

Short communication

First fossil record of the oribatid family Liacaridae (Acariformes: Gustavioidea) from the lower Albian amber-bearing site of Ariño (eastern Spain)

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ABSTRACT

We describe the first beetle mite (Oribatida) found in the lower Albian (Lower Cretaceous) amber-bearing site of Ariño, located in the Teruel Province (eastern Iberian Peninsula). It represents the first fossil record of the family Liacaridae (Acariformes: Gustavioidea). A new species, *Liacarus (Procorynetes) shtanchaevae* Arillo and Subías sp. nov., is described and compared with the living species of the subgenus *Liacarus (Procorynetes)*. Notes on its biogeography and palaeobiology are provided. It corresponds to the first Cretaceous record of an extant oribatid subgenus and bears witness to the wide range of distribution that the ancient representatives of the subgenus may have had. Most of the oribatid species from Cretaceous ambers belong to living genera, which reflects the high degree of morphological stasis, or bradytely, over the evolutionary history of oribatid mites since the Early Cretaceous.

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1. Introduction

Beetle mites (Oribatida) are common in almost all terrestrial ecosystems, and comprise more than 10,000 described species (Subías, 2004, updated online version 2019). Some estimations have placed the number of oribatid species in the world fauna as high as 50,000–100,000 (Schatz and Behan-Pelletier, 2008). However, because of their minute size, they are rarely found in the fossil record, especially in pre-Cenozoic strata, and are mostly associated with amber deposits from the Cretaceous onwards. The oldest oribatid mites date from the Middle Devonian (Norton et al., 1988; Subías and Arillo, 2002). Only 16 oribatid species have been described in Cretaceous ambers from Lebanon, Spain, Taimyr, and Canada (Arillo et al., 2016, 2019, 2020); the species from Lebanon (Barremian) corresponds to the oldest oribatid in amber (Arillo et al., 2019). Regarding the oribatid fossil record, an outstanding upper Albian amber outcrop is San Just (Maestrazgo Basin, Teruel

Province, Spain), which contains five species (Arillo et al., 2009, 2010, 2012, 2016): *Trhypochthonius lopezvallei* Arillo, Subías and Shtanchaeva, 2012, *Cretaceobodes martinezae* Arillo, Subías and Shtanchaeva, 2010, *Ametroproctus valeriae* Arillo, Subías and Shtanchaeva, 2009, *Tenuelamellarea estefaniae* Arillo and Subías, 2016 (in Arillo et al., 2016), and *Hypovortex hispanicus* Arillo and Subías, 2016 (in Arillo et al., 2016).

Nowadays, oribatids inhabit a wide range of habitats, such as plant litter, soil, mosses, lichens, rock surfaces, bark, and leaves (Schatz and Behan-Pelletier, 2008).

Liacaridae is a forest soil dwelling family of oribatids with an almost cosmopolitan distribution, being present in all continents, except for Antarctica and Australia. It is included in the superfamily Gustavioidea. Four fossil species and one subspecies belonging to the Gustavioidea are known: three species of the family Astegistidae (*Cultroribula jurassica* Krivolutsky, 1977 (in Krivolutsky and Krasilov, 1977) from the Tithonian, in the Burea River Basin, in Far East Russia, and *Cultroribula lauta* Sellnick, 1931 and *Cultroribula superba* Sellnick, 1931, both from Eocene Baltic amber), one species of the family Xenillidae, *Xenillus tegeocraniformis* (Sellnick, 1919) from Baltic amber, and one subspecies of the family Ceratoppiidae, *Ceratoppia bipilis fossilis* Sellnick, 1919 from Baltic amber. To date,

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the families Metrioppiidae, Tenuialidae, Gustaviidae and Multoribulidae lack any fossil record. Some living species of oribatids are found as subfossils, as it is the case of the liacarid species *Adoristes* (*Adoristes*) *ovatus* (Koch, 1839) and *Liacarus* (*Liacarus*) *coracinus* (Koch, 1841) from Quaternary deposits of northern Europe (Dunlop et al., 2012).

Here, we describe a new oribatid species from the lower Albian (Lower Cretaceous) amber-bearing site of Ariño, which belongs to a living genus and subgenus of the family Liacaridae and represents the first fossil record of the family worldwide.

