

# Phylogeny of snout butterflies (Lepidoptera: Nymphalidae: Libytheinae): combining evidence from the morphology of extant, fossil, and recently extinct taxa

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## Abstract

Snout butterflies (Nymphalidae: Libytheinae) are morphologically one of the most unusual groups of Lepidoptera. Relationships among libytheines remain uncertain, especially in the placement of the recently extinct *Libythea cinyras* and two fossils, *L. florissanti*, and *L. vagabunda*. The aim of this study is to present the first phylogenetic hypothesis of Libytheinae utilizing all available morphological data from extant and extinct species. Forty-three parsimony-informative characters were coded, and the all-taxa analysis resulted in six most parsimonious trees (length 92 steps, CI = 0.66, RI = 0.82). The subfamily was resolved as monophyletic and was split into Old World and New World clades. Inclusion of extinct species with considerable missing data had little effect on relationships of extant taxa, although Bremer support values and jackknife frequencies generally decreased if extinct species were included. In order to preserve the monophyly of extant genera, two fossils are assigned to *Libytheana* for the first time (*L. florissanti* comb. n. and *L. vagabunda* comb. n.). This study demonstrates the value of morphological data in phylogenetic analysis, and highlights the contribution that can be made by scoring extinct taxa and including them directly into the analysis.

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Unusual morphological features and well preserved fossils of snout butterflies (Nymphalidae: Libytheinae) have long fascinated morphologists, taxonomists, and paleontologists studying the Lepidoptera. Libytheines have an extraordinarily long labial palpus or 'snout' projecting from the front of the head (Fig. 1), and a fully developed female foreleg that is reduced in all other Nymphalidae. The 12 extant species (Fig. 2) include some broadly distributed migratory continental species and others that are restricted to isolated islands (Shields, 1985a; Kawahara, in press). Unlike most Nymphalidae, the larva of snout butterflies lacks horns or spines, and superficially resembles the larva of Pieridae (Fracker, 1915; Shirozu and Hara, 1960; Shields, 1989). Such characteristics led many traditional studies to treat

libytheines as a separate butterfly family (e.g. Hering, 1921; Holland, 1931; Peile, 1937; Shirozu, 1960).

Following the advent of modern cladistic methodology (Hennig, 1950, 1965, 1966), libytheines were included in Nymphalidae as a subfamily, because they share uniquely with Nymphalidae the presence of longitudinal ridges on the antenna (Kristensen, 1976; Ackery et al., 1998). Morphological and molecular phylogenetic analyses support the inclusion of Libytheinae within Nymphalidae (e.g. de Jong et al., 1996; Weller et al., 1996; Brower, 2000; Wahlberg et al., 2003, 2005a), and more precisely, libytheines are considered to be sister to the remaining Nymphalidae because they lack apomorphic features such as the simple female foreleg (Ehrlich, 1958; Ackery, 1984; Scott, 1985; Scott and Wright, 1990; Harvey, 1991; Martin and Pashley, 1992; de Jong et al., 1996; Freitas, 1999; Freitas and Brown, 2004). However, relationships within the subfamily have not been examined in a modern cladistic

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Fig. 1. Lateral view of the libytheine head (anterior = left). The 'snout' or labial palpus extends forward from the front of the head.

context as phylogenetic studies that included snout butterflies have focused on higher nymphalid relationships with typically only one or two extant libytheine exemplars.

Historically, there have been attempts to resolve relationships of libytheine species. Pagenstecher (1901) assigned all then known extant taxa to three subgenera, *Dichora* Scudder, *Hypatus* Hübner, and *Libythea* Fabricius, and relationships following Pagenstecher are shown in Fig. 3a. Hering (1921) examined distributional



Fig. 2. Adult representatives of Libytheinae. Right dorsal surface shown. Scale 1 cm. (a) *Libythea celtis*, Russia; (b) *L. lepita*, Japan; (c) *L. myrrha*, India; (d) *L. collenettei*, French Polynesia; (e) *L. narina*, Philippines; (f) *L. geoffroy*, Papua New Guinea; (g) *L. labdacca*, Cameroon; (h) *L. laius*, Mozambique; (i) *Libytheana carinenta*, Brazil; (j) *L. fulvescens*, Dominica; (k) *L. motya*, Cuba; (l) *L. terena*, Dominican Republic. All are males except *L. motya*.

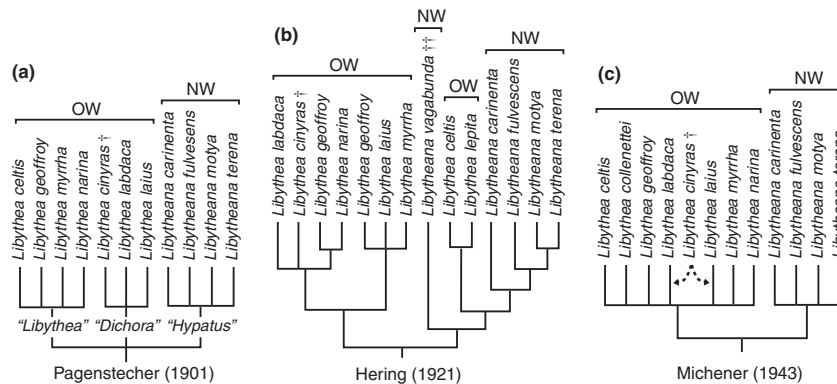


Fig. 3. Previous hypotheses of libytheine relationships. (a) Pagenstecher (1901). (b) Hering (1921). (c) Michener (1943). For the purpose of consistency between trees, taxon names in figures follow the names recognized in Kawahara (in press). OW, Old World; NW, New World; †, recently extinct; ††, fossil.

patterns and external features of adults, and published the most comprehensive work on libytheine relationships to date. He hypothesized an ancestral split within the subfamily into an Old World and a predominantly New World lineage (Fig. 3b). Subsequently, Michener (1943) synonymized *Dichora* with *Libythea*, and introduced the replacement name *Libytheana* for the invalid name *Hypatus* Hübner (Hemming, 1967; Kawahara, in press). Michener classified all New World species in *Libytheana*, and distinguished this genus from the putatively monophyletic Old World *Libythea*, but relationships among species in the subfamily remain largely uncertain (Fig. 3c).

Of particular interest is the phylogenetic position of extinct snout butterflies. Hering (1921) postulated that the fossil *Libytheana vagabunda* is the putative sister species to taxa currently placed in *Libytheana* and the Old World *Libythea celtis* group (Fig. 3b). This fossil shares a unique combination of morphological features found in extant genera, and for this reason was originally described in the monotypic genus *Prolibythea* Scudder. After examining the fossil, Shields (1985b) included the species in *Libythea* because of its close resemblance to the Asian *Libythea lepita*. Shields (1985b) further placed a second libytheine fossil, *Barbarothea florissanti*, in *Libythea* because of its similarity to *Libythea geoffroy*. However, neither Shields' fossil assignments nor the monophyly of the currently recognized genera have been tested in a modern phylogenetic framework. Consequently, this paper aims to: (i) present a cladistic analysis of Libytheinae; (ii) test Michener's (1943) postulate that extant genera form monophyletic Old World and New World groups; (iii) refine our understanding of libytheine morphology by assessing character homology; (iv) test how the inclusion of the three extinct taxa with abundant missing data affects relationships of extant taxa.

