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REVIEW AND CLADISTIC ANALYSIS OF THE GENERIC-LEVEL TAXA OF MORIONINI BRULLÉ (COLEOPTERA: CARABIDAE)

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Abstract.—A cladistic analysis based on adult morphological characters shows that monophyly of the tribe Morionini Brullé (Coleoptera: Carabidae), including *Stereostoma* Murray, is unambiguously supported by only one character, moniliform antennae. Under an explicit accelerated transformation optimization the prominent form of the temples also supports the Morionini node. *Cnemalobus* Guérin-Ménéville (Cnemalobini) is found to be the sister-group to Morionini. A clade of *Stereostoma* + *Morionidius* Chaudoir (Morionini *incertae sedis*) is sister to the remaining morionine genera (Morionina). Under this hypothesis *Stereostoma* and *Cnemalobus* have independently derived a significant number of character states. Morionina is designated as a subtribal clade defined in this analysis to include seven genera (*Buderes* Murray, *Moriosomus* Motschulsky, *Hyperion* Laporte, *Hyperectenus* Alluaud, *Morion* Latreille, *Megamorio* Chaudoir and *Platynodes* Westwood). A new record for New Guinea and first reported male specimens of *Morionidius doraei* Chaudoir are presented and described. Characteristics of the female reproductive tract are clarified for *Morionidius*. Notes on the present systematic status of the included taxa, references for species-level identification for members of each supra-specific group and a key to genera and subgenera for adult specimens of Morionini is provided.

Key Words.—Harpalinae, Generic key, Ground beetles.

In the process of identifying material housed at the University of California Bohart Museum, Davis that had been collected at the Ivimka Research Station, Papua New Guinea, I found two specimens that were clearly members of Morionini but where quite different from *Morion* Latreille, the only genus of Morionini reported from that country. Ultimately, working with original descriptions, I was able to attribute them to the genus *Morionidius* Chaudoir. During this process I found that there was no single key to all genera of the tribe and not all genera are treated in the various regional keys. Given this dearth and having specimens of all genera at hand, I present a key and list of references so that material may be identified and to help stimulate research on this interesting group of ground beetles. Additionally, the morphological matrix and exemplar taxa included in the cladistic analysis provides a summary of character data and a starting point for the more extensive study needed for the group.

MATERIALS AND METHODS

Overall methods follow Will (2002). Sources of material for this study are from the following institutions and were kindly provided by the curators listed: Essig Museum of Entomology, University of California, Berkeley, Ca. [EMEC], Cheryl Barr; Bohart Museum of Entomology, University of California, Davis, Ca. [UCDC] Lynn Kimsey and Steve Heydon; Carnegie Museum of Natural History, Pittsburgh, Pa. [CMNH], Robert Davidson; California Academy of Sciences, San Francisco, Ca. [CASC], David Kavanaugh and Roberta Brett; Museum of Comparative Zoology, Harvard, Ma. [MCZC], Phil Perkins.

In addition to consulting previously published accounts and general inspection of external characteristics of numerous museum specimens, the following species were

examined for male and/or female reproductive systems: *Morion aridus* Allen ♂♀; *M. cordatus* Chaudoir ♂♀; *M. crassipes* Sloane ♂; *M. monillicornis* (Latreille) ♂♀; *M. simplex* Dejean ♂♀; undetermined *Morion* spp. from Malaysia ♂♀; Madagascar ♂♀; Mexico ♂♀; Dominican Republic ♂; Papua New Guinea; *Megamorio basilewskyi* Straneo ♂♀; *M. camerunus* Straneo ♂; *M. gabonicus* (Alluaud) ♂; *Platynodes westermanni* Westwood ♂♀; *Platynodes* spp. ♂; *Moriosomus seticollis* Straneo ♂♀; *M. sylverstris* (Motschulsky) ♂♀; *Buderes oberti* ♂♀; *Hyperion schroetteri* ♂♀; *Hyperectenus aenigmaticus* Alluaud ♀; *Sterostoma angolensis* ♀; *Sterostoma* 3 spp. ♂ or ♂♀.

Summary of species names is based on the catalogues of Lorenz (1998a, b). The key is based on examination of specimens from all genera and published keys by Straneo (1949, 1952, 1958, 1991), Allen (1968), and Jeannel (1948). Female tract terminology follows Liebherr & Will (1998).

Cladistic Methods.—The character matrix was assembled and resulting cladograms viewed in WinClada (Nixon 1999–2002). Parsimony analysis was done by submitting the matrix from WinClada to NONA (Goloboff 1999) using a 100 Mult* replicates holding 25 trees per replicate.

Character polarity is set by placing the root between the ingroup and selected outgroup taxa (Watrous &Wheeler 1981). Two possible character optimizations that may, but do not always (Maddison & Maddison 2000: 100), represent the extremes of character optimization were examined. These were accelerated transformation optimization (ACCTRAN), which places character state changes as close to the root of the cladogram as possible, thereby preferring reversals in homoplasious characters and delayed transformation optimization (DELTRAN), which places character state changes as apical as possible, thereby preferring parallelism or convergence of states (Swofford & Maddison 1987; Maddison & Maddison 2000). Most characters have only one possible parsimonious optimization and so are un-ambiguously shown on the cladogram. Other characters that can be optimized in alternative equally parsimonious ways (e.g., ACCTRAN, DELTRAN) are either not considered to provide support for any nodes or an explicit optimization is selected and discussed below.

Outgroup Taxa.—Three outgroup taxa were selected to test monophyly and root the resultant cladograms. Two of the outgroup taxa have been associated with Morionini by previous authors and have a number of potentially significant similarities. *Catadromus* W.S. Macleay (Pterostichini auct.) was included in Morionini by Moore (1965) and *Cnemalobus* Guérin-Méneville (Cnemalobini) has been associated with Morionini by Roig-Juñent (1993) and Liebherr & Will (1998). *Cuneipectus* Sloane (Cuneipectini auct.) is an isolated pterostichine taxon putatively sharing several homologous characteristics with Morionini. The proposed close association of morionines with Scaritini based on larval characters (van Emden 1953; Lindroth 1969) has been shown to be incorrect (Bousquet 2001; Arndt 1993; Maddison et al. 1999; Ober 2000) and the majority of evidence supports a position as within Harpalinae.

Characters.—Adult anatomy was examined for characteristics that could be coded as discrete states and were thought to potentially vary in a way that they could provide grouping information for taxa (Table 1). In the analysis all characters were equally weighted and are binary and non-additive, except as noted below. Three characters are not parsimony infor-mative (28, 29, 31) and so do not contribute to the grouping of taxa or tree statistics, but are in-cluded for discussion purposes only. Characters used in the cladistic analysis are as follows:

1. *Post-ocular margin and temple*: margin slightly emarginate, temple not prominent = 0 (Figs. 1A, 2C); margin deeply emarginate but temple relatively small, moderately

Table 1. Taxon × Character matrix. $ = subset polymorphic [0,1]; * = full polymorphism; ? = unknown/ambiguous.

