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BIOLOGY AND IMMATURE STAGES OF *THECESTERNUS HIRSUTUS* PIERCE (COLEOPTERA, CURCULIONIDAE) IN NORTH-EASTERN MEXICO

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Abstract.—*Thecesternus hirsutus* Pierce (Thecesterninae) was studied in north-eastern Mexico as a biocontrol agent against *Parthenium hysterophorus* L. (Asteraceae), an introduced weed pest in Australia, and field and laboratory observations on the previously little-known biology of this weevil are reported. There is one generation per year. The larval stage overwinters. Larvae hatch from eggs laid in the soil surface, burrow down to the host's roots, on which they feed externally, causing a gall-like swelling at each feeding-site, and construct earthen cells around themselves and the feeding-sites. Although its host range is highly specific, including only a few closely related species of *Parthenium, T. hirsutus* does not seem promising as a biocontrol agent because larval feeding does not cause significant damage to the plants. Larvae and pupae are described for the first time for the Thecesterninae and larval morphology clearly places this group in the section Phanerognatha of the Curculionidae.

The Thecesterninae are a small North American subfamily of large weevils whose biology has been little studied and whose immature stages have never been reported. The subfamily contains one genus, *Thecesternus,* with seven species (O'Brien and Wibmer, 1982), and the adults are characterized structurally by their unlobed tarsi, the short, broad rostrum which fits into a deep emargination in the prothorax, and the triangular form of the prosternum which lies posterior to this emargination (Kissinger, 1964). Blatchley and Leng (1916) quoted a report by [C. V.] Riley (no reference cited) of the adults cutting off grape blossoms, while Kissinger (loc. cit.) states that they are to be found under stones and dried cow dung. Apart from these references there seems to be virtually no published information on the biology of the group.

From 1978 to 1983 one of us (McClay) was engaged in studies of the natural enemies of the annual weed *Parthenium hysterophorus* L. (Asteraceae) in north-eastern Mexico on behalf of the Department of Lands of Queensland, Australia. This plant, native to the neotropics, was introduced into Australia in the 1950's, and since 1973 has become a serious problem in cattle-raising areas of central Queensland (Haseler, 1976). The studies in Mexico were aimed at identifying potential biocontrol agents for use against it in Queensland, and were carried out from a base at Monterrey, Nuevo Leon.

During these studies, large curculionid larvae were found feeding externally on the roots of *P. hysterophorus*. Adults reared from these larvae were identified by D. R. Whitehead of the Systematic Entomology Laboratory, IIBIII, USDA, in Washington, D.C. as *T. hirsutus* Pierce. While this species was being evaluated as a possible biocontrol agent for *P. hysterophorus*, observations were made of its life-history, habits and host-specificity, and larvae and pupae were collected for detailed morphological study.

Collections were made at a number of sites in the vicinity of Monterrey. *Thecesternus hirsutus* was found to be locally common, favoring dry, stony, well-drained sites subject to little disturbance. It was collected mainly as larvae, which when collected partly-grown could be reared through to pupation in the laboratory on an artificial diet (Harley and Willson, 1968). Adults were rarely found in the field.

Although the evaluation suggested that *T. hirsutus* was not a promising biocontrol agent for *P. hysterophorus*, material has been sent for further study to the Department of Lands laboratories at Sherwood, Queensland. If it is confirmed to be sufficiently host-specific, this species may eventually be released onto infestations of *P. hysterophorus* in Queensland.

The descriptions of the immature stages presented here will help future investigators to identify larvae and pupae of this genus and to establish the correct systematic position of the subfamily Thecesterninae within the Curculionidae.

Life History

Information on the life history was derived mainly from observations on weevils kept in an open insectary on potted plants of *P. hysterophorus* under ambient conditions.

The eggs are laid in the soil surface either at the base of the host plant or within the area of the root system, and covered with a few mm of soil. If oviposition is not completed, the site appears as a small conical pit in the soil surface. Females observed ovipositing adopted a characteristic "head-up" position with the tip of the abdomen inserted in the soil surface and being moved back and forth to excavate the oviposition hole. The egg is smooth and pale yellow, ovoid, approximately 1.40×1.04 mm in size. Owing to the concealed oviposition site, the duration of the egg stage is not known exactly.

