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Author(s): Omar M. Amin , Richard A. Heckmann , Ali Halajian , Atif el-Naggar and Sareh Tavakol Source: Comparative Parasitology, 81(1):33-43. 2014. Published By: The Helminthological Society of Washington DOI: <u>http://dx.doi.org/10.1654/4664.1</u> URL: <u>http://www.bioone.org/doi/full/10.1654/4664.1</u>

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Description of *Moniliformis kalahariensis* (Acanthocephala: Moniliformidae) from the South African Hedgehog, *Atelerix frontalis* (Erinaceidae) in South Africa

Omar M. Amin, 1,6 Richard A. Heckmann, 2 Ali Halajian, 3 Atif el-Naggar, 2,4 and Sareh Tavakol 3,5

¹Institute of Parasitic Diseases, 11445 E. Via Linda, # 2-419, Scottsdale, Arizona 85259, U.S.A. (e-mail: omaramin@aol.com),

² Department of Biology, 401 WIDB, Brigham Young University, Provo, Utah 84602, U.S.A.

(e-mail: richard_heckmann@byu.edu),

³ Department of Biodiversity (Zoology), University of Limpopo, Turfloop Campus, Private Bag X1106, Sovenga, 0727 Polokwane, South Africa (e-mail: ali_hal572002@yahoo.com),

⁴ College of Women for Arts, Science and Education, Ain Shams University, Cairo Egypt (e-mail: amonagar@yahoo.com), and

⁵ Department of Fisheries, Islamic Azad University, Tonekabon Branch, Tonekabon, Iran

ABSTRACT: Moniliformis kalahariensis Meyer, 1931 (Moniliformida Schmidt, 1972: Moniliformidae Van Cleave, 1924) is redescribed from long, unsegmented juveniles and pseudosegmented mature adults collected from the South African hedgehog Atelerix frontalis Smith, 1831 (Erinaceidae) in South Africa. The species has not been taxonomically treated since Meyer's original description of only segmented adults from the same host, A. frontalis, as well as from the unusual host, the Namaqua sandgrouse, Pterocles namaqua (Gmelin, 1789) (Pteroclididae), in Botswana and from cystacanths from Blattella (Phyllodromia) germanica Linnaeus, 1767 (Blattidae Karny, 1908) in Bombay, India. Despite the generous space Meyer devoted to the description of mature adults of M. kalahariensis in 1931, and his shorter description in 1932, both accounts lacked considerable important information. We examined some of Meyer's original adults and cystacanths from Berlin's Museum für Naturkunde by optical microscopy and by scanning electron microscopy (SEM). Meyer did not measure or illustrate the proboscis hooks but reported 14 hook rows with 9-10 hooks each in his adult and cystacanth specimens. The proboscis of our juvenile and adult specimens from South Africa had 16 hook rows each with 9-11 hooks. One adult from Meyer's specimens that we examined using SEM had at least 16 proboscis hook rows, and one of his cystacanths had 14 hook rows each with 10-12 hooks. Our report provides new illustrations and morphometric data of the long juvenile and mature adults and gives the full range of measurements of proboscis armature. We further describe, for the first time, the 2 apical pores on the proboscis in all stages; the proboscis hooks and their lateral slits and the spiniform hooks in adult worms; hook roots; the reproductive system in both males and females (only the size and placement of testes were reported and an egg was illustrated by Meyer in 1931 and 1932); sensory pores; and the sensory plates near the posterior end of adult males. Lastly, we also describe the large unsegmented juveniles to which Meyer made no reference.

KEY WORDS: *Moniliformis kalahariensis*, Acanthocephala, cystacanth, juveniles, adults, hedgehog, South Africa, description, SEM.

Moniliformis kalahariensis Meyer, 1931 (Moniliformida Schmidt, 1972: Moniliformidae Van Cleave, 1924) has not been treated taxonomically since Meyer's 1931 original description of pseudosegmented adults from the South African hedgehog, Atelerix frontalis Smith, 1831 (Erinaceidae) and from the unusual host, the Namaqua sandgrouse Pterocles namaqua (Gmelin, 1789) (Pteroclididae) in Botswana as well as of cystacanths from the German cockroach Blattella (Phyllodromia) germanica Linnaeus, 1767 (Blattidae Karny, 1908) in Bombay, India. Despite the generous space Meyer (1931) devoted to the

description of mature adults of *M. kalahariensis* and his shorter description of the same species the following year (Meyer, 1932), both accounts lacked considerable important information. Other descriptions of this species, e.g., Petrochenko (1958), were repetitions of the original description using Meyer's (1931, 1932) own line drawings. We collected many long, unsegmented juveniles (not described by Meyer) and pseudosegmented mature adults from *A. frontalis* in South Africa and studied them by optical microscopy and by scanning electron microscopy (SEM). We also examined some of Meyer's original adults and cystacanths from Berlin's Museum für Naturkunde (Hartwich et al., 1998) using both light microscopy and SEM. In the present work, we

