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The Biology of *Scapter* and its Cuckoo Bee, *Pseudodichroa* (Hymenoptera: Colletidae and Anthophoridae)

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The present paper is intended to make known information on the nests of the paracolletine genus *Scapter* and on the behavior of its nomadine cleptoparasite *Pseudodichroa*. Although the Paracolletini are found in the southern continents of the world and northward to Arizona in the Western Hemisphere, *Scapter* is probably restricted to southern Africa. *Scapter* has both spring and autumn species and ranges across the whole southern end of the continent, but it is most abundant in species and individuals in the spring in the western part of Cape Province, where our observations were made. *Pseudodichroa* (tribe Ammobatini) contains only two described species, *capensis* (Fries) and *fumipennis* Bischoff. The type of the former from "Kapland"³ is identical with the smaller of the two species we studied. The larger species agrees closely with the descrip-

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FIG. 1. Nesting site of *Scapter longula* and *crassula* north of Kommetjie, Republic of South Africa.

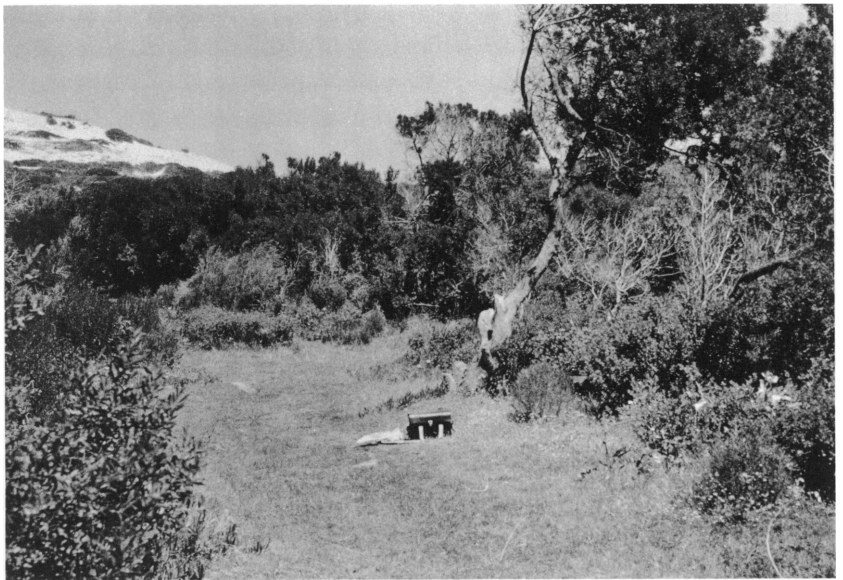


FIG. 2. Nesting site of *Scapter alfkeni* south of Kommetjie, Republic of South Africa.

tion of *P. fumipennis* and therefore is tentatively assigned to it. Although the type of *P. fumipennis*, now lost, presumably came from Java, even Bischoff (1923) questioned the correctness of the locality because almost all related genera are African. The locality is placed in still graver doubt because nomadines tend to be host specific and because the two examples of *Pseudodichroa* that we studied attacked a host genus found only in Africa. *Pseudodichroa*, known from about 40 specimens, seems restricted to the western part of Cape Province in the spring.

