Arboreal beetles of neotropical forests: *Agra* Fabricius, the *cayennensis* complex (Coleoptera: Carabidae: Lebiini: Calleidina)

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The neotropical carabid genus *Agra* contains more than 2 000 species. One monophyletic lineage, the *cayennnensis* group, was selected for phylogenetic analysis to underpin a biogeographic study pertaining to the Amazon Basin. The *cayennensis* group containing 10 subgroups and more than 150 species, arose and radiated in the basin, subsequently invading Central and Middle America 3 times, and as far as Texas once. The fact that such major radiation occurred within the basin, not only at the species level, but to a higher plain, the subgroup level, forces us to look for evolutionary driving forces that act relatively quickly and at a fine geographic resolution in order to account for the megadiversity found there today.

1. Introduction

The neotropical carabid genus *Agra*, whose range extends from southern Texas to northern Argentina contains more than 2 000 species (most of which are undescribed and most of which live in the Amazon Basin or nearby areas) making it the largest monophyletic lineage at the generic level known of predatory beetles. *Agra* is monophyletic by virtue of the extendable, or telescopic, ovipositor and arrow-head phallus, as well as the tubular prothorax and large array of secondary sexual features in both males and females. Its putative sister is the African/Madagascan genus *Callidiola* (Erwin 1982).

Reasons for the rise of *Agra* to dominance after the fragmentation of Gondwanaland include its successful invasion of the uppermost reaches of tropical angiospermus tree canopies, morphological (superspecialist) adaptations for canopy life including gigantism relative to its micro-habitat, agility, maximal radiation in fragmented forest mosaics during the Pleistocene, and tolerance for relatively diverse climatic regimes, both altitudinally and latitudinally. All other arboreal carabids in the Amazon Basin and other neotropical forests are much smaller in size, or like another dominant group, *Calleida*, live in the understory and/or in the shrub zone beneath the understory. In addition, females have a totally unique feature not found in any other carabids, an extensible ovipositor that is capable of reaching 1/2 to 2/3 the length of the body, thus their larvae most likely exploit a niche not accessible to other carabids. However, where they oviposit, the gen-

eral behavior, and the life history of *Agra* members are entirely unknown.

Although a possible artifact of sampling, very few species are known which have extensive ranges. Even in the western Amazon Basin, where canopy fogging as a method of collecting has been used for more than a decade, most *Agra* species are still known from single localities, thus species turnover or beta diversity is remarkably high. Species are adapted to microhabitats both in the understory and in the canopy and at any one site there are dozens of species distributed across the landscape. For example, there are 56 species known from Barro Colorado Island in the Panamá Canal. Some species groups are now known to be confined to microhabitats, thus ecological characters have the potential of enhancing morphological ones for the purposes of classification. The putatively least derived lineage of *Agra* occurs in non-forested habitats (savannas) in northern Argentina and southern Brazil and individuals have been collected on grasses in open habitats (W. Steiner, pers comm.), although they may actually depend on isolated tree canopies in the savanna for reproduction. The hypothesized sister lineage of *Agra*, *Callidiola* and relatives were found in evergreen forest habitats in Madagascar (W. Steiner, pers comm.).

Questions arise as to how a group such as this could have diverged from its sister and then speciated to the extent it has in such a short period of time in the neotropics, i.e. post drift. The forest refugium hypothesis (Haffer 1969) is an obvious explanation, but this idea has been challenged by palynologists (Colinvaux 1987). Further, it's proposed extent could not totally account for the pattern seen today in *Agra* distributions (Erwin and Pogue 1988); other possibilities such as hydrological features which create micro-vicariant events may add to the dynamic of speciation (Salo *et al*. 1986), and there are new findings in archeology (Meggers 1994ab) that relate massive amazonian forest fires to long-term El Niño climatic cycles, thus a potential further mechanism of range disruption that might lead to speciation. Likely, all of these and perhaps other factors have influenced the evolution of this remarkable group of carabid beetles.

What, then, do the *Agra* themselves and their distributions tell us about the evolution of amazonian-centered lineages, indeed, what do they tell about neotropical speciation and post-gondwanian radiation in general? In order to answer these questions, we need to know the history of the genus and this, then, is dependent on a firm phylogenetic understanding of the group.

