Architis nitidopilosa, a neotropical pisaurid with a permanent catching web (Araneae, Pisauridae)

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Summary

Architis nitidopilosa Simon 1898 (Pisauridae) was studied in tropical Panama. Males, females and penultimate stages all build large, permanent catching webs. The 3-dimensional web consists of a short, horizontal funnel which widens at both openings to form two extensive vertical sheets. Females reduce this web to a nursery. Earlier instars build a somewhat different catching web around a hole in a leaf. The phylogenetic position of the web of *Architis* within the Pisauridae and web-building in general in Pisauridae is discussed.

Introduction

When Carico (1981) wrote his revision of the neotropical genus *Architis* he added 5 new species to the hitherto known 2 species. All of these species are known only from museum specimens and virtually nothing is known about the living animals. Thus, apart from an occasional note in a vial in the collection made by Chickering in Panama in the 1930s, our knowledge of the natural history of *Architis* is still that of Simon when he described the first species in 1898. During studies in Panama, *Architis* was found to be common in some localities and easily observed. Thus, as an addition to Carico's genus revision, the following paper gives some notes on the natural history of *A. nitidopilosa*.

Description of the species

For a good morphological description of both sexes see Carico (1981). As far as the colour is concerned, Carico himself remarked that his species description is somewhat vague because of the great age of the material. Therefore, a short description is added here. The colouration is similar in both sexes and shows some variation. Generally, living specimens show 5 bright white bands on the cephalothorax (Carico's "indistinct dusky") which are more or less parallel. The median band reaches from the front to the fovea, the lateral bands fork below the anterior lateral eyes and meet at the hind angle of the cephalothorax. The lower line is sharply defined and follows the broadest circumference of the prosoma. The upper line possesses two side-branches which are sometimes reduced to spots. Similar white, glossy hairs which form these lines are found on the opisthosoma where they cover the sides and form dorsally a "Y" with a long median line. The red and brown dorsal side, the annulated legs (bright brown with grey-green spots and red-brown rings), the sternum covered and surrounded by white hairs, and the brown-white striped lung-covers, give the living spiders an easily recognisable appearance. These distinct patterns disappear in alcohol and the white hairs become brown.

Distribution and habitat

Records of *A. nitidopilosa* are known from Panama, south to Colombia, Venezuela, the Guianas, and into central Brazil (Carico, 1981). In Panama, the species was studied at several forest localities near Gamboa, 25 km NW of Panama City. The forest here can be classified as tropical monsoon forest. The spiders are rather common in the stratum of herbs and lower bushes. They occur inside the forest but were also found frequently on road-sides, avoiding directly insolated places. This was revealed by a census of both sides of a trail with similar plant structure (i.e. possible web-building sites). On the more isolated side of the 10 m long and 5 m wide trail I found 2 *Architis* and 23 on the shadier side. The retreat of the spider, a funnel, is normally situated 50-100 cm above the ground, the highest webs were found on hanging branches of trees at a height of 2.5-3.0 m, the lowest webs were found 30-40 cm above ground (Fig. 1). The distribution of *A. nitidopilosa* within its habitat is highly irregular with a maximum density of 3-5 adult spiders per m^2. Normally, clusters can be found of 2-10 spiders, whereas the species is absent over larger distances between the clusters. Juveniles occur at much higher population densities. In the early wet season (April), a density of 38 juvenile spiders per m^2 was found on a slope with dry grass.

The web

Penultimate and adult spiders of both sexes build a 3-dimensional web. It might be characterized as a space web with a horizontal funnel in its centre (Figs. 2, 3). This funnel is 5-10 mm long and is open at both ends. At both openings the funnel widens to form an extensive, vertical sheet 10-20 cm wide and 20-30 cm high (adult female). The left and right sides of these sheets tend to touch each other. Above, the web becomes more irregular and is suspended by single threads which may function as support for the web or as catching threads for flying insects. The general shape of the web is highly variable and depends in its detail on the attachment possibilities which the web site (i.e. the plant) offers. The web can be found between two forked stems, in an umbel or panicle of grasses or herbs, or under larger leaves. Depending on the location, the funnel may show a more excentric position, and the web may show a more square, triangular, or round shape (Fig. 4). Additionally, in the dry season, the web tends to be built more frequently on dry grass stems or dry branches whereas during the wet season preferred web sites are under large leaves. This may be interpreted as a protectional behaviour against web damage by heavy rainfall. Normally, the web is built at night and in the early morning. During the first night, the spider builds the funnel and nearby web parts, and on 1 or 2 successive nights, the web is enlarged to its final size. The spider stays in its web for several weeks.

