Allogynaspis flechtmanni, a new genus and species of the subfamily Macrochelininae (Acari: Mesostigmata: Macrochelidae) from southeastern Brazil, with comments on cheliceral dentition, reproductive strategies, and postepigynal platelets

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Abstract

Allogynaspis flechtmanni n. gen., n. sp. is described from litter bordering a stream in a forested area of Itatiaia National Park in southeastern Brazil. Although it shares a number of traits with the free-living macrochelid genera Nothrholaspis and Macrholaspis, the new species presents a unique combination of characters that argues against its inclusion in either genus, or in any other recognised macrochelid genus. A dichotomous key that distinguishes Allogynaspis from related macrochine genera is included in the text.

Key words: Macrochelidae, Nothrholaspis, Macrholaspis, Geotrupacarus, gnathotectum, epigynal shield, sperm access system, phoresy

Introduction

The Macrochelidae is an ecologically and behaviourally diverse family of predatory gamasine mites, many of which occupy insular and often unstable habitats such as dung or carrion and rely on phoretic associations with flying hosts to move from deteriorating to fresh substrates. Other members of the family have retained the simple, free-living edaphic lifestyle typical of many gamasine predators and occur in more or less permanent or predictable habitats such as forest litter, rotting plant debris or beach wrack (Krantz 1998). Among these presumably early derivative forms are the macrocheline genera Macrholaspis Oudemans (Macrocheles opacus group of earlier authors) and Nothrholaspis Berlese (Macrocheles carinatus group of earlier authors (Hyatt & Emberson 1988, Krantz 1998, Emberson 2010), and M. (Scleritholaspis) of Mašán (2003). The presence of three (occasionally fewer) pairs of platelets in the integument behind the epigynal shield in both of these genera, along with the development of strong para-anal cribral extensions bordering the anal opening, a serrate dorsal cheliceral seta, and the sharing of a free-living non-phoretic life style lend credence to Emberson’s (2010) observation that, despite differences in gnathotectal and dorsal setal characters, Macrholaspis could well be considered a subgenus of Nothrholaspis. Emberson (2010) and Mašán (2003) considered Macrholaspis and Nothrholaspis to be Palaeartic in distribution, but representatives of both genera have also been collected in North America (Krantz, pers. observ.).

In March of 2000, I recovered several females and a small number of nymphs of an undescribed macrochelid species from litter at a riparian site in southeastern Brazil that displays strong morphological affinities with both Macrholaspis and Nothrholaspis. Morphological traits shared with Macrholaspis include a strongly tapered dorsal shield with all dorsal setae pilose (M. evansi Balogh is exceptional in having four pairs of smooth median dorsal setae (Balogh 1958)) and a generally punctate sternal shield that lacks distinct reticulation in the anterior portion (M. dentatus (Evans & Browning) is an exception to the latter (Evans & Browning 1956)). A pair of conical teeth flank the capitular setae of the gnathosoma (Fig. 4), structures that also have been seen in some New World Macrholaspis (Oregon State Arthropod Collection). Notable characters shared only with Nothrholaspis are the...
clavate, pilose condition of the robust marginal and submarginal dorsal shield setae (Fig. 15) and the presence of strong medioventral spines at the base of the bifid distal median process of the gnathotectum (Fig. 7). Additionally, a rugose, unpaired sacculus similar to that found in the new species has been observed in an undescribed *Nothrholaspis* species from western North America and probably occurs in other species of the genus as well.

Similarities to *Nothrholaspis* and *Macrholaspis* notwithstanding, the new species displays a suite of morphological and distributional traits that argue against its inclusion in either genus. The unique form of the epigynal shield (Fig. 2), the proximal dentition of the fixed cheliceral digit (Fig. 5), and the morphology of the sperm access system (Fig. 8) are especially noteworthy, but key among the observed disparities is the absence of recognisable postepigynal platelets. While females of all known *Nothrholaspis* and virtually all known *Macrholaspis* species have three pairs of rounded or elongate platelets between the epigynal and ventri-anal shields (known exceptions are *M. georgicus* Bregetova with one pair and *M. morikawai* Ishikawa with two pairs (Mašán 2003)), females of the new species have instead a single pair of small, narrow sclerites at the level of the anterior margin of the ventri-anal shield just above opisthogastatic setae Zv1 (Fig. 2, vs) (the single pair of platelets of *Macrholaspis georgicus* are instead medially positioned above ventri-anal setae Jv1 (Bregetova 1977)). An unpaired, more medial sclerite also has been observed on the right or left side of the opisthogaster between Zv1 and Jv1. Based on their structure and position, these sclerites are not typical postepigynal platelets, nor do they appear to be epigynal in origin.

