

# New barklice (Psocodea, Trogiomorpha) from Lower Cretaceous Spanish amber

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**Abstract:** Barklice are insects belonging to the order Psocodea. They are herbivorous or detritivorous, and inhabit a wide range of environments. Their oldest fossil record dates back to the late Carboniferous, but it was not until the Cretaceous that they became much more diverse. However, their fossil record could be affected by taphonomic processes due to their tiny size and soft bodies. Here, we present new psocid specimens from five amber-bearing outcrops in Spain that are Albian in age. One of the specimens, a well-preserved psocid nymph assigned to †Archaeatropidae, lacks evidence of debris-carrying behaviour. Some of the specimens belong to the previously known species *Archaeatropos alavensis* Baz & Ortuño and *Preempheria antiqua* Baz & Ortuño (Trogiomorpha: Atropetae), providing new anatomical and biogeographical information. Furthermore, we describe a new species, *Libanoglaris hespericus* sp. nov. (†Archaeatropidae). The diagnosis for the family †Archaeatropidae is emended. The

abundance of psocids in Cretaceous amber and their virtual absence in compression outcrops could be due to taphonomic bias. Considerations on the phylogenetic placement of trogiomorphan families and the relationships between †Archaeatropidae and †Empheriidae are included. Today, the least diverse psocid suborder is Trogiomorpha, but this suborder comprises the majority of the Cretaceous psocodean species described to date, possibly due to palaeobiological or evolutionary constraints. Trogiomorphan could have been relegated to marginal habitats by niche competition with psocomorphans. Debris-carrying behaviour in response to predatory pressure might not have been widely distributed, geographically or phylogenetically, in the Cretaceous psocid nymphs.

**Key words:** Psocodea, Trogiomorpha, barklice, amber, Cretaceous.

PSOCIDS, commonly known as barklice and booklice, are hemimetabolous insects that are a few millimetres in length and are characterized by well-developed chewing mouthparts (Mockford 1993). They are considered cosmopolitan, inhabiting a wide range of habitats such as trees, rocks, caves, bird and mammal nests, ground litter, and domestic environments (New 1987). Psocids, accounting for more than 5000 living species, are herbivorous or detritivorous and feed on microorganisms and the remains of dead arthropods, thereby playing a key role as nutrient recyclers of organic matter (New 1987). Psocids are included in the order Psocodea alongside parasitic lice (Phthiraptera), with the previously known 'Psocoptera' forming a paraphyletic group (Johnson *et al.* 2018). Psocodea contains three suborders (Smithers 1972; De Moya *et al.* 2021): Trogiomorpha, Troctomorpha and Psocomorpha.

The oldest known psocodean record dates back to the late Carboniferous (Nel *et al.* 2013). A major diversification of the group took place during the Cretaceous, with 70 species described from amber dating to this period (Álvarez-Parra *et al.* 2020a, table 1; plus material subsequently described, including the new species described here). However, the lack of a pre-Cretaceous record could be due to taphonomic bias. The Cretaceous fossil record of psocids has expanded significantly in recent years with the description of the basal family †Cormopsocidae (Yoshizawa & Lienhard 2020), which has been found to be very diverse (Wang *et al.* 2021). The three psocodean suborders already existed during the Cretaceous (Álvarez-Parra *et al.* 2020a). Trogiomorpha includes the families †Cormopsocidae (not assigned to an infraorder, although its placement in a more basal clade outside Trogiomorpha cannot be excluded, *sensu* Yoshizawa & Lienhard 2020),

Prionoglarididae (within Prionoglaridetae), Psyllipsocidae (within Psyllipsocetae), †Archaeatropidae, †Empheriidae, Psoquillidae, Trogiidae and Lepidopsocidae (all five within Atropetae) (Yoshizawa *et al.* 2006). The fossil record of Trogiomorpha includes 57 species dating from the Barremian to the Quaternary (Table 1), most of which were found in amber and only four in copal. Trogiomorphan species from compression fossil sites are unknown to date. The families with the highest number of fossil species are the extinct families †Archaeatropidae and †Empheriidae. The former is a psocid family that has been identified only from Cretaceous ambers (Lebanon, Spain, France and Myanmar) and which includes 11 species in seven genera dating from the Barremian to the Cenomanian (Álvarez-Parra *et al.* 2020a; Cumming & Le Tirant 2021) (Table 1). †Empheriidae specimens are known from Cretaceous (Spain, Myanmar and Russia) and Eocene (France and Baltic) ambers, and comprise 11 species in eight genera dating from the Albian to the Priabonian (Hakim *et al.* 2021a) (Table 1). The phylogenetic position of both families might be more basal to the rest of the families belonging to the infraorder Atropetae (Yoshizawa & Lienhard 2020). The taxonomical relationships of †Archaeatropidae and †Empheriidae have been questioned, given that Li *et al.* (2020) described a new genus (assigned to †Empheriidae) with diagnostic characters of both families. The palaeobiology of archaeatropids and empheriids remains unknown.

The study of psocids from Spanish amber was initiated by Baz & Ortuño (2000), who erected the family †Archaeatropidae and later studied †Empheriidae and Manicapsocidae (Troctomorpha). Five psocid species from Spanish amber have been identified to date (all of them from Álava amber) (Baz & Ortuño 2000, 2001a, b): *Archaeatropos alavensis* Baz & Ortuño, 2000, *Empheropsocus arilloi* Baz & Ortuño, 2001b, *Empheropsocus marginelabrus* Baz & Ortuño, 2001b, *Manicapsocidus enigmaticus* Baz & Ortuño, 2001a and *Preempheria antiqua* Baz & Ortuño, 2001b. More than 100 psocids from Spanish amber are pending investigation, most of them from Álava amber.

Here, we describe new psocid specimens belonging to Trogiomorpha from five amber-bearing outcrops of the Iberian Peninsula. The first psocid nymph known from Spanish amber and a new species are described. Furthermore, the finding of new specimens belonging to known species adds further detail to previous anatomical information. We also address phylogenetic and palaeobiological topics regarding the Cretaceous Trogiomorpha.

## GEOLOGICAL SETTING

The specimens studied here correspond to bioinclusions in amber pieces obtained from the El Soplao (Cantabria

Autonomous Community) and Peñacerrada I (Burgos Province) fossil sites, and the Ariño, the Arroyo de la Pascueta and San Just fossil sites in Teruel Province. These amber-bearing outcrops are distributed along the north and east of the Iberian Peninsula, corresponding to the coastal areas of the Iberia Island during the Albian (Fig. 1).

El Soplao and Peñacerrada I are located in the Basque–Cantabrian Basin, which is related to the opening of the North Atlantic Ocean during the Oxfordian–Aptian rifting period (Martín-Chivelet *et al.* 2002). The El Soplao outcrop is in the western margin of the Basque–Cantabrian Basin and belongs to the Las Peñas Formation, with the amber deposited in a deltaic–estuarine environment under a marine influence (Najarro *et al.* 2009). This outcrop is considered Albian in age (Najarro *et al.* 2009). Peñacerrada I (which, together with the Peñacerrada II outcrop was known as Álava amber) is located in the eastern margin of the Basque–Cantabrian Basin, belonging to the Utrillas Group (Barrón *et al.* 2015). The depositional environment corresponds to the top of the filling sequences of abandoned fluvial channels in inter-distributary deltaic bays (Martínez-Torres *et al.* 2003). Peñacerrada I dates back to the late Albian based on its palynological content (Barrón *et al.* 2015).

The amber-bearing outcrops of Ariño, San Just and Arroyo de la Pascueta are in eastern Spain, located in the Maestrazgo Basin. Ariño amber is interesting because it appears to be associated with dinosaur bones in the bonebed level AR-1 (Alcalá *et al.* 2012; Álvarez-Parra *et al.* 2020b, 2021). This level belongs to the Escucha Formation and is early Albian in age based on the charophyte, ostracod and palynological assemblages it contains (Tibert *et al.* 2013; Villanueva-Amadoz *et al.* 2015). The palaeoenvironment corresponded to a freshwater swamp plain, including alkaline shallow lakes, with a marine influence in a subtropical or tropical climate (Tibert *et al.* 2013; Villanueva-Amadoz *et al.* 2015; Álvarez-Parra *et al.* 2021). The San Just outcrop is also attributed to the Escucha Formation and has been dated to the middle to lowermost upper Albian based on the palynological assemblage it contains (Peñalver *et al.* 2007; Villanueva-Amadoz *et al.* 2010). A recent palynological study constrained the dating to the upper Albian. The amber is found in a level that is rich in organic matter and fusinite, which is associated with a freshwater swamp plain (Peñalver *et al.* 2007; Villanueva-Amadoz *et al.* 2010). The little-studied Arroyo de la Pascueta amber outcrop is also assigned to the Escucha Formation and was initially dated to the lower–middle Albian (Gomez *et al.* 2000; Peñalver & Martínez-Delclòs 2002). However, as in the case of the San Just outcrop, a recent palynological study indicated the age to be late Albian. The sedimentology of the outcrop has been interpreted as a swamp in a lower

