

Distribution and speciation of carabid beetles in the Galápagos Archipelago (Ecuador)

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Abstract

During several recent expeditions, we collected carabid beetles on most of the important islands of the Galápagos Archipelago. About 40 species belonging to 11 genera are known to us from the islands. No less than 90% of the species are endemic to one or more islands in the archipelago. In this communication, the distribution patterns (concerning 75% of the known species) are described in relation to morphological, ecological and dispersal power characteristics of these species. This leads to suggestions of how and when speciation might have occurred in different groups. The extent of individual distribution patterns as well as the degree of radiation having occurred in different taxa suggest a variety of modes of speciation ranging from large to small scale allopatric and parapatric speciation events. Cases of parapatric speciation are suggested in sister species with adjacent ranges but without obvious ecological or geographic barriers between them. They are further substantiated by a possible case of incipient speciation by means of reproductive character displacement ('Wallace-effect'). A suspected case of introgressive hybridization leads to the hypothesis of allopatric speciation (separation by altitude/habitat) and secondary contact of the sister species. Finally, two species seem to have been unintentionally introduced recently. In conclusion, the carabid beetles of Galápagos show a wide variety of distribution and speciation patterns and contribute in this way to the well known fascination of these islands for the ecologist and evolutionary biologist.

Key-words: Speciation, evolution, carabid beetles, Galápagos Islands.

Résumé

Nous avons, lors de nos récentes expéditions, collectionné des carabes sur la plupart des îles importantes. 40 espèces appartenant à 11 genres sont connues pour les îles. Près de 90% des espèces sont endémiques dans une ou dans plusieurs îles de l'archipel. Nous décrivons dans cet article les modèles de distribution (ceci pour 75% des espèces connues) en rapport avec les caractéristiques morphologiques, écologiques et de capacité de dispersion. L'ampleur des modèles de distribution individuelles, ainsi que le degré de radiation survenu dans différents taxa, suggèrent une diversité de modes de spéciation (allo- et parapatriques).

Des cas de spéciation parapatric sont suggérés dans des espèces soeurs ayant des aires adjacentes sans barrières écologiques ni géographiques apparentes. L'hypothèse est confortée par

un cas possible de spéciation naissante par 'l'effet Wallace'. Un cas possible d'hybridation introgressive nous amène à formuler l'hypothèse d'une spéciation allopatric (séparation altitude/habitat) avec contact secondaire entre les espèces. Deux espèces ont probablement été introduites récemment et involontairement. En conclusion, les Carabidae des Galápagos montrent une large diversité de modèles de distribution et de spéciation, et contribuent ainsi à la fascination bien connue pour ces îles des écologistes et biologistes évolutionnistes.

Mots-clés: Spéciation, évolution, Coléoptères Carabiques, îles Galápagos.

1. Introduction

Oceanic islands have had an important role in the history of evolutionary biology and are continuing to serve as crucial sites for evolutionary studies. Galápagos certainly is one of the most famous archipelagoes where much biological investigation has been, and continues to be, performed. Today, the evolutionary and ecological dynamics of the plants and vertebrates are fairly well known. In comparison, most invertebrate groups are the poorest known components of the terrestrial biota and yet they are the most diverse and have the greatest research potential for general conclusions on island biology (e.g. PECK, 1990).

As part of a long term study started in 1982 and during several recent expeditions (1982, 1986, 1988, 1991), most of the important islands and volcanoes were sampled by us in complete transects or in altitudinal gradients for their invertebrate fauna (especially spiders and carabid beetles, cf. BAERT & MAELFAIT, 1986a,b; BAERT et al., 1989a,b, 1991; DESENDER et al., 1988, 1989, 1990a,b, 1991, 1992). Our studies have to be situated within the field of evolutionary ecology and involve different steps, starting from systematics and taxonomy. We are at the same time involved in several smaller case studies on different aspects of ecology, reproductive biology, population dynamics and dispersal power of the species as well as on population genetics.

In this communication we will report on distribution and speciation patterns in carabid beetles. Since our recent expeditions, carabids are now known from all major

islands and even from several very small or satellite islands. About 40 species belonging to 11 genera are known to us from the islands. The most recent previous account on Galápagos carabids mentioned 35 species (PECK & KUKALOVA-PECK, 1990), which means that we are describing several species as new or at least new for the islands. The distribution patterns (concerning 75% of the known species) will hereafter be described in relation to morphological, ecological and dispersal power characteristics of the species. This leads to suggestions of how and when speciation might have occurred in different groups. Of course many of our present conclusions are only tentative because several necessary data are still lacking or need to be more elaborated in the future.

2. Environmental setting and climate (cfr. Fig. 1)

The Galápagos Archipelago straddles the equator in the Pacific Ocean about 1000 km west of the Ecuadorian coast of continental South America. The islands are strictly volcanic in origin, being the product of outpourings from the Galápagos hotspot, now situated near the western islands. In general the southeastern islands appear to be the oldest whereas the northern and western islands appear to be the youngest (SIMKIN, 1984). Volcanic activity continues today, especially on younger islands.

There are about 15 larger islands in Galápagos. They are heterogeneous in many features, especially in area, elevation and isolation. Isabela is the largest one, more than 100 km long and unusual because it comprises six major volcanoes separated by low-lying land, chiefly barren lava flows. The peaks are reaching about 1200-1700 m of altitude. Together with Fernandina and the northern islands Darwin, Wolf, Pinta, Marchena, Genovesa and Santiago, these younger islands (without rocks dated older than 0.7 million years) have extensive areas of fairly recently formed lava. The more central islands Pinzón, Floreana, Santa Cruz and Baltra range from 100 to 850m in elevation and have rocks in the 0.7-1.5 million years range. Española and San Cristóbal have been estimated near 3 million years old and reach only 300 respectively 800m of elevation.

