

OBSERVATIONS ON THE BIOGEOGRAPHY OF  
THE GENUS *GOLIATHUS* (INSECTA: COLEOPTERA)<sup>1</sup>

LEON CROIZAT<sup>2</sup>

SUMMARY

The biogeography of the beetle genus *Goliathus* in Africa is detailed. The pattern of its distribution is in line with the general biogeography of other animals and plants on the continent and may be explained through geological and organic co-evolution.

KEY WORDS: *Goliathus* - Insecta: Coleoptera - taxonomy - biogeography - Africa.

Dr J.T. Wiebes has been good enough to send me a copy of his work (Wiebes 1968) on the taxonomy of *Goliathus* Lamarck *sensu lato* [goliath beetle, Insecta-Coleoptera: Cetoniidae] on the understanding that the distribution of its species would prove biogeographically interesting. The surmise of this brilliant entomologist will be, of course, amply supported by the observations and comments in this short article. Viewing the subject strictly from the standpoint of the classifying entomologist, Wiebes has managed to materialize patterns of dispersal that, to a striking extent, support the general biogeography of Africa. This congruence of biogeography with taxonomy is important because it shows that the two are indeed inseparable.

It will perhaps be remarked by some readers that, not being a specialised entomologist, I lack status to judge on the taxonomy of a coleopterous insect, whether Wiebes' or somebody else's. This remark is only correct to the extent that I am not qualified to decide on whether, for instance, the two races which Wiebes assigns to species *G. goliatus* are not in themselves full species. The student of dispersal is not immediately concerned with this level of *formal taxonomy*, though he may not be wanting trenchant ideas on some of its aspects (see Croizat 1962: 500 ff.).

On the other hand, and on account of his cogent interest in evolution considered under the double aspect of space and time, the biogeographer is by no means incompetent to take stock of *taxogeny*. *Taxogeny* is the discipline enquiring into the process of biological form-making (genus-making, speciation, etc. in a broad sense) without raising immediate questions of rank and nomenclature.

Incompetent, as obviously I am, concerning the *taxonomy* of these Cetoniidae, I am rather less than fully so when faced by the task of judging the geographic ranges that Wiebes assigns to one or other of the taxa *Goliathus*, and of certain aspects of their form-making. This is a very basic issue. No naturalist will ever believe that throughout its history, this or

---

<sup>1</sup> Editor's note: Croizat wrote this article in 1969. Thanks to Mrs. C. Croizat for loan of the manuscript. The article was submitted by Dr M. Heads, Biology Department, University College of Winneba, P.O. Box 25, Winneba, Ghana, from whom reprints are obtainable.

<sup>2</sup> Deceased 1982.

that insect, bird or plant has been privileged to have the free run of palaeogeographic and actual maps provided by Dame Nature for its own special use. Indeed, it is statistically demonstrable (see Croizat 1952, 1958, 1961, 1968a, 1968b, 1968c) that the very same tracks, the very same loci, recur in the dispersal of sundry animal and plant groups. Not only that, but also some of the major tracks in question are closely bound with basic features of tectonics and general geology, thus proving that life and the earth evolved together. *Goliathus*, naturally, is no exception to this fundamental rule. Were I to suppress the name *Goliathus* altogether in the pages of this article and replace it with the symbol X (see Croizat 1961, 1b: 1451 ff.), I could claim that the patterns of distribution of this beetle belong instead to some bird or plant in full assurance that neither the entomologist nor the ornithologist nor the botanist could contradict. It so happens indeed, that the patterns in question are perfectly congruous with those of other life as I propose to demonstrate. Whether one calls it *Goliathus* or X, it is still the same biogeography throughout.

This pointed conclusion jars of course against the belief, now widely current, that biogeography is not a science in its own right, but just the more or less casual appendage of this or that specialised form of research such as taxonomy or ecology. Lamentably, this belief is false, and its by-products catastrophic to the detriment of advancing knowledge. It leads on to as many "zoogeographies" and "phytogeographies" as there are plants, animals and naturalists specialized in one or other of their families or genera. Somebody postulates "centres of origins" which somebody else denies; someone else visualizes "migrations" running diametrically opposed to the "migrations" postulated by others, and so on without end. I have not been the first to discover and expose this pernicious state of mind: a well-known North American ecologist, Stanley A. Cain, had already seen it in 1943 (see original quotation and comments in Croizat 1962: 595), showing that no less than 13 different criteria were being employed — none satisfactory — to determine the "centre of origin". He tartly concluded as follows: "what is most needed in these fields [biogeography] is a complete return to inductive reasoning with assumptions reduced to a minimum and hypotheses based on demonstrable facts and proposed only when necessary. In many instances the assumptions arising from deductive (i.e. fundamentally aprioristic) reasoning have so thoroughly permeated the science of geography [sic], biogeography, and have so long been part of its warp and woof, that students of the field can only with difficulty distinguish fact from fiction".

Heeding the warning by Cain (I am not aware if he laboured to implement what he so clearly perceived, but I, at least, tried to behave otherwise from 1952), my readers and I will examine the biogeography of *Goliathus* strictly on the strength of what it factually exhibits, without any guess, surmise or theory as to, for example, *Goliathus* having "extended" its range by "casual migrations" to make us deviate from the record. What *Goliathus* did will become clear by this distribution, reasoned according to common sense, and in no other way or manner.

#### THE CLASSIFICATION AND DISTRIBUTION OF *GOLIATHUS*

Wiebes structures the genus *Goliathus* Lamarck *sensu lato*, dividing it into four subgenera and 11 species (two of them raceless), as follows:

- i. Subgenus *Goliathus* — three species: *G. goliatus* (three subspecies, *goliatus*, *regius*, *orientalis*); *G. albosignatus* (two subspecies, *albosignatus*, *kirkianus*); *G. cacticus* (raceless);
- ii. Subgenus *Argyrophegges* — one species: *G. kolbei* (raceless);
- iii. Subgenus *Fornasinius* — four species: *G. fornasini* (raceless); *G. russus* (raceless); *G. aureosparsus* (raceless); *G. higginsi* (raceless);
- iv. Subgenus *Hegemus* — three species: *G. pluto* (raceless); *G. vittatus* (raceless); *G. peregrinus* (raceless).

