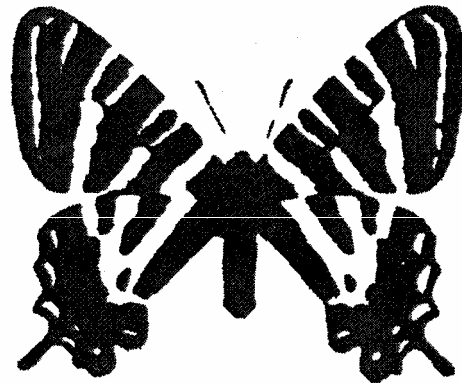


Biology of the snout butterflies (Nymphalidae, Libytheinae)
Part 1: *Libythea* Fabricius

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Biology of the snout butterflies (Nymphalidae, Libytheinae)

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Abstract This study reviews the distribution, habitat, behavior, life history, larval host plant, dispersal ability, adult diet, mimicry, camouflage, predators, parasitoids, and microbiological data (chromosome number, pterin pigment, and genetic information) for all species in the Old-World snout butterfly genus *Libythea*. The adult of each species typically lands at damp spots on the ground, and visits flowers in low elevation mountains. Novel data from my field observations are also included. The male typically is territorial, and both sexes cryptically rest on branches. Most species are found in forests and disturbed habitats, and usually have one or two annual generations. The egg is generally laid on buds of *Celtis* (Celtidaceae), and in nearly all cases, the larva feeds on leaves of this plant genus. Little is known about the developmental stages of *Libythea cinyras* Trimen, *L. collenettei* Poulton & Riley, and *L. narina* Godart.

Key words Adult diet, behavior, dispersal, habitat, host plant, *Libythea*, Libytheinae, life history, microbiology, migration, mimicry, parasitoid, predator.

Introduction

The Libytheinae are well known for their characteristically long labial palpi and the relatively few species in the subfamily. The monophyletic subfamily has an unusual global distribution, with several widespread species and five that are restricted to islands (Kawahara, 2001). Previously, Pagenstecher (1901, 1902, 1911) revised the snout butterflies into three genera and ten species. Subsequently, Michener (1943) erected *Libytheana* for all New World taxa. Taxonomic checklists by Shields (1984) and Okano (1987) treated seven species in *Libythea* and five in *Libytheana*. Due to the taxonomic instability, a formal revision of the Libytheinae was conducted (Kawahara, accepted) which yielded nine species in *Libythea* and four in *Libytheana*. Nomenclature presented in this paper follows the revision of Kawahara (accepted).

Shields (1985*a*, 1987*a*, *b*) reviewed the biology of snout butterflies, but his papers focused on zoogeography, migration, pterin pigments, and some of the information has become outdated. Publications on the butterflies of the world (*e. g.* Seitz, 1906–1924; Lewis, 1974; d’Abrera, 1977–1997) included discussions and images of Libytheinae, but in each case, not all libytheine species were included. Motono (1993) illustrated numerous habitus photographs, but did not include color images of all species, and there was very little written on biology. The goal of this study is to review libytheine biology according to the taxonomy of a modern revision, present dorsal and ventral habitus images of all species, and include information from personal field observations and all obtainable literature dated before 2003. Due to the length of this paper, the biology of *Libytheana* will be presented in a separate publication.

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Species accounts

Libythea celtis (Laicharting, 1782) (Figs 1–2)

Distribution. Southern Europe and northwestern Africa to western India and southern Russia (Fig. 19).

Habitat. Small towns, villages (Chinery, 1989), cities, shrublands (Pamperis, 1997), bushy areas with scattered deciduous trees (Tolman & Lewington, 1997), and along small roads (Gómez-Bustillo & Fernández-Rubio, 1974). The adult is also found near gardens, agricultural sites (Muñoz Sarios, 1995), *Celtis* plants (Kirby, 1896; Higgins & Riley, 1970; Lyneborg, 1974), rivers (Hesselbarth, 1995), seashores and clearings, but not from dense forests or alpine zones (Pamperis, 1997). It is usually found below 1,500 m, but is occasionally found up to 3,000 m (Fruhstorfer, 1914).

General behavior. The adult flies close to the ground and frequently lands on flowers, but also flies rapidly above trees, and is most active between 22–28°C (Puységur, 1967). It also lands on the ground to drink water (Muñoz Sarios, 1995; Tennent, 1996; Tolman & Lewington, 1997). Pamperis (1997) noted a perched adult displaying the ventral surface of the forewing when disturbed. He believed the purpose of this behavior is to scare predators, but it is odd given that *L. celtis* lacks eyespots or other characteristic wing patterns that are typically correlated with anti-predator startle behaviors. Eitschberger *et al.* (1991) claimed that the over-wintered adult returns to the same breeding area from which it is born, but this hypothesis requires testing.

Mating behavior. In an observation of *L. celtis* in France, Vidau (1984) reported two adults coming in contact during flight, falling nearly vertically in the grass, and then remaining motionless for several seconds. Afterwards, they flew to a nearby branch and closed their wings. This behavior is somewhat similar to Shinshu Konchu Gakkai's (1979) report of mating behavior in *L. lepita*.

Generations. In Europe, the adult is typically reported from June–August, and from late March–late April after over-wintering (Tolman & Lewington, 1997). *Libythea celtis* lives approximately ten months (Puységur, 1967), but reported generation times are not the same across its distribution. Algeria and Tunisia: mid-June–autumn, and after hibernation in March and April (Tennent, 1996); Greece: February–October (Pamperis, 1997); Russia: June–September (Tuzov *et al.*, 2000); Spain: June–August, reappearing in the spring (Manley & Allcard, 1970; Gómez-Bustillo & Fernández-Rubio, 1974); Turkmenistan: March–September (Tshikolovets, 1998). Most publications stated that *L. celtis* is univoltine, but some sources (*e. g.* Berge, 1910; Verity, 1950) claimed there are two annual generations. *Libythea celtis* probably has more than one annual generation in warmer parts of its distribution.

Oviposition. The female only oviposits if there are buds on the larval host plant. The egg is laid in the angle between a young shoot and its parent twig (Chapman, 1912). The female walks along a branch tip, rotating 180° and then bends her abdomen to make contact with the bud and lays an egg (Benoit, 1993). If the bud is developed into a leaf, the egg is oviposited on the petiole or on the undersides of the leaf. In captivity, 13 eggs were laid in leaf axils and 43 beneath nearly fully grown leaves (Chapman, 1912). At Montpellier, France, oviposition takes place between March 20 and April 27 (Puységur, 1967).

Ovum. 0.7 mm high and 0.5 mm wide, with a regular lattice of approximately 34 longitudinal ribs, pronounced transverse ribs, a rounded summit, and a smooth base. It is whitish or greenish-white with a pearly luster (Chapman, 1912) or shining white (Puységur, 1967).

