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## A revision of the genus *Afroheterozercon* (Acari: Heterozerconidae)

HANS KLOMPEN<sup>1</sup>, MILAN AMIN<sup>2</sup> & BEVERLY SWAIM GERDEMAN<sup>3</sup>

<sup>1</sup>Acarology Collection, Ohio State University, 1315 Kinnear Rd., Columbus, OH 43212, USA. E-mail: klompen.1@osu.edu

<sup>2</sup>Undergraduate Biology Program, Ohio State University, Columbus, OH, USA. E-mail: amin.57@buckeyemail.osu.edu

<sup>3</sup>Northwestern Washington Research and Extension Center, Washington State University, 16650 State Route 536, Mount Vernon, WA 98273, USA. E-mail: mitehunter1@hotmail.com

<sup>4</sup>Corresponding author

### Abstract

Six new species of *Afroheterozercon*, *A. mahsbergi*, *A. sanghae*, *A. goodmani*, *A. gabonensis*, *A. tanzaniensis* and *A. madagascariensis*, are described from a range of localities in sub-Saharan Africa, bringing the total number of described species in the genus to ten. These mites appear to be common on especially larger millipedes. Distribution data suggest locality, rather than host, specificity. A preliminary analysis of relationships provided relatively weak resolution and no evidence of geographically restricted lineages.

**Key words:** Diplopoda, Heterozerconidae, taxonomy

### Introduction

Mites in the family Heterozerconidae are distributed throughout most tropical and subtropical regions, with the exception of the Australian faunal region. The adults of most species are found attached to medium to large (> 4cm) millipedes, while immatures appear to live off-host either in millipede nests (Gerdeman *et al.* 2000) or in the litter (Gerdeman & Garcia 2009(2010)). Adults of the genus *Amheterozercon* Fain 1989 (= *Zeterohercon* Flechtmann & Johnston 1990) are exceptional in that they are parasitic on snakes (Squamata, Serpentes) and worm lizards (Squamata: Amphisbaenidae). Feeding biology for the adult millipede associates is still not clear, however immatures are predatory and have been observed feeding on immature mites (e.g. Oribatida) and other small arthropods (e.g. Collembola) (Gerdeman *et al.* 2000; Gerdeman & Garcia 2010). So far, only 14 species have been described in the entire family, but this is clearly an underestimate of actual diversity. The current study was undertaken to address this issue, by describing a wider range of taxa, starting with African material.

The genus *Afroheterozercon* Fain, 1989 was described to accommodate adults of three species described from the Democratic Republic of Congo, *A. spirostreptus* (Fain 1988) from *Spirostreptus cornutus* Attems, *A. pachybolus* (Fain 1988) from *Pachybolus macrosternus* Cook, and *A. ancoratus* Fain 1989 from a termite nest (*Cubitermes* sp.). The genus is characterised by the presence of series of anchor-shaped spines on the latero-ventral region of the opisthosoma, and a specific pattern of setal modifications on the femur of legs II in the male (Fain 1989). We also include *Heterozercon cautus* Berlese 1924 (= *Afroheterozercon cautus* (Berlese) comb. nov.), described from “East Africa”. The brief description of this species (Berlese 1924) is not clear on the shape and degree of development of the lateral spines (he mentions “Margo lateralis ventris scutulis minimus subrotundatis 10 numero, seriatis, ornatus”, which may refer to the lateral spines). The description does specify the presence of a single, massive and curved spine on femur II of the male (“calcar robusto”), another condition that is unique to *Afroheterozercon*. A more complete analysis of evidence favoring inclusion of *H. cautus* in *Afroheterozercon* is presented below. After this change all reported Heterozerconidae from sub-Saharan Africa are assigned to the genus *Afroheterozercon*.

As part of this study eight species were identified, two of which correspond to described species, *A. spirostreptus* and *A. pachybolus*, while the remaining six are new. The three species previously described by Fain are (partially) redescribed and figured, along with the six new species, to provide consistent data for comparative studies.

## Material and methods

Specimens were cleared in lactophenol and slide mounted in Hoyer's medium (Walter & Krantz 2009). They were studied with phase contrast and differential interference contrast (DIC) microscopy. Pencil drawings were prepared using a drawing tube attached to a Zeiss Axioskop compound microscope. Resulting images were scanned and redrawn in Adobe Illustrator® (Adobe Systems Inc., San Jose). Other specimens were drawn in Illustrator based on high resolution photographs using the extended depth option in the NIS Elements software package on a Nikon Eclipse 90i compound microscope (Nikon Instruments Inc, Melville, NY). Palpal chaetotaxy follows Evans (1963a), leg chaetotaxy Evans (1963b,1969), and idiosomal chaetotaxy Lindquist & Evans (1965), all as implemented by Gerdeman & Klompen (2003). Measurements were prepared using the NIS Elements software package. Idiosomal length is measured from the base of the gnathosoma to the end of the opisthosoma; width is measured at the broadest point. Width of the movable digit is measured just above the base, at the widest part of the actual digit. All measurements are in micrometres ( $\mu\text{m}$ ) in the format: average (range), and are summarised in Tables 1–2. Measurements are restricted to those structures found to be variable among the taxa studied. Characters examined (Table 3) were processed in the matrix development mode of vSysLab (Johnson 2010), and exported as both proto-species descriptions and as a NEXUS file for systematic analysis (Table 4). Individual specimens examined are identified by OSAL numbers. Complete data for each specimen are available on-line through the OSAL database (<http://www.biosci.ohio-state.edu/~acarolog/collection/index.html>). Millipede hosts from Central African Republic and Gabon were preserved individually. A small label with the text “Mites removed, H. Klompen“ plus a field number was added to each individual host allowing direct association of individual mites with individual millipede hosts. Host depository and, where available, specimen ID or field number for the host, are listed in brackets. Phylogenetic and character distribution analyses were conducted using, respectively, PAUP\* (Swofford 2002) and MacClade 4 (Maddison & Maddison 2002).

Depositories are identified by the following acronyms: BUW: Biozentrum der Universität Würzburg, Germany; CASEnt: California Academy of Sciences, San Francisco, CA; FMNH: Field Museum of Natural History, Chicago, IL; IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels; ISZA: Istituto Sperimentale per la Zoologia Agraria, Florence; OSAL: Ohio State University Acarology Collection, Columbus, OH; ZSM: Zoologische Staatssammlung, Munich.

Descriptions are restricted to those structures we found to be variable among species of *Afroheterozercon*. Thus we do not present detailed descriptions or images of the palps, the subcapitulum, the dorsum, legs III–IV or elements of legs I–II. These structures are either invariant among the species in the genus or what variation there is cannot be scored or described consistently. The variability in these structures will be the subject of a separate project. Meanwhile, a broad overview of the structure of the palps, subcapitulum, dorsum, and leg chaetotaxy in Heterozerconidae can be found in Gerdeman & Klompen (2003).

## Taxonomic section

### *Afroheterozercon* Fain, 1989

*Afroheterozercon* Fain, 1989: 147.

**Diagnosis.** Adults with a series of “anchor-shaped” lateral spines in the adults (Fig. 3). Combined sternal and ventral (= sternitovenral) shield in the male fused with the peritrematal / metapodal / endopodal shields (also in *Maracazercon* Fain 1989) (Fig. 3). Femora II of the male each with seta *pv1* shaped as a long, thick, curved spine (Fig. 5A); ventral setae of genua and tibiae II not conspicuously spinose.

TABLE 1. Comparative measurements for adult males of *Afroheterocercon* species. NA= not applicable, structure not present in this species.

	<i>mahsbergi</i> 4	<i>pachybolus</i> 6	<i>sanghae</i> 4	<i>spirostrepti</i> 5	<i>gabonensis</i> 4	<i>goodmani</i> 5	<i>ancoratus</i> 1	<i>tanzaniensis</i> 2	<i>madagascariensis</i> 4
length idiosoma	708 (571-811)	685 (649-727)	735 (670-807)	980 (909-1022)	853 (794-917)	806 (786-843)	799	766 (757-774)	653 (613-726)
width idiosoma	499 (442-552)	547 (513-579)	586 (581-590)	754 (716-799)	686 (647-706)	570 (552-583)	627	692 (687-697)	534 (517-566)
length fixed digit	68 (57-72)	45 (41-49)	72 (71-73)	74 (73-75)	57 (48-64)	51 (44-58)	72	90 (87-93)	80 (77-84)
chelicera	89 (84-91)	77 (71-83)	95 (89-100)	125 (118-128)	91 (87-98)	95 (91-98)	94	76 (72-80)	70 (68-72)
length moveable digit	9 (8-10)	10 (7-12)	18 (17-20)	17 (16-20)	23 (19-29)	19 (18-20)	17	18 (17-20)	11 (9-13)
width movable digit	65 (54-72)	57 (52-61)	77 (76-79)	152 (140-161)	65 (57-72)	54 (50-60)	79	96 (92-100)	80 (77-84)
length spermatodactyl									
total									
basal section	18 (15-20)	18 (16-20)	33 (28-36)	30 (20-36)	21 (14-32)	11 (6-14)	13	41 (38-44)	33 (30-36)
distal section	27 (19-31)	25 (20-27)	22 (21-23)	86 (80-90)	27 (22-35)	28 (27-30)	42	22 (20-23)	26 (23-28)
length cheliceral shelf	107 (104-110)	71 (65-78)	NA	NA	NA	NA	NA	NA	NA
width cheliceral shelf	26 (25-28)	19 (16-22)	NA	NA	NA	NA	NA	NA	NA
seta Z5	86 (76-95)	84 (70-95)	68 (60-79)	73 (62-80)	64 (49-73)	61 (58-64)	79	89 (89-90)	58 (50-70)
seta S5	17 (14-20)	24 (22-27)	39 (33-43)	30 (27-37)	43 (40-50)	21 (18-25)	39	49 (48-49)	15 (13-16)
ratio setae Z5 / S5	4.2-6.1	2.7-3.8	1.4-2.0	2.2-2.7	1.2-1.8	2.5-3.6	2.0	1.8-1.9	3.6-4.9
seta pa	45 (43-49)	51 (48-54)	70 (67-73)	74 (73-75)	67 (60-76)	67 (60-72)	65	68 (65-71)	47 (39-55)
seta po	13 (12-13)	21 (21-26)	24 (23-25)	22 (21-22)	21 (18-24)	21 (17-25)	18	23 (21-24)	23 (20-27)
femur I seta al1	90 (84-95)	105 (94-112)	136 (130-151)	110 (100-121)	108 (101-116)	99 (90-102)	121	120 (120-120)	79 (75-84)
femur I seta al2	40 (35-43)	34 (30-37)	48 (47-49)	66 (63-70)	54 (52-56)	48 (46-49)	48	60 (57-63)	36 (34-37)
ratio setae al1 / al2	2.1-2.5	2.9-3.4	2.7-3.2	1.5-1.8	1.9-2.2	2.0-2.1	2.5	1.9-2.1	2.1-2.4
femur II seta av1	35 (27-38)	38 (31-43)	51 (46-54)	73 (68-80)	53 (52-54)	45 (44-46)	55	54	34 (30-36)
femur II seta pv1	57 (54-59)	55 (53-58)	69 (66-74)	75 (67-82)	56 (51-60)	50 (48-53)	58	58 (56-60)	45 (41-49)
width femur II seta pv1	16 (15-18)	16 (15-18)	17 (16-18)	22 (21-23)	17 (15-18)	21 (19-22)	14	17 (16-17)	14 (13-15)
ratio setae av1 / pv1	0.5-0.7	0.5-0.8	0.7-0.8	0.8-1.1	0.9-1.0	0.8-1.0	1.0	0.9-1.0	0.7-0.8
genu II seta av1	11 (10-12)	5 (5)	35 (33-36)	28 (22-33)	29 (27-33)	15 (13-16)	45	19 (19)	18 (17-18)
genu II seta pv1	9 (9-10)	10 (8-14)	15 (14-16)	29 (23-33)	17 (16-19)	12 (10-13)	22	20 (17-23)	10 (9-11)

**TABLE 2.** Comparative measurements for adult females of *Afroheterozercon* species.

	mahsbergi	pachybolus	sanghae	spirostreptus	gabonensis
N	4	6	3	4	1
length idiosoma	753 (736–780)	862 (734–1033)	909 (904–913)	1202 (1028–1315)	848
width idiosoma	601 (550–626)	695 (586–814)	763 (754–771)	919 (776–1141)	694
length moveable digit chelicera	118 (107–127)	102 (101–104)	127 (118–143)	155 (148–165)	137
width movable digit	15 (13–16)	10 (9–12)	13 (12–14)	17 (15–18)	16
seta Z5	81 (80–83)	97 (82–115)	72 (57–91)	87 (82–96)	77
length seta S5	13 (10–14)	24 (20–26)	41 (40–44)	29 (24–34)	40
ratio setae Z5 / S5	5.6–8.3	3.4–4.8	1.4–2.1	2.6–3.1	2.8
length seta pa	48 (43–51)	57 (51–62)	70 (67–73)	78 (63–92)	79
length seta po	13 (11–15)	20 (14–23)	22 (19–24)	21 (20–21)	20
femur I seta all	93 (89–101)	119 (104–130)	119 (101–140)	120 (107–141)	127
femur I seta al2	43 (39–47)	40 (35–43)	53 (47–61)	65 (54–73)	57
ratio setae all / al2	2.0–2.3	2.8–3.1	1.9–2.9	1.7–2.0	3.2

continued.

