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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, A. Aiello (1984; Robbins and Aiello, 1982) in Panamá, P. DeVries (1986) along with D. Janzen and A. Young in Costa Rica, the Muyshondts (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

Table 1. Characters of juvenile Ithomiinae and their distribution of states within the subfamily (see codes below)

Character	TV ZO	EL PV	TT TR	TT HA	AE OL	AT CL	PA DE	EU HY	OY CR	AH ME	ML ET	ML LD	MT TH	PL EU	PI NG	TH PS	SC KR	SA RO	FB OL	MN PO	MN LY	TL LO	VM CR	CL LE	OT CN	NG OR	HS EG	OL AQ	ET EU	RH CN	GA XN	NP SU	HL OU	HT EU	HT NI	MI CY	IT DR	CS CN	CR NE	CR TU	DI DE	HY PS	PR HY	ES CL	ES CA	ES PH	PT CA	PT EU	GD ZA	GR NE	GR AN	PS ER	PS QD	MC SA	HP AD	HE ED
EGGS																																																								
In clusters								X						X						X	X													X		X								X	X											
Truncate																																																	X							
Pointed apex														X				X	X	X	X																																			
Near leaf edge									X	X	X	X	X			X													X																											
Axes ratio	B	B	B	B	B	B	B	C	B	B	B	B	B	B	B	B	C	B	D	D	D	A	B	B	C	C	C	C	A	B	B	A	A	B	B	A	A	A	A	B	A	A	A	A	A	A	A	B	A	A	A	A	B	A	A	A
Upper side of leaf																				X	X																																			
Near hole or vein																																							X		X	X														
On Apocynaceae	X	X	X	X	X																																																			
Relatively large	X	X	X	X	X		X	X					X		X		X		X	X	X			X			X	X																												
FIRST INSTAR LARVA																																																								
Dark head capsule	X	X	X	X	X	X	X	?	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	?	X	X	X	X	?	X	X	X			X											X				X	X			
*Dark legs		X	X	X	X	X	?	?	X	X	X	X	X	X	X	X		?	?	X	X		?	?		?					?																									
Thoracic tubercles	ln	st	st	st	st	st	?	?	st	st	st	st	ab	ab	st	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	?	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab
LAST INSTAR LARVAE																																																							
Danaiform body rings	dv	re	re	re	re	dv	?	?	re	?	re	re	re	dv	?							re		re		?																														
Broken body rings				X	X		?	?	X	?	X	X			?							X		X		?																														
Dorsal patterns							?	?		?					?								X			?								X					X	X	X	X					X	X		X	X	X	X			
Head capsule color	bk	or	bk	bk	bk	db	?	?	bk	?	bk	bk	bk	rd	?	bk	bk	bk	bk	br	bk	bk	or	bk	bk	?	bk	bk	or	or	cl	bk	bk	bk	cl	bk	bk	cl	bk	bk	cl	cl	cl	bk	cl	cl	bk	bk	cl	bk	bk	bk	bk	cl	cl	cl
Head capsule w/light areas			X	X		X	?	?	X	?	X	X			?							X	X	X		?								X			X		X	X				X			X	X		X	X	X	X			
Variable head pattern							?	?		?					?											?																		X			X	X								
Prothoracic "neck ring"		X	X	X	X		?	?	X	?	X	X			?	X	X	X	X	X	X	X		X	X	?	X	X	X		X	X	X	X	X	X	X		X	X	X	X					X	X			X					
Neck ring color		or	or	wt	or		?	?	wt	?	or	or			?	wt	wt	wt	wt	wt	wt	or		or	wt	?	wt	wt	wt		wt	wt	wt	wt	wt	wt	wt		wt	wt	wt	wt					or	or			or					
Neck ring protuberances							?	?		?					?				?	X	X					?																														
Lateral stripe							?	?		?					?								ab	cp	cp	?	cp	cp	ab	cp	ab	cp	cp	cp	cp	cp	cp	cp	cp	cp	cp	cp	cp	cp	cp	cp	cp	cp	cp	cp	cp	cp	cp			cp
Lateral stripe broken							?	?		?					?									X		?															X	X	X	X	X		X	X		X	X	X	X			
Lateral protuberances							?	?		?					?	st	st	st	st	ln	ln					?																														
Double lateral tubercles							?	?		?					?								X	X		?																														
Sublateral semicircles	ab	ab	ab	ab	ab	ab	?	?	ab	?	ab	ab	ab	ab	?	ab	ab	ab	ab	ab	ab	ab	ab	ab	dv	?	dv	dv	dv	dv	dv	dv	dv	dv	dv	dv	dv	re	re	re	re	re	re	re	re	re	re	re	re	re	re	re	re	re	re	re
Filaments: segment	mt	ms	ms	ms	ms	ms	?	?	ms	?	ms	ms	ab	ab	ms	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	?	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab
Filaments: length	ln	ln	ln	ln	ln	st	?	?	ln	?	ln	ln			?																																									
Filaments: apex white						X	?	?		?					?											?																														
Legs black	X	X	X	X	X	X	?	?	X	?	X	X	X	X	?	X		?	?	X	X		X	X	X	?			X	X	X	X	X	X	X	X								X												