The face of the *geographic distribution* of these 11 species in four subgenera, would not be other than it is if, unsatisfied with Wiebes' classification, we turned his 11 species into 33 and reduced his subgenera to two. The genus would cover as much ground, distributed basically as it is across Africa including the lower latitudes, under either formal classification. The notion that biogeography is ancillary to so-called "perfect classification" is one I have examined and exploded (Croizat 1968b: 219-262) once before. The truth is that, understanding of necessity, *taxogeny* as a general biological process over space through time, a competent biogeographer can, and in fact does, assist the taxonomist in the task of more deeply and fully appreciating the ultimate causes of taxon-making and, therefore, as a corollary, how best to formally classify. As a concrete subject of biogeographic enquiry, Wiebes' classification of *Goliathus* in Africa is just as valid a tool of analysis and synthesis as is, for example, Traylor's classification of certain Estrildidae birds on the same continent; my judgement of the two, of course, being that of a student of dispersal and *taxogeny*, not of a naturalist specialised in formal classification. Obviously, whenever formal taxonomy closely agrees with dispersal — which as we will presently see, is true of Wiebes' disposition of *Goliathus* — the conclusion is bound to follow that taxonomy and biogeography perform smoothly in the premises. Therefore, in all probability, *both are good*. This does not mean that this or that species in particular is unassailable from the stand-point of the specialised entomologist or ornithologist. It does mean, however, that both the biogeographer and the classifying naturalist know, in principle, their own job, and so qualify to collaborate fruitfully.

Having published well over 8000 pages on biogeographic matters, I need not refer my readers in detail to this or that title and citation on any particular subject. Suffice it to state here that a pattern of dispersal is well-known — classical, I should call it — which splits Africa into two halves, western and eastern, according to longitude. Just to orient the attention of my readers, I will give here an example drawn from the standard checklist of ornithology (Peters 1931-1968, 4: 21). If I choose to mention a bird as an example, this is not because I fancy myself as a better ornithologist than entomologist — I am neither — but the checklist in question is complete and organic to an extent that greatly exceeds what is being offered by other branches of botany or zoology.

Here, then is the example furnished by a genus of cuckoos, *Cercococcyx*.

- i. *C. mechowi* (raceless) — Sierra Leone eastward to Northern Uganda, across Zaire and southward to Angola;
- ii. *C. olivinus* (raceless) — Ghana to Cameroon, Zaire (Katanga), Angola;