	<i>goodmani</i>	<i>ancoratus</i>	<i>tanzaniensis</i>	<i>madagascariensis</i>
N	2	1	3	4
length idiosoma	1020 (942–1097)	948	887 (884–890)	712 (647–796)
width idiosoma	718 (620–816)	774	850 (831–869)	595 (557–643)
length moveable digit chelicera	109 (107–110)	121	118 (117–119)	106 (99–111)
width movable digit	13 (12–13)	12	13 (13–14)	12 (11–13)
seta Z5	60	83	94 (76–105)	69 (57–77)
length seta S5	24	32	44 (41–46)	15 (13–17)
ratio setae Z5 / S5	2.5	2.6	1.8–2.3	4.0–5.4
length seta pa	71 (70–71)	72	59 (53–63)	49 (48–51)
length seta po	23 (19–27)	23	22 (19–24)	21 (17–26)
femur I seta all	97 (94–100)	111	127 (124–130)	91 (87–97)
femur I seta al2	51 (46–55)	47	66 (63–69)	42 (39–47)
ratio setae all / al2	1.8–2.2	2.4	1.9–2.0	2.0–2.3

**Type species.** *Heterozercon spirostreptus* Fain, 1988: 237.

Other species included are *Afroheterozercon cautus* (Berlese, 1924), nov. comb.; *Afroheterozercon pachybolus* (Fain, 1988): 241; *Afroheterozercon ancoratus* Fain, 1989: 153; *Afroheterozercon mahsbergi* **nov. sp.**; *Afroheterozercon sanghae* **nov. sp.**; *Afroheterozercon gabonensis* **nov. sp.**; *Afroheterozercon goodmani* **nov. sp.**; *Afroheterozercon tanzaniensis* **nov. sp.**; *Afroheterozercon madagascariensis* **nov. sp.**

One of the main species-level characters in *Afroheterozercon* is the shape of the male spermatodactyl. Unfortunately, this structure is difficult to describe unambiguously, so we present both line drawings and photographs (Figs 1, 2). For the descriptive sections the following might aid in clarifying terminology. Fain (1989) recognised the following elements for the chelicerae of female Heterozerconidae: digits very long and thin; fixed digit with a few small teeth apically; movable digit with a comb of setiform processes along the entire dorsal surface, ventrally with two thin, cylindrical or blade-like processes (e.g. arrow Fig. 1D). Between the digits are two transparent membranes (interdigital membranes), covered by tiny spicules. The dorsal seta and lyrifissure *ia* are present in the usual positions. In the males, the spermatodactyl arises from the base of the fixed digit (Figs 1, 2). For discussion purposes the spermatodactyl is separated into a basal section (the size of which may vary dramatically), the “coiled” middle section where the sperm duct appears to twist around (coils may be tight or extended), and the distal section (usually thin, straight, finger-like, but broad or hooked in other taxa). The fixed

digit (FD Fig. 1A) itself is reduced in size and is often quite thin; it may be straight, end with a distinct hook, or carry a subterminal spine. The movable digit (MD Fig. 1A) may be robust and hook-like, or quite thin with a bulbous base. In either case it retains the comb of setiform processes. The two membranes (IM Fig. 1D), the dorsal seta and lyrifissure  $i\alpha$  are retained in the males. In a few species (*A. pachybolus*, *A. mahsbergi*, possibly *A. cautus*) a thick, sclerotised structure appears between the digits, seemingly a modification of the larger interdigital membrane (SPIM Fig. 1A).

The order of species treatment roughly follows a transect from northwest to southeast across the Afrotropical Region, followed by brief comments on the status of *A. cautus*.

***Afroheterozercon mahsbergi* nov. sp.**

(Figs 1A, 2A, 3, 4A, 5A)

**Diagnosis.** In the male, chelicera with a thin movable digit (width 8–10  $\mu\text{m}$ ) and large interdigital membrane partially modified into a sclerotised process (Fig. 1A); shields carrying setae *St1* partially connected to the sternitoventral shield (Fig. 3B); adults with a high length ratio of posterior marginal setae *Z5* / *S5* (4.2–8.3), mostly due to short setae *S5*; femoral setae *pl2* on legs I absent. Among the smaller species in the genus.

**Description.** Male chelicera (Figs 1A, 2A): spermatodactyl short; base short, coiled section tight, distal extension relatively short, finger-like. Fixed digit straight with a small terminal hook; movable digit thin with a bulbous base. Large interdigital membrane partially modified into a sclerotised process. Male venter (Fig. 3B): shields including setae *St1* partially connected to the sternitoventral shield. Setae *pa* relatively short, length < 3/4 length of setae *Z5*. Setae *S5* relatively short, length < 1/2 length of setae *Z5*. Posterior marginal sclerite with 5–6 tiny setae (usually 6 in female). Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 15–21 / side. Female venter (Fig. 3A): setae *S5* relatively short, length < 1/2 length of setae *Z5*. Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 20–24 / side. Male leg I chaetotaxy (Fig. 4A): coxal setae relatively thin, setiform (same in female). Trochanteral setae *al* with distinct barbs; setae *ad* and *pl* without barbs. Trochanteral setae *av1* relatively short; length less than, or equal to, setae *pl*. Femoral setae *pl2* absent. Femoral setae *ad3* relatively short; length less than 2/3 length of setae *pd2*. Femoral setae *pd1*, *al2* and *v2* without distinct barbs. Femoral setae *al1* and *al2* of average length; length ratio setae *al1* / *al2* between 2.1 and 2.5. Male legs II chaetotaxy (Fig. 5A): femoral setae *pv1* moderately wide (<20  $\mu\text{m}$ ). Setae *av1* relatively short (length ratio *av1* / *pv1* less than 0.8). Femoral setae *pd1* relatively short; length 2/3 length of setae *ad1*. Femoral setae *ad2* without distinct barbs. Genua with a distinct ventrodistal outgrowth. Genua setae *av1* short; length subequal to that of setae *pv1*. Tibial setae *av1* without distinct barbs. Adult legs III chaetotaxy: all trochanteral setae setiform.

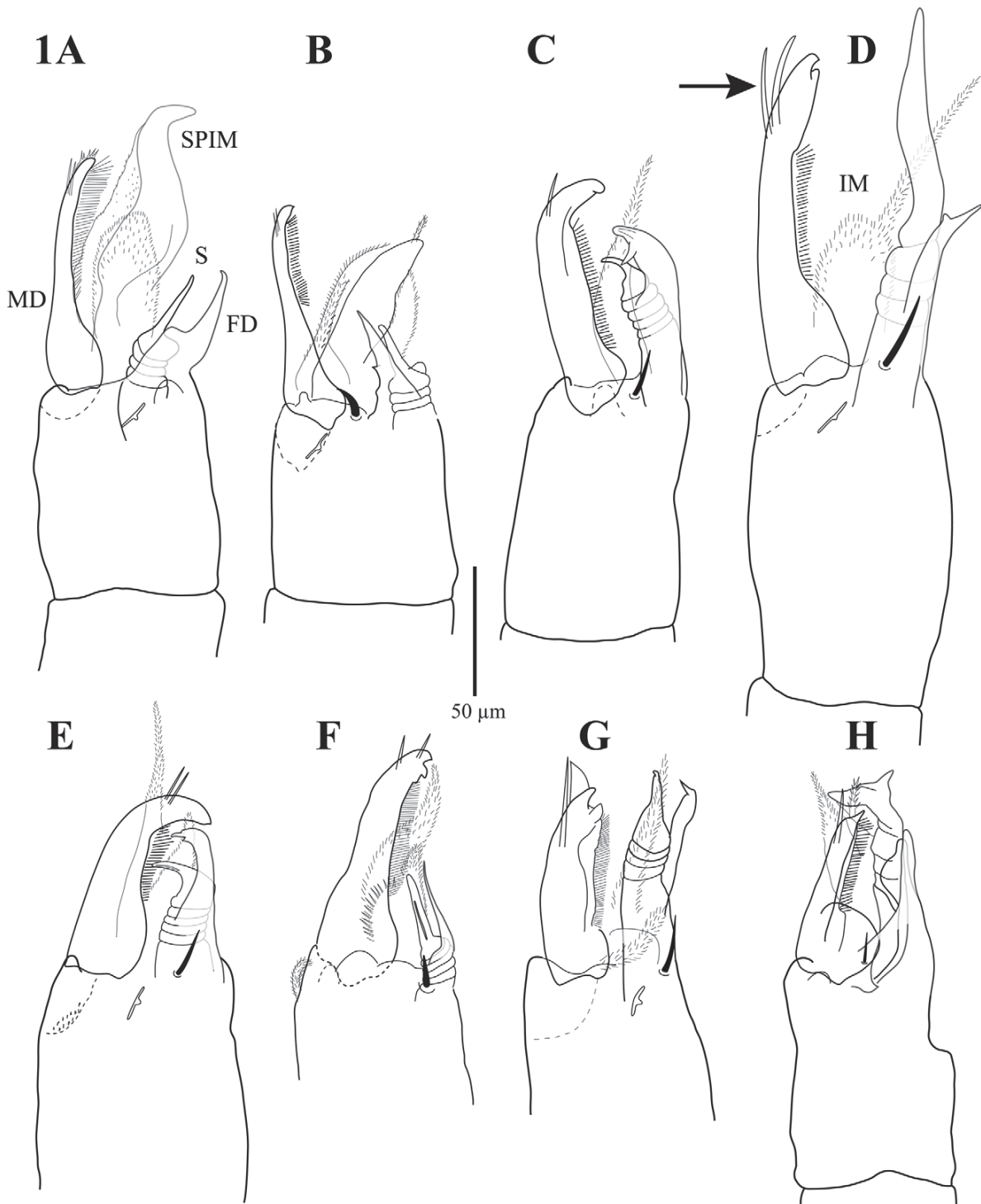
**Material examined.** Holotype male (OSAL003042): Côte d'Ivoire, Zanzan, Comoé Nat. Pk., 2001, coll. Mahsberg, D., hand collected from *Pelmatojulus tigrinus* Hoffman & Mahsberg (Pachybolidae) (host at BUW). Same data: OSAL003035, 003041, 003127-30, M; OSAL003036-40, 0003125-26, F. Same locality, date and collector, AL006578, ex *Peridotopyge, togoensis* Demange and *Peridotopyge, maliensis* Pierrard (Odontopygidae) (hosts at BUW): OSAL003045, 003047, M; OSAL003044, 003046, F. Same locality, date and collector, ex *Lacinogonus* sp. (Odontopygidae) (host at BUW): OSAL003050-51, M; OSAL003049, 003052, 003122-24, F.

**Deposition of types.** Holotype male, OSAL003042, deposited at OSAL. Paratypes at FMNH and ZSM.

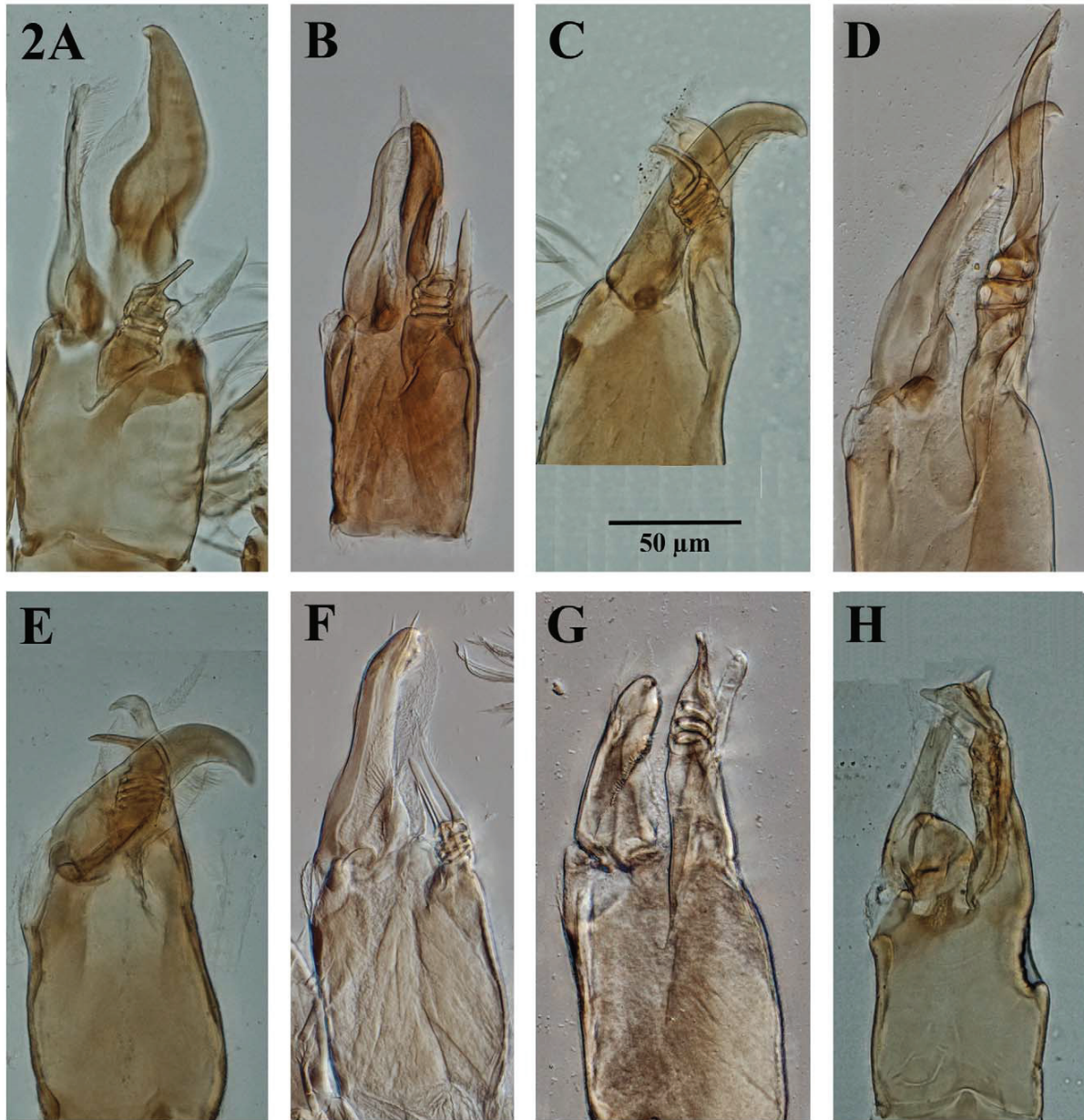
**Etymology.** This species is named in honor of Dr. Dieter Mahsberg, Universität Würzburg, who collected the specimens.

