New classification of the family Sejidae (Acari: Mesostigmata) based on morphological analyses

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Abstract
Relationships in the family Sejidae are examined based on analysis of 74 morphological characters. Synonymy of Willmannia Balogh and Liroaspis Banks with Sejus Koch is supported, while synonymy of Epicroseius Berlese is not. Nine species of Sejus are transferred to Epicroseius, and Sejus congoensis and S. solaris are transferred to Africasejus n. gen. A total of five genera is recognized in Sejidae: Sejus, Epicroseius, Adenosejus Lekveishvili and Krantz, Africasejus, and Zuluacarus Trägårdh. New diagnoses are proposed for the family and its genera.

Keywords: Acari, morphology, phylogeny, Sejidae

Introduction
The family Sejidae is a moderately diverse group of mesostigmatid mites. The family is widely distributed in the warm temperate and tropical regions of the world, with its constituent species often associated with wood. The second nymphal instar, the deutonymph, may be dimorphic, with one “normal” (homeomorphic) morph and a heteromorphic morph specialized for phoresy, often on cerambycid beetles.

Recent studies (Lekveishvili and Klompen 2004b) have clarified the family level groupings in the infraorder Sejina (including the surprising affinities with the Heterozerconidae and Discozerconidae), but relationships within Sejidae remain to be resolved. The primary aim of the current study is to resolve relationships within the Sejidae and to review the existing generic classification for the family.

The current study is based on morphological data only. To do this the taxon set is drastically increased relative to the infraorder revision study (Lekveishvili and Klompen 2004b). In addition, the number of morphological characters is also expanded. A secondary goal of this study is to discuss explicitly these characters in terms of homology decisions and character state designations.
Historical review

The taxonomic history of the family Sejidae is one characterized by wild swings in generic concepts, and a distinct lack of integration. The family was defined by Berlese (1913) based on the genus *Sejus* Koch, 1836 with type species *Sejus togatus* Koch, 1836. He also included a second genus *Epicroseius* Berlese, 1905, but did not mention *Liroaspis* Banks, 1902, with type species *L. americana* Banks, 1902. Confusion regarding the type species and genus ensued when Oudemans (1938) noted that Koch (1843) had designated *Sejus viduus* Koch, 1843 as type species for *Sejus* and proposed the name *Dwigubskia* Oudemans, 1938 as a replacement name for *Sejus* Koch, 1836. The issue was resolved by Lindquist and Evans (1965) who noted that the assignment by Koch (1843) of *Sejus viduus* as type species for *Sejus* was contrary to the rules of the International Code of Zoological Nomenclature, as the generic name was already associated with *Sejus togatus* in 1836. Thus *Dwigubskia* is a junior synonym. They also synonymized *Sejus* Koch, 1843 with *Cheiroseius* Berlese, 1916 (Asciidae). In subsequent years two more genera were proposed: *Zuluacarus* Trägårdh, 1906 and *Willmannia* Balogh, 1938. In a revision of the entire family Hirschmann and colleagues (Hirschmann 1991; Hirschmann et al. 1991) described many new species, redescribed several others, and synonymized *Epicroseius*, *Liroaspis*, *Zuluacarus*, and *Willmannia* with *Sejus*. Instead, Hirschmann proposed 10 species groups, without designating any formal taxonomic rank for any of these. Finally, after examining specimens of *Sejus krantzi* Hirschmann, 1991 and *S. manualkrantzi* Hirschmann, 1991, both described based solely on drawings in a reference book, Lekveishvili and Krantz (2004) synonymized the two species, and erected the genus *Adenosejus* Lekveishvili and Krantz, 2004, to accommodate the species. This has brought the total number of nominal genera to six.

Materials and methods

**Taxon selection**

Twenty-seven species of Sejidae, two species of Ichthyostomatogasteridae, one species each of Uropodellidae and Heterozerconidae, and *Archaeopodella scouplifera* were included in the analysis. Inclusion of Heterozerconidae was based on the results of our previous study where heterozerconine families are included in Sejina (Lekveishvili and Klompen 2004b). Efforts were made to include the type species of all named sejid genera and representatives of all of Hirschmann’s (Hirschmann 1991) “species groups”. Exceptions include the type species of *Epicroseius* and *Zuluacarus* (*E. angelioides* Berlese, 1905 and *Z. termitophilus* Trägårdh, 1906) which were excluded because of insufficient data for analysis. Species of Sejidae for which fewer than 50% of characters could be coded were also excluded from the analysis. In addition to described species, five new species were included. *Microgynium incisum* Krantz, 1961 (Microgyniina) and *Zercon* sp. (Zeronina) were selected as outgroups. Including more distant outgroups was problematical in terms of establishing defensible homologies.

Characters were coded by direct observation of specimens, or based on original descriptions and drawings (when specimens were not available). Seventy-four characters were coded, including gnathosomal, idiosomal and leg characters of all instars except the heteromorphic deutonymphs. Description of characters and character states and the final character matrix are presented in Appendices 1 and 2, respectively.
Material examined

The following abbreviations are used: OSAL, Ohio State University Acarology Collection; OSAC, Oregon State University Arthropod Collection; UMMZ, University of Michigan Insect Collection; ZSMC, Zoologische Staatssammlung, München.