⁶ Corresponding author.

describe our South African population of *M. kalahariensis* with emphasis on new features not previously reported by Meyer (1931, 1932) to cover the full range of morphological variation of that species and provide further information on cystacanth morphology using material originally obtained by Meyer (1931) from a Bombay German cockroach, *Blattella (Phyllodromia) germanica.*

MATERIALS AND METHODS

Forty-five specimens were collected from 2 road-killed hedgehogs, 5 specimens from 1 hedgehog on the University of Limpopo grounds, Turfloop, Polokwane, Limpopo Province (23°53'35.7"S; 29°44'12.9"E) on 17 September 2012, and 40 specimens from the other hedgehog in Mohlonong Village, Mashashane, Limpopo Province, South Africa (23°53'49.9"S; 29°07'56.6"E) on 1 November 2012. These specimens were dissected out of the hedgehogs' intestines shortly after capture and were used for microscopical and SEM studies. Some cystacanths from the German cockroach in India, as well as adults from Botswana from Meyer's collection obtained courtesy of Dr. Birger Neuhaus, Curator, Museum für Naturkunde, Berlin, were also studied using both light microscopy and SEM.

For light microscopy studies, worms were punctured with a fine needle and subsequently stained in Mayer's acid carmine, destained in 4% hydrochloric acid in 70% ethanol, dehydrated in ascending concentrations of ethanol (70%, 80%, 90% [twice], 100%), cleared in 100% xylene, and then in 50% Canada balsam and 50% xylene; each step was for 24 hr. Whole worms were then mounted in Canada balsam. Measurements are in micrometers (µm) unless otherwise noted. Measurements are reported as the range followed by the mean values in parentheses. Width measurements represent maximum width. Measurements of the width of the proboscis receptacle include the encasing spiral muscles. Trunk length does not include the proboscis, neck, or bursa.

For SEM studies, specimens previously fixed in 70% ethanol were placed in critical-point drying baskets and dehydrated using an ethanol series of 95% and 100% for at least 10 min per soak followed by critical-point drying (Lee, 1992). Samples were mounted on SEM sample mounts, gold–palladium coated, and observed with a SEM (XL30 ESEMFEG; FEI, Hillsboro, Oregon). Digital images of the structures were obtained using digital imaging software attached to a computer.

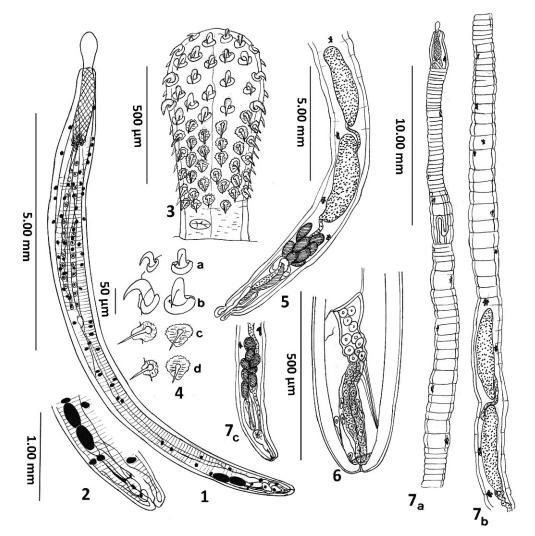
RESULTS

The following results are based on light microscopy and SEM studies of about 30 of the 45 specimens of *M. kalahariensis* collected from 2 road-killed hedgehogs, *A. frontalis*, in Limpopo Province, South Africa, in 2012. Adults from the hedgehog and sandgrouse in Botswana, and cystacanths from the German cockroach in India from Meyer's collection obtained from the Berlin's Museum für Naturkunde, were also studied using light microscopy and SEM. Other specimens from South Africa were also used for transmission electron microscopy and histopathological studies, which will be reported elsewhere. Meyer's (1931, 1932) descriptions of the egg and cystacanths were adequate and well illustrated. Only the SEM of these stages, as well as those of the juveniles recovered from the definitive host, are provided herein. A complete description of the juveniles, not previously reported by Meyer, is provided.

