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Lycosidae: the grassland spiders

Rudy Jocqué[1], *Mark Alderweireldt*[1]

Abstract: The hypothesis is formulated that the Lycosidae co-evolved with grassland and dispersed with the expansion of this type of habitat. Arguments that sustain this view are the abundance of Lycosidae in open habitats with low vegetation and their relative rareness in dense forest, the lack of typical hunter adaptations to achieve grip on smooth surfaces and the fact that the family is only known in the fossil record from the Miocene onwards, which is in synchronization with the spreading of grassland.

Key words: adaptation, grip, Miocene, Araneae, Pisauridae

Introduction

Lycosidae or wolf spiders are a clearly delimited and well defined spider family both on somatic and behavioural characteristics. They have a unique eye pattern and a typical egg sac and spiderlings carrying behaviour. However, their systematics are particularly problematic because of the often faint distinctions between the different taxa, on specific as well as generic level. It has been suggested (Alderweireldt, Jocqué 1992, Wunderlich 2004) that Lycosidae are a family of recent evolutionary origin. Taxonomic revisions have in several cases been problematic as confronted with particular difficulties in species and genus delimitations and diagnoses (e.g. Alderweireldt 1996, 1999, Alderweireldt, Jocqué 1992, 2005). From these studies ample indications are found that at least certain groups of Lycosidae apparently demonstrate recent speciation processes.

But apart from these indications resulting from the taxonomic approach, no data have been put forward to support this opinion. The present paper is the first one that gathers a series of arguments to defend the recent origin of the family mainly based on the indications that Lycosidae are particularly well adapted to grassland habitats. It is hypothesised that Lycosidae have co-evolved with that type of vegetation.

Habitat preferences

The idea of promoting Lycosidae to the "grassland spiders" par excellence comes mainly from our experience with soil dwelling spiders in tropical as well as temperate habitats. Especially during field work in tropical Africa, some striking observations were made that asked for explanation. An example:

During our sampling campaigns (Jocqué *et al.* 2005) in the frame of a forest rehabilitation project in Ivory Coast (West Africa), we were confronted with the fact that Lycosidae, despite being a very widespread and very speciose spider family in Africa, are particularly scarce to even absent in dense (primary) forest. We were at first looking for a representative of the Lycosidae as indicator species in monitoring for several reasons. Many Lycosidae are diurnal and very active and therefore easy to spot and observe. As the females carry the egg sacs attached to the spin-

[1] Invertebrate non-insects section, Royal Museum for Central Africa, B-3080 Tervuren, Belgium. E-mails: rudy.jocque@africamuseum.be, malderweireldt@hotmail.com

nerets, these are easily collected during the reproductive season. The number and the size of the eggs can be used as good parameters to estimate the fitness and general condition of the parents and their populations (e.g. Alderweireldt, Maelfait 1988, Bonte, Maelfait 2001, Hendrickx *et al*. 2003). However, surprisingly, Lycosidae appeared to be rather rare in the forests of eastern Ivory Coast in contrast to the nocturnal Ctenidae, which proved to be absolutely ubiquitous. In areas where the forest canopy was opened, even locally, and were grasses (Poaceae) had formed a thin herb layer, Lycosidae (mainly *Pardosa injucunda* O.P-Cambridge) made their appearance. In locations devoid of grasses, Lycosidae remained absent. Several pitfall trap studies demonstrate that Lycosidae have been found to be the dominating spider group in a wide range of habitats. Russell-Smith *et al.* (1987, 1999), Van der Merwe, Dippenaar-Schoeman (1996), Warui *et al.* (2005) found them to be the dominating family in African savanna habitats. They are also abundant in other herb dominated vegetations such as swamps, but are particularly scarce in densely forested habitats.

