

Distribution and Ethology of *Priscomasaris* Gess (Hymenoptera: Vespidae: Masarinae: Priscomasarina) in Namibia

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Abstract.—Knowledge of the distribution and flower associations of the monospecific genus *Priscomasaris* is expanded. The nature of the provision, nesting situation, nest structure, and method of nest construction are recorded for the first time. *Priscomasaris namibiensis* Gess has been encountered solely in the Mopane Savanna/Northern Namib transition and Dwarf Shrub Savanna (of Giess 1971), all records falling within the northwestern extension of the Nama Karoo Biome (of Rutherford and Westfall 1986, as adapted by Lovegrove 1993). Flowers visited for nectar and pollen are of the families Aizoaceae (non-Mesembryanthema) and Molluginaceae. Nesting aggregations were located in sparsely vegetated areas of horizontally presented, stabilized, sandy soil. The nest is a multicellular burrow with its entrance surmounted by a mud-turret and with each excavated cell containing a constructed mud-cell. Water is used in excavation and construction. Evidence for bivoltinism is presented.

F.W. Gess (1998) described *Priscomasaris namibiensis* Gess, a new genus and species of Masarinae (Hymenoptera: Vespidae) from Namibia. He discussed its position within the subfamily, placing it in a new subtribe Priscomasarina, a sister group of Paragiina and Masarina combined. Its ethology is of particular interest as it represents the most primitive extant member of the Masarinae. F.W. Gess recorded female water collection behaviour and two forage plants but, as nests had not yet been discovered, could make no comment on nesting behaviour other than to suggest that water is most probably used in nest construction.

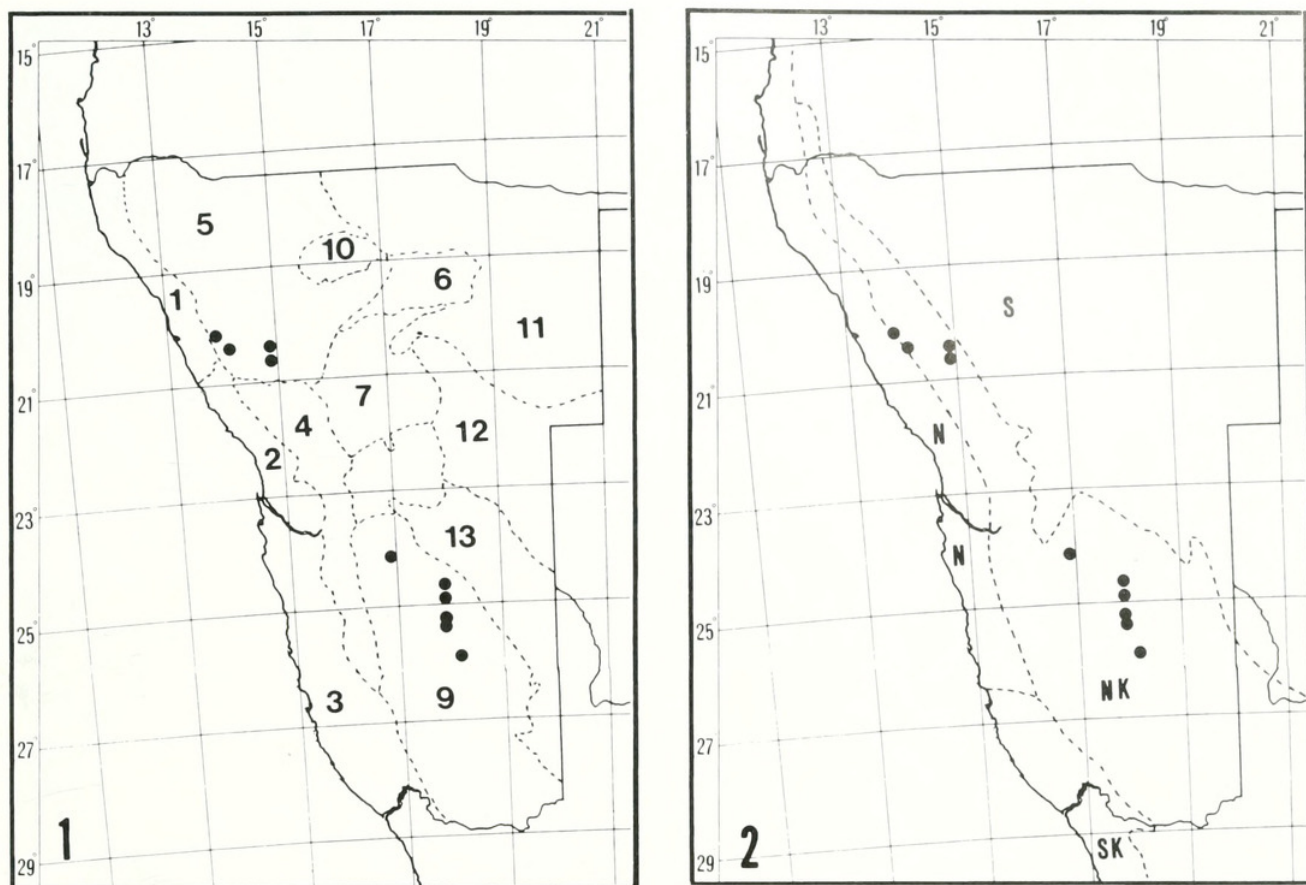
In March 2000 two nesting aggregations of *P. namibiensis* were discovered and investigated by the present author. This investigation forms the subject of the present paper.

Distribution.—Previously published (F.W. Gess 1998) and new collection records of *P. namibiensis* are listed in Appendix 1 under the vegetation types of Giess (1971) (Fig. 1) and biomes of Rutherford

and Westfall (1986) as adapted by Lovegrove (1993) (Fig. 2). It appears that *P. namibiensis* is a northern Nama Karoo species.

