

JUVENILE STAGES OF ITHOMIINAE: OVERVIEW AND SYSTEMATICS (LEPIDOPTERA: NYMPHALIDAE)

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ABSTRACT.—Larvae and pupae are illustrated and described for 66 species in 40 of the 53 genera of Ithomiinae (Lepidoptera: Nymphalidae); eggs are shown for 60 species in 43 genera. With the use of 60 polarized characters drawn from these stages, a preliminary phylogeny is presented for 51 species in 41 genera, and compared with the genus-level phylogenies based on adults only (concepts of Fox and D'Almeida) and based on a sum of 138 new adult and juvenile characters (170 derived states). Two new genera are described: *Ollantaya* Brown & Freitas n. gen. (Type-species *Ithomia canilla* Hewitson) and *Talamancana* Haber, Brown & Freitas n. gen. (Type-species *Dircenna lonera* Butler & Druce).

KEYWORDS: Apocynaceae, Bolivia, Brazil, characters, chemical preadaptation, coevolution, Colombia, colonization, Danainae, Dircennini, Ecuador, eggs, El Salvador, Gesneriaceae, Godyridini, Heliconiini, hostplants, Ithomiinae, Ithomiini, juveniles, larvae, Mechanitini, Melinaeini, Mesoamerica, Mexico, Napeogenini, Neotropical, Oleriini, *Ollantaya* n. gen., Panama, Peru, phylogeny, pupae, Solanaceae, South America, *Talamancana* n. gen., taxonomy, Tellervini, Tithoreini, Trinidad, Venezuela.

The potential contribution of juvenile (immature) stages to Lepidopteran systematics has rarely been fully exploited, since in many groups the early stages are hard to find and thus not available for analysis. In principle, juvenile stages should be useful in the understanding of relationships among taxa, especially at the genus-level and above, because juveniles, like embryonic or ontogenetic stages, conserve characters of older or sister lineages, diverging less than the more specialized adults (see Kitching, 1985 and references therein).

In Neotropical butterflies, the understanding of juveniles provided by the classical works of Müller (1886), Moss (1920, 1949), and D'Almeida (1922, 1935a, 1935b, 1936, 1938, 1939, 1944) in Brazil, has been expanded recently by diligent field workers like Comstock and Vázquez (1961) in México, Aiello (1984; Robbins and Aiello, 1982) in Panamá, P. DeVries (1986) along with D. Janzen and A. Young in Costa Rica, the Muysbondts (1976 and references therein) in El Salvador, and the New York Zoological Society group (Beebe, Crane and Fleming, 1960) in Trinidad. The only reasonably large group for which juveniles are known and published for over 90% of the species is the Heliconiini (Brown, 1981), widely used in laboratory studies and as "flying flowers" in greenhouses. Knowledge of juveniles falls short of 80% of the species even in the intensely studied Papilionidae (110 of the 142 native to the Americas; Tyler *et al.*, 1994), though most species-groups have been studied. In general, only when juveniles of all major species groups and genera have been discovered, described and studied, can a reasonable picture of the whole group be seen and understood. This is now true, after over 25 years of intensive work throughout the Neotropics, for the Ithomiinae (Drummond and Brown, 1987): a total of 41

of the 53 genera, and most subgroups in the larger genera, have been reared to the pupa (or mature larva, 2) by various scientists [all but one of the remaining genera are either monotypic (7) or bitypic (4) and close to known ones; nine of the 12 are already known as eggs or often first instar larvae]. These data (Table 1) present a picture of relationships between genera (Figure 1) somewhat different from that established on the basis of adult morphology only (Fox, 1940, 1949, 1956, 1960, 1961, 1967; Fox and Real, 1971; D'Almeida, 1941, 1978).

The combined data for juveniles (Table 1, Fig. 2-7) and adults led to a preliminary phylogeny for Ithomiinae genera and tribes (Fig. 1C). When linked to a preliminary phylogeny for the host plants (Brown *et al.*, 1991), the picture showed that primitive Ithomiinae moved initially from Apocynaceae (the probable ancestral food plants, shared with the sister group Danainae and still used today by the earliest Ithomiinae *Tellervo*, *Tithorea*, *Elzunia* and *Aeria*) onto more advanced groups of Solanaceae, while the most advanced ithomiine genera today use the earliest genera in the two subfamilies of Solanaceae: *Solanum* (especially trees in the Section *Geminata*) and *Cestrum* (Drummond & Brown, 1987; Brown, 1987). Since these genera, at the base of the two major radiations of the plant family, are chemically similar and show many more classes of defensive chemicals (several types each of alkaloids, terpenes, saponins, phenolics, and strong-smelling oils) than the more advanced genera used by primitive Ithomiinae (each of which shows its own limited and specialized secondary chemicals), the evolution of the insect/plant interface was described as "progressive colonization of better-defended plants through chemical tolerance and preadaptation," rather than "sequential coevolution of parasite and host groups by

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bb 31 trees; TREE 14:

Phylogeny based on adults only
(following Fox and D'Almeida)

mhennig length 723 ci 24 ri 67 trees 2
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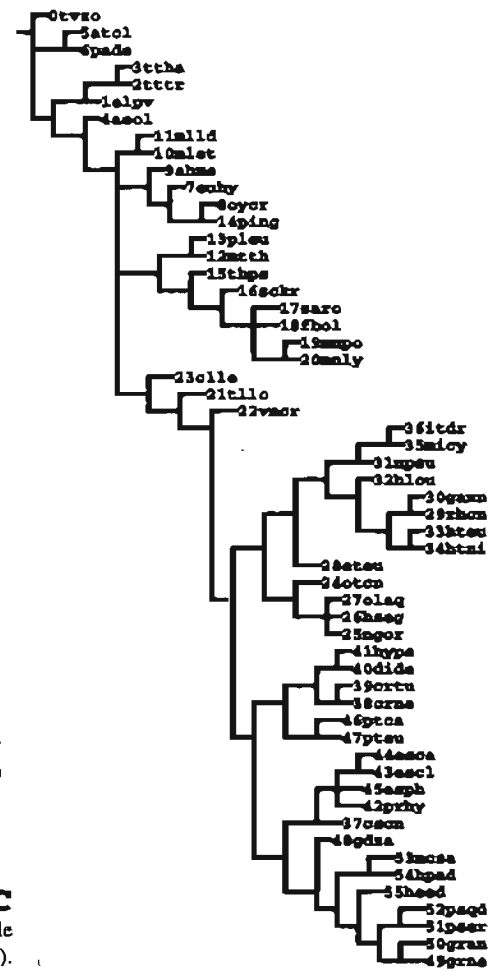
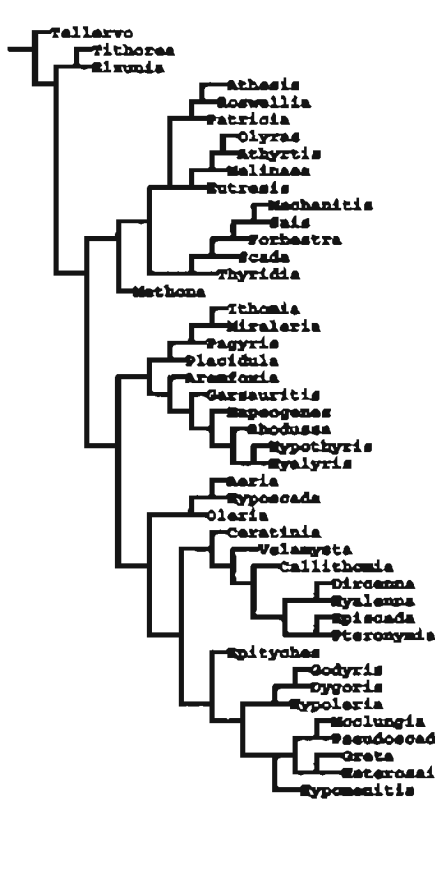
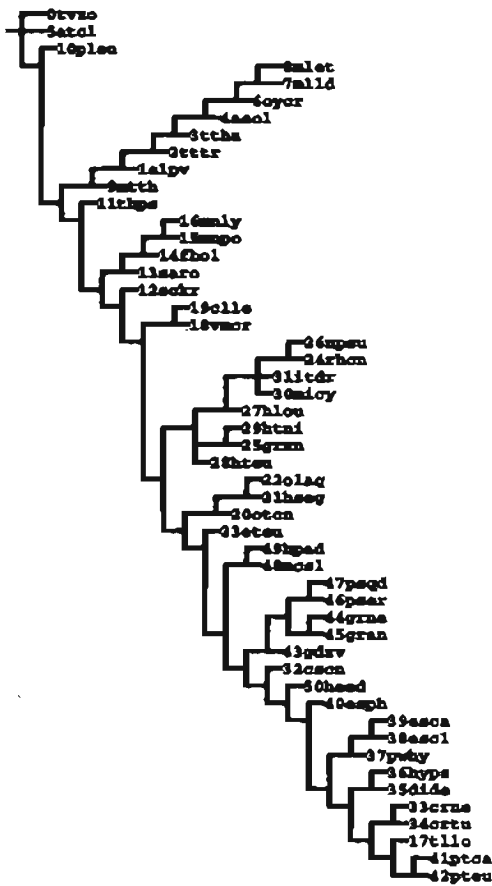


Figure 1. Phylogenetic hypotheses for Ithomiinae genera based on characters of juveniles only (A, see Table 1), on adult morphology only (B), or on many characters drawn from all stages, behavior and chemistry (C).

