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Author(s)	Kumata, Tosio
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A NEW STEM-MINER OF ALDER IN JAPAN,
WITH A REVIEW OF THE LARVAL TRANSFORMATION IN
THE GRACILLARIIDAE (LEPIDOPTERA)

By TOSIO KUMATA

Abstract

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Dendrorhycter marmoroides (n.g., n. sp.), a stem-miner of alder in Japan, is described. Its peculiar heteromorphic development in the larval stage is described, and the heterometamorphosis in the family Gracillariidae is reviewed. The larvae of the family are divided into 4 forms based on the structure and function: sap-feeding, tissue-feeding, spinning and quiescent forms. The patterns of the ontogenetic life-cycle are compared in 11 species belonging to 10 genera. The evolutionary trends of the family are discussed on the basis of the comparison, with notes on the origin and significance of the peculiar larvae of the sap-feeding, spinning and quiescent forms.

Author's address. Entomological Institute, Faculty of Agriculture, Hokkaidô University, Sapporo, 060 Japan.

Contents

Introduction	3
Descriptions of new taxa	
Genus <i>Dendrorocyter</i> nov.	3
<i>Dendrorocyter marmaroides</i> , sp. nov.	6
A review of the larval transformation in Gracillariidae	
Larval forms of Gracillariidae	12
Pattern of larval transformation	15
Origin and evolutionary significance of the peculiar forms	18
Concluding remarks	20
Acknowledgements	20
References	21
Plates	23

INTRODUCTION

Up to the present, three species of the Gracillariidae have been known as stem-miners of various trees in Japan: *Acrocercops astawrota* Meyrick feeding on Rosaceae (*Malus* and *Pyrus*) and first recorded by Nawa (1916); *Acrocercops* sp. on Fagaceae (*Castanea*), reported by Suenaga (1938); and *Spulerina corticicola* on Pinaceae (*Abies*, *Larix* and *Pinus*), described by Kumata (1964). Recently, I have found very long serpentine mines made by an unrecorded gracillariid species on the trunk and branch of *Alnus hirsuta* (Betulaceae) in Hokkaidô. At first sight this species appeared very closely related to the members of the genus *Marmara*, which also contains stem-miners but is restricted to North and Central America in distribution. After careful examinations of both the adult and larval characters, however, I have come to conclude that a new genus should be erected for the reception of the species, which is also new to science.

The new species undergoes a peculiar heteromorphic development in the larval stage as is the case with *Marmara*-species reported by DeGryse (1916) and Fitzgerald & Simeone (1971 b). On this occasion I would like to give a review of our present knowledge on the larval transformation of the Gracillariidae. The review, given in the latter pages of this paper, may not be complete, but I hope that it will contribute towards the study of this interesting pattern of growth.

The specimens studied are all deposited in the collection of Entomological Institute, Hokkaidô University. The method and terminology used in the larval study are the same as in Kumata (1977).

DESCRIPTIONS OF NEW TAXA

Genus *Dendrorycter* nov.

Type-species: *Dendrorycter marmaroides*, sp. nov.

♂ ♀. Face and head smooth-scaled; scales on face shortly hanging over labrum towards base of proboscis, which is moderately developed and naked. Ocellus absent. Maxillary palpus minute, slender, pointed, the apical segment being porrect. Labial palpus about 1/3 as long as fore tarsus, slender, smooth-scaled, drooping, pointed, the apical segment about as long as the second and about twice as long as maxillary palpus. Antenna a little longer than fore wing, simple; scape very slightly thickened, with a pecten of a few narrow scales. Thorax simple, without dorsal crest. Legs slender; middle tibia slightly thickened with scales apically, with a pair of apical spurs; hind tibia with a row of bristly scales on upper side, and with 2 pairs of spurs, the 1st pair originating at basal 1/3 and the other at apex; 1st tarsal segment of hind leg with a row of short bristly scales on upper side, but the scales are much shorter than those on the tibia and diminish towards apex of the segment. Fore wing lanceolate, acutely pointed apically, with 8 veins (Fig. 1, A), 4 of them terminating at costal margin; vein R_1 absent; veins R_4 and R_5 coincident; veins M_2 and M_3 absent; veins Cu_{1a} and Cu_{1b} coincident; vein An simple, nearly straight, terminating at apical 2/5 of dorsal margin; discoidal cell lanceolate, occupying about 11/13 length of wing. Hind wing a little shorter than and about half as wide as fore wing, narrowly attenuating towards apex, with 5 veins (Fig. 1, A); vein Rs simple, not divided into 2 branches; vein M_1 simple, rudimentary on basal part; veins M_2 and M_3 absent; veins Cu_{1a} and Cu_{1b} long-

stalked; cell open between Cu_{1a} and M_1 .

Male genitalia: Symmetrical, rather small in comparison with abdomen. Tegumen simple, round apically, without uncus, socius and gnathos; tuba analis short, reaching nearly apex of tegumen, with a subscaphium weakly sclerotized

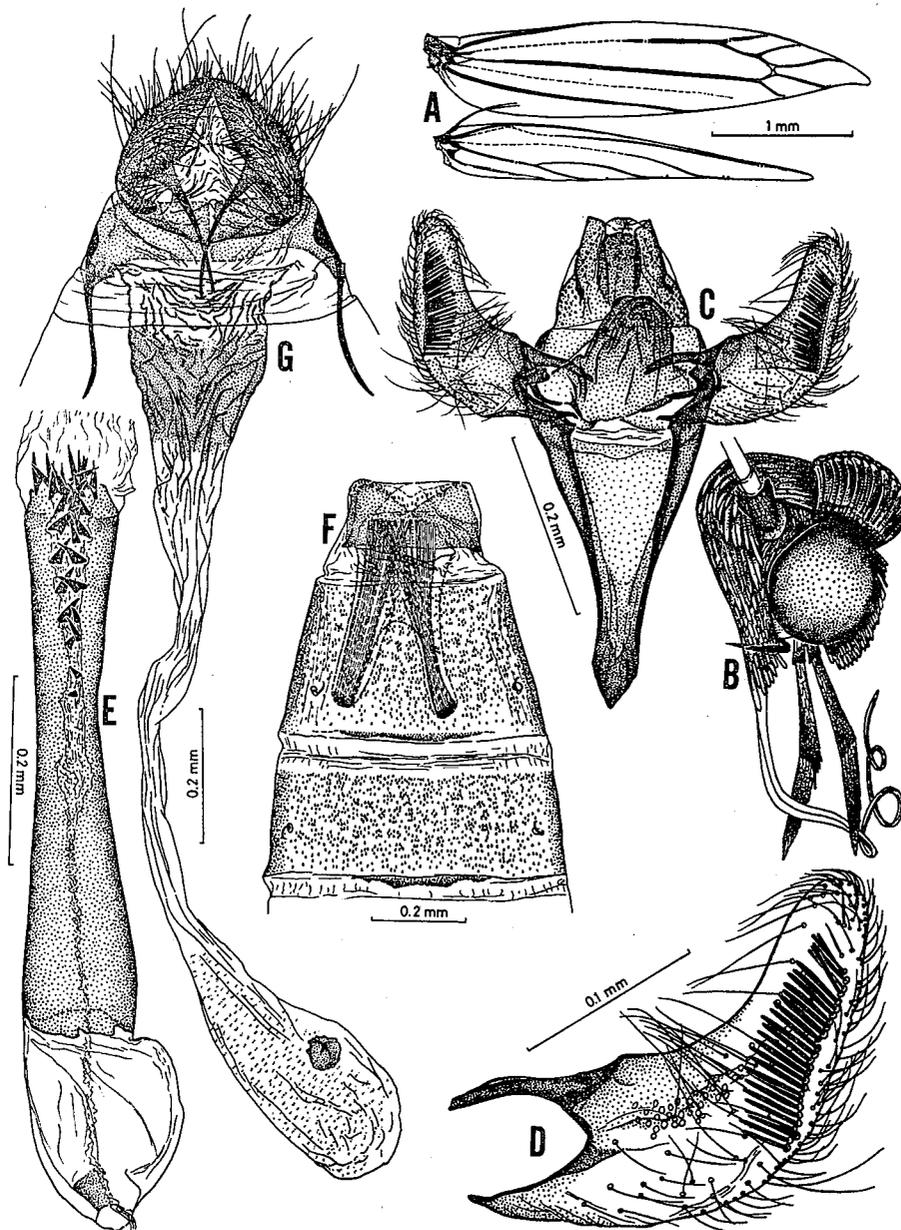


Fig. 1. *Dendrorhycter marmaroides*, gen. et sp. nov. A: Wing venation — B: head of adult in lateral view — C: male genitalia in ventral view — D: right valva — E: aedeagus — F: 6th to 8th abdominal segments of male in ventral view — G: female genitalia in ventral view.

and elliptical. Valva upturned at middle, narrowing apically, moderately setose inside, with a wide comb nearly occupying apical half of inner surface; transtillae incomplete, widely separated from each other, with labides slender. Juxta large, obovate, striated near apical area. Saccus about 1.7 times as long as valva, lanceolate, with a small patch bearing a few scent scales at each side near base. Aedoeagus very large, about 3 times as long as valva, straight, tubular, with acute cornuti arranged in a double row, each row consisting of about 15 spines, which diminish towards base of aedoeagus in size. Eighth abdominal segment with tergum alone moderately sclerotized, trapezoid in shape, and squamose along notched caudal margin; a pair of coremata inserted into body at intersegmental membrane between 8th and 7th abdominal segments; 8th sternum membranous, with a patch bearing a few minute orbicular scales at centre. Seventh abdominal segment like preceding ones in structure, without coremata.

