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THE LARVA OF *SPHINDOCIS DENTICOLLIS* FALL AND A NEW SUBFAMILY OF CIIDAE (COLEOPTERA: HETEROMERA)

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ABSTRACT. The larva of *Sphindocis denticollis* Fall is described, and its biology is briefly discussed. A new subfamily of Ciidae — the Sphindociinae — is proposed for *Sphindocis* and is formally characterized, while the Ciidae and Ciinae are redefined. Speculations are made concerning the phylogenetic relationships of the family Ciidae.

The monotypic genus *Sphindocis* Fall is based on a very interesting fungus-feeding beetle (*S. denticollis*) that is known only from the Transition Zone forests of the northern California coast. The genus was originally placed in the family Ciidae (Fall, 1917), but it was recently removed from that family and tentatively placed in the Tetratomidae (Lawrence, 1971). At the suggestion of R. A. Crowson, I made a more detailed study of the *Sphindocis* larva, comparing it and the adult with various Ciidae, Tetratomidae, Pterogeniidae, and related Heteromera. As as result, I have come to the conclusion that *Sphindocis* represents the closest living relative or sister group of the Ciidae and should either be returned to that family or form the basis for a new group of equal rank. The former alternative appears more reasonable, since the number of families in the Heteromera is already excessive. The following treatment includes a description of the *Sphindocis* larva, the proposal of a new subfamily for the inclusion of this genus, and a recharacterization of the family Ciidae and subfamily Ciinae.

The larval description is based on more than 50 specimens collected with adults in the fruiting bodies of *Trametes sepium*

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Berkeley growing on dead branches of madrone (*Arbutus Menziesii*) at the following localities in California: Alpine Lake, Marin County; 1 mi. N Piercy, 2 mi. N Piercy, 3 mi. S Leggett, and 4 mi. W Leggett, Mendocino County. Another eight specimens were collected without adults in a fruiting body of *Poria cinerascens* (Bresadola) Saccardo and Sydow growing on a Douglas fir (*Pseudotsuga Menziesii*) log at Alpine Lake. A single pupa was dug out of madrone wood beneath a fruiting body, which may indicate that the beetles require the woody substrate for pupation.

Most of the terms used in the larval description are those found in standard works, such as Böving and Craighead (1931) and van Emden (1942). For the three labial sclerites, I have used the terms prementum, mentum, and submentum, although Anderson (1936) has indicated that these are not homologous in all groups. Terminology for the ventral thoracic sclerotizations follows Watt (1970), while various other terms have been taken from Crowson (1955), Glen (1950), Rozen (1958, 1960), St. George (1924), and Snodgrass (1935).

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DESCRIPTION OF THE MATURE LARVA OF *Sphindocis denticollis* Fall

Body elongate and subcylindrical, lightly sclerotized except for head, anterior part of prothoracic tergum, and pygidium (upper part of ninth abdominal tergum). Length about 5 mm; width about 0.7 mm.

Head (Figs. 1–3) exserted, obliquely prognathous, subglobular, strongly convex dorsally, except for a broad, shallow concavity (c) extending from the middle of the epicranial stem to the upper part of the frontoclypeal triangle (fc); heavily sclerotized and yellowish brown in color, with fairly coarse and irregular punctation; vestiture consisting of numerous short setae and several longer ones, the origins of which are shown in Figures 1–3. Epicranial stem (es) about half as long as head width; frontal arms (fa) somewhat V-shaped and extending to antennal ridges (ar), which conceal antennal insertions; endocarina absent. Frontoclypeal area (fc) bearing two parallel, transverse sulci (ts) near epistomal margin (em). Epicranial

