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Vignettes of the history of neotropical carabidology

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Development of knowledge of Neotropical carabid taxonomic diversity is illustrated primarily in terms of rate of description of new genera, the pattern of which is paralleled by description of new family-group (tribal-subtribal) taxa. The rate of discovery of the latter is very low now, suggesting approach of an asymptote. New genera have been discovered at a rate of about 11 per decade for the past 40 years. Four periods of descriptive activity are recognized and related both to circumstances that influenced Western European cultural history generally, from 1758 to the present, and to the activities of primarily European specialists on Carabidae.

1. Introduction

History is not only development of a chronicle of past events, but is also a search for patterns and their causes or correlates. The exploration and elucidation of diversity of regional biotas is summarized in the scientific results achieved: species lists, monographs, *et cetera*. These achievements proceed from a background that belongs to other aspects of human endeavor. This background, which can enrich appreciation of the scientific achievements, is in the domain of history. The purpose of this paper, then, is to reveal something of the background of Neotropical carabidology, primarily for the benefit of those who find nearly irresistible the study of ground beetles. A detailed analysis, however, is too long for presentation in the present volume. Accordingly, I offer a few observations (vignettes) that provide a part of the detailed presentation.

This analysis is based on the Carabidae in a moderately restricted sense: excluded are the Trachypachidae, the rhysodids and tiger beetles. Relationships of these latter groups to the former are not settled.

Inspiration for this study came from reading Nelson Papavero's fine "Essays on the History of Neotropical Dipterology" (1971 and 1973). But more than inspiration came from these two volumes. The early history of entomological exploration by Europeans in the Neotropics, so carefully and painstakingly extracted from primary documents and other sources and explained by Papavero, is basic to my own endeavors. A more general treatment of Neotropical entomology was prepared by Hogue (1993: 3–13), and, considering the brevity of the account, it is a surprisingly rich source of information.

An under-exploited source of knowledge about the history of systematics is in checklists and catalogues of taxa, with their dated scientific names and associated names of authors. This information permits one to identify trends in rate of discovery (or publication), and thus trends in increase in knowledge. Also, it provides for correlating systematics with, for example, concurrent geopolitical events.

In this paper, I offer observations about the early stages of study of the Neotropical carabid taxa, about general trends in rate of description of genera, and recent developments in taxonomic treatments of tribes that are confined to the Neotropical Region or that show Neotropical-Afrotropical relationships.

My primary sources for this review were Blackwelder (1944), Erwin *et al*. (1977), Reichardt (1977), Madge (1989), and Erwin (1990). Information in these publications was supplemented by information in revisions and descriptions published since 1977. Older primary sources were consulted, as required, and cited, as appropriate.

2. Early Neotropical Carabidology (1758–1824)

2.1. Background

2.1.1. Philosophy and Collections

A proper appreciation of the beginnings of Neotropical carabidology requires a context based on circumstances current in the early part of the 18th Century that led to the flourishing of natural history in Western European culture. Mayr (1982: 100–103) provides a very good account, emphasizing that interest in organismic diversity at that time had an underpinning of recognition in the theory of Christian natural theology of the hand of the creator in similarities of organisms to one another and in their environmental relationships. At the time, this recognition was an adequate rationale for learning about and describing the taxa that were at hand, and served as a bridge between the religious domination of thought of previous centuries to the secularism that became dominant toward the end of the nineteenth century. Microscopes had been developed in the previous (17th) century, and with them it was possible to make the detailed observations required to characterize and identify plant and animal species, including those of small size, such as insects.

Interest in diversity was stimulated further by "the success of voyages and individual explorers bringing back exotic plants and animals from all continents" (Mayr 1982: 100). Farber (1982: 33) notes that "Traders, explorers, colonials, and voyageur-naturalistes provided a steady flow of new species, which broke into a deluge after 1815, when, following the cessation of the Napoleonic wars, nations undertook large scale expeditions and surveys".

The preservation of these specimens required care and maintenance, which took the form of natural history collections and ultimately museums. Such an institution, as noted by Winsor (1991: 267) is, at base, "just the mature version of the well-known human instinct for collecting".