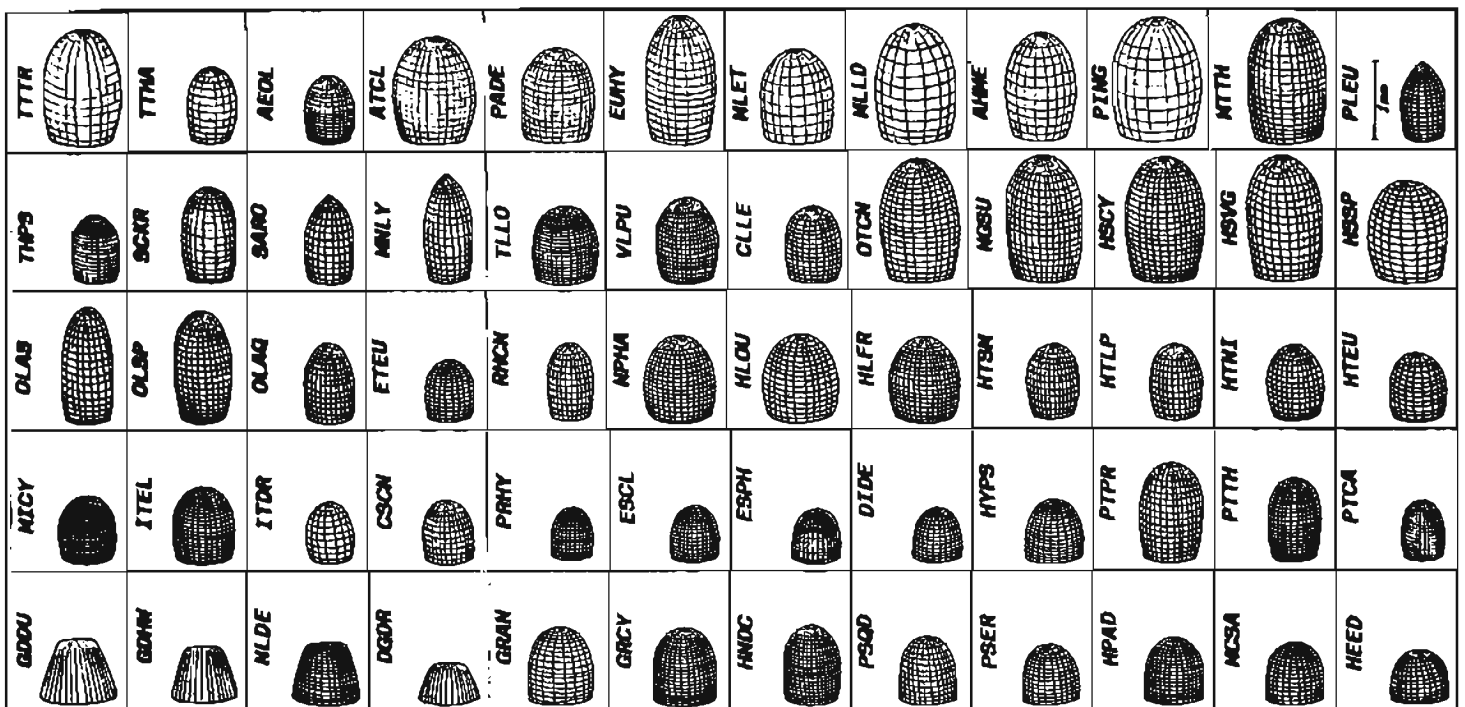


Fig. 2. Eggs of Ithomiinae, showing the principal characters used in Table 1, representing all tribes and most genera, except for *Tellervo* (see Orr in Ackery, 1987).



(See general legend for Figures 3-7 on following Figure)

Fig. 3: Sister-group and primitive genera. **DANAINAE:** A, *Ituna ilione* on *Ficus glabra*, Japi, São Paulo, Brazil; B, *Lycorea cleobaea* on *Carica lanceolata*, Colorado, RO, Brazil. **ITHOMIINAE, TELLERVINI:** C, *Tellervo zoilus* (AO) on *Parsonsia emarginata*, Cairns, Queensland. **TITHOREINI:** D, *Tithorea harmonia pseudonyma* on *Prestonia acutifolia*, Urucum, MS, Brazil; E, *T. h. gilberti* on *Prestonia* sp., Jaen, Cajamarca, Peru; F, *T. h. furia* on *Prestonia* sp., Acariçua, Portuguesa, Venezuela; G, *T. h. caissara* on *Prestonia coalita*, Serra Negra, SP, Brazil; H, *Tithorea tarricina tagarna* on *Prestonia* sp., La Merced, Junín, Peru (larva) and *T. t. purola* on *Prestonia* sp., Darién, Valle, Colombia; I, *Elzunia pavonii* (GL) on *Prestonia* sp. (same as for E), Jaen; J, *Aeria elara* (PM) on *Prestonia coalita*, Uberlândia, MG, Brazil; K, *Aeria eurimedia* on *Prestonia* sp., Caraballeda, N Venezuela; L, *Aeria olena* on *Prestonia coalita*, Campinas, SP; M, comparison of pupal sizes of *T. h. pseudethra* (left) and *Aeria olena* on *P. acutifolia*, Martinho Prado, SP. **MELINAEINI:** N, *Athesis clearista* on *Capsicum rhomboideum*, Caraballeda; O, *Olyras crathus* reared on *Juanulloa mexicana*, Portachuelo, Aragua, Venezuela; P, *Paititia neglecta* 1st instar (from expressed egg), Boca do Tejo, Acre (did not accept any plant given).



GENERAL LEGEND FOR FIGURES 3-7: Each species or population is indicated by a capital letter, usually between fifth instar larva on outer edge and pupa in center (other stages are indicated by E=egg, L1,L2,L3,L4=larval instars 1-4, PP=prepupa) (Photos by KB, or contributors: initials AO,IS,GL,JV,PM,WH).

