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#### 4.18. Elateriformia *Incertae Sedis*

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**Introduction.** This Chapter includes several elateriform family groups or genera whose phylogenetic relationships are currently in doubt. *Podabrocephalus* Pic, *Neocrowsonia* Kistner & Abdel-Galil and *Cydistus*

Bourgeois are rare taxa which have never been included in a phylogenetic analysis, while Pterotinae, *Harmatelia* Walker, *Stenocladus* Fairmaire and Ototretinae were removed from Lampyridae based on a cladistic analysis of a morphological data set by Branham & Wenzel (2001, 2003). All recent molecular analyses support the previous position of Pterotinae, Ototretinae and *Stenocladus* in Lampyridae (Bocakova *et al.* 2007; Sagegami-Oba *et al.* 2007; Stanger-Hall *et al.* 2007).

#### Podabrocephalidae Pic, 1930

**Distribution.** The only known species, *Podabrocephalus sinuaticollis* Pic, was described from Wallardi, Travancore (Pic 1913) and specimens have been seen from other localities in southern India.

**Biology and Ecology.** Nothing is known about the ecology of these beetles, and they are known only by adult males specimens.

**Morphology, Adult males** (Fig. 4.18.1 A). Length 3.8–5.2 mm. Body about 3.05–3.15 times as long as wide and more or less parallel-sided. Upper surfaces shining, dark reddish-brown with yellow legs and antennae, clothed with fine hairs (Fig. 4.18.1).

Head about 1.5 times as long as wide, not declined, not abruptly constricted posteriorly. Occipital region very long, without transverse occipital ridge or stridulatory file. Frontal region strongly deflexed and vertical at apex only. Eyes strongly protuberant, entire, finely faceted, without interfacetal setae; postocular carina extending from eye to posterior edge of head. Antennal insertions concealed from above; subantennal groove

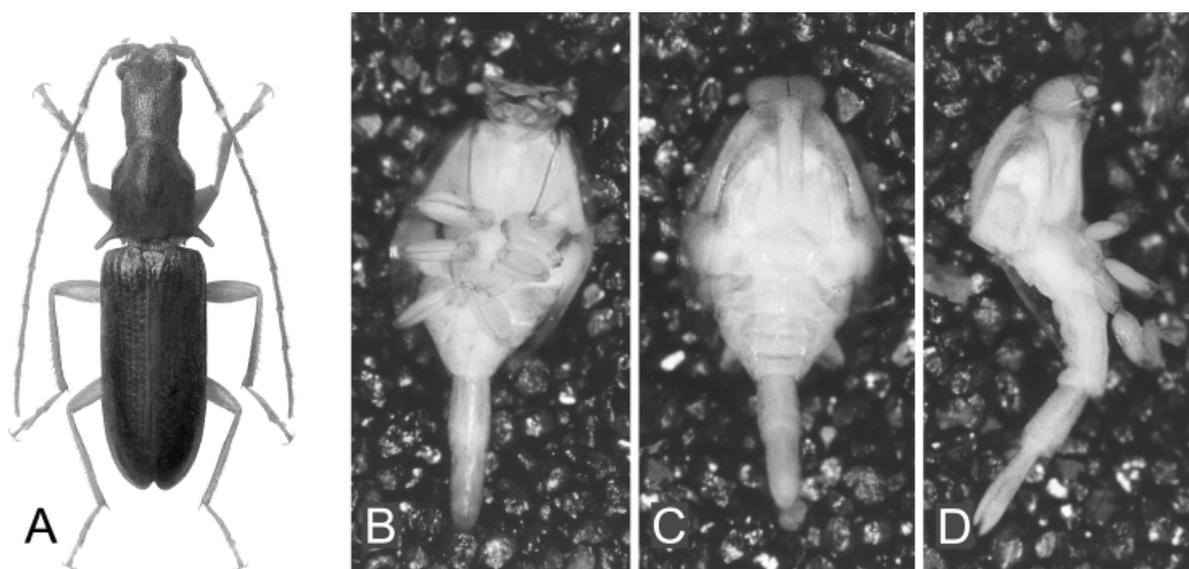


Fig. 4.18.1 A, *Podabrocephalus sinuaticollis* Pic, male, dorsal (© Ivo Jenis); B–D, *Neocrowsonia viatoricus* Kistner & Abdel-Galil, male: A, dorsal; B, lateral; C, ventral (© CSIRO Australia).

absent. Frontoclypeal suture absent; anterior edge of clypeus straight to convex. Labrum strongly transverse, subtruncate to slightly convex. Antennae 11-segmented, filiform, extending posteriorly beyond middle of elytra; clothed with long hairs. Mandibles very narrow and elongate, unidentate, strongly curved ventrally; mola and prostheca absent. Maxilla with single apical lobe; apical maxillary palpomere securiform. Ligula undivided; apical labial palpomere cylindrical to fusiform. Head ventrally with long paired subgenal ridges. Gular sutures narrowly separated. Corporotentorium narrow. Cervical sclerites present.

Pronotum about 0.9–0.95 times as long as wide and widest posteriorly; sides sinuate, not explanate; base not or slightly narrower than elytral bases; lateral pronotal carinae complete, simple, without raised margin; anterior angles not produced; posterior angles strongly produced posterolaterally, subacute; posterior edge distinctly sinuate; disc without paired basal impressions. Prosternum in front of coxae longer than shortest diameter of procoxal cavity, concave. Prosternal process incomplete, parallel-sided, strongly produced ventrally. Notosternal sutures complete. Procoxae projecting well below prosternum, without or with short concealed lateral extension. Trochantin concealed. Procoxal cavities slightly transverse, contiguous, externally broadly open, with narrow lateral extensions; internally open. Scutellar shield abruptly elevated, anteriorly simple, posteriorly acute. Elytra 2.2–2.3 times as long as wide and 2.2–2.8 times as long as pronotum; irregularly punctate, without scutellary striole; apices meeting at the suture; epipleuron complete. Mesoventrite partly or completely fused to mesanepisterna, which meet or are very narrowly separated at midline; anterior edge on same plane as metaventrite, without paired procoxal rests. Mesoventral cavity absent. Mesocoxae conical and projecting. Mesocoxal cavities narrowly separated and open laterally. Mesometaventral junction a complex fitting. Metaventrite with discrimen moderately to very long; postcoxal lines absent; exposed portion of metanepisternum very long and narrow. Metacoxae contiguous or narrowly separated, obliquely oriented, extending laterally to meet elytra or sides of body; plates weakly developed. Metendosternite with lateral arms short or absent; laminae absent; anterior process moderately long and anterior tendons moderately or very close together. Hind wing with moderately long apical field with three distinct sclerites, one longitudinal and two transverse; radial cell well developed, elongate with inner posterobasal angle narrowly acute; medial field with four free veins and no medial fleck; wedge cell absent; anal notch absent. Legs long and slender; tibial spurs distinct; tarsi 5-5-5 with penultimate tarsomere reduced and antepenultimate one strongly lobed beneath (pseudotetramerous); pretarsal claws toothed or bifid.

Abdomen with five ventrites, the first three of which are connate; ventrite 1 not much longer

than 2, without postcoxal lines. Intercostal process absent. Functional spiracles on abdominal segment VIII absent. Anterior edge of sternite VIII in male with median strut. Anterior edge of sternite IX in male without spiculum gastrale. Tergite IX truncate, X well developed and free. Aedeagus trilobate, symmetrical; anterior edge of phallobase without struts; parameres individually articulated to phallobase, not outwardly hooked; anterior edge of penis without struts.

**Phylogeny and Taxonomy.** Pic (1913) first compared this genus to members of the Cantharidae and later (1930) placed it in a new family close to Drilidae. Wittmer (1969) suggested that it might be a ptilodactylid on the advice of R. A. Crowson, who had examined a photo of the type. Such a relationship seems likely given the presence of pseudotetramerous tarsi, toothed pretarsal claws, a strongly oblique radial cell in the hind wing, three connate ventrites and no functional spiracles on segment VIII. However, the monophyly of Ptilodactylidae and its relationship to other groups, such as Cheloniidae and Cneoglossidae, are still disputed (Lawrence 2005). Lawrence & Newton (1995) placed the genus at the end of Elateriformia as *incertae sedis*.

### ***Neocrowsonia* Kistner & Abdel-Galil, 1986**

**Distribution.** *Neocrowsonia viatoricus* Kistner & Abdel-Galil, the only known species, occurs in Cape Province, South Africa.

**Biology and Ecology.** A number of specimens, including males and females, were collected in nests of the termite *Microhodotermes viator* (Latreille); larvae are unknown.

