

"SPIDER EAT SPIDER": THE PREDATORY BEHAVIOR OF *RHOMPHAEA* SP. FROM NEW ZEALAND

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ABSTRACT

Rhomphaea sp. from New Zealand captures other spiders which wander onto its web, and ventures onto other spiders' webs to capture the resident. *Rhomphaea* captures spiders by using aggressive mimicry to lure the victim and by throwing a sticky triangular net over the prey. The importance of this unusual method of capturing spiders is discussed in relation to the evolution of this spider.

INTRODUCTION

This work examines the predatory behavior of *Rhomphaea* Simon, a genus of elusive, solitary spiders whose predatory behavior is unknown other than that they eat other spiders (Eberhard 1979; Smith Trail 1980; Horton 1982). The behavior of *Rhomphaea* is of special interest because species from a closely related genus, *Argyrodes*, capture spiders by using stealth (Eberhard 1979), aggressive mimicry (Whitehouse 1986), and engage in an unusual form of foraging—kleptoparasitism (Vollrath 1976; Whitehouse 1986).

Currently there is conjecture surrounding the degree to which the genera *Argyrodes* and *Rhomphaea* are related. Exline and Levi (1962) merged *Rhomphaea* with the genus *Argyrodes*, but some workers disagree with the grouping (e.g., Simon 1895; Forster pers. comm.: opinion based on New Zealand species). More information on the foraging behaviors of the two groups of spiders is needed to ascertain if the behavioral characteristics of the two groups support the merger.

Because the taxonomy of *Rhomphaea* is incomplete, the species studied cannot be named. Two populations of *Rhomphaea* were studied; one at Christchurch, New Zealand (43.32°S; 172.37°E) and one at Te Aroha, New Zealand (37.32°S; 175.43°E). As there were no important behavioral differences between the two populations, data were pooled. Voucher specimens have been deposited at the Otago Museum, Dunedin, New Zealand.

METHODS

Field observations.—Surveys of feeding behavior were conducted in the field during both winter (May 1985) and spring (October 1985) in Christchurch and Te Aroha by inspecting bushes and fences. I recorded the type of web upon which

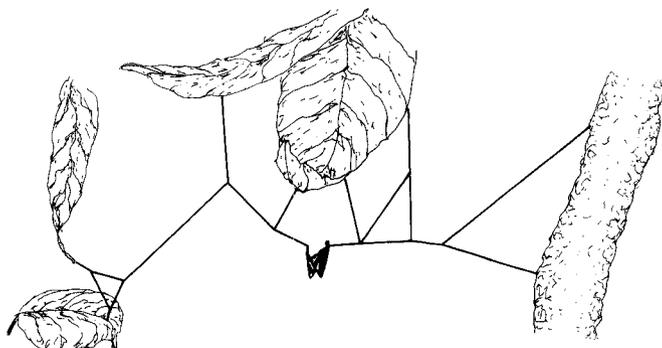


Fig. 1.—Web of *Rhomphaea* located in a bush. *Rhomphaea* is hanging in the middle of the main horizontal thread. Spider is roughly 3 mm long.

Rhomphaea was located, the surrounding habitat, and the activity in which the spider was engaged.

Laboratory studies.—Two types of encounters were staged. The first type was staged in small cylindrical containers (diameter = 5 cm; height = 6 cm) to facilitate spider interaction. The prey spiders were immature *Achaearana* sp. (Theridiidae), approximately the same size or slightly smaller than the *Rhomphaea*. *Rhomphaea* was either added to the *Achaearana* sp. cage or vice versa. Spiders were observed for 1-2 h during daylight.

The second type involved *Rhomphaea* responding to prey either on its own web, or on another spider's web. *Rhomphaea*, and potential prey spiders smaller than *Rhomphaea* (which included *Aranea pustulosa* (Walckenaer), *Badumna longinquus* (L. Koch), *Achaearana* sp., and *Leucauge dromedaria* (Thorell)) established webs in separate spider cages 20 cm long, 8 cm deep, 10 cm wide (see Jackson 1974 for a detailed description of cages). Observations began when either a prey spider was introduced to a cage containing *Rhomphaea* or *Rhomphaea* was introduced to a cage containing a prey spider. The ensuing interaction was observed for 1-2 h. After this period the spiders were often left together for 1-2 days to see if capture occurred.