## Materials and methods

### *General perspective on inclusion of extinct taxa with missing data*

Inclusion of extinct taxa with abundant missing data in parsimony analyses remains controversial. Those who oppose the inclusion of incomplete taxa argue that the large amount of missing data will result in poorly resolved trees because incomplete taxa often lack many informative characters (Patterson, 1981; Ax, 1987). Indeed, studies have shown that including taxa with abundant missing data can result in an increase in the number of trees (Gauthier, 1986; Nixon and Wheeler, 1992; Novacek, 1992; Wilkinson and Benton, 1995), and a decrease in branch support values (Wilkinson and Benton, 1996; Horovitz, 1999; Wilkinson, 2003; Cobbett

et al., 2007). For these reasons, some empirical studies have excluded potentially valuable incomplete taxa from their analyses (e.g. Liu et al., 2001).

Despite such practice, there is overwhelming evidence that incomplete taxa should not be excluded from parsimony analyses. Recent simulation work demonstrates that analyses including taxa with abundant missing data can lead to improved phylogenetic resolution and accuracy relative to analyses that exclude them (Wiens, 1998, 2005, 2006). Empirical studies have shown that inclusion of incomplete fossil taxa can often provide valuable character-state combinations that are not present in extant taxa (Donoghue et al., 1989; Novacek, 1992; Wilkinson, 1995; Kearney, 2002; Cobbett et al., 2007), thereby breaking long branches and increasing the chance of resolving the true phylogeny (Gauthier et al., 1988; Anderson, 2001; Poe, 2003; Wiens, 2005, 2006). Including extinct species also improves taxonomic breadth, which is the primary purpose of most empirical studies. Such a total evidence approach (Kluge, 1989) is taken in this study, as the most justified phylogenetic hypothesis is here considered to be the one that utilizes all available data.

### *Taxonomic material*

The 1981 libytheine specimens recently examined for a revision of the subfamily (Kawahara, in press) were studied for external morphology. Of these, 87 specimens were dissected fully, or in part, to further examine the appendages and genital morphology (Appendix 1). These dissections are deposited in the following collections: American Museum of Natural History, New York, USA (AMNH); Akito Y. Kawahara private collection, Fujinomiya, Japan (AYK); The Natural History Museum, London, UK (BMNH); Bernice P. Bishop Museum, Honolulu, USA (BPBM); Carnegie Museum of Natural History, Pittsburgh, USA (CMNH); Cornell University Insect Collection, Ithaca, USA (CUIC); Mayumi Takahashi private collection, Shizuoka, Japan (MTC); Tomoo Fujioka private collection, Ueno, Japan (TFC); and The National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

The extinct *Libythea cinyras*, known only from a poorly preserved holotype from Mauritius (Kawahara, 2006), was examined at The Natural History Museum, London. The holotype specimen of *Libytheana vagabunda* was examined at the paleontology collection of the Museum of Comparative Zoology at Harvard University. The fossil *L. florissanti* is presumably lost (Shields, 1985b) and could not be examined, but character states were scored from detailed images in the original description (Scudder, 1892). Both fossils were discovered from Eocene deposits dated at 34.07 Myr from the Florissant formations in Colorado (Meyer, 2003). These

fossils are here treated as New World taxa, because the Old World and New World were separated before the Eocene (Scotese and Sager, 1988).

Six outgroups were included in the study, *Pieris rapae* (L.), *Euselasia gelon* (Stoll), *Chersonesia rahria* (Moore), *Danaus plexippus* (L.), *Nymphalis polychloros* (L.), and *Pierella luna* (Fabricius). *Chersonesia rahria* was included in the analysis because a prior phylogenetic analysis of Nymphalidae placed this species close to the Libytheinae (Brower, 2000), and other taxa were chosen as additional outgroups. The position of the Libytheinae in Nymphalidae was not investigated in the present study, as the main goal was to understand species relationships within Libytheinae.

#### *Dissections, illustrations, and imaging*

Methods used for preparation of genitalia follow Winter (2000). The abdomen of a dried specimen was removed, placed in an uncapped glass vial containing 10% KOH, and heated on a hot plate for 10 min. The abdomen was then submerged in 95% EtOH and hairs and scales were removed with a fine brush. Male genitalia were separated from the abdomen by cutting the membrane between the genitalic ring and eighth abdominal segment. In females, the membrane between the sixth and seventh segment was cut to remove the genitalia, and the membranous structures were stained with Chlorazol Black dye. All genital dissections were placed in Falcon 24-cell sorting trays and compared. Legs, palpi, and antennae were heated in 10% KOH, cleaned, mounted on depression slides with glycerin jelly, and examined under a Leitz Dialux phase-contrast compound microscope. Illustrations were prepared using a camera lucida attached to a WILD M5 stereomicroscope, scanned and redrawn using Adobe Illustrator CS2. Habitus images were taken with a Nikon 4500 digital camera. For SEM images, the antenna and legs were removed from the specimen, dissected, dried, and sputter-coated with a 60 : 40 mixture of gold–palladium. SEM images were taken using an Amray 1810 microscope with a lanthanum hexaboride (LaB6) source at the Smithsonian Institution SEM facility. Morphological nomenclature follows Scoble (1992) except for wing venation terminology, for which I follow Wootton (1979) and recognize four forewing radial sector veins.

#### *Character coding*

Forty-three characters of adult morphology (Table 1) were coded and a data matrix was constructed with WINCLADA ver. 1.0 (Nixon, 2002; Appendix 2). Parsimony-uninformative characters were excluded, as they can influence calculations of branch support (Carpenter, 1992, 1996). Of the 43 characters, 25 were binary, and 18 were multi-state. Multi-state characters 8, 30, 33, 34,

and 38 were transformation series and coded as additive, while all remaining characters were non-additive. All characters were equally weighted.

#### *Phylogenetic analyses*

Parsimony analyses were conducted for (i) an all-taxa data set including all libytheine species, and (ii) seven data sets omitting one or more extinct taxa. The all-taxa analysis was considered to be the best estimate of relationships, and additional analyses were conducted primarily to examine the potential effect of including the three taxa with abundant missing data.

Cladistic analyses were performed with NONA ver. 2.0 (Goloboff, 1999), implementing the following commands: hold 1000, hold/100, mult\*1000, max\*, mswap+. Most parsimonious trees (MPTs) were examined with WINCLADA (Nixon, 2002) under unambiguous and ACCTRAN optimization. Character jackknife (Lanyon, 1985; Farris et al., 1996) and Bremer support (Bremer, 1988, 1994), were calculated in NONA. Jackknifing was conducted with 500 replications (TBR, mult\*100; hold/1), Bremer support values were calculated with commands that searched for suboptimal trees at least five steps longer than the shortest tree (h 5000; sub 1; find\*; h 10000; sub 2; find\*; h 15000; sub 3; find\*; h 25000; sub 4; find\*; h 32759; sub 5; find\*; bs;). The strict consensus (Sokal and Rohlf, 1981) and agreement subtrees (Cole and Hariharan, 1996) were used to describe results.

## **Results**

The all-taxa analysis resulted in six MPTs (length 92 steps, CI = 0.66, RI = 0.82), and the preferred tree is illustrated in Fig. 7. The six trees differed in the position of *Libytheana carinenta*, *L. fulvescens*, and nymphalid outgroups. Unambiguous taxon-defining character states found in all six MPTs are listed in Table 2. Three nodes were collapsed in the strict consensus, and the subfamily was resolved as monophyletic with strong support (Bremer support 3, jackknife 88; Fig. 8a).

