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Chromosome evolution in Neotropical Danainae and Ithomiinae (Lepidoptera)

KEITH S. BROWN, JR.¹, BARBARA VON SCHOULTZ² and ESKO SUOMALAINEN³

¹*Museu de História Natural, Departamento de Zoologia, Universidade Estadual de Campinas, São Paulo, Brazil*

²*Department of Biological and Environmental Sciences, University of Helsinki, Finland*

³*Deceased 1995*

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Chromosome numbers are given for 1011 populations of 242 species, representing the full range of taxa (49 of the about 52 presently recognized genera) in the Neotropical Nymphalid butterfly subfamily Ithomiinae (prime movers for mimicry rings), including many additional geographical subspecies from 47 regions from México and the Caribbean islands throughout all tropical South American countries to southern Brazil. Twelve Neotropical Danainae (in 3 genera), all but one with $n=29-31$, and the Australian *Tellervo* ($n=32$) served as sister groups for comparison. The numbers range near-continuously from $n=5$ to $n=120$ with modal values (33–84 counts) at $n=12-18$, and only 16 and 26 counts at the usual modal number of all butterfly groups, $n=30-31$. Superimposition of these changes in karyotype on a cladistic phylogeny of the subfamily indicates possible early halving of the complement to n about 14–15, followed by much variation in each genus and tribe. While at least 17 species in 15 genera show stable karyotypes over much of the Neotropics, at least 40 species show large geographical variation in number of chromosomes, rarely accompanied by any evidence for reduction in fertility or incipient speciation. The evolutionary opportunism of the members of this subfamily probably accompanies their known population biology and community ecology: they are common, shade-loving, highly gregarious (occurring in small multispecies “pockets” in deep forest) and often migratory as a community when the environment becomes unfavorable (too hot or dry).

Keith S. Brown Jr., Museu de História Natural, Departamento de Zoologia, Universidade Estadual de Campinas, C.P. 6109, São Paulo 13.083-970, Brazil.

As part of a broad survey of the genetics, ecology, systematic relationships and evolutionary patterns in butterflies of the Neotropics, the first author has fixed in Bouin/Hollande male gonads from over 2000 populations of these insects over the past 35 years, and the second and third have made chromosome preparations from this material by sectioning and staining with hematoxylin. Earlier papers in the series of reports covering the results of this work (de LESSE and BROWN 1971; SUOMALAINEN and BROWN 1984; BROWN et al. 1992) dealt with members of the Nymphalid tribe Heliconiini, for which the essentially complete data revealed a coherent pattern of chromosome evolution, except in the primitive and still enigmatic genus *Philaethria* ($n=12$ to 88). Outside this, only a single derived splinter group (*Laparus doris*) revealed appreciable variation in chromosome number, paralleling its color-pattern polymorphism. A further paper (EMMEL et al. 1995) included incomplete data on the Neotropical Papilionidae (74 populations of 50 species). The modal number $n=30$ was dominant in all branches of the family, with however some variation in each tribe ($n=23$ to $n=45$ in two distasteful species of Troidini, for example).

The Ithomiinae (Nymphalidae) are considered as prime movers in most Neotropical mimicry rings (BROWN and BENSON 1974; BROWN 1987) and show great inter- and intraspecific variation in color and pattern (BROWN 1979). Early work on their chromosomes (de LESSE 1967, 1970a, 1970b; de LESSE and BROWN 1971; WESLEY and EMMEL 1975) also showed large variations in their number, between subspecies or even within single populations. Although neither the systematic revision, nor the coverage in fixing all major taxa, nor the examination of chromosomes is complete for this subfamily of over 350 species (BROWN 1985; LAMAS 2004), enough data are now in hand to permit an overview of the patterns of chromosome evolution at the tribal and generic levels, especially in the more basal or isolated groups. These are presented and discussed here, along with preliminary data on all the genera (including new counts on over 1000 populations representing 242 species) and an overall summary of the emergent patterns in this complex group, which includes many large genera with highly variable karyotype. Based on the chromosome patterns, a supplementary revision is presented for the variable genera *Melinaea* and *Mechanitis* that

form the core of “tiger”-patterned black–yellow–orange mimicry complexes throughout the Neotropics.

For comparison, numbers are also reported for Neotropical species in the sister group of the Ithomiinae, the Danainae (ACKERY and VANE-WRIGHT 1984). While large in the Old World, this subfamily is small in the Americas (only 14 species); the members also serve as foci for large mimicry rings in all the continents, but tend to join Ithomiinae-based rings in the Neotropics.

MATERIAL AND METHODS

Field-fixing and laboratory sectioning and staining methods follow those detailed in the earlier papers in this series (SUOMALAINEN and BROWN 1984; BROWN et al. 1992). Thus, field-collected male butterflies (from over 3200 collecting days) were kept alive until just before dissection, within 12 h of capture. The fused and usually red-colored testis was removed dorsally with fine-tipped forceps through an incision between the sixth and seventh abdominal segments, described (size and color), and dropped into Hollande’s modification of Bouin (picric acid-cupric acetate-water 5:8:200 plus 49% formaldehyde-acetic acid 20:3 added afterwards). After at least 12 h (and up to many years), the material was washed in tap water, transferred to 80% alcohol with a unique number, sent to Finland and kept at low temperature. After paraffin blocking, the testis was sectioned to 10 μ m and stained with Heidenhain’s iron hematoxylin. Photographs (Leitz Orthomat camera, Agfa Agepe 35 mm film) or drawings if all chromosomes could not be seen in the same plane (Wild apparatus, bench level) were prepared of dividing meiotic nuclei (normally first metaphase) as observed through a 12.5 \times ocular and a 100 \times immersion objective. The final magnification is about 2500 \times .

Voucher specimens are deposited in the Museu de História Natural of the Universidade Estadual

de Campinas, São Paulo, Brazil, accompanied by their unique number.

RESULTS

Table 1 to 3 summarize results obtained to date for the Ithomiinae; Table 4 contains the results for the 12 American Danainae. In all, individuals from 1011 populations of Ithomiinae were fixed; 1437 individuals in 242 species and 592 subspecies gave usable karyotypes. The Tables include data published by previous authors, and a very few (8) counts on material fixed by the first author in HOAc-EtOH and later squashed and stained with aceto-lacto-orcein by P. C. Eliazar and T. C. Emmel (Univ. of Florida, Gainesville). The complete list of all individuals fixed can be downloaded from <http://www.oikos.ekol.lu.se> and from the author K. S. Brown upon request. Figure 1 shows the Ithomiinae results over a cladogram of this subfamily, constructed with over 150 characters and 240 derived states (BROWN and FREITAS 1994; FREITAS and BROWN 2004). Figure 2 shows the distribution of known numbers, from 5 to over 100 for genera and species of Ithomiinae; Fig. 3 gives similar results for the Danainae, including on a world scale. Selected chromosome complements (meiotic plates) are illustrated in Fig. 4–78.*

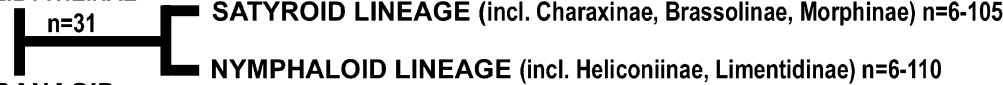
DISCUSSION

The modal class of chromosome complement in the Ithomiinae is $n = 14$ (Fig. 2), almost half that seen in most Lepidoptera including the sister groups Danainae (Fig. 3) and Tellervinae (SUOMALAINEN 1969; LORKOVIC 1990). The karyotype of butterflies has a constant total volume. Fissions and fusions, not polyploidy, are responsible for changes in chromosome numbers. Well over half of all Lepidoptera counted with $n = 14$ are Ithomiinae; almost half of the 52 genera in this subfamily are dominated by this class and neighboring ones, suggesting a very early and strong stabilization of the karyotype at this

*As this paper went to press, a new arrangement of the Ithomiinae appeared in the Catalogue of Neotropical Lepidoptera, part 4A (LAMAS 2004). This Catalogue disagrees little from this paper in the definitions and ordering of species, genera and tribes. It also unites or separates a number of the species and subspecies names used in Table 1–3 and 5–7, without major differences in the relations among them (indeed, the chromosome numbers help to support unity or separation of a number of species, mostly corresponding to the arrangement in the Catalogue). The most important divergences in higher classification (from that in Fig. 1) are as follows: (1) Tribe E (*Roswellia-Athesis-Patricia*) remains within the Melinaeini, with the first two genera united under the second name; (2) *Athesis* (*Roswellia*) *vitrata* becomes a full species; (3) *Athyrtis* is between *Eutresis* and *Olyras*; (4) *Methona* is placed as the earliest genus in the Mechanitini; (5) Napeogenini (tribe G) is anterior to Ithomiini (Tribe F); (6) *Rhodussa* and *Garsauritis* are joined with *Hypothyris*, while *Hyalyris* is anterior to *Napeogenes*; (7) *Ollantaya* is joined with *Oleria*; (8) *Ceratonia* is at the base of the Dircennini; (9) *Prittwitzia* and *Ceratiscada* are joined to *Episcada*; (10) *Episcada* has several species combined; (11) *Dygoris* is included in *Godyris*; and (12) *Hypomenitis* is combined into *Greta*. There are quite a few more minor differences, mostly species separations or unions that only time and biological work will resolve. The chromosome numbers help to resolve many of the differences in nomenclature between the lists.

