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# *Caeculus fedrae* sp. nov., a new fossil species of rake-legged mite (Acari: Caeculidae) from Baltic amber.

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## Original research

### ABSTRACT

*Caeculus fedrae* sp. nov. is described from a series of three exemplars from Baltic amber (Eocene). This species is the first fossil representative of the genus *Caeculus*, the first fossil species of the family not belonging to the genus *Procaeculus*, and the second species of the genus in Europe. Phylogenetic relationships, morphological features and paleoecological implications of the finding are discussed.

**Keywords** Caeculidae; Eocene; fossil; mite; Prostigmata

**Zoobank** <http://zoobank.org/5B10E209-4973-41A2-9815-4746C9AA5E1F>

## Introduction

Mites of the family Caeculidae Berlese 1883 are medium to large sized and common in arid habitats. One of the main characteristics are the spines on the legs, which are used to capture small arthropods (Walter *et al.* 2009). Currently, the family comprises about 100 extant species in seven accepted genera (Taylor *et al.* 2013). With regard to the fossil record, only four species are known, all belonging to the genus *Procaeculus*, from different amber deposits: *P. eridasonae* Coineau & Magowski, 1994, from Baltic amber (Middle Eocene); *P. dominicensis* Coineau & Poinar, 2001, from Dominican amber (Upper Eocene), *Procaeculus* sp. (Rivas *et al.* 2016) from Chiapas amber (Early Miocene) from mines in Simojovel, Mexico, and *P. coineaui* Porta, Proud, Franchi, Porto, Epele & Michalik, 2019, from Burmese amber (Upper Cretaceous).

The nominal genus of the family, *Caeculus* Dufour, 1932, comprises 21 extant species (Taylor *et al.* 2013; Bernard *et al.* 2020; Porta and Vazquez, 2020); only *C. echinipes* Dufour, 1832 is found in Europe while the rest of the species are distributed in North America. Yves Coineau (1974) proposed the genus *Pseudocaeculus* for some American species including *C. americanus* Banks, 1899. However, Taylor *et al.* (2013) pointed out that *Pseudocaeculus* is not an available name, since Coineau did not designate a type species. Bernard *et al.* (2000) published the first phylogeny of the genus based on morphological data and suggested that the common ancestor of *Caeculus* inhabited southwestern North America and that the lineage spread from North America to Europe. Here, we describe the first fossil species of the genus *Caeculus* from Baltic amber (Middle Eocene) which is also the first fossil caeculid mite not belonging to the genus *Procaeculus*, and the second species of the genus known from Europe.

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## Material and methods

The specimens are preserved in cut pieces of amber. Cutting of the amber pieces was made using a mini grinder Pro'sKit PT-5205U equipped with dental discs. For optical observation, specimens were prepared by sanding with a series of waterproof sandpapers and polishing with a fine cerium oxide paste and Chamois leather. To refer to each specimen of the type series we introduce the following abbreviations: Hol for the holotype, SMF Be 14264a, Par1 for the paratype SMF Be 14265a and Par2 for the paratype SMF Be 14264b. Hol and Par2 (SMF Be 14264b) belong originally to the same piece of Baltic amber. In Hol (Figs. 1A–B, 2) there are bubbles clinging on to the specimen's idiosoma, and the aspidosoma is broken in its anterior portion precluding the observation of the gnathosoma (Fig. 2). In Par1 (Fig. 3) the dorsal plates are partially degraded precluding the observation of chaetotaxy (Fig. 4B). Dorsal to Par2 (Fig. 1C) there is a fault in the amber piece precluding the observation of dorsal plates and setae with optical instruments, and the bubbles in the ventral side preclude the observation; some segments of legs I and II are missing. Specimens were studied and measured on Olympus BH-2, CH-2 and Reichert Zetopan compound microscopes. Drawings were made with a camera lucida mounted on an Olympus microscope using both transmitted and incident light. Photographs were taken with a camera on a Leica D2500, the Olympus BH-2 or the Reichert Zetopan. Terminology follows Coineau (1974) with the addition of notation of measures and ratios of leg segments as in Porta *et al.* (2019) and Porta and Vazquez (2020). Following Porta *et al.* (2021), a rational number,  $p$ , associated to an event is the estimation of the probability of this event obtained as the count of favorable cases divided by the count of total cases. Measurements are given in micrometers. Abbreviations Hol, Par1 and Par2 after or before some observation indicates that it corresponds to a specific exemplar; for example: tibia III with solenidium (Par1) means that the solenidium has been observed in the tibia III of the paratype 1. All specimens are deposited in the Senckenberg Naturmuseum Frankfurt (SMF).

## Results

### Family Caeculidae Oudemans, 1902

#### Genus *Caeculus* Dufour, 1832

Type species: *Caeculus echinipes* Dufour, 1832 by monotypy.

**Diagnosis** — (based on Coineau 1974) – *Caeculus* corresponds to caeculids with dorsal plates without intensive neotrichy,  $\omega$  solenidium dorsally located, famulus  $\varepsilon$  dorsal and hidden, famulus  $\kappa''$  recessive, hidden; eupathidia with the typical shape of 'baguette de tambour' (stick drum) of most of the genera of the family, legs with lateral claws equally sized in each tarsus, with trichobothria on all tarsi and tridactyly evident.

**Remark** — Except for the species *C. echinipes*, which has been studied in detail by Y. Coineau in his monograph on the family (1974), and two species recently described (Bernard *et al.* 2020; Porta and Vazquez 2020), all the other species of the genus need to be redescribed.

#### *Caeculus fedrae* sp. nov.

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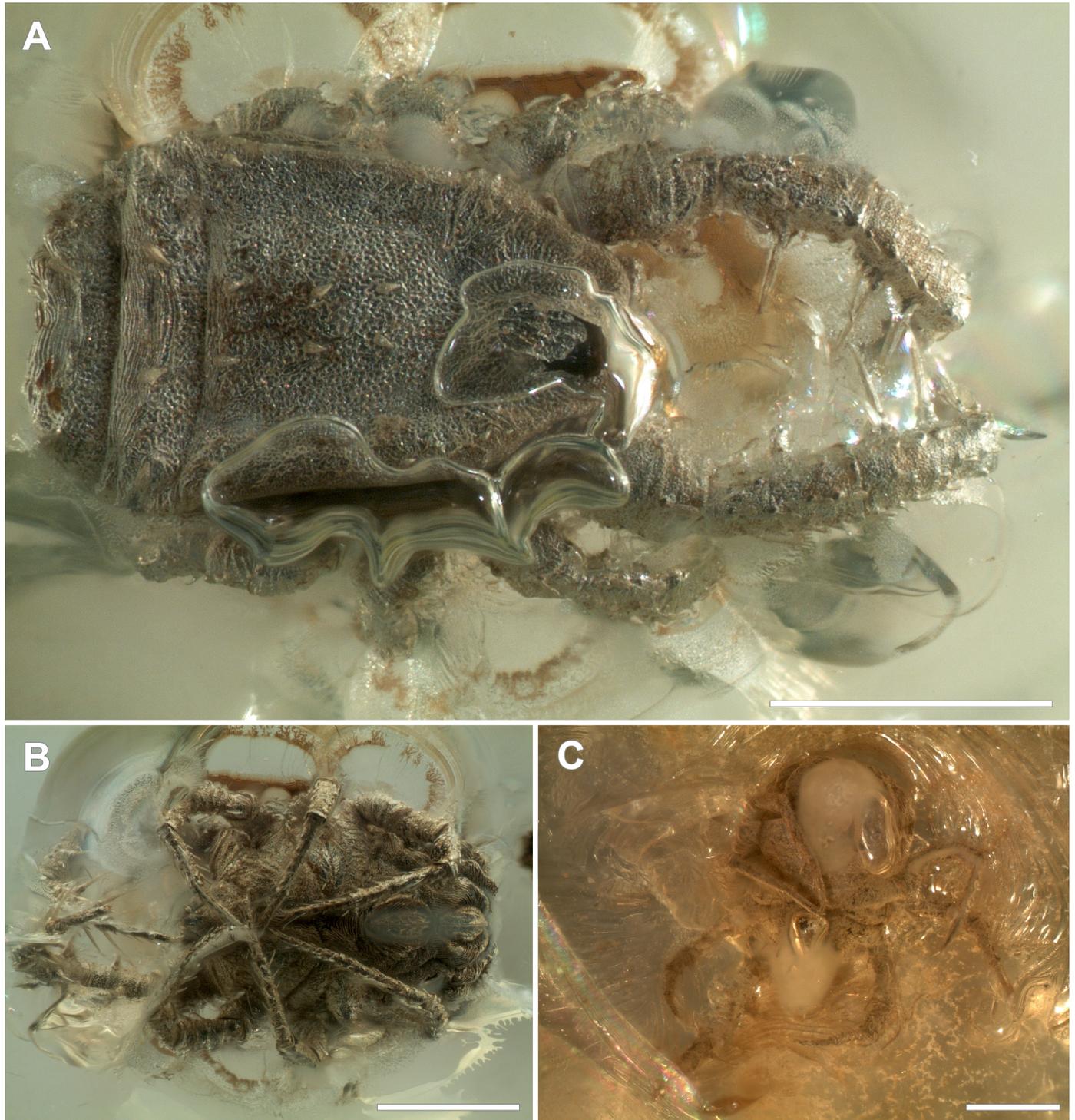
(Figs. 1–11)

#### Etymology

The specific name is a patronym in honor to Dr. Fedra Bollatti (IDEA-Conicet).

