Afrotropical mistletoe butterflies: Larval food plant relationships of *Mylothris* Hübner (Lepidoptera: Pieridae)

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**Abstract**  
A detailed list of larval food plants of *Mylothris* based on review of published records in the literature is presented. Food plants have been reported for some 23 species (40%), although in only eight species (14%) of butterflies have plants been identified to species level. The food plants represent two unrelated orders, Santalales and Polygonales, although nearly all records (93%) are from four closely related families in the former group. Within the Santalales, the family Loranthaceae, a diverse group of aerial stem-parasitic shrubs (mistletoes), is most frequently exploited. Only two species of *Mylothris*, *M. bernice* (Hewitson) and *M. rubricosta* (Mabille), which are closely related and possibly comprise a single species, are associated with Polygonaceae (Polygonales). Comparison of the morphology of the early stages of *M. bernice*, and other evidence, clearly indicates that *M. bernice/rubricosta* belong to *Mylothris* and do not represent a separate genus or sister group. Comments are made on these diverse food plant relationships within the context of a modern phylogeny of the Santalales and the evolution of parasitic plant feeding in butterflies in general. It is suggested that *Mylothris* had its major period of evolution and adaptive radiation on the Loranthaceae, probably sometime after the differentiation of most of the families or lineages in the Santalales (rather than on an earlier ancestral branch at or near the root of the Santalales evolutionary tree), and that this association has facilitated host switching multiple times. While more field data are clearly needed to ascertain the full extent of host specificity and range of mistletoe species exploited by *Mylothris*, this is unlikely to significantly change the patterns of food plant utilization seen at the higher taxonomic (ordinal and familial) levels. *Mylothris* represents one of only a few diverse groups of Lepidoptera, and insects in general, known to feed predominantly on African mistletoes.

**Keywords:** Africa, Lepidoptera, Loranthaceae, mistletoe, Mylothris, Pieridae, Polygonaceae, Santalales, Viscaceae

**Introduction**

*Mylothris* Hübner, the ‘Dotted Borders’, is a large genus of butterflies endemic to the Afrotropical Region, and represents a significant radiation within the family Pieridae. Ackery et al. (1995) recognized 55 species and numerous subspecies in their recent, comprehensive catalogue of the Region, but new taxa continue to be discovered and
described at species level (Hecq 2001). Notwithstanding the Ackery et al. (1995) faunal checklist, there are widely disparate opinions as to what level taxa constitute valid species and subspecies (compare regional taxonomic treatments between D’Abrera 1980; Berger 1981; Kielland 1990; Larsen 1991, for example), and the genus is in need of revision. Notable taxonomic complexes that remain unresolved include the M. yulei Butler group of species, the M. sagala Grose-Smith group of species, and the specific status of M. chloris/agathina and M. bernice/rubricosta, amongst others. The last taxonomic revision of the genus was by Talbot (1944), who recognized only 23 species, considerably fewer than his earlier estimate of 43 species (Talbot 1932), although the validity of Talbot’s arrangement was seriously questioned by van Son (1949) in his monograph of the South African butterfly fauna. Talbot (1944) recognized four species-groups, but van Son (1949) only two groups, according to differences in wing colour and form of the valva of the male genitalia. Clearly a detailed appraisal based on modern phylogenetic analysis of taxonomic characters, integrated with sound knowledge of ecology and life history based on field observations, is warranted.

The relationships and affinities of Mylothris have remained obscure. The adult butterflies phenotypically resemble many African species of Appias Hübner, Belenois Hübner and Dixiea Talbot, but this is almost certainly due to convergence, possibly a result of complex mimetic associations, rather than due to common ancestry. Klots (1933) placed the genus at the end of his classification of the Pieridae because he considered the genus to represent an independent lineage isolated from, or at least sister to, the rest of the Pierini, based on the presence of two unique and putatively specialized characters (synapomorphies): fore wing radial veins R3 and R4+5 being entirely fused, and a lobe-like structure on the inner wall of valva of the male genitalia. Talbot (1944), however, noted that Mylothris appeared to have a distant relationship with the Oriental–Australian genus Delias Hübner based on similarities in ecology, but felt that the pupa approximated more to that of Belenois. Trimen (1889), Holloway (1969), D’Abrera (1980), and Larsen (1991) all implied a possible relationship with Delias, pointing out a number of similarities, including larval food plant specialization, habitat distribution and flight behaviour. More recently, the late J. N. Eliot, in Corbet and Pendlebury (1992), suggested a close relationship with Delias and some genera in the Neotropical Catasticta Butler group. A recent phylogenetic analysis of the Pieridae, based on the nuclear gene EF-1α, however, has shown that the nearest relatives of Mylothris are 13 genera belonging to the Aporia Hübner, the Delias and the Catasticta groups of genera, provisionally assigned to the tribe Aporiini (M. F. Braby and N. E. Pierce, unpublished data).

