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SPECIATION AND GEOGRAPHICAL PATTERNS IN *PYROPHORUS* BILBERG, 1820 (COLEOPTERA, ELATERIDAE, PYROPHORINI)

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ABSTRACT

Comments on the speciation and geographical patterns in Pyrophorus as well a key to species are given. The genus is monophyletic, predominantly tropical and radiated in the forests of the Guiano-Brazilian sub-region.

INTRODUCTION

It is my intention in this paper to extend an earlier effort (Costa, 1968-1975) to synthesize certain information on the speciation and geographical patterns of the genus *Pyrophorus* Bilberg. In the previous papers, were only given a key to species, comments on the systematic position, redescriptions and descriptions of new species, bionomical data and the relationships with other genera of Pyrophorini.

Twenty six species belong to this genus. Costa (1968) considered *P. angustus angustus*, *P. angustus luscus* and *P. angustus hayekae* as subspecies. The more detailed study of all species of this genus, showed that it is more comprehensible to elevate these subspecies to species rank, than to create other new subspecies.

Information on the number of individuals examined, list of localities for each species (only the following new localities are added: for *P. divergens*: FRENCH GUIANA. Cayenne; COLOMBIA. Boyacá: Muzo; BRAZIL. Mato Grosso: Chapada and Tapajós, Minas Gerais: Barbacena and Uberaba; BOLIVIA. Beni: Reys and Rio Beni, La Paz: Asunta, Pando: Rio Mapiri; for *P. clarus*: VENEZUELA. Magdalena: Caracas and Cerro Tumuypejocha, Se. de Perijá; COLOMBIA. Cundinamarca: Honda, Boyacá: Muzo and Caldas: Pereira), list of abbreviations of collections and illustrations are the same presented in the previous papers and are not included here. As the key to species published in 1972 is in Portuguese and not phylogenetic, I found it useful to present an English version here.

Maps showing the known general distribution of each species are given. The shading of each area of maps 1, 3, 4 indicates the forested regions and is an adaptation of Starker (1950), Stuart (1966) and Hueck (1966).

This genus is characterized by a stout and robust shape; antennae short, luminous spots of the prothorax lateral; no apparent sexual dimorphism; male genitalia with median lobe very robust, gradually tapering to apex, with or without minute cuticular scales; female genitalia with well developed bursa copulatrix, very spiraled and with numerous long spines, spermatheca membranous and with many ramifications, median oviduct simple.

Pyrophorus Bilberg, 1820

Elater (pars) Linnaeus, 1758: 404; De Geer, 1774: 160; Olivier, 1790: 15; Fabricius, 1792: 218; 1801: 223; Herbst, 1801: 331; Latreille, 1804: 14; Illiger, 1807: 141.

Pyrophorus Bilberg, 1820: 20; Eschscholtz, 1829: 32; Castelnau, 1840: 235; Germar, 1841: 1; Candèze, 1863: 3; Champion, 1895: 463; Schenkling, 1927: 345; Blackwelder, 1944: 285; Navajas, 1952: 52-56; Costa, 1968: 61-83; 1969: 249-262; 1970: 69-76, 1971: 65-72; 1972: 199-227; 1975: 49-190.

Key to species

1. Luminous spots visible only on the pronotum 2
 Luminous spots visible dorsally on the pronotum and ventrally on the proepisternum 12
- 2(1). Lateral lobes of male genitalia short and rounded to apices 3
 Lateral lobes of male genitalia short and with a small lateral and subapical spine 9
- 3(2). Prothorax and luminous spots slightly convex 4
 Prothorax and luminous spots strongly convex 5
- 4(3). Pronotum homogeneously punctulate, luminous spots great, oval and oblique in relation to the lateral margin of the prothorax (Mexico and Central America)
 *strabus* Germar, 1841
 Pronotum heterogeneously punctulate, luminous spots smaller, rounded and not oblique in relation to the lateral margin of the prothorax (Central America) *jocundus* Costa, 1972
- 5(3). Pronotum homogeneously punctulate 6
 Pronotum strongly and heterogeneously punctulate, prothorax strongly convex anteriorly (Greater Antilles, Jamaica)
 *plagiophthalmus* Germar, 1841
- 6(5). Prosternum homogeneously punctulate; elytra coarsely punctulate mainly on the disc (Central America and West Indies)
 *mellifluus* Costa, 1972
 Prosternum heterogeneously punctulate 7