Maintenance.—Spiders were housed in a room with controlled temperature (22°C-25°C) and light (12:12, L:D). The daylight hours were reversed for the second series of tests and the spiders were observed during their night time.

RESULTS

Habitat.—*Rhomphaea* was found at night in its sparse web (ca 15 cm long) in bushes and other sheltered areas. The web consisted of one main thread, roughly horizontal to the substrate, which had other vertical (secondary) threads ascending from it (Fig. 1). It was usually strung below a branch or ledge in areas where webs of other spiders (such as *Badumna longinquus*, *Achaearana* sp., and *Cambridgei antipodiana* (White)) were common. *Rhomphaea* usually hung close to the middle of the horizontal thread, 3-8 cm below the branch or ledge. *Rhomphaea* only came out on its web at night. During the day it rested (usually among detritus) by hanging ca 5 mm below a branch or ledge on a single horizontal thread ca 4 cm long.

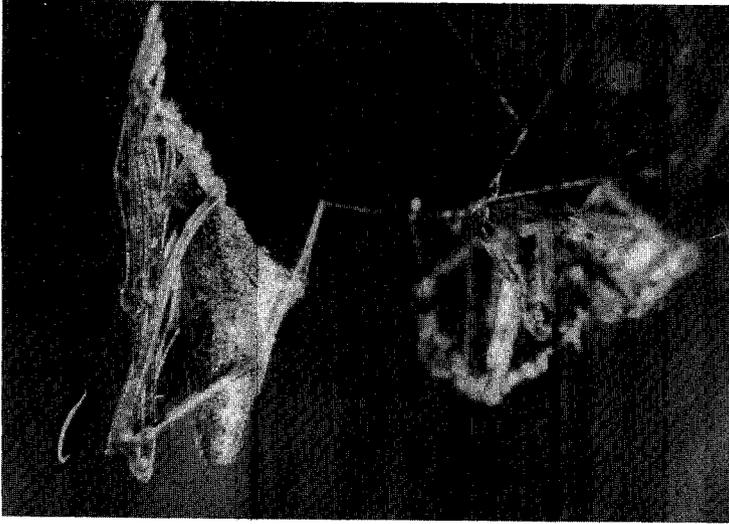


Fig. 2.—*Rhomphaea* (right, foreground) in hunched position next to its recently captured wrapped prey, an *Achaearanea* sp. (left, background). *Rhomphaea* is hanging dorsal side downwards with its legs pulled in close and flexed over its cephalothorax.

Cryptic appearance.—*Rhomphaea* is a small spider (body length: ca 3 mm), with a triangular abdomen, whose body and legs are various shades of light brown. This coloring enabled the spider to blend into its background of dried leaves and twigs. Camouflage was enhanced by the spider adopting the *hunched posture* (Fig. 2) in which all legs (except legs IV) were flexed sharply at the femur-patella joint so that the tibia lay against the femur, and the femora of all its legs lay against the triangular-shaped abdomen. Thus the whole animal resembled a triangular piece of leaf, making detection almost impossible (for a human).

Occasionally, *Rhomphaea* adopted the *extended posture* (Fig. 3), in which legs I and II were held directly anterior to the body.

Field observations.—Of 38 *Rhomphaea* found in the field, 31 were on their own web either in the hunched, extended, or alert posture (see below); two were

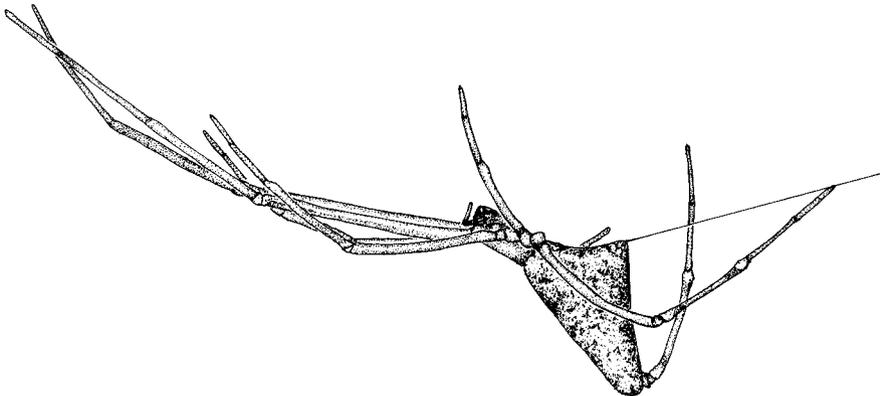


Fig. 3.—*Rhomphaea* in the extended posture. By extending legs I and II anteriorly in this manner, *Rhomphaea* resembles a twig.

