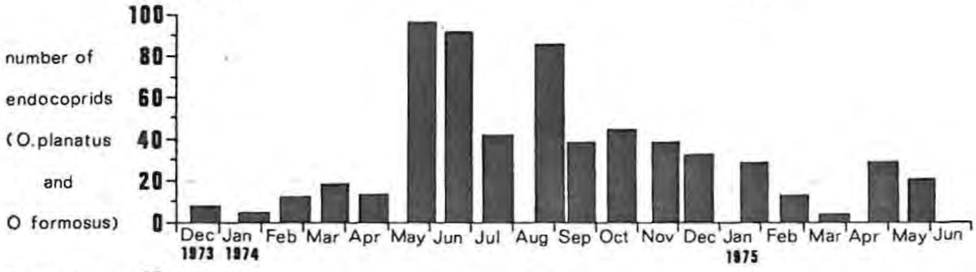
31



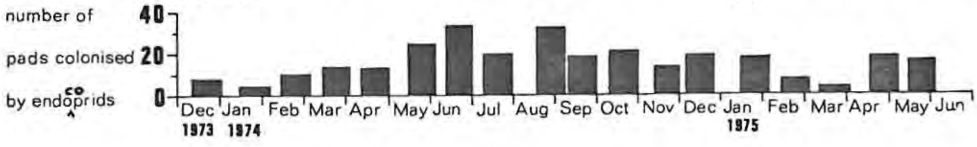
32



33



34



It can be seen that on the infrequent occasions that endocoprid broods were constructed in pads from which as much as 90% of the dung had been removed by paracoprids and telecoprids, only small numbers of balls were successfully completed. (Table 31). Usually, when dung burial percentages were as high as 90%, no endocoprid breeding was recorded (Figs 28 and 29 - December 1973 to February 1974) but as average dung removal was more often much less than 90%, the production of low numbers of brood balls usually continued in the face of competition by paracoprids and telecoprids (Figs 28 and 29 - February to May 1974 and January to April 1975).

Endocoprid breeding was only recorded in monitoring pads which were less than seven days old on four occasions. In most of these pads, paracoprid and telecoprid dung beetle activity had probably accelerated the rate of drying so that a suitable moisture content for endocoprid breeding was obtained more quickly. In intact pads, breeding by endocoprids did not usually commence until at least seven days after deposition, owing to the slower rate of desiccation. Most paracoprids had usually departed from the pads before the commencement of endocoprid breeding.

It might be expected that the lower the percentage dung removal by paracoprids and telecoprids and the slower the rate of desiccation, the greater would be the number of brood balls able to be completed by endocoprids, in cow pads at De Wildt. However, data indicate that dung removal activity inhibits actual commencement of the endocoprid breeding cycle, rather than brood production, since, once construction of the brood chamber had begun, a similar average number of brood balls

was ....

was produced in each chamber irrespective of dung removal percentages up to 80% (Table 31). This apparent anomaly may have resulted from disturbing the beetles before brood construction had been completed or through reduction in the rate of desiccation due to the cooling and moistening effects of rainfall.

Whilst the number of endocoprid broods per chamber may, or may not, be affected by percentage dung removal, Table 32 indicates that greater rapidity of desiccation may have been responsible for a higher percentage mortality of endocoprid larvae in pads from which much of the dung had been removed.

Although, during winter, the adults continued to fly from pad to pad, temperatures at De Wildt were usually too low to support endocoprid breeding and no brood balls were recorded in monitoring pads between mid May and mid August (Fig 29). *O. formosus* brood balls found on the 29th July, 1975 were the first examples of winter breeding observed there during the investigation. Observations of endocoprid breeding near Mkuze (27° 33'S 32° 02'E) during July (Tribe pers. comm.) suggests that on the much warmer coastal plain of Zululand breeding is continuous throughout the year.

5.5. Fluctuations in endocoprid numbers

Periods of declining or low percentage dung removal by paracoprids and telecoprids were followed by peaks in the numbers of endocoprids captured in De Wildt monitoring pads (Figs 28, 33, 34, 35 and 36). Observations and monitoring data suggest that, as well as being

a real ....

TABLE 32: The increasing percentage mortality of endocoprid larvae (*O. planatus* and *O. formosus*) with increasing percentage dung removal, from De Wildt monitoring pads, by paracoprids and telecoprids.

% Dung removal by paracoprids and telecoprids	Total number of endocoprid brood chambers	Total number of endocoprid brood balls	Number of dead larvae	Overall % mortality
0 - 20	57	275	9	3,3
21 - 40	8	27	5	18,5
41 - 60	3	13	5	38,5
61 - 80	8	33	6	18,2
81 - 100	2	2	1	50

a real increase due to enhanced endocoprid breeding success, the rise in numbers was probably also influenced by seasonal variations in the rate of pad desiccation for which no allowance was made in the experimental procedure.

The peaks, in early winter, which follow declining dung removal in late summer, are possibly a regular, annual occurrence. This conjecture is supported by records from De Wildt for 1974 and 1975 (Fig 33) and by field observations of increased endocoprid activity made in other areas during May 1973, e.g. Nelspruit (25^{0} 27'S 30^{0} 58'E). At De Wildt, the magnitude of these peaks was far greater in 1974 than in 1975. Monitoring pads imply that endocoprid breeding was totally suppressed prior to February 1974, due to high percentage dung burial activity by paracoprids and telecoprids. Thus there was possibly a synchronisation of brood ball construction which led to the dramatic increase in endocoprid numbers recorded during the following May when there was a probable, simultaneous, mass emergence of fillial adults. (Figs 29 and 33). The greater breeding success in 1975 was nullified by the flooding of most of the monitoring site which probably killed many larvae and interferred with pad colonisation leading to the low numbers recorded during autumn.

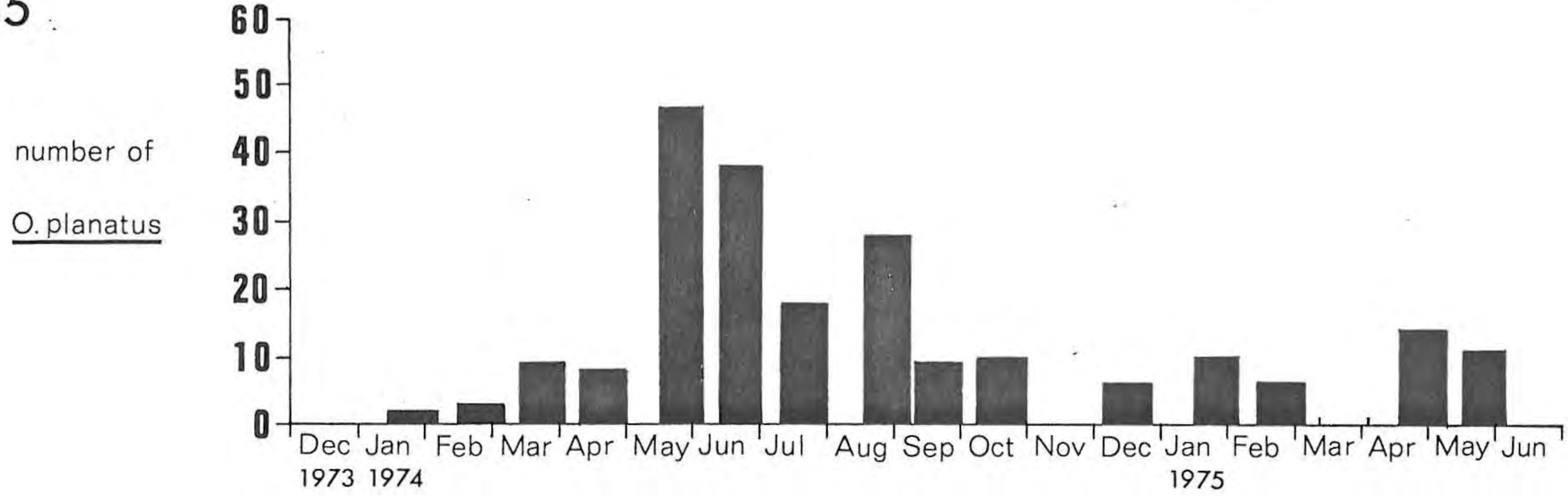
Monitoring conducted at De Wildt between February and July 1976 (Chapter 3.1.), when a method had been discovered for differentiating freshly emerged from older endocoprids, confirms that an influx of fresh emergences occurs in autumn. Table 33 shows that, during most months, freshly emerged specimens comprised only between zero and 17% of the

FIGURES 35 and 36 Numbers of endocoprid beetles recovered from the 60 pads of each De Wildt monitoring exercise.