**TABLE 1.** Checklist of fossil species belonging to Trogiomorpha (Psocodea).

| Infraorder       | Family           | Genus and species   | Type locality                            | Age                     | Notes  |
|------------------|------------------|---|--|-------------------------|--|
| Indet.           | Indet.           | <i>Empheriopsis vulnerata</i><br>Vishniakova, 1975  | Yantardakh<br>(Russia)                   | Santonian               | Transferred to<br>Trogiomorpha by<br>Mockford <i>et al.</i> (2013)       |
|                  | Indet.           | <i>Parapsyllipsocus vergereau</i><br>Perrichot <i>et al.</i> , 2003                                     | Archingeay-<br>Les Nouillers<br>(France) | Albian–<br>Cenomanian   | –  |
|                  | †Cormopsocidae   | <i>Cormopsocus baleoi</i> Hakim<br><i>et al.</i> , 2021   | Hukawng<br>Valley<br>(Myanmar)           | Early<br>Cenomanian     | –  |
|                  |                  | <i>Cormopsocus groehni</i><br>Yoshizawa & Lienhard,<br>2020   | Hukawng<br>Valley                        | Early<br>Cenomanian     | –  |
|                  |                  | <i>Cormopsocus neli</i> Hakim,<br>Azar & Huang <i>in</i> Hakim<br><i>et al.</i> , 2021b                 | Hukawng<br>Valley                        | Early<br>Cenomanian     | –  |
|                  |                  | <i>Cormopsocus perantiqua</i><br>(Cockerell, 1919)  | Hukawng<br>Valley                        | Early<br>Cenomanian     | Transferred to<br><i>Cormopsocus</i> by<br>Cumming & Le Tirant<br>(2021) |
|                  |                  | <i>Longiglabeillus edentatus</i><br>Wang, Li & Yao <i>in</i> Wang<br><i>et al.</i> , 2021               | Hukawng<br>Valley                        | Early<br>Cenomanian     | –  |
|                  |                  | <i>Longiglabeillus pedhyalinus</i><br>Wang, Li & Yao <i>in</i> Wang<br><i>et al.</i> , 2021             | Hukawng<br>Valley                        | Early<br>Cenomanian     | –  |
|                  |                  | <i>Stimulopsocus jiewenae</i><br>Liang & Liu, 2022  | Hukawng<br>Valley                        | Early<br>Cenomanian     | –  |
| PRIONOGLARIDETAE | Prionoglarididae | <i>Palaeosiamoglaris burmica</i><br>Azar, Huang & Nel <i>in</i><br>Azar <i>et al.</i> , 2017            | Hukawng<br>Valley                        | Early<br>Cenomanian     | –  |
|                  |                  | <i>Palaeosiamoglaris</i><br><i>inexpectata</i> Azar, Huang<br>& Nel <i>in</i> Azar <i>et al.</i> , 2017 | Hukawng<br>Valley                        | Early<br>Cenomanian     | –  |
|                  |                  | <i>Palaeosiamoglaris lienhardi</i><br>Azar, Huang & Nel <i>in</i><br>Azar <i>et al.</i> , 2017          | Hukawng<br>Valley                        | Early<br>Cenomanian     | –  |
|                  |                  | <i>Palaeosiamoglaris</i><br><i>hkamtiensis</i> Jouault <i>et al.</i> ,<br>2021                          | Hkamti<br>(Myanmar)                      | Early Albian            | –  |
|                  |                  | <i>Palaeosiamoglaris</i><br><i>hammanaensis</i> Hakim<br><i>et al.</i> , 2022                           | Hammana-<br>Mdeyrij<br>(Lebanon)         | Barremian               | –  |
| PSYLLIPSOCETAE   | Psyllipsocidae   | <i>Psyllipsocus</i> sp.   | Simojovel de<br>Allende<br>(Mexico)      | Early–Middle<br>Miocene | Nymph of <i>Psyllipsocus</i><br><i>sensu</i> Mockford (1969)             |
|                  |                  | <i>Psyllipsocus eocenicus</i> Nel<br><i>et al.</i> , 2005   | Le Quesnoy,<br>Oise (France)             | Ypresian                | –  |
|                  |                  | <i>Sinopsyllipsocus fushunensis</i><br>Zhang <i>et al.</i> , 2016                                       | Fushun<br>(China)                        | Ypresian                | –  |
|                  |                  | <i>Khatangia inclusa</i><br>Vishniakova, 1975   | Yantardakh                               | Santonian               | –  |
|                  |                  | <i>Annulipsyllipsocus andreneli</i><br>Hakim <i>et al.</i> , 2018a                                      | Hukawng<br>Valley                        | Early<br>Cenomanian     | –  |

(continued)

TABLE 1. (Continued)

| Infraorder | Family           | Genus and species  | Type locality            | Age                 | Notes  |
|------------|------------------|--|--------------------------|---------------------|--|
|            |                  | <i>Annulipsyllipsocus inexpectatus</i> Hakim <i>et al.</i> , 2018a                                     | Hukawng Valley           | Early Cenomanian    | –  |
|            |                  | <i>Concavapsocus parallelus</i> Wang <i>et al.</i> , 2019  | Hukawng Valley           | Early Cenomanian    | Probably does not belong to Psyllipsocidae <i>sensu</i> Jouault <i>et al.</i> (2021) |
|            |                  | <i>Psyllipsocus myanmarensis</i> Jouault <i>et al.</i> , 2021  | Hukawng Valley           | Early Cenomanian    | –  |
|            |                  | <i>Psyllipsocus yangi</i> Liang & Liu, 2021  | Hukawng Valley           | Early Cenomanian    | –  |
|            |                  | <i>Psyllipsocus yoshizawai</i> Álvarez-Parra <i>et al.</i> , 2020a                                     | Hukawng Valley           | Early Cenomanian    | –  |
|            |                  | <i>Libanopsyllipsocus alexanderasnitsyni</i> Azar & Nel, 2011  | Hammana-Mdeyrij          | Barremian           | Belongs to Pachytrictidae (Troctomorpha) <i>sensu</i> Mockford <i>et al.</i> (2013)  |
| ATROPETAE  | †Archaeatropidae | <i>Proprionoglaris axioperi erga</i> Azar <i>et al.</i> , 2015   | La Garnache (France)     | Cenomanian–Turonian | –  |
|            |                  | <i>Heliadesdakruon morganae</i> Cumming & Le Tirant, 2021  | Hukawng Valley           | Early Cenomanian    | –  |
|            |                  | <i>Proprionoglaris guyoti</i> Perrichot <i>et al.</i> , 2003   | Archingeay-Les Nouillers | Albian–Cenomanian   | Transferred to †Archaeatropidae by Mockford <i>et al.</i> (2013)                     |
|            |                  | <i>Prospeleketor albianensis</i> Perrichot <i>et al.</i> , 2003  | Archingeay-Les Nouillers | Albian–Cenomanian   | Transferred to †Archaeatropidae by Mockford <i>et al.</i> (2013)                     |
|            |                  | <i>Archaeatropos alavensis</i> Baz & Ortuño, 2000  | Peñacerrada I (Spain)    | Late Albian         | –  |
|            |                  | <i>Libanoglaris hespericus</i> sp. nov.  | Ariño (Spain)            | Early Albian        | –  |
|            |                  | <i>Archaeatropos randatae</i> (Azar & Nel, 2004)   | Jezzine (Lebanon)        | Barremian           | Transferred to <i>Archaeatropos</i> by Mockford <i>et al.</i> (2013)                 |
|            |                  | <i>Bcharreglaris amunobi</i> Azar & Nel, 2004  | Bcharreh (Lebanon)       | Barremian           | Transferred to †Archaeatropidae by Mockford <i>et al.</i> (2013)                     |
|            |                  | <i>Libanoglaris chehabi</i> Azar & Nel, 2004   | Hammana-Mdeyrij          | Barremian           | Transferred to †Archaeatropidae by Mockford <i>et al.</i> (2013)                     |
|            |                  | <i>Libanoglaris mouawadi</i> Azar, Perrichot, Néraudeau & Nel <i>in</i> Perrichot <i>et al.</i> , 2003 | Hammana-Mdeyrij          | Barremian           | Transferred to †Archaeatropidae by Mockford <i>et al.</i> (2013)                     |
|            |                  | <i>Setoglaris reemae</i> Azar & Nel, 2004  | Hammana-Mdeyrij          | Barremian           | Transferred to †Archaeatropidae by Mockford <i>et al.</i> (2013)                     |
|            | †Empheriidae     | <i>Empheria pertinens</i> (Enderlein, 1911)  | Baltic amber             | Lutetian            | Transferred to <i>Empheria</i> by Roesler (1940)                                     |
|            |                  | <i>Empheria reticulata</i> Hagen <i>in</i> Pictet-Baraban & Hagen, 1856                                | Baltic amber             | Lutetian            | –  |

(continued)

TABLE 1. (Continued)

| Infraorder | Family         | Genus and species  | Type locality                     | Age                              | Notes   |
|------------|----------------|--|-----------------------------------|----------------------------------|---|
|            |                | <i>Trichempheria villosa</i><br>(Hagen, 1882)  | Baltic amber                      | Lutetian                         | Transferred to<br><i>Trichempheria</i> by<br>Enderlein (1911) |
|            |                | <i>Eoempheria intermedia</i> Nel<br><i>et al.</i> , 2005                                 | Le Quesnoy,<br>Oise               | Ypresian                         | –   |
|            |                | <i>Jerseyempheria grimaldii</i><br>Azar <i>et al.</i> , 2010                             | Sayreville<br>(USA)               | Turonian                         | –   |
|            |                | <i>Empherium rasnitsyni</i><br>Hakim <i>et al.</i> 2021a                                 | Nizhnyaya<br>Agapa<br>(Russia)    | Late<br>Cenomanian               | –   |
|            |                | <i>Burmempheria</i><br><i>densuschaetae</i> Li, Wang &<br>Yao <i>in Li et al.</i> , 2020 | Hukawng<br>Valley                 | Early<br>Cenomanian              | –   |
|            |                | <i>Burmempheria raruschaetae</i><br>Li, Wang & Yao <i>in Li</i><br><i>et al.</i> , 2020  | Hukawng<br>Valley                 | Early<br>Cenomanian              | –   |
|            |                | <i>Empheropsocus arilloi</i> Baz &<br>Ortuño, 2001b                                      | Peñacerrada I<br>(Spain)          | Late Albian                      | –   |
|            |                | <i>Empheropsocus</i><br><i>marginelabrus</i> Baz &<br>Ortuño, 2001b                      | Peñacerrada I                     | Late Albian                      | –   |
|            |                | <i>Preempheria antiqua</i> Baz &<br>Ortuño, 2001b  | Peñacerrada I                     | Late Albian                      | –   |
|            | Psoquillidae   | <i>Eorhyopsocus magnificus</i><br>Nel <i>et al.</i> , 2005                               | Le Quesnoy,<br>Oise               | Ypresian                         | –   |
|            | Trogiidae      | <i>Paralepinotus fushunensis</i><br>Azar <i>et al.</i> , 2018                            | Fushun                            | Ypresian                         | –   |
|            |                | <i>Cretolepinotus tankei</i> Cockx<br><i>et al.</i> , 2020                               | Pipestone<br>Creek<br>(Canada)    | Late<br>Campanian                | –   |
|            |                | <i>Eolepinotus pilosus</i><br>Vishniakova, 1975  | Yantardakh                        | Santonian                        | –   |
|            |                | <i>Eolepinotus zherikhini</i><br>Hakim <i>et al.</i> , 2021a                             | Timmerdyakh-<br>Khaya<br>(Russia) | Late<br>Cenomanian<br>– Turonian | –   |
|            | Lepidopsocidae | <i>Nepticulomima mortua</i><br>(Hagen, 1865)   | Zanzibar?<br>copal                | Quaternary                       | Transferred to<br><i>Nepticulomima</i> by<br>Enderlein (1911) |
|            |                | <i>Perientomum incultum</i><br>(Hagen, 1865)   | Zanzibar?<br>copal                | Quaternary                       | Transferred to<br><i>Perientomum</i> by<br>Enderlein (1911)   |
|            |                | <i>Thylacella eversiana</i><br>Enderlein, 1911   | Zanzibar?<br>copal                | Quaternary                       | –   |
|            |                | <i>Thylax fimbriatum</i> Hagen,<br>1866  | Zanzibar?<br>copal                | Quaternary                       | –   |
|            |                | <i>Echmepteryx (Loxopholia)</i><br><i>dominicanus</i> Hakim <i>et al.</i> ,<br>2018b     | Dominican<br>amber                | Early–Middle<br>Miocene          | –   |
|            |                | <i>Thylacella eocenica</i> Nel<br><i>et al.</i> , 2005                                   | Le Quesnoy,<br>Oise               | Ypresian                         | –   |