Although Mylothris is distributed widely in Africa, the greatest concentration of species occurs in the region embraced by the Rift Valleys (i.e. eastern Congo, Uganda, western Kenya, western Tanzania), with a secondary peak in species richness in the mountains near the Gulf of Guinea (Cameroon) (Talbot 1944). The majority of species are limited to cool-temperate montane evergreen forest, typically between 1000 and 2000 m with at least one species occurring up to 3200 m (Talbot 1944; Kielland 1990; Larsen 1991; Ackery et al. 1995), and few have adapted to lowland forest (<500 m), savannah, woodland, open disturbed areas, and suburban environments. Very few species occur outside the continent: three species are endemic to Madagascar, one is confined to the Comoro Islands (Talbot 1944; Ackery et al. 1995), and another is limited to the south-western mountains of Arabia (Asir, Yemen) (Larsen 1984).

The larval food plants, general biology and natural history of Mylothris have been well known for some time (Trimen 1889), but there are surprisingly few species for which the
life histories have been described. Detailed information on the morphology and behaviour of the early stages is really only available for three species in South Africa, namely *M. agathina* (Cramer), *M. trimenia* (Butler) and *M. rueppellii* (Koch) (Clark 1949, 1978, 1994; van Son 1949; Pringle et al. 1994; Henning et al. 1997), although anecdotal information is available for others elsewhere in the range (e.g. Berger 1979). The usual food plants reported are mistletoes in the Loranthaceae, but plant species from at least six other families have been listed (Ehrlich and Raven 1965; van Someren 1974; Ackery 1991; Larsen 1991). Kroon (1999) provided a list of food plants for a few species of *Mylothris* in his catalogue of South African Lepidoptera, but there is no comprehensive account that lists all the plants eaten for the genus as a whole; hence, it is difficult to make broad generalizations about diet breadth, ecological preferences, and degree of host specificity within this interesting group of butterflies. Indeed, reliable information on the food plant associations of phytophagous insects forms the very basis of our understanding of co-evolution of animal–plant interactions, host specificity, species diversity, and community ecology (e.g. Ehrlich and Raven 1965; Janz and Nylin 1998; Wahlberg 2001).

The purpose of this paper is to provide an up-to-date list of the larval food plants of *Mylothris* based on a review of published records scattered in the literature. Such information is desirable as it provides a framework for studies of patterns of host plant utilization within the wider family Pieridae, as well as for comparative studies with other mistletoe-feeding pierids in South-East Asia–Australia and South America (M. F. Braby and K. Nishida, unpublished data; M. F. Braby et al., unpublished data). In addition, I provide brief descriptions of the early stages of *M. bernice* (Hewitson) and make comments on its taxonomic placement, mainly because this species is exceptional to the general pattern and is ecologically removed from others in the genus.

**Materials and methods**

Biological and entomological journals and books were surveyed to locate records of association between plants and *Mylothris* butterflies. While I consider this review thorough it is by no means exhaustive and I apologise in advance to readers for any records that may have been omitted. Most records were derived from recent secondary sources (books) that provided regional faunistic treatments for various countries, although considerable effort was made to locate primary sources (usually historical records) providing food plant data. In many cases, the historical literature was found to be inadequate, providing little more than family or an obsolete genus name. Nomenclature for butterflies follows Ackery et al. (1995), while that for plants follows Polhill and Wiens (1998) for the Loranthaceae and Viscaceae, and the Missouri Botanical Garden (2003) for the other families.

A “record” was defined as a unique butterfly–plant association. However, a large number of these (20 records, or 43%), were found to report larval food plants to only family level (as Loranthaceae), or simply as “Loranthus”. The genus *Loranthus* Jacq. is now used in the restricted sense to include only two species in Europe and Asia (B. A. Barlow, personal communication) and thus is no longer a valid generic name in the Afrotropical Loranthaceae. While many, if not all, of the records which list plants as “Loranthaceae” or “Loranthus” may indeed refer to the Loranthaceae, these records have been listed as Santalales until further evidence becomes available. Many early accounts documenting larval food plants were published when the Viscaceae were not recognized as a family distinct from the Loranthaceae. In this way, the possibility that some records may have been reported in error, and in fact refer to the Viscaceae, is minimized. With the recent
detailed publication on African mistletoes by Polhill and Wiens (1998), all species of Loranthaceae and Viscaceae can now be reliably identified to the level of genus and species. The larval food plant records of *Hevea brasiliensis* Müll. Arg. (Euphorbiaceae) and *Theobroma cacao* L. (Sterculiaceae), both for *M. yulei* in Kenya (Le Pelley 1959; Larsen 1991; Ackery et al. 1995), are considered to be in error (S. Collins, personal communication) and are not listed below. Both plants are common host trees for mistletoes in Africa (B. A. Barlow, personal communication), and the presence of early stages of the butterfly on these trees does not necessarily imply that they are in any way edible and serve as larval food plants. Indeed, in Cameroon, S. Collins (personal communication) once found many final instar larvae and pupae of *M. yulei* on the trunk of *Hevea*, suggesting that the larvae may descend from the mistletoe clumps to pupate on the host tree.

Descriptions of the final instar larva and pupa of *M. bernice* are based on material collected from Tanzania (Irundi Hill, Mufindi) by C. Congdon and I. Bampton on 21 April 2002, and kindly sent to the author for detailed examination and comparison with those published for other species of *Mylothris*. However, since previous illustrations of the pupae of *Mylothris* are insufficient for detailed comparison, I have included drawings of the pupa of *M. agathina* based on material collected from Kenya (Nairobi) by S. Collins in 2001.