- 7(6). Elytra finely punctate-striate; male with eyes slightly greater than normal, very small luminous spots on the prothorax (Lesser Antilles, St. Lucia) *mellitus* Costa, 1972
Elytra strongly punctate-striate 8
- 8(7). Prothorax bisinuate on the margins; luminous spots slightly oblique in relation to the lateral margin of the prothorax (Mexico, Central America, Guianas; Lesser Antilles: Guadeloupe, Dominica, Martinica)
..... *phosphorescens* Castelnau, 1840
Prothorax not bisinuate; luminous spots parallel to the lateral margins of the prothorax; two small smooth zones on the median part of the pronotum (Lesser Antilles: St. Vincent)..... *indulcatus* Costa, 1972
- 9(2). Prosternum homogeneously punctulate; luminous spots strongly convex; directed to the outer margin of the prothorax; elytra strongly punctate-striate mainly on the median region (Atlantic and Amazonian region; Mexico and West Indies) *tuberculifer* Eschscholtz, 1829
Prosternum heterogeneously punctulate 10
- 10(9). Elytra finely punctate-striate (Atlantic and Amazonian forest) *divergens* Eschscholtz, 1829
Elytra strongly punctate-striate 11
- 11(10). Luminous spots oblique in relation to the lateral margin of the prothorax; elytra with a small apical sutural spine (Bolivia, Brazil, Paraguay and Argentina)
..... *punctatissimus* Blanchard, 1843
Luminous spots parallel to the lateral margin of the prothorax; elytra slightly raised and rounded to apices (Paraguay) *everus* Costa, 1972
- 12(1). Lateral lobes of male genitalia short and with a small lateral subapical spine; median lobe well developed and without cuticular scales; luminous spots of the prothorax elliptical (Northern Venezuela) .. *stupendus* Costa, 1972
Lateral lobes of male genitalia more or less elongate, median lobe variable 13
- 13(12). Lateral lobes of the male genitalia slightly elongated, median lobe straight, less developed, with or without a few minute cuticular scales 14
Lateral lobes of the male genitalia strongly elongated, median lobe more developed and with numerous minute cuticular scales 19
- 14(13). Pronotum with punctures very fine and scarce (Guianas and Eastern Amazonia) *hayekae* Costa, 1968
Pronotum with punctures very distinct 15
- 15(14). Prothorax and luminous spots very convex (Mexico, Central America and Northern Brazil) *indistinctus* Germar, 1841
Prothorax and luminous spots not so convex 16

16(15). Pronotum strongly and homogeneously punctulate; elytra finely punctate-striate (Bolivia, Peru and Ecuador)
..... *angustus* Blanchard, 1843
Pronotum heterogeneously punctulate 17

17(15). Prosternum strongly punctulate 18
Prosternum finely and scarcely punctulate on the middle, slightly dense on the margins (Colombia and Ecuador)
..... *dulcifer* Costa, 1972

18(17). Prosternum heterogeneously punctulate, luminous spots rounded; hind angles of the pronotum slightly divergent (Northwestern corner of South America)
..... *clarus* Germar, 1841
Prosternum homogeneously punctulate, luminous spots slightly oval, hind angles of the pronotum strongly divergent (Ecuador) *magnus* Costa, 1972

19(17). Punctures on the pronotum extremely dense and coarse; elytra strongly punctate-striate on the latero-anterior region (Mexico to Rio de Janeiro, Brazil)
..... *noctilucus* Linnaeus, 1758
Punctures on the pronotum very distinct but not very dense; elytra finely punctate-striate 20

20(19). Prothorax convex, pronotum homogeneously punctulate, prosternum finely and scarcely punctulate (Eastern Ecuador) *pisticus* Costa, 1972
Prothorax slightly convex, pronotum heterogeneously punctulate 21

21(20). Prosternum homogeneously punctulate 22
Prosternum heterogeneously punctulate 23

22(21). Antennae with segment two subequal to three; abdominal luminous organ of large size (Costa Rica)
..... *ingens* Costa, 1972
Antennae with segment two smaller than segment three; abdominal luminous organ of median size (Costa Rica and Panama) *avunculus* Costa, 1972

23(20). Luminous spots slightly convex (Colombia and Ecuador) ..
..... *validus* Costa, 1972
Luminous spots flat 24

24(23). Prosternum strongly punctulate 25
Prosternum finely punctulate (Mexico to Panama)
..... *veriloquus* Costa, 1972

25(24). Front with punctures umbilicate and dense (Mexico, Central America and Colombia) *luscus* Candèze, 1889
Front with punctures fine and not umbilicate ((Northwestern corner of South America) *expeditus* Costa, 1972

According to the male genitalia the species of this genus may be subdivided as follows:

Genitalia A (*phosphorescens* group) (figs. 9 and 10 from Costa, 1969; figs. 1-3, 6 and 9 from Costa, 1972), characterized by the lateral lobes short and rounded to the apices. Belonging to this group are: *strabus* Germar, *jocundus* Costa, *plagiophthalmus* Germar, *mellifluus* Costa, *mellitus* Costa, *phosphorescens* Castelnau and *indulcatus* Costa.

