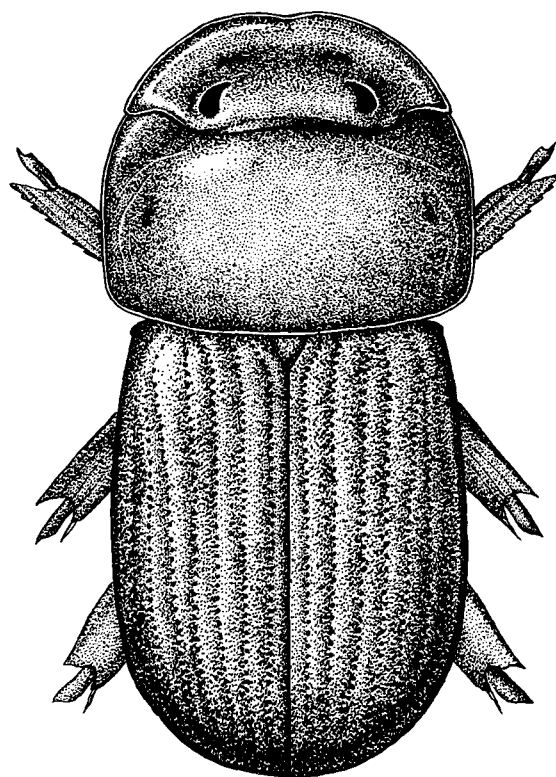




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Fig. 1. Habitus of *Brasilucanus acomus* Ratcliffe, new species.

**A Review of the Penichrolucaninae with Analyses of Phylogeny and Biogeography, and
Description of a Second New World Species from the Amazon Basin (Coleoptera:
Lucanidae)**

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ABSTRACT

The Penichrolucaninae is a small subfamily of very rare Lucanidae consisting of Brasilucanus alvarengai Vulcano and Pereira (Brazil, Guyana), B. acomus, new species (Brazil), Penichrolucanus copricephalus Deyrolle (Malaysia), P. elongatus Arrow (Malaysia), P. leverii Arrow (Solomon Islands), P. nicobaricus Arrow (Nicobar Islands), and P. sumatrensis Arrow (Sumatra). A monophyletic origin for the subfamily is indicated because all included taxa share (1) an extremely dorso-ventrally compressed body and (2) fused tarsomeres. No other lucanid adults possess these character states. This paper discusses two alternate biogeographical hypotheses to explain the current distribution of these beetles. The first postulates a Holarctic radiation in the Paleogene with subsequent retreat to tropical refuges in Malaya (post-Miocene) and South America (post-Pliocene). The second postulates a Gondwanan origin and radiation with subsequent vicariance to South America due to continental drift (Upper Cretaceous), dispersal from Africa to Asia (Miocene), and possible extinction in Africa (Miocene onward). A new species of Brasilucanus is described from Amazonian Brazil, a key to genera and species is presented, illustrations of important characters and geographic distribution of taxa are given, and analyses of phylogeny and biogeography are examined.

RESUMO

Os Penichrolucaninae, grupo pequeno e raro, compreende as seguintes espécies: Brasilucanus alvarengai Vulcano e Pereira (Brasil, Guiana); Penichrolucanus copricephalus Deyrolle (Malásia), P. leverii Arrow (Ilhas Salomão), P. nicobaricus Arrow (Ilhas Nicobar) e P. sumatrensis Arrow (Sumatra). Brasilucanus acomus sp.n. (Brasil, Amazonas) é descrita. Apresento chave de identificação para gêneros e espécies, ilustrações dos caracteres mais importantes, distribuição geográfica e análise filogenética e biogeográfica. Dois caracteres, comuns a todos taxa, indicam a origem monofilética desta sub-família: (1) corpo extremamente comprimido e (2) tarsômeros fundidos. Estes caracteres não aparecem nenhum outro Lucanidae. Duas hipóteses biogeográficas são propostas para explicar a distribuição destes besouros. Na primeira, postulo radiação Holártica durante o Paleogenio com retração subsequente em refúgios tropicais na Malásia (post-Mioceno) e na América do Sul (post-Plioceno). No segundo modelo, proponho origem Gondwanica, com subsequente radiação vicariante à América do Sul devido a deriva continental (Cretáceo Superior), dispersão da África à Ásia (Mioceno) e extinção provável na África (Mioceno, em diante).

INTRODUCTION

The Penichrolucaninae is a distinctive, highly aberrant group of stag beetles. Were it not for their antennae, one would not easily recognize them as stag beetles at all. Moreover, they are exceedingly rare. Based upon collections and literature records with which I am familiar, only

three of the seven known species are represented by more than a single specimen. Penichrolucanines are denizens of dense, equatorial forests in the Amazon Basin, Solomon Islands, and in Malaysia. The locality records (figs. 10-11) represent a disjunct distribution in the extreme. Nothing is known of habits of adults, life cycle, or immature stages of these taxa except that adults of one species were taken in rotting wood. These taxa may be myrmecophilous or termitophilous because penichrolucanine adults show many of the same character states seen in adults of known myrmecophiles such as the paussine Carabidae and the Cremastocheilini of the Scarabaeidae. These states include dorsal-ventral flattening, reduced or compacted tarsomeres and flattened and closely appressed femora. Myrmecophily would also help to explain their current rarity, *i.e.*, they have not been sought out in nests of ants or termites. Based on my own extensive collecting in the type locality of the new species described herein, I believe that adults are not attracted to lights.

Prior to this study, only one specimen had been reported from the New World: the type of *Brasilucanus alvarengai* Vulcano and Pereira. A second specimen of this species was located in the collection at Cornell University. A third specimen, representing a new species from Brazil, is described below.

Arrow (1949) established the subfamily Penichrolucaninae to accommodate five distinctive species in the Malaysian genus *Penichrolucanus*. This genus was formed by Deyrolle (1863) when he described *P. copricephalus* from Malacca (Melaka) in Malaya. Arrow (1935) then described *P. elongatus* from Kuala Lumpur in Malaya, *P. nicobaricus* from Nicobar Island off the northern tip of Sumatra, and *P. sumatrensis* from Palembang in Sumatra. The most recently described Old World species, *P. leverii* Arrow, came from Guadalcanal in the Solomon Islands.

Vulcano and Pereira (1961) briefly reviewed the Penichrolucaninae and described a new genus and species from Jacaré-a-Canga in extreme western Pará state in Brazil, *Brasilucanus alvarengai*. This represented the first reported occurrence of the subfamily in the New World. A second specimen of *B. alvarengai*, this from Guyana, is here reported: "Tumatumari, Potaro R., BR. GUIANA, VI-29-1927, Cornell University, Lot 760, Sub 117." The Guyana specimen clearly indicates that this species occurs both north and south of the Amazon River. Distribution on both sides of the Amazon River is significant from the standpoint of biogeography because the Amazon was a large inland sea during pluvial periods of the Pleistocene (Haffer, 1969; Simpson and Haffer, 1978; Vuilleumier, 1971). Biogeographical data are discussed later in this paper.

The authors of *Brasilucanus* considered it distinct from *Penichrolucanus* because adults of the former genus were characterized by distinct setae dorsally and ventrally, mandibles completely hidden by the clypeus in dorsal view, and greatly expanded and/or shortened femora and tibiae. Discovery of a second species of *Brasilucanus* requires alteration of the generic diagnosis. This is discussed under "Remarks" in the new species description.

I describe below a new species of *Brasilucanus* taken at Reserva Ducke, a forest study site 26 km NE of Manaus, Amazonas, Brazil. This species is the second known from the New World and the first described from a "black water" forest region in the Neotropics.

The Penichrolucaninae, then, consists of two genera with seven species known from approximately 14 specimens. The subfamily was not even reported from the New World until 1961, a fact that is indicative of rarity of these taxa. Consequently, I believe that new taxa may yet be found in South America, Asia, and perhaps also in Africa (see discussion on biogeography).

Key to Adults of the Penichrolucaninae

- 1 Mandibles completely hidden by clypeus in dorsal view. New World species (*Brasilucanus*) 2
- 1' Mandibles exposed in dorsal view. Malaysian species (*Penichrolucanus*) 3
- 2 (1) Head, pronotum, elytra, and femora setigerously punctate *B. alvarengai* Vulcano and Pereira
- 2' Head, pronotum, and femora glabrous, impunctate *B. acomus* Ratcliffe, n. sp., p. 63
- 3 (1') Elytra lacking punctures on interneurs or on intervals. Color nearly black *P. elongatus* Arrow
- 3' Elytra with interneurs punctate or not and/or punctate on intervals. Color reddish brown 4
- 4 (3') Elytra with interneurs impunctate. Meso- and metatibiae just beyond middle with small spines *P. leverii* Arrow
- 4' Elytra with interneurs punctate. Meso- and metatibiae lacking small spines just beyond middle 5
- 5 (4') Anterior tibia with only small, lateral serrations (fig. 4) *P. nicobaricus* Arrow
- 5' Anterior tibia with distinct, large, lateral teeth (fig. 6) 6
- 6 (5') Mandibles nearly right angled externally *P. sumatrensis* Arrow
- 6' Mandibles not distinctly angulate externally, rounded instead *P. copricephalus* Deyrolle

Brasilucanus acomus Ratcliffe, new species

(Figs. 1, 5, 10)

