

Handbook of Zoology

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Arthropoda: Insecta

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DE GRUYTER

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Coleoptera, Beetles

Volume 3:
Morphology and Systematics
(Phytophaga)

DE GRUYTER

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ISBN 978-3-11-027370-0
e-ISBN 978-3-11-027446-2
ISSN 2193-4231

Library of Congress Cataloging-in-Publication Data

A CIP catalogue record for this book is available from the Library of Congress.

Bibliografic information published by the Deutsche Nationalbibliothek

The Deutsche Nationalbibliothek lists this publication in the Deutsche Nationalbibliografie; detailed bibliographic data are available in the Internet at <http://dnb.dnb.de>

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Typesetting: Compuscript Ltd., Shannon, Ireland
Printing and Binding: Hubert & Co. GmbH & Co. KG, Göttingen
Printed in Germany
www.degruyter.com

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2.3 Disteniidae J. Thomson, 1861

Petr Svacha and John F. Lawrence

Distribution. A moderately large (over 300 species) and widely distributed family (absent from New Zealand and Australia) that is predominantly tropical and subtropical, with only a few species penetrating into temperate areas, exceptionally surpassing 45° latitude (*Distenia japonica* Bates in Sakhalin). Arid zones are avoided. Disteniids are present in South America (except for Chile and Uruguay; in Argentina known only from Misio-nes; Di Iorio 2005), Central America (including some Caribbean islands), southern North America (numerous species in Mexico but only one in the eastern United States), the Afrotropical region (including Madagascar and some adjacent islands), the eastern Palaearctic region (northeastern China, Korean Peninsula, Japan and the Ussuri region,

Sakhalin and Kurile Islands in Russia; absent from the western Palaearctic and Siberia), the Oriental region including southeastern Asian islands and some Melanesian islands (New Britain, Bougainville, several islands of Fiji; not known from New Guinea or New Caledonia; Lingafelter 2007).

Biology and Ecology. The larval biology of Cyrtopini and Heteropalpini is unknown. The slender larvae of Disteniini feed in or under bark and sometimes later in the sapwood of dead or dying trees and shrubs, often assuming a characteristic curved position resembling some buprestid larvae. A Madagascan species of *Nethinius* Fairmaire was also found in a half-dead liana. Pupation occurs usually in sapwood. The relatively well known East Asian island species *Distenia japonica* (sometimes incorrectly treated as a synonym of *D. gracilis*; Danilevsky 2012) is polyphagous on broadleaved trees and conifers (see Gressitt 1951; Ohbayashi & Niisato 2007); the mainland *D. gracilis* feeds underground on roots of broadleaved trees, although larvae return to root bases for pupation (Cherepanov & Cherepanova 1975). The North American *Elytrimitatrix undata* (Fabricius) also feeds on roots (Craighead 1923). The Oriental *Dynamostes audax* Pascoe (Dynamostini) was recently found in Yunnan (Lin *et al.* 2010), and some specimens were reared from larvae found in May in rainforest at approximately 1000 m in a standing half-dead stem of an unidentified broadleaved tree about 30–40 cm in diameter; larvae fed under dead bark together with some cerambycids; pupation was not observed (X. Zhu, personal communication). Disteniid adults are usually winged and both sexes are capable of flight (verified in some Disteniini); only two related wingless Oriental genera are known: *Clytomelegena* Pic (Fig. 2.3.1 F, 2.3.2 C; Lin & Murzin 2012) and *Olemehlia* Holzschuh. Adults of some species (e.g., some Madagascan *Nethinius*) are at least partly diurnal, but many disteniids are predominantly crepuscular or nocturnal and are often attracted to light. Very little is known about adult feeding; some taxa possibly do not feed at all (?*Cyrtonops* White), but captive adults of Madagascan *Nethinius* sp. fed on honey, whereas pellets of unidentified particulate food (but not pollen) were found in the guts of several Disteniini (*America* Santos-Silva & Tavakilian, *Elytrimitatrix* Santos-Silva & Hovore, *Distenia* Le Peletier & Audinet-Serville).

Morphology, Adults (Fig. 2.3.1, 2.3.2; no specimens of Heteropalpini were available for dissection). Length 5–40 mm; body about 2.7–6 times as long as wide; sides subparallel or elytra distinctly tapering (expanded behind middle in flightless myrmecoform *Clytomelegena* and *Olemehlia*). Coloration usually brownish to black, occasionally metallic and/or variegated. Upper surfaces bearing longer erect setae and/or short decumbent hairs, the latter sometimes forming patterns on the elytra.

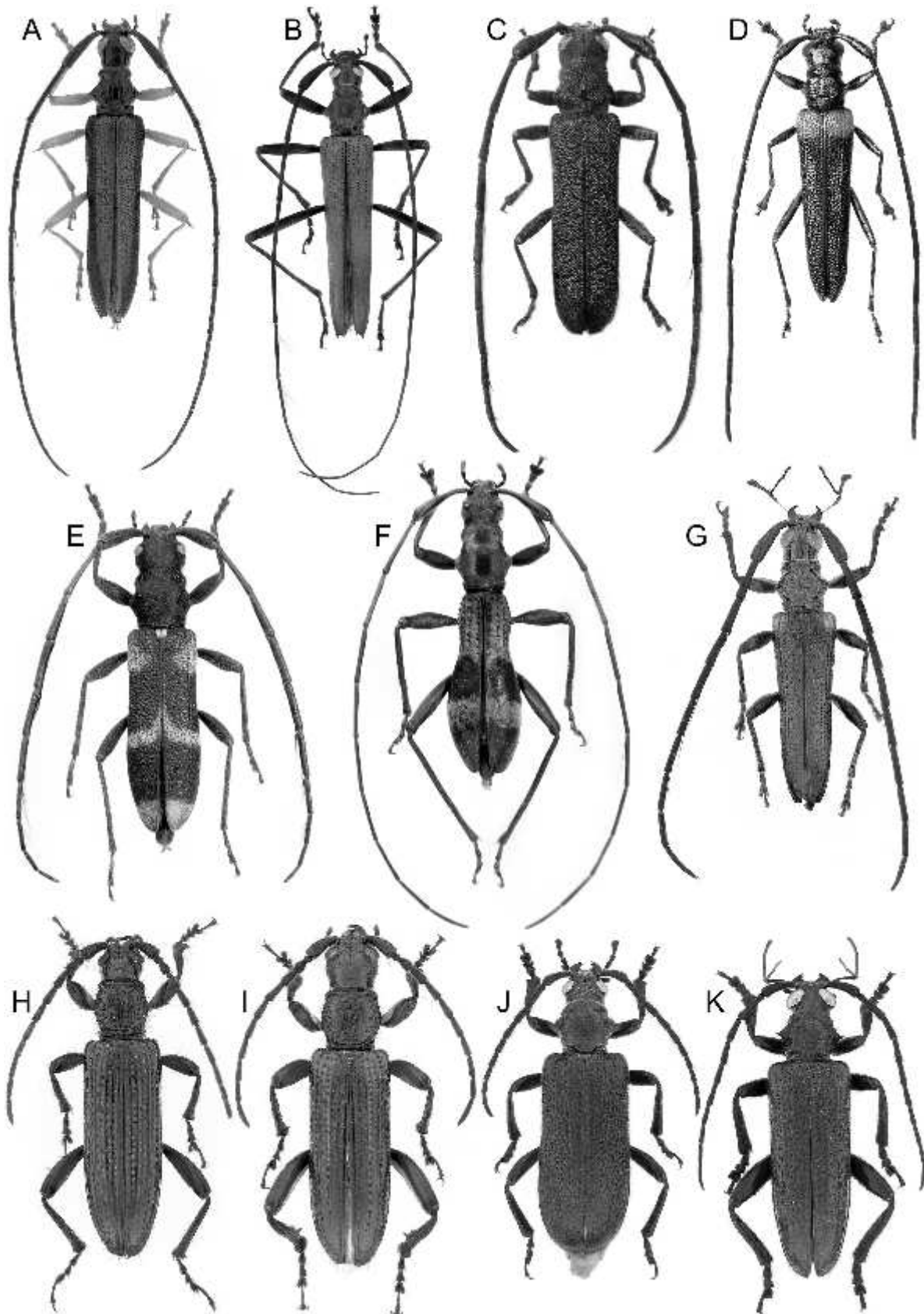


Fig. 2.3.1 Adults of Disteniini (A–F), Heteropalpini (G), Dynamostini (H, I), and Cyrtonopini (J, K), dorsal view. A, *Distenia suturalis* Bates, female, 20 mm; B, *Typodryas callichromoides* J. Thomson, male, 23 mm; C, *Cometes hirticornis* Le Peletier & Audinet-Serville in Latreille, male, 9 mm (© I. Jeniš); D, *Paracometes acutipennis* (Buquet), male, 12 mm (© I. Jeniš); E, *Tengius ohkuboi* Matsushita, female, 8 mm; F, *Clytomelegena kabakovi* (Murzin), female, 11 mm; G, *Pseudocometes argutulus* (Buquet), male, 13 mm; H, *Dynamostes audax* Pascoe, female, 19 mm; I, *D. audax*, male, 20 mm; J, *Cyrtonops metallicus* Hüdepohl, female, 19 mm; K, *Cyrtonops* sp. (Sri Lanka), male, 25 mm.

