REDESCRIPTION OF *SCHIZOSTHETUS LYRIFORMIS* (McGRAW AND FARRIER, 1969) (PARASITIFORMES: PARASITIDAE), WITH REVISION OF THE GENUS

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ABSTRACT - *Schizosthetus lyriformis* (McGraw and Farrier, 1969) is redescribed for all instars, emphasizing ontogenetic changes in sensillar and gland patterns of all body parts. This approach allows recognition of some previously unreported patterns. Major positional shifts of lyrifissures over ontogeny appear correlated with the formation of the peritremes, and some setae of leg tarsi 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.

Key words - Mesostigmata, Parasitidae, *Schizosthetus*, bark beetles, development.

INTRODUCTION

Parasitidae is among the most common and widely distributed families of soil and litter mites in the Holarctic. 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 Parasitinae 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 (Hennessey and Farrier, 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*, *Coleogamasus* Tichomirov, 1967, *Eugamasus* Berlese, 1892, *Vulgarogamasus* Tichomirov, 1969, and *Neogamasus* 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-Bals (1975, 1981, 2002) have helped out for the Pergamasinae, but some additions for Parasitinae seem overdue.

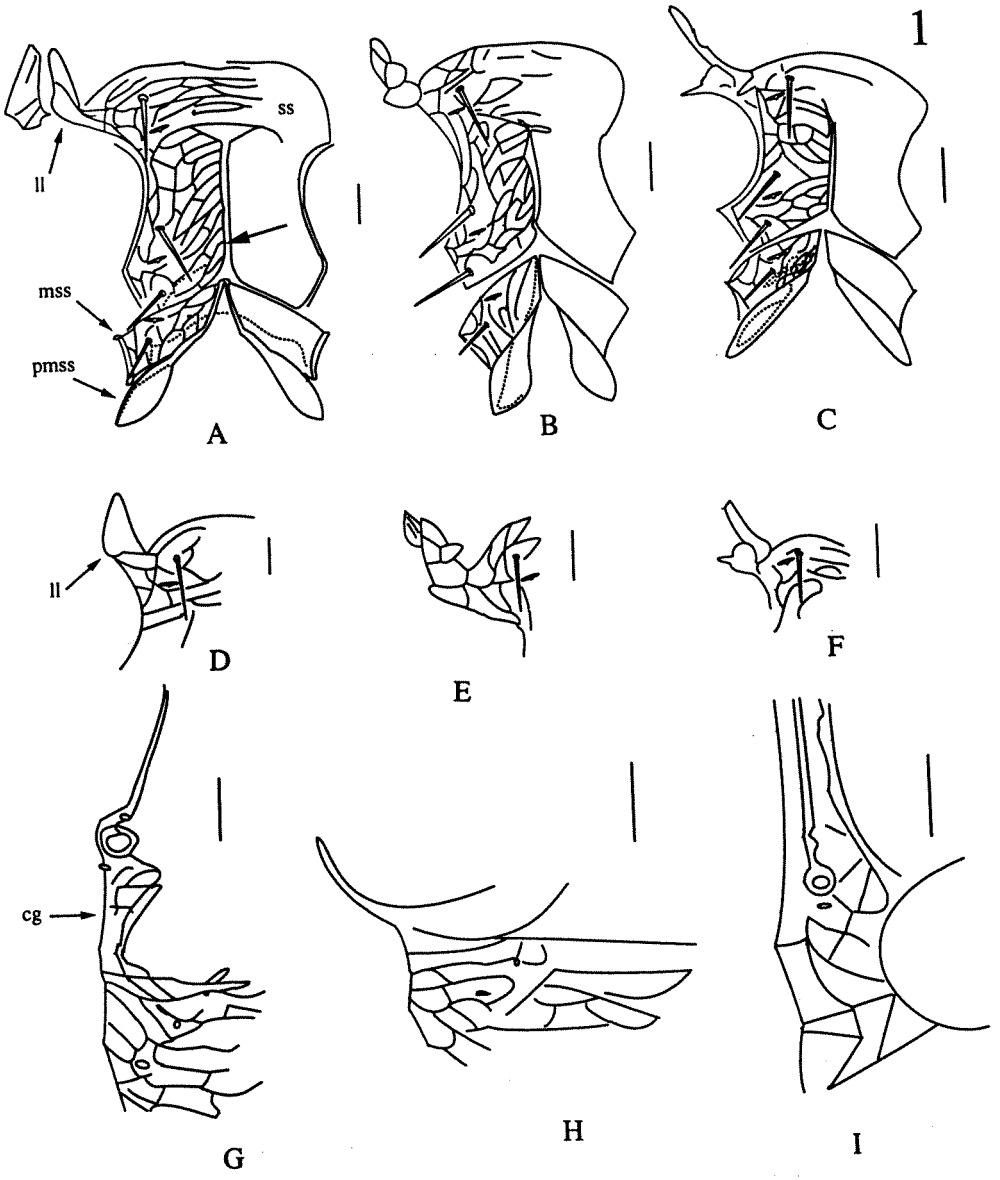

Fig. 1. Variable characters within *Schizosthetus* - Sternal shield (ss), anterior lateral lobes (ll), metasternal shield (mss) and parametasternal shield (pmss) of female: A, *Schizosthetus lyriformis;* B, *S. simulatrix;* C, *S. vicarius.* Large arrow indicates split in sternal shield. Anterior lateral lobes of male: D, *S. lyriformis;* E, *S. simulatrix;* F, *S. vicarius.* Cingulum (cg) of female: G, *Schizosthetus lyriformis;* H, *S. simulatrix,* cingulum absent; I, *S. vicarius.* All scale bars 50 μm.

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 lyrifissure 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 (Hyatt, 1980), and finding or rearing those instars can be difficult (Bhattacharyya, 1962). However, detailed studies of immatures are often the only way to resolve homology questions in adults.

The genus *Schizosthetus* Athias-Henriot, 1982 is a good example to illustrate the above problems. McGraw and Farrier (1969) described the type species as *Eugamasus lyriformis* McGraw and Farrier, 1969 based on general characteristics of the tectum, cornicula, and chelicera. Tichomirov (1977) transferred it to *Vulgarogamasus* based on the absence of denticles on the lateral margin of the genital shield, a characteristic he considered typical of *Eugamasus*. Athias-Henriot (1978b) clarified the concept of *Eugamasus* by noting the characteristic bifid shape of the anterior-lateral palp genu setae (*al1*, *al2*). In a later paper, Athias-Henriot (1982) proposed *Eugamasus lyriformis* as type of a new genus, *Schizosthetus*. The main character for this genus is the longitudinal split of the sternal 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 "pores." In contrast, Athias-Henriot (1982) concentrated on the adults of *S. simulatrix* and *S. vicarius*, providing a detailed discussion of idiosomal lyrifissures and glands while almost completely ignoring the legs and the immature 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 *Schizosthetus lyriformis*, including the gnathosomal 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 *Schizosthetus*.

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 idiosoma; 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).

Schizosthetus Athias-Henriot

Schizosthetus Athias-Henriot, 1982: 208.