All fossil records correspond to amber or copal (for the limits of the term copal, see Solórzano-Kraemer *et al.* 2020). Undescribed trogiomorphans have been reported from Aptian Congolese amber (Bouju & Perrichot 2020) and Campanian Tilin (Myanmar) amber (Zheng *et al.* 2018). Note that there is controversy about the origin of the Zanzibar copal, which probably corresponds to copal obtained from different areas of East Africa (Delclòs *et al.* 2020). The new species described in this paper is shown in bold.

delta plain with freshwater and marine inputs (Gomez *et al.* 2000).

## MATERIAL AND METHOD

Amber pieces were prepared following the methodology of Corral *et al.* (1999). They were cut, polished and embedded in prisms of epoxy resin, which facilitates the preservation and protection of amber pieces. Observations with reflected and transmitted light, photography and drawing of the specimens were acquired using an Olympus CX41 compound microscope with an attached sCMEX-20 digital camera and a camera lucida tube. ImageFocusAlpha version 1.3.7.12967.20180920 was used to take the photographs. Figures were prepared using Photoshop CS6. The anatomical nomenclature and systematic classification follow the works of Smithers (1972, 1990), Mockford (1993), Lienhard (1998) and Baz & Ortuño (2000).

This study includes 18 fossil psocid specimens. Their prefixes and provenances as well as the public Spanish institutions in which they are housed are given here.

*Institutional abbreviations.* AP, Arroyo de la Pascueta amber, housed in the Museo Aragonés de Paleontología, Teruel, Spain; AR-1-A, Ariño amber, housed in the Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis), Teruel, Spain; CES, El Soplao amber, housed in the Colección Institucional del Laboratorio de la Cueva El Soplao in Celis, Cantabria, Spain; CPT, MAP, San Just amber, housed in the Museo Aragonés de Paleontología, Teruel, Spain; MCNA, Peñacerrada I amber, housed in the Museo de Ciencias Naturales de Álava in Vitoria-Gasteiz, Álava, Spain; SJ-10, SJNB2012, San Just amber, housed in the Museo Aragonés de Paleontología, Teruel, Spain.

## SYSTEMATIC PALAEOLOGY

Order PSOCODEA Hennig, 1966

Suborder TROGIOMORPHA Roesler, 1940

Infraorder ATROPETAE Pearman, 1936

Family †ARCHAEATROPIDAE Baz & Ortuño, 2000

*Type genus.* *Archaeatropos* Baz & Ortuño, 2000.

*Included genera and species.* *Archaeatropos alavensis* Baz & Ortuño, 2000 (Albian, Spain); *Archaeatropos randatae* (Azar & Nel, 2004) (Barremian, Lebanon); *Bcharreglaris amunobi* Azar & Nel, 2004 (Barremian, Lebanon); *Heliadesdakruon morganae* Cumming & Le Tirant, 2021 (Cenomanian, Myanmar); *Libanoglaris chehabi* Azar & Nel, 2004 (Barremian, Lebanon); *Libanoglaris mouawadi* Azar, Perrichot, Néaudeau & Nel in Perrichot *et al.*, 2003 (Barremian, Lebanon); *Proprioglaris axioperi erga* Azar *et al.*, 2015 (Cenomanian–

Turonian, France); *Proprioglaris guyoti* Perrichot *et al.*, 2003 (Albian–Cenomanian, France); *Prospeleketor albianensis* Perrichot *et al.*, 2003 (Albian–Cenomanian, France); and *Setoglaris reemae* Azar & Nel, 2004 (Barremian, Lebanon).

*Original diagnosis.* Belonging to the suborder Trogiomorpha. Inner side of 2nd maxillary palpal segment with sensillum. Antennae with segments secondarily annulated. Forewing: veins (except Cu<sub>2</sub>) and margin with long setae. Basal sector of Sc well developed curving to meet R. Distal section of Sc directed backward. Pterostigma not thickened. M + Cu strongly curved. Crossvein from R<sub>1</sub> to R<sub>s</sub>. Areola postica long and slender, Cu<sub>1b</sub> shorter than Cu<sub>1a</sub>. Veins Cu<sub>2</sub> and IA ending together on wing margin (nodulus). Hind wing: M 2-branched. Cu<sub>2</sub> only slightly sinuous. Sc short, not passing into R. IA and 2A fused basally, dividing near margin, with IA strongly curved. Tarsi 3-segmented. Coxal organ present on hind legs. Hind tibia and tarsus together longer than abdomen. Claws without preapical tooth or, if present, very small. Ovipositor valvulae as follows: external valve (v<sub>3</sub>) as an elongate and setose lobe; dorsal valve (v<sub>2</sub>) small, rudimentary; ventral valve (v<sub>3</sub>) absent. Paraprocts with a strong posterior spine. Subgenital plate apparently membranous without sclerifications (Baz & Ortuño 2000).

*Emended diagnosis.* Antennae with 18 or more flagellomeres; inner side of the second maxillary palpomere possessing a sensillum; forewings: row of setae along the veins except Cu<sub>2</sub>, basal sector of Sc well developed and curving to meet R<sub>1</sub>, pterostigma not thickened, M + Cu strongly curved, crossvein from R<sub>1</sub> to R<sub>s</sub>, areola postica long and slender, Cu<sub>1b</sub> shorter than Cu<sub>1a</sub>, veins Cu<sub>2</sub> and A ending together in a nodulus; hind wings: Sc short not passing into R, with R<sub>s</sub> and M two-branched, basi-radial cell four-angled, IA and 2A fused basally and dividing near the margin with IA strongly curved; coxal organ present on hind legs; hind tibia and tarsus together longer than abdomen; tarsi three-segmented; ovipositor valvulae: external valve as an elongate and setose lobe, dorsal valve small and rudimentary, ventral valve absent; paraprocts with a strong posterior spine; subgenital plate apparently membranous without sclerifications.

*Remarks.* The original diagnosis of †Archaeatropidae proposed by Baz & Ortuño (2000) was based only on the species *Archaeatropos alavensis* due to monotypy. The diagnoses of the genus and the species were the same as the original diagnosis of the family. After the description of the family †Archaeatropidae, several genera and species have been identified that belong to this family. Therefore, an emended diagnosis was necessary to better accommodate the new taxa and to differentiate them from *A. alavensis*.

The character ‘antennae with 18 or more flagellomeres’ has been included in the emended diagnosis because this is typical in the species of the group (*Archaeatropos alavensis*, 20/21; *Archaeatropos randatae*, 22; *Bcharreglaris amunobi*, 25; *Heliadesdakruon morganae*, 25; *Libanoglaris chehabi*, 21; *Libanoglaris mouawadi*, 20; and *Proprioglaris guyoti*, 18). *Setoglaris reemae* (with at least 10 flagellomeres) is an exception, but the antennae seem to be incomplete (Azar & Nel 2004). The number of





**FIG. 1.** Palaeogeographical reconstruction of western Europe from 100 Ma showing the location of the amber-bearing outcrops that yielded the studied specimens (psocid silhouettes). Map modified from Scotese (2001). Psocid silhouette redrawn from Lienhard *et al.* (2012, fig. 1).

flagellomeres in *Propionoglaris axioperi erga* and *Prospelektor albianensis* is unknown. The characters ‘secondary annulations on flagellomeres’ and ‘preapical tooth on pretarsal claws’ are unstable in the family. All of the members of the family show a sensillum on the second maxillary palpomere, except for the genus *Propionoglaris* (Perrichot *et al.* 2003). Fourth maxillary palpomere with hatchet-shaped apex is typical of both †Archaeatropidae and †Empheriidae. Regarding the forewing venation, the character ‘distal section of Sc directed backward’ is a putative autapomorphy of the genus *Archaeatropos*, as Mockford *et al.* (2013) indicated. Therefore, it has been removed from the emended diagnosis. The hind wings of archaeatropids show two-branched Rs and a four-angled basi-radial cell, with these two characters included in the emended diagnosis. The mention of the vein Cu<sub>2</sub> with a slightly sinuous path in the hind wings has been removed from the emended diagnosis because it is nearly straight or slightly curved in some specimens. In the original diagnosis the ventral valve of the ovipositor was incorrectly called ‘v3’ instead of ‘v1’.