Prolegs: black plate	X	X	X	X	X	X	?	?	X	?	X	X	X	X	?	X		?	?	X	X				X	?				X		X												X												
Anal prolegs:black plate	X	X	X	X	X	X	?	?	X	?	X	X	X	X	?	X			?	X				X	X	?						X												X												
Cuticle furry							?	?		?				X	?											?															X	X														
Abdominal cones (8th)	X				X	X	?	?		?					?							X	X	X		?																					X	X								
Anal cap					X		?	?	X	?	X	X			?							X				?													X	X			X	X	X	X	X	X								
Anal plate with black	X	X	X	X		X	?	?	X	?	X	X	X	X	?	X								X		?																														
Ventral color	dk	dk	dk	dk	dk	dk	?	?	wt	?	rd	rd	dk	dk	?	wt	wt	wt	wt	wt	wt	wt	wt	wt	wt	?	wt	wt	wt	wt	wt	wt	wt	wt	wt	wt	wt	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr
Leaf rolling							?	?		?					?											?															X	X		X												
PUPAE																																																								
Color	yl	yl	yl	yl	wt	yl	?	?	wt	?	yl	yl	yl	wt	?	yl	yl	?	yl	yl	yl	yl	?	yl	gr	?	gr	gr	gr	wt	wt	wt	wt	wt	wt	wt	wt	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr	gr
Color variable							?	?		?					?			?					?			?										X	X																			
Reflections absent	X					X	?	?	X	?	X	X	X		?			?					?			?																														
Reflections variable							?	?		?				X	?			?					?			?				X	X	X	X	X	X	X	X																			
Reflective area		tt	tt	tt	tt	tt	?	?		?				tt	?	tt	tt	?	tt	tt	tt	tt	?	tt	rs	?	rs	rs	rs	tt	tt	tt	tt	tt	tt	tt	tt	tt	tt	tt	tt	tt	tt	tt	tt	tt	tt	tt	rs	rs	rs	rs	rs	rs	rs	rs
Pupal angle	sr	bn	ob	ob	ob	bn	?	?	ob	?	bn	bn	sr	sr	?	sr	ob	?	sr	sr	sr	bn	?	bn	ob	?	ob	ob	bn	ob	bn	ob	bn	bn	bn	ob	ob	bn	bn	bn	bn	bn	bn	bn	bn	bn	bn	bn	bn	bn	bn	bn	bn	bn	bn	bn
Thor/Abd notch shallow	X	X	X	X	X		?	?		?	X	X	X	X	?	X	X	?	X	X	X		?			?			X																											
Abdomen bent distally							?	?		?			X	X	?	X		?	X	X	X		?			?																														
*Abdominal shelf (3th)	re	dv	dv	dv	dv	re	?	?	dv	?	ab	ab	ab	re	?	re	ab	?	?	re	re	ab	?	dv	ab	?	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab
*Abdomen compressed	X					X	?	?		?	X	X		X	?			?				X	?	X		?			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Three pairs of tubercles						X	?	?	X	?	X	X		X	?			?					?	X		?													X	X	X	X														X
Ocular caps rounded	X	X	X	X		X	?	?	X	?	X	X	X	X	?			?				X	?			?																														
Cremaster basal warts	ab	cx	cx	cx	ab	ab	?	?	cx	?	sl	sl	cx	ab	?	sl	ab	?	ab	ab	ab	ab	?	ab	ab	?	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab	ab
Cremaster color	bk	bk	bk	bk	bk	rd	?	?	bk	?	bk	bk	bk	bk	?	bk	rd	?	bk	bk	bk	cl	?	bk	rd	?	rd	cl	bk	rd	rd	rd	rd	rd	rd	rd	rd	bk	rd	rd	cl	cl	cl	rd	rd	cl	rd	rd	bk	bk	bk	bk	cl	rd	bk	cl
Abdominal black spots	X	X	X	X	X	X	?	?	X	?	X	X	X	X	?	X		?	?	X	X		?	X		?				X	X	X	X	X	X	X	X												X	X	X	X	X	X		
Pattern of black spots	sp	rw	rw	rw	rw	rw	?	?	ad	?	sp	sp	rw	ad	?	rw		?		rw	rw		?	sp		?				rw	rw	rw	rw	rw	rw	rw	rw												sp	sp	sp	sp	sp	sp		
8Abd dorsal black stripe	X	X	X	X	X		?	?	X	?	X	X	X	X	?	X		?		X	X		?	X		?																														
*8Abd ventral black stripe		X	X	X	X		?	?	X	?			X	X	?		X	?	X	X	X		?	X		?				X	X	X	X	X	X	X	X																			
EHTs not sclerotized							?	?		?					?			?				X	?		X	?	X	X										X	X	X	X	X	X	X	X	X	X	X								
Alar marks absent							?	?		?					?			?					?			?															X	X				X										
Pattern of alar marks	sp	ll	ll	ll	ll	tl	?	?	ll	?	sp	sp	ll	tl	?	ll	ll	?	ll	ll	ll	sp	?	sp	sp	?	sp	sp	sp	tl	tl	tl	tl	tl	tl	tl	tl	sp	sp	sp			sp	sp	sp		sp	sp	sp	sp	sp	sp	sp	sp	sp	sp

EXPLANATION OF CODES IN BODY OF TABLE: X = presence of a feature; 5th Character: A=<1.2, B=1.2 to 1.5, C=1.5 to 1.7, D=>1.7.
Other characters (alphabetically): ab=absent, ad=additional rows, bk=black, bn=bent (near 90°), cl=colorless, cp=complete or entire, cx=complex and subdivided, db=dark brown, dk=dark, dv=developed or conspicuous, gr=green, ll=long lines, ln=long, mt=metathorax, ms=mesothorax, ob=obtuse (near 120°), or=orange, rd=red, re=reduced or obsolescent, rs=restricted to small areas, rw=rows, sl=simple, sp=sparse dots, sr=straight (near 180°), st=stubby or short, tl=transverse lines, tt=total, wt=white, yl=yellow. *Tellervo* (TVZO, leftmost column) has 0-states (most primitive) for all characteres except for those with asterisks.