Fig 4: Primitive Ithomiinae (conclusion). MELINAEINI: A, *Melinaea ludovica paraiya* on *Dyssochroa viridiflora*, Jacarepaguá, RJ, Brazil; B, *Melinaea menophilus* on *Hawkesiophyton ulci*, Jaru, RO, Brazil; C, *Melinaea ethra* on *D. viridiflora*, Mongaguá, SP; D, *Melinaea lilis* on *Juanulloa mexicana*, Las Tuxtlas, Veracruz, E Mexico; E, Eggs of *Eutresis hypereia* (Caraballeda, Venezuela) laid on *J. mexicana* in captivity MECHANITINI: F, *Methona megisto* on *Brunfelsia nire*, Theobroma, RO; G, *Methona themisto* on *Brunfelsia australis*, Campinas, SP; H, *Placidula euryanassa* on *Brugmansia suaveolens*, São Vicente, SP (including larvae in MeOH to show ringed pattern better); I, same from Jacarepaguá, RJ; J, *Thyridia psidii* (large pupa JV) on *Cyphomandra divaricata*, Campinas, SP; K, *Scada theuphia* on *Solanum (Bassovia) nt. trizygum*, Ariqueemes, RO; L, *Mechanitis lysimnia* on *Cyphomandra betacea*, Itatiaia, RJ; M, *M. lysimnia* (JV) on *Solanum paniculatum*, Campinas; N, *M. lysimnia* on *Lycopersicon esculentum*, Campinas; O, *M. polymnia* on *Solanum goodspeedi*, Caranavi, Bolivia; P, *M. polymnia* on *S. variable*, Sumaré, SP.



Fig. 5: Transitional Ithomiinae (less primitive); see general legend on Fig. 4. [NEW TRIBE]: A, *Velamysta cruxifera* on *Lycianthes* sp., Rio Blanco E of Baños, Ecuador; B, *Callithomia lenea xantho* on *Solanum* (sect. *Jasminosolanum*) *flaccidum*, Martinho Prado, SP; C, *Talamancana lonera* (WH) on *Cyphomandra betacea*, San Vito, Costa Rica. OLERINI: D, *Ollantaya canulla* on *Lycianthes* sp., Mina Pichita, Chanchamayo, Junin, Peru; E, *Hyposcada egra* reared to pupa on *Juanulloa mexicana*, 70 Km N of Manaus, AM; F+G, *Oleria aquata* on *Solanum swartzianum*, Mongaguá, SP; H, same from Juiz de Fora, MG. [NEW TRIBE?] I, *Eptryches eupompe* on *Aureliana lucida*, Japi, SP. ITHOMIINI: J, *Miraleria cymothoe* on *Brugmansia suaveolens*, San Antonio above Caracas, Venezuela; K, *Ithomia lichyi* on *A. lucida*, Japi, SP; L, *Ithomia agnosia* on *Acnistus arborescens*, Campinas, SP. NAPEOGENINI: M, *Napeogenes sylphis acreana* on *Lycianthes* sp., S of Ariqueemes, RO, Brazil; N, *Napeogenes inachia pyrois* on *Lycianthes* sp., N of Manaus, AM; O, *Garsauritis xanthostola* on *Solanum insidiosum*, N of Manaus, AM; P, *Hyalyris oulita metella* on *Solanum appressum*, Naranjal, Junin, Peru; Q, *Hyalyris oulita* ssp. on *Solanum* sp., Incel, E Ecuador; R, *Rhodussa cantobrica* on *Lycianthes* sp., Brasília, Acre, Brazil; S, *Hyalyris excelsa* (egg and larva, WH), Monteverde, Costa Rica; T, egg of *Hypothyris euclea* on *Solanum rugosum*, S of Ariqueemes, RO.



Fig. 6: More advanced Ithomiinae. **NAPEOGENINI:** A, *Hypothesis daphnis amapaensis* on *Solanum asperum*, Lourenço, Amapá, Brazil; B, *Hypothesis ninonia daeta* (lower larva IV) on *Solanum paniculatum*, Campinas, SP; C, *Hypothesis euclea laphria* on *Solanum asperum*, Linhares, ES, Brazil; D, *Hypothesis euclea leucania* on *Solanum umbellatum*, Santa Rita, Panamá; E, *Hypothesis mamercus* ssp. on *Solanum insidiosum*, Jaru, RO, Brazil; F, *Hypothesis lycaste limosa* on *Solanum rugosum*, Bajo Calima, Valle, Colombia. **DIRCENNINI:** G, *Pteronymia carlia* on *Solanum* (Sect. *Geminata*) *inaequale*, Japi, SP; H, *Pteronymia aletta* on *Solanum* (Sect. *Geminata*) sp., Rio Frio, Táchira, Venezuela; I, *Pteronymia vestilla* on *Solanum* (Sect. *Geminata*) sp., Carajás, Pará, Brazil; J, *Pteronymia pronuba* on *Markea* sp., Mina Pichita, Chanchamayo, Junin, Peru; K, *Pteronymia euritea* on *Solanum* (Sect. *Geminata*) *pseudoquina*, Angelo Frechiani, ES, Brazil; L, *Pteronymia latilla* on *Solanum nr. ripense*, La Victoria, Aragua, Venezuela; M, *Ceratinia tutia* (WH) on *Solanum* (Sect. *Leiocarpa*) sp., Turrialba, Costa Rica.



