

Retreat architecture and construction behaviour of an East African idiopine trapdoor spider (Araneae, Idiopidae)

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Summary

The arboreal retreat of an East African idiopine spider is provided with a trapdoor with tabs on its edge. Videotape analysis of retreat construction shows that the trapdoor is constructed by virtually the same door-moulding behaviour programme observed so far in ctenizids (*Ummidia* and *Hebestatis*) and antrodiaetids (*Aliatypus*), a construction programme very different from the door-cutting behaviour of another idiopid trapdoor spider, *Arbanitis gilliesi*. The evidence indicates that, in the Idiopidae, the door moulding programme is primitive and door-cutting is derived. The door-edge tabs may increase the spider's prey-sensing radius and allow the door to be closed more securely. Observations of door closing, prey capture, and soil ejection behaviours are presented.

Introduction

In spite of the large number of trapdoor-building mygalomorph spider taxa and the fascinating diversity of trapdoor structure, surprisingly little is known about the functions and design features of these doors and virtually nothing is known about their evolutionary history. The facts that all known Mesothelae construct trapdoors and that eight of the 15 mygalomorph families contain large numbers of trapdoor-building species suggest that the trapdoor is the plesiomorphic retreat entrance construct for Mygalomorphae. However, Bristowe (1930), Main (1976), Gertsch (1979), Coyle (1986) and Mayo (1988) have argued that, because of the wide diversity of trapdoor form, the existence of two very different trapdoor construction programmes, and the simplicity of the behavioural shift which probably permitted the evolution of the trapdoor from a collar door in the Antrodiaetidae, trapdoors may have originated independently a number of times during mygalomorph evolution. Such evolutionary plasticity would be similar to that which Eberhard (1990) has detected in the evolution of aerial webs.

In order to test hypotheses about the evolution of trapdoors, it is important to (1) understand the functions of trapdoor design features and consequently the selection pressures responsible for their evolution (Coyle, 1986) and (2) describe the trapdoor construction behaviours of different taxa. These behavioural characters not only increase the number of characters available for phylogenetic analysis but also allow one to recognise homologous constructs in the same manner as homologous anatomical structures are revealed by developmental similarity. To our knowledge, descriptions of trapdoor-building behaviour have been published for only seven

mygalomorph species (representing seven genera in five families). Five of these species mould the door from pellets of excavated soil while the other two simply cut the door out of one end of the sealed retreat. The door-moulding species include the ctenizids, *Ummidia carabivora* (Atkinson) (Atkinson, 1886a,b,c; Coyle, 1981), *Bothriocyrtum californicum* (O.P.- Cambr.) (Passmore, 1933), and *Hebestatis* sp. (Mayo, 1988); the antrodiaetid, *Aliatypus thompsoni* Coyle (Mayo, 1988); and the migid, *Migas distinctus* O.P.- Cambr. (Todd, 1945). (Main's (1957) sketchy account of door construction by the aganippine idiopids indicates that these are also probably door-moulders.) The two door-cutting species are the nemesiid, *Nemesia meridionalis* (O. Costa) (Moggridge, 1873), and the idiopid, *Arbanitis gilliesi* (O.P.- Cambr.) (Todd, 1945). These two construction modes are so different that they (and their products) are not likely to be homologous. Careful observation of entrance construction behaviour in other mygalomorph taxa may tell us much about trapdoor evolution and may even help test mygalomorph phylogenies.

In this paper we describe door and retreat structure, construction behaviour, and other aspects of the behaviour of an East African idiopine spider. Unlike the arbanitine idiopid *A. gilliesi* (Todd, 1945), but like (apparently) the aganippine idiopids (Main, 1957), this species employs door-moulding.

Materials and methods

Seven idiopine spiders (six females and a juvenile) were collected in their tubular retreats on a tree trunk at Hunter's Campsite, a semi-cleared spot in the edge of a forest at an elevation of 320 m in the Shimba Hills National Reserve south of Kwale, Kenya, on 31 March 1989. Fourteen spiderlings were living with the largest female in her retreat. In the absence of any revisionary work on the Idiopinae it is difficult to determine the species or genus to which these obviously conspecific specimens belong. However, based on Raven's (1985) description of idiopine genera and Griswold's (1984) key, this species, because it lacks the posterior pair of sternal sigilla, does not have the anterior region of the chelicerae narrowed, and has a normal (not saddle-shaped) third tibia, is either in the genus *Ctenolophus* or its sister genus, *Idiops*. Figures 1–3 show characters useful for eventual identification to genus and species. The specimens are deposited in the American Museum of Natural History and the National Museums of Kenya.