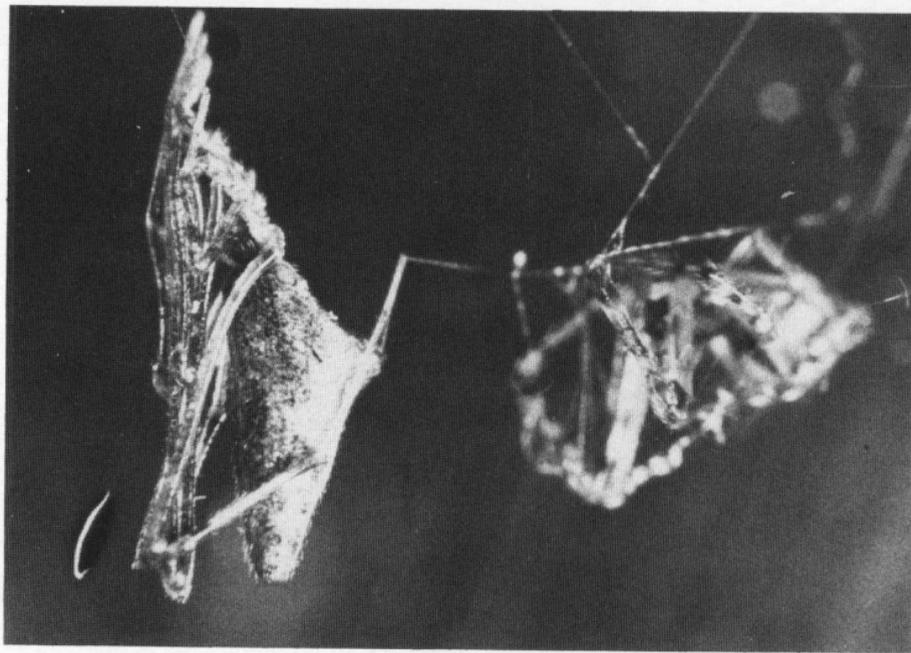


Fig. 2.—*Rhomphaea* (right, foreground) in hunched position next to its recently captured wrapped prey, an *Achaearanea* sp. (left, background). *Rhomphaea* is hanging dorsal side downwards with its legs pulled in close and flexed over its cephalothorax.

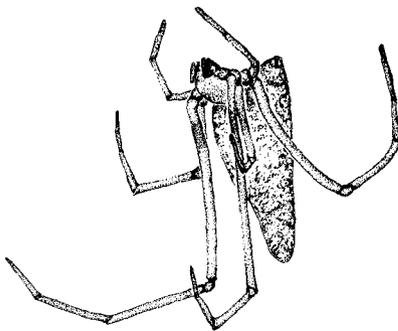


Fig. 4.—The alert posture was assumed by *Rhomphaea* when another spider moved on the same web.

on their own web interacting with other spiders (one *Rhomphaea* had wrapped up an *Achaearanea* sp.; the other was responding to an araneid that was moving onto its web); five were in the webs of other spiders (*Badumna longinquus* (*Rhomphaea* had caught this spider), *Argyrodes antipodiana*, *Leucauge dromedaria*, and two theridiid webs (web owners were not present)).

Elements of predatory behavior.—*Alert posture*: In the alert posture (Fig. 4), *Rhomphaea* extended legs I so that the femora were parallel and dorsal, the tibiae were angled ca 120° to the femora and pointed anteriorly and slightly laterally, while the metatarsi and tarsi were flexed slightly. The femora of legs II (which were lateral to legs I) were also extended dorsally while the tibiae were extended anteriorly. The metatarsi and tarsi of legs II were angled anteriorly so that the tarsal tip was ventral to the animal's mouthparts. Legs III were held ventrally to the spider.

Rotary probing: During rotary probing the spider moved its leg I (mainly at the coxa-trochanter joint) causing the tarsal tip of the leg to describe a circle (diameter: ca 2-6 mm; duration: ca 0.3-1.0 s).