The extinct *Libythea cinyras*, *Libytheana vagabunda*, and *L. florissanti* were missing 39.5, 67.4, and 76.7% of characters, respectively. Omission of extinct taxa generally did not affect relationships of extant species. Exclusion of all extinct taxa resulted in a two MPTs (length 90 steps, CI = 0.67, RI = 0.83; Fig. 8b), and support was high for the monophyly of Libytheinae (Bremer support > 5; jackknife 99) and *Libytheana* (Bremer support > 5; jackknife 100). The maximum agreement subtree denotes overall topological congruence between the all-taxon trees and all trees resulting from analyses excluding at least one extinct taxon (Fig. 8c). Relationships of extant species in *Libythea* did not change with the omission of one or more extinct

Table 1  
 Characters coded for phylogenetic analysis

Character	Coding	Comments
1. Club of antenna	(0) gradually incrassate (Fig. 6a); (1) abruptly incrassate (Fig. 6b)	–
2. Three raised ventral carinae on antennal flagellum	(0) absent; (1) present (Fig. 4a)	The three carinae on the antenna is thought to be the single apomorphy defining the Nymphalidae (Kristensen, 1976; Ackery et al., 1998)
3. Flap-like lobe on ventral surface of patagium	(0) reduced; (1) complete	Ehrlich (1958, p. 355) described this character as 'patagia membranous except for a small lateral sclerotic area on each'
4. Anepisternum of mesothorax	(0) absent; (1) present	–
5. Precoxal suture	(0) absent; (1) present	–
6. Parepisternal suture	(0) absent; (1) present	–
7. Prescutum	(0) oblique to almost vertical, with metanotum not appearing truncated; (1) approximately vertical or with upper end slightly anterior to lower end	Character 95 of de Jong et al. (1996)
8. Foreleg	(0) reduced in both sexes; (1) reduced in male (Fig. 4b) but developed in female (Fig. 4c); (2) developed in both sexes	Character 43 of de Jong et al. (1996); and within Nymphalidae this character is unique to Libytheinae. The foreleg morphology led some studies on butterfly higher relationships to recognize the snout butterflies as a separate family (Ehrlich and Ehrlich, 1967; Shields, 1989), to treat them as a basal nymphalid (Ackery, 1984; Scott and Wright, 1990; de Jong et al., 1996), or to group them with some riodinids, which also have a reduced male foreleg, but a developed female foreleg (Mengel, 1905; Seitz, 1906-1924)
9. Spines on tibia of foreleg	(0) absent; (1) two; (2) more than two	–
10. Claws on female foreleg	(0) absent; (1) present (Fig. 4c)	–
11. Pulvilli of claws of pterothoracic leg	(0) vestigial; (1) reduced; (2) developed	Character 55 of de Jong et al. (1996)
12. Spines on tibia of pterothoracic leg	(0) absent; (1) two; (2) more than two	–
13. Mesoscutellum overhanging metascutum	(0) absent; (1) present (Fig. 6c)	This character was first described as 'metatergum essentially overhung by mesotergum' (Ehrlich, 1958, p. 355)
14. Forewing radial sector	(0) three branches; (1) four branches (Fig. 5a,b)	–
15. Forewing Rs2	(0) with base closer to fork of Rs3 + Rs4 than discal cell apex (Fig. 5a); (1) with base midway between fork of Rs3 + Rs4 and discal cell apex (Fig. 5b)	Michener (1943) first described this character to define <i>Libytheana</i>
16. Basal spur on forewing cubitus	(0) absent; (1) present	–
17. Forewing discocellular recurrent veins	(0) absent; (1) weak; (2) distinct	Character 12 of de Jong et al. (1996)
18. Forewing vein M1–M2	(0) not curved towards wing base; (1) slightly incurved (Fig. 5a,b); (2) incurved sharply angled	Character 13 of de Jong et al. (1996)
19. Forewing posterior anal vein 2a	(0) absent; (1) present	–
20. Hindwing M3 and CuA1	(0) well separate; (1) connate (Fig. 5c,d)	–
21. Hindwing humeral vein	(0) short; (1) long, straight; (2) long, curved distally (Fig. 5c,d)	–
22. Hindwing discal cell	(0) intermediate, 41–59% of wing length; (1) long, 60% or more of wing length; (2) short, 40% or less of wing length	Character 29 of de Wahlberg et al. (2005a)
23. Hindwing cross-vein M1–M2	(0) forming angle with M2 (Fig. 5c,d); (1) curving into M2 smoothly; (2) running more or less straight into M2	Character 36 of de Jong et al. (1996)
24. Outer margin of axillary 3	(0) straight or convex; (1) concave	Character 80 of de Jong et al. (1996)
25. Triangular mark at base of forewing discal cell	(0) absent (Fig. 5a); (1) present (Fig. 5b)	–

Table 1  
(Continued)

Character	Coding	Comments
26. Band from forewing costal margin to M3:	(0) absent (Fig. 5a); (1) discontinuous (Fig. 5b); (2) continuous (Fig. 2k,l)	Shields (1985a) illustrated this character, and presented the continuous band as a putative synapomorphy of <i>Libytheana</i>
27. Band across forewing cells M1 and M2	(0) absent; (1) proximal (Fig. 5b); (2) distal (Fig. 5a)	The proximal position of this band was presumed to be a synapomorphy of <i>Libythea</i> (Shields, 1985b)
28. Distal mark of forewing cell M3	(0) absent (Fig. 5b); (1) present (Fig. 5a)	–
29. Forewing apex	(0) smooth (Fig. 5b); (1) falcate (Fig. 2e); (2) sharply falcate (Fig. 5a)	–
30. Triangular mark in Sc + R1 cell of hindwing	(0) absent (Fig. 5c); (1) blurred (Fig. 5d); (2) discrete	–
31. Single, wide band across hindwing cells M1–M3	(0) absent; (1) present (Fig. 5c,d)	–
32. Lobe at terminus of CuA2 of hindwing	(0) absent; (1) present	–
33. Ratio of forewing length (measured by length from base of forewing to apex) to palp length	(0) < 3.8; (1) 4–5.8; (2) > 6	–
34. Eighth abdominal tergum of male	(0) simple; (1) bifid (Fig. 6d); (2) trifid (Fig. 6e)	The bifid state found in <i>Libythea</i> is the ‘bifid superuncus’ of Corbet and Pendlebury (1978). Michener (1943) first described the spines on the posterior margin of the median process in the trifid state, and Friedlander (1984) illustrated and described the spines in detail
35. Uncus	(0) curved dorsad (Fig. 6f); (1) curved ventrad (Fig. 6g).	–
36. Shape of saccus	(0) short; (1) attenuate (Fig. 6h); (2) T-shaped (Fig. 6i)	–
37. Phallus	(0) straight (Fig. 6j); (1) curved dorsally (Fig. 6k); (2) sigmoid (Fig. 6l)	–
38. Position of apical point of juxta	(0) dorsal margin (Fig. 6m); (1) lateral, between dorsal and ventral margins (Fig. 6n); (2) ventral margin (Fig. 6o)	–
39. Dorsal margin of valva	(0) weakly curved ventrad (Fig. 6p,q); (1) strongly curved ventrad (Fig. 6r)	–
40. Apical spine on valva	(0) absent (Fig. 6p,q); (1) present (Fig. 6r)	–
41. Eighth abdominal sternum of female	(0) reduced (Fig. 6s); (1) developed (Fig. 6t)	–
42. Corpus bursa with triangular signa	(0) absent; (1) present	The triangular signa are present in <i>Libythea</i> , and Kawahara (2003) illustrated this structure
43. Microtrichia on membrane of bursa copulatrix	(0) absent; (1) present	–

taxa, but within *Libytheana*, the sister-group relationship of *L. carinenta* and *L. fulvescens* changed when one or more were excluded. Removing extinct taxa generally decreased the number of MPTs and increased the number of nodes with jackknife frequencies > 50 and Bremer support values  $\geq 2$  (Table 3).

