Immatures of The Solitary Bee Camptopoeum Friesei (Andrenidae: Panurginae: Panurgini) and of Its Cleptoparasite Parammobatodes Minutus (Apidae: Nomadinae: Ammobatini)

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Immatures of the Solitary Bee *Camptopoeum friesei* (Andrenidae: Panurginae: Panurgini) and of its Cleptoparasite *Parammobatodes minutus* (Apidae: Nomadinae: Ammobatini)

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ABSTRACT

Descriptions of the mature larva and pupa of *Camptopoeum* (*Camptopoeum*) *friesei* Mocsáry are presented as are the descriptions of the mature oocytes and postdefecating larva of its cleptoparasite, *Parammobatodes minutus* (Mocsáry). The larva of *C. friesei* is compared to that of *C.* (*Camptopoeum*) *clypeare* Morawitz and *C.* (*Camptopoeum*) *frontale* (Fabricius), as is the mature oocyte of *P. minutus* with that of *P. rozeni* Schwarz. The descriptions of the pupa of *C. friesei* and the mature larva of *P. minutus* are the first such accounts for their respective genera.

INTRODUCTION

This paper presents new information concerning the immature stages of two distantly related bees whose lives are intertwined: the solitary andrenid bee *Camptopoeum* (*Camptopoeum*) *friesei* Mocsáry and its nomadine cleptoparasite *Parammobatodes minutus* (Mocsáry). The mature larvae of only two species of *Camptopoeum* have been described to date (Dorn, 1971; Rozen, 1988), and no pupa of the genus has been studied. Herein I describe the mature larva and pupa of *C. friesei*, and compare them with immatures of related taxa. Neither the larva nor pupa of any species of *Parammobatodes* has been described and illustrated, although the mature oocyte of *P. rozeni* Schwarz was studied (Rozen and Özbek, 2003). While the pupa of the genus remains unknown, the mature larva of *P. minutus* is described below and compared with those of other ammobatines, as is its mature oocyte. This new information would not be available now without the field efforts of the persons acknowledged at the end of this paper.

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The egg of *Parammobatodes minutus* will eventually be found embedded in the cell wall of its host, as is characteristic of all Nomadinae (Michener, 2007). The cleptoparasitic association of *P. minutus* with *C.* (*Camptopoeum*) *frontale* (Fabricius) has been long known (e.g., Friese, 1923), and Warncke (1983) recorded *C. friesei* as another host. Retrieval of the larva of *P. minutus* from the nest of *C. friesei* now confirms that association.

METHODS AND TERMINOLOGY

Some specimens were examined with a Hitachi S-5700 scanning electron microscope (SEM) after being critical-point dried and coated with gold/palladium. Others were decapitated, and heads and bodies were then cleared in an aqueous solution of sodium hydroxide, stained with Chlorazol E Black, and examined while in glycerin with light microscopes.

As pointed out elsewhere (Rozen, 2008), a thin, transparent secretion covers the post-defecating larvae of panurgines (as well as of other bees), which, after drying, possibly affords protection against desiccation during diapause. This material, of unknown origin, is generally not noticed when specimens are examined with a light microscope but obscures integumental sculpturing and other microscopic surface features when specimens are coated with gold/palladium for SEM evaluation. I had originally assumed that the secretion appeared as the larva entered diapause, for younger last larval instars seemed to be free of it. However, figure 8 is of a predefecating larva, and, as can be seen in figure 11, the thin secretion was inadvertently torn away from the lower part of the right maxillary apex, revealing the deeply wrinkled integument beneath. This suggests that the secretion appears earlier than the onset of diapause, but, since the specimen was clearly less covered than a diapausing larva (fig. 6), it may also indicate that the application of the material is accomplished slowly during the last larval stadium. SEM studies of last larval instars of various known ages should yield insight into this matter. Similarly, dissections of last larval instars to reveal the condition of their salivary glands before and after this coating substance is applied might determine
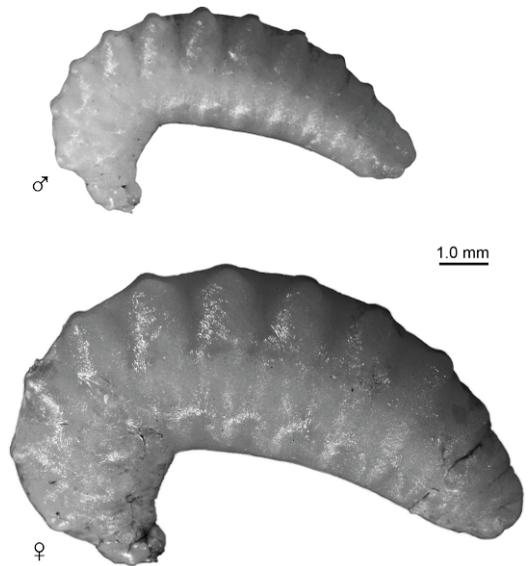

Fig. 1. Macrophotograph of male (above) and female (below) postdefecating larvae of *Camptopoeum friesei*, lateral views; scale (= 1.0 mm) refers to both figures.

whether the salivary glands are the source of the coating and possibly explain the peculiar sculpturing of the integument surrounded by the U-shaped salivary opening (fig. 12).

The term *verrucose* (meaning wartlike texture) used below refers to deeply wrinkled integument. Etymologically and entomologically it is akin to *varicose* (meaning swollen, lumpy) used in describing a specialized, raised, somewhat wrinkled patch of integument on the pupa also treated below. On some bee pupae, such wrinkled integument seems to be found on parts of the anatomy that contact the substrate. As used here, these terms express differences in degree of wrinkling more than anything else, although the function of the very deep wrinkling of the verrucose labiomaxillary area almost certainly serves a different purpose from that of the milder wrinkling of varicose areas on bee pupae.

