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Taxonomy

Revision of the Bark Beetle Genera Within the Former Cryphalini (Curculionidae: Scolytinae)

Andrew J. Johnson,[1,9] Jiri Hulcr,[1,2] Miloš Knížek,[3] Thomas H. Atkinson,[4] Michail Yu. Mandelshtam,[5] Sarah M. Smith,[6] Anthony I. Cognato,[6] Sangwook Park,[7] You Li,[1] and Bjarte H. Jordal[8]

[1]School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611, [2]Entomology and Nematology Department, University of Florida, Gainesville, FL 32611, [3]Department of Forest Protection Service, Forestry and Game Management Research Institute, Strnady, Jíloviště, Praha 5, Zbraslav CZ-15600, Czechia, [4]Texas Natural History Collections, Integrative Biology, University of Texas at Austin, Austin, TX 78712, [5]Department of Forest Protection, Wood Science and Game Management, Saint-Petersburg State Forest Technical University named after S.M. Kirov, Institutskii per., 5, 194021 Saint-Petersburg, Russia, [6]Department of Entomology, Michigan State University, East Lansing, MI 48824, [7]Research Institute of Forest Insect Diversity, Namyangju 12113, South Korea, [8]University Museum of Bergen, University of Bergen, P.O. 7800, 5020 Bergen, and [9]Corresponding author, e-mail: andrewjavanjohnson@gmail.com, ajj@ufl.edu

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Abstract

Cryphalini Lindemann, 1877 are a speciose group of mostly miniscule beetles. The tribe Cryphalini is reviewed here which resulted in taxonomic and nomenclatural changes. This revision follows a recent molecular phylogenomic re-analysis focused on the tribe and related scolytine taxa. The analysis demonstrated that the tribe is polyphyletic, as found in other molecular phylogenies. To ensure monophyletic classification, we present a revision of the former tribe with two tribes resurrected, one described, and several genera transferred to other existing tribes. Additionally, extensive generic synonymy, and new combinations are presented. A key, photographs, and illustrations are provided to enable an accurate determination of genera. The revised Cryphalini contains only *Cryphalus* Erichson, 1836 (=*Hypocryphalus* Hopkins, 1915 **syn. nov.**; *Margadillius* Hopkins, 1915 **syn. nov.**). Coriacephilini Johnson **trib. nov.** contains only *Coriacephilus* Schedl, 1939. Ernoporini Nüsslin, 1911 **stat. res.** contains *Eidophelus* Eichhoff, 1876 (=*Scolytogenes* Eichhoff, 1878 **syn. nov.**; *Ptilopodius* Hopkins, 1915 **syn. nov.**; *Ernoporicus* Berger, 1917 **syn. nov.**; *Cryphalogenes* Wood, 1980 **syn. nov.**); *Ernoporus* Thomson, 1859 (=*Ernocladius* Wood, 1980 **syn. nov.**; *Allothenemus* Bright and Torres, 2006 **syn. nov.**); *Hemicryphalus* Schedl, 1963; and *Procryphalus* Hopkins, 1915. Trypophloeini Nüsslin, 1911 **stat. res.** includes the genera *Afrocosmoderes* Johnson and Jordal **gen. nov.**; *Atomothenemus* Bright, 2019; *Cosmoderes* Eichhoff, 1878 (=*Allernoporus* Kurentsov, 1941 **syn. nov.**); *Hypothenemus* Westwood, 1834 (=*Periocryphalus* Wood, 1971 **syn. nov.**); *Macrocryphalus* Nobuchi, 1981 **stat. res.**; *Microcosmoderes* Johnson and Jordal **gen. nov.**; *Microsomus* Bright, 2019; *Pygmaeoborus* Bright, 2019; and *Trypophloeus* Fairmaire, 1864. Xyloterini LeConte, 1876 is maintained, containing *Indocryphalus* Eggers, 1939; *Trypodendron* Stephens, 1830 and *Xyloterinus* Swaine, 1918. *Acorthylus* Brèthes, 1922, *Cryptocarenus* Eggers, 1937, *Neocryphus* Nunberg, 1956, *Stegomerus* Wood, 1967, and *Trypolepis* Bright, 2019 are transferred to Corthylini LeConte, 1876. *Stephanopodius* Schedl, 1963 is transferred to Xyloctonini Eichhoff, 1878. As a consequence of generic synonymy, the following new or resurrected combinations are proposed: *Cosmoderes euonymi* (Kurentsov, 1941) **comb. nov.**; *Cryphalus aciculatus* (Schedl, 1939) **comb. nov.**; *Cryphalus afiamalus* (Schedl, 1951) **comb. nov.**; *Cryphalus angustior* Eggers, 1927 **comb. res.**; *Cryphalus asper* (Broun, 1881) **comb. nov.**; *Cryphalus bakeri* (Eggers, 1927) **comb. nov.**; *Cryphalus basihirtus* Beeson, 1929 **comb. nov.**; *Cryphalus bidentatus* (Browne, 1980) **comb. nov.**; *Cryphalus brevior* (Schedl, 1943) **comb. nov.**; *Cryphalus carinatus* (Browne, 1980) **comb. nov.**; *Cryphalus confusus* (Hopkins, 1915) **comb. nov.**; *Cryphalus corpulentus* (Schedl, 1942) **comb. nov.**; *Cryphalus cylindripennis* (Schedl, 1959) **comb. nov.**; *Cryphalus cylindrus* (Browne, 1950) **comb. nov.**; *Cryphalus densepilosus* (Schedl, 1942) **comb. nov.**; *Cryphalus dilutus* Eichhoff, 1878 **comb. res.**; *Cryphalus discrepans* (Schedl, 1965) **comb. nov.**; *Cryphalus discretus* Eichhoff, 1878 **comb. res.**; *Cryphalus erythrinae* (Hopkins, 1915) **comb. nov.**; *Cryphalus fici* (Browne, 1986) **comb. nov.**; *Cryphalus glabratus* (Schedl, 1959) **comb. nov.**; *Cryphalus granulatus* (Schedl, 1942) **comb. nov.**; *Cryphalus imitans* (Schedl, 1951) **comb. nov.**; *Cryphalus interponens* (Schedl, 1953) **comb. nov.**; *Cryphalus kalambanganus* (Schedl, 1943)

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comb. nov.; *Cryphalus laevis* (Browne, 1980) **comb. nov.**; *Cryphalus laticollis* (Browne, 1974) **comb. nov.**; *Cryphalus longipennis* (Browne, 1970) **comb. nov.**; *Cryphalus longipilis* (Browne, 1981) **comb. nov.**; *Cryphalus magnus* (Browne, 1984) **comb. nov.**; *Cryphalus malayensis* (Schedl, 1942) **comb. nov.**; *Cryphalus mangiferae* Stebbing, 1914 **comb. res.**; *Cryphalus margadilaonis* (Hopkins, 1915) **comb. nov.**; *Cryphalus mindoroensis* (Schedl, 1943) **comb. nov.**; *Cryphalus minor* (Schedl, 1943) **comb. nov.**; *Cryphalus minutus* (Hopkins, 1915) **comb. nov.**; *Cryphalus mollis* Schedl, 1955 **comb. res.**; *Cryphalus moorei* (Schedl, 1964) **comb. nov.**; *Cryphalus nigrosetosus* (Schedl, 1948) **comb. nov.**; *Cryphalus nitidicollis* (Schedl, 1975) **comb. nov.**; *Cryphalus obscurus* (Hopkins, 1915) **comb. nov.**; *Cryphalus ovalicollis* (Schedl, 1942) **comb. nov.**; *Cryphalus papuanus* (Schedl, 1973) **comb. nov.**; *Cryphalus piliger* (Schedl, 1975) **comb. nov.**; *Cryphalus polynesiae* (Schedl, 1979) **comb. nov.**; *Cryphalus quadrituberculatus* (Schedl, 1963) **comb. nov.**; *Cryphalus reflexus* (Browne, 1980) **comb. nov.**; *Cryphalus robustus* Eichhoff, 1872 **comb. res.**; *Cryphalus rotundus* (Hopkins, 1915) **comb. nov.**; *Cryphalus sandakanensis* Schedl, 1937 **comb. res.**; *Cryphalus spathulatus* (Schedl, 1938) **comb. nov.**; *Cryphalus striatulus* (Browne, 1978) **comb. nov.**; *Cryphalus striatus* (Hopkins, 1915) **comb. nov.**; *Cryphalus sumatranus* (Schedl, 1939) **comb. nov.**; *Cryphalus triangularis* (Schedl, 1975) **comb. nov.**; *Cryphalus tutuilaensis* (Schedl, 1951) **comb. nov.**; *Eidophelus absonus* (Schedl, 1975) **comb. nov.**; *Eidophelus afer* (Schedl, 1970) **comb. nov.**; *Eidophelus africanus* (Schedl, 1977) **comb. nov.**; *Eidophelus aitutakii* (Beaver and Maddison, 1990) **comb. nov.**; *Eidophelus alniphagus* (Nobuchi, 1975) **comb. nov.**; *Eidophelus alternans* (Schedl, 1975) **comb. nov.**; *Eidophelus amanicus* (Eggers, 1919) **comb. nov.**; *Eidophelus ankius* (Schedl, 1979) **comb. nov.**; *Eidophelus apicalis* (Schedl, 1971) **comb. nov.**; *Eidophelus approximatus* (Schedl, 1975) **comb. nov.**; *Eidophelus aspericollis* (Eichhoff, 1878) **comb. nov.**; *Eidophelus ater* (Eggers, 1923) **comb. nov.**; *Eidophelus australis* (Schedl, 1942) **comb. nov.**; *Eidophelus badius* (Nobuchi, 1975) **comb. nov.**; *Eidophelus bambusae* (Browne, 1983) **comb. nov.**; *Eidophelus bangensis* (Eggers, 1927) **comb. nov.**; *Eidophelus basilaris* (Wood, 1960) **comb. nov.**; *Eidophelus birosimensis* (Murayama, 1958) **comb. nov.**; *Eidophelus braderi* (Browne, 1965) **comb. nov.**; *Eidophelus brimblecombei* (Schedl, 1972) **comb. nov.**; *Eidophelus buruensis* (Eggers, 1926) **comb. nov.**; *Eidophelus camelliae* (Nobuchi, 1975) **comb. nov.**; *Eidophelus candidus* (Nobuchi, 1975) **comb. nov.**; *Eidophelus capucinus* (Schedl, 1971) **comb. nov.**; *Eidophelus caucasicus* (Lindemann, 1877) **comb. nov.**; *Eidophelus ceylonicus* (Schedl, 1959) **comb. nov.**; *Eidophelus cicatricosus* (Schedl, 1942) **comb. nov.**; *Eidophelus coccotrypanoides* (Schedl, 1939) **comb. nov.**; *Eidophelus communis* (Schaufuss, 1891) **comb. nov.**; *Eidophelus confragosus* (Sampson, 1914) **comb. nov.**; *Eidophelus corni* (Kurentsov, 1941) **comb. nov.**; *Eidophelus corpulentus* (Schedl, 1965) **comb. nov.**; *Eidophelus corrugatus* (Schedl, 1950) **comb. nov.**; *Eidophelus creber* (Schedl, 1975) **comb. nov.**; *Eidophelus crenatus* (Sampson, 1914) **comb. nov.**; *Eidophelus cylindricus* (Schedl, 1959) **comb. nov.**; *Eidophelus darwini* (Eichhoff, 1878) **comb. nov.**; *Eidophelus devius* (Schedl, 1975) **comb. nov.**; *Eidophelus dubiosus* (Wood, 1960) **comb. nov.**; *Eidophelus eggersi* (Schedl, 1962) **comb. nov.**; *Eidophelus euphorbiae* (Wood, 1980) **comb. nov.**; *Eidophelus excellens* (Schedl, 1979) **comb. nov.**; *Eidophelus exiguus* (Wood, 1980) **comb. nov.**; *Eidophelus exilis* (Yin, 2001) **comb. nov.**; *Eidophelus eximius* (Schedl, 1942) **comb. nov.**; *Eidophelus expers* (Blandford, 1894) **comb. nov.**; *Eidophelus fagi* (Fabricius, 1798) **comb. nov.**; *Eidophelus fijianus* (Schedl, 1950) **comb. nov.**; *Eidophelus formosanus* (Browne, 1981) **comb. nov.**; *Eidophelus fugax* (Schedl, 1975) **comb. nov.**; *Eidophelus fujisanus* (Nobuchi, 1975) **comb. nov.**; *Eidophelus fulgens* (Schedl, 1975) **comb. nov.**; *Eidophelus fulgidus* (Schedl, 1975) **comb. nov.**; *Eidophelus fulvipennis* (Nobuchi, 1975) **comb. nov.**; *Eidophelus ghanaensis* (Schedl, 1977) **comb. nov.**; *Eidophelus glabratus* (Yin, 2001) **comb. nov.**; *Eidophelus gracilis* (Schedl, 1950) **comb. nov.**; *Eidophelus granulatus* (Wood, 1960) **comb. nov.**; *Eidophelus grobleri* (Schedl, 1962) **comb. nov.**; *Eidophelus hirtus* (Wood, 1974) **comb. nov.**; *Eidophelus hobohmi* (Schedl, 1955) **comb. nov.**; *Eidophelus hylesinopsis* (Schedl, 1975) **comb. nov.**; *Eidophelus incultus* (Yin, 2001) **comb. nov.**; *Eidophelus indicus* (Wood, 1989) **comb. nov.**; *Eidophelus insularis* (Nobuchi, 1975) **comb. nov.**; *Eidophelus insularum* (Krivolutskaya, 1968) **comb. nov.**; *Eidophelus jalappae* (Letzner, 1849) **comb. nov.**; *Eidophelus javanus* (Schedl, 1942) **comb. nov.**; *Eidophelus kanawhae* (Hopkins, 1915) **comb. nov.**; *Eidophelus landolphiae* (Schedl, 1961) **comb. nov.**; *Eidophelus leprosulus* (Browne, 1974) **comb. nov.**; *Eidophelus longipennis* (Eggers, 1936) **comb. nov.**; *Eidophelus magnocularis* (Yin, 2001) **comb. nov.**; *Eidophelus marquesanus* (Beeson, 1935) **comb. nov.**; *Eidophelus mauritianus* (Schedl, 1965) **comb. nov.**; *Eidophelus micans* (Eggers, 1927) **comb. nov.**; *Eidophelus minor* (Eggers, 1927) **comb. nov.**; *Eidophelus minutissimus* (Schedl, 1943) **comb. nov.**; *Eidophelus mus* (Schedl, 1975) **comb. nov.**; *Eidophelus nanulus* (Wood, 1960) **comb. nov.**; *Eidophelus nigellatus* (Schedl, 1950) **comb. nov.**; *Eidophelus nubilus* (Wood, 1960) **comb. nov.**; *Eidophelus ocularis* (Schedl, 1965) **comb. nov.**; *Eidophelus onyanganus* (Schedl, 1941) **comb. nov.**; *Eidophelus opacus* (Schedl, 1959) **comb. nov.**; *Eidophelus pacificus* (Schedl, 1941) **comb. nov.**; *Eidophelus papuanus* (Schedl, 1974) **comb. nov.**; *Eidophelus papuensis* (Wood, 1989) **comb. nov.**; *Eidophelus paradoxus* (Wood, 1992) **comb. nov.**; *Eidophelus parvus* (Hopkins, 1915) **comb. nov.**; *Eidophelus pityophthorinus* (Schedl, 1943) **comb. nov.**; *Eidophelus pleiocarpae* (Schedl, 1957) **comb. nov.**; *Eidophelus polisquamosus* (Yin, 2001) **comb. nov.**; *Eidophelus praeda* (Browne, 1978) **comb. nov.**; *Eidophelus puererae* (Choo and Woo, 1989) **comb. nov.**; *Eidophelus pumilionides* (Schedl, 1977) **comb. nov.**; *Eidophelus pumilus* (Wood, 1960) **comb. nov.**; *Eidophelus punctatulus* (Nobuchi, 1976) **comb. nov.**; *Eidophelus punctatus* (Schedl, 1951) **comb. nov.**; *Eidophelus puncticollis* (Schedl, 1950) **comb. nov.**; *Eidophelus pygmaeolus* (Schedl, 1971) **comb. nov.**; *Eidophelus quadridens* (Browne, 1983) **comb. nov.**; *Eidophelus ramosus* (Beeson, 1935) **comb. nov.**; *Eidophelus robustus* (Schedl, 1955) **comb. nov.**; *Eidophelus rugosus* (Schedl, 1943) **comb. nov.**; *Eidophelus rusticus* (Wood, 1974) **comb. nov.**; *Eidophelus semenovi*

(Kurentsov, 1941) **comb. nov.**; *Eidophelus separandus* (Schedl, 1965) **comb. nov.**; *Eidophelus setifer* (Wood, 1974) **comb. nov.**; *Eidophelus sodalis* (Schedl, 1965) **comb. nov.**; *Eidophelus spessivtzevi* (Berger, 1917) **comb. nov.**; *Eidophelus spirostachius* (Schedl, 1958) **comb. nov.**; *Eidophelus splendens* (Schedl, 1975) **comb. nov.**; *Eidophelus squamatilis* (Schedl, 1977) **comb. nov.**; *Eidophelus squamosus* (Schedl, 1942) **comb. nov.**; *Eidophelus squamulosus* (Eggers, 1936) **comb. nov.**; *Eidophelus stephegynis* (Hopkins, 1915) **comb. nov.**; *Eidophelus takahashii* (Nobuchi, 1975) **comb. nov.**; *Eidophelus tarawai* (Beaver, 1990) **comb. nov.**; *Eidophelus tonsus* (Schedl, 1969) **comb. nov.**; *Eidophelus tricolor* (Lea, 1910) **comb. nov.**; *Eidophelus trucis* (Wood, 1974) **comb. nov.**; *Eidophelus uncatus* (Schedl, 1971) **comb. nov.**; *Eidophelus usagaricus* (Eggers, 1922) **comb. nov.**; *Eidophelus varius* (Schedl, 1975) **comb. nov.**; *Eidophelus venustus* (Schedl, 1953) **comb. nov.**; *Eidophelus yunnanensis* (Yin, 2001) **comb. nov.**; *Eidophelus zachvatkini* (Krivolutskaya, 1958) **comb. nov.**; *Ernoporus corpulentus* (Sampson, 1919) **comb. nov.**; *Ernoporus exquisitus* (Bright, 2019) **comb. nov.**; *Ernoporus guiboutiae* (Schedl, 1957) **comb. nov.**; *Ernoporus minutus* (Bright and Torres, 2006) **comb. nov.**; *Hypothenemus attenuatus* (Eggers, 1935) **comb. nov.**; *Hypothenemus loranthus* (Schedl, 1942) **comb. nov.**; *Hypothenemus novateutonicus* (Schedl, 1951) **comb. nov.**; *Hypothenemus pullus* (Wood, 1971) **comb. nov.** Following assessment of diagnostic characters, the following species were transferred to a different genus: *Afrocosmoderes madagascariensis* Schedl, 1961 **comb. nov.**; *Afrocosmoderes caplandicus* (Schedl, 1965) **comb. nov.**; *Afrocosmoderes grobleri* (Schedl, 1961) **comb. nov.**; *Afrocosmoderes niger* (Schedl, 1961) **comb. nov.**; *Afrocosmoderes pellitus* (Schedl, 1953) **comb. nov.**; *Afrocosmoderes pennatus* (Schedl, 1953) **comb. nov.**; *Eidophelus concentralis* (Schedl, 1975) **comb. nov.**; *Eidophelus inermis* (Browne, 1984) **comb. nov.**; *Eidophelus insignis* (Browne, 1984) **comb. nov.**; *Eidophelus kinabaluensis* (Bright, 1992) **comb. nov.**; *Eidophelus philippinensis* (Schedl, 1967) **comb. nov.**; *Eidophelus podocarpi* (Bright, 1992) **comb. nov.**; *Ernoporus imitatrix* (Schedl, 1977) **comb. nov.**; *Ernoporus minor* (Schedl, 1942) **comb. nov.**; *Ernoporus parvulus* (Eggers, 1943) **comb. nov.**; *Indocryphalus sericeus* (Schedl, 1942) **comb. nov.**; *Macrocryphalus elongatus* (Schedl, 1965) **comb. nov.**; *Macrocryphalus punctipennis* (Schedl, 1965) **comb. nov.**; *Microcosmoderes shoreae* (Schedl, 1953) **comb. nov.**; *Stegomerus parvatis* (Wood, 1974) **comb. nov.**; *Stephanopodius dubiosus* (Schedl, 1970) **comb. nov.** Twenty-nine secondary homonyms were created following genus synonymy, and are designated replacement names: *Afrocosmoderes schedli* Johnson **nom. nov.** (=*Euptilius madagascariensis* Schedl, 1963 **syn. nov.**); *Cryphalus amplicollis* Johnson **nom. nov.** (=*Cryphalus laticollis* Browne, 1984 **syn. nov.**); *Cryphalus eggersi* Johnson **nom. nov.** (=*Cryphalus confusus* Eggers, 1927 **syn. nov.**); *Cryphalus fuscus* Johnson **nom. nov.** (=*Cryphalus cylindrus* Browne, 1984 **syn. nov.**); *Cryphalus gracilis* Johnson **nom. nov.** (=*Cryphalus laevis* Browne, 1984 **syn. nov.**); *Cryphalus luteus* Johnson **nom. nov.** (=*Margadillius fulvus* Browne, 1984 **syn. nov.**); *Cryphalus minusculus* Johnson **nom. nov.** (=*Hypocryphalus minutus* Browne, 1980 **syn. nov.**); *Cryphalus ozopemoides* Johnson **nom. nov.** (=*Hypocryphalus montanus* Schedl, 1974 **syn. nov.**); *Cryphalus pellicius* Johnson **nom. nov.** (=*Hypocryphalus pilifer* Schedl, 1979 **syn. nov.**); *Cryphalus punctistriatulus* Johnson **nom. nov.** (=*Cryphalus striatulus* Browne, 1981 **syn. nov.**); *Cryphalus schedli* Johnson **nom. nov.** (=*Hypocryphalus formosanus* Schedl, 1952 **syn. nov.**); *Cryphalus solomonensis* Johnson **nom. nov.** (=*Margadillius terminaliae* Browne, 1984 **syn. nov.**); *Cryphalus spissepilosus* Johnson **nom. nov.** (=*Cryphalus densepilosus* Schedl, 1943 **syn. nov.**); *Cryphalus storckiellae* Johnson **nom. nov.** (=*Cryphalus striatus* Browne, 1974 **syn. nov.**); *Cryphalus takahashii* Johnson **nom. nov.** (=*Euptilius exiguus* Browne, 1984 **syn. nov.**); *Eidophelus alstoniae* Johnson **nom. nov.** (=*Chiloxylon sumatranus* Schedl, 1970 **syn. nov.**); *Eidophelus brighti* Johnson **nom. nov.** (=*Hemicryphalus minutus* Bright, 1992 **syn. nov.**); *Eidophelus brownei* Johnson **nom. nov.** (=*Euptilius papuanus* Browne, 1983 **syn. nov.**); *Eidophelus furvus* Johnson **nom. nov.** (=*Cryphalophilus ater* Schedl, 1972 **syn. nov.**); *Eidophelus levis* Johnson **nom. nov.** (=*Eidophelus gracilis* Browne, 1984 **syn. nov.**); *Eidophelus lucidus* Johnson **nom. nov.** (=*Lepicerinus pacificus* Schedl, 1959 **syn. nov.**); *Eidophelus minusculus* Johnson **nom. nov.** (=*Eidophelus minutissimus* Schedl, 1962 **syn. nov.**); *Eidophelus niger* Johnson **nom. nov.** (=*Ernoporicus ater* Nobuchi, 1975 **syn. nov.**); *Eidophelus parvulus* Johnson **nom. nov.** (=*Cryphalus parvus* Browne, 1984 **syn. nov.**); *Eidophelus rhododendri* Johnson **nom. nov.** (=*Hemicryphalus squamosus* Bright, 1992 **syn. nov.**); *Eidophelus schedli* Johnson **nom. nov.** (=*Cryphalomorphus ceylonicus* Schedl, 1959 **syn. nov.**); *Eidophelus yinae* Johnson **nom. nov.** (=*Scolytogenes venustus* Yin, 2001 **syn. nov.**); *Hypothenemus marginatus* Johnson **nom. nov.** (=*Periocryphalus sobrinus* Wood, 1974 **syn. nov.**); *Hypothenemus squamosulus* Johnson **nom. nov.** (=*Ptilopodius squamosus* Schedl, 1953 **syn. nov.**). Two replacement names are now unnecessary: *Cryphalus striatulus* (Browne, 1978) **stat. res.** (=*Hypothenemus brownei* Beaver, 1991 **syn. nov.**); *Macrocryphalus oblongus* Nobuchi, 1981 **stat. res.** (=*Hypothenemus nobuchii* Knížek, 2011 **syn. nov.**). We also acknowledge the original description of several species by Eichhoff, 1878a which have been widely referenced as a later description (Eichhoff, 1878b). The following taxonomic changes are provided to acknowledge the changes: *Cryphalus horridus* Eichhoff, 1878a (=*Cryphalus horridus* Eichhoff, 1878b **syn. nov**); *Cryphalus numidicus* Eichhoff, 1878a (=*Cryphalus numidicus* Eichhoff, 1878b **syn. nov**); *Cryphalus submuricatus* Eichhoff, 1878a (=*Cryphalus submuricatus* Eichhoff, 1878b **syn. nov**); *Eidophelus aspericollis* (Eichhoff, 1878a) (=*Eidophelus aspericollis* Eichhoff, 1878b **syn. nov**); *Hypothenemus arundinis* (Eichhoff, 1878a) (=*Hypothenemus arundinis* Eichhoff, 1878b **syn. nov**); *Hypothenemus birmanus* (Eichhoff, 1878a) (=*Hypothenemus birmanus* Eichhoff, 1878b **syn. nov**); *Hypothenemus fuscicollis* (Eichhoff, 1878a) (=*Hypothenemus fuscicollis* Eichhoff, 1878b **syn. nov**); *Hypothenemus rotundicollis* (Eichhoff, 1878a) (=*Hypothenemus rotundicollis* Eichhoff, 1878b **syn. nov**). Subjective species-level changes are minimal. The following synonymies are proposed: *Cryphalus papuanus* (Schedl, 1973) (=*Ernoporus*

antennarius Schedl, 1974 **syn. nov.**); *Eidophelus concentralis* (Schedl, 1975) (=*Margadillius concentralis* Schedl, 1975 **syn. nov.**). A neotype for *Periocryphalus sobrinus* Wood, 1974 and its replacement name *Hypothenemus marginatus* **nom. nov.** is designated at USNM due to the holotype being lost and replaced with a different species.

Key words: taxonomy, systematics, phylogeny, forest entomology

Introduction

Bark and ambrosia beetles (Curculionidae: Scolytinae) are an insect group of high economic and scientific importance because they include pests of forests and crops. Scolytines exhibit a wide array of feeding strategies but are primarily composed of two distinct groups: bark and ambrosia beetles. True to their common name, bark beetles are phloeophagous and feed predominantly on phloem of dead, dying and living trees. Ambrosia beetles bore into the xylem of a dead or dying tree and cultivate a symbiotic fungus (Kirkendall et al. 2015). Despite this diversity, scolytines are commonly collectively referred to as bark beetles. Scolytines include a handful of species that are notorious forest pests which kill trees on a landscape scale, but the overwhelming majority of species are benign in their native habitats. The cryptic nature of boring under bark and into wood makes scolytines difficult to detect and as a result many species have become established outside of their native range. Over the last 50 years, international trade has led to an exponential increase in the establishment of exotics and as a result, many invasive scolytine species are emerging (Kirkendall and Faccoli 2010, Haack and Rabaglia 2013, Hughes et al. 2017). These species are often difficult to identify because they arrive from regions that have been historically understudied. Despite more than a century of bark beetle systematic research, there are no identification resources for most of the world's approximately 6,000 species (Hulcr et al. 2015). While identification of some bark beetles is important due to their pest status, there are thousands of other scolytine species which have no known economic impact yet are ecologically significant due to their role as one of the first decomposers of woody material (Stokland 2012). Our ability to identify these is no less important as they represent a treasure trove of biodiversity.

Scolytines have evolved an unprecedented variety of genetic and reproductive strategies, symbioses with fungi and associations with various hosts or substrates (Kirkendall et al. 2015, Gohli et al. 2017, Johnson et al. 2018). Many species are also becoming endangered, as their hosts or ecosystems succumb to pressures of the Anthropocene (e.g., Wagner and Todd 2016). In order to facilitate description, understanding and preservation of this unique species diversity, it is imperative that the higher-level classification is clarified.

The least well-documented group of bark beetles is almost certainly the Cryphalini. In almost every recent treatment of the group, the inappropriate delineation of genera is acknowledged (Wood 1986a, 2007; Alonso-Zarazaga and Lyal 2009). The polyphyly of the group as a whole and of individual genera has also been clearly documented in molecular studies (Jordal and Cognato 2012, Gohli et al. 2017, Johnson et al. 2018, Pistone et al. 2018). Even from a morphological perspective, there has never been a thorough analysis that recovered a monophyletic Cryphalini; the classification was always based on taxonomists' intuition, cursory morphological analyses, or the acknowledgement of the non-monophyly of genera (Wood 1986a). The large number of species with few utilized morphological diagnostic characters undoubtedly limited the resolution in the classification of cryphalines.

However, resolution of even difficult scolytine groups is possible when detailed morphological analysis and molecular phylogenetics are combined, as shown for many other groups such as Micracidini (Jordal and Kaidel 2017).

History of Cryphalini Classification

The first mention of Cryphalini as a group name was by Lindemann in 1877. The group-concept was much broader, including *Pityophthorus* Eichhoff, 1864, *Hypoborus* Erichson, 1836, *Hylocurus* Eichhoff, 1872, and *Xyloctonus* Eichhoff, 1872, all of which are currently placed in separate tribes.

Eichhoff described many of the contemporary genera, plus several which are now junior synonyms (Eichhoff 1878a). Most contemporary Cryphalini genera were classified in 'Cryphalidae' which was a much narrower concept than previously described, containing the known Cryphalini genera (except *Eidophelus* Eichhoff, 1876) plus *Hypoborus* and *Liparthrum* Wollaston, 1854 (Hypoborini) and what is now the genus *Pityoborus* Blackman, 1922 (Corthylini). Other groups, such as contemporary Micracidini LeConte, 1876 and Xyloctonini Eichhoff, 1878, were explicitly described as different tribes.

This approximate group concept of Cryphalini remained until Hopkins presented a major reclassification of Scolytinae in 1915, with a group 'Cryphalinae' in an even broader sense including the contemporary tribes Xyleborini and some genera in the current Dryocoetini Lindemann, 1877 and Corthylini LeConte, 1876. Most of the contemporary Cryphalini are contained in Hopkins 'Division I, Subdivision A', a group described based on the type of vestiture ('with scales, rarely with hairs') and the pattern of asperities along the anterior margin of the pronotum. The characters used to describe and diagnose the genera within the Cryphalini include the presence of distinct elytral strial punctures, the shape of the lateral margins of the pronotum, the degree to which the pronotum was produced, the apex of the elytra, and most importantly, the morphology of the antennae. *Eidophelus* was considered in a different subdivision with *Dendroterus* Blandford, 1904 and some other genera now placed in Dryocoetini.

Balachowsky (1949) presented a clarified classification of bark beetles which reflects most contemporary tribes. While restricted to the fauna of France, it clearly described Cryphalini as different from Hypoborini. Wood (1954) evaluated the North American Cryphalini genera and species, representing the contemporary scope of the tribe for the region. Two additional genera from East Asia were described by Nobuchi (1981), inferred partly by new sets of characters from the proventriculus (Nobuchi 1969). While these alone enabled identification of most scolytine genera, they were not widely adopted as a diagnostic set of characters.

Schedl was a major contributor to Cryphalini systematics. While very prolific in describing new species, his classification of Cryphalini

did not settle any of the considerable confusion and his nomenclatural practices were not consistently valid (see Wood and Bright 1992). Schedl described five genera in the contemporary Cryphalini, but four of these are now regarded as junior synonyms.

The most recent treatment of Cryphalini was Wood's (1986a) review of all scolytine tribes and genera. In this review, Cryphalini was diagnosed based on the combination of the ascending costal margin of the elytra, by the base of the elytra that is unarmed (or rarely armed with a continuous line, not crenulations), by the declivous (steeply sloped) pronotum usually armed with serrations and asperities, by the concealed head when viewed dorsally, by the eye that is 'usually' entire and 'less commonly emarginated', by the antennal funicle with no more than five segments, by the antennal club which is 'strongly flattened' and never truncate, by the lateral margins of the pro- and mesotibiae armed with denticles, and by the metanepisternum which has a posterior margin concealed by the elytron.

Wood and Bright brought significant order to the chaos of the classification of Scolytinae as a whole, including Cryphalini. Many genera were synonymized, and a small number was described. Their compilation of the catalogs (Wood and Bright 1987; Wood and Bright, 1992) is a milestone in scolytine systematics and provides a very useful starting point for taxonomic reviews. *Allothenemus* Bright and Torres, 2006 was subsequently described. During the final stages of this manuscript preparation, four further genera were described in Cryphalini: *Atomothenemus* Bright, 2019, *Microsomus* Bright, 2019, *Pygmaeoborus* Bright, 2019, and *Trypolepis* Bright, 2019.

Contemporary Molecular Phylogenetics

All published molecular phylogenies to date found Cryphalini polyphyletic (Jordal and Cognato 2012, Gohli et al. 2017, Johnson et al. 2018, Pistone et al. 2018). *Hypothenemus*, *Cryphalus* and *Trypophloeus* are typically grouped with Xyloterini, *Cryptocarenus* is nested among Corthylini (genetically similar to *Araptus* Eichhoff, 1872 or *Dacnophthorus* Wood, 1975), *Stephanopodius* is sister to or nested in *Glostatus*, and several other genera, including *Eidophelus*, *Ernoporus*, *Scolytogenes* and *Procryphalus* are found in another clade.

Cryphalini genera are frequently reported as polyphyletic. *Hypocryphalus* and *Cryphalus* are intermixed (Johnson et al. 2017, Johnson et al. 2018), as are *Ptilopodius*, *Ernoporicus* and *Scolytogenes* (Johnson et al. 2018). Our most recent phylogenomic treatment of most scolytine tribes with special focus on Cryphalini is the first that resolved deep nodes and clearly demonstrated the relationships between most genera and tribes (Johnson et al. 2018, but see also Pistone et al. 2018). The phylogeny by Johnson et al. (2018) serves as the background for the present reclassification (Fig. 1).

This review and revision of genera brings together history, morphology and genetics to synthesize a biologically meaningful classification of genera currently placed in Cryphalini sensu Wood 1986a. With a molecular phylogeny as the scaffold, external and internal characters are assessed for their utility in classification, and most species are placed into genera. The genera are redescribed based on a consistent set of characters. A dichotomous key, as well as photos are presented to illustrate the morphological diversity of the genera and to assist identification of the former Cryphalini genera.

Materials and Methods

Materials Examined

Type and nontype material were studied from the institutions listed in Table 1. Additional nontype specimens were examined for dissection and to gather sequencing information. All specimens examined are presented in Supp Table 1 (online only). A morphological matrix was made for specimens representing all species included in this analysis, primarily types or material with genetic information.

The numbers of specimens for each genus is summarized in Table 2. Specimens examined were assigned to species based on the similarity of their external morphology to that of identified specimens, usually types if available, or internal morphology if presented in past literature (particularly Tsai and Li (1963)). Some characters were used to determine species but were not used for morphological analysis and are not necessarily scored in the morphology matrix. These include difficult to code characters such as the shape and the vestiture, or autapomorphies. Preliminary diagnoses of genera for undetermined specimens were based on the identification key by Wood (1986a) or based on overall similarity to described species.

Representatives of genera were photographed using various camera-microscope arrangements, predominantly using a digital SLR (Canon rebel t3i) mounted on an Olympus UIS2 system (BX53 microscope) with 5×–40× objectives, lit with diffused halogen lights or a camera flash. All photos are focused stacked (Helicon Focus, Helicon Soft). Photographs were edited for color balance, light levels and contrast, with background objects removed for clarity using Photoshop (Photoshop CC, Adobe 2015).

Molecular Phylogenetics

Molecular phylogenies were taken from previous studies involving large datasets of tens or hundreds of genes (Johnson et al. 2018, Pistone et al. 2018).

Phylogenies were expanded using available data mined from GenBank (www.ncbi.nlm.nih.gov/genbank/) and BOLD (v3.boldsystems.org/) sequence repositories. The partial nuclear large subunit ribosomal gene (28S) was used for phylogenetic placement of additional species. Additional specimens were also added to the dataset. Extractions were made with DNeasy extraction kit (Qiagen, USA), and 28S gene was amplified using PCR following methods by Sequeira et al. (2000), that used the primers GAGAGTTMAASAGTACGTGAAAC and CCTGACTTCGTCCTGACCAGGC, and sequenced using Sanger sequencing.

Three sequences were omitted from analyses due to erroneous identities (AF308395, AF308388, KY805970); each of them closely matched species from a different genus suggesting a cross-contamination. One sequence was omitted due to poor alignment suggesting nontarget amplification (JX263691). Duplicates of species were omitted following confirmation of identity.

The sequences were aligned using MAFFT (Katoh and Standley 2013), and inferred using maximum likelihood (RAxML V.8.2.3) (Stamatakis 2014) constrained to the trees by Johnson et al. (2018).

Trees were estimated constrained or unconstrained to the topology found by Johnson et al. (2018). A tree was first made including all outgroups to confirm tribal placement of specimens. The well-supported (>95% likelihood bootstrap) clades identified were then analyzed individually and recalculated to better estimate relative branch lengths. The most closely related genera to the identified separate clades of former Cryphalini were used as outgroups for the separate analyses. Sequences of *Scolytomimus* Blandford, 1895, *Xyloctonus* Eichhoff, 1872, *Strombophorus* Hagedorn, 1909, and *Hapalogenius* Hagedorn, 1912 were used as outgroups for a clade with *Cryphalus*, *Hypothenemus*, *Trypophloeus*, *Coriacephilus* and *Trypodendron* and *Cryphyophthorus* Schedl, 1953, *Styracoptinus* Wood, 1962, *Liparthrum*, and *Hypoborus* were used as outgroups for the *Ernoporus*/*Procryphalus*/*Eidophelus* clade.

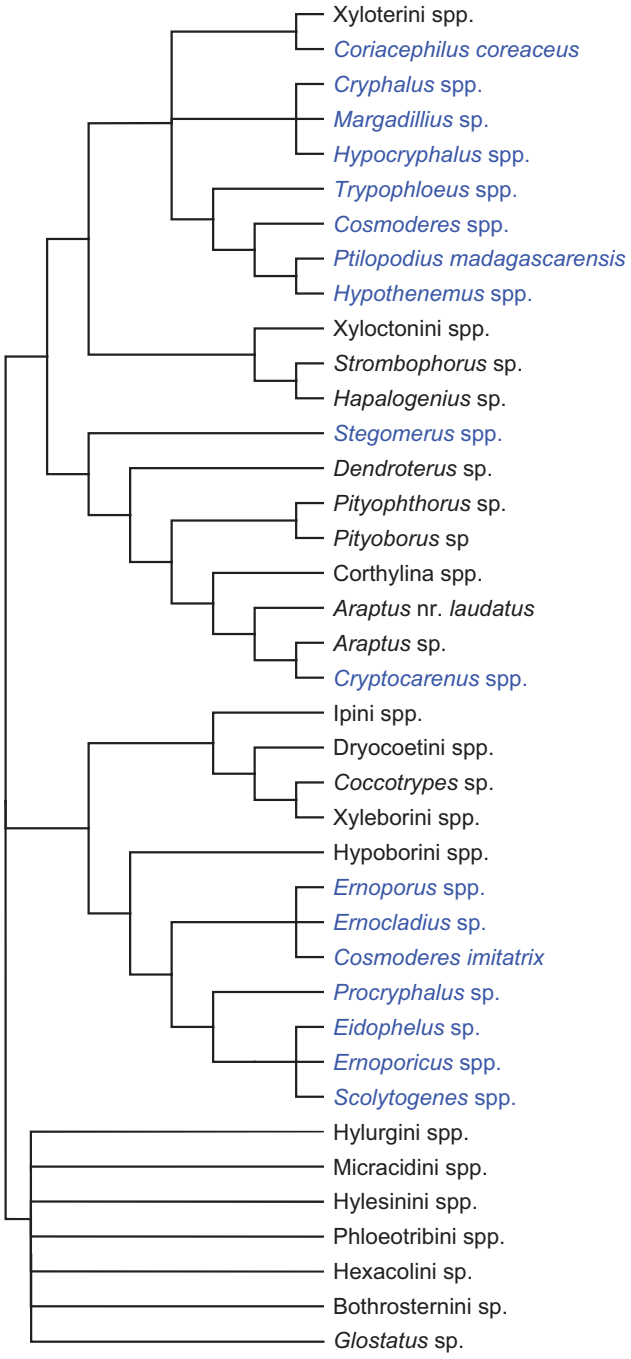

Figure 1. Simplified cladogram inferred from a >100-gene phylogeny presented in Johnson et al. (2018). Blue text represents genera of Cryphalini sensu (Wood 1986a)

Morphology

External morphological characters were taken from Wood (1986a) or defined by the senior author during this study. External morphology was observed using a dissecting microscope (mostly Olympus SZX16, plus dissecting microscopes available at museums), or a compound microscope (Olympus BX53). Some characters were scored based on photographs of type material. Terminology was based on conventional scolytine literature (Wood 1986a, Lyal 2018) and is illustrated in Figs. 2 and 3. Characters, character states, and references are presented in the Supplementary material.

Specimens were dissected under a microscope to study internal characters, primarily the proventriculus and aedeagus. Specimens were all photographed from at least a lateral view for digital vouchering prior to dissection. Specimens with large series from the same collecting event were dissected in soapy water and discarded after use. Specimens from dubious series, rare collecting events, or museum types were dissected in 95% ethanol, and remains were pinned, slide mounted, and/or stored in ethanol.

The proventriculus was extracted from the specimen, soaked in NaOH if appropriate, cut in one or two places, and unrolled onto a microscope slide with water. The proventriculus slide mounts were photographed from the internal face. For male specimens, the aedeagus was also dissected, cleared using NaOH, and temporarily mounted on a slide with water or permanently mounted in Euparal (BioQuip Inc., USA). The aedeagus was

Table 1. Acronyms used for entomological collections, based on Evenhuis (2018)

Acronym	Repository
AMNH	USA, New York, New York, American Museum of Natural History
AMNZ	New Zealand, Auckland, Auckland Institute and Museum
AMS	Australia, New South Wales, Sydney, Australian Museum
ANIC	Australia, Australian Capital Territory, Canberra City, CSIRO, Australian National Insect Collection
BMNH	United Kingdom, London, The Natural History Museum [formerly British Museum (Natural History)]
BPBM	USA, Hawaii, Honolulu, Bernice P. Bishop Museum
CAS	USA, California, San Francisco, California Academy of Sciences
CNC	Canada, Ontario, Ottawa, Canadian National Collection of Insects
FMNH	USA, Illinois, Chicago, Field Museum of Natural History
FRIM	Malaysia, Kuala Lumpur, Forest Research Institute
FSCA	USA, Florida, Gainesville, Division of Plant Industry, Florida State Collection of Arthropods
IFRI	India, Uttarakhand, Dehradun, Forest Research Institute
IPKE	Germany, Eberswalde, Institut für Pflanzenschutzforschung Kleinmachnow Bereich Eberswalde
IRSM	France, Paris, Institut de Recherche Scientifique de Madagascar Tananarive
ITLJ	Japan, Ibaraki, Tsukuba, National Institute of Agro-environmental Sciences
IZCAS	China, Beijing, Chinese Academy of Sciences, Institute of Zoology
MCZ	USA, Massachusetts, Cambridge, Harvard University, Museum of Comparative Zoology
MHNG	Switzerland, Geneva, Muséum d'Histoire Naturelle
MNHN	France, Paris, Muséum National d'Histoire Naturelle
MZPW	Poland, Warszawa [=Warsaw], Polish Academy of Science, Museum and Institute of Zoology
MZSP	Brazil, São Paulo, São Paulo, Museu de Zoologia da Universidade de São Paulo
NHMB	Switzerland, Basel, Naturhistorisches Museum
NHMW	Austria, Wien, Naturhistorisches Museum Wien
NHRS	Sweden, Stockholm, Naturhistoriska riksmuseet
OSAC	USA, Oregon, Corvallis, Oregon State University, Oregon State Arthropod Collection
PPST	Japan, Tokyo, Plant protection Station
QM	Australia, Queensland, South Brisbane, Queensland Museum
RBINS	Belgium, Brussels, Royal Belgian Institute of Natural Sciences
RMCA	Belgium, Tervuren, Musée Royal de l'Afrique Centrale
RMNH	Netherlands, Leiden, Naturalis Biodiversity Centre [formerly Rijksmuseum van Natuurlijke Historie]
SAM	Australia, South Australia, Adelaide, South Australian Museum
SANC	South Africa, Pretoria, South African National Collection of Insects
SEMC	USA, Kansas, Lawrence, University of Kansas, Snow Entomological Museum
SZMN	Russia, Novosibirsk, Institute of Animal Systematics and Ecology, Siberian Zoological Museum
TMSA	South Africa, Gauteng, Pretoria, Ditsong National Museum of Natural History [formerly Transvaal Museum]
USNM	USA, Washington D.C., National Museum of Natural History, [formerly, United States National Museum]
UUZM	Sweden, Uppsala, Uppsala University
ZIN	Russia, St. Petersburg, Russian Academy of Sciences, Zoological Institute
ZMHB	Germany, Berlin, Museum für Naturkunde der Humboldt-Universität
ZMUC	Denmark, København [= Copenhagen], University of Copenhagen, Zoological Museum
ZMUM	Russia, Moscow, Moscow State University, Zoological Museum

photographed dorsally and/or ventrally (conventionally only dorsally are displayed). Photos of internal structures are taken using Olympus BX53 with 20× and 40× objectives, using a mounted dSLR. Photos of the proventriculus and genitalia were typically stacked images (Helicon Focus V. 6.0, Helicon Soft.). The terminology for the proventriculus (Fig. 4) follows Nobuchi (1969) and Jordal and Kaidel (2017). The proventriculus was illustrated with the anterior side on the top of the page, contrary to Nobuchi (1969). Aedeagus morphology (Fig. 5) terms follows Glossary of Weevil Characters (Lyal 2018) which differs from traditional and recent terms used in Scolytinae-specific literature.

All specimens included in the molecular phylogeny had their morphology scored. The retention index and the consistency index were calculated for all scored characters using the phangorn package for R (Schliep 2010) (Table 3). This was used to help inform arbitrary generic limits and provide a basis for the notes for diagnosis of genera.

Resolving Taxonomy and Nomenclature

Taxonomic and nomenclatural acts, including descriptions of genera, synonymy of genera, descriptions of species, synonymy of species, new combinations of species, and suppression of species, were initially mined from literature, especially from Wood and Bright (1987, 1992), Bright and Skidmore (1997, 2002), Bright (2014), Alonso-Zarazaga and Lyal (2009), and Alonso-Zarazaga et al. (2017), and verified with the original descriptions.

The reclassification of tribes and genera were based on reciprocal monophyly. Taxonomic changes were only made to fulfill reciprocal monophyly, or to describe morphologically or ecologically distinct groups of species (in terms of genera) or groups of genera (in terms of tribes and sub-tribes) without conflicting with reciprocal monophyly.

Most, but not all, references for taxonomic and nomenclatural acts (e.g., described genera, synonymy of genera, described species, and synonymy of species) were checked directly by the authors. The information was stored as a database (SQLite 3.0) and queried to generate the current valid names and their junior synonyms.

Unless explicitly stated, the authority of the taxonomic and nomenclatural changes are all the authors of this monograph.

