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Archaeodictyna ulova, new species (Araneae: Dictynidae), A Remarkable Kleptoparasite of Group-Living Eresid Spiders (*Stegodyphus* spp., Araneae: Eresidae)

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ABSTRACT

A new species of Dictynidae, *Archaeodictyna ulova*, was found living in the communal retreats of two species of group-living eresid spiders, *Stegodyphus mimosarum* Pavesi and *Stegodyphus dumicola* Pocock, in Natal and the eastern Transvaal regions of South Africa. A species description and diagnosis are given, with observations of behavior in the field and laboratory. The dictynid lays its egg sacs throughout the eresid retreats, lives

as an inquiline in the nest interior, and feeds communally with the eresids on prey items which the eresids catch. *A. ulova* was never found living independently or with spiders other than the two eresids, and did not remain in nests which were abandoned by the eresid hosts. Ratios of *A. ulova* to eresids in nests were variable, but reached as high as 0.22. Scelionid wasps parasitized eggs of *A. ulova* within the eresid nests.

INTRODUCTION

Kleptoparasitic (prey-stealing) interactions among spiders are widely known, with kleptoparasites recognized from at least five families: Mysmenidae (Griswold, 1985; Platnick and Shadab, 1978), Salticidae (Jackson, 1985; Jackson and Blest, 1982), Symphytognathi-

dae (Vollrath, 1979), Theridiidae (Kaston, 1965; Vollrath, 1984; Whitehouse, 1986), and Uloboridae (Bradoo, 1979). In all previously known cases, the kleptoparasites rely on stealth to avoid detection and attack by their hosts, or are so small relative to the host as

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to apparently escape detection (Vollrath, 1984, 1987). Of great interest then is the discovery of a kleptoparasitic spider which infiltrates and integrates into colonies of communal nonterritorial spiders, and which is apparently treated as a conspecific by its hosts (Meikle-Griswold, 1986). In conjunction with the study of the natural history of two species of group-living eresid spiders (*Stegodyphus mimosarum* Pavesi and *S. dunicola* Pocock), a new species of *Archaeodictyna* Caporiacco (Dictynidae) was found occupying the *Stegodyphus* retreats and sharing the prey.

S. mimosarum and *S. dunicola* (also known as *Magunia dunicola*, sensu Lehtinen, 1967) are both group-living (Dewar and Koopowitz, 1970; Wickler, 1973). They are communal nonterritorial (sensu Jackson, 1978), and cooperative (sensu Smith, 1982). Both species are obligately group-living as juveniles, and facultatively group-living and quasisocial as adults (sensu Wilson, 1971; Meikle-Griswold and Griswold, in prep.). Their distributions overlap throughout summer rainfall areas of southern Africa, but *S. mimosarum* is more often found in proximity to water. Colonies (groups of individuals sharing a retreat) are usually found in thorny shrubs or trees, where they construct dense silken communal retreats (nests), surrounded by cribellate trap-webbing. Nest interiors are composed of interconnected silken tubes. The nests are variably shaped, usually ovoid, with the longest dimension ranging from 3 to 50 cm. Nests are often found unoccupied by host spiders.

Nests of *S. dunicola* and *S. mimosarum* were often found to have kleptoparasitic spiders such as *Argyrodes* sp. (Theridiidae) and *Portia* sp. (Salticidae) in and around the trap-web. These caught small prey in the eresid web, retreated to the edge of the web to feed, and never entered the host retreats (i.e., pilferers, sensu Vollrath, 1984). *Archaeodictyna ulova* lives as an inquiline within colonies of *S. mimosarum* and *S. dunicola* (Meikle-Griswold, 1986). *A. ulova* is completely tolerated by its hosts, and often builds up to large numbers in host colonies. The dictynids interact closely with the *Stegodyphus* hosts, and apparently are not recognized as "different" when they join in group-feeding on prey items (i.e., peculators, sensu Vollrath, 1984).

A. ulova is described in this paper. This is the first record of kleptoparasitism in the family Dictynidae, and the first record of a spider kleptoparasite that lives as an inquiline and is apparently accepted as a member of a host colony of group-living spiders.

MATERIALS AND METHODS

Nest associates of the eresid spiders *Stegodyphus mimosarum* and *Stegodyphus dunicola* were studied as part of a larger study on the phenology and colony survival of these two eresid species (male and female voucher specimens of each species are deposited in the American Museum of Natural History, New York; British Museum (Natural History), London; California Academy of Sciences, San Francisco; and Musée Royal de L'Afrique Centrale, Tervuren). Field observations of *A. ulova* were made monthly from their first discovery in October 1985, until October 1986, at the Spioenkop Dam Nature Reserve, in eastern South Africa (28°41'S: 29°28'E, elev. 900 m). Feeding behavior and interactions with *Stegodyphus* hosts were observed in situ. Habitats at Spioenkop where *A. ulova* was abundant were searched monthly for evidence of this species living independently or as a kleptoparasite with other spiders.