	Characters 1–35						
	5	10	15	20	25	30	
Cuneipectus	00001	00210	02100	00000	00000	01001	00100
Catadromus	00000	02210	02100	00000	00000	00000	00100
Cnemalobus	00000	00200	20000	20000	00001	00001	01100
Stereostoma	00110	00001	23001	20100	01011	11110	110?0
Hyperion	21001	11210	13011	?1100	10001	01000	00111
Megamorio	11001	12210	12211	10111	10101	10000	00111
Platynodes	21001	12210	11211	12111	10101	00000	00111
Buderes	11001	00210	13311	10000	00101	01000	10110
Morionidius	10100	00011	14011	10000	01011	*10*1	000?0
Hyperectenus	11001	10210	13311	10000	00101	10000	0011?
Moriosomus	11000	10110	13311	10000	10101	01000	00111
Morion	00111	11001	1$210	133*1	10100	10101	000*0

prominent = 1 (Fig. 1B); margin deeply emarginate and temple markedly prominent = 2 (Fig. 2A). Considered additive to set adjacency between most similar states. The temple is the post-ocular region of non-ocular cuticle behind eye and above the gena.

2. *Maxillary setae*: positioned near base of palpifer = 0 (Fig. 3A); positioned near middle of palpifer = 1 (Fig. 3B). In most Harpalinae and nearly all pterostichine-like taxa the single setae of the palpifer is positioned near the base, within 1–2 puncture diameters from the basal margin. In many morionines and all Caelostomini the setae is positioned near the middle of the palpifer. Many Australian pterostichines, including *Cuneipectus*, have two setae on the palpifer, one near the midline and one near the base. In *Cuneipectus*, however, the apical-most seta is position near the dorsal margin of the palpifer rather than centered laterally. It is assumed in this analysis that the setae in morionines is the basal seta in a more apical position and not a midline setae with the basal seta absent. A broader-scaled analysis is needed to test the homology of all plurisetose taxa.

3. *Apical labial palpi*: fusiform = 0; securiform = 1.

4. *Setae of the anterior margin of labrum*: 6 setae = 0 (Fig. 3C); 2 or 4 setae = 1 (Fig. 3D). Non-informative and deactivated. A smaller number of setae along the margin of the labrum is a derived character within *Stereostoma* Murray.

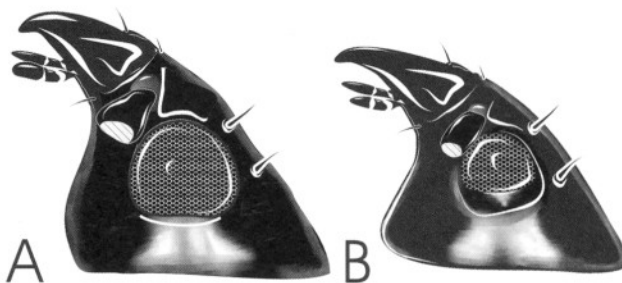5. *Form of the anterior margin of labrum*: nearly straight = 0 (Fig. 3D); clearly emarginate = 1 (Fig. 3C).

Figure 1. Left lateral view of head of A- *Stereostoma* (*Stereodema*) sp. and B- *Morionidius doraei* Chaudoir.
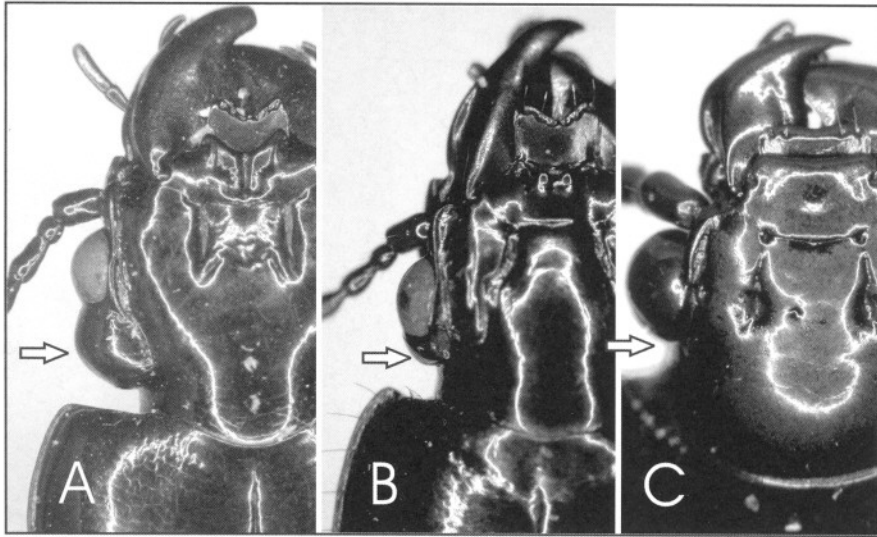
Figure 2.   Dorsal view of left side of head with arrow indicating temples in A- *Platynodes westermanni* Westwood, B- *Morion* sp. and C- *Stereostoma* (*Stereodema*) sp.

6. *Form of the margin of clypeus*: laterally convergent to apex and straight across apical margin = 0 (Fig. 3D); lateral concavity and apically emarginate = 1 (Fig. 3C).

7. *Frontal furrows*: entirely narrow throughout, narrow ending punctiform or effaced = 0; broad poorly defined = 1; broad, deep, sharply defined = 2. Considered additive to set adjacency between most similar states.

8. *Apex of mentum tooth*: simple, acute form = 0; simple, blunt form = 1; bilobed = 2. Considered nonadditive as all states are considered equidistant in similarity.

9. *Basal antennomeres*: 3 without dense pubescence = 0; 4 without dense pubescence = 1.

10. *Lateral edge of antennomeres 5–11*: entirely pubescent = 0; with glabrous region = 1. Glabrous region is a thin shiny region on the narrow edge of the antennomeres.

