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Eggs, Ovariole Numbers, and Modes of Parasitism of Cleptoparasitic Bees, with Emphasis on Neotropical Species (Hymenoptera: Apoidea)

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CONTENTS

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ABSTRACT

The shapes, sizes, and chorionic ornamentation of mature oocytes/eggs are described along with ovariole and mature oocyte numbers of six lineages of primarily South American cleptoparasitic bees. This information is related to whether the eggs are introduced into brood chambers that are still open and being provisioned by the host female or whether the chambers have already been closed by the host females. The lineages, all in the Apidae, are as follows: (1) *Kelita* (Nomadinae: Brachynomadini), (2) *Isepeolus* and *Melectoides* (Apinae: Isepeolini), (3) *Leiopodus* (Apinae: Protepeolini), (4) *Rhathymus* (Apinae: Rhathymini), (5) *Mesoplia* and *Epiclopus* (Apinae: Ericrocidini), and (6) *Exaerete* (Apinae: Euglossini).

A table in the section on Discussion and Analyses summarizes information on mature oocyte/egg size (egg index), total number of mature oocytes, mature oocytes per ovariole, and ovariole number (ovariole formula) for all taxa of cleptoparasites, worldwide, that have been studied to date. It shows that almost all of the Nomadinae have more than the plesiomorphic number of ovarioles, a feature also found in two of the three studied genera of the Ericrocidini. All other cleptoparasitic lineages lack extra ovarioles. The potential selective advantage of extra ovarioles is discussed. Also discussed is whether the large number of mature oocytes carried by cleptoparasites might result, in part, from the length of time required for chorion deposition after the oocytes reach maturity.

The table shows not only that the mature oocytes/eggs of cleptoparasitic bees in general tend to be smaller than those of solitary bees, but that the mature oocytes/eggs of those cleptoparasites that hide their eggs in open host brood cells are significantly smaller than those that introduce their eggs into cells that have been closed by the host. The potential selective advantages of small egg size in cleptoparasitism are explored.

Lastly, the unusual modified shapes of mature oocytes/eggs and the thick chorions of cleptoparasites that oviposit in open host cells are attributed to ways of protecting the eggs from discovery and damage by returning host females.

Appended is a scanning electron micrograph of the micropyle of the North American *Stelis elongativentris* Parker (Megachilidae: Anthidiini), the ovariole and oocyte statistics of which have been published earlier. Also appended are a description and illustrations of the oocyte of *Coelioxys novomexicana* Cockerell (Megachilidae: Megachilini).

INTRODUCTION

Eggs of cleptoparasitic bees display considerable variation in size, shape, and chorionic ornamentation. Methods by which cleptoparasites introduce their eggs into host cells and by which the host offspring (eggs or larvae) are killed also vary among lineages. Furthermore, some cleptoparasites exhibit an increased number of ovarioles, presumably an adaptation enabling them to have more mature oocytes ready to be deposited in quick succession. This paper presents new information regarding these matters with respect to six groups of cleptoparasitic Apidae (sensu Roig-Alsina and Michener, 1993; Michener, 2000) found primarily or exclusively in South America: *Kelita* (Nomadinae: Brachynomadini), *Isepeolus* and *Melectoides* (Apinae: Isepeolini), *Leiopodus* (Apinae: Protepeolini), *Rhathymus* (Apinae: Rhathymini), *Mesoplia* and *Epiclopus* (Apinae: Ericrocidini), and *Exaerete* (Apinae: Euglossini). Also included is new descriptive information about the mature oocytes of the North American ericrocidine genus *Ericrocis*. Finally, this paper summarizes (see table 1) published data regarding eggs/oocytes and ovariole numbers of all cleptoparasitic bees studied to date. Appended is information about two North American species belonging to the megachilid genera *Stelis* and *Coelioxys*.

MATERIALS, METHODS, AND TERMINOLOGY

MATERIALS: Information about *Isepeolus luctuosus* (Spinola), *Melectoides triseriatus* (Friese), and *Kelita tuberculata* Ehrenfeld and Rozen resulted from fieldtrips to Chile in October and November 2000 and in October 2001. On the latter trip, females of *Kelita toroi* Ehrenfeld and Rozen and *Epiclopus gayi* Spinola were also collected for this study.

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TABLE 1

Number of Ovarioles and Number and Sizes of Mature Oocytes/Eggs of Cleptoparasitic Bees

Taxa arranged by family, subfamily, and tribe according to Michener (2000). Numbers in the first three columns are means if more than one specimen has been examined. Numbers in the next to last column refer to the following citations in References: (1) Alexander and Rozen, 1987; (2) Iwata, 1955; (3) Rozen, 1986a; (4) Rozen, 1992; (5) Rozen and Roig-Alsina, 1991; (6) Rozen and McGinley, 1991; (7) Iwata, 1960; (8) Iwata, 1965; (9) Rozen, 1994b; (10) Roig-Alsina and Rozen, 1994; (11) Alexander, 1996; (12) Rozen et al., 1997; (13) Rozen, 1997; (14) Rozen, 2001; (15) Garófalo and Rozen, 2001; and (16) Alves-dos-Santos et al., 2002; (17) Rozen and Özbek, 2003. Boldfaced citations in last column refer to the species listed in the first column; citations in regular type refer to another species in the genus listed in the first column. For explanation of shading, see text.

Taxon	Egg index	No. total mature oocytes	Mature oocytes /ovariole	Ovariole formula	No. of specimens	Refs. to egg index, ovariole, oocyte data	Refs. to mode of parasitism
HALICTIDAE							
HALICTINAE							
Sphecodes esakii Strand & Yasumatsu	0.36	9	1.50	3:3	2	2	Sick et al., 1994; Bohart,
Sphecodes japonica Cockerell	—	4	0.67	3:3	2	2	1970
Sphecodes sp. A	0.57	6	1.00	3:3	1	1	
Sphecodes sp. B	0.76	—	—	3:3	1	1	
MEGACHILIDAE							
MEGACHILINAE							
Tribe Anthidiini							
Euaspis basalis Ritsema	0.53	3.5	0.58	3:3	3	1, 7	**Iwata, 1933**
Stelis elongativentris Parker (as *Stelis* sp.)	0.61	2.67	0.44	3:3	3	1	**Rozen, 1987**
Tribe Dioxyini							
Dioxys cincta (Jurine)	0.39	7	1.17	3:3	4	17	**Rozen & Özbek, 2003**
Dioxys pacificus Cockerell	0.77	1.5	0.23	3:3	2	1	
Dioxys pacificus Cockerell				3:3	4	17	
Dioxys p. pomonae Cockerell	0.66	—	—	—	—	17	**Rozen & Favreau, 1967**
Tribe Megachilini							
Coelioxys brevis Eversmann	0.40	5	0.83	3:3	1	2	Iwata, 1939; Baker,
Coelioxys decipiens Spinola	—	4	0.67	prob. 3:3	1	8	1971;
Coelioxys fenestratus Smith	0.54	18	3.00	3:3	1	2	Ramirez-A. et al., 1996;
Coelioxys novomexicana Cockerell	0.46	—	—	3:3	1	this study	Michener, 2000. Michener
Coelioxys yanonis Matsumura	—	2	0.33	3:3	1	2	stated that some species lay
Coelioxys (Rhinocoelioxys) sp.	0.41	—	—	prob. 3:3	1	1	eggs after cell closure but
Coelioxys sp. (138)	—	9	1.50	3:3	1	2	gave no further details.
APIDAE							
NOMADINAE							
Tribe Hexepeolini							
Hexepeolus rhodogyne Linsley & Michener	0.44	11	0.61	11:9	1	4	**Rozen, 1992, 1994b**
Hexepeolus rhodogyne Linsley & Michener				9:8	1	11	
Tribe Brachynomadini							
Brachynomada roigi Rozen	0.23	20	—	—	1	9	**Rozen, 1994a**
Brachynomada scotti Rozen	0.28	14	0.78	9:9	1	13	**Rozen, 1997**
Kelita chilensis (Friese)	0.30	7	0.70	prob. 5:5	1	3	**Rozen, 1970**
Kelita toroi Ehrenfeld & Rozen	0.25	10.63	—	~10:10	1	9	**Rozen, 1994a**
Kelita toroi Ehrenfeld & Rozen			0.54	7:9	1	this study	
Kelita toroi Ehrenfeld & Rozen				7:8	2	this study	

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TABLE 1
(Continued)

Taxon	Egg index	No. total mature oocytes	Mature oocytes /ovariole	Ovariole formula	No. of specimens	Refs. to egg index, ovariole, oocyte data	Refs. to mode of parasitism
NOMADINAE (Continued)							
Tribe Brachynomadini (Continued)							
Kelita toroi Ehrenfeld & Rozen				12:12	1	this study	
Kelita toroi Ehrenfeld & Rozen				8:8	1	this study	
Kelita toroi Ehrenfeld & Rozen				11:11	1	this study	
Kelita tuberculata Ehrenfeld & Rozen	0.38	6.5	0.67[a]	5:4[a]	2	this study	
Melanomada chica Snelling	0.39	5	0.3?	9:?6	1	9	Rozen & Snelling,
Melanomada margaretae Rozen	0.40	5	0.30	9:8	1	9	1986
Paranomada nitida Linsley & Michener	0.26	>18	0.90	10:10	1	11	Rozen, 1977
Paranomada nitida Linsley & Michener				10:10	1	9	
Triopasites penniger (Cockerell)	0.30	11	0.79	7:7	2	11	**Rozen, 1977**
Tribe Nomadini							
Nomada articulata Smith (as *Centrias articulata)*	0.28	—	—	5:5	3	1	Linsley & MacSwain,
Nomada banksi Cockerell	0.30	15.5	1.55	5:5	3	1	1955
Nomada illinoensis Robertson	—	—	—	5:4	1	1	
Nomada japonica Bischoff	0.39	21.13	2.15	5:5	6	2	
Nomada pyrifera Cockerell	0.50	14.5	1.45	5:5	2	2	
Nomada vicina Cresson	0.39	8	0.80	5:5	1	1	
Nomada sp. nr. *glabella* Thompson	0.38	8.67	0.90	5:5	2	2	
Nomada ("Gnathias") sp.	—	—	—	5:5	1	1	
Tribe Epeolini							
Doeringiella grandis (Friese) (as *Triepeolus* sp. R)	0.49	2	0.20	5:5	1	1	**Rozen, 1984**
Doeringiella pectoralis (Robertson) (as *Triepeolus pectoralis*)	0.62	5	0.50	5:5	1	1	Torchio,1986; Rozen, 1989
Epeolus scutellaris Say	0.76	6.33	0.45	7:7	4	1	Rozen & Favreau,
Epeolus zonatus Smith	0.53	8.5	0.85	5:5	2	1	1968;
Epeolus sp.	0.56	4	0.40	5:5	1	1	Torchio & Burdick,
Epeolus japonicus Bischoff	1.00	6.5	0.54	6:6	2	2	1988
Tribe Ammobatoidini							
Ammobatoides abdominalis (Eversmann)	0.27	15	1.50[a]	5:5	2	14	**Rozen, 2001**
Holcopasites calliopsidis (Linsley)	—	—	—	5:6	1	1	Rozen, 1965
Holcopasites eamia (Cockerell)	0.23	10	1.00	5:5	3	11	
Holcopasites insoletus (Linsley)	0.26	7.33	0.73	5:5	2	11	
Holcopasites insoletus (Linsley)				5:5	1	17	
Holcopasites prob. *tegularis* Hurd & Linsley	0.41	6.5	0.65	5:5	4	11	
Holcopasites tegularis Hurd & Linsley	0.45	4	0.40	5:?5	1	17	
Tribe Biastini							
Biastes brevicornis (Panzer)	0.18	32	1.60	~10:10	1	17	
Neopasites cressoni Crawford	0.31	14.5	1.16	6:6	2	11	**Torchio et al., 1967**
Neopasites cressoni Crawford				7:6	3	11	
Neopasites cressoni Crawford				5:6	1	12	
Rhopalolemma rotundiceps Roig-Alsina	0.38	20.7	0.58[a]	17:14+[a]	3	12	**Rozen et al., 1997**

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TABLE 1
(Continued)

Taxon	Egg index	No. total mature oocytes	Mature oocytes /ovariole	Ovariole formula	No. of specimens	Refs. to egg index, ovariole, oocyte data	Refs. to mode of parasitism
NOMADINAE (Continued)							
Tribe Townsendiellini							
Townsendiella pulchra Crawford	0.62	6.18	0.44	7:7	2	6	**Rozen &**
Townsendiella pulchra Crawford				7:7	3	11	**McGinley, 1991**
Tribe Neolarrini							
Neolarra californica Michener	0.33	13.75	1.325	5:5	3	1	
Neolarra californica Michener				5:6	1	1	
Neolarra vigilans (Cockerell)	—	11	1.10	5:5	1	1	
Neolarra (Neolarra) sp.	—	—	—	5:5 (or 5:4)	1	1	
Tribe Ammobatini							
Ammobates carinatus Morawitz	0.47	6	0.50	6:6	1	1	
Oreopasites (Oreopasites) favreauae Rozen (as *Oreopasites* sp. A)	0.49	7	0.74	5:4	1	1	**Rozen, in Bohart, 1970**
Oreopasites (Oreopasites) favreauae Rozen (as *Oreopasites* sp. A)	—	—	—	5:5 (or 6:4)	1	1	
Oreopasites (Oreopasites) vanduzeei Cockerell	—	—	—	approx. 11 total	1	3	
Oreopasites (Oreopasites) vanduzeei Cockerell				Prob. 5:5	1	3	
Oreopasites (Oreopasites) vanduzeei Cockerell	0.35	11.5	0.80[a]	5:5[a]	2	17	
Oreopasites (Perditopasites) barbarae Rozen	0.63	8	0.80	5:5	2	17	
Oreopasites (Perditopasites) linsleyi Rozen	0.60	5	0.50	5:5	1	17	
Parammobatodes rozeni Schwarz	0.41	7	0.58	6:6	1	17	
"*Parammobatodes*" *orientana* (Warnke)	0.52	8.5	1.06	4:4	2	17	
Pasites maculatus Jurine	0.47	13	1.44 or 1.63	4:4 or 4:5	1	17	**Rozen, 1986b**
Sphecodopsis (Pseudodichroa) capensis (Friese)	0.72[b]	—	—	—	—	17	**Rozen & Michener, 1968**
Sphecodopsis (Pseudodichroa) fumipennis (Bischoff)	0.67[b]	—	—	—	—	17	**Rozen & Michener, 1968**
Tribe Caenoprosopidini							
Caenoprosopis crabronina Holmberg	0.40[a]	28.5	2.75	6:6	1	5	**Rozen & Roig-A., 1991**
Caenoprosopis crabronina Holmberg	—			5:5	1	11	
Caenoprosopina holmbergi Roig-A.	0.48	12	1.00	6:6	1	5	
APINAE							
Tribe Isepeolini							
Isepeolus luctuosus (Spinola)	0.45	4.7	0.60[b]	4:4[b]	6	this study	
Isepeolus viperinus (Holmberg)	0.47	3	0.38	prob. 4:4	1	11	
Melectoides triseriatus (Friese)	0.47	5	0.63	4:4	1	11	
Melectoides triseriatus (Friese)				4:4[c]	5	this study	
Tribe Osirini							
Epeoloides coecutiens (Fabricius)	0.70	4.4	0.55	4:4	5	14	
Osirinus lemniscatus Roig-Alsina	0.79	3.5	0.44	4:4	2	11	
Parepeolus aterrimus (Friese)	0.88	1	0.13	4:4	1	11	
Tribe Protepeolini							
Leiopodus abnormis (Jörgensen)	0.31	8	1.00	4:4	1	10	**Roig-A. & Rozen, 1994**
Leiopodus lacertinus Smith	0.25	9.5	1.19	prob. 4:4	2	10	**Roig-A. & Rozen, 1994**

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TABLE 1
(Continued)

Taxon	Egg index	No. total mature oocytes	Mature oocytes /ovariole	Ovariole formula	No. of specimens	Refs. to egg index, ovariole, oocyte data	Refs. to mode of parasitism
APINAE (Continued)							
Tribe Protepeoline (Continued)							
Leiopodus singularis (Linsley & Michener)	0.32	12.2[b]	1.50[b]	4:4	5	11	**Rozen et al., 1978**
Leiopodus singularis (Linsley & Michener)				—	1	10	
Leiopodus trochantericus Ducke	0.24	10+	1.25?	prob. 4:4	1	10	
Tribe Tetrapedini							
Coelioxoides waltheriae Ducke	0.68	2[d]	0.25[d]	4:4	4	16	**Alves-dos-Santos et al., 2002**
Tribe Rhathymini							
Rhathymus bicolor Lepeletier & Serville	0.61	4	0.50	4:4	1	this study	Camargo et al., 1975
Rhathymus sp. A	0.58	3.5	0.44	4:4	4	this study	
Tribe Ericrocidini							
Epiclopus gayi Spinola	0.74	2	0.20	5:5	1	this study	
Ericrocis lata (Cresson)	0.79	2	0.20	5:5	1	1	
Ericrocis lata (Cresson)				5:5	1	this study	
Mesoplia prob. *rufipes* (Perty)	0.74	4	0.50	4:4	1	1	Vinson et al., 1987
Mesoplia rufipes (Perty)	0.76	2	0.25	4:4	3	this study	**Rozen, 1991**
Tribe Melectini							
Melecta albifrons albovaria Erichson	0.59	3	0.38	4:4	3	17	Rozen & Özbek, 2003
Thyreomelecta kirghisia Rightmyer & Engel	0.68	4	0.50	4:4	1	17	
Thyreus japonicus (Friese)	0.85	3.5	0.44	4:4	2	2	
Thyreus lieftincki Rozen	0.82-0.84	—	—	—	—	17	**Rozen, 1969**
Xeromelecta californica (Cresson)	0.59	5.3	0.67	4:4	3[e]	17	**Torchio & Trostle, 1986**
Zacosmia maculata desertorum Cockerell	0.74	6	0.75	4:4	1	1	**Torchio & Youssef, 1968**
Tribe Euglossini							
Exaerete smaragdina (Guérin-Méneville)	0.55	2	0.25	4:4	2	15	**Garófalo & Rozen, 2001**

[a] Based on one specimen.
[b] Based on five specimens.
[c] One of five specimens had an ovarian formula of 4:3.
[d] Based on three specimens.
[e] A fourth specimen had no mature oocytes and presumably had just emerged from the pupal stage.