**Taxonomic remarks.** In the male, the presence of a thin movable digit is shared with *A. pachybolus* and *A. madagascariensis*. The partial sclerotisation of the large interdigital membrane is also shared with *A. pachybolus* (and possibly *A. cautus*). Finally, male *A. mahsbergi* share with *A. pachybolus* and *A. sanghae* a connection of the shields containing setae *St1* with the sternitoventral shield, although the connection is only partial in *A. mahsbergi* and *A. sanghae*, while complete in *A. pachybolus* (Fig. 6B). The high length ratio of setae *Z5* to *S5* appears to be unique, as is the absence of setae *pl2* on femora I.

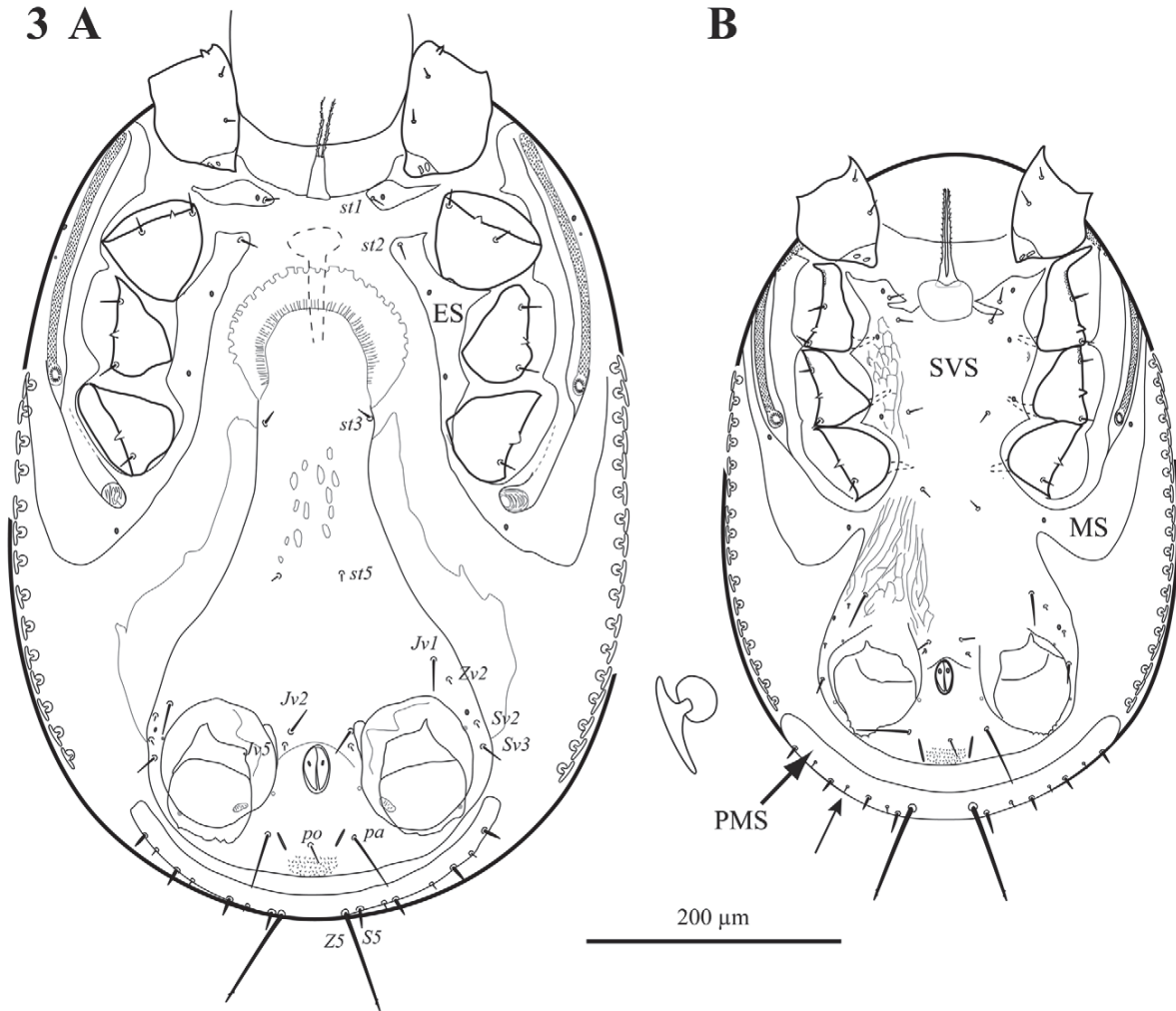
**Biology.** Even though we recovered this species from four different hosts in two different families, we found no recognisable differences based on host species. This is consistent with low levels of host specificity, although this conclusion has to remain tentative given the relatively small sample size.



**FIGURE 1.** *Afroheterozercion* spp., chelicerae male. A, *A. mahsbergi* **nov. sp.** (OSAL003051); B, *A. pachybolus* (Fain) (OSAL092084); C, *A. sanghae* **nov. sp.** (OSAL053288); D, *A. spirostreptus* (Fain) (OSAL053950); E, *A. gabonensis* **nov. sp.** (OSAL92096); F, *A. goodmani* **nov. sp.** (OSAL102681); G, *A. tanzaniensis* **nov. sp.** (OSAL53955); H, *A. madagascariensis* **nov. sp.** (OSAL053962). Abbreviations: FD: fixed digit; IM: interdigital membrane; MD: movable digit; S: spermatodactyl; SPIM: sclerotised portion interdigital membrane. Arrow to ventral blade-like processes.



**FIGURE 2.** *Afroheterozercus* spp., chelicerae male, photographs. A, *A. mahsbergi* nov. sp. (OSAL003045); B, *A. pachybolus* (Fain) (OSAL092070); C, *A. sanghae* nov. sp. (OSAL053288); D, *A. spirostreptus* (Fain) (OSAL053952); E, *A. gabonensis* nov. sp. (OSAL053942); F, *A. goodmani* nov. sp. (OSAL102681); G, *A. tanzaniensis* nov. sp. (OSAL053955); H, *A. madagascariensis* nov. sp. (OSAL053962).



**FIGURE 3.** *Afroheterozercon mahsbergi* nov. sp., venter adults. A, female (OSAL003040); B, male (OSAL003042). Inset, detail “anchor-shaped” lateral spines. Abbreviations: ES: endopodal shield; MS: metapodal shield; PMS: posterior marginal sclerite; SVS: sternitoventral shield. Small arrow: “tiny seta” on posterior marginal sclerite.

***Afroheterozercon pachybolus* (Fain)**

(Figs 1B, 2B, 4B, 5B, 6)

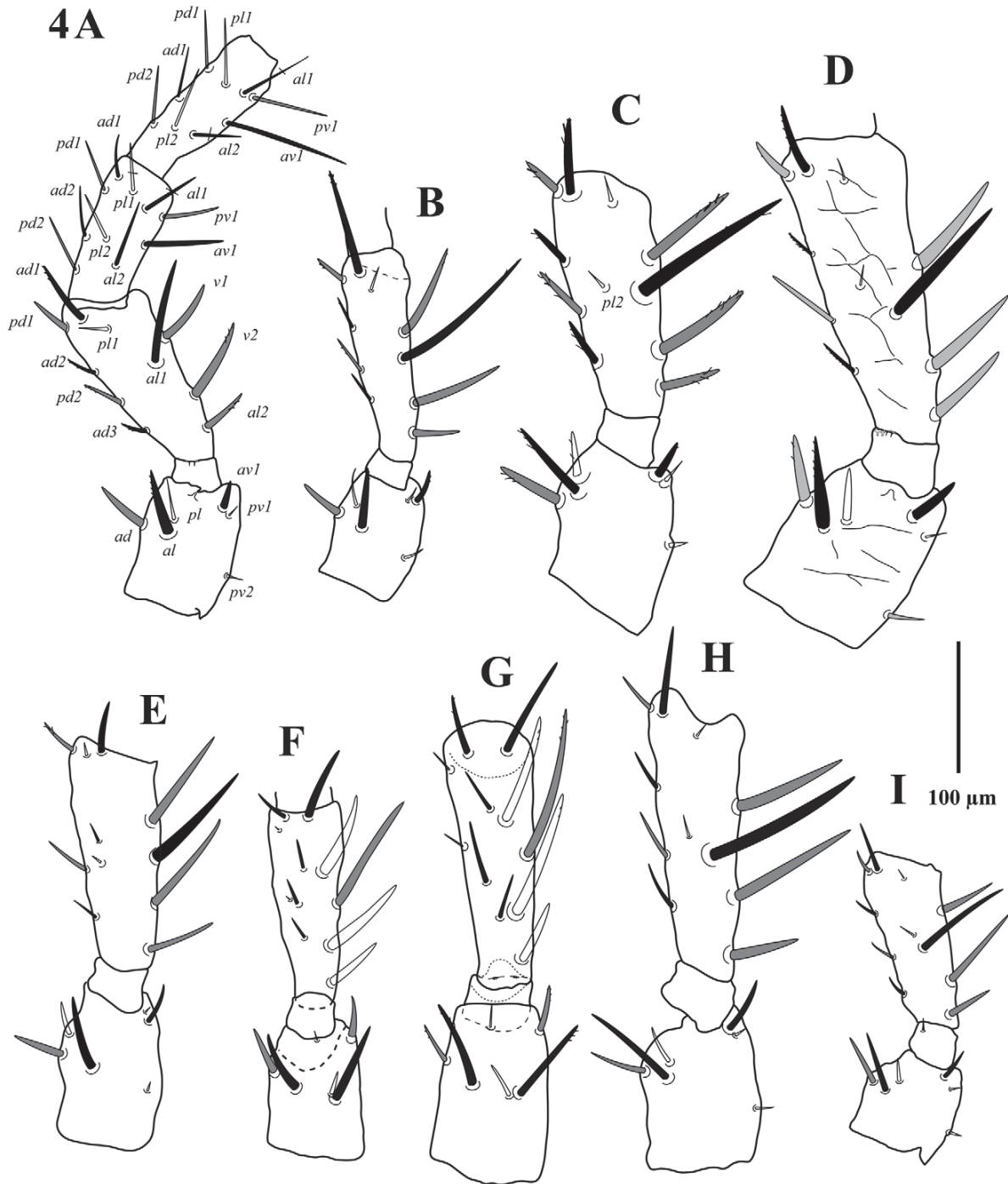
*Heterozercon pachybolus* Fain, 1988: 241.

*Afroheterozercon pachybolus*.— Fain, 1989: 153

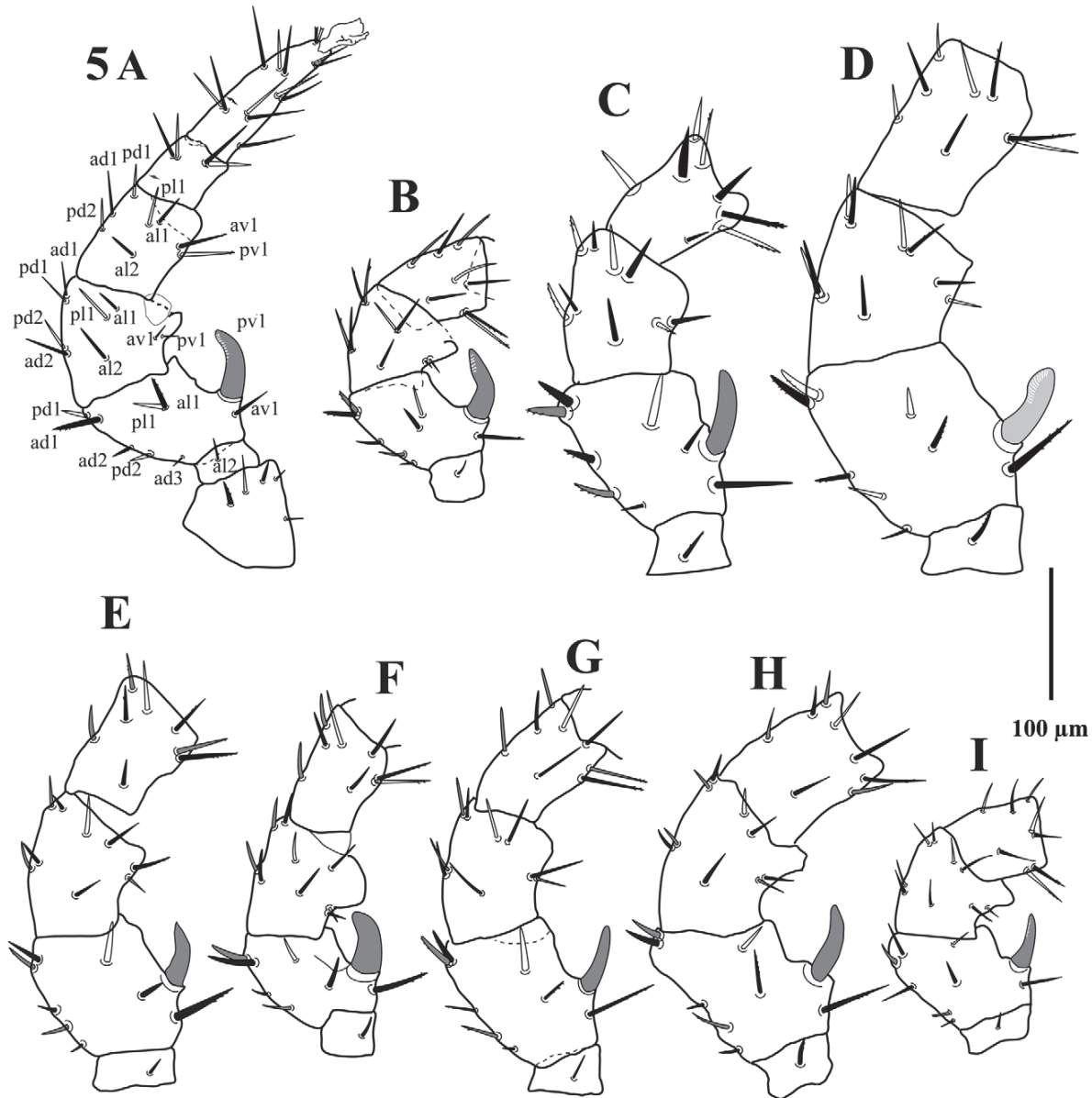
**Diagnosis.** Movable digit in male thin, fixed digit and spermatodactyl short; large interdigital membrane partially modified into a sclerotised process; shields including setae *St1* broadly connected to the sternitoventral shield. Adults with relatively small numbers of lateral spines (13–16).