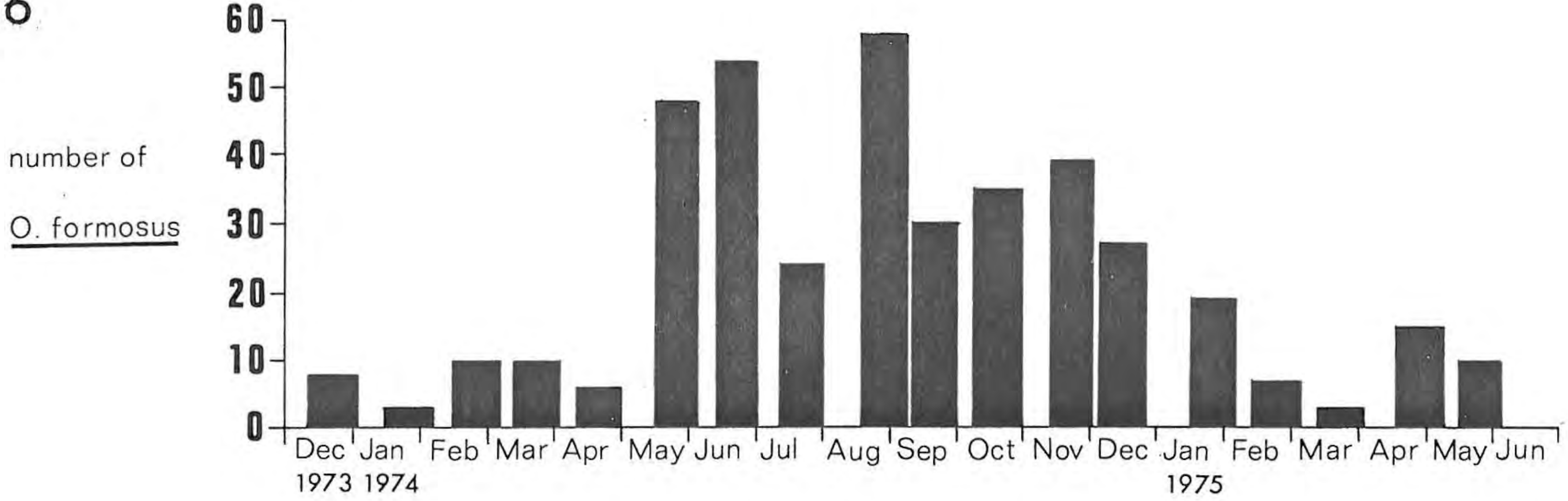
FIGURE 35 *O. planatus*

FIGURE 36 *O. formosus*

35


number of
O. planatus
60
50
40
30
20
10
0
Dec
1973
Jan
1974
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
1975
Feb
Mar
Apr
May
Jun

36


number of
O. formosus
60
50
40
30
20
10
0
Dec
1973
Jan
1974
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
1975
Feb
Mar
Apr
May
Jun

population whereas, during May, freshly emerged beetles comprised 38% of the population. This real increase in endocoprid numbers may account for only a proportion of the peaks recorded during autumn in previous years since it is possible for an apparent increase to result from the much slower rate of pad desiccation during the cooler months. This extends the period during which pads remain attractive to endocoprids, so promoting a greater buildup in numbers than is seen in summer. However, there is no evidence that this effect would not be countered by reduced frequency of flying to fresh dung due to the longer duration of pad colonisation.

TABLE 33: Number of endocoprid beetles (*O. planatus* and *O. formosus*) recovered from 30 monitoring pads set at De Wildt between February and July 1976, showing fluctuations in the numbers of young specimens entering the population based on an examination of setal wear.

Month 1976	Stages of wear*			% of younger specimens	Total number of beetles
	1	2	3		
February	1	4	7	8	12
March	1	3	2	17	6
April	1	8	4	8	13
May	6	6	4	38	16
June	0	2	2	0	4
July	0	5	2	0	7

*Stages of wear
1) Setae more or less intact. Little wear visible. Recently emerged specimens.
2) Setae bent and thinned out but still well represented as tufts etc.
3) Less than 5 setae left.

(2 and 3 were older specimens).

5.6. Summary

During the wet summer (Fig 32 - late October to March), sampling at De Wildt showed fair to high removal of dung from cow pads by paracoprids and telecoprids (Fig 28) which, together with high temperatures (Fig 31), promoted rapid pad desiccation so that endocoprid breeding success (*O. formosus* and *O. planatus*) was relatively low or completely suppressed (Fig 29). The peak period of endocoprid arrival was within the first few days (Fig 26) and the duration of pad colonisation by most specimens was short (less than seven days) (Fig 27). Only one sample of 15 pads was removed during this period of peak presence by endocoprids (after three days - e.g. November/December, 1974 - Fig 27) and the total numbers captured were often low.

In autumn (April to early May), sampling continued to show low to fairly high removal of dung (Fig 28) mainly due to burial by the autumn active paracoprid, *Onitis caffer*. Declining temperatures (Fig 31) decreased the rate of pad desiccation which often resulted in an increase in the duration of pad colonisation by endocoprids (Fig 27) especially if there was cool, wet weather (e.g. 1975). Whilst endocoprid breeding continued, during 1974, it was not significantly more successful than it had been during late summer and, during 1975, it actually declined during autumn (Fig 29).

During the dry winter (Fig 32 - late May to early August), sampling at De Wildt showed that with the onset of still lower temperatures and the cessation of the rains, dung removal declined to zero (Fig 28) due to a marked reduction in activity by paracoprids and telecoprids which either died or became dormant in the soil. The further decrease in temperature (Fig 31) resulted in a still slower rate of pad

desiccation ....

desiccation which led to later arrival and a further extension in the duration of colonisation by endocoprids (Figs 26 and 27) so that up to three samples of 15 pads (compared to the one of summer) were taken during peak or near peak presence by species of *Oniticellus (s. str.)* (after 7, 14 and 21 days - e.g. May/June 1974 - Fig. 27). Therefore the increased totals of endocoprids captured during a complete monitoring period, during winter, are artificially high, compared with those of summer, due to experimental procedure. Data do, however, suggest that the marked rise in endocoprid numbers recorded during early winter is partially due to influx of freshly emerged specimens (Table 33). No endocoprid breeding was recorded at De Wildt during winter, due to the low temperatures (Figs 29 and 31).

Before the first rains, during spring 1974 (Fig 32 - late August to early October), temperatures rose (Fig 31) sufficiently to support endocoprid breeding (Fig 29) which was recorded in 50 - 60% of the two, and three week old, monitoring pads which were intact in the absence of dung removal by paracoprids and telecoprids (Fig 28). The rate of pad desiccation remained fairly slow owing to the minimal amount of shredding but the timing of arrival by endocoprids and the duration of pad colonisation became variable (Fig 27). The peak in the numbers of endocoprids captured continued to be recorded from the later samples (Fig 26) during each three week, monitoring exercise.

6. PREDATORS, PROTECTIVE MECHANISMS AND PARASITOIDS

As endocoprids spend practically the whole of their lives in dung pads, it could be expected that they suffer from predation to a greater extent than burrowing species. As a consequence protective mechanisms may have developed.

As opposed to the brooding endocoprids which are often found in older pads, *O. egregius* is rarely, if ever, seen in pads more than 14 days old. Protective mechanisms in this species are apparently of greater complexity than those of the other endocoprids and those of many other dung beetles which are able to retreat into their burrows. As there is no direct evidence to show that the mechanisms described below are, in fact, protective, suggestions as to their functions are purely speculative.

6.1. Predators

Field observations have been made of various mammalian, avian and insect predators preying upon dung beetles. This includes francolin (Fam. Phasianidae) in the Kruger National Park and meerkats (Fam. Viverridae) near Pietersburg. Field observations in Australia and laboratory observations in South Africa show that Amphibia and reptiles may also feed on dung beetles.