Although the islands are lying astride the equator, they show a remarkably seasonal but very unpredictable climate. The major influences on the climate are cool water masses originating off the coast of Peru and flowing northwestwards and warm water masses originating to the north and flowing southeastwards. Seasonality takes the form of a hot and wet period from approximately January to May and a cooler and drier period for the rest of the year. The amount of rain varies from place to place: more rain falls on high islands and at higher altitudes until about 800-1000 m where an inversion zone occurs, higher parts being dryer again. Higher

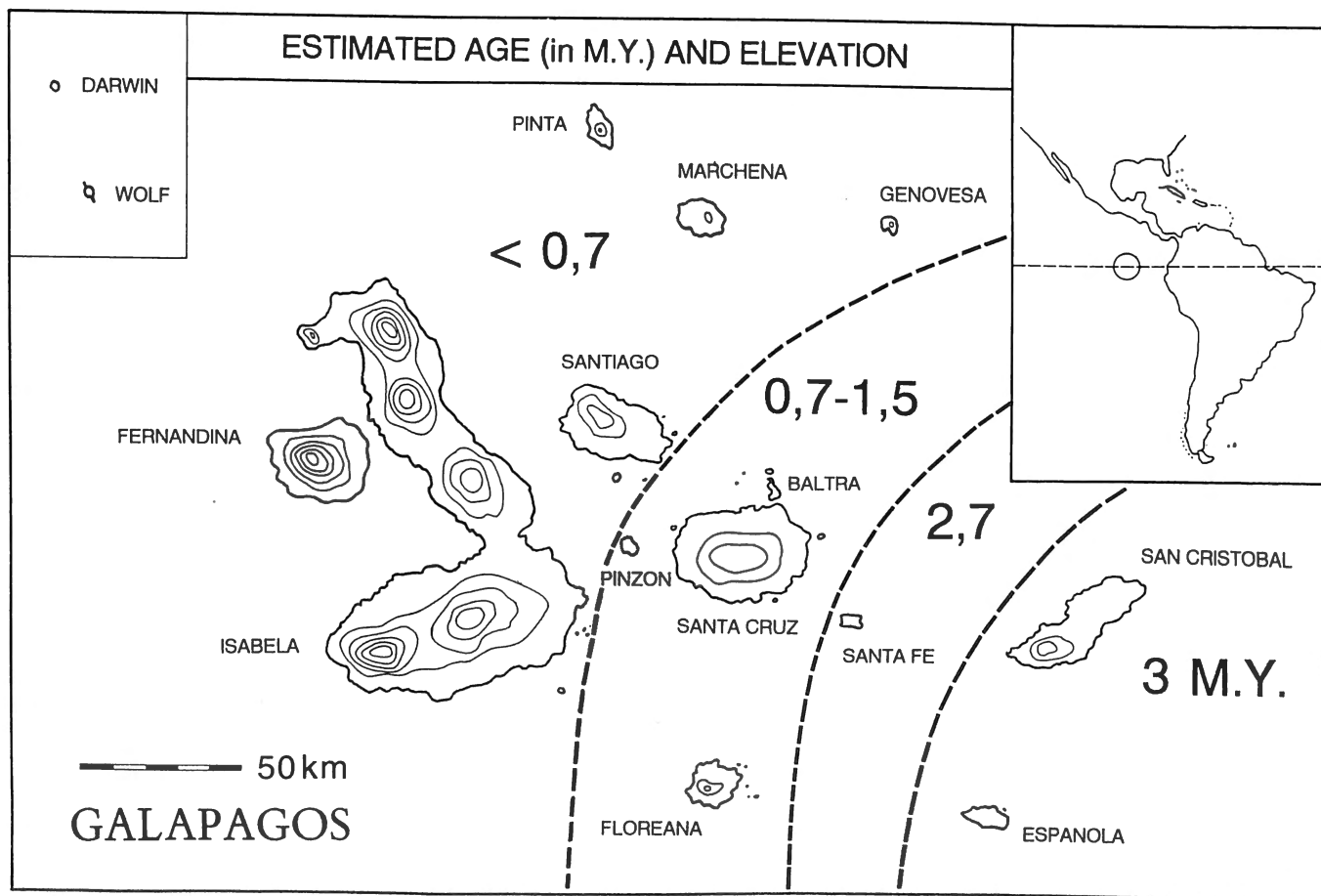


Fig. 1. — Environmental setting, estimated age (in Million Years) and elevation (250m intervals) of the Galápagos Islands.

volcanoes have large areas that tend to be cooler and more mesic than any habitats on the smaller, lower islands. Southern sides receive more rain than northern sides due to prevailing wind directions from the southeast. The archipelago however in general is arid because rainfall is erratic in occurrence and quantity. Heaviest and most extensive rains are associated with so-called 'El Niño' events (intertropical convergence zone more to the south, cfr. DESENDER et al., 1992).

3. Results

Let us first overview the ratio of endemic to other distribution types in Galápagos carabids. As shown in table 1, 90% of these carabids are endemic to one or more islands in the archipelago. Two species only are natives, also occurring on the South American mainland. We furthermore suspect that two species have been introduced recently and unintentionally. Such a high level of endemism is only matched by few other terrestrial arthropods in Galápagos. It is certainly due to the isolation of the archipelago, difficulties for colonizing species to establish a population in the harsh environment of

Galápagos, as well as to the relatively low dispersal abilities of many carabid beetles. It is interesting to note that most of the endemic species, limited in occurrence to one island only, are known to us as brachypterous species and thus are not expected to be able to reach other islands frequently. We are at the moment however not inclined to think that this relationship between reduced dispersal power and restricted endemic distributions always has to be interpreted as direct and causal.

Grouping of the observed distribution patterns within each suspected monophyletic species group yields several patterns, which we will now overview from the more simple to the more complex.

3.1. A first type of distribution concerns genera or subgenera represented by one species only, endemic to the islands, but known from several islands in the archipelago. We recognize three such cases among Galápagos carabids. These species are all possessing full wings and we have observed flight activity and/or the possession of functional flight muscles in each case.

