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A note on facultative kleptoparasitism in *Prionyx kirbii* (Hymenoptera: Sphecidae) as a consequence of multi-specific shared nesting site, with description of its prepupa

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Observations of a female of *Prionyx kirbii* at an aggregation of *Stizus continuus* revealed an alternative nesting behaviour of the first wasp due to the presence of the second one. The overlap of some resources (prey, kind of soil) allowed *P. kirbii* to act as a kleptoparasite of *S. continuus*. The observed female often re-used as nests pre-existing *S. continuus* emergence holes, but no *S. continuus* nests. The prey were obtained sometimes by stealing the grasshoppers from *S. continuus* nests and/or by attacking the females while carrying the prey. From a review of interspecific kleptoparasitism among sphecoid wasps it appears that family Sphecidae includes the highest number of facultative parasitism cases and this finding is discussed. In addition, the description of the prepupa of *P. kirbii* is given and is shown to be in agreement with the description of the mature larvae of the other species of the genus.

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1. Introduction

Sphecoid wasps (Sphecidae and Crabronidae) often nest in large aggregations (e.g. Evans 1966 & 1974, Evans & Hook 1986, Rosenheim 1990). As the physical nesting requirements (like soil compactness, soil moisture and amount of vegetation among others), are similar in many cases for different species, nesting sites are often shared by a number of species. When this occurs, interspecific interactions may become frequent and lead to nest usurpation (Matthews 1983, Hook

1987), kleptoparasitism (Kurczewski & Spofford 1998, Casiraghi *et al.* 2003) or, more rarely, nest sharing (McCorquodale & Thomson 1988). Facultative kleptoparasitism and brood parasitism (i.e. use by a wasp of another wasp's prey to feed her own brood) could have been an intermediate step in the evolution of the obligate kleptoparasitism and brood parasitism typical of genera such as *Nysson* and *Stizoides* (Evans 1966, Wcislo 1987).

In this paper we report a few observations taken on a single female of *Prionyx kirbii* (Vander Linden) (Hymenoptera: Sphecidae), a common species of the old world, nesting in the same area where a large aggregation of *Stizus continuus* Klug (Hymenoptera: Crabronidae) had been established for many years (Asìs *et al.* 1988 & 2006). The behavioural consequences of the coexistence of the two wasps are analyzed.

Prionyx females usually establish their nests on bare, compact soil. The unicellular or, in few cases, multicellular nests are filled with Orthopthera Acrididae to feed the larvae. One grasshopper is usually provided to each larva (Evans 1958, Benz 1959, Bohart & Menke 1976). Depending on the species, nests are constructed before or after hunting the prey. Some species close the nest temporarily before hunting (Evans 1958, Genise 1980, Grissell 1981). *P. kirbii* belongs to the group of species that dig the nest before hunting and make a temporary closure before the provisioning trip (Ferton 1902, Fabre, 1914, p. 202, Benz 1959, Bohart & Menke 1976). *P. kirbii* females usually hunt one large prey, sometimes two, if they are too small (Benz 1959). There is only one report of Ferton (1902) of a nest with two cells, one with two-prey, the other with only one, but his finding is dubious. The nests structure consists of a vertical burrow from 3 to 4 cm deep followed by an horizontal section of about 4 cm (Benz 1959).

S. continuus females dig (multicellular) nests before hunting on bare and compact soil, provisioning them massively with grasshoppers (several for each cell). The nest remains closed during hunting flights (Asìs *et al.* 1988). The nest of *S. continuus* is composed of a main burrow (oblique to the soil surface) about 50 cm long from which 3–8 secondary tunnels depart, each of them ending in a brood cell. Generally 1–2 accessory burrows (false nests 2–3 cm long, see Evans 1966) are dug close to the nest entrance (Asìs *et al.* 1988).

Our aims are twofold. Firstly, we report observations on an unusual strategy adopted by *P. kirbii* to obtain prey and nest; secondly, we describe the mature larva of *P. kirbii*, in order to provide traits to separate this species from others of the genus.

2. Material and methods

Observations were made on a single female of *P. kirbii* between 24.VI.2003 and 10.VII.2003, the date when the wasp was collected for determination. *P. kirbii* was observed on an aggregation of the solitary wasp *Stizus continuus*, in an area of salt-marsh (*ca.* 9 m × 15 m), characterized by a bare, compact soil, covered (30% of the surface approximately) by *Arthrocnemum fruticosum* (L.) and *Juncus maritimus* Lam. and bounded by *Pinus pinaster* Aiton and *Phragmites australis* (Cav.). The female was marked with non-toxic paints to permit identification on field. Nests dug and provisioned by the wasp were marked with a coloured stick placed in the ground close to the entrances.