Female genitalia: Papilla analis short, wide, densely setose almost on whole surface; apophysis posterioris slender, much widened basally. Eighth abdominal segment short, about 1/3 as long as the 7th segment; apophysis anterioris slender, about as long as apophysis posterioris. Ostium bursae situated on ventrum of 8th abdominal segment, large, without any sclerous genital plate. Antrum long, narrowing towards ductus bursae, striated, much sclerotized on median area; ductus bursae moderate in length, membranous; corpus bursae pyriform, membranous, with a signum which is a minute elliptical plate. Seventh abdominal segment like preceding segments in structure.

Remarks: In the very reduced wing venation, the new genus *Dendrororycter* may be closely related to the genus *Marmara*. The members of the latter genus are restricted to North and Central America in distribution and are known as stem-miners or rarely leaf-miners in the larval stage. The new genus is readily distinguished from *Marmara* as follows: - 1) In *Dendrororycter* the vein R_1 of the fore wing is absent, whereas in *Marmara* it is present. 2) In *Dendrororycter* the hind wing has the vein Cu_{1a} stalked with Cu_{1b} , and lacks M_2 , while in *Marmara* it lacks Cu_{1a} and has M_2 stalked with M_1 . 3) In *Dendrororycter* the valva is simple and composed of only one large lamella, but in *Marmara* it is divided into three lamellae, that is, a narrow, spatulate costal part, a wide dorsal part and a hairy processus basalis of costa.

Although the present genus has a very reduced wing venation like the members of the subfamily Lithocolletinae, it certainly belongs to the subfamily Gracillariinae by having the radial sector of the hind wing arched upwardly and approaching to the subcostal vein near the base. This is also true of *Marmara*. On the other hand, in the Lithocolletinae the radial sector runs nearly parallel with the median vein towards the base of the wing.¹⁾ On account of the bristly hind tibia and tarsus, *Dendrororycter* may be referred to the *Acrocercops*-group of the Gracillariinae and near the genus *Spulerina*, some species of which are also stem-miners in larval stage.

1) The importance of these characters in separating the family into 2 subfamilies Lithocolletinae and Gracillariinae has been overlooked for a long time. The genus *Chrysaster* Kumata, 1961, which was not dealt with in my paper entitled "Taxonomic studies of the Lithocolletinae of Japan" (1963), is now referred to the Lithocolletinae on the basis of the character of the radial sector.

Dendrorhycter marmaroides, sp. nov.

Adult

♂ ♀. Expanse of wings: 7.0–8.8 mm. (7.0 mm. in holotype, 7.9 mm. in average of 8 specimens). Length of fore wing: 3.3–4.2 mm. (3.3 mm. in holotype, 3.7 mm. in average of 9 specimens).

Colour: Head and face black with a coppery lustre under some light, with vertex between antennae slightly paler. Maxillary palpus entirely black. Labial palpus whitish, somewhat leaden-metallic under some light, with a longitudinal, narrow, blackish line outside except for apical extremity. Antenna pale ochreous, faintly annulated with a little darker colour; scape and its pecten entirely blackish. Thorax black with a coppery lustre, with a broad, silvery-whitish band on each pleural area. Legs blackish; basal halves of fore and hind coxae, and median area of hind femur silvery-whitish; a postmedian ring of mid tibia, a subbasal ring and preapical one of hind tibia white and broad; fore and mid tarsi white, with 2 black rings, one placed at middle and the other at apex; hind tarsus black, with 2 broad, white rings, one situated just beyond middle and the other near apex; all tibial spurs whitish apically. Fore wing black with a coppery lustre under some light, with markings silvery-white; a transverse band placed at basal 1/5 of wing, straight, perpendicular to costa or very slightly oblique inwardly, slightly widened towards dorsal margin; 1st pair of costal and dorsal blotches at middle of wing, quadrate, perpendicular to margins, the costal one being a little longer than the dorsal one and situated a little basally than the latter; 2nd pair of blotches just opposite at apical 1/4 of wing, wedge-shaped, the costal one a little larger than the dorsal; a spot at apex of wing round; a small spot sometimes situated on costa between 2nd costal blotch and apical spot; cilia dark gray, with fringe line and terminal margin around apex of wing blackish narrowly. Hind wing dark fuscous, with cilia dark gray. Abdomen dark fuscous; ventrum with a broad, silvery-white band on apical margin of each segment.

Male genitalia: Valva with a comb consisting of 28–29 teeth; coremata a little longer than 7th abdominal segment. The other characters as given under the genus.

Female genitalia: As given under the genus.

Larva

Three larval forms are distinguished: sap-feeding, spinning and quiescent forms. The sap-feeding form appears first and has at least 6 instars (Fig. 5). The spinning form is the last larval instar, and is devoted to forming the cocoon. The quiescent form occurs between the sap-feeding and spinning forms, and may agree with what Fitzgerald & Simeone (1971 b) called "pseudo-pupa" in *Marmara fraxinicola*. It is wholly concealed within the skin of the preceding instar throughout its existence. The exuviated head-capsule is, therefore, usually kept within that of the final sap-feeding instar.

Spinning form (last instar). Colour: Head and body evenly creamy-yellowish, with a dark pigmentation around ocelli.

Structure: Head (Figs. 2, B & 4, C) round, broadly angulated posterolaterally, with posterior dorsal prolongations much developed; adfrontal and coronal sutures absent. Frontoclypeus elongate-quadrangular, nearly parallel-

