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Bionomics of a Pollen-collecting Wasp, *Paragia tricolor* (Hymenoptera: Vespidae: Masarinae), in Western Australia

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Abstract

At a perennial nest-site 40 km north-east of Perth, females of *Paragia tricolor* nested for about one month in late summer/early autumn while males patrolled bushes nearby. The nests in clayey soil were characterized by mud entrance turrets, vertical shafts and horizontal cells whose cemented earthen walls were polished and waterproof internally. Each cell received a loose egg prior to being mass-provisioned with a loaf of pollen-nectar mixture and plugged with mud. *Eucalyptus calophylla* was the sole food source. Shafts of completed nests had blind diverticulae and were sealed with mud partitions. Mature larvae spun cocoons, defaecated and entered diapause. Depredators associated with nests were a wasp, *Carinafoenus* sp. (Gasteruptiidae), and a mite, *Tyrolichus casei* (Acaridae).

Some distant populations of *P. tricolor* became active in December or January and fed at another *Eucalyptus* species.

Introduction

The vespid subfamily Masarinae (*sensu* Carpenter 1982) occurs world-wide and, although very incompletely studied, is notable in that those species whose habits are known provision their nests with pollen and nectar, much as do the bees. An overview of the biology of Masarinae may be obtained from the works of Richards (1962), Malyshev (1968), Torchio (1970), Zucchi *et al.* (1976), Gess and Gess (1980) and Dorr and Neff (1982).

In Australia, the subfamily is represented by four endemic genera whose habits remain largely unknown. Wilson (1869) recorded females of *'Paragia tricolor'*, later identified as *P. smithii* de Saussure (Richards 1962: 28), entering ground burrows with earth 'chimneys' in South Australia but revealed nothing of the nests' subterranean structure or contents. Riek (1970) commented that the food of Australian species is unknown and noted several plant genera whose flowers they frequent. Richards (1968) recorded *Goodenia cycloptera* R. Br. as a forage plant of two *Riekia* species.

The present paper results from the fortuitous discovery by Mr Eric McCrum of a nest colony of *P. tricolor* Smith near Perth and is the first detailed account of the biology of an Australian masarine.

Specimens collected during the course of this study are lodged in the Western Australian Museum, Perth (WAM).

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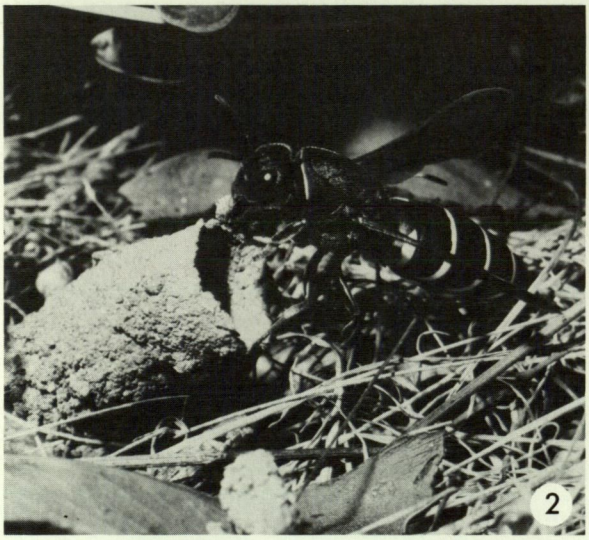
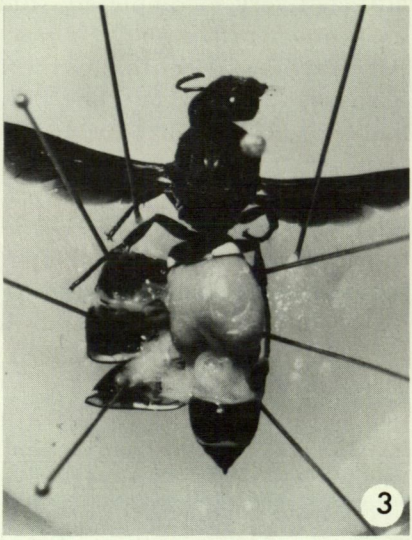




Figures 1-3 *Paragia tricolor*: (1) nest area at Noble Falls, W.A. (nests occurred in grassy area arrowed); (2) female emerging from nest turret carrying soil pellet in mandibles; (3) female dissected to show pollen-filled crop.

