Notes on the natural history of *Aspidolasius* branicki (Araneae: Araneidae) at Tinigua National Park, Colombia, with a revision of the genus

Alejandro Calixto

Department of Entomology, Texas A&M University, College Station, Texas 77843-2150, USA

and

Herbert W. Levi

Department of Invertebrate Zoology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138-2902, USA

Summary

Preliminary observations on the natural history of the spider *Aspidolasius branicki* were made during January 1994 and October 1998 in a rain forest at Tinigua National Park, Colombia. The species constructed a triangular orb-web, consisting of very thick and sticky golden-hued silk, attached by the frame to three supports and lacking a secondary frame. Diptera and Hymenoptera constituted the most common insects observed caught in *A. branicki* webs. The species preferred shrubby vegetation and areas with small trees for the deployment of its web. The density of *A. branicki* differed significantly between different habitats and it was found mainly in mature and degraded forests. This is the first report of this species from Colombia.

Introduction

The family Araneidae comprises more than 3,000 species and constitutes the largest family of orb-weaving spiders in the neotropics and worldwide (Shear, 1986). The phylogenetic position of this family and its intra-familial phylogeny have been recently reviewed (Griswold *et al.*, 1998; Scharff & Coddington, 1997). A great number of species within this family construct webs with viscous silk (Coddington, 1986). Some are nocturnal, hiding during the day and building their webs and feeding at night (Brown, 1981). The biology and behaviour of some tropical species have been studied intensively, with respect to habitat selection, foraging behaviour, mating behaviour, etc. (Robinson & Robinson, 1978; Eberhard, 1986; Riechert & Gillespie, 1986; Stowe, 1986).

Aspidolasius branicki (Taczanowski, 1879) is a common araneid in tropical areas of Colombia that has received little attention. This species has not been officially reported for this area, and there have been few revisions of this genus in the literature (Simon, 1887; Bonnet, 1995; Platnick, 2004), and none addressing the biology of this species. *Aspidolasius* is a poorly known monotypic genus that possesses many plesiomorphic traits (Levi & Coddington, 1991; Scharff & Coddington, 1997). This species has been reported from lowland tropical forests below 1,000 m in Peru, tropical savannas in Guyana, and cloud forests in Bolivia. Records are also presented here from Venezuela, Ecuador and Brazil, as well as from Colombia (Fig. 3). The biology and ecology of this species is not well known in spite of it being relatively abundant in some tropical areas. The objective of this paper is to provide a general overview of the natural history of this species, and a revision of the genus.

Material and methods

Study site

During January 1994 and October 1998, the web architecture, web placement, and diet of A. branicki were studied at the Centro de Investigaciones Ecológicas Macarena, Estacion Biologica Puerto Agujo, on the eastern side of the Tinigua National Park, Departamento del Meta, Colombian Amazon (2°40'N, 74°10′W), at an elevation of 350 m. The study area lies within the low tropical wet forest zone (Holdridge, 1967). Five forest types occur at this site: (1) mature forest, located mainly on hill ridges, characterised by 20-25 m high trees and continuous canopy, with emergent trees, reaching up to 30 m; (2) open degraded forest, localised in eroded areas, small valleys and around small streams, and composed mostly of vines, bamboos and a few trees between 20-25 m in height, resulting in a discontinuous canopy and a thick understory; (3) flooded forest, found in flatlands formed near the river, and characterised by a discontinuous canopy dominated by Ficus sp., Inga sp. and Cecropia sp. etc., the understory consisting mostly of "platanillo" (Heliconia sp.); (4) riparian forest, localised on recently formed sandy shores, covered mostly by graminoids and young Tessaria integrifolia and Cecropia trees; and (5) secondary forest, resulting from human disturbance, in the process of natural regeneration to forests of the other four types (Anonymous, 1997; Hirabuki, 1990; Stevenson et al., 1994, 2000).