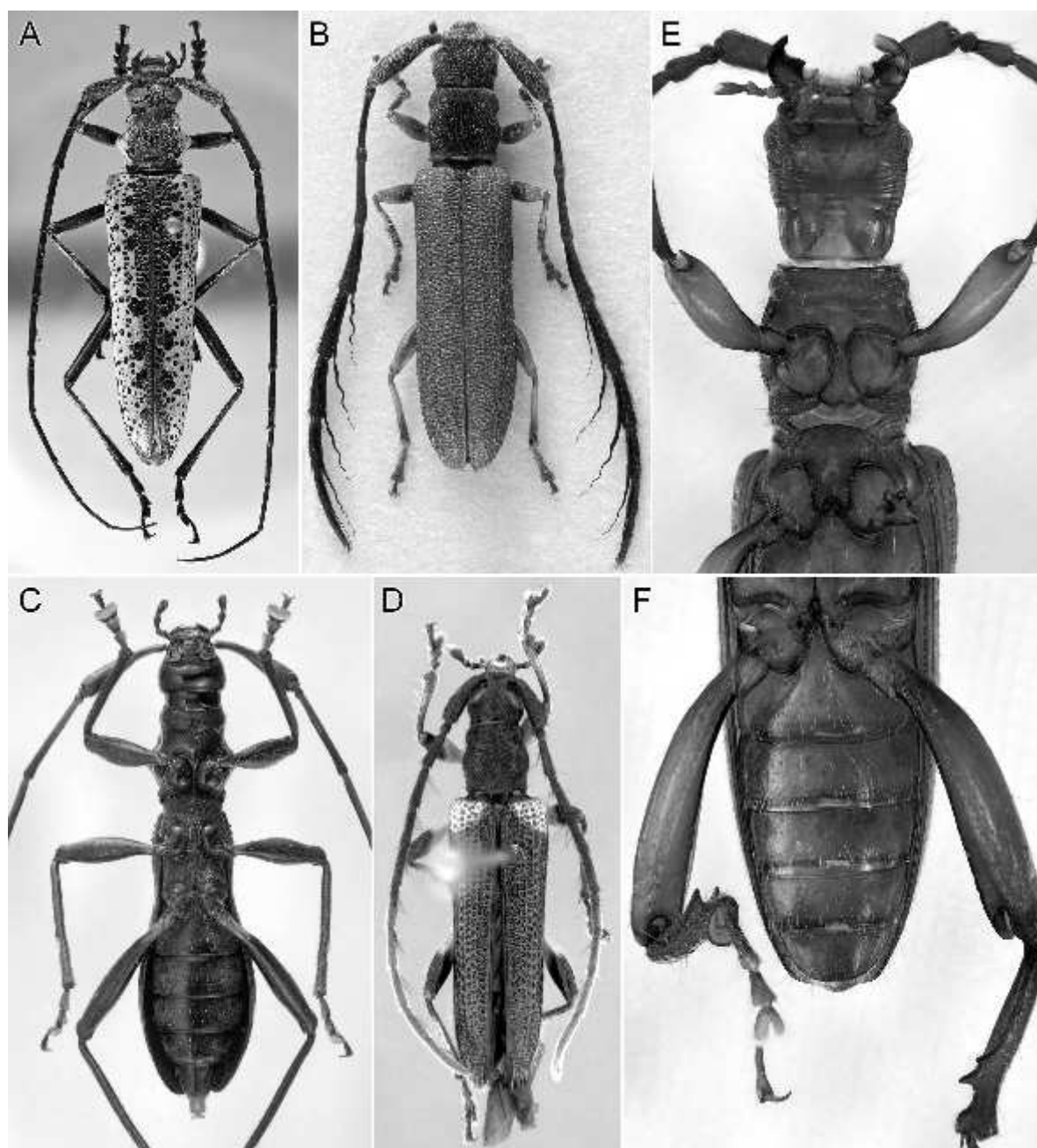


Fig. 2.3.2 Adults of Disteniini (A–C) and Dynamostini (D–F). A, *Disteniazteca pilati* (Chevrolat), female, dorsal view (© N. P. Lord & E. H. Nearn); B, *Villiersicometes wagneri* (Gounelle), ?male, dorsal view (© N. P. Lord & E. H. Nearn); C, *Clytomelegena kabakovi*, female, 11 mm, ventral view; D, *Aiurasyma potira* Martins & Galileo, male, 8.4 mm, dorsal view (© G. Biffi); E, *Dynamostes audax*, male, head, pro- and mesothorax, ventral view; F, *D. audax*, male, hind legs and abdomen, ventral view.

Head prognathous, short to moderately elongate, not or only slightly constricted posteriorly; sometimes forming a very broad neck and long, weakly defined temples. Occipital region without transverse ridge or stridulatory file. Frontal region not to moderately, gradually declined except for steeply declivous anterior margin; with median groove or line (marking deep internal carina) that may continue behind the eyes but does not reach the posterior cranial margin. Eyes small to large, slightly to strongly protuberant, usually shallowly emarginate (may be entire when small); finely

or coarsely faceted, without interfacetal setae. *Distenia japonica* (described by Gokan & Hosobuchi 1979 as *D. gracilis*) has a cone ommatidia with biconvex corneal lens and a large open rhabdom (corresponding with nocturnal habits) formed by two central and six peripheral retinula cells; central rhabdom fused at both ends with continuous circular peripheral rhabdom. Antennal insertions exposed from above, very close to mandibular articulations, facing laterally and more or less anteriorly; supported medially by prominent tubercles connected by more or less complete transverse

protuberance, sharply declivous anteriorly toward (and usually partly involving) postclypeus; short carina usually present behind antennal sockets; subantennal groove absent. Frontoclypeal ridge distinctly impressed, transverse or slightly V-shaped; pretentorial pits distinct and positioned in narrow space between antennal sockets and lateral postclypeus with mandibular articulations (Fig. 2.3.3 A). Anterior clypeus membranous; postclypeal sclerotization reaching more or less anterior to mandibular articulations; with straight or (*Cyrtonops*, Fig. 2.3.3 B) slightly raised and emarginate anterior margin. Labrum free, moderately

to strongly transverse, broadly rounded to truncate or slightly emarginate. Antennae 11-segmented, filiform; usually surpassing elytral apices, distinctly shorter than body in both sexes of *Cyrtonops* and *Dynamostes* Pascoe; scape long (occasionally almost reaching posterior margin of prothorax) and thickening distad, occasionally spinose; pedicel small (at most slightly longer than broad) but with large condyle fitting in broad distal opening of scape; all or at least some flagellomeres usually bearing characteristic long recumbent setae in large sockets placed in shallow longitudinal groove on posterior antennal face and typically

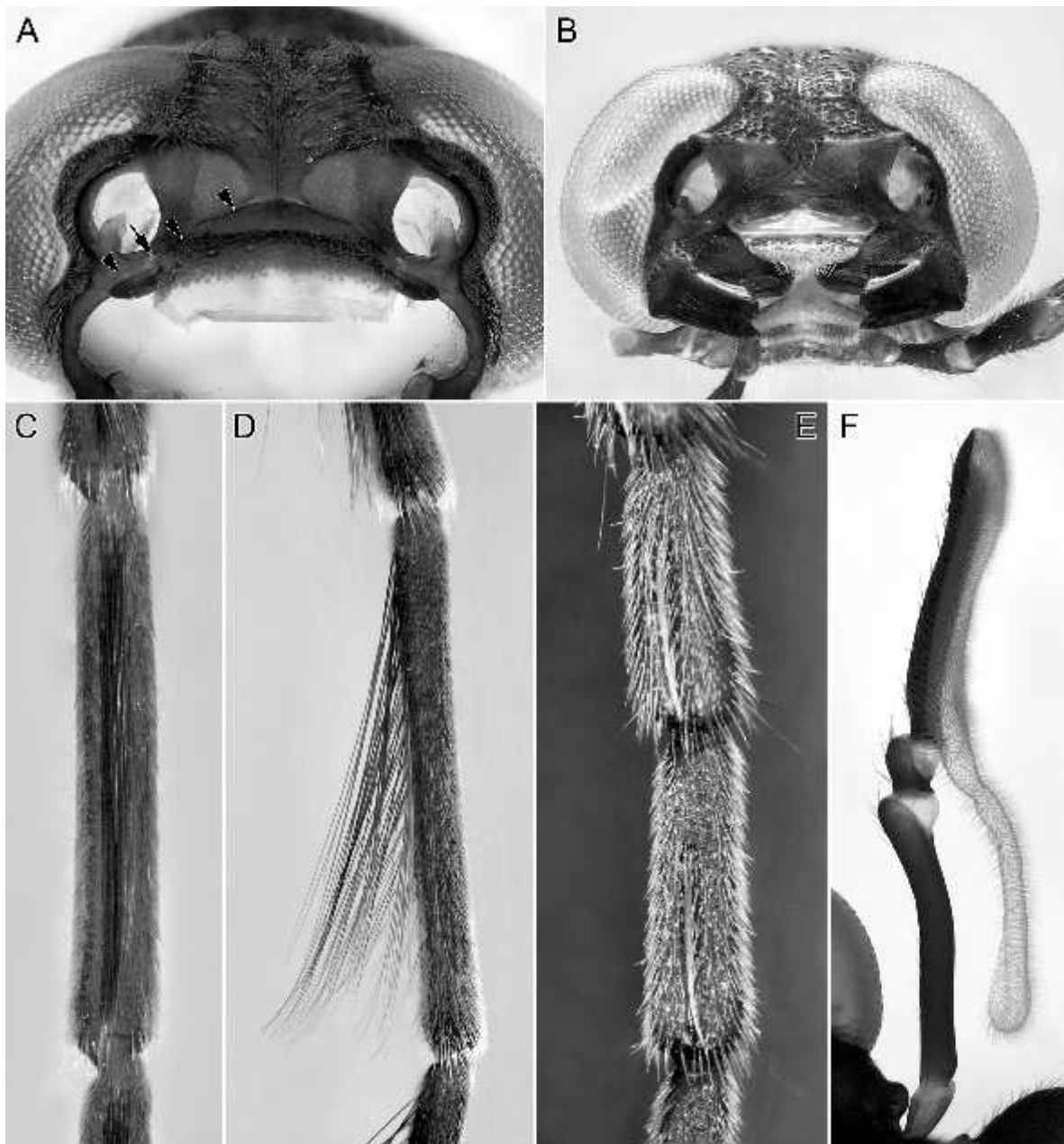


Fig. 2.3.3 Adults. A, *Elytrimitatrix undata* (Fabricius), female, head, anterior view (arrowheads mark the frontoclypeal sulcus, arrow points to right pretentorial pit); B, *Cyrtonops punctipennis* White, male, head, anterior view; C, *Elytrimitatrix undata*, female, fifth right flagellomere, posterior view (long setae in shallow groove); D, *E. undata*, male, sixth right flagellomere, dorsal view (long setae partly erect); E, *Dynamostes audax*, male, sixth and seventh right flagellomeres, posterior view (showing reduced but present long setae); F, *Cyrtonops punctipennis*, male, left maxillary palp, dorsal view.

