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MORPHOLOGICAL DESCRIPTIONS AND BIOLOGICAL AND PHYLOGENETIC DISCUSSIONS OF THE FIRST AND FINAL INSTARS OF FOUR SPECIES OF *MEGACERUS* LARVAE (COLEOPTERA: BRUCHIDAE)

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Abstract

The first and final larval instars of Megacerus discoidus, M. eulophus, M. insulatus, and M. maculiventris are illustrated and described. The chaetotaxy, head, antenna, clypeolabrum, epipharynx, mandible, maxilla, labium, leg, spiracle, and sulcus, and egg are described. In addition, scanning electron micrographs of the egg chorion of M. baeri, M. discoidus, and M. maculiventris are also included. A key to the final instars of M. baeri, M. discoidus, M. eulophus, M. insulatus and M. maculiventris is provided. A key to the first instar larvae of the foregoing species plus M. cubicus is also included. Our data suggest that the current subgeneric classification should be re-examined using both larval and adult characters.

A taxon represents a phylogenetic unit which has been defined by as many parameters (morphology, behavior, physiology, etc.) as possible. These parameters presumably reveal functional nucleic acid sequences (genes). Since some genes are operative at different times throughout the life cycle of a holometabolous insect it seems reasonable to include affinities and/or differences, of the various life stages (egg, larva, pupa, adult), in order that as many functional genes as possible can be used to construct a valid phylogenetic tree. A classification scheme using characters from all life history stages should provide a more accurate indication of phylogenetic affinities than one based solely upon adult characters.

Of the approximately 1,300 species of Bruchidae described (Johnson 1970), too few (approximately 100) descriptions of bruchid larvae have been published. The first significant contribution was that of Prevett (1971), in which larvae of 28 species were described. In 1976, Pfaffenberger and Johnson published the bionomics of 20 additional species (first instars only). Later, Arora (1978) published descriptions of the final instars of 36 species, while research on 9 species was published by Vats (1974) at about the same time. Each of these works provided descriptions using external morphological features. Vats (1982), however, described the tracheal systems of larvae of 8 species. He concluded that numbers of air sacs appeared to be useful in delineating bruchid subfamilies. Subsequent works (e.g., Muruaga De L'Argentier and Teran 1980; Pfaffenberger 1980, 1981) have provided important information.

The purpose of this paper is to provide additional descriptions of larvae in the genus *Megacerus*. Only the first and final instars of *M. baeri* (Muruaga De L'Argentier and Teran 1980) and the first instar of *M. cubicus* (Pfaffenberger 1980) have been described to date. Included here are descriptions of the first and final instars of *M. discoidus*, *M. eulophus*, *M. insulatus* and *M. maculiventris*. In addition, scanning electron micrographs (SEM) of egg choria are presented for *M. baeri*, *M. discoidus*, and *M. maculiventris*. These descriptions will contribute significant information in our eventual understanding of phylogenetic relationships within *Megacerus* and the family Bruchidae.

Megacerus baeri (Pic)

EGG (cf., Figs. 1-2, with Figs. 5a, 5b in Muruaga De L'Argentier and Teran 1980). Chorionic sculpturing a continuous, symmetrical pattern of spherical domes, each of which is pierced with a single aeropyle. Fig. 1 shows adhesive flange to be continuous, undulating band of mucilage which completely surrounds venter.

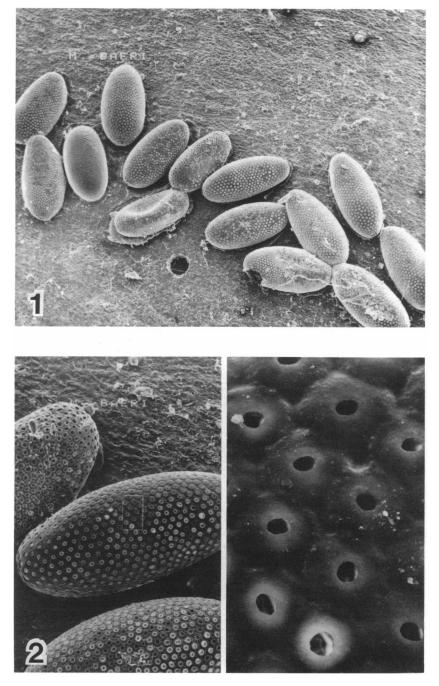
SIGNIFICANT CHARACTERS. Final instar: ocelli absent; inconspicuous epipharyngeal tormae; palpifer with 5 setae and 2 sensory pores; membranous palpifer with 6 setae; labium without submentum, mentum bordered laterally by 2 pairs of primary setae; 1 pair of shorter setae along proximal border of mentum; ligula with many fine spines. First instar: ocelli absent; epipharyngeal tormae absent; tooth formula, of prothoracic plate, is 1 + 1 + 4-6; absence of setae on 10th abdominal segment. Egg: chorion a continuous pattern of circular domes, each pierced with a single aeropyle.

All subsequent larval descriptions are compared to those of M. baeri (Muruaga De L'Argentier and Teran 1980).

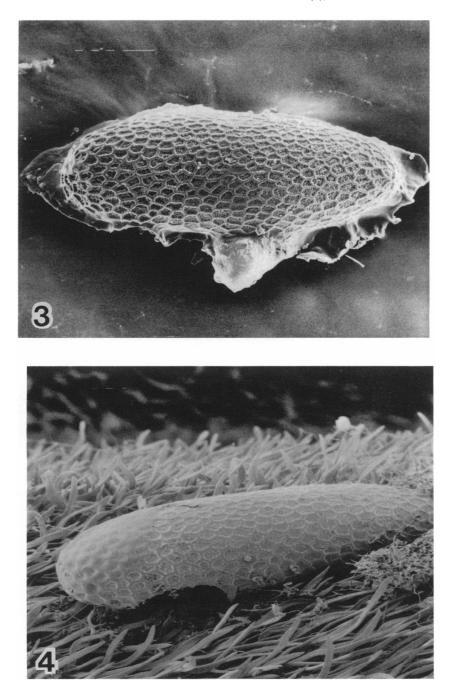
Megacerus discoidus (Say)

FINAL INSTAR. Body: length 3.0-5.0 mm, width 2.0-3.0 mm; C-shaped; robust; thorax increasing in width from pro- to metathorax; meso- and metathorax with single, dorsal plica; diameter of abdominal segments 1-5 subequal but less than metathorax and greater than segment 6; segments 6-10 strongly tapered toward button-like 10th segment; segments 1–9 with single dorsal plica; integument with yellow pigmentation on dorsomedial to lateral areas of prothorax; integument appearing naked but with numerous, submicroscopic setae mostly aligned in rows along crests of plicae and other elevated regions of integument. Head (Fig. 56; Figs. 3-4 in Pfaffenberger 1977): frons with proximomedially curved row of 3 decurved sensilla trichodea; 1 elongate trichoid sensillum on opposite sides of midline near distal border; ventral surface almost completely occupied by occipital foramen; mouthparts hypognathous. Antenna (Fig. 8): located at anterolateral margin of frons near superior base of mandible; 1 retractible segment; distal end with peripheral fringe of sharp, sclerotized projections, these extend midway down lateral aspect of segment; membranous base of antenna with 2 sensory pores, 1 ventrolateral and 1 dorsolateral. Clypeolabrum (Fig. 10): clypeus rounded laterally with anterolateral curvature; crescent-shaped base; labrum with dome-like outer margin and gradually convexed base; basal border paralleled with elongate, pigmented area bearing trichoid sensillum near each end (similar to distal clypeal setal pair of *M. baeri*); distally a median arc of 6 enlarged sensilla trichodea encompassing single, central

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Figs. 1-2. SEM micrographs of Megacerus baeri: 1, eggs; 2, chorionic sculpturing.



