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Web gigantism in Darwin's bark spider, a new species from Madagascar (Araneidae: *Caerostris*)

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Abstract. The remarkable bark spiders (genus *Caerostris*: Araneidae) are poorly known Old World tropical orb-weavers, whose diversity, currently at 11 species, is grossly underestimated. Most species build large webs at forest edges, clearings, and gardens, but in Madagascar, probably the hot spot of *Caerostris* diversity, at least one species occupies a unique ecological niche: casting its web across streams, rivers and lakes, so that the orb is suspended above water and attached to substrate on each riverbank via bridgelines up to 25 m. Here, we summarize current knowledge on *Caerostris* natural history, and specifically focus on the remarkable web architecture and biology of the newly described *Caerostris darwini* n. sp. Darwin's bark spider builds its web, a regular orb suspended above water, and maintains it with daily reinforcing of bridgelines and renewal of orb for many days. Web size ranged from 900–28,000 cm^2, with the largest measured web of about 2.8 m^2 being the largest orb ever measured, to our knowledge. With anchor lines capable of bridging over 25 m, it also builds the longest webs among all spiders—a unique form of web gigantism. We report on mass capture of ephemeropteran prey items in *C. darwini* n. sp. webs during a single day. Webs contained up to 32 mayflies that were subsequently wrapped *en masse* before the spider fed on them. We also provide the first evidence of kleptoparasitism in these webs both by other spiders (Argyrodinae) and by newly documented, undescribed symbiotic flies. *Caerostris* display extreme sexual size dimorphism with large females and small males, which is manifested in enigmatic sexual behaviors such as mate guarding, male-male aggressiveness, genital mutilation, mate plugging, and self castration. *Caerostris* is thus a promising candidate for evolutionary studies, and its diversity, biology, and phylogenetic relationships all deserve a closer scrutiny.

Keywords: Diversity, DNA barcode, genital mutilation, morphology, orb web architecture, sexual behavior, sexual size dimorphism

Spiders of the genus *Caerostris* (Araneidae), known in Africa under the vernacular 'bark spiders', are eye-catching orbweavers that are widespread throughout the Old World tropics. *Caerostris* spiders all make sizable orb webs, with some of the webs reported here, to the best of our knowledge, qualifying as the largest spider webs ever documented. *Caerostris* are also remarkable for their extreme sexual size dimorphism, with huge females and small males (Grasshoff 1984; Kuntner et al. 2008a). The large females are highly conspicuous when sitting in the center of their webs; however, their name stems from the habits of at least some species to mimic dead bark, twigs or thorns (Fig. 1), making them quite cryptic but also resulting in exceptional morphological diversity. Surprisingly, given the size of the spiders and their webs, virtually nothing is known about *Caerostris* natural history, and the genus is also poorly known taxonomically and phylogenetically.

Caerostris, first described by Thorell (1868), is a seemingly species-poor genus, with only 11 species recognized throughout the Old World tropics (Platnick 2010). Most descriptions have been based on female material alone (Grasshoff 1984), since the small males are cryptic and very rarely observed or collected. In the only taxonomic revision of the entire genus, Grasshoff (1984) only examined a total of 16 *Caerostris* males, and these only belonged to three widespread Afrotropical species, the type *C. mitralis* (Vinson 1863), *C. sexcuspidata* (Fabricius 1793) and *C. vicina* (Blackwall 1866). According to Grasshoff, an additional six species are known (females only) from the Afrotropics: *C. corticosa* Pocock 1902 from South Africa, *C. cowani* Butler 1882, *C. ecclesiigera* Butler 1882, *C. extrusa* Butler 1882 and *C. hirsuta* (Simon 1895), all from Madagascar, and *C. mayottensis* Grasshoff 1984 from Mayotte. Grasshoff also recognized two Asian species based on female material, *C. indica* Strand 1915 from Myanmar and the widespread *C. sumatrana* Strand 1915 (for the description of the male, see Jaeger 2007). The revision is devoid of biology, as it only mentions that female *Caerostris* construct orb webs (Grasshoff 1984:765).

Of the 11 currently recognized *Caerostris* species, six occur in Madagascar (Platnick 2010). However, this diversity is hugely underestimated; for example, we observed and collected female vouchers of perhaps seven species in sympatry in the Andasibe-Mantadia National Park alone (Fig. 2A, D–I), some diurnal and some nocturnal. We found that males of the diurnal species usually hide in vegetation away from female webs (Fig. 2B), and were thus able to collect more males during our three field expeditions than exist in all museum collections of all species worldwide (own data). Hence, a new global taxonomic revision is necessary to 1) match sexes of species previously known from females only, 2) understand *Caerostris* diversity better and describe new species, and 3) obtain *Caerostris* DNA data for taxonomic and phylogenetic investigations; this work is already underway in the authors' laboratories. The goal of this paper is to introduce some of the most striking aspects of *Caerostris* biology, based mostly on original observations of a new species from Madagascar, which we named *C. darwini* n. sp. precisely 150 yr after the date of the publication of Charles R. Darwin's *Origin of Species* (see Etymology).

