



Biological data on *Smicronyx* species with a first description of immature stages of *Smicronyx smreczynskii* Solari, 1952 (Coleoptera, Curculionidae)

by

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with 21 colour photos, 19 SEM photos and 6 drawings

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Abstract. The mature larva and pupa of *Smicronyx smreczynskii* Solari, 1952 are described and illustrated for the first time. Species and genus-specific characters are given, and a key to distinguish larvae and pupae of *Smicronyx smreczynskii* from those of *S. menozzii*, *S. fulvus* and *S. japonicus* (only larva) is provided. The habitat of the first record of *Smicronyx smreczynskii* in Greece is briefly described, and the extant distribution of the genus *Smicronyx* is studied under consideration of host plant use. On this basis, it is hypothesised that a *Cuscuta*-dwelling species spread from North America to the Old World at an early date (lower Oligocene?) - or it took the opposite route - with the consequence that independent radiation centres with different host plant family use arose in both parts of the world.

Zusammenfassung. Das letzte Larven- und das Puppenstadium von *Smicronyx smreczynskii* Solari, 1952 werden erstmalig ausführlich beschrieben und illustriert. Gattungs- und Artmerkmale von *Smicronyx*-Larven und Puppen werden vorgestellt, und es werden Bestimmungsschlüssel für *Smicronyx smreczynskii*, *S. menozzii*, *S. fulvus* und *S. japonicus* (nur Larve) vorgelegt. Der Lebensraum des Erstnachweises in Griechenland wird vorgestellt, und die aktuelle Verbreitung der Gattung *Smicronyx* wird unter Berücksichtigung ihrer Wirtspflanzennutzung untersucht. Auf dieser Grundlage wird die Hypothese aufgestellt, dass sich eine an *Cuscuta* lebende Art zu einem frühen Zeitpunkt (unteres Oligozän?) von Nordamerika in die Alte Welt ausgebreitet hat – oder sie nahm den umgekehrten Weg – mit der Folge, dass in beiden Teilen der Welt voneinander unabhängige Radiationszentren mit unterschiedlicher Wirtspflanzenfamiliennutzung entstanden.

Podsumowanie. Dojrzałe stadium larwalne i poczwarka *Smicronyx smreczynskii* Solari, 1952 zostały opisane i zilustrowane po raz pierwszy, wraz z podaniem cech charakterystycznych gatunkowo oraz cech charakterystycznych dla rodzaju. W pracy umieszczono klucz pozwalający na odróżnienie stadiów larwalnych i poczwarek *Smicronyx smreczynskii* od *S. menozzii* i *S. fulvus* oraz *S. japonicus* (tylko larwa). Opisano pierwsze stanowisko *S. smreczynskii* w Grecji i zbadano obecne rozmieszczenie rodzaju *Smicronyx*, biorąc pod uwagę wykorzystanie roślin żywicielskich. Na tej podstawie wysunięto hipotezę, że gatunek zamieszkujący *Cuscuta* rozprzestrzenił się z Ameryki Północnej do Starego Świata we wczesnym okresie (dolny oligocen?) - lub obrał odwrotną drogę - w wyniku czego w obu częściach świata powstały niezależne centra radiacyjne z różnymi rodzinami roślin żywicielskich.

Keywords. *Cuscuta*, gall, biology, morphology, larva, pupa, spreading, extant distribution.

1. Introduction

The genus *Smicronyx* is distributed over the Palaearctic region, Africa, America, Southeast Asia, and Australia. Alonso-Zarazaga et al. (2023) listed around 50 species for the Palaearctic region. According to Rheinheimer & Hassler (2010) the total number of species worldwide is around 130; Anderson et al. (2006), Haran et al. (2017), Haran (2018, 2021) added another 18 species. The tribe Smicronychini comprises a comparably small number of genera (5 - 6 according to Caldara et al. 2014: p. 615) and is well characterized by a small body size, a constriction in front of the eyes and a more or less scaly integument (Freude et al. 1983, Haran 2014).

Basic papers regarding taxonomy, phylogeny and biology of the American *Smicronyx* species were published by Anderson (1962) and of the French and German species by Hoffmann (1958) and Dieckmann (1986). Further works focused mainly on certain aspects of biology, phenology, distribution (Sorel 1971, Dieckmann 1986, Schott 1999, Heijerman & Alders 2000, Legalov 2010, Haran 2014, Haran et al. 2017, Yunakov et al. 2018), biological control (e.g., Anderson & Cox 1997) and the description of new *Smicronyx* species (Anderson 1974, Dieckmann 1990, Karasyov 1995, Anderson et al. 2006, Morimoto & Kojima 2007, Morimoto & Matoba 2009, Haran et al. 2017, Haran 2018, Haran 2021).

In the Palaearctic region, several *Smicronyx* species develop in semi-parasitic plants with little chlorophyll (*Cuscuta*, *Orobanche*). Their

larvae often induce galls (Dauphin 2002, Dieckmann 1986, Winkelmann 2019).

For some *Smicronyx* species there is information about pupae as well as early and late larval instars: Urban (1914), adopted from Scherf (1964), gave sparsely illustrated data about the morphology of the larval stages of *S. jungermanniae* (Reich, 1797), which, according to Dieckmann (1986) and to Heijerman & Alders (2000), refers to *S. smreczynskii*. On the other hand, Frilli (1966) described in detail the immature instars of another gall-producing species, *S. menozzii* Solari, 1952 (egg, mature larva, pupa), and he provided a table with the chaetotaxy of the larva. Moreover, Oseto & Braness (1979a) described in detail the mature larva and pupa of *Smicronyx fulvus* LeConte, 1876, and Korman & Oseto (1984) reported about sexual dimorphism of its pupae (without any other details). The mature larva of *S. japonicus* was quite precisely described by Morimoto & Matoba (2009), whereas the description of larva and pupa of *S. balassogloi* Faust, 1885 (under the name of *S. roridus* Marsham 1952), provided by Agrawal (1984), lack some important details and pure illustrations.

Due to the economic importance of two North American species of sunflower seed weevils, *Smicronyx fulvus* and *S. sordidus* LeConte, 1876, developing in the seeds of *Helianthus annuus* L., biology and larval development of these species were examined more thoroughly (Oseto & Braness 1979b, Oseto & Korman 1986, Brewer 1991).

Smicronyx smreczynskii Solari, 1952, the species, which is treated in this contribution, is distributed in Europe from France (Gironde), Denmark, the Netherlands, Finland and Sweden through Poland, Hungary, Moldova, Bulgaria, Ukraine to Georgia and through Russia to Siberia (Kemerovo, Tuva) (Legalov 2010, Alonso-Zarazaga et al. 2023). This species has been collected on dodder, mainly *Cuscuta europaea* L. (Sorel 1971, Dieckmann 1986), and on *C. scandens* Brot. (syn. *C. australis* R. Br.) (Dauphin 2002, Haran 2014), which grow along riversides (*C. europaea*) and in moist meadows and other wetlands (both) (Haran 2014 and own observations).

2. Materials & Methods

All specimens were fixed in 75% ethanol and examined under an optical stereomicroscope (Olympus SZ60 and SZ11) with calibrated oculars. The following measurements of the larval instars were made: body length (BL), body width (BW) (at the third thoracic segment), width (HW) of the head capsule and its height (HH, measured from the apex to the epistoma). The pupal measurements included body length (BL), body width (BW) (at the level of the mid-legs), head width (HW) (at the level of the eyes), length of rostrum (RL) and width of pronotum (PW). Drawings and outlines were made using a drawing tube (MNR-1) installed on a stereomicroscope (Amplival) and processed by computer software (Corel Photo-Paint X7, Corel Draw X7).

Slide preparation basically followed May (1994). The larvae selected for study under the microscope were cleared in 10% potassium hydroxide (KOH), then rinsed in distilled water and dissected. After clearing, the head, mouthparts and body (thoracic and abdominal segments) were separated and mounted on permanent microscope slides in Faure-Berlese fluid (50 g gum arabic and 45 g chloral hydrate dissolved in 80 g distilled water and 60 cm³ glycerol) (Hille Ris Lambers 1950).