Slide specimens examined. Asternolaelaps sp. OSAL (L—OSAL522, PN—OSAL14384–87, OSAL520–522, DN—OSAL14377–83, M—OSAL14373–76, F—OSAL14369–72, OSAL504); Uropodella laciniata Berlese, 1888, OSAL (M—OSAL3112, F—OSAL3109–11, 3113–14); Adenosejus krantzi (Hirschmann, 1991), OSAL (L—13639), OSAC (M—OSAC558–2, 558–3, F—OSAC558–1 (holotype)); Sejus togatus, OSAL (M—OSAL14364, F—1452); Liroaspius americana, OSAL (L, DN—OSAL14368, M—OSAL14366–67, F—OSAL14366); S. carolinensis Lekveishvili and Klompen, 2004, OSAL (L—OSAL4630–4631, PN—OSAL4632–4634, DN—OSAL4635, 4638, 4644, M—OSAL4640–4641 (paratypes), F—OSAL4636 (holotype)); Sejus congoensis Wisniewski and Hirschmann, 1991, ZSMC (L, PN, DN, F, M—U551, U624 (paratypes)); S. solaris Wisniewski and Hirschmann, 1991, ZSMC (L, PN, DN, F, M—U254, U796 (paratypes)); S. stebaevi Wisniewski and Hirschmann, 1991, ZSMC (M (holotype) and F (paratype)—U835); S. camerunis Wisniewski and Hirschmann, 1991, ZSMC (PN, DN, F—U621); S. posnaniensis Hirschmann and Kaczmarek, 1991, ZSMC (L, PN, DN, F, M—#12–19 (paratypes)); S. boliviensis Hirschmann and Kaczmarek, 1991, ZSMC (D, F, M—paratypes, A20032901–A220032907); Narceoheterozercon ohiensis Gerdeman and Klompen, 2003, OSAL (L—OSAL2958, PN—OSAL2968, DN—OSAL1255, M—OSAL1239 (paratypes), F—OSAL1259 (holotype)). New species: n. sp. 1, UMMZ (PN, F, M—BMOC 93–1300–043); n. sp. 2, OSAL (PN—OSAL13635, DN—OSAL13634, F—OSAL13628–13629, 13659, M—OSAL13630–13633); n. sp. 3, OSAL (DN—OSAL13587–13588, F—OSAL13585–13586, M—OSAL13584, OSAL508); n. sp. 4, OSAL (F—OSAL13589–13590, M—OSAL13591–13593, OSAL277); n. sp. 5, OSAL (PN—OSAL13594–13598, D—OSAL13599–13605, F—OSAL13606–13615, M—OSAL13616–13625). Outgroups: Zercon sp. (F—OSAL000426–430), Microgynium incisum (F—OSAL13637, M—13638).

Coding of the following species was based on original descriptions only: Japanasternolaelaps japanensis Hirschmann and Hiramatsu, 1984; Archaeopodella scopulifera Athias-Henriot, 1977; Sejus polonicus Hirschmann and Kaczmarek, 1991; S. hinangensis Hirschmann and Kaczmarek, 1991; S. rafalskii Wisniewski and Hirschmann, 1991; S. australis Hirschmann and Kaczmarek, 1991; S. cubanus Wisniewski and Hirschmann, 1991; S. mesoaficanus Wisniewski and Hirschmann, 1991; S. kikakhensis Hirschmann, 1991; S. marquesanensis Hirschmann, 1991; S. tanganicus Hirschmann and Kaczmarek, 1991; S. venezuelanensis Hirschmann and Wisniewski, 1994; S. novaezealandiae Fain and Galloway, 1993; L. armatus Fox, 1947; L. baloghi Athias-Henriot, 1960; Willmannia sejiformis Balogh, 1938; Epicroseius porosus Domrow, 1957; E. zimmermani Trägårdh, 1952; E. abinashi Bhattacharyya, 1966.

The data matrix was constructed using McClade v.4.05 (Maddison and Maddison 2002). Parsimony analyses were conducted in PAUP* (Swofford 2002) using heuristic searches with multiple random additions (1000 replicates). All characters were equally weighted. Branch support was assessed by calculating Bremer Support (BS) (Bremer 1988).
Analysis and results

The analysis yielded 73 equally most parsimonous trees (Figure 1) (length 259; CI = 0.37; RI = 0.66). Sejina s.s., that is without Heterozerconina, is supported, in contrast to molecular-based analyses which support inclusion of Heterozerconina within Sejina (Lekveishvili and Klompen 2004b). Within the limits of this analysis, Heterozerconina is the closest relative of Sejina s.s., and this relationship is relatively well supported (BS = 3).

The families Uropodellidae, Ichthyostomatogasteridae, and Sejidae are monophyletic, with Archaeopodella included in Ichthyostomatogasteridae. Ichthyostomatogasteridae and Sejidae are sister groups although support for this relationship is relatively weak (BS = 1). The family Ichthyostomatogasteridae itself is also weakly supported (BS = 1). New sp. 1 from the Philippines groups with Archaeopodella, and may belong in that genus. Relationships of Archaeopodella, Astenolaelaps, and Japanasternolaelaps are not resolved.

The family Sejidae is relatively well supported (BS = 3). There are four distinct groups defined in the family, three of which correspond to existing genus-level groupings. The (nova–meso) lineage (Figure 1) is moderately well supported (BS = 2). It includes the type species of the genera Sejus, S. togatus, Willmannia, W. sejiformis, and Liroaspis, L. americana. It will be referred to as Sejus. Similarly, the (zimm–marq) lineage is well supported (BS = 4) and includes all species previously assigned to the genus Epicroseius. This clade also includes some species (e.g. S. klakahensis, S. marquesanus, and S. tanganicus) previously classified within Sejus. These two lineages, Sejus and Epicroseius, form a well-supported clade (BS = 3). The two remaining lineages, one including S. solaris and S. congoensis, the other Adenosejus krantzi and n. sp. 2, are weakly supported (BS = 1). Both occupy more basal positions relative to Epicroseius and Sejus.

Relationships among the species of the (nova–meso) lineage are not well resolved, although a few species groups are defined. Sejus posnaniensis and Willmannia sejiformis are clustered together (BS = 1). Sejus stebaevi, L. americana, S. polonicus, S. togatus, S. hinangensis, and S. rafalskii form a clade which is also weakly supported (BS = 1). The lineage of (aust–meso) has relatively better Bremer support (BS = 2), although relationships within the group are not resolved. Relationships of S. novaezealandiae, n. sp. 3 and n. sp. 4 relative to other species of Sejus are not resolved.