Three of the spiders were kept alive and later observed indoors in North Carolina from October 1990 to March 1991. They were placed in small terraria, the floors of which were covered with 10–20 mm of fine, sifted, humus-rich soil for retreat construction. Indoor lighting generally corresponded to the natural North Carolina photoperiod regime. Retreat and trapdoor construction behaviours were recorded with a Panasonic WV-D5000 video recorder with a Micro-Nikkor 55 mm close-up lens. A total of seven retreats were built by the three spiders. Two virtually complete trapdoor construction sequences performed by two individuals were videotaped. Trapdoor

construction behaviour was analysed using slow motion and freeze-frame playback of the videotape.

Results

Retreat architecture

The spiders were collected in tubular silk-lined retreats constructed in clayey soil lodged in deep bark crevices 1.3–2.0 m above ground level on the tree trunk. Each retreat tube was short, at least slightly inclined, and was provided at its lower end with a dorsally hinged trapdoor inclined 45–80° above horizontal when closed (Fig. 4). The trapdoors were well camouflaged, being partly covered with the same moss protonema, filamentous blue-green algae, and fungal hyphae covering the retreat and adjacent soil and bark surfaces.

The following description and Figs. 4 and 5 are based on one retreat that was removed from the tree intact and photographed with its spider within. The inner dimensions of the retreat, which was approximately twice the length of the spider, were 18 mm long and 6–7 mm in diameter. The retreat was surrounded by a 2–6 mm thick layer of hard clayey soil which was thicker on the exposed side than against the bark surface. Trapdoor (Fig. 5) dimensions were: hinge width 7.0 mm, maximum diameter (parallel to hinge) 8.1 mm, minimum diameter (perpendicular to hinge) 6.5 mm, thickness 0.5–5.4 mm. The door's thickness varied so much because of a thick mass of soil, moss and algae attached to its outer surface centrally and near the hinge. The inner surface of the door was a thick smooth layer of silk. The door edge was bevelled and extended outwards as 14 closely-spaced tabs composed of silk (inner surface) and soil (outer surface) and ranging from 0.44–1.33 mm wide and 0.74–1.41 mm long.

The trapdoor of another spider, probably the large female with spiderlings, was collected and measured

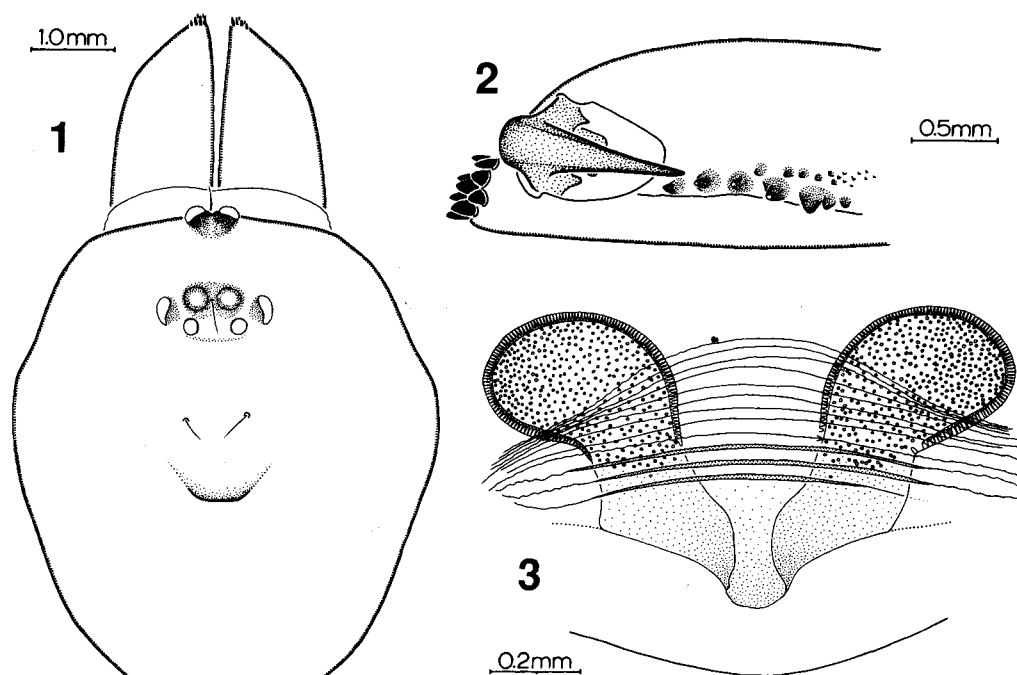
(Figs. 6, 7): hinge width 9.2 mm, maximum diameter 12.3 mm, minimum diameter 10.5 mm, maximum thickness 3.1 mm. The thickness of this door was also highly variable because its outer surface was very rough and partly covered with moss. Like the other door, the inner surface was smooth and silk-covered, and broadly and rather steeply bevelled around the edge. Tabs of silk plus soil were present but generally wider (0.48–1.48 mm) and shorter (0.26–0.74 mm) and more worn than those of the other door.

