The architecture of the physid musculature of *Physa acuta* Draparnaud, 1805 (Gastropoda: Physidae)

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ABSTRACT

The basommatophoran family Physidae possesses a remarkable but little known set of muscles called the “physid musculature”. Using *Physa acuta* as a model, this musculature was shown to be anatomically complex and associated in places with the columellar muscle. The physid musculature has two main components, the physid muscle _sensu stricto_ and the fan muscle, both of which have previously been named but not examined in detail. The physid muscle _s.s._ is branched with the larger branches running to the neck, head and foot, and the smaller ones to the lung floor and mantle. The fan muscle is not branched. We propose that the physid musculature is responsible for a unique ability of physids to rapidly flick their shells from side to side—a reaction that frequently enables them to escape predation. We suggest that during this movement the lung floor, which is strengthened by several bands of muscle from both the physid musculature and the columellar muscle, serves as a pivot for the rotating visceral hump and shell, while the main trunk of the physid muscle _s.s._ and its main branches provide a broad anchorage in the foot.

KEY WORDS: Physidae, *Physa acuta*, anatomy, physid musculature, columellar muscle, predator avoidance, shell twisting.

INTRODUCTION

Members of the freshwater pulmonate family Physidae possess a complex of muscles that is unique amongst gastropods. This complex was given the name “physid musculature” by Harry and Hubendick (1964) who provided a brief description of its structure and named its two main components, the physid muscle _sensu stricto_ and the fan muscle. Harry (1964) used the presence of the physid musculature as the main character separating the Physidae from the rest of the Basommatophora. Paraense (1986, 1987) identified the attachment (insertion) of the “physid muscle” in his re-descriptions of *Physa marmorata* Guilding, 1828 and *Physa cubensis* Pfeiffer, 1839 respectively. He did not comment further on this beyond noting that the roof of the pulmonary cavity was darkly but patchily pigmented except for that part covering its attachment which in the case of *P. marmorata* was lightly pigmented or unpigmented and in the case of *P. cubensis*, always unpigmented. As far as we know, no detailed studies have been made of the physid musculature.

Our attention was drawn to Harry and Hubendick’s (1964) description of this musculature as we looked for a mechanism to account for the well-known ability of physids to twist their shells rapidly through approximately 120° (180° according to Dawson 1911) in a clockwise direction and back. Dawson (1911) must in fact be credited with the hypothesis that this twisting is important in predator avoidance. He indirectly intimated this over 95 years ago from his observations on the sensitivity of the mantle of *Physa gyrina* Say, 1821 to external stimuli. He did not record the existence of the physid musculature, but rather argued that the strong shell-twisting reaction of *Physa gyrina* to a localized mechanical stimulus might be due to the reflection of the mantle over the shell.

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This manoeuvre is only seen in physids and is widely thought to serve as part of predator escape behaviours, e.g. Wrede (1927), Frieswijk (1957) and in particular, the elaborate avoidance responses 3–6 of Wilken and Appleton (1991). Observations on the predator-avoidance behaviour of invasive physids in Africa (Hofkin et al. 1991; Wilken & Appleton 1991; Maharaj et al. 1992; Appleton et al. 1993, 2004) confirm that these snails are able to escape slow-moving predators that hunt by ambushing their prey, viz. indigenous leeches and sciohyzid fly larvae as well as introduced crayfish, but not the fast-moving indigenous belostomatid bugs that actively pursue their prey. We therefore support Taylor (2003) in proposing that the physid musculature plays an important role in the ability of these snails to avoid predation. This ability to escape both indigenous and introduced predators has undoubtedly been a useful attribute in the colonization of many parts of Africa by Physa acuta Draparnaud, 1805 and Aplexa marmorata (Guilding, 1828) (= Physa marmorata Guilding, 1828) (Brown 1994).

In South Africa, P. acuta has colonized several major river systems and many smaller ones (de Kock & Wolmarans 2007). It occurs in a wide variety of habitats, particularly perennial rivers, streams and dams with muddy or stony substrata, from the coastal lowlands to an altitude of approximately 1500 m above sea level. In many of these habitats, it is the most common gastropod species present. A. marmorata has also become invasive in South Africa, but is found almost exclusively in standing water bodies notably swamps and ponds, both natural and artificial (Appleton & Dana 2005). Both species are still spreading.

Using P. acuta as a representative of the Physidae, this study provides a detailed description of the physid musculature and proposes that it plays the major role in shell-twisting. These specimens were previously known as P. cubensis Pfeiffer, 1839, but this species was placed into synonymy with P. acuta by Paraense and Pointier (2003). Although the type locality of P. acuta is the Garonne River, southern France, it is thought to have been translocated to Europe from the Americas (Dillon et al. 2001) sometime before 1805.

MATERIAL AND METHODS

Samples of adult P. acuta from several localities in Mexico and Brazil were relaxed in Petri dishes using two methods. (1) Snails were placed in fresh water with small pieces of tobacco for five to six hours at room temperature and then at 4°C in a refrigerator until they showed no signs of movement; they were then placed in 70% ethanol. (2) Snails were kept overnight in a 0.05% Nembutal solution after which they were placed in water at 70°C for ±40 seconds in order to kill them; the soft parts were then pulled from their shells and placed in a modified Railliet-Henry solution (Paraense 1986, 1987). Although both methods were effective, the physid musculature proved easier to dissect and follow in snails relaxed using method 1. Nevertheless, some variation was seen in the degree of relaxation of certain muscle bands which resulted in slight differences in their appearance, especially their width (e.g. Fig. 1C).

Written records were kept as dissections proceeded and drawings were made at different stages using a camera lucida. These drawings of the dissected muscles were redrawn within outlines of Physa taken from Taylor (1988) while referring to actual specimens at the same time. Finally, composite drawings were made in order to show
the whole complex of muscles and how it associates with the columellar muscle. The terms ‘left’ and ‘right’ are used in relation to the snail body.

A list of abbreviations used in the figures and text is given below. ‘P’ denotes a component of the physid musculature and ‘C’ a component of the columellar muscle.

- Pm – main trunk of the physid muscle s.s.
- Pm1–5 – branches of the physid muscle s.s.
- Plu – physid muscle fibres on lung floor
- Pp – pneumostome–mantle band
- Pf – fan muscle
- Cm – main trunk of the columellar muscle
- Cm1–4 – branches of the columellar muscle

RESULTS AND DISCUSSION

Rather than devise new names for the components of this complex of muscles, we have followed the terminology of Harry and Hubendick (1964) with new names given only to components they did not recognize. Thus, we accept the names “physid musculature” for the entire complex and ‘physid muscle s.s.’ and ‘fan muscle’ for its two main components. However, to avoid confusion between the ‘physid musculature’ as a complex and its major component, the ‘physid muscle s.s.’, these names are written in full or abbreviated as listed above each time they are used. The physid musculature of *P. acuta* is therefore described in terms of its two major components, their branches and associated structures. Since it is associated with the physid musculature in several places, the columellar muscle is described as well.

*The physid muscle sensu stricto*

The physid muscle s.s. (Pm) is the main trunk of the physid musculature. It is situated in the right hand part of the body and is almost as wide as the columellar muscle, the principal muscle of most gastropods. Its origin is in the right hand side of the right anterior pedal branch of the main trunk of the columellar muscle (Fig. 1A) and its insertion is, as shown in Fig. 1B, on the lower right hand side of the mantle (Harry & Hubendick 1964; Paraense 1986, 1987). The point of insertion is clearly visible as an elongate scar on the mantle, broadest close to the mantle collar and extending towards the mid-dorsal line, but tapering as it does so. The main axis of the physid muscle s.s. lies perpendicular to the foot and at an angle of ±120° to the columellar muscle. Since this study showed that there were more components to the physid muscle s.s. than identified by Harry and Hubendick (1964), they are described in terms of their association with (i) the upper portion of neck and head, (ii) the lung floor and pneumostome and (iii) the columellar muscle.