Genitalia B (*divergens* group) (figs. 7 from Costa, 1969; fig. 1 from Costa, 1971 and figs. 4-5 from Costa, 1972), the lateral lobes are short but with a small lateral and subapical spine. The following species belong here: *divergens* Eschscholtz, *tuberculifer* Eschscholtz, *evexus* Costa and *punctatissimus* Blanchard.

Genitalia C (*stupendus* group) (fig. 13 from Costa, 1972), similar to the genitalia B, differing by the very stout median lobe. A single species belongs to this group: *stupendus* Costa.

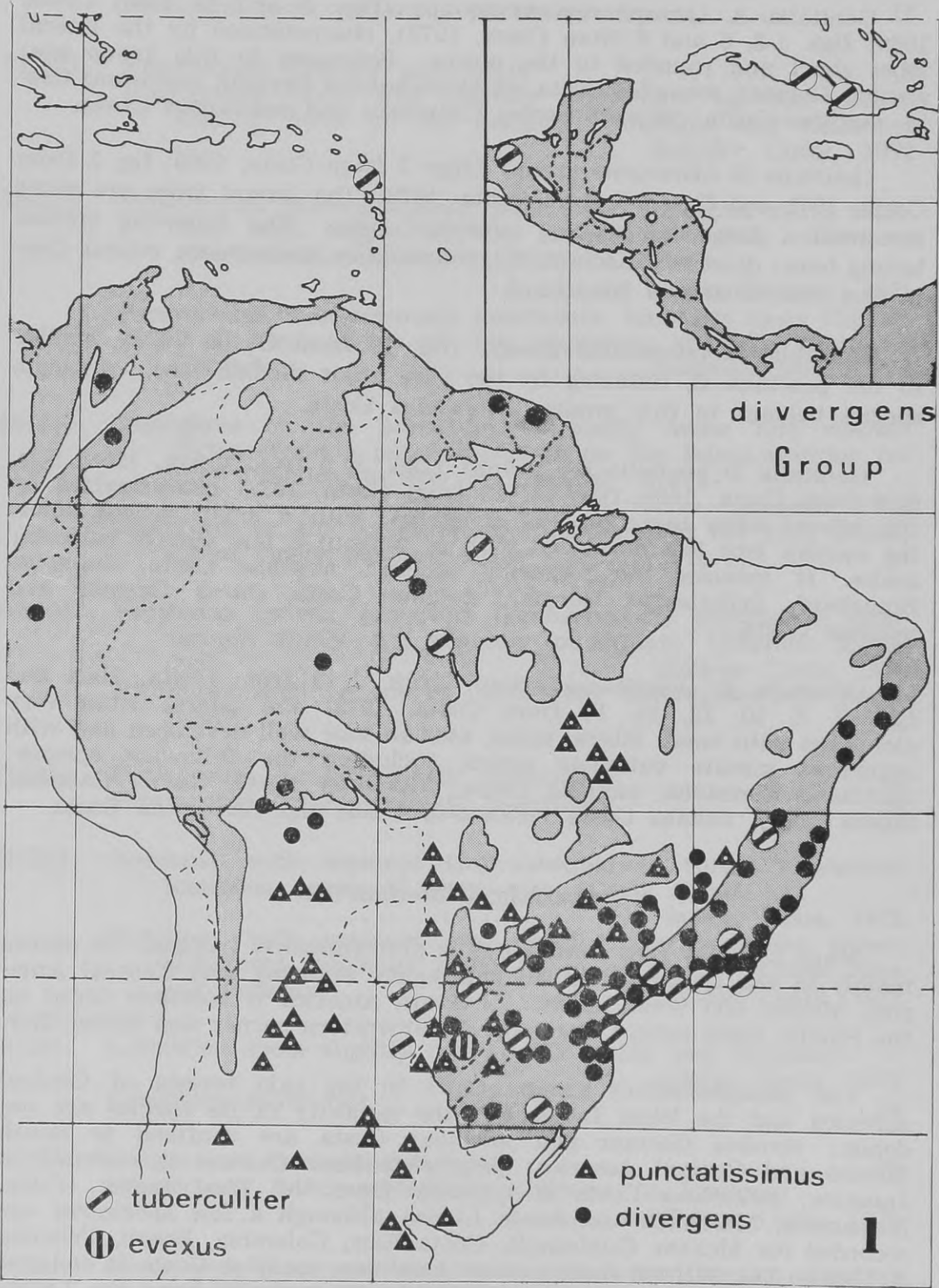
Genitalia D (*indistinctus* group) (figs. 3, 5 from Costa, 1968; figs. 6, 8 from Costa, 1969, figs. 11, 14 from Costa, 1972) characterized by the lateral lobes more or less elongated, with a small lateral spine, the median lobe less developed with or without a few minute cuticular scales. It includes the following species: *hayekae* Costa, *angustus* Blanchard, *indistinctus* Germar, *dulcifer* Costa, *clarus* Germar and *magnus* Costa.

