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Uropodella (Acari: Mesostigmata: Sejidae), mites unchanged from Eocene past to Holocene present

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Original research

ABSTRACT

The first record is presented of the sejoid genus *Uropodella* (family Uropodellidae, suborder Sejida) from Baltic amber, based on a well-preserved adult male. Morphologically, the specimen is as modern in structure as adults of the six known extant species of *Uropodella*. The diagnosis of the fossil in distinction to the extant species justifies naming it as a **new species**. This record traces the genus back to the Eocene, representing the oldest validated age for a mesostigmatan genus. A key to species of the genus *Uropodella* is given.

Keywords Parasitiformes; Sejida; fossil record
Zoobank http://zoobank.org/BD77235C-748E-4D6C-A917-C4394DCC0BFB

Introduction

Members of the suborder Sejida are considered to be among the most primitive of the acarine order Mesostigmata (Johnston 1982; Evans 1992). The Sejida encompasses the infraorder Sejina *sensu lato* (Lekveishvili and Klompen 2004), which includes the superfamily Heterozerconoidea and various other families of traditional Sejina *sensu stricto* (Lekveishvili and Klompen 2009). Phylogenetically, the genus *Uropodella* is considered basal to all other taxa of the Sejina *sensu stricto* (Lekveishvili and Klompen 2004). The Sejina *sensu stricto* consists of one superfamily, Sejoidea, with four families, Sejidae, Uropodellidae, Ichthyostomatogasteridae, and Reginacharlottiidae (Lekveishvili and Krantz 2004; Joharchi *et al.* 2021). In turn, the Uropodellidae contains only a single genus, *Uropodella* Berlese, 1888, currently with six extant species described from the Americas and Africa (Camin 1955; Athias-Henriot 1972; Hirschmann and Zirngiebl-Nicol 1984; Wisniewski and Hirschmann 1991). Because the fossil adult male is so similar morphologically to those of extant species, various aspects of its ways of life can also be assumed similar, as presented in the discussion. Moreover, because this male can be distinguished from the adults of all six of the described extant species, it is provided with a binomen as a new species and included in a key to species of this genus.

Material and methods

Provenance and deposition. The piece of Eocene Baltic amber mined at Usedom (a Baltic Sea island in Pomerania) containing the fossil mite treated herein originates from the private Collection of Christel and Hans-Werner Hoffeins (CCHH), original collection number CCHH-354-1. The piece is transferred to the collection of the Geological-Palaeontological Museum,

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Leibniz Institute for the Analysis of Biodiversity Change (LIB), Hamburg, Germany, collection number GPIH-05125.

Syninclusion: Acari: Acariformes, only an anterior part (gnathosoma and propodosoma) not further identifiable, in the depth of amber.

Amber preparation. The fragment measuring 4.5x3.5x0.8 mm, containing the mite, was trimmed from the original piece embedded in polyester resin and then polished on two sides, following protocols of Sidorchuk and Vorontsov (2018), to provide dorsal and ventral aspects of the mite. Other aspects were not assessed due to the trench in amber which crossed the mite in the frontal plane. For collection storage, after the study the specimen was covered by the same artificial resin (Hoffeins, 2001).

Imaging. For imaging, a Nikon E-800 compound microscope with dry (10x) and water (40x and 60x) objectives was used. As the body of the mite was mostly non-translucent, most of the micrographs were made in reflected light that limited the resolution. Stacks of images, comprising multiple focal planes, were obtained with an Olympus OM-D E-M10-II digital camera. Final images were focus-stacked using Helicon Focus Pro 7.6. Image stacks are available through Figshare (https://doi.org/10.6084/m9.figshare.21938027).

Terminology, systematics, measurements. Terminology used for morphological structures follows those of Evans (1992) and Alberti and Coons (1999). Classification and systematic concepts generally follow Lindquist *et al.* (2009) and Beaulieu *et al.* (2011). Measurements of structures are given in micrometers (µm) and rounded to the nearest 5 if beyond 30 mm; length, width and height relates in each case to the maximal dimension visible. As orientations of structures in amber were suboptimal, the measurements are to be treated as minimal estimates. Measurements are based on the one specimen available and limited to idiosomatic structures, as the legs are too folded and obscure for measuring. Notation for setae and gland-like structures are not attempted, in view of idiosomatic hypertrichy and obfuscation of other structures.