Moniliformis kalahariensis Meyer, 1931 (Moniliformida Schmidt, 1972: Moniliformidae Van Cleave, 1924) (Figs. 1–35)

Diagnosis

With characters of the genus Moniliformis. Juveniles long, slender, unsegmented, with many rounded giant nuclei (Figs. 1, 2, 13); females up to 32.00 mm long. Adults considerably longer than juveniles, pseudosegmented except posteriorly, beginning at level of male reproductive system, and anteriorly (Figs.7). Segmentation nontaeniate, earthworm-like (Figs. 22, 23, 33). Segments in variable states of expansion (relaxation) and contraction affecting total length (Figs. 7, 23). Shared structures larger in females than in males. Body wall aspinose with few amoeboid-stellate giant nuclei (Figs. 5, 7), many sensory pores (Figs. 22, 23, 34), electron-dense micropores throughout epidermal surface, and specialized sensory plates near posterior end of sexually mature males only (Figs. 24-27). Proboscis cylindrical, gradually widens anteriorly, somewhat rounded apically (Figs. 3, 14, 18, 30); apical end with 2 eccentric sensory pores in all stages (cystacanths, juveniles, adults) (Figs. 10, 15, 19, 31). Proboscis with16 (rarely 15) rows of 9-11(usually 10) hooks each. Anterior 4 (occasionally 3) hooks robust, with lateral slits, markedly curved posteriorly (Figs. 16, 20, 32), with robust roots embedded in prominent rounded base (Fig. 4a, b). Slits absent in cystacanths (Fig. 11) but begin developing in growing juveniles. Posterior 7 (occasionally 6) hooks slender, spine-like, straight, with rounded stubby base embedded in triangulate sheet with anteriorly serrated margin (Fig. 4c, d). Anterior rooted hook shortest. Second or third spiniform hooks from anterior longest. Hooks gradually decrease in size towards both ends of proboscis (Fig. 4). Marked neck with sensory pore in prominent, laterally oriented ovoid orifice (Figs. 3, 14). Proboscis receptacle encased in spirally arranged muscle layers with cephalic ganglion at its base.



Figures 1–7. Juveniles and adults of *Moniliformis kalahariensis* from *Atelerix frontalis* in South Africa. **1.** A juvenile male with underdeveloped reproductive system and embryonic giant nuclei (solid black). **2.** An enlargement of the posterior portion of the specimen in Figure 1. **3.** The proboscis of a female specimen showing the distribution of the 4 anterior rooted hooks and the posterior 5–7 spiniform hooks. Note the sensory structure on the neck. **4.** Lateral and frontal perspectives of hooks nos. 1, 4, 5, and 10–11, marked as a, b, c, and d, respectively, showing the curvature of the blade and the donut-like base of the prominent root of the anterior hooks no. 1–4 and the posterior 5–7 spiniform hook nos. 5–11 with posterior, knoblike root. **5.** Male reproductive system at the posterior end of the trunk. **6.** Reproductive system of a young female; note the thick uterus, multinucleated uterine bell, lack of vagina, the attachment of the vontral side of the distal end of the uterine bell to the body wall, the filament fibers connecting the anterior uterus to the body wall dorsally, and the presence of a permanent muscular "plug" at the posterior end of the body cavity. **7 a,b,c.** First, second, and third parts, respectively, of a whole mature male specimen showing the lack of segmentation anteriorly, posteriorly, around the reproductive system, and the earthworm-like expandable segments that vary in location in different worms.

Posterior end of receptacle with few pouches of nuclei (Fig. 1). Lemnisci long, filamentous, broader anteriorly, with many prominent nuclei, especially in younger specimens.