Observations on *P. kirbii* were made on a discontinuous base, since they were intermixed with a long term planned research on *S. continuus.*

In the following text, we will use the term "kleptoparasitism" to indicate when a wasp stole the host provisions from inside the nest and then carried them to her own nest or when she stole the host provisions attacking directly the host outside the nest; we will use the term "brood parasitism" if the wasp entered the host nest and oviposits on the host provisions, eventually eating the host egg.

The postdefecated larva (prepupa) was obtained at Saler, Valencia (6.IX.1992). The method employed to prepare the specimen, as well as the terminology of larval morphology and format used in the description follow fundamentally Evans (1987). The following abbreviations have been used in the description: d = diameter; h = height; l = length and w = width. Voucher specimens are deposited at the "Torres-Sala" Entomological Foundation (Valencia, Spain).

Table 1. Numbers of observations made on the female of *Prionyx kirbii* between 24.VI. and 10.VII.2003.

Date	Patrolling the area: stopping on *Stizus continuus* nests	Patrolling the area: "touching" *S. continuus* females	Attacking *S. continuus* females on on their nests	Carrying a prey to a nest their nests	Closing a nest definitively	Stealing a prey from *S. continuus* females
24.VI.	3		1			
25.VI.	4	1			1	
26.VI.	2	1	1**	1		1**
27.VI.		1***				
28.VI.	4			1	1	
29.VI.	2				1****	
30.VI.	2	1***		1*		
01.VII.		1				
02.VII.	1					1*****
03.VII.	4			1	1	
04.VII.	3	2				
05.VII.	5					
06.VII.	2					
07.VII.	2					
08.VII.	3				1	
09.VII.	4					
10.VII.	1					

* = prey carried deep in a grass area; nest not identified; ** = prey stolen from the wasp after an attack; *** = the *S. continuus* female flown away after the "touch"; **** = this nest did not correspond to an emerging hole of *S. continuus* as the other ones; *****=prey stolen from inside the nest.

3. Results

3.1. Behaviour of *P. kirbii*

Table 1 summarizes the results of the observations. The female of *P. kirbii* was observed for the first time on the 24.VI.2003, while patrolling the nesting site of *S. continuus*, and she frequented the area every day of the observation period. The patrolling behaviour included always a number of stops on some nests of *S. continuus* (open or closed). The stops lasted 5–30 seconds and, on average, the wasp stopped on a nest 0.8 times/minute (*range*: 0–5 min^{-1}, $SD = 1.31$, $n = 19$ observations that lasted more than 1 minute).

On some occasions (6 out of 42 contacts with the wasp) the *Prionix* female, while overflying a *S. continuus* nest when the owner was present at the entrance, flew rapidly down and "touched" the other wasp, disturbing her activity (in 2 cases out of 6, the female of *S. continuus* flew away for a while after the "touch"). Three times the female of *P. kirbii* attacked more violently a *S. continuus* female as she was opening her nest to enter with a prey. One time she caused the abandonment of the prey by the attacked wasp: at this point the female of *P. kirbii* took the prey, stung it and transported it away, stopping sometimes to sting again the grasshopper. The other two times the female of *S. continuus* did not abandon the prey, and *P. kirbii* flew away. On another occasion, *P. kirbii* waited on a closed nest the return of the owner with a prey and followed her inside the nest, coming out a few seconds later with the grasshopper. Even in this case the wasp re-stung the prey during the transport. Neither females nor males of *S. continuus* showed any aggressiveness toward *P. kirbii*.