The newly-hatched larva burrows down into the soil from the oviposition site and begins to feed externally on either a tap-root or a lateral root. A gall-like swelling soon begins to form at the feeding site, resulting from a proliferation of the cortical tissue of the root. The stele is little affected by the gall formation or the feeding of the larva. As the larva grows it forms around itself an earthen cell, which is attached around the edge of the feeding site on the gall. At first the cell is fairly fragile but later becomes reinforced by an interior layer of a dark brown papery material that gives it considerable toughness. Larvae feeding on artificial diet in the laboratory were observed taking drops of excreta from the anus into the mouthparts and spreading them on the surface of the diet block. This behavior is probably responsible under natural conditions for the formation of the reinforcing layer of the feeding cell.

The gall may be as large as 10 mm in diameter, and in the field up to 12 nearly-mature larvae have been found feeding on the roots of a single plant. Their feeding does not seem to have any significant detrimental effect on the growth of the plant. The normal duration of the larval stage in the field appears to be about 6 months. Larvae are often found on the roots of *Parthenium* plants growing several m from their nearest neighbors of the same species, indicating that the adults, although flightless, have a well-developed searching ability for the host plant.

Pupation takes place in the feeding cell. The duration of the pupal stage of individuals that were fed on the laboratory diet varied from 16 to 20 days. Detailed morphological descriptions of the larva and pupa are given below.

After eclosion the teneral adult remains in the cell for several days to harden up before cutting a hole in the cell and tunnelling up to the soil surface. Adults which emerged in the laboratory did not begin to feed until 14 to 24 days after eclosion. When maintained on potted plants of *P. hysterophorus,* they fed somewhat sparingly on the foliage, cutting pieces out of the edges of the leaves. Their mottled gray coloration provides a very effective disguise on the soil surface. Feeding, mating, oviposition and locomotion were all observed during daylight, but on some occasions the weevils were inactive during the day in cracks in the soil or in the corners of the cage. The adults are long-lived, some surviving for at least 10 months.

Phenology

From January to December of 1982, a site near the village of Dr. Gonzalez, about 54 km north-east of Monterrey, was visited at approximately monthly intervals in order to determine the seasonal occurrence of the different stages of the life-cycle. From these observations it is apparent that *T. hirsutus* has a mainly univoltine life-cycle, with the main period of oviposition occurring in September when the late summer rains lead to a flush of growth of *P. hysterophorus.* The larvae then feed over the autumn and early winter, ceasing to feed when they reach full development some time between December and February. Pupation occurs in early April and the adults emerge in April or May to feed over the summer and oviposit in September. The finding of a few early-instar larvae from May onwards, and of some pupae in September and October, suggests that some adults may oviposit in the spring, giving rise to a partial second generation over the summer. The timing of oviposition is probably influenced by the availability of the host plant in a suitable condition. In the insectary, adults which had emerged the previous year oviposited from February onwards.

Host-Specificity

Larvae were found in the field on roots of both *P. hysterophorus* and *P. confertum* DC. One larva found on *P. bipinnatifidum* Villanova near San Luis Potosi, SLP, was similar to those found on *P. hysterophorus* and *P. confertum,* but was not reared to the adult stage. Examination of the roots of other Asteraceae growing in the vicinity of *P. hysterophorus,* mainly at the Dr. Gonzalez site showed no larvae feeding on *Melampodium cinereum* DC, *Viguiera dentata* (Cav.) Spreng., *Ambrosia confertiflora* DC, *Dyssodia micropoides* (DC) Loes., *D. pentachaeta* (DC) Robins or *Chaetopappa* sp.

Host-specificity tests were also carried out in the insectary, in multiple-choice cages in which potted plants of *P. hysterophorus* and other species of Asteraceae were exposed to the adult weevils. The design of the test cages was such that the weevils could move freely from one plant to another and had access to both the plants and the soil surface in the pots. In this way both feeding and oviposition preferences could be studied. Five to seven weeks after setting up a test, the roots of all test plants were carefully cleaned of soil and checked for the presence of larvae. The other test plants used were *P. argentatum* Gray (the guayule rubber plant), *Helianthus annuus* L., *Ambrosia confertiflora* DC, *Bidens pilosa* L., *Xanthium* sp., *Lactuca sativa* L., *Cichorium intybus* L., and ornamental cultivars of coreopsis, zinnia and dahlia.