In regard to distribution, the discovery of the new species in a neotropical setting makes questionable its placement either in *Macrholaspis* or *Nothrholaspis*, neither of which has ever been recorded from the Neotropical realm. In a broader sense, the pilose condition of all of the ventral setae in both females and immatures (only the para-anal setae are smooth), coupled with the singular structure of the epigynal shield and the proximal dentition of the fixed cheliceral digit, augment a character cluster that precludes placement of the new species in any currently recognised macrochelid genus. Accordingly, it is described here as the monotypic representative of a new genus, *Allogynaspis*.

**Methods and materials**

Specimens were taken from litter on a stream bank in southeastern Brazil in March, 2000. Following Berlese funnel separation, recovered mite specimens were held in 70% ethyl alcohol and later cleared, mounted (Hoyer’s solution) and ringed with red insulating varnish (M.G. Chemicals, Burlington, Ontario, Canada) following protocols of Walter & Krantz (2009). A Zeiss GFL phase contrast laboratory microscope equipped with a Zeiss drawing tube was used for specimen examination and for preparation of illustrations. Measurements are given in micrometres. Adult and immature idiosomatic chaetotaxy follows Lindquist & Evans (1965) as later modified by Lindquist (1994) and Lindquist & Moraza (1998) and applied to the Macrochelidae by Halliday (1986). Leg and palpal chaetotaxies are based on a system developed by Evans (1963a, 1963b), and gland pore and poroid terminology are those elaborated by Kazemi *et al.* (2014) based on earlier systems developed by Athias-Henriot (1975) and Johnston & Moraza (1991), and later applied to the Macrochelidae by Knee (2017). It should be noted that the deutonymphal and protonymphal descriptions presented below are fragmentary due to inadequacies in available preparations.

**Systematics**

*Allogynaspis* n. gen.

Type species *Allogynaspis flechtmanni* n. sp., by monotypy.

**Diagnosis.** Female with general shield, setal, and integumental characters of *Macrholaspis* and *Nothrholaspis* except for the following: Dorsal shield abruptly narrowed posterior to coxae IV, without marginal crenulation or serration; with 29 pairs of setae (both J2 and J3 present), all of which may be considered pilose in the broad sense, but whose pilosity is notably robust and neither soft nor overly long; dorsal setae j1 widely separated, not
expanded. Epigynal shield unique for the family, posterior margin not rounded or truncate but instead convex medially and becoming concave laterally, sharply angled anterad at the posterolateral corners and attached there via membranous ligatures to strongly developed accessory sclerites. Underlying sperm access system with a median unpaired rugose sacculus and exceptionally long tubuli. Without postepigynal platelets, but rather with a pair of narrow sclerites above integumental setae Zv1, sometimes with an additional unpaired sclerite between Zv1 and anterior margin of ventri-anal shield. Gnathotectum with broadly attached, distally undivided lateral elements similar to those seen in some *Macrholaspis* species, but clearly longer than distal median elements, juncture of median elements displaying a series of spines as often seen in *Nothrholaspis* (Hyatt & Emberson 1988), lateral elements reduced or absent in earlier instars. Fixed cheliceral digit with a proximal pair of closely adjacent teeth, dorsal cheliceral seta weakly serrate on broadened distal margin.

*Allogynaspis flechtmanni* n. sp.  
(Figs 1–18)

With the general characteristics of the family as defined by Mašán (2003) and the tribe Macrochelini as defined by Emberson (2010).

