ANNALS OF THE TRANSVAAL MUSEUM
ANNALE VAN DIE TRANSVAAL-MUSEUM

VOL. 31 31 AUGUST 1978 No. 8

NEW TAXA OF FOSSIL AND RECENT MICROPTERIGIDAE WITH A DISCUSSION OF THEIR EVOLUTION AND A COMMENT ON THE EVOLUTION OF LEPIDOPTERA (INSECTA)

By PAUL WHALLEY

Department of Entomology, British Museum (Natural History),
London, SW7 5BD, England

(With four plates and two Text-figures)

ABSTRACT

Fossil and Recent Micropterigidae (Lepidoptera) and their evolution are discussed; descriptions are given of a fossil micropterigid from the Lower Cretaceous and two recent, new species from South Africa. The presence of a possible species of Incurvariidae in the Lower Cretaceous is noted. A summary of the factors affecting the evolution of the Lepidoptera is given.

INTRODUCTION

The origins and evolution of the Lepidoptera have long been a subject of interest. Recent discoveries of Mesozoic insects are giving us our first factual account of these early Lepidoptera. Parts of this paper summarize our present knowledge of some of the earliest fossils, describe a new fossil genus and species and indicate factors which may have been important both for evolution within the Lepidoptera and the evolution of the order itself.

A study was made of all the recent genera of Micropterigidae and the data obtained used to define two groups within the family and assign a place for the new fossil species. The evolution of the Lepidoptera, apart from its own intrinsic interest, is an important factor in the evolution of flowering plants. Fossil insects are generally considered rare (Hughes, 1976) and amongst insect fossils Lepidoptera form only a very small proportion. About 200 fossil lepidopterous specimens have been described but many are just fragments barely recognizable as Lepidoptera. Many fossils previously considered to be Lepidoptera are known to belong to other Orders; in fact until 1970, all other species described as lepidopterous from strata earlier than Tertiary, have proved to belong to different Orders (Crowson *et al.*, 1967: 523).

It was clearly realized that they must have occurred in the Mesozoic because the Lepidoptera known from the early Tertiary were far from primitive. In 1969 the head of a lepidopterous caterpillar was found in Canadian amber of Cretaceous age (Mackay, 1970: 1173). Subsequently adult Lepidoptera of Cretaceous age were recognized by Dr A. Mutuura in Canadian amber and by Dr A. Skalski in Siberian amber (personal communication). The latter is also describing a species of Micropterigidae from an impression on rock in the Lower Cretaceous of Siberia. Recent interest has centred on amber from the Lebanon of Lower Cretaceous age and much has already been published on this (Schlee & Dietrich, 1970; Schlee, 1970; Schlüter, 1976; etc.). This amber has been dated as Aptian (Acra *et al.*, 1972) or Neocomian (Schlee & Dietrich, 1970; Schlüter, 1976), see Table 1. Further evidence of the presence of Lepidoptera in the Mesozoic was published by Kühne *et al.*, (1973) who described lepidopterous scales from fossil resins of Cretaceous age from north-west France.

Riek (1976) described two species of Lepidoptera from the Triassic of South Africa (about 200 million years B.P.). He places them in the Paratrichoptera, a suborder which he transferred to the Lepidoptera, considering the Paratrichoptera ancestral to the Lepidoptera. In view of the age of these fossils, some 100 million years older than those currently recognized as lepidopterous, it is important to consider if the evidence presented does indicate their lepidopterous origin.

In his discussion, Riek states that the Paratrichoptera differ from other Lepidoptera in the presence of a well developed CuP vein in the forewing. However, there are many recent Lepidoptera with CuP, some are illustrated by Common (1970). The presence in the Triassic fossils of two crossveins from CuP to CuA and the apparent origin of the medial vein from CuA do not support the idea that they are lepidopterous insects. With the evidence available it is difficult to suggest an alternative, but perhaps a comparison with Trichoptera or even Diptera, with which they have some general similarities, should be made. I do not consider their lepidopterous nature has been proved.

Skalski (1976) discusses the state of our knowledge of amber Lepidoptera. He publishes a reconstruction of *Micropterix proavitella* Rebel (Baltic amber), together with a suggested phylogeny of the fossil and recent Micropterigidae. From his diagram it is apparent that he considers the Australian and New Zealand species, currently in *Sabatinca* Walker, as not being congeneric. He regards *Micropterix* Hübner as a Tertiary relict which arose in the Cretaceous of Laurasia, separately from other micropterigid genera. His re-examination of *Micropterix proavitella* from the Baltic amber leads him to suggest that it should be in a new genus, close to the Ethopian *Agrionympha* Meyrick. In the latter I agree with Skalski only in as much that it is not a *Micropterix*, but I believe it is closer to the Australian genus *Sabatinca.*

Amongst many insects in Lower Cretaceous amber from the Lebanon collected by Dr Aftim Acra, five lepidopterous specimens have been recognized. Although not in good condition between them it is possible to obtain information on the morphology of these early Lepidoptera. I had originally only four specimens and believed they were all the same species (Whalley, 1977). A subsequent specimen has shown that there are two distinct species which may well be in different families. Three specimens I consider to be Micropterigidae, but the other two I place tentatively in the Incurvariidae.

TAXONOMIC SECTION

Suborder: Zeugloptera, family: Micropterigidae

Genus *PARASABATINCA* gen. nov.

Type-species: *Parasabatinca aftimacrai* spec. nov.

This genus is separated from *Sabatinca* by the extra large spines on the legs, absence of ocelli and the apparent lack of a branch of Sc in the forewing, but this area is not too clear in the specimens examined. The fossil moths have scales similar to recent Micropterigidae, but it is not possible to be absolutely sure that cross-ribs are absent from the scales, the thickness of the amber preventing the use of very high magnifications. The head has mandibles and labial palpi very similar in shape to *Sabatinca* and *Micropterix*. There is no trace of the galea near the maxillary palpi which can be seen clearly from one side on the holotype. The labial palpi are two-segmented, possibly with a third segment (or praementum) but this cannot be clearly distinguished. The thorax has two small tegulae and both these and the wing shape are similar to recent Micropterigidae. A small four-spined 'frenulum' at the base of the costal margin of the hindwing is present, similar to *Sabatinca* but the jugum (if present) cannot be seen. The whole wing is covered with microtrichia which are particularly numerous in the area round the frenular bristles. The genus *Parasabatinca* is proposed for one species of which three specimens, in varying states of preservation, are known.

Type-locality: Lebanon, Lower Cretaceous amber, Aptian/Neocomian (see below).

Parasabatinca aftimacrai spec. nov., plates **11:** 1–3, **12:** 1–3, **13:** 1, **14:** 1.

Wingspan approximately 10mm, body length 10mm. Head with long scales, antennae with larger basal segment; maxillary palpi long, strongly reflexed, 3–4 times diameter of eye, four-segmented, but a fifth segment may be present; third segment curved; mandibles present, probably with small spine on outer surface. Forewing venation without any obvious branch to Sc (but area obscured in specimens), R_1 probably single, R_2 and R_3 with common stalk, similarly R_4 and R_5. Such hindwing venation as visible suggests a homoneurous condition. Scales on wing margin elongate, clavate or slender. Fore tibia with epiphysis, middle tibia with subapical spurs and several spines. Hindleg with very strong tibial spurs plus spines; tarsi five-segmented with terminal tarsal claw, half-circle of

4(?5) spines apically on tarsi. Abdomen and other structures not clear in specimen.

