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Richard A. B. Leschen
Rolf G. Beutel
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Scientific Editors

Richard A. B. Leschen
Landcare Research, New Zealand Arthropod Collection
Private Bag 92170
1142 Auckland, New Zealand

Rolf G. Beutel
Friedrich-Schiller-University Jena
Institute of Zoological Systematics and Evolutionary Biology
07743 Jena, Germany

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- lis americana* Brown (Coleoptera: Chrysomelidae). – *International Journal of Insect Morphology and Embryology* 8: 289–295.
- Monné, M. A. (2002): Catalogue of the Neotropical Cerambycidae (Coleoptera) with known host plant – Part V: Subfamilies Prioninae, Parandrinae, Oxypeltinae, Anoplodermatinae, Aseminae and Lepurinae. – *Publicações Avulsas do Museu Nacional* (Rio de Janeiro) 96: 3–70.
- Mulsant, E. (1839): *Histoire Naturelle des Coléoptères de France. Longicornes*. xi + 304 pp., 3 pls. Maisson, Paris.
- Napp, D. S. (1994): Phylogenetic relationships among the subfamilies of Cerambycidae (Coleoptera – Chrysomeloidea). – *Revista Brasileira de Entomologia* 38: 265–419.
- Penteado-Dias, A. M. (1984): Estudo comparativo do cordão nervoso nos Cerambycidae (Coleoptera). – *Revista Brasileira de Entomologia* 28 (3): 223–243.
- Peslier, S. & Mazel, R. (2009): Données éthologiques et notes sur la répartition de quelques espèces du genre *Vesperus* Dejean, 1821 (Coleoptera, Cerambycidae, Vesperinae). – *Revue de l'Association Roussillonaise d'Entomologie* 18 (2): 49–53.
- Prosen, A. F. (1960): Notas sobre la familia Anoplodermatidae (Coleoptera, Cerambycoidea). – *Anales del Instituto de Medicina Regional* (Tucumán) 5 (2): 87–100.
- Pu, F.-J. (1988): Coleoptera: Cerambycidae. Pp. 293–304 in Huang, F.-S., Wang, P.-Y., Yin, W.-Y., Yu, P.-Y., Lee, T.-S., Yang, C.-K. & Wang, X.-J. (eds.) *Insects of Mt. Namjagbarwa Region of Xizang*. Science Press, Beijing (in Chinese with English summary).
- Reid, C. A. M. (1995): A cladistic analysis of subfamilial relationships in the Chrysomelidae sensu lato (Chrysomeloidea). Pp. 559–631 in Pakaluk, J. & Ślipiński, S. A. (eds.) *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson*. Vol. 2. Muzeum i Instytut Zoologii PAN, Warszawa.
- Saito, A. (1990): Female reproductive organs of cerambycid beetles from Japan and the neighboring areas. I. Philini through Atimiini. – *Elytra* (Tokyo) 18 (2): 231–260.
- Santos-Silva, A., Heffern, D. & Matsuda, K. (2010): Revision of Hawaiian, Australasian, Oriental, and Japanese Parandrinae (Coleoptera, Cerambycidae). – *Insecta Mundi* 130: 1–120.
- Schiødte, J. C. (1864): Danmarks Cerambyces. – *Naturhistorisk Tidsskrift* (Ser. III) 2 (3): 483–576, pl. XX (in Danish and Latin).
- Schomann, H. (1937): Die Symbiose der Bockkäfer. – *Zeitschrift für Morphologie und Ökologie der Tiere* 32: 542–612.
- Sechi, D. (2012): Osservazioni sulla biologia di *Vesperus macropterus* (Coleoptera, Cerambycidae). – *Fragmenta Entomologica* 43 (1): 75–87.
- Sharp, D. (1884): Some observations on *Hypocephalus armatus*. – *Annales de la Société Entomologique de Belgique* 28: cvii–cxii.
- Svacha, P. & Danilevsky, M. L. (1987): Cerambycid larvae of Europe and Soviet Union (Coleoptera, Cerambycoidea). Part I. – *Acta Universitatis Carolinae (Biologica)* 30 [1986]: 1–176.
- Svacha, P., Wang, J.-J. & Chen, S.-C. (1997): Larval morphology and biology of *Philus antennatus* and *Heterophilus punctulatus*, and systematic position of the Philinae (Coleoptera: Cerambycidae and Vesperidae). – *Annales de la Société Entomologique de France* (N. S.) 33: 323–369.
- Thomson, J. (1860–1861): *Essai d'une Classification de la Famille des Cérambycides et Matériaux pour Servir à une Monographie de cette Famille*. Pp. i–xvi + 1–128 [1860], 129–396 + 3 pls. [1861]. By the author, Paris.
- (1864–1865): *Systema Cerambycidarum ou Exposé de Tous les Genres Compris dans la Famille des Cérambycides et Familles Limitrophes*. Pp. 1–352 [Livres 1–3, 1864], 353–578 [Livre 4, 1865]. H. Dessain, Liège.
- Verdugo-Páez, A. (2009): Descripción de *Vesperus barre-dai* (Coleoptera, Cerambycidae, Vesperinae), nueva especie de cerambycido de la Península Ibérica. – *Boletín de la Sociedad Andaluza de Entomología* 16: 21–32.
- Villiers, A. (1978): *Cerambycidae. Faune des Coléoptères de France I*. xxvii + 607 pp. P. Lechevalier, Paris.
- Vives, E. (2001): The systematic position of *Vesperoctenus flohri* Bates, 1891 and the taxonomic status of the Vesperidae (Coleoptera). – *Occasional Papers of the Consortium Coleopterorum* 4 (1): 35–44.
- (2005): Revision du genre *Vesperus* Dejean 1821 (Coleoptera: Cerambycidae). – *Annales de la Société Entomologique de France* 40 (3–4): 437–457.
- Wilcken, C. F., Orlato, C. & Ottati, A. L. T. (2005): Ocorrência de *Migdolus fryanus* (Coleoptera: Cerambycidae) em plantios de *Pinus caribaea* var. *hondurensis*. – *Revista Árvore* 29 (1): 171–173.
- Wu, W.-W. & Chiang [Jiang], S.-N. (2000): A taxonomic study of the male genitalia of some philid beetles with one new species in China (Coleoptera: Cerambycoidea). – *Acta Entomologica Sinica* 43 (1): 78–87 (in Chinese with English abstract).
- Yin, X.-M. (1994): Morphological observation of the immature and adult stages of the philid longicorn beetle (*Philus antennatus*) (Coleoptera: Cerambycidae). – *Journal of Southwest Agricultural University* 16: 265–269 (in Chinese with English abstract).

2.2 Oxypeltidae Lacordaire, 1868

Petr Svacha and John F. Lawrence

Distribution. Two genera (*Oxypeltus* Blanchard in Gay and *Cheloderus* Gray in Griffith) with three species (*Oxypeltus quadrispinosus* Blanchard in Gay, *Cheloderus childreni* Gray in Griffith and *C. penai* Kuschel; Cerda 1972, 1986) occur in central and southern Chile (*Oxypeltus* reaching Magallanes province) and in adjacent southwestern Argentina (all three species in Neuquén province, *Oxypeltus* also in Chubut), within the South American range of the tree genus *Nothofagus* (Nothofagaceae). Although the two species of *Cheloderus* are broadly sympatric, *C. penai* (the most restricted of the three

species occurring in Ñuble and Biobío to Osorno provinces in Chile, and Neuquén province in Argentina) prefers higher altitudes. The nearly flightless females and high host specificity would imply great vulnerability of this relict group without known relatives to forest fragmentation.