Systematic paleontology

Superorder Parasitiformes Reuter, 1909, *sensu* Krantz and Walter 2009

Order Mesostigmata G. Canestrini, 1891

Suborder Sejida Kramer, 1885

Infraorder Sejina Kramer, 1885, *sensu* Lekveishvili and Klompen 2004

Superfamily Sejoidea Berlese, 1885

Family Uropodellidae Camin, 1955

Genus *Uropodella* Berlese, 1888

Uropodella hoffeinsorum new species

Zoobank: 3E1FEF54-6C3E-4E68-9CFB-816E5B2274F4

Diagnosis

The fossil male mite is distinguished from adults of *Uropodella laciniata* (Berlese, 1888) and *sensu* Camin (1955), and of *U. nebulosa* Athias-Henriot (1972) in having the setae of the dorsal shields extremely thin, nearly smooth (though minutely ciliated), whereas these setae are described or shown as being thicker, leaf-like, pectinated on those two forms. Its distinction from *U. australis* Athias-Henriot, 1972 is based immediately on the idiosomatic shields of the latter being remarkably unsculptured. The dorsal shields of *U. cristata* Athias-Henriot, 1972 are each more clearly (1.1–1.4x) wider than long, with the posterior shield ca 1.5x longer than the anterior shield (based on measures and figures); whereas each of these shields is subequally