Nesting areas and sites.—Two nesting areas of *P. namibiensis* were located, both in Dwarf Savanna Shrub to the east of the Mariental-Keetmanshoop road and railway track: one 5 km south of Mariental (Fig. 3) and the other 7 km south of Gibeon railway siding. Both areas are associated with drainage lines that form part of the Fish River catchment. Rainwater pools, resulting from thundershowers, were present in association with the railway embankment through which the drainage channels have passage (Fig. 4).

The nests were aggregated above normal flood level within sparsely vegetated sites. In the Gibeon nesting area two small aggregations were discovered, each of no more than 10 nests, 9 to 11 metres from the water source. The soil was compacted sand with an inclusion of small pebbles and with a sufficient clay element to make it maleable when mixed with water. The



Figs. 1–2. Map of Namibia showing the distribution, based on collection records (Appendix 1), of *Prisco-masaris namibiensis* (dots). 1, The vegetation types of Giess (1971): 1 = Northern Namib; 2 = Central Namib; 3 = Southern Namib; 4 = Semi-desert and Savanna Transition (Escarpment Zone); 5 = Mopane Savanna; 6 = Mountain Savanna and Karstveld; 7 = Thornbush Savanna; 8 = Highland Savanna; 9 = Dwarf Shrub Savanna; 10 = Saline Desert with Dwarf Shrub Savanna Fringe; 11 = Tree Savanna and Woodland; 12 = Camelthorn Savanna (Central Kalahari); 13 = Mixed Tree and Shrub Savanna (Southern Kalahari). 2, The biomes of Rutherford and Westfall (1986) as adapted by Lovegrove (1993) (S = Savanna; N = Namib Desert; SK = Succulent Karoo; NK = Nama Karoo).

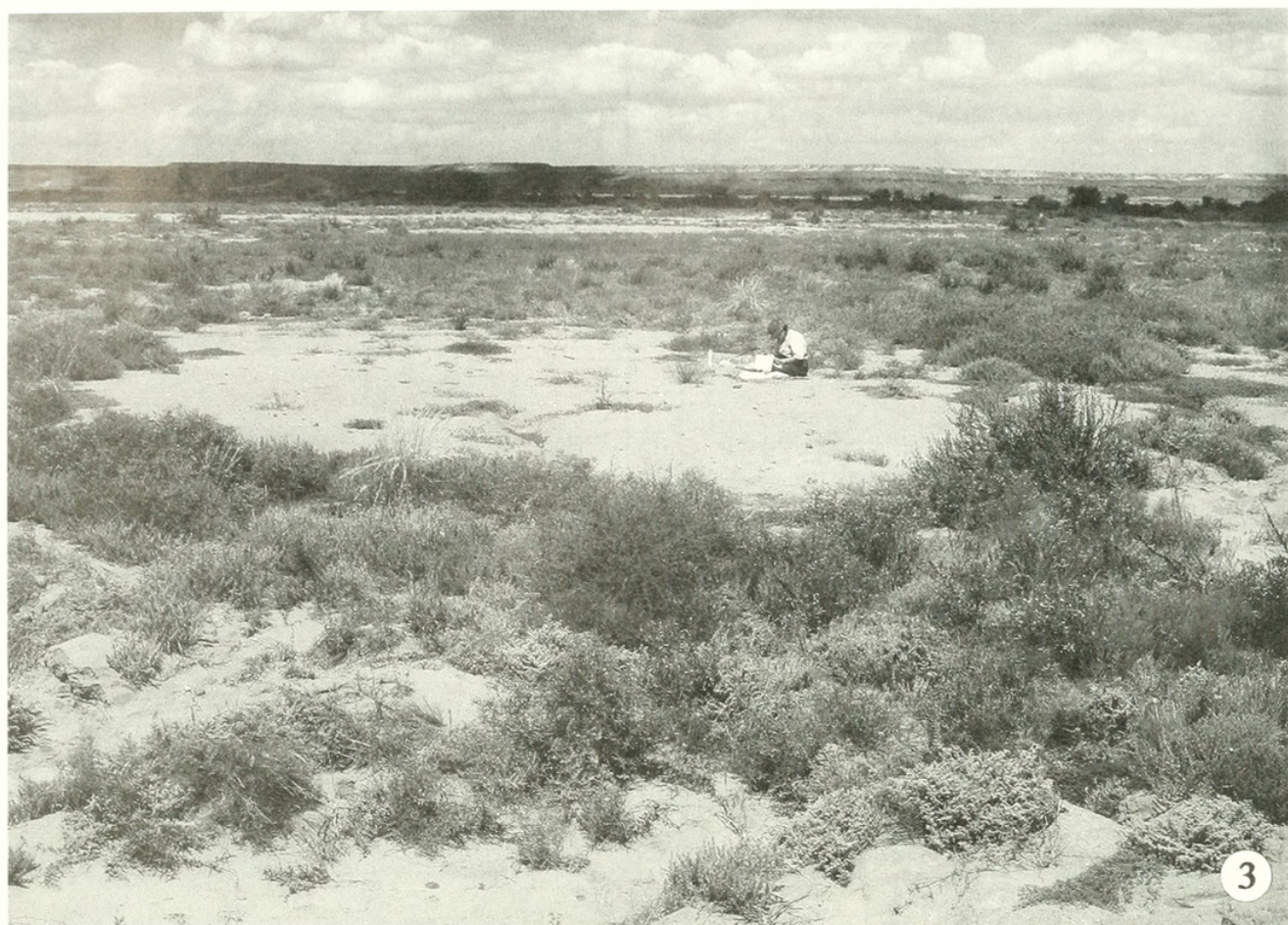
gravelly surface was scattered with pebbles and small plants. Individual nests were sited next to a pebble or small plant (Figs. 5–10).

