An Australian Masarine, *Rolandia angulata* (Richards) (Hymenoptera: Vespidae): Nesting and Evaluation of Association with *Goodenia* (Goodeniaceae)

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Abstract.—An account is given of some aspects of the nesting of *Rolandia angulata* (Richards) (Masarinae). This wasp nests in multicellular burrows in compacted sandy soil. The sloping entrance to the burrow, not surmounted by a turret, is concealed beneath a pebble, a plantlet or a suitable item of debris. The main thrust of the shaft is vertically downwards, however, at intervals it curves outwards to end in a horizontal cell so that each cell, except the last excavated and therefore deepest one, appears to be accessed by a lateral shaft. The cells are unlined. The architecture of the nest and the method of its construction are discussed. The association between *Rolandia angulata* and *Goodenia* (Goodeniaceae) flowers, the source of nectar and pollen, is evaluated. It is shown that the association with *Goodenia pinnatifida* Schldl., at least, is mutually beneficial. Indeed it is suggested that in some areas, at some times, *R. angulata* may be the most important potential pollinator of this plant.

The genus *Rolandia* Richards, 1962 is listed by van der Vecht and Carpenter (1990) as a junior synonym of *Metaparagia* Meade-Waldo, 1911. As the analysis on which this is based has not yet been published the generic name *Rolandia* is used in the present paper. *Rolandia* is restricted to Australia. Four species are known, two, *R. maculata* (Meade-Waldo) and *R. houstoni* Snelling, from Western Australia, a third, *R. borreriae* Snelling, from Northern Territory, and the fourth, *R. angulata* (Richards), the subject of this paper, from Queensland and New South Wales.

Rolandia angulata has been recorded from southwestern Queensland and northwestern New South Wales, from Cunnamulla [28.04S, 145.40E] (Richards 1968 as *Riekia angulata* and Snelling 1986) in the north to 90 km W of Cobar, Barnato Tanks [31.38S, 144.59E] (about 400 km south of Cunnamulla) (Richards 1968) in the south, and from three sites to the east of Cunnamulla, 80 km E of Cunnamulla (28.04S, 145.40E), 27 km W of St George (28.03S, 148.30E), and 85 km E of St George (28.03S, 148.30E) (27–29.x.1993, F.W., S.K. and R.W. Gess).

There is only one published observation on the nesting of *Rolandia*—that of *R. maculata* entering a turretless, simple, oblique, blindly ending burrow in sandy ground (Houston, 1984). However, Houston is currently investigating further the nesting of this species and has made some details available for comparison.

The investigations concerning *R. angulata* published in the present paper were undertaken by the authors during the course of a fieldtrip to Australia in October 1993. Voucher specimens have been deposited in the Albany Museum (*R. angulata*, the forage plants, and the bee visitors to the forage plants), the Australian National Insect Collection, Canberra (*R. angulata*), and the Australian National Herbarium, Canberra (the forage plants).

NESTING

Description of the Nesting Areas.—Two nesting areas of Rolandia angulata were lo-



Figs. 1–4. 1, *Eucalyptus* woodland between St George and Cunnamulla, southwestern Queensland; 2, *Acacia* scrub 80 km east of Cunnamulla, southwestern Queensland; 3, a nesting site of *Rolandia angulata* 27 km west of St George, southwestern Queensland; 4, a nest entrance of *Rolandia angulata* beneath a piece of plant debris (approximately \times 3.6).

cated between St George and Cunnamulla in southern Queensland, one 27 km west of St George on 28 October and the other 80 km east of Cunnamulla on 29 October, the former in dry open woodland dominated by *Eucalyptus* (Fig. 1) and the latter in dry open scrub dominated by *Acacia* (Fig. 2). Both areas had recently received rain in the form of localized thundershowers which had resulted in a growth of annuals which were in flower on the road verges and in the low lying areas. The soil in both areas was sandy, compact but friable. It was increasingly moist at least to the depth of the deepest nest cells, 38 cm.

Flowers Visited.—The only previous record of flower visiting by *R. angulata* is that of Richards (1968) for females collected on *Goodenia cycloptera* R.Br. in C.Sturt (Goodeniaceae) at Barnato Tanks. In the present study females and males were collected and observed visiting the yellow flowers of a prostrate herb also identified as *G. cycloptera* (Fig. 11) and an erect herb *Goodenia pinnatifida* Schldl. (Fig. 6) in the two areas where nests were discovered and

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also in the area 85 km east of St George. At the most easterly site, that is 85 km east of St George, both species of *Goodenia* were common. Travelling westwards to Cunnamulla it was observed that *G. cy-cloptera* rapidly became uncommon whereas *G. pinnatifida* became increasingly common and at the site 80 km east of Cunnamulla was the most common roadside herb. The abundance of *R. angulata* followed a similar pattern to that of *G. pinnatifida*.