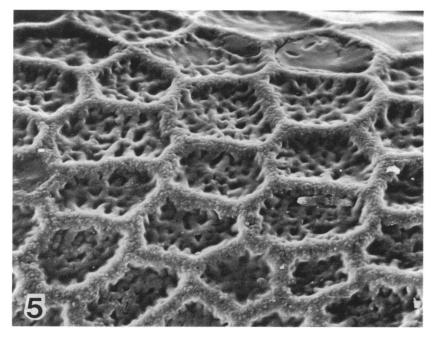
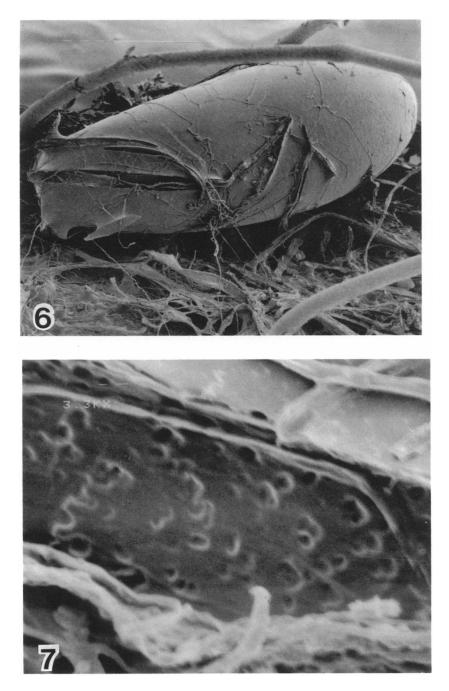


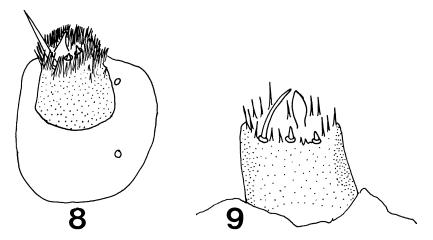
Fig. 5. SEM micrograph of *M. discoidus* egg, showing chorionic sculpturing and aeropyles.

sensillum trichodeum; posterolateral pair with sharp point, others with truncate ends; all 7 sensilla trichodea interspersed among dense mat of microtrichia that borders free margin of labrum. *Epipharynx* (Fig. 12): epipharyngeal groove lanceolate; each sensillum flanked proximolaterally by triangular patch of obliquely arranged, sclerotized, pointed projections. *Mandible* (Figs. 16–17): monocondylic, molar surface smooth basally and fluted apically; triangular dorsum with double scalloped, medioapical surface; triangularly arranged triplet of sensory pores on dorsal surface; most heavily pigmented near distal end; ventral surface with lateroproximal sensory pore flanked distally and proximally with single sensillum trichodeum. *Maxilla* (Fig. 18): cardo present, transversely oval to elongate with rounded to truncate ends with sinuate, posterior border; membranous stipes bearing approximately 16 sensilla trichodea (number of setae may be as few as 4 or as many as 23, but there always appears to be more setae on the right maxillary stipes than on the left); sclerite of palpifer with spinous, dorsal surface and bearing 2 elongate sensilla trichodea on ven-

(

Figs. 3-4. SEM micrographs of *Megacerus discoidus* egg: 3, circumscribing flange of mucilage; 4, exposes ventral emergence hole and site of seed penetration. Seed is that of *Ipomoea leptophylla*.



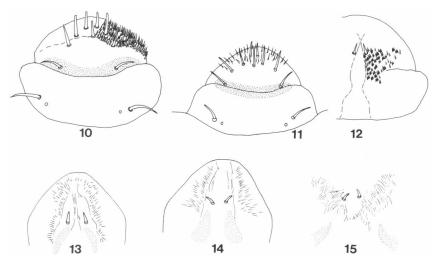


Figs. 8-9. Final instar antenna: 8, M. discoidus; 9, M. insulatus.

trolateral margin, single lateral sensory pore overlapping membranous and sclerotized borders of palpifer, 5 pointed sensilla trichodea equidistantly spaced along distal medioventral border, 2 finger-like sensilla basiconica between dorsomedial pair of sensilla trichodea, distomedial border occupied by 5 contiguous and 1 ventral adjunct peg-like setae; palpus with proximolateral and distomedial setae on dorsal surface of sclerite, membranous end bearing numerous sensilla basiconia. Labium (Fig. 20): submentum basically C-shaped with extended lateral borders, each anterolateral margin supporting pair of enlarged sensilla trichodea, shorter pair of sensilla trichodea along proximomedial border; mentum oval-shaped with U-shaped distal end, each arm of 'U' reinforced with elongate, deeply pigmented bars, proximal end of each bar flanked laterally by 1 decurved sensillum trichodeum; glossae fused distally with numerous sclerotized projections located at base of cleft between ligular lobes, pair of decurved, peg-like setae between sclerotized projections and pointed ends of mentum. Leg (Fig. 22): 4 fleshy segments, penultimate and basal segments with short mediolateral sensillum trichodeum, vertical row of 4 sensory pores extending from basal to penultimate segment, latter segment bearing 2 sensory pores, basal segment also with 2 sensory pores (one near posterolateral border). Spiracle (Fig. 26): enlarged thoracic pair, peritreme oval to round, atrial orifice lined with sclerotized projections.

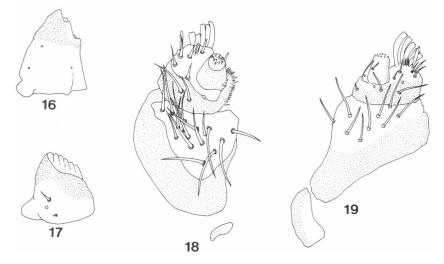
FIRST INSTAR. *Body* (See Fig. 1 in Pfaffenberger and Johnson 1976): 0.8 mm long by 0.4 mm wide, with greatest width among mesothoracic to 2nd abdominal segments, abdomen tapering to minute 10th segment; cuticle white with

Figs. 6–7. SEM micrographs of *Megacerus maculiventris* egg: 6, showing encompassing mucilage, with minimal attachment surface; 7, chorionic sculpturing. Egg appears to be secured by entrapped components of the seed surface.