Association with the upper portion of neck and head (Figs 1B–D)

The physid muscle s.s. (Pm) has five branches which are designated Pm1 to Pm5 in the figures. Two of these (Pm1 & 5) branch from the upper part of the physid muscle s.s. while the remaining three (Pm2–4) branch from the lower part (Fig. 1B). Pm1–4 pass down the upper portion of neck of the snail where they entwine to form a mesh-like tissue with fibres coming down from the columellar muscle (Fig. 1C). Two of these branches (Pm1 & 2) descend further towards the right and left sides of the body
respectively (Fig. 1B). Pm1 then radiates out over the right side of the head while Pm2 & 3 as well as the fourth branch (Pm4) run from the right to the left flank, after passing over the neck. From here Pm3 & 4 sink towards the foot. Just before doing so, they entwine with fibres running longitudinally within the body wall for almost the whole length of the body and with fibres of Pm5 coming from the right to the left but wrapping round behind the columellar muscle (Fig. 1B) before entering the foot where it is anchored. The middle two branches (Pm2 & 3) then run anteriorly towards the left side of the head, spreading out just above the male gonopore and left eye (Figs 1B, 1D) and sink into the spongy tissue of the sole where they are inserted.

Association with the lung floor and pneumostome (Figs 2A, 2C)

Thin parallel bundles of fibres (Plu) from the main trunk of the physid muscle s.s. cross laterally over the floor of the lung cavity towards the left at approximately the level of the anterior corner of the pneumostome (Fig. 2A). In addition, fibres from the columellar muscle cross the lung floor but in an antero-posterior direction, i.e. at right
angles to those from the physid muscle s.s. (Fig. 2A). There are also some fibres running diagonally from right to left over the lung floor. These fibres reach the mantle collar but their origin was not seen. It is thus clear that the lung floor is well supplied with muscle fibres. It also effectively divides the body cavity into two sub-cavities, the lower of which includes the mouth, buccal mass and male and female genitalia while the upper contains the visceral hump. The muscle fibres associated with the lung floor correspond to the structure in *Lymnaea catascopium* Say, 1817 that Walter (1969) called the “transverse membranous mid-body (‘cervical septum’)”, but which was difficult to separate from the lung floor in *P. acuta*.

The anterior corner of the pneumostome together with the lung floor are of particular interest because three different bands of muscle fibres converge there, one from above and two from below. Because of their proximity to each other, these bands are thought to combine to play a role in the swinging of the shell (see below). They are (i) the pneumostome–mantle band of muscle fibres (Pp) crossing from the mantle roof (Figs 2B, 2C); (ii) fibres on the lung floor coming from the main trunk of the physid muscle (Plu); and (iii) those coming from the columellar muscle (Figs 2C, 3A). The diagonal fibres on the lung floor (Fig. 2A) were not seen in all specimens dissected. The lung floor is thus strengthened by fibres from both the physid muscle s.s. and columellar muscle, but mostly the former, giving it the appearance of thickened scar tissue. This is in contrast to the ‘membranous’ structure described for *L. catascopium* by Walter (1969).
Not only does this reinforced lung floor form the partition between the upper and lower body cavities (Figs 2A, 3A), but it is thought to have a pivotal function in shell-twisting as well (see below).

*The columellar muscle* (Figs 2A, 3B, 3C, 4A)

The columellar muscle originates on the columella and is inserted in the foot. In *P. acuta* it comprises three parts, upper, middle and lower. The upper part has four elements all of which attach to the shell and are indicated Cm1–4 in Fig. 3C. The right hand of these elements (Cm1) descends to the right side of the head while the two middle elements (Cm2 & 3) descend to the foot. For part of their length, these three elements are united longitudinally to their contiguous neighbour or neighbours. The left hand element (Cm4) is divided in its mid-portion to form two sections (Figs 3B, 3C). The uppermost of these sections attaches to the edge of the mantle below the distal part of the digestive tract. It then fans out laterally to the left side to mesh with the connective tissue of the inner lung wall (Fig. 2A), i.e. at the “angle of the body whorl” behind the rectum and renal duct. This section of the lung wall, which lies against the columella, thus consists of connective tissue reinforced by columellar muscle fibres.

The lower part of Cm4 radiates both laterally and dorsally towards the head and snout as a wide band of fibres (Figs 3B, 4A, 4C). As it does so, it allows the passage of

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**Fig. 3.** (A) Transverse view of the body at the level of the lung floor as seen from below showing the physid muscle s.s. (Pm) and columellar muscle (Cm). Fibres from the Pm (Plu) and columellar muscle (Cm) cross the lung floor (fine detail indicated in upper right hand corner of the lung floor). The lung floor is surrounded by mantle collar tissue. (B) Dorsal view of *P. acuta* with the visceral hump removed to show the dorsal components of the columellar muscle (Cm). These have been flattened slightly. No detail is shown on the lung floor. (C) Above – dissection of the columellar muscle (Cm) and its four elements (slightly flattened). Below – detail of Cm overlying Pm4 and Pm5 fibres as they pass into the foot.
the vas deferens and the female and male gonopores (Fig. 4A). As they pass towards the head, some Cm4 fibres entwine with those of the physid muscle s.s. (Pm) but most lie above it as it crosses over the upper portion of the neck from the right to the left side of the body (Figs 1B–D). Within the head the fibres are so closely associated with the skin, that it is impractical to separate them either from the dorsum or the flanks or to determine whether they originate or insert there. In the foot, the main trunk of the columellar muscle (Cm) runs posteriorly but does not reach the tip of the tail (Fig. 1A). Anteriorly Cm divides into two thick branches that run longitudinally towards the head, tapering as they do so. These pedal branches were referred to as horns by Elves (1961) in his histological study on Physa fontinalis. In addition, a thin layer of fibres from the bottom of the main trunk of the columellar muscle runs anteriorly along the foot floor but does not quite reach the head.

These three bundles of muscle fibres in the foot (the main columellar trunk and its two anterior horns) lie on top of the thick, spongy skin and enclose a cavity in which the buccal mass, nerve ring and lower genital ducts lie. This cavity becomes shallower as it approaches the head. The main trunk of the physid muscle s.s. (Pm) is anchored primarily in the anterior right horn of Cm though some of its fibres can be seen to entwine with the left horn (Fig. 1A).

Association with the physid musculature (Figs 1B, 1C, 3C)

The posterior branch of the physid muscle s.s. (Pm5) runs behind the main trunk of the columellar muscle (Cm) (Figs 1B, 1D, 3C) from the right to the left side of the
body, following the Cm into the foot. Some of the descending Pm5 fibres entwine with fibres descending from the columellar muscle (Cm4) and also with fibres from an anterior branch of the trunk of the physid muscle s.s. (Pm4) that pass over the upper part of the neck from the right to the left (Figs 1A, 1D).

The fan muscle and pneumostome–mantle band of muscle fibres (Figs 1D, 2B, 2C, 4B)

As described by Harry and Hubendick (1964), the fan muscle consists of a number of thin but broad bundles of fibres radiating from its origin at the mantle end of the physid muscle s.s. across the roof of the right half of the mantle cavity (Figs 1D, 2C, 4B). We agree with the above authors that these fibre bundles have no clear insertions, but end diffusely in the tissue of the mantle roof. Some of these fan muscle fibres entwine in a perpendicular fashion with the pneumostome–mantle band of fibres (Pp) which appears to originate on the mantle collar. This band runs from the mantle collar (at the anterior corner of the pneumostome) across the middle of the right hand half of the mantle roof (Figs 2B, 2C, 4B) from one side to the other and disappears in the mantle roof in the vicinity of the spermatheca. It is widest near the anterior corner of the pneumostome but becomes narrower by a factor of 5 as it reaches the spermatheca.

Interaction between the physid musculature and columellar muscle

Figures 4B and 4C show the components of the physid musculature and columellar muscle together in composite diagrams in order to demonstrate their complexity and interrelationship. We agree with Taylor (2003) that the physid musculature enables physid snails to twist their shells rapidly as a predator escape manoeuvre in the manner described earlier but no mechanism has been proposed for this action. We therefore present one below.

Function of the physid musculature

The following attempt to identify the mechanism responsible for swinging the shell is based on the description of the physid musculature given above. It is based entirely on dissection and is therefore speculative. Further research into the mechanics of the physid musculature may modify this opinion.

We propose that the components of the physid musculature responsible for swinging the shell are the fan muscle (Pf), the 5th branch of the physid muscle s.s. (Pm5) and the pneumostome–mantle band (Pp). The physid musculature as a whole facilitates the swinging movement by (i) strengthening the lung floor so that it supports the rotating visceral hump and (ii) providing a broad anchorage in the head and foot for the contractions of the effector muscles Pf and Pm5 during rotation. Note that Pp has no attachment to the foot but originates on another solid structure, the mantle collar. The lung floor is strengthened by the meshing of fibres from both the physid musculature (Plu) and the columellar muscle. Anchorage in the foot is provided by the origin of the physid muscle s.s. (Pm) in the right hand pedal branch of the columellar muscle and the individual attachments of its branches (Pm1–5) in the tissues of head and foot.