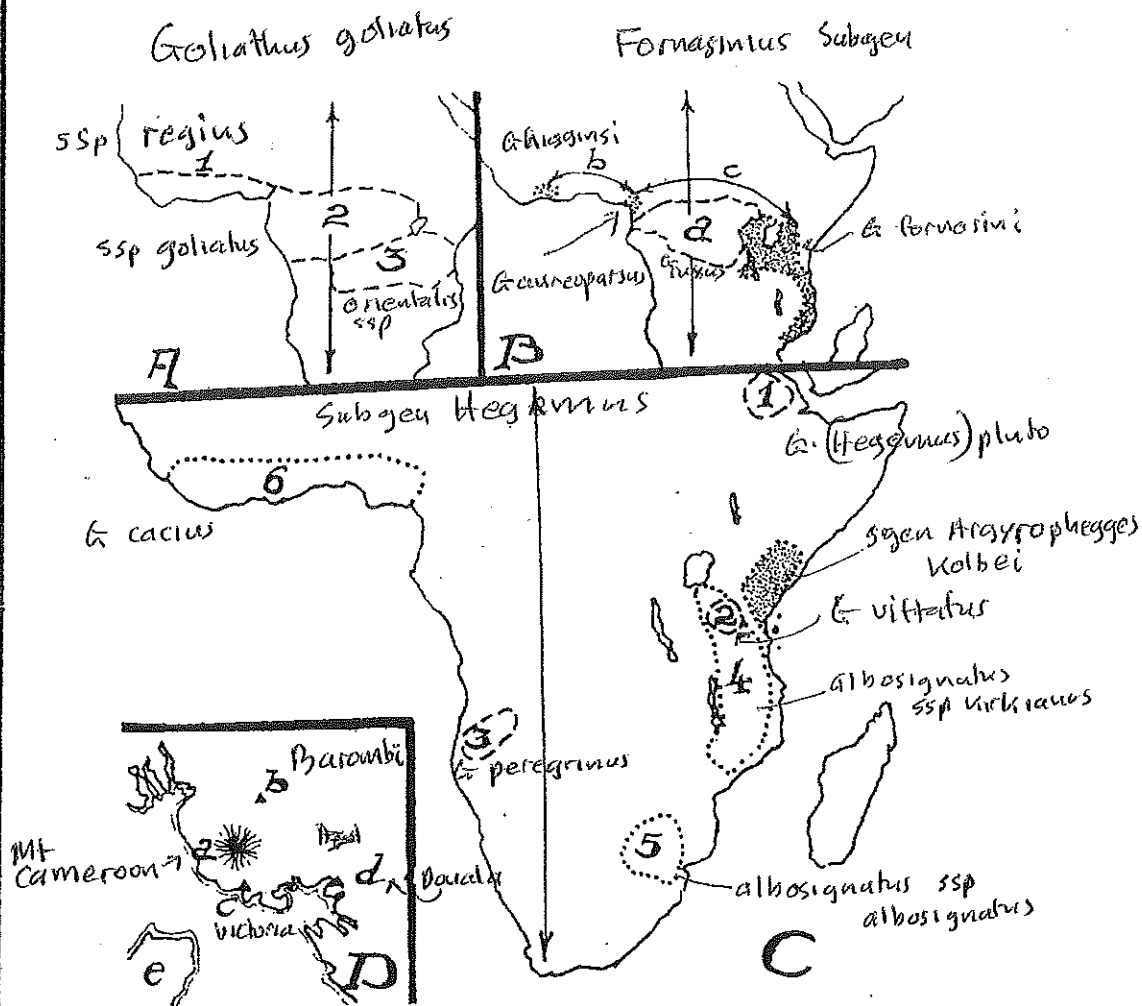


FIG. 1. A. The distribution of *Goliathus goliatus* by subspecies: 1 *regius* (western); 2 *goliatus* (nominate, central); 3 *orientalis* (eastern). The arrow corresponds to longitude 20°E and splits Africa in half (after Wiebes 1968). B. The distribution of *Goliathus* subgenus *Fornasinius*. Arrow b makes contact between *G. higginsii* (left) and *G. aureosparsus* (right). Arrow c makes contact between *G. aureosparsus* and *G. fornasini* (stippled). These three species resemble one another more than *G. russus* (a, dash line) resembles any of them. Note: (i) *G. russus* is surrounded by an arc of forms (*G. higginsii*, *G. aureosparsus*, *G. fornasini*) similar to one another all the way from the Ivory Coast (*G. higginsii*) to Mozambique (southern end of *G. fornasini*'s distribution), and is "isolated" within this arc; (ii) the species in the "wings of the dispersal", that is away from its centre, are related by similarity. C. The distribution of other *Goliathus* species: 1 *G. (Hegemus) pluto*; 2 *G. (Hegemus) vittatus*; 3 *G. (Hegemus) peregrinus*; 4 *G. (Goliathus) albosignatus* subsp. *kirkianus*; 5 *G. (Goliathus) albosignatus* subsp. *albosignatus*; 6 *G. (Goliathus) caciw*; stippled *G. (Argyrophegges) kolbei*. After Wiebes 1968. D. Some localities on the Nigeria/Cameroon border: a Mt. Cameroon; b Barombi; c Victoria; d Douala; e northern end of the island of Fernando Po. Barombi, Mt. Cameroon and Victoria are politically part of Nigeria and virtually contiguous with Cameroon on its southeastern boundary.

- iii. *C. montanus* (races as given) — Highlands of the Zaire-Uganda-Tanzania boundary, from the Ruwenzori to Lake Tanganyika, with *montanus* in Tanzania (apparently confined to the Uluguru and Usambara plateaux) and *patulus* in Malawi.

A glance at the above reveals that species *mechowi* and *olivinus* are distributed to the west and the two races of species *montanus* to the east.

Since *dispersal forever repeats*, it will not surprise my readers that *Goliathus* too, is distributed along lines matching the distribution of *Cercococcyx* (and endless other examples). If we split Africa into two by an axis drawn along the longitude between westernmost Cyrenaica and the Cape of Good Hope (Fig. 1), we readily classify *Goliathus* and its species and races into *western* and *eastern* as follows: (a) Western — *G. goliatus regius*, *G. cacicus*, *G. aureosparsus*, *G. higginsi*, *G. peregrinus*, and (b) Eastern — *G. goliatus orientalis*, *G. albosignatus* (all races), *G. fornasini*, *G. pluto*, *G. vittatus*, *G. kolbei*; giving a total of five western taxa and seven eastern taxa.

Out of this brutally geographic classification remain two forms, *G. goliatus goliatus* (nominate) and *G. russus*, which happen to be intersected about half-way by the Cyrenaica-Cape of Good Hope divide. Technically speaking, these two taxa could be termed central. There is, however, every justification to identify them as actually western (see comments under Mabira below).

In sum, *Goliathus* in Africa is equally split between west and east, thus matching the distribution of numerous plants and animals. This being the case, I would not wish the responsibility of proving that *Goliathus* has dispersed by chance, flying haphazardly from one to the other corner of Africa from this or that putative "centre of origin". The face of the record is, on the contrary, clearcut and precise, and is similar to countless other cases of distribution of the same type. If I were to postulate "chance dispersal" for *Goliathus*, I ought to do the same for *Cercococcyx*, a bird, and *Macaranga*, a Euphorbiaceae plant (Pax & Hoffman 1931: 128), thus turning the whole world dispersal into a nightmare of "chance" (see Croizat 1968a: 10), "casual distribution" and "double invasions", making an academic farce of the workings of nature that reach cosmic proportions over space through time.

#### OBSERVATIONS ON CERTAIN LOCALITIES

Assured that the dispersal of *Goliathus* is the same in its own right and by comparison with that of the rest of creation, let us look at certain of the localities which turn up in the records of *Goliathus* as reported upon by Wiebes. A "feeling" for localities is a fundamental end of biogeographic science, as my readers will soon learn.

1. **Mabira.** This locality (a forest and small river in Uganda within the triangle Lake Victoria—Lake Edward—Lake Albert) is a thoroughly standard station for groups of *western* origin which reach the easternmost limit of their dispersal in Uganda. A telling example from bird life (Peters 1931-1968, 10: 24-25) is in a genus which is familiar from the Old World: *Erithacus erythrothorax* (by races) — *erythrothorax* (nominate), Sierra Leone, Liberia, Ghana, southern Nigeria; *gabonensis*, coastal region of Cameroon and Gabon, Fernando Po; *xanthogaster*, southern and southeast Cameroon, Zaire along the middle Congo river; *mabirae*, eastern half of the forests of the Upper Congo in Zaire, and Uganda (forest patches east to Mabira). As we saw, *Cercococcyx mechowi*, which rates as fundamentally

western as does *E. erythrothorax*, ends its eastern distribution, according to Peters, in "Northern Uganda". The reader will not sin by imprudence if he suspects that this cuckoo, too, is not unknown around Mabira. As an informed student of dispersal would anticipate, Mabira also turns up in the records of *Goliathus*. As a matter of fact, it marks the eastern end of the distribution of *G. goliatus goliatus*, and likewise that of *G. russus*. These two taxa, it will be recalled, are geographically *central*, but biogeographically rather *western*.

2. **Barombi—Cross River—Kribi.** These three localities crowd by the shore of the Gulf of Guinea and its immediate hinterland. They stand right at the heart of one of the most important biogeographic centres of Africa, indeed in the world. This node (the "Nigerian Triangle") is so conspicuous that I spotted it in 1952 (Croizat 1962). Other authors had had inkling of it (see Croizat 1968b: Figs. 30, 31).

