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11.22. Trictenotomidae Blanchard, 1845

Darren A. Pollock and Dmitry Telnov

Distribution. The family consists of only two genera: *Autocrates* Thomson (4 species) and *Trictenotoma* Gray (9–10 species). Species in this family have a somewhat restricted distribution; their combined ranges include the southeastern Palaearctic and Oriental regions: Nepal, Korean peninsula, central and southeastern China, India, Sri Lanka, Myanmar, Bangladesh, Thailand, Malaysia (including Borneo), Vietnam, Laos, Cambodia, and Indonesia East to Sulawesi [Gebien 1911; Pouillaude 1914; Telnov & Lee 2008].

Biology and Ecology. For such large and presumably sought-after beetles, the adults of which are seemingly collected fairly easily, it is surprising that so little is known about the life history of species of *Trictenotoma* or *Autocrates*. Only one larval description has been published (see below), with no indication of the biological context of the larva. It has been assumed, perhaps without adequate evidence, that the larvae are inhabitants of decaying logs. Adults are active nocturnally, and are collected most commonly at light. Collections have also been made from fallen trees and on rotten wood, sometimes subcortically, and also on tree fungi. Recent attempts to collect live larvae of trictenotomids in 2004–2006 by the second author and M. Barclay (Natural History Museum) were not successful [Gahan 1908; Lameere 1916; Lawrence 1982; Lawrence 1991].

Morphology, Adults (Fig. 11.22.1 A–D). Total body length 32–80 mm. Body slightly flattened to moderately convex. Dorsal and ventral surfaces clothed with distinct short appressed hairs or setae, more conspicuously on specimens of *Trictenotoma*.

Head prognathous. Width behind eyes narrower than prothoracic width. Eyes large, vertically oriented (higher than long), notched slightly around antennal insertions, without interfacetal setae. Antennal insertions widely separated, concealed from above by projecting canthus. Frontoclypeal suture absent. Clypeus projecting anteriorly between mandibular bases, anterior margin almost straight. Subantennal cavity on the head indistinctly developed. Antennae 11-segmented, robust, longer than half body length. Basal antennomere (scape) elongate, distinctly widened distally, greater than lengths of antennomeres 2 and 3 combined; antennomere 2 short, submoniliform; antennomeres 3–8 filiform, elongate, only slightly widened distally; distal end of antennomere 8 simple (*Trictenotoma*), or with lateral projection (*Autocrates*). Antennomeres 9–11 forming loose, 3-segmented terminal club; antennomeres 9–10 flabellate, slightly more distinctly so in males; surfaces of all antennomeres almost completely glabrous, except for distal surfaces of 9–11 with very dense sensillar fields. Labrum reduced in size, partly visible, free and distinctly transverse, heavily sclerotized, except at base; anterior margin with dense fringe of setae. Mandibles very large (maximum size in male *Autocrates*) and conspicuous, as long or longer than head, projecting anteriorly, with (*Autocrates*) or without (*Trictenotoma*) being conspicuously upturned distally; lateral margins smooth, or with large notch (in some *Autocrates*); apices unidentate; mola small, at extreme base of mandible; prostheca reduced, represented by a small fringe of setae; inner margins of mandibles with several terebral teeth, more numerous in number in *Autocrates*; dorsal surface of mandibles concave mesally, usually with rugose macrosculpture; rugosity also present along lateral regions of mandibles in males of some *Trictenotoma*; ventral groove present on both mandibles, with long row of dense microtrichia. Maxilla with distinct galea and lacinia; lacinia reduced in length, inconspicuous; galea relatively long, slender, beset with dense setae; palpi 4-segmented; distal palpomere subtriangular, expanded. Mentum distinctly concave, with elongate centrally directed setae: labial palpi 3-segmented, with dense setae on palpomeres 1 and 2.