Visits to the flowers by female *R. angulata* were abundant by 10h00 and continued through the heat of the day and the afternoon. Visits became fewer in the late afternoon and ceased after 17h00. Males were observed to patrol the flowers and only later in the day to visit them for nectar.

All plants flowering together with the two *Goodenia* species, most notably several Asteraceae and a *Wahlenbergia* species (Campanulaceae), were sampled for flower visitors. None was being visited by *R. angulata*.

Provision.—Provision in the form of a firm, white pollen loaf was obtained from each of three cells. Pollen from the loaves was examined microscopically and found to match that obtained from the *Goodenia* flowers.

Mate location.—During the morning males patrolled the flowers where they sought the females. They did not alight on the flowers but rested on a neighbouring plant, for example on a grass stem, or on the ground. Numerous attempted copulations at flowers were observed and a single attempt to copulate with a nest-excavating female was noted. Several instances of a male and female grappling on the ground next to plants and of "hot pursuit" were noted.

Description of the Nest.—The nest (n = 8) consists of a subterranean burrow (Fig. 5) excavated in horizontal sandy soil in a clearing (Fig. 3). The entrance is concealed beneath a pebble, a plantlet or a suitable

item of debris (Fig. 4). It is a simple hole 3–4 mm in diameter, not surmounted by a superstructure. For approximately the first 10 mm the shaft slopes gently downwards. Thereafter its main thrust is vertically downwards, however, at intervals it curves outwards to end in a horizontal cell so that each cell, except the last excavated and therefore deepest one, appears to be accessed by a lateral shaft. These "lateral shafts" radiate out through 360° each deeper than that preceding it.

The diameter of the shaft narrows at a depth of approximately 80 mm and then continues constant. The first cell in the nests investigated was at a depth of between 180 and 370 mm, the "lateral shafts" were 30 mm in length, and the cells 13 mm long and 4 mm in diameter at the widest point. A lateral shaft is packed with sand after the cell which terminates it has been provisioned. Up to seven cells per nest were recorded. The cells are unlined.

Method of Construction of the Nest and Provisioning.-Water is not required for the excavation of the nest as the sandy soil, though compact, is friable. The sand extracted from the burrow is carried out of the shaft held between the head and the prosternum, the genae being fringed with ammochaetae. Whilst excavation is in progress, the female, when leaving the nest, backs out. During the initial stages of burrow excavation the extracted sand is dropped in flight in a more or less constant area to one side of the entrance and about 120 mm from it. As the burrow becomes deeper the extracted sand is dropped further from the nest in a constant arc about 250 mm from the entrance. The sand being scattered, there is no detectable accumulation and so no tumulus develops.

The presence of a recently hatched larva in a sealed, fully provisioned cell indicated that mass provisioning is practised. The sand used for packing a shaft leading to a cell is almost certainly obtained with-

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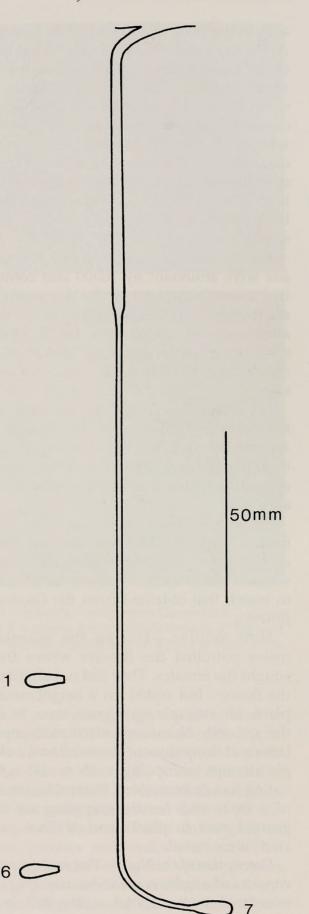
in the nest during the excavation of the shaft leading to the next cell.

