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The Papilionidae (Lepidoptera): Co-evolution with the Angiosperms

By

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With 2 figures

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Summary

RICHARD D. & GUÉDÈS M. 1983. The Papilionidae (Lepidoptera): co-evolution with the Angiosperms. — *Phyton* (Austria) 23 (1): 117—126, 2 figures. — English with German summary.

The Papilionidae appears to have co-evolved with two lines of Angiosperms, the one rooted in the *Magnoliales* or rather their ancestors, the other in the *Rosales-Myrtales* or their ancestors. The Papilionini (Graphiini) is especially interesting in being adapted to a lineage including the *Magnoliales*, *Rutales*, *Umbellales* and *Asterales*, whose existence is clear on phytochemical and morphological grounds. It is stressed that morphological differentiation does not go necessarily hand in hand with adaptive co-evolution: whereas the whole of the Troidini remained adapted to the *Aristolochiaceae*, the single genus *Papilio* (Papilionini) "learned" to feed on a succession of related families culminating in the *Compositae*, and still remained unchanged at even the genus level.

Zusammenfassung

RICHARD D. & GUÉDÈS M. 1983. Die Papilionidae (Lepidoptera): Coevolution mit den Angiospermen. — *Phyton* (Austria) 23 (1): 117—126, 2 Abbildungen. — Englisch mit deutscher Zusammenfassung.

Die Papilionidae haben anscheinend mit zwei Linien der Angiospermen coevoliert, nämlich mit einer, die im Bereich der *Magnoliales* oder eher ihrer

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Vorfahren wurzelt, und einer, die auf *Rosales-Myrtales* bzw. deren Vorfahren zurückgeht. Die Papilionini (Graphiini) sind besonders interessant, weil sie an Arten aus Ordnungen (*Magnoliales*, *Rutales*, *Umbellales*, *Asterales*) angepaßt sind, die einer auch aus phytochemischen und morphologischen Gründen zunehmenden Entwicklungslinie der Angiospermen angehören. Es wird hervorgehoben, das morphologische Differenzierungen nicht parallel mit coevolutiver Anpassung gehen müssen: Während die ganze Tribus der Troidini an *Aristolochiaceae* angepaßt geblieben ist, hat die Gattung *Papilio* Vertreter einer ganzen Folge von Familien als Fraßpflanzen angenommen und sich dabei aber nur innerhalb des Niveaus der Gattung differenziert.

Introduction

Although many authors mentioned the adaptation of the Papilionidae and their caterpillars to egg-laying and feeding on more or less definite families and genera of Angiosperms, it seems that no peculiar attention has been paid to a possible co-evolution between them and the Angiosperms. With co-evolutionary thought now so pervasive, and co-evolution with Angiosperms having been discussed by EHRlich & RAVEN 1960 as regards the Lepidoptera as a whole, such a study is certainly in order, the more so as many of the Papilionidae appear to be adapted to some of the putatively primitive Angiosperms.

Host Plants of the Papilionidae

We have compiled a list of the host plants of the Papilionidae by drawing mainly on works by D'ABRERA 1971—1979, HAUGUM & LOW 1978—1979, HIGGINS & RILEY 1980, TYLER 1975, VIETTE & PAULIAN 1968, WILLIAMS 1969, also taking advantage of personal communications from various entomologists (see acknowledgments).

Few species are normally monophagous, *Baronia brevicornis* SAL. being a notable exception by feeding exclusively on *Acacia cymbispina* SPRAGUE & RILEY. Even fewer prove monophagous when offered various plants in the laboratory. The most selective butterflies and caterpillars seem to be the Parnassiinae and those of the Papilionidae that feed and lay eggs on *Aristolochia*. Many others of the Papilionidae have caterpillars that will at least occasionally feed on a vast array of plants, especially those of the North-American group centred on *Papilio glaucus* L. (BROWER 1958). Caterpillars of the latter have been found on more than 15 different plant families, as a rule rather primitive ones, especially the *Betulaceae*, *Lauraceae*, *Magnoliaceae*, *Oleaceae*, *Platanaceae*, *Rosaceae*, *Salicaceae*. Only *Papilio eurymedon* LUCAS feeds mostly on the *Rhamnaceae*. These butterflies, are advanced, and probably became secondarily adapted to their varied host families. This may have occurred at an early date since all or most of their host families were in existence by the Cretaceous. *Eurytides branchus* DOUBL. belongs to the Papilioninae Papilionini (Graphiini) and basically