Barombi is located (Fig. 1d) about 75 km northwest of Douala, between the Mungo and Mene rivers. The Cross River has one of its sources not far to the north of Barombi. Kribi is on the coast about 125 km south of Douala. The entire sector is a formidable node of endemism and distribution, to which of course *Goliathus*, too, is subservient. As a matter of fact: (i) This node stops the dispersal of *G. goliathus regius* eastward; (ii) it does the same as regards *G. cacticus*; (iii) it marks the range of *G. aureosparsus*; (iv) it stops the dispersal westward of *G. goliatus goliatus*; (v) Barombi, one of the classic botanical stations of Africa (the same collectors, Preuss for instance, sent plant and insect specimens to Europe) is for the moment the only known station of *G. aureosparsus*; (vi) Kribi, a station in the records of *G. goliatus goliatus*, is a classical locus for the dispersal of one of the most striking avian relics of Africa (and even more, of the world). This is also the case with the genus *Picathartes* (two species), with *P. gymnocephalus* from the dense forests of Upper Guinea, i.e. Sierra Leone to Togo, and *P. oreas* from similar forests in Lower Guinea, i.e. Cameroon. Kribi is known in connection with this bird (Bannerman & Hoffmann 1931: 1251). Reichenow, the author of the species, might have originally received it from there, rather than from Victoria, which is also in Cameroon.

A similar dispersal range might be found for *Goliathus* if this genus is carefully investigated. It is well known from Chapin's reports (Rand 1951), and also from evidence presented by myself (Croizat 1968b: Fig. 27a), that there are marked disconnections in the range of plants and animals distributed on both sides of, for example, Togo/Benin. There is little doubt that a sector of western Africa has "foundered" or "crumbled" into the waters of the Gulf of Guinea - the geological process in play is of little significance to students of dispersal (Croizat 1968b: 406 ff.). Only a fairly exhaustive knowledge of the ranges of *Goliathus* in this sector could throw light on the point above and beyond the records now available, but it is not impossible that, for example, the discontinuity between *G. higginsii* and *G. aureosparsus* in the ranks of subgenus *Fornasinius* has this origin. Breaks of the kind are already authenticated with plants, for example *Cleistanthus* (Croizat 1968b).

3. **Uluguru—Usambara.** It is a matter of common knowledge for the student of dispersal that the highlands and tablelands of Tanzania are a major sector of dispersal and endemism in Africa, with connections far flung across the world (see Croizat 1958, 1: Fig. 16). Among these highlands, the Uluguru and Usambara plateaux easily rank as bio-geographically the most important. In *Goliathus*: (i) species *kolbei*, sole member of the subgenus *Argyrophegges*, is palpably massive on Usambara; (ii) species *albosignatus* subsp. *kirkianus* is,

without doubt, present in the Uluguru region. The latter is also recorded further south on Mt. Mulanje (Malawi) which ranks as yet another marked centre of endemism. The nominate subspecies (*albosignatus*) is reported south of the Limpopo river to the approaches of Pretoria (Magaliesberg, west of Pretoria). Its distribution (map in Wiebes 1968: Fig. 3e) resembles that of *Barberton*, which I noted years ago as an important biogeographic node (Croizat 1952: Fig. 13; 1962: 293), its status having recently been confirmed on strictly phytogeographic grounds by Nordenstam (1969). So far, it appears *Goliathus* is not known in the Chimanimani region of Zimbabwe and Mozambique, an outstanding biogeographical area. However, further exploration may well alter the picture, considering that the Chimanimani mountains stand between the disconnected ranges of the two subspecies of *G. albosignatus*. A record from Usambara also turns up in the range of *G. fornasini*, the distribution of which seems, judging from Wiebes (1968), to be mainly coastal south of Zanzibar—Dar es Salaam, but to veer inland towards Zaire to the north. Distribution of this type is quite standard (see Croizat 1968b: Figs. 26c, 28a) and of overall significant importance.

4. Ethiopia—Tanzania—Angola. These three centres are included in the distribution of the three species of *Goliathus* subgenus *Hegemus*, one of which, *G. vittatus*, appears to be wedged squarely between Uluguru and Usambara (Croizat 1968b: Fig. 6m). They are part of a standard African circuit of dispersal, and *Aloe*, for example, significantly highlights the three (Croizat 1968b: Fig. 39f).

It seems useless to extend this enumeration when what I have stated is sufficient to orient the thoughts of readers. At any rate, *G. russus*, a species to which I will presently return, has its extreme eastward extent at Kampala on the shores of Lake Victoria in Uganda, and westward extent at the Dja river. Kampala has similar biogeographical importance as Mabira (Mabira turns up in two collections of *G. russus*). The Dja (or Ja) river (on the maps of the formerly German Kamerun it is spelt Dscha; Dscha Posten is located right at the sources of the river, just north of Lomie, c. 250 km southeast of Yaounde) waters a region also well known for its endemisms, e.g. the bird *Ploceus batesi*, raceless in South Cameroon (type locality, Ja River). In sum, if the reader needs supporting evidence, he is sure to find it abundantly throughout the records of the natural sciences.

#### ON "WING DISPERSAL" AND GENERALITIES OF FORM-MAKING OVER SPACE THROUGH TIME

Commenting presently on subjects other than localities, Wiebes (1968: 30) tells us: "The species here united in subgenus *Fornasinius* seem to form a superspecies. One, *G. russus*, differs more from the other three than *G. fornasini*, *G. aureosparsus* and *G. higginsii* differ from one another; it may represent a semi-species, wedging in between the allospecies *G. fornasini* and *G. aureosparsus*. The close similarity of the East African and West African forms is suggestive of a former connection that is now lost. There are many more examples of this phenomenon in other groups of African Cetoniidae. I prefer to postpone a possible explanation of this geographical pattern until these other groups have been treated".

The geographic pattern in question is a classical example of what I have called *wing dispersal* (Croizat 1962: 876). In substance the species "in the wings" (here, *G. higginsii*, *G.*

*aureosparsus*, both western, and *G. fornasini*, eastern) are closer to one another than the central, *G. russus*, is to any of them, which of course is a geographical paradox (Fig. 1b).