The juvenile web

Juvenile spiders build 2-dimensional webs. The spiderling sits in a hole or slit in a leaf, sometimes only 5 to 10 mm in diameter. On both sides the hole is surrounded by silk, with some silken threads on each surface of the leaf. These "signal threads" are spun at irregular distances from each other. The shape of the total silk-covered area is also irregular. The position of the spiderling in its leaf hole (4 ipsilateral legs on each side of the leaf) and its reaction to prey are the same as in the adult spider.

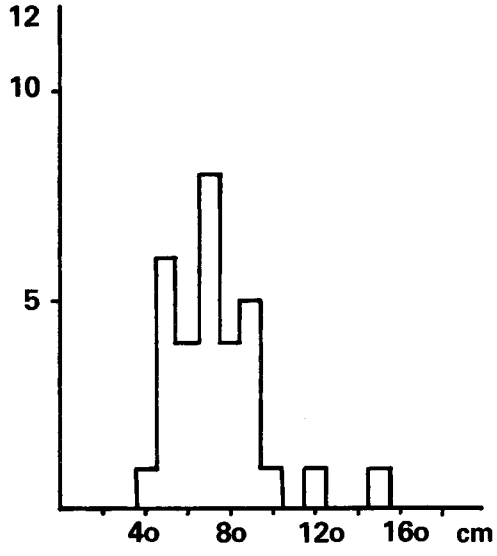

Fig. 1: Height distribution of 31 webs of *Architis nitidopilosa* (height = distance from the retreat to the ground).

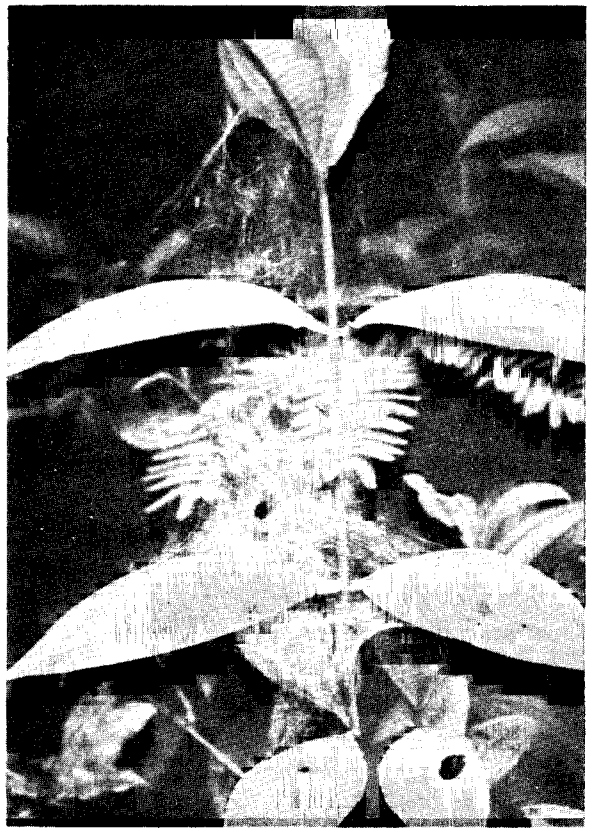

Fig. 2: Permanent catching web of adult *Architis nitidopilosa.*

The position of the spider

The spider sits inside the funnel with its head downwards, and the 4 legs of each side of the body outside the funnel, thus, touching the sheet on each side (Fig. 3). Apart from descriptions by Lenler-Eriksen (1969) and Carico (1985), this position is not known in any other spider species. In this position the spider immediately perceives vibrations of entangled prey and can also escape in dangerous situations to either side of the funnel. The spider is not clearly nocturnal or diurnal. During the day it normally sits inside the funnel, but responds quickly to vibrations and catches prey. At night, the spider is more frequently found on the sheet, maybe looking (or waiting?) there for prey, or cleaning (?) or repairing the web. In captivity, feeding and drinking (*A. nitidopilosa* like many other tropical spiders needs to drink regularly) was readily performed by day and at night.