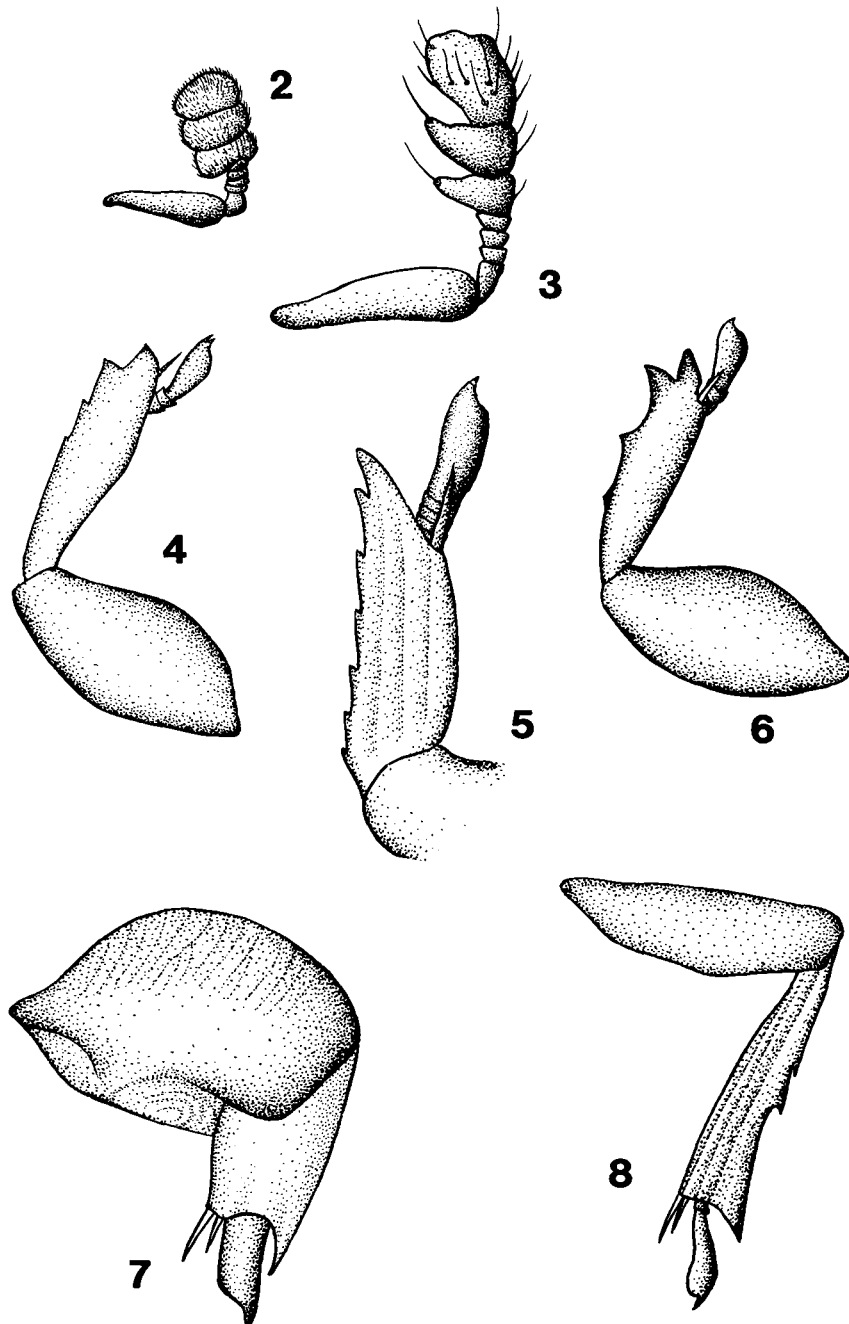
Type Material.— Holotype male, labeled "BRASIL, T. Pimental col., Reserva Ducke, Manaus, Am., 4-VII-1970." Type deposited at the United States National Museum.

Holotype.— Length 10.1 mm; width across pronotum 5.0 mm; width across humeri 4.4 mm. Body shape rectangular, strongly dorso-ventrally compressed. Color reddish brown, margins piceous. *Head*: Surface smooth, impunctate. Clypeus distinctly, broadly emarginate at center. Eye twice as long as wide in dorsal view. Mentum with disc smooth, impunctate. Antenna with eight segments; club large, loose. *Pronotum*: Surface smooth, impunctate; each side with two extremely fine rugae extended parallel to lateral margin and single ruga extended obliquely across anterior angle from side of pronotum to base of head behind eye. Sides and base with marginal bead, lateral margins broadly explanate. Scutellum small, subsemi-oval. *Elytra*: Surface with six interneurs between suture and humerus; interneurs moderately, deeply impressed, weakly punctate within, punctures obsolete at apical declivity. Intervals smooth, impunctate. Lateral margin narrowly explanate. Humerus with small, feeble tooth externally. *Legs*: Femora and tibiae about 2/3 as wide as long in ventral view; surface impunctate, without setae. Foretibia (fig. 5) with three weak, but distinct, longitudinal ridges on dorsal surface and five or six on ventral surface; apex with two strong teeth, lateral margin with five minute serrations. Foreleg with tarsomeres 1-4 subequal in length, tarsomere 5 longer than rest together. Meso- and metatarsi each with segments fused into single segment.

Derivation of specific epithet.— From the Greek *akomos* meaning without hair. So named because of its glabrous body surface (relative to *B. alvarengai*).

Remarks.— Adults of *Brasilucanus acomus* are separated from those of *B. alvarengai* by the absence of punctures or setae from head, pronotum, elytral intervals, disc of the mentum, and ventral surfaces of the femora and tibiae.

The generic diagnosis originally given by Vulcano and Pereira (1961) for *Brasilucanus* included setigerous punctures of the dorsum and venter. This distinction is reduced to species-level significance in view of the lack of setigerous punctures on *B. acomus* adults. The



Figs. 2-3. Antennal club of *Penichrolucanus leveri* and *Brasilucanus alvarengai* respectively (after Vulcano and Pereira, 1961).

Fig. 4. Anterior tibia of *Penichrolucanus nicobaricus* (after Arrow, 1935).

Fig. 5. Anterior tibia of *Brasilucanus acomus*.

Fig. 6. Anterior leg of *Penichrolucanus leveri*.

Fig. 7. Posterior leg (ventral view) of *Brasilucanus alvarengai* (after Vulcano and Pereira, 1961).

Fig. 8. Posterior leg (ventral view) of *Penichrolucanus leveri* (after Vulcano and Pereira, 1961).

principal differences between *Brasilucanus* and *Penichrolucanus* are: (1) the mandibles are exposed in *Penichrolucanus* and hidden in *Brasilucanus*; (2) femora and tibiae are very broad in *Brasilucanus* (fig. 7) while much less so in *Penichrolucanus* (fig. 8); and (3) the club of the antenna is consistently more compact and shorter in *Penichrolucanus* (fig. 2) than *Brasilucanus* (fig. 3).

The specimen of *B. acomus* was taken in July during the dry season in this area. It is unknown how the specimen was collected, but it was probably taken from dead wood or by surface gleaning. Light trapping was rarely, if at all, conducted at the type locality in 1970 when the specimen was collected. Moreover, I collected extensively at Reserva Ducke over a two year period with light traps, pitfall traps, and surface gleaning and failed to collect any additional specimens. This attests not only to the rarity of this species but also to the fact that adults do not come to lights.

SYNOPTIC CHECKLIST OF THE PENICHROLUCANINAE

<i>Penichrolucanus copricephalus</i> Deyrolle 1863: 483.	Malaya
<i>Penichrolucanus elongatus</i> Arrow 1935: 122.	Malaya
<i>Penichrolucanus leverii</i> Arrow 1938: 61.	Guadalcanal, Solomon Islands
<i>Penichrolucanus nicobaricus</i> Arrow 1935: 123.	Nicobar Islands
<i>Penichrolucanus sumatrensis</i> Arrow 1935: 124.	Sumatra
<i>Brasilucanus alvarengai</i> Vulcano and Pereira 1961: 475.	Amazonian Brazil, Guyana
<i>Brasilucanus acomus</i> Ratcliffe, n. sp. 1984: 63.	Amazonian Brazil

PHYLOGENY

Introduction

Phylogenetic relationships among these stag beetles have not been previously addressed. Indeed, the higher classification of the Lucanidae in general is unsettled (Holloway, 1960; Moore, 1978). I believe, however, that it is not premature to propose such relationships even though data for these organisms are few. It may even be advantageous to formulate such a relationship hypothesis now to stimulate further interest in these elusive beetles. Assuming further specimens and data are forthcoming, then our phylogenetic considerations will grow by accretion. The added benefit of this is, of course, that new data will provide a test of congruity for any preceding hypothesis. I propose a hypothesis of relationship based upon which animals share derived states of the same homologous character (synapomorphies). The operational philosophy for establishing this hypothesis is that of Hennig (1966) and the many subsequent developers of cladistic methods.

Character Analysis

Adults within this subfamily all share peculiar modifications. The independent appearance of these non-lucanid structures in two separate groups of Lucanidae seems extremely improbable and so the Penichrolucaninae are viewed most parsimoniously as a monophyletic lineage. The characters that bind the taxa together in a phylogenetically unified lineage are: (1) the dorso-ventrally compressed body; and (2) the peculiar form of the tarsomeres which are fused into a single segment in the meso- and metatarsi. No other lucanid adults possess body form and tarsal characters like those seen in the Penichrolucaninae. Because penichrolucanines are so unique, they warrant subfamily status as proposed by Arrow (1949) and reiterated by

Benesh (1960). Didier and Séguéy (1953) (possibly only following Roon [1910]) placed the penichrolucanines in the Figulinae, but I cannot agree with this because of their unique characters.

Characters and their states were derived from specimens of *Brasilucanus* and *Penichrolucanus* and from a careful analysis of the literature for *Penichrolucanus*. There is an inherent disadvantage in obtaining character data from literature sources, particularly when descriptions are brief or do not describe the same characters. Fortunately, a single author described all but one of the *Penichrolucanus* species, and these narratives were detailed enough to establish character states. Three species on the cladogram lack apomorphies, and this is attributed to failure to find suitable characters because of a lack of specimens in series from which to glean data. Four of the seven species are known from only a single specimen. I believe that synapomorphies do exist for these species, but that more material for study is necessary to ascertain what they might be.

The out-group method of Watrous and Wheeler (1981) was used to polarize characters into ancestral and derived states. The sister group of the Penichrolucaninae has not been identified. Character polarizations were based largely on the Figulinae as the out-group because the Figulinae share more morphological affinity with the Penichrolucaninae than any other subfamily. While this may not show relationship in and of itself, it is suitable for the comparisons of characters. The remainder of the Lucanidae was used as the broader out-group when both states of a character were encountered in the Figulinae. Characters and their polarities are shown in Table 1.

Characters

Distinctly depressed body form (apotypic state of character 1) and fused tarsomeres in the meso- and metatarsi (apotypic state of character 2; figs. 7-8) are possessed by all the taxa in this group, and this binds them together in a monophyletic lineage. No other lucanid adults possess these character states. The gena (character 3) is greatly expanded and laterally flared, and this is viewed as apotypic. All species have this character state except *P. leverii* which has secondarily lost it. Eyes (character 4) are interpreted for these beetles as derived when dorsally large as in *Penichrolucanus* as opposed to the small eyes of *Brasilucanus*. Small eyes in lucanids are not always plesiotypic as exemplified by South African *Colophon* species which have secondarily reduced eyes and wings and are restricted to mountain summits. Mandibles (character 5) are exposed in all lucanid adults except those of *Brasilucanus*, a state that is interpreted as plesiotypic for *Penichrolucanus*. Hidden mandibles in *Brasilucanus* are unique and, therefore, apotypic. The presence of two tubercles on the head (character 6) in *P. nicobaricus* and *P. sumatrensis* is synapotypic. The figuline *Caprinigidius trifurcatus* Didier and some species of *Figulus* possess one or three tubercles on the head, but a bituberculate head is lacking. A small, compact antennal club (character 7; fig. 2) is plesiotypic (*Penichrolucanus*), and a more open, looser club (fig. 3) is apotypic (*Brasilucanus*). The more primitive scarabaeoid adults have a small, compact antennal club.