Description

Males (based on 5 juveniles and 4 mature adults, with sperm, from South African hedgehogs): Trunk 11.25 mm long by 0.77–1.12 (0.94) mm wide (juveniles); 44.25-75.00 (59.62) mm long by 1.62-1.75 (1.68) mm wide (adults). Proboscis 728-780 (745) long by 333-374 (349) wide (juveniles); 780 long by 384 wide (adult). Proboscis with 15-16 (15.7) (rarely 15) usually straight rows of 9-11 (10.0) (usually 10) hooks each. Length of rooted hooks from anterior: 25-32 (28), 35-50 (42), 42-60 (50), 50-55 (54) (juveniles); 29-30 (29), 41-47 (44), 55-57 (56), 55-56 (55) (adults). Length of spiniform hooks from anterior: 55-65 (61), 65-72 (67), 55-67 (64), 60-70 (64), 45–65 (52), 37–55 (46), 35–45 (41) (juveniles); 67-75 (71), 75-77 (76), 65-75 (70), 60-62 (61), 57-60 (58), 35-40 (38) (adults). Proboscis receptacle 1.32-1.58 (1.43) mm long by 0.30-0.54 (0.38) mm wide (juveniles); 1.52 mm long by 0.52 mm wide (adult). Lemnisci 7.00-13.25 (10.08) mm long by 0.16-0.17 (0.16) mm wide (juveniles); 18.75 mm long by 0.17 mm wide (adult). Reproductive system in posteriormost part of trunk; underdeveloped, with cement glands occasionally absent in juveniles. Testes ovoid in juveniles (Figs. 1, 2) but elongate in adults (Figs. 5, 7). Cement glands in cluster of 8, largest anteriorly, short distance from posterior testis in adults (Figs. 5, 7). Common sperm duct ventral to common cement gland duct; both adjacent to Saefftigen's pouch (Figs. 5, 7). Anterior testis 333-676 (504) long by 166-208 (187) wide (juveniles); 3.50-6.87 (5.64) mm long by 0.75-1.25 (1.07) mm wide (adults). Posterior testis 302-728 (515) long by 156-208 (182) wide (juveniles); 4.05-5.55 (5.02) mm long by 0.95-1.32 (1.08) mm wide (adults). Cement glands 73-94 (83) long by 73-83 (78) wide (juveniles); 0.87-2.50 (1.56) mm long by 0.50-1.07 (0.74) mm wide (adults). Saefftigen's pouch 520 long by 177 wide (juvenile); 1.62-1.75 (1.68) mm long by 0.50-0.57 (0.54) mm wide (adults).

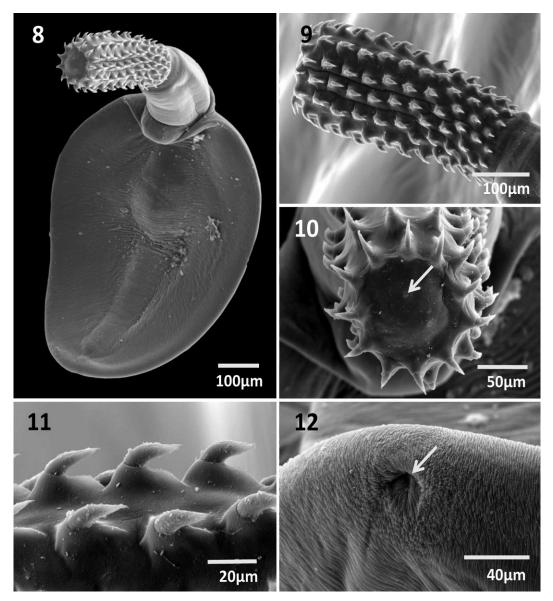
Females (based on 5 juveniles and 3 adults with eggs from South African hedgehogs): Trunk 8.25-32.00 (17.07) mm long by 0.62-0.85 (0.77) mm wide (juveniles); 51.25-81.25 (64.92) mm long by 2.00-2.25 (2.17) mm wide (adults). Proboscis 780-863 (821) long by 333-406 (372) wide (juveniles); 763-863 (812) long by 374-426 (402) wide (adults). Proboscis with 16 (15.7) (occasionally 15) usually straight rows of 9-11 (10.0) (usually 10) hooks each. Length of rooted hooks from anterior: 25-32 (28), 40-50 (46), 55-65 (58), 55-65 (57) (juveniles). Length of spiniform hooks from anterior: 55-70 (62), 55-80 (67), 52-82 (67), 60-72 (64), 50-69 (59), 42-67 (57), 35–51 (42) (juveniles). Proboscis receptacle 0.88-1.45 (1.24) mm long by 0.23-0.41 (0.32) mm wide (juveniles); 1.75–1.80 (1.77) mm long by 0.47 -0.55 (0.51) mm wide (adults). Lemnisci 4.73-10.75 (8.71) mm long by 0.10-0.21 (0.16) mm wide (juveniles); 13.75-16.25 (15.00) mm long by 0.24-0.27 (0.25) mm wide (adults). Reproductive system lacks vaginal muscles, with thick, double-walled uterus, many nuclei in uterine bell, well-developed ligaments holding distal end of uterus to body wall, short ligaments distally nucleated on opposite side near posterior end of trunk, and muscular plug at inner posterior tip of trunk (Fig. 6). Whole reproductive system 572–946 (720) long; uterus 343–624 (457) long, uterine bell 208–343 (263) long. Eggs ovoid, notched at one pole, 73–114 (96) long by 31–62 (48) wide (Figs. 29, 35; and Meyer, 1931, Fig. 33).

