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LARVA AND PUPA OF *CLEONIDIUS ERYSIMI* (FALL) WITH A DISCUSSION OF THE PHYLOGENETIC POSITION OF LIXINI (*SENSU* KUSCHEL) (COLEOPTERA: CURCULIONIDAE)

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I first met Don Whitehead in December of 1980 when I visited him in Washington to discuss a topic in weevil systematics suitable for a Ph.D. dissertation. With his help and advice I eventually selected North American Cleoninae as the group I would study. Not only was Don instrumental in the selection of my dissertation topic but he was also the reviewer of the published version which appeared in 1988; his insightful and in-depth commentary greatly improved the final product. All those who have ever discussed phylogenetics with Don know of his keen interest in the subject and his unique means of demonstrating relationships (he brought new meaning to the term "hand cladistics" and I suspect was often frustrated that he only had ten fingers). I feel that it is appropriate that the present paper, which continues to deal with the Cleoninae and their phylogenetic relationships, be dedicated to his memory.

Abstract. – The last instar larva and pupa of Cleonidius erysimi (Fall) are described. Larvae mine the roots and crowns of Lobularia maritima (L.) Dev., an introduced species of Cruciferae, in southern California. Pupation takes place in the larval mines. The presence of mandibular setae in the pupa of traditional Adelognatha, and Lixini, Thecesternini, Pachyrhychina (sensu Kuschel), and Ithycerus noveboracensis (Forster) suggests this character state is symplesiotypic. A review of the phylogenetic placement of Lixini (sensu Kuschel) is confused by conflicting character state distributions.

Key Words: Curculionidae, immature stages, phylogeny

Recent systematic revision of adults of the New World weevils placed in the tribe Cleonina of the tribe Lixini (*sensu* Kuschel) (= tribe Cleonini of the subfamily Cleoninae in Anderson [1988]) questioned the traditional placement of all New World Cleonina in the genus *Cleonis* Dejean (O'Brien and Wibmer 1982), and instead showed there to be four rather distantly related genera represented: *Cleonis* Dejean (1 introduced species), *Stephanocleonus* Motschulsky (6 native species), *Apleurus* Chevrolat (8 native species), and *Cleonidius* Casey (19 native species) (Anderson 1988). Whereas phylogenetic relationships of *Cleonis, Stephanocleonus* and *Apleurus* were considered to be with various other traditional Cleonina, relationships of *Cleonidius* were more difficult to firmly establish, but appeared to be with one or more subgenera of the extremely speciose, geographically widespread and structurally diverse genus *Lixus* Fabricius of the

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subtribe Lixina as well as with a genus of traditional Cleonina, *Cylindropterus* Chevrolat (Anderson 1988). These relationships were established solely on the basis of the distribution of adult character states largely because of the unavailability of other life stages representative of both Old, but especially, New World species.

In a review of the immature stages of American Curculionoidea, Burke and Anderson (1976) noted that larvae and/or pupae have been sufficiently well-described for only the introduced Cleonis piger (Scorpoli) and Rhinocyllus conicus (Froelich), and for but two native species of Lixus, L. scrobicollis (Boheman) (Boving and Craighead 1930) and L. concavus Say (Peterson 1951). Immature stages of species of Apleurus, Cleonidius, and North American Stephanocleonus (an unidentified Palearctic species was very briefly described by Scherf [1978]) have not previously been described. Immature stages of a number of Old World Lixini (sensu Kuschel) have been very briefly described and diagrammatically illustrated by Scherf (1964).

This paper describes the pupal and last larval instars for Cleonidius erysimi (Fall) and thus represents the first description of the immature stages of that genus. Unfortunately, few meaningful phylogenetic interpretations can be made of characters of immature Cleonidius because of the general lack of broad taxonomic representation within the tribe, particularly those taxa apparently closely related to Cleonidius as determined on the basis of adult characters. Although nothing can be said of the phylogenetic relationships of Cleonidius and other Lixini (sensu Kuschel) based on character states of the immature stages, the phylogenetic relationships of Lixini (sensu Kuschel) and other Curculionidae can be discussed in this light.

Terms for the pupa follow those of May (1978); for the larva, those of Anderson (1947) and Ahmad and Burke (1972), and May (1977) for the alimentary canal. Pupae

were examined in alcohol with a binocular dissecting microscope. Larvae were prepared for examination as in Ahmad and Burke (1972). They were examined in glycerine in depression slides with a compound microscope with interference contrast.

