North American myrmecophilous beetles of the genus *Cremastocheilus:* discussion of their classification and review of the subgenera *Trinodia* and *Anatrinodia* (Coleoptera: Cetoniidae)

by J. Krikken

Rijksmuseum van Natuurlijke Historie, Leiden, the Netherlands

Communicated by Prof. J.T. Wiebes at the meeting of October 26, 1981

ABSTRACT

The taxonomy of the subgenera *Trinodia* Casey and *Anatrinodia* Casey, genus *Cremastocheilus* Knoch, a Nearctic group of myrmecophilous scarab beetles, is reviewed. The subgenera of *Cremastocheilus* are keyed and mentioned in an annotated checklist. The monospecific subgenus *Anatrinodia* is re-instated. The characters of the *Cremastocheilus* species are examined, with special reference to *Trinodia* and *Anatrinodia*. The 13 *Trinodia* and *Anatrinodia* species are keyed and mentioned in an annotated checklist. Their phylogeny is briefly discussed. One new *Trinodia* species is described from Mexico. For five species-group names lectotypes are designated.

1. INTRODUCTION

This paper has resulted from an analysis of the morphological diversity in the North American genus *Cremastocheilus* Knoch. Such an analysis is one of the prerequisites for a proposed worldwide reclassification of the whole tribe, the Cremastocheilini (sensu Schenkling, 1921). In material sent for this purpose by the California Academy of Sciences there appeared to be some misidentifications in *Cremastocheilus*, which could be rectified by studying the relevant type-specimens. In the end, however, one Mexican species was left that did not match any of the descriptions and type-specimens. This apparently new species is here described and compared with its relatives by means of a concise review of the subgenus concerned, *Trinodia* Casey.

The subgenera of *Cremastocheilus* are diagnosed and discussed. The characters of all the *Cremastocheilus* species available to me were examined, with special reference to *Trinodia* and *Anatrinodia* Casey. The latter is a

monospecific subgenus incorrectly abandoned by recent authors. The species of these two subgenera are keyed in the present paper, and mentioned in a checklist, which is followed by nomenclatural notes. The new *Trinodia* species is formally described. The phylogeny of the *Cremastocheilus* subgenera and of the *Trinodia* and *Anatrinodia* species is discussed. The species of the two remaining subgenera (see section 2) require the study of much more material, and therefore a revision of the whole genus is postponed. Moreover, my primary objective is a supraspecific reclassification, not a full-scale species-level revision.

The *Cremastocheilus* species are probably all myrmecophilous (sensu Wilson, 1971), but in a manner different from what early authors, like Wheeler (1910), thought. Cazier & Mortenson (1965) were the first to report that, instead of being peaceful synoeketes or symphiles, as suggested by the expanded mentum and antennal scapi, and by the prothoracic trichomes, *Cremastocheilus* actually are ant predators. The final truth, however, may be more complicated, as recently indicated by Kloft et al. (1979), who, by means of radio isotope experiments, established the existence of intimate contacts between the ants and their guests. A good parallel to the mixed symphilous–predatory nature of the Cremastocheilini is found in the paussid beetles (cf. Darlington, 1950), a group of ant predators with sophisticated trichome systems in the derivative groups. Not only Cremastocheilini bearing trichomes are associated with ants: many others without trichomes have inquilinous habits, including the widespread New World genus *Genuchinus* Westwood (cf. Krikken, 1981). Glandular areas with distinct trichomes (thick bushes of setae) occur, apart from *Cremastocheilus*, in two remotely related genera of Afrotropical Cremastocheilini only: *Aspilus* Schaum (trichomes along prothoracic base) and *Lecanoderus* Kolbe (trichome on pygidium). *Aspilus* is found with ants, *Lecanoderus* with ants and termites. As for *Cremastocheilus*, much of the biological information available has been summarized by Cazier & Statham (1962); recently new information was given by Alpert & Ritcher (1975), and, as already mentioned, by Kloft et al. (1979). Ratcliffe (1977) described larva and pupa of *C.* (*Anatrinodia*) *wheeleri*.

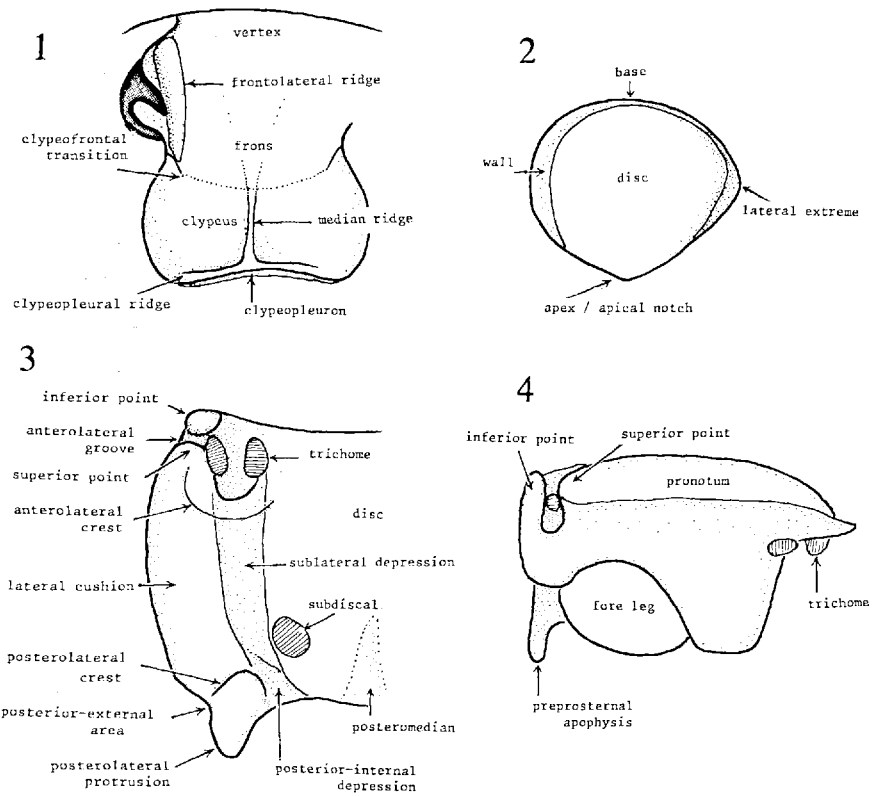
2. THE GENUS, AND A DICHOTOMOUS KEY TO ITS SUBGENERA

As a genus, *Cremastocheilus* stands out by the prothoracic exudatory areas with associated grooves and trichomes. No other cremastocheiline genus has the anterolateral prothoracic grooves characterizing *Cremastocheilus* (cf. also keys in Howden, 1971, Krikken, 1976a), not in the New World, nor anywhere else. Therefore, ruling out parallel evolution, the presence of these grooves constitutes a perfect synapomorphy. Usually, the pronotum of *Cremastocheilus* is broad and has projecting posterolateral angles. Potts (1945) in his key included names of ca. 45 species and subspecies; one more was added since, in *Trinodia*. Some of the names will certainly prove to be synonyms, others need further research as to their validity (see also section 7). In the present paper the species are grouped in four subgenera, instead of three (as has

been done recently, e.g. by Howden, 1971). The monospecific group *Anatrinodia* Casey (1915) is here considered so different from the other *Cremastocheilus* that it is re-instated as a subgenus. No distinct synapomorphy has been found that would justify a simple inclusion in one of the other subgenera. The phylogeny of the subgenera is briefly discussed in section 9. They can be keyed as follows (see figures; terminology, fig. 1–4).