NYMPHALIDAE

LIBYTHEINAE



DANAOID LINEAGE

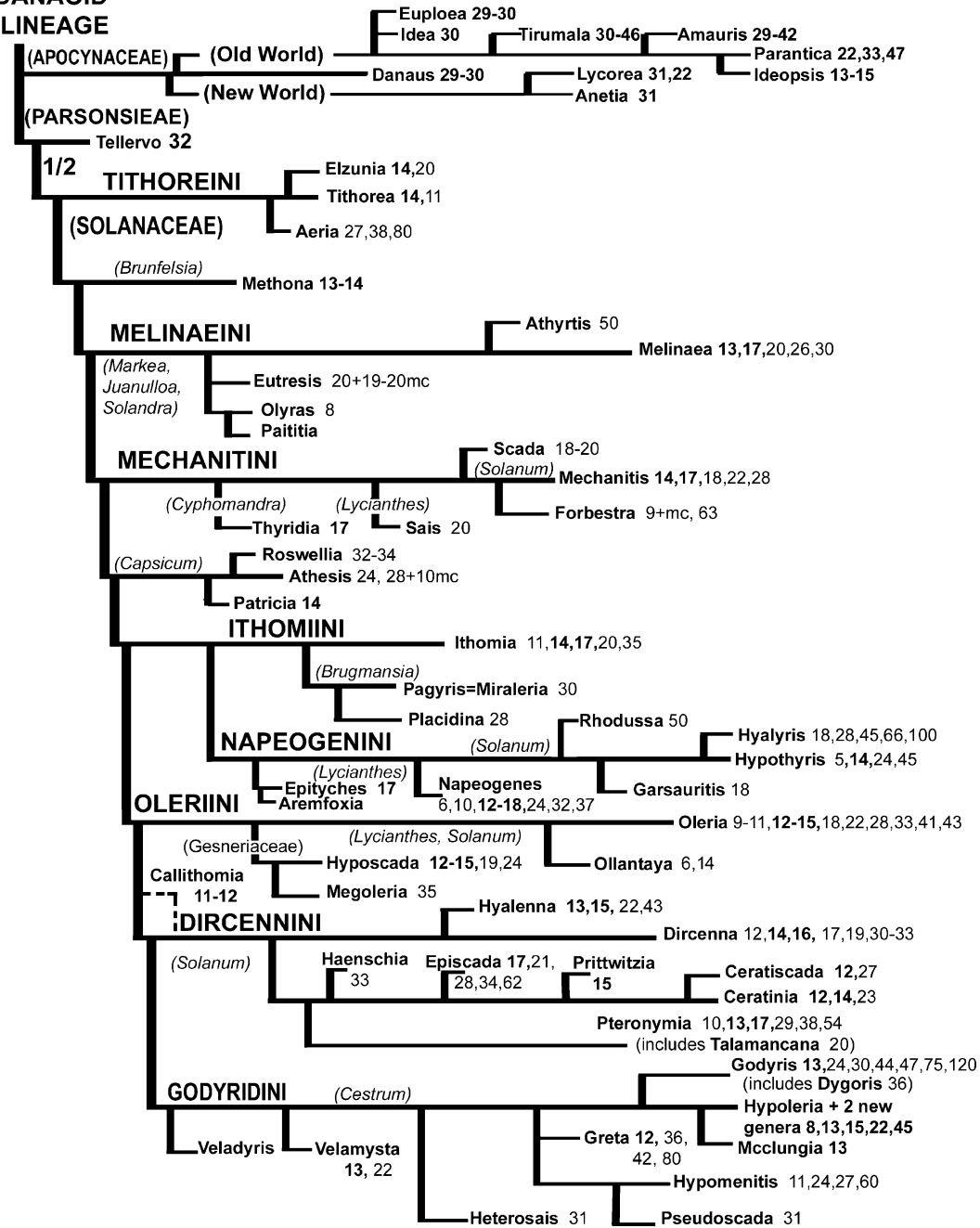


Fig. 1. The chromosome numbers of Danainae and Ithomiinae over a cladogram of these subfamilies. The systematics and cladogram are based on BROWN and FREITAS (1994) and FREITAS and BROWN (2004), with important contributions of LAMAS (2004) and (for molecular data) N. WAHLBERG and A. BROWER (work in progress with AVFL). The origin of the Ithomiinae has evidently been accompanied by an approximate halving of the modal lepidopteran n = 31 to a new modal n = 14. The further diversification of the group has included both fusions and fissions. This process has run in parallel with the acquisition of novel larval food plants, shown in parentheses. The food plants contain noxious chemicals; the butterflies have not only adapted to tolerate these but also to use them as chemical defences (BROWN 1987). For details of the chromosome numbers consult the Tables.

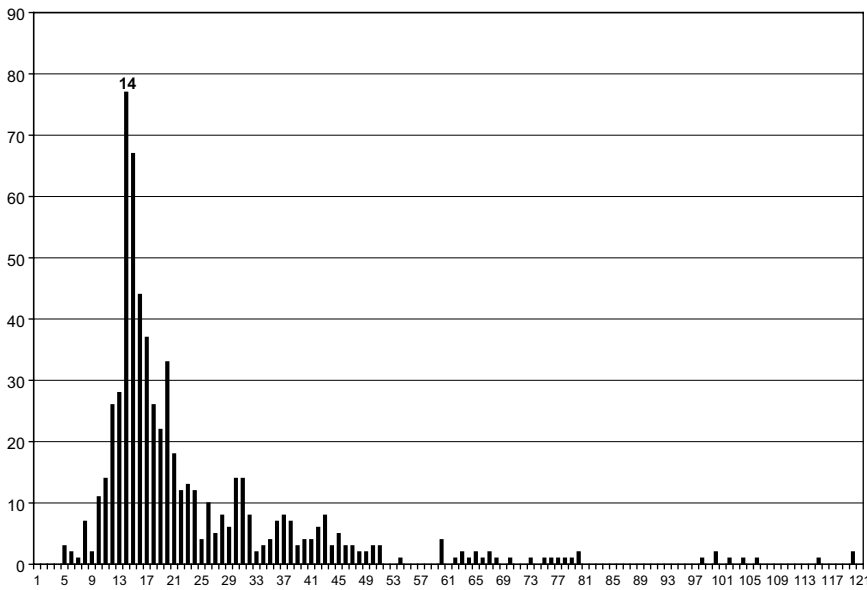


Fig. 2. The distribution of known chromosome numbers, from $n=5$ to 120 for species and subspecies of Ithomiinae.

level (Fig. 1). As expected, the chromosomes of species with a low chromosome number are larger than the ones of species with high numbers. In contrast, very few species (11) in only six genera show $n=30$ or 31, and $n=29$ is only rarely seen as a variant of $n=30$ or higher in the Ithomiinae. The extraordinary radiation of ithomiine genera and species with numbers between 11 and 20 might be compared with that of the genus *Heliconius* with a nearly stable complement of 21 chromosome pairs

(BROWN et al. 1992), but there is an important difference. Unlike *Heliconius*, the Ithomiinae show excessive infrageneric and even infraspecific variation in karyotype, confirming the observations of earlier authors (de LESSE 1967, 1970a, 1970b; de LESSE and BROWN 1971; WESLEY and EMMEL 1975). Most of the larger genera present very complex patterns of chromosome number variation, as do some older genera (Fig. 1), and very few general tendencies are discernible.

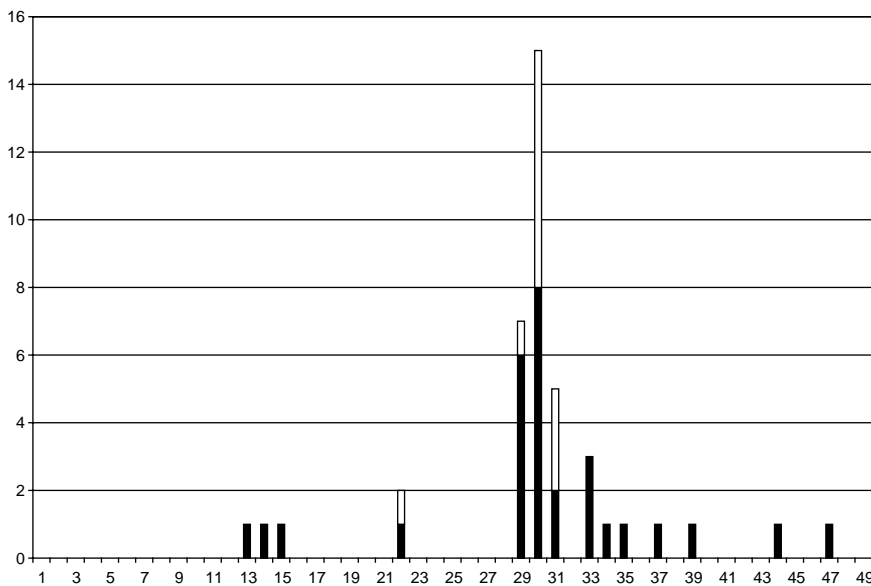


Fig. 3. The distribution of known chromosome numbers for the Danainae. The light part of the columns shows the numbers for the Neotropical species, while the shaded parts show the distributions for the Old World species according to ACKERY and VANE-WRIGHT (1984, pp. 92–93).

The haploid chromosome numbers within the subfamily Ithomiinae range from $n=5$ through $n=120$. We may note here that $n=5$ is the lowest haploid number recorded for any lepidopteran (FREEMAN 1969). The total range of variation within the subfamily is one of the most extensive ones within the Animal Kingdom. KANDUL et al. (2004) have shown that the haploid chromosome numbers within the Palearctic lycaenid butterfly genus *Agrodiaetus* range from $n=10$ to $n=125$. This range of variation within a genus is second only to one held by the genus *Apiomorpha* of coccids, hemipteran insects that like lepidopterans have holokinetic chromosomes. The Ithomiine genus *Godyris* has an about equally extensive range: from $n=13$ through $n=120$. Several other genera, e.g. *Aeria*, *Hyaliris* and *Greta* have only slightly less extensive ranges of haploid chromosome number variation.

A parsimonious scheme (Fig. 1) over a cladogram updated from that in BROWN and FREITAS (1994) suggests reduction of the complement to $n=14$ as early as the second New World node (*Tithorea*), with larger numbers then appearing very regularly in series in later genera. An alternative might conserve the larger number through all radiations to the most advanced genera (*Pseudoscada* and *Heterosais*, both with $n=30-31$), with reductions in almost all branches, accompanied or followed by later increases, but this requires many more steps. The choice is not easy to make, however; and any narrative explanation of such a complex pattern is somewhat forced (a "just-so story"). It seems best to simply accept a profound and repeated instability in the genome and karyotype of these mimetic insects, perceivable even in today's reality within the boundaries of well-defined and acceptable species and populations (Table 1-3, Table 5-8). It would be in accord with current suggestions about chromosomal lability accompanying evolutionary opportunism (WAHRMAN and GOUREVITZ 1973), which is a characteristic of mimetic groups, as discussed in earlier papers in this series

(SUOMALAINEN and BROWN 1984; BROWN et al. 1992).