**Adult female** (Figs 1–8, 14–15).

*Dorsal idiosoma* (Fig. 1) Dorsal shield averaging 787 (703–917) in length, width of shield at level of coxae III averages 575 (526–648) (n=10), tapered in posterior portion and abruptly narrowed behind coxae IV at level of setae Z3 (Z2 of Knee 2017), exposing considerable posterolateral and posterior opisthonotal integument, shield with foveolate pattern anteriorly, blending into roughly rugose area at level of setae j4–j6 and displaying a punctate-reticulate pattern posterior to j6. Dorsal shield setae j1 widely separated, longer than j2 (67 vs 42), similar in length and ornamentation to j3–5; dorsal shield setae z1, j5–6, s2, z5–6, and J2–3, 5 considerably shorter (23–26) than remaining median, marginal and submarginal shield setae which, when viewed dorsoventrally, are seen to be weakly clavate with a rounded tip and ornamented with a number of short hairs antiaxially, paraxial setal surface smooth and with strongly bipectinate margins (Fig. 1, detail). Setae J2 inserted anterior to poroid pairs idm2–3 rather than between them, J3 at level of Z3 and anterior to poroids idm4 (see Halliday 1986 for a discussion of position and identity of J setae). Variation in setal position may occur both between specimens and from one side of the dorsal shield to the other; e.g., the distance between the insertions of seta z2 and the diminutive seta s2 on the right side of the illustrated specimen is greater than on the left side so that insertions of setae r2 and r3 shift closer to the shield margin, with the insertion of seta r3 appearing on the ventrally infolded margin; without unpaired setae on opisthonotal portion of dorsal shield as seen in some *Macrholaspis* species (Emerson 2010). With 16 pairs of lyrifissures and six pairs of gland openings as typical for the family (Knee 2017). Adjacent integumental setae shorter than marginal dorsal setae but with similar robust pilosity, typically appearing pointed terminally rather than clavate; idiosomatic integument generally striate-crenulate (Fig. 15), sometimes appearing spiculate.

*Ventral idiosoma* (Figs 2–4) Integumental and shield setae pilose except for smooth para-anaals on ventri-anal shield; base of tritosternum (Fig. 3) 2½ times longer than wide (40), bipectinate lacinae long (130), normally produced. Sternal shield (Fig. 2) with basic ornamentation pattern similar to that of *Macrholaspis opacus* (Koch) (Mašán 2003), densely punctate except around insertions of sternal setae, without clear reticulation or linear pattern, portion of shield below poroids iv2 appearing more densely punctate than anterior portion; shield margin typically notched above posterolateral angles, or with paired shield fragments laterad from setae st3 when notches are absent. Setae st1 longer than st2–3 (102 vs 77), closely inserted, without basal pilosity; st4 shorter (~42), inserted on small elliptical metasternal shields, poroid iv3 on anterior shield margin or in integument above it. Epigynal shield punctate, with weakly developed reticulation, epigynal setae (st5) similar in length to st3, but considerably more pilose; poroids iv5 in integument behind juncture of shield with accessory sclerites. With a single pair of small, narrow sclerites above opisthogastric setae Zv1, sometimes with an additional unpaired sclerite between Zv1 and ventri-anal shield setae Jv1 (Fig. 2, vs). Ventri-anal shield narrowly pyriform and punctate-reticulate, sometimes irregularly notched laterally, with three pairs of pilose ventri-anal setae (44), here considered JV1–3; para-anal setae smooth and postanal seta strongly pilose as in *Macrholaspis* species (Mašán 2003), para-anaals somewhat longer than ventri-anaals (48), postanal seta shorter (28) than para-anaals, its base often obscured by overhanging anal shield ridge; cribrum densely spiculate, with narrow para-anal cribral elements.
extending anteriorly to level of para-anal setae; opisthogastric setae mostly longer than ventri-anals (56–58), opisthogaster with three pairs of poroids (Fig. 4, ivo), gland gv2 well removed from posterior margin of coxae IV. Peritrematic shields fused to dorsal shield at level of coxae II, peritremes extend anteriorly and then anterodorsally above coxae I along margin of dorsal shield to a position just above insertions of setae z1, stigmata strongly produced, laterad from coxae III-IV.