Similar observations were made in forests in Congo D.R. near Kisangani (Juakaly, pers. comm.), Gabon (Pauwels, pers. comm.), Malawi, Comoros, Rwanda, Guinea and Equatorial Guinea (own observations). More or less the opposite seems to be true for Ctenidae. Figs 1 and 2 summarise some pitfall data for Lycosidae in a gradient of different habitat types. In nocturnal transects, along which spiders with grate-shaped tapeta were caught according to a distance sampling protocol (Jocqué *et al.* 2005), lycosids were so rare in the dense forest patches, that it was decided to concentrate on Ctenidae alone. Lycosidae numbers increase with the area covered by the herb layer which is negatively correlated with the degree of canopy closure. The tendency in Ctenidae is exactly the opposite. The less degraded the forest, the more abundant they become. Lycosidae and Ctenidae thus seem to counterbalance each other in a habitat gradient. The proportion of Lycosidae/Ctenidae might therefore be an excellent and easy to use indicator for forest quality (see Jocqué *et al.* 2005).

About webs, claws and claw tufts

Lycosidae versus Ctenidae

Jocqué (1995) and Dippenaar-Schoeman, Jocqué (1997) attracted the attention to the fact that there is a tendency in spiders to abandon the habit of webbing and return to the hunting strategy. The majority of spider species are indeed hunters. In almost all spider families consisting of mainly web building spiders, there are taxa that have switched to a hunting way of life (e.g. Alderweireldt 1994; overview in Jocqué 1995). As far as known, these almost invariably belong to the more derived taxa. Lycosidae are an excellent example of this tendency. The more ancestral taxa in the family are purely web-inhabiting. Among these are *Hippasa, Aulonia* and *Amblyothele*. But the majority of the wolf spiders have turned into a purely hunting life style. Typical for web building spiders is the presence of three tarsal claws: one dorsal pair of large claws, and one smaller, more ventrally inserted, unpaired claw. This is shown on the scanning EM picture in Fig. 3a. The third tarsal claw appears to be an adaptation for life on a web and is present in almost all webbing spiders.

Most hunting spiders on the other hand have lost the third claw and many have developed extensive scopulae and well developed claw tufts, as shown in Fig. 3b. The latter provide the owners with a perfect grip on smooth surfaces (Fig. 3d) thanks to the so called "Van der Waals forces" (Kesel *et al.* 2003). These forces are based on the dipole-dipole attraction between large molecules provided there is close contact between them. The tips of claw tuft setae are finely divided, resulting in several hundreds of thousand of contact points between the leg tip and the substrate.

Ctenidae are a perfect example of a family with very well developed claw tufts. This adaptation makes them very well equipped to move over very smooth surfaces such as forest tree

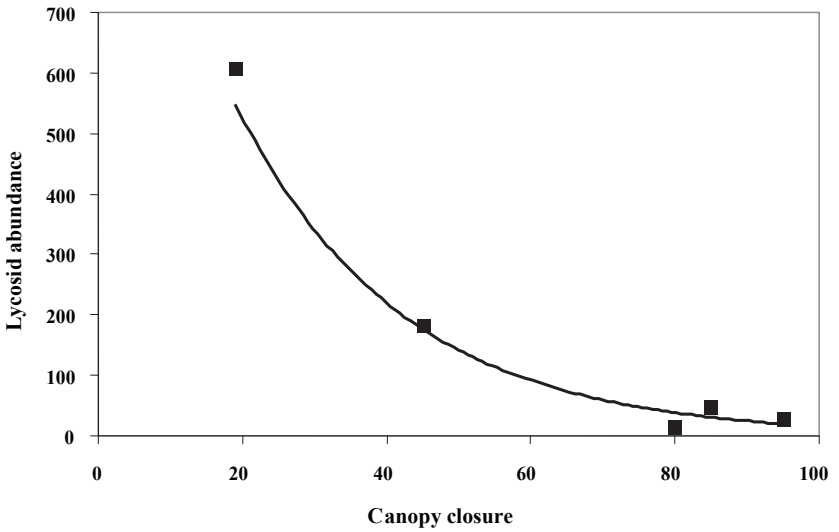

Fig. 1. Number of Lycosidae captured during a two-year trapping cycle in five stations with different tree density in eastern Ivory Coast (Jocqué, unpublished).