Adults of the two species of *Rhathymus* and the one of *Mesoplia* were collected by Dr. Maria Cristina Gaglianone at a nesting site of *Epicharis nigrita* Friese. All specimens collected by her bear the same data. She (in litt.) stated that one species of *Rhathymus* was *R. bicolor* Lepeletier and Serville, distinguishable from the other because of its dark mesosoma contrasting with the red metasoma. The other species, uniformly red, did not agree with specimens of *R. unicolor* (Smith) available to her, and is therefore termed *Rhathymus* species A in this paper. She identified the *Mesoplia* as *M. rufipes* (Perty), the

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name used here. However, the legs of the specimens in Kahle's solution seemed far redder than those on the specimen, similarly preserved, treated (as *M.* probably *rufipes*) by Alexander and Rozen (1987). They were also redder than those of dried specimens, identified as *M. rufipes* in the collection of the American Museum of Natural History. I dissected all specimens provided by Dr. Gaglianone in January 2001 while I was visiting the Bee Laboratory at the University of São Paulo, São Paulo, Brazil.

METHODS: In the last half century there has been considerable interest in the comparative morphology of the female reproductive tract of bees and in the size and structures of bee eggs (and mature oocytes) (e.g., see reference in table 1) because such information has phylogenetic significance and might relate to bee behavior, ecology, and sociality. Iwata (1955, 1960, 1965) described and discussed these matters for Aculeate Hymenoptera in general. Subsequently, Iwata and Sakagami (1966), working on bees alone, developed an index whereby the size of an egg (or mature oocyte) could be related to the body size of the female. The index is calculated by dividing the length of the egg or mature oocyte (E) by the distance between the outer extremities of the tegulae (M), that is, egg index = E/M. The system has been used with slight modification, as explained by Alexander and Rozen (1987) and Alexander (1996), for all subsequent studies listed in table 1. In addition, Iwata and Sakagami (ibid.: table 2) developed a classification of eggs based on their sizes relative to the body sizes of the female, as follows:

> *dwarf* ($E/M \leq 0.50$); *small* ($0.50 < E/M \leq 0.75$); *medium* ($0.75 < E/M \leq 1.00$); *large* ($1.00 < E/M \leq 1.10$); *giant* ($1.10 < E/M$).

Because eggs of cleptoparasitic bees tend to have thick, conspicuous chorions, I consider oocytes to be mature once the ova are completely surrounded by chorion. Because the thick chorion gradually builds up on such oocytes, tubercles and other features gradually appear and presumably can account for considerable variation among the mature oocytes of a female. See the introduction and remarks sections of *Leiopodus abnormis*, below, for a case in point.

Although much of the information about ovariole number and oocyte size and morphology has come from dissecting specimens preserved in Kahle's solution, I developed a new technique on the most recent trip to Chile. I dissected freshly killed females by rupturing the conjunctiva between the second and third metasomal segments both dorsally and ventrally. Then, gripping the anterior and posterior parts of the body with two pairs of forceps, I gently pulled them apart. The crop and midgut remained with the anterior part, while the ovaries remained with the rest of the metasoma. I subsequently removed terga and sterna of segments three and four to reveal the usually perfectly arrayed and separated ovarioles, which were then placed in Kahle's solution to be counted later. This technique avoids the distortion and adhesion usually found in specimens preserved intact, in which the full crop presses against the ovaries.

Data presented in table 1 are the same as those summarized by Alexander and Rozen (1987) and Alexander (1996), augmented to include the recent literature on the subject and new data described below with respect to *Kelita*, *Isepeolus*, *Melectoides*, *Rhathymus*, *Mesoplia*, *Epiclopus*, and *Ericrocis* (as well as *Coelioxys*).

TERMINOLOGY: Rozen (2001) described a pedunculate process arising from the mature oocyte of *Ammobatoides abdominalis* (Eversmann) and suggested that it might be the micropylar apparatus. This has now been supported by new findings (Rozen and Özbek, 2003) with respect to solitary and other cleptoparasitic bees, as well as by Erickson et al. (1986) with respect to honey bees. As varied as these openings are among different groups of bees, their constant presence and position at the anterior end of eggs and mature oocytes leave little doubt as to their function.

In all bees, the anterior end of the developing oocyte is pointed toward the anterior end of the female, so that all eggs are deposited posterior end first, and the micropyle is always found at the anterior end of the egg. However, problems exist distinguishing between dorsal and ventral surfaces in some cases, and the use of these terms needs to be explained. In the description of the mature oocyte of *Kelita toroi*, I refer to the flat surface seen in lateral view as the dorsal surface because I suspect that in all Nomadinae the

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micropylar process is dorsal (Rozen et al., 1997; Rozen, 2001; Rozen and Özbek, 2003). In *Isepeolus luctuosus*, the observed deposited egg clearly indicated that the micropyle was dorsal. Considering the similarity of egg anatomy of *I. luctuosus* and *Melectoides triseriatus*, there is no question about which surface is dorsal in the latter. However, in *Rhathymus*, *Epiclopus gayi*, and *Mesoplia rufipes* (as well as in the Melectini), the micropyles were apical on curved cylindrical oocytes with rounded front ends. While their shape appears radially symmetrical around their long axes, their microstructure is invariably bilaterally symmetrical, particularly in the vicinity of their micropyles (figs. 30, 35, 38, 43). In the descriptions pertaining to these taxa, I have used the terms outcurved and incurved to refer to the long surfaces of the oocytes. I suspect that the outcurved surface is dorsal because eggs of most solitary bees are deposited with the incurved surface facing the provisions, as with the ventral surface of the emerged larva.

I originally used the phrase ''mode of parasitism'' to refer to certain variables pertaining to the biology of cleptoparasitic bees (Rozen, 1991). These include: Is the cleptoparasitic egg introduced into the host cell before the host has sealed it, or does the parasite female insert her egg into a cell after it has been sealed? If the latter applies, does she open the cell, reach in and eliminate the host offspring with her mandibles, and replace it with her own egg, or does she make only a small hole in the cell wall or closure and oviposit through it? Is the host offspring eliminated by the female parasite or by her offspring, which has modified head structures enabling it to find and kill its competitor for the stored provisions? Which larval instar is so equipped to do this? These are all interesting questions when one studies the behavior, ecology, development, and anatomy of these organisms. Because the present contribution focuses on the anatomy and size of cleptoparasitic oocytes/eggs, particularly as these attributes relate to the cleptoparasite's way of gaining access to host cells, emphasis is placed on the first question: *Is the cleptoparasitic egg introduced into the host cell before the host has sealed it, or does the parasite female insert her egg into a cell after it has been sealed by the host?*

BRACHYNOMADINI

Kelita toroi Ehrenfeld and Rozen

The eggs/oocytes and ovariole counts of this species were previously reported by Rozen (1994a); the mature oocyte is redescribed here to provide additional details. Specimens examined for the current study were initially dissected in the field shortly after being killed, as described in Materials, Methods, and Terminology. Consequently, ovariole counts were more reliable, as was the recognition of mature oocytes, than if dissections had been made on whole specimens preserved in Kahle's solution. The average egg index of 0.25 is based on all known specimens.

DESCRIPTION OF MATURE OOCYTE (figs. 1–4): Length 0.43 mm, maximum width 0.23 mm lateral view, maximum width slightly less dorsal view (N = 19); egg index 0.23–0.29 (dwarf). Shape bilaterally symmetrical; dorsal surface (figs. 1, 2) incurved to nearly flat as seen in lateral view (the slightly outcurved dorsal surface depicted by Rozen [1994a: fig. 2] is atypical but visible on some oocytes (the median ridge in fig. 1 is an artifact resulting from critical-point drying); front end more narrowly rounded and tapering more than posterior end as seen in lateral view; maximum width in lateral view near midsection, in dorsal view usually posterior to midsection; hook-shaped micropylar process present at anterior end (figs. 1–4) with perhaps five or six pores opening posteriorly; length of process apparently somewhat variable (that of figs. 6, 7 long). Chorion moderately thick throughout, reflective, clear as seen through stereoscopic microscope, without ornamentation or other unusual external features except for micropylar process; under SEM examination, chorion with faint polygonal pattern (fig. 2) but without other significant features.

MATERIAL STUDIED: Six females, Chile: Limari Prov., Parque Nacional Fray Jorge, 21-X-2001 (J.G. Rozen, A. Ugarte, C. Espina).

REMARKS: The shape of the mature oocytes shows considerable variation even when taken from a single female.

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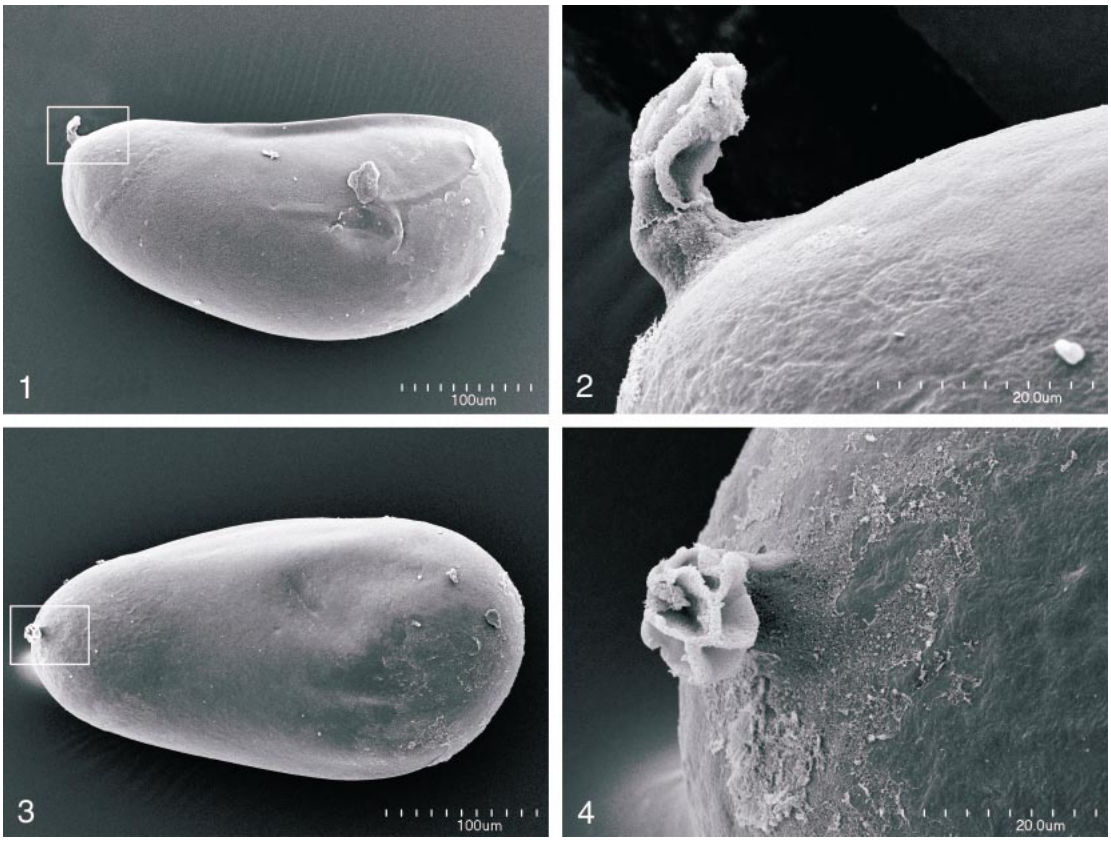

Figs. 1–4. SEM micrographs of mature oocytes of *Kelita toroi*. **1.** Entire oocyte, lateral view, anterior end toward left; apparent longitudinal ridge along top an artifact presumably created by critical-point drying. **2.** Close-up of micropylar process outlined by rectangle in fig. 1. **3.** Entire oocyte, dorsal view. **4.** Close-up of micropylar process outlined by rectangle in fig. 3.

Kelita tuberculata Ehrenfeld and Rozen

Except for its smaller size, the mature oocyte of *Kelita tuberculata* differs little from that of *K. toroi*.

DESCRIPTION OF MATURE OOCYTE (figs. 5–8): Length 0.35–0.40 mm; dorsal and lateral maximum widths about 0.19 mm (N = 13); egg index 0.36–0.39 (dwarf). Shape, micropyle, and chorionic features as described for *Kelita toroi*. Other features as described for *K. toroi*.

MATERIAL STUDIED: Two females, Chile: Limari Prov., 1 km E Parque Nacional Fray Jorge, 25-X-2000 (J.G. Rozen).