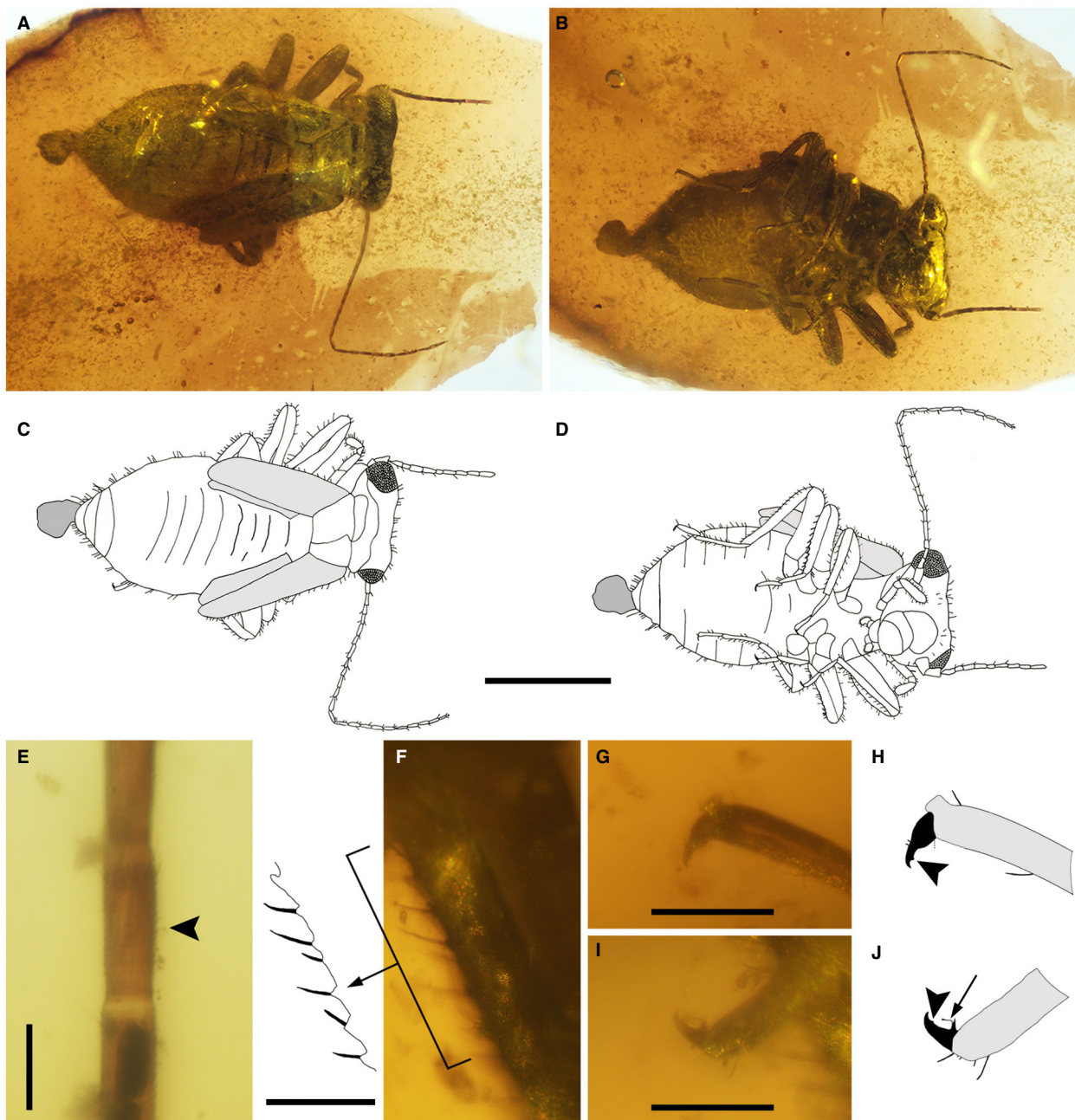
†ARCHAEATROPIDAE indet.

Figure 2

*Material.* SJNB2012-12-02: a complete nymph, sex unknown. The amber piece contains a total of 36 syninclusions: three

psocids, one thrips, two hemipterans, nine hymenopterans, 15 dipterans, two undetermined insects, three spiders, and probable spiderweb threads.

*Description.* Complete immature specimen, sex unknown. Brown body 1.26 mm long, covered by fine hairs (Fig. 2A–D). Head 0.48 mm wide, with a broad vertex and two prominent compound eyes separated by 0.30 mm, lacking ocelli; left antenna incomplete with scape, pedicel and nine flagellomeres, with secondary annulations; right antenna completely preserved with scape, pedicel and 25 flagellomeres of similar lengths (*c.* 0.05 mm), with secondary annulations (Fig. 2E) and with a pair of distal, fine hairs; marked labrum and clypeus, with differentiable anteclypeus and postclypeus; maxillary palps four-segmented, covered by fine hairs, a sensillum visible on the left second maxillary palpomere, length of maxillary palpomeres: I 0.04 mm, II 0.08 mm, III 0.03 mm, IV 0.13 mm, fourth maxillary palpomere with hatchet-shaped apex; visible mentum, paraglosses and labial palps two-segmented with a round apex and covered by fine hairs, length of labial palpomeres: I 0.02 mm, II 0.04 mm; lacinia not visible. Wing buds placed over the body; forewing buds 0.55 mm long, up to half the length of the abdomen, elongate and slender with a sharp apex, no visible venation, few fine hairs on costal and radial margins; hind wing buds 0.4 mm long, present under forewings, no visible venation



**FIG. 2.** Psocid nymph (Psocodea, Trogiomorpha, †Archaeatropidae) from the upper Albian amber of San Just (Teruel Province, Spain), SJNB2012-12-02, sex unknown. A–B, habitus in the dorsal and ventral view, respectively. C–D, camera lucida drawings of the habitus in dorsal and ventral view, respectively. E, detail of the left antenna in ventral view, with the secondary annulations indicated by an arrowhead. F, detail of the left midtibia and interpretation of the ctenidiobothria. G–H, detail of the pretarsal claw in the right hind leg, with the preapical tooth indicated by an arrowhead, both images are at the same scale. I–J, detail of the pretarsal claw in the left foreleg, with the preapical tooth indicated by an arrowhead and the pulvillus by an arrow, both images are at the same scale. A–D at the same scale. Scale bars represent: 0.5 mm (A–D); 0.05 mm (E–J).

or tracheation nor fine hairs. Legs completely preserved and covered by fine hairs, with thick femora, thin tibiae and two-segmented tarsi (typical for nymphs); a rounded mark on coxa

of right hind leg (possibly coxal organ); two distal spurs on tibiae, and ctenidiobothria visible on midtibiae (Fig. 2F); length of tarsomeres of forelegs and midlegs: proximal 0.11 mm, distal



0.08 mm; tarsomeres of hind legs longer: proximal 0.20 mm, distal 0.09 mm; distal tarsomere with a pretarsal claw bearing one small preapical tooth, pulvillus present (Fig. 2G–J). Abdomen 0.84 mm long. Genitalia not visible. A structure at apex of abdomen could correspond to a coprolite.

*Remarks.* Nymphal stages of psocids resemble the adult body form and markings. They are characterized by a lack of ocelli, the presence of shorter antennae with fewer flagellomeres than in adults, and the presence of wing buds and two-segmented tarsi (Smithers 1972; Mockford 1993). The number of nymphal instars of psocids is usually six, but it is reduced in some species (New 1987). Wing buds emerge during the second instar (Smithers 1972). There are few reports of nymphal fossil psocids (e.g. Mockford 1969; Vishniakova 1975; Azar *et al.* 2015), and they are usually poorly preserved, hindering their study. Mockford (1969) described a psocid nymph from Miocene Mexican amber from Chiapas that had enough characters to assign it to the living genus *Psyllipsocus* (Trogiomorpha: Psyllipsocidae). Interestingly, Poinar & Vega (2020) identified a parasitic fungus adhering to a female psocid nymph (Troctomorpha: Troctopsocidae) that acted as the host. Recently, new psocid immatures have been described from Burmese amber (Kiesmüller *et al.* 2021; Xu *et al.* 2022).

The high number of flagellomeres (25) in SJNB2012-12-02 and the presence of a labial palpus with a minute proximal segment and a rounded distal segment led to its inclusion in Trogiomorpha (Smithers 1972; Mockford 1993). Considering that nymphs have fewer flagellomeres than adults, the imago of the corresponding species could show an extraordinarily high number of flagellomeres. The presence of a sensillum on the second maxillary palpomere links the specimen to the infraorder Atropetae or to the subfamily Speleketorinae (Prionoglaridetae: Prionoglarididae). Some species of the genera *Psyllipsocus* (Psyllipsocidae) and *Palaeosiamoglaris* (Prionoglarididae) also have a sensillum on the second maxillary palpomere (Lienhard & Ferreira 2015; Liang & Liu 2021; Hakim *et al.* 2022). Unfortunately, Atropetae and Prionoglaridetae are supported by the character states of the adults only (Yoshizawa *et al.* 2006). Speleketorinae is an interesting group in that some members show sex-reversed genital organs (female penis). The representatives of this subfamily are thought to have a Gondwanan origin (Yoshizawa *et al.* 2019). Specimens of this subfamily have secondarily annulated flagellomeres, trichobothria on the legs (absent in Prionoglaridinae) and a preapical tooth on the pretarsal claws, as observed in SJNB2012-12-02. Known Prionoglarididae specimens have half the number of flagellomeres or even fewer than the studied specimen, which would exclude it from this family (Lienhard 2000, 2004; Lienhard & Ferreira 2013). Speleketorinae lacks a fossil record to date, in contrast to the abundance of Atropetae specimens in Cretaceous amber. The assigning of SJNB2012-12-02 to Atropetae is reinforced by its somewhat triangular head, typical for this group. Furthermore, the extant nymphs of Speleketorinae are almost completely related to cave environments.

When comparing SJNB2012-12-02 to Atropetae specimens, the combination of ‘flagellomeres with secondary annulations’, ‘sensillum on the second maxillary palpomere’ and ‘pretarsal claws bearing a preapical tooth and pulvillus’ excludes it from the families Lepidopsocidae, Trogiidae, Psoquillidae and †Empheriidae

(Smithers 1972; Mockford 1993; Baz & Ortuño 2001b). The SJNB2012-12-02 nymph meets the diagnostic characters of †Archaeatropidae (Baz & Ortuño 2000). The feature ‘hatchet-shaped apex of fourth maxillary palpomere’ is typical of archaeatropids and empheriids. Regarding the archaeatropid genera, the specimen resembles *Bcharreglaris* (which includes only the species *B. amunobi* from Barremian Lebanese amber), based on the characters that they share, including the same number of flagellomeres (Azar & Nel 2004). *Heliadesdakruon morganae* also shows 25 flagellomeres (Cumming & Le Tirant 2021). The species *Archaeatropos alavensis* is present in San Just, as discussed below. SJNB2012-12-02 differs from *A. alavensis* only by the number of flagellomeres, which could be variable (Baz & Ortuño 2000). Therefore, it is plausible that the nymph belongs to this species. Nonetheless, we prefer not to assign the specimen to a specific group given the lack of data on nymphal fossil psocids. Furthermore, the description of a new species based on a nymph would be problematic. This finding is interesting because the exceptionally well-preserved nymph is tentatively assigned to †Archaeatropidae, a psocid family restricted to the Cretaceous.