The photographs were taken using an Olympus BX63 microscope and processed with Olympus cellSens Dimension software. The larvae selected for SEM imaging (scanning electron microscope) were first dried in absolute ethanol (99.8%), then rinsed in acetone, treated by CPD (Critical Point Drying) and finally gold-plated. TESCAN Vega 3 SEM was used to examine selected structures.

The general terminology and chaetotaxy follow Anderson (1947), May (1994), and Marvaldi (1999, 2003); the antennae terminology follows Chaika & Tomkovich (1997) and Zacharuk (1985).

3. Results

3.1 Material studied, host species identification and habitat information

All larvae and pupae were obtained from galls on *Cuscuta campestris* Yunck. (Figure 3) in Northern Greece near Eratino close to Kavala airport (province of Eastern Macedonia and Thrace), in a small ruderal area, immediately adjacent to the road (at 40°55'58"N, 24°37'47"E), with a large cover of *Cuscuta* parasitizing on *Chondrilla juncea* L. or a very similar-looking plant species and on small plants growing close to the ground, perhaps grasses or annual Fabaceae (Figures 1, 2). The yellow-orange colour of the *Cuscuta* cover was noticed from the road. Other plant species present at this site: *Avena* spec., *Bromus* spec., *Eryngium campestre* L., *Foeniculum vulgare* Mill., *Juncus* spec., *Sambucus ebulus* L., *Solanum elaeagnifolium* Cav., further monocots, annuals and others. The ruderal habitat close to the road was limited by a semiruderal grass and rush zone and by shrubs and trees (*Pinus*) (Figure 1).



Fig. 1. Habitat of *Smicronyx smreczynskii*, a weakly disturbed ruderal place with temporarily wet parts south of Eratino, its host plant (*Cuscuta campestris*), conspicuous from afar by its orange colour, and the accompanying vegetation with violet flowers of *Solanum elaeagnifolium*.



Fig. 2. *Cuscuta campestris* on *Chondrilla juncea* from the study site in Northern Greece. Identification was based on orange stem colour, morphology of the flower (acute petals, well visible tube scales, styles of equal length, head-shaped stigma), and on the shape of the fruit. The small leaves of *Chondrilla juncea* were already withered.

For identification of the *Cuscuta* species, the following sources were used:

- The Flora of Greece website to define and limit the possible *Cuscuta* species. (<https://portal.cybertaxonomy.org/flora-greece/content>)
- The key of Rothmaler (1976) and the atlas of Rothmaler et al. (1991) with detail drawings of many *Cuscuta* species to identify the species.
- The key of Meikle (1977) to exclude certain species, not present in the key of Rothmaler (1976): *Cuscuta monogyna* Vahl, *C. palaestina* Boiss. and *C. planiflora* Ten.
- The pictorial key of Meyer (<http://www.blumeninschwaben.de/>) allowed to distinguish between the similar species *C. campestris*, *C. scandens* and *C. suaveolens* Ser. and was used on 17.6.2023.

Cuscuta approximata Bab. was excluded by its yellowish, rarely reddish stem colour, and *C. brevistyla* A. Rich. by its usually short style (Jahn & Schönfelder 1995).

Important characters for species recognition: stem orange, ovary with two styles of same length, stigma head-shaped, broad, petals triangular and acute (not rounded at tip), scales in the tube of the corolla well visible, fruit spherical, flat (Figure 2).

This interaction is not documented by Gaertner (1950). She only listed *Cuscuta gronovii* Willd. as a parasite of *Chondrilla juncea*.

Winkelmann (2019), who re-collected this species three years later, obviously at the same locality after a short verbal description, did not report about the finding circumstances: neither about collecting time nor

about locality data (except "North of Greece"); furthermore he was unable to identify the *Cuscuta* species, its host plant, and to describe its habitat or the accompanying flora. Therefore, this data gap can be closed or reduced now with this publication.

Larvae: 4 exx. on 31.05.2016.

Pupae: 3 exx. ♂, 1 ex ♀, 2 exx. on 31.05.2016.

Two adult weevils were received some days later. Julien Haran confirmed species identity.



Fig. 3. Different galls of *Smicronyx smreczynskii* on *Cuscuta campestris*.

3.2 Morphological description

Larval morphology of *Smicronyx smreczynskii*

BL: 1.90–2.20 mm; BH: 0.77–0.93 mm (at the level of metathorax); HW: 0.43–0.45 mm.

Live larva pure white, with light yellow head capsule. Body moderately stout, slightly curved, rounded in cross section (Figure 4A, B). Prothorax prominent, pronotal shield invisible; meso- and metathorax similar

to each other, together as wide as prothorax, divided dorsally into two lobes (prodorsal and postdorsal lobes almost equal in size). Pedal lobes of thoracic segments weakly isolated, flat. Abdominal segments I–III of similar size, smaller than metathorax. Segments IV–IX tapering towards posterior body end. Abdominal segments I–VII divided into prodorsal and postdorsal folds of similar size; segment VIII dorsally partially divided; segment IX dorsally undivided. Spiracular, epipleural and pleural lobes of segments I–VII conical, well isolated; on segment VIII spiracular lobe fused to dorsal lobes. Segment IX reduced, divided into lateral, pleural and sternal lobes. Abdominal segment X completely hidden inside previous segment, divided into four lobes, almost of equal

size. Anus situated terminally. Body sparsely covered with minute asperities.

Chaetotaxy: setae various in length, hair-like, transparent (what made observation very difficult). Thorax (Figure 4C): prothorax with 8 *prns* (six elongated, 2 short), 2 elongated *ps* and 1 minute *eus*. Meso- and metathorax each with 1 minute *prs* and 3 *pds* (2 elongated and 1 short), 1 minute *as*, 2 *ss*, various in length, 1 elongated *eps*, 1 elongated *ps* and 1 minute *eus*. Pedal areas of thoracic segments each with 5 *pda* of various length. Abdomen (Figure 4D, E): segments I–VII with 1 short *prs*, 3 *pds*, various in length, 2 *ss* (one short, one elongated), 2 *eps*, various in length, 2 *ps* of equal length, 1 elongated *lsts* and 2 minute *eus*. Abdominal segment VIII with 2 *pds* and 2 *eps*, both various in length, 2 *ps* of equal length, 1 elongated *lsts* and 2 minute *eus*. Abdominal segment IX with 3 *ds*, various in length, 2 minute *ps* and 2 minute *sts* (Figure 4D, E). Abdominal segment X without setae. All spiracles bicameral; thoracic (Figure 4F) placed laterally between pro- and mesothorax; abdominal spiracles (Figure 4G) placed antero-medially on segments I–VII, on segment VIII medio-dorsally.

Head capsule. Head (Figure 5A–D) narrowed bilaterally; endocarina very short, reaches 1/6 of the frons; frontal sutures distinct along entire length up to antennae; stemmata (*st*) visible, placed at the end of frontal suture. Setae of head minute to elongated, hair-like, transparent. Cranial setae: elongated *des*₁ placed medially, elongated *des*₂ placed posterolaterally, elongated *des*₃ placed on the margin of frontal suture, *des*₄ absent, elongated *des*₅ placed anterolaterally, *fs*₁ and *fs*₂ absent, minute *fs*₃ placed anteromedially, elongated *fs*₄ placed anteromedially, and elongated *fs*₅ placed anterolaterally, medium *les*₁ placed posterolaterally, elongated *les*₂ placed anterolaterally, and two minute *ves*, postepicranial area with 6 *pes*. Antennae (Figure 5E) placed on each side at anterior margin of head, close to internal border of frontal suture; membranous basal segment convex, semi-spherical, bearing conical, moderately elongated sensorium and 2 sensilla styloconica (*ss*).