surpassing distal end of flagellomere (Fig. 2.3.3 C, D); those setae are absent on flagellomere 1 in *Tengius* Matsushita, are fewer and shorter (not surpassing segments) in Dynamostini, particularly in *Dynamostes* where present only on flagellomeres 2–8 (Fig. 2.3.3 E), and are absent in Cyrtonopini. Mandible short and broad to moderately long (*Dynamostes*, Fig. 2.3.2 E), more or less abruptly curved mesally; apex bidentate (*Cyrtonops*, Fig. 2.3.3 B), more or less broadly truncate or rounded (most species, Fig. 2.3.4 A), or sharply pointed (*Nethinius*; mandible in latter genus also with particularly prominent, longitudinal lateroventral carina, Fig. 2.3.4 B); incisor edge simple or with one or two teeth, in some cases with row of long hairs; molar plate usually well-defined (often finely striate or with other microsculpture), surrounded anteriorly by desclerotized area with fine microtrichia (Fig. 2.3.4 A, B); molar plate less distinct in Dynamostini, with only small central area of distinct microsculpture and smaller desclerotized area in *Dynamostes*; both structures absent in *Cyrtonops* (molar region partly visible in Fig. 2.3.3 B); prostheca absent. Maxilla with

distinct, setose galea and lacinia without obvious pollinophagous modifications (such as elongate bases and long curved setae), both relatively small in *Cyrtonops*; lacinia without uncus; palps tetramerous; terminal palpomere always with larger sensory area in males, often fusiform or moderately truncate in females and apically expanded and more or less triangular in males; in Cyrtonopini and Heteropalpini broadened in females and uniquely modified in males (Fig. 2.3.1 G, K, 2.3.3 F) where palpomere 2 is long, 3 very short, 4 (terminal) again long with sensory area expanded along its entire mesal face and projecting basally into a finger-like process. Ligula with more or less broad membranous anteriorly straight or very shallowly emarginate apical flap (small in *Cyrtonops*); never typically bilobed but in *Nethinius* with paired membranous lobes sharply folded back on ventral side; labial palps trimerous; terminal palpomere normal, fusiform (some females) to strongly expanded apically (many males). Metantennal slits oblique and converging, broadly separated to virtually touching anteriorly. Gula not defined laterally

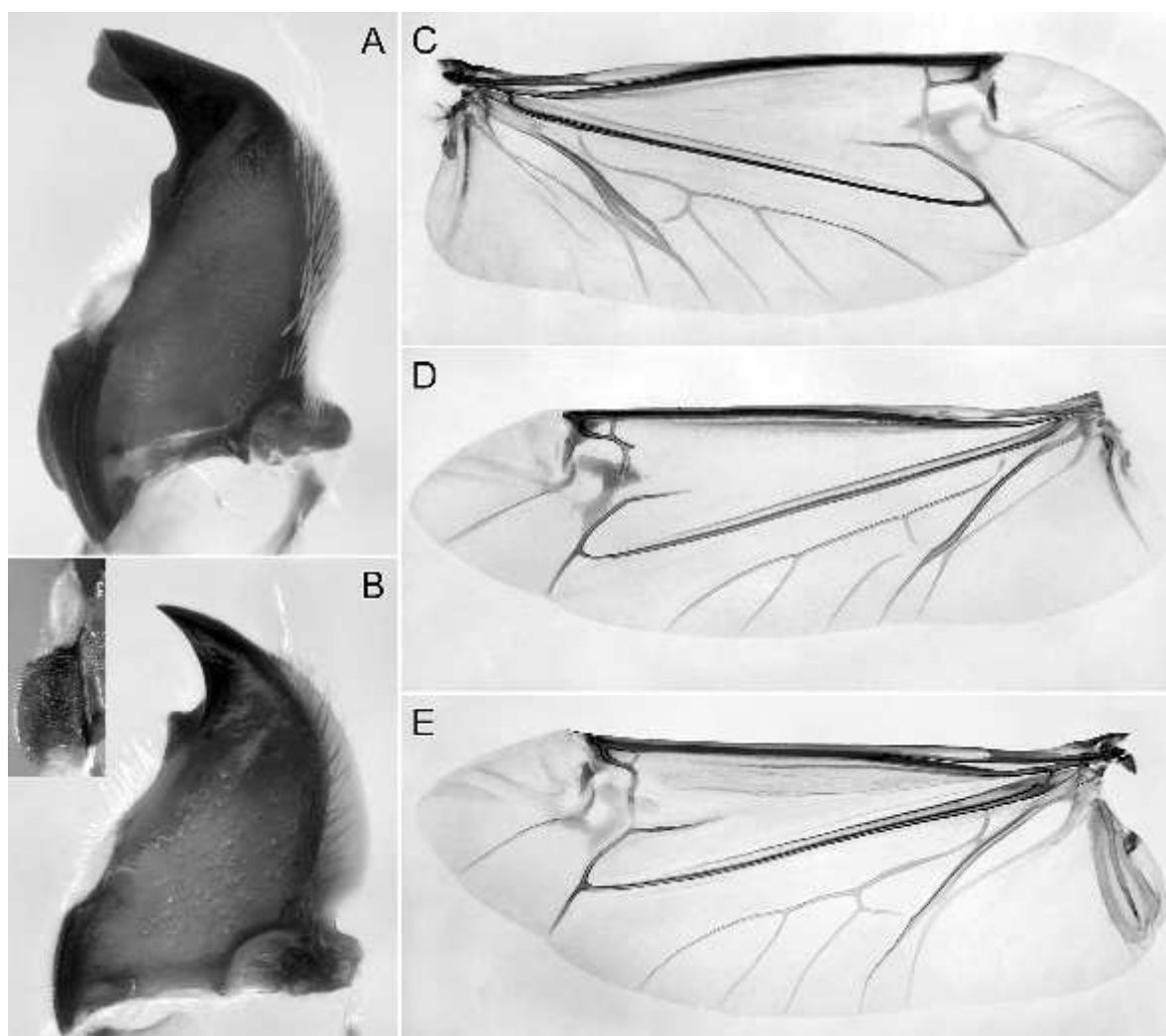


Fig. 2.3.4 Adults. A, *Elytrimitatrix undata*, female, right mandible, dorsal view; B, *Nethinius* sp., male, right mandible, dorsal view (inset shows molar plate in dorsomedial view); C, *Elytrimitatrix undata*, female, right wing; D, *Distenia japonica* Bates, female, left wing; E, *Cyrtonops* sp. (Sri Lanka), male, left wing.

anterior to those slits, fused with submentum; the latter strongly projecting between maxillary bases. Tentorial bridge broad, roof-like or, in taxa with approximate metatentorial slits, almost cylindrical anteriorly where the bases of metatentorium become subcontiguous; pre- and metatentorial arms sclerotized and firmly fused with each other; dorsal arms absent or only bases distinctly sclerotized. Cervical sclerites rudimentary or absent.

Prothorax 0.65–1.2 times as long as wide, usually widest and bearing a lateral spine or distinct tubercle at approximately the middle (sides broadly rounded and without tubercle in *Dynamostini* and *Micronoemia Aurivillius* of *Disteniini*); often constricted anteriorly and less distinctly posteriorly; base distinctly narrower than elytral bases except for flightless *Clytomelegena* (Fig. 2.3.1 F, 2.3.2 C) and *Olemehlia*; pronotum not explanate or margined laterally, without produced anterior angles; anterior edge usually with narrow margin or bead; posterior angles obtuse or right, posterior edge more or less straight or evenly rounded; disc frequently with smooth or otherwise distinguished raised areas, without paired basal impressions. Prosternum in front of coxae slightly shorter to slightly longer than shortest diameter of procoxal cavity, flat to moderately convex. Prosternal process usually more or less complete, narrow, parallel-sided and rounded, truncate or slightly expanded at apex; very short and pointed in *Cyrtonops*, broader and strongly expanded apically in *Dynamostes* and *Aiurasya* Martins & Galileo. Notosternal sutures incomplete or indistinct. Procoxal cavities usually narrowly separated and more or less circular (lateral coxal angles completely covered by prosternal flaps), confluent and lateral angles and trochantins partly exposed in *Cyrtonops*; open externally except for *Dynamostes* (Fig. 2.3.2 E) and *Aiurasya*, broadly closed internally; visible procoxae usually subglobular and moderately projecting below prosternum, but strongly prominent in *Cyrtonops*. Mesoscutum straight or shallowly emarginate anteriorly, with median endocarina and divided and usually large stridulatory plate (Fig. 2.3.5 A); endocarina slightly shifted to left side (making division asymmetrical) in single available specimen of *Saphanodes* Hintz (holotype of *S. apicalis* [Chevrolat]). Scutellar shield small, more or less abruptly elevated above mesoscutum, anteriorly simple, posteriorly broadly rounded to truncate. Elytra fully covering abdomen, 2.2–4.2 times as long as combined width and 2.7–5 times as long as pronotum; irregularly punctate, or with as many as ten puncture rows (often obliterated posteriorly); rarely punctation indistinct (*Thaigena* Holzschuh); scutellary striole missing; elytral apices meeting or almost meeting at suture, in some cases with inner (sutural) and/or outer spines; epipleura absent or incomplete. Mesoventrite separated by complete sutures from mesanepisterna, which are broadly separated at midline; anterior edge on same plane as metaventrite, in species with externally open procoxal cavities usually with paired horizontal or