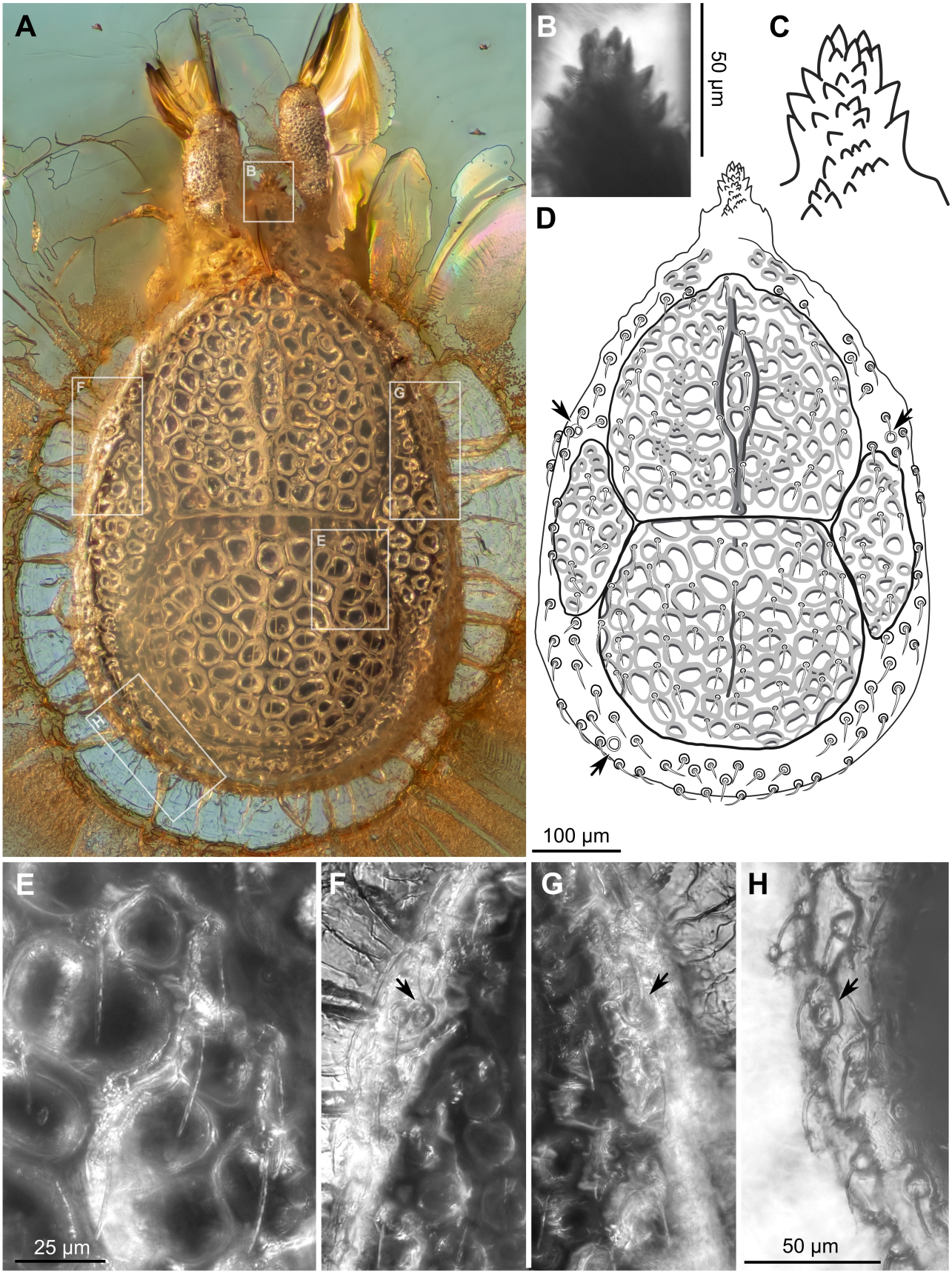

Figure 1 Dorsal images of adult male, *Uropodella hoffeinsorum*, **sp. nov.**; A – habitus image, micrograph; B – enlarged photo of anterodorsal idiosomal vertex or prosostège *sensu* Athias-Henriot 1972; C – drawing of idiosomal vertex; D – line drawing; E – enlarged reflected light micrograph of finely ciliate dorsal setae; F, G, H – enlarged micrographs of ring-like structures (arrows) amidst setae. All micrographs except B are focus-stacked; F, G, H to same scale.

as wide as long, with the posterior shield at most 1.1x longer than the anterior shield on the fossil.

Description

Adult male

(Figures 1–2)

Dorsal idiosoma — Broadly oval in form, length 710 (including podonotal vertex projection of ca 90), greatest width near mid-level 440; dorsal surface with extensive anterior vertex, and anterior and posterior dorsal shields of similar dimensions, flanked on either side by a lateral shield (Figures 1A, D); all shields hypertrichous with small (15–20) thin, nearly smooth, slightly ciliate setae (Figure 1E), strongly ornamented with coarse foveae, lateral margins of shields smooth; shields flanked by soft, slightly tuberculated cuticle, similarly hypertrichous with small, nearly smooth setae inserted individually on small sclerotized bases (Figures 1H, 2F). Dorsal idiosoma extended anteriorly into a projecting, coarsely spinose vertex or "prosostège" *sensu* Athias-Henriot, 1972 (Figures 1B, C); anterior dorsal shield with midline ridge along posterior third of length, that ridge divided antero-medially on mid-third of shield (Figures 1A, D), midline length 270, greatest width slightly posterior to mid-level 280; posterior dorsal shield without horn-like processes bearing setae, with midline ridge developed along most of its length, and with slight indications of a parallel mid-lateral ridge on either side (Figure 1A), midline length 295, greatest width near mid-level 300; lateral dorsal shields narrowly rounded at either end, each 195–200 in length, maximum width near mid-level 78–80; dorsal shield setae difficult to discern, exceedingly thin, slightly ciliated (Figure 1E); surrounding soft cuticle with a mostly single series or rim of similarly small, nearly as thin setae anteriorly, becoming more numerous as two or more such series posterad the lateral shields; soft cuticle with a ring-like structure amidst setae closely anterad each lateral shield and also one posterad the posterior dorsal shield (visible only unilaterally) (Figures 1D, F, G, H, arrowed).

