



A brief introduction to the phylogeny of Iranian Lepidoptera*

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CHAPTER 3

A brief introduction to the phylogeny of Iranian Lepidoptera*

REZA ZAHIRI¹ & HOSSEIN RAJAEI²

The order Lepidoptera (Insecta), with roughly 160,000 described species, is the largest lineage of plant-feeding organisms on Earth (COMMON 1990; SCOBLE 1992; NIEUKERKEN et al. 2011). Still, many more lepidopteran species are awaiting to be discovered and it has been estimated that the number of species in the order will reach 400,000 or more (KRISTENSEN et al. 2007). Together with the other three megadiverse lineages of phytophagous organisms—Coleoptera, Diptera and Hymenoptera—Lepidoptera accounts for nearly 81% of all described species of living insects (POGUE 2009). The fossil records of these fragile insects are sparse and best represented as inclusions in amber and as larval mines in fossil leaves. Recent discoveries show that lepidopterans (including glossata) were flying on the planet at least 201 million years ago (mya) (VAN ELDIJK et al. 2018). The latter study dated back the presence of a proboscis to at least 70 mya, before the emergence of flowering plants. Another ancient fossil record of the order is *Archaeolepis mane* Whalley, 1985, which consists of three tiny wings on a piece of rock from the Early Jurassic (ca. 190 mya) of Dorset, England (GRIMALDI & ENGEL 2005).

The lepidopteran clade mainly diversified in the Cretaceous (145–66 mya) and early Tertiary (66–23 mya), together with the diversification of angiosperm (= flowering) plants (Fig. 1). Thus, Lepidoptera appears to be an old clade having mostly radiated recently. Recent phylogenomic studies estimate that the origin of the stem lineages of the many holometabolous insect orders dates to the Late Carboniferous (~300 mya), with spectacular diversifications within Lepidoptera having occurred around the Early Cretaceous, contemporarily with the radiation of flowering plants (MISOFF et al. 2014).

The monophyly of Lepidoptera and its systematic position within the class Insecta are well established (KRISTENSEN 1998). The order has a sister-group relationship to caddisflies (Trichoptera), with which it constitutes the higher-rank taxon Amphiesmenoptera. The close relationship between Lepidoptera and Trichoptera has essen-

tially never been disputed and is supported by strong morphological (KRISTENSEN 1997), molecular (WHEELER et al. 2001; WHITING 2002) and paleontological (GRIMALDI & ENGEL 2005) evidence. Lepidoptera and Trichoptera probably diverged from a common ancestor in the late Triassic (over 210 mya) (MISOFF et al. 2014).

It is believed that Lepidoptera underwent a burst of rapid radiation during the Cretaceous, together with the rise of flowering plants, and that many of the ditrysian superfamilies came into existence over a relatively short period (GRIMALDI & ENGEL 2005). Such an explosive radiation has left little evidence about the relationships between groups, because of the short evolutionary intervals between divergences. This evolutionary pattern of rapid diversification could partly explain why some ancient relationships within the Lepidoptera phylogeny are not fully resolved and remain uncertain.

A modern classification system should reflect the phylogeny of the group, i.e., the taxonomic groupings should correspond to monophyletic groups or “clades” (AARVIK et al. 2017), and relationships among the clades should represent true evolutionary relationships based on shared characters (synapomorphies). Most of the current Lepidoptera families are believed to be monophyletic and have stable defining traits (apomorphic characters). However, the superfamilies have proven difficult to resolve with morphology (mainly due to convergent evolution and shared ancestral characters, i.e., symplesiomorphies) and molecular data (mainly due to artefacts or insufficient data, lack of phylogenetic signal, homoplasy, sparse taxon sampling, etc.). As a result, the molecular revolution in lepidopterology is still in its infancy and numerous surprises are expected in the future (MUTANEN et al. 2010; KAWAHARA et al. 2019; ROTA et al. 2022).

A tentative phylogeny of Lepidoptera based on the lineages known from Iran was derived from REGIER et al. (2013) and KAWAHARA et al. (2019), and its graphic representation (Fig. 1) is adopted from AARVIK et al. (2017). The family Micropterigidae is the most basal lineage of the

