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Remarks on evolution of Salticidae (Arachnida: Araneae)

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Salticidae, taxonomy, phylogeny

Abstract. The hypotheses on origin, relationships and evolution of jumping spiders are reviewed. Morphological, behavioural and distributional data support the concept on web-building descendants of Salticidae. The fossil Baltic amber inclusions and continental faunas suggest the explosive evolution of the family at least from the upper Mesozoic.

INTRODUCTION

Jumping spiders represent the largest spider family, with about 4500 nominal species and over 500 genera described from all over the world. They display huge morphological diversity (Wanless, 1984; Figs 1–2), spectacular mating and hunting behaviour (Jackson, 1982a, 1986), various habitat preferences and are known both from present and fossil faunas (Wunderlich, 1986).

Though the relationships within the family have been the subject of investigations for almost a century, the results are not satisfactory (Coddington & Levi, 1991). Except for Simon's classification (1901–1903), the studies concentrated mostly on separate genera and subfamilies and/or on regional faunas (e.g. Wanless, 1988; Prószyński, 1976; Maddison, 1988; Żabka, 1991). The aim of this paper is to review some of the previous hypotheses and to provide remarks on salticid phylogeny.

MORPHOLOGY, FOSSILS, DISTRIBUTION AND SOME PRACTICAL PROBLEMS

The valuation of characters and the scope of genera and higher taxa is a basic aim in taxonomic research. Frequently, the characters are selected arbitrarily, depending on arachnologists' research topics and technical possibilities rather than on character weightening. The criteria in salticid taxonomy are mostly morphological, which include cuticular and genitalic structures (stridulatory and sensory organs, epigyne and palps), cheliceral teeth and tubercles and other special features. Only some genera or subfamilies are precisely diagnosed (e.g. Prószyński, 1971; Wanless, 1984, 1988; Griswold, 1987), partly because in many unrelated taxa the routine features are similar (Figs 3–4) and in such cases new, more sophisticated criteria (SEM, behaviour, molecular data) are highly recommended.

Simon (1901–1903) was the first who divided salticids into sections (Unidentati, Fissidentati, Pluridentati) and subfamilies/groups. Though with some evident errors (e.g. *Bianor* and *Harmochirus* in different sections), the classification was based on

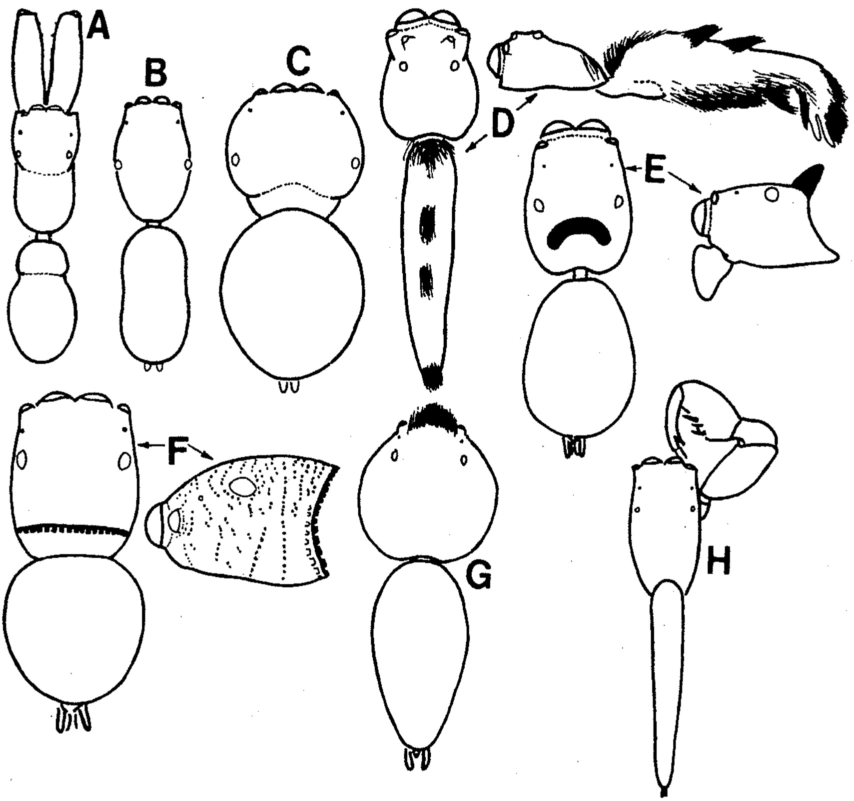

Fig. 1. Body form in Salticidae. A—Myrmarachne, B—Rhombonotus, C—Simaethula, D—Asemonea, E—Diolenius, F—Coccorchestes, G—Mopsus, H—Goleta.

