NEOTROPICAL MICROLEPIDOPTERA XXV.

NEW LEAF-MINING MOTHs FROM CHILE, WITH REMARKS ON THE HISTORY AND COMPOSITION OF PHYLLOCNISTINAE
(LEPIDOPTERA: GRACILLARIIDAE)

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ABSTRACT.– Prophyllocnistis epidrimys n. gen., n. sp., and Phyllocnistis puyehuensis n. sp., are described from Chile. The larva of Prophyllocnistis epidrimys is a serpentine leafminer on Drimys winteri chilensis (DC) A. Gray and D. winteri andina Reiche. Morphologically, the species appears most allied to the North American Metriochroa psychotriella Busck, which is also recognized as a member of the subfamily Phyllocnistinae along with the Old World genus, Cryphiomystis. Either the last instar larva or pupa of Prophyllocnistis epidrimys is heavily parasitized by a braconid, Clinocentrus sp. The life history of Phyllocnistis puyehuensis is unknown. The known stages of both species are fully illustrated. The leaf mines of Prophyllocnistis resemble those of the earliest gracillarid fossil mines known from the Cenomanian of the earliest Upper Cretaceous (97 m.y.a.). Discovery of the latter suggests that all three subfamilies of the Gracillariidae arose when the angiosperms were beginning to radiate.


For more than a century, the family placement of the largely cosmopolitan genus Phyllocnistis has vacillated among the Gracillariidae, Tineidae, Lyonetiidae, or Phyllocnistidae (Heinemann and Wocke, 1870). As early as 1928, Meyrick correctly associated the genus with the Gracillariidae. Primarily on the basis of several synapomorphies of the larva, notably a hypermetamorphic development with early sapfeeding instars, Phyllocnistis most recently has been treated as a subfamily of Gracillariidae (Davis, 1983, 1987; Common, 1990). Recent studies by the author and David Wagner have shown that Metriochroa, at least as typified by its type species, M. psychotriella Busck, is also a member of this subfamily. Metriochroa is represented in Europe reportedly by at least one species and in southern Africa by three serpentine leaf-mining species (Vари, 1961). Busck (1900) stated that Metriochroa was allied to Omix (since recognized as Callisto and Parornix), a member of the Gracillariinae. Several larval and pupal characters, as well as similar mine morphology and biology, associate Metriochroa with Phyllocnistis. Metriochroa psychotriella is of further interest in possessing five pairs of crochets on abdominal segments 2 - 6 of the last (spinning) larval instar, as noted by Busck (1900). Last instar larvae of Phyllocnistis lack crochets. Crochets on A2 are unknown in other Gracillariidae and are rarely present in this family on A6 (in Artofodina Kumata, 1985, Metriochroa, and Phyllocnistis, described herein). Crochets on A2 are known to occur elsewhere only in the Zygaenoidea (e.g., Dalceridae and Megalopygidae), where they also are found on A7 (Steinh and McFarland, 1985; Epstein, 1988).

All known phyllocnistine larvae construct long, slender, subepidermal, serpentine leaf mines (ophionome) containing a usually dark, median frass line deposited under the leaf epidermis. There are no tissue-feeding instars and, hence, no granular frass, but only 3 or more sap-feeding instars and one nonfeeding, highly specialized, spinning instar (Davis, 1987). The latter constructs a flimsy cocoon within the slightly broader termination of the mine. Because this type of mine is believed characteristic for all Phyllocnistinae, other genera described in the literature exhibiting this type of larval feeding are believed to be members of this subfamily. For example, Vари (1961) states that Metriochroa is allied to Cryphiomystis. The larval habits of Cryphiomystis described by Vари also indicate the placement of this genus in Phyllocnistinae.