Cicindela galapagoensis, at first sight, shows an erratic distribution (Fig. 2). In this species, dispersal is probably very efficient (nearly all known specimens have even been

Table 1. Endemism in the carabid beetle fauna of Galápagos.

genus	# species (approx.)	ENDEMIC 1 ISLAND	ENDEMIC > 1 ISLAND	NATIVE	INTRODUCED RECENTLY
<i>Agonum</i>	3 (?)	3			
<i>Bembidion</i>	2		2		
<i>Bradycellus</i>	5 (?)	4	1		
<i>Calosoma</i>	4	3		1 (?)	
<i>Cicindela</i>	2		1		(1)
<i>Mystroceridius</i>	2	2			
<i>Pentagonica</i>	1				(1)
<i>Pterostichus</i>	12	12			
<i>Scarites</i>	2	2			
<i>Selenophorus</i>	3 (?)		3		
<i>Tachys</i>	4 (?)		3	1	
TOTAL	40	26	10	2	(2)
PERCENTAGE		65%	25%	5%	(5%)

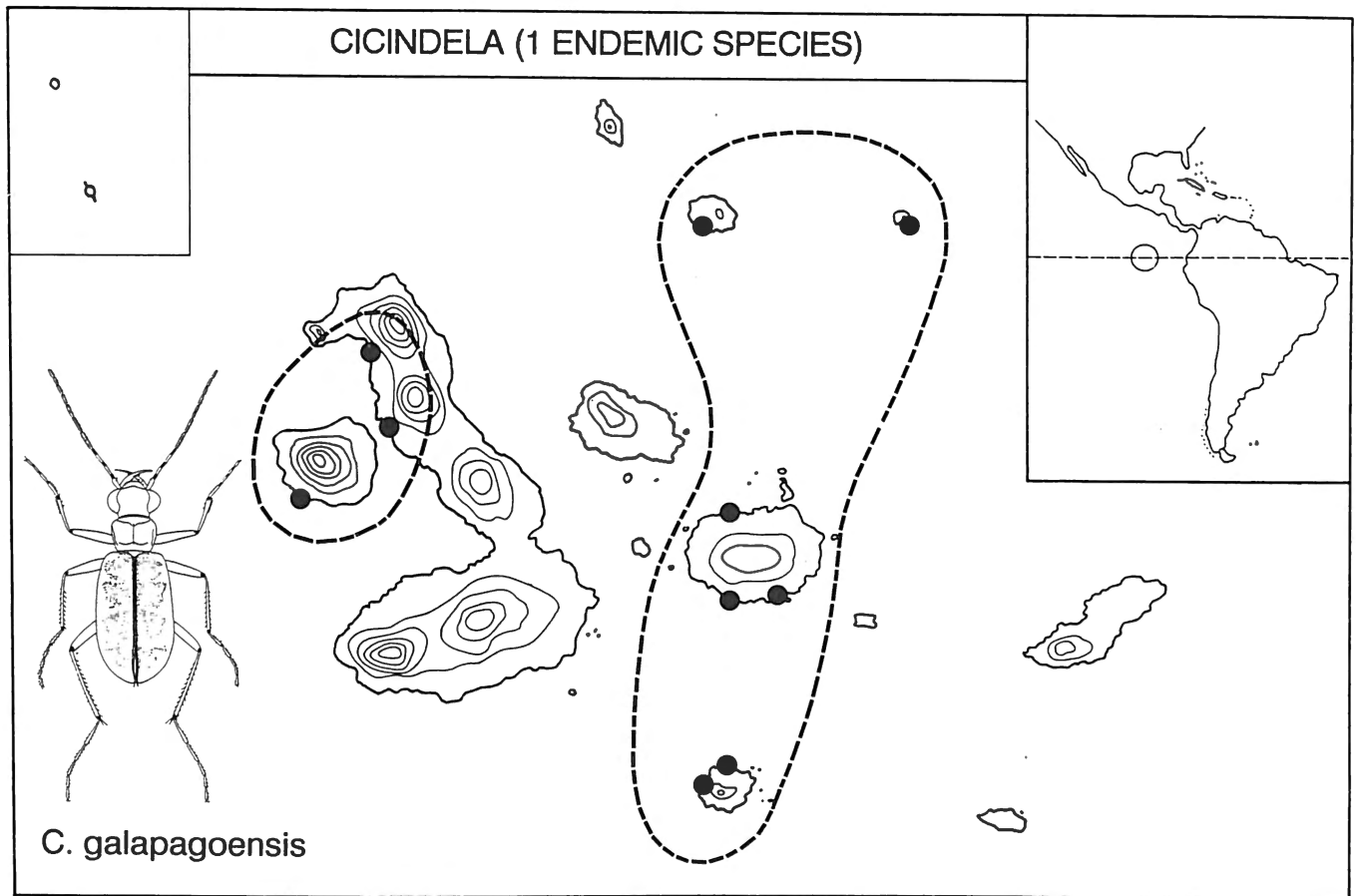


Fig. 2. – Geographical distribution of *Cicindela galapagoensis* in the Galápagos Archipelago.