slightly declined procoxal rests; mesoventral cavity absent. Mesocoxal sockets subcircular, moderately to widely separated; broadly open laterally in *Cyrtonops*, narrowly open to closed in *Disteniini* and *Heteropalpini*, closed in *Dynamostini*; mesocoxae round, moderately projecting. Mesometaventral junction a complex fitting. Metaventrite with discrimen moderately to very long; postcoxal lines absent; exposed portion of metanepisternum very long and narrow. Metacoxae contiguous or narrowly separated, horizontally oriented, extending laterally to meet elytra; plates absent. Metendosternite (Fig. 2.3.5 B) with lateral arms moderately to very long; laminae and anterior process absent; anterior tendons fine and placed more or less far apart on lateral arms. Hind wing (Fig. 2.3.4 C–E) fully developed except for apterous *Clytomelegena* and *Olemehlia*; apical field moderately long, with only one (posteriormost) distinct sclerotized radial vein remnant; radial cell proximally closed (see remark under *Dynamostini*), with posterobasal angle right or obtuse; crossvein r3 short or absent and often fused for most/all of its length with r4; r4 in some cases interrupted before reaching RP; spur usually short or absent (relatively distinct in some *Nethinius*, but variable even between right and left wing of the same specimen); RP surpassing r4 proximally, moderately long; medial field with five free veins and no medial fleck; mp₃₊₄-cu often absent; CuA₁₊₂ and CuA₁ present but former often interrupted basally; CuA₂ in some cases also disconnected (Fig. 2.3.4 D); wedge cell usually absent but narrow yet distinct in *Elytrimitatrix undata* (Fig. 2.3.4 C) and rudiments present in several other *Disteniini* (Santos-Silva & Hovore 2007 a); anal lobe well-developed, without embayment; AP₃ may be more or less surrounded by sclerotization in *Cyrtonops* (Fig. 2.3.4 E). Legs moderately to very long, usually slender; strong particularly in males of *Cyrtonops* and *Dynamostes*; trochanterofemoral joint strongly oblique, with base of femur sometimes abutting coxa; femur, particularly in some American taxa, with apical spine on anterior side (Fig. 2.3.1 A); tibial spurs 2-2-2; inner protibia and outer mesotibia near apex usually with oblique, hairy grooves (antenna cleaners similar to those in cerambycid subfamily Lamiinae; reduced in *Cyrtonops*, possibly in connection with loss of long flagellar setae); hind legs enlarged in males of *Dynamostes* and some *Cyrtonops*, in former hind tibiae with two large teeth on inner side, in latter inner edges of femora and tibiae tuberculate or spinose. Tarsi 5-5-5, pseudotetramerous with tarsomere 4 strongly reduced and tarsomere 3 enlarged and ventrally (bi)lobed; tarsomeres 1–3 each with dense ventral pads (slightly reduced on tarsomere 1 in some species); pretarsal claws simple, without setae, divaricate; empodium present, bi- or usually multisetose.

Abdomen with five visible sterna (III–VII), first not much longer than second, without postcoxal lines; intercoxal process acute or narrowly rounded, completely hiding sternum II. Functional spiracles located in lateral membranes of

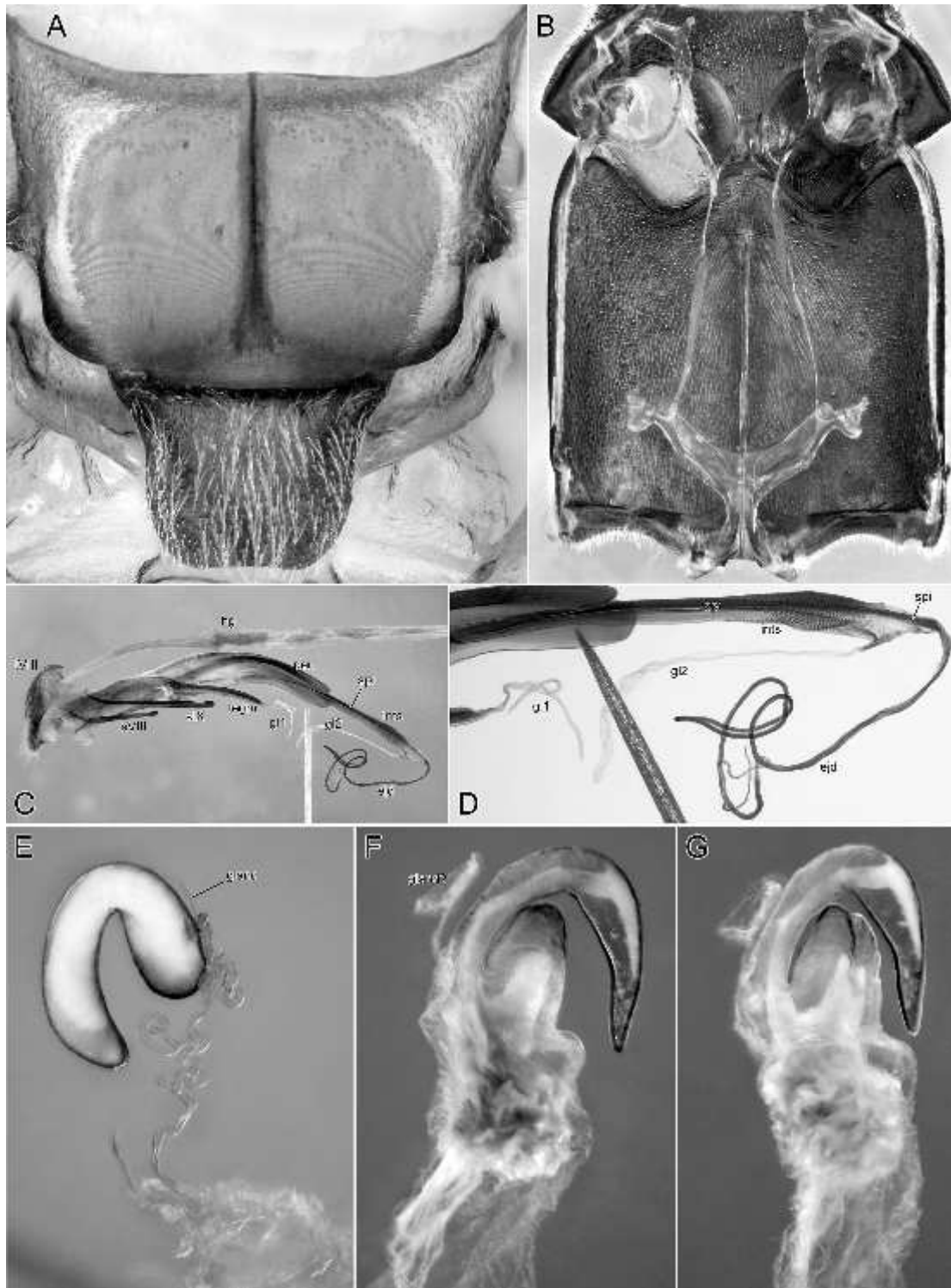


Fig. 2.3.5 Adults. A, *Distenia japonica*, female, mesoscutum with divided stridulatory file and scutellum, dorsal view; B, *Elytrimitatrix undata*, female, meso- and metathoracic venter, dorsal view (showing metendosternite with broadly separate anterior tendons approaching posterior tendons of mesothoracic endoskeleton); C, *E. undata*, dissected male terminalia, lateral view; D, *E. undata*, same preparation as in C, different illumination; E, *America berkovi* Santos-Silva & Tavakilian, female, spermatheca (spermathecal gland only partly visible, opens into distalmost part of slightly sclerotized coiled duct); F and G, *Cyrtanops piceatus* Holzschuh, female, spermatheca, lateral (F) and lateroventral (G) view. ejd, ejaculatory duct (containing a sclerotized rod along most of its length, which enters the canal in the spine on internal sac, visible in D); gl1, bifurcate gland (?) opening at anterior tip of tegmen; gl2 (held down by a pin), unpaired gland (?) opening at base of retracted internal sac (close to secondary gonopore) and thus at its apex when everted; hg, hindgut; ints, internal sac; pen, penis; sVIII, anterior apodeme of sternum VIII; sIX, anterior apodeme of sternum IX (spiculum gastrale); spi, spine projecting at secondary gonopore (terminal genital opening on everted internal sac); tVIII, tergum VIII; tegm, anterior tip of tegmen.

segments I–VII. Male terminalia (Villiers 1980; Lin *et al.* 2010 for *Dynamostes*; Fig. 2.3.5 C, D): Tergum VIII sclerotized; anterior edge of sternum VIII with median strut and anterior edge of sternum IX with spiculum gastrale. Terga IX and X fused and membranous. Aedeagus cucujiform, symmetrical; anterior edge of phallobase without strut; parameres fused to phallobase but free from each other; broad struts on anterior edge of penis present but sometimes fused except for apices (*Cyrtonops*); internal sac variable; ejaculatory duct unpaired, containing long sclerotized rod; gonopore projects into a sclerotized spine (usually very long as in Fig. 2.3.5 D, but very short in *Nethinius*). Female terminalia (Villiers 1980; Saito 1990; Lin *et al.* 2010 for *Dynamostes*; Fig. 2.3.6 A) with sternum VIII bearing anterior apodeme (spiculum ventrale) and segment VIII not protruding; ovipositor moderately long, virtually without basal paired pockets; four pairs of baculi present (proctigeral, dorsal, paraproctal and usually broad coxital baculi; *cf.* Fig. 2.4.19 O); styli distinct, terminal. Vagina broad; bursa copulatrix short; spermatheca (Fig. 2.3.5 E–G, 2.3.6 A) present, terminally attached on bursa; duct present or absent, occasionally with its distal part sclerotized, thickened and closely associated with spermatheca, making it appear very complex; spermathecal gland small, inserted on distal spermathecal duct or its sclerotized derivatives. Single dissected female of *Cyrtonops* lacking distinct spermathecal duct; simple sickle-shaped spermatheca attached to anterior tip of bursa copulatrix, which terminates as peculiar sclerotized bilobed knob (Fig. 2.3.5 F, G). Gut usually functional (hindgut well-developed and often containing food pellets; slightly reduced and not containing food in dissected *Cyrtonops*); stomodeal valve (posterior end of foregut) in dissected species without sclerotized armature.