MATURE LARVAE OF *CAMPTOPOEUM FRIESEI*

Figures 1–15

Dorn (1971) described the mature larva of *Camptopoeum* (*C.*) *frontale*, as did Rozen
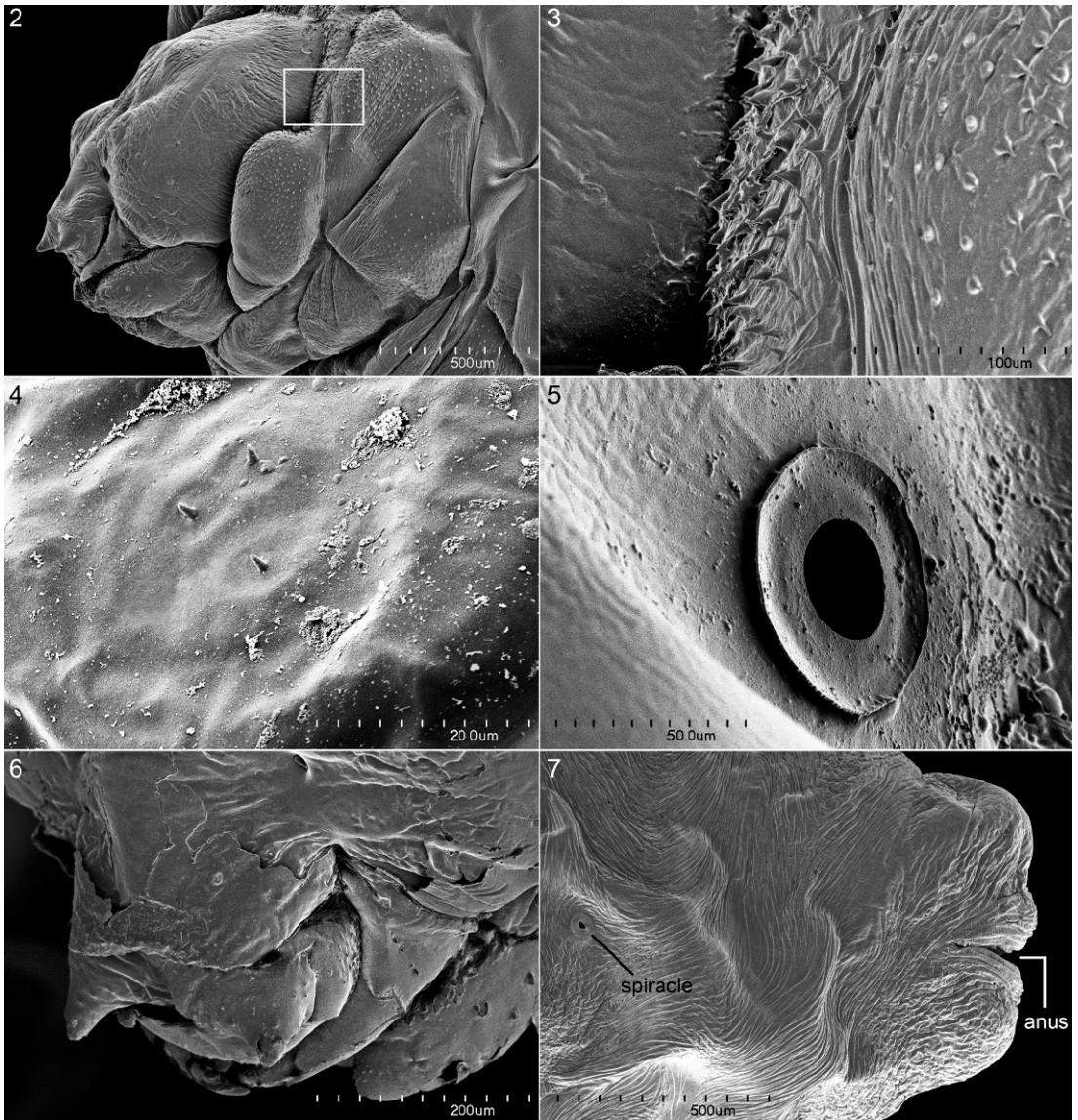
Figs. 2–7. SEM micrographs of last larval instar of *Camptopoeum friesei*. **2.** Head and prothorax of predefecating larva, near lateral view. **3.** Close-up of integument identified by rectangle in fig. 2, showing spiculation. **4.** Antennal papilla of same, showing lack of projection and three cone-shaped sensilla. **5.** Spiracle of same, showing saucerlike peritreme and projecting rim. **6.** Clypeus and mouthparts of postdefecating larva after sonication, demonstrating thick coating of secretion only partly removed by sonication. **7.** Apex of abdomen of postdefecating larva, lateral view, showing wrinkling of integument, left spiracle of abdominal segment 8, and anus on segment 10.

(1988) for the postdefecating larva of *C. (C.) clypeare* Morawitz (as *C. bakeri* Rozen, fide Patiny, 1999). The following description of the larva of *C. friesei* refers to both the post-defecating and predefecating forms.