many metric and structural characters; nothing better has been proposed as far as the whole family is concerned. From morphological and ethological data it seems that the pluridents are the most primitive and unidents the most derived. Recent research (Jackson, 1982a,b, 1986; Jackson & Hallas, 1986; Jackson & Blest, 1982; Hallas & Jackson, 1986) has provided evidence that some archaic behavioural features present in pluridents can be extremely useful not only for species-level taxonomy but also for the studies on family origin.

The distributional patterns have been neglected in analysing the relationships. It is clear, however, that the geological history of continents was crucial for today's taxonomic composition of continental faunas and vice versa. Analysed on the generic and species levels, the faunas are very distinctive and highly endemic—especially as far as southern

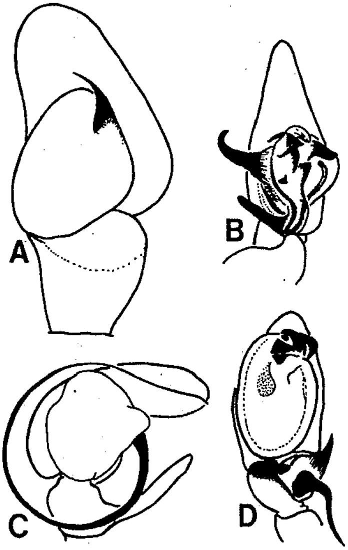

Fig. 2. Simplicity and complexity of salticid genitalia. A—Uroballus, B—Onomastus, C—Afraflacilla, D—Gelotia.

continents are concerned (Żabka, 1991) and prove that the family must have existed before Gondwana begun to split apart. The continental arcs have taken the salticids, at that time being (only and/or already) represented by present subfamilies (?). With limited dispersal abilities (Horner, 1975; Salmon & Horner, 1977; Greenstone et al., 1987), the salticids evolved in isolated unique biota. It seems that in taxonomic studies the independent origin of todays continental, highly endemic faunas should be the basic principle.

The oldest fossil salticid records come from the Eocene and Oligocene Baltic amber. The inclusions represent both today's and extinct subfamilies (Prószyński & Żabka, 1980, 1983; Cutler, 1984; Wanless, 1984; Wunderlich, 1986; Żabka, 1988) and are almost useless for research on the family origin. They are, however, very important for the studies on evolution rate, age of a particular genera and their zoogeographic history.

THE FAMILY ANCESTORS

Two groups of hypotheses based on morphological and/or behavioural characters descend Salticidae from cursorial or web-building spiders.

1. The Salticidae—Anyphaenidae—Clubionidae hypothesis discussed by Coddington and Levi (1991) placed salticids within Gnaphosoidea. The three families basically do not build webs and have lost cylindrical glands and spigots, the characters being typical for higher Entelegyne. However, as stated by Coddington and Levi themselves, the loss may well have been secondary. In many tropical genera the ability is still retained (e.g. in Spartaeinae) or has appeared as a new character.