CODES FOR SPECIES IN TABLE 1 AND PHYLOGENIES:

aeol=*Aeria olena*
ahme=*Athyrtis mechanitis*
atcl=*Athesis clearista*
clle=*Callithomia lenea*
crne=*Ceratinia neso*
crtu=*Ceratinia tutia*
cscn=*Ceratiscada canaria*
dide=*Dircenna dero*
elpv=*Elzunia pavonii*
esca=*Episcada carcinia*
escl=*Episcada clausina*
esph=*Episcada philoclea*
eteu=*Epityches eupompe*
euhy=*Eutresis hypereia*
fbol=*Forbestra olivencia*
gaxn=*Garsaur. xanthostola*
gdza=*Godyris zavaleta*
gran=*Greta andromica*
grne=*Greta nero*
heed=*Heterosais edessa*
hlou=*Hyalyris oulita*
hpad=*Hypoleria adasa*
hseg=*Hyposcada egra*
hteu=*Hypothyris euclea*
htni=*Hypothyris ninonia*
hyps=*Hyalenna pascua*
itdr=*Ithomia drymo*
mcsa=*Mcclungia salonina*
micy=*Miraleria cymothoe*
mlet=*Melinaea ethra*
mlld=*Melinaea ludovica*
mnpo=*Mechanitis polymnia*
mnly=*Mechanitis lysimnia*
mtth=*Methona themisto*
ngor=(New gn.-1) *orestilla*
npsu=*Napeogen. sulphurina*
olaq=*Oleria aquata*
otcn=*Ollantaya canilla*
oycr=*Olyras crathis*
pade=*Patricia dercyllidas*
ping=*Paititia neglecta*
pleu=*Placidula euryanassa*
prhy=*Prittwitzia hymenaea*
pser=*Pseudoscada erruca*
psqd=*Pseud. quadrifasciata*
ptca=*Pteronymia carlia*
pteu=*Pteronymia euritea*
rhcn=*Rhodussa cantobrica*
saro=*Sais rosalia*
sckr=*Scada karschina*
thps=*Thyridia psidii*
tllo=*Talamancana lonera*
tvzo=*Tellervo zoilus*
ttha=*Tithorea harmonia*
tttr=*Tithorea tarricina*
vmcr=*Velamysta cruxifera*

Additional codes (Fig. 2)
dgdr=*Dygoris dircenna*
gddu=*Godyris duilia*
gdhw=*Godyris hewitsoni*
grcy=*Greta cyrcilla*
hlfr=*Hyalyris frater*
hndc=*Hypomenitis dercetis*
hscy=*Hyposcada cyrene*
hssp=*Hyposcada* sp.
hsvg=*Hyposcada virginiana*
htlp=*Hypothyris leprieuri*
htsm=*Hypothyris semifulva*
itel=*Ithomia ellara*
ngsu=(New gn.-1) *susiana*
nlde=(N. genus-2) *derama*
npha=*Napeogenes harbona*
olas=*Oleria astraea*
olsp=*Oleria* sp.
ptpr=*Pteronymia pronuba*
ptth=*Pteronymia thabena*
vlpu=*Velamysta pupilla*