ISEPEOLINI

Most immature stages of *Isepeolus* have been known for many years (Michener, 1957; Lucas de Oliveira, 1966; Rozen, 1966, 1991, 2000a) and recently the mature larva of the sister genus *Melectoides* was described (Michelette et al., 2000). The first instar of *Isepeolus viperinus* (Holmberg) has tremendously elongate curved mandibles, clearly indicating that it is hospicidal. However, unknown were characteristics of the egg and whether the female enters open host cells that are still being provisioned or whether she introduces her eggs into cells that have been previously sealed by the host. Claude-Joseph (1926) reported that female *Isepeolus* oviposits on the provisions. Roig-Alsina (1991) suggested that the eggs might actually be hidden in the host cell, thus implying that the cell is attacked before cell closure. His suggestion was based on the female's modified sixth sternum, convergent with nonhomologous modifications in the

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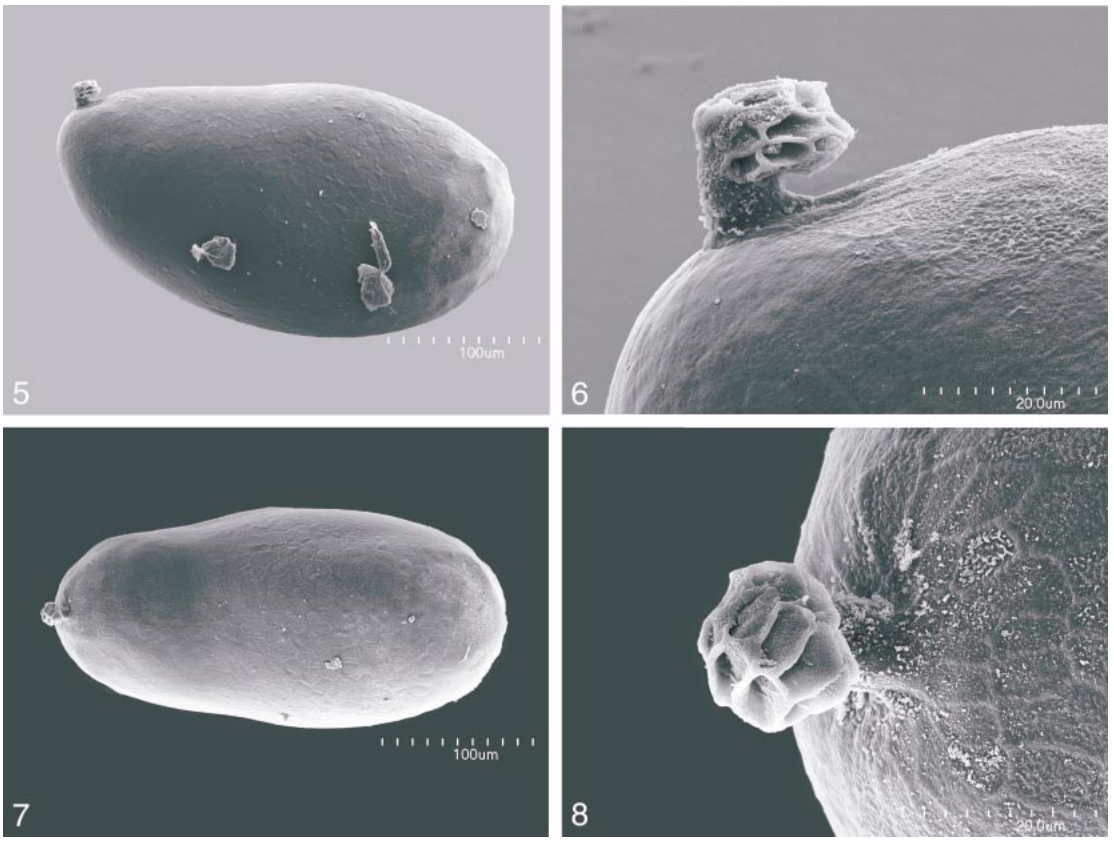

Figs. 5–8. SEM micrographs of mature oocytes of *Kelita tuberculata*. **5.** Entire oocyte, lateral view, anterior end toward left. **6.** Close-up of micropyle, lateral view. **7.** Entire oocyte, dorsal view. **8.** Close-up of micropyle, dorsal view.

Protepeolini and Nomadinae, which are known to enter open cells and hide their eggs in the cell walls.

On a fieldtrip to Chile in October and November 2000, I collected and preserved in Kahle's solution the cellophanelike linings of the cells of colletines from holes in vertical banks in Limari and Elqui provinces in the hope of recovering information about isepeoline eggs and how they are introduced into the host cells. Adults of both *Isepeolus luctuosus* and *Melectoides triseriatus* were collected at the nesting sites. I found three eggs of *I. luctuosus* on the cell linings of either *Colletes* or possibly *Mourecotelles*. (Subsequently, the partial remains of a chorion were also recovered from a cell lining, collected dry, containing a vacated cocoon of *I. luctuosus*).

Two eggs (one of which had hatched) were side by side in one cell, and the other was in another cell. Each cell contained a cast, darkly pigmented head capsule to which was attached the transparent, clear cast body skin of a first instar. The egg from the other cell had not hatched and presumably had been killed by the first instar, whose chorion was not detected. The chorion of the hatched egg had split anteriorly and longitudinally along one side at the time of eclosion, and the first instar presumably then killed the unhatched egg.[2] The cast first-instar exoskeletons were split longitudinally along the dorsal midline,

[2] The presumption that the intact eggs of *Melectoides triseriatus* were killed by the first instars of the same species is based on the fact that with many cleptoparasites, a first instar will kill the eggs or first instars of others of its kind that it encounters. I looked for puncture marks or tears in the chorions of the two eggs but was unable to see external damage.

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starting just behind the head; the head capsule of each was completely intact, as were the mandibular apodemes.

The identification of the cleptoparasite as *Isepeolus luctuosus* and not *Melectoides triseriatus* is based on the following: (1) the eggs were associated with distinctive first-instar head capsules morphologically nearly identical to those of *I. viperinus* (Michener, 1957; Lucas de Oliveira, 1966; Rozen, 1991), thereby indicating they belonged to the Isepeolini; (2) adults of *M. triseriatus* and *I. luctuosus* were the only isepeolines collected on that trip and a subsequent one to the two provinces in October 2001; and (3) on the second trip, females of *M. triseriatus* were preserved for dissection, and a colletid cell containing a pupal *I. luctuosus* in a cocoon had the shed head capsule preserved in the fecal material surrounding the cocoon. The head capsule was identical to the two recovered with the eggs the previous year. Furthermore, mature oocytes of *M. triseriatus* have a distinctively thick dorsal chorion unlike the thin one of *I. Luctuosus*, and they lack the roughened posteroventral patch characteristic of eggs and mature oocytes of *I. luctuosus* (see diagnosis under Description of Mature Oocyte of *Melectoides triseriatus*, below, for other features distinguishing the oocytes of the two species).

The only inconsistency between the eggs and mature oocytes of *Isepeolus luctuosus* is in their lengths. The eggs are longer (1.63–1.75 mm; N = 3) than the mature oocytes (1.08–1.30 mm; N = 7). This presumably results from the female depressing the egg as she attaches it to the cell lining, thereby making the egg dorsoventrally thinner and more elongate and wider than the mature oocyte.

Isepeolus luctuosus (Spinola)

Because of pronounced dissimilarities, the eggs and mature oocytes of this species are described separately below.

DESCRIPTION OF EGG (fig. 9): Length (not including the flange; see Remarks) 1.63–1.75 mm (N = 3), maximum width 0.69–0.92 mm (N = 3), maximum dorsal/ventral thickness approximately 0.25–0.38 mm (N = 2); egg index not calculated since intertegular distance of female unknown, but see description of mature oocyte. Shape greatly dorsoventrally flattened relative to width, bilaterally symmetrical along its moderately straight long axis; anterior end subtruncate in dorsal/ventral outline, posterior end tapering abruptly with rounded apex in dorsal/ventral outline; sides in dorsal/ventral outline gently curved with greatest width near middle, tapering somewhat more posteriorly than anteriorly in dorsal/ventral outline; micropyle a rosette on dorsal surface just posterior to anterior end as seen through stereomicroscope (for details, see description of mature oocyte, below). Color of ovum apparently slightly yellowish. Chorion dorsally and ventrally smooth, clear, except posterior end conspicuously, finely roughened ventrally; eclosion line not evident through stereoscopic exam-

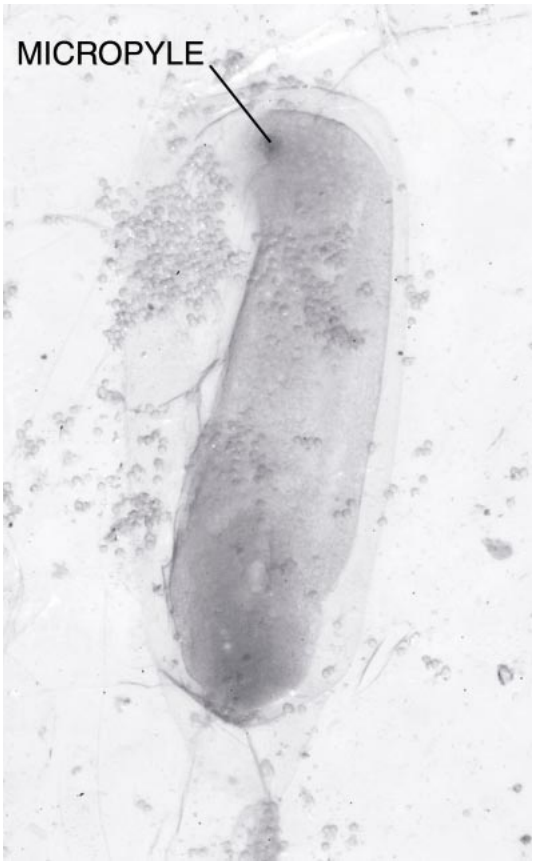

Fig. 9. Macrophotograph of egg of *Isepeolus luctuosus* attached to cellophanelike lining of host cell. Egg presumably killed by first instar of another individual.

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ination, but see description of mature oocyte; chorion of hatched egg apparently split along front and one side.

MATERIAL STUDIED: Three eggs, Chile: Limari Prov., Las Placetas, 6-XI-2000 (J.G. Rozen); one partial chorion same except 2-XI-2000. Las Placetas is a village a few kilometers southeast of Pisco Elqui.

REMARKS: The three eggs were glued longitudinally to the inner surface of the cellophanelike interior lining (two separated layers of lining clearly distinguishable, with threadlike strands extending from one layer to the other, as described by Torchio, 1965, for *Colletes ciliatoides* Stephen and by Rozen and Favreau, 1968, for *Colletes compactus compactus* Cresson). The inner surface was identifiable because the outer surface supported the fine filaments that ran to the outer layer. The inner lining was complete (i.e., without holes).

I interpret the extremely flattened appearance of these eggs to be an artifact created by their adhering so closely to the cell lining, in contrast to the more cylindrical mature oocyte (below). What causes the adhesion is unknown; it could result from a sticky ventral surface of the chorion itself or may be created by the female secreting some transparent substance on the lining at the time of egg deposition. The egg not only adheres to the surface, but it may also impress the lining to partially accommodate the thickness of the egg. Consequently, the egg projects little into the cell lumen. When first examined, the pointed posterior end of the egg appeared to be free from the cell lining. On closer examination, I detected a thin, totally transparent sheet of colorless, cellophanelike material (faintly visible in fig. 9) extending from the posterior end a short distance, where it was attached to the cell lining. Examination of the mature oocyte (fig. 10) revealed a flange of finely wrinkled chorion circumscribing the entire dorsal/ventral outline of the oocyte. On the oocyte, the flange drapes down and is more or less appressed to the body of the oocyte. It is longer toward the rear of the oocyte than on the sides or front. On the deposited egg, the flange extends out and attaches to the cell lining, thus forming a continuum with the cell lining that presumably helps to hide the egg from the returning host.

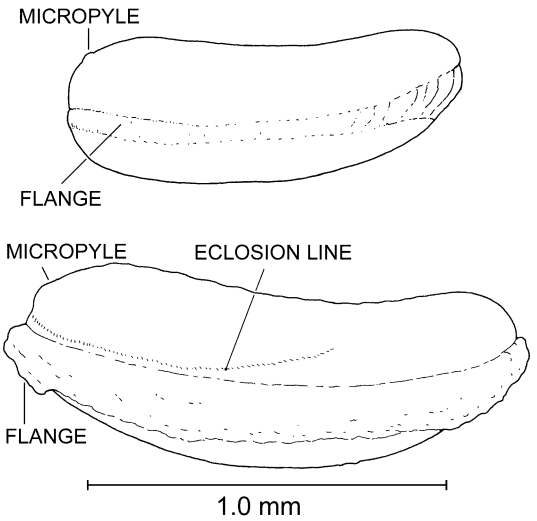

Fig. 10. Diagrams of mature oocytes of *Isepeolus luctuosus* (above) and *Melectoides triseriatus* (below), anterior ends toward left. Scale line refers to both.

Although the rear part of the flange was detected on the egg, I am uncertain whether the sides of the egg in figure 9 are outer boundaries of the flange or of just the body of the oocyte. Examination of freshly deposited eggs should lead to a better understanding of their structure.

There is strong circumstantial evidence that female *Isepeolus luctuosus* enters host cells that are still open to oviposit. The ventral surface of her egg is attached firmly to the cell lining, and she must somehow manipulate it with her metasoma to extend the flange and to stretch and dorsoventrally flatten the chorion as she oviposits. Cleptoparasites (i.e., Melectini, Ericrocidini, Tetrapediini, Rhathymini, *Exaerete*) that open closed host cells insert eggs that are freestanding or loosely attached to the cell closure or wall; their eggs are the more typical elongate ellipsoid eggs without flanges, similar to those of solitary bees. Further, it is unlikely that the parasite female would have time to open the elaborately folded cell closure of cellophanelike material, attach her egg to the lining, and then refold the closure, all while the host female was away gathering food for the next cell to be provisioned in the linear cell series. Eggs of parasites that open host cells

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tend not to be dwarfs and are obviously not concealed from returning foraging hosts because the host has finished with the cell after its egg deposition and cell closure. Cleptoparasites (e.g., Nomadinae, Protepeolini) that oviposit in cells still being provisioned while the host is away tend to have dwarf eggs that are hidden in various ways in the cell wall. *Melectoides triseriatus* has dwarf eggs (Alexander, 1996; table 1, herein), as do the two species of *Isepeolus* (table 1), and the egg of at least *I. luctuosus* is hidden by being flattened with a smooth exposed dorsal surface and flange that become a continuum with the cell lining. The oocyte of *M. triseriatus* is also fitted with a flange, suggesting similar concealment.

The lengthwise attachment of the eggs of *Isepeolus luctuosus* to the cell lining corresponds to the hole molds on the outer surfaces of the cocoons of *Melectoides bellus* (Jörgensen) illustrated by Michelette et al. (2000), which were questionably attributed to lengthwise cleptoparasitic oviposition holes in the cells wall of *Canephorula apiformis* (Friese). Lengthwise attachments of cleptoparasite eggs to cell surfaces are also known for the nomadine tribes Hexepeolini (Rozen, 1994b) and Biastini (Rozen et al., 1997), both of which oviposit in cells before they are closed.

The egg-laying behavior of *Isepeolus luctuosus* can be compared with that of other cleptoparasites that lay their eggs in colletine cells. Rozen and Michener (1968: figs. 5, 8–12) reported on the egg deposition of *Sphecodopsis* (*Pseudodichroa*) *capensis* (Friese) in nests of *Scrapter longula* (Friese) and *Sph.* (*P.*) *fummipennis* Bischoff in those of *Sc. crassula* Cockerell. Rozen and Favreau (1968: figs. 1, 2) described the egg deposition of *Epeolus pusillus* Cresson in the nests of *Colletes compactus compactus*. Torchio and Burdick (1988: figs. 1–19) provided an exceptionally detailed account of the egg deposition habits of *E. compactus* Cresson in the cells of *C. kincaidii* Cockerell. All of these parasitic bees enter the host cells while the cells are still open, so that their eggs are subject to discovery by host females returning with provisions. However, only *Isepeolus* deposits her eggs lengthwise on the inner surface of the cell lining. All others make small holes in the cell lining and insert their eggs through them so that only the anterior ends of the eggs are flush with the lining. In *Epeolus*, the exposed end of the egg is a flat or domed surface, presumably helping to obscure the egg from a returning host. With both species of *Sphecodopsis*, the anterior end of the egg is similarly modified but in addition has a thin flange radiating in all directions over the cell lining. This flange, appressed to the lining, is presumably a homolog of the flange identified in eggs of other ammobatines (Rozen, 1986a, 1986b; Rozen and Özbek, 2003) and may help seal the hole from liquids that might seep in or out (nests of *Scrapter* were in very moist sand) and/or may assist in hiding the egg from the host female.

DESCRIPTION OF MATURE OOCYTE (figs. 10–12): Length 1.08–1.3 mm, maximum diameter 0.35–0.50 mm (N = 7); egg index 0.31 (dwarf). Shape bilaterally symmetrical along its gently curved long axis with dorsal surface incurved; anterior end broadly rounded, posterior end more narrowly rounded; widest diameter near anterior end; midsection of oocyte very gradually tapering posteriorly; flange of finely wrinkled chorion circumscribing entire dorsal/ventral outline of egg; flange folded ventrally so closely to sides of egg below line of attachment that it is nearly invisible, not forming a conspicuous ridge as in *Melectoides triseriatus*; flange more visible toward posterior ends of oocytes because of series of elongate, blisterlike folds as seen in lateral view (fig. 10); micropyle a dorsal, slightly elevated rosette near anterior end consisting of perhaps 40 openings (as judged from fig. 12). Ovum white. Chorion of flange clear, presumably finely wrinkled; chorion elsewhere clear, reflective, and smooth except for finely roughened area ventrally at posterior end; eclosion (hatching) line not visible on uncoated oocyte, but visible on coated oocyte as a narrow band of polygonal plaques with elevated outlines extending around front of oocyte and along both sides, much as in *Melectoides triseriatus* (fig. 10).

