REDESCRIPTION OF SCHIZOSTHETUS LYRIFORMIS (McGraw and Farrer, 1969) (PARASITIFORMES: PARASITIDAE), WITH REVISION OF THE GENUS

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ABSTRACT - Schizosthetus lyriformis (McGraw and Farrer, 1969) is redescribed for all instars, emphasizing ontogenetic changes in vestiture and gland patterns of all body parts. This approach allows recognition of some previously unreported patterns. Major positional shifts of lyriformes over ontogeny appear correlated with the formation of the peritremes, and some setae of leg terg II-IV are unexpectedly variable in both shape and presence. In addition, the two remaining members of the genus are briefly redescribed, with a new diagnosis for the genus. Schizosthetus is strongly associated with bark beetles, with a geographic range matching that of their most common hosts.

Keywords - Mesostigmata, Parasitidae, Schizosthetus, bark beetles, development.

INTRODUCTION

Parasitidae is among the most common and widely distributed families of soil and litter mites in the Holartic. Even so, systematic relationships and classification of the family are still poorly resolved. The entire family was last revised by Micherdzinski (1969). Since that revision some regional studies have been published, e.g., Tichomirov (1977) for the former Soviet Union, Hyatt (1980) for Parasitidae in the United Kingdom, and Tseng (1995) for Taiwan. While many new taxa have been described, most of these descriptions have been in smaller studies. With different authors using different generic concepts, classification at the generic level within the family is unfortunately unstable (Hennexey and Farrer, 1989). For example, Micherdzinski (1969) and Tichomirov (1977) recognized 7 genera, while Karg (1971) recognized only 6. On the other extreme, Athias-Henriot, in a long series of papers (e.g. 1978a, 1978b, 1980, 1981, 1982), recognized a total of 22 genera worldwide. There are several reasons for the instability of parasitid mites classification. First, there are differences in taxonomic hierarchy. For example, Tichomirov (1977) recognized 5 subgenera of genus Parasitus Latreille, 1795: Parasitus, Coleogomosus Tichomirov, 1967, Euaggregateus Berlese, 1882, Vulgarogomosus Tichomirov, 1969, and Neogomosus Tichomirov, 1969. Other authors recognized the last 3 of these subgenera as genera. This is a relatively minor problem. Second, different researchers define the same genus based on different, and often single, characters, leading to incompatible groupings among researchers. This is much more serious.

An additional problem has presented itself. Most contributions to the knowledge of Parasitidae in the last 40 years have been by Athias-Henriot and colleagues. Athias-Henriot's work covers the world fauna, and provides a wealth of detail. Unfortunately she never summarized her classification or presented a generic key. Moreover, it is not easy to work with her publications as she rarely provided complete habitus drawings, instead relying on numerous densely packed detail drawings, and descriptions filled with terms that are often less than perfectly defined. Various studies by Juvara-Balis (1975, 1981, 2002) have helped out for the Pergamasini, but some additions for Parasitidae seem overdue.
Finally, descriptions are usually incomplete in terms of developmental patterns or coverage of all body structures. There are a few descriptions that show either the ontogenetic development of structures of the legs (Evans, 1963a, 1969), or the lyrifissures and gland patterns (Athias-Henriot, 1982), but none has presented complete, detailed, descriptions of all instars and all body structures in a single study. There are reasons for ignoring immatures. These instars show few differentiating characteristics (Hysatt, 1980), and finding or rearing these instars can be difficult (Bhattacharyya, 1962). However, detailed studies of immatures are often the only way to resolve homology questions in adults.

The genus Schizothorax Athias-Henriot, 1982 is a good example to illustrate the above problem. McGraw and Farrier (1969) described the type species as Eugomarus lyriformis McGraw and Farrier, 1969 based on general characteristics of the tectum, cornicles, and chelicerae. Tichomirov (1977) transferred it to Vulgaromurus based on the absence of denticles on the lateral margin of the genital shield, a characteristic not considered typical of Eugomaurus. Athias-Henriot (1978a) clarified the concept of Eugomaurus by noting the characteristic bifid shape of the anterior-lateral palp genu setae (al1, al2). In a later paper, Athias-Henriot (1982) proposed Eugomaurus lyriformis as type of a new genus, Schizothorax. The main character for this genus is the longitudinal split of the genital shield of the female. She also added two newly described species to this genus. The original description of S. lyriformis (McGraw and Farrier, 1969) is one of the better attempts at providing a full description. All instars were described and illustrated for the idiosomal setation, but the legs were largely ignored and the authors missed many idiosomal glands and lyrifissures especially in the larval and protonymphal instars. Moreover, they did not distinguish glands from lyrifissures, and included both under the term "peres." In contrast, Athias-Henriot (1982) concentrated on the adults of S. similatriz and S. vicarius, providing a detailed discussion of idiosomal lyrifissures and glands while almost completely ignoring the legs and the immatures instars.

The availability of large series of specimens of S. lyriformis of all instars, allowed us to address all of the above questions. We present a complete redescription of Schizothorax lyriformis, including the idiosomal structures, idiosomal setation, lyrifissure and gland patterns, and the leg setation for all instars. Specific terminology is redefined and specific structures are illustrated. Second, large numbers of specimens from different localities allowed an assessment of geographical variability, which is used in revising the genus Schizothorax.

MATERIAL AND METHODS

Terminology for the leg chaetotaxy is based on Evans (1963a) except for the tarsi of legs II-IV, which is based on Evans (1969). Pedipalp chaetotaxy is based on Evans (1963b). Designations of lyrifissures and glands are based on Johnston and Moraza (1991), and idiosomal chaetotaxy on Lindquist and Evans (1965). Other terminology generally follows Evans (1992); terminology differing from Evans (1992) is identified in the text.