11. *Apex of antennomere 4*: with a ring of 6 long setae = 0; with many shorter setae mostly laterally = 1; lateral patches as in antenomeres 5–11 = 2. Considered additive to set adjacency between most similar states.
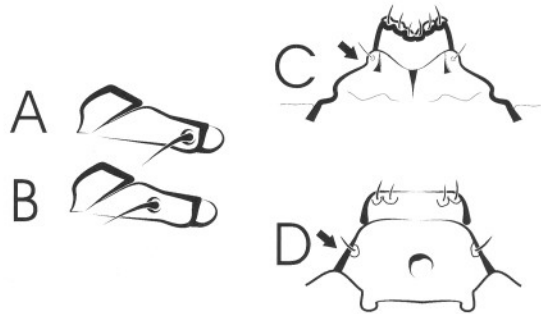

Figure 3.   Mouth parts, lateral view of maxillary palpifer showing seta A- in position near base and B- in position near midline; clypeus and labrum of C- *Morion* sp. and D- *Stereostoma* sp., arrow indicates lateral convex margin.
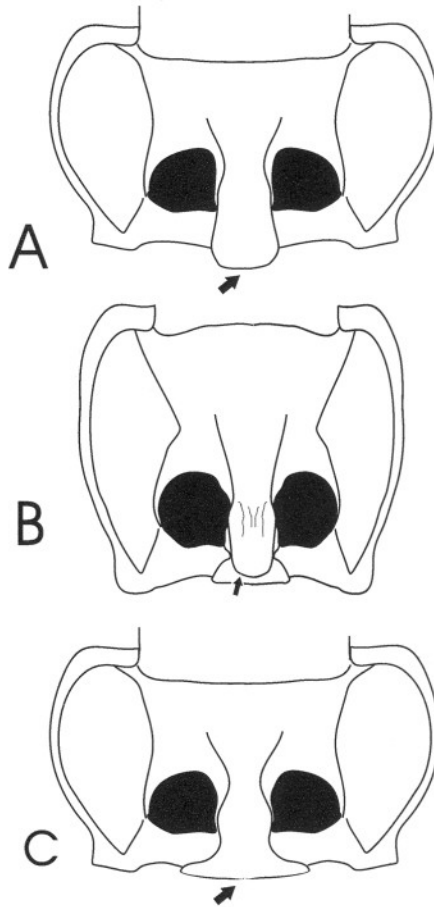
Figure 4. Ventral view of pronotum. C- *Megamorio* sp., B- *Hyperion schroetteri* (Schreibers), C-*Platynodes westermanni* Westwood. Arrow indicates modified tip of prosternum.

12. *Setae on apex of antennomere 3*: none $= 0$; two apical $= 1$; four apical $= 2$; six apical $= 3$; eight apical $= 4$. Considered nonadditive as it is not possible to establish homology of individual setae between lesser and more numerous setal states.

13. *Setae on apex of antennomere 2*: none $= 0$; one apical $= 1$; two apical $= 2$; six apical $= 3$. Considered nonadditive as it is not possible to establish individual setal homology between lesser and more numerous setal states.

14. *Antennomere 1*: with one long medial seta $= 0$; no setae $= 1$.

15. *Form of antennomeres*: filiform $= 0$; moniliform $= 1$.

16. *Smooth median region of antennomeres*: pubescent $= 0$; with scattered setae not sharply delimited $= 1$; glabrous and clearly delimited $= 2$. Considered additive to set adjacency between most similar states.

17. *Prosternal process*: blunt or cuneiform, only slightly wider dorsad of ventro-apical margin $= 0$ (Fig. 4A); broadened laterally dorsad of apical margin $= 1$ (Fig. 4B); broadened laterally at ventro-apical margin $= 2$ (Fig. 4C). Considered additive to set adjacency between most similar states.

18. *Umbilicate punctures in basal third of elytra*: single line of 6–8 punctures in interval 9 or touching stria 8 (as in the "normal" pterostichine arrangement) = 0; punctures supernumerary, 10–16 or more punctures in two lines, single dense line or alternating in position and size, placed in interval 9 or stria 8 = 1.

19. *Umbilicate puncture of elytral interval 9 in apical third*: single staggered row (as in the "normal" pterostichine arrangement) = 0; double or triple lines of setigerous punctures = 1.

20. *Elytral interval 7*: slightly convex to flat = 0; rounded or sharply carinate = 1.

21. *Elytral interval 9*: uniform width or narrowed near apex = 0; widening and very broad at apex = 1.

22. *Elytral interval 10*: absent = 0; present in apical third = 1.

23. *Parascutellar stria*: present either separate and shallowly impressed or anastomosing with stria one = 0; absent = 1.

24. *Base of stria 1*: present = 0; absent = 1.

25. *Elytral external plica*: visible = 0; not externally visable = 1.

26. *Elytral internal plica*: attains margin = 0; separate from margin = 1.

27. *Elytral discal puncture on interval 3*: present = 0; absent = 1.

28. *Apex of tarsomere 5*: open = 0; closed = 1. This is an autapomorphy for *Stereostoma* and so not informative in the analysis. In *Stereostoma* the dorsal and ventral surfaces of tarsomere 5 is fused together apically between the tarsal claws. In all other carabid taxa I have studied the apex is open.

29. *Tarsomere form*: slender, typical = 0; heavily built, nearly quadrate = 1. The form of the tarsomeres is variable in taxa like *Morion* and *Moriosomus* Motschulsky and some taxa have rather heavily built but elongate tarsomeres making it difficult to catagorize some individuals. The character may be informative within the genera but has been deactivated here.

30. *Transverse medial sulci of abdominal ventrites*: absent = 0; sulci present = 1.

31. *Basal crenulate sulci on abdominal ventrites*: absent = 0; present = 1.

32. *Abdominal ventrites*: glabrous, except paramedial ambulatory setae = 0; with transverse row of setae = 1.

33. *Female appended gland duct diverticula*: absent = 0 (Figs. 5A–B); present = 1 (Figs. 5C–D).

34. *Female appended gland duct diveticula terminates as*: a blunt tube = 0 (Fig. 5D); expanded bulb = 1 (Fig. 5C).

35. *Male median lobe endophallus*: simple or sparsely toothed = 0; with a rod-like process = 1 (Fig. 6).

RESULTS AND DISCUSSION

Results of the Analysis.—The analysis returned a single most parsimonious tree (MPT) of length = 65 steps, CI = 0.64 and RI = 0.69 (Fig. 7). Morionini was found to be monophyletic and of the included outgroups, *Cnemalobus* is the sister-group of Morionini. The clades supported by the most synapomorphies are 1. *Cnemalobus* + *Morionini*; 2. *Stereostoma* + *Morionidius*; 3. *Buderes* + the remaining morionine genera and 4. *Platynodes* + *Megamorio*.