Biology and Ecology. Oxyptelid beetles are diurnal and can be usually found on or around their larval hosts. Adult feeding has not been reported in literature. The morphology of adult mouthparts does not suggest non-feeding or florivory and appears compatible with feeding on solid plant tissues. The gut of a dissected female of *C. childreni* contained distinct fibrous plant fragments, and the beetles may possibly feed on fresh bark or other tissues of their host trees. In captivity, females of *C. childreni* occasionally fed on apples (Cameron & Real 1974). Males are strong fliers, whereas females, although winged, almost do not fly and, at least in *C. childreni*, probably produce a long-range pheromone because males are attracted to virgin females (Cerde 1972; Cameron & Real 1974; Gara *et al.* 1978; J. E. Barriga, personal communication). Larvae of all three species develop in living *Nothofagus* trees. *Quercus* and *Myrtus* (currently *Amomyrtus*) *luma* have been also cited for *C. childreni* (Germain 1900: 86–104, *vide* Duffy 1960), but although the local name “coleóptero de la luma” would imply an association with *Amomyrtus luma* (or some other Myrtaceae growing in the region), no reliable data confirming development in this species were found (Cerde 1972). The record from *Quercus* might also require confirmation. The following hosts were listed in Monné (2002): *Nothofagus antarctica*, *N. dombeyi*, *N. procera* and *N. pumilio* for *O. quadrispinosus*, *N. dombeyi*, *N. obliqua* and *Quercus* sp. (probably the above record) for *C. childreni* and *N. pumilio* and *N. antarctica* for *C. penai*. *Nothofagus antarctica* should probably be excluded for the latter species as it was erroneously listed in Kuschel’s (1955) original description of *C. penai* based on material actually collected by Luis Peña on *N. pumilio* (Cerde 1972 and references therein). According to Cameron & Real (1974), females of *C. childreni* attach eggs solitarily on the bark of stems and branch bases of living *Nothofagus* trees. The peculiar reduced female external genitalia serve for collecting debris from the bark surface. At oviposition, the collected material is used for camouflaging the egg. The egg stage lasts several months. Larvae penetrate the bark and gradually excavate a J-shaped gallery oriented upward and leading deep into the wood. That gallery serves as a shelter, and the larva returns for feeding to a broadened flat subcortical cavity around the entrance. Healing tissue produced by the host plant causes a swelling around that cavity and probably serves as the main larval food because the subcortical cavity is of limited size. The gallery is gradually enlarged as the larva grows and long wooden fibers are expelled through a small hole in the bark at the original oviposition site. The larval development is completed after approximately 5–6 years. Pupation occurs at

the top of the larval gallery, and the pupal chamber is separated by a wad of wood fibers; the pupa lies in the cell with its head downward. Pupae were found from September to January, adults from November to May. According to E. Krahmer and J. E. Barriga (personal communication), larvae of *Oxyptelus* develop for at least 2 years in living *Nothofagus* and pupate in April and May in branches. The pupal chamber is constructed in late summer. It is plugged at both ends with long wood fibers and separated by two girdles (Fig. 2.2.7 C) so that, particularly in thinner branches up to approximately 2 cm, the part with the pupal cell usually is broken off by wind and falls to the ground. Adults overwinter in the fallen branch fragments and emerge the next summer.

Morphology, Adults. Moderately sized to large (13–45 mm), robust, not depressed. Surface shiny metallic. Various parts green to blue; elytra with red tinge; color partly depending on viewing angle (Fig. 2.2.1 A, C). Body approximately 2.65–3 times as long as wide. Head, pronotum, scutellar shield and undersurfaces clothed with pale long hairs (Fig. 2.2.1 B) (shorter, sparser and less widespread, particularly in females of *Cheloderus childreni*); elytra and middle of abdominal venter largely glabrous.

Head moderately declined in *Oxyptelus*, strongly so (with mouthparts pointing almost ventrally) in *Cheloderus*; with small slightly protuberant temples behind and slightly below the eyes (often poorly visible dorsally), in *Oxyptelus* moderately constricted behind eyes to form a broad neck. Occipital region without transverse ridge and without median groove. Frontal region more or less impressed medially but without distinct median endocarina. Eyes moderately large, deeply emarginate, with ventral lobes much larger and almost touching anterior cranial margin but not extending onto ventral side; finely faceted, without interfacetal setae; ommatidial structure unknown. Antennal insertions exposed from above, moderately distant from mandibular articulations, located within eye emarginations, supported medially by raised tubercles; facing laterally or anterolaterally, not connected with mandibular articulation by a distinct elevation but a more or less distinct sulcus connecting antennifer to frontoclypeal boundary (epistomal suture); subantennal groove absent. Frontoclypeal sulcus distinct, curved to broadly V-shaped, without deep paramedian impressions; pretentorial pits laterodorsal, close to mandibular articulations, broadly open. Clypeus large, extensively sclerotized. Labrum free, partly retractile, transverse, rounded anteriorly. Antennae in both sexes shorter than body, 11-segmented (last flagellomere may be appendiculate); scape short, curved and dilated distally; pedicel very short and ring-like; flagellum slightly flattened and serrate, without long pilosity; first flagellomere short (clearly shortest of all, particularly in *C. childreni*) and its apical margin emarginate anteroventrally (Fig. 2.2.1 B). Mandible (Fig. 2.2.1 B, D) short and broad, moderately to strongly curved mesally, with bidentate apex; incisor edge simple, without row of

