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Research article

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Three new species of the genus *Megalothorax* (Collembola: Neelidae) from France

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Abstract. Three new species of *Megalothorax* are described from France. *Megalothorax calvignacensis* sp. nov. was discovered in the Lot department and is characterized by a dense grey pigmentation unusual in *minimus*-group. *Megalothorax cellarincola* sp. nov. was discovered in several cellars in the ancient city center of Clermont-Ferrand. *Megalothorax poinsoetae* sp. nov. is the first apparent littoral species of the genus and is characterized by strong lanceolate chaetae on the back of the head, and some thickened to lanceolate chaetae dorsally on the trunk. For each species, we provide a detailed morphological description and a molecular phylogenetic placement within the genus *Megalothorax*, based on the near complete nuclear rDNA operon. We inserted the species in the open key of the *Megalothorax* of the world (Schneider *et al.* 2023; last updated by Panina *et al.* 2025). The molecular analysis allowed to place *M. cellarincola* and *M. poinsoetae* among the *incertus*-group sensu Schneider & D'Haese (2013). *Megalothorax calvignacensis* is found to belong to the *minimus*-group.

Keywords. Springtails, morphology, integrative taxonomy, chaetotaxy, littoral species.

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Introduction

Adequate assessment of biological diversity is a typical problem for groups of minute organisms where morphological features are difficult to observe and to interpret. The genus *Megalothorax* Willem, 1900 is a typical example of a taxon with a cryptic diversity. As a consequence, it has not received much attention

since their discovery in 1900. However, the group displays very interesting aspects: (i) it yields multiple unique morphological characters among Collembola: for example, cuticular process on forehead or cuticular channels on abdomen (Schneider & D’Haese 2013; Panina *et al.* 2022, 2025). It is much more diverse than previously thought (Schneider & D’Haese 2013; Papáč & Kováč 2013; Schneider *et al.* 2016, 2018, 2023; Papáč *et al.* 2019; Panina *et al.* 2022, 2025; Schneider & Panina 2023).

In line with previous work, we use methods of integrative taxonomy, which combine methods of classical morphological taxonomy with molecular approaches to fill the gaps in knowledge in the species richness, the evolution and the diversity of *Megalothorax*, one of the smallest collembolans around the world.

At the current stage of development of the *Megalothorax* tree of life stand out three clades, referred to as the following morphological species-group: *minimus*-group, *incertus*-group and *anterolenis*-group (Schneider & D’Haese 2013; Schneider *et al.* 2023). The original sets of morphological character states provided for the *minimus* and *incertus*-group has then been shown to be not fully conserved within those groups (Panina *et al.* 2022; Schneider & Panina 2023), underlying the need to combine morphology and molecular data in order to precisely understand the interspecies relations.

In this work, we report three new species of *Megalothorax*, discovered in France. We provide thorough morphological descriptions. We also sequenced the near complete nuclear rDNA operon of each of those species, to place them in the molecular phylogenetic tree of the genus *Megalothorax* (Schneider & D’Haese 2013, most recently updated in Panina *et al.* 2025).

Material and methods

Sampling

Each species was sorted from bulk soil mesofauna community, extracted from sampled substrate into 96% ethanol using Berlese funnels. The ethanol-preserved animals were stored in fridge (~4°C).

Morphological investigation

Photographs of specimens in ethanol were made using a Panasonic Lumix G7 mounted on a Leica S8APO, at 8× magnification. Specimens were cleared in lactic acid and were mounted on permanent microscope slides using Marc-André II medium. Observations were made using a Leica DM2500 microscope at various magnifications, up to 100×, using phase contrast. Hand drawings were made with drawing tube and were digitized and annotated using Photoshop, Inkscape and Concepts for Android.

Molecular phylogeny

For each species the near complete rDNA operon was amplified with a single long-range PCR, according to the protocol described in Schneider *et al.* (2023), for sequencing on Oxford Nanopore MinION. The libraries were prepared using the Nanopore Native Barcoding Kit 24 V14. and sequenced overnight on a Flongle Flow Cell, ver. R.10. Bases were called from raw reads using Dorado ver. 0.5.0, using the highest accuracy mode. Reads were demultiplexed using a custom script, combining the following tools: BLAST ver. 2.14.1+ (blastn and blastn-short), SeqKit ver. 0.13.2 (Shen *et al.* 2024), and Minimap2 ver. 2.24-r1122 (Li 2018). The backbone phylogeny of species of *Megalothorax* from Schneider & D’Haese (2013) – last version in Panina *et al.* (2025) – was updated with the newly sequenced individuals. The rDNA operon was partitioned as described in Panina *et al.* 2025: 18S rDNA, ITS regions, 28S rDNA d1 to d2, 28S rDNA d3 to end. Legacy mitochondrial loci COI and 16SrDNA were not obtained for the three species, however we included the one previously acquired for other species in the overall dataset. Each partition was aligned using Muscle ver. 5.1 (Edgar 2022), at the exception of the pre-aligned protein coding gene COI. We used ModelTest-NG ver. 0.1.7 (Darriba *et al.* 2020) to select the best maximum

likelihood (ML) models for each partition according to BIC. The best ML tree was searched using RAxML-NG ver. 1.2.0 (Kozlov *et al.* 2019) with 500 bootstrapping repetitions.

Open Key

We updated the Open Key of the *Megalothorax* species of the World (Schneider *et al.*, 2023; last update Panina *et al.* 2025) to include the three new species (accessible on the Xper3 platform, direct access link: <https://app.xper3.fr/xper3GeneratedFiles/publish/identification/-9016514619991831667/mkey.html>)

Abbreviations for morphological terms

a0	= unpaired chaetae on forehead
a1, a2	= labral chaetae
Abd. I–IV	= abdominal segments I–IV
Ant. I–IV	= antennal segments I–IV
Bp	= basal postero-median lamella of claw
la, lp	= lateral antero-basal and postero-basal lamella of claw
mol	= maxilla outer lobe
Or	= organite of Ant. IV
pr.a	= prelabral anterior chaetae
S1, S4	= long S-chaetae on Ant. III
S2, S3	= short S-chaetae on Ant. III
s	= sensillum
s1, s2, s3	= swollen sensilla on body
S-chaetae	= specific cylindrical chaetae on ant. III–IV
sf 1, sf 2	= sensory field on head
sf 3, sf 4, sf 5	= sensory field on thorax
sf 6, sf 7	= sensory field on abdomen
Sx, Sy	= S-chaetae of Ant. IV
vt	= ventral tube
wrc	= free wax-rods (“free wax rod generating crypt” in Schneider & D’Haese 2013).
X-chaeta	= special chaeta on ant. IV

Institutional abbreviations

MNHN	= Muséum national d’Histoire naturelle, Paris
MSPU	= Moscow State Pedagogical University, Moscow
SMNG	= Senckenberg Museum of Natural History Görlitz, Görlitz

Remark

In the species description, the presence or absence of chaetae are reported relatively to the chaetotaxy of *Megalothorax minimus* Willem, 1900 sensu Schneider & D’Haese 2013.

Results

Taxonomy

Class Collembola Lubbock, 1870
Family *Neelidae* Folsom, 1896
Genus *Megalothorax* Willem, 1900

Megalothorax calvignacensis sp. nov.

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Figs 1A–C, 2–3, 8, Tables 1–2

Diagnosis

Megalothorax calvignacensis sp. nov. belongs to the *minimus*-group (Schneider & D’Haese 2013). The peculiar feature of this species is the black-grey colour of the body, common in the *incertus*-group (*M. nigropunctatus* Schneider & D’Haese, 2013, *M. perspicillum* Schneider & D’Haese, 2013), but firstly seen in the *minimus*-group.

Although the new species is morphologically similar to several species of the genus – namely *M. granulosus* Schneider & D’Haese, 2013, *M. minimus* Willem, 1900 sensu Schneider & D’Haese, 2013, *M. willemi* Schneider & D’Haese, 2013, it exhibits several distinctive features. In chaetotaxy, *M. calvignacensis* sp. nov. resembles *M. granulosus*, apart from the absence of chaetae β_1 , γ_2 , η_4 (vs their presence in *M. granulosus*). In addition, the second pair of dorsal globular sensilla s_3 is present in *M. calvignacensis* (vs absent in *M. granulosus*). Both species have a smooth mucro, 2+2 chaetae on the manubrium, an unpaired chaeta a_0 on forehead and flame-shaped inner sensilla.