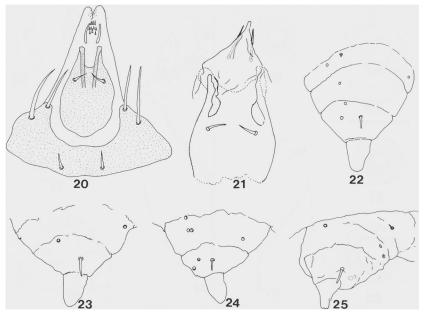
Figs. 10-11. Final instar clypeolabrum: 10, M. discoidus; 11, M. eulophus.

Figs. 12-15. Final instar epipharynx: 12, M. discoidus; 13, M. eulophus; 14, M. insulatus; 15, M. maculiventris.



Figs. 16–17. Final instar mandible of M. discoidus: 16, dorsal surface of left mandible; 17, ventral surface of right mandible.

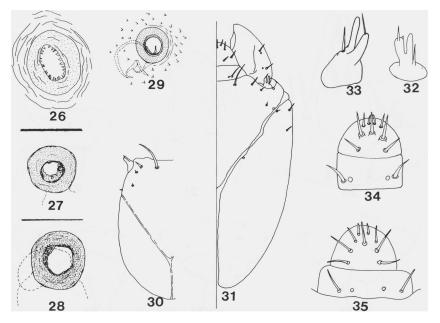
Figs. 18–19. Final instar: 18, left maxilla of *M. discoidus*; 19, right maxilla of *M. eulophus*.



Figs. 20-21. Final instar labium: 20, M. discoidus; 21, M. maculiventris.

Figs. 22–25. Final instar leg: 22, M. discoidus; 23, M. eulophus; 24, M. insulatus; 25, M. maculiventris.

deeply pigmented head capsule, prothoracic plate and abdominal spine; chaetotaxy of uniformly arranged primary (long) and secondary (short) setae. Head (Fig. 30): truncate frontoclypeal border. Antenna (Fig. 32): single bifid segment with proximomedial lobe subtended laterally by trichoid sensillum, this lobe somewhat longer than enlarged anterolateral lobe, the latter supporting 2 sensilla trichodea. Clypeolabrum (Fig. 34): rectangular clypeus with truncate attachment to hemispherical labrum; sensillum trichodeum and proximate, medial pore located in each proximolateral corner of clypeus; labrum with central arc of 5 sensilla trichodea with 3 central sensillae appearing to arise from elevated base; 4 smaller sensilla trichodea form arc near distal margin of labrum and in front of central arc of 5 sensillae. Epipharynx (Fig. 36): dome-shaped distal end with truncate base; centrally located pair of converging sensilla trichodea. Prothoracic plate (Fig. 40): X- or H-shaped; actinomorphic with 5-8 pairs of teeth; teeth arranged in 1 + 1 + 3-6 (cf. Fig. 15-A in Prevett 1971); plate with 4 pairs of setae (arrangement similar to that of *M. baeri*); remaining setal pairs and pair of sensory pores equidistantly spaced along medial border of anterior arms; second pair of setae 1/3 to 1/2 again as long as other setal pairs; sensory pore located between 3rd and 4th setal pairs; enlarged sensory pore located near distal end of anterior arm; plate bordered laterally by circular cluster of sclerotized projections which encompass centrally located sensory pore; single sensillum trichodeum located along anteromedian aspects of cluster. Prothorax (Fig. 44; Tables 1, 6): with 8 setae, excluding those associated



Figs. 26–29. Final instar abdominal spiracle: 26, M. discoidus; 27, M. eulophus; 28, M. insulatus; 29, M. maculiventris.

Figs. 30-31. First instar head capsule: 30, M. discoidus; 31, M. insulatus.

Figs. 32-33. First instar antenna: 32, M. discoidus; 33, M. maculiventris.

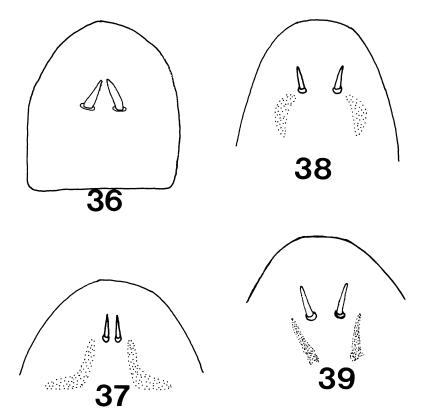
Figs. 34-35. First instar clypeolabrum: 34, M. discoidus; 35, M. maculiventris.

Segment	Pro- dorsum	Post- dorsum	Spira- cular area	Epi- pleuron	Hypo- pleuron	Ster	num	Pro- thorax
Mesothorax	ď′	A a″		Ee'		u	R	2
Metathorax	ď	A a″		e'		u	R	5
Abdomen								6
1	ď	A a″	s'	Ε	н	u		8
2	ď	A a″	s's″		Hh	u		10
2–5	ď	A a″	s'		н	u		12
6	ď	A a″	s′		Hh	u		14
7	d′*	A a″	s'		Hh	u		16
8	d′*	A a″			н	u		
9 10 g**		Aa'a"			н	u	x	

Table 1. Distribution of setae on Megacerus discoidus, first instar.

* Without proximate sensory pore.

** Dorsolateral seta on 10th abdominal segment.

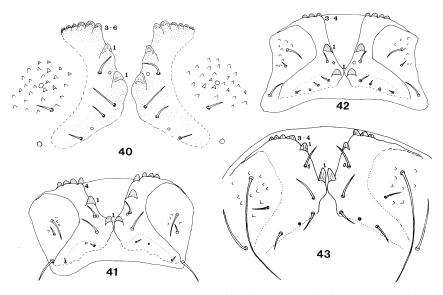


Figs. 36–39. First instar epipharynx: 36, M. discoidus; 37, M. eulophus; 38, M. insulatus; 39, M. maculiventris.

Segment	Pro- dorsum	Post- dorsum	Spira- cular area	Epi- pleuron	Hypo- pleuron	Sternum	Pro- thorax
Mesothorax		Aa'a″		Ee'		u R	2
Metathorax		Aa'a″		e'		u R	3
Abdomen							5
1	d′	Α	s′	E	h	uх	6
2	ď	A a″	s's″	E	h	u x	7
3-5	d′	A a″	s′	Е	h	uх	8
6	ď	A a″	s'	Ee'	h	vx	10
7	d′*	A a″	s'	Ee'	h	vx	11
8	d′*	A a″		Ee'	h	vx	16
9	d′*	A a″		E	h	х	
10							

Table 2. Distribution of setae on Megacerus eulophus, first instar.

* Without proximate sensory pore.