DIAGNOSIS: *Camptopoeum friesei*, like *C. clypeare* (Rozen, 1988) and presumably *C. frontale* (Dorn, 1971: fig. 1B), can be distinguished as mature larvae from those of other known panurgines by the conspicuous, pillow-
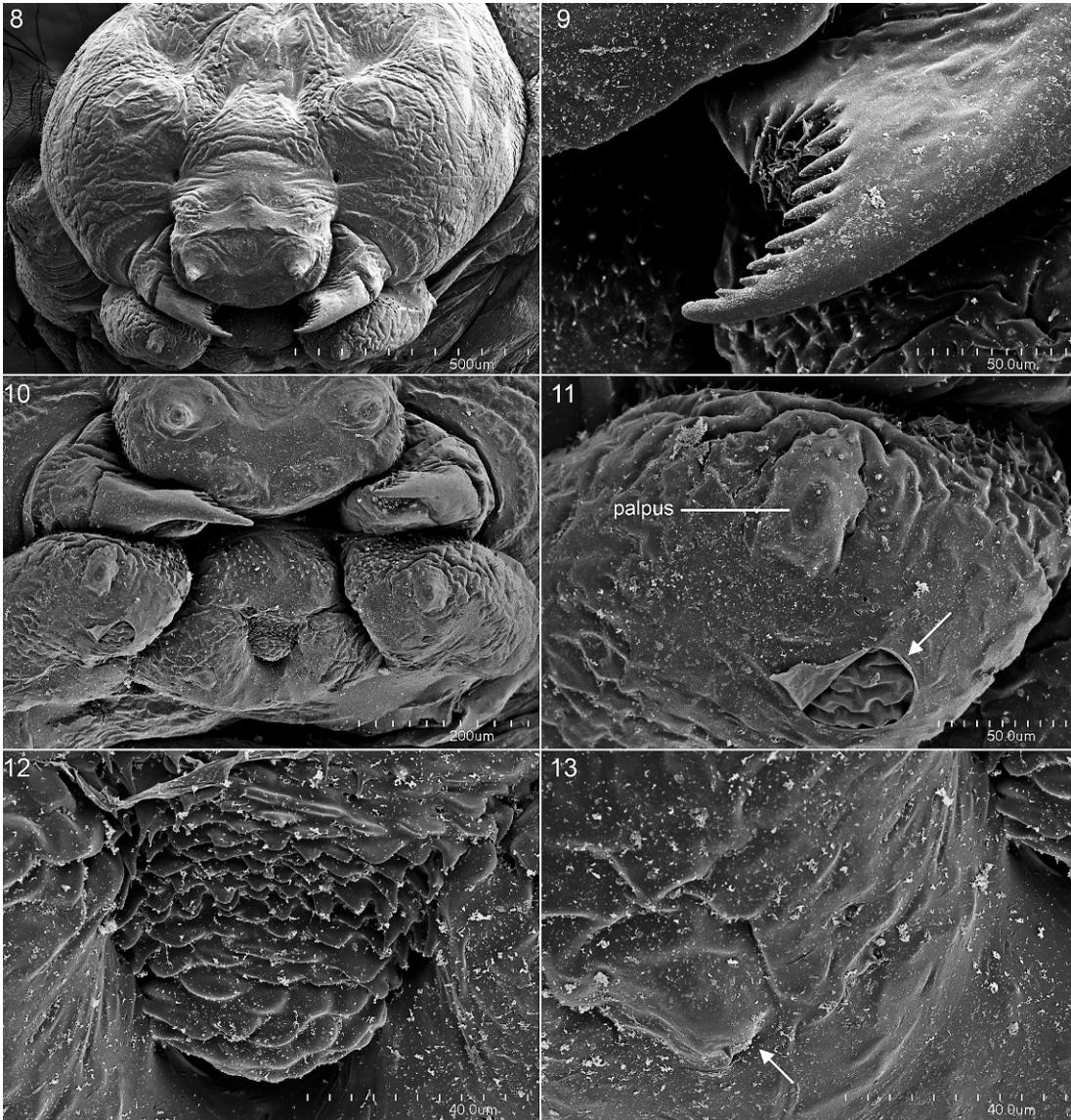
Figs. 8–13.   SEM micrographs of last larval instar of *Camptopoeum friesei*. **8.** Head of cleared specimen, approximate frontal view. **9.** Close-up of left mandible, showing teeth along upper apical edge and cuspal teeth farther back. **10.** Mouthparts of same specimen as above but tilted back to show details. **11.** Close-up of right maxilla, showing numerous sensilla on and around palpus and torn flap of dried secretion exposing verrucose integument (arrow) beneath. **12.** Close-up of U-shaped salivary opening, showing sculpturing of area bounded by it. **13.** Close-up of right labial palpus (arrow) with single cone-shaped sensillum.

like (in predefecating larva, fig. 2) or flat (in postdefecating larva, Rozen, 1988: figs. 5–7) extension of the pronotum that comes forward on each side to cover the lateral surface of the head just above the posterior tentorial pit. The function of these flaps is currently not understood. See the treatment of larval *C. clypeare* for other features whereby the genus can be separated from other Old World panurgines (Rozen, 1988). The distinctive verrucosity of the labiomaxillary region strongly resembles that of the last larval instar
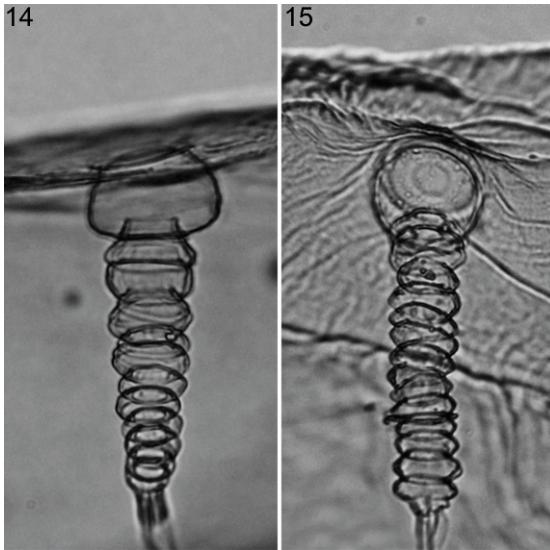
Figs. 14, 15. Macrophotographs of spiracles from cleared specimens, lateral views. **14.** *Camptopoeum friesei*. **15.** *Parammobatodes minutus*.

of *Calliopsis zebrata* Cresson (Andrenidae: Panurginae: Calliopsini) (Rozen, 2008), the only other panurgine larva that has been examined with an SEM to date. This character will probably be found widely among other panurgines.

HEAD: Integument with scattered sensilla that are not setiform; dorsal surfaces of maxilla and hypopharynx densely spiculate (figs. 2, 3); sides and undersurface of epipharynx spiculate; integument of head capsule wrinkled, that of dorsal surface of maxillary apices and labial apex deeply verrucose (figs. 8, 10, 11). Integument unpigmented except mandibular apices darkly pigmented, anterior tentorial pits pigmented, and maxillary palpi faintly pigmented.

Head moderately small compared with body size (figs. 1, 2); head capsule distinctly wider than length measured from top of vertex to lower clypeal margin in frontal view. Tentorium complete, including dorsal arms, moderately well developed. Anterior tentorial pit well removed from anterior mandibular articulation (fig. 8); posterior tentorial pits in normal position; postoccipital ridge uniformly moderately developed; median longitudinal thickening of head capsule (coronal ridge)

absent; hypostomal ridge moderately developed, its posterior section curving inward to meet tentorial bridge and postoccipital bridge without giving rise to dorsal ramus; pleurostomal ridge moderately developed; epistomal ridge laterad of (below) anterior tentorial pit moderate in length; ridge between pits absent. Parietal bands evident as integumental scars (figs. 2, 8). Antennal prominence rather weak (fig. 2); antennal disc as seen on cleared specimen moderately small, its diameter almost one-half distance from its lowest rim to center of anterior tentorial pit (distances measured in maximum profile); antennal papilla scarcely projecting, bearing 3–4 sensilla, which are cone shaped, projecting more than two times basal diameter (fig. 4). Vertex evenly rounded, but with low projection on each side above and somewhat mesad of antenna. Labrum projecting anteriorly as far as clypeus in lateral view (fig. 2), spiculate laterally, and with pair of acutely pointed, sensilla-bearing tubercles (figs. 2, 8).