1. Fore tarsal segments 4–5 remarkably "inflated". Head with very distinct frontolateral ridges ..... *Macropodina*
– Distal segments of fore tarsi not "inflated". Head without frontolateral ridges 2

2. Clypeus with median ridge. Pronotum with lateral cushions well separated from medial part. Anterolateral corners of prothorax "auriculate", i.e. with a long upturned inferior point ..... *Trinodia*
– Clypeus without all three features, except that *Anatrinodia* has ill-separated, poorly pronounced lateral pronotal cushions 3
3. Dorsal contours of pronotum strongly rectangular, anterolateral corners with thick trichome. Clypeus and mentum strongly laterally expanded ..... *Anatrinodia*
– Dorsal contours of pronotum different, sides rounded or sinuate, with more or less projecting posterolateral angle. Clypeus and mentum not strongly laterally expanded ..... *Cremastocheilus*



Figs. 1–4. Morphological terms employed in this paper. Composite diagrams of *Cremastocheilus* head (1), mentum, (2), prothorax, dorsal view (3) and lateral view (4).

3. CHECKLIST OF GENUS-GROUP NAMES IN *CREMASTOCHEILUS*

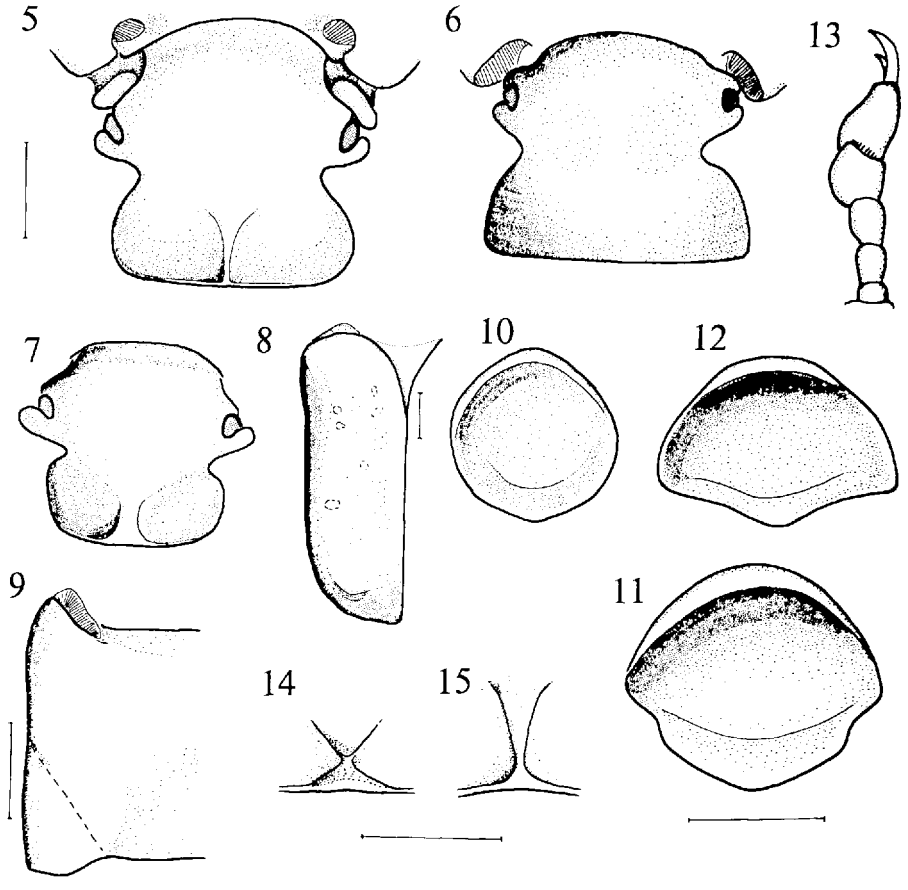
Six genus-group names are available for the species usually combined with *Cremastocheilus*. One is considered a junior synonym, *Myrmecotonus*, of which *Myrmeceia* would be an emendation.

Anatrinodia Casey, 1915: 369 (as subgenus of *Trinodia*), type-sp. *Cremastocheilus wheeleri* LeConte (Casey, 1915). – Midwestern U.S.A., southern Canada, 1 sp.

Cremastocheilus Knoch, 1801: 15, type-sp. *Cremastocheilus castaneus* Knoch (monotypy). – U.S.A., southern Canada, Mexico, ca. 20 spp.

Macropodina Casey, 1915: 344 (as genus, incl. 2 spp.), type sp. *Cremastocheilus planatus* LeConte (Casey, 1915). – S.W. U.S.A., 3 spp.

Myrmeceia Mann, 1914: correction slip, replacement for *Myrmecotonus*. – Unjustified emendation (cf. Howden, 1971).



Figs. 5–15. Details of *Cremastocheilus* species. – 5–7, heads, full-face view, of: 5, *mentalis*, Patagonia; 6, *wheeleri*, Wet Mts; 7, *academicus*, holotype. 8, left elytron of *academicus*, holotype. 9, left half of pronotum of *wheeleri*, Wet Mts. 10–12, mentum of: 10, *academicus*, holotype; 11, *quadricollis*, Houston; 12, *wheeleri*, Wet Mts. 13, fore tarsus of *Macropodina*. 14–15, clypeal median ridge ("nose") of two *Cremastocheilus* species: 14, *hirsutus*, Prescott; 15, *saucius*, lectotype. – Scale lines are 1 mm; same elements, same scale.

Myrmecotonus Mann, 1914: 17, type-sp. *Cremastocheilus knochii* LeConte (original designation). – Synonym to *Cremastocheilus*.

Trinodia Casey, 1915: 365 (as genus, and as subgenus, incl. 6 spp.), type-sp. *Cremastocheilus saucius* LeConte (Casey, 1915). – Southern U.S.A., Mexico, 12 spp.

4. TAXONOMIC CHARACTERS OF INFRAGENERIC IMPORTANCE

The characters of the numerous known species of *Cremastocheilus* have never been studied in such a way that comparison through the entire genus was made possible. I believe that this is due to:

1. the, at first sight, overwhelming morphological diversity within the genus;
2. the absence of a consistent morphological terminology;
3. the neglect of characteristic details of shape, of head, pronotum, and mentum.
4. the unjustified emphasis placed on characters of microsculpture, pilosity and colour; and
5. the total absence of any kind of phylogenetic interpretation of the diagnostic characters.

In figs. 1–4 an ad hoc terminology is proposed for the morphological features important in the infrageneric classification of all *Cremastocheilus*. It is hoped that this terminology will prove to be a useful tool in a future revision of the entire genus. The figures represent a sum of all the morphological features observed, and they are, consequently, not as such based on actual specimens (some of the features are mutually exclusive).

The following list gives the characters and character states that proved to be important for distinguishing the species-group taxa of *Cremastocheilus*. It is based on a survey of ca. 40 species-group taxa, including all known *Trinodia* and *Anatrinodia* species. The species in these two subgenera are compared by means of a synoptic table of characters further below (section 5). Phylogenetic aspects are discussed in section 9. Characters of supposed phylogenetic importance are marked with an asterisk.

Head

*1–1a, clypeus without median ridge; b, with median ridge. Subgeneric character.

1–2a, clypeopleuron narrow; b, broad (more than 0.25 of length of mentum).

1–3a, clypeopleural crest narrow, sharp; b, broad.

*1–4a, lateral flange of clypeus normally expanded; b, very strongly expanded. Subgeneric character.

1–5a, clypeofrontal transition gradual (in profile); b, abrupt.

1–6a, vertex moderately; b, very strongly constricted.

1–7a, clypeus anteromedially without tufted setae (those on clypeopleuron excluded); b, with tufted setae.

1–8a, clypeopleural crest without fringe of long setae (may have short setae; fresh specimens); b, with fringe of long setae.