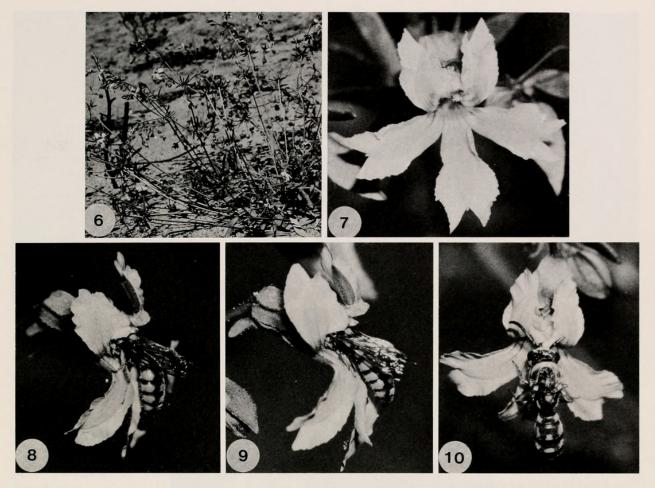
The fully fed larva spins a white cocoon which completely fills the cell. Like the sealed cell it is therefore rounded at the inner end and truncate at the outer end.

Discussion of Nesting .- The nest of R. angulata is essentially similar to that of R. maculata, which is described by Houston (pers. comm.) as a vertical burrow in sandy soil, about 300 mm deep and unlined, with unlined cells at the lower end. Thus the basic nest type for these two species of Rolandia can be defined as a multicellular sub-vertical burrow in horizontal ground excavated by the nester, without an entrance turret and with excavated cells not containing constructed cells. When compared with the seven basic nest types recognized for the Masarinae as a whole by Gess and Gess (1992) this appears to fit Nest type 1 except for the lack of an entrance turret. When the method of construction is compared with that of the species listed for this nest type, a basic difference is apparent. Water is used in the excavation and construction of Nests of type 1, like nests of types 2 and 3, whereas the nests of the two Rolandia species are excavated without the use of water. This is possible due to the friable nature of the soil in which they are sited. As noted in Gess and Gess (1992) nesting in friable soil in the Vespidae is probably derived rather than primitive as in the Pompilidae and Sphecidae. The nest type of the two Rolandia species is therefore seen as a sub-type which can be derived from Nest type 1.

Both species of *Rolandia* carry sand, extracted from the shaft, out of the burrow held between the head and the prosternum, the genae being fringed with am-

Fig. 5. Plan of vertical section of a nest of *Rolandia angulata*. Cells 2—5 followed cell 1, radiating out in sequence through 360° and at successively greater depths.





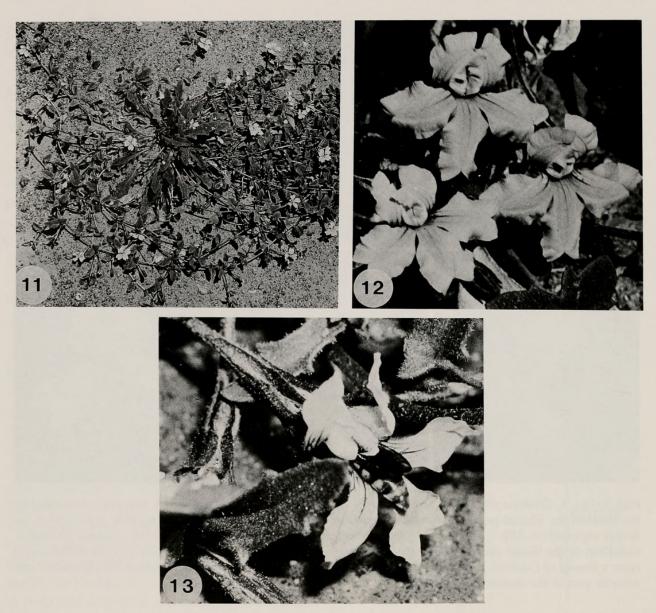
Figs. 6–10. 6, *Goodenia pinnatifida*, an erect herb; 7, a flower of *Goodenia pinnatifida*, indusium concealed by the bases of the adaxial petals; 8, *Rolandia angulata* entering a flower of *Goodenia pinnatifida*, indusium of the flower exposed (\times 2.8); 9, *Rolandia angulata* in nectar drinking position in a flower of *Goodenia pinnatifida*, indusium of the flower fitting snugly over the wasp's mesosoma (\times 2.8); 10, *Rolandia angulata* withdrawing from a flower of *Goodenia pinnatifida*, showing dusting of pollen on the head, dorsum of the prothorax, and anterior part of the mesoscutum (\times 2.8).

mochaetae. The possesion of ammochaetae fringing the genae is a generic character (Snelling 1986) and it is therefore expected that all members of the genus excavate their nests in a similar manner. The only other vespid genus recorded as having a psammophore for the removal of the spoils of excavation is *Pterochilus* (Eumeninae) (Bohart 1940) for which nesting in vertical burrows in friable soil by two species has been described (Isely 1914 and Evans 1956).