Ventral idiosoma — Holoventral shield with lateral margins slightly undulated, ornamented over entire surface with coarse foveae as on dorsal shields (Figures 2A, C), length from anterior margin between bases of legs I and II to hind margin 495; maximum width at posterior mid-level 390; minimum width between legs IV 135; shield with a pair of long furrows demarcating genitiventral area extending obliquely from between legs IV nearly to transverse level of anal opening near where greatest transverse interval between furrows 235. Tritosternum with broad, trapezoidal base with pilose laciniae separated at base. Form of anterior sternal area structures indiscernible. Genital opening with a sclerotized circular rim at level between bases of legs II, well behind anterior margin of holoventral shield. Anal opening protrudent, covered by a small, circumscribed, smooth, disc-like area, ca 50 long, 35 wide, flanked by a pair of minute anal valves with three pairs of setae (Figures 2D, E).

Gnathosoma — Chelicerae and ventral gnathosomatic structures indiscernible.

Legs — Leg segments roughened, tuberculated in surface texture, with some larger spines forming setal bases; leg I tarsus with apical subdivision, delineating an acrotarsus (Figure 2B, arrow); all legs with paired claws; details of rich setation and other structures mostly indistinct, but an elongated macroseta evident dorsally on genu of legs III, IV. Legs with rows of thick leaf-like setae (Figure 2G).

Etymology

The fossil species name is dedicated to Christel and Hans-Werner Hoffeins, who collected the piece of amber and discovered the mite inside.

Remarks

This fossil mite is an adult male because it both (1) presents a small, circular genital opening between the level of legs II on sternitigenital shielding that is (2) coalesced with peritrematal and ventrianal shielding to form a holoventral shield. Its configuration of dorsal shields