Sampling methods

Surveys were made along two linear transects $(100 \text{ m} \times 2 \text{ m})$ by direct counting (Southwood, 1978) in each of the five habitat types, and using the "looking up" and "looking down" method proposed by Coddington et al. (1991), to determine the relative density of this species. Webs were made more easily visible by using corn starch dusted onto the web using an ear syringe. The following data were recorded for each web: height (from the centre of the web to the ground); total numbers of radii (upper and lower), spirals and points where the web was attached to supports; web orientation (using a professional Suuntom mirror compass for precise directional measurements and indicating whether the web was northward-oriented in relation to the spider's position, i.e. if the dorsum of the spider was facing northward the web orientation was recorded in that direction); spider body length (using a precision vernier calliper); and number of insects seen caught on the web (whether the spider fed on them or not was not determined). For practical reasons, the densities of spiders were recorded only at heights between 0-225 cm, but it is likely that the species also occurs at greater



Fig. 1: A Web of *Aspidolasius branicki* (^φ) with three anchor lines and lacking a secondary frame; the orb is approximately 95 mm in diameter (vertical) and 85 mm (horizontal). **B** *A. branicki* ^φ facing head down on web with legs flexed.

heights. The prey, and in some cases the web itself, were collected and placed in 70% ethyl alcohol for analysis in the laboratory. Insects were examined and determined to order, and in some cases to family, except for four alate ants that were identified to genus. The stratum within the habitat where the web was found was designated by the terminology adopted by Valderrama (1996): litter (HJC), small plants <90 cm high (PLT), shrubs with a diameter at breast height <5 cm and 1.5–5 m high (ABT), small trees with diameter >5 cm and 2–5 m high (V-T), trees more than 5 m high (ARB), buttress roots (RIZ), horizontal trunks (H-T) and cavities in the trunks (C-T).

Behavioural observations

Ad libitum observations (i.e. there were no constraints on the duration of the observation period, how many individuals were observed, or what data or observations were recorded (Altmann, 1974) were made on the construction behaviour for ten *A. branicki* webs. Each web was observed periodically and followed for 5 consecutive days or until the spider was no longer observed.

Data analysis

A Chi-square test (Zar, 1996) was used to compare habitat and microhabitat preferences (values were significantly different when p<0.05). Pearson correlation coefficient tests (Zar, 1996) were used to determine any association between the web location (based on height), the size of the spider, and numbers of radii, spirals, supports, and prey found caught in the web.

Taxonomic revision

Voucher specimens of the spiders collected were deposited in the Museum of Comparative Zoology, Harvard University; Laboratorio de Zoologia y Ecologia Animal, Universidad de los Andes, Colombia; and Instituto de Ciencias Naturales, Universidad Nacional de Colombia. The specimens used for the came from the following collections: revision AMNH=American Museum of Natural History, New York, USA (N. Platnick, L. Sorkin); BMNH=Natural History Museum, London, UK (P. Hillyard, F. Wanless); CAS=California Academy of Sciences, San Francisco, California, USA (W. J. Pulawski, D. Ubick, C. Griswold); MCZ=Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MNHN=Muséum National d'Histoire Naturelle, Paris, France (J. Heurtault, C. Rollard); MUSM=Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (D. Silva D.); PAN=Polska Akademia Nauk, Warszawa, Poland (J. Prószynski, A. Slojewska, W. B. Jedryczkowski); USNM=National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (J. Coddington, S. F. Larcher).

Results

A total of 71 spiders were observed during this study, 37 found in January 1994 and 34 in October 1998. The body length of these spiders ranged between 1–12 mm (mean= 6.3 ± 2.4 SD). Ninety percent of the spiders were positioned on the web hanging head down and with the dorsum facing to the north. The threads of the web consisted of a very thick and sticky silk of golden colour, with the web usually close to vertical. A triangular shaped web was observed, resulting from three points of support (Fig. 1), resembling in shape the web of some species of *Micrathena* Sundevall, *Acacesia* Simon, *Wagneriana* F. O. P.-Cambridge and *Wixia* O. P.-Cambridge (Levi, 1993). None of the webs had secondary frames supporting the radii.

Webs were found in only three of the five habitats described; mature, open degraded and secondary forests. The density of webs was significantly higher in mature forests (57.7%), followed by open degraded forests (39.4%) and secondary forests (2.8%) (χ^2 =33.31; 2 df;



Fig. 2: A Relative abundance of *A. branicki* in different habitats; percentage of total numbers found in mature, degraded and secondary forests; **B** Relative abundance in different strata in all 3 habitats (ABT=shrubs 1.5-5 m high, V-T=small trees 2-5 m high, ARB=trees >5 m high).