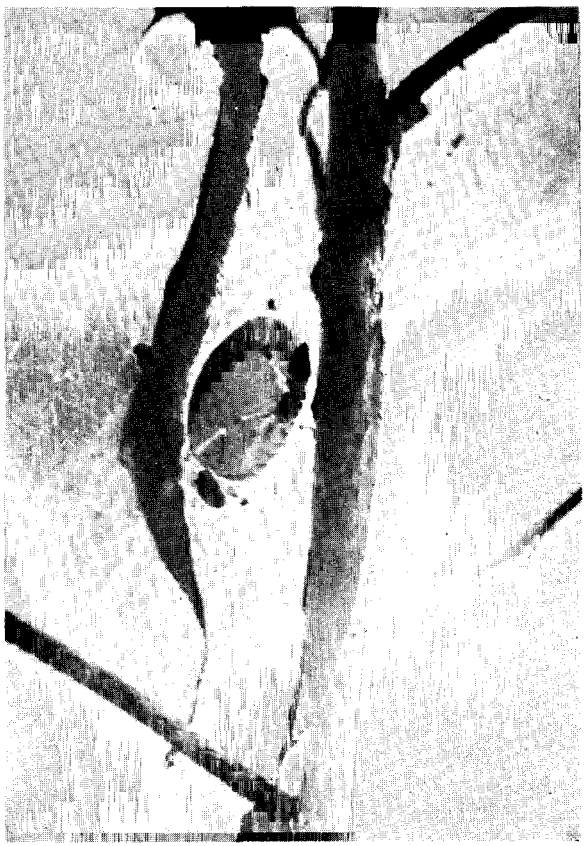

Fig. 3: Position of adult *Architis nitidopilosa* in retreat.

Senses

Although *A. nitidopilosa* is a web-building spider (most of which are not visually oriented) it reacts to optical stimuli over a considerable distance. The behaviour of *Architis* resembles much more that of a salticid than an araneid or linyphiid web-building spider. The spider sees somebody approaching at a distance of at least ¾ m and may react by shaking the legs or by flight behaviour. *Architis* observes the moving tip of a pair of forceps at a distance of 5-10 cm and, when sitting on the sheet, reacts by orientation movements in a way comparable to salticids. The spider also reacts to vibrations of the web (e.g. by struggling insects) and of the ground (e.g. by approaching persons). The eyes seem to be mainly accommodated to long distances because insects close to the spider (1-3 cm) are caught only when they move.

Escape behaviour

A. nitidopilosa shows 3 escape tactics: (1) Flight towards the opening of the funnel opposite to the source of danger and waiting on the sheet near the opening. This is the most frequently observed behaviour. (2) Flight onto the sheet, occasionally with subsequent climbing up on the suspension threads. (3) Jumping out of the web and running on the neighbouring vegetation to hide under a leaf. This is only done in case of emergency. During the jump the spider remains connected with the web by a drag-line.

Prey capture behaviour

A. nitidopilosa reacts differently to flying prey hitting the web and ambulatory prey that crawl into the web. Flying insects are caught by a jump, which is made from the funnel and reaches distances of at least 5 cm. In the field, this was frequently observed as a catching behaviour towards Nematocera, Brachycera and small Coleoptera. In most cases observed, however, the spider did not manage to capture the prey. Insects that become entangled in the web are caught by being picked up with the chelicerae. Depending on the kind of vibration and

on the "internal condition" of the spider, the reaction time varies from immediately to no reaction at all. During feeding experiments the reaction of *Architis* to prey was found to be much less predictable than that of *Araneus* or *Argiope* species (Araneidae). To capture prey, the spider runs very fast to the insect, stops in front of it and touches the prey with one of the first legs, apparently testing the prey in some way. If the prey is acceptable to the spider it is picked up with the chelicerae and brought back to the funnel. If the prey is found unacceptable the spider quickly returns to its funnel. The examination of the prey takes a very short time (one second or less). Sometimes, the spider repeats the whole sequence a second or even a third time. If an insect becomes entangled in the upper suspension threads of the web the spider shakes the whole web until the prey falls down onto the sheet.