Support for clades is distributed among the various body regions scored, but most unambiguous support comes from 1. elytral characters- nine synapomorphies; 2. antennal characters- eight synapomorphies and 3. head and mouth parts- eight synapomorphies.
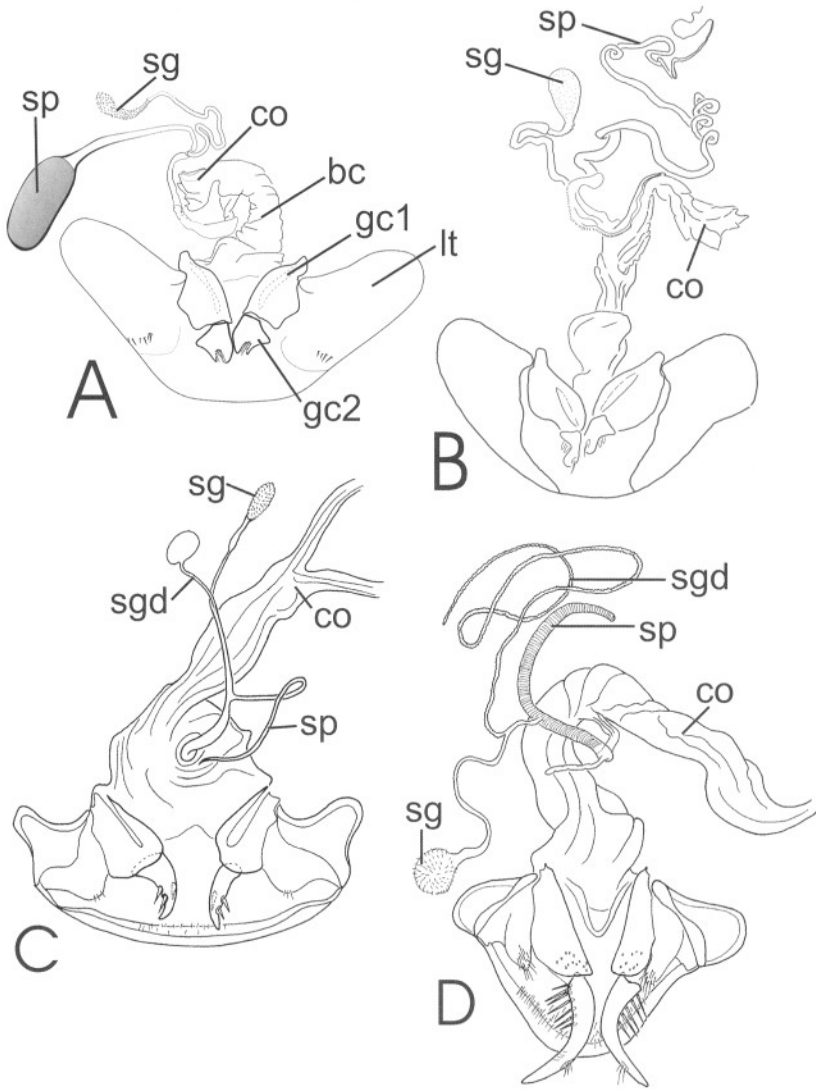
Figure 5. Ventral view of female reproductive tract of A- *Morionidius doraei* Chaudoir, B- *Stereostoma* (*Stereodema*) sp., C- *Morion monilicornis* Latreille and D- *Cnemalobus obscurus* Brullé. sp = spermatheca; sg = spermatheca appended gland; sgd = gland duct diverticula; gc1 = gonocoxite-1; gc2 = gonocoxite-2; lt = laterotergite IX; co = common oviduct; bc = bursa copulatrix. C-D from Liebherr & Will (1998).

Explicit optimization hypotheses were used for characters 1 (accelerated), 14, and 34 (both delayed), otherwise only unambiguously optimized characters are used to support nodes in the resulting cladogram.

Clade: *Cnemalobus + Morionini*

Cladistic Diagnosis/Characters.—Monophyly supported by three unambiguously optimized and unreversed synapomorphies (characters 11, 16, 25; Fig. 7). Two (11, 16)
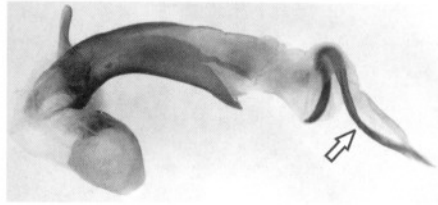
Figure 6. *Hyperion schroetteri* (Schreibers) left lateral view of median lobe of the aedeagus with endophallus everted, arrow indicates sclerotized rod.

entail characteristic pubescence and chaetotaxy of the antennae. All included taxa have reduced pubescence or a glabrous medial region on the antennomeres. Character 25, no externally visible elytral plica, is shared by all taxa. All taxa have a well developed ridge on the inner surface of the elytron, but this ridge does not extend beyond the margin of the elytra and so is not visible externally. The loss of the externally visible plica is a common feature in many carabid tribes (Liebherr 1986).

The synapomorphies from the pattern found here, numerous homoplasious similarities between *Cnemalobus* and *Stereostoma* (discussed under *Stereostoma* below), general similarities of the head of adults, features of the mouthparts of larvae (Roig-Juñent 1993) and female tract (Liebherr & Will 1998) all point to a close relationship between *Cnemalobus* and some pterostichine-grade taxon, most likely, as presented here, as sister to Morionini.

Tribe: Morionini Brullé 1835

Recognitory Diagnosis.—The combination of moniliform antennomeres, prominent eyes (except in *Hyperectenus* Alluaud), elytral plica not externally visible, expanded apex of the protibia with a apico-laterally produced spine (except in *Morionidius*), and projecting dentiform process above the insertion point of the antenna is characteristic of members of this tribe. Presently there are 92 named species in the tribe, the majority (63) in *Morion* and *Stereostoma*.

Additionally, all species in the tribe are deep black to piceus brown, rather shiny and typically large sized, most about 15–30 mm (range 8–80 mm). Most species are *Morion*-like in general form, elongate, parallel-sided and somewhat depressed and subpedunculate. However, many of the genera, which contain about a third of the species, are much more compact and convex in form. All have deeply impressed frontal impressions on the head and deep, linear pronotal basal impressions.