Collections of biological specimens developed initially because of a "naive interest in the 'rare and fabulous' bound by a stylized and symbolic concept of natural objects" (Cohen & Lachner 1969: 759). Collections of biological specimens evolved from accumulations of the "wonder cabinets" of royalty and other wealthy folk. Such cabinets included a grand mixture of various human artifacts and paintings, mineralogical specimens, and preserved remains of large or otherwise striking animals, and plants that were especially pleasing to the eye, or purportedly had medicinal value. "The conception of a natural history cabinet was more that of a collector's than of a savant's, and consequently aesthetic considerations were as important as scientific ones" (Farber 1982: 49).

Establishment of collections as purposeful instruments of scientific enquiry was part of a naturalistic perception of the universe as distinct from the preceding religious perception that had dominated Western European culture since the Dark Ages (Ritterbush 1969). William Bullock, in London, for example, had in the early 19th Century, a private collection of natural history material which was intended both for entertainment and to instruct members of the public about the wonders of nature (Farber 1982: 51).

2.1.2. Colonization and exploration

Spain and Portugal were the dominant European colonial powers in the New World tropics, especially Spain, during the 16th and 17th centuries. Toward the end of the 17th century, Spanish power began to wane, in part because of a shortage of funds as a result of conducting expensive wars with the Protestant nations in Western Europe, and in part because of being unable to populate with colonists, and thus control, the outer reaches of its New World empire, particularly in the West Indies. The other European sea powers, Spain's enemies (both in com-

merce and religion) in the Old World, taking advantage of Spanish weakness, gained a foothold in the West Indies both by trade with the Spanish colonists, and by warfare on land and at sea. English, French, Dutch and Danish colonies were established during the 17th century on various West Indian islands, and as well, in the mainland of what are now the Guianas.

Throughout the 17th and into the 18th century, islands and settlements in the Guianas changed hands, according to the fortunes of war (Parry & Sherlock 1963, Pares 1963). But the colonies prospered, after a fashion, providing to Europe a bountiful harvest of sugar, logwood for dye, salt, and other commodities. These settlements provided also bases of operations and opportunities for explorer naturalists, desirous of procuring biological material for study and description.

Brazil, under Portuguese control, had been closed to citizens of other European nations. For example, Alexander von Humboldt, on his great expedition through the American tropics from 1799 to 1804, was not permitted to enter Portuguese territory (Papavero 1971: 38). Changed circumstances in Portugal led to a change in policy in its New World possession, and in 1807, the Brazilian government took a more liberal attitude, permitting into the country non-Portuguese European naturalists with diplomatic connections (Papavero 1971: 49).

The South American coast was explored by naval expeditions sent out at various times by the governments of England, France, the Netherlands, Austria, Prussia and Russia. Ships' doctors were trained in natural history as well as in medicine, and some of them were excellent observers and avid collectors, their material going to the national or royal museums of their respective countries.

2.2. Taxonomic work

Until 1825, little was published about Neotropical ground beetles. In that year, the first volume of Dejean's (1825–1831) five-volume worldwide treatment of carabid taxa appeared, in which he described 39 species from the Neotropical Region, most of them new. Many more were described in his subsequent volumes that appeared during the next six years, as well as by subsequent workers. Dejean was the first specialist on Carabidae. His impact was enormous, and Lindroth (1973: 125) referred to him as "the great name in coleopterology during the early nineteenth century".

Prior to the beginning of the 19th Century, descriptions of Neotropical carabids were included in general descriptive publications by, for example, Linnaeus (1758, 1766, 1767), Fabricius (1775, 1781, 1787, 1792) and Olivier (1790, 1795). A hint of a classification of taxa between order and genus is evident in their sequence but nothing was specified; Winsor (1976) noted that the published sequence of genera within orders could reveal an author's beliefs about inter-ordinal relationships.

With no categories between genus and order, a formal subordinal classification had no basis. Latreille (1802) provided a remedy for this situation, introducing additional categories, including family, and ranks equivalent to tribes and subtribes (Ball 1979: 68–69). Bonelli (1810), who accepted Latreille's family-level arrangement, introduced a different system of sub-familial classification of carabids that became the basis of the present system (Ball 1979: 82–85, fig. 8). Also, the introduction of categories between genus and order had the effect of rendering genus-level taxa less inclusive, thus providing potential for recognition and description of many more genera than had been recognized previously.