Morphology, Larvae (Fig. 2.3.6 B). Known only in Disteniini. Described for *Elytrimitatrix* and *Distenia* (e.g., Craighead 1923; Gardner 1931; Kojima 1959; Duffy 1968; Mamaev & Danilevsky 1975; Cherepanov 1979; Svacha & Danilevsky 1987; Svacha *et al.* 1997; Lawrence *et al.* 1999 a), undescribed material available also for *Tengius* (two sp.), *Noemia incompta* Gressitt and several Madagascan species of *Nethinius*.

Body unsclerotized, extremely elongate, with slightly broader and flattened thorax and subcylindrical abdomen. All surfaces lightly pigmented, except for mouth frame (anterior cranial margin supporting mouthparts) and mandibles. Vestiture consisting of moderately dense, short, simple setae, and large fields of fine spine-like microtrichia on some body regions contacting gallery walls.

Head (Fig. 2.3.6 C, 2.3.8 C; for terminology see Fig. 2.4.22) prognathous, about half of it retracted into prothorax; cranium transverse, distinctly flattened, widest behind the middle, with sides evenly rounded; posterodorsally deeply notched; epicranial halves meeting almost at one point at frontal base, duplicate dorsomedian region

and coronal suture absent; frontal arms broadly V-shaped, indistinct in posterior pale frontal region (yet functioning as cleavage lines at ecdysis); anteriorly reaching cranial margin below antennal sockets, not interrupting their sclerotized rings. Median frontal endocarina complete, reaching epistomal margin, which is constructed as in Cerambycidae (i.e., incorporating postclypeus), sclerotized and sloping to step-like, without epistomal or frontal carinae; bearing six main and often several supplementary epistomal setae, median main pair not shifted posteriorly. Pretentorial pits indistinct; pretentorial arms as in Cerambycidae (short posteromedial rods). Clypeus membranous, trapezoidal, filling space between mandibular articulations, lacking setae. Labrum free, strongly transverse, sclerotized basally, broadly rounded and setose anteriorly; epipharynx with long tormae curved backward and reaching to sides of posterior raised epipharyngeal region. Pleurostoma sclerotized and moderately raised, without subfossal process. One fused composite main stemma present on each side (indistinct in *Elytrimitatrix*); small dorsal additional stemma visible in some specimens of *Nethinius*; ventral stemma absent. Antennae short, moderately retractile, three-segmented; antennomere 2 shorter than broad to ring-like, bearing prominent conical sensorium. Mandibles symmetrical, short and broad; basal part bearing two lateral setae; inner face simple, without molar plate; apical part with simple blunt apex, straight cutting edge, and two distinct inner keels (occasionally with some transverse connecting ridges; Fig. 2.3.7 A); pseudomola not distinctly developed, only present as small rudiment at dorsal angle (not visible in dorsal view). Maxillolabial complex (Fig. 2.3.8 D) more retracted than in Cerambycidae (cardo/stipes border distinctly posterad of mandibular condyle); maxillary articulating area large and divided into two parts; posterior portion larger and fused with submentum. Cardo large, free, with extensive undivided sclerotization, in some cases with minute lateral seta; stipes distinctly longer than wide; mala fixed, stout, subcylindrical, apically rounded, densely setose; not arising from palpiger, which is distinct and lacks a dorsolateral process; palp moderately long, three- or (*Noemia* Pascoe and some *Nethinius*) two-segmented; terminal palpomere with one lateral digitiform sensillum. Mentum not fused with submentum; labial palpigers widely separated; palps two-segmented; ligula well-developed, broadly rounded, with sparse ventroapical setae and broad apical and dorsolateral area of microtrichia; dorsal ligula and hypopharyngeal region very lightly sclerotized (hypopharyngeal sclerome absent) and separated from each other by narrow membranous zone. Hypopharyngeal bracon absent. Hypostomal rods absent, hypostomal region fused with epicranium. Gula absent. Metatentorial pits not distinct, metatentorial invaginations extremely broad, occupying entire lateral margin of ventral part of occipital foramen and fusing into a plate-like tentorial bridge lying in

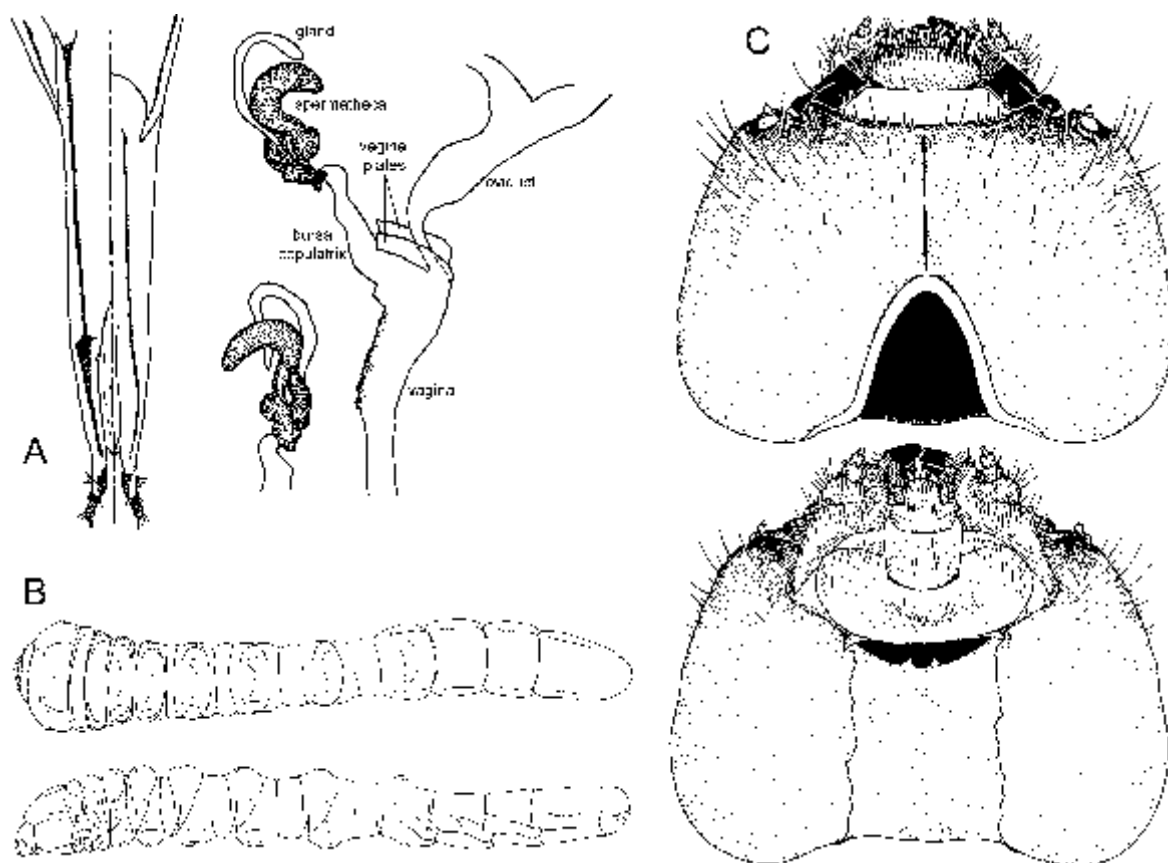


Fig. 2.3.6 A, *Distenia japonica*, female, ovipositor (left half in ventral view, right half in dorsal view) and internal genitalia showing a complex spermatheca with associated sclerotized coiled duct (from Saito 1990, as *D. gracilis*); B, *D. japonica*, larva, dorsal and lateral view; C, *D. japonica*, larva, head in dorsal and ventral view (B and C modified from Svacha & Danilevsky 1987).

the same plane with hypostomal region and anteriorly bearing paired fine branches reaching inside the cranial cavity toward the frontal region but not connected with pretentorial arms (Fig. 2.3.6 C, 2.3.8 B).

Thorax (Fig. 2.3.9 C) broadened and flattened. Prothorax about as long as meso- and metathorax combined and slightly wider. Pronotum delimited by long lateral furrows that slightly converge anteriorly; anterior protergal pigmentation missing or very pale (and then interrupted by lateral furrows); posterior pronotum and small adjacent lateral regions microspiculate (Fig. 2.3.9 A). Prothoracic venter (Fig. 2.3.9 B) with more or less separate epimeron and nearly fused coxal, basisternal and sternellar regions (faint oblique impressions divide this fold into what may be homologues of the cerambycid coxosternum and sternellar fold, both of composite origin), and with fused epipleuron, episternum and lateral presternum; median presternal region separated by anteriorly converging impressions (homology with cerambycid mediopresternal limits uncertain); base of median region always distinctly microspiculate; spinasternum indistinct; spina at most present as rudimentary fovea; other prosternal endoskeletal elements and pleural apodeme absent. Meso- and metanota simple or (metanotum) with indistinct lateral impressions; usually

microspiculate; particularly mesonotum with narrow anterior separate region. Wing discs absent. Epipleuron divided into two parts; mesoepipleural spiracle-bearing area not protruding into prothorax; mesothoracic spiracle placed on border with alar lobe, annular-multiforous, with broadly oval peritreme and variable number of distinct marginal chambers (Fig. 2.3.9 D); vestigial metathoracic spiracle present. Pleuron undivided and broadly separating coxal region from epipleuron. Sterna usually microspiculate; transsternal lines present as indistinct lateral rudiments. Coxa not prominent, medially separated from sternum by distinct impression. Distal legs (Fig. 2.3.10 B) small and very widely separated; trochanter small, distinct medially, reduced laterally; femur and tibiotarsus weakly sclerotized; pretarsus narrowly conical, very weakly sclerotized but microasperate, lacking setae.