Cystacanths (from the German cockroach using Meyer's [1931] specimens): Eccentric apical sensory pores (2) present (Fig. 10); thin elliptic trunk wide at shoulder; otherwise consistent with the description of Meyer (1931).

Specimens deposited: Voucher specimens were deposited in the Harold W. Manter Laboratory (HWML), University of Nebraska's State Museum, Lincoln, Nebraska, U.S.A. Collection numbers: HWML 49824 (juvenile male); 49825, 49826 (juvenile females); 49827, 49828 (adult males); and 49829, 49830 (adult females).

REMARKS

Our South African juvenile specimens were smaller than adults in all structures except the proboscis and proboscis armature, which appear to be of similar sizes. Early development of attachment structures to ensure the establishment of initial infections has been reported in other species of acanthocephalans, e.g., Neoechinorhynchus cylindratus (Van Cleave, 1913) Van Cleave, 1919 (Neoechinorhynchidae) and Pomphorhynchus bulbocolli Linkins in Van Cleave, 1919 (Pomphorhynchidae); see Amin (1986 and 1987, respectively). Juveniles up to 32.00mm long remain unsegmented and underdeveloped with undeveloped reproductive system. Small juvenile males barely show testes and have no cement glands. Largest juveniles have small, underdeveloped reproductive structures with barely discernible ducts (Figs. 1, 2), if at all. In our collection juvenile specimens were found in the same digestive tracts as the adults. It is surprising that Meyer (1931) did not refer to juveniles, which suggests that he may not have encountered them. He did not state how many worms he collected and from how many hosts. He may have



Figures 8–12. SEM of cystacanths of *Moniliformis kalahariensis* from *Blattella germanica* from Meyer's (1931) materials collected in Bombay, India. **8.** A whole cystacanth with leaf-thin trunk, a longitudinally elevated center, long neck, and fully everted proboscis with flattened apical end. **9.** The proboscis of the specimen in Figure 8 showing the imperfect longitudinal hook rows, some of which may have up to 12 hooks per row (second row from right). **10.** En face view of the apical end of the same proboscis in Figure 9 showing the 2 eccentric apical sensory pores (arrow points to one pore) found in all developmental stages of *M. kalahariensis*. **11.** A lateral view of the anterior hooks of the same proboscis showing the lack of the lateral slits that appear to develop only in maturing juveniles and adults. **12.** The gonopore of the cystacanth in Figure 8 showing the pattern of the rough topography of the epidermis.

encountered small numbers of individuals from old, established infections lacking juveniles.

As noted above, our light microscopy observations of 1 of the 9 cystacanths from Meyer's original collection in the Berlin's Museum für Naturkunde generally agree with Meyer's (1931, Fig. 35) description. Two other cystacanths were studied by SEM. The SEM images show a thin, elliptic trunk with a wider shoulder than shown by Meyer (1931) and with a prominent anteriorly partitioned part that includes most of the proboscis receptacle (Fig. 8). The proboscis is more flattened anteriorly than in adults and has 14 rows each with 11 (occasionally 12) hooks. Some hook rows are irregular or incomplete as seen in some juveniles and adults (Fig. 9). Two eccentric apical sensory pores are found on the cystacanth proboscis (Fig. 10) consistent with those discovered in juveniles and adults. The lateral slits of the anterior rooted hooks appear to develop in later stages, as they were absent in the cystacanth stage (Fig. 11). The genital pore is shown in Figure 12 within an elaborate matrix of dermal topography.