In the Mariental nesting area numerous nests were distributed over a site c 100 metres square. The soil was compacted sand of an even consistency with a sufficient clay element to make it maleable when mixed with water. The surface was compacted sand scattered with an occasional pebble and “mat” plant. Most commonly nests were grouped beneath or between the spreading branches of semi-prostrate *Gisekia africana* (Lour.) Kuntze (Molluginaceae) (Fig. 16), a forage plant of *Prisco-masaris*, and of a “mat” forming species of *Indigofera* (Papilionaceae), the flow-

ers of which it does not visit (Fig. 17). Less commonly nests were exposed but were then positioned next to a pebble or small plant.

Water collection.—As stated by F.W. Gess (1998) females visit pools of water in drainage channels and river beds in order to obtain water, apparently for use in nest construction. When they were common, very large numbers were present on and flying over the water. When filling their crops they always alight on the water surface, never at the water’s edge. Whilst on the water surface the wings are held erect.

Flower visiting.—Both sexes of *P. namibiensis* visit flowers. Those recorded were all small shallow flowers of Molluginaceae and Aizoaceae. The Molluginaceae were



Figs. 3–4. Nesting area south of Mariental (24.40S 17.57E). 3, Habitat. 4, Water source.

pink flowered *Gisekia africana* (Lour.) Kuntze (Fig. 16) (between Palm and Khorixas) and white flowered *Limeum* of three species: *L. argute-carinatum* Wawra & Peyr. (Fig. 12) (west of Khorixas, between Khorixas and Uis, and south of Mariental), *L. myosotis* H. Walter (Fig. 13) (between Khorixas and Uis), and *L. sulcatum* (Klotsch) Hutch. (Fig. 11) (southwest of Bullsport). The Aizoaceae (non-Mesembryanthema) were purplish-pink flowered *Sesuvium sesuvioides* (Fenzl) Verdc. (Fig. 15) (south of Mariental) and pink and white flowered *Trianthema parvifolia* E. Mey. ex Sond. (Fig. 14) (also south of Mariental). All yield nectar, easily imbibed by this short "tongued" wasp, and pollen, requiring no specialized "harvesting" behaviour. Other plants in flower at the foraging sites were not visited.

Priscomasaris is not the sole visitor to the flowers of any of its forage plants. The Molluginaceae are widespread and are visited by a range of wasps and bees (Gess and Gess unpublished catalogue of flowers visited by aculeate wasps and bees in semi-arid areas in southern Africa). The Aizoaceae attract a narrow range of wasps and bees—*S. sesuvioides* is principally visited by *Ceramius damarinus* Turner (Vespidae: Masarinae), which uses it as its source of provision for its nests (S.K. Gess 1999), and a species of *Parafidelid* (Fidelidae). *T. parvifolia* is principally visited by *Quartiniella turneri* Schulthess and several *Quartinia* species.

At the site near Bullsport, where *Priscomasaris* males and females were visiting the flowers of *L. sulcatum*, some males and an occasional female were collecting nectar from the extrafloral nectaries of young plants of the herb *Chamaesyce glandulifera* (Pax) Koutnik (Euphorbiaceae).