Between 1758 and 1825, 43 species of carabids were described (Tables 1 and 2), and it is interesting to note the nature of the beetles on which these descriptions were based. Except for the type material of *Selenophorus sinuatus* (Gyllenhal), the specimens were relatively large (mostly more than 10 mm in length), macropterous (except for the brachypterous *Enceladus gygas* Bonelli), and many were either colorful, graceful in form, or both. The one exception, *Selenophorus sinuatus*, is a widespread, probably commonly encountered species in the West Indies. Adults are small in size (length ca. 4–5 mm), but the body surface is rather metallic, and thus the beetles are moderately conspicuous, at least.

The species do not represent a random sample of the Neotropical carabid fauna. Being conspicuous and winged, these beetles could have been encountered at light, at night, or seen in the daytime, resting on vegetation or running in leaf litter, on the ground. Probably they were collected because of their relative conspicuousness and perhaps because they were attracted to human habitation by light.

Twenty two of these species represented what were found later to be 15 genera (16, if *Distichus* Motschulsky is accepted as separate from *Scarites* Fabricius): one, *Enceladus* Bonelli, remains as monobasic (adults of its single species, *E. gygas* Bonelli, 1813, are the largest carabids in the New World — see the frontispiece in Reichardt (1977)), but the others are more diverse (each presently with from 33 (*Pelecium* Kirby 1819) to several hundred (*Selenophorus* Dejean 1829)).

In contrast, 21 species represent the genus *Agra* Fabricius 1801, a taxon unplumbed with respect to species-level diversity, a current estimate being more than 2 000 (Erwin and Pogue 1988: 162). Adults of *Agra* are among the most visually pleasing carabids that inhabit the Neotropical Region.

Table 1. Species of Neotropical Carabidae described prior to 1825, and their describers[1].

Epithet	Author	Date: Page	Pres. Genus	Locality
americana	Linnaeus	1758: 415	Galerita	Surinam
aequinoct.	Linnaeus	1763: 395	Pheropsophus	Guianas
surinamens.	Linnaeus	1766: 619	Colliuris	Fr. Guiana
suturalis	Fabricius	1775: 238	Ceroglossus	Argentina
complanatus[2]	Fabricius	1775: 242	Pheropsophus	Guianas
amethystina	Fabricius	1787: 203	Calleida	Fr. Guiana
acuminata	Olivier	1790: 340	Calophaena	Colombia
bifasciata	Olivier	1790: 347	Calophaena	Brazil
pallipes	Fabricius	1792: 159	Apenes	West Indies
tridentata	Olivier	1795: 53	Agra	Brazil
cayennensis	Olivier	1795: 53	Agra	Fr. Guiana
fallax	Olivier	1795: 71	Chlaenius	Fr. Guiana
occidental.	Olivier	1795: 64	Galerita	Fr. Guiana
planus[2]	Olivier	1795: 62	Pheropsophus	Guianas
rufipes	Fabricius	1801: 225	Agra	Brazil
aenea[3]	Fabricius	1801: 224	Agra	Fr. Guiana
elongata	Fabricius	1801: 229	Colliuris	Surinam
integer	Fabricius	1801: 196	Selenophorus	Hispaniola
sinuatus	Gyllenhal	1806: 203	Selenophorus	West Indies
dentipes	Olivier	1811: 620	Ozaena	Brazil
gygas	Bonelli	1813: 460	Enceladus	Fr. Guiana
orientalis	Bonelli	1813: 169	Scarites	Surinam
glabrata	Bonelli	1813: 467	Scarites	Colombia
cyanipes	Kirby	1819: 378	Pelecium	Brazil
multiplicata	Klug	1824: 39	Agra	Brazil
rufescens	Klug	1824: 14	Agra	Brazil
immersa	Klug	1824: 27	Agra	Brazil
femorata	Klug	1824: 36	Agra	Brazil
excavata	Klug	1824: 20	Agra	Brazil
gemmata	Klug	1824: 28	Agra	Brazil
geniculata	Klug	1824: 30	Agra	Brazil
ruficornis	Klug	1824: 33	Agra	Brazil
infuscata	Klug	1824: 15	Agra	Brazil
exarata	Klug	1824: 35	Agra	Brazil
brevicollis	Klug	1824: 25	Agra	Brazil
attenuata	Klug	1824: 26	Agra	Brazil
variolosa	Klug	1824: 18	Agra	Brazil
catenulata	Klug	1824: 29	Agra	Brazil
aterrima	Klug	1824: 17	Agra	Brazil
cuprea	Klug	1824: 41	Agra	Brazil
chalcoptera	Klug	1824: 23	Agra	Brazil
chalcites	Germar	1824: 15	Notiobia	Brazil
cupripennis	Germar	1824: 16	Notiobia	Argentina

[1] Sequence is based on date of description of the species, and within dates, alphabetically by genus.
[2] Junior synonym of Pheropsophus aequinoctialis Linnaeus.
[3] Junior synonym of Agra cayennensis Olivier.