Mouthparts. Clypeus (Figure 6A, B) approximately 3.5 x longer than wide, with two *cls* relatively short, placed posteriorly, and single sensillum (*clss*) placed posteriorly between *cls*. Transverse, median furrow reaching 3/4 of the clypeus. Anterior margin of clypeus distinctly concave. Labrum (Figure 6A, B) approximately 2.5 x longer than wide, anterior margin sinuated; *lrs*₁ very long, placed posteromedially, *lrs*₂ elongated, placed anteromedially and short *lrs*₃, placed posterolaterally. Epipharynx (Figure 6C) with 3 prominent *als* and 2 medium *ams*, two *mes*, various in size, placed between labral rods. Labral rods (*lr*) nearly reniform, slightly converged posteriorly (Figure 6C); mandible (Figure 7) narrowed, bifid, apical tooth much higher than internal one. Cutting edge smooth, with very small additional protuberance. Setae: *mds*₁ and *mds*₂ minute, hair-like, both placed medially in shallow pits. Maxillolabial complex (Figure 8A, D) very wide, on stipes with 1 elongated *stps*, and 2 elongated *pfs*. Mala with 5 digitate *dms*, various in size (1st to 3rd elongated, 4th and 5th short) and a group of 4 *vms*, various in size and shape (1st and 2nd sharp, elongated, 3rd small, digitate, 4th sharp, medium-sized). Maxillary palpi with two palpomeres; basal palpomere distinctly wider than distal one. Length ratio of basal and distal palpomeres almost 1:1. Basal palpomere with minute *mps* and 1 pore (Figure 8B, C). Distal palpomere with 1 digitiform sensillum (*ds*) and a group of 11 apical sensilla basiconica and a single sensillum ampullaceum on the terminal receptive area (*tra*) (Figure 8E). Surface of mala smooth. Labium with wide, cup-shaped prementum, with 1 elongated *pms*, placed medially (Figure 8D). Ligula concave, with 2 minute *ligs*. Surface of labium smooth. Premental sclerite tridentate; postmentum very wide, membranous with 3 *pms*: short *pms*₁ situated posterolaterally, elongated *pms*₂ placed mediolaterally and medium *pms*₃ placed posteriorly. Labial palpi one-segmented. Each palpus with single pore, and a group of 12 apical sensilla basiconica, and 2 ampullacea on the terminal receptive area (Figure 8F). Surface of labium covered with prominent nodular cuticular processes.

Description of the pupa of *Smicronyx smreczynskii*

Male - BL (body length): 2.05 mm; BW (body width): 1.05 mm; HW (head width): 0.275 mm; RL (rostrum length): 0.50 mm; PW (pronotum width): 0.64 mm.

Female - BL: 2.35–2.50 mm; BW: 1.12–1.25 mm; HW: 0.31–0.35 mm; RL: 0.65–0.70 mm; PW: 0.69–0.72 mm.

General habitus and chaetotaxy (Figure 9A, B). Body white, slender, head and rostrum cuticle covered with fine asperities (Figure 9F). Rostrum elongate, in ♂ 3.8x, in ♀ 4.0x as long as wide, reaching mesocoxae. Pronotum 1.75 x as wide as long, sinuated laterally (Figure 9C–E). Mesonotum and metanotum almost of same size. Abdominal segments I–VI of equal length, segment VII semicircular, segment VIII narrow, segment IX terminal, with urogomphi (*ur*) laterally situated, slightly recurved, moderately elongate, each with sclerotized, sharp apex (Figure 10A–F). Spiracles placed dorso-laterally on abdominal segments I–VI, functional on segments I–V, vestigial on segment VI. Chaetotaxy (numbers of setae given for one side of the body): setae variable in size, hair-like, all placed on prominent protuberances. Rostrum with 1 minute *es*, 1 medium *rs*, and 2 relatively elongated *pas*. Head with 1 minute *sos* and 1 prominent *vs* (Figure 9C, D). Pronotum with 1 elongated *as*, 1 elongated *ls*, 2 *s/s* (one medium, one elongated), 2 *ds* (one medium, one minute), and 2 elongated *p/s*. Meso- and metathorax with 2 medium-sized setae, placed medially on dorsum (Figure 9E). Abdominal segments I–VI with 3 elongated setae (*d*₁ and *d*₂ placed anteromedially, *d*₃ anterolaterally). Segments VII and VIII with 2 setae dorsally each. All dorsal setae robust, placed on elongate protuberances (Figure 10B–D). Each side of segment IX with moderately elongate urogomphus. Each urogomphus with 2 setae (*v*_{1,2}) of various lengths (Figure 10E, F). Lateral parts of abdominal segments I–VIII each with a single minute seta (Figure 10A). Ventral parts of abdominal segments without setae. Each femur with one elongated, hair-like seta (Figure 10A).

Biological data of American *Smicronyx* species

There are over 70 named *Smicronyx* species in North America north of Mexico (Anderson 2002). According to Anderson (1962), most *Smicronyx* species from Asteraceae develop in or between the seeds, and species from *Cuscuta* (Convolvulaceae) in stems, galls or fruits. He summarized information about all weevil-plant interactions with special focus on breeding, which usually may be regarded as well-founded host plant interactions or host plant confirmation (Tab. 1).

Table 1. Host plants of *Smicronyx* species in North America according to Table 1 of Anderson (1962) and Anderson et al. (2006)

Asteraceae: *Ambrosia* (2 *Smicronyx* (*Pseudomicronyx*) species), *Haplopappus* (1 *Smicronyx* (*Desmoris*) species), *Helianthus* (2 *Smicronyx* (*Desmoris*) species), *Helenium* (2 *Smicronyx* (*Pachyphanes*) species), *Iva* (2 *Smicronyx* (*Pseudomicronyx*) species): 9 species from subgenera apart from *Smicronyx* s. str.
Convolvulaceae: *Cuscuta* (7 *Smicronyx* (s. str.) species)
Euphorbiaceae: *Croton* (1 *Smicronyx* (*Pachyphanes*) species)
Fabaceae: *Vachellia* (1 *Smicronyx* (s. str.) species)
Malvaceae: *Abutilon* (1 *Smicronyx* (s. str.) species), *Callirhoe* (1 *Smicronyx* (*Pachyphanes*) species)

Anderson (1962) summarized the number of observations of *Smicronyx* species on certain plant genera. In *Rudbeckia*, which was not listed as host plant, there are six observations of an association with *Smicronyx* species. In *Parthenium* there were only three observations, but it was recognized later as a host plant of *Smicronyx lutulentus*, demonstrating that there may be further undetected host plants of *Smicronyx* species missing in Anderson's list.

In many cases it may be sufficient to list a plant as host plant without any breeding efforts, if there is information about characteristic feeding tracks or direct feeding of the weevil (which may be exceptionally also take place on non-host plants, too). A regular presence on a certain plant species may be another criterion, if a refuge status of the plant or other reasons can be excluded (e.g., Colonnelli & Osella 1998; or the "Aufbäumen" or "Aufbaumen" of Apionids, climbing or flying to trees for biotope change; Dieckmann 1977: p. 17).

There are two cases of introductions of American *Smicronyx* species: a species from *Parthenium* (Asteraceae) was introduced to South Africa for reasons of biological control (Haran 2021), and another one from Texas, living on *Ambrosia* (Asteraceae), was found in Krasnodar (Anderson et al. 2006), demonstrating that *Smicronyx* species from Asteraceae are not original species of the "Old World".

In 22 of 78 North American *Smicronyx* species there are well-founded host plant data. This may seem low, but it is regarded representative for the *Smicronyx* species of this area, even if some species living on further plant families are overlooked. Numerous undescribed species occur in Mexico and Central America (Prena, pers. comm.).

→ There are data from 10 species, which develop on Asteraceae (from 6 genera): seven from Convolvulaceae (exclusively on *Cuscuta*), one from Euphorbiaceae (*Croton*), one from Fabaceae (*Vachellia*) and two from Malvaceae (*Abutilon* and *Callirhoe*).

→ Main host plants groups are Asteraceae and *Cuscuta*. Anderson (1970) described a possible mechanism, how the host plant spectrum was expanded from *Cuscuta* to Asteraceae: Due to the parasitism of *Cuscuta*, the inclusion of a new host plant of a *Smicronyx* species was always directed from *Cuscuta* to other plants and not vice versa. Anderson (1970) observed *Smicronyx* larvae boring and moving in the stems of *Cuscuta* host plants, where they fed and pupated afterwards. It can be stated that

- Asteraceae host North American *Smicronyx* species from three other subgenera than *Smicronyx* sensu stricto.
- Malvaceae and Fabaceae host one *Smicronyx* sensu stricto species each. Both host plant genera, *Abutilon* and *Vachellia*, prefer steppe and semidesert habitats.
- *Cuscuta* is present in warm and temperate zones of North America; usually habitats are unshaded.