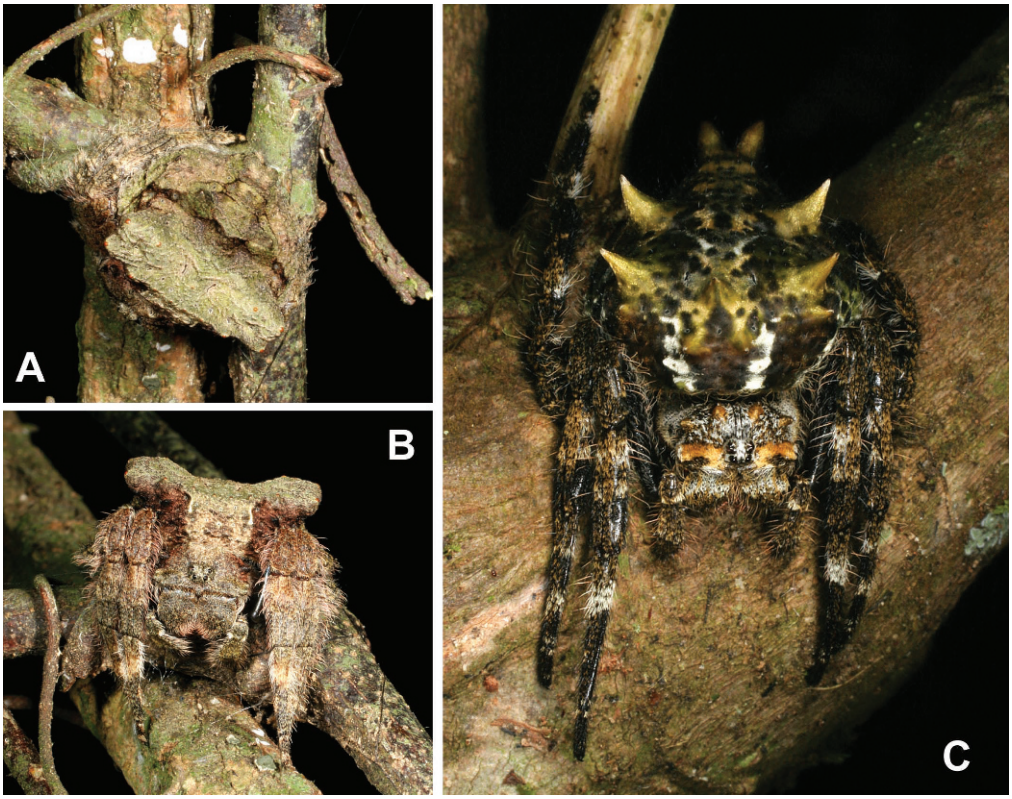

Figure 1.—Extreme crypsis of bark spiders, *Caerostris* spp: A. Bark, lichen, or what…?; B. Same female *Caerostris* spider from a different angle, South Africa; C. Female *Caerostris* from Madagascar.

We provide a preliminary assessment of *Caerostris* diversity on Madagascar and present the first natural history observations made on the newly described diurnal species, provide information on female and male sexual biology including genital damage, describe egg sac structure, and provide preliminary information on prey and prey capture. Additionally, we present the data on kleptoparasitism in *Caerostris* webs by other spiders (Argyrodinae) and by newly discovered undescribed dipterans (Fig. 4). Our main focus is on the biology and web architecture of the new riverine *Caerostris* species due to it combining extraordinary web architecture with exceptional silk mechanical properties (Agnarsson et al. 2010). In addition, we contrast this newly understood biology of the new species with certain aspects of the biology of other diurnal and nocturnal *Caerostris* species, based on preliminary and opportunistic observations from Madagascar (2001, 2008, 2010) and South Africa (2001).

Based on our observations on *C. vicina*, African *Caerostris* do not maintain webs diurnally, but cryptically hide during the day and construct large webs (up to 1.5 m across), often in the forest edge or clearings, at night. However, in Madagascar *C. darwini* n. sp. occupies a unique ecological niche: females cast their giant webs across streams, rivers and lakes, suspending the orb directly above the water on anchor threads that can span up to 25 m (M. Gregorič pers. comm.), attached to vegetation on each side of the river (Fig. 3). Although some other spiders build webs above water (Eberhard 1990), no others can, to our best knowledge, routinely utilize as habitat the air column immediately above sizeable rivers and up to several meters above water. We thus provide baseline information that we hope will inspire further work on this poorly known, but remarkable group of spiders. We believe *Caerostris* spiders have the potential to become exemplar organisms in the study of web biology (e.g., Blackledge & Hayashi 2006; Swanson et al. 2006; Agnarsson et al. 2009, 2010) and sexual behavior studies related to antagonistic interactions between the highly dimorphic sexes (e.g., Miller 2007;Kuntner et al. 2009b, c).

METHODS

Literature review.—We reviewed the literature on *Caerostris* biology, and summarize it along with our own observations (behavioral descriptions follow Eberhard 1982; Scharff & Coddington 1997; Griswold et al. 1998; Kuntner et al. 2008a). The only published accounts on *Caerostris* natural history appear in popular science works on common African species (Yates 1968; Filmer 1991; Dippenaar-Schoeman & Jocque 1997; Leroy & Leroy 2000). Nothing has been published on the biology of *Caerostris* species from Madagascar or Asia (Grasshoff 1984; but, see Jaeger 2007).

Field methods.—Fieldwork took place 21–25 April 2001 around Namorona River in Ranomafana NP (elev. 1000 m, see locality data below) and Fianarantsoa Province, eastern Madagascar; and 29 March–24 April 2008 in and around the two patches of forest protected by the Andasibe-Mantadia National Park (Périnet special reserve and Mantadia forest), in Toamasina Province, eastern Madagascar (elev. 900–1000 m, see locality data below). Additional data on *C. darwini* n. sp. comes from February–March 2010 fieldwork from both the above reserves and from Tzimbazaza Zoo in