Cladistic Diagnosis/Characters.—Monophyly is supported by a single unambiguously optimized synapomorphy, moniliform antennomeres (character 15; Fig. 7). This characteristic is found in several other groups of Carabidae, and in *Hyperion* Laporte the antennae are submoniliform. For this reason antennal form is not considered to be a character of high weight. Under an accelerated transformation optimization five additional characters would support this node (characters 1, 12, 14, 27, 34). Two of those (12, 27) are also synapomorphic changes under the delayed transformation optimization, but there is no compelling reason to choose between the two optimizations for the highly variable (across Carabidae), plurisetose condition of antennomere 3 or presence/absence of the discal puncture of elytral interval 3. Loss of the single seta of antennomere 1 (characters 14) and the form of the apex of the diverticula of the appended gland (character 34) are treated under the delayed transformation optimization and so do not support this
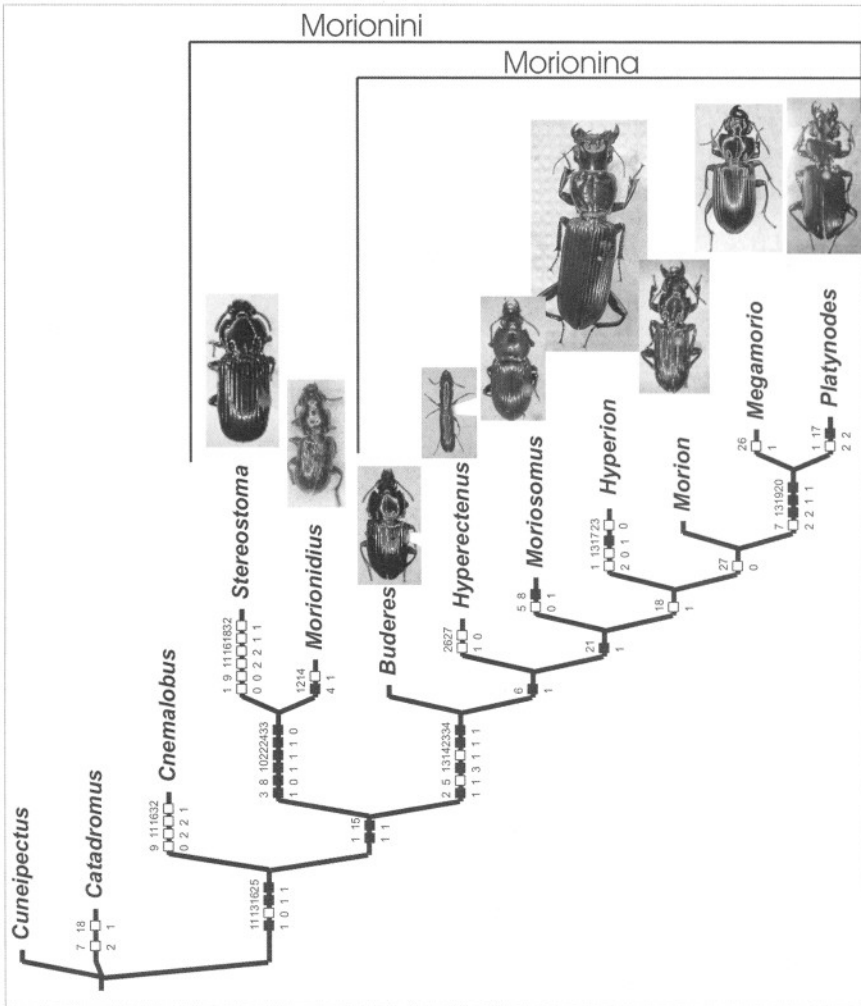
Figure 7. Cladogram for Morionini taxa showing unambiguous and characters with specific transformation optimization hypotheses (1- accelerated; 13, 34-delayed). Numbers to left of branches are character numbers and numbers to right of branches are the character states. Black rectangles mark forward changes and white rectangles mark homplasious changes. Images of beetles correspond to names on terminals but are not to scale.

node. Those characters are discussed below. The prominent eyes and similarity of the form of head suggest that moderately developed temples (character 1) is the ancestral condition for Morionini and so this transformation also supports the monophyly of Morionini. Overall there is little support for a monophyletic Morionini including *Stereostoma* and *Morionidius*.

Allen (1968) listed five features he considered to characterize the tribe: moniliform antennae, elytral plica internal, 4–12 setae on lateral margin of the pronotum, stria 8 with alternating setigerous punctures, and the rod-like process of the endophallus. Aside from the moniliform antennae, none of these is found to be definitive for the tribe as a whole. Most of these are known only in the more derived *Morion*-like genera and exception are

common, e.g., *Hyperion* lacks pronotal setae, *Buderes* and *Hyperectenus* lack the additional setigerous punctures of stria 8, and *Stereostoma* does not have the process of the endophallus. Probably Allen's review of the New World taxa simply overlooked variation in the Australian and African members of the tribe.

<div align="center">

Morionini *incertae sedis*

Clade: *Stereostoma* + *Morionidius*

</div>

Cladistic Diagnosis/Characters.—Monophyly is supported by six non-homoplasious synapomorphies (characters 3, 8, 10, 22, 24, 33; Fig. 7). One character state that is unique for these two taxa, the narrow, glabrous lateral edge of antennomeres 5–11 (character 10). All other character state changes are, with the exception of the simple and acutely formed apex of the mentum tooth (character 8) and absence of the base of stria 1 (character 24), uncommon in Harpalinae taxa and represent significant synapomorphies for this clade. The presence of securiform apical labial palpi (character 3) is scattered throughout the family and often associated with groups that have feeding specializations, e.g., cychrines and chaetodactylines. Whether this is the case in these taxa is unknown. All other taxa in this analysis and most other pterostichine-grade species have only nine elytral intervals, though a tenth interval is found in various taxa, e.g., *Haploferonia* Darlington and *Rhabdotus* Chaudoir, that are not thought to be closely related. Development of a tenth interval (character 22) in *Morionidius* is evidenced by a flat interval in the apical third of the elytron. In *Stereostoma* the interval is sharply carinate and begins at about the mid-point of the elytron. Except in this clade, the appended-gland duct diverticula of the female reproductive tract (character 33) is present. The exemplar taxa included in this analysis are representative of all clades of pterostichine-like taxa which have this structure, except for the distantly related South American and Australian euchroine pterostichines (Will 2000). The absence of this diverticula is a synapomorphic loss for *Stereostoma* and *Morionidius*.

<div align="center">

Stereostoma Murray 1857

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Recognitory Diagnosis.—Large deep-bodied species with prominent eyes that lack the prominent temples found in other morionine taxa (Fig. 2C).

Stereostoma (s.str.) contains six species from western Africa. Members of this subgenus lack the maxillary and antennal characteristic of *Stereostoma* (*Stereodema*) Chaudoir. The condition of the maxillae and antennae are most likely plesiomorphic in *Stereostoma* (s.str.) and this group is probably paraphyletic relative to *Stereodema*. No identification key is available for these species.

The 22 species of *Stereostoma* (*Stereodema*) are known from western and west-central Africa. Included species (except *S. praecellens* Müller) are separable using Straneo's (1991) key to species.