MATERIAL STUDIED: Two females, Chile: Elqui Prov., Las Placetas, 2-XI-2000 (J.G. Rozen); three females, same except 14-X-2001 (J.G. Rozen, A. Ugarte, C. Espina).

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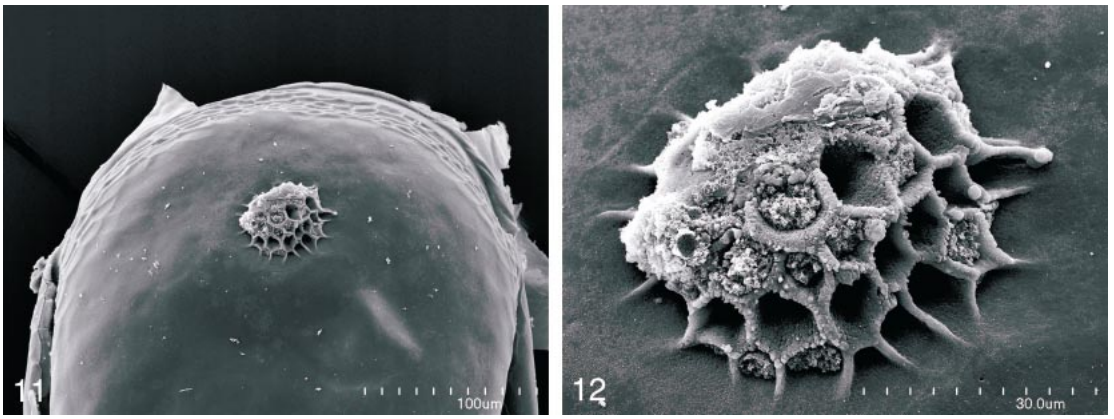

Figs. 11, 12. SEM micrographs of anterior end of mature oocyte of *Isepeolus luctuosus*. **11.** Dorsal view; note polygonal pattern of eclosion line anterior to micropyle. **12.** Close-up of micropyle.

Melectoides triseriatus (Friese)

The mature oocyte of this species differs from that of *Isepeolus luctuosus* as follows: (1) the flange is much more conspicuous; (2) the eclosion line is evident; (3) the dorsal chorion is much thicker compared with the ventral chorion and with the dorsal chorion of *I. luctuosus*; (4) the rear flange material does not form blisterlike swellings; and (5) the rear venter of the oocyte is not roughened compared with the rest of the ventral chorion.

DESCRIPTION OF MATURE OOCYTE (figs. 10, 13–15): Length 1.25–1.48 mm, maximum dorsal-view width 0.40–0.60 mm, maximum lateral-view width 0.38–0.50 mm (N = 9); dorsal width almost always greater than lateral width; egg index 0.47 (all specimens) (dwarf). Shape bilaterally symmetrical along its gently curved long axis with dorsal surface incurved; both ends rounded with maximum width and height about midsection; as seen in lateral view (figs. 10, 15), posterior end tapering more than anterior end; flange of finely wrinkled chorion circumscribing entire dorsal/ventral outline of oocyte; flange folded ventrally so that it more or less adheres to sides of oocyte below line of attachment, thus giving appearance that oocyte has a rounded ridge; rear flange not forming blisterlike swellings; micropyle a dorsal rosette near anterior end. Ovum white. Chorion of flange clear but wrinkled; rest of chorion faintly uneven on outer surface, clear except inner surface finely etched, hence somewhat milky; chorion of dorsal surface three times thicker than that of ventral surface; eclosion line a fine, silvery band easily split by manipulation with forceps, extending about two-thirds length of oocyte from anterior end on dorsal surface, as seen in figures 10 and 13.

MATERIAL STUDIED: Five females, Chile: Elqui Prov., Las Placetas, 15-X-2001 (J.G. Rozen, A. Ugarte, C. Espina).

REMARKS: Even before dissection, mature oocytes of this species were easily identified by the lateral ridge (formed by the folded flange) seen through the follicular tissue of the ovariole.

PROTEPEOLINI

Information about the egg indices and ovariole and oocyte numbers for four species of *Leiopodus* (summarized in table 1) has been presented by Roig-Alsina and Rozen (1994) and Alexander (1996), and mature oocytes/eggs of these species have been described and illustrated by Rozen et al. (1978) and Roig-Alsina and Rozen (1994). Added here is information about the micropyle and surface microstructure of the mature oocytes of three of the species examined by SEM. The specimens examined are the same as those described by Roig-Alsina and Rozen (1994) except that the specimen of *L. singularis* was no longer available; please see

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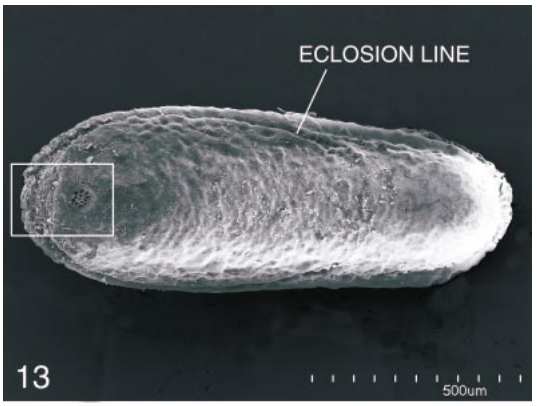

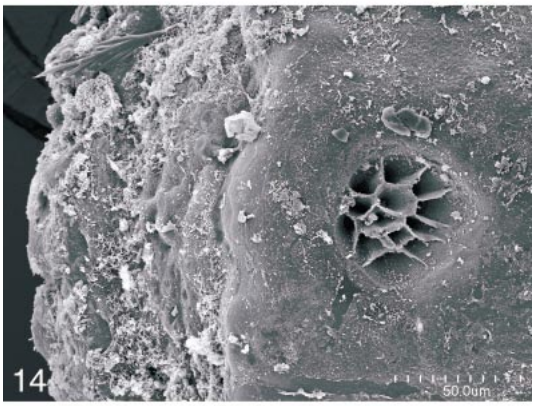

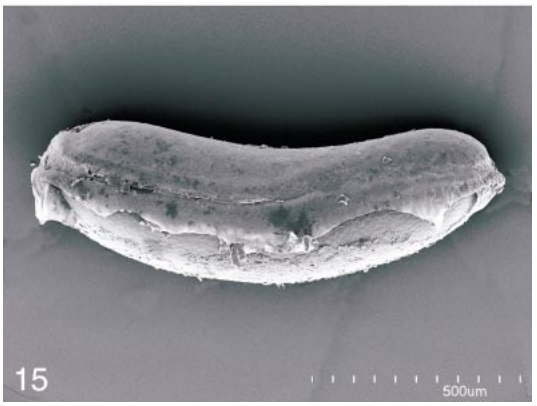

Figs. 13–15. SEM micrographs of mature oocyte of *Melectoides triseriatus*, anterior end toward left. **13.** Entire oocyte, dorsal view. **14.** Close-up of micropylar area as outlined by rectangle in fig. 13. **15.** Entire oocyte, lateral view.

their publication for collection data and general oocyte shape.

The striking differences in the oocytes of the four species *Leiopodus* were documented by Roig-Alsina and Rozen (1994), and the following accounts enhance these differences.

Leiopodus abnormis (Jörgensen)

Rozen and Özbek (2003) pointed out that the chorion of many cleptoparasitic bees is thicker than that of other bees and that the deposition of the chorion over an ovum after it is fully formed may take place over a greater period of time than that of other bees. Consequently, an early mature oocyte of cleptoparasites may have a different appearance than a late mature oocyte. I am almost certain that the great variation in the external appearance of mature oocytes of this species can be attributed to the various stages of chorionic deposition. This is because of the correlation of the size of the opercular tubercles with the extent of containment of the micropyle by the opercular rim, as is more fully explained under Remarks. The following description is based on what I think to be a late-stage mature oocyte.

DESCRIPTION OF MATURE OOCYTE (figs. 16–19): Chorion smooth under stereomicroscopic examination; under SEM examination, chorion at least of anterior part of oocyte (including the operculum) without patterning; opercular rim elevated so that disc recessed except for large paired tubercles that extend well beyond the rim (fig. 16); micropyle with pores tightly clustered and deeply recessed within micropylar aperture of the anterior edge of rim.

REMARKS: Figure 18 is thought to show an early-stage mature oocyte with the paired opercular tubercles just starting to be deposited. The opercular rim is elevated and evinces a polygonal patterning around its inner slope. The multipored micropyle cluster is well exposed (except for some follicular tissue that seems to be, but is not, a bridge of the chorionic opercular rim, fig. 18) and a faint polygonal patterning is apparent on the sides of the oocyte.

Figure 19 is interpreted to be an intermediate stage of chorionic deposition with the paired opercular tubercles partly developed but not extending beyond the elevated rim. The polygonal patterning is clearly visible on both surfaces of the rim, and the micropyle

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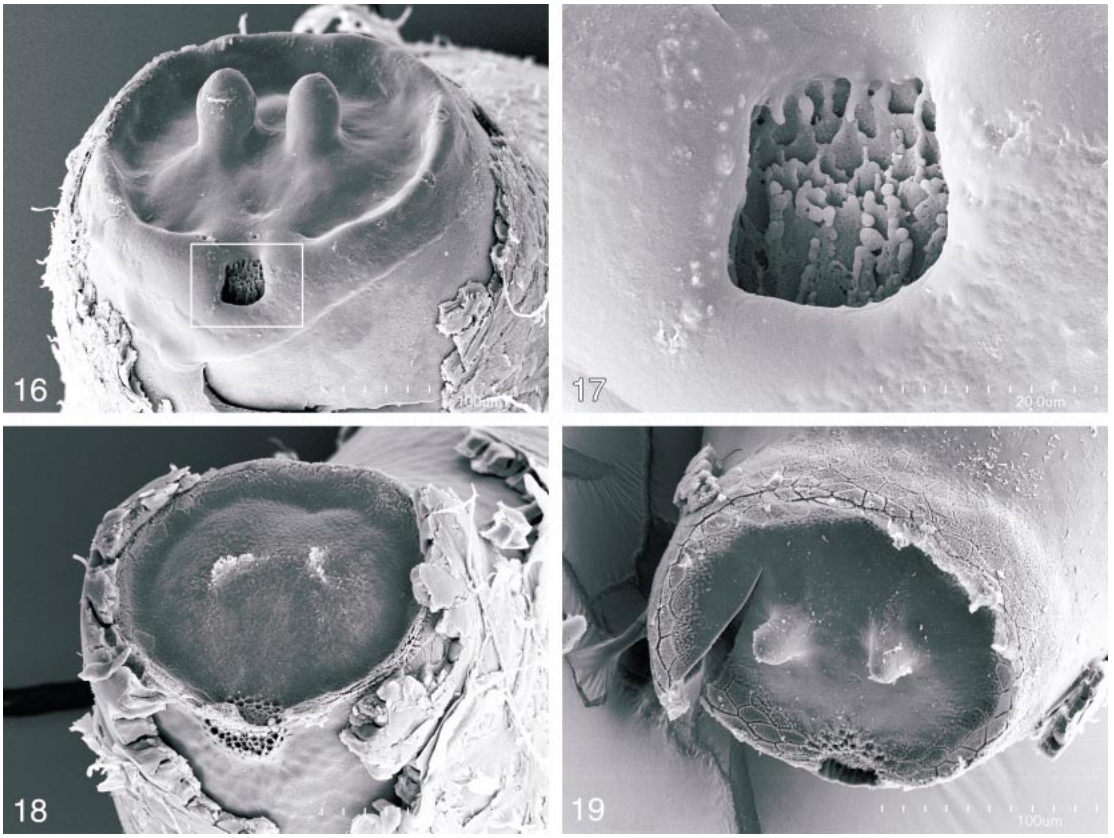

Figs. 16–19. SEM micrographs of operculum of mature oocyte of *Leiopodus abnormis*. **16.** Late stage, anterodorsal view. **17.** Close-up of micropyle; note opercular rim causing micropyle to be recessed. **18.** Early stage mature oocyte, with tubercles starting to be deposited, rim thin, and micropyle exposed (except for follicular debris appearing to divide it) anterodorsal view. **19.** Intermediate-stage mature oocyte, with tubercles partly developed and micropyle becoming recessed by rim, posterodorsal view.

aperture of the rim has enclosed the micropylar cluster.

Leiopodus lacertinus Smith

DESCRIPTION OF MATURE OOCYTE (figs. 20–24): Chorion smooth under both stereomicroscopic and SEM examination; opercular rim distinct but scarcely elevated; operculum nearly flat, without tubercles; micropylar aperture at anterior edge of rim; micropyle recessed on presumed late-stage mature oocyte (fig. 23). Unlike in other studied species of *Leiopodus*, oocyte with ventral band of forward-curving, hooklike chorionic projections (figs. 21, 22).

Leiopodus trochantericus Ducke

DESCRIPTION OF MATURE OOCYTE (figs. 25–28): Under both stereomicroscopic and SEM examination, dorsal surface of chorion irregularly uneven (fig. 25); opercular rim with edges rounded, slightly elevated; opercular disc with paired indistinct uneven protrusions; micropylar aperture of rim on anterior edge of rim; micropylar cluster of pores not visible on late-stage mature oocytes because it is obscured by follicular debris but distinct on somewhat earlier stage mature oocyte (fig. 28).

REMARKS: Figure 27 is considered to show an earlier stage mature oocyte because the opercular rim is sharper and the disc of the

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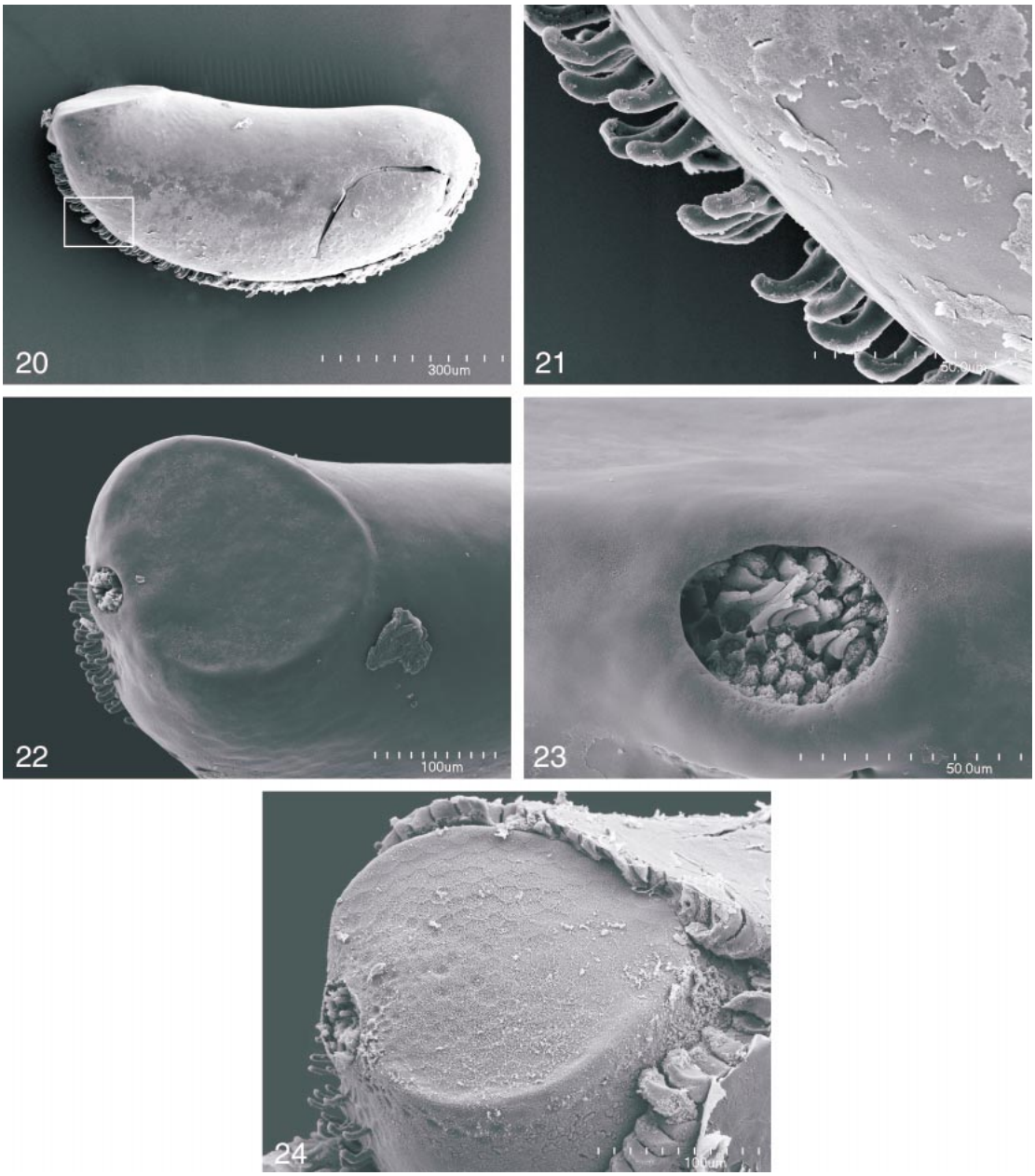

Figs. 20–24. SEM micrographs of mature oocyte of *Leiopodus lacertinus*. **20.** Entire oocyte, lateral view. **21.** Close-up of hooked ventral chorion projections in rectangle in fig. 20. **22.** Anterior end of oocyte, dorsolateral view, showing smooth operculum and position of micropyle, of presumed late-stage mature oocyte. **23.** Micropyle of presumed late-stage oocyte with most pores closed by debris, frontal view. **24.** Anterior end of oocyte, dorsolateral view, showing polygonal pattern suggesting that this is an early-stage mature oocyte.