1–9a, clypeus anteromedially (on median ridge) without whitish tomentum (fresh specimens); b, with whitish tomentum.

1–10a, clypeopleuron (i.e. anterior side) without setae (fresh specimens); b, with short setae all over; c, with very long setae.

1–11a, frons anteriorly without dense fringe of setae (fresh specimens); b, with dense fringe of setae.

*1–12a, frontolateral ridge absent; b, present. Subgeneric character.

Pronotum

2–1a, medially not impressed; b, with more or less impressed midline.

*2–2a, sublateral depression absent; b, distinct, although variable (pronotum with lateral "cushions"). Subgeneric character.

*2–3a, inferior point of anterolateral groove not developed; b, present, but indistinct in dorsal view; c, distinct in dorsal view ("auriculate"). Subgeneric character.

2–4a, anterolateral groove with 2 trichomes; b, with 1 trichome; c, with 3 (apparently separate) trichomes; d, trichomes absent/indistinct.

2–5a, anterolateral groove posteriorly not limited by crest; b, posteriorly limited by crest.

2–6a, posterolateral crest absent/indistinct; b, distinct.

2–7a, posterior-internal depression absent/indistinct; b, distinct, shallow; c. distinct, deep (a cavity).

*2–8a, posterior section of external border not sinuate-emarginate; b, posterior-external border (dorsal view) sinuate; c, posterior-external emargination deep.

2–9a, posterolateral angle not projecting (fresh specimens); b, projecting; c, reduced, "blunted" (fresh specimens).

2–10a, only posterior-external thoracic trichome present; b, posterior internal trichome also distinct (not a mere fringe of sparsely set setae); c, no distinct trichomes in posterolateral area of thorax.

*2–11a, lateral border of pronotum, apart from posterior-external emargination, arcuate (dorsal outline); b, straight or slightly sinuous.

2–12a, pronotum normally wide; b, very narrow ($\leq$0.7 of elytral width combined).

Elytra

3–1a, disco-lateral transition of elytra gradual; b, abrupt.

3–2a, disc without light tomentum; b, with light tomentum (sometimes also on pronotum).

Mouthparts, etc.

*4–1a, mentum posteriorly entire, rounded; b, entire, angulate; c, shallowly emarginate; d, deeply notched.

*4–2a, lateral extremes of mentum entire, not greatly expanded; b, greatly expanded, more or less angulate; c, emarginate.

4–3a, mentum not ridged or walled marginally; b, slightly concave or with low marginal ridge; c, with marginal wall.

4–4a, mentum with length/width ratio ca. 1; b, length/width ratio much less than 1.

Pectus

5–1a, preprosternal apophysis long; b, short (length/width ratio in profile less than 2).

Abdomen

6–1a, sternites 1–4 without trichome-like fringe; b, with trichome-like fringe.

6–2a, propygidial spiracles not produced; b, moderately produced (ratio height/diameter less than 1); c, strongly produced (ditto 1 or more).

Legs

7–1a, fore tibia normally wide (apart from subpedunculate base); b, strongly dilated.

7–2a, fore tibia with 3 external denticles; b, with 2 external denticles.

7–3a, fore tibia with distinct terminal denticle on underside; b, without terminal denticle.

*7–4a, (fore) tibial bases normally wide; b, subpedunculate (sinuate internally).

*7–5a, middle and hind tibiae more or less slender; b, dilated-complanate, narrow; c, dilated-complanate, wide.

7–6a, external protrusion of middle and hind tibia at 0.3–0.6 from apex; b, 0.25 or less from tibial apex; c, protrusion (sub)obsolete.

7–7a, femora not strongly complanate; b, strongly complanate.

*7–8a, tarsal segments all subcylindrical to club-shaped ; b, hind tarsal segments complanate (width/height ratio 2 or less); c, segments 4–5 of fore tarsi "inflated". Subgeneric character.

7–9a, tarsi all 5-segmented; b, 4-segmented.

Other characters

8–1a, colour predominantly black or very dark brown; b, ditto, but abdomen and/or legs more or less reddish; c, predominantly reddish.

8–2a, dorsal side predominantly shiny; b, opaque.

8–3a, dorsum (apart from clypeus) in fresh specimens glabrous, with a few long setae, or with short setae; b, with numerous very long setae.

8–4, range in total length, in mm.

A phylogenetic qualification (autapomorphous, plesiomorphous, parallel, see also section 9) may be applied to several of these 46 characters, especially on the basis of outgroup occurrence and specialisation (directional arguments 1 and 10 of De Jong, 1980). Several of the characters listed may have to be rephrased; a few may prove to be redundant, others may have to be added. Details of microsculpture and pilosity are hard to describe, especially in a list like the one above, where the states should be applicable to all *Cremastocheilus*. Certain characters require the study of series of fresh specimens. Some characters separating twin species (i.e. the closest possible relatives) are not included in the list if they are only conditionally applicable.

5. SYNOPTIC TABLE OF *TRINODIA* AND *ANATRINODIA* SPECIES

The character states for the 13 known *Trinodia* and *Anatrinodia* species are given in the synoptic table reproduced overleaf. Between parentheses = character state poorly pronounced; hyphen = intermediate state occurs; oblique dash = both states occur; question mark = to be checked on more specimens.

The grouping of the *Trinodia* species is based primarily on the pronotal shape, as defined by characters 2–1, 2–8, and 2–9 of the above list. In *Trinodia* five types of pronotum may be recognized (cf. diagrammatic figs. 16–23): A, with 2–1a, 2–8a, 2–9b; B, with 2–1a, 2–8a, 2–9c; C, with 2–1a, 2–8b, 2–9b; D, with 2–1b, 2–8b, 2–9b; E, with 2–1b, 2–8c, 2–9b. The pronotum of *Anatrinodia* (F, fig 21) is very different. The tibial and tarsal characters are also very important, particularly 7–1, 7–4, 7–5 and 7–9. Characters of restricted importance (including the twin species characters alluded to in the end of section 4) are given in the dichotomous key further below.

All the characters are listed, i.e. also those that are of no diagnostic value within *Trinodia*, being similiar for all species mentioned. In this way, however, the table also serves a descriptive function.

Synoptic table of character states:

	1-Head												2-Pronotum												
	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	
mentalis	b	b	a	a	a	b	a	b	b	b	a	a	a	b	c	a	a	a	b	a	b	b	a	a	mentalis
planipes	b	b	a	a	a	b	a	b	b	b	a	a	a	b	c	a	a	a	b	a	b	a-b	a	a	planipes
constricticollis	b	b	a	a	a	b	a	b	b	c	b	a	a	b	c	c	a	a	c	a	c	a	a	b	constricticollis
academicus	b	b	a-b	a	a	b	a	(b)	b	b	a	a	a	b	c	a	a	a	b	b	b	a	a	a	academicus
opaculus	b	b	a	a	a	b	a	b	b	b	a	a	a	b	c	c	a	a	b	b	b	a	a	a	opaculus
lengi	b	b	a	a	a	b	a	a	b	b	a	a	a	b	c	a	a	a	b	b	b	a	a	a	lengi
stathamae	b	b	a	a	a	b	a	b	b	b	a	a	b	b	c	a	a	a	c	b	b	a	a	a	stathamae
spinifer	b	b	a	a	a	b	a	b	b	b	a	a	b	b	c	a	a	a	c	b	b	a	a	a	spinifer
quadricollis	b	b	a	a	a	b	a	b	b	b	a	a	b	b	c	c	a	a	b	c	b	b	a	a	quadricollis
hirsutus	(b)	b	a	b	a	b	a	a?	b	b	a	a	b	b	c	a	a	a	b	c	b	b	a	a	hirsutus
saucius	b	b	a	a	a	b	a	a?	b	b	a	a	b	b	c	a	a	a	b-c	c	b	b	a	a	saucius
excavatus	b	b	a	a	a	b	a	a?	a	a	a	a	b	b	c	a	a	a	c	c	b	a	a	a	excavatus
wheeleri	a	a	a	b	a	a	a	a	a	a	a	a	a	a-b	a	b	a	a	b	a	a	b	b	a	wheeleri