Size of prey

A. nitidopilosa is a very selective spider. No insects larger than the spider (5-8 mm) are accepted. The size range of prey under natural conditions was found to vary from 2.3-6.6 mm in spiders of 5-7 mm body length. Under experimental conditions no prey larger than the spider's body size was accepted, sizes of 1/3 to 2/3 of the spider's size were most frequently accepted. This limitation to small size with a limit below the spider's body size is not generally found in spiders. Especially in web-building spiders (Nentwig, 1980; Murakami, 1983) the use of the web or other thread-using behaviour (e.g. in Hersiliidae or Oecobiidae which run around the prey) can help the spider in overwhelming larger prey. Though *A. nitidopilosa* builds a web, it does not use silk to overwhelm the prey and shows no wrapping behaviour.

Prey-specific behaviour

According to feeding experiments in a natural population, the spider reacts to different prey taxa as follows. Heteroptera, Coleoptera, and non-winged Formicidae are normally not accepted. They were examined briefly, then the spider returned to its funnel while the prey remained struggling. In a few cases the spider attacked small ants (1 mm) or bugs (3 mm) with a short bite, but all were then refused as prey. Quite often the spider did not react at all to struggling ants or bugs. Possibly *A. nitidopilosa* discriminates at least some kinds of prey on the nature of their vibration. Ants may be ignored because they were found to run quite often on to the plants to which the web is attached and *Architis* recognises them as being dangerous. Ensifera and Caelifera often move very slowly when entangled and at long intervals, so that the spider in numerous cases did not react to the prey. Obviously, slowly moving insects are not considered as prey. If the grasshopper moved rapidly enough the spider ran out and overwhelmed it immediately. Diptera and Auchenorrhyncha are normally accepted after a brief contact with one of the first legs. Other spider species which

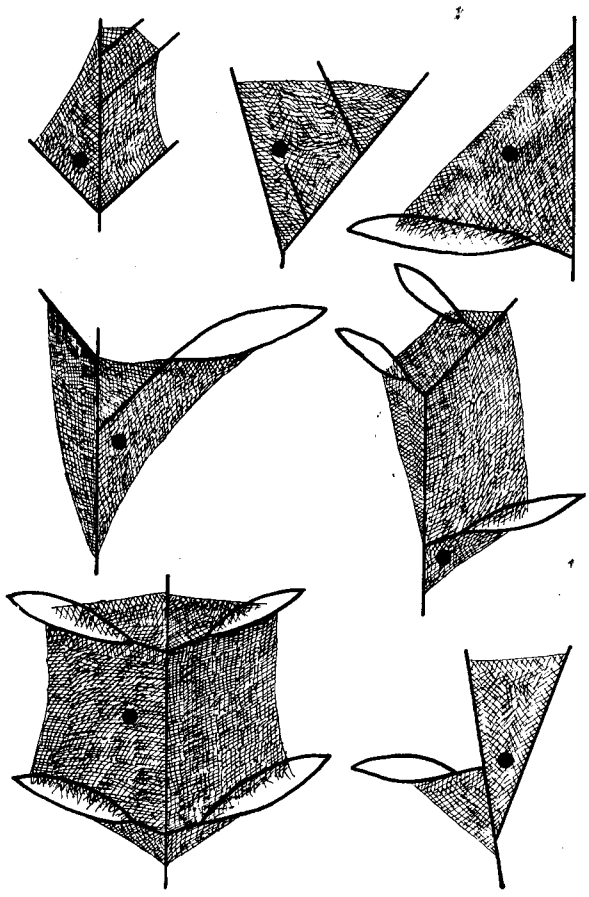

Fig. 4: Variation in shape of the web of *Architis nitidopilosa*, schematically (black lines = supporting vegetation, branches, leaves; hatched area = web; black spot = retreat).

fell into the web of *Architis* tried to escape as soon as possible. *Architis* showed either no reaction at all or ran towards the other spider in the manner of a "defensive attack". In feeding experiments, however, it never tried to overwhelm another spider but returned to the funnel after standing just in front of the other spider for a short while. In nature, *A. nitidopilosa* was observed feeding on Brachycera, Nematocera, winged Formicidae, Saltatoria (Caelifera, Ensifera incl. Gryllidae), Auchenorrhyncha and a small juvenile thomisid (*Onocolus* sp.). Additionally, in the webs remains were found of Salticidae (2-4 mm), Curculionidae (3-4 mm), Lepidoptera, Thysanoptera and Psocoptera (all 1-2 mm). It could not be decided whether these were caught by *Architis* or whether carcasses had fallen into the web.