All specimens (adults and juveniles from South Africa, adults from Botswana, and cystacanths from Bombay) had in common the presence of 2 eccentric sensory pores on the apical end of the proboscis. Our adult specimens from South Africa were smaller than Meyer's (1931) specimens (males 44.25-75.00 mm long, females 51.25-81.25 mm long) compared to 140-150-mm long males and females from Botswana. Meyer (1931) did not report on juveniles or measure the proboscis or proboscis hooks. He did, however, count 14 rows of 9-10 hooks each in adults and cystacanths and distinguished between the anterior robust hooks and the posterior spiniform hooks without reference to their roots. Our specimens had 16 rows (rarely 15 in 1 male and 1 female), each with 9-10 hooks (occasionally 11 and maybe 12 in 1 cystacanth). Meyer (1931) did not note the persistence of giant nuclei in the adults or observe the pouched nuclei at the posterior end of the proboscis receptacle. These pouched nuclei are similar to those characteristic of the genus Fessisentis Van Cleave, 1931. In Meyer's (1931) material, the testes measured 5.00 mm long while the eggs measured 110×57 . In our specimens from South Africa, anterior and posterior testes measured 3.50-6.87 (5.64) and 4.05-5.55 (5.02) mm long, respectively, and the eggs were somewhat smaller, 73–114 (96) \times 31–62 (48). Meyer's (1931) eggs (his Fig. 33) did not show the notch at one pole that we observed in his specimens from Botswana (Fig. 35) as well as in our specimens from South Africa (Fig. 29). Meyer (1931) also reported 6 cement glands; we counted 8. Yamaguti (1963) reported the number of the cement glands in Moniliformis as "6(?)-8." We regard the above comparison as an expression of a wider range of intraspecific variation of M. kalahariensis, which also covers characteristics not reported by Meyer (1931, 1932).

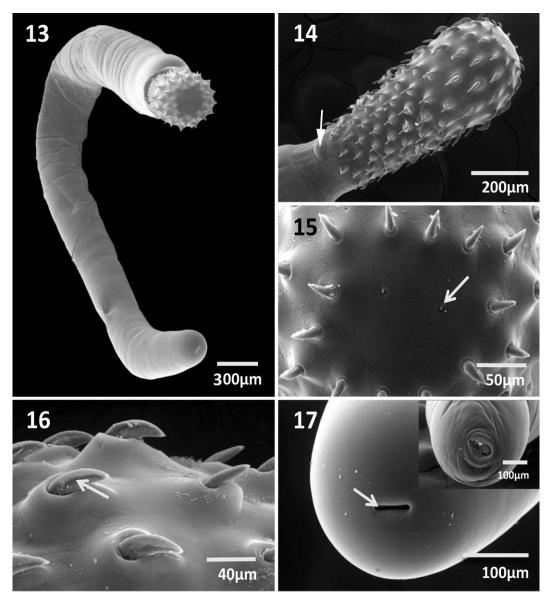
DISCUSSION

Meyer (1931, 1932) described segmented mature adults of *M. kalahariensis* from the South African hedgehog, *A. frontalis*, and from the Namaqua sandgrouse, *P. namaqua*, in Botswana as well as cystacanths from the German cockroach, *B. germanica*, in Bombay, India across the Indian Ocean from Africa. The present report deals with adults, juveniles, and cystacanths of *M. kalahariensis* from *A. frontalis* in South Africa.

We do not know the arthropod intermediate host(s) in Africa or the definitive host(s) in India. We do know, however, that the German cockroach was reported to be a cosmopolitan species that is chiefly indoors but which also occurs in forests and open landscapes (Wille, 1920; Marshall, 1985). As such, it could feasibly serve as a potential intermediate host in Africa as well.

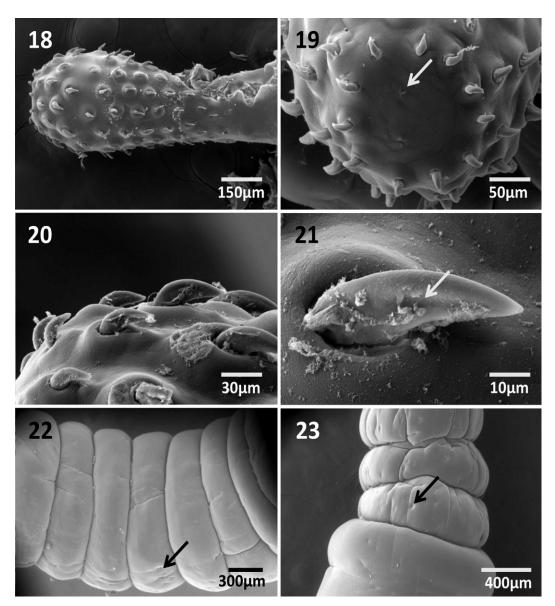
Four species of hedgehogs occur in Africa. The 3 other species of hedgehogs are not found in central or southern Africa. The South African hedgehog, A. frontalis, does not occur in the Indian subcontinent, although other species do. These include the Indian hedgehog, Paraechinus micropus Blyth, 1846 (found in the Bombay area where the intermediate host of M. kalahariensis was reported) and the Indian long-eared hedgehog, Hemiechinus collaris Gray, 1830 (found in all parts of India including the Bombay area as well as in the Corbett National Park and Gir Wildlife Sanctuary). Two other species of hedgehogs occur in Pakistan and elsewhere in Asia and the Middle east and have ranges that may overlap the Bombay area; the long-eared hedgehog, Hemiechinus auritus Gmelin, 1770 and Brandt's hedgehog, Paraechinus hypomelas Brandt, 1836 (see Hutterer, 2005). Examination of these 4 species of hedgehogs, especially the first 2, for parasites may reveal the presence of infections with M. kalahariensis.

