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Ecology, Behavior, and Mature Larva of a New Species of the Old World Bee Genus *Camptopoeum* (Andrenidae: Panurginae)

JEROME G. ROZEN, JR.[1]

ABSTRACT

The nesting biology of *Camptopoeum bakeri* Rozen, new species, is described and compared with accounts in the literature dealing with congeners, all of which nest in the ground. Subjects include ecological conditions of the nest site, nest architecture, provisioning, development, and cuckoo bee parasitism. As the first treatment of the immatures of the genus, its mature larva is described and compared with other known panurgine larvae. The taxonomic description of the adult is included at the end.

INTRODUCTION

Because little has been recorded about the nesting biology of the bees in the Palearctic genus *Camptopoeum* (Rozen, 1967), the following information is presented concerning a heretofore unknown species in the genus. *Camptopoeum bakeri,* formally described below, was one of three species of *Camptopoeum* flying in the vicinity of Quetta, Baluchistan, Pakistan, during May 1984. Its last-stage larva is also described, the first such account for any member of the genus.

I follow the traditional classification (Michener, 1944; Rozen, 1965) of the Panurginae rather than that of Warncke (1972). Ruz (1987) in a recent analysis of the cladistic relationships of the Panurginae showed that *Camptopoeum* belongs to the monophyletic assemblage of Old World genera (including *Panurginus* which also occurs in the New World). Where possible, comparisons are made with these Old World forms below.

Specimens of *Camptopoeum* and a possibly associated ammobatine cuckoo bee are in the collections of the American Museum of Natural History, the National Museum of Natural History, and Donald B. Baker. The

[1] Curator, Department of Entomology, American Museum of Natural History.

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Fig. 1. *Camptopoeum bakeri,* nesting site, near Pishin, Baluchistan, Pakistan. Nests widely scattered in this field.

larvae and cell samples are in the American Museum of Natural History.

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The following persons contributed substantially to the fieldwork for this project: Ronald J. McGinley, National Museum of Natural History; Sarfraz Lodhi, American Museum of Natural History; and Ian Stupakoff, a student at City College of the City University of New York.

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This manuscript has been critically reviewed by Dr. Beth B. Norden, Smithsonian Institution, Dr. Alvin H. Shinn, William Paterson College of New Jersey, and Mr. Donald B. Baker, Surrey, England.

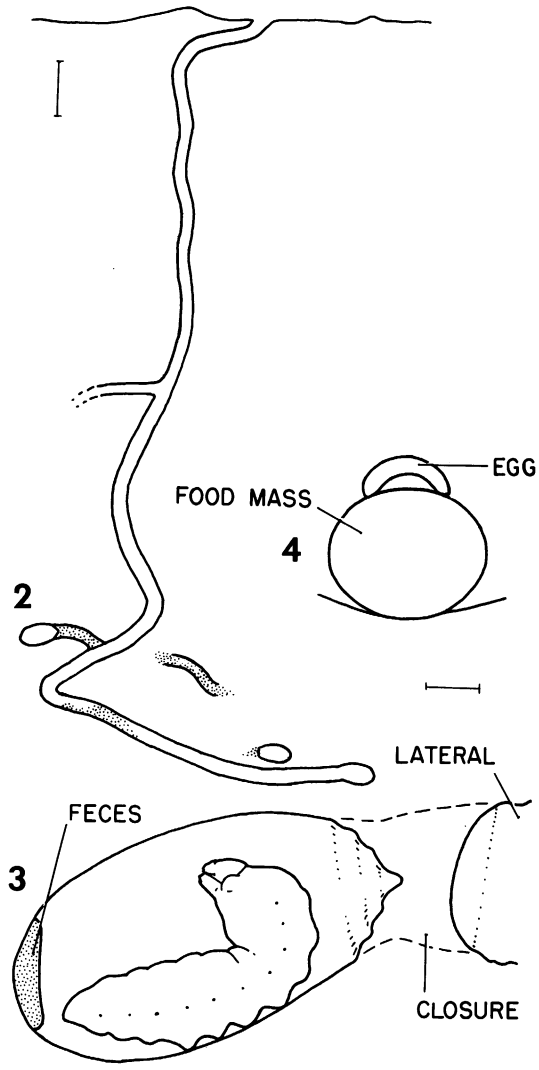
NESTING BIOLOGY

Numerous females of *Camptopoeum bakeri* foraged on the thistle, *Cousinia bipinnata* Boisier, at Pishin, 40 km north of Quetta, Baluchistan, Pakistan, on May 23, 1984. However, only three females were discovered entering the ground over a three-day period. Two were found about 50 m from one another on May 25, and the third, 100 m away, on May 27. The first nest tunnel entered a crack in the soil but was lost; the other two led to nests. All were in the immediate vicinity of the thistle. The following notes refer to the

two completely excavated nests, each of which contained a single female.