**Description.** Male chelicera: spermatodactyl very short, with a thin, straight distal section (Fig. 1B, 2B). Fixed digit short, pointed, with a small basal spur; movable digit straight, thin. Large interdigital membrane partially modified into a sclerotised process. Male venter (Fig. 6B): shields including setae *St1* broadly connected to the sternitoventral shield. Setae *pa* relatively short, length < 3/4 length of setae *Z5*. Setae *S5* relatively short, length < 1/2 length of setae *Z5*. Posterior marginal sclerite with 6 (rarely 7) tiny setae (also in female). Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 13–16. Female venter (Fig. 6A): setae *S5* relatively short, length < 1/2 length of setae *Z5*. Number of anchor-shaped spines on the latero-ventral region of the





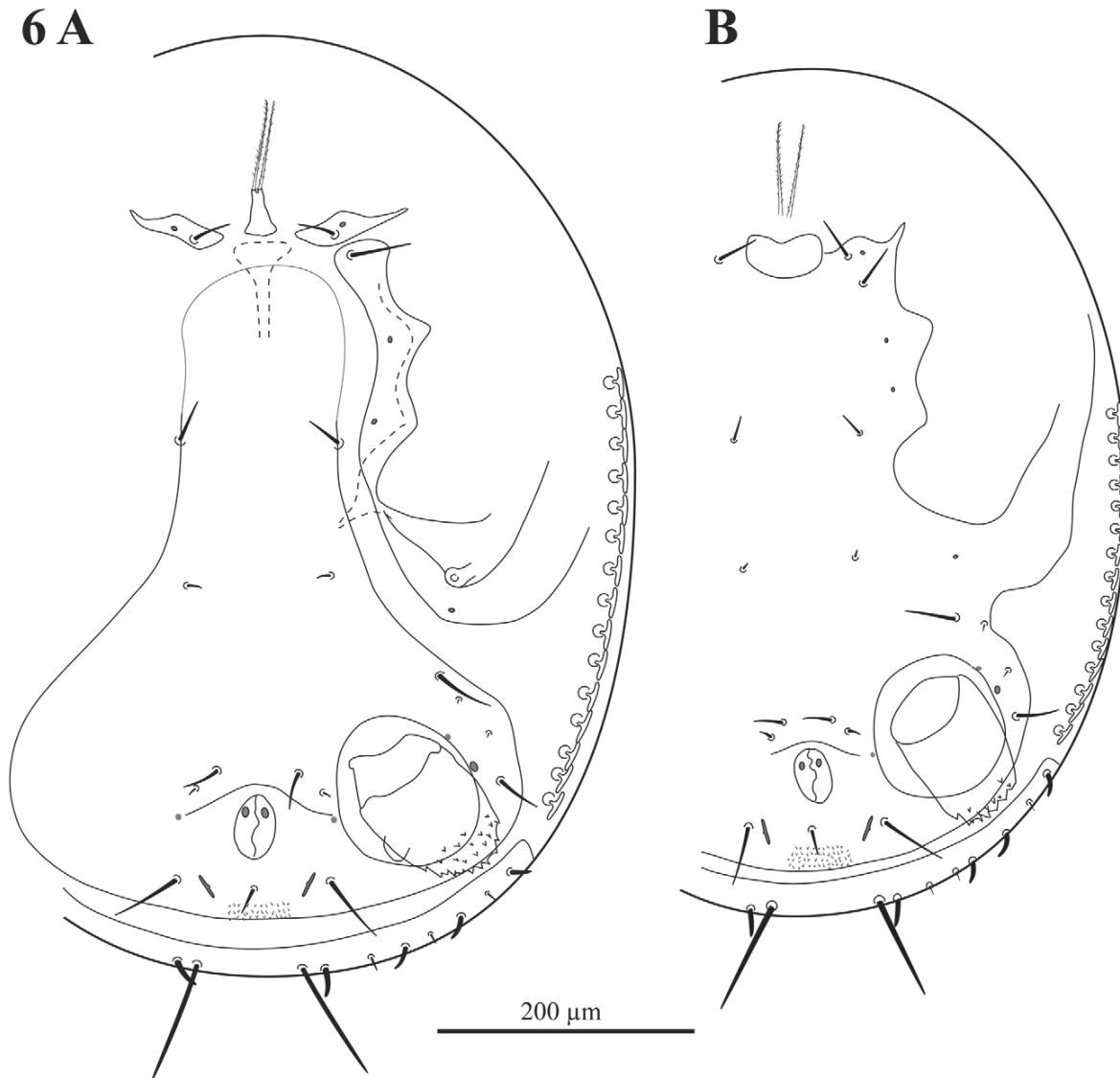
**FIGURE 4.** *Afroheterozercus* spp., partial leg I, male. A, *A. mahsbergi* **nov. sp.** (OSAL003042); B, *A. pachybolus* (Fain) (OSAL053989); C, *A. sanghae* **nov. sp.** (OSAL053998); D, *A. spirostrepius* (Fain) (OSAL053950); E, *A. gabonensis* **nov. sp.** (OSAL053942); F, *A. goodmani* **nov. sp.** (OSAL102682); G, *A. ancoratus* Fain (holotype); H, *A. tanzaniensis* **nov. sp.** (OSAL053955); I, *A. madagascariensis* **nov. sp.** (OSAL053961).



**FIGURE 5.** *Afroheterozercion* spp., partial leg II, male. A, *A. mahsbergi* nov. sp. (OSAL003042); B, *A. pachybolus* (Fain) (OSAL053989); C, *A. sanghae* nov. sp. (OSAL053998); D, *A. spirostreptus* (Fain) (OSAL053950); E, *A. gabonensis* nov. sp. (OSAL053942); F, *A. goodmani* nov. sp. (OSAL102682); G, *A. ancoratus* Fain (holotype); H, *A. tanzaniensis* nov. sp. (OSAL053955); I, *A. madagascariensis* nov. sp. (OSAL053961).

opisthosoma 14–16. Male legs I: chaetotaxy (Fig. 4B): coxae I setae spinose (also in female). Trochanteral setae *av1* relatively short; length less than, or equal to, setae *pl*. Trochanteral setae *ad*, *al* and *pl* without distinct barbs. Femoral setae *pl2* present. Femoral setae *ad3* length relatively long; length subequal to that of setae *pd2*. Femoral setae *pd1*, *al2* and *v2* without distinct barbs. Femoral setae *al2* unusually short, setae *al1* moderately long; length ratio setae *al1* / *al2* more than 2.7. Male legs II, chaetotaxy (Fig. 5B): femoral setae *pv1* moderately wide (<20  $\mu$ m). Setae *av1* relatively short (length ratio *av1* / *pv1* less than 0.8). Femoral setae *pd1* distinctly shorter than setae *ad1*. Femoral setae *ad2* without distinct barbs. Genua with a distinct ventrodiscal outgrowth. Genual setae *av1* very short; length half of that of setae *pv1*. Tibial setae *av1* with distinct barbs. Adult legs III, chaetotaxy: one or more trochanteral setae spine-like.

**Material examined.** Democratic Republic of Congo, forest of Kwango river, 5°S 17°E, 19 April 1964, coll. A. Fain, ex *Pachybolus macrosternus*, male holotype, IRSNB. New material: Central African Republic, Sangha-Mbaéré, Parc National Dzanga-Ndoki, 510 m, Mabéa Bai, 1–7 May 2001, coll. B. L. Fisher, ex pitfall trap, with unidentified millipede (host at CASEnt, field number AL6647): OSAL053989-91, 053994, 053997, male. Same locality, date, collector, ex pitfall trap with unidentified millipede (CASEnt AL6667): OSAL092084, M; OSAL092083, female. Same locality, date, collector, ex pitfall trap with unidentified millipede (CASEnt AL6683): OSAL092069-71, male; OSAL092072-73, 092095, female. Same locality, date, collector, ex pitfall trap with unidentified millipede (CASEnt AL6694): OSAL092087, 092090, males; OSAL092088-89, 092091-92, females.



**FIGURE 6.** *Afroheterozercus pachybolus* (Fain), venter adults. A, female (OSAL092091); B, male (OSAL092084).

**Deposition of specimens.** New material deposited at CASEnt and OSAL.

**Taxonomic remarks.** Our specimens correspond in most available details to the description by Fain (1988, 1989). The one discrepancy concerns the number of anchor-shaped lateral spines, 17–18 according to the description (Fain 1988), but 13–15 in our specimens and in Fain's figures (1988, 1989). Examination of the male holotype showed 15 lateral spines, suggesting the number in the description by Fain (1988) is inaccurate. The original description was based on one specimen only. The current description adds data on multiple male

specimens and includes the first notes on the female. In the male, *A. pachybolus* resembles *A. goodmani* by having a short spermatodactyl and short fixed cheliceral digit, and *A. mahsbergi* by sharing the thin movable digit, the partial sclerotisation of the large interdigital membrane, and the fusion of the shields carrying setae *St1* with the sternitoventral shield. It differs from both of those species by the male chelicerae that combine a short spermatodactyl and fixed digit with a thin movable digit, the presence of sclerotisation of the interdigital membrane, plus complete fusion of the shields carrying setae *St1* with the sternitoventral shield.

***Afroheterozercon sanghae* nov. sp.**

(Figs 1C, 2C, 4C, 5C, 7)

**Diagnosis.** Male chelicera with a distinct subterminal spine on the fixed digit and a relatively long basal section of the spermatodactyl, shields carrying setae *St1* partially connected to the sternitoventral shield, and unusually long setae *al1* on femora I. In adults length ratio of setae *Z5* to *S5* unusually small (1.4–2.1) due to relatively long setae *S5* and short setae *Z5*.

**Description.** Male chelicera: spermatodactyl of medium length, with a relatively long basal section (Figs 1C, 2C). Fixed digit robust, relatively long, with a distinct subterminal spine, resulting in a somewhat bifid appearance; movable digit robust, hook-like. Interdigital membranes normal. Male venter (Fig. 7B): shields including setae *St1* partially connected to the sternitoventral shield. Setae *pa* long, length > 3/4 length of setae *Z5*. Setae *S5* relatively long, length > 1/2 length of setae *Z5*. Posterior marginal sclerite with 6 tiny setae. Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 17 / side. Female venter (Fig. 7A): setae *S5* relatively long, length > 1/2 length of setae *Z5*. Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 18–22 / side. Male legs I, chaetotaxy (Fig. 4C): coxal setae relatively thin, setiform (same in female). Trochanteral setae *ad*, *al* and *pl* with distinct barbs. Trochanteral setae *av1* relatively short; length less than, or equal to, setae *pl*. Femoral setae *pl2* present. Femoral setae *ad3* length relatively long; length subequal to that of setae *pd2*. Femoral setae *pd1*, *al2* and *v2* with distinct barbs. Femoral setae *al1* very long, setae *al2* average length; length ratio setae *al1* / *al2* more than 2.7. Male legs II, chaetotaxy (Fig. 5C): femoral setae *pv1* moderately wide (<20  $\mu\text{m}$ ). Setae *av1* relatively short (length ratio *av1* / *pv1* less than 0.8). Femoral setae *pd1* relatively long; length subequal to that of setae *ad1*. Femoral setae *ad2* with distinct barbs. Genua without a distinct ventrodiscal outgrowth. Genua setae *av1* relatively long; almost twice as long as setae *pv1*. Tibial setae *av1* with distinct barbs. Adult legs III, chaetotaxy: one or more trochanteral setae spine-like.

**Material examined.** Holotype male (CASEnt 9039945), Central African Republic, Sangha-Mbaéré, Parc National Dzanga-Ndoki, 510m, Mabéa Bai, 1–7 May 2001, coll. B. L. Fisher, (BLF4003), ex pitfall trap in rainforest; on unidentified millipede (host at CASEnt, field number AL006647). Same data: OSAL053992, 053996, 053998, males. Central African Republic, Sangha-Mbaéré, Reserve Spéciale de Forêt Dense de Dzanga-Sangha, 10–17 May 2001, coll. B. L. Fisher (BLF4083), ex pitfall trap, halfway up rocky slope in rainforest; on unidentified millipede (CASEnt AL006727): OSAL053286, 0053288, male; OSAL053287, 053289-90, F. Central African Republic, Sangha-Mbaéré, Poli Lodge, Bayanga, 325m, 6 July 1998, J. W. Wenzel, ex unidentified millipede (OSAL AL05530): OSAL003032, male; OSAL003033-34, females.

**Deposition of types.** Holotype male deposited at CASEnt (CASEnt 9039945). Paratypes at CASEnt and OSAL.

**Etymology.** This species is named after the prefecture, Sangha-Mbaéré, in which the material was collected.

**Taxonomic remarks.** The males of *A. sanghae* share with *A. pachybolus* and *A. mahsbergi* the connection of the shields containing setae *St1* with the sternitoventral shield, but the connection is only partial in *A. sanghae* and *A. mahsbergi*, and complete in *A. pachybolus*. *Afroheterozercon pachybolus* and *A. mahsbergi* differ from *A. sanghae* by the presence (vs. absence) of sclerotisation of the interdigital membrane and by thin, rather than robust, movable digits. *Afroheterozercon sanghae* shares the distinct distal hook of the movable digit in the male, the number of lateral anchor-shaped spines (in both males and females), and the length ratio of setae *Z5* / *S5* with *A. ancoratus* and *A. gabonensis*. The males of *A. sanghae* differ from both of those species by the fusion of the shields carrying setae *St1* with the sternitoventral shield, and by the presence of a distinct subterminal spine on the fixed digit of the male chelicera.