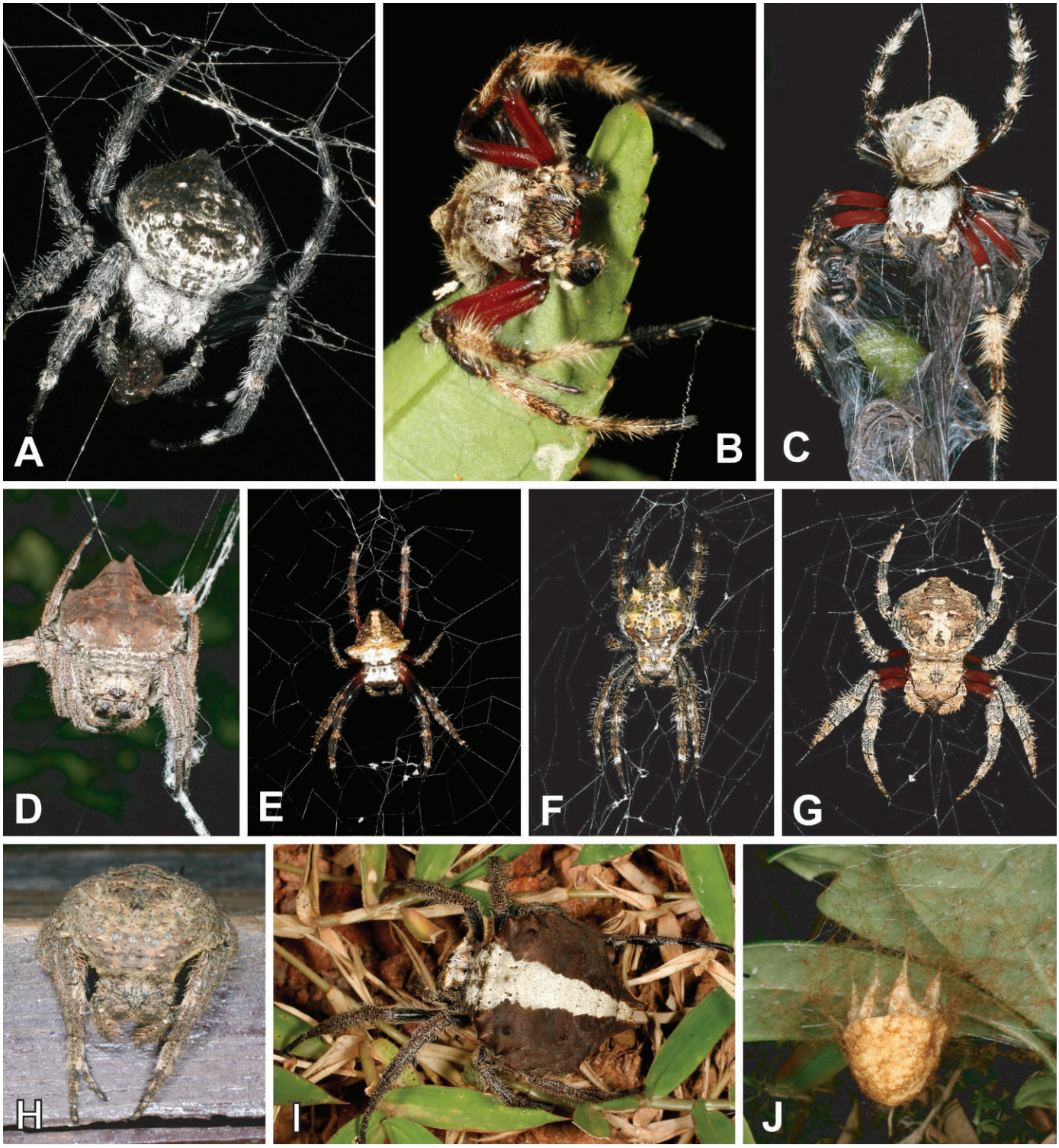

Figure 2.—A glimpse into Madagascar *Caerostris* diversity, all from a single reserve, Andasibe-Mantadia NP. A–C. The commonly encountered riverine species, *C. darwini* n. sp.: A. Female feeding at hub; B. Male hiding in vegetation near female web; C. Male feeding on prey caught and wrapped by female. D–I. Females of six other morphospecies in sympatry. J. Egg sac of undescribed *Caerostris* species from Madagascar.

Antananarivo, Madagascar. Additional, more sporadic data on *Caerostris* natural history are from Phinda Reserve and Tembe Elephant Park, South Africa during March–April 2001. Vouchers of all morphospecies are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

In Andasibe-Mantadia NP we encountered webs of about six different morphospecies (possibly new species, but

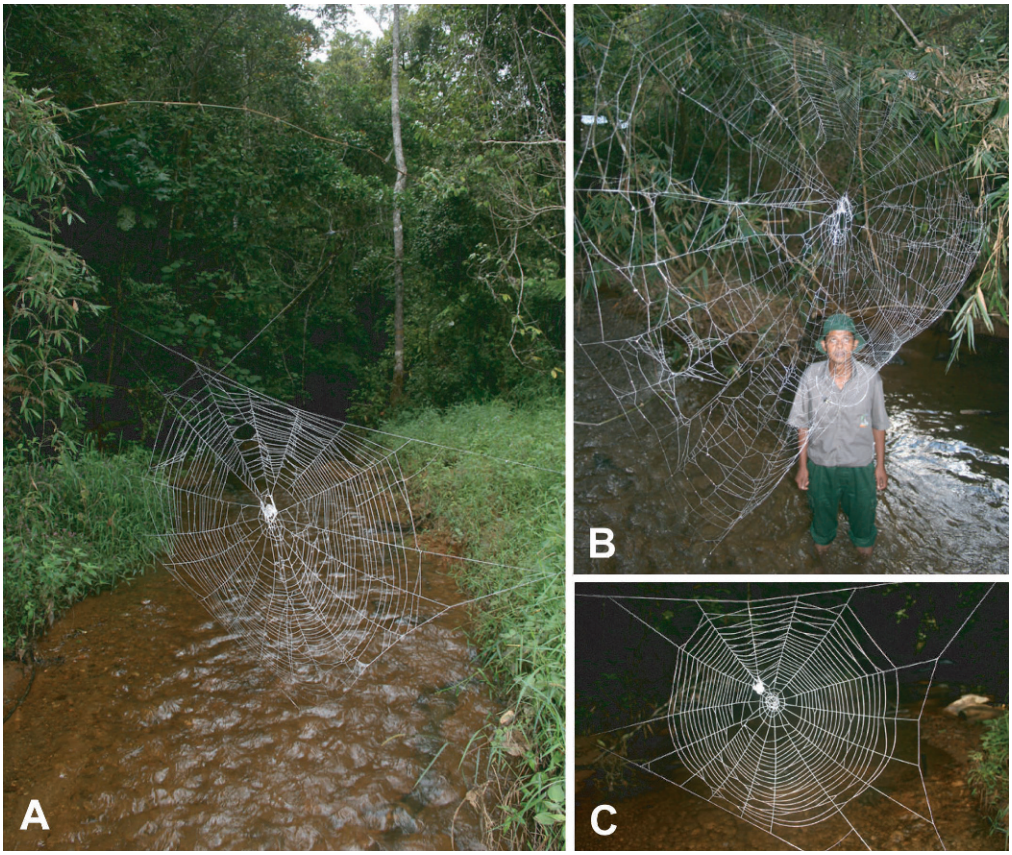

Figure 3.—*Caerostris darwini* n. sp. webs cast over streams and rivers in Andasibe-Mantadia NP, Madagascar.

represented by females only) along the road, at forest edges and in clearings, and of the focal species *C. darwini* n. sp., across streams and rivers (Figs. 2, 3). We also observed numerous *C. darwini* n. sp. along and across rivers in Ranomafana. We measured webs in the field, and when possible, we photographed each web for subsequent measuring. The parameters measured, all described elsewhere (Kuntner & Agnarsson 2009; Kuntner et al. 2008b), were 1) web width; 2) web total height; 3) distance from top web frame to hub; 4) maximal mesh width; 5) total bridge line length; 6) number of radii; 7) hub height above water/ground; and 8) maximal distance between sticky spirals. All web measurements are in cm, presented as the range and average ± SD.

Webs were also examined for prey items as well as kleptoparasitic organisms, and vouchers were collected. The web, and the vegetation to which the web was attached, was surveyed for egg sacs and for adult males. Prey items were photographed and collected for identification. Observations were made on web building and architecture, prey wrapping and feeding, including interactions between the spider host and kleptoparasites sharing her food, and on sexual biology.

Coddington's sound test involved a human emitted noise (humming) made close to the spider sitting at the web hub.

Taxonomic methods.—We used Grasshoff's (1984) revision of *Caerostris* to differentially diagnose *C. darwini* n. sp. from all other known species. Previously, Kuntner et al. (2008:fig. 16) used this species as an outgroup exemplar in a phylogenetic study focusing on nephilid spiders, and illustrated its genital anatomy. Here, we illustrate, diagnose and describe this new species (taxonomic methods follow Kuntner 2007), and provide the barcode COI sequence for reference (standard CO1 primers used; T. Blackledge pers. comm.).

