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FOSSIL BUTTERFLIES AND THE EVOLUTION OF LEPIDOPTERA OAKLEY SHIELDS

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ABSTRACT

The meager Cenozoic fossil record of butterflies is traced. Although pre-Tertiary fossils are so-far lacking, their development likely paralleled that of their angiosperm foodplants which probably arose in Early Mesozoic or Late Paleozoic times. The geological and morphological evidence herein suggests that primitive moths originated in the Permian, with primitive butterflies evolving from the Castnioid line soon thereafter, sometime in the Triassic. The major radiation of Lepidopteran families was already completed by the Upper Jurassic-Early Cretaceous when continental drift began, judging by their present-day, world-wide distribution.

INTRODUCTION

FOSSIL BUTTERFLIES ARE GREAT RARITIES, though moth fossils are more abundant. Butterflies' frail bodies and powers of flight may explain why they are rarely fossilized (Fox, 1948). Of 15,000 insect fossils from the Florissant beds of Colorado examined by Scudder (1889a), only 8 were butterflies. In all, about 41 specimens are known to science, many discovered about a century ago; all known occurrences derive from Cenozoic deposits (Table 1). Scudder's papers on fossil butterflies (1875, 1889b) are classics; he was without a doubt the most solid authority in this field. His interpretation of the affinity of *Apanthesis leuce*, however, was in error (Comstock, 1961).

The purpose of this paper is to review the scattered literature of the fossil record for butterflies and to determine at what evolutionary stage and geologic time interval the butterfly-moth lines diverged.

CENOZOIC BUTTERFLIES

By the lower Oligocene, the subfamilies Hesperinae, Satyrinae, Parnassinae, Coliadinae, Pierinae, Libytheinae, and Nymphalinae (plus an unplaced lycaenid) were present, signifying that all the major families of butterflies had developed by that time (Table 1). According to Zeuner (1962), "The Oligocene and Miocene species are very closely related to existing forms,

and are in no way more primitive," an opinion shared by Comstock (1961).

I concur with Wangrin (1939) that the fossil in an Oligocene nodule from Szczecin (= Stettin), Poland, is a butterfly with the head, body, and (two?) wings preserved, after viewing the figure (a pierid?). This locality was a seacoast, as many mollusks, some fish, a seacow, crabs, and a single bryozoan are known (Wangrin, 1939), and it is currently near the coast. No other insects are known. Similarly the two Gabbro, Italy, butterflies are from a seacoast locality. These Upper Miocene deposits are limestones containing calcareous algae, foraminifera, corals, and mollusks, with intercalations of pebbles not uncommonly, and rarely sands and clays (Desio, 1973, p. 590).

For butterflies, the richest fossil deposits are located at Florissant, Colorado. These are lacustrine beds with abundant plant and insect remains dated from the upper part of the Lower Oligocene, deduced from its relationship with other fossil floras, fossil vertebrates, and lithologic correlation (MacGinitie, 1953). The climate at that time was subhumid and warm temperate. Its butterfly fauna displays affinities to the Neotropics (Scudder, 1889a), although the two libytheids (I have examined the fossil *Prolibytha* and the description of *Barbarothesa*) are related to living species from southeastern Asia and the Indo-Australian regions, respectively. The butterflies from the calcareous marls of the gypsum quarries of Aix-en-Provence, France, mostly show Indo-Malayan affinities, while the two hesperiids from Aix and Rott display a relationship to subtropical North American genera (Scudder, 1875, 1889a). Saporta (1872) notes that the fossil angiosperm flora of Aix is related on the generic level primarily to southeastern Asia (see also Scudder, 1875, pp. 79-80). Two of the Radoboj butterflies from Yugoslavia display a "subtropical temperate American" affinity while the third, *Mylothrites pluto*, is African (Scudder, 1875).

Conditions apparently favorable for the preservation of butterfly wings include the margins of lakes, rivers, streams, and seacoasts, particularly during the Lower Oligocene and Miocene. In Oligocene-Miocene times, clay, sand, silt, mud, shale, limestone, marls, volcanic ash and dust, lacustrine, and freshwater deposits are common. This was a period of range erosion, basin fill, volcanic outpourings, and faulting, with plentiful fossils of mammals, plants, insects, soft-bodied invertebrates, etc.

The head capsule of a microlepidopteran larva in Canadian amber of the Cretaceous period is widely believed to be the

first evidence of Lepidoptera before the Tertiary (see MacKay, 1970). Recently some lepidopteran scales of a probable Micropterygidae were discovered in amber from the lowermost Upper Cretaceous (Cenomanian) of northwestern France (Kühne, Kubig, & Schlüter, 1973; Schlüter, 1975).