Trapdoors constructed in captivity were the same general shape as those found in nature, but were thinner and flatter (Figs. 10, 11), without the strongly concave outer surface and correspondingly bevelled edges of the field-collected doors (Figs. 4–7). The thresholds of the entrances constructed in captivity flared outwards at least slightly. All retreats constructed in captivity were approximately horizontal and the door plane varied from 30–80° above the horizontal.

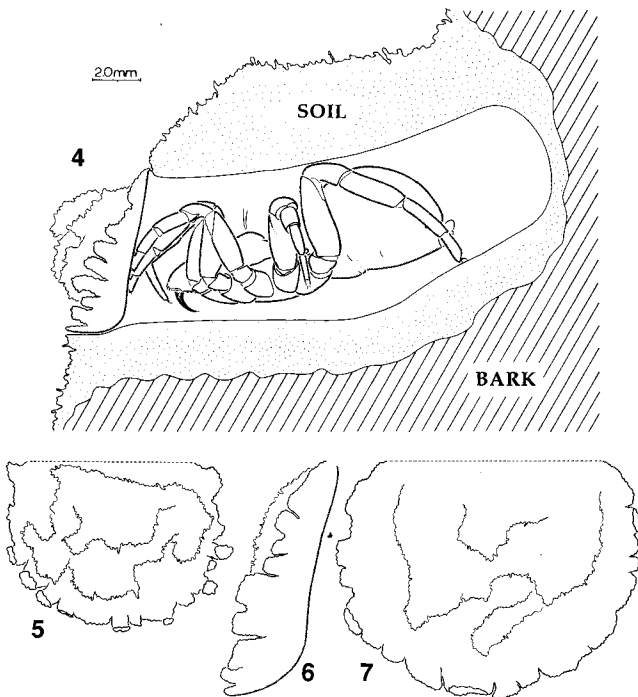
Descriptive statistics for the entire sample of trapdoors (two collected in field and six constructed in the lab): maximum diam. = 8.1–12.3 (9.86 ± 1.19), minimum diam. = 6.2–10.5 (7.49 ± 1.25), hinge width = 6.9–9.2 (8.16 ± 0.84), min. diam. (100)/max. diam. = 69–85 (75.6 ± 5.1), hinge width (100)/max. diam. = 75–90 (81.9 ± 5.9).

Construction behaviour

Retreat construction, which usually began in the evening or after nightfall and often continued into the next day, can be somewhat arbitrarily divided into three phases: (1) the initial excavation, (2) retreat tube construction, and (3) trapdoor construction. In phase 1 the spider excavates a shallow depression by digging small loads of soil with its chelicerae and depositing them a short distance to the side. Phase 2 begins when silk is added to this



Figs. 1–3: Idiopine female from Hunter's Campsite, Shimba Hills N R, S Kwale, Kenya. 1 Carapace and chelicerae, dorsal view; 2 Left chelicera, ventral view; 3 Spermathecae, cleared, dorsal view.



Figs. 4–7: Field-collected retreat and doors of idiopine females from Shimba Hills, Kenya; drawn from photographs, collected retreat, and preserved spider. **4** Spider holding trapdoor shut; mid-sagittal section of retreat and side view of door showing tabs; **5** Outline of trapdoor in Fig. 4, outer surface; **6, 7** Side view and view of outer surface of another trapdoor.

deposited soil to initiate side-wall construction. These walls are enlarged by adding more soil loads and silk. The application of silk between the two walls at the top rear begins the roof. Soil loads and silk are then applied alternately to the roof extending it towards the front of the retreat. The transition from phase 2 to phase 3 is subtle because the door is essentially an extension of the retreat roof, which is constructed, in part, with behaviour patterns similar to those used in door construction.