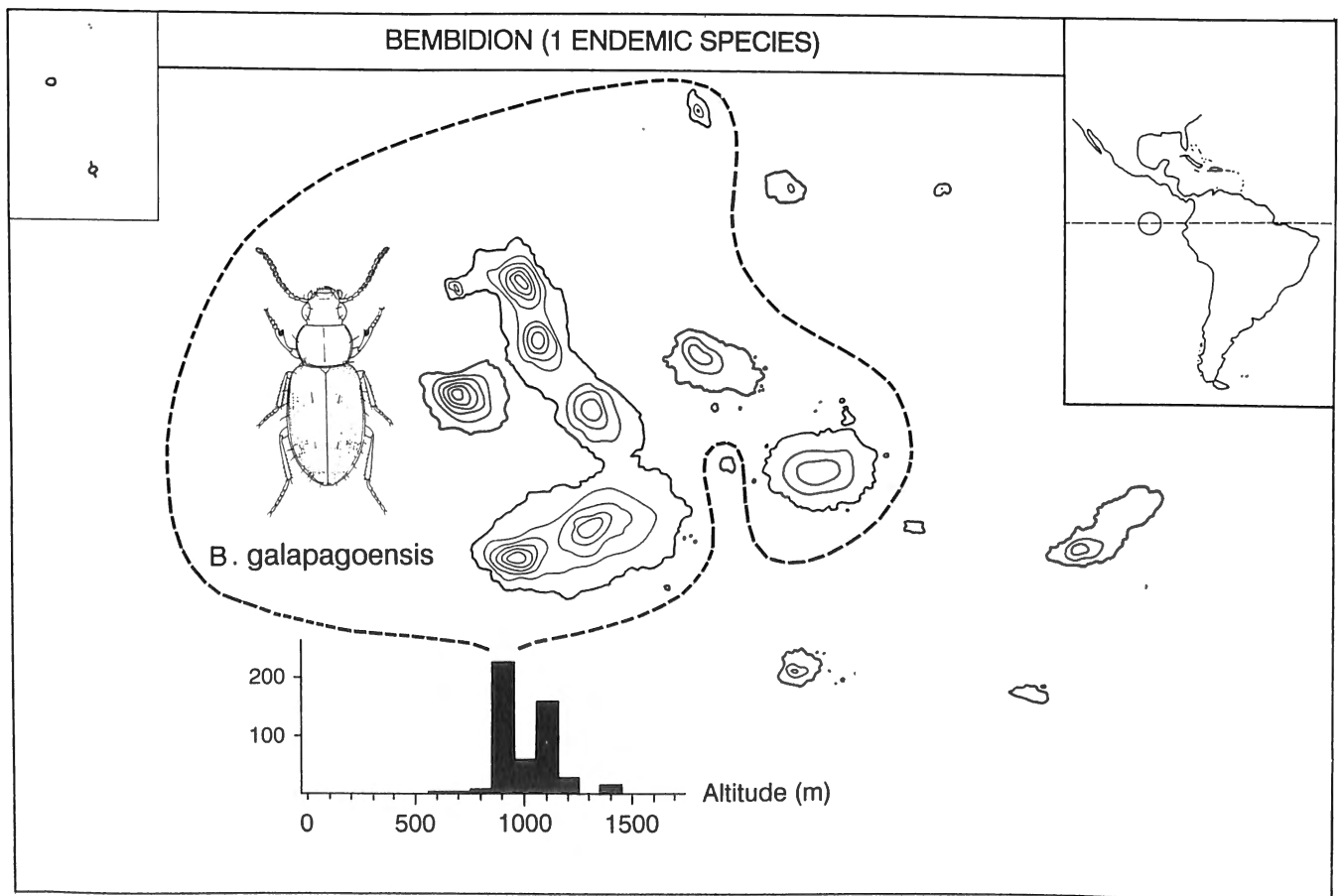


Fig. 3. – Geographical distribution of *Bembidion galapagoensis* in the Galápagos Archipelago.

collected during flight) and we therefore expect that the distribution should correspond to the geographic distribution of the habitat (sandy beaches near lagoons) in which it potentially can occur. This is indeed the case, the only exceptions being sites which are known to be not yet well sampled. As dispersal from one area to another probably takes place more or less continuously, opportunities for evolution in isolation or extensive radiation and speciation are expected to be rather rare.

A comparable case is observed in the small species *Bembidion galapagoensis* (Fig. 3). Again, at first sight, the geographical distribution is somewhat strange because not all major islands of the archipelago are inhabited by this species. Ecological data on the altitudinal distribution (cfr. Fig. 3) and habitat preference however clearly show this species to prefer open and more mesic habitats at higher altitude, zones which are simply absent from the lower older islands of the archipelago. Maybe this is an indication that the foundation event which led to the subsequent speciation of this species occurred in more recent times of the history of the archipelago.

A somewhat more complex case occurs in the genus *Selenophorus* (Fig. 4), represented in Galápagos by 2 or 3 endemic species, which again occur on several islands each. Again these species are all constantly full-winged and flight activity has been recorded, be it to a much lesser degree as in f.e. the cicindelid species, which are

much stronger fliers. The geographical distributions of these *Selenophorus* do not overlap and again there seems to be an associated difference in ecological preference, illustrated indirectly in their altitudinal frequency distribution (cfr. Fig. 4). An intriguing, but as yet unanswered, question is how to explain the absence of the 'lowland' species from the higher and younger western islands. Maybe gene flow is already reduced to such an extent because different groups of islands are more or less isolated (f.e. due to prevailing wind and ocean current directions). Moreover, as already mentioned, these species are probably weak fliers, able to perform only short distance flights.

In conclusion, these first cases of distribution types seem to have resulted each from allopatric speciation events on a relatively large scale, allopatry in the sense of the entire archipelago or a group of islands as compared to mainland distributions of ancestral species.

3.2. A second type of distribution patterns concerns species groups with again more than one endemic, each of which are now moreover restricted in their occurrence to a single island only, i.o.w. species groups which have radiated in the archipelago.