DESCRIPTION OF NESTING AREA: Pishin, somewhat less than 2000 m in elevation, is an agricultural area in a shallow drainage system surrounded by desert. Annual precipitation (100 to 200 mm) is restricted to the winter months, and the mean annual temperature is approximately 7°C. The forage plant and nests occurred in a vast fallow field (fig. 1) hundreds of meters long and wide, lacking trees except along the road that bordered it on one side. Although Friese (1926) reported that *Camptopoeum frontale* (Fabricius) and also *C. friesei* Mocsary nested in sloping and even vertical surfaces, the terrain at Pishin was horizontal. Previously tilled, the field was now fallow and dominated by several species of plants blooming at the time of this investigation. The most common was an unidentified red-flowered legume, and second most common was *Cousinia bipinnata.* The low-growing vegetation (generally less than 0.5 m tall) with few leaves and covering less than 50 percent of the ground surface provided little shade. The soil, often with a thin crust on the surface, was less consolidated below (almost powdery in places) and compact, hard, and dry at the cell level. We collected many species of bees at this locality, including a few foraging *Camptopoeum schewyrewi* Morawitz on *C. bipinnata.*

The entrance (fig. 2) of the first nest was open, devoid of tumulus, and appeared slightly elongate because the entrance tunnel ran obliquely for 1.5 cm just below the surface before descending vertically. Its tunnel, 2.0 mm in diameter and circular in cross section, was open and without plugs of soil at the upper levels. Although it appeared to branch at about 7 cm in depth, the branch became narrow and may have been a tunnel of some other insect. Several filled tunnels, intersecting the main burrow between the depth of 10 and 12 cm, may have been from a previous generation of bees. The main tunnel below the 8 cm level became wider and remained 3.0 mm in diameter to its end. The lower part of the tunnel wall was possibly coated with a fine lining of slightly harder material than the surrounding soil. This lining, if indeed different from the substrate, was nevertheless water absorbent when tested with



Figs. 2–4. *Camptopoeum bakeri.* **2.** Nest number 1, side view. **3.** Cell and closure showing fecal mass and postdefecating larva, side view. Lateral portrayed as if fill had been removed. **4.** Pollen mass and egg, side view. Scales = 1 cm (fig. 2) and 1 mm (figs. 3, 4).

a water droplet. The main tunnel, more meandering below 10 cm, was open most of the way but was loosely filled in the vicinity of the two lower cells.

The upper cell (fig. 3), at the depth of about 12 cm, contained a postdefecating larva and was connected to the tunnel by a short, filled lateral 1 cm long and 3.0 mm in diameter. Another cell, about 14 cm deep, also closely adjoined the main burrow and contained a

pollen mass and egg. The open third cell held unworked loads of provisions as discussed below. Because the larva was completely quiescent and the fecal mass completely dry and black, the postdefecating larva may have been the progeny of the previous generation; this would also account for the great disparity between the life stages in this single nest.

The entrance to the second nest, in a narrow crack in the soil, was not found, but the open main tunnel was uncovered 8 cm below the surface. It descended at about a 45° angle, and the first cell, containing a first instar, was discovered at the 17 cm level. It was connected to the main tunnel by a filled lateral, more than 4 cm long and bent sideways at nearly 45°. This lateral generally descended but rose again shortly in front of the cell. The main tunnel bent sharply at the point where the lateral diverged, and continued to descend at about 45°. The second cell, containing an egg, at a depth of about 18 cm, was far removed from the first, and was connected to the main tunnel by a filled lateral no more than 1 cm long. Shortly below this connection the main tunnel turned again and rose somewhat before opening into the cell at a depth of about 19 cm. This cell contained unworked loads of provisions, just as was the case with the lowest cell in the first nest. In this species, laterals may normally rise before joining the cells, because even closed cells with short laterals tended to be higher than the obliquely descending main tunnels. Overall nest configuration needs further study before it is understood.