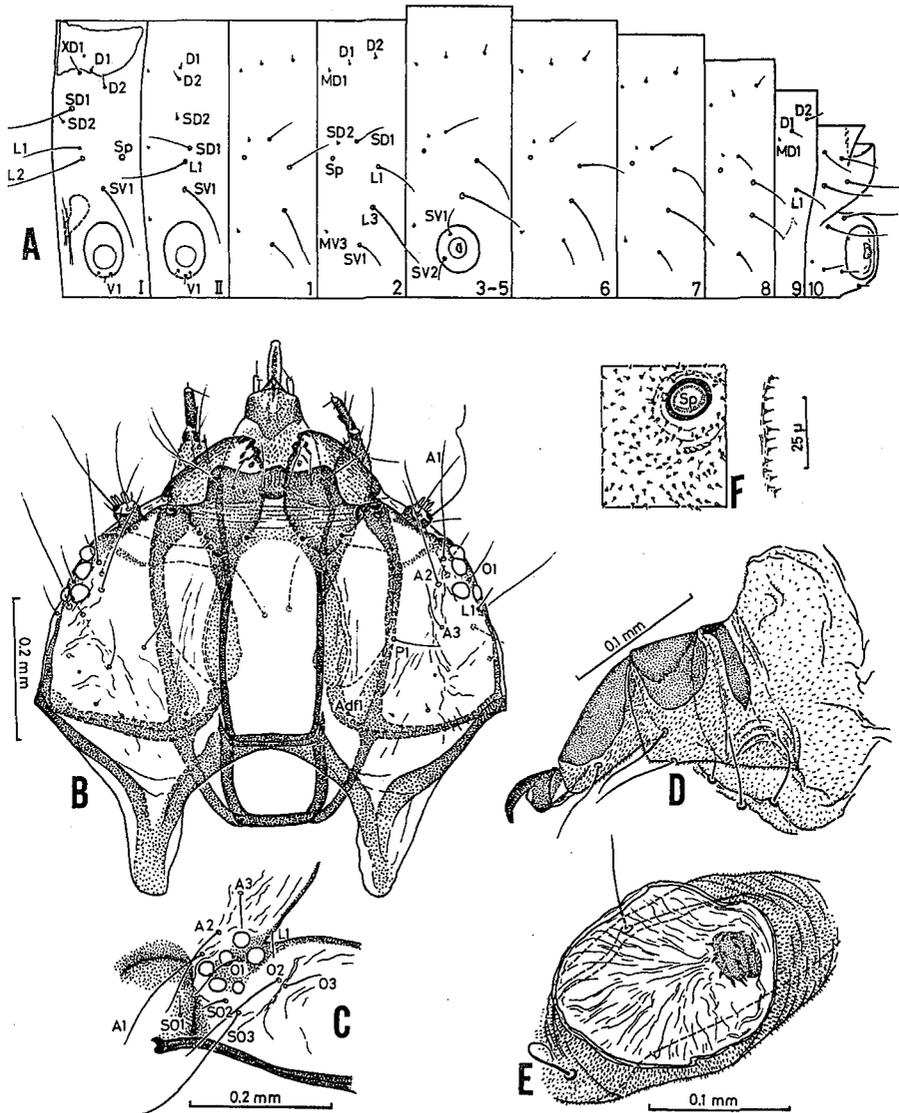


Fig. 2. *Dendrorhycter marmoroides*, gen. et sp. nov. (spinning larva). A: Setal map of thorax (I & II) and abdomen (1-10) — B: head in dorsal view — C: ocelli and adjacent setae — D: mesothoracic leg — E: ventral proleg of 5th abdominal segment — F: spinules of body surface.

sided, with frontal setae absent. Epicranial setae Adf_2 and P_2 absent; setae A_1 , A_2 , O_2 and SO_3 long and nearly same in length; seta A_3 posterior to A_2 ; seta SO_1 set close and ventral to antenna; seta L_1 short, set close and posterior to 1st ocellus; setae Adf_1 , E_1 and E_2 very minute, and rudimentary. Ocelli (Fig. 2, C) 6 on each side, arranged in a semicircle; seta O_1 at centre between 1st and 3rd ocelli. Antenna (Fig. 3, I) not segmented, with 2 long sensilla trichodia, 3 sensilla basiconica, 2 small sensilla basiconica and 1 short sensillum trichodium all on the

apex. Labrum (Fig. 3, C) short, vertical, shortly trilobed apically, with 3 pairs of setae arranged in a transverse line near apical margin, and with a pair of slender epipharyngeal setae. Mandible (Fig. 3, F) rather flat dorso-ventrally, with 2 obtuse teeth; mesial margin oblique and finely crenulate. Labiomaxillary part (Fig. 4, F) as in usual lepidopterous larvae; spinneret long, truncated apically, about 2.4 times as long as labial palpus, with ventro-median ridge narrowly sclerotized on basal 3/4; postmentum without median sclerite around labial setae; maxillary palpus slender, long, with apical segment about 2.5 times as long as 2nd segment and having a sensillum basiconicum at middle of mesial side; maxillary galea not visible.

Body cylindrical, strongly tapering posteriorly. Thoracic legs (Fig. 2, D) well developed; coxa entirely membraneous, with 2 setae set close to seta V_1 ; tarsus sclerotized on its dorsal side, with 1 seta on outer side near apex. Ventral prolegs (Fig. 2, E) on 3rd to 5th abdominal segments, well developed, without crochets, but its central sclerite bears many crochet-like spines; anal proleg without crochets or crochet-like spines. Spinules of body surface (Fig. 2, F) minute, pointed, dense. Chaetotaxy of body as shown in Fig. 2, A. Prothorax with a pair of gland-like pouches on ventrum anterior to legs; setae XD_2 , L_3 and SV_2 absent; D_1 microscopic, nearer to XD_1 than to D_2 , which is a little longer than D_1 ; SD_2 very minute, anterolateral to SD_1 ; L_1 and L_2 anterior to spiracles, long, about as long as SV_1 . Mesothorax and metathorax bearing 7 setae on each side except for proprioceptors; setae L_2 and L_3 absent; SD_1 long, closer to L_1 than to SD_2 , which is very minute and about as long as D_1 and D_2 . In 1st to 8th abdominal segments seta V_1 absent; lateral group of setae composed of L_1 and L_3 , L_3 being longer than L_1 ; subventral group represented by SV_1 alone except on ventral prolegs, which have 2 setae (SV_1 and SV_2); D_1 and D_2 very short, the former being slightly anterolateral to the latter; proprioceptor MV_3 absent on the 8th segment. In 9th abdominal segment setae are MD_1 , D_1 , D_2 and L_1 ; D_1 anterolateral to D_2 as in preceding abdominal segments.

Quiescent form. This form may belong to the 7th larval instar. The skin, even of the head-capsule, is not well sclerotized. Though the appendages are little more than mere outlines in the external pellicle, they are distinct and similar to those of the spinning form in shape.

Head (Fig. 4, B) a little wider than long, round laterally, with posterior dorsal prolongations inconspicuous. Frontoclypeus open posteriorly as in spinning form. Epicranial setae all reduced to minute conical projections, their positions being similar to those of corresponding setae in spinning form. Ocelli inconspicuous (absent?). Antenna (Fig. 3, H) a low prominence, with 2 rather long, 3 moderately long and 3 minute projections at its top. Labrum completely absent. Mandible tightly fused with epicranium, without any hinges; apical teeth 4, the 3rd from outer side being the longest. Labium and maxilla (Fig. 4, E) with appendages much reduced in size; spinneret short, about as long as wide; labial palpus in a minute tubercle at side of spinneret, much wider than long, with 2 microscopic projections on its top; premental and postmental setae represented by microscopic projections; maxillary palpus very short, represented by an unsegmented tubercle at top of maxilla, with 1 or 2 small projections near top and 3 minute projections near base; setae of stipes reduced to minute projections.

Body very weak and membraneous, with thoracic legs seen merely in a paired

large protuberances on ventral surface of each segment; ventral and anal prolegs not visible. All setae of body are in minute, rudimentary projections, but agree with those of the spinning form in position.

Sap-feeding form. The number of instars passed by this form is not certain, but seems at least 6 (Fig. 5).

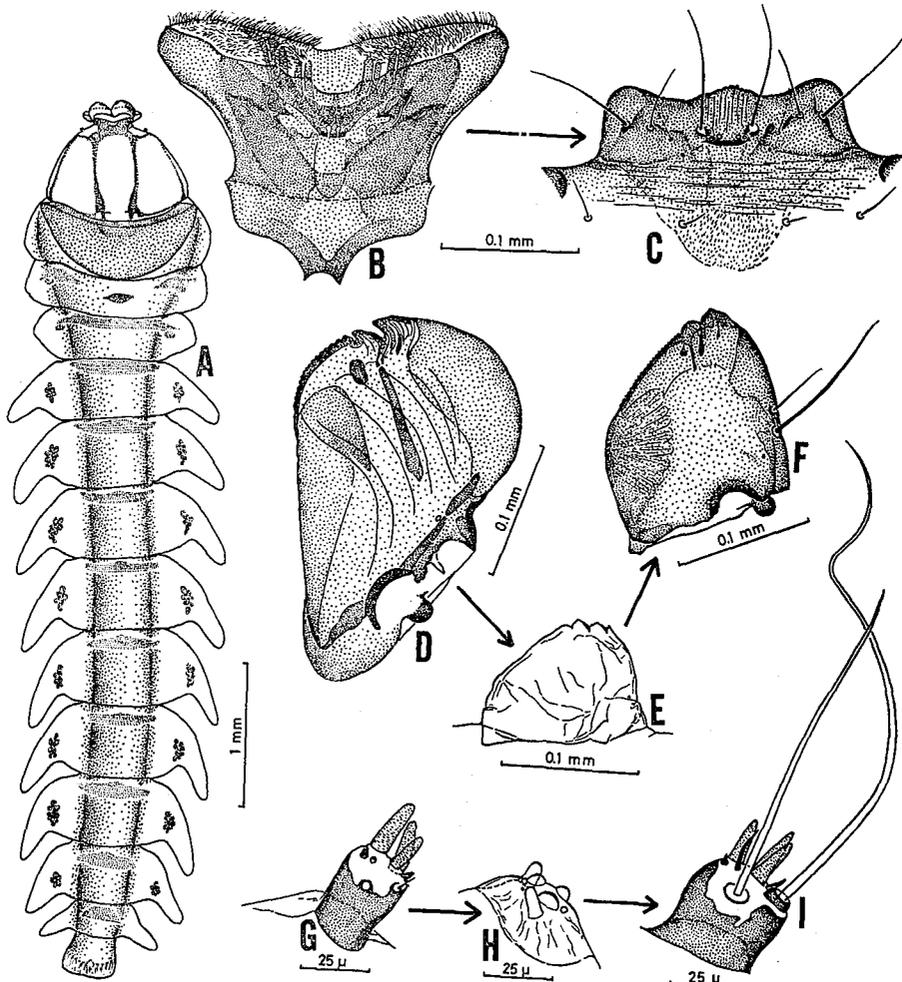


Fig. 3. *Dendrorhycter marmaroides*, gen. et sp. nov. (larva). A, B, D & G: Final instar of sap-feeding form — E & H: quiescent form — C, F & I: spinning form. A: Sap-feeding larva in dorsal view — B & C: labrum — D, E & F: mandible — G, H & I: antenna.