#### Type material

Holotype, SMF Be 14264a, adult, sex indeterminate in Baltic amber (Eocene), and 2 paratypes, SMF Be 14264b and SMF Be 14265a, both adults of sex indeterminate also from Baltic amber.



**Figure 1** *Caeculus fedrae* sp. nov., A–B Hol, A habitus dorsal; B habitus ventral; C. Par2, habitus ventral. Scale bars A–C, 500  $\mu$ m.

**Type locality**

Baltic Sea coast, Yantarny settlement (formerly Palmnicken), Sambia (Samland) Peninsula, the Kaliningrad Region, Russia.

### Diagnosis

*Aspidosoma* relatively short, slightly downturned (Fig. 3A), with anterior border with a median concavity (Fig. 5C–D), with two setae in the region *Pp* (Fig. 2); seta *Po* impair and short and trichobothria *bo* spatulate (Fig. 5F–G). The regressive chaetotaxy of the dorsal plates is unique for the genus *Caeculus*, plate *D* with only a pair of setae in each the series *a*, *b* and *c*; *b2* absent in plate *L*; *M* plate with only 4 setae and *ds* absent. Other diagnostic characters are dorsal plates cuticle with alveoli (Fig. 4A–B), plate *M* (Figs. 2, 3) fused; leg I trochanter (Fig. 6A, D) with two pedunculated seta on *l'* series, femur undivided in all legs (Figs. 6A, 9D, 10C–D); two setae in the series *v'* of femur I, with *v'* spiny, straight, with blunt end (Fig. 6A, C) and *vl'* much shorter, curved and pectiolated, two subequal spiny setae (the two distal) on genu I series *v'* (Fig. 6A–B) and two on tibia (Fig. 7A, C).

### Remarks

The three fossil specimens are considered adults based on the relative sizes of the anal and genital plates (Figs. 1B, 3C) and the presence of at least six setae on the genital plate of the holotype (Coineau 1974). The new fossil species is assigned to the genus *Caeculus* based in the chaetotaxy of the dorsal plates (Fig. 2), the shape of the leg eupathidia (e.g. Fig. 6); the presence of trichobothria and tridactyly in all leg tarsi (Figs. 8, 9A–C, 10E, 11F–G) and the position of the  $\omega$  solenidium and the famulus  $\epsilon$  in the dorsal facies of the tarsi I (Fig. 8). It must be noted here that *C. fedrae* sp. nov. differs from other fossil caeculids, all belonging to the genus *Procaeculus*, by the shape of eupathidia, the evident tridactyly and the bases of the trichobothria *bo* (Porta et al. 2019).

### Description

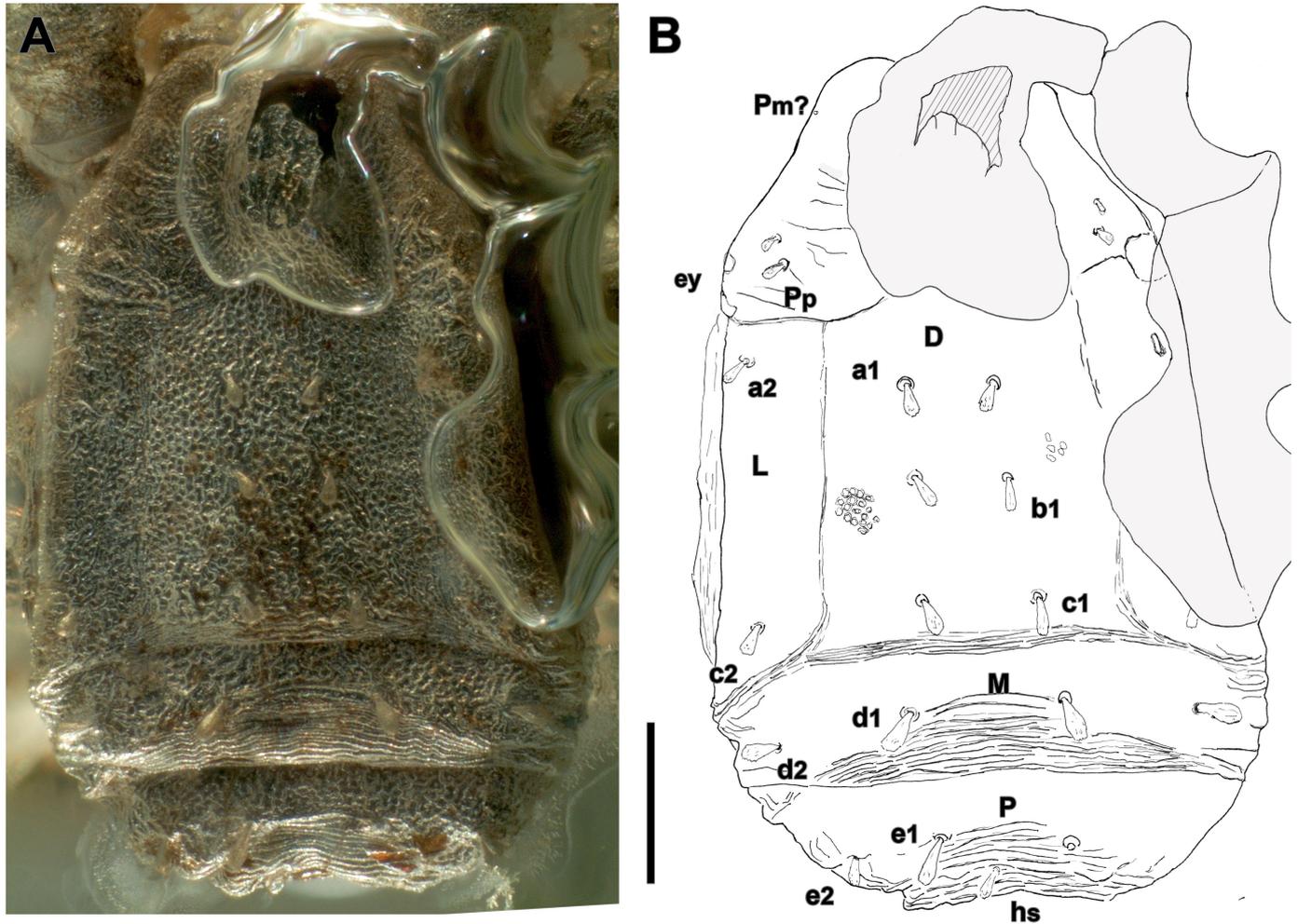
Body color: grayish brown.

**Idiosoma** — subtrapezoidal in dorsal view (Figs. 1A, 2, 3A), 1120 (940–1100) long, 640 (640) wide at the level of coxa IV, cuticle of dorsal plates, coxae and hypostome with alveoli (Fig. 4), membranous integument striate.

**Aspidosoma** — slightly downturned (Figs. 2, 3A), anterior margin 235 long in Par1, with a median concavity (Fig. 5C–D), posterior margin 451 wide in Hol. Seta *Po* (Fig. 5F–G) impair, pectiolated and small, 41 long, observable in Par1; trichobothria *bo* in Par1 spatulate, broadening in the distal end, 46–60 long. Apparently, one small seta *Pa*, in the left anterior margin of Par1 (Fig. 5D), only one insertion *Pm* observable in the left lateral margin of Hol (Fig. 2B), sector of the *Pp* with 2 setae in Hol, 23–32 long (Fig. 2B). Lateral eye plates not separated from other dorsal plates; anterior pair of eyes diameter 18–20, posterior pair 23.