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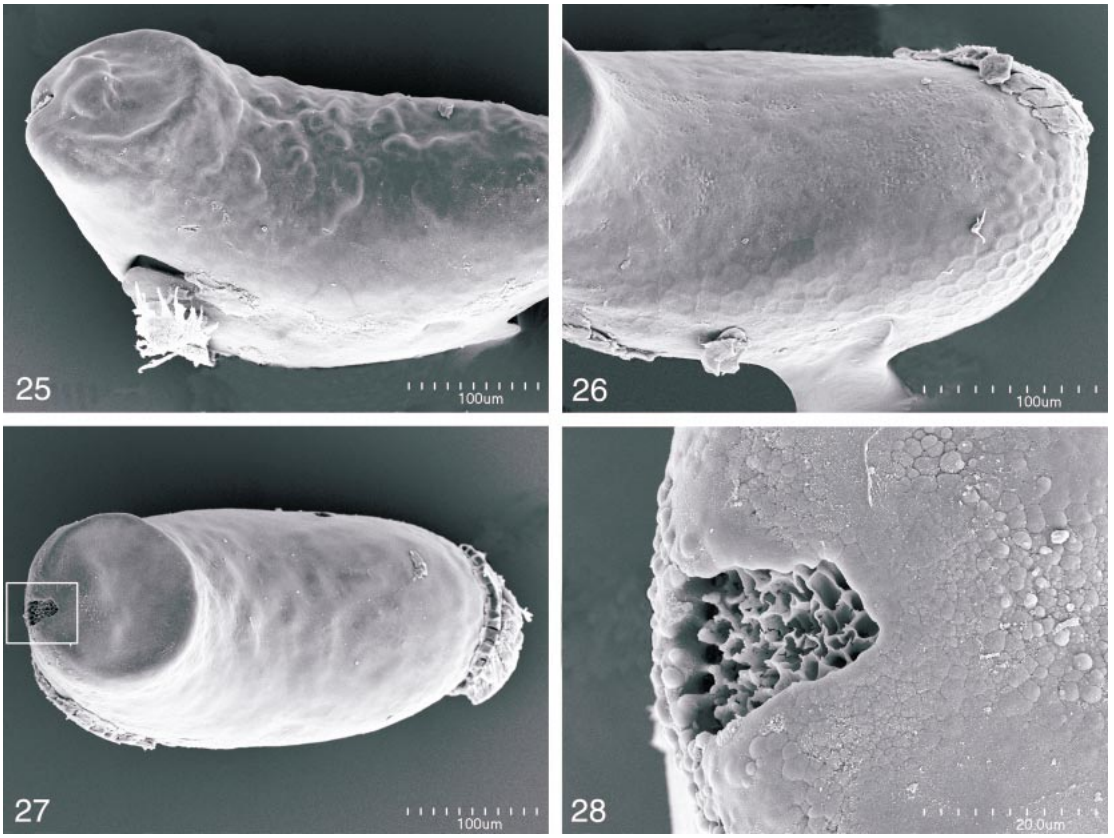

Figs. 25–28. SEM micrographs of mature oocyte of *Leiopodus trochantericus*. **25.** Entire late-stage oocyte (except for posterior tip), dorsolateral view; note uneven dorsal chorion behind operculum. **26.** Posterior part of early-stage oocyte, dorsolateral view, with dorsal chorion nearly smooth and strong polygonal pattern at posterior end. **27.** Intermediate-stage mature oocyte, nearly dorsal view, with dorsal chorion becoming uneven. **28.** Close-up of micropylar area identified by rectangle in fig. 27.

operculum and dorsal surface are far more even than those shown in figure 25. Because of the distinct polygonal patterning of the posterior and lateral parts of the chorion, figure 26 may show an even earlier stage.

RHATHYMINI

As summarized by Rozen (2000b), the eggs of *Rhathymus* (Camargo et al., 1975; Rozen, 1991) are introduced into cells that have already been sealed by the host female, and they hatch into larvae capable of killing the host offspring. However, the present study is the first to record (table 1) the number of ovarioles per ovary for any species of this monotypic tribe. The ovarian formula of 4:4 exhibited by both *R. bicolor* and *R.* species A is plesiomorphic in the Apidae.

Rhathymus bicolor Lepeletier and Serville

DESCRIPTION OF MATURE OOCYTE (figs. 29–31): Length 2.8–3.3 mm, maximum diameter 0.65–0.73 mm (N = 4); egg index 0.61 (small). Shape approximately symmetrical along its moderately curved long axis; rounded at both ends, with widest diameter near anterior end, then gradually tapering posteriorly; anterior pole not or scarcely produced; micropyle (fig. 30) a cluster of pores at anterior pole; pores directed toward outcurved surface. Chorion viewed through stereomicroscope smooth, dull, with inconspicuous polygonal pattern; boundaries of polygons more reflective than surfaces of polygons; as viewed by SEM, chorion surface with numerous shallow channels radiating from mi-

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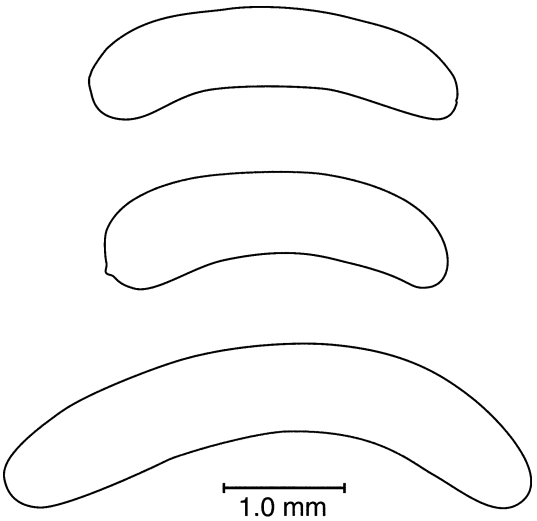


Fig. 29. Diagrams of mature oocytes of (from top to bottom) *Rhathymus bicolor*, *Rhathymus* species A, and *Epiclopus gayi*, lateral views, anterior ends to the left. Scale line (= 1.0 mm) refers to all figures.

cropylar pores toward outcurved surface; polygons immediately surrounding pores moderately conspicuous, with raised borders, becoming less conspicuous posteriorly.

MATERIAL EXAMINED: One female, Brazil: São Paulo, Luiz Antônio, Estação Ecológica de Jatai, 2-XI-2000 (M.C. Gaglianone), nesting site of *Epicharis nigrita*.

Rhathymus species A

DESCRIPTION OF MATURE OOCYTE (figs. 29, 32–36): Length 2.3–2.9, maximum diameter 0.55–0.73 mm (N = 14); egg index 0.54–0.65 (small); anterior pole produced as small elevation with micropylar pores clustered next to it toward outcurved surface (figs. 34, 35); other features as described for *Rhathymus bicolor*.

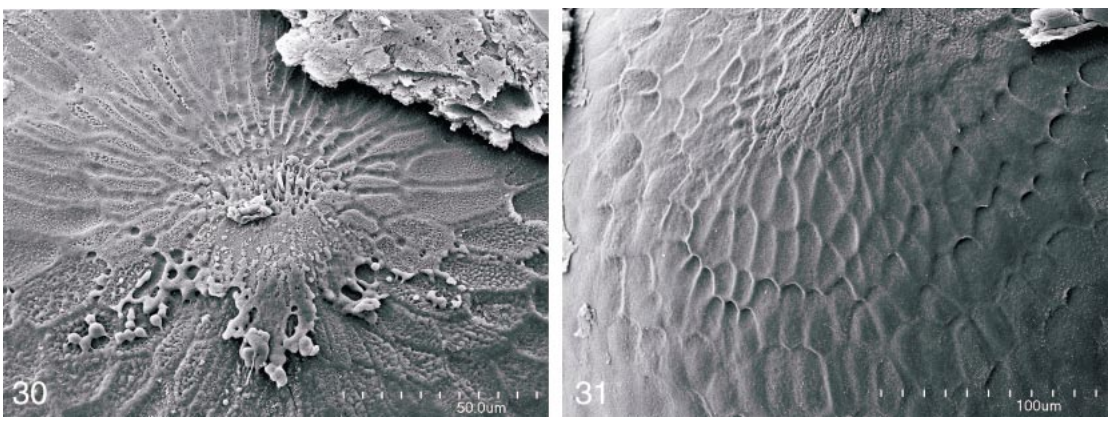
MATERIAL STUDIED: Four females, Brazil: São Paulo, Luiz Antônio, Estação Ecológica de Jatai, 2-XI-2000 (M.C. Gaglianone), nesting site of *Epicharis nigrita*.

ERICROCIDINI

Epiclopus gayi Spinola

The ovarian formula of this species is 5:5, like that reported for *Ericrosis lata* (Cresson) in table 1. These two species are the only cleptoparasites other than the Nomadinae reported to have more than the plesiomorphic number of ovarioles for their family.

DESCRIPTION OF MATURE OOCYTE (figs. 29, 37–42): Length 4.0–4.05 mm, maximum diameter 0.68 mm; egg index 0.74 (small). Shape approximately symmetrical along its moderately curved long axis, nearly parallel-sided; rounded at both ends; micropyle consisting of tight cluster of pores directed toward outcurved surface at anterior end (figs. 37, 38). Chorion dull, with microscopic sculpturing as seen through stereomicroscope; as seen through SEM, chorion with



Figs. 30, 31. SEM micrographs of mature oocyte of *Rhathymus bicolor*. **30.** Micropylar area. **31.** Polygonal pattern just below micropyle on incurved side.

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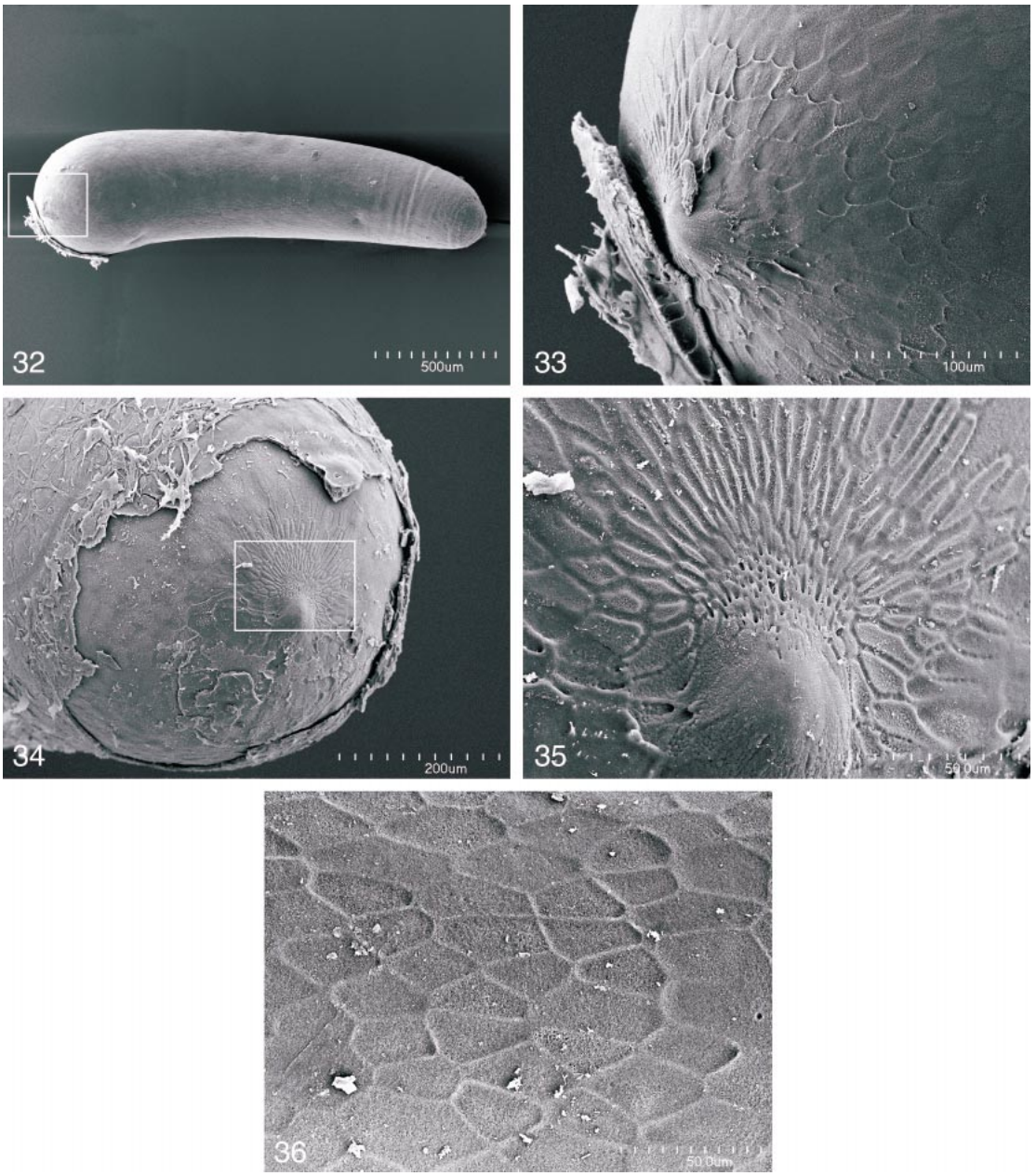

Figs. 32–36. SEM micrographs of mature oocyte of *Rhathymus* species A. **32.** Entire oocyte, incurved surface. **33.** Close-up of micropylar area identified by rectangle in fig. 32. **34.** Anterior end of oocyte of another specimen showing small elevation at anterior pole. **35.** Close-up of rectangle in fig. 34, showing micropyle just above elevation. **36.** Chorionic patterning at midbody.

strong polygonal pattern defined by incised borders anteriorly and on outcurved surface; adjacent to micropylar cluster on outcurved surface, polygons elongate, directed toward cluster; on outcurved surface polygons persist with flat smooth surfaces (figs. 39, 40); on incurved surface chorion nodular and quickly losing incised borders (figs. 39, 41).