Abdomen (Fig. 2.3.6 B, 2.3.9 C) long and narrow, more than five times as long as thorax; anteriorly distinctly pseudosegmented; dorsal and ventral intersegmental zones overlapping and dorsal one more anterior (as in Cerambycidae); dorsal intersegmental area expanded and forming more or less complete intersegments anterior to abdominal segments I–VI; intersegments very large anterior to segments IV–VI (Fig. 2.3.8 A). Dorsal and ventral

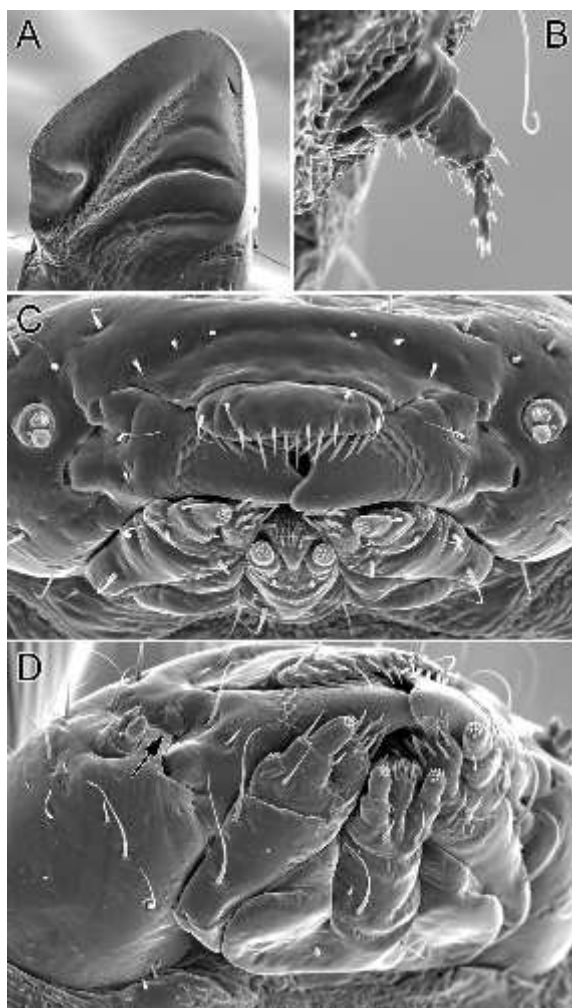


Fig. 2.3.7 SEM. A, *Distenia japonica*, later instar, apical part of left mandible, mesal view; B–D, *Nethinius* sp., first instar larva, left hind leg, anterior view (B), head, anterior view (C) and lateroventral view (D, arrow points to very inconspicuous pretentorial pit) (A and C from Svacha *et al.* 1997).

microasperate or microgranulate/microrugose ambulatory ampullae present on segments I–VI, those on II–V strongly prominent laterally and impressed in the middle; sixth ampullae much smaller; all with distinct lateral impressions and usually a pair of faint oblique discal impressions. Functional spiracles present on segments I–VIII, subequal, much smaller than mesothoracic spiracle and with marginal chambers on average fewer (some spiracles may bear only two in small species and/or early larval instars). Epipleuron distinctly protuberant on segments VII–IX and posteriorly on VI; fused with spiracular area on I–V; fused region divided by oblique furrow, particularly on II–V; poorly defined epipleural tubercles present on segments I and VI; virtually not defined on other segments but original posterodorsal extremity marked by small invaginated sclerite on I–VII; invaginated sclerites not surrounded by pleural discs (Fig. 2.3.9 C). Segments VII–IX long (IX much longer than wide), with simple terga and sterna; tergum IX without sclerotized armature. Segment

X subterminal, short and round, partly fused with IX. Anus slightly shifted posteroventrally, triradiate with very short ventral radius (relatively distinct in *Noemia*) to transverse. Digestive tube (Danilevsky 1976; Semenova & Danilevsky 1977; Svacha *et al.* 1997; Fig. 2.3.10 A) without defined crop or proventriculus; midgut straight (not looped as in Cerambycidae), without anterior mycetomes; first hindgut fold may be twisted above anus. Six Malpighian tubules present; crytonephridial condition weakly developed. Nerve cord with eight abdominal ganglia; ganglionic complex VIII shifted to segment VII; connectives paired.

First instars (Fig. 2.3.7 B–D) available for *Distenia japonica* and *Nethinius*. Basically similar to later instars, but much less elongate (larvae before hatching lie straight in fusiform eggs). Intersegments very short. Abdominal segments VII–IX transverse in larvae which are not inflated. Setation sparse, some setae longer. Legs basically similar to later instars, not distinctly longer. Spiracles with two marginal chambers and without a broadly open atrium. Egg bursters not identified; empty egg shells were possibly opened by mandibles (hatching not observed). In species of *Nethinius* with two-segmented maxillary palps, the reduction occurs also in first instars (Fig. 2.3.7 C, D).

Morphology, Pupae (Fig. 2.3.10 C–E). Described for *Distenia* (Cherepanov & Cherepanova 1975; Cherepanov 1979; Nakamura 1981), available also for *Nethinius*. Exarate, moderately depressed. Integument thin and unsclerotized except for small abdominal tergal spines; setae short and sparse, present also on distal femora, absent on antennae. Head bent ventrally, with the mouthparts pointing caudally. Both antennae looped together in a joint oval (not separately as in most Cerambycidae). Functional abdominal spiracles present on segments I–VI. Abdominal dorsum with sparse (*Nethinius*) or numerous (*Distenia*) small sclerotized spines that may become larger on terminal abdominal region but tergum IX without distinct urogomphi or unpaired caudal spine.

Phylogeny and Taxonomy. Disteniidae J. Thomson, 1861 is considered a *nomen protectum* and Cométites Blanchard, 1845 (derived from *Cometes* Le Peletier & Audinet-Serville, a genus currently classified in Disteniini) a *nomen oblitum* (Monné & Santos-Silva 2008).

The group was traditionally treated within Cerambycinae (when that subfamily was accepted in a broad sense, including all current cerambycid subfamilies except for Prioninae, Parandrinae and Lamiinae) either close to the present Lepturinae, or to various groups of then uncertain position. Gahan (1906) and many subsequent authors listed Disteniinae as a separate subfamily, and it was explicitly excluded from Cerambycidae by Linsley (1961, 1962) based on “scalpriform mandibles, the clypeus oblique to the frons, a nonhylecoetoid metendosternite, wings lacking a spur in the

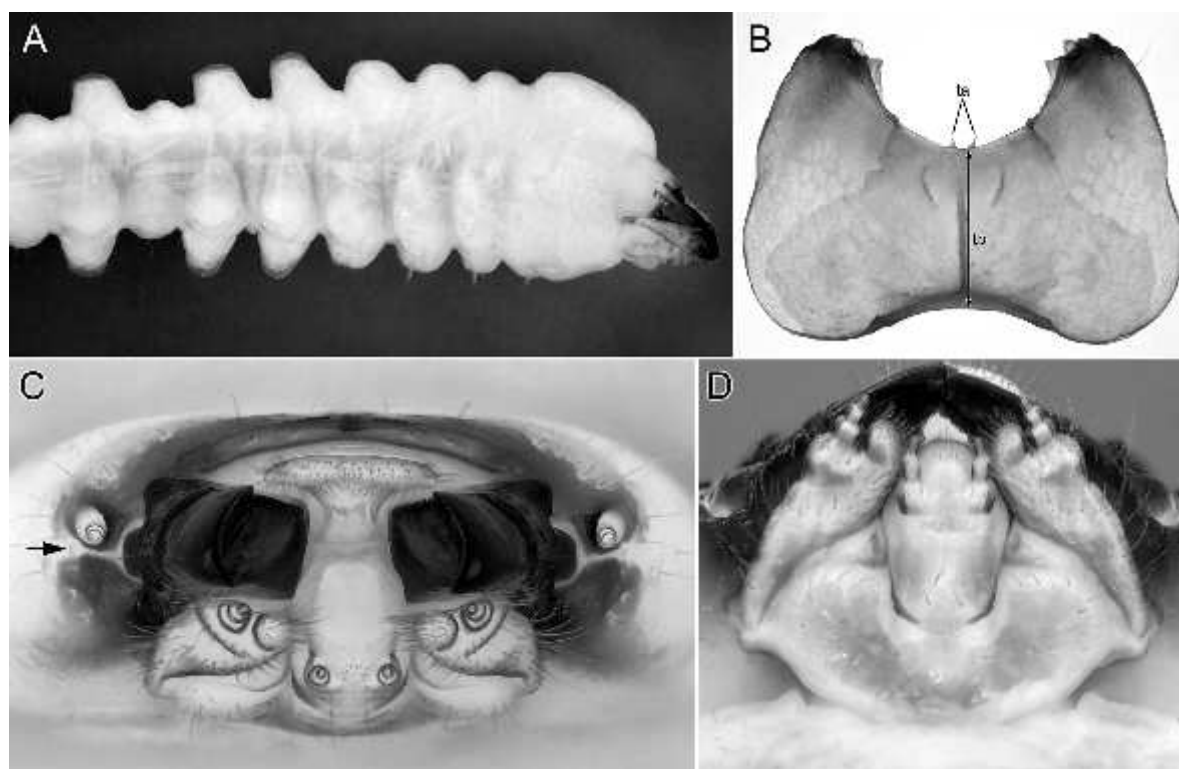


Fig. 2.3.8 Larvae. A, *Nethinius* sp., later instar, lateroventral view (showing large pigment spot of main stemma and first three of the strongly protuberant bilobed ambulatory ampullae on abdominal segments II–V); B, *Distenia japonica*, ventral half of cranium, dorsal view; C, *D. japonica*, head, anterior view (arrow points to small main stemma); D, *D. formosana*, maxillolabial complex, ventral view. ta, slender metatentorial arms on anterior margin of tentorial bridge, cut to short stubs; tb, tentorial bridge.

radio-medial crossvein [present crossvein r4; the lack of spur was incorrectly regarded as unique among Phytophaga], and larvae with retracted ventral mouthparts, the gula and hypostoma absent, and the skin of the prothorax attached directly to the submentum”.