Mandible in outer or inner views tapering evenly to narrowly pointed apex; dorsal apical edge with linear row of sharp teeth (fig. 9) that broadens at cusp; ventral apical edge without teeth; cusp moderately produced in dorsal and ventral views; apical concavity not facing hypopharyngeal surface; outer mandibular surface with small, seta-bearing tubercle toward base; dorsal surface faintly, irregularly wrinkled, nonspiculate. Labiomaxillary region weakly projecting in lateral view (fig. 2), but maxilla well developed, projecting well beyond apices of labium and hypopharynx in lateral view (fig. 2). Cardo, stipes faintly evident because more darkly stained than surrounding integument on cleared specimen; articulating arm of stipital sclerite questionably evident although hypopharyngeal groove pronounced; maxillary palpus (figs. 8, 10, 11) positioned at apex of maxilla, large, conspicuous, although projecting less that basal diameter. Labium weakly divided into prementum and postmentum; premental sclerite questionably evident as faintly darker area on stained specimen; labial palpus small, scarcely projecting, contrasting with large maxillary palpus. Salivary opening (figs. 10, 12) a U-shaped slit subtending hypopharyngeal groove, without lips; salivary duct attached to bottom of U; area

bounded by U-shaped slit deeply sculptured (fig. 12). Hypopharynx projecting forward, more or less as far as labial apex, but both recessed compared with maxillary apices (fig. 2).

BODY (figs. 1, 2): With fine, scattered, nonsetiform sensilla and with spiculate areas as follows: prothorax (figs. 2, 3) with large sharply pointed spicules densely and uniformly arranged on dorsal and lateral surfaces behind head and on lateral flaps; spicules gradually becoming fine on lower sides of body and ventrally; other body segments with spicules along dorsal midline well developed but elsewhere fine, inconspicuous, absent on lateral body surfaces. Body form of postdefecating larva moderate (fig. 1); intersegmental lines moderately weakly incised on predefecating and postdefecating forms; dorsal intrasegmental lines not evident; paired dorsal tubercles on postdefecating larva present but low on all thoracic segments and on abdominal segments 1–6, diminishing on abdominal segments 7, more so on 8, scarcely noticeable on 9; all tubercles low, rounded to conical (i.e., not transverse); on predefecating larva tubercles even less pronounced; integument of apices weakly minutely wrinkled; abdominal segment 9 not produced ventrally; abdominal segment 10 positioned medially on 9 as seen in lateral view (figs. 1, 7); anus apical on 10. Spiracles small, subequal in size, not on sclerites or tubercles; peritreme (fig. 5) present, moderately narrow, not as wide as diameter of atrial opening; atrium (fig. 5) projecting beyond body wall, with rim, globose; atrial wall (fig. 14) smooth (without denticles or ridges); primary tracheal opening with collar; atrium in lateral view (fig. 14) moderately large; subatrium of moderate length, of about 12 chambers; wide outer chambers tapering to narrow inner chambers. Male with median, transverse integumental scar on venter of abdominal segment 9; female with pair of opaque white subcutaneous imaginal bodies each on venter of abdominal segments 7–9, with those on 9 closest and than those on 7 the farthest apart.

MATERIAL EXAMINED: 1 predefecating and 4 postdefecating larvae, AUSTRIA: Burgenland: Illmitz, Reserve Seewinkel-Neusiedlersee, VII-18-2007 (J.S. Ascher); 1 predefecating, 1 postdefecating larvae, same except: (M.G. Rightmyer); 5 postdefecating larvae, same except VII-21-2007 (G. Hölzler), from nest #1 and #2.

REMARKS: Preserved with these specimens were the remnants of some of the provisions as well as a juvenile larva. The remnants were the thin, transparent outer coatings of the food mass with a layer of adherent pollen grains. This indicates that this bee coats the surface of the provisions with a clear material that is not water- or preservative soluble, probably like that of the Calliopsini and some Perditini. Thus, this is the first Old World panurgine known for this behavior, although, unexpectedly, this trait also occurs in certain New World Rophitinae (Halictidae) (Eickwort et al., 1986; Rozen, 1993).

PUPA OF *CAMPTOPOEUM FRIESEI*

Figures 16, 17

The following is the first pupal description of any species of *Camptopoeum*. Terminology and format follow Neff and Rozen (1995) and Rozen and Yanega (1999). Because the more developed pupa was damaged during excavation, the illustration of the anterior end was based on that specimen and the metasoma was drawn from the second specimen. Because the second pupa was considerably smaller than the first, its illustration is slightly more magnified.

DIAGNOSIS: The pupa of this species lacks a tubercle near the base of the outer surface of the hind tibia, whereas the existence of such a tubercle is found in most Andrenidae the pupae of which have been described. The absence of this tubercle also occurs in *Melitturga* (Yager and Rozen, 1966: figs. 15, 16), *Perdita* (Michener and Ordway, 1963; Yager and Rozen, 1966: fig. 18), *Neffapis* (Rozen and Ruz, 1995), *Oxaea* (Roberts, 1973), and *Protoxaea* (Rozen and Rozen, in press). The short but distinct terminal spine (fig. 17) and a clearly identified transverse depression between the mesoscutum and mesoscutellum (fig. 16) found in *C. friesei* will immediately separate its pupa from that of *Oxaea* (Roberts, 1973: figs. 7) and also *Protoxaea* (Rozen and Rozen, in press), which
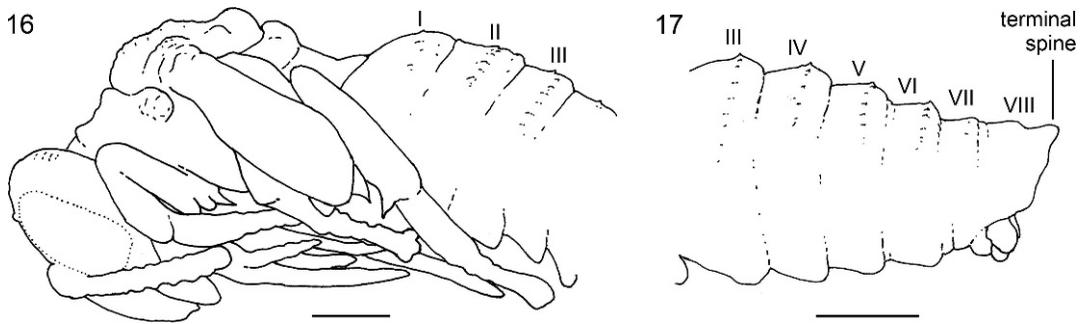
Figs. 16, 17.   Diagrams of pupa of *Camptopoeum friesei*, lateral views, drawn from different specimens to different scales. **16.** Anterior part of body. **17.** Posterior part of metasoma, with short terminal spine. Scales (= 1.0 mm) refer to closest figures.