## Discussion

### *Extinct taxa with abundant missing data*

Extinct taxa were excluded from analyses in various combinations to examine whether their abundant missing data were affecting relationships among extant

species. Incomplete taxa generally did not affect relationships among extant species, but changed the number of MPTs, and their exclusion tended to increase node support. Contrary to the general perception that removing incomplete taxa yields better resolution and fewer MPTs, two analyses in the present study resulted in a greater number of MPTs when incomplete taxa were excluded (Table 3). If *Libytheana vagabunda* is omitted alone or excluded with *Libythea cinyras*, the number of MPTs increased to 12. The difference in the number of MPTs is not large, but these results are consistent with a survey of published studies that included various degrees of incomplete taxa (Kearney, 2002). Exclusion of taxa with missing data can, but do not always, result in fewer MPTs; rather, it is the distribution of available character

Table 2  
Summary of nodes, taxa, and taxon-defining character states

Clade	Taxon	Taxon-defining character states
A	Libytheinae	<b>3(0): reduced flap-like lobe on ventral surface of patagium; 7(1): prescutum approximately vertical or with upper end slightly anterior to lower end; 13(1): mesoscutellum overhanging metascutum (Fig. 6c); 23(0) hindwing cross-vein M1–M2 forming angle with M2 (Fig. 5c,d); 24(1): concave outer margin of axillary 3; 30(1): blurred triangular mark in Sc + R1 of hindwing (Fig. 5d); 34(1): bifid male eighth abdominal tergum (Fig. 6d)</b>
B	<i>Libythea</i>	15(0): Forewing Rs2 with base closer to fork of Rs3 + Rs4 than discal cell apex (Fig. 5b); 37(2): phallus sigmoid (Fig. 6l); <b>39(1): dorsal margin of valva strongly curved ventrad (Fig. 6r); 42(1): corpus bursa with triangular signa</b>
C	<i>Libythea</i> (excl. <i>L. collettei</i> )	31(1): single, wide band across hindwing cells M1–M3 (Fig. 5c,d); <b>40(1): apical spine on valva (Fig. 6r)</b>
D	<i>L. cinyras</i> group	38(2): position of apical spine of juxta at ventral margin (Fig. 6o)
E	<i>L. cinyras</i> + <i>L. narina</i>	30(2): discrete triangular mark in Sc + R1 of hindwing.
F	Core <i>Libythea</i>	33(1): ratio of forewing length to palp length > 4–5.8
G	<i>L. labdaca</i> + <i>L. laius</i>	30(2): discrete triangular mark in Sc + R1 of hindwing; 32(1): lobe at terminus of CuA2 of hindwing (Fig. 2g,h)
H	<i>L. myrrha</i> group	<b>29(2): forewing apex sharply falcate;</b> 30(0): triangular mark in Sc + R1 of hindwing absent (Fig. 5c)
I	<i>L. celtis</i> + <i>L. lepita</i>	1(0): club of antenna gradually incrassate (Fig. 6a)
J	<i>L. florissanti</i> + <i>L. vagabunda</i>	1(0): club of antenna gradually incrassate (Fig. 6a)
K	<i>L. carinenta</i> + <i>L. fulvescens</i>	31(1): single, wide band across hindwing cells M1–M3 (Fig. 5c,d)
L	<i>L. motya</i> + <i>L. terena</i>	<b>26(2): continuous band from forewing costal margin to M3 (Fig. 2k,l);</b> 30(2): discrete triangular mark in Sc + R1 of hindwing

Nodes and unambiguous character states found in all six MPTs are listed. Apomorphies in bold; node numbers correspond to nodes in Fig. 7.

Table 3  
Effect of removing extinct taxa with abundant missing data

Extinct taxa removed	MPTs	L	CI	RI	Total nodes	Nodes collapsed	Node support	
							BS ( $\geq 2$ )	JK ( $> 50$ )
None	6	92	0.66	0.82	19	3	3	3
<i>L. cinyras</i>	6	92	0.66	0.82	18	3	3	3
<i>L. florissanti</i>	6	92	0.66	0.82	18	3	3	3
<i>L. vagabunda</i>	12	91	0.67	0.83	18	5	2	3
<i>L. cinyras</i> , <i>L. florissanti</i>	6	92	0.66	0.82	17	3	3	3
<i>L. cinyras</i> , <i>L. vagabunda</i>	12	91	0.67	0.83	17	5	3	4
<i>L. florissanti</i> , <i>L. vagabunda</i>	2	90	0.67	0.83	17	1	4	8
All	2	90	0.67	0.83	16	1	5	9

states in the data set that can influence its number (Novacek, 1992; Kearney, 2002).

The number of branches with strong support generally increased as extinct taxa were removed from the data set (Table 3). If no taxa were omitted, only three nodes had jackknife frequencies  $> 50$ , whereas omission of all extinct taxa resulted in nine. These results are consistent with prior studies demonstrating that supplementing a data set with incomplete taxa tends to result in trees with lower branch support (Wilkinson and Benton, 1996; Horovitz, 1999; Wilkinson, 2003; Cobbett et al., 2007), but does not justify the exclusion of incomplete taxa prior to analysis.

#### Comparison with previous studies on libytheine relationships

In general, results presented here were most consistent with the classification of Michener (1943), who separated

the subfamily into Old World and New World genera. Michener erected the genus *Libytheana* based on four putative characters that distinguish *Libytheana* from *Libythea*: position of forewing Rs2 with base midway between fork of Rs3 + Rs4 and discal cell apex (Char. 15 : 1, Fig. 5b), labial palp length (Char. 33 : 2, Fig. 2), trifold eighth abdominal tergum with spines at apex of median process (Char. 34 : 2, Fig. 6e), and valva without an apical spine (Char. 40 : 2, Fig. 6p,q). The former three can be used as diagnostic characters to distinguish libytheine genera, but only the trifold eighth abdominal tergum was found to be a synapomorphy of *Libytheana* under ACCTRAN optimization.

Most studies on the systematics of Libytheinae did not include fossil taxa (Pagenstecher, 1901; Michener, 1943; Shields, 1984; Okano, 1987), and the phylogenetic position of fossil libytheines has remained uncertain. Hering (1921) tentatively placed *Libytheana vagabunda* ancestral to New World Libytheinae + Old World

*L. celtis* group, based largely on superficial similarity. Shields (1985b) associated the two libytheine fossils with extant *Libythea* because morphological features of these fossils resemble those of certain extant taxa from Southeast Asia. However, all analyses from the present study placed the two fossils in a clade with extant New World *Libytheana*. The subfamily was split into Old World and New World clades, rejecting both Hering's and Shields' postulates, but supporting Michener's Old World/New World hypothesis.