Nearly horizontal, cells (fig. 3) in both nests were elongate ovoids; one tilted about 20° from horizontal, the front end higher than the rear. A closed cell measured 6.5 mm long from its rear to the outer rim of the closure; an open cell, 7.2 mm long from its rear to the constriction at the entrance. Four cells ranged in maximum diameter from 3.7 to 4.0 mm. The ceiling of at least one (fig. 3) was clearly somewhat vaulted compared with the floor, and the plane of its closure was not at right angles to the long axis of the cell. The inner surfaces of the cells were smooth, as pale as the surrounding soil, and gave no indication of having a special soil lining. Presumably lined with a transparent secretion, cells were water retardant at the rear and somewhat so on the sides but readily absorbent to water droplets placed on the ceiling.

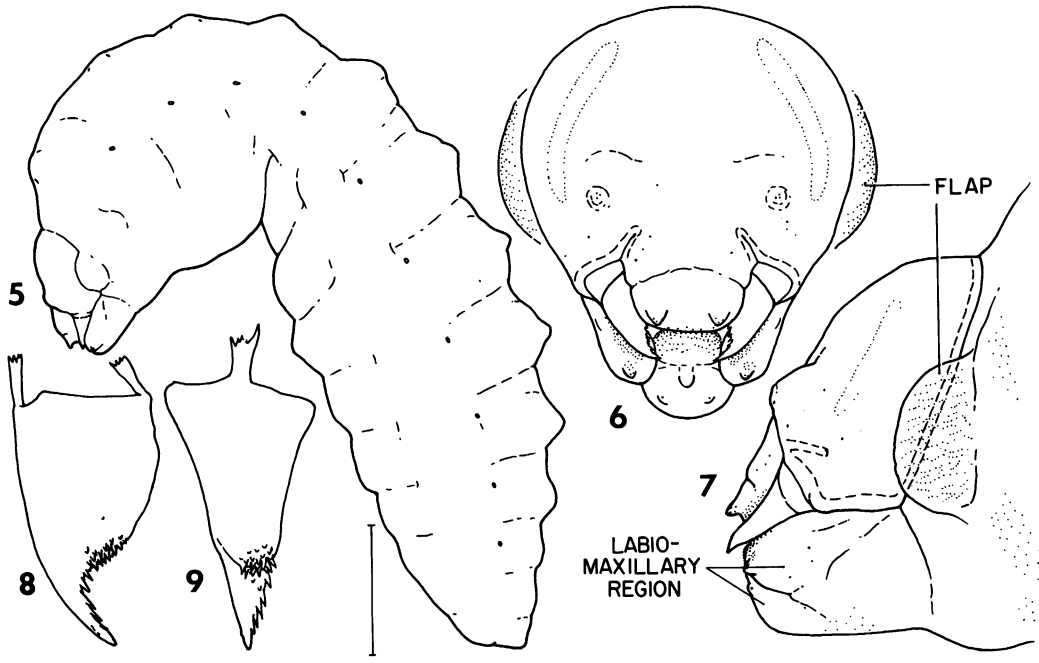
Two cell closures (fig. 3) were deeply concave (almost conical) on the inside where they were vaguely spiraled, with three to four coils to the radius. The outer surface of one closure was clearly specially worked, being very smooth, and evenly concave. This surface was absorbent to a water droplet. The closure was 1.0 mm thick at the middle and about 3.0 mm at the periphery.

PROVISIONING: Many species of *Camptopoeum* seem to be restricted to gathering pollen from thistles. Friese (1926) reported that *C. frontale* foraged on flowers of *Centaurea* and *C. friesei* foraged on *Carduus*. Both *C. bakeri* and *schewyrewi* gathered from *Cousinia bipinnata* at Pishin, and I collected a male and female of *C. persicum* Cockerell on an unidentified thistle at Jalogir, a small village between Pishin and Quetta, on May 16, 1984.

One open cell contained 10 oblong, moist pollen masses, obviously each representing the load from one hind leg. Hence the female had completed five foraging trips and presumably was leaving for the sixth when we captured her. One completed food mass (fig. 4) was a flattened sphere, 3.2 mm in maximum diameter and 2.5 mm high. Tan and dull on the surface, it was not coated with either a waterproof secretion or sticky nectar, and was homogeneously mealy-moist throughout, as were the leg loads. Unfortunately the position of the provisions in the cell could not be determined. Another food mass, conforming to the above description in every way, seemed to rest on the middle floor of the cell.