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). Palp 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 *gdz5* poorly developed or absent in the deutonymph and adults. Deutonymph lacking acrotarsus on legs I. Cingulum

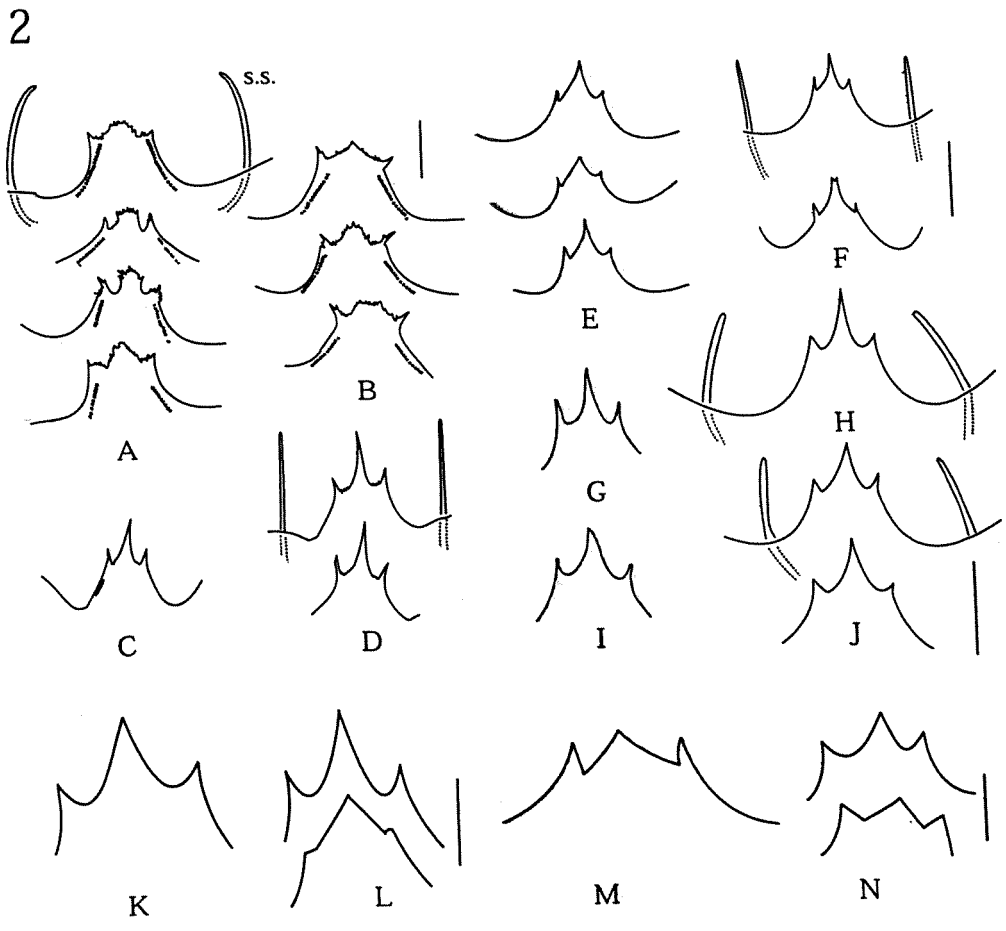

Fig. 2. *Schizosthetus lyriformis*, gnathotectum - A-B, larva; C-D, protonymph; E-F, deutonymph; G-H, female; I-J, male. A, C, E, G, and I based on material from Louisiana; B, D, F, H, and J based on material from California. *S. simulatrix*: K, female; L, male; *S. vicarius*: M, female; N, male. All scale bars 25 µm.

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

***Schizosthetus lyriformis* (McGraw and Farrier)**

Eugamasus lyriformis McGraw and Farrier, 1969: 19; *Parasitus (Vulgarogamasus) lyriformis* (McGraw and Farrier, 1969), Tichomirov, 1977: 148; *Schizosthetus lyriformis* (McGraw and Farrier, 1969), Athias-Henriot, 1982: 208.

DIAGNOSIS - Cingulum narrow (Fig. 1G). Glands *gdz5* and setae *Sv1* 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. Opisthonotal shield of the female with only 15 pairs of setae. Setae *pv1* on tarsi II of the male spine-like (finger shape) with poorly developed base, setae *av1* setiform (Fig. 9C). Ventrianal shield of female with 8 pairs of setae.

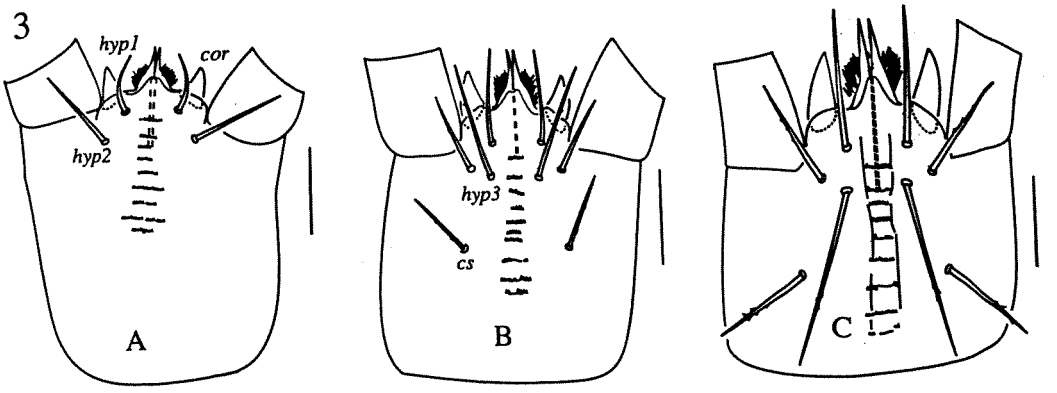

Fig. 3. *Schizosthetus lyriformis*, subcapitulum - A, larva; B, protonymph; C, female. A and B based on material from Louisiana. All scale bars 25 μm. Abbreviations: *cor* = corniculus; *c.s.* = palpcoxal seta; *hyp.1-3* = hypostomal setae.

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 stylets (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 malae, 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, antiaxial lyrifissure *ia* distinct. Dorsal seta (ds) inserted near lyrifissure *id*. Simple pilus dentilus (pd) between second and third tooth of the fixed digit. Arthrodial membrane process (ar) comb-like. Pedipalps (Figs. 5A-B) - With 5 segments and a 3-tined pretarsal claw (= apotele). Tibia and tarsus fused, but line of separation still visible. Trochanter bare. Femur with 4 setae (*al, dl, d2, pl*); seta *al* of characteristic shape, with three processes; setae *dl*, *d2*, and *pl* barbed. Small structure in dorsal distal position on site of future lyrifissure. Genu with 5 setae (*al, dl, d2, d3, pl*); seta *all* rod-shaped; all genual 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, z2, z4, z5, s4*). Setae *z5* (117 [113-122]; N= 5) and *s4* (145 [137-150]; N= 5) much longer than other podonotal setae. Setae *z5* 3-4x as long as other setae (*j5, j6*) of the dorsal hexagon. Four pairs of lyrifissures present (*idj3, idj6, ids4, ip1*). Lyrifissure *ip1* anterolateral to seta *s4*. Opisthonotal region with 9 pairs of setae (*J2, J3, J4, Z2, Z3, Z4, s6, S2, S3*), all subequal in length; setae *J4* slightly wider at their base than remaining setae. Dorsal opisthosoma with 5 pairs of lyrifissures (*idJ3, idJ4, idJ5, idZ1, ids6*) and 1 pair of glands (*gdS2*). Lateral to setae *s6* 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 or 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, laciniae barbed. Sternal region bears 3 pairs of setae (*st1-3*) of subequal length. Opisthogastric region with 4 pairs of setae (*Jv1, Jv2, Jv5, Zv2*). Paranal setae (*pa*) long, inserted on the corner of the anal shield or rarely off of the shield (82 [72- 88]; N= 5). Unpaired postanal seta (*po*) invariably very long (215 [208 -228]; N= 5). All ventral setae simple. Anal valves each carrying a small euanal seta (*eu*). Opisthogaster with 2 pairs of lyrifissures, one flanking seta *po* (*ivp*), the other (*ivo4*) posterolateral to setae *Zv2*.