2. Systematics of Liacaridae

The systematics of the family Liacaridae is controversial. Woolley (1972) proposed to group it under the superfamily Liacaroidea with Astegistidae, Metrioppiidae, Xenillidae, and Tenuialidae, but Subías (2004, updated online version 2019) grouped these five families alongside Gustaviidae, Ceratoppiidae and Multoribulidae inside the superfamily Gustavioidea. Xenillidae was erected as a family that shares anatomical features with Liacaridae (Woolley and Higgins, 1966), although some authors consider it as a synonym of the latter (e.g., Weigmann, 2006; Norton and Behan-Pelletier, 2009; Dunlop et al., 2012). Nonetheless, we prefer to follow the systematics established by Subías (2004, updated online version 2019), and consider Liacaridae and Xenillidae as different families based on the body sculpture, the morphology of the histerosomal setae and the depth of the rostral grooves (Ryabinin and Zaitsev, 2019).

Analysis of the 18S rRNA gene (Schaefer and Caruso, 2019) does not shed light on the phylogeny of Gustavioidea; *Xenillus* seems to be linked to *Euzetes* Berlese, 1908 (Ceratozetoidea: Ceratozetidae) and *Ceratoppia* (Gustavioidea: Ceratoppiidae) seems to be outside the clade of the superfamily, closer to *Banksinoma* Oudemans, 1930 (Opplioidea: Thyrisomidae).

The inner systematics of the family has also changed over time. Woolley (1972) included six genera (*Liacarus* Michael, 1898, *Adoristes* Hull, 1916, *Opsioristes* Woolley, 1967, *Rhaphidosus* Woolley, 1969, *Dorycranosus* Woolley, 1969, and *Procorynetes* Woolley, 1969). Later, Subías (2004, updated online version 2019) considered *Rhaphidosus*, *Dorycranosus* and *Procorynetes* as subgenera of *Liacarus*, thus recognising six genera: *Liacarus* (with four subgenera, *Liacarus*, *Rhaphidosus*, *Dorycranosus*, and *Procorynetes*), *Adoristes* (with two subgenera, *Adoristes* and *Goedeveilla* Shtanchaeva, Subías and Arillo, 2010), *Birsteiniius* Krivolutsky, 1965, *Opsioristes*, *Planoristes* Iturrondobeitia and Subías, 1978, and *Scarabacarus* Shtanchaeva and Subías, 2010.

Currently, the subgenus *Liacarus* (*Procorynetes*) is considered to include eight species (Subías, 2004, updated online version 2019). These are *Liacarus* (*Procorynetes*) *altaicus* (Krivolutsky, 1974), *Liacarus* (*Procorynetes*) *andinus* (P. Balogh, 1984), *Liacarus* (*Procorynetes*) *breviclavatus* Aoki, 1970, *Liacarus* (*Procorynetes*) *clavatus* Fujikawa and Aoki, 1970, *Liacarus* (*Procorynetes*) *espeletiae* (P. Balogh, 1984), *Liacarus* (*Procorynetes*) *globifer* (Kramer, 1897), *Liacarus* (*Procorynetes*) *huvsgulensis* Bayartogtokh, 2010, and *Liacarus* (*Procorynetes*) *nigerrimus* Berlese, 1916. The subgenus *Liacarus* (*Liacarus*) is the most diverse of the genus, comprising 61 species and three