Figs. 40-43. Prothoracic plate: 40, M. discoidus; 41, M. eulophus; 42, M. insulatus; 43, M. maculiventris.

with the prothoracic plate; sternite with numerous, posteriorly directed, sclerotized projections. *Mesothorax* and *Metathorax* (Fig. 44; Tables 1, 6): with secondary seta (d') and proximate sensory pore on prodorsum; metepipleuron with 1 secondary seta; mesohypopleuron with spiracle. *Leg* (Fig. 48): transverse distance between appendages increasing with each succeeding segment. *Abdomen* (Fig. 50; Tables 1, 6): prodorsum not apparent on segment 9; postdorsa 1–8 with single primary (A) and secondary (a") setae; dorsum of 9th segment

Segment	Pro- dorsum	Post- dorsum	Spira- cular area	Epi- pleuron	Hypo- pleuron	Sternum	Pro- thorax
Mesothorax		Aa'a″		Ee'		u R	2
Metathorax		Aa'a″		e'		u R	3
Abdomen							5
1	ď	A	s′	E	h	uх	6
2	ď	A a″	s's″	Е	h	uх	7
3–5	ď	A a″	s'	Ε	h	u x	8
6	ď	A a″	s'	Ee'	h	uх	10
7	d′*	A a″	s'	Ee'	h	u x	12
8	d′*	A a″		Ee'	h	u x	16
9	d′*	A a″		Ε	h	х	
10							

Table 3. Distribution of setae on Megacerus insulatus, first instar.

* Without proximate sensory pore.

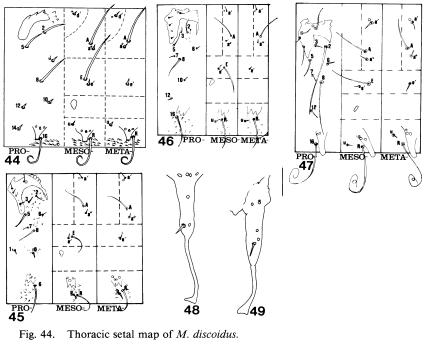


Fig. 45. Thoracic setal map of M. eulophus.

Thoracic setal map of M. insulatus. Fig. 46.

Fig. 47. Thoracic setal map of M. maculiventris.

Figs. 48-49. First instar leg: 48, M. discoidus; 49, M. eulophus.

Table 4.	Distribution of setae on	Megacerus maculiventris,	first instar.

Segment	Pro- dorsum	Post- dorsum	Spira- cular area	Epi- pleuron	Hypo- pleuron	Sternum	Pro- thorax
Mesothorax		Aa'a″		Ee'		u R	2
Metathorax		Aa'a″		e'		u R	3
Abdomen							5
1	ď	Α	s′	Е	h	vx	6
2	ď	A a″	s's″	Е	h	VX	7
3-5	ď	A a″	s′	E	h	vx	8
6	ď	A a″	s′	Ee'	h	vx	12
7	ď	A a″	s′	Ee'	h	vx	16
8	d′*	A a″		Ee'	h	vx	
9	d′*	A a″		Е	h	x	
10							

* Without proximate sensory pore.

M. baeri.***						
		(¥)	(B)	(C)	(Î)	(E)
Ocelli	pairs	1	1	-	-	
Antenna	# of setae # of conical sensilla	- F	- F	3 -	- e	3 -
Clypeus	pairs of setae pairs of sensory pores					
Labrium	 # of anterior setae # of anteromedian setae # of median setae # of posterior setae # of median sensory pores # of posterior sensory pores 	4-00	00-0	00-0	00-0	4-00
Epipharynx	pairs of median setae pairs of lateral setae	- 1	- 1	- 1	- 1	- 1
Maxilla	Cardo: setae Stipes: # of sensory pores # & position of setae seta S	- - (4)11-23M -	- - -0M	M6	- - 6-12M	– – –

Table 5.* Character summary of final instar larvae of: (A) Megacerus discoidus, (B) M. eulophus, (C) M. insulatus, (D) M. maculiventris, (E) M hoori ***

		(Y)	(B)	(C)	(Î)	(E)
Maxilla (cont.)	Palpifer: # & position of setae # of sensory pores Palp: setae # of segments Mala: # of spatulate setae # of other setae	2M, 2S 1 YZ** 1 5-6 5	2M, 2S 2 2 1 6	2M, 2S 2 2 1 5 6	2M, 2S 2 Z 5-6 6	4M, 5S 2 Z 1 6
Labium	Mentum: pairs of setae Ligula: pairs of setae Submentum: # of lateral setae # of anteromedian setae # of posterior setae	0 0	40	40	4 0	4 0
Leg Anal segment	# of segments # of lobes	3(4?) 2	6 0	6 0	3(4?) 2	ю 0
* Modification of Prevett (1 ** See Fig. 3 in Prevett 1971 *** From Muruaga De L'Arg. M = membrane; S = sclerite.	* Modification of Prevett (1971), see pp. 258-259. ** See Fig. 3 in Prevett 1971. *** From Muruaga De L'Argentier and Teran 1980. M = membrane; S = sclerite.					

Table 5.* Continued.

		(A)	(B)	(C)	(D)	(E)	(F)
Ocelli	pairs	_	1	_	1	1	1
Antenna	# of segments	1	1	1	1	1	1
	# of lobes	2	2	2	2	2	2
	# of setae	2	1	2	2	2	2
Prothoracic	# teeth-posterior arm	46	3-4	3–6	4	3–4	3-4
plate	# median teeth	1	1	1	1	1	1
	# anterior teeth	1	1	1	1	1	1
	# of setae	4	3	4	4	4	4
	# of sensillae	2	2	4	4	4	4
Legs	# of segments	2	2	2	2	2	2
U	expanded foot	+	÷+	+	+	+	+
	(Pro/Meso-Meta)						
	# of setae	1/1	2/1	1/1	1/1	1/1	1/1
	# of sensillae	5/6	0/0	6/6	5/5	5/5	5/5
Chaetotaxy	(Primary/Secondary)						
•	Prothorax	3/5	4/3	4/4	3/6	4/7	4/4
	Mesothorax	3/4	3/3	3/4	3/4	3/4	3/4
	Metathorax	2/4	3/3	2/4	2/4	2/4	2/4
	Abdomen						
	1	2/5	2/2	3/4	2/5	2/5	2/5
	2	2/7	2/5	2/6	2/7	2/7	2/7
	3-5	2/6	2/4	2/4	2/6	2/6	2/6
	6	2/7	2/4	2/5	2/7	2/7	2/7
	7	2/7	2/4	2/5	2/7	2/7	2/7
	8	2/6	2/4	2/4	2/6	2/6	2/6
	9	2/4	2/4	2/4	2/4	2/4	2/4
	10	-	1/2	—/1	—	-	-
Anal segment	# of lobes	2	2	2	2	2	2

Table 6. Character summary of the first instar larvae of: (A) Megacerus baeri,* (B) M. cubicus,** (C) M. discoidus, (D) M. eulophus, (E) M. insulatus, (F) M. maculiventris.

