

## CHAUDOIR'S STUDIES OF THE TAXA *AGRINA* AND *BRACHINITAE* (COLEOPTERA: CARABIDAE)

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### ABSTRACT

The Baron Maximilien de Chaudoir's system for agrine Lebiini and brachinines was developed by use of similarity among included taxa as determined by readily observable structural features of representative adults. In both groups, most easily recognizable taxa are listed first, and their character states are today regarded as apotypic. The following groups are progressively less clearly defined, more inclusive, and more plesiotypic in their character states. Hence, Chaudoir's systems of arrangement are inverse with respect to those which would be required by application of current cladistic methods. Chaudoir's career as a taxonomist extended from late pre-Darwinian to early post-Darwinian time (1835–1881), but evidence is not found in his publications about agrines and brachinines to suggest that he was influenced by ideas about evolution. He seems to have implicitly recognized natural order, but worked in the light of his own time, place, and contemporaries. His contributions are of value today at a practical, rather than a theoretical, level.

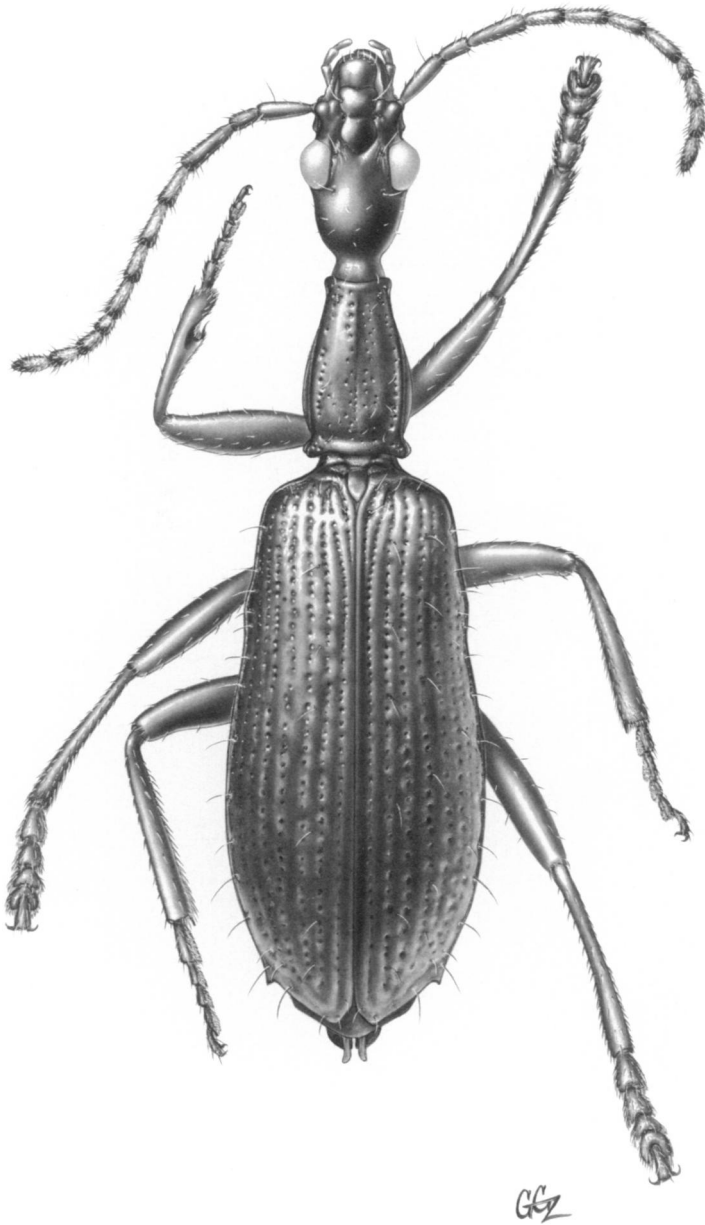
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“... it would be exceedingly interesting to know the thoughts of our predecessors about arrangement of taxa, and especially the thoughts of those who did not have the benefit of exposure to evolutionary theory.”