Stegodyphus dunicola and *S. mimosarum* nests were collected by the authors from Spioenkop, Mkuzi Game Reserve (northern Natal, 27°40'S: 32°11'E, elev. 130 m), Kruger Park (eastern Transvaal, 25°07'S: 31°31'E, elev. 550 m), the Cederberg (32°32'S: 19°17'E, elev. 940 m), and Kamiesberg (30°18'S: 18°05'E, elev. 1220 m) mountains (western Cape Province); large numbers of nests were also collected at Etosha Park in Namibia (18–19°S: 15–17°E, elev. 1000–1200 m) by E. Griffin of the Windhoek State Museum. Nests were dissected, and counts were made of the *Stegodyphus* inhabitants and all nest associates.

Individuals of *A. ulova* were reared and observed in the lab, using several techniques: (1) *A. ulova* and *S. mimosarum* or *S. dunicola* were reared together in glass shell vials or in 9 cm diam. petri dishes, with folded paper strips or corks included as a substrate for silk attachment. The spiders were fed fruit flies (*Drosophila melanogaster*), mealworms

(*Tenebrio molitor* larvae), cockroaches (*Blattella germanica*), or gryllid crickets. (2) *A. ulova* was reared in webs constructed in vials or petri dishes by *S. mimosarum* or *S. dumicola*, but with the eresids subsequently removed. These spiders were fed live *Drosophila*. (3) *A. ulova* was reared in groups of conspecifics only, in glass vials containing paper strips for silk attachment. Here they were fed incapacitated fruit flies, as the web in these vials was not sufficient to entangle active *Drosophila*. All of the rearing setups were given drops of water every 2 to 3 days.

In the descriptions all abbreviations are standard for the Araneae. All measurements are in millimeters.

OBSERVATIONS

A. ulova was found in nests of *S. mimosarum* and *S. dumicola* at the Spioenkop Dam Nature Reserve, and in a nest of *S. mimosarum* from the Kruger National Park. No specimens were found in *S. dumicola* nests collected in the western Cape Province, or in Etosha Park, Namibia, or in one *S. mimosarum* nest collected from Mkuzi Game Reserve.

A. ulova occurred year round at Spioenkop, in *S. dumicola* and *S. mimosarum* nests we examined monthly for 15 months. They were patchily distributed, mainly in areas with the highest densities of *S. mimosarum* colonies, for which they showed an apparent predilection. Of nests that were dissected from a variety of localities at Spioenkop, 54.5 percent of host-occupied *S. mimosarum* nests (6 of 11) contained *A. ulova*, whereas only 6.5 percent of host-occupied *S. dumicola* nests (2 of 31) did (table 1). *A. ulova* was never found living independently or with other spiders, and did not remain in nests which contained no living eresid hosts. Of the nests dissected, 42.9 percent of host-unoccupied *S. mimosarum* nests (3 of 7), and 4.3 percent of host-unoccupied *S. dumicola* nests (3 of 69) showed previous *A. ulova* occupation, as evidenced by old *A. ulova* egg sacs. Such egg sacs were laid throughout the host nests, both inside the interior tunnels of the nest core (fig. 3), and on the outside of the nest core. Egg sacs contained from 1 to 10 eggs ($\bar{x} = 5.7$, $N = 96$ egg sacs). Many of the *A. ulova* egg sacs

TABLE 1
Host-Occupied *Stegodyphus* Nests Containing *A. ulova* Inquilines, Collected at Spioenkop and Dissected

