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10.6. Biphyllidae LeConte, 1861

Andrew R. Cline and Floyd W. Shockley

Distribution. Biphyllidae is cosmopolitan, occurring in all zoogeographic regions except New Zealand, with highest diversity in the tropics. The family includes six genera and approximately 200 species (Lawrence 1982; Goodrich & Springer 1992). Schenkling (1934) provided the most recent world catalogue. In the Old World, *Biphyllus* Dejean occurs with highest diversity in Africa and Japan (Wollaston 1873; Reitter 1889; Miwa 1931) but also occurs in Taiwan, Sumatra, Australia (Schenkling 1934) and the Russian Far East (Nikitsky 1992). *Althaesia* Pascoe contains three species from Australia (Blackburn 1894; Lea 1921), two from Papua-New Guinea (Pascoe 1860; Arrow 1929), and one from Indonesia (Grouvelle 1913). *Diplocoelus* Guérin-Ménéville occurs sporadically in the Old World, with most species inhabiting Australia (Lea 1921 a, b, 1922); however, two

species are known from Europe (Reitter 1909; Winkler 1924). Within the Nearctic, two *Diplocoelus* and one *Anchorius* Casey species are known (Casey 1900; Goodrich & Springer 1992; Goodrich 2002). *Anchorius* also includes undescribed species from Central and South America. In the Neotropics, *Anobocoelus* Sharp contains four described species (Schenkling 1934; Blackwelder 1945) and an indigenous unnamed species on the Galapagos Island of Santa Cruz (Peck 2006), as well as 39 species of *Gonicoelus* Sharp (Blackwelder 1945). From 54 species known throughout the Neotropics, no overlap of species occurs between Central and South America (Blackwelder 1945).

Biology and Ecology. Adult and larval biphyllids may be found in leaf litter, fruiting bodies of pyrenomycetous Ascomycota fungi, and under bark of dead trees or fallen branches. *Anchorius* larvae were reported from under fermenting bark of mesquite (*Prosopis* sp.) (Lawrence 1991). *Diplocoelus brunneus* LeConte adults have been collected from dead oaks infested with *Hypoxyylon* fungi (Donisthorpe 1935; Lawrence 1977; Crowson 1981, 1984; Goodrich & Springer 1992; Downie & Arnett 1996), and also have been sifted from dead leaves of maple, beech and other hardwood trees. *Diplocoelus rudis* (LeConte) adults were found under moist, loose bark of fallen oaks, hickory, and pines (Goodrich & Springer 1992). Some biphyllids, including *Anchorius*, some *Diplocoelus* and *Gonicoelus* in Costa Rica, have been collected 'en masse' at freshly cut stumps of hardwoods as well as on split stalks of palms (*Iriarteia* sp.) spotted with Ascomycota molds (Cline pers. obs.). *Gonicoelus* larvae also have been collected under bark of hardwoods (Lawrence 1991). Species of *Biphyllus* have been reported to feed on spores and stromata of *Daldinia* (Wollaston 1865; Ganglbauer 1899; Crowson 1955; Vogt 1967; Hingley 1971), whereas *Diplocoelus* have been taken in association with *Tubercularia* (Palm 1959) and *Nammularia* (Dajoz 1966). Hammond & Lawrence (1989) also indicated *Biphyllus* and *Diplocoelus* on *Xylaria* and *Cryptostroma*. Jones (2000) reported *Biphyllus lunatus* (Fabricius) feeding on a *Cryptostroma* fungus specific to sycamore trees (*Acer* sp.) in England. Some Australian biphyllids have been found on rotting flower stalks of *Xanthorrhoea* and rotting cycad cones (Lawrence 1991).

Morphology, Adults (Fig. 10.6.1 A–E). Length 2.0–6.5 mm. Body oblong to elongate-oval, moderately convex to flattened; color yellowish brown to reddish brown to black, typically uniform but occasionally bicolored; moderately to strongly pubescent, dorsal surface with erect and decumbent hairs in more or less distinct striae, pubescence shorter and subdepressed ventrally.