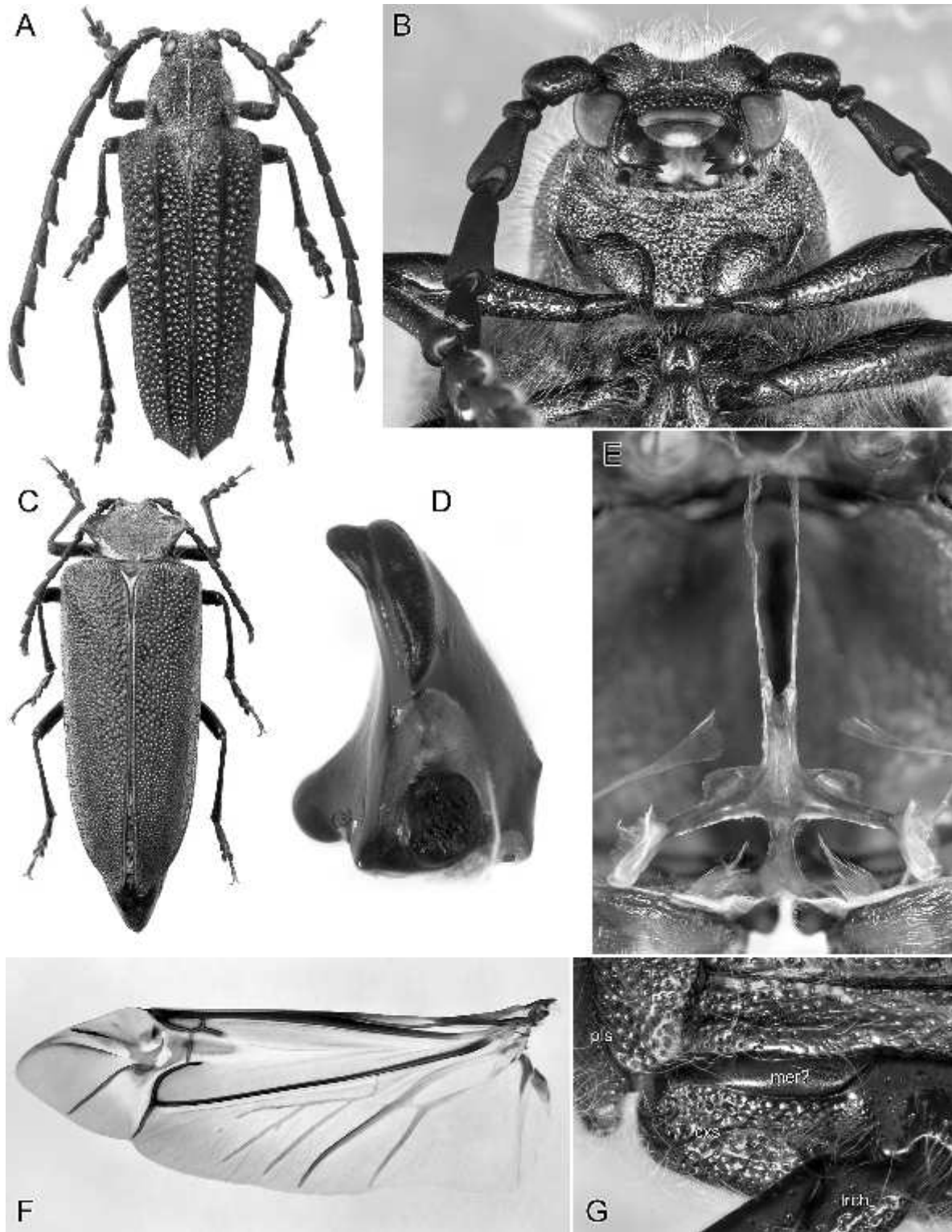


Fig. 2.2.1 Adults. A, *Oxypeltus quadrispinosus* Blanchard in Gay, male, dorsal view, 17 mm (© I. Jeniš); B, *O. quadrispinosus*, male, head and anterior thorax, ventral view; C, *Cheloderus childreni* Gray in Griffith, female, dorsal view, 41 mm (© I. Jeniš); D, *C. childreni*, male, right mandible, mesal view; E, *O. quadrispinosus*, female, metendosternite, dorsal view; F, *O. quadrispinosus*, male, left wing (particularly the conformation of MP_{3+4} is strongly individually variable); G, *O. quadrispinosus*, right hind coxal region, ventral view. cxs, coxal sulcus; mer?, enlarged distinctly delimited region probably belonging to coxal meron; pls, metapleural sulcus; trch, trochanter.

hairs; molar plate well-developed, subcircular and coarsely rugose; anteriorly largely enclosed by membranous region bearing dense microtrichia but not

projecting into a prostheca. Maxilla with distinct, densely setose galea and lacinia, the latter shorter and without uncus. Labial ligula membranous,

bilobed, moderately large. Maxillary palp tetramerous, labial palp trimerous, both short and with fusiform terminal segments. Subgenal ridges absent. Metatentorial slits widely separate. Gular sutures more or less distinct along entire gular length; gula fused with submentum, which projects slightly between maxillary bases. Tentorial bridge intermediate, firm but not broad and roof-like; pre- and metatentorium connected; dorsal tentorial arms present. Cervical sclerites very large.

Pronotum subquadrate or slightly transverse; pair of large flattened triangular laterodorsal projections present in *Cheloderus* (Fig. 2.2.1 C), apparently homologous to paired smooth elongate protuberances in *Oxypeltus* (certainly non-homologous to lateral pronotal carinae of some other cerambycoids); base distinctly narrower than elytra; sides without spines, lateral pronotal carinae absent or vestigial; anterior pronotal angles not produced; posterior angles broadly rounded to subacute; disc without paired basal impressions. Prosternum in front of coxae flat and shorter than shortest diameter of coxal cavity, particularly short in *Cheloderus*. Prosternal process complete, broad, parallel-sided, strongly elevated between and receding dorsally behind coxae. Notosternal sutures complete. Procoxal cavities moderately broadly separated, strongly transverse, angulate laterally, not concealing lateral coxal angles and trochantins, externally open (*Cheloderus*) or closed (*Oxypeltus*), internally closed. Procoxae prominent but not projecting below elevated prosternal process (Fig. 2.2.1 B), without secondary articulation. Mesoscutum short, with broad, shallow emargination anteriorly; with median endocarina; without stridulatory plate; scutellar shield large, acutely triangular, not sharply separated from or abruptly elevated above mesoscutum. Elytra covering abdomen (in some cases slightly dehiscent posteriorly), 2.2–2.5 times as long as combined width; irregularly punctate, without scutellary striole, epipleura very short or absent; elytra of *Oxypeltus* with paired longitudinal ridges terminated anteriorly by prominent parascutellar tubercles, also with tuberculate humeri. Elytral apices distinctly bispinose in *Oxypeltus* and more or less distinctly so in males of *Cheloderus*, whereas in females particularly the outer spine is usually reduced. Mesoventrite separated by complete sutures from mesanepisterna, the latter broadly separated at midline; sharply sloping, anterior edge on different plane than metaventrite, without paired procoxal rests. Mesocoxae subglobular with short lateral angle, moderately projecting, separated by much less than own width; cavities very broadly open laterally to mesepimeron. Mesometaventral junction strongly raised, as high as or raised above mesocoxae; junction complex, with metaventral knob fitting into mesoventral cavity (Fig. 2.2.1 B). Metaventrite with very long discrimen; postcoxal lines absent; transverse (katapisternal) suture more or less complete; exposed portion of metanepisternum short and broad anteriorly. Metacoxae narrowly separate, horizontally oriented, may or (particularly in females of *Cheloderus*)

may not extend laterally to elytral margins; anteriorly with large and well-defined separate area, possibly a posterior expansion of otherwise hidden metacoxal meron (Fig. 2.2.1 G; it is small or usually indistinct in other cerambycoids); coxal plates absent. Metendosternite with lateral arms moderately long; laminae reduced; anterior process present, moderately long and bearing closely associated anterior tendons (Fig. 2.2.1 E). Wings (Fig. 2.2.1 F) present; apical field relatively short (very short and not completely folded in females of *Cheloderus*), with short sclerite just apicad of radial cell, three radial vein remnants and longitudinal sclerite crossing r4; radial cell moderately large, elongate, closed proximally; r3 (at least its distinct part) not longer than cell and longitudinal; r4 with spur rudimentary to absent; basal portion of RP only shortly surpassing r4; medial spur reaching wing margin at a distinct embayment; medial field without medial fleck and usually with five free veins (but number individually variable); at least rudiments of mp_{3+4} -cu present; CuA_2 attached only to MP_{3+4} before its fork; CuA_{1+2} in studied specimens vestigial or absent (and MP_{3+4} thus appears to have typically three branches, although venation of this region is rather variable and veins may be added or lost); wedge cell absent; anal lobe large, without embayment. Legs moderately long, slender; trochanterofemoral joint strongly oblique yet base of femur separated from coxa; tibiae only slightly expanded apically, each with well-developed spurs (2-2-2); fore and mid tibiae without antennal cleaners; tarsi 5-5-5, pseudotetramerous (tarsomere 4 very small and sunken in cavity of tarsomere 3); tarsomeres 1–3 broad, with dense ventral pads, tarsomere 3 deeply bilobed; pretarsal claws simple, without setae, free, moderately divergent; empodium very small (concealed when claws are flexed) and aetose.

Abdomen with five visible sterna (III–VII); first not much longer than second, without postcoxal lines; intercoxal process acute; sternum II invisible. Functional spiracles present on segments I–VII, located in lateral membrane. Terga I–VII well-sclerotized, with metallic coloration. Terminalia strongly modified and very different from remaining cerambycoids (see also Fragoso 1985). Males (Fig. 2.2.2 A, 2.2.3 A–C) with tergum VIII sclerotized and forming genital capsule; sternum VIII desclerotized and without apodeme. Segments IX and X reduced and membranous; sternum IX without spiculum gastrale. Aedeagus of reduced cucujiform type, symmetrical; tegmen ring-like with long anterior strut; parameres fused into small unpaired process (*Cheloderus*, Fig. 2.2.3 B, C) or completely lost (*Oxypeltus*, Fig. 2.2.3 A); penis more or less evenly sclerotized, slightly flattened and ventrally curved, with long narrow paired anterior struts; endophallus (internal sac) entirely within sclerotized distal capsule of penis when inverted, short and bulbous when everted, with a sclerotized apical rod (Kasatkin 2006). Ejaculatory duct thin, unpaired, containing a very long sclerotized rod (Fig. 2.2.3 A, B). Female terminalia (Fig. 2.2.2 B–D,

