IMMATURE STAGES OF *RHYPARONOTUS ALTARENSIS* (OLLIFF) (COLEOPTERA: CURCULIONIDAE: MOLYTINAE), WITH COMMENTS ON LARVAL CHARACTERS IN ANCHONINI AND MOLYTINAE

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Abstract.—The last instar larva and pupa of *Rhyparonotus altarensis* (Olliff) (Curculionidae: Molytinae: Anchonini), from Ecuador, are described and illustrated. Larval characters are compared with those of other Molytinae, e.g., Molytini, Hylobiini, and Phrynixini, and their phylogenetic value is discussed.

The subfamily Molytinae (recently demoted to a tribe Molytini of Curculioninae, see Kuschel, 1995) resulted from the amalgamation of about 30 tribes and subfamilies by Kuschel (1987), to which Dinomorphini (Thompson, 1992) and Bagoini (Morrone, 1997) were subsequently added (see Appendix). This cosmopolitan subfamily comprises more than 3,000 species and 300 genera (Thompson, 1992). Although several authors have treated molytines as a distinct taxon, either of tribal (May, 1993; Kuschel, 1995; Morrone & Roig-Juñent, 1995; Marvaldi, 1997) or subfamilial rank (Wibmer & O'Brien, 1986; Kuschel, 1987; Thompson, 1992; May, 1994; Zimmerman, 1994; Morrone, 1997), it is debatable whether or not this highly speciose group really represents a natural taxon. Calder (1989) has pointed out the enormous diversity of anatomical features among some of the taxa included in Kuschel's Molytinae, suggesting that this taxon was not a monophyletic group. May (1994) considered that the larvae of many genera included in Molytinae diverge so far from the typical Hylobius that a diagnosis of the group "would serve no useful purpose." Doubts on the monophyly of Molytinae are shared by other authors (Robin Craw, pers. comm.).

The molytine tribe Anchonini is a relatively small group (about 200 species), ranged in the Americas (from the USA to Bolivia), Japan and the Oriental region (Faust, 1892; Morimoto, 1982; O'Brien & Wibmer, 1982; Wibmer & O'Brien, 1986; Voisin, 1992, 1993). Our cursory review of the literature shows that knowledge about the biology and immature stages of this taxon is very scarce. A brief larval description of *Anchonus* Schoenherr, based on larvae of unidentified species from Bahamas and Panama, was provided by Anderson (1952), who also intended a larval definition of the tribe Anchonini. However, little confidence can be given to that tribal diagnosis as it was based on larvae of taxa not currently placed in Anchonini, except those assigned to *Anchonus*. A recently fallen *Croton* sp. tree (Euphorbiaceae) in Ecuador provided one of us (JJM) the opportunity to collect specimens of *Rhyparonotus*

altarensis (Olliff). When the bark of the tree was removed, three mature larvae, two pupae, and one adult of this species were discovered.

Our main objective is to describe the immature stages of this anchonine species. Furthermore, we discuss the phylogenetic value of some characters that could help elucidating the placement of the tribe Anchonini, as well as testing the monophyly of the subfamily Molytinae.

The specimens examined for this study have the following collection data: EC-UADOR Napo: 52 km N Tena, 6500 feet, under bark of *Croton* sp., 24-V-95, J. J. Morrone coll., det. by associated adult, 3 mature larvae, 2 pupae. The immature specimens have been deposited in the collection of the Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), and the associated adult in the collection of the Museo de Zoología, Facultad de Ciencias (UNAM). Techniques for dissection of larvae and terminology and abbreviations here applied are those used in Marvaldi (1998). Pupae were studied following May (1987, 1994).

IMMATURE STAGES OF RHYPARONOTUS ALTARENSIS (OLLIFF)

Description. *Mature larva* (Figs. 1–14). Maximum size 13.28 mm \times 3.75 mm. Head width 2.20 mm. Body robust, cuticle finely spiculate, setae rather short except for long dorsal and pleural setae on AVII–IX; AVII and AIX transverse, depressed.