A Zeiss Axioskop® compound microscope with a drawing tube was used for initial pencil drawing at magnifications of 400-1000x using phase contrast and differential interference contrast (DIC) illumination. These drawings were scanned and imported into Adobe Photoshop® (Adobe Systems Incorporated, San Jose) and used as templates for final illustrations in Adobe Illustrator® (Adobe Systems Incorporated, San Jose). Specimens collected in California are considered to be the standard, described in this study, but some drawings were taken from material originating in Louisiana (noted in figure legends). The reason for drawing the specimens from California is practical: more specimens of all instars were available from California.

Specimens were measured with an ocular micrometer. Measurements are presented in micrometers (μm) in the format: average (range; number measured). Length is measured from the tip of the hypostome to the posterior end of the idiosome; width is measured at the widest point of the body.

Depositories of specimens: United States National Museum, Washington, D.C. (USNM); John Moser collection at the USDA Forest Service, Southern Research Station, Pineville, Louisiana (JM), Musée d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland (MHNG), Acarology Laboratory at Ohio State University, Columbus, OH (OSAL).

Schizothorax Athias-Henriot


DIAGNOSIS (updated from Athias-Henriot, 1982)

- Sternal shield of female longitudinally split from posterior border anterior to the level of the first pair of sternal setae (st1) (Figs. 1A-C). Paup femur of deutonymph and adult with anterior lateral setae (al) divided into three branches: one long, arrow-shaped, anterior branch, and two thin, shorter branches; palp genu with anterior lateral setae (al1) and (al2) rod-like. Idiosomal gland pair 4a:5 poorly developed or absent in the deutonymph and adults. Deutonymph lacking acrotrichia on legs I. Cingulum
Fig. 2. *Schizostethus lyriformis*, gnathotectum. A-D, larva; E-F, protonymph; G-H, deutonymph; I-J, male. A, C, E, G, and I based on material from Louisiana; B, D, F, H, and J based on material from California. S. simulatrix: K, female; L, male; S. vicarius: M, female; N, male. All scale bars 25 μm.

(Figs. 1G-I) present or absent. Ventral shield of the female holotrichous, with 6 to 8 pairs of setae.

*Schizostethus lyriformis* (McGraw and Farrier)


**Diagnosis** - Cingulum narrow (Fig. 1O). Glands gdR5 and setae SvJ present in deutonymph and adults. Setae r4 on the podonotal shield in adults. Glands gdR3 in deutonymph and female always on the dorsal membrane in opisthosomal region. Opisthosomal shield of the female with only 15 pairs of setae. Setae pvJ on tarsi II of the male spine-like (finger shape) with poorly developed base, setae ovJ setiform (Fig. 9C). Ventral shield of female with 8 pairs of setae.
**LARVA** - Very weakly sclerotized. Length 376 (330-451; N=7), width 283 (244-292; N=7).

**Gnathosoma** - Gnathotectum (Figs. 2A-B) with three processes, medial process slightly longer than lateral ones. Medial process usually broad and toothed; lateral processes generally small, smooth, and pointed. With series of very small teeth near (not on) the lateral margin of the gnathotectum proper. Salivary stylos (Fig. 2A: s.s.) prominent. Subcapitulum (Fig. 3A) well developed. With 3 pairs of setae: anterior hypostomal setae (hyp1, Evans and Till, 1979) and external posterior hypostomal setae (hyp2) simple. Cornicula (cor) horn-shaped, stout, inserted dorsally. Lateral lips (= internal male, hypostomatic processes) distinct, fringed, longer than cornicula. Labrum not visible. Deutosternum with nine transverse rows of denticles. Eighth row wider than other rows, with 15-18 teeth; other rows with 7 to 12 teeth. Chelicerae (Fig. 4A) - Fixed (fd) and movable (md) digits subequal in length. Fixed digit usually with four recurved teeth, rarely tridentate; movable digit tridentate. Dorsal lyrifissure id poorly visible in this instar, antialial lyrifissure ia distinct. Dorsal seta ds inserted near lyrifissure id. Simple pilus dentilis (pd) between second and third tooth of the fixed digit. Arthrobal membrane process (ar) comb-like. Pedipalps (Figs. 5A-B) - With 5 segments and a 3-tined pretarsal claw (= apotele). Tibias and tarsius fused, but line of separation still visible. Trochanter bare. Femur with 4 setae (fd, dl, d2, p3); seta al of characteristic shape, with three processes; setae d1, d2, and p3 barbed. Small structure in dorsal distal position on site of future lyrifissure. Genu with 5 setae (al, d1, d2, d3, p2); seta al rod-shaped; all general setae smooth. Tibia with 12 simple setae (3 ventral, 3 lateral, 6 dorsal); one anteroventral seta unusually small, spinose. Tarsus with 11 setae.