In southern Africa, hadeda (*Hagedashia hagedash* (Latham)) and sacred ibis (*Threskiornis aethiopicus* (Latham)) are often observed in cattle pastures. Cow pads in their vicinity are found to be riddled with puncture marks probably made by the birds' probing beaks. Dung beetles found in the gut contents of sacred ibis from the Pretoria area consisted mainly of *Euoniticellus intermedius*, *Onthophagus gazella* and *Onitis alexis*

(material .....

(material courtesy of R. Clarke). No endocoprids were found, as predation tends to be more intense in fresher pads where dung beetle densities are greater, predation of endocoprids (by ibis) would probably be slight due to their low abundance and frequent occurrence in older pads.

Insect predators of dung beetles exhibit two main types of behaviour. The first type includes those which wait close to the pad and catch the beetles as they fly to the dung e.g. asilids (Paschalidis, Bernon pers. comms.). The second type constitutes the predatory beetles which actually colonise dung pads. Those of the families Histeridae and Passalidae are especially noteworthy and many observations have been made of histerids preying upon small Scarabaeinae.

6.2. Protective Mechanisms

The dorsal surface of *O. egregius* is metallic blue-black with a yellow border. The ventral surface is mottled yellow and gold. If disturbed, *O. egregius* actively flip themselves onto their backs and remain still holding the median and metathoracic legs away from the body. This exposes the undersurface which is coloured similarly to the shredded fibres of rhinoceros or elephant dung and renders them inconspicuous. *O. formosus* and *O. pictus* possess a cryptic black and yellow pattern both ventrally and dorsally. They also exhibit thanatosis (remain still) when disturbed and hold their hind two pairs of legs away from the body. Whilst it appears that they do not actively turn onto their backs, the extension of the legs often produces a similar result.

Further mechanisms are employed by *O. egregius* which are probably protective. If picked up, this species often releases a brown fluid from the lateral edge of the anterior abdominal segments just posterior to the metathoracic legs. The odour is similar to oil of wintergreen, and it may be distasteful or discourage predators. In addition, the front legs which are held close to the body may be released under tension with sufficient force to lift the beetle as much as 60 cm into the air. It may serve as an escape mechanism and might conceivably frighten off vertebrate predators.

If disturbed, *O. planatus* may exhibit thanatosis with all legs held close to the body but, usually, it immediately races towards the base of the pad. It was suggested that this endocoprid might mimic predatory species of the genus *Hister* (Bornemissza pers. comm.). Whilst there is no direct evidence, the fast gait of *O. planatus* is very similar to that of histerids and both are black and extremely dorso-ventrally flattened. The wings of each have a similar black and white pattern whilst the wings of the other endocoprids are unpatterned and translucent. The hard exoskeleton and the unpleasant odour released by histerids might cause them to be distasteful to predators and suitable as models for mimicry.

6.3. Parasitoids

The larvae of most dung beetles of the subfamily Scarabaeinae are enclosed in broods deep in the soil. No insect parasitoids have been reported from such species, However, there is a small minority of beetles whose broods are situated on or close to the surface. These would be expected to be more susceptible to parasitism. Such species include endocoprids and some African *Sisyphus* which cement their broods to stalks in the undergrowth, e.g. *S. spinipes* Thunberg (Paschalidis 1974).

O. formosus, which invariably constructs its brood chamber in the pad, is the only species from which insect parasitoids have so far been recorded. These are respectively, *Bombylius sp.* (Diptera - Bombyliidae)

and ....

and *Oniticellobia sublaevis* Bouček (1976) (Hymenoptera - Pteromalidae).

Bombylius sp. has been recovered from brood balls collected near Messina and De Wildt near Pretoria. Of 17 brood balls found in a single *O. formosus* chamber at De Wildt, 12 were pierced by emergence holes whilst 5 parasitised broods remained intact. Each contained a single *Bombylius* pupa. They were placed in damp peat and emerged after approximately two weeks. The pupal exuviae were found on the surface of the peat but how they break out of the brood balls and how oviposition is achieved has not been observed. Bombyliidae are principally parasitoids of Orthoptera although the biology of many is unknown.

Oniticellobia sublaevis has been collected on only one occasion from a single chamber containing a total of five parasitised brood balls. This was found 7 km south of Messina. The parent *O. formosus* female was not in attendance. Four of the broods were opened and found to contain from eight to 16 small, hymenopterous pupae. Emergence commenced three days later, and continued for three days (9th to 11th September). The 16 pupae from the unopened ball all exited within a short space of time (11th September) from the same small hole bored through the thin spot of the wall. In opened balls the wasps emerged over a longer period. The size of the chamber within the brood balls and, the presence of the thin spot in most cases, suggests that the endocoprid progeny survive until at least the third larval instar when parasitised by both *Bombylius* and *Oniticellobia*.

Attempts to breed *Oniticellobia* were unsuccessful and they all died between the 9th and 12th October (28 to 33 days after emergence).

7. POTENTIAL USE OF ENDOCOPRIDS IN AUSTRALIA

The introduction of old world dung beetles into Australia was undertaken to accelerate the removal of cow dung from the surface, which it was expected would reduce the numbers of dung breeding flies, successfully completing their life histories. This present research on endocoprids was carried out as a part of this project following suggestions by Bornemissza (1969) that the group might play an important role in fly control. These suggestions were based on laboratory observations of *O. cinctus* (an Asian endocoprid). Since this species had not been observed to tunnel in the soil (Bornemissza 1969) it was not originally thought that endocoprids would play a role in dung control. This conclusion was reinforced by observations of African species, three of which, *(O. pictus, O. formosus* and *T. dimidiatus)*, have never been observed to bury dung whilst the remaining two *(O. planatus* and *O. egregius)* only make shallow excavations immediately under dung masses, which are seldom deeper than about 5 cm and are solely for breeding purposes. However, suggestions were later made (CSIRO Annual Report 1976) that, by their shredding action, endocoprids (principally *O. formosus*) may aid the breakdown of winter or dry season pads by promoting their mechanical dispersal with the first rains. This is not now thought likely since, for promotion of complete disintegration, large numbers of beetles would have to colonise each pad, and results from De Wildt, show that only about 50% of the monitoring pads were, in fact, colonised. Of these, 92% contained only one to four individuals whilst over 50% contained only one. The maximum of 16 endocoprids, (14 *O. formosus;* 2 *O. planatus*) found in a single winter pad, at De Wildt, was exceptional.

It is ....

It is probable that the numbers are regulated at this low level since evidence from endocoprid breeding performance at De Wildt suggests that three, or more, female endocoprids of the same species per cow pad inhibit each others' breeding activity (Chapter 4.2). Therefore it would be advantageous for the population to be limited to two or less females per pad. Below, or at this limit, especially if every pad were colonised, maximum breeding potential might be realised whereas above this limit, breeding would probably be inhibited and numbers would thus decline. The probable regulation of endocoprid numbers and the restricted number of brood chambers per pad will therefore render this group of little value in promoting large scale mechanical breakdown of dung pads.

Although endocoprids bury little dung, Bornemissza (1969) implied that their activities in dung pads might combat dung breeding fly pests directly. Furthermore, owing to the probability that they were less influenced by ambient soil moisture than paracoprids and telecoprids, it was suggested (Bornemissza 1969) that they might be especially important to fly control when conditions were too harsh for other dung beetle activity. But, several observations of endocoprid activity in Africa indicate that their use in this respect will probably be minimal. Firstly, it seems that most endocoprids may arrive at dung pads after fly eggs have hatched. Secondly, in intact pads, endocoprid breeding does not usually commence until after the elapse of seven days (Chapter 5.4.) whereas bushfly larval development requires only 6 - 8 days for completion (Hughes *et al.* 1972). Thirdly, laboratory observations suggest that the small numbers of beetles which usually colonise pads in the field would probably not interfere with fly maggot activity in any case, since laboratory breeding by single pairs of *O. egregius* was often inhibited

in ......

in maggot infested rhinoceros dung. The presence of these beetles did not appear to affect the emergence of numerous, large, healthy flies.