Within *Libythea*, *L. celtis* and *L. lepita* were recovered as sister species (Fig. 7, Clade I). Morphologically

these species are very similar, and numerous authors treat them as conspecific (Pagenstecher, 1901, 1902, 1911; Gaede, 1932; Nagano and Esaki, 1933; Shirozu, 1960; Fujioka, 1975; Kawazoe and Wakabayashi, 1976; Igarashi and Fukuda, 2000; but see also Yoshimoto, 1999; Kawahara, in press). Hering (1921) placed the two taxa as sister species in his tree, but believed that they evolved independently from the African and Indo-Australian species of *Libythea*. He therefore hypothesized that *L. celtis* and *L. lepita* are the sister-group to *Libytheana*. The phylogeny from the present study contradicts Hering's prediction.

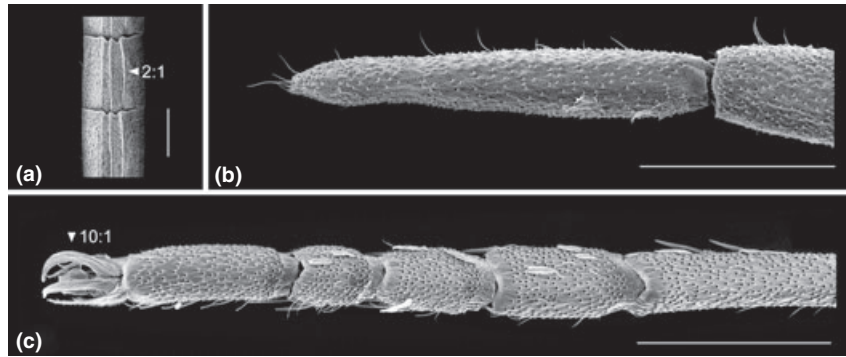


Fig. 4. Antenna and forelegs of adult *Libythea celtis*. (a) Antennal segments with three longitudinal ventral carinae (2 : 1), scale 200  $\mu\text{m}$ . (b,c) Scale 500  $\mu\text{m}$ , (b) Male foreleg, (c) female foreleg with claw (10 : 1).

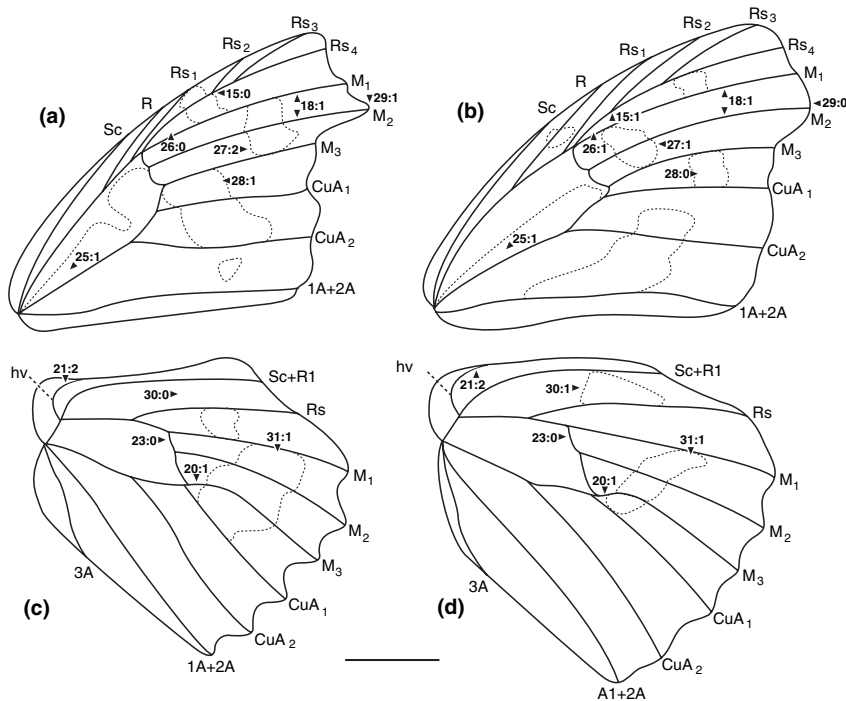


Fig. 5. Wing venation and marking patterns of Libytheinae. Character and character states noted. Scale 5 mm. (a,c) *Libythea celtis*, (b,d) *Libytheana carinenta*.



The extinct Mauritian *L. cinyras* was recovered in a clade with *L. geoffroy* and *L. narina* (Fig. 7, Clade D). *Libythea geoffroy* and *L. narina* have been hypothesized to be closely related (Shields, 1985a), but the association of *L. cinyras* with these species is in stark contrast to past associations of that species with various African taxa. Pagenstecher (1901) grouped *L. cinyras* with *L. labdaca* and *L. laius* in a then-recognized African subgenus, *Dichora* Scudder, while Hering (1921) placed *L. cinyras* close to the Madagascan *L. labdaca ancoata*. Shields (1984) and Okano (1987) also associated *L. cinyras* with African Libytheinae, treating *L. cinyras* as a subspecies of *L. laius* and *L. labdaca*, respectively. Unlike these studies, all analyses presented here placed *L. cinyras* with Southeast Asian *L. geoffroy* and *L. narina*, a grouping that is supported by the apical point of the juxta at the ventral margin (Char. 38 : 2; Fig. 6o).

Interestingly, *L. collenettei* is the sister taxon to the remaining *Libythea* species, but with weak support (Bremer support 1, jackknife < 50; Fig. 8a). The

phylogenetic position of *L. collenettei* is striking, as it has a very isolated distribution restricted to the Marquesas Islands in the Pacific (Shields, 1987; Kawahara, 2003). The two characters responsible for placing this taxon at the base of *Libythea* are both characters of absence: the lack of a single, wide band across hindwing cells M1–M3 (Char. 31 : 0), and the absence of a spine at the apex of the valva (Char. 40 : 0, Fig. 6p,q). If fossils are removed and branch support calculated, the core *Libythea* clade (all *Libythea* species excluding *L. collenettei*) remains weakly supported (Bremer support 1, jackknife 60; Fig. 8b). If these two characters are coded as ambiguous for *L. collenettei* and analysed, one MPT results, in which *L. collenettei* is the sister taxon to the clade containing *L. cinyras*, *L. geoffroy*, and *L. narina*. Based on phenotypic similarity and zoogeography, *L. collenettei* has been thought to be closely allied with the eastern Indonesian *L. geoffroy* (Waterhouse, 1937; Shields, 1987). For the above-mentioned reasons, I consider the position of *L. collenettei* as tentative, and this hypothesis should