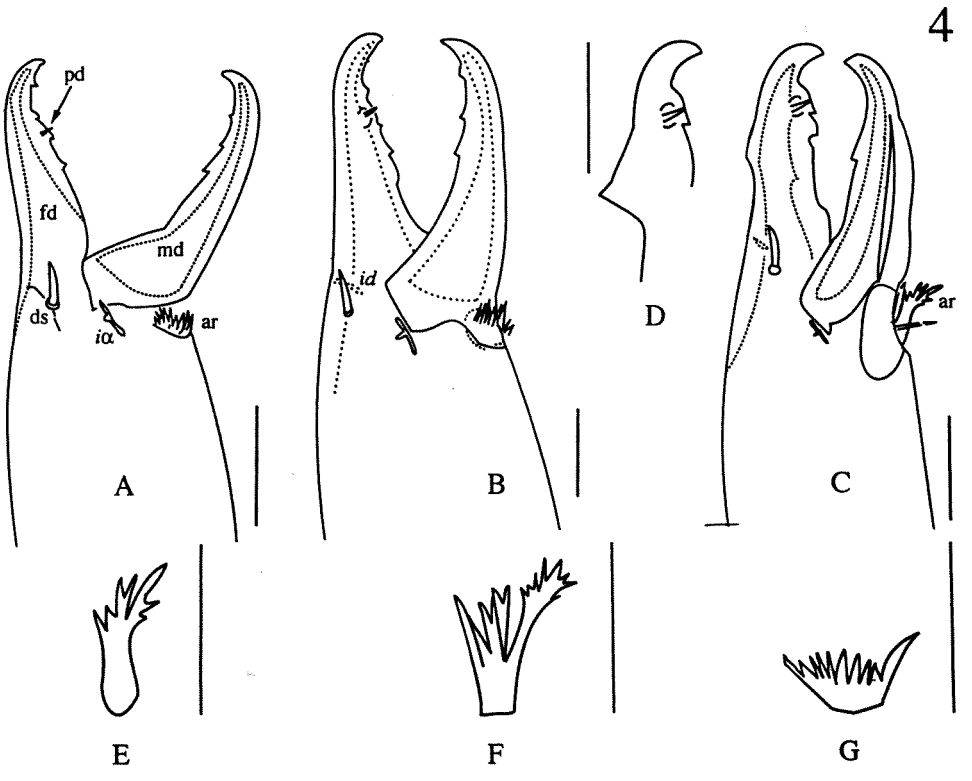

Fig. 4. *Schizosthetus lyriformis*, chelicera - A, larva; B, deutonymph; C, male. Figure A based on material from Louisiana. Fig. D, *S. simulatrix*, male chelicera. Figs. E-G, male, arthrodial membrane process: E, *Schizosthetus lyriformis*; F, *S. simulatrix*; G, *S. vicarius* Abbreviations: ar = arthrodial membrane process; d.s. = dorsal seta f.d.= fixed digit; *iα* = antiaxial lyrifissure; *i.d.*= dorsal lyrifissure; m.d. = movable digit; p.d. = pilus dentilus. All scale bars 25 μm.

Legs (Fig. 7) - Three pairs of legs present, each with 6 distinct segments (podomeres); pretarsus (apotele) 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 (*av, pv*). Coxae I with seta *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 III 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, pl2*), femora II with 7 setae (*al1, ad1, ad2, pd1, pd2, v1, 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, pd2, av1, pv1, pl1*); genua II-III lacking ventral setae (*av1, pv1*). Setae *pd2* proximal to other dorsal setae on all genua. Tibiae - I with 8 setae (*al1, ad1, ad2, av1, pv1, pd1, pd2, pl1*); tibiae II-III lacking setae *ad2*. Setae *pd2* I-III 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 whorls. First whorl with up to 6 setae (*al1, ad1, pd1, pl1, av1, pv1*), second with 4 setae (*al2, av2, 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*

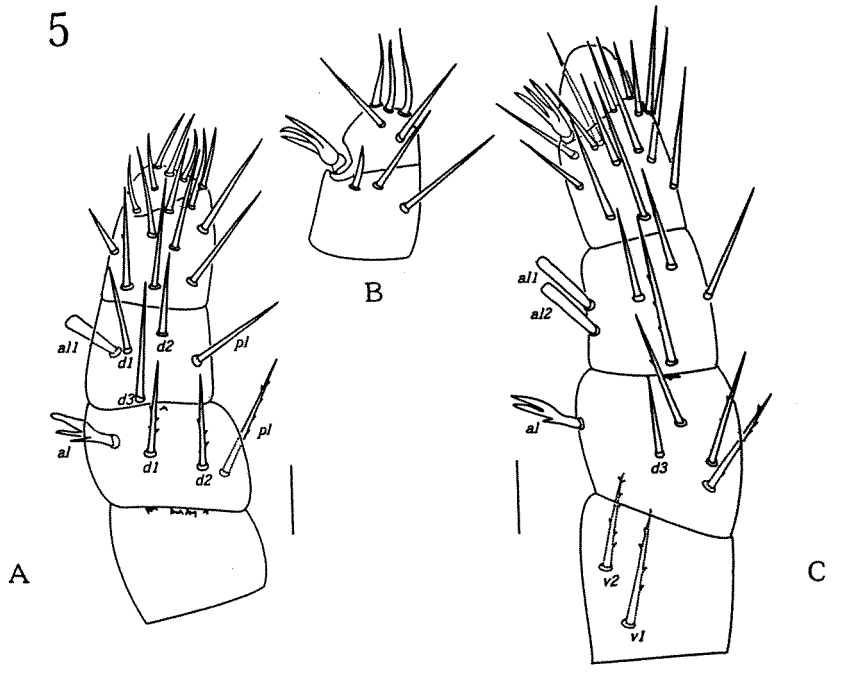

Fig. 5. *Schizosthetus lyriformis*, pedipalp - A, larva, dorsal view; B, larva, ventral view of tibia and tarsus; C, deutonymph. All figures based on material from Louisiana. All scale bars 25 μm.

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 (*cs*), 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 *s6* shifted from opisthosomal to opisthonotal region. Setae *r3* very long (157 [142-169]; N= 5). Setae *s4* and *z5*, 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 *z5* still 2-3X longer than setae *j5* and *j6*. Lyrifissure *ids5* added near seta *r5*. Opisthonotal region - 6 setae added (*J1, J5, Z1, S1, R1, Rv1*). 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 (*idS1, idS3, idJ1*) and 1 pair of glands (*gdz6*) added. Venter (Fig. 8B) - Tritosternum as in larva. Sternal region with 1 pair of sternal setae (*st.5*) and 2 pairs of lyrifissures (*iv1, iv2*) added. One pair of ventral setae (*Zv1*), 2 pairs of lyrifissures (*ivo1, ivo2*), and 1 poorly developed pair of glands (*gv2*) added in opisthogastric region. Anal shield bigger but retaining its triangular shape. Paranal and postanal setae much shorter than in larva (postanal seta still longer than paranal setae). Euanal setae absent but vestiges still visible. Cribrum present posterior to postanal seta. Stigmata present lateral to coxae IV, round in shape, and associated with short peritremes and a pair of lyrifissures (*ip2*).

Legs - Legs IV added in this instar (Fig. 9A). Coxae I to III as in larva. Coxae IV with only setae *av* on distal