Stereostoma (s.lat.) lacks many of the characteristics presumed to be derived for typical morionines. The most obvious morionine features of the head, e.g., the prominent temples and emargination of the labrum and clypeus, are not observed in *Stereostoma*. Several autapomorphies distinguish *Stereostoma*, including the complete enclosure of the apex of tarsomere 5 (character 28), apical margin of the labrum with only 4 setae in some species (6 in all other Morionini, character 4), and supernumary setae of the pronotal margin (found in some *Morion* and *Moriosomus* species). The moniliform antennomeres in *Stereostoma* differ from other morionines by having a complete absence of setae on the shiny median (broad) surface of antennomeres 5–11 and sharply delimited edges between this area and the densely pubescent lateral region. Other taxa have irregularly scattered

setae on the median surface and the boundary between the dense lateral pubescence and shiny median surface is not well defined. The eyes of *Stereostoma* species are very prominent, a condition found in various other carabid groups, e.g., Caelostomini and Cratocerini. The prominence of the eye itself is quite different from the enlarged eye and markedly prominent temples in other morionines.

Based on the MPT, *Cnemalobus* and *Stereostoma* have four characters that are homoplasious (characters 9, 11, 16, 32), three are antennal characters and one is the additional setae on the abdominal ventrites. Moving *Stereostoma* to a position as sister of *Cnemalobus* allows these to be synapomorphies for that clade and requires only a single additional step in the cladogram over all. This suggest that *Stereostoma*, which has some characteristics with various morionine taxa, e.g., double rows of setae of elytral interval 9 (character 18), internal plica distant from the elytral margin (character 26), and crenulate basal sulcus on abdominal ventrites (character 31), none of which are synapomorphies, may be convergent on the body form of Morionini taxa and independently evolved these characteristics.

Morionidius Chaudoir 1880

Recognitory Diagnosis.—Small to medium sized, deep-bodied species readily recognized from all other morionines by the transverse sulci on the abdominal ventrites.

Five species distributed in the Oriental region. No key to species exists. Sciacky & Beneš (1997) discuss some attributes and possible affinities of *Morionidius*, but only in comparison to *Morion* and *Stereostoma*. They note, as did Chaudoir (1880), that *Morionidius* and *Stereostoma* share the expanded apical labial palpomeres and have a significant number of shared characteristics of other morionines. The results of the cladistic analysis presented here are also consistent with these previous authors' conclusions. Features of the head and eyes are intermediate between those found in *Stereostoma* and other morionines. The eyes in *Morionidius* species are very prominent, like *Stereostoma*, but have prominent tempora as in other morionines (Fig. 1B). The labrum is also intermediate in form, very slightly emarginate, not straight as in *Stereostoma* nor deeply emarginate as in *Morion*. *Morionidius* lacks the prominently developed lateroapical spine of the protibia, which is very large in all other morionines. The transverse sulci of the abdominal ventrites in *Morionidius* is not found in any other morionine taxa, but is found in *Cnemalobus*, *Cuneipectus*, and various other pterostichine-grade taxa.

The female reproductive structures of *Morionidius* species are quite different and probably derived relative to those of other morionine taxa. The strikingly notched gonocoxite-2 (Fig. 5A) is likely a synapomorphy for the genus, however, not all taxa have been examined for this state. Sciacky & Beneš (1997) illustrate the female reproductive tract of *M. inexpectatus* Sciacky & Beneš, showing a system with a strongly sclerotized, ovoid spermatheca only and no appended gland or gland duct diverticula (Sciacky & Beneš 1997: 71, fig. 6). In the single female of *M. charon* Andrewes available to me, there is a similarly formed spermatheca, but also a well developed appended gland (Fig. 5A). There is no gland duct diverticula, however. The loss of the gland duct diverticula is a synapomorphy for *Stereostoma* and *Morionidius* (Figs. 5A–B). Notched gonocoxites and a sclerotized spermatheca is also found in species of *Tshitsherinella* Semenov (Chaetodactylini). Both of these taxa also have securiform labial papli and sulcate abdominal ventrites. Chaetodactylines are known to be parasites of scarab beetles (Jeannel 1948) and it is possible that *Morionidius* also has a parasitic lifestyle that led to the
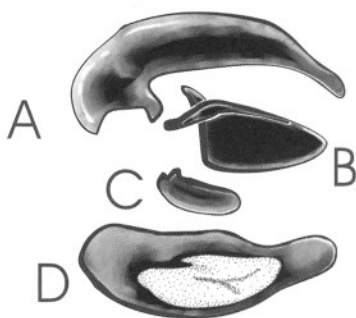
Figure 8. *Morionidius doraei* Chaudoir median lobe of aedeagus, A- left lateral view, B- left paramere, C- right paramere, and D- dorsal view.

independent acquisition of these features. Chaetodactylines do not have any of the apomorphic features found in morionine-like taxa.

In addition to the first report of the internal female reproductive structures in *M. charon*, I present here a new country record and first reported males for the type species of the genus, *Morionidius doriae* Chaudoir. Two male specimens labeled "Papua New Guinea/ Gulf: Ivimka Res./Station/Lakekamu/Basin 120 m 7°44′ S/146°30′ E 24.XI./1999 S.L. Heydon/Hg-vapor light" and "Papua New Guinea/Gulf: Ivimka Res./Station/Lakekamu/ Basin 120m 7°44′ S/146°30′ E 18.IV.00/T.A. Sears MT" were identified in the University of California, Davis, Bohart Museum of Entomology.

This species was described from a single female specimen collected in Borneo (Sarawak) (Chaudoir 1880: 384). The males agree in all regards with the original description, are 8 mm in overall length and with the following sexual characteristics: protarsomeres 1–3 symmetrically expanded with two rows of dense articulo-setae ventrally; last ventrite with one pair of paramedial setae; median lobe of aedeagus (Fig. 8) simple, apex bent slightly to the right, expanded toward tip, ostium dorsal.

Subtribe: Morionina

Cladistic Diagnosis/Characters.—The seven included genera share one unambiguous and unreveresed synapomorphy (characters 2), two unambiguous but subsequently reversed changes (characters 5, 23), one homoplasious change (character 13), and two state changes that support this node under a delayed transformation optimization (characters 14, 34).