G. E. Ball, 1979

The man who we celebrate, Baron Maximilien de Chaudoir, was, during the first half of his career, just such a predecessor; during the last half, the *Origin of Species* . . . (Darwin 1859) was in circulation and Chaudoir must have heard of it. In this paper, I attempt to determine, by analysis of two groups on which he worked (the genus *Agra* and supertribe Brachinitae), whether Chaudoir was influenced by Darwin's theory and adapted his arrangement of taxa accordingly. This is particularly interesting in a historical sense because Chaudoir was Russian born and raised, then steeped in French tradition by living in France and Belgium in his later life and associating with the great taxonomists there. Although Russia certainly adopted 'Darwinism' politically and socially, many of Chaudoir's Russian contemporary taxonomists (e.g. Mannerheim, Motschulsky, and Ménétrié) did not convey any such evolutionary principles in their works; nor did the French and Belgians with whom Chaudoir was very closely associated.

Chaudoir's studies of *Agra* began with his 1847 revision and 9-page redescription and placement of the genus. (Fig. 1 illustrates the habitus of a typical adult). As noted by Basilewsky (this symposium), the detail provided shows the importance he gave generic descriptions, which must be regarded as a work of descriptive art. For his first *Agra* paper, Chaudoir knew only 52 species, but he attempted to classify them into two divisions. Under each, he ordered the species by similarity. One species, *A. klugii* Brullé, was listed 53rd because,



**Fig. 1.** Habitus of *Agra latipes* Chaudoir, Ega (Tefê), Amazonas, Brazil, (dorsal aspect with alternate legs splayed to show degree of lateral compression).



having not seen material, he was unfamiliar with it. Chaudoir's two divisions were based on configuration of the elytral apex: bidentate versus tridentate/bisinate. Between 1847 and 1866, Chaudoir became acquainted with 20 or so more species, and read descriptions of 34 more (mostly Klug's) regarded at the time as *Agra*; he also recognized an additional 7 species as belonging to *Agridia*, a new genus he described in 1861, the members of which have flattened legs. So on the basis of 116 species, Chaudoir attempted his final classification of *Agra sensu lato* (Table 1). In this classification, he included two genera, one of which included two divisions, *spuriae* and *ingenuae*, and the latter comprised of 6 species groups. To fill these categories with taxa, a combination of characters was used including the following: structures of the mouthparts, e.g. shape of lateral lobes of the mentum; tarsal form and vestiture; degree of tibial compression; form of elytral interneurs; shape and vestiture of head; and degree of pronotal punctation.

Subsequent revisors (Liebke 1940, 1941; Straneo, 1955, 1957, 1958, 1965a, 1965b, 1968, 1979) more or less continued Chaudoir's system, adding or splitting groups and describing new species based on few additional characteristics; although they figured male genitalia, they made little systematic use of them. Erwin (1982a, 1982b, 1983) reported that female genitalia and rigorous use of traditional characteristics with some additional ones provided excellent data for systematization and used cladistics to achieve a classification. Preliminary analysis indicates the system is an inversion of that suggested by Chaudoir.

Chaudoir's studies of brachinines began with a description of *Pheropsophus maculatus* (1835:440; see Fig. 2) in his very first paper at the age of 19, and ended with his major monograph (1876). He maintained an interest in these beetles throughout his career. His collection of them was rich in species; and according to Putzeys (1875), Chaudoir planned a second monograph about groups not treated in the first one. However, due to Chaudoir's illness in the late 1870's and eventual death in 1881, this second monograph was not produced.

In December of 1874, Chaudoir offered the Société Entomologique de Belgique a monograph of the "Brachynides" in which he summarized all he knew about the group and its species, except for the *Brachinus* of North America (treated earlier by him in 1868) and *Brachinus* and other groups of Europe, the Mediterranean area, and western Asia, all of which were reserved for his second monograph.

In the 1874 monograph, published in 1876, he agreed with the American and German schools of the time in "subfamilial ranking" of the brachinines (Table II). It was this rank that both LeConte (1853) and Schaum (1860) assigned, equating brachinines with "Carabides" and "Scaritides," *et cetera*. LeConte called his Brachinini "Subfamily I" of the Carabidae (which excluded "Cicindelidae"). Chaudoir, however, used the ending for present day familial status, "idae." His basis of rank was the extra exposed segments of the abdomen, '7 in both sexes' (later it was discovered that females have 8 exposed). LeConte and Horn (1883) declared this character 'blown out of proportion' and relegated Brachinini to tribal status. Chaudoir (1876) meanwhile had adopted the higher rank by using a different spelling, one which was later stabilized by code to be familial level; such ranking has been carried throughout French-dominated literature, as has the rank of other groups the North American school presently ranks as tribes and/or subtribes. Jeannel's (1942, 1948) system differed from that of Chaudoir only by reversing the place of *Aptinus* and *Crepidogaster*, and

