

FOODPLANT ASSOCIATIONS OF THE URANIINAE
(URANIIDAE) AND THEIR SYSTEMATIC,
EVOLUTIONARY, AND ECOLOGICAL SIGNIFICANCE

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ABSTRACT. Larval and adult foodplant records for the moth subfamily Uraniinae (*sensu* Sick 1937) are reviewed. Reliable larval foodplant records for all seven genera include only the genera *Omphalea* L., *Endospermum* Benth., and *Suregada* Roxb. ex Rottl. (Euphorbiaceae), and this specialization on Euphorbiaceae supports Sick's concept of Uraniinae (based on metathoracic and tympanal morphology) as a monophyletic group. Whereas *Omphalea* is known to be fed on only by larvae of the three strictly day-flying genera (*Urania* Fabricius, *Chrystridia* Hübner, and *Alcides* Hübner), *Endospermum* is a recorded foodplant for *Alcides* and three primarily nocturnal genera (*Lyssa* Hübner, *Urapteroides* Moore, and *Cyphura* Warren). The latter two genera have been traditionally included in the Microniinae, as has been *Urapteritra* Viette, whose larval foodplant *Suregada* is reported here for the first time. Some ecological and evolutionary aspects of uraniine larval foodplant specialization are discussed. A putative phylogeny of Uraniinae based on published hearing organ and larval morphology is presented, and the phylogenetic significance of larval foodplant relationships evaluated. Adult foodplants (nectar resources) for the diurnal uraniines are summarized, and the possibility of their role in the moths' reproductive or predator defense ecology is briefly discussed.

Additional key words: Microniinae, *Omphalea*, *Endospermum*, *Suregada*, Euphorbiaceae.

SYSTEMATICS OF THE URANIIDAE

Diurnal members of the uraniid subfamily Uraniinae are renowned for their iridescent colors, rivalling the most exquisite butterflies. There are approximately 50 described species in 7 genera, distributed throughout the tropics: *Urania* ca. 6 spp., *Chrystridia* 2 spp., *Alcides* ca. 7 spp., *Lyssa* ca. 7 spp., *Urapteritra* ca. 8 spp., *Urapteroides* 3 spp., and *Cyphura* ca. 15 spp. (D. C. Lees, unpubl. data). Although there are no modern cladistic studies of the subfamily, Sick (1937) provided a basis for the generic arrangement of the group and its subfamilial relationships. Only two genera of the Uraniinae *sensu* Sick have been revised: *Lyssa* (Altena 1953) [= *Nyctalemon* Dalm.—see Fletcher 1979:121] and *Urapteritra* (Viette 1972). Viette separated *Urapteritra* from *Urapteroides* (Gaede 1926-30) on the basis of distinct genitalic differences and on the absence in *Urapteritra* of the stalked condition in the veins CuA₁ and M₃ of both sets of wings, which is present in both *Urapteroides* (Hampson 1895) and *Cyphura* (Westwood 1894). Traditionally, Uraniidae has been placed in the superfamily Geometroidea; males and fe-

males of the Geometridae possess a pair of tympanal organs on the first abdominal sternite (=sternite 2; abdominal sternite 1 is absent). However, there is a clear sexual dimorphism in the position of these organs in uraniines: although they occur in females on the anterior of abdominal sternite 2, in males they are found laterally at the junction of abdominal tergites 2 and 3 (Eltringham 1924b, Kennel & Eggers 1933, Sick 1937, Minet 1983), a synapomorphy with the Microniinae and the Epiplemidae *sensu auct.*

Following the suggestions of Sick (1937), Minet (1983, 1986) redefined the Uraniidae and erected a separate superfamily for them, the Uranioidea, reducing the Epiplemidae (ca. 700 spp. worldwide) to the rank of subfamily along with the Uraniinae and Microniinae (=Acropterinae of Sick). (Later, Minet (1991:87) returned the Uraniidae to a revised Geometroidea along with the Sematuridae and the Geometridae.) Minet (1983) concurs with Sick (1937) that the Indo-Australasian genera *Urapteroides* and *Cyphura* (conventionally regarded as microniines) are best placed in the Uraniinae based on tympanal and thoracic morphology.

Characters. Sick's three uraniid subfamilies form a monophyletic group defined by the synapomorphies in Table 1. The Microniinae *sensu auct.* (including *Cyphura* and *Urapteroides*) are all delicate conspicuous whitish moths with pointed wing apices, oblique dark cross-striations, and predator-deflection markings on the hindwing tails. The frenulum is absent or vestigial (both microniines and uraniines appear to substitute the conventional type of wing-coupling with expansion of the humeral angle of the hindwing, allowing a looser amplexiform coupling method: Common 1970:849–851). Although this "gestalt" concept of Microniinae may seem appealing, the patterns are very likely to be homoplasious anti-predator adaptations. Color patterns remarkably similar to those of various Microniinae *sensu auct.* reoccur in (a) the Neotropical Epipleminae, e.g., *Aorista* Warr., *Meleaba* Wkr., and *Psamathia* Wkr. (= *Micronioides* Mesm.); (b) an Old World epiplemine (*Epiplema himala* Btlr.); (c) the Old World Geometridae (e.g., *Ourapteryx* Leach); and (d) the Neotropical oxytenid genus *Asthenidia* Westwood. Microniinae is Palearctic, whereas Epipleminae and Uraniinae are pantropical.

Posture. Resting posture often is phylogenetically distinctive within the Lepidoptera. All uraniids possess a generally splayed-out day-time resting position, apparently the plesiomorphic condition within the group, but wing posture varies among uraniid subfamilies. The epipleminae, with cryptic coloration, are distinct in folding the hindwings alongside the abdomen, and frequently warp the forewings rather than extending them flat (Gaede 1926–30:390, Common 1970, Sugi 1987).

TABLE 1. Characters defining the Uraniidae (*sensu* Sick 1937 & Minet 1983) and its constituent subfamilies.

	Refs.†
Apomorphies defining Uraniidae	
1. Females with a unique conformation of tympanic cases and tympana, deriving from the first abdominal sternite (sternite 2) where they are anterior-laterally situated	1, 2, 3
2. Males with a unique conformation of hearing organs, with tympana, tympanic projections, countertympana, and tympanic cavities deriving from abdominal tergites 2 & 3	1, 2, 3
3. Females with scolopal body of scoloparium inverted	3, 4
4. Presence of a spiniform endosclerite ("Coxalzapfen") from the metathoracic epimeron next to the secondary arm of the furca	3, 4
Other characters [plesiomorphies?]	
5. Forewing vein R ₅ sharing a common stalk with M ₁ or joined at the base with M ₁ (also occurs in epicopeids)	3, 5, 6
6. Forewing vein R ₅ well separated from R ₁ -R ₄	3, 7
7. Larvae with full complement of prolegs (=16 legs)	5
8. Larvae without secondary setae; primary setae on tubercles	8, 9, 10
9. Eggs domed/spherical ("upright"), with projecting ribs	6, 11
Apomorphies defining Uraniinae	
1. Metathoracic epimerons of females modified into ±concave, oval covers in front of or laterally over abdominal tympana	3, 4
2. Known larval foodplants in the Euphorbiaceae (all genera specialists on <i>Omphalea/Endospermum/Suregada</i> , plants with polyhydroxy alkaloids)	12
Other characters [loss/reduction/absence characters]	
3. Mesothoracic anepisterna reduced or absent	3, 13
4. Female metacoxa <i>not</i> covered with projecting scales [scales form protective covers over tympana in Epipleminae and Microniinae]	3, 4
5. Strengthening conjunctiva between female intersegmental thoracic-abdominal membrane and tympanum less extended than in Epipleminae and Microniinae	4
6. Hindwing frenulum lost	12
Apomorphies defining Microniinae (<i>sensu</i> Acropterinae of Sick 1937)	
1. Angle of countertympanum to tympanum in males obtuse, ca. 120° [note: angle acute, ca. 60-80° in Uraniinae and ca. 45° in Epipleminae; ca. 100° in <i>Decetia</i>]	3, 4
2. Known larval foodplants in the Asclepiadaceae (<i>Dregia volubilis</i> Benth. ex Hook for <i>Acropteris ciniferaria</i> (Walker) in Sri Lanka and <i>Marsdenia tomentosa</i> C. Morr. & Decne for <i>A. cf. sparsaria</i> (Walker) in Taiwan [note: Olacaceae (<i>Olox wightiana</i> Wall) recorded for <i>Decetia subobscurata</i> Walker in India]	14, 15
Other characters [loss/reduction character]	
3. Frenulum absent or vestigial [note: frenulum present in <i>Decetia</i> Wkr. and <i>Paradecetia</i> Swinhoe]	3, 7
Characters defining Epipleminae [clear autapomorphies unknown]	
1. Male tympanum separated posteriorly from countertympanum by a sclerified arm (in Uraniinae/Microniinae by a narrow membranous strip)	3
2. Frenulum and retinaculum present (best developed in males)	3

TABLE 1. Continued.

	Refs.†
3. Hindwing humeral angle weakly expanded with humeral vein vestigial/absent in contrast to Uraniinae and Microniinae	3, 7
4. Hindwing vein 3A present or atrophied	3
5. Larval foodplants include Rubiaceae, Caprifoliaceae, Oleaceae, Daphniphyllaceae, Bignoniaceae, and Verbenaceae (just as in Sphingidae)	8, 16

† References: 1. Eltringham 1924b; 2. Kennel & Eggers 1933; 3. Minet 1983; 4. Sick 1937; 5. Hampson 1895:110-113; 6. Minet 1986; 7. Common 1970:849-851; 1990:381-385; 8. Holloway et al. 1987:171-172; 9. Kühn 1887; 10. Moore 1884-87:398-403, pl. 186; 11. Macleay 1834; 12. Current paper; 13. Brock 1971; 14. T. R. D. Bell 1901 MS; 15. J. Rawlins, pers. comm.; 16. Sugi 1987.

Members of the *Decetia* group are also drab, but their resting posture has not been described. The remainder of the Microniinae and the Uraniinae (*sensu stricto*) extend the wings flat, but appear to differ in alighting behavior. Microniines have a labored, conspicuous flight, normally crepuscular or nocturnal. They are easily disturbed by day, after which they flutter slowly for a short distance before alighting again, on or often underneath a leaf (Gaede 1933:97; Bell 1901 MS; D. C. Lees, pers. obs. for *Aploschema* Warren and *Acropteris* Geyer in Cameroon). Uraniines generally alight on top of a leaf, then reverse their position so that the head points downward, a tactic that confuses predators by drawing attention to the hindwing tails (Seitz 1940:829). Microniines and uraniines also may be aposematic, relying for protection by day on their bright contrasting colors, even at rest. For example, *Urapteritra* spp. in Madagascar may rest on top of leaves and are disinclined to move even when disturbed (J. Minet, pers. comm.). A clear exception is the genus *Lyssa*, which has a more cryptic brown coloration with disruptive white bands and rests in dark places or under leaves (Altena 1953:40-41). The nocturnal roosting posture of uraniines is also generally spread-out, with forewings slightly lowered over hindwings, observed in *Urapteritra fasciata* (Mabille) (D. C. Lees, pers. obs.) and *Urania fulgens* Wkr. (N. G. Smith, pers. obs.). However, *Chrysidia* spp. [and reportedly "microniines" (Gaede 1933:97)] rest at night with wings held vertically over the back like many butterflies (D. C. Lees, pers. obs.; Lucas 1876).

Foodplants. Foodplant records are useful in evaluating the phylogenetic relationships, based on morphological characters, of the uraniid subfamilies and the seven genera placed in the Uraniinae in this paper. Although foodplant records strongly support the monophyly of the Uraniinae *sensu* Sick (Table 1), the Epipleminae *sensu auct.* (for which Minet 1983 can find no convincing autapomorphies) and Microniinae *sensu* Minet appear more vulnerable taxa: more detailed morphological studies ultimately may prove them to be paraphyletic. Epipleminae are apparently associated with a suite of hostplants also found within

the Sphingidae (Table 1). The inclusion of *Decetia* Wkr. and *Paradecetia* Swh. among the microniines (Minet 1983) on the basis of tympanal characters alone (Table 1) is questionable (see also Sick 1937) because it ignores their distinctive wing-shape, which is different from the rest of the microniines; the pectinated antennae in *Decetia*; the presence of a well-developed hindwing frenulum; and a foodplant record on Olacaceae for *Decetia*, contrasting with apparent specialization on milkweeds (Asclepiadaceae) in the case of the microniine genus *Acropteris* (Table 1). Although the female tympana of *Decetia* have yet to be described (see Sick 1937), the appropriate solution may be the erection of a new uraniid subfamily for *Decetia* and *Paradecetia* (along with *Auzea* Walker).

LARVAL FOODPLANT RECORDS FOR THE URANIINAE

Uraniine foodplant records, widely dispersed in the literature, are summarized in Table 2, together with all known unpublished records. *Omphalea* L. (Euphorbiaceae) was first reported as the larval foodplant of *Urania* by Macleay (1834) and as that of *Chrysidia* by Camboué (1889, 1892). Our review indicates that the genera *Urania* and *Chrysidia* are specialists feeding exclusively on this pantropical plant genus (see Table 2). Furthermore, *Alcides metaurus* (Hopffer 1856) (= *A. zodiaca* (Butler 1869), synonymy as yet unpublished) from Queensland, North Australia, recently has been reported to feed on the *Omphalea* species endemic to the region (Coleman & Monteith 1981). *Endospermum* Benth. (Euphorbiaceae) was first reported as a uraniine foodplant for *Urapteroides* by Browne (1937), for *Lyssa* by Szent-Ivany and Carver (1967), and for *Alcides* by Coleman and Monteith (1981), and has subsequently proved to be a widespread uraniine foodplant in the Indo-Australasian region (Table 2).