**Idiosoma** - Dorsum (Fig. 6A) - Discrete shields absent. Transverse suture separating podosoma and opisthosoma weakly developed, not reaching lateral margin of the dorsum. All dorsal setae simple. Podonotal region (Krantz 1978; pronotal of Evans 1992) carries 9 pairs of setae (j1, j3, j4, j5, j6, x2, x4, x5, x6). Setae x2 (117 [113-122]; N=5) and x4 (145 [137-150]; N=5) much longer than other podonotal setae. Setae x3 3-4x as long as other setae (j5, j6) of the dorsal hexagon. Four pairs of lyrifissures present (id2, id4, id6, id8, ip1). Lyrifissure ip1 anterolateral to seta id4. Opisthonotal region with 9 pairs of setae (j2, j3, j4, x2, x3, x4, x5, x6, x2, x3), all subequal in length; setae x4 slightly wider at their base than remaining setae. Dorsal opisthosome with 5 pairs of lyrifissures (id13, id14, id25, id27, id66) and 1 pair of glands (gs22). Lateral to setae x6 is a set of structures composed of 3 elements: a large and rounded, a very small, and an elongated structure. These structures may include more lyrifissures and glands, but their exact nature is not clear. Venter (Fig. 6B) - Anal shield well defined and triangular. Tritosternum with a rectangular base, longer than wide and narrowing distally, lamellae barbed. Ster nal region bears 3 pairs of setae (a1-3) of subequal length. Opisthogastric region with 4 pairs of setae (jv1, jv2, jv5, zv2). Paranatal setae (pa) long, inserted on the corner of the anal shield or rarely off the shield (82 [72-88]; N= 5). Unpaired postanal seta (pa) invariably very long (215 [208-228]; N=5). All ventral setae simple. Anal valves each carrying a small canal seta (eu). Opisthogastric with 2 pairs of lyrifissures, one flanking seta po (hyp), the other (ivo4) posterolateral to setae zv2.
Legs (Fig. 7) - Three pairs of legs present, each with 6 distinct segments (podomeres); pretarsus (spotele) with paired claws and a rounded pulvillus. Legs I more slender than legs II-III, pretarsus smaller and narrower; setae shorter and less barbed than on legs II-III. Coxae - All coxae with 2 ventral setae (ov, pv). Coxae I with setae pv distal to av. A ventral gland present at base of coxae I. Trochanters - I and II each with setae al, pv1, pv2, and pl, trochanter II with setae al, ad1, pv1, and pv2. Femora - Each femur with a single lyrifissure on proximal third of segment. Basifemur not defined. Femora I with 10 setae (al1, al2, ad1, ad2, ad3, pd1, v1, v2, pl1, p12), femora II with 7 setae (al1, ad1, ad2, pd1, vd1, al2, pl1), and femora III with 5 setae (al1, ad1, ad2, pd1, v1). All setae distal to lyrifissure. Genua - I with 8 setae (al1, ad1, ad2, pd1, pv1, pv1, pv1, pl1); genua II-III lacking ventral setae (ovl, pvl). Setae pd2 proximal to other dorsal setae on all genua. Tibiae - 1 with 8 setae (al1, ad1, ad2, ov1, pv1, pd1, pd2, pl1); tibiae II-III lacking setae ad2. Setae pd2 I-II proximal to other tibial setae. Tarsi - Peripodomeric fissure on proximal third of each tarsus incomplete or absent. Position fissure indicated by a single ventral lyrifissure and a small lyrifissure-like dorsal structure. An additional dorsal lyrifissure present in middle third of tarsi II-III. Acrotarsus absent. Tarsi I with 30 sensilla of varying shape (Fig. 7B). Tarsi II-III with up to 16 setae distributed in 4 whirls. First whorl with up to 6 setae (al1, ad1, pd1, pl1, ov1, pv1), second with 4 setae (al2, ov2, pv2, pl2), third with only 2 setae (ad3, pd3), and fourth whorl, basal to incomplete peripodomeric fissure, with 4 setae (al4, pl4, ad4, pd4). Terminal setae ad1 and pd1 II-III very small or absent: seta ad1...
Fig. 5. *Schizothetus lyriformis*, pedipalp - A, larva, dorsal view; B, larva, ventral view of tibia and tarsus; C, deutonymph. All figures based on material from Louisiana. All scale bars 25 μm.

Present on 88% of tarsi II and 29% of tarsi III, seta pd1 present on 17% of tarsi II and 38% of tarsi III (N= 24). Tarsi III with seta pd3 very long, more than 2x as long as seta ad3.

**Protonymph** - Length 509 (473-554; N= 5), width 313 (263-392; N= 5).

**Gnathosoma** - Gnathotectum (Figs. 2C-D). Median and lateral processes become sharply pointed. Medial process 3x as long as lateral processes. Serration generally absent, except sometimes on the curved area between the lateral and medial processes. Small teeth near the lateral margin of gnathotectum proper less developed than in the larva. Subcapitulum (Fig. 3B) - Two pairs of setae added, the internal posterior hypostomal setae (hyp3) and the palpcoxal setae (es), both lightly barbed. Labrum still not visible. Deutosternum as in larva, but width of eighth row of denticles less distinct than in previous instar. Chelicerae - Dorsal lyrifissure id more prominent. Other characteristics as in larva. Pedipalps - Trochanter adding 1 ventral setae (v1), tarsus adding 4 setae; setation of other segments as in larva.

**Idiosoma** - Dorsum (Fig. 8A). Dorsal shields indistinct or absent. Podonotal region: 4 pairs of setae added (j2, r2, r3, r5). Setae r6 shifted from opisthosomal to opisthonotal region. Setae r4 and r5, which were very long in the larva, much shorter in this instar, 54 (43-63; N= 5) and 85 (75-105; N= 5), respectively. Setae r5 still 2-3X longer than setae j5 and j6. Lyrifissure id3 added near seta r5. Opisthonotal region - 6 setae added (j1, j5, z1, s1, r1, rvl). Setae j5 slightly wider than other setae and 2x as long as other dorso-central (j) setae; other opisthonotal setae subequal in length. Total of 3 pairs of lyrifissures (id1, id3, idu1) and 1 pair of glands (gd6) added. Venter (Fig. 8B) - Trilobosternum as in larva. Sternal region with 1 pair of sternal setae (st5) and 2 pairs of lyrifissures (iv1, iv2) added. One pair of ventral setae (v2v1), 2 pairs of lyrifissures (iv1, iv2), and 1 poorly developed pair of glands (gv2) added in opistogastric region. Anal shield bigger but retaining its triangular shape. Paranal and postanal setae much shorter than in larva (postanal setae still longer than paranal setae). Ectal setae absent but vestiges still visible. Coibrum present posterior to postanal setae. Stigmata present lateral to coxae IV, round in shape, and associated with short peritremes and a pair of lyrifissures (lp2).