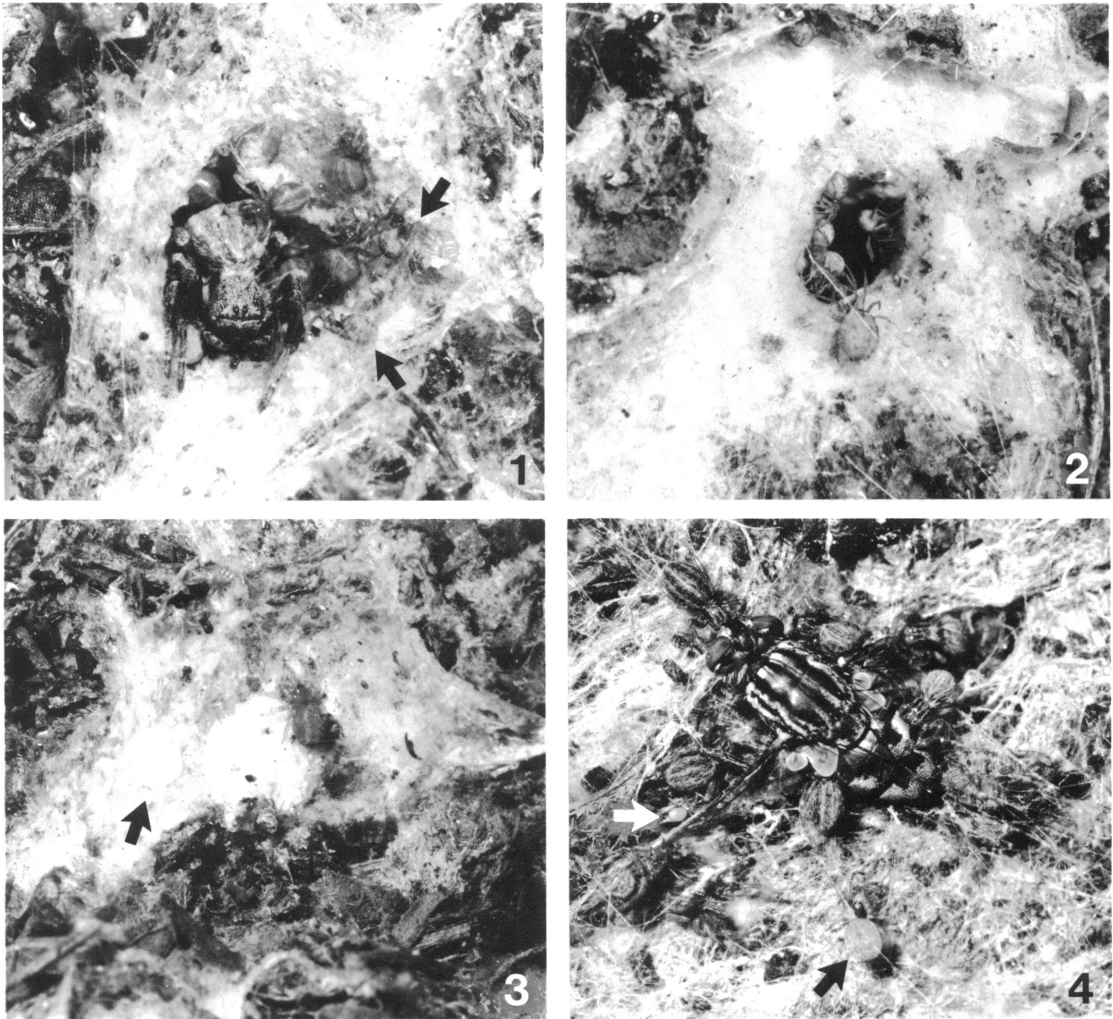
Host species	Collection date	No. spiders in nest	
		Host	<i>A. ulova</i>
<i>S. mimosarum</i>	Jan. 1986	294	64
<i>S. mimosarum</i>	Feb. 1986	156	24
<i>S. mimosarum</i>	Mar. 1986	161	1
<i>S. mimosarum</i>	Apr. 1986	75	1
<i>S. mimosarum</i>	May 1986	100	26
<i>S. mimosarum</i>	Oct. 1986	119	18
<i>S. dumicola</i>	Oct. 1985	121	9
<i>S. dumicola</i>	Nov. 1985	26	2

laid on and in the eresid nests were parasitized by small scelionid wasps (*Idris* sp., det. L. Masner). We should note that *Stegodyphus* egg sacs ($N > 100$) were never found to contain scelionid egg parasitoids.

A. ulova and its eresid hosts spend most of the daylight hours within the silken tubes of the nest core (figs. 1, 2). Just after dusk, when the host eresids emerge from the nests to extend and repair the trap-web, *A. ulova* spiders also come out onto the web. They appear to put down drag lines as they wander over the trap-webs, but they were never seen to card out cribellate silk. Individuals of *A. ulova* never made cribellate silk in mixed-species laboratory colonies, or when maintained individually or in groups of *A. ulova* only, although they do have a well developed calamistrum and cribellum.

During locomotion, *A. ulova* frequently waved the first pair of legs and tapped on the web. Physical contacts with other spiders, both hosts and conspecifics, usually resulted in briefly increased tapping on the body or legs of the spider contacted. These tapping movements are similar to those described by Jackson (1979) for the dictynids *Mallos gregalis*, *M. trivittatus*, and *Dictyna calcarata*. When an *A. ulova* individual approached a potential feeding situation, other spiders, or potential prey items, its tapping pattern became more rapid and jerky.