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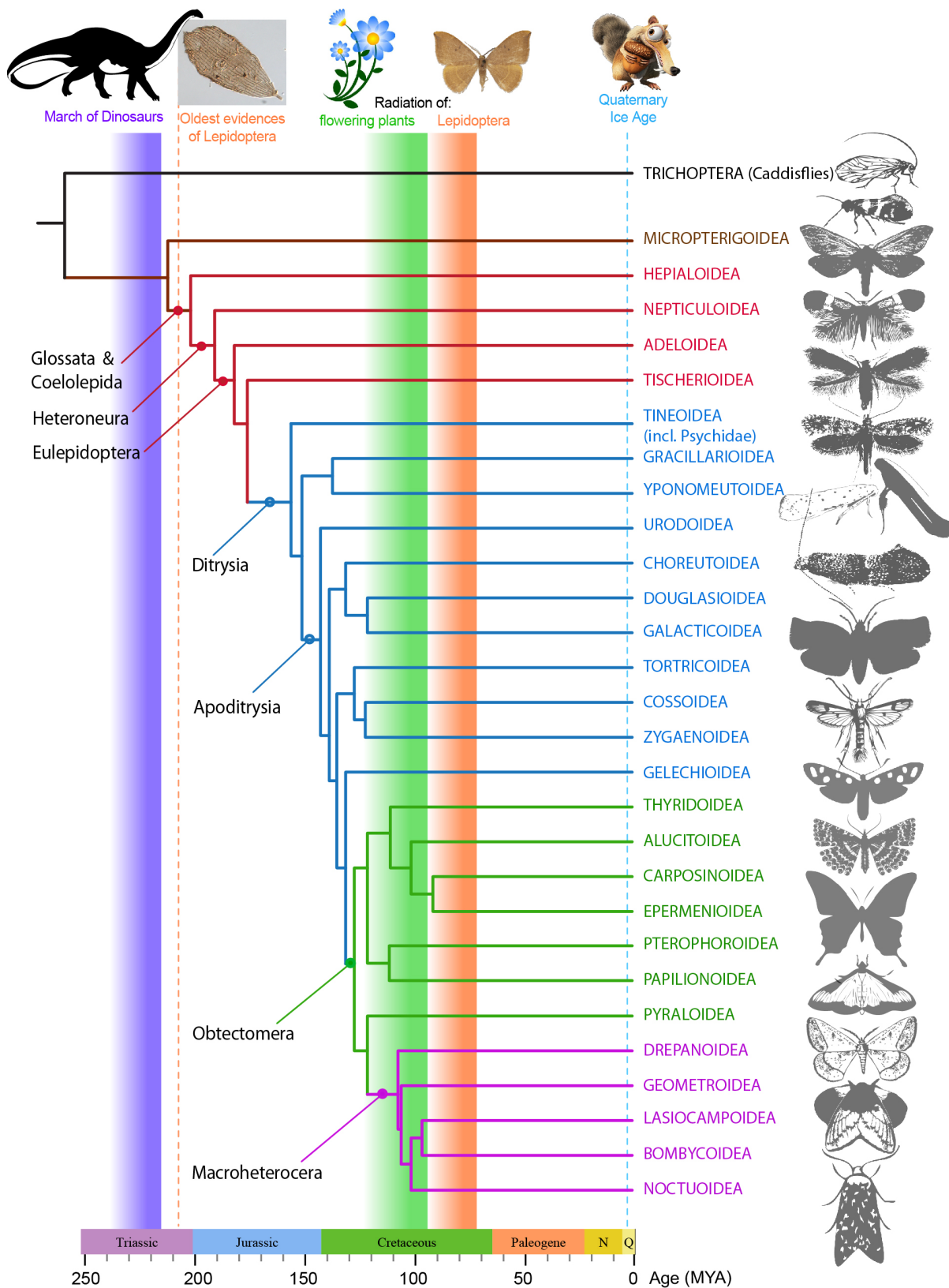


Fig. 1. Tentative phylogeny of the Lepidoptera of Iran. Based on REGIER et al. (2013) and KAWAHARA et al. (2019), with graphics adopted from AARVIK et al. (2017).

order and the only member of the clade Aglossata in Iran. This clade, together with the superfamily Micropterigoidea and the family Micropterigidae, is known only from two species firstly recorded from Iran (from the Hyrcanian forests in North Iran) in this catalogue. Adult micropterigid moths have not evolved a proboscis and retain the ancestral use of functional mandibles like their sister lineage caddisflies, hence their common name “mandibulate moths” (or Aglossata) (KRISTENSEN 1998). Additionally, their bodies are covered by solid scales (vs. hollow scales in Coelolepida). They are generally small in size and diurnal. Their larvae have retained, like most caddisflies, the probably ancestral amphiesmenopteran diet consisting of plant detritus. Micropterigid larvae feed on fungal hyphae, liverworts and other substrates among the forest leaf litter, and some feed on the foliage of angiosperms; the adults feed on pollen. This primitive lepidopteran moth family has a homoneurous wing venation in which the venation of the fore- and hindwings is alike.

The large, monophyletic group comprising all other moths, Glossata, includes those with a “proboscis”, constituted by a pair of elongated maxillary galeae covered with rows of minute processes (legulae). The pair of galeae is “zipped” together medially and forms a tube (KRENN & KRISTENSEN 2000). Glossatan larvae are equipped with a spinneret on the apex of the pre-labial hypopharyngeal lobe. Secretions are exuded at the tip of this spinneret in the form of silk, which is used for constructing larval retreats and webs (e.g., for ballooning and making pupal cases or cocoons). Nearly all adult specimens of the clade Glossata (except members of the superfamily Eriocranioidea, which has not yet been recorded in Iran) have body and wings covered with hollow scales (clade Coelolepida).