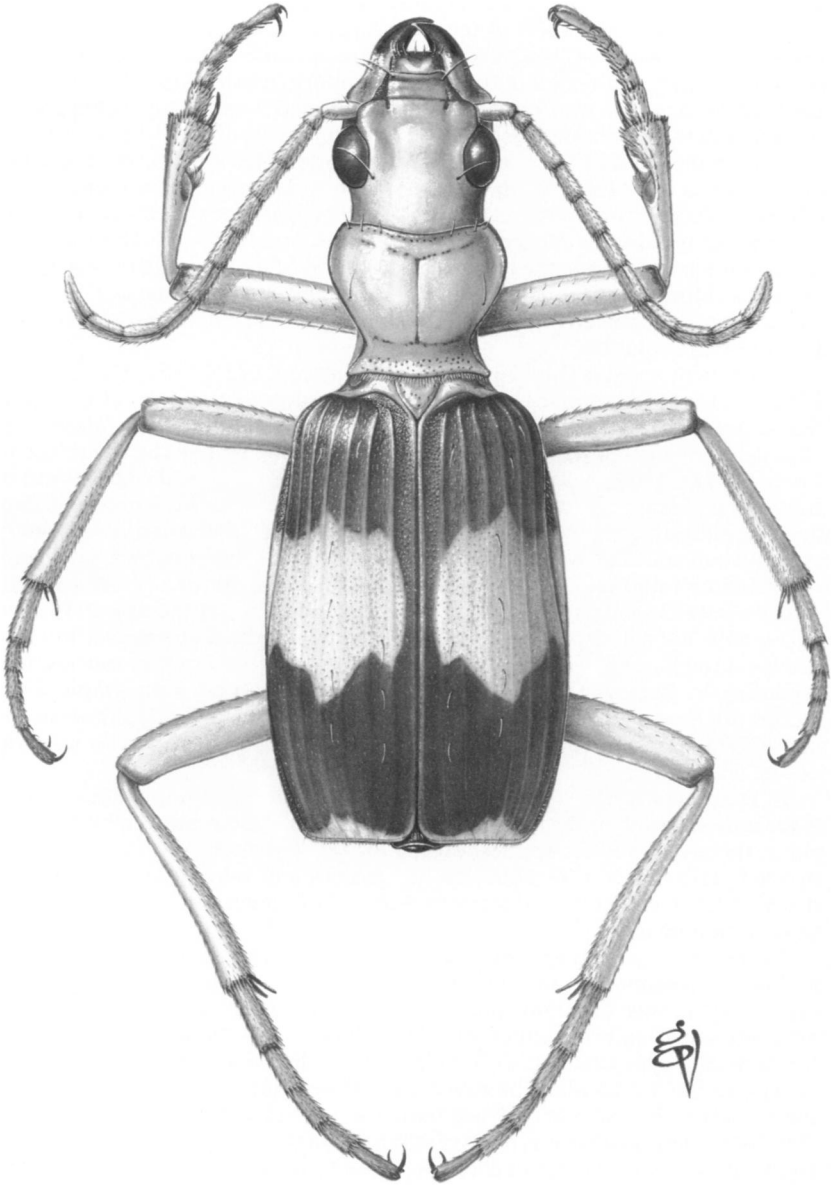


Fig. 2. Habitus of *Pheropsophus aequinoctialis* (Linné) (= *maculatus* Chaudoir), Rio Reventazon, Costa Rica.

elevating the latter to supertribal level. His system was based on phylogenetic considerations, and he pointed out that *Crepidogaster* had primitive characteristics. Had he used today's cladistic descriptive terms, his analysis would be considered quite modern. Erwin's (1970) system was achieved cladistically with *in*-group and *ex*-group comparisons, distribution of character states throughout the Carabidae, and determination of sister groups. The results bear no resemblance to that of Chaudoir and nearly inverts the order of taxa, as in *Agra*. Recognizing the different levels of rank begun by Chaudoir and carried to, at least, Jeannel's day by the French school, and noting the evolution of classification to the present day, we can now more closely examine the 'system' on which the classification, or arrangement of taxa, of Chaudoir is based.