Overall resolution and support levels are relatively weak, a situation resulting from inclusion of several taxa with large amounts of missing data. Exclusion of such taxa (as done in the more limited morphology based analysis by Lekveishvili and Klompen 2004b), achieves some improvements in both resolution and support level (results not shown), but is far less general, and results in some odd relationships, including inclusion of Archaeopodella in Sejidae. Overall, we prefer the total evidence analysis as explaining more of the overall character state pool and being more general, even if resolution and support levels are lower.

Discussion

Relationships

Our recent analysis of relationships among the families of Sejina and Heterozerconina (Lekveishvili and Klompen 2004b) suggested the possibility that the family Sejidae was paraphyletic if it excluded Archaeopodella. This result was somewhat surprising given that Archaeopodella is generally considered to be intermediate between Ichthyostomatogasteridae and Sejidae (Athias-Henriot 1977). Notably, this result was based entirely on
Figure 1. Consensus tree based on morphological analyses; H, Heterozerconidae; U, Uropodellidae; Ichthyo, Ichthyostomatogasteridae; Adeno, Adenosejus; Africa, Africasejus. See Appendix 2 for other abbreviations.
morphological characters, as molecular data were not available for the only described species in this genus, *Archaeopodella scopulifera*. The expansion of the current morphological character and taxon set suggest a different arrangement of *Archaeopodella* (within Ichthyostomatogasteridae), and monophyly of the family Sejidae. Notably, the arrangement of *Archaeopodella scopulifera* and n. sp. 1 (with all instars found on a Philippine rat), appears to make ecological sense, as it groups all taxa associated in some form with vertebrates into a single family, the Ichthyostomatogasteridae. *Asternolaelaps* collections include several records of vertebrate nest associations (Sellnick 1953; Womersley and Domrow 1959), and the only known collection of *Japanasternolaelaps* was from a stable (Hirschmann and Hiramatsu 1984).

Within Sejidae, the established pattern of relationships is somewhat consistent with the species groups of Hirschmann (1991), with one exception: the odd placement of his *Sejus krantzi* (*posnaniensis* group) and *S. manualkrantzi* (*solaris* group). These two taxa have been synonymized (Lekveishvili and Krantz 2004), and re-classified within the genus *Adenosejus*, a lineage that is quite distinct from most other Sejidae (e.g. Lekveishvili and Klompen 2004b). The current analysis also provides some higher-order arrangements for the multitude of species groups proposed by Hirschmann. For example, the (sola–cong) lineage (Figure 1) unites the *solaris* and *congoensis* species groups, the (nova–meso) lineage unites the *posnaniensis*, *camerunis*, *boliviensis*, *togatus*, *rafalskii*, and *stebaevi* groups, and the (zimm–marq) lineage (our *Epicroseius*) is equivalent to Hirschmann’s *tanganicus* group.

**Classification**

Based on results from the current and previous (Lekveishvili and Klompen 2004b) analyses, we support the synonymy of *Willmannia* Balogh and *Liroaspis* Banks, as proposed by, respectively, Hirschmann (Hirschmann et al. 1991) and Lindquist and Evans (1965). The type species of these genera are included in the (nova–meso) lineage. On the other hand, we reject the proposed synonymy (Hirschmann et al. 1991) of *Epicroseius* with *Sejus*. The (zimm–marq) and the (nova–meso) lineages are quite distinct. Moreover, the (zimm–marq) lineage includes all species previously referred to as *Epicroseius*. Although the type species of *Epicroseius*, *E. angelioides*, is not explicitly included in the analysis, the limited amount of available data (e.g. absence of claws on legs I, two-pronged gnathotectum, divided pygidial shield) are fully consistent with placement in the (zimm–marq) lineage. This lineage can thus be classified as *Epicroseius* Berlese. It also includes n. sp. 5 from Australia. Its sister group, the (nova–meso) lineage, which includes the type species of *Sejus*, *S. togatus*, will retain the generic designation of *Sejus*. It includes n. sp. 3 and n. sp. 4, both from Australia. Sister group relationships between *Epicroseius* and *Sejus* are supported by the shared presence of posterior projections in the protonymph. n. sp. 2, recovered for all instars from litter in the Great Smoky Mountains National Park, groups with *A. krantzi*, and will be classified within *Adenosejus*. Among the species included in this analysis, this leaves only *S. solaris* and *S. congoensis*, which do not fit into any of the generic groups proposed above. For this group we propose a new genus, *Africasejus*, n. gen.

The final named genus group in Sejidae is the monotypic genus *Zuluacarus* (Trägårdh, 1906) described from South Africa. As noted above, the species and genus descriptions of *Zuluacarus* are very incomplete, preventing us from including this species in the analysis. Only a few characters can be scored. The presence of a two-pronged gnathotectum is a synapomorphy shared with *Epicroseius*, but the presence of an ambulacrum on legs I (a plesiomorphic character) is inconsistent with such a placement. None of the other
characters that can be scored (dorsal and posteromarginal shields in adults, two pairs of projections, position of genital orifice) are informative, and so we tentatively place *Zuluacarus* near *Epicroseius*. Notably, this arrangement is similar to that proposed by Hirschmann (1991), who placed *S. termitophilus* in the *tanganicus* group (our *Epicroseius*). The genus and species are classified as *incertae sedis*.

**Diagnoses**

Based on the above, we propose the following updated diagnoses for the family *Sejidae* and the genera included in the *Sejidae*.