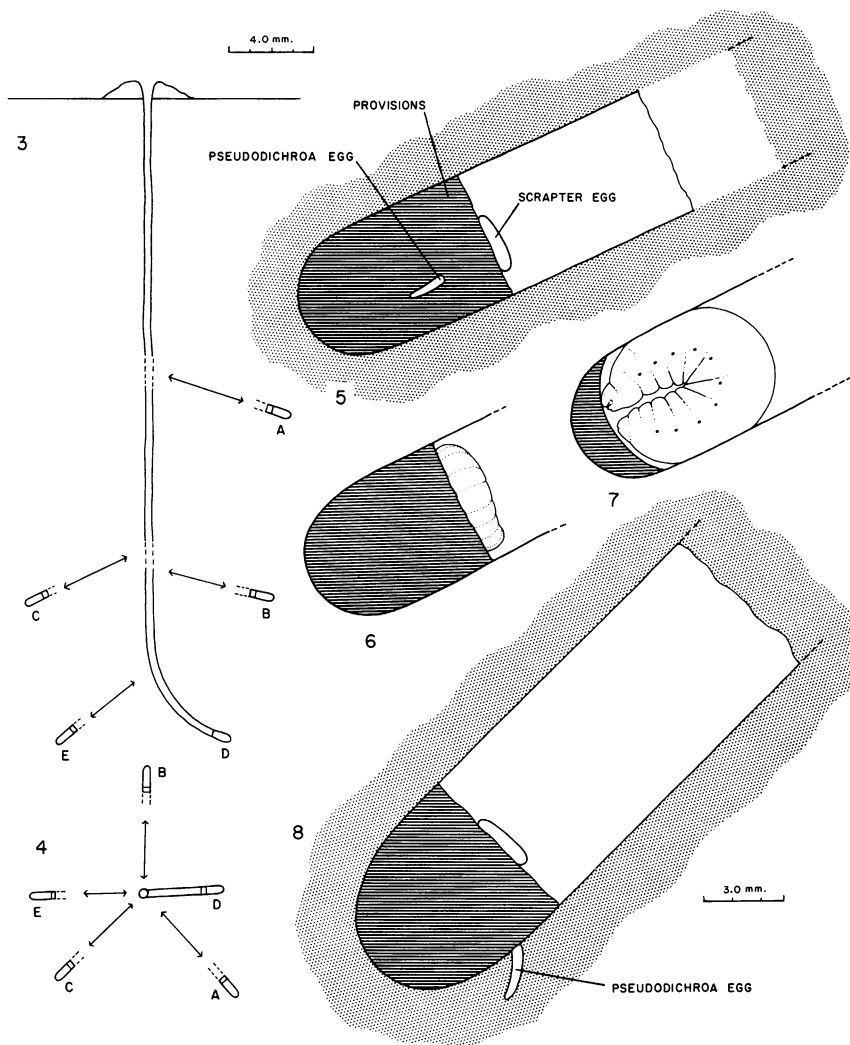
Details of the larval structure of both host and parasite will be presented in subsequent papers by the first author. Adults collected during the course of the field investigations are housed in the American Museum of Natural History and in the Snow Entomology Museum of the University of Kansas.

NESTING SITES

Scapter longula (Friese)¹ and *S. crassula* Cockerell² were found nesting just north of the small town of Kommetjie on the Cape of Good Hope Peninsula, Republic of South Africa, October 29, 1966. The nesting area was studied for several days and revisited on November 8 and 9, by which time *S. longula* was less common, and last observed December 1, when no live adults of *Scapter* were present. One site, consisting solely of *S. longula*, was situated a few yards northwest of the main road, whereas the other (fig. 1), inhabited by both species, occupied the clear area adjacent to the road, across from the first site. Both were between $\frac{1}{4}$ and $\frac{1}{2}$ mile from the ocean and were not subject to flooding by the sea. The first site was horizontal, whereas the second sloped gently; both consisted of moist, even-grained sand, white on the surface and gray beneath, with no stones and some roots. At the cell level of both species, the substratum was very moist, so that excavated sand would hold its form, but water could not be squeezed out of it by hand. The wet sand had a strong odor of decomposed organic matter. Neither site was shaded during most of the day, and only widely scattered low shrubs dotted the areas. The pollen plant of *Scapter longula* was a yellow composite growing within 40 feet of the first site; the pollen source of *S. crassula* was not discovered.

¹ Identification based on specimens of *Scapter longula* (Friese, 1912) in the British Museum (Natural History) and the United States National Museum, Smithsonian Institution.

² Compared in the British Museum, by Michener, with the type of *S. crassula* Cockerell (1932) and that of *S. turneri* Cockerell (1933a), which is the same (new synonymy).