Vibrating techniques: Four vibratory behaviors were observed: standard bouncing, palpating, shuddering, and small pulling. *Standard bounces* occurred intermittently during normal locomotion, just prior to locomotion, or in response to vibrations on the web. Movement by legs III and IV caused the body to oscillate smoothly dorso-ventrally (amplitude: ca 1 mm; duration: 0.5 s per bounce) in bouts of ca nine bounces. To *palpate*, the spider held its long palps in front of the body with the femur directed dorsally and the tibia, metatarsus and tarsus pointing ventrally (towards the silk). *Rhomphaea* moved its palps rapidly dorso-ventrally with the tarsi contacting the silk alternatively at the end of each ventral stroke (rate: ca six per s; amplitude: ca 0.3 mm; duration of bout was variable but was ca 2 s). During *shuddering*, the body of the spider oscillated so rapidly dorso-ventrally that it became a blur (amplitude: ca 0.5 mm; duration: ca 0.25 s). Bouts of shudders occurred at the rate of one per 1-2 s. To *small pull*, all legs in contact with silk were flexed slightly (ca 0.5 mm; duration: 0.1 s; rate: two per s) at the trochanter-femur joint, pulling the silk towards the body and then releasing it slowly in a smooth movement.

Pre-attack behavior: Before attacking its prey, *Rhomphaea* hung from the web by legs I, grasping its dragline with a leg II (Fig. 5a). It then drew more silk out of its spinnerets with first one leg IV and then the other. Thus the tarsi of both legs IV and one leg II held a triangle of silk (Fig. 5a). Large droplets of glue were

present on the silk as it was drawn out of the spinnerets. These covered the thread between the legs IV and continued over half way up the sides of the triangle towards leg II. Almost as soon as the net was complete, *Rhomphaea* scooped.

Scoop: When the approaching prey was 2-3 mm away, *Rhomphaea* scooped (Fig. 5b) by moving the triangular net towards the prey with both legs IV in unison. As legs IV moved the net towards the prey, the leg II that was holding the upper corner of the net also moved towards the prey. If the net adhered to the prey, up to ca three more nets were cast over the victim at a rate of ca two per s. If *Rhomphaea* missed the prey with the scoop, it immediately ate the triangular net.

Post-attack behavior: Once the prey was entangled, *Rhomphaea* approached and began wrapping it quickly with alternating sweeps of legs IV (ca six attachments per s) for ca 2 s. It bit the prey's leg then either continued to wrap or paused a few seconds while the victim's struggles subsided. A wrapped prey was covered with only enough strands of silk to bundle its legs against its body (Fig. 2). Finally the prey was carried higher in the web via a thread from the prey to the spider's spinnerets that was held by leg IV.

Sequences of behavior observed in the laboratory.—*Rhomphaea* first responded to prey spider's movements by assuming the alert posture. If the prey continued to move, *Rhomphaea* often began luring it by palpating, shuddering and/or giving small pulls while in the alert posture. The prey spider usually responded to the displays by rushing towards the predator who assumed the pre-attack posture (the resulting vibrations continued to lure the prey), and attacked by scooping.

Rhomphaea frequently made mistakes when it scooped. Sometimes the pre-attack position was assumed too soon, and *Rhomphaea* either scooped in front of the victim missing it, or the prey stopped short. One *Rhomphaea* in a densely woven juvenile *Achaearanea* sp. web scooped in the opposite direction to the prey.

Rhomphaea on its own web caught *Leucauge dromedaria* and *Achaearanea* sp. at least once, and attempted to catch *Aranea pustulosa*. On the prey's web *Rhomphaea* caught *Achaearanea* sp. and *Aranea pustulosa*. The prey responded at least once to palpating and small pulls by moving towards *Rhomphaea*. Surprisingly, simply walking on the web routinely lured prey (8 out of 15 recorded observations). However, *Rhomphaea* often rotary probed or palpated while walking, and these movements may have been what actually attracted the prey.