Before hatching, it becomes grey (Benoit, 1993) or brownish-pink (Chapman, 1912). Brown coloration may indicate that the egg of *L. celtis* contains ommochromes (Shields, 1987c). Benoit (1993) suggested that egg color may change to match the color of the developing leaf. This is likely, but further observations are necessary.

Larva. The final instar is typically 28–30 mm long (Gómez de Aizpúrua, 1988), with a green head and black mandibles (Verity, 1950). The rest of the body is green, and there is a yellow dorsal median line (Gómez de Aizpúrua, 1988), two white lines, and a row of black dots along both sides of the body (Verity, 1950). The body is dark green below these lateral lines (Muñoz Sariot, 1995). Four molts were recorded in captivity, and the larva becomes dark when reared in abundance (Puységur, 1967).

All instars rest cryptically on the mid-vein of the leaf. The larva is usually very calm, but can be very active (Gómez de Aizpúrua, 1988). When disturbed, it drops from the leaf and suspends itself with silk (Villiers, 1835), which can be 2–3 m long (Tolman & Lewington, 1997). In Spain, the larva is found on *Celtis australis* in May and June (Gómez de Aizpúrua, 1988), but in France, it is readily found in April, May (Puységur, 1967), and July (Berce, 1867). The cited sources should be examined for further details.

Pupa. According to Chapman (1900) and Gómez de Aizpúrua (1988), the pupa is 13–15 mm long. It lacks hairs, bears a dorso-ventrally 6 mm tall mesothoracic hump, and a 3 mm hump on the fifth abdominal segment (Chapman, 1900). The pupa is usually green, but can be grey (Puységur, 1967; Gómez de Aizpúrua, 1988), bluish (Puységur, 1967), or spotted with black (Chapman, 1900). Reasons for color variation remain unknown, but several color forms may exist to enhance camouflage.

According to Puységur (1967), the best time to find the pupa in Montpellier, France, is May 15–June 10. The pupa is often found under a leaf of the host plant (Godart, 1822), and the pupa twitches from side to side when disturbed (Chapman, 1900). Friedrich (1986) reported that the larva can become entangled in silk when reared in high density in captivity. Based on reports by Boisduval (1832) and Ruckstuhl (1982), pupal duration is 10–15 days. Chapman (1900) reported further details on morphology, and Puységur (1967) described details on adult emergence.

Host plants. Celtidaceae: *Celtis australis*, *C. caucasica*, *C. glabrata*, *C. tournefortii*. Plants in families other than Celtidaceae include: Rosaceae: *Prunus cerasus*; Ulmaceae: *Ulmus minor*, *U. glabra*; Urticaceae: *Urtica* sp. The larva reluctantly accepts leaves of *Ulmus minor* and *U. glabra*, and the reports on Rosaceae and Urticaceae are probably erroneous. Host plant data were extracted from: Laicharting (1782); Godart (1822); Kirby (1896); Kuznetzov (1960); Degtjareva (1981); Tennent (1996); Tolman & Lewington (1997); Tuzov *et al.* (2000); John & Makris (2001).

Dispersal. *Libythea celtis* is believed to disperse within its confined residential range during late summer (Puységur, 1967; Tolman & Lewington, 1997). Luquet (1977) believed that *L. celtis* displaces with time from low to high elevation. According to Dietzel (1987), *L. celtis* rapidly spread northward across Hungary during the 1940's and 1950's. Since *L. celtis* was found in areas without many *Celtis* plants, this butterfly probably dispersed from its main population.

Aggregations of *L. celtis* are reported from Greece (Boyd & Pyle, 2000), and Italy (Verity, 1950), but without migratory movement (migration in this paper refers to a dispersal event involving swarms of butterflies). Preossecker (*vide* Verity, 1950) reported the only known migration of *L. celtis*. He described an event in which several hundred adults flew from



Figs 1–18. Habitus images of *Libythea* spp. Scale bar=1 cm. Dorsal and ventral sides are shown for each specimen (dorsal wing surface at left, ventral wing surface at right), except for *L. cinyras*, which is the holotype. 1. *L. celtis*, ♂, Russia: Kirgizia, Kirgizaskii Ridge, Ala-Archa, Ak-Sai, 74°30'E 42°33'N, 17-21-vii-1979, J. A. Vaněk leg. (TFC). 2. *Ditto*, ♀, France: St. Maxime, 10-vi-1921, A. F. Pinhey leg. (BMNH). 3–4. *L. cinyras*, holotype ♂, Mauritius: Moka Dist., 25-vii-1865, C. Barkley leg. (BMNH). 5. *L. collenettei*, ♂, Marquesas: Ua Pou, Poohekaei summit, SW of Hohoi, 20-viii-2001, R. Englund leg. (BPBM). 6. *Ditto*, ♀, Marquesas: Nuku Hiva, Toovi Plat., near base of Takau Ridge, 2,500 ft, 24-viii-2001, R. Englund & S. Jordan leg. (BPBM). 7. *L. geoffroyi geoffroyi*, ♂,

Vipacco towards Prawald in Italy.

Adult diet. Water from puddles, nectar, and plant secretions. In the French Cevennes Mountains, 15–20 over-wintered adults fed on secretions from an apple tree (Feltwell, 1983).

Nectar sources include: Asteraceae: *Cirsium* sp.; Cistaceae: *Cistus creticus*; Cucurbitaceae: *Cucumis sativus*; Ericaceae: *Erica cinerea*; Lamiaceae: *Mentha* sp.; Ranunculaceae: *Clematis vitalba*; Rosaceae: *Prunus cerasus*, *Rubus fruticosus*, *R. sanctus*; Rutaceae: *Citrus* sp. Nectar source data were extracted from: Puységur (1967), Manley & Allcard (1970), Gómez-Bustillo & Fernández-Rubio (1974), Shields (1985b), John & Makris (2001).

Predators and parasitoids. Thompson (1946) reported *Compusilura concinnata* (Diptera: Tachinidae), and Puységur (1967) observed *Bactromyia aurulenta* (Diptera: Tachinidae) emerging from over 40% of reared pupae. Godart (1822) reported *Apechthis compunctor* (Hymenoptera: Ichneumonidae), and Puységur (1967) noted a possible braconid parasitoid. A fungus, *Isaria* sp. (Hypocreales: Clavicipitaceae) can devastate larval populations (Puységur, 1967).

Chromosome number. $N=31$: Yugoslavia (Lorković, 1941).

Pterin pigments and aberrations. Absent in specimens from Spain (Shields, 1987b). A gyandromorph was collected in Ardèche, France, on March 10, 1997 (Lentenois, 1998).