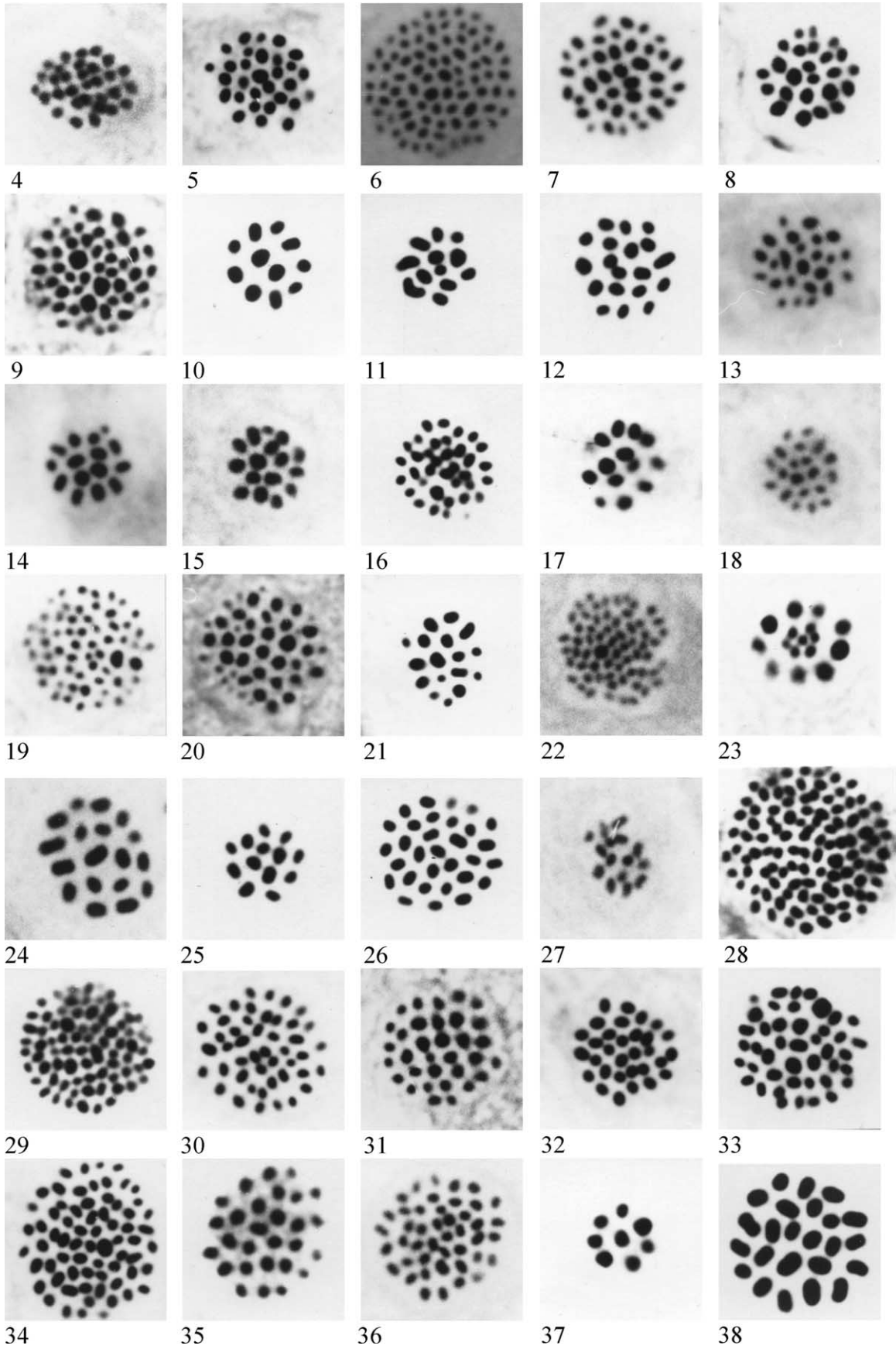
In contrast, the New World Danainae show a very stable chromosome complement at the usual mode for Lepidoptera, $n=29-31$ (Table 4, Fig. 3; two haploid chromosome sets are illustrated in Fig. 4 and 5). Only *Lycorea pasinuntia*, a recent species restricted to the Amazon/Guiana region, deviates from the norm. In their much larger radiation in the Old World tropics, the Danainae show some tendency for increase of number (up to $n=35-47$) with only a single species with 13-15 (ACKERY and VANE-WRIGHT 1984; Fig. 3). We thus regard the primitive number of the Danaoid lineage (Fig. 1; FREITAS and BROWN 2004) of Nymphalidae as 30-31, with early stabilization in the Ithomiinae of numbers about half this. The great variability can then be understood as a result of marked chromosomal instability within populations, long evolutionary time, and many ecological opportunities for radiation and differentiation associated with a mimetic life-style and selection regime, with frequent isolation in allopatric regions of favourable super-humid vegetation (cloud forests, gallery forests, and hilly regions near rivers, lakes or oceans).

Details of various groups

a. Small and monotypic genera and their closest relatives. — In the Ithomiinae, the species, the genera, and their relationships have been traditionally and quite stably defined by wing venation, minor wing-color elements, and morphology of male genitalia and hairpencils, plus palps and legs of both sexes. Recent addition of information on female genitalia and early stages produced only a few important rearrangements to the generally well-accepted systematics (MIELKE and BROWN 1979; BROWN 1985). The contrasting lability of the ithomiine chromosome complement is seen even within the smallest of the recognized genera, which with 2-3 species often show great variation in karyotype, and if monotypic, often show a greatly different number from that typical of the nearest genera. Table 5 summarizes these comparisons and

Fig. 4-78. Selected photograph of male meiotic metaphases of the Danaine (Fig. 4-5) and Ithomiinae (Fig. 6-78) species. Magnification for Fig. 4-38 is $\times 1700$ and for Fig. 39-78 $\times 1400$. Additional photographs are available on <http://www.fmnh.helsinki.fi/Ithomiinae>.

Fig. 4-38. (4) *Anetia briarea*, $n=31$. (5) *Danaus erippus*, $n=30$. (6) *Aeria elara*, $n=80$. (7) *A. eurimedia agna*, $n=38$. (8) *Athesis clearista*, $n=24$. (9) *Athyrtis mechanitis*, $n=50$. (10) *Callithomia hezia beronilla*, $n=11$. (11) *C. lenea zelia*, $n=12$. (12) *Ceratinia tutia chanchamaya*, $n=19$. (13) *Ceratiscada canaria*, $n=24$. (14) *Dircenna dero ca. dero*, $n=15$. (15) *Dircenna dero euchytna*, $n=16$. (16) *Dygoris dircenna*, $n=36$. (17) *Elzunia humboldt bomplandii*, $n=14$. (18) *E. pavonii*, $n=20$. (19) *Episcada carcinia*, $n=60$. (20) *E. philoclea*, $n=42$. (21) *Epityches eupompe*, $n=17$. (22) *Forbestra equicola* ssp., $n=63$. (23) *F. proceris*, $n=9+7$ mc. (24) *Garsauritis xanthostola*, $n=18$. (25) *Godyris kedema*, $n=13$. (26) *G. nepos hewitsoni*, $n=31$. (27) *G. nero*, $n=15$. (28) *G. petersii*, $n=\sim 105$. (29) *G. sappho*, $n=77$. (30) *G. z. zavaleta*, $n=46$. (31) *Haenschia derama*, $n=33$. (32) *Heterosais giulia nephele*, $n=31$. (33) *Hyalenna pascua*, $n=43$. (34) *Hyaliris antea frater*, $n=68$. (35) *H. oulita* ssp., $n=28$. (36) *Hypoleria (Brevioleria) sarepta goiana*, $n=44$. (37) *Hypoleria* near *pachiteae* or *plithenes*, $n=8$. (38) *Hypothyris mamercus*, $n=24$.



permits an overview of chromosomes in closely related pairs of taxa. Whether a change in chromosome number was an important component in the process that led to reproductive isolation between incipient species is a subject that cannot be evaluated by experiment today; but it does seem that a change in the number of chromosomes has at least accompanied differentiation in other morphological characters, which possibly restrict gene flow or hybridisation.

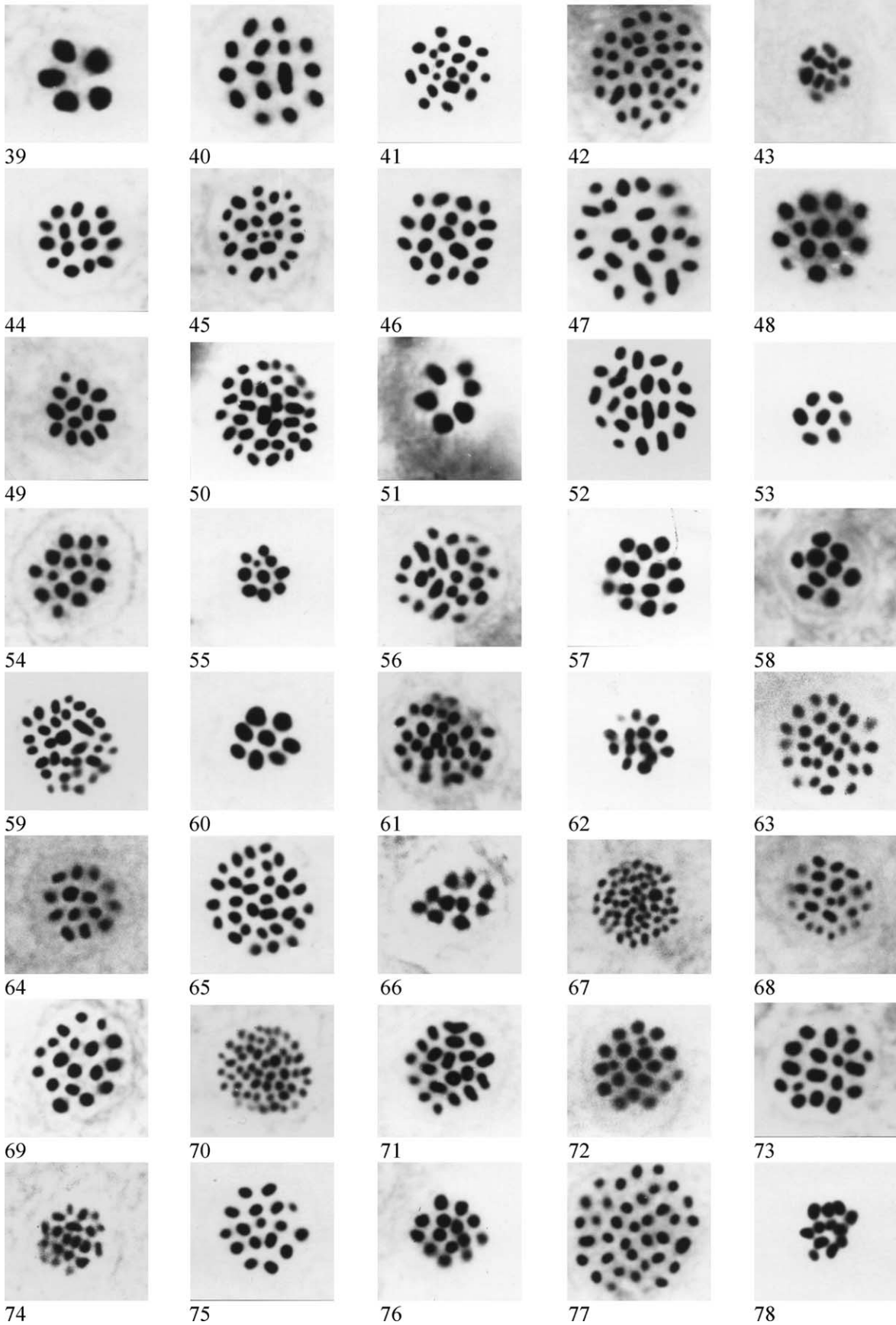
b. Variation within a genus or species. — Although definition of species is not always clearly and objectively possible in some groups of Ithomiinae, due to uniform morphology or confusing color-pattern characters, many genera have been adequately revised in recent years (BROWN 1979, 1980, 1985; BROWN and FREITAS 1994) and their species limits defined. The two most difficult primitive genera, *Melinaea* and *Mechanitis*, have repeatedly been subjected to new revisions as further data came to light (FORBES 1948; D'ALMEIDA 1951, 1978; FOX 1960, 1965, 1967; BROWN 1977, 1979; LAMAS 1988, 2004), and are once again partially revised in the last paragraph (g) of this section (Table 7–8), on the basis of the new chromosome information. Very complex patterns, still not completely characterized, are seen in some large derived genera, discussed briefly in paragraph (e). Outside of these cases, a number of well-accepted and integrated species of Ithomiinae show appreciable geographic variation in chromosome numbers (not due to variable microchromosomes), with or without evidence for partial barriers to gene flow in mixed populations (Table 6). These cases are of special interest to the geneticist, for they may be in an intermediate stage of species formation, and could be expected to show unusual cytogenetic phenomena, ecological peculiarities, and possible mosaic evolution in different parts of their ranges. Mostly members of larger mimetic groups or species groups, and significantly concentrated in the tribe Napeogenini (G, Table 2), they need to be carefully examined for further geographical variation and possible reduction of fertility in zones of subspecies intergradation, or between geographically isolated or distant populations.