	3-Elytra		4-Mouthparts				5-	6-Abdomen		7-Legs									8-Other				
	1	2	1	2	3	4	1	1	2	1	2	3	4	5	6	7	8	9	1	2	3	4	
mentalis	b	a	b	a	b	a	a	a	b	b	b	b	a	c	b	b	a	a	c	b	b	12-13	mentalis
planipes	b	a	b	a	b	a	a	a	b	b	b	b	a	c	b	b	a	a	b	b	b	12-14	planipes
constricticollis	b	a	b	a	b	a	a	a	a-b	a	b	b	a	a	a	a	a	a	c	b	a	11-13	constricticollis
academicus	b	(b)	a	a	b	a	a	a	b	a	b	b	a	a	a	a	a	a	a	b	a	9-10	academicus
opaculus	b	a	b	a	b	a	a	a	b	a	b	b	a	a	a	a	a	a	a	b	a	10-11	opaculus
lengi	b	a	a	a	b	a	a	a	b	a	b	b	a	a	a	a	a	b	a-b	b	a-b	9-10	lengi
stathamae	b	b	b	a	c	a	a	a	b-c	a	b	b	a	a	a	a	a	a	b	b	b	8-9	stathamae
spinifer	b	a	b	a	c	a	a	a	b-c	a	b	b	a	a	a	a	a	a	b	b	b	7-8	spinifer
quadricollis	a	b	b	c	b	a	b	a	b	a	b	b	a	a	c	b	b	a	a/c	a	b	12-13	quadricollis
hirsutus	a	a	b	a	a	a	b	a	b	a	b	b	b	b	a	b	b	a	c	b	b	12	hirsutus
saucius	a	a	b	a	a	a	b	a	b	a	b	b	b	b	a	b	b	a	c	a	a	9-11	saucius
excavatus	a	a	a-b	a	a-b	a	b	a	b	a	b	b	b	a-b	a	b	b	a	c	b	a	10-11	excavatus
wheeleri	b	a	b	b	c	b	b	a	c	b	b	b	a	c	a	b	b	a	a	b	a	10-11	wheeleri

6. DICHOTOMOUS KEY TO *TRINODIA* AND *ANATRINODIA* SPECIES

For more details, see synoptic table overleaf and figures of pronotal and other characters; terminology, figs. 1–4[1]).

1. Clypeus with median ridge connected with high clypeopleural ridge. Pronotum with distinct lateral cushions. Inferior point of anterolateral pronotal angle very distinct from above .... (*Trinodia*) 2
– Clypeus without median ridge, without high clypeopleural ridge. Pronotum without distinct lateral cushions. Inferior point of anterolateral pronotal angle invisible from above ..... (*Anatrinodia*) *wheeleri*
2. Pronotum very narrow, with shortened, blunt posterolateral angle (fresh specimens), type B ..... *constricticollis*
– Pronotum wider, with projecting acuminate posterolateral angle (fresh specimens) 3
3. Pronotal side with straight, non-sinuate posterior section, type A. Pronotal midline not impressed. Legs flattened 4
– Pronotal side with more or less strongly sinuate posterior section 5
4. Predominant colour reddish-brown ..... *mentalis*
– Predominant colour black ..... *planipes*
5. Pronotal sides posteriorly very strongly sinuate-emarginate, type E 6
– Pronotal sides posteriorly moderately sinuate, types C, D 9
6. Fore tibia subpedunculate (base internally sinuate) 7
– Fore tibia simple (base internally not sinuate) ..... *quadricollis*
7. Details of posterolateral and anterolateral parts of prothorax, figs. 33, 34. Middle and hind tibiae very narrow (fig. 41) 8
– Details of posterolateral and anterolateral parts of prothorax, fig. 35. Middle and hind tibiae moderately narrow (fig.40) ..... *excavatus*
8. Dorsum strongly setose (fresh specimens!), derm of dorsum, pectus and abdomen opaque. Clypeus with median ridge reduced (fig. 14) ..... *hirsutus*
– Dorsum glabrous or inconspicuously setose, derm shiny. Clypeus with median ridge narrow, elongate (fig. 15) ..... *saucius*
9. Posterior-internal depression of pronotum deep. Midline of pronotum impressed 12
– Posterior-internal depression of pronotum shallow. Midline of pronotum not impressed ... 10
10. Median ridge of clypeus broad. Posterolateral angle of pronotum acute, strongly turned outward. Tarsi robust, 5-segmented ..... *academicus*
– Median ridge of clypeus narrow. Posterolateral angle of pronotal less strongly turned outward 11
11. Tarsi robust, 4-segmented. Postclypeopleural impression moderately deep ..... *lengi*
– Tarsi slender, 5-segmented. Postclypeopleural impression very deep ..... *opacus*
12. Pronotum and head with extensive whitish tomentous markings and with very long setae ... *stathamae*
– Pronotum and head without such markings, with shorter setae ..... *spinifer*

7. CHECKLIST OF *TRINODIA* AND *ANATRINODIA* SPECIES

In this list each name is followed by: author and reference to first description; original status, if different from present; location of type(s), for abbreviations cf. Acknowledgements; approximate known distribution, type-locality; ant host (genera). Some synonymic and other nomenclatural notes are added further below.

---

[1] In consulting the figures one should bear in mind that various details are subject to individual and geographical variation and to wear.

academicus Krikken, present paper (subg.*Trinodia*), holotype in CAS! – Mexico (type-loc. Rio Linares). Host unknown.

constricticollis Cazier, 1940: 127 (subg. *Trinodia*), holotype in Robinson coll.–Arizona (type-loc.Bonita). With ants *Myrmecocystus*, cf. *Pogonomyrmex*.

excavatus Cazier, 1940: 133 (subg. *Trinodia*), holotype in USNM! – Mexico (type-loc. Durango). With ants of unidentified myrmicine genus.

hirsutus Van Dyke, 1918: 13 (subg. *Trinodia*), lectotype in CAS! – Arizona (type-loc. Prescott). With ants *Pogonomyrmex*.

lengi Cazier, 1938: 86 (subg. *Trinodia*), holotype in Cazier coll.–Arizona (type-loc. Palmerlee). With ants cf. *Myrmecocystus;* also with myrmicines.

mentalis Cazier, 1940: 129 (subg. *Trinodia*), holotype in Cazier coll.–Arizona (type-loc.Nogales). With ants *Dorymyrmex, Novomessor, Pogonomyrmex*.