Door construction involves the following behaviour patterns:

Digging: The spider extends its fangs and raises its chelicerae slightly. Then, as the prosoma is lowered towards the substrate, the chelicerae are lowered simultaneously to engage the soil. It is probable that the fangs cut into the soil at this point and are then flexed as the chelicerae (and soil load) are lifted. During the digging process the pedipalps are extended and then flexed, often against the substrate, and sometimes pull loose soil particles back to the soil load held by the chelicerae. The pedipalps then come to rest with metatarsi and tarsi in front of and below the soil load and remain in this position while the load is being carried.

Pivoting: The spider reverses its direction by flexing its body laterally and rotating clockwise or counter-clockwise about a dorsoventral axis running approximately through the pedicel. Clockwise pivoting is achieved by stepping backwards with the right legs while the left legs step forwards; counter-clockwise pivoting is achieved by the reverse stepping pattern.

Rolling: The spider walks sideways up the retreat wall (from an upright position on the retreat floor to an

inverted position on the retreat ceiling) or down the wall.

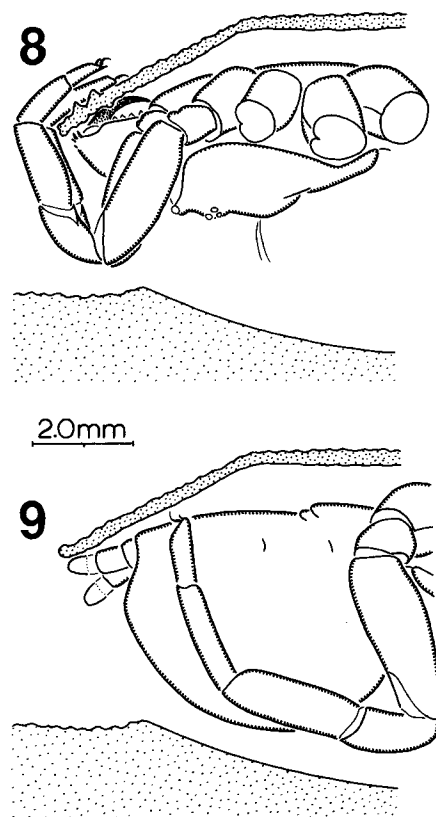
Door shape testing: The tips of the pedipalps and first legs are alternately lifted and lowered to repeatedly touch the edge of the door. This pattern nearly always immediately precedes soil release.

Soil releasing: The chelicerae alternate in an up and down motion with the fangs extending as the chelicerae are lifted and flexing just before the chelicerae are lowered. At the same time, the pedipalps are extending and flexing to guide the soil as it is released and (with large soil loads) to help push the soil from the chelicerae.

Door moulding: Immediately after the soil is released on the edge of the developing door it is repeatedly (usually 3–5 times) squeezed between the ventral (and perhaps anterior) surface of the chelicerae and the ventral surface of the distal articles of the pedipalps (and often the first legs) (Fig. 8).

Silk application: Each posterior lateral spinneret is flexed at its base towards the substrate and then lifted away in a continuing rhythmic movement while releasing silk (Fig. 9). The spinnerets move alternately; as one is bent to the substrate the other is lifted away. Lateral movements of the spinnerets occur occasionally, bringing them closer together or spreading them apart. The abdomen and whole body also shift about to direct silk application, which, although focused on the just-released soil, includes a wider area of the door under-surface. Although difficult to observe, the small posterior median spinnerets were seen applying silk on two occasions.

The following sequence of behaviour patterns is repeated again and again during door construction:



Figs. 8, 9: Door construction behaviour patterns; side views drawn from videotaped images and preserved specimen. **8** Door moulding; **9** Silk application.

digging — pivoting — rolling — door shape testing — soil releasing — door moulding — pivoting — silk application — rolling. Occasionally digging is preceded by pivoting instead of being followed by it, so that the spider excavates soil from the front portion of the retreat while facing out of the entrance. On at least one such occasion a spider gathered soil just outside the entrance by extending and flexing the pedipalps and first legs to pull the soil to the chelicerae; this was followed by rolling, releasing and door moulding. Rarely the spider adds soil to and moulds the entrance rim (door threshold). Often there is a pause of several seconds to several minutes between pivoting and rolling; as the door nears completion these pauses become longer and the spider occasionally pulls the door forcefully inwards, presumably testing its fit. The wide variation in the duration of trapdoor construction (6 to over 12 h) both within and among individuals was primarily the result of variation in the duration of pauses between behaviour patterns.