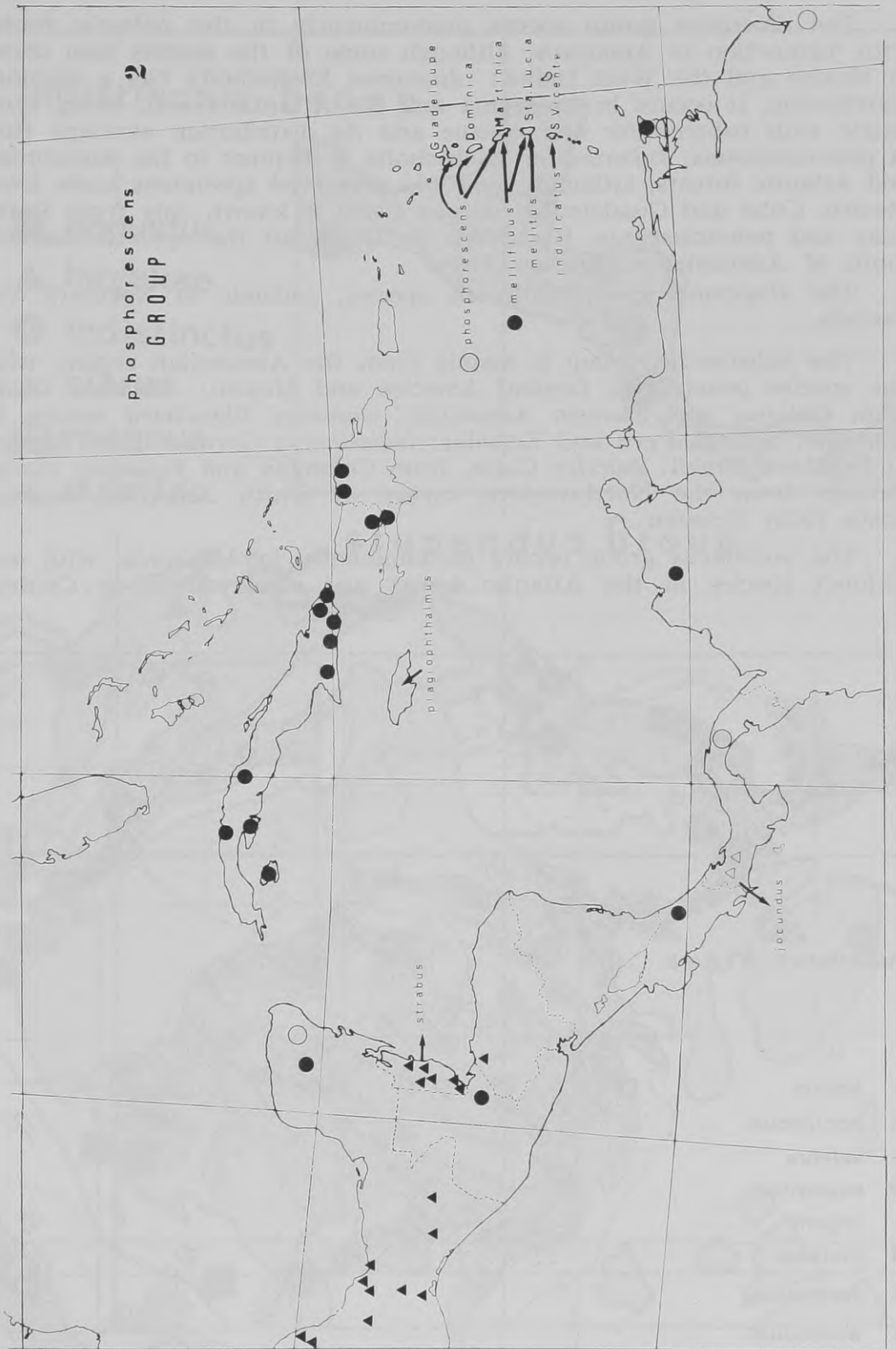
Genitalia E (*noctilucus* group) (figs. 1, 2 from Costa, 1968 and figs. 7, 8, 10, 12, 15, 16 from Costa, 1972) the lateral lobes very elongated with small lateral spine, median lobe well developed and with numerous minute cuticular scales, including the following species: *noctilucus* Linnaeus, *pisticus* Costa, *expeditus* Costa, *luscus* Candèze, *ingens* Costa, *validus* Costa, *avunculus* Costa and *veriloquus* Costa.