p < 0.05) (Fig. 2A). In these habitats webs were observed in only three microhabitats; shrubby vegetation (ABT=69%), small trees (V-T=21.1%) and trees >5 m(ARB=9.8%) (Fig. 2B); densities were significantly different among these microhabitats ($\chi^2 = 42.02$; 2 df; p < 0.05). Webs were observed only at heights ranging from 0.25–2 m (mean= 1.18 ± 0.51 SD). The number of radii observed in the webs ranged between 25-55 (mean = 35.8 ± 10.5 SD), and spirals between 9–45 (mean = 31.4 ± 8.7 SD). No significant relationships were found between spider size, height of web, and the numbers of radii or spirals (Pearson p > 0.05). Out of a total number of 116 prey caught and observed in A. branicki webs, the most numerous were Diptera (30.2%) and Hymenoptera (30.2%). Unidentified remains of other arthropods constituted 11.2% of the observed material. Other groups observed were Coleoptera (6.9%), Hemiptera (6.0%), Homoptera (4.3%), Lepidoptera (4.3%), Neuroptera (2.6%), Araneae (2.6%), Orthoptera (0.9%) and Strepsiptera (0.9%) (Table 1). Owing to practical limitations, no observations were made at heights above 225 cm. Previous observations of the vertical distribution of some spider species at the study site (Calixto, 1997) suggested that this species prefers the lower stratum of the forest. Further investigation is needed to verify whether this species also uses higher strata within the habitats.

Web construction (n=10) began between 0548 and 0600 h, when the first spiders were observed active when the spiders launched a bridgeline. The web had been totally removed (main lines were removed in most

cases) between 1800 and 1815 h, and the spider sought shelter among nearby foliage. An average of 44.5 min (SD=2.8) was spent in constructing the web, beginning with launch of the bridgeline and finishing with the sticky spiral. The steps and estimated times for the construction of the web can be summarised as: (1) placing of the bridgeline (mean= 4.7 ± 0.9 s, SD); positioning of three frame lines (mean = 4.9 ± 1.7 min); (3) placing the radii (mean= 15.6 ± 2.4 min); (4) placement of the temporary spiral beginning near the hub and working outwards (mean = 9.6 ± 2.4 min); (5) removal of the temporary spiral and placement of the sticky spiral (mean= 15.6 ± 3.4 min); (6) final modification of the hub, typically resulting in an asymmetrical hub with an irregular hole (mean = 14.8 ± 2.3 s). The spider was finally observed in the centre of the web with the legs

| Order | Family | Ν | % |
|-------------------------|----------------|-----|------|
| Araneae | | | |
| Calcontoro | Araneidae | 3 | 2.6 |
| Coleoptera | Chrvsomelidae | 1 | 0.9 |
| | Curculionidae | 1 | 0.9 |
| | Lycidae | 1 | 0.9 |
| | Scarabaeidae | 2 | 1.7 |
| | Scirtidae | 1 | 0.9 |
| | Staphylinidae | 1 | 0.9 |
| | Not identified | 1 | 0.9 |
| Diptera | | | |
| | Culicidae | 1 | 0.9 |
| | Psychodidae | 1 | 0.9 |
| | Sciaridae | 1 | 0.9 |
| | Syrphidae | 1 | 0.9 |
| TT 1 (| Not identified | 31 | 26.7 |
| Hemiptera | Nahidaa | 2 | 26 |
| | Pantatamidaa | 1 | 2.0 |
| | Cercopidae | 1 | 0.9 |
| | Not identified | 2 | 1.7 |
| Homontera | Not identified | 2 | 1.7 |
| | Cicadellidae | 2 | 1.7 |
| | Delphacidae | 1 | 0.9 |
| | Membracidae | 1 | 0.9 |
| | Not identified | 1 | 0.9 |
| Hymenoptera | | | |
| | Aphelinidae | 1 | 0.9 |
| | Braconidae | 1 | 0.9 |
| | Diapriidae | 1 | 0.9 |
| | Eupelmidae | 2 | 1.7 |
| | Formicidae | 4 | 3.4 |
| | Ichneumonidae | 3 | 2.6 |
| | Perilampidae | 1 | 0.9 |
| T | Not identified | 22 | 19.0 |
| Lepidoptera | Not identified | 5 | 1 2 |
| Neurontera | Not identified | 5 | 4.5 |
| reuroptera | Chrysopidae | 1 | 0.9 |
| | Not identified | 2 | 1.7 |
| Orthoptera | | | |
| | Acrididae | 1 | 0.9 |
| Strepsiptera | | | |
| | Stylopidae | 1 | 0.9 |
| Unidentified arthropods | | 13 | 11.2 |
| Total | | 116 | 100 |
| | | | |

Table 1 Arthropods collected in A. branicki webs.

flexed (Fig. 1). Some individuals built their web at the same site for several days. In two cases, webs were placed at the same site for 11 consecutive days before the spider disappeared.