His system began with identification of similarity in form of the whole beetles and some of their more easily observed structural characteristics. Chaudoir's methods were comparative as expressed in most of his descriptions. Lindroth (1969:xxxvi) laid particular stress on this descriptive method and made tremendous use of it in his monumental 'Ground-beetles of Canada and Alaska' (1961-1969). However, unlike that of Lindroth, Chaudoir's *system* was based on gross comparisons, thus some of his alignments of taxa were due to convergent and/or parallel development at the species level (e.g., in *Agra*, the *platyscelis/formicaria* groups; in *Brachinus*, the *mexicanus/costipennis=cognatus* groups) and group trends (*Mastax/Crepidogaster*) at the generic level. Lindroth, on the other hand, aligned species on the basis of male genitalia plus other characteristics, and used similarity in easily observable external features mostly for the purposes of field recognition of taxa.

So little other than pure description is stated in Chaudoir's works that almost nothing can be deduced about his ideas on evolution (pre- or post-Darwin 1859) and its importance in systematization and classification. As noted by Ball and Erwin (this symposium), the light of evolutionary theory did not brighten early in the French school, and there is no evidence that Chaudoir was at all influenced (see minutes of the Société Entomologique de France, 1835 to 1883). The general Frenchman's attitude on the subject was summarized by Bosanquet (1845) in reference to the early book alluding to evolution by Chambers (1844) (see Darlington 1981).

We are thus left with an analysis of Chaudoir's comparative techniques and their result in the final listing of taxa to get at his ideas, or lack thereof, of phylogeny. In both *Agra* and the brachinines, the most easily recognizable taxa (Fig. 4) are listed first. Those groups with the most apotypic features (as we would designate them today) are placed first in the boxes and listed first in the series of monographic descriptions. As one proceeds through the list of names of taxa (Fig. 3), the groups become less clearly defined, more inclusive, and more plesiotypic in the character suites used by Chaudoir. It must be remembered that optical equipment was less developed than at present, so observations made during Chaudoir's time were at relatively macroscopic levels compared with today, and internal structures such as male and female genitalia were not used at all (see Ball 1979, Fig. 5). In this light, it is interesting that Chaudoir's systems of *Agra* and brachinines, in addition to the trends just mentioned, also begin with taxa whose individuals are of larger size and end with those of smaller size.

Hence, Chaudoir's systems are inverse with respect to what current analyses demonstrate through use of cladistics, or even as listed by evolutionary eclectics (Ball 1979). Consequently, his classifications, in terms of individual sizes and

TABLE II.  
HISTORY OF CHANGES IN THE CLASSIFICATION OF BRACHINITAE

	CHAUDOIR 1876	SCHAUM 1860	JEANNEL 1942-48	ERWIN 1970
Taxon:	Brachinidae	Brachinini	Brachinidae	Brachinida
	<div style="border: 1px dashed black; padding: 2px;">           Aptinus  <u>Pheropsophus</u>            Brachinus  <u>Styphlomerus</u>  <u>Crepidogaster</u>            Mastax         </div>	<div style="border: 1px dashed black; padding: 2px;">           Aptinus  <u>Crepidogaster</u>  <u>Pheropsophus</u>  <u>Brachinus</u>  <u>Mastax</u> </div>	<div style="border: 1px dashed black; padding: 2px;">           Crepidogastritae            Crepidogastrini            Crepidogaster            Brachinitae            Pheropsophini  <u>Pheropsophus, etc. (3*)</u> </div>	<div style="border: 1px dashed black; padding: 2px;">           Crepidogastrini            Crepidogaster, etc. (1)         </div>
			<div style="border: 1px dashed black; padding: 2px;">           Brachinini            Mastacina  <u>Mastax</u> </div>	<div style="border: 1px dashed black; padding: 2px;">           Brachinini            Mastacina  <u>Mastax</u> </div>
			<div style="border: 1px dashed black; padding: 2px;">           Brachinini            Pheropsophina  <u>Pheropsophus, etc. (2)</u> </div>	<div style="border: 1px dashed black; padding: 2px;">           Pheropsophina  <u>Pheropsophus, etc. (2)</u> </div>
			<div style="border: 1px dashed black; padding: 2px;">           Aptinus  <u>Styphlomerus, etc. (2)</u>  <u>Mastax</u> </div>	<div style="border: 1px dashed black; padding: 2px;">           Aptinus  <u>Styphlomerus, etc. (3)</u> </div>
			<div style="border: 1px dashed black; padding: 2px;">           Brachinini            Brachinus, etc. (5)  <u>Aptinus</u>  <u>Styphlomerus, etc. (2)</u>  <u>Mastax</u> </div>	<div style="border: 1px dashed black; padding: 2px;">           Brachinini            Brachinus, etc. (3)         </div>

\* Numbers indicate associated genera.

complexity of readily observable structures, are almost mirror images of the phylogenetic sequences we are discovering today. It is likely that other taxonomists of Chaudoir's day may have arrived at similar conclusions in regard to arrangement simply because of methods, a point for all modern coleopterists to bear in mind. It should be noted here though, that both Agrina and Brachinitae bear such striking characteristics that they did not afford Chaudoir the opportunity to show much perception, at least from a modern point of view. His work on other groups, such as the difficult pterostichines, may provide better insights.