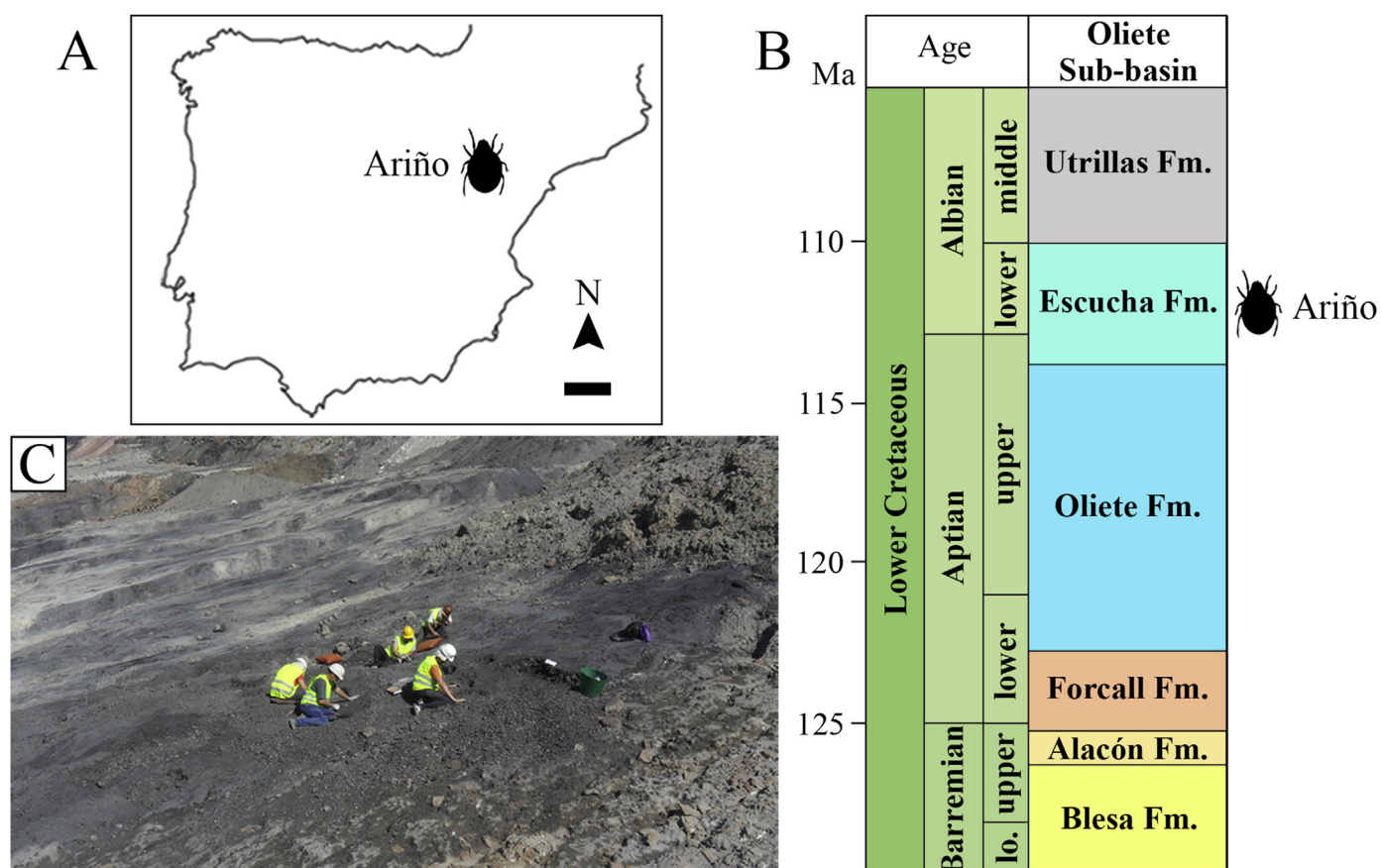


Fig. 1. Geographical and stratigraphic location of the lower Albian amber-bearing site of Ariño (Teruel Province, Spain); type locality of the oribatid species described: A) map of the Iberian Peninsula showing the location of Ariño (41° 1' N, 0° 33' W); B) approximate location of the Ariño site in the Lower Cretaceous stratigraphy of the Oliete Sub-basin, based on Aurell et al. (2018); C) amber excavation in the bonebed level AR-1 of Ariño, July 2019. Scale bar = 100 km (A).