c. Chromosome number variation within populations. — Certain species of Ithomiinae show variation in chromosome number in different individuals of the same population, and sometimes even in different dividing cells in the same gonad. Although this phenomenon is well known in some species, especially in Lycaenidae (LORKOVIC 1941; de LESSE 1960; EMMEL et al. 1973), it is not common in animals and suggests truly extraordinary mechanisms of gametogenesis.

In the Ithomiinae, small variation in number was observed quite frequently in dividing cells from a single individual, usually amounting to no more than 1–2 chromosomes or 5–10% of the total complement (Table 1–3). This and larger intrapopulational variation (not always shown in the Tables and probably not related to experimental technique or microscope/sectioning variation), was seen most often in the same species that showed large geographical variation in number, marked with an asterisk (*) in Table 6. Greatest variation was seen in the Napeogenini, as for variation between populations. de LESSE (1967) noted this in *Napeogenes stella* ($n=11-13$) in Victoria, Colombia, where very different numbers ($n=12, 15$) were also seen in *Ceratinia iolaia*. Further species which show notable chromosome variations in single populations, not in Table 6, include several *Melinaea* (*M. mnasias*, *M. lilis*, *M. maenius*, *M. marsaeus*; see paragraph (g)), *Scada zibia* ($n=17-19$), most *Mechanitis* (see paragraph (g)), *Oleria ilderina* ($n=28-30$), *Rhodussa cantobrica* ($n=45-51$), *Napeogenes aethra deucalion* ($n=12-14$), *N. ithra* ($n=14-16$), *Hypothyris semifulva* ($n=15-17$), *Ithomia amarilla* ($n=15-18$), *I. pellucida* ($n=12-14$), *Godyris zavaleta* ($n=35-45$), *Hypomenitis ortygia* ($n=88-95$), *Greta diaphanus* ($n=69-74$), *Pseudoscada erruca* ($n=29-31$) and *Heterosais giulia* ($n=29-31$). All these examples help to emphasize the appreciable lability shown by the chromosome complement of a wide range of Ithomiinae during meiosis; it is not known whether this can give an excess of defective or inviable gametes or zygotes.

d. Microchromosomes and supernumeraries. — Some of the variation seen in observed chromosome numbers, especially when these are large, is due to a

Fig. 39–78. (39) *H. thea*, $n=5$. (40) *Ithomia amarilla*, $n=15$. (41) *I. ellara*, $n=20$. (42) *I. salapia derasa*, $n=35$. (43) *Mcclungia cymo salonina*, $n=10$. (44) *Mechanitis lysimnia elisa*, $n=15$. (45) *M. menapis*, $n=24$. (46) *Melinaea lilis lateapicalis*, $n=20$. (47) *M. (ludovica?) crameri*, $n=23$. (48) *Methona grandior*, $n=14$. (49) *Napeogenes apulia*, $n=13$. (50) *N. cyrianassa* ssp. nov., $n=32$. (51) *N. harbona domiduca*, $n=6$. (52) *N. inachia pyrois*, $n=22$. (53) *N. verticilla*, $n=7$. (54) *Oleria astraea thiemei*, $n=15$. (55) *O. deronda innocentia*, $n=10$. (56) *O. egra*, $n=23$. (57) *O. ilderina priscilla*, $n=14$. (58) *O. victorine graziella*, $n=9$. (59) *O. zelica*, $n=32$. (60) *Olyras crathis*, $n=8$. (61) *Pagyris cymothoe*, $n=30$. (62) *Patricia deryllidas*, $n=14$. (63) *Placidina eurynassa*, $n=28$. (64) *Prittwitzia hymenaea centralis*, $n=14$. (65) *Pseudoscada timna*, $n=31$. (66) *Pteronymia donella donata*, $n=10$. (67) *P. hara semonis?*, $n=54$. (68) *P. oneida asopo*, $n=24$. (69) *P. zerlina*, $n=18$. (70) *Rhodussa cantobrica nundina*, $n=51$. (71) *Sais rosalia* ssp., $n=20$. (72) *Scada karschina*, $n=20$. (73) *S. zibia*, $n=18$. (74) *Talamancana lonera*, $n=20$. (75) *Thyridia psidii ino*, $n=17$. (76) *Tithorea harmonia dorada*, $n=14$. (77) *Velamysta peninna*, $n=38$. (78) *V. phengites*, $n=12$.



variable number of microchromosomes which appear in the dividing plates (Fig. 20 and 23). This is most evident in the genus *Forbestra* (tribe D, Table 1), where two species (*F. olivencia* and *F. proceris*) have a low basic number ($n=9$) and a variable amount (1–8) of additional minute chromosomes; the third (*F. equicola*) has a high number ($n=60-65$), with most chromosomes very small like the microchromosomes of the other two species. This tendency for fragmentation must be important in the over-all complex chromosome evolution of the Ithomiinae, for it appears throughout the subfamily, especially in the most variable or advanced groups. Among other species notable for variable microchromosomes or variable large numbers are (with tribe letters in parentheses) the following (not all shown in the Tables): (A) *Aeria elara* ($n=76-82$), (C) *Eutresis hypereia* (39–40, half of these very small), (D) *Scada batesi* ($n=43$, two very small), (E) *Athesis clearista* ($n=24-28+10$ mc), (G) *Hyaliris metella* ($n=98-100$), (J) *Godyris telesilla* ($n=100-120$), *G. zygia* ($n=75$), *G. zavaleta* ($n=36-46$) and *Hypomenitis theudelinda* (n = about 100).

e. Large and poorly defined genera (Table 2, 3, 7 and 8). — The largest genera of the Ithomiinae are all composed of primarily transparent-winged species in the most advanced radiations: (F) *Ithomia* (22 species), (G) *Napeogenes* (23), (H) *Oleria* (40), and (I) *Pteronymia* (46). With the chromosome numbers in hand, it becomes apparent that a number of somewhat smaller genera are also confusing in their patterns of species differentiation; (G) *Hyaliris* (13 species), (H) *Hyposcada* (8), (I) *Callithomia* (only 3?), *Dircenna* (7), *Hyalenna* (only 5?), and *Episcada* (20), (J) *Godyris* (14), *Hypoleria* sensu lato (13; divisible into three genera), *Hypomenitis* plus *Greta* (30), and *Pseudoscada* (4, possibly divisible into 2 genera). All of these genera also have transparent wings in most species and races, with few useful characters for identification, and variable and often poorly understood genital morphology. While it could be expected that the chromosome numbers, even though highly variable in some of these genera, would eventually help in the recognition of monophyletic units which may correspond to the typically widespread species known in other genera, the intraspecific variations mentioned in the above paragraphs will continue to make species determinations difficult in these fifteen genera. At the present, the chromosomes give suggestive support to a majority of species separations and subspecies associations as shown in Table 2 in *Ithomia*, *Napeogenes*, *Hyposcada*, *Hyalenna*, *Episcada*, *Godyris*, *Hypoleria* and *Hypomenitis*, but need to be further expanded and correlated with other morphological characters. While some

limited systematic progress might be claimed for *Oleria* and *Greta*, many more counts are still needed in these genera. The genera *Hyaliris*, *Dircenna* and *Pteronymia* remain chaotic, in some cases even worsened by the chromosome information, and the numbers are relatively uninformative in *Callithomia* and *Pseudoscada*.

f. Widespread species or genera with very stable karyotypes. — In contrast to the cases discussed in previous sections and presented in Table 5–6, a number of species and genera seem to have attained a remarkably stable chromosome complement over ranges covering most of the Neotropical region (Table 1–3). The following widespread and highly differentiated species have essentially identical numbers (in parentheses) in all regions examined (range shown after number): *Tithorea harmonia* (14) Mexico-Argentina, *Aeria eurimedia* (36–40) Costa Rica-Rondônia, *Aeria elara* (76–80) Venezuela-S. Brazil, *Methona* spp. (13–14) Venezuela-S Brazil, *Thyridia psidii* (17) Costa Rica-S Brazil, *Sais rosalia* (20) N Venezuela-SE Brazil, *Ithomia agnosia* (18) N Venezuela-S. Brazil, *Hypothyris leprieuri* (20) Guyane-SW Brazil, *Ceratinia neso* (14) N Venezuela-SW Brazil, *Prittwitzia hymenaea* (15) N Venezuela-Argentina, *Hypoleria ocalea* (10–11) N Colombia-SC Brazil, *Mclungia cymo* (11) Venezuela-SE Brazil, *Pseudoscada* spp. (30–31) N Colombia-Argentina, and *Heterosais* spp. (31) Panamá-SC Brazil. No simple pattern emerges for this list of “stable” species, neither in the stabilized number (10 to 80), the generic or ecological characteristics (from rare in deep forest to migratory and eurytopic), nor the phylogenetic position (the two extremes of the subfamily are included), but at least they may be recognized and used as controls for future studies of karyotype variation, its mechanisms and its influences.

g. Supplementary revision of the genera Melinaea and Mechanitis. — Table 1 contains the chromosome numbers for 168 populations of essentially all the species and most of the subspecies in two genera of large, common “tiger-striped” Ithomiinae. In *Mechanitis* (Table 7), the chromosome data confirm the union of *macrinus* with “*doryssus*”, *labotas* and *solaria*, but separate this Transandean complex ($n=22-24$) from *M. lysimnia* ($n=15-20$), the widest spread – $n=23$ versus 15 – occurring where the two species are potentially sympatric in eastern Colombia. The three principal subspecies of *lysimnia* have different numbers (*nesaea*, $n=17$; *lysimnia*, $n=19$ and *elisa*, $n=15$), but these usually intergrade in color-pattern and number ($n=16, 18$) whenever they meet. In two places in southern Mato Grosso and southern Bahia, however, two subspecies occur together or nearby with

Table 1. Summary of chromosome numbers in *Tellervo* and in the “primitive” radiation of *Ithomiinae*. Locality codes are shown at the end of Table 2. Localities in **bold** indicate places of origin of material for meiotic metaphases shown in Fig. 6 through 78.