The larval foodplant of the genus *Urapteritra* is reported here for the first time. Larvae of two species were discovered in Madagascar in January 1991 feeding on two different species of *Suregada* Roxb. ex Rottl. (= *Gelonium* Roxb. ex Willd.) (Euphorbiaceae) (Table 2).

Records of other purported uraniine foodplants are widespread in the literature. None have been confirmed to date. *Mangifera indica* L. (Anacardiaceae) was incorrectly stated as the larval foodplant of *C. rhipheus* (Boisduval 1833, Sganzin & Boisduval 1873; but see Guenée 1877, Mabille 1889), and of the closely related *C. croesus* from East Africa (Pinhey 1975:79, and subsequently by Sevastopulo 1981; but see Sevastopulo 1986). It is likely that mango flowers are a nectar resource for adult *Chrysidia* (see Table 8), as may be flowers of *Terminalia catappa* L. (Combretaceae) (T. Grant, pers. comm.), also unconvincingly reported as a larval foodplant by Pinhey. *Chrysidia rhipheus*,

like *Urania* spp., characteristically engages in territorial behavior alighting upside down on leaves of mango trees (Lucas 1869), and perhaps on foliage of other adult nectar sources; such behavior may have misled some authors (e.g., E. Pinhey, pers. comm.). *Eugenia malaccensis* L. (Myrtaceae) has been reported more than once as the larval foodplant of *Lyssa zampa* (Btlr.) and *Urapteroides astheniata* (Gn.) (Corbett & Dover 1927, reiterated by Altena 1953:38 and Barlow 1982:136). This is now recognized as a transcription mistake for *E. (Endospermum) malaccense* Benth. (syn. *E. diadenum* (Miq.) Airy Shaw) (Y. P. Tho, pers. comm., H. S. Barlow, pers. comm.). *Pittosporum* sp. (Pittosporaceae) has been reported as an *Alcides* foodplant by Szent-Ivany and Carver (1967), a record which should also be treated with caution in the absence of confirmation (Coleman & Monteith 1981). See Table 2, note 10, as regards a vague record of a palm as a *Lyssa* foodplant (Boisduval 1874). The description of the larval foodplant of a *Lyssa* sp. from N.E. Sulawesi (Kühn 1887) is too imprecise for certain identification (but see Table 2, note 9).

GEOGRAPHICAL DISTRIBUTION OF URANIINE LARVAL FOODPLANTS

Because of the apparent high degree of specialization of uraniines on their euphorbiaceous foodplants, it is of value to summarize the available botanical information on the species and their distribution (Tables 3, 4, 6). This has potential for pinpointing the gaps in knowledge of uraniine foodplant relationships, and, by comparison with data on moth distribution, might reveal if other foodplants are likely to be involved.

Omphalea, a genus of trees and large canopy-spreading lianas with about 16 species (Table 3), at least two of which are sometimes cultivated for their edible seeds in the Neotropics (Gillespie 1990), has so far been found to be the larval foodplant for seven species within three uraniine genera (Table 2). Eight species of *Omphalea* are known in the Neotropics, from Mexico to Amazonian South America and the atlantic coastal forests of Brazil, and sporadically through the Greater and Lesser Antilles. An additional eight species have a relict distribution in the Paleotropics, occurring in Tanzania, Madagascar, Queensland, New Guinea, the Bismarck Archipelago, Solomon Is., Sulawesi, Philippines, Borneo, Malaysia, Thailand, Laos, and Myanmar [Burma] (Gillespie 1990), including a new species discovered during recent fieldwork in Madagascar (Gillespie, unpubl. data). Cladistic analyses suggest that the Neotropical and Afrotropical species form a monophyletic group defined by a unique set of male floral characters, whereas the three Indo-Australasian species form a more plesiomorphic clade (Gillespie 1988, 1990). The disjunct distribution of the day-flying uraniines, which

TABLE 2. Extended.

											Rearing locality†	
<i>E. medullosum</i>											•	Cub: W¹
<i>E. myrmecophilum</i>											•	Cub: NW, Matanzas
<i>E. labios</i>											•	Cub: W, Mogotes
<i>E. moluccanum</i>											•	Jam: N, Ocho Rios
<i>E. diadenum</i>											•	Cub: E, Punta Maisi²
<i>E. sp.</i>											•	
<i>Suregada boivintiana</i> (Euphorbi-)											•	
<i>S. decidua</i>											•	
<i>Quisqualis indica</i> (Combret-)											•	Mex: Veracruz
<i>Pittosporum sp.</i> (Pittospor-)											•	Pan: N & S
"Palm" (Arec-)											•	Amaz: Surinam
											•	Trin
											•	Mad: E
											•	Mad: W, Lac Bemamba
											•	Mad: W, Bemaraha
											•	Mad: NW, Ankarana
	<	j	>								•	PNG: E, Sogeri⁸
	•	•	•							k	•	PNG: E, Rouna Falls, Port Moresby⁴
	•	•	•								•	NQd: upper Mulgrave R.
	j	•	•								•	NQd: Bamaga, Cp. York
	j	•	•								•	NQd: Mission Beach)
	•	<	>	k	>						•	PNG: E, Brown R.⁷
	•	<	>	j	>						•	PNG: E, Sogeri⁸;
	j	•	•	•	•						•	NQd: Cape Tribulation
	•	j	•	•	•						•	NQd: Cape York
	•	•	•	•	•						m	Phil¹⁰
	•	•	•	•	n	•	•	•	•	•	•	pMal: Selangor
	•	•	•	•	•	•	•	•	o	•	•	Thai: Bangkok¹²
	•	•	•	•	p	•	•	•	•	•	•	pMal: Selangor
	•	<	>	q	>	•	•	•	•	•	•	Sol¹³
r	•	•	•	•	•	•	•	•	•	•	•	NQd: Cape Tribulation

TABLE 2. Continued.

Moth taxon††	Larval foodplants* (Confirmed foodplants in bold) Species (Family—aceae)	<i>Omphalea oppositifolia</i> (Euphorbi-)	<i>O. triandra</i>	<i>O. hypoleuca</i>	<i>O. trichotoma</i>	<i>O. oleifera</i>	<i>O. diandra</i>	<i>O. palmata</i>	<i>O. sp. nov.</i>	<i>O. occidentalis</i>	<i>O. queenslandiae</i>	<i>Endospermum macrophyllum</i> (Euphorbi-)
<i>U. anerces</i> (Meyrick)		•	•	•	•	•	•	•	•	•	•	s
<i>Cyphura semi- obsoleta</i> Warr.		•	•	•	•	•	•	•	•	•	•	•
<i>Urapteritra fasciata</i> (Mabille)		•	•	•	•	•	•	•	•	•	•	•
<i>U. ?piperita</i> (Oberthur) ¹⁴		•	•	•	•	•	•	•	•	•	•	•

* In captivity, *Urania* larvae will feed on other species of *Omphalea* tested (N. G. Smith, D. C. Lees, pers. obs.); these records are all from the wild.

† See Tables 3, 4 and 5 for authors of plant names.

†† Notes (superscripts):

1. As "*O. triandra* Linn.," which does not occur in Cuba; however, Macleay's illustration clearly shows the hostplant to be *O. trichotoma*.
2. Voucher photographs show *Urania* larvae hanging down on threads (Fig. 1A); larvae are not *U. boisduvalii* and by elimination are assumed to be *U. poeyi*.
3. There is a color figure of *A. agathysus* larvae descending from an unspecified tree in Lae, Papua New Guinea, in D'Abrera (1974:60).
4. An *E. moluccanum* specimen in the Rijksherbarium, Leiden, was originally identified as a *Pittosporum* sp., so it is perhaps conceivable that such a misidentification could have been made in this case.
5. There are 3 larvae of *A. metaurus* collected by A. S. Meek in the BMNH collection, and, as they were collected at Cedar Bay, S. of Cooktown, it is likely they were reared on *E. medullosum* rather than one of the other two recorded foodplants.
6. The identity of the population of *Lyssa* in North Queensland, not recognized by Altina (1953), requires clarification, and is here referred to as *L. ?macleayi*. Previously it has been referred to in the literature as *L. patroclus* (Coleman & Monteith 1981), but the figure in D'Abrera (1974:60) resembles *L. macleayi*. Altina (1955: 13-14) was in any case unsure that the two taxa deserve specific status.
7. The moth host is described as "*L. patroclus goldiei* Dr.," referable to *L. macleayi macleayi* (see Altina 1953: 15). This foodplant is described as "*Endospermum* sp. nov. (Hoogland 1967, pers. comm.)," which is most likely to be referable to *E. labios* Schodde 1967, although there does exist a collection of *E. myrmecophilum* from Brown R. (see Table 6).
8. Ray Straatman reared his uraniines at Sogeri on a myrmecophilous species that he called "*E. formicarum*" (syn. *E. moluccanum*) (R. Straatman, pers. comm.), but Monteith and Wood (1987) suggest this was *E. myrmecophilum*.
9. Kühn (1887) describes and figures a larva of *Lyssa "patroclus"* from Tombugu, N. Sulawesi, which might be either *L. monoetius celebensis* or *L. zampa dilutus* (Altina 1953). The foodplant is described briefly as "an abundant shrub in mangrove swamp with glabrous blue-green bark, and simple ovate, acuminate leaves, the younger ones large hand[sized?] and trifid." *Endospermum peltatum* Merr. in N.E. Sulawesi has non-peltate

almost exactly corresponds to the range of the Neotropical, Afrotropical, and Australasian (but not the Malesian) *Omphalea* species, is suggestive of a very specialized and ancient relationship, perhaps even predating the final break-up of Gondwanaland in the mid-late Cretaceous, ca. 100-65 million years BP (Coleman & Monteith 1981). Although a vi-

TABLE 2. Continued.

											Rearing locality†	
<i>E. medullosum</i>	<i>E. myrmecophilum</i>	<i>E. labios</i>	<i>E. moluccanum</i>	<i>E. diadenum</i>	<i>E. sp.</i>	<i>Suregada boivintiana</i> (Euphorbi-)	<i>S. decidua</i>	<i>Quisqualis indica</i> (Combret-)	<i>Pittosporum</i> sp. (Pittospor-)	"Palm" (Arec-)		Fiji
•	•	•	•	•	•	•	•	•	•	•		NG
•	•	•	•	•	•	•	•	•	•	•		Mad: E, Perinet
•	•	•	•	•	•	•	t	•	•	•		Mad: SW, Beza Mahafaly, nr. Betioky

(acuminate) as well as peltate leaves, occurring in wet forest including swamps (Schaeffer 1971); however, younger divided leaves are not described. [A species of *Suregada*, *S. racemulosa* (Merr.) Croiz. (? = *S. trifida* (Elm.) Croiz.) has appropriately shaped leaves but is known only from the Philippines].

10. The record states only that a larva of this species that, was lightly hairy with 16 feet was reared by Lorquin on "une espèce de palmier (qu'entendit-il par ce nom?)".
11. The descriptions given of *L. ?zampa docile* larvae by Corbett & Dover (1927) mention the absence of hairs and tubercles, and are thus suspect. The two paintings (dorsal and lateral view) on which the descriptions were based, apparently held in the Department of Agriculture at Kuala Lumpur (Altena 1953:26, 37), have not been examined.
12. A voucher slide shows a reared *L. zampa zampa* adult resting on *Quisqualis indica* leaves, but the larvae were described as "orange, with long hairs", and the observer agreed they did not resemble the illustration of a *L. zampa* (or *L. monoetius*) larva in Kühn (1887). This shows short hairs on raised tubercles, as does a preserved larva of *L. ?macleayi* from Mission Beach, reared by D. Kitchin (see Fig. 1E). Thus this record requires confirmation.
13. As "*E. myrmicaria*"; *E. myrmecophilum* does not occur in the Solomons (Schaeffer 1971), so the record probably refers to one of the other two ant mutualist species (see Table 4).
14. *Urapteritra piperita* and *U. falcifera* (Weymer) are the two sympatric species; of these, the former has been recorded from Betioky (Viette 1972).

† References: a. Macleay 1834; b. N. G. Smith, pers. obs.; c. Gosse 1881; d. L. J. Gillespie, pers. comm.; e. N. G. Smith, Smiths. Inst. Res. rep. No. 7, Winter 1974; Smith 1982; f. Hofmann 1881; g. Guppy 1907; h. Camboué 1889, 1892; Eltringham 1924a; Catala 1940; i. D. C. Lees, pers. obs.; j. Monteith & Wood 1987; k. Szent-Ivány & Carver 1967; l. Coleman & Monteith 1981; m. Boisduval 1874; n. Y. P. Tho, pers. comm. [see also Barlow 1982]; o. A. R. Pittaway, pers. comm.; p. Browne 1937, 1938, 1940 [see also Corbett & Dover 1927]; q. CAB Int. Inst. of Entomol. economic card index, Natural History Museum, South Kensington; r. G. Monteith, pers. comm.; reared from pupa by D. Kitchin; s. Robinson 1975:315; t. L. L. Holloway, pers. comm., photographs of larvae and hostplant (Fig. 1G).

carriage explanation for the distributions seems sufficient, the possibility of more recent long-distance dispersal of moths or plants cannot be ruled out: the moths are renowned for their population explosions and migratory abilities and at least two *Omphalea* spp. are reported to disperse their seeds on ocean currents (Guppy 1917, Johnston 1949).