**Morphology, Adults** (Fig. 4.18.1B–D). Length 1.8–2.5 mm. Body about 1.9–2.15 times as long as wide, widest at junction of pronotum and elytra; convex dorsally and flattened ventrally; abdomen strongly tapering posteriorly. Upper surfaces shining, very lightly pigmented, white to cream-colored, with head yellowish-brown and legs yellow. Vestiture of short, sparsely distributed setae.

Head slightly wider than long, widest anteriorly, broadly rounded posteriorly; strongly declined; not abruptly constricted posteriorly to form neck. Occipital region with long median endocarina; without transverse occipital ridge. Eyes absent. Antennal insertions located in circular fossae concealed from above by sharp carina extending across entire frontoclypeal region, with mesal emargination flanked by pair of sharp teeth; subantennal grooves absent. Frontoclypeal suture absent. Labrum strongly transverse, subtruncate to slightly convex, not visible from above, apparently fused to clypeus. Antennae very short, apparently

8-segmented, and strongly clavate, with many sensilla on apex of terminal antennomere. Mandibles short and broad, strongly curved mesally, unidentate, with subapical tooth on incisor edge, with complete internal perforation; mola and prosthema absent. Maxilla with slender galea and subtriangular lacinia; palp 4-segmented. Labial palp 2-segmented. Gula short and broad. Corporotentorium absent. Cervical sclerites present.

Pronotum about 0.62–0.67 times as long as wide, widest posteriorly; sides straight; base not narrower than elytral bases; lateral carinae complete, simple, without raised margin; anterior angles not produced; posterior angles subacute; posterior edge more or less straight; disc with median raised area beginning near anterior end and more prominent posteriorly forming hook-like prominence. Prosternum in front of coxae much longer than shortest diameter of procoxal cavity, slightly convex, with short chin piece. Prosternal process parallel-sided, apically rounded. Notosternal sutures complete, open anteriorly, forming small antennal cavities. Procoxae not projecting, without concealed lateral extensions. Trochantin concealed. Procoxal cavities more or less circular, narrowly separated, externally broadly open; internally open. Scutellar shield concealed by posterior edge of pronotum. Elytra 0.65–0.75 times as long as combined width and 1.05–1.15 times as long as pronotum; more or less impunctate; apices independently rounded and separated by broad gap, exposing much of abdomen; epipleuron incomplete. Mesoventrite partly or completely fused to mesanepisterna; anterior edge on same plane as metaventrite, without paired procoxal rests or mesoventral cavity. Mesocoxae not projecting. Mesocoxal cavities widely separated, open laterally. Mesometaventral junction absent or weakly indicated due to fusion of mesoventrite and metaventrite. Metaventrite short, without discrimen or postcoxal lines; exposed portion of metanepisternum not clearly delimited. Metacoxae contiguous, obliquely oriented, extending laterally to meet elytra or sides of body; plates weakly developed. Metendosternite with lateral arms moderately long; laminae and anterior process absent; anterior tendons on lateral arms or not apparent. Hind wings absent. Legs moderately well developed; trochterofemoral joint oblique; tibiae slightly wider at about middle; tibial spurs absent; tarsi 5-5-5 with long divided, membranous lobed beneath first four tarsomeres; pretarsal claws simple.

Abdomen with four ventrites, the first belonging to segments I–VI, which are completely fused ventrally and apparently fused to metathorax, but more or less distinct in dorsal view. Segment VII short and cylindrical. VIII more than twice as long and subcylindrical; slightly widened apically, with functional spiracles. Part of genital capsule (segments IX and X) exposed. Anterior edge of segment IX in male more or less rounded. Tergite IX truncate. X well developed and free. Aedeagus

trilobate, symmetrical; phallobase short and broad; parameres partly fused together forming tube, but apically free and articulated to phallobase, not outwardly hooked; anterior edge of penis with short struts. Ovipositor telescopic with long bacculi; coxites setose and styli not apparent.

#### Larvae unknown.

**Phylogeny and Taxonomy.** Kistner & Abdel-Galil (1986) placed *N. viatorica* in the family Throscidae based partly on the presence of “membranous adhesive lobes on the first four tarsal segments of each leg” and “grooves for the reception of the antennae, although these are shorter than in free-living Throscidae”. Although the genus was included in the subfamily Throscinae (Triaxagidae of Crowson 1967), Lawrence & Newton (1995) noted that the long, divided, membranous, lamellae on tarsomeres 1–4 are characteristic of lissomine Elateridae, a group formerly included in Throscidae. The placement of this peculiar beetle is still questionable.

#### Cydistinae Paulus, 1972

**Distribution.** The genus *Cydistus* Bourgeois (1908) contains six species from Asia Minor and Central Asia.

**Biology and Ecology.** Natural history and immature stages are unknown.

**Morphology, Adult males** (Fig. 4.18.2). Length 7.5–9 mm. Body about 4.6–5 times as long as wide; flattened, sides more or less parallel. Upper



Fig. 4.18.2. *Cydistus lurcheri* Bourgeois, male, dorsal, with left hind wing unfolded; line = 2.5 mm (© M. Branham).

surfaces clothed with distinct hairs (Fig. 4.18.2). Head not declined, not abruptly constricted posteriorly; posterior edge weakly bisinuate. Occipital region without transverse ridge or stridulatory file. Frontoclypeal region moderately strongly declined anteriorly. Eyes strongly protuberant, entire, finely faceted, without interfacetal setae. Antennal insertions exposed, separated by about twice the diameter of one socket; subantennal groove absent. Frontoclypeal suture absent; anterior edge of clypeus convex. Labrum free, membranous and strongly transverse, with deeply emarginate anterior edge. Antennae 12-segmented, bipinnate from antennomeres 4–11; each ramus slender, subcircular in cross-section, apically acute and arising basally; antennomere 12 laterally compressed and narrowly rounded at apex. Mandibles narrow and elongate, with slightly widened base; strongly, evenly curved mesally; sharply unidentate; mola and prostheca absent. Maxilla with galea and lacinia short; galea broadly rounded; lacinia narrowly rounded, without uncus, both densely setose; apical maxillary palpomere securiform. Ligula membranous, moderately emarginate; apical labial palpomere fusiform. Gular sutures narrowly separated; gula longer than wide. Corpotentorium absent. Cervical sclerites present.

Pronotum about 1–1.2 times as long as wide, widest posteriorly; sides almost straight, slightly sinuate; base not or slightly narrower than elytral bases; lateral carinae incomplete, simple, without raised margin; anterior angles more or less right, not produced; posterior angles broadly rounded; mesal lobe formed by strongly produced posterior edge slightly emarginate, without raised margin; disc without paired basal impressions. Prosternum in front of coxae distinctly longer than shortest diameter of procoxal cavity, flat to moderately convex; anterior edge produced to form chin piece. Prosternal process absent or very short and broadly rounded. Notosternal sutures complete. Procoxae projecting well below prosternum, without concealed lateral extension. Trochantins exposed, setose. Procoxal cavities strongly transverse, contiguous, externally broadly open, without narrow lateral extensions; internally open. Scutellar shield not abruptly elevated, anteriorly simple, posteriorly broadly rounded. Elytra about 1.6–1.75 times as long as wide and 1.75–1.9 times as long as pronotum; irregularly punctate, without scutellary striole; apices independently rounded and separated by gap, exposing three or more tergites; epipleuron incomplete. Mesoventrite separated by complete sutures from mesanepisterna, which are distinctly separated at midline; anterior edge on same plane as metaventrite, without paired procoxal rests. Mesoventral cavity absent. Mesocoxae conical and projecting. Mesocoxal cavities weakly developed, contiguous, moderately oblique, open laterally (closed by mesanepisternum and mesepimeron). Mesometaventral junction absent. Metaventrite convex, with very short discrimen; postcoxal

lines absent; exposed portion of metanepisternum very long and narrow. Metacoxae narrowly separated, strongly oblique, extending laterally to meet elytra; plates weakly developed. Metendosternite with lateral arms very short; laminae absent; anterior process long and anterior tendons very close together. Hind wing about 2.3 times as long as wide; apical field very short, with three slender sclerotisations forming sigmoid figure; radial cell about 0.25 times wing length and 4.5 times as long as wide, its inner posterobasal angle obtuse; r3 short and slightly oblique; RP long, extending to basal fourth; R-M loop narrow and acute; medial spur slightly curved and extending to margin; medial field with five free veins; MP<sub>3+4</sub> with basal cross-vein but no spur; CuA<sub>1</sub> joining MP<sub>4</sub> near its base; wedge cell absent; anal lobe well developed; AP with 2 distinct branches; anal notch absent. Femoral attachment of mid trochanter strongly oblique with base of femur separate from coxa. Legs moderately long and slender; tibial spurs absent or inconspicuous; tarsi 5-5-5; tarsomeres without ventral lobes; pretarsal claws simple.