Two major clades are recognized within Coelolepida. The clade Exoporia, which mainly includes the superfamily Hepialoidea (or ghost moths and relatives), is characterized by the lack of an internal connection between the corpus bursae and the ovaries of the female reproductive system (i.e., absence of a ductus seminalis). Only one species of ghost moth, *Hepialus humuli* (Linnaeus, 1758), is known from Iran.

The other clade within Coelolepida is Heteroneura, which comprises over 99% of all Lepidoptera. The main synapomorphic character of heteroneuran Lepidoptera is a reduction in the branching of the Radius veins of the hindwing, as well as the development of a more effective wing coupling system called the frenulo-retinacular system (in contrast to homoneuran Lepidoptera, which have a similar venation system on both the fore- and hindwings and whose wings are coupled with the so-called Jugal system).

The most basal group within Heteroneura known from Iran is the superfamily Nepticuloidea with 35 reported species in the family Nepticulidae, a diverse lineage with

819 species worldwide. The family includes some of the smallest lepidopterans, with a wing length of merely 1.5 mm. Most of the larvae are leafminers.

Within the clade Heteroneura, all taxa except the superfamily Nepticuloidea are recognized as belonging to the Eulepidoptera clade, characterized by several synapomorphies including a more advanced coupling of the two halves of the proboscis. The superfamilies Adeloidea and Tischerioidea are the two most primitive eulepidopteran lineages, with only eight species known from Iran. All remaining Eulepidoptera belong to the clade Ditrysia, in which the female genitalia have two separate openings: the gonopore, for mating, and the ovipore, for egg-laying. Ditrysia include about 98% of lepidopteran diversity and include the butterflies and Microlepidoptera (Fig. 1).

Both morphological (NIELSEN 1989; KRISTENSEN & SKALSKI 1998) and molecular (e.g., MUTANEN et al. 2010) evidence for the monophyly of Ditrysia is quite convincing. The “monotrysonian” grade is more basal, and in contrast to Ditrysia has a single female genital opening and is now considered polyphyletic (MUTANEN et al. 2010).

The superfamily Tineoidea is the most basal lineage among Ditrysia and is represented by 100 species in Iran. Phylogenetic resolution is poor within Ditrysia, but some larger clades can be morphologically recognized.

All Ditrysia apart from Tineoidea, Gracillarioidea and Yponomeutoidea are united in the clade Apoditrysia, characterized by modifications of sternite II (i.e., reduced apodemes) of the adult (MINET 1983; KRISTENSEN & SKALSKI 1998) and a specific chaetotaxy in the larvae. In the clade Apoditrysia, the recently described Ustyurtiidae (superfamily Urodoidea) is the most basal family. In this catalogue, we report both the superfamily and the family from Iran based on a single species, *Karwandania chimabacchella* Amsel, 1959, described from the Sistan-o-Baluchestan province by AMSEL (1959).

The next clade contains three monophyletic groups: the superfamilies Douglassioidea, Choreutoidea and Galacticoidea, with 15 known species in Iran altogether.

The next monophyletic assemblage is a group containing the superfamilies Tortricoidea, Cossioidea and Zygaenoidea. This clade is globally highly diverse and represented by over 400 species in Iran, with many more species still awaiting discovery (LANDRY et al. 2023). Two families, Zygaenidae and Cossidae, are among the best-known families in Iran (e.g., KEIL & TARMANN 1997; HOFMANN & KEIL 2011; KEIL 2014; HOFMANN & TREMEWAN 2017, 2020; ALIPANAH et al. 2021).

The superfamily Gelechioidea is sister to the clade Obtectomera. With about 18,490 described species in ca. 1,480 genera, this superfamily is among the most diverse lineages of so-called Microlepidoptera. They are especially diverse in semi-arid habitats and mountains, which are common in Iran. Gelechioidea are overall rather small

and often dull-coloured, and as such are considered difficult to identify.

Within Apoditrysia, Obtectomera are characterized by the first four abdominal segments in the pupa usually being immobile, rendering the pupa unable to wriggle out of the surrounding substrate before hatching, and by a modification of the pulvillus of the pretarsus of the imago. Obtectomera include most of the larger moths and butterflies plus several superfamilies of micromoths, but not Cossioidea, Zygaenoidea, Sesioidea and Tortricioidea among others. The first clade within Obtectomera includes four superfamilies: Thyridoidea, Alucitoidea, Carposinoidea and Epermenioidea. The sister lineage to this clade contains two superfamilies: the butterflies (Papilionoidea) and Pterophoroidea. Pyraloidea are the sister-group to a monophyletic Macroheterocera containing the macromoth superfamilies Drepanoidea, Geometroidea, Lasiocampoidea, Bombycoidea and Noctuoidea. The latter is the most diverse superfamily of Lepidoptera, with approximately 1,368 described species and many undescribed and unnamed species in Iran.

The name Macroheterocera (alternatively Macrolepidoptera) has been variously used, often as a collective term for all larger Lepidoptera, separating them from Microlepidoptera. This is in some ways practical, but neither Macrolepidoptera nor Microlepidoptera are monophyletic groups.


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