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Evolutionary patterns in chromosome numbers in neotropical Lepidoptera

I. Chromosomes of the Heliconiini (Family Nymphalidae: Subfamily Nymphalinae)

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Chromosome counts in meiotic metaphase plates in the gonads of 67 of the probable 68 species of mimetic neotropical heliconian butterflies (Nymphalidae), representing 1524 individuals in 617 subspecies and geographically separate populations from southern Texas to northern Argentina, revealed a consistent haploid number of n = 21 in the genus *Heliconius* (except for the most advanced species with n = 33, 37, 56, and 60) and n = 31 in the more primitive genera (*Eueides*, *Dryas*, *Dryadula*, *Agraulis*, and *Dione*), with a transitional genus (*Neruda*) showing three species with n = 28–32, 21–22 + 5–10 "microchromosomes", and 20–22 + 1–5 "microchromosomes". The genus *Laparus*, with a single polymorphic species *doris*, probably an offshoot of early *Heliconius*, shows wide karyotypic variation (n = 20–30, 38) sometimes even within a single individual. The two most primitive genera also show much variation: *Podotricha* has two species with n = 9 and n = 26–29; and *Philaethria* shows many phenotypically similar species, two with n = 29 and a still uncertain number (at least 3) with n = 88 (most common), 67–72 (most widespread), 62 (very restricted geographically), 52, 21, and 12. Several interspecific hybrids (*Heliconius cydno* × *H. melpomene*) showed normal chromosome pairing, while deficient pairing was seen in intersubspecific hybrids in *Eueides tales* and *Heliconius sara*. The importance of these results in the evolutionary study of polytypic tropical species is discussed.

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Introduction

This paper is the first in a series of comprehensive summaries and analyses of patterns in the evolutionary modification of chromosome numbers in diverse groups of Neotropical Lepidoptera. The three laboratories cooperating in these papers have had interests in chromosome evolution among the butterflies for more than 20 years. As part of long-term studies of the evolution and ecology of Neotropical Lepidoptera (e.g., BROWN 1987), the first author has dissected and fixed thousands of testes of butterflies in all parts of tropical America since 1969, using a variety of methods (EMMEL 1969; DE LESSE and BROWN 1971). The majority of the material fixed by the first author has been examined by sectioning in the laboratory of the fourth author, as part of a general study of chromosome evolution in the Lepidoptera, including Neotropical species (SUOMALAINEN 1965, 1969, 1971; SUOMALAINEN et al. 1972, 1973; SUOMALAINEN and BROWN 1984). In addition, a substantial amount of material fixed by Brown in glacial acetic acid–absolute ethanol has been examined by Emmel & Eliazar.

We have placed emphasis in these studies on groups already found in previous publications (DE LESSE 1967, 1970a,b; DE LESSE and BROWN 1971) and our own surveys to show unusual chromosome variations, or to be judged to be important in the overall evolutionary patterns of the Lepidoptera, or to possibly demonstrate generalized processes in the area of tropical evolution. The Heliconiini, the first of these groups to be essentially completed, will be reported and discussed in this paper. Future papers are planned to discuss special problems

such as *Philaethria* (SOUMALAINEN and BROWN 1984), certain groups of Ithomiinae, Danainae, Charaxinae and other groups, as patterns become discernable and the coverage of species nears completion for each case.

Chromosomes of the Heliconiini (Family Nymphalidae: Subfamily Nymphalinae)

The heliconians or passion-flower butterflies are highly variable in color pattern, and usually participate in diverse mimicry rings wherever they occur in the Neotropics (BROWN 1981, 1987; TURNER 1981). They are suspected to be undergoing rapid present-day evolution, or to have radiated rapidly in the recent past, in a number of genera and species groups (see reviews in BROWN 1981 and SHEPPARD et al. 1985). Several early reports (MAEKI and REMINGTON 1961; DE LESSE 1967, 1970a,b) revealed a number of interesting aspects of the cytogenetics of this group. These authors showed that the primitive genera (*Agraulis*, *Dione*, *Dryas*, *Eueides*) had a near-identical chromosomal complement, with n = 31, the modal number for the butterflies in general (and also moths and caddisflies; SUOMALAINEN 1969). The first members counted for the genus *Heliconius*, however, showed n = 21, a modal number independent, for the most part, of the evolutionary position of those species in the genus, and also independent of strong geographic differentiation into polytypic color pattern complexes related to local mimicry rings.

Notable exceptions to the modal number of n = 31 included the primitive genus *Podotricha* (n = 9 for one species, n = 28–29 for the other, the latter being mimetic of a species of *Heliconius*; VANE-WRIGHT et al. 1975); the derived *Heliconius* splinter-genus *Laparus*, whose only species *doris* showed a variable n = 24–27 in those studies; the primitive *Heliconius aoede*, later separated by TURNER (1976) into the new taxon *Neruda*, with n = 23 including two microchromosomes; and the morphologically most evolved group of *Heliconius*, the *sapho*-related species (EMSLEY 1965; BROWN 1972, 1981), with n = 33 or 56.

Two subsequent papers by SUOMALAINEN et al. (1972, 1973) showed further interesting aspects in Heliconiini chromosomes. *Philaethria dido* from Trinidad, regarded by EMSLEY (1963) as the most primitive of the Heliconiini, showed n = 21 like the modal number for the genus *Heliconius*. Additionally, oogenesis in *Heliconius* was shown to be unaccompanied by chiasmata, thereby prohibiting recombination (unlinking of genes in the same chromosome) in females of those species. Other results for the 14 species of the tribe from Trinidad fell into the established n = 31/21 pattern, as did further numbers published by DE LESSE and BROWN (1971). WESLEY and EMMEL (1975) gave further information on Trinidad Heliconiini chromosomes, including numbers of n = 24/30 and 38 for *Laparus doris*, and n = 19, 20 and 29 for the relatively advanced species *Heliconius sara*, occurring on that island as a mixture of two subspecies (*magdalena* and *thamar*). Wesley and Emmel emphasized the probability that the Heliconiini might be one of the most interesting groups for further chromosome studies, because of the possibility that the observed variations might be linked with rapid evolution of mimetic patterns in these butterflies.

We have now fixed a wide range of populations (617) of all known Heliconiini species except for one little-studied *Eueides* species, which is evolutionarily "flanked" by species with uniform numbers of n = 31 and thus not expected to deviate from this pattern. The present work, in connection with evolutionary studies based on morphology, genetics, biology and foodplant choice, provides a broad understanding for the mechanisms of radiation in this important tropical group, offering the basis for the planning and interpretation of experimental studies in the future (BROWN 1981; TURNER 1981).

Material and methods

Field-collected (or, at times, laboratory-reared) male and occasionally female butterflies were kept alive in glassine envelopes, in a shaded belt box or side pack, until dissection was possible (usually in the evening of the same day; even in cool weather, the butterflies rarely remained active for more than 24 hours, and usually had to be dissected within 10 hours of capture). Immediately after pinching of the thorax, the butterfly was either treated as described by EMMEL (1969) or, in the fixing by K. S. Brown, pinned with wings open on a piece of cardboard, extended taut with a pin through the end of the abdomen, opened at the fifth or sixth abdominal segment dorsally with fine-tipped forceps, and pressed on the abdomen until the fused testicles (or ovaries), usually easily identified, became visible at the short incision. The gonads were described (size and color, and any unusual characteristics) and immediately removed to fixing solution. Each butterfly took about 2–3 min to dissect in this fashion;

a maximum of nearly 100 could be dissected and fixed by one person in an evening's work.

For 3:1 absolute ethanol–acetic acid fixing (Carnoy 1, EMMEL 1969) and for fixing in Carnoy's solution II (Carnoy II, ethanol–chloroform–acetic acid 6:3:1), the fixative was mixed immediately before use; for fixing in Hollande's modification of Bouin's solution (picric acid–cupric acetate–water 5:8:200 plus 40 % formaldehyde–acetic acid 20:30 added afterwards), the fixative was prepared in tubes before the trip. The first two solutions esterified and evaporated rapidly, and the fixed material had to be transferred within a few days to 80 % alcohol and stored below 0°C. The Bouin-Hollande fixative evaporated slowly, and material could be transferred as much as years later to 80 % alcohol after a brief wash with water; this material did not require refrigeration.

In all material fixed by K. S. Brown, small (6 × 50 mm) test tubes were used, and numerous testicles of different sizes and colors were fixed in multiple compartments divided by cotton wads. In this way, as many as fifty species could be fixed in a single tube, and thousands of butterflies were often prepared on a single trip. In the later separation of this material to labelled individual compartments for chromosome examination in Finland or Florida, occasional doubts arose as to the exact original identity of some testes, especially those which changed greatly in size or color after a long time in the fixative. Such cases were always noted during the work-up and, when doubts continued after the counting, the results from these testes were ignored in later interpretations. The small amount of information thus lost was presumed to be compensated by the great convenience, efficiency and volume of the field work and fixing; anomalous results were in almost all cases later confirmed or else definitely assigned to other species.