Abdomen with eight free ventrites; ventrite 1 not much longer than 2, without postcoxal lines. Intercoxal process absent. Functional spiracles on abdominal segment VIII present. Anterior edge of sternite VIII in male without median strut. Anterior edge of sternite IX in male without spiculum gastrale. Tergite IX slightly to moderately emarginate. Tergite X well developed and free. Aedeagus trilobate, symmetrical; anterior edge of phallobase without struts. Parameres individually articulated to phallobase, not outwardly hooked. Penis divided into dorsal and ventral lobes; anterior edge without struts.

**Phylogeny and Taxonomy.** *Cydistus* was placed by its describer (Bourgeois 1885) near the Drilidae and is included in that family in most catalogues, including that of Wittmer (1944). Crowson (1972) moved *Cydistus* to the family Phengodidae, along with several other Old World taxa now included in Rhagophthalmidae, based mainly on the 12-segmented antennae and shortened elytra. Paulus (1972) proposed a subfamily Cydistinae within the family Karumiidae, which Crowson (1971) later moved from Cantharoidea to Dascilloidea. Lawrence (2005) excluded it from Karumiinae based on the simple tibial spurs, elongate radial cell and absence of a tentorium. One feature supporting the inclusion of *Cydistus* in Phengodidae is the fact that antennomeres 2 and 3 are both short and simple, and the paired rami arise from the bases of antennomeres 4–11. Within the Elateroidea, biramose, 12-segmented antennae with rami beginning on 4 occur elsewhere only in the elaterid genus *Pityobius* LeConte. In spite of similarities to Phengodidae, *Cydistus* differs from all members of that family in having 1) the prosternum extending well in front of the procoxae, 2) AP<sub>3+4</sub> forked in the hind wing, and 3) the penis divided into dorsal and ventral

lobes. All three of these features also occur in Das-cillidae. It also differs from all phengodids except *Cenophengus* LeConte in having long, well separated gular sutures. The placement of this genus even to superfamily remains questionable.

### Pterotinae LeConte, 1861

**Distribution.** The genus *Pterotus* LeConte includes two species occurring in western North America. *P. obscuripennis* LeConte occurs from western Washington and Oregon to northern Baja California, while *P. curticornis* Chemsak is known from south-eastern California (Chemsak 1987).

**Biology and Ecology.** Larvae of *Pterotus obscuripennis* occur in moist forest habitats on the forest floor and normally prey on slugs (Mollusca: Gastropoda), including species of *Limax* and *Prophysaon*, but may also feed on small snails. The larvae pierce the prey with their perforate mandibles and inject a fluid thought to contain digestive enzymes and a neurotoxin. Larvae are luminescent, producing a yellow-green light from a pair of compact, spherical light organs located ventrolaterally on segment VII. Larvae may glow at various times (e.g., while feeding), but the strongest light is produced when the larva is disturbed. Similar luminous organs are located on the pupa and larviform female. The winged males apparently lack light organs. [Dean 1979.]

**Morphology, Adult males.** (Fig. 4.18.3 A). Length 9.5–12 mm. Body about 3.05–3.25 times as long as wide; more or less parallel-sided or slightly wider posteriorly; slightly flattened. Densely clothed with short, subdecumbent hairs (Fig. 4.18.3 A).

Head not or slightly declined, not abruptly constricted posteriorly; posterior edge deeply biemarginate. Occipital region without transverse ridge or stridulatory file. Frontoclypeal region moderately declined at apex. Eyes strongly protuberant, entire, finely faceted, without interfacetal setae. Antennal insertions exposed from above; slightly raised and separated by about the diameter of one socket; subantennal grooves absent. Frontoclypeal suture absent; anterior edge of clypeus slightly concave. Labrum strongly transverse; apex slightly convex. Antennae 11-segmented, uniflabellate, with long, slender, flattened rami arising from bases of antennomeres 3–10. Mandible very narrow and elongate; strongly, evenly curved and unidentate; mola and prostheca absent. Maxilla with broad, setose galea; lacinia highly reduced, without uncus; apical maxillary palpomere fusiform. Ligula simple, setose; apical labial palpomere fusiform. Gular sutures narrowly separated. Corpotentorium absent. Cervical sclerites present.

Pronotum about 0.6–0.65 times as long as wide, widest posteriorly; sides more or less straight,



Fig. 4.18.3. *Pterotus obscuripennis* LeConte: A, male, dorsal, line = 5 mm; B, larva, lateral, line = 5 mm; C, larval head & thorax, lateral. (© M. Branham).

somewhat explanate; base not or slightly narrower than elytral bases; lateral carinae complete, simple, without a raised margin, more or less continuous with anterior edge; anterior angles not produced; posterior angles right or slightly acute; posterior edge weakly bisinuate; disc with small paired basal impressions and vague median longitudinal groove. Prosternum front of coxae shorter than shortest diameter of procoxal cavity, flat to moderately convex. Prosternal process absent. Notosternal sutures complete. Procoxae projecting well below prosternum, without concealed lateral extensions. Trochantins exposed. Procoxal cavities strongly transverse, contiguous, externally broadly open, without narrow lateral extensions; internally open. Scutellar shield not abruptly elevated, anteriorly simple, posteriorly truncate. Elytra about 2.6–2.8 times as long as wide and 6.15–6.35 times as long as pronotum; irregularly punctate without scutellar striole; with several vaguely indicated longitudinal carinae; apices independently rounded, separated by narrow gap and concealing all abdominal tergites; epipleuron narrow and incomplete. Mesoventrite separated by complete sutures from mesanepisterna, which are distinctly separated at midline; anterior edge on same plane as metaventrite, without paired procoxal rests. Mesoventral cavity absent. Mesocoxae conical and projecting, with exposed, glabrous trochantins. Mesocoxal cavities contiguous, moderately to strongly oblique; open laterally (closed by both mesanepisternum and mesepimeron). Mesometaventral junction absent. Metaventrite moderately strongly convex, with long discrimen; sides straight; postcoxal lines absent; exposed portion of metanepisternum long and narrow. Metacoxae contiguous or narrowly separated, obliquely oriented, extending laterally to meet elytra; plates complete but very narrow. Metendosternite with lateral arms short; laminae absent; anterior process short and anterior tendons close together. Hind wing about 2.33 times as long as wide; apical field about 0.15 times total wing length, with weak anterior and posterior oblique sclerites; radial cell large, about 0.25 times wing length with inner posterobasal angle more or less right; cross-vein r3 short and oblique; RP extending to basal fourth; medial field with five free veins; MP<sub>3+4</sub> with basal cross-vein and spur; CuA<sub>1</sub> joining MP<sub>4</sub> near its base; wedge cell absent; anal lobe well developed, AP undivided; anal notch absent. Legs moderately long and slender; femoral attachment strongly oblique with base of femur separate from coxa; tibial spurs well developed; tarsi 5-5-5; ventral lobe of penultimate tarsomere present, slightly emarginate at apex; pretarsal claws simple.

Abdomen with eight free ventrites; ventrite 1 not much longer than 2, without postcoxal lines. Intercoxal process absent. Functional spiracles on abdominal segment VIII present. Anterior edge of sternite VIII in male without median strut. Anterior edge of sternite IX in male without spiculum

gastrale. Tergite IX deeply emarginate. Tergite X well developed and free. Aedeagus trilobate, symmetrical; anterior edge of phallobase without struts; parameres individually articulated to phallobase, not outwardly hooked; anterior edge of penis without struts.

**Morphology, Larviform Females.** Length 25–35 mm. Body larviform, without elytra or hindwings. Brown in color, moderately densely clothed with short hairs.

Head capsule small, transverse, capable of complete retraction within prothorax. Heavily pigmented, posteriorly trisinate. Epicranial stem moderately long, with underlying endocarina. Frontal arms V-shaped. Antennal insertions widely separated and barely exposed from above. Eyes small but multifaceted. Labrum fused to head capsule. Antennae 7-segmented; antennomeres 1 and 2 together almost as long as remaining ones combined; antennomere 7 reduced and subequal in length to sensorium. Mandibles strongly curved, falciform, with moderately broad base and narrowly acute apex. Ventral mouthparts strongly retracted; maxillary articulating area absent. Cardines obliquely longitudinal; stipes elongate; mala 1-segmented, articulated, broadly rounded and densely setose; palp 4-segmented, apical palpomere conical. Labium consisting of prementum and postmentum, the latter more or less connate with maxillae; ligula absent; labial palps short and 2-segmented with apical palpomere conical. Gular region short and lightly sclerotised.

Thoracic segments subequal in length. Prothoracic presternum, large, triangular, undivided. Legs moderately long, with projecting coxae, short triangular trochanter, elongate femur and tibia, 4-segmented tarsus and pretarsus consisting of 2 claws.