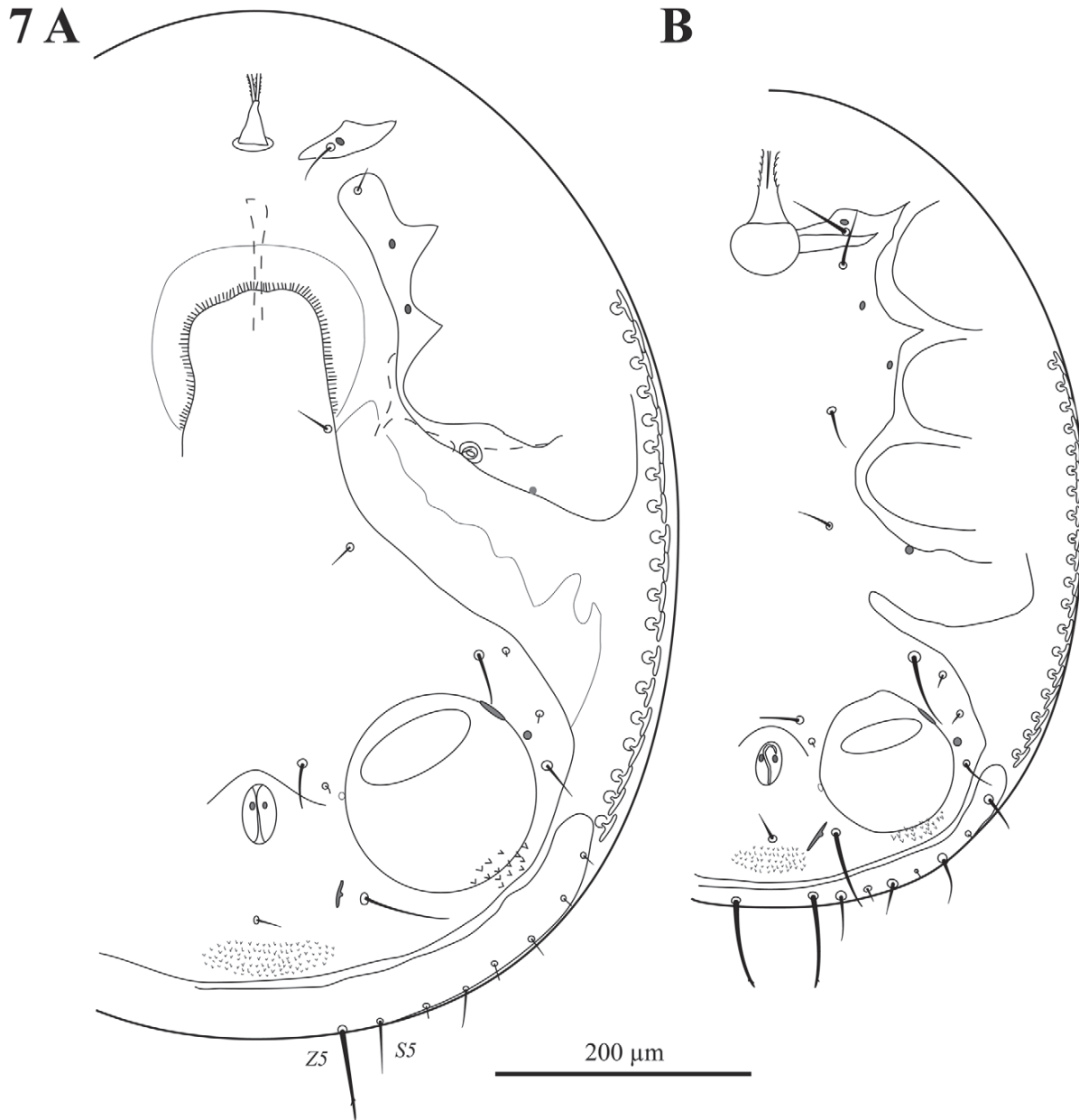


FIGURE 7. *Afroheterozercon sanghae* nov. sp., venter adults. A, female (OSAL003034; B, male (OSAL053998).

***Afroheterozercon spirostreptus* (Fain)**

(Figs 1D, 2D, 4D, 5D)

*Heterozercon spirostreptus* Fain, 1988: 237.

*Afroheterozercon spirostreptus*.— Fain, 1989: 153.

**Diagnosis.** Male chelicera with long movable digit (118–128 μm) and a very long spermatodactyl, especially the distal section (80–90 μm); shields carrying setae *St1* not connected to the sternitoventral shield; with an unusually small length ratio of femoral setae *al1* to *al2* (1.6–1.7). Adults always with more than 6 tiny setae on posterior marginal sclerite. In adults with relatively small numbers of lateral spines. The largest species examined.

**Description.** Male chelicera (Fig. 1D, 2D): spermatodactyl long; base long, coiled section extended, distal section very long and flap-like. Fixed digit of medium length, with a small subterminal knob; movable digit well developed, robust, with a small terminal tooth. Interdigital membranes normal. Male venter: shields including setae *St1* not connected to the sternitoventral shield. Setae *pa* relatively long, length  $> 3/4$  length of setae *Z5*. Setae *S5* relatively short, length  $< 1/2$  length of setae *Z5*. Posterior marginal sclerite with distinctly more than 6 tiny setae (same in female). Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 13 / side. Female venter: setae *S5* relatively short, length  $< 1/2$  length of setae *Z5*. Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 12–17 / side. Male legs I, chaetotaxy (Fig. 4D): coxal setae setiform (same in female). Trochanteral setae *av1* relatively short; length less than, or equal to, setae *pl*. Trochanteral setae *ad* and *al* with distinct barbs; setae *pl* without barbs. Femoral setae *pl2* present. Femoral setae *ad3* length relatively short; length  $< 2/3$  of that of setae *pd2*. Femoral setae *pd1*, *al2* and *v2* without distinct barbs. Femoral setae *al2* relatively long, setae *al1* of average length; length ratio setae *al1* / *al2* less than 1.7. Male legs II, chaetotaxy (Fig. 5D): femoral setae *pv1* wide ( $> 20 \mu\text{m}$ ). Setae *av1* relatively long (length ratio *av1* / *pv1* more than 0.8). Femoral setae *pd1* relatively long; length subequal to that of setae *ad1*. Femoral setae *ad2* with distinct barbs. Genua without a distinct ventrodiscal outgrowth. Genua setae *av1* relatively long; length subequal to that of setae *pv1*. Tibial setae *av1* with distinct barbs. Adult legs III, chaetotaxy: one or more trochanteral setae spine-like.

**Material examined.** Democratic Republic of Congo, Congo-Central, Mayumbe forest, Chiloango, Madiakoko, 25 March 1964, coll. A. Fain, ex *Spirostreptus cornutus*, 2 males, paratypes, 2 females, paratypes, IRSNB. New material: Gabon, Ogooué-Maritime, Monts Doudou, camp 1, 110m, Réserve de la Moukalaba-Douboua, 12.2 km NW Doussala, 25 February–03 March 2000, coll. S. M. Goodman, ex Spirostreptida (host at FMNH, AL6492): OSAL053950, 053952, M; OSAL053951, female. Same locality, date and collector, ex Spirostreptida (FMNH, AL006503): OSAL053947, 092068, 092100, male; OSAL053946, female. Hosts at FMNH, specimen numbers FMNH-INS-5479–5486.

**Deposition of specimens.** New material deposited at FMNH and OSAL.

**Taxonomic remarks.** Our specimens correspond quite well to the description by Fain (Fain 1988, 1989). The only notable discrepancy is in the number of anchor-shaped lateral spines in the female. Fain (1988) reported 12–13 in the description, matching the 12–15 noticed in our specimens, but Fain's Fig. 1 shows 16–18 lateral spines (Fain 1988), matching the numbers observed in the paratypes examined. The number of spines in the male matches better (13–14 in Fain's description and figures, the paratypes examined and our specimens). We do not believe that this difference by itself is sufficient to warrant a new species, although it is certainly possible that the material grouped under this name may represent a species complex. The extremely long spermatodactyl and movable digit of the chelicera, and the presence in both adults of distinctly more than 6 tiny setae on the posterior marginal sclerite easily differentiate this species from all other *Afroheterozercon*.

***Afroheterozercon gabonensis* nov. sp.**

(Figs 1E, 2E, 4E, 5E, 8)

**Diagnosis.** Male chelicera with a distinct terminal hook in both the spermatodactyl and the fixed digit; shields carrying setae *St1* not connected to the sternitoventral shield; low length ratio of setae *Z5* to *S5* (1.8–1.9). Adult with a very high number of lateral spines (18–24).

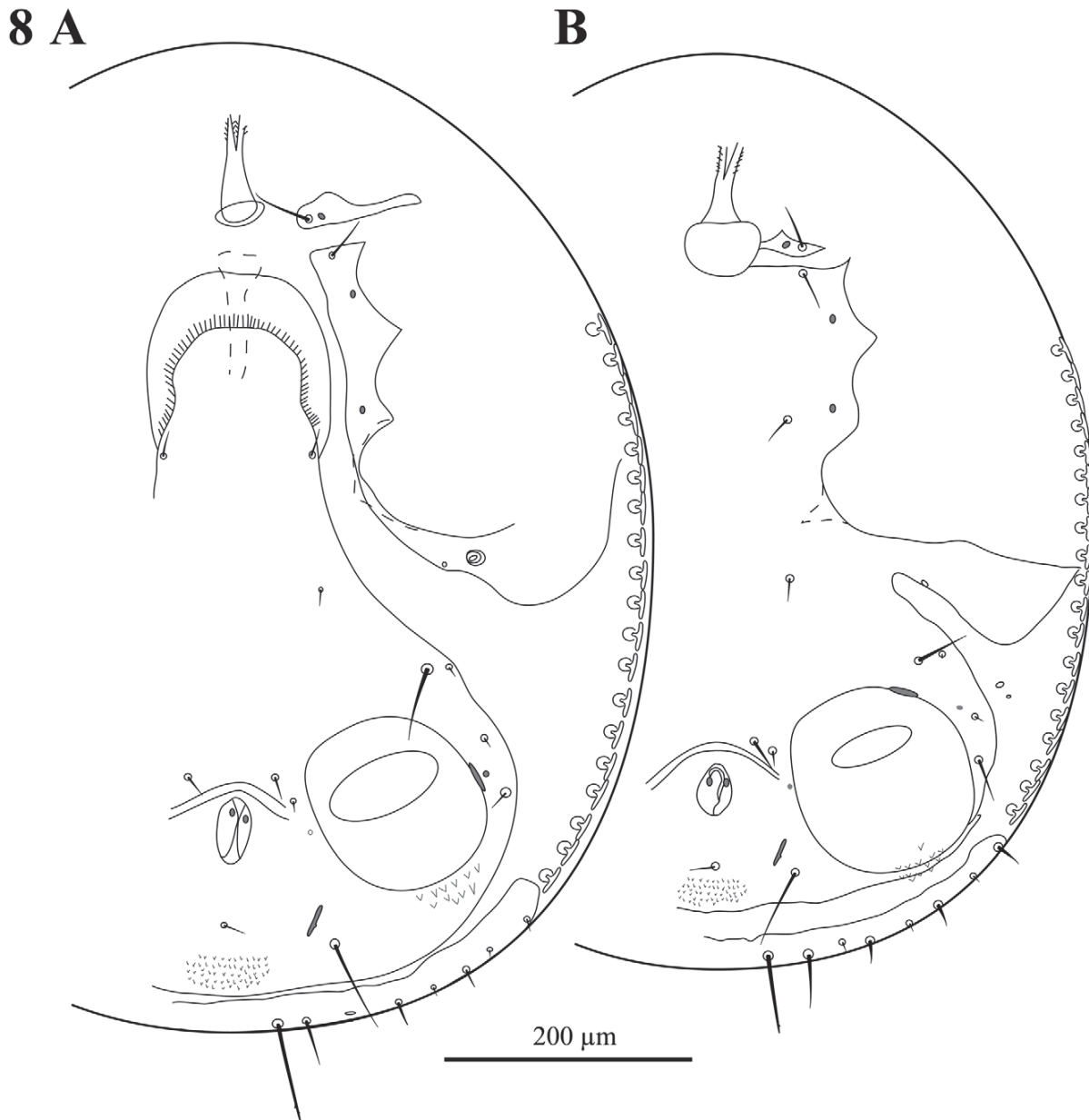
**Description.** Male chelicera (Figs 1E, 2E): spermatodactyl of medium length; base of medium length, distal section relatively thin, finger-like, with a distinct terminal hook. Fixed digit sturdy, with a distinct terminal hook; movable digit robust, strongly curved. Interdigital membranes normal. Male venter (Fig. 8B): shields including setae *St1* not connected to the sternitoventral shield. Setae *pa* relatively long, length  $> 3/4$  length of setae *Z5*. Setae *S5* relatively long, length  $> 1/2$  length of setae *Z5*. Posterior marginal sclerite with 6 tiny setae. Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 18–22 / side. Female venter (Fig. 8A): setae *S5* relatively short, length approximately  $1/2$  length of setae *Z5*. Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 22–24 / side. Male legs I, chaetotaxy (Fig. 4E): coxal setae setiform (same in female). Trochanteral setae *av1* relatively long; distinctly longer than setae *pl*. Trochanteral setae *ad*, *al* and *pl* without distinct barbs. Femoral setae *pl2* present. Femoral setae *ad3* length relatively short; length less than  $2/3$  that of setae *pd2*. Femoral setae *al2* and *v2* without distinct barbs; setae *pd1* with barbs. Femoral setae *al1* and *al2* of average

length; length ratio setae *al1* / *al2* between 1.9 and 2.2. Male legs II, chaetotaxy (Fig. 5E): femoral setae *pv1* moderately wide (<20  $\mu$ m). Setae *av1* relatively long (length ratio *av1* / *pv1* more than 0.8). Femoral setae *pd1* relatively long; length subequal to that of setae *ad1*. Femoral setae *ad2* without distinct barbs. Genua without a distinct ventrodistal outgrowth. Genual setae *av1* relatively long; length almost twice that of setae *pv1*. Tibial setae *av1* with distinct barbs. Adult legs III, chaetotaxy: one or more trochanteral setae spine-like.