In all material fixed by Emmel and Eliazar, testes were placed in individual 2-dram glass vials with individual labels. As many as 130 were fixed per day in the field, with no possibility of later confusion, thanks to using a separate vial for each testis.

Ethanol–acetic acid fixed material was studied in Florida by high-pressure squashing in lacto-aceto-orcein (EMMEL 1969; WESLEY and EMMEL 1975) and examination under 100× oil immersion planapochromatic objectives with a total magnification of 2000×. All preparations were then photographed with a Zeiss camera on 35 mm Panatomic X film for a permanent record. Bouin and Carnoy II fixed material was sent to Finland and sectioned to 100 μm, then stained with Heidenhain's iron hematoxylin. Photomicrographs and drawings were prepared of the dividing meiotic cells whenever possible and indicated. The photographs were taken on Agfa Agepe 35 mm film with a Leitz Orthomat camera and 100× immersion objective, and magnified to approximately 2700×. If the chromosome set of a species could not be adequately photographed, the chromosomes were presented in a drawing. Certain karyotypes judged to be important for this study were both drawn and photographed. The drawings were made at bench level with a Wild drawing apparatus (V = 2.5×) using a 100× immersion objective and a 12.5× ocular. The final linear magnification of the drawing text figures is about 2000×. All figures represent male meiosis; whenever possible, the first metaphase is shown. If the preparation contained only second metaphases, this stage was represented. A second metaphase can be recognized by the smaller size of the chromosomes.

In the Heliconiini, about 70 % of the testicles gave countable metaphases by the squash method. Almost all material fixed in Bouin or Carnoy II gave counts by sectioning. In the broad range of butterflies fixed (all groups), the corresponding figures were about 40 % and 80 %; the higher percentages in the Heliconiini are ascribable to continuous or delayed spermatogenesis in these long-lived and iteroparous butterflies.

While ethanol–acetic acid fixing and squashing is far more convenient in the laboratory and microscopy stage of the work, fixing for this procedure is relatively laborious in the field (as is fixing in Carnoy II, which also must be prepared from separate reagents just before use and rapidly evaporates). The vials and chemicals may require special handling unavailable in many parts of the American tropics, to avoid irretrievable loss; the low proportion of successful counts is probably due to these factors, since evening accommodations were often bare ground with candlelight, humidity levels allowed moisture into the chemicals, and no refrigeration was available at most sites. Fixing in Bouin-Hollande offers greater simplicity in the field stage, but involves much more laborious laboratory methods. It is preferred when highly limited, irreplaceable material, captured far from population centers or the laboratory, must be preserved. For more routine studies of large numbers of insects, on shorter trips in more accessible places, the ethanol–acetic acid method is the better choice.

The collecting localities, totalling over a thousand, cover the entire Neotropics and are grouped by country or region in the results. The total number of fixing days is presently near 3000; of populations fixed of Heliconiini, well over 600.

Results

Table I presents a composite summary of all our results of counts on the Heliconiini, also including other published results that we have been able to locate for members of this tribe. The codes used for the localities, testis size and colors are explained at the end of the Table, and follow the standard practice of DE LESSE (1970a,b) with the addition of an approximate size factor (the testes in the living adult will diminish with the age of the male, but in general the categories hold over a broad range of individuals). The complete table of individuals is deposited with the Editors of this Journal and also with each of the authors, and is available to interested readers. Selected chromosome complements are illustrated in Fig. 1–156 (Plates 1–6).

Discussion

The most striking aspect of the data collected in the present study is that the most primitive heliconian group (*Philaethria*) in the New World presents the most variable chromosome picture [n = 12 to 88, in what was once regarded as a single species, *dido* (EMSLEY 1963); widely different numbers from single localities, sometimes in phenotypically identical specimens]. The supposedly three species in the genus (BROWN and MIELKE 1972; BROWN and BENSON 1977; BROWN 1981) are extremely stable in color-pattern, habitat, and behavior; in terms of mimicry, they serve, (doubtfully, to some observers) as occasional models for the similarly green Batesian mimic *Siproeta stelenes*, varying geographically in parallel (see YOUNG 1972; YOUNG and MUYSHONDT 1973). They occur from southern Mexico to southern Brazil, though the two more primitive species (*pygmalion* and *wernickei*, both with n = 29) are restricted to open habitats in the Amazon and the eastern coast of Brazil, respectively. The remainder of the chromosome morphs (*n* = 12 with or without many micro-chromosomes, 21, 50–52, 62, 67–72 and 88) are easily divided into four morphospecies, one restricted to the Colombian Chocó (n = 62; SALAZAR 1991), one occurring from Costa Rica to eastern Brazil (n = 88, corresponding to the type of *dido*, with restricted green on the ventral surface; four subspecies, three still undescribed); a highly variable complex including the type of *diatonica*, with numbers near 70, occupying the extremes of the range of the *dido* complex; and a pointed-wing species with no name applicable and at least three geographic subspecies (n = 52). The further numbers of n = 12 and 21, possibly including *ostara*, occur in various regions and present a still undefined relationship with sympatric populations with n = 67–72. The systematics of this unusual group will be further discussed in a forthcoming publication by Brown and Suomalainen (see also SUOMALAINEN and BROWN 1984).

This pattern does not conform to that of the other genus in the tribe with highly variable numbers (*Laparus*), whose single species *doris* is strongly and mimetically polymorphic, associating with two or three different mimicry rings in the same locality, from Mexico to the limits of Amazonian Brazil and Bolivia; it has been suggested to be a Batesian mimic (BROWER et al. 1963; Benson 1971), and shares with *Philaethria* only a strong flight and dispersal ability.

Laparus chromosome polymorphism, probably resulting from chromosome fragmentation, has been specifically linked to adaptive rearrangement of genes related to mimicry, allowing "rapid evolution as a result of predator selection among new color morphs . . . a generally useful strategy for butterfly species faced by marginal environments and strong predator pressures" (WESLEY and EMMEL 1975). Similar and extensive intraspecific and intrageneric variation in karyotype has now been verified by us in a wide variety of mimetic groups, showing both the local polymorphism and extensive geographical differentiation (papers in preparation). Such an explanation is not relevant, however, to *Philaethria*, all of whose chromosome morphs are nearly identical in juvenile and adult morphology, and all of which share a single weakly mimetic wing color-pattern (SUOMALAINEN and BROWN 1984 and in preparation). The very different chromosome numbers in the *P. dido* complex are wide-spread: n = 67, from Mexico to southern Brazil; n = 88, from Costa Rica to eastern Brazil; n = 52, over the entire Amazon/Orinoco region. Present evidence indicates polymorphism of chromosome number in a single interbreeding population in some points, and as many as four externally recognizable species with different numbers flying together in others (southwestern Venezuela, n = 21/52/72/88; and western Colombia, n = 52/62/72/88).

Such a pattern seems more likely to have been derived from a long history for this complex, probably the most primitive American heliconian, than from rapid evolution associated with mimetic adaptation. Possibly, the wide variations in South American climate, vegetation, and topography over the Cenozoic, including the entire Andean orogeny and silting in of the Upper Amazonian lakes, led to many opportunities for allopatric speciation accompanied by karyotype revolutions in the complex, followed by rapid spreading out with fixation of different numbers in different species in some parts with highly heterogeneous environment (like the pre-Andean regions), assimilation of polymorphisms into a single population in more homogeneous areas, and even complete dominance of a single morph (n = 88) over vast regions of low-productivity dense lowland rain forest. As no simple rationalization can account for the extraordinary karyotype diversification in the otherwise very conservative *P. dido* complex, its variability must emphasize the necessity for caution in the interpretation of chromosome evolution, especially if only a few counts are available for limited populations or individuals — often the rule, especially for widespread but difficult-to-capture species like *P. dido*.

The only other departure from n = 31 in the primitive heliconians is in the relatively specialized though primitively rooted, partially mimetic genus *Podotricha* (EMSLEY 1963; VANE-WRIGHT et al. 1975). Here again, mimetic pressure does not explain the difference between the two species, since the conservative karyotype (n = 26–29) is found in the member with the derived mimetic wing-pattern and wide distribution (*P. telesiphe*), while the apparently derived karyotype (n = 9) appears in the species with a more conservative color-pattern (like *Dione*) and relict distribution. Notably, these are also ancient Andean species that probably accompanied the entire process of mountain-building on the western rim of South America. Once again, this points to the need for care in interpreting results of chromosome counts in terms of evolutionary processes presumed from other observations or organisms.