Based on the foregoing, I see in this carabidologist, the Baron Maximilien de Chaudoir, a man of his own time, a man of his own culture and 'scientific' environment, and a member in good standing of the Latreillean Period (Ball 1979) when the family Carabidae was recognized and reasonably well-defined. He did things well (e.g., descriptions, collections), perhaps better than most of his contemporaries, he knew many forms in nature because of his field work, he insisted on type comparisons rather than identification through literature whenever possible, and he took numerous trips to museums to make such comparisons. However, I find him neither innovative, creative, nor adaptive (at least as indicated in his writings), in that he carried on, throughout his entire career, the descriptive style laid down by Dejean; he did little with higher classification, methods, or collection techniques; and he paid little heed to the major philosophical event which occurred at the midpoint of his career. In short, Chaudoir the taxonomist was a keenly observant descriptive artist rather than a scientist; he merely did better the same things others had done before, including implicit understanding of the *scala naturae*. In explanation, I mean by 'artist' the fact that systematics is a continuum from art to science. Tax-

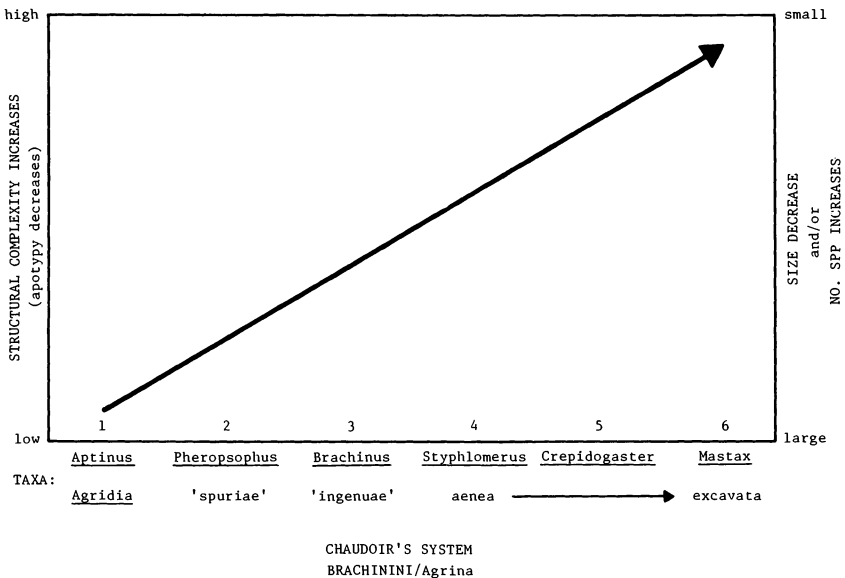


Fig. 3. Chaudoir's listed system of Brachinini and Agrina in relation to structural complexity (decreased gross apotypy), decreased size, and number of species.



