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Evolution and chemistry relations in butterflies of Parnassiinae (Lepidoptera, Papilionidae)

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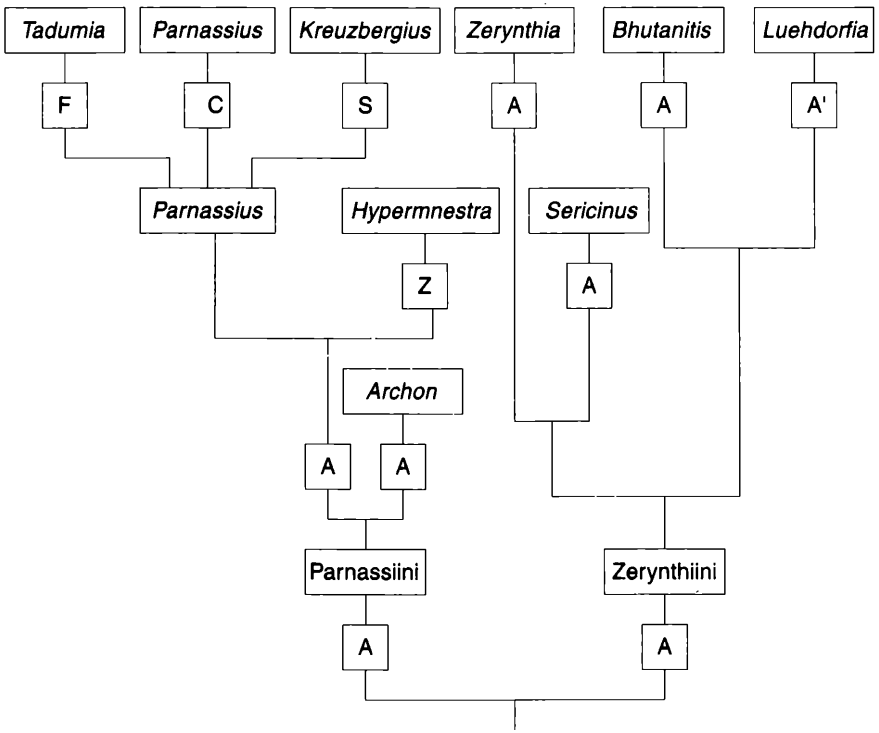
Very often toxic substances of the metabolism of plants determine via the control of food behaviour of phytophagous insects the coevolution of plants and insects (FRAENKEL, 1959; EHRLICH & RAVEN, 1965). There is more information about some species of Danaidae, Heliconidae and Pieridae in the research of the role of secondary metabolism (ROTHSCHILD, 1973; HARBORN, 1985).
The subfamily Parnassiinae has not been studied in this respect due to some mistaken data about the trophic relations of its species. But last time the foodplants of Parnassiinae species were determined (ACKERY, 1975; KREUZBERG, 1984, 1987) and the basic toxic substances of secondary metabolism have been found (table 1). Toxic substances of these papilionid's foodplants (Aristolochiaceae, Fumariaceae, Crassulaceae, Saxifragaceae, Scrophulariaceae) are used for chemical protection against predators and endoparasits and as oviposition attractants.

The Papilionidae have divided into subfamilies at the end of the Cretaceous Period. The Parnassiinae were formed in the euroasiatic part of Laurasia, the recent genera were formed during the Miocene and the early Pliocene Periods. In the beginning the primitive Papilionidae used species of Annonaceae and Aristolochiaceae as foodplants (HANCOCK, 1982). For many species of Annonaceae, Aristolochiaceae and Fumariaceae the presence of isochynoline alkaloids is known. The aristolochid acids in Aristolochiaceae originated from primitive isochynoline alkaloids by biosynthesis (LUKNER, 1979). The progressive evolution in the Parnassiinae has two aspects: the morphology of the insects and the chemistry of the foodplants.

The main factor of origination of *Parnassius* and *Hypermnestra* is the change of distribution of Aristolochiaceae during the Miocene Period by climatic changes. Following this, the Parnassiinae found foodplants with similar alkaloids: the Fumariceae with isochylonine alkaloids also and Zygophyllaceae with indol alkaloids. Due to historical changes of the climate some arid areas (300 mm water per year) were formed in Asia (map 1). The first of these zones (east coast of Tetis Sea) is the centre of *Hypermnestra* origination, and the second is the centre of *Parnassius* origination (Nanshan-Kunlun). The other genera of Parnassiinae did not occupy new adaptive zones, because their foodplants did not change their geographical distribution. But it is very interesting that *Luehdorfia* (very specialized in morphological characters) feeds on the specialized plant *Asarum* with its specialized aristolochoid secondary substances (alpha-Asaron etc.). Only one genus of Parnassiinae (*Parnassius*) has a great ecological and geographical adaptive radiation on the basis of the chemical and ecological specialization of its foodplants.

Table 1: Trophical and chemical relations in Parnassiinae

insect genus	plant genus	chemical substances
Archon, Zerynthia, Sericinus, Bhutanitis	*Aristolochia* (Aristolochiaceae)	aristolochid acids, isochynoline alkaloids
Luehdorfia	*Asarum* (Aristolochiaceae)	phenols (alpha-Asaron, etc.), glycosids
Hypermnestra	*Zygophyllum, Halimiphillum* (Zygophyllaceae)	indol alkaloids, glycosids
Parnassius (subgenus *Tadumia*)	*Corydalis, Cysticorydalis, Dicentra, Fumaria* (Fumariaceae)	isochynoline alkaloids
Parnassius (subgenus *Parnassius*)	*Sedum, Pseudosedum, Rhodiola, Clementsia, Rosularia, Orostachys, Sempervivum* (Crassulaceae), *Saxifraga* (Saxifragaceae)	piperidine alkaloids, glycosids
Parnassius (subgenus *Kreuzbergius*)	*Lagotis, Veronica* (Scrophulariaceae)	glycosids



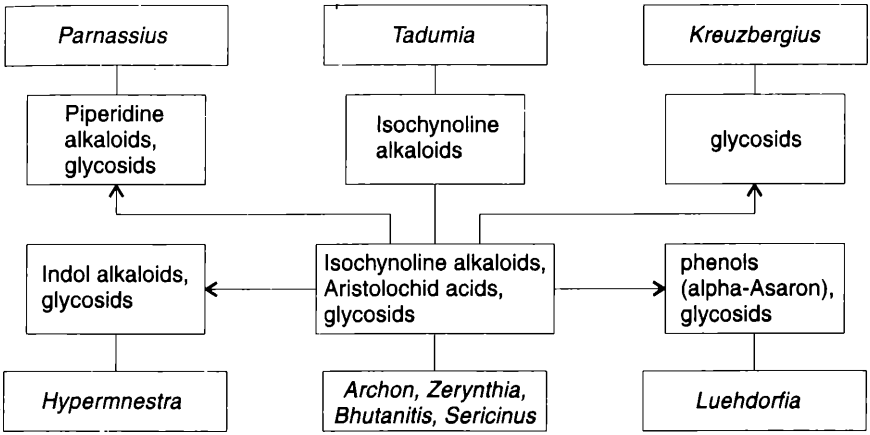


Fig. 2: The ways of chemical specialisation in Parnassiinae

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Fig. 1. Phylogenetic scheme of trophic relations in Parnassiinae:
A – Aristolochiaceae (*Aristolochia*), A' – Aristolochiaceae (*Asarum, Asiasarum*), Z – Zygophyllaceae, F – Fumariaceae, C – Crassulaceae, S – Scrophulariaceae.

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