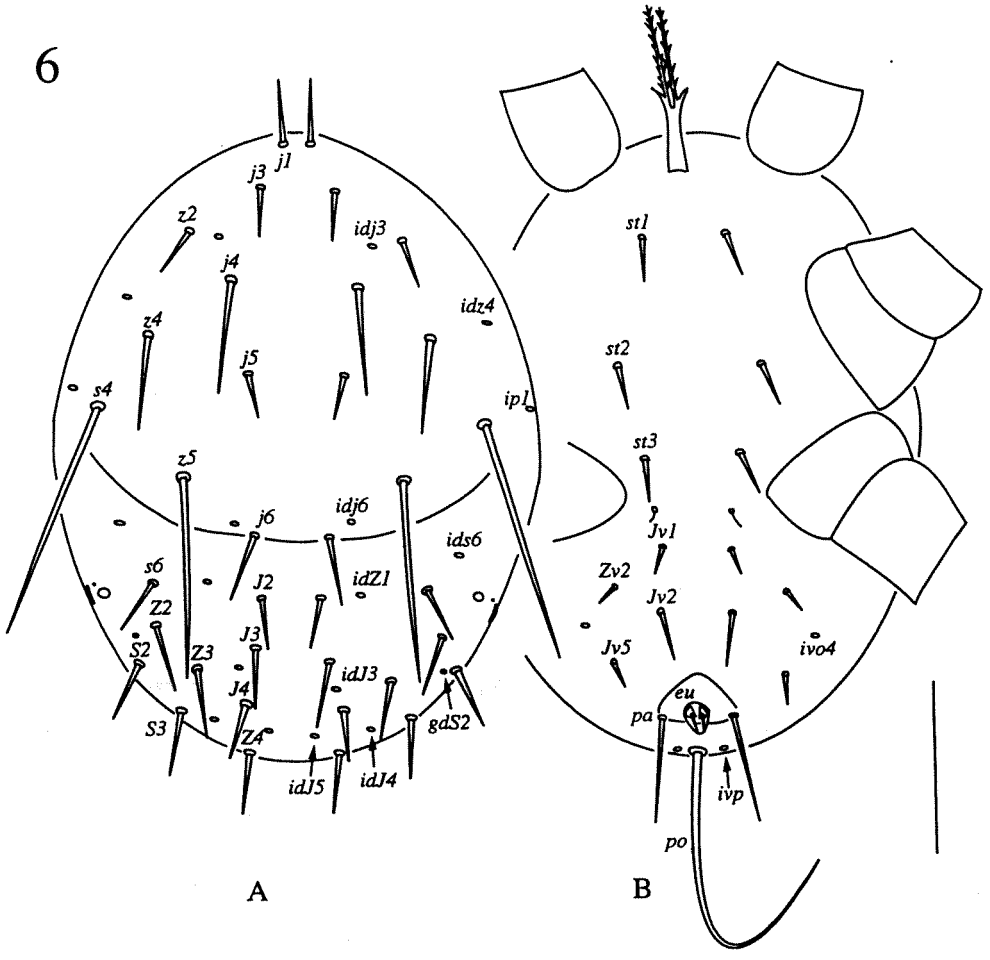

Fig. 6. *Schizosthetus lyriformis*, larva, idiosoma - A, dorsal view; B, ventral view. Scale bar 100 µm.

part of segment. Trochanters - I to III largely as in larva. Trochanters IV each with four setae (*al*, *ad1*, *av1*, *pv2*). Femora - I with poorly expressed, but complete peripodomeric 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 peripodomeric 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*, *av1*, *pv1*, *pl1*). Seta *ad1* very long. Tarsi - Peripodomeric 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 basitarsi 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*.

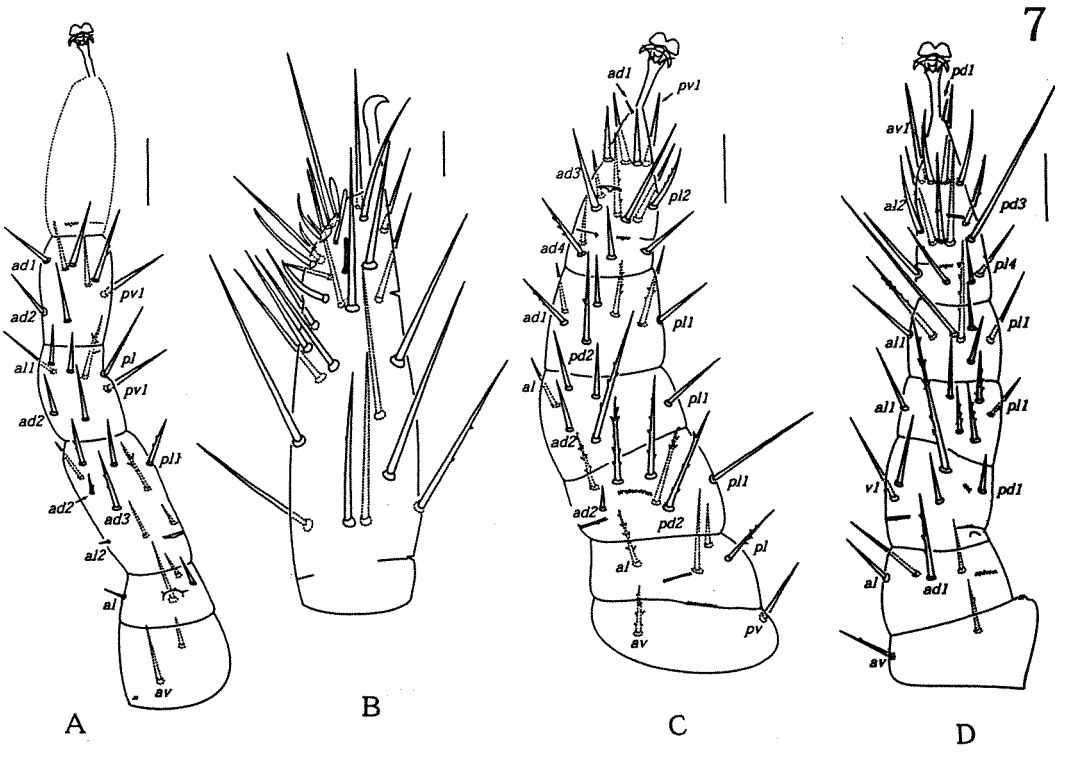

Fig. 7. *Schizosthetus lyriformis*, larva, legs - A, leg I; B, tarsus I; C, leg II; D, leg III. Figure A based on material from Louisiana. All scale bars 25 μm.

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. Deutosternum forming 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 *v1*, both setae barbed. Femur adding setae *d3*, genu adding rod-like seta *al2*, tibia adding 2 setae. Dorsodistal lyrifissure on femur distinct. Number of tarsal setae as in protonymph.

Idiosoma - Dorsum (Fig. 10A). Podonotal shield: length 404 (395-413; N= 5); width 432 (395-442; N= 5). Opisthonotal 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. Opisthonotal shield distinctly narrower than podonotal shield. All setae smooth. Podosomal region with 22 pairs of setae, adding 8 pairs relative to the protonymph (*z1, z3, z6, s1, s2, s3, r4, r6*). Setae *s2* and *r4* inserted off the shield on the membrane. Most podosomal setae similar in size, but setae *z1*, *s1*, and *s2* very small, and setae *r3* very long (174 [163-188]; N= 5). Dorsal hexagon setae *z5* 2x as long as setae *j5* and *j6*. A pair of lyrifissures (*idj1*), and 4 pairs of glands (*gdj2, gdj4, gdz5, gds6*) added. Lyrifissures *ip1* shifted ventro-laterally, now closely associated with the peritremes. Glands *gdj4* may be multiple, while glands *gdz5* are weakly developed. Muscle attachment scars (sigilles) as illustrated (Fig. 10A). Opisthosomal region with 22 pairs of setae, by addition of 8 pairs of setae (*Z5, S4, S5, R2, R3, R4, R5, rv6*). All *R*, *rv*, and *Rv* setae, plus setae *S4*, *S5*, and *Z5* inserted off the shield on the membrane. Setae *J5* 1.5x as long as other dorso-central (*J*) setae. Three pairs of lyri-