#### Genus ARCHAETROPOS Baz & Ortuño, 2000

*Type species.* *Archaeatropos alavensis* Baz & Ortuño, 2000.

*Other species.* *Archaeatropos randatae* (Azar & Nel, 2004).

*Emended diagnosis.* Antennae with 20–22 flagellomeres; maxillary palps with the fourth palpomere longer than the second palpomere; forewings: distal sector of Sc straight or curved, directed towards the wing base; claws without a preapical tooth or, if present, a very small preapical tooth.

#### *Archaeatropos alavensis* Baz & Ortuño, 2000

##### Figures 3–5

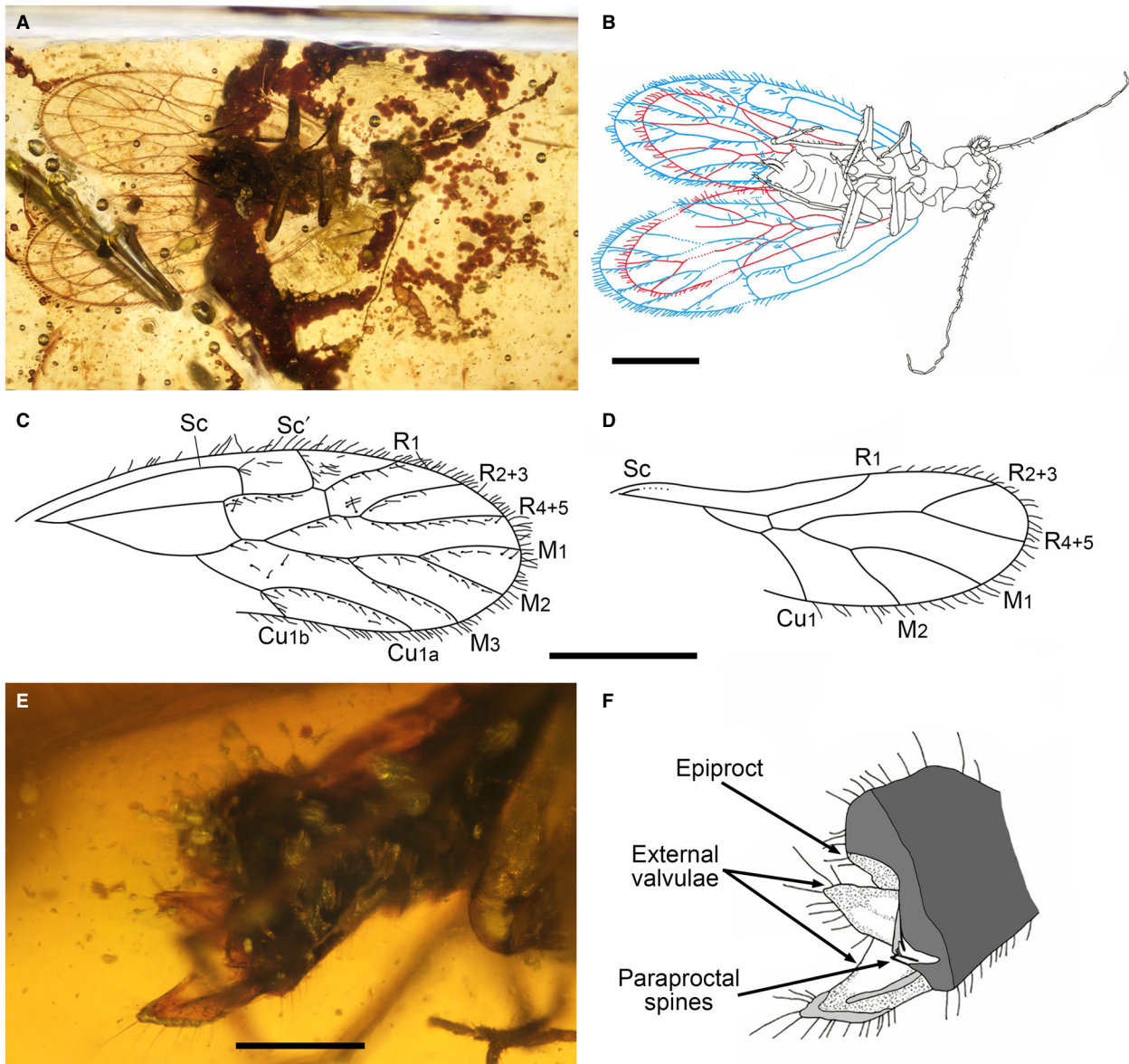
*Material.* CES.445: an almost complete specimen, sex unknown. CES.465: a complete specimen, female. CES.495.4: wing remains, with three hymenopterans as syninclusions. CES.526.5: a partial specimen, sex unknown, with a cockroach, a mite, a hymenopteran, a dipteran, a psocid and a thrips as syninclusions. CES.586.2: forewings and partial body remains, with a psocid of the genus *Libanoglaris* as a syninclusion. MCNA-14912.1: an almost complete specimen, sex unknown, with an undetermined wing as a syninclusion. MAP-7812: a complete specimen, female, with two hymenopterans, a bethylid and a platygastriid as syninclusions. (SJ-10-50) SJ2: an almost complete specimen, sex unknown. AP-11.1: an almost complete specimen, sex unknown, with an undetermined larva, a cockroach and a dipteran as syninclusions.

*Other material examined.* MCNA-8834, holotype, female. MCNA-8646, allotype, male.

*Emended diagnosis.* Flagellomeres secondarily annulated; forewings: margin setose, distal sector of Sc curved and directed towards the wing base; hind wings: margin setose.

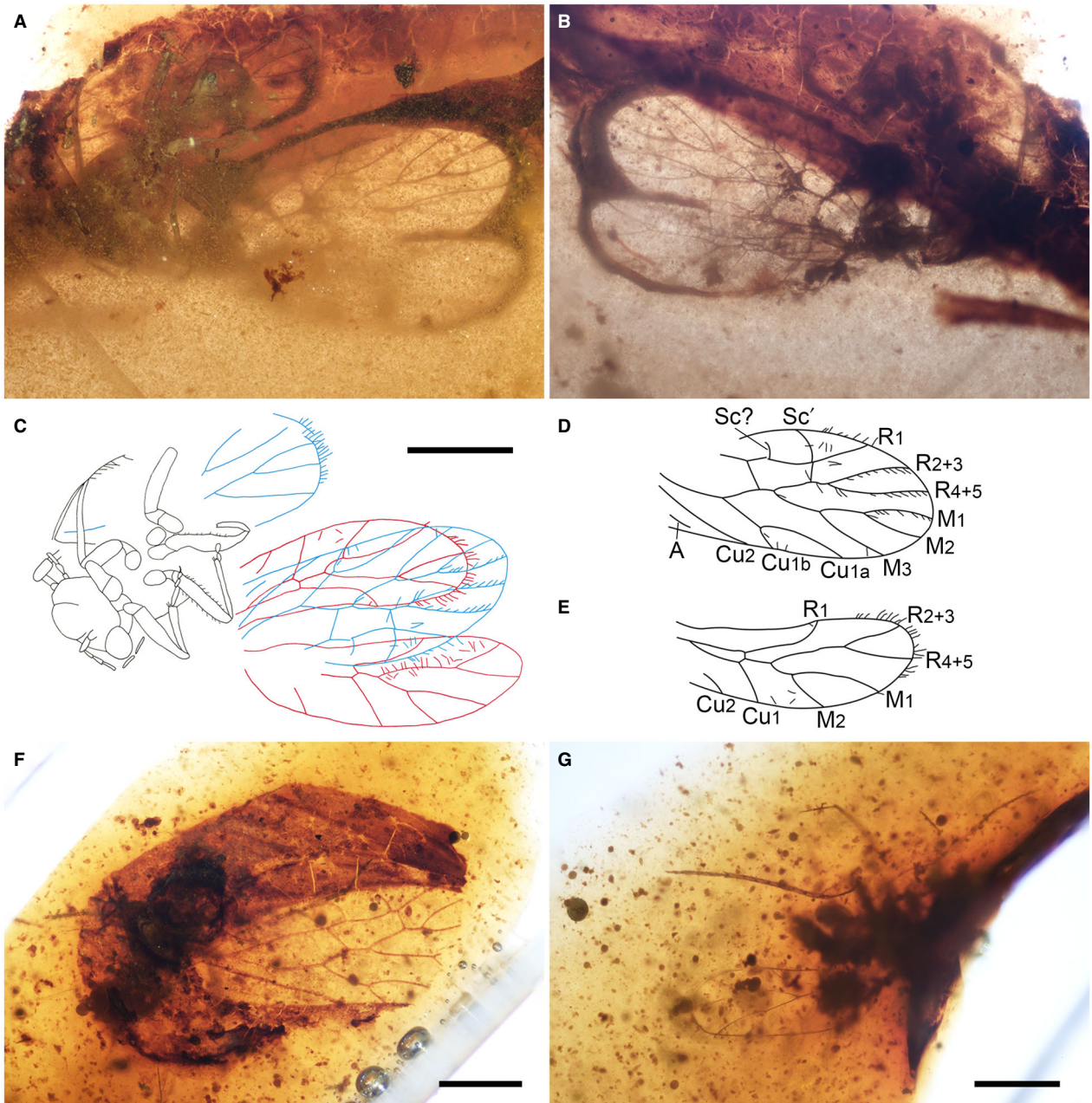
**Description.** Body length of the two completely preserved specimens is 1.35 mm (MAP-7812) and 1.62 mm (CES.465). Body covered by fine hairs. Head as long as wide and measuring *c.* 0.38 mm, with a broad vertex and two prominent compound eyes, ocelli not visible probably due to poor preservation of the vertex of the specimens; antennae incomplete with narrow and slightly elongate flagellomeres similar in shape, *c.* 0.05 mm long, secondarily annulated and with distal fine hairs (MAP-7812 has 20 flagellomeres); clypeus with a narrow anteclypeus and a bulging postclypeus; maxillary palp four-segmented, covered by fine hairs, with a sensillum on the second palpomere, fourth

palpomere broadened preapically (hatchet-shaped apex) and longer than second palpomere, length of maxillary palpomeres in CES.465: I 0.03 mm, II 0.06 mm, III 0.04 mm, IV 0.10 mm; other mouthparts not visible. Thorax with slightly bulging pronotum; wings with complete venation; measurements and description of the wings mainly follow those of specimen MAP-7812. Forewing (Figs 3C, 4D) hyaline, 1.60–1.95 mm long and 0.60–0.70 mm wide, wing margin setose with closely packed linear spicules parallel to margin, one row of setae along veins; basal sector of Sc long, distally curved and directed towards R<sub>1</sub>; distal sector of Sc curved and directed towards the wing base,



**FIG. 3.** New specimen of *Archaeatropos alavensis* Baz & Ortuño, 2000 (Psocodea, Trogiomorpha, †Archaeatropidae) from the upper Albian amber of San Just (Teruel Province, Spain), MAP-7812, female. A–B, photograph and drawing of the habitus in ventral view, with the forewings shown in blue and the hind wings in red. C–D, forewing and hind wing, respectively, both images are at the same scale. E–F, photograph and drawing of the female genitalia, respectively. Scale bars represent: 0.5 mm (A–D); 0.2 mm (E, F).