MATERIAL EXAMINED: Holotype in Lebanese amber, coll. Dr Aftim Acra, in BMNH (amber embedded in plastic); paratype 1: Data as holotype (head missing), in BMNH (amber mounted on slide in Euparal, figured in Whalley, 1977); paratype 2: Data as holotype, in BMNH (amber with scales and fragments of specimen mounted on slide in Euparal).

All specimens from Lower Cretaceous, Aptian (Acra *et al.*, 1972) or Neocomian (Schlee & Dietrich, 1970), variously dated about 100–130 million years B.P.

Although there are some differences between the fossils and recent species, I do think these are sufficient to justify placing the fossil in a new genus and I believe the species clearly belongs in the Micropterigidae. The mandibles, together with the strongly reflexed maxillary palpi, are very similar to both *Sabatinca* and *Micropterix*. In the fossil the very strongly developed spurs on the legs resemble *Sabatinca* rather than *Micropterix*, but they are more prominent even than in *Sabatinca*. The density of microtrichia on the wing membrane is similar to that found in recent genera.

The most conspicuous differences between *Sabatinca* and *Parasabatinca* are in the wing venation, but only part of the wing of the latter genus is known. *Parasabatinca* does not appear to have ocelli, or if they are present they are very small and obscured in the fossil; all recent Micropterigidae have ocelli. *Parasabatinca* has many morphological features which are also present in recent species and, if ocelli are absent as well, it can be regarded as a rather specialized micropterigid. Loss of ocelli occurs in many lepidopterous families and too much significance should not be attached to this feature in this genus.

In Table 2 the characteristics of the fossil and three recent genera are summarized. The family Micropterigidae now has, albeit with few examples, species from 100 million years ago to the present day and they provide us with morphological data unparalleled by any other family in the Lepidoptera. The fossils are:

Parasabatinca aftimacrai spec. nov., Lower Cretaceous (about 100 million BP), Lebanon.

Undopterix Skalski, in press, *Paleont. Zh.* Lower Cretaceous (about 80 million years BP), Siberia.

Micropterigidae, Kühne *et al.*, 1973. *Mitt. dt. ent. Ges.* **32:** 61. Upper Cretaceous (about 65 million years BP), France.

Micropterix proavitella Rebel, 1935. *Dt. ent. Z. Iris* **49:** 185 Eocene/Oligocene (about 40 million years BP), Baltic amber.

Micropterix species (to be described by E.A. Jarzembowski), Oligocene, Isle of Wight (U.K.), about 35 million years BP. Single wing impression on rock.

Micropterix pervetus Cockerell, 1919. *Entomologist* **52:** 193. Miocene (about 8 million years BP), but this Burmese amber might be redated when more information is available. Recent Carbon dating by the British Museum (Dr R. Burleigh, *in litt.*) give 30.000 years BP for a sample.

Other Burmese amber has insects which have similarities to much older ones (Dr D. Lewis, pers. comm.). I have re-examined the type of *M. pervetus* and both Rebel's original figures of *M. proavitella,* together with Skalski's recent reconstruction (1976) and transfer them both now (p. 77-78) to the genus *Sabatinca.*

From a study of the external morphology of modern genera, the family can be divided into two groups, the Micropterigoid-group and the Sabatincoid-group. The former contains the genera *Micropterix* Hübner, *Epimartyria* Walsingham, *Paramartyria* Issiki and *Neomicropteryx* Issiki, while the latter contains *Sabatinca* Walker, *Agrionympha* Meyrick, *Micropardalis* Meyrick, *Palaeomicroides* Issiki, *Parasabatinca* Whalley and *Undopterix* Skalski. The two groups are separated primarily on the bifurcation of R_1 and the post apical position (see later) of R_5 in the forewing. There are, naturally, certain characters peculiar to individual genera. For example *Neomicropteryx* has lost the epiphysis on the fore tibia, and it is also lost in one of the species of *Epimartyria* (Dr D. Davis, *in litt.*). The epiphysis on the fore tibia is present in most Lepidoptera and is generally regarded as a basic lepidopterous character. It is, however, lost in some families, sometimes only in one or two species in a genus (Thyrididae: Whalley, 1971; Hepialidae: Robinson, 1977). The bifurcation of the subcostal vein in the forewing is characteristic of all recent micropterigid genera and is also present in some Dacnonypha and Monotrysia, but is virtually unknown in the Ditrysia.

The first radial vein of the forewing may be bifurcate or single in the Micropterigidae, it is bifurcate in the genera in the Sabatincoid-group, with the possible exception of *Parasabatinca* where it cannot be seen, although it is clearly bifurcate in the Lower Cretaceous *Undopterix* from Siberia; bifurcation of the first radial vein is unusual in the Lepidoptera. The sternal organs on the 4th or 5th abdominal segments (sternal abdominal glands, Davis, 1975: 10) present in recent genera of micropterigids cannot be seen in the fossils. All the recent genera have a pair of ocelli, mandibles and strongly reflexed maxillary palpi. The position of the termination of R_5 on the wing margin in relation to the apex of the forewing differs in the two groups. In the Micropterigoid-group, R_5 in the forewing terminates on the costal margin, whereas in the Sabatincoid-group R_5 either terminates apically or, more usually, post-apically on the wing margin.

Recent species in the Sabatincoid-group have a southern hemisphere distribution in Australia-New Zealand, with a single genus in Africa. The Micropterigoid-group has a northern hemisphere distribution. The presence of fossil species of *Sabatinca* from Burma (Miocene), North-western Europe (Eocene/Oligocene), the Lebanon and Siberia (both Lower Cretaceous) suggests that formerly this genus was far more widespread but has been replaced by the Micropterigoid-group, leaving currently the Sabatincoid-group very much on the periphery of the present distribution of the Micropterigidae as a typical relict-group type of distribution.

Two new species of the modern genus *Agrionympha* from South Africa, recently submitted for study by Dr L. Vári, Pretoria, are described below.

Agrionympha capensis spec. nov., plate **14:** 2–3.

♀: Wing 3,5mm (apex to centre of mesothorax). Head with long yellow-brown scales; base of antennae covered with roof of long scales, below antenna with single long scales projecting from antennal base; labial palpi strongly reflexed. Tegulae small. Epiphysis on fore tibia; middle leg tibia with circle of scales but no spurs, hind tibia with two median and two long apical spurs with circlet of spines at apex. Forewing iridescent purple with prominent yellow-white fasciae, median fascia incomplete in anterior third, antemedial fascia angled L-shaped, continued to wing base; Sc and R_1 bifurcate, R_5 on wing margin posterior to apex. Hindwing brown, pointed, rather parallel sided.

Genitalia with rounded anal papillae and short bursa.

♂: Unknown.

MATERIAL EXAMINED: ♀-Holotype: South Africa, Knysna, Garden of Eden (C.P.), 16–20.I.1955, A.J.T. Janse, in Transvaal Museum; ♀-paratype: South Africa, Jonkershoek (C.P.), 19.II.1977, L. & G. Vári, in British Museum (Nat. Hist.); ♀-paratype: South Africa, Hermanus (C.P.), 26.II.1977, L. & G. Vári, in Transvaal Museum.

This species can be distinguished from *A. pseliacma* Meyrick and the following new species *A. vari* by the pattern of the forewing. In the three specimens examined, the thickness of the basal part of the L-shaped antemedial fascia varies to some extent.

Agrionympha vari spec. nov., plate **14:** 4.

♀: Wing 4mm (apex to centre of mesothorax). Head, antennal base, forewing colour, etc. as in preceeding species. Externally differing only in forewing pattern and hindwing shape. Post median fascia interrupted with smaller posterior part, antemedian fascia a whitish transverse band, basal longitudinal white streak not reaching antemedian fascia. Hindwing similar to *A. capensis* but broader and less sharp at apex.

