

## “Issidisation” of Fulgoroid Planthoppers (Homoptera, Fulgoroidea) as a Case of Parallel Adaptive Radiation

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**Abstract**—The term “issidisation” is proposed to describe the formation of the specific box-like body shape (including elytra) in several families of planthoppers (Acanaloniidae, Caliscelidae, Issidae, Nogodinidae, and Tropicuchidae). Parallel radiation resulting from adaptation to semi-arid and arid conditions is considered the cause of issidisation. The possibly rapid rate of evolution of higher Fulgoroidea and especially Issidae is discussed. Pyrogenic renewal of Mediterranean-type communities is hypothesized to be the cause of sympatric speciation in the Mediterranean insects.

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Parallelism, as well as convergence and reversal, is a form of homoplasy. Parallel evolution is the phenomenon of distantly related and geographically separated groups becoming independently adapted to similar ecological conditions and acquiring similar structural and behavioral traits (Fain and Houde, 2004). A considerable amount of data accumulated over the recent decades suggests that “parallel appearance of characters at different levels is more than common in evolution” (Zelenkov, 2011). In particular, such phenomena as “mammalisation” of theriodonts (Tatarinov, 1976), “arthropodisation” (Ponomarenko, 2005), and “ornithisation” of theropod dinosaurs (Kurochkin, 2006) were described; parallel radiation was demonstrated in various groups of placental mammals (Madsen et al., 2001) and neognathous birds (Fain and Houde, 2004).

The group of “issidoid” or “tropicuchoid” families including Issidae Spinola, Caliscelidae Amyot et Serville, Acanaloniidae Amyot et Serville, Tropicuchidae Stål, and Nogodinidae Melichar is a notorious problem in the modern taxonomy of fulgoroid planthoppers. In my opinion, these families should be collectively referred to as the “issidoid group” since Issidae is the senior name (Spinola, 1839). There are many publications devoted to the problems of differentiating these families and revealing their relationships (Yeh et al., 1998, 2005; Emeljanov, 1999, 2009; Gnezdilov, 2003b, 2007, 2009b, 2012a, 2012b; Gnezdilov and Wilson, 2006; Shcherbakov, 2006, 2007; Urban and

Cryan, 2007; Szewo and Stroiński, 2010; Hamilton, 2012).

Previously, the families Issidae, Caliscelidae, and Acanaloniidae together with some genera of the families Tropicuchidae, Nogodinidae, and Ricaniidae were traditionally considered within the family Issidae *sensu lato* due to the so-called “issidoid” habitus: a box-like body shape, subbrachypterous (with the fore wings barely covering the abdomen) or brachypterous, a broad metope, and a transverse coryphe (Melichar, 1906; Fennah, 1954; O’Brien and Wilson, 1985); the head parts are named here according to Emeljanov (1995).

The system of the family Issidae *sensu lato* was reconsidered based on the results of morphological studies of the male and female genitalia (Gnezdilov, 2008). The polyphyletic nature of Issidae *sensu lato* was also inferred from molecular data (Yeh et al., 2005; Urban and Cryan, 2007). The process was initiated by Fennah (1978, 1984) who revised the family Nogodinidae. I recently suggested that the family Issidae should be limited to the nominotypical subfamily with 3 tribes: Issini Spinola, 1839, Hemisphaeriini Melichar, 1906, and Parahiraciini Cheng et Yang, 1991 (Gnezdilov, 2003a, 2009a, 2012b). Based on the characters of male and female genital morphology, some of the suprageneric taxa previously included in Issidae were distinguished as distinct families Caliscelidae and Acanaloniidae (Emeljanov, 1999; Gnezdilov, 2012a), thus restoring the family rank originally

proposed by Melichar (1906) and supported by Muir (1930). Some other taxa were transferred to other families: Trienopininae Fennah and Gaetuliina Fennah, to the family Tropiciduchidae; Tonginae Kirkaldy and Colpopterini Gnezdilov, to the family Nogodinidae; Adenissini Dlabola, to the family Caliscelidae (Gnezdilov, 2003b, 2007, 2012b; Gnezdilov and Wilson, 2006). The subfamily Pharsalinae Gnezdilov was established in the family Ricaniidae (Gnezdilov, 2009b) for the genus *Pharsalus* Melichar, 1906, originally described within Issidae (Melichar, 1906). However, despite the revisions and attempts at building cladograms, there is still no consensus on the relationships within the “issidoid” group of families. The different views on the phylogeny of these families were reviewed by Urban and Cryan (2007). Reliable apomorphies of the above families should be found in order to solve this problem.