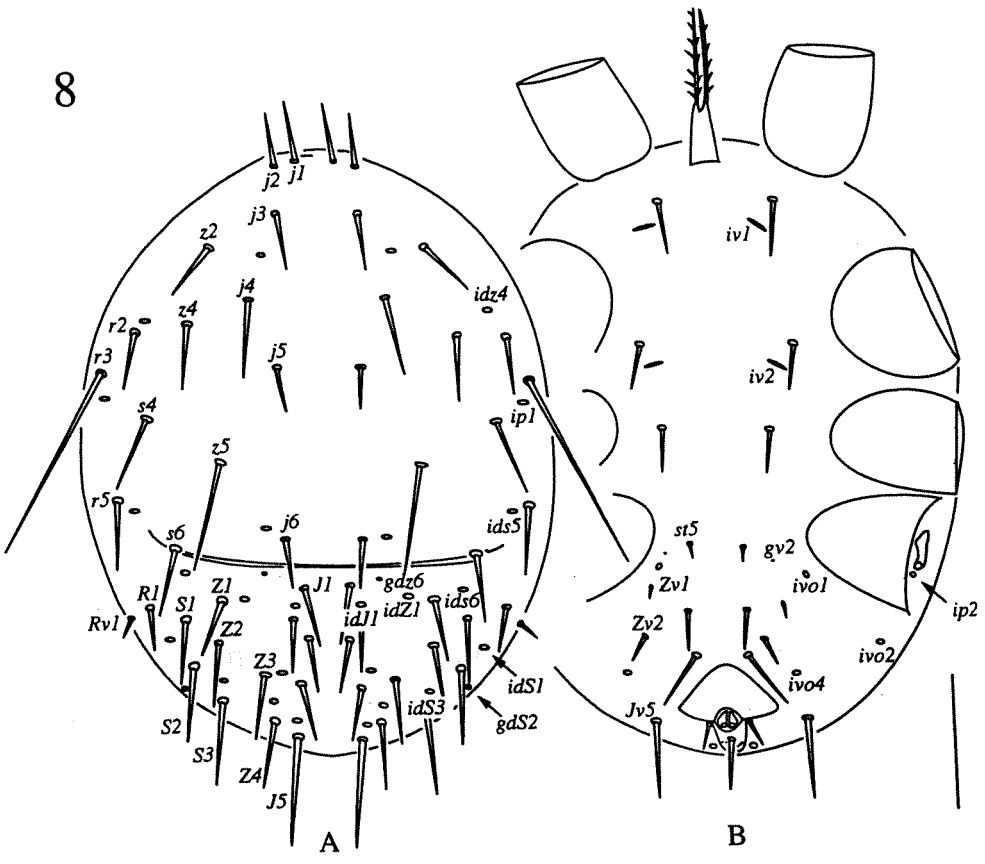

Fig. 8. *Schizosthetus lyriformis*, protonymph, idiosoma - A, dorsal view; B, ventral view. Scale bar 100 μm.

fissures (*idJ2, 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 *ip1* and gland *gp* (added) closely associated with anterior peritrematal shield, lyrifissure *ip2* as in protonymph.

Legs (Fig. 11) - Coxae - 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 peripodomeric fissure associated

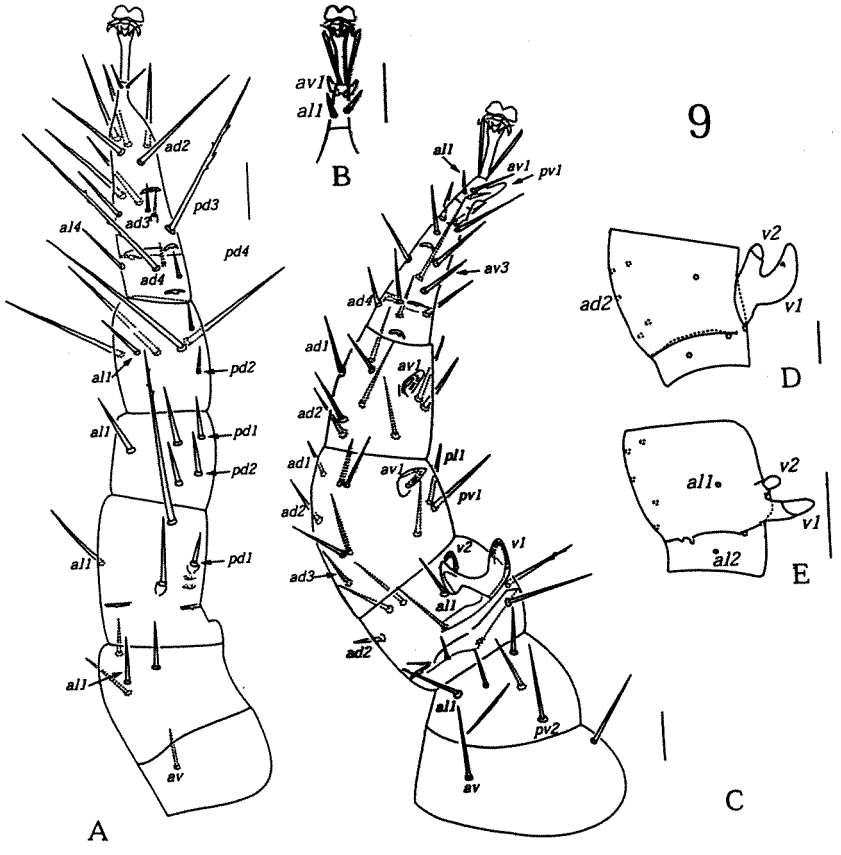

Fig. 9. *Schizosthetus lyriformis*, legs - A, leg IV, protonymph, dorsal view; B, distal part of tarsus II, female, dorsal view; C, leg II, male, ventral view; D, *S. simulatrix*, femur II, male, ventral view; E, *S. vicarius*, femur II, male, ventral view. All scale bars 50 μm.

with 2 lyrifissures. Three setae added on femur I (*pd2, v3, v4)*, 3 on femur II (*al2, ad3, v3*) 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, av2, pv2, 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 *l1* and *v1* setae. One ventral setae (*av3*) (*mv* of Evans, 1963a) added on tarsi II-IV. Presence of terminal setae *ad1* and *pd1* 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).

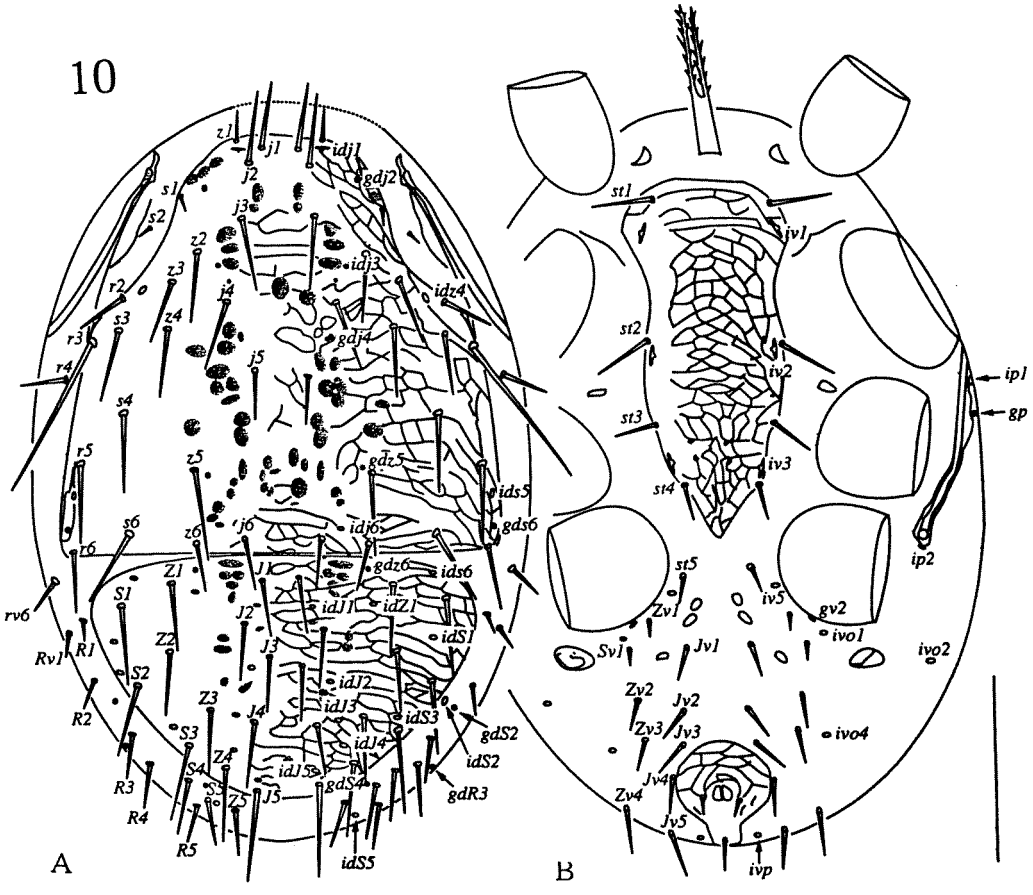

Fig. 10. *Schizosthetus lyriformis*, deutonymph, idiosoma - A, dorsal view; B, ventral view. Scale bar 200 μm.

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 deutonymph.