**Material examined.** Holotype male (OSAL053942): Gabon, Mt. Doudou, camp 3, 585–660 m, Aire d'Exploitation Rationnelle de Faune des Monts Doudou, 25.2 km NW Doussala, 52.6 km NW Mourindi, -2.2272, 10.3945, 14–20 March 2000, S. M. Goodman, ex Spirostreptida (host in FMNH, AL6508) in mid-level rainforest. Same data: OSAL003119-21, 053943-44, 092096-99, M; OSAL053941, 053945, females. Hosts at FMNH, specimen numbers FMNH-INS-5477-5478.

**Deposition of types.** Holotype male, OSAL053942, deposited at FMNH. Paratypes at FMNH and OSAL.

**Etymology.** This species is named after the country in which the material was collected.



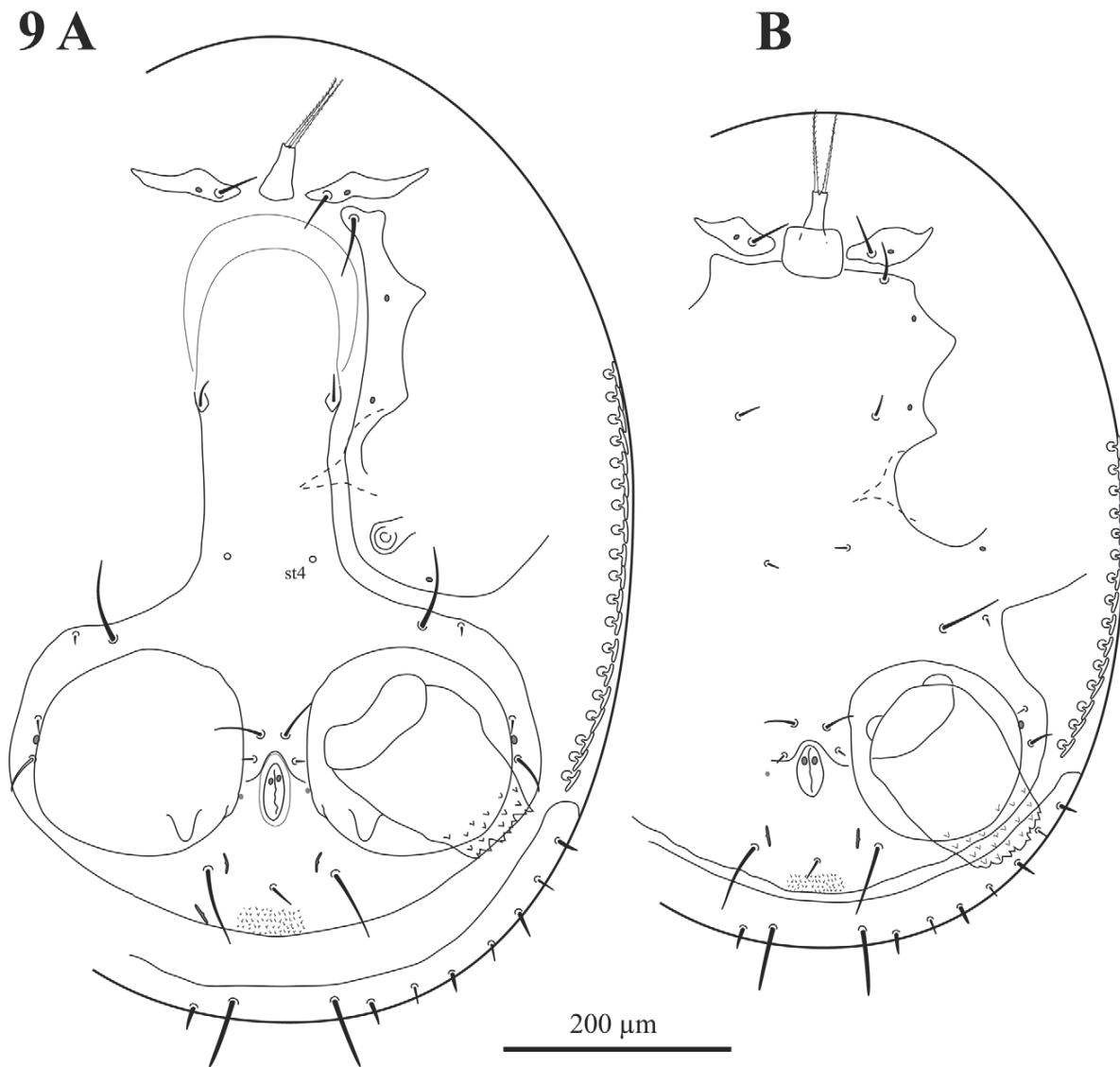
**FIGURE 8.** *Afroheterozercion goodmani* nov. sp., venter adults. A, female (OSAL053949); B, male (OSAL102681).

**Taxonomic remarks.** *Afroheterozercon gabonensis* shares the robust development of the cheliceral digits, the number of lateral anchor-shaped spines in both males and females, and the length ratio of setae *Z5* / *S5* with *A. ancoratus* and *A. sanghae*. However, it differs from *A. sanghae* by the lack of fusion of the shields carrying seta *St1* with the sternitoventral shield, and the lack of a subterminal spine on the fixed digit of the male chelicera, and from *A. ancoratus* by the hooked (not straight) distal portion of both the spermatodactyl and fixed digit, and the smaller length ratio of femur I setae *al1* / *al2* (1.9–2.2 vs. 2.5).

***Afroheterozercon goodmani* nov. sp.**

(Figs 1F, 2F, 4F, 5F, 9)

**Diagnosis.** Male chelicera with a short spermatodactyl with a very short basal section; shields carrying setae *St1* not connected to the sternitoventral shield; with a short, but relatively wide, spur on femora II (setae *pv1*).



**FIGURE 9.** *Afroheterozercon gabonensis* nov. sp., venter adults. A, female (OSAL053741); B, male (OSAL053942).



**Description.** Male chelicera (Figs 1F, 2F): spermatodactyl short; basal part very short, coiled section tight, distal extension relatively thin, finger-like, and straight. Fixed digit short, straight, pointed; movable digit robust, relatively straight with a distinct subterminal tooth. Interdigital membranes normal. Male venter (Fig. 9B): shields including setae *St1* not connected to the sternitoventral shield. Setae *pa* relatively long, length subequal to setae *Z5*. Setae *S5* relatively short, length < 1/2 length of setae *Z5*. Posterior marginal sclerite with 6 tiny setae. Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 13–17 / side. Female venter (Fig. 9A): setae *S5* relatively short, length < 1/2 length of setae *Z5*. Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 18–21 / side. Male legs I, chaetotaxy (Fig. 4F): coxal setae spinose (same in female). Trochanteral setae *av1* relatively short; length less than, or equal to, setae *pl*. Trochanteral setae *ad*, *al* and *pl* without distinct barbs. Femoral setae *pl2* present. Femoral setae *ad3* length relatively long; length subequal to that of setae *pd2*. Femoral setae *pd1*, *al2* and *v2* without distinct barbs. Femoral setae *al1* and *al2* all of average length; length ratio setae *al1* / *al2* between 2.0 and 2.1. Male legs II, chaetotaxy (Fig. 5F): femoral setae *pv1* wide (>20 µm). Setae *av1* relatively long (length ratio *av1* / *pv1* more than 0.8). Femoral setae *pd1* distinctly shorter than setae *ad1*. Femoral setae *ad2* without distinct barbs. Genua with a distinct ventrodiscal outgrowth. Genual setae *av1* relatively short; length subequal to that of setae *pv1*. Tibial setae *av1* with distinct barbs. Adult legs III, chaetotaxy: one or more trochanteral setae spine-like.

**Material examined.** Holotype male (OSAL102681): Gabon, Ogooué-Maritime, Monts Doudou, camp 1, 110 m, Réserve de la Moukalaba-Douboua, 12.2 km NW Doussala, 25 February–3 March 2000, coll. S. M. Goodman, ex Spirostreptida (host at FMNH, label AL6503). Same data: OSAL053948, 092076, 102682, males; OSAL053949, female. Same locality, date, collector, ex Spirostreptida (FMNH, AL6494): OSAL092086, male; OSAL092085, female. Hosts at FMNH, specimen numbers FMNH-INS-5479-5486.

**Deposition of types.** Holotype male, OSAL102682, deposited at FMNH. Paratypes at FMNH and OSAL.

**Etymology.** This species is named in honor of Dr. Steven Goodman, Field Museum of Natural History, who collected the material from Gabon.

**Taxonomic remarks.** The short spermatodactyl and poorly developed fixed digit resemble those structures in *A. pachybolus*, but *A. goodmani* males lack the sclerotised process of the interdigital membrane and have robust, not thin, movable digits. The short, but very robust setae *pd1* on femora II are unique within *Afroheterozercon*.

### ***Afroheterozercon ancoratus* Fain 1989** (Figs 4G, 5G)

*Afroheterozercon ancoratus* Fain, 1989: 153.

**Diagnosis.** Male chelicera with a thin, straight distal section of the spermatodactyl, and a smooth, lightly curved fixed digit; shields carrying setae *St1* not connected to the sternitoventral shield; length ratio of setae *Z5* to *S5* relatively low (~ 2.0).

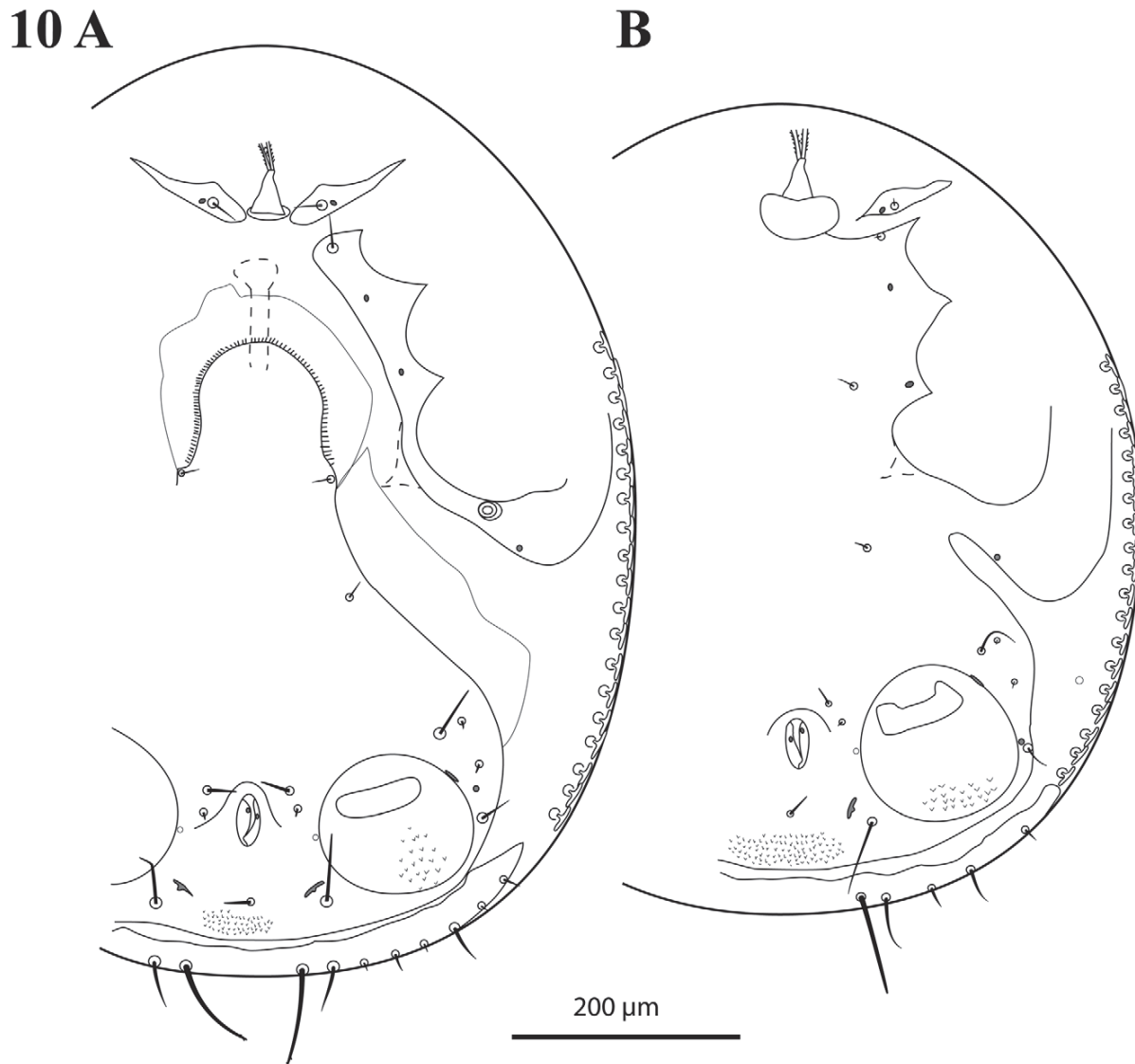
**Description** (largely based on Fain 1989, with additions based on examination of types). Male chelicera: spermatodactyl of medium length, with a thin, straight distal section. Fixed digit of moderate length, robust, ending in a point; movable digit well developed, slightly curved, with a small distal tooth. Interdigital membranes normal. Male venter: shields including setae *St1* not connected to the sternitoventral shield. Setae *pa* relatively long, length > 3/4 length of setae *Z5*. Setae *S5* ~1/2 length of setae *Z5*. Posterior marginal sclerite with 6 tiny setae (also in female). Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 16–19 / side. Female venter: setae *S5* relatively short, approximately 1/2 length of setae *Z5*. Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 20–24 / side. Male legs I, chaetotaxy (Fig. 4G): coxae I setae setiform (same in female). Trochanteral setae *av1* relatively short; length less than, or equal to, setae *pl*. Trochanteral setae *ad*, *al* and *pl* with distinct barbs. Femoral setae *pl2* present. Femoral setae *ad3* length relatively short; length about 2/3 x that of setae *pd2*. Femoral setae *pd1* with, setae *al2* and *v2* without, distinct barbs. Femoral setae *al2* of average length, setae *al1* very long; length ratio setae *al1* / *al2* ~ 2.5. Male legs II, chaetotaxy (Fig. 5G): femoral setae *pv1* moderately wide (<20 µm). Setae *av1* and *pv1* of average and similar length (length ratio *av1* / *pv1* ~ 1.0). Femoral setae *pd1* subequal in length to setae *ad1*. Femoral setae *ad2* without distinct barbs. Genua without a distinct ventrodiscal outgrowth. Genual setae *av1* relatively long; length almost twice that of setae *pv1*. Tibial setae *av1* with distinct barbs. Adult legs III, chaetotaxy: one or more trochanteral setae spine-like.