Feeding behavior was observed both in the field and in lab colonies. In the field, prey entangled in the *Stegodyphus* trap-web at-



Figs. 1–4. *Archaeodictyna ulova*, n. sp., in nests of *Stegodyphus mimosarum* Pavesi from Spioenkop, Natal, South Africa. 1. Adult *S. mimosarum*, juvenile *S. mimosarum*, and adult *A. ulova* (arrows) at entrance to tube on surface of nest. 2. *A. ulova* adults at nest entrance tube. 3. Interior of nest with egg-sacs of *A. ulova* (arrow) and *S. mimosarum*, with juvenile of *S. mimosarum*. 4. Mass feeding on sarcophagid fly on nest surface by *S. mimosarum* and *A. ulova* (arrows).

tracted both *A. ulova* and *Stegodyphus* from the interior of the nest (fig. 4). In 9 of 10 cases recorded, *Stegodyphus* was the first to attack and subdue the prey, while *A. ulova* remained several centimeters away from the attack. After the prey was subdued and *Stegodyphus* was feeding, *A. ulova* walked over the feeding *Stegodyphus* until an empty place was found where they could feed or until a *Stegodyphus* moved and an *A. ulova* could take its place (fig. 4). In one case, an *A. ulova* touched the

prey item before a *Stegodyphus* encountered it. The *A. ulova* in this case did not attempt to bite the prey. On average, *A. ulova* waited 18 minutes to begin to feed after *S. mimosarum* had begun ($N = 7$, range 5–24 min). *A. ulova* frequently continued to feed after its hosts had stopped.

In the lab, *A. ulova* living with colonies of *Stegodyphus mimosarum* or *S. dumicola* showed different behaviors depending on the size of the prey. Large prey such as cock-

roaches or crickets was often noticed and touched first by *A. ulova*, but was never attacked or subdued by the kleptoparasites. The prey sometimes began to struggle more vigorously in the web when *A. ulova* touched them, and this often attracted *Stegodyphus* which would then attack the prey. *A. ulova* would begin to feed after *Stegodyphus* had subdued the prey. In lab colonies, it was apparent that *A. ulova*, by walking on the hosts and tapping them rapidly with the forelegs, often caused *Stegodyphus* to shift feeding positions or to leave the prey.

When individuals of *Drosophila melanogaster* were put into small colonies of *Stegodyphus* and *A. ulova* in the laboratory, *A. ulova* often approached, touched, and bit the *Drosophila* before the *Stegodyphus* did. If the *Drosophila* did not struggle after the initial bite, *Stegodyphus* often did not notice the potential prey. *A. ulova* then fed either individually or in groups of up to six on the *Drosophila*. When a single *A. ulova* made the initial bite, other *A. ulova* often joined within 1–10 minutes. Pure *A. ulova* colonies in vials with recently made *Stegodyphus* webbing could attack, subdue, and feed on *Drosophila* which became entangled. *A. ulova* noticed and encountered, but did not bite, larger prey items. Pure *A. ulova* colonies in vials without *Stegodyphus* webbing made loose, smooth sheets from their draglines. *Drosophila* flies rarely became entangled in this webbing, and nearly always escaped before any *A. ulova* individuals were able to attack them. Damaged *Drosophila* individuals which were unable to walk were attacked and fed upon by the *A. ulova*.

Egg sacs of *A. ulova* required from 16 to 21 days ($N = 5$) to hatch in the lab (at ca. 70–77°F). Spiderlings matured in about 5 to 7 weeks. There was no parental care of egg sacs or offspring. Females laid egg sacs at 12–20 day intervals, usually laying a total of 2 or 3. Newly hatched *A. ulova* spiderlings fed on prey, but were too small to subdue even an incapacitated *Drosophila*. Generations overlapped, although in lab colonies, parents generally died at about the time their first offspring became sexually mature.

Dispersal was never observed in nature. In the lab, *A. ulova* individuals of all stages abandoned dwindling and dying *Stegodyphus*

colonies. Dispersal and host-finding behaviors require more study.