Head prognathous, visible from above, inserted in prothorax to base of eyes; surface punctate;

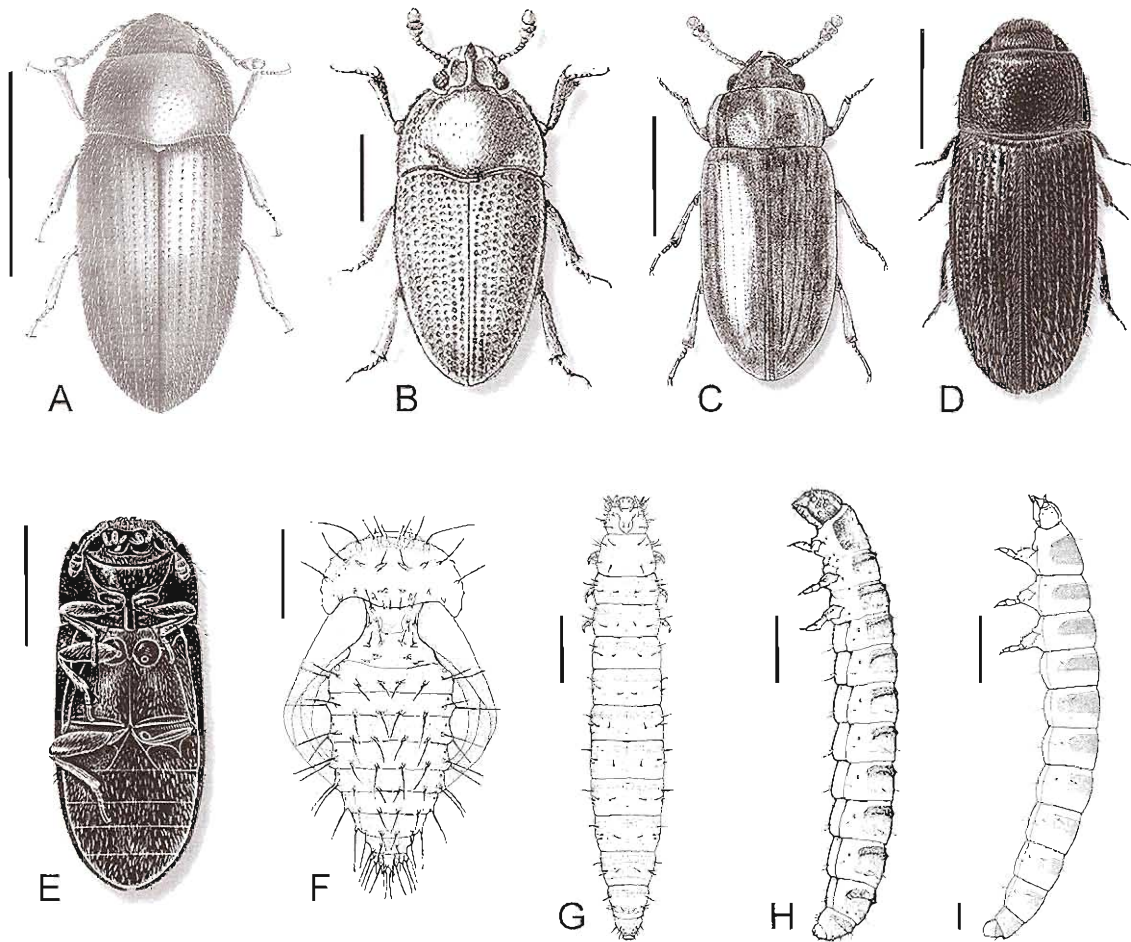


Fig. 10.6.1. A, *Biphyllus frater* Aube, adult, dorsal (modified from Delobel & Tran 1993; © Maurice Tran, ORSTOM); B, *Gonicoelus unicornis* Sharp, adult, dorsal (modified from Sharp 1902); C, *Diplocoelus fagi* Guérin-Méneville, adult dorsal (from Hansen 1950, © Danmarks Fauna and Zoological Museum, University of Copenhagen); D, *Diplocoelus punctatus* Lea, adult, dorsal; E, *Diplocoelus punctatus* Lea, adult, ventral, (from Lawrence *et al.* 1999 a; © CSIRO); F, *Diplocoelus amplicolis* Reitter, pupa, dorsal (from Costa *et al.* 1988; © Museu de Zoologia da Universidade de São Paulo, Brazil); G, *Diplocoelus amplicolis* Reitter, larva, dorsal (from Costa *et al.* 1988; © Museu de Zoologia da Universidade de São Paulo, Brazil); H, *Diplocoelus fasciatus*, larva, lateral (from Lawrence and Britton 1994, © CSIRO); I, *Anchorius lineatus* Casey, larva, lateral (from Lawrence 1991; © J. Lawrence). Lines = 1 mm.