Megalothorax calvignacensis sp. nov. is similar to *M. minimus* by its smooth mucro, an unpaired chaeta a_0 and similar chaetotaxy. In *M. calvignacensis* present chaeta ζ_1 (vs absent in *M. minimus*), but in *M. calvignacensis* absent chaeta β_1 (vs present in *M. minimus*). In addition, *M. calvignacensis* has flame-shaped inner sensilla (vs T-shaped in *M. minimus*). Adult specimens can be easily recognized from *M. minimus* by the pigmentation, orange in *M. minimus* (Fig. 1B, D–E).

With another widespread species, *M. willemi*, the new species shares the presence of flame-shaped inner sensilla, smooth mucro, an unpaired chaeta a_0 and similar chaetotaxy. However, in *M. calvignacensis* sp. nov. the chaeta β_1 is absent (vs present in *M. willemi*) and the chaeta ζ_1 is present (vs absent in *M. willemi*); and *M. willemi* lacks pigmentation.

Etymology

Megalothorax calvignacensis sp. nov. is named after its type locality, the commune of Calvignac.

Type material

Holotype

FRANCE • 1 ♀; Lot, Calvignac, mosses on rock face; 1.78475° E, 44.46041° N; 178 m a.s.l.; 25 Dec. 2023; Guy Bariviéra leg.; sample code nos 46-Q23-086, SMNG, slide no. SMNG-APT-AA04651.

Paratypes (9 ♀♀)

FRANCE • 5 ♀♀; Lot, Calvignac, mosses on rock face; 1.78475° E, 44.46041° N; 178 m a.s.l.; 25 Dec. 2023; Guy Bariviéra leg.; Apterygota collection SMNG, slides nos SMNG-APT-AA04652 to SMNG-APT-AA04655, tube no. SMNG-APT-EA-003-001 • 2 ♀♀; same data as for preceding; MSPU, slides nos LD 46-Q23-086-A, LD 46-Q23-086-B • 2 ♀♀; same data as for preceding; MNHN, slides nos 46-Q23-086A, 46-Q23-086B.

Other material examined

FRANCE • 6 specs in ethanol; Lot, Calvignac, mosses on rock face; 1.78475° E, 44.46041° N; 178 m a.s.l.; 25 Dec. 2023; Guy Bariviéra leg.; Apterygota collection SMNG, tube no. SMNG-APT-EA-003-001
• several specs in ethanol; same data as for preceding; MNHN.

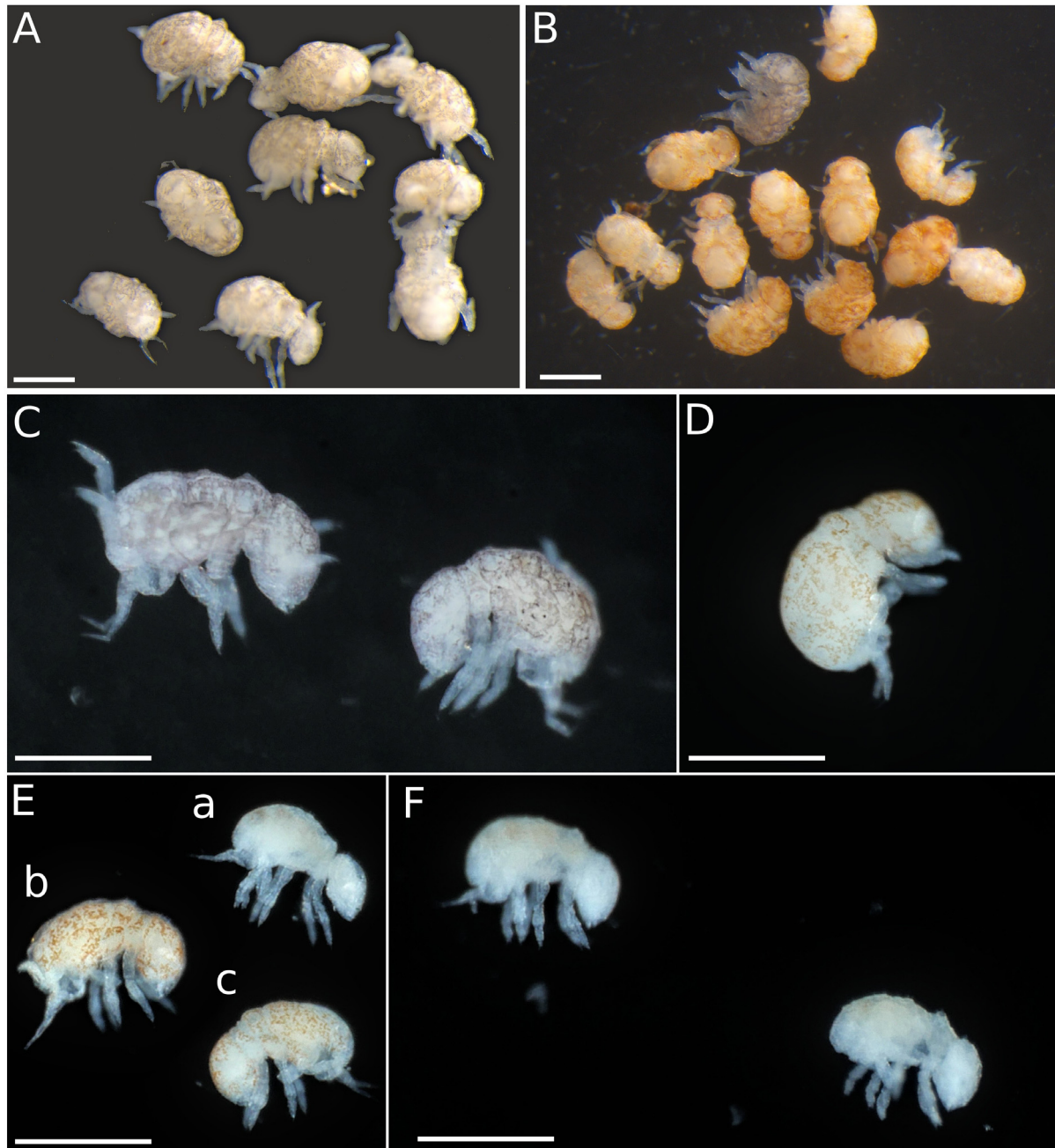


Fig. 1. Specimens of *Megalothorax* Willem, 1900 in ethanol. **A.** *M. calvignacensis* sp. nov. (MNHN). **B.** Grey individual = *M. calvignacensis* sp. nov. (MNHN); orange individuals = *M. minimus* Willem, 1900. **C.** *M. calvignacensis* sp. nov., paratypes, ♀♀ (SMNG). **D.** *M. minimus* (SMNG), co-occurring with previous. **E.** a = *M. cellaricola* sp. nov., paratype, ♀, (SMNG); b–c = co-occurring *M. minimus* (SMNG). **F.** *M. poisotae* sp. nov., paratype, ♀♀, (SMNG). All scale bars = 200 um.

Description

GENERAL ASPECT. Habitus and segmentation typical of the genus. Body length up to 500 μm . Specimens grey in alcohol (Fig. 1A–C). General chaetotaxy typical of the genus, trichobothria not studied. All chaetae ordinary, not lanceolate.

INTEGUMENT. Secondary granulation made of the usual dorsal rough granule. Integumentary channels extending laterally and dorsally in anterior and posterior parts of head. Anterior canal branching. Channels connection with linea ventralis roundabout-like.

SENSORY FIELDS AND WAX RODS (Fig. 2A). Sensory fields (sf 1–6) and their inner sensilla, as well as wax rod crypts wrc 1–7 with typical distribution of the genus. All inner sensilla of sensory fields are flame-shaped, the inner sensilla of sf 2 broad.