Head (Figs. 1, 2) exposed, subcircular, orange-brown pigmented. Frontal line visible in entire length, slightly angulate before apex. Endocarina absent. Postoccipital condyles well developed, obtuse-angled, pigmented. Setae: fs4,5 long, subequal, fs3 very short, fs1,2 minute; des1,3,5 long, subsequal, des2 shorter but well developed, des4 very small; des3 on epicranium but close to frontal line, pes minute; les1 short, les2 long; vcs1,2 short, subequal. Only anterior stemmata distinct, as black pigmented spots. Antennae (Figs. 1, 3) small, set obliquely on anterior margin of head, partially overhung by frontal projection, antennal sensorium broadly conical. Clypeus (Fig. 4) pigmented at base, with cls1,2 well developed. Labrum (Fig. 4) transverse, completely pigmented, the anterior margin slightly projected medianly; lms3 well developed but shorter than lms1,2; lateral labral sensilla at same level than lms1 and as widely separated as *lms2*; labral rods (Fig. 5) strong, joined at base with a distinct stem, Y-shaped. Epipharynx (Fig. 5) with ams1 larger as ams2 and subequal to als; mes1 as widely separated as mes2; sensillum clusters locate between mes1 and mes2 and near base of labral rods. Mandibles (Fig. 6) bidentate at apex, with a distinct median projection on cutting edge, mds1,2 aligned longitudinally, mds1 short, mds2 very small, scrobe indistinct. Maxillae (Figs. 7, 8) with 5 vms and a row of 7 dms; dms1 more slender than other dms; a patch of minute spinules present below palpus. Labium (Fig. 7) with pms2 and pms3 pairs separated by same distance, pms1 less widely separated; premental sclerite trident-shaped, with subtriangular posterior extension.

Thorax (Fig. 11). Spiracle (Fig. 9a) large, with pigmented and finely annulated airtubes, dorsally directed. Pronotum (Fig. 11) with 9 setae plus 2 small epipleural setae. TII, III (Fig. 11) with 1 *prs*; 4 *pds* (*pds1,2* short, *pds3,4* long); alar area with 1 *as*; spiracular area with 2 small setae. Pedal area (Fig. 10) with 6 setae (*z* absent) plus minute x', setae *t* and *w* long, others short; 2–5 sensilla present between *v* and *w*.

Abdomen (Figs. 11–14). Spiracles (Figs. 9b, c) of different size, with close-set annuli, those of AI–VII (Fig. 9b) smaller than thoracic spiracle, being the interme-

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Figs. 1–6. *Rhyparonotus altarensis*, larva. 1, head, dorsal; 2, head, ventral; 3, antenna; 4, clypeus and labrum; 5, epipharynx; 6, mandible. Scales, 1,2 = 1 mm; 3 = 0.1 mm; 4-6 = 0.5 mm.

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Figs. 7–10. *Rhyparonotus altarensis*, larva. 7, maxilla and labium, ventral; 8, maxilla, dorsal; 9, spiracles (a, thorax; b, AIV; c, AVIII); 10, pedal area. Scales = 0.5 mm.

diate ones smallest, airtubes dorsally directed; AVIII spiracle (Fig. 9c) placed on dorsum and larger than other 7 and than thoracic one, with airtubes posteriorly directed. AI–VII (Figs. 11–13) with *prs* small, vestigial on AVIII; AI–VII with 5 *pds*: *pds3.5* longer than others, distinctly longer and stronger on AVII; AI–VI with *ss1.2* on spiracular area; AVII with *ss2* shifted to postdorsum and *pds2* set ahead of other *pds*. AVIII (Fig. 13) with 3 *pds* which appear to correspond with *pds4* (minute), *pds5* (large and strong) and *ss2* (minute) of preceding segments. AIX (Figs. 13, 14) with 2 unequal *ds*. AX (Fig. 14) ventral, 4-lobed, anus transversal, lateral lobes smallest bearing 1 small seta.