DISCUSSION

Aggressive mimicry.—*Rhomphaea* produces vibrations on the web of the prey spider which cause the prey to respond to *Rhomphaea* as if it were food caught on the web, and run towards *Rhomphaea* who is therefore an aggressive mimic. By thus manipulating the behavior of the potentially dangerous prey, *Rhomphaea* presumably enjoys greater ease and less danger when catching prey than if the prey's behavior was uncontrolled. The advantages resulting from manipulating the prey's behavior have probably resulted in the majority of specialized web-invading araneophagic spiders adopting aggressive mimicry (see Whitehouse 1986).

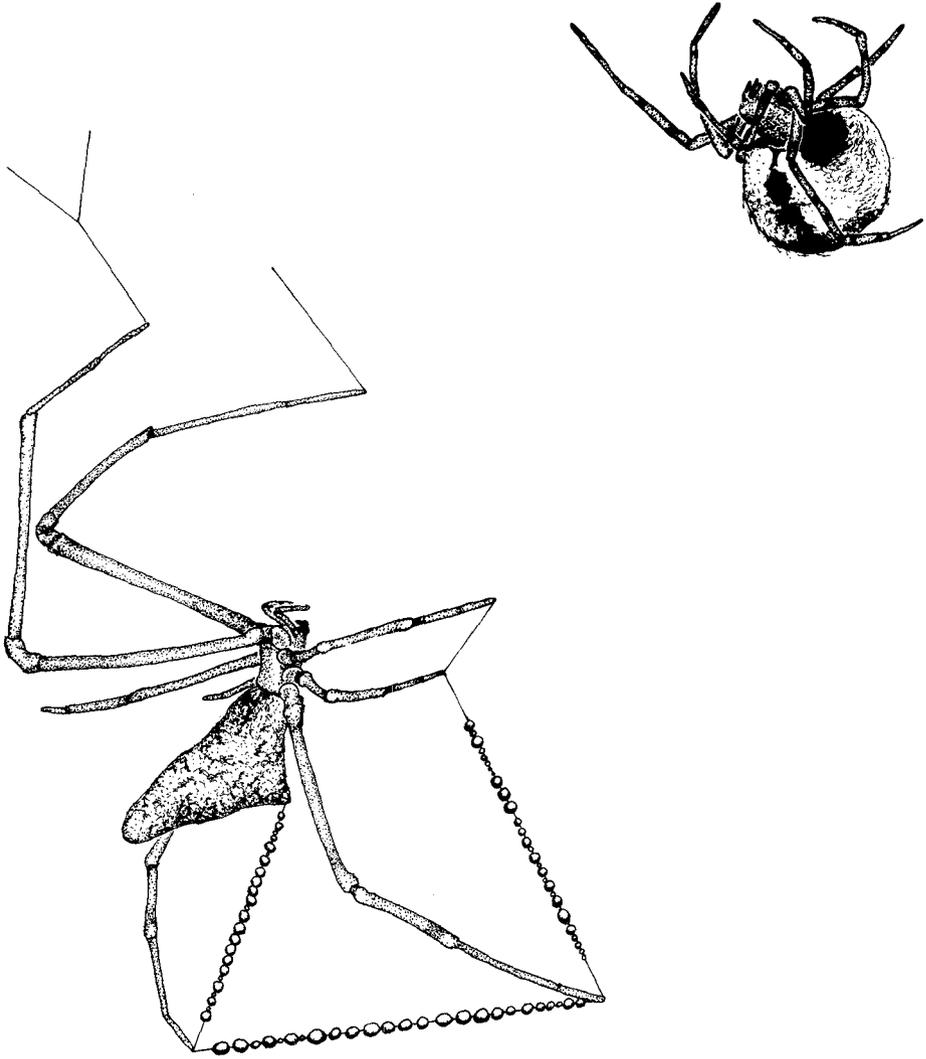


Fig. 5a.—*Rhomphaea* (bottom, left) holding its triangle net just prior to catching the *Achaearanea* sp.

These advantages may explain why *Rhomphaea* employs specialized vibratory techniques even though walking alone was effective at luring prey. *Rhomphaea* responded to prey lured while walking by momentarily stopping, perhaps to “read” the vibrations of the prey accurately. *Rhomphaea* may thus need to stop in order to accurately gauge where to cast the net.

The standard bounce rarely lured prey, and may be primarily defensive, rather than predatory. Stick-mimicking phasmids and mantids rock backward and forward or side to side in a manner suggested to resemble a leaf or stem being gently blown by a breeze in the forest (Robinson 1969). The standard bounce also fits this imagery, and may be used by *Rhomphaea* to conceal itself from its own visually hunting predators.