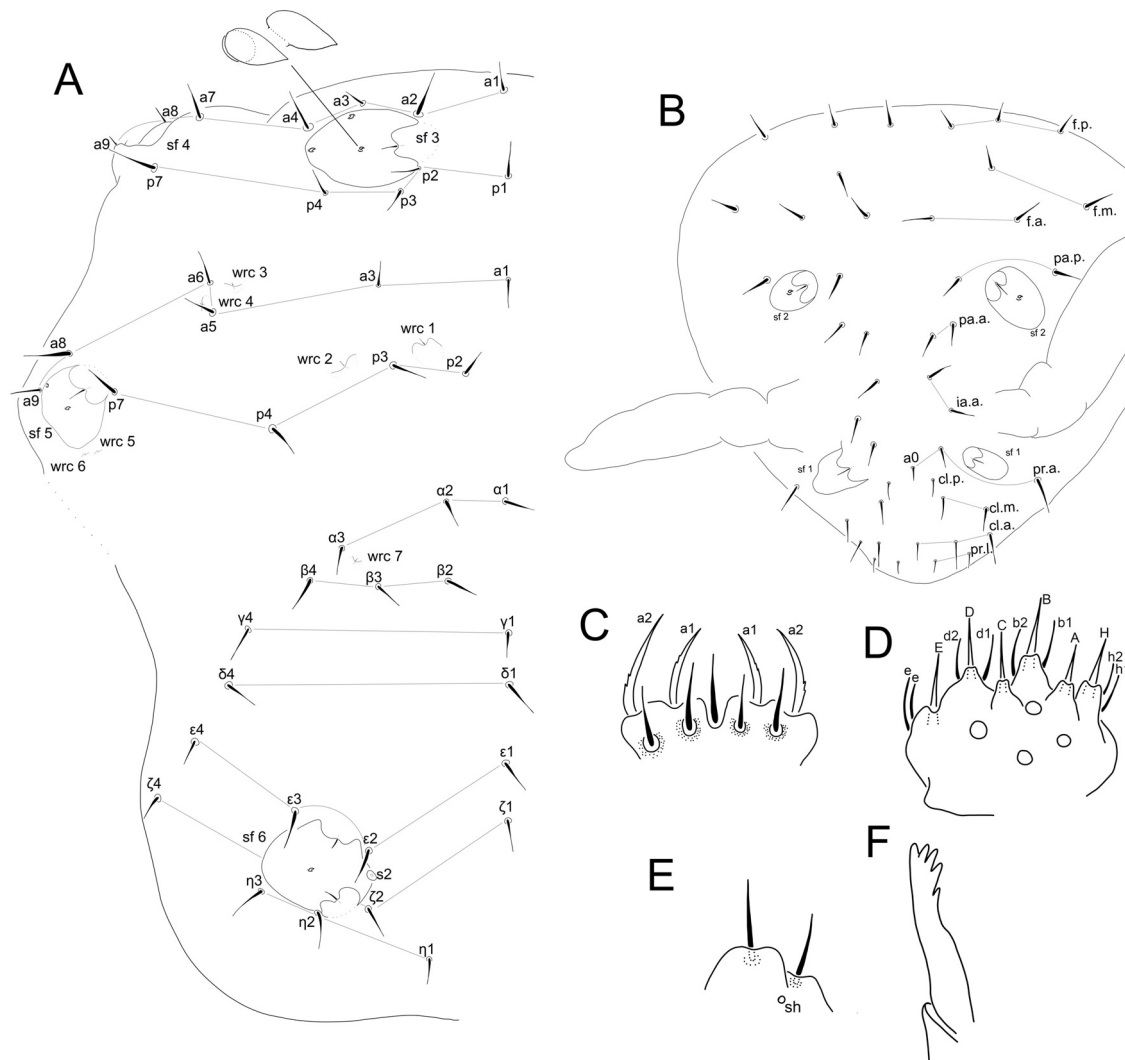


Fig. 2. *Megalothorax calvignacensis* sp. nov., holotype, ♀ (slide no. SMNG-APT-AA04651) **A.** Trunk tergites chaetotaxy, dorsal view (sf 4 not shown). **B.** Head, dorsal view. **C.** Labrum. **D.** Labial palp. **E.** Maxillary outer lobe without sublobal hair (sh). **F.** Mandibula. Abbreviations: see Material and methods. Images are not to scale.

MOUTHPARTS. Labrum as typical of the genus (Fig. 2C). Chaetae a1 pointing inward, with two teeth. Chaetae a2 with two small teeth. Labium with 4+4 proximal chaetae (Fig. 2D). Basomedian field with 3+3 chaetae. Labial palp (Fig. 2D) typical of the genus (A, B, C, D, E, b1, b2, d1, d2, 2e, H, h1, h2). Oral fold and maxillary outer lobe typical of the genus, without sublobal hair (Fig. 2E). Maxillary head without strong modification. Mandibula ordinary (Fig. 2F).

Head chaetotaxy. Forehead chaetotaxy as on Fig. 2B. Clypeal-labral formula: a0; 2, 4, 5, 4, 5, 4. Chaeta a0 present. Dorsal posterior area with 18 ordinary chaetae (Fig. 2B). Ventral side with three pairs of post-labial chaetae. Trend for posterior chaetae to be longer and stronger than anterior chaetae.

ANTENNAL CHAETOTAXY (Fig. 3A–B). Ant. I and II with one and four chaetae, respectively. Ant. III with seven chaetae and two long S-chaetae (S1 and S4). Striations of Ant III sensory organ short sensilla (S2 and S3) distinguishable in light microscopy. Ant. IV with seven chaetae (X-chaeta present) and ten S-chaetae. Sensory organ with Sx, Sy, Or, a, Sa. Organite (Or) of Ant IV short, seems apically flared. Summary on antennal chaetotaxy provided in Table 1.

BODY CHAETOTAXY. Th. II with 12+12 chaetae, 1+1 tubular and curved s1-sensilla (Fig. 2A). All chaetae ordinary. Th. III with 10+10 chaetae (some chaetae more lanceolate), 6+6 free wax-rods (wrc1–6). Chaeta a6 is longer and stronger than chaeta a5. Abd I–V terga with 20+20 ordinary chaetae, with 1+1 wrc (wrc 7 ordinary), 1+1 globular sensilla s2 (Fig. 2A). Sensilla s3 absent.

LEGS CHAETOTAXY. Typical of the genus (Table 2), consisting of ordinary chaetae of variable size (Fig. 3C–E).

CLAWS. Claw III bulkier than claw I and II. Claws subequal in unguis length (with a trend as unguis I > unguis II > unguis III). Unguis basal and posterior auxiliary lamellae well developed (Fig. 3C–E). Unguiculus 0.5–0.6 as long as unguis.

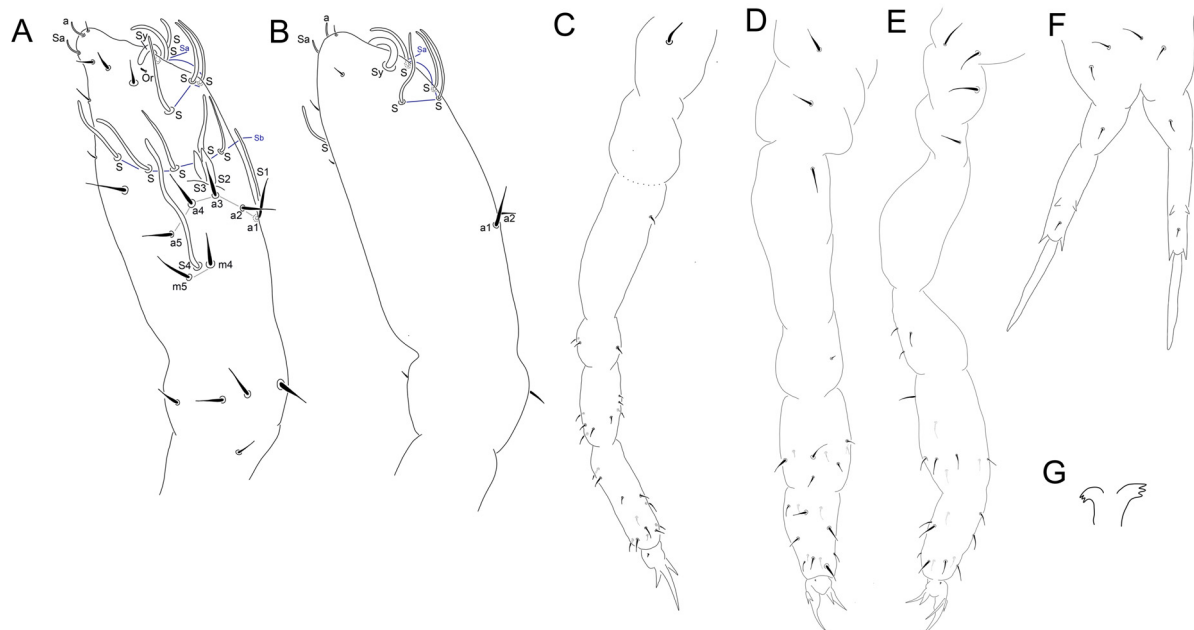


Fig. 3. *Megalothorax calvignacensis* sp. nov., holotype, ♀ (slide no. SMNG-APT-AA04651). **A.** Antenna, anterior view. **B.** Antenna, posterior view. **C.** Leg I. **D.** Leg II. **E.** Leg III. **F.** Furca, posterior view. **G.** Retinaculum. Abbreviations: see Material and methods. Images are not to scale.