### Results

*Larval food plants*

Table I summarizes the literature documenting the larval food plants recorded for each species of *Mylothris*. For each butterfly species, the plant (to species level), country and source of reference are given where this information was available. A total of 46 different butterfly–plant associations were found, although it is likely that at least 10 records are duplicates. For example, the records of *Ximenia* sp. and *Osyris* sp. listed for *M. agathina* in Kenya may in fact refer to the same species of plants recorded for this butterfly in South Africa, namely *X. caffra* and *O. lanceolata*, respectively. Furthermore, two of the records listed for *M. chloris* (Fabricius) may refer to *M. agathina* because of the taxonomic uncertainties of these two taxa (*M. agathina* is often treated as a subspecies of *M. chloris*). If these potential duplicate records are removed, the maximum number of different butterfly–plant associations is 36.

Inspection of the data in Table I indicates a general paucity of information for *Mylothris* as a whole. While food plants have been reported for some 23 species of butterfly (representing about 40% of the known species in the genus), in only eight species have the plants been identified to species level. In other words, detailed information on food plant usage is only available for about 14% of the known species. The paucity of records precludes generalizations to be made about the degree of host specificity within species. Two common and widespread species in central Africa, *M. agathina* and *M. sagala*, clearly feed on a wide range of plant genera representing two or three families within the Santalales and appear to be relatively unspecialized “oligophages”, especially *M. agathina*. The degree of specificity within other species, however, is unknown. Two fairly widespread species, *M. asphodelus* Butler and *M. rueppelli*, and the more restricted *M. trimenia* from south-eastern Africa, are recorded from only one or two species of Loranthaceae and these butterflies are possibly more specialized in their ecological requirements.
Table I. List of larval food plants recorded for species of *Mylothris* (butterfly species are listed alphabetically in the absence of a modern systematic framework for the genus).

| Butterfly species | Plant order/family | Plant genus | Plant species | Country | Reference |
|-------------------|--------------------|-------------|---------------|---------|-----------|
| *M. agathina* (Cramer) | Loranthaceae | *Agelanthus* | *kraussianus* (Meisn.) Polhill and Wiens | South Africa | Henning et al. (1997) |
| *M. agathina* | Loranthaceae | *Agelanthus* | *natalitus* (Meisn.) Polhill and Wiens | South Africa | Williams (1996) |
| *M. agathina* | Loranthaceae | *Erianthemum* | *dregel* (Eckl. and Zeyh.) Tiegh. | South Africa | Platt (1921), van Son (1949) |
| *M. agathina* | Loranthaceae | *Oncocalyx* | *quinquenervius* (Hochst.) Wiens and Polhill | South Africa | Platt (1921), Dickson and Kroon (1978) |
| *M. agathina* | Loranthaceae | *Tapinanthus* | *oleifolius* (J. C. Wendl.) Danser | South Africa | Trimen (1889), van Son (1949) |
| *M. agathina* | Loranthaceae | *Tapinanthus* | *rubromarginatus* (Engl.) Danser | South Africa | Henning et al. (1997), Pringle et al. (1994) |
| *M. agathina* | Olacaceae | *Ximenia* | *caffra* Sond. | South Africa | Henning et al. (1997), Pringle et al. (1994) |
| *M. agathina* | Olacaceae | *Ximenia* | – | Kenya | Larsen (1991) |
| *M. agathina* | Santalaceae | *Colpoon* | *compressum* Berg. | South Africa | Williams (1984, 1994), Claassens and Dickson (1986), Henning et al. (1997), Pringle et al. (1994), van Son (1949), Sevastopulo (1973, 1975, 1987), van Someren (1974) |
| *M. agathina* | Santalaceae | *Osyris* | *lanceolata* Hochst. and Steud. ex DC. | Kenya, South Africa | van Son (1949), Sevastopulo (1973, 1975, 1987), van Someren (1974) |
| *M. agathina* | Santalales | *Osyris* | “Loranthus” spp. | Kenya, Tanzania, South Africa | Larsen (1991), van Son (1949), van Someren (1974), Sevastopulo (1987), Kielland (1990), Larsen (1991) |
| *M. asphodelus* (Butler) | Loranthaceae | *Agelanthus* | *krausei* (Engle.) Polhill and Wiens | Tanzania | Congdon and Collins (1998) |
| *M. bernice* (Hewitson) | Polygonaceae | *Persicaria* | *attenuata* subsp. *pulchra* (Blume) K. L. Wilson | Tanzania | Kielland (1990) |
| *M. chloris* (Fabricius) | Santalaceae | *Osyris* | – | – | Ackery et al. (1995) |
| *M. chloris* | Viscaceae | *Viscum* | – | – | Ackery et al. (1995) |
| *M. chloris* | Santalales | “Loranthus” | – | Kenya | Larsen (1991) |
| *M. crathayi* (Butler) | Santalales | – | – | Tanzania | Kielland (1990) |
Table I. (Continued).