Idiosoma - Dorsum (Fig. 12A). Podonotal shield: length 454 (441-464; N= 5); width 482 (457-498; N= 5). Opisthonotal 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 opisthonotal shield. With the exception of the very long setae *r3*, and the relatively short setae *s1* and *s2*, all dorsal setae subequal in length. Setae *z5* subequal in length to setae *j6* and *z6*. Lyrifissures and glands largely as in deutonymph; glands *gds6* shifted axial, becoming more distinct due to the presence of a surrounding oval or round zone. Opisthosoma - Setae *J5* 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. Lyrifissures and glands as in deutonymph but glands *gdS4* 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: ll) relatively wide at their base, narrowing smoothly towards the distal apex. Metasternal shields large, each carrying

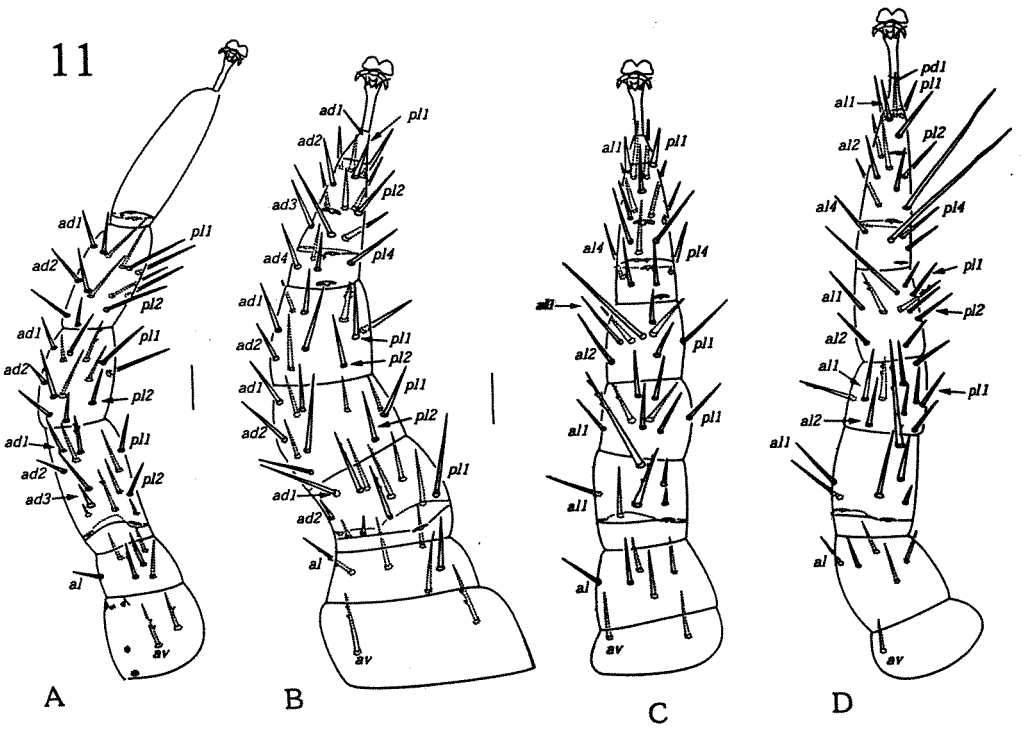

Fig. 11. *Schizosthetus lyriformis*, deutonymph, legs - A, leg I; B, leg II; C, leg III; D, leg IV. All scale bars 50 μm.

l seta (*st4*) and 1 lyrifissure (*iv3*). Parametasternal shield (Fig. 12B: pmss) flanking genital shield, medially convex. Genital shield triangular, its base hinged at corners to ventrianal shield. Genital shield with setae *st5*. Endogynium oval shaped (Fig. 12C). Opisthogastric region. Ventral shield fused with anal and metapodal shields to create a ventrianal shield, connected to peritrematal shield by a so-called "cingulum" (Figs. 1G, I, 12B: cg). Number of setae, lyrifissures, and glands as in deutonymph. Setae *Jv5* and *Zv4* off the shield inserted on the membrane. Cribrum (Fig. 12: cr) well developed. Stigmata as in deutonymph; peritrematal shield well defined.

Legs - Pretarsus I shorter than in deutonymph. Acrotarsal fissure on tarsi II-IV basal to first whorl of setae (Fig. 9B), not distal as in deutonymph. Setae *ad1* and *pd1* on tarsi II-IV thin and distinctly elongated; their tops arrow-shaped. Presence of terminal setae *ad1* and *pd1* II-IV: setae *ad1* present on 100% of tarsi II, 75% of tarsi III, and 38% of tarsi IV; setae *pd1* present on 50% of tarsi II, 75% of tarsi III, and 100% of tarsi IV (N= 8). Setae *l1* and *v1* on tarsi II-IV short and spinose (Fig. 9B).

MALE - Length 958 (916-1026; N= 5), width 521 (490-566; N= 5).

Gnathosoma - Gnathotectum (Figs. 2I-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 spermatotreme forming a slit or opening that closes on two sides. Arthrodial 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). Opisthonotal shield: length 290 (296-336; N= 5), width 484 (456-524; N= 5). Dorsal shields large, covering nearly entire dorsum. Podonotal and opisthonotal 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 *gdS4* absent and glands *gdS2* always posterolateral to lyrifissures *idS2*. Venter (Fig. 13B) - Tritosternum and presternal platelets as in

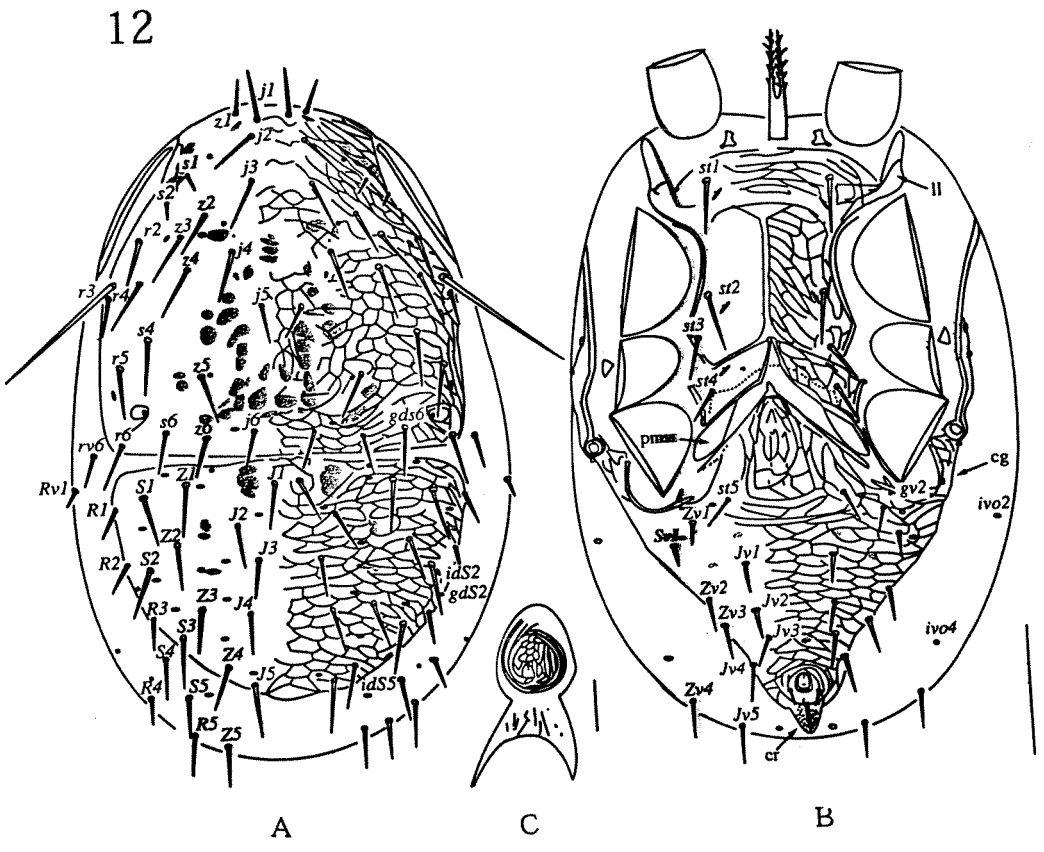

Fig. 12. *Schizosthetus lyriformis*, female, idiosoma - A, dorsal view; B, ventral view; C, endogynial sclerite. Abbreviations: cg= cingulum, ll= anterior lateral lobes, pmss = parametasternal shield. Scale bar 200 μm (A, B) and 50 μm (C).

deutonymph. Anterior lateral lobes of sternal shield as in female but a little wider at their base (Fig. 1D). Holoventral shield, but border of ventrianal shield faintly visible (Fig. 13B, dotted lines). Number of setae, lyrifissures, and glands in the opisthogastric region as in deutonymph, but all inserted on holoventral shield. Stigmata as in female; peritrematal portion of holoventral shields fused laterally with podonotal shield.