Two related *Scarites* species are known from Galápagos (Fig. 5), one species from a restricted zone on San Cristóbal, the other from the southern part of Isabela,

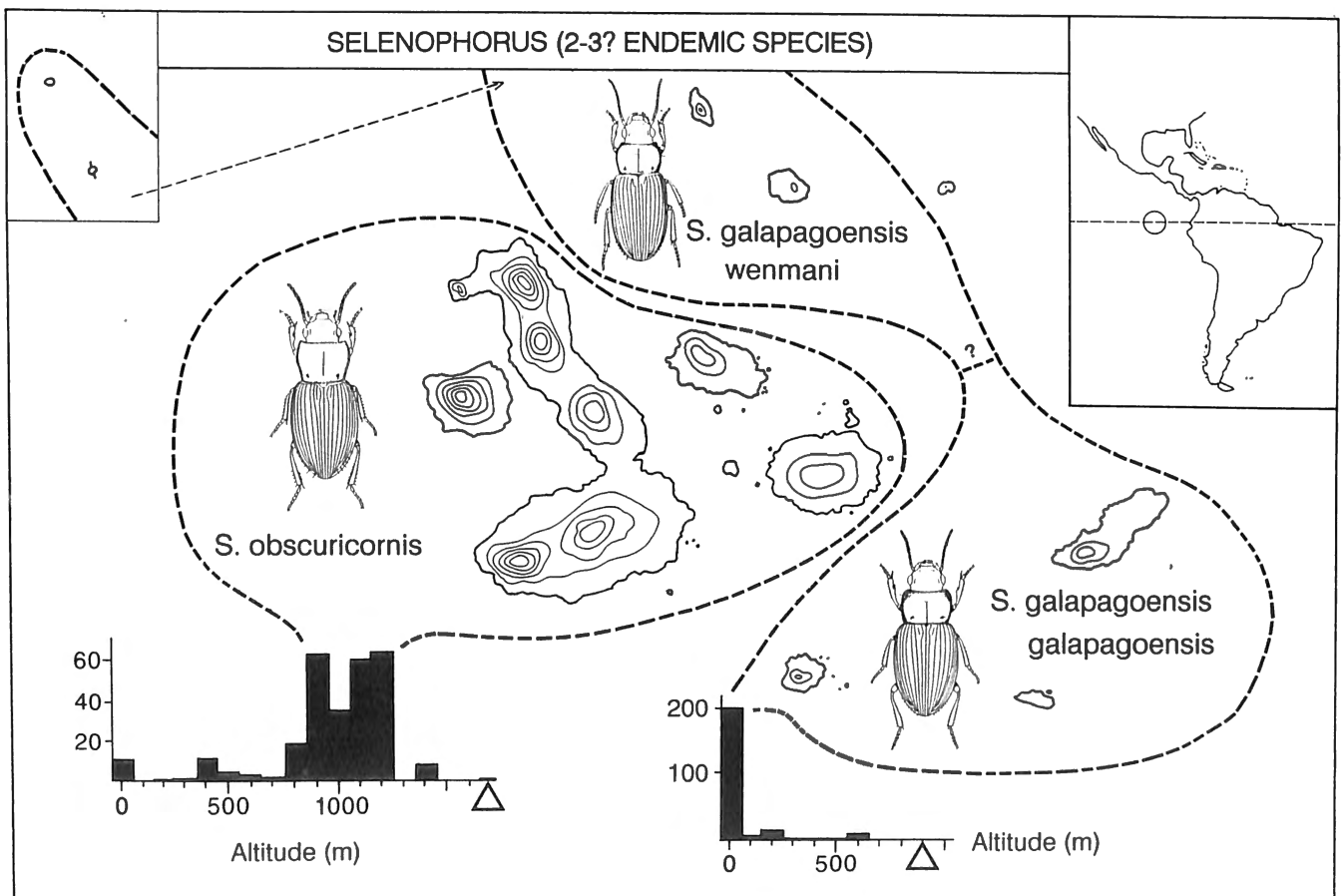


Fig. 4. — Geographical distribution of the *Selenophorus* species in the Galápagos Archipelago.