**Sejidae** Berlese, 1913

**Diagnosis**

Posterior edge of the female genital shield at the level of the posterior edge of coxae IV; female *st1* platelets (if present) not fused with each other or with the *st2* platelets (except in *S. stebaevi*, in which the *st1* platelets are fused to each other); posterior projections (tails) present in at least the larva (except in *S. congoensis* which never carries such projections).

**Remarks**

Most species have posterior idiosomal projections in all instars, but the larval projections may be lost in the protonymph (*Sejus solaris, Adenosejus*) or deutonymph (*S. posnaniensis* and possibly *S. seiiformis*). The number of genital setae in the female (at least three pairs) has been used as a key character for the family *Sejidae* (Krantz 1978; Evans and Till 1979). However, *Adenosejus krantzi, S. hinangensis, S. rafalskii, Epicroseius porosus, E. tanganicus, E. abinashi*, and n. sp. 5 have only two pairs of genital setae and *S. congoensis* has only one pair. Clearly this character is not unambiguous.

**Adenosejus** Lekveishvili and Krantz, 2004

**Diagnosis**

Hypostomal seta *hyp1* setiform (character 7), very large and spiniform setae on the legs; enlarged idiosomal glands.

**Species included**

*A. krantzi*, type species; n. sp. 2.

**Remarks**

Setiform hypostomal setae 1 is a plesiomorphic character shared by most groups of Mesostigmata including Uropodellidae and Ichthyostomatogasteridae. Presence of large, spiniform leg setae and enlarged idiosomal glands are characters not found in any of those groups or in other *Sejidae*. *Adenosejus* appears to be most basal in the family *Sejidae*.
**Africasejus** n. gen.

**Diagnosis**
Female sternal setae *st1* (character 48) inserted in soft cuticle; sides of tritosternal base with denticles (character 38).

**Species included**
*Africasejus congoensis* (Wisniewski and Hirschmann, 1991), n. comb., type species, and *A. solaris* (Wisniewski and Hirschmann, 1991), n. comb.

**Remarks**
*Africasejus* occupies a basal position relative to *Sejus* + *Epicroseius*. Both species included were described from specimens discovered under the bark of tropical hardwood, imported into Poland. The OSAL collection includes an additional specimen of *Africasejus congoensis* (OSAL 14363) recovered from tropical hardwood imported from tropical Africa into a US harbour.

**Epicroseius** Berlese, 1905

**Diagnosis**
Two-pointed gnathotectum; dendritic processes lateral of tritosternum; presence of seta *pv3* on tarsus IV. The latter is an unique character for Mesostigmata.

Based on these characters, nine species of *Sejus* are transferred to the genus *Epicroseius*. The following new combinations are proposed: *E. klakahensis* (Hirschmann, 1991) n. comb.; *E. marquesanus* (Hirschmann, 1991) n. comb.; *E. tanganicus* (Hirschmann and Kaczmarek, 1991) n. comb.; *E. indicus* (Hirschmann and Kaczmarek, 1991) n. comb.; *E. javensis* (Hirschmann and Kaczmarek, 1991) n. comb.; *E. oblitus* (Hirschmann, 1991) n. comb.; *E. savannakhetianus* (Hirschmann and Kaczmarek, 1991) n. comb.; *E. vitzthumiangelioides* (Hirschmann, 1991) n. comb.; *E. vitzthumiseurati* (Hirschmann, 1991) n. comb.

**Other species included**
*Epicroseius angelioides*, type species; *E. seioides* Berlese, 1910; *E. seurati* Berlese, 1918; *E. scutatus* Berlese, 1923; *E. zimmermani*; *E. porosus*; *E. abinashi*; and n. sp. 5.

**Remarks**
Validity of several of these species is unclear since they were described from single specimens in poor condition. These include: *Epicroseius klakahensis*, *E. marquesanus*, *E. vitzthumiangelioides*, *E. vitzthumiseurati*, *E. oblitus*, and *E. javensis*.

**Sejus** C. L. Koch, 1936

*Liroaspis* Banks, 1902 (Lindquist and Evans, 1964).
*Willmannia* Balogh, 1938 (Hirschmann, 1991).
Diagnosis

Sternal platelets \textit{st1} and \textit{st2} in female are not fused (character 55); posterior mesonotal shields in female are not fused to each other.

Species included

\textit{Sejus togatus}, type species; \textit{S. acanthurus} Canestrini, 1884; \textit{S. americana} (Banks, 1902); \textit{S. italicus} Berlese, 1916; \textit{S. paricornis} Berlese, 1916; \textit{S. bicaudus} Berlese; \textit{S. insulanus} Trägårdh, 1931; \textit{S. sejiformis} (Balogh, 1938); \textit{S. armatus} (Fox, 1947); \textit{S. baloghi} (Athias-Henriot, 1960); \textit{S. bakeria} Hirschmann, 1991; \textit{S. australis}; \textit{S. boliviensis}; \textit{S. geometricus} Hirschmann and Kaczmarek, 1991; \textit{S. hinangensis}; \textit{S. polonicus}; \textit{S. posnaniensis}; \textit{S. bugrovskii} Wisniewski and Hirschmann, 1991; \textit{S. cameruns}; \textit{S. cubanus}; \textit{S. mesoafricanus}; \textit{S. rafalskii}; \textit{S. stebaevi}; \textit{S. novoaezealandiae}; \textit{S. venezuelanus}; \textit{S. carolinensis}; n. sp. 3; and n. sp. 4.

Remarks

Balogh separated the genus \textit{Willmannia} from \textit{Sejus} based on the absence of posterior projections in adults (immatures are unknown). Since these projections are present in the larva and protonymph of \textit{S. posnaniensis}, a species which is very close to \textit{W. sejiformis} (it may even be a synonym), it can be assumed that they are present in the same stages of \textit{W. sejiformis} as well. The absence of posterior projections in the adults is apomorphic for \textit{S. sejiformis} and \textit{S. posnaniensis}, but continued recognition of \textit{Willmannia} would leave a paraphyletic \textit{Sejus}.