DESCRIPTION OF LAST INSTAR LARVA Figs. 1–6

Body (Fig. 1).—Robust, slightly curved. Asperites minute, various in degree of development, apices acutely pointed, evenly distributed over body except in areas surrounding bases of setae and in primary folds of body cuticle. Color creamy white except for head (medium to dark brown), pronotum (pale yellowish-brown), prothoracic pleural area and meso- and metanotal pedal areas (very pale golden yellow).

Head (Figs. 2-5).-Free. Mouthparts directed ventrally. Width of head capsule 1.44-1.59 mm (n = 4). Frontal sutures distinguishable throughout length, incomplete anteriorly. Epicranial suture distinct throughout length, length approximately one-half length of head capsule. Anterior ocellus small, indistinct; posterior ocellus absent. Basal article of antenna bearing tall, circular, cone-like accessory projection and three or four minute setae. Endocarina distinct, approximately one-half length of frons. Hypopharyngeal bracon present. Frons with five pairs fine, apically tapered, frontal setae (fs 1-5); fs 1 slightly shorter than fs 2, 4-5which are subequal in length; fs 3 very short. Two pairs frontal sensillae (fsl 1-2); fsl 1 situated near midline between fs 1 and fs 2; fsl 2 located equidistant between fs 3 and fs 4, immediately posteriad of line joining fs 3 and fs 4. Five pairs dorsal epicranial setae (des 1-5); des 1, 3, 5 very long, tapered apically, subequal in length; des 2, 4 slightly shorter, subequal in length; des 1 situated slightly posterolaterad of confluence of epicranial and frontal sutures; des 2 situated distinctly laterad, slightly posteriad of des 1; des 4 situated slightly posterolaterad of des 3, des 3 situated very close to frontal

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Figs. 1–6. Last instar larva of *Cleonidius erysimi* (Fall). 1, lateral view of larva (scale line = 1.75 mm). 2, frontal view of head (scale line = 0.5 mm). 3, ventral view of epipharynx (scale line = 0.1 mm). 4, dorsal view of left mandible (scale line 0.1 mm). 5, ventral view of maxillae and labium (scale line = 0.1 mm). 6, lateral view of alimentary canal (scale line = 1.5 mm).

suture. Four pairs very small, peg-like, postepicranial setae (pes 1–4) arranged in an arc directed from vertex to des 2. Three pairs dorsoepicranial sensillae (desl 1–3); desl 1 situated posteriad of des 1, slightly anteriad of pes 1; desl 2 situated slightly laterad of des 1, mediad of des 2, slightly closer to des 1 than to des 2; desl 3 situated posteriad of des 5. Two pairs lateral epicranial setae (les 1–2); les 1 shorter than les 2; les 2 subequal in length to des 1, 4–5. Two pairs ventral epicranial setae (ves 1–2); moderately long, subequal in length. Clypeus with two pairs short, stout, clypeal setae (cls 1–2); cls 1 longer than very short cls 2; also with single pair clypeal sensillae (clsl) close to anterior margin of frons. Labrum with two pairs short, stout, labral setae (lms 1–2); lms 1 longer than very short lms 2; lms 2 situated laterad and slightly anteriad of lms 1; also with one pair lateral labral sensillae (lmsl) situated between lms 1 and lms 2; and single median labral sensilla (mlmsl) situated on midline at anterior clypeal margin. Epipharynx with six or seven very short, peglike, anteromedian setae (ams); and four pairs short, stout anterolateral setae (als). Labral rods well-developed, convergent posteriorly; with two pairs short, stout, epipharyngeal median spines (msp 1-2); msp 1 longer and stouter than msp 2; single pair epipharyngeal sensory pores situated between msp 1 and msp 2. Mandibles with single apical tooth and with two mandibular setae (mds 1-2); mds 1 longer than very short, stout mds 2. Maxillary palpus with two subequal in length articles; apical article with number of small, cone-like projections at apex. Stipes with four setae (sts 1-4); sts 1, 3–4 moderately long, subequal in length; sts 2 very short. Mala with six stout dorsal (dmsa) and five linearly arranged stout ventral setae (vsma). Labial palpus of two articles. Premental sclerite with long anterior and posterior processes. One pair long, slender, premental setae (prms); three pairs short, stout, glossal setae (gls) and numerous minute asperites along apical margin. Postmentum with three pairs setae (pms 1-3); pms 1 very long, tapered apically; pms 2 shorter than pms 1; pms 3 shorter than pms 2; pms 2 and pms 3 situated close together in anterolateral angle of postmentum.