transverse occipital ridge present. Eyes large, globose, coarsely faceted, interfacetal setae present but not elongate. Antennal insertions concealed from above; subantennal grooves present between eyes and mandibular bases and extending behind eyes. Frontoclypeal suture absent. Labrum transverse. Antennae 11-segmented, usually with 3-segmented club (2-segmented in *Biphyllus*). Mandibles moderately large, curved and apically bidentate, mola well-developed. Maxilla with lacinia elongate, three times as long as wide, apex rounded; long setae present on medial and apical margins; galea wider than lacinia, twice as long as wide with long setae as in lacinia, apex of galea densely setose or spinose; maxillary palps 4-segmented, slender. Labium with mentum transverse, trapezoidal; labial palps 3-segmented, slender,

terminal palpomere often securiform or subulate. Head ventrally with pair of distinct setose tubular invaginations opening laterally into base of subantennal groove. Gular sutures either broadly separate or absent. Tentorial arms well-separated, corpotentorium narrow.

Pronotum transverse, with well-developed lateral margins, sometimes finely crenulate or serrulate, often with one or two pairs of longitudinal sublateral carinae (several pairs in *Anchorius*), and occasionally an additional pair of basal grooves or foveae present. Prosternal process parallel-sided. Procoxae transversely oval, with concealed or barely exposed trochantins. Procoxal cavities internally and externally closed, with very small lateral extension. Scutellar shield transverse, sides diverging posteriorly. Elytra 1.2–2.2 times as long as wide,

distinctly punctate with 10 rows of punctured striae and usually a scutellary striole. Epipleura gradually narrowed and complete. Mesocoxal cavities ovate, narrowly separated, open laterally (mesepimeron reaching middle of coxal cavities), trochantins exposed. Metaventrite longer than abdominal ventrite 1, slightly convex, discripen present, sinuate postcoxal lines forming an axillary space on each side (sometimes with an additional pair of straight postcoxal lines). Metacoxae transverse, slightly grooved, well-separated. Metendosternite of typical cucujoid type with elongate lateral arms; ventrolateral and anterior processes reduced or absent, laminae well-developed. Hindwings well-developed; apical field with transverse linear sclerite just distad of radial cell, which is well-developed; crossvein R3 oblique, R4 complete, sometimes with apical spur; r-m loop moderately broad; basal portion of RP very short or absent; medial spur almost reaching wing margin where there is a weak embayment; medial field with three or four free veins, the anteriormost (MP_{3+4}) extending into medial fleck; wedge cell present or absent; anal lobe well-developed, separated by deep, notch-like embayment. Trochanters short, somewhat heteromeroid in appearance; femora slender to moderately robust; tibiae slender, broadening apically; protibiae usually with spines or spurs apically; tarsal formula 5-5-5, tarsomeres slender, 2-4 with slender pubescent lobes, penultimate reduced, fifth as long or longer than other tarsomeres combined. Claws simple.

Abdomen with 5 free ventrites; ventrite 1 longer than second, with one or two pairs of straight, diverging postcoxal lines and narrowly rounded to acute intercoxal process. Sternites VIII and IX in male with anterior struts. Aedeagus symmetrical. Anterior edge of tegmen with single median strut and opposing paired struts. Parameres fused to phallobase, sometimes free from each other. Female sternite VIII with short spiculum ventrale. Ovipositor 3-6 times as long as wide, and almost as long as ventrites 3-5 combined; gonocoxites cylindrical; length of combined gonocoxites shorter than paraprocts, proximal lobe of gonocoxite and broad, distal lobe long and narrow; subapical gonostyli well-developed, with long setae subequal in length to stylus. Spermatheca sclerotized and with associated gland. [Lawrence 1999 a; Lawrence & Britton 1994; Goodrich & Springer 1992; Goodrich 2002.]

Morphology, Larvae (Fig. 10.6.1 G-I). Length 2.5-10 mm. Body elongate, parallel-sided, cylindrical to slightly flattened, straight or slightly curved ventrally; dorsal surface sclerotized and lightly to moderately pigmented, smooth, with scattered, simple setae; no asperites present, but protergum with one or more sclerotized plates.