Figs. 11–14. *Rhyparonotus altarensis*, larva. 11–13, one side, dorsolateral; 11, TI–III, AI; 12, AIV; 13, AVI–X. 14, AIX, X, caudal view. Scales = 1 mm.

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Figs. 15, 16. Rhyparonotus altarensis, pupa, habitus. 15, ventral; 16, dorsal. Scale = 5 mm.

Pupa (Figs. 15, 16). Maximum length 11.95 mm. Setae as in Figs. 15, 16. Cuticle glabrous. Setae orange-brown, tapering, moderately strong on head and pronotum, smaller on abdomen, mounted on small tubercles. Antennal club smooth. Each femur with a pair of unequal setae. Secondary pterotheca shorter than primary. Spiracles distinct, with dark peritreme. AIX with prominent posterior processes, each with a small associated seta located laterally at base.

DISCUSSION

The larva of *Rhyparonotus altarensis* presents some characters that are similar to those of *Anchonus* spp. indet. studied by Anderson (1952), such as: endocarina absent, antennae overhung by frontal projection, labrum completely pigmented with anterior margin produced medianly, maxillary mala with 7 *dms*, AI–VII (typical abdominal segments) with 3 dorsal folds, spiracle on AVIII dorsal and larger than those of anterior segments, and body asperities fine. These features may be useful to diagnose the tribe in the larval stage, but they are also present among other molytine larvae. The anchonine larvae herein studied and those examined by Anderson (1952) are different, however, in characters involving the position of *des3*, shape of labrum and position of lateral sensilla, shape of labral rods, arrangement of *als* on epipharynx, structure of mandible on cutting edge (inner margin), orientation of spiracular airtubes on AI–VII, relative length of *pds5* on AI–VII, and number of *pds* on AVIII and AIX. These characters may be diagnostic at generic level within Anchonini.

According to May (1993), Molytinae comprise two distinct elements: "live tissue feeders" (=tribes Molytini and Hylobiini), with modal mouthparts, and "inhabitants

of dead wood" (=tribe Phrynixini), with mouthparts adapted to xylophagy. The larvae of *Rhyparonotus* herein studied, apparently subcortical borders in dying trunks, fall in the former group, characterized by the pigmented head, transverse labrum, clear hypopharingeal bracon, broadly conical antennae, and maxilla with 2 setae on palpifer and 7 *dms*, plus TII, III with long *pds4*. These characters, however, appear to be plesiomorphic when compared with other weevil larvae, and thus, provide no evidence for monophyly. The latter group may correspond instead with a monophyletic group, because although several mouthpart characters defining it are hypothesized as "adaptations for xylophagy" (May, 1993), their maxillae with 3 setae on palpifer and 10 *dms*, and the short *pds4* on TII, III may be apomorphies of *Phrynixus* and its allies.

May (1993) considers "labral rods separate, subparallel or bowed" to diagnose Molytinae (from the Australian Region). However, larvae of Rhyparonotus herein studied, as well as those of Heilipodus erythropus (Rosado-Neto, 1980), belonging to the tribe Hylobiini, show Y-shaped labral rods (joined at base with a distinct stem), which could be phylogeneticaly informative. It is worth noting that, among other Curculionidae, labral rods Y-shaped define the larvae of Cryptorhynchinae, which can be distinguished from those of Molytinae by their lateral AVIII spiracles (May, 1993, 1994). We have noted that the 3 pds on AVIII of Rhyparonotus larvae (and probably other molytines, as suggested by figures in literature) appear to correspond with pds4, pds5 and ss2 of preceding segments. This is different in larvae of Rhytirrhinini and some Aterpini (Cyclominae), that lack pds5 and ss2 on AVIII (Marvaldi, 1998). Although there are examples of molytine larvae with des3 on frontal line or on frons (e.g., Anderson, 1952:291; May, 1993:82), those of typical Molytinae (e.g., Hylobius) have des3 on epicranium. The latter character allows separation from the morphologically similar larvae of Aterpini with des3 always on frons or on frontal line (May, 1994). To this could be added that most (though not all) larvae of Molytinae have only 2 ds on AIX. All these characters also provide separation from larvae of Rhytirrhinini, which in addition are diagnosed by their very reduced lateral labral setae. Larvae of Molytinae, with distinct postoccipital condyles and AVIII spiracles on dorsum, can be separated quite easily from those of Cossoninae and Scolytinae (Marvaldi, 1997), but they are difficult to distinguish, morphologically, from some Curculioninae s. str. (May, 1993, 1994).