This paper examines one monophyletic lineage of *Agra*, indeed, one part of the largest and most complex in the genus which by present count contains the following 10 subgroups and in excess of 150 species.

The *cayennensis* complex

The *cayennensis* group

Diagnosis: The following features in combination define the *cayennensis* group members-antennomere 8 coequal in length with 7 in males, 1/2 the length of 7 in females; prosternal process bifid in males, planular in females; middle tibia more or less rounded in x-section; middle and hind tibiae in male slightly to markedly arcuate and flattened antero-mesially, rounded in females; arcuate-flattened portion of tibiae markedly setose (brushy) or totally devoid of vestiture; elytral interneurs not well organized, of large foveae or of medium-sized foveae interspersed with punctulae; female stylus moderately long, somewhat flattened dorso-ventrally.

Member subgroup distributions:

— *cayennensis* subgroup – Brazil, Ecuador, French Guiana, Surinam, Guyana, Perú, Venezuela (no localities south of the south bank of the Rio Amazonas/Solimoes except one outlier in Mato Grosso, Brazil)

— *rufescens* subgroup – Brazil (south eastern), Bolivia, Perú (middle), French Guiana, Costa Rica (Amazonian and South Atlantic Forest)

— *darlingtoni* subgroup – Brazil (mid and south eastern), Bolivia, Colombia, Costa Rica, Ecuador, French Guiana, Panamá, Perú (Amazonian and South Atlantic Forest with northern vicargroup in Panamá and Costa Rica)

— *tarnieri* subgroup – Brazil (middle and eastern, to Bahia), Bolivia, French Guiana, Guyana, Surinam, mid and southern Perú (southern, northeastern Amazonian and South Atlantic Forest)

— *phallica* subgroup – Brazil, Bolivia, Colombia, Costa Rica, Panamá, Paraguay, Perú (middle) (Amazonian and cis-andean to Panamá and Costa Rica)

— *multipunctata* subgroup – Brazil (eastern), Perú

(middle) (southern Amazonian and South Atlantic Forest)

— *resplendens* subgroup – Brazil (eastern), Bolivia, Central and Middle America deep into México with outlier in Texas, Venezuela, Trinidad, Tobago (eastern and southern Amazonian, South Atlantic Forest, with a northern vicar-group in middle America to Texas)

— *cyanosticta* subgroup – Brazil (southeastern) (South Atlantic Forest with a single outlier at Belém)

— *vulgaris* subgroup – Brazil (northeastern), Guyana, Perú (middle) (middle Amazonian).

— *beegees* subgroup – Brazil (upper Amazonian), Guyana (eastern Amazonian).

Preliminary key to subgroups (males only). (Females can be identified at the group level only by features of their styli. Keys and illustrations will be published elsewhere.)

Most character states used below can be found illustrated in group revisions published earlier (see Erwin and Pogue, 1988, for bibliography).