Genitalia with rounded anal papillae and short bursa.

♂: Unknown.

♀-Holotype: South Africa, Mariepskop (Tvl.), 24–25.I.1956, L. Vári; ♀-paratype: South Africa, Worcester, Fairy Glen (C.P.), 15–19.X.1966, Vári and Potgieter, both in Transvaal Museum.

This species differs from *A. pseliacma* in the interrupted post median fascia, in which the fascia is complete across the wing. From *A. capensis* it can be distinguished by the lack of the fusion of the stripe at the base of the wing and the antemedian fascia. There is also a slight difference in the shape of the hindwing apparent when the two species are examined together.

Suborder: MONOTRYSIA, family: INCURVARIIDAE.

Genus *INCURVARITES* Rebel

Rebel (1934) proposed this genus for a species in Baltic amber, *I. alienella* Rebel. From the Lebanese amber there are two specimens which I regard as belonging to the Incurvariidae. Unfortunately neither is complete, in one specimen the head is missing and the wings are so tightly superimposed that identification of the wing veins is not practical. The other specimen is merely a few fragments of wing and scales, plate **13:** 3–4.

The most striking feature of these specimens, which are clearly lepidopterous and which separates them from the Lebanese amber Micropterigidae, is the wing margin scales. In the specimens of *Incurvarites,* the scales have a highly toothed apex, whereas clavate scales or simple ones are present in *Parasabatinca* and recent Micropterigidae. I have examined wing margin scales from all recent families which are loosely classified as Microlepidoptera, plus a sample of the Macrolepidoptera. The scales from the Lebanese amber specimens are similar to those in the Incurvariidae, especially in specimens of *Prodoxus* Riley. One of the specimens has an epiphysis on the fore tibia and very spiny legs. Unfortunately, neither are in good enough condition to describe or to be absolutely certain of their taxonomic position, but certainly the scales suggest Incurvariidae, plate **13:** 2.

However, it is possible to consider that there were two distinct species, probably distinct families (Micropterigidae, Incurvariidae) present together in the Lower Cretaceous.

EVOLUTION SECTION

Evolution of the Micropterigidae

In the light of the fossil evidence from the Mesozoic and Tertiary some of the plesiomorphous characters can be given with more certainty. These characters in the Micropterigidae include:

1. Mandibles
2. Reflexed maxillary palpi
3. Strongly spurred hind tibia
4. Strong spines at apex of tarsi
5. Posterior margin termination of R_5 in forewing
6. Microtrichia on wing membrane
7. Epiphysis on fore tibia
8. Scales on the wing
9. Sc bifurcate*
10. R_1 bifurcate*

The apparent absence of ocelli in the Cretaceous *Parasabatinca* is unexpected, all recent species of Micropterigidae have ocelli. However, in the Lepidoptera and Trichoptera, ocelli may be present in some species, while absent from others in the same genus. The presence or absence of ocelli may not necessarily be a significant character in their relationship.

Sabatinca pervetus (Cockerell) (**comb. nov.**) from Burmese amber has the venation typical of the genus with a bifurcate R_1, and R_5 terminating post-apically. The presence of the genus in Burma is interesting, neither the genus nor the family Micropterigidae are represented in the modern

---

*These features are visible on *Undopterix* from the Lower Cretaceous of Siberia, information and photo kindly supplied by Dr A. Skalski.

fauna. In the older Baltic amber (Eocene/Oligocene, *Sabatinca proavitella* (Rebel) (**comb. nov.**) shows that 30–40 million years BP the genus occurred far from the known recent distribution, and even further back in time, the typical Micropterigidae of the Sabatincoid-group occurred widely in the northern hemisphere. The recent discovery of a species of *Micropterix* in the Oligocene of the Isle of Wight (U.K.) is especially interesting and is roughly of the same age as the Baltic amber *Sabatinca*. This suggests a separation of the two genera at an even earlier period.

The fossil record shows that at least from the Lower Cretaceous to the Miocene, a period of roughly 100 million years, the Sabatincoid-group was more widespread than at present. Gradually it contracted its distribution from the Palaearctic as time progressed, in a south-easterly direction. We have one piece of recent evidence which also points to a more widespread occurrence of the Sabatincoid-group in former times. In Southern Africa, the genus *Agrionympha* has more characters in common with *Sabatinca* (Table 2) from Australia-New Zealand and is presumably a relict genus. While the genus *Agrionympha* may have evolved in isolation in Southern Africa, its close common ancestry with *Sabatinca* seems very probable. *Parasabatinca* from Lebanon and *Undopterix* from Siberia, both present in the Lower Cretaceous, show that while the distribution may have changed, the general morphology of the Micropterigidae has remained unchanged for over 100 million years.

The implications are that the Micropterigoid-group evolved later from a Sabatincoid-like ancestor and the separation was earlier as the presence of *Micropterix* in the Oligocene shows. They have remained successful in the Palaearctic with some 60 extant species, far more than are known in the other group, about 23 species. It is possible that speciation of the Micropterigoid-group may have been assisted by isolation during the various glaciations in the Palaearctic, but against this one must set the apparent morphological stability of the group; certainly the distribution of the recent Palaearctic species should be examined in the light of this suggestion. There are no Micropterigidae fossils known from the New World and only one extant genus, *Epimartyria*. This has many of the characters of *Micropterix* and is certainly in the same group; it may even be congeneric with *Micropterix*, but this needs further study. It is therefore probably derived from a common ancestor with the Palaearctic *Micropterix*, rather than directly from the more ancient Sabatincoid-group.

The biology of the modern species is not well known. The adults feed on pollen of various angiosperms, generally herbaceous species, which may have been rare in the Lower Cretaceous, accepting the recent account of angiosperm evolution (Hughes, 1976). However, the record is poor and it is not improbable that there were more angiosperm-type plants at that period.

The fossil moths provide clear evidence of Lepidoptera in the Lower Cretaceous and, because they were already relatively specialized, I propose an earlier date for the separation of the Lepidoptera from the Trichoptera-Lepidoptera stem-group than the Cretaceous origin hitherto suggested (Zeuner, 1962). Fossils in the Jurassic should be carefully examined for evidence of lepidopterous insects.

FACTORS INFLUENCING THE EVOLUTION OF THE LEPIDOPTERA

Angiosperms have long been considered to have had an important effect on the evolution of the Lepidoptera, evolving over the same geological period (Zeuner, 1962; Common, 1975). The earliest angiosperms have been recognized from Lower Cretaceous rocks, but they do not become abundant until later in the Cretaceous or early Tertiary (Hughes, 1976). The dependence of most Lepidoptera on flowering plants as food for the larvae and on the nectar in their flowers for the adult butterfly or moth is inextricably linked with the dependence of many flowering plants, particularly those with tubular corollas, on Lepidoptera for pollination. Hughes (1976) points out that sculptured exine of pollen, which is usually associated with, although may not be a direct result of, insect pollination, first appeared in the Lower Cretaceous. This was certainly contemporary with the early Micropterigidae (Whalley, 1977). The co-evolution of flowering plants and Lepidoptera probably developed not only from mutual benefits but also from mutual antagonism. This antagonism involved the plant developing chemicals to combat the insect attack while the insects responded to these changes in plant chemistry by their own evolutionary processes. The insect/plant relationship through 'pest pressure' is discussed by Gillett (1962). More recently the Insect/Plant Relationships were the subject of a symposium (van Emden, 1972).

