TABLE 1
Ovariole and Oocyte Statistics for *Ammobatoides abdominalis* and *Epeoloides coecutiens*
(For explanation of terms, refer to Materials and Methods.)

Taxon	Egg index	Total no. mature oocytes	Mature oocytes per ovariole	Ovarian formula	No. specimens examined
Ammobatoides abdominalis	0.27	15.0	1.50	5:5	2
Epeoloides coecutiens	0.70	4.4	0.55	4:4	5

tures. This suggests that different cleptoparasitic lineages do not have the same potential for evolving these special features or perhaps the circumstances of the biology of the host and/or cleptoparasites do not require these features. Described herein are the oocytes (and eggs) and number of ovarioles of two Palearctic species, both belonging to the Apidae but representing different cleptoparasitic lines according to Roig-Alsina and Michener (1993): *Ammobatoides abdominalis* (Eversmann) (Nomadinae: Ammobatoidini), a cleptoparasite of *Melitturga* (Andrenidae: Panurginae), and *Epeoloides coecutiens* (Fabricius) (Apinae: Osirini), a cleptoparasite of *Macropis* (Melittidae: Melittinae). Comparing these two species emphasizes the kinds of morphological adaptations associated with cleptoparasitism that have evolved in two cleptoparasites that did not share a common cleptoparasitic ancestor.

Observations are also presented on the biology of *Ammobatoides abdominalis* made at the time and place the adults were collected.

MATERIALS AND METHODS

Ovaries were dissected from females that had been preserved in Kahle's solution. The metasoma was cut along each side with iridectomy scissors, and terga 1–4 were lifted off to expose the ovaries. After the midgut and Malpighian tubes were excised, the basal sterna were removed in the case of *Epeoloides coecutiens,* leaving the ovaries, lateral oviducts, and common oviduct attached to the sting apparatus and the apical sterna and terga. Ovarioles were then counted, and mature oocytes were dissected from them by scraping and pulling ovariole tissue from the chorion. In the case of *Ammobatoides abdominalis,* ovarioles were counted after the midgut and Malpighian tubes had been excised but before the sterna were removed.

Oocytes were deemed mature if they evidenced a chorion, which was fairly easily detected because of the sculpturing present in both of these species. These oocytes probably correspond to categories A and B of Iwata (1955) since some were fully formed and others, with a thin chorion, were slightly misshaped. Data concerning the number of ovarioles and oocytes and sizes of oocytes are summarized in table 1. The egg index, also recorded there, is the average oocyte length divided by the width of the mesosoma measured between the outer rim of the tegulae (Iwata and Sakagami, 1966). The ovarian formula, as used by Alexander (1996), represents the number of ovarioles in each of the two ovaries.

Because oocytes could not be removed from the ovarioles without some distortion, they are diagrammed to show their shape (figs. 1–3). Scanning electron micrographs of oocytes of both species (figs. 4–14) were taken to examine details of sculpturing and chorionic microstructure after specimens had been critical-point dried and coated with gold palladium. Because the chorion on some of the oocytes was torn during dissection and/or treatment, observation of the fine internal structure of the chorion itself was possible through examination of the torn edges.

All specimens examined for this study, including the parasitized cell of *Melitturga*

Figs. 1, 2. Diagram of oocyte of *Ammobatoides abdominalis,* lateral and dorsal views, respectively, anterior end at top. Shaded area represents pitted region of chorion; unshaded area, smooth region of chorion.

Fig. 3. Diagram of oocyte of *Epeoloides coecutiens,* lateral view. Scale bars = 1.0 mm.

Figs. 4–9. SEM micrographs of oocytes of *Ammobatoides abdominalis.* **4.** Entire oocyte, lateral view, anterior end to left. **5.** Enlargement of anterior end, showing anterior point and pedunculate process. **6.** Another view of pedunculate process, enlarged. **7.** Torn chorion of dorsal rough surface of oocyte showing outer fenestrated layer and, where it is removed, exposing the consolidated inner layer. **8.** Posterior end of oocyte showing shallowly pitted posterior pole and edge or torn chorion (outlined) enlarged in figure. **9.** Enlarged section of torn chorion showing filmlike layer of outer surface and thick, consolidated inner layer.

clavicornis (Latreille), are in the collection of the American Museum of Natural History.