GEOGRAPHICAL DISTRIBUTION

Maps 1-4 show that *Pyrophorus* is predominantly tropical. It occurs mainly in the Guiano-Brazilian sub-region, entering also Central America, Mexico and West Indies. In South America it does not occur on the Pacific coast except along the Northwestern corner and below 35°S.

The *phosphorescens* group occurs in the rain forests of Central America and the West Indies and the majority of its species are endemic: *strabus* Germar and *jocundus* Costa are confined to South Mexico and Central America; *plagiophthalmus* Germar is endemic in Jamaica; *mellifluus* Costa is typically from the West Indies (Cuba, Hispaniola, Martinica and Santa Lucia) although a few specimens are recorded for Mexico, Guatemala, Costa Rica, Colombia, Brazil, Trinidad & Tobago but without more precise localities; *mellitus* Costa is endemic to Santa Lucia; *phosphorescens* Castelnau is typically from the Lesser Antilles (Guadeloupe, Dominica and Martinica) although a few records come from Mexico, Panama, Guiana (Essequibo), French Guiana





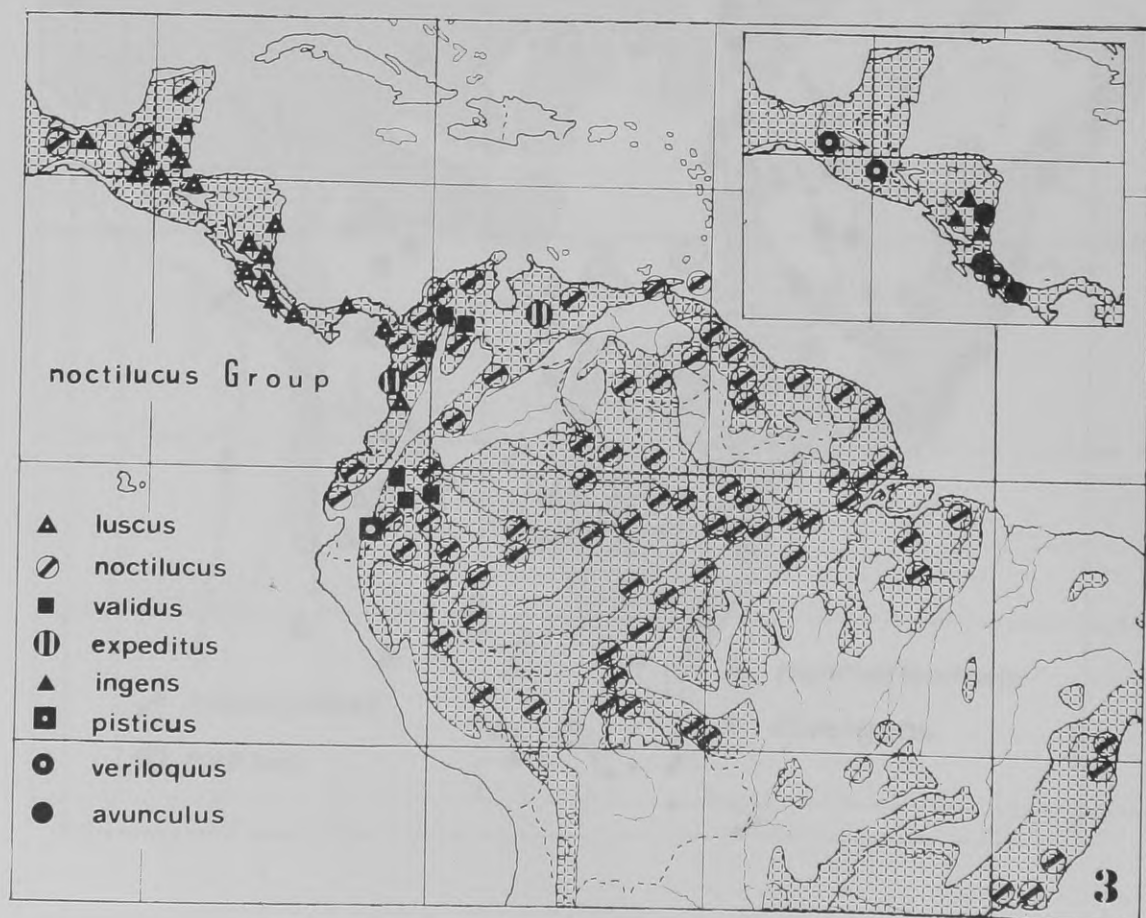
(Cayenne), Brazil and Trinidad & Tobago, some of these are from imprecise localities; and, *indulcatus* Costa, endemic to St. Vicent.