FOSSIL RECORD

Leaf mines resembling Phyllocnistis have been reported on fossil Cedrela leaves (Meliaceae) from the early Eocene of Wyoming (Hickey and Hodges, 1975). I have examined much
Fig. 1-4. 1. Type locality of Prophyllocnistis epidrimys new sp., Antillanca, Parque Nacional Puyehue, Chile; dominant vegetation: Nothophagus antarctica and Drimys winteri andina. 2. Leaf mines (2) of Prophyllocnistis epidrimys on Drimys winteri chilensis. 3. Prophyllocnistis epidrimys, holotype ♂, forewing length 4.3mm. Phyllocnistis puyehuensis new sp., holotype ♂, forewing length 2.8mm.

earlier phyllocnistine leaf mines collected by D. Dilcher from the Dakota Formation of Kansas and Nebraska that date to the Early Cenomanian (97 m.y.a; Harland et al., 1989) and within 25 million years of the initial angiosperm radiation (Labandeira and Dilcher, 1993). The host of these mines is a magnoliid dicot, currently not assignable to an order within the subclass. Some of these Cenomanian mines resemble those made by Prophyllocnistis epidrimys, n. sp., from Chile, particularly with regard to the broad, median frass trail and similar oval pupation chamber constructed away from the leaf margin. Prophyllocnistis mines the leaves of Drimys, a genus of Winteraceae and one of 7 extant families recognized by Heywood (1993) in the order Magnoliales. Possessing such primitive features as vesselless wood and unspecialized flowers (Carlquist, 1987; Friis and Endriss, 1990; Heywood, 1993), the Winteraceae are generally believed to represent one of the earliest clades of the flowering plants (Gottsberger, 1988). However, it has been proposed that the absence of vessels may represent a derived condition in the Winteraceae as well as in three other extant angiosperm families that share this feature (Doyle and Donoghue, 1986; Donoghue, 1989). The earliest records of the Magnoliales probably extend into the Albian (Friis and Crepet, 1987; Doyle and Donoghue, 1993) or certainly to the uppermost Albian or lowermost Cenomanian (ca. 97 m.y.a.) near the Upper and Lower Cretaceous boundary (Crane and Dilcher, 1984; Dilcher and Crane, 1984; Upchurch and Dilcher, 1990). It is during this period that much of the diversification and radiation of the flowering plants is believed to have occurred (Stewart and Rothwell, 1993). Pollen of the Drimys type is known from upper Late Cretaceous sediments (Maastrichtian, 65-74 m.y.a.) of southern Australia and New Zealand (Müller, 1981). Pollen similar to that of Winteraceae has been reported even earlier from the Aptian-Albian (ca. 112 m.y.a.) of Israel (Walker, Brenner and Walker, 1983) and the Late Barremian or Early Aptian of equatorial Africa (Doyle, Hutton, and Ward, 1990a, b). Both the host affinities of Prophy- llocnistinae and particularly the resemblance of its mine morphology to the earliest known Cenomanian leaf mines are indications that Phyllocnistinae are a more ancient lineage than previously
believed. Relatively specialized adult morphology and especially larval biology and morphology demonstrate that Phyllocnistinae appeared later in history than the more generalized Gracillariinae. The absence of an externally feeding larval stage (present in some Gracillariidae) and the presence of a highly specialized last larval instar in Phyllocnistinae are strong evidence of their more derived status. Eventually, the fossil record may reveal that leaf mines of Gracillariinae appeared even earlier than the Cenomanian. Unfortunately, in contrast to the typically long, very distinctive phyllocnistine mine, the much smaller, early instar mines of the most primitive Gracillariinae will be extremely difficult to verify. It seems likely that all three main lineages (i.e., Gracillariinae, Lithocolletinae, and Phyllocnistinae) of the Gracillariidae arose sometime during the Early Cretaceous, not long after the first angiosperms appeared and apparently radiated along with their hosts.