A total of 5 nests of *P. kirbii* were located in the nesting area of *S. continuus*, and 4 of them were identified as re-used emerging holes of *S. continuus*, but no nest of *S. continuus* was observed to be actively usurped by *P. kirbii*. A total of 4 prey-carryings by *P. kirbii* were observed, but no more than one to each nest. A fifth prey was carried in a peripheral area with dense vegetation, but the wasp disappeared in the grass and the nest was not found. Considering that the observed 5 nests were closed definitively by the wasp within one-two days since they were first recorded, and that the female was observed for a period of 17 days, probably many other unde-

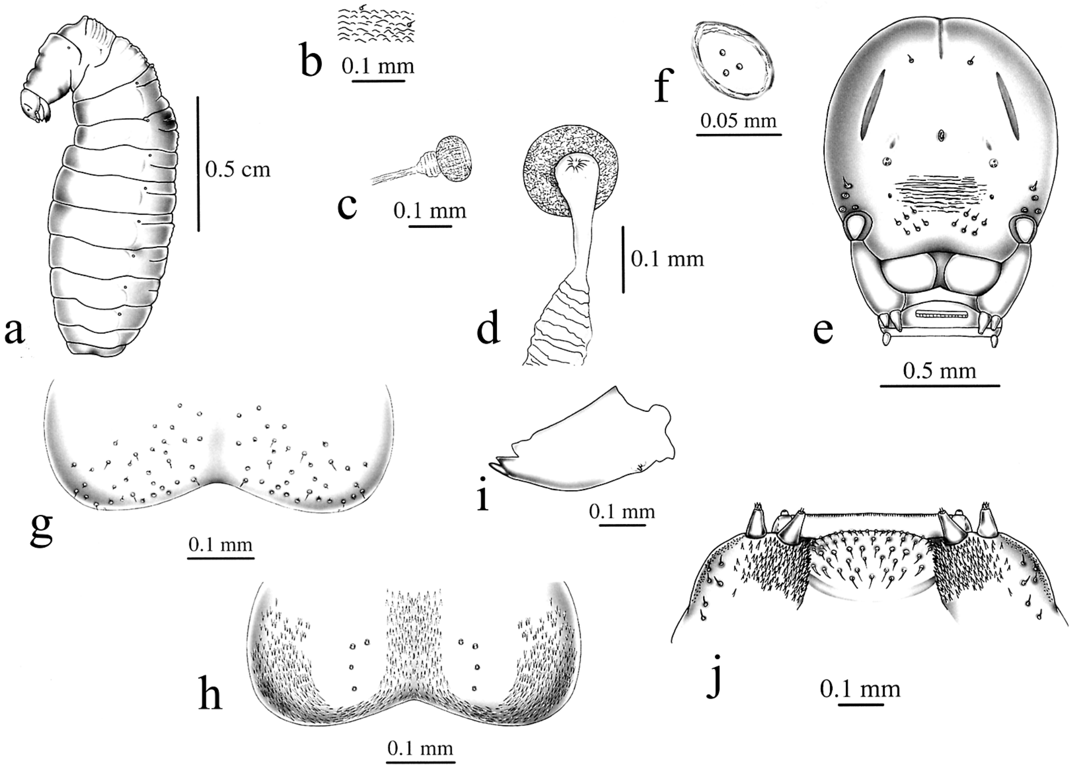

Fig. 1. Prepupa of *Prionyx kirbii* (Vander Linden). – a. General aspect (lateral view). – b. Portion of integument. – c–d. Abdominal spiracle. – e. Cranium (frontal view). – f. Antennal orbit (frontal view). – g. Labrum. – h. Epipharynx. – i. Left mandible. – j. Maxilla and Labium.

tected nests belonging to the same individual were been present in the area.

3.2. Description of the prepupa of *P. kirbii*

General aspect (Fig. 1a). Body (l = 13.5 mm, maximum w [3rd abdominal segment] = 4.3 mm) hymenopteriform, elongate, strongly curved at the level of the third thoracic segment, with the thorax and first abdominal segment narrow with respect to the rest, yellowish, weakly sclerotized, except for spiracles. Anus terminal, a transverse slit. Pleural lobes convex. Integument (Fig. 1b) with large spinules (l of spinules = 30 mm, w basal = 10 mm) arising from plate-like bases, with the exception of those of the thoracic segments (l = 5 mm) which are small and arranged in such a way that they have the appearance of transverse grooves, and with sparse setae (l = 3–7 mm). Spiracles (Fig. 1c–d) all in a single line, on mesothorax, metathorax, and first 8 abdominal segments; atria (d = ma) goblet-shaped; walls lined with ridges forming small and irregular polygons; opening into subatria armed with long spines; subatria comparatively small (d = 64 mm), with 6 swellings. Cranium (Fig. 1e) (w = 0.9 mm, h [height measured to apex of clypeus] = 1.1 mm) higher than wide, yellowish, with sparse setae (l = 5 mm) and some punctations close to mandibular insertion; vertex depressed medially; coronal suture and parietal bands present, brown; antennal orbits (Fig. 1f) (58 × 43 mm) with membrane of the orbit convex, with 3 sensilla. Frons with five depressions, near epistomal suture and base of clypeus transversely furrowed; frontoclypeal suture unpigmented; clypeolabral suture well defined. Clypeus with 12 setae (l = 5 mm). Labrum (Fig. 1g) (maximum w = 470 mm; maximum h = 150 mm) bilobate; base smooth; anterior margin weakly pigmented with small sensilla; each lobe surface with sparse setae (l = 5mm) and dense conical sensilla (w = 3 mm); epipharynx (Fig. 1h) densely spinulose (l of *spinules* = 25 mm, basal w