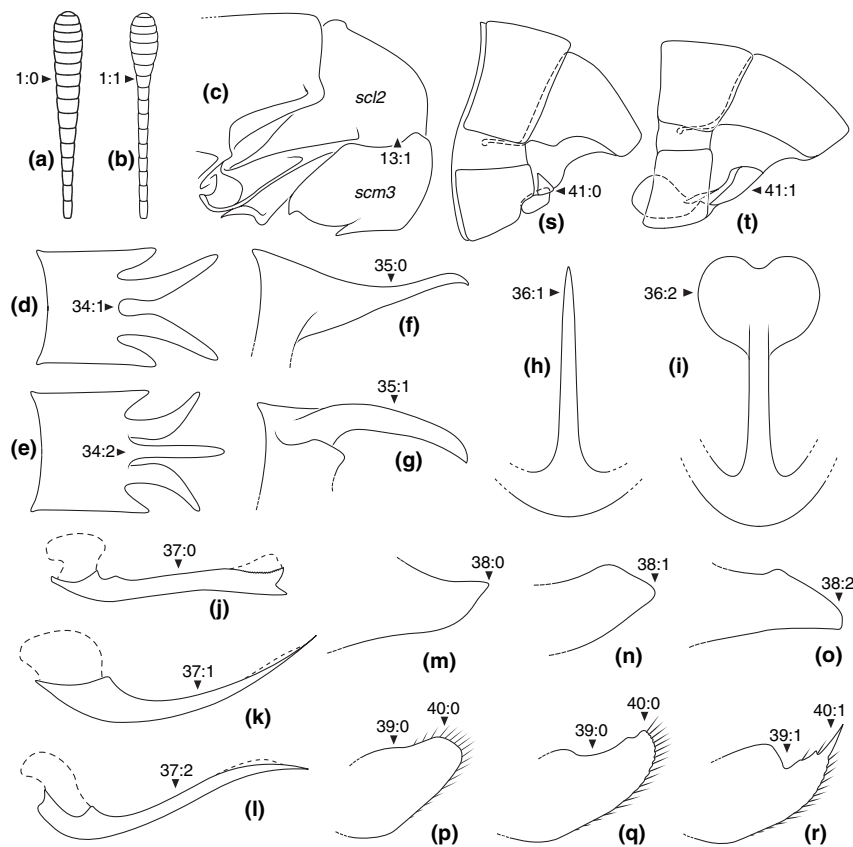


Fig. 6. Schematic illustrations of some morphological characters. (a) Club of antenna gradually incrassate (*L. celtis*); (b) abruptly incrassate (*L. carinenta*). (c) Mesoscutellum (sc12) overhanging metascutum (scm3; *L. labdaca*). (d) Eighth abdominal tergum of male bifid (*L. lepita*); (e) trifid (*L. carinenta*). (f) Uncus, lateral view, curved dorsad (*L. labdaca*); (g) curved ventrad (*L. carinenta*). (h) Saccus, ventral view, elongate (*L. celtis*); (i) T-shaped (*L. carinenta*). (j) Phallus, lateral view, straight (*P. luna*); (k) curved (*L. carinenta*); (l) sigmoid (*L. celtis*). (m) Position of apical point of juxta, dorsal (*L. carinenta*); (n) lateral (*L. celtis*); (o) ventral (*L. geoffroy*). (p,q) Apical spine on valva absent (*L. terena* and *L. collenettei*, respectively); (r) present (*L. geoffroy*). (s) Eighth abdominal sternum of female, reduced (*L. celtis*); (t) developed (*L. carinenta*).

be verified when a more comprehensive character sampling from additional sources of data becomes available.

*New combinations for fossil taxa*

In all analyses including fossils, *L. florissanti* (Scudder) and *L. vagabunda* (Scudder) form a monophyletic group with *Libytheana*. This contradicts previous hypotheses, as these two fossils have traditionally been

associated with Asian *Libythea* (Scudder, 1889; Shields, 1985b). Specifically, these authors note the resemblance of the hindwing lobe, overall antennal shape, and size of the fossils to modern Asian taxa. However, none of the authors examined the position of the forewing Rs2 vein, a key diagnostic feature of extant genera (Michener, 1943). Both fossils undoubtedly have a forewing Rs2 vein that arises intermediately between fork Rs3 + Rs4 and discal cell apex (Char. 15 : 1, Fig. 5b), a character state common to all extant *Libytheana* (Appendix 2). In

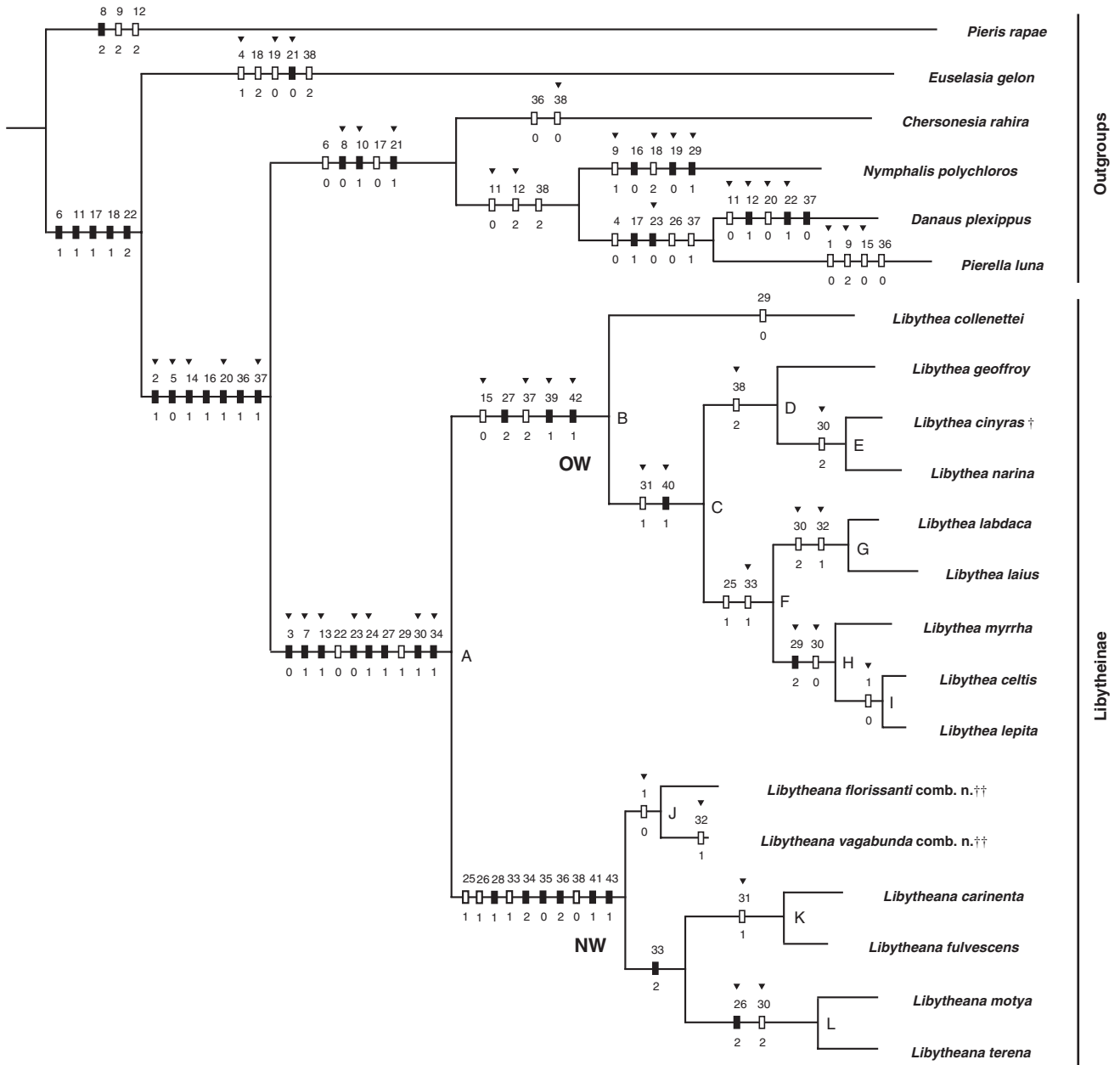


Fig. 7. One of six MPTs with the all-taxa data set (length 92 steps, CI = 0.66, RI = 0.82). The number above each rectangle refers to the character in Table 1, the number below the rectangle is the character state. A dark rectangle indicates a unique character state change, a white rectangle indicates a parallelism or reversal. A triangle indicates an unambiguous character state, all other character states are present if mapped with ACCTRAN optimization. Nodes within the ingroup with unambiguous character states are labelled.

order to preserve the monophyly of extant genera, the two fossil taxa are here for the first time included in *Libytheana*.