Abdomen moderately broad. Terga not extending laterally beyond sterna. Tergum IX about half as long as VIII, not extending onto ventral surface. Light organs on segments VII and VIII. Spiracles located near dorsal edges of laterotergites. Ovipositor short; undivided coxite narrowed apically, with short, cylindrical, terminal stylus.

**Morphology, Larvae.** (Fig. 4.18.3 B, C). Body elongate and more or less parallel-sided. Dorsal and ventral surfaces more or less heavily pigmented except on segments VII and VIII, finely tuberculate, shiny and densely clothed with short hairs (Fig. 4.18.3 B). Head small, prognathous, retractable; posterior edge of head capsule trisinate with sclerotised rim: Epicranial stem very short; frontal arms V-shaped, contiguous at base, with paired endocarinae beneath them. With one moderately large stemma on each side. Frontoclypeal suture absent. Labrum completely fused to head capsule. Antennae 3-segmented, moderately long; with palpiform sensorium as long as or longer than minute

antennomere 3. Mandibles symmetrical, unidentate, narrow and falcate, with internal perforation; mesal edge with sclerotized retinaculum and brush of hairs extending from retinaculum to base. Ventral mouthparts strongly retracted; maxillary articulating area absent. Cardo externally divided and longitudinally oriented; stipes longer than wide; galea, articulated and 2-segmented; lacinia reduced to short, broad lobe; upper surface of maxilla densely clothed with hairs; palp 4-segmented, palpomere 1 longer than remaining ones combined and palpomere 4 conical. Labium consisting of prementum and postmentum, the latter completely or almost completely connate with maxillae; ligula absent; labial palps 2-segmented, separated by more than width of first palpomere. Hypopharyngeal sclerome absent. Subparallel hypostomal rods extending to posterior edge of head; ventral epicranial ridges absent. Gular sutures separate; gula wider than long.

Prothorax not longer than meso- and metathorax combined. Thoracic terga subequal in length, without patches or rows of asperities or carinae. Prosternum without armature. Legs well developed, 5-segmented; pretarsus claw-like with two setae lying side by side or obliquely situated; mesocoxae separated by one to two basal coxal diameters (Fig. 4.18.3 C).

Abdomen less than twice as long as thorax. Abdominal terga not extending laterally beyond edges of sterna. Terga and sterna without patches or rows of asperities. Paired luminous organs present ventro-laterally on segment VII, one per side. Abdominal segment IX excluding appendages shorter than segment VIII; M not or only slightly extending onto ventral surface, not forming articulated plate; without paired urogomphi; sternum IX well developed, simple, not enclosed by sternum VIII. Segment X with several asperated, tubular, protrusible holdfast organs; anal region posteriorly oriented. Spiracles biforous, not placed at ends of spiracular tubes, located at the upper edges of laterotergites; those on VIII the same size as others on abdomen, facing laterally. [Dean 1979.]

**Phylogeny and Taxonomy.** *Pterotus* was traditionally placed in a tribe Pterotini of the family Phengodidae, following LeConte (1881). However McDermott (1964–1966) moved the tribe to Lampyridae and added the Old World genus *Harmatelia* Walker (see below). According to McDermott, this group was somewhat intermediate between Lampyridae and Phengodidae. Crowson (1972) retained Pterotinae excluding *Harmatelia*. In cladograms produced by Branham & Wenzel (2001, 2003) and based on morphological data, *Pterotus* was placed outside Lampyridae at the base of a clade containing Lycidae, Cantharidae, Omethidae, Telegeusidae and Phengodidae, while in those of Stanger-Hall *et al.* (2007) based on sequence data from nuclear and mitochondrial genes, the genus formed a monophyletic group with *Rhagophthalmus*

Motschulsky within a lampyrid clade containing *Pristolytus* Gorham and several genera of Orotretinae and Luciolinae.

### ***Harmatelia* Walker, 1858**

**Distribution.** Three species of *Harmatelia* are known from Sri Lanka.

**Biology and Ecology.** Green (1912) observed luminescence in the male of *Harmatelia bilineata* Walker, which was produced by a series of small spots, two on the mesothorax and eight on the abdomen, apparently associated with the spiracles. Immature stages are unknown.

**Morphology, Adult males.** (Fig. 4.18.4). Length 6–7 mm. Body 2.9–3.0 times as long as wide more or less parallel-sided and slightly flattened. Surface densely clothed with decumbent hairs.

Head moderately to strongly declined, transverse, not abruptly constricted posteriorly. Occipital region without transverse ridge or stridulatory file; posterior edge biemarginate. Frontal region weakly declined at apex. Eyes moderately small, slightly protuberant, entire, finely faceted, without interfacetal setae. Antennal insertions slightly

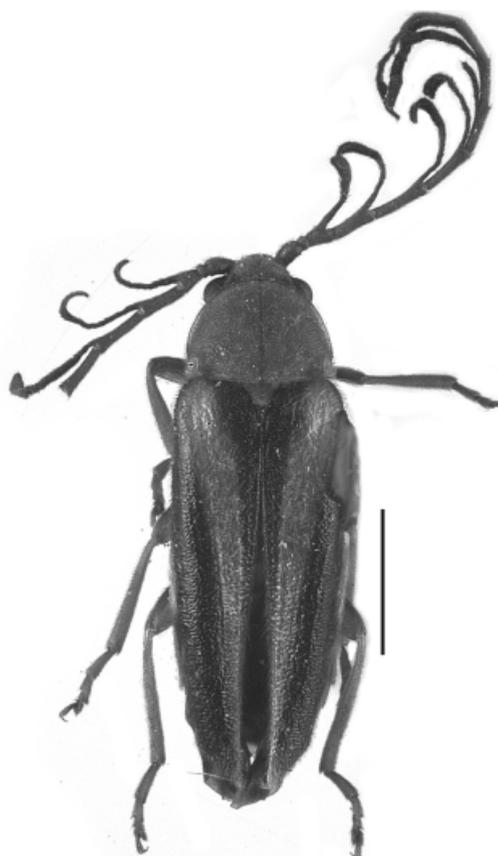


Fig. 4.18.4. *Harmatelia bilineata* Walker, male, dorsal, line = 2.5 mm (© M. Branham).

exposed from above; separated by slightly more than the diameter of one; subantennal grooves absent. Frontoclypeal suture absent; anterior edge of clypeus slightly concave. Labrum free and strongly transverse with apex weakly concave. Antennae 11-segmented, uniflabellate, with long, flattened rami arising subapically from antennomeres 3 to 10 (Fig. 4.18.4). Mandible very narrow and elongate, strongly but gradually curved mesally, with sharply acute apex; mesal surface of mandibular base simple; mola and prostheca absent. Maxilla with acuminate, densely setose galea and lacinia, the latter without uncus; apical maxillary palpomere fusiform. Ligula densely setose; apical labial palpomere fusiform. Subgenal ridges absent. Gular sutures well separated. Corpotorium absent. Cervical sclerites present.

Pronotum 0.7 times as long as wide, with maximum width at middle; sides curved anteriorly, sinuate posteriorly; pronotal base slightly narrower than elytral bases, lateral carinae complete, simple, slightly raised, continuous with anterior edge; anterior angles absent; posterior angles laterally produced and right or slightly acute; posterior edge weakly rounded, distinctly margined, with small notch on each side just mesad of posterior angles; disc with median longitudinal furrow, small paired basal impressions and a short, weak carina on each posterior angle. Prosternum in front of coxae shorter than shortest diameter of procoxal cavity; flat or slightly convex. Prosternal process absent. Notosternal sutures complete. Procoxae projecting well below prosternum, without concealed lateral extensions. Trochantins exposed, slender, glabrous. Procoxal cavities strongly transverse, broadly open externally, without narrow lateral extensions; open internally. Scutellar shield not abruptly elevated; anteriorly simple, posteriorly truncate. Elytra about 2.3–2.4 times as long as wide and 3.8–3.9 times as long as pronotum; irregularly punctate, without scutellary striole, with weak longitudinal carinae; apices almost meeting at the suture but independently rounded separated by narrow gap; epipleuron absent or incomplete. Mesoventrite separated by complete sutures from mesanepisterna, which are distinctly separated at midline; anterior edge on same plane as metaventrite, without paired procoxal rests. Mesoventral cavity absent. Mesocoxae conical and projecting, with exposed trochantins. Mesocoxal cavities at middle contiguous, strongly oblique, open laterally; partly closed by both mesanepisternum and mesepimeron. Mesometaventral junction absent. Metaventrite convex, with straight sides and moderately short disc; postcoxal lines absent; exposed portion of metanepisternum moderately elongate. Metacoxae contiguous, slightly oblique, extending laterally to meet elytra; plates weakly developed. Metendosternite with lateral arms short; laminae absent; anterior process moderately long and anterior tendons moderately close together. Hind wing relatively short and broad (about 2.25 times as long

as wide), with very short apical field; radial cell narrowly elongate with broadly obtuse and more or less rounded inner posterobasal angle; cross-vein r3 absent; RP long, extending to basal fourth; medial field with five free veins and no medial fleck; wedge cell well developed, 1.5 times as long and wide and apically subtruncate; anal lobe well developed; AP undivided. Legs moderately long and slender; tibial spurs absent; femoral attachment of mid trochanter strongly oblique with base of femur separate from coxa; tarsi 5-5-5; penultimate tarsomere short, with ventral lobe which is deeply emarginate at apex; pretarsal claws simple.