Observations

Nesting Site

The nest aggregation studied was at Noble Falls on Wooroloo Brook, about 40 km north-east of Perth. The nests were in an area of gently sloping, lightly grassed soil at the edge of a granite exposure and only a few metres from the perennial stream (Figure 1). The surface soil was a compacted loam which gave way at 20-30 cm depth to a hard sandy clay. Bordering the open ground were various shrubs, mostly *Acacia* species. The site was in dry sclerophyll forest dominated by *Eucalyptus calophylla* R. Br. and adjacent to cleared farmland where this same species occurred more sparsely. It was on a north-facing slope which received full sun most of the day. A strand line of flood debris occurred along the lower margin of the nesting area when first found but the area would not be inundated except in periods of abnormally high flooding.

Seasonality

Mr McCrum discovered the nesting site on 24 April 1982 when a single female entered a turreted burrow. Eight other turrets were located over an area of about 2 m^2. No live adults were observed when I visited the site on 8 May 1982 but seven nests were located by their turrets and excavated. Most had been abandoned while incomplete and five of six brood cells taken contained mouldy provisions and immature larvae. One contained a mature larva in a cocoon. Possibly nesting had been disrupted by earlier heavy rains.

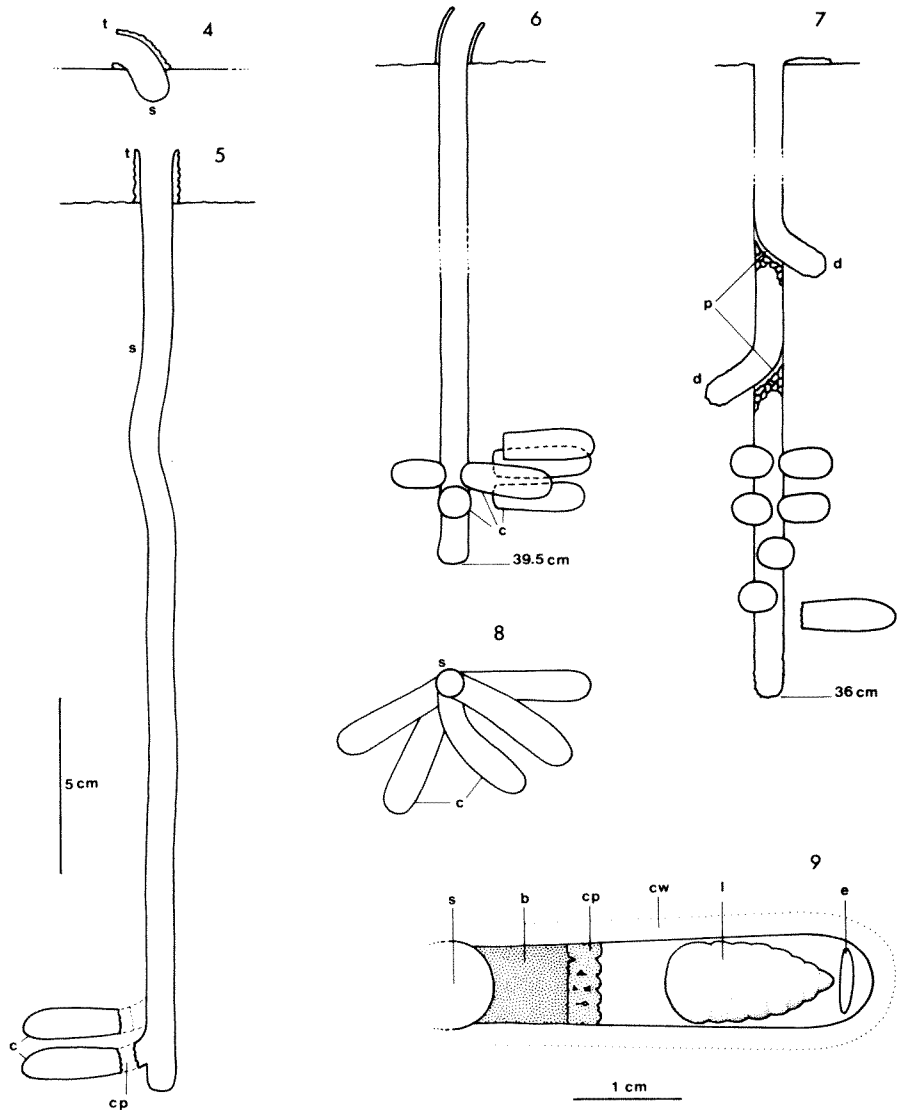
The Noble Falls site was revisited on 18 December 1982 and 13 February 1983 to check for activity but adults and turrets were absent. On 8 March 1983, adults of both sexes were active and nesting was well-advanced. Twelve turrets were found in the same ground occupied in 1982 and most were visited by females. Three nests (two active and one old and vacated) were excavated on 8 and 11 March. The active nests contained freshly provisioned cells with eggs and immature larvae. On 30 March, three closed nests containing mature larvae in cocoons were excavated, no adults were present and most turrets were collapsed (probably by rain).