Observations on all ten webs during the five day period showed that attack and prey manipulation behaviours mainly followed those already described for some other araneids such as *Argiope* Audouin and *Cyrtophora* Simon, where detection and location of the prey is followed by immobilisation by biting, manipulation, moving the prey, and feeding (Robinson, 1969; Robinson & Olazarri, 1971; Lubin, 1980; Eberhard, 1982). However, during all the observations, when prey was directly observed being caught in the web, *A. branicki* was never observed to wrap the prey or move it to a specific site for feeding, but simply fed on the prey where it was caught.

Casual observations were made on potential predators of *A. branicki*. Two species of hummingbirds *Phaetornis* sp. (hermits) and *Campylopterus largipennis* (grey-breasted sabrewing) were observed collecting the web for nest construction and the spider to feed to nestlings. Squirrel monkeys (*Saimiri sciureus*) and black-capped capuchins (*Cebus apella*) were also observed several times searching for spiders and collecting them by removing the spiders from the webs with their hands and eating them.

Discussion

Aspidolasius branicki was observed constructing an orb-web with three anchor lines and lacking a secondary frame, and built with very thick, sticky silk. The triangular shaped web resembles that of some species of Micrathena, Acacesia, Wagneriana and Wixia (Levi, 1985, 1993). The asymmetrically placed hub, with many loops and widely open in the centre, the long frame lines, and many closely spaced loops of sticky spiral, and the diurnal use of the orb, all resemble webs of Micrathena sp. (Shear, 1986). Scharff & Coddington (1997) raised some questions concerning the behaviour of hitherto unobserved araneids such as A. branicki, referring to preliminary observations on the behavioural characters described by Eberhard (1982). On such character is that during radius construction, araneids cut and reel up the exit line as they return to the hub, and the finished radial line is single (character 76 in Scharff & Coddington, 1997), whereas in uloborids, cyrtophorids and nephilids the radius is double; in Aspidolasius a single radial line was observed. A second character is the resting posture at the hub (character 82 in Scharff & Coddington, 1997): the spider rests either with legs I and II extended, or with those legs flexed; Aspidolasius always rested with them flexed.

At this specific locality, *A. branicki* was found most commonly in shrubby vegetation and in mature forests, which indicates a preference of this species for these types of microhabitat and habitat, probably as a response to the availability of suitable web supports and prey. However, further studies are needed since this first study was not intended to describe in detail the behav-



Fig. 3: Distribution of *Aspidolasius branicki* in Colombia and South America.

iour and ecology of this species, but to provide some basic information for future investigations of this species, which appears to be abundant in Colombia and fairly easy to observe.

Taxonomic revision

Aspidolasius Simon, 1887

- *Inca* Taczanowski, 1879: 104. Type species *Inca branickii* Taczanowski by monotypy. Name preoccupied by *Inca* Lepeletier & Serville, 1828 (Coleoptera) and *Inca* Jardine, 1850 (Aves) (Neave, 1939: 771).
- Aspidolasius Simon, 1887: 187. New name for *Inca* Taczanowski (Neave, 1939: 322). The gender is masculine (Bonnet, 1955: 765).

Diagnosis: The square carapace and oval, wide, abdomen with two posterior, lateral humps (Figs. 4–7) distinguish female *Aspidolasius* from most other araneids, and the abdomen shape distinguishes it from araneids that have a similar carapace (*Encyosaccus* Simon, 1895 and *Gasteracantha* Sundevall, 1833). Unlike males of *Encyosaccus* and *Gasteracantha*, males of *Aspidolasius* also have a square carapace (Figs. 8–11), and the male also has the abdomen covered with a sclerotised plate (Fig. 12).