4. Discussion

Morphology of preimmature instars

Due to the fact that the paper of Urban (1914) contains only several drawings of larvae and neither a description nor an illustration of the general chaetotaxy of the body, it is impossible to decide, whether the description refers to *S. jungermanniae* or, as suggested by Dieckmann

(1986) and Heijerman & Alders (2000), to *S. smreczynskii*. Some discrepancies between the morphology of *S. smreczynskii* and *S. jungermanniae* of Urban (1914) may be the result of using different nomenclature of chaetotaxy.

Moreover, the rather imprecise and unillustrated description of the pupa does not allow to confirm their identity. On the other hand, the paper of Korman & Oseto (1984) presented the sexual characters of *Smicronyx fulvus* pupae, which are in fact typical for all known pupae of weevils: male gonothecae undivided, female gonothecae divided. According to Korman & Oseto (1984), tubercles on the subcontiguous lobes seem to be diagnostic for *S. fulvus*. Other details about chaetotaxy are missing.

Taking into consideration the descriptions of *Smicronyx menozzii* by Frilli (1966), *S. japonicus* by Morimoto & Matoba (2009), and *S. fulvus* by Oseto & Braness (1979a), the study of *S. smreczynskii* allows to regard the below-listed characters as generally valid for larvae of the genus *Smicronyx*:

(1) head more or less narrowed; (2) fs_{1-3} minute or absent, fs_4 , fs_5 elongate; (3) stemmata present; (4) endocarina short; (5) mandible narrowed, bifid, teeth unequally high; (6) epipharynx with 2 *ams* and 2-3 *als*; (7) 2 *mes* (mes_1 much longer than mes_2); (8) labial palpi one-segmented; (9) all spiracles bicameral; (10) dorsal lobes of abdomen divided into pro- and postdorsal lobes; postdorsal lobe divided into two folds, various in size; (11) mature larva with: 8-12 *prms*, 3-5 *pds*; 2 *ss*, 2 *eps*, 2 *ps*, 1 *lsts* and 2 *eus*.

And for pupae: (1) body rather elongate; (2) ur present, rather short; (3) head with: 1 *vs*, 0-2 *sos*; (4) rostrum with: 1-2 *pas* and 1 *rs*; (5) pronotum with: 1 *as*; 2 *ds*; 2 *pds*; 1-2 *sls*; 1-2 *ls*; (6) meso- and metanotum with 2 *ds*; (7) abdominal segments 1-6 with 3 *ds* each; (8) each femora with a single seta.

These differences are used here to provide keys to *Smicronyx* larvae and pupae:

Key to mature larvae of three *Smicronyx* species

1. Clypeus with transverse, median furrow reaching 3/4 of its length; epipharynx with 3 *als*; labral rods nearly reniform; pronotum with 8 *prms*, abdominal segments I-VII with 3 *pds* ***S. smreczynskii***
- Clypeus without transverse, median furrow; epipharynx with 2 *als*; labral rods elongated; pronotum with 9-11 *prms*, abdominal segments I-VII with 4-5 *pds* **2**
2. fs_2 medium; *clss* absent; pronotum with 9 *prms*, abdominal segments I-VII with 4 *pds* and without *prs* ***S. menozzii***
- fs_2 minute or absent, *clss* present; segments I-VII with 5 *pds* and single *prs* **3**
3. Head suboval, fs_2 minute, pronotum with 10 *prms* ***S. fulvus***
- Head distinctly narrowed bilaterally; fs_2 absent, pronotum with 11 *prms* ***S. japonicus***

Key to pupae of *Smicronyx* species

1. Rostrum with 1 *es* and 2 *pas*; head with 1 *sos* ***S. smreczynskii***
- Rostrum without *es* and 1 *pas*; head with 0 or 2 *sos* **2**
2. Head with 2 *sos*; pronotum with 1 *ds* and 3 *pds*; gonothecae without tubercles on subcontiguous lobes ***S. menozzii***
- Head without *sos*; pronotum with 2 *ds* and 2 *pds*; gonothecae with tubercles on subcontiguous lobes ***S. fulvus***

About distribution and host plant use of *Smicronyx* species

The genus *Smicronyx* is distributed over great parts of the world, but its range and its host plant use are not to explain at first view (Rheinheimer & Hassler 2010, p. 589) and may lead far back into the past. Some facts and conclusions about the evolution of host plant use are presented here: The range of the genus comprises the Palaearctic region, with a main occurrence in the southern parts (e.g., Mediterranean

region, North Africa, Near East), Pakistan, Central Asia to Japan, North and Central America, and a few isolated places in South America and in Northern Australia. From Siberia, South America, the Oriental region (Southeast Asia) and from Australia only a small number of species were recorded, five from Siberia (2 exclusive), three from South America, eleven from the Oriental region, and two described (and a few undescribed) species from Australia (Anderson 1962, Caldara et al. 2014, Karasyov & Okrajko 1998, Legalov 2010) (Tab. 2).

Table 2: Number of described *Smicronyx* species in different parts of the world (all used sources cited in the text)

	Europe	Africa	Asia I: Near East and Central Asia	Asia II: Japan	Asia III: SE Asia	North Australia	North America	South America
A	22	34	20	5	10	2	78	3
B	10	26	14	2	8	2	78*	3

A: Total species numbers; B: Number of exclusive species; *: Central America included. American and Palaearctic possible radiation centres coloured.