LEPIDOPTERA EVOLUTION

The present-day distribution of related butterflies in tropical regions on separated continents suggests that their radiation occurred prior to continental drift and seafloor spreading, i.e. before Upper Jurassic-Early Cretaceous times. For example, the Morphinae-Amathusiinae and Ithomiinae are confined to the Neotropics and Indo-Australian regions and are absent from Africa. The Riodininae are worldwide but with their greatest development in the Indo-Australian and Neotropical regions. The Neotropical Heliconiinae (2 genera) is closely paralleled by the Oriental *Cethosia* (Clark, 1927). The Pyrginae genus *Celaenorrhinus* occurs in tropical America, Asia, and the Orient (Evans, 1949). Neotropical-African links occur in the Acraeinae and Charaxinae. The Eunicini, a large tribe of Nymphalidae, is confined to South America except for *Asterope* from Africa (Carcasson, 1964, p. 152). *Hypanartia* is developed in tropical America, Africa and one or two species on Mauritius and neighbouring islands; *H. delius* from West Africa closely resembles certain American species (Eliot, 1947).

The Lepidoptera likely arose in a symbiosis (i.e. coevolved) with the first flowers (Forbes, 1932; Wangrin, 1939; Comstock, 1961; Eaton, 1963; Owen, 1971, p. 148; Common, 1975), as most modern species use angiosperms for larval food and adult nectar. Lepidoptera and Trichoptera arose from a common ancestor; the latter date back to the Permian (Ross, 1967). According to Kristensen (1975, pp. 32-33), Trichoptera and Lepidoptera share numerous biological characteristics that place them in the same monophyletic superorder (Amphiesmenoptera), but that Lepidoptera did not evolve from Trichoptera because their larvae differ in certain fundamental characters. No angiosperms are supposedly known before the Early Cretaceous, and there is a lack of fossil evidence regarding ancestral forms; "the evolutionary advancement and diversity commonly attributed to Early Cretaceous representatives of the angiosperms has been interpreted to imply either (1) their relatively rapid evolution in middle Mesozoic time, or (2) their extended pre-Cretaceous

existence" (Scott, Barghoorn, & Leopold, 1960). Axelrod (1961, 1970) marshalls evidence for angiosperms originating in moist tropical upland (but not highland) regions during Permo-Triassic time, long before they began to invade the lowland sites of deposition in the Early Cretaceous, as indicated by many primitive living angiosperms persisting in upland sites. He notes that the extraordinary rate of evolution demanded of the vegetative plant body by a middle Mesozoic origin is highly improbable. Croizat (1968) thinks angiosperms originated soon after the Permo-Carboniferous glaciers had destroyed the Paleozoic flora. Hawkes & Smith (1965) reason that angiosperms originated in Permian (or Carboniferous) times in Gondwanaland before the onset of continental drift. Indeed, Radforth & Rouse (1956) report references to a tricolpate pollen in a Jurassic sediment and tetra-porate pollen resembling *Alnus* (Betulaceae) from Mississippian strata of Russia.

Butterflies no doubt originated from a moth line that was the common ancestor of the Cossidae and Castniidae (Forbes, 1960, p. 58) or directly from Castnioid stock (Brock, 1971). Miller (1970) emphasizes that Hesperioidea are morphologically closely allied to the Castniidae. One Pyrginae, *Euschemon*, still retains the frenulum and retinaculum of moths (Turner, 1947, p. 316). The most primitive moths are the Homoneura consisting of the Micropterygoidea and the Hepialoidea; the most primitive family is the Micropterygidae, with biting mouth-parts and neuration similar to the most primitive family of Trichoptera, the Rhyacophilidae, and to the Upper Permian *Belmontia* of Paramecoptera from the Upper Coal-Measures of Newcastle, N. S. W. (allied to Mecoptera and Protomecoptera) that Tillyard believes from his detailed analysis to be the common ancestor of the Trichoptera and Lepidoptera (Tillyard, 1919; Turner, 1947). Friese (1970) thinks Hepialoidea rather than Micropterygoidea should be regarded as the most primitive lepidopteran group, based on a number of previously neglected characteristics interpreted according to Hennig's phylogenetic rules. Turner (1947, p. 313) postulates a hypothetical family Protocossidae to link Cossidae-Tineidae remotely with the stem from which Micropterygoidea and Hepialoidea arose. Nisulescu (1970) has discovered rudimentary mandibles in *Castnia daedalus*, so perhaps Castniidae itself is close to the Micropterygoidea line. Tindale (1963) has proposed that butterflies should be regarded as a subordinal group (*Schizoneura*) approximately

equal in importance to the rest of the Heteroneura and separate also from the Homoneura, based on a deep division between the forewing vein stems ($R_2 + R_3$) and ($R_1 + R_3$) in early pupal stages in the higher families of butterflies and *Euschemon*. Thus butterfly radiation probably occurred near the beginning of moth evolution, perhaps sometime in the Triassic, filling the diurnal niche along with primitive day-flying moths like the Castniidae.