feeds on the *Magnoliaceae* and *Annonaceae*, but sometimes takes some of the *Verbenaceae*. *Parides daemonius* ALPH. and *Battus*, of the *Papilioninae* *Troidini*, sometimes feed on the *Rosaceae* and *Rutaceae*, whereas as the other *Troidini* they generally feed on the *Aristolochiaceae*. Some *Graphium* species, of the *Papilionini*, are found on the *Rutaceae* or *Apocynaceae*, while the genus *Graphium* basically feeds on the *Annonaceae*.

When such secondary adaptations are set aside, and one tabulates the plant family or families accepted by most species of a genus, or most generally consumed by them, a far more homogeneous gamut of hosts becomes obvious (Table 1). As will soon appear, these families are readily arranged in two phyletic lines.

Table 1
Main plant families hosts to the genera of *Papilionidae*

Genera of <i>Papilionidae</i>	Plant families
<i>Archon</i>	<i>Aristolochiaceae</i>
<i>Armandia</i>	?
<i>Baronia</i>	<i>Leguminosae Mimosoideae</i>
<i>Battus</i>	<i>Aristolochiaceae</i>
<i>Cressida</i>	?
<i>Drurya</i>	?
<i>Euryades</i>	<i>Aristolochiaceae</i>
<i>Eurytides</i>	<i>Annonaceae, Magnoliaceae</i>
<i>Graphium</i>	<i>Annonaceae</i>
<i>Hymermestra</i>	<i>Zygophyllaceae</i>
<i>Iphiclides</i>	<i>Rosaceae</i>
<i>Lamproptera</i>	<i>Combretaceae</i>
<i>Luhedorfia</i>	<i>Aristolochiaceae</i>
<i>Motasiona</i>	?
<i>Ornithoptera</i>	<i>Aristolochiaceae</i>
<i>Pachlioptera</i>	<i>Aristolochiaceae</i>
<i>Papilio</i> (excl. glaucus group)	<i>Rutaceae, Umbelliferae, Compositae</i>
<i>Parides</i>	<i>Aristolochiaceae</i>
<i>Parnassius</i>	<i>Crassulaceae, Fumariaceae, Saxifragaceae</i>
<i>Protographium</i>	<i>Annonaceae</i>
<i>Teinopalpus</i>	?
<i>Troides</i>	<i>Aristolochiaceae</i>
<i>Zerynthia</i>	<i>Aristolochiaceae</i>

Evolution of Host Plants

Table 2 gives SPORNE's last Advancement Index (1980) for the relevant Angiosperm families. The Advancement Index (AI) seems to us to offer a rather reliable measure of phyletic advancement, and one that is in reasonable accordance with the fossil record (GUÉDÈS 1979). In Table 2, some

families are included that are not found in Table 1, because providing only casual hosts to the Papilionidae. These include the *Rhamnaceae*, *Oleaceae*, *Piperaceae*, *Salicaceae* and *Lauraceae*.

Table 2
Advancement Index of families hosts to the Papilionidae
(secondary hosts in brackets)

<i>Magnoliaceae</i>	25
<i>Annonaceae</i>	40
(<i>Salicaceae</i>)	44
(<i>Rhamnaceae</i>), <i>Rutaceae</i>	45
<i>Combretaceae</i>	47
<i>Fumariaceae</i> , <i>Leguminosae</i> , <i>Rosaceae</i> , <i>Saxifragaceae</i>	48
<i>Aristolochiaceae</i>	50
(<i>Lauraceae</i>)	52
<i>Crassulaceae</i> , <i>Zygophyllaceae</i>	55
<i>Umbelliferae</i>	57
(<i>Piperaceae</i>)	60
<i>Oleaceae</i>	62
<i>Compositae</i>	72

It is clear (see also Fig. 2) that most host families have an AI in the range 40–60, with two exceptions: the *Magnoliaceae* below at AI 25 and the *Compositae* above at AI 72.