| Butterfly species | Plant order/ family | Plant genus | Plant species | Country | Reference |
|-------------------|---------------------|-------------|---------------|---------|-----------|
| M. jacksoni       | Santalales          | “Loranthus” | –             | Tanzania–Kenya | Kielland (1990), Larsen (1991) |
| Sharpe            |                     |             |               |         |           |
| M. kilimensis     | Santalales          | “Loranthus” | –             | Tanzania | Kielland (1990) |
| Kielland          |                     |             |               |         |           |
| M. kiusuensis     | Santalales          | “Loranthus” | –             | Zaire–Rwanda | Berger (1979) |
| Grünberg          |                     |             |               |         |           |
| M. nubila         | Santalales          | “Loranthus” | –             | Uganda  | Sevastopulo (1975) |
| (Möschler)        |                     |             |               |         |           |
| M. ochracea       | Santalales          | “Loranthus” | –             | Western-central Africa | Ackery et al. (1995) |
| Aurivillius       |                     |             |               |         |           |
| M. poppea         | Santalales          | “Loranthus” | spp.          | Uganda, South Africa | van Son (1949, van Someren (1974) |
| (Cramer)          |                     |             |               |         |           |
| M. rhodope        | Santalales          | “Loranthus” | –             | –       | Ackery et al. (1995) |
| (Fabricius)       |                     |             |               |         |           |
| M. rhodope        | Santalales          | “Loranthus” | –             | Ghana   | T. Larsen (personal communication) |
| (Mabille)         |                     |             |               |         |           |
| M. ruandana       | Santalales          | “Loranthus” | spp.          | Uganda  | van Someren (1974) |
| Strand            |                     |             |               |         |           |
| M. rubricosta     | Polygonaceae        | Persicaria  | barbata (L.) H. Hara | Kenya–Uganda | van Someren (1974); Sevastopulo (1975) |
| (Mabille)         |                     |             |               |         |           |
| M. rubricosta     | Polygonaceae        | Persicaria  | –             | Kenya, Tanzania | Ehrlich and Raven (1965), Kielland (1990), Larsen (1991) |
| (Koch)            |                     |             |               |         |           |
| M. rupeppelli     | Loranthaceae        | Tapinanthus | oleifolius (J. C. Wendl.) Danser | South Africa | Henning et al. (1997); Pringle et al. (1994) |
| (Koch)            |                     |             |               |         |           |
| M. rupeppelli     | Loranthaceae        | Tapinanthus | rubromarginatus (Engl.) Danser | South Africa | Williams (1994), Henning et al. (1997); Pringle et al. (1994) |
| (Koch)            |                     |             |               |         |           |
| M. rupeppelli     | Santalales          | “Loranthus” | spp.          | Tanzania–Kenya–Uganda, South Africa | van Someren (1974), Kielland (1990), Larsen (1991) |
| (Koch)            |                     |             |               |         |           |
| M. sagala         | Loranthaceae        | Erianthemum | dregei (Eckl. and Zeyh.) Tiegh. | Kenya | van Someren (1974) |
| Grose-Smith       |                     |             |               |         |           |
| M. sagala         | Loranthaceae        | Oncocalyx  | fischeri (Engl.) M. G. Gilbert | Kenya | van Someren (1974) |
| (Koch)            |                     |             |               |         |           |
| M. sagala         | Loranthaceae        | Oncocalyx  | sulfureus (Engl.) Wiens and Polhill | Kenya | van Someren (1974) |
| (Koch)            |                     |             |               |         |           |
| M. sagala         | Loranthaceae        | Phragmanthera | ussienisis (Oliv.) M. G. Gilbert | Kenya | van Someren (1974) |
| (Koch)            |                     |             |               |         |           |
| M. sagala         | Viscaceae           | Viscum      | –             | Kenya   | van Someren (1974) |
| (Koch)            |                     |             |               |         |           |
| M. sagala         | Santalales          | –           | –             | Tanzania | Kielland (1990) |
The plants recorded being eaten by *Mylothris* are listed taxonomically in Table II to present a deeper perspective from a botanical point of view. At the higher taxonomic levels (order, family), the food plants listed represent two unrelated plant orders, Santalales and Polygonales, but the most striking aspect is the overwhelming number of plants recorded from the Santalales (93%) compared with the Polygonales (three records, or 7%). Within the Santalales, four of the five families occurring in Africa (Olacaceae, Loranthaceae, Santalaceae, Viscaceae) are utilized as food plants, with the Loranthaceae being by far the most exploited group (65% of records for those positively identified to family level). If the 20 “Santalales” records (which refer to mistletoes in either the Loranthaceae or Viscaceae) are accepted as being Loranthaceae, as originally reported in the literature, then the frequency of host usage for this family rises to 80%. Within the Loranthaceae, plant genera from both the tapinanthoid and taxilloid groups are represented. Relatively few butterfly species are known to feed on Santalaceae and Viscaceae, and only *M. agathina* is recorded on Olacaceae. Only two closely related species, *M. bernice* and *M. rubricosta* (Mabille), are recorded associated with the Polygonales (Polygonaceae).