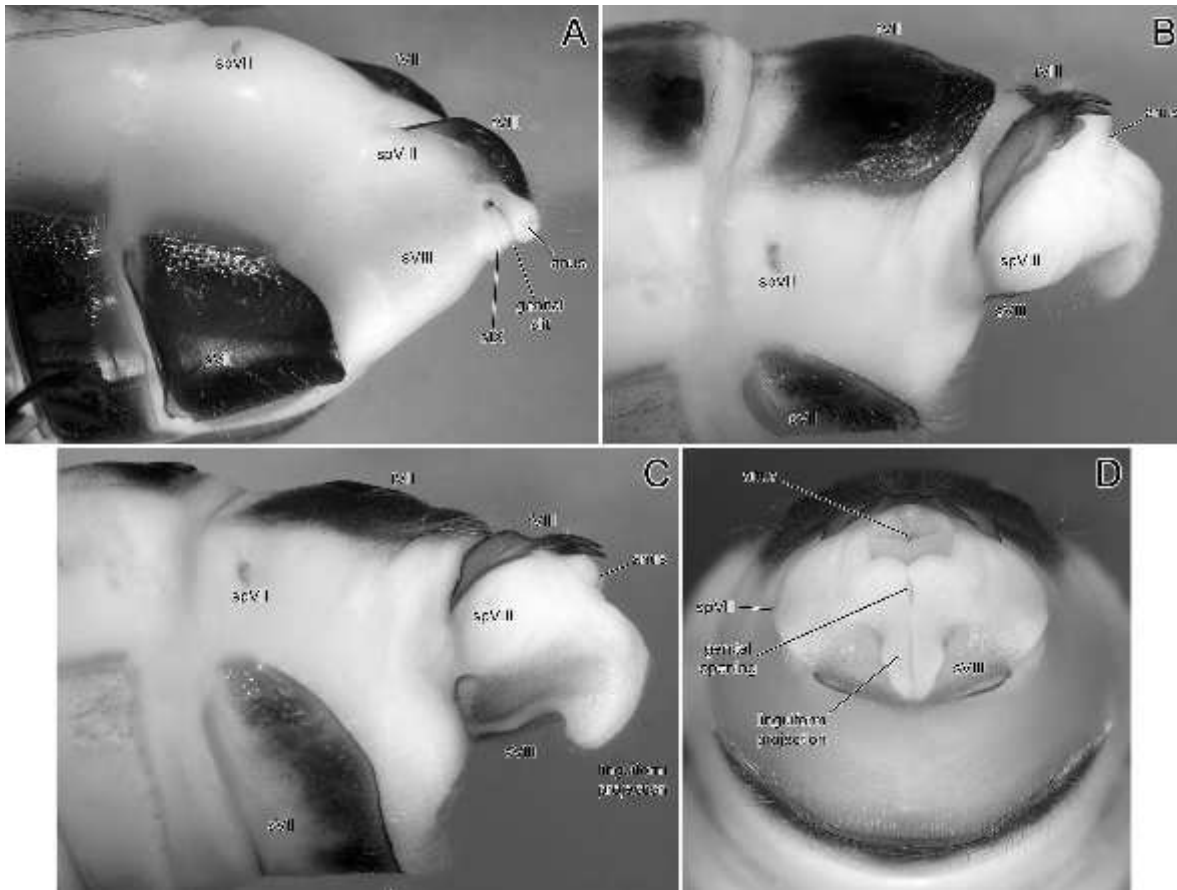


Fig. 2.2.2 *Oxypeltus quadrispinosus*, abdominal end of freshly moulted adults before the fat reserves are resorbed and membranes infolded. A, male, lateroventral view; B–D, female: B, laterodorsal view; C, lateroventral view; D, caudal view. s, sternum; sp, spiracle (vestigial on segment VIII); t, tergum.

2.2.3 D–F) with sclerotized and posteriorly dentate tergum VIII (a structure scraping debris for egg masking); membrane between sternum VII and VIII enlarged (“debris pocket” of Fragoso 1985); sternum VIII with anterior apodeme (spiculum ventrale), desclerotized along midline; posteriorly forming fleshy linguiform projection lateroventrally surrounding a simple membranous egg outlet (no distinct sclerotized ovipositor present). Vagina broad; bursa copulatrix virtually absent; spermathecal duct coiled and slightly sclerotized distally; spermatheca sclerotized, C-shaped, with moderately long gland on distalmost part of duct in *Cheloderus* (Fig. 2.2.3 F); *Oxypeltus* with small, spindle-shaped, poorly sclerotized capsule and a small gland far from terminal capsule (Fig. 2.2.3 D, E). Gut functional (hindgut often filled with food particles).

Morphology, Larvae (Duffy 1960; Svacha & Danilevsky 1987; Svacha *et al.* 1997). Body (Fig. 2.2.4 A, 2.2.6 A, B) soft, white, non-depressed, moderately elongate, almost parallel-sided. Setae simple, sparse and very short. Large body areas [posterior pronotum, posterior margin of prosternum, prothoracic coxal area and pleuron, pterothoracic terga and sternum, ambulatory ampullae (Fig. 2.2.6 E),

and some others] covered with microspines, on some sclerotized prothoracic regions in the form of small sclerotized granules.

Head (Fig. 2.2.4 B, 2.2.5 A, B; for terminology see Fig. 2.4.22) narrow and deeply retracted, prognathous; cranium elongate due to posteriorly expanded epicranial lobes with parallel and approximate dorsal inner margins (not fused as stated in Duffy 1960; i.e., without cranial duplication behind frontal base and with epicranial halves touching dorsally at “one point” immediately behind fusion of frontal lines; coronal suture absent); shape of posterior cranium individually variable. Frontal arms distinct, functioning as cleavage lines (at least during larval/pupal ecdysis), in part secondary as in Cerambycidae (see Fig. 2.4.27 E–I and cerambycid larval description); strongly curved to almost angulate, meeting at nearly 180°, anteriorly passing below antennae (not entering antennal openings) and (almost) reaching cranial margin. Frons entirely sclerotized, rugose and bearing a procurved transverse protuberance (its lateral ends more anterior), with distinct median endocarina; labrum and clypeus also sclerotized and fused with each other and with frons, forming a broadly trapezoidal nasale. Pretentorium as in Cerambycidae; pretentorial pits unusually