TAXONOMY

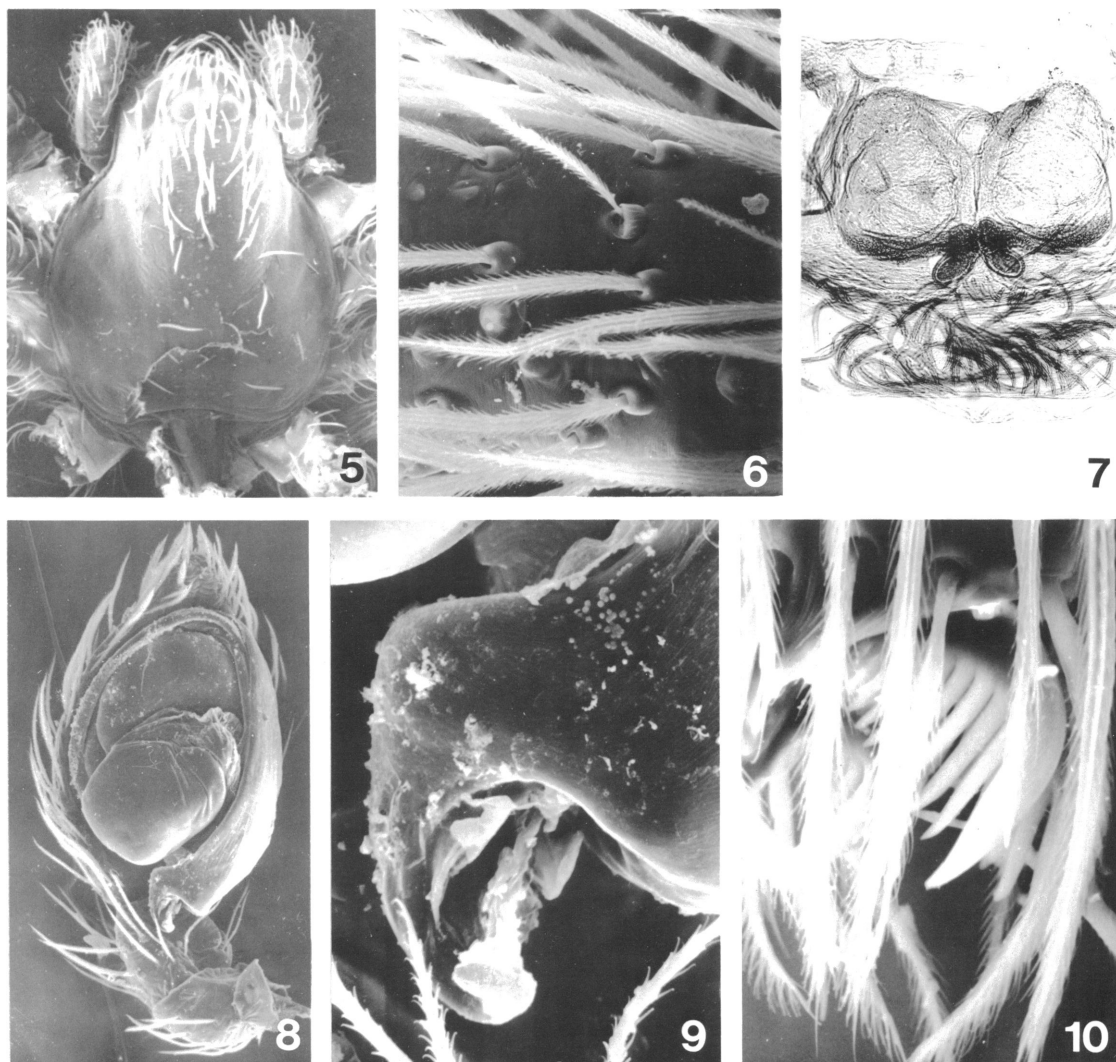
Archaeodictyna ulova, new species

Figures 5–13

TYPES: Holotype male, South Africa, Natal, Spienkop Dam, south shore, 30 km SW Ladysmith, elev. 900 m (28°41'S : 29°28'E), from nest of *Stegodyphus mimosarum* in *Acacia karroo* in mixed grasslands and dry bushveld, 9 July 1986, T. Meikle-Griswold and C. Griswold, deposited in the Natal Museum (type no. 3391). Paratypes, same locality, various dates, from nests of *Stegodyphus mimosarum* and *S. dumicola*, 18 males, 12 females: 1 pair each in British Museum (Natural History), London; National Collection, Pretoria; National Museum of Zimbabwe, Bulawayo; Musée Royal de L'Afrique Centrale, Tervuren; National Museum of Natural History, Washington, D.C.; California Academy of Sciences, San Francisco; and American Museum of Natural History, New York; remainder in Natal Museum.

ETYMOLOGY: The specific name is from the Zulu word for loafer or one who lives off the work of others.

DIAGNOSIS: *Archaeodictyna ulova* may be distinguished from all other African species currently (Lehtinen, 1967) placed in *Archaeodictyna* by details of the male palpus (figs. 8, 9, 12, 13) and internal genitalia of the female (fig. 7). Differentia of the other African *Archaeodictyna* are as follows: *anguiniceps* (Simon) 1899—male carapace elongate anteriorly, female genitalia with membranous bursae narrower, sclerotized receptacula relatively larger; *conducta* (O. P. Cambridge) 1876—apex of conductor broader and lateral chamber of receptaculum very large; *consecuta* (O. P. Cambridge) 1872—palpal conductor broader for entire length, tibial ctenidium longer, and bursae broader; *gertschi* (Berland and Millot) 1939—embolic base subapical; *longipes* (Berland) 1914—apex of conductor enlarged, strongly curved, extending to base of tibia, female with dorsolateral dark bands on abdomen; *montana* (Tullgren) 1910—embolic origin more basal and apex of conductor broader; *tazzeiti* Denis 1954—ctenidia of palpal tibia longer, bifid; *tullgreni* (Caporiac-



