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Original article

The biology of a *Patellapis (s. str.)* species (Hymenoptera: Apoidea: Halictidae): sociality described for the first time in this bee genus*

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Abstract – The sweat bees are socially diverse and therefore make ideal subjects for the study of insect sociality. A small nest aggregation of an undescribed species of *Patellapis* (s. str.) was studied in the western South African winter rainfall area to provide information on nest architecture, floral hosts, seasonality and kleptoparasites. A single excavated nest was inhabited by eight females and consisted of a main burrow with several lateral tunnels. Observations indicate that this *Patellapis* species probably has a communal nesting behaviour; sociality is recorded for the first time within this bee genus. Analyses of provisioned nest cells and scopal pollen loads of females revealed that this species is polylectic (generalist), collecting pollen from plant species occurring in high abundance, namely Asteraceae, Zygophyllaceae and Oxalidaceae. The species is parasitized by the cuckoo bee *Sphecodopsis semirufa* (Cockerell), which is recorded for the first time to attack a halictid bee.

***Patellapis* / sweat bee / biology / nest / communal / sociality / Halictidae**

1. INTRODUCTION

The Namaqualand in western South Africa is renowned to be a "hotspot" of biodiversity (Myers et al., 2000) where plant-pollinator interactions are supposed to play a major role for coevolutionary processes and speciation (Johnson, 1996; Cowling et al., 1998; Johnson and Steiner, 2003). This region with its world wide unique overlap of plant and bee diversity centres (Kuhlmann, 2005) is characterised by an unusual selective regime of low, highly predictable rainfall, very rare prolonged droughts, and mild, seasonal temperature ranges (Cowling et al., 1999) which is responsible for the species richness and the high degree of endemism in both plants and bees (Cowling and Hilton-Taylor, 1994). The bee fauna of Namaqualand and its ecology is poorly investigated (Whitehead et al., 1987). This is especially true for the diverse halictid bee genus *Patellapis* Friese, which comprises about 160 species, most of them confined to southern Africa and especially the South African winter rainfall area (Michener, 1978; Pauly, 1999). Species of this genus occur in high abundance and they are assumed to play a major role as pollinators (Timmermann, 2005) but data on their biology is not available.

Sweat bees (Halictidae) are of particular biological interest because of their diversity in social behaviour (Sakagami and Michener, 1962). Halictid social behaviour is characterised by the housing of a number of individuals in the same nest, and, in some genera and subgenera, by a division of labour and castes (Lin, 1964). Halictid bees show a wide spectrum of social behaviour ranging from strictly solitary (brood rearing nests are each cared by a single female) to eusociality, with

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communal and semisocial life as presumed intermediate forms (Sakagami, 1974; Richards, 1994). Because of their substantial intraspecific (Richards, 2000; Soucy and Danforth, 2002) and interspecific (Michener, 1974; Wcislo et al., 1993) variability in social behaviour, halictid bees are ideal for researching social evolution and the evolutionary origins of sociality (Crespi, 1996; Danforth, 2002). Phylogenetic analyses have revealed that eusociality is of recent origin, evolving in three independent lineages within the subfamily Halictinae and including frequent reversals from eusociality to solitary nesting (Danforth, 1999, 2002; Danforth et al., 2003; Brady et al., 2006). In contrast, communal and semisocial nesting seems to have evolved independently from eusociality (Danforth, 2002). But halictine social behaviour is not only extremely variable, but also ecologically and evolutionarily labile – reversals to solitary behavior seem to be quite common among the sweat bees (Richards, 1994). Due to geographic and climatic variation, some halictid species may even exhibit more than one type of sociality. *Lasioglossum* (*Evylaeus*) *calceatum* (Scopoli), for example, is social in lower altitudes but at higher altitudes reverts to solitary behaviour (Sakagami and Munakata, 1972), and populations of *Augochlorella striata* (Povancher) in Nova Scotia showed, that many foundresses are unable to establish matrifilial societies in areas with short foraging seasons (Packer, 1990). Other examples of socially polymorphic halictines are *Halictus rubicundus* (Christ) (Eickwort et al., 1996), *Halictus sexcinctus* (Fabricius) (Richards, 2001; Richards et al., 2003), and *Lasioglossum malachurum* Kirby (Richards, 2000).

This paper provides the first information on the nesting biology and social organisation of a *Patellapis* species and gives strong support for an additional case of independent evolution of sociality in halictid bees (Danforth, 2002). This is of particular interest because *Patellapis* s.l. (sensu Michener, 2000) represents the most recent clade within the Halictini (Danforth et al., 2008) and is therefore of interest for understanding patterns of social evolution.