Abdomen with eight free ventrites. Ventrite 1 not much longer than 2, without postcoxal lines. Abdominal process absent. Functional spiracles on abdominal segment VIII present. Spiracles located on lateral edges of sternites. Anterior edge of sternite VIII in male without median strut. Anterior edge of sternite IX in male without spiculum gastrale. Tergite IX slightly emarginate. Tergite X well developed and free. Aedeagus trilobate, short, broad and symmetrical; anterior edge of phallobase without struts; parameres individually articulated to phallobase but partly fused together and to base of penis; not outwardly hooked; anterior edge of penis with short, paired struts.

**Phylogeny and Taxonomy.** *Harmatelia* is one of a number of genera included in Drilidae by Wittmer (1944). McDermott (1964) moved it to Lampyridae within the subfamily Pterotinae. It was later moved to the lampyrid subfamily Otoretinae by Crowson (1972). In a cladogram produced by Branham & Wenzel (2001, 2003), the genus was placed at the base of a clade containing all cantharoid groups except Plastoceridae, Drilidae and Omalidae. Branham & Wenzel (2001) removed it from Lampyridae and moved it to Elaterioidea “*incertae sedis*” status.

### ***Stenocladus* Fairmaire, 1878**

**Distribution.** The genus *Stenocladus* is distributed throughout the Oriental region from the Ryukyu Islands of southwestern Japan, through China and Southeast Asia to Nepal, India and Sri Lanka. [Olivier 1910; Wittmer 1944; Ohba *et al.* 1996, 1997; Nakane 1997; Kawashima 1999; Kawashima & Satou 2004].

**Biology and Ecology.** Adult males of *Stenocladus* are primarily diurnal but may be attracted to lights at night, while adult females are probably nocturnal and rarely observed. *Stenocladus* larvae are completely nocturnal and mainly found on the ground in the forest litter at night. They emit a strong greenish continuous light, and feed mainly on earthworms (rarely terrestrial snails). Adult males of Japanese species have a pair of spot-like

luminescent organs at the sides of abdominal segment VII, while females emit a weak but continuous luminescence from most of the body, but also have a pair of spot-like luminescent organs at the sides of abdominal segment VII. [Ohba *et al.* 1996, 1997; Kawashima & Satou 2004].

**Morphology, Adult males** (Fig. 4.18.5 A, B). Length 5.8–10 mm. Body relatively long and slender; about 2.7–3.0 times as long as wide, subparallel-sided and slightly flattened. Weakly sclerotized. Bicolored or sometimes unicolorous. Upper surfaces densely clothed with short inclined hairs.

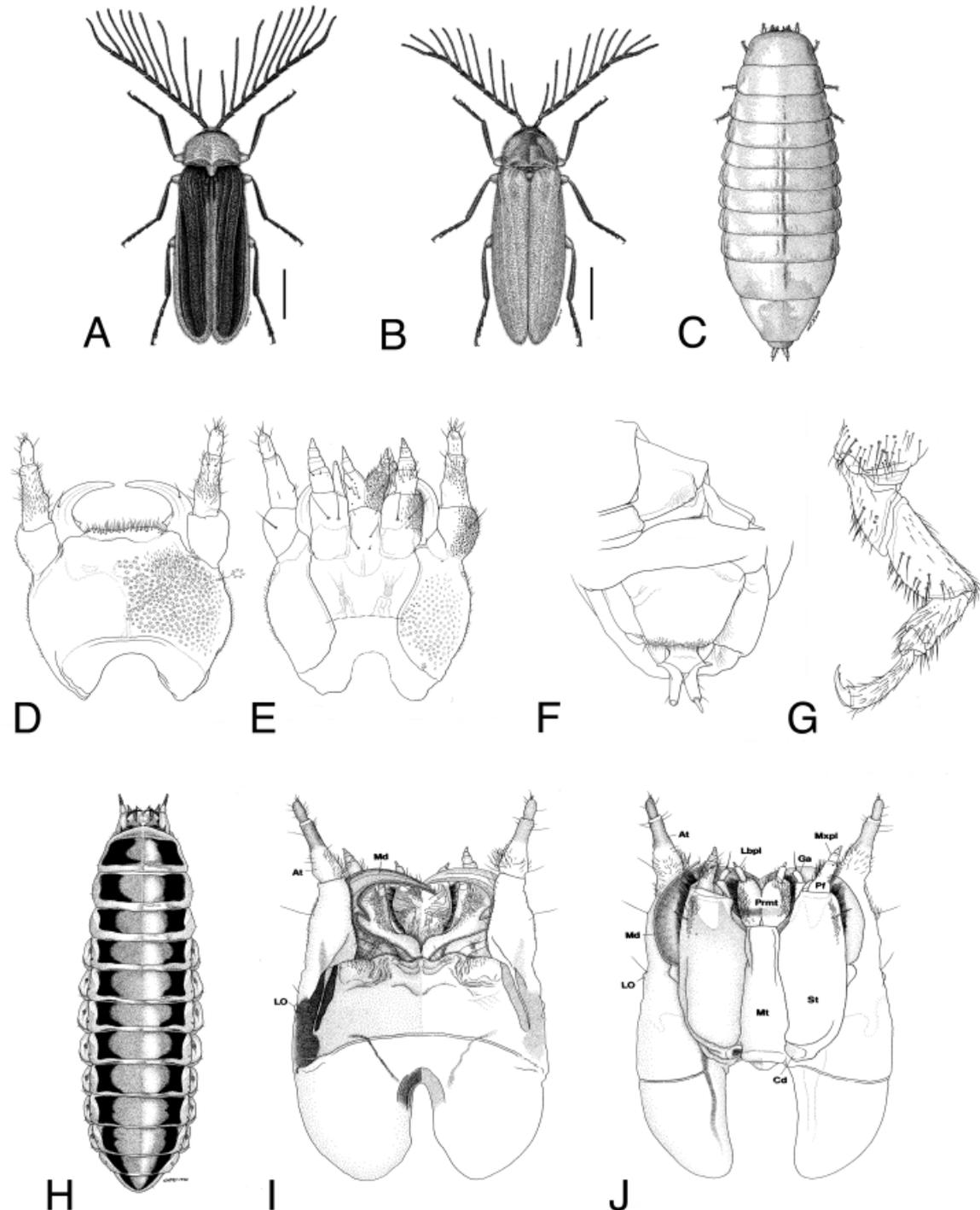


Fig. 4.18.5. *Stenocladus* spp.: A, *S. yoshimasai* Kawashima, male, dorsal, line = 2.5 mm; B, *S. flavipennis* Kawashima, male, dorsal, line = 2.5 mm; C, *S. flavipennis*, female, dorsal (© I. Kawashima); D–G, *S. flavipennis*, female: D, head, dorsal, line = 0.5 mm; E, head, ventral, line = 0.5 mm; F, abdominal apex, lateral & ventral, line = 0.5 mm; G, hind leg, line = 0.25 mm. H–J, *S. shirakii* Nakane, larva: H, habitus, dorsal; I, head, dorsal; J, head, ventral. (A, B from Kawashima 1999, © I. Kawashima; D–G from Kawashima & Satou 2004, © I. Kawashima; H–J from Ohba *et al.* 1996, © I. Kawashima).