**Material examined.** Democratic Republic of Congo, Congo-Central, Mayumbe forest, near Luki river, 23 Apr 1965, coll. R. P. Bouillon, ex nest *Cubitermes* sp. (Isoptera), 1 male, holotype, 1 female, paratype, IRSNB.

**Taxonomic remarks.** *Afroheterozercon ancoratus* shares with *A. spirostreptus* and *A. gabonensis* the robust male cheliceral digits, and the relative short (relative to setae *pd2*) setae *ad3* on femora I. It differs from *A. spirostreptus* in the much smaller male chelicera and the small number of tiny setae on the posterior ventral sclerite (among others). It differs from *A. gabonensis* in the shape of the male spermatodactyl and fixed digit (with very distinct hooks in *A. gabonensis*, largely straight in *A. ancoratus*), and shorter (relative to setae *pl*) setae *av1* on trochanter I.

*Afroheterozercon tanzaniensis* nov. sp.  
(Figs 1G, 2G, 4H, 5H, 10)

**Diagnosis.** Male chelicera with a long fixed digit (87–93  $\mu\text{m}$ ), relatively short movable digit, and a spermatodactyl with a very elongated basal section; shields carrying setae *St1* not connected to the sternitoventral shield; low length ratio of setae *Z5* to *S5* (1.8–1.9).



**FIGURE 10.** *Afroheterozercon tanzaniensis* nov. sp., venter adults. A, female (OSAL053958); B, male (OSAL053954).

**Description.** Male chelicera (Figs 1G, 2G): spermatodactyl medium long; base distinctly elongate, coiled section tight, distal extension short, finger-like, straight. Fixed digit strap-like, relatively long, with a small terminal spine; movable digit relatively short, robust, with a strong subterminal knob. Interdigital membranes normal. Male venter (Fig. 10B): shields including setae *St1* not connected to the sternitoventral shield. Setae *pa* relatively long, length > 3/4 length of setae *Z5*. Setae *S5* relatively long, length > 1/2 length of setae *Z5*. Posterior marginal sclerite with 6 tiny setae. Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 16–19 / side. Female venter (Fig. 10A): setae *S5* relatively long, approximately 1/2 length of setae *Z5*. Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 17–19 / side. Male legs I, chaetotaxy (Fig. 4H): coxal setae relatively thin, setiform (same in female). Trochanteral setae *av1* relatively long; length similar to, or exceeding that of, setae *pl*. Trochanteral setae *ad*, *al* and *pl* without distinct barbs. Femoral setae *pl2* present. Femoral setae *ad3* length relatively long; length subequal to that of setae *pd2*. Femoral setae *pd1*, *al2* and *v2* without distinct barbs. Femoral setae *al1* and *al2* relatively long; length ratio setae *al1* / *al2* more between 1.9 and 2.1. Male legs II, chaetotaxy (Fig. 5H): femoral setae *pv1* moderately wide (<20 µm). Setae *av1* relatively long (length ratio *av1* / *pv1* more than 0.8). Femoral setae *pd1* relatively long; length subequal to that of setae *ad1*. Femoral setae *ad2* without distinct barbs. Genua without a distinct ventrodiscal outgrowth. Genua setae *av1* moderately long; length subequal to setae *pv1*. Tibial setae *av1* with distinct barbs. Adult legs III, chaetotaxy: all trochanteral setae setiform.

**Material examined.** Holotype male (OSAL053955): Tanzania, Tanga, Mazumbai, 1 January 1981, coll. K. M. Howell, ex “common spirostrepsid” (no data on host depository). Same data: OSAL053954, male, OSAL053956–58, female.

**Deposition of types.** Holotype male, OSAL053955, deposited at OSAL. Paratypes at OSAL.

**Etymology.** This species is named after the country in which the material was collected.

**Taxonomic remarks.** The movable digit of the male chelicera, robust with a terminal tooth, is shared with *A. goodmani*, while the long, thin fixed digit resembles that in *A. ancoratus* and *A. mahsbergi*, but the combination of these two characteristics appears to be unique.

#### ***Afroheterozercon madagascariensis* nov. sp.**

(Figs 1H, 2H, 4I, 5I, 11)

**Diagnosis.** Male chelicera with a straight, thin movable digit and a highly unusual spermatodactyl with a distally expanded section; shields carrying setae *St1* not connected to the sternitoventral shield; unusually short setae *al1* on femora I (75–84 µm). In the adults a high length ratio of setae *Z5* to *S5* (3.6–5.4). The smallest species studied (length males 600–700 µm; females 650–800 µm).

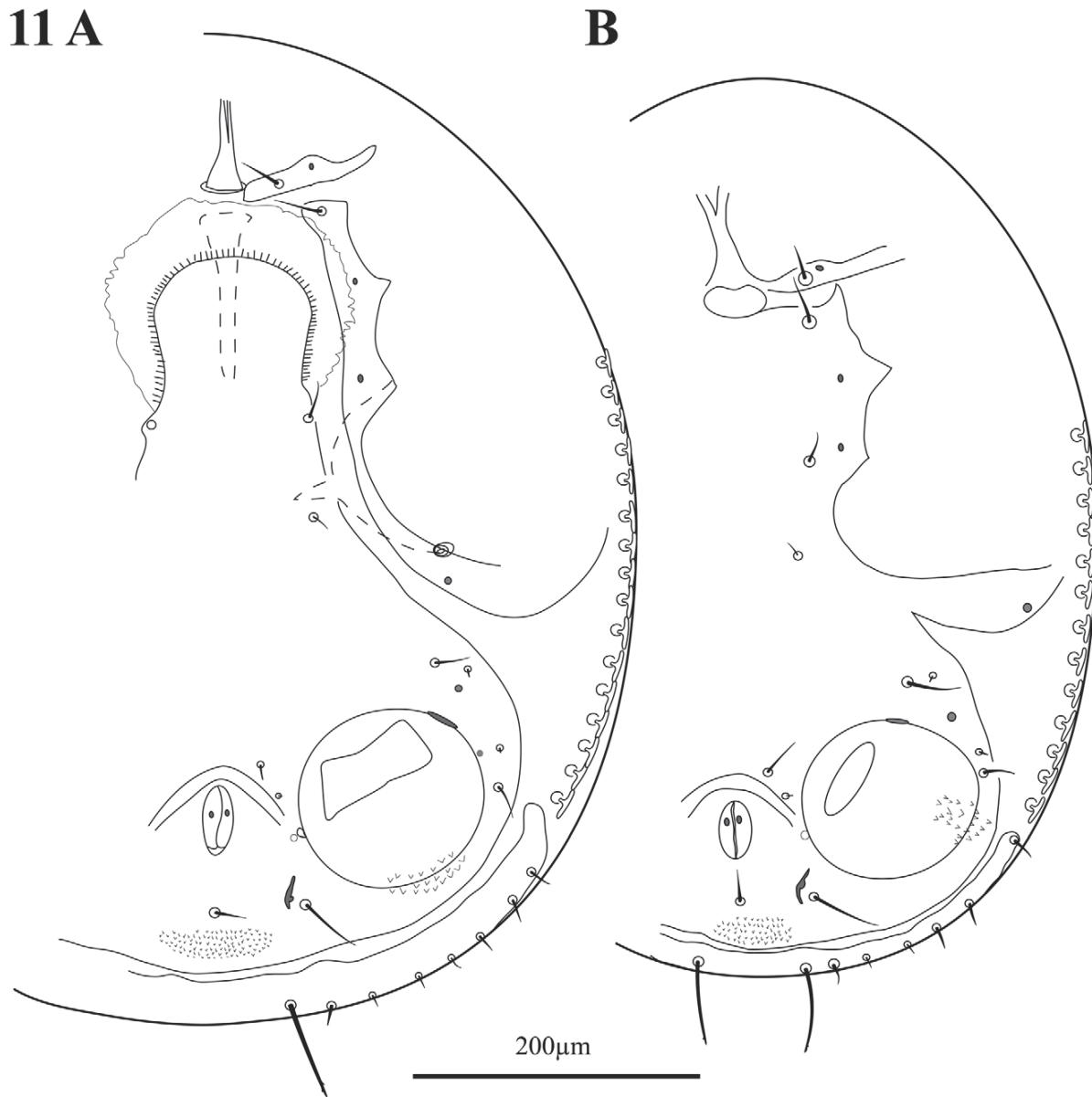
**Description.** Male chelicera (Figs 1H, 2H): spermatodactyl long; base of moderate length, coiled section extended, distal extension broad, ending in a widened, bifurcate section. Fixed digit weakly to moderately developed, straight; movable digit thin, straight, with a large bulbous base. Interdigital membranes normal. Male venter (Fig. 11B): shields including setae *St1* not connected to the sternitoventral shield. Setae *pa* relatively long, length > 3/4 length of setae *Z5*. Setae *S5* short, length < 1/2 length of setae *Z5*. Posterior marginal sclerite with 5–6 tiny setae. Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 13–15 / side. Female venter (Fig. 11A): setae *S5* short, length < 1/2 length of setae *Z5*. Number of anchor-shaped spines on the latero-ventral region of the opisthosoma 16 / side. Male legs I, chaetotaxy (Fig. 4I): coxal setae relatively thin, setiform (same in female). Trochanteral setae *av1* relatively long; length exceeding that of setae *pl*. Trochanteral setae *ad*, *al* and *pl* without distinct barbs. Femoral setae *pl2* present. Femoral setae *ad3* length relatively long; length subequal to that of setae *pd2*. Femoral setae *pd1*, *al2* and *v2* without distinct barbs. Femoral setae *al1* and *al2* relatively short; length ratio setae *al1* / *al2* between 2.1 and 2.4. Male legs II, chaetotaxy (Fig. 5I): femoral setae *pv1* moderately wide (<20 µm). Setae *av1* relatively short (length ratio *av1* / *pv1* less than 0.8). Femoral setae *pd1* distinctly shorter than setae *ad1*. Femoral setae *ad2* without barbs. Genua with a distinct ventrodiscal outgrowth. Genua setae *av1* relatively short; length distinctly exceeding that of setae *pv1*. Tibial setae *av1* with distinct barbs. Adult legs III, chaetotaxy: all trochanteral setae setiform.

**Material examined.** Holotype male (OSAL053960): Madagascar, Antsiranana, near Andrafiabe cave, 2.6 km E Andrafiabe, Reserve Speciale d'Ankaranana, ~50m, 20–27 January 2001, coll. S. M. Goodman, ex pitfall trap residue with multiple millipedes, in dry deciduous forest at base tsingy, collection no. FMHD#2001-41 (hosts at FMNH, specimen numbers FMNH-INS-3957 (Spirostreptida), FMNH-INS-5443 (Spirobolida), FMNH-INS-3960 (Spirobolida)). Same data: OSAL053959, 053961-63, 053974, male; OSAL 053964-73, 053975-88, 003131, female.

**Deposition of types.** Holotype, OSAL053960, deposited at FMNH. Paratypes at FMNH and OSAL.

**Etymology.** This species is named after the country in which the material was collected.

**Taxonomic remarks.** The thin moveable digit of the male spermatodactyl is shared with *A. pachybolus* and *A. mahsbergi*, but both of those species show a partial sclerotisation of the interdigital membranes. The shape of the distal part of the spermatodactyl is unique within the genus.



**FIGURE 11.** *Afroheterozeron madagascariensis* nov. sp., venter adults. A, female (OSAL053968); B, male (OSAL053961).

*Afroheterozercon cautus* (Berlese) com. nov.

*Heterozercon cautus* Berlese 1924: 251.

Fain (1989) noted "It is possible that *H. cautus* Berlese, 1924, described from East Africa, also belongs to this genus" (= *Afroheterozercon*). Re-examination of the type specimen (no. 221/40, Berlese acarotheca at ISZA) did not clarify the issue of presence or absence of lateral spines (the specimen is insufficiently cleared). It did reveal that, in addition to the presence of a single large spine-like seta on femur II of the male (seta *pv1* by our designation), the male spermatodactyl has a shape characteristic of *Afroheterozercon*. The chelicera appear to have the partially sclerotised interdigital membrane observed in *A. mahsbergi* and *A. pachybolus* (Figs 1A–B, 2A–B), while the spermatodactyl shows a tight coiled middle, and a short thin distal section. *Afroheterozercon cautus* differs from *A. mahsbergi* and *A. pachybolus* by the shape of the distal section of the spermatodactyl, straight in *A. mahsbergi* and *A. pachybolus*, while gently curved in *A. cautus*. Unfortunately, the condition of the type specimen does not allow us to score most characters examined for this study. We therefore have made no attempt to present a full re-description.

**Key to the species of the genus *Afroheterozercon* (males only).**

*Afroheterozercon cautus* is excluded due to insufficient data.