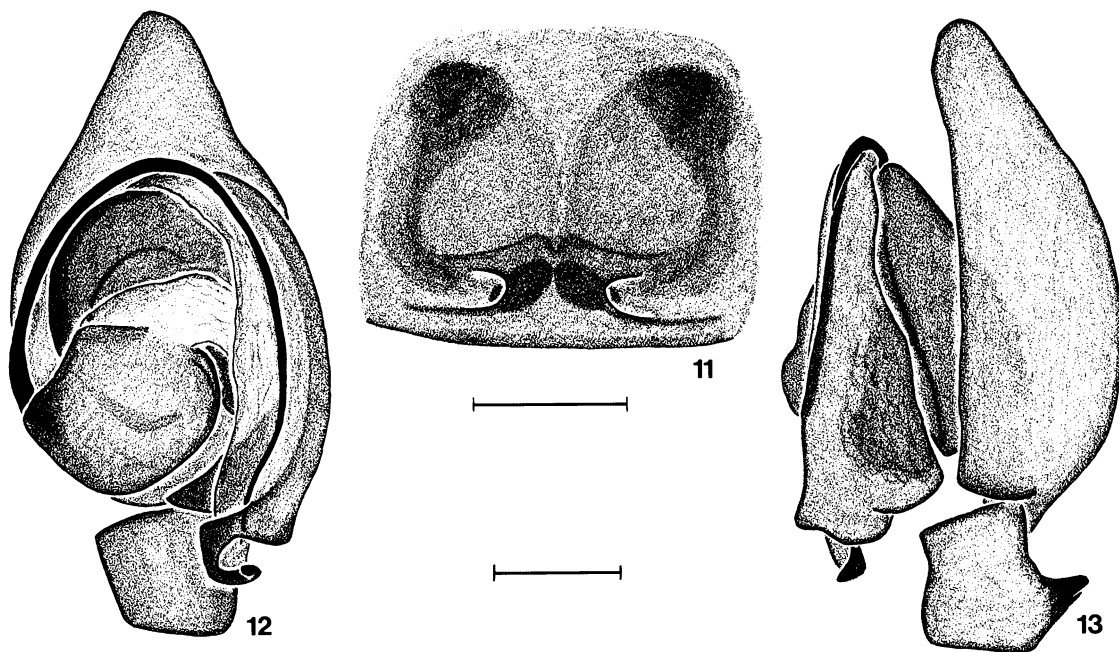
Figs. 5–10. *Archaeodictyna ulova*, n. sp. 5. Carapace of female, dorsal. 6. Dorsum of metatarsus IV of female, showing setae and trichobothrial base. 7. Spermathecae, cleared, dorsal view. 8. Male palpus, ventral. 9. Male palpus, apex of conductor. 10. Tarsus IV of female, claw.

co) 1949—palpal ctenidium longer, apex of conductor spiniform, reflexed.

MALE (holotype): Total length 1.76. Carapace brown on cephalic region, thoracic fovea, and striae radiating from foveal region, yellow-brown surrounding fovea, between lateral striae, and posteriorly; sparse white hairs on cephalic region and between eyes. Chelicerae brown, unmarked; venter, legs, and palpi pale yellow-brown, unmarked, all sparsely covered with dark hairs. Abdomen yellow-white, with faint anteromedian dark

longitudinal band and 3 pairs of faint, dark, posterodorsal spots, venter unmarked; sparsely covered with dark hairs.

Carapace 0.71 long, 0.61 wide, 0.25 high at OA; thoracic fovea a broad, shallow depression; clypeus low, 0.04 high, height $\frac{1}{5}$ diameter AME. Ocular area 0.31 wide, 0.12 long, width PER 1.19 times AER; ocular quadrangle slightly narrowed in front; distance AME-AME equal to AME diameter, AME-ALE $\frac{1}{3}$ AME, PME-PME equal to PME, PME-PLA $\frac{1}{5}$ PME, lateral eyes nearly



Figs. 11–13. *Archaeodictyna ulova*, n. sp., scale lines = 0.1 mm (upper scale line for fig. 11, lower for figs. 12, 13). 11. Female epigynum. 12. Left male palpus, ventral. 13. Left male palpus, retrolateral.

contiguous; ratio of eyes AM:AL:PM:PL, 1.13:1.25:1.13:1.00, diameter PME 0.04. Chelicerae 0.39 long, vertical, slightly swollen at base with small lateral boss, weakly carinate and bowed medially; fang furrow with 2 small teeth on promargin, 1 on retromargin; edge of fang weakly serrate. Sternum domed, smooth, margin entire, truncate posteriorly, 0.44 long, 0.45 wide; labium 0.17 long, 0.19 wide; palpal coxae converging but apices separate, 0.21 long, 0.13 wide.