DEVELOPMENT: Both eggs (fig. 4) were elongate and arched, and one measured 1.8 mm long and 0.4 mm in maximum diameter. Each was shiny whitish, and attached by its anterior and posterior ends centrally on top of the provisions.

As in other panurgines, development of *Camptopoeum bakeri* is probably rapid. Because of the seasonality of precipitation and flowering, this species is predicted to undergo only one generation a year, as has been reported by Friese (1926) for European congeners.



Figs. 5–9. *Camptopoeum bakeri,* postdefecating larva. **5.** Entire larva, drawn live, side view. **6.** Head, frontal view. **7.** Head, lateral view. **8.** Left mandible, ventral view. **9.** Left mandible, adoral view. Scale (fig. 5) = 1 mm.

The postdefecating larva (fig. 3) rested on its dorsum in the cell, with its head near the cell closure. Completely quiescent, the larva had not spun a cocoon, as is also characteristic of *Camptopoeum friesei* (Friese, 1926) and all known Panurginae. The single black dried fecal mass was attached to the rear of the cell. Disk-shaped, it was 2.2 mm in diameter, 0.5 mm thick, and surprisingly small considering the large size of the cell and larva.

ADULT ACTIVITY

Females of this species were observed foraging between 10 A.M. and 3 P.M. on clear warm days and may have been active both earlier and later. Their foraging flight, slow and deliberate from flower to flower, was not accompanied by obvious buzzing as in some other panurgines. Females transported pollen as a moist mass on only the anterior surface of the hind tibiae. This is in sharp contrast to the "bracelet" of moist provisions surrounding the hind tibia of *Nomadopsis* (Rozen, 1958) and some other panurgines.

No matings were observed and only a few males were collected visiting flowers, in contrast to numerous females seen and sampled.

PARASITISM

No parasites, parasitoids, or cleptoparasites were associated with nests, but females of an undescribed *Ammobates* cuckoo bee (identified by Donald B. Baker) occasionally patrolled the ground in the vicinity, and may have been nest associates of this bee.

Mature Larva, *Camptopoeum bakeri*
Figures 5–7

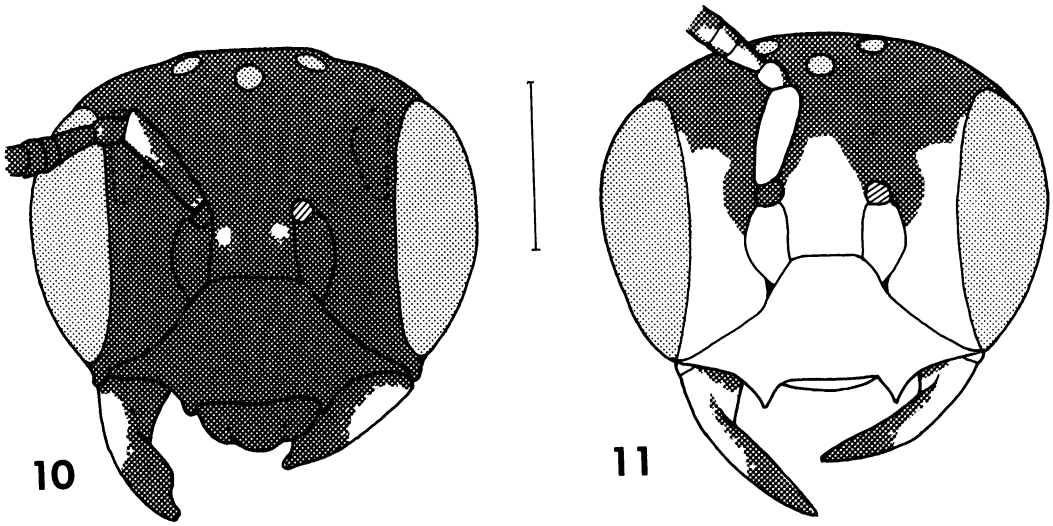
DIAGNOSIS: Larvae of this species can be distinguished from those of all other known panurgine genera by the flap of integument that projects forward and is appressed to each side of the head (figs. 6, 7). In addition, the larva of *Camptopoeum bakeri* can be differentiated from the larvae of each of the other Old World panurgine genera as follows (characters of the other genus given first, followed by features of *C. bakeri* given in parentheses): *Melitturga* (Rozen, 1965, 1971) (three species