Abbreviations.—The following anatomical abbreviations are used in the text and figures: ALE = anterior lateral eyes, AME = anterior median eyes, BH = basal hematodocha, C = conductor, CB = cymbium, CD = copulatory duct, E = embolus, EB = embolic base, Etm = embolus-tegulum membrane, FD = fertilization duct, PLE = posterior lateral eyes, PME = posterior median eyes, PP = pars pendula, S = spermatheca, SD = sperm duct, ST = subtegulum, T = tegulum.

RESULTS AND DISCUSSION

Our study revealed a high diversity of *Caerostris* in Madagascar (Figs. 1, 2), with several new species restricted to small remaining pockets of montane rainforest. The lack of available males still precludes a clear assessment of the numbers of new species, and we here only describe the one new species for which sufficient material of both sexes became available. Clear understanding of this diversity is critical to conserving these giant orbweavers and their habitat in the rapidly diminishing forests of Madagascar. *Caerostris* are strongly sexually dimorphic. Males are small, cryptic, and thus rarely discovered. These males are critical for identifying species and for phylogenetics. In addition to its conservation aspects, understanding Malagasy *Caerostris* diversity is also crucial to determine the evolutionary origin of web gigantism.

Our preliminary data suggest that *Caerostris* species exhibit two quite distinct biologies. The typical African and possibly

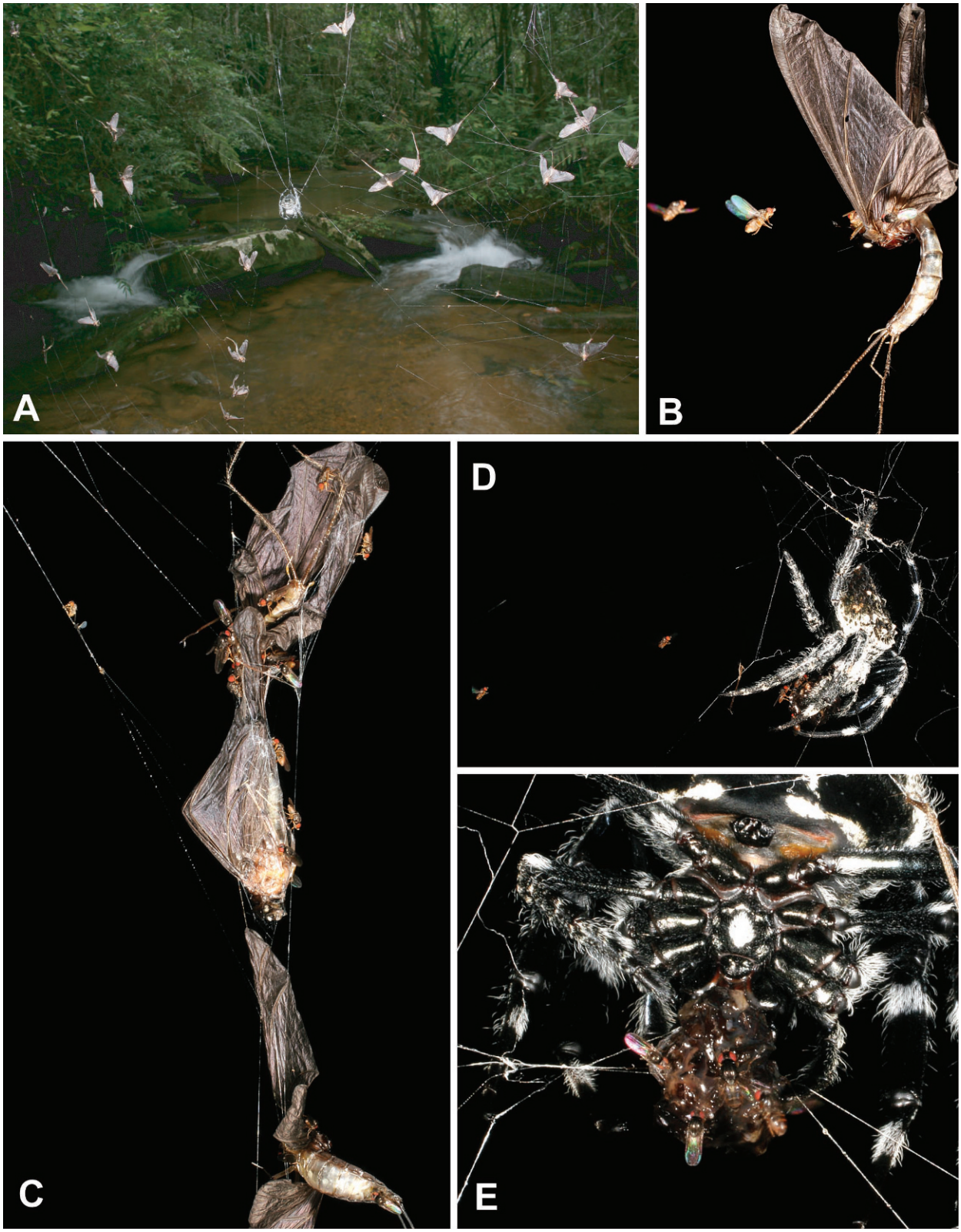

Figure 4.—*Caerostris darwini* n. sp. prey and their symbionts. A. Web with 22 newly caught mayflies. B–E. Kleptoparasitic flies interacting with spider and her prey: B. Landing on spider prey; C. At least 16 flies on and around three wrapped packages of spider prey; D. Flying in to feed with the spider female, who showed occasional aggressiveness; E. Close-up of feeding spider, involuntarily sharing food with four flies.

Asian species live away from webs cryptically on twigs during the day, resembling dead bark or twigs (Fig. 1A, B; see also Filmer 1991; Leroy & Leroy 2000). These species blend into the environment by their coloration and general morphology (flattened legs, hairy bodies with thorny projections (Fig. 1) and probably only build and occupy their webs at night (own data). The second lifestyle, typical of certain species from Madagascar and exemplified by *C. darwini* n. sp., is to live permanently in the web, which is typically spun over flowing bodies of water (Fig. 3). Smaller species in Madagascar utilize small streams and the large ones, like *C. darwini* n. sp., cast their impressive webs with anchor threads spanning on average 3.5 m, but up to 14 m wide over medium sized rivers that may be about 10 m wide (e.g., Namorona River at Ranomafana, 2001), and even 25 m wide over lakes (M. Gregorič pers. comm.).