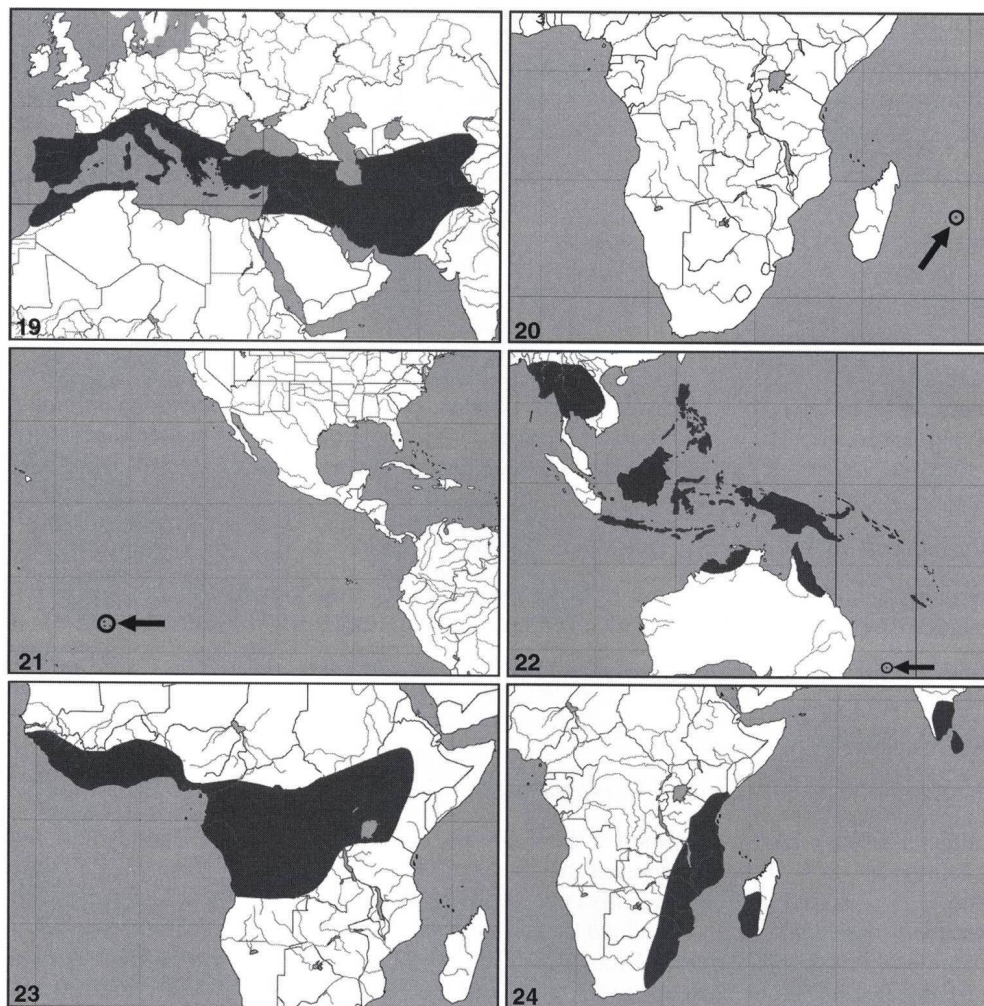
Gene sequences. *COI*, *EF1- α* , *Wingless* (Wahlberg *et al.*, 2003).

***Libythea cinyras* Trimen, 1866 (Figs 3–4)**

Distribution. There is one record from the Moka district on Mauritius (Fig. 20).

Status. The only known specimen is the holotype, collected by Colville Barclay and given to Trimen in 1865. Barclay reported the species to be “very scarce in Mauritius” (Trimen, 1866: 337). Based on Barclay’s observational notes, Manders (1907) believed that other specimens were present on the island when the holotype was collected. In the original description of *L. cinyras*, Trimen (1866) stated that E. L. Layard collected a similar specimen in Madagascar, which was deposited in the South African Museum. However, the specimen from Madagascar is most likely *Libythea labdaca*, because there are currently no specimens resembling *L. cinyras* in the South African Museum (Dawn Larsen, *pers. com.*). Trimen (1866) also stated that a similar specimen was collected in River Shiré, Mozambique, but later determined that the specimen was not *L. cinyras*, but *L. laius* instead (Trimen, 1879). The ancestor of *Libythea cinyras* probably flew to Mauritius and evolved on the island. Further studies are necessary to verify whether this species is extinct.

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- Indonesia: Timor Isl., Suai, Portug. 8–14-i-1913, E. Wahr leg. (BMNH). 8. *Ditto*, ♀, Indonesia: Timor Isl., Suai, Portug. i-1913, E. Wahr leg. (BMNH). 9. *L. labdaca labdaca*, ♂, Uganda: Mulange, 21–22-iii-1905 (CMNH). 10. *Ditto*, ♀, Cameroon: Batia, 2-iii-1929, A. I. Good leg. (CMNH). 11. *L. laius laius*, ♂, Malawi: Cholo, 10-x-1927 (CMNH). 12. *Ditto*, ♀, Cholo, 10-x-1927 (CMNH). 13. *L. lepita lepita*, ♂, Southeast Tibet: 7-iv-1913, F. M. Bailey leg. (AMNH). 14. *Ditto*, ♀, INDIA: Mishmi Hills, 4-v-1913, F. M. Bailey leg. (AMNH). 15. *L. myrrha myrrha*, ♂, Indonesia: Java (BMNH). 16. *Ditto*, ♀, Indonesia: West Java (BMNH). 17. *L. narina*, ♂, Indonesia: Lombok Isl., Sapat. iii-vi-1896 (BMNH). 18. *Ditto*, ♀, Philippines: Palawan Isl. (BMNH).