Prothorax transverse, ratio of length/width 0.55–0.65, widest near midlength; base of prothorax subequal in width to base of elytra at humeri. Pronotum convex dorsally, somewhat explanate

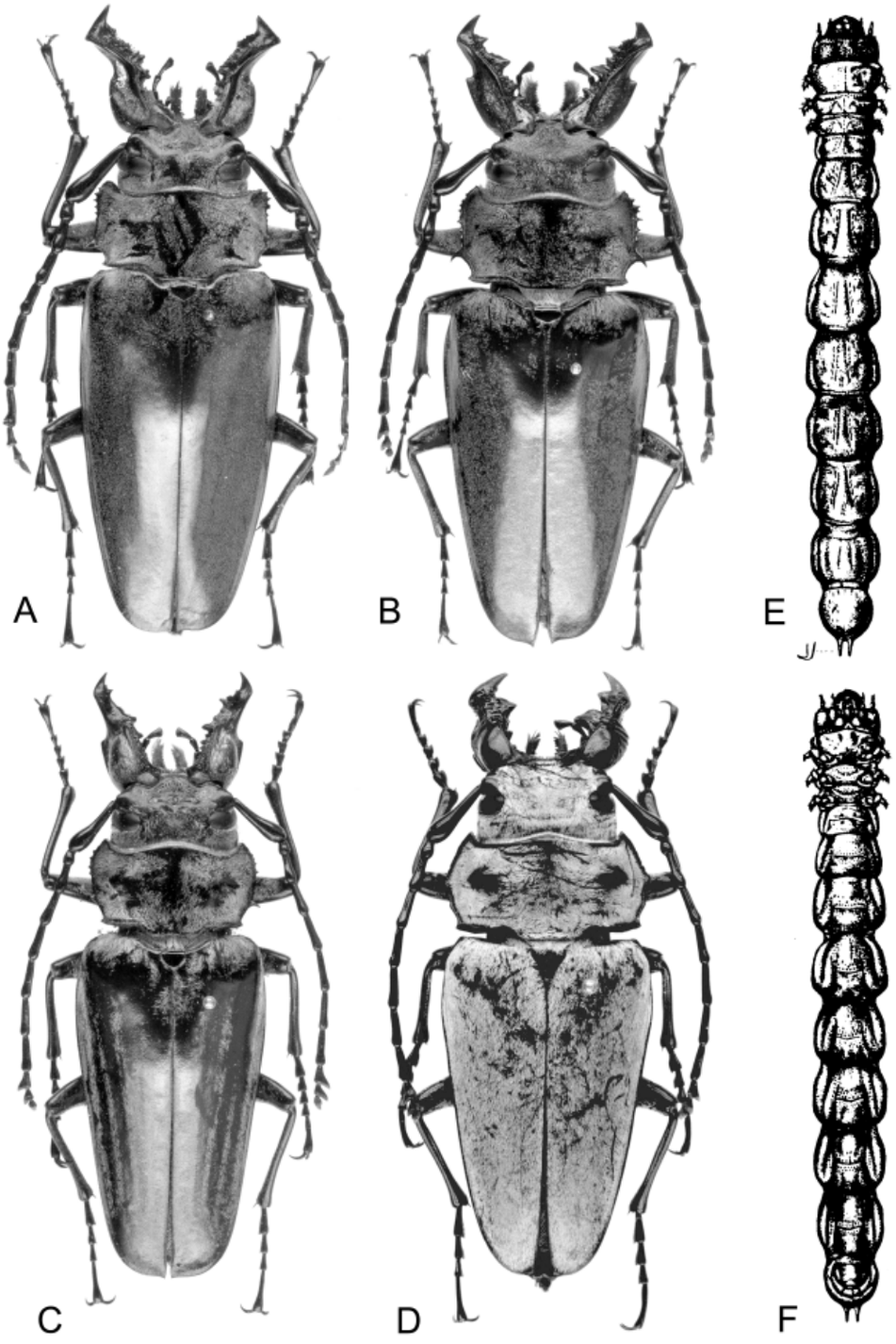

Fig. 11.22.1. A, *Autocrates aeneus* (Westwood), male (Nepal, Phewa Lake, 900 m., Pokhara). From Drumont (2006), by permission, length (excluding mandibles) = 58 mm; B, *Autocrates maqueti* Drumont, male (China, Guilin Co., Guangxi Province). From Drumont (2006), by permission, length (excluding mandibles) = 52 mm; C, *Autocrates oberthueri* Vuillet, male (China, Fujian Province, Wuyishan), length (excluding mandibles) = 56 mm; D, *Trictenotoma davidi* Deyrolle, male (China, Fujian Province, Wuyi-shan Mts.), length (excluding mandibles) = 54 mm; E, *Trictenotoma childreni* Gray, putative larva, dorsal, 120 mm (from Gahan 1908, by permission), length = 120 mm; F, *Trictenotoma childreni* Gray, putative larva, ventral (from Gahan 1908, by permission), length = 120 mm.