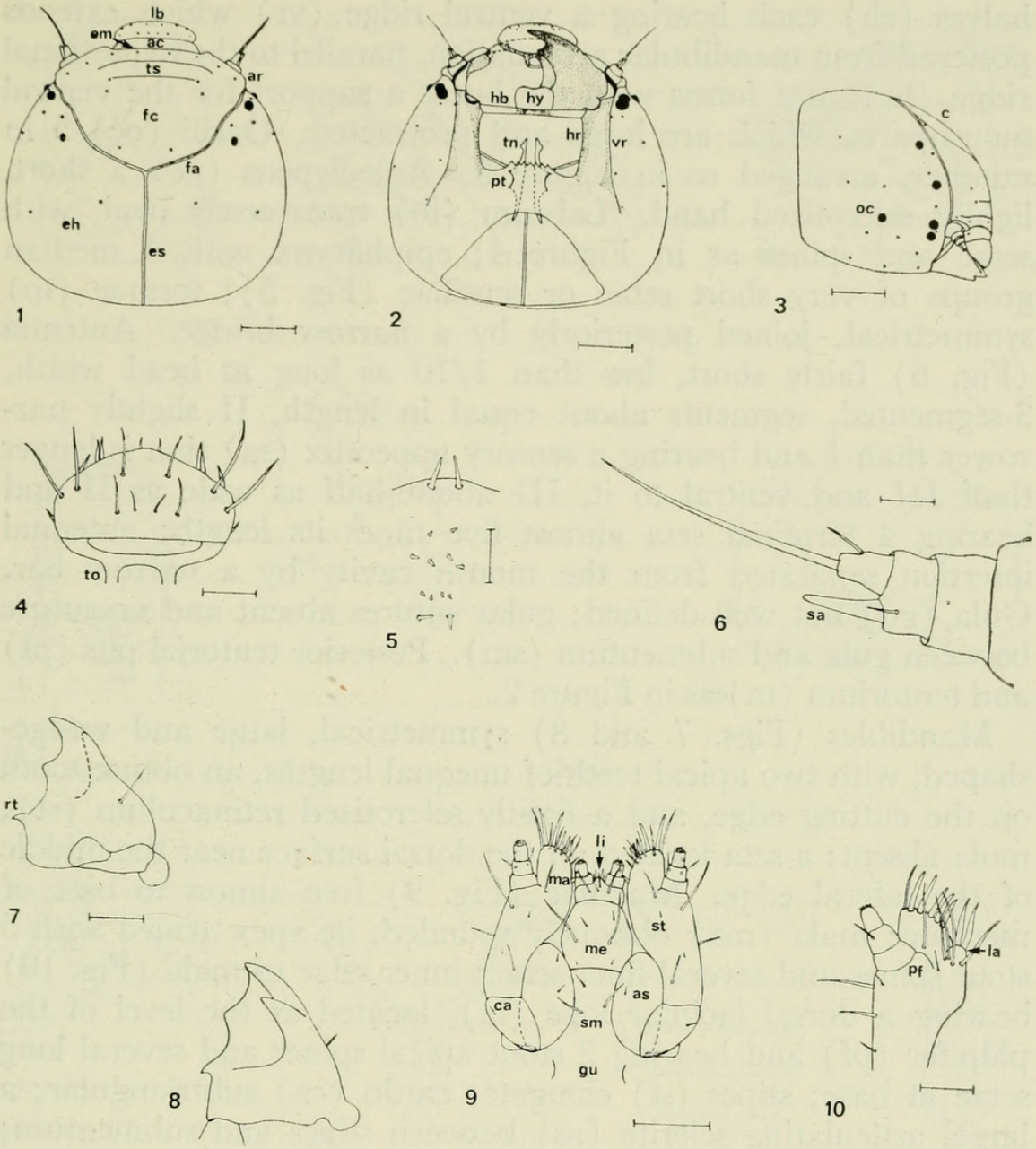

Plate 1

Figures 1–10. *Sphindocis denticollis* Fall, larva (1 line = 0.125 mm for 1–3, 9; 0.063 mm for 4, 7, 8, 10; 0.025 mm for 5, 6). Fig. 1. Head capsule, dorsal view, mandibles and ventral mouthparts removed (dots = setal origins). Fig. 2. Head capsule, ventral view, right mandible and ventral mouthparts removed. Fig. 3. Head capsule, lateral view. Fig. 4. Labrum-epipharynx, dorsal view. Fig. 5. Epipharynx, median portion. Fig. 6. Left antenna, lateral view. Fig. 7. Right mandible, dorsal view. Fig. 8. Left mandible, ventral view. Fig. 9. Ventral mouthparts and gular region, ventral view. Fig. 10. Apex of left maxilla, dorsolateral view.