Gnathosoma (Figs 4–5, 7) Lateral elements of gnathotectum (Fig. 7) broad basally and tapering distally, longer than distally undivided elements of bifid median process, which displays a series of strong medial ventral spines arising from gnathotectal stem; corniculi (Fig. 4, cn) long (120), extending nearly to terminus of palp femur, labrum plumose and nearly as long as corniculi, salivary styli (ss) distinct; hypostomatic setae smooth, setiform, h1 (100) and h3 (145) greatly exceeding length of h2 (50); caputial setae weakly pectinate, subequal in length to h2, laterocoxal setae (lc, van der Hammen 1964) distinct. Internal malar extensions of deutosternum elongate, narrow and strongly plumose; deutosternal groove with seven rows of denticles from level of setae h1 to capitular (postcoxal) setae, row 1 divided medially and with relatively few denticles on each side (8–10) and well separated from row 2, number of denticles in row 2 (~50) far greater than in row 3 (34) and decreasing further in succeeding rows, size of denticles increases in more posterior rows; row 7 with few (~20) relatively large denticles and generally flanked on each side by a series of 4–6 evanescent denticles located just below insertions of capitular setae (Fig. 4), additionally with a pair of large conical teeth laterad from capitular setae. Fixed digit of chelicera (Fig. 5) with a proximal pair of adjacent teeth reminiscent of bidentate tooth on movable cheliceral digit of females of more highly derived phoretic Macrocheles species (Krantz 1998) but without accompanying opposed ribbed surface on movable digit, additionally with a subterminal tooth internal to an elongate pilus dentilis, dorsal setae (Fig. 5, detail) weakly serrate on expanded distal face, often appearing smooth when seta is viewed dorsally; movable digit with a small median and a larger, more proximal tooth opposing paired teeth of fixed digit, internal arthrodial brush (90) considerably longer than external brush, comprised of overlying long hairs. Palptrochanter long (76), nearly length of palp femur; setae al1 of palp genu spinose, shorter than al2 (14 vs 26) and somewhat thickened.

Legs (Figs 6, 14) moderately to extremely long, with legs II-IV equaling or exceeding dorsal shield length, leg chaetotaxy typical for family (Evans 1963a), genu IV with six setae (1 2/1–2/0 0), coxal setae pilose. Legs I (~725) antenniform, narrower and somewhat shorter than legs II-III, with simple filiform setae on tarsus I, other segments with most dorsal and lateral setae distally pilose. Tarsal setae ad1/pd1 of legs II-IV smooth and acuminate, tarsal setae al1 and pl1 thickened and peg-like basally, often narrowed and acuminate distally. Legs II (~875) with smooth al setae on trochanter, femur and genu, other setae on these segments pilose; basitarsal setae (al3/pl3, ad3/pd3) and pd2 on tarsus II pilose, other tarsal smooth, spiniform; Setae of trochanters to tibiae III-IV mostly pilose distally; legs III (~910) with tarsal setae md, mv, pv1, ad2/pv2 and basitarsal setae pilose, other tarsal setae smooth. Legs IV long (1340–1390), nearly twice length of legs I and generally more than ½ times length of legs II-III, tarsus IV (Fig. 6) long (500–510), more than twice length of tibia, tarsal terminus between setae al1/p1 and av1/pv1 narrowed and elongate, distal portion of segment often inwardly curved, with normal complement of 18 setae, of which av1/pv1, av2/pv2, al2/pl2 and al3/pl3 are spiniform and greatly enlarged, al3 and pl3 weakly pectinate; other tarsal setae shorter, smooth (ad1/pd1) or pilose (md, mv, ad3/pd3).

Sperm access system (Fig. 8) with insemination pores (solenostomes) at bases of coxae III connecting to long (~500), narrow (~1.0), convoluted tubuli that are especially sinuous close to their origins at coxae III and which terminate in a median unpaired, rugose sacculus; sperm duct and seminal receptacle not seen.

Deutonymph (Figs 9, 17). Length of dorsal shield = 629 (548–670), (n=3). Dorsum obscure in preparations at hand, shield chelate, poroidotaxy/adenotaxy, and nature of shield margin not clear.

Ventral idiosoma (Fig. 9) Setal ornamentation as in female, st1–4 inserted on a posteriorly rounded shield defined primarily by absence of the striate-crenulate pattern seen in surrounding integument; insertions of st4 marginal, st5 and poroids iv5 in striated integument adjacent to posterior shield margin; with two pairs of opisthogastric poroids (ivo) internal to and flanking setae Zv2, glands gv2 in normal position behind coxae IV, opisthogastric region and setation pattern otherwise unclear in specimens at hand. Peritremes extend anteriorly and dorsally toward, but well short of, dorsal setae z1.