The fact that females of *Podotricha* are practically unknown, even where males are abundant, also suggests the possibility of unusual genetic mechanisms in this genus. Although female heliconians are always much more retiring than males, they can inevitably be found on favored flowers, and sex ratios in collections rarely exceed 10:1 in favor of males; in *Podotricha*, uniting all the world's collections and the extensive observations of recent field workers, the ratio remains near a thousand to one!

The different numbers exhibited by Peruvian and Ecuadorian populations of *P. telesiphe* (n = 26–27 and 28–29, respectively) are in accord with the "true" subspecies separation at the Rio Marañón suggested by VANE-WRIGHT et al. (1975); their prediction that white-banded *P.t. "telesiphe"* from southern Ecuador, which fly south of yellow-banded *P.t. tithraustes* in the upper Pastaza valley, should be closer to the latter subspecies, not to the Peruvian white-banded *P.t. telesiphe*, is borne out by the chromosome numbers observed (n = 28–29 in the upper Santiago, see Table 1). It would be interesting to get a count of an individual captured in the upper Marañón itself (specimens are known).

Morphological considerations (BROWN and HOLZINGER 1973) suggest that *Eueides* (always n = 31) grades into *Heliconius* (n = 21) through the species of the *aoede* group, placed by TURNER in his new (sub)genus *Neruda* (1976). The chromosome numbers are in excellent accord with this evolutionary hypothesis (Table 1; Fig. 24–35). *Neruda metharme* shows essentially the same number as the primitive genera (n = 30–32, several of the chromosomes being quite small, and missing in some southern populations). *N. godmani* has, in addition to 21–22 normally sized chromosomes, up to 10 small "microchromosomes", which from their mere appearance are difficult to identify as accessory chromosomes, fragments, or supernumeraries; their presence probably indicates extensive rearrangements in the complement. *Neruda aoede*, the most widespread, common and variable of the three species and, thus, probably the most derived, is very close to *Heliconius*, with 21 chromosomes plus a variably small number (2–5) of "microchromosomes". Apparently, the chromosome characteristics associated with the extreme mimetic plasticity in *Heliconius* are already present in *aoede*, which like *godmani* and *metharme* retains a primitive foodplant (*Dilkea*; see BENSON et al. 1976), but which, unlike them, is strongly polytypic, converging on prominent local ithomiine/heliconian color-patterns wherever it occurs in the Amazon Basin. While a few species of *Eueides* (n = 31) are also mimetically polytypic (*E. eanes*, *E. isabella*, *E. tales*, the latter participating in the same mimicry rings as *aoede*), their exuberance and abundance do not compare with those of many species of *Heliconius* with over 20 geographical subspecies (see Table 1).

The special significance of the number 21 in *Heliconius* is not known, but it seems noteworthy

Table 1. Summary of chromosome numbers in the Heliconiini

Genus	Species	n =	No. ssp. recogn.	No. ssp. fixed	No. fixed pops./inds.	Localities	Testis sizes	Testis colors
Philaethria	*pygmalion*	29	1	1	6/11	MT/PA/AM	m/ms	R/r/dR
	wernickei	·29	1	1	14/22	RJ4/SP5/ES/BA/SC	m/ms	R/Rr
	dido	··88·	4	4	38/106	AM10/MT2/PA5/ RO6/AC/PE/PB/ EE/AV/DA2/CH/ CZ3/AC/CC	m/ms/s	R/Rr/r
	diatonica	72·	2	2	3/17	OX/TV2	m/ms	R/Rr/r/G/yG
		·67–68·	4+	4	9/149	ES4/SP/RJ/BA/ PE/PA/OX/TV		
	constantinoi	62	1	1	1/1	CC	ms	G
	sp. nov.?	··52···	3+	3	7/25	ES/PA2/TV2	m/ms	R/Rr/r
	ostara?	·21···	2+	2	3/6	TR/TV/ES	ms	Rr
	sp. nov.?	12 + 19–25mc	2+	2	8/17	PA6/BO	s/ms/m	R/r
Podotricha	*telesiphe*	28–29	2	2	2/16	EE2	ml/m/ms	R/Rr/G
		26–27	1	1	1/2	CP	m	dR
	euchroia	·9·	4	3	7/25	VC2/CC/WE/EE2	ml/ms	R/dR/Rr
Dione	*juno*	31	5	5	12/23	WP/CV/WE2/MX/DF/ EB/EE/TR/CR/MT	m/ml/l	B/RB
	moneta	··31	3	3	4/5	SP/MX/OX	l/m	B/dB
	glycera	31	1	1	4/4	CP/VC	l/ml	B/RB
Agraulis	*vanillae*	31	8	7	13/28	MX2/TR/EE/AR/ CB2/WE/WP/C12	m/ml/l	B/RB/R
Dryadula	*phaetusa*	·31	1	1	6/9	CR/TR/AR/ES	ml	R
Dryas	*iulia*	··31	12	4	14/17	MX2/CR2/C13/ TX/EE/AN/TR/ GY/AR/WE	m/l	R
Eueides	*tibilia*	·31	6	3	9/15	ES/GO/VV/RR/ TV/RD/PA/AM	m/ms/s	R/Rr
	pavana	31	1	1	1/1	RJ	m	r
	lineata	31–32	4	1	1/2	AN	s/ms	R/Rr
	procula	31	7	2	6/13	RG/VC/EE	m/ms/s	R/Rr
	lampeto	31	10	1	1/1	AM	ms	r
	eanes	31	5	1	1/4	AC	ms	R
	isabella	·31·	17	5	5/23	OX/AN/TR/MG/WE	m/ms	R/Rr/G
	lybia	···31··	6	5	12/34	CT/CR/CZ/CC/ GY/VV/PA/AM/ MT/GO/TV	m/ms/s	Rr/R
	tales	·31·	13	7	12/30	VV/TV3/AM/PA/ RO/AM/AN	m/ms/ s/vs	Rr/r/ cr/OR/y/lr
		37			1/1	AM		
	aliphera	31	3	2	7/10	EE/CR/CZ/TR/AR	s/ms/m	R/Rr/r
Neruda	*metharme*	·31·	3	3	3/10	RO2/AC	m/ml/l	R/Rr/r/cr/dR
		··26–27 + 2–4mc			7/12	AM/RR/RO2/AV/AC		
	godmani	21–22· + 5–10mc	1	1	3/14	CC	ms/m/ml	R/dR/RB
	doede	·21· + 1–5mc	11	8	29/56	AP/AM6/RR2/PA7/ RO5/GY/EE/MT3	m/ml/l	R/r/rB/ RB/dR/Or
Laparus	*doris*	···25–27···	8	8	59/154	PA10/CR/RO6/ CZ3/WE/CH/AN/RG/ EV/AB/BO/AM8/TR/ PA/VV/EE2/MT3/LP/ AC/TV2/AP2/CP/CC2	l/ml/vl	R/Rr/r/cr/rB
		20, 24–27			1/1	CR		
		21, 25			1/1	RO		
		22			1/3	RG		
		24–30, 38			1/25	TR		
		24, 30			1/3	RO		
Heliconius	*hierax*	21, 22	2	2	3/3	VV/EE	m/ml/l	r/Rr
	hecuba	22–24	7	1	2/2	VV	l	dR
xanthocles-*wallacei* group	*xanthocles*	·21–22·	14	6	15/26	RO3/PA/MT/EE3/ VV/AV/AM	ms/m/ml	R/Rr/r/c
	egeria	21	4	2	4/4	PA/AM2	ms/m/ml	R/Rr
	astraea	21	2	1	4/6	AM/RO3	ml/l/vl	Rr/r
		24–25			1/1	RO		
	burneyi	21·	7	5	12/23	AV2/AM2/RO2/ EB/PA2	m/ml/l	Y/G/cr/Rr
	wallacei	21·	5	4	8/17	TR/GY/VV/EE/ AV/RO/RR/AP	m/ml	R/Rr/r/cOr

(*Table 1*, continued)