1.   Middle and posterior tibia markedly excavate antero-mesially; mesial surface markedly setose or not .. 2
1.'   Middle and posterior tibia slightly excavate antero-mesially; mesial surface moderately setose 8
2(1). Middle tibia markedly macromucrate ....
.... *cayennensis* subgroup
2'.   Middle tibia not or micromucrate 3
3(2'). Elytral apex with small lobe midway between lateral and sutural teeth .... *tarnieri* subgroup
3'.   Elytral apex straight between lateral and sutural apices 4
4(3'). Metasternum densely pubescent 5
4'.   Metasternum sparsely setiferous 6
5(4). Abdominal sterna 2–5 with undivided pubescent patch... *rufescens* subgroup
5'.   Abdominal sterna 2–5 with 2 bilateral patches ....
.... *darlingtoni* subgroup
6(4'). Elytron with obtuse sutural apex; interneurs of small foveae and punctures .... *resplendens* subgroup
6'.   Elytron with markedly dentate sutural apex; interneurs of large, course foveae 7
7(6'). Posterior tibia glabrous antero-mesially ....
.... *phallica* subgroup
7'.   Posterior tibia markedly setose antero-mesially ....
.... *multipunctata* subgroup
8(1'). Elytron bicolored, foveae dark, often metallic contrasting with pale surface .... *cyanosticta* subgroup
8'.   Elytron unicolored 9
9(8'). Elytral apex with small tooth midway between lateral and sutural teeth .... *vulgaris* subgroup
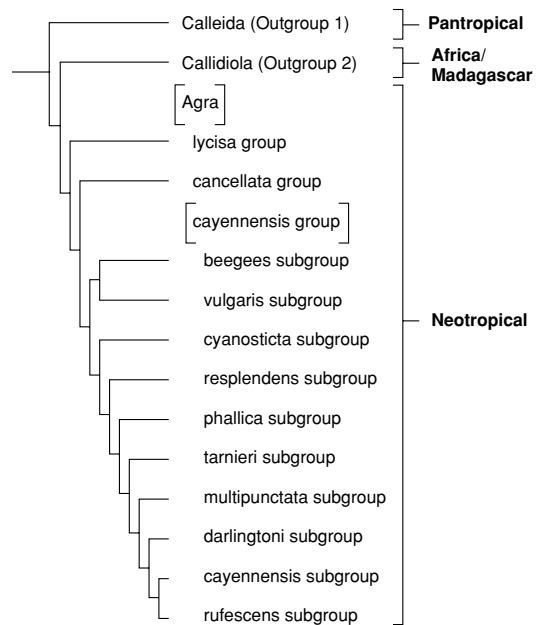

Fig. 1. Cladogram based on 60 characters of adult morphology for 10 subgroups of the *cayennensis* group using Hennig86; length 198 steps, CI = 0.65, RI = 0.60, 1 tree. After TSA, same tree, 169 steps, CI = 0.70, RI = 0.71.

9'.   Elytral apex straight between lateral and sutural apices .... *beegees* subgroup

2. Phylogeny

The purpose of this analysis is to provide a framework within which species of the *cayennensis* complex may be studied at a finer level and to analyze their distributions within a phylogenetic hypothesis. The program Hennig86, version 1.5, was used for the analysis and then Transformation Series Analysis (TSA) was performed on the data set (Mickevich 1982). The tree did not change after TSA, although it resulted from fewer steps and a better Consistency Index. The character set used, 60 characters (5.1 states average, number of states ranging from 2–15, with 11 2-state characters and 17 3-state ones), was extracted from that used for a study of the genus as a whole at the species level (106 characters) and will be described elsewhere. The cladogram (Fig. 1) based on these 60 characters of adult morphology for 10 subgroups of the *cayennensis* group resulted in 1 tree, length 198 steps, CI = 0.65, RI = 0.60.

Fig. 2. Distribution of subgroups using peripheral localities to circumscribe total range for detecting overlap.

After TSA, the same tree architecture, 169 steps, CI = 0.70, RI = 0.71. Fig. 1 depicts relationships among these characters with termini representing species subgroup within the *cayennensis* group and the sister relationship of *cayennensis* and *cancellata* groups. Fig. 1 also shows a sister group relationship between the *vulgaris* and *beegees* groups and these are the sister of the remainder of the subgroups. The *cyanosticta* subgroup is embedded within the evolution of all the groups, it is not basal. The *phallica* and *resplendens* groups are lower on the tree; these two also exhibit within group amphi-amazon distribution patterns; however, so does the *darlington* group which is subterminal on the tree. A notable trend seen in the cladogram is that basal groups have a less developed male leg morphology AND are of limited distribution, except the *resplendens* subgroup which is the most widespread of all groups.