Modern Lepidoptera, while popularly considered day or night-fliers, have very much modified habits adapted to flying at specific times of day or night, only the extremes of which are the true night or day-fliers. Virtually all butterflies fly by day, while more moths fly by night than day of the modern fauna. This is the only evidence that can be applied to fossils, that if they belong to, for example, certain moth families, then they may well have been night-fliers, the application of this can at best only be regarded as a working hypothesis. Zeuner suggested that butterflies had evolved from a night-flying ancestor: "It would thus appear that the Rhopalocera became day-fliers . . ."-Zeuner (1962: 312).

We now have evidence from the fossil record of mandibulate adult Lepidoptera from Lower Cretaceous deposits (Whalley, 1977) and evidence of haustellate Lepidoptera more recently from the middle of that period (Dr A. Skalski, Dr A. Mutuura, *in litt.*). By the early Tertiary there is fossil evidence of several recent families of Lepidoptera, including both butterflies and moths (Kuznetzov, 1941).

There is no direct evidence of the flight habits of fossil Lepidoptera. Only by inference from the habit of the modern extant species of the same family as the fossil can any analogies be drawn, and these must be viewed with caution. Using this analogy with recent Lepidoptera and taking the extreme conditions (i.e. ignoring crepuscular habits, etc.), these early Lepidoptera may have been day or night-fliers. If they flew in the dark then they were visually less apparent to any predators which were dependent on sight to catch their prey. If they flew by day they would be more obvious to these predators and could be caught in flight. Flying by day normally involves resting at night, conversely night-fliers rest in the day, when many predators hunt by sight. This must have led to the development of camouflage and methods of concealment at rest are importan as is clearly shown in the recent fauna where night-flying moths have developed patterns and colours to assist in day-time concealment; butterflies are experts at concealment as they alight.

As a working hypothesis if the early Lepidoptera were day-flying, what factors in the Cretaceous environment could have induced the night-flying habit? While many factors could have been important, here predation is considered. Invertebrate predators (e.g. Dragonflies) take Lepidoptera in flight (personal observation). Possible vertebrate predators that were present or evolving along-side the Lepidoptera were small mammals, birds, while the reptiles and amphibians were also taking a toll.

Birds would have provided additional predator-pressure, as well as the then existing invertebrate predators (perhaps with some predation from the now extinct pterosaurs). The increase in numbers and species of birds during the Mesozoic and early Tertiary and the consequent increase in predation of Lepidoptera in flight might have been sufficient to induce the development of a night-flying habit, or to provide a survival value to those which flew when the birds were not active. Birds in particular (with obvious specialized exceptions) are mainly day-time predators and, although much activity is also directed to seeking the insects at rest, the potential volume of aerial predation, which was a new situation in the late Mesozoic, cannot be ignored. There was an extensive avifauna in the Lower Eocene in Britain, with both sea and land birds represented (Harrison & Walker, 1977).

It is possible to speculate that in some cases, night-flying moths may have responded to predator-pressure in a similar way to the evolution of the bats (Chiroptera) from the early Tertiary by returning to the day-flying habit. It is interesting that the majority of day-flying moths, where we have data, are brightly coloured toxic species and therefore well protected against vertebrate predators hunting by sight. Some evidence for the development of day-flying moths from night-flying ancestors can be inferred from the Geometridae. Most species of Geometridae are night-flying (or crepuscular) and only a relatively few species are clearly adapted to day-flying (e.g. *Miliona* Walker).

If the earliest moths were day-flying, with night-flying developing later, then clearly the butterflies, which are currently mostly day-fliers, can either have evolved secondarily from night-flying Lepidoptera or directly from the early day-flying Lepidoptera without having a night-flying ancestor.

There is still little evidence from recent work on the relationship of the butterflies (Papilionoidea, Hesperioidea) with the other lepidopterous families, and no direct evidence on the possible flight habits of these early Lepidoptera. If one assumes they were day-flying then, and applying Occam's razor, deriving the butterflies from day-flying ancestors without the night-flying stage is worth considering as a plausible hypothesis.

THE EVOLUTION OF THE LEPIDOPTERA

Recognition of the differences between Lepidoptera and Trichoptera when based on limited fossil evidence is often very difficult. Some of the problems involved in separating these two orders were highlighted by the discussion over the position of the Zeugloptera (Hinton, 1946, 1958; Kristensen, 1975). The question was whether the Micropterigidae were 'true' Lepidoptera, or a separate order from either the Lepidoptera or Trichoptera. Kristensen keeps the Lepidoptera, including the Zeugloptera, as part of the superorder Amphiesmenoptera, which includes the Trichoptera as a separate, but closely related order.

Kristensen (1975) considers many characters of Lepidoptera; here I shall only consider those which might have been preserved in a fossil. Lepidopterous scales are generally characteristic, although similar scales do occur in the Trichoptera. The epiphysis on the fore tibia of Lepidoptera does not occur in the Trichoptera, but there are a few Lepidoptera where this is also absent. The various wing-coupling mechanisms in Lepidoptera are generally distinct from other groups and the wing venation is usually diagnostic. Other features which might be used to help the diagnosis, but which have not been sufficiently studied to be currently useful, are the shape of the thoracic tergites, the patagium, the tegulae and the arrangements of the spines on the legs.

The close relationship of the Lepidoptera and Trichoptera and their probable common origin is considered a reasonable hypothesis (Kristensen, 1975). The first recognizable trichopterous wing is Lower Permian (Crowson *et al.*, 1967), the first recognizable lepidopterous insect is Lower Cretaceous (considering the Triassic Lepidoptera of Riek, 1976 as not yet proven). This gives a time span of about 100 million years between the first recognizable Trichoptera and the first undisputed Lepidoptera. In deriving the two orders from a common ancestor one is left with the problem both of how their separate evolution took place and why we do not yet recognize Lepidoptera at an earlier date. Apart from the paucity of fossil records I believe that the facts can be explained on the basis of a hypothesis of differential rates of evolution between the adult and larvae. It is possible that the caterpillar-type larva differentiated before the adult lepidopterous characters developed. The environmental needs of the larvae and adult are so dissimilar that the rate of evolution of their separate characteristics, within the limits of its survival value for the species, need not have been at the same rate. Plants were available as food for the larvae before the angiosperm flowers and their associated nectaries were developed. There is also the evidence of insect borne pollen which first appeared in the Lower Cretaceous (Hughes, 1976: 96). This would imply that there were insects being attracted to flowers which had developed this pollen.

Differential rates of evolution of the Lepidoptera and Trichoptera are envisaged as proceeding in table 1. Given certain facts, this thesis can be developed. If we consider the number of fossil insect wings known from the Triassic to the Cretaceous which have not been identified or only loosely assigned to the Panorpoid complex, then we have the first fact. There were numbers of insects which were not trichopterous, nor were they recognizable as other recent groups. These are loosely grouped as the Panorpoid-complex. For the purpose of this argument we must assume that these insects were holometabolous with a larval organization of a caterpillar type and were terrestrial plant feeders. We know that holometabolous insects were present at that stage (Rodendorf, 1962). This caterpillar gave rise to an adult insect which I term a 'Panorpoid-imago', to indicate that we cannot recognize its modern affinities, certainly not from the wing fragments which are usually preserved.

If some of these caterpillars moved to an aquatic habitat, the resultant adult need not look very different from the stem-group adult, the Panorpoid-imago. Gradually, if the aquatic group specializes and the adults become more adapted to their particular environment, then the adults could differentiate more from the Panorpoid-imago ancestor. These would then come to represent our currently recognized Trichoptera. Meanwhile some further differentiation of the terrestrial caterpillar can take place in response to its environment; it may for example be able to make better use of its food or burrow into stems. If one projects this further, it is possible to have caterpillars, in the same sense that we would recognize them as such, that specialized for different habitats, whose adults would not yet be recognized as lepidopterous by our current definitions. The development of the flowering plants provided a stimulus for greater differentiation of the caterpillar and the adult stage which gradually assumed a lepidopterous type of organization.