In the laboratory, it was shown (Bornemissza 1970) that dung burial activity by the paracoprid, *Onthophagus gazella*, did reduce the breeding success of the bushfly. However, recent experiments conducted by M.M.H. Wallace, (*in litt.* to Dr. G.F. Bornemissza - February 3rd 1977) in Australia, indicate that predatory mites are also important in the control of flies. These mites are transported from pad to pad by dung beetles. Wallace *(in litt. Loc. cit.)* therefore suggested that endocoprids might be useful purely as phoretic hosts of mites, especially as they remain active during the dry season. Again there are several reasons why their usefulness may be strictly limited, particularly in summer.

Observations indicate that few endocoprids fly to pads younger than one day old. Out of 13 consecutive weeks' trapping (5 traps per week) conducted near Pretoria by P.D. Stickler (unpublished data), *O. planatus* was recovered within one day on only two occasions. The bushfly eggs on which the mites feed, hatch within 7 - 17 hours over a temperature range of 32^{0} to 21^{0}C (Hughes *et al.* 1972). Therefore, using De Wildt as an example, between October and March, when the mean daily temperature is above 21^{0}C, most endocoprids will arrive too late to play even an indirect role in fly control. Thus, during summer, the mites carried by the far more numerous paracoprids and telecoprids, which mostly arrive within the first 24 hours, will be far more effective in combatting dung breeding flies.

With the data available at present it is not possible to determine whether activity by endocoprids would have any impact on fly control during winter when most paracoprids and telecoprids are absent from the surface. Between April and September (inclusive) the mean daily temperature

at ......

at De Wildt is less than 21^{0}C. Assuming that bushfly eggs can develop under such cool conditions, the developmental period would be extended beyond 17 hours. The arrival of most endocoprids at dung pads in winter is much later than in summer (Chapter 5.3.) and it is unknown whether this would precede the hatching of bushfly eggs. However, assuming that the mites carried by endocoprids can be shown to be predators of bushfly eggs, or even small larvae, there is a possibility that endocoprids might play a minor role in fly control during the dry season despite their low abundance. This does not apply to winter rainfall areas where no endocoprids have been recorded.

It is my recommendation that endocoprids should be considered very low on the list of priorities if the decision is taken to introduce them without firm experimental evidence that they do play a part in fly control. *O. pictus, O. formosus* and *O. planatus* are the only species worth this consideration as the others show a strong preference for coarse fibred dung (Chapter 2.3.). *O. planatus* would probably provide the greatest control as observations indicate that the arrival of *O. pictus* and *O. formosus* at dung pads, is even later than that of the former species. An advantage in handling endocoprids is that, given sufficiently high laboratory temperatures, they may be bred at any time of the year without any of the diapause problems which have been experienced with many of the other introduced species.

8. THE ENDOCOPRID HABIT AND ITS EVOLUTION

The increased tolerance to potentially dry conditions shown by the genera *Oniticellus* (*s. str.*), and *Tragiscus*, is also found in several other genera and species of the tribe Oniticellini (Table 34). According to Halffter and Matthews (1966:149), this trend is allowed by their unspecialised breeding habits. But, whilst the nidification behaviour of some desiccation tolerant species is indeed unspecialised, that of others, including *Oniticellus* (*s. str.*) and *Tragiscus*, is much more complex.

Fairly simple behaviour is exhibited by species of *Drepanocerus* from the Congo (Zaire) which have been observed (Janssens 1953:5) to breed within pads in the manner of *Aphodius*, i.e. the eggs are laid freely in the dung. Another species of the same genus, observed in DBRU laboratory cultures, laid its eggs in a wad of dung constructed at the interface between the dung and the soil. More complex behaviour is shown by *Liatongus festivus* Steven. This species was reported by Medvedev (1952:224) to bury pear shaped broods under dung pads in Asia. There has long been controversy over its taxonomic position, and its nidification behaviour sets it apart from other *Liatongus* bred at the DBRU, e.g. *L. militaris*, which constructed broods in the manner of *Euoniticellus fulvus* (Goeze) (Fig. 37).

A few species of those genera which usually exhibit more complex dung burial and nidification behaviour, have also been observed to breed in or under pads. The larvae of *Trichillum sp.* (Coprini) live freely in pads (Ohaus 1909:88) similarly to the zairois *Drepanocerus* whereas *Eurysternus magnus* Laporte (Eurysternini), a South American species, has retained complex nidification behaviour and produces brood chambers which are similar in appearance to those of *Copris* except that they are constructed half in the pad and half in the soil (Howden, cited

by Halffter.....

TABLE 34 Dung age preference in African species of the genera of the tribe Oniticellini.

Genus	African species commonly found in older dung	African species usually found in fresh dung
Drepanocerus Kirby	*D. kirby* Kirby *D. laticollis* (Fahraeus) *D. sulcicollis* (Castelnau)	*D. ambiguus* (Kirby)
Drepanoplatynus Boucomont 1921	No information	
Euoniticellus Janssens 1953		*E. kawanus* (Janssens) *E. intermedius* (Reiche) *E. africanus* (Harold) *E. triangulatus* (Harold)
Liatongus Reitter 1893	*L. militaris* (Castelnau)	*L. spathulatus* (Roth)
Oniticellus (s.str.) (Serville) 1825	*O. egregius* Klug *O. formosus* Chevrolat *O. pictus pictus* (Hausman) *O. planatus* Castelnau	
Scaptocnemis Péringuey 1901	Insufficient observations	
Tiniocellus Péringuey 1901		*T. spinipes* (Roth)
Tragiscus Klug 1855	*T. dimidiatus* Klug	

by Halffter and Matthews (1966:152). Desiccation of the broods of *Oniticellus (s.str.)* and *Tragiscus* is probably reduced by the fact that they completely fill the chamber and are often bedded in dung shreds. Those of *Eurysternus* lie loosely in a spacious cavity but it has not been reported whether or not they possess a clay shell to protect against desiccation. As they conform to the definition (of endocoprids) formulated in Chapter 4.2., all those species which construct brood ovoids, or pears, in chambers positioned within, or immediately under the dung, should be considered endocoprids. As some of these species are taxonomically far removed from one another, the term "endocoprid" has no strict taxonomic validity and is purely an artificial grouping based on similarities in their biology.

Halffter and Matthews (1966:13) consider that the Scarabaeinae became specialised as dung feeders early in their evolution. Certainly a well developed dung beetle fauna (ca 250 species) utilises the droppings of the metatherian mammals of Australia. Assuming that, like the extant species, extinct marsupials also dropped pellets and, that the diminutive, early, placental mammals dropped small amounts of dung, the endocoprid habit could probably not have existed until the evolution of the larger eutherian herbivores, owing to the compact mass of dung required by endocoprids for successful breeding. Thus it is probable that endocoprids evolved from established coprophagous species comparatively recently.

Evolutionary trends in *Oniticellus (s.str.)* seem to have been towards increasing tolerance to desiccation, and temperature fluctuations probably resulting from their broods being buried more and more shallowly. This has possibly been in response to breeding under dry soil conditions. For example, in the laboratory, *Euoniticellus intermedius* buries its broods well beneath the pad at a depth of approximately 10 - 12 cm whereas an

european ....

european species, *E. fulvus*, constructs its broods in shallow burrows approximately 4 - 5 cm under the pad which may be an adaptation towards breeding in dry conditions (Aschenborn pers. comm.).

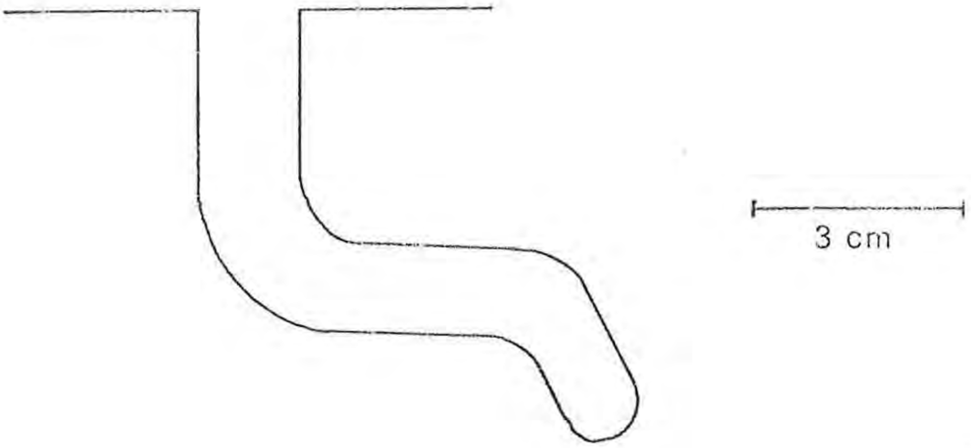
In endocoprid evolution, the increased likelihood of desiccation towards the soil surface has probably resulted in the development of more specialised nidification behaviour which agrees with Halffter and Matthews statement (1966:204) "that complex nesting behaviour ..... is a response to harsh environmental factors." As broods in shallow burrows are in closer proximity to the pad and its moisture content, reliance on soil moisture and the necessity to burrow may have gradually been lost. With the loss of burrowing the role played by the male in breeding behaviour is reduced to that of mating.