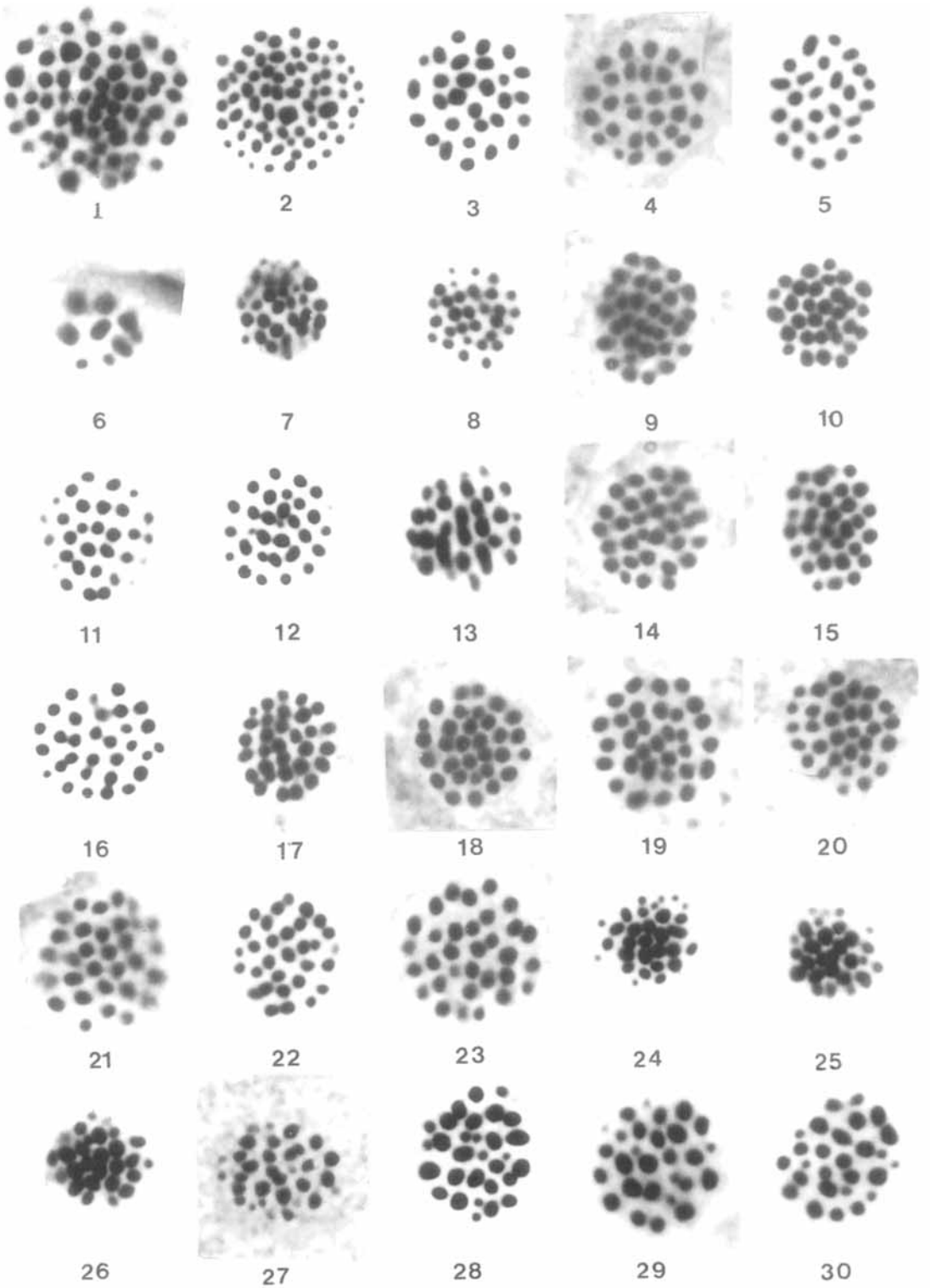
Genus	Species	n =	No. ssp. recogn/fixed		No. fixed pops/inds	Localities	Testis sizes	Testis colors
silvaniform	*nattereri*	21·	1	1	2/15	ES/BA	ms/m/ml	Rr/R/r/G/W
group	*numata*	···21	25	14	26/52	RO3/VV/EE/EB/MT/RJ/PA/AM2/AC/RR/MP/TV/ES/BA2	ms/m/ml	Rr/R/r
	ismenius	21	7	4	7/14	OX/AN/DA/CT	m/ml	R/r
	pardalinus	21·	10	5	6/19	LP/AC/VV/AM3	m/ml	R/Rr/r
	hecale	·21	29	14	19/35	CZ/CH/AN/VV/WE/EE/BO/CT/RO2/AC/RR/PA4	m/ml/l/vl	R/Rr/r
		21 + 3mc			1/1	RO		
	ethilla	·21	22	11	19/28	VV/TR/MT/DF/RJ2/HU/AM/TV/RO/PA3	m/ml/l	R/Rr/r/RB
	atthis	21	1	1	2/9	WE	ml	R
cydno-	*beseckei*	21	1	1	4/7	DF/MG/RJ/SP	ml	R/r/dR
-melpomene	*elevatus*	21	8	4	6/8	GY/RO3/PA/AM	m/ml/l	R/Rr/r
group	*luciana*	21	2	2	4/10	AV2/RR2	m/ml	R/dR
	timareta	21	2	2	2/7	EE2	l	R/Rr
	heurippa	21	1	1	1/5	VV	m/l	R
	(*cydno*) *pachinus*	21	1	1	1/11	CR	ml/l	r
	cydno	21	11	6	8/19	CZ/AN/WE2/CV/PT/TV	m/ml	R/r
	cydno × *melpomene*	21	(—)	(—)	4/4	AN/TV2	m/ml/l	R/Rr/r/lr
	melpomene	··21	29	13	22/45	CR/AN2/WE/TR2/VV/EE/AV/GY/RR/DA/RG/RO/AM2/PA2	m/ml/l	R/Rr/r/dR
erato-	*charitonia*	21	9	3	6/15	CI/WE/EE/WP/AN2	ms/s	R/Rr
group	*hermathena*	21	6	2	2/3	PA/AM	ms	R/r/dR
	hecalesia	21	6	3	3/6	CH/TV	m/ms	R/r
	clysonymus	21	4	2	5/10	EE/CC/WE2	ml/l	R/r
	hortense	21	1	1	3/4	MX/OX	m	R
	telesiphe	21	4	2	4/11	EE4	m/ml	R/dR
	erato	·21	28	17	23/43	MX/OX/GU/AN/TR/EE/WE/GY2/EB/AR DF/RR2/MP2/HU/RO	m/ms/s	R/Rr/r/dR/RB
sara-	*ricini*	21·	1	1	4/6	TR2/RO	ms	r/cr
-sapho	*demeter*	21	10	4	10/18	AM2/RO3/EB/PA	ms/s	R/Rr/r/cr/cY
group	*leucadia*	21·	2	1	7/9	EE/MT/AM/RO2/AC/PA	ms	R/Rr/r
	sara	··21	7	5	15/31	CZ/AN/WE2/VV/TR2/GY/DF/CC/RJ/EE/RO	s/ms/m/ml	R/cr/Rr/cY/Or/r
		29			1/1	TR		
	hewitsoni	21	1	1	2/2	CR	m	R
	antiochus	21·	6	5	18/32	RG2/VV/RR/RO/AM/PA3/LP/GO/BO/TV	s/ms/m/ml	R/r/G/Y/Or
	congener	33	3	2	3/16	EE2/VV	m/ms	R/Rr/r/cr
	eleuchia	·37	1	1	3/5	CZ/AN/VC	m/ms	r/G
	eleusinus	·59–60··	2	2	5/18	CC3/WE2	m/ms/s	R/r/cr/ly/G
	sapho	·56–57	4	4	6/26	OX/CC/AN/CZ/WE2	m/ms/s	Rr/r/cr

Chromosome number: A comma between numbers indicates different individuals; a dash, variation within individuals. Superscript dots before and after a number indicate variation in the number, as much as 3 over or under the given figure, infrequent but regular

Localities: Localities grouped by region; the number following indicates more than one population fixed within the region. Codes: AC = Acre, AM = Amazonas (Brazil), AN = north-central Colombia, AP = Amapá (Brazil), AR = northern Argentina, AV = Amazonas (Venezuela), BA = Bahia (Brazil), BO = Bolivar (Venezuela), CC = Chocó (W. Colombia), CH = W. Panamá, CI = Caribbean islands, CH = Chanchamayo (Peru), CR = Costa Rica, CT = N.W. Venezuela, CZ = Canal Zone, DA = E. Panamá, DF-Brasília (Brazil), EB = E. Bolivia, EE = E. Ecuador, ES = Espírito Santo (Brazil), EV = E. Venezuela, GO = Goiás (Brazil), GU = Guatemala, GY = Guianas, HU = Huallaga valley (Peru), LO = N.E. Peru, MG = Minas Gerais (Brazil), MP = upper Rio Marañón (Peru), MT = Mato Grosso (Brazil), MX = eastern Mexico, OX = S. Mexico, PA = Pará (Brazil), PB = Paraiba (Brazil), PE = Pernambuco (Brazil), PT = South Colombia, RG = N. Venezuela, RJ = Rio de Janeiro (Brazil), RO = Rondônia (Brazil), RR = Roraima (Brazil), SC = Santa Catarina (Brazil), SP = São Paulo (Brazil), TR = Trinidad, TV = Táchira (Venezuela), TX = S. Texas, VC = Valle de Cauca, W. Colombia, VV = Meta, E. Colombia, WE = West Ecuador, WP = western Peru