The apex of the protibia (character 8) is autapotypically bifid (fig. 4) in *P. nicobaricus*; this form of tibial apex was not seen in the Figulinae. Large, distinct, external teeth on the protibia (character 9; fig. 6) is considered apotypic on an *ad hoc* basis. Absence or presence of such teeth are both widespread in the family, and a more detailed analysis needs to be undertaken in order to resolve this polarity problem.

Table 1. Penichrolucaninae characters: plesiotypic and apotypic states.

No.	Character	Plesiotypic	Apotypic
1	Body convexity	convex	depressed
2	Tarsomeres	segments normal	segments fused
3	Gena	normal, rounded	laterally expanded
4	Eye size	small	large
5	Mandibles	exposed	covered
6	Tubercles on head	absent	present
7	Antennal club	small, compact	large, loose
8	Protibial apex	not bifid	bifid
9	Protibial teeth	weak, small	strong, large
10	Mid-metabial teeth	absent	present
11	Width of femora	slender	broad
12	Width of tibiae	slender	broad
13	Metatibial length	long	very short
14	Pronotal punctation	present	absent
15	Punctation of interneurs	absent	present
16	Dorsal setae	absent	present

I interpret the presence of several small teeth just behind the middle of the meso- and metatibia (character 10) as apotypic, a state present in all the penichrolucanine taxa except *P. leveri* (which is geographically isolated in the Solomon Islands) and *Brasilucanus*. Extremely wide femora (relative to length; character 11; fig. 7) are apotypic in *Brasilucanus* because no other lucanids possess such highly aberrant femora. Similarly, the marked width of the tibiae (relative to length; character 12; fig. 7) is apotypic as opposed to the more conventional, slender lucanid tibiae (fig. 8). All *Penichrolucanus* adults, except those of *P. leveri*, show a slight widening of the tibiae that becomes even more derived in *Brasilucanus*. Length of the metatibia (character 13) is considered apotypic when it is very short, and this constitutes a reduction of a once longer tibia. Only *P. elongatus* retains this character in a plesiotypic state. The tibia is considered long if its inside length is at least as long as the length of the pronotum.

The absence of pronotal punctures (character 14) is autapotypic and is seen only in *B. acomus*. The remainder of the Penichrolucaninae, as well as the outgroup, possess distinct pronotal punctation to some degree. Punctation within the elytral interneurs (character 15) is plesiotypic because this character is commonly found in the out-group. The presence of pronotal and elytral setae (character 16) is rare in the Lucanidae; presence of setae in *B. acomus* is autapotypic within the Penichrolucaninae.

Phylogenetic Relationships

In table 2 are listed the character state distributions for the taxa of Penichrolucaninae. A cladogram was produced (fig. 9) based on this set of character state distributions. The cladogram was constructed using the assumption that the most parsimonious arrangement of shared, derived character states with the fewest homoplasies (parallelisms, reversals) best infers genealogical relationship.

Table 2. Characters and Distribution of Phylogenetically Classified Character States¹ among the Species of Penichrolucaninae

No.	Character	Species ² and Character States						
		aco	alv	nic	cop	eln	sum	lev
1	Body convexity	1	1	1	1	1	1	1
2	Tarsomeres	1	1	1	1	1	1	1
3	Gena	1	1	1	1	1	1	0
4	Eye size	0	0	1	1	1	1	1
5	Mandibles	1	1	0	0	0	0	0
6	Tubercles on head	0	0	1	0	0	1	0
7	Antennal club	1	1	0	0	0	0	0
8	Protibial apex	0	0	1	0	0	0	0
9	Protibial teeth	0	0	0	0	0	1	0
10	Mid-metatarsal teeth	0	0	1	1	1	1	0
11	Width of femora	1	1	0	0	0	0	0
12	Width of tibiae	1	1	1	1	1	1	0
13	Metatarsal length	1	1	1	1	0	1	1
14	Pronotal punctation	1	0	0	0	0	0	0
15	Punctation of interneurs	1	1	1	1	0	1	0
16	Dorsal setae	0	1	0	0	0	0	0

¹Scores for character states: 0=plesiotypic; 1=apotypic.

²Abbreviations for specific epithets: aco=*acomus*; alv=*alvarengai*; cop=*copricephalus*; eln=*elongatus*; lev=*lever*; nic=*nicobaricus*; sum=*sumatrensis*.

Ranking of *Brasilucanus* and *Penichrolucanus* as genera is justified because the phyletic distance between them is broad; *Brasilucanus* has significant character states not shared by *Penichrolucanus*. It is not surprising that the two New World species have the most synapotypies, and it is not surprising that they cluster as sister species.

Penichrolucanus lever retains the most ancestral character states in the Old World taxa, which is in keeping with isolation and severely restricted gene flow from the parent stock in the region of the Malay Peninsula. The reduced genetic interchange in such isolated taxa permits retention of more ancestral character states. The four remaining Old World species are more derived than *P. lever*, more tightly clustered geographically, and probably have experienced greater or more recent gene flow amongst themselves. *Penichrolucanus nicobaricus* is not excluded from this interchange because the islands on which it occurs are not remote, isolated, oceanic islands but share the Asian continental shelf with the Malay Peninsula and Sumatra. Based on the current, limited data, synapotypies were not found for *P. copricephalus*. In spite of this, I have formed the cladogram to reflect what I believe to be the correct branching sequence for this species instead of showing its node as a trichotomy with *P. nicobaricus* and *P. sumatrensis*. This *ad hoc* hypothesis can be tested when further character data become available.

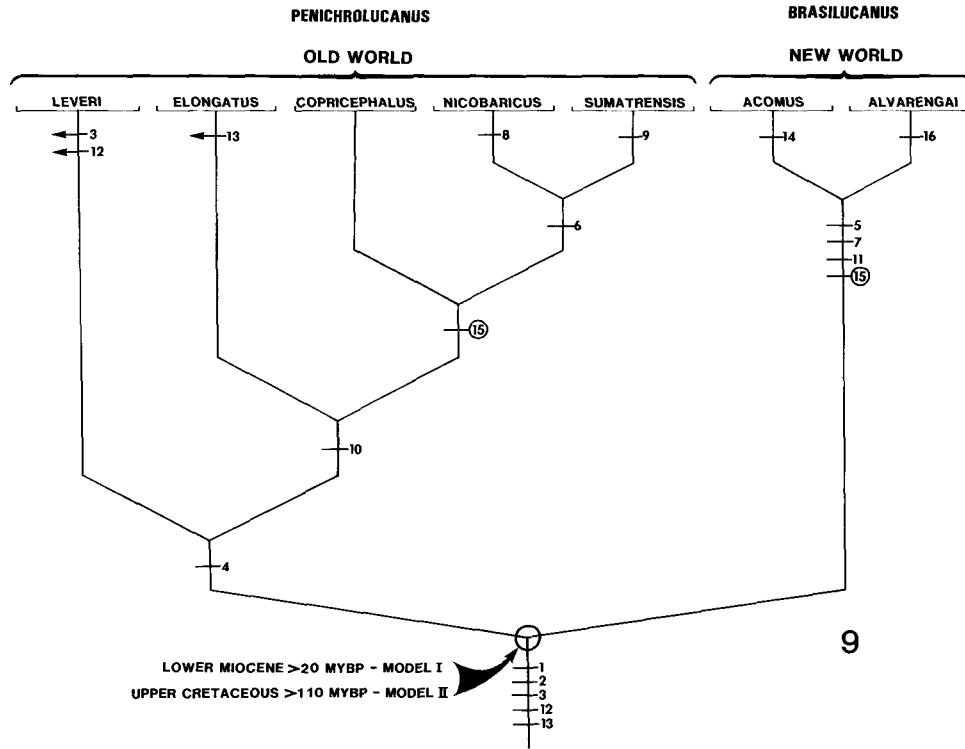


Fig. 9. Cladogram with proposed genealogical relationships of the species of Penichrolucaninae. Numbers refer to apotypic characters; horizontal lines indicate character advancement; arrows show character reversals.

BIOGEOGRAPHY

Life, unlike the inanimate, will take the long way round to circumvent barrenness --- L. Eisely.

Penichrolucanus and *Brasilucanus* are separated from one another by a world. How did this disjunct distribution happen given the monophyletic origin of the lineage? Fossil Penichrolucaninae are unknown, and it is not unreasonable to predict that they probably never will be found. Without fossil data, it becomes necessary to use a synthesis of data from plate tectonics, present and paleodistributions of other plants and animals, and phyletic relationships within the penichrolucanines to formulate a model to best explain the current distribution of these beetles. "It is a normal practice in science to infer from what is better and more completely known in order to discover the structure and the meaning of that which is less well or only partly known. The similarity of facts known on both sides of a controversy suggests that the best documented will be taken as a good model for the reconstruction of the structures still unknown on the other side" (Lavocat, 1980: 93). Ball (1975) also advocates deductive approaches to biogeographical reconstructions rather than narrative, inductive methods. I have



Fig. 10. Distribution of the species of *Brasilucanus*.