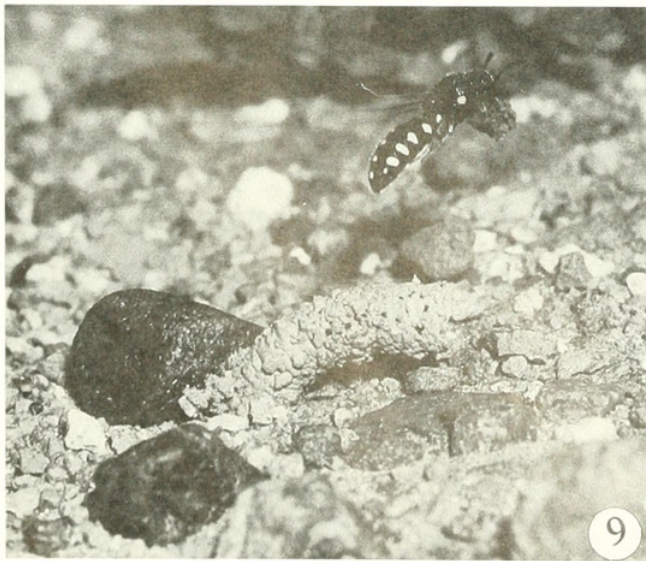
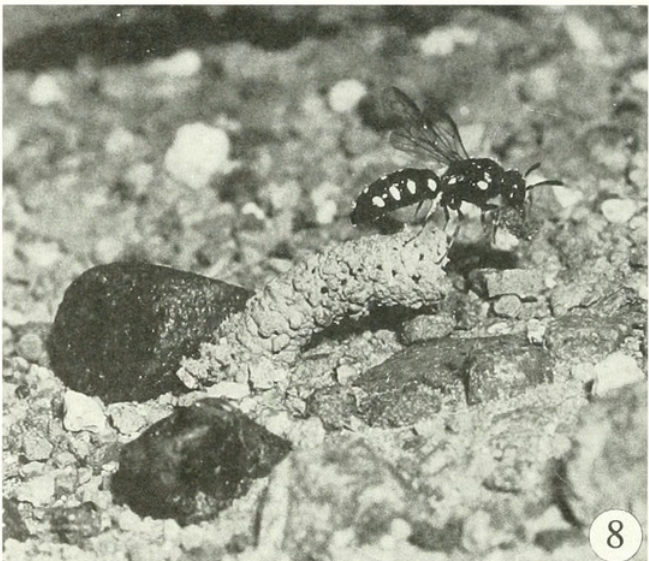
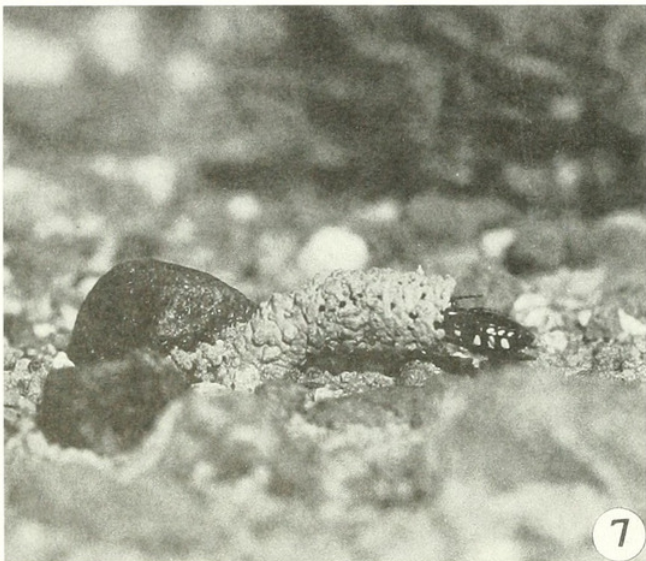
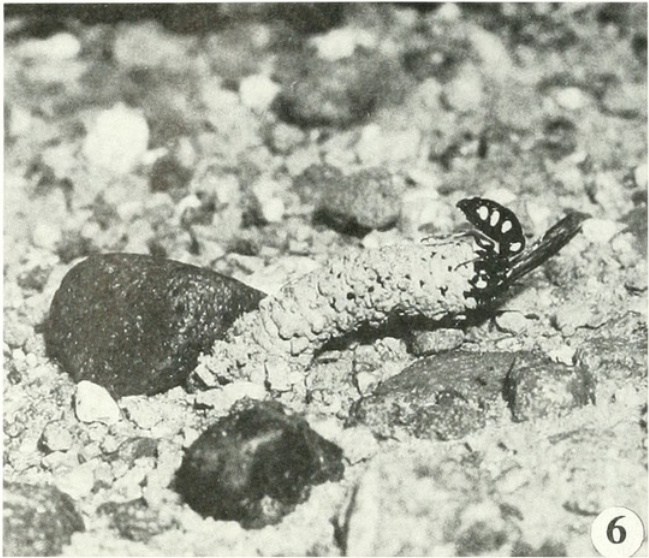
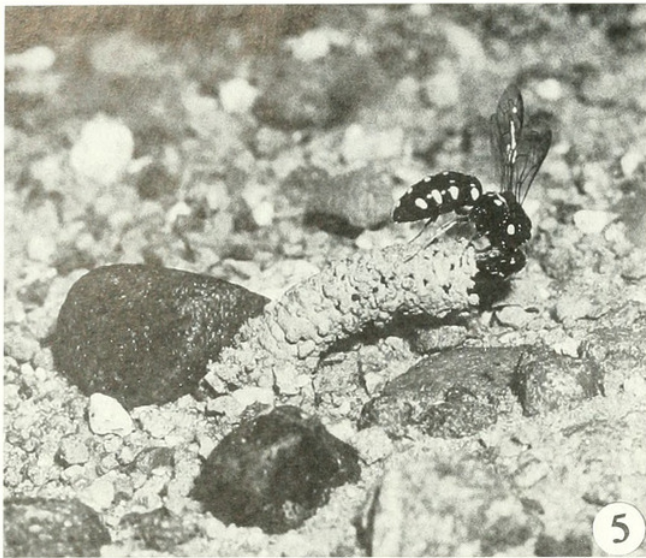
Provision.—The cell provision consists of a compact, firm, roughly cylindrical mass of pollen and nectar, rounded at the ends and with undulations along its length indicating deposition of individual "loads" of the pollen and nectar mixture. The pro-

vision mass, a "pollen loaf", remains loose within the cell. One complete "pollen loaf" was 8.17 mm in length and 3.0 mm in diameter (i.e. 0.12 mm less than the inner diameter of the constructed mud-cell). Samples of pollen from provision masses collected on 10, 22 and 31 March, and 2 April were examined microscopically. Four distinct pollens of 17.5, 20, 25 and 30 micromillimetres in diameter were present. These were compared with pollens from flowers visited by *Priscomasaris* and were found to match those of *T. parvifolia*, *L. argute-carinatum*, *G. africana* and *S. sesuvioides* respectively. The proportions of the different pollens varied. Samples taken on 22 March were mostly of *G. africana* and *S. sesuvioides* and those taken on 31 March and 2 April were principally of *T. parvifolia*.