Further studies on immature stages, including some less "typical" Molytinae, e.g., Petalochilini or Juanorhinini, are still needed in order to test the monophyly of Molytinae. Similarly, a more complete sample of larvae representative of Anchonini would be valuable to define this tribe at the larval stage and to ascertain the phylogenetic relationships of the Anchonini.

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Appendix. Tribes assigned to Molytinae (after Kuschel, 1987; Thompson, 1992; Morrone, 1997). Genera between brackets are those for which larvae have been described.

Acicnemidini Lacordaire Amalactini Lacordaire Anchonini Imhoff (Anchonus [Anderson, 1952]).

Dessini Thomson (Bassus [Saharf 1064; May 100/

Bagoini Thomson (Bagous [Scherf, 1964; May, 1994]).

Cholini Schoenherr

Cycloterini Marshall

Dinomorphini Lacordaire

Emphyastini Lacordaire

Euderini Lacordaire

Galloisiini Morimoto

Guioperini Lacordaire

Haplonychini Lacordaire

Hylobiini Kirby (=Heilipinae Faust) (Acles [Gardner, 1938]; Heilipodus [Rosado-Neto, 1980]; Heilipus [Böving & Craighead, 1930]; Hylobius [Gardner, 1938; Scherf, 1964; Anderson, 1991]; Kobuzo [Gardner, 1938]; Pagiophloeus [Gardner, 1934]; Paramecops [Gardner, 1934; Oberprieler, 1988]).

Ithyporini Lacordaire (=Conotrachelini) (*Conotrachelus* [Peterson, 1951; Anderson, 1991]).

Juanorhinini Aurivillius

Lepyrini Faust

Lithinini Lacordaire

Lymantini Lacordaire (genus indet. near Ithaura [Anderson, 1952]).

Mecysolobini Reitter (Mesalcidodes [Lee & Morimoto, 1988]).

Molytini Schoenherr (=Liparini Latreille) (Arecophaga [May, 1993]; Hadramphus [May, 1971, 1981]; Karocolens [May, 1987]; Liparus [Scherf, 1964]; Lyperobius [May, 1981]; Paedaretus [May, 1993]).

Nettarhinini Lacordaire

Omophorini Marshall

Pacholenini Lacordaire

Paipalesomini Marshall (Paipalesomus, Peribleptus [Gardner, 1993]).

Petalochilini Lacordaire

Phoenicobatini Champion

Phrynixini Kuschel (Megacolabus [May, 1973]; Notonesius [May, 1979]; Phrynixus [May, 1971, 1981]; Rhystheus [May, 1993]).

Pissodini Thomson (Pissodes [Anderson, 1947; Scherf, 1964]).

Sternechini Lacordaire (*Chalcodermus* [Peterson, 1951; Anderson, 1991]). Styanacini Chujo & Voss

Trypetidini Lacordaire (Heteramphus, Nesotocus [Anderson, 1952]).

Molytinae insertae sedis (Demyrsus, Melanotranes, Orthorhinus, Tranes [May, 1994]).



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