Web architecture and gigantism.—We documented webs of several *Caerostris* species in Andasibe-Mantadia NP. *Caerostris darwini* n. sp. was the most common species and well represented by both sexes. According to our observations, webs of *Caerostris* species are rather uniform and fairly typical araneid orbwebs (Fig. 3). All species make large orbs with a an open hub (rarely closed), gradual hub-loop to sticky-spiral transition, temporary spiral removed in finished web, relatively few radii, few or no secondary radii, and lacking a retreat or other auxiliary silk structures such as barrier web, and very rarely containing a stabilimentum (Kuntner et al. 2008a). We did not observe web construction in full, but new comprehensive data on *C. darwini* web construction will soon be made available (M. Gregorič pers. com.). One female *C. vicina* was observed partially building sticky spiral in Tembe Elephant Park, S. Africa. In a typical araneid fashion, she used the oL1 tap and removed the temporary non-sticky spiral; oL1 tap was also observed in another undescribed species in Périnet (2001), and in *C. darwini* n. sp. in Andasibe-Mantadia NP (2008). We encountered *Caerostris* webs mostly at forest edges or clearings, along rivers, and in the case of *C. darwini* n. sp., across rivers. The females typically rested in their webs head down (but often head up), during night. During day females of most species rested cryptically on bark away from the web (Fig. 1), *C. darwini* n. sp., on the other hand, was active day and night, sitting in the center of its web (Fig. 3A).

The *C. darwini* n. sp. webs were usually vertical, but sometimes inclined at 80, 70, or even 50 degrees ($n = 18$). They typically had open hubs (Fig. 3B, but see Fig. 3C), and the hubs were slightly displaced toward the top frame (Fig. 3A). The sticky spiral was circular and covered an area limited to the length of the shortest radii in the web. Many webs showed conspicuous sign of damage and repair, others had large open holes, suggesting that the spider does not immediately replace a damaged web, but continues to use it through periodic renewal. The *C. darwini* n. sp. female web data from Andasibe-Mantadia NP (2008) are summarized here as the range, average ± SD (all measurements in cm, $n = 18$ females): web width 31.5–105.0 (63.6 ± 21.7), web total height 30.0–130.0 (71.2 ± 30.3), distance from top web to hub 10.0–56.0 (28.5 ± 13.8), maximal mesh width 11.0–30.5 (17.6 ± 5.4), total bridge line length 180.0–700.0 (354.2 ± 152.7), number of radii 17–25 (21.8 ± 4.0), hub height above water 86.0–240.0 (152.3 ± 48.3), maximal distance between sticky spirals 0.8–3.5 (2.0 ± 0.8).

In comparison to *C. darwini* n. sp., the three other *Caerostris* species measured in Andasibe-Mantadia made denser webs with 34–36 radii and some secondary radii, with an average of 0.7 cm spacing between spirals. *Caerostris darwini* n. sp. webs had large capture areas (1900–28,000 cm^2 in size, area of capture spiral only), with the largest observed web exceeding even the giant *Nephila* orb webs (Kuntner & Coddington 2009). Additionally, the anchor threads may form the longest recorded bridgelines of any orb web, as they extend up to 25 m over rivers and lakes. How the spiders establish lines across the river, allowing the building of the web, is currently being researched (M. Gregorič pers. comm.).

Based upon the large size of the orbs as well as the spiders building them, and the webs' suspension on such extremely long anchor lines above water where the web is exposed to the elements, we might expect that the dragline silk of *C. darwini* would exhibit particularly high mechanical performance properties. In particular, high ability to absorb energy before breaking (high toughness) would help prevent bridgeline failure leading to webs collapsing into the water. Indeed, as we report elsewhere, *C. darwini* n. sp. silk is exceptionally tough, even compared to the already exceptional silk of other orbweavers (Agnarsson et al. 2010).

Prey capture and kleptoparasitism.—Although we observed numerous *Caerostris* webs over a long period of time, prey items were rarely observed in *C. darwini* n. sp. webs. Prey items include relatively small insects such as bees, small dragonflies and damselflies (M. Gregorič pers. comm.). However, on a single day we observed abundant mayflies (Ephemeroptera) emerging from the stream that were caught in large numbers in several webs (Fig. 4A). Up to 32 unwrapped prey items were counted in a single web. Prey were then subsequently wrapped *en masse*, the spider wrapping together several prey items before feeding on them. Most wrapped prey packages were heavily kleptoparasitized by flies (Fig. 4B, C), apparently undescribed and of several species and at least two families (P. O'Grady pers. comm.). Up to 10 flies were observed on a single package being consumed by the host spider, and numerous flies were constantly hovering around the spider and its prey. Flies were also found on prey items that had not been wrapped by the spider. The female spiders reacted aggressively toward the flies as they approached to feed directly on the prey in her mouth (Fig. 4D, E), and repeatedly shook their legs and web to chase off the flies. One male *C. darwini* n. sp. was observed eating prey wrapped by the female in her web; the male occasionally paused to chase off the flies (Fig. 2C).

Although flies have not been observed before in *Caerostris* webs, they are known kleptoparasites in certain other orbweaving spiders (Sivinski & Stowe 1980). Eisner et al. (1991) studied the flies belonging to three genera of Milichiidae and their kleptoparasitism in webs of the giant golden orbweaver *Nephila clavipes* (Linnaeus 1767) in Florida. These flies were chemically attracted to the spiders' heteropteran prey (stink- and squash bugs), but the spider host was not severely affected by such kleptoparasitism. *Nephila pilipes* (Fabricius 1793) from SE Asia also hosts flies in the web and on the body (Kuntner pers. obs.). Other families of flies have also been lured to spider webs (Chloropidae, Phoridae). Sivinski et al. (1999) reviewed kleptoparasitism in Diptera.

Spiders, dung-feeding scarab beetles as well as social and prey storing insects are common hosts because of the delay between prey acquisition and its consumption (e.g., spiders masticate and pre-orally digest their prey). These authors noted that flies associated with predators were mostly female, while scarab kleptoparasites were of both sexes.

Caerostris kleptoparasites often include other spiders. Argyrodine kleptoparasites, belonging to two potentially new, sympatric species, were found in about 30% of the *Caerostris* webs encountered in 2008, with 0–3 individuals per web (0.5 ± 0.9). In 2001, 11 argyrodines were observed in a single large (100 × 110 cm) *Caerostris* web (a third, undescribed species). Although these small spiders are known to steal food from their hosts in other orbweaving genera (e.g., *Nephila*, see Agnarsson 2003), our preliminary data lack notes on their behavior in *Caerostris* webs.