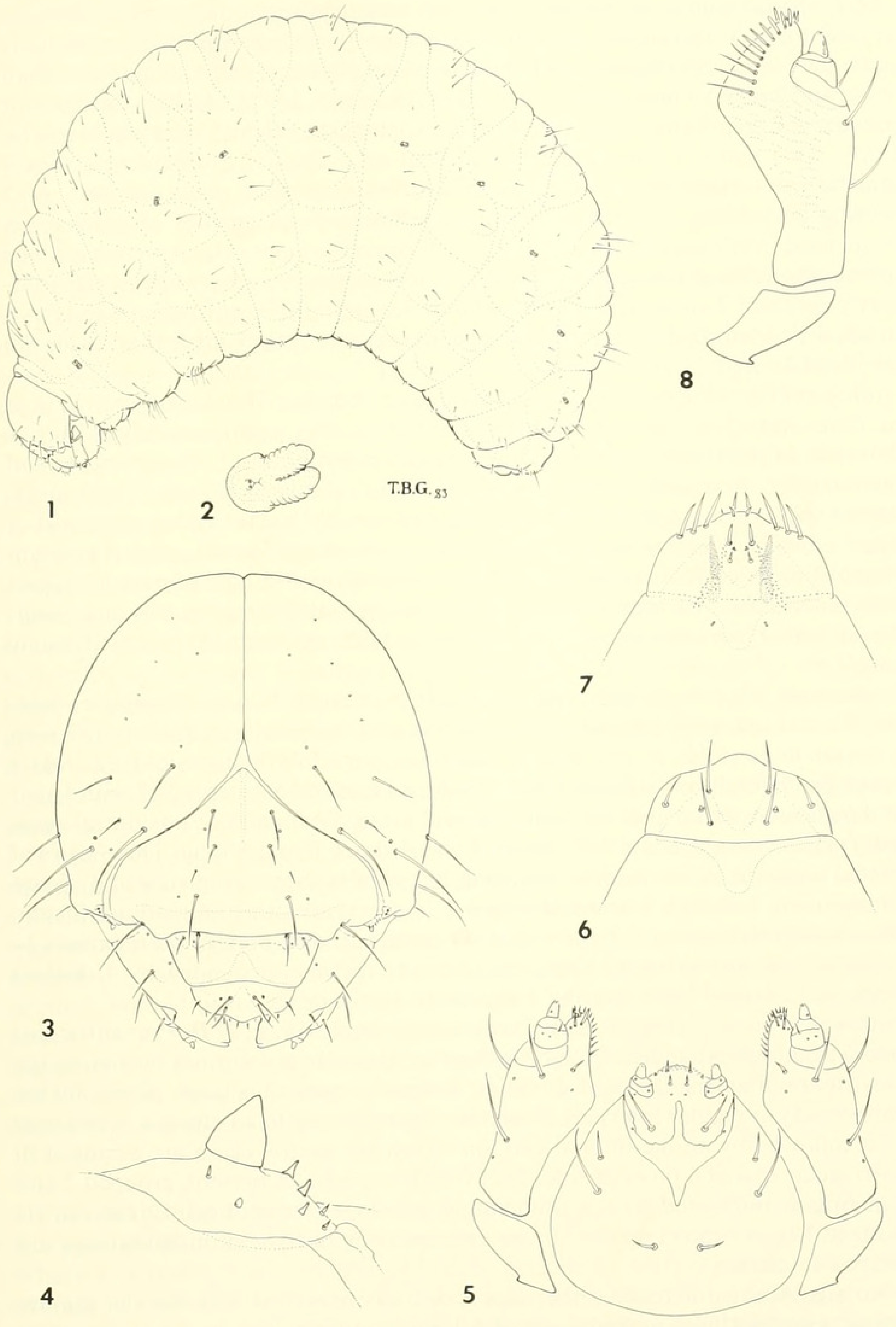
In these tests extensive feeding occurred on foliage of *P. hysterophorus,* while feeding was zero or negligible on all other test plants. Oviposition behaviour was seen frequently in the pots containing *P. hysterophorus,* but was never observed in those containing other test plants. Examination of the roots showed a mean of 9.7 larvae per plant of *P. hysterophorus* (range 0–24), while none were found on the roots of any other test plant.