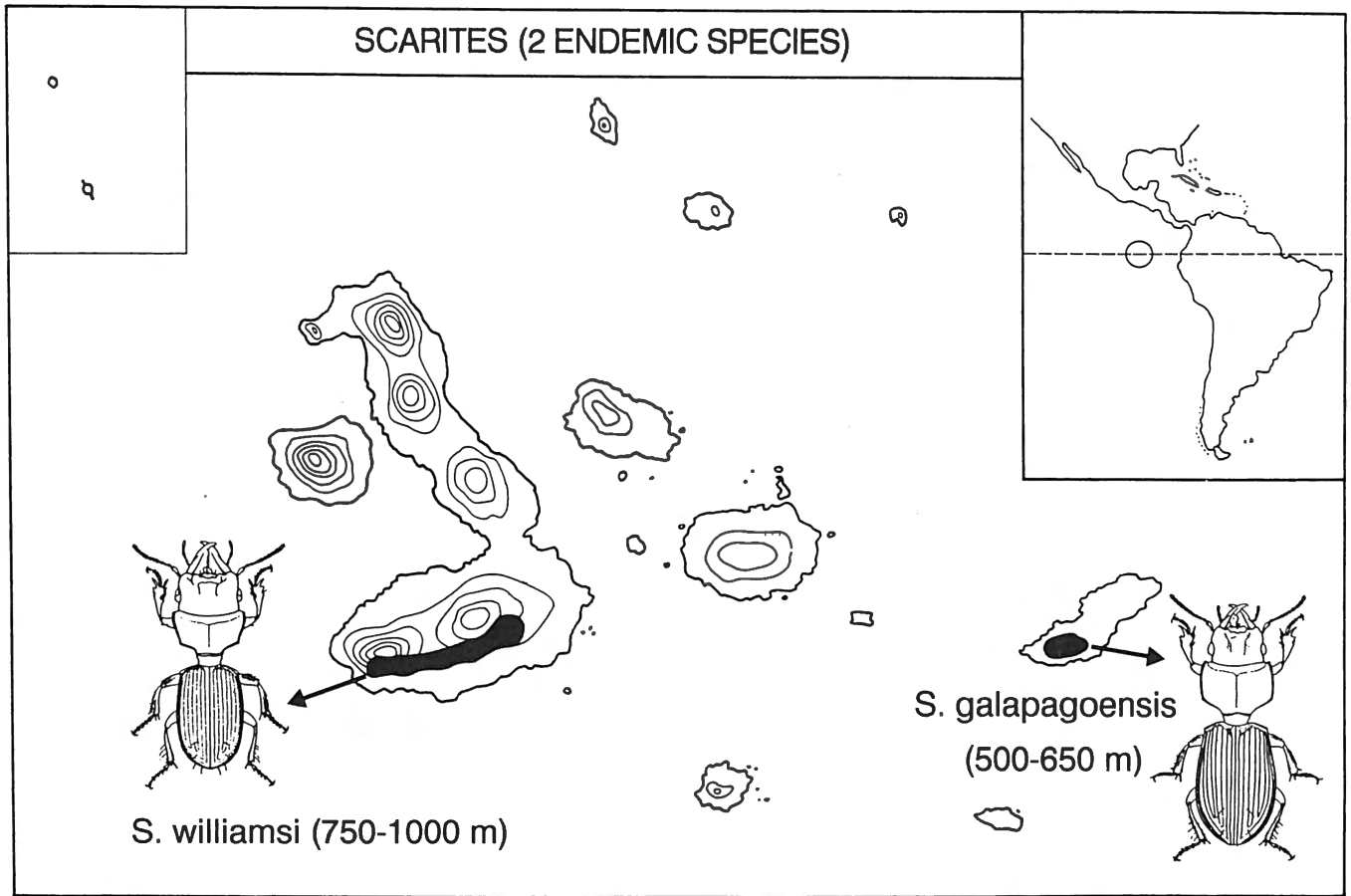


Fig. 5. — Geographical distribution of the *Scarites* species in the Galápagos Archipelago.

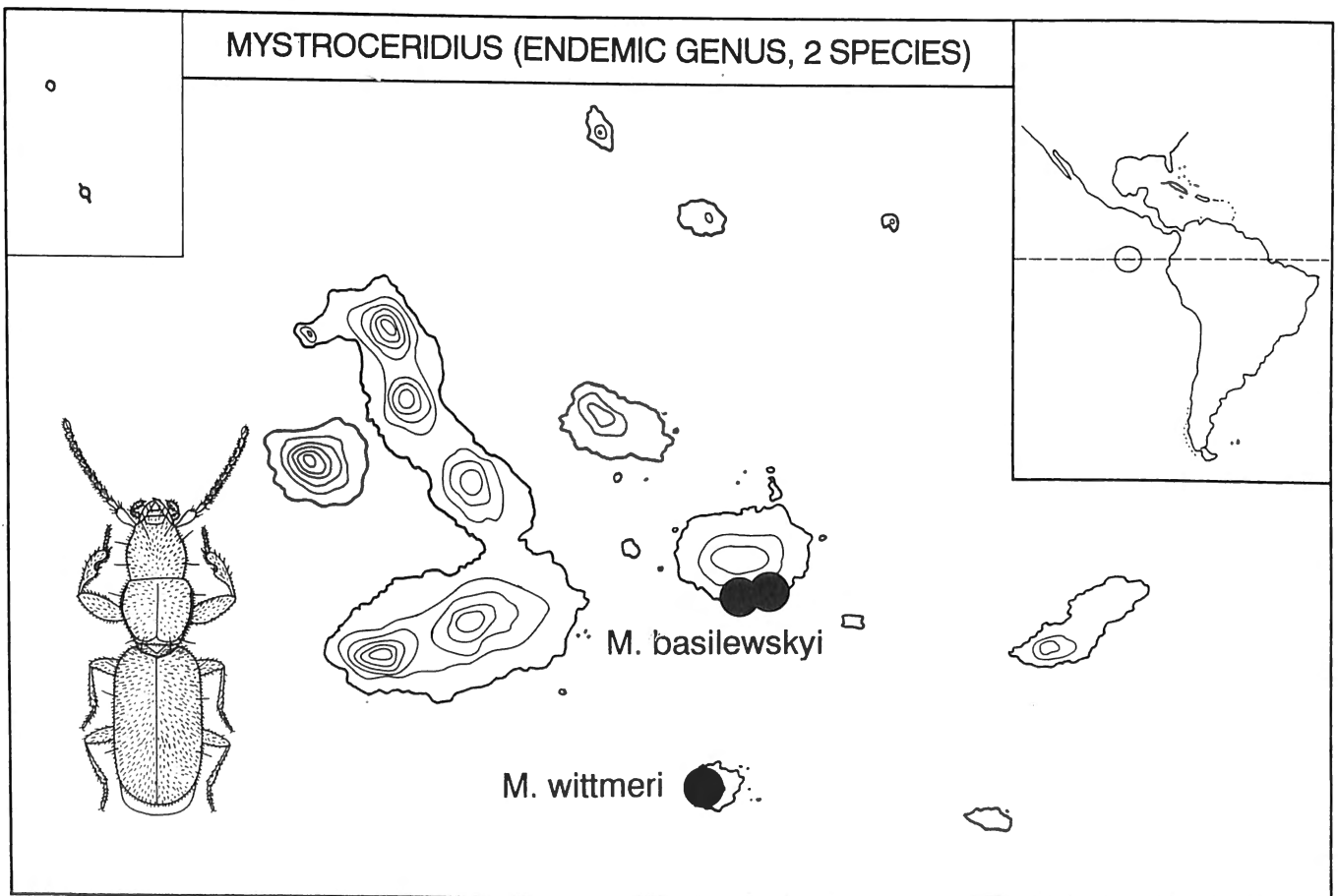


Fig. 6. — Geographical distribution of the *Mystroceridius* species in the Galápagos Archipelago.

again at a particular elevation. Both species are constantly brachypterous although many known relatives on the South American mainland are macropterous and able to fly. The species, about 2 cm in body length, show several special morphological adaptations to their predominant subterranean way of life and, as already mentioned, occur in an ecologically narrow zone. Their allopatric distribution, each species being confined to one island or even only part of it, suggests again the occurrence of allopatric speciation events in the past, but now on a smaller geographic scale and possibly at earlier stages in the history of the archipelago.