* See Muruaga De L'Argentier and Teran 1980.

** See Pfaffenberger 1980.

with 3 (Aa'a") setae; dorsum of 10th segment with single secondary (g) seta; spiracular area of 1st segment with integumental protrusions; first epipleuron with primary seta (E); all spiracular areas with integumental protrusions; 8th spiracular area asetiferous; spiracles oval; hypopleura 2 and 6–8 with primary (H) and secondary (h) setae; hypopleura 1, 3–5, and 9 with single primary (H) seta; sternites 1–5 with numerous, sclerotized, posteriorly pointed projections; sternites 1–8 and 10 asetiferous; 9th sternite bisetiferous.

EGG (Figs. 3-5). Length 1.0 mm; width 0.5 mm. Oval, greatest depth anteriorly, tapering to flattened posterior end; egg may be secured by encompassing band of mucilage (Fig. 3) or by strands of mucilage at posterior end; chorion a continuous pattern of hexagonic rings, each encompassing numerous aeropyles (Fig. 5).

SIGNIFICANT CHARACTERS. *Final instar:* ocelli absent; inconspicuous epipharyngeal tormae; each epipharyngeal sensillum flanked laterally by triangular patch of sclerotized, pointed projections; 2 sensory pores in membrane at base

16

of antenna; mandible with triad of sensory pores on dorsal surface; maxillary stipes with 4–23 setae; membranous palpifer with setae; sclerite of palpifer with 2 setae and sensory pore; C-shaped submentum bearing 3 setal pairs; oval mentum with U-shaped distal end; spiracular orifice lined with sclerotized projections. *First instar:* ocelli absent; epipharyngeal tormae absent; tooth formula, of prothoracic plate, is 1 + 1 + 3-6; plate bordered laterally by one seta and sensory pore; 1st abdominal segment with 3 primary setae (one on the epipleuron); 2nd abdominal hypopleuron with 2 setae (Hh); abdominal sternites 6–8 with 1 secondary seta; one seta (g) on 10th abdominal segment. *Egg:* chorion a continuous pattern of hexagonic rings, each with numerous aeropyles.

MATERIAL EXAMINED: 10 final instar larvae and 19 first instar larvae. Collected from seeds of *Ipomoea leptophylla*, 7-IX-79; 1, 5, and 10 mi E Elida, Roosevelt Co., New Mexico. Determined by association with reared adults.

BIOLOGICAL NOTES: The fruit of *Ipomoea leptophylla* is a thin walled, unicarpellate or bicarpellate capsule. Smaller capsules are unicarpellate, whereas larger capsules are bicarpellate. The latter bear two ovules in each carpel. The two ovules are flattened medially and adhere closely to the septum separating the two carpels. Outwardly, the two seeds are hemispherical and are usually of equal size.

Oviposition appears to be indiscriminate, with eggs being found in slits and breaks in the pedicel, on the septal surface of the ovary, as well as upon the surface of ripe capsules and seeds. Females appear to exhibit ovipositional preference for seeds retained within partially dehisced capsules, as opposed to those which have fallen to the ground, since no eggs were found upon dispersed seeds.

Once the mature pods are partially dehisced the female enters the capsule and oviposits 1-3 eggs upon the exposed seed surface. The usual form of emergence is through the ventral surface of the egg (Fig. 4). It utilizes purchase, gained from the egg chorion, to penetrate the thick seed testa. The larva may emerge dorsally from the egg, in which case its fate is undetermined; many larvae were observed wandering over the seed surface, but none was observed to penetrate the seed. As with other bruchid larvae, they excavate a pupation chamber in the seed. During their sojourn within the seed the larva appears to feed entirely upon the cotyledons, since in all seeds examined the radicle remained unmolested. Cannibalism also appears to occur, since only one adult has been observed to emerge from a seed with as many as 3 eggs on its surface.

Megacerus eulophus (Er.)

FINAL INSTAR. Body: length 2.5 mm; width 1.5 mm; color yellowish white; integument as in *M. baeri. Head:* yellowish, with anterior and lateral sides of epistoma, antennal sockets and mandibles more deeply pigmented; oval shaped, V_{10} longer than wide; sutures apparent; 1 pair of ocelli present; chaetotaxy as in *M. baeri*, except 1 pair of small setae behind sensory pores on frontal sutures. *Antenna:* distal segment cylindrical. *Clypeolabrum* (Fig. 11): clypeal portion membranous, with 1 pair of proximolateral setae subtended by single sensorium; labral portion with basal, sclerotized, transverse band bearing 1 pair of setae; located distally are 2 pairs of lateral, 1 pair of anteromedian, 1 pair of anterior, and 1 single median setae. *Epipharynx* (Fig. 13): tormae boomerang-shaped; groove converging distally; spinous mat paralleling longitudinal axis of epipharynx and forming continuous row around distal end of groove. *Maxilla* (Fig. 19; for symbolic setae, see Fig. 3 in Prevett 1971): mala poorly differ-

entiated from palpifer; palp with basal pore, lateral process, seta Z and truncate apical spines; mala with 5 spatulate, 1 lanceolate, 2 twin, and 3 simple setae; palpifer with 5 setae (including W) and 2 pores; membranous area of stipes with 9–10 setae. *Labium:* as in *M. baeri. Leg* (Fig. 23): 3-segmented; basal segment with 1 pore, median with 1 seta and 1 pore, apical devoid of pores or setae. *Spiracles* (Fig. 27): as in *M. baeri.*

FIRST INSTAR. Body: length 0.55 mm; yellowish white; head, prothoracic plate and abdominal spines, of first spiracular areas, more deeply pigmented; cuticle with segmental regions limited by fine strioles, latter more abundant on dorsum and spiracular areas; areolate structures on dorsum, epipleura and hypopleura of prothorax; posteriorly directed, spine-like projections on sterna and sensory pores on meso- and metathoracic postdorsa and 1-6 abdominal prodorsa as in M. baeri. Head: longer than wide; ocellus present on anterior extremity of each frontal suture; posterior to each ocellus are 1 sensory pore and 2 short setae. Antenna: basal sensory pore externally inconspicuous. Clypeolabrum: clypeal portion with two basal sclerotized areas each bearing 1 seta and 1 sensory pore; labral portion slightly sclerotized, with 1 pair of posterior, 1 pair of lateral, 1 pair of anteromedian, 1 pair of anterior, and 1 median single setae. Epipharynx (Fig. 37): tormae boomerang-shaped. Prothoracic plate (Fig. 41): X-shaped, apparently framed by slightly sclerotized cuticular area; teeth arranged in 1 + 1 + 4 pairs; with 2 short anterior and 1 longer posterior setae on each anterior arm; 1 long seta adjacent to sensory pore, close to medial border on median arm; posterior arms laterally expanded, with 1 pair of teeth on medial border, 4 on distal one; single tooth present medially on base of each median arm; 1 sensory pore is located between anterior setae on anterior arms. Chaetotaxy: primary and secondary setae with same distribution as in M. baeri, but primary ones shorter. Mesothorax and Metathorax (Fig. 45; Tables 2, 6): postdorsal setae inserted more anteriorly than in *M. baeri*; 1 metathoracic secondary seta on epipleuron, latter sometimes present in M. baeri. Leg (Fig. 49): first pair with 3 pores on basal segment; distal segment with 2 pores and 1 seta; 2nd and 3rd appendages as in M. baeri. Abdomen (Fig. 51; Tables 2, 6): as in *M. baeri. Spiracles:* without peculiar characters.