Newly constructed doors (18–40 days old, $n=3$) were very thin and lacked edge tabs, but older trapdoors (60–150 days old, $n=3$) appeared to be thicker centrally near the hinge and had a thicker silk lining and edge tabs. We observed spiders adding silk to the under-side of a 13 day-old door and a 20 day-old door. On a few occasions spiders were observed gently manipulating (as in door-shape testing) and/or adding small amounts of soil to the edges of older doors, actions that may have been part of edge-tab construction. Manipulation (with chelicerae) of the hinge area of completed doors, followed by silk application and repeated door opening (up to 90°) and closing was recorded several times. One individual was observed ejecting several loads of soil from a 13 day-old retreat; the door was opened about $25\text{--}30^\circ$ and the first legs and probably pedipalps were suddenly flexed behind the soil load (held in the chelicerae) and immediately extended rapidly to catapult the soil several cm from the retreat.

Prey capture behaviour

When the spider is in its foraging (prey-sensing) mode, the trapdoor edge is slightly above or resting loosely on the threshold (entrance rim) and extends slightly beyond it (Figs. 10, 11). Probably the spider is holding or at least touching the underside of the door, because the response (either a capture strike or door closing) to prey- or observer-generated door contact is often instantaneous. In all but one of the 40 prey captures observed (*Tenebrio* larvae and termite workers), the spider did not strike until the approaching prey touched the door; the exception occurred when the prey pushed a small lump of soil against the door edge and the spider grabbed the lump and missed the prey. The capture is extremely quick: the door pops open and the spider lunges with pedipalps and legs I and II extended; some or all of these reach over the prey and then flex to pull the prey to the chelicerae (which, at that moment, usually strike and insert fangs); the prey is quickly pulled into the retreat as the door falls shut. Typically the abdomen and tarsi III and IV do not leave the retreat entrance, although rarely tarsi III and part of the abdomen do. The duration of 10 video-recorded

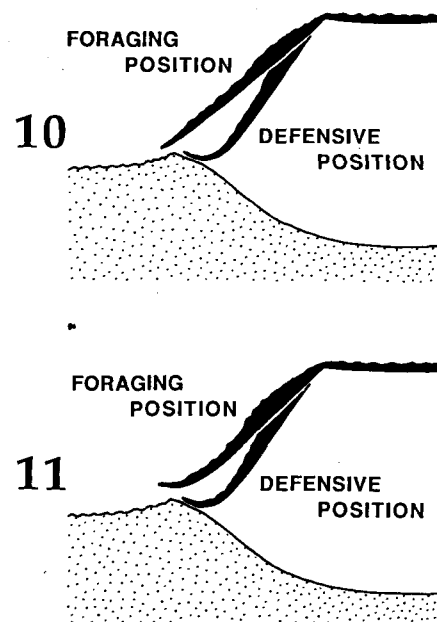
captures, from onset of the capture lunge to the disappearance of the spider and prey behind the trapdoor, ranged from 0.60 to 3.40 s (mean = 1.49 ± 0.89).

Defensive behaviour

Our attempts to grasp a door with forceps and open it were usually resisted by the spider which pulled the door tightly against the entrance rim, held it there, and continued to tug inwards in response to further probing. Although initially flat (Fig. 10) or weakly concave (Fig. 11), the peripheral portion of the door became more and more concave as the spider continued pulling on it, and the edge of the door bent more and more as it slid tightly into the entrance rim (Figs. 10, 11). Tapping the arena or the soil around the retreat elicited the same door-closing response. We were able to force open one spider's door enough to see that it was holding the door with the tarsal claws of legs I and II of both sides (Fig. 4); the chelicerae and pedipalps were not being used.

Discussion

The trapdoor construction behaviour patterns of this idiopine spider are very similar in both form and sequence to those of the only other door-moulding mygalomorphs whose trapdoor construction behaviours have been described in detail, the ctenizids *Ummidia* and *Hebestatis* (Atkinson 1886a,b,c; Coyle, 1981; Mayo, 1988) and the antrodiaetid *Aliatypus* (Mayo, 1988). Only minor differences exist; the idiopine, like *Ummidia* and *Aliatypus*, applies silk with alternate movements of its spinnerets and to a wide area in addition to the previous door-moulding focus, while *Hebestatis* applies silk with synchronous spinneret movements and only in the immediate area of door moulding.



Figs. 10, 11: Semi-diagrammatic mid-sagittal views of retreat entrances showing trapdoor open (in foraging position) and closed (in defensive position). **10** Door flat in foraging position; **11** Door concave in foraging position.