In our view the main host families may be arranged phyletically as depicted in Fig. 1. The *Magnoliaceae*, *Annonaceae* and *Lauraceae* derive from the stock of the *Magnoliales*. The relationship of the *Aristolochiales* to the *Magnoliales* is in accordance with CRONQUIST's (1968) and many others' suggestion. The *Rutaceae* is placed by CRONQUIST among the *Sapindales*, the latter belonging to the subclass *Rosidae*, whereas the *Magnoliales* belong to the *Magnoliidae*, but in CRONQUIST's own words (1968: 225) "the *Rosidae* are evidently derived from the *Magnoliidae*".

An impressive array of chemical traits links the *Rutaceae* to the *Magnoliales* (HEGNAUER 1973: 239). The *Zygophyllaceae* is generally considered to belong in the *Sapindales-Rutales*. A more debatable move is perhaps the placement of the *Umbelliferae* and especially the *Compositae* in the same lineage. The derivation of the *Umbellales*, including the *Umbelliferae*, from the *Sapindales-Rutales*, however, is suggested by CRONQUIST 1968 and endorsed by HEGNAUER 1971, 1973 on phytochemical grounds. The derivation of the *Asterales*, comprised of the only *Compositae*, from near the *Umbellales* is no doubt controversial, but seems well grounded on phytochemical data (PELT 1966, HEGNAUER 1973). In this connection, it must be recalled that