Head relatively large and weakly declined; not completely retracted into prothorax; slightly transverse, depressed above. Rather coarsely punctate on dorsal surface. Occipital region without any grooves or sutures. Eyes large, prominent, entire; separated from each other by 1 to 1.5 diameters in dorsal view, and slightly separated from mandibular bases. Antennal sockets located on both sides of declined frontal area and between eyes, not or barely visible from above; only a little separated from each other, distinctly oriented anteriorly. Clypeal region weakly deflexed or not; front-clypeal suture absent; anterior margin of clypeus almost straight or shallowly concave or emarginate. Labrum small, free, somewhat membranous, transverse or subquadrate; anterior edge almost straight. Antennae 11-segmented, long and slender, extending beyond middle of elytra; scape short, subcylindrical or clavate; pedicel highly reduced, almost as long as wide; antennomeres 3-10 pectinate or flabellate; each ramus arising from base of stem, about 2 to 6 times as long as stem and spatulate; antennomere 11 simple, spatulate, distinctly longer than all other segments (Fig. 4.18.5 A, B). Mandibles small, slender and gradually curved with acute apex; incisor edge simple; mola and prosthema absent. Maxilla with cardo minute and transverse; stipes longer than wide; galea 1-segmented, conical; lacinia reduced to flattened plate; apical palpomere conical or fusiform, with acuminate apex. Ligula membranous; apical labial palpomere conical with acute apex. Gular sutures relatively or well separated from each other, but gula more or less membranous. Cervical sclerites present.

Pronotum about 0.55–0.65 times as long as wide; widest posteriorly; sides curved anteriorly; lateral carinae complete, slightly raised, continuous along anterior edge, so that pronotum appears semicircular in dorsal view; anterior angles absent; posterior angles more or less acute and projecting laterally; posterior edge weakly trisinate, narrowly margined; disc with pair of small basal pits and sometimes with weak median furrow. Prosternum in front of coxae flat and shorter than shortest diameter of procoxal cavity. Prosternal process absent. Procoxae projecting below prosternum, without internal extensions. Trochantins exposed, slender, glabrous. Procoxal cavities strongly transverse, without narrow lateral extensions; broadly open externally; open internally. Scutellar shield not abruptly elevated; anteriorly simple, posteriorly broadly rounded. Elytra 2.2–2.5 times as long as wide and 5–5.7 times as long as pronotum; irregularly punctate and usually more or less rugulose, each with 4 weak longitudinal costae; apices independently rounded, separated by small gap; epipleuron incomplete. Mesoventrite separated by complete sutures from mesanepisterna, which are well separated at midline; anterior edge on same plane as metaventrite, without procoxal rests. Mesocoxae conical and projecting, with exposed, slender trochantins. Mesocoxal cavities contiguous;

open laterally; partly closed by mesanepisternum and mesepimeron. Metaventrite convex, with straight sides and short, vaguely indicated discimen; exposed portion of metanepisternum moderately long and narrow. Metacoxae contiguous, obliquely oriented, extending laterally to meet elytra. Hind wing about twice as long as wide; apical field very short, with vaguely indicated anterior and posterior oblique linear sclerites; radial cell about 0.3 times total wing length and almost 10 times as long as wide; base very short and weakly sclerotized, with inner posterobasal angle obtuse; cross-vein r3 absent; r4 long, slightly oblique and arising from about middle of cell; RP long, extending to basal fourth; R-M loop moderately broad; medial spur almost straight, extending to wing margin where there is a slight embayment; medial field with four free veins; MP<sub>3+4</sub> with curved basal cross-vein; wedge cell absent; cross-vein between Cu and MP<sub>4</sub> absent; AA<sub>4</sub> absent; anal lobe well developed; AP undivided; anal notch absent. Legs moderately long and slender; trochanterofemoral joint strongly oblique with base of femur separate from coxa; tibial spurs absent; tarsi 5-5-5; preapical tarsomere lobed beneath; pretarsal claws simple; empodium not visible in most specimens.

Abdomen with eight free ventrites corresponding to sternites II–IX: Ventrite 1 slightly shorter than 2, without postcoxal lines. Intercostal process absent. Last four ventrites gradually narrowing and terminal one (sternite IX) very small and broadly rounded or truncate. A pair of spot-like luminous organs present on segment VII, but not visible externally. Functional spiracles on abdominal segment VIII present; spiracles located in pleural membrane at lateral edges of sternites. Anterior edge of sternite VIII in male without median strut. Anterior edge of sternite IX in male without spiculum gastrale. Tergite IX deeply emarginate, almost divided into two parts. Tergite X well developed, free. Aedeagus trilobate, short and broad, more or less symmetrical; anterior edge of phallobase without struts; parameres individually articulated to phallobase but joined together and to base of penis dorsally; simple or slightly notched at apex; anterior edge of penis with short, diverging struts. [Nakane 1997; Kawashima 1999; Kawashima & Satou 2004.]

**Morphology, Adult females** (Fig. 4.18.5 C–G). Body larviform, without elytra or hindwings; elongate, more or less parallel-sided. Weakly sclerotized, pale yellow to milky white in color. Surfaces almost smooth, subglabrous, very sparsely clothed with setae (Fig. 4.18.5 C).

Head prognathous and slightly retracted; slightly longer than wide, somewhat depressed; sides somewhat arcuate; posterior edge deeply and broadly emarginate. Eyes minute, with six or fewer facets, but usually stemmata-like with only one facet in Japanese species. Epicranial stem and frontal arms absent. Frontoclypeal suture absent. Clypeal region

depressed, anterior edge subtruncate. Labrum fused to head capsule. Antenna short and stout, 3-segmented, borne on large antennifer; antennomere 1 more than twice as long as 2; antennomere 3 minute; sensorium dome-like. Mandibles almost symmetrical, strongly but gradually curved, narrowly rounded or subacute at apex; retinacula and mola absent, without internal perforation (canal visible internally but without apical opening) (Fig. 4.18.5 D). Ventral mouthparts moderately retracted; maxillary articulating area absent. Maxillae large; cardo only vaguely indicated and fused with basal parts of stipes and postmentum; stipes elongate; galea 1-segmented, elongate and conical; lacinia absent; palpifer cylindrical; palp 3-segmented, gradually narrowed from base to apical palpomere, which is conical and subacute. Labium consisting of prementum and postmentum, the latter more or less connate with maxillae; prementum distinctly notched at middle; labial palps 2-segmented with apical palpomere elongate and conical with subacute apex. Gular region lightly pigmented, so that head capsule appears ventrally open; gular sutures absent (Fig. 4.18.5 E).

Thoracic segments gradually decreasing in length and increasing in width posteriorly. Anterior edge of prothorax broadly arcuate. Thoracic legs short and stout, armed ventrally with spines on most segments; trochanter triangular, femur short and subcylindrical; tibiae very short and cylindrical, only half as long as femur; tarsal formula 2-2-2; basal tarsomere very short, simple, ring-like, apical one three to four times as long and a little longer than tibia; pretarsus consisting of paired, simple claws (Fig. 4.18.5 G).

Abdominal segments I to VII almost equal in length and width; more or less parallel-sided. Laterotergites and laterosternites clearly delimited by folds. Sides more or less abruptly converging on segments VIII and IX. Segment X not visible. Paired, spot-like luminous organs present on each side of segment VII. Ovipositor short; undivided coxite narrowed apically, with short, cylindrical, terminal stylus (Fig. 4.18.5 F). [Ohba *et al.* 1997; Kawashima 1998, 1999; Kawashima & Satou 2004.]

**Morphology, Larvae** (Fig. 4.18.5 H–J). Body elongate and more or less parallel-sided, slightly wider at middle. Dorsal surfaces heavily pigmented, bicolored, forming pattern; smooth and subglabrous; ventral surfaces lightly pigmented (Fig. 4.18.5 H).

Head moderately large and prognathous; partly retractable, slightly longer than wide with sides slightly rounded. Moderately to heavily pigmented anteriorly; depigmented posterior to transverse, slightly curved carina. Posterior edge of head capsule deeply emarginate. Stemmata on each side one; small with flattened lens; located behind antennal articulating membrane. Epicranial stem and frontal arms completely absent. Paired curved, slender endocarinae present in front of posterior

emargination. Frontoclypeal suture absent. Labrum completely fused to head capsule; anteriorly produced and bisinuate forming subacute nasale and broadly rounded paranasalia. Antennae moderately long, 3-segmented, with extensive basal membrane; antennomere 1 much longer than 2 but subequal in diameter; 3 minute and slender; sensorium dome-like. Mandibles symmetrical, narrow and falcate, with internal perforation opening just before narrowly acute apex; strongly and evenly curving mesodorsally; mesal edge with or without retinaculum; with fringe of very short hairs extending from base to about middle; mola absent (Fig. 4.18.5 I). Ventral mouthparts retracted; maxillary articulating area absent. Cardo divided by internal ridge, longitudinally oriented; stipes about 3 times as long as wide; galea articulated, 2-segmented, palpiform; lacinia absent; palp 4-segmented, with palpomere 1 longer than remaining ones combined; palpomere 4 narrowly conical. Labium consisting of prementum, mentum and submentum, the latter two completely connate with maxillae; mentum about 4 times as long as wide; subquadrate with blunt posterior edge; prementum apically bilobed, with median longitudinal endocarina; ligula absent; labial palps 2-segmented, separated by more than width of first segment; apical palpomere narrowly conical. Maxillae and hypopharynx densely clothed with long hairs. Hypopharyngeal sclerome absent. Hypostomal rods long and parallel but ending well before posterior edge of head. Ventral epicranial ridges absent. Hypostomal region depigmented, so that head capsule appears to be ventrally open; gular sutures absent (Fig. 4.18.5 J).