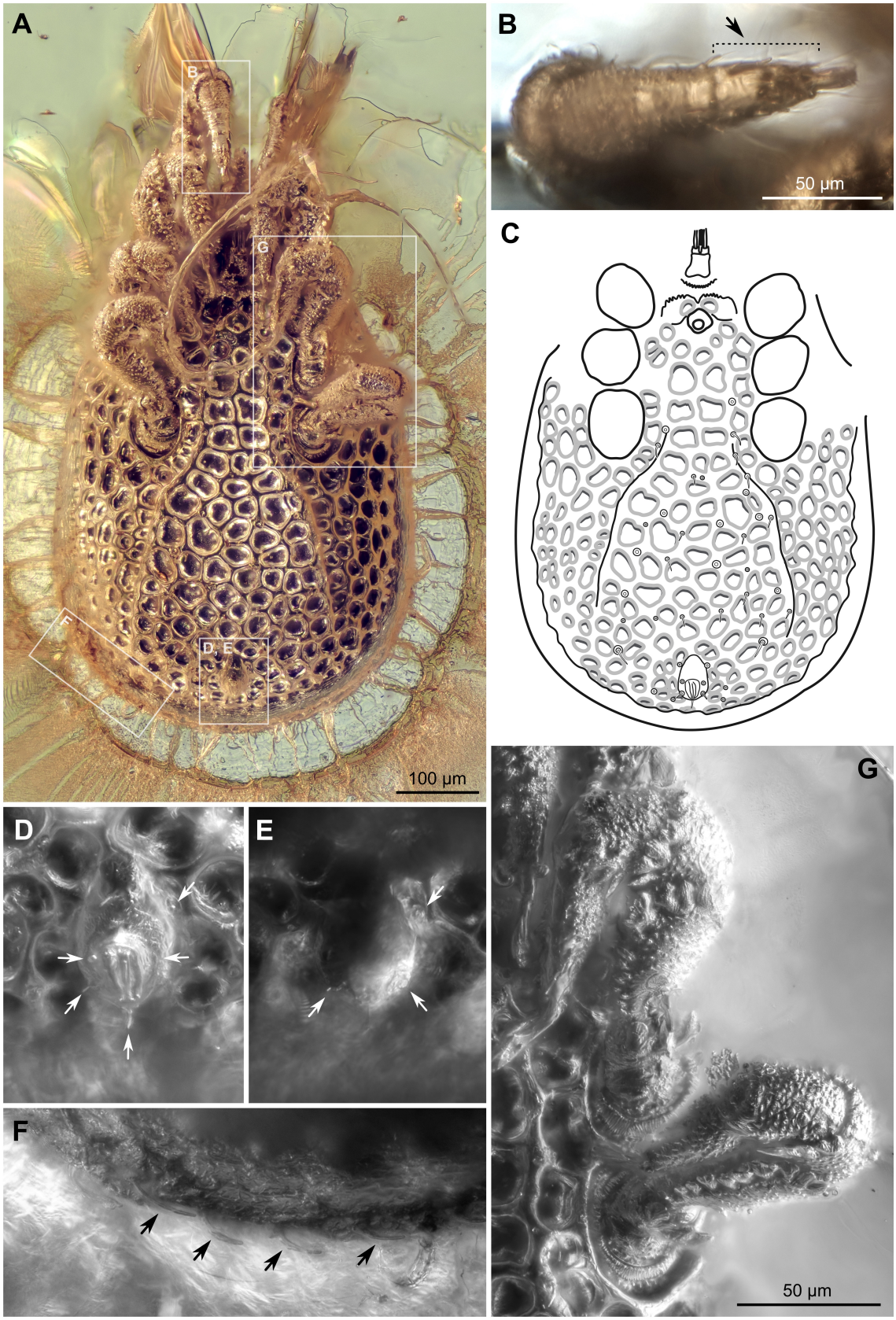

Figure 2 Ventral images of adult male, *Uropodella hoffeinsorum* , **sp. nov.**; A – habitus image, micrograph, showing circular, funnel-shaped genital opening, furrows delimiting sternitigenial area from more lateral parts of holoventral shield, and small, unornamented anal region; B – enlarged micrograph of tarsus I, showing tuberculated basal area, the apical subdivision delineating nearly smoothly surfaced acrotarsus.(arrow); C – ventral habitus drawing, legs omitted; D, E – reflected light micrographs of anal region of holoventral shield, showing small, protruding anal opening flanked by small anal sclerites; different focusing and directions of lateral lighting in D and E show alveoli of setae (arrows); F – micrograph showing thin smooth marginal setae (arrows, see also Fig.1G); G, legs III and IV. D-G to same scale.

(anterior and posterior, flanked by a lateral pair) is typical of both adult male and female sejine taxa. The fossil's species is assigned to the family Uropodellidae and its only recognized genus *Uropodella* by the following combination of attributes: (1) body with extensive dorsomarginal hypertrichy; (2) adult idiosoma with extensive anterior (podonotal) and posterior (opisthonotal) shields, flanked on either side by a mesolateral shield; these and ventral shielding (3) coarsely ornamented, foveolated; (4) apex of podonotum produced apomorphically into a prominent spiky knob (a vertex or prosostège *sensu* Athias-Henriot, 1972) over the gnathosoma; (5) male with ventral shields consolidated (holoventral shield); male genital aperture (6) subcircular, intercoxal between legs II, and (7) located behind level of anterior margin of sternitigenital part of ventral shielding; (8) anal opening small; (9) tritosternum with strongly developed base; (10) soft cuticle tuberculated.

The genus *Uropodella* was reviewed by Hirschmann and Zirngiebl-Nicol (1984), who provided keys to the six species recognized by them, including two newly named species based on material previously identified as *Uropodella sp.* by Krantz (1978, 2009) and provisionally as *Uropodella laciniata* by Camin (1955). Here, the names by Hirschmann and Zirngiebl-Nicol for two species are treated provisionally as nomina dubia, as they were not based on studies or deposition of specimens. However, they are included in the following key to species of the genus, in view of the fourth edition of the International Code of Zoological Nomenclature (1999), Article 13, seeming to accommodate them. Nevertheless, according to Recommendation 75E of the previous third edition of the Code (1985), which is no longer presented in the fourth edition (1999), a designation of Hirschmann & Zirngiebl-Nicol's names as "nomina dubia" seems appropriate until such time as some primary type specimens can be reexamined and published, with neotype designations, concerning material upon which Krantz's illustrations and Camin's illustrations and descriptions were based.