The species group including \textit{Sejus stebaevi}, \textit{S. americana}, \textit{S. polonicus}, \textit{S. togatus}, \textit{S. hinangensis}, and \textit{S. rafalskii} has characteristic anchor-shaped lateral extensions of the tritosternum in adults; in males the mesonotal and pygidial shields are fused forming an opisthonotal shield (except in \textit{S. stebaevi}; male of \textit{S. rafalskii} is unknown).

The species group including \textit{Sejus australis}, \textit{S. armatus}, \textit{S. boliviensis}, \textit{S. venezuelanus}, \textit{S. carolinensis}, \textit{S. baloghi}, \textit{S. cameruns}, \textit{S. cubanus}, and \textit{S. mesoafricanus} is supported by partially fused ventrianal and posteromarginal shields in the adults, and sickle-shaped lateral extensions of the tritosternum.

\textit{Sejus bakeria} is based on a drawing of \textit{Liroaspis armatus} in a textbook (Baker and Wharton 1952). Validity of this species is unclear.

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Appendix 1. Description of characters and character states

N/A = not applicable.

Figure 2. Chelicera (schematic). (A) With one row of teeth; (B) with two rows of teeth. pd, pilus dentilis.
Chelicera (Characters 1, 2)

1. Pilus dentilis: [0] present (Figure 2A, B); [1] absent.
2. Movable digit of chelicera: [0] with one row of teeth (Figure 2A); [1] with two rows of teeth (Figure 2B).

Figure 3. Gnathotectum. (A) Uropodella laciniata; (B) Narceoheterozercon ohioensis; (C) Africasejus solaris; (D) Sejus carolinensis; (E) Epicroseius sp.; (F) S. polonicus; (G) S. stebaevi; (H) S. rafalskii; (I) Zercon sp.
The derived state is shared by *Sejus togatus*, *S. polonicus*, *S. hinangensis*, *S. rafalskii*, and *S. stebaevi*.

**Gnathotectum (Characters 3–6, Figure 3)**

The shape of the anterior edge of the gnathotectum varies between families of Mesostigmata and within the Sejidae. It can be curved (Figure 3B, G–I), triangular (Figure 3C–F), or blunt (Figure 3A). It may also have from one to three prominent points arising from the anterior margin. Finally, the anterior margin may be serrate or smooth.

3. Gnathotectum of DN or adult: [0] with prominent points (Figure 3E, F, H, I); [1] prominent points absent (Figure 3A–D, G).

4. Number of prominent points on gnathotectum: [0] one (Figure 3H); [1] two (Figure 3E); [2] three (Figure 3F, I); N/A—no points.

5. Anterior edge of gnathotectum: [0] serrate (Figure 3C, D, G–I); [1] not serrate (Figure 3A, B, E, F).

6. Shape of gnathotectum: [0] curved (Figure 3B, G–I); [1] triangular (Figure 3C–F); [2] blunt (Figure 3A).

**Subcapitulum (Characters 7, 8)**

7. Hypostomal seta *hyp1*: [0] setiform; [1] membranous, inflated, with broad base and curved tip; [2] semi-membranous, slightly inflated, smooth.

![Subcapitulum of *Sejus carolinensis* (modified from Lekveishvili and Klompen (2004a) with permission of the *International Journal of Acarology*). *hyp1*, modified hypostomal seta 1; *hyp2–hyp3*, hypostomal setae 2–3; *cs*, coxal setae; *cn*, corniculi.](image-url)
In Sejidae seta hyp1 is modified as a membranous structure with a broad base and a curved tip (Figure 4). The shape of that tip varies a little among species and instars. *Adenosejus krantzi* and n. sp. 2 are the only members of the Sejidae with a setiform hyp 1 seta, the state found in all outgroups. The slightly inflated seta hyp1 of *Archaeopodella* seems to be somewhat intermediate between membranous and setiform, and is coded as semi-membranous.

8. Corniculi: [0] horn-shaped; [1] massive, bifurcate or trifurcate; [2] flat, lobed, membranous.

Horn-shaped corniculi are typical for most Mesostigmata and are retained in Sejidae (Figure 4). Modifications include massive trifurcate corniculi in Ichtyostomatogasteridae, and flat, lobed, and even membranous forms in Heterozerconidae.

**Dorsal shields (Characters 9–26, Figure 5)**

Sejina can have up to eight dorsal shields. The usually somewhat triangular podonotal shield covers the anterior half of the dorsum, the posterior half may carry up to four median (mesonotal) shields plus a pygidial shield. Larvae have podonotal and pygidial shields, but lack mesonotal shields. The mesonotals may or may not be added in protonymphs, but they are never fused. In deutonymphs and adults, the mesonotals can be fused to each other and/or to the podonotal or pygidial shields. Deutonymphs and adults of Uropodellidae add

![Figure 5. Dorsal shields of Sejina (schematic). PD, podonotal shield; PT, peritrematal shields; LT, lateral shields; AM, anterior mesonotal shield; PM, posterior mesonotal shields; PG, pygidial shield; PMG, posteromarginal shields; PP, posterior projections.](image-url)
separate shields lateral to the podonotal and opisthonotal shields, lateral shields. The only species of Sejidae where elements of these shields may be present is n. sp. 2, which has laterally extended mesonotal shields.

Coding for these characters can be problematic when shield fusion occurs. The coding approach chosen uses area as the basic unit, for example anterior mesonotal area or pygidial area. Thus a holodorsal shield, as found in adult Asternolaelaps and Heterozerconina, is coded as present for podonotal, all mesonotals, lateral, and pygidial shields as all those regions are covered by shields.