Supposed 6th instar — Colour: Head creamy whitish, somewhat transparent, slightly brownish around mouth-parts and ridges. Body evenly creamy-whitish.

Structure: Head (Fig. 4, A) very strongly flattened dorsoventrally, wedge-shaped, prognathous, with posterior dorsal prolongations well developed, slender and about half as long as frontoclypeus. Frontoclypeus open posteriorly, slightly

narrowed anteriorly, with frontal setae absent. Epicranial setae very minute, sometimes indicated by basal socket only, so that their arrangement is not always determined exactly. Ocelli much reduced in size, 3 or 4 on each side near anterolateral area of epicranium just behind antenna. Antenna (Fig. 3, G) unsegmented, nearly as long as wide, with 3 sensilla basiconica, 3 minute sensilla basiconica, 1

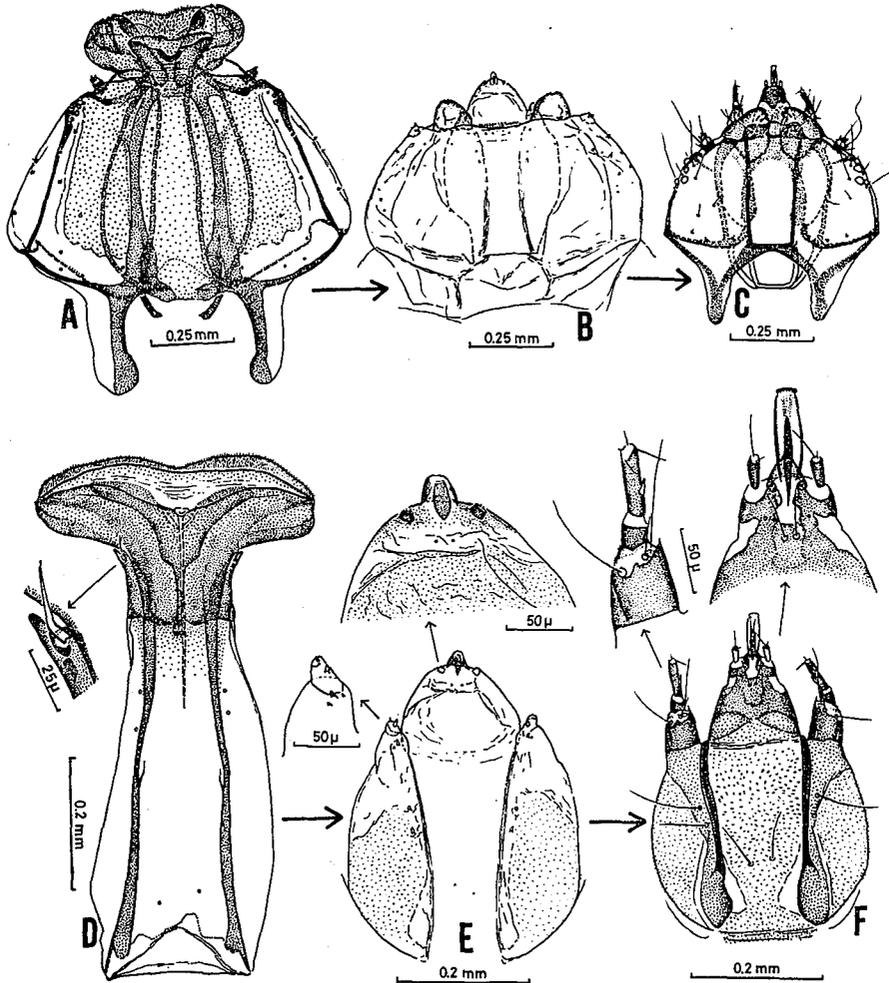


Fig. 4. *Dendrorhycter marmaroides*, gen. et sp. nov. (larva). A & D: Final instar of sap-feeding form — B & E: quiescent form — C & F: spinning form. A-C: Head in dorsal view — D-F: labiomaxillary part in ventral view.

short sensillum trichodium and 1 sensillum campaniformium at the top. Labrum (Fig. 3, B) expanded laterally, shallowly emarginate medially on anterior edge, with dense, fine hairs on apical area except medially, without any labral or epipharyngeal setae. Mandible (Fig. 3, D) very flat, with outer edge prominent and round, inner edge straight and hinge line oblique; 3 distal teeth of which the mesalmost is broad, round, and finely crenulate; about 7 fine grooves running on surface.

Labium and maxilla (Fig. 4, D) strongly modified and well prolonged; prelabium expanded laterally to form a large, transverse lamina, of which the apical edge is widely sinuate; labial palpi and spinneret absent; hypopharynx protruded a little beyond apical edge of labium, bilobed apically, covered with dense, minute hairs on apical area; postlabium oblong, slightly widened posteriorly. Maxillary galea narrow, merely reaching base of apical lamina of labium, with 1 bristle supposed to represent maxillary palpus (Fig. 4, D).

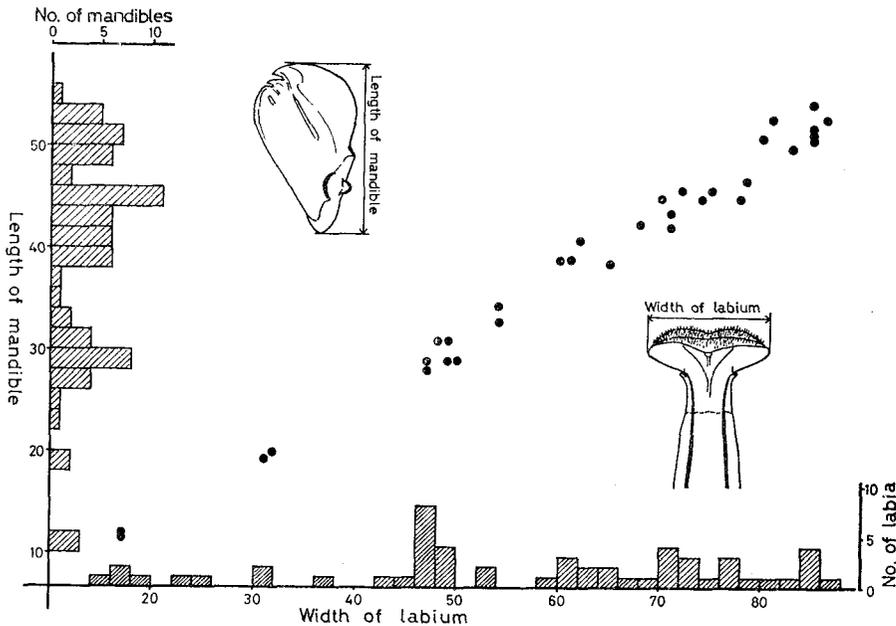


Fig. 5. Width of labium and length of mandible in sap-feeding larvae of *Dendrorhycter marmoroides*, gen. et sp. nov. Plotted in scatter diagram when mandible and labium are originated in the same head-capsule. Unit: 5 micra.

Body (Fig. 3, A) as well as head flattened dorsoventrally, with deep intersegmental constrictions. Prothorax covered dorsally with a large semicircular shield, with a band covered with transverse rows of small spines along the anterior margin of the shield. Mesothorax nearly as wide as prothorax, medially with a small dorsal sclerite, and near anterior margin with a pair of dorsal patches and a transverse ventral band, the patches and band covered with spines as in prothorax. Metathorax narrower, banded with spines on both dorsal and ventral sides. Abdominal segments except the 10th banded with spines as in metathorax, with a prominent lateral lobe on each side, the lobe suddenly narrowed on its apical half and directed more or less posteriorly. Tenth abdominal segment slender, produced posteriorly into a sclerotized dorsal lobe. All setae of body spine-like or represented by basal sockets. Thoracic legs and abdominal prolegs absent.