At the lower taxonomic levels (genus, species, subspecies), there is general lack of detailed information on the precise species of plants exploited by *Mylothris* (Table II). For instance, only 10 species representing five genera of plants have been reported for the Loranthaceae, and only the genus *Viscum* is recorded for the Viscaceae. These two families of plants are extremely diverse in Africa: the Loranthaceae are represented by 237 species in 21 genera, and the Viscaceae by 48 species in three genera (Polhill and Wiens 1998). The present records of mistletoes thus represent only a small fraction (25% of genera, 4% of species) of potentially available hosts. Given the large number of butterfly species in the genus and the high reporting rate of Loranthaceae, the range of mistletoes utilized by *Mylothris* must be considerably wider than available information indicates.
Table II. List of plants utilized by *Mylothris* (plants are listed taxonomically according to their higher classification).

| Plant order/family | Plant genus | Plant species | Butterfly species | Country          |
|-------------------|-------------|---------------|-------------------|------------------|
| Olacaceae         | Ximenia     | caffra        | *Mylothris agathina* | South Africa     |
| Olacaceae         | Ximenia     | –             | *Mylothris agathina* | Kenya            |
| Loranthaceae      | Oncocalyx   | sulphureus    | *Mylothris agathina* | South Africa     |
| Loranthaceae      | Oncocalyx   | quinquenervius | *Mylothris agathina* | South Africa     |
| Loranthaceae      | Oncocalyx   | quinquenervius | *Mylothris trimenia* | South Africa     |
| Loranthaceae      | Oncocalyx   | fischeri      | *Mylothris sagala*  | Kenya            |
| Loranthaceae      | Agelanthus  | krausei       | *Mylothris asphodelus* | Tanzania       |
| Loranthaceae      | Agelanthus  | kraussianus   | *Mylothris agathina* | South Africa     |
| Loranthaceae      | Agelanthus  | kraussianus   | *Mylothris trimenia* | South Africa     |
| Loranthaceae      | Agelanthus  | natalitia     | *Mylothris agathina* | South Africa     |
| Loranthaceae      | Tapinanthus | oleifolius    | *Mylothris agathina* | South Africa     |
| Loranthaceae      | Tapinanthus | oleifolius    | *Mylothris rueppellii* | South Africa |
| Loranthaceae      | Tapinanthus | rubromarginatus | *Mylothris agathina* | South Africa |
| Loranthaceae      | Erianthemum | drsei         | *Mylothris agathina* | South Africa     |
| Loranthaceae      | Erianthemum | drsei         | *Mylothris sagala*  | Kenya            |
| Loranthaceae      | Phragmanthera | usuiensis  | *Mylothris sagala*  | Kenya            |
| Viscaceae         | Viscum      | –             | *Mylothris chloris*  | –                |
| Santalaceae       | Colpoon     | compressum    | *Mylothris agathina* | South Africa     |
| Santalaceae       | Osyris      | lanceolata    | *Mylothris agathina* | Kenya, South Africa |
| Santalaceae       | Osyris      | –             | *Mylothris agathina* | Kenya            |
| Santalaceae       | Osyris      | –             | *Mylothris chloris*  | –                |
| Santalales “Loranthus” spp. | | | *Mylothris agathina* | Kenya, Tanzania, South Africa |
| Santalales “Loranthus” spp. | | | *Mylothris poppea* | Uganda, South Africa |
| Santalales “Loranthus” spp. | | | *Mylothris ruandana* | Uganda |
| Santalales “Loranthus” spp. | | | *Mylothris rueppellii* | Tanzania–Kenya–Uganda, South Africa |
| Santalales “Loranthus” – | | | *Mylothris chloris* | Kenya |
| Santalales “Loranthus” – | | | *Mylothris jacksoni* | Tanzania–Kenya |
| Santalales “Loranthus” – | | | *Mylothris kitwensis* | Zaire–Rwanda |
| Santalales “Loranthus” – | | | *Mylothris nubila* | Uganda |
| Santalales “Loranthus” – | | | *Mylothris ochracea* | Western-central Africa |
| Santalales “Loranthus” – | | | *Mylothris rhodope* | – |
| Santalales “Loranthus” – | | | *Mylothris spica* | Cameroon |
| Santalales “Loranthus” – | | | *Mylothris sulphurea* | – |
| Santalales – | – | | *Mylothris crawshayi* | Tanzania |
| Santalales – | – | | *Mylothris kilimensis* | Tanzania |
| Santalales – | – | | *Mylothris rhodope* | Ghana |
| Santalales – | – | | *Mylothris sagala* | Tanzania |
| Santalales – | – | | *Mylothris schumannii* | Kenya |
| Santalales – | – | | *Mylothris similis* | Tanzania |
| Santalales – | – | | *Mylothris talboti* | Tanzania |
| Santalales – | – | | *Mylothris yulei* | Kenya, Tanzania |
| Polygonaceae      | Persicaria | barbata       | *Mylothris rubricosta* | Kenya–Uganda |
| Polygonaceae      | Persicaria | attenuata     | *Mylothris bernice* | Tanzania |
| Polygonaceae      | Persicaria | –             | *Mylothris rubricosta* | Kenya, Tanzania |

Note that records listed under the Santalales refer to mistletoes in either the Loranthaceae or Viscaceae.
Larva and pupa of Mylothris bernice

Final instar larva. Head capsule dark brown, with numerous white setae; body pale brown, with a broad dark brown mid-dorsal band and a broader dark brown lateral band edged ventrally by a white lateral line, entire surface densely covered with small white protuberances (sockets) from which arise long white setae (up to 1 mm long); size 25 mm long.