ABD. IV STERNUM AND FURCA. Abd. IV sternum with 2+2 neosminthuroid chaetae and 2+2 chaetae. Manubrium with 2+2 posterior chaetae and 1+1 pegs with convex tip articulated with a corresponding concavity of the dens (Fig. 3G). Proximal subsegment of dens with a posterior chaeta (Fig. 3G); distal subsegment posteriorly with two basal spines and one chaeta at the middle. Anterior side of dens with five apical spines, spines without elongated apex (Fig. 3G). Dens ordinary, as in Fig. 3G. Mucro smooth, without teeth (Fig. 3G).

ABD. VI: ordinary with nine dorsal chaetae; each anal valve with a chaeta. Mature females with 8+8 ventral chaetae each anal valve with a chaeta av and several granular crests; mature females with 6+6 to 8+8 ventral chaetae. Genital plate: female with 2+2 chaetae. Male unknown.

TENACULUM AND VENTRAL TUBE. Tenaculum with 3+3 hook-like teeth (Fig. 3F). Ventral tube bulky with two apical pairs of chaetae.

Distribution and ecology

So far known only from the type locality, where it co-exists with *M. minimus*.

Molecular data

One topotype specimen sequenced (sample code 46-Q23-086), BOLD process id CSCOL002-25.

Megalothorax cellaricola sp. nov.

urn:lsid:zoobank.org:act:DC2D90F0-4C71-426E-9D20-466D80EAA45A

Figs 1E, 4–5, 8, Tables 1–2

Diagnosis

Megalothorax cellaricola sp. nov. can be attributed to the *incertus*-group in understanding of Schneider & D'Haese (2013). The new species shows all characters of this group: Abd IV sternum with 3+3 chaetae, inner sensilla of sensory fields globular, retinaculum with 4+4 teeth, connection of channels with linea ventralis crossed on the head, abdomen with 2+2 globular sensilla (s2, s3), basomedian fields of labium with 4+4 chaetae. Characters of *M. cellaricola* are the presence of s3 sensilla, globular inner sensilla and serrated mucro. Another unique character is the presence of strong lanceolate chaetae on the back of the head and almost all over the body (in other species only the setae of the back of the head are thickened and lanceolate in shape).

In chaetotaxy, the new species resembles *M. laevis* Schneider *et al.*, 2018, apart from the absence (vs presence in *M. laevis*) chaetae β_3 and ζ_4 on abdomen. In addition, *M. cellaricola* sp. nov. has chaeta β_2 (absent in *M. laevis*) and serrated mucro (vs smooth in *M. laevis*). *Megalothorax cellaricola* is similar in chaetotaxy to *M. perspicillum* Schneider *et al.*, 2013, excepting the presence of chaeta β_1 (vs its absence in *M. perspicillum*) and the absence of cuticular channels on the body (vs its presence in *M. perspicillum*). The widespread species *M. incertus* differs from the new species by the absence of chaeta a3 on thorax II (vs its presence in *M. cellaricola*).

Of the incompletely described species, the new species can be compared with *M. interruptus* Hüther, 1967 from Sudan, which is also closely related to *M. laevis*. In addition to the strong lanceolate chaetae on the back of the head and almost all over the body, *M. cellaricola* sp. nov. differs from *M. interruptus* in the serrated mucro (vs smooth mucro in *M. interruptus*) and 4+4 teeth on retinaculum (vs 3+3 in *M. interruptus*).

Etymology

The name is formed from the late latin ‘*cellarium*’ (‘storeroom’) and ‘*incola*’ (‘inhabitant’) and refers to the known habitat of this species.

Type material

Holotype

FRANCE • 1 ♀; Puy-de-Dôme, Clermont-Ferrand, Centre Ancient district; 3.084° E, 45.778° N (visited basements were within a 500 m radius of given geocoordinates); 19 Oct. 2014; Schneider leg.; underground basement, dry to humid soil, in some places with bait (pieces of vegetables); SMNG, sample code no. CS.017.FR, slide no. SMNG-APT-AA04656.

Paratypes (9 ♀♀, 1 ♂ and 3 juvs)

FRANCE • 6 ♀♀; Puy-de-Dôme, Clermont-Ferrand, Centre Ancient district; 3.084° E, 45.778° N (visited basements were within a 500 m radius of given geocoordinates); 19 Oct. 2014; Schneider leg.; underground basement, dry to humid soil, in some places with bait (pieces of vegetables) Apterygota collection SMNG, slides nos SMNG-APT-AA04657 to 62 • 1 ♂; same data as for preceding; Apterygota collection SMNG, slide no. SMNG-APT-AA04663 • 3 juvs; same data as for preceding; Apterygota collection SMNG, slides nos SMNG-APT-AA04664 to 66 • 3 ♀♀; same data as for preceding; MPSU, slides nos CS.17.FR-67, CS.016.FR-60, CS.018.FR-73.