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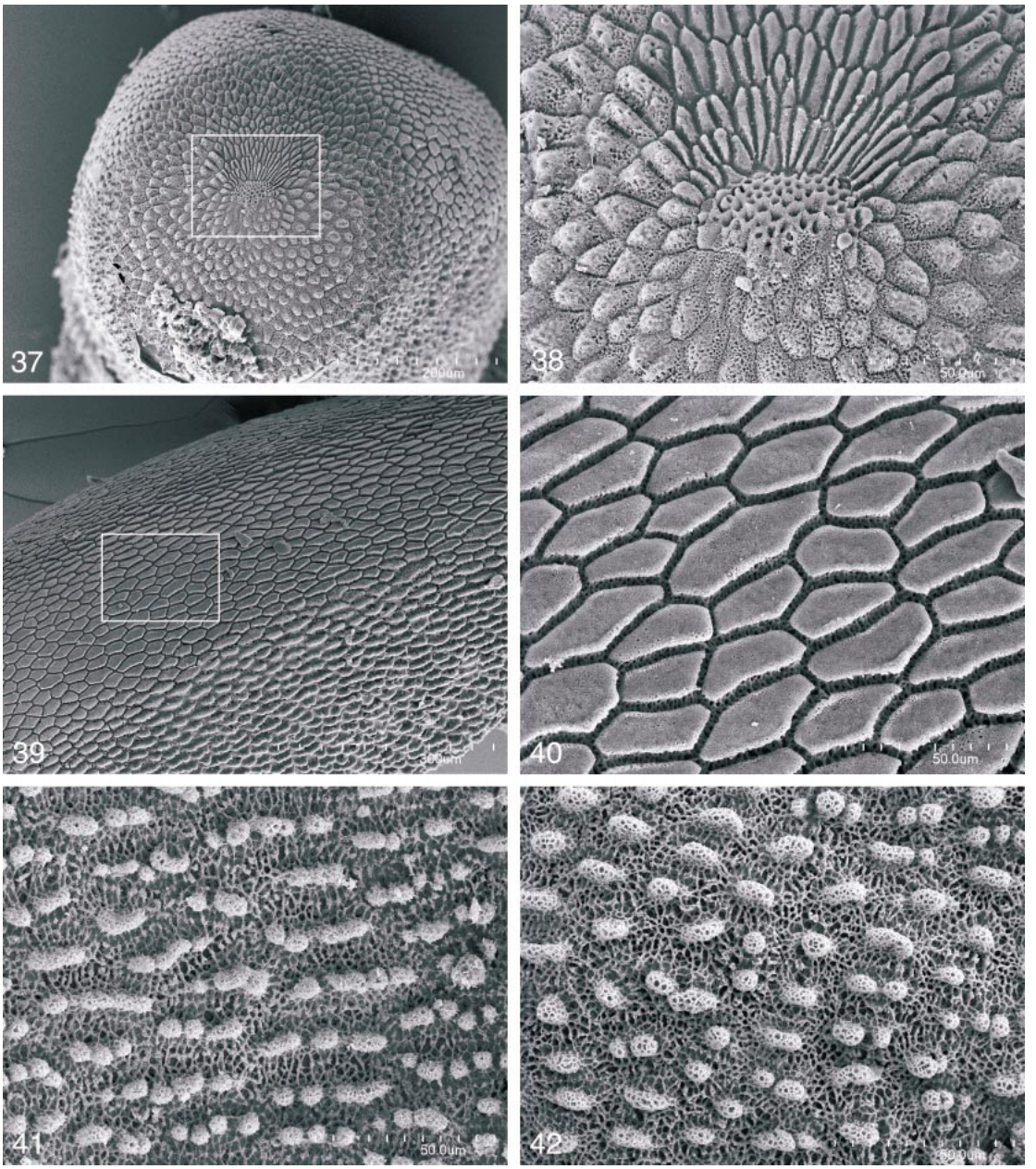

Figs. 37–42. SEM micrographs of mature oocyte of *Epiclopus gayi*. **37.** Anterior end. **38.** Close-up of micropylar area defined by rectangle in fig. 37. **39.** Midbody, showing smooth, platelike polygons defined by incised borders on outcurved (upper) surface and nodular patterning of incurved surface, lateral view. **40.** Close-up of outcurved surface in rectangle in fig. 39. **41.** Close-up of nodular surface at midbody. **42.** Close-up of nodular surface near posterior end.

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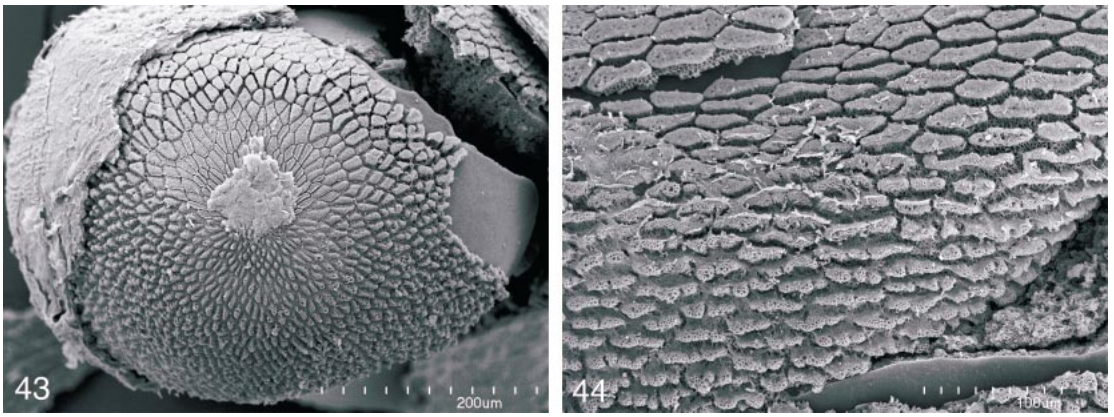

Figs. 43, 44. SEM micrographs of mature oocyte of *Ericrocis lata*. **43.** Anterior end with micropylar area barely visible just below follicular debris; note smooth, platelike, polygonal patterning on outcurved (upper) surface and nodular patterning on incurved surface. **44.** Midbody, showing platelike surface on outcurved surface changing to nodular patterning on incurved surface, lateral view.

MATERIAL STUDIED: One female, Chile, Limari Prov., Parque Nacional Fray Jorge, 21-X-2001 (J.G. Rozen, A. Ugarte, C. Espin a).

REMARKS: A noteworthy feature of the oocytes of this species is the difference in the microstructure of the chorion on the outcurved side compared to the incurved side. The smooth tilelike polygons of the outcurved surface contrast with the spongy nodular incurved surface. Although not found in *Mesoplia rufipes*, this feature is shared with *Ericrocis lata*, below. The egg deposition habits of both species should be investigated to ascertain a possible adaptive explanation that might account for this shift in microstructure from one surface of the egg to the other.

Ericrocis lata (Cresson)

Alexander and Rozen (1987) provided data on the number of ovarioles and oocytes of this species, which was then found to have an egg index of 0.77. Another specimen, whose mature oocytes are described here, had an egg index of 0.81, thus giving an average index of 0.79 for this species. Both specimens had an ovarian formula of 5:5.

DESCRIPTION OF MATURE OOCYTE (figs. 43, 44): Length 3.6 mm, maximum diameter approximately 0.6 mm; egg index 0.81 (medium). Shape approximately symmetrical along its moderately curved long axis, nearly parallel-sided; rounded at both ends; micropyle a cluster of pores at anterior pole (fig. 43). Chorion under SEM examination with strong polygonal pattern defined by incised borders anteriorly and on outcurved surface; adjacent to micropylar cluster on outcurved surface, polygons elongate, directed toward cluster; on outcurved surface polygons with flat smooth surfaces (fig. 44); on incurved surface chorion spongy nodular with distinct polygonal borders only near micropyle (fig. 43).

MATERIAL STUDIED: One female, Arizona: Cochise Co., 1 mi. E Douglas, 8-V-1989 (J.G. Rozen).

REMARKS: See Remarks under *Epiclopus gayi*, above.

Mesoplia rufipes (Perty)

Rozen (1991) reported that a female of this species inserted her egg through a small opening in the cell cap of the closed cell of *Epicharis albofasciata* Smith on Trinidad, and that *Aglaomelissa duckei* (Friese) deposited its eggs the same way in cells of *Centris carrikeri* Cockerell. However, Vinson et al. (1987) reported finding parasitized cells of *Centris flavofasciata* Friese, some of which exhibited small oviposition holes made by *Mesoplia* females in the closures while others did not. This suggests that *Mesoplia* may also attack open cells still being provisioned by the host.

The ovarian formula of this species is 4:4.

DESCRIPTION OF MATURE OOCYTE (figs. 45–

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50): Length 3.9–4.3 mm, maximum diameter 0.65–0.70 mm (N = 7); egg index 0.72–0.86 (small to medium). Shape approximately symmetrical around its gently curved long axis; front end round, slightly flatter below than above in lateral view; apparent protrusion at anterior pole presumably resulting from plumelike chorionic ornamentation (figs. 45, 46); midsection long, parallel-sided; posterior end tapering more gradually than anterior end in lateral view, narrowly rounded; micropyle elliptical cluster of pores, each more or less surrounded by blunt flattened filaments (figs. 46, 47); chorion microscopically sculptured, dull; under SEM examination, outcurved side of micropylar cluster bordered by elongate, peglike filaments (fig. 47); incurved side below micropylar array with protruding, plumelike mass of spongy filaments (fig. 46); extreme anterior end of chorion with strong polygonal pattern incised into spongy chorion, each polygon with one or two rounded nodules (fig. 50); polygonal pattern fading posteriorly, scarcely evident beyond distance of one oocyte diameter from anterior pole; nodular surface conspicuous throughout (fig. 49).

MATERIAL STUDIED: Three females, Brazil: São Paulo, Luiz Antônio, Estação Ecológica de Jatai, 2-XI-2000 (M.C. Gaglianone), nesting site of *Epicharis nigrita*.

EUGLOSSINI

Exaerete smaragdina (Guérin-Méneville)

The mature oocyte/egg of this species was recently described and illustrated by Garófalo and Rozen (2001), but the micropyle was not evident. SEM examination of one of the specimens studied by them now reveals that the micropyle is a multipored cluster at the anterior pole (fig. 51). Numerous narrow polygons with raised borders radiate from it, with these borders disappearing a short distance away.

ANALYSES AND RESULTS

Table 1 compiles available information about egg size relative to body size (i.e., the egg index), total number of mature oocytes, number of oocytes per ovary, and number of ovarioles per ovary, all with respect to mode of cleptoparasitism, starting from the pioneering works of Iwata (1955, 1960) and Iwata and Sakagami (1966) to the present (see references in caption to table 1). The following analyses and discussion are based on the data in this table.

NUMBER OF OVARIOLES: Table 1 reveals a strong tendency for the Nomadinae to have more ovarioles per ovary than the plesiomorphic number of 4:4 for the Apidae. The great variation in ovariole count is noteworthy and argues for dissecting longer series of females of other species at least in the Nomadinae. This variation exists among taxa and also intraspecifically (see especially the data for *Kelita toroi*). Elsewhere among cleptoparasitic bees, the ovarian formula remains consistent with the plesiomorphic number for their respective families, with the exception of the Ericrocidini where both *Epiclopus gayi* and *Ericrosis lata* have five ovarioles in each ovary, contrasting with *Mesoplia*, in the same tribe, retaining the plesiomorphic four ovarioles per ovary.

Does the increase in number of ovarioles function to increase the total number of eggs that an individual can produce, as suggested by Iwata (1955, 1964), Iwata and Sakagami (1966), and Alexander and Rozen (1987)? Iwata (1964: 418), basing his analysis on the number of ''mature ovarian eggs'' (i.e., mature oocytes), concluded that the reproductive capacity of bees (and wasps) was increased by having smaller eggs and/or an increase in ovariole number. If we consider the number of mature oocytes a measure of the reproductive capacity of cleptoparasitic bees, then data in column three, ''Total number of mature oocytes'', can be used to explore the question. The average total number of mature oocytes for taxa that normally have three or four ovarioles per ovary (the plesiomorphic number for their respective families) is 5.32 mature oocytes per individual. These taxa include the cleptoparasitic Halictidae, Megachilidae, ''*Parammobatodes*'' *orientana*,[3] and the nonnomadine cleptoparasitic Apidae ex-

[3] This species was originally described by K. Warnke as *Pasites* (*Parammobatodes*) *orientanus*. Its generic name here is placed in quotes because the species is thought to belong to a new genus, yet to be named, species of which attack the nests of *Nomioides*, as mentioned by Michener (2000: 643).

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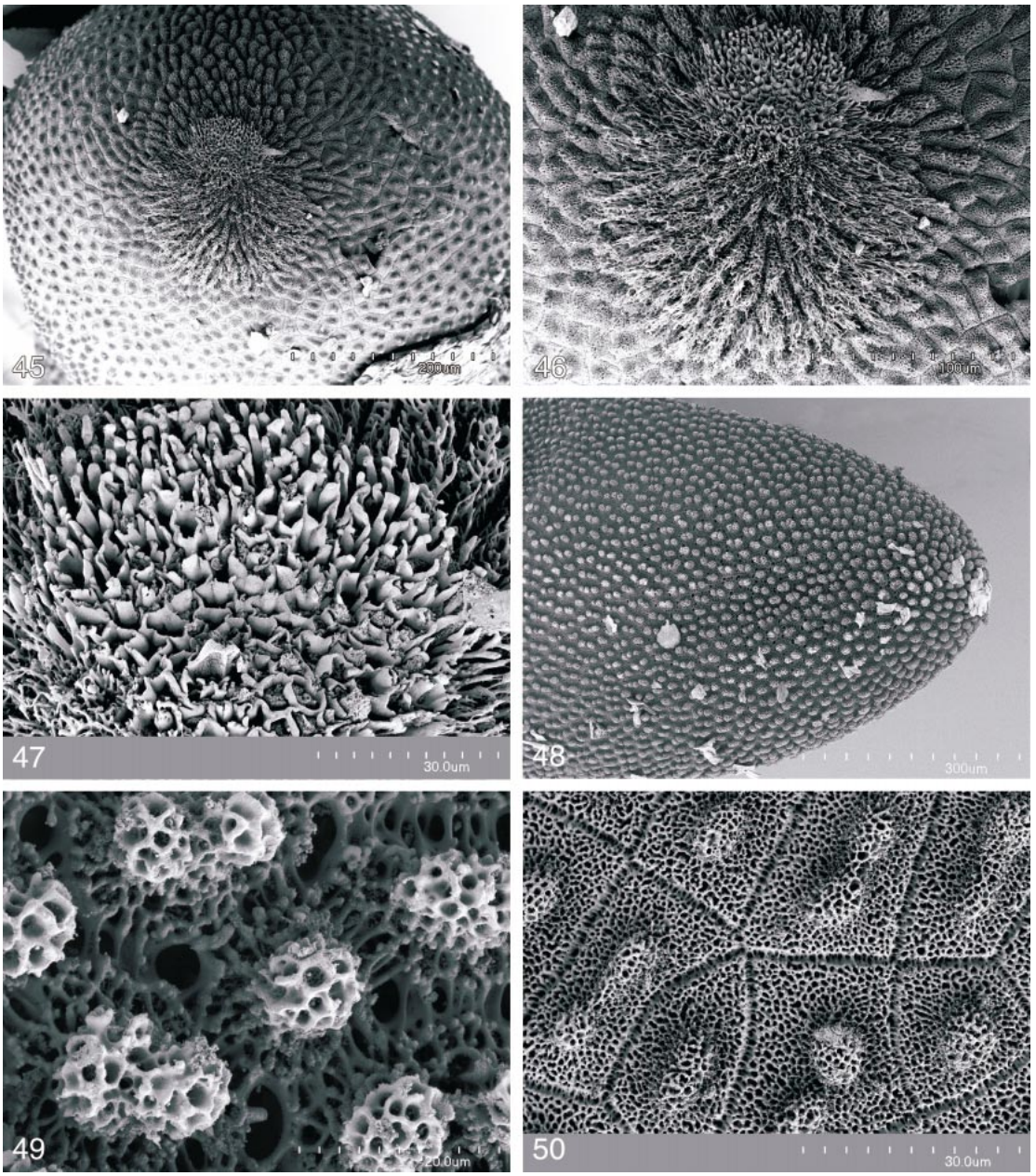

Figs. 45–50. SEM micrographs of mature oocyte of *Mesoplia rufipes*. **45.** Anterior end, frontal view. **46.** Close-up of micropylar area showing plumelike sculpturing below micropyle. **47.** Close-up of micropyle; note some pores filled with follicular debris. **48.** Posterior end of oocyte, lateral view. **49.** Close-up of chorion toward posterior end. **50.** Close-up of chorion near anterior end showing incised, polygonal pattern with one or two nodules per polygon.