examined): mandible apically bidentate, with single large cuspal tooth in addition to numerous normal-size teeth; maxillary palpus large; well-developed paired dorsal body tubercles on most segments and especially on anterior segments (mandible apically simple, without large cuspal tooth; maxillary palpus moderately small; paired dorsal body tubercles low, best developed on middle body segments). *Meliturgula* (Rozen, 1968) (two species examined) and *Poecilomelitta*[2] (larva of one species examined but not yet described): anterior body segments with pronounced dorsal tubercles; gena produced into low, rounded tubercle just above posterior mandibular articulation (gena normal, scarcely produced). *Panurgus* (Rozen, 1971; Rozen and Rozen, 1966) (four species examined): clypeus elongate; mandibular cusp projecting strongly ventrally (clypeus normally short; cusp not projecting ventrally). *Panurginus* (Rozen 1966, 1971) (four species examined): maxillary palpus large and down-curved; labium receding; tenth abdominal dorsum rounded, not projecting posteriorly beyond venter (maxillary palpus moderately small and not distinctly down-curved; labium strongly developed; tenth abdominal dorsum projecting posteriorly beyond venter). *Epimethea*: larva unknown but probably similar to that of *Camptopoeum*. *Mermiglossa* and *Plesiopanurgus*: larvae still unknown.

DESCRIPTION: *Head* (figs. 6, 7). Integument without setae but with scattered sensilla, unpigmented except for mandibular apexes, anterior tentorial arms, maxillary palpi, and labial palpi. Vertex not greatly produced on each side above antenna, gently rounded in profile (fig. 7); antenna arising from moderately low prominence; clypeus normally short; gena produced slightly just above posterior mandibular articulation. Tentorium complete and well developed; posterior thickening of head capsule and hypostomal ridge well developed; pleurostomal ridge weak; epistomal ridge below anterior tentorial pit well developed, mesad of pits absent; parietal bands faint. Unlike in any other known panurgine larva, anterior projection of integument immediately behind posterior thickening of head capsule extending forward as flattened, striospiculated flap obscuring posterior thickening above posterior tentorial pit (fig. 7). Each antenna a low convexity bearing three sensilla. Labrum bearing two moderate-sized tubercles; epipharynx spiculate laterally. Mandible (figs. 8, 9) moderately slender; apex slender and simple (i.e., without subapical tooth); upper apical margin serrate; lower margin nonserrate except for one or two minute denticles near apex; cusp moderately produced adorally, without large tooth as in *Melitturga,* not produced ventrally; cuspal teeth numerous; dorsal surface apparently nonspiculate basad of cusp. Maxilla, as seen in lateral view, projecting at most slightly beyond apex of labium; palpus moderately small, less conspicuous than labral tubercle; palpus not clearly directed downward; dorsal surface of maxilla spiculate, of palpus minutely spiculate. Hypopharynx spiculate but less so near hypopharyngeal groove; hypopharyngeal groove somewhat indistinct. Labium incompletely divided into prementum and postmentum; labial apex strongly projecting in comparison with other known panurgines, somewhat similar to that of *Meliturgula,* but entire labiomaxillary region of *Camptopoeum bakeri* more projecting and longer than that of *Meliturgula* or any other known panurgine larva with possible exception of some *Perdita*; labial palpus smaller than maxillary palpus. Salivary opening a distinct curved slit more or less extending to hypopharyngeal groove.

Body (fig. 5). Live and preserved larvae pale cream color. Much of integument finely spiculate; tenth abdominal segment at least not conspicuously spiculate, perhaps nonspiculate. Paired dorsal tubercles very low, rounded, not transverse; their apexes at most indistinctly spiculate; on postdefecating larva, tubercles scarcely evident on anterior and posterior body segments, more evident on middle body segments; pleural regions not produced; intersegmental lines shallowly incised; tenth abdominal dorsum projecting somewhat posteriorly. Spiracles with atrium projecting above body wall; atrial wall without teeth; peritreme present; primary tracheal

[2] Information on nesting biology as well as larval and adult anatomy suggests that these two genera may not be distinct, although Baker (1972) points out that there are major differences in male genitalia.