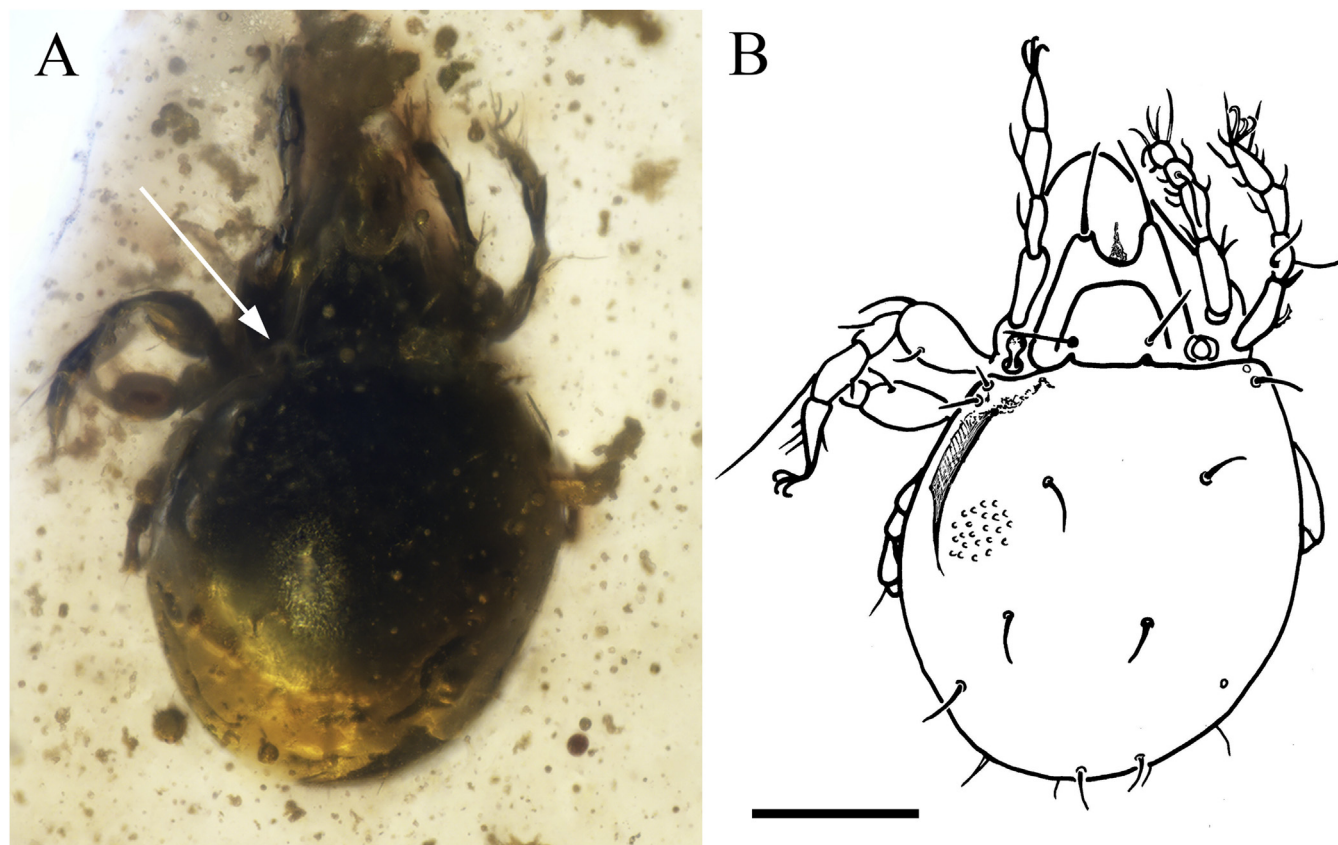


Fig. 2. *Liacarus (Procorynetes) shtanchaevae* sp. nov. (Oribatida: Liacaridae), from the lower Albian amber-bearing site of Ariño (Teruel Province, Spain), holotype AR-1-A-2019.45: A, B) photograph and drawing from dorsal view, both at the same scale, arrow in A indicates the sensilla. Scale bar = 100 μ m.

subspecies, while the subgenera *Liacarus (Dorycranosus)* and *Liacarus (Rhaphidosus)* include 36 (and one subspecies) and seven species respectively (Subías, 2004, updated online version 2019).

3. Material and methods

Fossiliferous Cretaceous amber from the Maestrazgo Basin (eastern Spain) has been known since Boscá (1910) mentioned the first apparent bioinclusions from calamine mines in the locality of Linares de Mora. To date, 31 amber-bearing outcrops have been reported in the basin, but only four of them show bioinclusions (Delclòs et al., 2007; Peñalver and Delclòs, 2010; Álvarez-Parra et al., 2021): Arroyo de la Pascueta, La Hoya, San Just and Ariño. The latter was excavated in 2019 and turned out to be a deposit that was very rich in bioinclusions, yielding the specimen studied here (Fig. 1).

The Ariño site is located in the Santa María open-pit mine (Ariño, Teruel, Spain). Geologically, it is in the Oliete Sub-basin of the Maestrazgo Basin, belonging to the Aragonese Branch of the Iberian Chain (Salas and Guimerà, 1996). The amber was found in the bonebed level AR-1 (Fig. 1), belonging to the middle member of the Escucha Formation and dated as lower Albian based on the charophyte, ostracod, and palynological assemblages (Tibert et al., 2013; Villanueva-Amadoz et al., 2015; Álvarez-Parra et al., 2021). This fossil site is highly significant as it has provided a diverse fossil record of plants, molluscs, ostracods, fish, turtles, crocodylians, and dinosaurs (Alcalá et al., 2012). It is the type locality of six vertebrate species, including two ornithischian dinosaurs, three ostracod species, and the mite species described here. The level AR-1 is mainly constituted of marls rich in organic matter (Álvarez-Parra et al., 2021). The Ariño palaeoenvironment is inferred as a

freshwater swamp plain with permanent alkaline shallow lakes, with salinity fluctuations due to marine influence, under a tropical or subtropical climate (Tibert et al., 2013; Villanueva-Amadoz et al., 2015). The presence of amber rich in arthropod inclusions in the bonebed level is interesting, as it increases the palaeoecological information about the habitat of the dinosaurs and other vertebrates (Álvarez-Parra et al., 2020a, 2021). The taphonomic conditions of this Konservat-Lagerstätte are under study and emphasize the significance of the fossil record found in this site (Álvarez-Parra et al., 2021).