Legs - Legs I, III and IV as in female, but ventral setae *av1* and *pv1* of tarsi III-IV longer than lateral setae and usually less spinose than in the female. Terminal setae *ad1* and *pd1* III-IV: seta *ad1* present on 62% of tarsi III, and 50% of tarsi IV; seta *pd1* 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*. Setae *al2* and *v3* basal to the peripodomeric fissure. Genu and tibia - setae *av1* hypertrophied to form short spurs, other setae as in deutonymph. Tarsus - seta *pv1* spinelike (finger-shaped) fused with cuticle segment (base of seta not visible), but seta *av1* setiform, longer than setae *al1* and *pl1*. Setae *ad1* and *pd1* as in female. Presence of terminal setae *ad1* and *ad2* 100% and 75% respectively (N= 8). Other tarsal setae as in female.

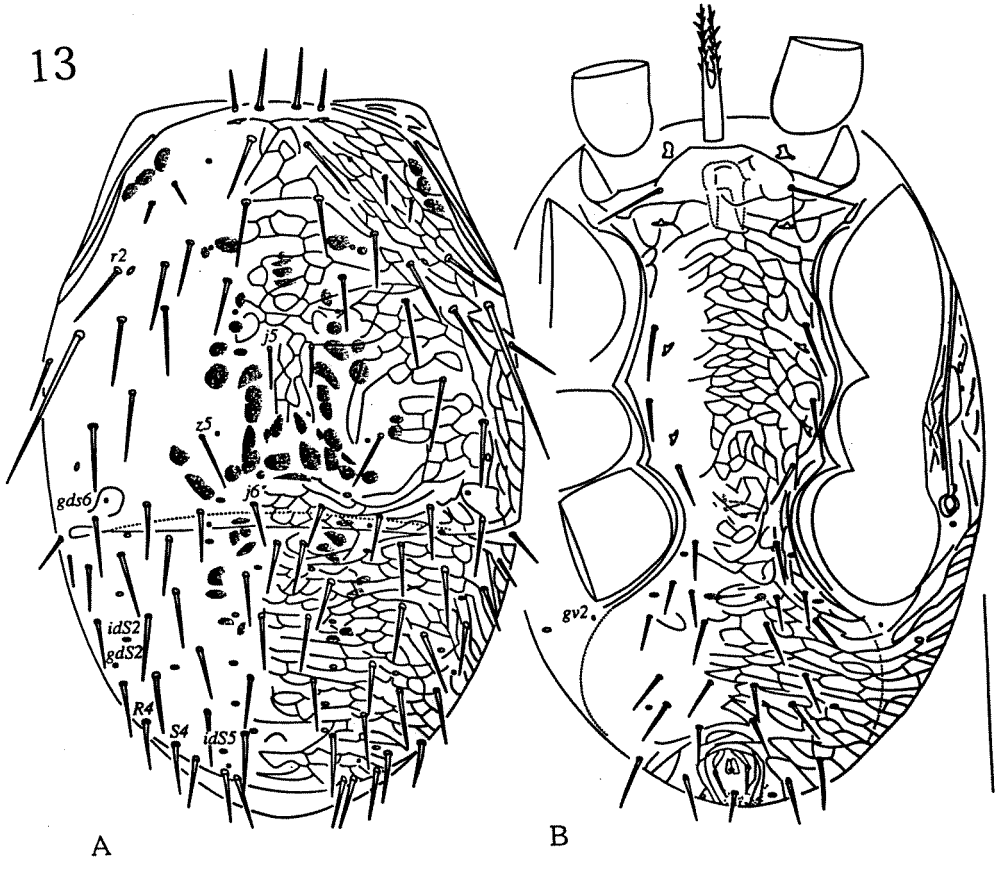

Fig. 13. *Schizosthetus lyriformis*, male, idiosoma - A, dorsal view; B, ventral view. Scale bar 200 μm.

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 *Dendroctonus frontalis* Zimmermann (Scolytidae) on *P. echinata*, 30 May 1966, J. R. McGraw, USNM. Allotype male (sp18). Other material - CANADA: Alberta, Grande Prairie, phoretic on *D. simplex* LeConte, ex eastern larch, 21 Feb 1965, R. Reid, 1DN, JM 3684. U.S.A.: California: Kern Co., Frazier Park, ex galleries of *Ips* sp. in *P. monophylla* Torrey and Frémont, 5 Feb 1966, D. Kinn and Y. Kinn, 6L 6PN 6DN 14F 6M; California; Kern Co. Tehachapi Mtn. Park, ex *D. valens* LeConte and *Onthotomicus latidens* in *Pinus jeffreyi* Greville and Balfour (Jeffrey pine), 16 Sep 1966, D. Kinn and D.E. Bright, 1DN; California: El Dorado Co., Blodgett Forest, ex *D. brevicomis* LeConte in *P. ponderosa* Douglas, 19 Jun 1964, I. Otvos, 3DN; same locality, ex *I. confusus* LeConte, 22 Jun 1965, A. Evitis and E. Johnson, 1DN; same locality, cages 5 and 6, ex *D. brevicornis* adult, 29 Jul 1965, 1DN; California: San Diego Co., Mt. Palomar, ex *D. brevicornis* gallery in *P. coulteri* D. Don (coulter pine), 14 Sep 1965, D. Kinn and D.E. Bright; California: Ventura Co., Scheideck, ex *P. monophylla* killed by *I. confusus*, 3 Jan 1969, D. Kinn and Y. Kinn , 1DN; same locality, ex under bark and *P. monophylla* killed by *I. confusus*, 24 Apr 1966, D. Kinn, Y. Kinn and N. Kinn, 1PN, 1M; California: Ventura Co., 1mi W Chuchupate Ranger Station, ex *P. monophylla* killed by *I. confusus*, 1 Aug 1968, D. Kinn and L. Browne,

2DN; same locality and source, 2 Aug 1968, D. Kinn and L. Browne, 1L 4PN 1DN 1F; California: Madera Co., Cedar Valley, ex dregs pheromone trap with *D. brevicornis*, 7 Jun 1982, P. Tilden, 1DN, JM 22,172; no locality data (probably California), cage 5, ex *D. brevicornis*, 2 Aug 1966, 3DN; tree #1591, ex *D. brevicornis* egg gallery, 1 Jul 1969, C. Dudley, 1DN; Wyoming: Carbon Co., Saratoga, ex *P. contorta latifolia* Douglas and *P. flexilis* E. James, Jun-Oct 1937, D. de Leon, lot 38-11,119, 2DN 1F 1M; Texas: Newton Co., Newton, ex galleries *D. frontalis* in *P. taeda* Linneaus (loblolly pine), 1 Jan 1965, 1F, JM2421; New Mexico: Lincoln Natl, For., Cloudcraft, ex inner bark *P. ponderosa*, 13 Aug 1975, M. Ellstrom, 2F 1M, JM 21,068, 21076, 21,077; Louisiana; Allen Parish, Elizabeth, ex inner bark *P. taeda* with *D. frontalis*, 14 Jun 1965, J. Moser, 4L 5PN 2F 3M, JM 4706, 4713, 4787, 4790, 4791, 4792,4828, 4993, 4894, 5083, 5084, 5087, 5088, 5126; same locality, phoretic on *Cylistix attenuata* LeConte (Histeridae) on *P. taeda* with *D. frontalis*, 14 Jun 1965, J. Moser, 3DN, JM 4764, 4771, 4775; same locality, under bark *P. taeda* with *I. avulsus*, 28 May 1965, J. Moser, 1L 1F 1M, JM 4464, 4482, 4485; Louisiana: Rapides Parish, ex gallery *D. frontalis*, May 1975, D. Kinn, 2L; Louisiana: Livingston Parish, Camp Livingston, ex inner bark *P. taeda* with *I. calligraphus* Germar, Feb 1976, 1F, JM 19,177; Arkansas, Pike Co., ex SL(RP), 5 Apr 1967, I. Brown, 1DN, JM 12,666. MEXICO: Chiapas, 5km S. Motozintia, ex galleries and inner bark with bluestain in *P. oocorpa* with *D. frontalis* emerging, 24 Apr 1998, J. Moser, 1F, JM 36,978. GUATEMALA: Puerta Tzantzia Solata, ex boring dust of *P. montezuma* with *D. frontalis*, 2 Feb 1972, E. W. Clark, 2PN, JM 15,790, 15,798. Most specimens deposited in OSAL, representative specimens of all instars in JM.