In Morionina taxa the maxillary palpifer setae (character 2) is very constant in being positioned well forward of the base (Fig. 3B). This character, which might be deemed of little weight, shows little variation among pterostichine-like taxa and the position and number of setae is quite useful for identifying several clades of pterostichines. Character 23, the absence of the parascutellar stria is a very rare condition in Harpalinae. This should not be confused with the condition where there is a short section of stria one, which is frequently absent, and the parascutellar stria is anastomosing with stria one (Will 2000). In *Stereostoma*, *Morionidius*, and the outgroup taxa there is no suggestion of the base of stria one and the parascutellar stria is clearly present. This innnermost stria in these taxa has its basal terminus at a narrowed portion of interval one and the base ends distant from the elytral basal puncture, which is at the base of stria 2. In Morionina, except for *Hyperion*, the base of the innermost stria (stria one) is ended at the elytral basal puncture, as is the
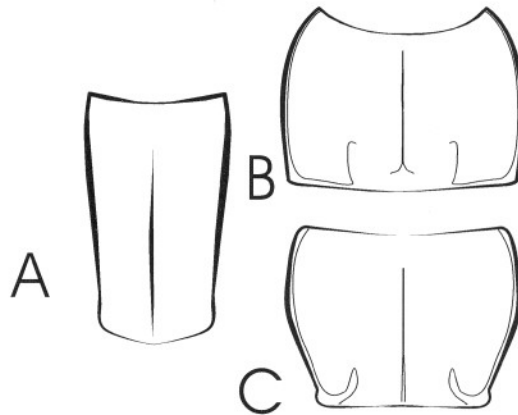
Figure 9. Dorsal view of pronota. A- *Hyperectenus aenigmaticus* Alluaud, B- *Buderes oberti* Murray and C- *Morion monilicornis* Latreille, setae omitted.

case for the base of stria one in other carabid taxa with both parascutellar striae and the base of stria one present. In a few individuals of various Morinina taxa, unilaterally, a few small punctures are visible in a position corresponding to the location where the parascutellar striae would be. Character 13, the presence of six setae on the apex of antennomere 2 supports this node but is reversed to the glabrous condition in *Hyperion*. Likewise, the emarginate apical margin of the labrum, hypothesized as the ancestral condition for the subtribe, is reversed to straight in *Moriosomus*.

Under a delayed transformation optimization two additional characters support this node (characters 14 and 34). This optimization implies that the single setae on antennomere 1 (character 14) would have been independently lost in *Morionidius* and the common ancestor of all Morionina. This is deemed more likely than the novel derivation of the seta implied by an accelerated transformation optimization, as this fixed seta is common to most Harpalinae and absence is rare. Under this optimization scheme, the apex of the diverticula of the appended gland (character 34) would be a novel transformation from an unexpanded to expanded apex of the diverticula and the loss of the diverticula in the ancestor of *Stereostoma* and *Morionidius* would have preceded its modification.

Buderes Murray 1857

Recognitory Diagnosis.—A single species from Africa with a relatively short, broad body-form, pronotum with lateral margins evenly rounded to base (Fig. 9B), and double clypeo-ocular sulci. This combination makes specimens of this genus easy to recognize from all other morionines.

Hyperectenus Alluaud 1935

Recognitory Diagnosis.—The highly modified cylindrical body shape is unmistakable among Morionini (Fig. 7, 9A).

Two named species from western and central Africa. However, as Straneo (1959:195) pointed out, *H. minor* Britton is most likely a small example of *H. aenigmaticus* Alluaud. The necessary comparison of types remains to be done.

Cladistic Diagnosis/Characters of Including Clade.—A single synapomorphic change in the form of the margin of clypeus from laterally convergent unto the apex and straight

across apical margin to lateral concave and apically emarginate (character 6, Fig. 3C–D) unites *Hyperectenus* and the remaining Morionina genera. The sclerotized rod in the male endophallus (character 35) is present in all taxa studied, however, a male specimen of *Hyperectenus* was not available and so the character state change remains ambiguous at this node. It would provide an additional synapomorphy for the node under an accelerated transformation optimization.

Moriosomus Motschulsky 1864

Recognitory Diagnosis.—Separable from all other morionini by the combination of robust body-form, pronotum with lateral margins rounded to near the base but with a short, distinct sinuation just in front of the hind angle, anterior margin of the labrum nearly straight and simple, median tooth of the mentum acutely formed. The genus includes two species from the Neotropical region treated by Straneo (1985).

Cladistic Diagnosis/Characters of Including Clade.—A single synapomorphy unites *Moriosomus* with the remaining morionine genera. In all included taxa the elytral interval 9 is noticeably wider near the apex, such that a more depressed, smoother and shinier region distinct from the rest of the elytra is present (character 21). A sclerotized rod in the male endophallus (character 35, Fig. 6) is present in all taxa studied; however, because no male specimens of *Hyperectenus* were available the character state change remains ambiguous at this node. Under a delayed transformation optimization this would be an additional synapomorphy for this node.

Hyperion Laporte de Castelnau 1834

Recognitory Diagnosis.—The genus includes a single species, *H. schroetteri* (Schreibers) from Australia. This is one of the largest species of Carabidae, with individuals reaching nearly 80 mm in length. Aside from its extraordinary size this species is distinguished by the combination of absence of setae on the pronotal margin, extremely prominent temples, and submoniliform antennae.

The antennal form is heavily built but not truly moniliform as in other morionine taxa, so this character (15) was scored as ambiguous for *Hyperion*. However, the tree topology does not change even if the analysis is done with the antennal form scored as filiform (tree length increases by one step).

Cladistic Diagnosis/Characters of Including Clade.—A single homoplasious synapomorphy supports the monophyly of the clade of *Hyperion* plus the remaining four genera, character 18, supernumerary setigerous umbilicate punctures near the humeral angle. This also occurs in *Stereostoma* (as a double row) and *Catadromus* (as a single dense row). In this character, *Hyperion* and some *Morion* are more similar to *Catadromus* than *Stereostoma*. The general body-form of all the included taxa is very similar and it is likely that *Morion* forms a grade from which all of these taxa, including *Hyperion*, are derived. Under an accelerated transformation scheme character 7—frontal furrows broad and poorly defined (state 1)—would be an additional synapomorphy for this node. However, given the variation in *Morion* species, there is no reason to prefer this optimization over a delayed optimization that places this change as apomorphic for *Hyperion*.

Morion Latreille 1810

Recognitory Diagnosis.—Member taxa are of the typical Morionini form, elongate, subpedunculate with moderately prominent temples. Essentially, *Morion* has the synapomorphic characteristics of Morionina, derived head, antennal elytral characters

(characters 6, 21, 18, 27), but lacks the derived features found in *Hyperion*, *Platynodes* Westwood and *Megamorio* Chaudoir.

This pantropical genus includes 41 named species, though undoubtedly many more remain to be described. More than half of the described species are treated in keys by Chaudoir (1880) and Allen (1968). Otherwise, regionally specific keys may used, e.g., those by Jeannel (1948), Darlington (1962), and Straneo (1958), but all lack some portion of the described taxa.

The genus has been divided by some authors into two subgenera (Jeannel 1948, Straneo 1952), *Morion* (s.str.) and *Morion* (*Neomorion*) Jeannel. I include this division in the key as no study has been conducted to support or refute the dichotomy and it may be useful as a starting point for study of the genus, even if it is an unlikely division. A comprehensive study of this genus, especially the African and Oriental species, would be very beneficial. It seems likely that *Morion* will be found to be a grade at this level and *Hyperion*, *Platynodes*, and *Megamorio* may be derived from it.