Although most known members of the Oniticellini, Onthophagini and Onitini remain relatively unspecialised in their breeding behaviour (Halffter and Matthes 1966:149) it is probable that the ancestors of the endocoprids bred in the manner of contemporary *Euoniticellus*. This genus, which is closely related to *Oniticellus (s.str.)*, is considered amongst the least specialised of the extant Scarabaeinae because the feeding and breeding burrows are indistinguishable (Halffter and Matthews 1966:124). A typical example is *E. fulvus* which packs a mass of dung into the end of a simple burrow (Farbre 1897:151). The egg is laid in a depression at the apex of this mass and a thin layer of dung is applied to the top to enclose the egg within a chamber (Fig 37). The method of nidification utilised by *O. egregius* may well have developed from this *Euoniticellus* type behaviour. The pit in which each brood is constructed probably represents an attenuated burrow (Fig 22). The lower mass of dung seen in the broods of *E. fulvus* (Fig 37d), is absent in *O. egregius*

so that ....

FIGURE 37: Manner of brood construction by *Euoniticellus fulvus*.

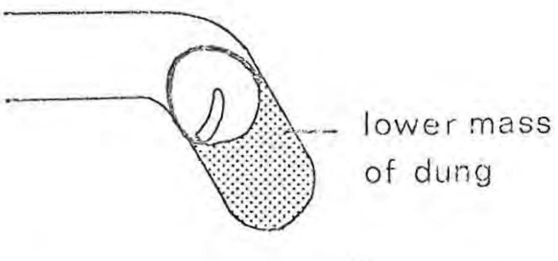
(a) Burrow excavated from under dung pad



(b) Dung packed into endof burrow

(c) Walls of egg chamber constructed and egg laid

(d) Apex of egg chamber sealed with thin layer of dung.



so that the brood of this species represents only the upper section around the egg chamber (Fig 22f). The clay shell was probably developed in response to increased desiccation close to the surface. The indications are that *O. egregius* breeding is restricted to the wet summer months in southern Africa, similarly to that of most other dung beetles. A disadvantage of breeding immediately under pads is the restriction of available breeding sites due to the activities of paracoprid and telecoprid dung beetles (Chapter 5.4.). It would thus be advantageous if the breeding period could have been continued a little beyond the end of the rains when dung removal is in decline. Further evolution may have led to the active colonisation of the pad, probably when dung removal was low. An advantage of breeding in the pad itself is that the larval cycle may be successfully completed utilising pad moisture only. This ability to breed independently of ambient soil moisture, and extension of the breeding season in the presence of reduced dung removal, has favoured the loss of aestivation through dry periods as continuous breeding can now occur. As temperatures have to be sufficiently high throughout the year for this to be possible, the endocoprid habit in *Oniticellus (s.str.)* and *Tragiscus* probably evolved in the tropics with the later radiation of these genera into the warmer parts of the temperate zone.

In the brooding species, *O. planatus*, the *egregius* style of brood construction has been retained (Fig. 23), though slightly modified to meet conditions in the pad where no pit can be utilised and the attainment of a suitable dung plasticity requires a drying period followed by rapid brood production. (Chapter 4.3.).

In ....

In the *Euoniticellus* style of brood construction, more dung is buried than is used by the larvae, whereas only the amount necessary to complete larval development is incorporated into the brood ovoids of *O. egregius* and the brood balls of the brooding endocoprids. This economy in time and energy expended on each endocoprid brood is an advantage which combined with other factors (Chapter 4.3.), makes for maximum rapidity in brood production.

Whilst *O. planatus*, and the Asian *O. cinctus*, have retained the alternative of constructing chambers in the soil, in *O. formosus*, *O. pictus* and *T. dimidiatus*, the most extreme endocoprid specialisation is seen with the restriction of brood chambers to the pad, the development of thin spots to aid emergence from dried out balls and further specialisation in brooding and brood construction (Chapter 4). The development of brooding behaviour has resulted in more infrequent breeding so that selection has favoured increased longevity in order that a viable population be maintained. For example, the species of the genera *Euoniticellus* and *Onitis* bred at the DBRU live approximately 30 and 105 days, respectively, whereas the African members of the brooding endocoprids have a mean life expectancy of 121 - 235 days (Table 23).

The evolutionary stages postulated above and below their selective forces and their consequences or advantages, have been indicated diagrammatically in Figure 38. These stages conform to the order of reduction in the size of the prosternal spur of *Oniticellus (s.str.)* described by Janssens (1953). It is probable that the endocoprid habit has been evolved independently by *T. dimidiatus*.

As most endocoprids lay their eggs over a short period, filial emergence occurs over an equally short period. Larval development begins whilst the broods are still being elaborated, with the result that parental abandonment of the chamber is allowed sooner than if they were completed one at a time. In this way more broods are completed per breeding cycle and more breeding cycles are accomplished in one lifetime.

Two trends are apparent in the evolution of endocoprid brooding. In the one, evolution has led to increased resistance to desiccation and earlier parental departure from the brood chamber. Whilst many *O. planatus* emerge only with their progeny, in the more desiccation resistant species parental abandonment of the brood chamber is at an earlier, immature stage (Chapter 4.5.). As the length of the life history in *O. planatus* and *O. formosus* has been shown not to be significantly influenced by the number of eggs laid (Tables 23 and 24), earlier abandonment of the chamber is another factor which allows a greater number of breeding cycles to be completed in one lifetime. In the second trend, during the 5 - 7 weeks period that the females tend their broods, they are removed from competition with other endocoprids which allows a higher breeding population to be maintained than is possible if the broods are abandoned soon after egg laying. This only applies where there is a limited number of breeding sites as there often is during summer.

The first trend towards increased resistance to desiccation appears to have increased the viability of the endocoprid larvae. However, the allowance of a shorter brooding period in relation to the stage of larval development at which parental daparture occurs would tend to return the brooding females to the active fraction of the population more frequently and increase competition for breeding sites between endocoprid females. However, with increased larval resistance to desiccation the species can theoretically remain viable with a smaller breeding population which will be a distinct advantage where the breeding sites are severely limited in number. Therefore, although these two trends might at first seem a contradiction in terms in that the one would tend to reduce the effectiveness of the other, they are, in fact, complementary in that both raise the viability of the population.

Willimzik (1930) pointed out that the presence of nidification or brooding behaviour influences the rate of egg production. Halffter and Matthews (1966:197) record that with increasing complexity of nidification and brooding, the number of follicles seen in the ovarioles becomes reduced, but this is not true of all brooding species. In *Copris hispanus* and *C lunaris* (L), Willimzik (1930) recorded a single follicle in the ovariole with sometimes a rudimentary second. Even so, egg production can take place with relative rapidity. Over a period of 77 days Lindquist (1935) induced a single female of *Copris remotus* Leconte, to lay 24 eggs in succession by removing broods soon after completion. Willimzik (1930) observed that only a fraction of the material in the terminal chamber of the ovariole is utilised for a single egg in *Copris* which may explain the ability to lay several eggs within a short period. In *Kheper nigroaeneus*, Tribe (1976:127) records up to three follicles in the ovariole but fecundity in this species was much lower than in *Copris*. Brooding in *Kheper* is probably of greater complexity than that of *Copris* whilst endocoprid brooding probably achieves a similar degree of organisation to that of the latter genus. However, the ovary in *Oniticellus (s.str.)* is not reduced at all from the state seen in their close, but unspecialised, relatives. (A mean range of 6 - 9 follicles with a maximum of 14 has been recorded for *O. planatus*). The rate of egg production is more rapid than in *Copris*. In the laboratory as many as 45 eggs may be laid within 29 days if female *O. planatus* are removed from their brood chambers and introduced to a fresh pad after 14 days.