Descriptions of Immature Stages

Larva.—The following description is based upon a series of 10 mature (final instar) larvae, of which 3 were dissected, collected at Garza Garcia, N.L., Mexico, Nov. 10, 1981, on roots of *P. confertum* by A. S. McClay and H. Miranda. Unless noted otherwise, the terminology used follows that of Anderson (1947).

Body: Stout, C-shaped, tapered at both ends (Fig. 1). Maximum length of entire specimens: 10.62 mm. Body white, with pale brown or unpigmented setae and tiny unpigmented asperities.

Head (Figs. 3–8): Convex dorsally, unretracted, slightly longer than wide; width of 8 measured: 1.40–1.60, mean 1.49 mm. Epicranium and frons light orange-brown, darkest dorsolaterally and around mouthframe. Epicranial suture slightly more than half length of epicranium. Five pairs of dorsal epicranial setae (des) present; des 3 and 5 longest, more than twice the length of des 4. Three pairs of dorsal epicranial sensilla present. Four pairs of minute posterior epicranial setae present. Two pairs of lateral epicranial setae present, subequal in length. Frontal sutures distinct, slightly sinuate, not reaching articulating membrane of mandible at anterior extremities. Frons with 5 pairs of setae (fs) and 2 pairs of sensilla; fs 4 and 5 subequal and distinctly longer than fs 1, 2, and 3. Endocarinal line distinct for approximately ⅓ length of frons. Two pairs of ventral epicranial setae present, subequal in length. Anterior ocellus present, its lens flat and its pigment divided into 2 equal spots; posterior ocellus vaguely indicated by a small subcutaneous pigment spot. Clypeus with 2 pairs of moderately long setae and 1 pair of basal sensilla. Labrum with 3 pairs of setae (lms) of which the inner 2 pairs (lms 1 and 2) are subequal, longer than lms 3, and with 2 basal sensilla but no median sensillum. Maxilla bearing 1 dorsal and 2 ventral setae on the stipes, a row of 10 or 11 dorsal malar setae, a group of 5 ventral malar setae of which 2 are short, 3 subequal to dorsal malar setae, and 4 ventral sensilla. Maxillary palpus of 2 articles, the first distinctly larger than the second and bearing 1 short ventral seta. Dorsal surface of maxilla partly covered with rows of microspicules. Premental sclerite of labrum trident-shaped with a pointed posteromedian process and an elongate anteromedian process. Labial palpi of 2 articles, the first distinctly broader than the second. Ligula bearing 2 pairs of short setae and 1 pair of rod-like sensilla. Three pairs of postmental setae (pms) present, of which pms 1 are more



Figs. 1–8. *Thecesternus hirsutus*, larva. 1, Entire larva, lateral view. 2, Abdominal spiracle. 3, Head, front view. 4, Antenna, dorsal view. 5, Labium and maxillae, ventral view. 6, Labrum, dorsal view. 7, Epipharynx, ventral view. 8, Right maxilla, dorsal view.

closely spaced than pms 2 or pms 3. Premental setae shorter than pms 2, subequal to pms 1 and 3. Hypopharyngeal bracon present, with a pair of pigmented spots near the center. Epipharynx with 3 pairs of anterolateral setae, 6 anteromedian setae, and 2 pairs of median setae (spines of Anderson, 1947), of which the anterior pair are longest. Labral rods (tormae) dark, elongate, slightly convergent posteriorly. Two pairs of sensilla clusters present on epipharynx; anterior pair, of 3 sensilla per cluster, posterior to 1st pair of median setae; posterior pair, of 2 sensilla per cluster, located posterior to labral rods. Asperities of epipharynx condensed into 2 paramedian stripes which converge anteriorly. Antenna a single membranous basal article bearing a subconical accessory sensory appendage (sensory cone) and 7 smaller processes. Mandibles stout, bifid at tips, orange-brown in basal ⅔, becoming dark brown at tips. Mandibular seta 1 more than twice the length of 2.