FIGS. 3, 4. Nest of *Scapter longula*, containing five cells. 3. Side view. 4. Top view.

FIGS. 5-7. Cells of *Scapter longula*, side view. 5. Recently provisioned cell, with egg of *S. longula* inside and with egg of *Pseudodichroa capensis* attached to outside. 6. End of cell, containing intermediate stage larva. 7. Same, containing nearly mature larva.

FIG. 8. Cell of *Scapter crassula*, containing egg of *Scapter* inside and egg of *Pseudodichroa fumipennis* attached to outside, side view.

Scales refer to figures 3 and 4 and figures 5-7, respectively.

Although *Scapter alfkeni* (Friese)¹ visited flowers near these two sites, it was not found nesting there. A single nest, in a small, barren spot in a pathway that was elsewhere covered with short grass, was excavated a short distance south of Kommetjie, November 9, 1966 (fig. 2). Exposed to the sun, the ground surface sloped about 10 degrees from the horizontal, and the soil was sandy though heavily laced with roots of nearby herbs and bushes. Other burrows, perhaps belonging to the same species, were within 7 cm. of the excavated burrow but could not be studied because of limited time. The pollen plant, a yellow composite, grew abundantly as close as 1 meter from the burrow. Many individuals of this species, of a species of *Scapter* with a red and black metasoma, and of *Parapolyglossa heterodoxa* Cockerell were active in the area.

NESTS OF *Scapter longula*

Burrow entrances were widely distributed over the two sites north of Kommetjie. All were in sand and unobscured by vegetation or other objects on the ground. Although some burrows were but a few inches apart, most were scattered.

The entrances of active burrows were usually surrounded by a symmetrical or nearly symmetrical tumulus 5 to 7 cm. in diameter and 1 to 2 cm. high, although at some active nests the eroded tumulus was less pronounced. The entrances were usually open; closed entrances were presumably temporarily clogged by the excavating activities of the bee within. Each nest had a single entrance and contained only one adult bee. Because of the few cells found per nest, we believe that a female normally constructs more than one nest. Most apparently had one or two cells, although one with five cells (figs. 3, 4) was uncovered.

The simple, unlined main burrow, circular in cross section, descends nearly vertically and lacks an antechamber. One or more unlined, nearly straight laterals branch from it, either at a sharp angle or as a more gentle curve, and descend at an angle from 15 degrees to 20 degrees from the horizontal. The lowest lateral curves or angles from the bottom of the main burrow which therefore has no blind end. Each lateral,

¹ Identification was based on "types" of "*alfkeni* Brauns" in the Transvaal Museum and specimens similarly identified in the British Museum (Natural History). However, Brauns seems not to have published the name, and as far as we know it was first printed by Friese (1924), a conclusion also reached for *S. caffra* "Brauns" by Cockerell (1933b). *Scapter alfkeni* is the same as *S. macrocephala* Cockerell (1933b) (new synonymy); the type was studied by Michener in the British Museum. It is also similar to and probably conspecific with *S. striata* Smith (1853).

TABLE 1
 NEST DIMENSIONS OF *Scapter*
 (Figures in parentheses indicate the number of measurements.)

	Diameter of Main Burrow (Mm.)	Diameter of Lateral (Mm.)	Cell Depth (Cm.)	Cell Length ^a (Mm.)	Cell Diameter (Mm.)
<i>Scapter longula</i>	4.0-5.0 (7)	4.0-4.5 (3)	18-44 (18)	13.0-15.0 (5)	4.0-5.0 (5)
<i>Scapter crassula</i>	5.0-6.0 (2)	—	75-85 (5)	18.0 (1)	6.0 (3)
<i>Scapter alfkeni</i>	3.0 (1)	—	13 (1)	11.0 (1)	3.9 (1)

^a That is, the length of the lining.

of approximately the same diameter as the main burrow, runs directly to a cell. The lateral is filled with the sand presumably excavated during the construction of the next lateral and cell. The last (lowermost) lateral constructed in a nest is apparently left open.