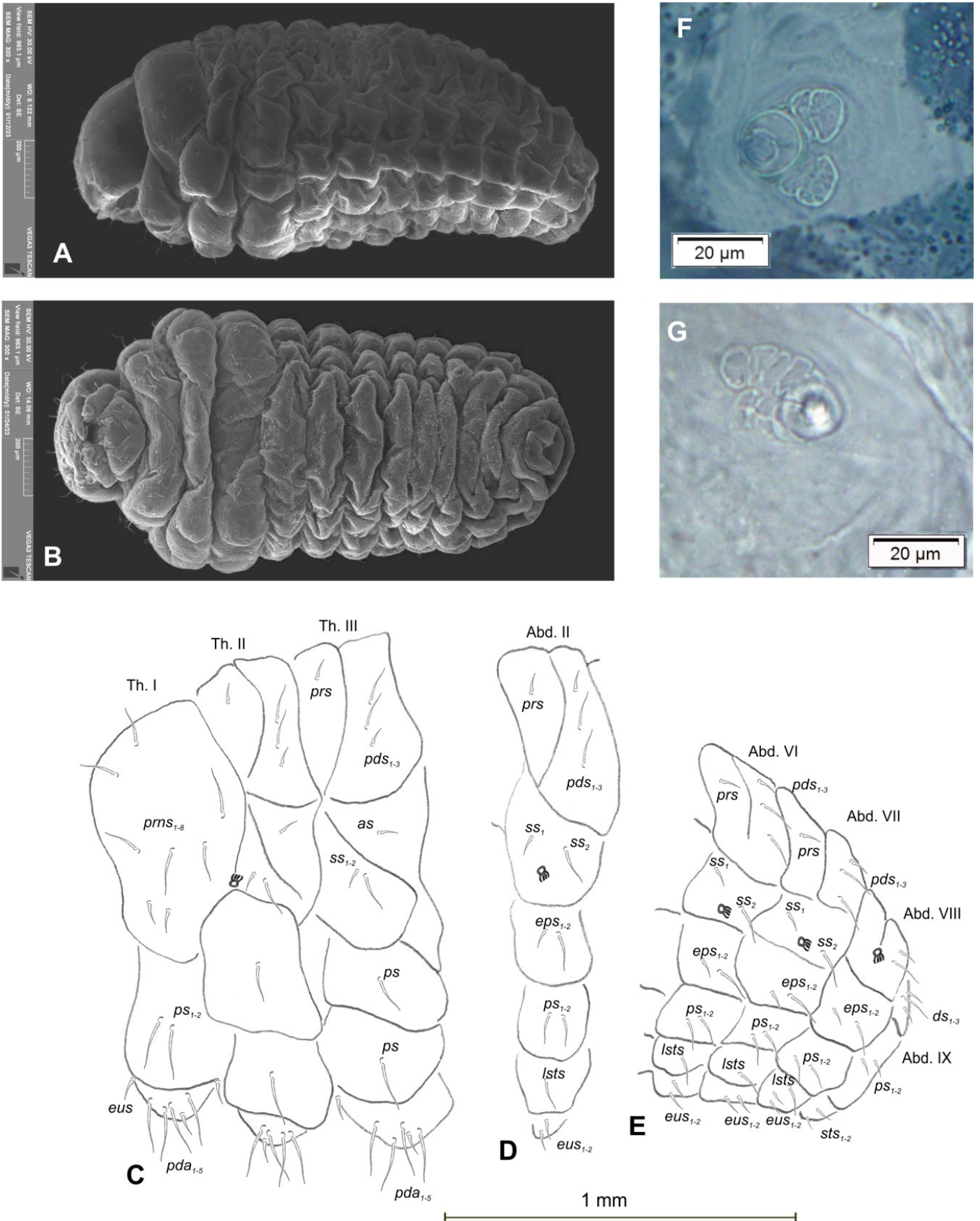


Fig. 4A-F: **A, B:** *Smicronyx smreczynskii* mature larva, habitus (SEM photos); **C-E:** chaetotaxy (drawings); **F:** thoracic spiracle; **G:** abdominal spiracle (photos). Abbreviations: Th. I–III—thoracic segments 1–3, Abd. I–X—abdominal segments 1–10, setae: *ds*—dorsal *eps*—epipleural, *eus*—eusternal, *ps*—pleural, *pda*—pedal, *pds*—postdorsal, *prns*—pronotal, *prs*—prodorsal, *ss*—spiracular, *sts*—sternal.

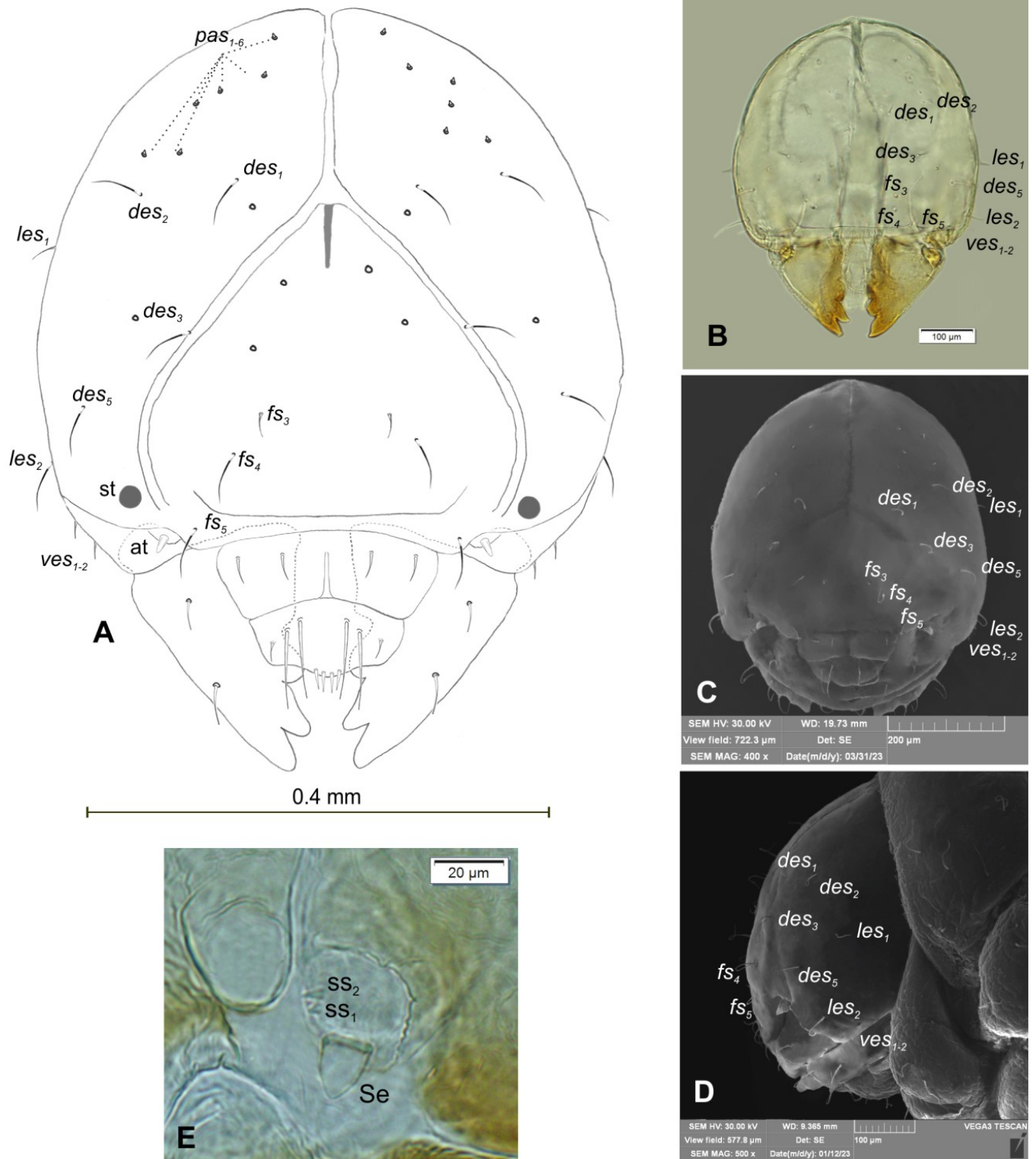


Fig. 5A-E. *Smicronyx smreczynskii* mature larva, head and antenna: A: chaetotaxy (drawing); B: chaetotaxy (photo); C, D: chaetotaxy (SEM photos); E: antenna (photo). Abbreviations: at – antenna, Se – sensorium, ss – sensillum styloconicum, setae: *des* – dorsal epicranial, *fs* – frontal, *les* – lateral epicranial, *pas* – postepicranial, *ves* – ventroepicranial.

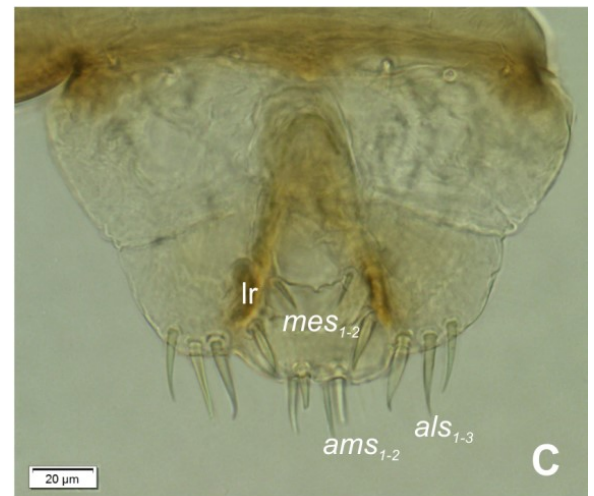
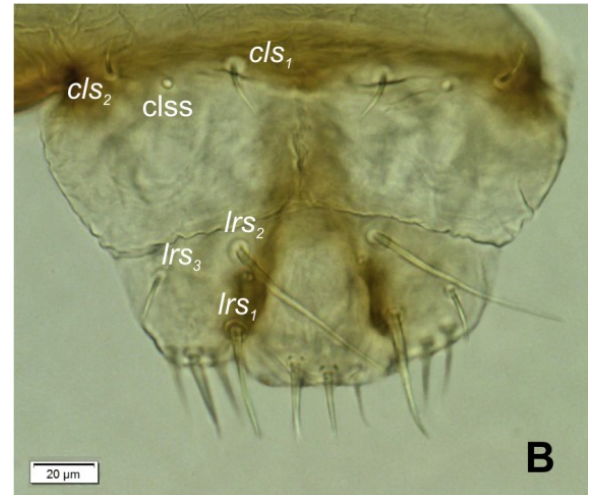
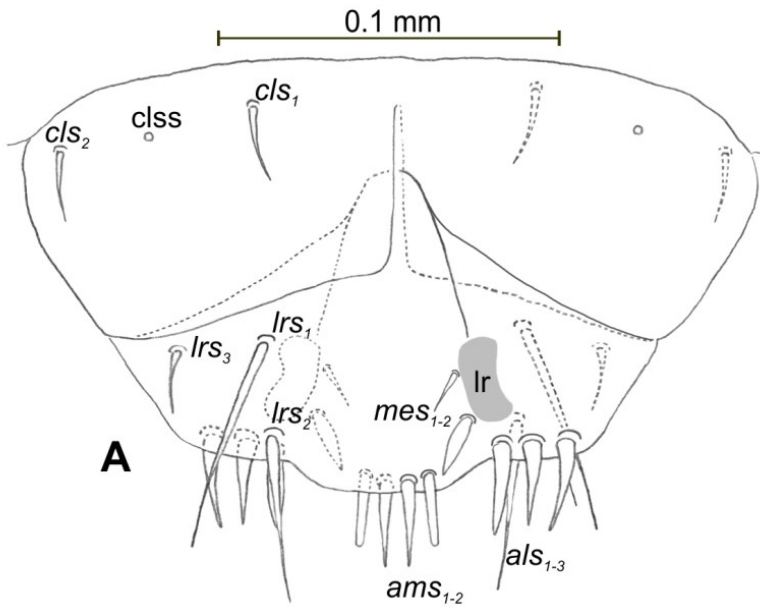