Comparable cases are found in three endemic *Agonum* species, again with a restricted ecological range and constantly brachypterous, in two *Myroceridius* species, as shown on Fig. 6, as well as in most of the *Pterostichus* species (Fig. 7), again all endemic to Galápagos. This genus has radiated more extensively in Galápagos and all of its species are more or less brachypterous and no longer able to fly and bridge large distances. This genus, however, brings us also to a more complicated pattern of distributions.

3.3. 'Mixed patterns'. Although many of the *Pterostichus* species most probably arose in allopatry on different islands (Fig. 7), there are also several cases of islands with two or even more species showing a more or less parapatric distribution. One of such species pairs on southern Isabela seems to show a case of incipient speciation by means of reproductive character displacement or reinforcement (the so-called 'Wallace effect'). Without going into much details (cfr. DESENDER et al., 1990a), genitalia characteristics, which are used in defining the species as reproductively isolated entities, have been compared. In a sympatric population they show much more differences between and more constancy within species as compared to an allopatric population. So these sister species with adjacent ranges but without obvious ecological or geographic barriers between them, seem to suggest parapatric or allo-parapatric speciation events and could well be cases of incipient speciation, i.o.w. evolution in action. Similar phenomena were observed for parapatrically occurring lycosid spiders (MAELFAIT & BAERT, 1986). We have studied such cases in more details during our 1991 expedition, but these new data have not yet been analyzed.

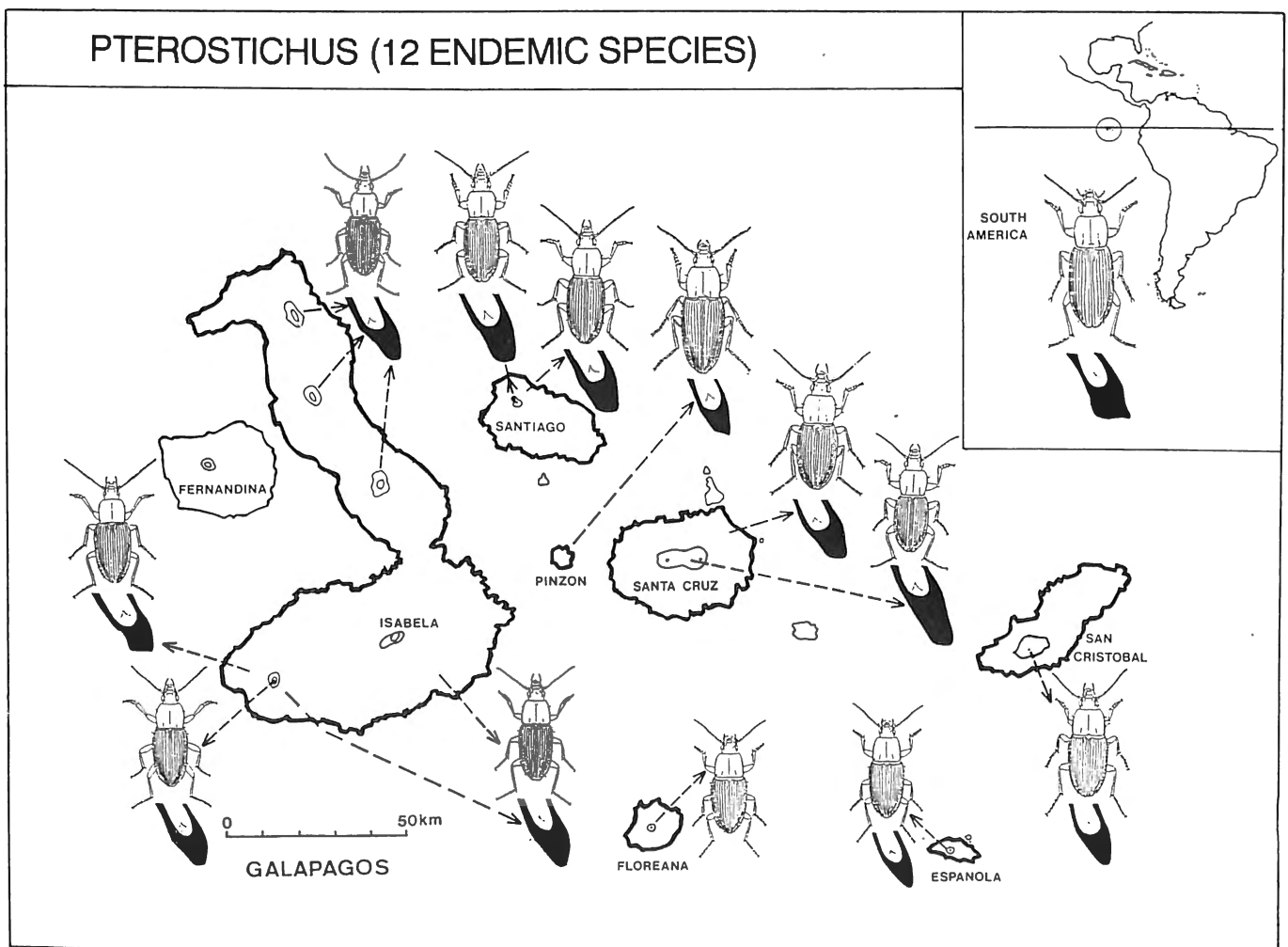


Fig. 7. — Geographical distribution of the *Pterostichus* species in the Galápagos Archipelago.