Although the group’s position had been questioned prior to Linsley (since the early 20th century), conclusions were sometimes based on poor knowledge of character variation in Disteniidae and Cerambycidae (see also Villiers 1980). Forbes’ (1922) comment on wing venation of *Distenia undata* (currently in *Elytrimitatrix*) as violating all definitions of Phytophaga stemmed from his poor knowledge of cerambycid wings, as disteniid wings possess no characters unknown in cerambycids. Linsley’s interpretation of the disteniid metendosternite as nonhylecoetoid (Linsley 1961, 1962; *contra* Villiers 1980: 19) implies a nonhylecoetoid metendosternite also in Parandrinae and many Prioninae (see Crowson 1938; the hylecoetoid metendosternite with laminae occurs in some Prioninae not known to Crowson). The broadly separated disteniid anterior tendons (Fig. 2.3.5 B) are unusual but present in some cerambycids. Thus, what remains to exclude disteniids from Cerambycidae is mainly the lack of the larval gula (Craighead 1923; Böving & Craighead 1931 and others), a presumed plesiomorphy as there are no obvious reasons to suspect the homology of the gula within Cerambycidae. Some later authors (Nakamura 1981: 7; Lawrence &

Newton 1982: 283) misinterpreted the broad tentorial bridge, an internal structure positioned above the nerve cord (Fig. 2.3.8 B), as a “concealed” gula or hypostoma. Larvae also differ from all known cerambycids by a straight midgut without a loop (polarity uncertain, possibly an apomorphy of slender disteniid larvae). The broad and bilobed or “scalpriform” adult mandibular apex (the simple apex in *Nethinius* and some other Disteniini may be derived), the approximate antennal sockets and mandibular articulations, and antennal tubercles associated with a protuberance abruptly sloping toward the postclypeus (Fig. 2.3.3 A, B) remain useful but are not diagnostic, and the polarity is uncertain. The characteristic long recumbent flagellar setae (Fig. 2.3.3 C–E) are probably autapomorphic for disteniids, but reduced in *Dynamostes* and absent in Cyrtonopini.

Unlike in Oxypeltidae and Vesperidae as presently defined (and most other chrysolmeloids), the disteniid larval epistomal margin (postclypeus with its setae fused with and forming the anterior margin of the frontal region) is constructed exactly as in Cerambycidae and may be a synapomorphy of the two families. Late instar disteniid larvae also have annular-multiforous spiracles (annular-biforous in Oxypeltidae and Megalopodidae, annular without marginal chambers in Vesperidae), lateral pronotal furrows, apparently homologizable mandibular and prosternal morphology, and a similar construction of the overlapping

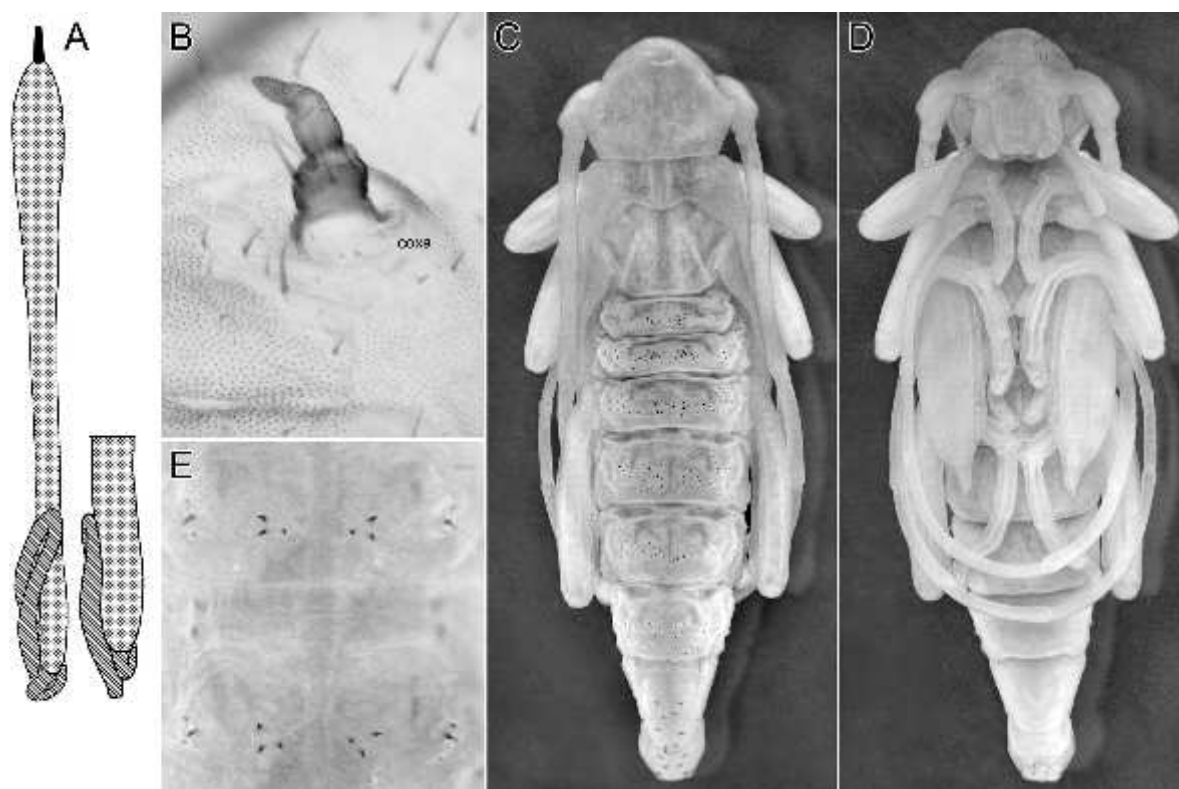


Fig. 2.3.10 A, larval digestive tract, diagrammatic, dorsal view, *Tengius* (left) and posterior part of gut of *Distenia* (right), foregut black, midgut stippled, hindgut crosshatched (from Svacha *et al.* 1997); B, *Distenia japonica*, larva, left middle leg, posteroventral view; C and D, *D. japonica*, female pupa, dorsal (C) and ventral view (D); E, *Nethinius* sp., female pupa, spines on abdominal terga III and IV.

bridging both hypostomal regions and separating the maxillolabial base from the prosternum). Larvae of Anoplodermatinae, which also lack a gula, were then very poorly known. Larvae of Philinae were unknown but the group's relationship to *Vesperus* had been repeatedly suggested before.

Taxa incorrectly placed in Disteniidae or its equivalents include *Dandamis* Gahan, containing *D. nigropunctatus* (Aurivillius), which was originally placed conditionally in *Cyrtanops* and is still occasionally treated in Disteniidae; it was considered a prionine cerambycid "allied to *Aegosoma* and *Sarmyodus*" by Gahan (1906), and the larva described by Duffy (1953, as *Megopsis*) is unquestionably prionine. Duffy (1968: 53) later questioned the identification solely because the larva was not similar to other Aegosomalatini, but it was actually similar to *Sarmyodus* Pascoe, and the reliably identified pupae with an almost prognathous head confirm a placement within the Prioninae because among the cerambycoids, prognathous pupae are known only in some prionines. Three Madagascan genera (*Apharsatus* and *Zulphis*: Fairmaire 1893; *Eupalelius*: Fairmaire 1896) were usually misplaced among disteniids in catalogues (e.g., Aurivillius 1912; Boppe 1921; Ferreira & Veiga-Ferreira 1959) because Fairmaire inappropriately compared them in the original descriptions with the disteniid genera *Phelocalocera* Blanchard and *Nethinius*. *Eupalelius* and *Zulphis* are now classified in Dorcasominae (Villiers *et al.* 2011; larvae of *Zulphis* are available and

support that placement). The position of *Apharsatus* has never been revised and the genus is still usually placed in Disteniini although it very probably does not belong there (as noted by Boppe 1921: 3) because according to the original description it does not share the universal disteniid placement of antennal sockets before eyes and approximate to the mandibular articulations.

The group is usually divided into four tribes (Bousquet *et al.* 2009, Löbl & Smetana 2010, both as Disteniinae; Bezark & Monné 2013): Disteniini, Dynamostini, Heteropalpini, and *Cyrtanopini*. Disteniini may be paraphyletic as they are defined solely by lacking apomorphic characters present in the other tribes (such as the externally closed procoxal cavities of Dynamostini and uniquely modified male maxillary palps of Heteropalpini and *Cyrtanopini*). The phylogenetic placement of *Cyrtanops* is ambiguous; depending on interpretation of characters, it could be basal or derived, and both alternatives would imply reversals and/or parallelisms. At present, we prefer the derived position as the large prominent pro- and mesocoxae may be apomorphic and responsible for the partly exposed lateral procoxal angles and broadly open mesocoxal sockets. The antennal grooves with long recumbent setae may be a plesiomorphic character within the family and its absence (associated with absence of the pro- and mesotibial cleaners) in *Cyrtanops* may be secondary. Regardless of some authors claiming absence of those setae also in Dynamostini (Gahan 1906;

Gressitt 1940; Villiers 1980; Martins & Galileo 2001 for *Aiurasya*), the setae are present (even if reduced) at least on several middle flagellomeres (Fig. 2.3.2 D, 2.3.3 E; A. Santos-Silva, personal communication for *Aiurasya*), and also the tibial cleaners are distinct. The unique male maxillary palps shared between Cyrtonopini and Heteropalpini may be a synapomorphy, even if the adults are dissimilar.