The data presented here are based on observations of a species new to science named *P.* sp. 1 here, which will be described in a forthcoming revision of *Patellapis* (Timmermann and Kuhlmann, unpubl. data).

2. MATERIALS AND METHODS

2.1. Study site

The study was carried out in the Nieuwoudtville Wild Flower Reserve (31°21′S 19°08′E; 760 m) in the South African winter rainfall area. Climatically, the Nieuwoudtville area is semi-arid with a mean annual rainfall of 341 mm (Snijman and Perry, 1987). The reserve falls within the vegetation type of the Nieuwoudtville dolerite renosterveld (Mucina and Rutherford, 2004) and is renowned for its high diversity of geophytes and annuals (Manning and Goldblatt, 1996).

2.2. Fieldwork

Fieldwork was conducted during the flowering seasons from August to October of 2002, 2004, and 2006. In each year, flower visiting individuals of *P.* sp. 1 were captured by using a sweep net during warm and sunny weather, mainly between 1100 and 1600 h, for the analyses of female scopal pollen loads. Observations on nesting individuals of *P.* sp. 1 were only made in 2006.

2.3. Nesting site

The gently sloping nesting site (5–10°), covering an area of approximately 110 m^2, was surrounded by some dolerite rocks and several medium sized shrubs in the dolerite hills of the Nieuwoudtville Wild Flower Reserve (Fig. 1a). The nesting area was sparsely vegetated and exposed to the sun. The flora included *Zygophyllum foetidum* Schrad. & J.C. Wendl. (Zygophyllaceae), *Felicia australis* (Alston) E. Phillips, *Osteospermum acanthospermum* (D.C.) Norl., *Rhynchopsidium pumilum* (L.f.) D.C., *Senecio* spec., *Ursinia anthemoides* (L.) Poir. (Asteraceae), *Lotononis maximiliani* Schltr. ex De Wild. (Fabaceae), *Diascia* spec., *Nemesia* spec. (Scrophulariaceae), *Galenia sarcophylla* Fenzl, *Tetragonia* spec. (Aizoaceae), *Oxalis pes-caprae* L., *Oxalis obtusa* Jacq. (Oxalidaceae), *Erodium*

Figure 1. (a) Nesting site of *P*. sp. 1 at the Nieuwoudtville Wild Flower Reserve, South Africa. (b) Nest entrance of *P*. sp. 1 (arrow). (c) Cuckoo bee *Sphecodopsis semirufa*. (d) Mating of *P.* sp. 1 on flower of *Felicia australis* (Asteraceae).

cicutarium (L.) L'Hér (Geraniaceae), *Spiloxene serrata* (Thunb.) Garside (Hypoxidaceae), *Bulbinella latifolia* Kunth (Asphodelaceae), *Cyanella hyacinthoides* L. (Tecophilaeaceae), and *Albuca maxima* Burm.f. (Hyacinthaceae). The top soil layer, approximately 8–10 cm thick, consisted of very dry, hard and crusted substrate. Deeper, the soil gradually became moister and less condensed with a composition of 36% clay, 28% silt, and 36% sand. The soil-particle-size analysis followed the pipette-method of Köhn and Köttgen (Kretzschmar, 1989). The soil on the surface as well as below contained some small stones and a few roots.

2.4. Nest observation and excavation

Nest entrances were difficult to find because they tended to be hidden under low growing plants and they did not possess tumuli (Fig. 1b). We identified nest entrances by observing the returning females entering them. As a result of the hard soil, we excavated only a single nest, but observations on other six active nests were also made. For nest observations, the nest entrances were covered with clear plastic cups to count the number of adult females within active nests. A single nest was excavated in order to describe the architecture following the methodology of Sakagami and Michener (1962). The nest was filled with liquid latex which was allowed to harden. By this method it was possible to follow the tunnels, to find brood cells and to reconstruct the architecture of the entire nest despite the very hard soil.

2.5. Pollen analyses

Host plants of *P*. sp. 1 were identified by analysing the content of female scopal pollen loads and larval food provisions of closed brood cells. The pollen was gently removed with an insect pin and embedded in Kaiser's glycerol gelatine on microscope slides. Pollen samples were identified by light microscopy at a magnification of 400× with the help of a pollen reference collection representing all plants flowering at the study site. The pollen composition was investigated by identifying 400 pollen grains randomly chosen from each sample. The pollen grains representing less than 5% per load were assumed to be contamination and neglected (Westrich and Schmidt, 1986).