3.4. Yet another carabid genus which has radiated in Galápagos, namely *Calosoma* (Fig. 8), shows again a different picture arising from the distribution patterns. In summary (more details were again already given earlier: DESENDER & DE DIJN, 1989, 1990, DESENDER et al., 1991) this group is represented by a winged species, occurring all over the archipelago, but wing polymorphic on younger volcanoes, where it occurs from the lowlands to the top zone as opposed to its preference for the lower arid and transition zone on older islands. This species most probably originated directly from a mainland stock. The three other *Calosoma* species of Galápagos are true endemics, limited each to the higher parts of one of the older islands and possibly derived from the lowland species in convergent habitat shifts to higher and more mesic pampa zones. They show brachypterism to varying degrees and their speciation sequence, as deduced from their morphological divergence from the presumed ancestral species, is in full agreement with the estimated age or time sequence of the origin of these different islands in the archipelago (cfr. DESENDER et al., 1991). This, in its turn, could indicate that the initial foundation event occurred in the early history of Galápagos. The most probably youngest of these derived species, *Calosoma galapageium* of the top zone of Santiago, seems to show some degree of introgressive hybridiza-

tion with the lowland species in a narrow zone of overlap. This can lead to the hypothesis of allopatric speciation due to separation by habitat and/or altitude and secondary contact of the sister species, but, alternatively, could also constitute an early step in allo-parapatric incipient speciation. Of course, again an intriguing subject for our future studies.

3.5. Introduced species. Finally, two carabid species seem to have been unintentionally introduced recently. Not only are these species both well known from the continent, very well able to fly, do they show an erratic (in the case of *Pentagonica flavipes*) or very restricted distribution in Galápagos (in the case of *Cicindela trifasciata*), but they have both only been found since the last important 'El Niño' event in 1982-1983. Both of these cases are analyzed in detail in another paper, where we also stress the importance of 'El Niño' events for evolution and conservation of invertebrates in Galápagos (DESENDER et al., 1992).

In conclusion, the carabid beetles of Galápagos show a wide variety of distribution and speciation patterns and contribute in this way to the well known fascination of these islands for the ecologist and evolutionary biologist.

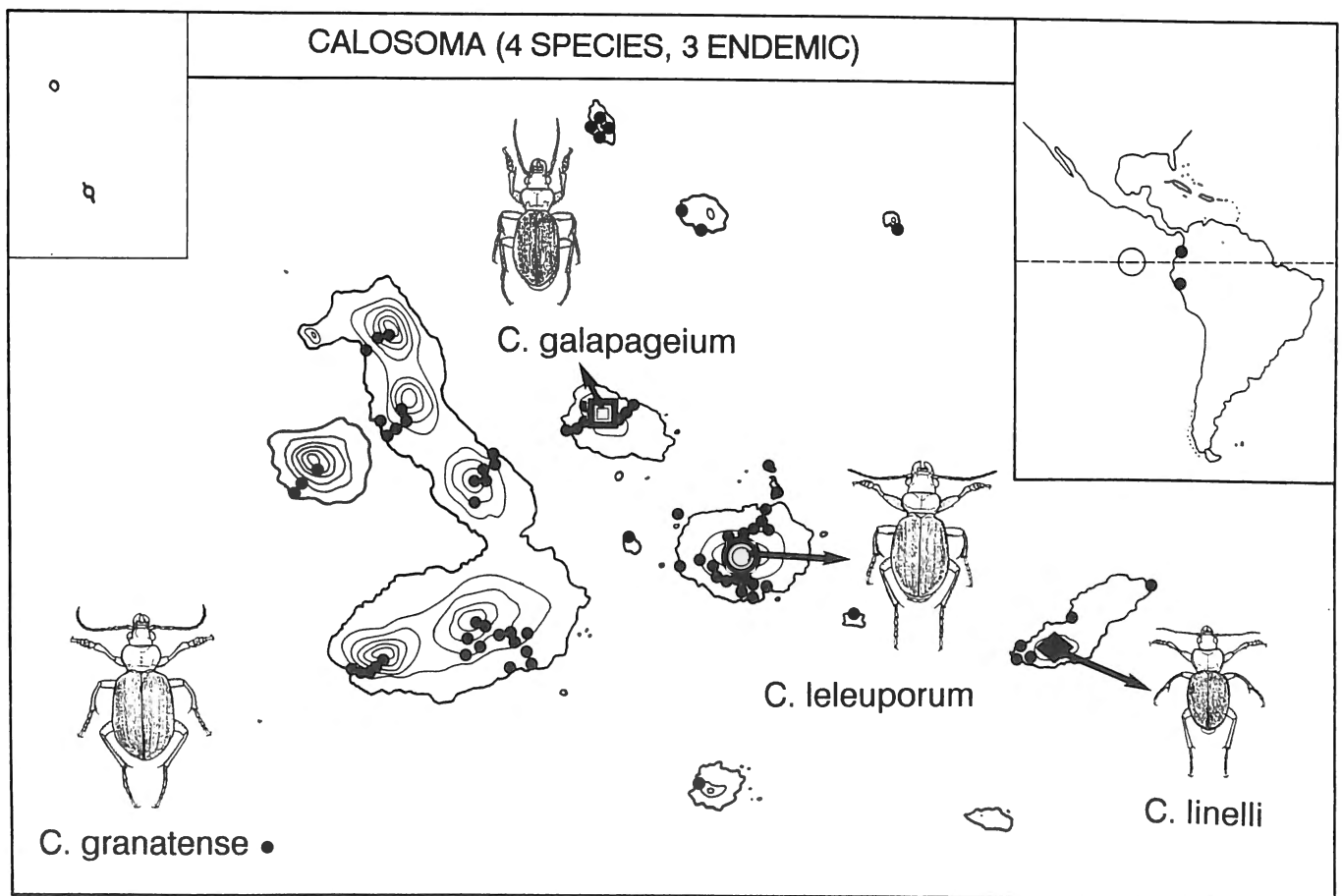


Fig. 8. — Geographical distribution of the *Calosoma* species in the Galápagos Archipelago.

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