EGG. Length 0.65 mm; width 0.31 mm. Color dull yellow. Suboval in outline, the wider and somewhat more raised. Dorsal surface strongly convex, ventral even. Egg chorion sculptured as in M. baeri (Muruaga De L'Argentier and Teran 1980). Translucent anchoring substance forming a flange around the egg.

SIGNIFICANT CHARACTERS. *Final instar:* ocelli present; epipharyngeal tormae boomerang-shaped; epipharyngeal hairs arranged parallel to longitudinal axis of epipharynx; membranous stipes with 9–10 setae; sclerite of palpifer with 3 setae and 1 sensory pore. *First instar:* ocelli present; epipharyngeal tormae boomerang-shaped; tooth formula, of prothoracic plate, is 1 + 1 + 4; abdominal sternites 3-8 with 2 secondary setae and no spinous projections.

BIOLOGICAL NOTES: In *Ipomoea rubriflora* O'Donell this species starts oviposition in February on green fruits. Generally a single egg is laid per capsule. Eggs are found on the outer face of sepals or, more frequently, on the external wall of fruits. They remain firmly stuck by the adhesive anchoring substance even after larval emergence. The first instar larva develops in about 8 days and emerges through the ventral wall of the broader end of the egg. Larvae are very active; they explore the seeds and bore an entrance hole to its interior, where they progressively make a circular cell until almost complete destruction of the contents occurs. Larvae reach maturity in about 20 days. Pupae are surrounded by frass and remains of seed contents loosely compressed, but no

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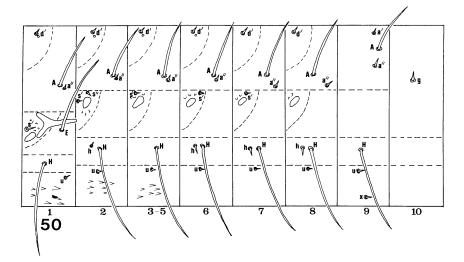


Fig. 50. Abdominal chaetotaxy of M. discoidus.

particular cocoon is apparent. They develop into adults in about 6 days. Adults emerge by the end of March through an exit hole partially prepared by mature larvae. In laboratory rearings, the life cycle lasts 90–110 days. When temperature is about 20°C, females lay eggs in the same places as in the field, but later, eggs are deposited on seeds, internal surfaces of the valve, or septa of partially open fruits. Several entrance holes were observed in seeds but only one larva develops within. Clear signs of mortality have been observed in the first and following instar larvae. In completely ripe seeds, first instar larvae are often caught in partially open galleries; hardness of the integument prevent them from reaching the inner part of seeds. Only 1.3% of seeds collected in

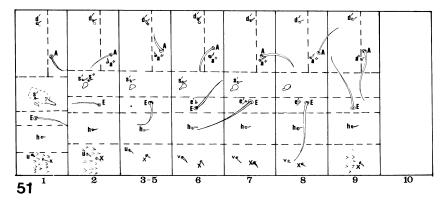


Fig. 51. Abdominal chaetotaxy of M. eulophus.

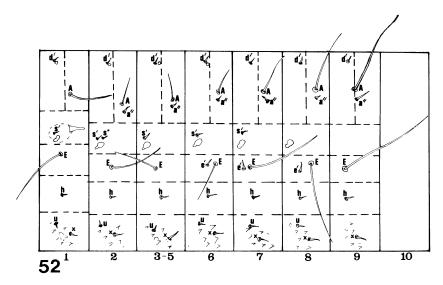


Fig. 52. Abdominal chaetotaxy of M. insulatus.

February 1980 were attacked by this bruchid. Host Plants: *M. eulophus* attacks seeds of *Convolvulus* and *Ipomoea*. It shares some of its host plants with *M. maculiventris* (Teran and Kingsolver 1977).

Megacerus insulatus Teran and Kingsolver

FINAL INSTAR. *Body:* length 3.6 mm; width 1.4 mm; color and integument as in *M. eulophus. Head:* one pair of ocelli present. *Antenna* (Fig. 9): larger sensillum basiconicum lanceolate. *Clypeolabrum:* similar to *M. eulophus. Epipharynx* (Fig. 14): tormae comma-shaped; distal convergence of groove not evident; spinous mat arranged parallel to longitudinal axis of epipharynx, not circumventing end of groove. *Mandible, Maxilla* and *Labium:* as in *M. baeri,* except for 9 setae on membranous area of stipes. *Leg* (Fig. 24): 3-segmented; basal segment with 4 pores, median with 1 seta and 2 nearby pores, apical bare. *Spiracles* (Fig. 28): 1st and last abdominal ones slightly larger.

FIRST INSTAR. *Body:* length 0.61 mm; yellowish white to greenish yellow; head, prothoracic plate and abdominal spines of 1st spiracular areas more deeply pigmented; spines, strioles, and sensory pores of cuticle as in *M. eulophus*; areolate structures abundant in prothorax and hypopleura of meso-, metathorax, and 1–9 abdominal segments, less numerous but equally conspicuous in spiracular areas and epipleura of same body segments. *Head* (Fig. 31): as in *M. eulophus. Antenna:* basal sensory pore externally visible; external appendix, of antenna, as long as internal plus its apical seta. *Clypeolabrum:* without sclerotized areas. *Epipharynx* (Fig. 38): tormae ()- to comma-shaped. *Prothoracic plate* (Fig. 42): as in *M. eulophus* but anterior and median arms less developed; secondary pore of median arm not so closely related to seta; tooth formula 1 + 1 + 3-4. *Chaetotaxy* (Figs. 46, 52; Tables 3, 6): primary and secondary setae with same distribution as in *M. baeri*; length of primary

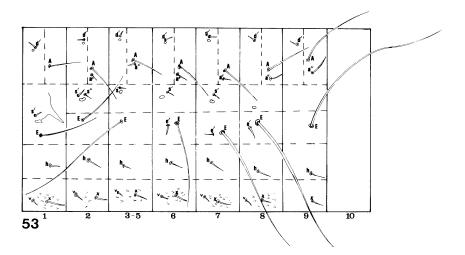


Fig. 53. Abdominal chaetotaxy of M. maculiventris.

setae equal to that of latter species; postdorsal setae of meso- and metathorax inserted more anteriorly than in *M. baeri*; 1 metathoracic secondary seta on epipleuron. *Leg:* as in *M. baeri. Spiracles:* without peculiar characters.