Life cycle

Adult spiders were found from March to August. The males disappear in June-July. Females build egg-cases from the end of May to mid-August with a peak in June. Chickering collected egg-sacs between 6 June and 30 July (Carico, 1981). Before a female builds an egg-case, it often reduces the size of the catching web. It will not maintain the upper parts, which are destroyed by the weather within a few days. The females often move to lower parts of the web and build a second funnel there. The egg-case is spherical, 4-5 mm in diameter, and consists only of a thin, dirty-whitish silk layer which holds the eggs. This egg-case is very similar to that of *Scytodes longipes* Lucas (Scytodidae) or *Pholcus phalangioides* (Fuesslin) (Pholcidae) and its silken walls are not nearly as thick as those of egg sacs of *Pisaura* (Pisauridae). In 6 examined cases the number of eggs was found to be 34, 39, 46, 67, 77 and 82 ($\bar{x}$ = 57.5). The female holds the egg-case with the chelicerae and presses it slightly against the sternum, bending its

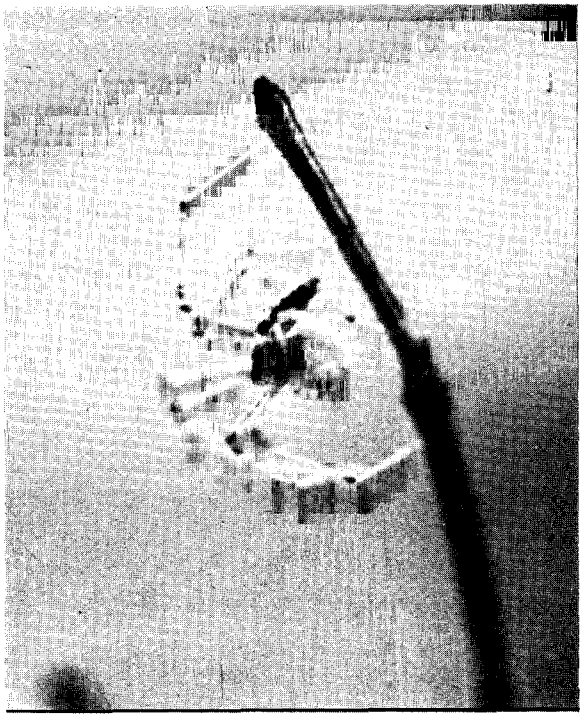

Fig. 5: Female *Architis nitidopilosa* with cocoon.

Fig. 6: Beginning of dispersal of the young of *Architis nitidopilosa*, cocoon and female are still in the web.

body around the eggs in the typical pisaurid way, with an angle of approx. 120° between cephalothorax and abdomen (Fig. 5). During the egg-carrying period the female does not feed or react to prey insects at all. It does not leave the funnel or place the egg sac anywhere else. The spiderlings hatch approximately 15 days after the eggs are laid. They stay the first day in the mother's web, but do not spread all over it (Fig. 6). There is no maternal care of the young and the mother reacts immediately to prey after the juveniles have emerged from the egg sac. From the second day on, the juveniles leave the adult web one by one until after some days all spiderlings have left their mother's web (Fig. 7). Now the mother rebuilds the upper part of the catching web but presumably dies in the following weeks. No adults were found from mid-August to mid-November. Juveniles are adult at the end of the year and a second reproduction period occurs in December/January. Thus, *A. nitidopilosa* has in Panama two generation cycles per year with the reproductive phase in the early and late wet season.