**Hysterosoma** — *Dorsal view* – with 5 dorsal plates *D*, (*L*), *M* and *P* (Figs. 2, 3). Unpaired dorsal plate *D* trapezoidal, 438 long, anterior margin 307 long, posterior margin 446 long in Hol (Fig. 2B), series *al*, *bl*, *cl*, only observable in Hol, each with a pair of setae situated near the median axis of the plate, length of setae *al*: 41, *bl*: 42–46, *cl*: 46; distance between setae insertions, *al-al*: 64, *bl-bl*: 69, *cl-cl*: 80, *al-bl*: 67, *bl-cl*: 90. Paired plates *L* 460 (400 Par1) long, 124 (115 Par1) wide; *a2*:30 (37 Par2), *b2* absent, *c2*: 37 long. Median posterior plate *M* with a median posterior concavity (Figs. 2, 3), 64 (77 Par1) long at median axis and 115 in the lateral margin of the body, 653 (531 Par1) wide, not divided in two plates, with 2 pairs of long setae, *d1* and *d2*, 60 and 46–57 long, respectively, *ds* absent, distance between setae insertions, *d1-d1*: 184, *d1-d2*: 156–161, *d2-d2*: 510. Posterior plate *P*, 64 (69 Par2) long, 483 (484 Par2) wide; with 4 setae (only insertion observable in some cases), *e1* and *e2*, 64 and 46 long, respectively; distance between setae insertions, *e1-e1*: 161, *e1-e2*: 96. Seta *hs* on posterior border of idiosoma, 35 long.

*Ventral view* – (Figs. 1B–C, 3C, 4C), coxae and hypostome cuticle with alveoli, membranous integument striate. Coxal setae clavate, coxa I with at least 4 setae, II and IV with at least 2, III and IV with at least 1. Genital opening 284 (189 Par1) long, 185 wide with 6 pairs of



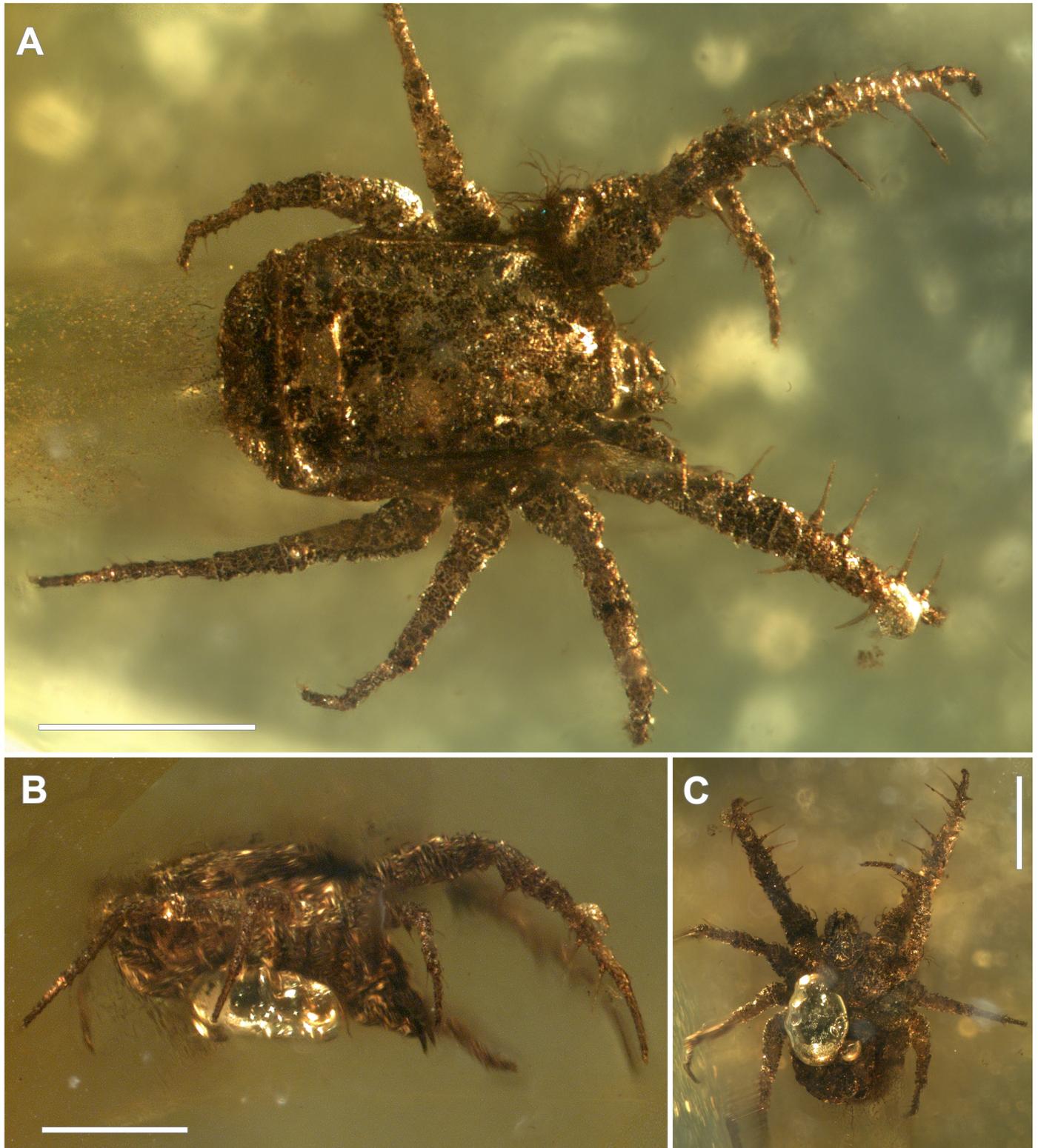
**Figure 2** *Caeculus fedrae* sp. nov., Hol, idiosoma dorsal, **A** photomicrographs; **B** schema. Scale bar 200  $\mu$ m.

genital setae in Hol, 14–16 long. Anal opening 192 (169) long, with at least a pair of clavate setae, 32 long. Only *ps3* and *ps2* observable in pseudoanal plates of Hol and Par1.

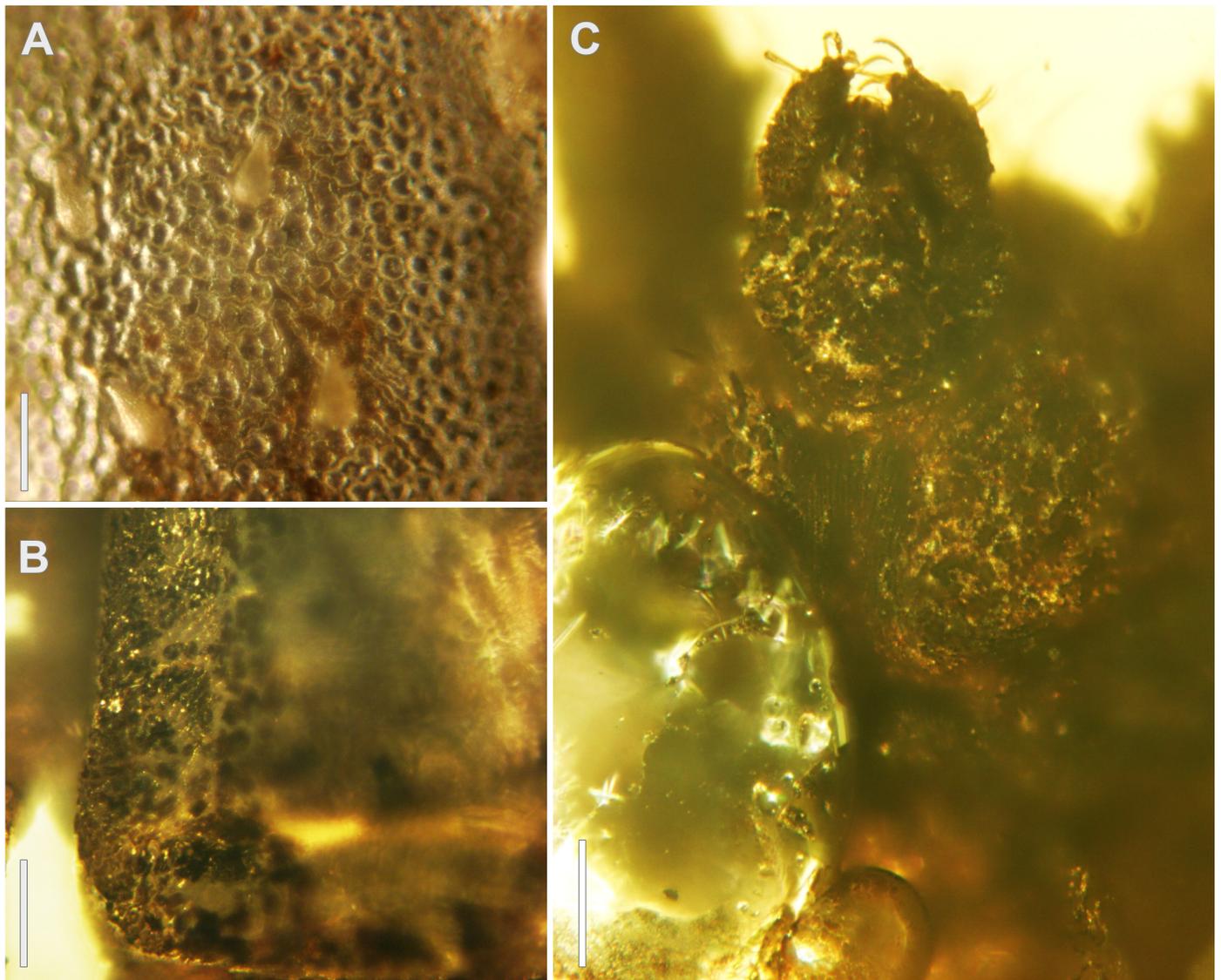
**Gnathosoma** — Chelicerae not observable. Palp only partially observed in Par1 in ventral (Fig. 5A–B) and lateral view, trochanter, femur and genu not observed, tibia with at least 5 setae, only seta *d* calcar, the rest of them clavate, only the contour of the tarsus visible in lateral view as well as two terminal eupathidia in ventral view. Subcapitulum (Fig. 4C) in Par1 posteriorly rounded, anteriorly subconical, 231 wide at level of palp insertion, 250 long, setae *m*, 28 long in Hol, *n* not visible, two pairs of adoral setae, *or* 1–2, 14–16 long.