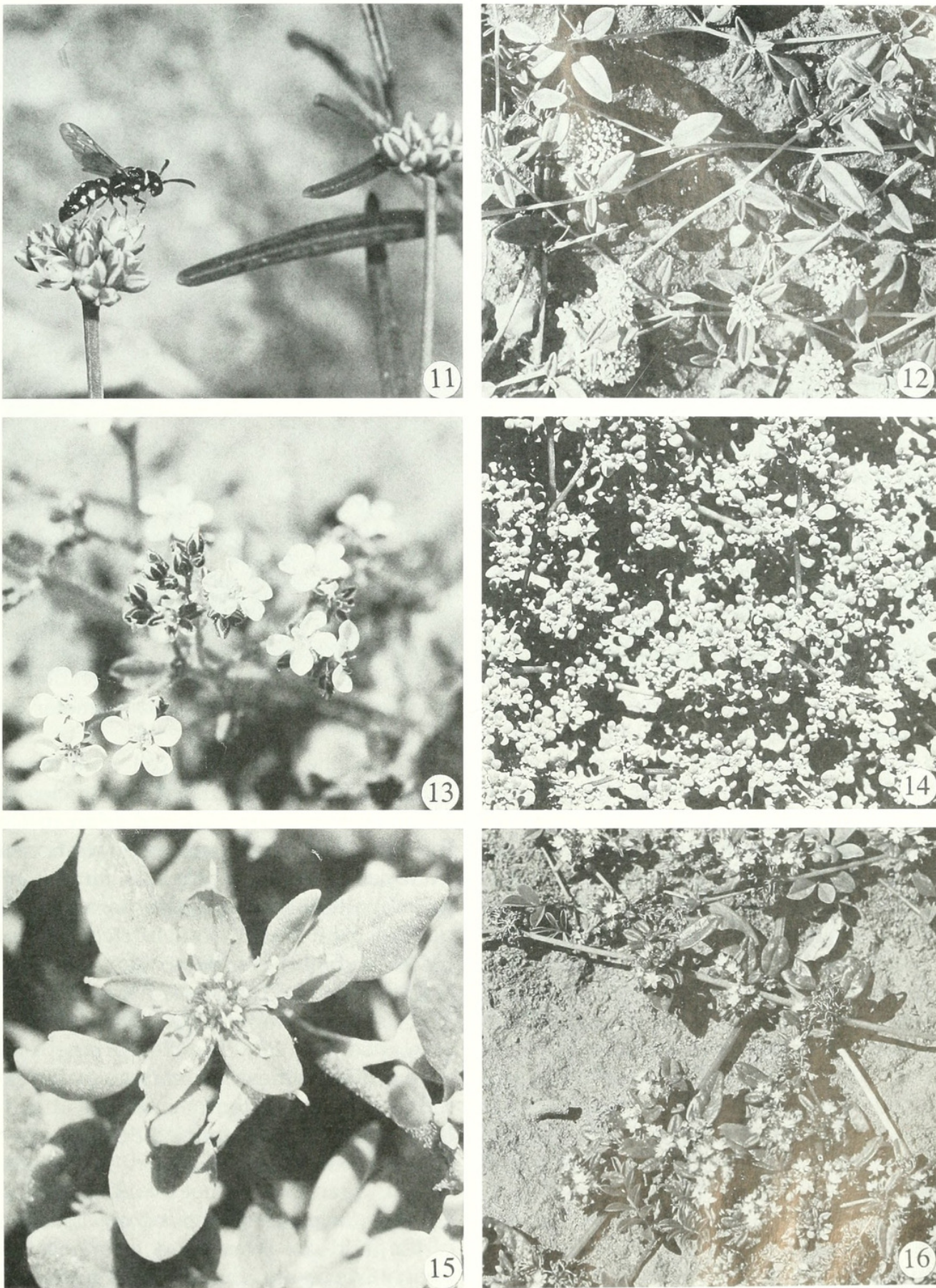
Male behaviour.—No males were found in nests or at water. In the morning, before the appearance of the females, males were observed flying to and fro over nesting aggregations and visiting flowers. After the females had made their appearance males were observed mounting them, both on the ground in the vicinity of the nests and on flowers. It was not possible to observe copulation.

Description and method of nest construction.—The description of the nest of *P. namibiensis* is based on investigations of 62 nests: four in the Gibeon nesting area on 9 March; and 22, 13, 5 and 18 at the Mariental nesting area on 10, 22 and 31 March and 2 April respectively. The method of construction is based on investigations of nests together with observations on nesting behaviour.

Description: The nest of *P. namibiensis* consists of a multicellular subterranean burrow (Figs. 19–23) surmounted by a curved, tubular mud-turret of the same diameter as the burrow opening and usually with its greater length parallel to the soil surface. The main shaft is vertical and is of equal diameter throughout its entire length. At its base it curves outwards to



Figs. 5–10. *Priscomasaris namibiensis* with nest entrance turret. 5 and 6, Preparing to enter nest entrance turret. 7, Entering nest entrance turret, ventral surface uppermost. 8, Preparing to leave nest to discard the mud-pellet held between mandibles. 9, Flying away from nest with a mud-pellet which will be dropped in the pellet-dropping area. 10, Adding mud to the rim of entrance turret. Actual length of wasp c 8 mm.



Figs. 11–16. Forage plants of *Priscomaris namibiensis*. 11, *Limeum sulcatum* (Molluginaceae), flowers white, *P. namibiensis* leaving after foraging on the flowers. 12, *Limeum argute-carinatum* (Molluginaceae), flowers white. 13, *Limeum myosotis* (Molluginaceae), flowers white. 14, *Trianthema parvifolia* (Aizoaceae: non-Mesembryanthema), flowers white or pink. 15, *Sesuvium sesuvioides* (Aizoaceae: non-Mesembryanthema), flowers purplish-pink. 16, *Gisekia africana* (Molluginaceae), flowers pink; entrance turret of *P. namibiensis* on left.

form a short lateral shaft which terminates in a sub-horizontal excavated cell in which is a constructed mud-cell. A second cell terminates a similar lateral shaft which leaves the vertical shaft at the same depth but at an acute angle from the first such that the two cells lie close together. Further cells in similar pairs are positioned almost immediately below the first pair, each pair deeper than that preceding it, so that the cells form a "stack" to one side of the main shaft. The largest number of cells found was 13.

Method of construction: When excavating a burrow, *P. namibiensis*, using its mandibles, extracts soil as moist mud-pellets. As nest constructing females make frequent visits to water it is almost certain that regurgitated water is used for moistening the soil.

At an early stage in shaft excavation the entrance turret is constructed from pellets extracted from the burrow. These are laid down around the rim of the entrance to the burrow in such a way that its inner diameter equals that of the main shaft (i.e. 3 mm). At the outset of turret construction the thickness of the wall is c 1 mm but after the turret has reached a height of a few millimetres is reduced to 0.5 mm. After the turret reaches a height of c 6 mm, pellets are usually added in such a way that the turret curves over, typically until the opening is vertical, after which they are added evenly around the circumference of the turret and the resultant horizontal tube is extended parallel with the soil surface for a further 13–17 mm, separated from it by a c 2 mm gap.

A female, when entering a nest, alights on the upper surface of the turret facing towards the opening (Fig. 5) and then curves over its lip (Fig. 6), entering and progressing along the passageway ventral surface uppermost (Fig. 7). When leaving the nest during shaft excavation she reverses the procedure emerging posterior end first, ventral surface uppermost and climbing out onto the upper surface (Fig.