halves (eh) each bearing a ventral ridge (vr) which extends posterad from mandibular articulation, parallel to the hypostomal ridge (hr), and forms with the latter a support for the ventral mouthparts, which are large and protracted. Ocelli (oc) 5 in number, arranged as in Figure 3. Anteclypeus (ac) a short, lightly sclerotized band. Labrum (lb) transversely oval, with setae and spines as in Figure 4; epipharynx with 4 median groups of very short setae or sensillae (Fig. 5); tormae (to) symmetrical, joined posteriorly by a narrow bridge. Antenna (Fig. 6) fairly short, less than 1/10 as long as head width, 3-segmented, segments about equal in length, II slightly narrower than I and bearing a sensory appendix (sa) that is longer than III and ventral to it, III about half as wide as II and bearing a terminal seta almost five times its length; antennal insertion separated from the mouth cavity by a narrow bar. Gula (gu) not well defined; gular sutures absent and no suture between gula and submentum (sm). Posterior tentorial pits (pt) and tentorium (tn) as in Figure 2.

Mandibles (Figs. 7 and 8) symmetrical, large and wedge-shaped, with two apical teeth of unequal lengths, an obtuse tooth on the cutting edge, and a lightly sclerotized retinaculum (rt); mola absent; a seta located on the dorsal surface near the middle of the lateral edge. Maxillae (Fig. 9) free almost to base of mentum; mala (ma) obliquely rounded, its apex armed with 5 stout spines and several finer setae; inner edge of mala (Fig. 10) bearing a dorsal laciniar lobe (la), located at the level of the palpifer (pf) and bearing 2 stout apical spines and several long setae at base; stipes (st) elongate; cardo (ca) subtriangular; a large, articulating sclerite (as) between stipes and submentum; palp 3-segmented. Labium with a short prementum, a subquadrate mentum (me), and a submentum (sm), which is raised above the gula but is not separated from it; ligula (li) short and rounded, bearing 4 setae at apex; palp 2-segmented. Hypopharynx (hy) subquadrate, without a sclerome; hypopharyngeal bracon (hb) lightly sclerotized except at base of hypopharynx.

Prothorax (Fig. 11) slightly longer than meso- or metathorax, its tergum (prt) well developed and extending onto lateral surfaces, heavily pigmented anteriorly, becoming very lightly pigmented posteriorly, with a median ecdysial suture; vestiture consisting of numerous short setae and 3 transverse rows of setae consisting of 12 (anterior edge), 8 (anterior third), and 10 (posterior third) setae; sternum consisting of a large, tri-