Endospermum, some species of which are of minor economic importance as a tropical softwood, has so far been found to be a host for seven species in four uraniine genera (Table 2). *Endospermum* is wide-

TABLE 3. Distribution of *Omphalea* species worldwide and the uraniine species that feed on them or are sympatric. Confirmed foodplants shown in bold. Arranged systematically (Gillespie 1990). Abbreviations: Pa = Sect. *Palminerviae* Pax & K. Hoffm.; Pe = Sect. *Peninerviae* Pax & K. Hoffm.; l = liana; t = tree/shrub. Locality abbreviations additional to Table 2: Braz = Brazil; Hisp = Hispaniola; Guat = Guatemala; Hond = Honduras; Tanz = Tanzania; CAM = Central America; IJ = Irian Jaya; Bis = Bismarck Arch. (NI = New Ireland); Myan = Myanmar [Burma]; Bor = Borneo; Sing = Singapore; Sul = Sulawesi. Italics signifies foodplant record as well as sympatry.

Plant species (Bold print: confirmed foodplant)	Uranine species* (Uranines confirmed to feed on <i>Omphalea</i> in bold)	Known distribution of plant: (Ref.)† (Bold print: diurnal uraniine sympatric)
<i>Omphalea brasiliensis</i>		Braz: atlantic rainforest, Bahia (Salvador & Vitoria) to Espirito Santo (Linhares): (1)
Muell. Arg. (Pe; l)		Mad: E rainforest, scattered small populations from Antongil Bay S. to Fianarantsoa: (2)
<i>O. oppositifolia</i> (Willd.) Gillespie [= <i>O. biglandulosa</i> (Pers.) Baill.] (Pe; t)		Jam: wet forest on limestone: (2); Haiti (introduced): (3)
<i>O. triandra</i> L. (Pe; t)	c	Hisp (Rep. Dominicana): cloud forest, La Vega & Banao: (3)
<i>O. ekmanii</i> Alain (Pe; t)	No <i>Urania</i> records	Cub: limestone Mogotes in west, Pinar del Rio: (4)
<i>O. hypoleuca</i> Grisebach (Pa; t)	d	
<i>Urania botsuvalti</i> Guerin		
<i>U. sloanus</i> (Cramer)		
<i>U. poeyi</i> Cundlach		
<i>U. fulgens</i> Walker		
<i>U. leilus</i> (L.)		
<i>U. brasiliensis</i> (Swainson)	a	
<i>Chrystridia rhipheus</i> (Drury)	a b	
<i>C. creesus</i> (Gerstaecker)		
<i>Aldes latona</i> (Druce)		
<i>A. aurora</i> Salvin & Godman		
<i>A. orontes</i> (L.)*		
<i>A. cydnus</i> (Felder)		
<i>A. arvus</i> (Felder)*		
<i>A. metaurus</i> (Höfner)		
<i>A. agathyrus</i> (Kirsch)		

TABLE 3. Continued.

Plant species (Bold print: confirmed foodplant)	Uranine species† (Uranines confirmed to feed on <i>Omphalea</i> in bold)										Known distribution of plant: (Ref.) (Bold print: diurnal uranine sympatric)				
	<i>Urantia boisduvalii</i> Guérin	<i>U. sloanus</i> (Cramer)	<i>U. poeyi</i> Gundlach	<i>U. fulgens</i> Walker	<i>U. leilus</i> (L.)	<i>U. brasiliensis</i> (Swainson)	<i>Chrystridia rhipheus</i> (Drury)	<i>C. croesus</i> (Gerstaecker)	<i>Alcides latona</i> (Druce)	<i>A. aurora</i> Salvin & Godman		<i>A. orontes</i> (L.)*	<i>A. cydneus</i> (Felder)	<i>A. aruus</i> (Felder)*	<i>A. metaurus</i> (Hopffer)
<i>O. commutata</i> Muell. Arg. (Pa; t)															Hispan (Haiti): Gonaives I.: (2)
<i>O. trichotoma</i> Muell. Arg. (Pa; t)	<i>d</i>														Cub: coastal limestone, N/NW, extreme E: (4)
<i>O. oleifera</i> Hemsley [= <i>O. cardiophylla</i> Hemsley] (Pa; t)			<i>e</i>	<i>f</i>	<i>f</i>										S Mex to Guat: (2); El Salvador: (2, 16)
<i>O. diandra</i> L.				<i>f</i>											Hond S through lowland Cam: (2);
[= <i>O. megacarpa</i> Hemsley] (Pa; l)					<i>g</i>										Amaz: (2); Trin & Tobago: (2); Grenada, cultivated: (2); Guadeloupe & Martinique: (2); St. Kitts, St. Vincent: (5)
<i>O. mansfeldiana</i> Mildbraed (Pa; l)		<i>i</i>	<i>d</i>												Jam: (6) (extinct?); Cub: NE near Baracoa: (7) SE Tanz: Lindi & Selous: Ebenda, Rufiji R., Kilwa: (8)

No *Urantia* records

Urantia not known to be a resident
Urantia not known to be a resident
Urantia not known to be a resident

g *h* *j*

TABLE 3. Continued.

Plant species (Bold print: confirmed foodplant)	Uranine species*† (Uranines confirmed to feed on <i>Omphalea</i> in bold)	<i>Urania boisduvalii</i> Guérin	<i>U. sloanus</i> (Cramer)	<i>U. poeyi</i> Gundlach	<i>U. fulgens</i> Walker	<i>U. leilus</i> (L.)	<i>U. brasiliensis</i> (Swainson)	<i>Chrystridia rhipheus</i> (Drury)	<i>C. croesus</i> (Gerstaecker)	<i>Alcides latona</i> (Druce)	<i>A. aurora</i> Salvin & Godman	<i>A. orontes</i> (L.)*	<i>A. cydnus</i> (Felder)	<i>A. arvus</i> (Felder)*	<i>A. metaurus</i> (Hopfer)	<i>A. agathyrsus</i> (Kirsch)
<i>O. sp. nov.</i> (Pa; t)		•	•	•	•	•	•	b	•	•	•	•	•	•	•	•
<i>O. palmata</i> Léandri (Pa; t)		•	•	•	•	•	•	b	•	•	•	•	•	•	•	•
<i>O. occidentalis</i> Léandri (Pa; t)		•	•	•	•	•	•	b	•	•	•	•	•	•	•	•
<i>O. queenslandiae</i> Bailey (Pa; 1/(t)) <i>O. papuana</i> Pax & K.		•	•	•	•	•	•	k	•	•	•	•	•	•	•	•

Known distribution of plant: (Ref.)†
(Bold print: diurnal uranine sympatric)

Mad: NW/N: limestone karst, Ankarana;
Montagne des Francais (E of Antsiranana): (9)

Mad: (W/NW): limestone karst,
Ankarafantsika,
Bemaraha and deciduous forest on sand, Trangahy, Manambolo R., **sublittoral forest W/SW Antsalova:** (10)

Mad: (W/NW): limestone karst,
Bemaraha,
Namoroka and dry sandy forest (Tsimpihy): (10)

NQd: Atherton/Cairns/Innisfail rainforest: (11)

NQd: Iron Range (Cp. York): (2);

TABLE 3. Continued.

Plant species (Bold print: confirmed foodplant)	Uranine species*† (Uranines confirmed to feed on <i>Omphalea</i> in bold)	<i>Urania botsduvalii</i> Guérin	<i>U. sloanus</i> (Cramer)	<i>U. poeyi</i> Gundlach	<i>U. fulgens</i> Walker	<i>U. lellus</i> (L.)	<i>U. brasiliensis</i> (Swainson)	<i>Chrystridia rhipheus</i> (Drury)	<i>Alcides latona</i> (Druce)	<i>A. aurora</i> Salvin & Godman	<i>A. orontes</i> (L.)*	<i>A. cydnus</i> (Felder)	<i>A. arnus</i> (Felder)*	<i>A. metaurus</i> (Hopfer)	<i>A. agathyrus</i> (Kirsch)
Hoffm. (Pa; l)	•	•	•	•	•	•	•	•	•	•	•	g	•	•	g
[= <i>Neomphalea gageana</i> Pax & K. Hoffm., = <i>N. papuana</i> Gage)	•	•	•	•	•	•	•	•	g	g	•	•	•	•	•
<i>O. bracteata</i> (Blanco) Merr. (Pe; (l/(t)))	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
[= <i>O. sargentii</i> Merr. (Pe; l)]	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
[= <i>O. malayana</i> Merr. (Pe; t)]	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
[= <i>O. grandifolia</i> Merr. (Pe; t)]	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•

Known distribution of plant: (Ref.)†
(Bold print: diurnal uranine sympatric)

NG: PNG, IJ;

Bis (NI);

Sol: Guadalcanal,

Treasury Is.: (12)
Flores (?); N/C Sul, Phil,
Bor, Sing, pMal, Thai,
Laos, Myan: (13)
[Bor]:(14)

[pMal, Phil: Luzon,
Bor: Sarawak]: (14)
[Phil: Luzon, Panay]: (15)

No diurnal uranine is sympatric;
Lyssa & *Urapteroides* are not known
to feed on *Omphalea*

* Diurnal uranines are recorded from the following main areas where *Omphalea* is not (excluding likely migrant records; subtitles refer to refs. below): *Urania botsduvalii*: Holguin Province, NE Cuba; *Alcides* spp.: Maluku, the table, *A. metaurus*, N. Cape York (C. B. Monteith, pers. comm.); *Chrystridia croesus*: Zanzibar. † References: *Omphalea* distribution: 1. Millers-Segovins 1873:74,514-515; K. S. Brown, Jr. pers. comm.; 2. Gillespie 1990:3. Logter 1971, 1986:178-181; 4. Leon & Alain 1953: 5. Adams 1972: 6. Hemsley 1855, Adams 1979: 7. C. Lees, pers. obs.; 8. Brown, Jr. pers. comm.; 9. L. J. Gillespie, pers. comm.; 10. Léandri 1938; 1954; D. C. Lees, pers. obs.; 11. Airy Shaw 1980a:661, 12. Airy Shaw 1980a:177-8; 1966; 1968; 13. Airy Shaw 1971:310-1; 1975:180-1, 1982: 31, 1983:38; 14. Airy Shaw 1973:180-1; 15. Airy Shaw 1983:38; 16. F. Seaton, pers. comm. ‡ References: uranine sympatricity (italics signify foodplant record as well): Gillespie, pers. comm.; f. N. C. Smith, pers. obs. g. National Collection, Natural History Museum, South Kensington; h. Guppy 1907; i. Townsend 1893; j. J. Kiehlund, j. Kingdon & W. B. Hynd, pers. comm.; k. R. Paulian, pers. comm.; l. Coleman & Monteith 1981.

spread in the Indo-Australasian region with approximately 13 species (Table 4), all trees, distributed from Assam east to southern China, south through Malaysia and the Philippines, to New Guinea and North Australia (Schaeffer 1971). The genus also occurs in the Andaman Islands and Sumatra as well as the New Hebrides and Fiji (Gowers 1976; Schaeffer 1971). There is a good correspondence between the overall range of *Urapteroides* spp. and *Lyssa* spp. with that of *Endospermum* (compare maps in Altena 1953 for *Lyssa* spp. and Schaeffer 1971 for *Endospermum* spp.—data are summarized in Table 4). Within its known range, *Endospermum* is uncollected from a number of island groups (mainly in the Papuan region) on which uraniines are known to occur (Franken 1984, Gowers 1976); these are listed in Table 4. Strikingly, both uraniine moths and *Endospermum* are completely absent from the archipelagos of the Lesser Sundas (Bali to the Timor Sea): these islands have a very pronounced dry season (van Steenis 1979). However, uraniines have been consistently reported from outside the range of *Endospermum* from Aru, Kai, and Tanimbar Is., C & S Sulawesi, Java and associated islands, and also from Sri Lanka (*Urapteroides astheniata*: Hampson 1895). The absence of records of *Endospermum* from these areas may be due to botanical undercollecting: remarkably, Java seems to be the only Indonesian island in the entire chain from Sumatra to the S.E. Moluccas with any comprehensive floristic treatment (see van Steenis 1979, Froden 1984). This explanation could also account for the apparent absence of *Omphalea* in the Moluccas.

There is no evidence that *Urapteroides* (or *Lyssa*) spp. feed on *Omphalea*. *Urapteroides* is the most widespread genus of Indo-Australasian Uraniinae, ranging from Assam to Queensland (*U. astheniata*), West Solomons, New Hebrides (*U. hyemalis* (Btlr.)), and Fiji (*U. anerces* Meyr.). This distribution is consistent with specialization on *Endospermum* spp. (Tables 4 and 5) throughout its range, but occurrence outside this range might be explained by adoption of an alternative foodplant or immigration, if not by gaps in floristic knowledge. Present evidence suggests that *Omphalea* does not constitute an alternative foodplant for *Urapteroides* because the larvae have a very characteristic feeding damage pattern (figured by Browne 1937; see also Fig. 1H) complete with a web that usually stays intact on herbarium specimens (often including droppings and occasionally head capsules or ova). An examination of all specimens of *Omphalea* and *Endospermum* in the herbaria of Royal Botanic Gardens (RBG), Kew, and Rijksherbarium, Leiden, revealed that although *Urapteroides*-type webs are fairly common on *Endospermum* spp. (Table 5), no such webs were found on Indo-Australasian *Omphalea* spp. However, records in Table 5 from

the New Guinea region and Solomons alternatively might be referable to *Cyphura* spp., should this genus have similar feeding habits.