**PROPHYLLOCNISTIS** Davis, *new genus*

**TYPE OF GENUS.–** *Prophyllocnistis epidrimys* Davis, *new sp.*

**ADULT.–** Small moths with slender forewings and lanceolate hindwings.  
*Head* (Fig. 46): Vestiture uniformly smooth, completely covered with moderately broad scales with rounded apices. Eye relatively small; interocular index ca. 0.6. Antenna ca. same length as forewing, smooth scaled, with a single row of slender scales encircling each segment; scape with pecten consisting of 4-6 dark brown piliform setae. Palpi moderately large. Haustellum naked, ca. 1.2X the length of labial palp. Maxillary palpus absent. Labial palp long, slender, with ratio of segments from base 1:2:4:1:9.  
*Thorax:* Forewing (Fig. 53) slender, maximum width 0.23 that of length; venation weak, reduced; R four-branched, R4 and 5 fused, extending to apex; M and CuA indistinct, single-branched. Discal cell faintly closed. Hindwing lanceolate; maximum width 0.16 that of length; frenulum consisting of a single, stout seta in both sexes; venation extremely reduced: M faint, single-branched; CuA single-branched, terminating near basal third; discal cell open. Foreleg with epiphysis absent; tarsal spurs 0-2-4. Metafurca with a pair of small dorsocaudal lobes.  
*Abdomen:* Without highly modified sclerites or scales; coremata absent.  
*Male genitalia* (Fig. 47-50): Uncus absent. Tegumen a moderately narrow ring dorsally. Vinculum of similar width and undifferentiated from tegumen, continuing anteriorly as an elongate, rodlike, saccus equal to length of entire genital capsule including saccus; cornuti absent.  
*Female genitalia* (Fig. 51-52): Ovipositor relatively short. Anterior and posterior apophyses of similar size, short, approximately equal in length to anal papillae. A8 a narrow band dorsally, about half the length of anterior apophysis. Bursa copulatrix short, only slightly surpassing anterior end of elongate A7; ostium membranous; ductus bursae moderately broad, with a dark, thickened, triangular lobe immediately anterior to ostium and with a series of 8-10 slender, longitudinal rods encircling ductus immediately caudad to corpus bursae; a cluster of minute spicules also imbedded in ventral wall of ductus just anterior to rods; corpus bursae very reduced, poorly differentiated from ductus and only slightly larger.  
**DISCUSSION.–** On the basis of wing venation, male genital structure and larval biology, this genus is most allied to *Metriochora* Busck and *Cryphiomystis* Meyrick. The latter differs from the former two in the loss of CuA in the forewing and in possessing the longest saccus (ca. 2X the length of the valva) in the male. Adult *Prophyllocnistis* can be distinguished from *Metriochora* by the greater reduction of the maxillary palpi (3-segmented in *Metriochora*), in having all veins arising separate from the cell and the loss of M1 in the forewing, the longer saccus (equal in length to the valva, compared to half the length in *Metriochora*), and by the considerably shorter female ductus bursae.

As mentioned in the introduction, the last instar larva of *Metriochora* differs from all other Gracillariidae in possessing five pairs of crochets on abdominal segments 2-6. *Prophyllocnistis* lacks crochets on A2 but still retains them on A3-6. The larva of *Cryphiomystis* is undescribed, but it has been reared from *Barchellia* and *Coffeea* (Rubiaceae) (Vari, 1961). *Metriochora* have been reared from *Psychotria* (Rubiaceae), in North America, and from *Pergularia* and *Tylophora* (Asclepiadaceae) (Vari, 1961), in South Africa.

**Prophyllocnistis epidrimys** Davis, *new sp.*

*Fig. 2-3, 5-53*

**Elachista rubella** Claude-Joseph, 1928:140 (nec Blanchard, 1852).

**ADULT (Fig. 3).–** Length of forewing 3.8-4.3mm.  
*Head:* Vestiture lustrous, silver gray, with paler, whitish suffusion over frons. Antenna ca. same length as forewing; basal 4/5 fuscous except for dull white on venter of scape and pedicel; apical fifth entirely white. Labial palpus with segments 1 and 2 white with dorsal suffusion of fuscous over distal half of 2; 3 mostly fuscous with white over venter surfaces.

*Thorax:* Lustrous dark silver gray to fuscous dorsally and over upper pleural area; white ventrally. Forewing fuscous marked with three white fascia, the basal two of which are interrupted at middle by fuscous; the outer, subapical fascia the most slender and complete; fringes fuscous except where white fascia intrude. Hindwing uniformly fuscous, more thinly scaled than forewing. Fore and midlegs dark fuscous dorsally, white ventrally; hindleg similar marked but much paler dorsally; apices of tibia and tarsal segments white.