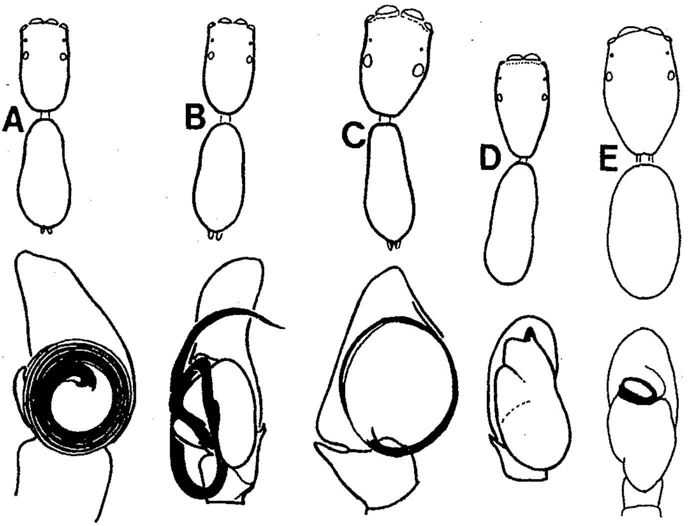

Fig. 3. Similar body form and different palpal organs in some ant-mimic genera of Salticidae. A—Sarinda (Panama), B—Ligonipes (Australia), C—Fluda (Brazil), D—Semora (Venezuela), E—Marengo (Sri Lanka).

2. The Salticidae—Clubionidae—Gnaphosidae hypothesis was proposed by Eberhardt (1986) for the three active hunters that perform similar silk manipulation.
3. The Salticidae—Thomisidae hypothesis presented by Loerbroks (1984) was based on similarities in palp structure of some representatives of both families. In fact, Salticidae do not perform any uniform palp pattern. It is generally simple but may be very complicated and accidental interfamily similarities are likely to occur.
4. The Salticidae—web-building spiders hypothesis proposed by Jackson and Blest (1982) and Jackson (1986) is based on the research of some tropical and subtropical jumping spiders (Portia and related genera) that perform web-building and cleptoparasitic behaviour. Spartaeinae and Lyssomaninae are subfamilies/groups where the web-building ability seems primitive and where other taxonomic characters (e.g. eye structure) prove their primitiveness. According to this hypothesis, some important steps in salticid evolution may be distinguished:

☐ Primary web hunters that build their own webs for catching prey; no representatives of this group are recorded so far.

☐ Primary cleptoparasites that build their own webs but also hunt in webs of other spiders (some Spartaeinae). Genus *Portia* is the best example of this level.

☐ Salticids that abandoned both the web and cleptoparasitic ways of life and perform active hunting behaviour. Amongst some of them secondary cleptoparasites or web hunters appeared (e.g. *Plexippus paykulli*).

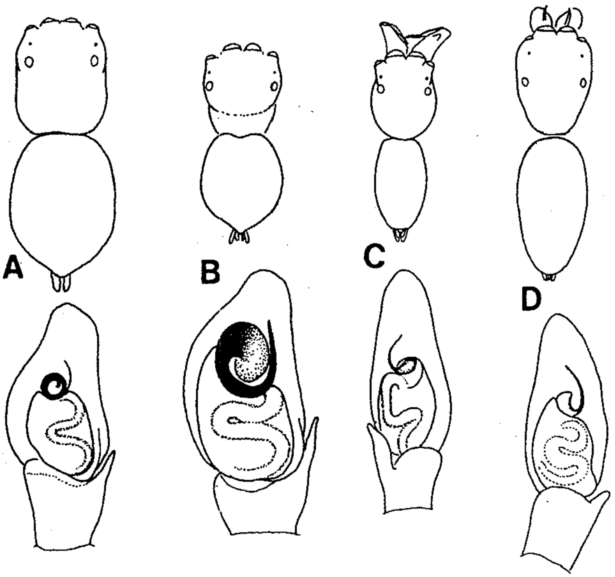

Fig. 4. Similar genitalic pattern in unrelated salticid genera. A—Zenodorus, B—Omoedus, C—Spilargis, D—Udvardya.

CONCLUSIONS

1. Any salticid classification should be based both on morphological and (if possible) on behavioural characters.
2. Genitalic characters, so important in other spider groups, may be misleading in analysing the salticid relationships because of the convergence resulting in similar patterns in unrelated taxa.
3. Complex and effective communication and recognition systems seem to be effective in preventing interspecific copulation.
4. Highly diversified fossil Eocene fauna proves that some subfamilies are at least 45–50 million years old. There is no fossil evidence of salticids existing before Tertiary but in the opinion of some arachnologists (e.g. Wunderlich, pers. comm.) their discovery is only a matter of time.
5. The high level of endemism of southern lands (e.g. Australia) is the result of post-Gondwanan isolation and evolution in unique conditions.
6. Because of lack of satisfactory and well documented classification for the whole family, the Simon's classification is recommended as temporary.

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