There are some 35 spp. of *Suregada* (Croizat 1942), entirely Paleotropical in distribution, with 13 spp. in Madagascar (Radcliffe-Smith 1991), eight spp. in Africa (Léonard 1958), including four spp. in East and South Africa (Palgrave 1977:432–434, Radcliffe-Smith 1987) (Table 6) and about 14 spp. in Indo-Australasia (D. C. Lees, pers. obs., Kew Herbarium). There is also a related genus, *Cladogelonium* Léandri (Léandri 1938), endemic to Madagascar, which, as the sister genus of *Suregada* (Radcliffe-Smith, pers. comm.) and being sympatric with *Urapteritra* spp. (Table 6), is a potential foodplant. The distribution of *Urapteritra* is consistent with the range of *Suregada* both in South and East Africa and in Madagascar as evident from museum and herbarium collections (D. C. Lees, unpubl. data; see Table 6). Eight species of *Urapteritra* are known from Madagascar (eastern rainforests and montane forests, western and southwestern dry deciduous forests; Viette 1972). One of these, *U. falcifera*, occurs in coastal eastern South Africa, Kenya, and Tanzania as well as in the southwestern forests of Madagascar. Two specimens of *U. falcifera* (Weymer) in the Natural History Museum, London, were bred by P. J. Leigh at Durban, Natal (where *Suregada* occurs), on an unspecified plant; a blown larval specimen from the same Leigh material exists at the Transvaal Museum in Pretoria, and also lacks foodplant data (C. B. Cottrell, pers. comm.). In Madagascar as in Africa the range of *Urapteritra* is considerably wider and stretches further south than that of the known *Omphalea* species (Table 3). This and the fact that no *Urapteritra* spp. were found recently during extensive fieldwork on Malagasy *Omphalea* species during the rainy season (D. C. Lees, pers. obs.) tends to suggest that *Urapteritra* does not feed on *Omphalea*. Similarly, it seems likely that *Chrysiridia* does not utilize *Suregada*. *Endospermum*, being absent from the Afrotropics, is not a potential natural foodplant of these two genera.

However, the remaining *Suregada* spp., widely distributed from India and South China to Australasia (Airy Shaw 1971, 1975, 1980a, 1980b, 1982, 1983) are potential uraniine foodplants. These are not tabulated here since no revision has been published and none are known to be foodplants. However, it will be of importance to discover whether any Indo-Australasian uraniines feed on the genus. Utilization of *Suregada* could explain some of the gaps mentioned in the distribution of *Endospermum* where uraniines occur. For example, *Lyssa zampa docile* (Butler) is apparently native to W. Java (Altena 1953), whereas *Endospermum* apparently is not (Backer 1963), although it is cultivated in the Bogor Botanical Garden (Schaeffer 1971). However, herbarium

TABLE 4. Distribution of *Endospermum* in Indo-Australasia and the uranine species that feed on them or are sympatric. Confirmed foodplants shown in bold. *Endospermum* spp. (all trees) arranged in approximate systematic order (Schodde 1967; Schaeffer 1971; Smith 1978, 1981; Airy Shaw 1980a:79; Monteith & Wood 1987). Potentially new unnamed taxa collected from Biak and Numfor Is., Irian Bay (Schodde 1967:401, Schaeffer 1971:191) not included. *Lyssa* spp. arranged after Altena 1953. Abbreviations: ** = species myrmecophilous (with *Camponotus quadricreps* Smith); * = twigs sometimes hollow but myrmecophily not known; # = inner bark odor foul, mousy; @ = inner bark odor like green beans; ? = identity of moth uncertain; localities not in Tables 2 and 3: Fij = Fiji Is.; Van = Vanuatu [New Hebrides]; NB = New Britain; Malu = Maluku [Moluccas]; Sum = Sumatra; HK = Hong Kong I.; IC = Indochina; pThai = peninsular Thailand; mThai = mainland Thailand. Italics signifies foodplant record as well as sympatry.

Uranine species*†	(Uranines confirmed to feed on <i>Endospermum</i> in bold)	<i>Aldes latona</i> (Druce)*	<i>A. aurora</i> Salv. & Godm.	<i>A. orontes</i> (L.)	<i>A. cydus</i> (Felder)	<i>A. arnus</i> (Felder)	<i>A. metaurus</i> (Hopffer)	<i>A. agathyrus</i> (Kirsch)	<i>Lyssa patroclus</i> (L.)*	<i>L. macleayi</i> (Montouzier)	<i>L. toxopeus</i> (Altena)	<i>L. mutata</i> (Butler)	<i>L. curvata</i> (Skinner)	<i>L. menoitus</i> (Hopffer)	<i>L. zampa</i> (Butler)	<i>Urapteroides aneres</i> (Meyr.)	<i>U. hyemalis</i> (Butler)	<i>U. asthenata</i> (Guenee)	<i>Cyphura</i> (Solomons spp.)*	<i>Cyphura</i> (Bismarcks spp.)	<i>Cyphura</i> (NG spp.)	<i>Cyphura</i> (Maluku spp.)	Plant species*‡ (Bold print: confirmed foodplant)	Plant distribution: (Ref.)*† (Bold print: uranine sympatric)
<i>Endospermum macrophyllum</i> (Muell. Arg.) Pax & Hoffm.*	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Fij: Vanua Levu, Viti Levu; Ovalau, Taveuni, Kadavu: (1)	
<i>E. robbieanum</i> A. C. Smith	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Fij: C. Vanua Levu: (1)	
<i>E. medullosum</i> L. S. Smith @ [? = <i>E. domati-</i> <i>phorum</i> Schaeffer, from E/C. PNG]	c	•	•	•	•	•	•	•	•	•	•	b	•	•	•	•	•	•	•	•	•	•	Van: SE Efate, Northern Is.: (2) Sol: (3), Santa Cruz Is.: (4) Admiralty Is.: (5) Bis: NB: (3), Normanby I.: (6) NG: PNG, IJ,	

TABLE 4. Continued.

Plant species [†] (Bold print: confirmed foodplant)	Plant distribution: (Ref.) [‡] (Bold print: uranine sympatric)																																				
	Sol	Bis	NB	(3)	NI	(6)	NG	PNG	IJ	(3)	Kar-Kar	Adi I.	(6)	Numfoor	Biak	Yapen	Salawati Is.	Kofiau Is.	Malu, S: Seram,	Ambon,	Malu, N: Bacan,	Morotai,	Ternate,	Halmahera,	Sul, NE,	Talau Is.:	(3)	Sum, N: Atjeh:	(3)	pMal:	P. Tioman:	(3)					
<i>E. moluccanum</i>																																					
(Teijsm. & Binnend)																																					
Kurz**#																																					
[= <i>E. formicorum</i> Becc.]																																					
<i>A. aurora</i> Saly. & Godm.																																					
<i>Alcides latona</i> (Druce) [#]																																					
<i>Endospermum</i> in bold)																																					
Uranine species [‡] (Uranines confirmed to feed on)																																					
<i>A. orontes</i> (L.)																																					
<i>A. cydnus</i> (Felder)																																					
<i>A. arnus</i> (Felder)																																					
<i>A. metaurus</i> (Hopffer)																																					
<i>A. agathyrsus</i> (Kirsch)																																					
<i>Lyssa patroclus</i> (L.) [#]																																					
<i>L. macleayi</i> (Montouzier)																																					
<i>L. toxopeus</i> (Altena)																																					
<i>L. mutata</i> (Butler)																																					
<i>L. curvata</i> (Skinner)																																					
<i>L. menoetus</i> (Hopffer)																																					
<i>L. zampa</i> (Butler)																																					
<i>Utraperoides anerces</i> (Meyr.)																																					
<i>U. hyemalis</i> (Butler)																																					
<i>U. astheniata</i> (Guenee)																																					
<i>Cyphura</i> (Solomons spp.) [‡]																																					
<i>Cyphura</i> (Bismarcks spp.)																																					
<i>Cyphura</i> (NG spp.)																																					
<i>Cyphura</i> (Maluku spp.)																																					

E. banghamit Merr.
E. ronaldit Schaeffer

specimens of the widely distributed species *Suregada glomerulata* (Bl.) Baill. from Java do show plausible uraniine damage (D. C. Lees, pers. obs.). Although an examination of herbarium specimens of *Suregada* spp. revealed no *Urapteroides*-type larval feeding webs (as in Fig. 1H), a specimen of *S. multiflora* (Juss.) Baill. at RBC, Kew, from Thailand contained a pupal exuvium that may be that of *U. astheniata* (D. C. Lees, unpubl.).

As uraniines do not occur outside the known range of these three euphorbiaceous foodplants, there is presently no unambiguous evidence for other larval foodplants within the group.

SYSTEMATIC AFFINITIES OF LARVAL FOODPLANT GENERA

Caution must always be exercised in championing lepidopteran hosts as plant chemotaxonomists since they might be simply exploiting biochemical homoplasy. The same allelochemicals might have arisen independently within the same family; there are plenty of examples of independent evolution of secondary compounds within unrelated families, e.g., mustard oils exploited worldwide by the pierid genus *Appias* within the Capparales and Euphorbiaceae (*Drypetes*) (D. C. Lees, pers. obs.). It does seem intriguing that all three euphorbiaceous uraniine larval foodplant genera were formerly grouped by Pax and Hoffman (1931) in separate subtribes of the same tribe Geloniae (subfamily Crotonoideae) on the basis of the valvate and imbricate condition of the male calyx. However, these characters are probable plesiomorphies (Gillespie 1990). More recent classifications based on pollen morphology have suggested affinities of *Omphalea* with *Plukenetia* L. in the Acalyphoideae: for example, these two genera share tricolpate pollen (L. J. Gillespie, pers. comm.; Webster 1975, supporting the indications of Croizat 1941 and Punt 1962). Nevertheless, this position is unsatisfactory in certain other respects: e.g., *Omphalea* possesses laticifers, uncharacteristic of Acalyphoideae (Rudall in press). Whereas the taxonomic affinities of *Omphalea* remain debatable, pollen morphology indicates that *Endospermum* has affinities with crotonoid genera such as *Te-*

←

† References: *Endospermum* distribution: 1. Smith 1978, 1981:540–542; 2. Gowers 1976; 3. Schaeffer 1971 and Airy Shaw 1971:258–9, 1975:109–110, 1980a:78–81, 1980b:628–9, 1982:18, 1983:24; 4. Franken 1984:182–3; 5. Airy Shaw 1980a:79; 6. Herbarium, RBC, Kew; 7. Monteith & Wood 1987; 8. Rijksherbarium, Leiden [Lelean & Stevens LAF 51208; NCF 21761, both with ants, but requiring confirmation]; 9. Schodde 1967.

‡ References: uraniine distribution: (italics signifies foodplant record; ? signifies doubt over identity of moth taxa, square brackets express reservation about record) a. Robinson 1975; b. Altena 1953, Semper 1896–1902:597–599; c. National Collection, Natural History Museum, South Kensington including Rothschild collection; d. Rijksmuseum van Natuurlijke Historie, Leiden; e. NHM, South Kensington accessions; f. Monteith & Wood 1987; g. G. B. Monteith, pers. comm.; Common 1990:107, 384; h. Zoölogisch Museum van de Gemeentelijke Universiteit, Amsterdam; i. H. S. Barlow, Y. P. Tho, pers. comm.; j. Browne 1937.

TABLE 5. Herbarium specimens of *Endospermum* showing damage and webs similar to the larval damage of *Urapteroides astheniata* figured by Browne (1937).

Species	Origin	Herbarium†	Specimen ref.
<i>E. macrophyllum</i>	Fij: Nabantini, Serua	RBG	CSIRO S1403/5
<i>E. medullosum</i>	W. Irian Jaya: Biak I.	RL	RL 961292897
<i>E. medullosum*</i> (as " <i>E. myrmecophilum</i> ")	N. Qld.: N. Kennedy, Mis- sion Beach (illustrated Fig. 1H)	RBG	B. Hyland 02050
<i>E. myrmecophilum</i>	PNG: Goldie R., Pt. Mores- by	RL	R. Pullen 3316
<i>E. myrmecophilum</i>	PNG: Brown R., 8 mi. W. of Karema	RL, RBG	R. Schodde 2665
<i>E. moluccanum</i>	N. Malu: Totedaku, Moro- tai	RBG	Kostermans 618
<i>E. moluccanum</i>	C. Malu: Ambon	RL	RL 903157173
<i>E. moluccanum</i>	Sol: SE Ranonnga	RL	BSIP 14317
<i>E. moluccanum</i>	Sol: SW Ranonnga	RL, RBG	BSIP 15640
<i>E. "nr. moluccanum"</i>	W. Irian Jaya: Sukarnapura	RBG	Kostermans & Soejang 14
<i>E. diadenum</i>	pMal: Forest Research In- stitute, Kepong, Selangor	RL	FRI 27661
<i>E. diadenum</i>	pMal: Kuala Lumpur, Se- langor	RBG	Ridley 3/3/1915
<i>E. diadenum</i>	pMal: Ulu Gombak Forest Reserve, Selangor	RBG	KFN 115660
<i>E. diadenum</i>	Bor: Kuching, Sarawak	RBG	Smythies 12517
<i>E. diadenum</i>	Bor: Kelumpang Forest Re- serve, Kunak, Sabah	RBG	SAN 79831
<i>E. diadenum</i>	SE. Bor [Kalimantan Sela- tan]: Balikpapan, Menta- wir	RBG	Saivreur 67
<i>E. "cf. macrophyllum"</i>	Bor: Meliau R., Beluran, Sabah	RL	SAN 99872
<i>E. peltatum</i>	pMal: Ulu Langit Forest Reserve. R., Selangor	RL, RBG	KFN 115652
<i>E. peltatum</i>	E. Bor [Kalimantan Ti- mur]: Sangkulirang, E. Kutei	RL, RBG	Kostermans 5854
<i>E. peltatum</i>	Phil: Surigao, Mindanao	RBG	No. 2895

† RL = Rijksherbarium, Leiden; RBG = Royal Botanic Gardens, Kew.