**FIG. 4.** New specimens of *Archaeatropos alavensis* Baz & Ortuño, 2000 (Psocodea, Trogiomorpha, †Archaeatropidae) from the upper Albian amber of San Just and Arroyo de la Pascueta (both in Teruel Province, Spain). A–E, specimen (SJ.10-50) SJ2, sex unknown: A–B, habitus in ventral and dorsal view, respectively; C, drawing of the habitus in ventral view, with the forewings shown in blue and the hind wings in red; D–E, left forewing and hind wing, respectively. F–G, habitus of the specimen AP-11.1 as preserved, sex unknown. A–E are at the same scale. Scale bars represent 0.5 mm.

joining margin at 1.00 mm from base;  $R_1$  slightly sigmoidal, reaching margin at 1.33 mm from wing base;  $R_s$  perpendicular to  $M$  or slightly oblique at its base, joining  $M$  at 0.78 mm from wing base; straight crossvein between  $R_1$  and  $R_s$ , forming a six-angled radial cell;  $R_s$  bifurcated into  $R_{2+3}$  and  $R_{4+5}$  at 1.18 mm from wing base, with both reaching the margin at 1.54 mm and 1.69 mm from wing base, respectively,  $R_{4+5}$  slightly sigmoidal;

$M_3$  emerging from  $M$  at 1.16 mm from wing base, showing a sigmoidal path and reaching the margin at 1.56 mm from wing base; separation of  $M_1$  and  $M_2$  at 1.39 mm from wing base, both are nearly straight, reaching the margin at 1.74 mm and 1.69 mm from wing base, respectively;  $Cu_1$  bifurcating into  $Cu_{1a}$  and  $Cu_{1b}$  at 0.89 mm from wing base, approximately at the same level as that of the bifurcation of  $R_s$  and  $M$ , areola postica

long and with a curved  $Cu_{1a}$  reaching the margin at 1.41 mm from wing base, while straight and short  $Cu_{1b}$  reaches the margin at 0.98 mm from wing base; nodulus between  $Cu_2$  and A visible in CES.526.5 specimen at 0.67 mm from wing base, nodulus is also tentatively visible in CES.495.4 and MCNA-14912.1 specimens, while the paths of  $Cu_2$  and A are compatible with the presence of a nodulus in the other specimens, although it is not visible in them. Hind wing (Figs 3D, 4E) hyaline, 1.12–1.45 mm long and 0.44–0.55 mm wide, with margin setose, membrane and veins without setae; Sc short and emerging near wing base, not reaching the wing margin or the other veins; elongate basi-radial cell four-angled;  $R_1$  distally curved, reaching the margin at 0.90 mm from wing base; Rs fused to M only for 0.10 mm, bifurcating at 0.68 mm from wing base; Rs dividing into  $R_{2+3}$  and  $R_{4+5}$  at 1.09 mm from wing base, both veins slightly curved and reaching the margin at 1.33 mm and 1.43 mm from wing base, respectively; M dividing into  $M_1$  and  $M_2$  at 0.86 mm from wing base,  $M_1$  is curved and reaches the margin at 1.31 mm from wing base, while  $M_2$  is sigmoidal and reaches the margin at 1.07 mm from wing base;  $Cu_1$  curved and reaching the margin at 0.78 mm from wing base;  $Cu_2$  and A are not visible or only partly visible in the studied specimens due to the poor preservation of the cubito-anal region of the hind wings. Legs covered by fine hairs; tarsi three-segmented; one distal spur visible in tibiae; interestingly, the tibiae and first tarsomeres of the hind legs of CES.465 seem to be longer than in the other specimens; length of tarsomeres of right midleg of MAP-7812: proximal 0.16 mm, middle 0.04 mm, distal 0.04 mm; pretarsal claws of distal tarsomeres without a preapical tooth or pulvillus, although a very small preapical tooth can be seen in some specimens. Abdomen c. 0.83 mm long in CES.465. Female genitalia (Fig. 3E, F) visible in the MAP-7812 and CES.465 specimens; external valvulae are two elongate lobes covered by long setae at apex and sides, and seem to have a membrane along the midline; dorsal and ventral valves not visible; two marked paraproctal spines; membranous epiproct. Genitalia of the other studied specimens are obscure.

*Remarks.* The number of flagellomeres, the presence of a sensillum in the second maxillary palpomere and the arrangement of the ovipositor valvulae (with external valves as elongate lobes bearing long setae) confirm the assignment of *Archaeatropos alavensis* to Atropetae in Trogiomorpha (Smithers 1972; Mockford 1993). The secondarily annulated flagellomeres, the forewings with a row of setae along the veins, the basal sector of Sc curving to meet  $R_1$  and the presence of a nodulus are characteristics of the family †Archaeatropidae, and differentiate it from the other families of Atropetae (Baz & Ortuño 2000). However, the recently described genus *Burmempheria*, belonging to †Empheriidae, shows some characters of †Archaeatropidae, such as the presence of a nodulus. Thus, the differences and putative relationships between these two families are discussed below. The diagnoses of the genus *Archaeatropos* and the species *A. alavensis* were the same as the original diagnosis of the family †Archaeatropidae (Baz & Ortuño 2000). Therefore, both have been emended to differentiate them from the other genera and species of the family.

As Mockford *et al.* (2013) indicated, the genus *Archaeatropos* is characterized by the distal sector of Sc being directed towards the wing base, a putative autapomorphy of the genus. This character is present in the two species of the genus. *Archaeatropos randatae*, from Barremian Lebanese amber, was first assigned to the genus *Libanoglaris* (Azar & Nel 2004), although its place in *Archaeatropos* (*sensu* Mockford *et al.* 2013) is suitable. *Archaeatropos randatae* differs from *A. alavensis* by having flagellomeres without secondary annulations (*A. alavensis* has secondary annulations), having a glabrous margin of the fore- and hind wing (setose in *A. alavensis*), and presenting a different shape of the areola postica (*A. alavensis* has a shorter  $Cu_{1b}$ ). *Archaeatropos randatae* has one preapical tooth on the pretarsal claws but this character in *A. alavensis* shows intraspecific variability, given that it is present in some specimens and absent in others. The specimens assigned to *A. alavensis* in this study share the same habitus and autapomorphies of the species, despite some minor differences that can be explained by intraspecific variability. *Psylloneura perantiqua* Cockerell, 1919 was transferred to the genus *Archaeatropos* by Mockford *et al.* (2013) based on the distal sector of Sc being directed towards the wing base, which is straight and, therefore, different from that of the other species of the genus. This species was described by Cockerell (1919) based only on the characters of the poorly preserved forewings and a partial antenna. Moreover, there were many important characters that could not be visualized, such as the basal sector of Sc joining  $R_1$ , the areola postica, the nodulus and most of the body characters. Recently, this species was again transferred to the genus *Cormopsocus* (†Cormopsocidae) based on the finding of a new complete specimen from Burmese amber (Cumming & Le Tirant 2021).

Notably, *A. alavensis* is the most abundant psocid species found in Albian Spanish amber. It is present in the amber outcrops of El Soplao, Peñacerrada I, San Just and Arroyo de la Pascueta. Therefore, it was distributed at least along the northern Iberia Island during this period. Many of the undescribed psocids from Peñacerrada I have a morphotype similar to that of *A. alavensis*, although a detailed study is required for confirmation.

#### Genus LIBANOGLARIS Azar, Perrichot, Néraudeau & Nel *in* Perrichot *et al.*, 2003

*Type species.* *Libanoglaris mouawadi* Azar, Perrichot, Néraudeau & Nel *in* Perrichot *et al.*, 2003.

*Other species.* *Libanoglaris chehabi* Azar & Nel, 2004.