Tables 1 and 2 show also the countries or regions from which the described specimens were taken: principally geographically marginal areas for eastern South America, and the West Indies. Middle America had not received the attention of the early collectors, nor had islands other than those of the West Indies.

2.3. The describers

Eight individuals described the carabid species during the period under review (see Table 3). The comments offered below reveal features that these Western European men of science held in common. Three were Scandinavians, two German, and one each, English, French and Italian. The preponderance of northern Europeans may be related directly to the early preeminence of Linnaeus in systematic entomology and his contemporary, Carl DeGeer, followed closely by Fabricius.

Five of them were professors: Linnaeus, University of Uppsala; Fabricius, Universities of Copenhagen and Kiel; Olivier, veterinary college, at Alfort; Germar, University of Halle; Bonelli, University of Turin. One was a director of an important museum: Klug, Berlin Zoologisches Museum. One, Gyllenhal, had a distinguished military career, taking up entomology upon retirement. And one, W. Kirby, was a devoted man of the cloth — the "rector of Barnham" for 68 years. They were well connected, and in position to sample rather freely the material that was arriving from overseas, as a result of the efforts of expeditions and individual collectors.

They were part of an unstructured, international community of scholars, among whom ideas, specimens and manuscripts moved rather freely. Kirby, in 1817, in an address to the Linnean Society of London, noted that Fabricius, Olivier and others were describing material from British collections because British entomologists had not busied themselves sufficiently with the specimens that they had at hand Further, he remarked that he was describing one hundred "... of the non-descript insects of my own cabinet... to give the public some account of our entomological treasures..." (Kirby 1819: 375).

All of these men were distinguished, having attained recognition, through their extensive publications, of at least the international entomological community in their own time. For each of them, except Bonelli, work on carabids was done as a part of far more general studies of insect diversity.

2.4. Sources of specimens

Noted here are individuals who collected the specimens, and/or collections from which the taxonomists

Table 2. Genera in which species described previous to 1825 are included at present.

Genera	No. Included Species
Ozaena Olivier	1
Ceroglossus Solier	1
Enceladus Bonelli	1
Pelecium Kirby	1
Chlaenius Bonelli	1
Apenes LeConte	1
Calleida Latreille & Dej.	1
Scarites Fabricius	2
Selenophorus Dejean	2
Notiobia Perty	2
Calophaena Klug	2
Colliuris DeGeer	2
Galerita Fabricius	2
Pheropsophus Solier	3
Agra Fabricius	21
Total Species	43
Total Genera	15

Frequency Distribution of Species in Relation to Genera	
No. Species	No. Genera
1	7
2	6
3	1
21	1

Countries Represented	No. Species
Brazil	23
Guianas	13
West Indies	3
Colombia	2
Argentina	2

Table 3. Describers of Carabidae, 1758–1824, and sources (collectors or collections) of their specimens.

Describer[1]		Collector or Collection	
Name	Nationality	Name	Biog. reference in Papavero (1971)
Linnaeus, C.	Swedish	Rolander, D.	page 9
Fabricius, J. C.	Danish	Banks, J.	16
		Bosc, L. A. G.	20
		Lund, N.T.	89
		Rohr, J. P. B. von	20
		Sehestedt, O.	21
Olivier, G. A.	French	Francillon	
		Holthuysen	112
		Mus. Paris	
		Tugni	
Gyllenhal, L.	Swedish	Forsström, J. E.	103
Bonelli, F. A.	Italian		
Kirby, W.	English	Hancock, D.	
Germar, E. F.	German	Langsdorff, G. H. von	50
Klug, J. C. F.	German	Olfers, I. F. N. M. von	69
		Sellow, F.	56
		Sieber, F. W.	48

[1] Names in sequence of date of first species description of a New World carabid by each author.

obtained the specimens on which they worked (see Table 3).

The publications of Marcgrave (1648), Piso (1658) and Merian (1705) that referred to or were based on observations of South American insects, in Brazil and Surinam, fired Linnaeus' interest in this part of the world. He encouraged several of his former students to undertake expeditions to South America. One of these individuals, Daniel Rolander, was in Surinam in 1755, where he made excellent collections, principally of plants (Papavero 1971: 8–9). He collected material of the first carabid species to be described from the Neotropical Region, *Galerita americana* (Linnaeus).