Thorax (Fig. 1): Pronotum lightly pigmented, bearing 11 setae on each side of midline. Spiracle bicameral; air tubes oriented dorsally, approximately as long as diameter of peritreme. Pleura bearing 2 setae on prothorax, 1 seta on meso- and meta-thorax. Alar areas both with 1 seta. Spiracular area of meso- and meta-thorax with 1 long and 1 short seta. Epipleura with 1 seta. Pedal areas with 8 setae, of which 3 are longer than the rest and 1 is minute. Sternal setae of medium length. Prodorsal folds of meso- and meta-thorax with 1 pair of median dorsal setae and 2 pairs of minute lateral setae. Postdorsal folds of meso- and meta-thorax with 4 pairs of setae, of which the second pair are short, the rest moderately long.

Abdomen (Figs. 1, 2): Eight pairs of lightly pigmented bicameral spiracles present, located laterally, with air tubes oriented posterodorsally. Segments 1–7 with 3 dorsal folds (folds II–IV) plus a small auxiliary fold behind fold IV; fold I developed laterally on segments 2–7. Prodorsal folds on segments 1–7 with 1 pair of dorsal setae and 1 pair of minute lateral setae. Five pairs of postdorsal setae (pds) present on segments 1–8, pds 1, 2 and 4 short, 3 and 5 long. Three pairs of pds on segment 9, the middle seta long, the others short. Epipleura and pleura on segments 1–8 with 2 setae of which 1 is short, the other of medium length. One short pedal seta and 2 pairs of short eusternal setae present on segments 1–9. Sternellum absent on all segments. Anus terminal, surrounded by 4 distinct lobes, the 2 lateral lobes bearing 1 short and 1 minute seta.

Alimentary canal (Figs. 9, 10): Terminology from May (1977): Proventriculus distinct but not expanded. Five or 6 large subglobular mycetomes encircling the constriction marking the cardiac valve. Anterior ventriculus large, deeply folded transversely at regular intervals. Posterior ventriculus with an anterior transverse twist followed by a longitudinal coil, on which the gastric caeca are arranged in an irregular row of 6 on each side. Six Malpighian tubules present, grouped 2 and 4 at origin, reinserted into a moderately developed cryptonephridium on the hindgut. Rectal bracon marked by an external constriction but membranous and difficult to discern.

No significant difference (other than size) was observed between the mature larvae described here and a series of 5 larvae (same collection data) that were clearly in an earlier instar, but no 1st instar larvae were available for study. Thus, it may be possible to identify most larvae of this species with the aid of the description and illustrations provided here, but if the 1st instar larva differs from later instars, as it does in some weevil genera, it may be difficult to identify.

Pupa.—The following description is based upon 4 pupae, of which 3 were reared from larvae collected at Dr. Gonzalez on Jan. 12, 1982, and 1 field collected at the same site between August and October, 1982. The terminology used here follows Burke (1968).

Body (Figs. 11, 12): Robust in form, white, with brown attenuate setae arising from tubercles of varying height. Length of 4 specimens: 8.72–11.62, mean 9.94 mm.

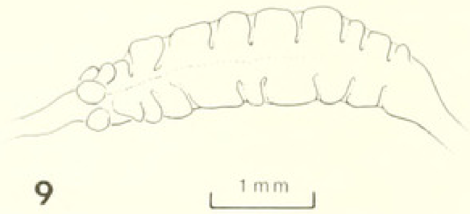
Head (Fig. 11): Convex dorsally, with impressed median ecdysial line. Rostrum very short, stout, untapered. Antennae thick, inserted at base of rostrum. Eyes not visible externally. Mandibles very stout, convex, 2-toothed, bearing 1 short seta. One pair of frontal setae, 3 pairs of supraorbital setae (1 pair short), 3–4 pairs of basirostral setae, and 3 pairs of distirostral setae present. Some tiny auxillary setae sometimes present on the rostrum.