Relationships: Aspidolasius has many characters that appear primitive: the female has a flat epigynum with a pair of depressions (Figs. 13–15); the male palpus lacks a radix, has a cone-shaped tibia (Fig. 16: TI) and the cymbium bears a tarsal organ (TO). The conductor may be the lobe of the tegulum (shown at 8 o'clock in Fig. 16) and the free sclerite is probably the median apophysis (Fig. 17). These male adaptations, along with the lack of grooves on the booklung covers, may be the result of its relatively small size. The embolus is in the shape of a coil and is not attached or supported by other structures (Figs. 17–18). However, the modified tapetum in the posterior median eyes suggests that the species belongs to the Araneidae. Superficially, *Aspidolasius* resembles the African *Caerostris* Thorell, 1868. *Aspidolasius* and 318

carapace" and having the "female carapace wider than long". *Distribution*: Only one American species is known, from the northern half of South America.

gasteracanthoid clade, because of a "reversal to a hirsute

Aspidolasius branicki (Taczanowski, 1879) (Figs. 1-18)

- Inca branickii Taczanowski, 1879: 105, pl. 1, fig. 24 (^Q). Female lectotype from Amable María [Depto. Junín], Peru, in PAN, examined.
- Paraplectana peruana Keyserling, 1880: 296, pl. 4, fig. 2 (d). Male holotype from Amable María [Depto. Junín], Peru, in PAN, lost. Keyserling, 1892: 5, fig. 5 (d); Roewer, 1955: 1615. New synonymy.
- Aspidolasius branicki: Simon, 1895: 870; Roewer, 1942: 893; Bonnet, 1955: 765.
- Aspidolasius bifurcatus Simon, 1897: 471. Female lectotype here designated and numerous paralectotypes from Moyobamba [Depto. San Martín], Peru, in MNHN, examined. Roewer, 1942: 893; Bonnet, 1955: 765. New synonymy.
- Aspidolasius smaragdus Mello-Leitão, 1948: 160. Immature holotype from Yawakuri River, Guyana, in BMNH, examined. Brignoli, 1983: 264. New synonymy.

Paraplectana peruviana: Bonnet, 1958: 3332.

Note: A male in the vial with the lectotype of *I. branickii*, in the original type series, belongs to *Enacrosoma*. Roewer (1942) does not list *peruana* with *Paraplectana*, but it is listed with synonymies in vol. 2b (1955), with the comment "nicht zu deuten." Roewer's comment is puzzling as Keyserling (1892: 5, fig. 5) published an adequate description and a minute, but good, illustration. Bonnet lists the species in *Paraplectana* and unjustifiably changed the spelling to *peruviana*.

Description: Female (from Meta, Colombia, in MCZ): Carapace dark orange-brown, with white, flattened setae in cephalic region. Chelicerae orange-brown. Endites, labium and sternum dark orange. Legs I–II dark brown, III–IV light orange-brown. Dorsum of abdomen light orange-brown, black around sides and posterior. Venter black with light, narrow, transverse line, running from near spinnerets in anterior lateral direction, becoming indistinct on sides. Eyes: PME same diameter as AME, laterals 0.5 diam. of AME. AME 0.9 diam. apart, PME 1.6 diam. apart, laterals separated by their radius. Ocular quadrangle slightly wider behind than in front. Height of clypeus 1.7 diam. of AME. Abdomen without sclerotised ring around spinnerets. Total length 8.3 mm. Carapace 4.6 mm long, 3.5 mm wide in thoracic region,



Figs. 4–18: Aspidolasius branicki (Taczanowski). 4–7 Female. 4 Eye region and chelicerae, frontal; 5 Carapace and chelicera, lateral; 6 Carapace, dorsal; 7 Habitus, dorsal. 8–12 Male. 8 Eye region, chelicerae and right palpus, frontal; 9 Carapace and chelicera, lateral; 10 Carapace, dorsal; 11–12 Habitus, dorsal. 13–14 Epigynum, ventral, virgin. 15 Epigynum, ventral, mated, with parts of embolus; 16 Left male palpus pulled apart; 17 Left embolus, subventral; 18 Left male palpus. Abbreviations: E=embolus, P=paracymbium, T=tegulum, TI=tibia, TO=tarsal organ. Scale lines=1.0 mm (4–12), 0.1 mm (13–18).

3.8 mm wide in cephalic region. Leg I femur 2.9 mm, patella+tibia 3.4 mm, metatarsus 1.9 mm, tarsus 1.1 mm. Leg II patella+tibia 3.3 mm, III 2.1 mm, IV 3.2 mm. Abdomen 5.7 mm long, 6.8 mm wide; 1.2 times wider than long.