**Legs** — (Figs. 6–11)

**Leg I** — (Figs. 6–8). Trochanter (Figs. 6A, C, 7A, C) 253 (220–253) long, 166 (142–156) wide with two setae on series *l'* (only one seta in addition an elevation of the cuticle in one setal insertion observable in Hol), 64 (46–60), 83+ (64–83) long, Hol with one elongated and peciolated seta on *d*, 60–64 long. Femur (Figs. 6A, C, 7A, C) 253–262 (230–240) long, 115–133 (115) wide with two setae on series *v'*, *v'* seta spiny, straight, with distal end blunt, 124 (101), 156+ (138+) long, ratios *Rf*: 1.08 (0.88), *RPref*+: 1.36 (1.2), seta *vI'* peciolated, curved, 46–51 long (27); with a spiny and blunt ended seta on series *v''*, 54 long in Par1; 4 peciolated setae on series *d*, 3 in series *l'* with *l'* eupathidial and the rest peciolated, 28–38 long, 3–4 setae on series *l''* with setae *l''* and *lI''* eupathidial in Hol and *l2''* also eupathidial en Par1. Genu (Figs.

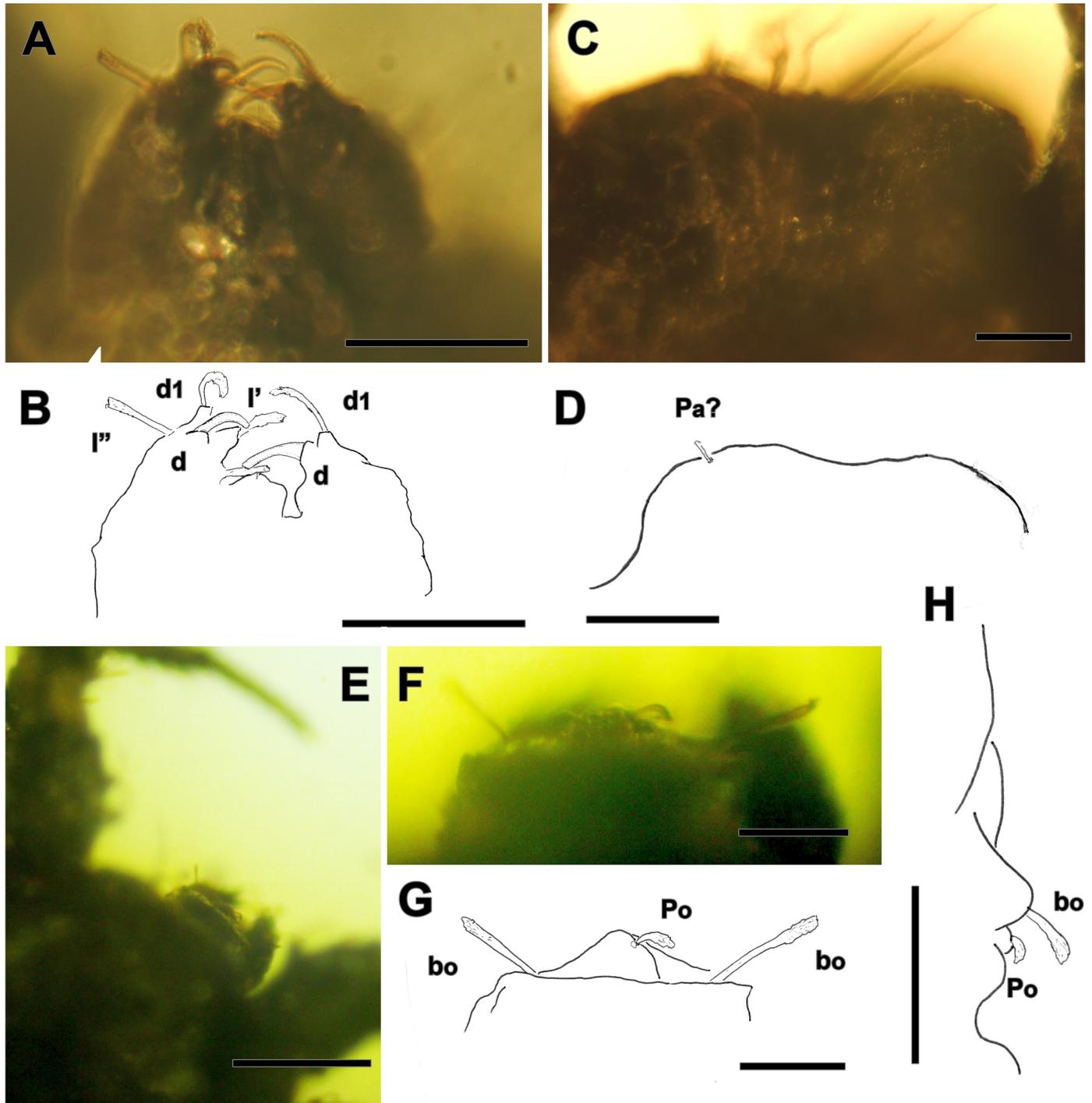


**Figure 3** *Caeculus fedrae* sp. nov., Par1, photomicrographs. **A** habitus dorsal; **B** habitus lateral; **C** habitus ventral. Scale bars A–C 500  $\mu$ m.



**Figure 4** *Caeculus fedrae* sp. nov., photomicrographs. **A** Hol, detail of the cuticle of plate *D*; **B** Par2, detail of the cuticle in left plate *L*; **C** Par2, ventral view of the anterior portion showing anterior coxae and hyposotome. Scale bars A, 50  $\mu$ m; B–C, 100  $\mu$ m.