Figs. 10, 11. *Camptopoeum bakeri,* head, adult, frontal view, diagrammatic. **10.** Female. **11.** Male. Scale = 1 mm.

opening with collar; subatrium moderate in length. Sexual characteristics unknown.

MATERIAL STUDIED: One postdefecating larva. Pishin, Baluchistan, Pakistan, May 25, 1984, J. G. Rozen, R. J. McGinley, S. Lodhi, I. Stupakoff. Nest no. 2, larva preserved July 5, 1984.

REMARKS: This larva agrees closely with the description of the subfamily presented by Rozen (1966), and reflects the fact that *Camptopoeum* is a "typical" panurgine. The distinguishing features of the larva tend to be idiosyncratic (autapomorphies) and do not seem to give clues as to the relationship of the genus to other Old World genera, which are themselves distinctive from one another (except for *Meliturgula* and *Poecilomelitta,* and ignoring *Epimethea* which will probably be similar to *Camptopoeum*). A cursory survey revealed no obvious close relationships between *Camptopoeum* and New World genera on the basis of larvae. A detailed global phylogenetic analysis awaits descriptions of more of the New World groups, particularly from South America.

Adult, ***Camptopoeum bakeri,*** new species

Figures 10–16

DIAGNOSIS: This species is similar to *Camptopoeum persicum.* Females of *bakeri* can be identified by their completely black clypeus (fig. 10) and paraocular areas; the only maculation on the head is a poorly defined pale mark on the supraclypeal area. Metasomal tergum V is usually completely black but if with maculations these light areas are irregular, small marks and do not form a distinct band as in females of *persicum, frontale,* and *schewyrewi.* The relatively smooth labrum of the female also immediately sets off the species from these others as described below. Males of *bakeri* can be distinguished from those of *persicum* by their shiny, more glabrous, less punctate yellow areas on the face and by the length of the first flagellomere being approximately 1.4 times maximum width. Males of *persicum* have a greater number of more conspicuous hairs on the face, the discal area of the clypeus is more punctate, and the first flagellomere is slightly shorter than its maximum diameter. Both males and females of *bakeri* are unusual because of their very long maxillae and labia, longer than those of *persicum, frontale, friesei,* and *schewyrewi.*

DESCRIPTION, FEMALE: Body length 5.7–6.2 mm (N = 159); length of forewing measured from apex of costal sclerite to wing tip: mean = 4.16 ± 0.19 mm (N = 20), holotype 4.5 mm.