Like Rolander, subsequent collectors about whom something is known, had deep interest and training in natural history, acquired with their medical degrees, or in the course of fulfilling their duties as employees of wealthy naturalists. Friedrich Sieber, for example, was employed as a preparator and curator by Count von Hoffmannsegg, and was sent by him to Brazil, to make collections of biological material (Papavero 1971).

Sir Joseph Banks was of the English landed gentry, and was instrumental in interesting the British government of the time in matters scientific. Lund and Sehestedt, former students of Fabricius, did not collect in the Neotropics, but because of their connections in the Danish diplomatic corps, they were able to obtain material through officials in the field, particularly in the West Indies. Both of them had extensive insect collections, which provided much material for their former professor of natural history.

2.5. Summary

The early history of Neotropical carabidology is best viewed in a general context. During the period 1758 through 1824, knowledge of insect diversity expanded markedly. Means of preparation and long-term (more or less) storage of specimens were assured through scientific collections established with governmental (or crown) support or by individuals of wealth and stature. These collections were cared for by persons employed for that purpose.

The basis for carabid study (as for all taxa) was strengthened markedly by Latreille's establishment of categories between genus and order. More specifically, Latreille (1802) established the taxon Carabici (= Carabidae) as a family. Both Latreille and Bonelli (1810, 1813) proposed useful systems of classification for the Carabidae.

The impression one gains about early collecting of Carabidae is that those specimens were acquired because they were easy to find, and because they were conspicuous in one way or another. Certainly, a systematic effort to sample a local fauna was not apparent in the results.

By the time (1825) that Dejean began his more systematic work to elucidate the Carabidae, he had a firm basis on which to build. Also, he had at his disposal an appreciable amount of material from the Neotropics (and elsewhere) that had been accumulated in France by the naval expeditions and land-based collectors who had visited the New World.

3. Progress in knowledge of diversity of the Neotropical carabid fauna (1825–1995)

This topic is addressed using principally quantitative information about genera, and subtribes and tribes (nomenclaturally, taxa of the family-group), on the assumption that increase in valid taxa recognized represents progress. Genera are treated first because, being more numerous, collectively they provide better data for consideration.

3.1. Genera

3.1.1. Quantitative aspects

Table 4 shows the pattern of increase in number of Neotropical genera between 1758 and the present. Included are only genera believed to be "native" — indigenous (with origin in the Neotropical Region, or earlier, in Gondwanaland, and occurring elsewhere now), or precinctive (origin in the Neotropical Region and present range confined thereto). See Frank and McCoy (1990) for a discussion of these terms.

An initial analysis, based on number of genera described per decade (1755–1764 to 1985–1984 and 1995) revealed the pattern summarized in Table 4, with four recognizable periods (I–IV). The average number of genera described per year over the entire time span (237 years) is 1.23. The averages for periods II and IV are above the overall average, espe-

cially period II, whereas the averages of periods I and III are below the overall average.

During period I, carabid specialists were not known, which is not surprising, considering the general state of knowledge of biodiversity then. The fruitful activities of the systematists of the time led very shortly in a temporal sense, to the need for specialization, which had also the salutary effect of enhancing the efficiency of the descriptive process. Specialization allowed for entry into the field of more workers, and the sharing of museum material that was brought from afar by the activities of the surveys and expeditions, noted above.

During period II, the first specialists on Carabidae appeared, the principal one being Baron Maximilien de Chaudoir, but le Comte Dejean, and later, Henry Walter Bates, then Assistant Secretary of the Royal Geographical Society (O'Hara 1995) were very active as well with studies of this family. Period II began with the first volume of Dejean's great work on carabids, and ended with Bates' treatment of the Carabidae of Middle America (1881–1884). During this time, thanks largely to Bates' efforts, knowledge of the Middle American carabid fauna increased markedly, though he contributed also to a substantial increase in knowledge of the South American ground beetles (papers published in 1871 and 1872, cited by O'Hara (1995: 215–216)).