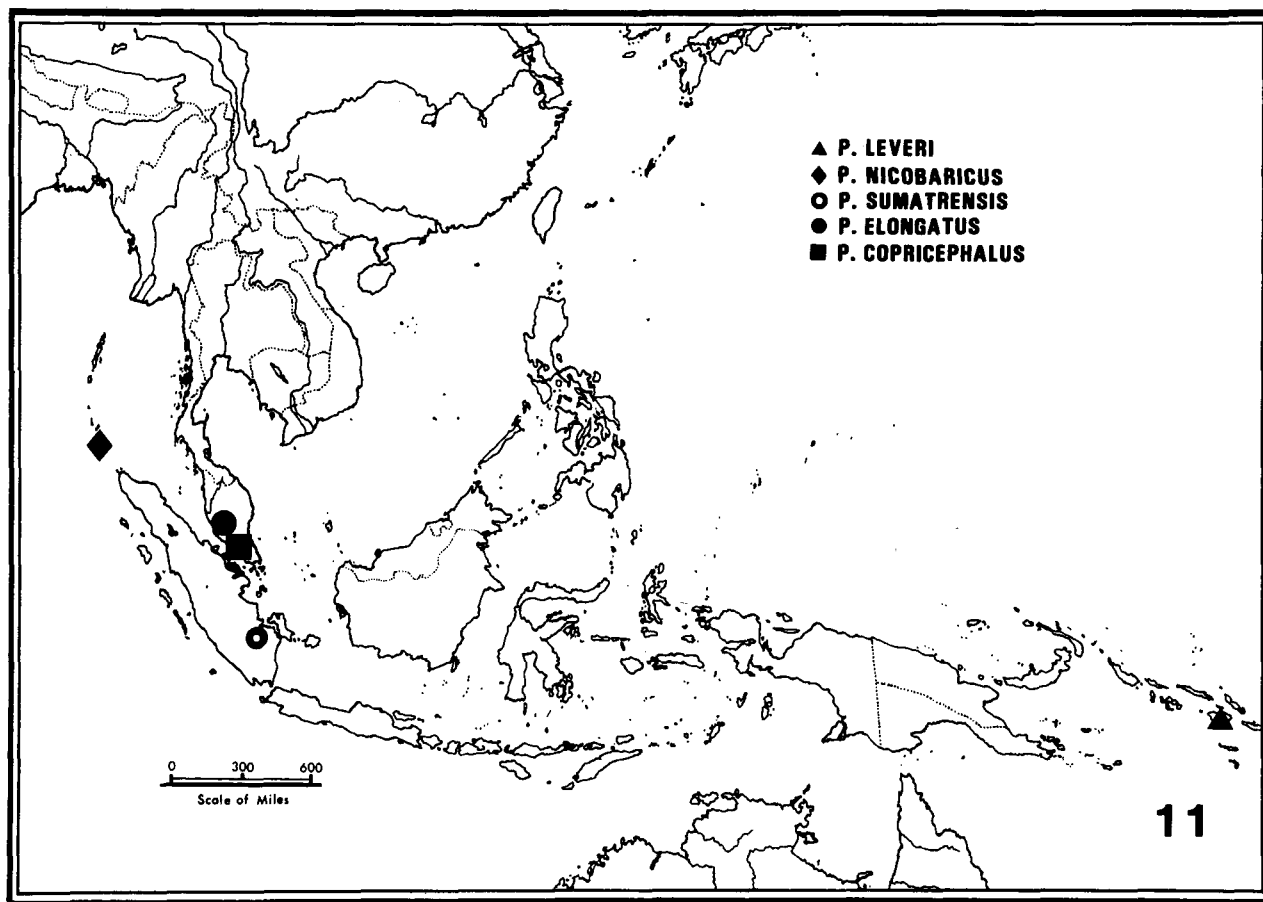


Fig. 11. Distribution of the species of Penichrolucanus.

attempted to follow these precepts.

Distribution of the Penichrolucaninae is shown in figs. 10-11. *Brasilucanus* is Neotropical, and *Penichrolucanus* is tropical Asian with one species crossing Wallace's Line to the Solomon Islands in the western Pacific. Two quite different models are proposed to explain the current distribution of these beetles. Each model is a maximum parsimony hypothesis, congruent with the cladogram, and is a blend of vicariance and dispersal paradigms of biogeography. Plate tectonics, as exemplified by sea floor spreading and continental drift, is implicitly assumed in this study.

Model I: Holarctic Origin

Within the framework of this model, the synthesis of data from other plants and animals, geology, and paleoclimatology favor the basal stock of the Penichrolucaninae being present in Holarctica, specifically either North America or eastern Asia, at least prior to the middle Miocene approximately 20 MYBP (million years before present) (figs. 12-13). Whether ancestral penichrolucanines originated in Asia or North America is unknown and probably unresolvable. It is of interest to note that North America has eight genera of Lucanidae, Latin America has 16 genera, Africa has nine genera, and Asia has 37 genera (Roon, 1910). Similar large differences favoring Asia at the species level are also present. Origins aside, it seems that the greatest *radiation* of Lucanidae has been in Asia.

Dispersal of ancestral Penichrolucaninae via Beringia occurred from Asia to America or *vice versa*. MacGinitie (1969), citing the distinct subtropical Asiatic element in the Eocene flora of the west coast of North America typified by the genera *Alangium*, *Canarium*, *Cinnamomum*, *Columbia*, *Cryptocarya*, *Mastixia*, *Neolitsea*, *Phytocrene*, and *Terminalia*, concluded that there must have been active dispersal around the northern Pacific in the early Tertiary. He continued by noting that this dispersal route is further indicated by the genera *Acalypha*, *Cissampelos*, *Chrysophyllum*, *Lucuma*, *Meliosma*, *Symplocos*, and others which occur as fossils in the Goshen and La Porte floras and which are both Neotropical and Palearctic in their present distribution. This distribution suggests strongly a much wider area of occupancy in the past, and this and similar evidence led MacGinitie (1969), Leopold and MacGinitie (1972), Dorf (1957) and others to conclude that a large area of subtropical to tropical forests once extended from the American tropics around the northern Pacific to the Asian tropics during the Paleogene.

There exists a distinct faunal similarity (suggesting warm climates) within the vertebrates between Asia and North America by the middle Miocene (proboscideans, primates, *Alligator*). Tapirs (order Perissodactyla) provide strong evidence for a subtropical to tropical dispersal route around the northern Pacific. Tapirs are and were primarily warm climate animals and are the only extant mammals found exclusively in the Asian and American tropics. Penichrolucaninae are also found only in the Asian and American tropics. Fossil evidence indicates tapirs were once much more widespread than they are today. Early tapiroids are found in Eocene and Oligocene deposits in North America, Mongolia and Korea (Radinsky, 1963), and true tapirs are found in the Miocene and later of Eurasia and North America (Romer, 1945; Schultz *et al.*, 1975). Tapir evidence indicates that there was good faunal interchange between North America and Asia in the late Eocene to early Oligocene. A complex pattern of alternating periods of faunal linkage and isolation between these two areas began in the Oligocene due to climatic changes and fluctuations in sea levels (Colbert, 1974; Cox, 1974). Beginning in the mid to late Miocene, climatic conditions were becoming too cool to permit

Genozoic	Quaternary	Pleistocene and Recent	1.8
	Tertiary	Pliocene	7
		Miocene	26
		Oligocene	37.5
		Eocene	53.5
		Paleocene	65
Mesozoic	Cretaceous	Upper Cretaceous	100
		Lower Cretaceous	136
	Jurassic	Upper Jurassic	162
		Middle Jurassic	172
		Lower Jurassic	192.5
	Triassic	Upper Triassic	205
		Middle Triassic	215
		Lower Triassic	225
	Paleozoic	Permian	Upper Permian
Lower Permian			280

12

Fig. 12. Geologic time scale from Permian to present. Numbers at right refer to age at beginning (MYBP). (after Seyfert and Sirken, 1973).

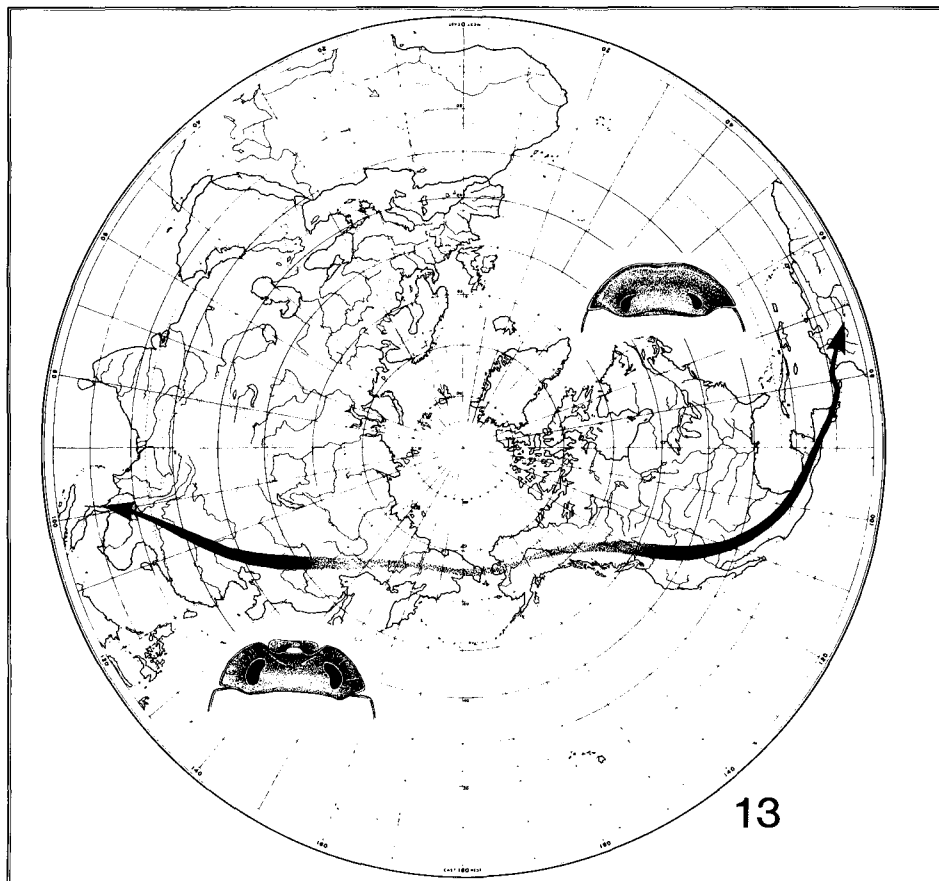


Fig. 13. Model I interpretation of biogeography showing generalized track of initial Holarctic radiation with subsequent retreat to tropical Malesia and tropical South America. Heads shown are *P. sumatrensis* and *B. acomus*.

dispersal of subtropical to tropical organisms between northern Asia and America (Michael Voorhies and Robert Hunt, personal communication, 1983). Warm climate plant and animal taxa retreated southwards. Tapirs, and presumably ancestral penichrolucanines, became extinct by the Pleistocene in what is now north temperate Asia and America, but they continued as relictual populations in tropical Asia and America.

In Asia, tapirs (one species) and penichrolucanines (five species) found refuge largely in tropical Malaya. In the New World, tapirs (three species) and penichrolucanines (two species) retreated southward to Central and South America. The closure of the Bering land corridor (due more to climate than physiography) marks the point of the *Brasilucanus*/*Penichrolucanus* dichotomy. All subsequent evolution of the *Brasilucanus* lineage in North America and their

eventual dispersal into South America would have occurred as an independent and parallel event to the evolution of the *Penichrolucanus* lineage in Asia and its dispersal into Malaya.