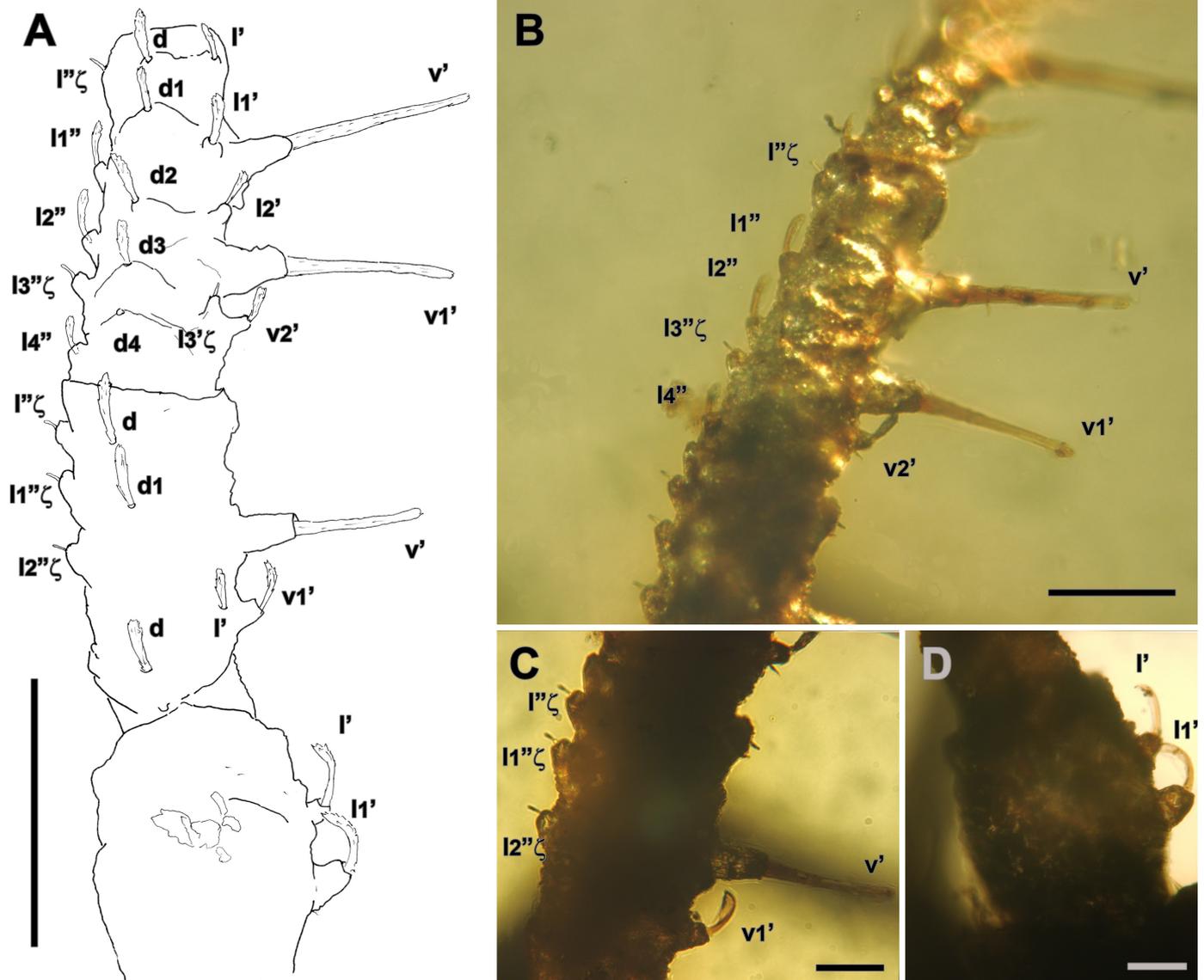
6A–B, 7A–B), 253–267 long, 87–92 wide in Par1 with the 2 distal setae on series  $v'$ , straight and spine shaped, subequal, 133–146 (124–138), 174–184+ (166–184) long, seta  $v2'$ , peciolated and curved, 32 long; 1 spiny seta observable in series  $v''$ , 138 (108), 175+ long; 4 peciolated setae on the series  $d$ ; 5 and 5–6 setae on each of the lateral series  $l'$  and  $l''$ , respectively, setae  $l'$ ,  $l2'$  ( $p=1/2$ ),  $l3'$ ,  $l''$  and  $l2''$  ( $p=2/3$ ) and  $l3''$  ( $p=1/2$ ) eupathidial. Tibia (Figs. 6A, 7) 338 long in Par1, with 3 setae in series  $v'$ , the 2 distal pointed and subequal, in Par1 133–138, 175–193+ long, the proximal,  $v2'$ , peciolated, 41–46, 64–69+ long in Par1, 2 subequal distal spiny setae observable on series  $v''$ , 138–140, 161+ long, in addition to 2 shorter,  $v2\gg$  and  $v3''$ , 62 and 31 long, respectively; Par1 with 5 setae in lateral series, setae  $l''$  and  $l3''$  eupathidial, series  $l'$  not observable solenidium  $\phi$  hidden inserted in the habitual dorsoantiaxial position in the distal part of the tibia observable in Hol (Fig. 8A),  $\kappa''$  not observed. Tarsus (Fig. 8), 253 (246 in Par1) long, 41 wide at base, with 5 setae in series  $l'$  and 4 in  $l''$  series, with  $l1''$ ,  $l2''$  and  $l'$  eupathidial; hidden solenidium  $\omega$  inserted dorsally (Fig. 8A) at the level of  $l2'$ ,  $\varepsilon$  famulus hidden, located in dorsal facies, near the solenidium; series  $v'$  with at least 4 setae; ( $er$ ) non eupathidial, ( $st$ ) not



**Figure 5** *Caeculus fedrae* sp. nov., Par2, A–B palp, from ventral view, photomicrograph and schema, respectively; C–D anterior portion of the aspidosoma, photomicrograph and schema, respectively; E–H insertion of the seta *Po* and trichoboria *bo*, E–F photomicrograph from dorsal view; G schema of F; H lateral view. Scale bars A–B, 100  $\mu$ m; C, 50  $\mu$ m; D, 100  $\mu$ m; E, 200  $\mu$ m; F–G, 50  $\mu$ m; H, 100  $\mu$ m.

observed, trichobothria *bt* short, 26 long; tridactyly present, with two the two lateral claws, *ol'* and *ol''*, subequal and the median, *oc*, shorter.

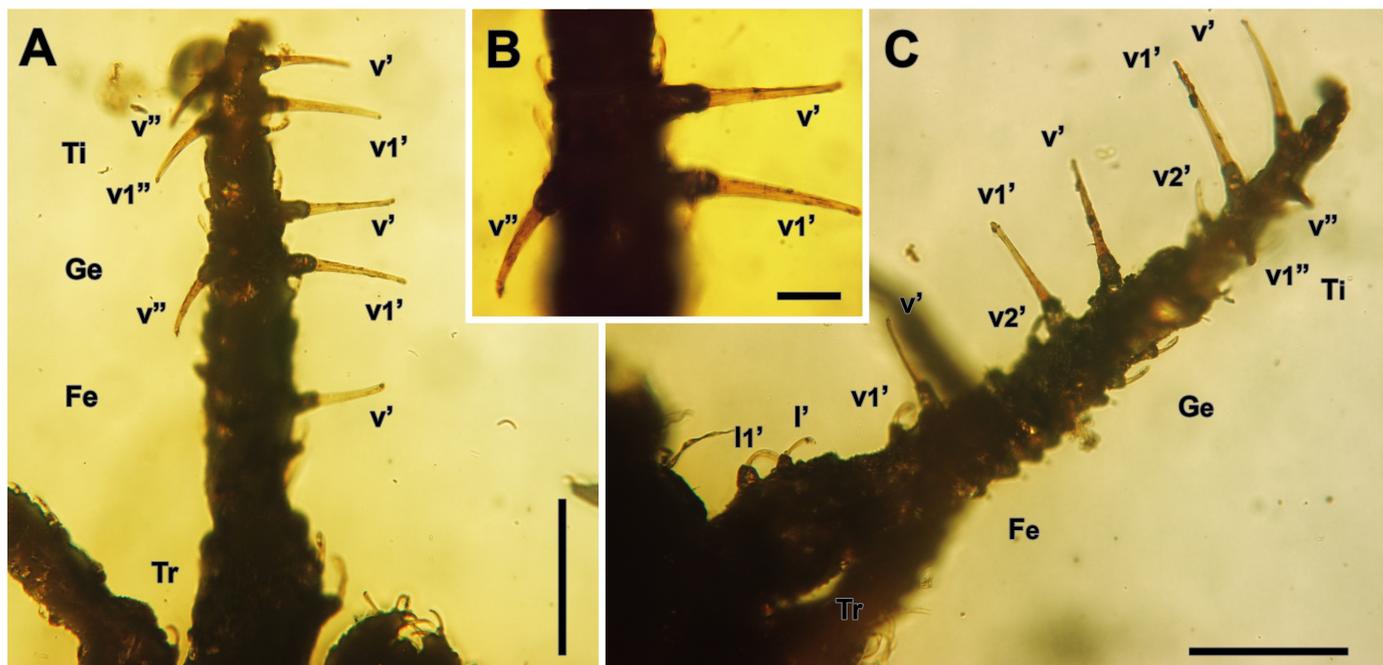
*Leg II* – (Fig. 9) Trochanter (Fig. 9D) in Par1 189 long, 92 wide with only one seta observable in each series *l'* and *d'*. Femur (Fig. 9D) 170 long, 87 wide, with 5 setae in series



**Figure 6** *Caeculus fedrae* sp. nov., Par2, left leg I, **A** trochanter to genu, dorsal view; **B–D** photomicrographs, **B** genu; **C** femur; **D** trochanter. Scale bars, A, 200  $\mu$ m; B, 100  $\mu$ m; C–D, 50  $\mu$ m.