The fan muscle and pneumostome–mantle band are the only components of the physid musculature that lie within the visceral hump, the part of the body that undergoes twisting. When they contract against the Pm with its branches 1–5 anchored in the head and foot, these two components will cause the shell + visceral hump to swing in
opposite directions. When the fan muscle and Pm5, which wraps around the columellar muscle (Cm), contract together, the hump will swing in a clockwise direction and when the pneumostome–mantle band contracts, the shell + visceral hump will swing anti-clockwise back to its normal position. This twisting pivots inside the body, at the base of the hump but dorsal to the foot—probably on the lung floor which as emphasized above is strengthened by several layers of muscle derived mostly from the physid musculature.

The effort required for the initial clockwise twisting is supplied jointly by the contraction of the fan muscle and Pm5 against the multiple anchorages provided by Pm in the pedal part of the columellar muscle and branches 1–4 of the Pm, which are buried broadly in the anterior pedal mass. The anti-clockwise return movement of the hump is effected by the pneumostome–mantle band (Pp) and will require less effort since it is returning to a normal or ‘resting’ position. It is possible that Pm4 also plays a role in this anti-clockwise rotation.

The function of the columellar muscle is to control the protraction and retraction of the snail’s head and foot out of and into its shell. This is very different from the function proposed here for the physid musculature, which therefore seems to be largely independent of the columellar muscle in terms of function though there are some anatomical associations.

CONCLUSIONS

The physid musculature is an elaborate complex of muscles that is unique to the basommatophoran family Physidae. Its broad main trunk originates in the pedal (basal) part of the physid muscle on the foot floor and is inserted as a single element on the roof of the pulmonary cavity. There are two principal components, the main trunk (the physid muscle s.s.) with its five branches and the unbranched fan muscle. Additional minor muscle bands strengthen the floor of the lung cavity. All these elements of the physid musculature are believed to play roles in the shell-twisting behaviour that is characteristic of physid snails.

Our conclusion that the physid musculature enables the visceral hump and shell to swing in an arc of approximately 120° and back rests on four premises. These are (i) that the origin of the main trunk (Pm) of the physid musculature in the pedal part of the columellar muscle and the attachments of its five branches (Pm1–5) in the tissues of the head and foot collectively provide a broad anchorage against which several of its components (Pf, Pm5 and Pp) can contract; (ii) that the Pm5 and Pf contract together to cause the shell to twist in a clockwise direction (Pm5 wraps around the columellar muscle so that when it contracts, it uses the trunk of the columellar muscle as a pivot); (iii) that contraction of the pneumostome–mantle band (Pp), which originates on the mantle collar, causes the shell to return to its resting position; and (iv) that the anterior corner of the pneumostome and the thick scar-like tissue of the lung floor provide a robust platform that serves as a base for the twisting forces exerted by these muscles. Contraactions of Pm1–4 seem unlikely to assist the twisting action provided by Pf and Pm5. However, these branches of Pm do have a supporting function by broadening the anchorage of the physid musculature in the pedal mass as noted above. If it can be shown that Pm4 plays a role in the anti-clockwise return the shell, Pm4 and Pm5 would be antagonistic muscles.
It is clear that the ability of physids to twist rapidly their shells in response to certain stimuli is at least partly responsible for some species, notably *P. acuta*, being able to defeat attacks from slow-moving predators by preventing them from making adequate contact with their shells. Indeed the physid musculature may have evolved within this Neotropical family in response to predation by such predators, i.e. glossiphoniid leeches, sciomyzid fly larvae and freshwater crayfish. Although the latter do not occur naturally in Africa, glossiphoniid leeches and sciomyzids do, and they are important predators of freshwater pulmonates there (Appleton *et al.* 2004). The ability to twist their shells is a pre-adapted escape manoeuvre that may have helped physids, particularly *P. acuta*, to become invasive in regions such as Africa where they have been introduced. Indeed, *P. acuta* is probably the most widespread invasive freshwater gastropod in the world.

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REFERENCES


Jumping spiders (Araneae: Salticidae) of the Ndumo Game Reserve, Maputaland, South Africa

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ABSTRACT

Salticids from the Ndumo Game Reserve (KwaZulu-Natal, South Africa) are described. In total 72 species of 38 genera were found, of which one genus Aenigma gen. n. and 14 species are described as new: Aenigma incognita sp. n., Btianor eximius sp. n., Evarcha mirabilis sp. n., E. striolata sp. n., Habrocestum africanum sp. n., Icius nigricaudus sp. n., Massagris natalensis sp. n., Phlegra arborea sp. n., Ph. certa sp. n., Pignus pongola sp. n., Pseudicius venustulus sp. n., Rhene pinguis sp. n., Thyenula fidelis sp. n., and Th. magna sp. n. Three specific names are synonymised: Cybra armata Wesolowska, 2006 with C. lineata Wanless, 1984; Pellenes pulcher Wesolowska, 1999 (junior homonym of P. pulcher Logunov, 1995) with P. tharinae Wesolowska, 2006; and Thyene strandi Caporiacco, 1939 with Th. natalii Peckham & Peckham, 1903. A new combination, Evarcha annae (ex Habrocestum annae Peckham & Peckham, 1903) is proposed. Twenty species are recorded from South Africa for the first time: Asemonea stella Wanless, 1980; Cybra boveyi Lessert, 1933; Evarcha elegans Wesolowska & Russell-Smith, 2000; E. ignea Wesolowska & Cumming, 2008; E. prosimilis Wesolowska & Cumming, 2008; Goleba puella (Simon, 1885); Heliophanus fascinatus Wesolowska, 1986; H. pauper Wesolowska, 1986; Hispo georgius (Peckham & Peckham, 1892); Menemerus minshullae Wesolowska, 1999; Modunda staintoni (O.P.-Cambridge, 1872); Myrmarachne laulengana Roewer, 1965; Nigorella plebeja (L. Koch, 1875); Pellenes epularis (O.P.-Cambridge, 1872); P. bulawayensis Wesolowska, 1999; P. tharinae Wesolowska, 2006; Pseudicius alter Wesolowska, 1999; Schenkelia modesta Lessert, 1927; Thyene bucculenta (Gerstaecker, 1873); and Th. semiargentea (Simon, 1884). The rich diversity of Salticidae collected in this study, and the proportion of new species relative to the total jumping spider fauna (19 %), highlight the need to maintain conservation efforts within Maputaland protected areas with management plans that also take invertebrate taxa into consideration.

KEY WORDS: Araneae, Salticidae, jumping spiders, taxonomy, new taxa, synonymy, new combination, new records, South Africa, protected areas.

INTRODUCTION

The Ndumo Game Reserve (NGR) is situated in the northern part of the KwaZulu-Natal Province, South Africa, and falls within the Maputaland bioregion (Fig. 1). The reserve lies close to the borders of South Africa, Swaziland and Mozambique. It is one of South Africa’s reserves formally protecting wetland and riparian ecosystems and is recognised as a RAMSAR site (Ramsar 2008). The reserve covers 10,117 ha and is structurally highly diverse, with a range of habitats including floodplain vegetation, subtropical bush, various types of savannah and woodland, and riparian forest with tall trees. The climate is subtropical.

The invertebrates of NGR are poorly known (Haddad 2003), but introductory studies of arachnids showed a very high diversity of spiders (over 430 species), representing the highest known diversity of the group from any reserve in South Africa; salticids were the most diverse family, with 82 species initially recorded (Haddad et al. 2006). The objective of this paper is to provide a full account of all jumping spiders found in the reserve, to re-evaluate the taxonomy of the Salticidae listed in the initial checklist (Haddad et al. 2006), and to provide notes on their biology and occurrence in different...
habitats. Following this more detailed study on the taxonomy of the family, the synonyms proposed here, and the identification of previously unidentified morphospecies listed in the initial checklist, the number of salticid species from the reserve is reduced from 82 to 72. Given the close proximity of NGR to several other reserves in Maputaland where surveys are currently under way, and the high levels of endemism of other taxonomic groups in Maputaland (e.g. plants), this paper will provide valuable baseline data for the identification of Salticidae in this region and elsewhere in South Africa, and for future evaluations of salticid endemism in Maputaland.