Fourteen of the 16 known species of sandgrouse, Pteroclididae, belong in the genus *Pterocles* Temminck, 1815. Pteroclidiformes are ground-dwelling birds restricted to treeless, open country such as plains, savannahs, and semideserts that are distributed across northern, southern, and eastern Africa as well as Madagascar, the Middle East, and India through central Asia. Sandgouse are generally seed eaters but also feed on termites and ants, among other insects, especially during the breeding season (Campbell and Lack, 1985). The Namaqua sandgrouse is found in Angola, Botswana, Namibia, South Africa, and Zimbabwe but not in India (Gooders, 1979; Crome, 1991). Nine of the 14 species of *Pterocles* are found



Figures 13–17. SEM of juveniles of *Moniliformis kalahariensis* from *Atelerix frontalis* in South Africa. **13.** A juvenile specimen showing the lack of segmentation. **14.** The proboscis of the specimen in Figure 13 showing its gradual anterior enlargement. Note the sensory orifice swelling at the left side of the neck (arrow). **15.** The apical end of the same proboscis in Figure 14 showing the 2 eccentric sensory pores (arrow) characteristic of this species. **16.** A lateral view of anterior proboscis hooks showing the complete development of lateral slits in the juvenile stage. **17.** Female gonopores showing the variable shape of the orifice depending on the state of contraction.

in central and southern Africa, of which 2 species are also found in India the Chestnut-bellied sandgrouse, *Pterocles exustus* Temminck, 1825 and the spotted sandgrouse, *Pterocles senegallus* Linn, 1771. Either one of these 2 species could also serve as a definitive host for *M. kalahariensis* in Africa or in India. Four other species are found only in India and Asia: the painted sandgrouse, *Pterocles indicus* Cabanis, 1868; the pin-tailed sandgrouse, *Pterocles alchata* Linn. 1766; the crowned sandgrouse, *Pterocles coronatus* Lichtenstein, 1823; and the black-bellied sandgrouse, *Pterocles orientalis*, Linn. 1758. Whether any of

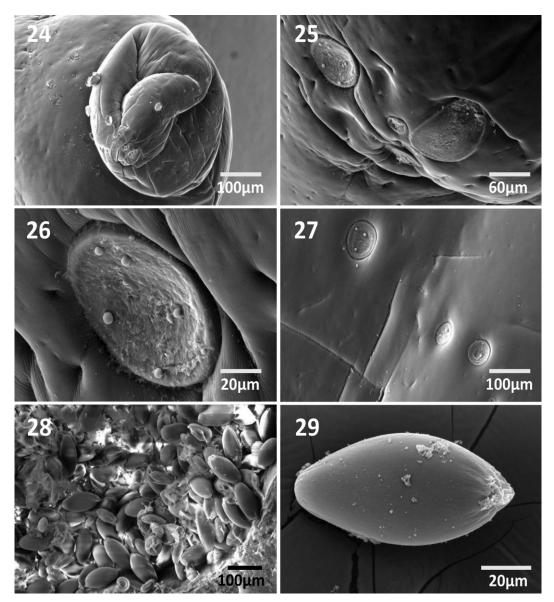


Figures 18–23. SEM of mature adults of *Moniliformis kalahariensis* from *Atelerix frontalis* in South Africa. 18. The proboscis of a female specimen showing its enlarged anterior end to be more rounded than in juveniles (Fig. 14). 19. The apical end of the same proboscis showing the paired sensory pores characteristic of *M. kalahariensis* (arrow points to 1 pore). 20. The full development of the longitudinal lateral slits in anterior proboscis hooks is shown in this lateral view. 21. A higher magnification of 1 proboscis hook showing the lateral slit as well as the dome-shaped topography of the hook insert area. 22. A part of the midtrunk of a worm showing the nontaeniate, earthworm-like segmentation characteristic of adult *M. kalahariensis*. Note the sensory pores (arrow). 23. Another segment of trunk from the same worm in Figure 22 showing part of an expanded segment (lower). Note the presence of many sensory pores (arrow).

these 4 species are involved in the life cycle of *M*. *kalahariensis* in India is an open question.