Testis sizes: vs = very small (less than 0.4 mm), s = small (0.4–0.7 mm), ms = medium small (0.7–1.0 mm), m = medium (1.0–1.3 mm), ml = medium large (1.3–1.6 mm), l = large (1.6–2.0 mm), vl = very large (2.0–3.0 mm) in fresh material

Testis colors: B = brown, cOr = clear orange, cr = clear rose, cY = clear yellow, DB = dark brown, dR = dark red, G = green, lr = light rose, ly = light yellow, Or = orange, R = red, r = rose, RB = red brown, rB = rose brown, Rr = rose red, W = white, y = yellow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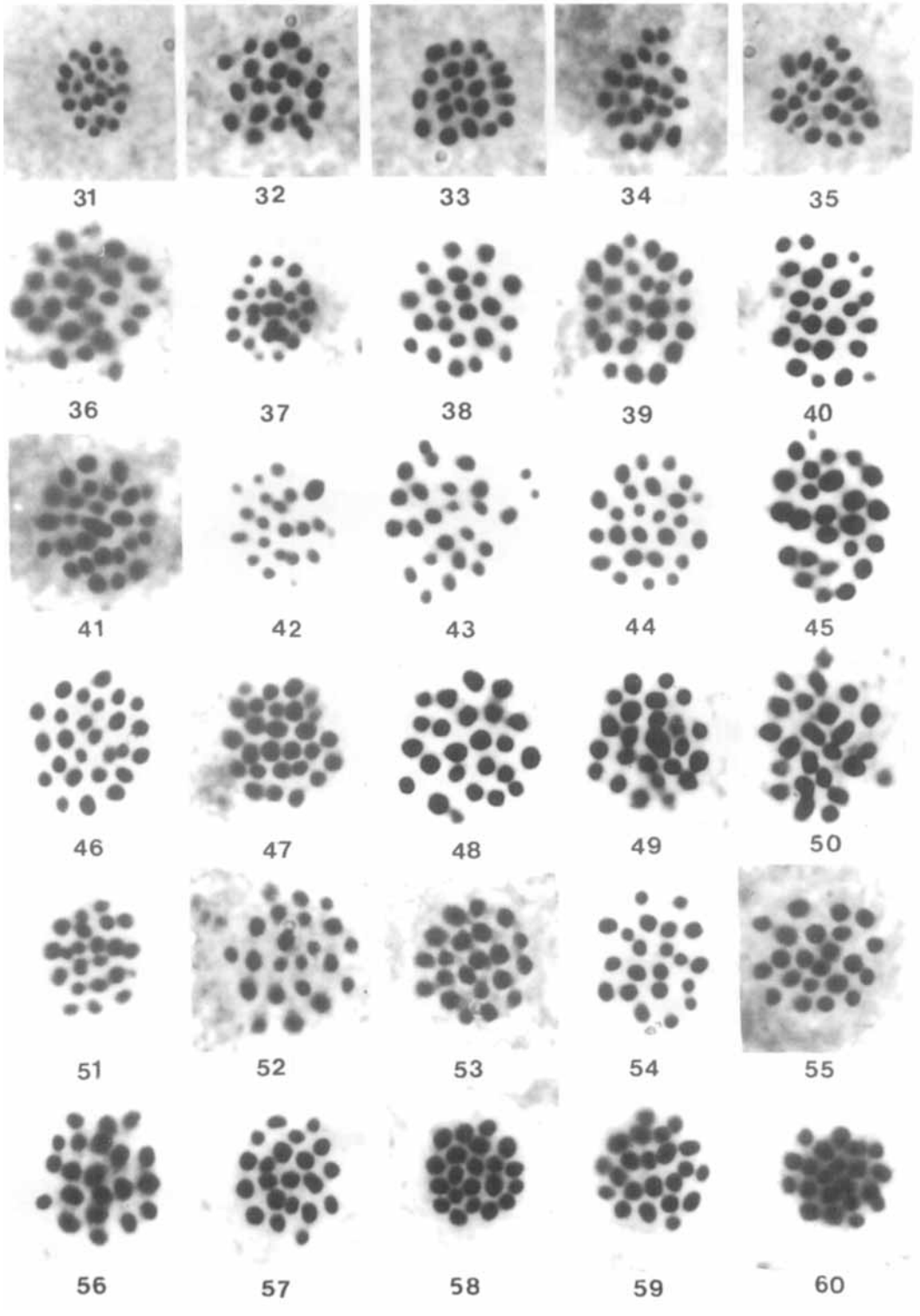
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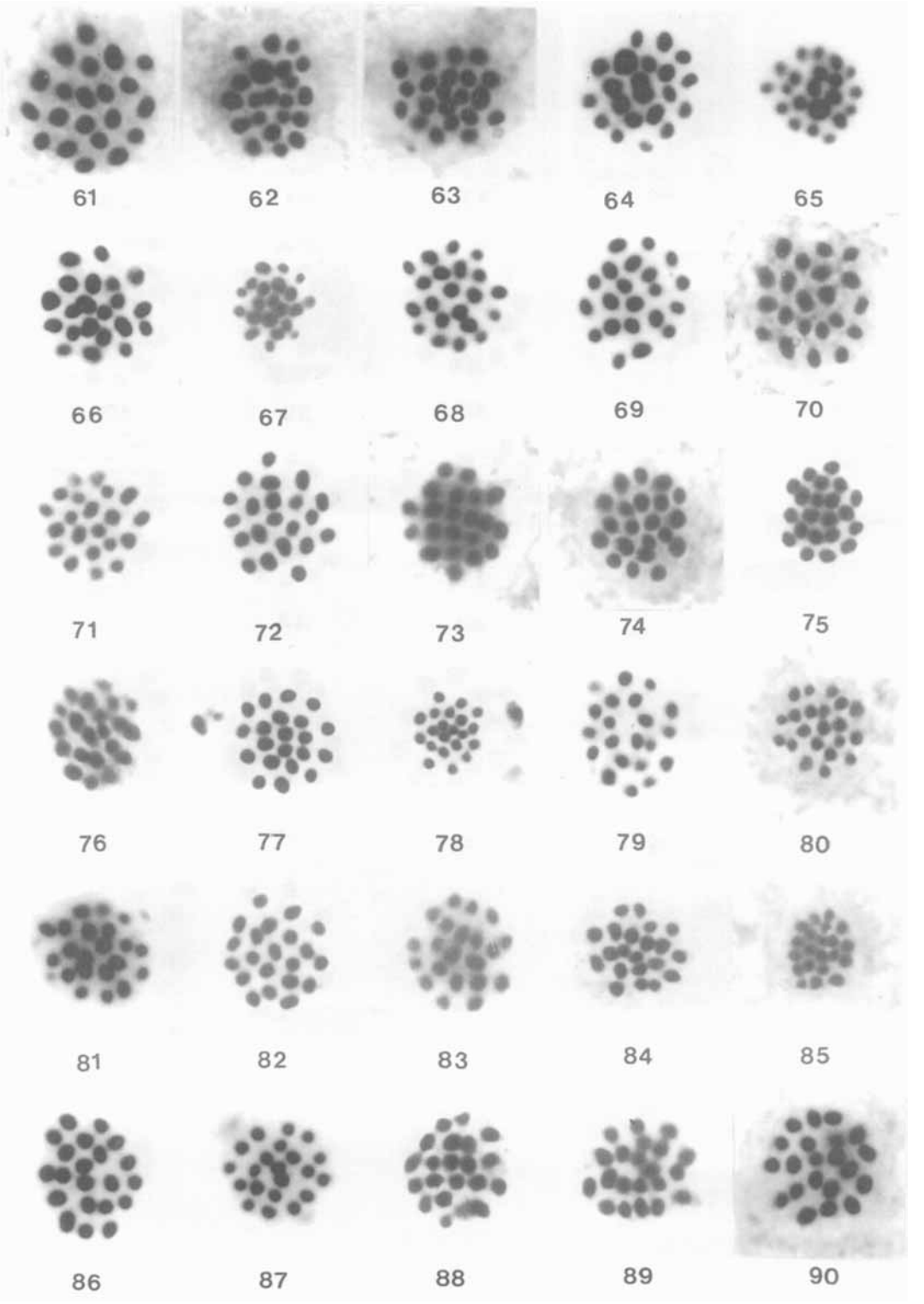
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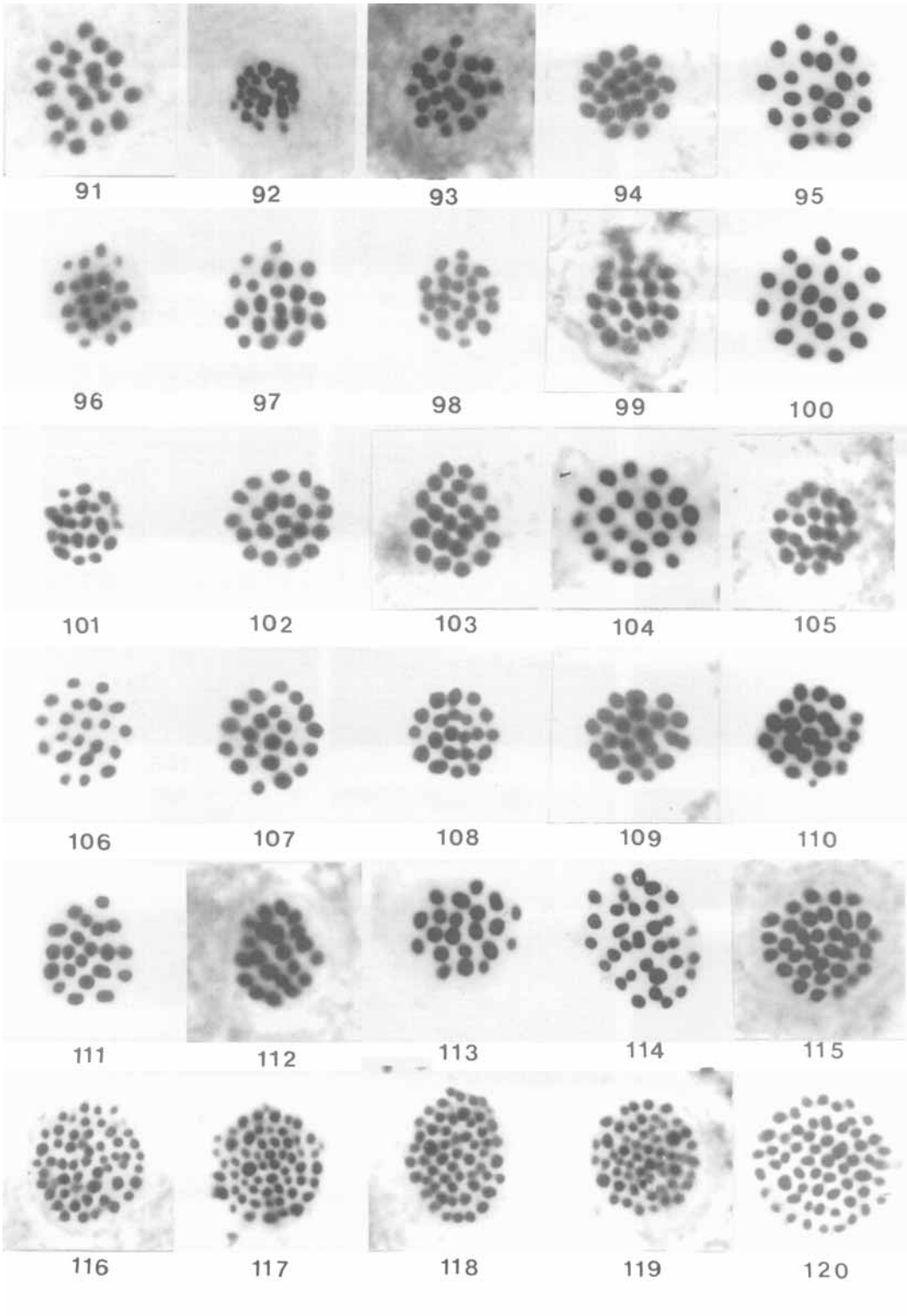
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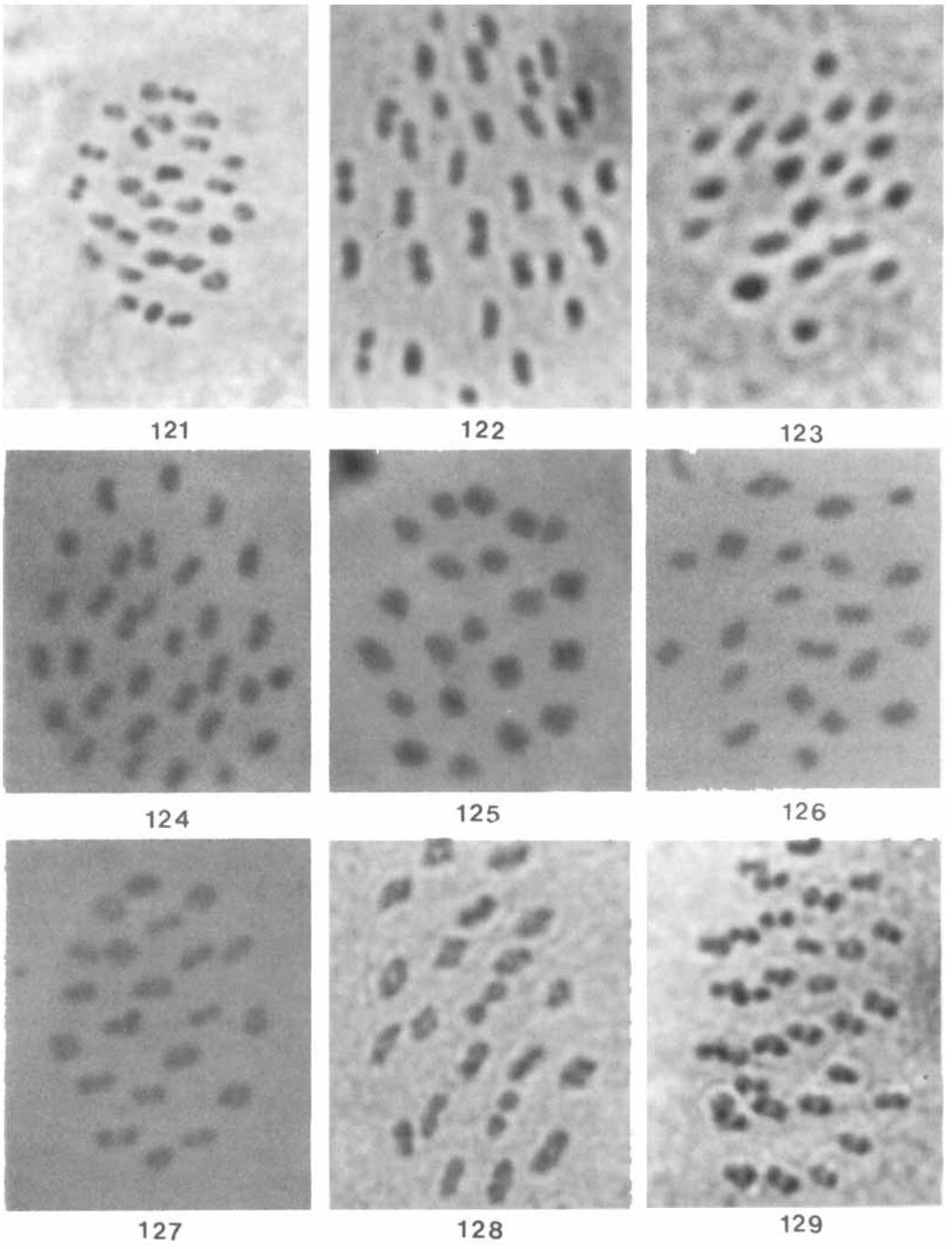
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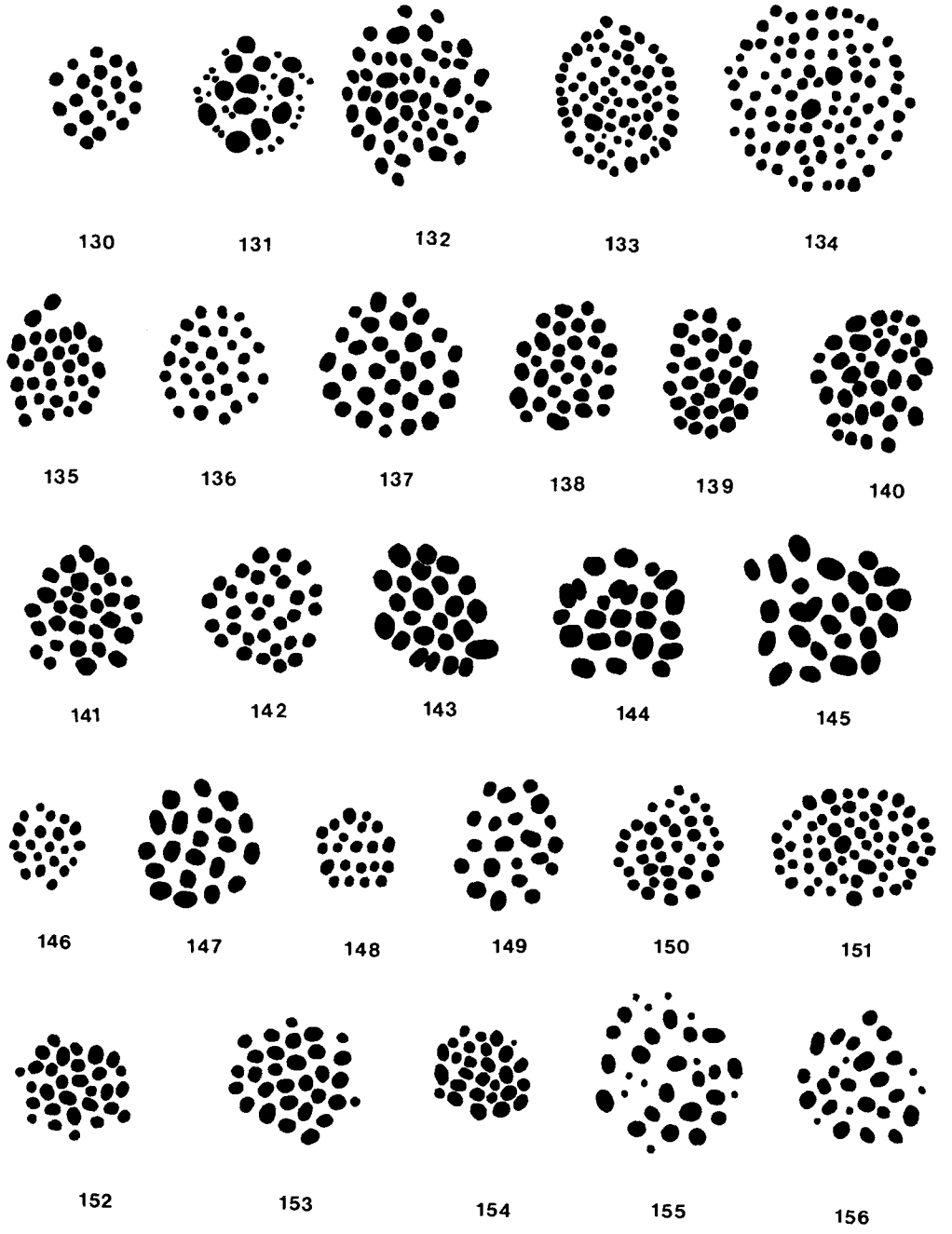