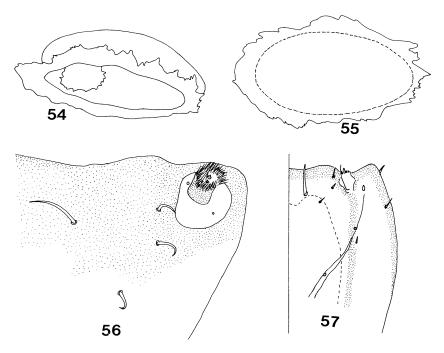
EGG (Figs. 54–55). Length 0.8 mm; width 0.3 mm. Color and characteristics as in M. eulophus, but ventral surface slightly concave.

SIGNIFICANT CHARACTERS. Final instar: ocelli present; epipharyngeal tormae ()- to comma-shaped; epipharyngeal hairs arranged linearly along longitudinal axis of epipharynx; membranous stipes with 9 setae. First instar: ocelli present; epipharyngeal tormae ()- to comma-shaped; tooth formula, of prothoracic plate, is 1 + 1 + 3-4; sensory pore, on basal arms, not equidistantly spaced between last 2 setae; 9th abdominal sternite with 1 seta and sclerotized projections (similar to *M. eulophus*), sclerotized projections also present on sterna 3-8, which distinguishes *M. insulatus* from *M. eulophus*.

BIOLOGICAL NOTES: The life cycle is similar to that of *M. eulophus*. Females start oviposition in mid February on partially ripe fruits and the adults emerge at the end of March. Eggs are laid isolated, in arcs or asymmetrical groups of 2 to 6, on the internal side of sepals. Under laboratory conditions (approximately 20°C), eggs are also found on seeds or inside fruit capsules. The life cycle lasts 55–70 days. In the field, approximately 10% of the seeds are destroyed by this species. Host Plants: *Ipomoea bonariensis* Hooker var. *chacoensis* O'Donell, from Argentina, Pcia. Salta, Salta Forestal (45 kms E Joaquin V. Gonzalez) 12-II-1980, Muruaga De L'Argentier coll. First citation of species and host plant for Argentina.

Megacerus maculiventris (Fahr.)

FINAL INSTAR. *Body:* length 2.8–3.0 mm; width 1.7–1.9 mm; color ivory white; mandibles, sclerotized parts of head, antennae, maxillae, and labium, reddish brown. *Head* (Fig. 57): ocelli present, seen as irregular black spots in fresh larva; slightly longer than wide, dome-shaped in outline; epistoma, an-



Figs. 54-55. M. insulatus egg: 54, ventral view; 55, dorsal view.

Figs. 56-57. Final instar head capsule: 56, M. discoidus; 57, M. maculiventris.

tennal sockets, and band on each side from epistoma forward to $\frac{1}{2}$ length of head more heavily sclerotized; from epistoma to sides of head, less sclerotized; sutures apparent; setae and sensory pores as in *M. eulophus*; 1 pair of pores midway between ocellus and vertex; longest epistomal setae slightly posterior to that in *M. baeri. Antenna:* distal segment cylindrical with sides more sclerotized. *Clypeolabrum:* as in *M. eulophus. Epipharynx* (Fig. 15): spinous mat arranged obliquely to longitudinal axis and converging posteriorly to circumvent groove; tormae awl-shaped; 1 pair of strong, short, curved setae. *Mandible:* external face with 1 basal seta and subtending sensory pore and 1 subapical seta. *Labium* (Fig. 21): more clearly defined at sides and base and less sinuate in front than in *M. baeri*; base of each ligular seta with vaguely visible sensory pore. *Leg* (Fig. 25): 3 (or 4?) segmented; distal segment bare, 2nd segment with 1 seta and 2 pores close to each other, 3rd with 3 pores and 1 small seta (probably belonging to a 4th, basal segment). *Spiracles* (Fig. 29): 1st and last abdominal pairs somewhat enlarged; atrium with minute granulations.

FIRST INSTAR. *Body:* length 0.7–0.8 mm; color whitish, with yellowish mouthparts, prothoracic plate, 1st spiracular spine and legs; brown head; cuticle areolate in prothorax, except at sides and in front of prothoracic plate where minute triangular spiniform plates are found; meso- and metathorax, and hypopleura 1–8 of abdomen, areolate. *Head:* slightly longer than wide; ocelli present. *Antenna* (Fig. 33): with external finger-like process longer than internal.

Clypeolabrum (Fig. 35): clypeal portion rectangular and broader than labral portion; setae and sensory as in *M. baeri*; labral portion with single arc of 8 setae, 2 proximal pairs 1/3 to 1/2 as long as apical pair; single elongate seta located distally inside apex of arc. *Epipharynx* (Fig. 39): tormae elongate, seta-shaped. Prothoracic plate (Fig. 43): framed by sclerotized cuticular area; actinomorphic; teeth arranged in 1 + 1 + 3 or 4 formula; 4 pairs of setae present; 2 anterior and 1 posteromedian on anterior arm, 1 with adjacent sensory pore close to median border of median arm; anterior arm enclosing sensory pore; basal teeth, of median arm, more acute than in M. baeri; posterior arms laterally expanded 1 pair of teeth on median border and 3-4 on distal arm. Prothorax (Fig. 47; Tables 4, 6): primary setae longer than in *M. baeri*. Mesothorax and Metathorax (Fig. 47; Tables 4, 6): postdorsal setae inserted more anteriorly than in M. baeri, only 1 seta on metathoracic epipleura; sternal primaries longer than in M. baeri. Leg: sensory pores and hairs distributed as in 2nd and 3rd pairs of M. baeri. Abdomen (Fig. 53; Tables 4, 6): primaries of epipleura and of 9th postdorsum, secondaries of hypopleura (especially 5-9) and posterior secondaries of 1-8 and that of 9th sterna, longer than in M. baeri; sensory pore of 6th abdominal prodorsum sometimes absent, occasionally present on 7th. Spiracles: similar to those in M. baeri.

EGG (Figs. 6-7). Length 0.65 mm; width 0.25 mm. Fusiform, section circular except in anchoring end where ventral surface is flattened in a variable extension. Eggshell translucent, thin, minutely punctate. For other features see significant characters.

SIGNIFICANT CHARACTERS. Final instar: ocelli present; epicranial sutures evident; epipharyngeal tormae awl-shaped; epipharyngeal hairs arranged obliquely to longitudinal axis of epipharynx; spiracle surrounded by numerous integumental projections. First instar: ocelli present; epipharyngeal tormae elongate and seta-shaped; tooth formula, of prothoracic plate, is 1 + 1 + 3-4; teeth on posterior arms actinomorphic; sensory pore, on basal arms, equidistantly spaced between last 2 setae; 9th abdominal sternite with 1 secondary seta and no sclerotized projections; primary epipleural setae 3-4 times as long as postdorsal primary setae. Egg: an SEM examination of a single egg (Figs. 6, 7) would indicate that its entire surface is covered with a thin layer of mucilage which secures the egg by adhering to any nearby object. Cracks in the mucilage (Fig. 7) reveal an irregular pattern of double and triple punctations, each of which appears to open into a single aeropyle.