lack a terminal spine[2] and in which the pupal mesoscutum and mesoscutellum form a single continuous curve in lateral view without a transverse depression separating two curved surfaces. The short and apically rounded terminal spine of *C. friesei* (fig. 17) easily identifies its pupa compared with that of *Perdita* with its elongate, apically pointed terminal spine (Michener and Ordway, 1963; Yager and Rozen, 1966: fig. 18). The lack of mesoscutellar tubercles of *C. friesei* distinguishes its pupa from that of *Melitturga*, in which the paired tubercles are pronounced (Yager and Rozen, 1966: figs. 15, 16).

DESCRIPTION: Length 7.9, 8.6 mm; body without setae.

Head: Scape and pedicel unmodified, without tubercles; flagellomeres unmodified. Mandible with large ventral tuberclelike swelling two-thirds distance to apex; malar area without tubercle. Vertex with pair of low, scarcely noticeable, median vertical tubercles mesad of lateral ocelli; median ocellar tubercle conspicuous; lateral vertical tubercles not evident, although area behind upper compound eye faintly varicose; frontal tubercles not evident. Surface of compound eye smooth. Proboscis long (corresponding to that of adult), so that glossa extends to middle of metasoma in lateral view.

**Mesosoma:** Lateral angles of pronotum faintly varicose; lateral lobes somewhat swol-len, varicose; mesoscutum without tubercles, but surface somewhat swollen and varicose on each side, so that median line deeply impressed; mesoscutellum without tubercles but produced on each side as low, faintly varicose mound separated from other by median depression; axilla slightly produced; metanotum slightly produced on each side. Tegula without tubercle, surface slightly varicose. Forewing without tubercle. Forecoxa with moderately slender apical tubercle; foretrochanter with ventral, rounded tubercle; forefemur produced at base as rounded projection; foretibia and -tarsus unremarkable. Mid- and hind coxa with apical, sharply pointed tubercle; midtrochanter with low rounded tubercle; hind trochanter apically produced but nontuberculate; mid- and hind femora and tarsi unremarkable.

Metasoma: Terga I–VI each with transverse row of very small, often sharply pointed tubercles; those of tergum I few in number; those of all terga most pronounced sublaterally, tending to be small or absent medially. Sterna without tubercles. Terminal spine apically rounded, perhaps slightly varicose apically, short, poorly differentiated from tergum VIII, which is well developed.

MATERIAL EXAMINED: 1 male pupa, AUSTRIA: Burgenland: Illmitz, Reserve Seewinkel-Neusiedlersee, VII-18-2007 (J.S. Ascher); 1 male pupa, same except: (M.G. Rightmyer).

REMARKS: Unfortunately the female pupa has not been collected, so that it is unknown if the leg tubercles might be different to accommodate adult setal development.

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[2]Roberts (1973: fig. 7) mistook part of the genitalic structure for the terminal spine, which is a projection from the last metasomal tergum. Neither *Oxaea* nor *Protoxaea* have a terminal spine (Rozen and Rozen, in press)
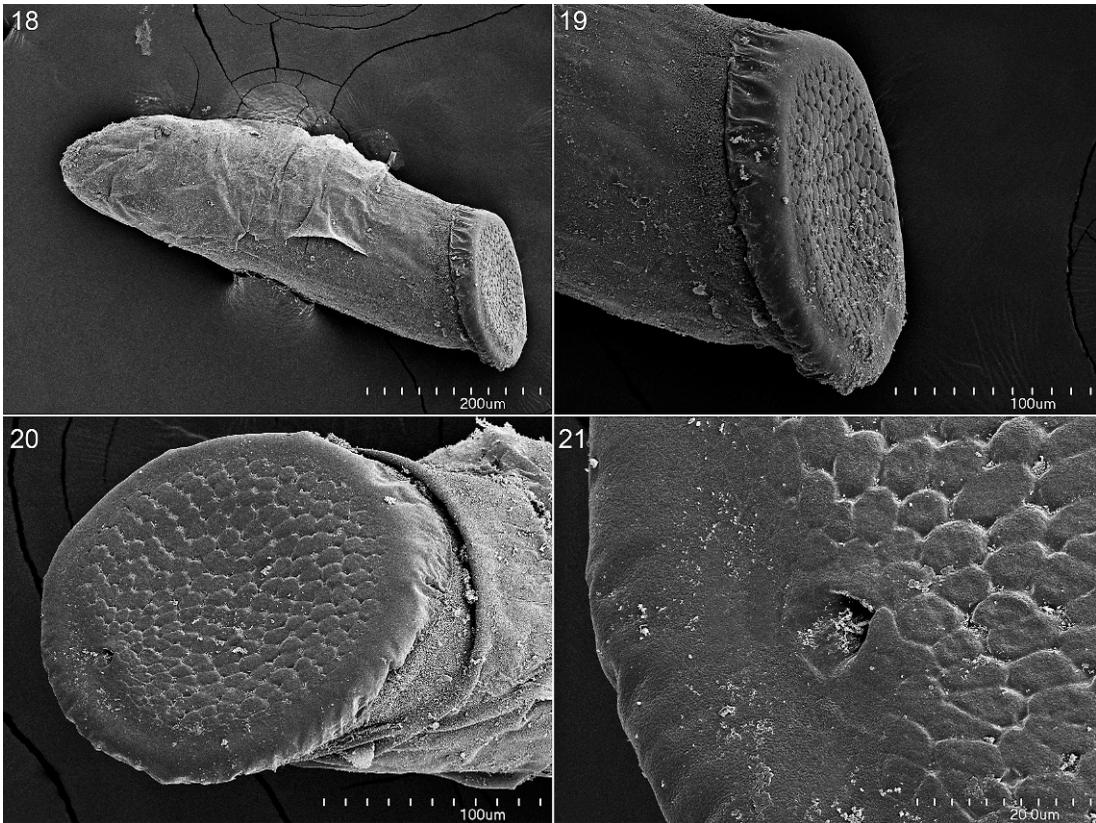
Figs. 18–21.   Oocytes of *Parammobatodes minutus*. **18.** Entire oocyte, anterior end toward right, lateral view, with chorion too badly damaged to demonstrate transverse dorsal folds. **19.** Close-up of operculum, showing flange draped over and clinging to rest of oocytes; flange almost certainly outstretched and continuous with surface of operculum after deposition in host cell, as in *Pasites maculatus* (see Rozen, 1986: figs. 5, 6), presumably an adaptation to obscure seam in cell wall so that returning host female will not detect parasite egg. **20.** Close-up of another oocytes, end view, showing texture of surface and micropyle on left. **21.** Close-up of micropyle.