Tribe	Genus	Species, subspecies	n =	No. fixed/counted			
				Pop./ind.	Ind.	Localities	
A	<i>Tellervo</i>	<i>zoilus zoilus</i>	32	3/5	1	QA3 (EMMEL et al. 1974)	
	<i>Aeria</i>	<i>o. olena</i>	27	3/3	3	AR(a),ES,SP	
		<i>eurimedia</i> (4 different)	°°38°°	10/16	7	AC3,CC3, RG3 ,RO	
	<i>Elzunia</i>	<i>elara</i> (3 different)	°°°°80°°	8/28	8	AC,AN,DF, GO ,MT,RG2,RO	
		<i>humboldt</i> (4 different)	14	5/8	1	AN,CC,EE,TV,VC	
	<i>Tithorea</i>	<i>pavonii</i>	°20	3/7	3	MP3	
		<i>harmonia</i> (16 different, from <i>salvadoris</i> to <i>caissara</i>)	°14	22/45	25	AM2,AN(a),AR(a), BO ,CM,EB,EV,GO(d),HU,MP,MT2,MX(b),PA,RG,RO2,RR2,SP,TR(e)	
	B	<i>Methona</i>	<i>t. tarricina, franciscoi, parola</i>	11	5/10	3	AN,CT2,VC2
			<i>m. megisto</i> , new ssp.	14	3/4	3	AM,MT,PA
			<i>curvifascia</i>	14	4/9	3	AC,EE2,HU
<i>g. grandior</i>			14	2/4	4	AC, AM	
<i>confusa</i> (3 different)			14	11/20	18	AC,AM2,CM,EB,EE2,RO2,RR,TV	
<i>themisto</i> ssp. nov.			14	1/1	1	GO(d)	
<i>singularis</i>			13	2/4	1	PB,PE	
C	<i>Olyras</i> <i>Eutresis</i> <i>Athyrtis</i> <i>Melinaea</i> (see details of this genus in Table 8)	<i>crathis</i> (4 different)	8	5/15	12	CC,EV, RG2 ,TV	
		<i>h. hypereia</i>	20+19-20	2/6	4	EV,RG	
		<i>mechanitis salvini</i>	°50°	8/13	11	AC2,RO6	
		<i>mnasias</i> (4 different)	°°26°°	5/7	5	AP,BA,CM,GY(c),RR	
		<i>l. ludovica</i>	17-23	12/19	18	AM5,AP2,GY(c),PA,RO,RR2	
		<i>paraiya; crameri</i>	°23°	4/5	5	BA,RJ(d),SPEV, BO	
		<i>i. idae, vespertina</i>	13	4/4	4	AN,CC,CZ,WE	
		<i>maelus</i> (8 different)	°15°°	10/23	18	AC2,AM2,EB3,EE,HU,RO	
		<i>lilis</i> (6 different)	°°22°°	7/11	11	CC,CH,EV,MX,OX,RG,TR(e),TV	
		<i>ethra</i>	°30	5/8	7	BA,ES,PE,RJ,SP	
		<i>mneme</i> (3 different)	°17	5/21	18	AM,AP2,GY(c),RO	
		<i>menophilus</i> (3 different)	°20°°	6/12	11	AC,EE(a),EE,RO3	
		<i>marsaeus</i> (4 different)	°17°	9/16	15	AC2,PA,RO4,VV2	
		<i>phasiana, satevis</i>	15	3/4	4	AC2,EB	
<i>maenius</i> (6 different)	°°22°°	10/18	17	AC,AP2,EE4,GY(c),RO,VV			
D	<i>Thyridia</i> <i>Sais</i> <i>Scada</i>	<i>psidii</i> (6 different)	17	11/15	12	AC,CH2, EE2 ,ES,GO,MP,MT2,RO	
		<i>rosalia</i> (6 different)	20	11/26	14	AC,ES,GO,MT,PA,RG,RO3,RR2	
		<i>z. zibia, xanthina, zeroca</i>	°18°	4/6	2	CC3 ,CH	
		<i>batesi; batesi quotidiana</i>	43	2/7	2	AC,EE	
		<i>reckia</i>	28?	3/9	1	BA2,PE	
		<i>ethica</i> (6 different)	°21°°	7/14	10	AC2,AM,EE,PA,RO,RR	
		<i>karschina</i>	20	2/7	3	BA ,ES	
		<i>kusa</i>	21	2/5	1	MP2	

Table 1 (Continued)

Tribe	Genus	Species, subspecies	n =	No. fixed/counted		
				Pop./ind.	Ind.	Localities
	<i>Mechanitis</i> (see details of this genus in Table 7)	<i>l. lysimnia</i>	18–19	5/10	7	AR(a),BA,GO,RJ(d),SP
		<i>nesaea, connectens</i>	16–17°	7/31	23	BA2;GO,MT2,PB,RO
		<i>meneclis, ocona, acreana, elisa</i>	15	7/26	15	CM,EB(a),EB2,EE,MT,RO
		<i>macrinus</i> (4 different)	22,23	4/8	5	CH,CZ,EV,RG
		<i>polymnia</i> (7, Transandean)	°18°°	11/31	24	AN(a),CC,CZ,EV,GU(a),MX,RG, VC2,VV,WE
		(9, Amazonian to SE Brazil)	°15°	27/58	43	AM,AP3,CM,DF(d),EB,EE,GO,HU, MG,MP,MT5,PA3,RJ,RO3,RR3
		<i>menapis</i> (4 different)	°°24–25°°°	8/19	14	AN(a),CC3,EV,RG,VC2
		<i>dariensis, mantineus</i>	20	2/5	4	DA,WE(incl. a)
		<i>mazaesus</i> (6 different, Amazon Basin)	14,15	7/15	14	AC,AM2,EE,RO,VV2
		(4 from peripheries)	°°16	10/36	21	EE3,CM,GY(c),PA2,RO,VV2
		<i>proceris</i>	9+6–8	2/4	4	AC2
		<i>olivencia</i> (4 different)	9+1–6	5/11	10	AC2,AM,EB,EE
		<i>equicola</i> (4 different)	°°°63°°	5/11	11	AC,AM,AP,EE,RO
E	<i>Roswellia</i>	<i>acrisione</i> (f), <i>a. vitrala</i>	32,34	2/4	2	EE(f),MP
	<i>Athesis</i>	<i>clearista, c. colombiensis</i>	24	5/11	8	AN,EV,RG2,VC
			28+10	1/2	2	RG
	<i>Patricia</i>	<i>d. deryllidas</i>	14	1/2	2	VC
		<i>d. demylus</i>	14	1/1	1	EE(f)

Explanation of Tables: nomenclature follows Lamas (2004) with few exceptions (Results, footnote). Superscript dots before and after a number indicate variation, as much as 3–6 over or under the given figure, encountered infrequently, rarely in the same population.

Localities are grouped by region; a number at the end indicates more than one population sampled within this region; a letter in parentheses indicates previous work (a = de LESSE 1967, b = de LESSE 1970a, c = de LESSE 1970b, d = de LESSE and BROWN 1971, e = WESLEY and EMMEL 1975, f = Eliazar and Emmel, pers. comm., g = MAEKI and REMINGTON 1960, h = MAEKI 1961).

Locality codes: AC = Acre (SW Brazil), AM = Amazonas (N Brazil), AN = NC Colombia, AP = Amapá (N Brazil), AR = N Argentina, AV = Amazonas (S Venezuela), BA = Bahia (Brazil), BO = Bolivar (SE Venezuela), CC = Chocó (W Colombia), CH = W Panama, CM = Chanchamayo (C Peru), CR = Costa Rica, CT = NW Venezuela, CZ = Canal Zone (Panama), DA = E Panama, DF = Brasília, DR = Dominican Republic, EB = E Bolivia, EE = E Ecuador, ES = Espíritu Santo (Brazil), EV = NE Venezuela, GO = Goiás (C Brazil), GU = Guatemala, GY = Guianas, HU = Huallaga Valley (C Peru), JM = Jamaica, LO = NE Peru, MG = Minas Gerais (Brazil), MP = upper Río Marañón (NW Peru), MT = Mato Grosso (Brazil), MX = SE Mexico, OX = S Mexico, PA = Pará (Brazil), PB = Paraíba (NE Brazil), PE = Pernambuco (NE Brazil), PT = S Colombia, QA = N Queensland (Australia), RG = N Venezuela, RJ = Rio de Janeiro (Brazil), RO = Rondônia (SW Brazil), RR = Roraima (N Brazil), SC = Santa Catarina (S Brazil), SP = São Paulo (SE Brazil), TR = Trinidad, TV = Táchira (SW Venezuela), VC = Valle de Cauca (W Colombia), VV = Meta (E Colombia), WE = W Ecuador.

Table 2. Chromosome numbers in "advanced" Ithomiinae: smaller or better-defined genera. Localities in **bold** indicate places of origin of meiotic metaphases shown in Fig. 4 through 78.