Legs - Legs IV added in this instar (Fig. 9A). Coxae I to III as in larva. Coxae IV with only setae av on distal
Fig. 6. Schistothecus lyriformis, larva, idiosoma - A, dorsal view; B, ventral view. Scale bar 100 \( \mu \text{m} \).

part of segment. Trochanters - I to III largely as in larva. Trochanters IV each with four setae (al, ad1, avl, pv2). Femora - I with poorly expressed, but complete peripodemic fissure in proximal third dividing each femur into a basi- and a telofemur. One lyrifissure added in fissure region. Femora II-IV not divided. Femora II with a single lyrifissure in region of future peripodemic fissure, femora III-IV with two lyrifissures (one added). Seta v2 added on femur II. Femora IV with four setae (al, ad1, ad2, pd1). Setae ad1 very long. Genua I to III as in larva. Genua IV each with 5 setae (al1, ad1, ad2, pd1, pd2). Tibiae - I to III as in larva. Tibiae IV with 7 setae (al1, ad1, pd1, pd2, avl, pv1, pl1). Seta ad1 very long.

Tarsi - Peripodemic fissure in proximal third of each tarsus complete. One dorsal lyrifissure added in fissure area, separate from lyrifissure-like structure. An additional dorsal lyrifissure added in the basal part of basitarso II-IV. Setae ad2 (md of Evans, 1963a) added on tarsi II-IV, positioned between the setae of whorl 1 and 2. Presence of terminal setae ad1 and pd1 II-IV variable: seta ad1 present on 100% of tarsi II, 25% of tarsi III, and 58% of tarsi IV, seta pd1 present on 50% of tarsi II, 25% of tarsi III, and 91% of tarsi IV (N = 12). Tarsi III: setae ad3 and pd3 subequal in length. Tarsi IV: seta pd3 much longer than ad3.
DEUTONYMPH - Very well sclerotized. Length 848 (813-917; N=5), width 474 (426-521; N=5).

Gnathosoma - Gnathotectum (Figs. 2E-F). Three-pronged, with median process 2.3x longer than lateral processes. Medial process rarely distally divided forming 2 prongs. Serration on processes and small teeth near lateral margin of gnathotectum proper lacking. Subcapitulum - Setae hyp3 relatively longer than in protonymph: 1.5x as long as setae hyp1, and 2x as long as hyp2. Setae hyp2 barbed. Deutosternal forking distinct gutter, 9 rows of deutosternal denticles of subequal width.

Chelicerae (Fig. 4B) - As in protonymph. Pedipalps (Fig. 5C) - Trochanteral seta v2 added, distal to seta vl, both setae barbed. Femur adding setae d2, genu adding rod-like seta a1, tibia adding 2 setae. Dorso-distal lyrifissure on femur distinct. Number of tarsal setae as in protonymph.

Idiosoma - Dorsum (Fig. 10A). Podonotal shield: length 404 (395-413; N=5), width 412 (395-442; N=5). Opisthonomal shield: length 222 (212-235; N=5) and width 358 (320-395; N=5). Both shields well defined with a reticulate pattern, but center of podonotal shield weakly reticulated. Opisthonomal shield distinctly narrower than podonotal shield. All setae smooth. Podosomal region with 22 pairs of setae, adding 8 pairs relative to the protonymph (s1, s3, s6, s1, s2, s3, r4, r6). Setae s2 and r4 inserted off the shield on the membrane. Most podosomal setae similar in size, but setae s1, s1, and s2 very small, and setae r3 very long (174 [163-188]; N=5). Dorsal hexagon setae s5 2x as long as setae j5 and j6. A pair of lyrifissures (idf1), and 4 pairs of glands (gdf2, gdf4, gdh5, gdh6) added. Lyrifissures ipf1 shifted ventro-laterally, now closely associated with the peritremes. Glands gdf4 may be multiple, while glands gdh2 are weakly developed. Muscle attachment scars (siquilles) as illustrated (Fig. 10A). Opisthonomal region with 22 pairs of setae, by addition of 8 pairs of setae (Z5, S4, S3, R2, R3, R4, R5, rv6). All K, rv, and Rv setae, plus setae S4, S3, and Z5 inserted off the shield on the membrane. Setae J5 1.5x as long as other dorso-central (j) setae. Three pairs of lyrifissure marks.
Fig. 8. *Schizostethus lyformis*, protonymph, idiosoma - A, dorsal view; B, ventral view. Scale bar 100 μm.

fissures (id12, idS2, idS5) and 2 pairs of glands (gdS2, gdS4) added. All glands off the shield (glands gdS2 occasionally on the edge of the shield). Lyrifissure idS2 and gland gdS2 may have one of three positions: both of them off the shield, both of them on the edge of the shield, or (most common) lyrifissure idS2 on the edge of the shield and gland gdS2 off. Usually gland gdS2 proximal to lyrifissure idS2, rarely inserted distally. Venter (Fig. 10B).

- Sternal and anal shields well defined and entirely reticulated. All setae smooth. Tritosternum as in protonymph, flanked by a pair of small crescent-shaped presternal platelets. Setae st4 and a pair lyrifissures (iv3) added to the sternal shield. Lyrifissures iv5 added near coxae IV.