* Monteith & Wood (1987); G. B. Monteith, pers. comm.

trorchidium Poepp. & Endl., *Klaineanthus* Pierre ex Prain (Punt 1962), *Adenocline* Turcz., *Cladogelonium* (Schaeffer 1971), and *Suregada* (Webster 1975). The finding that *Suregada* is a uraniine host appears reassuring because, apart from *Cladogelonium*, it is the most closely related genus placed within the Adenoclineae that occurs in Madagascar (Webster 1975). *Suregada* shares few synapomorphies with *Endospermum* (Gillespie 1990) but more closely related African genera occur outside the range of *Urapteritra*.

FOODPLANT DEFENSES: ECOLOGICAL SIGNIFICANCE FOR
URANIINE SPECIALISTS

Ants

Three Australasian species of *Endospermum* (see Table 4) have a mutualistic relationship with a black ant *Camponotus quadriceps* Smith (Monteith & Wood 1987), which inhabits the hollow twigs. This relationship is reflected by the local name of *E. moluccanum* (T. & B.) Kurz in the Solomon Is.: "Ai-Aofia", or "Chief Tree", presumably due to the clearance of surrounding saplings by ants (Whitmore 1966). Uraniine larvae living on foodplants with extrafloral nectaries have adaptations to defend themselves against ants, either by living under a silken web, or by dropping off on a silken line (e.g., see Browne 1937, Gosse 1881; Fig. 1). This silk-line or silk-web behavior, also possessed by epiplemines (Hampson 1895, Holloway et al. 1987), may have facilitated specialization on plants with extrafloral nectaries by ancestral Uraniidae; all *Omphalea* and *Endospermum* spp., in common with many other Euphorbiaceae, possess leaf nectaries attracting ants. Some species of *Suregada* also have secretions exuding from the leaf axils or base of the flower buds (A. Radcliffe-Smith, pers. comm.). An interesting dichotomy occurs in Madagascar. A *Urapteritra* sp. (probably *U. piperita* (Oberthür)) from the S.W. feeds on a *Suregada* species that attracts ants (Table 2, Fig. 1G); this species possesses silk-line and silk-web feeding adaptations (L. L. Holloway, pers. comm.). *Urapteritra fasciata* feeds in the eastern rainforest on another *Suregada* species that lacks ants (Table 2); this species apparently has lost these adaptations, possessing a free-feeding lifestyle in all instars, and using a minimum of silk for attachment (D. C. Lees, pers. obs.).

In concert with silk use, it seems likely that uraniine larvae also possess a chemical deterrent as a primary defense against extrafloral nectary recruits, since visiting ants generally completely ignore uraniine larvae (observed both for *Chrysidia* and *Urapteritra* in Madagascar: D. C. Lees, pers. obs., L. L. Holloway, pers. comm.). However, the presence of ant recruits and especially ant mutualists in some *Endospermum* spp. probably slows larval maturation and evidently deters oviposition. In North Queensland, plants of *E. myrmecophilum* L. S. Smith devoid of ant mutualists (usually those in open areas) are preferentially laid on and stripped by *Alcides metaurus* (G. B. Monteith, pers. comm.). Extrafloral nectaries of *Omphalea* spp. are also particularly attractive to polistiine wasps (D. C. Lees, pers. obs. in Madagascar), which are effective predators of early instar larvae (N. G. Smith, pers. obs. in Panama).

TABLE 6. Continued.

Plant species† (Bold print: confirmed foodplant)	Uranine species‡ (Uranines confirmed to feed on <i>Surgada</i> in bold)	<i>Urapteritra fasciata</i> (Mabille)	<i>U. swats</i> (Oberthür)	<i>U. falcifera</i> (Weymer)	<i>U. montana</i> Viette	<i>U. madagassaria</i> (Mabille)	<i>U. mabillet</i> Viette	<i>U. antisanakaria</i> (Oberthür)	<i>U. piperita</i> (Oberthür)	Plant Distribution† (Bold print: <i>Urapteritra</i> syntropic)
<i>S. adenophora</i> Baill.		•	•	•	•	•	•	•	•	Mad, SE: Vohipeno, Mananjary to Mad, SE: Ft. Dauphin
<i>S. grandifolia</i> A. R-Sm.		•	•	•	•	•	•	•	•	Mad, E: Ambila-Lemaitso
<i>S. nigriticaulis</i> A. R-Sm.		•	•	•	•	•	•	•	•	Mad, E: Analamazoatra Forest
<i>S. euclideanis</i> A. R-Sm.		•	•	•	•	•	•	•	•	Mad, W: Analavelona Massif (NE Toliara); Mad, SW: Zombitsy (E. of Sakaraha);
		•	•	•	•	•	•	•	•	Mad, W-C: Isalo Massif
<i>S. capuronii</i> Léandri		•	•	•	•	•	•	•	•	Mad, C: Ihosy to Ivohibe
		•	•	•	•	•	•	•	•	Mad, W: Marosalaza Forest, 50 km N of Morondava;
		•	•	•	•	•	•	•	•	Mad, SW: Sakaraha- Toliara;
		•	•	•	•	•	•	•	•	Aniamala- Andranovory;
		•	•	•	•	•	•	•	•	R. Fiherenana Gorges NE of Sakaraha;
		•	•	•	•	•	•	•	•	Ampanihy area
		•	•	•	•	•	•	•	•	Mad, S: Angavo Massif E of Antanimara;
		•	•	•	•	•	•	•	•	E of Ambovombe; Tsimele
		•	•	•	•	•	•	•	•	Mad, W: Bemaraha;
<i>S. decidua</i> A. R-Sm.		•	•	•	•	•	•	•	•	Morondava area incl. Andranomena to N,
		•	•	•	•	•	•	•	•	Mad, SE to Tanambao Forest (R. Maharivo)
		•	•	•	•	•	•	•	•	& S to Morombe
		•	•	•	•	•	•	•	•	Mad, SW: Toliara area (incl. lower R. Fiherenana,

TABLE 6. Continued.

Uranine species*† (Uranines confirmed to feed on <i>Suregada</i> in bold)	<i>Urapteritra fasciata</i> (Mabille)	<i>U. suavis</i> (Oberthür)	<i>U. falcifera</i> (Weymer)	<i>U. montana</i> Viette	<i>U. malgassaria</i> (Mabille)	<i>U. mabillet</i> Viette	<i>U. antstanakaria</i> (Oberthür)	<i>U. piperta</i> (Oberthür)	Plant Distribution† (Bold print: <i>Urapteritra</i> sympatric)
<i>S. croizatiana</i> Léonard	•	•	•	•	•	•	•	•	Zai: Kivu Prov.
<i>S. occidentalis</i> (Hoyle) Croizat	•	•	•	•	•	•	•	•	IvC; Gha; Nig
<i>S. ivorenensis</i> (Aubrev. & Pellegr.)	•	•	•	•	•	•	•	•	IvC
<i>S. gossweileri</i> (Moore) Croizat	•	•	•	•	•	•	•	•	Zai: Leopoldville Prov.

* *Urapteritra* spp. have also been collected from the following localities where *Suregada* have not (subscripts refer to references below): *U. malgassaria*: Mad, NE; Ananalova Forest S. of Vohimar, Firanakarana Forest, Navana, near Maroantsetra; *U. mabillet*: Mad, E; Tamatave/Alahakato forests; *U. suavis*: Mad, C; Lake Mantasoa (Andrangoloka, 1389 m.); *U. montana*: Mad, C; Antarifady Forest (Ankaratra); *U. piperta*: Mad, SW; Ankilirano, Mahafaly plateau; *U. falcifera*: Ken, Nairobi; SAF, Transvaal, Heestersfontein, Limberg (Polgeitersrus dist.); "Namaqualand" (=Namibia). Note: *Chalocentrum madagascariense* Léonard, a close relative of *Suregada*, has been collected from Tsingy de Bemaraha in W. Madagascar, and Bemarivo R. in the NE (Léonard, 1938) and it might be a foodplant of *Urapteritra* (it is sympatric with *U. piperta* in Bemaraha).

† References: *Suregada* nomenclature and distribution: Croizat 1942; Radcliffe-Smith 1991 for Madagascar spp.; Léonard 1958 for West African *Suregada* spp.; Palgrave 1977 for South African spp.; Radcliffe-Smith 1987 for East African spp.; C. Lees, pers. obs. in Madagascar; c. L. L. Holloway, pers. comm.; d. Transvaal Museum (C. B. Cottrell, pers. comm.); e. National Collection, Natural History Museum, South Kensington, including Rothschild Collection.

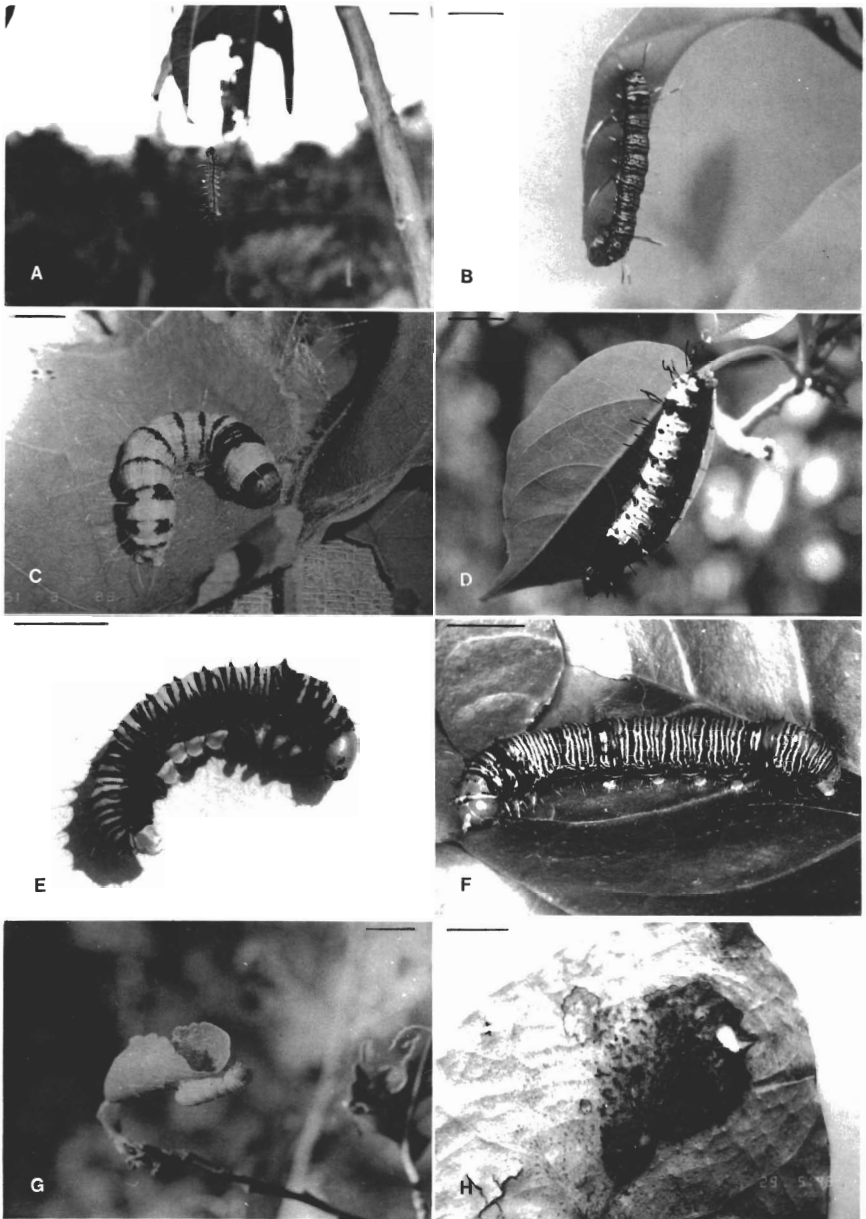


FIG. 1. Larval stages of Uraniinae. Horizontal bar = ca. 1 cm. **A.** Larva (3rd instar) of *Urania poeyi* showing silk-lining behavior on *Omphalea trichotoma*, Punta Maisi, E. Cuba, Mar 1989, L. J. Gillespie; **B.** Larva (4th instar) of *U. fulgens* on *O. diandra*, Atlantic forest, Panama, Jan 1988, D. C. Lees; **C.** Larva (5th instar) of *U. boisduvalii* on *O. hypoleuca* from Pinar del Rio, W. Cuba, Jun 1989, N. G. Smith; **D.** Larva (4th instar) of

Leaf Shape

Another foodplant defense may be leaf shape. Most species of *Omphalea* and *Endospermum* within the range of diurnal uraniines show a remarkable degree of variation in leaf form; in *Omphalea* deeply divided leaves occur on the same plant and in seedlings (Leon & Alain 1953, Smith in press a), and both peltate and non-peltate leaves occur in *Endospermum* species (Schaeffer 1971). In Madagascar, all four foodplants of *Chrysidia rhipheus* show such a range of form (D. C. Lees, pers. obs.). In the absence of other obvious specialist herbivores on these plants, it is possible such heterophylly may result from selective pressure by diurnal uraniine females that locate oviposition sites visually (see, e.g., Brown & Lawton 1991). One test of this hypothesis will be to assess leaf morphology of *Omphalea* and *Endospermum* species that occur outside the range of diurnal uraniines (as in Malesia). *Suregada* spp. in Madagascar show no such leaf shape plasticity and *Urapteritra* females there apparently oviposit nocturnally.