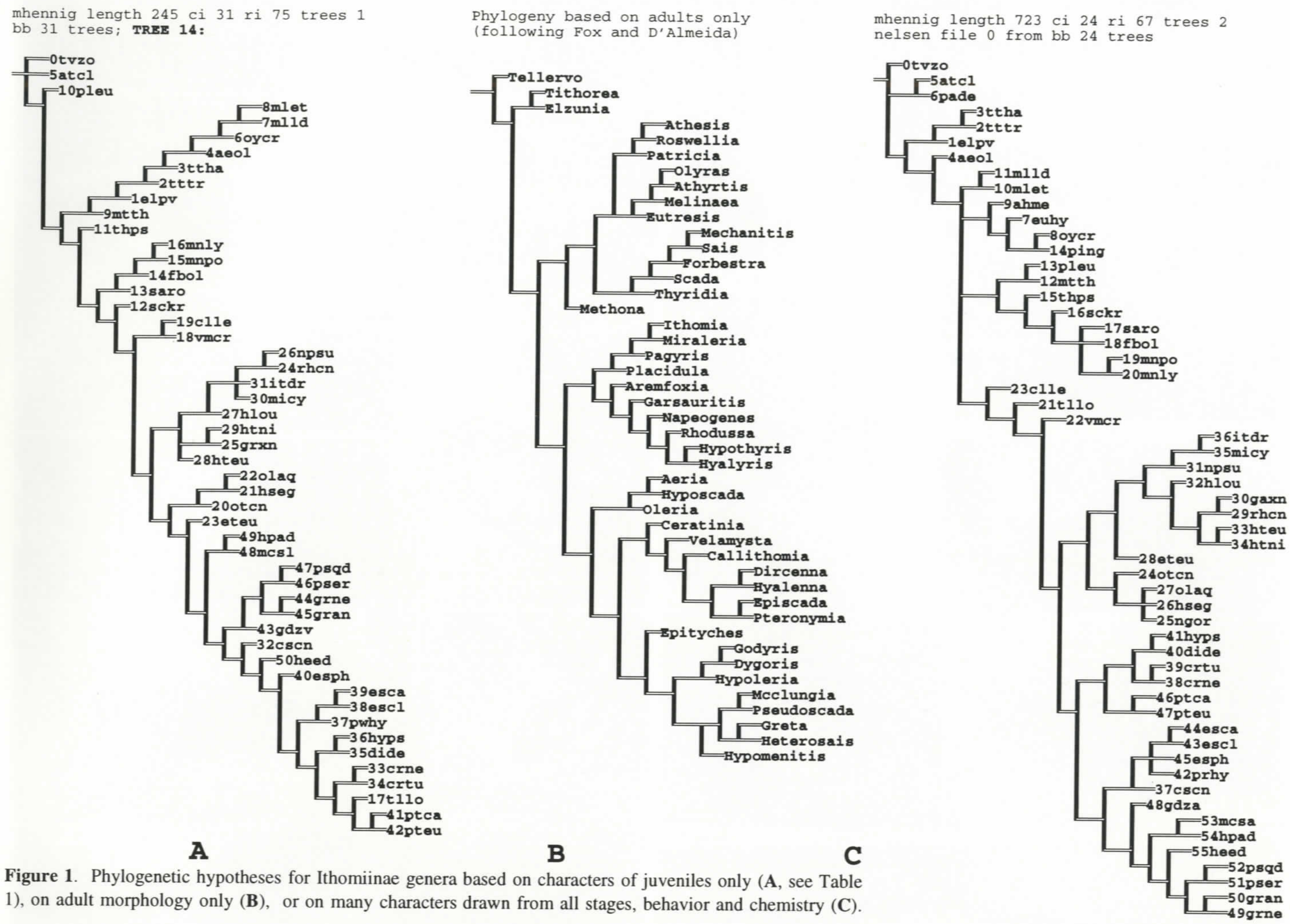

Figure 1. Phylogenetic hypotheses for Ithomiinae genera based on characters of juveniles only (**A**, see Table 1), on adult morphology only (**B**), or on many characters drawn from all stages, behavior and chemistry (**C**).