Coloration. Integumental background col-

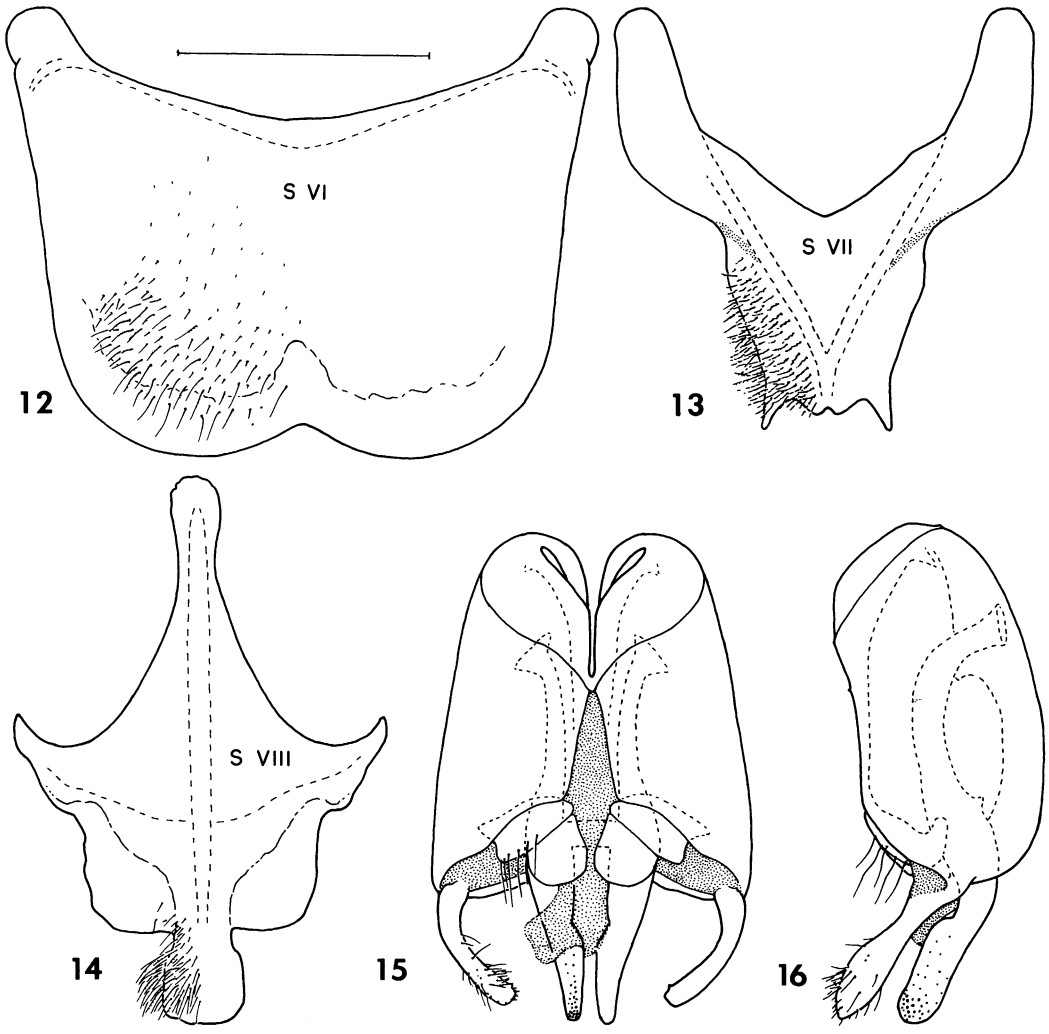
or very dark brown to black except metasomal venter brown to dark brown. Light maculations of head, mesosoma, metasoma pale cream color, about same hue as those of *Camptopoeum persicum* and *frontale,* less yellow than those of *schewyrewi.* Following cephalic areas maculate: supraclypeal area where maculation always poorly delineated and infuscated but most evident laterad of median line (in holotype, supraclypeal maculation reduced to two poorly delineated pale spots immediately below antennal sockets) (fig. 10); ventral surface of scape where pale maculations usually reduced to small tawny basal area and variably sized, more distinct apical maculation (rarely apical maculation extending to basal one). Pedicel usually with small indistinct apical maculation; flagellum brownish becoming tawny toward apex, without distinct pale maculations; bases of mandibles maculate. Following mesosomal areas maculate: posterior margin of pronotum except usually for median interruption; pronotal lobes; posterior edge of scutellar crest; rarely posterior margin of scutellum where maculations, when present, appear as irregular markings (in holotype these markings reduced to pair of barely visible lateral tawny spots); all of metanotum. Fore and middle femora with pale maculation at extreme apex; outer surface of fore and middle tibiae pale at base gradually darkening toward apex to tawny or light brown; inner surface of same infuscated; fore and middle tarsi tawny; hind tibia and tarsus pale brownish. Tegulae transparent except for basal opaque pale maculation; wings hyaline, at most faintly infuscated. Metasomal tergal pale bands narrow, rarely briefly interrupted, present on segments I–IV; tergum V usually completely dark, but very rarely with irregular, nonbandlike maculations; area basad of bands opaque very dark brown to black; marginal areas semitransparent brown; metasomal sterna without maculations.

Head. When seen from front (fig. 10), tangent of upper orbits immediately below level of median ocellus; lateral ocelli nearly reaching top of vertex, separated from vertex by less than diameter of median ocellus; facial foveae elongate, approximately three times as long as maximum width; lower median margin of clypeus well below level of lower orbits; clypeal disc weakly punctate, with very few setae; setae laterad of antennal sockets sparser and less plumose than those of *Camptopoeum persicum*; upper frontal area with setae numerous, decumbent, and so short and so appressed to integument that integument appears dull at first glance; these setae contrasting sharply with erect, very plumose setae of vertex behind ocelli. Basal smooth triangular area of labrum not set off from punctate, setose rest of labrum by ridge or carina; apex of triangle not projecting; hence labrum contrasting with that of *persicum, frontale,* and *schewyrewi* all of which have triangular area at least apically set off by sharp ridge and projecting median apex. Galea extremely long so that in repose tip of galea extending well beyond base of prementum and so that length of galea between insertion of maxillary palpus and tip approximately 1.5 times length of prementum; dorsal surface of galea strongly papillate, dull.