The amber piece containing the fossil mite was cut and embedded in an epoxy resin prism measuring 20 \times 13 mm following the methodology of Corral et al. (1999). This technique provides stabilisation and protection to the piece. The photograph of the specimen was taken using an Olympus CX41 compound microscope with an attached digital camera sCMEX-20, through the software ImageFocusAlpha version 1.3.7.12967.20180920. Drawings were made with the aid of an Olympus U-DA drawing tube attached to an Olympus BX50 compound microscope. The figures were prepared using Photoshop CS6 and GIMP 2.10. The specimen is housed at the Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain) with the fieldwork number AR-1-A-2019.45.

This manuscript has been registered in ZooBank under the number urn:lsid:zoobank.org:pub:FCEC0E9A-5AF3-49F5-87D0-420408C4F9E9.

4. Systematic palaeontology

Order Acariformes Zakhvatkin, 1952
Suborder Oribatida Dugès, 1834

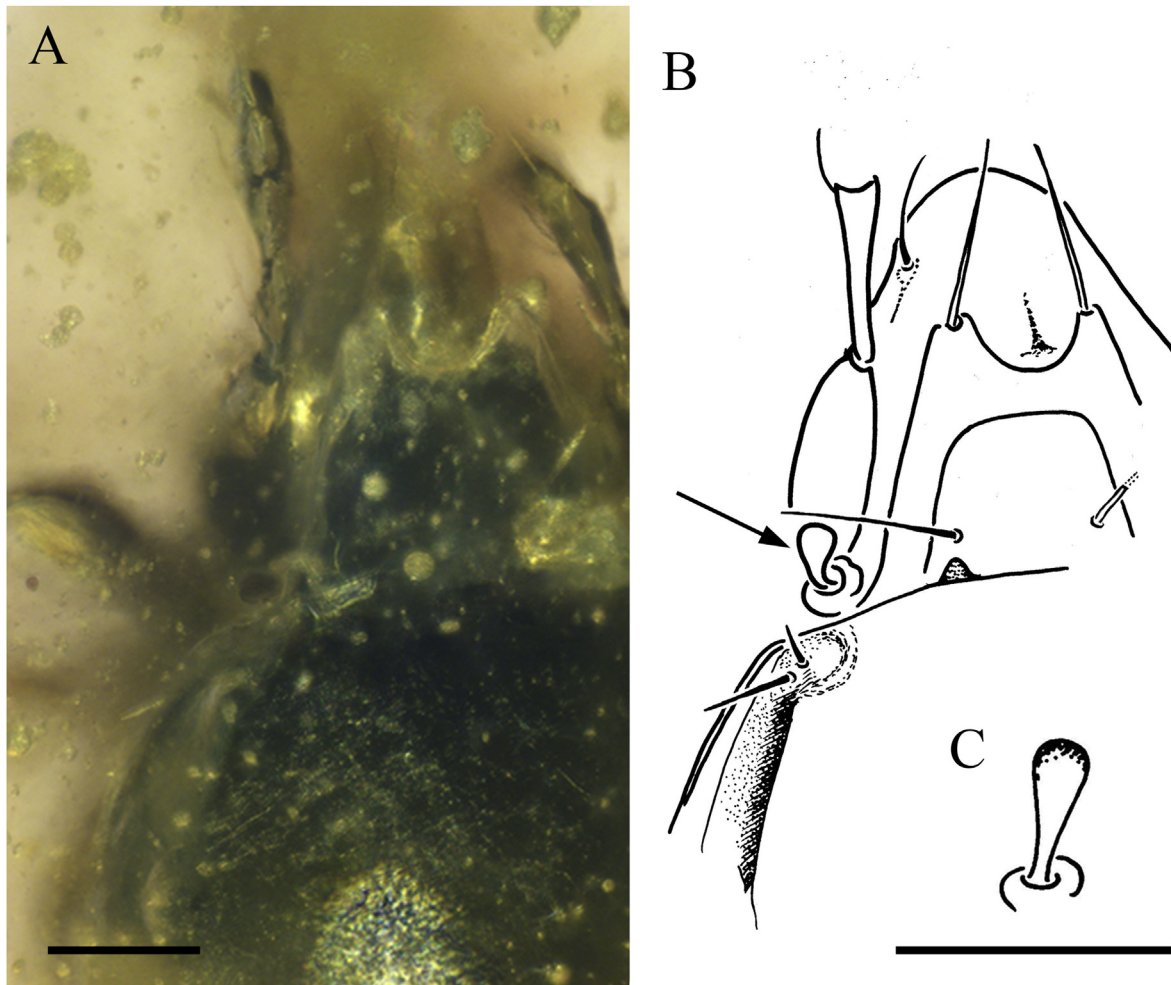


Fig. 3. *Liacarus (Procorynetes) shtanchaevae* sp. nov. (Oribatida: Liacaridae), from the lower Albian amber-bearing site of Ariño (Teruel Province, Spain), holotype AR-1-A-2019.45: A, B) photograph and drawing of the prodorsum region and anterior part of the notogaster, both at the same scale, arrow in B indicates the sensilla; C) drawing of the short and clubbed sensilla. Scale bars = 50 μ m.