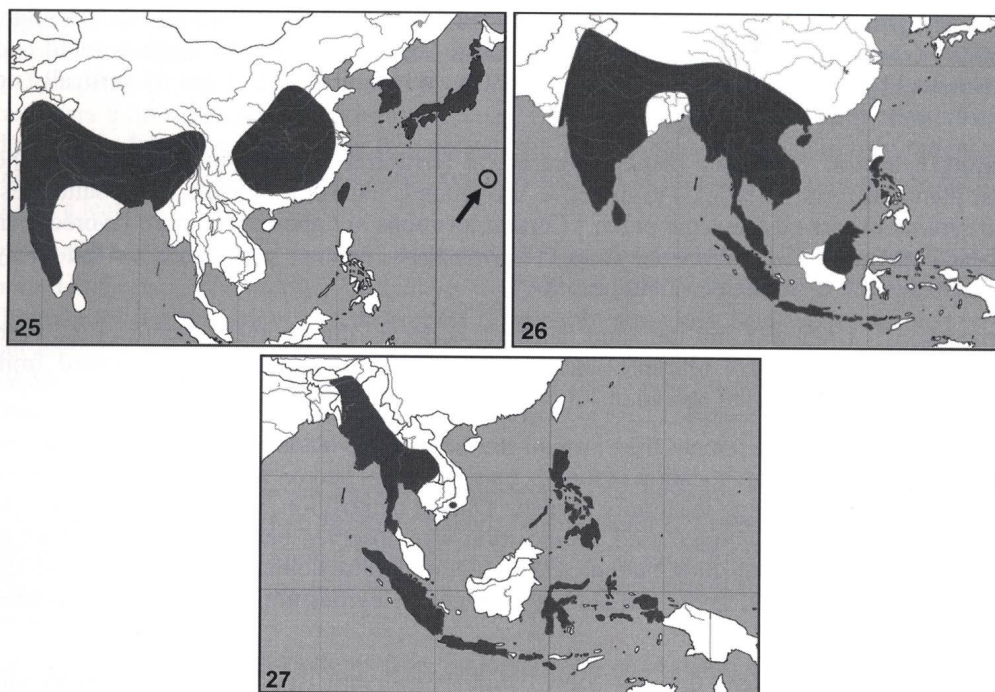
Figs 19–24. Distribution maps of *Libythea* spp. Distributions were determined from locality records provided by Shields (1985a) and museum specimens examined by Kawahara (2001). 19. *L. celtis*. 20. *L. cinyras*. 21. *L. collenettei*. 22. *L. geoffroyi*. 23. *L. labdaca*. 24. *L. laius*.

***Libythea collenettei* Poulton & Riley, 1928 (Figs 5–6)**

Distribution. Marquesas Islands: recorded from Nuku Hiva and Ua Pou (Fig. 21). In 2001, the adult was relatively common on Ua Pou, but only one specimen was seen on Nuku Hiva. It was absent on Fatu Hiva, Hiva Oa, and Mohotani (Ronald Englund, *pers. com.*).

Habitat. Reported from around a stream near sea level. Numerous adults were also observed near sea level at Hooumi Valley and on a 366 m ridge above Typee Valley (Poulton & Riley, 1928).

General behavior. The adult flies over streams near sea level (Poulton & Riley, 1928), and possibly lands at damp spots on the ground (Kawahara, 2003a).



Figs 25–27. Distribution maps of *Libythea* spp. 25. *L. lepita*. 26. *L. myrrha*. 27. *L. narina*.

Generations. Unknown, but there may be multiple annual generations (Kawahara, 2003a).

Host plant. *Celtis pacifica* (Celtidaceae) is believed to be the host plant (Shields, 1987d), but this was not observed or tested experimentally.

Dispersal. Unlikely, given its endemic distribution.

Adult diet. Unknown, but *L. collenettei* possibly feeds on a variety of flowers like other *Libytheinae*. For further details on *L. collenettei*, see Shields (1987d) and Kawahara (2003a).

***Libythea geoffroyi* Godart, 1822 (Figs 7–8)**

Distribution. Burma, Cambodia, China, Indonesia, Laos, Lord Howe Island, New Caledonia, New Guinea, northern Australia, Philippines, Solomon Islands and Thailand (Fig. 22).

Habitat. Residential areas and habitats along forests (Igarashi & Fukuda, 2000), especially monsoon forests (Johnson & Valentine, 1989). The adult is also found in vine thickets where the host plant occurs (Dunn & Dunn, 1991), along rivers (Fruhstorfer, 1914), and gravel roads (Tennent, 2002). Typically found up to 1,500 m, but the highest reported elevation is 1,828 m (Shields, 1985a).

General behavior. The adult basks on rocks in large groups (Parsons, 1991), and both sexes imbibe water from damp ground (Igarashi & Fukuda, 2000). Common & Waterhouse (1981) reported that the adult rests in shade, dense foliage, or under verandas of houses during the hottest times of day. However, on Cape York Peninsula of Australia, the adult is ac-

tive throughout the day, and is not encountered in shaded areas (Johnson & Valentine, 1989). *Libythea geoffroyi* generally flies close to the ground, and its flight is rapid and punctuated by periods of gliding (Parsons, 1991). When disturbed, it can fly vertically up into the canopy (Tennent, 2002).

Mating behavior. The male displays aggressive territorial behavior in clearings near the host plant. It rests on twigs 4–6 m above the ground, vigorously chases other butterflies, and returns to rest on the same perch. Certain locations are apparently more favored than others—when a male is removed from the population, another male lands on the newly evacuated perch (Johnson & Valentine, 1989).

Generations. Unknown, but the adult has been collected during every month of the year, suggesting that there are multiple annual generations. It is frequently observed from November to February, but less so in July and September (Shields, 1985*a*).

Oviposition. A gravid female flies around the host plant, lands, and taps leaves with its forelegs. Once a suitable location is found, a single egg is laid on a bud or the inner side of a fresh leaf so that the egg is slightly hidden. During oviposition, the female bends her abdomen and keeps her wings closed. Oviposition was observed between 1200–1300 hrs in both sun and shade (Igarashi & Fukuda, 2000). During these hours, the female rarely strays far from the host plant, and continuously engages in oviposition (Johnson & Valentine, 1989).

Ovum. 0.65 mm high and 0.4 mm wide, bullet shaped, and 10–11 projecting flanges surround the flat micropyle. The flanges become bifurcated or trifurcated into longitudinal ribs down the sides of the egg (Johnson & Valentine, 1989). Immediately after oviposition, the egg is pale cream colored, but eventually turns brown (Igarashi & Fukuda, 2000). The egg hatches in 2–3 days (Johnson & Valentine, 1989).

Larva. The first instar is 1 mm long, has a dark brown head capsule, a pale-green body covered in fine pubescence, and black legs and prolegs (Johnson & Valentine, 1989). The newly hatched larva eats approximately half of its transparent eggshell, begins feeding on young leaves, starting with the edge (Igarashi & Fukuda, 2000). The second instar is similar to the first, but the head capsule is pale green, with a black clypeus and dark stemmata. The third instar has a pale yellow-green head and body, but a white ventral surface. The body is covered in fine hairs, and a broad brown line is present along the dorsum, and a prominent yellow line on either side of the body. The young larva rests in a characteristic sigmoid shape, with its prolegs holding onto the substrate while the body is arched backwards with the head and thorax deflexed to touch the first pair of legs (Johnson & Valentine, 1989).

Fourth and fifth instars have a head capsule that is black on the ventral two-thirds and yellow on the dorsal third. The final instar is 27 mm long, and typically green, but the color can vary (Igarashi & Fukuda, 2000). Thoracic and terminal abdominal segments are yellowish, with a transverse row of silver spots, and the remainder of the body is greenish black and covered in fine hairs. The ventral surface is white and laterally bears a series of prominent white patches near the prolegs (Johnson & Valentine, 1989).