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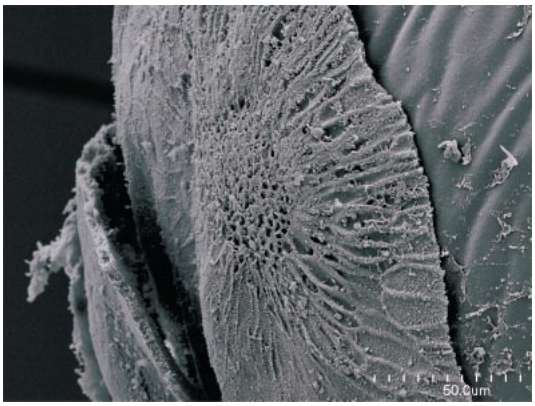

Fig. 51. SEM micrograph of anterior end of mature oocyte of *Exaerete smaragdina* showing multipored micropylar cluster and polygons with raised borders radiating from it.

cept for *Epiclopus gayi* and *Ericrocis lata*. The average total number of mature oocytes for the taxa that have extra ovarioles beyond the plesiomorphic number for their respective families is 10.91 mature oocytes per individual, more than twice the number compared with the first group. These taxa are *Ep. Gayi*, *Er. lata*, and all of the Nomadinae except for ''*Parammobatodes*'' *orientana*; *Pasites maculatus* was excluded from the calculations because of its ambiguous ovariole count. Thus, the average number of mature oocytes is significantly higher in species with extra ovarioles than in those with the plesiomorphic number in their families ($P < 1.7 \times 10^{-5}$, Wilcoxon rank sum test, one-sided). Although these figures seem to indicate that extra ovarioles confer a considerable advantage in increasing reproductive capacity, this situation is not clear. In the Ericrocidini, *Mesoplia*, which has the plesiomorphic number of mature oocytes, is shown to have more mature oocytes than *Ep. gayi* and *Er. lata*, each of which have five ovarioles per ovary. This sample is too small to be statistically significant, but the data hint that the extra reproductive capacity may be restricted to the Nomadinae alone.

Furthermore, if an increase in ovariole number increases reproductive capacity, then taxa with four ovarioles per ovary should have more mature oocytes than do those taxa with only three ovarioles per ovary. However, there is no significant difference in oocyte numbers between species in table 1 with an ovarian formula of 3:3 versus 4:4 ($P = 1.68$, Wilcoxon rank sum test, two-sided). Merely having more ovarioles, therefore, does not increase the reproductive capacity as a general rule among cleptoparasitic bees. The few oocytes per individual with four ovarioles is possibly associated with the fact that many cleptoparasitic taxa in this group (Osirini, Melectini, Ericrocidini, Rhathymini, and Euglossini) have very long but slender mature oocytes/eggs.

Thus, the situation is more complex than had been realized. One problem may be that the number of mature oocytes may not be a good measure of reproductive capacity.[4] As discussed in the next section, the apparent large number of mature oocytes in those taxa that hide their eggs in open cells may result at least in part from the increase in time required to develop thick chorions. This was demonstrated by the species of *Leiopodus* (figs. 16–28), which have the plesiomorphic number of ovarioles. Interestingly, the average number of mature oocytes per individual among the species in the genus is 9.93, not significantly different from 10.91 oocytes per individual for taxa with extra ovarioles ($P = 1.64$, Wilcoxon rank sum test, two-sided).

In conclusion, it appears obvious that an increase in numbers of ovarioles must play a role in increased reproductive capacity in such bees as *Apis* and perhaps other bees including the Nomadinae, but with the Nomadinae and perhaps with *Epiclopus gay* and *Ericrocis lata* extra ovarioles may serve to increase the likelihood that an egg will be ready to be deposited when the female discovers a host nest.

NUMBER OF MATURE OOCYTES: Alexander and Rozen (1987) concluded that cleptoparasites statistically tend to have a larger number of mature oocytes in their ovaries at a given time than do solitary bees. They (1987:

[4] As pointed out by Charles D. Michener (in litt.), who kindly reviewed this manuscript, ''longevity of a female bee is related to its potential reproductivity. For a short-lived insect [the number of mature oocytes] may be a good index of total productivity. But for a female *Ceratina* or *Braunsapis* that may live for 2+ years, if it has one egg at a time, it may none-the-less have a high total productivity.''

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159) reasoned, ''This may reflect that parasitic bees produce more eggs in their life span than do solitary bees and that as a result a larger number of eggs are ready for deposit in a short interval. However, it is also likely that there is selective advantage for parasitic bees to be able to oviposit in rapid succession.'' They were unaware that the chorions of cleptoparasites that introduce their eggs into open cells are thicker, at least on some surfaces, than those of solitary bees. This fact suggests another hypothesis that might explain, in part, the large number of mature oocytes found in these cleptoparasites, namely, in oogenesis a longer proportion of the entire developmental span is spent as a mature oocyte since more time is required to deposit chorionic material during the mature oocyte stage. Hence, in dissections, more mature oocytes would be encountered in various stages of having the chorions being deposited. This was evident in *Leiopodus abnormis*, *L. lacertinus*, and *L. trochantericus* (see figs. 16–28) where anatomical differences between early mature oocytes and late mature oocytes were detected. It was also noticed by Rozen and Özbek (2003) in a specimen of *Biastes brevicornis* (Panzer) that contained the remarkable number of 32 oocytes with chorions; of these, 13 appeared to have nearly or actually fully deposited chorions. While time required to deposit thick chorions may contribute to the large number of mature oocytes found in cleptoparasites that oviposit in open cells, we do not have a way of determining to what degree this influences the oocyte counts in these bees.

SIZE OF MATURE OOCYTES: Most authors have pointed out a tendency for cleptoparasitic bees to have eggs (or mature oocytes) that are smaller relative to the female's body size than the eggs of solitary bees. As Iwata and Sakagami (1966) pointed out, small eggs permit a cleptoparasitic female to have many on hand to liberate in quick succession. Many small mature oocytes can be carried within the confines of the female's metasoma whereas large mature oocytes occupy too much of the metasoma's capacity for more than the development of one or two at a time. Thus, cleptoparasites tend to be able to parasitize numerous host cells during a short period. Furthermore, small eggs are less likely to be discovered by returning host females (Rozen, 1994a). Indeed, the eggs of most parasitic bees (most, if not all, *Coelioxys*, apparently all Nomadinae, and all Protepeolini) that enter host cells before cell closure (and hence will be revisited by returning foraging hosts) are inserted in the cell wall[5] in such ways as to be less exposed to returning hosts. Although *Isepeolus* is the only certain exception, it flattens its egg against the cell lining in such a way that it is nearly a continuation of the cell lining and presumably, therefore, less detectable to the host female. The fact that these eggs often exhibit chorionic thickening and sculpturing that presumably resembles cell-wall texture supports the idea that returning host females exert considerable selection pressure on cleptoparasites.

Another possible explanation, yet to be tested, is that the embryos of dwarf to small eggs may develop more rapidly than do those of larger eggs. This was suggested for *Coelioxoides waltheriae* Ducke and it host, *Tetrapedia diversipes* Klug, where the parasite embyro developed in less than 1.5 days while the host egg took more than 4 days (Alves-dos-Santos et al., 2002). However, embryos of cleptoparasites apparently do not universally develop faster than those of the host; Torchio and Burdick (1988) reported that fully developed embryos of *Epeolus compactus* Cresson (egg length 1.3–1.7 mm) and its host *Colletes kincaidii* Cockerell (egg length 5 mm, Torchio et al., 1988) both took 6–8 days. We need to probe embryonic development rates of parasites and hosts; we may find that those of the parasites are finely tuned for the time to when the host eggs or larva can be destroyed.

If dwarfism is an adaptation for hiding eggs from returning host females, then we might predict that those cleptoparasitic lineages whose females attack cells that have not yet been closed by the host should have eggs that are smaller than those of lineages in

[5] One of the anonymous reviewers kindly pointed out that *Coelioxys texana* Cresson oviposits in the host's provisions, ''this probably common among parasites of taxa [of *Megachile*] in which the cell walls are not lined [with leaves or petals].'' The reviewer added the informative comment: ''Parasites probably lose a lot of eggs since the provisions are heavily kneaded with the mandibles before oviposition by the host . . . ''.

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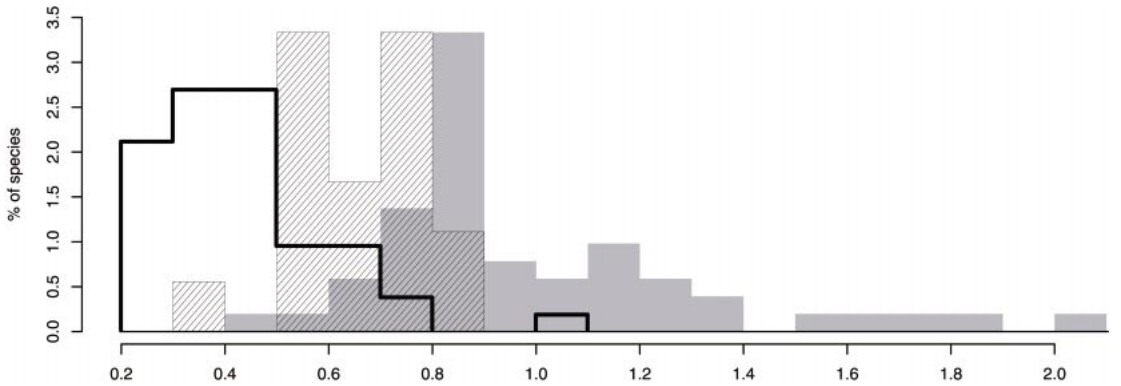

Fig. 52. Comparison frequency distributions for oocyte size (egg index) of cleptoparasitic bees that secrete their eggs in open host cells (dark outline), of those that introduce their eggs into cells that have already been sealed by the host (hatched), and of noneusocial, nonparasitic bees (gray). For further details, see text.

which cleptoparasites, in order to oviposit, open cells already closed by the hosts. To analyze whether this is the case, all species that introduce their eggs into closed host cells were shaded light gray in table 1, and all species that oviposit in cells that are still open were shaded dark gray (in both cases, citations in the column ''References to mode of parasitism'', table 1, are in boldface). Genera for which this information is unknown were left unshaded in the table. If the mode of parasitism of a congeneric species is known, it was assumed that other species in the genus will exhibit this same behavior (citations in ''References to mode of parasitism'', table 1, are not in boldface), and the genus was shaded according to its mode of parasitism.

However, two exceptions were identified. Although *Dioxys cincta* belongs in a genus where another species (Rozen and Favreau, 1967) has been recognized as ovipositing into closed host cells, the dwarf egg and the extensive chorionic ornamentation of *D. cincta* strongly suggest that the female introduces her eggs into open cells, unlike the other species (Rozen and Özbek, 2003). Therefore, this species is not shaded in table 1. The other exception is *Stelis elongativentris* in which it was originally assumed from indirect evidence (Rozen, 1987) that females entered cells that were still open. As reviewed by Torchio (1989) and Michener (2000), different species assigned to *Stelis* have variable behavior regarding ovipositing, and consequently more direct evidence should be uncovered before we can be certain of the oviposition habits of this species. It, too, is not shaded in table 1.

From the taxa shaded in table 1, the frequency distributions of oocyte size (egg index) (fig. 52) were graphed for cleptoparasites that introduced their eggs into closed cells and for those that introduce eggs into cells that are still open. This graph shows the strong tendency for eggs (mature oocytes) of the latter to be smaller than those of the former. On this diagram, the frequency distribution of the egg indices of 51 taxa of solitary bees[6] studied by Iwata and Sakagami (1966) were also plotted, revealing that cleptoparasitic bees of both categories have smaller eggs than do solitary bees, as already pointed out by Alexander and Rozen (1987). A statistical analysis confirms the visual impression that the distributions of egg-index values are different among the three groups: between open-cell and closed-cell cleptoparasitic bees, $P < 3 \times 10^{-6}$; between closed-cell and solitary bees, $P < 6.4 \times 10^{-6}$; between open-cell and solitary bees, $P < 1.2 \times 10^{-15}$ (Wilcoxon rank sum tests, two-sided).

[6] These taxa included all that Iwata and Sakagami (1966) coded solitary and all species of *Xylocopa* and *Ceratina*.

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SHAPE, CHORIONIC THICKNESS, AND CHORIONIC ORNAMENTATION OF MATURE OOCYTES: We can also expect that cleptoparasitic eggs inserted into cells that are still open will have (1) shapes and chorionic ornamentation that help hide the eggs and (2) a thicker chorion, at least on exposed surfaces, to protect the egg. Eggs introduced into closed cells should have simple, elongate-obovoid shapes and thin chorions similar to those of noncleptoparasitic bees, and they should be fully exposed in the cell lumen. Data concerning this matter have been insufficiently collected for the parasitic Halictinae and Megachilidae (but see remarks above concerning *Dioxys cincta*). The cleptoparasitic Apidae reveal that most of the Nomadinae (see references in the last column of table 1) have highly ornamented, often unusual-shaped eggs and all are hidden in various ways in cell walls, as is also true for the Protepeolini. In the Isepeolini, eggs of *Isepeolus*, with a flange surrounding their entire length, are hidden by being flattened against the cell lining. Those of *Melectoides*, similar in morphology to those of *Isepeolus*, may be deposited lengthwise in pits in the cell wall (Michelette et al., 2000). In contrast, eggs of the remaining cleptoparasitic apids have eggs that are normal in shape, are not hidden in, or on, cell walls, and have chorions that are not thick or greatly modified;[7] all of their eggs are deposited into cells that have already been closed by the host females. Figure 53 shows an assemblage of mature oocytes of some cleptoparasitic taxa from some of my recent publications, all reproduced to the same scale in lateral view. Those above the horizontal line are from cleptoparasites that oviposit in open cells and demonstrate the often-complex shapes attributed to their being hidden in or on cell surface. Those below the line are from taxa that introduce their eggs into cells that are closed and demonstrate the simple elongate-obovate shape comparable with eggs of nonparasitic bees.

[7] The nodular appearance of the chorion of *Coelioxoides waltheriae* Ducke might be considered an exception (Alves-dos-Santos, et al. 2002). However, the chorion of the unrelated *Epeoloides coecutiens* (Fabricius) is similarly modified (Rozen, 2001). One wonders if this ornamentation may relate to the fact that both are found in nests containing oil in the provisions. Another exception might be the currently unexplained shift in surface patterning from the outcurved to the incurved surfaces of the oocytes of *Epiclopus gayi* and *Ericrocis lata*.

One anonymous reviewer recommended summarizing the information concerning modes of parasitism, ovariole number, and egg size in light of bee phylogeny. Figure 54 is a cladogram depicting bee phylogeny on which have been plotted cleptoparasitic taxa that oviposit in closed nest cells (solid circles) and open nest cells (open circles). The question mark following the open circles associated with the Dioxyini refers to the assumption the *Dioxys cincta* is thought to oviposit in open host cells on the basis of its small egg size and heavily ornamented chorion in contrast to two North American *Dioxys* species. The plotting for Osirini is based on as yet unpublished information on *Protosiris* resulting from ongoing research started after this paper was submitted for publication.

One pattern that is immediately striking in this diagram is that de-novo origins of cleptoparasitic lineages seem to have been much more common among long-tongued bees (Megachilidae and Apidae) than among short-tongued bees (Colletidae, Halictidae, Andrenidae, and Melittidae). Such a conclusion is only partly true; the cladogram only plots those cleptoparasitic groups whose oviposition habits are known. Such information is unknown about seven independently evolved parasitic lineages in the Halictidae, one in the Colletidae, and one in the Andrenidae (i.e., an undescribed panurgine species in the collection of Padre J.S. Moure, Federal University of Paraná, Curitiba, Brazil) (Rozen, 2000b). By the same token, the modes of parasitism of *Bytinskia*, *Larinostelis*, and *Radoszkowskiana* in the Megachilidae and *Ctenoplectrina* and *Aglae* in the Apidae are unknown. In total, there have been 10 origins of cleptoparasitism among short-tongued bees and 19 among long-tongued bees. Thus, there appears to remain an unexplained disparity in the number of times that cleptoparasitic lifestyles have evolved between short-tongued and long-tongued bees as judged by extant taxa. The cladogram is uninformative about which mode of parasitism arose first or whether one form might be a precursor of the other form.