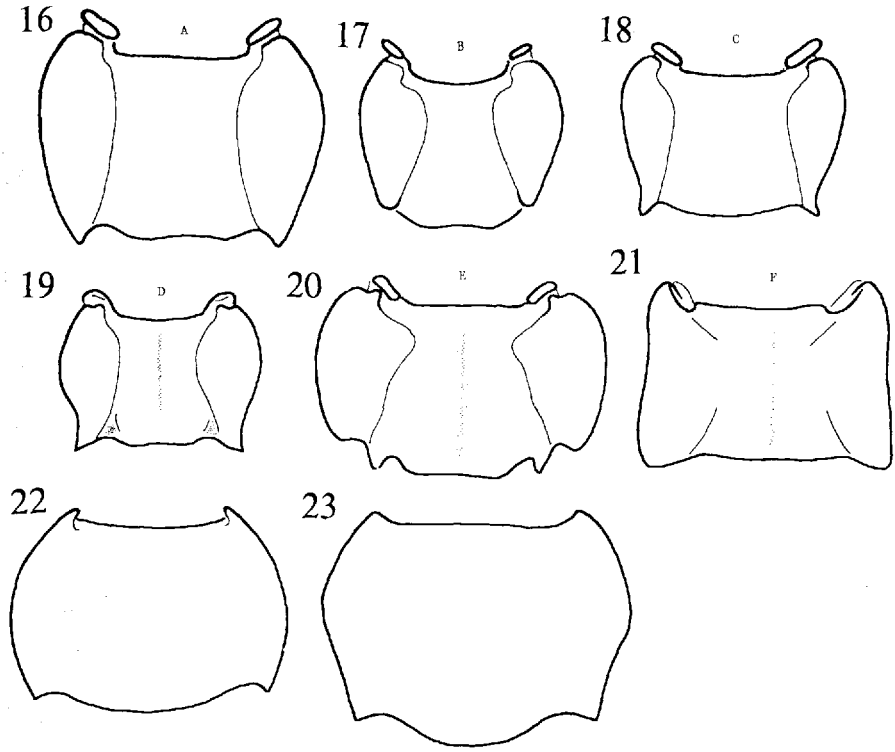
opaculus Horn, 1894: 399 (subg. *Trinodia*), lectotype in CAS! – Mexico: Baja California (type-loc. Pescadero), Arizona? With ants *Formica*?

planipes Horn, 1885: 127 (subg. *Trinodia*), lectotype in MCZ! – Arizona (type-loc. not detailed, Arizona). With myrmicine ants.

quadricollis (Casey, 1915: 368, *Trinodia*), holotype in USNM! Syn. nov. *setosifrons* (Casey, 1915: 367, *Trinodia*), lectotype in USNM! – Texas (type-loc. Waco), Kansas; Mexico. Host unknown.

saucius LeConte, 1858: 16 (subg. *Trinodia*), lectotype in MCZ! – Nebraska (type-loc. Lodge Pole Creek), Kansas, Colorado, Texas, New Mexico. With ants *Pogonomyrmex*.

spinifer Horn, 1885: 126 (subg. *Trinodia*), holotype in MCZ! – Texas (type-loc. not detailed, Texas), New Mexico. With ants *Pheidole*.



Figs. 16–23. Types of pronotum in the *Cremastocheilus* subgenera *Trinodia* and *Anatrinodia* and in their primitive relatives *Cremastocheilus* s. str. and *Centrochilus*. – 16, *mentalis* type (A); 17, *constricticollis* type (B); 18, *lengi* type (C); 19, *spinifer* type (D); 20, *saucius* type (E); 21, *Anatrinodia* type (F); 22, *Cremastocheilus schaumi* LeConte; 23, *Centrochilus howdeni* Krikken.

stathamae Cazier, 1961: 3 (subg. *Trinodia*), holotype in Cazier coll.? – Arizona (type-loc. Portal). With ants *Myrmecocystus, Novomessor.*

wheeleri LeConte, 1876: 516 (subg. *Anatrinodia*), holotype cf. in MCZ. – Colorado, Nebraska, New Mexico (type-loc. northern New Mexico). California.

Nomenclature:

The type-material relating to 8 species-group names of uncertain status had to be examined; they are listed here, in alphabetical order, with label data, comments, and lectotype designations, where appropriate.

excavatus Cazier, holotype from "Durango/Dgo. Mex./Wickham", USNM type no. 54790.

hirsutus VanDyke, lectotype, here designated, from "Prescott/Ariz./VI-11-1910", "Coll./J. Aug. Kusche", CAS type no. 3278.

opaculus Horn, lectotype, here designated, from "Pescadero", CAS type no. 62.

planipes Horn, lectotype, here designated, from "Ariz", MCZ type no. 3713.

quadricollis Casey, holotype from "Tex.", "Waco/4/12" USNM type no. 48709. Brownish black, older specimen, very similar to *setosifrons*, q.v.

saucius LeConte, lectotype, here designated, from "Pole Cr./Wood", "C. saucius/Pope Lec.", MCZ type no. 3786.

setosifrons Casey, lectotype, here designated, from "Clark Co. Ks/May–1962 ft/F.H. Snow", USNM type no. 48708. Red-brown, fresh specimen, very similar to *quadricollis*, q.v.

spinifer Horn, holotype from "Tex.", MCZ type no. 3711.

Species-group taxa like *spinifer* versus *stathamae*, and *planipes* versus *mentalis*, are so closely related that they may, eventually, turn out to have subspecific status.

8. *CREMASTOCHEILUS (TRINODIA) ACADEMICUS* SP. NOV.

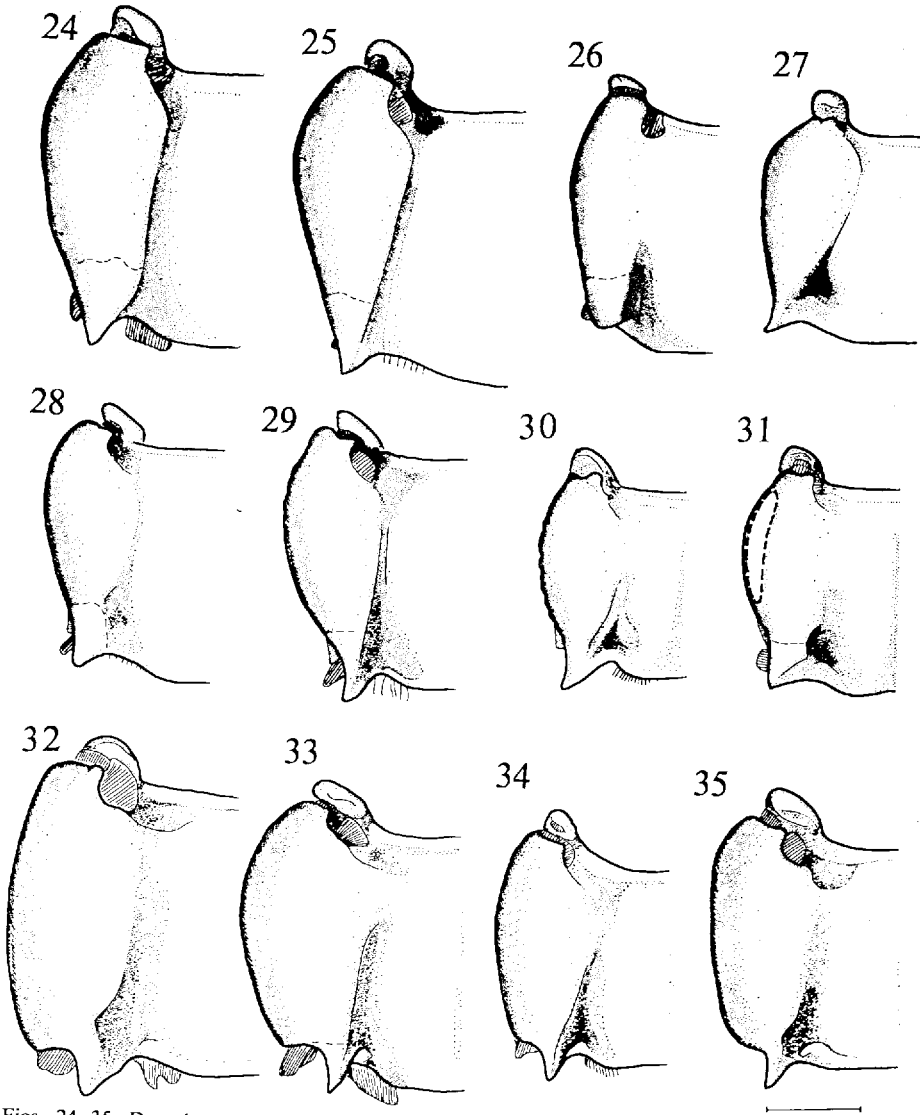
Holotype (male). – Approximate length 9.5, width 4, height 3 mm. Black, opaque, pilosity brownish, short everywhere; most microsculptural units with a minute seta. Habitus elongate-deplanate, like other *Trinodia* species.