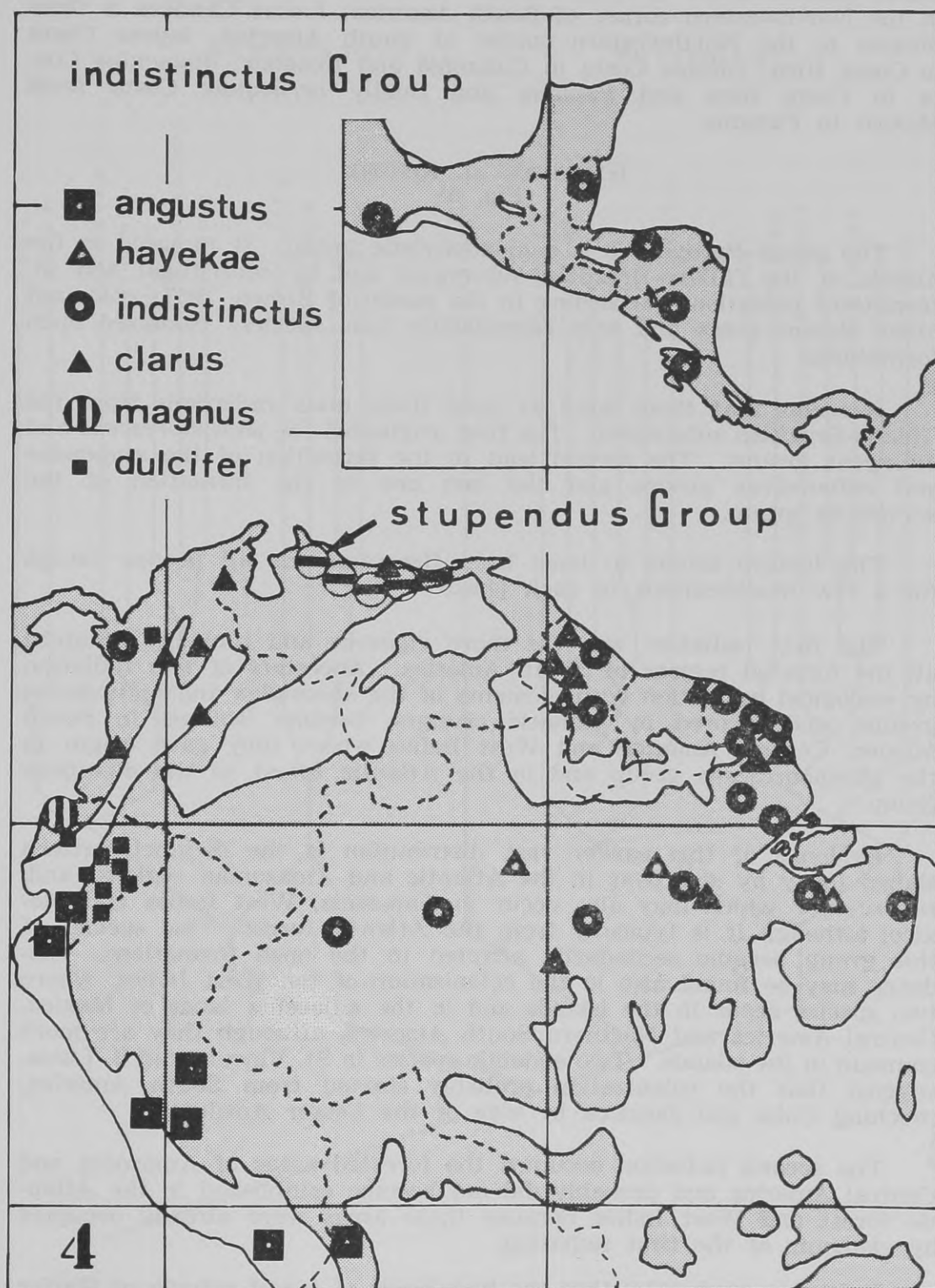
The *divergens* group occurs predominantly in the Atlantic forest with disjunction in Amazonia, although some of the species also occur in Mexico and the West Indies: *divergens* Eschscholtz has a disjunct distribution, it occurs in Amazonia and the Atlantic forest, being sympatric with *tuberculifer* and *evexus* and its distribution overlaps that of *punctatissimus*; *tuberculifer* Eschscholtz is disjunct in the Amazonian and Atlantic forests, although some old preserved specimens come from Mexico, Cuba and Guadeloupe; *evexus* Costa is known only from Paraguay and *punctatissimus* Blanchard occurs in all the open formations south of Amazonia to Buenos Aires.