Nomenclature

This paper and the nomenclatural act(s) it contains have been registered in Zoobank (www.zoobank.org), the official register of the

Table 2. Number of specimens of all proposed genera examined

Genus	Proposed tribe	Described species	Subjective synonyms	Species examined (undetermined)	Molecular phylogeny
Afrocosmoderes	Trypophloeini	7	0	5	2
Atomothenemus	Trypophloeini	1	0	0	0
Coriacephilus	Coriacephilini	5	1	3	1
Cosmoderes	Trypophloeini	15	2	10(3)	4(2)
Cryphalus	Cryphalini	252	54	121(9)	24(6)
Hypothenemus	Trypophloeini	220	244	72(10)	17(2)
Macrocryphalus	Trypophloeini	3	0	3	0
Microcosmoderes	Trypophloeini	1	0	1	1
Microsomus	Trypophloeini	1	0	0	0
Pygmaeoborus	Trypophloeini	1	0	0	0
Trypophloeus	Trypophloeini	15	13	4	6
Indocryphalus	Xyloterini	10	5	3	2
Trypodendron	Xyloterini	14	14	4	3
Xyloterinus	Xyloterini	1	1	1	1
Eidophelus	Ernoporini	152	23	70(11)	13(10)
Ernoporus	Ernoporini	19	6	10(3)	5(1)
Hemicryphalus	Ernoporini	3	0	2	1
Procryphalus	Ernoporini	4	4	4	3
Acorthylus	Corthylini	6	1	4	0
Cryptocarenus	Corthylini	16	10	12	4
Neocryphus	Corthylini	1	1	1	1
Stegomerus	Corthylini	9	0	7	2
Trypolepis	Corthylini	1	0	0	0
Stephanopodius	Xyloctonini	7	0	7(2)	1(2)

Numbers in brackets represent undetermined or undescribed species, not included in the total counts.

International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is urn:lsid:zoobank.org:pub:0CB0963A-2CEE-493F-AFF8-C5E1B2610B16

Results and Discussion

Molecular phylogeny and taxonomic changes

Thirty additional taxa were added to the phylogeny by Johnson et al. (2018) including several generic types. The major conclusions from the phylogeny were noted by Johnson et al. (2018). The additional taxa enabled a more thorough assessment of character evolution and corroborated generic synonymy.

A clade (Figs. 6 and 7) contained species from the previously recognized genera *Allernoporus*, *Coriacephilus*, *Cosmoderes*, *Cryphalus*, *Hypocryphalus*, *Hypothenemus*, *Indocryphalus*, *Trypophloeus*, *Trypodendron*, and *Xyloterinus*. Additional species from *Afromicracis* (Micracidini) and *Ptilopodius* were among this clade, although most species for these genera, including those that most closely match the type of each genus, were placed outside this clade.

The clade shares numerous diagnostic characters, such as an emarginated or divided eye, a postnotum which is separated from the mesonotum by a membrane (fused in most other Scolytinae) and the penis apodemes which are separate or only weakly fused. Among this clade, there are four clades which could correspond to tribes based on contemporary classification with enforced monophyly.

Indocryphalus, *Trypodendron*, and *Xyloterinus* are the genera of Xyloterini, the most senior group name in this clade, and have distinct characters such as completely divided eyes and presence of a mycangium on the hypomeron. This group name has remained in consistent use.

Three additional clades are present which, unless included in Xyloterini, would be paraphyletic if maintained as Cryphalini, and therefore warrant resurrection/description of tribe names to maintain monophyly while maintaining the use of Xyloterini.

The genus group names within the clade of Xyloterini were not all monophyletic. *Indocryphalus* was found to be paraphyletic (Fig. 6). This result provides an explanation for the conflicting hypotheses of the relations between the genera found with morphology by Cognato et al. (2015) and with molecular data by Johnson et al. (2018) and Pistone et al. (2018) because the taxa selected do not represent a monophyletic genus.

A clade containing *Hypothenemus* also includes two distantly related lineages, for which the morphology and biology differ substantially from *Hypothenemus*, and which are here described as new genera.

Another major group of the former Cryphalini taxa form a distantly related clade sister to Hypoborini, containing species previously included in the genera *Eidophelus*, *Ernoporus*, *Ernocladius*, *Hemicryphalus*, *Margadillius*, *Ptilopodius*, *Procryphalus*, and *Scolytogenes*.

Parts of the phylogeny were not fully resolved; the relationship between (*Ernoporus* + *Ernocladius* + *Margadillius parvulus*), *Cosmoderes imitatrix* and *Hemicryphalus* (Fig. 8) was poorly resolved in the phylogeny, with several of the inferred trees showing deviant relationships.

Several genera clearly belong to Corthylini: *Acorthylus*, *Cryptocarenus*, *Neocryphus* and *Stegomerus*, with *Cryptocarenus* and *Stegomerus* confirmed with molecular data. *Stephanopodius* is likely intermixed with *Glostatus*, and is transferred to Xyloctonini.

Macrocryphalus has been resurrected and is redescribed with three species. DNA sequences, morphology of the aedeagus, eye, and antennae suggest placement in Trypophloeini.

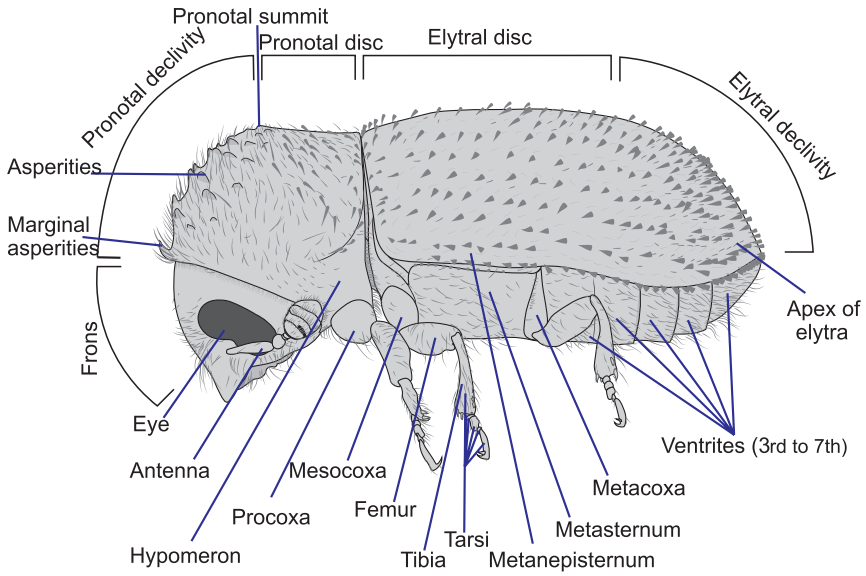

Figure 2. Labeled diagram of external morphology used in this study. Specimen illustrated is *Hypothenemus birmanus.*

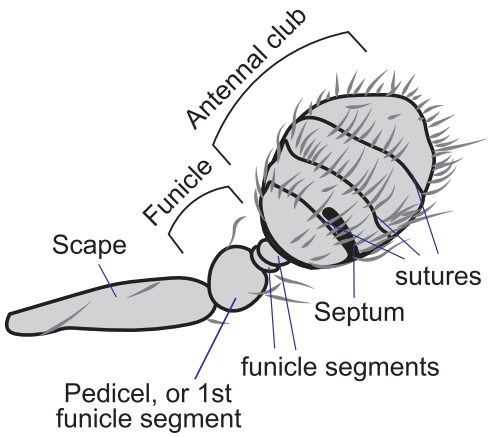

Figure 3. Labeled diagram of antennal morphology used in this study. Specimen illustrated is *Hypothenemus birmanus.*

Phylogenetic Value of Characters

Our phylogenetic analysis of morphological characters across Cryphalini sensu Wood, 1986a, combined with the phylogenetic placement of each examined species, enabled us to infer the relative phylogenetic information of each character, and thus a proxy for its value for systematics of this group (Table 3).

Eye

The shape of the eye has been widely used to describe and diagnose the genera of Cryphalini (Hopkins 1915; Wood 1982, 1986a, 2007). The emarginated eye is a useful character for diagnosing the three major clades of the former Cryphalini: The clade containing taxa grouping with *Cryphalus*, *Trypophloeus*, *Coriacephilus*, and *Trypodendron* has an emarginated or completely divided eye, whereas the clade containing *Ernoporus* and close relatives has an entire eye, and members that belong in Corthylini have a long and broadly emarginated eye. There are, however, notable exceptions which may mislead identification. *Hypothenemus georgiae* was originally described as the sole member of the genus *Trischidias* partly based on its entire eye, yet this trait can vary between specimens from the same collection (24 specimens USA: FL: Archbold bio. stn. *Quercus*, Deyrup coll; repository: UFFE 25365). The same applies to some other members of *Hypothenemus*, especially those which used to belong in the genus *Trischidias* (Atkinson, 1993). Similarly, some members of *Eidophelus*, which, for most specimens have entire eyes, have indication of an emargination. This is broader and shallower than usual in Cryphalini *s. str.*

Antennae

The number of funicle segments has been widely used to delimit many genera of Scolytinae, including Cryphalini (Hopkins 1915). This was apparently the last remaining diagnostic character for distinguishing *Hypocryphalus* and *Margadillius* from *Cryphalus* (Wood, 1986a). This character has low phylogenetic value (CI: 0.13; RI: 0.42) at the genus level, and we recommend that the number of funicular segments is not used to classify the former cryphaline genera. Some species (e.g., *C. dilutus* and *C. mangiferae*) have variable numbers of funicular segments (four or five), and the occurrence of three, four, or five funicular segments are scattered widely across the phylogeny of *Cryphalus*.

Several genera usually possess an antennal septum, which is a sclerotized subsurface structure visible as a dark line. This structure is difficult to observe without removal and slide mounting, especially if the antennal cuticle is dark. Furthermore, in the two speciose genera *Hypothenemus* and *Eidophelus* have multiple losses and gains of an antennal septum. However, most species in these genera possess a septum, which is transverse in *Hypothenemus* and oblique in *Eidophelus*.

Both the presence and shape of the antennal sutures have been used to diagnose Cryphalini genera. We found many instances where the presence and shape of the sutures varied among related species suggesting sutures have been lost or gained multiple times, which has undoubtedly lead to the confusing array of species described in the genera *Ptilopodius* and *Cosmoderes*. The presence of sutures is invariable in some genera (*Cryphalus* always have sutures) and variable in others (*Eidophelus* contains several unrelated occurrences, previously identified as *Ptilopodius*). *Ernoporus* has one species which does not have sutures. The shape of the antennal sutures has been found to be generally uninformative for delimiting genera (RI: 0.1; CI: 0.49).

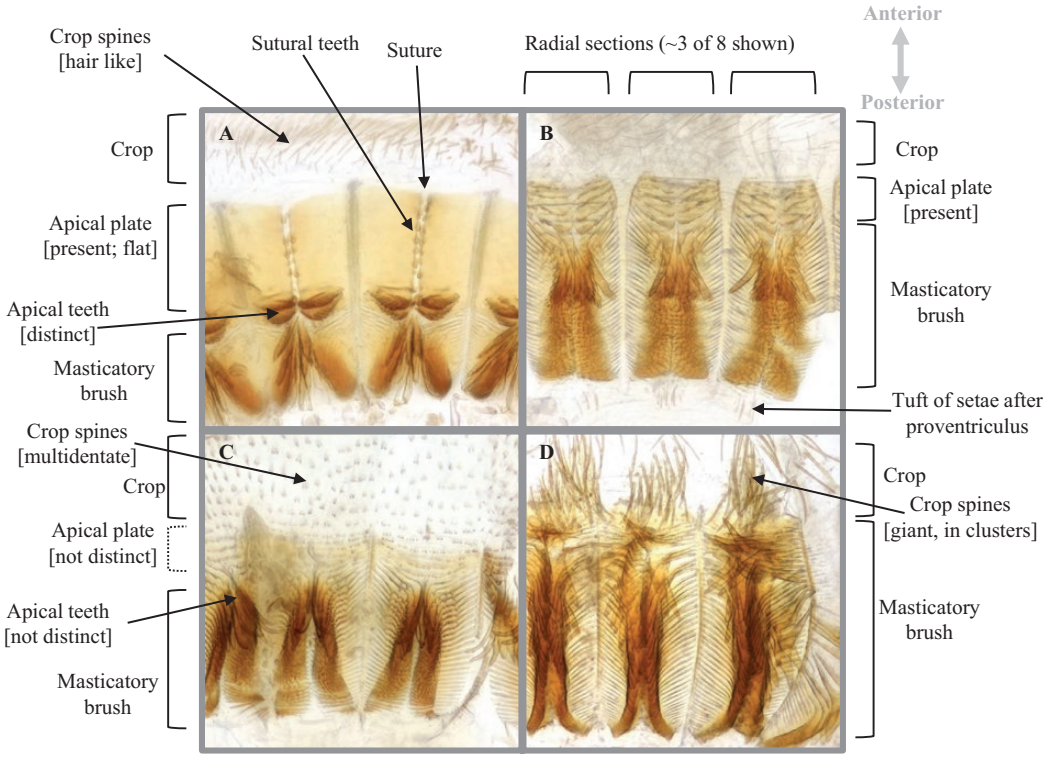

Figure 4. Labeled photos showing the variation in the proventriculus of former Cryphalini genera. A) *Cryphalus,* B) *Ernoporus,* C) *Eidophelus,* and D) *Procryphalus.*

Prothorax

The shape of the dorsolateral margin, whether there is a sharp edge versus a rounded edge, is a character that can be used to help delimit most Cryphalini genera. Sometimes the character is ambiguous in species with rugose texture, and variable in a few genera (e.g., *Cosmoderes*).

Several species have bifurcating setae on the hypomeron. This newly documented generic-level character is mainly restricted to several genera: *Cryphalus*, *Coriacephilus*, *Trypophloeus,* and *Cosmoderes*, and among the traditional cryphaline genera, only seen elsewhere in some *Ernoporus* species. In all these genera, the character is variable. However, it is present in 96% of the *Cryphalus* species sampled, and very sparse in most cases in species of other genera, so is likely a valuable diagnostic tool.

Mesothorax and Metathorax

The sclerotized part of the metathorax and the postnotum (first tergite) may be fused or separated by a flexible membrane, forming a key part of the classification of tribes (Wood, 1978). Contrary to Wood's assessment, this character is variable among the genera formerly placed in Cryphalini but matches the major phylogenetic division of genera, and therefore provides a basis for tribal-level reclassification.

The postnotum is also extended posteriorly in *Afrocosmoderes*, *Cosmoderes*, *Cryphalus*, *Indocryphalus*, *Hypothenemus*, *Macrocryphalus*, *Trypophloeus*, *Trypodendron,* and *Xyloterinus*, supporting our phylogenetic results and providing a synapomorphic character for a broader clade. This character was first noted by Jordal and Kaidel (2017).

Most Scolytinae have a projection on the anterior margin of the metanepisternum and a reciprocal groove on the underside of the elytra, but some have a reduced callus, or an oblique groove as an alternative locking mechanism (Wood 1978). Wood used this as a basis for the classification of tribes, particularly Corthylini which mostly possess an oblique groove. It is a variable character in the former Cryphalini. *Cryptocarenus* has an oblique groove, supporting the molecular placement in the tribe Corthylini (Pistone et al., 2018). Most Cryphalini, however, do not show an obvious locking structure, and it was therefore not recorded for most specimens.

The distance between the mesocoxae was not previously applied to the former Cryphalini. There is little variation within genera in the relative distance (narrowly separated versus widely separated), although exceptions were found in the speciose genera *Cryphalus* and *Eidophelus*. All species in *Cosmoderes* have contiguous mesocoxae, a character not seen in any other genera.

Legs

Among the former Cryphalini, the weakly bilobed third tarsal segment is found only in *Cryphalus* and *Stephanopodius*. This character also occurs in other tribes, so alone cannot reliably diagnose tribes or genera, but provides a strong diagnostic character when used in combination with other characters.

Proventriculus

The proventriculus (Fig. 4) is an organ in the upper gut which processes ingested material. It is a cylindrical structure with eight sections, comprised of inward pointing sclerotized structures for grinding food. This was first illustrated and described by

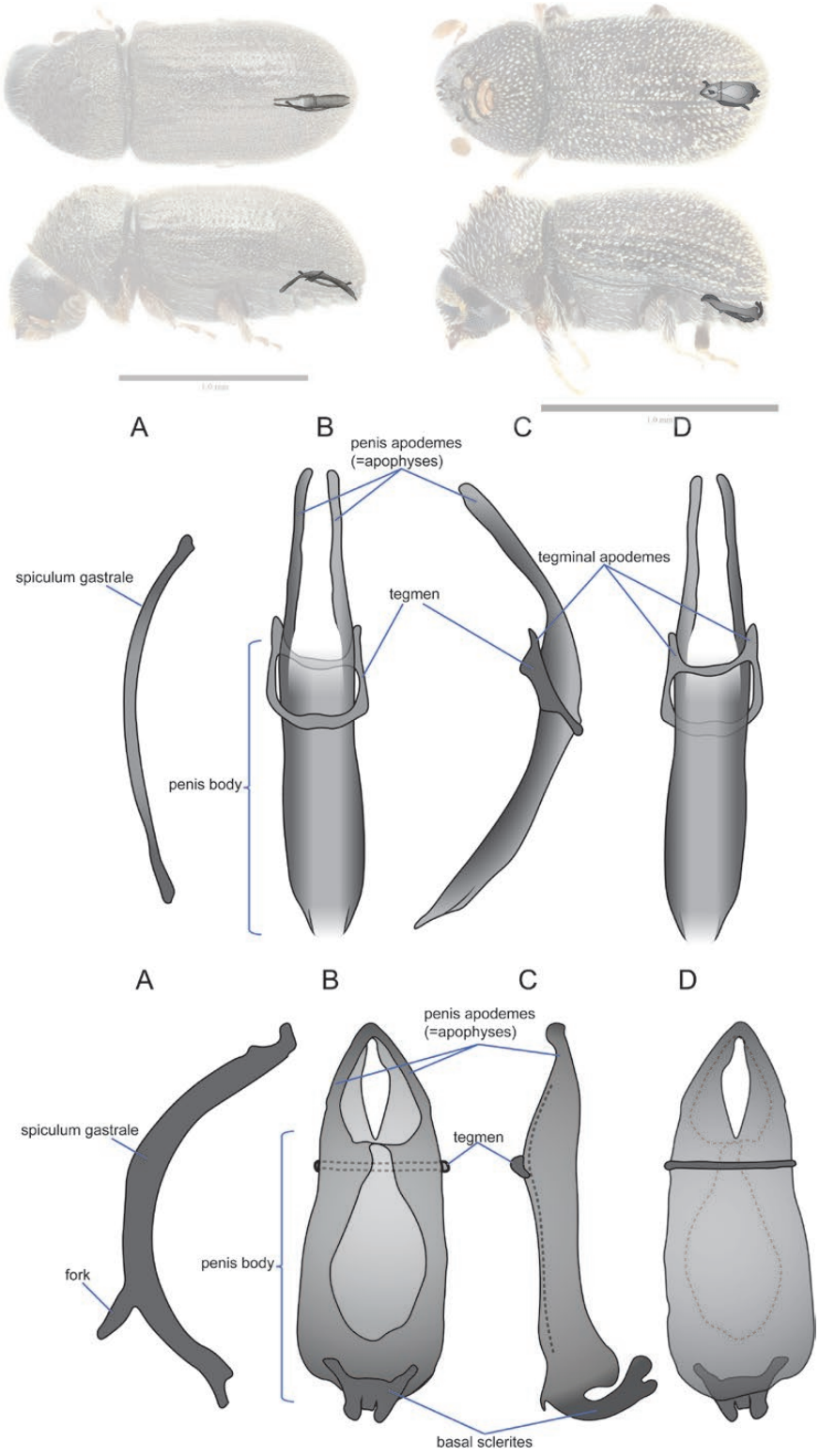

Figure 5. Labeled diagram of aedeagus with terminology. Top shows position of aedeagus in preserved beetles, middle shows aedeagus of *Cryphalus asperatus*, bottom shows aedeagus of *Ernoporus tiliae*. Sketches show A) spiculum gastrale, B) dorsal view, C) lateral view, and D) ventral view.

Nüsslin (1911b). Nobuchi (1969) carried out an extensive study across many genera, including six genera of former Cryphalini. The proventriculus of Mexican Scolytinae, including several former Cryphalini genera, were also recorded by López-Buenfil et al. (2001).

The characters used show strong phylogenetic signal, suggesting that they are very useful for classification of species into genera. We identified an undescribed character that was diagnostic for *Ernoporus*: a tuft of spatula-shaped setae on the posterior end of the masticatory brush (Figs 4b, 25). This feature is shared with

Table 3. Phylogenetic assessment of characters

Character	Consistency index	Retention index
Crop with multidentate spines	1	1
Frons of males with transverse carina	0.5	0.93
Third tarsal segment bilobed	0.5	0.95
Proventriculus apical teeth distinct	0.5	0.82
Eye shape	0.43	0.9
Frons median with file	0.33	0
Proventriculus with tuft of spatulate setae posteriorly	0.33	0.5
Male 6th ventrite visible	0.25	0.86
Crop with large sclerotized spines	0.25	0
Proventriculus anterior plate with side teeth present	0.17	0.17
Proventriculus anterior plate with complete rows of spines	0.17	0
Pronotum with concentric asperities	0.14	0.25
Pronotum dorsolateral margin with carina	0.14	0.63
Metatibia denticles distribution	0.14	0.76
Elytral declivity with spines	0.13	0.22
Frons with converging aciculations	0.13	0.3
Antennal funicle segments number	0.13	0.42
Antennal club number of sutures	0.13	0.45
Hypomeron with bifurcating setae	0.13	0.73
Pronotum produced	0.13	0.13
Elytral ground vestiture type	0.11	0.46
Antennal club sutures shape	0.1	0.49
Pronotal summit shape	0.1	0.22
Mesocoxae separation	0.1	0.69
Proventriculus apical plate present	0.1	0.57
Proventriculus sutural teeth present	0.1	0.63
Antennal funicle last segment wider	0.07	0.32
Antennal septum visible	0.07	0.61
Pronotum with scale-like setae	0.06	0.62
Metanepisternum posterior margin visible	0.04	0.3

some of the distantly related genera which are now transferred from Cryphalini to Corthylini.

The placement of the genera *Cryptocarenus* and *Stegomerus* in Corthylini using the molecular phylogeny is corroborated by the unusual morphology of the proventriculus, possessing synapomorphies such as a wide-open median suture of the apical plate, which were not observed in any other former Cryphalini genera. Nobuchi (1969) noted the similarity of *Cryptocarenus* with other Corthylini, hinting at a disagreement to Wood's placement of the genus in Cryphalini.

The enlarged apical plate in *Cryphalus* and the clade consisting of *Hypothenemus*, *Afrocosmoderes* and *Microcosmoderes* appears to have evolved convergently. Clusters of large crop spines are a valuable character for diagnosing the genera *Eidophelus*, *Hemicryphalus* and *Procryphalus*.

The morphology of the foregut of *Macrocryphalus* is remarkable. It has completely lost the sclerotized structures which make up the proventriculus. This was briefly noted in the description of the monotypic species (Nobuchi 1981) without noting its uniqueness among Scolytinae.

Aedeagus

The male genitalia of the specimens studied shows significant variation between species, genera and tribes (Fig. 4). The structures clearly differ between tribes to the point that assessment of character homology is difficult, especially with few specimens and without comparisons across other tribes of Scolytinae. Therefore, the diagnostic notes for the aedeagus should be considered preliminary.

The penis apodemes (=apophyses) show variation that strongly supports the separation of the former Cryphalini. *Ernoporus*, *Eidophelus,* and related genera have penis apodemes much shorter than the penis body, and are always fused at the apex, whereas *Cryphalus*, *Coriacephilus*, *Trypophloeus*, *Trypodendron*, and related genera have penis apodemes which are mostly as long as or longer than the penis body, and mostly separated at the apex. Rarely, the apex is weakly fused, (e.g., *Cryphalus mangiferae*). There was also variation in the profile of the penis apodemes which provided some phylogenetic signal; *Hypothenemus* and *Afrocosmoderes* have ribbon-shaped penis apodemes, related genera have cylindrical penis apodemes.

The tegmen also varies substantially between genera. Most former Cryphalini genera have the tegmen open dorsally (likely connected dorsally by non-sclerotized tissue not visible in the preparations). Only *Cryphalus* has a tegmen fused, completing a sclerotized ring. The tegminal apodemes are also very variable between genera, being either absent, a single median tegminal apodeme (=manubrium), two tegminal apodemes. The presence of tegminal apodeme exists in several distantly related scolytine tribes and other curculionid groups. The paired tegminal apodemes seen in most *Cryphalus* species are unique among all Scolytinae and all Curculionoidea.

The spiculum gastrale varies between genera in relative thickness, and whether they possess a fork. This structure is sometimes useful in grouping species in some scolytine genera (Tsai and Li 1963).

Taxonomy

The following generic diagnoses, description, and redescriptions include a checklist of species names. The following abbreviations are used to indicate taxonomic changes: trib. nov. (*tribus nova*) = new tribe; gen. nov. (*genus novum*) = new genus; syn. nov. (*synonymum novum*) = new synonymy; stat. res. (*status resurrectus*) = resurrected status; nom. nov. (*nomen novum*) = new name; comb. nov (*combinatio nova*) = new combination; and comb. res. (*combinatio resurrecta*) = resurrected combination. Valid species names are listed alphabetically, synonyms are listed chronologically. Alternative historical combinations used are not listed. The genus from which the species was originally described is listed in parentheses after the name. For taxa moved to a new genus, the previous genus is listed in square brackets. Additional notes on the status follow the name in parentheses. Remarks for a species name follow the list of synonyms. The type material examined, and synonyms are listed with the original combination. Valid subspecies are marked with the symbol '⊇' (indicating that they are a subset of).

Coriacephilini Johnson **trib. nov.**

Type of tribe

Coriacephilus Schedl, 1939.

Diagnosis

Tarsi with third segment cylindrical. Eye deeply emarginated. Antennal funicle with 3–5 segments. Antennal club with sutures and a complete septum. Hypomeron with bifurcating setae.

Female

See description of *Coriacephilus* below.

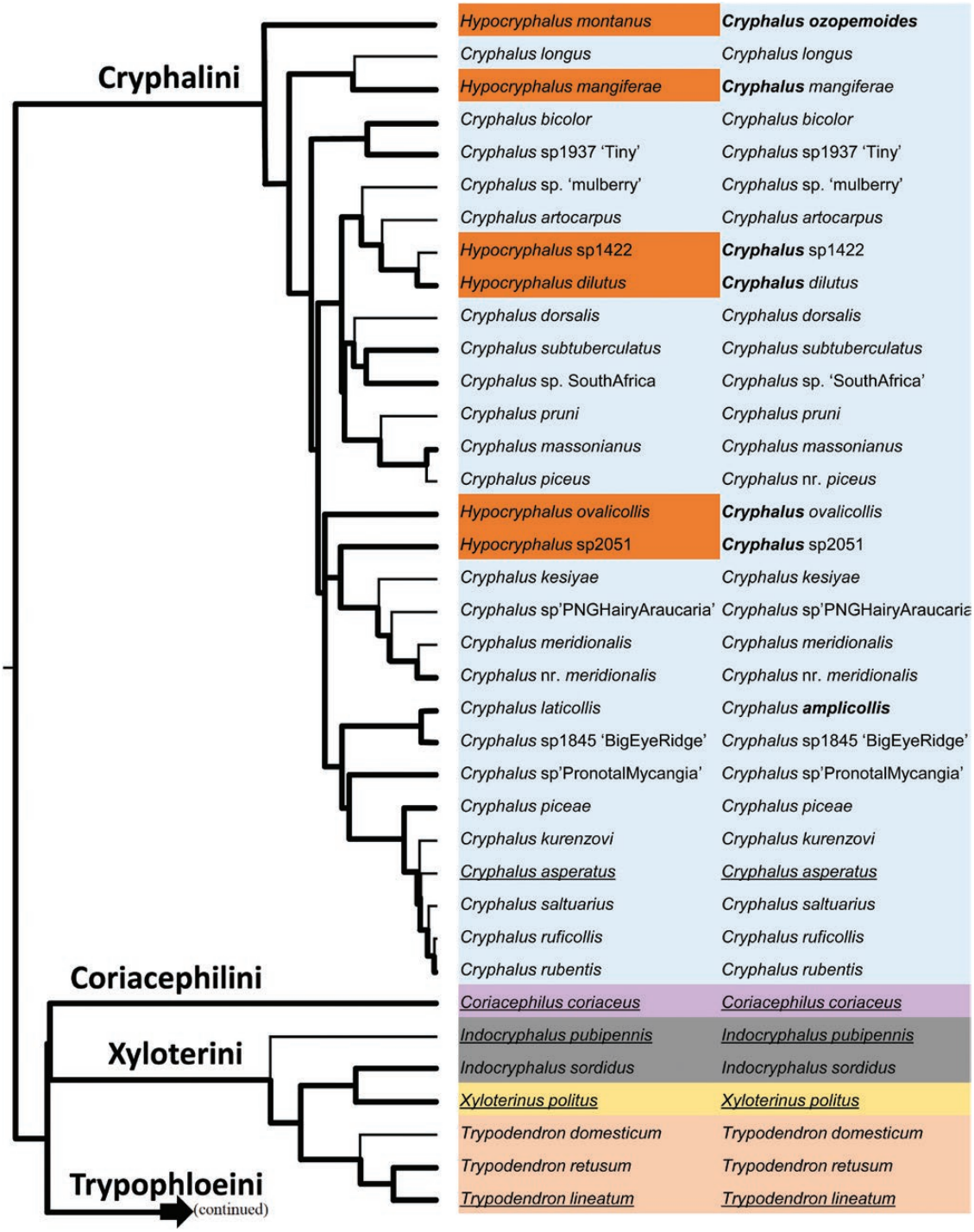

Figure 6. Phylogeny of Cryphalini, Coriacephilini, Xyloterini, and Trypophloeini, Part 1. Tree is made in RAxML, constrained to the tree by Johnson et al. (2018). Support values are not included due to artificial inflation by constraints. The constraint tree is indicated by a bold line. Outgroup taxa are omitted from the figure. Name pre- and post-revision are displayed, with changes marked in bold. Color boxes indicate genera. The type species of a genus is marked with underlined text.

Distribution

Southeast Asia.

Remarks

This tribe contains a single genus with five species, all rarely collected and poorly known, and with few good diagnostic characters. This tribe represents a phylogenetically distinct group which cannot be adequately placed in any other tribe.

Included genera

Coriacephilus Schedl, 1939

Coriacephilus Schedl, 1939b: 339 (Fig. 9)

Type of genus

Stephanoderes coriaceus Eichhoff, 1878.

Figure 7. Phylogeny of Cryphalini, Coriacephilini, Xyloterini, and Trypophloeini, Part 2.

Diagnosis

Coriacephilus can be separated from other Cryphalini by the combination of cylindrical third tarsal segments, deeply emarginated eye, antennae with sutures and septum, and bifurcating setae on the hypomeron.

Female

Eye deeply emarginated. Antennae with procurved sutures, the first darker indicating a complete septum. Antennae with four funicular segments. Hypomeron with bifurcating setae in most species. Pronotal disc present and prominent in all species with a mixture of hair-like setae pointing anteriorly. Elytra with flattened interstrial bristles and sparse hair-like interstrial ground vestiture. Proventriculus not examined. Aedeagus not examined.

Male

Unknown.

Distribution

All species are known from Southeast Asia.

Remarks

Five species known. No material was available for the study of internal morphology. All species are known from very few specimens. However, the validity of this genus being separate from *Cryphalus* and *Cosmoderes* is strongly supported with genetic evidence, placing *Coriacephilus coriaceus* as sister to Xyloterini. They are morphologically very similar to *Cryphalus*, most easily distinguished by the third tarsal segment which is not emarginated in *Coriacephilus*. A study of the internal morphology, or better genetic resources are

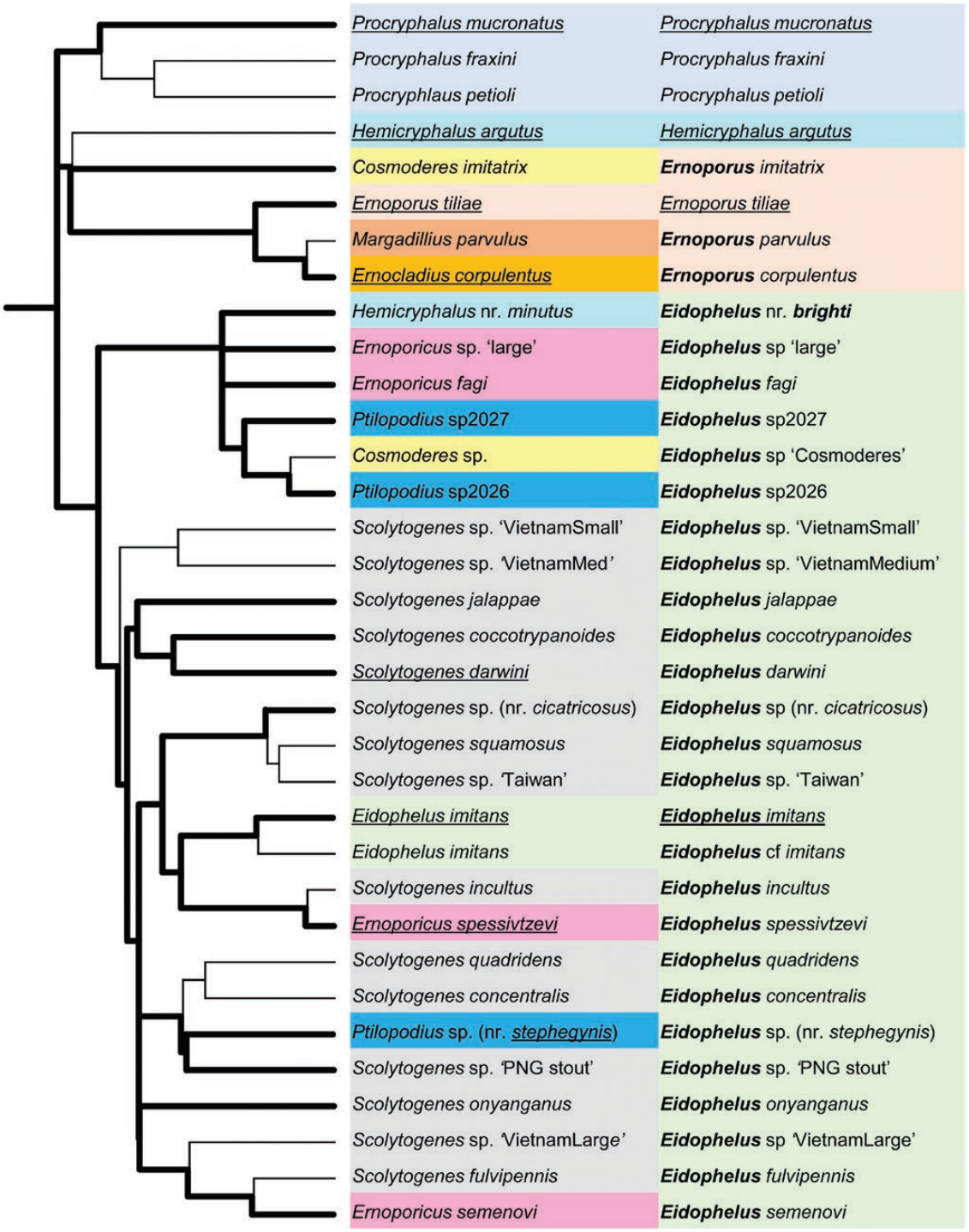

Figure 8. Phylogeny of Ernoporini. Tree is made in RAxML, constrained to the tree by Johnson et al. (2018). Support values are not included due to artificial inflation by constraints. The constraint tree is indicated by a bold line. Outgroup taxa are omitted from the figure. Name pre- and post-revision are displayed, with changes marked in bold. Color boxes indicate genera. The type species of a genus is marked with underlined text.

needed to provide better diagnostic characters for the reliable determination of this genus.

Type material examined

Holotype of *Stephanoderes coriaceus* Eichhoff, 1878 (NHMW); holotype of *Coriacephilus exiguus* Beaver, 2004 (QM); paratype of *Coriacephilus exiguus* Beaver, 2004 (BMNH); holotype of *Coriacephilus xyloctonoides* Schedl, 1939 (NHMW).

Included species

Coriacephilus coriaceus (Eichhoff, 1878b: 494) (*Stephanoderes*).
=*Cryphalus birmanus* Eggers, 1925: 153 (syn: Schedl, 1940c).
Coriacephilus cribripennis Schedl, 1943: 40.
Coriacephilus exiguus Beaver, 2004: 57.
Coriacephilus proximus (Eggers, 1925: 156) (*Cryphalus*).
Coriacephilus xyloctonoides Schedl, 1939b: 340.

Figure 9. Images of *Coriacephilus coriaceus*. Dorsal, lateral, and ventral photographs shown.

Cryphalini Lindemann, 1877

=Cryphaloideae Lindemann, 1877: 165.
=Cryphalidae Eichhoff, 1878b: 107.
=Cryphalini Weise, 1883: 181.
=Cryphali Blandford, 1898: 185.
=Cryphalinae Trédl, 1907: 40.
=Cryphalina Balachowsky, 1949: 200.

Type of tribe
Cryphalus Erichson, 1836.

Diagnosis
Tarsi with third segment bilobed. Eye emarginated. Antennal funicle with 3–5 segments. Antennal club with sutures and no septum. Hypomeron with bifurcating setae. Postnotum not fused with metanotum. Aedeagus with long penis apodemes, sometimes fused at apex, with a complete tegmen. Tegmen with pair of apodemes.

Female
See description of *Cryphalus* below.

Distribution
Eurasia, Southeast Asia, Africa, Oceania, North America, Central America (introduced), South America (introduced).

Remarks
The concept of Cryphalini is narrowly described, approximately following the group limits of Nüsslin (1911b) (including *Cryphalus* and excluding *Ernoporus* and *Trypophloeus*).

Included genera
Cryphalus Erichson, 1836.

Cryphalus Erichson, 1836: 61 (Figs. 10–12)

Synonymy
=*Pseudocryphalus* Ferrari, 1869: 252.
=*Taenioglyptes* Bedel, 1888: 398.
=*Cryptarthrum* Blandford, 1896a: 200.
=*Allarthrum* Hagedorn, 1912c: 355.
=*Dacryphalus* Hopkins, 1915: 42 **syn. nov.**
=*Ericryphalus* Hopkins, 1915: 38.
=*Hypocryphalus* Hopkins, 1915: 41 **syn. nov.**
=*Margadillius* Hopkins, 1915: 37 **syn. nov.**
=*Piperius* Hopkins, 1915: 39.
=*Toenioglyptes* Balachowsky, 1949: 205 (unavailable name).
=*Ernocryphalus* Murayama, 1958: 934.
=*Acryphalus* Tsai and Li, 1963: 604 (unavailable name).
=*Gugocryphelus* Tsai and Li, 1963: 603 (unavailable name).
=*Jugocryphalus* Tsai and Li, 1963: 604.

Type of genus
Bostrichus asperatus Gyllenhal, 1813.

Diagnosis
Cryphalus can be distinguished from similar genera by the combination of emarginated eyes, sutures on the antennae clearly visible but without a septum, by the weakly bilobed third tarsal segments, the proventriculus with a large apical plate, and the aedeagus that has a tegmen sclerotized completing a ring, usually with two tegminal apodemes.

Female
Eye emarginated. Antennae with three to five funicle segments. Antennal club with three visible procurved sutures, occasionally recurved, never septate. Frons convex, simple, sometimes with weak impression above epistoma, and sometimes with aciculations converging at epistoma. Pronotum with two or more marginal asperities, the margin produced in some species. Hypomeron with bifurcating setae (rare exceptions). Base of elytra sometimes with a slightly elevated ridge, straight to recurved. Angle of apex of declivity shallow, with the apex of each elytron obtuse (typically exposing part of the pygidium). Ground vestiture dense in most species (rarely sparse or absent), which can be hair-like, dagger-like or with tridentate scales. Metatibia with lateral denticles distributed over at least the apical quarter. Mesocoxae not contiguous, usually of a similar distance to distance between metacoxae or wider. Third tarsal segment weakly bilobed. Proventriculus with large apical plate, typically with sutural teeth and much larger apical teeth.

Male
Similar to female except sixth ventrite usually visible, frons with a transverse ridge, occasionally with enlarged setae on the protibiae and protarsi, and modified vestiture in the gular region. Penis apodemes typically as long as or longer than penis body, and separated or weakly fused at apex. Tegmen dorsally fused to form a ring. Tegmen with two short tegminal apodemes (absent in some species).

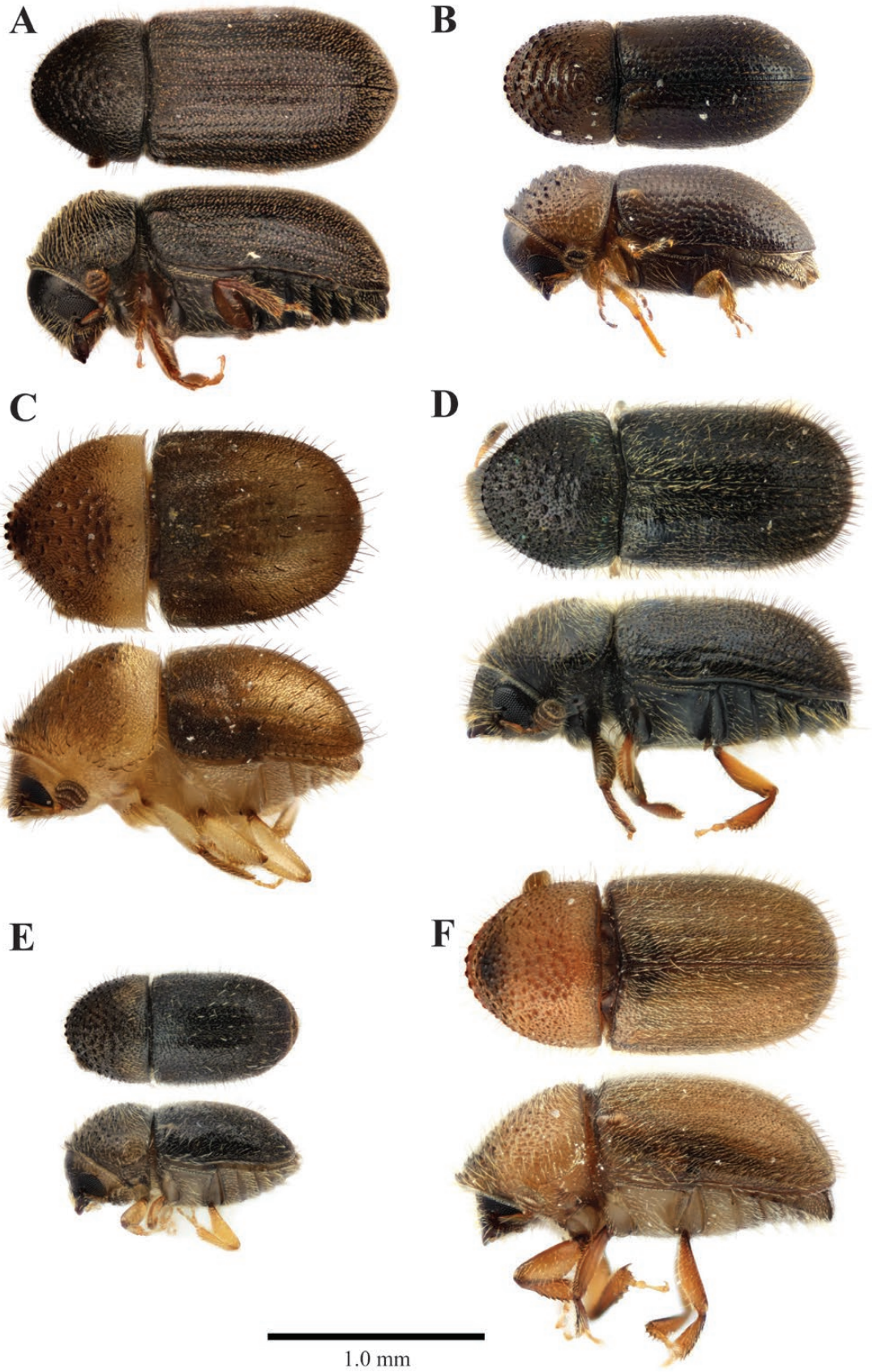

Figure 10. Images of *Cryphalus* spp.: Dorsal and lateral photographs of A) *C. asperatus,* B) *C. bicolor,* C) *C. dorsalis,* D) *C. kesiyae,* E) *C. amplicollis,* F) *C. meridionalis.*

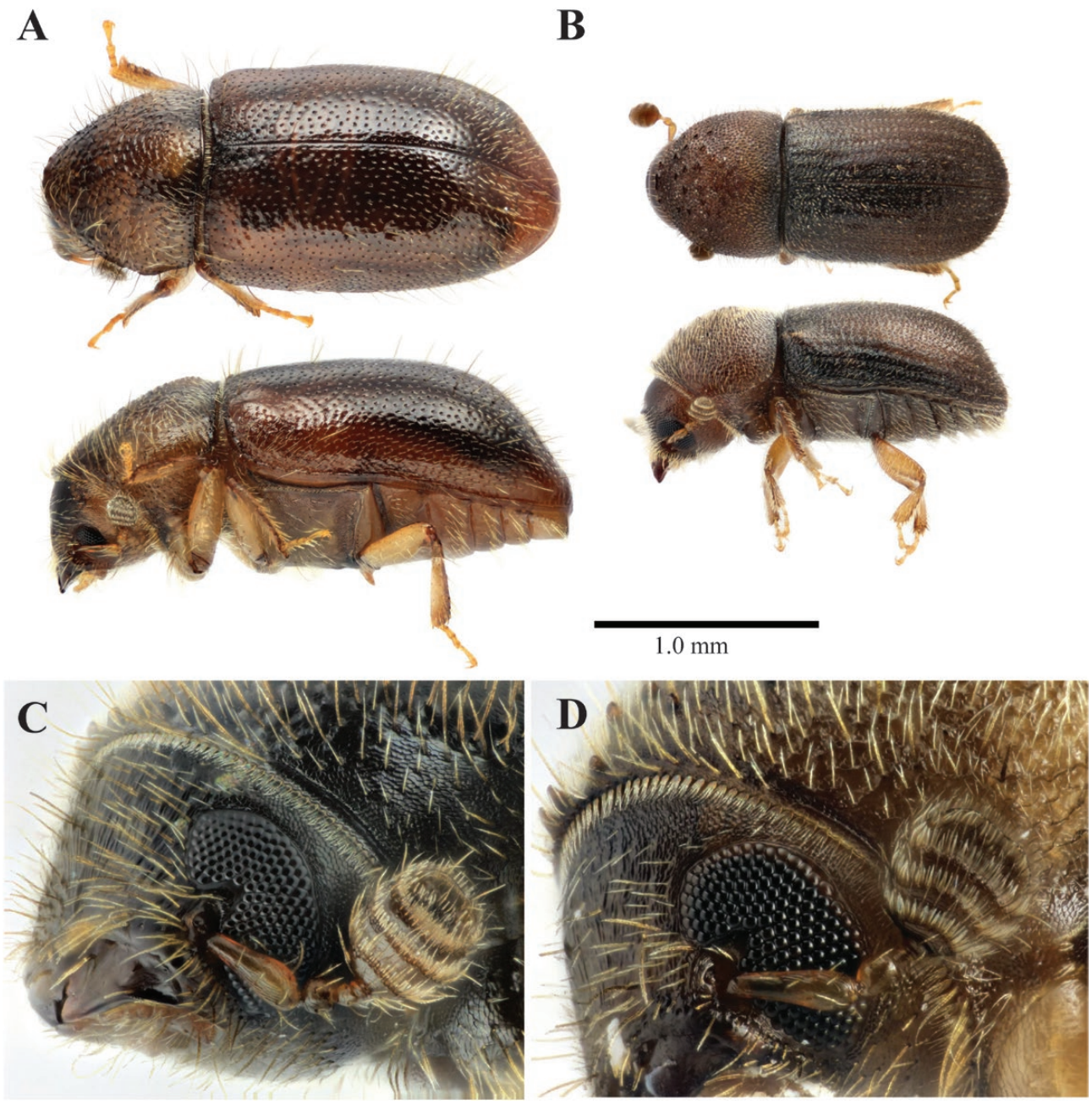

Figure 11. Images of *Cryphalus* spp.: Dorsal and lateral photographs of A) *C. ozopemoides,* B) *C. nr. piceus.* Eye, antennae, and frons of C) *C. kesiyae* and D) *C. mangiferae.*

Spiculum gastrale long, of a similar thickness to the penis apodemes, and without a fork. Basal sclerites not visible.

Distribution

Africa, Asia, Europe, Oceania, North America, Central America (introduced), South America (introduced).