Supposed 1st to 5th instars — Only exuviated head-capsules have been examined. The structures of head quite agree with those of the supposed 6th instar except for the size and the shape of the labrum. Labrum of 1st to supposed 3rd

instars distinctly trilobed anteriorly; lateral lobes sparsely hairy; median lobe slightly protruded beyond lateral lobes, round on terminal edge, with longitudinal striae on the surface.

Specimens examined: Adult — 3♂♂ & 6♀♀. Holotype; ♂ (G. sl. no. Grc-2040), Misumai, Sapporo, Hokkaidō, em. 13/vi/1975, ex *Alnus hirsuta*, breeding no. 1401. Paratypes: 2♂♂ & 2♀♀, with the same data as those for the holotype except date emerged, 9–19/vi/1975; 1♀, Misumai, Sapporo, em. 21/vi/1974, ex *A. hirsuta*, breeding no. 1272; 1♀, Sapporo, em. 28/vii/1957, ex *A. japonica*; 2♀♀, Apoi, Hidaka, Hokkaidō, em. 17/vii/1973, ex *A. hirsuta*, breeding no. 1162.

Larva — 3 larvae of spinning form, 1 of quiescent form, and 2 of sap-feeding form final instar; about 50 exuviated head-capsules of various instars of sap-feeding form. All collected from Misumai, Sapporo, early to late May, 1973–1975.

Food plant: *Alnus hirsuta* Turcz. and *Alnus japonica* Steud. (Betulaceae).

Larval habit: The larva makes a long linear mine just beneath the surface along the long axis of the young stem or branch of the food plant as in *Marmara fraxinicola* reported by Fitzgerald & Simeone (1971 b). The mine (Plate II) usually extends downwards. It is irregularly curved around the stem and is gradually broadened downwards with the larval growth. Eventually it often exceeds 1 m. in length. The final instar larva of the sap-feeding form suddenly broadens the mine into a large blotch which is about 5–6 cm. in diameter. The feeding activity seems to stop at the end of this stage. The larva is then transformed into the spinning form, through the quiescent form, within the mining cavity. Then, it leaves the mine through a semicircular slit made on the loosened epidermis of the stem. It seems that the migrating larva climbs the tree up. For in the field the cocoon is always found on the leaf above the last mining site with a slit. It is usually located on the lower surface of the leaf at the side of the main vein, boat-shaped, 6.5–8.0 mm. in longest diameter, and light brownish in colour, with many (14–42) white bubbles on the surface.

The seasonal life-cycle of the present species is poorly known, but it seems to be similar to that of *Marmara fraxinicola*. *Dendrorhycter marmaroides* may be univoltine, the adults having emerged in the middle of June to the middle of July under breeding conditions. The overwintering stage is perhaps the immature larva, because I have collected larvae of the 4th or 5th instar in the beginning of May, early spring in Hokkaidō.

A REVIEW OF THE LARVAL TRANSFORMATION IN GRACILLARIIDAE

Larval forms of Gracillariidae

Chambers (1877–78) reported for the first time that in the genus *Lithocolletis* (= *Phyllonorycter*) the larvae of early instars are peculiarly flattened with highly specialized mouth-parts, and that they suddenly change at 1 moult to the ordinary lepidopterous larval form. Since then the larval studies of the Gracillariidae have been carried on by Dimmock (1880), Trägårdh (1913), Heinrich & DeGryse (1915), Grandi (1931, 1933, 1959), Jayewickreme (1940), etc. Through their works, it is now well known that the heteromorphic development of the larvae is universal in the Gracillariidae (Hinton & Mackerras, 1970). These works deal with a limited number of species or give fragmentary descriptions of instars. According to them,

however, the larvae of the Gracillariidae can be divided into 4 distinct forms which differ not only in morphological structures but also in functional activities as given below.

1. Sap-feeding form. This name is first used by Trägårdh (1913), and is now accepted by many authors. This form is also called "flattened type" by Chambers (1877-78) and Braun (1908), "gracilariid type" by Chapman (1902) and "flat gracilariid type" by Heinrich & DeGryse (1915).

As described under *Dendrororycter marmaroides*, the sap-feeding form is distinctly characterized by the much flattened body and head; the head is more or less wedge-shaped, prognathous, with the frontoclypeus open and the mouth-parts remarkably modified. The labrum is much widened laterally to form the upper lamina of the mouth; it is usually devoid of obvious setae. The mandible is much flattened dorsoventrally, with a reduced number of apical teeth; the innermost tooth is more or less widened to form the median blade, which is sometimes crenulate along the whole apical edge, thus somewhat looking like a circular saw. The labium is very much simplified, widened in the apical area of the prelabium to form the lower lamina of the mouth; it lacks palpi; the spinneret is completely atrophied; the hypopharynx is well developed, very hairy at the apex, and usually produced anteriorly beyond the labium. The maxilla is much reduced in size in the apical part, with 1 or 2 lobes or spines at the apex. (For further description of the head, see Trägårdh, 1913.) The thoracic legs, and ventral and anal prolegs are entirely absent. Sometimes fleshy tubercles are present on the thoracic segments and on the 3rd to 5th or rarely on the 3rd to 6th abdominal segments, but they lack claws and crochets. The body setae are much reduced in length and sometimes represented only by their basal sockets, but the lateral setae are generally more or less prominent.

The sap-feeding form is exhibited by early 2 or more larval instars. In correspondence to the structural modification the larva of this form is peculiar in feeding behaviour. It usually mines the subepidermal or epidermal tissue of plant. The flattened body and the flattened head with prognathous mouth-parts may serve to mine such a thin layer of tissue. The mandibles, which are much modified as described above, may no longer be used in biting, but may be sawed through the plant-tissue. The larva thus absorbs sap flowing from the destroyed tissue. The hairy and developed hypopharynx may help the sap-flow into mouth-cavity. The labrum and prelabium, transformed into superposed laminae, hold the mandibles between them. The function of these laminae may be to prevent the sap from flowing out, or, as assumed by Trägårdh (1913) for *Phyllocnistis*, to protect the plant epidermis from the damage to be caused by the horizontally moving mandibles.

The apodous conditions seems to be correlated to the flattening of the body. The muscles associated with the legs must also be reduced, because these muscles are no doubt burdensome for such modification of the body.

2. Tissue-feeding form. This name was also proposed by Trägårdh (1913) in contrast with the sap-feeding form. This form is also named "cylindrical form" or "cylindrical type" by some authors.

The larva of this form is generalized in structure, and very similar in all respects to the free-living larvae of other microlepidopterous families. The head-capsule is round as usual, slightly lengthened anteriorly in the region of the genae in most species of *Phyllonorycter*, or slightly depressed dorsoventrally in the members of

Parectopa, *Liocrobyla* and their relatives. The mouth-parts are usually orthognathous, but semiprognathous or nearly prognathous in *Parectopa* and others. The labrum, mandibles, labium and maxillae show nothing peculiar in structure and quite resemble those of the ordinary lepidopterous larvae, though they show some differences among taxa. The body is cylindrical or subcylindrical, with the thoracic legs and abdominal prolegs completely developed in most of the species studied. In this family, however, the ventral prolegs are found on the 3rd to 5th or rarely on the 3rd and 4th abdominal segments. The body setae are more or less developed; especially D_2 , SD_1 and L_1 are well developed.

According to Heinrich & DeGryse (1915), the 3rd instar larva of *Neurobathra strigifinitella* is morphologically intermediate between the sap-feeding and tissue-feeding forms: its head-capsule is subcylindrical and ordinary in structure, but the body is completely apodous. They considered that it is transitional between the tissue-feeder and the sap-feeder. In my opinion, however, it should belong to the tissue-feeding form. The most important differences between the sap- and tissue-feeders are found in the mouth-parts, especially in the presence or absence of the spinneret on the labium.

The tissue-feeding form occurs in later larval instars, following the sap-feeding form, and covers 2 or more instars. Within the mine it feeds on the plant tissue by the ordinary manner.

3. Spinning form. Trägårdh (1913) mentioned the occurrence of this strange form at the last larval instar of *Phyllocnistis*, but he included it in the tissue-feeding form. It may be, however, better distinguished from the tissue-feeding form, because it does not feed. This form is often termed "prepupa".