8). Thus before flying away she is facing towards the turret opening. Whilst building the turret she remains curved around the rim (Fig. 10), rotating whilst placing mud with her mandibles and apparently supporting and tamping it with the tip of her abdomen.

When discarding a mud pellet, a female, holding the pellet in her mandibles, flies (Fig. 9) on a roughly circular path, dropping the pellets 10 to 30 cm from the nest. Usually the variation in distance of an individual's flight path is not more than 7 cm so that the pellets accumulate in a small area (Fig. 17).

The walls of the shaft are stabilized and smoothed with the addition of water. The diameter of the shaft (3 mm) is maintained constant throughout its length. There is no turning "bulb" such as that found in the nests of most species of *Ceramius* (S.K. Gess 1996). At a depth of 60–80 mm (average 69, $n = 17$) the shaft curves and after c 5 mm is expanded in the excavation of a cell of length c 15 mm and diameter c 5 mm.

Within the excavated cell a mud-cell (Figs. 19–23) is constructed, fitting closely within it but easily removed from it. On the outer surface evidence of deposition of mud-pellets is visible and a faint "fish scale" pattern similar to the more marked pattern exhibited by constructed cells of *Celonites* (S.K. Gess 1996) and *Pseudomasaris* (Torchio 1970) is discernable (Fig. 21). The inner surface of the mud-cell is smoothed (Fig. 20). The closed inner end is rounded whereas the outside tip of the mud-cell is consistently markedly papillate (Figs. 20–22). Apart from the tip, mud-cells are constant in diameter along their length, cigar-shaped, not ovoid.

The source of soil for the construction of the mud-cells was not determined. No quarry site within the nest was found. In nests with newly constructed open mud-cells there did not appear to be an excavated or partially excavated cell which could have been the source. As there is no



Fig. 17. Entrance turret of *Priscomasaris namibiensis* on right (arrow), discarded mud-pellets on left (arrow), amongst the branches of a species of *Indigofera* (Papilionaceae).

turning "bulb" such a source is also eliminated. The builders were carefully observed and were not bringing in soil from outside the nest. On numerous occasions, during nest investigation, loose dry soil was found in the main shaft from a depth of 50 mm downwards. It is highly unlikely that this soil had fallen into the shaft. It seems possible that, when a cell is excavated, extracted soil is not carried out as pellets but stored loose in the shaft and that the female coming and going from the nest can pass through the loose soil. This soil would then be available for mud-cell construction.

The constructed mud-cell walls appear to be harder and more brittle than those of the turret. This suggests that either, as in drying of concrete, slower drying of the mud used in mud-cell construction results in a "stronger" cementing or that something other than water is added to the

mud mixture. As *Celonites* and *Pseudomasaris* use nectar for bonding soil used in cell construction (S.K. Gess 1996 and Torchio 1970), nectar was considered a possibility. One gram of cell wall was tested for sugar content. Total sugars extracted amounted to only 3 milligrams, 0.6 micrograms of which were found to be glucose and 0.8 micrograms fructose. This appears to be too low a concentration of sugars to suggest deliberate use of nectar (Chris Whitely pers. com.) and therefore should be considered rather to be accidentally added from the crop which is used variously to carry nectar and water.

A mud-cell, in which oviposition and provisioning have been completed, is sealed with a mud-plug that fits into the neck of the cell, closing but not sealing it. After this plug has been constructed there is further addition of mud, extending across the plug and the rim of the mud-

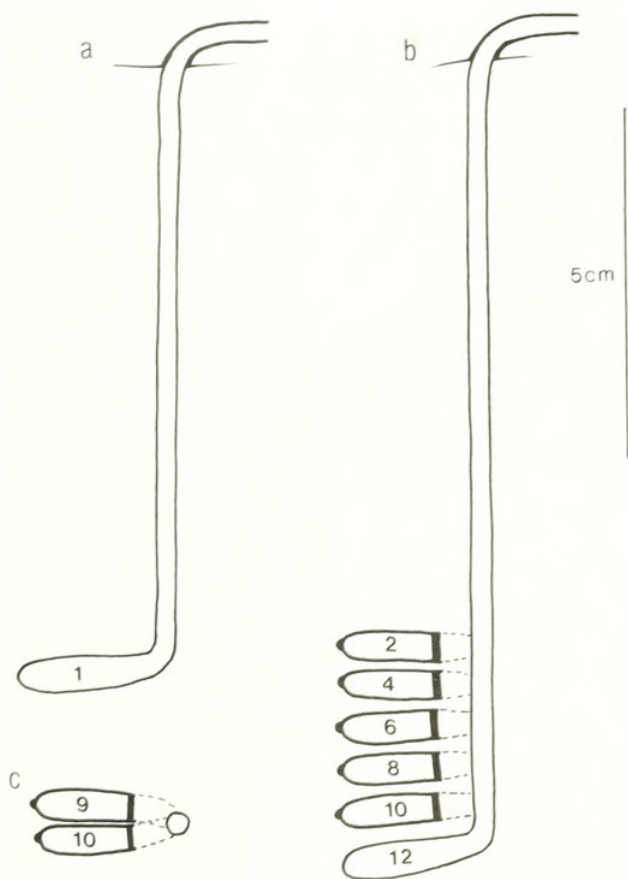


Fig. 18. Plans of two nests of *Priscomasaris namibien-sis*. a and b, vertical in single plane. a—nest with first cell only. b—nest with 12 cells. c, transverse in single plane.

cell, effectively sealing it. The remaining few millimetres of the lateral shaft are then filled with soil. Finally, where the shaft curves away from the vertical shaft, mud is used for sealing and plastering so that, when a nest with sealed cells is opened, there is no sign in the walls of the vertical shaft that any lateral shaft other than one leading to an open cell exists (Fig. 22).

A first cell having been completed and sealed off, a second lateral shaft leading to a second cell is excavated (and a mud cell constructed within it) at the same depth as the first and in the same plane, but at an acute angle from it.