Remarks

In total, 252 species known. Almost all species possess many split setae on the hypomeron which can easily separate species in this genus from most similar bark beetles. The presence, number, and arrangement of sutural teeth on the apical plate of the proventriculus have been extensively used to diagnose Chinese species (see Tsai and Li (1963)).

Many species are described. It is likely that several of the species names should be synonymized, but many types are in a poor condition with few external diagnostic characters known. The genus was previously split into three genera, including *Hypocryphalus* and *Margadillius* based primarily on the number of funicular segments. This is, however, a rapidly evolving character which may vary within a species and has a poor phylogenetic signal. The large number of species, particularly those described by Schedl, create many secondary homonyms. Where appropriate, these have been corrected.

Tsai and Li (1963) proposed three subgenera, *Cryphalus s. str.*, *Acryphalus,* and *Jugocryphalus*. The latter two are listed as unavailable names, based on an apparent lack of type designation (Alonso-Zarazaga and Lyal 2009). However, the types are indicated in the

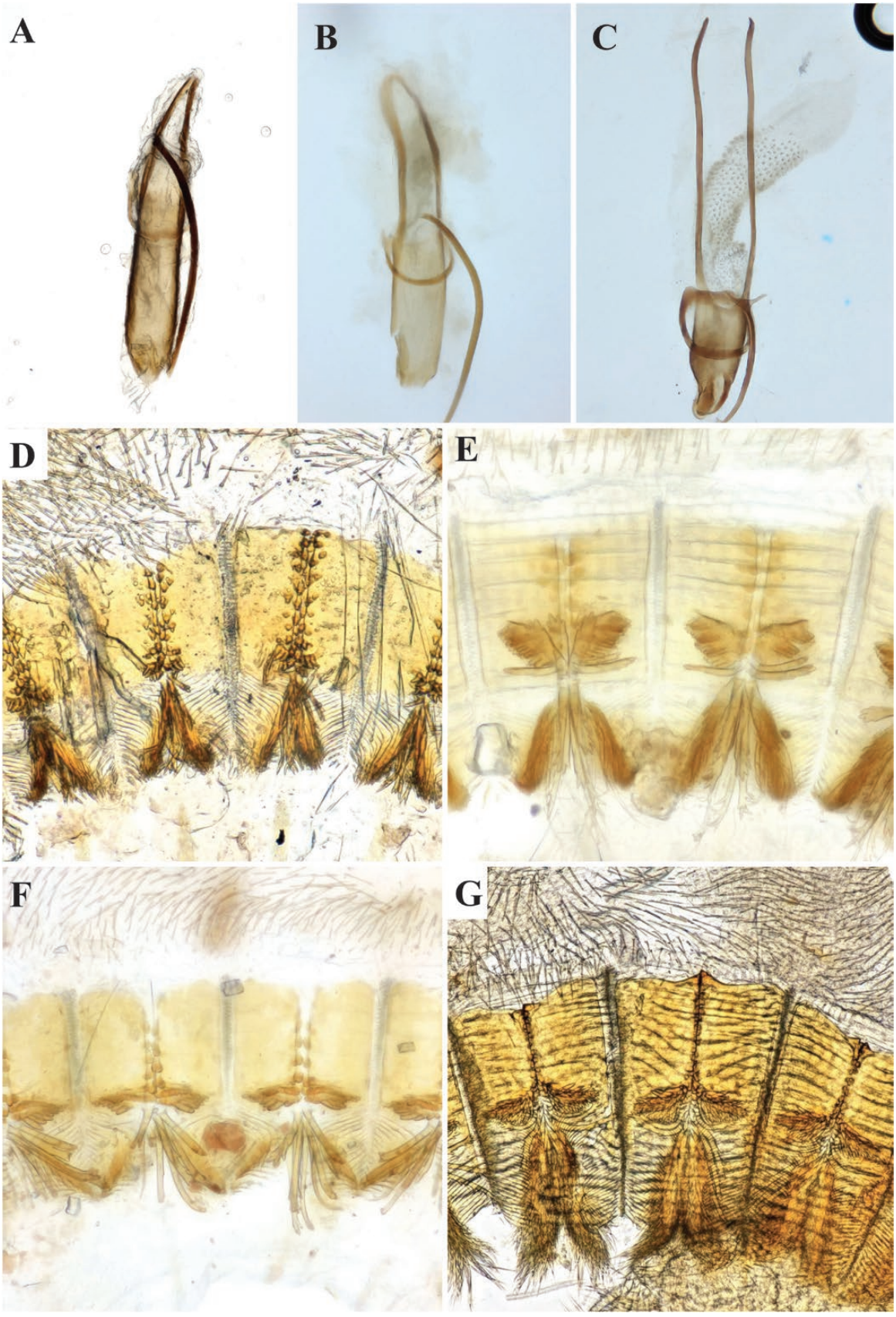

Figure 12. Images of *Cryphalus* spp.: Aedeagus of A) *Cryphalus asperatus*, B) *C. keysiae*, C) *C. mangiferae*. Proventriculus of D) *C. asperatus*, E) *C. dorsalis*, F) *C. mangiferae*, and G) *C. ozopemoides*.

original description of the subgenera ('亚属模' after the name, translating to 'type of subgenus'), with *Cryphalus lipingensis* the type of *Acryphalus*, and *Cryphalus fulvus* as the type of *Jugocryphalus*. Among the species described in the subgenera, the descriptions may represent monophyletic clades.

Where known, all species are monogamous with cave-like galleries feeding under bark.

Type material examined

Allotype of *Ernoporus antennarius* Schedl, 1974 (ANIC); paratype of *Ernoporus antennarius* Schedl, 1974 (NHMW); holotype of *Taenioglyptes aquilonius* Nobuchi, 1975 (ITLJ); holotype of *Cryphalus araucariae* Schedl, 1970 (ANIC); holotype of *Taenioglyptes artestriatus* Browne, 1970 (BMNH); holotype of *Ericryphalus artocarpus* Schedl, 1939 (BMNH); holotype and paratype of *Cryphalus asperulus* Schedl, 1948 (BMNH); paratype of *Cryphalus asperulus* Schedl, 1948 (BMNH); holotype of *Cryphalus ater* Browne, 1984 (BMNH); holotype of *Cryphalus basihirtus* Beeson, 1929 (BMNH); holotype of *Taenioglyptes bicarinatus* Nobuchi, 1975 (ITLJ); holotype of *Cryphalomorphus bicolor* Browne, 1983 (BMNH); holotype of *Hypocryphalus bidentatus* Browne, 1980 (BMNH); holotype of *Cryphalus brasiliensis* Schedl, 1976 (NHMW); paratype of *Ptilopodius brevis* Browne, 1970 (BMNH); allotype of *Cryphalus brevisetosus* Schedl, 1943 (NHMW); lectotype of *Cryphalus brevisetosus* Schedl, 1943 (NHMW); holotype of *Cryphalus brimblecombei* Schedl, 1948 (BMNH); holotype of *Cryphalus brunneus* Browne, 1984 (BMNH); holotype of *Cryphalus buloloensis* Browne, 1984 (BMNH); paratype of *Cryphalus buloloensis* Browne, 1984 (BMNH); holotype of *Margadillius carinatus* Browne, 1980 (BMNH); paratype of *Cryphalus carpini* Berger, 1917 (ZIN); holotype of *Cryphalus cylindricus* Browne, 1980 (BMNH); holotype of *Cryphalus cylindrus* Browne, 1984 (BMNH); holotype of *Dacryphalus cylindrus* Browne, 1950 (BMNH); paratype of *Cryphalus cylindrus* Browne, 1984 (BMNH); holotype of *Cryphalus dilutus* Eichhoff, 1878 (NHMW); holotype of *Cryphalus dipterocarpi* Wood, 1989 (USNM); holotype of *Taenioglyptes dissimilis* Nobuchi, 1975 (ITLJ); holotype and paratype of *Cryphalus diversicolor* Browne, 1984 (BMNH); holotype of *Cryphalus exiguus* Blandford, 1894 (BMNH); holotype of *Euptilius exiguus* Browne, 1984 (BMNH); holotype of *Cryphalus felis* Wood, 1989 (USNM); holotype of *Hypocryphalus fici* Browne, 1986 (BMNH); holotype of *Hypocryphalus froggatti* Nunberg, 1961 (BMNH); holotype of *Cryphalus fuliginosus* Blandford, 1895 (BMNH); holotype of *Cryphalus fulmineus* Wood, 1989 (USNM); holotype of *Margadillius fulvus* Browne, 1984 (BMNH); cotype of *Cryphalus garciniae* Nobuchi, 1959 (ITLJ); holotype of *Cryphalus grayi* Schedl, 1968 (ANIC); holotype of *Hypothenemus griseus* Blackburn, 1885 (BMNH); holotype of *Cryphalus helopioides* Schedl, 1953 (BMNH); holotype of *Taenioglyptes hirsutus* Nobuchi, 1975 (ITLJ); holotype of *Cryphalus inops* Eichhoff, 1872 (RBINS); holotype of *Taenioglyptes kagoshimensis* Nobuchi, 1975 (ITLJ); holotype and paratype of *Cryphalus kesiyae* Browne, 1975 (BMNH); paralectotype of *Cryphalus kurenzovi* Stark, 1936 (ZIN); holotype of *Hypocryphalus laevis* Browne, 1980 (BMNH); holotype and paratype of *Cryphalus laevis* Browne, 1984 (BMNH); type of *Cryphalus laricis* Niisima, 1909 (ITLJ); holotype and paratype of *Hypocryphalus laticollis* Browne, 1974 (BMNH); holotype of *Cryphalus longior* Browne, 1984 (BMNH); paratype of *Cryphalus longior* Browne, 1984 (BMNH); holotype and two paratypes of *Taenioglyptes longipennis* Browne, 1970 (BMNH); holotype of *Hypocryphalus longipilis* Browne, 1981 (BMNH); holotype of *Taenioglyptes longisetosus* Nobuchi, 1975 (ITLJ); holotype and paratype of *Margadillius magnus* Browne, 1984 (BMNH); holotype of *Hypocryphalus malayensis* Schedl, 1942 (BMNH); syntype of *Cryphalus mandschuricus* Eggers, 1929 (ITLJ); paralectotype and lectotype of *Cryphalus mangiferae* Stebbing, 1914 (BMNH); holotype of *Margadillius margadilaonis* Hopkins, 1915 (USNM); holotype of *Taenioglyptes meridionalis* Nobuchi, 1975 (ITLJ); Two paralectotypes of *Cryphalus minimus* Eggers, 1927 (NHMW, BMNH); holotype of *Hypocryphalus minutus* Browne, 1980 (BMNH); holotype of *Cryphalus mollis* Schedl, 1955 (BMNH); holotype of *Cryphalus montanus* Nobuchi, 1964 (ITLJ); paratype of *Hypocryphalus montanus* Schedl, 1974 (NHMW); holotype and paratype of *Cryphalus negrosensis* Browne, 1979 (BMNH); holotype of *Cryphalus nitens* Browne, 1980 (BMNH); holotype and paratype of *Cryphalus nitidipennis* Browne, 1984 (BMNH); paratype of *Cryphalus nothofagi* Browne, 1984 (BMNH); holotype of *Margadillius papuanus* Schedl, 1973 (ANIC); paratype of *Margadillius papuanus* Schedl, 1973 (NHMW); lectotype of *Cryphalus perminimus* Schedl, 1942 (NHMW; holotype of *Cryphalus pilosulus* Browne, 1980 (BMNH); holotype of *Taenioglyptes pulchellus* Nobuchi, 1975 (ITLJ); holotype and paratype of *Cryphalus punctatus* Browne, 1984 (BMNH); holotype of *Margadillius quadrituberculatus* Schedl, 1963 (NHMW); holotype of *Hypocryphalus reflexus* Browne, 1980 (BMNH); syntypes of *Cryphalus rhusii* Niisima, 1909 (ITLJ); syntypes (6) of *Cryphalus robustus* Eichhoff, 1872 (RBINS(5), BMNH(1)); holotype of *Hypocryphalus rotundus* Hopkins, 1915 (USNM); holotype of *Ericryphalus rugosus* Schedl, 1958 (BMNH); holotype of *Cryphalus samoensis* Beeson, 1929 (BMNH); syntype of *Cryphalus sandakanensis* Schedl, 1937 (BMNH); holotype of *Cryphalus sawadai* Nobuchi and Takahashi, 1965 (ITLJ); holotype of *Cryphalus scabripennis* Schedl, 1972 (BMNH); holotype of *Ericryphalus securus* Schedl, 1940 (BMNH); holotype of *Taenioglyptes sordidus* Nobuchi, 1975 (ITLJ); holotype of *Cryphalomorphus striatulus* Browne, 1978 (BMNH); holotype of *Cryphalus striatulus* Browne, 1981 (BMNH); holotype of *Cryphalus striatus* Browne, 1974 (BMNH); lectotype and 3 paralectotypes *Cryphalus swezeyi* Schedl, 1942 (BMNH(2), NHMW(2)); syntype of *Cryphalus swezeyi* Schedl, 1942 (BMNH); holotype of *Hypothenemus sylvicola* Perkins, 1900 (BMNH); holotype of *Cryphalus terminaliae* Browne, 1980 (BMNH); holotype of *Margadillius terminaliae* Browne, 1984 (BMNH); syntype of *Cryphalus trypanus* Sampson, 1914 (BMNH); holotype of *Cryphalus vestitus* Blandford, 1895 (BMNH); holotype and paratype of *Cryphalus vitiensis* Browne, 1974 (BMNH); holotype of *Cryptarthrum walkeri* Blandford, 1896 (BMNH).

Included species

Cryphalus abbreviatus Schedl, 1943: 35.

Cryphalus aciculatus (Schedl, 1939b: 341) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].

Cryphalus afiamalus (Schedl, 1951d: 148) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].

Cryphalus amplicollis Johnson **nom. nov.**

=*Cryphalus laticollis* Browne, 1984b: 288 **syn. nov.** (secondary homonym).

Remarks: A replacement name is proposed for *Cryphalus laticollis* Browne, 1984b because the name is now occupied by *Hypocryphalus laticollis* Browne, 1974. The replacement name is an adjective formed from *ampli* (= large) and *collis* (=collar).

Cryphalus angustior Eggers, 1927b: 300 **comb. res.** [*Hypocryphalus*].

Cryphalus aquilonius (Nobuchi, 1975: 52) (*Taenioglyptes*).

Cryphalus araucariae Schedl, 1970a: 214.
Cryphalus armatus Schedl, 1974: 459.
Cryphalus artestriatus (Browne, 1970: 553) (*Taenioglyptes*).
Cryphalus artocarpus (Schedl, 1939b: 432) (*Ericryphalus*).
=*Cryphalus artocarpus* Schedl, 1958d: 498 (syn: Schedl, 1975d).
=*Cryphalus brownei* Wood, 1992b: 79 (unnecessary replacement name).
Cryphalus asper (Broun, 1881: 742) (*Tomicus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus asperatus (Gyllenhal, 1813: 368) (*Bostrichus*).
=*Bostrichus abietis* Ratzeburg, 1837: 163 (syn: Wood, 1972b).
Cryphalus asperulus Schedl, 1948b: 26.
Cryphalus ater Browne, 1984d: 91.
Cryphalus babai Murayama, 1961: 29.
Cryphalus bakeri (Eggers, 1927c: 77) (*Stephanoderes*) **comb. nov.** [*Hypocryphalus*].
Cryphalus balanopselaphus Eggers, 1920: 21.
Cryphalus basihirtus Beeson, 1929: 227 **comb. nov.** [*Hypocryphalus*].
Cryphalus bellus Schedl, 1957b: 47.
Cryphalus bicarinatus (Nobuchi, 1975: 53) (*Taenioglyptes*).
Cryphalus bicolor (Browne, 1983b: 69) (*Cryphalomorphus*).
Cryphalus bidentatus (Browne, 1980b: 383) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus boettcheri Schedl, 1943: 38.
Cryphalus brasiliensis Schedl, 1976: 65.
Cryphalus brevior (Schedl, 1943: 40) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus brevipilosus Schedl, 1942c: 173.
Cryphalus brimblecombei Schedl, 1948b: 26.
Cryphalus brunneus Browne, 1984d: 93.
Cryphalus buloloensis Browne, 1984c: 67.
Cryphalus capucinicollis Schedl, 1950b: 47.
Cryphalus capucinoides Eggers, 1939b: 4.
Cryphalus capucinomorphus Schedl, 1950b: 48.
Cryphalus capucinus Schedl, 1938c: 425.
Cryphalus carinatus (Browne, 1980b: 382) (*Margadillius*) **comb. nov.** [*Margadillius*].
Cryphalus carpini Berger, 1917: 234.
Cryphalus carpinivorus Murayama, 1930: 14.
Cryphalus chamaeciparіae Niisima, 1910: 10.
Cryphalus chinlingensis Tsai and Li, 1963: 612.
Cryphalus ciliatipes Blandford, 1896b: 242.
Cryphalus cinereotestaceus (Motschulsky, 1866: 403) (*Hypoborus*).
Cryphalus compactus Lea, 1910: 139.
Cryphalus confusus (Hopkins, 1915: 38) (*Margadillius*) **comb. nov.** [*Margadillius*].
Cryphalus constrictus Schedl, 1942c: 174.
=*Cryphalus perminimus* Schedl, 1942d: 13 (syn: Schedl, 1958e).
=*Hypocryphalus constrictus* Schedl, 1942d: 22.
=*Hypocryphalus froggatti* Nunberg, 1961: 611 (syn: Schedl, 1962c).
Cryphalus corpulentus (Schedl, 1942d: 22) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus coryli Stark, 1936: 144.
Cryphalus cryptomeriae Niisima, 1908: 91.
Cryphalus cylindricus Browne, 1980b: 384.
Cryphalus cylindripennis (Schedl, 1959a: 483) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus cylindrus (Browne, 1950: 647) (*Dacryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus densepilosus (Schedl, 1942d: 21) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus dilutus Eichhoff, 1878a: 384 **comb. res.** [*Hypocryphalus*].
=*Cryphalus dilutus* Eichhoff, 1878b: 490 (syn: Johnson et al., 2017).
Cryphalus dipterocarpi Wood, 1989: 179.
Cryphalus discrepans (Schedl, 1965a: 58) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus discretus Eichhoff, 1878a: 385 **comb. res.** [*Hypocryphalus*].
=*Cryphalus discretus* Eichhoff, 1878b: 490 (syn: Johnson et al., 2017).
=*Cryphalus scabricollis* Eichhoff, 1878b: 491 (syn: Wood, 1989).
=*Cryphalus brevisetosus* Schedl, 1943: 36 (syn: Wood, 1989).
Cryphalus dissimilis (Nobuchi, 1975: 57) (*Taenioglyptes*).
Cryphalus diversicolor Browne, 1984d: 90.
Cryphalus dorsalis (Motschulsky, 1866: 403) (*Hypoborus*).
=*Hylesinus sericeus* Motschulsky, 1866: 402 (syn: Wood, 1969).
=*Hypoborus nebulosus* Motschulsky, 1866: 403 (syn: Wood, 1969).
=*Cryphalus indicus* Eichhoff, 1878a: 384 **syn. nov.**
=*Cryphalus indicus* Eichhoff, 1878b: 489.

Remarks: No formal synonymy has been proposed for this species name. Wood (1969) indicated that they are probably the same, and Wood and Bright (1992) listed the synonyms as above, choosing *Cryphalus dorsalis* as the valid name with *dorsalis* getting priority chosen by the first reviser. The nomenclature is being treated as valid, but the subjective synonymy is uncertain (see Mandelshtam and Nikitsky 2005).

Cryphalus dubiosus Schedl, 1963c: 66.
Cryphalus duplosquamosus Schedl, 1942d: 15.
Cryphalus eggersi Johnson **nom. nov.**
=*Cryphalus confusus* Eggers, 1927b: 395 **syn. nov.** (secondary homonym).

Remarks: A replacement name is proposed for *Cryphalus confusus* Eggers, 1927b, because the combination is already occupied following the transfer of *Margadillius confusus* Hopkins, 1915 to *Cryphalus*. The replacement name is a noun in the genitive case, honoring the original author.

Cryphalus elaboratus Schedl, 1950b: 51.
Cryphalus elongatus Schedl, 1962f: 105.
Cryphalus eriobotryae Johnson, 2019: 3.
Cryphalus erraticus Schedl, 1979c: 96.

Remarks: The original and subsequent spelling is *erraticum* as an adjective, which should be the masculine *erraticus*.

Cryphalus erythrinae (Hopkins, 1915: 38) (*Margadillius*) **comb. nov.** [*Margadillius*].
Cryphalus exiguus Blandford, 1894b: 82.
Cryphalus felis Wood, 1989: 180.
Cryphalus fici (Browne, 1986: 90) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus ficivorus Murayama, 1958: 933.
Cryphalus formosanus Schedl, 1942a: 175.
Cryphalus fugax Schedl, 1973b: 87.
Cryphalus fuliginosus Blandford, 1895: 319.
Cryphalus fulmineus Wood, 1989: 180.
Cryphalus fulvus Niisima, 1908: 92.
=*Cryphalus pini* Eggers, 1921: 39 (syn: Eggers, 1923b).
Cryphalus furukawai Murayama, 1934a: 59.
Cryphalus fuscus Johnson **nom. nov.**
=*Cryphalus cylindrus* Browne, 1984d: 92 **syn. nov.** (secondary homonym).

Remarks: A replacement name is proposed for *Cryphalus cylindrus* Browne, 1984d following the transfer of *Dacryphalus*

cylindrus Browne, 1950 from *Hypocryphalus*. The replacement name is an adjective, meaning either brown or indistinct.
Cryphalus garambaensis Nunberg, 1965: 25.
Cryphalus garciniae Nobuchi, 1959: 24.
Cryphalus giganteus Schedl, 1950a: 22.
Cryphalus gigas Schedl, 1975b: 218.
Cryphalus glabratus (Schedl, 1959a: 484) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus gracilis Johnson **nom. nov.**
=*Cryphalus laevis* Browne, 1984b: 288 **syn. nov.** (secondary homonym).
Remarks: A replacement name is proposed for *Cryphalus laevis* Browne, 1984b because the name is occupied by *Hypocryphalus laevis* Browne, 1980a. The replacement name is an adjective meaning slender or graceful.
Cryphalus granulatus (Schedl, 1942a: 176) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus helopioides Schedl, 1953b: 295.
Cryphalus hirsutus (Nobuchi, 1975: 52) (*Taenioglyptes*).
Cryphalus horridus Eichhoff, 1878a: 384.
=*Cryphalus horridus* Eichhoff, 1878b: 488 **syn. nov.**
Cryphalus imitans (Schedl, 1951d: 148) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus infimus Schedl, 1972c: 287.
Cryphalus intermedius Ferrari, 1867: 79.
Cryphalus interponens (Schedl, 1953a: 126) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus jeholensis Murayama, 1939: 143.
Cryphalus jezoensis Inouye and Nobuchi, 1957: 49.
Cryphalus juglansi Niisima, 1913: 3.
Cryphalus kagoshimensis (Nobuchi, 1975: 56) (*Taenioglyptes*).
Cryphalus kalambanganus (Schedl, 1943: 39) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus kesiyae Browne, 1975: 288.
Cryphalus kivuensis Schedl, 1957b: 48.
Cryphalus kolbei (Hagedorn, 1912c: 355) (*Allarthrum*).
Cryphalus kurenzovi Stark, 1936: 150.
=*Cryphalus punctulatus* Eggers, 1942: 29 (syn: Pfeffer, 1944).
=*Cryphalus ussuriensis* Eggers, 1942: 29 (syn: Schedl, 1952e).
Cryphalus kyotoensis Nobuchi, 1966a: 53.
Cryphalus laevis (Browne, 1980a: 374) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus laricis Niisima, 1909: 142.
Cryphalus laticollis (Browne, 1974: 67) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus latus Eggers, 1929a: 10.
=*Cryphalus premayaensis* Murayama, 1943: 97 (syn: Mandelshtam et al., 2007).
Cryphalus lepocrinus Tsai and Li, 1963: 619.
Cryphalus lipingensis Tsai and Li, 1959: 90.
Cryphalus longior Browne, 1984d: 91.
Cryphalus longipennis (Browne, 1970: 552) (*Taenioglyptes*) **comb. nov.** [*Hypocryphalus*].
Cryphalus longipilis (Browne, 1981: 128) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus longipilus Schedl, 1943: 34.
Cryphalus longisetosus (Nobuchi, 1975: 57) (*Taenioglyptes*).
Cryphalus longus (Eggers, 1926b: 136) (*Ernoporus*).
=*Cryphalus alni* Krivolutskaya, 1958: 145 (syn: Mandelshtam, 2002).
Cryphalus luteus Johnson **nom. nov.** [*Margadillius*].
=*Margadillius fulvus* Browne, 1984b: 289 **syn. nov.** (secondary homonym).
Remarks: A replacement name is proposed for *Margadillius fulvus* Browne, 1984b after its transfer to *Cryphalus*, because the name is already occupied by *Cryphalus fulvus* Niisima, 1908. The name is an adjective, meaning either brown or yellow, maintaining the original meaning.
Cryphalus magnus (Browne, 1984d: 88) (*Margadillius*) **comb. nov.** [*Margadillius*].
Cryphalus major Stebbing, 1903: 270.
=*Cryphalus morinda* Stebbing, 1903: 265 (syn: Wood, 1989).
Cryphalus malayensis (Schedl, 1942a: 176) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus malloti Schedl, 1943: 37.
Cryphalus malus Niisima, 1909: 144.
=*Cryphalus padi* Krivolutskaya, 1958: 144 (syn: Mandelshtam, 2002).
Cryphalus mandschuricus Eggers, 1929b: 10.
Cryphalus mangiferae Stebbing, 1914: 542 **comb. res.** [*Hypocryphalus*] (nomen protectum).
=*Cryphalus inops* Eichhoff, 1872a: 131 (syn: Wood, 1982) (nomen oblitum).
=*Hypothenemus griseus* Blackburn, 1885: 194 (syn: Wood, 1982) (nomen oblitum).
=*Hypocryphalus mangiferae* Eggers, 1928: 85 (syn: Eggers, 1930).
=*Cryphalus subcylindricus* Schedl, 1942d: 16 (syn: Schedl, 1958e).
=*Cryphalus mimicus* Schedl, 1942d: 17 (syn: Kalshoven, 1958).
=*Hypocryphalus opacus* Schedl, 1942d: 20.
Cryphalus margadilaonis (Hopkins, 1915: 38) (*Margadillius*) **comb. nov.** [*Margadillius*].
Cryphalus markangensis Tsai and Li, 1963: 618.
Cryphalus massonianus Tsai and Li, 1963: 613.
Cryphalus meridionalis (Nobuchi, 1975: 55) (*Taenioglyptes*).
Cryphalus mindoroensis (Schedl, 1943: 39) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus minimus Eggers, 1927c: 76.
Cryphalus minor (Schedl, 1943: 40) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus minusculus Johnson **nom. nov.** [*Hypocryphalus*].
=*Hypocryphalus minutus* Browne, 1980c: 495 **syn. nov.** (secondary homonym).
Remarks: A replacement name is proposed for *Hypocryphalus minutus* Browne, 1980c following its transfer to *Cryphalus*. The name is occupied by *Margadillius minutus* Hopkins, 1915. The replacement name is an adjective, and maintains the original meaning, referencing the very small size.
Cryphalus minutus (Hopkins, 1915: 37) (*Margadillius*) **comb. nov.** [*Margadillius*].
Cryphalus miyalopiceus Tsai and Li, 1963: 608.
Cryphalus mollis Schedl, 1955a: 288 **comb. res.** [*Hypocryphalus*].
=*Hypocryphalus tongaensis* Schedl, 1979c: 104 (syn: Beaver, 1987).
Cryphalus montanus Nobuchi, 1964: 129.
Cryphalus moorei (Schedl, 1964b: 247) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus neglectus Schedl, 1962d: 106.
Cryphalus negrosensis Browne, 1979: 85.
Cryphalus niger Schedl, 1942c: 172.
Cryphalus nigericus Browne, 1973: 289.
Cryphalus nigricans Schedl, 1943: 35.

Cryphalus nigrosetosus (Schedl, 1948b: 27) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus niponensis Inouye and Nobuchi, 1957: 51.
Cryphalus nitens Browne, 1980c: 494.
Cryphalus nitidicollis (Schedl, 1975b: 219) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus nitidipennis Browne, 1984d: 89.
Cryphalus nothofagi Browne, 1984c: 68.
Cryphalus numidicus Eichhoff, 1878a: 385.
=*Cryphalus numidicus* Eichhoff, 1878b: 487 **syn. nov.**
Cryphalus nyalubombeae Schedl, 1957b: 49.
Cryphalus obesus (Hopkins, 1915: 42) (*Dacryphalus*).
Cryphalus oblongus Niisima, 1910: 9.
Cryphalus obscurus (Hopkins, 1915: 41) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus orientalis Eggers, 1911: 122.
Cryphalus ovalicollis (Schedl, 1942c: 177) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus ozopemoides Johnson **nom. nov.** [*Hypocryphalus*].
=*Hypocryphalus montanus* Schedl, 1974: 460 **syn. nov.** (secondary homonym).

Remarks: A replacement name is proposed for *Hypocryphalus montanus* Schedl, 1974 following its transfer to *Cryphalus*, because the name is already occupied by *Cryphalus montanus* Nobuchi, 1964. The replacement name is an adjective, refenceing the gross similarity between this species and the genus *Ozopemon* Hagedorn, 1910, for which females have a very similar shape and overall appearance.

Cryphalus paganus Eichhoff, 1878b: 129.
Cryphalus palawanus Schedl, 1942a: 174.
Cryphalus pallidus Eichhoff, 1872a: 131.
Cryphalus papuanus (Schedl, 1973b: 87) (*Margadillius*) **comb. nov.** [*Margadillius*].
=*Ernoporus antennarius* Schedl, 1974: 461 **syn. nov.**
Cryphalus parvulus Niisima, 1910: 8.
Cryphalus pellicius Johnson **nom. nov.** [*Hypocryphalus*].
=*Hypocryphalus pilifer* Schedl, 1979c: 98 **syn. nov.** (secondary homonym).

Remarks: A replacement name is proposed for *Hypocryphalus pilifer* Schedl, 1979c following transfer to the genus *Cryphalus*, because the name is already occupied by *Cryphalus pilifer* Eggers, 1927b. The replacement name is an adjective, following the descriptive meaning of the name, meaning furry.

Cryphalus pexus Schedl, 1979b: 104.
Cryphalus piceae (Ratzeburg, 1837: 163) (*Bostrichus*).
=*Cryphalus hattorii* Kôno, 1938: 67 (syn: Inouye and Nobuchi, 1957).
=*Cryphalus subdepressus* Eggers, 1940d: 37 (syn: Wood, 1992a).
Cryphalus piceus Eggers, 1926b: 136.
Cryphalus pilifer Eggers, 1927b: 394.
Cryphalus piliger (Schedl, 1975b: 219) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus pilosellus Erichson, 1842: 212.
Cryphalus pilosulus Browne, 1980b: 385.
Cryphalus pilosus Tsai and Li, 1963: 606.
Cryphalus planicollis Schedl, 1978b: 74.
Cryphalus polynesiae (Schedl, 1979c: 105) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus procerus Schedl, 1953b: 296.
Cryphalus pruni Eggers, 1929b: 11.
Cryphalus pseudochinlingensis Tsai and Li, 1963: 610.
Cryphalus pseudotabulaeformis Tsai and Li, 1963: 613.
Cryphalus puberulus Schedl, 1942c: 171.
Cryphalus pubescens Hopkins, 1915: 39.
=*Cryphalus subconcentralis* Hopkins, 1915: 40 (syn: Wood, 1954).
Cryphalus pulchellus (Nobuchi, 1975: 54) (*Taenioglyptes*).
Cryphalus punctatostriatus Schedl, 1942a: 175.
Cryphalus punctatus Browne, 1984d: 66.
Cryphalus punctipennis Schedl, 1942c: 169.
Cryphalus punctistriatulus Johnson **nom. nov.**
=*Cryphalus striatulus* Browne, 1981: 127 **syn. nov.** (secondary homonym).

Remarks: A replacement name is proposed for *Cryphalus striatulus* Browne, 1981 because the name is occupied, following the revised status of *Cryphalomorphus striatulus* Browne, 1978. The new is formed from the diminutive of the adjective *punctatus* meaning punctured, and *s striatus* meaning with lines or rows.

Cryphalus pusillimus Schedl, 1942c: 171.
Cryphalus pusillus Schedl, 1943: 38.
Cryphalus quadrituberculatus (Schedl, 1963c: 64) (*Margadillius*) **comb. nov.** [*Margadillius*].
Cryphalus redikorzevi Berger, 1917: 232.
Cryphalus reflexus (Browne, 1980b: 383) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus resiniferi Schedl, 1943: 36.
Cryphalus rhusii Niisima, 1909: 145.
=*Cryphalus kurilensis* Krivolutskaya, 1968: 53 (syn: Mandelshtam, 2006).
Cryphalus robustus Eichhoff, 1872a: 131 **comb. res.** [*Hypocryphalus*].
Cryphalus rotundus (Hopkins, 1915: 41) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus rubentis Hopkins, 1915: 40.
Cryphalus ruficollis Hopkins, 1915: 40.
=*Cryphalus fraseri* Hopkins, 1915: 40 (syn: Wood, 1989).
=*Cryphalus approximatus* Hopkins, 1915: 41 (syn: Wood, 1954).
=*Cryphalus balsameus* Hopkins, 1915: 41 (syn: Wood, 1954).
=*Cryphalus amabilis* Chamberlin, 1917: 321 (syn: Wood, 1954).
=*Cryphalus grandis* Chamberlin, 1917: 323 (syn: Wood, 1954).
=*Cryphalus canadensis* Chamberlin, 1918: 88 (syn: Wood, 1954).
=*Cryphalus mainensis* Blackman, 1922b: 126 (syn: Wood, 1954).
=*Cryphalus ruficollis coloradensis* Wood, 1954: 1008 (syn: Wood, 1977c).
Cryphalus rufopilosus Schedl, 1942a: 174.
Cryphalus rugosus (Schedl, 1958b: 102) (*Ericryphalus*).
Cryphalus saltuarius Weise, 1891: 336 (nomen protectum).
=*Bostrichus asperatus* Ratzeburg, 1837: 163 (unavailable name).
=*Cryphalus scriba* Gozis, 1886: 31 (nomen oblitum).
Cryphalus samoensis Beeson, 1929: 224.
Cryphalus sandakanensis Schedl, 1937b: 548 **comb. res.** [*Hypocryphalus*].
=*Hypocryphalus maculatus* Browne, 1962a: 303 (syn: Wood, 1989).
Cryphalus sarawakensis Schedl, 1972h: 199.
Cryphalus sawadai Nobuchi and Takahashi, 1965: 3.
Cryphalus scabripennis Schedl, 1972h: 199.
Cryphalus schedli Johnson **nom. nov.** [*Hypocryphalus*].
=*Hypocryphalus formosanus* Schedl, 1952b: 62 **syn. nov.** (secondary homonym).

Remarks: A replacement name is proposed for *Hypocryphalus formosanus* Schedl, 1952b because the name is occupied by *Cryphalus formosanus* Schedl, 1942a. The replacement name is a noun in the genitive case, honoring the original author. The types of both species were unavailable for study.

Cryphalus scopiger Berger, 1917: 228.

Cryphalus securus (Schedl, 1940a: 436) (*Ericryphalus*).
Cryphalus sejugatus Schedl, 1965a: 54.
Cryphalus sichotensis Kurentsov, 1941: 152.
Cryphalus sidneyanus (Nördlinger, 1856: 75) (*Bostrichus*).
Cryphalus silvanus Schedl, 1951d: 145.
Cryphalus similis (Eggers, 1922: 168) (*Stephanoderes*).
Cryphalus simplex (Schedl, 1939b: 341) (*Ericryphalus*).
Cryphalus sinoabietis Tsai and Li, 1963: 606.
⊇*Cryphalus sinoabietis opienensis* Tsai and Li, 1963: 607.
Cryphalus solomonensis Johnson **nom. nov.**
=*Margadillius terminaliae* Browne, 1984c: 450 **syn. nov.** (secondary homonym).
Remarks: A replacement name is proposed for *Margadillius terminaliae* Browne, 1984c because the name is already occupied by *Cryphalus terminaliae* Browne, 1980b. The replacement name is a toponym derived from the type locality.
Cryphalus sordidus (Nobuchi, 1975: 51) (*Taenioglyptes*).
Cryphalus sparsepilosus Schedl, 1942c: 172.
Cryphalus spathulatus (Schedl, 1938b: 49) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus spissepilosus Johnson **nom. nov.**
=*Cryphalus densepilosus* Schedl, 1943: 36 **syn. nov.** (secondary homonym).
Remarks: A replacement name is proposed for *Cryphalus densepilosus* Schedl, 1943 because the name is now occupied by *Hypocryphalus densepilosus* Schedl, 1942d. The replacement name is formed from the adverb *spisse* (= densely) and the adjective *pilosus* (= hairy).
Cryphalus squameus Schedl, 1943: 38.
Cryphalus squamulosus Strohmeyer, 1911: 20.
Cryphalus storckiellae Johnson **nom. nov.**
=*Cryphalus striatus* Browne, 1974: 66 **syn. nov.** (secondary homonym).
Remarks: A replacement name is proposed for *Cryphalus striatus* Browne, 1974 because the name is now occupied by *Hypocryphalus striatus* Hopkins, 1915. The replacement name is a noun in the genitive case, named after the host plant *Storckiella*.
Cryphalus striatulus (Browne, 1978: 576) (*Cryphalomorphus*) **comb. nov.** [*Hypothenemus*].
=*Hypothenemus brownei* Beaver, 1991: 53 **syn. nov.** (unnecessary replacement name).
Remarks: *Cryphalus striatulus* (Browne, 1978) is transferred to *Cryphalus* based on the external diagnostic characters visible. The replacement name is no longer necessary.
Cryphalus striatus (Hopkins, 1915: 41) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus strigilatus Wichmann, 1914: 137.
Cryphalus strigipennis Schedl, 1950b: 50.
Cryphalus strohmeyeri Stebbing, 1914: 538.
=*Cryphalus indicus* Stebbing, 1902: 403 (syn: Stebbing, 1914) (Permanently invalid name due to primary homonymy).
Cryphalus subcompactus Lea, 1910: 140.
Cryphalus subgranulatus Schedl, 1943: 37.
Cryphalus submuricatus Eichhoff, 1878a: 385.
=*Cryphalus submuricatus* Eichhoff, 1878b: 492 **syn. nov.**
=*Cryphalus tuberculatus* Schedl, 1943: 37 **syn. nov.**
Cryphalus substriatus Schedl, 1942a: 174.
Cryphalus subtuberculatus Schedl, 1942c: 168.
Cryphalus subvestitus Schedl, 1959a: 482.
Cryphalus sumatranus (Schedl, 1939c: 38) (*Dacryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus sundaensis Schedl, 1942d: 14.
Cryphalus sylvicola (Perkins, 1900: 181) (*Hypothenemus*).
=*Ericryphalus henshawi* Hopkins, 1915: 38 (syn: Schedl, 1941b).
=*Piperius pini* Hopkins, 1915: 39 (syn: Schedl, 1963c).
=*Cryphalus swezeyi* Schedl, 1942b: 147 (syn: Wood, 1960).
=*Cryphalus dimorphus* Schedl, 1950b: 38 (syn: Beaver, 1991).
=*Cryphalus sylvicola obliquus* Schedl, 1950b: 48.
Cryphalus szechuanensis Tsai and Li, 1963: 614.
⊇*Cryphalus szechuanensis tehchangensis* Tsai and Li, 1963: 615.
Cryphalus tabulaeformis Tsai and Li, 1963: 609.
⊇*Cryphalus tabulaeformis chienzhuangensis* Tsai and Li, 1963: 610.
Cryphalus taiwanus Schedl, 1970c: 359.
Cryphalus takahashii Johnson **nom. nov.** [*Ernoporus*]
=*Euptilius exiguus* Browne, 1984c: 451 **syn. nov.** (secondary homonym).
Remarks: A replacement name is proposed for *Euptilius exiguus* Browne, 1984c because the name is occupied by *Cryphalus exiguus* Blandford, 1894b. The replacement name is a noun in the genitive case, honoring the original collector, K. Takahashi.
Cryphalus tenuis Schedl, 1942d: 16.
Cryphalus terminaliae Browne, 1980b: 384.
Cryphalus tetricus (Schedl, 1940a: 437) (*Ericryphalus*).
=*Cryphalus papuanus* Schedl, 1942c: 170 (syn: Schedl, 1979c).
=*Cryphalus grayi* Schedl, 1968: 265 (syn: Schedl, 1979c).
=*Ptilopodius brevis* Browne, 1970: 556 (syn: Schedl, 1972j).
Cryphalus theobromae Nunberg, 1956b: 208 (replacement name).
=*Cryphalus horridus* Graham, 1908: 113 (syn: Nunberg, 1956b) (permanently invalid name due to primary homonymy).
Cryphalus triangularis (Schedl, 1975a: 351) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus trypanoides Beeson, 1935a: 106.
Cryphalus trypanus Sampson, 1914: 383.
Cryphalus tutuilaensis (Schedl, 1951d: 147) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Cryphalus uapouensis (Beeson, 1935a: 107) (*Ericryphalus*).
Cryphalus upoluensis Schedl, 1951d: 144.
Cryphalus variolosus Schedl, 1950b: 49.
Cryphalus vestitus Blandford, 1895: 318.
Cryphalus viburni Stark, 1936: 151.
=*Cryphalus viburni* Eggers, 1942: 30 (syn: Pfeffer, 1944).
Cryphalus vitiensis Browne, 1974: 67.
Cryphalus walkeri (Blandford, 1896a: 200) (*Cryptarthrum*).
=*Coccotrypes hagedorni* Eggers, 1908: 216 (syn: Schedl, 1963c).
=*Cryphalus javanus* Schedl, 1954a: 148 (syn: Schedl, 1958e).
Cryphalus wapleri Eichhoff, 1872a: 131.
=*Cryphalus mekeoi* Schedl, 1972e: 61 (syn: Schedl, 1979d).
Cryphalus yamaguchii Inouye and Nobuchi, 1957: 55.
Cryphalus zimmermani Schedl, 1950b: 51.

Trypophloeini Nüsslin, 1911 **stat. res.**

=Trypophloeinae Nüsslin, 1911b: 375.

Type of tribe

Trypophloeus Fairmaire, 1864.

Diagnosis

Tarsi with third segment cylindrical. Eye emarginated. Antennal funicle with 3–5 segments. Antennal club with or without sutures, and at most a partial septum. Hypomeron with single setae, or rarely

mixed with a few bifurcating setae. Postnotum not fused with metanotum. Typically with scale-like interstrial bristles, and sparse interstrial ground vestiture.

Female
Eye emarginated just above the middle of the eye (or, rarely, entire in very small specimens). Antennae with three to five funicle segments. Antennal club usually flattened (conical in *Trypophloeus*). Pronotum declivous, with serrations and asperities. Pronotal summit usually distinct, profile of pronotal disc (viewed laterally) not obviously concave in most species. Elytra and pronotum typically with extensive vestiture. Metanepisternum with posterior margin obscured, barely visible. Scutellum visible, flat, and triangular. Postnotum not fused to metanotum. Proventriculus sometimes with a more strongly developed apical plate, but never with multidentate crop spines or a tuft of setae beyond the masticatory brush.

Male
Usually similar to female, except dwarfed and flightless in *Hypothenemus*. Some genera have typically sexually dimorphic frons. Aedeagus with separate penis apodemes, typically as long as the penis body.

Distribution
Worldwide, with the highest generic diversity in Asia.

Remarks
This tribe includes about half of the contemporary genera of Cryphalini, sensu Wood (1986a) and Bright (2019). The original description of the tribe (as a subfamily) was based on nonsclerotized parts of male genitalia, which was not examined. The biology of most species is poorly known. In outbreeding species, the female initiates the gallery and is joined by a single male. For inbreeding species (all *Hypothenemus*), a lone foundress produces multiple daughters and usually a single son which mate in their natal gallery before dispersal. Nuptial galleries in both inbreeding and outbreeding species are typically cave-like without egg niches, where eggs are laid communally. Larvae develop in independent tunnels made from feeding on phloem, or communally by extending the cave structure in bark and phloem (Browne 1961, Furniss, 2004).

Included genera
Afrocosmoderes Johnson and Jordal **gen. nov.**; *Atomothenemus* Bright, 2019; *Cosmoderes* Eichhoff, 1878; *Hypothenemus* Westwood, 1834; *Macrocryphalus* Nobuchi, 1981 **stat. res.**; *Microcosmoderes* Johnson and Jordal **gen. nov**; *Microsomus* Bright, 2019; *Pygmaeoborus* Bright, 2019; *Trypophloeus* Fairmaire, 1864.

Afrocosmoderes Johnson and Jordal **gen. nov.** (Fig. 13)

LSID:urn:lsid:zoobank.org:act:A1A4E099-E2A7-41AE-BC63-5CF6898B9932

Type of genus
Miocryphalus pennatus Schedl, 1953.

Diagnosis
Antennal club large without, or barely, visible sutures; pronotum with asperities, lateral margin with carina, hair-like setae present on the hypomeron; mesocoxae narrowly separated, third tarsal segment cylindrical, wings fully developed in males.

Female
Frons simple, convex. Eye distinctly emarginated above midlength. Antennae with two to four funicle segments including the pedicel. Antennal club flat, oval, with barely visible procurved sutures. Pronotum weakly declivous with summit on posterior half to two-thirds; with four to eight marginal asperities, small asperities on the pronotal declivity; a short carina marks the dorsolateral edge of the pronotum. Elytra simple, broadly rounded, with the posterolateral margin barely raised. Interstrial setae scale-like, with additional shorter ground vestiture fine to bristle-like. Scutellum visible, flat, U-shaped. Postnotum not fused to metanotum. Mesocoxae narrowly separated. Metatibiae with lateral, socketed denticles on at least apical quarter. Tarsal segments cylindrical Metanepisternum with its posterior margin barely visible below elytra. All setae on metanepisternum hair-like, not bifurcating. Proventriculus with developed apical plate occupying nearly half of the sclerotized area, divided by a median suture carrying sutural teeth.

Male
Very similar to female. The fifth ventrite is emarginated and the last tergite is visible ventrally. Penis apodemes shorter than rest of body, and ribbon-like, not fused at apex. Tegmen open dorsally. Tegmen with a median ventral apodeme. Spiculum gastrale weakly forked, and of a similar diameter to tegmen. Basal sclerites developed.

Distribution
Southeast Africa, Madagascar.

Etymology
The Latin name is composed by the adjective *afer* (stem *afr-*, and linking vowel *-o-*), in reference to the distribution in East Africa and Madagascar, and *Cosmoderes*, based on the morphological similarity to this genus. Gender masculine.

Remarks
Seven species known. *Afrocosmoderes* can be most easily distinguished from the sister group *Hypothenemus* by the antennae having a very short funicle, club without visible sutures and septum, and by the morphology of the male which is of a similar size of the female and has fully developed eyes and wings. This genus can be separated from the morphologically similar *Cosmoderes* by the sharp carina on the dorsolateral margin of the pronotum, and by the narrowly separated mesocoxae, and the much larger apical plate of the proventriculus with a median suture.

The transfer of *Erioschidias pellitus* Schedl, 1953 to this genus is based on overall appearance since the diagnostic characters are obscured on the type specimen. Several species are transferred from the genus *Afromicracis* Schedl, 1959 (Micracidini). There are a dozen undescribed species from Madagascar (Jordal, unpublished).