*Abdomen:* Fuscous dorsally, light gray venterally.

*Male genitalia* (Fig. 47-50): As described for genus.  
*Female genitalia* (Fig. 51-52): As described for genus.

**LARVA (Fig. 5-10, 13-36).–** With hypermetamorphic development; early instars with highly modified, depressed body for sap-feeding; maximum length 6.2 mm. Final instar non-feeding, with all mouthparts reduced or absent except for functional spinneret; body cylindrical, maximum length 4.2 mm. Body color uniformly pale yellow in all instars.

**Sap-feeding Instars**

*Head* (Fig. 13-18): Greatly depressed. Setae either lost or greatly reduced; all dorsal cranial setae lost except P1, P2, A1, A2, A3, and S and A3, which are minute (less than 4.5 μm in length); venral cranium devoid of conspicuous setae except for minute submarginal. Labrum (Fig. 14) well developed, almost as wide as both mandibles, with only 1-2 pairs of reduced lateral setae preserved; apex with a broad, rounded notch. Mandibles large, rounded, flattened plates with 10-12 minute serrations around apical margin (Fig. 17-18). Labial lobe trumpet shaped, 1.5X the width of labrum. Posterior hypopharyngeal spines extremely long, projecting caudally to base of labium (Fig. 16-17). Spinneret reduced to a simple, flushed opening ca. 10.4 μm in diameter at base of labium (Fig. 17). Maxillary and labial palp absent. Antenna (Fig. 15)
moderately elongate, consisting of a single long segment (length ca. 2.8X width), with three long, digitate sensilla and two minute, basiconic sensilla arising from apex; the longest scissum nearly 0.9 the length of segment. Stemmata absent.

Thorax and abdomen: Legs, prolegs, and ambulatory callosities absent. All setae extremely reduced to only a few microns in length. Body essentially naked except for bands of minute spines (Fig. 20) over T2-3, A9 of dorsum and T2-3, A1-9 of venter; spines on A3-6 divided into two patches. A7 with short, subacute pleural lobes; A8 with pleural lobes greatly lengthened as tubular processes ca. 3/4 the length of terminal process, the three processes together appearing as a tridentiform caudal appendage (Figs. 5, 19); pleural process of A8 sometimes with a row of small, ventral tubercles (Figs. 19, 21). Anal opening slitlike (Fig. 5, 19), at base of caudal process.

Spinning (Last instar) Larva

Head (Fig. 22-26): Approximately round, slightly depressed, with a prominent anterior lobe, consisting of fused hypopharynx and labium (Fig. 7, 23), projecting beyond labrum; anterior lobe essentially naked, without setae or spines except for a single pair of short spines lateral to base of moderately long labial palpus (Figs. 23, 26). Labial palpus 2-segmented, basal segment long, length ca. 2.5X width, bearing a single long sensillum from dorsal apex; apical segment short, spherical, with a single long, apical sensillum. Spinneret moderately short and stout. Cranial setae reduced in number, length, and distributed as shown in Fig. 7-8; F and AF absent; P1 and 2 closely associated; microdorsal setae absent. Labrum (Fig. 24) greatly reduced, fused to clypeus, with only 2-3 pairs of setae preserved. Stemmata absent. Antenna 2-segmented, with a short, bulbous, basal segment bearing two moderately long and one short sensilla; apical segment extremely reduced, bearing a single sensillum (Fig. 27). Maxilla reduced to a pair of smaller lobes on either side of large apical lobe; each maxillary lobe bearing two setae (Fig. 22-23). Tenentorium extremely reduced, slender (Fig. 8).

Thorax: Notal plates absent. Setae XD1, XD2, and D1 shortened; SD1 elongate; two pespiracular setae (L1, L2) present. Spiracle greatly reduced (Fig. 9). Legs vestigial, represented by flattened tubercules (Fig. 29).