Prothorax (Fig. 1).—(Setae described for one side of body). Pronotum with six moderately long setae arranged around perimeter of darkly sclerotized area. Spiracular area with two setae, anterior seta shorter than posterior. Spiracular bicameral, airtubes short, each with four or five annulations, peritreme elongate-oval in shape. Pleural region with two moderately long setae. Pedal area with seven setae arranged around perimeter of lightly sclerotized area.

Meso- and metathorax (Fig. 1).—(Setae described for one side of body). Prodorsum with single short seta (prs). Postdorsum with four setae (pds 1–4) arranged in a transverse line; pds 3–4 slightly longer than pds 1–2. Spiracular area with four short setae ar-

ranged in a longitudinal line. Epipleural region with single short seta (eps). Pleural region with single moderately long seta. Pedal area with six short setae arranged around perimeter of lightly sclerotized area. Sternellum with single short setae. Most setae (excluding pronotal setae and pds 3–4) subequal in length.

Abdomen (Fig. 1).-(Setae described for one side of body). Abdominal segments I-VII each with three folds; segment VIII with two folds. Prodorsum of each segment with single short seta (prs). Postdorsum with five setae (pds 1-5) arranged in transverse line on abdominal segments I-VI; pds 1-5 short, subequal in length on segments I-IV; pds 1-2, 4 longer than pds 3, 5 on segments V-VI. Abdominal segment VII with seven postdorsal setae (pds 1-7); pds 4, 6 shortest of series, pds 1-2, 4 subequal in length. Spiracles bicameral, present on abdominal segments I-VIII; peritreme circular, smaller than on prothorax; airtubes short, as long as diameter of peritreme, each with four or five annulations. Spiracular area with two setae (ss 1-2); ss 1 shorter than ss 2. Epipleural region with two short setae (ss 1-2); ss 1 shorter than ss 2. Epipleural region with two short setae (eps 1-2); eps 2 slightly longer than eps 1. Pleural region with two short setae (ps 1-2); ps 2 slightly longer than ps 1. Pedal area with single short seta. Eusternum with two short setae (eus 1-2). Abdominal segment IX with five short dorsal setae; one short epipleural seta; and, one short eusternal seta. Anus terminal.

Alimentary canal (Fig. 6).—Proventriculus short, numerous small mycetomes present around cardiac valve. Anterior ventriculus large, deeply folded with numerous variously sized and shaped protruding lobes, narrowed gradually to posterior ventriculus. Gastric caecae small, not numerous. Six malphighian tubules, grouped 4 + 2 on thickened portion of posterior ventriculus, rejoined to alimentary tract in uniform manner distant from rectal bracon and appressed for some length to well-developed,



Figs. 7–10. Pupa of *Cleonidius erysimi* (Fall). 7, frontal view of head. 8, dorsal view of pronotum and mesonotum. 9, dorsal view of metanotum and abdomen. 10, ventral view of abdomen. Scale line = 1.1 mm.

asymmetrically expanded cryptonephridium. Rectal bracon membranous, distinctly delimiting posterior end of cryptonephridium. Cryptonephridrium much longer than very short anal tube.

Specimens examined.—USA. CA. San Bernardino Co., Guadalupe, Los Alamos, 20.viii.1987, ex. crowns Lobularia maritima (L.) Dev. (Cruciferae), T. Seeno & J. Davidson (15 specimens). USA. CA. San Bernardino Co., Harris Ranch, Los Alamos, 25.vii.1986, ex. crowns Lobularia maritima (L.) Dev. (Cruciferae), J. Davidson (2 specimens). USA. CA. San Bernardino Co., Harris Ranch, Los Alamos, 14–21.vii.1987, ex. crowns and roots Lobularia maritima (L.) Dev. (Cruciferae) (1 specimen). Species identity was established based on co-occurrence of adults with larvae and pupae in mines in crowns and roots of the host plants. Specimens are deposited in CMNC, TAMU, USNM.

Description of Pupa Figs. 7–10

Body.—Length 9.6-13.0 mm (n = 9).