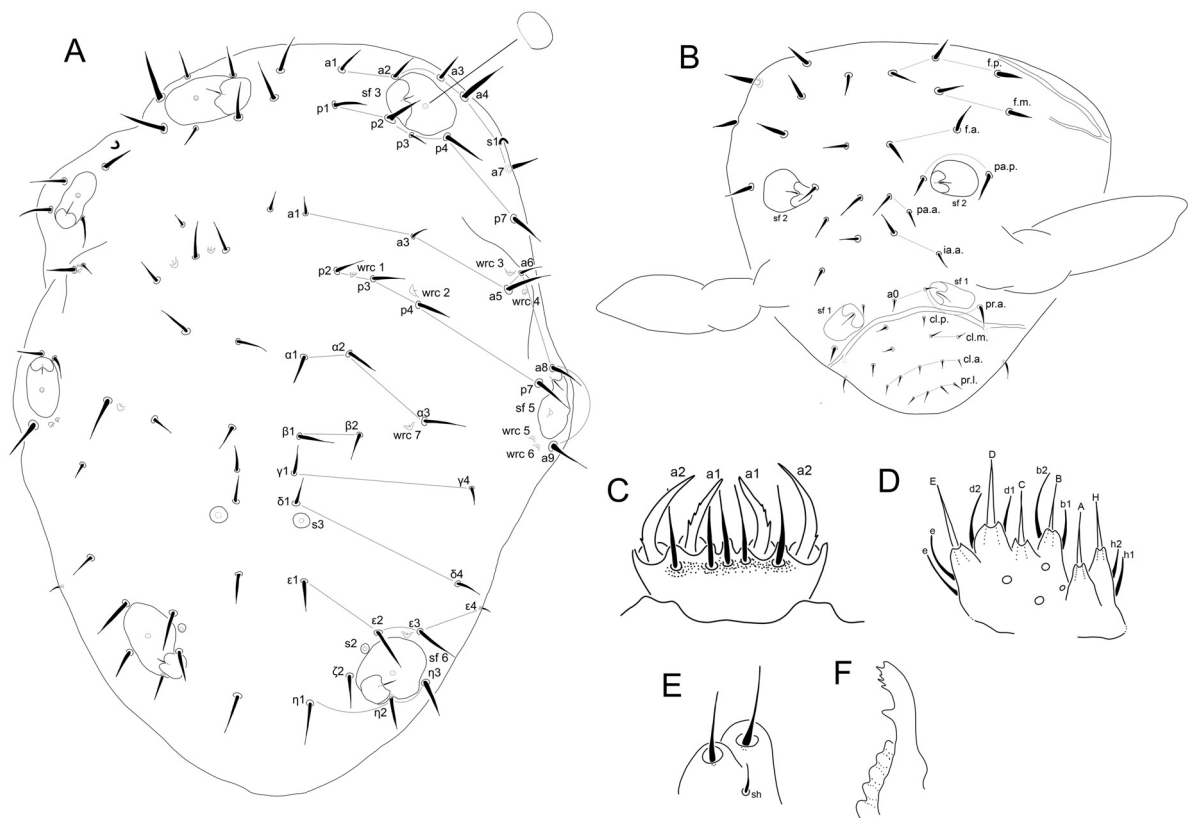


Fig. 4. *Megalothorax cellaricola* sp. nov. **A–B.** Holotype, ♀ (slide no. SMNG-APT-AA04656). **A.** Trunk tergites chaetotaxy, dorsal view (sf 4 not shown). **B.** Head, dorso-lateral view. **C–F.** Paratype, ♀ (slide no. SMNG-APT-AA04657). **C.** Labrum. **D.** Labial palp. **E.** Maxillary outer lobe with one sublobal hair (sh). **F.** Mandibula. Abbreviations: see Material and methods. Images are not to scale.

Other material

FRANCE • some specs kept in ethanol, number unknown due to possible ambiguity with co-occurring young *M. minimus*; same data as for holotype • several specs in ethanol, number unknown due to possible ambiguity with co-occurring young *M. minimus*; same data as for holotype; Apterygota collection SMNG, tubes no. SMNG-APT-EA-003-002–004.

Description

GENERAL ASPECT. Habitus and segmentation typical of the genus. Body length up to 300 µm. Specimens whitish in alcohol (Fig. 1E). General chaetotaxy typical of the genus, trichobothria not studied. Most chaetae lanceolate on body, but some are of ordinary morphology.

INTEGUMENT. Secondary granulation made of the usual dorsal rough granules. Integumentary channels extending laterally and dorsally in anterior and posterior parts of head. Anterior canal making the full circle around the head, branching near chaeta pr.a. (Fig. 4B). Channels connection with linea ventralis crossed.

SENSORY FIELDS AND WAX RODS (Fig. 4A–B). Sensory fields (sf 1–6) and their inner sensilla, as well as wax rods wrc1–7 with typical distribution for the genus. All inner sensilla of sensory fields are globular.

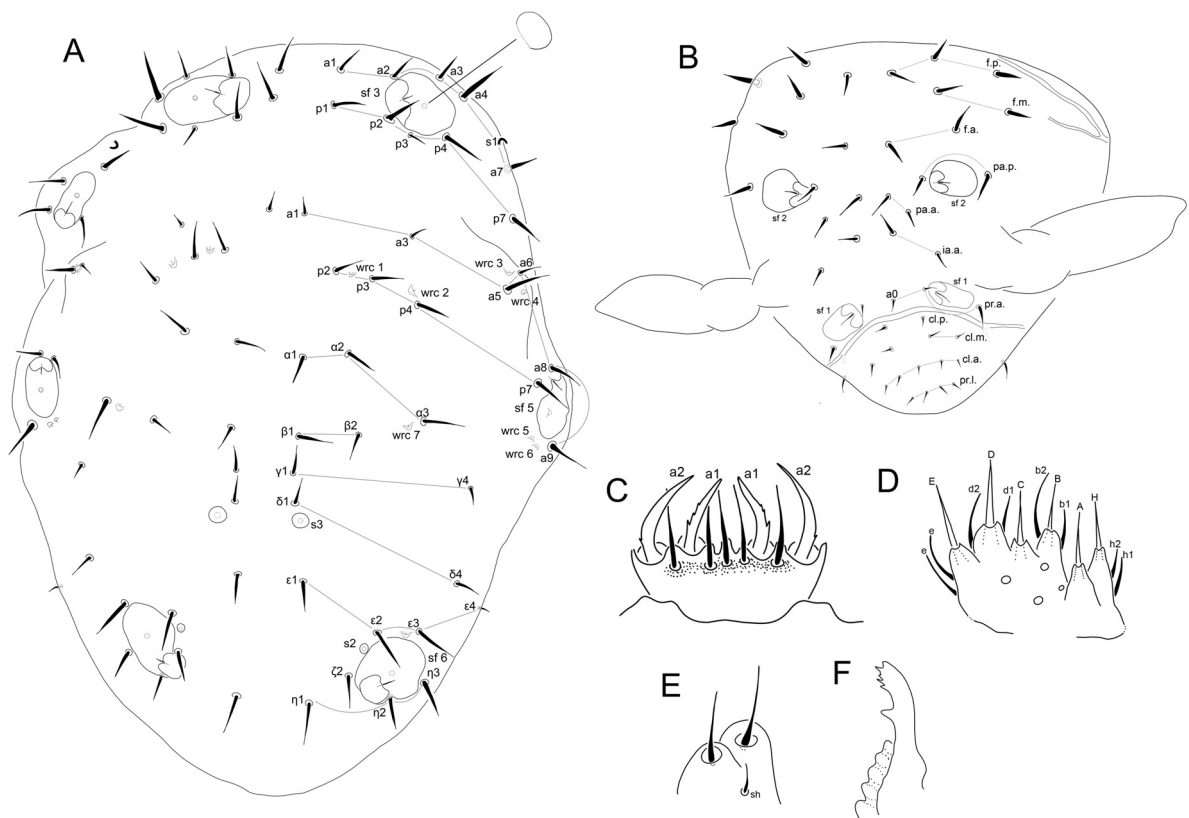


Fig. 4. *Megalothorax cellaricola* sp. nov. **A–B.** Holotype, ♀ (slide no. SMNG-APT-AA04656). **A.** Trunk tergites chaetotaxy, dorsal view (sf 4 not shown). **B.** Head, dorso-lateral view. **C–F.** Paratype, ♀ (slide no. SMNG-APT-AA04657). **C.** Labrum. **D.** Labial palp. **E.** Maxillary outer lobe with one sublobal hair (sh). **F.** Mandibula. Abbreviations: see Material and methods. Images are not to scale.

MOUTHPARTS. Labrum as typical of the *incertus*-group with tips of a1-chaetae pointing forward (Fig. 4C). Chaetae a1 with three external teeth. Chaetae a2 with one small external tooth. Labium with 4+4 proximal chaetae (Fig. 4D). Basomedian field with 3+3 chaetae. Labial palp (Fig. 4D), as common for the genus (A, B, C, D, E, b1, b2, d1, d2, 2e, H, h1, h2). Oral fold and maxillary outer lobe as typical of the genus, with one sublobal hair (Fig. 4E). Maxillary head without strong modification. Mandibula ordinary (Fig. 4F).

HEAD CHAETOTAXY. Forehead chaetotaxy as on Fig. 4B. Clypeal-labral formula: a0; 2, 4, 5, 4, 5, 4. Chaeta a₀ present. Dorsal posterior area with 18 strong lanceolate chaetae (Fig. 4B). Posterior chaetae lanceolate, longer and stronger than anterior chaetae. Ventral side with three pairs of post-labial chaetae.

ANTENNAL CHAETOTAXY (Fig. 5A–B). Ant. I and II with one and four chaetae, respectively. Ant. III with eight chaetae and two long S-chaetae (S1 and S4). Striations of Ant III sensory organ short sensilla (S2 and S3) distinguishable in light microscopy. Ant. IV with six chaetae (including X-chaeta) and ten S-chaetae. Sensory organ with Sx, Sy, Or, a, Sa. Organite (Or) of Ant IV short, seems apically flared. Summary on antennal chaetotaxy provided in Table 1.