Pupa (Figures 1–4). Pale pinkish brown, with obscure darker brown patches on wings and ventral surface of abdomen, and numerous small white protuberances on abdomen; head with a prominent anterior projection and a pair of small rounded subdorsal projections, anterior projection straight, stout, rounded at apex and covered with many small obscure protuberances; prothorax with a small, rounded dorsal ridge; mesothorax with a pronounced dorsal ridge subdivided into two prominent blunt, partially divided dark brown projections and a third less conspicuous dark brown projection posteriorly, a lateral rounded protuberance on wing-case and a lateral ridge (also on wing-case) which extends

Figures 1–6. Pupae of Mylothris spp. (1–4) M. bernice: (1) dorsal view; (2) lateral view; (3) lateral view of mesothorax showing dorsal ridge and projections; (4) lateral view of abdominal segments 7–8 showing dorsal projections. (5, 6) M. agathina: (5) dorsal view; (6) lateral view. Scale bars: 10 mm (1, 2, 5, 6); 1 mm (3, 4).
posteriorly to metathorax; metathorax with an inconspicuous narrow dorsal ridge; abdominal segments 1–8 each with a short, blunt dorsal projection at the anterior end of segment, those on segments 5–8 tipped dark brown; abdominal segment 1 with a small dorsolateral protuberance; abdominal segments 2 and 3 each with a pair of blunt dorsolateral projections, with the anterior projection black; abdominal segment 4 with a single dorsolateral projection anteriorly; abdominal segment 7 with an inconspicuous lateral protuberance posteriorly; anal segment relatively broad and flattened with cremastral hooks on upper and undersides near apex; spiracles dark brown; size 20 mm long. Attached to silken pad by central girdle, which passes over abdominal segment 1, and the cremaster.

Discussion

Despite the lack of detailed information on larval food plant utilization in *Mylothris*, two broad, general statements can be made based on available data. First, larvae of this genus are almost exclusively associated with plants in the order Santalales; only one species complex feeds on Polygonales. Second, within the Santalales, the family most frequently exploited is the Loranthaceae (65–80% of records). These findings are similar to that recorded for the Indo-Australian pierid genus *Delias* in which the frequency of plant usage among families is 77% for the Loranthaceae (M. F. Braby and N. E. Pierce, unpublished data). Of course, this assumes that the frequency of food plant reporting reflects a similar frequency of food plant utilization in nature. Of the different butterfly–plant associations (n=36, if potential duplicate records are excluded), larval food plants have been recorded for 23 butterfly species of *Mylothris*, which represents two-fifths of the genus. The documentation spans more than 110 years of natural history effort, although the majority of records have been reported in the past 30 years. Thus, the data set, although small, is still a reasonable sample size from which to draw general patterns of food plant association, although clearly more field data are needed to determine the degree of host specificity, ecological and taxonomic preferences, and range of mistletoe species exploited by *Mylothris*. However, it is doubtful that additional information will change these general conclusions: *Mylothris* butterflies can be recognized as one of only a few diverse groups of insects known to feed predominantly on African mistletoes (Polhill and Wiens 1998; Congdon and Bampton 2000). The genus also represents one of four diverse groups of pierid butterflies that feed predominantly on mistletoes throughout the world, the three others being *Delias* from the Australian–Oriental Region, the *Catasticta* group of genera from the Neotropical Region, and the *Hesperocharis* Felder group, also from South America (M. F. Braby and Nishida, unpublished data, M. F. Braby and N. E. Pierce, unpublished data). Such feeding patterns are exceptional in the Pieridae as most butterflies in this family feed on legumes and crucifers (e.g. Ehrlich and Raven 1965; Chew and Robbins 1984; Ackery et al. 1995; Janz and Nylin 1998).

The modern understanding of the systematics of the order Santalales is that it is a natural monophyletic group consisting of about six families of hemiparasitic angiosperms (Nickrent and Franchina 1990; Nickrent and Soltis 1995; Nickrent et al. 1998), with the Eremolepidaceae from Central and South America now generally regarded as belonging to the Santalaceae (Wiens and Barlow 1971). The proposed phylogenetic relationships of these families, based on combined nuclear 18S rDNA and *rbcL* sequences, is as follows: Olacaceae+((Loranthaceae+(Misodendraceae+Schoepfia))+(Opiliaceae+(Santalaceae+Viscaceae))) (Nickrent et al. 1998), although the level of statistical support (bootstrap
values) uniting some of these clades is poor while other parts of the topology are unresolved, particularly the monophyly of the Olacaceae and Santalaceae. Five of these families occur in tropical Africa, the Misodendraceae being the only family absent. In Africa, the Opiliaceae, Olacaceae and Santalaceae are all root-parasitic shrubs and trees (or sometimes lianas in the case of *Opilia*), whereas the Loranthaceae and Viscaceae are both aerial stem-parasitic shrubs and usually referred to as ‘mistletoes’. These latter plants in Africa parasitize dicotyledonous trees and shrubs, with about a third of the known species having specific associations with only one family of host trees (Polhill and Wiens 1998). Accepting the above phylogenetic reconstruction as correct, then the mistletoe habit has evolved independently at least four times in the Santalales (Nickrent et al. 1998) (the Misodendraceae and a few species of Neotropical Santalaceae are also aerial stem parasites).