Laticifers

A further defense common to both *Omphalea* and *Endospermum* spp. is the presence of laticifers (Rudall in press), which bear latex that is clear or oxidizing reddish but not milky or particularly copious. However, uraniine larvae have not been observed to utilize the leaf vein-cutting behavior (disc-cutting in early instars, midrib trenching in later instars) typical of latex-feeding larvae (Dussourd & Eisner 1987). Early instars instead strip-mine the leaves, eating out the inter-vein mesophyll tissue, whereas later instars of both *Urania* and *Chrysidia* have been observed to eat, in addition to leaves and fruit, tendrils and young stems bearing latex (N. G. Smith, D. C. Lees, pers. obs.). It would thus appear that later instar uraniine larvae are equipped to deal with the chemical defenses mobilized in the latex and that this latex does not pose a major mechanical problem in terms of mouthpart coagulation. The genus *Suregada* does not possess latex at all (D. C. Lees, pers. obs.), nor laticifers of the non-articulated type typical of Croton-

←

Chrysidia rhipheus on *Omphalea*, sp. nov., Ankarana, NW Madagascar, 2 Dec 1990, L. L. Holloway; E. Preserved larva (4th instar) of *Lyssa ?macleayi* from Cape Tribulation, N. Queensland, reared by D. Kitchin 1987 from *Endospermum medullosum*, D. C. Lees; F. Larva (5th instar) of *Alcides metaurus* on *Omphalea queenslandiae* from Bamaga, N. Queensland, N. C. Coleman; G. Larva (?4th instar) of *Urapteritra ?piperita* on *Suregada decidua* showing protective spinning, Beza Mahafaly, SW Madagascar, 18 Jan 1991, L. L. Holloway; H. Silk web spinning with frass typical of *Urapteroides atheniata* on *Endospermum medullosum* specimen AQ 0000126 from North Kennedy, Queensland, 8/10/68 at RBG, Kew, D. C. Lees.

ideae (P. Rudall, pers. comm.), once again raising a question over the phylogenetic position of the genus.

Secondary Plant Compounds

Until recently, examination of *Omphalea* secondary compounds was limited to an analysis of the seed oil of *O. diandra* L., a known purgative (Cash 1908). This oil was found to contain terpenes, sesquiterpenes, acid esters, and palmitic and oleic acids (Freise 1935). Horn et al. (1987) reported that *Omphalea* leaves contain high concentrations of a class of nitrogenous compounds known only since 1976: polyhydroxy alkaloids or alkaloidal glucosidase inhibitors (AGI's) (Fellows 1985, 1989). These compounds have toxic effects on some insect herbivores and antifeedant effects on others (Fellows et al. 1986), and are of considerable interest as they form a series mimicking certain sugars. DMDP (2R,5R-dihydroxymethyl-3R,4R-dihydroxypyrrolidine), resembling fructose, and HNJ (homonojirimycin), an alkaloid previously unknown in nature (Fellows 1989), have been reported from *O. diandra* (Horn et al. 1987, Kite et al. 1988).

AGI's may function in plants as competitive inhibitors of glycosidase synthesis, perhaps blocking the sugar-detecting apparatus of generalist herbivores on palpation (Fellows et al. 1986). They are known to be sequestered selectively by *U. fulgens* adults from the larval foodplant (Kite et al. 1990). Although there is no direct evidence that AGI's are noxious to avian predators, adult *U. fulgens* are rejected by jacamars in feeding trials (P. Chai, pers. comm.).

Strong biochemical similarities between *Omphalea* and *Endospermum*, the two foodplant genera so far examined in detail, suggest a chemical basis for the adoption of a new foodplant genus (Kite et al. 1991). Thus a priority for chemical investigations is to elucidate any differences in the fate of secondary plant compounds between *Lyssa* spp. (large, brown, "nocturnal" moths) and *Alcides* spp. (diurnal, apparently aposematic moths), which feed on the same species of *Endospermum* (Table 4). Preliminary results confirm the presence of AGI's in *Suregada* and in adults of *Urapteritra* (G. C. Kite, pers. comm.).

The apparent "immunity" of diurnal uraniines to predators such as tyrannid flycatchers has not gone unnoticed (Seitz 1913). It has been suggested that the aposematic appearance of adults [perhaps also the late instar larvae] of the three diurnal genera may result from the presence of toxic secondary compounds derived from the larval foodplant (Coleman & Monteith 1981). The mimicry of the New Guinean uraniine *Alcides agathyrsus* (Kirsch) by both sexes of *Papilio laglaizei* Depuiset (Jordan 1897, Poulton 1931) suggests adult toxicity directed towards avian predators in at least one uraniine.

Plant Chemistry and Uraniine Migration

Induced changes in larval foodplant secondary chemistry (Smith in press a) are currently being investigated as a possible ecological correlate of mass migration, a frequently noted behavioral feature in all three genera of diurnal uraniine adults (Smith 1972 for *Urania*), although migration also may occur in nocturnal genera. Captures aboard ships also suggest that *Lyssa* migrates (Altena 1953:39). Both species of the genus *Chrysidia* have been observed migrating in large numbers (Griveaud 1959, Lucas 1876, Pinhey 1975:79 and pers. comm.), as have populations of *Alcides* sp. in New Britain (P. Jolivet, pers. comm.) and *A. metaurus* in Queensland, which form large roosts on trees at night (King 1826:14, Smithers & Peters 1977). The large biomass of individual uraniine species that fly hundreds of miles in these spectacular mass migrations (Smith 1982, 1983), and the fact that *Urania* and *Chrysidia* larvae eat *Omphalea* flowers and fruit as well as defoliating entire plants (N. G. Smith, D. C. Lees, pers. obs.), suggest that these moths have a considerable negative impact on the reproduction of their foodplants and on the survival of seedlings (Dirzo 1984). A reduction in growth rate measured over a five year period in *Endospermum didennum* trees grown in Malaysian timber plots was attributed to the periodic mass herbivory by *Urapteroides astheniata* (Browne 1937, 1938, 1940). Thus attacked plants are likely to respond by changes in secondary compounds or nutrient levels (Smith 1983).

Morphologically and behaviorally distinct migratory and sedentary phases occur in *U. fulgens* (Smith in press b), and Smith (1982:342, 1983:83) proposed that an induced chemical response in the foodplant in response to repeated herbivory by several larval generations might provide the cue for production of migratory morphs. However, artificially simulated mechanical damage to foodplants has produced no clearcut pattern in induction of morph type (Smith 1982, in press a). Nevertheless, in Mexican as well as Central American foodplants of *U. fulgens* (Table 3), some individual plants after a sustained period of damage appear to become toxic to larvae causing high mortality levels (Smith 1982, 1983, R. Dirzo unpubl.). Experiments indicate that density changes are not the sole factor triggering the production of migratory morphs (Smith 1982), but if migratory phases are induced by a nutrient or chemical change, the mechanism remains unknown. There is at present no evidence that AGI's are involved in such a trigger, should one exist at all (Kite et al. 1991).

Although how it is mediated remains unknown, migration in uraniines presumably is selected for as a result of the widely oscillating population dynamics of strictly monophagous genera (Catala 1940:12, 13). Lack of intensive herbivory over long periods may result in lowered

moth-induced defenses (Smith 1983:81), allowing buildups in moth populations that culminate in mass local emergences; excessive defoliation would then be a critical factor. Sudden appearances of swarms of fresh individuals have been reported frequently for uraniines (Gosse 1851, Townsend 1893, Browne 1940, Smith 1972, Coleman & Monteith 1981, Smith 1982). Apparent population crashes might result from larval populations reduced by induced chemical defense, but are more likely caused by emigration of adults. Parasitoids, which also might be affected by foodplant allelochemistry, probably also play a role in uranine population dynamics: tachinid flies, but not Hymenoptera, have been reared from the pupae of *U. fulgens* (Smith in press a) and *Urapteroides astheniata* (Browne 1937), and hymenopteran parasitoids are known for *Chrysidia rhipheus* (A. Peyri ras, pers. comm.).

EVOLUTION OF DIURNALITY AND FOODPLANT SPECIALIZATION: PHYLOGENETIC HYPOTHESES

An evolutionary hypothesis that is in accord with the phylogeny of Uraniinae based on morphological characters and which explains foodplant exploitation patterns within the Uraniinae is that feeding on *Endospermum*, the only foodplant common to both nocturnal and diurnal uraniines, is plesiomorphic within the group. Once the biochemical leap was made to *Omphalea*, stockpiling of additional (as yet undefined) plant secondary compounds sequestered in the adult stage may have predisposed the moths (presumably through avian selection) to become obligately diurnal. Such a sequence has been suggested to have occurred within the Arctiidae (Rothschild et al. 1979:313, 314).

Diurnality

The term obligate diurnality for the three brightly colored genera is applied here because they have been observed in captivity and in the wild to be quiescent throughout the night, roosting nocturnally *en masse* during migrations (N. G. Smith, pers. obs. for *Urania*; D. C. Lees, pers. obs. for *Chrysidia*; Eltringham 1924a, Catala 1940:12, Paulian 1951:58, Coleman & Monteith 1981). However, crepuscular activity has been reported for *Alcides* (Boisduval 1874) and *Urania* (Skutch 1970) and both *Urania* and *Chrysidia* females oviposit in late afternoon or into dusk (Smith in press a, Alayo & Hernandez 1981, D. C. Lees, pers. obs. in Madagascar). As in the Arctiidae (Rothschild et al. 1979:313), nocturnality is best considered a plesiomorphy for the Uraniidae. Most if not all epiplemines, microniines, and uraniines, apart from the obligately diurnal uranine genera, appear to be nocturnal or crepuscular or both. *Lyssa* spp. do not seem to be exclusively nocturnal. Although individuals are frequently attracted to lights at night (Altena 1953), *L.*

zampa in Malaysia frequently may be seen flying spontaneously in the forest during the day (J. D. Weintraub, pers. comm.), behavior also recorded for *L. patroclus* (L.) (Altena 1953). One species, *L. mutata* (Btlr.) from the Solomon Is., which possesses a sheen of iridescent purple scales on the wings, has been observed flying freely at midday in a forest clearing, and being attacked by birds (Carpenter 1937). Conversely, the diurnal species *U. fulgens* (or *U. poeyi* H.-S.) occasionally has been observed coming to lights at night in Jamaica (Lewis 1944, 1945, Brown & Heineman 1972:12, T. Turner, unpubl.). *Cyphura* and *Urapteroides* [along with *Urapteritra*] are primarily nocturnal, and so the trend in development of diurnal behavior is in accordance with the morphologically derived cladogram (Fig. 2). However, this interpretation could be criticized on the basis that the hearing organs themselves probably are functionally modified for diurnal, nocturnal, or crepuscular predator evasion.

Uraniine Phylogeny

A phylogeny of the Uraniinae (Fig. 2) was constructed using published morphological (tympanic organ structure and larval morphology) apomorphies summarized in Table 7. Larval foodplants and diurnality have been added to allow interpretation of their roles in the evolution of the group. Larval foodplant patterns are consistent with the morphological data: each generic foodplant relationship need have arisen just once within the Uraniinae, with *Endospermum* the more plesiomorphic relationship within the group (excluding *Urapteritra*). Loss of *Endospermum* as foodplants in *Urania* and *Chrysidia* can be explained as a simple consequence of vicariance. Note that *Alcides* emerges as the most basal diurnal uraniine, with *Urania* and *Chrysidia* as sister taxa. The plesiomorphic status of *Alcides* was hinted at by Catala (1940:237, 258), perhaps somewhat unconvincingly on the basis of extensive temperature shock experiments in *C. rhipheus* pupae that produced adult color patterns similar to *Alcides aurora*.