Tribe	Genus	Species, subspecies	n =	No. fixed/counted				
				Pop./ind.	Ind.	Localities		
F	<i>Pagyris</i>	<i>cymothoe</i>	30	3/9	4	RG,TV,VV		
	<i>Placidina</i>	<i>euryanassa</i>	28	2/2	2	BA,RJ(d)		
	<i>Ithomia</i>	<i>iphianassa</i> (5 different)	°11–12	8/18	11	AN2,CC2,RG,VC,VV,WE		
		<i>p. pellucida</i> , ssp.	14	2/2	1	MPTV		
		<i>terra</i> (4 different)	15–17	4/6	5	CC,CH,CM,EE		
		<i>amarilla</i>	15–16°°	1/9	3	EE		
		<i>jucunda bolivari</i>	16	2/2	1	CH2		
		<i>diasia</i> (3 different)	17	5/12	10	CC3,CH,WE		
		<i>celemia plaginota</i>	17–18	1/3	2	CH		
		<i>agnosia</i> (4 different)	°18°	7/18	17	GO,EE3,PE,RG,RJ		
		<i>p. patilla, leila</i>	18	3/3	3	CH,GU(a),MX(a)		
		<i>lichyi</i> (3 different)	18	3/9	2	AC,BA,RJ(incl.d)		
		<i>h. hyala</i> , ssp.	19	2/5	2	CC,WE		
		<i>lagusa theuda, linda</i>	19	3/6	6	EE,VC2		
		<i>avella</i>	20	1/1	1	VC		
		<i>drymo</i>	20	2/4	4	ES,RJ(d)		
		<i>ellara</i>	20,21	1/2	2	CM		
		<i>salapia</i> (3 different)	34–35°°°	6/20	11	AC2,CM,EE3		
		G	<i>Epityches</i>	<i>eupompe</i>	17	2/4	2	BA,RJ
				<i>harbona domiduca</i>	6	1/1	1	CM
<i>Napeogenes</i>	<i>verticilla</i>		7	1/1	1	CM		
	<i>gracilis</i>		12	1/2	2	CM		
	<i>pharo</i> (4 different)		10,11,13	5/9	6	AC,PA,RO2,VV		
	<i>aethra deucalion</i> , ssp.		12,13,14	4/9	7	AC2,RO2		
	<i>a. apulia, lycora</i>		13	2/3	3	EE,VV		
	<i>sylphis</i> (4 different)		14°°	8/11	8	AM,AP,PA2,RO4		
	<i>s. stella, opacella</i>		°12,13,14	4/9	7	AN2(incl.a),CC2		
	<i>(stella?) duessa, jamariensis</i>		15	2/6	4	AC,RO		
	<i>cranto</i> ssp. nov.		18	1/1	1	WE		
	<i>inachia johnsoni, pozziana</i> (NW)		13,14	2/6	4	EE,VV		
	ssp. nov. (SW)		16,17,18	5/7	7	MT3,RO2		
	<i>pyrois</i> , 2 sspp. nov.(C)		22	3/5	2	AM2, PA		
	<i>(inachia?) sulphurina</i> , ssp. nov.		24,26,28	4/10	5	BA,PE3		
	<i>cyrianassa</i> (7, Amazon)		°32°	11/22	13	AM2,AP2,BO,PA,RO,3,RR2		
	<i>rhezia, yanetta</i>		35,37	4/9	5	BA2,ES2		
	<i>Hyaliris</i>		<i>leptalina</i> ssp. nov.	18	1/3	1	ES	
			<i>c. cana</i>	20	1/1	1	RG	
			<i>oulita? oulita lurida?</i>	26,28	2/8	2	CM,EB	
<i>o. ocna, adelinda</i>		°43	2/2	3	EE,VV			
<i>coeno</i> (4 different)		°48–49	4/23	12	MP,RG,TV,VV			

Table 2 (Continued)

Tribe	Genus	Species, subspecies	n =	No. fixed/counted		
				Pop./ind.	Ind.	Localities
		<i>excelsa</i> ssp. nov	60	1/2	2	TV
		<i>antea flebilis, frater</i>	°66°	2/7	6	CM,TV
		<i>metella</i>	98–100	1/5	3	CM
	<i>Garsauritis</i>	<i>x. xanthostola</i> , ssp. nov.	18,20	2/4	3	AM,AP
	<i>Rhodussa</i>	<i>cantobrica mundina</i> , ssp. nov	50–51	3/9	5	RO3
	<i>Hypothyris</i>	<i>thea, theatina, vestita</i>	5	4/6	5	AM2,PA2
		<i>(fluonia?) rowena</i>	9	1/3	2	VV
		<i>fluonia</i> (4 Amazonian ssp.)	°°15°°	5/14	6	AC2,GO,MT,RO
		<i>euclia</i> (8 Amazonian and Atlantic subspp.)	14°	18/42	32	AC,AM,AP2,BA,CM,EB2,EE3, ES, GO,MT,RG,RO,TR,TV
		<i>valora, philetaera</i>	°16°	4/10	7	AN,CC,CZ,VC
		<i>ninonia</i> (9 Amazonian subspp.)	°°16°°	16/46	36	AC,AP2,AM5,BO,MT,PA2,RO2, RR2
		<i>daeta</i>	18–19	4/9	8	BA,ES,MG(a),RJ(a)
		<i>evanescens</i>	21–23	3/10	9	BA2,PE
		<i>semifulva</i> (3 different)	°°17°°	5/10	8	AC2,RO3
		<i>v. vallonina</i> , ssp. n.	°°20°°	2/3	3	PA,RR
		<i>d. daphnis, madeira</i>	°20	2/9	4	AM,RO
		<i>leprieuri</i> (4 different)	°20	10/16	14	AC2,GY(c),MT3,RO4
		<i>anastasia</i> (3 different)	17,20,21	3/6	3	AC2,RO
		<i>mamercus</i> (4 different)	°24°°	6/13	7	AC,EE,RO4
		<i>lycaste</i> (5 different)	°°°45°°	5/11	7	CC,EV,GU(b),RG,VC
H	<i>Hyposcada</i>	sp.	12	1/2	2	CC
	(the genus <i>Oleria</i> is in Table 3)	sp.	12	1/2	1	AM
		<i>illinissa abida</i>	12	1/3	2	CC
		<i>attilodes?</i>	13	2/2	2	EE2
		<i>zarepha</i>	14	4	14	AP
		<i>illinissa</i> (4 different)	13,15	4/9	2	AM,EE,PT,RR
		<i>v. virginiana, consobrina</i>	15	2/2	2	AN,CC
		<i>anchiala</i> (3 different)	15	3/7	5	AC,EE,RO
		[like <i>makrena</i>]	19	1/1	1	EE
	<i>Megoleria</i>	<i>orestilla</i>	35	1/4	1	EE(f)
	<i>Ollantaya</i>	<i>aegineta cleobulina</i>	6?	1/1	1	CM
		<i>canilla</i>	14	1/3	2	CM
I	<i>Callithomia</i>	<i>hezia beronilla</i>	11	1/1	1	CC
		<i>alexirrhoe</i> (5 different)	12	6/6	5	AM,GY(c),MT,PA2,RO
		<i>lenea</i> (5 different)	12°°	12/19	11	BA,EB2,MT5,PA,RO,RR2
	<i>Dircenna</i>	<i>loreta</i> (4 different)	°12	12/21	14	EE3,MT,PA,RG,RO4,VV2
	(the genus <i>Pteronymia</i> is in Table 3)	<i>adina</i> (3 different)	14	4/8	7	EE2,RG,TV
		<i>dero</i> (4 different)	14,15	14/44	20	AC,CM,EB2,EE,ES2,GO,MG2, MT,PE,SP,VV

Table 2 (Continued)

Tribe	Genus	Species, subspecies	n =	No. fixed/counted		
				Pop./ind.	Ind.	Localities
		<i>"dero" euchytna</i> (Transandean)	16,17	7/12	11	AN(a),CH2,RG2,VC2
		<i>p. paradoxa</i> , ssp.	17	2/3	3	VC,WE
		<i>jemina</i> (5 different)	°19°	5/14	11	CH,CM,EB,EV,RG
	(may be hybrids or contaminants)	<i>"dero celtina"</i>	23	1/3	3	AR(a)
		<i>"dero rhoeo, dark"</i>	30,33	1/3	2	GO
	<i>Hyalenna</i>	sp. nov.	13	1/1	1	WE
		<i>a. alidella</i>	15	1/2	2	VC
		<i>minna</i>	22	1/2	2	CM
		<i>pascua</i>	43°	3/9	5	RJ,SP2
	<i>Haenschia</i>	<i>derama</i>	33	1/4	3	CM
	<i>Episcada</i>	<i>hemixanthe</i>	16	1/2	2	BA
		<i>mira</i>	17	3/5	3	AC,EE,VV
		<i>c. clausina, striposis</i>	°21°	3/5	4	EB,RJ(d),SP
		<i>montanella</i>	24	1/3	2	SP
		<i>munda</i>	26–27 + few	1/5	4	SP
		<i>philoclea</i>	28 + many	3/6	4	RJ,SP2
		<i>polita</i>	28°	5/6	4	AC2,CC,TV2
		<i>sylpha</i>	31	2/7	1	RG,TV
		<i>s. salvinia, cabenis</i>	°°34°	5/7	5	MX,OX,VC3
		<i>carcinia</i>	60–62	3/5	2	BA,SP2
	<i>Prittwitzia</i>	<i>hymenaea</i> (4 different)	°15	7/12	10	AR(a),BA,DF,GO,MG(d),RJ,RG
	<i>Ceraticscada</i>	<i>doto</i> ssp.	12	1/1	1	BO
		<i>canaria</i>	24,27	2/7	3	BA,ES
	<i>Ceratinia</i>	<i>iolaia</i>	12,14,15	1/5	5	AN(incl.a)
		<i>neso</i> (7 different)	14	9/21	14	BO,CM,EE2,RG,RO2,RR,VV
		<i>tutia</i> (10 different)	°°17°°°	17/32	17	AC3,AN,CC,CM,EE4,RG3,RO, VC,VV2
		<i>c. cayana, giparanaensis</i>	19 + 1,23	2/2	2	RO,RR
	<i>Talamancana</i>	<i>lonera</i>	20	1/1	1	CH
J	<i>Velamysta</i>	<i>phengites</i>	12	1/1	1	EE
		<i>pupilla cruxifera</i>	22	1/1	1	EE
		<i>peninna</i> ms. ssp.	38	1/3	2	CM
	<i>Dygoris</i>	<i>d. dircenna</i> , ssp. nov.	36	2/4	4	CM,VV
	<i>Godyris</i>	<i>kedema</i> (3 different)	13	3/9	4	EV,RG,VV
		<i>nero</i>	15	2/2	2	CH,OX
		<i>crinippa</i> ssp.	24	1/1	1	CM
		<i>nepos hewitsoni</i> , ssp. nov.	31,32	2/2	2	CM,EE
		<i>panthyale</i> ssp.	44	1/1	1	CM
		<i>duillia</i>	46,47	1/1	1	VV
		<i>zavaleta</i> (5 different)	°°°°40°°°°°°	7/27	17	CM,EE,RO3,TV,VV
		<i>zygia</i>	75	2/3	3	CH2
		<i>sappho</i>	77	1/2	1	CM
		<i>gonussa, petersii, telesilla</i>	98–120	5/11	9	AN,CC2,WE2

Table 2 (Continued)