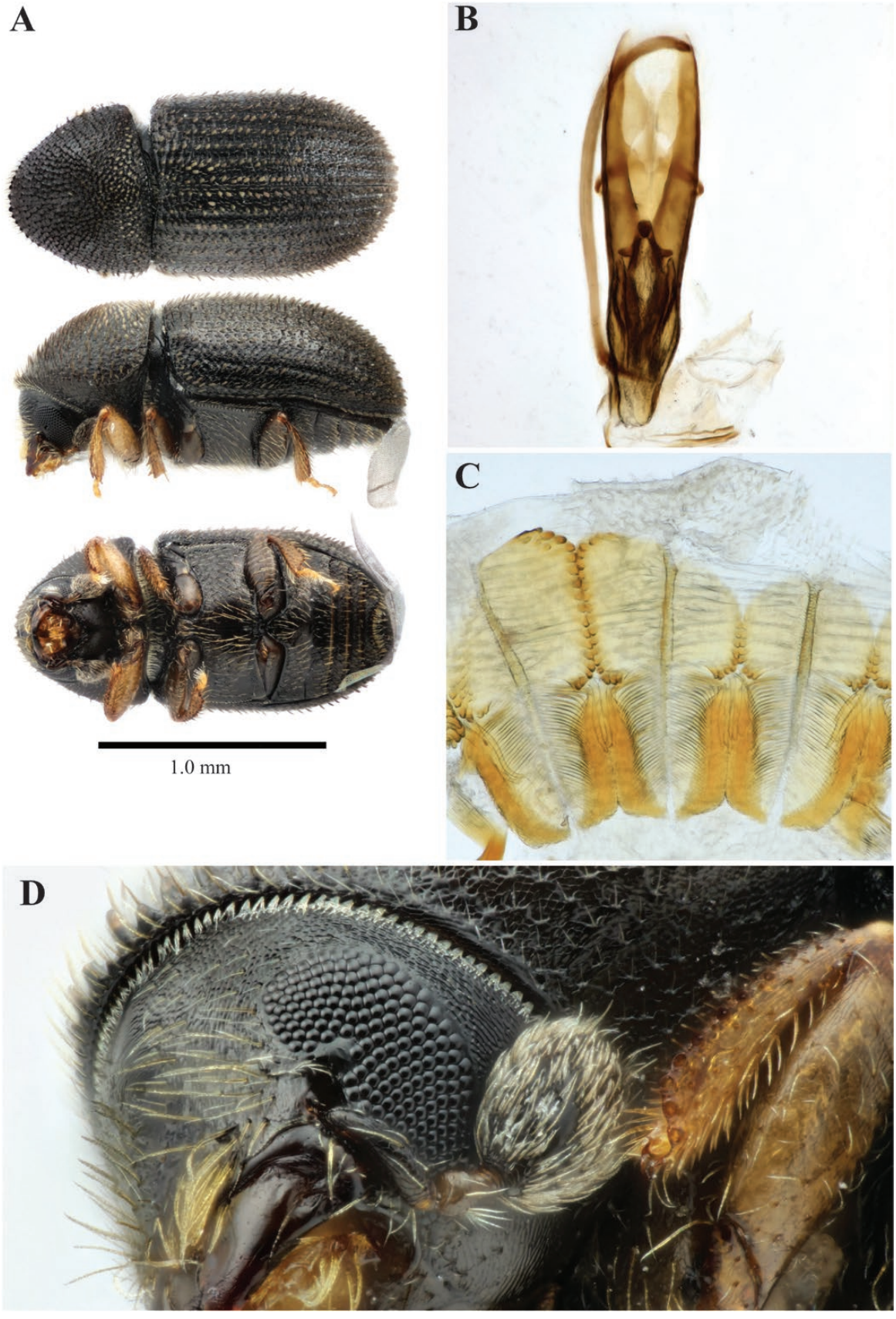

Figure 13. Images of *Afrocosmoderes* sp.: A) Dorsal, lateral and ventral photo of *A. pennatus*. B) Aedeagus of *A. pennatus*, C) Proventriculus of *A. pennatus*, D) Frons, eye, and antennae of *A. pennatus*.

Type material examined
Holotype and paratype of *Hypocryphalus caplandicus* Schedl, 1965, holotype and paratype of *Miocryphalus grobleri* Schedl, 1961 (SANC, NHMW), holotype of *Ptilopodius madagascariensis* Schedl, 1961 (MNHN), paratype of *Ptilopodius madagascariensis* Schedl, 1961 (NHMW), holotype of *Miocryphalus pennatus* Schedl, 1953 (NHMW), paratype of *Euptilius madagascariensis* Schedl, 1963 (NHMW).

Included species
Afrocosmoderes caplandicus (Schedl, 1965f: 115) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Afrocosmoderes grobleri (Schedl, 1961c: 349) (*Miocryphalus*) **comb. nov.** [*Afromicracis*].
Afrocosmoderes madagascariensis (Schedl, 1961b: 133) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].
Afrocosmoderes niger (Schedl, 1961b: 131) (*Erioschidias*) **comb. nov.** [*Cosmoderes*].
Afrocosmoderes pellitus (Schedl, 1953c: 79) (*Erioschidias*) **comb. nov.** [*Cosmoderes*].
Afrocosmoderes pennatus (Schedl, 1953c: 79) (*Miocryphalus*) **comb. nov.** [*Afromicracis*].
Afrocosmoderes schedli Johnson **nom. nov.** [*Cosmoderes*].
=*Euptilius madagascariensis* Schedl, 1963c: 65 **syn. nov.** (secondary homonym).

Remarks: A replacement name is proposed for *Euptilius madagascariensis* Schedl, 1963c due to the conflict with *Ptilopodius madagascariensis* Schedl, 1961b following the transfer of both species to *Afrocosmoderes*. The replacement name is a noun in the genitive case, honoring the original author.

Atomothenemus Bright, 2019: 106

Type of genus
Atomothenemus unicus Bright, 2019.

Diagnosis
Antennae with two funicle segments (including the pedicel), antennal club with horizontal sutures.

Female
Eye emarginated. Antennae with two funicle segments (including the pedicel). Antennal club with two horizontal sutures visible as rows of setae. Frons convex with weak impression in center. Marginal asperities broadly spaced. Pronotal summit distinctly elevated. Sparse scale-like setae on pronotal disc. Scale-like setae on pronotum. Total length approx. 0.8 mm.

Male
Unknown.

Distribution
Dominican Republic.

Remarks
Monotypic. This genus was described in the final stages of this manuscript preparation. Without molecular and internal characters examined, the placement within Trypophloeini is not confirmed. Only one specimen is known, the correct placement will be assessed when more specimens are available. Several of the diagnostic characters match *Hypothenemus distinctus* Wood, 1954 and *H. piaparolinae* Johnson, Atkinson and Hulcr, 2016, the latter is confirmed as *Hypothenemus* based on the proventriculus and molecular data.

Type material examined
Photograph of holotype of *Atomothenemus unicus* Bright, 2019.

Included species
Atomothenemus unicus Bright, 2019: 107.

Cosmoderes Eichhoff, 1878a: 387 (Figs. 14–15)

Synonymy
=*Cosmoderes* Eichhoff, 1878b: 495.
=*Erioschidias* Schedl, 1938b: 42 (unavailable name).
=*Cosmoderus* Chamberlin, 1939: 274 (unavailable name).
=*Allernoporus* Kurentsov, 1941: 159 **syn. nov.**
=*Vitideres* Beeson, 1941: 391 (unavailable name).
=*Erischidias* Schedl, 1942d: 9 (unavailable name).
=*Dendriops* Schedl, 1953a: 125.
=*Erioschidias* Wood, 1960: 21.
=*Vitideres* Beeson, 1961: 301 (unavailable name).
=*Pseudocosmoderes* Nobuchi, 1981: 16.
=*Vitaderes* Wood and Bright, 1992: 901 (unavailable name).

Type of genus
Cosmoderes monilicollis Eichhoff, 1878a.

Diagnosis
Body shape elongated, antennae with short funicle, antennal club large and without sutures, marginal asperities present, mesocoxae contiguous, anterior plate of proventriculus short.

Female
Overall shape elongate, more than 2.5 times as long as wide. Eye emarginated. Antennae with two or three funicular segments, and antennal club large, flattened, with no indication of sutures or a septum. Anterior margin of pronotum with 2–12 marginal asperities. Pronotum surface texture typically rugose. Lateral margins of pronotum rounded or with a carina on posteriolateral margin. Metatibiae with socketed denticles on the lateral edge distributed over at least apical third. Mesocoxae contiguous. The third tarsal segment cylindrical. Elytra with slightly flattened interstrial bristles. Ground vestiture sparse or absent, and hair-like if present. Proventriculus elongate, apical plate short, sometimes with a patch of teeth or granules near the median suture.

Male
Externally identical to females in most species, identified only through dissection of genitalia. In one undescribed species from Vietnam, sexual dimorphism is expressed in the male which has small tubercles on the frons and enlarged setae on the antennae (Johnson, unpublished). Penis apodemes of similar length to penis body, not fused at apex. Tegmen open dorsally. Tegmen with a median ventral apodeme. Spiculum gastrale without fork, of similar thickness to penis apodemes. Basal sclerites poorly developed.

Distribution
Africa, Asia, New Guinea, Australia, Oceania.

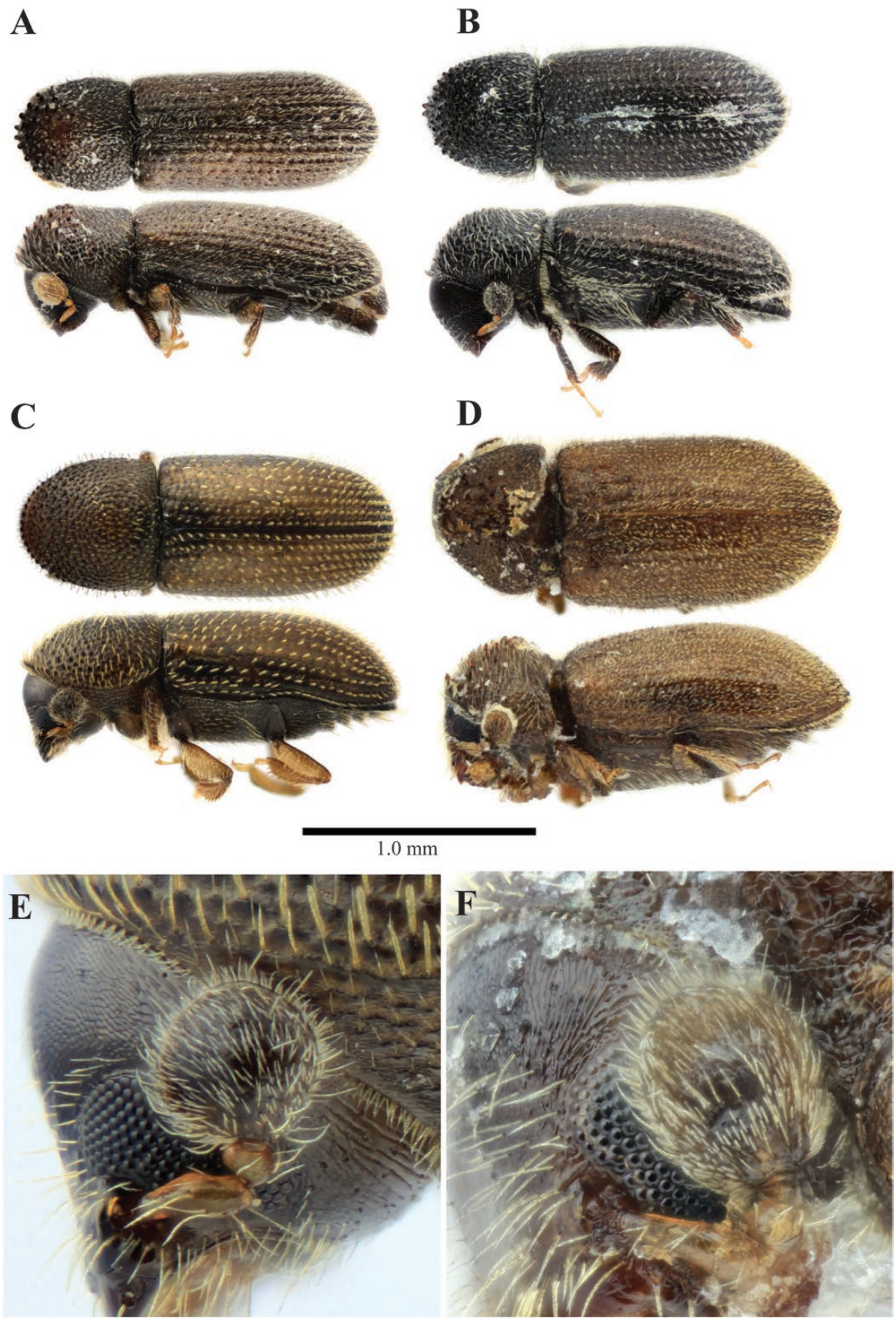

Figure 14. Images of *Cosmoderes* spp.: Dorsal and lateral photographs of A) *C. attenuatus*, B) *C. consobrinus*, C) *C. elegans*, D) *C. euonymi*. Eye and antennae of E) *C. elegans*, F) *C. euonymi*.

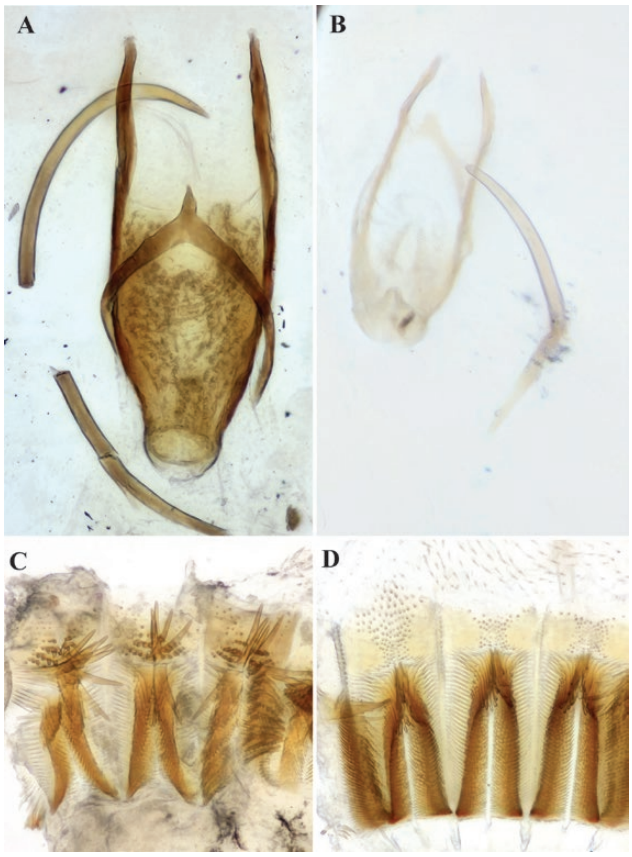

Figure 15. Images of *Cosmoderes* spp.: Aedeagus of A) *C. consobrinus* and B) *C. elegans*. Proventricuus of C) *C. attenuatus*, and D) *C. elegans*.

Remarks

Fifteen species known. The genus *Allernoporus* was found to be synonymous with this genus. *Allernoporus euonymi* is different from the generic type of *Cosmoderes* only by having two marginal asperities, bifurcating setae on the hypomeron, and ground vestiture on the elytra. These character states are found in other *Cosmoderes* species, and are typically variable in other Trypophloeini genera.

Specimens labeled as undetermined *Cosmoderes* spp. have been included in several phylogenetic studies (Jordal and Cognato 2012, Gohli et al. 2017, Pistone et al. 2018). These specimens were re-evaluated here and are in fact species of *Eidophelus*, indicated by the entire eye.

The biology of *Cosmoderes* is poorly known. Most specimens collected by the authors were from nonwoody material, especially vines. *Cosmoderes monilicollis* were observed to be monogamous with eggs laid in a cluster (Johnson, unpublished).

Type material examined

Holotype of *Cosmoderes consobrinus* Blandford, 1894 (BMNH); holotype of *Erioschidias cylindricus* Schedl, 1962 (NHMW); holotype of *Cosmoderes elegans* Schedl, 1975 (NHMW); paralectotypes (2) of *Allernoporus euonymi* Kurentsov, 1941 (ZIN); paratype of *Erioschidias frontalis* Wood, 1960 (USNM); lectotype of *Dendriops granulicollis* Schedl, 1953 (NHMW); holotype of *Cosmoderes papuanus* Schedl, 1975 (NHMW); holotype of *Erioschidias ruandae* Schedl, 1962 (NHMW).

Included species

Cosmoderes anticus (Schedl, 1975a: 343) (*Erioschidias*).
Cosmoderes attenuatus (Nobuchi, 1981: 17) (*Pseudocosmoderes*).
Cosmoderes consobrinus Blandford, 1894b: 86.
Cosmoderes corpulentus (Schedl, 1971d: 151) (*Erioschidias*).
Cosmoderes cylindricus (Schedl, 1962f: 103) (*Erioschidias*).
Cosmoderes elegans Schedl, 1975a: 342.
Cosmoderes elongatus (Eggers, 1939a: 4) (*Erioschidias*).
Cosmoderes euonymi (Kurentsov, 1941: 159) (*Allernoporus*) **comb. nov.** [*Allernoporus*].
Cosmoderes frontalis (Wood, 1960: 21) (*Erioschidias*).
Cosmoderes monilicollis Eichhoff, 1878a: 387.
=*Cosmoderes monilicollis* Eichhoff, 1878b: 496 (syn: Alonso-Zarazaga and Lyal, 2009).
=*Dendriops granulicollis* Schedl, 1953a: 125 (syn: Schedl, 1963c).
=*Erioschidias coriaceus* Schedl, 1959a: 474 (syn: Schedl, 1963c).
Cosmoderes papuanus Schedl, 1975a: 341.
Cosmoderes queenslandi (Schedl, 1938b: 43) (*Erioschidias*).
Cosmoderes ruandae (Schedl, 1962f: 104) (*Erioschidias*).
Cosmoderes setistriatus (Lea, 1910: 141) (*Cryphalus*).
Cosmoderes solitarius (Schedl, 1957b: 46) (*Erioschidias*).

Hypothenemus Westwood, 1834: 35 (Figs. 16–18)

Synonymy

=*Hypothonemus* LeConte, 1868: 154 (unavailable name).
=*Stephanoderes* Eichhoff, 1872a: 132.
=*Homoeocryphalus* Lindemann, 1877: 168.
=*Triarmocerus* Eichhoff, 1878a: 383.
=*Triarmocerus* Eichhoff, 1878b: 119.
=*Adiaeretus* Hagedorn, 1909: 744.
=*Trischidias* Hopkins, 1915: 12.
=*Stylotentus* Schedl, 1939d: 380 (unavailable name).
=*Chondronoderes* Schedl, 1940c: 589.
=*Epsips* Beeson, 1941: 373 (unavailable name).
=*Archeophalus* Schedl, 1941a: 392.
=*Pachynoderes* Schedl, 1941a: 393.
=*Lepiceroides* Schedl, 1957b: 59.
=*Ernophloeus* Nunberg, 1958: 484.
=*Stylotentus* Schedl, 1963a: 448.
=*Periocryphalus* Wood, 1971: 33 **syn. nov.**
=*Lepiceriodes* Schedl, 1977c: 499 (unavailable name).

Type of genus

Tomicus eruditus Westwood, 1834.

Diagnosis

Eye emarginated. Antennal club with partial septum, and straight, weakly procurved or sinuate sutures. Lateral margins of pronotum carinate. Hypomeron with hair-like or scale-like setae (not bifurcating). Third tarsal segment cylindrical. Male dwarfed and flightless. Species or specimens with deviations in the antennal club (lacking sutures or a partial septum) or eye (entire) are rarely encountered.

Female

Eye emarginated, except for some individuals of small species where this is not apparent. Frons variable, usually convex, sometimes with small to large concave region below level of eyes, or a small tubercle in the center. Antennal funicle with two to five segments. Antennae for most species with three approximately straight or weakly procurved sutures, and a partial septum. Larger species tend to have the sutures more procurved than smaller species. A small number of rarely collected species have no visible septum, and some of these have very poorly defined, procurved sutures. Pronotum with 2–10 marginal asperities. Pronotal declivity with asperities up to the summit, which may be elevated. A carina marks the

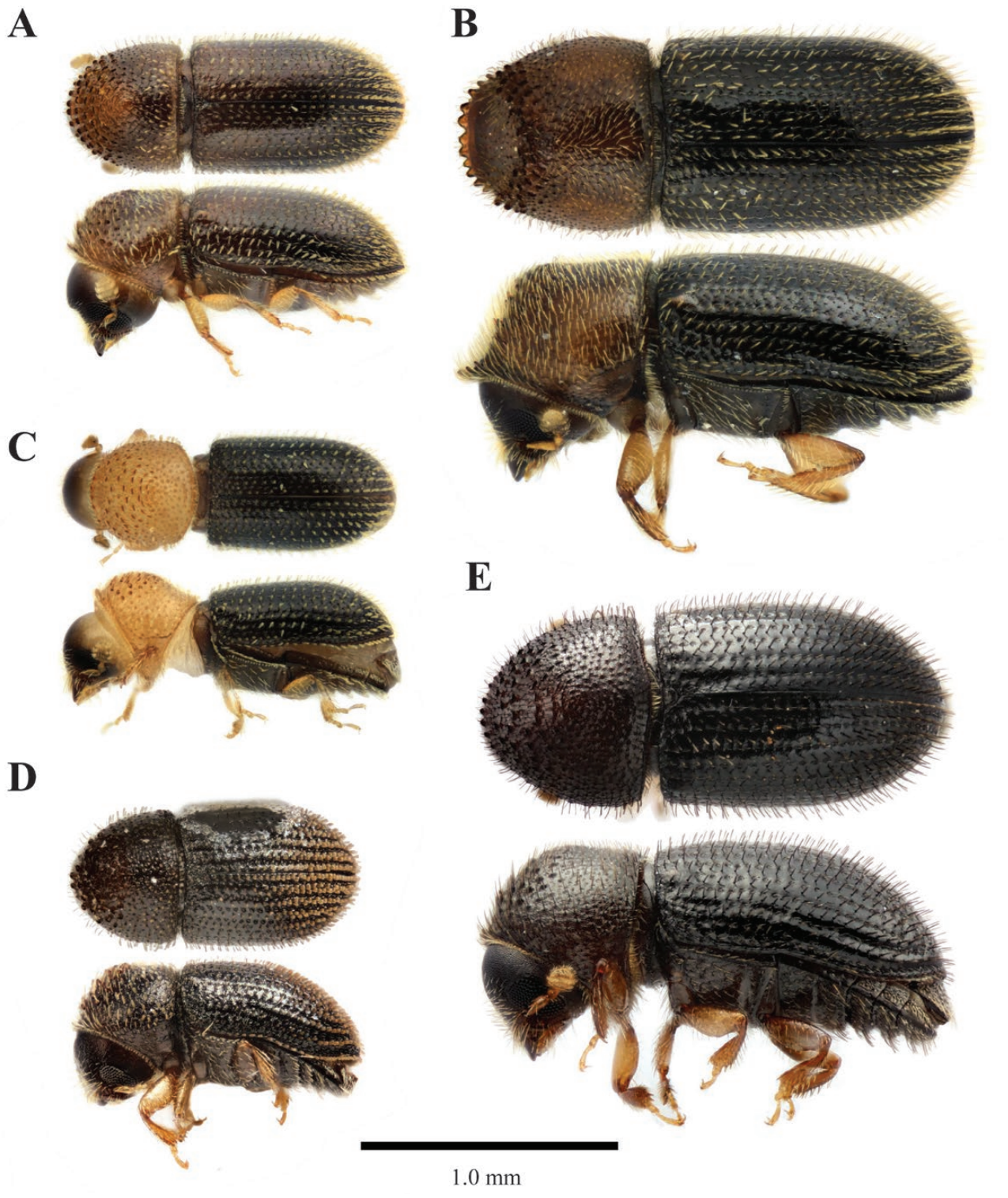

Figure 16. Images of *Hypothenemus* spp.: Lateral and dorsal photographs of A) *H.* areccae, B) *H. aulmanni,* C) *H. eruditus,* D) *H. georgiae* and E) *H. hampei.*

dorsolateral margin of the pronotum. The setae on the hypomeron are simple, never bifurcating. Elytra typically convex, rarely with granules or spines. Vestiture mostly consisting of interstrial rows of scale-like, less commonly hair-like, setae. Interstrial ground vestiture typically sparse or absent, and if present, usually restricted to the elytral apex. Apex of the elytra weakly elevated. Posterior margin of the metanepisternum typically covered by the elytra or barely visible. Metatibia with socketed denticles restricted to apical fifth. Third tarsal segment cylindrical. Proventriculus with well-developed apical plate, typically with transverse rows of teeth visible.

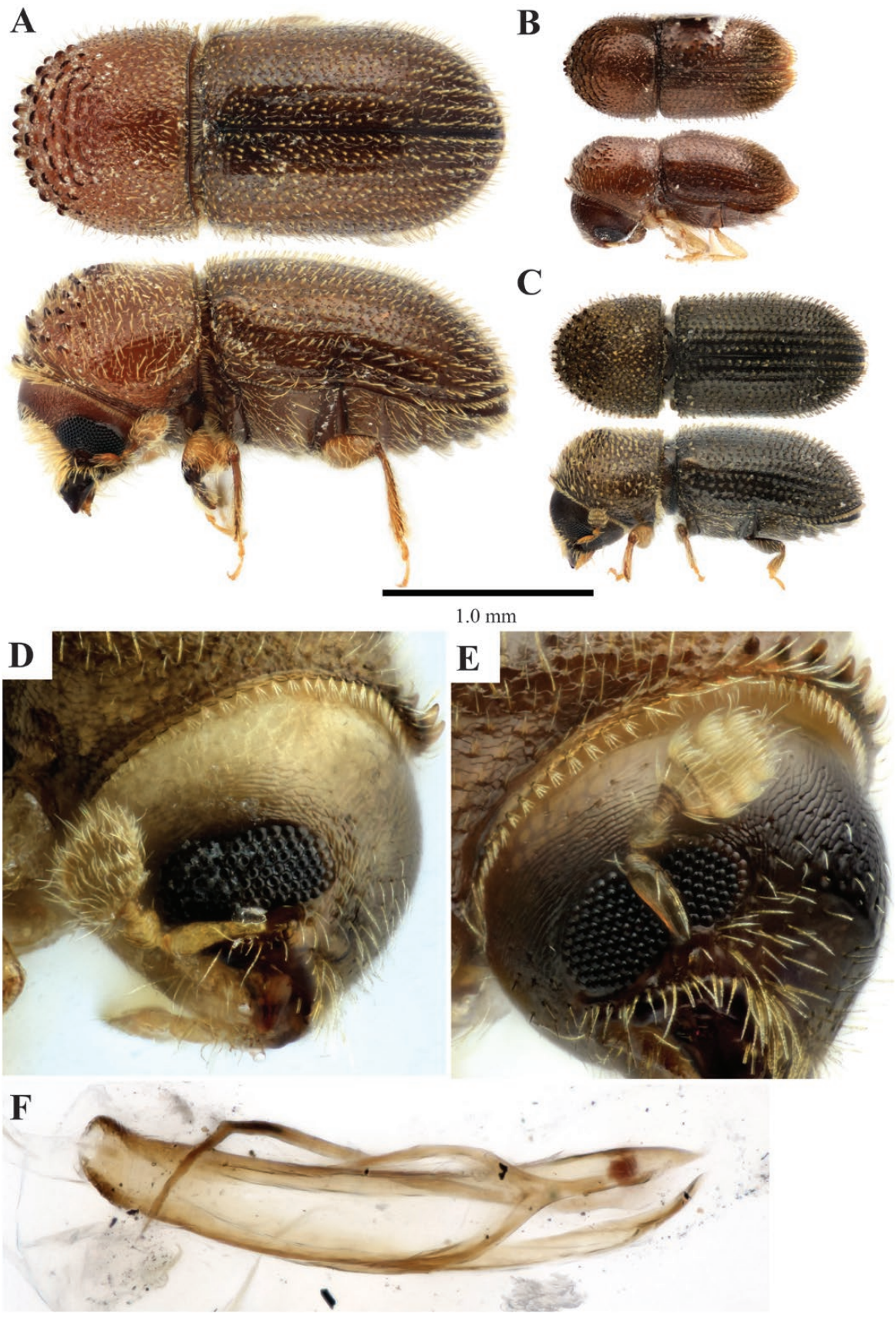

Figure 17. Images of *Hypothenemus* spp.: Lateral and dorsal photograph of A) *H. ingens*, B) *H. pullus*, C) *H. seriatus*. Eye and antennae of D) *H. piaparolinae* and E) *H. seriatus*, and aedeagus of F) *H. dissimilis*.

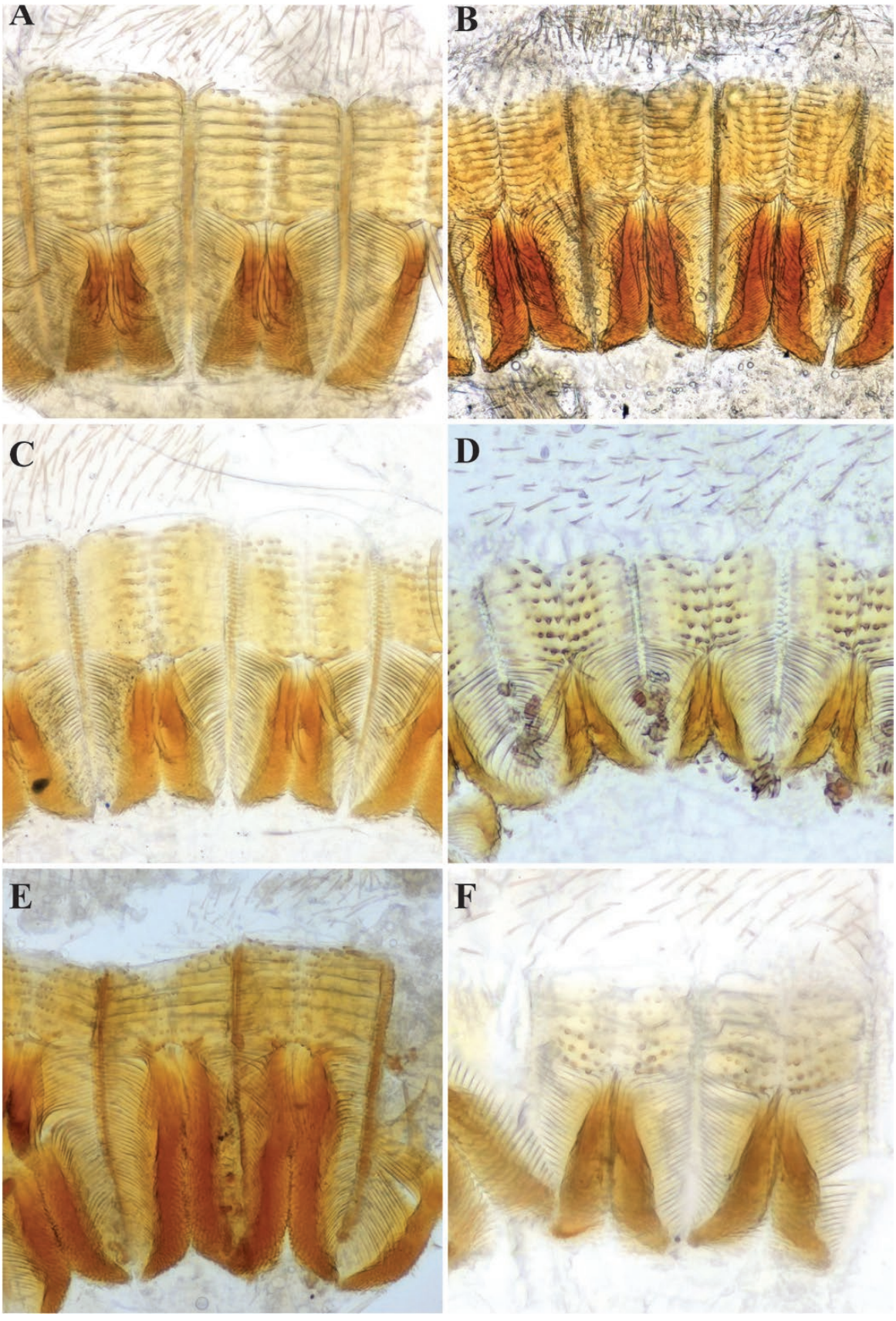

Figure 18. Images of *Hypothenemus* spp.: Proventriculus of A) *H. areccae*, B) *H. dissimilis*, C) *H. eruditus*, D) *H. georgiae*, E) *H. hampei*, and F) *H. piaparolinae*. Images not to scale.

Male

Usually much smaller than female with smaller eyes and vestigial wings, rarely found outside galleries. Penis apodemes of a similar length to penis body and flattened, ribbon-like, free at apex. Tegmen open dorsally, with a median ventral apodeme. Spiculum gastrale weakly forked, of a similar diameter to the tegmen (but smaller than the ribbon-like penis apodemes). Basal sclerites not visible.

Distribution

Worldwide in tropical and subtropical areas, rarely in temperate areas in Eastern North America and Eastern Asia.

Remarks

In total, 221 species known. *Hypothenemus* was originally described as a subgenus of *Tomicus* Latreille, 1802, thus the placement of parentheses for *Hypothenemus eruditus* (Westwood, 1834), which has not been widely used.

Trischidias is treated as a synonym following Bright (2019), which is similar to the species previously placed in *Periocryphalus*. They were previously diagnosed based on the entire eye (which is variable within species and often of a typical weak emargination of *Hypothenemus*), and by the antennae without a septum (which has been found in several unrelated *Hypothenemus* lineages as well). The relationship between *Hypothenemus* and *Trischidias* is long-standing, Wood (1954) remarked that they were 'obviously derived from *Hypothenemus*'. We confirm the placement within *Hypothenemus* with the type of the genus, corroborating previous phylogenies (Johnson et al. 2018)

Similarly, *Periocryphalus* Wood, 1971 is recognized here as a new synonym of *Hypothenemus*. The species in this genus are unusual, having antennae without visible sutures, stout body shape and a flared apical margin of the declivity. While internal morphological or genetic data were not available in this study, all external characters are in agreement with *Hypothenemus*.

Hypothenemus is a remarkably common genus in tropical and subtropical regions with several of the world's most abundant species in many forest localities. Also very frequently intercepted in global trade due to its wide range on host materials and high abundance. At least two species are obligate seed feeders and pests of certain crops. In addition to their common presence under bark, they are also known to reproduce in unusual plant material of grasses, vines, pith, leaf petioles, fruiting bodies of fungi (Deyrup, 1987), manufactured products (Browne, 1961), and even found in old galleries of other bark beetles (Johnson, unpublished).

Type material examined

Holotype of *Hypothenemus apicalis* Wood, 1974 (USNM); paratype of *Hypothenemus bauhaniae* Schedl, 1950 (BMNH); paratype of *Hypothenemus artocarpi* Browne, 1978 (BMNH); holotype of *Hypothenemus ascitus* Wood, 1971 (USNM); paratype of *Ernoporus nigrina* Schedl, 1967 (NHMW); cotype of *Stephanoderes attenuatus* Eggers, 1935 (NHMW); holotype of *Hypothenemus barinensis* Wood, 2007 (USNM); holotype of *Triarmocerus birmanus* Eichhoff, 1878 (NHMW); paratype of *Stephanoderes cryphalomorphus* Schedl, 1939 (BMNH); allotype of *Hypothenemus columbi* Hopkins, 1915 (USNM); holotype of *Cryphalus hispidulus* LeConte, 1868 (MCZ); holotype of *Stephanoderes cuneolus* Schedl, 1936 (NHMW); paratype of *Stephanoderes curtipennis* Schedl, 1950 (USNM); paratype of *Cryphalomorphus samoanus* Browne, 1977 (USNM); holotype of *Crypturgus dissimilis* Zimmermann, 1868 (MCZ); holotype of *Hypothenemus dolosus* Wood, 1974 (USNM); holotype of *Hypothenemus erectus* LeConte, 1876 (MCZ); paratype of *Tomicus eruditus* Westwood, 1834 (BMNH); paratype of *Stephanoderes erythrinae* Eggers, 1936 (BMNH); paratype of *Stephanoderes nanulus* Schedl, 1948 (BMNH); paratype of *Hypothenemus beameri* Wood, 1954 (BMNH); paratype of *Stephanoderes hirsutus* Wood, 1954 (BMNH); holotype of *Hypothenemus indigens* Wood, 1974 (USNM); lectotype of *Hypothenemus ingens* Schedl, 1942 (NHMW); paratype of *Stephanoderes javanus* Eggers, 1908 (NHMW); holotype of *Margadillius loranthus* Schedl, 1942 (NHMW); paratype of *Hypothenemus major* Browne, 1970 (BMNH); holotype of *Hypothenemus meridensis* Wood, 2007 (USNM); paratype of *Trischidias minutissimus* Wood, 1954 (NHMW); paratype of *Hypothenemus namosianus* Browne, 1983 (BMNH); holotype of *Hypothenemus nanellus* Wood, 1971 (USNM); holotype of *Archeophalus natalensis* Schedl, 1941 (NHMW); holotype of *Miocryphalus nigrinus* Schedl, 1965 (MRCB); paratype(?) of *Miocryphalus nigrinus* Schedl, 1965 (NHMW); holotype of *Eidophelus nitidus* Schedl, 1965 (NHMW); holotype of *Hypothenemus parvistriatus* Wood, 2007 (USNM); holotype of *Hypothenemus piaparolinae* Johnson, Atkinson and Hulcr, 2016 (USNM); holotype and paratype of *Periocryphalus pullus* Wood, 1971 (USNM); holotype and paratype of *Hypothenemus rugosipes* Wood, 2007 (USNM); holotype of *Ptilopodius shoreae* Schedl, 1953 (BMNH); holotype of *Hypothenemus solocis* Wood, 1974 (USNM); paratype of *Miocryphalus spinatus* Schedl, 1977 (NHMW); holotype of *Ptilopodius squamosus* Schedl, 1953 (BMNH); paratype of *Trischidias striatus* Atkinson, 1993 (TAMU); paratypes (10) of *Hypothenemus subterrestris* Johnson, Atkinson and Hulcr, 2016 (FSCA); holotype of *Hypothenemus suspectus* Wood, 1974 (USNM); holotype of *Hypothenemus teretis* Wood, 1971 (USNM); holotype of *Hypothenemus trivialis* Wood, 1974 (USNM); holotype of *Hypothenemus vesculus* Wood, 1974 (USNM); holotype of *Hypothenemus virolae* Wood, 2007 (USNM); holotype of *Hypothenemus vitis* Browne, 1970 (BMNH).

Included species

Hypothenemus aberrans Browne, 1973: 287.
Hypothenemus abhorrens Wood, 2007: 504.
Hypothenemus abruptus (Schedl, 1961b: 135) (*Stephanoderes*).
Hypothenemus acaciae (Eggers, 1920: 120) (*Cryphalus*).
Hypothenemus adscitus (Schedl, 1950b: 46) (*Stephanoderes*).
Hypothenemus adustus Bright, 2019: 122.
Hypothenemus aethiops (Schedl, 1965e: 26) (*Lepiceroides*).
Hypothenemus africanus (Hopkins, 1915: 30) (*Stephanoderes*).
=*Hypothenemus concavifrons* Bright and Torres, 2006: 405 (syn: Bright, 2019).
Hypothenemus agnatus (Eggers, 1924: 103) (*Stephanoderes*).
=*Stephanoderes tungamwansolus* Schedl, 1939d: 385 (syn: Beaver and Löyttyniemi, 1989).
=*Hypothenemus confusus* Eggers, 1940c: 235 (syn: Beaver and Löyttyniemi, 1989).
Hypothenemus alternatus (Eggers, 1943b: 73) (*Stephanoderes*).
Hypothenemus amakusanus (Murayama, 1934b: 287) (*Stephanoderes*).
Hypothenemus amplissimus Bright and Torres, 2006: 404.
Hypothenemus apicalis Wood, 1974a: 19.
Hypothenemus areccae (Hornung, 1842: 117) (*Bostrichus*).

=*Stephanoderes obscurus* Eichhoff, 1872a: 133 (syn: Wood, 1975b).
=*Stephanoderes depressus* Eichhoff, 1878b: 155 (syn: Wood, 1975b).
=*Hypothenemus vafer* Blandford, 1896b: 241 (syn: Wood, 1974b).
=*Stephanoderes fungicola* Eggers, 1908: 216 (syn: Eggers, 1929c).
=*Stephanoderes polyphagus* Eggers, 1924: 104 (syn: Wood, 1972b).
=*Stephanoderes hispidus* Eggers, 1925: 156 (syn: Wood, 1960).
=*Hypothenemus heterolepsis* Costa Lima, 1928: 117 (syn: Wood, 1972b).
=*Hypothenemus capitalis* Beeson, 1935a: 102 (syn: Wood, 1960).
=*Hypothenemus eupolyphagus* Beeson, 1940: 193 (syn: Wood, 1960).
=*Stephanoderes bambesanus* Eggers, 1940c: 232 (syn: Wood, 1989).
=*Stephanoderes subvestitus* Eggers, 1940c: 232 (syn: Wood, 1972b).
=*Stephanoderes martiniquensis* Eggers, 1941a: 99 (syn: Wood, 1972b).
=*Hypothenemus oahuensis* Schedl, 1941b: 110 (syn: Wood, 1960).
=*Hypothenemus subglabratus* Schedl, 1942c: 174 (syn: Beaver, 1991).
=*Hypothenemus bauhaniae* Schedl, 1950a: 19 (syn: Wood, 1989).
=*Stephanoderes occidentalis* Schedl, 1954b: 76 (syn: Wood, 1989).
Hypothenemus artocarpi Browne, 1978: 588.
Hypothenemus arundinis (Eichhoff, 1878a: 386) (*Stephanoderes*).
=*Stephanoderes arundinis* Eichhoff, 1878b: 157 **syn. nov.**
Hypothenemus ascitus Wood, 1971: 35.
Hypothenemus ater Eggers, 1932: 31.
Hypothenemus aterrimulus Wood, 1989: 178.
=*Lepiceroides aterrimus* Schedl, 1957b: 59 (syn: Wood, 1989).
Hypothenemus aterrimus (Schedl, 1951e: 104) (*Stephanoderes*).
Hypothenemus atomus Hopkins, 1915: 15.
=*Hypothenemus impressifrons* Hopkins, 1915: 15 (syn: Wood, 1954).
=*Hypothenemus marylandicae* Hopkins, 1915: 15 (syn: Wood, 1954).
=*Hypothenemus robiniae* Hopkins, 1915: 15 (syn: Wood, 1954).
=*Hypothenemus toxicodendri* Hopkins, 1915: 15 (syn: Wood, 1954).
=*Ernoporus nigrina* Schedl, 1967b: 7.
Hypothenemus atratus (Schedl, 1964c: 45) (*Stephanoderes*).
Hypothenemus attenuatus (Eggers, 1935: 306) (*Stephanoderes*) **comb. nov.** [*Afromicracis*].
Hypothenemus aulmanni Hagedorn, 1912b: 41.
=*Cryphalus tonsus* Eggers, 1919: 242 (syn: Beaver, 1999).
Hypothenemus avitus Bright and Poinar, 1994: 186.
Hypothenemus balachowskyi Menier, 1971: 141.
Hypothenemus baloghi (Schedl, 1967c: 226) (*Stephanoderes*).
Hypothenemus bambusae Browne, 1980d: 775.
Hypothenemus barinensis Wood, 2007: 505.
Hypothenemus bauhaniae (Schedl, 1950a: 20) (*Stylotentus*).
Hypothenemus bezaziani Peyerimhoff, 1935: 192.
Hypothenemus bicinctus Schedl, 1959a: 479.
Hypothenemus bidens Browne, 1973: 288.
Hypothenemus bifurcatus Bright, 2019: 127.
Hypothenemus birmanus (Eichhoff, 1878a: 384) (*Triarmocerus*).
=*Triarmocerus birmanus* Eichhoff, 1878b: 486 **syn. nov.**
=*Hypothenemus maculicollis* Sharp, 1879: 101 **syn. nov.** (syn: Browne, 1970).
=*Hypothenemus peritus* Blandford, 1894b: 84 **syn. nov.** (syn: Browne, 1970).
=*Hypothenemus farinosus* Blandford, 1896b: 241 **syn. nov.** (syn: Browne, 1970).
=*Hypothenemus validus valens* Sampson, 1914: 385 **syn. nov.** (syn: Browne, 1970).
=*Stephanoderes perkinsi* Hopkins, 1915: 21 **syn. nov.** (syn: Wood, 1972b).
=*Stephanoderes psidii* Hopkins, 1915: 32 **syn. nov.** (syn: Wood, 1972b).
=*Stephanoderes sterculiae* Hopkins, 1915: 32 **syn. nov.** (syn: Wood, 1972b).
=*Stephanoderes alter* Eggers, 1923a: 219 **syn. nov.**
=*Stephanoderes uter* Eggers, 1923a: 219 **syn. nov.**
=*Stephanoderes nibarani* Beeson, 1933: 10 **syn. nov.**
=*Stephanoderes ampliatus* Eggers, 1936c: 627 **syn. nov.**
=*Stephanoderes pacificus* Beeson, 1940: 197 **syn. nov.**
=*Stephanoderes castaneus* Wood, 1954: 1027 **syn. nov.**
=*Stylotentus dubius* Schedl, 1971b: 372 **syn. nov.**
Hypothenemus biseriatus (Eggers, 1919: 240) (*Stephanoderes*).
Hypothenemus bolivianus (Eggers, 1931: 29) (*Stephanoderes*).
Hypothenemus brevicollis (Eggers, 1927a: 177) (*Stephanoderes*).
=*Stephanoderes lamuensis* Eggers, 1935: 304 (syn: Beaver, 2011b).
Hypothenemus brevis Eggers, 1932: 30.
Hypothenemus californicus Hopkins, 1915: 19.
=*Hypothenemus tritici* Hopkins, 1915: 19 (syn: Wood, 1972b).
=*Hypothenemus thoracicus* Hopkins, 1916: 598.
=*Stephanoderes zeae* Schedl, 1973a: 169 (syn: Wood, 1989).
Hypothenemus camerunus (Eggers, 1922: 167) (*Stephanoderes*).
=*Stephanoderes brunneipes* Nunberg, 1960: 289.
Hypothenemus carbonarius Eggers, 1943b: 73.
Hypothenemus carinafrons Bright, 2019: 128.
Hypothenemus colae (Schedl, 1957b: 54) (*Stephanoderes*).
Hypothenemus collinus Bright, 2019: 129.
Hypothenemus columbi Hopkins, 1915: 18.
=*Hypothenemus abdominalis* Hopkins, 1915: 18 (syn: Wood, 1954).
=*Hypothenemus brunneipennis* Hopkins, 1915: 18 (syn: Wood, 1954).
=*Hypothenemus rufopalliatus* Hopkins, 1915: 18 (syn: Wood, 1954).
=*Hypothenemus amplipennis* Hopkins, 1915: 19 (syn: Wood, 1954).
Hypothenemus concolor Hagedorn, 1909: 744.
Hypothenemus costatus (Eichhoff, 1878a: 386) (*Stephanoderes*).
Hypothenemus crinatus Bright, 2019: 131.
Hypothenemus criticus (Schedl, 1937a: 398) (*Cryphalus*).
=*Hypothenemus alternans* Browne, 1970: 554 (syn: Schedl, 1972i).
Hypothenemus crudiae (Panzer, 1791: 35) (*Bostrichus*).
=*Cryphalus mucronifer* Wollaston, 1867: 116 (syn: Wood, 1989).
=*Cryphalus hispidulus* LeConte, 1868: 156 (syn: Wood, 1972b).
=*Hypothenemus nanus* Hagedorn, 1909: 744 (syn: Schedl, 1952e).
=*Stephanoderes differens* Hopkins, 1915: 25 (syn: Wood, 1972b).
=*Stephanoderes brasiliensis* Hopkins, 1915: 26 (syn: Wood, 1954).
=*Stephanoderes guatemalensis* Hopkins, 1915: 26 (syn: Wood, 1954).
=*Stephanoderes lecontei* Hopkins, 1915: 26 (syn: Wood, 1954).