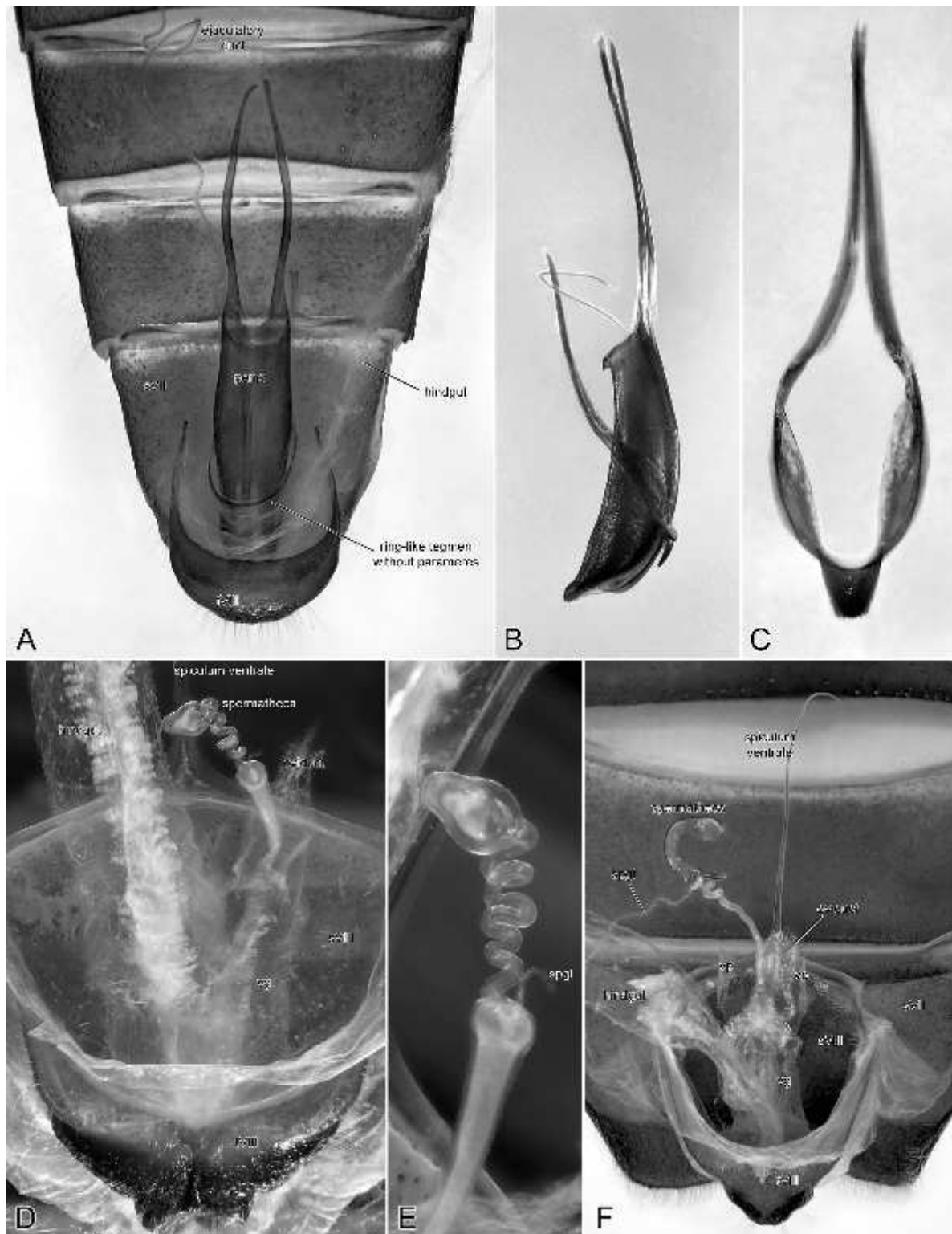


Fig. 2.2.3 Genitalia. A, *Oxyptelus quadrispinosus*, male, end of abdomen, dorsal view (terga removed except for VIII); B, *Cheloderus childreni*, penis (with part of ejaculatory duct) and tegmen, left lateral view (membranes removed); C, *C. childreni*, tegmen, dorsal view; D, *O. quadrispinosus*, female, end of abdomen, dorsal view (terga removed except for VIII); E, *O. quadrispinosus*, detail of spermatheca and spermathecal gland (may not be complete); F, *C. childreni*, female, end of abdomen, dorsal view (terga removed except for VIII). s, sternum; spgl, spermathecal gland; t, tergum; vp, paired vaginal plates (apodemes at anterior end of vagina, see Saito 1989); vg, vagina.

distinct (Fig. 2.2.5 B). Pleurostomal region swollen, without setae and subfossal process; low longitudinal ridge runs from ventral mandibular articulation posteriorly. Six stemmata on each side

arranged in three groups (Fig. 2.2.5 B), three in an oblique row laterad of the antennal socket (lower two with cornea contiguous to fused, although pigment spots often remain distinguishable), two

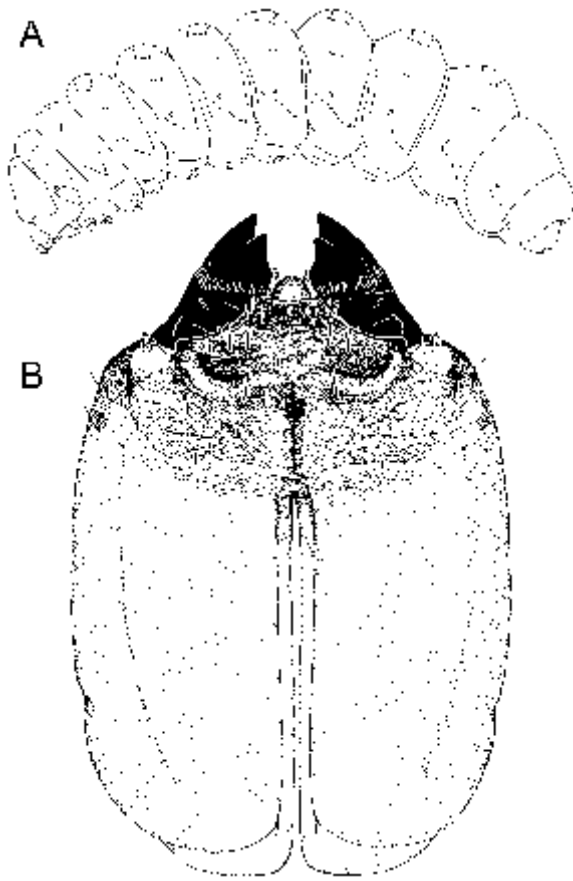


Fig. 2.2.4 Larvae. A, *Oxypeltus quadrispinosus*, larval habitus, left lateral view (from Svacha *et al.* 1997); B, *Cheloderus childreni*, head, dorsal view (from Svacha & Danilevsky 1987).

posterodorsally and one posteroventrally to the first group. Antenna trimerous, moderately long, with large connecting membrane and therefore deeply retractile; membrane smoothly continuous with cranial cuticle that does not form a distinct antennal ring; sensorium conical; antennal retractors attached on posterior frontal margin (Fig. 2.2.5 B, asterisk). Mandibles (Fig. 2.2.5 C, D) symmetrical, strongly sclerotized, with two dorsolateral setae on basal part (ventral one much more distal) and no mesal molar armature or articulated appendage; apical part with apex simple and separated from flat and shallowly bilobed dorsal edge by a distinct incision; in *Oxypeltus* medioapical face at base with cushion of short trichoid structures (Fig. 2.2.5 D; sometimes strongly abraded); position different from the penicillus of some Chrysomelidae (the structure was not found in a single, relatively intact mandible of *Cheloderus* that was studied). Maxillo-labial complex (Fig. 2.2.5 A) more retracted than in Cerambycidae (cardo/stipes border distinctly behind mandibular condyle). Maxillary articulating area sharply divided in two parts, with larger posterior plate-like part fused with submentum and entire fused region slightly sclerotized. Cardo large, free, bearing one short lateral seta, sclerite not distinctly divided; stipes long, maxillary palpiger small, poorly defined, without laterodorsal

process (Fig. 2.2.5 B); palp trimerous; last palpomere with one digitiform sensillum; mala with somewhat carinate inner face, extensively covered with dense long microtrichia with sparse interspersed setae. Distal labium slender; mentum long, almost fused with submentum; pigmentation of labial palpigers not fused medially; ligula entire, lacking setae and densely covered with microtrichia reaching far posteriorly along dorsolateral margin; hypopharyngeal part narrow and abruptly raised, without sclerome. Hypopharyngeal bracon absent. Short hypostomal rods present (ending blindly posteriorly); hypostomal plates not bridged by a sclerotized gula (i.e., connection between labial part of maxillo-labial base and prosternum remains membranous). Metatentorial pits not distinct, metatentorial invaginations very broad, fusing into a plate-like tentorial bridge (lying in same plane as hypostomal plates and misinterpreted by Duffy 1960 as a “concealed hypostoma”) and anteriorly bearing paired fine branches reaching deep into the cranial cavity toward the frontal region but not connected with pretentorial arms (Fig. 2.2.5 A, E).