Reference specimens of *P*. sp. 1, cuckoo bees, brood cells, soil, and pollen samples are deposited in the collection of the authors.

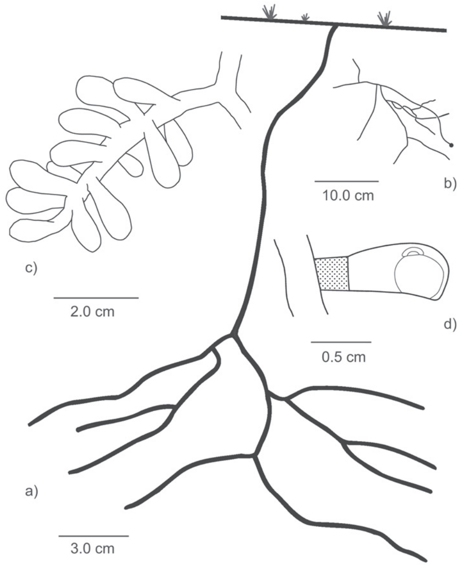

Figure 2. Nest of *P*. sp. 1. (a) Schematic representation of the nest. (b) Same nest, top view. The dot represents the nest entrance. (c) Part of a branch with brood cells. (d) Side view of a closed and provisioned brood cell.

3. RESULTS

3.1. Nest architecture

The following information was obtained from excavating a single active nest on 6 September 2006. The nest contained eight adult females. The entrance was 3.5 mm in diameter and did not possess a tumulus. The main burrow entered the ground obliquely for the first centimetre, and then the burrow descended more or less vertically. Three lateral tunnels branched from the main burrow at depths of 15 cm, 18 cm, and 21 cm. Two of them divided again with some of the secondary branches also ramified (Fig. 2a, b) to give eight laterals. Lateral tunnels extended 3–10 cm horizontally or slightly downward. The brood cells tended to be closely clustered along the branches (Fig. 2c). Eight to fifteen cells were clustered together and became more abundant towards the end of each branch. In total, 98 brood cells were observed for the whole nest, with 65 of them closed and 33 cells were open with unfinished larval food provisioning.

We made observations of *P*. sp. 1 on six other nests. The number of females belonging to a single active nest varied from three to seven specimens (one nest with three, two nests with four, two nests with five females, and one nest with seven females).

3.2. Brood cells

The nest cells were elongated ovals, slightly flatter on the lower surface than on the upper surface (Fig. 2d). All cells occurred in the moister substrate beneath the dry surface layer. They were found at depths of 17–27 cm with a maximum between 20–23 cm. The cells were primarily horizontal to subhorizontal in their orientation. In five of the cells the posterior end was slightly higher than the anterior end. Measurements of nine cells indicate an average cell length from rear to centre of closure of 8.7 mm (range 8.3–9.6 mm) and an average maximum width of 4.9 mm (range 4.6–5.1 mm). The cell walls were completely lined with a thin and shiny waterproof film (tested with a droplet of water). Cell closures consisted of soil material not identical to the surrounding substrate and had an average width of 2.5 mm (range 2.2–3.0 mm). A vague spiral structure could be detected on the inner side of only one closure, the other eight were smooth. Closures were slightly concave on the inside and had no lining.

The provisions in closed cells were spherical pollen-nectar balls of a pasty consistency with an average diameter of 4.2 mm (range 3.5–4.8 mm, n = 15). They were located on the bottom of the cells near the posterior end (Fig. 2d). Eggs were placed on the top of the provision with both ends attached to the masses (Fig. 2d). The whitish eggs were strongly arched and possessed a smooth, transparent chorion. Small to large sized larvae were also encountered but details of larval morphology and behaviour were not obtained.

3.3. Parasites

Nests of *P*. sp. 1 were parasitized by the cuckoo bee *Sphecodopsis semirufa* (Cockerell) (Apidae), which was abundant at the

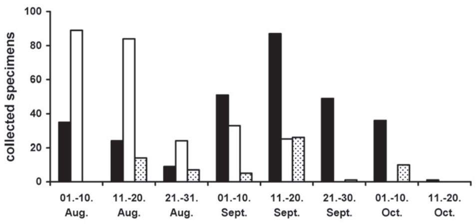

Figure 3. Seasonal activity pattern of *P*. sp. 1 (♀ black and ♂ white bars) and its parasite *Sphecodopsis semirufa* (♀ and ♂ dotted bars) at the Nieuwoudtville Wild Flower Reserve based on pooled records of the years 2002–2006 (*P*. sp. 1: n = 546, ♀ 292, ♂ 254; *S. semirufa*: n = 63, ♀ 47, ♂ 16).

nesting site (Fig. 1c). Both species showed an overlapping daily and seasonal activity pattern (Fig. 3).