Fig. 7. Advanced Ithomiinae; see general legend for Figs. 3-7 on Fig. 4. **DIRCENNINI:** A, *Ceratiscada canaria* on *Solanum* (Sect. *Geminata*) *laxiflorum*, São Mateus, ES, Brazil; B, *Ceratiscada hymen* (?) on *Solanum* (Sect. *Geminata*) sp., Mina Pichita, Chanchamayo, Junin, Peru; C, *Pritwitzia hymenaea* on *Solanum* (Sect. *Geminata*) *caavurana*, Campinas, SP; D, *Episcada philoclea* (pupa only) on *Solanum* (Sect. *Geminata*) *inaequale*, Extrema, MG, Brazil; E, *Episcada clausina striposis* on *Solanum inaequale*, Japi, SP; F, *Hyalenna pascua* on *Solanum* nr. *schwackeanum*, Japi, SP; G, *Dircenna dero* (IS) on *Solanum paniculatum*, Sumaré, SP; H, *Dircenna loreta acreana* on *Solanum grandiflorum*, Colorado, RO, Brazil. **GODYRIDINI:** I, *Godyris zavaleta* on *Cestrum* sp., Colorado, RO; J, *Greta andromica* on *Solanum* nr. *ripense*, Caraballeda, N Venezuela; K, *Pseudoscada erruca* on *Cestrum laevigatum*, Campinas, SP; L, *Hypoleria fallens* on *Cestrum* sp., Rocha Leão, RJ; M, *Hypoleria adasa* on *Cestrum amictum*, Japi, SP; N, *Meclungia salonina* (larva JV) on *Cestrum sendnerianum*, Sumaré, SP; O, *Heterosais edessu* on *C. amictum*, Mongaguá, SP.

mutual selection." As many Ithomiinae genera occur throughout tropical America and show the same restrictive host preferences from their northern to southern limits (Fig. 8), these relationships may be presumed to be very old, probably part of the adaptive genetic architecture that accompanied the formation of the Ithomiinae genera, just as each host plant genus would have a characteristic chemical profile over all the same range. As the plants advanced with blockage of biosynthetic pathways, permitting greater efficiency in the allocation of materials and energy (Gottlieb, 1982), their parasites advanced (probably at a later time) through development of enzymes, producing tolerance of the wider range of chemical micro-molecules found in the supposedly more primitive plants.

This scheme has recently been challenged by macromolecular (chloroplast-DNA) studies suggesting a different evolutionary picture for the Solanaceae (Olmsted and Palmer, 1992), that places the foodplants of the earliest Ithomiinae to use this family (Markea, Juanulloae, *Brunfelsia* and *Brugmansia*) as primitive, and woody *Solanum* as advanced. Even though this scheme does not agree with traditional concepts of plant advancement based on flower and fruit characters and growth habit, it must be taken seriously. Further study thus should be directed at the development of a rigorous phylogenetic hypothesis for the Ithomiinae, based on "Total Evidence": polarized states of characters from as many manifestations of the genome as possible, in all life stages including morphology, chemistry, behavior, macroscopic and microscopic, external and internal, for comparison with a final host plant phylogeny (being developed by M. Nee, S. Knapp and others).

This paper presents the data-base for 60 macroscopic characters of eggs, larvae and pupae (Table 1) of 49 of the 50 Ithomiinae genera for which any of these have been observed and recorded in usable form (juveniles of the fiftieth, *Pagyris*, are essentially identical to those of *Miraleria*; the two genera have been recently combined by Lamas, 1986). As preserved early stages are available for many of these (though in some cases all were reared through to pupae), microscopic characters are being investigated more fully by P.C. Motta, who has already finished an SEM study of the eggs (1989). The characters and derived phylogenies for eggs and for first instar larvae are being published separately. This paper illustrates in color (Fig. 3-7)

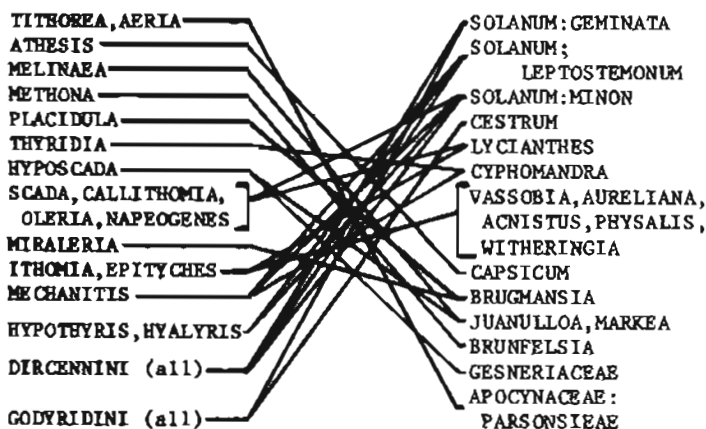


Fig. 8. Major widespread genera of Ithomiinae (left), linked (center) to their consistent hostplants (at right), both in order of advancement (top to bottom).