- 1. Posterior marginal sclerite with distinctly more than 6 tiny setae (male and female) (see small arrow Fig. 3B); spermatodactyl strongly elongate (Figs 1D, 2D) ..... *A. spirostreptus*
- Posterior marginal sclerite with only 6 (rarely 5 or 7) tiny setae; spermatodactyl much smaller ..... 2
- 2. Shields carrying setae *St1* connected with sternitoventral shield ..... 3
- Shields carrying setae *St1* not connected to sternitoventral shield ..... 5
- 3. Movable digit of chelicera robust; interdigital membranes not sclerotised (Figs 1C, 2C) ..... *A. sanghae*
- Movable digit of chelicera thin (< 13 µm); one interdigital membrane partially sclerotised (Figs 1A–B) ..... 4
- 4. Length ratio of setae *Z5* to *S5* very high, 4.2–6.1 (long *Z5*, short *S5*) (Fig. 3), setae *pl2* on femora I absent (males and females) ..... *A. mahsbergi*
- Length ratio of setae *Z5* to *S5* smaller, 2.7–3.8 (Fig. 6), setae *pl2* on femora I present ..... *A. pachybolus*
- 5. Fixed digit and spermatodactyl reduced (Fig. 1F) ..... *A. goodmani*
- Fixed digit chelicera and spermatodactyl well developed ..... 6
- 6. Distal end of spermatodactyl expanded; movable digit chelicera thin (<13 µm wide) (Figs 1H, 2H) ..... *A. madagascariensis*
- Distal end of spermatodactyl tapering, not expanded; movable digit chelicera robust ..... 7
- 7. Movable digit of chelicera not strongly curved but with a well-differentiated distal tooth; spermatodactyl long, especially in basal section (Figs 1G, 2G) ..... *A. tanzaniensis*
- Movable digit chelicera strongly curved, but distal teeth absent or weakly developed ..... 8
- 8. Distal sections of the fixed digit and spermatodactyl straight ..... *A. ancoratus*
- Distal sections of the fixed digit and spermatodactyl with well developed hooks (Figs 1E, 2E) ..... *A. gabonensis*

**Discussion**

**Biology.** Most of the material for *A. pachybolus* and *A. sanghae* is part of a large collection of millipedes (~100) that was preserved individually, allowing some inferences on incidence (percentage of millipedes infested) and abundance (average number of mites/infested host) at the mite genus level. Unfortunately we have not been able to get identifications of the millipede hosts, limiting us to treatment by relative size, which may reflect either different host species or immature vs. adult hosts. Incidence for "large" millipedes (N=50) was 76% and abundance was 12.0. Clearly these mites are not rare in appropriate circumstances. On the other hand recovery is very poor if hosts are not killed and preserved individually (or if preservative is changed without consideration of associates) because the mites rapidly drop from the host once those hosts are fluid preserved. There is a marked correlation between presence of heterozerconids and the size of the host millipede. Although incidence for "medium" sized millipede hosts (N=26) was comparable to that for "large" ones (72% vs. 76%), abundance was clearly lower (6.8 vs. 12.0). Both measures were much lower for "small" (N=14) millipedes, 29% and 1.3, respectively. This pattern matches that observed for the association of the North American species *Narceoheterozercon ohioensis* Gerdeman & Klompen 2003 and its millipede host, *Narceus annularis* (Rafinesque) (Gerdeman 2002). It is also similar to the

pattern observed for another group of mesostigmatid associates of the Central African Republic millipedes, members of the similar sized genus *Julolaelaps* (Iphiopsididae). Numbers for this genus are, respectively, 64% and 37.4, 48% and 15.7, and 7% and 1.0, for the "large", "medium" and "small" millipede size categories. The trends for the two taxa from the Central African Republic are similar with two small differences: (1) incidence, as well as abundance, drops strongly from "large" to "medium" millipedes in *Julolaelaps*, and (2) the drop in abundance across the host size categories is even more pronounced for *Julolaelaps* than for *Afroheterozercon*. A study of mite associates of millipedes in the eastern U.S. also noted the lack of (the relatively large) Mesostigmata on small millipedes (e.g. family Julidae, Blaniulidae). The few records of Mesostigmata in this study were from larger hosts (mostly Polydesmida: Euryuridae) (Farfan & Klompen 2012). Thus our records support the generally accepted notion that medium to large mites require relatively large-bodied hosts.

Males of *A. sanghae* and *A. pachybolus* were found on the same individual millipede (field number AL6647). Similarly, we found two species, *A. spirostrepti* and *A. goodmani*, on a single millipede in Gabon (field number AL6503). The presence of multiple species of Heterozerconidae on a single host individual has been suggested previously (Kethley, pers. comm.), and is hereby confirmed. Further studies are needed to assess how common this type of association is.

**Phylogeny.** A phylogenetic analysis of relationships in *Afroheterozercon* was attempted using the characters in Table 3, adding *Maracazercon jolivetii* Fain as outgroup (matrix in Table 4). Taxa included were all species in the genus except *Afroheterozercon cautus*, for which available data were insufficient (see above). Eight of the 29 characters (13–15, 18–20, 25, 28), all dealing with presence/absence of barbs on specific setae were subsequently excluded because of difficulties in character state determination, and the fact that these characters proved to be highly homoplasious (strong correlation with body size). The analysis based on the remaining 19 characters generated seven equally most parsimonious trees (length 39; CI= 0.56, RI= 0.57). A strict consensus tree supported only two groupings, (*A. madagascariensis* (*A. goodmani*, *A. mahsbergi*, *A. pachybolus*)). As expected, support is weak: Bremer support of 1 for these two lineages; jackknife analysis (1000 repetitions) provides weak support (63–69%) for three groupings, (*A. madagascariensis* (*A. goodmani* (*A. mahsbergi*, *A. pachybolus*))). Notably, two character reweighting procedures, successive approximations weighting (Farris 1969) and Goloboff fit (Goloboff 1993), both converged on one of the seven trees, so we selected that tree as the best solution given the data (Fig. 12).

**TABLE 3.** Characters scored for *Afroheterozercon* species.

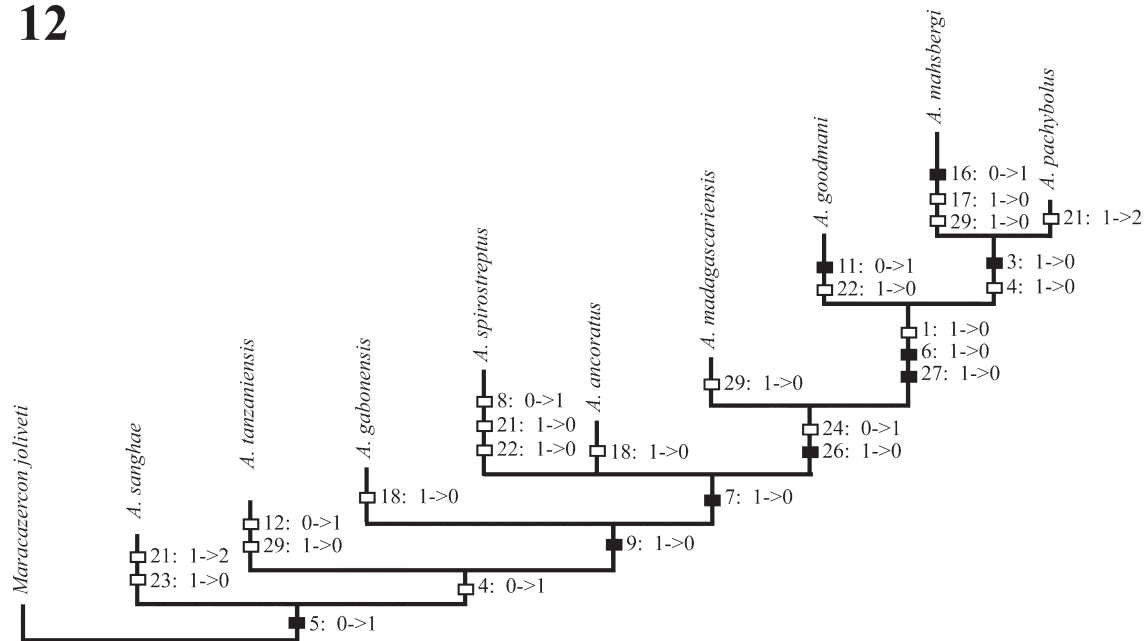
1. Fixed digit chelicera in male
  0. very short (less than 60  $\mu\text{m}$ )
  1. longer (more than 60  $\mu\text{m}$ ),
2. Width movable digit chelicera in male
  0. thin (less than 13  $\mu\text{m}$ )
  1. thick, robust (more than 17  $\mu\text{m}$ ),
3. Large interdigital membrane of chelicera in male
  0. partially sclerotized to a shelf-like process
  1. membranous
4. Shield containing setae *St1* in male
  0. connected to sternitoventral shield
  1. not connected to sternitoventral shield
5. Lateral spines in adult
  0. hook-shaped
  1. anchor shaped
6. Length of setae *pa* relative to setae *Z5* in male
  0. < 3/4 length of setae *Z5*
  1. > 3/4 length of setae *Z5*
7. Length of setae *S5* relative to setae *Z5* in male
  0. < 1/2 length of setae *Z5*
  1. > 1/2 length of setae *Z5*
8. Number of tiny setae on posterior marginal sclerite, adult:
  0. six
  1. distinctly more than six
9. Length of setae *S5* relative to setae *Z5* in female
  0. < 1/2 length of setae *Z5*
  1. > 1/2 length of setae *Z5*

10. Coxae I, male: setal shape
  0. setiform
  1. spinose
11. Coxae I, female: setal shape
  0. setiform
  1. spinose
12. Trochanters I, male: relative length of setae *av1*
  0. length less or equal to that of setae *pl*
  1. length exceeding that of setae *pl*
13. Trochanters I, male: setae *al* with distinct barbs
  0. present
  1. absent
14. Trochanters I, male: setae *ad* with distinct barbs
  0. present
  1. absent
15. Trochanters I, male: setae *pl1* with distinct barbs
  0. present
  1. absent
16. Femora I, male: setae *pl2*
  0. present
  1. absent
17. Femora I, male: relative length of setae *ad3*
  0.  $< 2/3$  length of setae *pd2*
  1. subequal in length to setae *pd2*
18. Femora I, male: setae *pd1* with distinct barbs
  0. present
  1. absent
19. Femora I, male: setae *al2* with distinct barbs
  0. present
  1. absent
20. Femora I, male: setae *v2* with distinct barbs
  0. present
  1. absent
21. Femora I, male: relative length ratio of setae *al1* / *al2*
  0. ratio less than 1.8
  1. ratio between 1.9 and 2.5
  2. ratio more than 2.7
22. Femora II, male: thickness seta *pv1*
  0. very thick ( $>20 \mu\text{m}$ )
  1. relatively thin ( $<20 \mu\text{m}$ )
23. Femora II, male: length seta *av1*
  0. shorter (length ratio setae *av1* / *pv1* less than 0.8)
  1. longer (length ratio setae *av1* / *pv1* more than 0.8),
24. Femur II, male: relative length of seta *pd1*
  0. subequal to seta *ad1*
  1. distinctly shorter than seta *ad1* ( $<80\%$ )
25. Femora II, male: setae *ad2* with distinct barbs
  0. present
  1. absent
26. Genua II, male:
  0. with a distinct ventro-distal outgrowth
  1. relatively smooth, ventral outgrowth absent or small
27. Genua II, male: setae *av1*
  0. short (length 10-15  $\mu\text{m}$ ), always similar in length to seta *pv1*
  1. well developed (length  $> 20 \mu\text{m}$ ), often distinctly longer than seta *pv1*
28. Tibiae II, male: setae *av1* with distinct barbs
  0. present
  1. absent
29. Trochanters III, adult: setal shape
  0. all setiform
  1. one or more spine-like

**TABLE 4.** Character matrix for *Afroheterozercon* species.

Character number	1		11111		11112		22222		2222	
	12345	67890	12345	67890	12345	67890	12345	6789	12345	6789
mahsbergi	00001	00000	00011	101?1	11011	0010				
pachybolus	00001	00001	10111	01111	21011	0001				
sanghae	11101	1101?	?0000	01000	21000	1101				
spirostreptus	11111	10100	00011	00111	00100	1101				
gabonensis	11111	110?0	01111	00011	11101	1101				
goodmani	01111	00001	10111	01111	10111	0001				
ancoratus	11111	1?000	00001	00011	11101	1101				
tanzaniensis	11111	110??	?1111	01111	11101	1100				
madagascariensis	10111	1000?	?1111	01111	11011	0100				
Maracazercon joliveti	01100	11110	00111	00111	11111	1111				

## 12



**FIGURE 12.** Phylogenetic tree *Afroheterozercon* species (see text and tables 3 & 4). Character changes indicated on the branches. Closed boxes indicate apomorphies; open boxes homoplasious changes. Only unambiguous character changes are listed.

The grouping of *A. madagascariensis*, *A. goodmani*, *A. mahsbergi*, and *A. pachybolus* is supported by the presence of a ventrodistal outgrowth on genu II of the male (character 26: 0). This structure is best developed in the latter three species, which are also characterised by short setae *pa* (char. 6: 0) and *avI* on genua II (char. 27: 0), and a very short fixed cheliceral digit (char. 1: 0). The grouping of *A. mahsbergi* and *A. pachybolus* is characterised by the partial sclerotisation of the large interdigital membrane of the chelicerae (char. 3: 0), and partial fusion of the shield containing setae *StI* with the sternitoventral shield (char. 4: 0). Given the poor resolution of relationships among the remaining taxa it seems overly speculative to discuss their affinities, other than to note that the topology in Fig. 12 is heavily influenced by the ratio of setae *S5* to *Z5*, in both females (char. 9: 0) and males (char. 7: 0).

The topology presented in Fig. 12 does not match any obvious broad biogeographical patterns. For example, the *madagascariensis* - *pachybolus* lineage includes species from the northern, western, and southern extremes of the known range. Additional collections from a broader range of localities in the Afrotropical region, and improved host identification may help improve support for phylogenetic relationships and allow more meaningful analyses of biogeography and host associations.



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