Cell construction progresses downward in nests with several cells, so that the oldest larva is closest to the surface. A cell is constructed, provisioned, an egg deposited, and the cell is closed before the next lateral and cell are started. The long axis of the cell (fig. 3) is a continuation of the axis of the lateral burrow, so that cells also slope from 15 degrees to 20 degrees from the horizontal. The cell (fig. 5), circular in cross section, has the same diameter as the lateral. The cell walls possess no special lining except for a nearly clear, colorless, tough, single-layered, cellophane-like membrane similar to that of other colletids. This lining does not cover the cell closure, and there is a space of 3 to 4 mm. between the end of the lining and the closure. Possibly because of the granular nature of the sand no special pattern, such as a spiral, can be detected on the inner face of the closure.

The dimensions of the nest components are given in table 1.

The bright yellow-orange provisions (fig. 5), which lack a fermented odor, are stored in the rear of the cell, so that the front end of the provisions forms a flat surface perpendicular to the long axis of the cell. The length of the provisions seems quite variable, ranging from 6.0 to 8.25 mm. (three measurements). The complete provisions in a recently closed cell are dry pollen on the inside, but are moist, probably with nectar, to a depth of about 0.25 mm. on all surfaces, both the exposed one and those in contact with the cell wall. Presumably the female deposits honey on the cell wall as she stores the pollen; the exposed surface must be kept dry until just before egg deposition.

TABLE 2
EGG DIMENSIONS (IN MILLIMETERS) OF *Scapter* AND *Pseudodichroa*
(Figures in parentheses indicate the number of measurements.)

	Length	Maximum Diameter
<i>Scapter longula</i>	2.10 (1)	0.50 (1)
<i>Scapter crassula</i>	2.20 (1)	0.60 (1)
<i>Scapter alfkeni</i>	2.00 (1)	0.45 (1)
<i>Pseudodichroa capensis</i>	1.50-1.80 (5)	0.25-0.30 (5)
<i>Pseudodichroa fumipennis</i>	1.90-2.00 (5)	0.38-0.40 (5)

The single, smooth, nearly straight, semitransparent white egg (fig. 5) lies on the sticky exposed surface of the provisions. The egg is slightly larger at one end, and both ends are rounded; its dimensions are given in table 2.

The egg hatches, apparently in less than a week, and the larva curls on the surface of the pollen mass so that nearly half of its body is submerged in the semiliquid coating (fig. 6). As the larva feeds, the quantity of the liquid in the cell increases, probably by absorption of water. By alternate contraction and expansion of its body, the larva slowly moves in a circular path. The young larvae and also those of intermediate size often turn their heads to the cell opening and actively open and close their sharp-pointed mandibles. This action may provide some defense against the larvae of the parasitic bee, *Pseudodichroa*. If so, this case would be the first known, in which a host larva defended itself against cuckoo bees.

When the larva grows to the extent that its curled body touches the cell wall on all sides, it reorients, so that both its anterior and posterior ends are directed toward the mass of provisions, while its mid-part loops toward the cell opening (fig. 7). At this time the cell normally contains such a large quantity of liquid that one would expect the now-large larva to drown. In this position it presumably finishes the food. Shortly afterward, it defecates but spins no cocoon.

The cell contents of this species are attacked by such organisms as mold and nematodes, in addition to the cuckoo bee *Pseudodichroa capensis*.

NESTS OF *Scapter crassula*

This species, less common than *S. longula*, was more or less restricted to one end of the roadside nesting site, where there were no nests of *S. longula*. The entrances were approximately as dense as those of *S. longula*.

elsewhere. The sand in the nesting area of *S. crassula* was drier on the surface than that in the site of *S. longula*, but at the cell level both were very moist. There was no indication that more than one female occupied a nest.