general features of larvae and pupae of 66 species representing 40 genera in all tribes of Ithomiinae, and two genera of Danainae (the sister-group, for comparison). As most juveniles are illustrated here for the first time, Table 1 compares their diagnostic characters (as developed for the phylogenetic analysis) and thus represents, along with the color photographs, description of these juveniles. Figure 2 includes line drawings of the eggs of 60 species in 43 genera, including 8 not illustrated on Fig. 3-7. Some further information on juveniles was taken from the studies mentioned above and also Brown and D'Almeida (1970), Drummond (1976), Haber (1978), Young (1972, 1973, 1974a, 1974b, 1974c, 1978a, 1978b), Orr in Ackery (1987), Brown (1980, 1987), and Freitas (1993).

DATA ACQUISITION

Several photographs of eggs, larvae and pupae in Fig. 3-7 were received from W. A. Haber, J. Vasconcellos-Neto, Ivan Sazima, P. C. Motta, Gerardo Lamas, and A. G. Orr, as indicated in the legends. Many of the eggs illustrated in Fig. 8 were expressed from field-captured females, and then let hatch to record larval and pupal stages (Brown and Benson 1974). This gave reasonable results (>50% hatching) in rainier periods, but little success in drier seasons when ithomiinae foodplants have no tender new leaves and the adults are in reproductive diapause. When the foodplant was not known, several plants used by close relatives or seen being inspected by females were offered to the larvae. Only three of the species illustrated (*Paititia neglecta*, *Olyras crathis* and *Hyposcada egra*) were not seen inspecting any potential host; the latter two were reared to adults on *Juanulloa mexicana* cultivated in Campinas (the egg and first instar of *Paititia*, shown in Fig. 2-PING and Fig. 3-P, are very close to those of *Olyras* but far from *Thyridia*). During the rearing of juveniles from distant places, switches to closely related plant species were often necessary and usually successful; many genera and species of Solanaceae were cultivated in Campinas for this purpose.

Many other juveniles were discovered on their natural host plants, often after observation of oviposition by a wild female. In most cases, both eggs and larvae were found on suspected hosts by turning over new or damaged leaves in the earlier hours of the day, or older (basal) leaves later.

Eggs were kept in closed containers and inspected daily until hatching (2-7 days), when the foodplant leaf was replaced by fresh tissue. Larvae were likewise maintained in tightly closed, humid glass or plastic dishes, with daily cleaning to avoid contamination. Pupae were kept in a more ventilated environment until emergence (5-10 days). Most recently emerged adults were used in *Nephila* bioassay (Brown, 1985, 1987) and then fixed in methanol for analysis.

Photographs of living juveniles were mostly taken with a Pentax Spotmatic camera equipped with a Spiratone Macrobel, 5 cm of rings, and a short 150mm f4.5 lens (Macrobel) or a small f3.5 lens (Macrostar), with ASA 400 Fujichrome or Ektachrome film, later transferred to prints on Kodak Gold 100 ASA film with a slide copier, using sunlight reflected off a rough white wall. Eggs were drawn freehand or with a camera lucida on a stereomicroscope.

GENERAL COMMENTS ON ITHOMINE JUVENILES

Table 1 shows that eggs are usually laid singly by a female landed on the lower side of a leaf (but *Mechanitis* lay bunches on the upperside); some genera lay near a vein or hole in the leaf, while others grasp the upperside while ovipositing near the edge of the underside (Drummond, 1976). Eggs are white or pale yellow, often subspherical, but may be elongated, flattened, or truncated (refer to Table 1 for the distributions of these characters). The chorion is divided by numerous horizontal and vertical ridges, and both the base and micropyle show significant variation (Motta, 1989, and in prep.).

First instar larvae have a uniformly colored head capsule, and taxonomically significant setal differences (Motta, in prep.). Primitive genera, including *Painitia*, show mesothoracic tubercles or buds, that grow to long flexible "feelers" in later instars. Body rings are present from early instars in most of these tubercled ("danaiform") larvae, and may develop, along with other color and pattern elements, in later instars in the more advanced genera; lateral projections may be single or multiple, round, squared or pointed. Head, leg and anal cap colors are quite variable. Many larvae bear a side stripe, and a few are "fuzzy" with dense short setae. Larvae from bunched eggs usually stay, feed and molt together until the fifth instar; solitary larvae normally rest in a characteristic "J" position (Table 1).

Ithomiine pupae may be straight, or strongly bent in the first or final abdominal segments. Most genera show 4 (rarely 6) anterior tubercles, and some have an abdominal "shelf." Ground color varies from white or yellow to green, often overlaid with variable black spotting or banding, and patches of brilliant iridescence; all these may vary within a population, or in accord with pupation site. The cremasters and EHTs show significant variation, as in the Danainae (Kitching, 1985). The distribution of all of these characters is shown in Table 1.

DESCRIPTIONS OF NEW GENERA OF ITHOMIINAE

OLLANTAYA Brown & Freitas, new genus

Type-species: *Ithomia canilla* Hewitson, 1874 (Fig. 10A).