All visits to the study site were made on days with fine, sunny, warm to hot weather, considered conducive to flight. Evidently *P. tricolor* produced a single generation of adults over twelve months at Noble Falls with emergence occurring in late February and activity ceasing by late March.

The foregoing observations and dates on several WAM specimens suggest that adult activity in the Darling Range-Perth region is confined to the months February-April. However, records from further north (Mullewa-Perenjori region) and further east (Coolgardie-Norseman region) indicate that activity there occurs in December and January.

Nests

Thirteen nests in various stages of development were excavated on 8 May 1982 and 8-30 March 1983. All active and recently completed nests, including some



Figures 4-9 Details of nests of *Paragia tricolor*: (4-7) profiles of nests in various stages of completion (schematic; turrets and shafts shown in section, cell chambers in outline; portions of shafts omitted from 6 and 7; measurements indicate depths): (4) early stage of excavation; (5-6) cell construction stage; (7) sealed and complete; (8) plan view of cell group depicted in 6 with closures omitted to show connections to shaft; (9) horizontal section through newly completed cell showing pollen loaf and egg (top views). 4-8 to same scale. Legend: b, barricade; c, cell(s); cp, cell plug; cw, cemented wall; d, diverticulum; e, egg; l, pollen loaf; p, partition; s, shaft; t, turret.

with shafts only a centimetre or so deep, had entrance turrets. Evidently, turrets are constructed in the initial stages of burrow excavation. Most turrets were situated amongst low dry grass and herbs and were vertical to moderately curved (Figures 2, 4-6). A few reclined on to the surface of bare ground and opened horizontally. Several occurred beneath the edges of tussocks and shrubs. Their height (or length) ranged from 15-30 mm. Internally, they were smooth and about 9.5 mm in diameter, while externally they varied from smooth to coarsely granular and were 11-14 mm in diameter. Tumuli were absent and only a few pellets of earth lay about the turrets.

Shafts were uniformly circular in cross-section, about 8.5 mm in diameter, and extended more or less vertically below the turrets. Their walls were not specially formed except in the lower extremities adjacent to the brood cells. Where cells were present, shafts varied in depth from 20-40 cm.

Nests under construction contained 1-6 cells, three recently completed nests contained 3, 7 and 8 cells, and an old vacated nest contained 14 (Figures 5-7, 16). Cells occurred at depths of 19-38 cm, mostly in the loam-clay interzone which was quite dry at the time of excavation. They were usually confined to one side of the shaft (Figure 8) and were sometimes in contact with one another.

Each cell was a horizontal, somewhat cylindrical chamber apparently connecting directly with the shaft. However, its 'throat' probably represents an extremely short access burrow. Cells (including access burrows) were 24-42 mm long and attained their maximum diameters of 8.5-9.5 mm near their rounded blind ends. They tapered gradually into their throats which were 1-2 mm narrower (Figure 9). The walls of cells were of cemented earth and about 2 mm thick. Whether these were built-in or formed by impregnation of the walls of excavated cavities was not clear, but some walls appeared darker than the yellow clay matrix. Their hardness permitted cells to be removed intact (Figure 15) after scraping away the softer matrix but they had no discrete external surfaces.

Internally, cell walls were very smooth, shiny and light chocolate brown. The gloss diminished towards the cell mouth (Figure 10). That the inner walls were waterproof was demonstrated when drops of water placed on them remained unabsorbed whereas others placed on the outsides were absorbed immediately. Microscopic examination revealed no special film or coating on the inner walls. A piece of cell wall soaked in water gradually disintegrated, the outer layers slumping first and the fine clay inner surface resisting longest. One complete, closed but unprovisioned cell exhibited a scaly pattern on its inner walls suggesting that they had been deposited as pellets 0.5-1.0 mm wide.

Following oviposition and provisioning, each cell was closed with a plug of cemented earth up to 10 mm thick. Plugs consisted of an inner partition (the cell plug proper), showing a concentric pattern of pellets on its rough inner surface, and a barricade of compacted soil (the access burrow filling) plastered smooth and flush with the shaft walls externally (Figure 9). Thus, cells were

undetectable from within the shafts. Where several cells had been sealed, the shaft walls were largely built-in and slightly glazed.