towards posterolateral margins, with (*Trictenotoma*) or without (some *Autocrates*) pair of small, circular raised areas on disc; lateral pronotal carinae complete; margin somewhat angulate and/or notched, with several sharp spines along margin in *Autocrates*; hypomera broad; anterolateral angles of pronotum distinctly produced anteriorly; posterolateral angles obtuse or right, often with spine; posterior

margin with distinct bead laterally only; posterior margin with truncate medial region. Anterior edge of large prosternum not produced anteriorly; prosternal process distinct, very wide and parallel-sided, completely separating procoxae; posterior extent of prosternal process with wide bead, either lobed (*Autocrates*) or distinctly notched (*Trictenotoma*), overlapping mesoventrite. Procoxal cavities slightly transverse, open externally and closed internally. Protrochantins slightly exposed. Scutellum distinct, moderately large, posterior margin U-shaped (*Autocrates*) or V-shaped (*Trictenotoma*), at same level as elytral bases; mesoventrite short, with medial groove for anterior edge of metaventrite and (in *Autocrates*) for apical part of prosternal process; mesothoracic coxal cavities closed internally, broadly separated by anterior extension of metaventrite, open laterally. Mesotrochantin visible. Metaventrite long and broad, with indistinct discrimen, beaded along anterior and posterior margins; anterior margin with distinct process (almost keel-like in some *Trictenotoma*), overlapping posterior extent of mesoventrite. Metacoxae distinctly transverse, narrowly separated. Metendosternite with arms separated from base; laminae absent; anterior tendons inserted at about midlength of furcal arms. Legs long, slender, all three pairs very similar in size and shape; trochanters heteromeroid; femora somewhat robust, distinctly broader than slender tibiae, with dense row of setae along anterior (front femur) and posterior (middle and hind femora) margin, especially well developed in *Autocrates*; in *Trictenoma* males each femur with small setal patch near base; tibiae with pair of small apical spurs; tarsal formula 5-5-4, tarsomeres simple, without lobes or accessory processes; distal tarsomere distinctly longer than preceding two tarsomeres, with pair of non-dentate claws; ventral surface of all (but last) tarsomeres with short, dense setae. Elytra fully sclerotized, covering entire abdomen, evenly convex and without distinct macrosculpture; ratio of elytral length/greatest elytral width 1.8–2.0; ratio of elytral length/pronotal length 3.3–4.0; lateral elytral margin almost straight or weakly sinuate, elytra distinctly tapered posteriorly; dorsal surface of elytra apunctate or irregularly, shallowly punctate; sutural stria and scutellar striole absent; apices meeting or almost meeting at the suture, armed with small tooth; epipleuron incomplete, distinct basally, but then abruptly reduced. Hind wing well developed, darkly pigmented; radial cell well developed, elongate; angle formed at base of radial cell right or obtuse; four free veins in medial field; wedge cell well developed; medial fleck and anal notch absent.

Abdomen with five free ventrites. Ventrite 1 longer than any following. Ventrite 5 in males with conspicuous emargination, absent in females. Tergite IX in male completely fused to tergite X. Inverted aedeagus elongate, slender; tegmen divided into short basal piece (basale) and considerably more elongate apical piece (apicale); very narrow, articulated accessory lobes present, inserted towards base of basale, with group of setae at base and apex; lateral lobes expanded, spatulate distally; apex of apicale with distinct notch; median lobe slender, without endophallus or accessory structures, attached to basal piece of tegmen via parameral struts. Ovipositor distinct, elongate, flexible; coxites 1-segmented, uniformly covered by very short setae; coxital and paraproctal baculi distinct; styli apical, short, subcylindrical. Spermatheca complex with six accessory lobes – four longer and two shorter; spermathecal gland very long, narrow, with single branch in *Trictenotoma* and two branches in *Autocrates*; bursa copulatrix very narrow, only slightly expanded at point of attachment of common oviduct.