Infraorder Brachypilina [Hull, 1918](#)
 Superfamily Gustavioidea [Oudemans, 1900](#)
 Family Liacaridae [Sellnick, 1928](#)

Genus *Liacarus* [Michael, 1898](#)
 (= *Leiosoma* [Nicolet, 1855 nom. praec.](#))
 (= *Leuroxenillus* [Woolley and Higgins, 1966](#))
 (= *Stenoxenillus* [Woolley and Higgins, 1966](#))
 Subgenus *Liacarus (Procorynetes)* [Woolley, 1969](#)
 Type species: *Liacarus (Procorynetes) nigerrimus* [Berlese, 1916](#)

Liacarus (Procorynetes) shtanchaevae Arillo and Subías sp. nov.
 (Figs. 2 and 3)

This new species has been registered in ZooBank under the number urn:lsid:zoobank.org:act:B70B5EB4-193B-4135-9E41-CF16BBB14088.

Holotype. Specimen number AR-1-A-2019.45, housed at the Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain).

Locality and horizon. Bonebed level AR-1 of the Ariño site, in the Santa María open-pit mine, Teruel, Spain. Maestrazgo Basin, middle interval of the lower sedimentary succession of the Escucha Formation, lower Albian ([Alcalá et al., 2012](#); [Álvarez-Parra et al., 2021](#)).

Etymology. The specific epithet is named after our oribatologist colleague Umukusum Ya. Shtanchaeva.

Diagnosis. *Liacarus (Procorynetes)* species with short lamellae and well-developed translamella. Short and clubbed sensilla.

Description. **Measurements:** Body length 397 μ m, body width 244 μ m (Figs. 2A and B).

Prodorsum: Anterior edge rounded. Short lamellae ending far from the anterior edge without cusps at the base of the lamellar setae. Well-developed translamella with arched anterior margin, without central tooth (Fig. 3A and B). Rostral, lamellar and interlamellar setae smooth and well developed. Exobothridial setae no visible. Short tailed sensilla with clubbed head slightly truncated (Fig. 3C). Tutorium absent.

Notogaster: Rounded and slightly punctuated. Seven pairs of smooth setae are visible (including two humeral pairs). Humeral region rounded, without pteromorphs. Porose area absent.

Ventral side: Poorly preserved and obscured. Distant anal and genital plates. Three pairs of adanal setae preserved, pair ad_1 being in post-anal position. Anal plates seem to bear two pairs of anal setae. Genital setae not visible. Epimeral region not visible.

Legs and chaetotaxy: Legs tridactylous. Legs I, II and III with slightly swollen femora. Chaetotaxy of legs partially preserved. Setae in femorae I slightly barbulated. Solenidia on Tibiae I and II visible.

5. Discussion

5.1. Taxonomy

The systematics of the genus *Liacarus* is mainly based on the shape of the sensillae. The new species clearly belongs to the subgenus *Liacarus* (*Procorynetes*), in view of the short tail and the clubbed head, slightly truncated, on its apex. Species within this subgenus present different types of lamellar shape. In some species, such as *L. (P.) huvsgulensis*, *L. (P.) clavatus*, *L. (P.) altaicus*, *L. (P.) andinus*, and *L. (P.) espeletiae*, the lamellae are very close to each other, without any translamellar development. Other species develop a short translamella with a medial tooth on its anterior margin, such as *L. (P.) breviclavatus* and *L. (P.) nigerrimus*. While *L. (P.) globifer* has a short translamella without medial tooth. Dubinina et al. (1966) noted that the shape of lamellae and lamellar cusps and the presence or absence of translamellar tooth have strong intraspecific variability (even in the same population) in the genus *Liacarus*.

Liacarus (Procorynetes) shtanchaevae sp. nov. is close to *L. (P.) globifer* but easily distinguished from that species by its developed translamella, shorter lamellae and shorter lamellar and interlamellar setae. Furthermore, the size of the new species is around 400 µm, while *L. (P.) globifer* is about 900 µm.