Abdomen: Setae generally reduced in length, with only D1 of A8-10 elongate; D1 and 2 present on all segments; SD and L unisetose on all segments, except SD absent on A9; A9 with only D1, D2, and L1 present. A3-6 with prolegs reduced; crochets arranged in a single row of 9-11 hooks (Figs. 30, 31); A10 without crochets. A9 and 10 with reduced pleural lobes.

PUPA (Fig. 11-12, 37-45).—Maximum length 4.5mm; diameter 0.8mm. Vertex with a stout, elongate, acute process (cocon cuter) exceeding length of head (Fig. 37-38). A single pair of long, clavate setae arising from frons midway between eye and cocon cutter. Antenna long and straight, extending to A10. Forewing extending almost to A6. Hindleg to middle of A6. Chaetotaxy as shown in Fig. 12. Setae moderately short, with simple apices except for frontal seta. Dorsum of A2-7 with dense concentration of minute spines randomly distributed over entire tergum, with largest spines anteriorly (Fig. 40). Tergum of A9 greatly reduced, with a pair of small spine-tipped tubercules (Figs. 42, 45). A10 prominently furcate (Fig. 43-44), with a pair of large, slightly divergent, acute processes from caudal apex; length of processes exceeding segments A8-9.

Fig. 5-12. Phyllocnistis epidrimys new sp., immature stages. 5. Sapfeeding penultimate instar, dorsal view. 6-10. Spinning last instar: 6. Ventral view of body. 7. Dorsal view of head. 8. Ventral view of head. 9. Chaetotaxy of thoracic segments 1-2 & abdominal segments 1,2,6,8,9. 10. Dorsal view of abdominal segments 8-10. 11-12. Pupa: 11. Ventral view. 12. Lateral view. All scales = 0.5mm.

LEAF MINE (Fig. 2).—An elongate, tortuous, upper surface, serpentine mine up to 21.5cm long and 2-3mm wide, with a 1-2mm wide, dark brown median frass line. Mine normally is not visible from underside of leaf. On larger leaves the mine is usually confined to one side of the midrib; with smaller leaves the entire leaf surface can be mined with the mine usually crossing the midrib beyond the distal fourth where the midrib is smaller. Near end of mine a small, elongate blotch, up to 5.5 mm wide and 14 mm long, is formed prior to last larval instar; blotch is usually formed away from leaf margin, which is never folded or pinched in. Pupation occurs within thin silken lining within blotch.

HOST.—Winteraceae: Drimys winteri andina Reiche and Drimys winteri chilenensis (DC.) A. Gray. For a discussion of these hosts see Davis (1991) and Smith (1943).


DISTRIBUTION.—Spotty but moderately widespread through the Valdivian Forest Province (Davis, 1986) along the coastal mountains and Andes from Talca Province south to Osorno, ranging in elevation from 500m to 1300m. Leaf mines (DRD 456) have also been collected at El Pantanillo (a small nature preserve), 17km southeast of Constitucion, Talca Province and at La Selva (west of Fundo Chacamo, DRD 456.2), in Cautin Province.

DISCUSSION.—The immature stages and life history of this species were briefly described by Claude-Joseph (1928) under the name Elachista rubella Blanchard. Both the distinctive female genitalia figured by Clarke (1967) as well as the unusual wing pattern of E. rubella show this species to be unrelated to Propyllocnistis and most likely not a member of Gracillariidae.

The egg of E. epidrimys is deposited on the basal third or fourth of the upper leaf surface. Upon eclosion, the larva bores through the epidermis and begins a tortuous, gradually enlarging, serpentine mine that can extend over 20cm. As the sap-feeding larva progresses it deposits a prominent, median, subepidermal frass line nearly the width of the mine. At the end of the serpentine sap-feeding stage, the larva widens the mine to form a small elongate blotch in which it molts to the last larval instar, a nonfeeding, spinning stage. The spinning larva proceeds to line the dorsal and ventral surfaces of the central portion of the blotch with silk, wherein it pupates. Larvae are most prevalent from August through October at lower elevations (Claude-Joseph, 1928) to as late as early December at higher elevations. The number of generations is not known, although no larvae have been noted after early January. The number of larval instars also was not determined, with four or five sap-feeding instars and one spinning instar suspected.