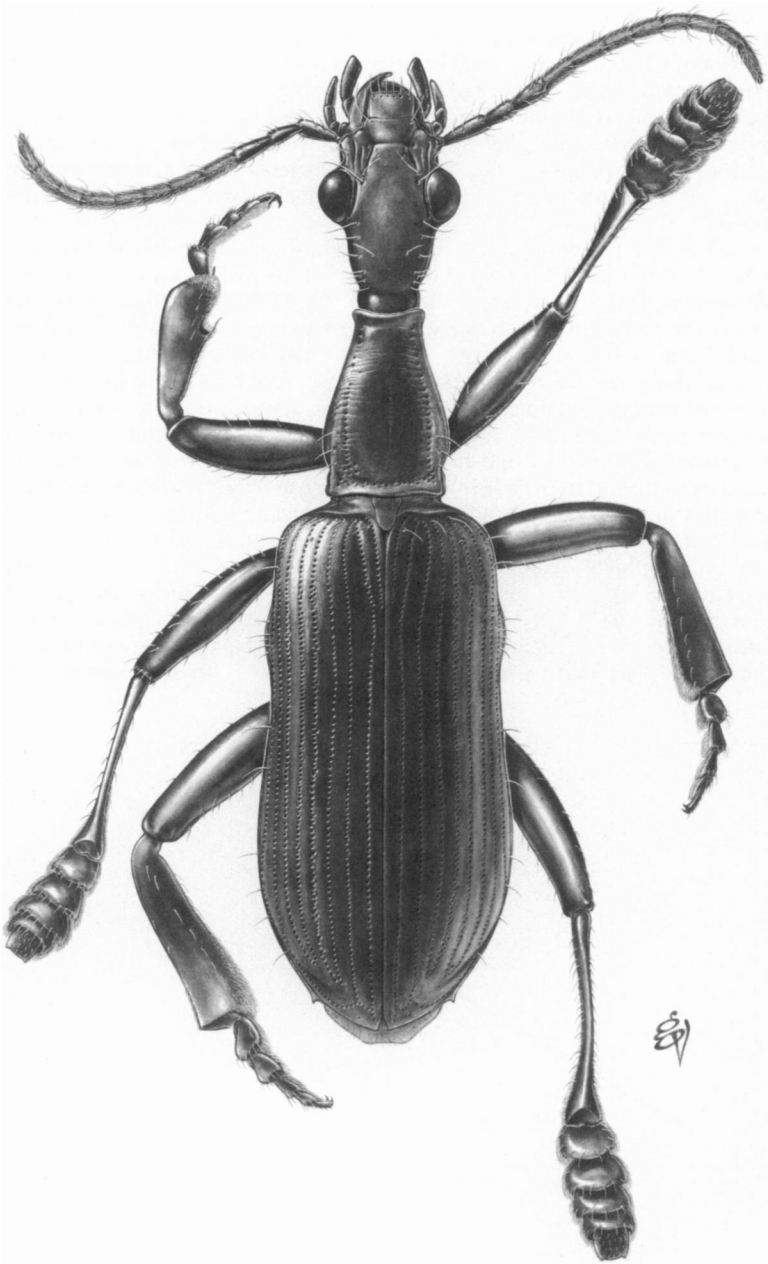


Fig. 4. Habitus of *Agra sasquatch*, Belém, Brazil, (dorsal aspect with alternate legs splayed to show degree of lateral compression).

onomy in the strict sense, the naming and describing of organisms, is an artform which requires keen observation and ability to put those observations into words (together with ability to comprehend and apply provisions of international codes). Even today, some taxonomists stop at this point. It is only when those observations are connected within a systematic framework, patterns are discerned, and hypotheses are erected and tested that the process becomes science; I see no evidence in Chaudoir's works on *Agrina* and *Brachinitae* of such science, except that he certainly had some idea that species could be arranged "naturally." Earlier in this symposium, Ball alluded to Chaudoir's perception of 'natural' systems or *scala naturae*. Based on an analysis of his treatment of *Agrina* and *Brachinitae*, it appears to me that his system was developed by use of similarity of readily observable structural characters and he aligned specimens accordingly. For his time, this course of study was appropriate and worthwhile. Today, however, we have the evolutionary framework to do much more and ought to be doing it. Our studies should be far more sophisticated than those of Chaudoir, but, still it is because of Chaudoir, and others, that we can do these more sophisticated studies, by building upon those of the past (Darlington 1979).

As one of the first carabidologists, Chaudoir made improvements to the system of classification and we can thank him for these; he was able to correctly record carabid structural features and define those which were diagnostic. Unfortunately, he was of a time when 'natural' systems were little understood and thus, like most of his immediate contemporaries, his "scientific" achievements were scant. His perception of the natural world was not that of Darwin, Wallace, or even Bates, but the question remains, 'what was his perception?'. When virtually no clues are available, it is impossible to decide whether his system based on similarity of structure was in turn based on an inherent feeling of the natural order of the world or a convenient way to arrange nearly similar objects in a box. Although we cannot *know* anything for sure, it is likely, in the case of the Baron, the latter can be rejected. He implicitly recognized natural order, but worked in the light of his own time, place, and contemporaries. It would be exceedingly interesting to know the systematic thoughts of this early carabidologist who lived both before and after the introduction of evolutionary theory and natural selection; I am sorry to say that these thoughts were buried with him 100 years ago!

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