Period III (1885–1924) is characterized by a striking decrease in description of carabid genera. The reasons for the marked decline probably are many and complex. First, European interest in the New World tropics seems to have declined, with emphasis and investment being placed instead in Africa and the Far East. Thus, the government surveys and expeditions that contributed so much to the growth of museums in the early part of the 19th Century were not being conducted in the New World. Second, the political unrest, both in Europe and in the South and Middle American republics, was not conducive to visits there by itinerant European naturalists. The unrest in Europe, beginning with the Franco-Prussian War in 1870–1871, was crystallized and terminated in the First World War (1914–1918), which was very disruptive to scientific endeavor, generally. Third, economic depression that developed in Western Europe in the closing decades of the 19th Century spread elsewhere, affecting support for museums and other cultural activities on other continents, including South America (Sheets-Pyenson 1988: 95–96). Fourth, the developing New World tropical nations had in place only a very limited system for support of taxonomic endeavor. Thus, the void left by the Europeans could not be filled, locally. Fifth, the political unrest of the time likely generated a certain amount of xenophobia, so that even the few naturalists who might have ventured into the New World tropics were discouraged from doing so. Thus, additional material proved difficult to obtain.

3.1.2. Nationalities of the describers

A superficial examination of this topic reveals, not surprisingly, that most of the Neotropical genera have been described by French, English, and German-speaking taxonomists, with the outstanding exception of the Ukrainian, Baron Maximilien de Chaudoir. Chaudoir, however, had strong Parisian connections (Basilewsky 1983: 466) which no doubt enabled him to obtain material from the New World that was available readily to French entomologists. These Western European nations had established large and very active museums (British Museum, in London; Museum National d'Histoire Naturelle, in Paris; and the Zoologisches Museum at the Universität zu Berlin, an institution with a royal endowment). Although unlike Great Britain and France, Germany was not a major sea power, a number of zealous German collectors, sent there by their institutions or wealthy private collectors, visited the New World tropics . As well, donations of private collections were made to the public institutions, and specimens were purchased and exchanged (Farber 1982: 61–62).

The most surprising feature of nationalities of the describers in Periods I to III is absence from the

Table 4. Historical periods and number of precinctive and indigenous Neotropical carabid genera described in each period.

	Years		Number of Genera	
Period	Range	Total	Described	Described per year
I	1758–1824	66	9	0.14
II	1825–1884	60	155	2.58
III	1885–1924	40	16	0.40
IV	1925–1995	71	112	1.56
TOTAL		237	292	1.23

Table 5. Family-group names of Carabidae (Madge, 1989) based on Neotropical genera

Name	Original: Author	Year[1]	Current: Subtribe	Tribe
Ctenodactylidae	Laporte	1834		Ctenodactylini
Agridae	Kirby	1837	Calleidina	Lebiini
Leptotrachelides	Chaudoir	1848		Ctenodactylini
Lachnophori	LeConte	1853		Lachnophorini
Cnemacanthides	Lacordaire	1854		Cnemacanthini
Anchonoderides	Lacordaire	1854		Lachnophorini
Antarctiides	Lacordaire	1854	Antarctiina	Pterostichini
Eucaeri	LeConte	1861		Lachnophorina
Pasimachides	Putzeys	1866	Pasimachina	Scaritini
Ardistomides	Putzeys	1866	Ardistomina	Scaritini
Gallerucidiae	Chaudoir	1872d	Gallerucidiina	Lebiini
Pentagonicinae	Bates	1873		Pentagonicini
Stenomorphidae	Laporte	1874	Harpalina	Harpalini
Euchroides	Chaudoir	1874	Euchroina	Pterostichini
Peleciides	Chaudoir	1880		Peleciini
Enceladini	Horn	1881	Enceladina	Siagonini
Catapiesinae	Bates	1882		Catapiesini
Pelmatellinae	Bates	1882	Pelmatellina	Harpalini
Nemotarsinae	Bates	1883a	Nemotarsina	Cyclosomini
Eucheilinae	Bates	1883a	Pericalina	Lebiini
Polpochilinae	Bates	1891b	Stenolophina	Harpalini
Tropopterides	Sloane	1898	Melisoderina	Psydrini
Microcephalides	Tschitsch.	1899b	Euchroina	Pterostichini
Trichopselaphini	Tschitsch.	1900	Harpalina	Harpalini
Micratopini	Casey	1914a	Tachyina	Bembidiini
Homopteridae	Wasmann	1920	Homopterina	Paussini
Merizodini	Sloane	1920	Merizodina	Zolini
Dercylini	Sloane	1923b	Dercylina	Oodini
Homaloderini	Jeannel	1926	Homaloderina	Trechini
Ceroglossina	Lapouge	1927		Ceroglossini
Cicindini	Csiki	1927b		Cicindini
Nototylini	Bänninger	1927		Nototylini
Eohomopterinen	Kolbe	1927a	Homopterina	Paussini
Tichonii	Csiki	1929	Euchroina	Pterostichini
Anisotarsi	Csiki	1932a	Anisodactylina	Harpalini
Barysomi	Csiki	1932a	Amblystomina	Harpalini
Forcipatorina	Bänninger	1937	Forcipatorina	Scaritini
Monolobini	Jeannel	1938		Migadopini
Barypitae	Jeannel	1941	Barypina	Broscini
Creobitae	Jeannel	1941	Creobiina	Broscini
Calophaenidae	Jeannel	1941		Ctenodactylini
Pachytelini	Jeannel	1946	Pachytelina	Ozaenini
Physeitae	Jeannel	1946	Physeina	Ozaenini
Brachygnathini	Basilewsky	1946	Brachygnathina	Panagaeini
Metiini	Straneo	1951	Antarctiina	Pterostichini
Chaetogenyina	van Emden	1958		Chaetogenyini
Tichonillina	van Emden	1958	Euchroina	Pterostichini
Cnidiina	Jeannel	1958	Perileptina	Trechini
Helluomorphina	Reichardt	1974	Helluomorphina	Helluonini
Cyrtolaina	Whiteh.& Ball	1975	Coelostomina	Pterostichini
Apenina	Ball	1982	Apenina	Lebiini
Notiokasiini	Kav. & Nègre	1982		Notiokasiini