From Upper Permian to Middle Triassic, arid or semi-arid climates were widespread (Kummel, 1970). The larvae of Hepialidae, Cossidae, and Castniidae feed within stems and roots (or externally on roots in the soil), perhaps originally as a response to increasing aridity (Common, 1970, p. 782). Likewise the Megathymidae, an archaic butterfly family formerly placed in the Castniidae, burrow as larvae into the basal leaves and roots of Agavaceae to feed in arid regions. The radiation of the primitive Lepidopteran families seems to fit an earth-expansion model in which the continents on the east and west sides of the Pacific were joined in a continuous landmass prior to the Upper Jurassic (Shields, 1975). I.e., Micropterygidae has an extremely wide distribution but with its headquarters in New Zealand, Hepialidae genera are greatest developed in Australia and the Neotropics (Paclt, 1953), Castniidae has its stronghold in the Neotropics, and Megathymidae is confined to southern North America and Central America (Eriocraniidae and Cossidae are generally distributed).

According to Davis (1975), the primitive family Neopseustidae resembles the Hepialoidea and Nepticuloidea in certain characters and is confined to southeast Asia and Chile.

Although some transoceanic movement following continental breakup did occur, it appears unlikely that any massive post-drift dispersal of the major butterfly groups took place between the tropical regions, since the intervening islands show no evidence of this and the Bering land bridge was never tropical. In the Pacific, small islands lying near continents such as the Galapagos, Samoa, Fiji, Carolines, and Guam are populated by a fair number of butterfly species compared with more distant islands like Napuka, Funafuti, Bikini, Rapa, Fanning, Canton, Gilberts, Wake, Necker, and Marquesas which are each composed of three (or less) migrant species. A similar pattern pertains to the Atlantic and Indian Oceans.

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TABLE 1. The known fossil record for butterflies.¹

Horizon	Locality	Deposit	Families	References
Upper Eocene or ?		Baltic	1 Lycaenid	Handlirsch,
Lower Oligocene		amber	(larva)	1906-1908
Upper Eocene or ?		Baltic amber	2 (?)	Larsen, 1974,
Lower Oligocene			papilionids	p. 34
Lower Oligocene	Florissant,	lacustrine	2 pierids,	Scudder, 1891;
	Colorado	beds	2 Libytheids,	Cockerell, 1907,
			7 nymphalids	1913; Handlirsch,
				1906-1908; Brown, 1976
Lower Oligocene	Aix-en-	calcareous	1 hesperiid,	Scudder, 1891;
	Provence,	marls of	1 papilionid,	Handlirsch,
	France	gypsum	1 pierid,	1906-1908;
		quarries	3 satyrids,	Theobald, 1937
			1 Lycaenid	

Lower Oligocene (Lattorfian)	Gurnet Bay, Isle of Wight	Osborne and Headon Beds of freshwater sands, clays, limestones	1 nymphalid	Zeuner, 1962
Middle Oligocene	Stolzenhagen near Szczecin, Poland	concretionary nodule of cemented marine sand	1 unplaced adult	Wangrin, 1939
Upper Oligocene	Rott, Rhine basin, Bavaria, Germany	lignite beds	1 hesperiid	Scudder, 1891; Handlirsch, 1906-1908
Lower Miocene	Radoboj, Yugoslavia	marls of lacustrine beds	1 pierid, 2 nymphalids	Scudder, 1891; Handlirsch, 1906-1908; Zeuner, 1942

TABLE 1. (continued).

Horizon	Locality	Deposit	Families	References
Middle Miocene (Karagan)	Stavropol, North Caucasus	continental deposits; "fragile rocks alternate with gray sandy clays"	2 nymphalids	Nekrutenko, 1965
Upper Miocene (Tortonian or Lower Messinian)	Gabbro, Italy (S. of Livorno, on the coast)	seacoast limestones	1 lycaenid, 1 papilionid	Handlirsch, 1906-1908
Upper Miocene (Sarmatian)	Randecker Maar, SW Germany	extremely fine shale called dysodil or paper-coal	1 pierid	Zeuner, 1942

Pleistocene	Shiobara, Japan	Lake deposits	1 papilionid	Fujiyama, 1968
Pleistocene	?	?	2 hesperiids, 1 nymphalid	Zeuner, 1962
Pleistocene or Recent	East Africa	amber	1 pierid	Zeuner, 1942
Quaternary	Re, Italy	lacustrine beds	1 lycaenid, 1 unplaced pupa	Handlirsch, 1906-1908
Recent (2000-3000 years)	Lindi and Bagamoyo, Tanzania	amber	1 nymphalid, 1 unplaceable adult	Evers, 1907

1 Leakey (1953) found undetermined Lepidoptera larvae and pupae in Miocene sandstone and clay beds from Rusinga and Mwafangano islands in Lake Victoria, Kenya.