I believe this model acquires added significance because of the similarities (distribution, climatic and habitat requirements) between these beetles and the tapirids. Tapiridae have a known fossil record which enables reconstruction of their history, and the similarities allow for cautious extrapolation to the Penichrolucaninae. Tapirid history (as well as that for many other Eurasian-American animals and plants) clearly indicates dispersal via Beringia to explain the overall pattern in distribution of higher taxa. Intracontinental vicariance can then account for many of the distributions of the lower ranking taxa.

New World.— Tapiridae penetrated South America in the late Pliocene (Keast, 1972a) in separate invasions at widely separated periods when climates and topographic features were different (Hershkovitz, 1972). About half of the extant Neotropical genera of mammals are derived from late Pliocene or Quaternary North American invaders (Keast, 1972a). Pre-Miocene dispersal of vertebrates between North and South America occurred probably uncommonly through a filter route according to the fossil record. This reduced amount of interchange agrees with the geologic evidence suggesting a relatively wide separation of the Americas in Cretaceous through Oligocene times (Gose *et al.*, 1980; Raven and Axelrod, 1974; Smith and Briden, 1977). An extensive faunal exchange occurred from the Pliocene on as Mesoamerica coalesced from a peninsula and islands (Woodring, 1954) comprising a sweepstakes dispersal route to a definite land bridge in the Pliocene approximately 5.7 MYBP (Lloyd, 1963). Formation of just such a dispersal route allowed for entry into South America of Nearctic, ancestral penichrolucanines.

The modern mammalian fauna of the Amazon Basin seems derived from the Brazilian and Andean uplands (Hershkovitz, 1972). Similarly, Camp (1952) stated that the flora of the central Amazon Basin was derived from surrounding uplands, and that it is a recent flora (late Pliocene or Pleistocene) characterized by many groups with often inadequately delimited genera and species. The relatively recent nature of the largely upland-derived fauna and flora is partially a result of the periodic marine transgressions in the Amazon Basin during the Pliocene and pluvials of the Pleistocene. Post-inundation, hence recent, invasion of the Central Amazon valley by Penichrolucaninae is indicated. The South American collecting sites for these beetles are all less than 100 meters in elevation and were probably submerged at times of high water during the Tertiary/Quaternary transition.

Lastly, the proposed Amazonian forest refugia of the Pleistocene (Brown *et al.*, 1974; Brown, 1977; Haffer, 1969, 1978, 1982; Müller, 1973; Prance, 1973, 1982; Simpson and Haffer, 1978; Tricart, 1974; Vuilleumier, 1971) undoubtedly affected penichrolucanine beetles. The refuge theory, in essence, states that during the Quaternary, lowland rain forests contracted during dry periods (glaciations usually) while savannas and other nonforest biotopes expanded. During wetter times the rain forests again expanded, and the nonforested grassland regions contracted. Each of the periods of the contraction can be viewed as a vicariance event that led to certain extinction for some species and potential speciation within other taxa. Subsequent expansion of forests allowed dispersal of previously isolated taxa. Duellman (1982), Livingstone (1982), Lynch (1982), and especially Endler (1982a, b) question the refuge theory and suggest that events other than Pleistocene forest contractions and expansions could be responsible for the present day diversity and distributions of the descendent tropical biota. Although distribution of a taxon in and of itself is inadequate support for the refuge theory, the increasing evidence provided by geomorphology, palynology, and paleoclimatology give

additional credence to this interpretation.

Penichrolucanine beetles are extremely rare today. Severe disruption of a formerly more continuous range during Pleistocene times due to climatic change accords well with their patchy distribution and rarity. The present distribution of *Brasilucanus* has a remarkable similarity to Haffer's (1969) bird refuges, Prance's (1982) angiosperm refuges, and to the Pleistocene vegetational refuges proposed by Ab'Sáber (1982) which were based on geological, climatological and pollen data. Penichrolucanines may be patchy in their distribution because they have not been able to disperse far from their hypothetical Pleistocene refuge areas where they occur today as endemic relicts. Failure to colonize or re-colonize after Pleistocene disruption of habitat or competitive exclusion by other animals would both help to account for current patchiness and rarity. New discoveries of *Brasilucanus* in South America would provide much needed additional data with which to test these suppositions. Even though the correlation between these proposed refuges and the distribution of *Brasilucanus* is tantalizing, I feel that these centers of diversity and endemism require further paleontological evidence to prove that they are indeed the result of Pleistocene refugia.

Asia.— While dispersal from the Holarctic source area may have begun in the late Eocene to early Oligocene, arrival at and radiation in the Sunda region was a later event. Establishment of Penichrolucaninae in Malaya and Sumatra by at least Miocene times is considered tenuous because much of this region was not even permanently emergent until the Miocene when the northward-moving Australian plate arrived in the vicinity of the Asian plate (Beaufort, 1951; Raven and Axelrod, 1972, 1974; Schuster, 1972; Umbgrove, 1938).

Sumatra, Java, and Borneo are separated from one another and from mainland Asia by shallow seas, many less than 100 meters in depth. Pacific sea levels fell as much as 100-180 meters below present depths during Pleistocene glacial maxima (Audley-Charles and Hooijier, 1973; Biswas, 1973; Geyh *et al.*, 1979; Keast, 1972b; Kuenen, 1950; Verstappen, 1975; Walker, 1982), and much of today's Sunda and Sahul island region was interconnected by dry land or by much larger islands with smaller water gaps. Ancestral Penichrolucaninae would have been able to disperse from mainland Asia over a land corridor or by a series of island stepping stones to the Sunda region. This is certainly so for many vertebrates (Sartono, 1973). Proboscideans, for example, dispersed from Indomalaya to Java, Borneo, Celebes, and Timor (Hooijier, 1967) and even to Mindanao and Luzon in the Philippines (Johnson, 1980). Fossil hippopotomids and giraffids are also known from the Pleistocene of Java (Hooijier, 1975; Keast, 1972b; Medway, 1972). Further, plant geographers have considered the ranges of the Southeast Asian endemic Dipterocarpaceae as good indicators for the existence of former land connections because of their limited powers of seed dispersal (Meijer, 1974). The subsequent rise of sea levels to current depths then fractured and isolated populations, restricted gene flow, and contributed to speciation in the biota of the entire Malayan region.

During the Pleistocene dry cycles, the Malesian¹ islands preserved a great part of the widespread mid-Miocene tropical flora (Meijer, 1982) and presumably fauna. There is growing evidence to indicate that during this period the lowland dipterocarp forests of the Malay Peninsula, Borneo, and Sumatra were preserved as a humid refuge surrounded on the east by

¹"Malesia", a Dutch term, is used for the area including Malaya (south of the Kra isthmus) and the islands commonly referred to collectively as the Indo-Australian Archipelago. This usage of Malesia in biogeography follows Walker (1982: 559, Fig. 30.4) and others.

an arid corridor which extended from Celebes to Java and the Lesser Sunda Islands (Meijer, 1982). This proposed plant refuge corresponds with the present distribution of the Penichrolucaninae in Malesia just as there is a similar conjunction of these beetles and proposed refuges in the Neotropics.

In view of documented swimming powers of modern elephants, Johnson (1980) argued cogently that historical insular biogeographies (such as in Malesia) may have to be re-evaluated, particularly when these reconstructions depend on the presence of proboscideans (again, as in the East Indies) to imply land bridges. The hypothesis proposed here does not require land bridges but only significant narrowing of water gaps. In so doing, the hypothesis of dispersal becomes not only more parsimonious, but also much more likely to have actually occurred. This is, I believe, in accord with known historical geology for the region and accommodates Johnson's concern for insular paleogeographic scenarios using proboscidean data.

The predominantly tropical fauna of the Sunda region is continental Asian almost completely and demonstrates clearly the pathway the Penichrolucaninae used to reach Sumatra, the continental Nicobar Islands, and possibly other areas in the Greater Sunda Islands and the Moluccas. Additional taxa of these beetles may yet be awaiting discovery in this region as well as in mainland Indochina.

Western Pacific.— *Penichrolucanus leveri* occurs on Guadalcanal in the Solomon Islands. The Solomons are an oceanic archipelago and have never been connected with New Guinea or the Indonesian islands to the west. This island arc evolved from a series of oceanic, volcanic welts which started to shoal in the Miocene (Hackman, 1971; Quantin, 1971; Tarling, 1971). Due to their late origin, the biota of these islands has a distinct immigrant pattern of dispersal of Indomalesian taxa which were carried to the Solomons across water barriers and *via* New Guinea (Darlington, 1957; Keast, 1972b; Raven and Axelrod, 1972).

Many lucanids seem to be good overwater dispersers (Howden, 1981) and one monobasic genus, *Apterochylus* Waterhouse, has even reached the Hawaiian Islands. The prevailing modern surface currents for the East Indies are essentially from Malaya, Sumatra, and Borneo eastward toward New Guinea, the Bismarks, and the Solomons. It is postulated that ancestors of *P. leveri* rafted to the Solomons from the Malayan source area. This reconstruction implies that actual over water dispersal would need to occur only from the then terrestrial, confluent Greater or Lesser Sunda Islands on the Asian continental plate across the Banda Sea to New Guinea on the Australian continental plate and then to the Solomons. The rationale for this route is that lowered sea levels during the Pleistocene permitted terrestrial (or nearly so) connections among many of the Malesian islands. Considering that Guadalcanal is Miocene in age, then colonization must have occurred later than this. It could be inferred that this colonization was not a recent event because the primitive character states retained by this species suggest long isolation from the parent stock.

Model II: Gondwanan Origin

This model proposes that the Penichrolucaninae are a much older lineage with origin and initial radiation in Gondwanaland. This would have happened at least prior to 110 MYBP which coincides with the early Albian break between Africa and South America (Dietz and Holden, 1970; Tarling, 1971; Veevers *et al.*, 1971). Although fossil plant and animal data tend to support this hypothesis, the fact remains that these beetles are unknown in Africa. This does not necessarily falsify the model of origin, but makes it slightly less acceptable in view of the

weight of the present evidence. It is presented as an alternate hypothesis based on the contingency that penichrolucanines now inhabit or once inhabited Africa. Figures 14-16 show the position of the continents resulting from drift and illustrate how ancestral Penichrolucaninae became isolated from one another.

South America.— The ancestors of *Brasilucanus* became separated from the African penichrolucanines by the rifting between South America and Africa. Ancestral *Brasilucanus* evolved in isolation during South America's long westward drift and developed unique character states not found in other members of the subfamily. As explained previously in the first model, Pleistocene forest refugia may have been the principal means by which the Penichrolucaninae survived in South America during past times of great climatic and ecological disruption. Hypothetical African taxa may not have been so fortunate.