MATERIAL AND METHODS

Field observations were conducted during several trips in the period 2000–2007. Spiders were collected by different methods: using pitfall traps, sifting leaf litter, turning rocks and logs, from tree bark, beating sheets, sweep-nets, by hand, and at light traps. All material of jumping spiders collected in a survey of fever tree bark (Haddad unpubl.) from five sites in the reserve (Banzi, Hotwe, Nyamiti and Shokwe Pans, and the Pongola River floodplain) was also included in this study. Unless otherwise stated, the specimens were all collected by the second author from Ndumo Game Reserve, South Africa. All material collected in the field was preserved in 70 % ethanol.

Eight broad habitat types can be recognised in NGR, and details of the vegetation are given in De Moor et al. (1977) and Haddad et al. (2006): *Acacia tortilis* (umbrella thorn Acacia) savannah (AS, Fig. 2), *Acacia xanthophloea* (fever tree) forest (AX, Fig. 3), deciduous broadleaf woodland (BW, Fig. 4), *Ficus sycomorus* (wild fig) forest (FF, Fig. 5), floodplain vegetation along the Pongola and Usutu rivers (FP, Fig. 6), riparian forest (RF, Fig. 7), sand forest (SF, Fig. 8), and subtropical bush (ST, Fig. 9), including *Acacia nigrescens* (knob thorn) woodland and Mahemane thicket. The abbreviations provided with each habitat type are used below, in descriptions of the habitat and biology of the salticid species.
Figs 2, 3. Habitats of the Ndumo Game Reserve, northern KwaZulu-Natal, South Africa: (2) *Acacia tortilis* savannah (AS); (3) *Acacia xanthophloea* forest, Hotwe Pan (AX).
Figs 4, 5. Habitats of the Ndumo Game Reserve, northern KwaZulu-Natal, South Africa: (4) Deciduous broadleaf woodland (BW) (photo courtesy Catharina Hanekom); (5) *Ficus sycomorus* forest, Shokwe Pan (FF).
Figs 6, 7. Habitats of the Ndumo Game Reserve, northern KwaZulu-Natal, South Africa: (6) Floodplain vegetation near Usutu River (FP); (7) Riverine forest, Pongola River (RF).
Figs 8, 9. Habitats of the Ndumo Game Reserve, northern KwaZulu-Natal, South Africa: (8) Sand forest (SF); (9) Subtropical bush, Mahemane thicket (ST).
Individuals were examined in 70% ethanol in a Petri dish. The genitalia were removed for study, and after examination were placed in microvials and stored with specimens in the same collection vials. The epigynes were macerated in 5% hot KOH for a few minutes, cleared in clove oil and examined under a compound microscope. In some cases (Myrmarachne spp., Thyene spp.) the epigynes were stained in Chlorazol black E alcohol solution. Drawings were made on a Citoval stereomicroscope with the aid of a reticular eyepiece. Digital photographs of the habitus of specimens were taken using a Nikon Coolpix 4500 attached to a Nikon stereomicroscope. Terminology is standard for spiders, and all measurements are given in millimetres.

The holotypes of the newly described species are deposited in the National Collection of Arachnida, ARC–Plant Protection Research Institute Pretoria, South Africa (NCA), and paratypes and other material are deposited in the NCA, National Museum, Bloemfontein, South Africa (NMBA), Natal Museum, Pietermaritzburg, South Africa (NMSA), and in the Royal Museum for Central Africa, Tervuren, Belgium (MRAC).

**TAXONOMY**

**Genus Aenigma** gen. n.

Etymology: From Latin *aenigma* (riddle), referring to the uncertain taxonomic position of the genus. Gender feminine.

Type species: *Aenigma incognita* sp. n.

Diagnosis: The habitus is typical for the majority of salticids (Fig. 210), with oval, medium high carapace and ovoid abdomen. Chelicera is long, promargin with two teeth, retromargin with single tooth. Legs medium long, with numerous spines.

Distinguished from other salticid genera by the unique form of the epigyne, by long and thin seminal ducts and, especially, by the shape of the receptacles, which are spherical with very long tail-like terminal parts.

Remark: Relationships of this genus will remain unresolved until the male of the type species is discovered.

Figs 10, 11. *Aenigma incognita* sp. n., holotype: (10) epigyne; (11) internal structure of epigyne.
Aenigma incognita sp. n.

Figs 10, 11, 210

Etymology: From Latin incognita (unknown).

Diagnosis: The female of this species is characterised by the structure of the epigyne, long and narrow seminal ducts, and receptacles with an elongated, narrow characteristic tail forming the final part. Male unknown.

Description:
Female.

Measurements: Carapace length 3.1, width 2.3, height 1.2. Abdomen length 3.3, width 2.4. Eye field length 1.6, anterior width 2.1, posterior width 2.2.

General appearance as in Fig. 210. Carapace ovoid, medium high, brown with slightly darker eye field and black rings surrounding eyes; traces of dark streaks radiating from fovea; some colourless bristles near eyes, sparse whitish hairs on slopes of carapace; small white scales frame anterior eyes ventrally, three parallel white lines below anterior lateral eyes, one of them across clypeus. Chelicerae long, unidentate, light brown, with dark patch on external sides; endites and labium brown with paler tips. Sternum yellow. Abdomen ovoid, on yellowish grey background mosaic composed of dense dark grey dots, with traces of paler chevrons medially; fine hairs covering abdomen, longer at anterior edge; sides of abdomen with small dark marks; venter yellowish with wide dark streak; spinnerets pale. Legs yellow with brownish spots; spines numerous; spination of leg I: femur 1-1-5 dorsally; patella pro- and retrolaterally 1; tibia 1-2 prolaterally, 1-1 retrolaterally, 2-2-0-2 ventrally; metatarsus 1-1 prolaterally, 1 retrolaterally, 2-2 ventrally. Palps yellow. Epigyne with two large rounded depressions near epigastric furrow (Fig. 10); internal structure as in Fig. 11, seminal ducts long, weakly sclerotised.


Habitat and biology: The holotype was collected from semi-aquatic vegetation on the banks of the Usutu River.

Genus Afromarengo Benjamin, 2004
Afromarengo coriacea (Simon, 1900)

Marengo coriacea: Simon 1900a: 401; Lawrence 1947: 36, fig. 22; Wanless 1978a: 261, fig. 1a–j, pl. 1a–c; Wesolowska & Russell-Smith 2000: 67, figs 171–174.
Marengo kibonotensis: Lessert 1925a: 439, figs 15–17.
Afromarengo coriacea: Benjamin 2004: 66, figs 4c, 57a–c, 58a–d, 59a–f.

See Wanless (1978a) for description of both sexes.

Material examined: 1♂ Between Main Camp and Vulture Restaurant, 26°54.276'S:32°18.664'E, broadleaf woodland, on bush, 3.xii.2000 (NMSA 21834); 2♀ Southern boundary fence, 26°55.578'S:32°19.081'E, deep sand forest, under tree bark, 11.i.2007 (NCA 2007/3034); 1♂ Western shore of Nyamiti Pan, 26°53.767'S: 32°16.557'E, A. xanthophloea bark, 6.ii.2005 (NCA 2008/598).

Distribution: Known from Congo, Kenya, Tanzania and South Africa.

Habitat and biology: This species was rare and was collected by beating foliage in BW. Adults were collected from beneath bark in AX and SF, close to colonies of Crematogaster ants.
Genus *Asemonea* O. P.-Cambridge, 1869

*Asemonea stella* Wanless, 1980

Figs 12, 13


Redescription:

**Female.**

Measurements: Carapace length 1.4, width 0.9, height 0.7. Abdomen length 2.0, width 1.2. Eye field length 0.5, anterior width 0.8, posterior width 0.6.

General appearance as in Fig. 12; small, light coloured spider. Carapace pear-shaped, eyes typical for Lyssomaninae, in four rows, situated on high tubercles; posterior median eyes relatively large; fovea sulciform; colouration of carapace creamy (light green in living individuals), two parallel black lines on thoracic part, eyes (except anterior median ones) surrounded by black rings. Mouthparts and sternum pale; chelicerae with five very small teeth on promargin and four on retromargin. Abdomen whitish with blackish pattern, characteristic star-shaped patch on centre of dorsum (Fig. 12); venter light; spinnerets white. Legs long and thin, last pair longest (with very long metatarsus), black spots on basis and tips of tibiae of all legs, also on metatarsi I and II; spines numerous, long, pale. Whole body covered with fine pale hairs. Epigyne with small depression posteriorly (Fig. 13).