Prothorax moderately enlarged and not broader than other body segments. Protergum large, strongly inclined, broadly pigmented; pronotum not distinctly delimited except for posterior indistinct rudiments of what may be homologues of cerambycid lateral furrows; sclerotization divided by a soft and flexible median zone, anteriorly with a pair of notches and posteriorly with a pair of paler protuberances just mesad of the rudiments of the lateral furrows; alar lobes partly divided posteriorly by longitudinal impression (indistinct in inflated specimens) laterally delimiting protergal sclerotization. Epipleuron broadly pigmented and delimited by anteriorly diverging lines. Propleuron separate; pleural sulcus indistinct except for deep invagination at upper margin (Fig. 2.2.6 A), projecting internally into a short pleural apodeme. Sternal region (Fig. 2.2.6 B) composed of large and broadly sclerotized anterior plate and narrow, medially constricted posterior fold (possibly sternellum) with laterally adjacent procoxae; posterior fold constricted medially at short but distinct internal process, possibly representing a spina; other sternal endoskeletal elements absent. Pterothorax with mesonotum not distinctly subdivided; postnotum not developed; metanotum divided by two feeble transverse lines. Wing discs absent. Mesothoracic spiracle not protruding into prothorax, narrowly oval, annular-biforous, with two small marginal chambers at upper end; vestiges of metathoracic spiracle distinct. Meso- and metapleuron large, undivided, broadly separating coxa from epipleuron. Mesosternum divided by single trans-sternal line with incomplete anterior oblique branches. Metasternum with (partly) duplicate transverse line. Small but distinct spina present between meso- and metasternum. Coxae poorly defined, unsclerotized; distal legs short (slightly longer than maxillary palps), stout, without any sclerotized articulating points; trochanter unsclerotized and extremely reduced

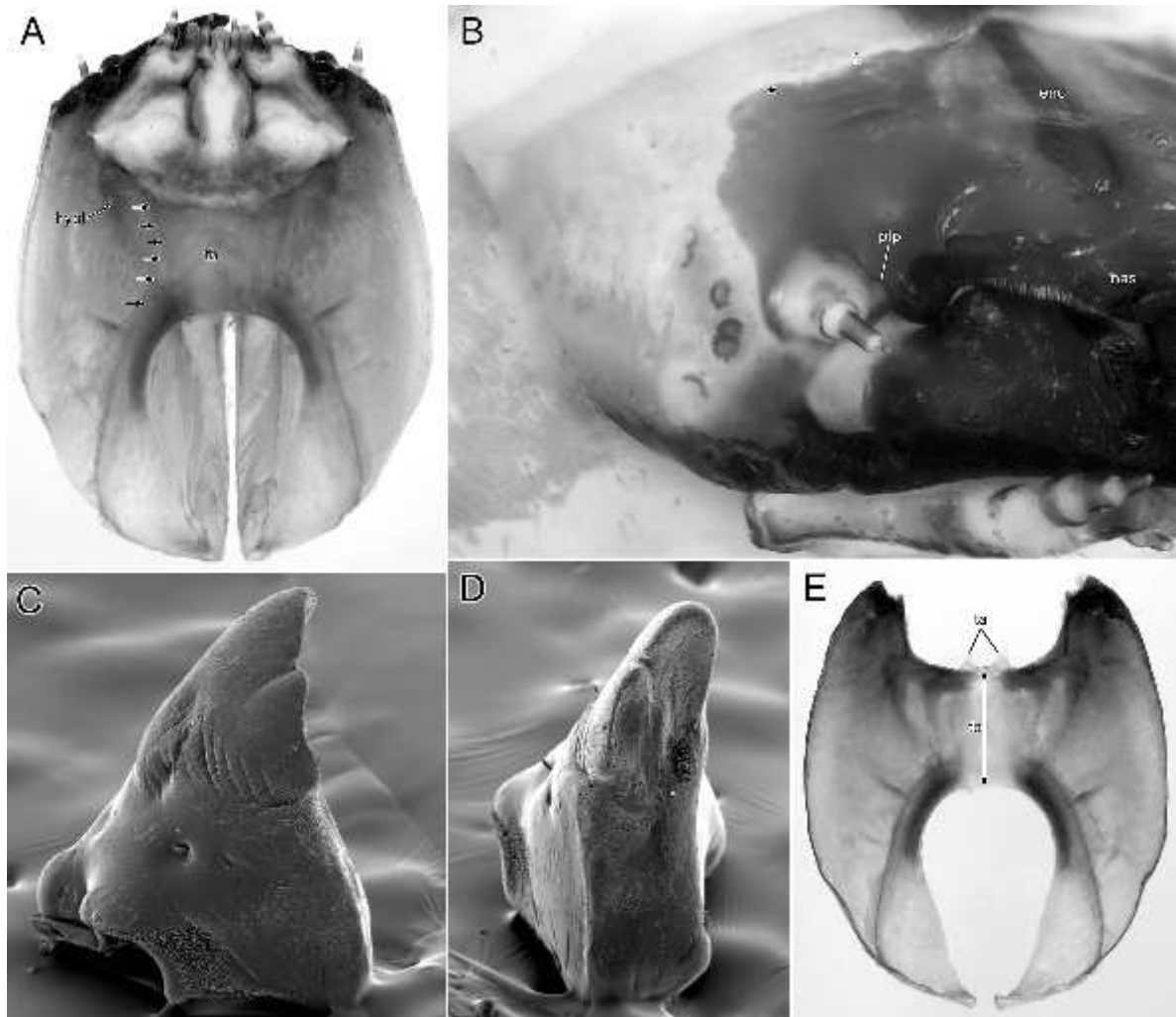


Fig. 2.2.5 *Oxypeltus quadrispinosus*, larva. A, head, ventral view; B, head, anterolateral view; C, left mandible, dorsal view; D, same, mesal view (C and D from Svacha *et al.* 1997); E, ventral half of cranium, dorsal view. enc, median frontal endocarina; fl, right frontal line; hypl, hypostomal lines; nas, sclerotized nasale; pip, right pretentorial pit; ta, slender metatentorial arms on anterior margin of tentorial bridge, cut to short stubs; tb, tentorial bridge; *, point of attachment of retractors of right antenna; arrows in A, broad metatentorial invagination.

laterally; femur annular; tibiotarsus slightly longer than broad; pretarsus stoutly conical, sclerotized and rugulose distally, without setae; desclerotized mesal side of femur and usually adjacent part of trochanter bearing patches of microspines.

Abdomen with broad, flat and poorly delimited dorsal and ventral ambulatory ampullae on segments I–VII (ventral ampullae not distinctly separate from protuberant epipleuron), both divided by two laterally converging transverse lines delimited by one distinct pair of lateral impressions (Fig. 2.2.6 E). Spiracles on segments I–VIII (Fig. 2.2.6 C) similar to mesothoracic spiracles but smaller. Epipleuron protuberant on segments I–IX; epipleural tubercles or discs not defined. Lateral intersegmental zones behind segments I–VI with dorsal infolding forked and embracing dorsal end of ventral infolding (Fig. 2.2.4 A, 2.2.6 A, F). Pleural lobes small, indistinct, posterolateral. Segments IX and X small, subterminal, tergum

IX unarmed. Anus triradiate, ventral radius long. Internal organs (*Oxypeltus* dissected): Foregut slightly asymmetrical, forming a moderately voluminous crop (Fig. 2.2.6 D); midgut not looped posteriorly; with broader anterior part without mycetomes and a posterior part bearing numerous small globular crypts; only very short distal parts of Malpighian tubules forming cryptonephric complex; hindgut simply looped, first fold not twisted above anus. Eight abdominal ganglia distinctly separated, connected by paired connectives; ganglionic complex VIII moved to posterior region of segment VII yet fully separate from seventh ganglion. First-instar larvae unknown.