On 30 March, two nests with sealed shafts were excavated. In both, the shaft had two blind diverticulae closed from the shaft below by cemented partitions (Figure 7). The latter were built upon plugs of mud pellets and were smooth and moulded so as to maintain the contours of the shaft into the diverticulae. Presumably they were constructed with soil excavated from the diverticulae. In one of these nests there was also a rough-walled lateral burrow below the cells.

Remains of old vacated nests were frequently encountered while excavating and were sometimes in very close proximity to new nests. One new shaft ran parallel to an old one with only 2-3 mm separation.

Provisions

Ten closed cells with fresh or partly consumed provisions were examined on 8 and 11 March 1983. In each case, the provisions consisted of a loaf of soft, moist, yellow pollen, wide enough at the cell plug end to almost occlude the cell lumen and tapering to the other end (Figures 9-12). The loaves had folds and annulations which probably represented successive deposits of food. This suggested that a female first deposits food in the median line of the floor near the cell base and subsequently alternates regurgitations to the left and right towards the cell mouth. Loaves varied considerably in size (lengths 16-24 mm) independently of cell size. They tasted sweet indicating that the pollen was moistened with nectar. Some loaves taken to the laboratory began to develop vesicles over their surfaces within a day suggesting that fermentation was occurring. This ceased as they dried.

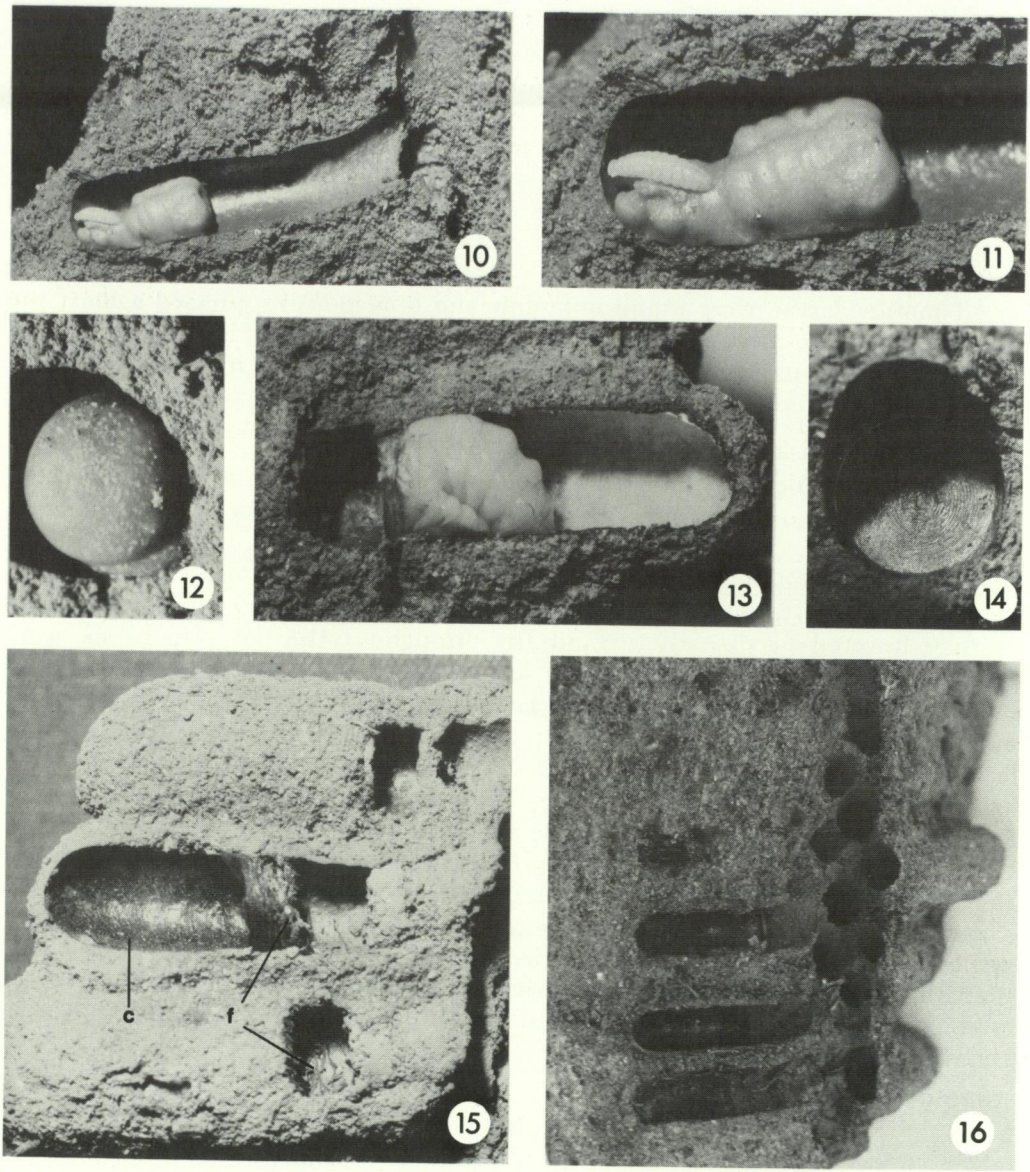
A female captured returning to her nest in which there were freshly provisioned cells was dissected and it was found that her pollen-filled crop occupied about two-thirds the volume of her abdomen (Figure 3). A full load would be equivalent to several folds in a pollen loaf.