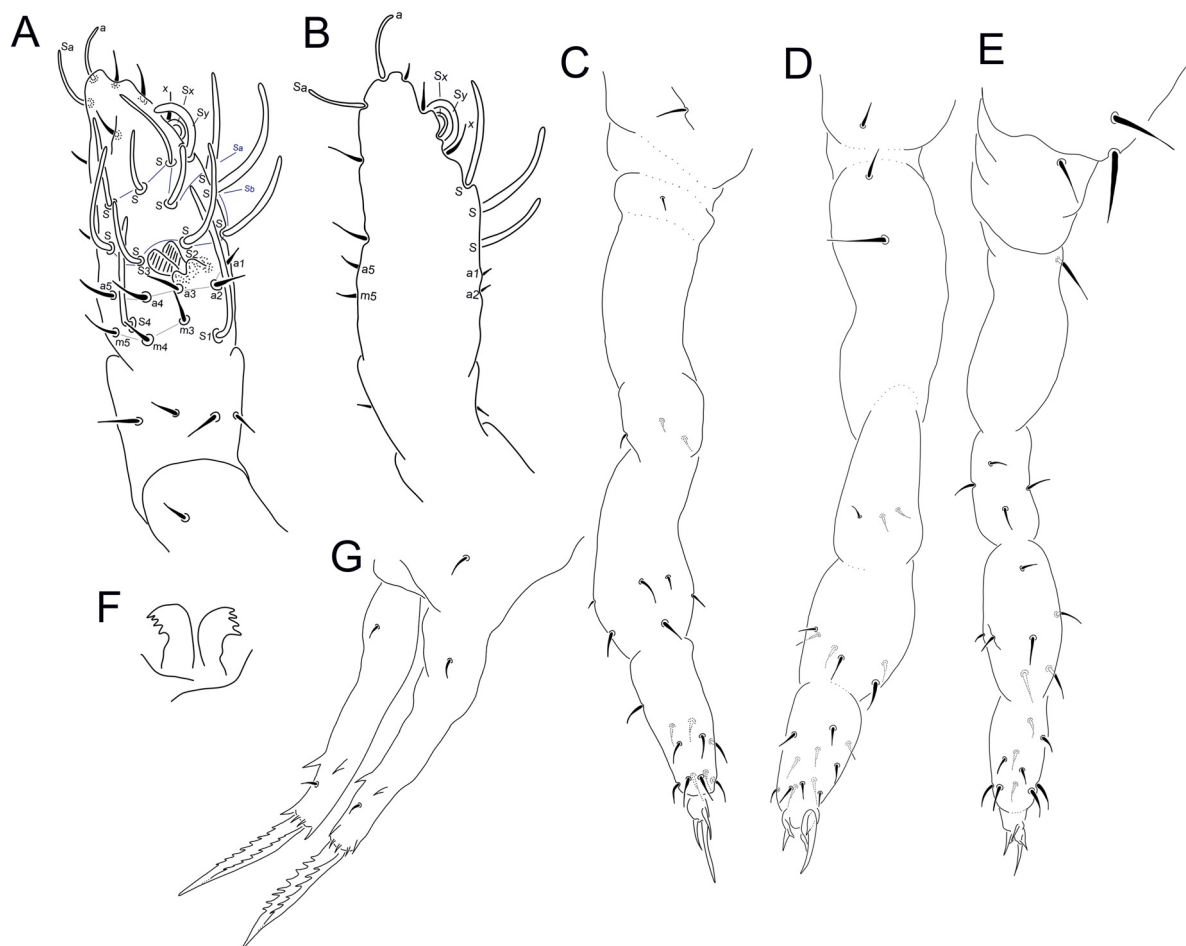


Fig. 5. *Megalothorax cellaricola* sp. nov. **A–E.** Holotype, ♀ (slide no. SMNG-APT-AA04656). **A.** Antenna, anterior view. **B.** Antenna, posterior view. **C.** Leg I. **D.** Leg II. **E.** Leg III. **F–G.** Paratype, ♀ (slide no. SMNG-APT-AA04657). **F.** Fetinaculum. **G.** Furca, posterior view, paratype. Abbreviations: see Material and methods. Images are not to scale.

BODY CHAETOTAXY. Th. II with 12+12 chaetae, 1+1 tubular and curved s1-sensilla (Fig. 4A). Chaetae a1, a4, p1, p2 and p4 longer and stronger than other, lanceolate. Th. III with 10+10 chaetae (some chaetae more lanceolate), 6+6 free wax-rods (wrc 1–6). Chaeta a5 is longer and stronger than chaeta a6. Abd I–V terga with 17+17 ordinary chaetae (some chaetae around sf 6 longer and lanceolate), with 1+1 wrc (wrc 7 ordinary), 2+2 globular sensilla s2 and s3 (Fig. 4A). Sensilla s3 bigger than s2.

LEGS CHAETOTAXY. Typical of the genus (Table 2), consisting of ordinary chaetae of variable size (Fig. 5C–E).

CLAWS. Claw III bulkier than claw I and II. Claws subequal in unguis length (with a trend as unguis I > unguis II > unguis III). Unguis basal and posterior auxiliary lamellae (Ia, Ip and Bp) well developed (Fig. 5C–E). Unguiculus 0.5–0.6 as long as unguis.

ABD. IV STERNUM AND FURCA. Abd. IV sternum with 2+2 neosminthuroid chaetae and 2+2 chaetae. Manubrium with 1+1 posterior chaetae (Fig. 5G). Proximal subsegment of dens with a posterior chaeta (Fig. 5G); distal subsegment posteriorly with two basal spines and one chaeta at the middle. Anterior side of dens with five apical spines, spines ordinary without elongated apex (Fig. 5G). Dens ordinary, as in Fig. 5G. Mucro with thin lamellae, with ~8 teeth on each posterior lamella (Fig. 5G).

ABD. VI. Typical of the genus: with nine dorsal chaetae; each anal valve with a chaeta av and several granular crests; mature females with 6+6 to 8+8 ventral chaetae. Genital plate: female with 2+2 chaetae. Male genital plate not studied (preparation unsuitable).

TENACULUM AND VENTRAL TUBE. Tenaculum with 4+4 hook-like teeth (Fig. 5F). Ventral tube bulky with two apical pairs of chaetae.

Distribution and ecology

Megalothorax cellaricola sp. nov. is so far only known from its type locality, where it coexists with *M. minimus*. It is an inhabitant of man-made subterranean habitats, similarly to *Megalothorax sanctistephani* Christian, 1998.

Molecular data

Two topotype specimens sequenced (sample code CS.17.FR and CS.16.FR), BOLD process id CSCOL003-25 and CSCOL004-25.

***Megalothorax poinsotae* sp. nov.**

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Figs 1F, 6–8, Tables 1–2

Diagnosis

Megalothorax poinsotae sp. nov. can be attributed to the *incertus*-group with the common character states combination: cross connection of head channels with linea ventralis, serrated mucro, presence of s3 sensilla on abdomen, globular inner sensilla, 2+2 chaetae in the basolateral field of labium, 3+3 chaetae on Abd. IV sternites and 4+4 teeth on the retinaculum.

This species is similar to *M. cellaricola* sp. nov. by the presence of strong lanceolate chaetae on the back of the head and some parts of the thorax. These species are distinguished by the chaetotaxy of the abdomen. In *M. poinsotae* sp. nov. chaetae p4 and ε1 are absent (vs present in *M. cellaricola*).

Etymology

The species is dedicated posthumously to Nicole Poinot, for her work on the taxonomy and ecology of Collembola in Provence. Poinot reported a so-called *M. minimus* (this species was ambiguously defined at the time) in the sansouire, an halophilous vegetal formation of Camargue (Poinot 1975).

Type material

Holotype

FRANCE • ♀; Var, Sainte-Maxime, plage de la Madrague, litter and algae among *Salicornia* L.; 6.65684° E, 43.31301° N; ca 1 m a.s.l.; 27 Jan. 2024; Deharveng and Bedos leg; SMNG, sample code no. 83-556, slide no. SMNG-APT-AA04667.