Fig. 6A-C. *Smicronyx smreczynskii* mature larva, mouthparts: **A:** chaetotaxy (drawing); **B:** chaetotaxy of clypeus and labrum (photo); **C:** chaetotaxy of epipharynx (photo). Abbreviations: clss – clypeal sensorium, setae: *ams* – anteromedial, *als* – anterolateral, *cls* – clypeal, *lrs* – labral.

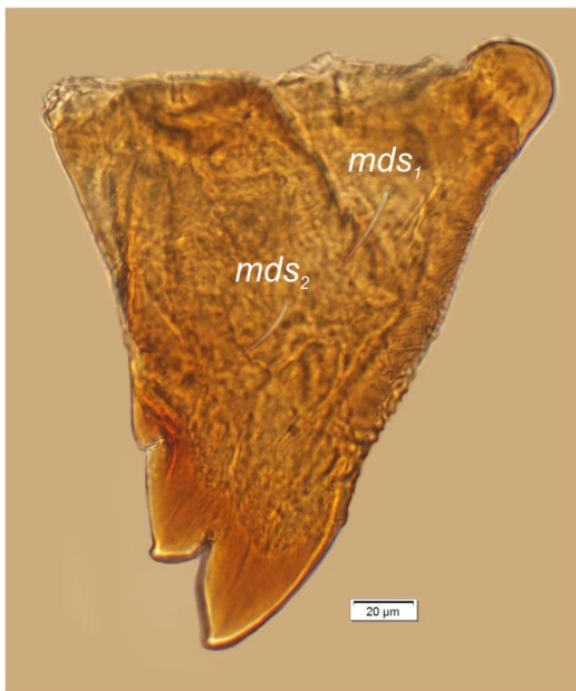


Fig. 7. *Smicronyx smreczynskii* mature larva, left mandible. Abbreviation: *mds* – mandibular seta.

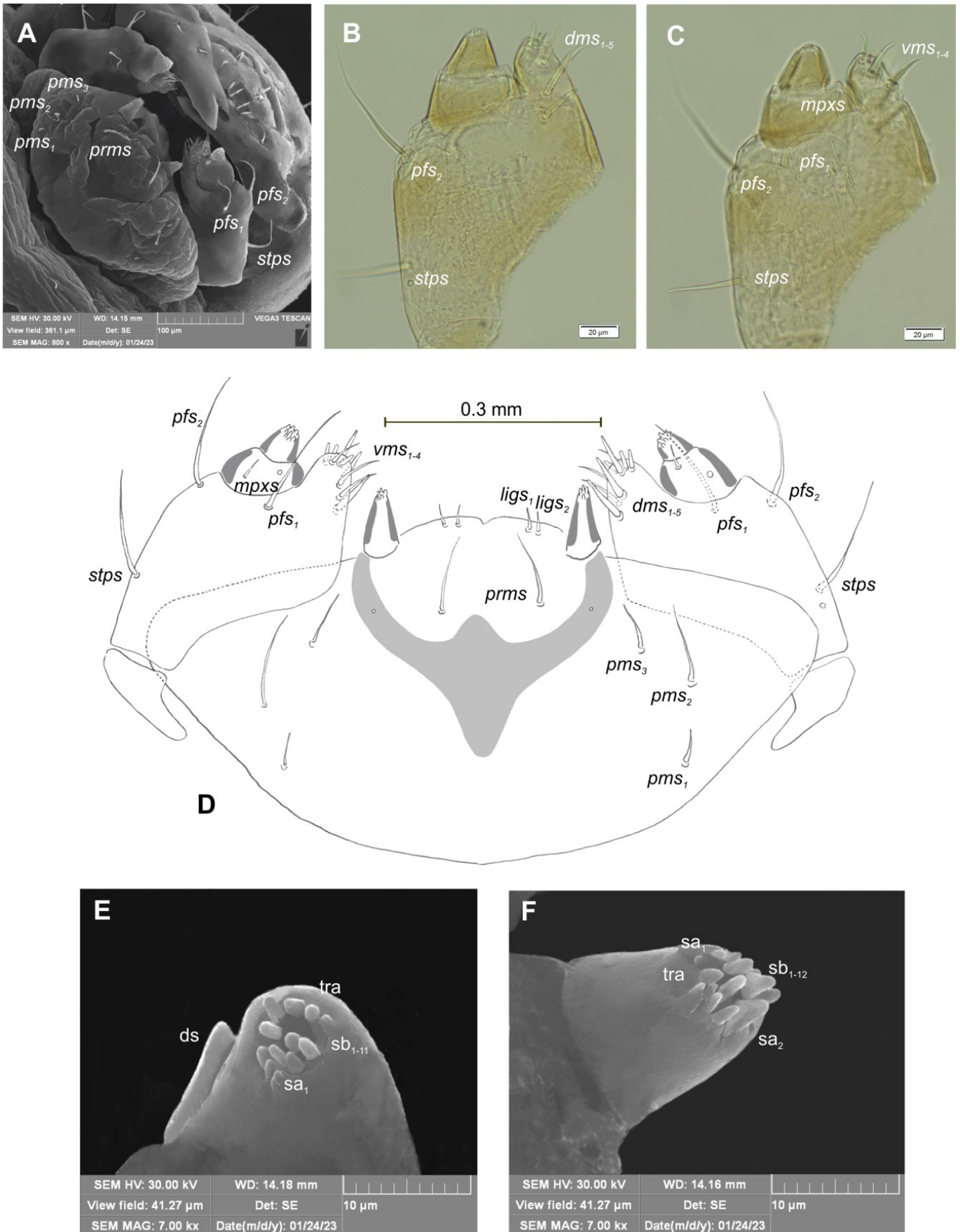


Fig. 8A-F. *Smicronyx smreczynskii* mature larva, mouthparts: **A:** maxillolabial complex (SEM micrographs); **B, C:** apical part of maxilla (pictures); **D:** maxillolabial complex, ventral aspect (drawing); **E:** apical part of distal maxillary palp (SEM micrograph); **F:** apical part of labial palp (SEM micrograph). Abbreviations: ds – digitiform sensillum, sa – sensillum ampullaceum, sb – sensillum basiconicum, tra – terminal receptive area, setae: *dms* – dorsal malar, *ligs* – ligular, *mbs* – malar basiventral, *mbs* – maxillary palp, *pfs* – palpiferal, *prms* – prelabial, *pms* – postlabial, *stps* – stipal, *vms* – ventral malar.