SYSTEMATIC DESCRIPTIONS

Ammobatoides abdominalis

BIOLOGY: I discovered males and females of the host bee, *Melitturga clavicornis* foraging from *Trifolium repens* Linnaeus on June 21, 1999, at the Central Asian locality identified below under Material Studied. Both sexes of *Ammobatoides abdominalis* were collected in the vicinity, feeding on the same plant. I searched for nests of the host bee near patches of *Trifolium* and found one, described below. Where *Ammobatoides* females were most abundant, I could see several patrolling at one time as they meandered low over the ground, a search flight typical of other nomadine bees.

The male flight behavior of *Ammobatoides abdominalis* was noteworthy. They perched on elevated prominences such as large stones on barren patches of ground. They swiftly and suddenly took pursuit when they observed other insects approaching on the wing. After chasing an insect, the male usually returned to the same perch. When I threw a small stone toward a perching male, he arose quickly to pursue. This test was conducted about 10 times, with some pebbles soaring 30 cm above them, and in most cases the males responded the same way. I have observed similar chasing behavior on the part of males of *Melitturga clavicornis* (Rozen, 1965b), *Meliturgula braunsi* (Friese) (Rozen, 1968), and *Xylocopa virginica* (Apidae: Xylocopinae) (unpubl. obs.), as have Linsley and Michener (1962) and Cazier and Linsley (1963) for *Protoxaea* (Andrenidae: Oxaeinae). In the case of *Melitturga, Protoxaea,* and *Xylocopa,* males hover in the air and chase oncoming insects (and pebbles). With *Meliturgula,* males rested on the ground, as did those of *A. abdominalis* when not chasing.

This behavior appears to be a form of territoriality. Cazier and Linsley (1963), after discussing the function and significance of male territorial behavior in *Protoxaea gloriosa* (Fox), suggested that it may reduce competition for nectar and pollen by other species and thereby allow a greater supply for conspecific females. However, this explanation does not readily explain such behavior on the part of a cleptoparasitic bee, which does not provision nests. Since males of the host *Melitturga clavicornis* exhibit aggressive behavior toward other insects, might territorial aggressiveness of the *Ammobatoides* male be reinforcing that of the host male and thereby assure the provisioning of more host brood cells?[2] The answer to this question is

[2] One of the anonymous reviewers disagreed with this possible explanation of territoriality in male *Ammobatoides.* He believed that it ''is most likely due to one of two reasons: (1) the males are establishing territories over a resource valuable to females (possibly host nests), and (2) the males are waiting for female *Ammobatoides* to mate with.'' He, of course, may be correct, but his explanations do not address how territoriality arose uniquely in *Ammobatoides* of all the Nomadinae. Nor do they acknowledge the peculiar fact that both host and parasite exhibit territoriality, accompanied by strong sexual dimorphism. Almost all hosts of the Nomadinae are nonterritorial. Why is territoriality not exhibited in these other cleptoparasites (even closely related ones such as *Holcopasites*)?

Figs. 10–14. SEM micrographs of oocytes of *Epeoloides coecutiens.* **10.** Entire oocyte, lateral view. **11.** Enlarged view of midsection of chorion, showing projecting nodules. **12.** Anterior pole, showing change in sculpturing (for further description, see text). **13.** Anterior pole, anterior view, of another oocyte showing sculpturing and torn chorion (outlined) depicted in Figure 14. **14.** Enlarged view of cross section of chorion.

unknown. An alternative explanation of this male behavior in *Ammobatoides* might involve spacing of males for dispersal and mate seeking.