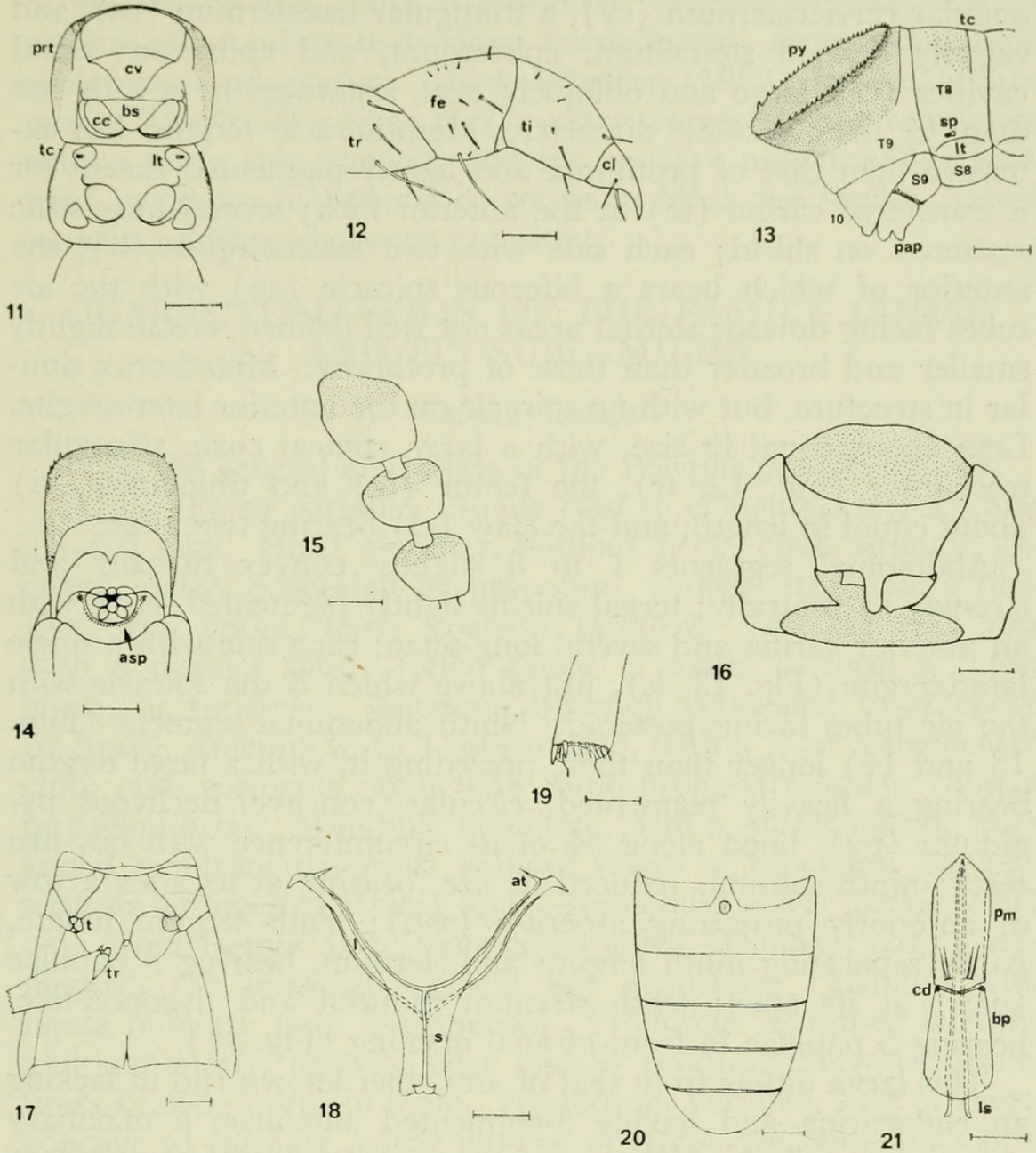

Plate 2

Figures 11–14. *Sphindocis denticollis* Fall, larva (1 line = 0.063 mm for 12; 0.250 mm for 11, 13, 14). Fig. 11. Prothorax and mesothorax, ventral view, legs removed. Fig. 12. Prothoracic leg, coxa and part of trochanter not shown. Fig. 13. Apex of abdomen, lateral view. Fig. 14. Apex of abdomen, ventral view. Figures 15–21. *Sphindocis denticollis* Fall, adult male (1 line = 0.063 mm for 15, 19; 0.250 mm for 16, 17, 20; 0.125 mm for 18, 21). Fig. 15. Antennal club. Fig. 16. Prothorax, ventral view, right coxa removed. Fig. 17. Meso- and metathorax, ventral view, left mesocoxa and metacoxae removed. Fig. 18. Metendosternite, dorsal view. Fig. 19. Apex of protibia. Fig. 20. Abdomen, ventral view. Fig. 21. Aedeagus, ventral view.

angular cervicosternum (cv), a triangular basisternum (bs), and vaguely defined sternellum, episternum, and epimeron; coxal cavities (cc) large and obliquely oval, separated by a little less than ¼ their greatest diameter. Mesothoracic tergum less extensive than that of prothorax and lightly pigmented except for a transverse carina (tc) at the anterior fifth; several long setae scattered on shield; each side with two laterotergites (lt), the anterior of which bears a biforous spiracle (sp) with the air tubes facing dorsad; sternal areas not well defined, coxae slightly smaller and broader than those of prothorax. Metathorax similar in structure, but with no spiracle on the anterior laterotergite. Legs about equal in size, with a large conical coxa, triangular trochanter (Fig. 12, tr), the femur (fe) and tibiotarsus (ti) about equal in length, and the claw (cl) bearing two setae.