Male (from Mato Grosso, Brazil, in AMNH): Carapace, chelicerae and sternum dark orange-brown. Dorsum of abdomen orange-brown to black, venter black, posterior of abdomen lighter than anterior. Eyes: PME 1.1 diam. of AME, laterals 0.5 diam. of AME. AME 0.7 diam. apart, PME 1.0 diam. apart. Ocular quadrangle wider behind than in front. Endite without tooth. Palpal patella without macroseta. Coxa I without hook. Tibia II thinner than I. No ring around spinnerets. Total length 2.2 mm. Carapace 1.22 mm long, 1.04 mm wide in thoracic region, 1.07 mm wide in cephalic region, 0.71 mm high. Leg I femur 1.01 mm, patella+tibia 1.18 mm, metatarsus 0.66 mm, tarsus 0.43 mm. Leg II patella+tibia 1.11 mm, III 0.53 mm, IV 0.78 mm. Abdomen 1.41 mm long, 1.53 mm wide.

Note: The embolus breaks off and remains in the epigynum after mating, part of the embolus inside the ducts, part visible externally. No males were found lacking the embolus. Only a few females were found without an embolus stuck in the epigynum (Figs. 13–14).

Males and females were matched because the long coiled embolus matches the long coiled connecting ducts of the female genitalia, and because most females have a broken piece of the long embolus extending from the epigynum (Fig. 15).

Variation: Total length of females 7.0–10.8 mm, males 2.1–2.5 mm. Illustrations made from a female (Fig. 6) from Depto. Meta, Colombia (MCZ), a female (Fig. 7) from Depto. San Martín, Peru (AMNH) and a male from Mato Grosso, Brazil (AMNH).

Diagnosis: The hairy, square carapace and the shape of the abdomen (Fig. 7) distinguish the female from all other American orb-weavers. The square carapace (Fig. 12) and the palpus with a coiled embolus (Figs. 16–18) distinguish the male from the small, superficially similar, *Witica cayana* Levi, 1986.

Material examined: VENEZUELA: Bolívar: Cerro Coroba, 420 m, Hato La Vergareña, 23 April 1955, 2º (J. J. Wurdack, AMNH). GUYANA: Canje Ikurua River, August-December 1961, 1º (G. Bentley, AMNH); Takutu Mountains, 6°15'N, 59°05'W, Mazaruni-Potaro Distr., 8 December 1983, 1º (P. J. Spangler, R. A. Faitoute, A. M. Hegyi, USNM); Yawakuri River, July 1919, 19 (Cattle Trail Survey, A. A. Abraham, BMNH). COLOMBIA: Caquetá: Río Orteguaza, August-September 1947, 1º (L. Richter, AMNH). Santander: Río Suarez, 800-1000 m, 11-17 August 1946, 39 (AMNH). Meta: Río Duda, Macarena, 1992, 49, voucher specimens (A. Calixto, MCZ). ECUADOR: Sucumbios: Reserva Faunistica Cuyabeno, Laguna Grande, 0°00', 76°10'W, 26 June 1988, early imm. (W. Maddison, MCZ). Napo: Selva Aliñahui, 450 m, 25 km E Puerto Napo, 01°00'S, 77°25'W, January-February 1991, 49 4 imm., December 1992, 2º (both E. S. Ross, CAS). PERU: Ucayali: Parque Nacional A. von Humboldt, 30 July 1986, 13 (D. Silva D., MUSM); Divisoria, Huanuco, 23 September-3 October 1946, 1 imm. (F. Woytkowski, AMNH). Pasco: Villa Rica, 1500 m, 28 July 1992, 19 (P. Hocking, MUSM). San Martín: Ekin, E. Tarapoto, 9-21 March 1947, 1 imm. (F. Woytkowski, AMNH); Mishiqui-yacu, 20 km NE Moyobamba, August 1947, 5º 2 imm. (F. Woytkowski, AMNH); Hara, 32 km SE Moyobamba, 1-30 June 1947, 19 (F. Woytkowski, AMNH). Huánuco: Dantas-La Molina, SW of Puerto Inca, 270 m, 09°38'S, 75°00'W, 18 Mav-1 June 1987, 1º 1 imm, (D. Silva D., MUSM). Monsón Valley, Tingo María, 12 October 1954, 1 imm. (E. I. Schlinger, E. S. Ross, CAS). Madre de Dios: Zona Reservada Pakitza, 11°56'S, 71°17'W, 356 m, 5 October 1991, 2º 13 (D. Silva D., MUSM); February-March 1992, 1º 2 imm. (I. Bohorquez M., MUSM); Cuzco Amazonico Lodge, 15 km E Puerto Maldonado, 28 May 1983, 1º (G. C. Hunter, CAS); Parque Nacional Manu, Totora Trail, night collection, 1 November 1987, 19 (I. Bohorquez M., MUSM); Cashu Trail, 3-20 November 1987, 2º (I. Bohorquez M., MUSM); Reservada Tambopata, 290 m, 12°50'S, 69°17'W, 17 July 1987, 19 3 imm. (D. Silva D., MUSM); 27 May-13 June 1988, 29 2 imm. (D. Silva D., MUSM); 5-20 September 1984, 29 1 imm. (I. Bohorquez, MUSM); 3-13 October 1987, 19 (R. Fernandez, MUSM). BRAZIL: Acre: Rio Purus, W Sena Madureira, Boca de Chandless, 9 September 1973, 1º 2 imm. (B. Patterson, MCZ). Rondônia: 62 km SW Ariquemes, 10°32'S, 62°48'W, 18-25 July, 3º 2imm. (CAS). Mato Grosso: Sinop, October 1975, 18 (M. Alvarenga, AMNH), February 1976, 23 (O. Roppa, AMNH). BOLIVIA: Beni: Estacion Biológica Beni, 8-14 September 1987, 19 13 2 imm. (J. Coddington, S. Larcher, D. Wilson, USNM).