Prothorax about as long as wide. Meso- and meta-thorax shorter and broader, without patches or rows of asperities or carinae. Terga relatively reduced, not extending laterally beyond sterna, without sharp lateral edges. Prothoracic presternum large and subtriangular, with lateral supporting rods and lightly pigmented longitudinal macula. Legs relatively short, 5-segmented, with long projecting coxae; trochanter and femur armed with long, stout setae; tibiotarsus with stout setae and dense brush of long hairs; pretarsus claw-like, with single stout seta and brush of long hairs extending well beyond its apex; coxae widely separated at base but sometimes approaching one another apically.

Abdomen slightly more than twice as long as thorax. Tergites more or less evenly pigmented with a variety of red, black and orange markings, especially in earlier instars. Anterolateral corners of tergites I–VIII each with laterally facing, oval gland opening. Sterna very lightly pigmented, except for more or less broadly V-shaped transverse markings on sternites II–VIII and a transversely quadrate marking on IX. Segment IX shorter than VIII, not extending onto ventral surface, not forming articulated plate; without paired urogomphi; sternite IX well developed, simple, not enclosed by sternite VIII. Segment X with weakly developed, tubular, protrusible, asperated holdfast organs; anal

region posteriorly oriented. Spiracles biforous, with posteriorly projecting air tubes; not placed at ends of spiracular tubes, located at the upper edges of laterotergites; laterally facing spiracles VIII of same size as others on abdomen. Luminous organs usually located on sides of abdominal segment VII as a pair of spot-like organs. [Ohba *et al.* 1996; Kawashima & Satou 2004.]

**Phylogeny and Taxonomy.** *Stenocladius davidis* Fairmaire was compared by its describer to the lampyrid genus *Magnoculus* McDermott, but was usually placed in Drilidae (Wittmer 1944) until Crowson (1972) moved the genus to the lampyrid subfamily Ototretinae. In a molecular phylogenetic study of Japanese fireflies, Suzuki (1997) found that the genus formed a clade with *Rhagophthalmus*, which was sister to that containing *Cyphonocerus* Kiesenwetter and several Lampyrinae, and in another molecular analysis of North American, Asian and European Lampyridae by Stanger-Hall *et al.* (2007), the genus was within a clade containing *Pollaclasis* Newman, *Cyphonocerus*, *Pterotus*, *Rhagophthalmus*, *Brachylampis* Van Dyke, *Drilaster* Kiesenwetter and several Luciolinae. In the morphological cladogram produced by Branham & Wenzel (2001, 2003), the genus clustered with four genera of Phengodidae and was moved into that family (2001).

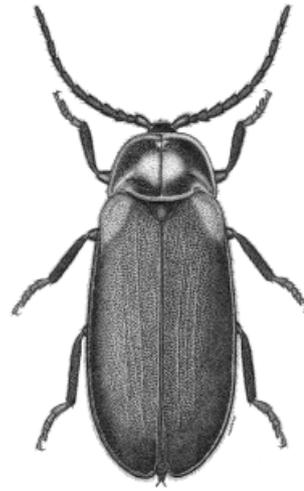
#### Ototretinae McDermott, 1964

**Distribution.** *Drilaster* and other genera of Ototretinae occur throughout the eastern Palaearctic and Oriental regions from India, China and Japan to Taiwan, the Philippines, Southeast Asia, and the East Indies. [Wittmer 1944; McDermott 1966; Satō 1968; Kawashima *et al.* 2005.]

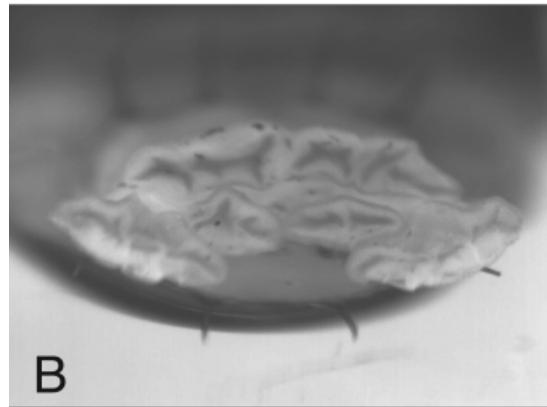
**Biology and Ecology.** Biological data is available for two genera only. Adult males and females of *Drilaster* are mainly diurnal insects, usually found on the upper surfaces of leaves at the forest edge, but sometimes they are collected and observed at night, both males and females being barely luminescent just after emergence from the pupa. *Drilaster* larvae are completely nocturnal, distinctly luminescent and feed on snails. They are usually found together with *Stenocladius* larvae in the same habitats in the Ryukyu Islands. [Ohba *et al.* 1996, 1997; Kawashima & Satou 2004.]

**Morphology, Adults** (Fig. 4.18.6 A) Length 3–10 mm. Body about 2–3.5 times as long as wide; slightly flattened to moderately convex. Upper surfaces usually densely clothed with decumbent hairs, sometimes mixed with erect hairs.

Head not to moderately strongly declined, but not concealed from above by pronotum; slightly transverse, not abruptly constricted posteriorly (Fig.



A



B

Fig. 4.18.6 A, *Drilaster axillaris* Kiesenwetter, female, dorsal (© I. Kawashima); B, *D. okinawensis* Nakane, larva, abdominal apex (© I. Kawashima).

4.18.6 A). Occipital region without transverse ridge or stridulatory file. Eyes small to moderately large, well separated from one another both dorsally and ventrally; slightly to strongly protuberant, entire, finely faceted, without interfacetal setae. Frontal region not to strongly deflexed at apex. Antennal insertions at least slightly exposed, moderately widely to narrowly separated; subantennal grooves absent. Frontoclypeal suture absent; anterior edge of clypeus straight to concave. Labrum small, free, slightly to strongly transverse, sometimes membranous. Antennae 11-segmented, usually filiform, serrate, unipectinate or uniflabellate from antennomere 3 to 10; occasionally moniliform or slightly widened at middle, rarely bipectinate or bipinnate. Mandibles small, very narrow and falcate, strongly, gradually curved mesally, unidentate; mola and prostheca absent. Maxilla with short, broad, more or less setose galea; lacinia highly reduced or absent; apical palpomere usually fusiform to slightly expanded and truncate or securiform. Ligula small, undivided, membranous; apical labial palpomere usually fusiform to securiform, but apical maxillary and labial palpomeres greatly enlarged and flattened in *Lamellipalpus* Maulik,

*Lamellipalpodes* Maulik, *Hyperstoma* Wittmer and *Eugeusis* Westwood. Subgenal ridges absent. Gular sutures moderately widely separated. Corpotentorium absent. Cervical sclerites well-developed.

Pronotum about 0.45–0.75 times as long as wide; usually widest posteriorly, with sides straight, strongly curved anteriorly or sinuate; base not or only narrower than elytral bases; lateral carinae complete, simple, often slightly raised and continuous along anterior edge; anterior angles not produced, usually absent; posterior angles usually more or less produced and rounded or acute, often embracing elytral humeri; posterior edge usually sinuate, sometimes straight, with or without raised margin; disc almost always with pair of relatively deep impressions or pits just mesad of posterior angles and often with shallow, median longitudinal groove. Flat prosternum in front of coxae much shorter than shortest diameter of procoxal cavity. Prosternal process absent. Notosternal sutures complete. Procoxae projecting well below prosternum, without concealed lateral extensions. Trochantins exposed, not appressed to sternum, glabrous, except in *Orotretadrilus*. Procoxal cavities transverse, contiguous, externally broadly open, without narrow lateral extensions; internally open. Scutellar shield well developed, not abruptly elevated; anteriorly simple, posteriorly acute to broadly rounded or truncate. Elytra 1.3–2.9 times as long as wide and 2.3–6 times as long as pronotum; sides subparallel or slightly widened apically, irregularly punctate or rugulose, sometimes with weak longitudinal carinae; apices conjointly or independently rounded, sometimes exposing one or two abdominal tergites; epipleura usually more or less complete, sometimes vaguely defined or absent. Mesoventrite separated by complete sutures from mesanepisterna, which are well separated from one another; anterior edge on same plane as metaventrite, without paired procoxal rests. Mesoventral cavity absent. Mesocoxae conical and projecting. Mesocoxal cavities confluent, poorly defined and more or less oblique; open laterally (closed by both mesepimeron and mesanepisternum). Mesometaventral junction absent. Metaventrite moderately to strongly convex, with straight side edges; discrimen short to absent; transverse (katapisternal) suture absent; exposed portion of metanepisternum moderately elongate. Metacoxae contiguous, strongly oblique, extending laterally to meet elytra; plates usually weakly developed but more or less complete, sometimes obliterated laterally. Metendosternite with lateral arms short or absent; laminae absent; anterior process short to moderately long and anterior tendons moderately or very close together. Hind wing about 1.7–2.25 times as long as wide; apical field less than 0.2 times total wing length, usually with vague, oblique anterior and posterior maculae; radial cell usually large and elongate with basal edge oblique but sometimes lacking; r3 short or absent; basal portion of RP long, often extending to basal fourth of wing; medial spur usually straight;