At a later stage in the evolution of the Lepidoptera the influence of the adult and caterpillar on one another shows in more specific ways, for example with the evolution of distasteful adults which may derive their toxins from plants eaten by the caterpillar (e.g. *Aristolochia*-feeding papilionids). Similarly, the selection of a specific food-plant by the adult for the monophagous caterpillar, shows dependence of the caterpillar on the adult.

Differential evolution of the adult and larva is probably an oversimplification of what must have been a series of complicated evolutionary events, but it is possibly one of the features of the evolution of the Trichoptera and Lepidoptera. The possibility of the existence of a fairly specialized larval condition before the corresponding (recognizable) adult condition should be considered as the search for lepidopterous fossils is pushed further back in the Mesozoic. The principle of differential evolution of the larvae and adults might well apply to other holometabolous groups of insects.

ACKNOWLEDGEMENTS

Professor Aftim Acra, Beirut, in spite of many difficulties, has made a remarkable collection of Lower Cretaceous fossil insects. I am indebted to him for the privilege of studying the material. Mr G.S. Bearne embedded and polished the specimens and Mr G.J. Elliott (both Department of Mineralogy) gave advice on the chemical nature of the resin. Mr R. Croucher (Department of Palaeontology) advised on various techniques for handling the material.

I am grateful to Dr L. Vári for arranging publication by the Transvaal Museum and editing of my paper. His advice and help have been invaluable. I have also studied the *Micropterix* specimens collected by him and named one species after him as a gesture of appreciation of his work on Lepidoptera. I would also like to express my thanks to the Authorities of the Transvaal Museum for publishing my paper.

My colleagues have been patient and helpful in discussing the facts and ideas, but do not necessarily agree with the latter. To all of them I offer my thanks.

TABLE 1. Differential evolution of Trichoptera and Lepidoptera.

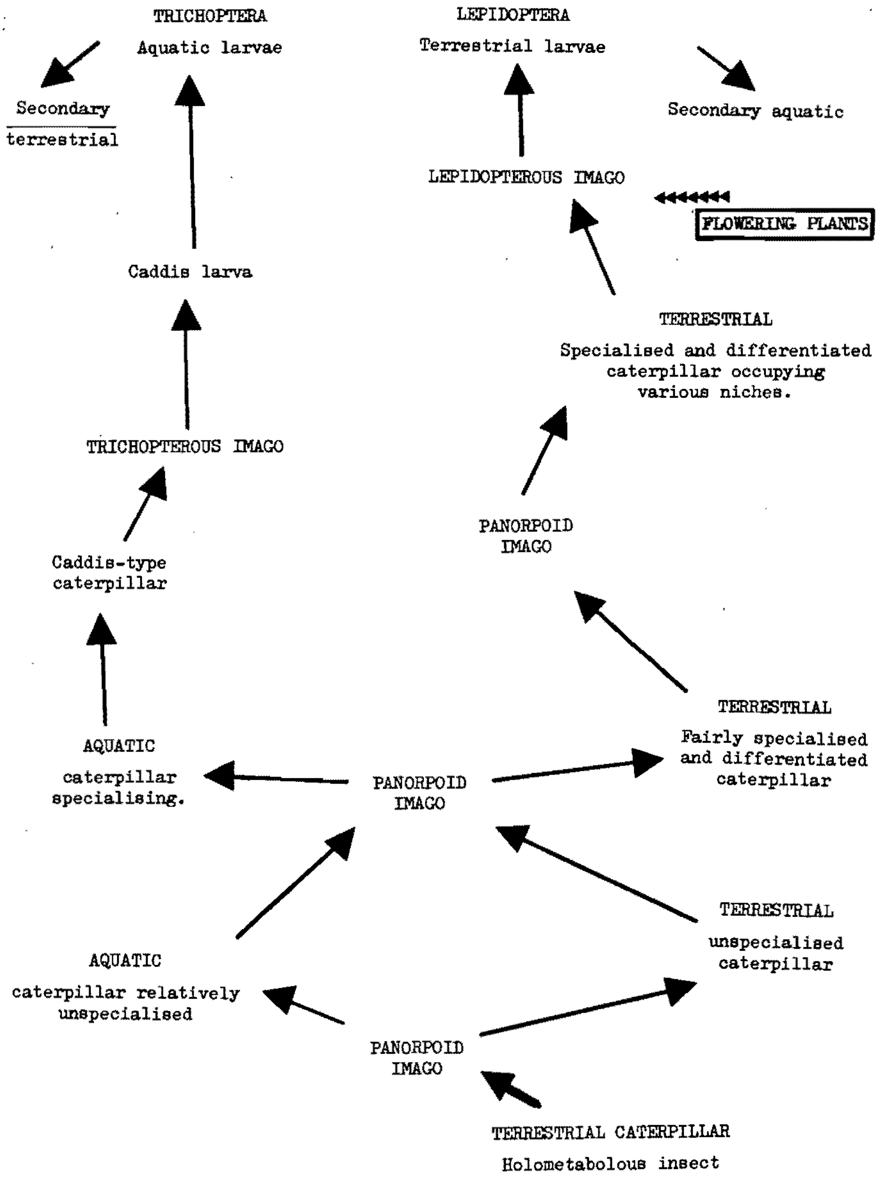


TABLE 2. Characteristics of the fossil and three recent genera of the Micropterigidae.

	Parasabatinca (fossil)	*Sabatinca* (recent)	*Agrionympha* (recent)	*Micropterix* (recent)
Mandibles	+	+	+	+
Ocelli	—	+	+	+
Maxillary palpi, long, reflexed . . .	+	+	+	+
Labial palpi two-segmented	+	+	+	+
Frenulum bristles	+	+	+	+
Jugum	?	+	+	+
Sc bifurcate in forewing	?	+	+	+
Microtrichia on wing membrane . .	+	+	+	+
R_1 forked in forewing	?	+	+	—
Apical cell in forewing	?	+	—	+
R_5 terminate on costal wing margin	—	—	—	+
Small tegulae	+	+	+	+
Epiphysis on fore tibia	+	+	+	+
Middle leg tibia with spines and spurs	+	+	—	—
Hind leg with strong subapical spurs	+	+	—	—
Tarsi with 2–3 or more strong apical spines	+	+	—	—

(+ Present; — Absent; ? Area obscured.)

BIBLIOGRAPHY

ACRA, A., MILKI, R. and ACRA, F., 1972. The occurence of Amber in Lebanon. L'Assoc. Libanaise Adv. Sci. Quatrième Réunion Scientifique: 7. [UNESCO abstract].

BROCK, J.P., 1971. A contribution towards an understanding of the morphology and phylogeny of the Ditrysian Lepidoptera. *J. nat. Hist.* **5**: 29–102.

COCKERELL, T.D.A., 1917. Insects in Burmese Amber. *Ann. ent. Soc. Am.* **10**: 323–9.

COMMON, I.F.B., 1970. Lepidoptera. *In*: The Insects of Australia: 765–866. Melbourne, Melbourne University Press.

——, 1975. Evolution and classification of the Lepidoptera. *A. Rev. Ent.* **20**: 183–203.

CROWSON, R.A., ROLFE, W.D.I., SMART, J., WATERSTON, C.D., WILLEY, E.C. and WOOTTON, R.J., 1967. *In*: The Fossil Record, Arthropoda: 499–534. London, Geological Society.