Acknowledgements

We thank C. Mejia, A. Dean and M. K. Harris for ideas in the development of this paper, and all the curators of the collections for making the specimens available. N. Scharff made available his world-wide knowledge of gasteracanthine spiders, made suggestions and sent his sketches of an expanded *Caerostris* palpus. We thank two anonymous reviewers and the editor for their comments to improve this manuscript. This study was partially supported by the CIEM, Universidad de los Andes and the Museum of Comparative Zoology, Harvard University.

References

- ALTMANN, J. 1974: Observational study of behaviour: sampling methods. *Behaviour* 49: 227–265.
- ANONYMOUS 1997: The study site: a brief description. Field studies fauna flora La Macarena, Colombia 10: 5.
- BONNET, P. 1955: Bibliographia Araneorum 2(1): 1–918. Toulouse.
- BONNET, P. 1958: *Bibliographia Araneorum* **2**(4): 3027–4230. Toulouse.
- BRIGNOLI, P. 1983: A catalogue of the Araneae described between 1940 and 1981. 1–755. Manchester University Press, Manchester.
- BROWN, M. V. 1981: Foraging ecology and niche partitioning in orb-weaving spiders. *Oecologia* 50: 380–385.
- CALIXTO, A. 1997: Spiders at the CIEM: a preliminary list. *Field* studies fauna flora La Macarena, Colombia 10: 33–37.
- CODDINGTON, J. A. 1986: The monophyletic origin of the orb web. In W. A. Shear (ed.), Spiders: webs, behavior and evolution: 319–363. Stanford University Press, Stanford.
- CODDINGTON, J. A., GRISWOLD, C. E., SILVA-DAVILA, D., PEÑARANDA, E. & LARCHER, S. F. 1991: Designing and testing sampling protocols to estimate biodiversity in tropical systems. In E. C. Dudley (ed.), The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology: 1: 44–60. Dioscorides Press, Portland, Oregon.
- EBERHARD, W. G. 1982: Behavioral characters for the higher classification of orb-weaving spiders. *Evolution* **36**(5): 1067–1095.
- EBERHARD, W. G. 1986: Effects of orb-web geometry on prey interception and retention. *In* W. A. Shear (ed.), *Spiders: webs, behavior and evolution*: 70–100. Stanford University Press, Stanford.