Head protracted and prognathous, moderately broad, slightly flattened. Epicranial stem absent or very short; frontal arms lyriform, contiguous

at base. Median endocarina absent. Six stemmata on each side. Frontoclypeal suture absent. Labrum partly fused to head capsule. Antennae short but well-developed, 3-segmented; sensorium on segment 2 conical or palpiform, much shorter than terminal segment. Mandibles symmetrical, bidentate, with accessory ventral process and sometimes with serrate incisor edge; mola well-developed and sickle-shaped, transversely ridged, with asetose hyaline lobe at base; prostheca bearing a brush of complex comb-like. Ventral mouthparts retracted. Maxillary articulating area well-developed. Maxilla with transverse cardo, elongate stipes, 3-segmented palps, and falciform mala bearing a dorsal row of spines along inner edge. Labium free almost to base of mentum; ligula transverse; labial palps 2-segmented, widely separated. Prementum present, postmentum quadrate to trapezoidal. Hypopharyngeal sclerome consisting of a transverse bar. Hypostomal rods short and diverging. Ventral epicranial ridges well-developed; gula transverse.

Legs well-developed, 5-segmented, nearly contiguous medially; clothed with short spines; pretarsus with 1 seta. Mesotergum, metatergum, and abdominal terga I-VIII each with a transverse carina near anterior edge. Tergum IX usually without urogomphi, if present short and fixed; sternum IX well-developed, simple. Segment X more or less cylindrical, forming a posteroventral pygopod. Spiracles annular-biforous, raised on short tubes; posteriorly or posterodorsally placed on segment VIII. [Costa *et al.* 1988; Lawrence & Britton 1994; Lawrence 1991; Lawrence *et al.* 1999 b; Goodrich 2002.]

Morphology, Pupae (Fig. 10.6.1 F). Length 2.0-4.0 mm. Aedealous and exarate. Color from yellowish brown to light brown; moderately pubescent with long erect hairs often associated with distinct spicules. Head partially visible from above with several minute spinose projections. Pronotum transverse, somewhat to highly convex; posterior angles prominent, apex rounded; dorsal surface with several to many large spicules with or without associated setae. Mesosoma and metatergum each with four pairs of prominent setose spicules, often arranged in transverse bands. Wing pads long and wrapping around abdomen to ventral midline. Abdominal segments I-VIII with two pairs of setose spicules dorsal and two pairs lateral; segment IX with a pair of distinct, minute urogomphi and two to four pairs of tubercles laterad of urogomphi, one pair distinctly ventral; segment I with large dorso-lateral annular spiracles; spiracles on segments II-VI smaller than those on segment I [Costa *et al.* 1988].

Phylogeny and Classification. Although biphyllids were always considered to be a well-defined group, sister-group relationships and placement

within Cucujoidea were historically contentious. Early 19th and 20th century coleopterists placed biphyllids within Mycetophagidae (LeConte 1861, 1863; Reitter 1877; Horn 1878; LeConte & Horn 1883), Cryptophagidae (Redtenbacher 1858; Jacquelin DuVal 1859; Wollaston 1862; Thomson 1863; Seidlitz 1891; Casey 1900; Reitter 1909; Leng 1920) and Erotylidae (Ganglbauer 1899; Winkler 1924; Roberts 1958; Crowson 1955; Vogt 1967). In the mid-20th century, biphyllids again were erroneously placed in Tenebrionoidea (Crowson 1960; Abdullah & Abdullah 1966; Abdullah 1973) based on superficial aedeagal and trochanteral similarities; despite the non-heteromeroïd tarsi and work by Falcoz (1926) that used adult characters and proposed an affinity with *Byturus* (Byturidae). Lawrence and Newton (1982) noted the biphyllid aedeagus was more similar to the cleroid sheath type than the tenebrionoid type and suggested a relationship to languriine Erotylidae (e. g., *Cryptophilus*). Shared features of larvae and adults also have indicated potential relationships to Bothrideridae, Nitidulidae, Protocucujidae and euxestrine Cerylonidae (Crowson 1955; Lawrence 1991). Crowson (1981, 1984) suggested the unique biphyllid pre-gular pits might be a type of mycangium; however, no evidence supports this claim. The pits do appear to present a potential synapomorphy for Biphyllidae, in combination with the metaventral and/or abdominal coxal lines, uniting members of this family.