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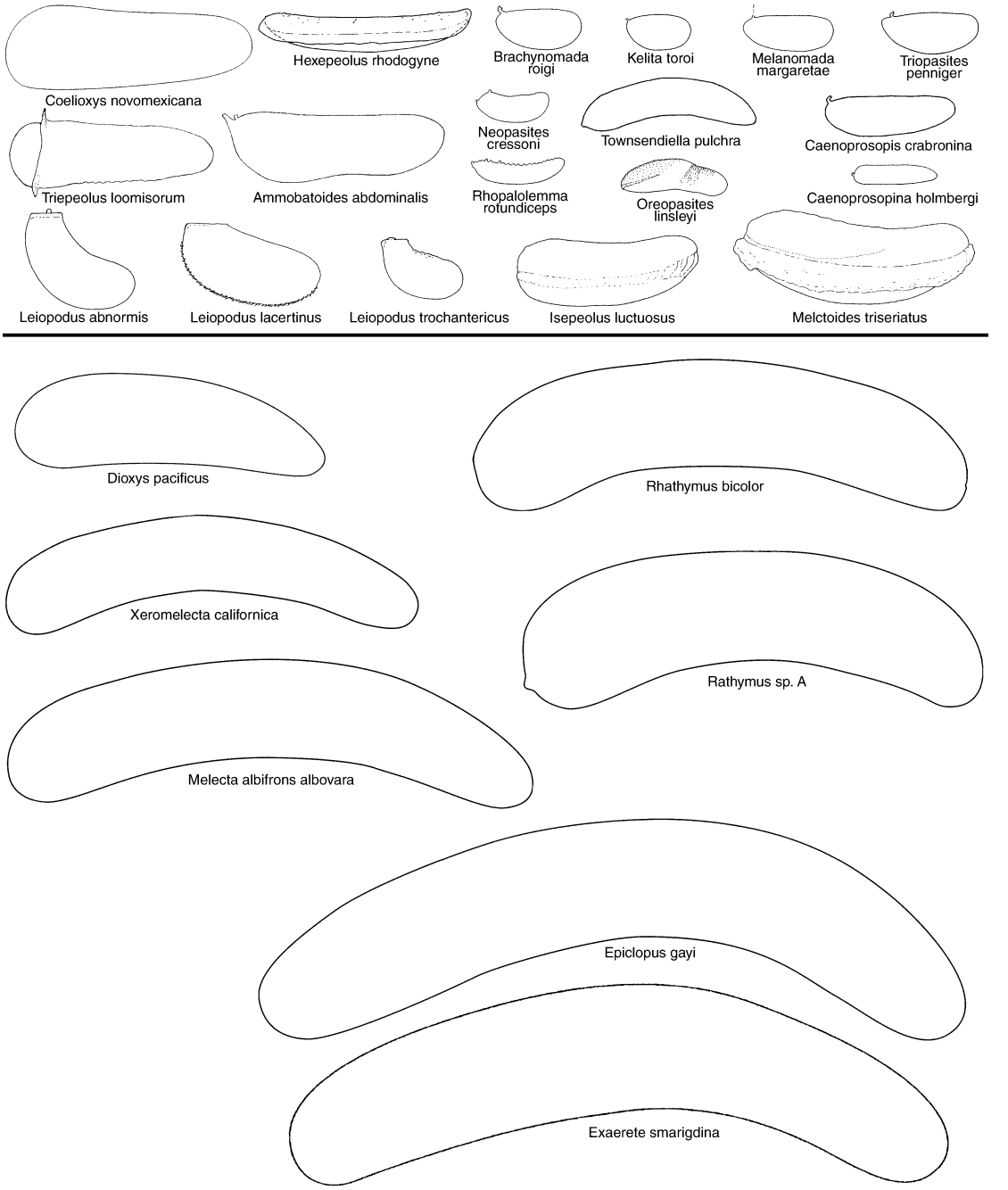

Fig. 53. Eggs of some cleptoparasitic bees from some of my recent publications, all reproduced in the same scale to illustrate the often complex shape of those that are hidden in open cells (above horizontal line) and the simple elongate shapes of those that are introduced into closed cells (below horizontal line). The size difference between the oocytes in these two categories is noteworthy, but is best analyzed in terms of oocyte length compared with body size of the female, i.e., the egg index; see Analyses and Results, subsection Size of Mature Oocytes.

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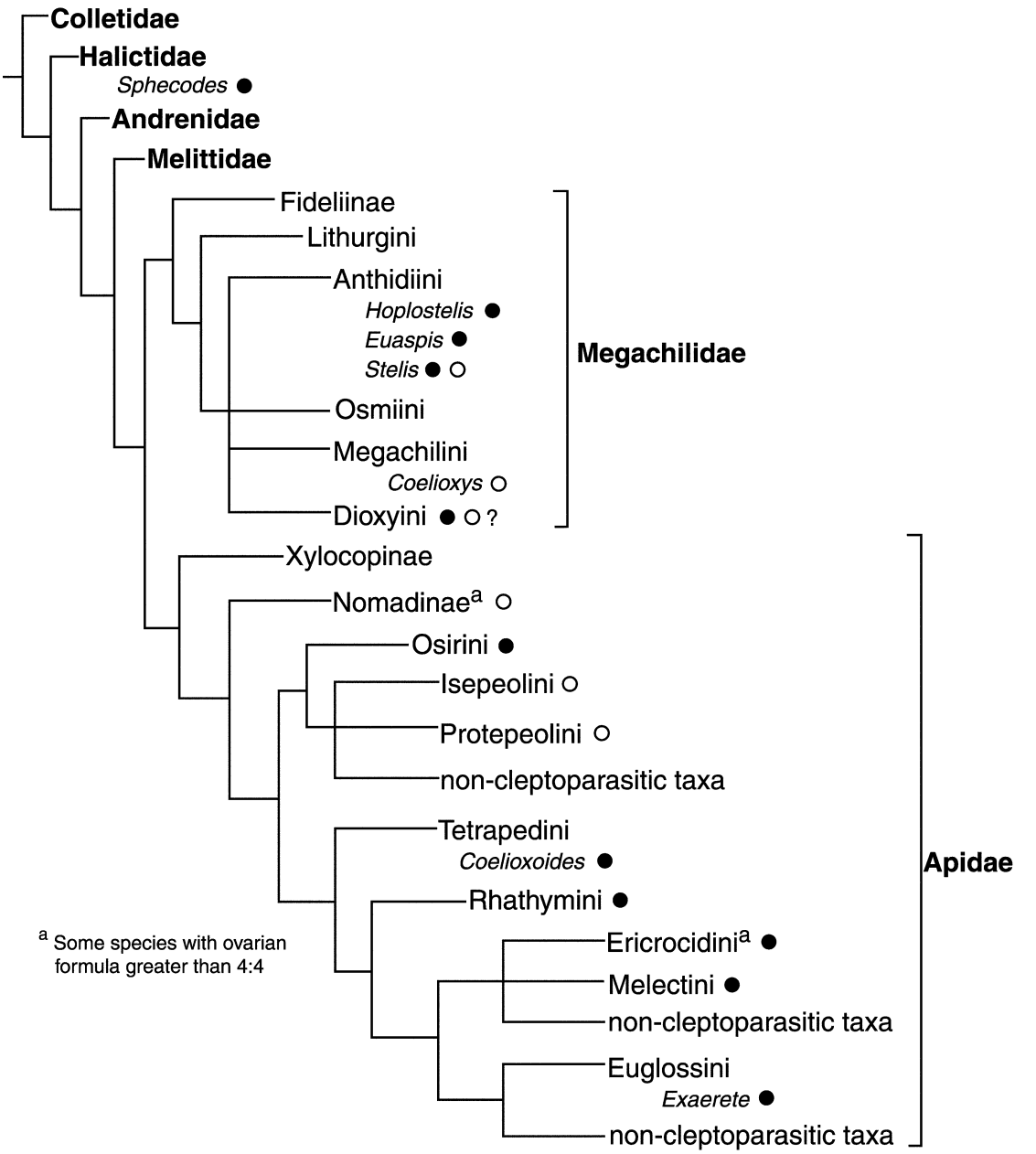

Fig. 54. Cladogram showing bee phylogeny upon which has been plotted the cleptoparasitic taxa that oviposit into nest cells that have not yet been closed by the host female (○) and the cleptoparasitic taxa that oviposit in nest cells that had been closed by the host female (●). Genera of cleptoparasites appear beneath the higher taxon to which they belong. If no generic name is listed beneath a cleptoparasitic taxon, all included genera are assumed to be cleptoparasitic with the same mode of parasitism. For discussion, see text. Cladogram modified from Engel (2001) and Michener (2000).

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A number of Scientific Assistants contributed greatly to the laboratory phase of this study. Valerie Giles took all of the SEM micrographs. Tam Nguyen photographed the egg of *Isepeolus luctuosus*. Steve Thurston arranged and labeled the illustrations and micrographs and prepared the histogram and cladogram. Eric Quinter edited the completed manuscript. I very much appreciate their expert assistance.

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APPENDIX

Because this paper summarizes oocyte and ovariole information for bees worldwide, it seems appropriate to include the following, even though *Stelis* and *Coelioxys* (*Boreocoelioxys*) are unknown from South America (Michener, 2000).

Stelis elongativentris Parker

Ovariole numbers and the egg index (table 1) of this North American species were recorded by Alexander and Rozen (1987); SEM micrographs of the micropylar area are placed on record herewith (figs. 55, 56). This specimen may or may not have been a late-stage mature oocyte.

Coelioxys (*Boreocoelioxys*) *novomexicana* Cockerell

Although South America has a rich fauna of *Coelioxys*, species in the subgenus *Boreocoelioxys* apparently do not occur there. Mature oocytes/eggs of other *Coelioxys* species have been described and/or illustrated by Graenicher (1905), Iwata (1939, 1955, 1965), and Baker (1971). All appear to have the shape of the egg of *C. novomexicana*, except for that of *C. decipiens* Spinola, which is described and depicted by Iwata (1965) as ''a mere sausage-shape''.

Although the dissected female had a single clearly recognizable mature oocyte, one or more other oocytes may not have been quite mature or might haven been undergoing reabsorption. Because of the uncertain nature of these statistics, they are not recorded in table 1.

DESCRIPTION OF MATURE OOCYTES (figs. 57–61):Length 1.7 mm, maximum diameter in lateral view 0.43 mm; egg index 0.46 (dwarf).

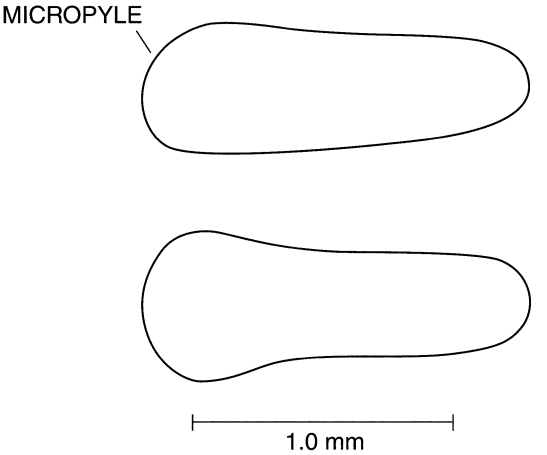
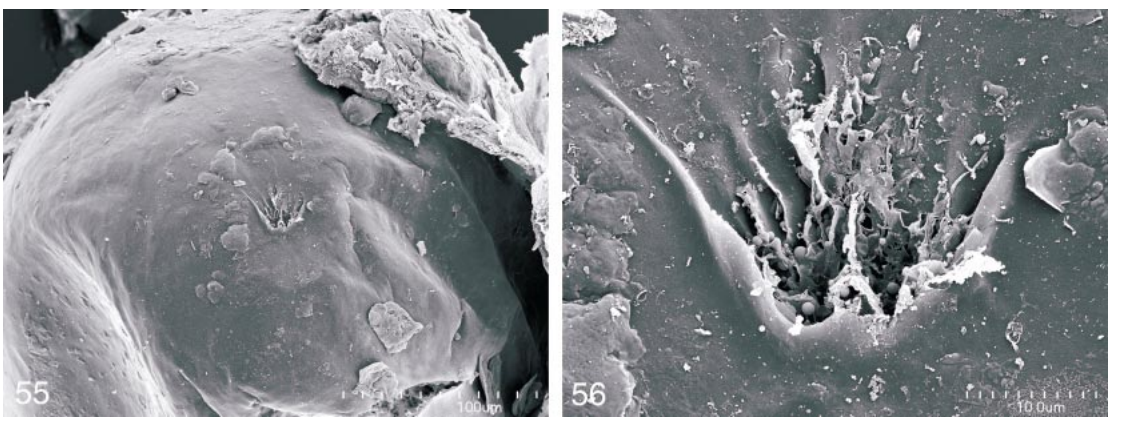


Fig. 57. Diagrams of mature oocyte of *Coelioxys novomexicana*, lateral and dorsal/ventral views, respectively; anterior ends toward the left; position of micropyle as noted.

Shape in lateral view (fig. 57) nearly straight, rounded at anterior end, with widest near anterior end, gradually tapering posteriorly to rounded posterior end (somewhat asymmetrical rounded front end in fig. 57, perhaps an artifact of preservation); shape in dorsal/ventral view (fig. 57) with anterior end expanded laterally, narrowing abruptly just behind anterior end, then tapering gradually to rounded posterior end; micropyle a cluster of pores at anterior end closer to presumed dorsal surface than to ventral surface. Chorion under stereoscopic exam-



Figs. 55, 56. SEM micrographs of mature oocyte of *Stelis elongativentris*. **55.** Anterior end, frontal view. **56.** Close-up of micropyle.

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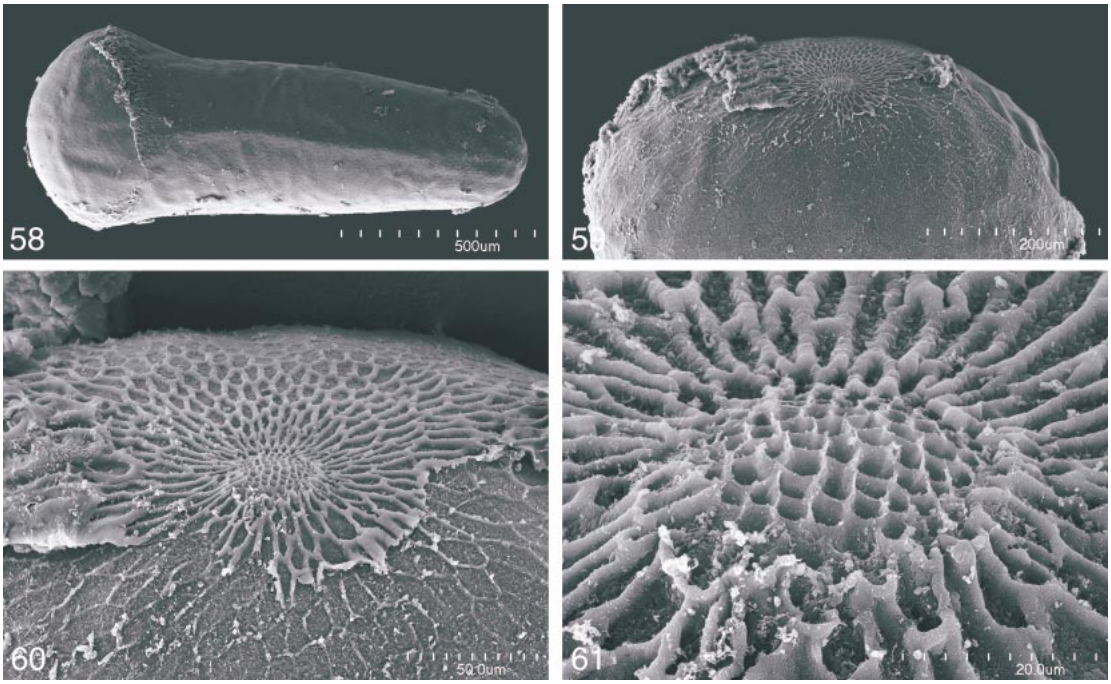

Figs. 58–61. SEM micrographs of mature oocyte of *Coelioxys novomexicana*. **58.** Entire oocyte, ventral view; anterior end toward the left. **59.** Anterior end, frontal view. **60.** Close-up of micropylar area; absence of strongly raised polygonal boundaries below unexplained but possibly due to dissection damage. **61.** Close-up of micropyle.

ination, moderately shiny and clear; under SEM examination with faint polygonal pattern that apparently becomes pronounced only at anterior end (figs. 59, 60); micropyle surrounded by strong polygonal pattern with raised borders, these polygons becoming narrowed and elongate, pointing toward micropyle (figs. 60, 61).

MATERIAL STUDIED: One female, Nevada: Clark Co., Spring Mountains, Lee Canyon, el. 6000 ft, 36° 23′01″N, 115°36′17″W, 5-VI-2002 (J.G. Rozen).

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