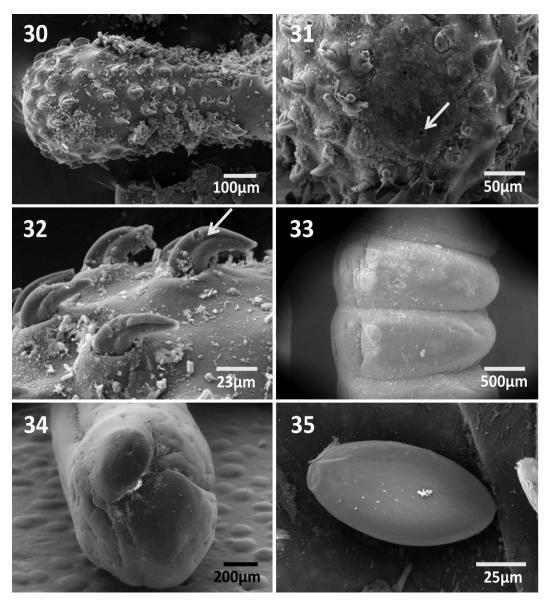
The description of *M. kalahariensis* from Botswana (Meyer, 1931) and our more-detailed description of the

same species from South Africa constitute a defacto new description. This description (1) reports a wider range of variation in size of trunk (males 44.25– 150.00 mm long, females 51.25–150.00 mm long),



Figures 24–29. SEM of mature adults and eggs of *Moniliformis kalahariensis* from *Atelerix frontalis* in South Africa. **24.** The posterior end of a male specimen showing many sensory pores on the trunk and sensory plates on the bursa. **25.** A view of a few sensory plates at the posterior extremity of the male in Figure 24. **26.** Higher magnification of the sensory plate shown in the upper left hand corner of Figure 25. **27.** Another type of sensory plate of a male flush with the epidermal surface, not raised as in Figures 24–26. **28.** One of many clusters of eggs in the body cavity of 1 segment of a gravid female demonstrating the high reproductive potential of females of *M. kalahariensis*. **29.** High magnification of a ripe egg showing the characteristic polar notch on 1 end (right).

eggs (73–110 \times 31–57), and of counts of both proboscis hooks (14–16 rows each with 9–11 hooks) and cement glands (6–8) (counted as 6 by Meyer, 1931, 8 by us, and 6(?)–8 by Yamaguti, 1963); (2) adds new measurements of proboscis hooks, the proboscis receptacle, lemnisci, and male and female reproductive structures; and (3) describes new features not previously reported by Meyer (1931) such as the apical proboscis and trunk sensory pores and plates, the shape of proboscis hooks and roots, the giant nuclei



Figures 30–35. SEM of 1 mature female of *Moniliformis kalahariensis* from *Atelerix frontalis* or from the Namaqua sandgrouse, *Pterocles namaqua*, collected in Botswana and from Meyer's (1931) original collection (or from both). Note the similarities with our adult specimens from *A. frontalis* from South Africa in the shape of the proboscis, hooks, eggs, and trunk segments (Figs. 18–29). The sensory plates (Figs. 24Y27) were not observed in the Meyer female specimen because they are only found in males. **30.** The proboscis of a female specimen. **31.** The apical end of the proboscis showing the 2 eccentric sensory pores (arrow points to 1 pore). **32.** Proboscis hooks with lateral slits. **33.** Typical nontaeniate trunk segments. **34.** Posterior end of a female. **35.** The notched egg characteristic of this species of acanthocephalan.

at the base of the proboscis receptacle, the nature of trunk segmentation, the persistent stellate-amoeboid giant nuclei in the trunk of adults, details of male and female reproductive systems, and the notched eggs. Moreover, our description of the South African material includes a complete description of the juveniles, which were not reported by Meyer (1931). We also add, using SEM, to the description of the cystacanths obtained from Meyer's material from German cockroaches collected in Bombay, India and

note the presence of the species-specific apical sensory pores on the cystacanth proboscis. Our light microscope and SEM comparisons with adults from Meyer's (1931) material confirm the conspecificity of all the materials examined.

ACKNOWLEDGMENT

We are grateful to Dr. Birger Neuhaus, Curator, the Berlin Museum für Naturkunde, for making available adults and cystacanths of the Meyer material for study.

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