At the nesting site *S. semirufa* was seen patrolling around nests, performing inspection flights slowly and very close to the ground, and landing at several nests to inspect the entrances with their antennae. After inspection females usually flew onto a stick or plant close to the entrance and remained motionless (sometimes several minutes), observing the nest entrance. Several times the pollen loaded host bee was seen to arrive at the burrow and enter while the cuckoo bee was waiting. When *P*. sp. 1 left the nest, *S. semirufa* flew to the entrance, stopped in front of it, inspected the nest again with its antennae and then entered. We observed three females of *S. semirufa* invading a nest, staying inside for three to eight minutes and leaving before the host female returned. Contact between the parasite and the host bee was not observed. Males of *S. semirufa* were regularly seen on flowers of *F. australis*, but no mating was observed.

3.4. Daily activity and seasonality

Females started flight activity on warm, clear or partly cloudy days at about 1115 h until 1700 h, but were most abundant from 1215 h to 1330 h. Periods of rainy and cloudy weather or incoming cold fronts disturbed bee activity, and the bees were not active outside nests. Females were seen particularly on flowers of *F. australis* and *Z. foetidum*, which occurred in high abundance close to the nesting site. Males were regularly seen later in the day on host flowers near nests, where they patrolled or held territories. Mating was observed once on a flower of *F. australis* on 11 September 2006 (Fig. 1d).

First observations at the nest aggregation were made on 27 August 2006, when nesting activities had already begun. When we last visited the site on 27 September 2006, nesting activity was greatly reduced. Only a few females and almost no males visited the food plants, indicating that the nesting season was ending. A last single female of *P*. sp. 1 was collected on 19 October in the vicinity of the nesting site. Protandry is suggested by seasonal activity data of the males. Collection records indicate a single generation per year that is restricted to the winterly flowering season between August and October (Fig. 3).

3.5. Pollen analyses

From August to October 2006 we collected 223 specimens (♀ 198, ♂ 25) of *Patellapis* spec. at the Nieuwoudtville Wild Flower Reserve. A total of 226 pollen samples were used for pollen analyses, including 161 samples from female scopal loads and 65 brood cells. *P*. sp. 1 collected pollen from eight host plants in seven plant families, including species of Asteraceae (*F. australis*, *R. pumilum*), Zygophyllaceae (*Z. foetidum*), Scrophulariaceae (*Diascia* spec.), Aizoaceae (*G. sarcophylla*), Oxalidaceae (*O. pes-caprae*), Asphodelaceae (*B. latifolia*) and Tecophilaeaceae (*C. hyacinthoides*) (Tab. I). Pollen from Asteraceae (62.7%) and Zygophyllaceae (33.2%) were represented at most. Both were present in 90% (Asteraceae) and 60% (Zygophyllaceae) of all pollen samples and ranged from 6–100% per sample. The other 4% of pollen originated from Scrophulariaceae, Aizoaceae, Oxalidaceae, Asphodelaceae, and Tecophilaeaceae (Tab. I). Of 95 pure pollen loads found, 74 only contained pollen of Asteraceae, and 21 exclusively consisted of Zygophyllaceae pollen. The remaining 131 pollen samples (58%) consisted of mixed pollen loads of

Table I. Composition of 226 pollen samples of *P.* sp. 1 from the Nieuwoudtville Wild Flower Reserve 2006. Other = unidentified pollen types.

Family	Host plant species	% (all loads)	Presence in samples	min.max. / load (%)
Asteraceae	*Felicia australis*, *Rhynchopsidium pumilum*	62.7	203 (89.8%)	6–100
Zygophyllaceae	*Zygophyllum foetidum*	33.2	135 (59.7%)	6–100
Scrophulariaceae	*Diascia* spec.	2.0	17 (7.5%)	6–100
Aizoaceae	*Galenia sarcophylla*	1.5	12 (5.3%)	8–63
Oxalidaceae	*Oxalis pes-caprae*	0.5	2 (0.9%)	30–75
Asphodelaceae	*Bulbinella latifolia*	< 0.1	2 (0.9%)	8–10
Tecophilaeaceae	*Cyanella hyacinthoides*	< 0.1	2 (0.9%)	8–15
Other		< 0.1	1 (0.4%)	6

different plant families, most of them (n = 99) containing a mixture of Asteraceae and Zygophyllaceae.