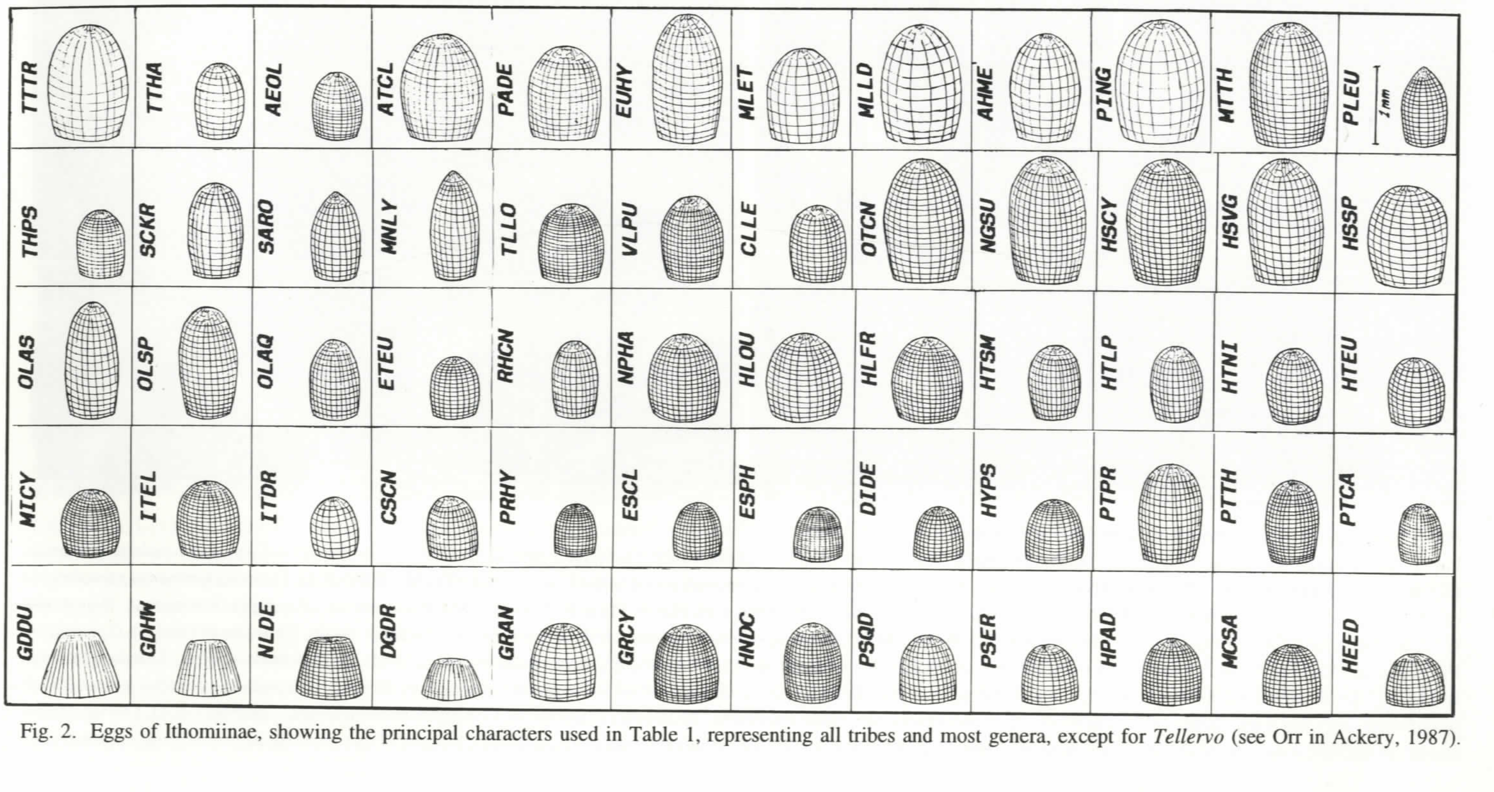

Fig. 2. Eggs of Ithomiinae, showing the principal characters used in Table 1, representing all tribes and most genera, except for *Tellervo* (see Orr in Ackery, 1987).

(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., Acarigua, Portuguesa, Venezuela; **G**, *T. h. caissara* on *Prestonia coalita*, Serra Negra, SP, Brazil; **H**, *Tithorea tarricina tagarma* on *Prestonia* sp., La Merced, Junin, Peru (larva) and *T. t. parola* 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*, Uberlandia, 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 crathis* 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 *Dyssochroma viridiflora*, Jacarepaguá, RJ, Brazil; **B**, *Melinaea menophilus* on *Hawkesiophyton ulei*, 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 mire*, 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 theaphia* on *Solanum* (*Bassovia*) nr. *trizygum*, Ariquemes, 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. variabile*, 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. **OLERIINI**: **D**, *Ollantaya canilla* 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**, *Epityches 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 Ariquemes, 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., Inecel, E Ecuador; **R**, *Rhodussa cantobrica* on *Lycianthes* sp., Brasileia, Acre, Brazil; **S**, *Hyalyris excelsa* (egg and larva, WH), Monteverde, Costa Rica; **T**, egg of *Hypothyris euclea* on *Solanum rugosum*, S of Ariquemes, RO.

Fig. 6: More advanced Ithomiinae. **NAPEOGENINI**: **A**, *Hypothyris daphnis amapaensis* on *Solanum asperum*, Lourenço, Amapá, Brazil; **B**, *Hypothyris ninonia daeta* (lower larva JV) on *Solanum paniculatum*, Campinas, SP; **C**, *Hypothyris euclea laphria* on *Solanum asperum*, Linhares, ES, Brazil; **D**, *Hypothyris euclea leucania* on *Solanum umbellatum*, Santa Rita, Panamá; **E**, *Hypothyris mamercus* ssp. on *Solanum insidiosum*, Jaru, RO, Brazil; **F**, *Hypothyris 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**, *Prittwitzia 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**, *Mcclungia salonina* (larva JV) on *Cestrum sendtnerianum*, Sumaré, SP; **O**, *Heterosais edessa* 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 Ithomiine 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 (Markeae, Juanulloeae, *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) 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).

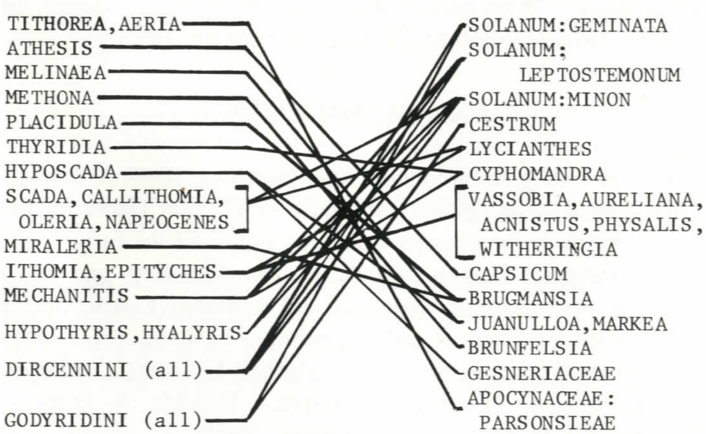

Fig. 8. Major widespread genera of Ithomiinae (left), linked (center) to their consistent hostplants (at right), both in order of advancement (top to bottom).

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 ithomiine 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 (Macrotel) or a small f3.5 lens (Macrotar), 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 camara lucida on a stereomicroscope.