Small triangular fragment of endopodal shield present between coxae II-III. Opisthogastric region adding 5 pairs of setae (Jv3, Jv4, Zv3, Zv4, Sv1). Glands gv2 well developed. Sclerotization includes 3 pairs of ventral platelets between setae st5 and Zv2, and small, oval, metapodal shields lateral to setae Sv1. Anal shield more rounded than in previous instars. Stigmata at level of coxae IV or between coxae III and IV, associated peritremes extending to level of coxae I; anterior section dorsal in position. Peritrematal shield present. Lyrifissure (p1) and gland gp (added) closely associated with anterior peritrematal shield, lyrifissure p2 as in protonymph.

Legs (Fig. 11) - Coxa - One ventral gland added to each coxa I. Trochanters - Two setae added on trochanters I (ad1, av1), only one on trochanters II-IV: av1 on trochanters II-III, pv1 on trochanter IV. Femora - II to IV with a complete peripodemeric fissure associated...
with 2 lyrifissures. Three setae added on femur I (pd2, v3, v4), 3 on femur II (al2, ad3, v2) and 1 on femora III-IV (pd2). Setae al2 and v3 II, and v1 III inserted on the basifemur. All added setae small. Femur III-IV: seta ad1 2-3x as long as seta pd1. Genua - Five setae (al2, ad3, pd3, pl2, av2) added on genu I, 5 setae (al2, ad3, av1, pv1, pl2) on genu II, 2 ventral setae (av1, pv1) on genu III, and 5 setae (al2, pd3, av1, pv1, pl1) on genu IV. Tibiae - Six setae (al2, ad3, pd3, av1, pv1, pl2) added on tibia I, 3 setae (al2, ad2, pl2) on tibia II, 1 seta (al2) on tibia III, and 3 setae (al2, pd3, pl2) on tibia IV. Setae av1 and pv1 on tibiae II and IV shorter and stronger than in the protonymph. Tibiae III-IV - seta ad1 3x as long as other dorsal setae. Tarsi - Subdistal fissure, forming acrotarsus, appears distally on tarsi II-IV, at same level as, or slightly distal to, the bases of the II and VI setae. One ventral setae (av2) (nv of Evans, 1963a) added on tarsi II-IV. Presence of terminal setae ad2 and pd2 II-IV: seta ad1 present on 100% of tarsi II, 21% of tarsi III, and 14% of tarsi IV; setae pd1 present on 35% of tarsi II, 14% of tarsi III, and 71% of tarsi IV (N= 14).

FEMALE - Length 1096 (1045-1144; N= 5), width 599 (566-627; N= 5).

Fig. 9. Schizostethus lyriformis, legs - A, leg IV, protonymph, dorsal view; B, distal part of tarsus II, female, dorsal view; C, leg II, male, ventral view; D, S. simulatrix, femur II, male, ventral view; E, S. vicarius, femur II, male, ventral view. All scale bars 50 µm.
Gnathosoma - Gnathotectum (Figs. 2G-H) - Angle between base of the median and lateral processes decreasing (relative to deutonymph). Lateral process relatively longer than in deutonymph. Subcapitulum (Fig. 3C) - Labrum poorly visible. Deutosternum, chelicerae, and pedipalps as in deutonymphs.

Idiosoma - Dorsum (Fig. 12A). Podonotal shield: length 454 (441-464; N=5), width 482 (457-498; N=5). Opisthonal shield: length 325 (299-348; N=5), width 454 (441-464; N=5). Both shields subequal in width. Total number of dorsal setae unchanged, but relative to deutonymph setae s2 and r4 shifted onto the podonotal shield, and setae R1, R2, and R3 onto the opisthonal shield. With the exception of the very long setae r3, and the relatively short setae s1 and s2, all dorsal setae sub-equal in length. Setae z5 subequal in length to setae j6 and x6. Lyristriphyses and glands largely as in deutonymph; glands gdsC shifted axial, becoming more distinct due to the presence of a surrounding oval or round zone. Opisthosoma - Setae J3 subequal in length to other shield setae. Setae overall relatively shorter than in deutonymph, e.g. setae J3 and J4 not extending to bases of next setae. Lyristriphyses and glands as in deutonymph but glands gdsD often absent. Muscle scars as in deutonymph. Venter (Fig. 12B) - Shield reticulation distinct. Tritosternum as in protonymph. Sternal shield medially split with cut extending anterior from the posterior border to the level of the setae st1. Anterior lateral lobes (Figs. 1A, 12B.l) relatively wide at their base, narrowing smoothly towards the distal apex. Metasternal shields large, each carrying
1 setae (st4) and 1 lyrifissure (iv3). Parametasternal shield (Fig. 12B, pesms) flanking genital shield, medially convex. Genital shield triangular, its base hinged at corners to ventral shield. Genital shield with setae st5. Endogynium oval shaped (Fig. 12C). Opisthogastric region. Ventral shield fused with anal and metapodal shields to create a ventrional shield, connected to peritremal shield by a so-called "cingulum" (Figs. 1G, 1, 12B: eg). Number of setae, lyrifissures, and glands as in deutonymph. Setae lv3 and 2v4 off the shield inserted on the membrane. Cribrum (Fig. 12: cr) well developed. Stigmata as in deutonymph; peritremal shield well defined.

Legs - Pretarsus I shorter than in deutonymph. Acetabular fissure on tarsi II-IV basal to first whorl of setae (Fig. 9B), not distal as in deutonymph. Setae adl and pdl on tarsi II-IV thin and distinctly elongated; their tops arrow-shaped. Presence of terminal setae adl and pdl II-IV: setae adl present on 100% of tarsi II, 75% of tarsi III, and 38% of tarsi IV; setae pdl present on 50% of tarsi II, 75% of tarsi III, and 100% of tarsi IV (N= 6). Setae ii and vi on tarsi II-IV short and spinose (Fig. 9B).