Cephalic contours, fig. 7. Clypeus with broad median ridge, clypeopleural crest broad; clypeopleuron broad, surface scabrous; clypeofrontal transition gradual; densely, finely punctate; punctures not distinctly annulate-striolate, their diameters ca. 0.3 of those of the pronotal disc; pilosity of head diminutive, except laterally on clypeopleural crest, where setae are abundant, with lengths mostly several times the diameter of the frontal punctures. Maximum width of head 2.2 mm.

Pronotal contours, fig. 27; vertigial constriction not accented by declivous anteromedian part of pronotum; pronotal disc without midline impression; lateral cushion distinct, but feebly convex; posterior-internal depression distinct, but shallow; posterolateral protrusion sharp, its underside with small trichome (partly worn away); anterolateral groove with trichomes (partly worn away) between superior and inferior points; internal part of superior point protuberant. Pronotal disc annulate-striolate; striolae circular to slightly elongate-elliptic, many of them with a longer seta; striolae crowded laterally, almost sparse along apex and base; their densities ca. 25/0.25 sq. mm; lateral cushions with smaller, scattered, subannulate punctures, mostly separated by 2–4 times their diameters, many with a seta ca. twice as long as the punctural

diameter; surface of posterolateral smooth, shiny. Median length of pronotum 2.0, maximum width 3.1 mm. Scutellum (fig. 8) with 12 arcuate striolae.

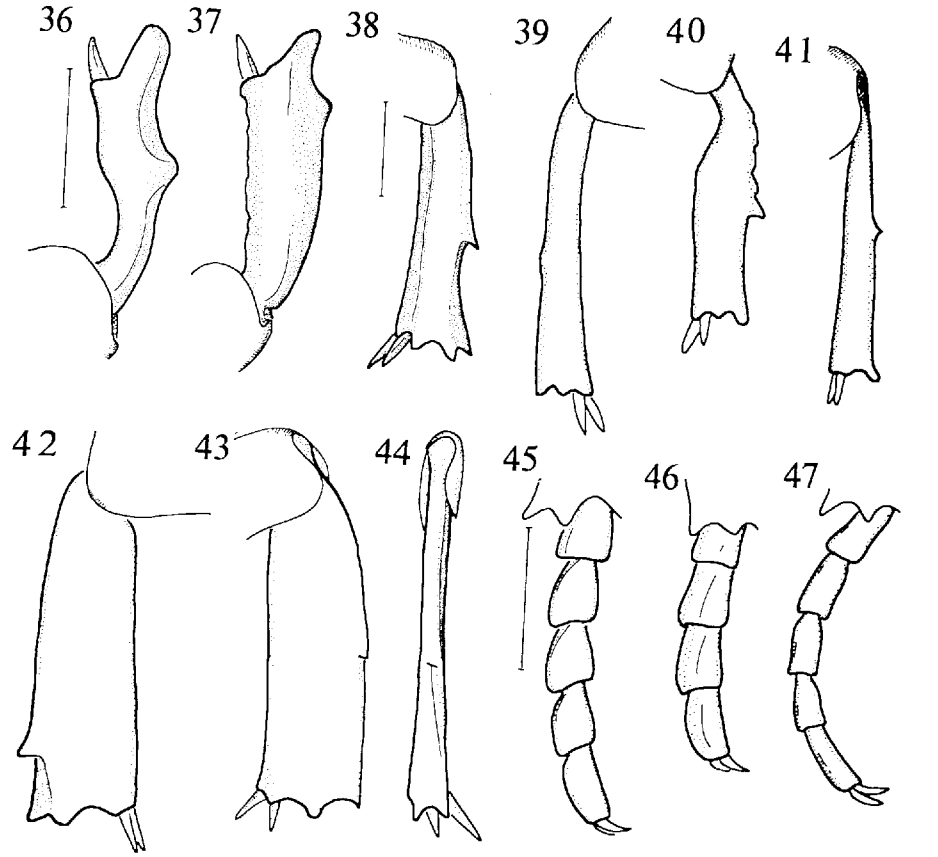
Elytral contours, fig. 8; elytral disc with sinuous and elongate-annulate striolae, many of them encompassing one or more minute punctures bearing a fine seta; some scattered speckles of whitish velutinous matter present; lateral and distal declivities of elytron with abundant fine punctures, nearly all bearing seta. Sutural length of elytra 4.2, maximum (longitudinal) length 5.7, maximum width combined 4.1 mm.



Figs. 24–35. Dorsal pronotal contours (left half) of *Cremastocheilus* (*Trinodia*) species. – 24, *mentalis*, Patagonia; 25, *planipes*, Tombstone; 26, *constricticollis*, Tombstone; 27, *academicus*, holotype; 28, *lengi*, Sta Catalina Mts; 29, *opaculus*, lectotype; 30, *spinifer*, Del Rio; 31, *stathamae*, Portal; 32, *quadricollis*, holotype; 33, *hirsutus*, Prescott; 34, *saucius*, lectotype; 35, *excavatus*, holotype. – Scale line is 1 mm; all drawn to same scale.

Mentum, fig. 10; surface of backward extension virtually smooth, perimarginal wall well-developed. Antennal scapus dilated as usual, subtrangular, posterolateral angle rounded. Preposternal apophysis short. Lateral parts of pectus abundantly multistriolate (proepisternum) to arcuate-striolate (rest, including hind coxa). Metasternal disc with abundant fine punctures, nearly all bearing a minute seta. Abdomen medially impressed, with abundant, scattered, arcuate-striolate (laterally) to simple punctures (medially), nearly all bearing a minute seta. Pygidium strongly convex, with abundant, scattered, simple punctures, nearly all bearing a minute seta; derm of pygidial apex shiny. Propygidial spiracles feebly protuberant.

Fore tibia (fig. 37) with 2 external denticles, spiniform apical-internal protrusion, and obtuse inferior-terminal angle; terminal spur long, tapering, just reaching tarsal segment 3. Middle and hind tibiae (fig. 38) with external protusion at ca. 0.4 from apex; apex of tibiae quadridentate, with terminal spurs normally acuminate, reaching ca. halfway tarsal segments 2. Tibial and