Fennah (1967) was one of the first to offer an explanation for the development of the combination of a stocky, almost ovoid body with brachyptery in fulgoroid planthoppers inhabiting the South African fynbos (a peculiar type of xerophilous shrubland endemic to the Cape Region). According to the cited author, such a constitution saves water by reducing the body surface, facilitates cold resistance and female fecundity, and enhances the hopping ability, whereas brachyptery facilitates mobility in the dense and coarse fynbos vegetation which would hinder flight. However, Kerzhner (1981), considering brachyptery in true bugs of the family Nabidae, noted that shortened wings were characteristic of species living in low and sparse vegetation. According to Emeljanov (1980), a denser integument and a more compact body may be regarded as morphological adaptations to arid climate in planthoppers of the subfamily Orgeriinae Fieber of the family Dictyopharidae Spinola.

In all appearances, the subbrachypterous (“issidoid”) morphological type is one of the most advantageous in arid habitats. For example, in South Africa and Madagascar, where representatives of the family Issidae are absent (except for one species, *Ikonza lawrencei* Hesse, 1925 from northern Namibia), the arid stations are inhabited by issidoid representatives of Mithymnini Fennah (Nogodinidae), Gaetuliini (Tropiciduchidae), and Ricaniinae (Ricaniidae).

A similar body shape in species inhabiting other communities, such as rain forests, has appeared for different reasons, possibly related to mimicry. Exam-

ples of this kind are members of the Oriental tribes Hemisphaeriini and Parahiraciini (Issidae) and probably the subbrachypterous planthoppers of the family Ricaniidae from Madagascar (Stroiński et al., 2011), which seem to imitate beetles. In particular, representatives of the genera *Gergithus* Stål (Hemisphaeriini) and *Globularica* Stroiński, Gnezdilov et Bourgoin (Ricaniidae, Ricaniinae) resemble ladybirds, whereas representatives of the tribe Parahiraciini, at least those with the lower part of the metope and the upper part of the postclypeus shaped as a proboscis (*Bardunia* Stål, *Fortunia* Distant, *Scantinius* Stål, etc.), seem to imitate weevils (Shelford, 1902; Gnezdilov and Wilson, 2007).

The ancestral forms of higher fulgoroid planthoppers are difficult to determine since their fossil records are scarce (Shcherbakov, 2006). According to the results of molecular analysis (Urban and Cryan, 2007), families of the issidoid group are young (advanced) taxa. Indeed, fossil representatives of Nogodinidae are known only since the Late Paleocene (Shcherbakov, 2006), those of Tropiciduchidae, since the Eocene (Szwedo et al., 2004; Shcherbakov, 2006), those of Issidae, since the Miocene (Stroiński and Szwedo, 2008), whereas no fossil data are available on Caliscelidae and Acanaloniidae (Szwedo, 2002; Shcherbakov, 2006). It should be borne in mind that the absence of fossil remains of a particular group does not prove that this group did not exist during a given geological epoch. Besides, insects inhabiting mountain and desert regions have minimum chances to be preserved as fossils (Zherikhin, 1980). According to the data of Szwedo (2002), families of the issidoid group must have originated at the Cretaceous–Neogene boundary and diverged widely during the Eocene–Miocene. In the opinion of Shcherbakov (2006), the latest radiation of higher fulgoroid families, including the taxa in question, occurred after the Cretaceous–Paleogene crisis, whereas the first higher fulgoroid planthoppers may already have been subbrachypterous and “issidoid.” I consider the latter assumption to be unlikely since subbrachypterous forms are specialized (advanced) and cannot be regarded as ancestors of the recent higher fulgoroid taxa. In fact, box-shaped subbrachypterous forms were already present in the Eocene: representatives of two tribes of the family Tropiciduchidae, namely Austrini Szwedo et Stroiński, 2010 (known only as fossils) and Gaetuliini Fennah (broadly represented in the recent fauna as well), were described from the Baltic amber (Szwedo and Stroiński, 1999, 2010).

It seems that we are dealing with almost simultaneous (at the geological scale) appearance of similar forms, adapted to arid conditions, in several fulgoroid families. This phenomenon was similar to the origin of the Cretaceous family Perforissidae Shcherbakov, which the author of this taxon regarded as “a neotenic derivative of the Mesozoic Fulgoridiidae and an early attempt at ‘constructing’ cicadellid forms based on lantern-flies, related to colonization of the first angiosperms in coastal habitats” (Shcherbakov, 2007). The fossil data on various groups show that homoplastic forms (in our case, Issidae-like ones) “often originate on the basis of similar ancestors, more or less simultaneously in different groups” (Rasnitsyn, 1996, cited after Rasnitsyn, 2005).