[1] References to first publication of family-group names are in Madge (1989: 470–474).

list of the names of Spanish and Portuguese entomologists. These nations did not take the opportunity offered by their extensive territorial holdings in the New World. Was this generally true for all taxa, or were the carabids simply one group among many ignored by Spanish and Portuguese entomologists interested in other taxa?

3.2. Taxa of the family-group: quantitative aspects

Prior to 1834, the new genus-group taxa of Neotropical Carabidae were either not placed in formally named subfamilial or tribal taxa, or were placed in taxa of this rank that were based on genera from elsewhere. Table 5 shows that, between 1834 and 1994, 52 family-group names were proposed that were based on Neotropical carabid genera (Madge 1989). The table shows also the fate of these names in terms of present-day use, for subtribes or tribes.

The data from Table 5 are summarized in Table 6, showing the relationship between number of names proposed in each of the periods identified previously. Not surprisingly, number of higher taxa proposed parallels the number of genera proposed, with a distinct depression in Period III, between 1885 and 1924. However, proportionally more names of higher taxa were proposed in Period IV (1925–1994) than in Period II (1825–1884 — cf. Table 4). This difference has probably two causes. First, the overall increase in numbers of lower taxa (cf. Table 4) requires more higher level taxa to group and ultimately to classify the former. Second, the more detailed analysis of carabid taxa using more character systems (Ball 1979: 71–75) provided an improved basis for discovering the relationships reflected in the higher level classification systems.

It seems clear that an asymptote has been approached for taxa above the rank of genus. Only two Neotropical groups based on newly discovered genus-group taxa (*Chaetogenys* van Emden and *Notiokasis* Kavanaugh and Nègre) have been proposed since 1882, when Bates named the Pelmatellinae, based on the then newly described genus *Pelmatellus*. Even then, chaetogenyines had been known in the form of *Camptotoma* (*s. str.*) since Reiche described the group, in 1843. Its distinctness had not been recognized until van Emden did so, though he did not appreciate the close relationship, indicated by Straneo (1977: 116), between *Chaetogenys* and *Camptotoma*.

3.3. Some recent advances

During the first international symposium of carabidologists in Washington, D. C., in 1976, a paper written by Hans Reichardt (1979), then recently deceased, was read, in which that author summarized the present status of the precinctive (or "endemic" — see Frank and McCoy (1990)) Neotropical tribes of Carabidae. He discussed also the Inabresian tribes (i.e., those with Afrotropical affinities — see Jeannel (1939) for a general discussion of the geographical distribution of the tribes of Carabidae). In the years intervening between the oral presentation of that paper and the present, each of these tribes was investigated more or less intensively, mostly by individuals who had been friends of Reichardt. The results are summarized in Tables 7 and 8.