Ehrlich and Raven (1965, p 593) suggested that mistletoe feeding in the Pierinae was a derived state, having evolved from a Capparaceae–Brassicaceae-feeding ancestor, “it would appear that the main diversification of this group occurred after it became associated with Capparidaceae–Cruciferae”. Chew and Robbins (1984) and Venables (1993) postulated that mistletoe feeding in the Pieridae may have evolved as a result of a radical host shift from the host tree (i.e. the butterfly’s ancestral food plant) to the parasitic plant growing on the trunks and branches of that tree. Indeed, Mooney (2003) concluded that, based on a review of associations between Lepidoptera and dwarf mistletoes (*Arceuthobium*, Viscaceae) and their conifer host trees (Pinaceae) in North America, such shifts between host trees and their mistletoe parasites, and vice versa, may be common in taxa which feed on either of these resources because of the close physical proximity of host and parasite. This close physical association between host and parasite would provide increased ecological opportunity, and the mechanism, for larvae to be exposed to taxonomically and chemically unrelated potential food plants. For instance, larval contact with the new potential food plant (parasite) could occur as a result of females ovipositing on or near the parasite, or as a consequence of larvae defoliating the host tree and exhausting their food supply. Natural genetic variation within the population may allow some larvae to detoxify, consume or otherwise supplement their diet with the new mistletoe food plant. If the mistletoe food plant happens to confer greater fitness than the host tree (e.g. through increased nutritional value, reduced chemical toxicity, reduced interspecific competition, escape from natural enemies, etc.) then, over evolutionary time, natural selection will favour those individuals feeding on the new food plant and females will preferentially oviposit on the parasite. Lamont (1983), for example, suggested mistletoes may be more nutritious than their hosts because of higher nitrogen content and mineral concentrations. If such a shift from host tree to parasite occurred in *Mylothris*, it could have taken place either in the Loranthaceae or Viscaceae (i.e. the aerial stem parasites); it is unlikely to have occurred on the root parasites because these plants usually grow some physical distance from the host tree (i.e. members of the Olacaceae and Santalaceae are less likely to come into contact with ovipositing females or larvae feeding on their host trees). Presumably, once the evolutionary shift to Loranthaceae or Viscaceae occurred, it was not too difficult for some butterflies to then exploit other chemically related families, such as the Olacaceae and Santalaceae, within the Santalales. Given the topology of the Santalales outlined above and the distribution of insect–plant associations across the tree, a major prediction would be that some species of *Mylothris* may also feed on the Opiliaceae.

Of the five families of Santalales in Africa, the Loranthaceae are by far the most diverse group, comprising 21 genera and some 237 species (Polhill and Wiens 1998). The
Viscaceae, by contrast, are represented by 48 species in only three genera, two of which are exceedingly small and have very limited distributions in eastern Africa (Barlow 1983; Polhill and Wiens 1998). The apparent preference for Loranthaceae in *Mylothris* may well reflect this wider availability of food resource, especially in the equatorial montane and submontane evergreen forests of the Afromontane and Guineo-Congolian chorological divisions, which are particularly species-rich in both the mistletoe plants (Polhill and Wiens 1998) and butterflies (Talbot 1944). The preference for Loranthaceae may also be related to an historical association and adaptive radiation with the Loranthaceae, especially if the ancestor of *Mylothris* fed on the Loranthaceae lineage before the evolution and major radiation of the Viscaceae lineage. Indeed, the phylogeny for the Santalales indicates that the Loranthaceae may be an older group than the Viscaceae (Nickrent et al. 1998). Given that no *Mylothris* species are known to feed exclusively on any one of the non-Loranthaceae families, an historical association with the Loranthaceae is even more likely, although a modern species-level phylogeny of *Mylothris* would be desirable to confirm this. A more ancient association with the Santalales is possible but seems unlikely given: (1) that the ancestral mode of parasitism in the Santalales is thought to be root parasitism (Nickrent et al. 1998), thereby reducing the likelihood of an early evolutionary host shift; (2) that so few butterflies are known to feed on the Olacaceae, Santalaceae and Viscaceae, especially the Olacaceae (the oldest and most “primitive” family, which is sister to the rest of the Santalales); and (3) that no species appear to be limited to these non-Loranthaceae families—the two or three species (*M. agathina/chloris, M. sagala*) which feed on Olacaceae, Santalaceae or Viscaceae also utilize Loranthaceae.