DAVIS, D.R., 1975. Systematic and Zoogeography of the family Neopseustidae with the proposal of a new superfamily [Neopseustoidea]. *Smithson. Contr. Zool.* **210**: 1–45.

DUGDALE, J.S., 1974. Female genital configuration in the classification of the Lepidoptera. *N.Z. Jl Zool.* **1**: 127–46.

DURDEN, C.J. and ROSE, H., 1978. The butterflies from the Middle Eocene. The earliest occurrence of fossil Papilionoidea (Lepidoptera). *Pierce-Sellards Ser. Tex. Memor. Mus.* **29**: 1–25.

Gillett, J.B., 1962. Pest Pressure, an underestimated factor in evolution. *In*: Taxonomy and Geography: 37–46, Public. No. 4. London, Syst. Association.

Hannemann, H.J., 1956. Die Kopfmuskular von *Micropteryx calthella* (L.), Lep. Morphologie und Funktion. *Zool. Jb* (*Anatomie*) **75**: 177–206.

Harrison, C.J.O. and Walker, C.A., 1977. Birds of the British Lower Eocene. *Tertiary Res. Special Paper* **3**: 1–52. London, Tertiary Research Group.

Hinton, H.E., 1946. On the homology and nomenclature of the setae of the Lepidopterous larvae with some notes on the phylogeny of the Lepidoptera. *Trans. R. ent. Soc. Lond.* **97**: 1–37.

——, 1958. The Phylogeny of the Panorpoid orders. *A. Rev. Ent.* **3**: 181–206.

Hughes, N.F., 1976. Palaeobiology of Angiosperm Origins: 1–242. Cambridge, Cambridge University Press.

Janse, A.J.T., 1942. The Moths of South Africa **4**: 1–183. Pretoria, National Research Council of South Africa.

Kristensen, N.P., 1975. The phylogeny of the hexapod "Orders". A critical review of recent accounts. *Z. zool. syst. Evol.-forsch.* **13**: 1–44.

Kühne, W.G., Kubig, L. and Schlüter, T., 1973. Eine Micropterygide (Lepidoptera, Homoneura) aus mittelcretazischem Harz Westfrankreichs. *Mitt. dt. ent. Ges.* **32**: 61–5.

Kuznetzov, N.J., 1941. A revision of the Amber Lepidoptera. *Acad. Sci. U.S.S.R.* **1941**: 5–135.

Mackay, M. R., 1970. Lepidoptera in Cretaceous Amber. *Science, N.Y.* **167**: 379–80.

Mutuura, A., 1972. Morphology of the female terminalia in Lepidoptera and its taxonomic significance. *Can. Ent.* **104**: 1055–71.

Razowski, J., 1974. Phylogeny and Classification of Lepidoptera. *Acta Zool. Crac.* **19**: 1–20.

Rebel, H., 1935. Bernstein-Lepidopteren. *Dt. ent. Z. Iris* **49**: 162–86.

Riek, E.F., 1976. A new collection of insects from the Upper Triassic of South Africa. *Ann. Natal Mus.* **22**: 791–820.

Robinson, G.S., 1977. A taxonomic revision of the genus *Callipielus* Butler (Lepid. Hepialidae). *Bull. Br. Mus. nat. Hist.* (Ent.) **35**: 101–21.

Rodendorf, B.B., 1962. Fundamentals of Palaeoentomology (Osnovy, Paleontologii). Arthropoda, Tracheata and Chelicerata: 1–560, Moscow. (in Russian)

Schlee, D., 1970. Insekten fossilien aus der unter Kreide, 1. Verwandtschaftsforschung an fossilien und rezenten Aleyrodina (Ins. Hemiptera). *Stuttg. Beitr. Nat.* **213**: 1–72.

Schlee, D. und Dietrich, H.G., 1970. Insektenführender Bernstein aus der Unterkreide des Libanon. *Neues Jb. Geol. Paläont. Mh.* **1970**: 40–50.

Schlüter, T., 1975. Nachweis verschiedener Insecta-Ordines in einem mittelkretazischen Harz Nordwestfrankreichs. *Ent. Germ.* **1**: 151–61.

——, 1976. Die Fossil Falle Harz. Die gegenwärtige Erforschungsstand. *Naturw. Rdsch., Stuttg.* **29**: 350–4.

Shields, O., 1976. Fossil Butterflies and the evolution of the Lepidoptera. *J. Res. Lepid.* **15**: 132–43.

Skalski, A.W., 1976. Les Lépidoptères fossiles de l'ambre. Etat actuel de nos connaissances. *Linn. Belg.* **6**: 154–208.

Smart, J. and Hughes, N.F., 1972. The insect and the plant: progressive palaeoecological integration. Insect/Plant Relationships. *Symposium R. ent. Soc. Lond.* **6**: 143–55. London, Blackwells.

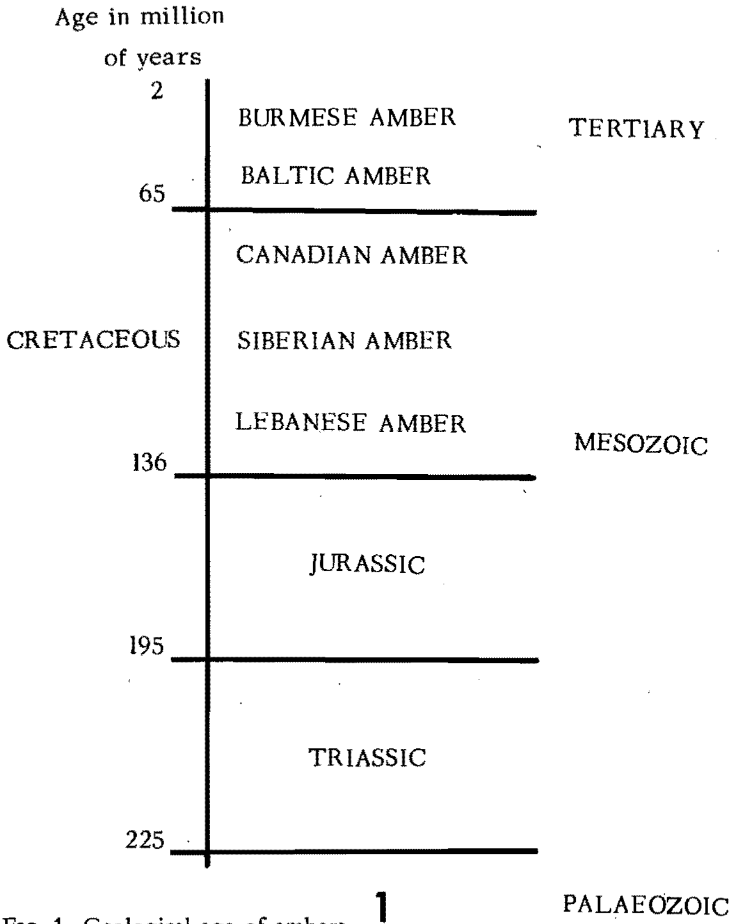
van Emden, H., 1972. Insect/Plant Relationships. *Ibidem* **6**: 1–198. London, Blackwells.

van Schepdael, J., 1974. Macrolépidoptères fossiles du domaine paléarctique. La Paléontologie au service de l'Ecologie. *Naturalistes Belg.* **55**: 3–37.

Whalley, P.E.S., 1971. The Thyrididae of Africa and its islands (Lepidoptera). *Bull. Br. Mus. nat. Hist.* (Ent.) Suppl. **17**: 1–198.