Leg formula 1243. Legs, palpi, and body sparsely covered with plumose hairs (fig. 6). Spines absent. Trichobothria: 2 dorsal near base of tibiae, 2 distal on metatarsi I and II, 1 distal on metatarsi III and IV; bothrium with posterior hood, trichome plumose (fig. 6). Claws pectinate (fig. 10), STC with 7–9 teeth, ITC with 3–5. Measurements of legs:

	I	II	III	IV	Palp
Femur	0.60	0.55	0.46	0.59	0.26
Patella	0.24	0.22	0.22	0.22	0.10
Tibia	0.51	0.43	0.32	0.39	0.08
Metatarsus	0.43	0.38	0.35	0.41	—
Tarsus	0.37	0.33	0.31	0.25	0.37
Total	2.15	1.91	1.66	1.86	0.81

Abdomen 1.12 long, 0.86 wide. Cribellum and calamistrum nonfunctional, reduced.

Palpus with short dorsal ctenidium on tibia (fig. 13). Bulb as in figures 8, 12, 13; embolus slender, arising proximally on anterolateral side of bulb, slender for entire length, apex obscured by conductor; conductor thickened distally, apex (fig. 9) bent mesally, then basally.

Variation. Total length 1.63–1.84. Carapace markings faint, yellow-brown and clear, or obscure, dark brown; abdomen with anterodorsal median dark band or pair of small spots, abdominal markings faint to bold, venter unmarked or with paired dark longitudinal marks anterolaterad of spinnerets and laterad of book-lungs. Carapace length 1.16–1.21 times width, height 0.42–0.50 width; ocular area 2.00–2.48 times wider than long; distance AME-AME $\frac{4}{5}$ -equal to AME diameter, AME-ALE $\frac{1}{3}$ - $\frac{2}{5}$ AME, PME-PME $\frac{3}{4}$ -equal to PME, PME-PLA $\frac{3}{4}$ -equal to PLA. Clypeal height $\frac{2}{3}$ - $\frac{4}{5}$ AME diameter, chelicerae length 8–11 times clypeal height. Sternum length 0.98–1.02 times width; labium width 1.12–1.36 times length.

FEMALE (paratype): Total length 2.04. Markings and structure essentially as in males, abdominal markings fainter.

Carapace (fig. 5) 0.86 long, 0.73 wide, 0.33 high at OA; clypeus 0.05 high. Ocular area 0.34 wide, 0.14 long; distance AME-AME equal to AME diameter, AME-ALE $\frac{2}{3}$ AME, PME-PME equal to PME, PME-PL $1\frac{1}{4}$ times PME; ratio of eyes AM:AL:PM:PL, 1.11:1.00:1.11:1.22, diameter PME 0.05. Chelicerae 0.39 long, vertical, noncarinate and weakly concave medially. Sternum 0.56 long, 0.50 wide; labium 0.17 long, 0.23 wide; palpal coxae 0.25 long, 0.13 wide.

Leg formula 1423. Palpal claw pectinate, with 6 teeth. Calamistrum a single row, posterodorsal, extending subbasally to subapically for most of metatarsus length. Measurements of legs:

	I	II	III	IV	Palp
Femur	0.76	0.69	0.59	0.71	0.29
Patella	0.29	0.27	0.25	0.29	0.12
Tibia	0.59	0.47	0.39	0.45	0.16
Metatarsus	0.55	0.49	0.41	0.51	—
Tarsus	<u>0.41</u>	<u>0.37</u>	<u>0.31</u>	<u>0.35</u>	<u>0.32</u>
Total	2.60	2.29	1.95	2.31	0.89

Abdomen 1.22 long, 0.96 wide. Cribellum small, entire. Epigynum (fig. 11) unsclerotized externally, receptacula visible, with paired copulatory pores. Spermathecae as in figure 7, with large anterior membranous bursae, small posterodorsal sclerotized receptacula, and lateral fertilization ducts.

Variation. Total length 1.80–2.90. Variation in markings as in male. Carapace length 1.18–1.24 times width, height 0.36–0.46 width; ocular area 2.29–2.54 times wider than long; distance AME-AME $\frac{4}{5}$ —equal to AME diameter, AME-ALE $\frac{2}{5}$ – $\frac{3}{5}$ AME, PME-PL $\frac{4}{5}$ – $1\frac{1}{3}$ times PME. Clypeal height about equal to AME diameter; chelicerae length 7–8 times clypeal height. Sternum length 0.98–1.12 times width; labium width 1.29–1.35 times length. Leg formula 1423 or 1(2 = 4)3.

ADDITIONAL MATERIAL EXAMINED: SOUTH AFRICA: Transvaal: 30 km SW Skukuza on Nahpe Road, Kruger National Park, elev. 1800 ft, from nest of *Stegodyphus mimosarum* on *Zizyphus mucronata*, 2♂, 10♀, 15 Dec. 1984, C. Griswold and T. Meikle-Griswold (Natal Museum).