=*Stephanoderes paraguayensis* Hopkins, 1915: 26 (syn: Wood, 1972b).
=*Stephanoderes trinitatis* Hopkins, 1915: 28 (syn: Bright and Torres, 2006).
=*Stephanoderes uniseriatus* Eggers, 1924: 103 (syn: Wood, 1972b).
=*Stephanoderes polyphagus* Costa Lima, 1924: 316 (syn: Wood, 1972b).
=*Stephanoderes largipennis* Toledo Piza Junior, 1924: 354 (syn: Costa Lima and Ravache, 1925).
=*Stephanoderes fallax* Costa Lima, 1924: 414 (syn: Wood, 1972b).
=*Stephanoderes lebronneci* Beeson, 1935a: 104 (syn: Wood, 1972b).
=*Stephanoderes hivaoea* Beeson, 1935a: 105 (syn: Wood, 1972b).
Hypothenemus cryphaloides (Eichhoff, 1878a: 384) (*Triarmocerus*).
=*Triarmocerus cryphaloides* Eichhoff, 1878b: 119 (syn: Alonso-Zarazaga and Lyal, 2009).
Hypothenemus cuneolus (Schedl, 1936: 24) (*Stephanoderes*).
Hypothenemus curtipennis (Schedl, 1950b: 45) (*Stephanoderes*).
=*Cryphalomorphus samoanus* Browne, 1977: 61.
Hypothenemus cylindraceus Schedl, 1972c: 287.
Hypothenemus cynometrae Schedl, 1957b: 50.
Hypothenemus delicatus Schedl, 1964c: 44.
Hypothenemus deprecator (Schedl, 1941a: 393) (*Pachynoderes*).
Hypothenemus dexter (Sampson, 1922: 141) (*Cryphalus*).
Hypothenemus dimorphus (Schedl, 1959b: 168) (*Stephanoderes*).
Hypothenemus dipterocarpi Hopkins, 1915: 17.
=*Hypothenemus mangarevanus* Beeson, 1940: 196 (syn: Wood, 1972b).
Hypothenemus discordis Bright, 2019: 133.
Hypothenemus dissimilis (Zimmermann, 1868: 144) (*Crypturgus*).
=*Stephanoderes chapuisii* Eichhoff, 1872a: 132 (syn: Eichhoff, 1896).
Hypothenemus distinctus Wood, 1954: 1053.
Hypothenemus dolichocola Hopkins, 1915: 19.
Hypothenemus donisi (Schedl, 1957b: 46) (*Ericryphalus*).
=*Ericryphalus madagascariensis* Schedl, 1961b: 131 (syn: Wood, 1989).
Hypothenemus dorsosignatus (Schedl, 1950b: 46) (*Stephanoderes*).
=*Stephanopodius fijianus* Schedl, 1955a: 289 (syn: Beaver, 1991).
Hypothenemus dubitalis Bright, 2019: 134.
Hypothenemus ebenus Wood, 2007: 529.
Hypothenemus elephas (Eichhoff, 1872a: 132) (*Stephanoderes*).
=*Adiaeretus spinosus* Hagedorn, 1909: 745 (syn: Schedl, 1963a).
Hypothenemus emmi (Hagedorn, 1913: 254) (*Cryphalus*) (Fossil taxon).
=*Stephanoderes emmi* Eggers, 1919: 240 (syn: Eggers, 1927a).
Hypothenemus erectus LeConte, 1876: 356.
=*Hypothenemus validus* Blandford, 1904: 228 (syn: Wood, 1972b).
=*Stephanoderes cubensis* Hopkins, 1915: 32 (syn: Wood, 1972b).
=*Stephanoderes puncticollis* Hopkins, 1915: 32 (syn: Wood, 1972b).
=*Stephanoderes brunneicollis* Hopkins, 1915: 33 (syn: Wood, 1954).
=*Stephanoderes discedens* Schedl, 1950a: 23 (syn: Wood, 1976).
Hypothenemus eruditus (Westwood, 1834: 34) (*Tomicus*).
=*Bostrichus plumeriae* Nördlinger, 1856: 74 (syn: Bright, 2019).
=*Cryphalus aspericollis* Wollaston, 1860: 365 (syn: Schedl, 1960).
=*Bostrichus boieldieui* Perroud, 1864: 188 (syn: Eichhoff, 1878b).
=*Cryphalus obscurus* Ferrari, 1867: 17 (syn: Wood, 1974b).
=*Homoeocryphalus ehlersi* Lindemann, 1877: 168.
=*Stephanoderes germari* Eichhoff, 1878a: 386.
=*Stephanoderes myrmedon* Eichhoff, 1878a: 386.
=*Stephanoderes ehlersii* Eichhoff, 1878a: 387 (syn: Balachowsky, 1949).
=*Stephanoderes germari* Eichhoff, 1878b: 159 (syn: Wood, 1977c).
=*Stephanoderes myrmedon* Eichhoff, 1878b: 160 (syn: Wood, 1977c).
=*Stephanoderes ehlersi* Eichhoff, 1878b: 493.
=*Stephanoderes communis* Schaufuss, 1891: 11 (syn: Wood, 1992a).
=*Hypothenemus insularis* Perkins, 1900: 181 (syn: Wood, 1960).
=*Cryphalus tectonae* Stebbing, 1903: 263 (syn: Wood, 1989).
=*Cryphalus basjoo* Niisima, 1910: 9 (syn: Wood, 1972b).
=*Cryphalus striatopunctatus* Lea, 1910: 142 (syn: Wood, 1989).
=*Cryphalus tantillus* Lea, 1910: 142 (syn: Wood, 1989).
=*Hypothenemus tuberculosus* Hagedorn, 1912a: 339 (syn: Wood, 1989).
=*Cosmoderes schwarzi* Hopkins, 1915: 11 (syn: Wood, 1972b).
=*Hypothenemus bradfordi* Hopkins, 1915: 15 (syn: Wood, 1972b).
=*Hypothenemus flavosquamosus* Hopkins, 1915: 15 (syn: Wood, 1972b).
=*Hypothenemus asiminae* Hopkins, 1915: 16 (syn: Wood, 1954).
=*Hypothenemus hamamelidis* Hopkins, 1915: 16 (syn: Wood, 1954).
=*Hypothenemus myristicae* Hopkins, 1915: 16 (syn: Wood, 1972b).
=*Hypothenemus nigricollis* Hopkins, 1915: 16 (syn: Wood, 1972b).
=*Hypothenemus pruni* Hopkins, 1915: 16 (syn: Wood, 1954).
=*Hypothenemus rumseyi* Hopkins, 1915: 16 (syn: Wood, 1954).
=*Hypothenemus tenuis* Hopkins, 1915: 16 (syn: Wood, 1972b).
=*Hypothenemus koebelei* Hopkins, 1915: 17 (syn: Wood, 1972b).
=*Hypothenemus lineatifrons* Hopkins, 1915: 17 (syn: Wood, 1972b).
=*Hypothenemus mali* Hopkins, 1915: 17 (syn: Wood, 1972b).
=*Hypothenemus parvus* Hopkins, 1915: 17 (syn: Wood, 1972b).
=*Hypothenemus sacchari* Hopkins, 1915: 17 (syn: Wood, 1972b).
=*Hypothenemus webbi* Hopkins, 1915: 17 (syn: Wood, 1972b).
=*Hypothenemus flavipes* Hopkins, 1915: 18 (syn: Wood, 1972b).
=*Hypothenemus pallidus* Hopkins, 1915: 18 (syn: Wood, 1972b).
=*Hypothenemus punctifrons* Hopkins, 1915: 18 (syn: Wood, 1954).
=*Hypothenemus nigripennis* Hopkins, 1915: 19 (syn: Wood, 1954).
=*Hypothenemus ferrugineus* Hopkins, 1915: 20 (syn: Wood, 1972b).
=*Hypothenemus heathi* Hopkins, 1915: 20 (syn: Wood, 1972b).
=*Hypothenemus punctipennis* Hopkins, 1915: 20 (syn: Wood, 1972b).
=*Stephanoderes flavicollis* Hopkins, 1915: 24 (syn: Wood, 1972b).

=*Stephanoderes pygmaeus* Hopkins, 1915: 24 (syn: Wood, 1972b).
=*Stephanoderes cylindricus* Hopkins, 1915: 25 (syn: Wood, 1989).
=*Stephanoderes elongatus* Hopkins, 1915: 25 (syn: Wood, 1972b).
=*Stephanoderes subconcentralis* Hopkins, 1915: 25 (syn: Wood, 1972b).
=*Stephanoderes unicolor* Hopkins, 1915: 25 (syn: Wood, 1972b).
=*Stephanoderes evonymi* Hopkins, 1915: 26 (syn: Wood, 1954).
=*Hypothenemus bicolor* Eggers, 1919: 241 (syn: Schedl, 1957b).
=*Hypothenemus ehlersi rotroui* Peyerimhoff, 1919: 255 (syn: Balachowsky, 1949).
=*Hypothenemus juglandis* Blackman, 1922a: 88 (syn: Wood, 1954).
=*Hypothenemus pusillus* Eggers, 1927a: 173 (syn: Wood, 1989).
=*Stephanoderes intersetosus* Eggers, 1928: 85 (syn: Wood, 1972b).
=*Hypothenemus lezhavai* Pyatnitskiy, 1929: 15 (syn: Schedl, 1963a).
=*Stephanoderes gracilis* Eggers, 1929b: 51 (syn: Wood, 1974b).
=*Hypothenemus citri* Ebeling, 1935: 21 (syn: Wood, 1954).
=*Stephanoderes erythrinae* Eggers, 1936c: 628 (syn: Wood, 1972b).
=*Hypothenemus argentinensis* Schedl, 1939a: 408 (syn: Wood, 1989).
=*Hypothenemus cylindricus* Schedl, 1939a: 409 (syn: Wood, 1989).
=*Hypothenemus bicolor* Schedl, 1939c: 32 (syn: Schedl, 1957b).
=*Hypothenemus asaroriensis* Beeson, 1940: 195 (syn: Wood, 1989).
=*Hypothenemus dubiosus* Schedl, 1940b: 207 (syn: Wood, 1972b).
=*Stephanoderes subcylindricus* Eggers, 1940c: 233 (syn: Schedl, 1957b).
=*Stephanoderes transatlanticus* Eggers, 1941a: 99 (syn: Wood, 1972b).
=*Hypothenemus mauiensis* Schedl, 1941b: 110 (syn: Wood, 1989).
=*Hypothenemus glabratus* Schedl, 1942a: 175 (syn: Schedl, 1963a).
=*Archeophalus ealaensis* Eggers, 1944: 94 (syn: Schedl, 1957b).
=*Stephanoderes nanulus* Schedl, 1948a: 263 (syn: Wood, 1989).
=*Hypothenemus guadeloupensis* Schedl, 1951e: 98 (syn: Wood, 1989).
=*Hypothenemus parilis* Schedl, 1951e: 100 (syn: Wood, 1989).
=*Hypothenemus obscuriceps* Schedl, 1952a: 339 (syn: Wood, 1989).
=*Hypothenemus hirtipennis* Schedl, 1952a: 450 (syn: del Río, Lanteri and Suárez, 2005).
=*Stephanoderes tigrensis* Schedl, 1952a: 452 (syn: Wood, 1989).
=*Hypothenemus glabratellus* Schedl, 1953b: 292 (syn: Schedl, 1963a).
=*Hypothenemus parcius* Schedl, 1957b: 49 (syn: Wood, 1989).
=*Hypothenemus cylindripennis* Schedl, 1957b: 51 (syn: Wood, 1989).
=*Stephanoderes ituriensis* Schedl, 1957b: 55 (syn: Wood, 1989).
=*Hypothenemus vianai* Schedl, 1958c: 42 (syn: Wood, 1989).
=*Hypothenemus mesoleius* Schedl, 1959a: 480 (syn: Wood, 1989).
=*Hypothenemus minutulus* Schedl, 1972g: 225 (syn: Wood, 1989).
=*Cryphalus minutus* Schedl, 1978a: 299 (syn: Wood, 1989).
Hypothenemus euphorbiae (Schedl, 1961b: 135) (*Stephanoderes*).
Hypothenemus exceptus Bright, 2019: 139.
Hypothenemus exiguus (Wood, 1986b: 273) (*Trischidias*).
Hypothenemus eximius Schedl, 1951e: 99.
Hypothenemus externedentatus Schedl, 1959a: 480.
Hypothenemus flavus Hopkins, 1915: 17.
Hypothenemus fuscicollis (Eichhoff, 1878a: 386) (*Stephanoderes*).
=*Stephanoderes fuscicollis* Eichhoff, 1878b: 148 **syn. nov.**
=*Stephanoderes sundaensis* Eggers, 1927b: 396 **syn. nov.**
=*Hypothenemus aequaliclavatus* Schedl, 1939c: 33 **syn. nov.**
=*Ernophloeus costalimai* Nunberg, 1958: 170 **syn. nov.**
=*Hypothenemus ghanaensis* Schedl, 1962b: 67 **syn. nov.**
=*Hypothenemus comosus* Bright, 1972: 50 **syn. nov.** (syn: Bright, 2019).
Hypothenemus georgiae (Hopkins, 1915: 12) (*Trischidias*).
Hypothenemus glabratulus (Schedl, 1957a: 192) (*Stephanoderes*).
=*Hypothenemus parvistriatus* Wood, 2007: 517 (syn: Bright, 2019).
Hypothenemus glabripennis (Hopkins, 1915: 32) (*Stephanoderes*).
Hypothenemus gossypii (Hopkins, 1915: 25) (*Stephanoderes*).
=*Hypothenemus beameri* Wood, 1954: 1056 (syn: Wood, 1962).
Hypothenemus grandis Schedl, 1939d: 384.
Hypothenemus granulatus Bright, 2019: 144.
Hypothenemus hampei (Ferrari, 1867: 11) (*Cryphalus*).
=*Stephanoderes coffeae* Hagedorn, 1910: 1 (syn: Schedl, 1970b).
=*Xyleborus coffeivorus* Weele, 1910: 1 (syn: Strohmeyer, 1910).
=*Stephanoderes cooki* Hopkins, 1915: 27 (syn: Schedl, 1959a).
=*Xyleborus cofeicola* Campos Novaes, 1922: 67 (syn: Costa Lima, 1924).
=*Stephanoderes punctatus* Eggers, 1924: 101 (syn: Wood, 1972b).
=*Stephanoderes glabellus* Schedl, 1952a: 452 (syn: Wood, 1989).
Hypothenemus hirsutus (Wood, 1954: 1020) (*Stephanoderes*).
Hypothenemus hystrix (Eggers, 1919: 242) (*Adiaeretus*).
Hypothenemus ignotus Bright, 2019: 146.
Hypothenemus improvidus Bright, 2019: 147.
Hypothenemus incognitus (Schedl, 1967c: 227) (*Stephanoderes*).
Hypothenemus indigens Wood, 1974a: 20.
Hypothenemus indigenus Bright and Peck, 1998: 245.
Hypothenemus indistinctus Bright, 2019: 147.
Hypothenemus ingens Schedl, 1942d: 18.
=*Cryphalomorphus grandis* Schedl, 1969: 49 (syn: Wood, 1989).
Hypothenemus inordinatus Bright, 2019: 148.
Hypothenemus insulanus Bright, 2002: 146.
=*Hypothenemus pacificus* Bright and Peck, 1998: 246 (syn: Bright and Skidmore, 2002).
Hypothenemus interstitialis (Hopkins, 1915: 28) (*Stephanoderes*).
=*Hypothenemus ceibae* Hopkins, 1915: 20 (syn: Bright, 2019).
=*Stephanoderes interpunctus* Hopkins, 1915: 28 (syn: Wood, 1954).
=*Stephanoderes approximatus* Hopkins, 1915: 29 (syn: Wood, 1954).
=*Stephanoderes flavescens* Hopkins, 1915: 29 (syn: Wood, 1954).
=*Stephanoderes obliquus* Hopkins, 1915: 30 (syn: Wood, 1954).
=*Stephanoderes opacipennis* Hopkins, 1915: 30 (syn: Wood, 1954).
=*Stephanoderes quadridentatus* Hopkins, 1915: 30 (syn: Wood, 1954).
Hypothenemus intricatus (Schedl, 1950a: 25) (*Stephanoderes*).

Hypothenemus japonicus (Niisima, 1910: 10) (*Cryphalus*).
Hypothenemus javanus (Eggers, 1908: 215) (*Stephanoderes*).
=*Stephanoderes obesus* Hopkins, 1915: 30 (syn: Wood, 1957b).
= *Stephanoderes brunneus* Hopkins, 1915: 31 (syn: Bright, 2019.
=*Stephanoderes frontalis* Hopkins, 1915: 31 (syn: Wood, 1954).
=*Stephanoderes philippinensis* Hopkins, 1915: 31 (syn: Wood, 1975b).
=*Stephanoderes bananensis* Eggers, 1922: 167 (syn: Wood, 1972b).
=*Stephanoderes kalshoveni* Schedl, 1939c: 35 (syn: Wood, 1972b).
=*Stephanoderes cryphalomorphus* Schedl, 1939e: 14 (syn: Wood, 1977a).
=*Stephanoderes bituberculatus* Eggers, 1940a: 126 (syn: Wood, 1977a).
=*Stephanoderes subagnatus* Eggers, 1940b: 101 (syn: Wood, 1972b).
=*Stephanoderes pistor* Schedl, 1951e: 102 (syn: Wood, 1976).
=*Stephanoderes prosper* Schedl, 1951e: 103 (syn: Wood, 1976).
Hypothenemus kamathi Beaver, 1995: 16.
Hypothenemus kraunhiae Murayama, 1950: 50.
Hypothenemus lefevrei (Schedl, 1952d: 8) (*Stephanoderes*).
Hypothenemus leprieuri (Perris, 1866: 194) (*Dryocoetes*).
=*Stephanoderes albipilis* Reitter, 1887: 195 (syn: Eggers, 1940e).
=*Dryocoetes kraussei* Wichmann, 1911: 210 (syn: Eggers, 1921).
Hypothenemus leptosquamus Bright, 2019: 152.
Hypothenemus liberiensis (Hopkins, 1915: 31) (*Stephanoderes*).
=*Stephanoderes theobromae* Eggers, 1932: 32 (syn: Wood, 1968).
Hypothenemus liliputianus Bright, 2019: 152.
Hypothenemus lineatus (Eggers, 1927a: 175) (*Stephanoderes*).
Hypothenemus longipennis (Eggers, 1935: 305) (*Stephanoderes*).
Hypothenemus longipilis Schedl, 1952a: 451.
Hypothenemus loranthus (Schedl, 1942d: 8) (*Margadillius*) **comb. nov.** [*Margadillius*].
Hypothenemus macrolobii (Eggers, 1940c: 234) (*Stephanoderes*).
Hypothenemus madagascariensis Schedl, 1953c: 82.
Hypothenemus magnus (Eggers, 1924: 102) (*Stephanoderes*).
Hypothenemus major Browne, 1970: 555.
Hypothenemus malayensis (Schedl, 1977c: 499) (*Lepiceriodes*).
Hypothenemus mallyi (Hopkins, 1915: 32) (*Stephanoderes*).
=*Stephanoderes soussouensis* Eggers, 1943b: 74 (syn: Wood, 1972b).
Hypothenemus malus (Schedl, 1957b: 56) (*Stephanoderes*).
Hypothenemus mangovorus Schedl, 1961b: 134.
Hypothenemus marginatus Johnson **nom. nov.**
=*Periocryphalus sobrinus* Wood, 1974a: 22 **syn. nov.**

Remarks: A replacement name is proposed for *Periocryphalus sobrinus* Wood, 1974 following the generic synonymy of *Hypothenemus* and *Periocryphalus*, creating conflict with *Stephanoderes sobrinus* Schedl, 1965a. The replacement name is an adjective, referencing the prominent posterolateral margin of the elytra. The holotype of *Periocryphalus sobrinus* Wood, 1974 at BMNH is lost and erroneously replaced with a *Cnesinus* sp., which clearly does not match the species description. A paratype at USNM collected from the same location on a different date matches the original and subsequent descriptions of the species. (Labeled 'PARATYPE // Periocryphalus // sobrinus // S. L. Wood 1972 //// Periocryphalus //sobrinus//.72 Wood // S. L. Wood // RS/RGS Exp. Brazil // 12′31′S 51′46′W //// R. A. Beaver F03 // 7.XI.1968 //// S. L. Wood Collection //// USNMENT 01448187'.) Since this species is the type of the genus *Periocryphalus*, the stability of the name-bearing type is critical. Therefore, the single remaining specimen in the type series at USNM is designated as a neotype of *Periocryphalus sobrinus* Wood, 1974a, and subsequently, the neotype of *Hypothenemus marginatus* Johnson.

Hypothenemus marshalli (Eggers, 1936b: 36) (*Stephanoderes*).
Hypothenemus mateui (Schedl, 1965g: 198) (*Stephanoderes*).
Hypothenemus melanarius (Schedl, 1953c: 80) (*Cosmoderes*).
Hypothenemus melasomus (Lea, 1910: 140) (*Cryphalus*).
Hypothenemus meridensis Wood, 2007: 506.
Hypothenemus miles (LeConte, 1878: 433) (*Cryphalus*).
Hypothenemus minor (Eggers, 1927a: 178) (*Adiaeretus*).
Hypothenemus modestus (Murayama, 1940: 236) (*Cryphalus*).
Hypothenemus morigerus (Schedl, 1957b: 57) (*Stephanoderes*).
Hypothenemus morio (Eggers, 1940b: 101) (*Stephanoderes*).
Hypothenemus morosus Schedl, 1965a: 57.
Hypothenemus mozambiquensis Eggers, 1943b: 75.
Hypothenemus mulongensis (Eggers, 1940c: 235) (*Stephanoderes*).
Hypothenemus multidentatulus (Schedl, 1962f: 95) (*Stephanoderes*).
Hypothenemus multidentatus (Hopkins, 1915: 28) (*Stephanoderes*).
=*Stephanoderes ferrugineus* Hopkins, 1915: 29 (syn: Wood, 1972b).
=*Stephanoderes nitidifrons* Hopkins, 1915: 31 (syn: Wood, 1972b).
=*Hypothenemus hopkinsi* Browne, 1963b: 53 (syn: Wood, 1972b).
Hypothenemus multipunctatus (Schedl, 1939c: 36) (*Stephanoderes*).
Hypothenemus muticus (Schedl, 1961b: 136) (*Stephanoderes*).
Hypothenemus namosianus Browne, 1983a: 78.
Hypothenemus nanellus Wood, 1971: 34.
Hypothenemus nanoparvus Bright, 2019: 154.
Hypothenemus natalensis (Schedl, 1941a: 392) (*Archeophalus*).
Hypothenemus nesiotus Bright, 2019: 154.
Hypothenemus nigropiceus (Schedl, 1951c: 20) (*Stephanoderes*).
Hypothenemus novateutonicus (Schedl, 1951e: 105) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].
Hypothenemus obscurifrons Bright, 2019: 155.
Hypothenemus obscurus (Fabricius, 1801: 395) (*Hylesinus*).
=*Stephanoderes asperulus* Eichhoff, 1872a: 133.
=*Stephanoderes cassiae* Eichhoff, 1878b: 152.
=*Hypothenemus kuennemanni* Reitter, 1902: 140 (syn: Wood, 1972b).
=*Stephanoderes moschatae* Schaufuss, 1905: 8 (syn: Wood, 1972b).
=*Stephanoderes rufescens* Hopkins, 1915: 29 (syn: Wood, 1972b).
=*Stephanoderes buscki* Hopkins, 1915: 30 (syn: Wood, 1972b).
=*Stephanoderes amazonicus* Eggers, 1934: 78 (syn: Wood, 1972b).
=*Hypothenemus emarginatus* Schedl, 1942d: 11 (syn: Wood, 1972b).

Remarks: Bright (2019) noted that *Hypothenemus seriatus* (Eichhoff, 1872) was a junior synonym of *H. obscurus* (Fabricius, 1801), as it was synonymized by Wood (1954), based on a specimen compared with the type by Eggers, but the synonymy was largely ignored (including by Wood). We consider the synonymy originally proposed by Wood to be rejected. *Hypothenemus obscurus* is a highly damaging pest which is not present in some areas where *H. seriatus* is present. We found that the species were sister in the phylogeny. The morphological differences have been well documented (Vega et al., 2015), and they are genetically distinct (Mitchell and Maddox 2010, Johnson et al 2018). It is possible that there is much more variation than documented which may make definitive identification by morphology difficult or impossible, but more evidence would be needed to justify grouping the distinct morphotypes as one species, as well as alternative recognition of the pestiferous beetles which devastate the macadamia and other tropical nut industries. The economic and policy implications of the synonymy could hinder the necessary biosecurity measures to prevent the pest species establishing in other areas.

Hypothenemus opacus (Eichhoff, 1872a: 132) (*Stephanoderes*).

=*Hypothenemus dolosus* Wood, 1974a: 21 (syn: Bright, 2019).
Hypothenemus paradoxus Schedl, 1964c: 45.
Hypothenemus parallelus (Hopkins, 1915: 25) (*Stephanoderes*).
Hypothenemus parasquamosus Bright, 2019: 160.
Hypothenemus parvulosus Bright, 2019: 160.
Hypothenemus parvulus Browne, 1984d: 93.
Hypothenemus paulus Bright, 2019: 162.
Hypothenemus perappositus (Schedl, 1934: 91) (*Stephanoderes*).
Hypothenemus perexiguus Bright, 2019: 162.
Hypothenemus perhispidus (Eggers, 1927a: 177) (*Stephanoderes*).
Hypothenemus perpunctatus (Eggers, 1940c: 233) (*Stephanoderes*).
Hypothenemus piaparolinae Johnson, Atkinson and Hulcr, 2016: 418.
Hypothenemus pilosus Hopkins, 1915: 20.
Hypothenemus ponticus Bright, 2019: 164.
Hypothenemus praecellens (Schedl, 1972c: 288) (*Stephanoderes*).
Hypothenemus pubescens Hopkins, 1915: 19.
=*Hypothenemus subelongatus* Hopkins, 1915: 19 (syn: Wood, 1972b).
=*Stephanoderes opacifrons* Hopkins, 1915: 25 (syn: Wood, 1972b).
=*Hypothenemus minutissimus* Schedl, 1952a: 450 (syn: Wood, 1989).
Hypothenemus pubipennis (Eggers, 1935: 305) (*Stephanoderes*).
Hypothenemus puertoricensis (Bright and Torres, 2006: 409) (*Trischidias*).
Hypothenemus pullus (Wood, 1971: 33) (*Periocryphalus*) **comb. nov.** [*Periocryphalus*].
Hypothenemus pygmaeomorphus Bright, 2019: 166.
Hypothenemus rotundicollis (Eichhoff, 1878a: 385) (*Stephanoderes*).
=*Stephanoderes sculpturatus* Eichhoff, 1878a: 385 **syn. nov.** (syn: Eichhoff, 1896).
=*Stephanoderes rotundicollis* Eichhoff, 1878b: 45 **syn. nov.**
=*Stephanoderes sculpturatus* Eichhoff, 1878b: 45 **syn. nov.**
=*Stephanoderes quercus* Hopkins, 1915: 32 **syn. nov.**
Hypothenemus rubrithorax Bright, 2019: 168.
Hypothenemus ruficeps Perkins, 1900: 181.
Hypothenemus rugifer (Schedl, 1965d: 9) (*Pachynoderes*).
Hypothenemus ruginosus Wood, 1989: 178.
=*Pachynoderes rugifer* Schedl, 1977a: 395 (syn: Wood, 1989) (Permanently invalid name due to primary homonymy).
Hypothenemus rugosipes Wood, 2007: 515.
Hypothenemus sambesianus Eggers, 1943b: 74.
Hypothenemus sapporoensis (Niisima, 1910: 3) (*Cryphalus*).
Hypothenemus sassaensis (Eggers, 1924: 102) (*Stephanoderes*).
Hypothenemus schedli Browne, 1963b: 54.
=*Stephanoderes pubescens* Schedl, 1942d: 18 (syn: Browne, 1963b).
Hypothenemus scutiae (Schedl, 1959c: 708) (*Stephanoderes*).
Hypothenemus seoulensis Choo and Woo, 1989: 58.
Hypothenemus seriatus (Eichhoff, 1872a: 133) (*Stephanoderes*) **stat. res.**
=*Stephanoderes pulverulentus* Eichhoff, 1872a: 133 (syn: Wood, 1973).
=*Stephanoderes vulgaris* Schaufuss, 1897: 209 (syn: Wood, 1972b).
=*Stephanoderes georgiae* Hopkins, 1915: 26 (syn: Wood, 1972b).
=*Stephanoderes minutus* Hopkins, 1915: 26 (syn: Wood, 1972b).
=*Stephanoderes texanus* Hopkins, 1915: 26 (syn: Wood, 1954).
=*Stephanoderes ficus* Hopkins, 1915: 27 (syn: Wood, 1954).
=*Stephanoderes fiebrigi* Hopkins, 1915: 27 (syn: Wood, 1954).
=*Stephanoderes floridensis* Hopkins, 1915: 27 (syn: Wood, 1954).
=*Stephanoderes pini* Hopkins, 1915: 27 (syn: Wood, 1954).
=*Stephanoderes salicis* Hopkins, 1915: 27 (syn: Wood, 1954).
=*Stephanoderes tamarindi* Hopkins, 1915: 27 (syn: Wood, 1972b).
=*Stephanoderes lucasi* Hopkins, 1915: 28 (syn: Wood, 1954).
=*Stephanoderes soltaui* Hopkins, 1915: 28 (syn: Wood, 1954).
=*Stephanoderes virentis* Hopkins, 1915: 28 (syn: Wood, 1954).
=*Stephanoderes nitidipennis* Hopkins, 1915: 29 (syn: Wood, 1972b).
=*Stephanoderes nitidulus* Hopkins, 1915: 29 (syn: Wood, 1977c).
=*Stephanoderes pecanis* Hopkins, 1915: 29 (syn: Wood, 1954).
=*Stephanoderes subopacicollis* Hopkins, 1915: 30 (syn: Wood, 1977c).
=*Stephanoderes niger* Hopkins, 1915: 31 (syn: Wood, 1972b).
=*Hypothenemus robustus* Blackman, 1922a: 88 (syn: Wood, 1954).
=*Hypothenemus cassavaensis* Schedl, 1938a: 453 (syn: Wood, 1989).
=*Stephanoderes hawaiiensis* Schedl, 1941b: 112 (syn: Wood, 1989).
=*Stephanoderes darwinensis* Schedl, 1942c: 178 (syn: Wood, 1972b).
=*Hypothenemus striatulus* Schedl, 1942d: 12 (syn: Wood, 1989).
=*Hypothenemus marovoayi* Schedl, 1953c: 81 (syn: Wood, 1989).
=*Stephanoderes andersoni* Wood, 1954: 1045 (syn: Wood, 1972b).
=*Stephanoderes liquidambarae* Wood, 1954: 1046 (syn: Wood, 1972b).
=*Stephanoderes asperatus* Schedl, 1967c: 226 (syn: Wood, 1989).
Hypothenemus setiferous Bright, 2019: 169.
Hypothenemus setosus (Eichhoff, 1868: 391) (*Hypoborus*).
=*Stephanoderes congonus* Hagedorn, 1912a: 337 (syn: Wood, 1975b).
Hypothenemus simoni (Reitter, 1887: 194) (*Stephanoderes*).
Hypothenemus sobrinus (Schedl, 1965a: 58) (*Stephanoderes*).
Hypothenemus socialis (Schedl, 1957b: 57) (*Stephanoderes*).
Hypothenemus solitarius (Schedl, 1950a: 24) (*Stephanoderes*).
Hypothenemus solivagus Bright, 2019: 171.
Hypothenemus solocis Wood, 1974a: 21.
Hypothenemus sparsedentatus (Schedl, 1942c: 178) (*Stephanoderes*).
Hypothenemus sparsus Hopkins, 1915: 20.
=*Hypothenemus similis* Hopkins, 1915: 20 (syn: Wood, 1954).
=*Stephanoderes tridentatus* Hopkins, 1915: 31 (syn: Wood, 1954).
Hypothenemus spinatus (Schedl, 1977b: 282) (*Miocryphalus*).
Hypothenemus spinicollis (Schedl, 1965a: 59) (*Stephanoderes*).
Hypothenemus spinosus (Schedl, 1979c: 98) (*Lepiceroides*).
Hypothenemus squamosulus Johnson **nom. nov.** [*Ptilopodius*].
=*Ptilopodius squamosus* Schedl, 1953b: 294 **syn. nov.** (secondary homonym).

Remarks: A replacement name is proposed for *Ptilopodius squamosus* Schedl, 1953b after transferring this species from *Ptilopodius*, since the combination is already occupied by *Stephanoderes squamosus* Hopkins, 1915. The new name is the diminutive of the adjective *squamosus* (= scaly), referring to the scale-like setae on the pronotum and elytra.

Hypothenemus squamosus (Hopkins, 1915: 26) (*Stephanoderes*).
Hypothenemus stigmosus (Schedl, 1951e: 101) (*Stephanoderes*).
=*Stephanoderes garciae* Schedl, 1958c: 42 (syn: Wood, 1989).
Hypothenemus striatus (Atkinson, 1993: 422) (*Trischidias*).
Hypothenemus styrax (Schedl, 1942a: 177) (*Stephanoderes*).
Hypothenemus subacuminatus (Schedl, 1942a: 177) (*Stephanoderes*).
Hypothenemus subterrestris Johnson, Atkinson and Hulcr, 2016: 421.
Hypothenemus suspectus Wood, 1974a: 22.

Hypothenemus tectus Bright, 2019: 173.
Hypothenemus teretis Wood, 1971: 35.
Hypothenemus teteforti (Menier, 1971: 141) (*Stephanoderes*).
Hypothenemus tredli (Reitter, 1908: 55) (*Cryphalus*).
Hypothenemus tristis (Eichhoff, 1876: 200) (*Stephanoderes*).
=*Stephanoderes taihokuensis* Schedl, 1952b: 63. (syn: Beaver, 2011a).
=*Hypothenemus cosmoderoides* Murayama, 1961: 30 (syn: Beaver and Liu, 2010).
Hypothenemus trivialis Wood, 1974a: 20.
Hypothenemus tuberosus (Schedl, 1942d: 19) (*Stephanoderes*).
Hypothenemus turnbowi Bright, 2019: 173.
Hypothenemus ustulatus Bright, 2019: 174.
Hypothenemus vernaculus Bright, 2019: 174.
Hypothenemus versicolor Bright, 2019: 176.
Hypothenemus vesculus Wood, 1974a: 21.
Hypothenemus villosus Bright, 2019: 176.
Hypothenemus virolae Wood, 2007: 509.
Hypothenemus vitis Browne, 1970: 554.
Hypothenemus winkleri (Reitter, 1907: 192) (*Stephanoderes*).
Hypothenemus woodi Bright, 2019: 153 (replacement name).
=*Trischidias minutissimus* Wood, 1954: 1069 (syn: Bright, 2019).
Hypothenemus xanthophloeae (Schedl, 1957b: 58) (*Stephanoderes*).

Macrocryphalus Nobuchi, 1981: 14 stat. res. (Fig. 19)

Type of genus
Macrocryphalus oblongus Schedl, 1965.

Diagnosis
The teardrop-shaped antennae, rounded lateral margins of the pronotum, separated mesocoxae, and absence of a sclerotized proventriculus diagnose members of this genus.

Female
Eye acutely emarginated. Frons with an abrupt concavity lined with long, golden setae which converge toward its median. Antennae with five funicle segments. Antennal club flattened, teardrop-shaped (narrower at base). Antennae with a single procurved suture. Pronotum armed with five to seven marginal asperities, and more than 30 asperities on the pronotal declivity, leading to a slightly elevated summit.

Lateral margins of pronotum rounded. Vestiture of pronotum is hair-like to slightly flattened; setae on the hypomeron simple. Scutellum visible. Elytra simple and convex. Striae not visible. Interstrial bristles slightly flattened, and ground vestiture and strial setae presumably intermixed, confused and hair-like. No sclerotized structure (crop and proventriculus) visible in the upper gut.

Male
Similar except the vestiture of the frons is much shorter. Most males are of a similar size to females and have functional wings. Penis apodemes of a similar length or shorter than penis body, separated at apex. Tegmen without apodemes, open dorsally. Spiculum gastrale of a similar diameter to penis apodemes. Basal sclerites complex and developed.

Distribution
East Asia, East Africa.

Remarks
Three species known. The phylogenetic placement of this genus remains unknown. Molecular data, obtained after the analyses, confirm the placement in Trypophloeini. The transfer of two African species from *Afromicracis* Schedl, 1959 to this genus is dubious and based on external appearance only.

Type material examined
Holotype of *Miocryphalus elongatus* Schedl, 1965 (NHMW); holotype of *Macrocryphalus oblongus* Nobuchi, 1981 (ITLJ); holotype of *Miocryphalus punctipennis* Schedl, 1965 (NHMW).

Included species
Macrocryphalus elongatus (Schedl, 1965c: 366) (*Miocryphalus*) **comb. nov.** [*Afromicracis*].
Macrocryphalus oblongus Nobuchi, 1981: 14 **stat. res.** [*Hypothenemus*].
=*Hypothenemus nobuchii* Knížek, 2011: 86 **syn. nov.** (unnecessary replacement name)
Macrocryphalus punctipennis (Schedl, 1965c: 367) (*Miocryphalus*) **comb. nov.** [*Afromicracis*].

Microcosmoderes Johnson and Jordal **gen. nov.** (Fig. 20)

(LSID: urn:lsid:zoobank.org:act:9503C4F2-A4A1-4BAB-9EB6-8C5061CD118A)

Type of genus
Ptilopodius shoreae Schedl, 1953: 293.

Diagnosis
Microcosmoderes can be diagnosed from other Trypophloeini genera by the rounded apical margin of the pronotum (without marginal asperities), by the males with fully developed wings, the proventriculus with a very long and saw-toothed apical plate, a cylindrical third tarsal segment, and the antennal club with one faint suture.

Female
Eye very weakly emarginated. Frons with a transverse, short, barely visible carina just below level of eyes. Cuticle behind eyes with weakly visible striations. Antennae with four funicle segments. Antennal club flattened and round; posterior face with a single, weakly indicated procurved suture; anterior face with a transverse suture near base. Anterior margin of the pronotum smooth, numerous asperities behind margin towards a slightly elevated summit. Pronotal disc coarsely punctured near to summit; a weakly visible carina at the base of the lateral margin only. Elytra convex, without distinct sculpturing. Interstrial bristles slightly flattened and spatula-shaped. Interstrial ground vestiture absent. Proventriculus: apical plate longer than posterior plate, without median suture, with about 15 recurved sharp edges containing many small sharp teeth; closing teeth branched at tips, femoral teeth long and abundant.

Male
Similar to female with no apparent external sexual dimorphism. Penis apodemes of a similar length or longer than penis body, separated at apex. Tegmen open dorsally, with a median ventral apodeme nearly as long as penis apodemes. Spiculum gastrale slightly thicker than penis apodemes, with a weak fork. Basal sclerites visible.

Distribution
Peninsular Malaysia to Borneo.

Etymology
The name is composed by the Latinized form of Greek adjective *mikros*, meaning small, and the name of the related genus *Cosmoderes* in reference its morphological similarity to this genus. Gender masculine.

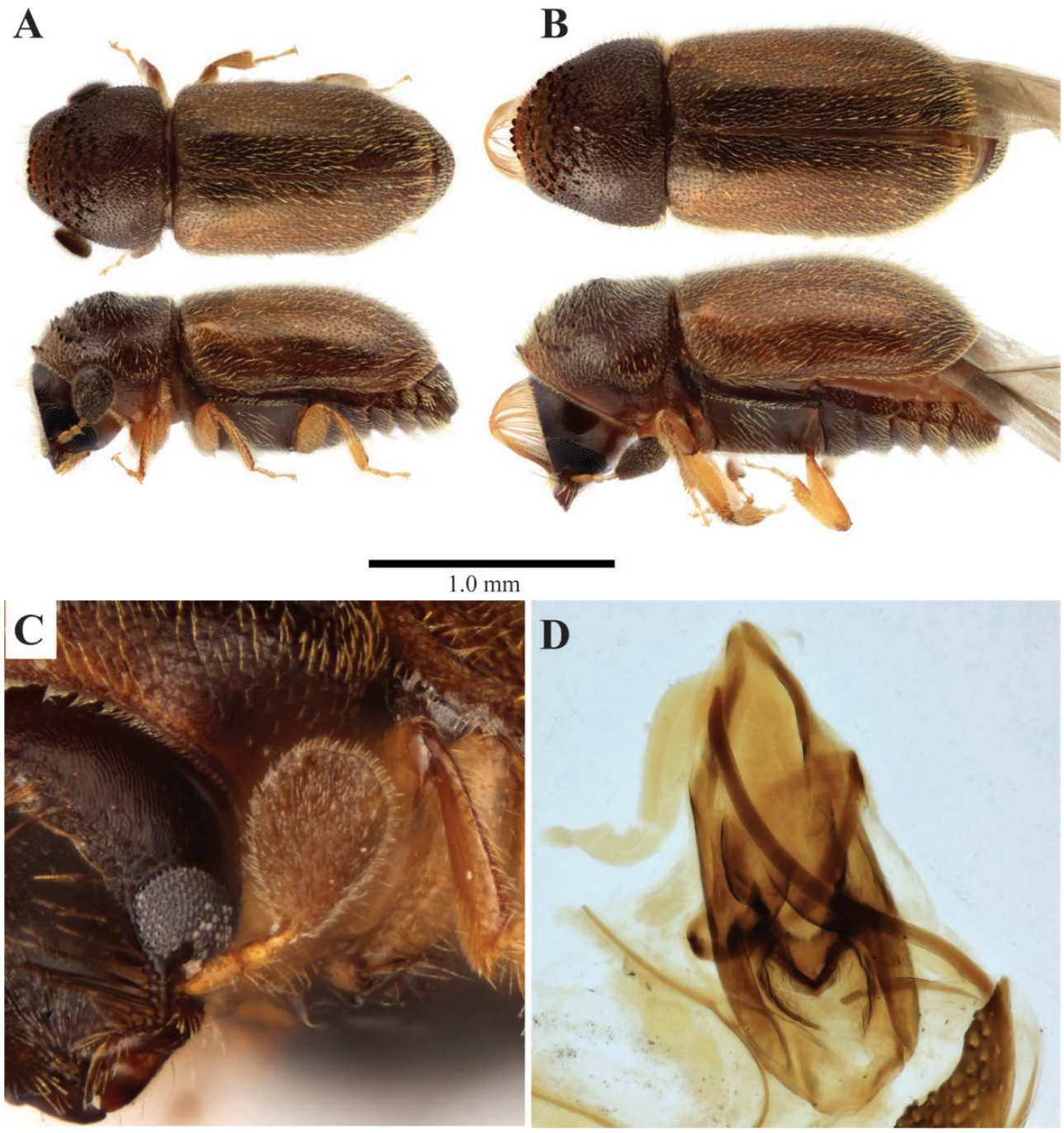

Figure 19. Images of *Macrocryphalus oblongus*: Dorsal and lateral photographs of A) male and B) female, D) Antennae of female, and D) aedeagus.

Remarks

Monotypic. *Microcosmoderes* was previously determined as a *Ptilopodius* (=*Eidophelus*) sp. following Wood's key to genera and used with that designation (Jordal and Cognato 2012, Pistone et al. 2018).

The biology of this genus is not known; the species was found in a small twig. Browne (1961) notes that the species is inbreeding (similar to *Hypothenemus*), but we studied a male which had functional eyes and wings which suggest that males disperse and mate outside the parental gallery (typical of an outbreeding species). Based on Browne's inferred habits of this species (Browne 1961), it is likely that it feeds gregariously, a trait correlated with, but not limited to, inbreeding in bark beetles (Kirkendall 1983, Jordal and Cognato 2012, Johnson et al. 2018).

Type material examined

Holotype of *Ptilopodius shoreae* Schedl, 1953 (BMNH).

Included species

Microcosmoderes shoreae (Schedl, 1953b: 293) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].

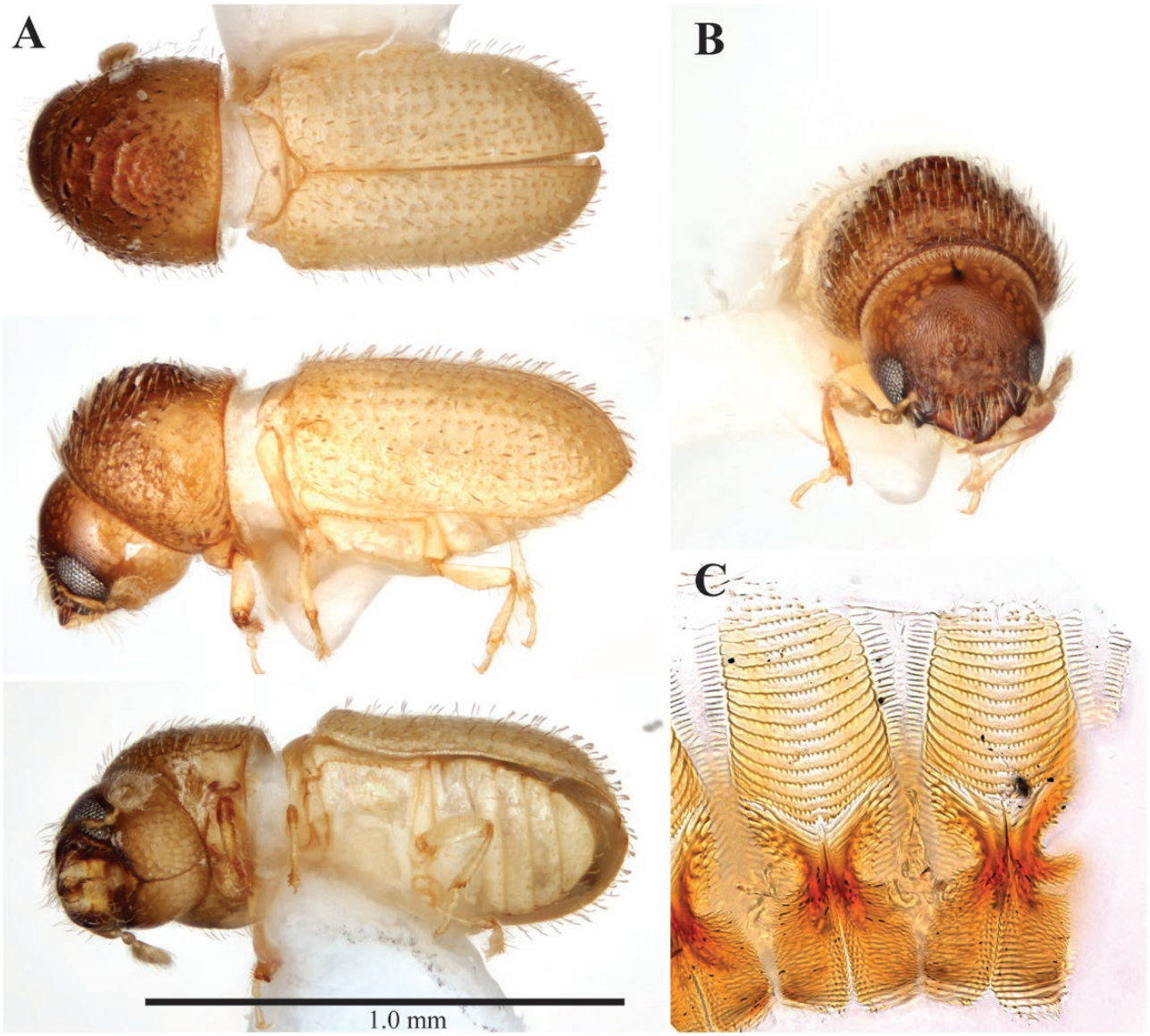

Figure 20. Images of *Microcosmoderes shoreae*: A) Lateral, dorsal, and ventral photograph, B) frons, and C) proventriculus.

Microsomus Bright, 2019: 178

Type of genus

Microsomus atomus Bright, 2019.

Diagnosis

This genus can be distinguished from other Trypophloeini by the antennae, with a single, procurved suture, and by the lack of any vestiture on the elytra.

Female

Eye weakly emarginated. Antennal club with single, procurved suture marked by setae. Four marginal asperities. Punctures on elytra broad. No discernable vestiture on elytra.

Male

Unknown.

Distribution

Saint Croix (U.S. Virgin Islands).

Remarks

Monotypic. This genus was described in the final stages of this manuscript preparation. Without molecular and internal characters examined, the placement within Trypophloeini is not confirmed. Only one specimen is known, the correct placement will be assessed when more specimens are available.

The genus-group name is also a homonym of *Microsomus* Burlini, 1957, a subgenus of *Stylosomus* Suffrian, 1848 (Coleoptera: Chrysomelidae: Cryptocephalinae). We refrain from creating a replacement name for the genus until specimens have been assessed.

Type material examined

Photograph of the holotype of *Microsomus atomus* Bright, 2019.

Included species
Microsomus atomus Bright, 2019: 178.

Pygmaeoborus Bright, 2019: 178

Type of genus
Pygmaeoborus cubensis Bright, 2019.

Diagnosis
Similar to *Hypothenemus* except antennae with single suture indicated by dense setae on apical third.

Female
Antennae with three funicle segments. Antennal club without sutures except a single procurved suture indicated by dense setae on the apical third. Frons convex. Pronotum armed with six widely spaced marginal asperities. Lateral margins marked by a barely distinct fine raised line. Setae on hypomeron single and hair-like. White scale-like setae cover pronotum and elytra. Strial punctures large. Overall shape elongate, more than 3 times long as wide.