OVARIAN STATISTICS AND MATURE OOCYTE OF *PARAMMOBATODES MINUTUS*

Figures 18–21

Table 1 provides ovarian statistics for *Parammobatodes minutus* as well as those presented for *P. rozeni* Schwarz (Rozen and Özbek, 2003; Rozen, 2003), the only other congeneric species for which there is information. The egg index, a statistic developed by Iwata and Sakagami (1966), permits comparisons of the size of the egg or mature-oocyte of species with different body sizes. The index is calculated by dividing the length of the egg (or that of the mature oocytes) by the distance between the outer rims of the tegulae of the female from which the egg was taken. One can then compare the resulting figures (indices) of different sized adults to determine if their eggs are larger, smaller, or of the same size irrespective of body size. Iwata and Sakagami (1966: table 2) proposed a classification of the indices consisting of five size categories. Indices of both *P. rozeni* and *P. minutus* fall well within *dwarf*, the smallest category. This is not surprising since eggs of cleptoparasitic bees tend to be among the smallest of all groups of bees (Rozen, 2003). Furthermore, eggs of all other Ammobatini (representing five additional genera) that have

TABLE 1
Number of Ovarioles and Number and Size of Mature Oocytes of Two Species of *Parammobatodes*
Data for *P. rozeni* from Rozen and Özbek (2003) and Rozen (2003). Numbers in first three columns are average values of the two specimens of *P. minutus*

Taxon	Egg index	Mature oocytes (no.)	Mature oocytes/ ovariole	Ovariole formula	No. of specimens
P. rozeni	0.41	7	0.58	6:6	1
P. minutus	0.36	12.5	0.75 or 0.77	7:8 or 8:8	2

been examined are either *dwarf* or *small* (ibid.).

The values of the other statistics in table 1 are consistent with those of other Nomadinae (Rozen, 2003) in that the ovariole number (number of ovarioles per ovary) is elevated compared with the plesiomorphic number (4:4) for Apidae including other cleptoparasitic lineages. Also, the total number of mature oocytes is high compared with solitary bees, but this is usually the case with cleptoparasitic bees irrespective of their families (Rozen, 2003). The adaptive significance of these phenomena has been discussed by Alexander and Rozen (1987) and Rozen (2003).

DIAGNOSIS: As with other Ammobatini (Rozen and Özbek, 2003) the mature oocyte of this species has an operculum the surface of which slants obliquely from the long axis of the oocyte. The oocyte is slightly smaller that that of *P. rozeni*, but otherwise they are nearly identical, although the more regular patterning of the operculum of *Parammobatodes minutus* (fig. 20) seems to contrast with the less uniform patterning of that of *P. rozeni* (Rozen and Özbek, 2003: fig. 38). Both species are unusual in that the operculum is strongly tinted; that of *P. rozeni* ebony colored while that of *P minutus* is more or less amber but always paler than ebony. The range of color depth of the operculum is likely due to the age of the oocyte after it reached maturity: the older the mature oocyte, the darker its color.

Because mature oocytes have opercula that are tinted amber, they are easy to identify although very earlier mature oocytes may be colorless because of the gradations in ages of their maturity. Oocytes, counted through the follicular tissue, take on the shape of the mature oocytes before becoming mature. Hence, a few mature oocytes may have been mistaken for a premature oocyte because they

had not yet acquired any color. In addition to those with tinted opercula, two tinted opercula unattached to oocytes were found in separate ovarioles next to the calyx of one ovary of one specimen. With *Parammobatodes rozeni*, such opercula without attached oocytes were considered reabsorbed (Rozen and Özbek, 2003), as seems to be the case here.

DESCRIPTION OF MATURE OOCYTE (figs. 18–21): Length of longest oocyte (measured from front edge of operculum to posterior tip) 0.68 mm, maximum width behind operculum 0.19 mm; average egg index 0.37 (N = 2) (*dwarf*). Shape (fig. 18) nearly straight, with anterior thick, flat operculum slanting posteriorly on dorsal surface; operculum oval with distinct flange that drapes over and covers sides of oocyte; opercular length (exclusive of draped flange) (0.21 mm) greater than width; opercular surface somewhat uneven as seen through stereomicroscope; as seen with SEM, opercular surface with large circular area pebbled in low relief, becoming smooth toward periphery (fig. 20). Micropyle (fig. 21) a somewhat irregular and nonelevated hole near anterior edge of operculum (for further description, see Remarks below). Operculum amber, transparent; rest of chorion clear, seemingly colorless, shiny, and without surface sculpturing when examined with SEM; dorsal surface of oocyte with series of transverse folds (as in Rozen and Özbek, 2003: figs. 37, 44).

MATERIAL EXAMINED: Oocytes from specimens collected: AUSTRIA: Burgenland: Illmitz, Reserve Seewinkel-Neusiedlersee, VII-22-2007 (G. Hölzler).