The larva of this form exclusively spins the cocoon. In this respect it distinctly differs from the larva of the last tissue-feeding instar, for the latter spins only in the late part of the instar. In the Gracillariidae this form is known to occur at the last 1 or 2 larval instars in a few species belonging to *Cameraria*, *Marmara* and *Metriochroa*. It also occurs in other genera including the present new genus and *Chrysaster*.

In spite of the functional difference, morphologically this form is certainly similar to the tissue-feeding form. However, it shows some modifications in the mouth-parts and legs. The most remarkable structure of the mouth-parts is the prelabium with a prominent spinneret and a pair of palpi on the anterior extremity. The labrum is more or less reduced in length, especially in *Metriochroa*. The mandible is also reduced into a small triangular sclerite in some species. The maxilla is somewhat simplified in structure especially on the apical part. The thoracic legs are often developed as usual, but sometimes reduced into protuberances without claw. The abdominal prolegs are also often reduced into small protuberances without crochets. The various modifications of these organs seem to be correlated with the spinning site. In *Metriochroa* and *Cameraria*, which exclusively pupate inside the mine, the spinning larva shows the reduced mandibles and thoracic legs. On the other hand, in *Marmara*, *Dendrorhycter* and *Chrysaster*, which usually pupate outside the mine, it bears more or less developed mandibles and legs. In the former genera the mandible seems to have no function at all, while in the latter it is used to make a hole or slit on the plant epidermis through which the larva escapes from the mine.

4. Quiescent form. The presence of this form in the larval stage of the

Gracillariidae was first reported by DeGryse (1916) in *Marmara fulgidella*. He wrote: "This period, it was found, is marked by a special stage similar to the pseudo-pupal stage of the Meloidae". Recently, it is found in another species, *Marmara fraxinicola*, by Fitzgerald & Simeone (1971 a & b). I have also observed it in the present new species and *Chrysaster hagicola*.

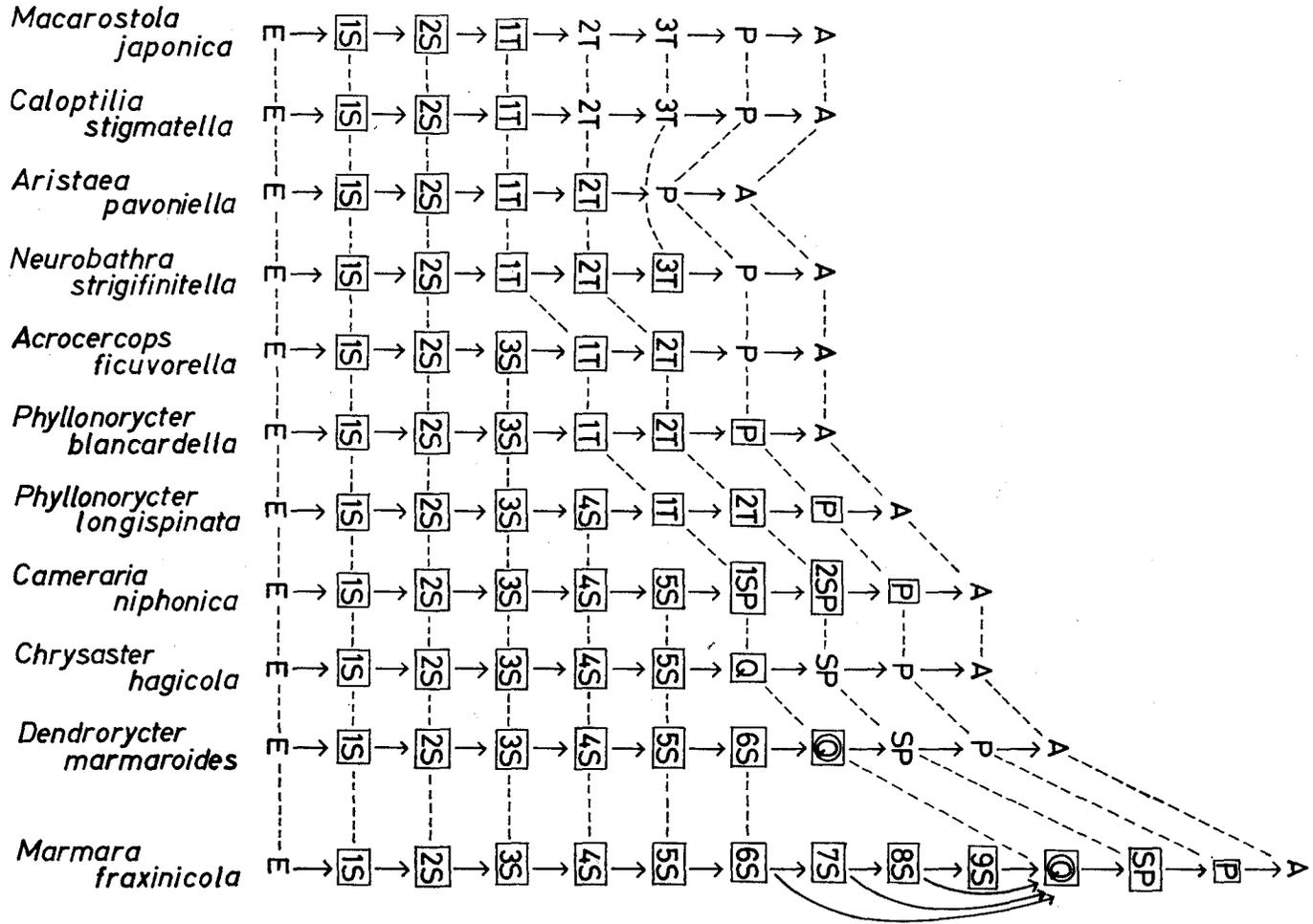
This form occurs in 1 instar between the sap-feeding and spinning forms. In *Marmara* and *Dendrorhycter*, so far as known, throughout its instar it is in a "pharate phase" as termed by Hinton (1946 & 1971). It is wholly contained within the cuticle of the preceding instar (final sap-feeding instar). The spinning stage is then formed within the quiescent larva. Upon its emergence, the spinning larva casts the skins of both the final sap-feeding and quiescent instars at once. On the other hand, in *Chrysaster hagicola* the quiescent form is an independent instar isolated from the final sap-feeding larva, though the period of the instar is shortened. Whether it is pharate or independent, the quiescent form completely lacks ability to move like a true pupa.

As described under *Dendrorhycter marmaroides* the present form is peculiar in structure. The whole body surface is very weakly sclerotized, even in the head-capsule. All the appendages are merely outlined in the external pellicle like those of a true pupa, while their parts are distinct and are easily identified. The characters of the sap-feeding form are lost, while those of the spinning form are foreshadowed, especially in the labium. The head-capsule is also rather similar to that of the spinning form, but it is slightly depressed dorsoventrally, rather broad, shortened, without posterior dorsal prolongations, and with apodemes nearly obliterated. The labrum is reduced in length and coalesced into clypeal region. The mandible is subatrophied and united with the cranial wall, thus it has no function. The spinneret and palpi of the labium are also subatrophic. The maxilla is tightly fused with postlabium, but with an atrophic palpus. The antenna is less prominent, unsegmented, with small projections. All the legs are rudimentary, and are represented by oaired ventral tubercles without claw and crochets. All the trichotactic setae are much reduced into minute conical projections.

The description given above is mainly based on *Dendrorhycter marmaroides*. In *Chrysaster hagicola*, however, this form is not so much specialized, and is slightly more similar to the spinning form in structure. The antenna is well developed, with normal sensory setae and papillae. The thoracic legs are also developed, but the apical claws are atrophied. All the trichotactic setae are short, but well reserved as in the spinning larva. These differences between *Dendrorhycter* and *Chrysaster* may partially owe to the difference between the pharate and independent conditions of the form, and partially to the taxonomic difference, for *Dendrorhycter* belongs to Gracillariinae and *Chrysaster* to Lithocolletinae.

Pattern of larval transformation

Figure 6 shows the ontogenetic life-cycles of 11 species which are selected from different genera of the Gracillariidae. The data used, except for *Dendrorhycter marmaroides*, originate with the following authors: Heinrich & DeGryse (1915) for *Neurobathra strigifinitella*; Pottinger & LeRoux (1971) for *Phyllonorycter blancardella*; Fitzgerald & Simeone (1971 a & b) for *Marmara fraxinicola*; Kumata (1977) for *Macarostola japonica* and *Aristaea pavoniella*. The data of the remaining species have been obtained by my own observations, but not yet been published.