GENERAL COMMENTS ON ITHOMIINE 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 *Paititia*, 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 oleriine 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 Oleriini. 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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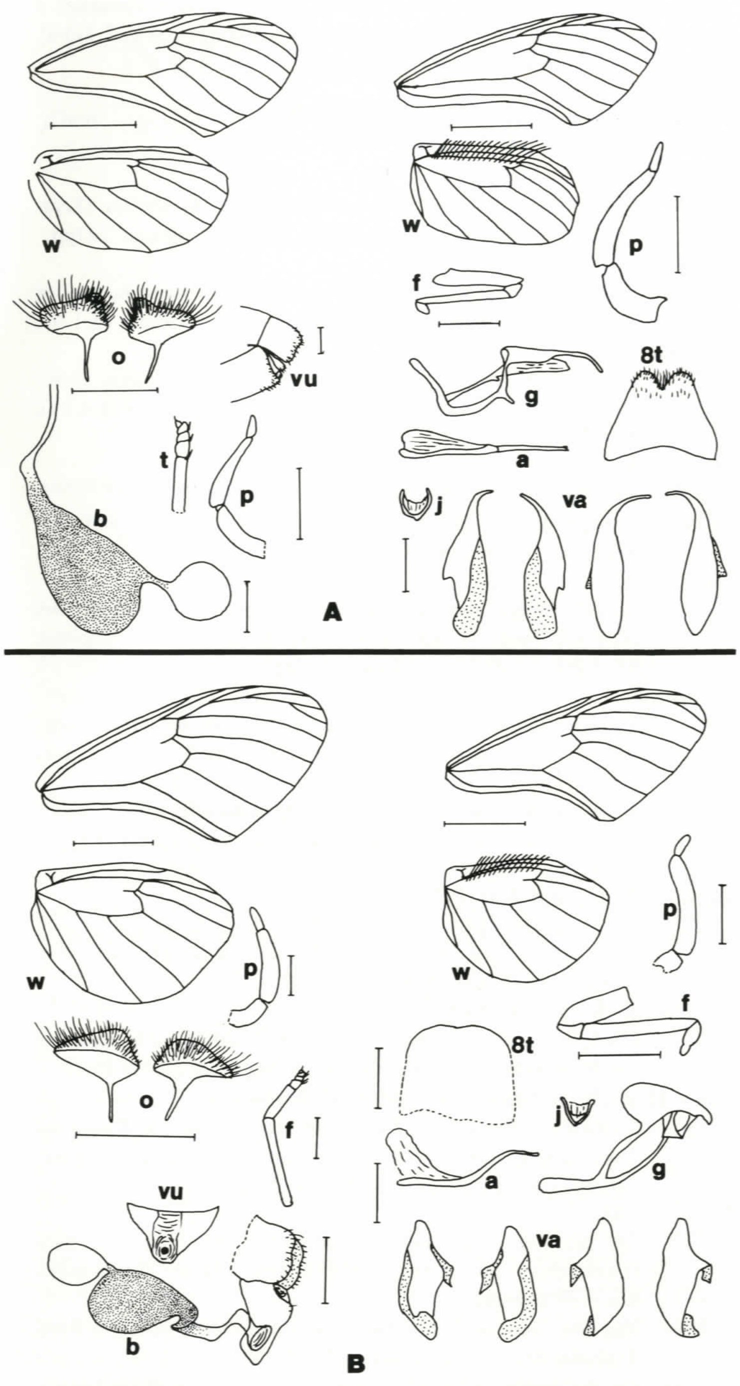

Fig. 9. Morphological aspects of adults of *Ollantaya canilla* (**A**, upper) and *Talamancana lonera* (**B**, lower); ♀ at left, ♂ at right, codes: **a**, aedeagus; **b**, bursa copulatrix; **f**, foreleg; **g**, genitalia; **j**, juxta; **o**, ovipository lobes; **p**, palpus; **va**, views of valves;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

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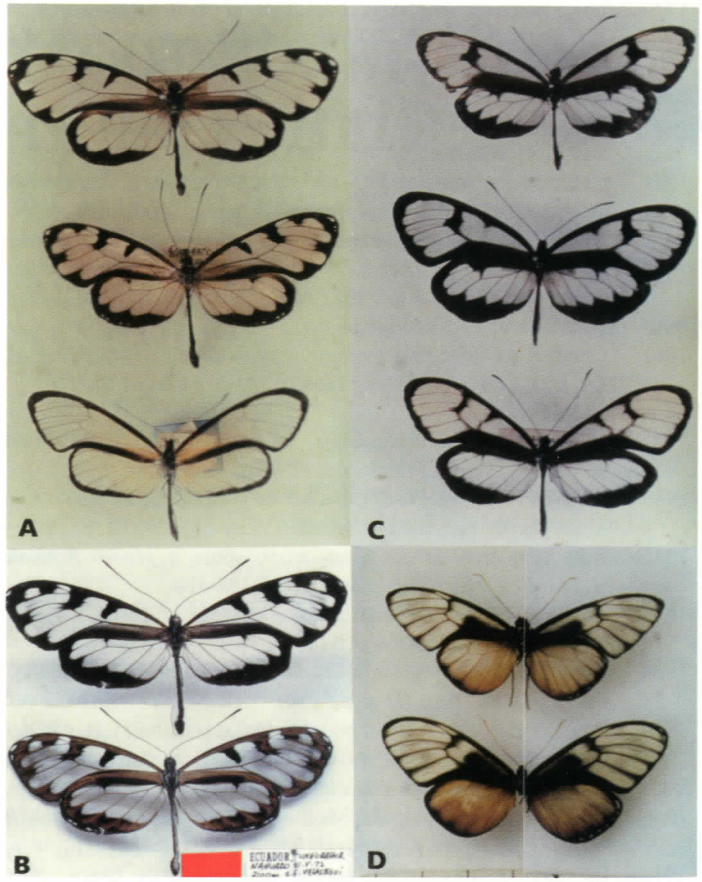

Fig. 10. Adults of *Ollantaya* and *Talamancana*: **A**, *O. baizana* ♂ and ♀ (Ecuador), *O. canilla* ♂ (Peru); **B**, *O. baizana* ssp.; **C**, various subspecies of *O. cleobulina*; **D**, *T. lonera* ♂ (upper) and ♀, dorsal (left) and ventral.