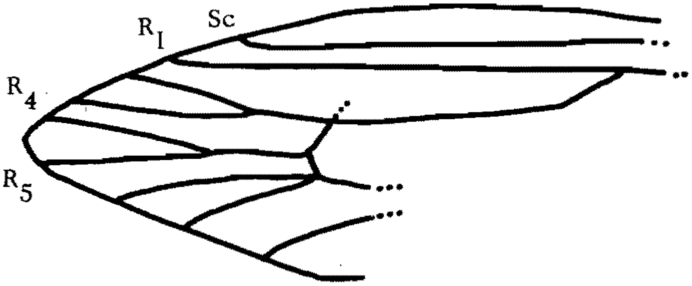
——, 1977. Lower Cretaceous Lepidoptera. *Nature, Lond.* **266**: 526.

Zeuner, F.E., 1962. Notes on the evolution of the Rhopalocera. *11. Int. Congr. Ent. 1960*, **1**: 310–3.



1

FIG. 1. Geological age of ambers.



2

FIG. 2. *Parasabatinca aftimacrai* spec. nov., forewing venation.

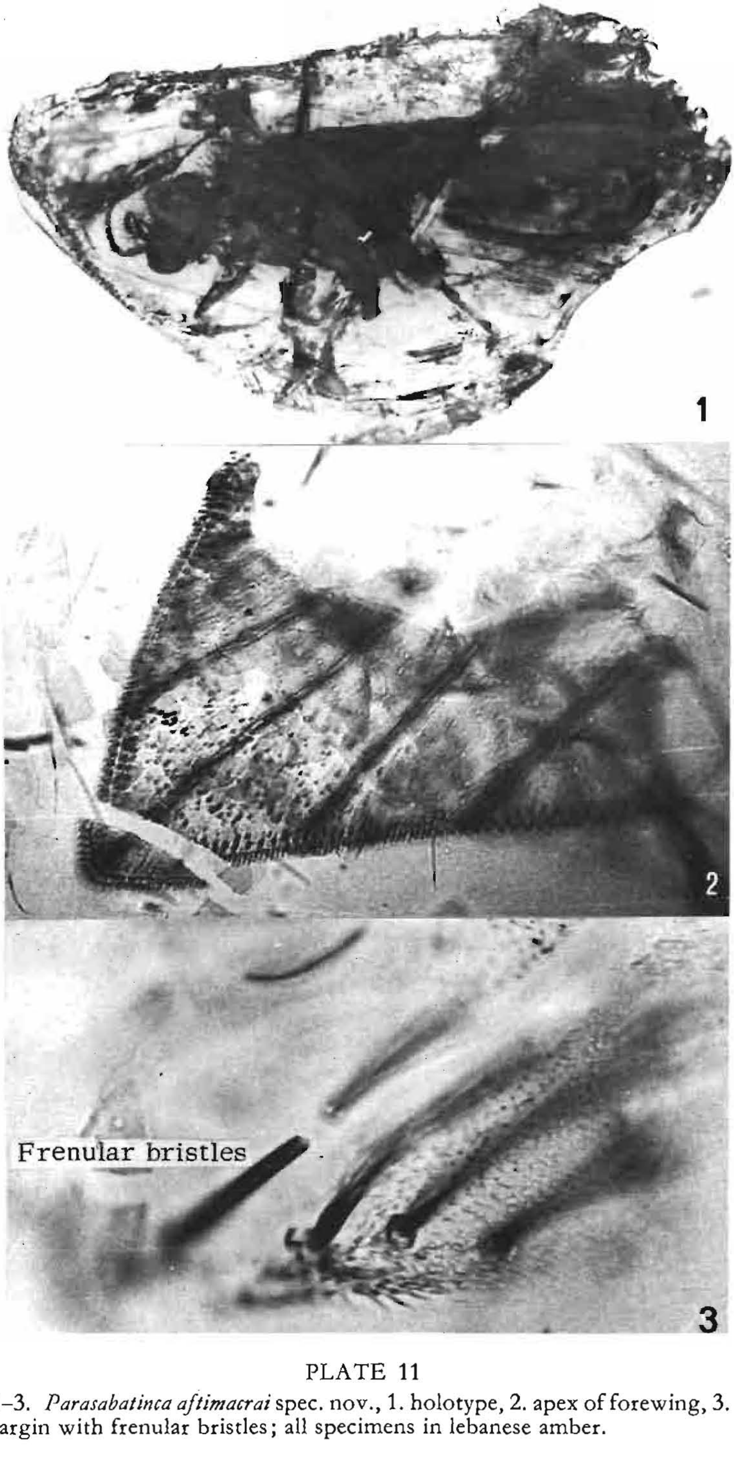


PLATE 11

FIGS. 1–3. *Parasabatinca aftimacrai* spec. nov., 1. holotype, 2. apex of forewing, 3. costal margin with frenular bristles; all specimens in lebanese amber.