Synopsis (Fig. 9A): Adults are characterized by (a) extremely elongated wings, (b) very elongated male uncus and valves, (c) bilobed eighth tergite, (d) tubular gnathos, (e) long straight narrow aedeagus, (f) T-shaped hindwing humeral vein, (g) long undivided hairpencil, (h) fully reduced male foretibia + tarsus, (i) female ovipository lobes with broad base and very narrow apophysis, (j) signum bursae strong and (k) vulvar plates narrow and simple. Character (a) is extreme among Ithomiinae, (b) is found in *Olyras*, *Thyridia* and many *Hyposcada*, (d) is known only in *Patricia*, (f), (g) and (j) are primitive, (e) is frequent and (h) and (i) normal in advanced ithomiine genera. Character (j) separates, while (e), (k) and the typically olerine early stages (Fig. 5D) link *Ollantaya* closely and convincingly with its probable sister genus, *Hyposcada*. Almost all of these characters and the juveniles separate *Ollantaya* from the genus in which *canilla* is usually placed, *Pteronymia*.

Comments: Other members of this genus include *Leucothyris baizana* Haensch, 1903 (Fig. 10A) as well as an undescribed subspecies of the same from the Abitagua valley in Ecuador (Fig. 10B; both these might be northern vicariants conspecific with *O. canilla*), and *Ithomia cleobulina* Hewitson, 1876 and its various

subspecies (Fig. 10C), usually placed in *Pteronymia* like *O. canilla*.

Ollantaya species are encountered very locally and usually in sparse and seasonal populations (three types of rarity, reflected in the sparse material in museums), flying at 2-6m above the ground inside dense cloud forests at altitudes between 1500 and 2200m, with more than 2000mm yearly precipitation, on the eastern slopes of the Andes from N. Ecuador to C. Bolivia. Both may be rarely seen below Mina Pichita (1600-1800m), W. of San Ramon, Junin, Peru.

Very recently (1993) we learned, from unpublished notes of Richard M. Fox that were commented upon in an unpublished manuscript by Herman G. Real, that Fox had independently separated *O. canilla* to be placed in a new genus of Olerini. Fox did not comment on this with the first author in the 60s, nor in any of his published materials including his list of genera (1961). **Etymology:** Ollanta was a mythical Inca chieftain.

TALAMANCANA Haber, Brown & Freitas, new genus

Type-species: *Dircenna lonera* Butler & Druce, 1872 (Fig. 10D); no further species have been found in this genus.

Synopsis (Fig. 9B): Adults are characterized by (a) in the male genitalia, a fully sclerotized scoop-like gnathos, (b) a recurved narrow aedeagus, (c) male forewing veins R2 to R5 short-stalked with M1, (d) bifurcate hindwing humeral vein, (e) hindwing recurrent vein (in discal cell) a basal prolongation of M2 in the male, slightly below M2 in the female, (f) HW veins RS and M1 fully fused in the male, arising from the upper corner of the cell in the female, (g) a single long hairpencil in the male, (h) a partly fused male foretibia/tarsus, (i) broad base to the female ovipository lobes with long tapered apophysis, (j) strong signum bursae, (k) broad fused vulvar plate surrounding the ostium, and (l) female foretarsus 5-segmented. The typical dircennine genitalia (see Brown & D'Almeida, 1970) are accompanied by a combination of characters shared with nearby genera including *Ceratinia* (a,b,d,e,g,j,l), *Velamysta* (a,b,d,e,j,l), *Callithomia* (d,g,i,l only), *Pteronymia* (a,d,f,l only), and *Dircenna* (a,i,j,k only). Character (h) is seen in *Mechanitini* and one species of *Melinaea* (*ludovica*). The early stages (Fig. 5C) were found on *Cyphomandra* (like only *Thyridia* and some *Mechanitis*) and most resemble those of *Ceratinia* or *Pteronymia* (larva) or *Callithomia* (pupa). **Comments:** This apparently monotypic genus is found rarely in rich wet cloud forests in the higher mountains of Costa Rica to W. Panamá (Chiriqui endemic region).

Etymology: These mountains form the Talamanca massif, an isolated large island during long periods of the Tertiary.