5.2. Distribution of the *Liacarus (Procorynetes) spp.*

Living *Liacarus (Procorynetes) spp.* seem to show a cold climate distribution (Fig. 4). Palaeartic species are found in boreal areas or at high elevations. *Liacarus (Procorynetes) altaicus* was described from elfin woodlands of *Pinus sibirica* and tundra in Altai Republic (Krivolutsky, 1974) and later, Behan-Pelletier (1978) found this species in different arctic and subarctic localities in Canada. Furthermore, *L. (P.) huvsgulensis* was discovered in the banks of the river Borsog in the east side of Lake Khuvsgul (Khövsgöl) at a height of 1645 m in samples of mosses and litter from forests of *Larix sibirica* (Bayartogtokh, 2010).

Concerning the Japanese species, *L. (P.) breviclavatus* was discovered in *Abies veitchii* var. *sikokana* smoking trees with insecticides on Mount Ishizuchi (1890 m) in the island of Shikoku (Aoki, 1970), and *L. (P.) clavatus* was described in a Glehn's spruce (*Picea glehnii*) forest near Obihiro in the island of Hokkaido (Fujikawa and Aoki, 1970).

The fifth Palaeartic species, *L. (P.) globifer*, was described from Greenland and later recorded in shrub samples from Kandalaksha on the shores of the White Sea (Dzhaparidze, 1987).

The two Neotropical species, *L. (P.) andinus* and *L. (P.) espeletiae*, were sampled in *Espeletia hartwegiana* dead leaves in Huila, Colombia, at a height of 3700 m (Balogh, 1984).