The position of *Urapteritra* is uncertain because nothing has been published on the tympanic organs, although genitalic characters have been examined (Viette 1972). Similarity in wing shape and patterning to *Urapteroides* and *Cyphura* combined with the minor difference in hindwing venation suggests that *Urapteritra* may be basal to the white group of uraniines. As *Suregada* has its greatest species concentration in Indo-Australasia, it seems likely that *Cyphura*, or *Urapteroides*, or both, may feed on *Suregada* in this region. Because *Chrysidia* does not appear to feed on *Suregada* in Madagascar (D. C. Lees, pers. obs.), this genus seems unlikely to be one of the foodplants of the diurnal clade. It seems more parsimonious to assume that *Suregada* was added

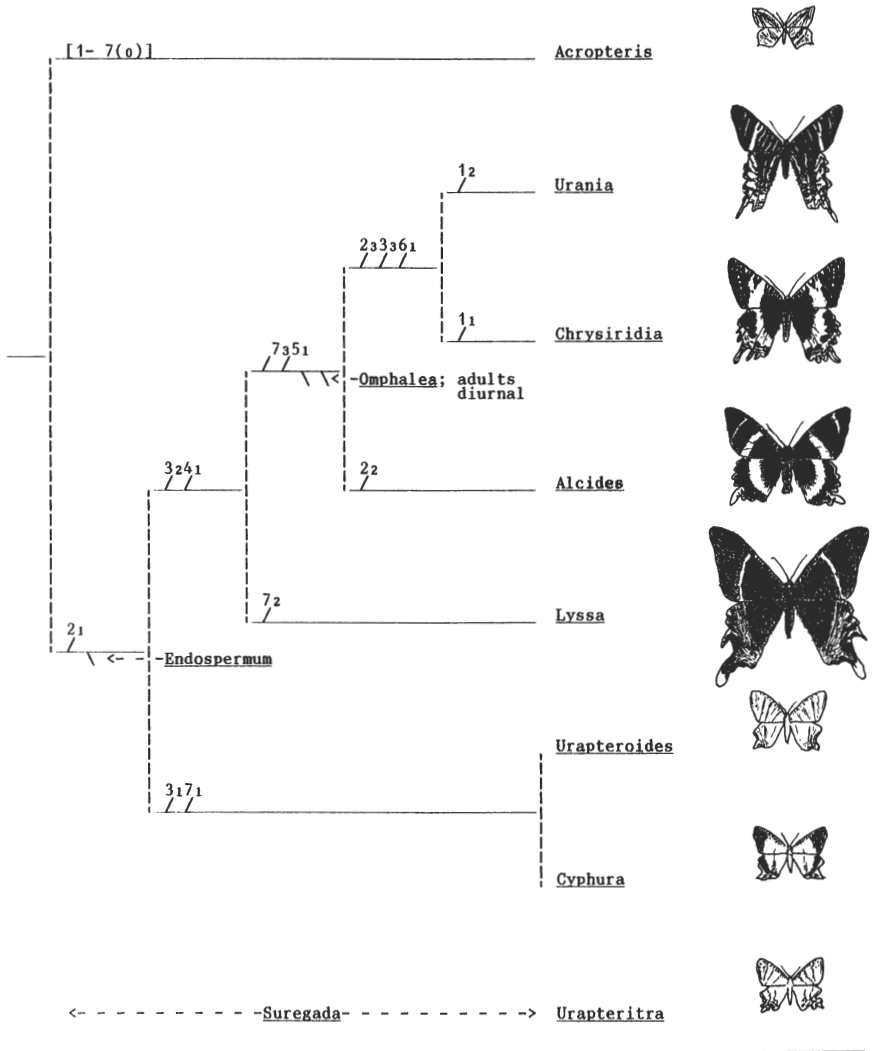


FIG. 2. Phylogeny of the Uraniinae based on larval setal morphology (Bell 1901 MS, Browne 1937, Kühn 1887, Coleman & Monteith 1981, Eltringham 1924a, Guppy 1907) and hearing organ (abdominal and thoracic) morphology (Sick 1937, Minet 1983) (characters 1-7, Table 7). Tree rooted on *Acropteris* (Microniinae) as an outgroup. A computer run using Hennig 86 (J. S. Farris) using the ie option produces one tree, length 14, consistency index 1.00, retention index 1.00. Unordering of multistate characters in the computer run makes no difference to the cladogram topology (characters are arbitrarily numbered). Foodplant associations and adult obligate diurnality are added to this tree. Species drawn as representatives of each genus are: *Acropteris ciniferaria* (Walker), *Urania leilus*, *Chrysidia rhipheus*, *Alcides agathyrsus*, *Lyssa curvata*, *Urapteroides atheniata*, *Cyphura multistrigaria* and *Urapteritra piperita* (*Urapteritra* is not included in the analysis due to absence of published data). Scale bar = 10 cm.

TABLE 7. Character matrix for Fig. 1.

Taxa†	Character number‡						
	1	2	3	4	5	6	7
ACRO	0	0	0	0	0	0	0
URAN	2	3	3	1	1	1	3
CHRY	1	3	3	1	1	1	3
ALCI	0	2	2	1	1	0	3
LYSS	0	1	2	1	0	0	2
CYPH	?	1	1	0	0	0	1
URAP	0	1	1	0	0	0	1

† Code: ACRO = *Acropterus* (outgroup); URAN = *Urania*; CHRY = *Chrysidia*; ALCI = *Alcides*; LYSS = *Lyssa*; CYPH = *Cyphura*; URAP = *Urapteroides*.

‡ Details of characters:

Character state:	apomorphy			plesiomorphy
	3	2	1	0
Character:				
1. Larval last instar spatulate setal state*	—	024 0000 00220	088 6666 66664	All simple.
2. ♀ metathoracic epimeron: devt. type of tympanal cover#	Ventrally lobed LC.	Unlobed LC.	Unlobed AC.	Not developed.
3. ♀ tympanal case: ratio of dorso-ventral height to that of sternite 2	ca. ¼	≤ ½	ca. ½	≥ ¾
4. ♀ tympanum: depth	—	—	Close to surface.	Relatively sunken.
5. ♀ tympanum: angle to body axis	—	—	Very acute (close to plane of sternite).	Perpendicular.
6. ♀ tympanal cases: 3- and 2-dimensional shape	—	—	Hemispherical; oval.	Flattened; nearly circular.
7. ♂ tympanum: angle to counter-tympanum	ca. 60°	ca. 70°	ca. 80°	ca. 120°

* Spatulate setal formulae (spatulate setae per segment) are derived from *Urania leilus* (Cuppy 1907) and *Chrysidia rhipheus* (Eltringham 1924a). Other species may differ: indeed in *U. boisduvalii*, the spatulate condition is lost (Macleay 1834), perhaps concomitant with a change to nocturnal feeding behavior (the larva is concealed by day under a web).

= modifications of metathoracic epimerons include central oval areas forming shallowly concave (protective and/or sound-reflective) tympanal covers, either lateral to the tympana, entirely covering the tympanic organs and orientated inwardly (LC) or anterior to the tympana and orientated posteriorly (AC). See Sick (1937) for figures.

to the foodplant repertoire of an independent clade than lost by sympatric ancestors of the diurnal clade. In this respect it is critical to know whether *Lyssa* feeds on *Suregada*: such a discovery might support a change in the topology of the cladogram. The evidence for *Endospermum* as the most plesiomorphic foodplant of the Uraniinae seems the most convincing, as vicariance could also account for its loss by *Urapteritra*.

Although the three known foodplant genera are not closely related enough to provide a useful generic phylogeny, once species phylogenies of each uraniine genus and the foodplant genera are clarified, it will be of interest to compare these trees. For example *Chrysidia* and *Urania*, sister taxa and the most derived uraniine genera, feed on a monophyletic group of relatively advanced Neotropical and Afrotropical species of *Omphalea* (Gillespie 1990; see Table 3). Also, *Alcides* (at least in Australia) retains the plesiomorphic uraniine foodplant re-

lationship with *Endospermum* as well as feeding on *Omphalea queenslandiae* Bailey, a representative of an apparently plesiomorphic clade of three Indo-australasian *Omphalea* species (Gillespie 1988, 1990, and pers. comm.), which retains the plesiomorphic euphorbiaceous trait of well developed sepal disc glands in the male flower (Airy Shaw 1966, 1969). Although the foodplant relationships of the diurnal genera appear broadly consistent with the phylogeny shown in Fig. 2, it seems at this stage unlikely that parallel cladogenesis at the species level will be demonstrable for individual foodplant genera. For example, there does not seem to be any clearcut pattern of foodplant specialization between penninerved and palmatinerved Afrotropical and Neotropical *Omphalea* species (Table 3). Recent comparisons of phylogenies of phytophagous specialists and their foodplants generally have suggested sequential colonization (Drummond 1986, Miller 1987) rather than parallel cladogenesis or even diffuse coevolution (see Mitter & Brooks 1983) although there are exceptions (Farrell & Mitter 1990).

Biogeography

Biogeographic analysis of the moth/foodplant distributions may be useful to interpret the phylogeny presented in Fig. 2. For example, the absence of nocturnal uraniines in the Neotropics might simply reflect the absence of *Endospermum* or *Suregada* in western Gondwanaland. This perhaps supports an eastern (Australasian) origin for uraniines. As with epiplemines, greatest species concentrations of uraniines are found in Indo-Australasia. A scenario based on vicariance is that ancestral Uraniinae specialized on *Endospermum*, and prior to the final breakup of Gondwanaland the diurnal lineage colonized an ancestral form of *Omphalea* (most likely via an oviposition response to a common allelochemical). Colonization of *Suregada* by an ancestor of *Urapteritra* might have occurred independently before the separation of Australasia with Africa and Madagascar. Evidence for this may be found in the foodplant associations of Australasian species of *Urapteroides*, *Cyphura*, or both. Vicariance acting on the original colonization of the foodplant genera by the ancestral uraniines seems sufficient without the need to invoke long-distance dispersal, including use of land bridges. One difficulty is that euphorbiaceous pollen is known only from the early Miocene (Muller 1984) whereas the above vicariance explanation requires this foodplant association to be in place not only before the final separation of Africa and South America (ca. 100 mBP) but prior to the separation of Australasia from Africa.

Nevertheless, a Gondwanaland origin for uraniines seems compatible with the present evidence. Altena (1953) suggests that the least derived *Lyssa* species occur to the east of its Indo-Australasian range and the

same may be true of *Urapteroides* (D. C. Lees, unpubl.). In this interpretation, both genera apparently managed to bridge the Wallace line to Sulawesi; *Alcides* evidently did not [although two specimens of *A. orontes* (L.), perhaps vagrants, exist in the NHM, South Kensington labelled "N. Celebes": Table 4]. *Alcides* is represented in North and South Maluku [Moluccas] (Table 3), where *Omphalea* has not been recorded, but where it should certainly be checked for. *Endospermum moluccanum* (Teijsm. & Binnend) Kurz is a likely foodplant for *A. aruus* (Felder), *A. orontes* and *A. cydnus* (Felder) (Table 4), but it is interesting that *Alcides* apparently has not managed to colonize the species of *Endospermum* and *Omphalea bracteata* (Blanco) Merr. that occur a little further west in Sulawesi. The lack of a diurnal uraniine within the range of *O. bracteata* (Table 3) might in fact be interpreted as further evidence for the Gondwanaland (eastern) origin of uraniines. Furthermore, it is possible that *Omphalea* is a recent colonist of South-East Asia via seed dispersal on ocean currents since the merging of the Asian and Australian plates. The occurrence of just one variable species of *Omphalea* throughout South-East Asia (Gillespie 1990) supports this hypothesis. Tentative evidence suggests that *Urapteritra* is a relatively recent colonist of East Africa from Madagascar, the center of diversity of *Urapteritra*, since *Suregada* species also occur in West Africa, where *Urapteritra* does not occur (Table 6).

ALTERNATION OF LARVAL FOODPLANTS:

IMPLICATIONS FOR CONSERVATION OF MIGRATORY URANIINES

Conservation of uraniines has as much merit on aesthetic grounds as, for example, conservation of papilionids, but has received relatively little attention, despite the fact that the moths are localized in many of the world's most threatened and diverse tropical habitats.

An interesting feature of most diurnal uraniines is their reliance on two or more geographically isolated larval foodplant populations between which they seasonally migrate, often in huge numbers. This certainly includes *Urania fulgens*, *U. boisduwalii* Guérin, *U. poeyi* (H.-S.), *Chrysidia rhipheus* and *Alcides metaurus* (Table 3). *Chrysidia rhipheus* in Madagascar is a particularly good example of alternate larval foodplant dependence: adults migrate between populations of three different *Omphalea* species in dry deciduous forest in the west and one rainforest species in the east (Table 3; D. C. Lees, unpubl. data; Griveaud 1959 mentions west-east migrations). Although western foodplant populations (deciduous trees) are protected by reserves in areas on limestone karst, the *Omphalea* species in the east, being the sole evergreen foodplant, is probably crucial to the moth's continued survival, but this species occurs in widely scattered populations mostly

outside reserves and is threatened by deforestation (D. C. Lees, unpubl.; Catala 1940:6, 7, 13).

Coupled with the frequently reported wide fluctuations in the size of local populations, dependence on alternate foodplants probably renders island uraniine populations particularly vulnerable to environmental stress (e.g., hurricanes and habitat loss) and, eventually to inbreeding. Sadly, the most spectacular *Urania* species, *U. sloanus* (Cramer) from Jamaica, was last reported as long ago as 1894 or 1895 (Lewis 1944, Perkins 1944) and is likely to be extinct (T. Turner, unpubl.). Although habitat loss in Jamaica may have been a factor in its demise, substantial tracts of primary forest still remain. The reported foodplant of *U. sloanus* on the North coast at Ocho Rios, *Omphalea triandra* L. (Gosse 1881: see Table 3) apparently is still widespread in wet forest on limestone in the island (Adams 1972). However, it is likely that that moth also feeds on *O. diandra*, reported, although not recently, from Portland County (Adams 1972, Hemsley 1885), a former locality for the moth (Townsend 1893). Periodic swarms of moths at flowering trees in the Blue Mountains of Portland were intervened by years of great scarcity (Townsend 1893). The population of *U. sloanus* apparently crashed below a sustainable level, perhaps a victim of loss of one of its larval foodplants.