LITERATURE CITED

Ackery, P. R.

1987. The danaid genus *Tellervo* (Lepidoptera: Nymphalidae): a cladistic approach. *Zool. J. Linn. Soc.* (London), 89:273-294.

Aiello, A.

1984. *Adelpha* (Nymphalidae): deception on the wing. *Psyche* (Cambridge, Ma.), 91:1-45.

Beebe, W., J. Crane, and H. Fleming

1960. A comparison of eggs, larvae and pupae in 14 species of heliconiine butterflies from Trinidad, W.I. *Zoologica* (New York), 45:111-154.

Brown, K. S., Jr.

1980. A review of the genus *Hypothyris* Hübner (Nymphalidae), with descriptions of three new subspecies and early stages of *H. daphnis*. *J. Lepid. Soc.* (Los Angeles), 34:52-172.

1981. The biology of *Heliconius* and related genera. *Ann. Rev. Ent.* (Palo Alto), 26:427-456.

1985. Chemical ecology of dehydropyrrolizidine alkaloids in adult Ithomiinae (Lepidoptera: Nymphalidae). *Rev. Brasil. Biol.* (Rio de Janeiro), 44:435-460.

1987. Chemistry at the Solanaceae/Ithomiinae interface. *Ann. Missouri Bot. Garden* (St. Louis), 74: 359-397.

Brown, K. S., Jr., and W. W. Benson

1974. Adaptive polymorphism associated with multiple Müllerian mimicry in *Heliconius numata* (Lepid: Nymphalidae). *Biotropica* (College Park), 6:205-228.

Brown, K. S., Jr., and R. F. D'Almeida

1970. The Ithomiinae of Brazil (Lepidoptera: Nymphalidae). II. A new genus and species of Ithomiinae with comments on the tribe Dircennini D'Almeida. *Trans. Amer. Ent. Soc.* (Philadelphia) 96:1-18.

Brown, K. S., Jr., J. R. Trigo, R. B. Francini, A. B. B. Morais, and P. C. Motta

1991. Aposematic insects on toxic host plants: coevolution, colonization, and chemical emancipation. *In* Price, P.W., Lewinsohn, T.M., Fernandes, G.W., and Benson, W.W. (eds.), *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*, 357-402. New York: J. Wiley.

Comstock, J. A., and L. Vázquez G.

1961. Estudios de los ciclos biologicos en Lepidopteros Mexicanos. *An. Inst. Biol. Univ. Mex.* (Mexico City), 31:349-448.

D'Almeida, R. Ferreira

1922. *Mélanges Lépidoptérologiques. I. Études sur les Lépidoptères du Brésil.* Berlin: Friedlander & Sohn. 226pp.

1935a. Les *Actinote* de la partie orientale de l'Amérique du Sud. *Ann. Acad. Brasil. Sci.* (Rio de Janeiro), 7:69-88, 89-112, 13 pl.

1935b. Nota supplementar ao nosso artigo sôbre o género *Actinote* Hübn. *Rev. Ent.* (Rio de Janeiro), 5:486-488.

1936. Revisão das *Terias* americanas (Lepid.: Pieridae). Parte II. *Mem. Inst. Oswaldo Cruz* (Belem), 31:189-247, 18 pl.

1938. Estudo sôbre três géneros da subfamília Ithomiinae (Lepid.: Rhop.). *Mem. Inst. Oswaldo Cruz* (Belem), 33:381-394, 3 pl.

1939. Revisão das espécies americanas da superfamília Danaoidea (Lep.: Rhopalocera), Parte I—Família Danaidae, subfamília Danainae. *Mem. Inst. Oswaldo Cruz* (Belem), 34:1-114, 30 pl.

1941. Contribuição ao estudo dos Mechanitidae (Lep. Rhopalocera) (4ª nota). *Pap. Avuls. Dept. Zool. São Paulo*, 1:79-85.

1944. Estudos biológicos sôbre alguns lepidópteros do Brasil. *Arq. Zool. Est. São Paulo*, 4:33-72, 3 pl.

1978. *Catálogo dos Ithomiinae Americanos (Lepidoptera).* Curitiba, PR: CNPq/Univ. Fed. Paraná. 405pp.

DeVries, P. J.

1986. Hostplant records and natural history notes on Costa Rican butterflies. *J. Res. Lepid.* (Beverly Hills), 24: 290-333.

Drummond, B. A., III

1976. *Comparative Ecology and Mimetic Relationships of Ithomiine Butterflies in Eastern Ecuador.* Ph.D. Thesis, Univ. Florida, Gainesville. 361pp.

Drummond, B. A., III, and K. S. Brown, Jr.

1987. Ithomiinae (Lepid.: Nymphalidae): summary of known larval foodplants. *Ann. Missouri Bot. Garden* (St. Louis), 74:341-358.

Fox, R. M.