The behavior of the final instar is similar to that of *L. celtis* in that it lifts the anterior portion of its body from the leaf surface, and when threatened, the larva secretes a silken thread and drops from the leaf. The suspended larva thrashes violently for several seconds before becoming motionless. When disturbance ceases, it ascends the thread using its forelegs and mouthparts. Larval duration is 11–13 days (Johnson & Valentine, 1989).

Pupa. The following description is abstracted from Johnson & Valentine (1989) and Igarashi & Fukuda (2000). The pupa is 12–15 mm long, 6 mm wide, pale green or brown, and suspended by the cremaster at an acute angle beneath a leaf of the host plant. The thorax bears a dorsal, ridge-like protrusion along which lies a prominent yellow line. Pupal duration is 4–8 days, and during this period, the pupa moves about rigorously when disturbed. Although the pupation site remains unknown, it is probably spun in places such as under a leaf.

Host plants. Celtidaceae: *Celtis paniculata* and *C. philippensis*. Sapindaceae: *Pometia pinnata*. Ulmaceae: *Aphananthe philippinensis*. d'Abbrera (1977) claimed that *Cryptocarya* sp. (Lauraceae) is a host plant, but this report is probably erroneous because larvae died without eating leaves when provided with leaves from *C. triplinervis* (Johnson & Valentine, 1989). The report of Sapindaceae as a larval host plant is also questionable. Host plant references: d'Abbrera (1977), Common & Waterhouse (1981), Johnson & Valentine (1989), Fox (1995), Igarashi & Fukuda (2000).

Dispersal. There is no known report of a migration in the literature for this species, but several adults were collected on Iriomote Island, Japan (Asahi & Shinkai, 1979) which is over 800 km from the closest known established population in the Philippines. Straatman (*pers. com.*, *vide* Shields, 1987a) and Parsons (1999) reported aggregations of adults in New Guinea.

Adult diet. The adult drinks fluids from puddles, surfaces of damp stones, and sites of fires. They also visit flowers of *Eupatorium* sp. (Asteraceae), and *Poinciana* sp. (Fabaceae), and *Lantana* sp. (Verbenaceae). Nectar source data were extracted from: Fukuda *et al.* (1983), Parsons (1991), Fox (1993, 1995), Igarashi & Fukuda (2000), Tennent (2002).

Parasitoids. Unidentified tachinid flies (Johnson & Valentine, 1989).

Mimicry and camouflage. Nicéville (1890) believed the male mimics *Euploea* sp. (Nymphalidae: Danainae). The combined distribution of *E. tulliolus* and *E. leucostictos* is similar to the range of *L. geoffroyi* (Shields, 1985a). Since *Euploea* contains toxins that protect them from predators (Ackery & Vane-Wright, 1984), and because *L. geoffroyi* and the two *Euploea* species have partly overlapping distributions, *L. geoffroyi* may be mimicking *Euploea*. Experiments are necessary to test this hypothesis.

Pterin pigments. Xanthopterin and a faint trace of erythropterin (Shields, 1987b).

***Libythea labdaca* Westwood, 1851 (Figs 9–10)**

Distribution. Western and Central Africa south of the Sahara Desert (Fig. 23).

Habitat. The adult is typically found along forest margins from 800–1,800 m altitude (Kielland, 1990), especially in tropical evergreen forests and savanna woodlands with over 150 cm of annual rainfall. The highest recorded elevation is 2,438 m (Shields, 1985a). The butterfly is abundant in some years but very rare during others (Holland, 1920).

General behavior. The adult flies in shaded parts of forests and lands on the trunk or branches with its wings closed and head facing down (Williams, 1994). It is also attracted to damp spots on the ground and flies rapidly in a jerky fashion (Larsen, 1991).

Mating behavior. Little has been reported on mating behavior other than that the male is territorial (Williams, 1994).

Generations. Unknown, but labels from dried museum specimens indicate an abundance of

adults from November to May, suggesting that there may be more than one annual generation.

Ovum. Undescribed, but possibly similar to the ovum of *L. laius*, because a phylogenetic study of Libytheinae (Kawahara, 2001) grouped *L. labdacca* and *L. laius* as sister species.

Host plants. Celtidaceae: *Celtis africana*, *C. intergrifolia*, *C. soyauxii*, possibly *C. adolphi-friderici*, *C. prantlii*, and *C. zenkeri*. Rosaceae: *Prunus cerasus*. Given the specificity of *Libythea* to *Celtis* plants, the report on *Prunus* is probably erroneous. Nectar source data were extracted from: Shields (1987a), Williams (1994), Santin (1998).

Dispersal. Williams (1958) compiled dates and directions of migratory movement of *L. labdacca* in six African countries, and showed that there are two main migration events, one in the spring (typically directed southward), and another in the fall (directed both northward and southward). Migrations are usually observed from 1000–1800 hrs and migrating adults travel at a speed of 10–12 km per hour, and the adult typically flies between the ground and 4.5 m (Shields, 1987a), but occasionally above trees at a height of 30 m (Williams, 1939).

Leston & Wink (1975) estimated that one billion butterflies migrated in Ghana during March and April 1972. Shields (1987a) reported a 2:1 male to female ratio during migrations. Migrations are reported for the following years: 1914, 1915, 1919, 1925–30, 1932, 1935, 1938, 1946, 1948–50, 1953, 1964, 1966, 1969, 1971–72, 1977, 1980, 1988. Rainey (*vide* Johnson, 1969) suggested that migrations are confined to the Intertropical Convergence Zone (ITCZ), but the significance of this correlation remains unknown. See Shields (1987a) for further details on individual migration events.

Adult diet. Water from puddles and perspiration from vertebrates (Williams, 1971). Larsen (1991) claimed that the adult does not visit flowers, but this seems unlikely given the large number of reported flower visitation records for other Libytheinae (*e. g.* *Libythea celtis*, *Libytheana carinenta*).

Chromosome number. $N=31$: Entebbe, Uganda (De Lesse, 1968; 1970).

Pterin pigments. Absent (Shields, 1987b).

***Libythea laius* Trimen, 1879 (Figs 11–12)**

Distribution. Eastern Africa, Madagascar, southern India, and Sri Lanka (Fig. 24).

Habitat. Savannas, tropical semi-deciduous forests, subtropical forests and woodlands (Shields, 1985a) usually up to 2,000 m (Kielland, 1990). In southern Africa, *L. laius* prefers moist forests (Migdoll, 1988).

General behavior. *Libythea laius* frequently lands on moist ground, twigs (Kielland, 1990; Larsen, 1991), perspiring humans (Williams, 1971), and on the bark of its host plant (Migdoll, 1988). The adult flies rapidly, approximately 50 cm from the ground along gravel roads, frequently landing on the ground or on the stem of a shrub, but immediately flies away when it senses movement (Kawahara, *pers. obs.*, Tulear, Madagascar).