Comparisons with the genera *Ariamnes* and *Argyrodes*.—*Ariamnes*: Exline & Levi (1962) merged the genus *Ariamnes* with *Rhomphaea* and *Argyrodes*.

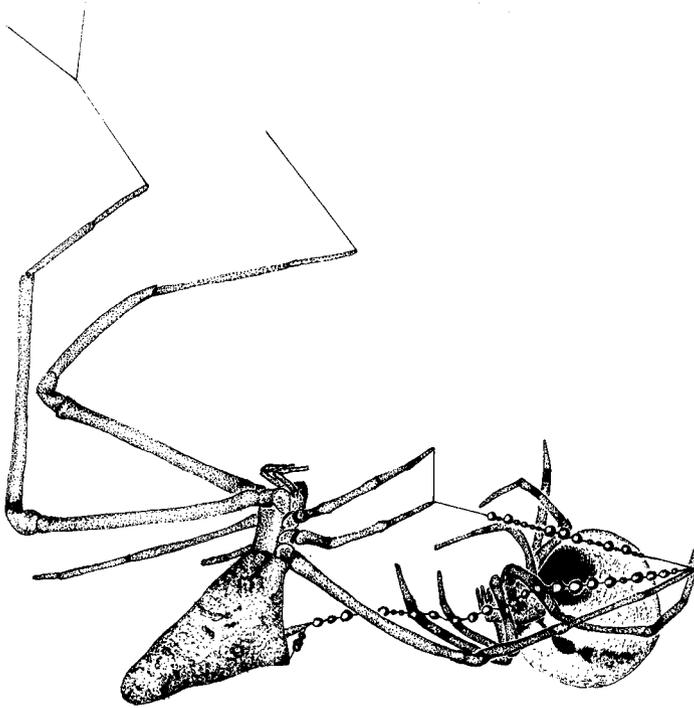


Fig. 5b.—*Achaearana* sp. is lured towards a *Rhomphaea* which scoops with a triangle net, catching the spider. To scoop, legs IV are rotated ventrally at the trochanter-femur joint.

Ariamnes colubrinus (Keyserling) (Clyne 1979) and *Ariamnes attenuatus* (O. P. Cambridge) (Eberhard 1979) use a similar scooping behavior to that of the New Zealand *Rhomphaea* to catch their prey. However, *Ariamnes* has relatively longer legs than *Rhomphaea* and unlike *Rhomphaea*, neither species of *Ariamnes* appears to use a leg II to form a complete triangle. By using leg II the triangular net is no longer apexed at the spider who may thus enjoy greater safety from the prey should the net be misthrown. Another difference is that *Ariamnes attenuatus* has modified hairs with which to hold the sticky silk (Eberhard 1979) whereas New Zealand *Rhomphaea* has no such hairs (Whitehouse unpubl. data). A third difference is that *Ariamnes* is only known to catch spiders and flies on its own web, while *Rhomphaea* ventures onto foreign webs to capture prey.

Argyrodes: This genus is well known for its kleptoparasitic species some of which are also araneophagic. *Argyrodes antipodiana* uses a different method to lure and capture spiders than species from the genera *Rhomphaea* and *Ariamnes*. Instead of ensnaring them in a net, *A. antipodiana* lunges, encircling the prey with legs I and II, and pulls the spider in towards its mouth (Whitehouse 1986). This method is similar to that used by species of *Mimetus* (Jackson & Whitehouse 1986).

Evolution.—The degree to which the genera *Argyrodes*, *Ariamnes*, and *Rhomphaea* are related and whether they should be treated as one or three genera is unclear. Presumably their common ancestor was a web-builder which caught prey by wrapping it with silk in a manner similar to that of many other theridiids such as *Achaearana* sp. The behavioral repertoires of *Argyrodes*,

Ariamnes and *Rhomphaea* have diverged in different directions from such an ancestor. The genus *Argyrodes* (as represented by *A. antipodiana*) now lunges at prey with legs I. In contrast the New Zealand *Rhomphaea*, and species of *Ariamnes* all catch prey by scooping. This behavior may be a synapomorphy linking *Rhomphaea* more closely to *Ariamnes* than *Argyrodes*.

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