*Libytheana florissanti* (Scudder, 1892) comb. n.

= *Barbarothea florissanti* (Scudder, 1892) (Scudder, 1892): 23, pl. 3, Figs 1–5.

= *Libythea florissanti* (Scudder, 1892); (Shields, 1985b): 13.

*Libytheana vagabunda* (Scudder, 1889) comb. n.

= *Prolibythea vagabunda* Scudder (1889); Scudder, (1889): 465, pl. 53, Figs 4–9.

= *Libythea vagabunda* (Scudder, 1889); (Shields, 1985b): 13.

Type: Museum of Comparative Zoology, Cambridge, Massachusetts. No. 5, Field #16,353, *Libytheana vagabunda*, Type, Scudder Collection, Florissant, Colorado.

**Conclusions**

This is the first phylogenetic analysis utilizing all available data from both extant and extinct Libytheinae.

The all-taxa analysis resulted in six trees which contrasted with two previous hypotheses of libytheine relationships (Pagenstecher, 1901; Hering, 1921). One reason for the difference in relationships is that these prior studies did not execute a cladistic analysis to justify phylogenetic conclusions. Trees presented here support Michener’s (1943) postulate of an ancestral Old World/New World split in the subfamily, but challenge the homology of some of his morphological characters that united particular libytheines. Only a limited amount of data were available for extinct species, but inclusion of these taxa resulted in a justifiable assignment to an extant genus. Supplementing the data set with incomplete taxa did not substantially reduce phylogenetic resolution despite recommendation to exclude them from phylogenetic analysis *a priori* (Patterson, 1981; Ax, 1987).

Recent phylogenetic studies based on molecular and morphological data have considerably advanced our understanding of butterfly relationships, especially within Nymphalidae (Brower, 2000; Wahlberg and Nylin, 2003; Wahlberg et al., 2003, 2005b; Freitas and Brown,

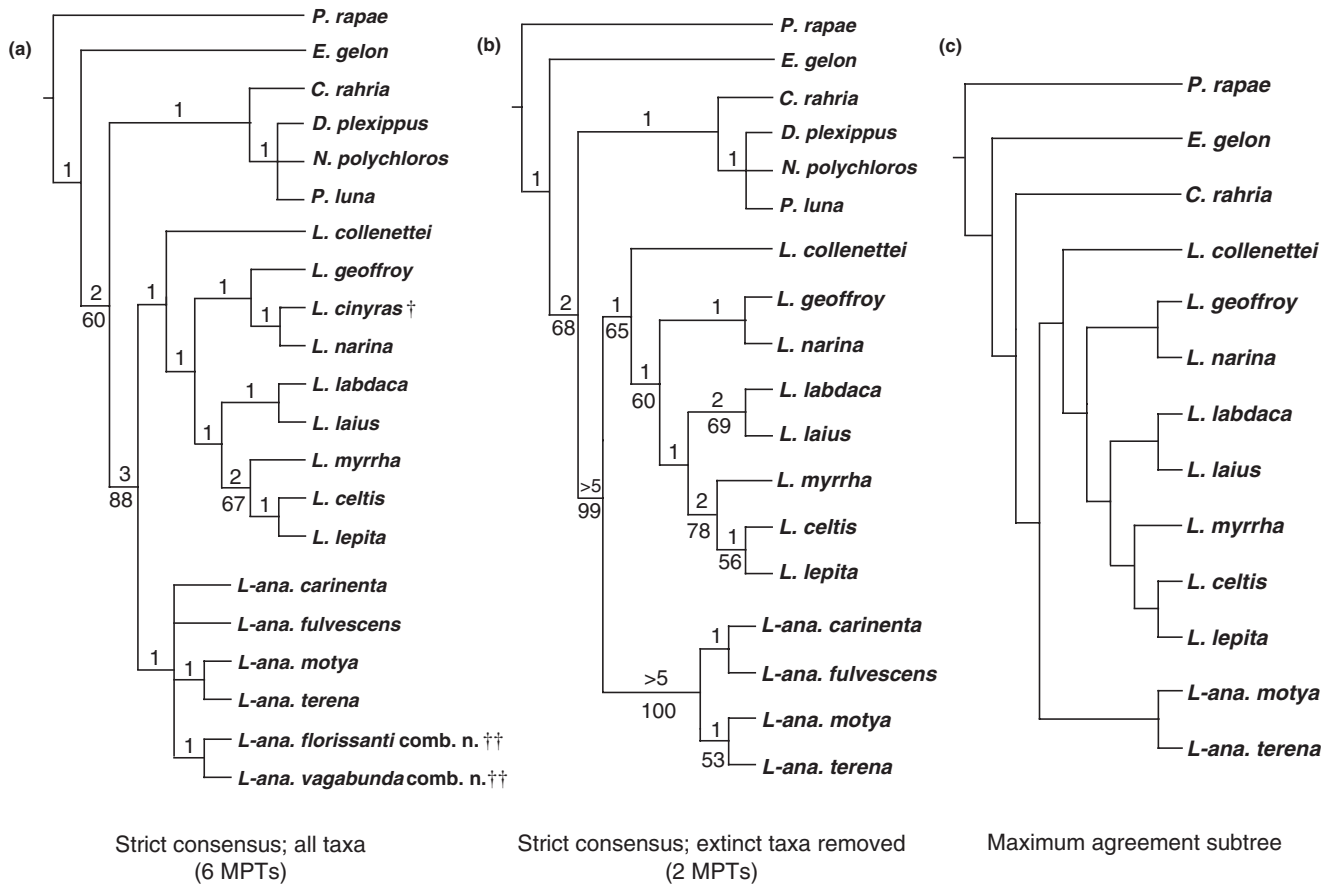


Fig. 8. Assessing the topological impact of omitting fossils. (a) Strict consensus of six most parsimonious trees if all taxa are included. (b) Strict consensus if extinct taxa are omitted. (c) Maximum agreement subtree showing relationships which are congruent between the six all-taxa trees and all trees resulting from analyses excluding at least one extinct taxon. All unsupported nodes are collapsed; numbers above branches indicate Bremer support, numbers below are jackknife frequencies.

2004; Peña et al., 2006; Simonsen et al., 2006). However, well preserved butterflies are uncommon in the fossil record, and morphological characters of extinct taxa are rarely scored for inclusion in phylogenetic analyses. Most studies use available fossils to date phylogenies, which, without careful examination of fossil morphology, may lead to misleading relationships and incorrect estimation of the timing of events (de Jong, 2007). Without cladistic studies that include fossils as terminal taxa, we cannot test their classification and examine the fundamental historical patterns of morphological character evolution.

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## Appendix 1

Specimens examined for both genitalia and external morphology. Refer to text for repository abbreviations.