In this figure, the successive stages of growth are expressed by symbols, and the patterns of the transformation are compared among the species. As far as I know, the pattern is fairly stable in a genus. However, in the genus *Phyllonorycter* the number of the sap-feeding instars is variable; it is usually 3 or 4; moreover, according to Ujiye (1976), the sap-feeding stage of *P. ringoniella* consists of 2 instars in early generations, while 3 instars in the succeeding generations. It is also reported by Fitzgerald & Simeone (1971 b) that the sap-feeding larva passes through 6 to 9 instars in *Marmara fraxinicola*.

As shown in the figure, the number of the larval instars varies with species in a very wide extent from 4 in *Aristaea pavoniella* to 11 in *Marmara fraxinicola*. So far as I am aware, the basic number of the larval instars in this family has not yet been discussed. As the genus *Macarostola* has many primitive characters in the wing venation and larval chaetotaxy, it is considered to be the most primitive in the Gracillariidae (Vári, 1961; Kumata, 1977). If this assumption is right, the basic number of larval instars should be 5, and the basic pattern of the larval transformation should be that shown by *Macarostola*, that is, the pattern with 2 sap-feeding instars succeeded by 3 tissue-feeding instars. This pattern is also seen in *Caloptilia stigmatella*, and the genus *Caloptilia* is also a primitive group. Any number of instars other than 5, either decreased or increased, therefore, might be a derived character.

Aristaea pavoniella has only 4 larval instars, and the decrease appears to have been caused by losing 1 instar in the tissue-feeding form. The genus *Aristaea* is related to *Caloptilia*, and shows some derived characters in the wing venation and larval chaetotaxy (Kumata, 1977). Moreover, most members of *Aristaea*, including *pavoniella*, are leaf-miners throughout the larval period. On the other hand, in most species of *Macarostola* and *Caloptilia* the larvae are leaf-miners in the first 3 instars (the last of them belongs to tissue-feeding form), then they leave the mine to make a leaf-roll or leaf-fold, within which they continue feeding. This pattern seems to be primitive in the family, in which many forms are highly adapted to mining plant tissue.

The increase of instars mainly occurs in the sap-feeding form. The known extreme in this tendency is provided by *Marmara fraxinicola*, in which the sap-feeding stage consists of 6 to 9 instars. In *Acrocercops ficuvorella* and *Phyllonorycter blancardella* the number of larval instars is 5 as in *Macarostola japonica* and *Caloptilia stigmatella*. But the former 2 species differ from the others in having 1 more sap-feeding instar and dropping 1 tissue-feeding instar; in other word, the transformation occurs at the 3rd moult (between the 3rd and 4th instars) in *A. ficuvorella* and *P. blancardella*, while at the 2nd moult in *M. japonica* and *C. stigmatella*. In *Phyllonorycter longispinata* the transformation occurs at the 4th moult, thus the sap-feeding stage consists of 4 instars. These species of *Acrocercops* and *Phyllonorycter* are leaf-miners throughout the larval period; those of *Phyllonorycter* even pupate inside the mine-cavity.

In the species belonging to the genera *Macarostola*, *Caloptilia*, *Aristaea*, *Neurobathra*, *Acrocercops* and *Phyllonorycter*, the sap-feeding form is succeeded by the

Fig. 6. Comparison of ontogenetic life-cycles in 11 species of the Gracillariidae. A: Adult; P: pupa; 1T to 3T: 1st to 3rd tissue-feeding instars; 1S to 9S: 1st to 9th sap-feeding instars; SP: spinning instar; Q: quiescent instar; E: egg. The instars within a square are mining, and those within a circle are in pharate phase. The broken lines indicate corresponding instars.

tissue-feeding form after 1 moult. In *Cameraria niphonica*, which has 5 sap-feeding instars in the larval stage, the sap-feeding form is no longer transformed into the tissue-feeder but into a nonfeeding spinning form, which is represented by 2 instars. The larva actually finishes feeding at the end of the 5th sap-feeding instar. The larva of the 1st spinning instar exclusively lines the plant-epidermis with silk threads at the pupating site within the mine, then the larva of the 2nd spinning instar makes a cocoon. In comparison with the transformation in *Phyllonorycter longispinata*, these spinning larvae seem to be modified tissue-feeders, with a change of function from feeding to spinning.

In the larval stage of *Chrysaster hagicola*, the sap-feeding form spent in 5 instars is transformed into the quiescent form, then the latter changes to the spinning form after a moult. Similar transformations are seen in *Dendrorhycter marmaroides* and *Marmara fraxinicola*, although in these species the sap-feeding instars are more numerous and the quiescent form is a pharate phase throughout its existence. These species differ from *C. niphonica* in having 1 quiescent instar and 1 spinning instar in the later larval stage instead of 2 spinning instars. This suggests that the quiescent form has originated in the 1st spinning instar with the reduction of functions in spinning and locomotion. It is noteworthy that the quiescent form, whether pharate or independent, occurs in those species which have 5 or more instars in the sap-feeding stage and complete feeding within this stage.

Origin and evolutionary significance of the peculiar forms

The larval heteromorphic development in the Gracillariidae is caused by the intervention of such peculiar forms as the sap-feeding, spinning and quiescent forms in the course of larval growth. In Lepidoptera, such a heterometamorphosis is also known in the Epipyropidae and Phyllocnistidae. The larva of the Epipyropidae is external parasite on Homoptera, and the heterometamorphosis is adaptive to the parasitic life (Clausen, 1940; Snodgrass, 1954). On the other hand, in the Phyllocnistidae, which includes only one genus *Phyllocnistis*, the larva mines the tissue of leaves, twigs or stems of plants like that of the Gracillariidae. Moreover, it passes through 3 sap-feeding instars and 1 spinning instar in the larval stage likewise. The occurrence of the peculiar forms in the Gracillariidae and Phyllocnistidae is evidently associated with the mining habit of the larva as discussed by many authors (Chambers, 1830; Chapman, 1902; Trägårdh, 1913; DeGryse, 1916; Jayewickleme, 1940; Grandi, 1959; etc.).

1. Sap-feeding form. Since it was first reported by Chambers in 1877-78, this form has attracted the attention of many workers especially for its origin and significance. Chambers (1880) himself published his consideration on its evolutionary significance. After him it is a primitive form of the lepidopterous larva because of its early appearance in the larval stage and its simple structure. Chapman (1902) rejected Chamber's view, and argued that "each larval instar is a stage, comparable to the pupal or imaginal stage in its individual importance, and it may undergo changes without necessarily involving any other instar, which holds to it the attitude of a separate stage". He concluded that "the Gracillarian form arose by modification in the first instar, and thence moved forward into the second, and in other cases further". His conclusion suggests that the sap-feeding form is an example of "caenogenesis" of de Beer (1958), after whom "evolutionary novelties may have made their first appearance at any stage of the life-history,

early or late". Chapman's assumption has been followed by authors.

The characters of the sap-feeding form may be divided into simple characters, which Chambers may have considered as primitive, and complicated ones. The simple characters includes the apodous condition of the body, the labium without spinneret and palpi, the very short maxilla without complicated palpi or apical lobes, the mandible with a few apical teeth, etc. These characters can be considered as reductive states associated with the flattening of the body and head with prognathism. Trägårdh (1913) and Jayewickleme (1940) compared in detail the structure of the sap-feeding form with that of other lepidopterous leaf-mining larvae, and showed various stages of reduction in many features. The complicated characters are the extremely widened prelabium and labrum, the flattened mandible somewhat similar to a circular saw, etc. These characters are specializations associated with the feeding behaviour as already discussed. These specializations tend to be strengthened with instars.

Grandi (1954) argued that majority of the characters peculiar to the sap-feeding form, including the flattening of the body and head, are states adapted to its sap-feeding behaviour. It is no doubt that they are closely related to the mining habit of the larva that mainly lives in such thin layers as the epidermal or subepidermal tissue of plants. This may have been a new adaptive zone for the leaf-mining Lepidoptera. In the Gracillariidae the larva passes through at least 2 instars in this form, and phylogenetically advanced species tend to have more instars. This family, with a very wide distribution over the world and with rich numbers of species, is undoubtedly a flourish group, and this might owe to the exploitation of the new adaptive zone by means of the sap-feeding behaviour and the flattened body with a prognathous head.

2. Spinning form. In the Gracillariidae and Phyllocnistidae the larva spins the cocoon in the last instar, whether the cocoon is made rough or dense. The tissue-feeding larva can spin the cocoon as a prepupa in the late stage of the final instar. On the other hand, the sap-feeding larva is unable to make the cocoon, because it has no spinneret, one of the spinning organs. Accordingly, it must be transformed into a spinning form, when it has completed taking food. So far as based on the comparisons of the patterns of the larval transformation and the larval structures, the spinning form in question must have arisen from the last 1 or 2 instars of the tissue-feeding form with the reduction of feeding activity.