MALE - Length 958 (916-1026; N= 5), width 521 (490-566; N= 5). Gnathosoma - Gnathostegum (Figs. 21-J) and subcapitulum as in female. Deutosternum usually as in female, rarely with 10, instead of 9 rows. Chelicerae (Figs. 4C, E) - Fixed digit with only two teeth and movable digit with only one tooth. Movable digit with spermatotome forming a slit or opening that closes on two sides. Arthrostral membrane process (ar) shaped like a thick rod, with distal branches (Fig. 4E). Pedipalps - As in deutonymph.

Idiosoma - Dorsum (Fig. 13A) - Podonotal shield: length 443 (430-449; N= 5); width 501 (457-553; N= 5). Opisthognathal shield: length 290 (296-336; N= 5), width 484 (456-524; N= 5). Dorsal shields large, covering nearly entire dorsum. Podonotal and opisthognathal shield adjoined or partly overlapping. All dorsal setae inserted on the shields, relative lengths as in female. Lyrifissures and glands as in female. Distal part of peritremes completely dorsal. Glands g2S4 present and glands g2S2 always postceralateral to lyrifissures id32. Venter (Fig. 13B) - Tritosternum and presternal platelets as in
deutonymph. Anterior lateral lobes of sternal shield as in female but a little wider at their base (Fig. 1D). Holoven- 
trual shield, but border of ventralial shield faintly visible (Fig. 13B, dotted lines). Number of setae, lyrifissures, 
and glands in the opisthogastric region as in deutonymph, 
but all inserted on holovenstral shield. Stigmata as in fe-
male; periatrial portion of holovenstral shields fused 
larly with podonotal shield.

Legs - Legs I, III and IV as in female, but ventral 
setae avl and pvl of tarsi III-IV longer than lateral setae 
and usually less spinose than in the female. Terminal 
setae adl and pdl II-IV: seta adl present on 62% of tarsi 
III, and 50% of tarsi IV; seta pdl present on 50% of tarsi 
III, and 100% of tarsi IV (N= 8). Leg II (Fig. 9C) - Coxae 
and trochanters - as in deutonymph. Femur -enlarged. 
Setae v1 and v2 hypertrophied to form spurs; each seta v1 
modified as a large spur (apophysis) with a curved shape, 
seta v2 as a short auxiliary spur. Seta v1 extending from 
its base to approach the base of setae v2. Seta ad2 and 
v3 basal to the peripodomial fissure. Genitalia - 
setae avl hypertrophied to form short spurs, other setae 
as in deutonymph. Tarsus - seta pvl spindike (finger-
shaped) fused with cuticle segment (base of seta not 
visible), but seta avl setiform, longer than setae ad1 and pdl.

Setae adl and pdl as in female. Presence of terminal 
setae adl and od2 100% and 75% respectively (N= 8). 
Other tarsal setae as in female.
MATERIAL EXAMINED

Type material examined - U.S.A.: North Carolina; Yadkin Co., ex Ips avulsus Eichhoff (Scolytidae) and I. grandicollis Eichhoff on Pinus echinata Miller, 30 May 1966, J. R. McGraw, USNM. Paratypes (2) female (sp20), North Carolina; Yadkin Co., ex Dendrocotinus frontalis Zimmerman (Scolytidae) on P. echinata, 30 May 1966, J. R. McGraw, USNM. Allotype male (sp18).


DIAGNOSIS - Cingulum absent (Fig. 1H). Setae SvI and glands g2g5 present. Setae r4 off podonotal shield in female. Opisthonal shield with 15 or 16 pairs of setae in adults (setae S4 may be inserted on the shield). Gland pair g3r3 on dorsal membrane of opisthosomal region in deutonymph and female. Ventral shield of female with only 6 setae (Sv3 and Jv- off the shield).

The deutonymph and adults have recently been redescribed by Kalk et al. (in press).

COMMENTS - Deutonymph in most details as deutonymph of S. lyriformis. Adults. Medial process of gnathotremum longer than lateral processes. In male, lateral processes appear shortened (Fig. 2K-L). Arthrodial membrane process of chelicer in male short and distally divided (Fig. 4F). Dorsal projection on the fixed cheliceral digit of the male much more developed than in S. lyriformis (Fig. 4D). The latter difference was also noted by Athias-Henriot (1982). Idiosomal dorum largely as in S. lyriformis but in female setae r4 off podonotal shield while setae S4 are sometimes inserted on the margin of the opisthosomal shield. Retractility of podonotal shield in the central area distinct. Positions of glands g2g2 and lyriformia id2 id2 as in S. lyriformis. Vent. Axial margin of parameseral shield highly convex (Fig. 1B) - Anterior lateral lobes of sternal area of adults distinctive (especially in the male) (Figs. 1B, E). Legs - Apophyses on femora II of the male generalized, but larger and longer than in the other species (Fig. 9D). Setae avl and pvl on tarsi II of both sexes spinelike, resembling condition in female S. lyriformis (Fig. 9B).

MATERIAL EXAMINED

Previously published localities - SPAIN: Canary Islands; PORTUGAL (Athias-Henriot 1982), GERMANY (Moser and Bogenschütz, 1984); SLOVAKIA, several localities (Kalitè et al., in press).

_Schizosthetus vicarius_ Athias-Henriot


**DIAGNOSIS** - Cingulum large (Fig. 1). Setae _sv1_ and glands _ghd5_ absent. Setae _sd_ on podonotal shield of adult. Opisthontal shield of female with 28 or 29 pairs of setae. Glands _ghd3_ on opisthontal shield. Ventrianal shield of female with 8 pairs of setae.