Tribe	Genus	Species, subspecies	n =	No. fixed/counted		
				Pop./ind.	Ind.	Localities
	<i>Greta</i>	<i>p. polissena, umbrana</i>	12	3/6	1	CH,WE2
		<i>(andromica?) andania</i>	°36°	2/8	5	CM,EE
		<i>a. andromica, lyra</i>	°42°	8/18	6	AN2(a),CC,CH,RG,TV,VC,WE
		<i>morgane oto</i>	°°47°	3/5	2	CH,MX(b),OX
		<i>quisqueya</i>	70	1/6	2	DR
		<i>diaphanus</i>	78	1/5	2	JM
		<i>annette</i>	73,80	4/4	2	CH,OX3
		<i>cyrilla?</i>	24	1/1	1	CM
		<i>dercetis</i>	27	4/7	2	EE2,RG,TV
		<i>enigma</i>	42	1/3	3	WE
<i>Hypomenitis</i>	<i>alphesiboea</i>	60	2/2	1	EE,VV	
	<i>ortygia ssp.</i>	68	1/1	1	CM	
	<i>ochretis</i>	"very many"	2/2	1	AN,VC	
	<i>theudelinda</i>	about 100	1/6	2	EE(f)	
	<i>cymo</i> (4 different)	°11	6/9	4	BO,GO2,MG2,MT	
	<i>fallens</i> (3 different)	13	4/12	5	AC,RJ,RO	
	<i>aelia pachiteae, plisthenes</i>	8	14/28	11	AC3,BA,DF(d),GO2,MG,MT2, RO3,SP	
	<i>orolina</i> (5 different)	°15°	7/15	6	AC2,DF,GO,MT,RO,SP	
	<i>ocalea</i> (4 different)	10,11	6/15	9	AN2,MT2,RG,RO	
	<i>adasa</i> (3 different)	20°	4/8	3	ES,GO,RJ(d),RR	
<i>Hypoleria</i>	<i>lavinia</i> (4 different)	26,29–30	5/10	6	CC2,CZ,TV,WE	
	<i>alema</i> (12 different)	36–38, 40–43	16/34	15	AC2,AP,BA,EE,ES,GO,MT4,PA,PE, RO2,VV	
	<i>sarepta virginia</i> , +2 different	44,45	6/11	8	AC3,AM2,SP	
	<i>erruca</i>	°30°	7/12	4	ES,MG4,RJ2	
	<i>timna</i> (5 different)	°31°	12/34	16	AC2,AN(a),CC2,CH,C-M,EE2,RG,VV,WE	
<i>Pseudoscada</i>	<i>florula</i> (4 different)	30–31	7/23	11	AC2,BA2,EE,ES,RJ	
	<i>acilla quadrifasciata</i> , ssp.	31	5/16	13	GO(d),MT3,RO	
	<i>giulia</i> (5 different)	°°31	15/31	20	AN(a),CH,CM,EB,EE,HU,MT3, RG,RO3,VV,WE	
<i>Heterosais</i>	<i>edessa</i>	30–31	4/7		PE,BA,ES2	

Table 3. Chromosome numbers in two large, poorly resolved genera: *Oleria* and *Pteronymia*. Localities in **bold** indicate places of origin of meiotic metaphases shown in Fig. 54–59 and 66–69.

Tribe	Genus	Species, subspecies	n =	Pop./ind.	Ind.	Localities		
H	<i>Oleria</i>	<i>victorine graziella</i>	9	2/6	4	RG2		
		<i>deronda valida</i>	10	1/1	1	CM		
		<i>fasciata</i>	11	1/2	1	CM		
		<i>gunilla lota, lubilerda</i> +2	10,11	5/15	5	AM2,EE2,VV		
		<i>amalda, a. modesta</i>	12	3/8	3	CC2,WE		
		<i>olerioides</i>	12	1/1	1	CM		
		<i>peruicola</i>	13	1/2	2	CM		
		<i>makrena</i> ?+2	°13°	7/16	6	CC,CH,CM,CZ,VC,WE2		
		<i>manora</i>	14	2/5	4	RO,RJ(d)		
		<i>cyrene</i>	14	1/6	5	CM		
		<i>aegle</i>	14,15	1/2	2	AP		
		<i>ilerdina priscilla, quintina</i>	°14°	6/25	18	AC2,CM,EB2,HU		
		<i>alexina didymaea</i> +2	°°15	7/10	6	PA,RO,RR,EB		
		<i>a. astraea, burchelli, similigena</i>	°15	5/25	12	AC2,AM,AP, BA3 ,EE,ES		
		<i>p. paula</i>	16	2/3	3	MX2(b)		
		<i>phenomoe</i>	18,19	3/8	2	RG,TV2		
		<i>onega crispinilla</i> +1	°22	4/12	5	AC3,CH		
		<i>e. egra, divisa</i>	23–24	3/11	2	AM2,AC		
		<i>e. estella</i>	27–28	2/5	4	EE2		
		<i>padilla pseudmakrena</i> +2	30	3/12	2	CM,RG,VV		
		<i>o. onega, ilerda, machadoi</i> +1	30°	5/8	5	AP2,CM,EE,VV		
		<i>zelica</i> (2 different)	32,29	2/7	7	VE, WE		
		<i>athalina</i>	41	1/1	1	CM		
		<i>aquata</i> (3 different)	°°43°°	8/26	7	AC,BA2,ES,GO,MT2,RO		
		I	<i>Pteronymia</i>	<i>donella donata</i>	10	1/1	1	DA
				<i>alida</i>	13	1/2	1	RG
				<i>vestilla</i> ? (2 different)	14	3/6	5	AN,PA,VC
<i>sylvo</i>	14			5/7	2	AR(a),GO,MG,RJ(d),RO		
<i>euritea</i>	14			2/6	6	ES,RJ(d)		
<i>cotytto</i>	15			1/1	1	MX(b)		
<i>são guntheri</i> , ssp. nov. (Lamas)	15			2/3	1	AC,CM		
<i>artena</i> (3 different)	15			3/4	3	EE,TV,VV		
<i>forsteri</i>	16			1/1	1	AC		
<i>latilla</i> (3 different)	16			3/11	5	CC,RG,TV		
<i>veia linzera</i> +4	°°17°			7/10	9	CM,EE,HU,TV,VC2, WE		
<i>o. oneida</i>	20			1/1	1	EE		
<i>granica</i> ?	23			1/1	1	EE		
<i>oneida</i> ? <i>asopo</i> (2 different)	°24°°			4/7	3	EE2 ,RG,TV		
<i>zerlina nubivaga</i>	26			1/2	1	RG		
<i>aletta</i>	26			4/10	3	AN,CC,RG,TV		
<i>teresita thabena</i>	38			1/10	2	EE(f)		
<i>hara semonis</i> ?	54			1/2	1	VC		

Table 4. Chromosome numbers of the American *Danainae*. The taxonomic division follows ACKERY and VANE-WRIGHT (1984). The numbers $n = 29$ for *D. eresimus* and ($n = 29-30$) for *D. gilippus* come from MAEKI (1961); the number for *D. plexippus* comes from a population kept at the University of Madras, India (RAO and MURTY 1975).

Tribe	Genus	Species, subspecies	n =	No. fixed/counted		
				Pop./ind.	Ind.	Localities
A	<i>Anetia</i>	<i>thirza</i>	31	1/2	1	OX
		<i>briarea</i>	31	1/5	2	DR
		<i>pantheratus</i>	31	1/2	1	DR
B	<i>Lycorea</i>	<i>cleobaea</i> (2 different)	30	2/2	2	AN(a),RJ(d)
		<i>pasimuntia</i> (3 different)	22	10/17	10	AC3,AM3,EV,GY(c),RO2
		(<i>Ituna</i>) <i>ilione</i> (2 different)	30	3/5	4	EE2(incl. a),VV
C	<i>Danaus</i>	<i>cleophile</i>	30	1/2	1	DR
		<i>plexippus</i>	30	1/1	?	Madras, India
		<i>erippus</i>	30	1/2	2	SP
	(Anosia)	<i>eresimus</i> (5 different)	°30	6/8	5	CT,DR,DA,EV,MX(gh)
		<i>plexaure</i>	30–31	1/2	2	BA
		<i>gilippus</i> (2 different)	29°	3/6	3	BA,ES,MX(gh)

Not counted: *Anetia jaegeri*, *A. cubana*.

Table 5. Chromosome number comparisons in monophyletic sister-groups (within small genera, or between them and their closest relatives).

Tribe (Fig. 1)	Genus (most primitive or widespread species)	n/n	More advanced or restricted species, or putative sister-genus
A	<i>Elzunia humboldt</i>	14/20	<i>Elzunia pavonii</i>
	<i>Tithorea harmonia</i>	14/11	<i>Tithorea tarricina</i>
	<i>Aeria olena</i>	27/38, 80	<i>Aeria eurimedia</i> , <i>A. elara</i>
E	<i>Athesis clearista</i>	24/14	<i>Patricia</i> (2 spp.)
C	<i>Olyras crathis</i>	8/20 + 19–20 mc	<i>Eutresis hypereia</i>
	<i>Melinaea</i> (10 spp.)	13–30/50	<i>Athyrtis mechanitis</i>
D	<i>Thyridia psidii</i>	17/18–43	<i>Sais rosalia</i> , <i>Scada</i> spp.
	<i>Mechanitis lysimnia</i>	15–19/22–23	<i>Mechanitis macrinus</i>
	<i>Forbestra olivencia</i>	9 + mc/63	<i>Forbestra equicola</i>
I	<i>Callithomia</i> (3 spp.)	11–12/12–38	<i>Velamysta</i> spp.
H	<i>Ollantaya canilla</i>	14/6	<i>Ollantaya aegineta cleobulina</i>
	<i>Hyposcada</i> (11 spp.)	12–15/9–43, 35	<i>Oleria</i> (>20 spp.), <i>Megoleria susiana</i>
G	<i>Epityches eupompe</i>	17/6–37	<i>Napeogenes</i> spp.
F	<i>Pagyris cymothoe</i>	30/11–35	<i>Ithomia</i> spp.
G	<i>Garsauritis xanthostola</i>	18–20/50–51	<i>Rhodussa cantobrica</i>
I	<i>Hyalenna</i> sp. nov., <i>H. alidella</i>	13,15/22, 43	<i>Hyalenna minna</i> , <i>H. pascua</i>
	<i>Ceraticada doto</i>	12/24–27	<i>Ceraticada canaria</i>
	<i>Prittwitzia hymenaea</i>	15/17–62	<i>Episcada</i> spp.
J	<i>Dygoris dircenna</i>	36/13–120	<i>Godyris</i> spp.
	<i>Meclungia salonina</i>	11/8–45	<i>Hypoleria</i> spp.
	<i>Heterosais</i> , <i>Pseudoscada</i>	31, 30–31/12–100	<i>Greta</i> , <i>Hypomenitis</i>

Table 6. *Ithomiine species with appreciable geographic variation in their chromosome numbers, in different localities (see also Table 7–8). Asterisk (*) indicates variation within populations also.*