Fig. 1–129. Photographs of male meiotic metaphases of the Heliconiini species. Photographs by Suomalainen (1–120), magnification approximately 2.700×. Photographs by Emmel (121–129), magnification approximately 2.850–2.950×.

Plate 1, Fig. 1–30.

1. *Philaethria constantinoi*, n = 62
2. *P. diatonica*, n = 67
3. *P. wernickei*, n = 29
4. *P. pygmalion*, n = 29
5. *Podotricha telesiphe*, n = 26
6. *P. euchroia*, n = 9

7. *Dione juno miraculosa*, n = 31
8. *D. juno suffumata*, n = 31*
9. *D. glycera*, n = 31
10. *Agraulis vanillae lucina*, n = 31
11. *Eueides lineata emsleyi*, n = 31
12. *E. lineata emsleyi* (reared), n = 31
13. *E. lampeto* subsp. nov., n = 31
14. *E. procula procula*, n = 31
15. *E. procula edias*, n = 31
16. *E. tales xenophanes*, n = 31
17. *E. vibilia vibilia*, n = 31
18. *E. vibilia unifasciatus*, n = 31
19. *E. isabella dianasa*, n = 31
20. *E. tales cognata*, n = 31
21. *E. lybia olympia*, n = 31
22. *E. l. lybia*, n = 31
23. *E. l. lybia*, n = 32
24. *Neruda metharme*, n = 30
25. *N. metharme*, n = 27
26. *N. metharme*, n = 27 (same ind. as 25)
27. *Neruda godmani*, n = 22 + 10 "microchr."
28. *N. godmani*, n = 21 + 10 "MC"
29. *N. godmani*, n = 21 + 7 "MC"
30. *N. godmani*, n = 21 + 6 "MC"

* one bivalent out of focus

Plate 2. Fig. 31–60.

31. *Neruda aoede faleria*, n = 21
32. *N. aoede bartletti*, n = 21
33. *N. aoede eurycleia*, n = 22
34. *N. aoede eurycleia*, n = 21
35. *N. aoede astydamia*, n = 21 + 2–5 "MC"
36. *Laparus doris aristomache*, n = 25
37. *L. doris eratonius*, n = 25
38. *L. doris eratonius*, n = 22
39. *L. doris amathusius*, n = 25
40. *L. doris eratonius*, n = 25
41. *L. doris amathusius*, n = 27
42. *L. doris delila*, n = 21
43. *L. doris delila*, n = 25
44. *L. d. doris*, n = 25
45. *L. d. doris*, n = 25
46. *L. d. doris*, n = 26
47. *L. d. doris*, n = 27
48. *L. doris viridis*, n = 24
49. *L. doris obscurus*, n = 24
50. *L. doris obscurus*, n = 24
51. *Heliconius hecuba choarina*, n = 22
52. *H. hierax*, n = 22
53. *H. hierax*, n = 21
54. *H. xanthocles melittus*, n = 21
55. *H. xanthocles paraplesius*, n = 22
56. *H. xanthocles flavosia*, n = 21
57. *H. xanthocles meridionalis*, n = 21
58. *H. wallacei flavescens*, n = 21
59. *H. wallacei flavescens*, n = 22
60. *H. wallacei wallacei*, n = 21

Plate 3, Fig. 61–90.

61. *Heliconius burneyi/ada*, n = 21
62. *H. burneyi ada*, n = 21
63. *H. astraea rondonia*, n = 21
64. *H. egeria egerides*, n = 21
65. *H. egeria hyas*, n = 21
66. *H. nattereri* (Bahia), n = 21
67. *H. nattereri* (Espirito Santo), n = 21
68. *H. pardalinus orteguaza*, n = 21
69. *H. pardalinus lucescens*, n = 21
70. *H. numata messene*, n = 21
71. *H. numata aristiona*, n = 21
72. *H. numata mirus*, n = 21
73. *H. numata mirus/silvana*, n = 21
74. *H. numata silvana*, n = 21
75. *H. atthis*, n = 21
76. *H. numata silvaniformis*, n = 21
77. *H. numata ethra*, n = 21
78. *H. numata robigus*, n = 21
79. *H. numata geminatus*, n = 21
80. *H. ismenius ismenius*, n = 21
81. *H. hecale nigrofasciatus*, n = 21 + 3 "MC"
82. *H. hecale melicerta*, n = 21
83. *H. ethilla metalilis*, n = 21
84. *H. ethilla chapadensis*, n = 21
85. *H. ethilla narcaea*, n = 21
86. *H. luciana luciana*, n = 21
87. *H. luciana watunna*, n = 21
88. *H. elevatus perchlora*, n = 21
89. *H. elevatus aquilina*, n = 21
90. *H. besckei*, n = 21

Plate 4, Fig. 91–120.

91. *Heliconius heurippa*, n = 21
92. *H. cydno* × *melpomene*, n = 21
93. *H. cydno* × *melpomene*, n = 21
94. *H. melpomene melpomene*, n = 21
95. *H. timareta* ssp. nov., n = 21
96. *H. cydno chioneus*, n = 21
97. *H. cydno weymeri*, n = 21
98. *H. cydno haenschi*, n = 21
99. *H. hermathena sheppardorum*, n = 21
100. *H. telesiphe telesiphe*, n = 21
101. *H. charitonia simulator*, n = 21
102. *H. clysonymus clysonymus/hygiana*, n = 21
103. *H. clysonymus hygiana*, n = 21
104. *H. hecalesia formosus*, n = 21
105. *H. ricini*, n = 21
106. *H. demeter eratosignis*, n = 21
107. *H. sara sara*, n = 21
108. *H. sara sprucei*, n = 21
109. *H. sara apseudes*, n = 21
110. *H. antiochus zobeide*, n = 21
111. *H. antiochus antiochus*, n = 21
112. *H. antiochus alba*, n = 21
113. *H. antiochus salvini*, n = 21

114. *H. congener aquilionaris*, n = 33
115. *H. congener congener*, n = 33
116. *H. sapho sapho*, *n* = 56
117. *H. sapho chocoensis*, n = 57
118. *H. sapho chocoensis*, n = 56*
119. *H. sapho candidus*, n = 56
120. *H. eleusinus primularis*, n = 59
* one bivalent out of focus

Plate 5, Fig. 121–129.

121. *Podotricha telesiphe titraustes*, n = 28
122. *Dryas julia*, n = 31
123. *Heliconius pachinus*, n = 21
124. *Eueides isabella ecuadorensis*, n = 31
125. *Heliconius cydno alithea*, n = 21
126. *H. melpomene cythera*, n = 21
127. *H. erato lativitta*, n = 21
128. *H. clysonymus*, n = 21
129. *Dryadula phaetusa*, n = 31

Plate 6, Fig. 130–156.