Distribution: Known from Kenya and Tanzania, also reported from Queensland in Australia. Recorded for the first time in South Africa.

Habitat and biology: This species was collected from broad-leaved woody plants, where its pale green colouration is cryptic.

*Asemonea sp.*

Figs 14, 15

The only specimen represents a new, undescribed species. Unfortunately, the epigyne was lost during preparation. For this reason we refrain from giving a formal scientific name for the species until discovery of new specimens. Male unknown.

Description:

**Female.**

Measurements: Carapace length 1.5, width 1.2, height 0.6. Abdomen length 2.1, width 1.3. Eye field length 0.5, anterior width 0.9, posterior width 0.6.

General appearance in Fig. 14; small, pale spider; shape of body as in other *Asemonea* species (see above). Carapace whitish cream, with two dark dots on thoracic part posteriorly; eyes (except anterior medians) surrounded by black rings. Chelicerae with four small teeth on both margins. Abdomen also whitish, with only a few blackish marks (Fig. 14). Legs white with black patches at basis and tips of tibiae and on retro-
lateral side of tarsi terminally (all legs); probably black tarsal patches are a diagnostic feature for the species (usually tarsi are the lightest segments of legs); first leg with four pairs of spines on tibia ventrally and three pairs on metatarsus. Epigyne oval, very weakly sclerotised, with small depression posteriorly (Fig. 15); seminal ducts long.


Habitat and biology: This species was collected by beating foliage in SF. Apart from the female, several immatures were collected that may be conspecific with this species.

Figs 12–15. Asemonea stella (12, 13) and Asemonea sp. (14, 15): (12, 14) habitus; (13, 15) epigynes.
Genus *Baryphas* Simon, 1902

*Baryphas ahenus* Simon, 1902

*Baryphas ahenus*: Simon 1902a: 42; 1903a: 681, figs 807–809; Peckham & Peckham 1903: 207, pl. 24, fig. 2; Lessert 1925b: 349, fig. 13; Prószyński 1987: 5; Wesolowska & Cumming 2008: 169, figs 2–8.

See Wesolowska & Cumming (2008) for description of both sexes.


Distribution: Species common in southern Africa.

Habitat and biology: This widespread species was commonly collected from foliage along the Pongola and Usutu River floodplains, and in ST, where it was common on low-growing shrubs (e.g. *Croton* sp.). Predominantly immature spiders were sampled, and were thus not preserved.

Genus *Bianor* Peckham & Peckham, 1886

*Bianor eximius* sp. n.

Figs 16–19, 211

Etymology: From Latin *eximius* (exceptional).

Diagnosis: The female of this species has large white patches on the abdomen. It is distinguished from congeners by the very long seminal ducts (the longest of all species in the genus), forming three loops, and the multi-chambered receptacles (two-chambered in other species). Male unknown.

Figs 16–19. *Bianor eximius* sp. n., holotype: (16) abdominal pattern; (17) first leg; (18) epigyne; (19) internal structure of epigyne.
Description:

**Female.**

Measurements: Carapace length 1.2, width 1.2, height 0.6. Abdomen length 1.7, width 1.3. Eye field length 0.6, anterior width 0.9, posterior width 1.2.

General appearance as in Fig. 211; small spider; shape of body typical for the genus. Carapace blackish, anterior part of eye field and thoracic part sparsely covered with white scales; long dark setae near eyes; clypeus low, with white hairs. Mouthparts and sternum dark brown, only inner margins of endites slightly paler. Abdomen ovoid, black, with five large white patches and band along anterior margin composed of light hairs (Fig. 16); abdomen dark ventrally; spinnerets dark. First leg slightly thicker than others (Fig. 17); legs dark yellow, femora tinged with grey. Palps light. Epigyne typical for the genus, with central pocket (Fig. 18); seminal ducts very long, forming a few loops, receptacles multi-chambered (Fig. 19).


Habitat and biology: Collected from leaf litter in partial shade in BW.

**Genus Cyrba** Simon, 1876

**Cyrba boveyi** Lessert, 1933

Figs 20–23, 238

*Cyrba boveyi*: Lessert 1933: 145, fig. 63; Wanless 1984a: 463, figs 11a–f.

See Wanless (1984a) for descriptions of both sexes.

Redescription:

**Male.**

Measurements: Carapace length 2.3–2.4, width 1.4–1.5, height 0.8. Abdomen length 2.5–2.6, width 1.1–1.3. Eye field length 0.9–1.0, anterior width 1.3–1.5, posterior width 1.2–1.4.

General appearance in Fig. 238; medium-sized spider; whole body densely covered with short, bright reddish orange hairs. Carapace slightly elongate, moderately high in cephalic part and sloping gently posteriorly; eye field trapeziform, slightly wider anteriorly; some brown bristles in vicinity of eyes; fovea prominent; clypeus low, clothed in white hairs. Chelicerae light brown, pluridentate, promargin with three, retromargin with four teeth; endites orange with lighter inner margins, labium and sternum yellowish orange. Abdomen elongate, dorsum bright orange with scattered brown bristles, venter yellowish; spinnerets grey. Legs yellowish orange, only first pair with black tibiae and metatarsi; pedipalps with black cymbium. Palpal patella with blunt apophysis (Figs 20–23); tibial apophysis with recurved row of long black scales; tegulum rounded, rather flat, with furrow near base of embolus and long process at prolateral edge (Figs 20, 21).

Material examined: 3♂ Between Crocodile Farm and Main Camp, 26°54.431'S:32°19.045'E, broadleaf woodland, under logs, 1.xii.2000 (NCA 2008/2025); 4♂ Between Main Camp and Vulture Restaurant, 26°54.276'S:32°18.664'E, broadleaf woodland, under logs, 2.xii.2000 (NCA 2009/677).

Distribution: Species known from Angola, Kenya and Mozambique; recorded for the first time from South Africa.
Figs 20–23. *Cyrba boveyi*: (20, 21) palpal organ, ventral views; (22) palpal organ, lateral view; (23) tibial apophysis, dorsal view.
Habitat and biology: *C. boveyi* was a common ground-dwelling salticid in BW and was regularly found in silk retreats beneath logs and rocks, particularly in sunny areas. It was frequently found in the vicinity of colonies of large ants (*Camponotus* and *Streblognatha*), and dense aggregations of spitting spiders (*Scytodes caffra* Purcell, 1904) and violin spiders (*Loxosceles spinulosa* Purcell, 1904). Several immature specimens were collected from *A. xanthophloea* bark low on the tree trunks.

*Cyrba lineata* Wanless, 1984

Figs 24, 25, 239

*Cyrba lineata*: Wanless 1984a: 465, figs 13a–h.
*Cyrba armata*: Wesołowska 2006a: 618, figs 1–5. **Syn. n.**

See Wesołowska (2006a) for description of male, and Wanless (1984a) for description of female; general appearance of male in Fig. 239.

**Redescription:**

**Female.**

Measurements: Carapace length 2.5–2.7, width 1.7–1.8, height 0.9–1.1. Abdomen length 3.0–3.8, width 1.9–2.4. Eye field length 1.0–1.1, anterior width 1.7–1.8, posterior width 1.6–1.7.

Medium-sized spider. Carapace longer than wide, moderately high, with gently sloping posterior part; light brown to dark brown at margins; eye field slightly darker than thoracic area, in one specimen two black spots on eye field centre, eyes surrounded by black rings; short brown hairs on carapace, some long bristles near eyes; anterior eyes fringed by white hairs; fovea long, sulciform; clypeus low with short white hairs. Chelicerae brown, promargin with three, retromargin with four teeth; mouthparts brown, sternum light brown. Abdomen ovoid, blackish, with narrow longitudinal white line and light patch on mytiliform field; in other specimens abdomen grey with three lighter chevrons posteriorly; abdomen covered in short dark hairs; venter dark grey with two yellowish lines; spinnerets grey. Legs light brown, femora tinged with black, first pair of legs with darker tibiae and metatarsi; last pair of legs longest; leg hairs and spines

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![Image 24](https://bioone.org/journals/African-Invertebrates.on 14 Nov 2019)

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![Image 25](https://bioone.org/journals/African-Invertebrates.on 14 Nov 2019)

Figs 24, 25. *Cyrba lineata*: (24) epigyne; (25) internal structure of epigyne.
brown. Epigyne with acute lobes of caudal ledge and two pockets (Fig. 24); internal structure as in Fig. 25, receptacles spherical with very thick walls.