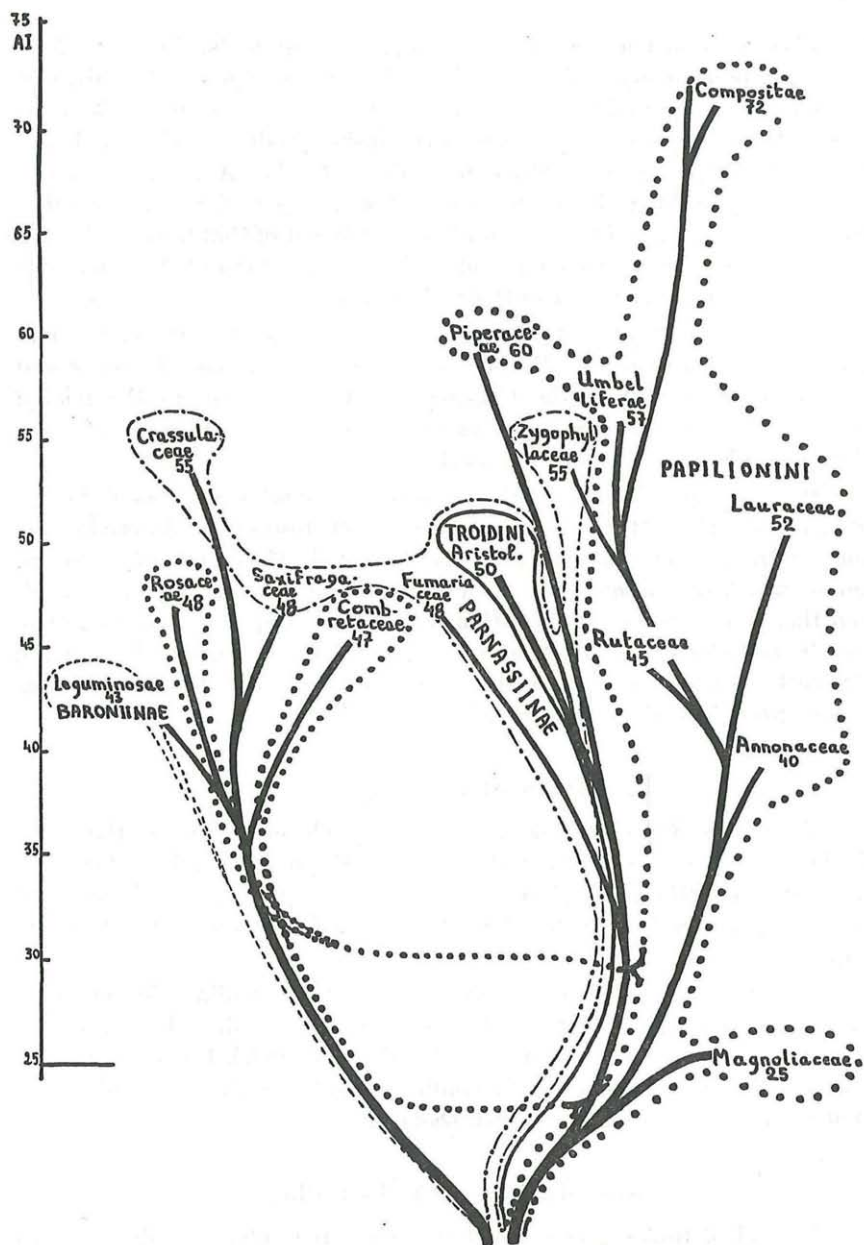


Fig. 1. Possible phylogeny of host families, account being taken of the Advancement Index. Families hosts to various taxa of the Papilionidae are enclosed in boxes as follows: — — — — Baroniinae, Papilionini, ————— Troidini, — Parnassiinae. Advancement Index on the left scale and near family names

it is also far from unconceivable on morphologic grounds. The *Umbellales* have an inferior ovary and unitegmic ovules with an apparently univalent integument, as opposed to the single integument of e. g. some of the *Rosaceae* and *Ranunculaceae*, corresponding to the fusion product of the usual two. These are characters they share with the *Asterales*. A composite head, moreover, is nothing else than an umbel with sessile flowers. The calyx reduction in the *Umbellales* is somewhat reminiscent of that in the *Asterales*, both taxa have haplostemonous androecia, and other morphologic features could be adduced in support of their relationship.

Some of the Papilionidae live on another lineage of Angiosperms, and this is centred around the *Rosales*, with the *Saxifragaceae*, *Rosaceae* and *Leguminosae*, as well as the *Combretaceae* which belong to the related *Myrtales*. The *Leguminosae* is present through *Acacia cymbispina* only, this in turn host to the single genus *Baronia*.

It seems questionable that the *Rosales-Myrtales* are rooted in the *Magnoliales*. The latter are advanced in various respects, and deriving the *Rosales* from them can hardly be contemplated. They and other orders, among which the *Rosales*, may well come from a pro-angiospermous stock and there seems to be no indication that pro-Angiosperms were more like the *Magnoliales* than the *Rosales*, except perhaps in their pollen. In the circumstances, we have shown the *Magnoliales*- and *Rosales*-centred lineages as two independent ones (Fig. 1).

Evolution of the Papilionidae

EHRlich & MUNROE 1960 attempted a phylogenetic tree of the Papilionidae which seems the best documented at present. It is rather near that by FORD 1944 and replaces to advantage the phylogenies put forward by MUNROE 1961 in a paper that although written before the 1960 one appeared after it.

In EHRlich & MUNROE's mature view, the Baroniinae branches off first in evolution as a dead-end line, then the Parnassinae becomes individualized. This leaves the primitive Papilioninae which become split into the Troidini and Papilionini (Graphiini). *Papilio* is the most advanced genus in the Papilionini, along with *Dabasa*.

Co-evolution with Host Plants

Perusal of tables 1 and 2 makes it clear that plant families host to single genera of butterflies are located in one or the other half of the evolutionary range evidenced by the Advancement Index. A genus living on the *Magnoliaceae* may also be found on the *Annonaceae*, but not on families with an AI above 40. Conversely, genera living on the *Umbelliferae* (AI 57) may occur on the *Rutaceae* (AI 45) and *Compositae* (AI 72), but not on