Abdominal segments 1 to 8 slightly convex dorsally and strongly so ventrally; tergal shields lightly pigmented, each with an anterior carina and several long setae; each side with a single laterotergite (Fig. 13, lt), just above which is the spiracle with the air tubes facing posterad. Ninth abdominal segment (Figs. 13 and 14) longer than those preceding it, with a large tergum bearing a heavily pigmented, circular, concave, declivous pygidium (py), lined along ¾ of its circumference with saw-like teeth; ninth sternum reduced in size, bearing at its apex a row of anteriorly projecting asperites (asp); tenth tergum lunate, partly separating ninth tergum and sternum, bearing 3 papillae (pap) at its apex; tenth sternum reduced and pygopod-like, bearing 5 papillae in front of anal opening (Fig. 14).

This larva differs from that of any other known ciid in lacking an endocarina and having 3-segmented antennae, a maxillary articulating sclerite, biforous spiracles, and subanal asperites on the ninth sternum. The presence of an endocarina has never been noted for the Ciidae, probably because it is directly beneath the epicranial stem and does not extend anterad of the frontal arms, as it does in various other Heteromera. The epicranial stem in *Sphindocis* is an ecdysial line, whereas in other Ciidae it coincides with an internal ridge. The reduced antennal segmentation in most ciid larvae represents a fusion of the last two segments. Symmetrical mandibles also occur in other Ciidae, but asymmetry appears to be the more common condition. Biforous spiracles appear to be unique to *Sphindocis,* but a peculiar type of accessory air tube has been observed in at least one other ciid (unpublished). The concave pygidium of *Sphindocis,* which occurs in other Ciidae, such as *Cis melliei* (Coquerel, 1849),

in the tenebrionid genus *Meracantha* (Hyslop, 1915), and in various other substrate-dwelling beetle larvae, represents a type of defensive adaptation, which Wheeler (1928) termed phragmosis. The fruiting body of *Trametes sepium* is often resupinate with a fairly thin context, and the concave and heavily sclerotized pygidium in *Sphindocis* serves to block the shallow larval tunnel against predators or parasites.

CHARACTERIZATION OF THE FAMILY CIIDAE AND ITS SUBFAMILIES

Ciidae Leach

With the general characters of the Polyphaga: Cucujoidea.

Adult. Form variable, usually oval to elongate, convex. Size 0.5–6.0 mm. Head globular, without neck, often strongly declined, partly concealed by pronotum, without stridulatory files. Eye oval, entire, fairly coarsely facetted. Frontoclypeal area with a distinct suture, often raised in males to form a ridge, horns, or tubercles. Antennal insertion concealed from above by frons. Antenna 8- to 11-segmented, with a 2- or 3-segmented club, club segments often with multi-pronged sensillae (absent in *Sphindocis*). Mandible bidentate, with a simple cutting edge and a quadrangular mola without ridges or tubercles. Maxilla with an articulated lacinia and 2-segmented galea (*Sphindocis*) or a fixed lacinia and 1-segmented galea (Ciinae), palp 4-segmented, the terminal segment not securiform. Labium with ligula reduced, palp 3-segmented. Pronotum margined laterally and posteriorly, anterior edge usually produced forward, sometimes bearing horns in male. Prosternum variable, long or short, concave to carinate, coxae globose or transverse, sometimes projecting, contiguous to broadly separated, without internalized lateral extensions, trochantin usually concealed; procoxal cavities open internally, narrowly open or closed externally (posteriorly). Elytra not striate, humeri tuberculate, epipleura very narrow, extending almost to apex. Scutellum small and subtriangular, sometimes absent. Wing venation often reduced, subcubital fleck present, anal region with four veins (*Sphindocis*) or only one (Ciinae). Mesosternum transverse, sometimes extremely reduced, coxae globose and narrowly separated, coxal cavities not closed outwardly by sterna, trochantins exposed or not. Metasternum subquadrate, with or without median suture, without coxal lines, coxae narrow, transverse, subcontiguous. Metendosternite with a long median stalk (*Sphindocis*) or none (Ciinae),