Distribution: Species known only from South Africa.

Habitat and biology: C. lineata was common under logs and rocks in AS and BW, and was collected from underneath logs and in leaf litter in AX, RF and ST. All of the material was collected during winter.

Remarks: The species is distinguishable by the presence of epigynal pouches. C. lineata was hitherto known only from the female. C. armata was recently described from Kosi Bay in KwaZulu-Natal (approximately 60 km east of NGR), on the base of single male, and Wesolowska (2006a) suggested that it may be the missing sex of C. lineata. The similar morphology and occurrence of the two sexes in the same locality (NGR) allows for the synonymisation of their names.

**Cyrba nigrimana** Simon, 1900

Figs 26–28


*Cyrba nigrimana*: Wanless 1984a: 465, figs 12a–g.

See Caporiacco (1947) for description of male.

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Figs 26–28. *Cyrba nigrimana*: (26) cheliceral dentition; (27) epigyne; (28) internal structure of epigyne.
Redescription:

**Female.**

Measurements: Carapace length 2.6, width 1.7, height 0.8. Abdomen length 2.7, width 1.8. Eye field length 1.1, anterior width 1.6, posterior width 1.5.

Medium-sized spider. Carapace elongate, sloping gently posteriorly; eye field short, slightly wider anteriorly; carapace orange-brown, eyes surrounded by black rings; fovea elongate, sulciform, clearly visible; clypeus low, clothed in long white hairs. Chelicerae brown, three teeth on promargin and four small teeth on retromargin (Fig. 26). Abdomen elongate oval, narrower than carapace, dark grey, covered with dense, short, greyish hairs; venter grey; spinnerets grey. Legs moderately long and slender, last pair longest; legs light brown, only tibiae and metatarsi of first pair black; hairs covering legs long, brown; one pair of ventral spines on metatarsus I, three pairs on tibia. Pedipalps blackish. Epigyne with notch in posterior edge and posterior depression in shape of inverted heart (Fig. 27); receptacles elongated (Fig. 28).


Distribution: Species described from South Africa (Pretoria, Gauteng Province and Makapan, Limpopo Province). Also reported by Caporiacco (1947) from Eastern Africa, but this record is doubtful.

Habitat and biology: Collected from leaf litter in BW and under logs in ST.

Remark: This species has elongate receptacles, whereas those of the other members of the genus are spherical.

**Genus Evarcha** Simon, 1902

*Evarcha annae* (Peckham & Peckham, 1903), **comb. n.**

Figs 29–31

**Habrocestum annae**: Peckham & Peckham 1903: 238, pl. 27, fig. 4; Prószynski 1987: 39.

Redescription:

**Female.**

Measurements: Carapace length 3.5, width 2.7, height 1.4. Abdomen length 4.2, width 2.9. Eye field length 1.6, anterior width 2.4, posterior width 2.5.

Carapace brownish orange, eye field dark brown, eyes with black rings; anterior part of eye field sparsely covered with white hairs, some surrounding anterior eyes; on thoracic area light hairs longer, but not numerous. Chelicerae unidentate; labium and endites orange, sternum lighter. Abdomen oval, yellowish, with series of chevrons formed by small grey spots (Fig. 29); sides and venter pale; sparse brown bristles on dorsum, longer at anterior edge of abdomen; spinnerets pale. Legs dark yellow, bearing brown hairs and spines. Epigyne small, rounded, with two shallow depressions (Fig. 30); internal structure as in Fig. 31; seminal ducts short, receptacles spherical.

**Male.** Unknown.


Distribution: Previously known only from the type locality, Durban in South Africa.
Habitat and biology: Known only from a single female collected from leaf litter in ST. Remarks: The body proportions and the presence of a wide epigynal pocket suggest that this species should be placed in the genus *Evarcha*, but establishment of closer relationships with other congeners will be possible only after finding the male of this species.

*Evarcha dotata* (Peckham & Peckham, 1903)

*Habrocestum dotatum*: Peckham & Peckham 1903: 239, pl. 27, fig. 6.
*Hyllus ventrilineatus*: Strand 1906: 665.
*Hyllus dotatus*: Logunov 2004: 87, figs 1, 2.

See Wesolowska & van Harten (1994, 2007) for descriptions of both sexes.

Distribution: Species widely distributed in the Afrotropical Region; known also from Yemen.

Habitat and biology: This widespread species was common on low-growing foliage of herbaceous plants and in sweep netting samples, and was also occasionally observed at the base of grass tussocks and in leaf litter, in AS, BW and ST.

_Evarcha elegans_ Wesołowska & Russell-Smith, 2000

Figs 32, 33

_Evarcha elegans_: Wesołowska & Russell-Smith 2000: 26, figs 37–44; Wesołowska & Tomasiewicz 2008: 14, figs 52, 53.

See Wesołowska & Russell-Smith (2000) for description of both sexes.

Redescription:

**Female.**

Measurements: Carapace length 2.5, width 1.9, height 1.0. Abdomen length 2.7, width 1.6. Eye field length 1.2, anterior width 1.6, posterior width 1.7.

Carapace orange, ocular area slightly lighter, eyes with black rings; near eyes some light setae. Abdomen grey, posteriorly slightly darker, with yellowish median serrate band; sides whitish yellow, venter light with two lines formed by dark marks; spinnerets pale, their tips darker. Legs yellowish orange, spines light. Epigyne oval, with two broadly spaced openings (Fig. 32); seminal ducts very poorly sclerotised, wide, forming loop (Fig. 33).


Distribution: Previously known only from the type locality, Mkomazi Game Reserve in Tanzania. Recorded from South Africa for the first time.

Habitat and biology: Collected from the foliage of shrubs in ST.

_Evarcha ignea_ Wesołowska & Cumming, 2008

Figs 34–37, 212

_Evarcha ignea_: Wesołowska & Cumming 2008: 175, figs 22, 23.

Redescription:

**Male.**

Measurements: Carapace length 1.9–2.3, width 1.5–1.8, height 0.8–1.0. Abdomen length 1.6–2.2, width 1.1–1.4. Eye field length 0.9–1.0, anterior width 1.4–1.5, posterior width 1.5–1.6.

General appearance as in Fig. 34. Carapace dark brown, with thin black line along margins, vicinity of eyes black; brown setae form median streak on thorax and band...
Figs 34–41. *Evarcha ignea* (34–37) and *Evarcha mirabilis* sp. n., holotype (38–41): (34) habitus of male; (35, 39) palpal organs, ventral views; (36, 40) palpal organs, lateral views; (37) tibial apophysis, lateral view; (38) abdominal pattern; (41) tibial apophysis, dorsal view.
along edge of flat part of thorax; long brown bristles near eyes, white hairs scattered on thoracic plain, forming large patch on eye field posteriorly; anterior eyes surrounded by orange scales; clypeus high, clothed in bright reddish scarlet scale-like hairs (Fig. 212), reaching to sides of carapace. Chelicerae unidentate; labium and endites brown, sternum yellow tinged with grey. Abdomen russet brown with yellowish pattern (Fig. 34), light posterior chevrons joined to large patch in some specimens; in one specimen delicate small orange scutum anteriorly on dorsum; sparse long dark setae cover abdomen, denser and longer at anterior edge; venter grey, in one specimen yellow with three streaks composed of dark dots; spinnerets yellowish grey. Legs brown with lighter rings on patellae and tibiae basally, and yellowish metatarsi and tarsi; leg hairs and spines brown. Pedipalps brown; tibial apophysis straight and wide, with small notch in tip (Figs 36, 37); tegulum with posterior lobe, embolus nestling to tegulum (Fig. 35).

Female. Unknown.


Distribution: Species described from Zimbabwe, recorded for the first time from South Africa.

Habitat and biology: This species was collected from the bases of grasses and from leaf litter in BW and ST. Two males were captured beneath bark in SF.

_Evarcha mirabilis_ sp. n.