Gnathosoma. Gnathotectum similar to that of female (Fig. 7) except that lateral elements are more narrowly
attached to central stalk and narrow throughout, similar in length (27) and width to elements of distal bifid median process; deutosternal groove with seven rows of denticles between h1 and the capitular setae, but with capitular row weakly produced, with fewer denticles in row 2 than in adult (~32 vs ~50) and decreasing to ~26 in row 3, and further in succeeding rows; row 7 without flanking denticles below capitular setae, but with a conical tooth flanking each capitular seta as in female. Chelicerae (Fig. 17) without proximal adjacent teeth on fixed digit as seen in female, median and the more proximal tooth of movable digit subequal in size; condition of dorsal cheliceral seta unclear but, based on preceding and succeeding stages, presumed to be weakly serrate on expanded distal face.

**Protonymph** (Figs 10–13, 16, 18).

Length of idiosoma =456 (451–462), width at level of coxae III= 339 (325–333) (n=2).
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Dorsal idiosoma (Figs 10, 16) weakly ornamented, shield margins weakly defined; dorsal setal shape and ornamentation similar to those of adult female, shield chaetomes of 11 pairs of podonotals and eight pairs of...
opisthonotals normal for the instar (Halliday 1986, Krantz & Redmond 1987), although a supernumerary seta occurs on opisthonotal shield of illustrated specimen (viz., Z3 on the left side in Fig. 10); putative setae J3 with insertions at level of poroids idm4.


*Ventral idiosoma* (Figs 12, 13) Sternal shield defined by absence of integumental striae, shield strongly narrowed posterior to insertions of st3; st1–3 with ornamentation as in later stages, with pilosity largely confined to distal portions; st5 (Figs 12, 13) short, palmate, with 4–6 distal “fingers” and inserted in integument behind sternal
shield. Anal shield small, ovate, weakly defined, anal valve complex wider than long (30x20); opisthogaster with only four observed pairs of setae (ventri-anals Jv1–3 and Jv5), in addition to the strongly produced, smooth para-
anal and pilose postanal seta; with two pairs of poroids (ivo) laterad from Jv2. Stigmata above anterior margin of
coxae IV, peritremes short (35), extending laterad from stigmata and curved anteriorly.

**Gnathosoma** as in female except for the following: gnathotectum (Fig. 11) with distal bifid process as in later
stages, but lateral elements absent; deutosternal groove with only six rows of denticles between setae h1 and
capital setae, row 2 with fewer denticles than in deutonymph (~22 vs ~32) and decreasing in succeeding rows.
Without ancillary denticles below capital setae, but with paired conical teeth flanking capital setae as in later
stages. Fixed digit of chelicera (Fig. 18) without adjoining proximal teeth, subterminal, median and proximal teeth
of movable digit weakly developed; dorsal cheliceral seta weakly serrate on broadened distal face.

**Legs** (Fig. 16) similar to those of later stages, including presence of enlarged, spiniform setae on tarsus IV, seta
mv absent; visible setal segmental chaetomes corresponding to those presented by Evans (1963a) for protonymphal
**Pergamasus**

### The following key serves to differentiate *Allogynaspis* n. gen. from similar macrochelinine genera

1. Sternal shield with strong uniformly reticulate pattern, weakly punctate. Phoretic on geotrupine beetles in southeastern USA .
   - Sternal shield variously ornamented but not as above. Free-living forms 2
   - Dorsal shield tapered posteriorly, exposing opisthontal integument; all dorsal shield setae typically pilose. 3
   - Dorsal shield not tapered posteriorly, more or less covering opisthontal dorsum; with at least some median dorsal setae
     smooth. Halocrite 3

2. Sternal setae smooth; epigynal shield with rounded posterior margin; anal shield typically rounded or subcircular. Halocrite .
   - Sternal setae pilose; posterior margin of epigynal shield convex medially and becoming concave laterally; anal shield longer
     than wide. Neotropical  Allogynaspis new genus

### Type material. Holotype and nine paratype females, four paratype deutonymphs and two paratype protonymphs ex
mixed, damp organic litter on the banks of a minor tributary of Rio Campo Belo, Itatiaia National Park, Rio de
Janeiro state, Brazil (22° 22’ S, 44° 39’ W), 900m altitude, 3 March, 2000 (G.W. Krantz, coll.). Holotype female to
National Museum of Natural History, Washington, D.C.; paratypes to Oregon State Arthropod Collection,
Corvallis; Acarology Laboratory, The Ohio State University, Columbus; Canadian National Collection, Ottawa;
Luiz de Queiroz College of Agriculture, University of São Paulo, Piracicaba; Australian National Insect Collection,
Canberra.