The insular Cuban endemic *U. boisduvalii* (Smith in press b), whose appearance and morphology indicate long isolation from continental *Urania* populations, may also be at risk; the limestone "Mogote" stacks of Pinar del Rio in Western Cuba, now fortunately a biosphere reserve, appear crucial to its survival, but populations of its alternate foodplant on northern coastal limestone are greatly diminished (N. G. Smith, pers. obs.). The other Cuban species, *U. poeyi*, apparently also uses alternate foodplants because it migrates between localities for *O. diandra* in N.E. Cuba and *O. trichotoma* M.A. in E. Cuba (L. R. Hernandez, pers. comm.). This population probably represents a more recent colonization of the island from Central America; adult specimens and recent photographs of larvae (Fig. 1A; Table 2, ref. 2) suggest it is conspecific with *U. fulgens*. *Urania* specimens taken occasionally in Jamaica this century appear to be migrants, possibly *U. poeyi* from Cuba (Lewis 1944, T. Turner, unpubl., M. J. C. Barnes, pers. comm. with slide). Strikingly, in contrast to Cuba, no *Urania* has been reported for Hispaniola, despite the presence of two endemic and one introduced species of *Omphalea* (Table 3). Perhaps this is due to extinction resulting from loss of larval foodplant; e.g., *O. commutata* M.A. is a casualty of deforestation in Haiti and may survive now only on Gonaives Island (L. J. Gillespie, pers. comm.).

ADULT RESOURCES OF THE URANIINAE AND
THEIR ECOLOGICAL SIGNIFICANCE

Many recent studies on the chemical ecology of Lepidoptera have revealed the significance of compounds in adult foods, such as pyrrolizidine alkaloids in nectar of Asteraceae and Boraginaceae, to the reproductive success and anti-predator defense systems of these insects, especially the Danainae, Ithomiinae, Arctiinae, and Ctenuchiinae (Ackery & Vane-Wright 1984, Brown 1984, Boppré 1986, Goss 1977). As a basis for the future study of the chemical ecology of adult uraniines, known adult resources are documented here (Table 8).

Our survey of *Urania*, *Chrysidia*, and *Alcides* indicates that visual cues play a large role in nectar source selection. All diurnal species prefer white or whitish-yellow flowers. Most flowers visited are also densely filamented, with projecting conspicuous stamens, imparting a "bottle-brush" appearance, particularly those in the Leguminosae: Mimosoideae, Myrtaceae, and Combretaceae, or else are composed of clusters or panicles of small flowers (Table 8). *Urania fulgens* adults are readily attracted to white cotton wool balls soaked in sugar solution, useful to feed them in the laboratory and field. By no means all white flowers elicit a response; the flowers and floral bracts of *Omphalea oppositifolia* in Madagascar are white and showy, but adults of *Chrysidia rhipheus* were never seen to visit them (D. C. Lees, pers. obs.). *Lyssa* adults appear to be fruit specialists; Ribbe observed them on putrefying bananas (Pfeiffer 1925:127), on which *L. zampa docile* (Btlr.) has also been photographed feeding at night (Yong 1983:13). Semper (1896-1902:598) observed that they come to flowering trees in the evening.

Nectar sources may play an important role in the reproductive or defense ecology of uraniines. Species of the genus *Inga* Scop. (Leguminosae: Mimosaceae), an important nectar resource in the Neotropics, are extremely attractive to *Urania* moths during their short flowering period, as well as to many papilionid, pierid, and heliconiine butterfly species (D. C. Lees, pers. obs.). A sample of moths taken from an *Inga* sp. in Peru showed a predominance of males of *U. leilus* (L.) compared with a *Combretum* sp. flowering nearby (Table 9). This result agrees with observations of migrating *U. fulgens* on an *Inga* sp. filmed in Panama (Table 10) where males constituted about 72-83% of readily sexed individuals. This apparent sex bias in flower-visiting *Urania* has yet to be explained, but may result from differential exploitation of nectar chemicals.

Flowers of at least 13 species of *Inga*, although rich in amino acids, lack pyrrolizidine alkaloids (S. Koptur, pers. comm.). There is at present

TABLE 8. Adult nectar resources of Uraniinae. Arrangement of plant families follows Cronquist (1981); arrangement of genera and species in alphabetical order; flower color observed given (bold print) or obtained from miscellaneous botanical treatments [w = white, y = yellow, o = orange, g = green, p = pink, v = violet, r = red]; S = densely Staminate/filamented flowers; C = flowers in dense Clusters or panicles. Confirmed records shown in bold. Locality abbreviations as in Tables 2, 3, 4 and 6 plus Sur = Surinam; CR = Costa Rica; in cap = captivity (*U. leilus* from Trinidad).

Family Species	Nectar source	Color	C/S	Taxon nectaring†					Locality	
				<i>U. sloanus</i> (Cramer)	<i>U. fulgens</i> Walker	<i>U. leilus</i> (L.)	<i>Chrystridia rithpeus</i> (Drury)	<i>C. croesus</i> (Cestaecker)		<i>Alcides metaurus</i> (Hopffer)
Lauraceae										
<i>Persea americana</i> P. Mill (= <i>gratissima</i>)		w-g/y	C	•	1	•	•	•	•	Pan
<i>Ocotea</i> sp.		w		2	•	•	•	•	•	Cub
Theaceae		y	C	•	4	•	•	•	•	Jam CR
<i>Camellia chinensis</i> Kuntze		w + y	S	•	•	•	5	•	•	Mad
Capparaceae		w-p		•	•	6	•	•	•	In cap
Rosaceae		w	S	•	•	•	7	•	•	Mad: Tana
<i>Eriobotrya japonica</i> Lindl.		y-o	?	•	8	•	•	•	•	Pan
Caesalpinaceae										
<i>Pterocarpus ?offinialis</i> Jacq.										
Mimosaceae										
<i>Acacia</i> spp.		w	S	•	•	•	•	•	•	9
<i>Albizia</i> sp.		w	S	•	10	•	•	•	•	Qld Pan

TABLE 8. Continued.

Family Species	Nectar source	Color	C/S	Taxon nectaring†					Locality		
				<i>Urantia boisduvalii</i> (Guérin)	<i>U. sloanus</i> (Cramer)	<i>U. fulgens</i> Walker	<i>U. leilus</i> (L.)	<i>Chrystridia rhyphus</i> (Drury)		<i>C. croesus</i> (Gerstaecker)	<i>Aldes metaurus</i> (Hopffer)
Apocynaceae											
<i>Aspidosperma sessiliflorum</i> M.A.		w-y	?	•	•	•	17	•	•	•	Trin
Solanaceae											
<i>Cestrum diurnum</i> L.		w	C	18	•	•	•	•	•	•	Cub
Boraginaceae											
<i>Cordia ?cylindrostachya</i> R. & S.		w	C	•	•	•	19	•	•	•	Trin
Ehretiaceae											
<i>Ehretia tinifolia</i> L.		w	C	18	•	•	•	•	•	•	Cub
Verbenaceae											
<i>Lantana camara</i> L.		w-p	C	•	•	•	•	•	20	•	Ken: Mombasa In cap
			C	•	•	•	6	•	•	•	In cap
			C	•	•	•	•	•	•	21	Qld garden
			C	22	•	•	•	•	•	•	Cub
Buddlejaceae											
<i>B. fallowiana</i> Balf & Smith		v	C	•	•	•	6	•	•	•	In cap
<i>Buddleia madagascariensis</i> Lam.		y	C	•	•	•	6	•	•	•	In cap
Anacardiaceae											
<i>Mangifera indica</i> L.		w-g	C	•	•	•	•	•	20	•	Ken: Mombasa Jam
				•	•	•	•	•	•	•	•
				22	•	•	•	•	•	•	Cub

TABLE 8. Continued.

Family Species	Nectar source		Color	C/S	Taxon nectaring†					Locality
	<i>U. sloanus</i> (Cramer)	<i>U. fulgens</i> Walker			<i>U. letus</i> (L.)	<i>Chrystridia rhipheus</i> (Drury)	<i>C. croesus</i> (Gerstaecker)	<i>Alcides metaurus</i> (Hopffer)		
Rubiaceae										
<i>Ixora</i> sp.			O-F	•	•	•	•	•	•	Trin
Asteraceae										
<i>Eupatorium pauciflorum</i> Rafin			w	C	•	•	•	•	•	Sur: Paramaribe
Areaceae										
<i>Roystonea regia</i> O. F. Cook			w-y	C	22	•	•	•	•	Cub: Pinar del Rio

† References: 1. N. C. Smith, pers. obs.; 2. Gundlach 1881:284-285; 3. Gosse 1851; 4. Skutch 1970 (author notes that nearby yellow flowers of *Cassia spectabilis* and red trumpets of *Spatheodea campanulata* ignored); 5. B. Jacsó, pers. comm.; 6. D. C. Lees, pers. obs.; 7. Sibree 1915:110 (as blue-gum and loquat); 8. Lundy 1953 (as dragon blood tree and ragoon creeper); 9. C. Sankowsky, pers. comm.; 10. Smith 1982 (*Albizia* as *Leucaena*); Skutch 1970: 11. BBC TV [*Butterflies in Australia*] documentary, Mar. 1989; 12. B. Courtin, pers. comm.; 13. Bealden & Broedien 1970: 14. BBC, TV, "Through Animal Eyes", Feb. 1985; 15. T. Grant, pers. comm.; Pinhey 1975, pers. comm.; [*Terminalia* and *Mangifera* recorded as larval foodplant-adult foodplants?]; 16. Cabala 1940: 17. Quesnel 1975 (author notes that nearby purple flowers of *Lonchocarpus punctatus* [= *L. violaceus* H. B. & K.] ignored); 18. Macleay 1884; 19. Guppy 1907 (as black sage); 20. D. C. Sevastopulo, pers. comm.; 21. A. S. Wheeler, pers. comm.; 22. L. R. Hernandez, pers. comm.; 23. Gosse 1880; Lewis 1944.

TABLE 9. Numbers of *Urania leilus* at flowers in S. E. Peru (D. C. Lees). Bushes were 5–10 m apart; time of sampling was 0700–1230 h each day (the bushes did not flower synchronously). Only netted individuals were sampled and their sex determined by the presence or absence of a prothoracic leg hair brush borne and extruded only by males. Expected frequencies are shown in parentheses on the basis of equal sex ratios.

Flower	Date	No. males (no. expected)	No. females (no. expected)	Total
<i>Inga</i> ? <i>quaternata</i> Poepp. & Endl. (Mimosaceae)	11 Oct 86	7 (4)	1 (4)	8
<i>Combretum laxum</i> Jacq. (Combretaceae)	15 Oct 86	5 (4.5)	4 (4.5)	9
Total		12	5	17

H₀: No. males = no. females at *Inga*.

H₁: No. males > no. females at *Inga*.

Chi-squared (1 tailed, 1 df) = 4.625, P < 0.025, H₀ rejected.

no evidence that *Urania* moths use any plant secondary compounds in nectar for defense, despite the fact that their range of nectar sources does include *Eupatorium* (Table 8) and some Boraginaceae, noted pyrrolizidine alkaloid sources (Brown 1984). However, the importance of amino acids in the competitive mating systems of many Lepidoptera is now better understood (Goss 1977, Drummond 1984), and could explain the skewed sex ratios on *Inga*, if males visit *Inga* flowers to replenish proteins transferred to the females during mating. Amino acids such as proline play an important role in flight metabolism of migrating moths, and the presence of multiple spermatophores in the much heavier migrating females (Smith in press a) is consistent with the hypothesis that male investment in reproduction includes a contri-

TABLE 10. Sexes of migrating *Urania fulgens* filmed at the flowers of an *Inga* sp. in Panama (Margarita, Colon Prov.), September 1983 (N. G. Smith). Six samples (A–F) were taken from a 16 mm film (speed 24 frames per minute), total duration 7.4 minutes. Each sample consisted of advancing the film frame by frame until 10 frame samples were counted. The frames with moths the least agitated were counted, and individuals assigned a sex only where at least two of three sexually dimorphic criteria of shape, size, and wing bar coloration (Smith 1982) were clearly visible. Samples A to F are not assumed to be independent. Sex ratio of individuals in the migration appeared to be 1:1.

Sample	No. of males	No. of females	% males	No. not sexed	Total	% males of total
A	211	63	77.0	59	333	63.4
B	116	13	89.9	41	170	68.2
C	168	10	94.4	22	200	84.0
D	119	29	80.4	17	165	72.1
E	228	79	74.3	33	340	67.1
F	268	54	83.2	28	350	76.6
Mean			83.2			71.9

bution of energy for female flight (and thus dispersal ability) as well as for egg production.

Urania males are attracted to urine-soaked sand and sweat from clothes (D. C. Lees, pers. obs. for *U. leilus* in Peru), and *Alcides* spp. in Papua New Guinea participate in puddling behavior, suggesting that salts or nitrogenous compounds or both may be replenished during this activity.

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