Figs 38–41

Etymology: From Latin _mirabilis_ (admirable).

Diagnosis: The male of the species is closely related to _Evarcha maculata_ Rollard & Wesołowska, 2002 from the Nimba Mountains, but has a distinctly wider tibial apophysis with an additional tooth (compare Fig. 40 herein with fig. 6B in Rollard & Wesołowska 2002). Female unknown.

Description.

_Male._

Measurements: Carapace length 1.9, width 1.4, height 0.8. Abdomen length 1.7, width 1.1. Eye field length 0.9, anterior width 1.3, posterior width 1.4.

Carapace rather high, dark brown, with two lighter semicircular areas on thoracic region (behind last row of eyes); anterior eyes surrounded with fawn scales; long brown bristles near eyes, white scale-like hairs scattered on eye field and on thoracic plain, denser behind anterior eyes; clypeus low, dark brown. Chelicerae unidentate; labium and endites brown, sternum orange. Abdomen russet brown with yellowish pattern, only transverse band at anterior margin white (Fig. 38); long dark setae at anterior edge of abdomen; venter dark yellow; spinnerets grey. Colouration of legs contrasted; coxae, trochanters and basal halves of femora yellow, distal parts of femora, patellae and tibiae almost black, metatarsi and tarsi yellow. Pedipalps contrasted; femur black, remaining segments yellow; tibial apophysis very broad at base, pointed at tip, with two dorsal teeth (Figs 40, 41). Tegulum rounded, with posterior lobe, embolus short (Fig. 39).

_Evarcha mustela_ (Simon, 1902)

_Viciria mustela:_ Simon 1902a: 48; 1903a: 743, figs 885, 886; Lessert 1936: 297, figs 94, 95.

_Viciria morigera:_ Peckham & Peckham 1903: 232, pl. 26, fig. 6.

_Viciria parmata:_ Peckham & Peckham 1903: 234, pl. 26, fig. 5.


See Wesolowska & Cumming (2008) for description of both sexes.

Material examined: 1 ♀ Between Crocodile Farm and Main Camp, 26°54.431'S:32°19.045'E, broadleaf woodland, beats, short shrubs, 10.xii.2000 (NMSA 21841); 1 ♀ Crocodile Farm, 26°54.426'S:32°19.185'E, broadleaf woodland, beats, short bushes, 10.xii.2000 (NMBA 11603); 2♂ same locality, beats, short shrubs, 8.xii.2002 (NCA 2009/679); 2♂ 1 ♀ 26°52.464'S:32°16.050'E, subtropical bush, _A. nigrescens_ woodland beats, foliage, 8.xii.2000 (NCA 2008/2034).

Distribution: Known from western and southern Africa.

Habitat and biology: The species was occasionally collected by beating foliage of shrubs in BW and ST. This species was only collected in summer.

_Evarcha prosimilis_ Wesolowska & Cumming, 2008

Figs 42–46


Redescription:

Measurements (male/female): Carapace length 2.3–2.4/2.3, width 1.9/2.0, height 0.9/0.9. Abdomen length 2.0–2.1/2.9, width 1.3–1.4/2.2. Eye field length 1.0–1.2/1.0, anterior width 1.6/1.5, posterior width 1.7/1.6.

_Male._

Carapace oval, brown, vicinity of eyes black; sparse white hairs on eye field, forming small patch behind anterior median eyes; longitudinal streak composed of brown hairs on thoracic area; glaring orange scales encircling anterior eyes, except scales surrounding anterior laterals from above, which are white; clypeus high, covered with orange reddish hairs. Mouthparts dark brown, sternum orange-brown. Abdomen light brown with white yellowish pattern; two transverse bands in anterior half, large leaf-shaped patch, and pair of submarginal spots in posterior half. Abdomen covered with brown and whitish hairs; venter yellow, with three longitudinal lines of small dark marks, in second specimen whole venter dark; spinnerets greyish. Legs yellow with brown rings, tarsi light, first and second pairs slightly darker than posterior pairs; leg hairs and spines brown. Pedipalps dark brown, white hairs forming spots on tips of palpal femur and patella dorsally; tibial apophysis with notch (Figs 43, 44), embolus double (Fig. 42).

_Female._

Carapace light brown, traces of striae on thoracic part, black rings around eyes; clypeus low, brownish, with thin white line on lower clypeal margin; two parallel white lines on lateral slopes of carapace, below anterior lateral eyes; anterior eyes surrounded by small fawn scales, some long brown bristles on eye field anteriorly. Mouthparts brownish with light tips, sternum yellowish. Abdomen darker than in male, mottled, pattern com-
posed of small greyish brown patches on yellowish background, posteriorly a few darker chevrons; brownish and grey hairs cover abdomen; venter light with brownish marks; spinnerets greyish beige. Legs yellow with brownish rings proximally and distally on segments; spines and leg hairs brown. Epigyne as in Fig. 45, receptacles multi-chambered (Fig. 46), only initial chambers strongly sclerotised.


Distribution: Species known from northern Tanzania and Zimbabwe; recorded for the first time in South Africa.

Habitat and biology: Collected from leaf litter and the bases of grass tussocks in AS, BW and ST, and from pitfall traps in FP.

Figs 42–46. *Evarcha prosimilis*: (42) palpal organ, ventral view; (43) palpal organ, lateral view; (44) tibial apophysis, dorsal view; (45) epigyne; (46) internal structure of epigyne, dorsal view.
Remarks: This species resembles *E. culicivora* Wesołowska & Jackson, 2003 from Kenya, but the male has a shorter embolus (compare Fig. 42 herein with fig. 6 in Wesołowska & Jackson 2003); the females are very similar and telling them apart is problematic. It is also similar to *E. picta* Wesołowska & van Harten, 2007 from Yemen, but the male of the latter species has a wider tibial apophysis, and the female has an epigyne with a strongly sclerotised posterior rim (see figs 38, 41 in Wesołowska & van Harten 2007).

‘*Evarcha*’ *striolata* sp. n.

Figs 47–49, 213, 214

Etymology: From Latin *striolata* (striped); the name refers to the abdominal pattern.

Diagnosis: The structure of the palpal organ is similar to that of *E. infrastriata* (Keyserling, 1881) from Australia. *E. striolata* is easily distinguished from its congeners by the characteristic striped abdominal pattern. Female unknown.

Description.

*Male.*

Measurements: Carapace length 2.1, width 1.6, height 0.8. Abdomen length 2.0, width 1.1. Eye field length 0.9, anterior width 1.4, posterior width 1.5.

General appearance in Figs 47, 213, 214. Carapace high, sloping abruptly posteriorly; dark orange with black rings surrounding eyes; surface almost bald, only a few colourless delicate bristles near anterior eyes; clypeus low, with few delicate hairs. Mouthparts and sternum dark yellow. Abdomen narrower than carapace, slightly elongate, narrowing posteriorly, striped (Fig. 47); two brown streaks separated by three yellowish ones on dorsum, dark streaks on sides; these brown stripes are formed by dense dark hairs; venter light yellow with two thin dark lines joined by transverse line in front of base of spinnerets; spinnerets pale. Legs yellowish, covered with short brown hairs, spines numerous; legs of pair III longest. Pedipalp (only right pedipalp present) pale; tegulum rounded, embolus encircling tegulum; tibial apophysis long, straight, thin (Figs 48, 49).


Habitat and biology: The holotype was collected from the base of grasses under a fever tree in AX.

Remarks: The species slightly differs from other *Evarcha* by the body shape. Its taxonomic position is tentative. Only discovery of the female and examination of its genitalia will enable confirmation of this placement.

Genus *Festucula* Simon, 1901

*Festucula lawrencei* Lessert, 1933

Figs 50–52


See Wesołowska & Russell-Smith (2000) for description of both sexes.
Redescription:

**Female.**

Measurements: Carapace length 2.2, width 1.2, height 0.5. Abdomen length 5.5, width 1.4. Eye field length 0.9, anterior width 1.0, posterior width 1.1.