A similar pattern to *Mylothris* in frequency of larval food plant utilization within the Santalales occurs in the African lycaenid tribe Iolaini (Congdon and Bampton 2000). The vast majority of Iolaini feed on plants in the Loranthaceae, but a few butterflies, representing three genera, also exploit Olacaceae (*Ximenia, Olax*) and Viscaceae (*Viscum*). The distribution of food plants across butterfly taxa again suggests a major radiation on the Loranthaceae, followed by occasional shifts to related families, although a modern phylogeny of the tribe is desirable to test this.

Larval feeding on Polygonales is perhaps more difficult to explain, particularly since this group of plants is unrelated to the Santalales (e.g. Cronquist 1981). It is exceptional to the general pattern observed in *Mylothris*. Indeed, *M. bernice* and *M. rubricosta* represent the only species in the entire Pieridae known to feed on plants in this order (M. F. Braby and N. E. Pierce, unpublished data).

*M. bernice* and *M. rubricosta* are very closely related and form a taxonomic complex; in the past they were conventionally treated as a single species until Berger (1981) treated *rubricosta* as a distinct species. Several authors have subsequently expressed reservations about this taxonomic decision (Kielland 1990; Larsen 1991). Both species are unusual in that the upperside of the fore wing possesses a narrow orange-red costal streak, which becomes broader at the base in the cell (in other white-coloured species with orange-red markings on the fore wing, the marking is limited to the base of the wing, usually displayed as a broad patch in and below the cell). Talbot (1944) thought *M. bernice* should be placed into a species-group of its own, but van Son (1949) placed it into the *chloris* species-group based on careful study of the genitalia and wing pattern. Comparison of the larval morphology, pupal morphology (of *M. bernice*: Figures 1, 2) and male genitalia (of *M. rubricosta*: Talbot 1944; van Son 1949), together with a phylogenetic analysis of pierid genera based on nuclear and mitochondrial genes (M. F. Braby and N. E. Pierce, unpublished data; M. F. Braby et al., unpublished data), clearly indicate that *M. bernice/M.
rubricosta belong to Mylothris and do not represent a separate genus. The form of the pupa in Mylothris is most distinctive: unique characters include the mesothoracic dorsal ridge divided into three raised blunt projections (each partially divided) (Figure 3), the eight abdominal mid-dorsal blunt projections (Figure 4), and the small lateral projection on abdominal segment 7. The pupa of M. bernice possesses all of these characters and closely resembles that of M. agathina (Figures 5, 6) in profile and in the possession of other features, such as the anterior projection and the distribution of the six dorsolateral projections on abdominal segments 1–4. Thus, there is currently no morphological evidence to suggest that M. bernice/M. rubricosta form a deep sister lineage to all other species of Mylothris but, according to the systematic classification of van Son (1949) in which the genus comprises two main divisions, are nested within the chloris species-group. Clearly there is a need for a modern phylogenetic hypothesis of Mylothris and better understanding of species relationships, but the implication from the present systematic framework is that Polygonaceae feeding is a derived state, having evolved from a mistletoe-feeding ancestor.

M. bernice and M. rubricosta are locally common in papyrus swamps, marshes and riverine places where the Persicaria larval food plant grows (Kielland 1990; Larsen 1991). If larval feeding on Polygonaceae by these species represents a secondary host shift from the Santalales, the mechanism for this switch is by no means clear. A phylogenetic study of the Pieridae suggests that Santalales feeding has evolved independently three times in the family but has been secondarily lost at least seven times (M. F. Braby and N. E. Pierce, unpublished data). In these extreme cases the butterflies have exploited unusual (novel) food plants which appear to represent the host trees that support the (now ancestral) mistletoe food plants. In the African Iolaini, one species feeds exclusively on Sapotaceae within an otherwise large Santalales feeding clade (Congdon and Bampton 2000), and presumably represents a similar radical host shift from the parasite to the parasite’s host plant. In the case of Mylothris, however, species of African Loranthaceae and Viscaceae, which grow only on woody plants, do not parasitize herbaceous Persicaria (Polhill and Wiens 1998; R. Polhill, personal communication) and further field work on the ecology of M. bernice and M. rubricosta is needed to understand the butterflies’ relationship with Polygonaceae. In the Rift Valley of Uganda–Kenya–Tanzania, Persicaria barbata and P. attenuata typically grow very locally in areas surrounded by diverse woody vegetation that support a high diversity of mistletoes, especially in Tanzania (R. Polhill, personal communication). It is possible that a shift occurred from a species of Loranthaceae or Viscaceae in these woodlands growing in close proximity to the papyrus swamps. For example, close physical contact between Loranthaceae and Persicaria could occasionally arise where the foliage of low-growing clumps of mistletoes happens to touch herbaceous plants on the ground.

In conclusion, Mylothris probably had its major period of evolution and adaptive radiation on the Loranthaceae lineage, sometime before the evolution of the Viscaceae but after the differentiation of most of the other Santalales families or lineages, rather than on an earlier ancestral branch at or near the root of the Santalales evolutionary tree. Once the Loranthaceae association had been established, this may have facilitated host switching to related (and possibly non-related) families multiple times. A modern, robust phylogeny of the genus would provide additional evidence to test these hypotheses.

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