The probable reason for the absence of ovarian reduction in *Oniticellus (s.str.)* lies in the positioning of the brood chambers. *Copris* and *Kheper* construct their brood chambers at depth, in the soil, which confers the advantage of stable conditions. These are listed by Halffter and Matthews (1966:177) as relatively constant humidity (less fierce desiccation than at the surface), reduced fluctuation in temperature, an assured dung supply and protection from predators. In the case of endocoprids just the opposite applies. Whilst brooding is well developed, the degree of adversity offered by environmental factors, and the removal of dung by other beetles, has selected against the reduction of the number of follicles, and the rate of egg laying seen in other brooding species. In fact, specialisations have developed which boost fecundity (Chapter 4). Amongst these are, increased longevity and a higher egg laying potential than their close non - endocoprid relatives, mechanisms to maintain a rapid rate of egg laying without feeding and a dual stage mode of brood construction which allows rapid egg laying but, at the same time, provides adequate protection against desiccation.

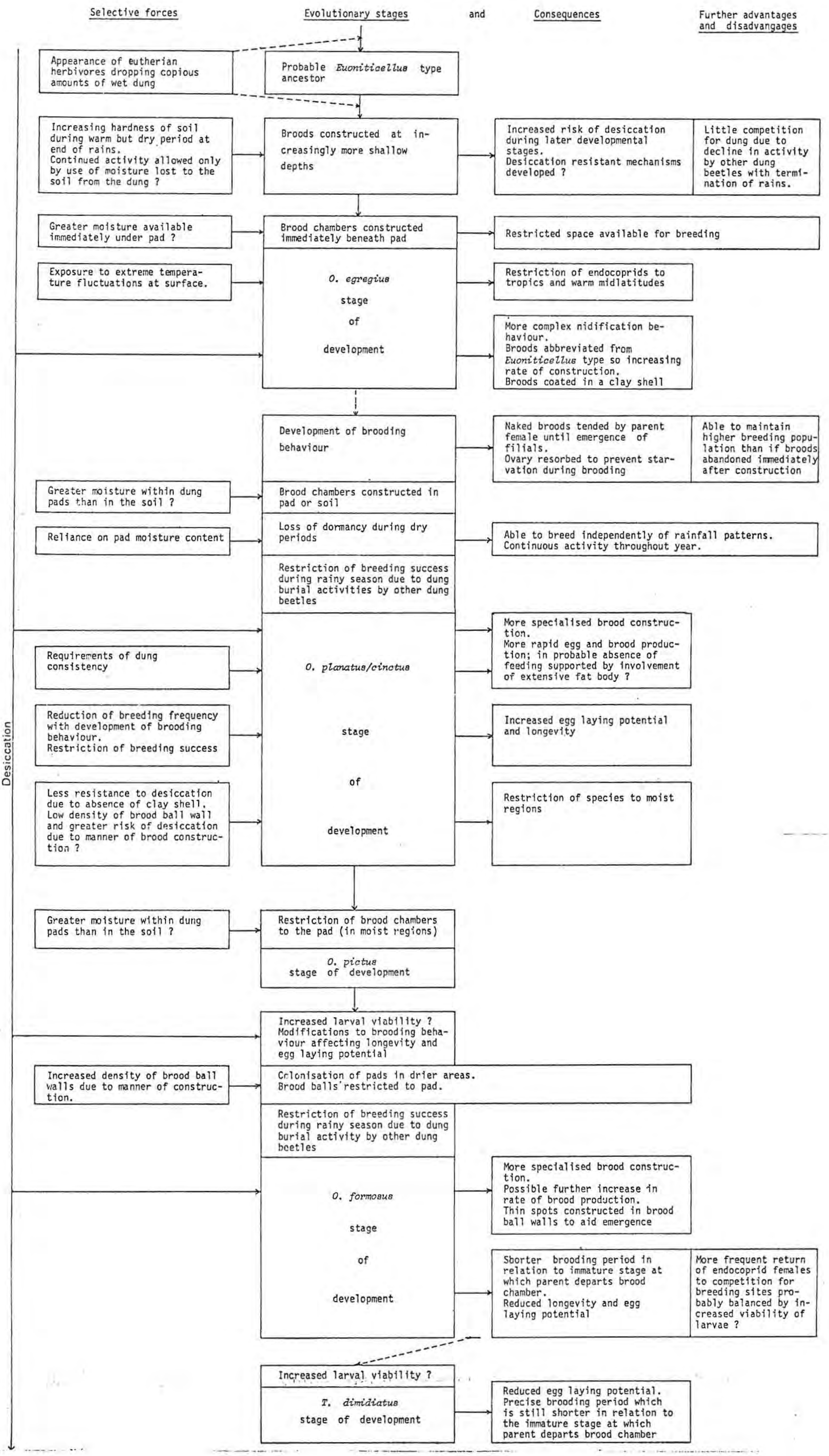
As the position of endocoprid brood chambers exposes them to surface temperature fluctuations it is no advantage to overwinter as dormant larvae and all species which are able to construct their chambers actually within dung pads pass the winter as active adults. Dissections show that, although during winter *O. formosus* from De Wildt continue feeding, their ovaries remain relatively undeveloped with rudimentary follicles visible only at the proximal end of the ovariole. The fat body around the gut is often bright yellow. Continuous winter activity results in endocoprids being able to take immediate advantage of increased temperatures in order to commence breeding activity. In *Kheper nigroaeneus*, a brooding species which overwinters in the soil as a dormant adult, the gut was completely collapsed after aestivation and 2 - 3 weeks feeding was required before egg laying began. (Tribe 1976:128).

In conclusion, I see the endocoprids as having become an

extremely ......

an extremely specialised group through their adoption of the habit of breeding within or immediately beneath dung pads where they have been exposed to extreme temperature fluctuations, the danger of rapid desiccation and competition for dung with paracoprids and telecoprids. Although their abundance is often low, they exhibit a very widespread distribution and must therefore be considered as successful.

Figure 38: Diagram showing the postulated direction, selective forces and consequences of endocoprid evolution in southern Africa.



SUMMARY

1) The biology and ecology of the endocoprid dung beetles of the Aethiopian zoogeographic region has been studied in the field and laboratory. Work has centred mainly on *Oniticellus planatus* and *O. formosus* although information has also been supplied on *O. egregius, O. pictus* and *Tragiscus dimidiatus*.

2) The taxonomy of *Oniticellus (s.str.)* and *Tragiscus* has been discussed with the recommendation that *O. planatus* and *O. pseudoplanatus* be synonymised.

3) It has been suggested that endocoprid distribution is chiefly controlled by temperature, rainfall and the density of suitable large dung masses. On the basis of distribution it has been suggested that the taxonomic status of the subspecies of *O. pictus* should be reviewed. Endocoprids (genus *Oniticellus (s.str.)*) are found throughout the warmer regions of Africa and Asia. *Tragiscus* is found only in Africa.

4) Methods are described for monitoring endocoprids in the field, for distinguishing freshly emerged from older specimens, and for breeding endocoprids under laboratory conditions.

5) It has been shown that endocoprids breed within or just beneath large dung masses unlike most other members of the Scarabaeinae which actively bury dung and construct their broods at depth in the soil.

6) It has been shown that there is a restriction of breeding sites available to endocoprids due to the removal of dung by other Scarabaeine beetles and the limited space available within dung pads.

This ....

This has resulted in low endocoprid population numbers, a disadvantage which has been countered by highly specialised but opportunistic breeding habits.

7) The requirements of dung plasticity have limited the time available for breeding activity by most endocoprids (excluding *O. egregius*) so that both the reproductive system and the reproductive behaviour (cf. *O. planatus*) are geared to rapid egg and brood production. Large numbers of follicles are able to be produced over a short period. In the probable absence of feeding, this has possibly been allowed by the involvement of a well developed fat body. The broods are tended by the parent female during larval development and the follicles are gradually resorbed, probably to prevent starvation. Ovarian recovery is rapid once feeding recommences. Behavioural mechanisms have developed which boost the number of broods constructed and the rapidity with which they are produced.