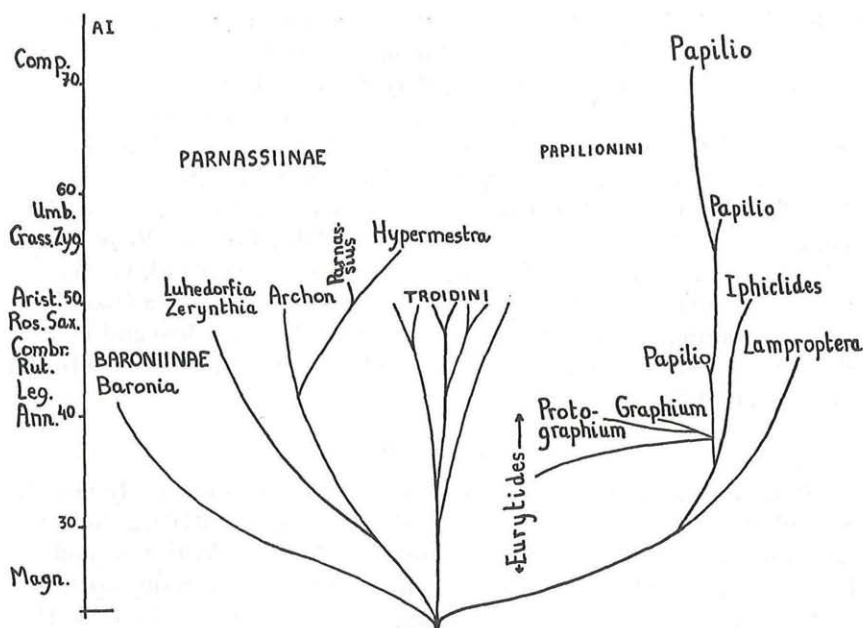


Fig. 2. Possible phylogeny of the Papilionidae (modified after EHRlich & MUNROE 1960). The genera are arranged in such a way as to indicate their probable relationships and the Advancement Index of their main host families (left scale). Generic names of the Troidini (Ornithoptera, Troides, Parides, Pachlioptera, Euryades, Cressida, Battus) have been omitted for space reasons. Ann. Annonaceae, Arist. Aristolochiaceae, Combr. Combretaceae, Comp. Compositae, Crass. Crassulaceae, Leg. Leguminosae, Magn. Magnoliaceae, Rut. Rutaceae, Sax. Saxifragaceae, Umb. Umbelliferae, Zyg. Zygophyllaceae. Only some important families are mentioned on the abscissa

families with an AI below 45. This seems to point to some correlation between plant and butterfly evolution.

A slightly modified form of EHRlich & MUNROE's phylogeny is presented in Fig. 2. It readily parallels plant phylogeny. The Papilionidae may have lived first on some kind of pro-Angiosperm ancestors to the *Rosales*, *Myrtales* and *Magnoliales*. The Baroniinae evolved with the rosalean line, having now become adapted to one of the *Mimosoideae*. The Parnassiinae at first evolved with the *Aristolochiaceae* or its ancestors, becoming or remaining adapted to that family at AI 50. One of the Parnassiinae (*Hypermestra*), however, became adapted to the *Zygophyllaceae* at AI 55 within the same lineage. The genus *Parnassius* developed an adaptation to the *Saxifragaceae* (AI 48) and the *Crassulaceae* (AI 55) of the *Rosales*. It is also found on some of the *Fumariaceae* (AI 48). As the latter seems to belong

to the Magnolioid line with which most of the Parnassiinae were evolving, it may be that the *Fumariaceae* is the basic host to Parnassius with the *Saxifragaceae* and *Crassulaceae* secondary though highly successful adaptations (Fig. 1). While this was going on, the Papilioninae were developing on the Magnolioid line. The Troidini, like the Parnassiinae, adapted to the *Aristolochiaceae* or its ancestors. The Papilionini remained on their ancestral Magnolioid lineage for their most part, but some diverged to the rosalean line. Eurytides, Protographium, Graphium specialized on the *Magnoliaceae* and *Annonaceae* at AI 25 and 40, but Papilio went far up with the lineage through the *Rutaceae* (AI 45) and *Umbelliferae* (AI 52) to the *Compositae* (AI 72). Lamproptera for its part went over to the sister line and became adapted to the *Combretaceae* at AI 47, while Iphiclides passed over to the *Rosaceae* at AI 48.