Provisional key to species of *Uropodella* adults, based on sexually non-dimorphic attributes

1. Dorsal and ventral idiosomal shields unsculptured, smooth . . . . . *U. australis* Athias-Henriot, 1972
— Dorsal and ventral idiosomal shields strongly sculptured, foveolate **2**

2. Dorsal shield setae keeled, thick, serrated or pectinate **3**
— Dorsal shield setae thin, not keeled, nearly smooth (almost imperceptibly ciliate) 7

3. Sternitigenital shield with anterolateral projections parallel, directed straight forward . . . . . *U. nebulosa* Athias-Henriot, 1972
- Sternitigenital shield with anterolateral projections divergent, directed between bases of legs I and II **4**

4. Sternal setae *st1*, *st2* on smooth tubercles . . *U. krantzi* Hirschmann & Zirngiebl-Nicol, 1984, **nomen dubium?** [=*U. sp.*, Ohio, USA *sensu* Krantz, 1978; Lindquist *et al.*, 2009]
— Sternal setae *st1*, *st2* on prickly/thorny tubercles or shaggy mounds **5**

5. Posterior dorsal shield ca 1.1–1.2x wider than anterior dorsal shield width . . . . . .*U. laciniata* Berlese, 1888, and *sensu* Zirngiebl-Nicol *in* Hirschmann & Zirngiebl-Nicol, 1984
— Posterior dorsal shield subequally (+/- 1.05x) as wide as anterior dorsal shield **6**

6. Epigynial shield 1.6x longer than wide . . . . *U. camini* Hirschmann & Zirngiebl-Nicol, 1984, **nomen dubium?** [=*U. laciniata sensu* Camin, 1985, not Berlese, 1888]
— Epigynial shield 1.3x longer than wide . . . . *U. congoensis* Wisniewski & Hirschmann, 1991

7. Dorsal shields each 1.1–1.4x wider than long, with posterior shield ca 1.5x longer than anterior shield . . . . . *U. cristata* Athias-Henriot, 1972

— Dorsal shields each subequally (+/- 1.05x) as wide as long, with posterior shield at most 1.1x longer than anterior shield ..... *U. hoffeinsorum* **sp. nov.**

Discussion

As noted by Joharchi *et al.* (2021), fossil mesostigmatic mites are extremely rare. Moreover, their posture in amber, with the legs usually folded onto the undersides of the body, leaves them extremely difficult to image micrographically and understand their morphological details. The fossil male *Uropodella* at hand from Baltic amber of Eocene age, 54.5−37 Ma (Weitschat & Wichard 2010) has relatively good preservation that allows its certain determination to genus and even to morphological proximity with adults of extant species. An unusual detail appears to be the presence of a small, ring-like structure closely anterad the anterior margin of each lateral dorsal shield (Figures 1F, G). Camin (1955) noted such structures in his description of *Uropodella laciniata* as follows: "…lateral to the anterior median dorsal shield and just anterior to the lateral dorsal shields are a pair of minute, ring-shaped platelets without setae" (Figure 3A). A structure similar in size and location was illustrated for *Uropodella cristata* by Athias-Henriot (1972, figure 207) without descriptive comment. Similarly formed and located structures were illustrated for *Uropodella congoensis* Wisniewski & Hirschmann (1991, figure 2) and for *Adenosejus krantzi* (Hirschmann & Zirngiebl-Nicol, 1984) by Hirschmann (1991), as copied in Lekveishvilli and Klompen (2009), who regarded them perhaps to be gland-pore complexes. A similar structure shown by Athias-Henriot (1972, again figure 207) for *Uropodella cristata* is located on soft cuticle posterolaterad the posterior dorsal shield. Her caption noted it as "pustule OS4 dans un microsclérite piligère", albeit the microsclerite is drawn as having but one seta. She defined "pustule" as a specialized, dorsal, solenostome-bearing organ. Again, a structure similar in size and position is evident on one side of this fossil (Figure 1H). This detail is notable in being peculiar to only some sejine mites, and a further indication of how well and clearly preserved is this fossil specimen.