anterior tendons arising near the apices of the lateral arms. Tarsal formula in both sexes 4–4–4 (occasionally 3–3–3), tarsi simple, the first three segments small and subequal, terminal segment elongate, claws simple. Trochanters oblique, completely (Ciinae) or only partly (*Sphindocis*) separating coxa from femur. Tibial spurs usually absent; 2 reduced spurs in *Sphindocis*. Outer edge of protibia often expanded and modified at apex. Abdomen with 5 visible sternites, the first 2 (III and IV) connate (*Sphindocis*) or not (Ciinae). First visible sternite (III) without coxal lines, often with a median pubescent fovea in male. Aedeagus of inverted heteromeroid type, with ventral tegmen and dorsal median lobe.

Larva. Body elongate and subcylindrical, lightly sclerotized, except at anterior and posterior ends. Head subglobular, obliquely prognathous, with well-developed epicranial stem and Y-shaped frontal arms, endocarina present (Ciinae) or not (*Sphindocis*); ventral epicranial ridge present behind mandibular articulation. Ocelli usually 5, occasionally fewer or none. Antennal insertion concealed from above and separated from mouth cavity by a narrow bar. Antenna short, 2- or 3-segmented, with a long sensory appendix on segment II and a very long terminal seta. Gular area short, sutures present or absent. Mandibles large and wedge-shaped, usually somewhat asymmetrical, with 2 apical teeth, a simple cutting edge, often with a lightly sclerotized retinaculum, mola usually absent. Maxilla free at least to middle of mentum, with a narrow articulating membrane (Ciinae) or a large articulating sclerite (*Sphindocis*) between stipes and submentum; mala obliquely rounded, inner edge with a dorsal laciniar lobe; palp 3-segmented. Labium with short prementum, subquadrate mentum, and elongate submentum, the last separated from gula by suture or not; ligula short and rounded, with 2 or 4 setae; palp 2-segmented. Hypopharynx without sclerome. Thoracic terga well developed and extending onto sides; prothorax slightly larger than meso- or metathorax; prosternum with a large triangular cervicosternum; procoxae large and fairly close together; spiracle annular (Ciinae) or biforous (*Sphindocis*), located on anterior latero-tergite of mesothorax. Legs fairly short and broad, subequal; claw with 2 setae. Abdominal spiracles located above latero-tergites. Ninth tergum variously modified, usually heavily sclerotized and with urogomphi; tenth sternum reduced and pygopod-like; anal opening surrounded by several papillae.

Sphindociinae, New Subfamily

Adult. Antenna 11-segmented, with 3-segmented club (Fig. 15); club segments without multi-pronged sensillae. Maxilla with an articulated lacinia and a 2-segmented galea. Pronotum (Fig. 16) with lateral margins broadly crenulate, so that several round teeth are formed; procoxal cavities with a slight lateral extension, which may expose part of trochantin. Mesocoxal cavities (Fig. 17) with exposed trochantins (t). Metendosternite (Fig. 18) with a long stalk (s), a narrow lamina (l), and the anterior tendons (at) near the apices of lateral arms. Hindwing with well-developed anal region, bearing 4 veins and a wedge cell. Trochanter (Fig. 17, tr) of heteromeroid type, obliquely joined to femur so that the latter is in direct contact with coxa at one point. Tibial apices (Fig. 19) simple, with 2 reduced spurs. Abdominal sternites III and IV connate (Fig. 20), III with a median pubescent fovea in male. Aedeagus (Fig. 21) with a large basal piece (bp), with two apical condyles (cd), a well-sclerotized ventral paramere (pm) with 2 pairs of setae near its base, and a membranous median lobe with 2 lateral struts (ls).

Larva. Head without endocarina, with 5 ocelli. Antenna 3-segmented. Mandibles symmetrical, without mola and with lightly sclerotized retinaculum. Maxilla free almost to base of mentum, with a large articulating sclerite between stipes and submentum. Spiracle biforous. Ninth tergum bearing a concave pygidium surrounded by saw-like teeth; ninth sternum bearing a row of asperites.