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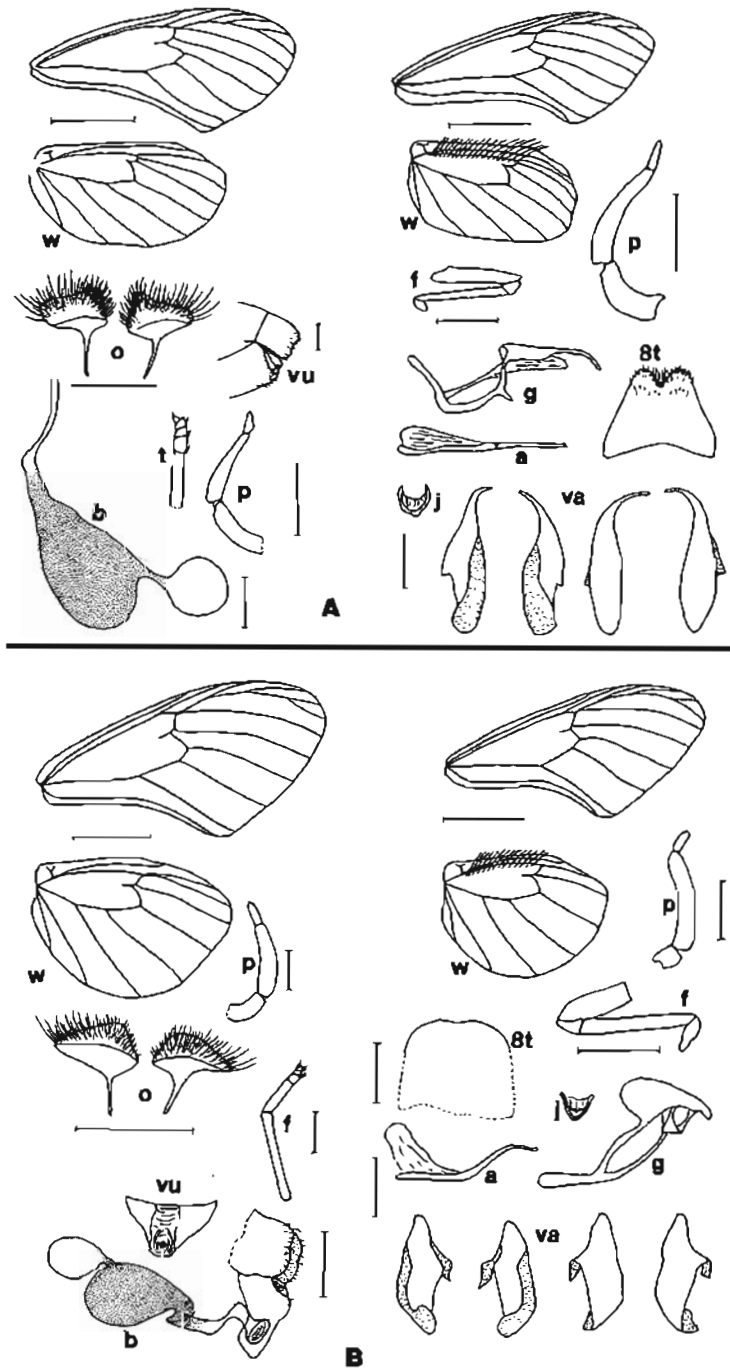


Fig. 9. Morphological aspects of adults of *Ollantaya canilla* (A, upper) and *Talamancana lonera* (B, lower); ♀ at left, ♂ at right, codes: a, aedeagus; b, bursa copulatrix; f, foreleg; g, genitalia; j, juxta; o, ovipository lobes; p, palpus; va, views of valves; vu, vulvar plate and ostium; w, wing venation; 8t, eighth tergite. Bar scale = 1cm (wings) or 1mm (other).

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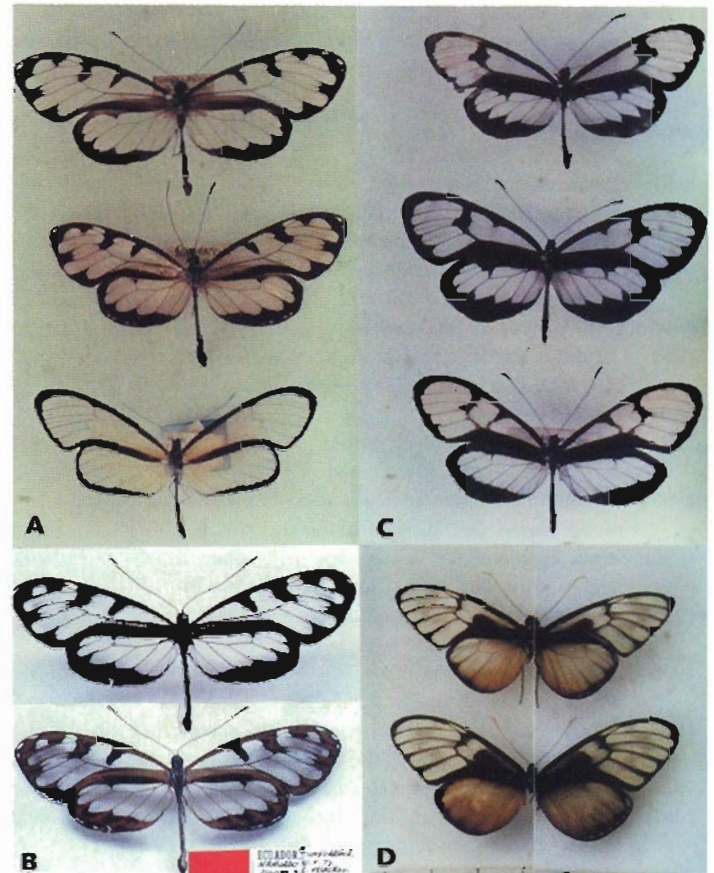


Fig. 10. Adults of *Ollantaya* and *Talamancana*: A, *O. baizana* ♂ and ♀ (Ecuador), *O. canilla* ♂ (Peru); B, *O. baizana* ssp.; C, various subspecies of *O. cleobulina*; D, *T. lonera* ♂ (upper) and ♀, dorsal (left) and ventral.

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