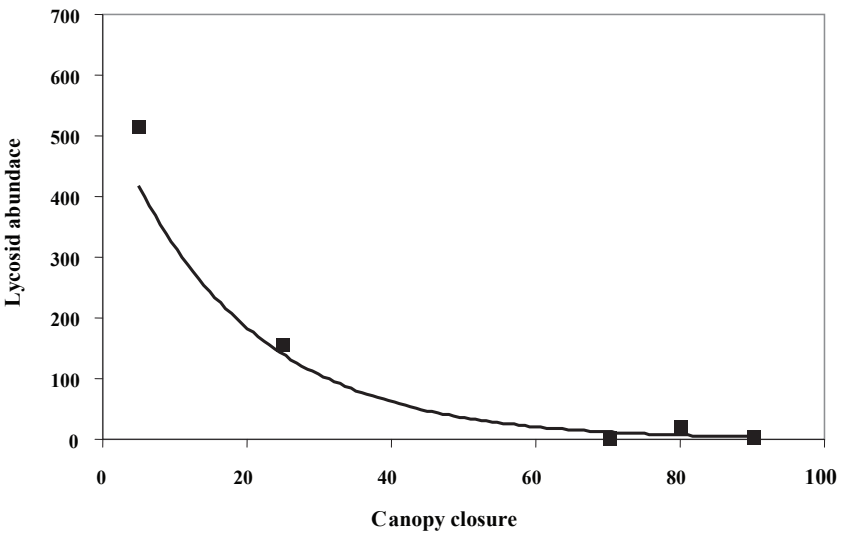

Fig. 2. Number of Lycosidae captured during a one-year trapping cycle in five stations with different tree density in eastern Congo D.R. (Juakaly, unpublished)

leaves. For some species, e.g. *Petaloctenus* (see Jocqué, Steyn 1997), the leaves of forest tree saplings is their preferred substrate. In these tropical forests, tree leaves are very smooth (Fig. 3d) and provided with a drip tip to evacuate excess of water in order to prevent algal growth (Wolfe 1985, Wolfe, Upchurch 1986, 1987). Lycosidae on the other hand, are not equipped with such an adaptation like claw tufts and are as a consequence rarely seen on forest leaves. However, most grasses and many herb species have either a rough surface (Fig. 3c) or are provided with an extensive layer of hairs. In many cases this is an adaptation to prevent excessive transpiration. But on such a surface a claw tuft is useless for good grip. In contrast to this, claws provide a much better adherence and it is therefore easily understood why Lycosidae move remarkably easy over herbs and grasses.