**COMMENTS** - Deutonymph unknown. Adults - Gnathottergum with medial and lateral processes similar in length and shape (Figs. 2M-N); lateral processes in male clearly larger at their base than in the female (Fig. 2N). Arcbrochial brush of chelicerae comb-shaped in both male and female (Fig. 4G). Dorsal process on fixed cheliceral digit of chelicera in male less distinct than in _S. lyriformis_ or _S. similatrix_. Idiosomal dorsum as in _S. lyriformis_ except that setae _j6_ are slightly longer than setae _z5_ and _j5_ (based on only one specimen); glands _ghd5_ absent. Opisthontal shield with 28 or 29 pairs of setae; setae usually long, extending beyond the insertion point of the next seta. Gland pairs _gds2_ and _gdr3_ and lyrifissures _id82_ on opisthontal shield, distant from the shield margin. Posterior marginal reticulation characteristically wavy. Venter with axial margin of parameternal shield straight (Fig. 1C). Anterior lateral lobes of sternal area of female and male short, narrow and smooth (slightly shorter and wider in male), with a distinct projection at their base (Figs. 1C, F). Legs - Apophyses of femora II of the male generalized and smaller than in the other species (Fig. 9E). Tarsal setae _avl_ and _pvl_ II in the male spine-like but smaller than in the other two species.

**MATERIAL EXAMINED**

Type material examined - U.S.A.: Oregon, Lane Co., Andrews Experimental Forest, ex moss and soil on trunk of _Pseudotsuga menziesii_, 1977, D. Voegtlin, USNM. Paratype female (AS631) and male (AS633).

**DISCUSSION**

**DEVELOPMENT IN S. lyriformis** - Most of the observations presented in this study agree with previous studies on the family (Athias-Henriot, 1982; Evans 1963a, 1963b, 1969; Hyatt 1980; Micherdzinksi, 1969). However, this study generated some previously unreported, or at least not emphasized, information. First, the detailed study of idiosomal glands and lyrifissures throughout ontogeny illustrated a notable positional shift for lyrifissures _ipl_. In the larva and protoynymph these lyrifissures are positioned distinctly dorsal (podonotal region), but they shift ventrolateral to become associated with the peritremes in the deutonymph and adult. Second, the odd structures near setae _a6_ in the larva (a large rounded shape associated with a very small structure and an elongated structure). The possibility that these structures are the first step towards developing stigmata is of some interest for developmental patterns in all Mesostigmata. Third, _S. lyriformis_ shows a variability in the presence/absence of terminal tarsal setae _avl_ and _pvl_ II-III. Such variability was not reported in the classic study by Evans (1963a) on _Pergamasus_ leg ontogeny. At the very least this suggests that while leg chaetotaxy is generally conserved within Parasitidae, some intra- and perhaps inter-specific variability may occur. In the same context we note the sexual dimorphism in the shape of the _vl_ setae on tarsus II of _S. lyriformis_. Finally, we comment on the development of relative setal lengths. Whether or not the setae of the dorsal hexagon are of the same length and shape is often used as a key character for adult (and deutonymphal) Parasitidae. Development in _S. lyriformis_ shows that this character may have an ontogenetic component. These setae are quite different in length in the larva, but gradually become more similar in size during development, culminating in near identical setae in the adults.

**CLASSIFICATION OF THE GENUS** - The longitudinal split in the sternal shield of the female easily distinguishes _Schizosthetus_ from all other genera of Parasitidae. This characteristic is not known in any other lineage of Parasitidae or in closely related taxa, and can thus be considered derived, supporting the monophyly of _Schizosthetus_. What is still unclear is the status of the related genera into which _Schizosthetus_ species have previously been placed. Athias-Henriot (1978b) clarified the concept of _Eugamasus_ pointing out a unique character that distinguishes deutonymphys and adults of this genus from all other genera: the bifid shape of palp genu setae _a2_ and _a12_. However, there is no unique character or set of characters that defines _Vulgarogamasus_. Based on currently available data, this genus is almost certainly paraphyletic, and in great need of revision. In terms of key characters, _Vulgarogamasus_ can be distinguished from _Schizosthetus_ by the absence of the split sternal shield in the female, but it is much more difficult to distinguish _Vulgarogamasus_ from _Schizosthetus_ in the male. For example, the pedipalpal setae of _Vulgarogamasus bicuspidus_ Ewing, 1913 have the same shape as in _Schizosthetus_. In the deutonymph, _Schizosthetus_ can be distinguished from _Eugamasus_ and _Vulgarogamasus_ by the absence of an acrotarsus on tarsi 1.
Table 1. Comparative characteristics of Schizocassidus species.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th><em>S. lyriformis</em></th>
<th><em>S. simulatrix</em></th>
<th><em>S. vicarius</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Cingulum (female)</td>
<td>Narrow (Fig. 1G)</td>
<td>Absent (Fig. 1H)</td>
<td>Wide (Fig. 1I)</td>
</tr>
<tr>
<td>Glands gzd5 (DN, Ad)</td>
<td>Present</td>
<td>Present</td>
<td>Absent</td>
</tr>
<tr>
<td>Glands gzd3 (DN, Ad) on opisthnotonal shield</td>
<td>No</td>
<td>No</td>
<td>Yes (DN unknown)</td>
</tr>
<tr>
<td>Setae Svl (DN, Ad)</td>
<td>Present</td>
<td>Present</td>
<td>Absent</td>
</tr>
<tr>
<td>Shape anterior lateral lobes (Ad)</td>
<td>Edges smooth (Figs. 1A, D)</td>
<td>With anterior protuberance (Figs. 1B, E)</td>
<td>Narrow, anterior edge smooth, posterior edge with projection (Figs. 1C, F)</td>
</tr>
<tr>
<td>Setae av1 and pv1 on tarsi II (male)</td>
<td>pv1 spinelike; av1 simple (Fig. 9C)</td>
<td>Both spinelike</td>
<td>Both spinelike, relatively small</td>
</tr>
<tr>
<td>Number of setae on ventrional shield (female)</td>
<td>8</td>
<td>6</td>
<td>8</td>
</tr>
</tbody>
</table>

Abbreviations: DN, deutonymph; Ad, adult.