REMARKS: Almost certainly the egg of this species when found in the host cell will have its posterior end bent under (or over) the anterior part of the egg as has been reported for *Pasites maculatus* Jurine (Rozen, 1986: figs. 6, 9) and *Oreopasites* (Bohart, 1970). Evidence of this is

the dorsal transverse folding of the chorion at midsection that allows the stretching of the chorion necessary to accommodate the U-shaped bending of the egg. This phenomenon is unique to the Ammobatini genera, the eggs or oocytes of which have been studied. However, it is not found in *Sphecodopsis* (*Pseudodichroa*),[3] perhaps because of the cell lining of the host, *Scrapter* (Colletidae) (Rozen and Michener, 1968). The lining is cellophanelike, similar to that of *Colletes*. If it is separated from the cell wall as reported by Rozen and Favreau (1968) for *Colletes*, then perhaps the egg does not need to be bent U-shaped since it would lie in the empty space between lining and cell wall.

The micropylar duct of *Parammobatodes minutus* appears to penetrate the thick chorion of the operculum diagonally, and the parallel ridges at its entrance on the surface (similar to those of *Pasites maculatus* [Rozen and Özbek, 2003: fig. 47]) suggests that duct may lead to a multipored, true micropyle below or it may be a remnant of it. This suggestion is not unreasonable since by far most bee taxa have multipored micropyles even including some Ammobatini such as *Ammobates carinatus* Morawitz and a number of species of *Oreopasites* (Rozen, 2003: figs. 26, 31, 36). A recessed micropyle of this sort, thus, might have come about through selection pressure for the bee egg to have a thick exposed chorion as protection against the mandibles of the host female. The ontogenetic changes in the oocyte of *Leiopodus abnormis* Jörgensen (Rozen, 2003: figs. 16–19) (a presumably unrelated cleptoparasitic bee in the Protepeolini) during late oogenesis give credence to this idea.

POSTDEFECATING LARVA OF *PARAMMOBATODES MINUTUS*

Figures 22–25

DIAGNOSIS: The mature larva of *Parammobatodes minutus* strongly resembles those of other Ammobatini in having a body form

that tapers both anteriorly and posteriorly and that often has pronounced body segmentation (McGinley, 1981; Rozen, 1954, 1966, 2008; Rozen and McGinley, 1974). Internal head ridges tend to be reduced or even lacking, especially the postoccipital ridge, and the labiomaxillary region is greatly fused and recessed, with the labial palpi scarcely evident. On all, the hypopharynx is nonspiculate, and mandibles tend to be short and robust basally. The following key will separate the larvae of taxa that have been described to date (references to their descriptions cited parenthetically after their name).

KEY TO KNOWN MATURE LARVAE OF AMMOBATINI

1. Body with distinct paired dorsolateral tubercles (fig. 22; Rozen, 2008: fig. 12) 2
– Body without distinct paired body tubercles (Rozen, 1954: fig. 1, 1966: fig. 59; Rozen and McGinley, 1974: figs. 1, 10, 18), although in *Oreopasites* dorsolateral area on many terga slightly produced forming dorsolateral angle (or "hip") on each side 3
2(1). Each parietal swollen, directed forward as seen in lateral view (Rozen, 2008: fig. 15); mature larva extremely small, less than 4 mm long. *Chiasmognathus pashupati* Engel (Rozen, 2008)
– Each parietal normally sloping posteriorly as seen in lateral view (fig. 25); mature larva larger, longer than 6.5 mm long . . . . *Parammobatodes minutus* (Mocsáry) (present study)
3(1). Labral tubercles far apart, distance between them about four-times basal diameter (Rozen and McGinley, 1974: fig. 15); upper frons with median swelling (ibid.: figs. 15, 16) . . . . *Ammobates carinatus* Morawitz (Rozen and McGinley, 1974)
– Labral tubercles more closely set, distance between them at most twice, to less than, basal diameter (Rozen, 1954: fig. 5; Rozen and McGinley, 1974: figs. 16, 23[4]); upper frons without median swelling (Rozen, 1954: fig. 6; Rozen and McGinley, 1974: figs. 8, 24) . . 4

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[3]Perhaps non-coincidentally, species of this subgenus have an egg the chorion of which is uniformly covered with a network of fine interconnecting ridges (Rozen and Michener, 1968: figs.9, 10; Rozen and Özbek, 2003: figs. 48, 49). Thus, it is probably stiffened and presumably not sufficiently elastic to bend.

[4]Although the illustration (Rozen and McGinley, 1974: figs. 23) of the labral tubercles of *Pasites histrio* (Gerstaecker) (= *Morgania histrio transvaalensis* Bischoff) seems to indicate that they are separated by a distance of more the twice their basal diameter, re-examination of the specimens confirms their separation by no more than two diameters.
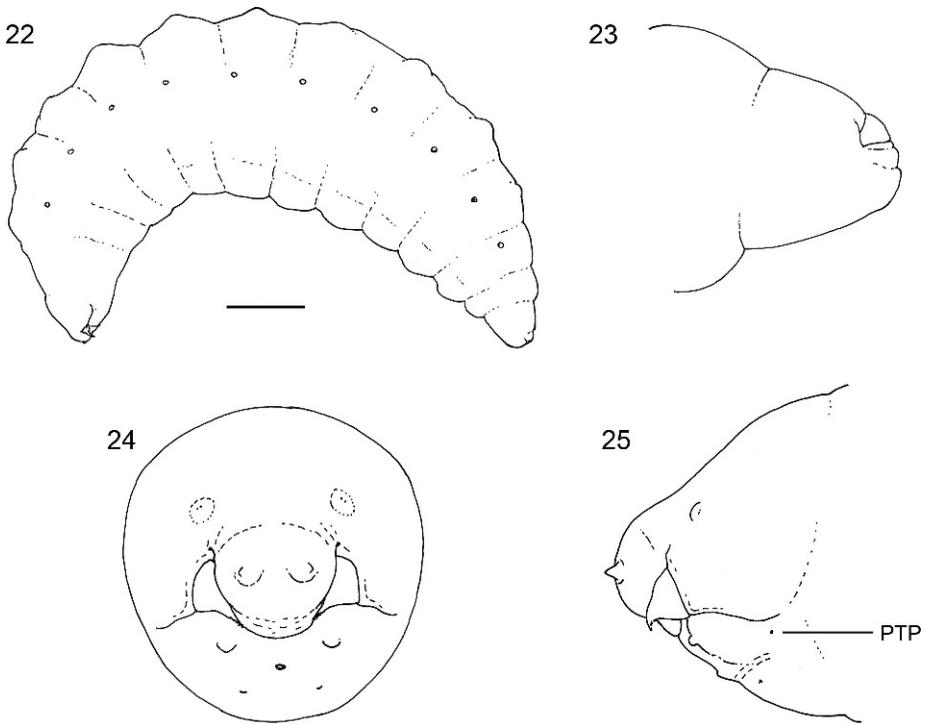
Figs. 22–25.   Diagrams of postdefecating larva of *Parammobatodes minutus*. **22.** Entire larva, lateral view. **23.** Close-up of terminal abdominal segments, lateral view. **24, 25.** Head, frontal and lateral views, respectively. PTP = posterior tentorial pit. Scale (= 1.0 mm) refers to fig. 22.