= 3 mm) centrally and laterally, with 8 sensory pores (d = 7 mm) medially distributed en 2 epipharyngeal sensory areas, each with 4 pores.

Mouthparts. Mandibles (Fig. 1i) (l = 370 mm, maximum w = 170 mm) robust, sclerotized, brown, teeth 3 and 4 dark brown, 2.2 × as long as wide, with two punctures close to the basal external margin, with 4 apical teeth, 3 superior teeth on about the same plane, the basal tooth on a lower plane. Maxillae (Fig. 1j) with sparse lateral setae (l = 11 mm), mesally densely spinulose, with very short spinules; maxillary palpi longer than wide (75 × 49 mm) with 5 apical sensilla; galeae (l = 75 mm, w = 30 mm) similarly formed, with 2 large apical sensilla. Labium (Fig. 1j) setose (l of the setae = 12 mm); labial palpi longer than wide (75 × 49), with 4 apical sensilla (d = 7.5 mm); salivary orifice (l = 450 mm) transverse.

4. Discussion

These are the first observations made on *P. kirbii* (as well as on the genus *Prionyx*) behaving as a kleptoparasite of a different species of sphecoid wasp, and provide new data on these interspecific relationships phenomena, which are probably more widespread than previously supposed among fossorial Hymenoptera. The observations are based on a single female. However, the behaviour is probably rare: in none of the 14 published works on the nesting habits of *Prionyx* spp. kleptoparasitic behaviour was detected (most important references quoted in the text; the complete list of works on *Prionyx* spp. could be found in Pulawski (1999)). For the much more investigated genus *Ammophila*, only in 4 out of more than 50 studies such behaviour was recorded (Table 2 and Pulawski 1999). This means that this behaviour is difficult to observe repeatedly. Accordingly, we consider this phenomenon worth of reporting in spite of the restricted data.

4.1. The behaviour of *P. kirbii* on the nesting site of *S. continuus*

The nesting behaviour exhibited by the observed female of *P. kirbii* showed characteristics that seem to be related to the presence in the same nesting area of several provisioning females of *S. continuus* (*ca.* 30 during the period). The overlap of the resources needed by the two species, in particular bare soil and grasshoppers (Evans 1958, Benz 1959, Asìs *et al.* 1988), would account for the observed phenomenona. Notwithstanding the lack of a continuous recording of the activity of *P. kirbii*, we have stated that, at least in part, the wasp used two resources obtained by *S. continuus* females: emergence holes (as nests) and prey (as food for the larvae). By a slight shift in her behaviour, the female of *P. kirbii* may become a true kleptoparasite of *S. continuus*, at least for what prey is concerned (strictly speaking, emergence holes re-use is not a parasitic action). This strategy should allow reduced the expenditure of energy in digging a nest, but probably it does not reduce the time necessary to find the prey. In fact, we observed no more than one nest provisioned and completed per day, the commonest value found in many other *Prionyx* species studied (Evans 1958, Genise 1980, Grissell 1981).