We recognize three species of Schizocassidus: *S. lyriformis*, *S. simulatrix*, and *S. vicarius*. The main character that distinguishes these species from each other is the cingulum, found only in the female (Table 1). Most other characteristics are shared between *S. lyriformis* and *S. simulatrix*. These two species are quite distinct from *S. vicarius*. For example, glands gzd5 and setae Svl are present in *S. lyriformis* and *S. simulatrix* but absent in *S. vicarius*, and glands gzd3 are positioned off the opisthnotonal shield in *S. lyriformis* and *S. simulatrix* while on the opisthnotonal shield in *S. vicarius* (Table 1). Distinguishing *S. lyriformis* from *S. simulatrix* is less simple. In female *S. simulatrix* setae r4 are inserted on the podonotal shield, setae S4 are sometimes inserted on the margin of the opisthnotonal shield, and only 6 pairs of setae are present on the ventrional shield, while in the other two species setae r4 are inserted on the podonotal shield, and the ventrional shield carries 8 pairs of setae. In *S. lyriformis* setae S4 are inserted on the opisthnotonal shield. In the male, the anterior lateral lobes (Figs. 1D-E) and the shape of the apical ventral setae on tarsi II allow species identification (Table 1). The deutonymphs of *S. lyriformis* and *S. simulatrix* are very similar, but differ by having the third set of small ventral sclerites fused to the base of setae Jvl (S. simulatrix) or free from those setal bases (S. lyriformis) (Kulak et al., in press). Although the deutonymph of *S. vicarius* is unknown, it seems likely, based on the condition in the adults, that it lacks glands gzd5 and setae Svl.

**DISTRIBUTION PATTERNS** - Based on the previous records of McGraw and Farrier (1969), Athias-Henriot (1982), and newly reported collections, the distribution of each species can be summarized as follows: *S. vicarius* has been found only in Oregon; *S. lyriformis* is distributed over most of North America, including Canada (Alberta, British Columbia), the United States (Louisiana, New Mexico, Colorado, North Carolina, South Dakota, Virginia, Wyoming, Tennessee, and California), Mexico, Honduras, and Guatemala; *S. simulatrix* has been identified from Europe and North Africa, specifically Slovakia, Germany, France, Portugal, and the Canary Islands (Spain). Even though deutonymphs of *S. lyriformis* and *S. simulatrix* cannot be distinguished with absolute certainty, we consider it very likely that available deutonymphs form Germany and Sweden also belong to this species. Unexamined material from Siberia reported by Tichomirov (1977) may belong to *S. simulatrix* based on the poor development of the lateral processes of the gnathosoma (based on a drawing by Tichomirov, 1977). However, the states for several important specific characters were not reported, and the status of that collection is considered undetermined. A lone male specimen from China (Gansu Prov., Sunan, ex Polygraphus polygonus trap dregs, 7 July 1982, Yin Hui-Fan, IM, JM 20069) adds to this uncertainty. If it belongs to *Schizocassidus* (because it is a male, generic identification is tentative), the shape of the anterior lateral lobes and presence of Svl identify it as new species with characteristics intermediate be-
between *S. simulatrix* and *S. lyriformis*. As might be expected, this overall distribution largely mimics the distribution of Scolytidae and pine trees.

The genus *Schizostethus* may be considered as relatively recent. This idea is based on the limited diversity (only three species) and the paucity of specific morphological characters that distinguish this obligate bark beetle associated genus from free living genera such as *Eugamurus* and *Vulgarogamurus*. From a systematic point of view *S. vicarius*, which is found only in Oregon, is most likely the sister group of the lineage including both of the other two species, *S. lyriformis* from North America and *S. simulatrix* from Europe. Given that both sister lineages occur in North America, and only one in Europe, it seems most likely that the ancestor of the entire genus occurred in North America. Dispersal from North America to Eurasia may have happened during periods when a land bridge formed in the Bering Sea. After dispersal to Northern Russia, further dispersal may have brought the genus to Europe. Meanwhile *S. lyriformis* dispersed over North America.

At the species level, the available data allow some comments on the population structure of *S. lyriformis*. The range of pine trees in North America was pushed back from north to south during the time of the ice ages. At the end of these ice ages pine trees started dispersing north again. Moser and Macías-Sánchez (2000) concluded that the appearance of *Dendroctonus frontalis* Zimmerman (Scolytidae) in the Southern United States might be a recent event, involving dispersal northwards from Mexico along with the pines. These authors suggested a movement northwards of the beetles along two routes, one west into California, the other along the Gulf coast into Louisiana and the Southeastern US. Although *S. lyriformis* is associated with many species of Scolytidae (Kinn, 1971; McGraw and Farrier, 1969) it is interesting to note that there are some small differences between the California and Louisiana / North Carolina populations of *S. lyriformis*. Some dorsal and lateral setae of tibia I and sometimes genu I in the deutonymphs and males (less common in females) are setiform in California specimens, but may be lightly fan-shaped setae in material from Louisiana and North Carolina. This pattern of variation is thus consistent with the proposed dispersal pattern of *D. frontalis*. More detailed studies of population variability over the entire range of *S. lyriformis* are required to further test the validity of the bark beetle / mite dispersal hypothesis.

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**REFERENCES**