Africa.— Penichrolucaninae are not known from Africa. Within the framework of this model, they should have occurred there in the past or may yet remain there undiscovered. If representatives of this group still exist in Africa, then they would probably be restricted to areas of wet rainforest like their American and Asian relatives. With these assumptions of habitat preference, penichrolucanines could be expected to occur only in the forested areas of extreme southern Ivory Coast, Ghana and Nigeria, the Cameroons, and the Congo and Ubangi River drainages. Coincidentally, these areas are similar to Laurent's (1973) postulated refuge areas of African lowland tropical forests.

Conversely, penichrolucanines may be extinct in Africa. Raven and Axelrod (1974) proposed a model reconstructing humid forests covering virtually all of Africa (except the south) until the Neogene (26 MYBP). These forests, extending over what is now the Sahara desert, could have been suitable habitat to ancestral Penichrolucaninae. Raven and Axelrod continue by characterizing the Miocene onward as a time of massive African extinctions resulting from dramatic climatic changes. Eastern Africa was uplifted approximately 2,400 meters since the Miocene, and arid climates have spread over the continent. Also beginning in the Miocene, the Benguela current brought cold water to the west coast of Africa. The changing climate subjected an area covered with rainforest to only seasonal precipitation. Moreover, the trend toward aridity was increased by Pleistocene arid cycles, a phenomenon further reducing the extent of tropical rainforests. Extinctions among the African biota were pronounced during the Neogene and later times, and these authors conclude that it is not surprising that Africa has the most impoverished of all tropical biotas. Livingstone (1982) noted that there has been no period of long stability for African forests.

Asia.— The position of Asia *vis-a-vis* Gondwanaland as well as Asian paleoclimates remain largely unknown. There may have been only poor links to Gondwana, but geological and paleontological studies are still inadequate in quality and quantity to position this area unambiguously relative to the other continental blocks (Tarling, 1980). How, then did the Penichrolucaninae get to Asia if they had a Gondwanaland origin? The history of distribution of elephants may help provide the answer.

Africa was variably joined to Europe prior to the early Paleocene, 63 MYBP (Dietz and Holden, 1970; Phillips and Forsyth, 1972; Pitman and Talwani, 1972; Smith, 1971). Dewey *et al.* (1973) suggested that Africa and Europe became more widely separated from the early Paleocene (63 MYBP) to about the upper Eocene (53 MYBP). Berggren and Couvering (1974) indicated that African reconnection with Eurasia may have occurred for a short period in the Eocene-Oligocene (approximately 40-35 MYBP). In any event, a close African-Eurasian connection was established in the middle Miocene about 18 MYBP (Cooke, 1972; Dewey *et al.*,

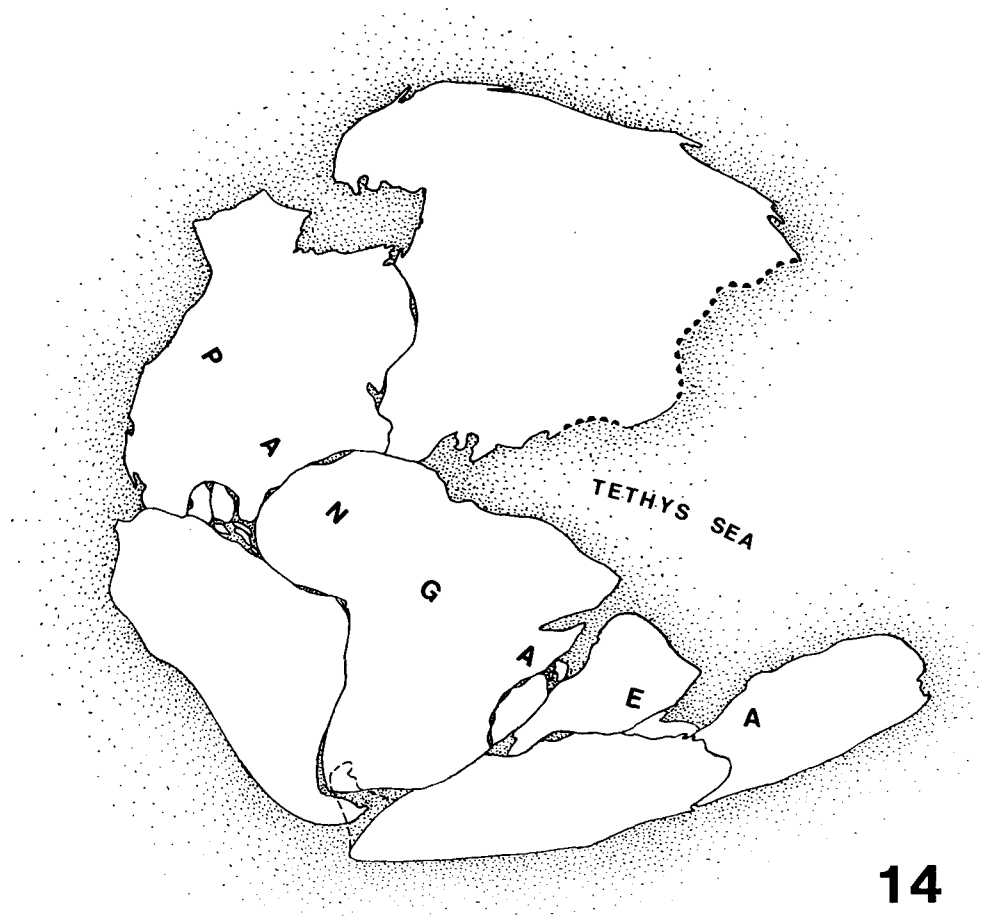


Fig. 14. Model II interpretation of biogeography. Continental drift (after Dietz and Holden, 1970). Reconstruction of Pangaea at the end of the Permian, 225 MYBP.

1973; Hallam, 1973) that ended Africa's long period of isolation from Eurasia. Eocene mammals of Africa are wholly endemic, but decreasing endemism is exhibited through the Oligocene and Miocene into the Pliocene, with the most frequented (if not the only) migration route being to and from western Asia (Coryndon and Savage, 1973). One of the best known groups, the proboscideans, first migrated to Asia in about early Miocene time; the later Miocene marks the time of strongest links for the whole mammal fauna (Hallam, 1981).

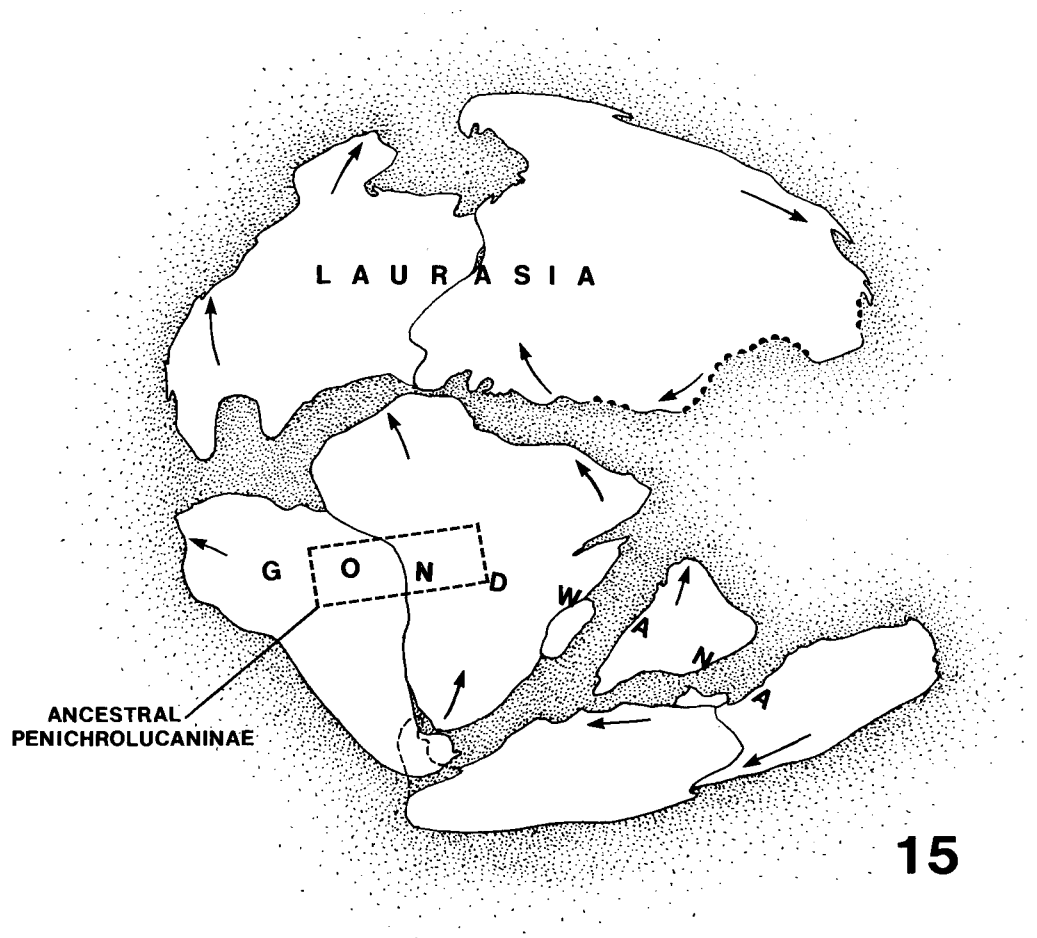


Fig. 15. Model II interpretation of biogeography. Continental drift (after Dietz and Holden, 1970). Initial rifting of Pangaea as of the end of the Triassic, 180 MYBP with proposed ancestral Penichrolucaninae established in Gondwana. Population boundary is simply to show occurrence on both continents.