Predators

No egg parasites were observed. This is at least partly due to the fact that *Architis* holds its egg-case in the mouth. However, Valerio (1981) reports that a similar holding manner does not protect *Scytodes intricata* Banks from heavy parasitism by a scelionid wasp. In one case Lepidoptera larvae fed on the plant where the web was built. By eating the plant, the caterpillars destroyed the web completely and the spider had to move. A subadult male of *Scytodes* sp. was observed while entering the web of an *Architis* male and killed the resident. Only one of several hundred observed webs possessed a kleptoparasite, a juvenile *Argyrodes* species (Theridiidae), and in one web a female of *Philoponella tingens* (Chamberlin & Ivie) (Uloboridae) had its own orb web.

Discussion

As a spider which builds a permanent catching web, *Architis nitidopilosa* is unusual among the pisaurids. It shares characters of a typical non-web building pisaurid (e.g. ambushing behaviour even in its web, egg-sac carrying with the jaws, leg posture, and good visual orientation), but also shows behavioural patterns of a typical web spider (e.g. web shaking).

There are further records of web building in the Pisauridae. Permanent catching webs are built by African species of *Euprosthenops, Euprosthenopsis, Vuattouxia,* and *Tetragonophthalma* (Gerhardt & Kästner, 1937; Blandin & Célérier, 1981) and by the Australian species of *Inola* (Davies, 1982). As far as is known, these webs represent a rather plesiomorphic web type (*sensu* Nentwig & Heimer, 1983), consisting of a large sheet in the vegetation and a funnel which leads in the case of the African species to a burrow in the ground. This type is similar to that of some Hippasinae (Lycosidae) or Agelenidae.

Juvenile spiders build webs in numerous other pisaurid species from Africa, America and Europe (Nielsen, 1932; Lenler-Eriksen, 1969; Carico, 1976, 1985; R. Nitzsche, pers. comm.). Conclusions on web building in the Pisauridae, however, seem to be impossible at the moment. The classical separation into 3 subfamilies (Pisaurinae, Thalassiinae and Dolomedinae, Gerhardt & Kästner, 1937) is considered to be artificial by several authors and major revisions at subfamily and family level have recently been produced (Lehtinen, 1967; Carico, in press). A general phylogenetic concept for the whole family does not yet exist.

If one considers the African and Australian species with a permanent catching web (as described above)

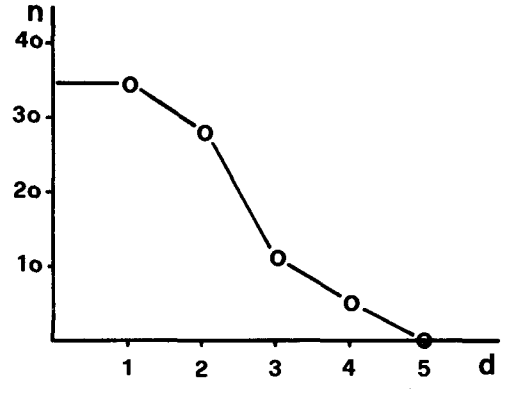

Fig. 7: The dispersal of young *Architis nitidopilosa.* After leaving the cocoon the spiderlings leave the mother's web within a few days.

to be less related to the European or American species, the permanent web of the neotropical *Architis nitidopilosa* is unique in this group. It may have evolved from a further-developed nursery web (which most – all? – pisaurid females build), or it could be a secondary catching web. The following arguments indicate that the last possibility is perhaps the most probable one: (1) The web of *A. nitidopilosa* with a central funnel, open at both ends, is unique. It resembles none of the known web types and within the general evolutionary lines as described by Nentwig & Heimer (1983) is certainly not related to webs of the African or Australian pisaurids. (2) The web is not restricted to females. Males and penultimates of both sexes build it as well. The catching web, thus, cannot be a precursor of the nursery web. Contrarily, females reduce their webs to a nursery. (3) The juvenile webs of *A. nitidopilosa* share some characteristics of the penultimate and adult web form. The position of the juvenile spider in its web is characteristic and similar to the position taken by adult spiders. (4) The web type of *Architis nitidopilosa* seems to be developed within this species or genus. It could also be interpreted as a trend to web enlargement, opposite to the general trend of web reduction in the Pisauridae.

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