Approximately half of the pupal chambers of P. epidrimys examined from Fundo Chacamo contained evidence of a braconid pupal parasite, Clinocentrus sp. The pupa of this parasitoid is
enclosed within an oval, white cocoon approximately 4.5mm long.

Two empty mines somewhat similar to that produced by *P. epidrimys* were found on *Drimys winteri chilensis* near the east end of Lago Tepuhueco, Chiloé Island, Chile on 25 December 1981. These differed in being located on the underside of the leaf and were less conspicuous with much thinner frass lines. Possibly these represent another species of *Prophyllocnistis* or merely an unusual feeding variation of *P. epidrimys*.

**Phyllocnistis puyehuensis** Davis, new sp.

ADULT (Fig. 4).—Length of forewing: 2.8mm.

*Head:* Vestiture lustrous white, completely covered with smooth, broad scales from vertex to base of haustellum and slightly overlapping eyes. Antenna ca. 0.8 the length of forewing, smooth scaled with one row of slender scales completely encircling each segment; scape and basal 2/3 of flagellum brown dorsally and white ventrally; distal 1/3 entirely white. Haustellum short, naked. Maxillary palpus minute, 1-segmented. Labial palpus straight and drooping, 3-segmented, smooth scaled, with basal 1/3 white, distal 2/3 brown.

*Thorax:* Lustrous white dorsally and ventrally. Forewing lustrous white with fuscos costal margin extending to apex; a broad, pale golden fascia, bordered by pale fuscos, traversing wing at distal third, broadest at costa and tapering to hind margin; a larger, brighter, golden spot also surrounded by pale fuscos at subapex, slightly separated by a narrow white band from prominent black apical spot; usually 4 pale fuscos striae visible on distal third of costal margin and 2 less distinct striae on hind margin and termen. Hindwing white with mostly gray costal fringe and white dorsal fringe. Legs generally grayish brown dorsally and white ventrally, with hind tibia almost entirely white; apex of tarsomeres pale gray.

*Abdomen:* Mostly light grayish brown dorsally with suffusion of white; uniformly white ventrally. Coremata present on A8 of male, consisting
Fig. 46-57. Adult morphology. 46-53. Prophyllocnistis epidrimys new sp.: 46. Head, anterior view. 47. Male genitalia, ventral. 48. Lateral view of fig. 47. 49. Right valva, mesal view. 50. Aedoeagus. 51. Female genitalia, lateral view. 52. Ventral view of fig. 51. 53. Wing Venation. 54-57. Phyilocnistis puyehuensis new sp.: 54. Male genitalia, ventral view. 55. Right valva, mesal view. 56. Aedoeagus. 57. Coremata of A8. Length of all scales = 0.5mm.
of a pair of lateral tufts of piliform setae (Fig. 57).

Male genitalia (Fig. 54-56).-- Uncus absent. Tegumen a small, weakly sclerotized, triangular lobe. Vinculum relatively large, U-shaped, ca. 0.4 the length of valva. Transtilla present, moderately well developed. Valva simple, extremely slender, width ca. 0.06 length, approximately same width throughout, slightly broader at base. Aedoeagus relatively robust, simple, tapering caudally, elongate (ca. 0.8 the length of entire genitalia), with elongate phallobase ca. 1.3X the length of aedoeagus.

Female and immature stages unknown.


**PARATYPE.** -- Same data as holotype: 1 σ', (ZMUC).

**HOST.** -- Unknown.

**DISTRIBUTION.** -- Known only from the type locality, which is situated in the cool, moist Valdivian forests of southern Chile (Davis, 1986).

**DISCUSSION.**-- *Phyllocnistis puyehuensis* differs from all known species of Neotropical *Phyllocnistis* in wing pattern, particularly by the absence of basal, longitudinal striae and by the presence of a single, broad, subterminal fascia across the distal third of the wing. Of the four *Phyllocnistis* described from neighboring Argentina (Davis, 1984), only one, *P. abatiae* Hering (1958), lacks basal striae. That species differs from *P. puyehuensis* in possessing a pair of smaller costal bands (strigulae) at the distal third of the forewing.

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