8) The duration of endocoprid colonisation and the timing of arrival at dung is shown to be related to the rate of pad desiccation which is chiefly controlled by temperature and degree of dung removal by other dung beetles. Precipitation may also play a part.

9) Predation by vertebrates and other insects has been noted and a number of mechanisms are described which are probably protective.

10) Two insect parasitoids of *O. formosus* larvae have been recorded.

11) The potential use of endocoprids in the Australian dung and fly control project has been discussed and it is recommended that their introduction be considered of low priority.

12) ....

12) It is suggested that the endocoprids evolved from *Euoniticellus* type ancestors and that their behaviour and complex nidification developed in response to harsh environmental factors, chiefly the danger of desiccation and competition for dung with other dung beetles.

13) From a consideration of brood and brood chamber construction it is suggested that *O. egregius* is a relatively unspecialised endo-endocoprid which may retain dry season aestivation and has not evolved much further than its probable *Euoniticellus* type ancestor. The broods are coated in clay and abandoned soon after construction.

14) Greater specialisation is shown by *O. planatus* and *O. formosus* which exhibit brooding behaviour, increasing longevity, more specialised brood protection, increased potential fecundity and continuous activity throughout the year. *O. formosus* shows greater specialisation in brood production than *O. planatus*.

15) Greatest specialisation is found in *T. dimidiatus* which exhibits a precise brooding period and low egg production. Brood construction is of a similar degree of specialisation to that of *O. formosus*. Activity is also continuous throughout the year.

16) The comparative biology of the five southern African endocoprids is summarised in Table 35.

TABLE 35 :

A comparative summary of the biology of five endocoprid dung beetles occurring in southern Africa.

The species are listed in the order of what is considered their degree of specialisation to the endocoprid habit.

SPECIES	Relative degree of development of prosternal spur (Chap.1)	Winter Aestivation	Dung age preference	Position of brood chamber	Mean number of broods/ chamber	Mean Fecundity (number of broods/ life-time)	Mean Longevity (LLH) (days)	Condition of outer shell of brood balls	Mean elaboration of broods mm	Brooding behaviour	Mean time spent in each brood chamber (days)	Stage of development of greatest % of immature stages when female departed brood chamber
O.egregius	Large	Perhaps	Fresh	Soil	7,5	*IBLH:- 65	98	Clay Shell	None	None	13 (24-25°C)	Egg / 1st instar larva
O.planatus	Small	None	Older	Soil or Pad	13,5	*LLH:- 52 IBLH:- 144	223	Naked	0,23	Present	48 (23-24°C)	Filial adult
O. pictus-pictus	Almost non-existent	None	Older	Pad	-	-	-	Naked	-	Present	-	-
O.formosus	Almost non-existent	None	Older	Pad	13,5	LLH:-59 IBLH:- 93	142	Naked	0,46	Present	44 (23-24°C)	Pupa
T.dimidiatus	-	None	Older	Pad	5,8	LLH:-19	177	Naked	-	Present	48 (23-24°C)	3rd instar larva

* LLH :- Female allowed to remain in the brood chamber until it emerged voluntarily.

* IBLH:- Female introduced to a fresh pad every 14 days (every seven days in the case of *O. egregius*).

ACKNOWLEDGEMENTS

My thanks are due to Dr. G.F. Bornemissza, head of the DBRU, for suggesting the endocoprids as a suitable topic for research.

The advice, constructive criticism and guidance offered by my long-suffering supervisor, Dr. V.C. Moran, of the Entomology Department, Rhodes University, Grahamstown, is sincerely appreciated.

As I was allowed to continue this study during working hours, I would like to express my gratitude to my employers, the Plant Protection Research Institute, South Africa, by whom I am locally engaged for the CSIRO, Australia.

I am indebted to Mr. G.C. Clarke of the farm, *Sandspruit*, near De Wildt, for his kind permission to conduct the majority of the field work, cited in this thesis, on his property. During my absence on field trips, this work could not have been continued without the much appreciated assistance of the staff members of the DBRU, past and present, especially Messrs. G.C. Culligan, I.D. Temby, G.D. Tribe and Miss W. Davis. The technical assistance given by Mr. F. Malebye was a great help in reducing the workload and is also greatly appreciated.

I am beholden to the various farmers elsewhere in the Transvaal who granted me permission to collect and make observations on their properties. I am especially grateful, in this respect to Mnr. J. du Preez of the farm, *Rustig*, near Middelburg, Mnr. F.G. Terblanche of the farm, *Waterval*, near Pietersburg, and Mnr. J.J. Roos who farms near Messina.

I ....

I thank Dr. J. Decelle of the Musée Royal de l'Afrique Centrale, Tervuren, Belgium, for forwarding specimens of *O. pseudoplanatus* and *O. planatus*. I also thank Mnr. G.L. Prinsloo of the National Collection, Pretoria, and Dr. Y. Cambefort of the Centre National de la Recherche Scientifique, Toulouse, France, for their criticism of the taxonomic section of this thesis. In addition, thanks are extended to Mr. P.D. Stickler (DBRU, affiliated to the Plant Protection Research Institute, Pretoria), and Mr. W. Bond of the Department of Forestry, Saasveld, George, for their comments on the first draft of this study, and to Mr. G.C. Temlett and Mnr. Marnovic of Pretoria Zoo, for supplies of white rhinoceros dung, without which life history studies of *O. egregius* and *T. dimidiatus* would have proved impossible. Further thanks are extended to Mr. P.D. Stickler for the provision of unpublished data. Lastly, but not least, I thank Mr. Galpin of the Weather Bureau, Pretoria, for the provision of much useful climatic data amassed by his department and Mr. R. Clarke of the Department of Agricultural Technical Services, Pretoria, for supplying data on the gut contents of Sacred Ibis.

REFERENCES

Anon., 1954. *Climate of South Africa. (W.B.19), Part 1, Climate Statistics*. The Government Printer, Pretoria and Cape Town : 158 pp.

Anon., 1960. *Tables of temperature, relative humidity and precipitation for the world*, M.O. 617. Her Majesty's Stationery Office, London : 694 pp.

Arrow, G.J., 1928. Polymorphism in horned beetles. *Trans. R. ent. Soc. Lond.*, 76 : 73-77.

Arrow, G.J., 1931. *The Fauna of British India, including Ceylon and Burma, Coleoptera Lamellicornia III (Coprinae)*, Taylor and Francis, London, V - XII, 428 pp. Cited by Janssens (1953).

Arrow, G.J., 1933. Notes on Coprid Coleoptera, with descriptions of a new genus and a few new species. *Ann. Mag. Nat. Hist.*, XII : 421 - 430. Cited by Janssens (1953).

Bailey, H.P., 1960. A method of determining the warmth and temperateness of Climate. *Geogr. Annlr.*, XLII : 1 - 16.

Balthasar, V., 1941. Neue Coprophage Scarabaeidae. *Mitt. münch. ent. Ges.* XXXI : 164-184. Cited by Janssens (1953).

Balthasar, V., 1963. *Monographie der Scarabaeidae und Aphodiidae der palaearktischen und Orientalischen Region.* Tschechoslowakische Akademie der Wissenschaften I : 391 pp.

Balthasar, V., 1964. Neue Oniticellinen-Arten. 119. Beitrag zur kenntnis der Scarabaeoidea (Coleoptera). *Beitr. Ent.*, 14 : 619 - 622.

Bornemissza, G.F., 1960. Could dung eating insects improve our pastures ? *J. Aust. Inst. agric. Sci.*, 26 : 54 - 56.

Bornemissza, G.F., 1969. A new type of brood care observed in the dung beetle *Oniticellus cinctus* (Scarabaeidae). *Pedobiologia*, 9 : 223 - 225.

Bornemissza, G.F., 1970. Insectary Studies on the control of dung breeding flies by the activity of the dung beetle *Onthophagus gazella* F. (Coleoptera : Scarabaeidae). *J. Aust. ent. soc.* 9 : 31 - 41.

Bouček. Z., 1976. African Pteromalidae (Hymenoptera) : new taxa, synonymies and combinations. *J. ent. Soc. sth. Afr.* 39 : 9 - 31.