The burrow entrances are nearly identical with those of *S. longula* but slightly larger (table 1), with the tumulus perhaps somewhat more copious. The main burrow was open in the two nests examined. It differed from that of *S. longula* not only in diameter but also in that it was lined in places with a dark material 0.5 to 0.75 mm. thick. This lining appeared to consist of sand incorporating considerable fine-grained black organic material; it was readily permeable to water and might have resulted from adherence of the dark sand below to the moist walls of the burrow as the bee ascended with freshly excavated loads.

The main burrow descended vertically and branched at various places along the way. In most cases the branches were filled with dark sand similar to the material coating the main burrow. In other places the fill was paler. In all cases the branches extended downward at an angle of 45 degrees or less from the vertical. With some, the branches apparently also divided, although the secondary branches may have been confused with filled burrows from previous years. The branches led to cells that tilted from 45 degrees to 90 degrees (i.e., vertical) from the horizontal. In contrast to *S. longula* and *alfkeni*, *S. crassula* does not leave a space between the cell closure and the cellophane-like lining of the cell; that is, the closure is in contact with the end of the lining (fig. 8).

The shape of the cell (fig. 8) is like that of *S. longula*. The wall of the cell was lined with a soft, dark material similar to the coating of the main burrow. Because of the soft nature of the moist sand in the nesting area, it was impossible to excavate the cells of any of the species without altering their shape to some extent.

The provisions, duller and darker than those of *S. longula*, occupy 6.0 mm. (two measurements) of the rear of the cell. They differ from those of *S. longula* by being a thick liquid throughout. The egg, placed on the exposed surface of the provisions, is nearly identical with that of *S. longula*; its dimensions are given in table 2. *Scapter crassula*, like *S. longula*, does not spin a cocoon, as judged by the old cells found in the nesting area.

NESTS OF *Scapter alfkeni*

The open entrance to the single nest of this species was surrounded

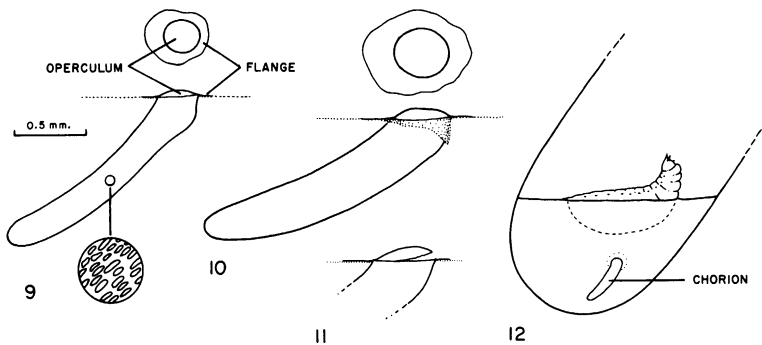
by an irregular, scanty tumulus. The main burrow descended almost vertically but was soon lost because of the difficulty of excavating through the network of roots. A single cell (table 1) was found in sand that was as moist as the cell substrate of the other two species. The cell was tilted at an angle of 20 degrees from the horizontal and was smaller than, though otherwise similar to, cells of *S. longula*. Its cellophane-like lining was open at the front end, and there was a 3.0 mm. space between it and the closure. The pollen mass, 5.0 mm. long, was like that of *S. longula* with respect to consistency and color and differed only in that the exposed surface, instead of being flat, was slightly produced in the center where it had also cracked. The egg, whitish, slightly curved, smooth, and shiny, lay with the anterior end down; its dimensions are given in table 2.