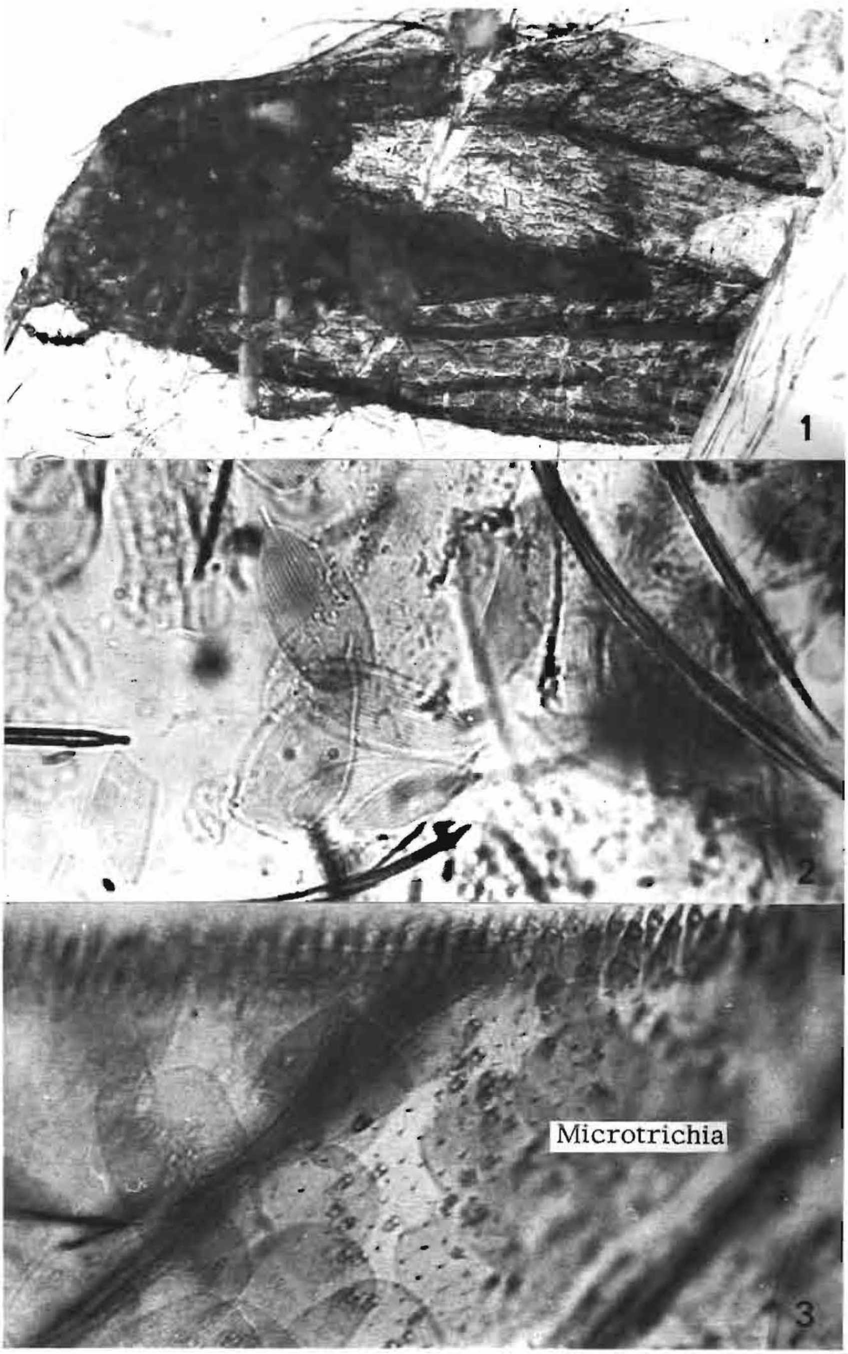


PLATE 12

FIGS. 1–3. *Parasabatinca aftimacrai* spec. nov., 1. paratype, 2. scales on forewing, 3. scales and microtricha on forewing; all specimens in lebanese amber.

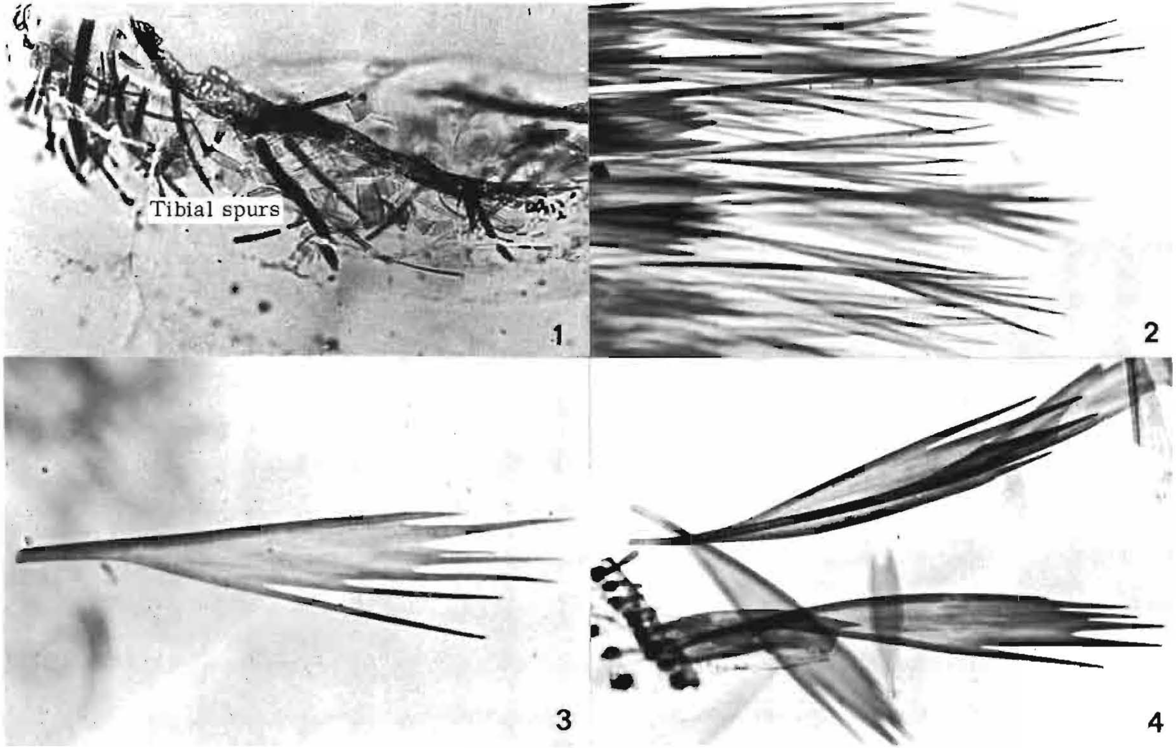


PLATE 13

FIG. 1. *Parasabatinca aftimacrai* spec. nov., two pairs of tibial spurs, femora incomplete, tarsi missing (right). 2–4. Forewing scales of Incurvariidae, 2. *Prodoxus* species (recent), 3 and 4. *Incurvarites* species; specimens 1 and 3–4 in lebanese amber.

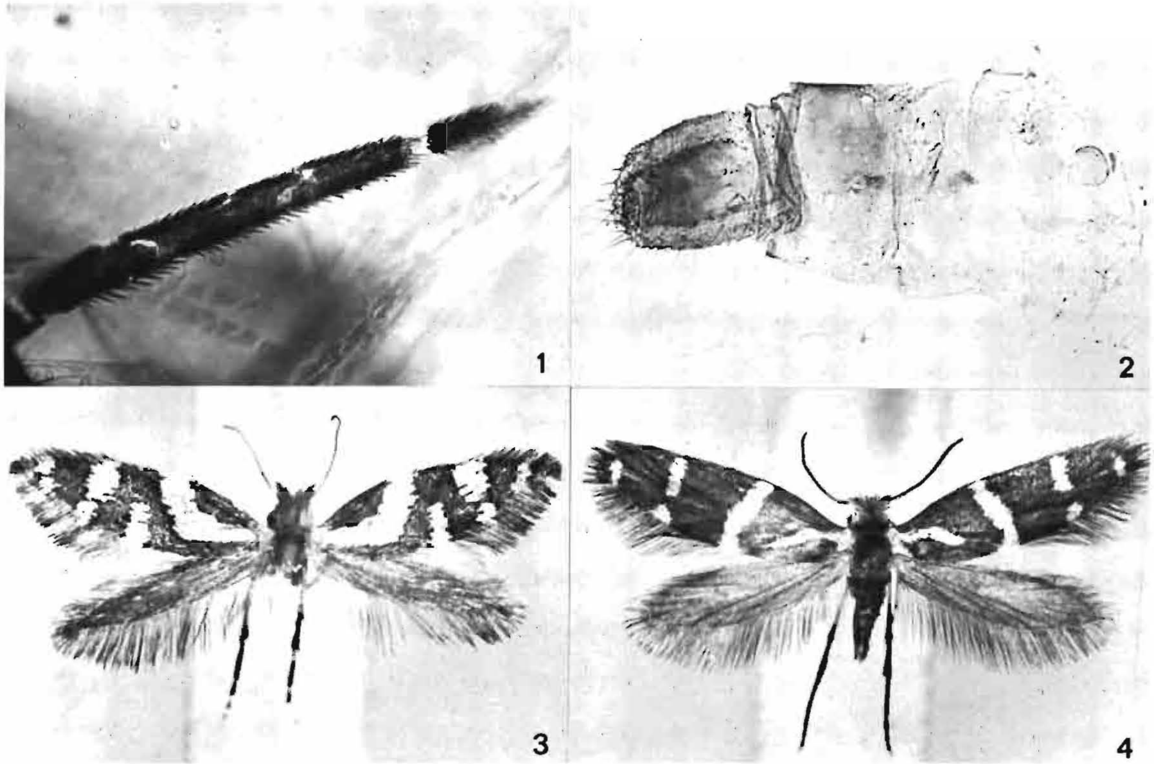


PLATE 14

FIG. 1. *Parasabatinca aftimacrai* spec. nov., hind tibial spur, in lebanese amber. 2 and 3. *Agrionympha capensis* spec. nov., 2. ♀-genitalia, 3. holotype. 4. *Agrionympha vari* spec. nov., holotype.