Additional scopal pollen loads from 2002 (n = 12) were very similar in content, dominated by pollen of Asteraceae and Zygophyllaceae (together 85%). In 2004 the pollen content of scopal loads (n = 11) was very different, consisting only of pollen from Oxalidaceae (76%) and Asteraceae (24%).

4. DISCUSSION

4.1. Sociality of the *Patellapis* species

Halictine bees are noteworthy among insects in the occurrence of different levels of social organization from strictly solitary to a complicated eusocial societies (Sakagami and Michener, 1962; Michener, 1974). Although, there is no strict correlation between social organisation and nest architecture (Sakagami and Michener, 1962), the communal sociality of *P.* sp. 1 seems to be very probable given the similarity in nest architectures of other communal halictid bees (Michener and Lange, 1958; Michener et al., 1979).

By definition, communality is the simplest form of insect social organisation (Paxton et al., 1996) where insects share a common nest in which each adult female provisions and produces its own offspring; there is a lack of reproductive division of labour and no overlap of generations (Michener, 1974). In such multi-female nests halictine bees tend to have various degrees of integration of joint and solitary nest construction (Sakagami and Michener, 1962). The nest's architecture is not an outcome of the work of a single bee, but a product of joint work by several nest mates. The joint and solitary sections in the nests are relatively easy to distinguish. The most distinct pattern consists of one main communal burrow and several private laterals. Each inhabitant makes one or more laterals of their own (Sakagami and Michener, 1962). The *P.* spec. 1 multifemale nest appears to be communal. The ramifying nest suggests clear separation of joint and solitary sections for reproduction; eight adult females with equally worn wings and mandibles shared a single nest consisting of eight lateral tunnels with aggregated brood cells. Furthermore, several provisioned brood cells from different laterals suggest no collaboration of foragers in cell provisioning. It is assumed that each female had her own branch and own cells or cell group. A higher social organization of *P.* spec. 1 cannot be excluded. However, eusociality is unlikely due to the single short activity period in winter.

The 33 open empty brood cells compared to only 8 actively provisioning foundresses of the examined nest are unusual among halictine bees. Similar observations have been made by *Sphecodogastra texana* (Cresson) from Kansas (Kerfoot, 1967) and *Lasioglossum* (*Dialictus*) *figueresi* Wcislo from Costa Rica (Wcislo et al., 1993). Whereas *S. texana* lack the closure of each completed brood cell, some females of *L. figueresi* reused old nests and some old brood cells within these nests. Both suggest, that one female simultaneously provision more than one brood cell. Observations on nesting sites of *P*. spec. 1 have shown, that this species neither reuses old nests, nor seals the brood cells after egg deposition. Multiple provision of brood cells by a single female was not observed, but all open brood cells were completely empty. This might suggest some additional kinds of social interactions.

Although the nest architecture indicates a communal organisation for *P*. sp. 1, the level of social organisation is nevertheless not totally clear. Confirmation of communal status requires detailed studies of intranidal reproductive behaviour (Paxton et al., 1996), but such a study is lacking for the *P*. sp. 1. Evaluation of the reproductive status of individuals that share a nest can provide support for their communal status. A study of genetic relatedness and reproductive status of nestmates of *P*. sp. 1 is planned.

4.2. Cuckoo bee of the *Patellapis* species

The cleptoparasitic bee genus *Sphecodopsis* Bischoff comprises 10 species all endemic to southern Africa (Eardley and Brothers, 1997; Michener, 2000). Among this genus only two host records are available. Rozen and Michener (1968) found eggs and larvae of *Sphecodopsis capensis* (Friese) in nests of *Scrapter niger* Lepeletier & Serville (as *Scrapter longula* (Friese)) (Colletidae) and *Sphecodopsis fumipennis* Bischoff in those of *Scrapter erubescens* (Friese) (as *Scrapter crassula* Cockerell). Their flight and inspection behaviour described in Rozen and Michener (1968) is identical with that of *Sphecodopsis semirufa* observed at nests of *P*. sp. 1. *Sphecodopsis* has not previously been recorded kleptoparasitizing halictine bees. *S. semirufa* probably has more than one host species, because it is distributed throughout the Karoo area (Eardley and Brothers, 1997), where *P*. sp. 1 has not been recorded.