Samples from all ten pollen loaves were examined microscopically and consisted entirely of one kind of myrtaceous pollen matching that of *Eucalyptus calophylla.*

Immatures

In each of two newly completed closed cells, a large (6.2 mm long, 1.4 mm wide), fusiform egg lay transversely and loosely in the inner end behind the pollen loaf (Figure 9). The eggs must have been deposited prior to commencement of provisioning as the females could not have got past the pollen loaves.

In other cells, small to medium-sized larvae fed at the tapered inner ends of pollen loaves (Figures 10, 11). All mature larvae found were enclosed in cocoons which were evidently constructed after completion of feeding and prior to defaecation. The cocoons consisted of a black to brown papery material closely applied to and not readily separable from the inner ends of cells. The inner end of each



Figures 10-16 *Paragia tricolor*: (10-11) cell opened from side to show young larva feeding on pollen loaf; (12) outer end of a pollen loaf; (13) cell with cocoon opened from side to show mature larva in resting position; (14) outer view of cocoon septum; (15) group of three cells partly opened to show faeces (f) and cocoon (c) of *Carinafoenus* sp.; (16) old vacated nest with fourteen cells exposed from the sides.

was rounded in conformity with the cell base, and the outer end was truncate and formed by a flat, circularly-striate septum (Figures 13, 14). A space up to 10 mm long remained between this septum and the cell plug. Cocoons varied in length from 17-24 mm. Silk strands were far more numerous in their walls nearest the septum than in the much thinner, more fragile walls of the inner end.

Black faecal material was deposited as a thin layer over the inner three-fifths or so of each cocoon and often also as thick scales at the inner end. This faecal layer was covered with white mould in numerous cocoons in recently completed nests (Figure 13).

All mature larvae were found immobile and unresponsive, pressed against the flat septa of their cocoons and out of contact with the faecal layers (Figure 13). Each rested with its head and forebody reflexed ventrally and its broad soft body occluding the cocoon lumen.

Associated Organisms

Two kinds of depredators were found in association with nests: a parasitoid wasp, *Carinafoenus* sp. (Gasteruptiidae), and a mite, *Tyrolichus casei* Oudemans (Acaridae).

Both sexes of *Carinafoenus* sp. were observed over the nesting area on 8 and 11 March 1983. The wholly orange-bodied wasps (21-23 mm long) were conspicuous as they hovered persistently to and fro throughout the day. Up to six were present at a time. Although none was seen to enter or leave a turret or pay particular attention to one, gasteruptiid larvae were found in three cells. One immature larva was found on a mouldy pollen loaf. Two mature larvae were found in their cocoons in cells. They differed conspicuously from the host larvae in being more slender, setose and active. Their cocoons were distinctive in having masses of black rod-like faeces outside the septa (Figure 15) and the septa were blacker and concave internally. Evidently, the larvae of *Carinafoenus* develop on the pollen stores, probably after destruction of the *Paragia* eggs.

Mites were found only in one cell where dozens of eggs and nymphs and several adults of *T. casei* occurred on a dried, shrunken pollen loaf. No *P. tricolor* immature was present. *T. casei* is a cosmopolitan pest of stored products (cheese, grain, flour and old honeycomb) and is not recorded as a close associate of Hymenoptera (A. Fain pers. comm.).