Since re-using a pre-existing burrow (the emergence tunnels of *S. continuus*) evidently reduces the time spent to obtain a nest, prey-finding should be the activity that mainly determines the time necessary to complete a nest. In fact, attacking a *S. continuus* female to steal her prey is greatly more dangerous and time-consuming than re-using an emergence hole, which is no more used by any *S. continuus* females and only attracts the attention of the males (Asìs *et al.* 2006). Moreover, although territorial *S. continuus* males attack conspecific males and males of the mutillid parasite *Nemka viduata* (Pallas), they were never observed to interfere with the activity of *P. kirbii*. In conclusion, we may suppose that the females of *P. kirbii* prefer to gain time and energy colonizing an emerging tunnel of *S. continuus*; subsequently, they first try to feed their larvae at the expense of *S. continuus* (prey). Anyway, usually after having lost time by patrolling the *S. continuus* nesting area in search of a prey in an “easier” way, they resume their “normal” hunting activity. Re-using *S. continuus* nests does not seem to be related to similarity in nest architecture of the two species. In fact *P. kirbii* females have been observed to dig their nests even inside already pre-existing nests of bees of the genus

Table 2. Observed facultative interspecific parasitism among different species of sphecoid wasps (Sphecidae and Crabronidae). The kind of behaviour of prey stealing is reported only for facultative kleptoparasitism.

Facultative kleptoparasitism		**Prey of the host**	**Kind of parasitic behaviour**	**References**
Parasite	**Host**			
*Ammophila kennedyi** (Murray) [S]	*Ammophila urnaria* Dahlbom [S]	Lepidoptera larvae	Theft of provisions from inside nests	Kurczewski *et al.* 1992
*Ammophila urnaria** [S]	*Ammophila kennedyi* [S], *Podalonia robusta* (Cresson) [S]	Lepidoptera larvae, Lepidoptera larvae	Theft of provisions from inside nests	Kurczewski *et al.* 1992; Kurczewski & Spofford 1998
Microbembex monodonta ** (Say) [B]	*Tachysphex terminatus* (F. Smith) [C], *Lyroda subita* Say [C], *Bembix pruinosa* Fox [B], *Ammophila harti* (Fernald) [S]	Orthoptera, Diptera, Diptera, Lepidoptera larvae	Prey theft outside the nest	Kurczewski, personal communication, quoted by Evans 1966, p. 378; Evans 1966, p. 376, 378
Passaloecus corniger Shuckard [P] [P]	*Passaloecus singularis* Dahlbom	Homoptera	Theft of provisions from inside nests	Danks 1970
Passaloecus corniger [P]	*Passaloecus gracilis* (Curtis) [P]	Homoptera	Theft of provisions from inside nests	Corbet & Backhouse 1975
Passaloecus corniger [P]	*Passaloecus insignis* (Vander Linden) [P]	Homoptera	Theft of provisions from inside nests	Corbet & Backhouse 1975
Passaloecus corniger [P]	*Psenulus atratus* (F.) [P]	Homoptera	Theft of provisions from inside nests	Chevalier 1923, quoted by Evans & West-Eberhard 1970, p. 212
*Podalonia affinis** (Kirby) [S]	*Ammophila sabulosa* L. [S]	Lepidoptera larvae	Theft of provisions from inside nests	Field 1989, 1992; Casiraghi *et al.* 2003
Ammophila kennedyi [S]	*Podalonia robusta* [S]	Lepidoptera larvae	Theft of provisions from inside nests	Kurczewski *et al.* 1992
Prionyx kirbii Vander Linden [S]	*Stizus continuus* (Klug) [B]	Orthoptera	Theft of provisions from inside nests; Prey theft outside the nest	Present study
Stictia signata (L.) [B]	*Stictia heros* (Fabricius) [B]	Diptera	Prey theft outside the nest	Sheehan 1984

Table 2 continued.

Facultative brood parasitism		**Prey of the host**	**References**
Parasite	**Host**		
*Ammophila kennedyi** [S]	*Ammophila urnaria* [S]	Lepidoptera larvae	Kurczewski *et al.* 1992
*Ammophila urnaria** [S]	*Ammophila kennedyi* [S]	Lepidoptera larvae	Kurczewski *et al.* 1992
*Podalonia affinis** [S]	*Ammophila sabulosa* [S]	Lepidoptera larvae	Field 1989, 1992
Liris niger (Fabricius) [C]	*Sphex maxillosus* (Fabricius) [S]	Orthoptera	Fabre 1914, p. 102

S = Sphecidae; Crabronidae: B = Bembicinae, P = Pemphredoninae, C = Crabroninae; * species that appear both as facultative kleptoparasites and brood parasites; ** this species is a strict scavenger, according to Evans 1966, p. 376.

Halictus (Benz 1959). However, burrowing a new nest is very time-consuming activity: 22 minutes/cm, according to Benz (1959). Even if some amount of labour should be necessary to adapt a foreign nest, it could be worth doing it.