Description, Larva (Fig. 11.22.1 E–F) (based on description of *Trictenotoma childreni* [Gahan 1908]; quoted sections below are taken directly from this reference). Total length 120 mm. General color pale yellowish-white; head reddish brown with front margin and mandibles black. Head and anterior segments somewhat flattened and depressed. Legs well developed. Segment IX narrower and somewhat shorter than VIII, obtusely rounded behind and apically with two posteriorly produced processes, which are curved upwards and sharply pointed at the end.

Head distinctly prognathous, transverse, with lateral margins rounded. Dorsal surface punctuate. Frontal arms of epicranial suture distinct, lyriform, extended to near antennal insertions; stem of coronal suture present ("a sutural line beginning at the occiput, extends a very short distance forwards in the middle and then branches into two curved lines forming a horse-shoe-shaped impression, from the anterior ends of which, transverse lines may be seen running to the sides of the head to end just before the antennal supports"); Stemmata absent. Distinct labrum fused to clypeus, transverse, anterior margin fringed with setae. Antennae 3-segmented; antennomere 3 very short and narrow; antennomere 2 distinctly shorter and narrower than 1 (no indication from description or illustration of sensorium on antennomere 2). Mandibles large, curved, asymmetrical, tridentate apically; left mandible with two teeth along inner margin. Maxilla with cardo appearing 2-segmented; stipes relatively broad, ending in distinct, 3-segmented palpi; mala with deep distal cleft, bearing shallowly bifid uncus. Mentum relatively narrow; ligula much shorter than 3-segmented palpi. Hypostomal rods apparently present (Gahan 1908: fig. 1, not explicitly mentioned in the description).

Prothorax distinctly transverse, widest slightly posterior of front margin. Surface smooth, impunctate. Meso- and metathorax similar in shape and size, shorter than prothorax, distinctly transverse. Tergites with transverse series of "short small longitudinal carinae near the front margin, and a set of smaller tubercles forming an oblique patch

on each side". Sternites anteriorly with patch of small asperities ("corneous granules"), and posteriorly on each side with a "few more elongate granules or carinae"; thoracic spiracle very large, vertically elliptical (other details about spiracles missing from description). Legs short but distinct, 5-segmented, similar in shape and size on all thoracic segments; coxae very widely separated by ventral sclerites; femora relatively short, widened distally; tibiae attached somewhat obliquely to femora, each with single, large pretarsal claw.

Nine recognizable abdominal segments relatively similar in shape and size. Segment IX distinctly shorter than any preceding segment. Tergites I–VII with "median, triangular, faintly depressed, paler-coloured area, at each side of which is a series of small longitudinal carinae". Tergite VIII without such adornment. Tergite IX with pair of transverse, curved carinae just anterad of urogomphi. Sternite I without carinae or "granules". Sternites II–VIII with "submedian transverse depression, with a granulated area in front and another behind it". Sternite IX with transverse group of granules near anterior margin, enclosing transverse anus. Urogomphi slender, short, parallel, inserted very close together. Abdominal spiracles present dorsolaterally on segments I–VIII.

Phylogeny and Taxonomy. The superficial resemblance of trictenotomids to Lucanidae and Cerambycidae, particularly Prioninae, has obscured the phylogenetic placement of the family. Westwood (1848: 47) had no "hesitation in referring the insect to the section "Longicornes", notwithstanding the internally produced terminal joints of the antennae.., the heteromerous tarsi, and the structure of the organs of generation". Upon examination of the putative larva of *Trictenotoma childreni*, Gahan (1908) noted many similarities between this larva and those of Pythidae, Pyrochroidae and Oedemeridae. It was suggested that the trictenotomids should be placed at the beginning of the "heteromerous series". Lameere (1916) commented upon the various family placements of *Trictenotoma* and *Autocrates*, stating finally that these genera were most certainly Heteromera (Tenebrionoidea) based on the adult tarsal formula and the features of the described larva of *T. childreni*. Two of the early describers of Trictenotomidae placed the constituent taxa in two different families: Lucanidae by Gray (1832), and Cerambycidae (or "Longicornes") by Westwood (1848). These two placements perhaps seem reasonable, given the denticulate lateral pronotal margins in some species, the large mandibles of males, and the loose, three-segmented antennal club.