The *stupendus* group with one species, endemic to Northern Venezuela.

The *indistinctus* group is mainly from the Amazonian region, with one species penetrating Central America and Mexico: *hayekae* Costa from Guianas and Eastern Amazonia; *angustus* Blanchard occurs in Northern Bolivia, Peru and Ecuador; *indistinctus* Germar, from Mexico to Northern Brazil; *dulcifer* Costa, from Colombia and Ecuador; *clarus* Germar from the Northwestern corner of South America; *magnus* Costa from Ecuador.

The *noctilucus* group occurs predominantly in Amazonia, with one disjunct species in the Atlantic forest and some others in Central





America and Mexico: *noctilucus* Linnaeus has a vast distribution from Mexico to Rio de Janeiro being disjunct in the Brazilian open formations; *pisticus* Costa is from Eastern Ecuador; *expeditus* Costa occurs in the Northwestern corner of South America; *luscus* Candèze is from Mexico to the Northwestern corner of South America; *ingens* Costa in Costa Rica; *validus* Costa in Colombia and Ecuador; *avunculus* Costa in Costa Rica and Panama and finally *veriloquus* Costa from Mexico to Panama.

HYPOTHETICAL HISTORY (Fig. 5)

The genus *Pyrophorus* is a monophyletic group. It radiated in the forests of the Guiano-Brazilian sub-region and by centrifugal and intermittent pulsations (according to the model of Brown, 1957) colonized other distant areas and only secondarily (one species) colonized open formations.

It seems that there were at least three main radiations from the Guiano-Brazilian sub-region. The first originated the *phosphorescens* and *divergens* groups. The second led to the formation of the *stupendus* and *indistinctus* groups and the last one to the formation of the *noctilucus* group.

The history seems to have been the same for all groups except for a few modifications in each phase.

The first radiation was the more vigorous and probably occupied all the forested regions of South America. Ancestors of this radiation by ecological competition with elements of the *stupendus* and *indistinctus* groups, and favored by climatic changes, became isolated in South Mexico, Central America and West Indies where they gave origin to the *phosphorescens* group and in the Atlantic forest to the *divergens* group.