Previously published localities (all McGraw and Farrier, 1969) - CANADA: Alberta, Grande Prairie; British Columbia, Radium Hot Springs; USA: Colorado, Douglas Co., Castle Rock and Larimer Co., Red Feather Lakes; Louisiana, Allen Parish, Elizabeth; North Carolina, Beaufort, Davie, Durham, Granville, Rowan, Wake, and Yadkin counties; South Dakota, Lawrence Co., Deadwood; Tennessee, Anderson Co., Oak Ridge; Virginia, Hardin and Tyler counties; Wyoming, Johnson Co., Buffalo and Teton Co., Teton; MEXICO: Puebla; HONDURAS: Cedros.

Schizosthetus simulatrix Athias-Henriot

Schizosthetus simulatrix Athias-Henriot 1982: 212; *Vulgarogamasus* sp. Moser and Bogenschütz 1984: 442; *Schizosthetus simulatrix* Athias-Henriot 1982, Kaluz, Masan and Moser, in press.

DIAGNOSIS - Cingulum absent (Fig. 1H). Setae *Sv1* and glands *gdz5* present. Setae *r4* off podonotal shield in female. Opisthonotal shield with 15 or 16 pairs of setae in adults (setae *S4* may be inserted on the shield). Gland pair *gdR3* on dorsal membrane of opisthosomal region in deutonymph and female. Ventrianal shield of female with only 6 setae (*Zv3* and *Jv4* off the shield).

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

COMMENTS - Deutonymph in most details as deutonymph of *S. lyriformis*. Adults. Medial process of gnathotectum longer than lateral processes. In male, lateral processes appear shortened (Fig. 2K-L). Arthrodial membrane process of chelicera 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 dorsum largely as in *S. lyriformis* but in female setae *r4* off podonotal shield while setae *S4* are sometimes inserted on the margin of the opisthonotal shield. Reticulation of podonotal shield in the central area distinct. Positions of glands *gdS2* and lyrifissures *idS2* as in *S. lyriformis*. Venter. Axial margin of parametasternal 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 *av1* and *pv1* on tarsi II of both sexes spinelike, resembling condition in female *S. lyriformis*(Fig. 9B).

MATERIAL EXAMINED

Type material examined - Data unclear, probably PORTUGAL: Tomar (LU 28), ex *Pinus pinaster*, C. M. Baeta Neves, MHNG. Paratype male (AP8) and female (AP5). Other material - FRANCE: region Parisienne, associated with *Ips typographus* and *I. sexdentatus*, 1979, F. Lieutier, 1F 1M, JM 28185, 23189; Forest of Orleans, phoretic on *I. sexdentatus* ex *Pinus sylvestris*, May 1986, F. Lieutier, 4 DN, JM 31662, 32590, 34523, 34529; GERMANY: 25km SE Freiburg, ex *Trypodendron lineatum* pheromone trap water dregs, 12 May 1981, H. Bogenschütz, 1DN, JM 24608; same locality and source, 16 Jun 1981, H. Bogenschütz, 1F, JM 24722; same locality, ex *I. typographus* pheromone trap water dregs, 19 May 1981, H. Bogenschütz, 1DN, JM 24515; ex *I. typographus* pheromone trap water dregs, June 1980, H. Bogenschütz, 1DN, JM 24940; SWEDEN: 18km E Uppsala, ex *I. typographus* dregs pheromone trap, 24 May 1983, J. Regnander, 1DN, JM 25233; same locality, ex *I. typographus* dregs pheromone trap, 8 Jun 1983, J. Regnander, 3DN, JM 25251, 25273, 25286.

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

Schizosthetus vicarius Athias-Henriot

Schizosthetus vicarius Athias-Henriot, 1982: 214.

DIAGNOSIS - Cingulum large (Fig. 1I). Setae *Sv1* and glands *gdz5* absent. Setae *r4* on podonotal shield of adult. Opisthonotal shield of female with 28 or 29 pairs of setae. Glands *gdR3* on opisthonotal shield. Ventrianal shield of female with 8 pairs of setae.

COMMENTS - Deutonymph unknown. Adults - Gnathotectum 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). Arthrodial 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. simulatrix*. Idiosomal dorsum as in *S. lyriformis* except that setae *j6* are slightly longer than setae *z5* and *j5* (based on only one specimen); glands *gdz5* absent. Opisthonotal 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 *idS2* on opisthonotal shield, distant from the shield margin. Posterior marginal reticulation characteristically wavy. Venter with axial margin of parametasternal 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 *av1* and *pv1* 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; Micherdzinki, 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 *ip1*. In the larva and protonymph 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 *s6* 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 *ad1* and *pd1* 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 *v1* setae on tarsi 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 deutonymphs and adults of this genus from all other genera: the bifid shape of palp genu setae *al1* and *al2*. 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 bifurcus* 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 I.

Table 1. Comparative characteristics of *Schizosthetus* species.

	S. lyriformis	*S. simulatrix*	*S. vicarius*
Cingulum (female)	Narrow (Fig. 1G)	Absent (Fig. 1H)	Wide (Fig. 1I)
Glands *gdz5* (DN, Ad)	Present	Present	Absent
Glands *gdR3* (DN, Ad) on opisthonotal shield	No	No	Yes (DN unknown)
Setae *Sv1* (DN, Ad)	Present	Present	Absent
Shape anterior lateral lobes (Ad)	Edges smooth (Figs. 1A, D)	With anterior protuberance (Figs. 1B, E)	Narrow, anterior edge smooth, posterior edge with projection (Figs. 1C, F)
Setae *av1* and *pv1* on tarsi II (male)	*pv1* spinelike; *av1* simple (Fig. 9C)	Both spinelike	Both spinelike, relatively small
Number of setae on ventrianal shield (female)	8	6	8

Abbreviations: DN, deutonymph; Ad, adult.

We recognize three species of *Schizosthetus*: *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 *gdz5* and setae *Sv1* are present in *S. lyriformis* and *S. simulatrix* but absent in *S. vicarius*, and glands *gdZ3* are positioned off the opisthonotal shield in *S. lyriformis* and *S. simulatrix* while on the opisthonotal shield in *S. vicarius* (Table 1). Distinguishing *S. lyriformis* from *S. simulatrix* is less simple. In female *S. simulatrix* setae *r4* are inserted off the podonotal shield, setae *S4* are sometimes inserted on the margin of the opisthonotal shield, and only 6 pairs of setae are present on the ventrianal shield, while in the other two species setae *r4* are inserted on the podonotal shield, and the ventrianal shield carries 8 pairs of setae. In *S. lyriformis* setae *S4* are always inserted off the opisthonotal 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 *Jv1* (*S. simulatrix*) or free from those setal bases (*S. lyriformis*) (Kaluz *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 *gdz5* and setae *Sv1*.

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 gnathotectum (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 polygraphus* trap dregs, 7 July 1982, Yin Hui-Fen, 1M, JM 20069) adds to this uncertainty. If it belongs to *Schizosthetus* (because it is a male, generic identification is tentative), the shape of the anterior lateral lobes and presence of *Sv1* identify it as new species with characteristics intermediate be-

tween *S. simulatrix* and *S. lyriformis*. As might be expected, this overall distribution largely mimics the distribution of Scolytidae and pine trees.

The genus *Schizosthetus* 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 *Eugamasus* and *Vulgarogamasus*. 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-Sámano (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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