9. Lateral dorsal shields in adults: [0] present; [1] absent.
10. Mesonotal shields in protonymph: [0] present; [1] absent.
11. Homeomorphic deutonymph, anterior mesonotal shields: [0] partially fused with podonotal; [1] not fused with podonotal.

The anterior mesonotal shields in some homeomorphic deutonymphs may be fused to the podonotal shield. The line of fusion is usually still visible. This condition is found in some Epicroseius and Africasejus congoensis.

12. Homeomorphic deutonymph, anterior mesonotal shields: [0] fused to each other; [1] not fused.
13. Homeomorphic deutonymph, anterior and posterior mesonotal shields: [0] fused to each other; [1] not fused.
14. Homeomorphic deutonymph, posterior mesonotal shields: [0] fused to each other; [1] not fused.
15. Homeomorphic deutonymph, posterior mesonotal shields: [0] fused to pygidial; [1] not fused.
16. Anterior mesonotal shields in male: [0] fused with podonotal; [1] not fused with podonotal.

There is only one sejid species, Africasejus solaris, that has the anterior mesonotal shields fused to the podonotal shield in the male. This type of fusion has not been observed in any other species of the family. This hypothesis of homology is based on (1) the presence of slightly differentiated areas resembling the mesonotal shields on the large anterior shield, and (2) the presence of a large number of additional setae on that anterior shield which can only be explained by assuming fusion of the anterior mesonotals and the podonotal.

17. Anterior mesonotal shields in male: [0] fused with each other; [1] not fused with each other; [2] partially coalesced.

The mesonotal shields in Epicroseius species are surrounded by secondarily sclerotized cuticle, an arrangement designated as "partially coalesced". Coding of this character has to be approached with some care. The level of secondary sclerotization appears to be age dependent. In one (new) species of Epicroseius we have observed specimens that can be assigned, conditionally, to four groups (Figure 6) depending on level of secondary sclerotization. In the first group the four mesonotal shields are well defined. In the second group the mesonotal shields are embedded in a poorly delimited zone of secondary sclerotization. Specimens in the third group show an almost rectangular, and much better defined, zone of sclerotization around the mesonotals and in the most sclerotized specimens
(fourth group) the rectangular shield of secondary sclerotization is very well developed and the original mesonotal shields are hard to distinguish.

Because type material of most *Epicroseius* species was not available to us we had to rely on original descriptions and drawings. Trägårdh (1951) states that *E. zimmermani* has “a median shield, with two cuneiform areas which are presumably the remnants of anterior mesonotal shields, now almost completely coalesced with the postero-median shields, the lateral and posterior margins of which are rather indistinct”. In his description of *E. porosus* Domrow (1956) describes the median shield as “rectangular, entirely covered by striated cuticle, except for four small transverse exposed areas”. It seems, that in older adults of *Epicroseius* the mesonotal shields are always coalesced, but in teneral specimens the secondary sclerotization may not always be present.

18. Anterior and posterior mesonotal shields in male: [0] fused; [1] not fused; [2] partially coalesced.
19. Posterior mesonotal shields in male: [0] fused with each other; [1] not fused; [2] partially coalesced.
20. Posterior mesonotal shields in male: [0] fused with pygidial; [1] not fused.

The males of some Sejidae have their mesonotal shields fused with the pygidial forming an opistthonotal shield. The same condition is also found in *Uropodella* and n. sp. 2.

21. Posterior mesonotal shields in female: [0] about same size or larger than anterior shields; [1] smaller than anterior shields; N/A—shields are fused.
22. Female anterior mesonotal shields: [0] fused with each other; [1] not fused; [2] partially coalesced.
23. Female posterior mesonotal shields: [0] fused with each other; [1] not fused; [2] partially coalesced.
24. Pygidial shield in larva: [0] present; [1] absent.
25. Pygidial shield in protonymph: [0] present; [1] absent.
26. Pygidial shield in adults: [0] divided; [1] not divided.

In the diagnosis of *Epicroseius angioides*, the type species of genus, Berlese (1905) states that the posterior (pygidial) shield is divided in two by a longitudinal strip of soft cuticle. Later, in the description of *E. scutatus*, he refers to the pygidial shield as two shields, fused together. Trägårdh (1951) follows Berlese in his description

![Figure 6. Secondary sclerotization in *Epicroseius* n. sp. 3. (A–D) first to fourth levels.](image)
of *E. zimmermani*. In contrast, Domrow (1956) describes it as “posterior shield with sclerotized median longitudinal strip without setae; lateral margin well sclerotized, remainder reticulated”.

All specimens of *Epicroseius* have a pygidial shield with a median longitudinal strip that suggests a groove rather than a line of fusion. We call this the median groove. The sclerotization level of the groove area is about the same as that of the lateral strips which are also present in all *Epicroseius* (Figure 7A). The groove is absent in most other Sejina or in the outgroups. N. sp. 2 shows a similar median groove dividing the pygidial shield, but lacks the lateral strips (Figure 7B).

**Posteromarginal shields (Characters 27–29, Figure 5)**

Posteromarginal shields are not developed in immatures. In adults they may be present or absent. They can be fused to each other or to the pygidial or ventrianal shields.

27. Posteromarginal shields in adults: [0] present; [1] absent.

28. Posteromarginal shields in female: [0] fused with each other; [1] not fused with each other; N/A—shields absent.

29. Posteromarginal shields in female: [0] fused with pygidial shield; [1] not fused with pygidial shield; N/A—shields absent.

30. Two pairs of projections in larva: [0] present; [1] absent.

Most Sejidae have two pairs of posterior projections in the larvae bearing setae J5 and Z5. The exception is *Africasejus congoensis*, in which the larva lacks projections. They are also absent in the outgroups.