EVALUATION OF ASSOCIATION WITH FLOWERS VISITED

Both *R. angulata* males and females obtain nectar and possibly pollen for their own nourishment and females collect nectar and pollen for provisioning their nestcells apparently solely from *Goodenia* flowers. They are therefore probably dependant on *Goodenia* flowers. To determine whether or not the association between the wasp and the flowers is mutually beneficial or not, that is whether or not the wasp in addition pollinates the flowers, requires a consideration of the functional morphology of the flowers, the behaviour of the wasps in the flowers, and wasp/ flower fit.

Goodenia flowers are distinctly two lipped. The lower wings of the two adaxial petals are differentiated in their lower parts into auricles which envelop the



Figs. 11–13. 11, *Goodenia cycloptera*, a prostrate herb; 12, three flowers of *Goodenia cycloptera*, indusium concealed by the bases of the adaxial petals; 13, *Rolandia angulata* in nectar drinking position in a flower of *Goodenia cycloptera*, indusium of the flower pressed down on the wasp's folded wings (× 3.3).

indusium in the flower (Figs 7 and 12) so that it is only exposed when an insect visitor pushes the corolla lobes apart as it seeks the nectar at the base of the flower (Figs 8 and 13). The indusium is a cup at the top of the style and the surrounding stigmatic initial that collects and retains pollen from the stamens, which dehisce in the bud, and presents it thus to the pollen vector (Carolin, Rajput and Morrison 1992). Later the stigmatic initials mature and grow out of the indusium and collect pollen from pollen vectors. *R. angulata* when visiting the flowers for nectar always alights on the lower lip and then pushes its way in beneath the indusium so that, if the flower is in the pollen presenting phase, the wasp receives pollen on its head. When it is in the nectar drinking position in a flower of *G. pinnatifida*, the mesosoma (Fig. 9) is snugly capped by the indusium but, when it is in a flower of *G. cycloptera*, which is deeper, it is the folded wings which are pressed beneath the indusium (Fig. 13). On emerging from a flower of *G. pinnatifida* it can be clearly

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seen to have been well dusted with pollen not only on the head but also on the dorsum of the prothorax and the anterior part of the mesonotum (Fig. 10). When coming thus laden with pollen to a flower with receptive stigmas the wasp would be ideally suited to pollinate it. It is not clear, however, whether *R. angulata* would effectively pollinate the deeper flowers of *G. cycloptera*. It is possible that pollen may be transferred from its head to a receptive stigma but the pollen received on the wasp's wings is unlikely to be successfully transferred.

It is concluded that, within its limited distribution, *R. angulata* is a potential pollinator, at least, of the widespread species *G. pinnatifida* with which it therefore has a mutually beneficial association. However, at none of the sites was *R. angulata* the sole visitor to the *Goodenia* flowers.

At the most easterly site a second masarine, Riekia nocatunga Richards, which was also recorded from Goodenia fascicularis F.Muell. & Tate at Kondar to the southeast, was a relatively abundant visitor to G. pinnatifida. Furthermore the flowers of both species of Goodenia, particularly those of G. cycloptera, were visited abundantly by bees. The most common species was Leioproctus (Chrysocolletes) moretonianus (Cockerell) (Colletidae) which was also recorded from Goodeniaceae at several sites in Queensland by Michener (1965). Less common visitors were a second, but slightly smaller, species of Leioproctus (Chrysocolletes) and a species of Megachile (Megachilidae). Relatively uncommon visitors were six further species of Megachile, an additional colletid, a halictid, a few anthophorids and the honey-bee. Travelling westwards the bees were uncommon at the site 27 km west of St George and at the site 80 km east of Cunnamulla all but the second species of Leioproctus (Chrysocolletes) were absent. At the latter site a third much smaller species of Leioproctus was also recorded. However, R. angulata was the

only abundant visitor suggesting that in some areas, at some times, it may be the most important potential pollinator of *G. pinnatifida*.

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