*l'* and at least 1 in *l''*, respectively; *l'* eupathidial. Genu (Fig. 9A, D) in Par1 184 long, 69 long, with 4 setae in series *l'* all pectiolated, Hol with 2 setae in ventral series *v''*, *v''* seta elongated, 78, 92+ long. Tibia (Figs. 9A–B) in Par1 207 long, with 4 setae on ventral series *v''* (6 in Par2), 5 setae on lateral series *l''*, *l'* eupathidial in Par2, solenidium  $\phi$  not observable. Tarsus (Fig. 9B–C) with 5 setae on lateral series *l''* and *l'* (4 in Par2); solenidium  $\omega$  and famulus  $\epsilon$  as in leg I (Hol), each ventral series *v'*, with at least 4 setae; *er'* non eupathidial, trichobothria *bt* 25 (32 in Par2) long; tridactyly present (Fig. 9C, arrow) with the two claws *ol'* and *ol''* subequal.

*Leg III* – (Figs. 10, 11) Trochanter (Fig. 10A, C, F–G) in Par1 130–156 long, 115–124 wide, with 2 setae in series *l'*. Femur in Par1 133–147 long, 81–87 wide, with 2 setae in series *l'* with *l'* eupathidial. Genu 147 long, 64 wide in Par1, with 4 setae on series *d* (Hol); 4 setae in lateral series *l'* with only seta *l'* eupathidial. Tibia (Fig. 11A, D), 285–317 (322 Par2) long, 46 (46 Par2) wide, *RTi* 6.2–6.3 (7 in Par2) with 6 setae on ventral series *v''* (5 in Par2), 3 setae in series *d*, 6 setae in lateral series *l'* in Hol, 5 in Par1; 5 setae in series *l''* with setae *l1''*, *l2''*



**Figure 7** *Caeculus fedrae* sp. nov., Par2, **A** right leg I, ventral view; **B** same, detail of the spines of the (*v*) series of the genu; **C** right leg I, ventral view. Scale bars A, 200 µm; B, 50 µm; C, 200 µm.

( $p=1/3$ ),  $l3''$  ( $p=2/3$ ) and  $l4''$  ( $p=1/2$ );  $l'$  eupathidial in Hol, Par1 and Par2 and  $l4'$  eupathidial only in Hol, solenidium  $\phi$  inserted in dorsoantiaxial position in the distal part of the tibiae. Tarsus 202 (221 Par2) long, (32 Par) wide at base, with 3 setae in ventral series  $v'$ , pair (*er*) non eupathidial, trichobothria *bt* 110 (92 Par2) long; tridactyly present, with the two lateral claws  $ol'$  and  $ol''$  subequal.

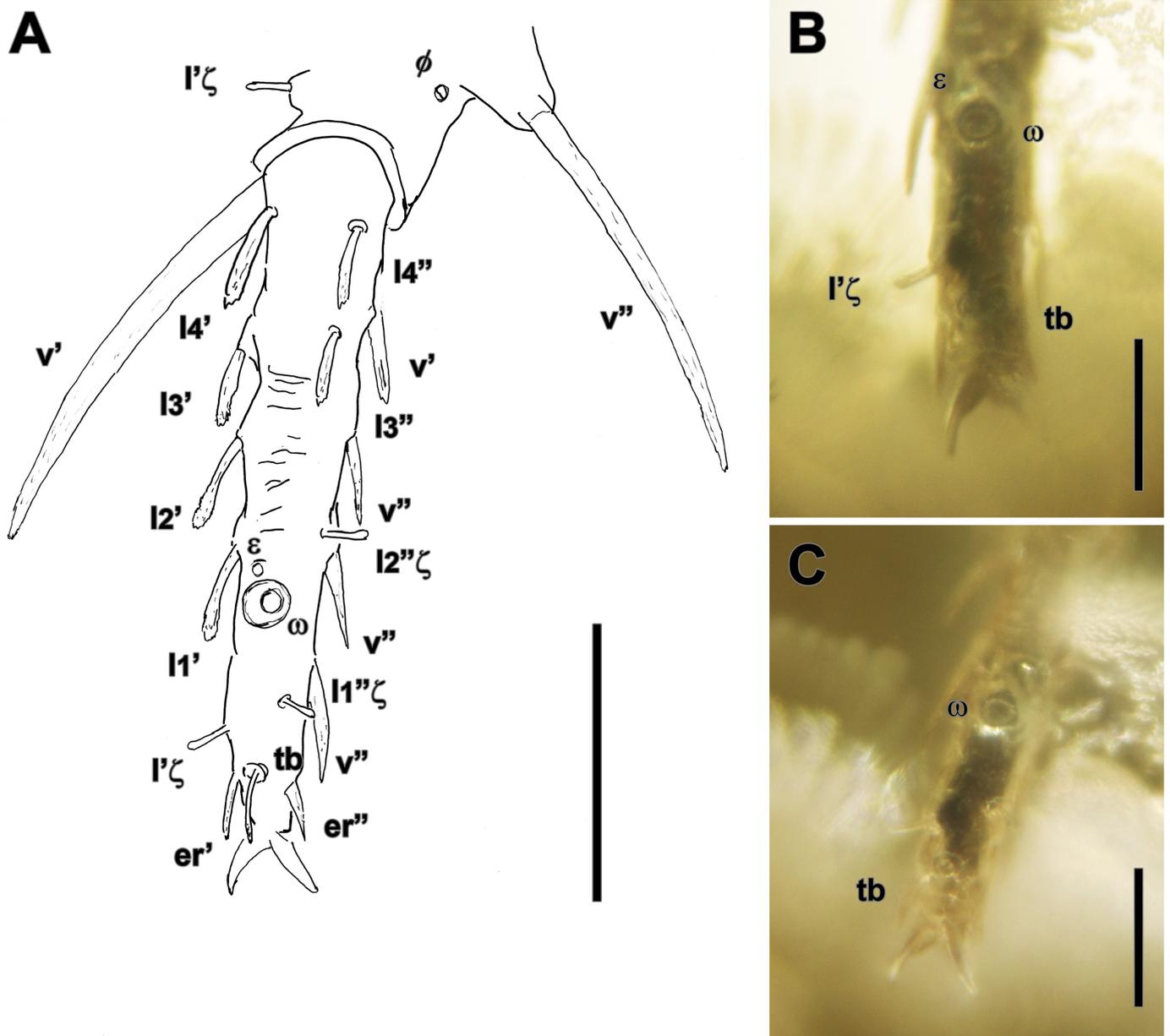
**Leg IV** – (Figs. 10, 11) Trochanter (Fig. 10A, D) in Par1 253 long, 120 wide, with 1 seta on each *d* and *v* series. Femur 161 long, 78 wide, with 2 setae on series  $l'$ , distal seta  $l'$  eupathidial. Genu of Par1 166 long, 55 wide, with 4 setae in lateral series  $l'$ ; setae  $l''$  and  $l'$  eupathidial in Hol. Tibia (Figs. 10B, D, 11B, E), 345 (253–381) long, 60 wide, with 4–5 setae in ventral series  $v'$ , 5–6 setae in lateral series  $l'$  and 5 on  $l''$ , setae  $l''$ ,  $l3''$ ,  $l'$  and  $l3'$  eupathidial, solenidium  $\phi$  apparently absent. Tarsus (Figs. 10B, E, 11B–C, F–G) 207–216 (230 in Par2) long, 37 wide at base, with 5 setae in ventral series  $v''$  (4 in Par2), 3 on lateral series  $l''$  with  $l1''$  eupathidial in the left leg of Hol ( $p=1/2$ ); (*er*) non eupathidial; trichobothria *bt* 115 (106 in Par1, 124 in Par2) long; tridactyly observable (Fig. 11F, arrow), with the two claws  $ol'$  and  $ol''$  subequal, 28 long.