Male
Unknown.

Distribution
Cuba, USA (Florida).

Remarks
Monotypic. This genus was described in the final stages of this manuscript preparation, from a single specimen. Two additional specimens were observed from Florida. Without molecular and internal characters examined, the placement within Trypophloeini is not confirmed.

Type material examined
Photograph of the holotype of *Pygmaeoborus cubensis* Bright, 2019.

Included species
Pygmaeoborus cubensis Bright, 2019: 179.

Trypophloeus Fairmaire, 1864: 105 (Fig. 21)

Synonymy
=*Glyptoderes* Eichhoff, 1878b: 34.

Type of genus
Bostrichus binodulus Ratzeburg, 1837.

Diagnosis
This genus can be diagnosed by the emarginated eye, by the cone-shaped antennal club with slightly recurved sutures, and by the rounded lateral margins of the pronotum.

Female
Eye emarginated. Frons simple with no extensive sculpturing or of vestiture. Cuticle behind eyes reticulated or aciculated. Antennae with five funicle segments. Antennal club conical, sutures recurved or straight. Pronotum armed with four to six marginal asperities, with the median of the margin slightly projected. Pronotal declivity with more than 30 asperities leading to a slightly elevated summit. Lateral margins of the pronotum rounded, hypomeron with mostly hair-like setae, sometimes with a small number of bifurcating setae. Elytra broadly convex, sometimes with interstriae 4 slightly raised. Vestiture comprised of hair-like or scale-like interstrial bristles and ground vestiture.

Male
Similar to female except anterior margin of pronotum slightly more projected. Elytral interstriae 4 sometimes with small tubercles or spines near declivity. Penis apodemes of a similar length to penis body, separated at apex. Tegmen open dorsally. Median ventral face of tegmen without apodeme or with only a slight projection. Spiculum gastrale with a fork, and of similar thickness to the penis apodemes. Basal sclerites visible.

Distribution
East Asia, Europe, North Africa, North America.

Remarks
Fifteen species known. Found primarily on *Salix* and *Populus* (Salicaceae), and *Alnus* (Betulaceae). Larvae develop communally for the first instar, then independently to complete development (Furniss 2004).

Type material examined
Holotype of *Trypophloeus populi* Hopkins, 1915 (USNM); holotype of *Trypophloeus salicis* Hopkins, 1915 (USNM); holotype of *Trypophloeus concentralis* Hopkins, 1915 (USNM).

Included species
Trypophloeus alni Lindemann, 1875a: 136.
=*Trypophloeus holdhausi* Wichmann, 1912: 186 (syn: Balachowsky, 1949).
Trypophloeus binodulus (Ratzeburg, 1837: 163) (*Bostrichus*).
=*Cryphalus grothii* Hagedorn, 1904: 232 (syn: Reitter, 1913).
=*Trypophloeus spiculatus* Eggers, 1927d: 122 (syn: Sokanovskiy, 1954).
=*Trypophloeus populi* Kurentsov, 1941: 164 (syn: Krivolutskaya, 1996).
=*Trypophloeus berezinae* Stark, 1952: 285 (syn: Sokanovskiy, 1954).
=*Trypophloeus kurenzovi* Nunberg, 1956b: 208 (syn: Krivolutskaya, 1996).
=*Trypophloeus kurenzowi* Schedl, 1959d: 42 (syn: Krivolutskaya, 1996).
Trypophloeus bispinulus Eggers, 1927d: 121.
Trypophloeus dejevi Stark, 1936: 152.
=*Trypophloeus dejevi* Eggers, 1942: 31 (syn: Pfeffer, 1944).
Trypophloeus discedens Palm, 1950: 142.
=*Trypophloeus palmi* Hansen, 1956: 183 (syn: Süda, 1996).
Trypophloeus grandis Schedl, 1964a: 99.
Trypophloeus granulatus (Ratzeburg, 1837: 164) (*Bostrichus*).
=*Cryphalus granulatus* var. *tredli* Hagedorn, 1904: 232 (unavailable name).
Remarks: *Cryphalus tredli* Reitter, 1908 was erroneously listed as a synonym of *Trypophloeus granulatus*, without the original genus in Wood and Bright (1992) (p. 845), in addition to its correct entry as a valid species in *Hypothenemus*. *Cryphalus granulatus* var. *tredli* Hagedorn, 1904 was described without locality data, so cannot be considered even a subspecies.
Trypophloeus klimeschi Eggers, 1915: 188.

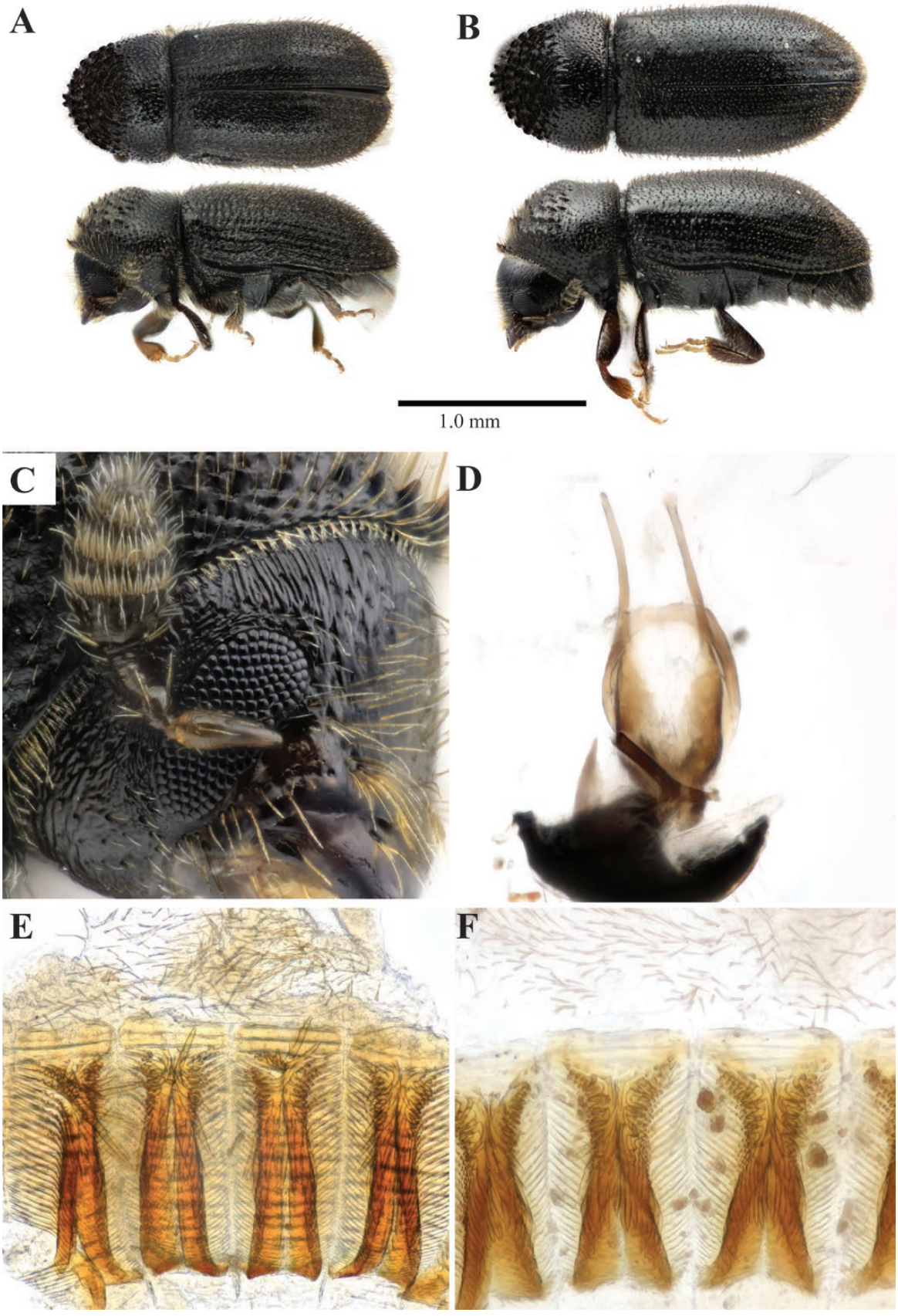

Figure 21. Images of *Trypophloeus* spp. Lateral and dorsal photographs of A) *T. granulatus*, B) *T. populi*, C) *T. granulatus*, D) *T. populi*, E) *T. dejevi*, F) *T. granulatus.*

Trypophloeus niger Stark, 1936: 152.
Trypophloeus populi Hopkins, 1915: 37.
Trypophloeus rybinskii Reitter, 1895: 72.
⊇*Trypophloeus rybinskii corsicus* Eggers, 1912: 113 (syn: Balachowsky, 1949).
=*Trypophloeus rybinskii salicis* Stark, 1952: 283 (Permanently invalid name due to primary homonymy).
Trypophloeus salicis Hopkins, 1915: 36.
=*Trypophloeus concentralis* Hopkins, 1915: 36 (syn: Wood, 1954).
Trypophloeus striatulus (Mannerheim, 1853: 235) (*Cryphalus*).
=*Cryphalus nitidus* Swaine, 1912: 349 (syn: Wood, 1969).
=*Cryphalus punctipennis* Hopkins, 1915: 37 (syn: Wood, 1954).
Trypophloeus thatcheri (Wood, 1954: 994) (*Cryphalus*).
Trypophloeus tremulae Stark, 1952: 287.

Xyloterini LeConte, 1876

=Xyloteri LeConte, 1876: 356.
=Xyloteroideae Lindemann, 1877: 165.
=Xyloteridae Eichhoff, 1878b: 411.
=Trypodendrinae Trédl, 1907: 70 (Unavailable name).
=Xyloterinae Nüsslin, 1911a: 432.
=Xyloterini Reitter, 1913: 28.
=Xyloterina Balachowsky, 1949: 196.
=Trypodendrina Nunberg, 1954: 16.
=Trypodendrini Browne, 1961: 45.
=Trypodendroninae Wood, 1978: 114.

Type of tribe
Xyloterus Erichson, 1836.

Diagnosis
Eye divided. Mycangia present on females.

Female
Female: Frons typically convex. Eye completely divided. Antennae with five funicle segments. Pronotum in dorsal view broadly rounded anteriorly, mostly with marginal asperities. Lateral margins of pronotum rounded. Vestiture typically with only hair-like setae. All tarsal segments cylindrical. Tibiae flattened with socketed denticles extending over at least apical quarter. A fungus-carrying organ (mycangium) visible as a setose opening on the latero-ventral side of the prothorax on the hypomeron.

Male
Similar to female in most characters, but pronotum in dorsal view quadrate and in *Trypodendron*, frons typically concave. Penis apodemes of a similar length or longer than penis body, separated at apex. Tegmen with a median apodeme or no apodemes, open dorsally. Spiculum gastrale reduced, much thinner than the thickness of penis apodemes. Basal sclerites complex and developed. Males of *Xyloterinus politus* are reportedly flightless and do not leave the natal gallery.

Distribution
Holarctic and Southeast Asia.

Remarks
All thorough molecular studies to date have indicated a strongly supported nested position among several former Cryphalini genera, sister to *Coriacephilus* or *Cryphalus*. We note that *Indocryphalus* may be paraphyletic based on the two taxa included in some molecular studies and with morphology (Cognato et al. 2015).

Included genera
Indocryphalus Eggers, 1939; *Trypodendron* Stephens, 1830; *Xyloterinus* Swaine, 1918.

Indocryphalus Eggers, 1939b: 6 (Figs. 22 A, B, E, F)

Synonymy
=*Dendrotrypum* Schedl, 1951a: 76 76 (unavailable name).

Type of genus
Indocryphalus malaisei Eggers, 1939b.

Diagnosis
Antennal club without indication of sutures. Mycangia on hypomeron either vertical (dorso-ventrally elongate) or horizontal (antero-posteriorly elongate).

Female
As described for tribe. Antennal club without an indication of a suture. Mycangia on hypomeron either vertical (dorso-ventrally elongate) or horizontal (antero-posteriorly elongate).

Male
Similar to female except lacking mycangia, and pronotal declivity less steep. Aedeagus as described for tribe, tegmen without apodemes.

Distribution
East and Southeast Asia.

Remarks
Ten species known. *Erioschidias sericeus* Schedl, 1942d is transferred based on the divided eyes.

Type material examined
Syntype of *Xyloterus intermedius* Sampson, 1913 (BMNH); holotype *Ptilopodius kalshoveni* Schedl, 1954a (NHMW); holotype and allotype of *Indocryphalus machili* Wood, 1988 (USNM); syntype of *Trypodendron pubipennis* Blandford, 1894b (BMNH); holotype of *Trypodendron sordidum* Blandford, 1894a (BMNH); holotype of *Trypodendron tropicum* Browne, 1950 (BMNH).

Included species
Indocryphalus aceris (Niisima, 1910: 4) (*Xyloterus*).
=*Xyloterus dainichiensis* Murayama, 1954: 191 (syn: Beaver, 2000).
Indocryphalus intermedius (Sampson, 1913: 445) (*Xyloterus*).
=*Indocryphalus malaisei* Eggers, 1939b: 7 (syn: Browne, 1970).
Indocryphalus machili Wood, 1988: 197.
Indocryphalus major (Eggers, 1926b: 148) (*Trypodendron*).
=*Xyloterus ashuensis* Murayama, 1950: 51 (syn: Beaver, 2000).
Indocryphalus pasohensis Beaver, 2000: 167.
Indocryphalus pubipennis (Blandford, 1894b: 125) (*Trypodendron*).
Indocryphalus sericeus (Schedl, 1942d: 10) (*Erischidias*) **comb. nov.** [*Cosmoderes*].
=*Ptilopodius kalshoveni* Schedl, 1954a: 149 (syn: Schedl, 1958e).
Indocryphalus sordidus (Blandford, 1894a: 577) (*Trypodendron*).

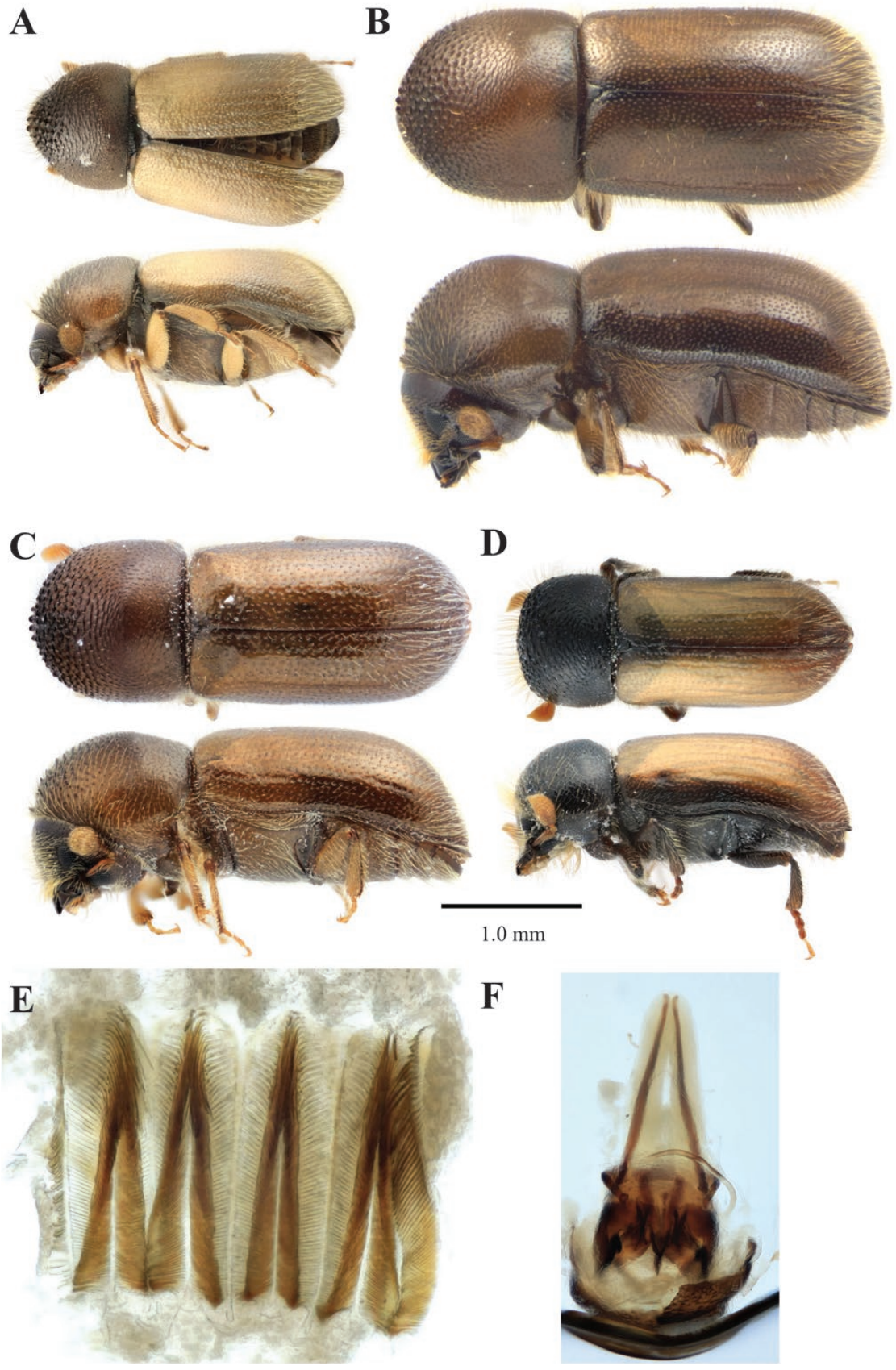

Figure 22. Images of Xyloterini spp.: Lateral and dorsal photographs of A) *Indocryphalus pubipennis* (male), B) *I. sordidus* (female), C) *Xyloterinus politus* (female), and D) *Trypodendron domesticum* (male). E) Proventriculus of *I. pubipennis*. F) Genitalia of *I. pubipennis*.

=*Trypodendron sinensis* Eggers, 1941b: 225 (syn: Beaver, 2000).
Indocryphalus suongmu Cognato, Smith and Pham, 2015: 6.
Indocryphalus tropicus (Browne, 1950: 648) (*Trypodendron*).

Trypodendron Stephens, 1830: 353 (Fig. 22 D)

Synonymy
=*Xyloterus* Erichson, 1836: 60.
=*Tripodendron* Redtenbacher, 1845: 151 (unavailable name).
=*Trypodendrum* Agassiz, 1846: 380.
=*Xyloteres* Redtenbacher, 1847: 36 (unavailable name).
=*Xylotrophus* Gistel, 1848: 4.
=*Trypodendrum* Gistel, 1856: 368 (unavailable name).

Type of genus
Dermestes domesticus Linnaeus, 1758.

Diagnosis
Antennal club with a single acutely procurved suture. Mycangia on hypomeron horizontal (antero-posteriorly).

Female
As described for tribe. Antennal club with a single acutely procurved suture. Mycangia on hypomeron horizontal (antero-posteriorly).

Male
Frons flattened or concave. Pronotum distinctly quadrate. Mycangia absent. Aedeagus as described for tribe; tegmen with apodemes.

Distribution
Holarctic.

Remarks
Fourteen species known.

Type material examined
Photograph of syntype of *Xyloterus retusus* LeConte, 1868 (MCZ); photograph of holotype of *Xyloterus scabricollis* LeConte, 1868 (MCZ).

Included species
Trypodendron betulae Swaine, 1911: 216.
Trypodendron domesticum (Linnaeus, 1758: 356) (*Dermestes*).
=*Bostrichus limbatus* Herbst, 1783: 24 (syn: Fabricius, 1801).
=*Apate limbata* Fabricius, 1792: 33 (syn: Fabricius, 1801).
⊇*Xyloterus domesticus apicalis* Endrödi, 1957: 309.
⊇*Xyloterus domesticus toracalis* Endrödi, 1957: 309.
Trypodendron dorjitenzingi Schmutzenhofer, 1988: 487.
Trypodendron gaimaense (Murayama, 1937: 359) (*Xyloterus*).
Trypodendron impressum Scudder, 1876: 83 (Fossil taxon).
Trypodendron laeve Eggers, 1939c: 122.
=*Trypodendron piceum* Strand, 1946b: 172.
Trypodendron lineatum (Olivier, 1800: 18) (*Bostrichus*).
=*Apate bivittata* Kirby, 1837: 192 (syn: Eichhoff, 1872b).
=*Bostrichus cavifrons* Mannerheim, 1843: 297 (syn: Eichhoff, 1872b).
=*Trypodendron vittiger* Eichhoff, 1881: 298 (syn: Schwarz, 1886).
=*Trypodendron borealis* Swaine, 1917: 21 (syn: Wood, 1957a).
=*Trypodendron granulatum* Eggers, 1933c: 51 (syn: Schedl, 1951a).
=*Trypodendron meridionale* Eggers, 1940d: 38 (syn: Schedl, 1951a).
⊇*Xyloterus lineatus lineellus* Endrödi, 1957: 309.
⊇*Xyloterus lineatus pauper* Endrödi, 1957: 309.
Trypodendron niponicum Blandford, 1894b: 124.
Trypodendron proximum (Niisima, 1909: 165) (*Xyloterus*).
Trypodendron pulchellum (Murayama, 1957: 585) (*Xyloterus*).
Trypodendron retusum (LeConte, 1868: 158) (*Xyloterus*).
Trypodendron rufitarse (Kirby, 1837: 193) (*Apate*).
=*Trypodendron ponderosae* Swaine, 1917: 22 (syn: Wood, 1957a).
Trypodendron scabricolle (LeConte, 1868: 158) (*Xyloterus*).
Trypodendron signatum (Fabricius, 1792: 363) (*Apate*).
=*Bostrichus quinquelineatus* Adams, 1817: 312.
=*Bostrichus waringii* Curtis, 1840: 279 (syn: Schedl, 1951a).
=*Xyloterus quercus* Eichhoff, 1864: 381.
=*Trypodendron suturale* Eggers, 1933b: 52 (syn: Schedl, 1951a).
=*Trypodendron obtusum* Eggers, 1939c: 121 (syn: Schedl, 1951a).

Xyloterinus Swaine, 1918: 44 (Fig. 22 C)

Type of genus
Bostrichus politus Say, 1826.

Diagnosis
Antennal club with a single weakly procurved suture. Mycangia on hypomeron horizontal (antero-posteriorly elongate).

Female
As described for tribe. Antennal club with single weakly procurved suture. Mycangia on hypomeron horizontal (antero-posteriorly elongate).

Male
Similar to female except much smaller mycangia not present, and the pronotal declivity is less steep. Aedeagus as described for the tribe, tegmen without apodemes.

Distribution
Nearctic.

Remarks
Monotypic.

Type material examined
None.

Included species
Xyloterinus politus (Say, 1826: 256) (*Bostrichus*).
=*Xyloterus unicolor* Eichhoff, 1872a: 136.

Ernoporini Nüsslin, 1911 **stat. res.**

=Ernoporinae Nüsslin, 1911b: 375.
=Eidophelinae Murayama, 1954: 200 (Unavailable name).
=Eidopherinae Murayama, 1954: 200.

Type of tribe
Ernoporus Thomson, 1859.

Diagnosis
Eye entire, rarely broadly emarginated. Antennae with three to five funicle segments. Postnotum fused with metanotum. Penis apodemes short and fused.

Female
Eye entire, oval (rarely with a weak emargination in species with disproportionally large eyes). Antennal funicle with three to five funicle segments (usually four). Antennal club flattened, sometimes with a single complete or partial septum. Third tarsal segment cylindrical. Basal margin of elytra smooth, rounded. Elytral apex typically vertical. Vestiture typically with many scale-like setae.

Male
Similar to female, sometimes indistinguishable externally. Rarely with sexually dimorphic frons or pronotal declivity. Penis apodemes shorter than penis body, fused at the apex. Tegmen open dorsally.

Distribution
Worldwide, but very few species and genera in the Americas.

Remarks
The original description for the higher classification was based on only one species, *Ernoporus tiliae*. The description of the new tribe was based solely on the characters of the nonsclerotized structures of the male reproductive system, which were not studied here.

Included genera
Eidophelus Eichhoff, 1876; *Ernoporus* Thomson, 1859; *Hemicryphalus* Schedl, 1963; *Procryphalus* Hopkins, 1915

Eidophelus Eichhoff, 1876: 200 (Figs. 23–26)

Synonymy
=*Idophelus* Rye, 1877: 362 (unavailable name).
=*Lepicerus* Eichhoff, 1878a: 388 **syn. nov.**
=*Scolytogenes* Eichhoff, 1878a: 387 **syn. nov.**
=*Lepicerus* Eichhoff, 1878b: 501 **syn. nov.**
=*Scolytogenes* Eichhoff, 1878b: 497 **syn. nov.**
=*Lepidocerus* Rye, 1880: 103 **syn. nov.**
=*Cryphalomorphus* Schaufuss, 1891: 12 **syn. nov.**
=*Letznerella* Reitter, 1913: 68 **syn. nov.**
=*Ernoporides* Hopkins, 1915: 34 **syn. nov.**
=*Hypothenoides* Hopkins, 1915: 11 **syn. nov.**
=*Ptilopodius* Hopkins, 1915: 11 **syn. nov.**
=*Ernoporicus* Berger, 1917: 242 **syn. nov.**
=*Neocryphalus* Eggers, 1922: 169 **syn. nov.**
=*Negritus* Eggers, 1923a: 141 **syn. nov.**
=*Lepicerinus* Hinton, 1936: 473 **syn. nov.**
=*Cylindrotomicus* Eggers, 1936c: 633 **syn. nov.** (unavailable name).
=*Eocryphalus* Kurentsov, 1941: 161 **syn. nov.**
=*Ernopocerus* Balachowsky, 1949: 211 **syn. nov.** (unavailable name).
=*Ernoporoides* Balachowsky, 1949: 201 **syn. nov.** (unavailable name).
=*Ernopocerus* Wood, 1954: 986 **syn. nov.**
=*Phellodendrophagus* Krivolutskaya, 1958: 107.
=*Cryphalophilus* Schedl, 1970c: 358 **syn. nov.**
=*Xylocryptus* Schedl, 1975a: 352 **syn. nov.**
=*Cryphalogenes* Wood, 1980: 91 **syn. nov.**
=*Ernpocerus* Wood, 1982: 858 **syn. nov.** (unavailable name).
=*Nigritus* Wood and Bright, 1992: 858 **syn. nov.** (unavailable name).

Type of genus
Eidophelus imitans Eichhoff, 1876

Diagnosis
Eidophelus can be diagnosed from superficially similar genera by the entire eye, by the lateral and basal margins of the pronotum marked by a carina, and by the antennal club which has a partial or absent septum, and by the proventriculus characters.

Female
Frons simple, convex. Eye oval shaped, rarely broadly emarginated. Antennae typically with four funicle segments. Antennal club large and flat, with a septum and sutures sometimes present. Pronotum sometimes with asperities on anterior margin. Pronotal summit rarely pronounced (i.e., protruding higher than most of the disc). Elytra with variable setae, from almost glabrous to dense scale-like or hair-like ground vestiture. Apex of elytra nearly or distinctly vertical. Mesocoxae separated, often much more than metacoxae. Metatibiae with denticles distributed over at least apical quarter. Proventriculus with apical plate shorter than rest of proventriculus (except *Eidophelus darwini*), with rows of granules, occasionally less sclerotized around the median suture (i.e., appearing open). Crop with thick spines or granules, in sclerotized clusters.

Male
Typically indistinguishable externally from the female. Some members of this genus have a sexually dimorphic frons (Johnson, unpublished), highly enlarged mandibles, or males have feather-like setae on the protarsi. Penis apodemes are much shorter than penis body, fused at apex. Tegmen open dorsally, of a similar thickness to penis apodemes. Median tegminal apodeme present, typically hooked at apex. Spiculum gastrale of a similar thickness or thicker than penis apodemes, with a fork. Basal sclerites visible.

Distribution
Worldwide except Antarctica, but most diversity is in Africa, Asia, Oceania, and Europe.

Remarks
In total, 152 species known. An extraordinarily diverse genus. The morphological variation in this genus has led to the description of many genera based on a limited number of characters, particularly in the antennae. However, there are no distinct groupings based on morphological characters, and many of the current genera are polyphyletic or represent smaller clades nested within the genus. The genera *Cryphalogenes*, *Ernoporicus*, *Ptilopodius*, and *Scolytogenes* are, therefore, all considered synonyms of *Eidophelus*.

Type material examined
Holotype of *Ernoporicus alniphagus* Nobuchi, 1975 (ITLJ); holotype of *Ernoporicus ater* Nobuchi, 1975 (ITLJ); holotype and paratype of *Ptilopodius bambusae* Browne, 1983 (BMNH); 2 paratypes of *Cryphalomorphus bangensis* Eggers, 1927 (NHMW); holotype of *Cryphalomorphus brimblecombei* Schedl, 1972 (QM);

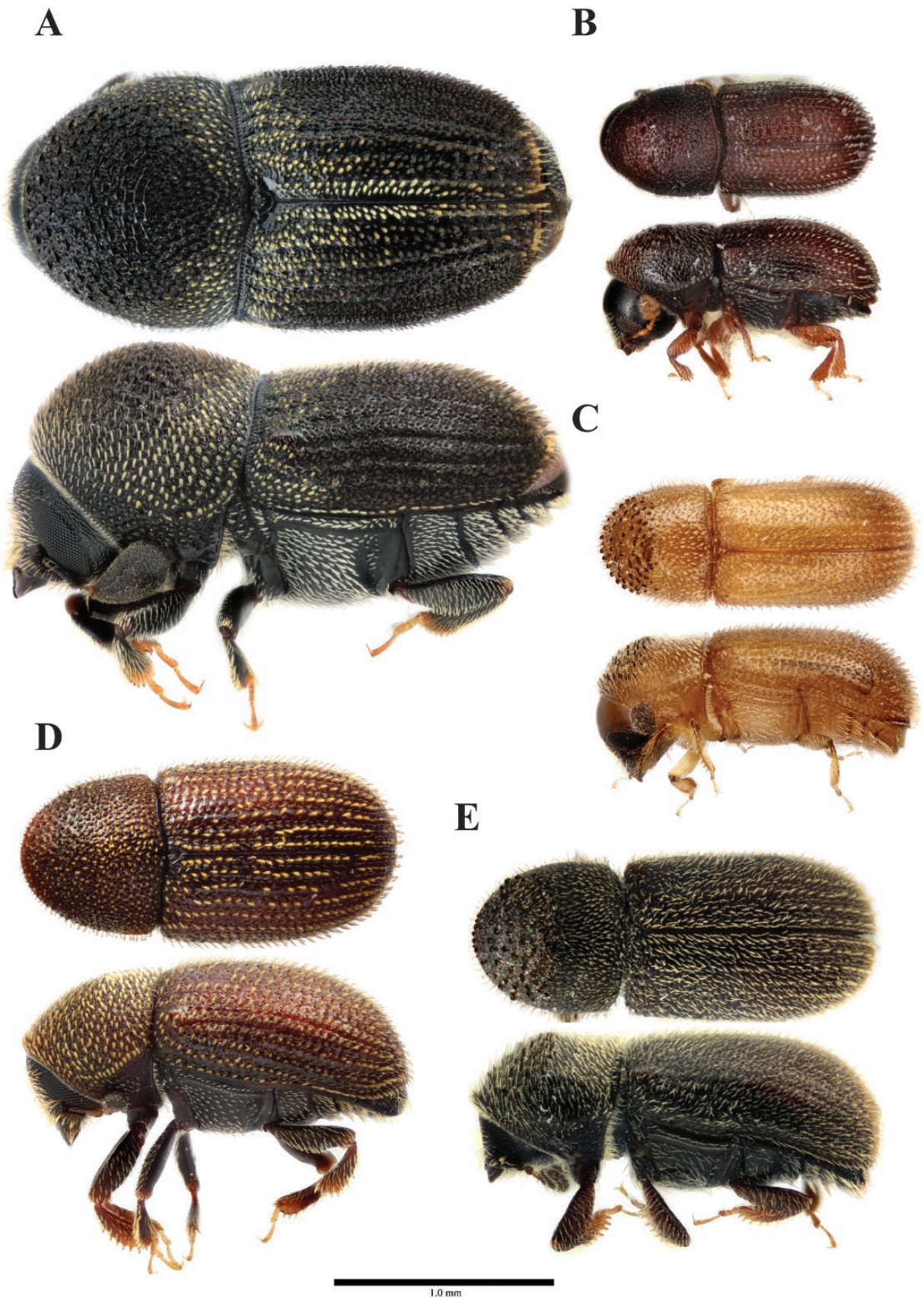

Figure 23. Images of *Eidophelus* spp.: Dorsal and lateral photos of A) *E. darwini*, B) *E. euphorbiae*, C) *E. jalappae*, D) *E. hylesinopsis*, E) *E. puerarae*.

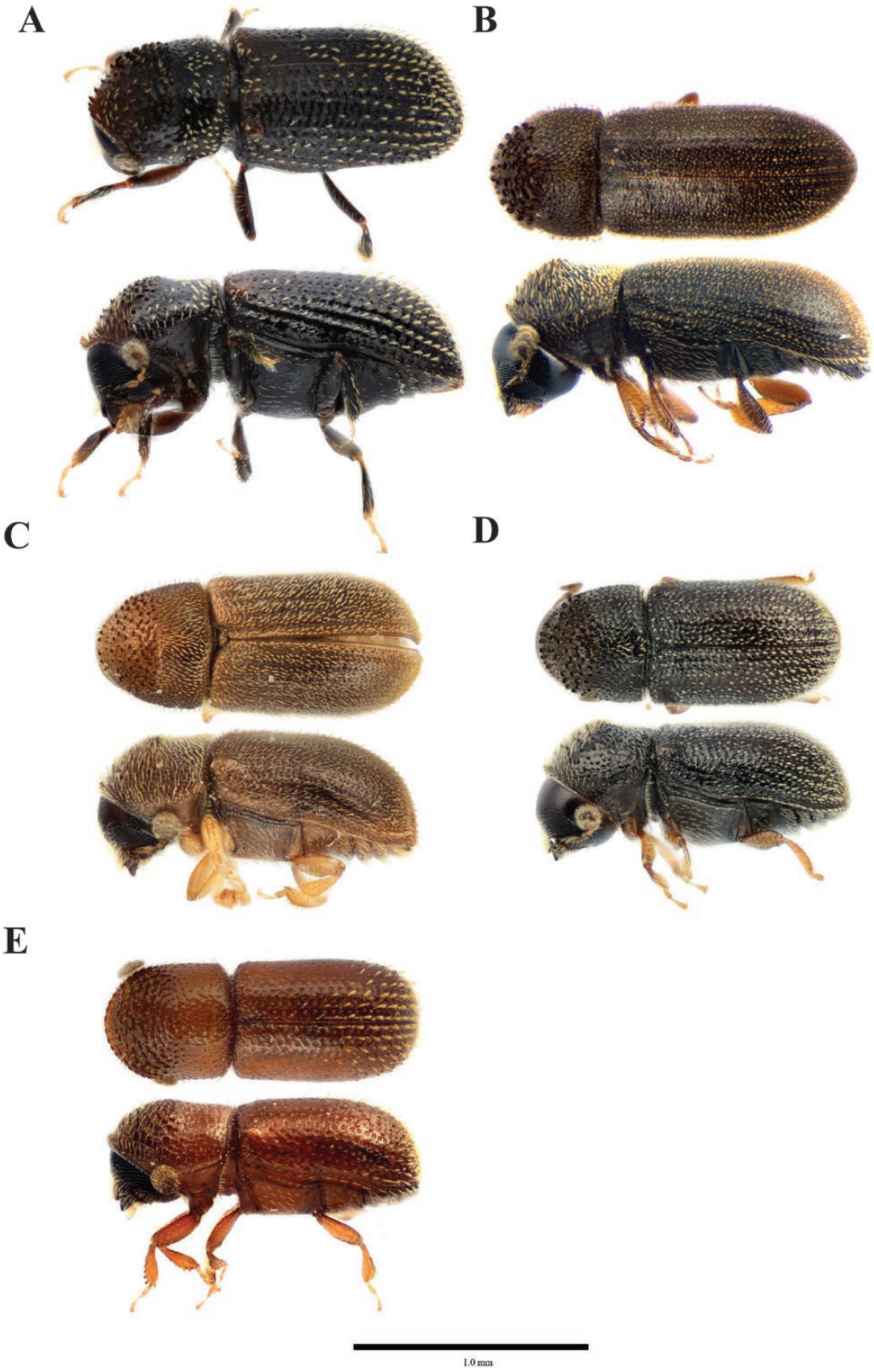

Figure 24. Images of *Eidophelus* spp.: Dorsal and lateral photos of A) *E. quadridens*, B) *E. fagi*, C) *E. semenovi*, D) *E. spessivtzevi*, E) *E. squamosus.*

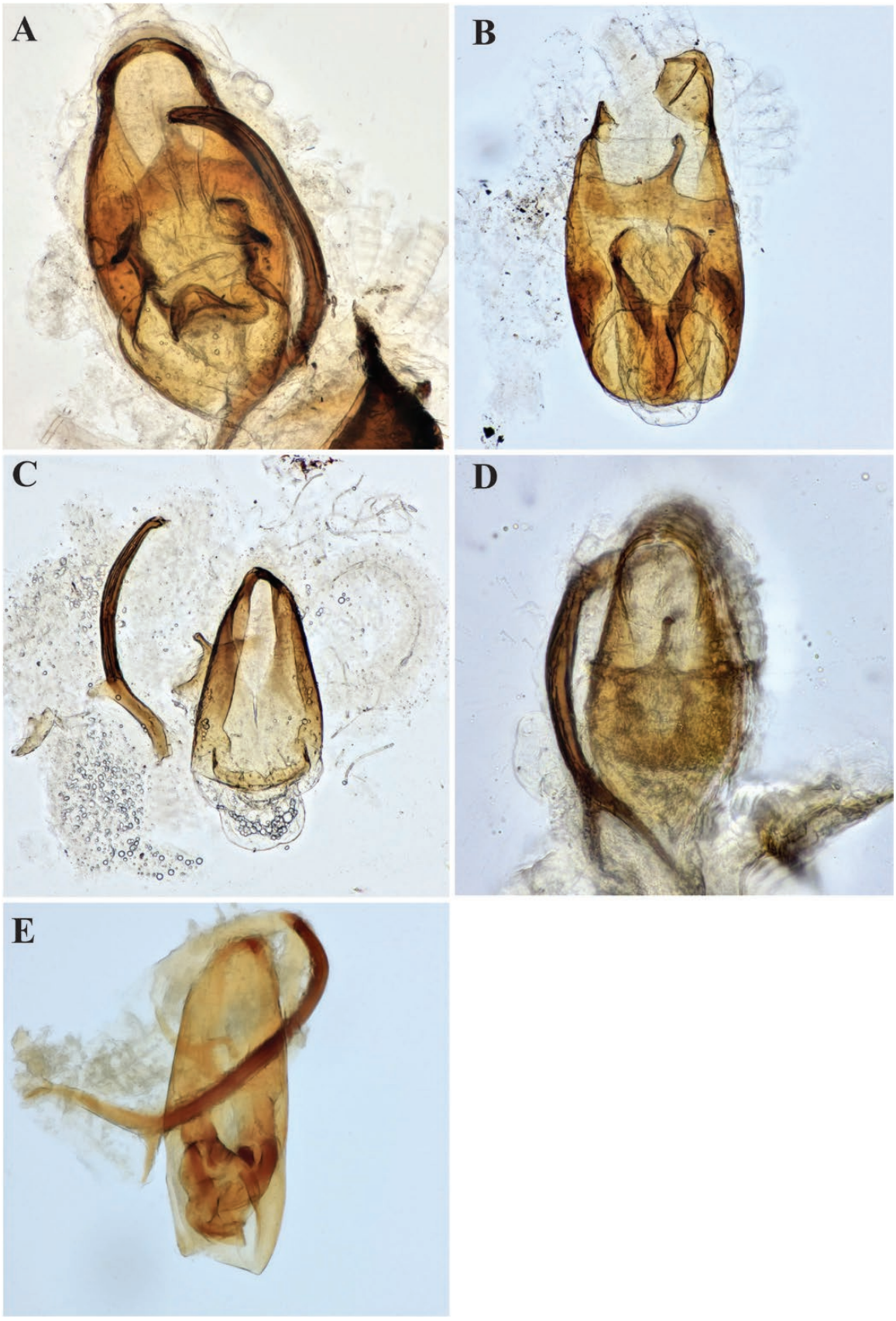

Figure 25. Images of *Eidophelus* spp.: Aedeagus of A) *E. darwini*, B) *E. fagi*, C) *E. incultus*, D) *E. squamosus*, and E) *E. fulvipennis*.

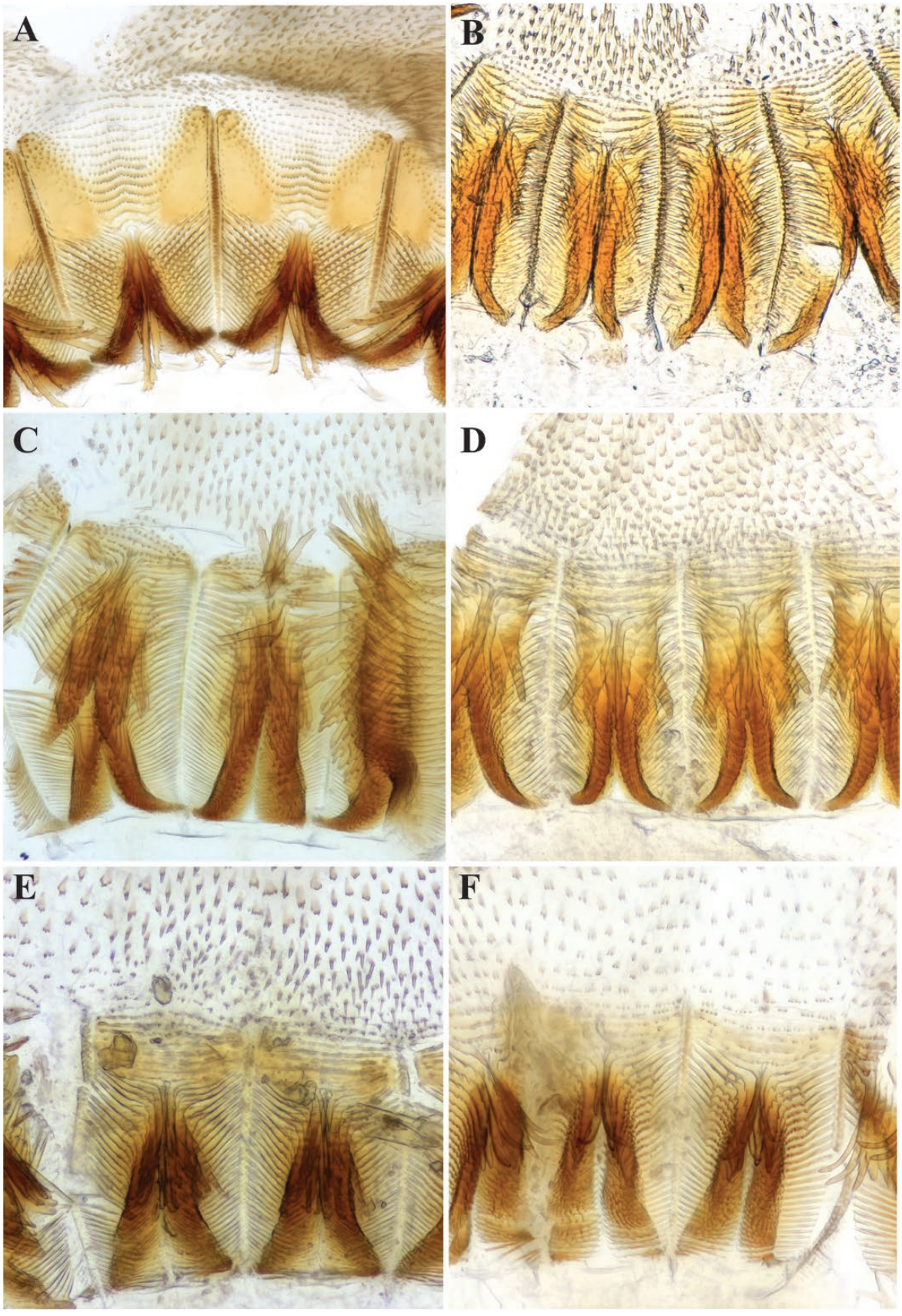

Figure 26. Images of *Eidophelus* spp.: Proventriculus of A) *E. darwini*, B) *E. fagi*, C) *E. hylesinopsis*, D) *E. jalappae*, E) *E. quadridens,* and F) *E. spessivtzevi.*

holotype of *Euptilius papuanus* Browne, 1983 (BMNH); holotype of *Cryphalomorphus buruensis* Eggers, 1926 (NHMW); holotype of *Cryphalomorphus camelliae* Nobuchi, 1975 (ITLJ); holotype of *Cryphalomorphus candidus* Nobuchi, 1975 (ITLJ); holotype(?) of *Lepicerinus coccotrypanoides* Schedl, 1939 (NHMW); syntype(?) of *Lepicerinus coccotrypanoides* Schedl, 1939 (BMNH); holotype of *Cryphalophilus concentralis* Schedl, 1975 (NHMW); holotype of *Margadillius concentralis* Schedl, 1975 (NHMW); holotype of *Cryphalomorphus confragosus* Sampson, 1914 (BMNH); holotype of *Cryphalomorphus scolytomimoides* Nobuchi, 1975 (ITLJ); paratype of *Ptilopodius dubiosus* Wood, 1960 (USNM); holotype and paratype of *Cryphalogenes euphorbiae* Wood, 1980 (USNM); holotype and paratype of *Cryphalogenes exiguus* Wood, 1980 (USNM); holotype [potentially mislabeled or misplaced] of *Hypothenemus expers* Blandford, 1894 (BMNH); holotype of *Lepicerinus fijianus* Schedl, 1950 (NHMW); holotype of *Ptilopodius formosanus* Browne, 1981 (BMNH); holotype of *Cryphalomorphus fujisanus* Nobuchi, 1975 (ITLJ); holotype of *Cryphalomorphus fulgidus* Schedl, 1975 (NHMW); holotype of *Cryphalomorphus fulvipennis* Nobuchi, 1975 (ITLJ); holotype of *Cryphalophilus ater* Schedl, 1971 (QM); paratype of *Cryphalomorphus granulatus* Wood, 1960 (USNM); holotype of *Cryphalomorphus grossepunctatus* Browne, 1974 (BMNH); holotype of *Cryphalomorphus hirtus* Wood, 1974 (USNM); holotype of *Cryphalomorphus hylesinopsis* Schedl, 1975 (NHMW); holotype of *Scolytogenes indicus* Wood, 1989 (USNM); holotype of *Hypothenemus inermis* Browne, 1984 (BMNH); holotype of *Hypothenemus insignis* Browne, 1984 (BMNH); holotype of *Cryphalomorphus insularis* Nobuchi, 1975 (ITLJ); holotype of *Ericryphalus elongatus* Nobuchi, 1975 (ITLJ); lectotype of *Ptilopodius javanus* Schedl, 1942 (NHMW); paratype of *Hemicryphalus kinabaluensis* Bright, 1992 (MK collection); holotype of *Cryphalomorphus leprosulus* Browne, 1974 (BMNH); holotype of *Cryphalomorphus longipennis* Eggers, 1936 (BMNH); paratype of *Hemicryphalus minutus* Bright, 1992 (MK collection); paratype of *Cryphalomorphus nanulus* Wood, 1960 (USNM); Two paratypes of *Cryphalomorphus nubilus* Wood, 1960 (USNM); Likely unlabeled holotype of *Ptilopodius pacificus* Schedl, 1941 (BMNH); holotype of *Cryphalus parvus* Browne, 1984 (BMNH); paratype of *Hemicryphalus podocarpi* Bright, 1992 (MK collection); holotype of *Ptilopodius praeda* Browne, 1978 (BMNH); holotype of *Scolytogenes punctatulus* Nobuchi, 1976 (ITLJ); holotype and paratype of *Hypothenemus quadridens* Browne, 1983 (BMNH); holotype and paratype of *Cryphalomorphus rusticus* Wood, 1974 (USNM); holotype and paratype of *Cryphalomorphus setifer* Wood, 1974 (USNM); holotype of *Ptilopodius spirostachius* Schedl, 1958 (BMNH); holotype of *Lepicerinus squamosus* Schedl, 1942 (NHMW); paratype of *Hemicryphalus squamosus* Bright, 1992 (MK collection); holotype of *Cylindrotomicus squamulosus* Eggers, 1936 (BMNH); holotype of *Ptilopodius stephegynis* Hopkins, 1915 (USNM); holotype of *Ernoporicus takahashii* Nobuchi, 1975 (ITLJ); holotype and paratype of *Cryphalomorphus trucis* Wood, 1974 (USNM).