Previously, Jeannel's (1926–1928) treatment of the Trechini introduced evolutionary concepts to study of carabid classification in the Neotropical Region. In most of the papers noted above, an evolutionary theme was a central and organizing component. Collectively, they are confirmatory of the ideas promulgated by Jeannel and Reichardt. They are an indirect tribute to Reichardt, recognizing his perceptiveness in bringing into focus these wonders of the Neotropical fauna, to the study of which he had dedicated himself. In marking the flowering of evolutionary thought as applied to the Neotropical Carabidae, they are also a tribute to Jeannel, who introduced such thought some 40 to 50 years previously.

Progress of the type noted above is dependent upon other advances, only one of which, accumulation of study material, is noted here. As recorded above, early collections of Neotropical insects included few carabids which must have been picked up primarily because of their conspicuousness.

Table 6. Numerical summary by time period of family-group names based on Neotropical carabid genera, with numbers of names used currently for subtribes and tribes.

Period	Years	Total No. Proposed-A	No. Recognized Subtribes	Tribes	Total No. Recognized-B	B/A %
I	1755–1824	0	0	0	0	0
II	1825–1884	20	8	5	13	65
III	1885–1924	8	4		4	50
IV	1925–1994	24	9	5	14	58

Concerted efforts to obtain representative faunal samples in the Neotropical Region was begun, evidently, by the collectors who contributed the material on which the volumes of the Biologia Centrali-Americana were based. This sampling was confined, however, to what could be accumulated principally at ground level or at least near the ground. Recently, concerted efforts have been made and techniques developed to sample the very rich insect fauna of the high canopy of tropical forests, with spectacular results. For a brief account, see Erwin (1989).

4. The nature of progress in Neotropical Carabidology

The advances, noted above, nonetheless, were made possible by those 19th Century workers, who, through their endeavors, made known an important portion of the diversity of Neotropical Carabidae. Their more extensive publications were not simply random arrays of descriptions, nor were they simply catalogues or dictionaries of diversity (Ball 1983: 529, Thompson 1983: 608–609). Though not declared as such, the taxa described by previous generations of carabid workers are first-order hypotheses about biodiversity, and they are tested by the new information discovered by subsequent generations. Bates used information that he had assembled about the Middle American carabid fauna to postulate faunal assemblages with common histories. Similarly, he tested the hypothesis of a close faunal resemblance among Chile, the equatorial Andes and the temperate zones of North America and Europe (O'Hara 1995: 210–211).

Table 7. Reichardt's (1979) precinctive Neotropical tribes of Carabidae and their present status.

Tribes	1979	1995	Publications
Nototylini	paussine affinities?	independent lineage (Nototylidae)	Deuve (1994)
Catapiesini	lebiomorph affinities postulated	lebiomorph affinities confirmed	Erwin (1985)
Agrini	lebiomorph affinities suggested	calleidine Lebiini confirmed	Erwin (1985)
Eucheilini	helluonine affinities suggested	pericaline Lebiini confirmed	Ball&Shpeley (1983)
Cnemacanthini	relationships uncertain revision required	Cnemalobini: species revised; relationship – nr. Pterostichini & Zabrini confirmed	Roig (1993, 1994)

Table 8. Reichardt's (1979) "South American...endemic [carabid] tribes with African relationships", and their present status.

Tribes	1979	1995	Publications
Cicindisini	relationships uncertain	Cicindini independent lineage, w/isopleuran affinities	Kavanaugh & Erwin (1991)
Siagonini	Inabresian affinities accepted, but not confirmed by detailed study	larval features of Neo. *Enceladus* & Afr. *Siagona* confirmatory	Erwin (1978); Moore (1972)
Apotomini	status of Brazilian exx. not confirmed	Brazilian exx. descr. as n. sp. of *Apotomus*	Erwin (1980)
Peleciini	affinities doubtful; revision required	genera & Neotropical spp. revised; affinities	Straneo & Ball (1989)
Pterostichini			
Dryptini	Inabresian affinities accepted	no change	
Hiletini	Inabresian affinities accepted	revision of genera and Neotropical species	Erwin & Stork (1985)

The point is that the results of previous taxonomic work made possible the application of evolutionary theory in further advancing knowledge of the Neotropical carabid fauna. As Darlington (1971) noted, progress in knowledge of taxa has been achieved by a series of steps, each of which, in retrospect, is rather short. Thus, progress has been evolutionary rather than revolutionary.

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