Thorax (Figs. 11, 12): Prothorax slightly broader than long, convex dorsally and laterally; setae moderately long and slightly curved, borne on tubercles of moderate height, including 2 pairs of widely separated anteromedian setae, 2 pairs of posteromedian setae slightly anterior to middle of pronotum, 3 pairs of anterolateral setae, and 2 pairs of posterolateral setae. Ocular lobes well developed. Three pairs of mesonotal and metanotal setae present. No anteronotal setae present on meso- or metanotum. Elytral pads thick, convex, and distinctly striate externally, apices nearly reaching tips of hind femora. Hindwing pads very short, hidden by elytral pads. Forecoxae subglobose, approximate, concealing most of prosternum. Midcoxae separated by a distinctly protuberant mesosternum. Hindcoxae widely separated by the metasternum.

Abdomen (Figs. 11, 12): Convex dorsally, slightly swollen through middle segments and slightly wider at that point than broadest width of prothorax. Segments 1–7 each bearing 4 pairs of discotergal setae, of which the innermost pair are short, and 1 pair of laterotergal setae, all of which increase progressively in length and tubercle height posteriorly, becoming prominent on segments 5–7. Eighth segment bearing 1 pair of discotergal and 1 pair of laterotergal setae on prominent tubercles. Anal segment bearing 2 pairs of setae of which 1 pair arise from tips of short, curved posterior processes. Two pairs of very short laterosternal setae present on all but the anal segment. Spiracles nearly round to oval, distinct on segments 1–7. Sternopleural area longitudinally wrinkled on all segments. Sexes are separable, females having a distinct pair of lobes anterior to the anus, but males with a single plate bearing 4 short setae in that area.

Discussion

The life cycle of *T. hirsutus* is well adapted to that of its host, *P. hysterophorus*, an opportunistic annual plant growing in an area of low and very seasonal rainfall. Where this insect was studied in Mexico, periods of highest rainfall occur on average in June and September, and each such period leads to a flush of growth of the plant. Adults emerging in early summer can thus usually build up reserves by feeding on the plants of the first flush, enabling them to survive until the plants of the second flush are available for oviposition. Larvae then develop on the roots



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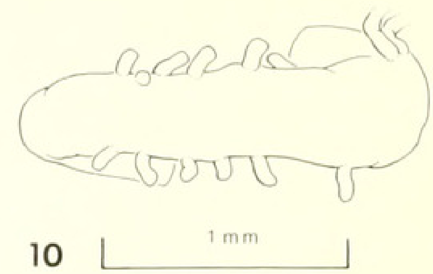

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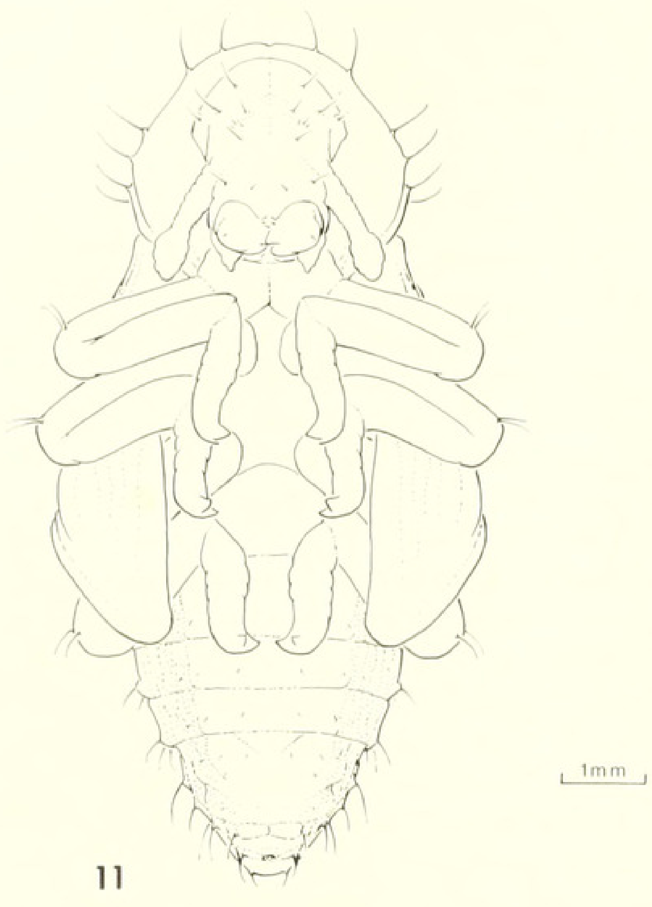