Head (Fig. 7).—Creamy white except for compound eye and mandibles which are light to dark brown in color in some specimens. All setae sessile, fine, tapered apically. One pair moderately long vertical setae (vs), subequal in length to each of two pairs supraorbital setae (sos 1-2) and pair orbital setae (os 1). One pair "ocular" setae situated on posterior portion of ocular area subequal in length to, or shorter than, each of vs, sos 1-2 and os 1. Five pairs postantennal setae (pas 1-5); pas 1-4 subequal but various in length, successively more distal in position; pas 5 situated laterad of, and slightly shorter than, pas 4. Rostrum short, extended only to base of prothoracic tarsi. One pair short to moderately long rostral setae (rs 1) situated immediately anterior to site of antennal attachment, subequal in length to pair lateral rostral setae (rls 1); rls 1 borne on distinct lateral tubercle at anterolateral angle of rostrum. Mandible with one pair very short, fine, mandibular setae (ms) at extreme anterolateral angle of mandible.

Prothorax (Fig. 8).-Pronotal setae sessile, fine, tapered apically; straight to slightly medially or anteriorly apically curved. One pair very long apical setae (aps), subequal in length to each of two pairs anterolateral setae (als 1-2), pair of lateral setae (ls 1), and lateralmost two of four pairs posterolateral setae (pls 3-4). Two pairs short to moderately long discal setae (ds 1-2) situated approximately equidistant from aps and pair moderately long basal setae (bs); ds 1 slightly shorter than ds 2 on most specimens, situated slightly posteromediad of ds 2. Aps, ds 2 and bs situated in longitudinal linear manner. Two pairs very long anterolateral setae (als 1-2); als 1 situated mediad and slightly anteriad of als 2. One pair long lateral setae (ls 1) situated posterolaterad of als 2 and anterolaterad of pls 4. Four pairs posterolateral setae (pls 1-4); pls 3-4 very long; pls 4 situated moderately anterolaterad of pls 3; pls 2 shorter than pls 1, 3-4, situated slightly mediad of pls 3; pls 1 moderately long, situated approximately equidistant from pls 2 and bs, laterad and various from slightly anteriad to slightly posteriad of bs.

Mesonotum (Fig. 8).—Six pairs short to moderately long, fine, straight, sessile mesonotal setae (msns 1–6); msns 4, 6 subequal in length, longest of series.

Metanotum (Fig. 9). – Five pairs short to moderately long, fine, straight, sessile metanotal setae (mtns 1–5); mtns 1–2 short, situated very close together in anterior onehalf of metanotum; mtns 3–5 longer than mtns 1–2, situated equidistant from each other in slightly anteriorly directed transverse linear manner.

Abdomen (Figs. 9-10). - Abdominal segment I with four pairs very short, very fine, sessile postdorsal setae (pods 1-4); two pairs short, fine laterodorsal setae (lds 1-2), the latter each borne on summit of very small, rounded, laterally directed tubercle. Abdominal segment II with five pairs very short, fine postdorsal setae (pods 1-5), each seta borne on summit of very small, rounded, posteriorly directed tubercle; two pairs short, fine laterodorsal setae (lds 1-2); one pair very short, fine, prodorsal setae (prds 1); and two pairs moderately long spiracular setae (ss 1-2), each borne on summit of small rounded tubercle, the bases of tubercles narrowly contiguous. Abdominal segments III-VII each with six pairs short postdorsal setae (pods 1-6); pods 1-2, 4, 6 short, very stout, darkly sclerotized, each borne on summit of apically darkly sclerotized, posteriorly directed, rounded tubercle; pods 3, 5 short to moderately long, fine, sessile or situated on summit of small, unsclerotized tubercle; two pairs short to moderately long laterodorsal setae (lds 1-2), each borne on summit of small rounded tubercle, lds 1 approximately onehalf length lds 2, lds 1 and lds 2 more closely situated on successively more posterior abdominal segments; one pair small, fine, sessile prodorsal setae (prds 1); and two pairs long to very long, fine spiracular setae (ss 1-2) each borne on summit of laterally directed rounded tubercles, tubercles slightly larger and bases increasingly contiguous on successively more posterior abdominal segments. Abdominal segment VIII with five