Adult Behaviour

Females returning to their burrows from foraging trips hovered in hesitantly and alighted either on the ground or on the rims of their turrets before entering them head first. They always reversed out of the turrets, indicating their inability to turn within the burrows. Nest-building was not observed except that a female was noted carrying a pellet of soil in her mandibles as she emerged from a turret (Figure 2) and returning without it after a brief flight. Clearly, most soil excavated must be carried well away from the burrows as no more than a few pellets lay around turrets.

On two observation days (8 and 11 March), up to ten males were in flight near the nesting area at any one time between about 8.30 a.m. and 2 p.m. They flew fairly quietly (except for a few with very ragged wings) and were very attentive to several shrubs without flowers on the margin of the nesting area. They flew erratically in and around the shrubs but seldom alighted. Territorial behaviour appeared to be absent as the flight paths of males interwove and only occasional chases were noted. One male pounced on and grappled with a female approaching her turret but copulation did not ensue. After midday the number of individuals patrolling gradually diminished until all had vanished by about 2 p.m.

Forage Plants

No adults were observed foraging at Noble Falls. However, examination of larval provisions (see above) suggested that Marri (*Eucalyptus calophylla*) was the sole source of pollen. Marri trees were virtually the only source of pollen and nectar at Noble Falls while adults were active in 1982 and 1983. In 1983, local flowering peaked in February prior to adult emergence and had almost ceased on 30 March (when activity had ended). The flowering period of Marri is recorded as February and March (Beard 1970) but irregular flowering earlier or later is not uncommon. Thus, the activity season of *P. tricolor* in the Darling Ranges coincides approximately with the flowering period of this plant.

Marri does not occur at all *P. tricolor* localities and on 20 January 1982 at Dedari (near Coolgardie) I collected 14 male and 2 female *P. tricolor* at flowers of White Mallee (*Eucalyptus cylindriflora* Maiden and Blakely). Probably the observed regional differences in activity periods (see Seasonality) are correlated with flowering times of different forage plants.

Discussion

Detailed comparison of the ethology of the Masarinae so far studied is hampered by insufficiency of data in some reports. However, it is clear that *P. tricolor* conforms generally to the pattern of behaviour described for most species and particularly for those members of the ground-nesting genera *Ceramius, Jugurtia* and *Trimeria* (Masarini). Some other Masarini (*Masaris, Pseudomasaris* and *Celonites*) differ radically from these genera in building aerial mud nests or nests in beetle burrows in logs.

The ground-nesters conform in nesting in hard clayey soil near water (which is required to produce mud) and in constructing entrance turrets, vertical shafts and separate earthen cells at the ends of lateral burrows (sometimes very reduced, as in *P. tricolor*). Eggs are deposited loosely in cells (unlike those of Gayellini which are attached by threads to the cell walls) and before the cells are provisioned with annulated loaves of moist pollen.

Some ground-nesters (e.g. *Ceramius capicola* Brauns and *C. lichtensteinii* [Klug]) construct bulbous enlargements of their shafts used by the wasps for

turning whereas others, including *P. tricolor,* do not. Also, some (such as *C. lichtensteinii, C. tuberculifer* Saussure and *Jugurtia confusa* Richards) construct mud cells within excavated chambers while others form only excavated cells. The method of cell construction employed by *P. tricolor* merits further attention as this study failed to determine whether the 2 mm thick mud walls of cells were built-in or formed by impregnation of the walls of excavated chambers by some cementing liquid. No roughed-out or obviously incomplete cells were discovered that might have shed light on this problem.

A polished inner cell wall, as occurs in *P. tricolor,* has been reported for *Trimeria howardii* Bertoni (Zucchi *et al.* 1976). In other genera, the walls are smooth but dull and, as with *Trimeria,* their water absorbency has not been reported. No explanation was obtained of how females of *P. tricolor* produce the lustrous and waterproof inner surfaces of their cells.

The shaft closures of *P. tricolor* have no known parallel amongst their ground-nesting relatives. Not only may the oblique mud septa serve as barriers to potential depredators but they may also deflect them into the diverticulae where (should they attempt to burrow deeper) they would expend their energies fruitlessly.

According to Richards (1962), the closest relatives of *Paragia* are the other Australian masarine genera about whose nesting habits nothing has been published. However, I have observed a female of *Rolandia maculata* (Meade-Waldo) and one of an undescribed *Riekia* species entering burrows in sandy ground. Both burrows were simple, oblique and ended blindly without any cells and neither had an entrance turret.

Acknowledgements

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