As in the case of *Xylocopa, Protoxaea, Melitturga,* and *Meliturgula,* males of *Ammobatoides* have compound eyes that converge above (contrasting with parallel inner orbits or inner orbits that diverge dorsally in females). The converging of the upper part of the male's eyes in these taxa presumably enhances the ability to detect oncoming flying insects. Male dorsal eye convergence is uncommon among cleptoparasites, but a similar sexual dimorphism, though less pronounced, occurs in *Epeoloides.* Whether it is accompanied by similar behavior is as yet unknown.

Because other differences between the sexes of *Melitturga clavicornis* and *Meliturgula braunsi* are suspected of being involved with male hovering/territoriality (Rozen, 1968), antennae and hind-wing differences were inspected in *Ammobatoides.* Male *Ammobatoides* exhibit no clublike modifications of the antennae as has been noted for the two panurgines, and their hind wings were of about the same proportions as those of the female, contrasting with those of *M. braunsi.*

In regard to sexual dimorphism of *Ammobatoides* not related to hovering/territoriality, color pattern and hair-length dissimilarities are pronounced. Females have the typical black head and mesosoma and red metasomal color pattern often found in such cleptoparasitic bees as *Sphecodes* and *Holcopasites.* This pattern is associated with short body hair. In contrast, males are all black with long, grayish hairs on the mesosoma, first metasomal tergum, and most metasomal sterna; they also have distinct pale apical hair bands on terga 2–6. The significance of this strong dimorphism is unknown.

In a single case, a female's search behavior differed from the wandering patrolling referred to above. A female sat on the ground, facing a tumulus. She shifted her position several times by hovering slowly, but she always alighted and remained facing the tumulus. Because such behavior of cleptoparasites has led to the discovery of host burrows in the past, I inverted a plastic drinking glass over the tumulus in an unsuccessful attempt to capture a departing female *Melitturga* or to slow the flight of a returning, pollen-laden female. Several hours later I excavated the nest.

Below the surface, the burrow meandered downward to a depth of 5 cm and then curved sideways to end in a single open cell that contained a flattened, apparently complete ball of provisions without a *Melitturga* egg. A search of the cell surface revealed an egg of *Ammobatoides abdominalis* inserted in a hole in the wall toward the rear of the cell. When first discovered, the egg was not visible, and the hole was covered with a raised, roughly circular piece (about 0.8 mm in diameter) of the cell lining with soil adhering to the underside. When I explored the raised area with forceps, the piece with the egg attached immediately broke away from the cell wall. This piece may have been the ''flap'', still attached on one side to the cell lining, as described for *Holcopasites* (Rozen, 1965a), but further observations are needed to confirm the attachment and whether any part of the egg is normally visible. It is unknown why the egg adhered to the flap, but it could have been either because the female had cemented it to the flap with a secretion or because it had been damaged as it broke away with the flap. Subsequent examination of the egg in the laboratory showed that the anterior end was pointed toward the wall surface and the textured anterior part (see description below) clung to the flap. One wonders if the textured sculpturing of the egg might provide a rough surface for gluing the egg to the flap.

The hole into which the egg had been inserted was 0.4 mm in diameter, about 0.8–0.9 mm in depth, and it penetrated at about 45° from the cell surface, that is, more sharply than that illustrated by Rozen (1965a: fig. 3) for *Holcopasites.*

The anterior end of the egg was identified by the fact that oocytes of bees are directed with their anterior end toward that of the mother; eggs are deposited posterior end first. The dorsal surface of the egg and oocyte of *Ammobatoides abdominalis* was presumed by the fact that the egg was inserted under the flap with the textured part attached to the flap so that the emerging first instar

would crawl out with its venter in contact with the cell wall.