Some family-level taxonomic confusion surrounded this group until the late 20th century. Lawrence and Newton (1995) noted the incorrect family-group author assignment used in Silfverberg (1992) and that Goodrich & Springer (1992) had referred to Biphyllidae Sharp (1900) in which Sharp apparently assumed *Biphyllus* Dejean and *Diphyllus* Berthold were independent. LeConte (1861) used the genus *Diphyllus* to establish the family-group name, but *Diphyllus* was an unjustified emendation of *Biphyllus* by Redtenbacher (1858). Under rule of priority, correction of this emendation and subsequent relegation of *Diphyllus* to junior synonym made LeConte's family-group name valid under the corrected name Biphyllidae. Current consensus places Biphyllidae within Cucujoidea (Crowson 1955), sister to Byturidae (Falcoz 1926; Barber 1942; Crowson 1955; Goodrich & Springer 1992). Leschen *et al.* (2005) recently performed a robust cladistic analysis of basal cucujoid families based on adult and larval morphology that, like the above previous efforts, yielded conflicting results. Adult morphology supported a sister group relationship to Erotylidae, but larval morphology supported a relationship to Byturidae. A combined molecular and morphological dataset may be required to resolve the proper placement of this family within Cucujoidea. No phylogenetic studies have yet been performed to assess intra-familial relationships at any level within Biphyllidae.

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10.7. Erotylidae Leach, 1815

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Distribution. There are approximately 258 presently recognized genera and over 3500 described species occurring worldwide and present mainly in forested environments where fungi or host plants occur. Apart from some members of Cryptophilinae and stored product pests, the family is absent from oceanic islands. The group is divided into six subfamilies and ten tribes. The subfamily Xenoscelinae (8 genera, 10 spp.) is widespread, but absent from temperate South America and the Nearctic. The subfamily Pharaxonothinae (5 genera, 24 described species) is widely distributed with genera that are restricted to Japan and southern Europe and the genus *Pharaxonotha* Reitter found in the tropical New World and Asia and possibly Africa. Two species, *Leucohimatium arundinaceum* (Forskål) and *Pharaxonotha kirschi* Reitter, are widespread stored product pests and there are many undescribed species in the largest genus *Pharaxonotha* (13 spp.). The subfamily Loberinae (5 genera, 79 spp.) is widely distributed with genera restricted to Madagascar, New Caledonia, and Central America. The world wide genus *Loberus* LeConte (the largest loberine genus with 75 spp.) and the New Caledonian genus *Paphezia* Zablony & Leschen (1 sp.) contain many undescribed species. One of the largest and most diverse subfamilies is the phytophagous Languriinae with three tribes. Hapalipini (3 gen., 74 spp.) is predominantly pantropical, with *Hapalips* Reitter the largest genus (57 spp.). Languriini (56 genera, >750 spp.) is mainly tropical, and absent from Europe, New Zealand, and Chile. Thalissellini (4 genera, 25 spp.) is Neotropical and contains many undescribed spp. The subfamily Cryptophilinae contains three tribes. Empocryptini (3 genera, 17 spp.) occurs in the Neotropics and temperate South America. Cryptophilini (5 genera, 33 spp.) is mainly pantropical, but the widespread genus *Cryptophilus* Reitter has some Holarctic species and *Cryptophilus integer* (Heer) is a widespread vagrant. Toramini (5 genera, 58 spp.) is widespread, mainly tropical with few species in temperate regions, and absent from much of the Pacific, Australia, and New Zealand. The largest and most widespread genus is *Toramus* (43 spp). The mycophagous subfamily Erotylinae is the largest consisting of five tribes, 172 genera, and 2563 species. Dacnini (14 genera, 92 spp.) has a worldwide distribution, occurs primarily in the Holarctic and Austral-Asian regions, with few members from the New World and African tropics. Encaustini (13 genera, 203 spp.) is pantropical and occurs primarily in southeastern Asia-Indonesia, with few African and Central American taxa. Megalodacnini (sometimes considered part of Encaustini by Węgrzynowicz 2002) (28 genera, 323 spp.) is distributed worldwide