Ciinae Leach

Adult. Antenna 8- to 10-segmented, with a 2- or 3-segmented club; club segments with at least 4 multi-pronged sensillae. Maxilla with a reduced and fixed lacinia and a 1-segmented galea. Pronotum with lateral margins never broadly crenulate or toothed; procoxal cavities without lateral extension, trochantin always concealed. Mesocoxal cavities with trochantins concealed. Metendosternite with median stalk very short and broad, so that arms may appear to arise independently. Hindwing with reduced anal region bearing a single vein. Trochanter of normal type, oblique but completely separating coxa and femur. Tibial spurs absent on all legs, apices of tibiae, especially protibiae, variously expanded and modified. Abdominal sternites free, III often with a median pubescent fovea in male. Aedeagus

with a small basal piece, without condyles, paramere variously modified at apex but without basal setae, and median lobe sclerotized and without lateral struts.

Larva. Head with endocarina, ocelli 5 or less. Antenna 2-segmented. Mandibles often asymmetrical, with or without mola and retinaculum. Maxillae free to about middle of mentum, without an articulating sclerite at its base. Spiracles annular. Ninth tergum variously modified, usually with two urogomphi; ninth sternum without asperites.

This subfamily includes all members of the family except *Sphindocis.*

DISCUSSION

The major justification for uniting *Sphindocis* and the Ciidae is the joint possession by the two groups of at least one feature — the distinctive laciniar lobe of the larval maxilla — which is certainly unique and derived. This particular type of structure is found in no other cucujoid beetle, and it is sufficiently complex and similar in the two groups to make convergence unlikely. There is no reason to believe that the cleft malar apex of the Zopheridae, Cephaloidae, and Synchroidae, or the various teeth, spines, or hooks (to which the word uncus is often applied) of *Anaspis,* the Oedemeridae, and various other Heteromera are homologous to this laciniar lobe. The loss of the mandibular mola and of the hypopharyngeal sclerome in the larva are also derived features, but it would be difficult to demonstrate their uniqueness. The lightly sclerotized and tooth-like "retinaculum" of the larval mandible appears to be unique in the Heteromera, but similar structures occur in a number of Clavicornia, suggesting that the character may be primitive. In the adult stage, the reduction of the ligula and the presence of an abdominal fovea in the male may both represent synapomophic conditions, but most other adult characters are shared by one or more Heteromera. The abdominal fovea is rare in this section of the Cucujoidea, although some Mycteridae and at least one mycetophagid have abdominal tufts or patches of hairs in the male. Foveae similar to those of ciids, however, do occur in certain Erotylidae among the Clavicornia (Delkeskamp, 1959).

The erection of a new subfamily for *Sphindocis* is based on numerous differences between this genus and all of the remaining ciids. In larval Ciinae, the antennae are reduced to two segments, an endocarina is present, the maxillary articulating area

is reduced to a narrow membrane, the spiracles are annular without a pair of contiguous air tubes, the ninth sternite lacks a row of asperites, and the gula and submentum are not fused, while in the adults of this subfamily, the antennae always have less than 11 segments, the club segments bear multi-pronged sensillae, the galea has only a single segment, the lacinia is not articulated, the anal region of the hindwing has only a single vein, the pro- and mesotrochantins are concealed, the trochanters are not heteromeroid, the tibial spurs are lacking, the abdominal sternites are free, and the median lobe of the aedeagus is sclerotized. Most of these characters are derived and several are obviously associated with reduction in size (hindwing, antennal segments of adult and larva, adult maxilla). The development of large and complex hygroreceptor sensillae on the antennal club probably represents an improvement in the ability to locate fungus sporophores, while the formation of a larval endocarina, reduction of the maxillary articulating area, the further enclosure of the pro- and mesocoxae, and the loss of tibial spurs may have been associated with the utilization of a tougher fungus substrate.

The relationships of the Ciidae to other heteromerous families are still somewhat obscure, and a detailed discussion must await a study now in progress on adult and larval Heteromera. Crowson (1966) suggested that the Ciidae, along with the Pterogeniidae, Tetratomidae, and Mycetophagidae, might be direct offshoots from a biphyllid-byturid type of heteromeran ancestor, and that the Pterogeniidae might represent the sister group of the Ciidae. I have agreed basically with Crowson's views (Lawrence, 1971), while allowing for the possibility that the ciids have evolved directly from a clavicorn ancestor, perhaps related to *Cryptophilus* or *Setariola* in the Languriidae.