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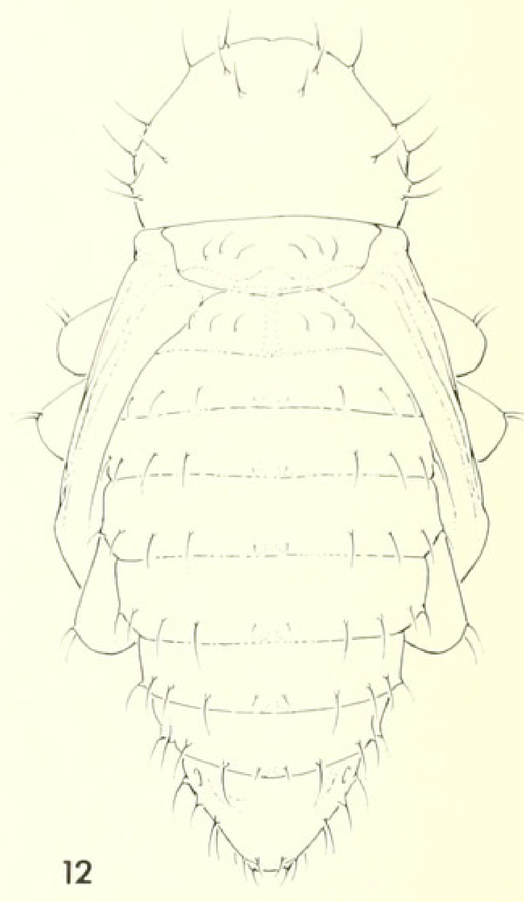

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Figs. 9–12. *Thecesternus hirsutus.* 9–10, Larva, alimentary canal. 9, Proventriculus and anterior ventriculus, with their juncture marked by rounded mycetomes. 10, Posterior ventriculus, ventral view, with gastric caecae attached laterally. 11–12, Pupa. 11, Ventral view. 12, Dorsal view.

of these plants and, by the time plant growth ceases due to the cooler, dryer winter conditions, many of these will have developed sufficiently to enable them to pupate the following spring. The life cycle seems sufficiently flexible to allow a summer generation to occur if plants are available for oviposition.

Both the field and insectary observations indicate a high degree of host-specificity, feeding and larval development being restricted among the Asteraceae to *P. hysterophorus, P. confertum* and probably *P. bipinnatifidum.* These species are closely related, being grouped by Rollins (1953) in the section *Argyrochaeta* of the genus *Parthenium,* and they resemble each other closely in their general morphology. The gall-forming response of the roots to larval feeding is indicative of a close biochemical or physiological adaptation of this insect to its host, and is thus further evidence of specificity.

Thecesternus hirsutus does not cause serious damage to its host plant, and does not appear to be a promising biocontrol agent. Defoliation caused by the adults is light, and the fact that larval feeding is confined to the cortical tissue of the root means that it is unlikely to affect the plant's water uptake. However, its host specificity seems to be such that it could be released without causing damage to other plants.

No comparison of the larvae of *T. hirsutus* with those of other weevil genera will be attempted here, except to note that the incomplete frontal sutures, elongate sensory appendage of the antenna, and 3 distinct dorsal folds in typical abdominal segments clearly place this larva in the Phanerognatha as defined by van Emden (1952). However, it seems possible that further comparison of this larva with those of other weevils may help to establish the phylogenetic position of the genus *Thecesternus* to a greater extent than has been possible on the basis of adult specimens alone.

Acknowledgments

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