31. Two pairs of projections in protonymph: [0] developed; [1] not developed.

Some Sejidae lose the projections in the protonymphal stage (*Adenosejus krantzi* and *Africasejus solari*).

32. Two pairs of projections in deutonymphs or adults (Figure 5): [0] developed; [1] not developed.

Only one species, *Sejus posnaniensis*, has projections in the larva and protonymph, but loses them in the deutonymph.

33. Dorsal setae: [0] short and leaf-shaped; [1] not short and leaf-shaped.

Most Sejidae have barbed dorsal seta except *Africasejus congoensis* which has short and leaf-shaped setae, a state shared with *Uropodella* and *Japanasternolaelaps*.

![Figure 7. Divided pygidial shield. (A) *Epicroseius* sp.; (B) *Adenosejus* n. sp. 2.](image-url)
34. Dorsal setae on tubercules (Figure 8): [0] present; [1] absent.

35. Marginal setae in adults: [0] five pairs of marginal setae serrate, with expanded tips; at least five times longer than the remaining dorsal setae; [1] all marginal setae about the same length as the remaining dorsal setae and without expanded tips. *Africaseius solaris* and *Adenoseius krantzi* have very long marginal setae with expanded tips.

**Tritosternum (Characters 36–41, Figure 9)**

36. Lateral extensions of tritosternum: [0] present (Figure 9A–C, F–H); [1] absent (Figure 9D, E).

37. Shape of lateral extensions: [0] inverted T-shaped (Figure 9A); [1] sickle-shaped (Figure 9B); [2] anchor-shaped (Figure 9C); [3] barbed (Figure 9F); [4] very small, spur-shaped (Figure 9G); [5] anteriorly serrate (Figure 9H); N/A—no lateral extensions.

38. Sides of base of tritosternum: [0] with denticles (Figure 9D); [1] without denticles (Figure 9A–C, E–H).

39. Surface of base of tritosternum: [0] with denticles (Figure 9D, G); [1] without denticles (Figure 9A–C, E–F, H).

40. Two or three pairs of dendritic processes lateral of tritosternum: [0] present (Figure 9E); [1] absent (Figure 9A–D, F–H).

The presence of these processes is characteristic for members of the genus *Epicroseius*. They are absent in other taxa.

41. Row of denticles posterior to tritosternum: [0] present; [1] absent.

Most Sejidae have a row(s) of denticles (small teeth) on both sides of, or posterior to, the base of the tritosternum. This is a character shared with most Heterozerconidae.

**Sternal and genital regions (Characters 42–60, Figures 10, 11)**

Sejidae have a divided sternal shield in both males and females.

Males can have two pairs of sternal platelets (very small shields) and a larger sternal shield (Figure 10). The platelets may be fused with each other and/or with the main sternal
shield. In most species setae \textit{st1}, \textit{st2}, and \textit{st3} are inserted on the sternal platelets. When platelets are absent, these setae are inserted on dentate areas or on soft cuticle. Sternal setae \textit{st4} and \textit{st5} are always inserted on the large sternal shield, which may bear additional setae. The presternal genital orifice is small, circular, and devoid of genital setae.

Females may have up to three pairs of sternal platelets, which bear \textit{st1}, \textit{st2}, and \textit{st4}, respectively, and one transverse platelet anterior to the genital shield, which bears setae \textit{st3} (Figure 11). Platelets bearing \textit{st4} may be fused with platelet bearing setae \textit{st3}. If platelets are absent, the setae are inserted on dentate areas or on soft cuticle (as in the male). Seta \textit{st5} is always inserted on the genital shield. The genital shield usually bears additional setae, from

Figure 9. Tritosternum. (A) \textit{Africasejus congoensis}; (B) \textit{Sejus carolinensis}; (C) \textit{S. hinangensis}; (D) \textit{A. solaris}; (E) \textit{Epicroseius} sp.; (F) \textit{Astermolaelpates} sp.; (G) \textit{Japanastermolaelpates} japonensis; (H) \textit{Archaeopodella} scopulifera.
two to four pairs, except in *Africasejus congoensis*, which has only *st5* on genital shield. The genital shield is situated between the centre or posterior edge of coxae II and the posterior edge of coxae IV.

42. Sternal seta *st1* in male: [0] on sclerotized platelet; [1] on dentate area; [2] on soft cuticule.
43. Sternal seta *st3* in male: [0] on sternal shield; [1] not on sternal shield.
44. Male sternal region with: [0] five pairs of setae; [1] more than five pairs of setae.

Figure 10. Sternal region of male (schematic). GO, genital orifice; st1–st2, sternal platelets 1–2; CI–CIV, coxa I–coxa IV.