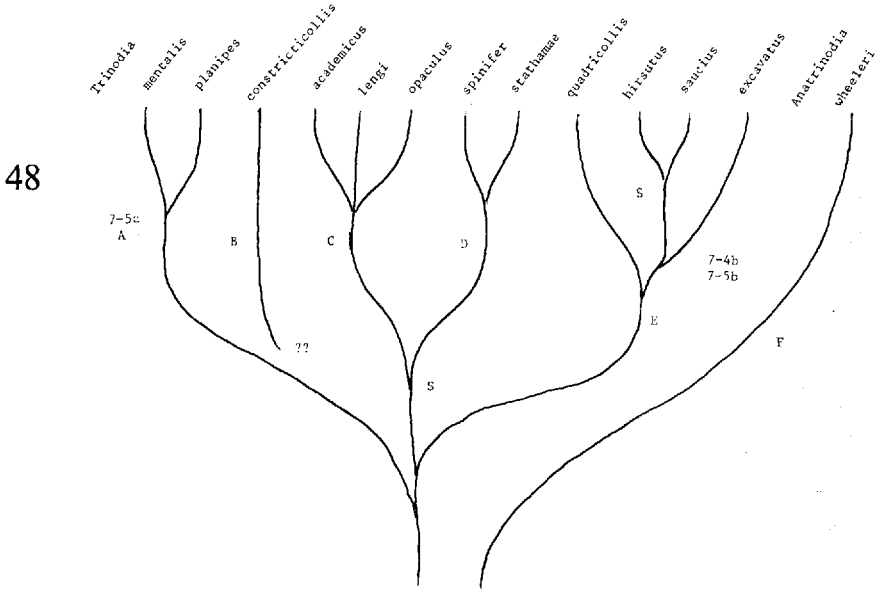


Figs. 36–47. Legs of *Cremastocheilus* species; ventral (36–43) and lateral views (44) of fore (36–37) and hind tibiae (38–44); right hind tarsi (45–47). – 36, *saucius*, Colorado; 37–38, *academicus*, holotype; 39, *quadricollis*, Houston; 40, *excavatus*, holotype; 41, *saucius*, Colorado; 42, *planipes*, Tombstone; 43–44, *wheeleri*, Wet Mts; 45, *academicus*, holotype; 46, *lengi*, Sta Catalina Mts; 47, *opaculus*, Pescadero. – Scale lines are 1 mm; same elements, same scale.

femoral derm largely rugulate-punctate. Tarsi 5-segmented, opaque, somewhat complanate (fig. 45); claws sickle-shaped, their length 1–1.5 times tarsal height.

Parameres simply lobiform.

Material examined. – Holotype and paratype male from "Rio Linares/20 mi. West/Linares, Mex/Nov. 16, 48" (California Academy of Sciences, San Francisco). Paratype scarcely different from holotype.



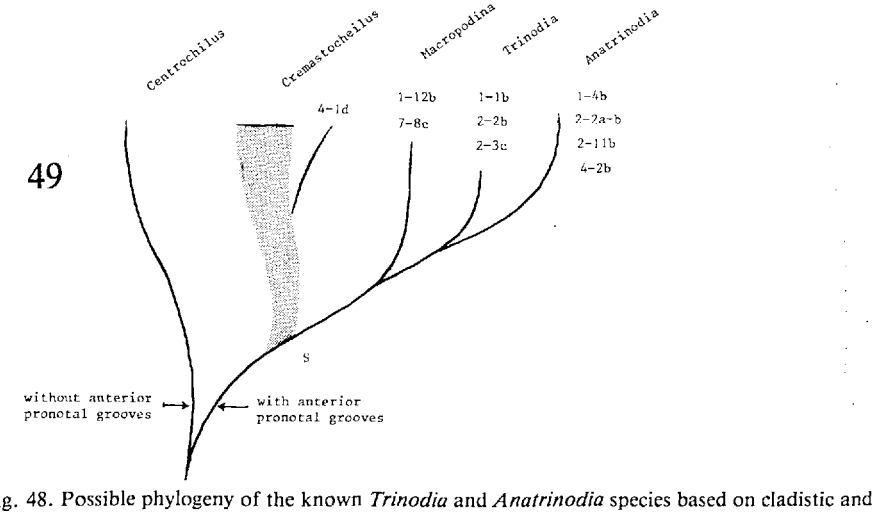


Fig. 48. Possible phylogeny of the known *Trinodia* and *Anatrinodia* species based on cladistic and phenetic considerations (see section 9). Capital letters denote pronotal type (see section 5 and figs. 16–21). S near branching points indicates that overall similarity has been considered. Figures denote apomorphous character states (see section 4).

Fig. 49. Possible phylogeny of the known *Cremastocheilus* subgenera and their cladistic twin *Centrochilus*. Shaded branch: no synapomorphies found. Further explanation under fig. 48.

9. PHYLOGENETIC DISCUSSION

For the criteria to be applied in the phylogenetic qualification of character states, see De Jong (1980), and my remark at the end of section 4. I believe that, like in other cremastocheiline genera (cf. also Krikken, 1976b), several of the characters mentioned above show transformation series representing a perfection of myrmecophilous adaptations (e.g. the development of glandular tissue and associated features, including prothoracic cushions, grooves, trichomes), thus justifying the reference to the specialisation criterium. But even if this criterium would appear unacceptable, several of the characters

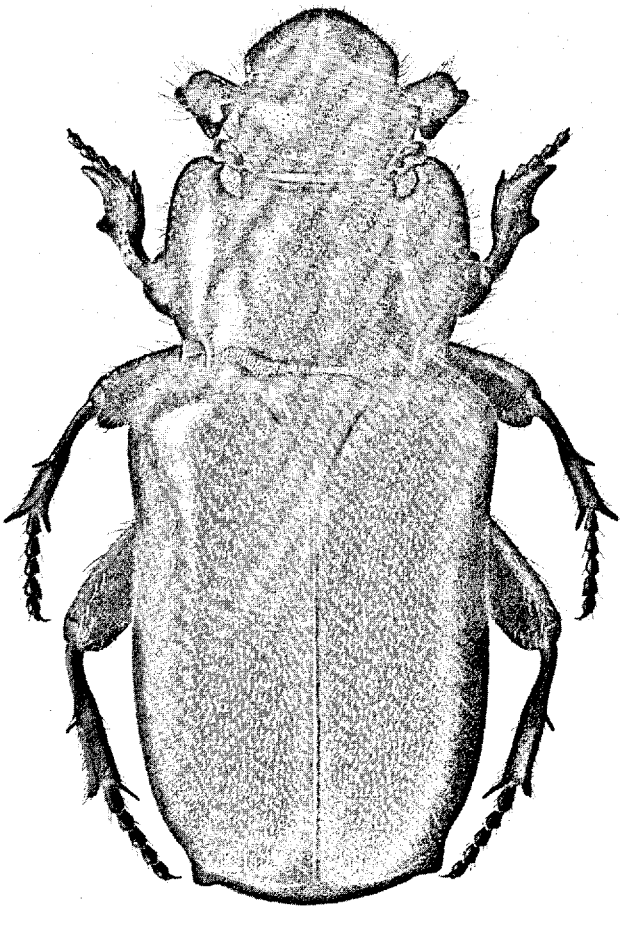


Fig. 50. Habitus of *Cremastocheilus* (*Trinodia*) *hirsutus*.

mentioned (e.g. the prothoracic peculiarities just mentioned) are so odd that the outgroup occurrence criterium would also warrant a correct phylogenetic qualification of the character states concerned.

The subgenus *Trinodia* is a derivative group[1] within *Cremastocheilus*, defined by three synapomorphous character states (section 4, 1–1b, 2–2b, 2–3c). The subgenus *Anatrinodia*, with its single species, should be placed very close to *Trinodia* if one considers, as I do, the pronotal cushions in a state transitional from 2–2a to 2–2b; *Anatrinodia* has three distinctly apomorphous character states (1–4b, 2–11b, 4–2b). The subgenus *Macropodina* does not share any synapomorphy with *Trinodia* and *Anatrinodia*, but has two synapomorphies of its own (character states 1–12b, 7–8c). The subgenus *Cremastocheilus* has no distinct synapomorphies of its own, but some species-groups do have them, like the one around *C. canaliculatus* Kirby (deeply notched mentum, character state 4–1d). Therefore, the subgenus *Cremastocheilus* as currently recognized is certainly not a strictly monophyletic taxon. The cladistic twin of the genus *Cremastocheilus* may be *Centrochilus* Krikken (1976), because all it seems to be missing for a place in *Cremastocheilus* are the anterolateral pronotal grooves, the generic synapomorphy (compare figs. 22 and 23). My ideas on the phylogeny of all these genus-group taxa are summarized in fig. 49.