4(3).   Labral tubercles separated by distance equal to, to twice, their basal diameter (Rozen and McGinley, 1974: fig. 23). . . . *Pasites histrio* (Gerstaecker) (= *Morgania histrio transvaalensis* Bischoff [Rozen and McGinley, 1974])

– Labral tubercles separated by distance clearly less than their basal diameter (Rozen, 1954: fig. 5; Rozen and McGinley, 1974: figs. 7) . . . . *Oreopasites* and *Sphecodopsis* (*Pseudodichroa*) *fumipennis* (Bischoff) (as *Pseudodichroa fumipennis* Bischoff)[5] (Rozen and McGinley, 1974)

[5]Rozen and McGinley (1974) regarded larval *Sphecodopsis* (*Pseudodichroa*) *fumipennis* (Bischoff) (as *Pseudodichroa fumipennis* Bischoff) as quite distinct from other ammobatines. Because their limited material consisted of only predefecating specimens, which have now deteriorated to some degree, we do not attempt here to separate this species from *Oreopasites* in the key. However, whereas all known predefecating larvae of the North American genus *Oreopasites* are normally slender, they can immediately be distinguished from physogastric predefecating larvae of the southern African *S. fumipennis*, which when fully fed has a maximum body width 4–5 times greater than its maximum head width.

DESCRIPTION: Length approximately 6.5 mm. **Head**: Unpigmented except for mandibular apices, mandibular internal ridges, and hypostomal ridge, which are weakly pigmented; sensilla nonsetiform; spiculation, including that of hypopharynx, absent.

Head size small compared with body; head capsule wider than long in frontal view (length measured from vertex to level of posterior mandibular articulation); as seen in lateral view (fig. 25), parietals at top of head sloping backward, not projecting forward as in *Chiasmognathus pashupati* Engel (Rozen, 2008: fig. 12). Tentorium absent except at pits (possibly because specimen was about to molt), existing tentorial arms short, fragile; anterior tentorial pit very small, close to anterior mandibular articulation; posterior tentorial pit small, below and posterior to curve of hypostomal ridge as ridge bends upward; postoccipital ridge not evident so that hypostomal ridge fading completely at its

posterior end and posterior margin of head capsule a faint line extending dorsolaterally to cervical fold; integument in front of posterior margin nonspiculate, integument behind margin becoming conspicuously spiculate. Median longitudinal thickening of head capsule absent; hypostomal ridge evident, becoming weaker posteriorly; pleurostomal ridge weak, not clearly defined; epistomal ridge mesad of anterior tentorial pits absent, weak laterad of pits. Parietal band not evident. Antennal prominence low; antenna positioned as in figs. 24, 25; antennal disc and papilla not clearly differentiated; papilla bearing two sensilla. Labroclypeal region strongly projecting beyond frontal area with labrum large, without sclerite, with two sharply defined, apically acute, small, sensilla-bearing tubercles that are separated by distance slightly less than their basal diameter; lower margin of labrum extending downward to meet hypopharynx where they join pharynx; lower part of labrum (epipharyngeal surface) overridden laterally by mandibular apices when mandibles are closed.

Mandible (too small to be dissected from head but interpreted through cleared head capsule) moderately long for an ammobatine, with base moderately developed (but not globular); apex strongly curved downward and sharply pointed; cusp and apical concavity not differentiated, without denticles; outer surface with scattered denticles; dorsal and ventral apical edges with conspicuous, sharply pointed, apically directed teeth. Maxilla strongly fused to labial region, its apex (except for palpus) small, surpassed by hypopharynx; galea and maxillary sclerites absent; palpus large at base, tapering rapidly to pointed apex, so that palpal length clearly shorter than basal diameter. Labium not divided into pre- and postmentum; premental sclerite absent; labial palpus presumably represented only by a sensillum somewhat posterior to salivary opening. Salivary opening simple, circular, without lips. Hypopharynx defined by mouth above, by maxillae laterally, but without hypopharyngeal groove below.

Body (figs. 22, 23): Without setae, with fine spicules on prothorax and on venters of other thoracic segments and anterior abdominal segments; integument without spines or sclerotized tubercles. Body form slender, elongate; intersegmental lines weakly incised between most body segments; dorsolateral intrasegmental lines not evident; thoracic and abdominal segments 1–8 with paired, low, conical (i.e., not transverse) dorsolateral tubercles, which do not project dorsally as far as body midline; paired tubercles absent on abdominal segments 9, 10; venter of abdominal segment 9 not produced; segment 10 longer than basal diameter in lateral view, not bulging ventrally, attached centrally to 9; anus a transverse slit, apical on 10; perianal area with dorsal and ventral lips (fig. 23). Spiracles faintly pigmented, subequal, moderately small; spiracles projecting beyond body wall, with rims; peritreme present, moderately wide; atrium globular; atrial wall without denticles or rings; primary spiracular opening with collar; subatrium (fig. 15) moderately long, with about 14 chambers, all of approximately equal diameter; thus, subatrium not tapering from outer most to inner most chamber as in *Camptopoeum friesei* (fig. 14). Sex characters unknown.

MATERIAL EXAMINED: 1 postdefecating larva, AUSTRIA: Burgenland: Illmitz, Reserve Seewinkel-Neusiedlersee, VII-18-2007 (J.S. Ascher).

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