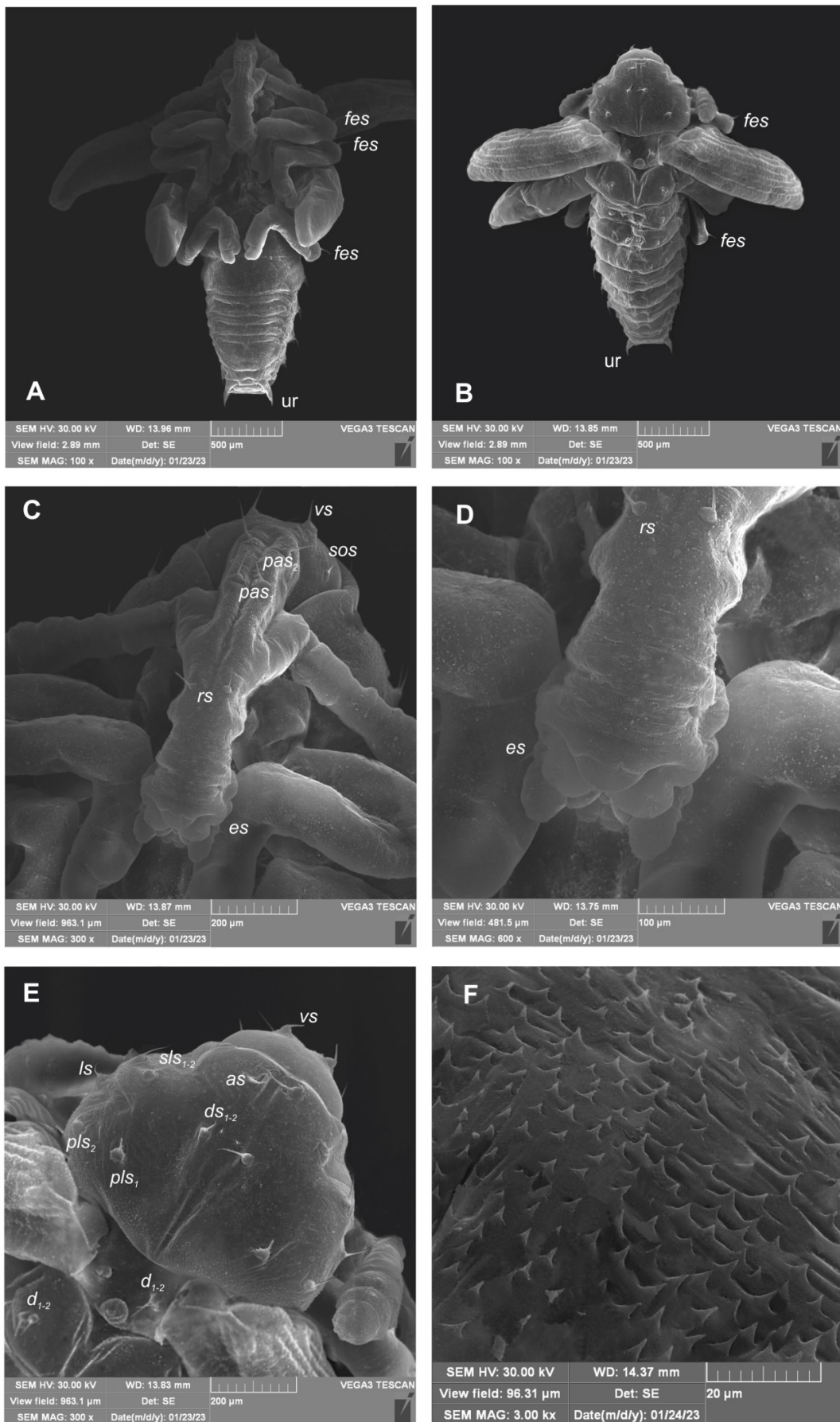


Fig. 9A-F. *Smicronyx smreczynskii* pupa, habitus (SEM micrographs): A: ventral view; B: dorsal view; C, D: head and rostrum; E: prothorax, dorsal view; F: prothorax, structure of cuticle. Abbreviations, setae: as – apical, d – dorsal, ds – discal, es – epistomal, ls – lateral, pas – postantennal, p/s – posterolateral, rs – rostral, s/s – superlateral, sos – superorbital, vs – vertical.

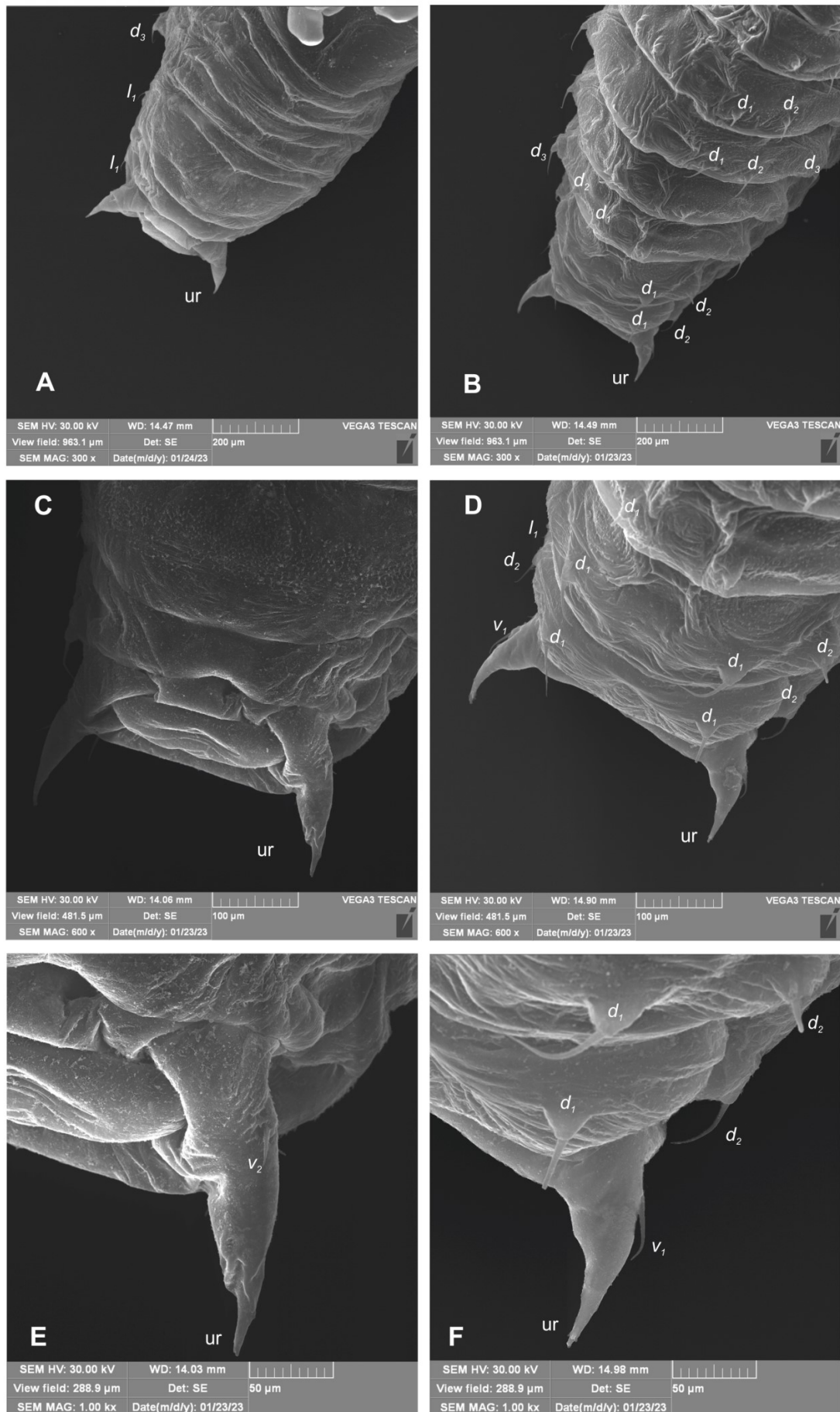


Fig. 10A-F: *Smicronyx smreczynskii* pupa, abdomen and urogomphi (SEM micrographs): **A, C**: abdomen, ventral view; **B, D**: abdomen, dorsal view; **E**: urogomphus, ventral view; **F**: urogomphus, dorsal view. Abbreviations: ur – urogomphus, setae: *d* – dorsal, *l* – lateral, *v* – ventral.