Apart from the excellence of its preservation, the present discovery is significant in representing the second oldest identified example of the infraorder Sejina of the Sejida, previously considered to be the most primitive suborder of mesostigmatic mites (Johnston, 1982), although currently considered less early derivative (Klompen 2000; Klompen *et al.* 2007). The oldest record is of a deutonymph of an unidentified genus, tracing the Sejida twice as many millions of years back to the mid-Cretaceous in Burmese amber, ca 100 Ma (Joharchi *et al.* 2021).

Comportment — In view of this fossil adult male mite being so similar morphologically to adults of extant species, various aspects of its ways of life are also assumed similar. (1) Association with woody habitats such as tree holes and insect galleries: (Camin 1955; Athias-Henriot 1972; Wisniewski and Hirschmann 1991); very dry, powdery tree holes appear to be a preferred habitat in Ohio, eastern U.S.A (Klompen, personal observations). (2) Fluid feeding: indicated by having a small anal opening, in contrast to particulate feeding and large anal opening (Evans 1992; Lindquist *et al.* 2009). (3) Tocospermic sperm transference: although details of the fossil's chelicerae are obscured, the male chelicerae of all sejine mites are unmodified for sperm transfer activity (Evans 1992). (4) See comments on anal plate structure, below.

Anal plate structure — The form of anal structures, with the anal opening being small and covered by a pair of minute anal valves (Figures 2D, E), may be an ontogenetic carryover from the deutonymph, in which indicating a secretive function as found in the phoretic form of deutonymphs of diverse extant uropodine and sejine taxa (Evans 1992). Based on the descriptions of immature instars of one form of *Uropodella* (Camin 1955), this form of external anal structure is carried over from that of the deutonymph. However, this is not to suggest that an adult male like this fossil could produce an adherent stalk.