Taxon	Locality	Repository
<i>Chersonesia rahria</i> (Moore)	3♂, 3♀, India, Lower Sikkim	AMNH
<i>Danaus plexippus</i> (L.)	1♂, 1♀, USA, Maryland, Prince Georges Co	USNM
<i>Euselasia gelon</i> (Stoll)	1♂, 1♀, French Guiana	USNM
<i>Nymphalis polychloros</i> (L.)	1♂, 1♀, Germany	USNM
<i>Pierella luna</i> (Fabricius)	3♂, 3♀, Panama, Canal Zone, Fort Clayton	AMNH
<i>Pieris rapae</i> (L.)	3♂, 3♀, USA, New York, Ithaca	AYK
<i>Libythea celtis</i> (Laicharting)	3♂, 2♀, Spain, Catalonia, Oliana	AMNH
	1♂, Spain, l'Ametilla	AMNH
<i>Libythea collenettei</i> Riley	1♀, French Polynesia, Marquesas Isl., Nuku Hiva	BMNH
	1♂, French Polynesia, Marquesas Isl., Nuku Hiva	BPBM
<i>Libythea geoffroy</i> Godart	1♂, 1♀, Indonesia, Nusa Barong Isl.	TFC
	1♂, 2♀, Indonesia, Bacan	CMNH
	1♂, Solomon Islands	CMNH
<i>Libythea labdacca</i> Westwood	1♀, Cameroon, Bafia	CMNH
	1♂, Cameroon, Bitye	CMNH
	1♂, Cameroon, Efulen	CMNH
	1♂, Cameroon, Lolodorf	CMNH
	1♂, Congo, Nola Sanga	CMNH
	1♂, Liberia, Bong Mts	CMNH
<i>Libythea laius</i> Trimen	1♂, 3♀, Malawi, Cholo	CMNH
	1♂, Kenya, Meru	USNM
	1♂, Kenya, Nairobi	USNM
	1♀, Madagascar	USNM
<i>Libythea lepita</i> Moore	1♀, China, Moupin	USNM
	1♂, China, Xian	TFC
	1♂, India, Kashmir	USNM
	1♂, 1♀, Japan, Shizuoka, Fujinomiya	AYK
	1♀, Japan, Yamanashi, Hinoharu	AYK
	2♂, Taiwan, Kaohsiung, Ruigui	MTC
	1♂, Taiwan, Puli, Nanshan	AYK
<i>Libythea myrrha</i> Godart	1♂, Burma, Tenasserim	CMNH
	1♂, Cambodia, Kampot, Komchai	AMNH
	1♂, India, Naga Hills	CMNH
	1♂, 1♀, India, Tamil Nadu	AMNH
	1♂, 1♀, Nepal, Kathmandu	CMNH
	1♂, 1♀, Sri Lanka, Colombo	CMNH
	1♀, Thailand, Rachaburi	CMNH
<i>Libythea narina</i> Godart	1♂, 1♀, Indonesia, Sumatra, Atjeh	CMNH
	1♂, Philippines, Luzon, Baguio	USNM
	1♀, Thailand, Pak Jong	CMNH
	1♂, 1♀, Thailand, Rachaburi	CMNH
<i>Libytheana carinenta</i> (Cramer)	1♂, Argentina, Iguazu Falls	CUIC
	1♂, Bolivia, Prov. del Sara	CMNH
	3♂, Brazil, Matto Grosso, Corumba	AMNH
	1♂, 1♀, Colombia, Magdalena	CMNH
	1♂, Costa Rica, Avangarez	AMNH

**Appendix 1**  
(Continued)

Taxon	Locality	Repository
	2♂, 1♀, Ecuador, El Oro, Lafebra	CMNH
	1♂, Honduras, San Pedro Sula	CUIC
	1♂, Mexico, San Juan Del Rio	CMNH
	1♂, Mexico, Nombre de Dios	CMNH
	1♂, Mexico, Yucatan, Chichen-Itza	CMNH
	2♂, USA, Arizona, Santa Rita Mts.	CMNH
	1♂, USA, Georgia, Clarke Co.	CMNH
	1♂, USA, Oklahoma, Payne Co., Stillwater	CMNH
	1♂, USA, Pennsylvania, Allegheny Co., Pittsburgh	CMNH
	1♂, USA, Tennessee, Shelby Co., Memphis	CMNH
	1♀, USA, Tennessee, Davidson Co., Nashville	CMNH
	1♂, USA, Texas, Webb Co.	CMNH
	1♀, USA, West Virginia	CMNH
	1♂, USA, Virginia, Nelson Co.	CMNH
<i>Libytheana fulvescens</i> (Lathy)	1♂, Dominica, 1km N. Colihaut	CMNH
	1♀, Dominica, Copt Hall	USNM
<i>Libytheana motya</i> (Hübner)	1♂, 2♀, Cuba, Guantanamo	CMNH
	1♀, Cuba, Loma del Gato	CUIC
	1♂, Cuba, Pinar del Rio	CMNH
<i>Libytheana terena</i> (Godart)	2♂, 1♀, Dominican Republic, Pedernales	CMNH

## Appendix 2

List of taxa examined and matrix of morphological characters for 15 libytheines and six outgroups. +, additive characters; ?, uncertain states; -, inapplicable states; †, extinct; ††, fossil.

	0	1	2	3	4
	123456789 +	0123456789	0123456789	0123456789 + ++ +	0123 + ++ +
<i>Chersonesia rabria</i> (Moore)	111????0	01001-??11	1122?--00	00000-0100	0000
<i>Danaus plexippus</i> (L.)	11111000	0010111211	0111001000	00000-12-0	00-0
<i>Euselasia gelon</i> (Stoll)	101100010	11000-0120	0022000000	00000-0020	0000
<i>Nymphalis polychloros</i> (L.)	111011001	0220110020	1122000001	00000-1120	-0--
<i>Pierella luna</i> (Fabricius)	011????02	022010?11	1121?-000	00000100-0	0000
<i>Pieris rapae</i> (L.)	101001022	12200-0001	0202000000	00000100-0	0000
<i>Libythea celtis</i> (Lacharting)	010010110	110110111	1200110202	010111211	1010
<i>Libythea cinyras</i> (Trimen) †	??0101?0	1?0110111	1200100201	21???????	????
<i>Libythea collenettei</i> Riley	110010110	110110111	1200100200	100011211	0010
<i>Libythea geoffroy</i> Godart	110010110	110110111	1200100201	110011221	1010
<i>Libythea labdaca</i> Westwood	110010110	110110111	1200110201	211111211	1010
<i>Libythea laius</i> Trimen	110010110	110110111	1200110201	211111211	1010
<i>Libythea lepita</i> Moore	010010110	110110111	1200110202	010111211	1010
<i>Libythea myrrha</i> Godart	110010110	110110111	1200110202	010111211	1010
<i>Libythea narina</i> Godart	110010110	110110111	1200100201	210011221	1010
<i>Libytheana carinenta</i> (Cramer)	110010110	110111111	1200111111	1102202100	0101
<i>Libytheana florissanti</i> (Scudder) ††	0???????	1??11?1?	1?00????1	?0???????	????
<i>Libytheana fulvescens</i> (Lathy)	110010110	110111111	1200111111	1102202100	0101
<i>Libytheana motya</i> (Hübner)	110010110	110111111	1200112111	2002202100	0101
<i>Libytheana terena</i> (Godart)	110010110	110111111	1200112111	2002202100	0101
<i>Libytheana vagabunda</i> (Scudder) ††	0??????1?	0??111?11	1?00?11??	?1???????	????