Tribe	Genus	Species	Localities	n =	Comments
E	<i>Athesis</i>	<i>clearista</i>	Colombia, W Venezuela NE Venezuela	24 28 + 10 mc	Related <i>Roswellia</i> has 32, 34
F	<i>Ithomia</i>	* <i>iphianassa</i>	C Colombia Venezuela, W Ecuador	10 12–13	Intergrade freely giving n = 11, 12
		<i>terra</i>	W Colombia Eastern Peru	14 17	n = 16 also known in between these
G	<i>Garsauritis</i>	<i>xanthostola</i>	Amapá, N Brazil Manaus, C Amazon	20 18	
	<i>Napeogenes</i>	* <i>inachia</i>	E Colombia Rondônia, SW Brazil Amapá-Para, N Brazil	13–14 16–18 22	The conspecificity of these populations might be questioned!
		<i>sulphurina</i>	Pernambuco, Bahia	24, 26, 28	
		* <i>stella</i>	Central Colombia W Colombia	11–13 12–14	Almost surely all are conspecific
	<i>Hypothyris</i>	* <i>ninonia</i>	Amazonian Brazil	15–18	Possibly not the same species
		* <i>n. daeta</i>	Eastern Brazil	18–23	
		<i>vallonia</i>	Roraima, N Brazil Pará, E. Brazil SW Venezuela	24 20–21 22	Sister sp. (<i>gemella</i>) has n = 18–20 in Roraima, Venezuela
		<i>fluonia</i>	E Colombia E Ecuador S-C Brazil	9 16–17 13	Conspecificity is quite certain for all these
		* <i>euclea</i>	C America– W Colombia Amazon to S Brazil	16–17 12–15	Intergrades in W Colombia, n = 16–17
		* <i>lycaste</i>	Guatemala W Colombia W Ecuador	48 42–45 50	
H	<i>Oleria</i>	* <i>aquata</i>	SE Brazil SW Brazil	46 43	
		<i>zelica</i>	W Colombia W Ecuador	29 33	Most species have the same number in both
I	<i>Dircenna</i>	<i>dero</i>	C America to W Ecuador S Brazil–Argentina	16–17 14–15	
	<i>Ceratinia</i>	* <i>tutia</i>	C America– W Colombia N Venezuela Acre, SW Brazil Rondônia, SW Brazil	15–16 19–20 15 18	Almost surely these are conspecific with each other
	<i>Ceraticada</i>	<i>canaria</i>	Bahia, E Brazil Esp. Santo, E. Brazil	24 27	
J	<i>Hypoleria</i>	<i>lavinia</i>	Costa Rica to W Colombia W Ecuador	26 29	
		<i>alema</i>	SW Venezuela	30	
		<i>oreas</i>	SW Brazil NE Brazil NW Brazil E Colombia	36 40–42 38, 40 37–38	

Table 7. Chromosomes and systematics of *Mechanitis* species and subspecies.

Species	Subspecies examined	Localities	n =	Comments
<i>lysimmia</i>	<i>menecles, ocona, acreana, elisa</i>	CM,EB,EE,MT,RO	15	no variation in these western ssp.
	<i>lysimmia</i>	AR,BA,RJ	18–19	Form “connectens” (GO,MT) has n = 16–17
	<i>nesaea</i>	BA,PB	17	Form “sulphurescens” has n = 18
<i>macrinus</i>	<i>macrinus, utemaia, solaris</i> , new ssp.	CH,CZ,EV,RG	22–24	Consistently higher n than <i>lysimmia</i> , for names see LAMAS (1988)
<i>polymnia</i>	<i>lycidice, isthmia, veritabilis</i> , <i>weneri, caucaensis, kayei</i> , <i>chimborazona</i> (Transandean)	AN,CC,CZ,EV,MX,VC,WE	17–19	Occasionally to n = 20 or more, especially in Sucre/Trinidad
	<i>bolivarensis, dorissides</i> , <i>proceriformis, eurydice</i> , <i>polymnia, mauensis</i> , new ssp., <i>angustifascia, casabranca</i>	MP,RR,VV,EE, CM,PA,AM,MT,CM, EB,HU,GO, MG,RJ	14–16	n = 16 seen very rarely, possibly due to non-pairing in an otherwise stable complement
<i>menapis</i>	<i>menapis, occasiva, caribensis</i> , new ssp.	DA,CC,VC,RG,EV	24–25	occasionally lower (22–23 in E Venezuela) or higher (28 in W Colombia)
	<i>dariensis, mantineus</i>	DA,WE	20	lowest numbers at extremes of range
<i>mazaesus</i>	<i>mazaesus, elevata, egaensis</i> , <i>pannifera, visenda, pothetoides</i> , various forms	GY,VV,EE,AM, RO,PA,AC	14–16	darker forms tend to lower numbers (14) in W Amazon and Andean foothills but most pops. have variable 14–16
	<i>messenoides, deceptus</i>	VV,EE,CM	15–16	very occasional counts of 14 seen

Table 8. Chromosomes and systematics of *Melinaea*.

Species	Subspecies examined	Localities	n =	Comments
<i>mnasias</i>	<i>eratosthenes, rondonia, thera</i> , <i>comma</i> , new ssp.	AP,CM,GY,RR, BA,PA,RO	23–27	Seems coherent and amply distinct; also includes 7–10 other ssp.
<i>iudovica</i>	<i>iudovica</i> (some populations)	AP,PA,RO,RR	17–19	Varies within populations or individuals
	<i>iudovica, paraiya</i>	AM,BA,GY	20–23	May be due to incomplete pairing at times
	<i>crameri, paraiya</i>	BA,BO,EV,RJ,SP	23,24	Highest n at extremes of range
<i>idea</i>	<i>idae, vespertina</i>	AN,CC,CZ,WE	13	Separated from <i>iudovica</i> by chromosomes
<i>ethra</i>	(none)	BA,ES,PE,RJ,SP	29,30	E Brazil; separated from <i>maelus/maeonis</i>
<i>maelus</i>	<i>zamora, maeonis, cydon</i> , <i>tarapotensis, flavomaculata</i> , <i>mnemopsis, scylax</i>	AC,AM,CH, EB,EE,HU,TV	14,15, 17	Consistent form of wing markings (FW Cu, HW cell) and low number
	<i>lamasi</i> , new ssp.	AC,RO	14–17	higher numbers can be seen in this region
<i>lilis</i>	<i>imitata, parallelis, lilis, dodona</i>	CH,CC,MX,OX RG	21–24	Variable within and between populations, includes also 7 more Transandean ssp.
	<i>sola, lateapicalis</i>	EV,TR,TV	20–21	Lowest n at NE, S extremes of range
<i>mneme</i>	<i>mneme, mauensis</i> , new ssp.	AM,AP,GY,RO	16,17	Consistent in pattern and number
<i>menophilus</i>	<i>menophilus, orestes, zaneka</i>	AC,EE,RO	19–22	Consistent E to E Pará
<i>marsaeus</i>	<i>messenina, mothone, clara</i> , <i>pothete</i>	AC,EE,TV,VV RO,PA	16–18	Also includes <i>marsaeus, macaria, rileyi</i> ; sympatric with <i>maelus, menophilus, maenius</i>
	<i>phasiana, satevis</i>	AC,EB	15	lowest numbers in SW, <i>satevis</i> was in <i>iudovica</i>
<i>maenius</i>	<i>mediatrix, isocomma, simulator</i> , <i>cocana, egesta, juruaensis</i>	GY,AP,VV,EE, RO,AC	20–23	Up to n = 25 in some areas; often hard to separate superficially from <i>marsaeus</i>

different numbers and without intermediate numbers. This might suggest incipient speciation, which is not affirmed here because elsewhere in the same states, the same pairs do intergrade. Trans- and cis-Andean populations of the widespread *polymnia* complex also show different numbers ($n=17-20$ versus $n=14-16$), but blend into each other in eastern Colombia, unlike *macrinus* and *lysimmia*. *M. menapis* has quite a variable number ($n=20$ to 28) but does not seem to be divisible for this reason only. The union of the mid-elevation *messenoides* with the low-elevation *mazaesus* is supported by both morphological and chromosome intergradation in many mixed populations, with variable $n=14-16$. *M. limnaea* and *M. bipuncta*, provisionally united with *lysimmia* in the latest revision (BROWN 1977), have not yet been fixed for counts. The within species and within population variation in number in *Mechanitis* is extraordinary and makes it tempting to simply forget about rigid species definitions in the genus, accepting each population or regional subspecies as a unit unto itself, without obligatory evolutionary links to others; but such would represent an appreciable loss of information necessary to proceed with further studies of the group.

The genus *Melinaea* (Table 8) continues to present similar doubts. Some changes to the arrangement in BROWN (1977), already incorporated into BROWN (1979 and later), are clearly indicated by the chromosome numbers. *M. lilis* ($n=20-24$) and *M. maelus* ($n=14-17$), sympatric in northeastern Colombia and southwestern Venezuela, parallel the *macrinus-lysimmia* case seen in *Mechanitis*, and both must be separated from *M. ethra* of southeastern Brazil ($n=29-30$); from its compatible number, *M. scylax* would seem to be a race of *M. maelus* isolated in western Costa Rica, in the middle of the *lilis* range. The Transandean *M. idae* ($n=13$) must be separated from the *M. ludovica* complex ($n=17-24$), whose subspecies vary appreciably in number within and between populations; the Bolivian *satevis* ($n=15$) would be more extreme for this species and may be associated with *M. marsaeus* (*M. m. phasiana* also shows $n=15$). While *M. mnasias* ($n=24-27$), *M. mneme* ($n=16-17$), and *M. menophilus* ($n=19-22$) seem to continue cohesive as in the previous revision, the rational distribution of many Amazonian and Andean populations associated with *M. marsaeus* and *M. maenius* among these two species continues to be problematical. Lower numbers ($n=15-17$) are associated with a widespread species (*marsaeus*) which can include both dark mid-elevation forms (*mothone* and *messenina*) and foothill forms like *macaria* and *satevis* ($n=15$), and extends east to Pará as *m. pothete*.

Other mid-elevation dark forms (*simulator*, $n=20$) and the foothill *egesta+hicetas* ($n=23-25$) fit better into *maenius* ($n=21-22$) which also shows a more strongly red-colored testis than *M. marsaeus*. Two similar "transitional *marsaeus (pothete × clara)*" from south of Ariquemes, Rondônia showed $n=18$ and 20, suggesting that one might be *maenius juruaensis*, or that the variations in these species may exceed the possibilities for final decision on separations or associations based on phenotype alone, requiring more sophisticated techniques to properly place all subspecies (*juruaensis* was associated with *maenius* in BROWN 1977, but with *marsaeus* in BROWN 1979). In a single location, the usual maximum number of easily distinguished phenotypes in this complex is five, but foothill or transitional areas may show several additional forms, often seeming to intergrade among themselves and with the primary types.

CONCLUSIONS

In conclusion we may note that the basal karyotype of Ithomiinae has originated through what appears to be a process of concerted fusion. The starting point has been $n=30-31$ as in Danainae and Tellervinae. Numbers have evolved further through fusions and fissions to as low as $n=5$ and as high as $n=$ about 120. Some genera have stable chromosome numbers, while others exhibit extensive variation among and within species. This variation seems to be geographically differentiated. We hope that understanding chromosomal differentiation will help to understand the taxonomy and ecology of this important neotropical group of butterflies.

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