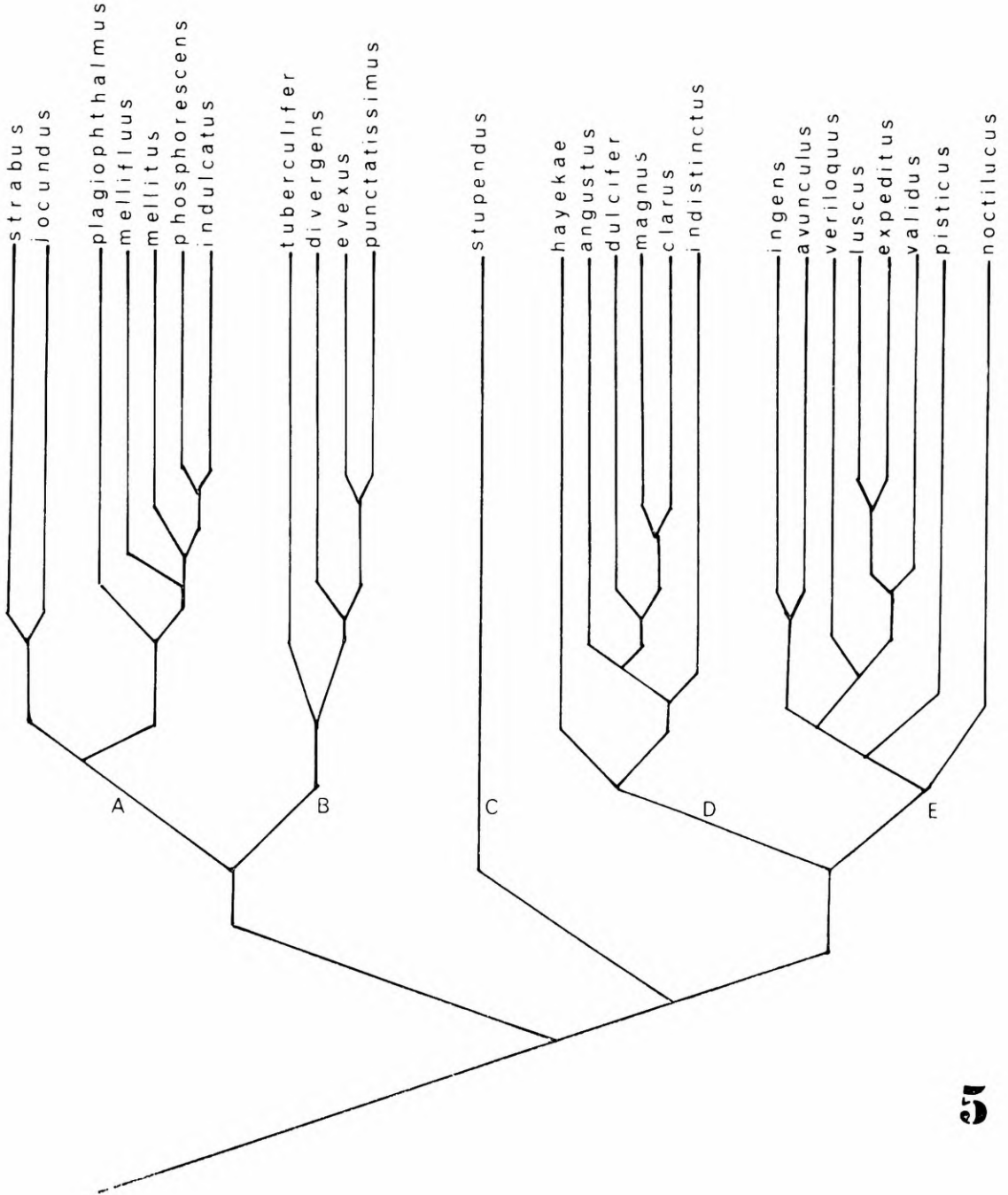
Evidence of this earlier vast distribution is the disjunct pattern shown today by *divergens* in the Atlantic and Amazonian regions; and, *tuberculifer* which may also occur in Amazonia, West Indies and Mexico, although it is typically from the Atlantic forest. One species of this group became secondarily adapted to the open formations. Evidence may be found also in the colonization of the West Indies, where two species occur in the islands and in the adjacent lands of Mexico, Central America and Northern South America, although they are more common in the islands. Two endemic species in St. Vincent and S. Lucia, suggest that the colonization probably started from South America, reaching Cuba and Jamaica by way of the Lesser Antilles.

The second radiation occupied the forested areas of Amazonia and Central America and probably did not become established in the Atlantic forest and West Indies because these areas were already occupied by elements of the first radiation.

It is very suggestive that the hypothesis of forest refugia of Haffer (1967, 1969, 1970, 1974) and Vanzolini and Williams (1970) might explain the origin of some of the species evolved in consequence of these radiations. According to these authors, differentiation of many

HYPOTHETICAL

PHYLOGENY



species may have been determined by the Quaternary vegetational history of South and Central America that includes alternations between drier and wetter episodes reflecting cycles of spreading and retreat of the forests. During the drier phase the forest was reduced to isolated patches "the refugia" in certain areas.

Comparing the present distribution of the *stupendus* and *indistinctus* groups, it seems that survival of the *stupendus* group only in the Northern Venezuela refuge, is a relict pattern. The *indistinctus* group was reduced to a few isolated patches: in Eastern Amazonia (*hayekae*); in Eastern Ecuador (*magnus*), in Eastern and Western Ecuador (*dulcifer*); in the Northwestern corner of South America (*clarus*); and one species with a more vast distribution from Northern Amazonia-Guiana, Central America and Mexico (*indistinctus*). It is very probable that *magnus* and *dulcifer* have originated in the Pacific Colombian refuge and this last species expanded into Western Ecuador. On the other hand, *clarus* is derived from ancestors that reinvaded South America from Central America and became isolated in the Caribbean Colombia refuge or in the Pacific Colombian refuge. Finally the more recent species (*indistinctus*) of this group penetrated Central America and Mexico from Northern Amazonia.

The third radiation also occupied all forested areas of South America, and by ecological competition with the groups formed earlier was prevented to establish in certain areas, as the Atlantic forest and the West Indies. In the areas where it now is sympatric with elements of others groups, it is probable that there was secondary adaptation to different habitats. Three species (*ingens*, *avunculus* and *veriloquus*) are typical from Central America and probably have evolved there. One species (*luscus*) also typically Central American reinvaded South America but does not go beyond the Northwestern corner. Species that probably have originated in the refugia are: *expeditus* in the Caribbean Colombian or Northern Venezuela refugia, *validus* in the Napo or Caribbean refugia and *pisticus* in the Napo refuge. Finally the more recent species (*noctilucus*) of this group has yet a vast distribution from Mexico to Rio de Janeiro.

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