Morphology, Pupae. Information based on female pupa of *Oxypeltus* (Fig. 2.2.7 A, B). The description and photograph of *C. childreni* in Cameron & Real (1974) is insufficient. Exarate (all appendages free), only very slightly depressed, white, soft, almost



Fig. 2.2.6 Larvae. A, *Cheloderus childreni*, head, thorax and first two abdominal segments, left lateral view; B, *Oxypeltus quadrispinosus*, head and thorax, ventral view; C, *O. quadrispinosus*, 7th right abdominal spiracle; D, *O. quadrispinosus*, gross morphology of larval gut, diagrammatic, dorsal view (foregut black, midgut stippled, hindgut crosshatched; from Svacha *et al.* 1997); E, *O. quadrispinosus*, fifth dorsal abdominal ampulla, cleaned cuticle stained with Chlorazol Black E; F, *O. quadrispinosus*, right side of abdomen cut horizontally immediately above spiracles, dorsal part viewed ventrally, showing intersegmental folds following segments II, III and IV. al, alar lobe; bst, basisternum; cx, coxa; dis, dorsal intersegmental zone; epl, epipleuron; epm, epimeron; epst, episternum; l1, l2, l3, pro-, meso- and metathoracic distal legs (without coxa); lfur?, possible homologues of lateral pronotal furrows of the Cerambycidae; pasc, parascutum (abdominal homologue of lateral part of pterothoracic scuta); pl, pleuron (fused episternum and epimeron); pll, pleural lobe (on abdominal segments); pn, pronotum; psc, prescutum; pst, presternum; sc, scutum; scl, scutellum; sp1, sp2, sp3, mesothoracic, metathoracic (vestigial and closed) and first abdominal spiracle; scpl, scutal plate of dorsal abdominal ampulla; spa, spiracular area (presumed abdominal homologue of pterothoracic alar lobes); stl?, presumed sternellum; stpl, prosternal plate of uncertain homology; vis, ventral intersegmental zone; *, invagination of propleural apodeme; ?, separate transverse fold on ventral abdominal ampulla (may belong to either basisternum or sternellum). For a more detailed discussion of terminology see Cerambycidae.

glabrous (minute setae present on some small tubercles/processes on abdominal terga I–VI). Head bent ventrally, with mouthparts pointing obliquely caudad. Antennae looped separately

between mid and hind legs, not coiled, without spines. Pronotum bears paired round and fleshy processes. Abdomen with functional spiracles on segments I–V (those on VI and VII distinct but

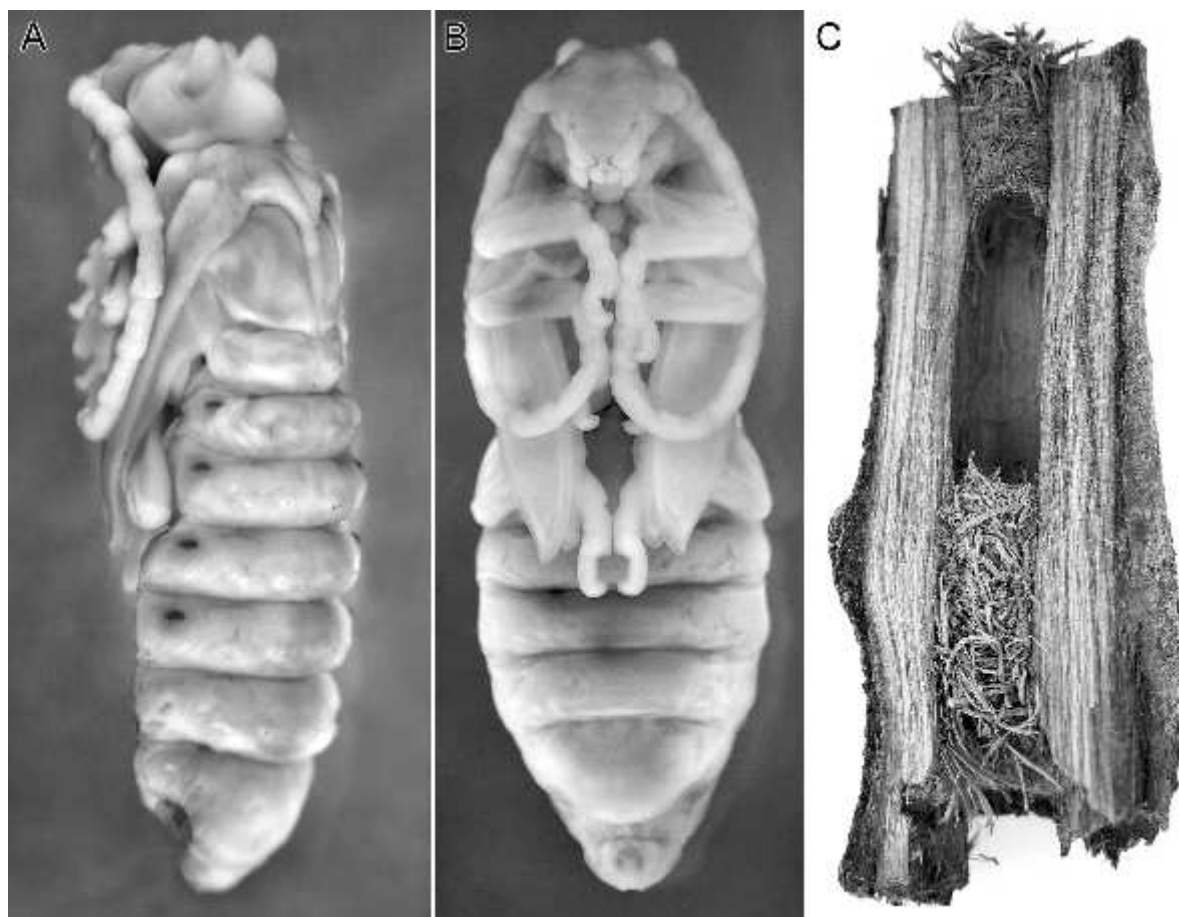


Fig. 2.2.7 *Oxypeltus quadrispinosus*. A, female pupa, dorsolateral view; B, same, ventral view; C, pupal chamber in about 2 cm thick girdled branch fragment of *Nothofagus dombeyi*.

obviously closed, VIII much less distinct), without gin traps; in female, sternum VIII very soft, wrinkled and with slightly marked prospective lingular process; segment IX reduced, tergum without urogomphi or spine, venter without paired lobes (corresponding with absence of ovipositor).

Phylogeny and Taxonomy. The group was revised by Cerda (1972). Both genera were originally classified as an aberrant, problematic group with possible affinities to members of the cerambycid subfamily Prioninae (in part because of the flat pronotal projections of *Cheloderus*, which are not homologous to the prionine lateral pronotal carinae). This concept was accepted by Thomson (1861), but later Thomson (1864) and Lacordaire (1868) removed the two genera from prionines. Thomson (1864) placed them in his Tribus Lepturitae and Division Necydalitae. This was a remarkably heterogeneous group containing (in addition to *Oxypeltus* and *Cheloderus*) 23 other genera currently belonging to three or (if Necydalinae and Lepturinae are separate) four different subfamilies of Cerambycidae. Lacordaire introduced a group named Oxypeltides in his broad subfamily named Cérambycides. Afterward, the group was generally classified in the non-prionine and non-lamiine parts of the Cerambycidae or its equivalents (e.g.,

“Longicornia”), frequently close to forms belonging to or resembling Lepturinae. Crowson (1955) also provisionally placed *Oxypeltus* and *Cheloderus* in his Lepturinae (characterized by himself as “a fairly extensive subfamily of rather uncertain limits” and containing present Dorcasominae and the genera *Vesperus* Dejean and *Mantitheus* Fairmaire of Vesperidae), mentioning that they have “Prionid-like facies, little posterior constriction of the head, and no mesonotal stridulatory file”. Discovery of the extraordinary larvae prompted Duffy (1960), who was otherwise very reserved concerning taxonomic changes, to elevate their rank to a cerambycid subfamily Oxypeltinae. The subfamily rank was accepted by other researchers, such as Cerda (1972, 1986), Monné (1994, 2002, 2006), Lawrence & Newton (1995), and Bousquet *et al.* (2009). Crowson (1981) combined the subfamily with Philinae, Vesperinae and Disteniinae in his family Disteniidae (though it should have been named Vesperidae based on priority). Based primarily on larval characters, Svacha & Danilevsky (1987) and Svacha *et al.* (1997) treated Oxypeltidae as a separate family (followed by Lawrence *et al.* 1999 b). Napp (1994) accepted this concept, although it was not clearly supported by her analysis of adult characters. Even though Monné & Giesbert (1994) placed Oxypeltini as a tribe in their

cerambycid subfamily Aseminae without explanation, recent works (Monné 2012; Bezark & Monné 2013) support the group as a family. Oxypeltidae is undoubtedly a monophyletic taxon bearing some striking apomorphies, which are either unique or have evolved in parallel in unrelated chrysomeloid groups. These characters are as follows: adult males with reduced or lost parameres (Fig. 2.2.3 A–C) and with sterna VIII and IX lacking apodemes; adult females without any traces of a sclerotized ovipositor (Fig. 2.2.2 B–D); elongated larval head with epicranial halves extended posteriorly, with approximated but separate parallel dorsomesal margins (Fig. 2.2.4 B, 2.2.5 A); maxillary mala covered with dense long microtrichia and only few scattered setae; completely fused and sclerotized nasale (Fig. 2.2.4 B, 2.2.5 B). Relationships to other chrysomeloid families are unclear. Oxypeltids were always classified in the cerambycid assemblage (i.e., together with the presently recognized families Vesperidae, Disteniidae and Cerambycidae), but monophyly of that assemblage is not reliably supported, and some larval characters (such as the tendency toward increased sclerotization and fusion of the labrum and clypeus, also occurring but less pronounced in the megapodid subfamily Palophaginae) or preliminary unpublished molecular data (D. McKenna *et al.*, in preparation) suggest possible closer relationships with the Megalopodidae.