## Discussion

### Morphology and Systematics

The new species present some morphological features that are remarkable for the genus *Caeculus* and deserves to be further discussed, namely: the aspidosomal shape; the leg chaetotaxy with entire femora, the chaetotaxy of the dorsal idiosomal plates and the presence of an impair seta *Po*.

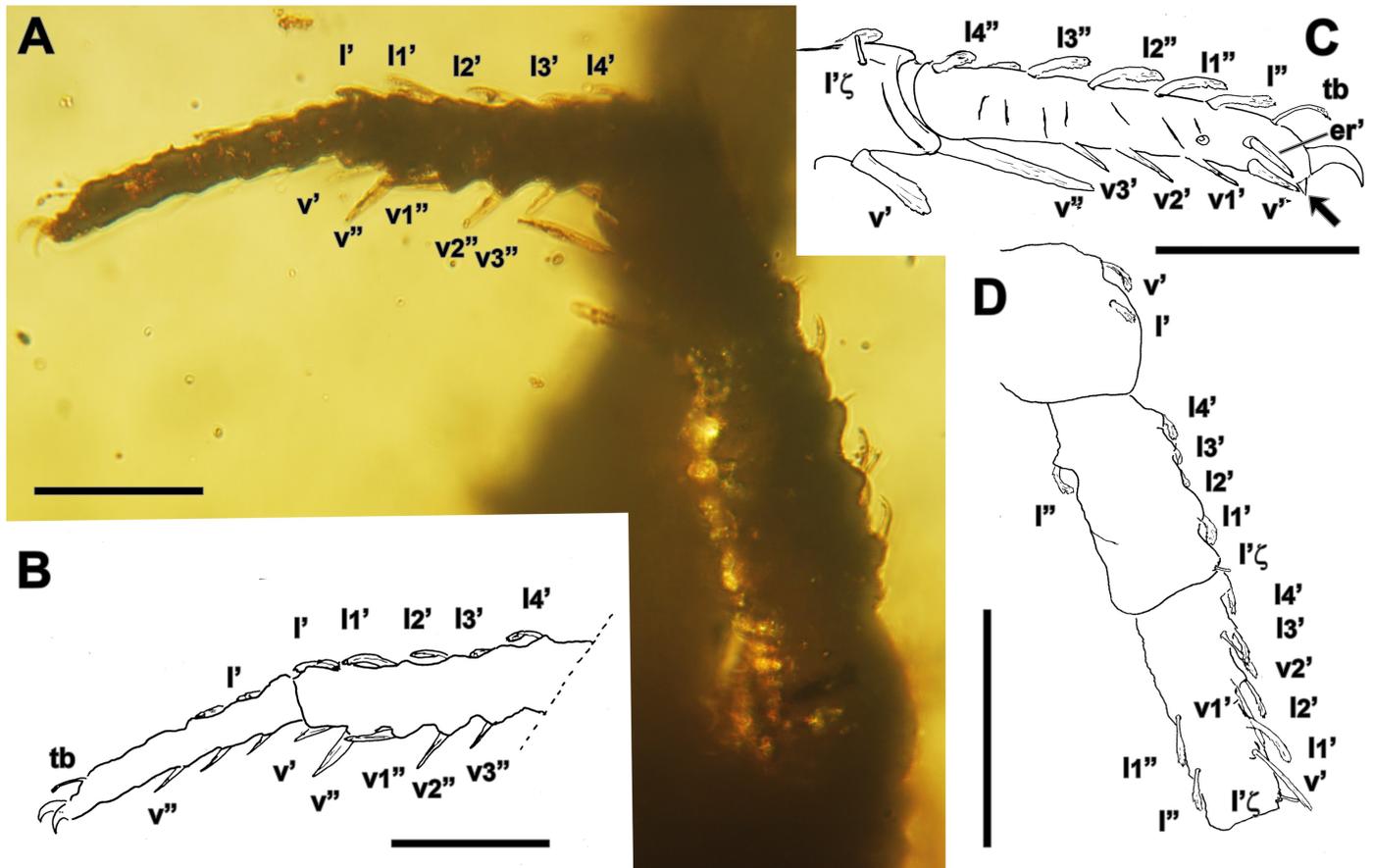
In contrast to most of the extant species of *Caeculus* the aspidosoma of *C. fedrae* sp. nov. is short, slightly downturned, and not horizontally extended over the gnathosoma, compared with most of the extant species of *Caeculus*. However, we refrain from proposing a new genus for this fossil species based on this peculiar morphology as *C. kerrulius* Mulaik, 1945 seems to



**Figure 8** *Caeculus fedrae* sp. nov., Hol, left leg I, tarsus, A schema, dorsal view; B–C photomicrographs. Scale bars A, 100  $\mu$ m; B–C, 50  $\mu$ m.

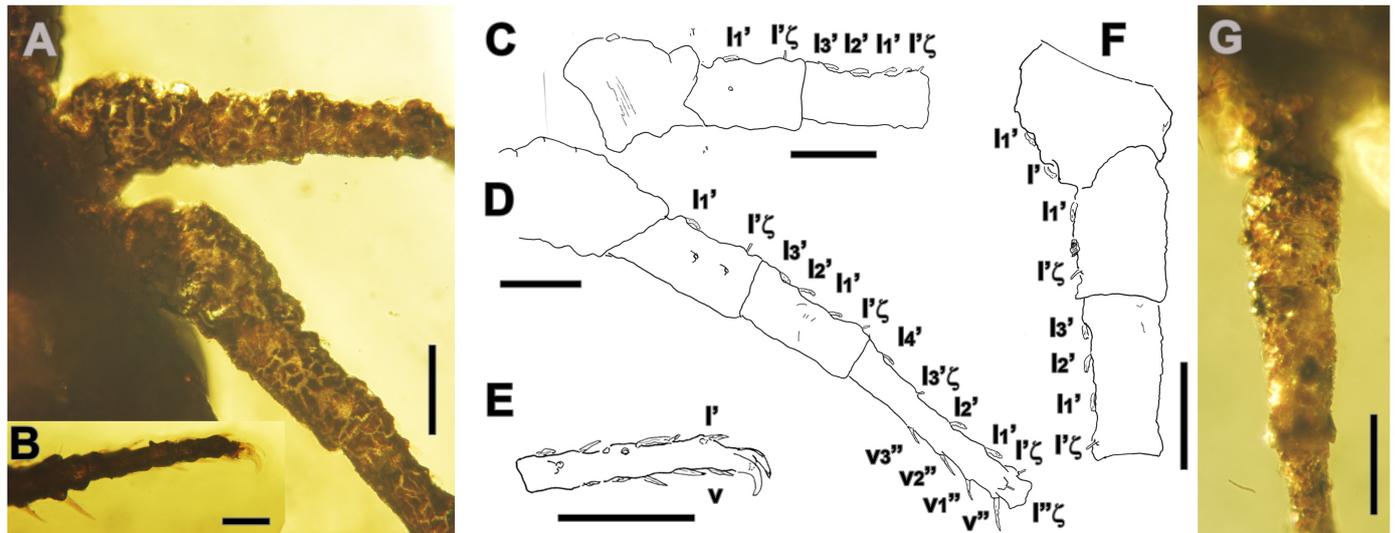
have a similar morphology of the aspidosoma (see Mulaik 1945: Figs. 1, 17), and species of *Neocaeculus* Coineau 1967 have great interspecific variation in this character (Taylor 2014).

The entire femora of all legs and the morphology of the series  $v'$  of leg I in the new species is also very unusual for the genus; only two species of *Caeculus* have undivided femora, according to the original descriptions, *C. americanus*, Banks 1899 and *C. clavatus* Banks 1905 (it will be interesting to reexamine Banks' specimens to confirm that their femora are truly entire). The series  $v'$  on the femur I is, however, very different in Banks' species: while in these species  $v'$  and  $vI'$  have similar shape and size, in *C. fedrae* sp. nov.  $vI'$  is pectiolated and much smaller than  $v'$ , which is spine-shaped (Fig. 6A, C). On the other hand, the chaetotaxy of the series  $v'$  in leg I of *C. fedrae* sp. nov. exhibits a high level of concordance with those of leg I of other species in the genus *Procaeculus*, namely *P. dominicensis* Coineau and Poinar,



**Figure 9** *Caeculus fedrae* sp. nov., leg II, A–B, D, Par2; C, Hol, A photomicrograph of left leg II from ventral; B same, schema of tarsus and tibia; C right tarsus; D same as B, trochanter to femur. Scale bars A–C, 100 µm, D, 200 µm.