Crowson (1955) stated that the trictenotomids belong with the "more primitive Heteromera", and that the family is sharply defined, "but of most uncertain relationships". He mentioned the description of the larva by Gahan (1908) and agreed that the larva is very similar to larvae of *Pytho* Latreille and *Pyrochroa* Geoffroy. For the first time, a third genus, *Trimitomerus* Horn, was included in Trictenotomidae based on similarities of the metendosternite. Later, Crowson (1981) merged the genera of Trictenotomidae into the Pythidae, without further explanation. Watt (1987) considered the Trictenotomidae to show significant similarities to both Pythidae and Boridae and suggested that all three be considered separate families. The genus *Ischyomius* Chevrolat, now thought to be in Pythidae (see Pollock 1998), was included in Trictenotomidae by Watt (1987), in the absence of described larvae. In this same work, a cladogram depicting the relationships among related families was presented, as follows: (Trictenotomidae + (Salpingidae + (Boridae + Pythidae))).

A similar conclusion was reached by Pollock (1994), who analyzed the "salpingid group" of families (*sensu* Watt 1987) plus Pyrochroidae. The analysis produced an unresolved trichotomy among Salpingidae, Pythidae, and Trictenotomidae, based on shared possession of parameral struts on the male genitalia. Pollock (1994) further stated that the arrangement of asperities on abdominal sternites II–IX of the *Trictenotoma* larva is an autapomorphy, although these asperities are similar to those seen in eurypine Mycteridae. The placement of Trictenotomidae near the Pythidae and Boridae was retained by Lawrence & Newton (1995) and Pollock & Lawrence (1995).

A novel hypothesis, which is reminiscent of Westwood's old placement, is that of Ferrer & Drumont (2003), who placed the Trictenotomidae near the Cerambycidae in Chrysomeloidea. This scenario was based primarily on the structure of the male genitalia: "The aedeagus of the Trictenotomidae is in fact closer [sic] related to the aedeagus of the Cerambycidae... despite its apparently better resemblance to Pythidae and Salpingidae" (Ferrer & Drumont 2003: 457). These authors account for the heteromerous tarsi of Trictenotomidae by invoking a "very special heteromery". Other features, which confirm the placement of the family among the "salpingid group" are not mentioned by Ferrer & Drumont (2003), particularly the larval description by Gahan (1908). A similar placement was suggested by Drumont (2006), who also recommended the establishment of the Cerambycoidea, comprising Trictenotomidae, Cerambycidae, Oxypeltidae, Disteniidae, and Vesperidae (these latter three taxa are treated as subfamilies of Cerambycidae by Lawrence & Newton 1995).

In a broad examination of larval Tenebrionoidea, Beutel & Friedrich (2005) postulated a sister-group relationship between Trictenotomidae and Pythidae, based on shared possession of plates on the ventral part of tergite IX, and asperities on sternum IX. In conclusion, it seems that the placement of Trictenotomidae within the "salpingid group" is firmly established, although its exact placement remains equivocal. Discovery of additional larvae of *Trictenotoma* and/or *Autocrates*, and

their description, will undoubtedly help to clarify the exact placement.

The only published information on immature stages is the description of a presumptive larva of *Trictenotoma childreni* by Gahan (1908). The association was based on the fact that the larva was found "by the side of the debris of pupae and imagines of *Trictenotoma childreni*, Gray". Unfortunately, nothing is mentioned regarding the habitat of this larva. Given the large size and the salient structural features, there seems no reason to doubt the provisional identity. Apparently, the specimen is in rather poor condition.

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11.23. Pythidae Solier, 1834

Darren A. Pollock

Distribution. As currently defined, Pythidae exhibit a partial amphitropical (Crowson 1980) distribution. Five genera, including two (*Trimitomerus* Horn and *Osphyoplesius* Winkler) provisionally placed in Pythidae pending discovery of larvae, comprise the northern temperate component of the family.