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Literature

- Bezark, L. G. & Monné, M. A. (2013): *Checklist of the Oxypeltidae, Vesperidae, Disteniidae and Cerambycidae (Coleoptera) of the Western Hemisphere, 2013 Edition (Updated through December 2012)*. 484 pp. Available at: <http://plant.cdfa.ca.gov/byciddb/documents.html>.
- Bousquet, Y., Heffern, D. J., Bouchard, P. & Nears, E. (2009): Catalogue of family-group names in Cerambycidae (Coleoptera). – *Zootaxa* 2321: 1–80.
- Cameron, R. S. & Peña, L. E. (1982): Cerambycidae associated with the host genus *Nothofagus* in Chile and Argentina. – *Turrialba* 32 (4): 481–487.
- Cameron, W. S. & Real, P. (1974): Contribución a la biología del coleóptero de la luma, *Cheloderus childreni* Gray (Coleoptera: Cerambycidae). – *Revista Chilena de Entomología* 8: 123–132.
- Cerda G., M. (1972): *Revisión de la Subfamilia Oxypeltinae (Coleoptera, Cerambycidae)*. *Publicación Ocasional No. 13*, 10 pp. Museo Nacional de Historia Natural, Santiago de Chile.
- (1986): Lista sistemática de los cerambycoides chilenos (Coleoptera: Cerambycidae). – *Revista Chilena de Entomología* 14: 29–39.
- Crowson, R. A. (1955): *The Natural Classification of the Families of Coleoptera*. 187 pp. Nathaniel Lloyd, London.
- (1981): *The Biology of the Coleoptera*. xii + 802 pp. Academic Press, London.
- Duffy, E. A. J. (1960): *A Monograph of the Immature Stages of Neotropical Timber Beetles (Cerambycidae)*. 327 pp., 13 pls. British Museum (Natural History), London.
- Fragoso, S. A. (1985): The terminalia as a basis for the classification of Cerambycidae (Coleoptera) subfamilies. Part II, Oxypeltinae. – *Revista Brasileira de Entomologia* 29: 165–168.
- Gara, R. I., Cerda M., L. & Kraemer, E. (1978): Sobre la emergencia y vuelo de dos cerambycoides chilenos: *Holopterus chilensis* y *Cheloderus childreni*. – *Turrialba* 28 (2): 117–121.
- Germain, P. (1900): Apuntes entomológicos. Los Lonjicórnios chilenos. – *Anales de la Universidad de Chile* 107: 79–104, 859–912.
- Kasatkin, D. G. (2006): The internal sac of aedeagus of longhorned beetles (Coleoptera: Cerambycidae): morphology, nomenclature of structures, taxonomic significance. – *Kavkazskii Entomologicheskii Byulleten* 2 (1): 83–104 (in Russian).
- Kuschel, G. (1955): Una nueva especie de *Cheloderus* Castelnau (Coleoptera, Cerambycidae). – *Revista Chilena de Entomología* 4: 251–254.
- Lacordaire, J. T. (1868): *Histoire Naturelle des Insectes. Genera des Coléoptères, Vol. 8*. 552 pp., pls. 81–91. Librairie Encyclopédique de Roret, Paris [dated 1869].
- Lawrence, J. F. & Newton, Jr., A. F. (1995): Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). Pp. 779–1092 in Pakaluk, J. & Ślipiński, S. A. (eds.) *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson*. Vol. 2. Muzeum i Instytut Zoologii PAN, Warszawa.
- Lawrence, J. F., Hastings, A. M., Dallwitz, M. J., Paine, T. A. & Zurcher, E. J. (1999 a): *Beetle Larvae of the World: Descriptions, Illustrations, Identification, and Information Retrieval for Families and Subfamilies*. CD-ROM, Version 1.1 for MS-Windows. CSIRO Publishing, Melbourne.
- (1999 b): *Beetles of the World: A Key and Information System for Families and Subfamilies*. CD-ROM, Version 1.0 for MS-Windows. CSIRO Publishing, Melbourne.
- Monné, M. A. (1994): *Catalogue of the Cerambycidae (Coleoptera) of the Western Hemisphere. Part XII. Subfamilies Parandrinae, Anoplodermatinae, Spondylidinae, Aseminae and Oxypeltinae*. 56 pp. Sociedade Brasileira de Entomologia, São Paulo.
- (2002): Catalogue of the Neotropical Cerambycidae (Coleoptera) with known host plant – Part V: Subfamilies Prioninae, Parandrinae, Oxypeltinae, Anoplodermatinae, Aseminae and Lepturinae. – *Publicações Avulsas do Museu Nacional (Rio de Janeiro)* 96: 3–70.
- (2006): Catalogue of the Cerambycidae (Coleoptera) of the Neotropical Region. Part III.

- Subfamilies Parandrinae, Prioninae, Anoplodermatinae, Aseminae, Spondylidinae, Lepturinae, Oxypeltinae, and addenda to the Cerambycinae and Lamiinae. – *Zootaxa* 1212: 1–244.
- (2012): Catalogue of the type-species of the genera of the Cerambycidae, Disteniidae, Oxypeltidae and Vesperidae (Coleoptera) of the Neotropical Region. – *Zootaxa* 3213: 1–183.
- Monné, M. A. & Giesbert, E. F. (1994): *Checklist of the Cerambycidae and Disteniidae (Coleoptera) of the Western Hemisphere*. xiv + 410 pp. Wolfsgarden Books, Burbank, California.
- Napp, D. S. (1994): Phylogenetic relationships among the subfamilies of Cerambycidae (Coleoptera – Chrysomeloidea). – *Revista Brasileira de Entomologia* 38: 265–419.
- Saito, A. (1989): Female reproductive organs of lepturine cerambycid beetles from Japan, with reference to their taxonomic significance (Part 1). – *Elytra* (Tokyo) 17 (1): 65–86.
- Svacha, P. & Danilevsky, M. L. (1987): Cerambycid larvae of Europe and Soviet Union (Coleoptera, Cerambycoidea). Part I. – *Acta Universitatis Carolinae (Biologica)* 30 [1986]: 1–176.
- Svacha, P., Wang, J.-J. & Chen, S.-C. (1997): Larval morphology and biology of *Philus antennatus* and *Heterophilus punctulatus*, and systematic position of the Philinae (Coleoptera: Cerambycidae and Vesperidae). – *Annales de la Société Entomologique de France* (N. S.) 33: 323–369.
- Thomson, J. (1860–1861): *Essai d'une Classification de la Famille des Cérambycides et Matériaux pour Servir a une Monographie de cette Famille*. Pp. i–xvi + 1–128 [1860], 129–396 + 3 pls. [1861]. By the author, Paris.
- (1864–1865): *Systema Cerambycidarum ou Exposé de Tous les Genres Compris dans la Famille des Cérambycides et Familles Limitrophes*. Pp. 1–352 [Livres 1–3, 1864], 353–578 [Livre 4, 1865]. H. Dessain, Liège.

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 (?*Cyrtionops* 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.