Wing dispersal has multifarious aspects, some seemingly "mysterious". It is so "utterly mysterious" that not a single zoogeographer has ever referred to any of the following: *Picumnus*, type of Picidae subfamily Picumninae, has about 26 different species in tropical America. A raceless monotypic genus *Verreauxia* of the same affinity is reported from western and central Africa (*V. africana*, from Nigeria to southern Cameroon (Yaounde!), Gabon, Zaire (to the Upper Ituri in the east, southward to the Kasai)). A third genus of two species, *Sasia*, inhabits the Indo-Malayan Region (South Tenasserim), marking, quite typically (Croizat 1958), the limit between the two: *S. abnormis*, south of Tenasserim to Malaya and Western Malaysia; and *S. ochracea*, north of Tenasserim to South China and the Western Himalayas. Remarkably, the species *P. innominatus* (Wiebes 1968), which ornithological opinion credits<sup>3</sup> uncontroversially to *Picumnus*, turns up as if from nowhere in the tropical Far East and Greater Sunda, with five races ranging from the northwestern Himalayas to Sumatra and Borneo (see Peters 1931-1968, 6: 97 ff.). To complete the record, the genus *Nesocittes* (*N. micromegas* in two races) is endemic to Hispaniola and the adjacent island of Gonave.

These birds are sedentary, small, indifferent volants (see Smythies 1960: Pl. 23). Therefore it is wholly against reason to imagine that *Picumnus innominatus* could have reached Malaysia and the Himalayas from Brazil, whether "across the Atlantic/Indian Ocean" or "across the Pacific". Similar "mysteries" turn up elsewhere (Croizat 1961, 1b: 1486 ff.), such as "American" Iguanidae being endemic to Madagascar, and whole sets of them can be collected (see Croizat 1962: 21 ff.), none of which has ever been explained in the light of current zoogeography and phytogeography.

The explanation is very simple: Form-making takes place by *recombination of characters* within an original genetic pool. In the case of *Picumnus* (Croizat 1962, 1968a), the original picumnine genetic pool, wide on pantropical scale to begin with, has yielded *Picumnus* and *Nesocittes* in the New World, *Verreauxia* in Africa, *Sasia* in the Indo-Malayan region, and, by a combination of characters "off focus" in terms of current geography, a species of *Picumnus* in the Indo-Malayan region. The same is found with plants where, for example, *Menodora* has North American species with varieties in South Africa.

No taxonomist would feel surprised if the genetic pool of a certain species A, for instance, should yield at the periphery of its range two subspecies/varieties that are strikingly similar at a distance of, let us say, about 100 km from one another. It remains to be seen why *Picumnus*, *Menodora* and Iguanidae should be "mysterious" for nothing more than recombining characters over a far more imposing stretch of miles overland and overseas. A biological process is not subservient to space: its premises being given, genetically and structurally, it will act at any distance.

<sup>3</sup> Tenasserim is without effect in the ranks of this piculet (Croizat 1962: Fig. 46). Its race, *P. innominatus malayorum*, is distributed to eastern India (Vizagapatam region), eastern Burma, Indo-China (Tonkin, Annam, Laos), Thailand ("western portion of the northern plateau (Chaiya Prakan, Chiang Mai, Lamphun) and in the northwestern portion of the eastern plateau (Loei)" [Deignan 1963: 84]), Malaya, Sumatra Borneo (where it is a "mystery bird" [Smythies 1960: 327]). It seems clear from the records that northern Thailand splits the dispersal of this bird into a western and eastern segment. The former runs the whole track from eastern Burma to Sumatra (Croizat 1968a: Fig. 32d), the latter runs part of a track from northeast Thailand-Indochina-Borneo (Croizat 1968a: Fig. 13).



Normally, when the gene pool is undergoing evolutionary flux, recombinant characters are numerous and more active. Hence, at the periphery of the optimum range, "older" forms are likely to appear together with characters similar to those which have been whittled down or eliminated in the most active sector of the pool.

In the case of *Goliathus* subgenus *Fornasinius*, Wiebes is right in visualizing a "connection to have existed that is now lost". This connection has been "lost" within the bosom of species *G. russus*, but has survived "in the wings of the dispersal" with species *G. fornasini*, *G. aureosparsus* and *G. higginsii* that are peripheral to *G. russus*. Likewise, in Picumnine woodpeckers - the "connection" has been lost in Africa (*Verreauxia*)<sup>4</sup>, but kept up in the wings of the dispersal (*Picumnus* in Tropical America, and *Picumnus* in Indo-Malaysia). By the same token, an "odd recombination of characters" in the dentition has turned the "Agamidae" into the Iguanidae that should be geographically proper to Madagascar. It is indeed very simple in essence, though multifarious in its geographic and taxonomic aspects. This being the case, no wonder Wiebes ran against other cases of the same sort in other groups of Ceteroniidae. Nothing is indeed more probable than the "species" in subgenus *Fornasinius* form a "superspecies"<sup>5</sup>. These species have been issued by a common progenitor *G. russus* + *fornasini* + *aureosparsus* which, over space through time, has come to differentiate into taxonomic ancestral forms all the way from the Ivory Coast to Tanzania (Usambara) across the body of Zaire. Nobody who marvels at this would not marvel if the very same "trick" were observed in the case of four subspecies, for example in Sumatra or Borneo or Zaire or Venezuela.

In conclusion, what has happened in subgenus *Fornasinius* of *Goliathus* tells, as clearly as we may like to have it, that the genetic pool of pre-*Goliathus*/*Goliathus* was originally widespread all over Tropical Africa, yielding in the course of further evolution different subgenera, species and subspecies around centres of differential taxonomic ancestral forms. This is standard not only for *Goliathus*, but, as we saw, for all manner of life, plant and animal. Were this not the case, we would not have marked centres of endemism with far flung similar connections in, for example, the Cameroons and Usambara, documentable as much in insects as in birds and plants (for example, *Cleistanthus* and *Euphorbia*).

In sum, it is not nature that works in ways that are devious, "mysterious" or "unfathomable". Rather, it is us who do not understand how simple are the rules under which she

<sup>4</sup> Precise semantics are the by-product of precise ideas, and I am not libelling the natural sciences in affirming that the "semantics" displayed in their literature sometimes leave much to be desired. The "connection" which was "lost" because of *Verreauxia* "intruding" between the "disjointed" ends of *Picumnus* has a different meaning. It is geographic in so far as it would, if present, join the map of Brazil to the Himalayas (where *Picumnus* species occur) and over the body of Africa (where *Verreauxia* occurs). It is phylogenetic in the sense that its loss, definite in the sense of classification by *Verreauxia* having replaced *Picumnus* in Africa, is not such against the background of the total picumnine genetic pool. In fact, this pool was so well knit and powerful that it proved advisable "to recombine" *Picumnus* species alike in both Venezuela and Borneo. It is biogeographic in that it is "zoogeographic" to anyone who would span its yawning lips with some "casual flight" or the like. May the reader imagine how fruitful an argument will be when conducted among parties who do not know what exactly to think of the "connection" in question.