4.3. Polylecty of *Patellapis* sp. 1

There is great diversity among bees in their patterns of pollen use, with a continuum from generalists that use pollen from many plant taxa of different families to specialists that collect pollen from just one plant species (Linsley, 1958; Cane and Sipes, 2006). Analyses of pollen collected by *P*. sp. 1 females showed that these bees are polylectic according to the definition of Cane and Sipes (2006) with strong preferences for plant species occurring in high abundance. In 2002 and 2006 *F. australis*, *R. pumilum* and *Z. foetidum* were the most abundant flowers at the nesting site and the preferred pollen plants of *P*. sp. 1. In 2004 *Oxalis pes-caprae* and *O. obtusa* were exceptionally abundant and the most important host plants. Flower visiting records by Gess and Gess (2004) support a relatively high incidence of polylecty in South African halictine bees with a strong preference for Asteraceae and Zygophyllaceae. Oxalidaceae as host plants for halictids are recorded here for the first time.

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Biologie de l'espèce *Patellapis* (*s.str.*, Hymenoptera : Apoidea : Halictidae) : première description d'un comportement social chez ce genre d'abeilles.

Halictidae / abeille / biologie / socialité / nidification / nid collectif

Zusammenfassung – Biologie einer *Patellapis*-Art (*s.str.*, Hymenoptera: Apoidea: Halictidae): Erste Beschreibung des Sozialverhaltens in dieser Bienengattung. Das Ziel dieser Untersuchung war es, erste Informationen zur Biologie der artenreichen Bienengattung *Patellapis* zu erhalten, deren Verbreitung weitgehend auf südafrikanische Gegenden mit Winter-Niederschlägen beschränkt ist. Wir untersuchten die Nestarchitektur, die Trachtpflanzen und die

Saisonalität und identifizierten den Kleptoparasiten einer neuen Art von *Patellapis* (s. str.), die wir vorläufig als *P*. sp. 1 bezeichneten. Eine kleine Nestaggregation dieser Art wurde in der Nähe von Nieuwoudtville (31°21′S 19°08′E; 760 m) (Abb. 1a, c) untersucht. Adulte Bienen flogen hier in der Umgebung des Nestbereiches von August bis Oktober 2006 (Abb. 3). Die Nesteingänge von *P*. sp. 1 waren nicht leicht zu finden, da sie meist unter bodennahen Pflanzen versteckt waren und keine Tumuli besaßen (Abb. 1b). Mehrere Weibchen wurden beobachtet, wie sie denselben Nesteingang benutzten. Dies lässt auf soziales Verhalten schließen. Um Nester beobachten zu können, wurden 7 Nesteingänge mit durchsichtigen Plastikbechern bedeckt und so die Anzahl der adulten Weibchen in diesen aktiven Nestern gezählt. Die Anzahl an Weibchen pro Nest reichte von drei bis acht. Wegen des harten Bodens gruben wir nur ein einziges Nest aus, um die Nestarchitektur zu beschreiben. Das Nest besteht aus einem einzigen Hauptgang mit mehreren seitlichen Tunneln (Abb. 2a). Insgesamt wurden 98 Zellen im Nest in einer Tiefe von 17–27 cm gefunden (Abb. 2c, d). Unsere Beobachtungen sowie die Nestarchitektur, die sehr ähnlich ist wie bei anderen kommunalen Halictiden, weisen darauf hin, dass *P*. sp. 1 kommunal nistet (die einfachste Form der sozialen Organisation bei Insekten). Dies ist die erste Beschreibung einer kommunalen Nestorganisation innerhalb der Gattung *Patellapis*. Dies lässt auf eine unabhängige Evolution des Sozialverhaltens in der Gattung *Patellapis* schließen. Bei den Pollenvorräten der Brutzellen sowie zusätzlich an 161 Pollenladungen von den Scopalhaaren der Weibchen wurden Pollenanalysen durchgeführt. Dabei zeigte sich, dass diese Bienenart ein Generalist (polylektisch) ist mit einem starken Übergewicht an Pflanzenarten aus den Gruppen der Asteraceae, Zygophyllaceae und Oxalidaceae (Tab. I). Die Kuckucksbiene *Sphecodopsis semirufa* (Cockerell) wurde als Kleptoparasit von *P*. sp. 1 bestimmt (Abb. 1c). Bisher wurde noch nie beobachtet, dass *Sphecodopsis* bei Halictiden parasitiert.

Patellapis **/ Furchenbienen / Biologie / Nest / kommunal / Sozialität / Halictidae**

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