The appearance of the spinning form is obviously associated with the increase of the sap-feeding instars, but not with a fixed number of instars. Figure 6 shows that it occurs in 1 or 2 instars following at least 5 instars of the sap-feeding form. In this connection it may be noteworthy that the basic number of the larval instars is assumed also to be 5 in the Gracillariidae.

The acquisition of the spinning form has divided the larval stage into 2 phases with different functions, feeding and spinning. It seems that this division enabled the sap-feeding form to increase instars further.

3. Quiescent form. This peculiar form is known in a limited number of species including the present new species *Dendrorhycter marmaroides*. In these insects the larva passes through 5 or more instars in the sap-feeding form, and the quiescent form is always intercalated between the final sap-feeding instar and the last larval instar (viz. the spinning instar).

As described and figured for *D. marmaroides* (Fig. 4, B), morphologically the

quiescent form is similar to the spinning form rather than to the sap-feeding one, but it is characterized by many reduced features. The most obvious difference between them is concerned with the functional activity. The quiescent form has completely lost function in feeding, spinning and moving. Moreover, it is a pharate phase throughout its existence in the genera *Dendrorhycter* and *Marmara*. When DeGryse (1916) first discovered it in the larval stage of *Marmara fulgidella*, he called it pseudo-pupa and mentioned that "the pseudopupa bears the same relation to the prepupal larva as the pupa bears to the imago". His statement is still acceptable at present.

According to Hinton (1963) the pupa of Endopterygota functions to bridge the gap between the larva specialized for feeding and the adult specialized for reproduction and dispersion. When the larval stage is sharply subdivided into 2 phases, feeding and spinning, the gap between these phases may become too wide to cross at 1 moult. Moreover, as already mentioned, the sap-feeding form grows more specialized with instars. An intercalation may be necessary to bridge the gap between them. The quiescent form in question seems to be such an intercalation, and to function to bridge the gap between the sap-feeding form specialized for feeding and the spinning form specialized for spinning.

A comparison of the larval transformations between *Chrysaster hagicola* and *Cameraria niphonica*, which are taxonomically closely related to each other, suggests that the quiescent form has originated in the 1st spinning instar. This form occurs in taxonomically different groups, that is, *Marmara* and *Dendrorhycter* belong to the subfamily Gracillariinae, while *Chrysaster* to the other subfamily Lithocolletinae; then, it must have been acquired independently in these subfamilies. The wholly pharate condition of the quiescent form in the genera *Dendrorhycter* and *Marmara* is quite mysterious. I have no idea about its evolutionary significance.

Concluding remarks

Our knowledge on the ontogenetic life-cycle of the Gracillariidae is still based on a limited number of species. As a result of this review, however, it is apparent that the most drastic event in the evolution of the Gracillariidae was the acquisition of the sap-feeding form in the early larval instars. The acquisition of this form may have opened the new adaptive zone of mining the thin epidermis of plants. The next step in the evolutionary trends may have been the prolongation of the sap-feeding stage. The variation of the number of the larval instars as seen in Fig. 6 mainly owes to the gradual increase of the sap-feeding instars, and the various patterns of the larval transformation may have appeared as a result of this evolutionary trend. The peculiar larvae of the spinning and quiescent forms are modifications of the tissue-feeding form (which agrees with the ordinary form of lepidopterous larvae) with the reduction of one or both of the feeding and spinning functions. These modifications might have been associated with the increase of the sap-feeding instars and the completion of feeding within the sap-feeding stage.

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PLATES

Plate I

- Fig. 7. Adult specimen of *Dendrocycter marmaroides*, gen. et sp. nov.
A: Holotype ♂.
B: Paratype ♀ (Misumai, Sapporo, Hokkaidō, ex *Almus hirsuta*).

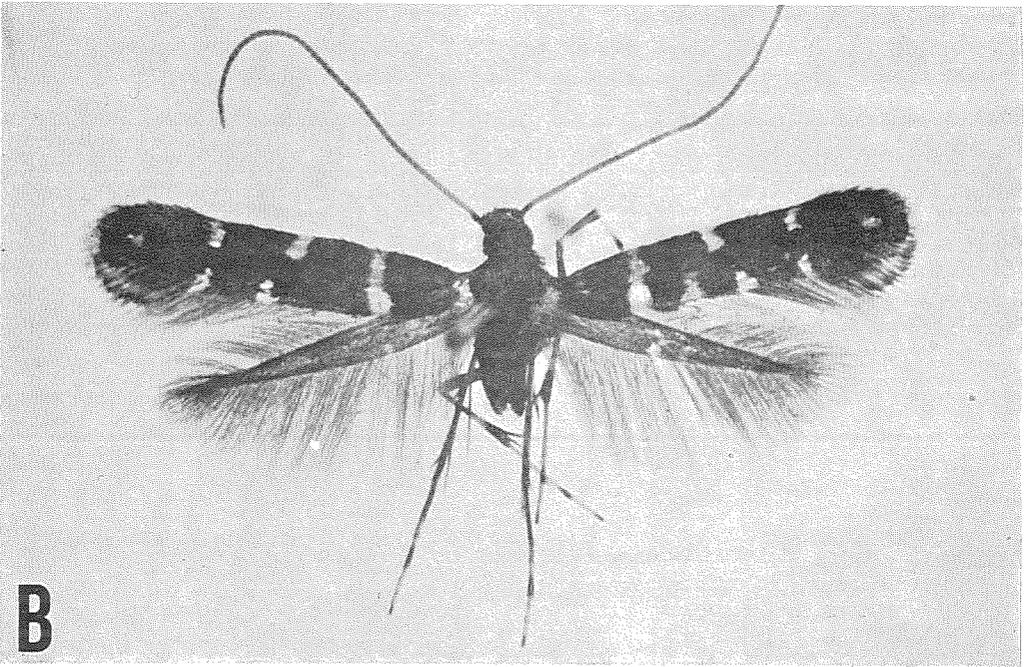
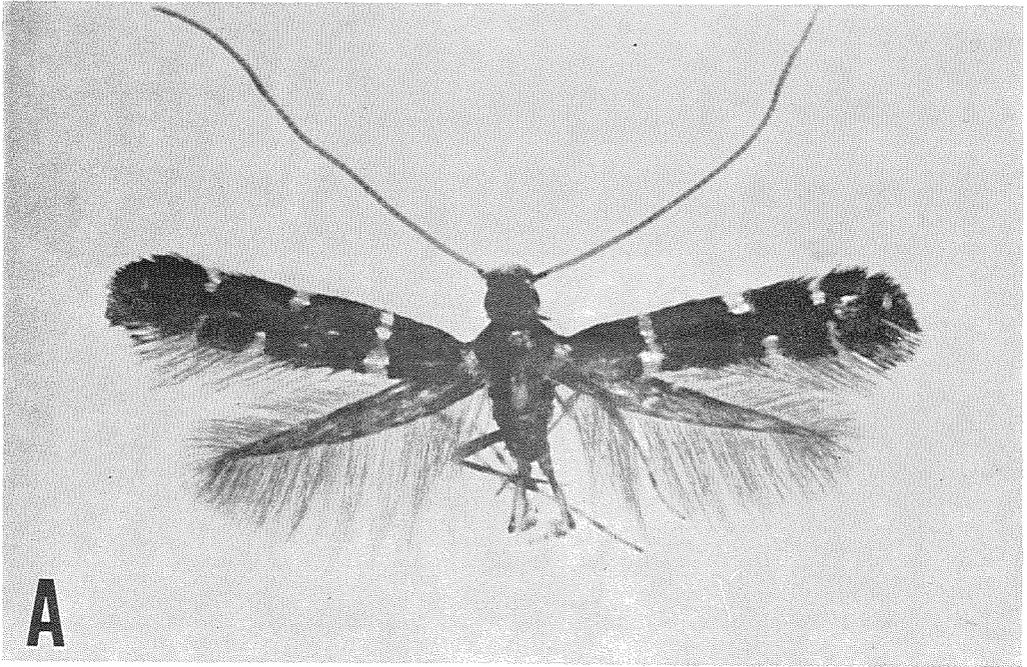


Plate II

Fig. 8. Mine of *Dendrocycter marmaroides*, gen. et sp. nov.
A: Mine on trunk of *Alnus hirsuta*.
B & C: Ditto, enlarged.