4.2. Interspecific facultative parasitism in sphecoid wasps: distribution and occurrence

Despite of the many studies devoted to intraspecific parasitism among solitary wasps (see Field 1992, for a review on its occurrence and performance in solitary Hymenoptera), very little information exists in literature about interspecific relationships (see Field 1992, for a brief review). Table 2 presents a summary of the actual knowledge on the occurrence of this phenomenon, restricted to the sphecid wasps (*sensu* Bohart & Menke 1976; now the family is split into Crabronidae, Sphecidae and Ampulicidae) and considering only facultative parasitism. According to Field (1992), one may classify the different patterns of interspecific kleptoparasitic behaviour as in the intraspecific case (see Table 2 and Field 1992). In fact, the tactic does not change if the host is the same or a related species showing similar nesting habits. Field (1992) notes that facultative parasitism may occur even between distant species (up to bees vs. wasps), because the parasite only needs a resource similar to that employed in its normal and non-parasitical behaviour. This seems to be true in particular for nest usurpation (without utilization of any other host resources). However, in the restricted field of facultative kleptoparasitism (and brood parasitism), sharing the same prey is not a sufficient condition and parasites and hosts have to be related species. In fact, there exists a considerable overlapping between nesting habits and phylogeny in sphecoid wasps: all the members of the same genus often use similar resources (Evans 1966, Bohart & Menke 1976). Things seem to work differently in the case of obligate brood parasitism, for which only the recognition of the host nest is required. Parasitism will be performed later, in the absence of the host, when its nest will be reopened and its egg destroyed (e.g. *Stizoides* spp., *Nysson* spp.). On the contrary, facultative brood parasitism and facultative kleptoparasitism have probably followed a pathway different from that of obligate brood parasitism. Supporting this view, facultative kleptoparasitism has been observed more frequently in behaviourally related genera like *Ammophila* and *Podalonia*, whose members share similar resources (Table 2). In associations between related species, parasitic females know the characteristics of the host's nest and may recognize it more easily.

A second point concerns the overlap of food resources. For example, species of the genus *Cerceris* often nest in sympatry (Evans 1971, Hook 1987, Evans & Hook 1986), but no records exist of interspecific kleptoparasitism or brood parasitism, even if interspecific nest usurpation was observed in some cases (Evans & Hook 1986, Hook 1987). This is probably due to the large variety of prey hunted by the different species, which rarely overlap. On the other hand, genera that greatly overlap their prey spectrum and nesting areas, as *Oxybelus* and *Bembix* (Bohart & Menke 1976), do not show any kind of reciprocal parasitism, probably because of the much different habits performed by these genera, which could prevent any efficient kleptoparasitism.

Unfortunately, data are too scarce to substantiate any hypothesis about the evolution of parasitic strategies in these wasps.

4.3. The prepupa of *Prionyx kirbii*

The description of the prepupa of *P. kirbii* is in reasonable agreement with the description of the mature larvae of the other species of the genus described: *P. atratus* (Lepeletier, 1845), *P. thomae* (Fabricius, 1775) (Evans & Lin 1956) and *P. viduatus* (Christ, 1791) (Tsuneki & Iida 1969). The prepupa of *P. kirbii* shares the following character states with the mature larvae of the three previously described species: (a) spiracles all in a single line, (b) cranium higher than wide, (c) mandibles without spinules on their upper surface and (d) thorax without welt-like elevations. However, the character states: (a) mandibles less than 2 times as long as maximum wide, and (b) galeae and maxillary palpi subequal in length (used by Evans and Lin (1956) to characterise the final larval stage of the tribe Sphecini, and the genus *Prionyx* Vander Linden, respectively), are not shown by *P. viduatus* and *P. kirbii*. Accordingly, they should not be used to characterise the respective taxa. In these latter species, the final larval stage has mandibles that are more than 2 times long than they are wide, and the *galeae* are longer than the maxillary palpi. Additionally, the prepupa of *P. kirbii* shares, with the mature larva of *P. viduatus* the following properties: (a) spinules of lacinial area not recurved, (b) an atrium with ridges forming small and irregular polygons, and c) inside of labium with ridges, as well as the characters described by Evans (1959) to characterise the Sphecinae (*sensu* Bohart & Menke 1976).

Unlike the other described species of *Prionyx*, *P. kirbii* exhibits a clypeus with setae.

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