pairs postdorsal setae (pods 1-5); pods 1, 3, 5 short, very stout, darkly sclerotized, each situated on summit of moderately large, posteriorly directed, darkly sclerotized tubercle; pods 2, 4 long, fine, each situated on summit of small, rounded tubercle; one pair prodorsal setae (prds); two pairs laterodorsal setae (lds 1-2) situated very close to each other; and two pairs long, fine, spiracular setae, slightly shorter in length than those on abdominal segment VII. All setae very slightly increased in length on successively more posterior abdominal segments unless otherwise noted. Ventrally with two pairs short, fine, sessile lateroventral setae (lvs 1-2) on each of abdominal segments IV-VII; and three pairs transversely linearly arranged, very short, fine, sessile midventral setae (mvs 1-3). Abdominal segment VIII ventrally with single pair short, fine, sessile lateroventral setae (lvs) and single pair short, fine, sessile midventral setae (mvs). Abdominal segment IX with pair of large, apically acuminate, darkly sclerotized, posteriorly directed processes (pp), each process with three or four moderately long, fine setae around and anterior to base, each seta borne on summit of variously developed, small, rounded tubercle. Basal region of processes to apical margin abdominal segment VIII slightly ventrally swollen.

Specimens examined.—USA. CA. Santa Barbara Co., Guadalupe, Los Alamos, 20.viii.1987, ex. crowns Lobularia maritima (L.) Dev. (Cruciferae), T. Seeno & J. Davidson (4 specimens). USA. CA. Santa Barbara Co., Harris Ranch, Los Alamos, 14– 21.vii.1987, ex. crowns Lobularia maritima (L.) Dev. (Cruciferae) (8 specimens). Specimens are deposited in CMNC, TAMU, USNM.

NATURAL HISTORY

This species is widely distributed throughout western North America from British Columbia east to Manitoba, south to southern California, Arizona and extreme west Texas (Anderson 1988). Adults

of Cleonidius erysimi have been collected from a variety of plants, most commonly Cruciferae, in a variety of habitats throughout the species range (Anderson 1988). Although Cruciferae were suspected as the larval host due to the abundance of associations of adults with plants of this family, the association of the immature stages with Lobularia maritima (L.) Desv. is the first confirmed larval host record. Lobularia maritima is an introduced, low, woody shrub of Mediterranean origin which is a common escapee from gardens; it generally grows along roadsides or in wasteplaces in California (Munz 1974). Lobularia maritima is cultivated for its seeds which are used in flower beds. Although seeds develop on infested plants, the plants are forced into early maturation and therefore, produce fewer seeds.

Cleonidius erysimi adults and immature stages were found associated with commercially planted L. maritima in Santa Barbara County, California. Natural vegetation in the areas surrounding the infestations was checked but no C. erysimi adults or immature stages were found. Infested plantings were in one-half to ten acre lots. Most infestations involved 10-15% of the plants but in some lots up to an estimated 70% of the plants were involved. Most infestations were dense nearest the service roads with evidence of activity getting lighter toward the center of the planting. One larva was present per plant and occupied the entire area inside the crown. Pupation takes place in the larval mine. Plants with purple flowers appeared to have the heaviest infestations. Larvae mine the roots and crowns of the plants; pupation takes place in the larval mine.

THE PHYLOGENETIC POSITION OF LIXINI

Anderson (1988) summarized evidence, albeit symplesiotypy, to suggest Lixini (*sen-su* Kuschel) as a primitive lineage within Curculionidae but otherwise could not resolve their precise relationships further. Such a proposal was made solely on the basis of character state distribution in adults. Whereas precise relationships are still left as unresolved, based on the present descriptions of the immature stages of *C. erysimi*, examination of pupae of *L. scrobicollis* (personal observation), and descriptions and figures of pupae of Lixini (*sensu* Kuschel) in Scherf (1964), some additional evidence bearing on this topic can now be considered.

The traditional division of Curculionidae into Adelognatha ("broad-nosed weevils") and Phanaerognatha ("long-nosed weevils") carries with it the implication that the two groups are sister-taxa. This is clearly not so, and as a result, the resolution of phylogenetic relationships in Curculionidae is proving to be a very complex problem, one brought about largely by conflicting character state distributions in a number of presumed primitive curculionid groups.