The Pterogeniidae resemble ciids both as adults and larvae, but the similarities may be due to the fact that both groups inhabit the woodier fungi. Adult pterogeniids differ from the Ciidae in having filiform antennae, securiform maxillary palps, a 5–5–4 tarsal formula, internally closed procoxal cavities, and distinct lateral lobes on the aedeagus. The larvae of *Pterogenius* and *Histanocerus,* which are being described elsewhere, differ from those of ciids in having a characteristically curved epicranial stem, an extensive mandibular mola with transverse ridges, a well-developed and molar-like hypopharyngeal sclerome, and no laciniar lobe on the maxilla.

The row of asperites at the apex of the ninth sternite in the *Sphindocis* larva is found outside the group only in the genus

Prostomis, which has been placed in a separate family of uncertain affinities. The row of asperites in the larvae of Pythidae, Pyrochroidae, and Othniidae is always at the base of the ninth sternite and is apparently not homologous to that of *Sphindocis.* The Prostomidae differ from ciids in having closed front and middle coxal cavities in the adult and a simple mala, well-developed mola, and hypopharyngeal sclerome in the larva.

The Tetratomidae have also been considered as a possible sister group of the Ciidae, and certain characters of both adult and larva tend to support this hypothesis. Adults of the Tetratomidae (excluding *Mycetoma,* removed by Crowson, 1966, and Viedma, 1966) and the related Mycetophagidae are similar to ciids in having internally and externally open procoxal and laterally open mesocoxal cavities, while the pisenine tetratomid *Eupisenus elongatus* (LeConte) bears a striking superficial resemblance to *Sphindocis.* The procoxal cavity in all tetratomids has a distinct lateral extension that exposes the trochantin; in *Sphindocis* there is a slight extension of the cavity, while in the Ciinae it is absent. The hindwing of *Sphindocis* is similar to that of tetratomids in having a wedge cell and subcubital fleck and differs in having four rather than five anal veins, while the metendosternite is essentially of the tetratomid type with a reduced lamina. In the Ciinae, both the hindwing and the metendosternite have undergone extreme reduction and modification.

The male genitalia of the Tetratomidae are variable, and Miyatake (1960) has described and illustrated two major types: that of *Pisenus,* with the basal piece ventral and bearing two ventral accessory lobes in addition to the parameres, which are free; and that of the Tetratomini, with the basal piece dorsal and bearing only parameres, which are at least partly fused together. In the genus *Penthe* (Penthini) the genitalia are of the tetratomine type, but in *Eupisenus,* a distinctive type occurs with the basal piece ventral and the parameres fused into a single piece notched at the apex; moreover, this single paramere bears near the base two clusters of six or seven setae, which are in the same positions as the two pairs of setae in *Sphindocis.* The median lobe is also like that of *Sphindocis* in being membranous with lateral struts that meet at the apex.

The larvae of Tetratomidae are also quite variable, but they differ consistently from those of Ciidae in having lyre-shaped frontal arms and no laciniar lobe on the maxilla. The mandible of *Pisenus* resembles that of the Mycetophagidae in having a mola with transverse ridges grading into tubercles or asperites on

the ventral surface (Hayashi, 1971; 1972). In *Eupisenus,* the mola is simple and concave and is bordered by two rows of teeth that grade into tubercles both dorsally and ventrally. In the Tetratomini (Crowson, 1964) the mola is further reduced with only three or four teeth, while in *Penthe* there is no mola. The hypopharyngeal sclerome, which can often be correlated with molar development, is well developed and tooth-like in *Pisenus,* consists of a transverse band in *Eupisenus* and the tetratomines, and is barely sclerotized in *Penthe.* It would not be difficult to derive the simple mandible and unsclerotized hypopharynx of the Ciidae from a form like *Eupisenus,* and it is also possible that the "retinaculum" of the Ciidae represents a remnant of the molar teeth in tetratomids, rather than a carry-over of the clavicorn retinaculum.

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