BIOLOGICAL NOTES: Flowers of Ipomoea purpurea var. purpurea are found from February to May. By mid-May, they are scarce, but fruits in every degree of maturity are found on the fading vines. Females are often seen within corollas, feeding on pollen; flowers are deserted before noon shrinkage. Eggs are laid on the external face of sepals, on fruit stalks, bracts, when fruits are still green, or on the internal face of valves on mature and partly dehisced fruits; they are loosely attached by their ends. Developed first instar larvae stay within the eggshell for a considerable time, probably awaiting seed maturation. They chew an exit hole on the dorsal or ventral surface of the eggshell and actively walk with the help of their legs and tips of their abdomens to find a suitable place for entering the fruit. Only one larva is able to develop per seed. Seeds maintained under laboratory conditions had mature larvae in them at the end of July. At the beginning of August larvae pupate and adults start to emerge by the end of the month. Most males have emerged before the females. Host Plants: Five species of Ipomoea have been recorded as host plants of maculiventris (Teran and Kingsolver 1977); in most cases, it shares them with

another species of the genus (*M. flabelliger, M. eulophus*). In Argentina, it probably is the only species found in *I. purpurea* (L.) var. *purpurea*. Our observations have been made in this species.

KEY TO SOME MEGACERUS FINAL INSTAR LARVAE

1.	Ocelli absent	2
1′.		3
2(1).	Labial submentum, C-shaped, sclerotized and bearing 2 lateral and 1 proximal pairs of setae; epipharyngeal sensillae flanked laterally	
	by triangular patch of sclerotized, pointed projections; sclerite of palpifer with 2 setae and 1 sensory pore M. discoidu	S
2′.	Labial submentum absent; epipharyngeal projections absent; scle- rite of palpifer with 5 setae and 2 sensory pores <i>M. baei</i>	
3(1).	Abdominal spiracles surrounded by numerous integumental pro- jections; epipharyngeal hairs arranged obliquely to longitudinal axis of epipharynx <u>M. maculiventru</u>	
3'.	Characters not as above	4
4(3).	Epipharyngeal tormae boomerang-shaped; epipharyngeal groove converging apically and bordered distally by fringe of hairs	
4′.	<i>Epipharyngeal tormae comma-shaped; epipharyngeal groove not converging distally; the latter not bordered distally by hairs</i>	
	KEY TO SOME MEGACERUS FIRST INSTAR LARVAE	

KEY TO SOME MEGACERUS FIRST INSTAR LARVAE

1.	Ocelli absent 2
1′. 2(1).	Ocelli present 3 First abdominal epipleuron with primary seta (E); spiracular areas
	of abdominal segments 2–8 with integumental protrusions; abdom- inal sternites 6–8 with single seta and no sclerotized projections;
2′.	10th abdominal segment with single secondary seta M . discoidus First abdominal epipleuron glabrous; spiracular areas without small integumental protrusions; abdominal sternites 6–8 with 2 second- ary setae and numerous sclerotized projections; 10th abdominal
	segment asetiferous
3(1).	Prothoracic plate with 3 pairs of setae and 1 pair of sensory pores;
	abdominal hypopleura 2-8 with 1 primary (H) and secondary (h)
	setae; abdominal sternites 1-8 asetiferous; 10th abdominal segment
	with 3 setae (Aa'a") M. cubicus*
3'.	Characteristics not as above 4
4(3).	Ninth abdominal sternite with 1 secondary seta and no sclerotized projections; primary epipleural setae 3-4 times as long as postdorsal primary setae; teeth on posterior arms of prothoracic plate actinomorphic M. maculiventris
4'.	Ninth abdominal sternite with single secondary seta and sclerotized
т.	projections; other characters not as above 5
5(4).	

8 with 2 secondary setae and spinous projections absent M. eulophus

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^{*} See Pfaffenberger (1980).

DISCUSSION

According to Teran and Kingsolver (1977), the genus Megacerus consists of three subgenera (Serratibruchus, Pachybruchus and Megacerus), of which the first and last are represented among the larvae described in this study. Serratibruchus includes M. maculiventris, whereas M. discoidus, M. eulophus, and M. insulatus, as well as M. baeri (Muruaga De L'Argentier and Teran 1980) and M. cubicus (Pfaffenberger 1980) are included within the subgenus Megacerus.

As is evidenced by the character summary (Table 5; Figs. 12–17 in Muruaga De L'Argentier and Teran 1980), there are numerous features which the final instars share in common. The more significant of these include: (1) single segmented antenna bearing 1 large and 2 small conical sensillae and 1 seta, (2) clypeus with 1 pair of setae and 2 sensory pores, (3) epipharynx with 1 pair of median setae, and (4) 1 pair of setae on labial mentum and ligula.

Some incongruency exists between the adult subgeneric and the final larval instar classifications. The most notable inconsistency is between *M. baeri-M. discoidus* and the remaining species, wherein the former species lack ocelli and possess 9 labral setae instead of 7. It is evident, on the basis of shared similarities (Table 5), that *M. eulophus*, *M. insulatus* and *M. maculiventris* form a well-defined cluster.

Like the final instars, the first instar larvae form a cohesive group (Table 6). Some of the shared characters include: (1) single segmented antenna; (2) bilobed antenna; (3) prothoracic plate characters which include, 1 pair of anterior teeth, 1 pair of median teeth, 3–6 pairs of posterior teeth; (4) 2-segmented legs with expanded foot; and (5) 1 seta present on meso-metathoracic appendages.

Significant differences do exist, however, which could be used to create 3 phylogenetic groupings. Group I would consist of M. baeri and M. discoidus since both (1) lack ocelli, (2) have as many as 6 teeth on posterior arms of prothoracic plate, and (3) have 6 sensillae on the basal segment of the mesometathoracic appendages. Group 2 would consist of M. cubicus, which has (1) 1 antennal seta, (2) 3 setal pairs on prothoracic plate, (3) 2 setae and no sensillae on prothoracic appendages, (4) no sensillae on thoracic appendages, and (5) 1 primary and 2 secondary setae on 10th abdominal segment. Group 3 would then include the remaining species (M. eulophus, M. insulatus and M. maculiventris). Upon examination of the characters (Table 6), one is impressed by the remarkable similarities which exist among these species.

Chorionic sculpturing of eggs might provide valuable clues to phylogenetic affinities (Figs. 2, 5, 7), but no chorionic patterns have been observed for M. *cubicus*, M. *eulophus*, and M. *insulatus*. Larval similarities and/or differences presented here indicate the need for a critical review of all first and final larval instars of Megacerus.

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