ACTIVITIES OF *PSEUDODICHROA*

The two species of this genus were encountered at the nesting sites of *Scapter longula* and *S. crassula*. The smaller, *Pseudodichroa capensis*, was recovered a number of times from the nests of *S. longula*, whereas *Pseudodichroa fumipennis* examined the burrows of *S. crassula*. Eggs and larvae of *P. capensis* and *fumipennis* were found in the nests of *S. longula* and *crassula*, respectively. The flight behavior of these two cuckoo bees was identical. Females flew low over the ground and often examined a nest entrance by alighting a short distance from it and walking to it. Usually they next flew onto a nearby stick or plant (one such plant was 6 cm. away) and stayed there motionless (up to 30 minutes), facing the nest entrance. Several times the pollen-laden *Scapter* was seen to arrive at the burrow and enter while the *Pseudodichroa* was waiting. When the host bee later left her nest, the *Pseudodichroa* flew to the entrance, walked around, and then entered. In one case two individuals of *Pseudodichroa* that had been watching the same entrance both went in immediately after the departure of the *Scapter*. From these observations, it seems that *Pseudodichroa* cannot determine whether the host bee is away from the nest without seeing it depart.

Of 17 cells of *S. longula*, five had one egg of *Pseudodichroa* each and one cell was infested with four eggs; the other 11 cells lacked such eggs. Of 17 cells of *S. crassula*, eight each had a single egg of *Pseudodichroa*, two had two eggs of *Pseudodichroa*, and seven were unparasitized. There was no indication of parasitism in the single cell of *S. alfkeni*. These rates of parasitism are high compared with those of other nomadine cleptoparasitic bees.

The egg (figs. 9, 10) in both species of cleptoparasites is long, slightly curved, whitish, with the posterior end tapering to a rounded point. The anterior end forms a convex operculum from which a nearly invisible flange radiates. The egg is inserted through a hole in the cellophane-like cell lining so that the entire egg, except for the flange and operculum, is embedded in sand. The hole is the same diameter as the end of the egg, and the flange is appressed to the cell lining on the inside of the cell. The flange seems to provide a nearly watertight seal so that liquids can neither enter nor leave the cell through the egg puncture,



FIGS. 9-12. *Pseudodichroa*. 9. Egg of *P. capensis*, top and lateral views; circle shows pattern on chorion. 10. Egg of *P. fumipennis*, top and lateral views. 11. Anterior portion of egg of *P. fumipennis* after hatching, lateral view. 12. Intermediate stage larva of *P. fumipennis* "swimming" on semiliquid provisions; note attached chorion.

Scale refers to figures 9-11.

and the connection is sufficiently strong that, if the lining is removed from the sand, the egg always remains attached. Upon hatching, the larva crawls out through a slit along the opercular margin toward the front of the cell (fig. 11). As with others of the Nomadinae, the entire chorion remains intact after the larva leaves. Both the flange and operculum are smooth or nearly so, whereas the rest of the chorion has a strong pattern (fig. 9) and is sufficiently thick that it does not collapse after hatching.

The metasoma of a specimen of *P. capensis* collected in 1920 was briefly boiled in a solution of potassium hydroxide, and eight identical egg chorions were removed from it. None contained an operculum and flange—the anterior end was open. In other respects, including the presence of sculpturing, these chorions were identical with those found

attached to *Scapter* cells. In addition there was at least one partly formed chorion that lacked sculpturing.

All eggs were inserted in the rear part of the cell, which is occupied by the provisions, so that, upon hatching, the first instar passed through the food before reaching the empty part of the cell. The posterior tip of the egg (figs. 5, 8, 12) is directed somewhat toward the rear of the cell at about a 45-degree angle, a possible requisite orienting the newly hatched larva toward the lumen.

Upon hatching, the young larva crawls toward the surface of the provisions, where it searches out and kills any siblings (if present) and the offspring of the host which, in each of the four cases examined, was a young larva and not an egg. The first instar is equipped with elongate, slender, curved mandibles, pigmented head capsule, and slender straight body. It lacks lateral body extensions, characteristic of some species of *Triepeolus*, and possesses two posterolaterally directed, eversible processes at the apex of the abdomen. This forked abdominal tip enables the first instar to push itself along. The larva is active and turns readily when touched. Often one was seen with its head pointed upward, a pose reminiscent of the first instars of the other members of the *Nomadinae*. The second-stage larva of at least *P. fumipennis* retains the forked tail but is strongly produced laterally, an adaptation presumably enabling it to float on the by now almost liquid provisions. As the larva (fig. 12) eats and molts, its venter expands. As a consequence, while the dorsum is nearly flat and flush with the surface of provisions, the venter bulges into the provisions. The dorsum is continuously rippling here and there, an activity that may help keep the spiracles free from the liquid. Although the abdominal region is expanded both laterally and ventrally, the thoracic region remains slender and surprisingly extensible. Often the older larva (fig. 12), like the first instar, reared its head high, at right angles to the body.