Paratypes (6 ♀♀)

FRANCE • 2 ♀♀; Var, Sainte-Maxime, plage de la Madrague; 6.65684° E, 43.31301° N; ca 1 m a.s.l.; 27 Jan. 2024; Deharveng and Bedos leg; litter and algae among *Salicornia* L.; Apterygota collection SMNG, slides nos SMNG-APT-AA04668 to 71 • 2 ♀♀; same data as for preceding; MPSU, slides nos 83-556–spec1, 83-556–spec2 • 2 ♀♀; same data as for preceding; MNHN, slides nos 83-556A, 83-556B.

Other material

FRANCE • several specs in ethanol; Var, Sainte-Maxime, plage de la Madrague, litter and algae among *Salicornia* L.; 6.65684° E, 43.31301° N; ca 1 m a.s.l.; 27 Jan. 2024; Deharveng and Bedos leg; Apterygota collection SMNG, tubes no. SMNG-APT-EA-003-005 • several specs in ethanol; same data as for preceding; MNHN.

Morphological description

GENERAL ASPECT. Habitus and segmentation typical of the genus. Body length up to 400 µm. Specimens whitish in ethanol. Body chaetotaxy sparse including chaetae, s-chaetae, trichobothria, neosminthuroid chaetae, wax-rods and inner sensilla within sensory fields 2–6. Most of chaetae lanceolate on body, but some are of ordinary morphology.

INTEGUMENT. Secondary granulation made of the usual dorsal rough granules. Integumentary channels not reaching the posterior part of the head, limited to short ventral channels forming a cross connection with the linea ventralis.

SENSORY FIELDS AND WAX RODS (Fig. 6A). Sensory fields (sf 1–6) and their inner sensilla, as well as wax rods wrc1–7 with typical distribution of the genus. Inner sensilla of sf 2 broad flame-shaped, the other s are globular.

MOUTHPARTS. Labrum as typical of the *incertus*-group with tips of a1-chaetae straightening up to point forward, a1 with two small external teeth, a2 external teeth imperceptible.

LABIUM. With 4+4 proximal chaetae, basomedian fields with 3+3 chaetae, basolateral fields with 2+2 chaetae (Fig. 6E). Labial palp (Fig. 6E) as common for the genus (A, B, C, D, E, b1, b2, d1, d2, 2e, H, h1, h2). Oral fold and maxillary outer lobe as typical of the genus, with two sublobal hair (Fig. 6F). Maxillary head without strong modification (Fig. 6C). Mandibula ordinary (Fig. 6D).

HEAD CHAETOTAXY. Forehead chaetotaxy as on Fig. 6B. Clypeal-labral formula: a0; 2, 4, 5, 4, 5, 4. Chaeta a0 present. Dorsal posterior area with 18 ordinary chaetae (Fig. 6B). Ventral side with three pairs of post-labial chaetae. Trend for posterior chaetae to be longer and stronger than anterior chaetae, including posterior lanceolate chaetae.

ANTENNAL CHAETOTAXY (Fig. 7A, B). Ant. I and II with one and four chaetae, respectively. Ant. III with nine chaetae and two long S-chaetae (S1 and S4). Striations of Ant III sensory organ short sensilla (S2 and S3) distinguishable in light microscopy. Ant. IV with five chaetae (X-chaeta present) and ten S-chaetae. Sensory organ with Sx, Sy, Or, a, Sa. Organite (Or) of Ant IV short, seems apically flared. Summary on antennal chaetotaxy provided in Table 1.

BODY CHAETOTAXY. Chaetotaxy of thorax and abdomen reduced. Th. II with 12+12 chaetae, 1+1 tubular and curved s1-sensilla (Fig. 6A). All chaetae ordinary. Th. III with 9+9 chaetae (chaeta p4 absent) and 5+5 free wax-rods (wrc 2 absent). Chaeta a5 is longer and stronger than chaeta a6. Abd I–V terga with 17+17 ordinary chaetae (chaetae β 3, β 4, ϵ 1 absent) with 1+1 wrc (wrc 7 ordinary), 2+2 globular sensilla s2 and s3 (Fig. 6A). Sensilla s3 bigger than s2.

LEGS CHAETOTAXY. Typical of the genus (Table 2), consisting of ordinary chaetae of variable size (Fig. 7C–E).

CLAWS. Claw III bulkier than claw I and II. Claws subequal in unguis length (with a trend as unguis I > unguis II > unguis III). Unguis basal and posterior auxiliary lamellae well developed (Figs 7C–E). Unguiculus 0.5–0.6 as long as unguis.

ABD. IV STERNUM AND FURCA. Abd. IV sternum with 2+2 neosminthuroid chaetae and 2+2 chaetae. Manubrium with 1+1 posterior chaetae (Fig. 7F). Proximal subsegment of dens with a posterior chaeta (Fig. 7F); distal subsegment posteriorly with two basal spines and one chaeta at the middle. Anterior side

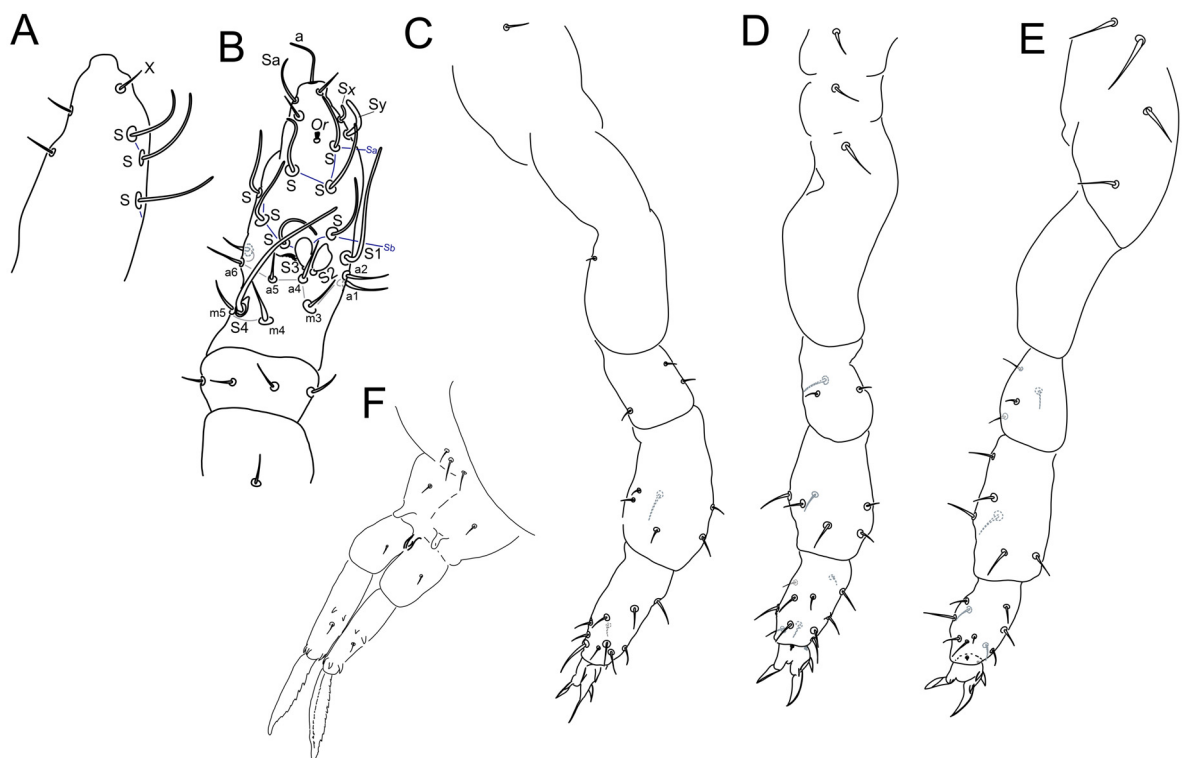


Fig. 7. *Megalothorax poinsotae* sp. nov. **A.** Holotype, ♀ (slide no. SMNG-APT-AA04667), antenna, posterior view. **B–F.** Paratype, ♀ (slide no. SMNG-APT-AA04668). **B.** Antenna, anterior view. **C.** Leg I. **D.** Leg II. **E.** Leg III. **F.** Furca, posterior view. Abbreviations: see Material and methods. Images are not to scale.

of dens with five apical spines, spines without elongated apex (Fig. 7F). Dens ordinary, as in Fig. 7F. Mucro serrated (Fig. 7F).