Included species

Eidophelus absonus (Schedl, 1975a: 344) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus afer (Schedl, 1970c: 359) (*Cryphalophilus*) **comb. nov.** [*Scolytogenes*].

Eidophelus africanus (Schedl, 1977a: 396) (*Stephanorhopalus*) **comb. nov.** [*Ernoporicus*].

Eidophelus aitutakii (Beaver and Maddison, 1990: 1367) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].

Eidophelus alniphagus (Nobuchi, 1975: 43) (*Ernoporicus*) **comb. nov.** [*Ernoporicus*].

Eidophelus alstoniae Johnson **nom. nov.** [*Scolytogenes*].

=*Chiloxylon sumatranus* Schedl, 1970c: 358 **syn. nov.** (secondary homonym).

Remarks: A replacement name is proposed for *Chiloxylon sumatranus* Schedl, 1970c because the name is already occupied by *Eidophelus sumatranus* Schedl, 1961a. The replacement name is a noun in the genitive case, named after the host plant, described as 'Pulai logs' = *Alstonia* sp.

Eidophelus alternans (Schedl, 1975a: 345) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus amanicus (Eggers, 1919: 239) (*Cryphalus*) **comb. nov.** [*Scolytogenes*].

Eidophelus ankius (Schedl, 1979c: 96) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus apicalis (Schedl, 1971c: 11) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus approximatus (Schedl, 1975a: 346) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus aspericollis (Eichhoff, 1878a: 388) (*Lepicerus*) **comb. nov.** [*Scolytogenes*].

=*Lepicerus aspericollis* Eichhoff, 1878b: 501 **syn. nov.**

=*Cryphalus stierlini* Eggers, 1911: 121 **syn. nov.** (syn: Eggers, 1929c).

Eidophelus ater (Eggers, 1923a: 142) (*Negritus*) **comb. nov.** [*Scolytogenes*].

Eidophelus australis (Schedl, 1942c: 175) (*Lepicerinus*) **comb. nov.** [*Scolytogenes*].

Eidophelus badius (Nobuchi, 1975: 44) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus bambusae (Browne, 1983b: 69) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].

Eidophelus bangensis (Eggers, 1927c: 75) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus basilaris (Wood, 1960: 30) (*Scolytogenes*) **comb. nov.** [*Scolytogenes*].

Eidophelus birosimensis (Murayama, 1958: 935) (*Ernocryphalus*) **comb. nov.** [*Scolytogenes*].

Eidophelus borneensis Browne, 1984a: 153.

Eidophelus braderi (Browne, 1965: 191) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

=*Cryphalomorphus orientalis* Schedl, 1971c: 11 (syn: Wood, 1992b).

Eidophelus brighti Johnson **nom. nov.** [*Hemicryphalus*].

=*Hemicryphalus minutus* Bright, 1992: 187 **syn. nov.**

Remarks: *Hemicryphalus minutus* Bright, 1992 is transferred to *Eidophelus* based on the eye shape, and shape of the pronotum. A replacement name for *Hemicryphalus minutus* Bright, 1992 is proposed because the name is already occupied by *Eidophelus minutus* Blandford, 1894b. The replacement name is a noun in the genitive case, honoring the original author.

Eidophelus brimblecombei (Schedl, 1972a: 146) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus brownei Johnson **nom. nov.** [*Ernoporus*].

=*Euptilius papuanus* Browne, 1983b: 70 **syn. nov.** (secondary homonym).

Remarks: *Euptilius papuanus* Browne, 1983b was previously recognized as a junior synonym of *Ernoporus antennarius* Schedl, 1974. This was likely a mistake since the two species differ greatly. Wood (1989) probably intended to synonymize *Ernoporus*

antennarius Schedl, 1974 and *Margadillius papuanus* Schedl, 1973b. Subsequently, the release from synonymy and the transfer of *Euptilius papuanus* Browne, 1983b to *Eidophelus* requires a replacement name because the name is already occupied by *Cryphalomorphus papuanus* Schedl, 1974. The replacement name is a noun in the genitive case, honoring the original author.

Eidophelus buruensis (Eggers, 1926a: 300) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus camelliae (Nobuchi, 1975: 45) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus candidus (Nobuchi, 1975: 47) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus capucinus (Schedl, 1971a: 283) (*Cryphalops*) **comb. nov.** [*Ernoporicus*].

Eidophelus caucasicus (Lindemann, 1877: 373) (*Ernoporus*) **comb. nov.** [*Ernoporicus*].

=*Cryphalus schreineri* Eichhoff, 1881: 185.

Eidophelus ceylonicus (Schedl, 1959a: 475) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].

Eidophelus cicatricosus (Schedl, 1942c: 176) (*Lepicerinus*) **comb. nov.** [*Scolytogenes*].

Eidophelus coccotrypanoides (Schedl, 1939b: 343) (*Lepicerinus*) **comb. nov.** [*Scolytogenes*].

Eidophelus communis (Schaufuss, 1891: 12) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus concentralis (Schedl, 1975a: 342) (*Cryphalophilus*) **comb. nov.** [*Scolytogenes*].

=*Margadillius concentralis* Schedl, 1975a: 344 **syn. nov.**

Eidophelus confragosus (Sampson, 1914: 386) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus corni (Kurentsov, 1941: 162) (*Hypothenemus*) **comb. nov.** [*Ernoporicus*].

Eidophelus corpulentus (Schedl, 1965a: 54) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus corrugatus (Schedl, 1950a: 19) (*Stephanorhopalus*) **comb. nov.** [*Scolytogenes*].

Eidophelus creber (Schedl, 1975a: 346) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus crenatus (Sampson, 1914: 385) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus cylindricus (Schedl, 1959a: 476) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus darwini (Eichhoff, 1878a: 387) (*Scolytogenes*) **comb. nov.** [*Scolytogenes*].

=*Scolytogenes darwinii* Eichhoff, 1878b: 497 (syn: Alonso-Zarazaga and Lyal, 2009).

=*Negritus similis* Eggers, 1923a: 142 (syn: Wood, 1985).

=*Negritus major* Eggers, 1927c: 69 (syn: Wood, 1985).

=*Scolytogenes cryptolepis* Schedl, 1951b: 55 (syn: Wood, 1985).

=*Cryphalomorphus scolytomimoides* Nobuchi, 1975: 50.

Eidophelus devius (Schedl, 1975c: 280) (*Cryphalophilus*) **comb. nov.** [*Scolytogenes*].

Eidophelus dubiosus (Wood, 1960: 19) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].

Eidophelus eggersi (Schedl, 1962e: 490) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

=*Cryphalomorphus minor* Eggers, 1927c: 76 (syn: Schedl, 1962e).

Eidophelus euphorbiae (Wood, 1980: 91) (*Cryphalogenes*) **comb. nov.** [*Cryphalogenes*].

Eidophelus excellens (Schedl, 1979c: 97) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus exiguus (Wood, 1980: 92) (*Cryphalogenes*) **comb. nov.** [*Cryphalogenes*].

Eidophelus exilis (Yin, 2001: 327) (*Scolytogenes*) **comb. nov.** [*Scolytogenes*].

Eidophelus eximius (Schedl, 1942d: 9) (*Erischidias*) **comb. nov.** [*Ernoporicus*].

Eidophelus expers (Blandford, 1894b: 85) (*Hypothenemus*) **comb. nov.** [*Scolytogenes*].

Eidophelus fagi (Fabricius, 1798: 157) (*Apate*) **comb. nov.** [*Ernoporicus*].

=*Bostrichus serratus* Panzer, 1795: 288.

=*Cryphalus (Ernoporus) thomsoni* Ferrari, 1867: 14 (syn: Ferrari, 1869).

Eidophelus fijianus (Schedl, 1950b: 42) (*Lepicerinus*) **comb. nov.** [*Scolytogenes*].

Eidophelus formosanus (Browne, 1981: 129) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].

Eidophelus fugax (Schedl, 1975a: 347) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus fujisanus (Nobuchi, 1975: 46) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus fulgens (Schedl, 1975a: 348) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus fulgidus (Schedl, 1975a: 348) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus fulvipennis (Nobuchi, 1975: 47) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus furvus Johnson **nom. nov.** [*Ptilopodius*].

=*Cryphalophilus ater* Schedl, 1972a: 146 **syn. nov.** (secondary homonym).

Remarks: A replacement name is proposed for *Cryphalophilus ater* Schedl, 1972a because the name is already occupied by *Negritus ater* Eggers, 1923a. The replacement name is an ajective, maintaining the meaning of the original name, meaning black, dark or obscure.

Eidophelus ghanaensis (Schedl, 1977b: 281) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus glabratus (Yin, 2001: 330) (*Scolytogenes*) **comb. nov.** [*Scolytogenes*].

Eidophelus gracilis (Schedl, 1950b: 44) (*Lepicerinus*) **comb. nov.** [*Scolytogenes*].

Eidophelus granulatus (Wood, 1960: 31) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus grobleri (Schedl, 1962b: 68) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus hirtus (Wood, 1974a: 18) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus hobohmi (Schedl, 1955c: 215) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus hylesinopsis (Schedl, 1975a: 349) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].

Eidophelus imitans Eichhoff, 1876: 150.

=*Phellodendrophagus elegans* Krivolutskaya, 1958: 150 (syn: Wood, 1989).

=*Ptilopodius nitidus* Schedl, 1959a: 475 (syn: Wood, 1989).

Eidophelus incultus (Yin, 2001: 325) (*Scolytogenes*) **comb. nov.** [*Scolytogenes*].

Eidophelus indicus (Wood, 1989: 184) (*Scolytogenes*) **comb. nov.** [*Scolytogenes*].

Eidophelus inermis (Browne, 1984d: 94) (*Hypothenemus*) **comb. nov.** [*Hypothenemus*].
Eidophelus insignis (Browne, 1984a: 151) (*Hypothenemus*) **comb. nov.** [*Hypothenemus*].
Eidophelus insularis (Nobuchi, 1975: 48) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus insularum (Krivolutskaya, 1968: 56) (*Hypothenemus*) **comb. nov.** [*Ernoporicus*].

=*Ericryphalus elongatus* Nobuchi, 1975: 42 (syn: Mandelshtam, 2006).

=*Hypothenemus krivolutskayae* Wood, 1992b: 79 (syn: Alonso-Zarazaga, 2005).
Eidophelus jalappae (Letzner, 1849: 99) (*Bostrichus*) **comb. nov.** [*Scolytogenes*].

=*Ernoporides floridensis* Hopkins, 1915: 34 (syn: Wood, 1966).

=*Ernoporides knabi* Hopkins, 1915: 34 (syn: Wood, 2007).

=*Hypothenemus ritchiei* Sampson, 1918: 295 (syn: Wood, 1966).

=*Cryphalomorphus caraibicus* Schedl, 1951e: 96 (syn: Wood, 1966).

=*Cryphalomorphus minutissimus* Schedl, 1951e: 97 (syn: Wood, 1977b).

=*Cryphalomorphus subtriatus* Schedl, 1952c: 360 (syn: Wood, 1966).

=*Cryphalomorphus alienus* Schedl, 1976: 65 (syn: Wood, 1989).
Eidophelus javanus (Schedl, 1942d: 10) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].
Eidophelus kanawhae (Hopkins, 1915: 35) (*Ernoporus*) **comb. nov.** [*Ernoporicus*].
Eidophelus kinabaluensis (Bright, 1992: 186) (*Hemicryphalus*) **comb. nov.** [*Hemicryphalus*].
Eidophelus levis Johnson **nom. nov.**

=*Eidophelus gracilis* Browne, 1984a: 152 **syn. nov** (secondary homonym).

Remarks: A replacement name is proposed for *Eidophelus gracilis* Browne, 1984a following the genus synonymy of *Eidophelus* and *Scolytogenes*, because the name is already occupied by *Lepicerinus gracilis* Schedl, 1950b. The name is an adjective, meaning smooth.
Eidophelus landolphiae (Schedl, 1961b: 133) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus leprosulus (Browne, 1974: 45) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus longipennis (Eggers, 1936a: 30) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus lucidus Johnson **nom. nov.** [*Scolytogenes*].

=*Lepicerinus pacificus* Schedl, 1959a: 477 **syn. nov.** (secondary homonym).

Remarks: A replacement name is proposed for *Lepicerinus pacificus* Schedl, 1959a following the genus synonymy of *Ptilopodius* and *Eidophelus*, because the name is already occupied by *Ptilopodius pacificus* Schedl, 1941b. The name is an adjective, with reference to its shiny appearance.
Eidophelus magnocularis (Yin, 2001: 326) (*Scolytogenes*) **comb. nov.** [*Scolytogenes*].
Eidophelus marquesanus (Beeson, 1935a: 101) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].

=*Ptilopodius zimmermani* Schedl, 1951d: 143 (syn: Beaver, 1991).
Eidophelus mauritianus (Schedl, 1965a: 56) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus micans (Eggers, 1927b: 396) (*Stephanoderes*) **comb. nov.** [*Scolytogenes*].
Eidophelus minor (Eggers, 1927c: 69) (*Negritus*) **comb. nov.** [*Scolytogenes*].
Eidophelus minusculus Johnson **nom. nov.**

=*Eidophelus minutissimus* Schedl, 1962a: 191 **syn. nov.** (secondary homonym)

Remarks: A replacement name is proposed for *Eidophelus minutissimus* Schedl, 1962a because the name is now occupied by *Ptilopodius minutissimus* Schedl, 1943. The replacement name is an adjective, and maintains the original meaning, referencing the very small size.
Eidophelus minutissimus (Schedl, 1943: 34) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].
Eidophelus minutus Blandford, 1894b: 88.
Eidophelus mus (Schedl, 1975a: 349) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus nanulus (Wood, 1960: 29) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus nigellatus (Schedl, 1950b: 44) (*Lepicerinus*) **comb. nov.** [*Scolytogenes*].
Eidophelus niger Johnson **nom. nov.** [*Ernoporicus*].

=*Ernoporicus ater* Nobuchi, 1975: 43 **syn. nov.** (secondary homonym).

Remarks: A replacement name for *Ernoporicus ater* Nobuchi, 1975 is proposed because the name is already occupied by *Negritus ater* Eggers, 1923a. The name is an adjective, following the meaning of the original name, meaning black.
Eidophelus nitidus Schedl, 1965b: 26.
Eidophelus nubilus (Wood, 1960: 30) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus ocularis (Schedl, 1965c: 368) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus onyanganus (Schedl, 1941a: 391) (*Letznerella*) **comb. nov.** [*Scolytogenes*].

=*Cryphalomorphus similaris* Schedl, 1965d: 8 (syn: Browne, 1973).
Eidophelus opacus (Schedl, 1959a: 477) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus pacificus (Schedl, 1941b: 111) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].
Eidophelus papuanus (Schedl, 1974: 459) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus papuensis (Wood, 1989: 179) (*Scolytogenes*) **comb. nov.** [*Scolytogenes*].

=*Xylocryptus papuanus* Schedl, 1975a: 352 (secondary homonym).
Eidophelus paradoxus (Wood, 1992b: 80) (*Scolytogenes*) **comb. nov.** [*Scolytogenes*].

=*Cryphalomorphus papuanus* Schedl, 1979c: 97 (secondary homonym).
Eidophelus parvulus Johnson **nom. nov.** [*Cryphalus*].

=*Cryphalus parvus* Browne, 1984a: 152 **syn. nov.** (secondary homonym).

Remarks: *Cryphalus parvus* Browne, 1984a is transferred to *Eidophelus* based on the cylindrical third tarsal segment, on the entire eye, and on the near-vertical apex of declivity. A replacement name is subsequently proposed due to the name being occupied by *Hypothenoides parvus* Hopkins, 1915. The replacement name is the diminutive of the adjective *parvus* (=small), emphasizing that particularly small body size.
Eidophelus parvus (Hopkins, 1915: 11) (*Hypothenoides*) **comb. nov.** [*Scolytogenes*].

Eidophelus philippinensis (Schedl, 1967a: 126) (*Erioschidias*) **comb. nov.** [*Cosmoderes*].
Eidophelus pityophthorinus (Schedl, 1943: 39) (*Lepicerinus*) **comb. nov.** [*Scolytogenes*].
Eidophelus pleiocarpae (Schedl, 1957b: 51) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus podocarpi (Bright, 1992: 188) (*Hemicryphalus*) **comb. nov.** [*Hemicryphalus*].
Eidophelus polisquamosus (Yin, 2001: 329) (*Scolytogenes*) **comb. nov.** [*Scolytogenes*].
Eidophelus praeda (Browne, 1978: 589) (*Ptilopodius*) **comb. nov.** [*Scolytogenes*].
Eidophelus puerarae (Choo and Woo, 1989: 58) (*Scolytogenes*) **comb. nov.** [*Scolytogenes*].
Eidophelus pumilionides (Schedl, 1977c: 500) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus pumilus (Wood, 1960: 29) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus punctatulus (Nobuchi, 1976: 72) (*Scolytogenes*) **comb. nov.** [*Scolytogenes*].
=*Cryphalomorphus punctatus* Nobuchi, 1975: 49.
=*Cryphalomorphus nobuchii* Schedl, 1980: 118 (syn: Choo and Woo, 1989).
Eidophelus punctatus (Schedl, 1951b: 55) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus puncticollis (Schedl, 1950b: 43) (*Lepicerinus*) **comb. nov.** [*Scolytogenes*].
=*Cryphalomorphus grossepunctatus* Browne, 1974: 63 (syn: Beaver, 1991).
Eidophelus pygmaeolus (Schedl, 1971c: 12) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus quadridens (Browne, 1983b: 71) (*Hypothenemus*) **comb. nov.** [*Scolytogenes*].
Eidophelus ramosus (Beeson, 1935b: 115) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].
Eidophelus rhododendri Johnson **nom. nov.** [*Hemicryphalus*].
=*Hemicryphalus squamosus* Bright, 1992: 188 **syn. nov.** (secondary homonym).
Remarks: A replacement name for *Hemicryphalus squamosus* Bright, 1992 is proposed because of the transfer to *Eidophelus*, where the name is already occupied by *Lepicerinus squamosus* Schedl, 1942c. The replacement name is a noun in the genitive case, named after the host plant.
Eidophelus robustus (Schedl, 1955b: 32) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus rugosus (Schedl, 1943: 34) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].
Eidophelus rusticus (Wood, 1974a: 18) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus samoanus Schedl, 1972b: 268.
Eidophelus schedli Johnson **nom. nov.** [*Scolytogenes*].
=*Cryphalomorphus ceylonicus* Schedl, 1959a: 477 **syn. nov.** (secondary homonym).
Remarks: A replacement name for *Cryphalomorphus ceylonicus* Schedl, 1959a is proposed because the name is occupied by *Ptilopodius ceylonicus* Schedl, 1959a. The replacement name is a noun in the genitive case, honoring the original author.
Eidophelus semenovi (Kurentsov, 1941: 161) (*Eocryphalus*) **comb. nov.** [*Ernoporicus*].
Eidophelus separandus (Schedl, 1965a: 56) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus setifer (Wood, 1974a: 18) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus sodalis (Schedl, 1965a: 55) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus spessivtzevi (Berger, 1917: 243) (*Ernoporicus*) **comb. nov.** [*Ernoporicus*].
Eidophelus spirostachius (Schedl, 1958a: 557) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].
Eidophelus splendens (Schedl, 1975a: 350) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus squamatilis (Schedl, 1977c: 500) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus squamosus (Schedl, 1942c: 175) (*Lepicerinus*) **comb. nov.** [*Scolytogenes*].
Eidophelus squamulosus (Eggers, 1936c: 633) (*Cylindrotomicus*) **comb. nov.** [*Scolytogenes*].
Eidophelus stephegynis (Hopkins, 1915: 11) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].
Eidophelus sumatranus Schedl, 1961a: 72.
Eidophelus takahashii (Nobuchi, 1975: 43) (*Ernoporicus*) **comb. nov.** [*Ernoporicus*].
Eidophelus tarawai (Beaver, 1990: 149) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].
Eidophelus tonsus (Schedl, 1969: 49) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus tricolor (Lea, 1910: 141) (*Cryphalus*) **comb. nov.** [*Scolytogenes*].
Eidophelus trucis (Wood, 1974a: 19) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus uncatus (Schedl, 1971b: 373) (*Cryphalophilus*) **comb. nov.** [*Ptilopodius*].
Remarks: *Cryphalomorphus ater* Schedl, 1972a:146, nomen nudum, was listed as a synonym of this species (Wood and Bright, 1992), but this is likely an error, probably misinterpreted from the genus transfer of *E. uncatus* and *Cryphalophilus ater* Schedl, 1972a:146, by Beaver (1991).
Eidophelus usagaricus (Eggers, 1922: 169) (*Neocryphalus*) **comb. nov.** [*Scolytogenes*].
Eidophelus varius (Schedl, 1975a: 350) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Eidophelus venustus (Schedl, 1953c: 78) (*Ptilopodius*) **comb. nov.** [*Ptilopodius*].
Eidophelus yinae Johnson **nom. nov.** [*Scolytogenes*].
=*Scolytogenes venustus* Yin, 2001: 328 **syn. nov.** (secondary homonym).
Remarks: A replacement name for *Scolytogenes venustus* Yin, 2001 is proposed because the name is occupied by *Ptilopodius venustus* Schedl, 1953c. The replacement name is a noun in the genitive case, honoring the original author.
Eidophelus yunnanensis (Yin, 2001: 324) (*Scolytogenes*) **comb. nov.** [*Scolytogenes*].
Eidophelus zachvatkini (Krivolutskaya, 1958: 149) (*Eocryphalus*) **comb. nov.** [*Ernoporicus*].

Ernoporus Thomson, 1859: 147 (Figs. 27–29)

Synonymy
=*Cryphalops* Reitter, 1889: 94.
=*Stephanorhopalus* Hopkins, 1915: 35.
=*Euptilius* Schedl, 1940c: 589.
=*Ernocladius* Wood, 1980: 93 **syn. nov.**
=*Allothenemus* Bright and Torres, 2006: 400 **syn. nov.**

Type of genus
Apate tiliae Panzer, 1793.

Diagnosis
This genus can be diagnosed by the combination of the entire eye, by the pronotum with concentric rows of asperities, by the distinct summit, and by the proventriculus which has anteriorly pointing spines posterior to the masticatory brush.

Female
Robust body shape, less than 2.1 times as long as wide. Eye oval shaped. Antennae with three or four funicle segments. Antennal club in most species with sutures straight to profoundly procurved. Pronotum with two or more marginal asperities. Asperities on the pronotum always arranged in concentric rows, leading to a distinct summit. Sides of pronotum rounded, sometimes with a weakly visible carina extending slightly from the posterior edge. Elytra with scale-like interstrial bristles. Apex of elytra vertical. Proventriculus with a simple, short apical plate. Crop spines hair-like. An area of anteriorly pointing spine-shaped or spatula-shaped setae is present beyond the masticatory brush.

Male
Similar to females, except for a more produced anterior margin of the pronotum, typically with feather-like setae on the protarsi and two or more spines on the posteroventral margin of the seventh tergite. Penis apodemes much shorter than penis body, fused at apex. Tegmen open dorsally, much narrower than penis apodemes. Tegminal apodemes absent. Spiculum gastrale thicker than penis apodemes, with a fork. Basal sclerites sometimes visible. Sometimes large hook-like end plates are present.

Distribution
Asia, Europe, Africa, Caribbean (likely introduced), Australia (introduced).

Remarks
Nineteen species known. *Ernoporus* are most easily recognized by the stout appearance with concentric asperities on the pronotum, though a few members of *Eidophelus* also share this feature, as well as *Acorthylus* and *Neocryphus*. The tuft of setae posterior to the proventriculus has not been observed in any other Ernoporini, but is present in other genera such as *Acorthylus* and at least some *Stegomerus* species.

Several species were previously placed in the genus *Euptilius*, presented separately in Fig. 25. These are characterized by antennal club with profoundly procurved sutures and extensive split setae on the hypomeron. No fresh specimens were available for study and no genetic information exists. However, based on the external morphology as well as a dissection of the proventriculus, there was no justification for resurrecting this genus based on the information available (Wood 1980). All the characters which are distinctive are present in other *Ernoporus* species (procurved antennal sutures, split setae on the pronotum), although to a much lesser extent. Members of this species group have a very similar appearance to *Neocryphus*, but differ in the antennal club and the eye shape.

The genera *Ernocladius* and *Allothenemus* closely match the characters for this genus. *Ernocladius* was described as distinct from *Ernoporus* based on the interstrial ground vestiture being absent on the elytral disc and sparse or absent on the declivity, by the antennal funicle with only two segments, and by the procurved sutures of the antennal club (Wood 1980). This combination of characters is not consistent within the groups, and is not stable across other genera. *Allothenemus* was described based on the unique morphology compared to former Cryphalini from the Americas, but also matches the diagnostic characters of *Ernocladius* and closely matches some Asian species. It is likely that the species represent non-native species based on the distribution and the close similarity to *Margadillius minor* Schedl, 1942. *Erioschidias imitatrix* Schedl, 1977 is transferred from *Cosmoderes*, supported by internal and external morphology and molecular phylogenetics. Several species formerly in the genus *Margadillius* have been moved here. The previous misclassification is unsurprising, since a specimen in Schedl's collection (NHMW) labeled as a homeotype (which is usually specimen that was directly compared to and that matches the primary type) of *Margadillius margadilaonis*, was in fact a misidentified member of *Ernoporus*.

Type material examined
Holotype of *Euptilius armatus* Browne, 1981 (BMNH); holotype and paratype of *Ernoporus concentralis* Eggers, 1936 (BMNH); allotypes (x2) of *Cryphalus corpulentus* Sampson, 1919 (BMNH); holotype of *Erioschidias imitatrix* Schedl, 1977 (NHMW); holotype of *Ernoporus japonicus* Nobuchi, 1966 (ITLJ); syntypes (x2) of *Margadillius minor* Schedl, 1942 (NHMW and BMNH); holotype of *Margadillius parvulus* Eggers, 1943 (NHMW); paratype of *Euptilius thailandicus* Schedl, 1967 (NHMW); holotype of *Euptilius tuberculatus* Browne, 1981 (BMNH).

Included species
Ernoporus acanthopanaxi (Niisima, 1913: 4) (*Cryphalus*).
Ernoporus armatus (Browne, 1981: 129) (*Euptilius*).
Ernoporus concentralis Eggers, 1936c: 629.
Ernoporus corpulentus (Sampson, 1919: 113) (*Cryphalus*) **comb. nov.** [*Ernocladius*].
=*Margadillius corpulentus sundri* Schedl, 1969: 48 (syn: Wood, 1989).
Ernoporus dispar (Schedl, 1972f: 49) (*Cryphalops*).
Ernoporus exquisitus (Bright, 2019: 105) (*Allothenemus*) **comb. nov.** [*Allothenemus*].
Ernoporus guiboutiae (Schedl, 1957b: 53) (*Miocryphalus*) **comb. nov.** [*Ernocladius*].
Ernoporus imitatrix (Schedl, 1977c: 499) (*Erioschidias*) **comb. nov.** [*Cosmoderes*].
Ernoporus inermis (Schedl, 1939b: 343) (*Stephanorhopalus*).
Ernoporus japonicus Nobuchi, 1966b: 52.
Ernoporus melodori (Hopkins, 1915: 36) (*Stephanorhopalus*).
Ernoporus minor (Schedl, 1942a: 176) (*Margadillius*) **comb. nov.** [*Margadillius*].
Ernoporus minutus (Bright and Torres, 2006: 400) (*Allothenemus*) **comb. nov.** [*Allothenemus*].
Ernoporus parvulus (Eggers, 1943b: 75) (*Margadillius*) **comb. nov.** [*Margadillius*].
Ernoporus quadridens (Schedl, 1971a: 284) (*Cryphalops*).
Ernoporus shimanensis Murayama, 1953: 36.
Ernoporus thailandicus (Schedl, 1967a: 127) (*Euptilius*).
Ernoporus tiliae (Panzer, 1793: 14) (*Apate*).
=*Cryphalus ratzeburgi* Ferrari, 1867: 11.
=*Cryphalus lederi* Reitter, 1889: 93.
=*Ernoporus eggersi* Kurentsov, 1941: 155 (syn: Sokanovskiy, 1954).
=*Ernoporus starki* Eggers, 1942: 31 (syn: Schedl, 1952e).
Ernoporus tuberculatus (Browne, 1981: 128) (*Euptilius*).

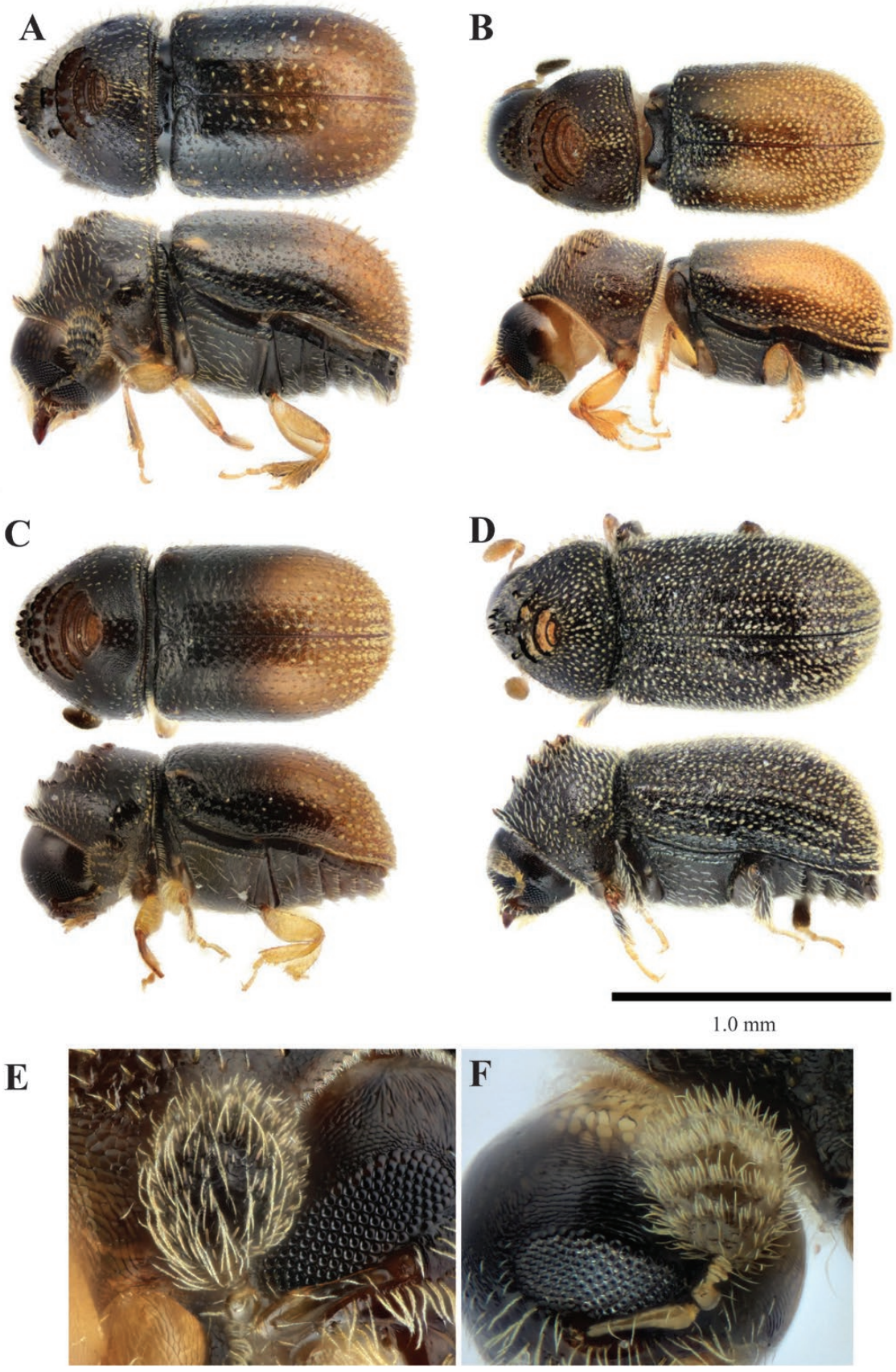

Figure 27. Images of *Ernoporus* spp.: Dorsal and lateral photos of A) *E. corpulentus*, B) *E. imitatrix*, C) *E. parvulus*, and D) *E. tiliae*. Eye and antennae of E) *E. imitatrix* and F) *E. parvulus*.

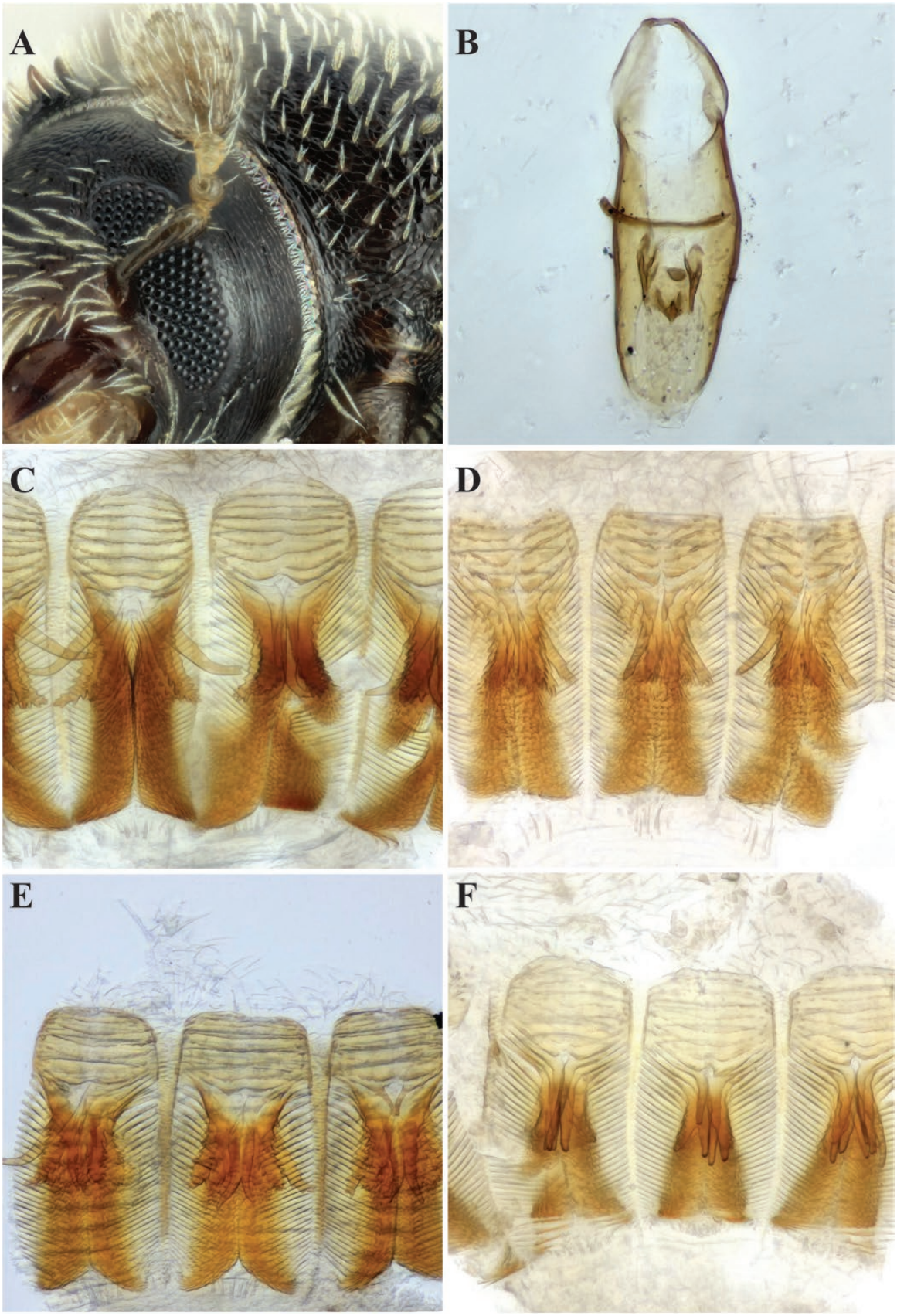

Figure 28. Images of *Ernoporus* spp.: A) *Ernoporus tiliae* showing eye and antennae, B) male genitalia of *E. imitatrix.* Proventriculus of C) *E. corpulentus,* D) *E. imitatrix,* E) *E. parvulus,* and F) *E. tiliae.*

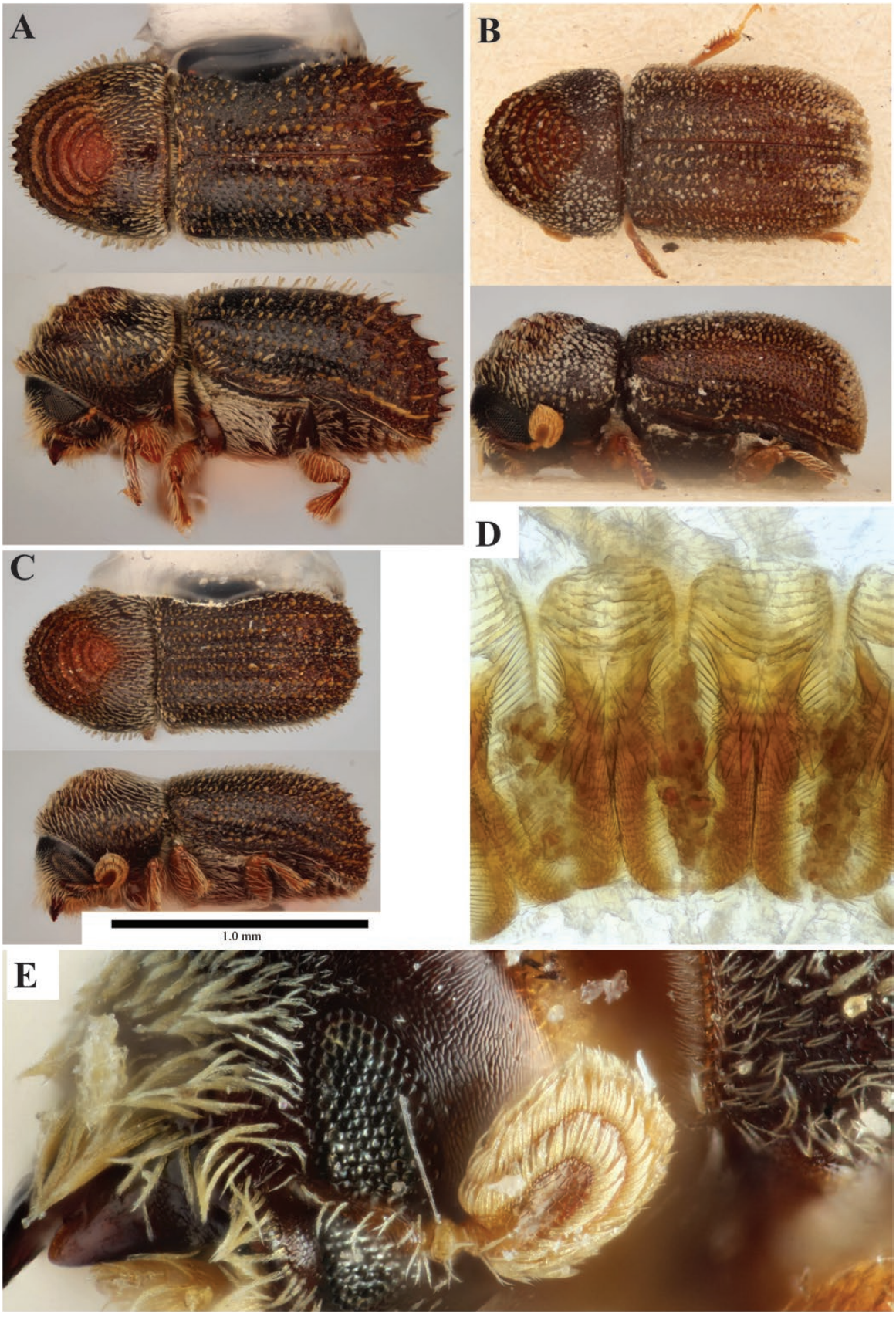

Figure 29. Images of *Ernoporus* spp.: Dorsal and lateral photographs of A) *E. armatus* (holotype), B) *E. concentralis* (lectotype), C) *E. tuberculatus* (holotype). Proventriculus of D) *E. concentralis*, E) eye and antennae of *E. concentralis*.

Hemicryphalus Schedl, 1963b: 264 (Fig. 30)

Type of genus

Eidophelus argutus Wood, 1960.

Diagnosis

Hemicryphalus can be diagnosed by the broadly emarginated, slightly tapered eye shape, by the straight or weakly procurved sutures on the antennal club, by the lateral margin of the pronotum which has a fine carina, and by the proventriculus which has clusters of long, giant spines.

Female

Eye broadly emarginated. Frons with abundant plumose setae. Antennal funicle 4-segmented. Antennae with straight or slightly procurved sutures, with an incomplete septum on both sides of the frist suture. Pronotum glossy. Pronotum with distinct raised line marking the lateral edge. Pronotum width slightly less than the elytra. Elytra with sparse vestiture. Under the elytra, the cuticle is poorly sclerotized, almost transparent. Proventriculus with short apical plate. Crop spines in bundles, not distributed with radial symmetry and is a mixture of hair-like and large sclerotized setae with multiple spines on its tip.

Male

Externally similar to female except with much less elaborate vestiture on the frons. Penis apodemes much shorter than penis body, fused at apex. Tegmen open dorsally, and of a similar thickness to penis apodemes. A very small median tegminal apodeme is present. Spiculum gastrale thicker than penis apodemes, with a fork. Basal sclerites visible.

Distribution

Pacific islands.

Remarks

Three species known. Superficially similar to some *Eidophelus* formerly in *Ernoporicus*, and in *Eidophelus* sensu Wood and Bright 1992, which can be distinguished by the antennae in *Hemicryphalus* having straight sutures with complete septa versus procurved sutures with or without a partial septum, by the eye shape being broadly emarginated instead of oval shaped, and most reliably by the proventriculus having clusters of large, rod-like crop spines instead of short, tooth-like crop spines.

Several species described in this genus from Borneo are transferred to Eidophelus, based on the procurved antennal sutures, overall shape and a close similarity to an undescribed species from montane Java, which is confirmed by molecular data and internal morphology to be nested among other *Eidophelus*.

Type material examined

Holotype *Eidophelus atomus* Wood 1960 (USNM); Two paratypes *Eidophelus argutus* Wood 1960 (USNM).

Included species

Hemicryphalus argutus (Wood, 1960: 33) (*Eidophelus*).
Hemicryphalus atomus (Wood, 1960: 34) (*Eidophelus*).
Hemicryphalus incomptus (Wood, 1960: 32) (*Eidophelus*).

Procryphalus Hopkins, 1915: 33 (Fig. 31)

Type of genus

Procryphalus populi Hopkins, 1915.

Diagnosis

Distinguished from other Ernoporini and former Cryphalini by the rounded lateral margins of the pronotum, by the eye oval, sometimes weakly emarginated, with the top half wider than the lower half, and by the proventriculus with clusters of giant spines.

Female

Elongate in appearance, at least 2.7 times as long as wide. Frons convex, slightly elongate. Eye oval, sometimes weakly emarginated, with the top half wider than the lower half. Antennae with four funicle segments. Antennal club with one complete septum, and an additional straight suture. Pronotum with marginal asperities, sometimes anteriorly projected. Pronotum constricted and narrower than elytra. Lateral margin of pronotum rounded. All species mature black with pale scales. Proventriculus with large, sclerotized crop spines in clusters just anterior to the anterior plate.

Male

Externally similar to female. Penis apodemes much shorter than penis body, fused at apex. Tegmen open dorsally, and of a similar thickness to penis apodemes. A very small median tegminal apodeme is present. Spiculum gastrale thicker than penis apodemes, with a fork. Basal sclerites visible. Genitalia very similar to *Hemicryphalus*.

Distribution

Holarctic, with one additional species from tropical Southeast Asia (Thailand).

Remarks

Four species known. Externally very similar to some species of *Eidophelus*, distinguished only by the antennae, by the rounded lateral margin of the pronotum, and by the proventriculus which has clusters of large long spines compared to sclerotized contiguous short spines in *Eidophelus*. The recent transfer of *Dryocoetiops petioli* to *Procryphalus* (Beaver et al. 2019) is supported by several multi-gene phylogenies (Jordal and Cognato 2012, Pistone et al. 2018) and the similar aedeagus and proventriculus (short apical plate with clusters of long crop spines). Very similar and dubiously distinct from *Hemicryphalus*, but available molecular data did not support the morphological similarity.

Type material examined

Holotype *Cryphalus mucronatus* LeConte, 1879 (MCZ); 'Cotype' *Ernoporus fraxini* Berger, 1917 (NHMW).

Included species

Procryphalus fraxini (Berger, 1917: 238) (*Ernoporus*).
Procryphalus mucronatus (LeConte, 1879: 518) (*Cryphalus*).
=*Procryphalus idahoensis* Hopkins, 1915: 34 (syn: Wood, 1954).
=*Procryphalus populi* Hopkins, 1915: 34 (syn: Wood, 1954).
Procryphalus petioli (Beaver, 1990: 281) (*Dryocoetiops*)
Procryphalus utahensis Hopkins, 1915: 33.
=*Procryphalus aceris* Hopkins, 1915: 33 (syn: Wood, 1954).
=*Procryphalus salicis* Hopkins, 1915: 33 (syn: Wood, 1954).

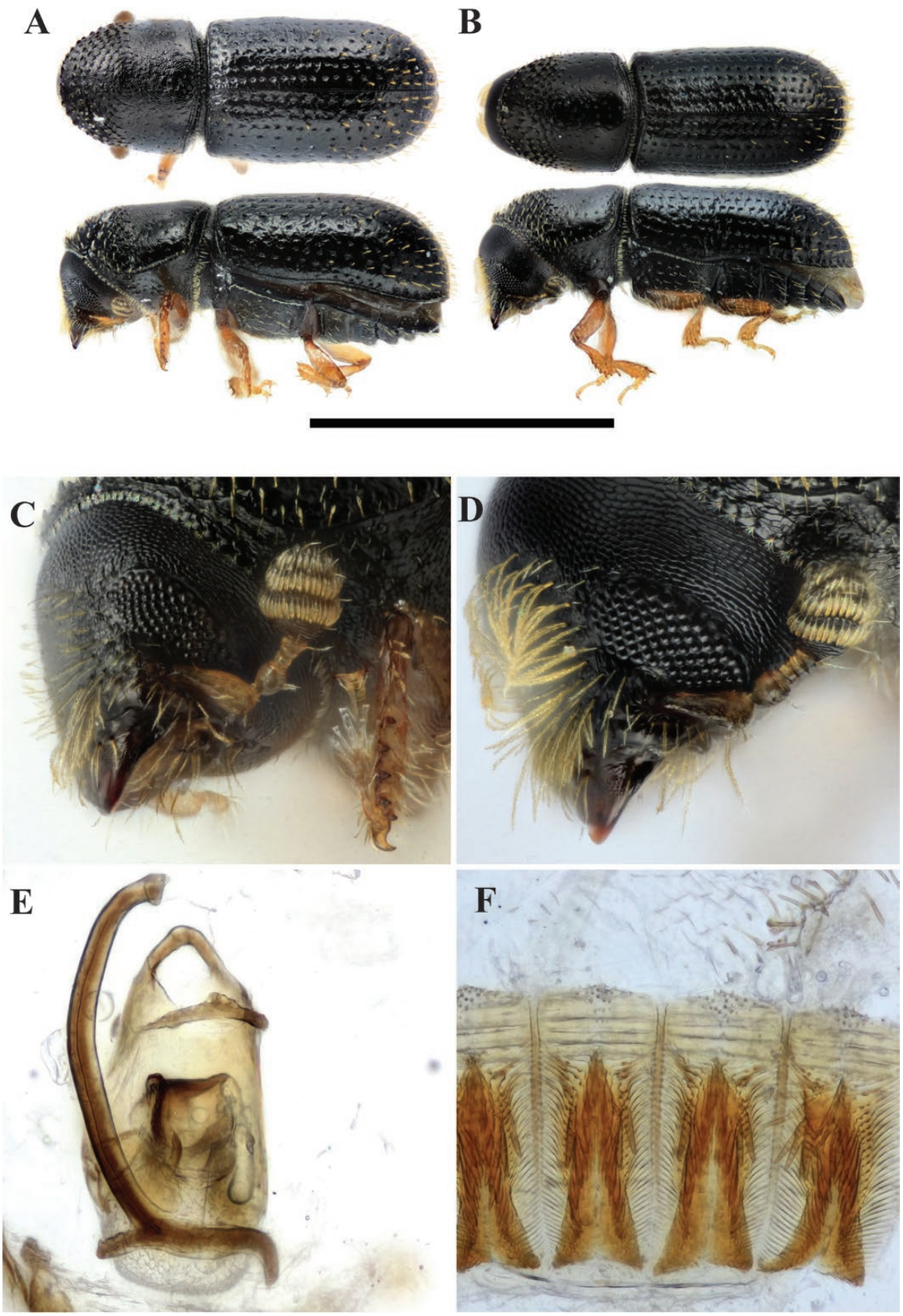

Figure 30. Images of *Hemicryphalus argutus*: Dorsal and lateral photographs of A) male and B) female, eye, and antennae of A) male and B) female, E) aedeagus, and F) proventriculus.