DISCUSSION

The nests of *Scapter* are of the general type known for the genus *Leioproctus* (*sensu lato*; see Michener, 1965), in the *Paracolletini*, in South America (for information and references, see Michener, 1957) and Australia (for references, see Michener, 1965, p. 42). The nests of *Leioproctus* have cells shaped more or less like those in *Andrena* or *Halictus*, larger in diameter than the burrows leading to them, with smooth walls of soil on which the cellophane-like secreted cell lining is deposited. On the contrary, cells of *Scapter* are of the same diameter as the burrows leading to them.

The genus *Colletes* constructs cells that, depending on the species, may or may not be larger in diameter than the burrows leading to them. Some species place cells in linear series in burrows not enlarged for the cells (see Friese, 1912b; Michener, 1957; and others). Other species put a single cell at the end of each lateral burrow. Among such species the cells may be of greater diameter than the lateral burrows, as in *C. cunicularius* (Linnaeus) (Malyshev, 1935) and *compactus* Cresson (Rozen and Favreau, in press). However, in some species that construct isolated cells, these have the same diameters as the burrows (e.g., *C. ciliatoides* Stephen, see Torchio, 1965). In this respect such nests resemble those of *Scapter*.

Cells of *Colletes* differ from those of the Paracolletini, including *Scapter*, in being closed by a cellophane-like membrane and in often being constructed rather intricately of such membranes and of fibers of the same material (Michener, 1957; Torchio, 1965; Rozen and Favreau, in press).

The provisions in *Leioproctus* consist of a ball of firm pollen with the egg laid on top of it, as in *Halictus*. In *Colletes* the provisions are semiliquid, and the egg is attached by one end to the cellophane-like lining of the cell, in the space above the provisions. In *Scapter* the situation is intermediate between that of *Leioproctus* and that of *Colletes*. The provisions fill the distal part of the cell as in *Colletes*, although they are at first firm, only later with absorption of water becoming semiliquid. The egg, however, is laid on top of the provisions as in *Leioproctus*.

In most biological respects *Pseudodichroa* is similar to other genera of the Nomadinae. Like those of other nomadines, the females of *Pseudodichroa* search for burrows by flying low over the surface of the ground. They differ from *Neopasites*, *Holcopasites*, and *Oreopasites*, New World relatives, by spending more time waiting at nest entrances and less time flying from burrow to burrow. As with other nomadines, eggs are embedded in the cell wall. Superficially the position of the egg and its form resemble those of *Triepeolus remigatus* (Fabricius) (Bohart, 1966) and *Epeolus pusillus* Cresson (Rozen and Favreau, in press) in that the anterior apex (operculum) of each egg appears nearly flush with the cell wall. Like the egg of *E. pusillus*, but unlike that of *T. remigatus*, it gradually tapers posteriorly, and it intersects the cell wall at an acute angle so that its anterior end is directed toward the front of the cell. It differs from all known nomadine eggs by having a flat flange that radiates from the operculum.

The slender, crawling first instar, with prognathous, pigmented head capsule and large sickle-shaped mandibles, is similar to the first instars

of other nomadines. It seeks out and destroys the young larva of the host. As with all parasitic bees, the larval stage feeds on the provisions supplied by the host female. As with other nomadines, the instars that follow the first have a far less modified head capsule than does the first. The subsequent instars of *Pseudodichroa* are unique in their navicular shape, an apparent adaptation for floating on the semiliquid provisions.

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