The highly similar door-building behaviour of these four taxa supports the hypothesis that their trapdoors are homologous. Outgroup comparison (the Ctenizidae, Actinopodidae and Migidae together constitute the sister group of the Idiopidae (Raven, 1985)) supports the hypothesis that this door-moulding programme is plesiomorphic for the idiopids and that the door-cutting mode of construction observed in the arbanitine idiopid *Arbanitis gilliesi* (Todd, 1945) has evolved independently. The possibility that the trapdoor of *Aliatypus* is homologous to the idiopine and ctenizid doors seemingly contradicts the hypothesis, supported by outgroup comparison, that the *Aliatypus* trapdoor evolved from a collar door (Mayo, 1988). However, Mayo discovered that the only difference between collar and trapdoor construction programmes in the Antrodiaetidae is one of simple orientation, so it is conceivable that the door-construction programme common to both ctenizids and antrodiaetids was present in their fornicephaline ancestor and that in the atypid-antrodiaetid lineage the programme shifted easily between trapdoor and collar/turret construction. The observations of door-moulding in the Mesothelae (Klingel, 1967; Haupt, 1979) suggest that it is the plesiomorphic mode of door construction in the Mygalomorphae.

The soil ejection behaviour of this idiopine appears similar to that observed by Coyle (1981) for *Ummidia* during its second phase of burrow excavation and by Passmore (1933) for *Bothriocyrtum californicum*. However, *Ummidia* uses only its pedipalps to catapult the soil; its first legs hold the door open. The idiopine prey-capture attempt which appeared to fail because of the soil clump present just outside the threshold supports Coyle's (1981) suggestion that such interference could foster selection for soil ejection behaviour.

A noteworthy finding of this study is the gradual transformation of the trapdoor, over a period of weeks and months, from the thin, flat, rather smooth-edged flap constructed initially, to one that has edge tabs, is thicker, and is peripherally concave. Such gradual but rather profound changes, and the observed behaviours which help produce them, indicate an even larger and longer term expenditure of door-construction behaviour by trapdoor spiders than has heretofore been appreciated.

We have not encountered in the literature a description of a trapdoor with tabs on its edge. Two non-exclusive hypotheses for the functions served by these tabs occur to us. (1) They may increase the prey sensing effectiveness of the door. Since these spiders strike only at prey which touch the door, even the small increase in door radius caused by these tabs may result in the detection and capture of significantly more prey. Linear litter, silk lines, and tabs attached to and radiating out from entrance rims are characteristic of some burrowing spider taxa, and apparently increase the prey-sensing area (Main, 1957, 1976; Coyle, 1986), but they typically radiate much further than these idiopine tabs. (2) The edge tabs may allow the door to be pulled further into and be held more securely within the entrance by the spider. The spaces between the tabs permit them to converge and therefore bend more and with less resistance as the door is being pulled into the threshold than would a continuous edge of equal extent.

This would make it easier for the spider to pull the door into the threshold a given distance and therefore possibly more difficult for a predator to detect the door edge and prise it open.

Defensive door-holding behaviour appears to vary widely among trapdoor spiders, and especially so within the Idiopidae. Some trapdoor spiders, like the ctenizid *Bothriocyrtum californicum* (Passmore, 1933) and the arbanitine idiopids *Cataxia* and *Arbanitis* (Main, 1985), hold the door shut with their fangs. Others, like the aganippine idiopids, hold the door shut with their hind legs (Main, 1985). Holding a door shut with the first and second legs, as our East African idiopine and *Cyclocosmia torrea* Gertsch & Platnick do, might be a way of keeping the chelicerae free for defensive use. Crome's (1962) analysis of *Conothele arboricola* Pocock specimens preserved in their nests indicates that this ctenizid species sometimes uses only its fangs and at other times only its pedipalps and first legs to hold its door shut.

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***Kilifina*, new generic name for *Kilifia*, preoccupied (Araneae, Mysmenidae)**

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Baert & Murphy (1987) described a mysmenid spider from Kenya for which they erected a new genus they named *Kilifia* after the type locality.

Dr Mark Judson kindly drew our attention to the fact that the genus name *Kilifia* had already been used by De Lotto in 1965 for the description of an African soft-scale insect (Coccidae).

Therefore we propose here the generic name *Kilifina* to replace *Kilifia*, preoccupied. The type species thus becomes *Kilifina inquilina* (Baert & Murphy, 1987).

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