Disteniini J. Thomson, 1861. Distribution that of the family. The largest tribe with approximately 300 species; generic classification unsatisfactory and in need of revision in many regions; recent comprehensive taxonomic studies are available only for the New World taxa (Santos-Silva & Hovore 2007 a–d, 2008 a, b; Santos-Silva & Tavakilian 2009; Santos-Silva & Martins in Martins 2010). The only generic name currently used for both Old World and New World species of Disteniini is *Distenia* Le Peletier & Audinet-Serville (synn. *Aphelles* Blessig; *Sakuntala* Lameere; *Thelxiope* J. Thomson, preoccupied; *Thomsonistenia* Santos-Silva & Hovore, *nom. nov. pro Thelxiope*). Old World genera currently in use: *Capnethinius* Adlbauer (Afrotropical: South Africa); *Clytomelegena* Pic (Oriental; syn. *Noeconia* Murzin; Lin & Murzin 2012); *Melegena* Pascoe (Oriental); *Micronoemia* Aurivillius (Seychelles); *Nericonia* Pascoe (Oriental); *Nethinius* Fairmaire (Afrotropical: Madagascar and adjacent islands; occasionally treated as a synonym of *Noemia*); *Noemia* Pascoe (Oriental); *Nupseranodes* Adlbauer (Afrotropical: South Africa); *Olemehlia* Holzschuh (Oriental: Vietnam); *Phelocalocera* Blanchard (Mauritius, Reunion); *Phelocalocerella* Villiers (Mauritius, Reunion); *Saphanodes* Hintz (Afrotropical); *Tengius* Matsushita (Japan); *Thaigena* Holzschuh (Oriental: Thailand); *Typodryas* J. Thomson (Oriental; syn. *Psalanta* Pascoe). New World genera and subgenera currently in use (Santos-Silva & Martins in Martins 2010; Bezark & Monné 2013): *Abauba* Santos-Silva & Tavakilian; *America* Santos-Silva & Tavakilian; *Arietocometes* Santos-Silva & Tavakilian; *Cometes* Le Peletier & Audinet-Serville; *Cupecuara* Santos-Silva & Tavakilian; *Basisvallis* Santos-Silva & Hovore (subgenus of *Distenia*); *Disteniazteca* Santos-Silva & Hovore; *Elytrimitatrix* Santos-Silva & Hovore; *Grossifemora* Santos-Silva & Hovore (subgenus of *Elytrimitatrix*); *Hovorenstia* Santos-Silva; *Novantinoe* Santos-Silva & Hovore (*nom. nov. pro Antinoe* J. Thomson, preoccupied); *Myopsocometes* Santos-Silva & Tavakilian; *Oculipetilus* Santos-Silva & Hovore; *Paracometes* Villiers; *Villiersicometes* Santos-Silva (*nom. nov. pro Microcometes* Villiers, preoccupied).

Adults (Fig. 2.3.1 A–F, 2.3.2 A–C) with antennae longer or even much longer than body; long recumbent setae always present on (almost) all flagellomeres (in some cases indistinct on one or two apical segments, completely missing on flagellomere 1 in *Tengius*). Mandible with distinct mola and associated desclerotized region; apex scalpriform, broadly rounded, rarely (mainly *Nethinius*, Fig. 2.3.4 B) with simple sharp pointed apex. Male maxillary palps normal. Prothorax usually with

lateral tubercles or spines, but sides convex and without tubercles in *Micronoemia*: figures in Adlbauer (2004) (placed in *Nethinius*) or Vives (2009). Prosternal process narrow but usually complete (rarely slightly expanded apically, very narrow and slightly shortened in *Nethinius*); procoxal cavities open externally; lateral procoxal projections and trochantins concealed. Mesocoxal cavities narrowly open to closed laterally. Wing rarely with wedge cell; *Clytomelegena* (Fig. 2.3.1 F, 2.3.2 C) and *Olemehlia* apterous. Legs simple (femora of some species with apical spine, Fig. 2.3.1 A), occasionally very long; lobe of tarsomere 3 deeply cleft.

Dynamostini Lacordaire, 1868. Name based on *Dynamostes audax* Pascoe from the Oriental Region (southern Himalayas): Nepal, northern India, and Yunnan (Lin *et al.* 2010). The genus, although formally unplaced, was apparently considered prionine by its author (“this most remarkable form has no very obvious affinity with any genus of Prionidae yet known”: Pascoe 1857: 90). It was left as of uncertain taxonomic position by Thomson (1861: 379, in Cérambycites; 1864: 309, in Prionites). Lacordaire (1868) created a monogeneric tribe Dynamostides and placed it (together with Thaumastides and Spondylides) in “Légion I. Cérambycides aberrants” of his broad subfamily named Cérambycides. *Dynamostes* was moved to Disteniinae by Gahan (1906).

Adults of *Dynamostes* (Fig. 2.3.1 H, I, 2.3.2 E, F) are robust, relatively large (ca. 20 mm), parallel-sided, somewhat flattened. Color rusty brown to brown-black. Pronotum and elytra often with slightly darker median/sutural and lateral stripes. Antennae much shorter than body in both sexes; recumbent setae in grooves short and restricted to flagellomeres 2–8 (Fig. 2.3.3 E; rather indistinct, particularly on 2 and 8). Mandibular apex scalpriform; molar plate and associated desclerotized region poorly developed, but molar region prominent. Maxillary palps normal; last segment more or less truncate. Prothorax longer than broad, sides without tubercle or spine and coarsely longitudinally rugose. Prosternal process moderately broad and expanded apically; procoxal cavities externally closed (Fig. 2.3.2 E); lateral procoxal projections and trochantin concealed. Mesocoxal cavities closed laterally. Wing without wedge cell; the wing depicted by Villiers (1980: Fig. 65; examined by us) with a proximally open radial cell and only a distal disconnected rudiment of MP₄ may be aberrant as a closed radial cell and a complete bifurcate MP₃₊₄ was present in both wings of another male. Legs moderately long, in males stronger and with hind legs more enlarged; hind tibia in males with two inner ridges ending as large teeth (Fig. 2.3.2 F); lobe of tarsomere 3 deeply cleft.

Santos-Silva & Martins (2004) added to this tribe the Neotropical *Aiurasya potira* Martins & Galileo (Fig. 2.3.2 D; Colombia), originally described without tribal placement (Martins & Galileo 2001). This species shares with *Dynamostes* the pronotal sides

without spine or tubercle and externally closed procoxal cavities. *Aiurasya* is less robust and much smaller (length of the holotype male 7.9 mm), has longer antennae (about as long as body in males, much shorter in females), recumbent flagellar setae better developed and present on all flagellomeres (A. Santos-Silva, personal communication), coarsely punctate sides of the prothorax, and hind legs in males not distinctly enlarged and lacking tibial teeth. Known specimens of *Aiurasya* are dark castaneous, with pale bases of the femora and more or less pale parts of the tibiae and elytral humeri, and a slight metallic tinge on the dark part of elytra.

Heteropalpini Villiers, 1961. Neotropical region, northern part of South America from French Guyana and northern Brazil to Colombia, Ecuador and Peru (P. Demez, personal communication). The two genera *Heteropalpus* Buquet and *Pseudocometes* Villiers (Fig. 2.3.1 G) comprise approximately three or four species. Only one male of *P. argutulus* (Buquet) was available, and no specimens were dissected for this work.

Adults with antennae longer than body in both sexes; all flagellomeres with long recumbent setae. Mandibular apex scalpriform; mola present. Male maxillary palps similar to those in *Cyrtonopini*; process longer and indistinctly annulate. Prothorax with lateral tubercles. Procoxal cavities open externally; prosternal process narrow but complete; lateral procoxal projections and trochantins concealed. Mesocoxal cavities narrowly open (*Heteropalpus*: A. Santos-Silva, personal communication) or closed laterally. Wing without wedge cell. Legs simple; lobe of tarsomere 3 deeply cleft.

Cyrtonopini Gressitt, 1940. The only genus *Cyrtonops* White (syn. *Cladopalpus* Lansberge) comprises eleven species (the status of some of them is uncertain) in the Oriental region, reaching Taiwan, Borneo, Sumatra and Java. The genus was treated as a member of Prionidae by its author (White 1853: 32) who described and depicted a female; in a footnote, he briefly mentioned the peculiar maxillary palp of one available male specimen, considering it a malformation (and thus possibly allowing the subsequent description of *Cladopalpus*). *Cyrtonops* was poorly known to Thomson (1861: 284, 381, 1864: 309) and Lacordaire (1868: 162) who both based its placement in their Prionitae or Prionides, respectively, on White's original description and figure. The genus was placed in Disteniinae by Gahan (1906).

Adults (Fig. 2.3.1 J, K) robust, yellow-brown to black; abdomen and parts of legs may be pale; rarely elytra with blue metallic luster (Bornean *C. metallicus* Hüdepohl). Antennae shorter than body, without long recumbent flagellar setae. Mandible without molar plate; apex bilobed to bidentate. Male maxillary palps as in Fig. 2.3.3 F. Prothorax short and with lateral spines. Procoxal cavities open externally; prosternal process short and partly hidden between prominent contiguous procoxae, their lateral projections and trochantins

partly exposed. Mesocoxal cavities open laterally. Wing without wedge cell; AP₃ may be surrounded by distinct sclerotization (Fig. 2.3.4 E). Legs moderately long, strongly developed; hind legs in males usually enlarged and with dentate inner margins of femur and tibia; pro- and mesotibial cleaning devices virtually absent (more or less distinct in remaining three tribes; corresponds with presence or absence of long recumbent flagellar setae); tarsi broad and lobe of tarsomere 3 only moderately emarginate, not deeply cleft.

Acknowledgments

We are grateful to X. Zhu (Shanghai, China) for biological information on *Dynamostes audax*; to G. Biffi (Museum of Zoology, University of São Paulo), I. Jeniš (Náklo, Czech Republic), N. P. Lord (Department of Biology, University of New Mexico, Albuquerque) and E. H. Nearn (National Museum of Natural History, Washington, DC), for permission to use their photographs; to J. Hájek (Department of Entomology, National Museum, Prague), Meiyang Lin (Institute of Zoology, Chinese Academy of Sciences, Beijing), S. W. Lingafelter (Systematic Entomology Laboratory, National Museum of Natural History, Washington, DC) and N. Ohbayashi (Miura, Japan) for loan or gift of specimens; to A. Santos-Silva (Museum of Zoology, University of São Paulo) for information on the morphology of *Aiurasya potira* and valuable comments on the manuscript; to P. Demez (Ica, Peru) for information on the occurrence of Heteropalpini in Peru. P. Svacha acknowledges support from the Institute of Entomology (RVO:60077344).

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