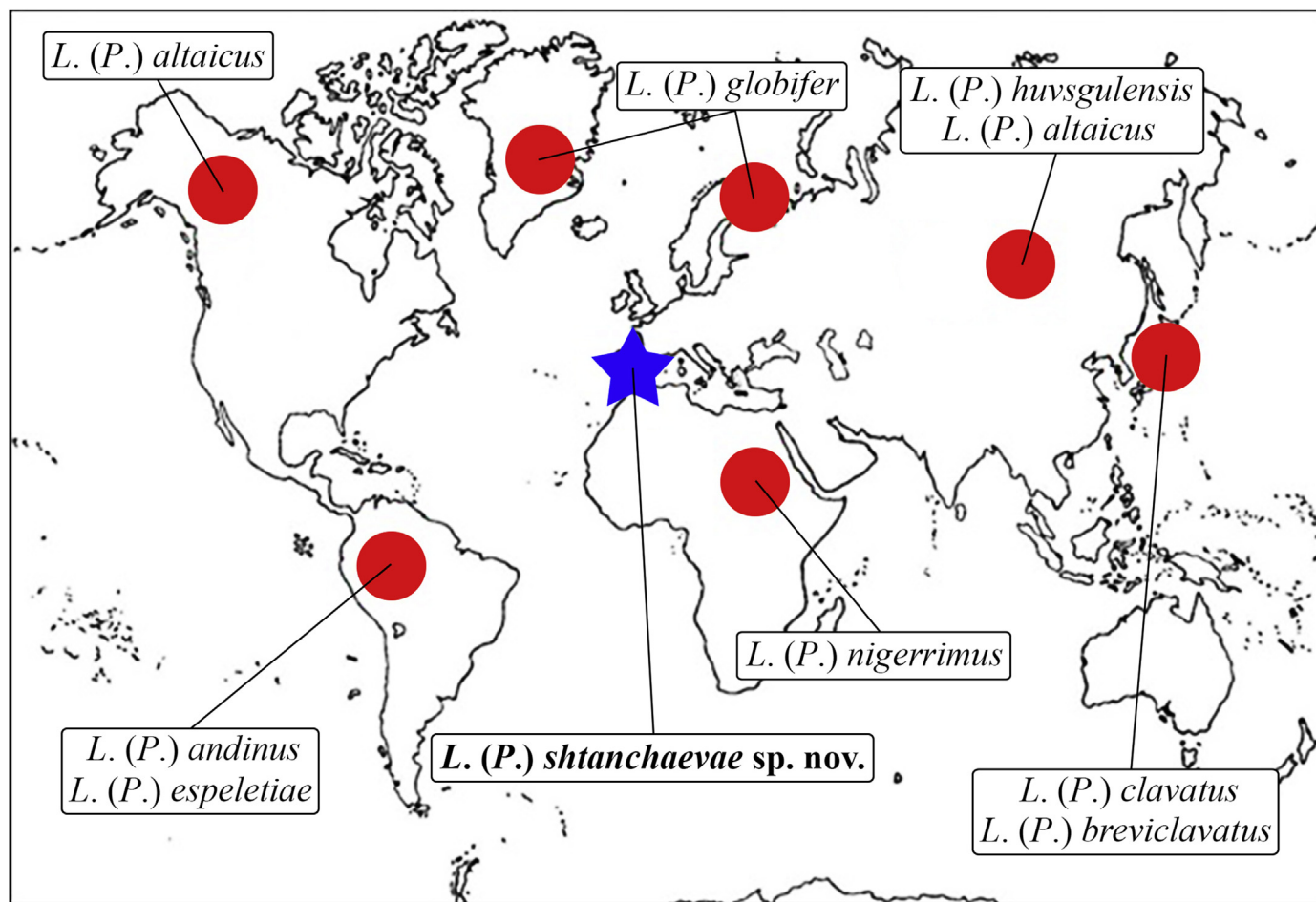


Fig. 4. Distribution of the *Liacarus (Procorynetes) spp.* (Oribatida: Liacaridae). Red dots correspond to the living species, and the blue star represents the type locality of the new fossil species from the lower Albian (Lower Cretaceous) amber-bearing site of Ariño. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Finally, the only African species, *L. (P.) nigerrimus*, was described from “East Africa”, the label of the holotype reading “Africa Orientale, Alluau et Jeannel” (Castagnoli and Pegazzano, 1985). We know that Charles A. Alluau and René Jeannel made an expedition to East Africa in 1911–1912 to study equatorial alpine fauna and they collected samples in both Mount Kenya and Mount Kilimanjaro. Therefore, the holotype must come from one of these mountains.

The presence of *L. (P.) shtanchaevae* sp. nov. during the early Albian of the Iberian Peninsula is interesting, as it corresponds to the only species of the subgenus living under a warm climate and at low altitude where the resiniferous forest thrived. Therefore, the *Liacarus (Procorynetes)* spp. seems to follow a common pattern of a relict distribution which was wider in the past, and today is restricted to cold areas or high elevations in the Holarctic and high mountains in the Afrotropical and Neotropical ecozones (Fig. 4).

5.3. Morphological stasis in oribatid mites

The new species described here belongs not just to a living genus, but to a living subgenus. This is the only case so far of a specimen of a living oribatid subgenus in the Cretaceous. However, its finding is not surprising, as oribatid mites are an important example of bradytely within arthropods: that is, long-term morphological stasis over the geological time (Simpson, 1944). Most of them have preserved a highly similar habitus and morphology since the Cretaceous that makes them almost indistinguishable from the living representatives. To date, 17 oribatid species have been described from Cretaceous ambers, 15 of them listed by Arillo et al. (2020), with the additions of the species from Lebanese amber (Arillo et al., 2019) and the species described here. Interestingly, 13 of these species belong to living genera – that is, 76% of the oribatid species from Cretaceous ambers – suggesting bradytely for these genera in particular and oribatids in general. The only four extinct oribatid genera recorded in Cretaceous ambers are: *Eocamisia* Bulanova-Zachvatkina, 1974 (Santonian, Russia), *Rasnitsynella* Krivolutsky, 1976 (in Krivolutsky and Ryabinin, 1976) (Santonian, Russia), *Strieremaeus* Sellnick, 1919 (Albian, Spain, also recorded in Eocene Baltic and Rovno ambers), and *Cretaceobodes* Arillo, Subías and Shtanchaeva, 2010 (Albian, Spain). Bradytely has usually been related to groups inhabiting mesic microhabitats, such as the leaf litter on forest soil (Yamamoto et al., 2017). Besides the oribatids, some beetles, psocids, and springtails are leaf litter inhabitants with Cretaceous species belonging to living genera (Sánchez-García and Engel, 2016; Yamamoto et al., 2017; Álvarez-Parra et al., 2020b). The body plan and general habitus of the oribatids have remained stable and almost unchanged at least since the Early Cretaceous, occupying a similar litter habitat to their living representatives. However, the evolutionary patterns over the history of the oribatids are not well known, and the description of new fossil species may draw attention to the outstanding morphological stability of this group.

6. Concluding remarks

Liacarus (Procorynetes) shtanchaevae sp. nov., from the lower Albian amber-bearing site of Ariño, represents the first fossil record of the Liacaridae, and the first Cretaceous species belonging to a living oribatid subgenus. It is the seventeenth oribatid species from Cretaceous amber described to date, and thus increases the known palaeodiversity of the group. Considering the biology of the extant representatives of the family, it may be a leaf litter dweller of the resiniferous forest community. However, the environmental conditions of its ecosystem, close to the sea and under a tropical or subtropical climate, differ from those of the living species of the

subgenus, which inhabit cold environments at high latitudes or high mountains at middle latitudes. Therefore, the new species shows that the living species of the subgenus may be relict, since the ancient representatives occupied a wider range of habitats and distribution.

Acknowledgements

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