DESCRIPTION OF MATURE OOCYTES (figs. 1, 2, 4–9): Size small relative to distance between outer rim of tegulae (i.e., egg index 0.27); length 1.02–1.06 mm; maximum diameter 0.30–0.31 mm; total number of mature oocytes per ovariole 14–16. Shape (figs. 1, 2, 4) bilaterally symmetrical with anterior dorsal surface slightly flattened and anterior ventral surface bulging; oocyte slightly constricted ventrally somewhat more than halfway posteriorly; maximum diameter of anterior part somewhat greater than that of posterior part as seen in lateral view; anterior end produced as sharp, curved point, which appears irregularly roughened under SEM examination (fig. 2); small, pedunculate process (figs. 5, 6), presumably the micropylar apparatus (Margaritis and Mazzini, 1998), occurring midline at base of point on dorsal surface[3]; this process with large, deep, angular pits (presumably micropylar pores, ibid.); each side of oocyte with apparent ridgelike line arising from anterior point and gradually fading posteriorly; under SEM examination (fig. 4, 5), line consisting of a number of irregular alveoli marking boundary between deeply pitted dorsal surface and smooth lower surface of anterior part of oocyte; posterior end of oocyte broadly rounded. Color nearly white.

Chorion under stereoscopic examination (figs. 1, 2) smooth, transparent, shiny except finely pitted area extending along dorsal surface from pointed anterior end between lateral lines almost to posterior end. Chorion under SEM examination (figs. 4, 5) minutely, roughly pitted except dorsal surface more coarsely pitted almost to posterior end; chorion at posterior pole with faint, evenly distributed, shallow depressions (fig. 8); chorion of roughly pitted area in cross section (fig. 7) consisting of two layers, outer one of spongelike matrix with many holes, and inner one, of about equal thickness, of consolidated, finely granulate matrix lacking fenestrations; chorion of smooth, shiny area in cross section under high magnification (fig. 9) consisting of film of more coarsely granular outer material and thick layer of consolidated, finely granular material lacking fenestrations.

REMARKS: The egg index of this species is low, reflecting the small size of the oocyte relative to female body size. Alexander (1996) listed the egg index of several species of the related *Holcopasites* as also being low compared with that of many other Nomadinae. The shape and pattern of chorion ornamentation of the oocyte of *Ammobatoides abdominalis* is not known to occur in any other cleptoparasite. The pedunculate process at the base of the anterior point, first noticed by Molly Rightmyer, is a peculiar feature, as is the anterior point. The process was not clearly visible under stereoscopic examination because of light glare of the nearly white eggs. It was also sometimes obscured because of specimen orientation under SEM viewing, but almost certainly is present in all oocytes.

Although Rozen (1965a: fig. 3) illustrated the egg of *Holcopasites*, eggs/oocytes of that genus should be examined with a scanning electron microscope so that they can be compared with those of *Ammobatoides abdominalis*.

MATERIAL STUDIED: Two females, Kyrgyzstan: Dzhalal-abad, Chandalash R. 6 km N jct Chatkal R., 1630 m, 41°44′19″N, 70°52′22″E, VI-20–1999 (J. G. Rozen, J. K. Bouseman).

Epeoloides coecutiens

BIOLOGY: Observations have not yet been made on how and when the egg of any Osirini, including *Epeoloides*, is introduced in the host cell. Furthermore, the method of elimination of the host immature (be it egg or larva) is also unknown. To date, most known cleptoparasitic Apidae have early (usually first) instars with modified head capsules and long, sharply pointed mandibles that kill the host egg or usually young larva. Such Apidae include the Nomadinae, Melectini, Isepeolini, Rhathymini, Ericrocidini, Protepeolini, and Tetrapedini (see Rozen, 1991, and references therein; information on Tetrapedini [i.e., *Coelioxoides*] is new and will be reported fully elsewhere). The only

[3] This process was seen on many, but not all, of the oocytes. Its absence from some presumably results from being accidentally scraped away during dissection.

recorded exception is *Exaerete*; Bennett (1972) provided a detailed description of a female *E. dentata* (Linnaeus) opening the closed cell of *Eufriesea surinamensis* (Linnaeus), removing the host egg, and crushing it with her mandibles.