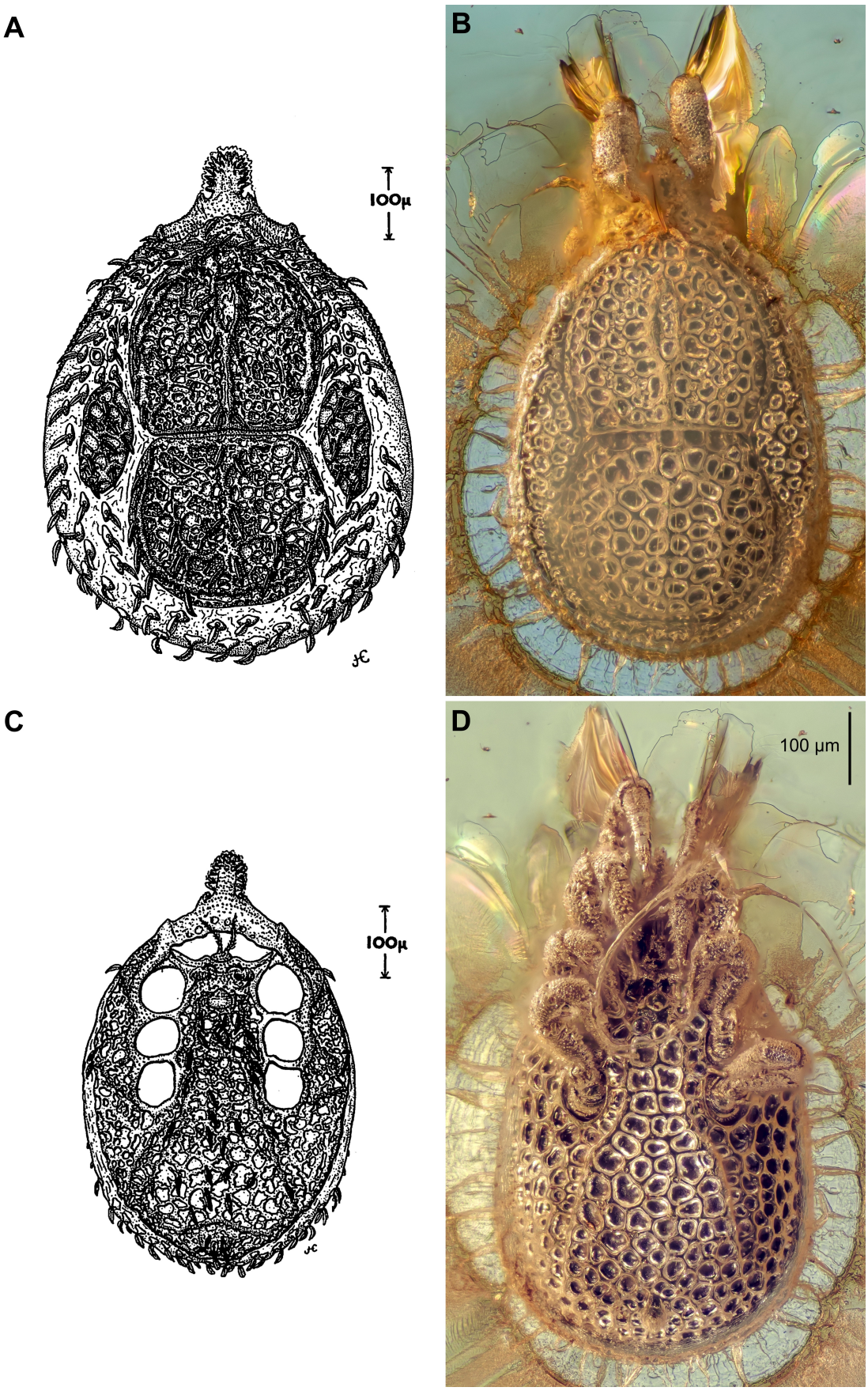

Figure 3 Comparison of adults of *Uropodella laciniata sensu* Camin (1955) with those of *U. hoffeinsorum*, **sp. nov**. A, B – dorsal aspects of female *U. laciniata* (from Camin, 1955) and male *U. hoffeinsorum*, **sp. nov.**; C, D – ventral aspects of adult males of *U. laciniata* (from Camin, 1955) and *U. hoffeinsorum* **, sp. nov**. All drawings and micrographs to same scale.

Johnston (in Norton *et al.* 1993) suggested a close phylogenetic relationship of the suborders Sejina, Microgyniina and Uropodina, without providing explicit evidence. However, this relationship is consistent with a major, life-history modification of deutonymphal phoretic dispersal among mites of these suborders in attaching to hosts by anal secretions, an autapotypical attribute unknown among other Parasitiform mites. In noting that the anal plate structure of *Uropodella* deutonymphs is quite similar to that in the heteromorphic deutonymph of thinozerconoid Uropodina, Kethley (1983) hypothesized that the presence of a heteromorphic deutonymph in *Uropodella* and other non-pedicelate uropodines is derivative relative to the condition of having only a single, homeomorphic deutonymphal instar as found in "primitive" Sejina (*Archaeopodella* and *Epicroseius*). He suggested a subsequent loss of the homeomorphic deutonymph in *Uropodella* and higher uropodines. However, this notion would imply paraphyly of the Sejina relative to Uropodina, and species with specialized deutonymphs have since been described in *Epicroseius* (Hirschmann *et al.*, 1991), suggesting that this hypothesis needs reconsideration (Lekveishvili and Klompen 2004).

Forever small – another example — The idiosomatic sizes of extant adult *Uropodella*, based on five species (females of *laciniata* Berlese, 1888, *australis* and *cristata* of Athias-Henriot, 1972, *congoensis* of Wisniewski and Hirschmann, 1991, *laciniata sensu* Camin, 1955, and males of *laciniata sensu* Camin, 1955, *congoensis* of Wisniewski and Hirschmann, 1991), have lengths of 581 to 763 and widths of 310 to 545 µm. Adult males average ca 0.85 smaller than adult females, based on measurements of two species, *congoensis* and *laciniata sensu* Camin. The fossil male body size of 620 length by 438 µm width fits within those extant body size ranges, so as to be another example of related mites being "forever small", based on data presented by Sidorchuk (2018). Moreover, the morphological aspects of this fossil are so similar to those of extant *Uropodella* species, even to the dorsal shield ornamentation and topographic undulations of *U. laciniata sensu* Camin, 1955 (Figure 3), to suggest that it represents what could be an extant form that dates back to the Eocene epoch.

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