<sup>5</sup> I need not insist that taxonomists arguing whether *Goliathus* subgenus *Fornasinius* actually consists of a "superspecies", or only of four "subspecies", or of four "species" not forming a "superspecies", or of some "species" mixing up with some other "semispecies", etc., will far more quickly and easily put an end to their toils if they are informed about "wing dispersal" as a general process of form-making.

operates. Slaves to outworn notions of "zoogeography" and "phytogeography", resting on the thin fare of original Darwinian speculation and theory (Croizat 1962), we imagine "centres of origin" issuing "migrations" by "casual means", and turn mileage into the standard of "zoogeography" and "phytogeography". This is all wrong: A genuine science of dispersal (panbiogeography as I happen to call it) has *the factual process of form-making through time over space* as its main concern, not speculation about the "mysterious means" that took *Picumnus* from the Himalayas to Brazil (or, who knows, just the other way round), or Iguanidae flying in the "eye of a storm" from Mexico to Madagascar, and similar nonsense.

Naturally, I could not believe that *Goliathus* landed in Africa from Europe, or Asia or America (where Cetoniidae also exist, Croizat 1961, 1b: 1624-1625). Not so at all—the ancestors of this genus were part and parcel of a vast assemblage of pre-cetoniid insects that assuredly was in Africa at no later time than, for example, the ancestors of the Euphorbiaceae genus *Cleistanthus* (Croizat 1968b) or of the Lentibulariaceae genus *Utricularia* (Croizat 1968b). That the species of *Goliathus* subgenus *Fornasinus* stand as a "super-species", or indeed as subspecies of a polytopic Rassenkreis, is an important taxonomic question, but in no way as important a *taxogenetic* and *biogeographic* issue as I understand the terms. The ancestors of *Cleistanthus* and *Utricularia* were in Africa before the "Gondwanic landmass" broke apart and dissolved to form the "modern" continents, that is earlier than 150 million years ago. This date is not speculative for, affirmed in all my works on strictly biogeographic grounds, it has now been confirmed by the very latest findings of geophysics and tectonics (Heirtzler 1968).

Obviously, I could not believe that *Goliathus* yields valid evidence to demonstrate that its range has "expanded" by more or less "casual means" and "migrations". I would admit that these beetles have occupied wider and more extensive ranges in Africa when, for instance, the tropical forest ranged farther to the north than it does now (Aubreville 1949: 66). However, there is a far cry between granting this, which is well attested and borne out by positive facts (such as the occurrence of relics "off place", whether in present-day dry or wet Africa), and indulging in arbitrary, unsupported theorizing about the evolutionary history of *Goliathus* (and creation in general) calling for hypothetical "migrations" and casual "dispersal" at some time during the "Tertiary". Not so at all - *Life is logical for it is bound to laws*, and the first task of the naturalist is to research these laws instead of theorising how these laws should be to square with the pet dreams of this or that theorist.

Strictly as an introduction to the subject - much more indeed could and ought to be done by teaming together the taxonomist and the biogeographer/taxogenist - I think I have shown that the excellent work of Wiebes on *Goliathus* contributes materially not only to the advance of the classification of Coleoptera, but to biogeography and taxogeny as well. The taxa Wiebes presents, and the loci they occupy, offer propitious, constructive grounds for analyses that reach above and beyond classification to enter the field of general evolution in terms of space and time.

The question inevitably arises why it so often happens that work of outstanding taxonomic and systematic merit ends with "zoogeographic" or "phytogeographic" conclusions that dispute its substance and stultify its message. It often looks as though a naturalist extremely careful of his classification is at the same time absolutely footloose in regard to his "biogeography". For example, see the "zoogeography" of Chase & Hobbs (1969: 13 ff.) who affirm the glaring falsehood that: "The apparent disparity in number of species present in Dominica and the neighbouring islands of Guadeloupe and Martinique [has little significance]". In contrast (Croizat 1958, 1: 602-745; 1961, 1b: 550-684; and the biogeographic

revision of Blackwelder's classic Checklist of Antillean Coleoptera in Croizat 1962: 146-149), the whole of it is "overlooked" by the authors above.

The often enormous disparity between the taxonomy and the biogeography of an author is the by-product of (a) inadequate and faulty basic teaching, and (b) lack of proper orientation. It occurs to no one to give a course at University level in, for example, statistics and biometry consisting of vague theories and compilations as to what these disciplines should be. However, hardly anyone thinks today of biogeography except as a confused array of theoretical premises; no effort is being made to create in the student a feeling for localities, to teach him the rudiments of comparative analysis of factual records of dispersal.

Graver still is the neglect of advances in fields that have much to contribute and to receive from biogeography as a science. In the last 15 years, geophysics has made great progress, and since *earth and life evolve together* it should be logical that geophysics and biogeography team up.

We now have concrete chronological data from geophysics (Hiertzler 1968) for the separation of Africa and America - "poles of spreading" are indicated in Africa and the Western Pacific not so remote from the "gates of angiospermy" that I (Croizat 1952) happened to mark out some 20 years ago<sup>6</sup>. It is palpable (Croizat 1952) that the major tracks outlined by the biogeographer are congruent with the patterns of "sea-floor spreading" identified by the geophysicist. Nothing of this, alas, influences the thinking of natural history, which, as to "geographic distribution", still trots today (Croizat 1962) after the Darwinian carrots of 1858.

It is statistically documented that the basic threads of the dispersal of plants and animals centre on the southern continents, and, with higher animal life in particular, on the continent which we call today Africa (see all my works). Some of the tracks out of Africa followed by mammals (Croizat 1961, 1b: 1211 ff., 1229 ff.) to this day, began to run with Dinosauria in the Triassic.