For example, the origin of the main orders of birds is believed to have been “accompanied by rapid cladogenesis, so that phylogenetic relations between the orders are extremely difficult to resolve even by the modern molecular methods” (Zelenkov, 2011). The molecular cladogram pattern for Hemiptera can also be interpreted as an indication of rapid diversification of the main groups within the order (Cryan and Urban, 2012). There is an amazing hypothesis by Easteal (1999, cited after Madsen et al., 2001) according to which the primitive Cretaceous placental mammals diverged phylogenetically even before they acquired morphological differences corresponding to the rank of orders. This hypothesis agrees with the idea that “transformations of the genotype can occur, and in fact do occur, without any changes in the phenotype” (Groditsky, 2001), by changes in the genetic polymery of a character. By analogy, one may assume that the difficulties in outlining the families Issidae, Caliscelidae, Acanaloniidae, Tropiduchidae, and Nogodinidae result from rapid evolution of these groups. It is known that “non-uniform rates and stability of directions of evolution are its inherent properties,” whereas “large morphofunctional changes are saltational by their nature” (Emeljanov and Rasnitsyn, 1991).

The number of seminal follicles varies between congeneric species and between different genera of West Palaearctic representatives of the tribe Issini (Maryńska-Nadachowska et al., 2006; Kuznetsova et al., 2010), whereas some more primitive families of fulgoroid planthoppers, such as Dictyopharidae Spinola and Delphacidae Leach, are characterized by a stable number of seminal follicles within tribes and subfamilies (Emeljanov and Kuznetsova, 1983). Con-

trary to the opinion of Emeljanov and Kuznetsova (1983) that polymerization of seminal follicles is typical of more primitive groups, this trend is observed in a number of higher fulgoroid families: not only Issidae but also Nogodinidae, Ricaniidae, and Flatidae (Kuznetsova et al., 1998). Thus, polymerization may indicate a comparatively young (advanced) status of these families, in which the number of follicles has not yet completely stabilized at the level of supraspecific taxa. This is an example of the rule of initial diversity (Mamkaev, 1968) reflecting “high structural variation at early stages of evolution of a given taxon” (Rasnitsyn, 2002), which may be considered an indication that the families Issidae, Nogodinidae, Ricaniidae, and Flatidae are at early stages of their evolution.

In particular, diversification of the family Issidae in the West Palaearctic may be reasonably connected with aridization of the Mediterranean landscapes. Typical Mediterranean communities can be traced in the northern hemisphere only since the Miocene–Pliocene (Zherikhin, 1995), whereas the recent Mediterranean climate was formed only 5–10 million years ago as the result of a global decrease in temperature and precipitation and changes in the atmospheric circulation patterns, which started after the Paleocene–Eocene thermal maximum due to formation of the Antarctic and Greenland ice caps in the Pliocene (Axelrod, 1973; Suc, 1984, cited after Ackerly, 2009).

Having analyzed the diversification patterns in plants, Linder (2008) found that the younger taxa diverged at greater rates as compared to older ones. These rates were assumed to decrease with time in all the taxa. This trend may be present in animal taxa as well.

The West Palaearctic fauna of the family Issidae is characterized by a great number of narrow endemics. In particular, five largest genera, including from 20 to 79 species each, are distributed in the Ancient Mediterranean region (*Kervillea* Bergevin: 20 species; *Bubastia* Emeljanov: 22; *Issus* Spinola: 32; *Tshurtshurnella* Kusnezov: 40; *Mycterodus* Spinola: 79 species). No species with narrow trophic preferences, which could account for sympatric speciation, have been found in the family so far. In my opinion, one of the factors of sympatric speciation may be pyrogenic renewal of Mediterranean communities: the initial population of a species becomes fragmented due to fires and the resulting micropopulations then become isolated. This mechanism of sympatric speciation in

plants was considered by Cowling and co-authors (1996); it may be also realized in phytophagous insects with a certain allowance for their motility. In case of frequent fires, the species with broad trophic preferences, common among Issidae, are the least vulnerable.

Most issidoid species and genera of fulgoroid planthoppers are associated with sub-arid and arid landscapes; in particular, the faunas of the Mediterranean, the south of the US, and South Africa are highly diverse. Therefore, arid conditions can be regarded as one of the factors (possibly the main factor) of issidisation, i.e., development of the external traits typical of the family Issidae *sensu stricto* and more specifically, the genus *Hysteropterum* Amyot et Serville, by representatives of various families of fulgoroid planthoppers. The cases of mimicry considered above represent an exception. In other words, issidisation is the result of parallel adaptive radiation in certain families of planthoppers, rather than an indication of close relations between them. It is quite possible that radiation of higher fulgoroid planthoppers including the family Issidae occurred relatively fast.

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