Smicronyx s. str. and the closely related genus (or subgenus of *Smicronyx*) *Afrosmicronyx* is distributed over great parts of Africa (North Africa as part of the Palaearctic region, the Sahel zone, East Africa, South Africa) (Alonso-Zarazaga & Lyal 1999, Haran 2018, 2021). Host plants in Europe, Asia and Africa are in the families Convolvulaceae (genus *Cuscuta* only), Gentianaceae and Orobanchaceae, whereas in America Asteraceae play the most important role: Anderson (1962) listed 52 *Smicronyx* species in four subgenera (*Desmoris*, *Pachyphanes*, *Pseudomicronyx*, and *Smicronyx* s.str.) from North America. Nine species live on 6 genera of Asteraceae. Seven American species are known to live on *Cuscuta* (Convolvulaceae) like in Europe, Africa and Japan, where most species inhabit this genus. In North America, *Smicronyx* s.str. use additionally: Euphorbiaceae (1 species on *Croton*), Fabaceae-Mimosoideae (1 species on *Vachellia*), and Malvaceae (one species each on *Abutilon* and on *Callirhoe*). The American host plants are expanded over the following five orders (most important bolded): **Asterales**, Fabales, Malpighiales, Malvales, and **Solanales** (see APG 2016).

American *Smicronyx* of the nominotypical subgenus, which is present in the Palaearctic region, too, inhabit with one exception *Cuscuta*. The other American *Smicronyx* species were placed in other subgenera or inhabit plant genera that do not occur in the Palaearctic region (except introduced).

From these data it can be stated that genus *Smicronyx* has a North American radiation centre with four subgenera there and a spread of the species over five host plant families from five orders.

In the "Old World" the situation is rather different. Host plant use in the Palaearctic region and in Africa obviously remained restricted to three orders of Lamiales: **Solanales** (with Convolvulaceae), **Gentianales** (with Gentianaceae), and **Lamiales** (with Orobanchaceae). This picture could at best change only gradually with research into host plant interactions of the rather great number of unknown relations.

Palaearctic and African *Smicronyx* s. str. mainly use *Cuscuta* species as host plants, but a few species are also found on Gentianaceae (genera see below), Orobanchaceae (*Buchnera* and *Striga*) and on *Convolvulus* and an unidentified genus of Convolvulaceae (Karasyov 1995, Haran 2018).

The subgenus *Chalybodontus* and the closely related genera *Afrosmicronyx* (up to 2013 a subgenus of *Smicronyx*) and *Sharpia* may be involved in these evolutionary processes, as they use the same host plant families like *Smicronyx* (*Smicronyx*) species. *Afrosmicronyx* and *Smicronyx* (*Chalybodontus*) species live, as far as it is known, on Orobanchaceae (*Cistanche*, *Cynium*, *Orobancha*, *Phelipaea*, *Sopubia*, and *Striga*) (Hoffmann 1958, Haran & Perrin 2017, Haran 2018, 2021). The mainly Asian, but also African genus *Sharpia* is known to live on *Convolvulus* species and *Cressa cretica* L. (Convolvulaceae) (Friedman 2017, Haran et al. 2017), demonstrating the strong limits and the close relations of these Smicronychini genera and subgenera.

In Europe three species, *Smicronyx funebris* Tournier, 1874, *S. reichii* (Gyllenhal, 1836) and *S. swertiae* Voss, 1953, live on Gentianaceae (*Centaurium*, *Gentianella* (incl. *Gentianopsis*), and *Swertia*). In South Africa and Japan one further species each, *Smicronyx san* Haran, 2021, and *S. gentianae* Morimoto & Kojima, 2007, are known to use this family, too (host plants in Africa are *Chironia*, *Orphium*, and *Sebaea* and in Japan *Gentiana*; Haran 2021, Morimoto & Matoba 2009). Two of five Japanese species live on *Cuscuta*, one on *Gentiana* (*G. scabra* Bunge), and in two species the host plants are unknown.

It is unknown, which relevant chemical compounds are common to all three plant families and which mutation may have happened to enable this conspicuous inclusion of two new host plant families. An important precondition may have been same use of dry and warm habitats with *Cuscuta* and with certain species of Gentianaceae and Orobanchaceae, but it does not explain the exclusion of many other plant families, which are also regularly attacked by *Cuscuta* species, see for example the list of Gaertner (1950).

It is a striking fact that there are at least two groups of plants, the Gentianaceae and the Orobanchaceae families, which are not inhabited in North America by any *Smicronyx* species, and, vice versa, in the Palaearctic Asteraceae, Euphorbiaceae, Malvaceae and Fabaceae are not used by any *Smicronyx* species. This may be also helpful to recognize introduced species.

These data show that there was an independent radiation in the Old World and that both are linked by a *Smicronyx* sensu stricto species from *Cuscuta*, which is regarded as the basic plant genus for these evolutionary processes in the "Old" and in the "New World".

Some more hypothetical ideas about the natural history of *Smicronyx* species

Only a few or perhaps a single species from *Cuscuta* may have spread from America to the Old World or the other way round. The first records of a *Smicronyx* or a Smicronychini species have been backdated to the early Oligocene (Alonso-Zarazaga & Lyal 1999).

The *Smicronyx antiquus* record of Förster (1891) from the French locality of Brunstatt (close to the German and Swiss borders) is from the 'lowest Middle Oligocene' ("unterstes Mitteloligocän"). This historical period, no longer in use in current time scales, is now part of the Rupelium (Gradstein et al. 2004). It may be backdated to around 30 – 31 million years BC (see for example Eberle et al. 2017). Legalov (2020) confirmed the tribe Smicronychini but set *Smicronyx* in quotations marks by this expressing some doubt on genus assignment. The first record of a Smicronychini species, *Smicrorhynchus mcgeeii* Scudder (1893) from Florissant, Colorado, may be a few million years older and is backdated to early Oligocene, too.

Recently, *Smicronyx* species are usually to find at nearly any place with *Cuscuta* species with high probability (predictability), especially in dry and warm areas. Haran et al. (2017) listed six *Smicronyx* (s. str.) and one *Smicronyx* (*Chalybodontus*) species from Israel, most of them from many sites. A low number of species, such as *S. coecus* (Reich, 1797) and *S. smreczynskii*, inhabit *Cuscuta* species in moist habitats, too, and they are distributed further to the North; but likewise, their habitats have to be unshaded. During Middle Oligocene water-land distribution was similar as today with a few exceptions, which are not relevant in this context. The average temperature was around 5 ± 2 °C above today's temperature (see Hansen et al. 2013). Hence, climate should have been warm enough, at least temporarily, to allow species adapted to lower temperatures, such as *Smicronyx smreczynskii* or *S. coecus* or their ancestors, to spread from the northern parts of North America to the Palaearctic region over Alaska and Yakutia. In any case, it should be a rare event in such small species of mainly warm regions (most of them range between 2 and 3 mm).

A preference for warm and often dry areas can be recognized in North America as well as in the Palaearctic and Africa (see maps of Anderson 1962 and most of the localities given by Haran 2021). The absence from great parts and the presence in only two disjunct areas of South America is another interesting fact: very probably radiation and main spread of the species did not occur before a land bridge between North and South America was present. Unfortunately, the time period, when a land bridge was formed between North and South America is under debate: 3 or 15 million years (Montes et al. 2012, O'Dea et al. 2016, Arnold 2017). Both dates coincide with the fact that they are much younger than spreading and first record in Central Europe and in North America between 30 to 35 million years ago.

The host plants in South America are unknown, but should also belong to one of the families, which are present in the climatically warmest parts of North America (and Mexico). The preference of warm and dry habitats of *Smicronyx* species can be additionally concluded from the absence in higher mountain areas, where Gentianaceae are present with high species numbers, e.g. in the Pyrenees, Alps, Balcans, Caucasus and Himalayas, but obviously no further *Smicronyx* species have evolved there; see for example the distribution of *Gentiana* in: Meusel & Jäger (2011).

It seems noteworthy that 3 (or 15) million years were obviously too short for a similar secondary evolution in South America compared with the Palaearctic region and Africa. In specialized stenophagous weevils, the adoption of new plant species, genera or even families, seems to be a rather slow process (see discussion for *Carpinus* in Sprick & Floren 2008: p. 248f.). They usually remain for long times, so to speak, stuck in their niches. There is a rather different situation on volcanic archipelagos, which, in a sense, act as an engine of evolution (see Machado 2007, Stüben 2022).

We tried to summarize information from different disciplines and are aware that there are still many data gaps (e.g. undescribed species, unknown plant relations, gaps in knowledge about distribution and

others). We look forward to seeing how future studies will change our perspective.

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