**Etymology.** The generic name *Allogynaspis* derives from the Greek *allos* meaning “other” or “different”,
combined with the Greek *gyn* plus *aspis*, referring to the distinctive morphology of the epigynal shield. The
specific name honors Dr. Carlos H.W. Flechtmann, University of São Paulo (ESALQ), Piracicaba SP, Brazil, a
valued colleague and friend who co-hosted my visits to southeastern Brazil in 2000 and 2001, and who introduced
me to Itatiaia National Park and to the river bank where *A. flechtmanni* was found.

### Discussion

*Allogynaspis flechtmanni* shares a number of similarities with the basal macrochelaine lineage that includes
*Nothrholaspis* and *Macrholaspis sensu* Emberson 2010, but it displays an array of characters that includes an
epigynal shield whose configuration (Fig. 2) is autapomorphic for the genus, widely separated and unexpanded
dorsal shield setae j1, distinctive gnathotectal and cheliceral morphologies, and elongate legs IV whose tarsal
setation includes four pairs of greatly enlarged spiniform setae. Enlarged setae often occur on tarsi II-IV in other
Macrochelinidae, but those of tarsi IV of the female and nymphal stages of *A. flechtmanni* are especially striking
(Fig. 6). Their presence throughout ontogeny suggests a function common to all postlarval instars, one perhaps
related to defense or, considering their riparian habitat, to locomotion across water films.

The female of *A. flechtmanni* has a single pair of small postepigynal sclerites above setae Zv1 (an additional
unpaired element may be present medially from seta Zv1), while *Nothrholaspis* and *Macrholaspis* always or
virtually always have three pairs of well developed platelets between the insertions of Zv1. The sclerites of *A. flechtmanni* occur at the level of the anterior margin of the ventri-anal shield rather than adjacent to the posterior margin of the epignyal shield or nearer the ventri-anal shield as in *Macrholaspis* or *Nothrholaspis* species. The location and reduced state of these sclerites suggest that they do not share the epignyal origins of the comparatively robust platelets seen in the free-living *Nothrholaspis* and *Macrholaspis*, but rather are fragments of a primitively larger ventri-anal shield that were left behind as the shield underwent reduction in sclerotisation. As such, these ventri-anal fragments (Fig. 2, vf) can be considered an autapomorphy (R.B. Halliday, pers. correspondence), one that signals a major divergence from a lineage in which females have postepigynal platelets derived from the epignyal shield. Like *Nothrholaspis* and *Macrholaspis*, adult females of the habitat-isolated and niche-specialised phoretic macrocheline genus *Geotrupacarus* (Krantz and Mellott 1968, Krantz 2009) have three pairs of postepigynal platelets, but they appear to first arise as small sclerites between genital setae st5 and ventri-anal setae Jv1 in the protonymphal stage, persisting also in the deutonymph (Krantz & Royce 1992). If these elements are homologues of the adult female postepigynal platelets, their presence in the nymphal stages of *Geotrupacarus* negates the possibility that they arose as fragments of secondarily reduced female epignyal or ventri-anal shields and effectively isolates *Geotrupacarus* from the free-living lineage represented by *Nothrholaspis*, *Macrholaspis* and *Allogynaspis*, calling into question the true origins of postepigynal platelets in the Macrochelidae.