Fig. 130–134. Meiotic chromosome sets of the *Philaethria dido* complex from different localities (drawn).
130. Trinidad (secondary spermatocyte metaphase), n = 21
131. Mosqueiro, Pará, Brazil, n = 12 + 25 "michrochromosomes"
132. Tachira, Venezuela, n = 52
133. Linhares, Espirito Santo, Brazil, n = 67 + 2 "MC"
134. Vilhena-Pimenta Bueno, Rondônia, Brazil, n = 87

Fig. 135–156. Meiotic metaphase plates in spermatocytes (drawn).
135. *Dione juno juno*, n = 31
136. *Dryadula phaetusa*, n = 31
137. *D. iulia delila*, n = 31
138. *Eueides pavana*, n = 31
139. *E. tales tales* × *E. tales pythagoras*, n = 31
140. *E. tales tales* × *E. tales pythagoras*, n = 37; a part of chromosomes, probably 6 + 6 have remained unpaired
141. *E. tales pseudeanes*, n = 31
142. *E. aliphera gracilis*, n = 31
143. *Laparus doris aristomache*, n = 24
144. *L. doris eratonius*, n = 24
145. *L. doris viridanus*, n = 25
146. *Heliconius demeter beebei*, n = 21
147. *H. sara magdalena*, n = 21
148. *H. sara brevimacula*, n = 21
149. *H. leucadia pseudorhea*, n = 21
150. *H. eleuchia eleuchia*, n = 37
151. *H. eleusinus eleusinus*, n = 59
152. *Neruda metharme*, n = 30
153. *N. metharme*, n = 30
154. *N. metharme*, n = 28
155. *N. godmani*, n = 21 + 10 "MC"
156. *N. aoede astydamia*, n = 21 + 5 "MC"

that the most evolved, polytypic, and mimetic species in the transitional triad, indeed the only one of the three normally encountered in the field (as *metharme* is exceedingly rare and local though widespread, and *godmani* is confined to the superhumid jungles of western Colombia), has already attained this number in the majority of populations examined (Table 1).

Further deviation from n = 21 then occurs, aside from the monotypic splinter genus *Laparus* (probably related to the *wallacei*-group of *Heliconius*), only at the end of the evolutionary line, in the most advanced *sapho*-group. One of the species, peripheral and geographically highly restricted (*hewitsoni*, possibly a northern outlier of *antiochus*, which is widespread in South America) shows the standard n = 21; this is often accompanied by 1–2 additional chromosomes in *antiochus* itself. An eastern Andean species (*congener*), not strongly polytypic, shows a uniform n = 33, of uncertain derivation. The three common species in the Trans-Andean region show n = 37, 56, and 60 chromosomes, suggesting a progressive fragmentation of the complement along a single radiating line, such as must have occurred at the other end of the tribe in *Philaethria*. Presaging this process is the occasional observation of fragmentations in species immediately antecedent to the *sapho*-group, such as *demeter* (n = 21–23), *sara* (one count of n = 29 in a probably hybrid individual, possibly a result of inadequate pairing), and also in *antiochus* (n = 21–22).

The material examined includes a number of intraspecific and interspecific hybrids found in nature. In one case involving the subspecies of *Eueides tales* from north and south of the Rio Negro which do not often meet, a hybrid gave incomplete chromosome pairing (Fig. 140) with a count of n = 37; other intersubspecies hybrids, with the possible exception of the above-mentioned *sara*, have shown the usual n = 21 or 31. A number of interspecific hybrids between *H. melpomene* and *H. cydno*, which frequently cross in nature, were examined; *all* showed normal chromosome pairing (n = 21). Many of these hybrids probably possess reasonable

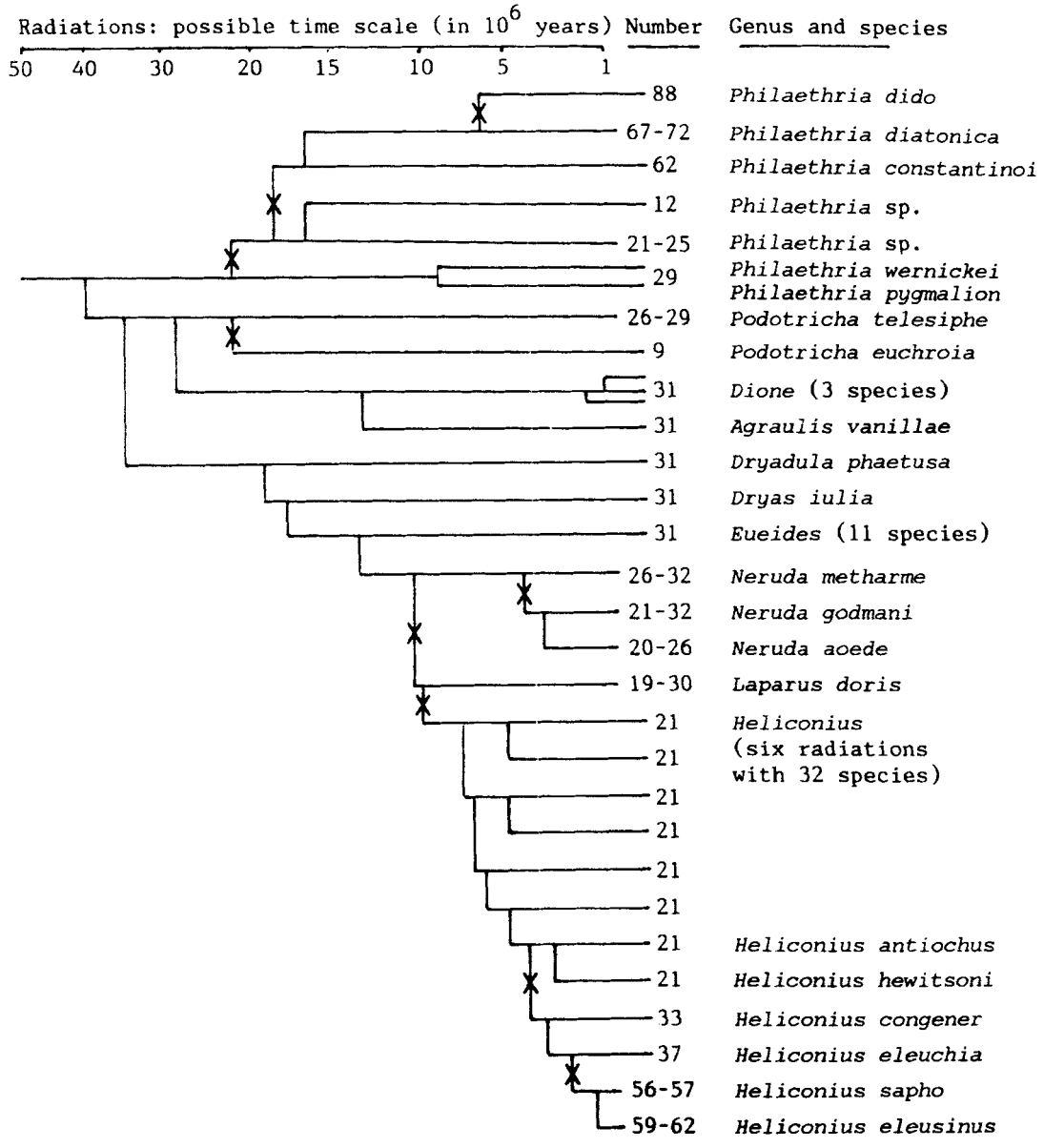

Fig. 157. Evolution of chromosome numbers in the Heliconiini. Adapted from BROWN (1981). X = notable modification of chromosome number.

fertility, and may have given rise to some unusual local species or subspecies like *H. heurippa*, through hybrid stabilization and fixation in the distant past. Since closely related species of *Heliconius* and *Eueides* have the same chromosome numbers and probably homologous genes at many loci (SHEPPARD et al. 1985), it is possible that hybridizations between them could have contributed in an important manner to heliconian evolution.

The overall phylogenetic picture of the Heliconiini (BROWN 1981) is presented in Fig. 157, with the chromosome characters indicated for each taxon. The present survey of this group, while essentially confirming the previously observed patterns, not only reveals an interesting and previously unsuspected transition between the two modal numbers in exactly the subgroup where this occurs in morphological characters, but also identifies four fur-

ther anomalous groups where more extensive studies of the chromosome and evolutionary processes would be exceptionally interesting: *Philaethria*, *Podotricha*, *Laparus*, and the *Heliconius sapho*-group. The first two represent a complex picture of old chromosome evolution, still incompletely understood, while the last two are examples of rapid modern chromosome evolution which need careful study.

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