Mesosoma and Metasoma. Mesoscutum shiny, with setae very short, inconspicuous and punctures reduced in size and numbers so that area between tegulae with only scattered punctures; hence scutum shinier and more glabrous than that of *persicum, frontale,* or *schewyrewi*; ventral median groove of thorax deeper and more conspicuous than those of these other species, and with ventral episternal setae longer; these setae directed posteromedially.

DESCRIPTION, MALE: Body length 6.0–7.0 mm (N = 2); length of forewing measured from apex of costal sclerite to wing tip 3.9 (allotype)–4.4 mm (N = 2).

Coloration. Integumental background color (including that of metasomal venter) very dark brown to black. Light maculations of head, mesosoma, metasoma, and legs pale cream color, about same hue as those of *Camptopoeum persicum* and *frontale,* less yellow than those of *schewyrewi* and *friesei.* Following cephalic areas maculate: clypeus, subantennal areas, paraocular areas to well above level of subantennal sockets (fig. 11), supraclypeal area to well above antennal sockets (fig. 11) but not reaching median ocellus (dark frontal area reaching down laterad of antennal socket and outer subantennal suture on each side, fig. 11); ventral surface of scape (except for basal ball), pedicel, and first



Figs. 12–16. *Camptopoeum bakeri,* male, setae and sensilla shown on left. **12.** Metasomal sternum VI. **13.** Metasomal sternum VII. **14.** Metasomal sternum VIII. **15, 16.** Genitalia. All ventral views except figure 16, lateral view. Scale (all figures) = 0.5 mm.

three flagellomeres (other flagellomeres tawny), labrum, bases of mandibles. Following mesosomal areas maculate: entire posterior margin of pronotum; pronotal lobes; posterior edge of scutellar crest; most of metanotum. Fore coxa with small anteromesal pale maculation; fore trochanter with small apical pale ring or mark; apical one-third of fore femur maculate; all of fore tibia light except for vague dark area on inner surface; fore tarsus maculate except gradually darkening to tawny apically; middle leg as described for fore leg except coxa and trochanter completely dark; hind coxa and trochanter each with small apical light area; apical area of hind femur and all of tibia light; tarsus light, gradually turning tawny apically. Tegulae and wings as described for female. Metasomal tergal pale bands narrow, uninterrupted medially; area basad of bands opaque, very dark brown to black; marginal areas semitransparent, nonpigmented so that integument of following segment visible. Metasomal sterna without maculations.

Head. When seen from front (fig. 11), tangent of upper orbits slightly below level of

median ocellus; lateral ocelli nearly reaching top of vertex; lower margin of clypeus well below level of lower orbits. Clypeal disc weakly punctate so that integument appears shiny; setae of clypeus small, sparse, thin. Antenna elongate, so that first flagellomere 1.4 times maximum width. Galea as described for female.

Mesosoma. Mesoscutum covered with moderate-length, erect, conspicuously plumose, grayish pubescence so that integument partly obscured; this pubescence similar to that of vertex, gena, and mesepisternum.

Metasoma. Apical sterna and genitalia as illustrated (figs. 12–16); some setae on sterna VI and VIII plumose, those of sternum VII very plumose.

TYPES: *Holotype female:* Pakistan: Baluchistan Province, Pishin, 40 km north of Quetta, May 25, 1984 (Rozen, Lodhi, Stupakoff); allotype, same except May 27, 1984. *Paratypes:* 157 female and 2 male, same locality, May 23 to 27, many on thistle, collected by S. Lodhi, R. J. McGinley, J. G. Rozen, and I. Stupakoff; 1 female, Pakistan: Baluchistan Province, Pringabad, south of Quetta, on coriander, R. J. McGinley. Holotype and allotype in the American Museum of Natural History; paratypes primarily in the American Museum of Natural History and the Smithsonian Institution.

ETYMOLOGY: This species is named in honor of Donald B. Baker, an eminent authority on Palearctic bees, who first recognized this species as undescribed.

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