Mating behavior. The male actively flies at tree tops and perches with its wings open on branch tips and awaits a female (Trimen, 1887). This behavior is similar to the male mate-locating behavior described by Rutowski *et al.* (1997) for *Libytheana carinenta*.

Generations. The adult is active from February to October in India (Fruhstorfer, 1914), and is documented from every month in Kenya (Sevastopulo, 1974) and southern Africa

(Williams, 1994). These data suggest that *L. laius* may have multiple annual generations in some parts of its distribution.

Oviposition. The only known published information on oviposition is that the egg is laid singly on the leaf of the host plant (Williams, 1994).

Ovum. 0.8 mm high and 0.45 mm wide, with a truncate summit and 21–45 longitudinal ribs (Clark & Dickson, 1964). The egg is whitish immediately after oviposition, but becomes pale-salmon after a few days, and may therefore contain ommochromes (Shields, 1987c).

Larva. Williams (1994) noted that the larva is cylindrical with fine hairs. Clark & Dickson (1964) stated that the final instar is pale pea-green, with a brown sub-spiracular band and a green dorsal line on segments 2–11. Spiracles are black with a yellow rim, and stemmata are brown.

Pupa. Pale green, 13 mm long, yellow stripes define the dorsal ridge. The pupa bears a thoracic and abdominal hump, the former being less prominent than the latter (Clark & Dickson, 1964).

Host plants. Celtidaceae: *Celtis africana*, *C. australis*, *C. mildbraedii*, *C. soyauxii*. Host plant data were extracted from: Clark & Dickson (1964), Shields (1987a), Williams (1994), Santin (1998).

Dispersal. Migrations occur around or soon after the rainy season (Larsen, 1991). *Libythea laius* is abundant in some years, but nearly absent in others (Sevastopulo, 1974). The male to female ratio during migrations is 3:1 (Shields, 1987a), and an east-to-north direction of migration was observed (Gifford, 1965). Vossler (*vide* Aurivillius, 1919) reported a migration in Amani, Tanzania, on May 14, 1904, when there was a gentle north-westerly wind. A large swarm traveled from south to north between 9 am and noon. *Libythea laius* did not land on flowers, but some rested on the masonry of houses or on the ground.

Adult diet. Water from puddles and perspiration from vertebrates (Williams, 1971). Trimen (1887) stated that *L. laius* visits flowers, but he did not report specific plant names.

Mimicry. Swanepoel (1953) claimed that the adult resembles *Sallya natalensis* (Nymphalidae: Eurytelinae) when at rest, but this needs to be tested experimentally.

Pterin pigments. Absent (Shields, 1987b).

***Libythea lepita* Moore, 1857 (Figs 13–14)**

Distribution. India and Pakistan, east to China, Korea and Japan (Fig. 25). *Libythea lepita* was previously considered the same species as *L. celtis*, but the taxonomic status has been debated (Yoshimoto, 1999). Due to consistent differences in wing patterns between eastern and western populations, the two have formally been separated, and both names are valid (Kawahara, accepted). For further discussion on taxonomic history and how to distinguish the two species, see Kawahara (accepted).

Habitat. The adult is frequently encountered in residential areas (*e. g.* parks, temples, and cemeteries), around lowland forests (especially those in which their host plant occurs), but also in mountainous regions, particularly near rocky outcrops, roads, and streams. It is fairly common in Japan during the early spring and early summer (Kawazoé & Wakabayashi, 1976; Shinshu Konchu Gakkai, 1979; Fukuda *et al.*, 1983). In India, it is very common between May and October from 1,219 m to 2,133 m (Hannington, 1910), but rare in Sri

Lanka (Ormiston, 1924).

General behavior. In Japan, the newly emerged adult typically aggregates with other adults in midsummer around damp places on the ground. When disturbed, it immediately takes flight, and lands on a nearby branch and remains motionless with its wings closed (Peile, 1937). This behavior is similar to other Libytheinae such as *Libytheana carinenta* (Kawahara, 2003b). After a week or two, some adult *Libythea lepita* aestivate for the rest of the summer and become active again in the fall before hibernating for the winter. In the spring, adults copulate and the female oviposits on buds of the host plant before dying (Fukuda *et al.*, 1983).

The following are my observations on adult behavior, taken on March 23, 2003, between 1000 and 1300 hrs, 17°C, at Inako, Yamanashi prefecture, Japan, at 200 m. Nine adults (some fresh, but many with damaged wings) were observed on separate occasions flying along a gravel road beside a stream. Most flew close to the ground (<1 m), but occasionally flew as high as 5 m. *Libythea lepita* actively flew when the sun shone, and usually perched on the ground in the sun within ten seconds after taking flight. If clouds covered the sun, each adult landed with its wings closed on the ground or on branches.

Mating behavior. Kitahara (1989) observed mating behavior on Mt Bodai, Yamanashi Prefecture, Japan, on March 27, 1986, around noon. The male displayed territorial behavior: it chased other butterflies and flying insects and frequently rested on the ground. A male was observed resting on the ground with wings open at a 130–140° angle and antennae pointed forward. A female landed nearby, at which point he flew and immediately landed behind her, and walked towards her. As he approached, he walked from side to side and vibrated his wings. Kitahara believed that the male was responding to her pheromones. When beside her, she pushed her abdomen down with his head repeatedly for 30–40 seconds while she kept her wings closed. This behavior suggests that the male uses its labial palpi during courtship, but additional observations are necessary because there are no other reports of libytheine courtship involving labial palpi.

After this unusual behavior was observed, the male flew to a point 20 cm from her, landed, and fully opened his wings. She then fully opened her wings, and he flew approximately 10 cm off the ground and circled her in a radius of 20 cm. Courtship continued with the female flying and landing approximately 6 m away and closing her wings. He immediately followed and landed behind her, and as before, vibrated his wings. She then landed in another spot close by, and once again, he flew, landed, and vibrated his wings as he walked towards the female from behind. In total, this scenario (the female flying and landing, the male flying and landing behind her and walking towards her while vibrating his wings, the female remaining still with her wings closed) was observed at four locations on the ground.

Shinshu Konchu Gakkai (1979) reported an observation of copulation in late March in Nagano, Japan. Females that had just come out of hibernation mated with males that were flying around the host plant. A male and a female circled each other in flight, close enough that their wings collided and made snapping sounds. She eventually landed on the host plant, and he landed near her and walked towards her. She circled the branch several times and gently opened and closed her wings, at which point, he bent his abdomen and copulated. During copulation, the pair remained fairly still with their wings closed, but separated and hid in deep vegetation after an hour. Labial palpi were not reported to have been used during courtship.