Boucomont, A. 1921. Synopsis des Oniticellini d'Afrique. *Revue zool. afr.* IX ; 197 - 233. Cited by Janssens (1953).

Chapman, R.F., 1969. *The insects, structure and function.* The English Universities Press, London. SBN 340 04988 X : 819 pp.

CSIRO, 1976. *Division of Entomology, Annual Report, 1975 - 76.* 15. Biological control of dung : 104 - 109. Canberra, A.C.T.

Drury, 1837. *Ill. Exot. Ent.*, ed. J.O. Westwood, I : 78. Cited by Janssens (1953).

Farbre, J.H., 1897. *Souv. ent.,* V : 1 - 167. Cited by Halffter and Matthews (1966).

Ferrar, P., 1973. The C.S.I.R.O. dung beetle project. *Wool Technol. Sheep Breed.* 20 : 73 - 75.

Ferrar. P., 1975. Disintegration of dung pads in north Queensland before the introduction of exotic dung beetles. *Aust. J. exp. Agric. Anim. Husb.,* 15 : 325 - 329.

Ferrar. P. and Watson, J.A.L. 1970. Termites (Isoptera) associated with dung in Australia. *J. Aust. ent. Soc.,* 9 : 100 - 102.

Ferreira, M.C., 1966. Os Escarabideos da Sub-região natural da Africa do sul. *Mems. Inst. Invest. cient. Mocamb.,* 8, Série A : 35 - 51.

Ferreira, M.C., 1972. Os Escarabideos de Ãfrica (Sul do Sãara) I.*Revta. Ent. Mocamb.* 11. (1968 - 1969) : 5 - 1088.

Gardner, J.C.M., 1929. Immature stages of Indian Coleoptera. 6. *Indian Forest Rec.,* 14 : 27 - 30.

Gillet, J.T.E. and Boucomont, A. 1927. *Coleopterorum catalogus, Scarabaeidae: Coprinae, Termitotroginae,* Partes 30 et 90. W. Junk, Berlin, 1911 - 1927 : 103 - 264.

Gomes Alves, M.L., 1950. Alguns Escarabideos de Mocambique. *Anais Jta. Invest. Colon.,* 5 : 147 - 179. Cited by Janssens (1953).

Halffter, G. and Edmonds, W.D. 1972. A taxonomic and biological study of the immature stages of some New World Scarabaeinae (Coleoptera : Scarabaeidae). *An. Esc. nac. Cienc. biol., Méx.,* 19 : 85 - 122.

Halffter, G. and Matthews, E.G., 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera : Scarabaeidae). *Folia ent. Méx.*, 12 - 14 : 1 - 312.

Harold, E. von. 1869. *Catalogus coleopterorum hucusque descriptorum synonymicus et systematicus, 4, Scarabaeidae.* E.H. Gummi, Monachii; E. Deyrolle fils, Paris : William and Norgate, London : 979 - 1346. Cited by Janssens (1953).

Hughes, R.D.; Greenham, P.M.; Tyndale-Biscoe, M. and Walker, J.M. 1972. A synopsis of observations on the biology of the Australian bushfly (*Musca Vetustissima* Walker). *J. Aust. ent. Soc.*, 11 : 311 - 331.

Janssens, A., 1939. Coprini (Coeleoptera Lamellicornia). Inst. Parcs Nat. Congo Belge. *Explor. Parc. natn. Albert. Miss. G.F. de Witte*, (1933 - 1935), 29 : 1 - 104.

Janssens, A., 1940. Monographie des *Scarabaeus* et genres voisins (Coleoptera Lamellicornia). *Mém. Mus. r. Hist. nat. Belg.*, 2e Série, 16 : 1 - 81.

Janssens, A., 1953. Oniticellini (Coleoptera Lamellicornia). Inst. Parcs. nat. Congo Belge. *Explor. Parc. natn. Upemba Miss G.F. de Witte*, (1946 - 1949), II : 1 - 118.

Judulien, F., 1899. Quelques notes sur plusieurs coprophages de Buenos Aires. *Revta. Mus. La Plata*, 9 : 371 - 380. Cited by Halffter and Matthews (1966).

Klemperer, H.G. and Boulton, R., 1976. Brood burrow construction and brood care by *Heliocopris japetus* (Klug) and *Heliocopris hamadryas* (Fabricius) (Coleoptera, Scarabaeidae). *Ecol. ent.*, 1 : 19 - 29.

Köppen, W., 1931. *Grundriss der klimakunde*. W. de Guyter, Berlin and Leipzig : 388 pp. Cited by Bailey (1960).

Kraatz, G., 1895. Zwei neue Westafricanische *Oniticellus* - Arten. *Dt. ent. Z.*, XXXIV : 142 - 144. Cited by Janssens (1953).

Landin, B.-O., 1961. Ecological studies on dung beetles (Col. Scarabaeidae). *Opusc. ent.*, Suppl. 19 : 1 - 228.

Lengerken, H. von., 1954. *Die Brütfürsorge und Brutpflegeinstinkte der Käfer*. Akademische Verlagsgesellschaft Geest und Portig K.-G., Leipzig. 383 pp. Cited by Halffter and Matthews (1966).

Lindquist, A.W., 1935. Notes on the habits of certain Coprophagus beetles and methods of rearing them. *U.S. Dept. agric. Circular* 351 : 1 - 10.

Medvedev, S.I., 1952. Lichinki plastinchatousykh zhukov fauny SSSR. *Opred. faune SSSR*, 47 : 1 - 242. Cited by Halffter and Matthews (1969).

Ohaus, F., 1909. Bericht über eine entomologische studienreise in Sudamerika. *Stettin. ent. Ztg.*, 70 : 3 - 139. Cited by Halffter and Matthews (1966).

Orbigny, H.d'., 1916. *Voyage de M. Guy Babault dans l'Afrique orientale anglaise*, 1912 - 1913, Imprimerie Gênêrale Lahure, Paris : 1 - 31.

Paschalidis, K.M., 1974. The genus *Sisyphus* Latr. (Coleoptera : Scarabaeidae) in Southern Africa. MSc. Thesis, Rhodes University, Grahamstown, RSA. : 189 pp.

Pêringuey, L. 1901. Catalogue of the Coleoptera of South Africa. *Trans S.Afr. phil. Soc.*, XII :

Paulian, R. 1945. *Faune de l'Empire Francais III.* Coléoptères Scarabaeides de l'Indochine, Libraire Larose, Paris, 225 pp. Cited by Janssens (1953).

Prasse, J. 1957a. Nahrungserwerb koprophager Pillenwälzer *(Sisyphus schaefferi* (L.) und *Gymnopleurus geoffroyi* Fuessl.). *Wiss. Z. Martin-Luther-Univ. Halle-Wittenb.*, 6 : 439 - 444. Cited by Halffter and Matthews (1969).

Rommel, R. 1961. Ernährungsbiologie und Brutpflegeverhalten des spanischen Mondhornkäfers *Copris hispanus* (L.) (Colept. Scarab.). *Biol. Zbl.*, 80 : 327 - 346. Cited by Halffter and Matthews (1966).

Serville, A.J.C. 1825.*Encycl. Meth.*, X : 356. Cited by Janssens (1963).

Stuckenberg, B.R. 1969. Effective temperature as an ecological factor in Southern Africa. *Zoologica Afr.* 4 : 145 - 197.

Tribe, G.D., 1976. The ecology and ethology of ball rolling dung beetles (Coleoptera : Scarabaeidae). MSc. thesis. University of Natal, Pietermaritzburg, RSA. : 160 pp.

Waterhouse, D.F., 1974. The biological control of dung. *Scient. Am.*, 230 : 100 - 109.

Weir, J.S., 1971. The effect of creating additional water supplies in a central African national park. The Scientific management of animal and plant communities for conservation. The 11th symposium of the British Ecological Society, University of East Anglia, Norwich, 7 - 9 July, 1979. Blackwell, Oxford : 367. Cited by Ferrar (1973).

Wernstedt, F.L., 1972. *World climatic Data.* Climatic Data Press, Lemont, Pennsylvania : 522 pp.

Willimzik, E., 1930. "Uber den Bau der Ovarien verschiedener Coprophager Lamellicornier und ihre Beziehung zur Brutpglege. *Z. Morph. Ökol. Tiere,* 18 : 669 - 700.