Figure 11. Sternal and genital regions of female (schematic). GS, genital shield; st1–st4, sternal platelets 1–4; CI–CIV, coxa I–coxa IV.
45. Male sternal region with: [0] six pairs of setae; [1] seven pairs of setae; [2] nine pairs of setae; [3] more than nine pairs of setae; N/A—with five pairs of setae.
46. \textit{st1} areas in male if sclerotized: [0] fused with each other; [1] not fused with each other; N/A—not sclerotized.
47. \textit{st2} areas in male if sclerotized: [0] fully fused with \textit{st3} area; [1] partially fused with \textit{st3} area; [2] not fused with \textit{st3} area; N/A—not sclerotized.
48. Seta \textit{st1} in female: [0] on sclerotized platelet; [1] not on sclerotized platelet.
49. Seta \textit{st2} in female: [0] on sclerotized platelet; [1] not on sclerotized platelet.
50. Seta \textit{st3} in female: [0] on sclerotized platelet; [1] not on sclerotized platelet.
51. Seta \textit{st4} in female: [0] on sclerotized platelet; [1] not on sclerotized platelet.
52. Sternal setae \textit{st3} and \textit{st4} in female: [0] on the same platelet; [1] not on the same platelet; N/A—not on platelet.
53. Female \textit{st1} areas if sclerotized: [0] smooth; [1] not smooth; N/A—not sclerotized.
54. Female \textit{st1} areas if sclerotized: [0] fused with each other; [1] not fused with each other; N/A—not sclerotized.
55. Female \textit{st1} and \textit{st2} areas if sclerotized: [0] fused; [1] not fused; N/A—not sclerotized.
56. Anterior edge of genital shield: [0] at the middle of coxae II; [1] posterior to coxae II; [2] at the anterior edge of coxae IV.
57. Posterior edge of genital shield: [0] at the posterior edge of coxae IV; [1] behind coxae IV; N/A—fused with ventral.
58. Female genital shield with: [0] one pair of setae; [1] more than one pair of setae.
59. Female genital shield with: [0] two pairs of setae; [1] three pairs of setae; [2] four pairs of setae; [3] five pairs of setae; [4] 10 or more pairs of setae; N/A—one pair of setae.
60. Platelets between sternal and ventrianal shields in male: [0] two pairs; [1] more than two pairs; [2] no small platelets; N/A—area between sternal and ventrianal shields is sclerotized.

Some Sejidae have two or more pairs of sclerotized platelets between the sternal and ventrianal shields. They are absent in other groups.

61. Male genital orifice: [0] presternal, between coxae II; [1] midsternal, between coxae III.

\textit{Ventrianal shield (Characters 62–64, Figure 12)}

Ventrianal shields are mostly large, but vary in shape and relative size. They may or may not be fused with the posteromarginal shields (if present).

62. The width of female ventrianal shield: [0] about half or less of the width of the opisthosoma (Figure 12A–C); [1] about three-fourths to two-thirds of the width of the opisthosoma (Figure 12D); [2] almost equal to the width of the opisthosoma (Figure 12E, F).
63. Ventrianal shield in adults: [0] fully fused with posteromarginal shields; [1] partially fused with posteromarginal shields; [2] not fused with posteromarginal shields.
64. Anus: [0] enlarged; [1] small.
65. Metapodal shields in deutonymphs or adults: [0] present; [1] absent.
66. Metapodal shields in deutonymphs or adults situated: [0] axial; [1] laterally; [2] shifted dorsolaterally; N/A—absent.

67. Metapodal shields in deutonymphs or adults: [0] medium size, oval; [1] reduced to two or three miniplatelets; [2] large triangular; [3] long and narrow; N/A—absent.

68. Metapodal shields in male: [0] fused with ventrianal; [1] not fused with ventrianal; N/A—absent.

69. Claws on legs I: [0] absent in immatures and adults; [1] absent in immatures, present in adults; [2] present in immatures and adults.

Absence of claws on leg I in all instars defines the genus *Epicroseius*. Immatures of Heterozerconidae lack claws on tarsi I, but add them in the adults.

70. Setae *av4* and *pv4* on tarsus IV: [0] present (Figure 13); [1] absent.

These setae are inserted on the intercalary sclerite of tarsus IV, between the basitarsus and telotarsus. This character is often used as characteristic for the infraorder Sejina.

71. Seta *pv3* on tarsus IV: [0] present; [1] absent.

Seta *pv3* on tarsus IV is found in *Epicroseius* and absent in all other groups.

Figure 12. Female ventrianal shield. (A) *Africosejus solaris*; (B) *Sejus australis*; (C) *S. boliviensis*; (D) *S. stebaevi*; (E) *S. togatus*; (F) *Adenosejus krantzi*.
72. Very large and spiniform setae on legs: [0] present; [1] absent.
73. Acrotarsus on leg I: [0] present; [1] absent.
74. Dorsum of idiosoma: [0] without large glands; [1] with two pairs of large glands; [2] with more than two pairs of large glands.

The dorsum of Mesostigmata is covered with a number of small glands, but two pairs of very large glands are present in *Africasejus congoensis*, Ichthyostomatogasteridae, and Uropodellidae. One pair is on the podonotal shield or near that shield and another pair is on the posterior margins of the pygidial shield. *Adenosejus* species have more than two pairs of large glands.
## Appendix 2. Matrix of morphological character states

| Character State | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|-----------------|---|---|---|---|---|---|---|
| Zercon (Zerc)   | ?  | 0  | 0  | 0  | 0  | 0  | 0 |
| Microgynium (Micr) | 1  | 0  | 0  | 0  | 0  | 0  | 0 |
| Narceoheterozon (Narc) | 0  | 1  | 0  | 0  | 0  | 0  | 0 |
| Asternolaelaps (Astl) | 1  | 1  | 1  | 0  | 1  | 1  | 1 |
| Japanasterolaelaps (Japn) | 0  | 1  | 1  | 0  | 0  | 0  | 0 |
| Uropodella (Urpd) | 0  | 0  | 1  | 2  | 0  | 0  | 0 |
| Archaeopodella (Arch) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. kranzii (kran) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. solis (sola) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. congensis (cong) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. sagittatus (sag) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. hensens (hens) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. parvus (parv) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. americana (amer) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. novaeezlandiae (nov) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. posnaniensis (posn) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. sejiformis (seji) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. australis (austr) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. armatus (arma) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. boliviensis (bol) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. venezuelans (ven) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. carolinensis (caro) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. baloghii (bal) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. camerunensis (came) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. cubanus (cub) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. mosquirostris (moso) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. sp. 3 (sp3) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| A. sp. 4 (sp4) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| E. porus (porus) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| E. zimmermani (zimm) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| E. tanganica (tang) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| E. abinashi (abin) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| E. klahokensis (klak) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |
| E. marquesanus (marq) | 0  | 0  | 0  | 0  | 0  | 0  | 0 |

? = data is not available; – = not applicable.