- HIRABUKI, Y. 1990: Vegetation and land form structure in the study area of La Macarena: a physiognomic investigation. *Field studies new world monkeys La Macarena Colombia* **3**: 35–48.
- HOLDRIDGE, L. R. 1967: *Life zone ecology*. 1–206. Tropical Science Center, San Jose, Costa Rica.
- KEYSERLING, E. 1880: Neue Spinnen aus Amerika. Verh. zool.-bot. Ges. Wien **29**: 293–350.
- KEYSERLING, E. 1892: Epeiridae, part 1. *Die Spinnen Amerikas* **4**(1): 1–208. Nürnberg: Bauer und Raspe.
- LEVI, H. W. 1985: The spiny orb-weaver genera *Micrathena* and *Chaetacis* (Araneae: Araneidae). *Bull. Mus. comp. Zool. Harv.* **150**: 429–618.
- LEVI, H. W. 1993: The Neotropical orb-weaving spiders of the genera *Wixia, Pozonia,* and *Ocrepeira* (Araneae: Araneidae). *Bull. Mus. comp. Zool. Harv.* **153**: 47–141.
- LEVI, H. W. & CODDINGTON, J. A. 1991: Systematics and evolution of spiders (Araneae). A. Rev. Ecol. Syst. 22: 565–592.
- LUBIN, Y. D. 1980: The predatory behavior of *Cyrtophora* (Araneae: Araneidae). J. Arachnol. 8: 159–185.
- MELLO-LEITÃO, C. F. de 1948: Contribuição ao conhecimento da fauna araneológica da Guianas. Anais Acad. bras. Cienc. 20: 151–196.
- NEAVE, A. S. 1939: *Nomenclator Zoologicus* **1**(A–C): 1–957. London: Zoological Society.
- PLATNICK, N. I. 2004: The world spider catalogue. Version 5.0. <http://research.amnh.org/entomology/spiders/catalog/ INTRO1>
- RIECHERT, S. E. & GILLESPIE, R. M. 1986: Habitat choice and utilization in web-building spiders. In W. A. Shear (ed.), Spiders: webs, behavior and evolution: 23–48. Stanford University Press, Stanford.
- ROBINSON, M. H. 1969: Predatory behavior of Argiope argentata (Fabricius). Am. Zool. **9**: 161–173.
- ROBINSON, M. H. & OLAZARRI, J. 1971: Units of behavior and complex sequences in the predatory behavior of Argiope argentata (Fabricius) (Araneae: Araneidae). Smithson. Contr. Zool. 65: 1–36.

- ROBINSON, M. H. & ROBINSON, B. C. 1978: Thermoregulation in orb-web spiders: new descriptions of thermoregulatory postures and experiments on the effects of posture and coloration. *Zool. J. Linn. Soc.* 64: 87–102.
- ROEWER, C. F. 1942: *Katalog der Araneae von 1758 bis 1940* **1**: 1–1040. Bremen.
- ROEWER, C. F. 1955: *Katalog der Araneae von 1758 bis 1940, bzw. 1954* **2b**: 927–1751. Bruxelles.
- SCHARFF, N. & CODDINGTON, J. A. 1997: A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneidae). Zool. J. Linn. Soc. 120: 355–434.
- SHEAR, W. A. 1986: *Spiders: webs, behavior and evolution.* 1–492. Stanford University Press, Stanford.
- SIMON, E. 1887: Quelques observations sur les arachnides. Annls Soc. ent. Fr. (6) 7: 158–159, 167, 175–176, 186–187, 193–195.
- SIMON, E. 1895: *Histoire naturelle des Araignées* **1**(4): 761–1084. Paris.
- SIMON, E. 1897: Etudes arachnologiques. 27e mémoire. XLII. Descriptions d'espèces nouvelles de l'ordre des Araneae. Annls Soc. ent. Fr. 65: 465–510.
- SOUTHWOOD, T. R. E. 1978: *Ecological methods with particular* reference to the study of insect populations. Chapman & Hall, New York.
- STEVENSON, P. R., QUIÑONES, M. J. & AHUMADA, J. A. 1994: Ecological strategies of woolly monkeys (*Lagothrix lagotricha*) at Tinigua National Park, Colombia. *Am. J. Primatol.* 32: 123–140.
- STEVENSON, P. R., QUIÑONES, M. J. & CASTELLANOS, M. C. 2002: Guía de frutos del río Duda La Macarena, Colombia. 1–467. Asociación para la defensa de la reserva de la Serranía de La Macarena. IUCN, Bogotá, Colombia.
- STOWE, M. 1986: Prey specialization in the Araneidae. *In* W. A. Shear (ed.), *Spiders: webs, behavior and evolution*: 101–131. Stanford University Press, Stanford.
- TACZANOWSKI, L. 1879: Les Aranéides du Pérou central. Trudy russk. ent. Obshch. (=Horae Soc. ent. Ross.) 15: 102–136.
- VALDERRAMA, C. 1996: Comparación de la distribución vertical de arañas constructoras de telas orbiculares en tres zones de un bosque nublado. M.Sc. thesis. Facultad de Ciencias Biologicas, Universidad de los Andes, Colombia.
- ZAR, H. J. 1996: Biostatistical analysis (3rd edn). Prentice Hall.