DISCUSSION

Ecological and behavioral factors favoring kleptoparasitism were listed by Brockmann and Barnard (1979) in a review of kleptoparasitism in birds. These included: (1) high host concentrations, (2) large quantities of food available, (3) large or high-quality food items, (4) habits of host that make food temporally or spatially predictable, (5) long prey-handling time by host that makes prey more vulnerable to kleptoparasitism, (6) little likelihood of host escape or retaliation, and (7) kleptoparasites moving with agility among their hosts. These conditions all apply to the living habits of *S. mimosarum* and *S. dumicola* and the kleptoparasite *A. ulova*. (1) Host concentrations are locally high. Colonies of *S. mimosarum* and *S. dumicola* are patchily distributed, but populations are dense within colonies and colony clusters. We found *S. mimosarum* and *S. dumicola* nests to be most abundant in areas of high prey density: e.g., near watercourses and lakes, or in areas with many large grazing mammals. At the Spioenkop site, *A. ulova* was most frequently found in a lakeshore area with the highest density of *S. mimosarum* nests. (2) These colonies were nearly always found either handling prey or with recent prey items dead on the nest exterior, suggesting that large quantities of food were available. (3) A wide spectrum of prey types were captured, ranging from small parasitic Hymenoptera to large grasshoppers and mantids. In the field, we observed *A. ulova* feeding alongside *S. mimosarum* on prey items generally at least two times the size of *S. mimosarum*. However, smaller prey items were often pulled into the nest interior by *Stegodyphus*, and in these cases, feeding was impossible to observe. (4) Food is spatially predictable from the point of view of *A. ulova* (i.e., on trap-web or nest surface), as long as the host spiders continue to repair and extend the trap-web and catch prey. (5) Long prey-handling time makes prey vulnerable to kleptoparasitism. After being subdued, large prey items were usually fed upon for more than one hour. (6) Host escape with the prey is unlikely since *A. ulova* have access to the hosts' entire trap-web and retreat. Host retaliation is unlikely as *Stegodyphus* are remarkably tolerant of other spi-

ders. Various researchers have shown that inhibition of aggression in group-living *Stegodyphus* species is not a property of colony membership or even restricted to members of the same species. By transferring individuals between colonies several miles apart, Wickler (1973) showed that there was no within-colony recognition of nest-mates in *S. mimosarum*. We performed a similar experiment using marked individuals. These were accepted into the new colonies, where they participated in prey-capture and food-sharing. We found this also to be the case with *S. dunicola*. Additionally, we combined colonies of *S. mimosarum* and *S. dunicola*, and found that mixed colonies persisted in the lab and on our verandah for several months. Interactions during prey capture and feeding appeared qualitatively the same as in single-species groups, and individuals touched one another frequently. This lack of species-level discrimination demonstrates the potential ease of infiltration and integration of heterospecifics. Kullman (1972) reported that intra- and interspecific tolerance, and inhibition of biting in *S. sarasinorum* (another group-living, cooperative species) are mediated by tactile and chemical cues on the integument. It is possible that similarities in cuticular structure and/or semiochemicals aid in the integration of *A. ulova* into *Stegodyphus* colonies. (7) Finally, *A. ulova* spiders move with ease through the trap-web and interior tubes of *Stegodyphus* nests. *A. ulova* is a cribellate spider, as are the *Stegodyphus* hosts. The hackled-band silk of trap-webs and retreats constructed by most members of the family Dictynidae are similar to those of the family Eresidae, and this may be an advantageous preadaptation to infiltrating *Stegodyphus* nests.

While *A. ulova* apparently benefits in terms of energy savings by not constructing trap-webbing or helping to catch prey, it is not yet known whether the relationship between *A. ulova* and its hosts is parasitic, commensal, or possibly even mutualistic. Ward and Enders (1985) showed that in groups of *S. mimosarum*, increasing group size resulted in a decreased amount of overall food extraction per spider per unit of time. They also found a significant decline in individual biting times as group size increased. This implies that in-

creasing the number of spiders feeding on a prey item decreases an individual spider's energy gain from that unit of prey. Possibly, *A. ulova* has an adverse impact on its hosts, i.e., it increases feeding-group size without reciprocally contributing to prey capture. Observations of *A. ulova* actively displacing *Stegodyphus* from prey items indicate that this relationship may be detrimental to the hosts. This impact might be minimized by the fact that *A. ulova* tends to join feeding groups during the later stages of prey consumption by the hosts. Laboratory observations showed that *A. ulova* could even have a beneficial effect by causing trapped insects to struggle in the web, attracting *Stegodyphus* to prey that might otherwise have been missed.

These observations raise a number of questions concerning both the specific interactions of *A. ulova* with its *Stegodyphus* hosts, and more generally, the mechanisms and limits of tolerance in group-living spiders: Does *A. ulova* cause a significant energy loss in its host species? Does it play a role in causing the hosts to abandon old nests? How do the dictynids locate host nests? What are the physical and behavioral factors that allow *A. ulova* to integrate so well into *Stegodyphus* nests? It is possible that highly integrated kleptobionts like *A. ulova* may provide useful data for understanding the mechanisms of tolerance and recognition in group-living spiders.

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