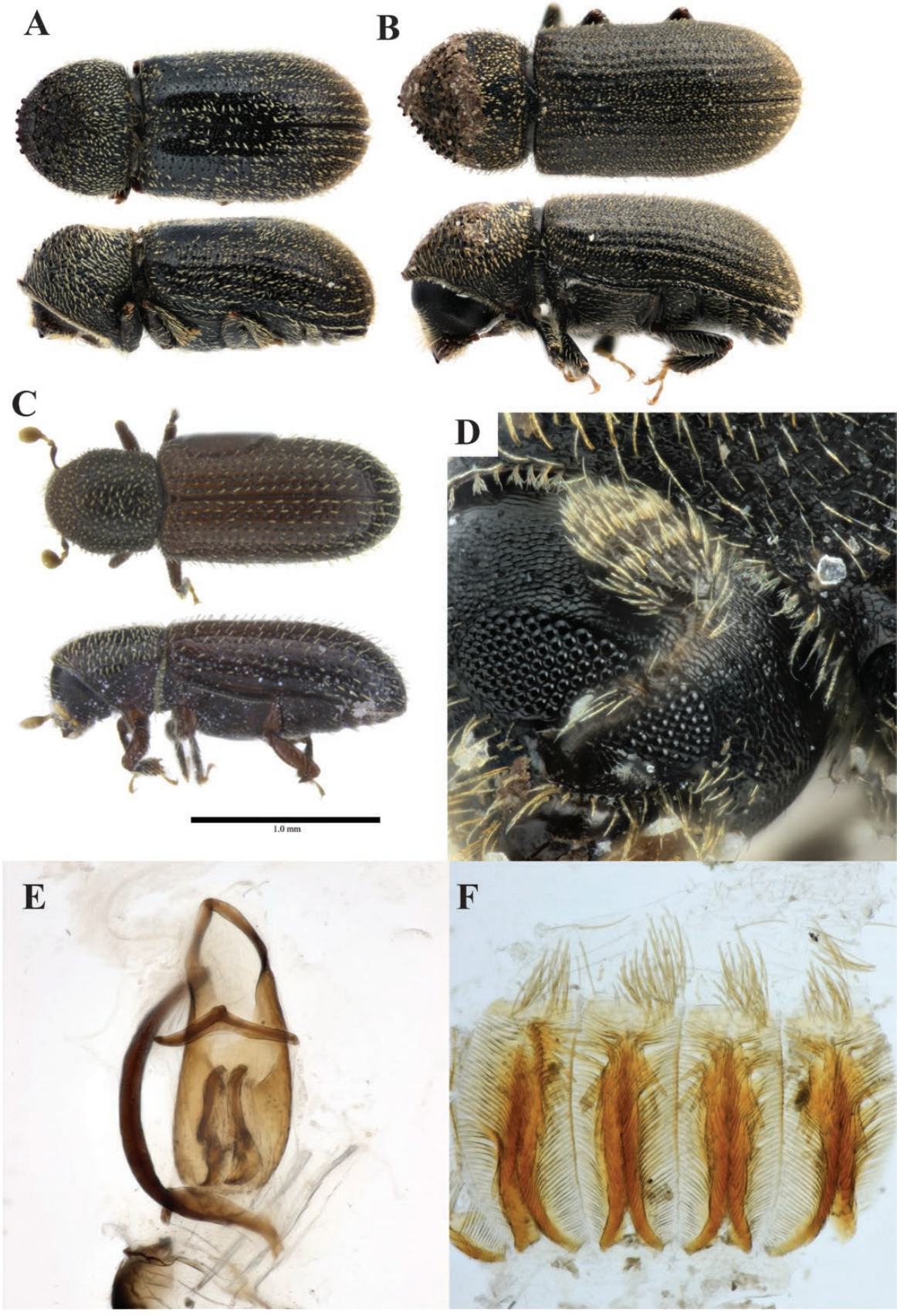

Figure 31. Images of *Procryphalus* spp.: Dorsal and lateral photographs of A) *P. fraxini*, B) *P. mucronatus*, C) *P. petioli*, D) eye and antennae of *P. mucronatus*, E) male genitalia of *P. mucronatus*, F) proventriculus of *P. mucronatus*.

Corthylini LeConte, 1876

Type of tribe
Corthylus Erichson, 1836.

Distribution
Most genera and species are only known from the Americas.

Remarks
Corthylini is one of the most diverse tribes in terms of number of genera and species. Some former Cryphalini are transferred, but a full review of the taxonomy, the diagnostic characters and generic limits are beyond the scope of this study.

Genera transferred from Cryphalini
Acorthylus Brèthes, 1922; *Cryptocarenus* Eggers, 1937; *Neocryphus* Nunberg, 1956; *Stegomerus* Wood, 1967.

Acorthylus Brèthes, 1922: 304 (Fig. 32)

Synonymy
=*Phacrylus* Schedl, 1938d: 24.

Type of genus
Acorthylus asperatus Brèthes, 1922.

Diagnosis
This genus can be diagnosed from all other Scolytinae by the unique second funicle segment which is much larger than the first.

Female
Eye long and broadly emarginated. Antennae with an enlarged second funicle segment. Antennal club large, with two sutures, septate on both sides, approximately symmetrical. Pronotum with a distinct summit. Asperities on the anterior margin present. Asperities on the pronotal declivity are arranged in concentric giving an obtuse arc-shaped area of asperities. Dorsolateral margin of pronotum rounded. Hypomeron with extensive bifurcating setae. Elytra convex, without any distinct sculpturing.

Male
Similar to female. Aedeagus not examined.

Distribution
South America.

Remarks
Six species known. Although this was not confirmed with any molecular data, this genus is transferred based on the broadly emarginated eye, the bisulcate declivity, but the apical plate of the proventriculus which is wide open, and by the similarity of this genus to *Stegomerus* which has been confirmed by molecular data to be Corthylini.

Type material examined
Lectotype of *Phacrylus bosqi* Schedl, 1938 (NHMW); holotype of *Acorthylus frontalis* Wood, 2007 (USNM); paratype of *Phacrylus pruni* Wood, 1971 (USNM).

Included species
Acorthylus asperatus Brèthes, 1922: 305.
Acorthylus bosqi (Schedl, 1938d: 24) (*Phacrylus*).
=*Ernoporus squamulosus* Eggers, 1943a: 356 (syn: Schedl, 1964d).
Acorthylus frontalis Wood, 2007: 485.
Acorthylus gracilis (Schedl, 1972d: 58) (*Phacrylus*).
Acorthylus pruni (Wood, 1971: 33) (*Phacrylus*).
Acorthylus robustus (Schedl, 1952a: 453) (*Phacrylus*).

Cryptocarenus Eggers, 1937: 79 (Fig. 33)

Synonymy
=*Cryptocarenus* Eggers, 1933a: 10 (unavailable name).
=*Tachyderes* Blackman, 1943: 35.

Type of genus
Cryptocarenus diadematus Eggers, 1937.

Diagnosis
Cryptocarenus can be diagnosed from other Scolytinae by the combination of a broadly emarginated eye, metatibiae with spines only on the distal end (as in *Hypothenemus*), and an oblique groove instead of a spine or callus below the base of the elytra, and by the dwarfed, flightless males.

Female
Eye long and broadly emarginated. Antennae with five funicle segments. Antennal club flattened, rounded, with three sutures, the first segment sometimes completely septate. Pronotum with 6–14 marginal asperities, and many more on the pronotal declivity. Lateral margins of pronotum with a clearly visible carina. Elytra broadly convex, slightly bisulcate on the declivity. Vestiture sparse in most species, typically with spatulate interstrial bristles and barely visible strial setae. Metatibia with denticles only on the apex. Proventriculus with many lateral spines on apical plate, and backward pointing spines posterior to the proventriculus.

Male
Similar to female, but often much smaller, with reduced eyes, and flightless. Aedeagus not examined.

Distribution
Eastern North America, tropical areas of North and South America, Africa (introduced).

Remarks
16 species known. This genus is transferred from Cryphalini based on molecular data (Gohli et al. 2017, Johnson et al. 2018, Pistone et al. 2018), as well as characters such as an oblique groove instead of a spine or callus below the base of the elytra.

Phylogenetically, it appears to be nested within *Araptus* and/or sister to *Dacnophthorus*. Very few members of *Araptus* were included in the analyses, so it would be inappropriate to make any further changes before a more thorough review of this genus and related genera.

Type material examined
Holotype of *Cryptocarenus amazonicus* Wood, 2007 (USNM); holotype of *Cryptocarenus barinensis* Wood, 2007 (USNM); paratype of *Cryptocarenus brevicollis* Eggers, 1937 (USNM); holotype of *Cryptocarenus coronatus* Wood, 1971 (USNM); holotype of *Cryptocarenus frontalis* Wood, 2007 (USNM); holotype of *Cryptocarenus lepidus* Wood, 1971 (USNM); holotype of *Cryptocarenus pubescens* Wood, 1986 (USNM); holotype of *Cryptocarenus spatulatus* Wood, 1986 (USNM); holotype of *Cryptocarenus tropicalis* Wood, 2007 (USNM).

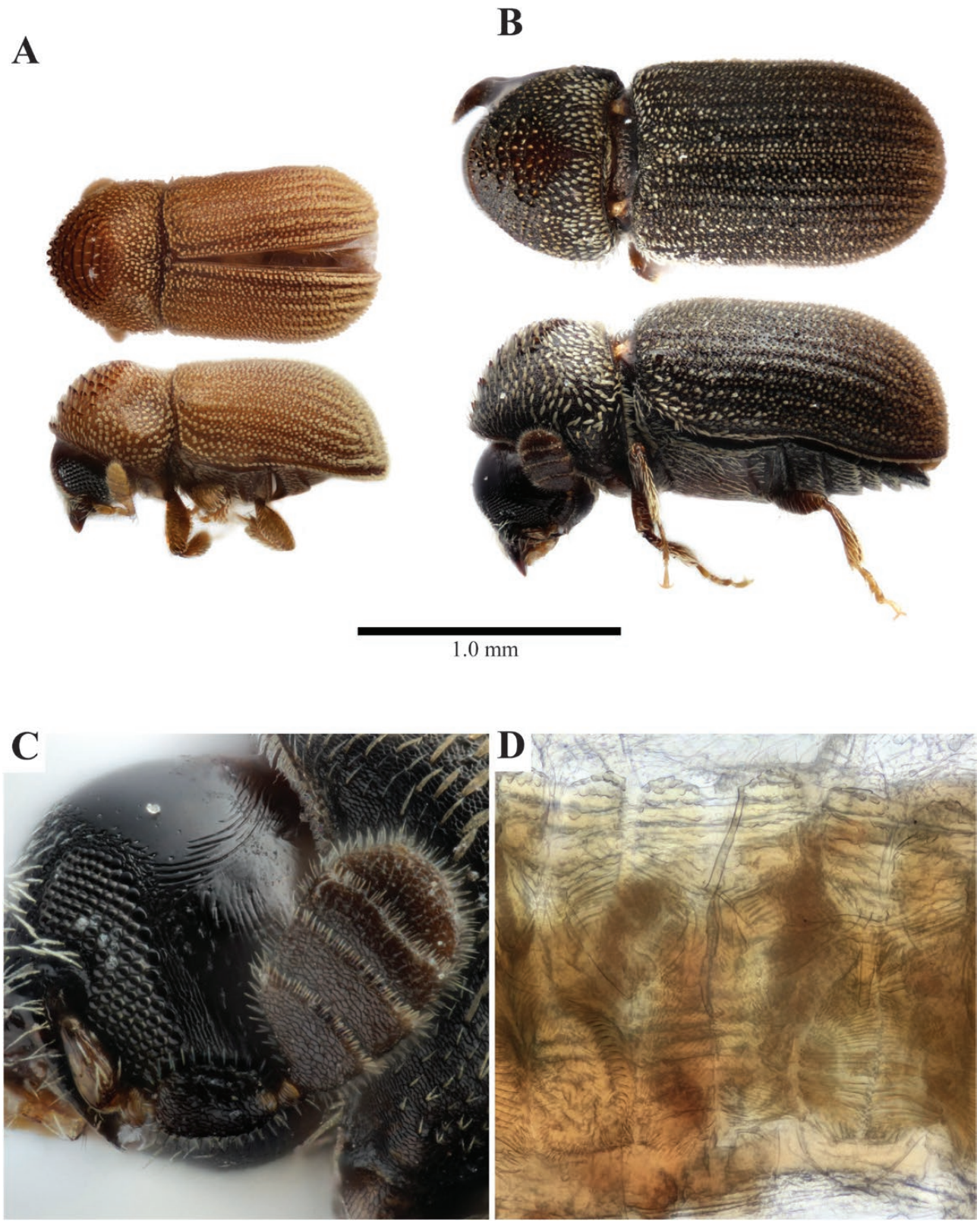

Figure 32. Images of *Acorthylus* spp.: Dorsal and lateral photos of A) *A. gracilis*, B) *A. pruni*. Eye and antennae of C) *A. pruni*, and proventriculus of D) *A. pruni*.

Included species

Cryptocarenus amazonicus Wood, 2007: 492.
Cryptocarenus barinensis Wood, 2007: 496.
Cryptocarenus beaveri Wood, 2007: 495.
Cryptocarenus brevicollis Eggers, 1937: 81.
=*Cryptocarenus coronatus* Wood, 1971: 36.
Cryptocarenus diadematus Eggers, 1937: 80.
Cryptocarenus frontalis Wood, 2007: 495.
Cryptocarenus harringtoni (Blackman, 1943: 38) (*Tachyderes*).
Cryptocarenus heveae (Hagedorn, 1912a: 338) (*Stephanoderes*).

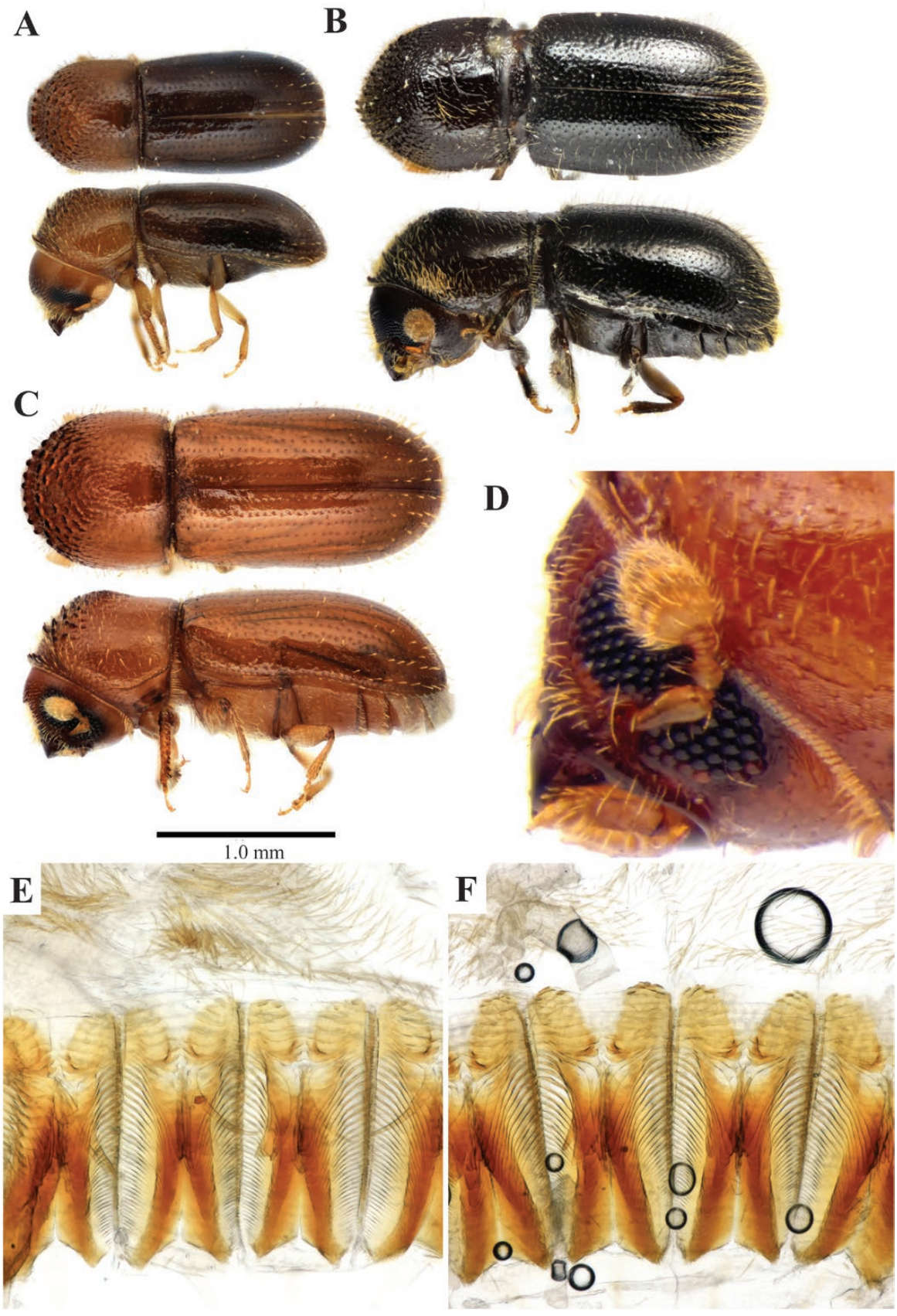

Figure 33. Images of *Cryptocarenus* spp. Dorsal and lateral photographs of A) *C. heveae*, B) *C. pubescens* and C) *C. seriatus*, D) eye and antennae of *C. seriatus*, proventriculus of E) *C. heveae* and F) *C. seriatus*.

=*Stephanoderes caraibicus* Eggers, 1937: 82 (syn: Wood, 1975b).
=*Stephanoderes punctifrons* Schedl, 1939a: 410 (syn: del Río, Lanteri and Suárez, 2005).
=*Tachyderes parvus* Blackman, 1943: 36 (syn: Wood, 1962).
=*Miocryphalus brasiliensis* Schedl, 1951e: 96 (syn: Wood, 2007).
=*Stephanoderes porosus* Wood, 1954: 1014 (syn: Wood, 1957b).
=*Stephanoderes acaciae* Schedl, 1958c: 45 (syn: Wood, 2007).
Cryptocarenus laevigatus (Blandford, 1904: 230) (*Hypothenemus*).
Cryptocarenus lepidus Wood, 1971: 36.
Cryptocarenus pilosus Eggers, 1937: 81.
Cryptocarenus pubescens Wood, 1986b: 271.
Cryptocarenus pygmaeus Schedl, 1965c: 370.
Cryptocarenus seriatus Eggers, 1933a: 10.
=*Cryptocarenus adustus* Eggers, 1933a: 11 (syn: Wood, 1972a).
=*Tachyderes floridensis* Blackman, 1943: 36 (syn: Schedl, 1962d).
=*Cryptocarenus bolivianus* Eggers, 1943a: 356 (syn: Wood, 1975a).
Cryptocarenus spatulatus Wood, 1986b: 272.
Cryptocarenus tropicalis Wood, 2007: 491.

Neocryphus Nunberg, 1956a: 139 (Fig. 34)

Type of genus
Neocryphus argentinensis Nunberg, 1956.

Diagnosis
This genus can be diagnosed by the combination of a broadly emarginated eye, antennae with a second funicle segment smaller than the first, and a large antennal club.

Female
Eye long and broadly emarginated. Frons with an arc-shaped transverse carina at upper level of eyes, lined with scale-like setae. Cuticle above and behind eye striate. Antennae with four funicle segments. Antennal club large, with three slightly procurved sutures. Pronotum with two marginal asperities, and pronotal asperities in approximately concentric rows. Pronotum and hypomeron covered in extensive scale-like and bifurcating setae. Elytra with extensive scale-like setae. Declivity with deeply impressed striae and raised interstriae.

Male
Presumably similar to female.

Distribution
South America.

Remarks
Monotypic. This genus is transferred to Corthylini based on the eye shape and the bisulcate declivity. This genus is dubiously distinct from *Acorthylus* and *Stegomerus* based on antennal characters. No material was available for dissection or molecular analyses, so there is insufficient evidence to warrant taxonomic changes. Distinguished from *Acorthylus* based on the second funicle segment, which is a similar size to the third.

The observed specimen has a unique morphology of the protibiae; the mucro extends approximately a third of the length of the rest of the protibia, and appears to widen at its tip. This structure has not been described from Cryphalini or any Scolytinae. It is potentially a sexually dimorphic character, although only one individual of an unknown sex was studied.

There is a remarkable similarity between this genus and some members of *Ernoporus*, which have very similar sculpturing on the pronotum and elytra, and very similar vestiture. The two genera can be distinguished by the eye shape and the antennal club.

Type material examined
None.

Included species
Neocryphus argentinensis Nunberg, 1956a: 141.
=*Phacrylus cristatus* Schedl, 1979a: 61 (syn: Wood, 2007).

Stegomerus Wood, 1967: 129 (Fig. 35)

Type of genus
Stegomerus vulgaris Wood, 1967.

Diagnosis
Stegomerus can be diagnosed by the short, almost spherical antennal scape, the antennal club, which is mostly symmetrical and with one or two visible procurved sutures, by the rounded lateral margin of the pronotum with bifurcating setae on the hypomeron, and the broadly divided apical plate of the proventriculus.

Female
Eye long and broadly emarginated. Frons simple and convex. Antennal scape short, almost spherical. Antennae with five funicle segments. Antennal club with procurved sutures. Lateral margins of pronotum rounded. Hypomeron with bifurcating setae. Proventriculus with open median suture in the apical plate. Crop spines stout. A cluster of spines is present on the posterior side of the proventriculus.

Male
No obvious external differences from the female. Aedeagus not examined.

Distribution
Central America, South America.

Remarks
Nine species known. We transfer *Cryphalomorphus parvatis* Wood, 1974 from *Eidophelus* based on the diagnostic characters above. The species may be conspecific with *Stegomerus pygmaeus* Wood, 1967.

Type material examined
Holotype and paratype of *Stegomerus chiriquensis* Wood, 1967 (USNM); paratype of *Stegomerus mexicanus* Wood, 1967 (USNM); holotype and paratype of *Stegomerus mirandus* Wood, 1971 (USNM); holotype and paratype of *Stegomerus montanus* Wood, 1967 (USNM); holotype and paratype of *Cryphalomorphus parvatis* Wood, 1974 (USNM); holotype of *Stegomerus pygmaeus* Wood, 1967 (USNM); holotype and paratype of *Stegomerus vulgaris* Wood, 1967 (USNM).

Included species
Stegomerus chiriquensis Wood, 1967: 131.
Stegomerus diversus Bright, 2019: 181.

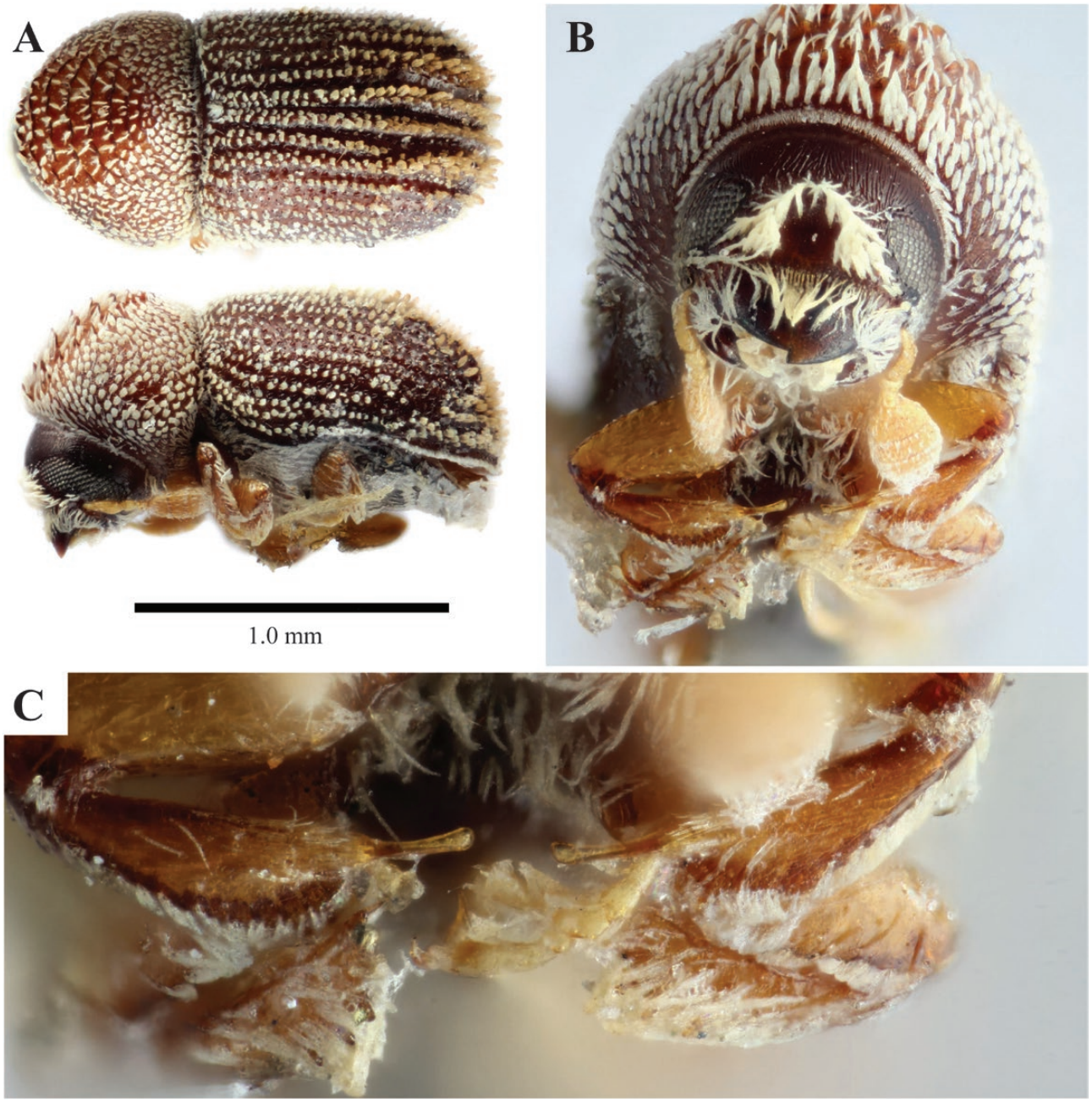

Figure 34. Images of *Neocryphus argentinensis*. A) Dorsal and lateral photographs. B) Frontal view. C) Photograph of protibial showing unusual projection at the apex.

Stegomerus longipennis Wood, 2007: 482.
Stegomerus mexicanus Wood, 1967 133.
Stegomerus mirandus Wood, 1971: 32.
Stegomerus montanus Wood, 1967: 132.
Stegomerus parvatis (Wood, 1974a: 17) (*Cryphalomorphus*) **comb. nov.** [*Scolytogenes*].
Stegomerus pygmaeus Wood, 1967: 130.
Stegomerus vulgaris Wood, 1967: 134.

Trypolepis Bright, 2019: 182

Type of genus
Trypolepis antillica Bright, 2019.

Diagnosis
This genus can be diagnosed from the similar *Acorthylus* and *Neocryphus* by the antenna, which has only two funicle segments, with the first (pedicel) of a similar size to the second, and from the superficially similar *Ernoporus* by the broadly emarginated eye.

Female
Eye broadly emarginated. Antennae with two funicle segments (including pedicel) of a similar size. Antennal club large, flat, with a single suture. Frons with a weakly concave region above epistoma. Pronotum with two asperities just behind margin, plus asperities in

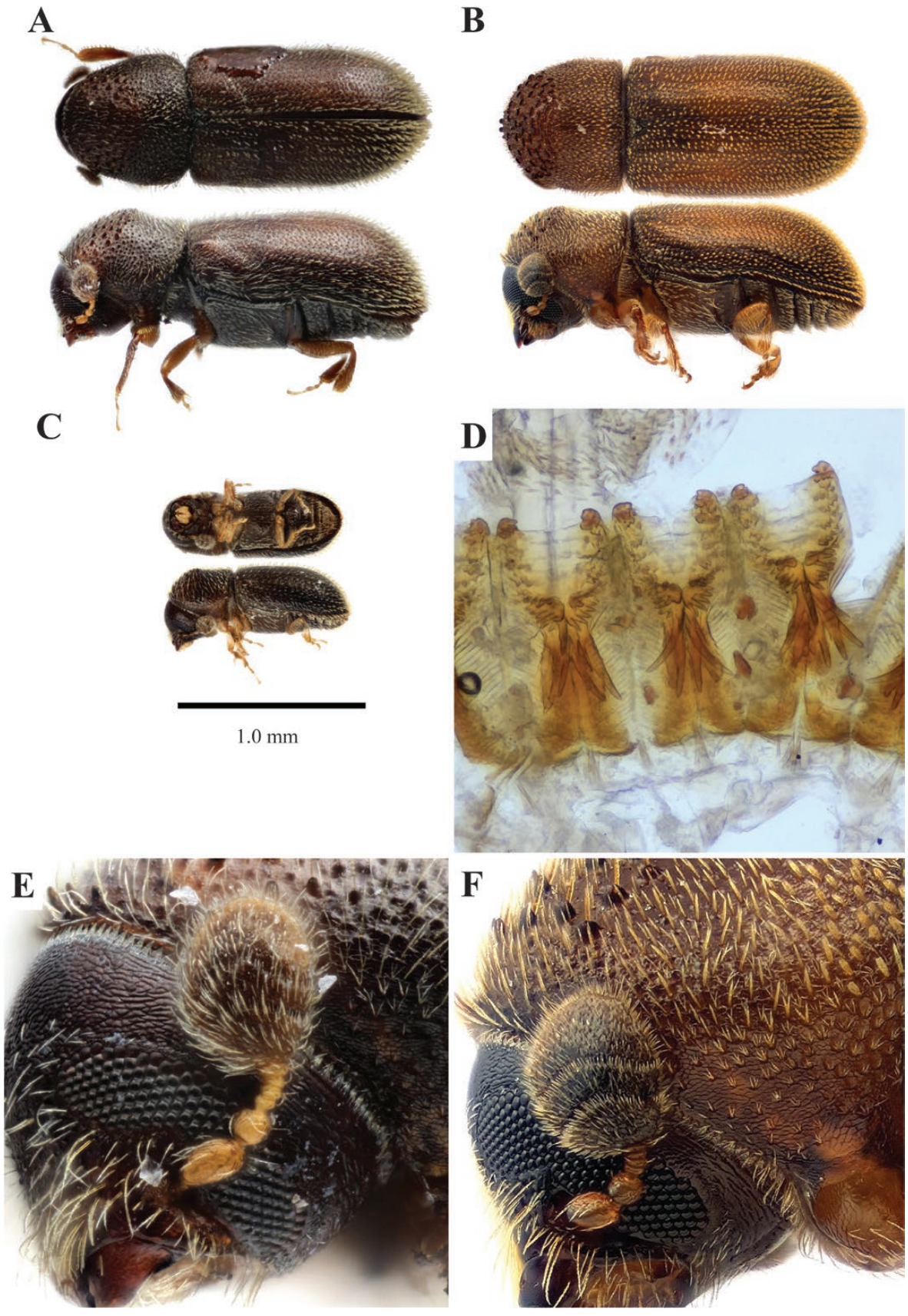

Figure 35. Images of *Stegomerus* spp.: Dorsal and lateral photographs of A) *S. montanus*, B) *S. vulgaris*, C) Ventral and lateral photograph of *S. pygmaeus*, D) Proventriculus of *S. pygmaeus*, eye, and antennae of E) *S. montanus*, and F) *S. vulgaris*.

concentric rows on pronotal slope. Pronotal summit distinct. Declivity vertical at the apex.

Male
Unknown.

Distribution
Grenada (West Indies).

Remarks
Monotypic. This species was described during the later stages of the preparation of this manuscript. Based on the description and the photos, it is clearly very similar to *Acorthylus* and *Neocryphus*, differing only by the antennal funicle.

Type material examined
Photo of holotype of *Trypolepis antillica* Bright, 2019.

Included species
Trypolepis antillica Bright, 2019: 182.

Remarks: The original spelling, *antillicum*, is corrected to be feminine to match the gender of the genus.

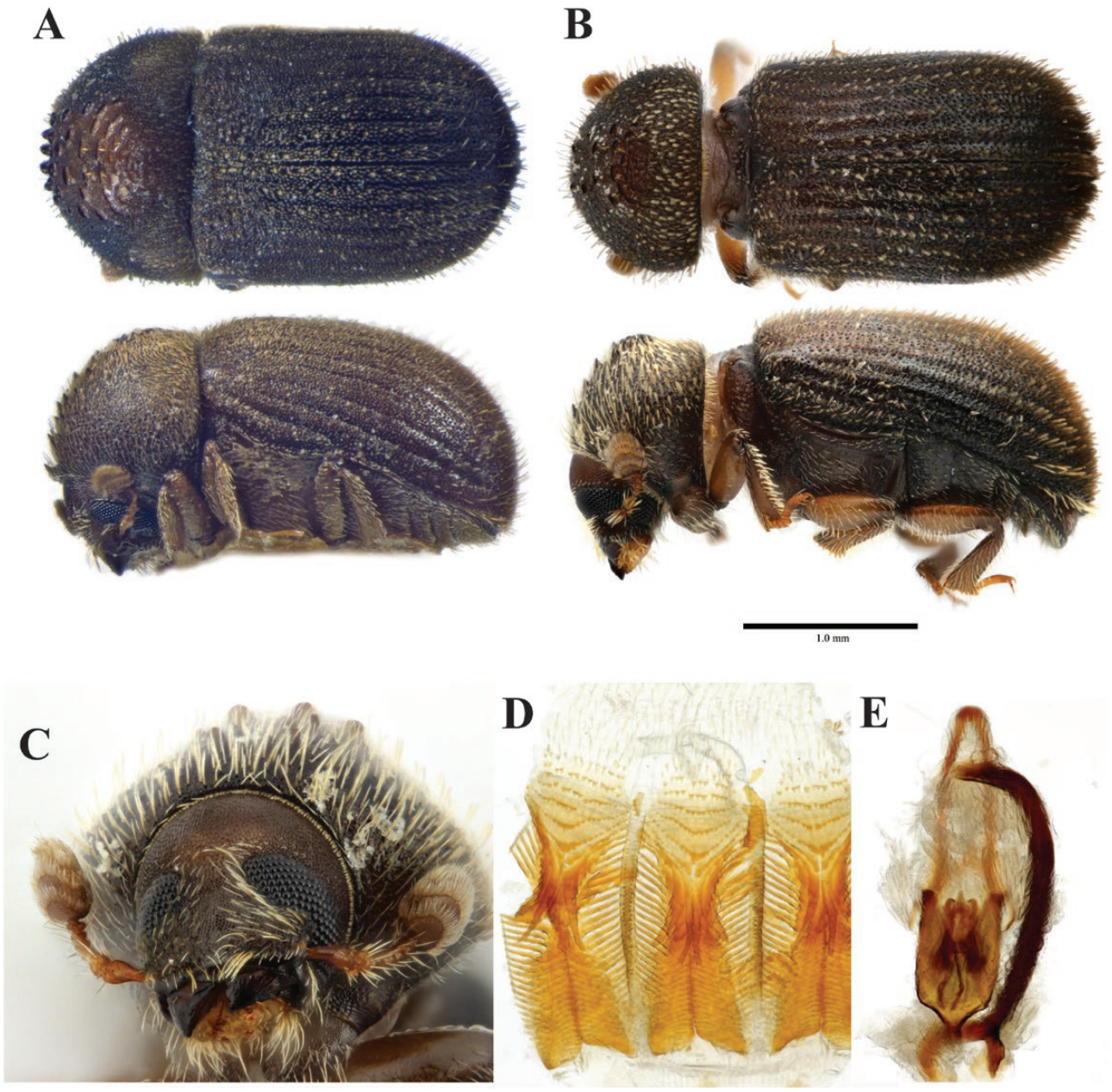

Figure 36. Images of *Stephanopodius* spp.: Dorsal and lateral photographs of A) *Stephanopodius ghanaensis*, B) *S. dubiosus*; C) head of *S. dubiosus*; D) proventriculus of *S. dubiosus*, and E) aedeagus of *S. dubiosus*.

Xyloctonini Eichhoff, 1878b

Type of tribe
Xyloctonus Eichhoff, 1872a.

Distribution
Africa, Southeast Asia and Oceania.

Genera transferred from Cryphalini
Stephanopodius Schedl, 1963

Stephanopodius Schedl, 1963a: 633 (Fig. 36)

Synonymy
=*Stephanopodius* Schedl, 1941a: 396 (unavailable name).
=*Cryphalomimus* Browne, 1962b: 75 (permanently invalid primary homonym).
=*Cryphalomimetes* Browne, 1963a: 242.
=*Cryphalmomimetes* Wood, 1980: 95 (unavailable name).

Type of genus
Stephanoderes dispar Eggers, 1936.

Diagnosis
Stephanopodius can be distinguished by the pronotum strongly arched, laterally inflated and rounded, with very rough asperities near the summit, by the antennal club nearly segmented, with two or three distinct sutures or grooves marked by thick, plumose setae, and by the metatibiae with lateral edge angulate and denticles only on apical margin, and by the bilobed third tarsi.

Female
Frons sexually dimorphic, male variously impressed with short erect setae, female frons convex. Eyes elongated, broadly sinuate on anterior margin. Antennal club with two or three distinct sutures or grooves marked by thick, plumose setae or bundles of fine setae. Funicle 5-segmented. Pronotum strongly arched, with very rough asperities, concentric on summit appearing cup-like; males usually without marginal asperities. Elytra densely setose, with dense ground vestiture of scale-like setae and longer hair-like or more commonly scale-like interstrial setae. Procoxae contiguous. Metatibiae, sometimes also other tibiae, with lateral edge near apex angular, with denticles restricted to apical margin. Third tarsal segment bilobed.

Proventriculus with short apical plate, with rows of granules. Crop spines hair like. Tuft of spatulate setae posterior to the proventriculus.

Male
Similar to female. Penis apodemes fused at apex. Spiculum gastrale much thicker and more sclerotized than penis apodemes, with a fork.

Distribution
Sub-Saharan Africa.

Remarks
Seven species known. The relationship between this genus and the Xyloctonini genus *Glostatus* Schedl has been suggested by Pistone et al. (2018) based on molecular data. Most species are likely nested among or near *Glostatus*. A revision of the two genera is in progress by BHJ. The placement of *Glostatus* and *Stephanopodius* within Xyloctonini is not congruent with molecular phylogenies.

Type material examined
Paratype of *Stephanoderes dispar* Eggers, 1936 (BMNH); holotype and paratype of *Hypocryphalus dubiosus* Schedl, 1970 (SANC).

Included species
Stephanopodius dispar (Eggers, 1936b: 35) (*Stephanoderes*).
Stephanopodius dubiosus (Schedl, 1970d: 117) (*Hypocryphalus*) **comb. nov.** [*Hypocryphalus*].
Stephanopodius ghanaensis (Schedl, 1962b: 66) (*Hypocryphalus*).
Stephanopodius giganteus Schedl, 1950a: 26.
Stephanopodius mkulumusius (Eggers, 1919: 241) (*Stephanoderes*).
Stephanopodius squamosus Nunberg, 1973: 9.
Stephanopodius usambaricus Schedl, 1941a: 396.

Key to Genera of Former Cryphalini and Xyloterini

This key is made with the diagnostic characters to enable identification of the tribes Coriacephilini, Cryphalini, Trypophloini, Xyloteini, or Ernoporini. Corthylini genera are not included since a thorough review of the tribe would be needed to accurately place the genera in a key. *Atomothenemus* Bright, 2019, *Microsomus* Bright, 2019, and *Pygmaeoborus* Bright, 2019, all from the West Indies, were described during the final preparation of the manuscript and not included in this key.

1a. Eye emarginated (with exceptions for some specimens <1.0 mm) or divided. Lower part of elytral declivity usually sloping. Mesocoxae usually narrowly separated similar to metacoxae, or contiguous. Postnotum separated from metathorax by a continuous membrane. Aedeagus with separated (rarely weakly fused) penis apodemes, typically as long as or longer than penis body **2**

1b. Eye oval (with exceptions of specimens with proportionally large eyes, and *Procryphalus* and *Hemicryphalus*, have long, broadly emarginated eyes). Lower part of elytral declivity usually vertical. Mesocoxae usually more widely separated than metacoxae. Postnotum fused to metathorax. Aedeagus with fused penis apodemes that are much shorter than penis body. (Ernoporini) **12**

2a. Eye completely divided. Females with a visible mycangium on the hypomeron. Males sometimes with a barely declivous pronotum or flattened pronotal margin. (Xyloterini) **10**

2b. Eye emarginated (rarely oval). No mycangium on hypomeron of females **3**

3a. Third tarsal segment bilobed. Lateral margins of pronotum always with carina along dorsolateral margin. Split setae on hypomeron usually present. Interstrial ground vestiture usually dense. Antennae always with sutures (which can be recurved or procurved). Body generally rounded. (Cryphalini) ..... ***Cryphalus***

3b. Third tarsal segment cylindrical. Lateral margin of pronotum with or without carina along dorsolateral margin. Hypomeron without, or rarely with very few bifurcating setae. Interstrial ground vestiture usually sparse, especially on elytral disc. Antennae with or without sutures. Body usually more elongated **4**

4a. Eye deeply emarginated. Antennal club with procurved sutures and a complete septum along the first suture. Lateral margins of pronotum rounded or with weak carina and hypomeron with bifurcating setae. Interstrial ground vestiture hair-like. Distributed only in Asia (rarely collected). (Coriacephilini) ..... ***Coriacephilus***

4b. Not in combination as described above. (Trypophloeini).....**5**

5a. Lateral margins of pronotum always rounded. Antennal club cone-like with horizontal sutures and elongate, with a pointed apex. Distributed in temperate climates in hosts including *Salix*, *Populus* or *Alnus*. Proventriculus with short apical plate, less than one fifth of the sclerotized part .....***Trypophloeus***

5b. Lateral margins of pronotum rounded or with carina. Antennal club flattened, with or without sutures, usually transverse or procurved, apex rounded. Various hosts, widespread distribution, in tropical to temperate areas. Proventriculus with apical plate much more than one fifth of total length (except not sclerotized in *Macrocryphalus*).....**6**

6a. Lateral margins of pronotum rounded. Antennal funicle always with five segments. Antennal club shape tapered proximally, with a weakly visible procurved suture. Elytra covered in hair-like interstrial ground vestiture. Striae not apparent. Proventriculus not sclerotized.....***Macrocryphalus***

6b. Lateral margins of pronotum with carina. Antennal funicle with 2–5 segments. Antennal club shape and sutures variable. Elytra interstrial ground vestiture variable. Striae usually visible (except some *Afrocosmoderes*). Proventriculus fully sclerotized **7**

7a. Mesocoxae contiguous. Body shape elongate, more than 2.3x as long as wide. Antennae always with 2–3 funicular segments, with the first segment longer than the subsequent funicle segments combined. Antennal club flat and without sutures..... ***Cosmoderes***

7b. Mesocoxae narrowly separated. Body shape stout to elongate. Antennae with 3–5 funicle segments. Antennal club flat, with or without sutures or septum.....**8**

8a. Antennal club without sutures or weakly visible procurved sutures. Metatibia with denticles covering at least apical quarter, pointing outwards and distally ..... ***Afrocosmoderes***

8b. Antennal club usually with straight or slightly procurved sutures and a partial septum (rare exceptions are known). Metatibia with denticles restricted to apex, usually pointed distally.....**9**

9a. Antennal club with three sutures and usually a partial septum. Pronotum with marginal asperities. Males smaller, with vestigial wings, and with eyes much smaller than females .....***Hypothenemus***

9b. Antennal club with one transverse suture and one barely visible procurved suture near apex. Pronotum with no marginal asperities. Males of a similar size, with fully developed wings and with eyes similar to females ..... ***Microcosmoderes***

10a. Antennal suture (indicated by differences in vestiture) acutely procurved. Males with distinctly flattened frons and dorsally subquadrate to quadrate pronotum. Tegmen with median apodeme..... ***Trypodendron***

10b. Antennal suture (indicated by differences in vestiture) broadly procurved. Males with flat or convex frons, and pronotum dorsally rounded. Tegmen without median apodeme.....**11**

11a. Antennal club uniformly pubescent to base. Male and female of a similar size. Females with longest axis of mycangia either vertical (dorso-ventrally) or horizontal (antero-posteriorly) .....***Indocryphalus***

11b. Antennal club with basal area corneous. Male distinctly smaller than female. Females with longest axis of mycangia horizontal (antero-posteriorly) .....***Xyloterinus***

12a. Stout, less than 2.2x as long as wide. Pronotum with distinct summit, asperities in irregular concentric rows. Lateral margins of pronotum rounded, at most with a small carina along the posterior edge. Setae on hypomeron divided in some species. Proventriculus crop with thin spines, no enlarged crop spines or multidentate spines. Proventriculus posterior to the masticatory brush with a tuft of spatulate setae ... ***Ernoporus***

12b. Proportions variable. Pronotal summit variable, asperities may occur in irregular concentric rows or scattered. Pronotum with carina along dorsolateral edge (except *Procryphalus*, which has longer body proportions). Setae on hypomeron always hair-like (if present). Proventriculus crop with enlarged clusters of crop spines or multidentate spines. Proventriculus posterior to the masticatory brush smooth, without a tuft of spatulate setae **13**

13a. Base of pronotum constricted, narrower than the base of the elytra. Antennae with straight sutures, the first suture being completely septate. Dorsolateral margin of pronotum rounded. Proventriculus simple, crop with clusters of very large crop spines.....***Procryphalus***

13b. Base of pronotum as broad as the base of elytra, not constricted. Antennal sutures variable, sometimes with partial septum. Dorsolateral margins of pronotum marked with carina. Proventriculus and crop variable.....**14**

14a. Eye long and tapered ventrally. Antennal club with three transverse sutures. Symetrical incomplete septum along first suture. Crop spines include several large long sclerotized spines. Distributed only in the Pacific islands ..... ***Hemicryphalus***

14b. Eye usually elongate-oval shaped. Antennal club flattened, sutures often procurved or absent, oblique partial septum sometimes present. Proventricular crop spines well-developed as short, socketed spines. Widespread in Europe, Africa, Asia and Oceania, rare in tropical and subtropical Americas .....***Eidophelus***

Conclusions

Cryphalini has been a notoriously challenging tribe in scolytine systematics. A comprehensive review of the genera using morphology, and, where available, molecular information has enabled an evidence-based classification system in agreement with the evolutionary history.

However, a small number of the changes were not completely backed up with comprehensive evidence and will need confirmation when more material and resources become available.

This project has not resolved all species level conflicts, for which many likely synonyms were noted but excluded from the scope of the study. Resolving some species, such as several *Hypothenemus* spp. and *Cryphalus* spp. is formidable, due to likely high numbers of cryptic and pseudocryptic species (Kambestad et al., 2017), as well as the loss or lack of diagnostic characters of type material of many species.

There is also a great undescribed diversity of species in Cryphalini and Ernoporini, many of which were encountered during this study. The advances in molecular systematics and photography provide an unprecedented toolkit to tackle species-level taxonomy, and further enable the study of their ecology and evolution.

Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

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