Generations. In Japan, there is typically one annual generation, but two are reported from the following localities: Amamioshima (Kubo, 1958), Fukushima (Tsunoda, 1984), Gunma

(Suzuki, *unpubl.*, *fide* Fukuda *et al.*, 1983), Kumamoto (Fukuda *et al.*, 1983), Nagano (Aonuma, 1971), Osaka (Fukuda *et al.*, 1983), Tochigi (Nishiyama, 1983), and Yamanashi (Suzuki, *unpubl.*, *fide* Fukuda *et al.*, 1983). There may be three generations in Nagano, because a larva found in mid-late October became an adult in November (Shinshu Konchu Gakkai, 1979), but direct field observations are necessary because this larva was reared indoors. There may also be several generations in the Ryuku Islands (Fujioka, 1975).

In a comprehensive study of the life histories of Japanese butterflies, Fukuda *et al.* (1983) explained how two generations may occur annually. An over-wintered adult appears in February (southern Japan) or March (mainland Japan), at which point, copulation and oviposition take place. Its offspring emerge as adults from the end of May to early June, and most aestivate after a week or two of activity, but some remain active and copulate. The active female oviposits in June and July, and its young become adults between July and August. This second generation is briefly active in the fall before hibernating for the winter with others from the first generation. Under this scenario, the over-wintered adults are a mixture of first and second-generations.

- Fukuda *et al.* (1983) also noted that bud presence on the host plant can greatly influence generation number. For example, in the southern islands of Japan, a storm may damage the host plant, causing buds to emerge during the fall. Under such circumstance, the aestivated butterfly resumes activity and begins ovipositing. This may be why in Okinawa, the larva and adult can be found throughout the year (Higa, 1981, 1982).

Oviposition. Oviposition occurs in the following manner: a gravid female lands on the host plant, opens her wings at a 90–120° angle, walks towards the branch tips, bends her abdomen, and oviposits. She usually lays only one egg per bud, but in some cases will lay several. The over-wintered female lays eggs beginning in mid-late April in Japan. Oviposition lasts 2–3 seconds, and usually occurs around noon on trees less than 2 m high (Shinshu Konchu Gakkai, 1979), but sometimes takes place on trees 7–8 m tall (Fukuda *et al.*, 1983).

Ovum. The egg is barrel-shaped, 0.8 mm high, 0.4 mm wide, with 20–30 longitudinal ribs. At first, it is milky-white or light yellow, but becomes dark brown before hatching in 4–9 days (Takeuchi, 1929; Shirôzu & Hara, 1960; Shinshu Konchu Gakkai, 1979; Igarashi & Fukuda, 2000).

Larva. Numerous authors (*e. g.* Nagano, 1933; Shirôzu & Hara, 1960; Igarashi & Fukuda, 2000) described the morphology of the final instar. The head capsule is 2.6 mm wide, green, concave at the vertex, and is covered with short hairs which are black on the upper half of the head and white on the lower half. Stemmata, mouthparts, and antennae are black. The body is uniform in width, and every segment has three annulations, each of which bears numerous hairs. There are small black spots on the dorsum, and small yellow spots laterally. The final instar is typically 25 mm long, light green, with a narrow yellow dorso-medial line, but can also be purplish or dark brown-green with a dark dorsal stripe and purple lateral stripe.

Akayama (1980, 1981) examined color variation in larva reared at different population densities but fed *ad libitum*. He discovered that a caterpillar reared in isolation turned pale green, but one reared with many other larvae became dark. A larva reared in high density develops more rapidly, is more active, spends less time resting, and becomes a smaller adult than those in isolation. On Honshu, Japan, larval duration is 30–35 days for the first generation, and 7–12 days for the second (Shinshu Konchu Gakkai, 1979).

Aonuma (1971) documented larval feeding behavior in detail. The first and second instar feed towards the tip or at the center of leaves, and produces circular bite marks. The third and fourth instar usually feeds only on the apical third of the leaf, although larval population density can affect this behavior. The final instar perches in the center of the upper surface of the leaf with its head pointed towards the petiole.

When threatened, the larva usually lifts its thoracic legs off the surface, arches its thorax and tucks its head under (Igarashi & Fukuda, 2000). It can also spin a thread and hang from the plant, but if the thread is broken, it can find its way back to the base of the host plant and walk up the trunk (Shinshu Konchu Gakkai, 1979). Refer to the original references for further details on larval morphology and behavior.

Pupa. The pupa is green, grey, or spotted black and white. The black and white form was not reported from the second generation, and a pupa found in a dark place is darker than one in a location with more light (Nagano, 1933). Pupation occurs under the leaves or on the stem of the host plant, but can also take place on other artificial substrates (Fukuda *et al.*, 1983). Pupation lasts approximately twelve days for the first generation, and seven for the second (Shinshu Konchu Gakkai, 1979). Nagano (1933) and Shirôzu & Hara (1960) reported further details on pupal morphology.

Host plants. Celtidaceae: *Celtis boninensis*, *C. tetrandra* (= *C. formosana*), *C. jessoensis*, *C. sinensis*, *Trema orientalis*. Fukuda *et al.* (1983) believed that *Ulmus laciniata* may be utilized above 1,600 m, but this was not formally tested. Females displayed oviposition behavior on *Broussonetia kazinoki* (Moraceae) in Japan, but rarely laid eggs (Fukuda *et al.*, 1983). Host plant data were extracted from: Kono & Sawamoto (1939), Shirôzu & Hara (1960), Fujioka (1975), Kawazoé & Wakabayashi (1976), Shinshu Konchu Gakkai (1979), Fukuda *et al.* (1983).

Dispersal. *Libythea lepita* is not known to migrate. Akayama (1981: 341) stated, “[*L. lepita*]. . . seems to live in comparatively stable conditions, its population density seems not to fluctuate widely and food shortage is unlikely to occur, since its host *Celtis sinensis* supplies the larvae with enough food regularly every year. It is not, therefore, surprising that there is no record of migration accompanied with [a] sudden outbreak... while there are many records in other species.” However, this species has been found in large numbers on occasion, in areas with its host plant and in areas without (Kawahara, *pers. obs.*). Like *L. celtis*, this species probably disperses to higher elevations as the summer progresses.

Adult diet. Fluids from aphids, animal carcasses, stems and fruits. The adult is also attracted to sap from *Quercus* trees (Fagaceae) and nectar from the following plants: Aquifoliaceae: *Ilex pedunculosa*; Asteraceae: *Erigeron annulus*, *Eupatorium chinense*; Brassicaceae: *Brassica rapa*, *Cardamine flexuosa*, *Raphanus sativus*; Clethraceae: *Clethra barbinervis*; Ericaceae: *Pieris japonica*; Fabaceae: *Astragalus sinicus*; Lauraceae: *Lindera obtusiloba*; Liliaceae: *Allium fistulosum*; Malvaceae: *Hibiscus syriacus*; Oleaceae: *Ligustrum obtusifolium*; Polygonaceae: *Fagopyrum esculentum*; Rosaceae: *Prunus mume*, *P. salicina*, *P. tomentosa*; Salicaceae: *Salix gracilistyla*; Scrophulariaceae: *Veronica didyma*, *V. persica*; Stachyuraceae: *Stachyurus praecox*. Nectar source data were extracted from: Kawazoé & Wakabayashi (1976), Shinshu Konchu Gakkai (1979), Fukuda *et al.* (1983).