On the completion and sealing off of the second cell a third lateral shaft with cell is excavated almost immediately below the first after a slight deepening of the vertical shaft. A fourth shaft and cell follows almost immediately below the second in the

same plane as the third. Excavation of further lateral shafts with cells follows this pattern so that a double "stack" of sub-horizontal cells (excavated cells each containing a constructed mud-cell) forms to one side of the vertical shaft.

Of the 22 nests investigated at Mariental on 10 March 5 (22.7%) had not yet reached the stage of lateral shaft excavation, 4 (18.2%) had reached lateral shaft excavation but not cell excavation, 6 (27.3%) had one cell each, and 5 (22.7%) had two cells. Twelve days later 12 nests were investigated, 4 (33.3%) had one cell each, 1 (8.3%) two cells, 2 (16.7%) three cells, 2 (16.7%) four cells, 1 (8.3%) 11 cells, and 1 (8.3%) 13 cells.

Taking two as possibly the largest number of cells per nest on 10 March and 13 twelve days later, it is estimated that it is possible that a cell could be prepared, oviposited into and provisioned in a single day. This is of course a very rough estimate but would be comparable with the rate observed for *Celonites latitarsis* Gess (Gess and Gess 1992) and *Masarina strucki* Gess (Gess, Gess and Gess 1997).

Life history.—From two nests each with a constructed mud-cell, empty except for an egg, it was possible to establish the positioning of and appearance of the egg. The eggs were white, slightly curved, more rounded at one end than at the other, 2.6 and 2.22 mm in length and 0.72 and 0.68 mm in diameter at mid-length. Each egg was positioned across the inner end of the mud-cell, cemented at its narrower end to the mud-cell wall.

A larva initially feeds only from one side of the mass of provision so that the "pollen loaf" extracted from a cell with a feeding early instar larva is not of even diameter along its length, but has an acentric process at the inner end, the length of the process in relation to the length of the provision being in proportion to the size of the larva.

The larva consumes the entire provision and then defecates at the inner end of the

mud-cell. The fecal mass forms a mustard coloured deposit on the inner surface of the mud-cell to a distance of 3–4 mm from the inner end. Microscopic examination revealed that it contains a mass of empty pollen grain walls, in no way macerated, with the pores widely extended. In addition approximately half-way along the length of the mud-cell an irregular mass of white crystalline matter is deposited. In several of the cells investigated fungal hyphae bearing penicillate sporangiophores and white spores covered the fecal mass.

The mud-cell walls from the edge of the fecal layer to approximately 10 mm from the inner end of the cell are lined by the larva with a parchment-like silken layer. At approximately 10 mm from the inner end of the cell it constructs a seal. Viewed from within the mud-cell the seal is in the shape of a round, flat-bottomed dish and viewed from the mud seal looking into the cell it has the appearance of a truncated cone. Both surfaces are brown and varnished in appearance. Between the inner and outer sloping walls is a series of silken parchment-like lamellae (Fig. 23). The central disc which forms the bottom of the inner "dish" and outer inverted "truncated cone" is thin and translucent. As the silken covering of the mud-cell walls only extends to the fecal mass there is not a complete cocoon.

On emerging the adult "cuts" out the flat, varnished "bottom" of the dish-like seal leaving a circular lamellate collar in place. The "varnished" disc is left pushed to one side.

Voltinism.—The findings suggest that there can be at least two generations of *P. namibiensis* per year. Clearly the nests investigated on 9 and 10 March were all recently started by recently emerged females. Those investigated on 22 March were a mixture of recently started nests and nests of which the initiation was probably contemporary with those investigated on 10 March. This suggested an initial staggered emergence of females. The nests

investigated on 31 March and 2 April, after a week of rains, were all recently started. These could have been initiated by a fresh flush of females of the same generation as the nest builders of 10 March or a second generation of adults.

That *P. namibiensis* is possibly bivoltine was demonstrated further, when, later in April, a male and two females emerged from three mud-cells collected on 22 March from nests of actively nesting females, there being no evidence of re-use of natal nests.

DISCUSSION

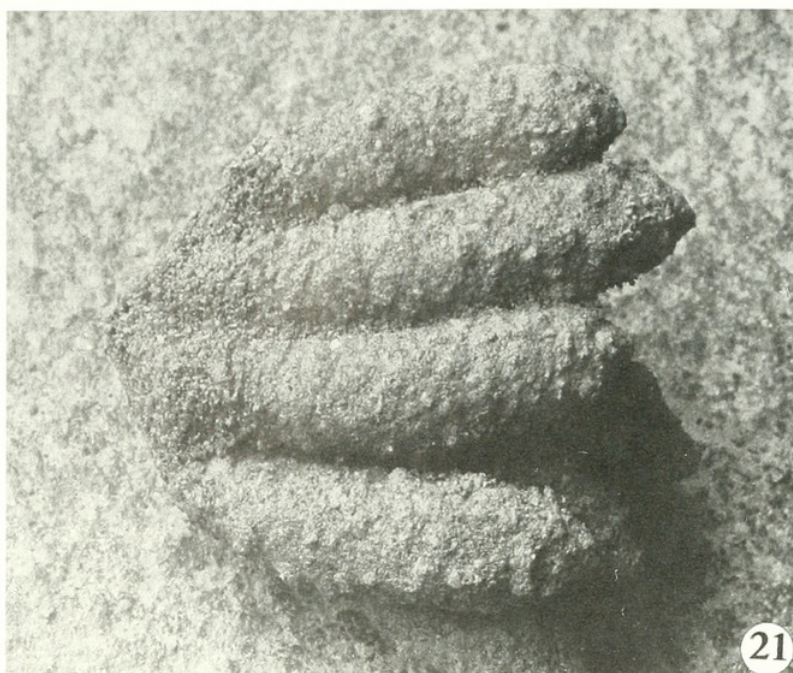
Gess and Gess (1980 and 1992) and S.K. Gess (1996) discussed possible evolutionary sequences in the Masarinae. They suggested a sequence from the excavation of burrows with excavated cells only (as practised by *Ceramius damarinus* of species Group 4, *Ceramius* species of Group 8 and *Trimeria howardi*) through excavated burrows with constructed earthen-cells within excavated cells with earth for construction being derived from within the burrow (as practised by *Ceramius* species of groups 2, 3, 5, 6, and 7, at least three species of *Paragia* and at least two species of *Jugurtia*) to the presumably more advanced construction of aerial earthen-cells (as typically practised by *Celonites*, *Pseudomasaris* and *Gayella*).