DESCRIPTION OF MATURE OOCYTES (figs. 3, 10–14): Size moderately large relative to distance between outer rim of tegulae (i.e., egg index 0.70); length 2.02–2.11 mm; maximum diameter 0.37–0.38 mm; total number of mature oocytes per ovariole 4–5. Shape (figs. 3, 10) approximately symmetrical along its moderately curved long axis, elongate, rounded at anterior end, gradually, evenly tapering posteriorly, narrowly rounded posteriorly; maximum diameter immediately behind anterior end; micropylar pore(s) not identified and hence apparently lacking, corresponding to situation in *Apis* and *Bombus* (Bronskill and Salkeld, 1978). Color nearly white.

Chorion dull throughout, appearing granular under low-power magnification, but actually with small, evenly spaced, projecting, rounded nodules under high power or under SEM examination (figs. 10–14); extreme anterior end (fig. 12, 13) without nodules but with pattern of elongate ovoids defined by raised borders; these ovoids becoming more elongate toward anterior pole of oocyte so that raised borders obliterate centers of ovoides, there remaining only incised channels separating raised borders; chorion in cross section under high magnification (fig. 14) consisting of outer spongy, columnar matrix that is somewhat thicker than consolidated, nonfenestrated inner layer; inner layer possibly comprised of two layers.

REMARKS: Alexander (1996) provided information on the egg indices of *Osirinus lemniscatus* Roig-Alsina and *Parepeolus aterrimus* (Friese), both of which were somewhat greater than that of *Epeoloides coecutiens.* Hence, all three representatives of the Osirini have eggs that tend to be large relative to body size compared with many other cleptoparasites.

MATERIAL STUDIED: Five females, Germany: North Bavaria, Bayreuth, Ecological-Botanical Garden of the University of Bayreuth, 49°55.7′N, 11°34.9′E, VII-1–1999 (P. Hartmann).

DISCUSSION AND CONCLUSIONS

Alexander and Rozen (1987) and Alexander (1996) summarized the known data on the number of ovarioles and size of mature oocytes of cleptoparasitic apids. Additional data have been presented by Rozen (1994, 1997), Roig-Alsina and Rozen (1994), and Rozen et al. (1997).

These accounts reveal that almost all Nomadinae have more ovarioles per ovary than do other Apidae, which almost always have an ovarian formula of 4:4 (exceptions are *Psithyrus, Ericrocis*, and *Apis*). *Ammobatoides abdominalis* with a formula of 5:5, therefore, is consistent with the other Nomadinae. *Epeoloides coecutiens* maintains the formula of 4:4, the plesiomorphic condition in the Apidae, as do the other members of the Osirini. This supports the conclusion of Roig-Alsina and Michener (1993) that the Osirini are not closely related to the Nomadinae.

This conclusion also seems supported by the pronounced difference in oocyte size relative to body size (i.e., the egg index) between *Ammobatoides abdominalis* and *Epeoloides coecutiens.* The oocytes of *A. abdominalis* (egg index 0.27) is similar not only to that of three species of the ammobatoidine genus *Holcopasites* (egg indices 0.23–0.41) (Alexander, 1996) but also to that of most other Nomadinae. The oocyte of *E. coecutiens* (egg index 0.70), though somewhat smaller than those of other Osirini (egg indices 0.79–0.88) (ibid.), is substantially larger than those of most Nomadinae. While the oocyte size of *E. coecutiens* is large compared to that of *A. abdominalis*, it is still smaller than that of most solitary bees (Alexander and Rozen, 1987: fig. 1). Interestingly, the known egg indices of the Osirini (0.70–0.88) closely match those of the Melectini (0.74–0.85) and Ericrocidini (0.74–0.77) (Alexander, 1996). Females of the latter tribes do not enter open cells and hide their eggs in the cell wall (as do the Nomadinae and Protepeolini, which have small eggs); rather, each female makes a small hole in the closed host cell (presumably through the cell closure) through which she inserts the tip of her metasoma to deposit an egg. Egg deposition is unknown for any of the

Osirini, but, if it is found to be like that of the Melectini and Ericrocidini, then a pattern would appear to be established between inserting a *small* egg in a closed cell to which the host female will no longer return and hiding a *smaller* egg in the cell wall from a returning host female.

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