20019; *P. eridanosae* Coineau and Magowski, 1994; *P. mexicanus* (Mulaik & Allred, 1954); *P. oregonus* (Mulaik & Allred, 1954) and *P. willmanni* (Vitzthum, 1933) (see Coineau 1969). All species of *Procaeculus* also present undivided femora. It must be mentioned, however, that most species of the genus *Procaeculus* have been collected from trees, as was noted for Coineau and Magowski (1994) in order to explain why this is the only genus present in fossil amber. Then, considering that the fossil arthropods found in Baltic amber seem to be mainly bark-dwelling species (Dunlop *et al.*, 2018), the similarity between the legs I of *C. fedrae* sp. nov. and those of some *Procaeculus* may be a convergent morphological adaptation to bark-dwelling lifestyle (although undivided femora I are found in many *Neocaeculus* species that are terrestrial, e.g. Taylor *et al.* (2014), they present a different pattern of the *v'* series). The oligotrichy of the dorsal plates *L* and *D* of *C. fedrae* sp. nov. is unique for the genus. Following the studies of the ontogeny of the setae of the dorsal plates in the Coineau (1974), the setae present in *C. fedrae* sp. nov. constitutes the minimal set possible in adults caeculids. The same condition has been reported for some psammophile caeculids belonging to *Microcaeculus* (Coineau 1974) and *Andocaeculus* Coineau, 1974 (Porta *et al.* 2020) and is considered a derived condition, resulting from a process of “*évolution régressive par retardement*” of the dorsal plates chaetotaxy. Furthermore, the other caeculid species described from Baltic amber, *Procaeculus eridanosae*, shares the same condition, unique also for its genus. It could be interesting to study if there is some correlation between the presence of oligotrichy in the dorsal plates and some ecological constraints in modern caeculids in order to make paleoecological



**Figure 10** *Caeculus fedrae* sp. nov., legs III and IV, Par2, **A** photomicrograph dorsal view of the right leg III and IV, from trochanter to genu; **B** photomicrograph of the right tarsus IV; **C** right leg III, dorsal view from trochanter to genu; **D** right leg IV, dorsal view from trochanter to tibia; **E** right tarsus IV; **F–G** scheme and photomicrograph of the left leg III from trochanter to genu. Scale bars A, 100 µm; B, 50 µm; C–G, 100 µm.

inferences.

According to the proposed character evolution by Coineau (1974), the presence of a single seta *Po* in *C. fedrae* sp. nov., must be considered derived especially for the genus *Caeculus*, where the plesiomorphic condition would be a pair of setae. This author even reported the transition from a pair to a impair seta *Po* in the course of the ontogeny of *C. echinipes*. The same condition as in *C. fedrae* sp. nov. occurs at least in three North American species of the genus. The presence of this derived condition in the new taxon, a putative internal node in the phylogeny of the family, is of great value for the dating and study of the morphological changes during the evolution of this family.

### Distribution of the genus *Caeculus*

So far, only one species of the genus, *C. echinipes*, is reported from Europe. It has been suggested that its wide distribution (Fig. 12B) may be a consequence of a postglacial distribution process (Franz 1952). In contrast, the genus *Caeculus* is rather diverse in the Nearctic Region (Fig. 12A) with 20 species covering, as a whole, a wide range (data from Banks 189; 1905; Bernard *et al.* 2020; Enns 1958; Franz 1952; Hagan 1985; Higgins and Mulaik, 1957a, b; McDaniel and Boe 1990; Mulaik 1945; Mulaik and Alfred 1954; Nevin 1943; Porta and Vazque Rojas 2020). Based on their first phylogeny of the genus, Bernard *et al.* (2020) suggest the possibility of the North American southwest origin of the genus, followed by a dispersal event to Europe of an ancestor of *C. echinipes*. The discovery of a new fossil species in Europe presenting so many morphological particularities suggest that modifications of the hypothesis about the origins of the genus may be necessary. From our point of view, based on the empirical data of the genus *Andocaeculus*, ecological constrains take a prevalent role in the evolution of some morphological characters as leg and idiosoma chaetotaxy, the introduction of molecular data may be necessary for robust phylogenetic inference concerning this family.



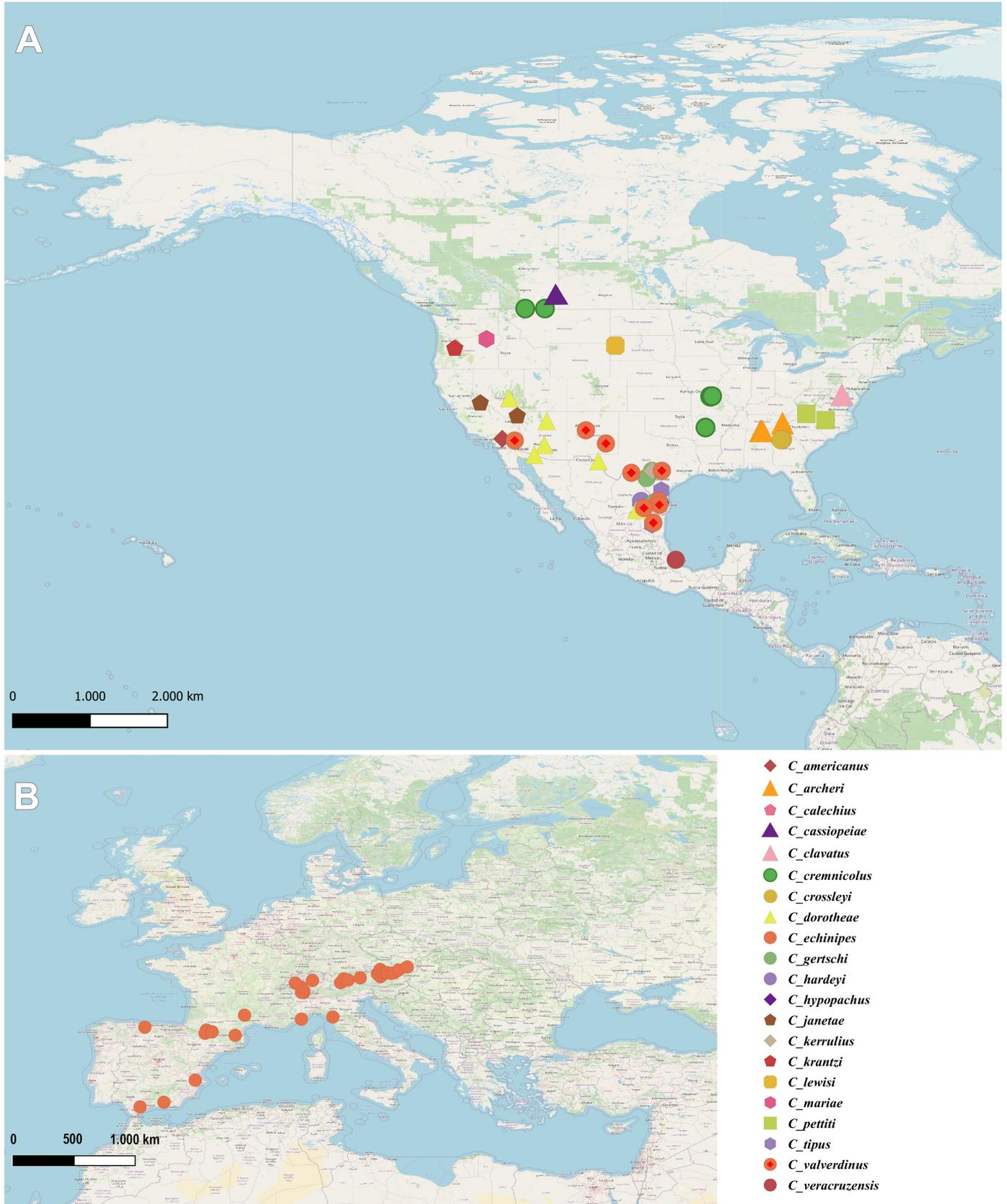


Figure 12 Distribution of the extant species of the genus *Caeculus*, A American species; B *Caeculus echinipes*.

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