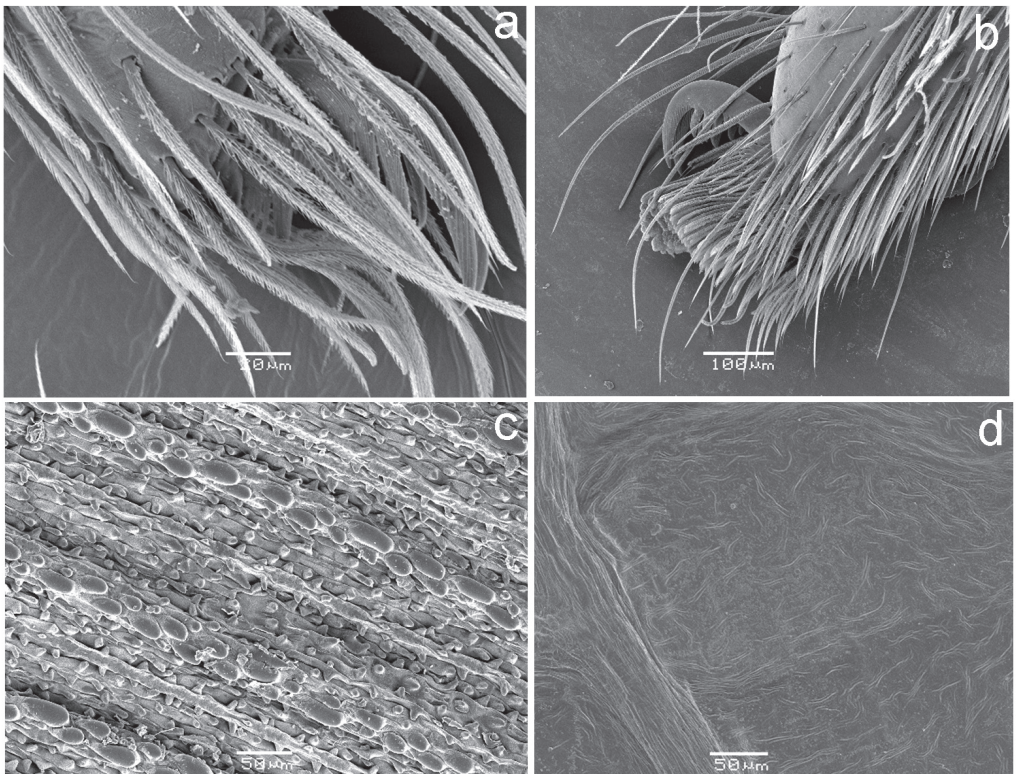

Fig. 3. a – tip of tarsus of a three clawed spider; b – claw tufts and scopulae; c – rough surface; d – smooth surface.

This reasoning is confirmed by observing actively hunting, non-web building members of the Pisauridae (e.g. *Charminus*, *Cispius*, *Pisaura*). They also have retained the third claw and wander around on herbs, grasses and lower bushes. Pisauridae are indeed spiders of the lower shrub and upper herb layer par excellence although one clade including *Thalassius, Dolomedes, Hygropoda* and *Hypsithylla*, appears to have developed fishing behaviour. However, they also hide in high shrubby vegetation during periods of inactivity. This explains why Pisauridae are rare or absent in pitfalls but are frequently caught in pan traps and Malaise-traps. The nursery webs of *Pisaura* for instance are most often constructed in high grasses or between branches of low bushes with rough surfaces. Claw tufts are useless in these conditions, while the third claw proves crucial to move easily through this kind of vegetation. Just like Lycosidae they are absent in higher strata and only very exceptionally found in canopy fogging samples (De Bakker, pers. comm.).

The fossil record

Recent studies of the presence of the spider families in the fossil record are particularly instructive. The fascinating study of Penney (2004) shows that the first records of Lycosidae are as recent as the Miocene. As illustrated in his cladogram Lycosidae seem to have evolved far more recently than most other spider families. The striking observation however is that the Miocene period is exactly the period in which grassland habitats dominated by Poaceae have become a major habitat occupying by now a large proportion of the surface of continents. Crepet, Feldmann (1991) summarise data about the earliest remains of grasses in the fossil record. Although grass pollen occurs sporadically since the Eocene (Salard-Chebaldaeff 1981), evidence of grassland communities in Africa does not appear until the mid-Miocene, about 14 million years ago (Jones 1997,

Retallack 1992). Pickford (1985) provides evidence for co-evolution of some elements in the fauna with grasses dating back from that period. Similarly, the synchronisation of lycosid radiation and the expansion of grassland habitats can therefore be regarded as a plausible phenomenon.

The hypothesis

Combining all the observations explained above, we emit the following hypothesis: Lycosidae originated fairly recently in the evolutionary history of spiders and were exclusive web spiders until the Miocene. As far as the habitat structure is concerned, they had fairly simple demands as they were providing their own substrate in the shape of a sheet web. The spreading of grasslands from the Miocene onwards provided the Lycosidae with an excellent habitat that gave them the possibility to spread as hunters without particular new adaptations: the combination of acute vision and their perfect grip on rough surfaces were the perfect requisites to become the grassland hunters par excellence. Thanks to this, they were able to radiate quickly to become today one of the most speciose families on the African continent (Alderweireldt, Jocqué 1994) and beyond. It is therefore stated that Lycosidae have co-evolved with the expansion of grassland habitats and by extension in all kinds of open habitats with short vegetation, since the Miocene.

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Lycosidae – тревните паяци

Р. Жоке, М. Алдервейрелд

(Резюме)

В настоящата статия е изказана хипотезата, че паяците от семейство Lycosidae са произлезли съвместно с тревните съобщества и са разширили ареала си заедно с експанзията на този тип хабитат. Аргументите, които подкрепят тази хипотеза са: обилието от представители на това семейство в открити местообитания с ниска растителност, сравнително рядкото им присъствие в гъсти гори, липсата на типичните ловни приспособления за улавяне на жертва на гладка повърхност, както и фактът, че семейството е известно във фосилната летопис едва от миоцена насам, което е в синхрон с появата и експанзията на тревната растителност.