medial field usually with five free veins, but sometimes reduced to three or four; MP<sub>3+4</sub> with basal cross-vein but no spur; wedge cell often well developed and apically truncate, sometimes absent; anal lobe well developed, AP undivided; anal notch absent. Legs moderately long and slender; trochanterofemoral joint strongly oblique with base of femur separate from coxa; tibial spurs usually present but sometimes very short and not easily visible beyond apical setal fringe; tarsi 5-5-5; preapical tarsomere lobed beneath; pretarsal claws simple; empodium not usually visible.

Abdomen with six to eight free ventrites. Ventrite 1 not much longer than 2, without postcoxal lines. Intercoxal process absent. Luminescent organs present or absent, sometimes not obvious on dried specimens; usually present on sternite VI as paired spots, sometimes occupying entire sternite VI or sternites VI and VII. Functional spiracles on abdominal segment VIII present; spiracles located at lateral edges of sternites. Anterior edge of sternite VIII in male without median strut. Anterior edge of sternite IX in male without spiculum gastrale. Tergite IX shallowly to deeply emarginate. Tergite X well developed; usually free but sometimes partly fused to tergite IX. Aedeagus trilobate, short and broad, symmetrical; anterior edge of phallobase without struts; parameres individually articulated to phallobase, but usually joined together and to base of penis dorsally; simple or apically bifurcate; anterior edge of penis sometimes with short struts and complex endophallus. Sternite VIII in female with long anterior, spiculum ventrale. Ovipositor short to moderately long, slender, flattened, lightly sclerotized; paraprocts much longer than coxites, which are weakly divided with short, terminal, palpi-form styli. [Gorham 1883 a, b, 1885; Maulik 1921; Pic 1930; Wittmer 1938, 1944; McDermott 1964; Satô 1968; Crowson 1972; Nakane 1977; Branham & Wenzel 2001; Kawashima *et al.* 2005; Kawashima 2007; Brancucci & Geiser 2007.]

**Morphology, Larvae (*Drilaster*).** Body elongate and somewhat fusiform, slightly widened at middle. Dorsal surfaces more or less heavily pigmented, relatively smooth, shiny and subglabrous; ventral surfaces partly or lightly pigmented, except for sterna VII–IX.

Head small, prognathous, partly retractable, longer than wide. Posterior edge of head capsule more or less sinuate. Epicranial stem moderately long. Frontal arms V-shaped, extending anteriorly to mandibular articulations, bases contiguous. Median endocarina absent. With one moderately large stemma on each side. Frontoclypeal suture absent. Labrum completely fused to head capsule; anterior edge of nasale slightly produced and sinuate with distinct mesal emargination. Antennae 3-segmented, moderately long; antennomeres 1 and 2 elongate and of equal width; 3 much shorter and narrower; sensorium dome-like and oblique. Mandibles symmetrical, narrow and falcate with

internal perforation opening just before apex; strongly, gradually curved mesally with acute apices overlapping; mesal edge with broad, sclerotized, shelf-like retinaculum extending from base to about middle and completely lined with stiff setae; mola absent. Ventral mouthparts strongly retracted; maxillary articulating area absent. Cardo externally divided and longitudinally oriented; stipes longer than wide; galea articulated and 2-segmented; lacinia absent; upper surface of maxilla densely clothed with hairs; palp 4-segmented; palpomere 1 longer than remaining ones combined and palpomere 4 narrowly conical. Labium consisting of prementum, mentum and submentum, the latter two completely connate with maxillae; mentum more lightly pigmented than postmentum; prementum apically bilobed, with three internal supporting rods; ligula absent; palp 2-segmented, separated by more than width of first palpomere; apical palpomere narrowly conical. Hypopharyngeal sclerome absent. Subparallel hypostomal rods extending to posterior edge of head. Ventral epicanial ridges absent. Hypostomal region depigmented, so that head capsule appears to be ventrally open; gular sutures absent.

Prothorax about as long as wide. Meso- and metathorax shorter and broader, without patches or rows of asperities or carinae. Terga extending laterally beyond sterna, but without sharp lateral edges. Prothoracic presternum large and subtriangular, with lateral supporting rods and lightly pigmented longitudinal macula. Legs well developed, 5-segmented, with long projecting coxae; trochanter, femur and tibiotarsus armed with long, stout setae; pretarsus claw-like with two setae lying side by side or obliquely situated; coxae widely separated at base but approaching one another apically.

Abdomen less than twice as long as thorax. Abdominal terga extending laterally well beyond sterna but without sharp lateral edges; well developed laterotergites and very slender laterosternites present on ventral surface. Paired dorsal gland openings on segments I–VI; pigmentation weak or lacking on segments VII and VIII. Abdominal segment IX shorter than segment VIII, not extending onto ventral surface, not forming articulated plate, without paired urogomphi. Sternum IX well developed, simple, not enclosed by sternum VIII. Segment X with three pairs of asperated, tubular, protrusible holdfast organs (Fig. 4.18.6 B); anal region posteriorly oriented. Spiracles biforous, not placed at ends of spiracular tubes; located at upper edges of laterotergites; those on segment VIII the same size as others on abdomen, facing laterally. Luminous organs normally located at sides of segment VII. [Hayashi 1991.]

**Phylogeny and Taxonomy.** This taxon is meant to encompass most of those genera included in the family Drilidae by Wittmer (1944) but differing from true drilids in having a much shorter prosternum and lacking pretarsal setae (Crowson

1972). McDermott (1964) included only *Drilaster* Kiesenwetter (as *Ototreta* Olivier) and *Brachylampis* in his lampyrid subfamily Otoretinae, while Crowson specifically mentioned those taxa he was able to examine (e. g., *Drilaster*, plus *Picodrilus* Wittmer, *Ceylanidrilus* Pic, *Lamellipalpus*, *Mimophaeopterus* Pic, *Harmatelia* Walker, *Stenocladius*). *Ototretadrilus* Pic was placed by Crowson (1972) in a separate lampyrid subfamily, while *Harmatelia* and *Stenocladius* are discussed above. Other “drilid” genera or subgenera included by Wittmer which may belong here include *Baolacus* Pic, *Bicladon* Pic, *Brachypterodrilus* Pic, *Eugeusis*, *Falsophaeopterus* Pic, *Falsophrixothrix* Pic, *Flabellotreta* Pic, *Gorhamia* Pic, *Hyperstoma* Wittmer, *Lamellipalpodes*, *Mimophaeopterus* Pic, *Monodrilus* Pic, and *Pachytarsus* Motschulsky. Of the remaining genera in Wittmer’s catalogue, *Drilonius* Kiesenwetter is now placed in Omethidae, *Platerodrilus* Pic in Lycidae and *Phrixothrix* Olivier in Phengodidae, while *Cydistus* is discussed above. In cladograms produced by Branham & Wenzel (2001, 2003) containing 37 lampyrid genera and 25 outgroups and based morphological features of adult males, *Brachylampis* is considered to be a basal member of the Lampyridae, while *Harmatelia* and *Drilaster* are both basal to a clade including all other cantharoids, except Plasteridae, Drilidae and Omalisidae. In Suzuki’s (1997) study of Japanese fireflies, based on 16S mitochondrial RNA, two species of *Drilaster* were placed at the base of a clade including *Stenocladius*, *Rhagophthalmus* and seven genera of Lampyridae. In the cladogram produced by Stanger-Hall (2007), *Brachylampis* and *Drilaster* formed a clade well within Lampyridae and basal to one containing *Pollaclasis*, *Cyphoncerus*, *Stenocladius*, *Pterotus*, *Rhagophthalmus*, *Pristolytus* and several Luciolinae. In cladograms based on COI, 16S, 18S and 28S by Bocakova *et al.* (2007), *Drilaster*, *Flabellotreta*, *Mimophaeopterus* and *Ototretadrilus* consistently formed a clade either nested well within Lampyridae, or as sister-group to the remaining lampyrid genera.

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