3. Biogeography

Fig. 2 resulted from finding, for each subgroup, the peripheral localities at which individuals were collected and connecting these with a line. Amazonian and Central American limits were only connected for the *phallica* group since several species in this subgroup were found in amazonian and inter-Andean Colombian localities, thus linking Panamá with the Amazon Basin. Four patterns emerge: 1) the Amazonian-South Atlantic Forest pattern with 6 groups occupying it; 2) the North-amazonian pattern with 3 groups; 3) the Amphi-amazonian pattern with 2 groups; and the South Atlantic Forest pattern with only 1 group. Only the *cyanosticta* subgroup seems to be isolated outside of Amazonia; all the other groups are overlapping in some way, although they too are in part vicariant within group with a

northern and southern unit of species — for example, both the *resplendens* and *darlingtoni* subgroups are amphi-amazonian with numerous species occurring in Central America (to Texas in *resplendens*) and again in Amazonia + South Atlantic Forest. The amphi-amazonian pattern was pointed out previously for the *formicaria* and *fiestameli* groups (Erwin & Pogue 1988). The north amazonian pattern also occurs in the *formicaria* group (*ibid*).

Two anomalies lie in the data as presented. One species of the *cynosticta* subgroup has been collected in Belém and one species of the *cayennensis* subgroup was collected in the Xingu area, in both cases hundreds or a thousand kilometers from the rest of the species. In both cases, these remote species are represented by a single specimen.

In summary, it is clear that the center of origin for the *cayennensis* group is the Amazon Basin; all subgroups are found there except, perhaps, *cynosticta* subgroup, if the Belém record is proved false. Even if *cyanosticta* is found to be solely in the South Atlantic Forest today, its sister, the combined taxa from *resplendens* to *rufescens* groups (see cladogram) are northern Amazonian in part, thus *cyanosticta* or its ancestor occurred at one time in the Basin, perhaps being replaced by more advanced members of the *cayennensis* group depicted higher on the tree (Fig. 1) as the result of a taxon pulse (Erwin 1985). The fact that such major radiation occurred within the basin, not only at the species level, but to a higher plain, the subgroup level, forces us to look for evolutionary driving forces that act relatively quickly and at a fine geographic resolution in order to account for the megadiversity found there today. What are the possibilities? Of those listed above, the one with the least study is the latest to be introduced — the long term cyclic impact of El Niño on both the forest and the populations of organisms using that forest. Will drought and subsequent fires be extensive enough to isolate forest patches as suggested for the pleistocene forest refugia? Will these isolated forests exist long enough for vicariant speciation? How do populations of insects respond to drought ridden tropical forests even when they don't burn? What are the effects of shorter cycles on these same populations, for example, the 4 year El Niño cycle? Is there a connection between cyclic abundance highs and lows and dispersal that might lead to a founder effect across isolated forest patches?

References

Colinvaux, P. 1987: Amazon diversity in the light of the paleoecological record. — Quatern. Sci. Rev. 6: 93–114.

Erwin, T. L. 1982: Agra, arboreal beetles of Neotropical forests: erythropus group systematics (Carabidae). — Syst. Ent. 7: 39–71.

— 1985: The taxon pulse: A general pattern of lineage radiation and extinction among Carabid beetles. — In: Ball, G. E. (ed.), Taxonomy, phylogeny, and zoogeography of beetles and ants: A Volume dedicated to the memory of Philip Jackson Darlington Jr. 1904 –1983: 437–472. Dr. W. Junk b.v. Publishers, The Hague.

Erwin, T. L. & Pogue M. G. 1988: Agra, arboreal beetles of Neotropical forests: Biogeography and the forest refugium hypothesis (Carabidae). — In: Heyer, W. R. & Vanzolini, P. E. (eds.), Neotropical distribution patterns: proceedings of a 1987 Workshop: 161–188. Proceedings of the Brasilian Academy of Sciences.

Haffer, J. 1969: Speciation in Amazonian forest birds. — Science 165: 131–137.

Meggers, B. J. 1994a: Biogeographical approaches to reconstruction the prehistory of Amazonia. — Biogeographica, 70(3): 97–110.

— 1994b: Archeological evidence for the impact of Mega-Nino events on Amazonia during the past two millennia. — Climatic Change 28: 321–338.

Mickevich, M. F. 1982: Transformation Series Analysis. — Syst. Zool. 31: 461–478.

Salo, J., Kalliola R., Häkkinen I., Mäkinen Y., Niemelä P., Puhakka, M., & Coley P. D. 1986: River dynamics and the diversity of Amazon lowland forest. — Nature 322: 254–258.