As for the *Trinodia* species, the importance of the pronotal characters has been stressed in section 5, and in my attempt to establish a phylogeny it is assumed that the pronotal types A–E (figs. 16–20) constitute a transformation series: A has simply projecting posterolateral angles, whereas B–E have them progressively modified. I do not claim to know the cladistic details of the modification process (e.g. in the way of character cladograms), and admit that the transformation series may be based partly on overall similarity. Superposed on these pronotal types are two synapomorphies for the *saucius* group (character states 7–4b, 7–5b), and an additional character state (7–5c) for the *planipes-mentalis* pair. In two cases it is considered reasonable to invoke the argument of overall similarity to connect different lineages (*lengi* and *spinifer* groups, the *saucius-hirsutus* pair); the position of *constricticollis* remains obscure. All these considerations are summarized in fig. 48; the resulting phylogeny is undoubtedly capable of improvement.

10. ACKNOWLEDGEMENTS

In various ways I received help from a number of institutions and individuals, for which I am very grateful. Some sent me *Cremastocheilus* specimens, especially the California Academy of Sciences, other institutions were visited during a tour through the United States and Canada in 1976. The hospitality of the European museums is also gratefully acknowledged. The institutions that sent types on loan are followed by their abbreviations (used in section 7).

[1] Derivative is here meant as possessing more apomorphous character states than is the case with other more or less related groups. The subgenus *Cremastocheilus* would then qualify as primitive.

California Academy of Sciences (CAS), San Francisco (D.H. Kavanaugh); Museum of Comparative Zoology (MCZ), Cambridge, Mass. (M.K. Thayer); National Museum of Natural History, Smithsonian Institution (USNM), Washington D.C. (R.D. Gordon); American Museum of Natural History, New York City (L.H. Herman); Field Museum of Natural History, Chicago (E.H. Smith, H.S. Dybas); Canadian National Collection, Ottawa (E.C. Becker); H.F. Howden, Ottawa; British Museum (Natural History), London (R.D. Pope); Muséum National d'Histoire Naturelle, Paris (A. Descarpentries); Institut für Landwirtschaftwissenschaften, Abteilung Taxonomie der Insekten, Eberswalde D.D.R. (G. Morge); Museum für Naturkunde, Zoologisches Museum, Berlin (F. Hieke, J. Schulze).

The habitus drawing was produced by H. Heijn.

11. REFERENCES

Alpert, G.D. & P.O. Ritcher – Notes on the life cycle and myrmecophilous adaptations of *Cremastocheilus armatus* (Coleoptera: Scarabaeidae). Psyche **82**, 283–291, 5 figs. (1975).

Casey, T.L. – A review of the American species of Rutelinae and Cetoniinae. Memoirs Coleoptera **6**, 1–394 (1915).

Cazier, M.A. – A generic revision of the North American Cremastocheilini with description of a new species. (Coleoptera-Scarabaeidae). Bull. southern Cal. Acad. Sci. **37**, 80–87, 8 figs. (1938).

Cazier, M.A. – New North American myrmecophilous Scarabaeidae (Coleoptera *Cremastocheilus*). Bull. Brooklyn ent. Soc. **35**, 122–133, 2 figs. (1940).

Cazier, M.A. – A new species of myrmecophilous Scarabaeidae, with notes on other species (Coleoptera, Cremastocheilini). Amer. Mus. Nov. **2033**, 12 pp., 3 figs. (1961).

Cazier, M.A. & M.A. Mortenson – Bionomical observations on myrmecophilous beetles of the genus *Cremastocheilus* (Coleoptera: Scarabaeidae). J. Kansas ent. Soc. **38**, 19–44, 6 figs. (1965).

Cazier, M.A. & M. Statham – The behaviour and habits of the myrmecophilous scarab *Cremastocheilus stathamae* Cazier with notes on other species (Coleoptera: Scarabaeidae). J.N.Y. ent. Soc. **70**, 125–149 (1962).

Darlington, P.J. – Paussid beetles. Trans. Amer. ent. Soc. **76**, 47–142, 207 figs., 3 maps (1950).

Horn, G.H. – Descriptions of new North American Scarabaeidae. Trans. amer. ent. Soc. **12**, 117–128 (1885).

Horn, G.H. – The Coleoptera of Baja California. Proc. Cal. Acad. Sci. (2) **4**, 302–449, pls. 7–8 (1894).

Howden, H.F. – Key to the New World Cremastocheilini, with notes and description of a new genus (Coleoptera: Scarabaeidae). Proc. ent. Soc. Washington **73**, 224–230, 8 figs. (1971).

Jong, R. de – Some tools for evolutionary and phylogenetic studies. Z. zool. Syst. Evolut.-Forsch. **18**, 1–23, 2 figs. (1980).

Kloft, W.G., R.E. Woodruff & E.S. Kloft – *Formica integra* (Hymenoptera: Formicidae) IV. Exchange of food and trichome secretions between worker ants and the inquilinous beetle. *Cremastocheilus castaneus* (Coleoptera: Scarabaeidae). Tijdschr. Ent. **122**, 47–57, 20 figs. (1979).

Knoch, A.W. – Neue Beyträge zur Insectenkunde, 2c. Part **1**, xii ± 208 pp., 9 pls. Leipzig (1801).

Krikken, J. – New genera of New World Cremastocheilini, with revisional notes (Coleoptera: Cetoniidae). Zool. Meded. Leiden **49**, 307–315, 16 figs., 1 pl. (1976a).

Krikken, J. – Taxonomy of the African genus *Placodidus* Péringuey (Coleoptera: Cetoniidae). Proc. Kon. Ned. Acad. Wetensch. (C) **79**, 367–380, 41 figs., 1 pl. (1976b).

Krikken, J. – Taxonomic review of the New World genus *Genuchinus* Westwood (Coleoptera: Cetoniidae). Proc. Kon. Ned. Acad. Wetensch. (C) **84**. 403–417, 30 figs., 1 pl. (1981).

LeConte, J.L. – Catalogue of Coleoptera of the regions adjacent to the boundary line between the United States and Mexico. J. Acad. Philad. (N.S.) **4**, 9–42 (1858).

LeConte, J.L. – New species of Coleoptera, collected by the expeditions for geographic surveys West of one hundredth meridian &c. Report Chief of Engineers, Washington, **1876**, 516–520 (1876).

Mann, W.M. – Some myrmecophilous insects from Mexico. Psyche **20**, 171–181, 3 figs.; correction slip (1914).

Potts, R.W.L. – A key to the species of Cremastocheilini of North America and Mexico (Coleoptera, Scarabaeidae). Bull. Brooklyn ent. Soc. **40**, 72–78 (1945).

Ratcliffe, B.C. – Descriptions of the larva and pupa of *Osmoderma subplanata* (Casey) and *Cremastocheilus wheeleri* LeConte (Coleoptera: Scarabaeidae). J. Kansas ent. Soc. **50**, 363–370, 12 figs. (1977).

Schenkling, S. – Scarabaeidae: Cetoninae. Coleopt. Catalogus **72**, 431 pp. (1921).

Van Dyke, E. – Some new beetles in the families Cantharidae (Lampyridae), Ptinidae, and Scarabaeidae, from western North America, with notes upon others. Bull. Brooklyn ent. Soc. **13**, 1–15 (1918).

Wilson, E.O. – The insect societies, x + 548 pp. figs., frontispiece. Cambridge, Mass. (1971).

Wheeler, W.M. – Ants. Their structure, development and behaviour, xxv + 663 pp., 286 figs., frontispiece. New York (1910, reprinted 1914).