Predators and parasitoids. Sparrows regularly feed on the larva, and vespid wasps attack large caterpillars and make them into “meatballs” (Fukuda *et al.*, 1983). In Japan, *Paradrino longicornis* (Tachinidae) emerged from a pupating larva (Shima, 1984).

Chromosome number. $N=31$: Japan (Maeki, 1953*a, b*; Maeki & Makino, 1953), Taiwan (Maeki & Ae, 1969).

Pterin Pigments and aberrations. Euthyropterin and isoxanthopterin were prominent from Taiwanese specimens (Shields, 1987*b*). Hirose (1934) studied variation in wing patterns and Kasahara (1936), Fujioka (1975), and Motono (1993) presented wing pattern aberrations.

Gene Sequence. *ND5* (Yagi *et al.*, 1999).

Libythea myrrha Godart, 1819 (Figs 15–16)

Distribution. India to Malaysia, Brunei, Indonesia, and Philippines (Fig. 26).

Habitat. The adult is found in tropical evergreen rainforests and semi-deciduous forests (Shields, 1985*a*), especially along roads and banks around forest streams. Common below 2,000 m, but can be found up to 3,000 m in northern India. Habitat data were extracted from: Moore (1880, 1901), Elwes (1888), Manders (1890), Fruhstorfer (1914), Peile (1937), Woodhouse & Henry (1942), Shields (1985*a*), Haribal (1992), Satyamurti (1994).

General behavior. The adult lands on twigs with its wings closed (Leech, 1893; Marshall & Nicéville, 1886; Moore, 1901; Satyamurti, 1994), and it flies rather high around the host plant (Seitz, 1910). In India, the adult commonly lands at puddles in May, June, August and October (Peile, 1937), and if it takes flight, it usually flies a few yards before returning (Woodhouse & Henry, 1942).

Generations. According to Seitz (1910), there are two generations in the northern portion of its distribution, and the adult is found all year round in the south. Most museum specimens were collected between March–July and from September–October throughout its distribution (Kawahara, 2001). The few specimens collected in August suggests that there may be at least two annual generations, but further studies on life history are necessary.

Oviposition. The egg is deposited on a bud or young leaf of the host plant. The female favors host plants that are in a forest near a river, stream, or a damp place open to sunlight (Nicéville, 1900; Bell, 1910).

Larva. The first several instars remain undescribed. The following information on the final instar was compiled from Bell (1901, 1910). The caterpillar is 26 mm long, 4.5 mm wide from segments 4–10, and is typically dark green, but sometimes brownish. There is a light yellow line on segments 4–12 that is approximately two-thirds the width of each segment along the dorsum. There is also a thin lateral yellow supra-spiracular band on either side of the body.

The head capsule is somewhat rounded, with a shallow depression at the vertex, which is green with brown markings. The head is smooth, but is covered with minute, dark bristles, and there are pale hairs around the mandibles. Head capsule width is 2.25 mm, which is about the same width of the anterior margin of the prothorax. The antenna is reddish, the labrum is green, and the stemmata are black. Three thin, depressed transverse lines divide each thoracic and abdominal segment into four sub-regions. Minute, bristle-like black hairs cover the dorsal surface of these sub-regions, and these hairs are also sometimes found on the ventral surface. The body narrows at the final abdominal segment, where the dorsal margin slopes at an approximate 45° angle. Spiracles are oval and light yellow with a black margin.

The larva lives on undersides of leaves and eats everything but ribs and veins. When disturbed, it draws its true legs off the surface of the substrate and curls its head down to one side. It can also drop from the plant, and use silk to suspend itself.

Pupa. According to Bell (1901, 1910), the pupa is smooth and slightly shiny, and is light green with yellow ridges and a black marking on the dorsum. It is 12.5 mm long, the width of the head is approximately 3 mm, and that of the thorax is 5 mm. The pronotum is trapezoid, and the lateral edges are straight. Together, the dorsal margins of the pro- and mesothoracic segments form a ridged thoracic hump. The dorsal edge of the abdomen forms an abdominal hump at the margin of the fifth and sixth segments. The dorso-ventral depth of the thoracic and abdominal hump is 5 mm and 6 mm respectively. The abdomen is bent at an acute angle posterior to the eighth and ninth segments. Thoracic spiracles are depressed narrow slits, but other spiracles are oval, pale, and directed anteriorly.

Host plant. Celtidaceae: *Celtis tetrandra* (Bell, 1901; 1910).

Migration and dispersal. There is one report of a migration in Sri Lanka (Shields, 1987a).

Adult diet. Water from puddles (Woodhouse & Henry, 1942) and nectar from *Anaphalis* sp. (Asteraceae) (Haribal, 1992).

Mimicry. The adult mimics *Pantoporia hordonia* (Nymphalidae: Nymphalinae) in Sri Lanka (Longstaff, 1912).

Pterin pigments. Erythropterin and xanthopterin (Shields, 1987b).

Libythea narina Godart, 1819 (Figs 17–18)

Distribution. Burma, Thailand, Vietnam, Philippines, and Indonesia (Fig. 27). Possibly from Borneo.

Habitat. Generally uncommon (Antram, 1924; Wynter-Blyth, 1957), but the adult is found in tropical evergreen forests. The highest recorded elevation for this species is 1,828 m (Shields, 1985a).

Generations. In Thailand, the adult was collected in February, June, July, September and November (Pinratana, 1988), suggesting there may be multiple annual generations in at least some parts of its distribution.

Pterin pigment. Xanthopterin was found in specimens from Thailand (Shields, 1987b).

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摘 要

テングチョウ13種の生活態. 1. テングチョウ属 (河原章人)

今まで世界のさまざまな学者がテングチョウ類について研究発表してきた。この論文にはこれまで発表されたテングチョウの命名法、生息地、生態、成虫食、食草、移住、天敵の、擬態、カムフラージュ及び、クロモソーム数、プテリン色素などをまとめて報告し、私の新しい観察と研究を含める。テングチョウ類のほとんどは2,000 m以下の低い山の森林や荒らされている環境に生息する。花によくとまり、年1-2回発生し、雄が縄張りをもつ。♀は普通エノキ (Celtidaceae: *Celtis*) の新芽に産卵し、幼虫はこの葉を食べる。小さな島に生息する4つの固有種の幼生期については過去に観察や研究が少ない。また、テングチョウ4種は移住することが知られている。本報では、テングチョウ属9種の生活態をまとめる。

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