The progressive ontogenetic development of the gnathotectum from protonymph to female and the increase of denticular rows from six in the protonymph to seven in the deutonymph and adult female of *A. flechtmanni* are not unique for the family, but the palmate condition of the genital setae (st5) of the protonymph (Fig. 13) is noteworthy. Also of interest is the large conical tooth flanking each capitular setae on the gnathosomatic venter of all postlarval stages of *A. flechtmanni* (Fig. 4). Paired conical teeth also occur in North American specimens of *Macrholaspis* in the OSAC Collection, but they have not been observed in available *Nothrholaspis* specimens. The terminally rounded, slightly clavate condition of many of the median, marginal and submarginal dorsal shield setae of *A. flechtmanni* (Fig. 1, detail) also is seen in *Nothrholaspis* species (Evans & Browning 1956, Mašán 2003), as is the presence of short secondary hairs on their antialarial surfaces. Ornamentation of the integumental idiosomatic setae of *A. flechtmanni* is similar to that of the dorsal shield setae, but they are neither clearly clavate nor rounded distally (Fig. 15).

It was mentioned earlier that the proximal pair of adjacent teeth on the fixed cheliceral digit of female *A. flechtmanni* (Fig. 5) is reminiscent of the median bidentate tooth on the movable digit of females of many highly derived phoretic macrochelids. However, a grasping function related to phoresy seems unlikely in this case in that *A. flechtmanni* appears to be a free-living species occupying a continuous riparian habitat and would have no apparent need for phoretic transport. In support of a possible phoretic function, however, the adjacent fixed digit teeth are absent in protonymphs and deutonymphs of *A. flechtmanni*, instars that generally are non-phoretic in macrochelids that have phoretic females (Krantz 1998). At the same time, it should be noted that females of some phoretic macrochelid genera (e.g. *Geotrupacarus*, *Neopodocinum*) lack the cheliceral bidentate tooth usually associated with phoresy, and that males of *Geotrupacarus* and males and nymphs of *Neopodocinum* and those of other more highly derived macrochelids (e.g., the *dimidiatius* species group of *Macrocheles*) may, without benefit of a bidentate cheliceral tooth, routinely attach to the same scarabaeine beetle hosts as those on which their female counterparts are found (Krantz 1965, 1998, 2007; Krantz and Mellott 1968, Krantz & Royce 1992, Costa 1969, Lindquist et al. 2009).

The unusual morphology of the laelapid-type sperm access system of the female of *A. flechtmanni* is worthy of special note. Rather than having relatively short tubuli as seen in *Macrholaspis dentatus* Evans & Browning (~180) (specimen in OSAC Collection), *A. flechtmanni* has highly convoluted, uniformly narrow tubuli whose extraordinary length far exceeds the actual distance between the sacculus and each of the paired insemination pores on coxae III. Unlike the paired, seemingly separate saccular elements in *M. dentatus* and other species of *Macrholaspis* (Mašán 2003), *A. flechtmanni* has an unpaired, more or less rounded, rugose median sacculus (Fig. 8) similar to that of an undescribed species of *Nothrholaspis* collected in northern California (GWK, pers. observ.) and to *Dissoloncha superba* Falconer, a geholaspinine macrochelid species common to littoral habitats in the Holarctic realm (Takaku 1997).

Males of *A. flechtmanni* were not found among the specimens collected at the type locality, nor are males known for the majority of described species of *Macrholaspis* (Johnston 1970, Emberson 2010). *Nothrholaspis*, along with the free-living macrocheline genus *Geholaspis*, also include species that are known or believed to
produce only female progeny (Filipponi 1964, Oliver 1971). While arrhenotoky is common among phoretic macrochelids occurring in temporary insular habitats, Manning & Halliday (1994) note that free-living non-phoretic species of *Macrocheles* occupying continuous habitats such as leaf litter or compost in Australia generally are thelytokous (and incidentally lack the bidentate tooth on the movable cheliceral digit that would facilitate phoresy). The possibility that *A. flechtmanni* also is thelytokous is reinforced by its open litter habitat and lack of a typical cheliceral adaptation for phoresy. If males are present and fertilisation does occur, and barring the possibilities either of alteration in sperm cell form as the cells pass through the tubulus, or of transient enlargement of the tubulus to better accommodate sperm cell passage (Alberti & Hänel 1986, Di Palma *et al.* 2017), the unusual nature of the tubuli could limit sperm transfer to the sacculus, ultimately affecting fertilisation rate.

Further collection at the Itatiaia site to determine whether males are present, in addition to rearing and cytological studies, should be undertaken to clarify the reproductive strategy of this species.

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