Adelognatha appear to represent a monophyletic group based on a number of apotypic features; in adults, the deciduous mandibular cusp and resulting mandibular scar, and in larvae, the accessory sensory appendage of the antenna distinctly wider than tall and the frons lacking an endocarina. May (1970, 1978) suggested that the occurrence of mandibular setae in pupae of only Adelognatha was thus associated with the presence of the deciduous cusp in the adult. Absence of the deciduous mandibular cusp in adults of species of Pantorhytes (Pachyrhynchina), but the presence of mandibular setae in pupae, suggested the secondary loss of the cusp in this taxon (May 1978). Mandibular setae, however, are now known in pupae of *Ithycerus noveboracensis* (Forster) (Sanborne 1981), Thecesternus hirsutus Pierce (McClay and Anderson 1985), Cleonidius erysimi (Fall) and Lixus scrobicollis (Boheman) (personal observation), and Cleonis pigra (Scopoli) (Scherf 1964). Adults of each of these species do not possess a deciduous mandibular cusp. If absence of the cusp is truly a unique secondary loss (as

suggested by May 1970, 1978) and presence of mandibular setae is apotypic, their presence in the pupa suggests inclusion of these taxa in a monophyletic group, sister to the paraphyletic traditional Adelognatha. If, however, it is not assumed that the mandibular setae of pupae are associated with the presence of the deciduous cusp in the adult, then the alternative proposal, that presence of mandibular setae in the pupa is an independent apotypic feature, can be considered. Such would result in Adelognatha, Ithycerus noveboracensis, Pachyrhynchina, Thecesternini and Lixini (sensu Kuschel) as a monophyletic group but with relationships further unresolved. Either of these arrangements is fraught with problems and thus it appears best if a third alternative is considered: that the presence of mandibular setae in the pupa is a plesiotypic character state, not related to the presence of deciduous cusps in the adults.

Kuschel (in press) has recently proposed the unification of traditional Adelognatha with Ithycerus noveboracensis (Forster) and a number of other presumed primitive Curculionidae (including Pachyrhynchina and Thecesternini among others, but not Lixini), as the Brachycerinae. Inclusion of Ithycerus noveboracensis is at least in part based on the presence of mandibular setae in pupae of this species as well as a number of other features of the adult and immature stages (Kuschel in press). That pupae of Lixini (sensu Kuschel) are now known to possess mandibular setae suggests, if the presence of the setae were considered apotypic, inclusion of this taxon in Brachycerinae (sensu Kuschel in press); however, among other characters used by Kuschel (in press) to define Brachycerinae, some support this placement whereas others dispute it. Adult Lixini agree with the Brachycerinae (sensu Kuschel in press) in having the epistoma raised in relation to the surrounding area (although this is not so in some Lixus species and may be correlated with increased overall rostrum length), mandibles plurisetose, underside of elytra lacking stridulatory files, sclerolepidia absent, and bladal part of sternite 9 of male extensively pigmented. Adult Lixini disagree in not having the proximal and distal hemisternites (gonocoxites I and II) of the female distinct (proximal hemisternite [gonocoxite I] is lacking), fore coxae placed posteriorly on the prosternum, and in the rostrum being sexually dimorphic (although this is not true for many traditional Cleonina) and where natural history information is available, in being used (in females of at least some Lixus species) to excavate the oviposition site. As far as larval characters are concerned, Lixini disagree in that des 1 is not situated in the dorsoepicranial suture or on the frons, and, where natural history information is available, they are known to be endophytic in roots and stems.

Anderson (1988) was unable to suggest a sister-group relationship between Lixini (sensu Kuschel) and any other Curculionidae and suggested a primitive phylogenetic position in Curculionidae, apparently near Molytini, but cautioned that this could not be further resolved as it was based solely on symplesiotypy. The now apparent phylogenetic position near traditional Adelognatha is not inconsistent with this previous suggestion of a primitive phylogenetic position for Lixini, but disputes the claim of a close relationship to Molytini. At present, Lixini as a Curculionini (sensu Kuschel in press) is supported by only one apotypic character; that of not having the proximal and distal hemisternites (gonocoxites I and II) of the female distinct (proximal hemisternite [gonocoxite I] is lacking). On the other hand, apotypic characters suggesting Lixini as Brachycerinae are: bladal part of sternite 9 of male extensively pigmented, and, for some of the species, having the epistoma raised in relation to the surrounding area and the rostrum not sexually dimorphic.

At present Lixini are best left as Curculioninae in the new scheme of Kuschel (in press), but special note should be taken of their heretofore unrecognized close and perhaps transitional relationship with Brachycerinae.

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