Males and sexual biology.—Most male *C. darwini* were found on the female web's bridge lines, and on leaves in vegetation to which they are attached. At most two males were found associated with a single (sub)adult female web (0.5 ± 0.6). In Andasibe-Mantadia (2008), adult females had at most one male associated with their web, but subadult females had sometimes more than one male effectively waiting for their maturation, a common pattern of pre-copulatory mate guarding in orbweaving spiders (see below). In Ranamofana (22 April 2001) we observed the here-designated type specimens (holotype male, paratype male and female) engaging in sexual behavior (Fig. 5). First, a male was found copulating with a large female, while she was at the hub of the web in a copulation position head facing upwards, with no mating thread present. This male (M1) had the right palpal hematodochae expanded and copulated only with that palp (Fig. 5 shows that he lacked the left palp). During copulation, a second male (M2) approached the hub from the web periphery. M1 aggressively chased the intruder off the female web to the anchor line. M2 retreated and waited, while M1 returned to the hub. The female had at first not moved from the copulating posture, but later switched to the usual head down position at hub before M1 could return to resume mating. On M1 return, she aggressively shook the web towards him, and he retreated a short distance. Then M2 approached the female on another thread, and she reacted aggressively, and he also retreated. M1 then tried to re-approach. Approaching involved no signaling; the male simply walked directly to the female. He stopped when she responded aggressively and groomed his expanded right palp. M2 attempted to re-approach, but the female again responded aggressively and the male retreated. No further attempts occurred, and all the animals were collected (see Types).

Caerostris darwini n. sp. exhibits mating behaviors reminiscent of sexually dimorphic nephilid and certain araneid spiders (see e.g., Kuntner et al. 2009a–c): males plug female copulatory openings with embolic parts, and they sometimes lack one or both palpal distal parts (eunuchs, Fig. 5). However, in *Caerostris* such males retain the cymbium whereas in nephilid eunuchs the palpal breaking point is between the tibia and tarsus (Kuntner 2005, 2007). Adult males were observed in the webs of subadult females, presumably a form of pre-copulatory mate guarding. In one case a mated male with no palps (full eunuch) was collected in the web of a subadult female, apparently mate-guarding her, which is a paradox also known from nephilids. However, despite the extreme sexual size dimorphism and apparent male-male antagonism in *Caerostris*, males do not appear to accumulate in female webs in large numbers, as is the case in some comparable orbweavers such as nephilids (Miller 2007; Kuntner et al. 2009b, c).

Other observations.—*Caerostris vicina* repeatedly reacted to Coddington's sound test by rapidly flexing their legs (South Africa). When a grasshopper was thrown in her web she bit it immediately, then held the prey in her chelicerae for a long time. Later she wrapped it slightly.

The egg sac architecture of *Caerostris* is unlike any other araneids, a dumbbell-shaped sac with ridged edges and one side of the sac attached to a leaf (Fig. 2J). The egg sac is placed away from the web, but close to the attachment of anchor threads to the substrate.

Conclusions.—Future work should aim to gain a clearer understanding of *Caerostris* diversity and biology for several reasons. First, it is critical to conserve these giant orbweavers and their habitat in the rapidly diminishing forests of Madagascar. Second, *Caerostris* appears to have evolved extraordinary silk, which allowed the spiders to conquer a unique ecological niche (Agnarsson et al. 2010). Third, an array of ecological interactions takes place in these fascinating spiders, including the newly discovered kleptoparasitic flies. Fourth, the genus may provide an interesting model for sexual selection studies, as *Caerostris* species seem to display a number of sexual behaviors very similar and potentially homologous to those in araneids and nephilids, such as mate guarding, male accumulation, male-male aggressiveness, male genital mutilation and mate plugging, and self castration (Kuntner et al. 2008a, 2009a–c). All these behaviors and sexual dimorphism observed in this enigmatic group makes them excellent models for future evolutionary studies, especially if such can be based on comprehensive biodiversity data, encompassing all known species in the group in a robust phylogenetic framework.

TAXONOMY

Family Araneidae

Genus *Caerostris* Thorell 1868 (Bark spiders)

Caerostris Thorell 1868; Simon 1895; Grasshoff 1984; Jaeger 2007; Platnick 2010; *Trichocaris* Simon 1895.

Type species.—*Epeira mitralis* Vinson 1863, designated by Thorell 1868:4.

Diagnosis.—Species of *Caerostris* of both sexes differ from other araneid spiders by the combination of the following morphologies: prosoma and opisthosoma wider than long, prosomal head region much elevated from the thoracic region, with one or two pairs of carapaceal projections, and with the median and lateral eyes grouped into separate elevations (Fig. 1C), the presence of a frontal rostrum (FigS. 1B, 2B), the presence of unpaired and/or paired projections on flattened opisthosoma (Figs. 1, 2), the flattened tibiae I, II, IV, and hairy legs with spatulate setae on femur IV (Grasshoff 1984:figs. 43–48). Female *Caerostris* epigynum is well sclerotized (Fig. 4E) and has conspicuous copulatory chambers and a pair of hooks (Fig. 6F). Male palpal subtegulum is of exaggerated proportions, the palp lacks paracymbium, and