Discussion

It seems essential to point out that co-evolution is obviously not the cause of the divergence of taxa. While they were differentiating, both the Parnassiini and Papilionini became adapted to the *Aristolochiaceae*, and yet they came to differ from each other in such a way as to warrant separation as the tribe level. Because they were apparently unable to adapt to other plants, they were restrained by the range limitation of their host family. Papilio on the other hand, the most enterprising genus in the family, managed to adapt to newly evolved and highly successful families of the Magnolioid line, so taking advantage of the wide distribution of the *Umbelliferae* and *Compositae*. It also developed secondary adaptations to unrelated plants, and so radiated even further. But while evidencing, such a high adaptability as far as nutritional requirements are concerned, Papilio remained homogeneous enough in the characters of its comprising taxa to be considered as a single genus. Co-evolution was then limited to acquisition of sensorial and/or enzymatic capabilities, no morphologic differentiation attending at what is generally considered as the genus level.

With respect to Angiosperm classification, our co-evolutionary data seem interesting in affording a further argument for the occurrence of a lineage rooted near the ancestors of the *Magnoliales*, and whose present representatives include the *Magnoliales*, *Laurales*, *Rutales*, *Umbellales* and *Asterales*. It is not very surprising that co-evolutionary data are in agreement with phytochemical ones, since insect attraction depends on chemicals. As explained, the existence of this lineage is far from improbable on morphological grounds as well.

The relation of the *Aristolochiales* to that lineage is also confirmed by our data.

As the *Magnoliaceae* is apparently the most primitive and oldest-appeared family of host plants to the Papilionidae, it may be that Eurytides, which lives partly on it, is the most ancient genus. Since, however, it also

lives on the *Annonaceae*, it might be basically linked to this, are as *Graphium* and *Protographium*, not being necessarily older than the two latter. Only secondarily would it have become adapted to the *Magnoliaceae*.

It may be that most of the Papilionidae as we know them differentiated at about the same time on plants at AI 40–50. This may have occurred at the turn of the Cretaceous. The occurrence of the *Annonaceae*, *Rosaceae* and *Leguminosae-Mimosoideae* is doubtful before the Eocene. However, there is no indication on ancestors of either the present butterflies or their host plants, so past adaptations are obscure. This difficulty in interpreting co-evolutionary data is discussed by REGENFUSS 1978. Since the Papilionini feed on families all through the Magnolioid line, it is reasonable to believe their ancestors to have been adapted to the unknown ancestor(s) of this line, but we cannot decide whether the Parnassiinae first became adapted to some common ancestor of the *Saxifragaceae* and *Crassulaceae*, or separately to each of these families once they became distinct, as hypothesized on Fig. 1. In the same way, it is tempting to believe that *Iphiclides* fed on the ancestors of the *Rosales* before adapting to the present *Rosaceae*, and in Fig. 1 we thus considered that it passed to the rosalean line not long before the subline leading to the *Rosales* became individualized. The latter divergence, however, may itself have occurred sooner than indicated, i. e. the ancestor(s) to the *Rosales* may have had an AI below 35. *Iphiclides* or its ancestor(s) may also have lived on the Magnolioid line until more recently, then passing to the already differentiated *Rosaceae*. The disjunct area of *Iphiclides* (Europe and North America on the one hand, Himalaya on the other) points to an ancient origin of this genus. Further data for settling the problem might come from chemical studies of attractive plant substances. *Iphiclides* is related to butterflies living on the *Annonaceae*. If it is attracted to the *Rosaceae* by chemicals similar to those attracting its relatives to the *Annonaceae*, it will be probable that it passed to some of the *Rosaceae* recently, because the latter happened to produce the same chemical(s) as the ancestral *Annonaceae*. (Even so, these chemicals might have long appeared in the *Rosaceae* or their ancestors, *Iphiclides* then adapting to that family at an early date.) If, as seems more probable, attractive chemicals of the *Rosaceae* are quite different from those in the *Annonaceae*, becoming adapted to them will have to be considered as a lengthy process that went on while the *Rosaceae* were themselves evolving, and *Iphiclides* or its ancestors already were on this line, attracted by less distinct chemical(s). It is hoped that identifying attractive chemicals from various host plants of the Papilionidae will be a matter for future researches.

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