Cladistic Diagnosis/Characters of Including Clade.—A single homoplasious character (27), loss of the puncture of elytral interval 3, supports this node. Given the frequency that this puncture is apparently lost or multiplied among taxa throughout the family, it is not possible to give much weight to this change alone.

Clade: *Megamorio* + *Platynodes*

Cladistic Diagnosis/Characters.—Four synapomorphies support this clade: frontal furrows broad, deep, sharply defined (character 7), two setae on apex of antennomere 2 (Character 13), umbilicate puncture of elytral interval 9 with double or triple lines of setigerous punctures in apical third (character 19), and carinate form of elytral interval 7 (character 20).

Megamorio Chaudoir 1880

Recognitory Diagnosis.—Generally formed like a large, slightly depressed *Morion* but with sharply carinate elytral intervals 7–8.

I have had access to a limited number of specimens of this genus and it is possible that this and *Platynodes* may prove to be congeneric. Study of the types for all included species is needed. A key to species was provided by Straneo (1949). Six species are attributed to this genus, all restricted to Africa.

Platynodes Westwood

Recognitory Diagnosis.—One species from Africa. Easily recognized by flat body-form (Fig. 10B), the broadly expanded apex of the prosternal process (character 17, Fig. 4c), very large and prominent temples, non-carinate elytral interval 8 and rounded- or sub-carinate elytral interval 7.

The literature seems unclear about the relationship of this species and *Megamorio*. Specimens which I have examined are of a wide size range and vary in ways that indicate there may be a number of undescribed species in collections. However, until the necessary study of types is complete new taxa cannot be properly delimited.

Key to the Genera and Subgenera of Adult Morionini

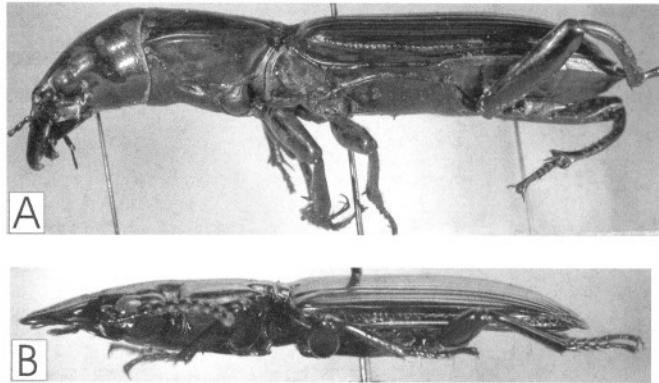1. Hind margin of eye deeply emarginate (Fig. 1B). Large, prominent, well-developed temples (Figs. 2A–B) 2

Figure 10. Left lateral view of A- *Hyperion schroetteri* (Schreibers) and B- *Platynodes westermanni* Westwood.

1′. Hind margin of eye only slightly emarginate (Fig 1A). Without prominent temples (Fig. 2C) . . . . *Stereostoma* s.lat 10

2(1). Temples not as prominent as eye, about one half the size of eye, usually less (Fig. 2B) 3

2′. Temples markedly prominent, as prominent and as large as eye or more (Fig. 2A) 4

3(2). Body form broad, convex. Pronotal margins rounded. Pronotum cordiform in most species (Figs. 9B–C) 5

3′. Body form cylindrical-elongate (Fig. 7). Pronotal margins straight, converging to base. Pronotum very elongate, rectangular (Fig. 9A) . . . .
. . . . *Hyperectenus* Alluaud [Africa]

4(2′). Body form very compressed dorso-ventrally (Fig. 10B). Pronotum with lateral setae. Prosternal process apex extremely broad (Fig. 4C) . . . .
. . . . *Platynodes* Westwood [Africa]

4′. Body form more convex (Fig. 10A). Pronotum without lateral setae. Prosternal process dorsad of apical margin somewhat broadened laterally (Fig. 4B) . . . .
. . . . *Hyperion* Laporte de Castelnau [Australia]

5(3). Apical labial palpomere fusiform. Abdominal sterna without transverse medial sulci (shallow, crenulate basal sulci present in *Buderes* Murray) 6

5′. Apical labial palpomere securiform. Abdominal sterna with transverse medial sulci . . . . *Morionidius* Chaudoir [Oriental/Austral]

6(5). Elytral interval 7 or 8 flat or convex 7

6′. Elytral intervals 7 and 8 carinate. Body form and pronotal shape in most species very similar to *Platynodes* (Fig. 7) . . . . *Megamorio* Chaudoir [Africa]

7(6). Pronotum cordiform or lateral margins sinuate near base. Clypeo-ocular sulci single. Ventrites smooth 8

7′. Pronotal margins evenly rounded to base (Fig. 9B). Clypeo-ocular sulci double. Base of abdominal ventrites with shallow transverse crenulate sulcus . . . . . .
. . . . *Buderes* Murray [Africa]

8(7). Medial tooth of mentum clearly bilobed. *Morion* s.lat. [world-wide] 9

8′. Medial tooth of mentum simple, apex entire, or, in some individuals, at most slightly indented medially . . . . *Moriosomus* Motschulsky [Neotropical]

9(8). First protarsomere in male without prominent medio-apical denticle . . . .
. . . . *Morion* (s.str.) Latreille
9′. First protarsomere in male with prominent medio-apical denticle . . . .
. . . . *Morion* (*Neomorion*) Jeannel
10(1′). Maxillae prominently curved, moderately stout. Third antennomere only slightly
longer than second . . . . *Stereostoma* (s.str.) Murray [Africa]
10′. Maxillae straight, thick and fusiform. Third antennomere distinctly longer than
second . . . . *Stereostoma* (*Stereodema*) Chaudoir [Africa]

CONCLUDING REMARKS

The taxa included in Morionini have a readily recognizable form, however, the inclusion of *Stereostoma* and *Morionidius* is supported by few derived features. The relationships of tribal-level taxa in Harpalinae is currently being studied using morphological and DNA sequence characters. Preliminary results in that study, based on a much smaller a set of Morionini ingroup taxa, are similar to that of the morphological analysis presented here (D. R. Maddison, Univ. of Arizona, Tucson AZ and K. W. Will, unpublished). Ultimately all these data will be combined to help us better understand the relationships of these taxa to the other members of the subfamily.

Within the clearly monophyletic Morionina the pan-tropical, species rich genus *Morion* and the African *Platynodes* and *Megamorio* have substantial possibilities for study in terms of alpha-level taxonomy, biogeography, and behaviors. As suggested by Erwin (1991) these beetles and their larvae are active, voracious predators in subcortical and deadwood microhabitats and as such a complete study of their systematics and a complete taxonomy will be essential for important future work on their ecology.

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