General appearance in Fig. 50; very long and slender spider. Carapace slightly elongate, not broadening along its whole length, very flattened, eye field short; dorsum of carapace dark brown, with light brown band medially on thoracic part; along sides dark yellow streak, but margins framed by dark line; clypeus very low, clothed in white hairs; delicate, short whitish hairs sparsely cover carapace. Chelicerae, labium and sternum dark brown, maxillae brown with light inner margins. Abdomen very long and thin, striped, with two marginal brownish grey streaks and broad median whitish streak; sides of abdomen

Figs 47–49. *Evarcha striolata* sp. n., holotype: (47) habitus, lateral view; (48) palpal organ, ventral view; (49) palpal organ, lateral view.
whitish, three dark stripes on venter; spinnerets dark. Legs relatively short, the third pair shortest; first legs slightly thicker than others, with slightly swollen tibia, armed with three prolateral ventral spines, and two pairs of spines on metatarsus ventrally; leg I brown, remaining legs whitish yellow. Stridulatory apparatus consists of row of setae located on carapace sides, below lateral eyes, and a few bristles on prolateral surface of femora of first legs. Epigyne with shallow depression, partially plugged with waxy secretion (Fig. 51); internal structure in Fig. 52, receptacles elongate.


Distribution: Species known from Angola and Tanzania; recorded for the first time from South Africa.

Habitat and biology: The female and a large number of immatures were collected by sweeping long grasses in BW. This species is clearly a grass-dwelling specialist, demonstrated by its elongate body form and colour, which is cryptic on grass stalks.
Genus *Goleba* Wanless, 1980

*Goleba puella* (Simon, 1885)

Figs 53–61

*Asamonea puella*: Simon 1885: 27; Roewer 1965: 4, figs 5a–c.

*Asemonea puella*: Clark 1974: 12, figs 2, 3.

*Goleba puella*: Wanless 1980: 246, figs 22a–e, 23a–c, 29.

Redescription:

Measurements (male/female): Carapace length 2.5/2.5, width 1.9/1.9, height 0.8/0.7. Abdomen length 3.2/4.5, width 1.3/2.2. Eye field length 0.8/0.8, anterior width 1.3/1.2, posterior width 0.9/1.0.

**Male.**

General appearance as in Fig. 53. Carapace pear-shaped, yellowish (probably green in live specimens), with black rings surrounding eyes (except anterior medians), and traces of parallel brownish stripes on the thoracic part; eyes placed in four rows, posterior median eyes relatively large (as in other Lyssomaninae spiders), all eyes on high tubercles; fovea sulciform; clypeus medium high, with band composed of reddish hairs (Fig. 54), band extending to lateral margins of carapace. Mouthparts and sternum yellow. Chelicerae pluridentate, four teeth on promargin and five on retromargin, dorsal surface of chelicerae with transverse brown band (Fig. 54). Abdomen narrower than carapace, elongate, yellow, with poorly defined pattern formed by reddish hairs; venter pale; spinnerets yellow. Legs slender, long, especially long metatarsi; legs yellowish, only femora with brown stripes on prolateral surfaces; spines numerous, robust, long. Pedipalps pale; palpal femur with big ventral tubercle (Fig. 59); cymbium narrow terminally (Fig. 58); tibia with ventral and retrolateral apophyses, the latter one hooked (Figs 57, 58); tegulum irregular, with median tegular apophysis and two small lobes (Fig. 56); spermophore meandering, embolus stout (Figs 55, 56).

**Female.**

Slightly larger than male, abdomen not as slender; whole body yellowish white, only eye rings blackish. Epigyne rounded, shown in Fig. 60; internal structure as in Fig. 61; accessory glands very long, tubule-like.


Distribution: Species hitherto known from Angola, Congo, Ghana and Kenya; recorded for the first time from South Africa.

Habitat and biology: This pale green species was occasionally collected from foliage of woody plants in BW, RF and ST.

Genus *Habrocestum* Simon, 1876

*Habrocestum africanum* sp. n.

Figs 62–67

Etymology: The specific name refers to Africa.
Diagnosis: The male of the species is closely related to *H. formosum* Wesołowska, 1999 from Zimbabwe, but has a wider tibial apophysis, longer tegulum and smaller embolus (compare Figs 64, 65 herein with figs 13–15 in Wesołowska 1999a). The female resembles *H. tanzanicum* Wesołowska & Russell-Smith, 2000 from Tanzania, but can be recognised by the smaller copulatory openings and more elongate spermathecae (more compact in *H. tanzanicum*, compare Figs 66, 67 herein with figs 56, 57 in Wesołowska & Russell-Smith 2000).
Description.

Measurements (male/female): Carapace length 1.9/2.1–2.2, width 1.4/1.7–1.8, height 0.9/1.0. Abdomen length 1.4/2.5, width 1.1/1.7–2.1. Eye field length 1.1/1.1, anterior width 1.4/1.4–1.5, posterior width 1.3/1.3.

Male.

General appearance as in Fig. 62; small spider. Carapace high with very steep posterior slope (Fig. 63); eye field short, distance between anterior lateral eyes slightly larger than between posterior lateral ones; carapace dark brown, vicinity of eyes black; short greyish hairs cover thoracic part, denser on carapace slopes, orange hairs on eye field, numerous brown bristles near eyes; anterior eyes surrounded by short hairs, orange above eyes and whitish below; clypeus light brown. Chelicerae fissidentate; mouthparts brown, sternum dark yellow. Abdomen small, narrower than carapace, dark yellow with brown pattern (Fig. 62); venter yellow, tinged grey; brown hairs on abdomen. Legs dark yellow with brown spots, first pair slightly darker; legs III longest (especially
long femora); spines numerous, long, brown; leg hairs brown. Pedipalps brown, along prolateral sides of femur, patella and part of cymbium dense white hairs; palpal organ shown in Figs 64, 65; tibial apophysis straight, embolus short.

**Female.**

Resembles male. Endites with pale inner margins. Pedipalps yellow. Epigyne rounded with deep pocket at epigastric furrow (Fig. 66); internal structures strongly sclerotised, shown in Fig. 67.


**Habitat and biology:** Specimens were collected from the soil surface and from leaf litter in thorny thickets in ST. Occasionally collected from the foliage of low shrubs and from fever tree bark in AX.

**Genus Harmochirus** Simon, 1885

**Harmochirus luculentus** Simon, 1886


*Harmochirus albibarbis*: Peckham & Peckham 1895: 171, pl. 16, fig. 3; Wesołowska 1994: 198, figs 1–3.

*Valloa elegans*: Peckham & Peckham 1903: 218, pl. 24, fig. 10.


See Logunov (2001) for description of both sexes.

**Material examined:** 1 ♂ Crocodile Farm, Pongola R. floodplain, 26°54.426'S:32°19.185'E, under tree bark, 12.1.2007 (NCA 2007/3075); 1 ♀ Near NRC picnic site, 26°52.742'S:32°11.088'E, A. tortilis savannah, sweeps, grass, 29.xi.2000 (NCA 2008/2039).

**Distribution:** Species widespread in the Afrotropical Region.

**Habitat and biology:** This rare species was collected from tall grasses in AS. One male was collected from under tree bark along the Pongola River floodplain.

**Genus Heliophanus** C. L. Koch, 1833

**Heliophanus claviger** Simon, 1901

Figs 68–72

*Heliophanus claviger*: Simon 1901a: 56, fig. 9; Wesołowska 1986: 15, figs 54–63.

See Wesołowska (1986) for description of both sexes.

**Redescription:**

**Male.**

Measurements: Carapace length 2.3, width 1.8, height 0.8. Abdomen length 2.4, width 1.7. Eye field length 0.8, anterior width 1.3, posterior width 1.5.

General appearance in Fig. 68. Carapace dark brown, eye field black with metallic lustre, reticulate-punctured; white hairs form patch between anterior median eyes and...
two light streaks extending from anterior lateral eyes to thoracic part of carapace (Fig. 68); endites and labium brown with light tips, chelicerae and sternum dark brown. Abdomen oval, dark brown, with white band along anterior abdominal edge, extending to sides, and two pairs of rounded spots, one of them at midpoint and second at spinnerets (Fig. 68); venter pale yellow; spinnerets dark. Legs yellow with brown rings; pedipalps brown, with white scales on tibia dorsally and on cymbium; tegulum triangular, embolus short (Fig. 69); two tibial apophyses (Figs 69–71); palpal femur with small process ventrally (Fig. 72).


Distribution: Known only from South Africa.

Habitat and biology: This rare and distinctive species was collected from foliage of short shrubs in BW. Several immature specimens were collected from A. xanthophloea bark around Hotwe, Nyamiti and Shokwe Pans, and along the Pongola River floodplain.