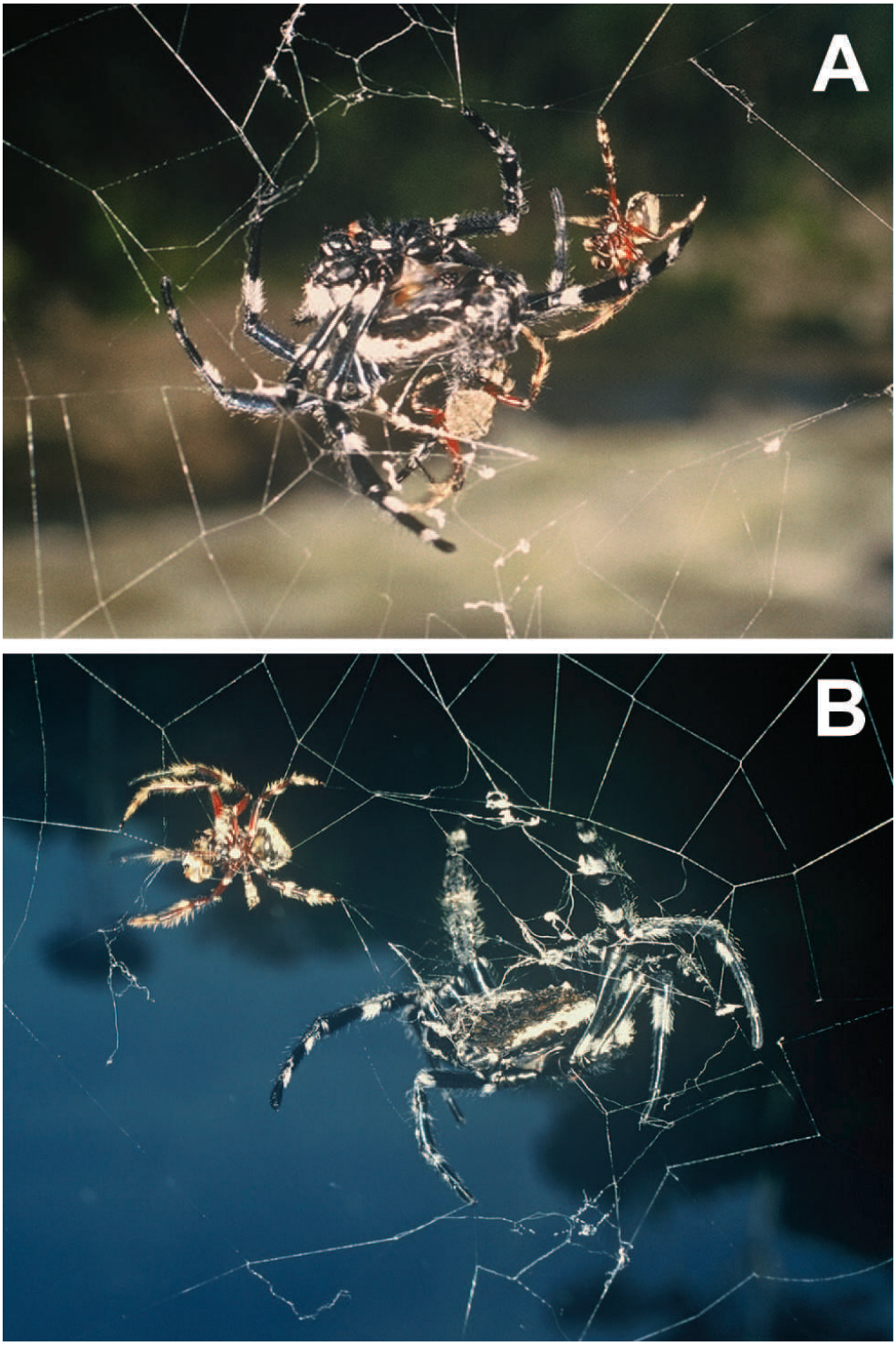

Figure 5.—Observations of *Caerostris darwini* n. sp. sexual behaviors, from Ranomafana: A. Single-palped male (“eunuch”, below the female) and an intact intruder (to the right of the female) compete for a female at the hub of her web; B. The “eunuch” prevails, but fails to mate for the second time. See text for details.

has a fully enclosed embolus in a terminal sclerite (Fig. 6A–C) termed here the conductor (see Kuntner et al. 2008a).

Taxonomic history.—Thorell (1868) described the genus *Caerostris*. Simon (1895:831) erected the group Caerostreae within Argiopinae of the family Argiopidae, to include *Caerostris* and *Trichocaris* Simon 1895. Grasshoff (1984) considered *Trichocaris* a junior synonym of *Caerostris*, which he placed in the araneid subfamily Araneinae. However,

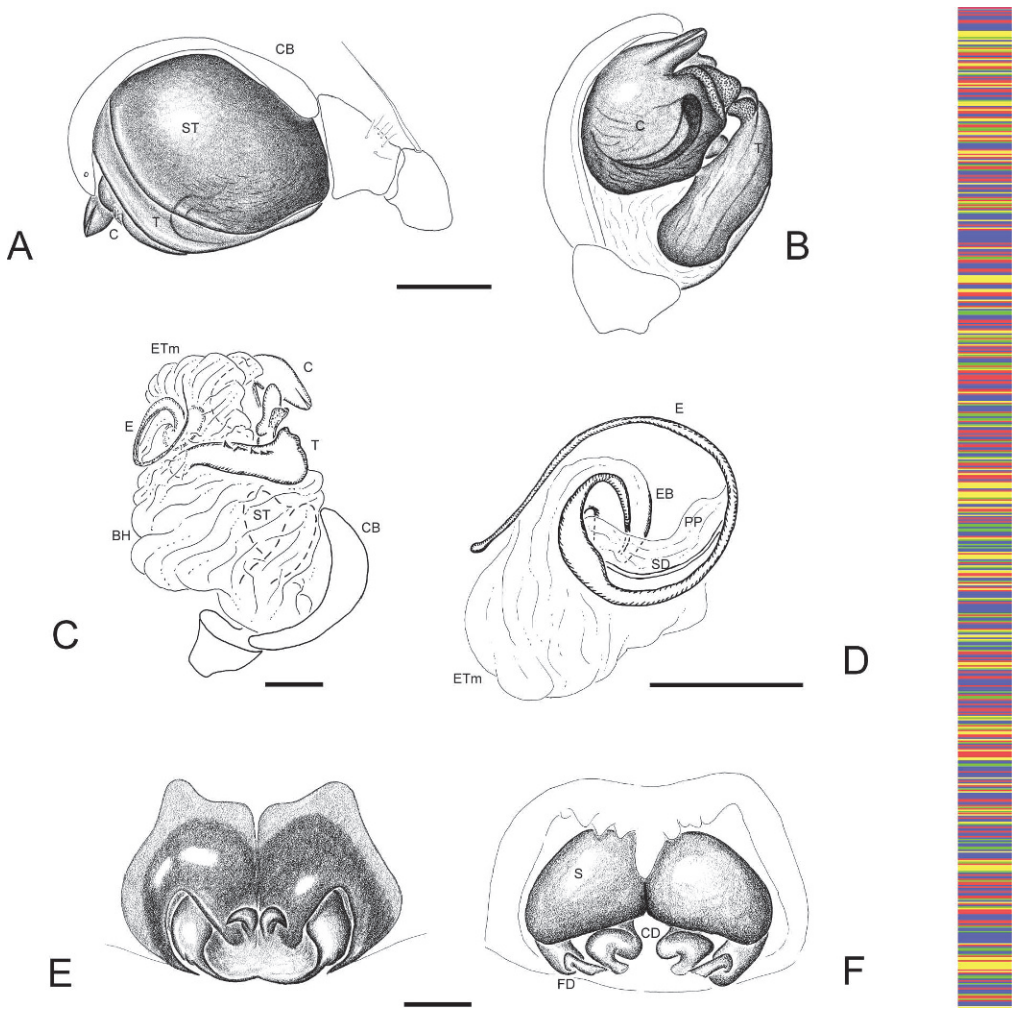

Figure 6.—*Caerostris darwini* n. sp.: A. Male left palp, retrolateral view; B. Same, ventral view; C. Male right palp, expanded; D. Detail of embolus showing pars pendula (PP); E. Female epigynum, ventral; F. Same, dorsal. Scale bars = 0.5 mm. CO1 barcode (female from Andasibe-Mantadia NP) provided on the side.

phylogenetic analyses based on morphological and behavioral characters place *Caerostris* into the 'argiopoid clade' (Scharff & Coddington 1997; Kuntner et al. 2008a). According to Scharff & Coddington (1997), *Caerostris* and *Aspidolasius* Simon 1887 form a doublet within 'gasteracanthoids'. In order to establish a *Caerostris* ground plan, Scharff & Coddington (1997) examined *C. sexcuspidata* and *C. vicina* [=*C. vinsoni*], and Kuntner et al. (2008:fig. 16) examined *C. darwini* n. sp. Jaeger (2007) described the male of the SE Asian species, *C. sumatrana* Strand 1915, from Laos.