It is a matter of common knowledge that insects living in the Early Tertiary can hardly be distinguished from their descendants extant today, in spite of which their dispersal (e.g. *Asilidae*, Croizat 1962: 328 ff.) is easily analyzed. No naturalist with a smattering of palaeontology is ignorant of the fact that just as in the scale of absolute time plants preceded animals, fishes, reptiles, birds and mammals, life received sometime between the Carboniferous and Triassic a very powerful fillip towards general "modernisation", for it is by the Triassic-Jurassic that the ancestors of "modern" plants (*Angiospermae*), "modern" birds (*Archaeopteryx*, etc.), "modern" mammals (*Microleptidae*, *Triconodonts*, etc), and "modern" reptilians appear in the palaeontological records.

Reliable evidence is now available from geology (Harland & Rudwick 1964) that some 600 million years ago a "Great Infra-Cambrian Ice Age" swept the earth. After a conclusive review of the data and inferences in their hands, Harland and Rudwick (1964) stress the fact that this glaciation heralded the appearance of a fauna which precluded to at least the lower forms still living, and conclude: "A causal connection between the Infra-Cambrian Ice Age and the appearance of the Cambrian fauna thus appears possible, and perhaps probable. Certainly, a climatic event of an intensity unparalleled in the later history of the earth seems to have been closely followed by a biological event of profound significance in the history

<sup>6</sup> These "gates", *inter alia*, prompted one of the reviewers of my earliest major work (Croizat 1952) to ask the question whether I was: "Nu been genie of alleen maar een fanaat".

of Life". Had the authors been familiar with efficient biogeography (let us give it its proper name, *panbiogeography*), they would understand that the text I have quoted applies as well to the Permo-Carboniferous Ice Age approximately 200-300 million years ago (paraphrased: A causal connection between the Permo-Carboniferous age and the appearance of the Mesozoic fauna precluding to the eventually modern one thus appears possible, and perhaps probable). Certainly, a climatic event of an intensity unparalleled in the later history of the Earth seems to have been closely followed by a biological event of profound significance in the history of life. Indeed, it is after the Permo-Carboniferous ice ages had spent their fury that mammals, birds, etc. began to appear, yet conclusively precluding to living ones. It is also noted that the threads of modern dispersal lead precisely to the continents of the southern hemisphere, the hemisphere which bore the brunt of the glaciations of 250-300 million years ago.

How a glaciation affects life is not speculative, for, in a sense, we can easily judge its effects from the Pleistocene to recent times (earlier ice ages were much longer). Life that has reached a climax stage is wiped out wholesale or allowed to survive as relics, individually or in association (Croizat 1962: 226 ff.). Its place is taken by life more competent under the new conditions (Croizat 1958, 1: 30 fn.; 1961, 1b: 1174 ff.) and by genetically plastic "weedy" plants and animals (Croizat 1962: 368) which, in the process of further evolution, "radiate" structurally and ecologically (*structural and ecological evolution are by no means synonymous!*), gradually reaching the climax stage of their development, thus becoming ready for their eventual demise at the next major revolution of geology. Because of this, both the Infra-Cambrian and Permo-Carboniferous Ice Ages had the same effect on life, heralding the advent of new forms of plants and animals.

Some will still claim that this is "inference" and unproven. I will suggest that they take a good long look at all my works, in the pages of which hundreds of different patterns of dispersal are painstakingly and methodically analyzed to establish just the exact opposite.

Naturally, we do not exactly know, step by step, how the Permian and Triassic ancestors of the life we call "modern" (because it lives with us) initially radiated. However, beginning with the Mid-Jurassic we have data in hand justifying searching, concrete analyses. For example, Madagascar got separated from continental Africa by the Mozambique Channel around Mid-Jurassic times, and contacts between it and the body of Africa since then have only been temporary and of comparatively short duration. If it is possible that certain forms of life (e.g. *Hippopotamus*) reached Madagascar taking advantage of such connections in the Late Cretaceous/Tertiary, it is downright impossible that hundreds of species of *Euphorbia*, so typically Malagasy that their origin can be told at a glance, stem from comparatively late ancestors. It is obvious that prior to the Mid-Jurassic their ancestors had settled in Madagascar before its separation and then gradually evolved into well-marked, strictly local forms. The same must have happened with *Euphorbia* in southern South Africa. In sum (Croizat 1965), these plants were already distributed all over "Africa" before the Mid-Jurassic. By the same token, certain ancestral "pre-Ericoideae" had by then already laid the cornerstone of the distribution of modern Rhododendroideae in Malaysia (c. 275 species according to Sleumer 1966), and in the Eastern Himalayas/Burma (c. 600 species), leaving the Ericoideae to occupy southern South Africa in large numbers (at least 600 species). The two groups presently occupy radically different floral regions (Croizat 1962: Fig. 53) and cross paths in Europe without overlapping, thus again disputing the claim that dispersal is "chance".

It is time to put an end to this cursory review of vital evidence which seems to be unknown to the majority of naturalists today. Informed of it, I will certainly not believe that the ancestors of *Goliathus* reached Africa at any later epoch than the Mid-Jurassic/earliest Cretaceous, for by then "modern" angiospermous plants had, without doubt, settled in Africa as well as in Madagascar, Malaysia and the Cape. I am not prepared to grant that the origin of the modern insects was later to that of Angiosperms. Knowing something of the biogeography of the world in general, and of Africa in particular, I am not easily convinced that *Goliathus* would "migrate" by "chance" when it is clearly written on the face of its records that this belief runs against the facts.

### CONCLUSIONS

The conclusions of this short article are both general and particular in nature, and are as follows:

1. Of a general nature:
  - a) *Properly understood, biogeography is a primary biological science in its own right. It collaborates with other sciences (geology, taxonomy, ecology, evolution), but is ancillary to none.*
  - b) *Biogeography is to be viewed and applied as an essentially exact science. Its task is not to forge theories of how life should have evolved over space through time, but to methodically study the records of geographic distributions of plants and animals in order to determine on a statistical, comparative basis of enquiry exactly how life *did* evolve. Only on the basis of positive enquiry, and no other, can laws and rules of biogeographic and taxogenetic significance be deduced.*
  - c) *"Modern" life had its inception in the aftermath of the Permo-Carboniferous Ice Ages. We cannot fully establish the details of its earlier radiations because we lack positive data on it. However, beginning with the Mid-Jurassic (approximately 100 million years ago), we have data at hand to begin *concrete* analyses of dispersal of plants and animals.*
  - d) *The main centres of diversity for "modern" life were established no later than 170-140 million years ago, and are the same for plants and animals. The centres of diversity then established on land and still extant (for example, southern South Africa, the approaches of the Eastern Himalayas, the sectors Congo-Gabon to Cameroon-Nigeria-Sierra Leone, Usambara-Uluguru, Greater Sunda-Thailand, etc.) can be traced forward to the present, which shows that they never substantially altered in status.*
  - e) *It is obvious that, for example, the ancient centres of life established between Sierra Leone and Cameroon, Usambara-Uluguru and the rest of Eastern Africa, have varied in extent depending on dry or wet ages. An insect bound to the dense forest, for example, will, using its ordinary *means of survival* and turning them into *means of dispersal*, migrate hundreds of miles with the forest when this expands. However, these *migrations* are not to be confused with the original *radiation*, and less, can be credited for having*

wiped out the ancient centres of diversity as in (c) and (d) above. In sum, and quite concretely, there were ages when *Goliathus* could be found in the central Sahara and ages when this insect would not be found even in places where it lives today, everything depending on cycles of wet and dry weather. However, there was never a time when the whole of the dispersal of *Goliathus* in West and East Africa was managed by climate, chance, casual migrations and the like (see ecological "lag" in Croizat 1958, 2a: 28, 68, 132, 136) leading to the obliteration of the primeval ranges of the genus, whether west or east. To anyone who is unsure, I suggest that he ponders the *wing dispersal* evident in *Goliathus* subgenus *Fornasinus*.

f) Whatever claim is made by "zoogeography" that is not based on the records of life - as these read - and a coherent, logical interpretation of their significance on a comparative basis, may as well be dismissed as *prima facie* unfounded.

## 2. Of a particular nature:

a) At the very least, as a sound working hypothesis, it can be accepted that the proximal ancestors of *Goliathus* reached Africa at no later time than the late Jurassic/early Cretaceous. By then the main loci of the eastern and western centres of diversity still extant in Africa had already been established.

b) Of course, *Goliathus* in Africa does not stand isolated. Its history over space through time is bound with that of its allies in Europe, America and Asia. In other words, *Goliathus* is that fragment of cetoniid life which, in Africa, vicariates with consanguineous stock endemic to other continents. The concept of *vicariism* is basic in biology, from the race to the family.

c) The current geographic distribution of *Goliathus* is similar to that of other groups of life, and the localities which turn up in its scores are significant beyond the limits of the genus.

## ACKNOWLEDGEMENT

Dr J.T. Wiebes is to be congratulated for having contributed with his study of *Goliathus* an outstanding accretion of knowledge of taxonomy, taxogeny and biogeography. I may not judge the formalities involved by specialized classification, but as to taxogeny and biogeography, I think I have reason to rate the work commented upon in these pages as I have just done.

## REFERENCES

- AUBREVILLE, A. (1949). *Contribution a la Paleohistoire des Forets de l'Afrique tropicale*. Soc. Edit. Geogr. Mar. Col., Paris.
- BANNERMAN, D.A. (1953). *The Birds of West and Equatorial Africa* (Vols. 1, 2). Oliver and Boyd, Edinburgh.

- CHASE, F.A. & HOBBS, H.H. JR. (1969). The freshwater and terrestrial Decapod Crustaceans of the West Indies with special reference to Dominica. *Bull. Smithsonian Inst.* 292.
- CROIZAT, L. (1952). *Manual of Phytogeography*. The Hague.
- CROIZAT, L. (1958). *Panbiogeography* (Vols. 1, 2a, 2b). Caracas, Venezuela.
- CROIZAT, L. (1961). *Principia Botanica* (Vols. 1a, 1b). Caracas, Venezuela.
- CROIZAT, L. (1962). *Space, Time, Form: The Biological Synthesis*. Caracas, Venezuela.
- CROIZAT, L. (1965). An introduction to the subgeneric classification of *Euphorbia* L., with stress on the South African and Malagasy species. *Webbia* 20: 573 ff.
- CROIZAT, L. (1968a). The biogeography of the tropical lands and islands east of Suez-Madagascar, with particular reference to the dispersal and form-making of *Ficus* L. and different other vegetal and animal groups. *Atti Ist. Bot. Lab. Critt. Univ. Paiva*, Ser. v 4: 1-400.
- CROIZAT, L. (1968b). Introduction Raisonnee a la Biogeographie de l'Afrique. *Mem. Soc. Broteriana Coimbra* 20: 1-451.
- CROIZAT, L. (1968c). The biogeography of India: A note on some of its fundamentals. Proceedings of the symposium on recent advances in tropical ecology (Varanasi, India). Part 2: 544 ff.
- DEIGNAN, H.G. (1963). Checklist of the birds of Thailand. *Bull. Smithsonian Inst., US Natl. Mus.* 226: 1-263.
- HARLAND, W.B. & RUDWICK, M.J.S. (1964). The Infra-Cambrian Ice Age. *Scientific American* 211(2): 28 ff.
- HEITZLER, J.R. (1968). Sea-floor spreading. *Scientific American* 219(6): 60 ff.
- NORDENSTAM, B. (1969). Phytogeography of the genus *Euryops* (Compositae): A contribution to the phytogeography of Southern Africa. *Opera Botanica (Lund)* 23: 1 ff.
- PAX, F. & HOFFMANN, K. (1931). Euphorbiaceae. In: Engler & Prantl, *Nat. Pflanzenf. Zweite Aufl.* 19(c): 11 ff.
- PETERS, J.L. (1931-1968). *Check-List of Birds of the World, I-XIV*. Harvard University, Boston.
- RAND, A.L. (1951). Birds from Liberia with a discussion of barriers between Upper and Lower Guinea subspecies. *Fieldiana (Zool.)* 22(9): 558 ff.
- SLEUMER, H. (1966). *Rhododendron. Flora Malesiana*, Ser. 1, 6(4): 473-674.
- SMYTHIES, B.E. (1960). *The Birds of Borneo*. Oliver and Boyd, Edinburgh.
- WIEBES, J.T. (1968). Catalogue of the Coleoptera: Cetoniidae in the Leiden Museum. 1: *Goliathus* Lamarck sensu lato. *Zool. Meded. Mus. Nat. Hist. Leiden* 43(3): 19 ff.