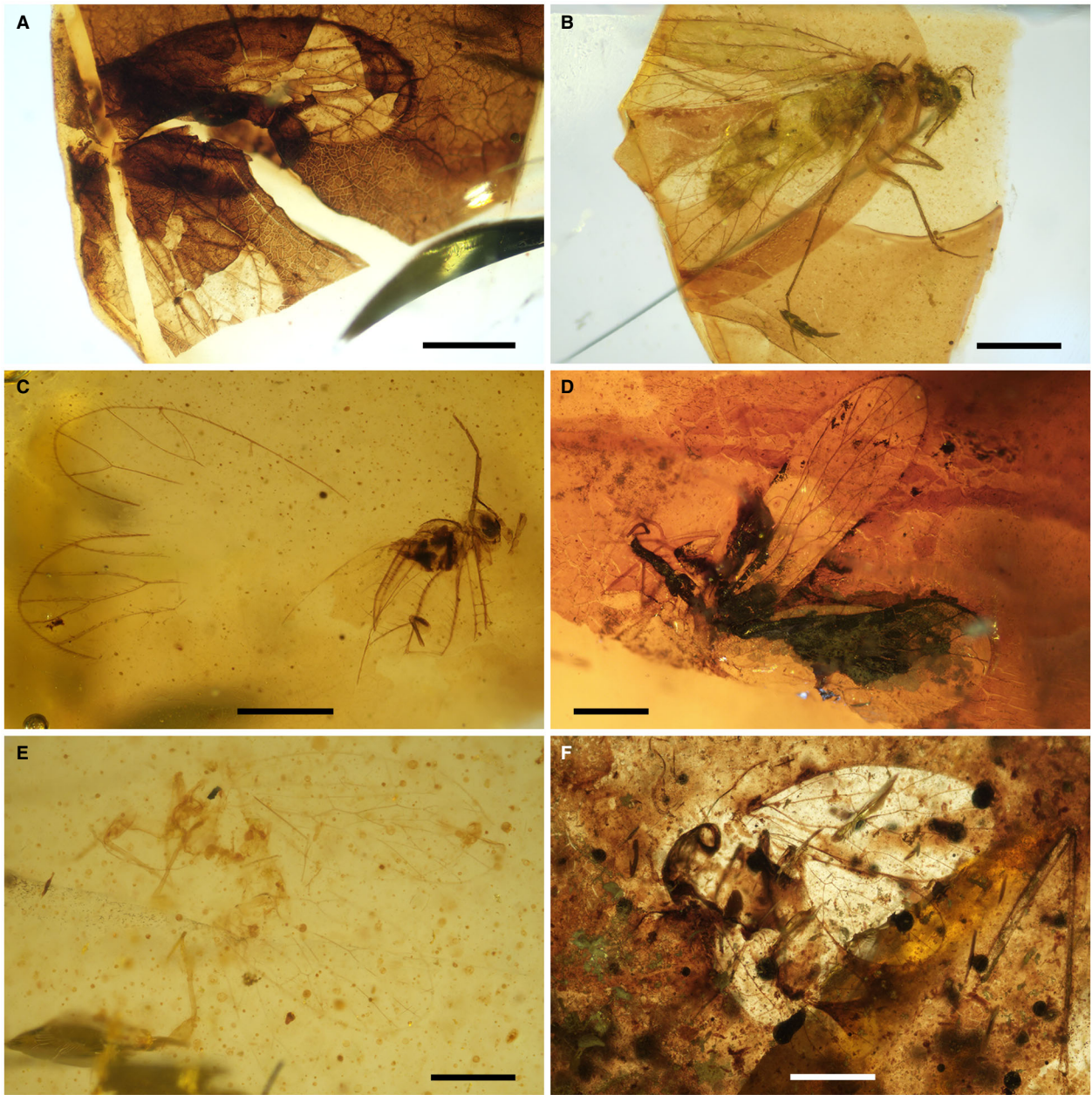
#### *Libanoglaris hespericus* sp. nov.

Figures 6–8

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*Derivation of name.* After Hesperia, from the Greek *Ἑσπερίς*, the ancient name for the western lands of the Mediterranean Sea, based on the location of the type locality of the new species





**FIG. 5.** New studied specimens of *Archaeatropos alavensis* Baz & Ortuño, 2000 (Psocodea, Trogiomorpha, †Archaeatropidae) from the Albian amber of El Soplao (Cantabria Autonomous Community, Spain) and the upper Albian amber of Peñacerrada I (Burgos Province, Spain). A, specimen CES.445, sex unknown. B, specimen CES.465, female. C, specimen CES.495.4, sex unknown. D, specimen CES.526.5, sex unknown. E, specimen CES.586.2, sex unknown. F, specimen MCNA-14912.1, sex unknown. Scale bars represent 0.5 mm.

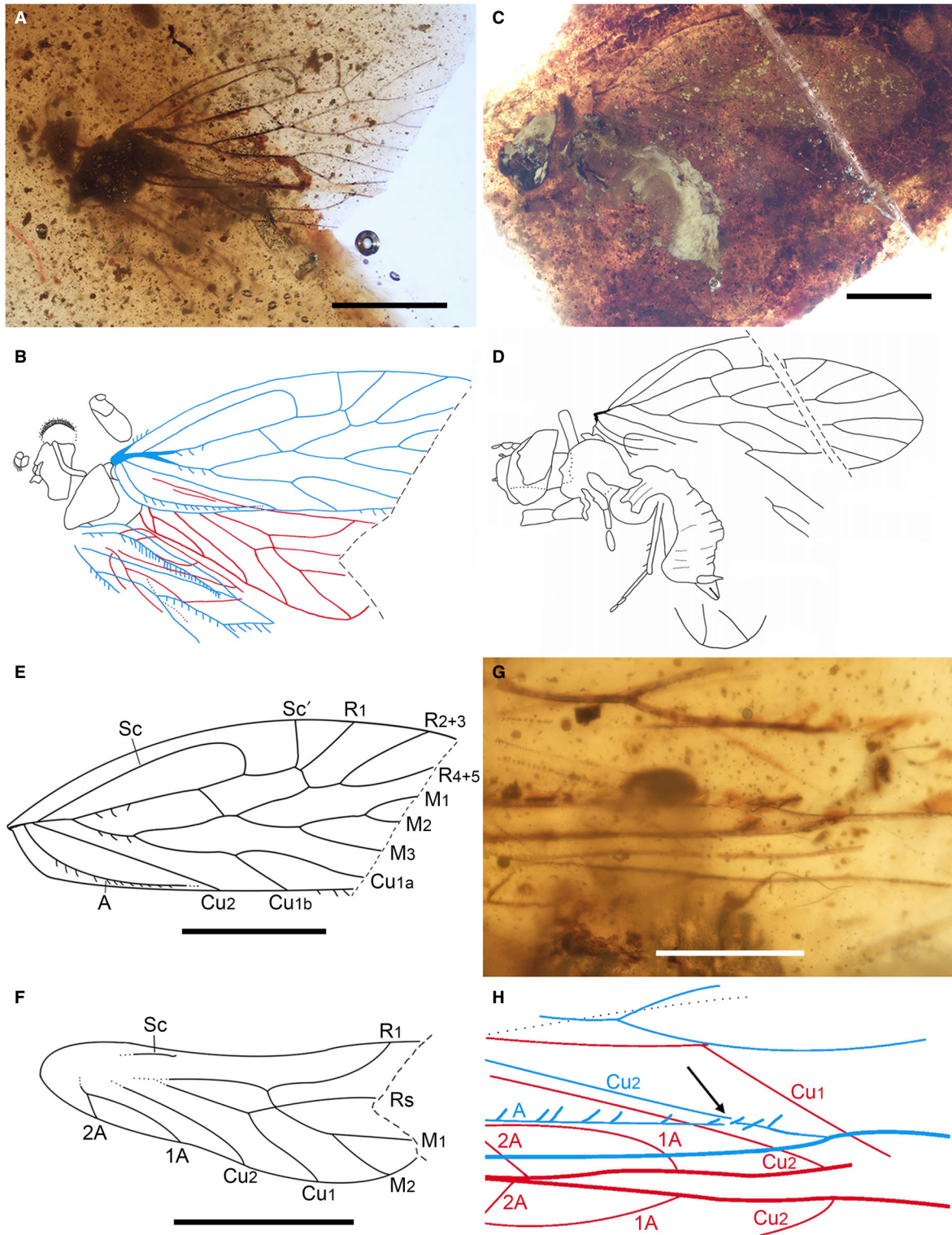
in relation to that of the other species of the genus (from Lebanon).

*Type specimens.* Holotype AR-1-A-2019.35: an incomplete macropterous specimen with clearly visible venation (Fig. 6A, B), sex unknown. Paratype AR-1-A-2019.69.1: an almost complete specimen, the right forewing and some body characters are visible (Fig. 6C, D), sex unknown, with a specimen that could be a

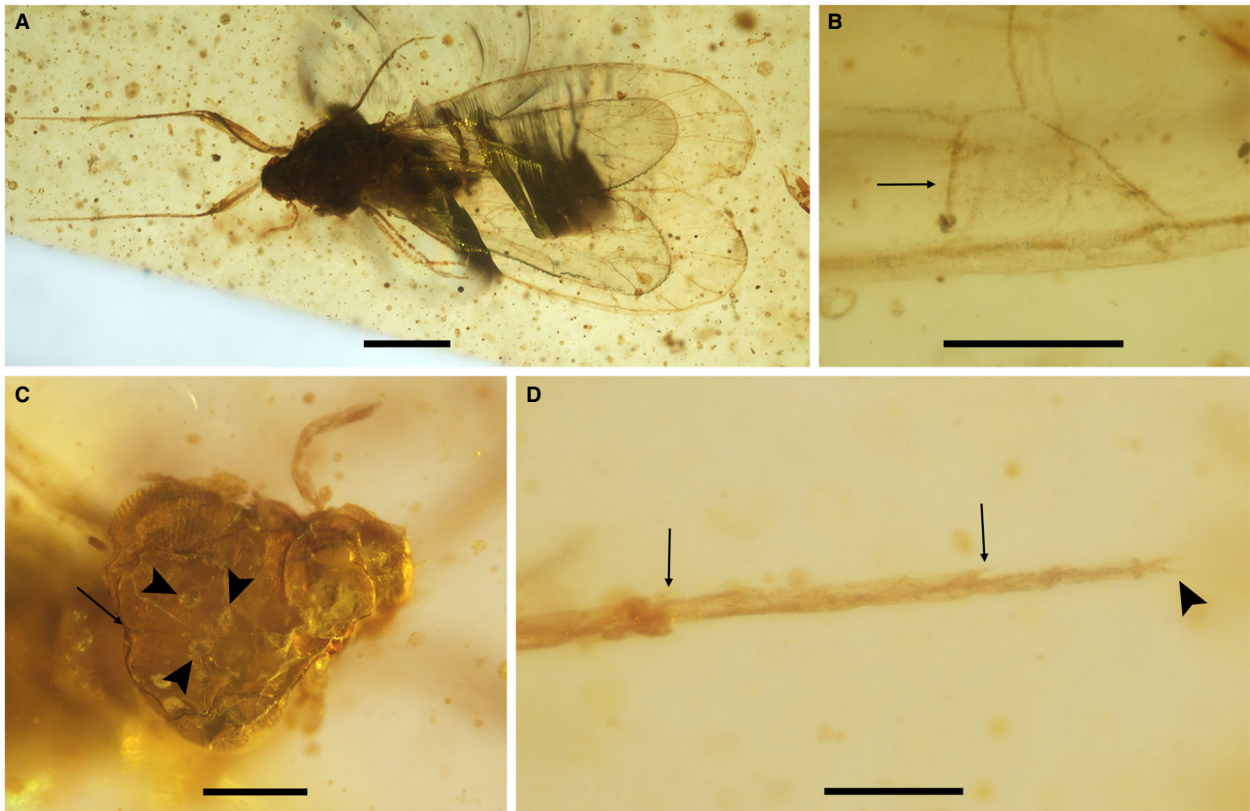
dipteran as a syninclusion. Both are housed at the Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis).