Caerostris darwini new species (Darwin's bark spider)
Figs. 2A–C, 3, 4A, D, E, 5, 6

Types.—Male holotype, male paratype, female paratype in National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), labeled: MADAGASCAR: Fianarantsoa Province, Ranomafana NP. Research station at Namorona River and surrounding forest, elev. 1000 m, 21°15′S, 47°25′E, 21–25.iv.2001. Agnarsson & Kuntner.

Etymology.—The species description was prepared on 24 November 2009, precisely the 150th anniversary of the publication of the first edition of Darwin's book *On the Origin of Species*. The species is thus named in honor of Charles R. Darwin, 200 years after his birth.

Diagnosis.—*Caerostris darwini* n. sp. somatic morphology resembles that of *C. vicina*, *C. sexcuspidata* and *C. extrusa*. However, female *C. darwini* n. sp. differ from all other Afrotropical *Caerostris* species by the well defined separate epigynal chambers and the pair of hooks positioned in the posterior part of the epigynal plate rather than anteriorly to medially (Fig. 6E, compare with Grasshoff 1984:figs. 16, 17, 19, 20, 23, 24, 26, 27, 29, 30, 31, 34, 37, 39). Male *C. darwini* n. sp. differ from all other Afrotropical *Caerostris* species by the massive conductor with a straight tip, by the relatively shorter pars pendula and relatively longer and spatulate embolus ending (Fig. 6A–D, compare with Grasshoff 1984:figs. 13, 14, 15, 22).

DNA barcode.—*Female from Andasibe-Mantadia NP:* TATATTTTATTTTCGGAATTTGAGCAGGAATAGTTGGCTCATCTTTAAGAATAATTATTCGAACAGAATTAGGAATACCAGGCTCTTTAATCGGAAATGATCAAATTTTTAATGTAATTGTTACAGCTCATGCATTTATTATAATTTTTTTTATAGTAATACCAATTATAATTGGGGGATTCGGAAACTGACTTGTACCCCTTATACTGGGGGCCCCAG-

ATATAGCATTCCCTCGAATAAATAACATAAGATTTT-
GACTACTCCCACCATCCCTTTCCCTACTTACTATAAG-
AAGAATTGTAGAAAATGGAGCAGGCACTGGTTGAA-
CTGTTTATCCCCCCCTATCCTCAAATATCGGACACGC-
TGGTAGATCAGTAGACTTAACTATTTTCTCCCTTCAT-
CTTGCAGGAATTTCTTCAATTTTAGGGGCTATCAATT-
TTATCACAACAGTAATCAATATACGTTCAAAGGGAA-
TATCACTAGACCAAATACCTTTATTTGTATGATCAGT-
TGTAATTACAGCTTTACTTCTTTTACTTTCTCTACCT-
GTTTTAGCAGGTGCTATCACAATACTACTAACTGAC-
CGAAATCTAAATACCTCTTTTTTTGACCCAGCAGGA-
GGGGGCGACCCCATTTTATACCAACATTTA

Description.—*Female (paratype):* Base color black (live) to red-brown (in ethanol), but prosoma, opisthosoma and appendages in live spider partly white due to setae color (Fig. 2A). Total length 17.9. Prosoma 6.2 long, 8.6 wide. Sternum 3.7 long, 3.9 wide, widest between second leg coxae, with paired tubercles between all leg coxae, black with a white center (Fig. 4E; but, this not visible in ethanol). AME diameter 0.28, PME 0.28, AME separation 0.42, PME separation 0.91, PME–PLE separation 2.47, ALE–PLE separation 0.54. Leg I length 34.9 (femur 9.8, patella 5.2, tibia 7.9, metatarsus 9.1, tarsus 2.9). Opisthosoma 12.8 long, 14.5 wide. Dorsum with paired lateral and caudal humps (Fig. 2A). Epigynum as diagnosed (Fig. 6E, F), spermathecae juxtaposed, spermathecae and ducts heavily sclerotized, frontal inner wall denticulated (Fig. 6F).

Male (paratype): Base color red and light brown (live and in ethanol), but prosoma, opisthosoma and distal parts of appendages in live spider whitish due to setae color, and femora strikingly red and glabrous (Fig. 2B, C). Total length 5.7. Prosoma 3.0 long, 3.1 wide. Sternum 1.3 long, 1.4 wide; unicolor red, without conspicuous humps. AME diameter 0.22, PME 0.17, AME separation 0.18, PME separation 0.59, PME–PLE separation 0.86, ALE–PLE separation 0.07. Leg I length 15.0 (femur 4.1, patella 2.0, tibia 3.6, metatarsus 4.1, tarsus 1.2). Opisthosoma 3.3 long, 4.3 wide. Dorsal paired humps inconspicuous, but unpaired frontal hump present. Pedipalp as diagnosed, with extensive membranes between the sclerites, a denticulated tegulum and long embolus with spatulate ending (Fig. 6A–D).

Variation.—*Female:* Prosoma length 6.2–6.7; total length 17.9–22.0. *Male:* Prosoma length 2.7–3.0; total length 5.7–6.1.

Additional material examined.—Numerous males and females to be deposited in USNM from the type locality and the following, all collected by I. Agnarsson and M. Kuntner: MADAGASCAR: *Toamasina Prov.*, Andasibe-Mantadia NP, Tsakoka. Montane rain forest, at or above river, elev. 952 m, S18°47′54″, E48°25′34″, 30 March and 24 April 2008; Andasibe-Mantadia NP, Mantadia. Montane rain forest edge, at or above stream, elev. 952 m, S18°51′18″, E48°25′42″, 30 March and 24 April 2008; Andasibe-Mantadia NP, Périnet Spec. Res., Montane rain forest streams and rivers, elev. 900–1000 m, S18°56′10″, E48°25′11″, 29 March–23 April 2008.

Natural history.—The species inhabits montane rainforests and their edges in eastern Madagascar, where they construct their webs over water (small streams to medium sized rivers, even lakes). See Results for details.

Distribution.—Eastern Madagascar, currently known from Ranomafana NP and Andasibe-Mantadia NP.

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