1940. A generic review of the Ithomiinae (Lepidoptera: Nymphalidae). *Trans. Amer. Ent. Soc.* (Philadelphia), 46:161-207.

1949. The evolutionary systematics of the Ithomiidae (Lepidoptera). *Bull. Univ. Pittsburgh*, 45:1-12.

1956. A monograph of the Ithomiidae (Lepidoptera). Part I. *Bull. Amer. Mus. Nat. Hist.* (New York), 111-176, 9 pl.

1960. A monograph of the Ithomiidae (Lepidoptera). Part II. The tribe Melinaeini Clark. *Trans. Amer. Ent. Soc.* (Philadelphia), 86:109-171.

1961. A checklist of the Ithomiidae. I. Tribes Tithoreini and Melinaeini. *J. Lepid. Soc.* (Los Angeles), 15:25-33.

1967. A monograph of the Ithomiidae (Lepidoptera). Part III. The tribe Mechanitini Fox. *Mem. Amer. Ent. Soc.* (Lanham), 22:1-190.

Fox, R. M., and H. G. Real

1971. A monograph of the Ithomiidae (Lepidoptera). Part IV. The tribe Napeogenini Fox. *Mem. Amer. Ent. Inst.* (Gainesville), 15: 1-368.

Freitas, A. V. L.

1993. Biology and population dynamics of *Placidula euryanassa*, a relict ithomiine butterfly (Nymphalidae; Ithomiinae). *J. Lepid. Soc.* (Los Angeles), 47:87-105.

Gottlieb, O. R.

1982. *Micromolecular Evolution, Systematics and Ecology.* Berlin: Springer-Verlag,. 170pp.

Haber, W. A.

1978. *Evolutionary Ecology of Tropical Mimetic Butterflies (Lepidoptera: Ithomiinae).* Ph.D. Thesis, Univ. Minnesota. 227pp.

Kitching, I. J.

1985. Early stages and the classification of the milkweed butterflies (Lepidoptera: Danainae). *Zool. J. Linn. Soc.* (London), 85:1-97.

Lamas-M., G.

1986. Revisión del genero *Pagyris* Boisduval (Lepidoptera, Nymphalidae: Ithomiinae). *An. Inst. Bio. Univ. Mex.* (Mexico City), 56:259-276.

Moss, A. M.

1920. The Papilios of Pará. *Novit. Zool.* (Tring), 26:295-319.

1949. Biological notes on some Hesperiidae of Pará and the Amazon. *Acta Zool. Lilloana* (Tucuman), 7:27-79, 5 pl.

Motta, P. C.

1989. *Análise Filogenética de Ithomiinae (Lep.: Nymphalidae) com Base nos Ovos: Relação com Plantas Hospedeiras.* Campinas, SP: UNICAMP, M.Sc. Thesis. 294pp.

Müller, W.

1886. Südamerikanische Nymphalidenraupen. Versuch eines natürlichen Systems der Nymphaliden. *Zool. Jahrb.* (Jena), 1: I-X, 1-255, 4 pl.

Muyshondt, A., A. Muyshondt, Jr., and P. Muyshondt

1976. Notas sobre la biologia de lepidopteros de El Salvador. I. *Revta. Soc. Mex. Lepid.* (Mexico City), 2:77-90.

Olmsted, R. G., and J. D. Palmer

1992. A chloroplast DNA phylogeny of the Solanaceae: subfamilial relationships and character evolution. *Ann. Missouri Bot. Garden* (St. Louis), 79:346-360.

Robbins, R. K., and A. Aiello

1982. Foodplant and oviposition records for Panamanian Lycaenidae and Riodinidae. *J. Lepid. Soc.* (Los Angeles), 36: 65-75.

Tyler, H. A., K. S. Brown, Jr., and K. H. Wilson

1994. *Swallowtail Butterflies of the Americas: A Study in Biological Dynamics, Ecological Diversity, Biosystematics and Conservation.* Gainesville: Scientific Publ. 376pp.

Young, A. M.

1972. On the life cycle and natural history of *Hymenitis nero* (Lepidoptera: Ithomiinae) in Costa Rica. *Psyche* (Cambridge, Ma.), 79:284-294.

1973. The life cycle of *Dircenna relata* (Ithomiidae) in Costa Rica. *J. Lepid. Soc.* (Los Angeles), 27:258-267.

1974a. On the biology of *Godyris zavaleta caesiopicta* (Lepidoptera: Nymphalidae: Ithomiinae). *Ent. News.* (Philadelphia), 85:227-238.

1974b. A natural historical account of *Oleria zelica pagasa* (Lepidoptera: Nymphalidae: Ithomiinae) in a Costa Rican mountain rain forest. *Stud. Neotrop. Fauna* (Amsterdam), 9:123-140.

1974c. Notes on the biology of *Pteronymia notilla* (Ithomiidae) in a Costa Rican mountain forest. *J. Lepid. Soc.* (Los Angeles), 28:257-268.

1978a. The biology of the butterfly *Aeria eurimedea agna* (Nymphalidae: Ithomiinae: Oleriini) in Costa Rica. *J. Kansas Ent. Soc.* (Lawrence), 51:1-l0.

1978b. Notes on the biology of the butterfly *Hypoleria cassotis* (Bates) (Nymphalidae: Ithomiinae) in northeastern Costa Rica. *Brenesia* (San Jose), 14-15:97-108.