ABD. VI. Typical of the genus: with nine dorsal chaetae; each anal valve with a chaeta. Mature females with 8+8 ventral chaetae. Genital plate: female with 2+2 chaetae. Male unknown.

TENACULUM AND VENTRAL TUBE. Tenaculum with 4+4 hook-like teeth. Ventral tube bulky with two apical pairs of chaetae.

Distribution and ecology

So far known only from the type locality, it is the first species of *Megalothorax* to be found in a true littoral habitat (Salicornetium). Three species of Collembola were present in the same sample with *Megalothorax poinsotae* sp. nov.: an *Hypogastrura* sp., and two typically littoral species of Isotomidae: *Archisotoma* sp. and *Halisotoma* sp.

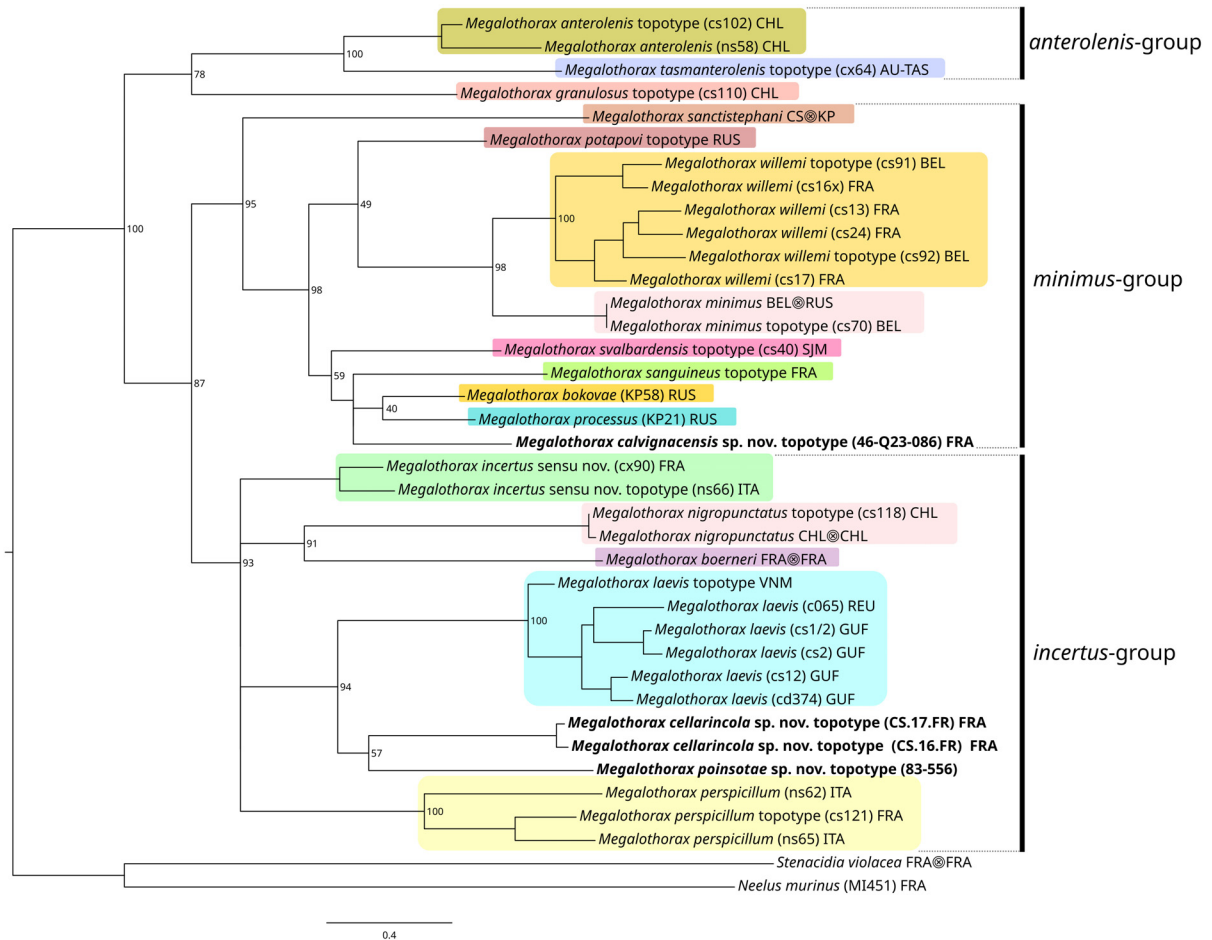


Fig. 8. Maximum likelihood phylogenetic tree of the genus *Megalothorax* Willem, 1900 based on molecular data. Nodes labels = bootstrap support (not shown when 100% or for infra-specific nodes. OTUs labels: in parenthesis = specimens number; either country indicated in ISO-3166-1 alpha3 or region indicated in ISO-3166-2; chimeric OTUs are denoted with a ⊗, left indicates origin of the mtDNA, right indicates origin of the nrDNA.

Table 1. Summary of the chaetotaxy of the antennae.

	<i>M. calvignacensis</i> sp. nov.			<i>M. cellaricola</i> sp. nov.			<i>M. poinsotae</i> sp. nov.		
	chaetae	S	Sg	chaetae	S	Sg	chaetae	S	Sg
Ant I	1	0	0	1	0	0	1	0	0
Ant II	4	0	0	4	0	0	4	0	0
Ant III	8	0	2	7	0	2	9	0	2
Ant IV	6	10	0	6	10	0	5	10	0

Table 2. Summary of the chaetotaxy of the legs.

	<i>M. calvignacensis</i> sp. nov.			<i>M. cellaricola</i> sp. nov.			<i>M. poinsotae</i> sp. nov.		
	leg I	leg II	leg III	leg I	leg II	leg III	leg I	leg II	leg III
epicoxae	1	1	2	1	1	2	1	1	2
subcoxae	0	1	1	0	1	1	0	1	1
coxae	1	1	1	1	1	1	1	1	1
trochanter	3	3	4	2	3	4	3	3	4
femur	6	6	7	8	8	8	6	6	6
tibiotarsus	12	12	10	12	12	11	11	12	10
pretarsus	2	2	2	2	2	2	2	2	2

Molecular data

One topotype specimen sequenced (sample code 83-556), BOLD process id CSCOL001-25.

Discussion

Until recently, no real distinction was made within edaphic European species of *Megalothorax* falling within the original description of *Megalothorax incertus*: whitish specimens with a serrated mucro and without exceptional morphological traits. Since Schneider & Panina (2023), and including two new species in this work, five European species can now be recognized, namely *M. incertus*, *M. boeneri*, *M. perspicillum*, *M. cellaricola* sp. nov. and *M. poinsotae* sp. nov. The two new species stand out from the others due to their enlarged lanceolate chaetae. A similar or even more spectacular chaetae enlargement is also observed in *M. australis* Delamare Deboutteville & Massoud, 1963, *Megalothorax massoudi* Deharveng, 1978 and *Megalothorax potapovi* Schneider *et al.*, 2016 (*minus*-group).

Interestingly, the use of the full rDNA operon does not allow to resolve all the relations within the species-group *minus* and *incertus* (Fig. 8). Most striking is the ambiguity at the base of the *incertus*-group. We note that two relations are well supported: the sistership of *Megalothorax nigropunctatus* (Chilean species) and *Megalothorax boeneri* Schneider & Panina 2023 (European species) and the sistership of *M. laevis* (cosmopolitan, tropical species) with *M. cellaricola* sp. nov. and *M. poinsotae* sp. nov. (the exact configuration of this triplet being unclear).

Modern sampling effort of species of *Megalothorax* mostly occurred in Europe. Despite this bias, it is possible to estimate that the *minus*-group as it is known now birthed in the Palearctic, as all the species are known from Palearctic natural habitats, and only the cosmopolitan species *minus* and *willemi*

were formally identified in other parts of the world, probably being recent invaders. The *incertus*-group, while mostly known from Europe, also includes some species native from the southern-hemisphere (*M. nigropunctatus*, *M. laevis*). Further exploration outside of the Palearctic would be desirable to further capture the diversity of the *incertus*-group and improve its phylogenetic resolution.

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