That *P. namibiensis* constructs earthen-cells (mud-cells) within excavated cells suggests that this behaviour is plesiomorphic for Masarinae and that excavation of cells without constructing cells within them is, for Masarinae, derived.

Descriptions of nesting by *Euparagia scutellaris* Cresson (Williams 1927, Clement and Grissell 1968 and Trostle and Torchio 1986) do not suggest that *Euparagia* (Euparagiinae, formerly included in Masariidae) constructs earthen-cells within excavated cells. Similarly, there appears to be no evidence for construction of cells in self-excavated cells by any Eumeninae. It would seem that construction of earthen-



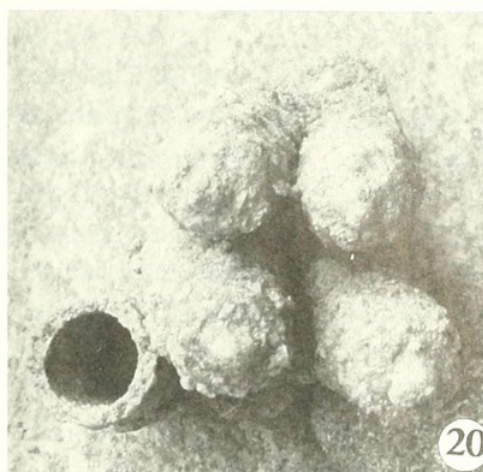
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Figs. 19–23. Nest burrow and constructed mud-cells of *Priscomasaris namibiensis*. 19, Burrow cut in vertical plane. 20, Constructed mud-cells, four viewed end on (note papillate inner end of mud-cells) and one cut transversely to show thickness of cell wall and smoothed inner surface. 21, Group of constructed mud-cells from cut main shaft which is showing “fish-scale” pattern. 22, Group of constructed mud-cells sealed off from larva and silken parchment-like closure. 23, Constructed mud-cell cut longitudinally, showing fully grown larva and silken parchment-like closure.

cells within self-excavated cells is, in the Vespidae, probably restricted to Masarinae. Indeed, construction of cells within self-excavated cells by aculeate wasps appears to be restricted to Masarinae and certain Apoidea, the two groups of aculeates that provision with pollen and nectar.

The egg of *E. scutellaris* is, like that of Eumenidae, attached to the cell wall by a thread (Trostle and Torchio 1986) suggesting that attachment of the egg by a thread is plesiomorphic for Vespidae. It is therefore of note that the egg of *P. namibiensis*, like that of all other Masarinae, for which the egg is known, is not attached by a thread.

S.K. Gess (1996) stated that as a general rule at temperate latitudes pollen wasps appear to be univoltine but that Zucchi *et al.* (1976) suggested that *T. howardi* in subtropical South America may be bivoltine. It is therefore of particular interest that it has now been demonstrated that *P. namibiensis* is bivoltine. This suggests that the recorded second flush of nesting by *Jugurtia confusa* Richards (Gess and Gess 1980) after late summer rain in the Eastern Cape of South Africa may indicate that under optimal summer conditions *Jugurtia* may also be bivoltine. It is therefore possible that whether or not pollen wasps in southern Africa are uni- or bi-voltine varies from year to year with varying spring and summer rainfall patterns.

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- 20.17S 14.05E, between Palm and Khorixas (F. W. and S. K. Gess, 31.iii.1997)
- 20.26S 14.54E, 15.5 km by road west of Khorixas (F. W. and S. K. Gess, 31.iii.1997)
- 20.31S 14.56E, 23 km by road from Khorixas to Uis (F. W. and S. K. Gess, 1.iv.1997)
- 9—Dwarf Shrub Savanna (falling within the Nama Karoo Biome)
- 24.11S 16.56E, southeast of Bullsport (F. W. and S. K. Gess, 11.iii.2000)
- 24.40S 17.57E, 5 km south of Mariental by road to Keetmanshoop (F. W. and S. K. Gess, 10 and 31.iii.2000 and 2.iv.2000)
- 24.58S 17.55E, 43 km south of Mariental by road to Keetmanshoop (F. W. and S. K. Gess, 4.iv.1997)
- 25.17S 17.50E, 7 km south of Gibeon railway siding by the Mariental/ Keetmanshoop road (F. W. and S. K. Gess, 9.iii. and 3.iv.2000)
- 25.24S 17.54E, 97 km south of Mariental by road to Keetmanshoop (F. W. and S. K. Gess, 4.iv.1997)
- 25.53S 18.07E, Tses, 161 km south of Mariental by road to Keetmanshoop (F. W. and S. K. Gess, 4.iv.1997 and 17.iv.1998)

APPENDIX 1

Collection records of *Priscomasaris namibiensis* Gess listed under the vegetation types of Giess (1971) (given by number and name, see also Fig. 1) and the biomes of Rutherford and Westfall (1986) as adapted by Lovegrove (1993) (see Fig. 2).

5—Mopane Savanna (falling within the Nama Karoo



Gess, Sarah K. 2001. "Distribution and Ethology of *Priscomasaris* Gess (Hymenoptera: Vespidae: Masarinae: *Priscomasarina*) in Namibia." *Journal of Hymenoptera research* 10, 16–28.

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