This model suggests that the Penichrolucaninae dispersed from Africa to Asia. When they did this is unknown, but the middle Miocene and later is most suitable for this hypothesis for it was during this time period that there began an abundant interchange of organisms, particularly tropical organisms, between Africa and Eurasia. Proboscideans, hippopotamids, and giraffids, for example, dispersed from Africa to Indomalesia. These animals today are primarily savanna dwelling forms, but this is not considered true for their shorter limbed ancestors which occupied forests or gallery woodlands. Raven and Axelrod (1974) report an

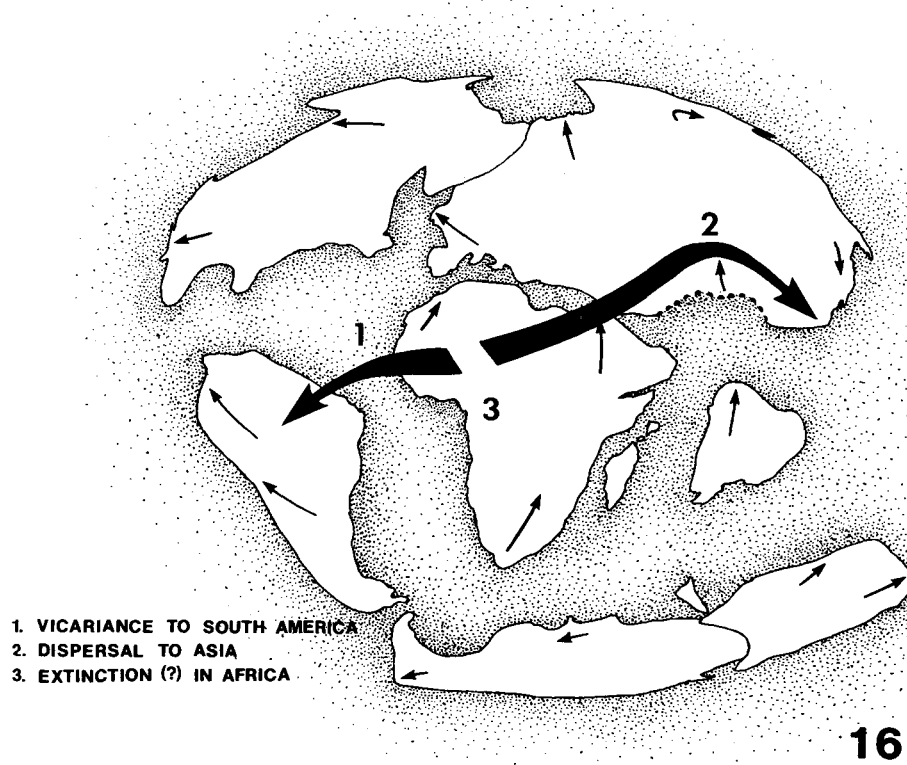


Fig. 16. Model II interpretation of biogeography. Continental drift (after Dietz and Holden, 1970). Continents as they appeared at the end of the Cretaceous, 65 MYBP and how rifting accounts for present day distribution.

almost complete floristic continuity at family and often generic level between Africa and Southeast Asia that indicates ease of migration between these two areas into early Paleogene time and again in the Neogene when overland connections were restored. Dispersal from the Malayan Peninsula to the islands of the Sunda region and then to the Solomons in the western Pacific would then be the same as already outlined in the first model.

REJECTED DISPERSAL HYPOTHESES

The preceding two biogeographic interpretations seem most likely to me based on evidence currently available. The following hypotheses are discussed and found unacceptable.

South American Origin

The data do not support a post-rifted, South American origin for the subfamily. To do so would imply upper Cretaceous dispersal to Antarctica and Australia that would then have taxa raft to Asia when the Australian and Asian plates collided in the Miocene. Although there has been substantial Malaysian biotic introgression to Australia, there has been virtually no movement from Australia to Malaysia (Carne, 1957; Keast, 1972b; Raven and Axelrod, 1974).

Radiation from South America into North America and then to Asia via the Bering Strait is another possibility. This route would require a post-Pliocene movement because it was not until this time that a Panamanian land bridge was established (5.7 MYBP) in Central America to permit dispersal from South America into North America. It is doubtful that a rainforest habitat would have been available to these animals at this time along the entire route. Such a route also implies rapid dispersal over a very long distance.

I believe both of these ideas are untenable in view of what we know of past and present animal dispersal and earth history.

Indian Rafting

India probably did not serve in the capacity of a Noah's Ark and raft the ancestors of *Penichrolucanus* from a Gondwanan origin to the shores of Asia. India drifted 9,000 km during 200 million years of isolation (Dietz and Holden, 1970) and crossed latitudinal belts of climate which led to widespread impoverishment of its indigenous biota (Raven and Axelrod, 1974). India collided with Asia by the middle Eocene, 45 MYBP (Powell and Conaghan, 1973). Upper Eocene mammal faunas there are distinctly Laurasian in character as is the Recent biota. Floristically, India has few endemics compared to other tropical regions (Raven and Axelrod, 1974). It seems apparent that the long period of Indian drift was characterized by conditions too harsh to permit survival of presumed rainforest inhabiting ancestors of *Penichrolucanus*, even if they did occur in India in the past.

Summary

- 1a. The Penichrolucaninae originally radiated from holarctic Asia or North America prior to the middle Miocene, approximately 20 MYBP. The subfamily is known from both the Old World and New World tropics implying antiquity for the group.
- 1b. Retreat to the tropical refuges of Indomalaysia occurred post-Miocene and to tropical South America post-Pliocene when water barriers were reduced or eliminated and as tropical climates in northern latitudes deteriorated. Both plants and tapirs in the Old and New Worlds demonstrate parallel distributions with the Penichrolucaninae.
- 2a. An alternate hypothesis suggesting a Gondwanan origin and radiation prior to the middle Cretaceous (approximately 110 MYBP) is not ruled out although it seems less likely due to absence of penichrolucanines in Africa.
- 2b. In this second model, occurrence in South America resulted from vicariance between Africa and South America. Representatives of the subfamily remain undiscovered or else are extinct in Africa. If still present in Africa, they would be found in the belt of tropical forests surrounding the Congo and Ubangi Rivers. The ancestors of *Penichrolucanus* dispersed from Africa to Asia, probably during the middle Miocene.
- 3a. Both models converge at this point to suggest dispersal to insular Malaya and Sumatra during periods of glacial maxima in the Pleistocene when sea levels were lowered in this area.
- 3b. The ancestors of *P. leverii* dispersed from a Sunda source to the Solomon Islands probably by sweepstakes dispersal no sooner than the Miocene (time of Solomons formation) and probably not later than the Pleistocene. Long isolation of this taxon is inferred by its retention of primitive character states.

4. The conclusions of the biogeographical analysis (either scenario) support, by congruence, the hypothesis of relationships proposed for the subfamily.

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LITERATURE CITED

- Ab'Sáber, A.N. 1982. The paleoclimate and paleoecology of Brazilian Amazonia. *In*, G.T. Prance (ed.), *Biological Diversification in the Tropics*, pp. 41–59. Columbia University Press, New York.
- Arrow, G. 1935. A contribution to the classification of the coleopterous family Lucanidae. *Transactions of the Royal Entomological Society of London* 83: 105–125.
- . 1938. Some notes on stag-beetles (Lucanidae) and description of a few new species. *Annals and Magazine of Natural History (Ser. 11)* 2: 49–63.
- . 1949. *The Fauna of British India Including Pakistan, Ceylon, Burma, and Malaya. Coleoptera, Lamellicornia, Vol. IV. Lucanidae and Passalidae*. Taylor and Francis, Ltd., London.
- Audley-Charles, M.G. and D.A. Hooijer. 1973. Relation of Pleistocene migrations of pygmy stenodonts to island arc tectonics in eastern Indonesia. *Nature* 241: 197–198.
- Ball, I.R. 1975. Nature and formulation of biogeographical hypotheses. *Systematic Zoology* 24: 407–430.
- Beaufort, L.F. de. 1951. *Zoogeography of the Land and Inland Waters*. Macmillan, New York.
- Benesh, B. 1960. *Coleopterorum Catalogus Supplementa*. Lucanidea (sic). W. Junk, Gravenhage.
- Berggren, W.A. and J.A. Van Couvering. 1974. Neogene geochronobioclimatopaleomagnetostatigraphy: a Mediterranean synthesis. *Abstracts and Papers, 1974 Annual Meeting of the Geological Society of America*, pp. 1022–1024.
- Biswas, B. 1973. Quaternary changes in sea-level in the South China Sea. *Bulletin of the Geological Society of Malaysia* 6: 229–255.
- Brown, K.S., Jr. 1977. Centros de evolução refúgios quaternários e conservação de patrimônios

- genéticos na região neotropical: padrões de diferenciação em Ithomiinae (Lepidoptera: Nymphalidae). *Acta Amazonica* 7: 75–137.
- _____, P.M. Shepard and J.R.G. Turner. 1974. Quaternary refugia in tropical America: evidence from race formation in *Heliconius* butterflies. *Proceedings of the Royal Society of London (B)* 187: 369–378.
- Camp, W.H. 1952. Phytophyletic pattern on lands bordering the South Atlantic basin. *Bulletin of the American Museum of Natural History* 99: 205–212.
- Carne, P.B. 1957. *Systematic Revision of the Australian Dynastinae*. Division of Entomology, CSIRO, Melbourne.
- Colbert, E.H. 1974. *Wandering Lands and Animals*. Hutchinson, London.
- Cooke, H.B.S. 1972. The fossil mammal fauna of Africa. In, A. Keast, F.C. Erk and B. Glass (eds.), *Evolution, Mammals, and Southern Continents*, pp. 89–139. State University of New York Press, Albany.
- Coryndon, S.C. and R.J.G. Savage. 1973. The origin and affinities of African mammal faunas. In, N.F. Hughes (ed.), *Organisms and Continents Through Time*. Palaeontological Association of London, Special Papers in Palaeontology No. 12: 121–135.
- Cox, B.C. 1974. Vertebrate paleodistributional patterns and continental drift. *Journal of Biogeography* 1: 75–94.
- Darlington, P.J., Jr. 1957. *Zoogeography: The Geographical Distribution of Animals*. John Wiley and Sons, Inc., New York.
- Dewey, J.F., W.C. Pitman III, W.B.F. Ryan and J. Bonin. 1973. Plate tectonics and the evolution of the Alpine system. *Bulletin of the Geological Society of America* 84: 3137–3180.
- Deyrolle, H. 1863. Nouveau genre de lucanide. *Annales de la Société Entomologique de France* 1863: 485–487.
- Didier, R. and E. Ségué. 1953. *Catalogue Illustré des Lucanides du Globe. Texte*. Paul Lechevalier, Paris.
- Dietz, R.S. and J.C. Holden. 1970. Reconstruction of Pangaea; breakup and dispersion of continents, Permian to Present. *Journal of Geophysical Research* 75: 4939–4956.
- Dorf, E. 1957. The Earth's changing climates. *Weatherwise* 10: 54–59.
- Duellman, W.E. 1982. Quaternary climatic-ecological fluctuations in the lowland tropics: frogs and forests. In, G.T. Prance (ed.), *Biological Diversification in the Tropics*, pp. 389–402. Columbia University Press, New York.
- Endler, J.A. 1982a. Pleistocene forest refuges: fact or fancy? *Ibid*, pp. 641–657.
- _____. 1982b. Problems in distinguishing historical from ecological factors in biogeography. *American Zoologist* 22: 441–452.
- Geyh, M.A., H.R. Kudrass and H. Streif. 1979. Sea-level changes during the late Pleistocene and Holocene in the Strait of Malacca. *Nature* 278: 441–443.
- Gose, W.A., G.R. Scott and D.K. Swartz. 1980. The aggregation of Mesoamerica: paleomagnetic evidence. In, R.H. Pilger, Jr. (ed.), *The Origin of the Gulf of Mexico and the Early Opening of the Central North Atlantic Ocean*, p. 51–54. Symposium Proceedings, Louisiana State University and Louisiana Geological Survey, Baton Rouge.
- Hackman, B.D. 1971. The Solomons fractured arc. *Record of Proceedings, Twelfth Pacific Science Congress* 1: 366.
- Haffer, J. 1969. Speciation in Amazonian forest birds. *Science* 165: 131–137.
- _____. 1978. Distribution of Amazon forest birds. *Bonner Zoologische Beiträge* 29:

- 38–78.
- _____. 1982. General aspects of the refuge theory. In, G.T. Prance (ed.), *Biological diversification in the Tropics*, pp. 6–24. Columbia University Press, New York.
- Hallam, A. 1973. Distributional patterns in contemporary terrestrial and marine animals. In, N.F. Hughes (ed.), *Organisms and Continents Through Time*. Palaeontological Association of London, Special Papers in Palaeontology No. 12: 93–105.
- _____. 1981. Relative importance of plate movement, eustasy, and climate in controlling major biogeographical changes since the early Mesozoic. In, G. Nelson and D.E. Rosen (eds.), *Vicariance Biogeography. A Critique*, p. 303–330. Columbia University Press, New York.
- Hennig, W. 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana.
- HersHKovitz, P. 1972. The Recent mammals of the Neotropical Region: a zoogeographic and ecological review. In, A. Keast, F.C. Erk and B. Glass (eds.), *Evolution, Mammals, and Southern Continents*, pp. 311–431. State University of New York Press, Albany.
- Holloway, B.A. 1960. Taxonomy and phylogeny in the Lucanidae (Insecta: Coleoptera). *Records of the Dominion Museum* 3: 321–365.
- Hooijer, D.A. 1967. Indo-Australian insular elephants. *Genetica* 38: 143–162.
- _____. 1975. Quaternary mammals west and east of Wallace's Line. In, G.-J. Barstra and W.A. Casparie (eds.), *Modern Quaternary Research in Southeast Asia*, pp. 37–46. A.A. Balkema, Rotterdam.
- Howden, H.F. 1981. Zoogeography of some Australian Coleoptera as exemplified by the Scarabaeoidea. In, A. Keast (ed.), *Ecological Biogeography of Australia*, pp. 1009–1035. W. Junk, the Hague.
- Johnson, D.L. 1980. Problems in the land vertebrate zoogeography of certain islands and the swimming powers of elephants. *Journal of Biogeography* 7: 383–398.
- Keast, A. 1972a. Continental drift and the evolution of the biota on southern continents. In, A. Keast, F.C. Erk and B. Glass (eds.), *Evolution, Mammals, and Southern Continents*, p. 23–87. State University of New York Press, Albany.
- _____. 1972b. Australian mammals: zoogeography and evolution. *Ibid*, p. 195–246.
- Kuenen, P.H. 1950. *Marine Geology*. John Wiley & Sons, Inc., New York.
- Laurent, R.F. 1973. A parallel survey of equatorial amphibians and reptiles in Africa and South America. In, B.J. Meggers, E.S. Ayensu and W.D. Duckworth (eds.), *Tropical Forest Ecosystems in Africa and South America: a Comparative Review*, pp. 259–266. Smithsonian Institution Press, Washington, D.C.
- Lavocat, R. 1980. The implications of rodent paleontology and biogeography to the geographical sources and origin of Platyrrhine primates. In, R.L. Ciochon and A.B. Chiarelli (eds.), *Evolutionary Biology of the New World Monkeys and Continental Drift*, pp. 93–102. Plenum Press, New York.
- Leopold, E.B. and H.D. MacGinitie. 1972. Development and affinities of Tertiary floras in the Rocky Mountains. In, A. Graham (ed.), *Floristics and Paleofloristics of Asia and Eastern North America*, pp. 147–200. Elsevier, New York.
- Livingstone, D.A. 1982. Quaternary geography of Africa and the refuge theory. In, G.T. Prance (ed.), *Biological Diversification in the Tropics*, pp. 523–536. Columbia University Press, New York.
- Lloyd, J.J. 1963. Tectonic history of the south Central-American orogen. In, O.E. Childs and B.W. Beebe (eds.), *Backbone of the Americas*, pp. 88–100. American Association of

- Petroleum Geologists Memoir No. 2.
- Lynch, J.D. 1982. Relationships of the frogs of the genus *Ceratophrys* (Leptodactylidae) and their bearing on hypotheses of Pleistocene forest refugia in South America and punctuated equilibria. *Systematic Zoology* 31: 166–179.
- MacGinitie, H.D. 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. *University of California Publications in Geological Sciences* 83: 1–140.
- Medway, L. 1972. The Quaternary mammals of Malesia: a review. *In*, P. and M. Ashton (eds.), *The Quaternary Era in Malesia*, pp. 63–98. Department of Geography, University of Hull, England.
- Meijer, W. 1974. Plant geographic studies on Dipterocarpaceae in Malesia. *Annals of the Missouri Botanical Gardens* 61: 806–818.
- . 1982. Plant refuges in the Indo-Malesian Region. *In*, G.T. Prance (ed.), *Biological Diversification in the Tropics*, pp. 576–584. Columbia University Press, New York.
- Moore, B.P. 1978. A new Australian stag beetle (Coleoptera: Lucanidae) with Neotropical affinities. *Journal of the Australian Entomological Society* 17: 99–103.
- Müller, P. 1973. *The Dispersal Centers of Terrestrial Vertebrates in the Neotropical Realm. Biogeographica II*. W. Junk, the Hague.
- Phillips, J.D. and D. Forsyth. 1972. Plate tectonics, paleomagnetism, and the opening of the Atlantic. *Bulletin of the Geological Society of America* 83: 1579–1600.
- Pitman, W.C. III and M. Talwani. 1972. Sea-floor spreading in the North Atlantic. *Bulletin of the Geological Society of America* 83: 619–646.
- Powell, C.M. and P.J. Conaghan. 1973. Plate tectonics and the Himalayas. *Earth and Planetary Science Newsletter* 20: 1–12.
- Prance, G.T. 1973. Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon Basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. *Acta Amazonica* 3: 5–28.
- . 1982. Forest refuges: evidence from woody angiosperms. *In*, G.T. Prance (ed.), *Biological Diversification in the Tropics*, pp. 137–158. Columbia University Press, New York.
- Quantin, P. 1971. On the nature and fertility of volcanic ash soils derived from Recent volcanic eruptions in the New Hebrides Archipelago. *Record of Proceedings, Twelfth Pacific Science Congress* 1: 5–6.
- Radinsky, L. 1963. Origin and early evolution of North American Tapiroidea. *Bulletin of the Peabody Museum of Natural History* 17: 1–106.
- Raven, P.H. and D.I. Axelrod. 1972. Plate tectonics and Australasian paleogeography. *Science* 176: 1379–1386.
- . 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* 61: 539–673.
- Romer, A.S. 1945. *Vertebrate Paleontology*. University of Chicago Press, Chicago.
- Roon, G. van. 1910. *Coleopterorum Catalogus* 29 (Pars 8. Lucanidae). W. Junk, Berlin.
- Sartono, S. 1973. On Pleistocene migration routes of vertebrate fauna in southeast Asia. *Bulletin of the Geological Society of Malaysia* 6: 273–286.
- Schultz, C.B., L.D. Martin and R.G. Corner. 1975. Middle and Late Cenozoic tapirs from Nebraska. *Bulletin of the University of Nebraska State Museum* 10: 1–21.
- Schuster, R.M. 1972. Continental movements, “Wallace’s line” and Indomalayan-Australasian

- dispersal of land plants: some eclectic concepts. *Botanical Review* 38: 38–86.
- Seyfert, C.K. and L.A. Sirkin. 1973. *Earth History and Plate Tectonics*. Harper and Row, New York.
- Simpson, B.B. and J. Haffer. 1978. Speciation patterns in the Amazonian forest biota. *Annual Review of Ecology and Systematics* 9: 497–518.
- Smith, A.G. 1971. Alpine deformation and the oceanic areas of the Tethys, Mediterranean, and Atlantic. *Bulletin of the Geological Society of America* 82: 2039–2070.
- Smith, A.G. and J.C. Briden. 1977. *Mesozoic and Cenozoic Paleogeographic Maps*. Cambridge University Press, Cambridge.
- Tarling, D.H. 1971. Gondwanaland, paleomagnetism and continental drift. *Nature* 229: 17–21, 71.
- _____. 1980. Continental drift and biological evolution. *Carolina Biology Readers* 113: 1–32.
- Tricart, J. 1974. Existence de périodes sèches au Quaternaire en Amazonie et dans les régions voisines. *Revue de Géomorphologie Dynamique* 4: 145–158.
- Umbgrove, J.H.F. 1938. Geological history of the East Indies. *Bulletin of the American Association of Petroleum Geologists* 22: 1–70.
- Veevers, J.J., G. Jones and J.A. Talent. 1971. Indo-Australian stratigraphy and the configuration and dispersal of Gondwanaland. *Nature* 229: 383–388.
- Verstappen, H.Y. 1975. On palaeoclimates and landform development in Malesia. *In*, G.-J. Barstra and W.A. Casparie (eds.), *Modern Quaternary Research in Southeast Asia*, pp. 3–35. A.A. Balkema, Rotterdam.
- Vuilleumier, B.S. 1971. Pleistocene changes in the fauna and flora of South America. *Science* 173: 771–780.
- Vulcano, M.A. and F.S. Pereira. 1961. A subfamília Penichrolucaninae representada em América (Col., Lucanidae). *Studia Entomologica* 4: 471–480.
- Walker, D. 1982. Speculations on the origin and evolution of Sunda-Sahul rain forests. *In*, G.T. Prance (ed.), *Biological Diversification in the Tropics*, p. 554–575. Columbia University Press, New York.
- Watrous, L.E. and Q.D. Wheeler. 1981. The out-group comparison method of character analysis. *Systematic Zoology* 30: 1–11.
- Woodring, W.P. 1954. Caribbean land and sea through the ages. *Bulletin of the Geological Society of America* 65: 719–732.