*Other material.* CES.586.1: a complete specimen, the body is anterodorsally compressed (Fig. 7), the wings are folded roof-like so that the venation is unclear, sex unknown, with a psocid (*Archaeatropos alavensis*) as a syninclusion.





**FIG. 6.** Type specimens of *Libanoglaris hespericus* sp. nov. (Psocodea, Trogiomorpha, †Archaeatropidae) from the lower Albian amber of Ariño (Teruel Province, Spain). A–B, habitus of the holotype specimen AR-1-A-2019.35 in ventral view, sex unknown, with the forewings shown in blue and the hind wings in red in B. C–D, habitus of the paratype specimen AR-1-A-2019.69.1 in dorsal view, sex unknown. E–F, forewing and hind wing, respectively, of holotype AR-1-A-2019.35. G–H, detail and interpretive drawing of the nodulus of the right forewing of holotype AR-1-A-2019.35, respectively, with the nodulus indicated by an arrow in H, forewing is shown in blue and the hind wings in red. Scale bars represent: 0.5 mm (A–F); 0.2 mm (G, H).



**FIG. 7.** *Libanoglaris hespericus* sp. nov. (Psocodea, Trogiomorpha, †Archaeatropidae) from the Albian amber of El Soplao (Cantabria Autonomous Community, Spain), CES.586.1, sex unknown. A, habitus in the dorsal view. B, pterostigma area of the left forewing, showing the straight distal sector of Sc (arrow) joining the wing margin at a right angle. C, head in the dorsal view (epicranial suture indicated by an arrow, ocelli indicated by arrowheads). D, right foreleg, distal spurs of the tibia and the proximal tarsomere are indicated by arrows, while the pretarsal claws lacking a preapical tooth are indicated by an arrowhead. Scale bars represent: 0.5 mm (A); 0.2 mm (B, C); 0.1 mm (D).

*Diagnosis.* Wings glabrous except for the forewings with fine hairs in the basal parts of R and M + Cu, and a row of setae along A; forewings: crossvein from R<sub>1</sub> to Rs straight, Rs oblique basally, bifurcation of Cu<sub>1a</sub> and Cu<sub>1b</sub> at the same level as that of the joining of Rs with M.

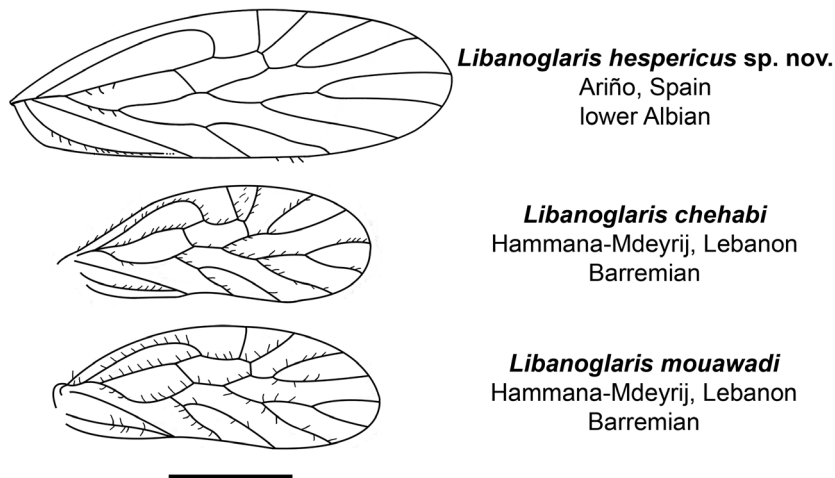
*Description.* Body almost glabrous or covered by a few fine hairs. Head 0.52 mm wide, with broad vertex showing three ocelli (Fig. 7C); prominent compound eyes separated by 0.32 mm; antennae preserved in AR-1-A-2019.69.1, showing scape, pedicel and first flagellomere of the right antenna without secondary annulations; bulging postclypeus; mouthparts obscure. Description of venation is based on the holotype AR-1-A-2019.35, which presents visible veins although it is lacking a wing apex (Fig. 6E–H); forewing 1.88–2.16 mm long and 0.60–0.71 mm wide (Fig. 6E), hyaline, with a glabrous margin except for a few fine hairs in the basal part of the costal margin of AR-1-A-2019.35; basal parts of R and M + Cu covered by fine hairs; basal sector of Sc long, showing a strong curve before fusion with R<sub>1</sub>, to which it is fused for 0.18 mm, basal sector of Sc is not visible in CES.586.1; distal part of Sc straight and reaching the costal margin at 1.07 mm from the wing base to form

almost a right angle; pterostigma area not thickened and without setae; straight crossvein from R<sub>1</sub> to Rs; length of R<sub>1</sub> from where the distal part of Sc emerges to the crossvein from R<sub>1</sub> to Rs is variable (Fig. 7B), longer in CES.586.1 than in the holotype AR-1-A-2019.35; Rs oblique basally and fused to M for 0.05 mm, emerging from M at 0.80 mm from wing base, and distally branching into R<sub>2+3</sub> and R<sub>3+4</sub> at 1.17 mm from the wing base, both veins slightly curved; radial cell closed, six-angled and elongate, more than threefold longer than wide; curved M + Cu<sub>1</sub>, 0.22 mm long, bifurcating at 0.44 mm from wing base; M<sub>3</sub> emerging from M at 1.01 mm from wing base and continuing mostly straight, M branching into M<sub>1</sub> and M<sub>2</sub> at 1.24 mm from wing base; Cu<sub>1</sub> 0.37 mm long, bifurcation of Cu<sub>1a</sub> and Cu<sub>1b</sub> at the same level as that of the joining of Rs with M, at 0.79 mm from wing base, Cu<sub>1a</sub> showing a slight curve and extending towards the wing apex, Cu<sub>1b</sub> straight, shorter than Cu<sub>1a</sub> and reaching the margin at 0.99 mm from the wing base, both forming an elongate areola postica; straight Cu<sub>2</sub> extending towards the wing margin, which it reaches at 0.77 mm from the wing base; A covered by a row of setae, showing a strong curve and extending towards Cu<sub>2</sub>, joining in a nodulus (Fig. 6G, H). Hind wing hyaline (Fig. 6F), without setae or fine hairs in the margin

or in the veins, 1.65 mm long in CES.586.1 (only specimen showing hind wings that are complete in length) and 0.34–0.45 mm wide; Sc does not reach the wing margin, ending free in wing membrane;  $R_1$  reaching the margin at 0.98 mm from the wing base; Rs makes contact with M at a point, but they do not fuse, although Rs and M are fused for 0.23 mm in CES.586.1; Rs two-branched; basi-radial cell four-angled; M basally fused with  $Cu_1$ , length of M from its separation from  $Cu_1$  to its joining with Rs is 0.08 mm, distal free part of M is 0.18 mm long, bifurcation of  $M_1$  and  $M_2$  is at 0.83 mm from wing base;  $Cu_1$  separating from M and reaching the margin at 0.83 mm from wing base; slightly curved  $Cu_2$  reaching the margin at 0.62 mm from wing base; A separating into 1A and 2A at 0.14 mm from wing base, 1A is curved and 2A is straight, both reaching the margin at 0.43 mm and 0.20 mm from the wing base, respectively. Forelegs of CES.586.1 are completely preserved; thick femora 0.43 mm long; thin tibiae 0.70 mm long; tarsi three-segmented (Fig. 7D); one distal spur in the tibiae and proximal tarsomere (Fig. 7D); length of tarsomeres: proximal 0.21 mm, middle 0.06 mm, distal 0.05 mm; two pretarsal claws in distal tarsomeres that lack a preapical tooth (Fig. 7D). Abdomen of AR-1-A-2019.69.1 and CES.586.1 poorly preserved; the former could be a female based on the morphology of the genitalia.

**Remarks.** *Libanoglaris hespericus* sp. nov. belongs to †Archaeatropidae (Trogiomorpha: Atropetae) based on the following characters: forewing with a well-developed basal sector of Sc that is curved and reaches R, a pterostigma area that is not thickened, a curved M + Cu, a crossvein from  $R_1$  to Rs, a long and slender areola postica, a shorter  $Cu_{1b}$ , compared with  $Cu_{1a}$ , the joining of  $Cu_2$  and A in a nodule, a short hind wing with Sc that does not reach R, a two-branched M, a four-angled basi-radial cell, basally fused 1A and 2A that branches near the wing margin, a curved 1A, and three-segmented tarsi. Within †Archaeatropidae, the three specimens are assigned to the genus

*Libanoglaris* based on the lack of secondary annulations in the flagellomeres and the venation of the wings (Perrichot *et al.* 2003). Other archaeatropid genera without secondary annulations are *Prospeleketor* and *Propionoglaris*, but the wing venations are clearly different (Perrichot *et al.* 2003). Both genera present forewings in which the distal sector of Sc is directed towards the wing apex (Perrichot *et al.* 2003), in contrast to the genus *Libanoglaris*, which presents a straight distal sector of Sc that joins nearly perpendicular to the anterior wing margin (Perrichot *et al.* 2003; Azar & Nel 2004). Furthermore, the three specimens fit within the genus *Libanoglaris* based on their wings without scales and without a sclerotized pterostigma, a forewing with the basal sector of Sc reaching R and fusing with it over a long stretch (basal sector of Sc not preserved in CES.586.1), an absence of a crossvein between the proximal sector of Sc and the wing margin, an elongate radial cell and an Rs that is oblique at its base, and a hind wing with a four-angled basi-radial cell (Perrichot *et al.* 2003). The number of flagellomeres, the characteristics of the mouthparts, and the absence of long sensillae in the median and posterior femora and tibiae, which are indicated in the diagnosis of *Libanoglaris* (Perrichot *et al.* 2003), cannot be observed in the specimens. The genus *Bcharreglaris* has forewings in which the distal sector of Sc is perpendicular to the wing margin (Azar & Nel 2004), but it has secondary annulations in the flagellomeres and a triangular pterostigma (vs a trapezoidal pterostigma in *Libanoglaris*). *Libanoglaris* includes two species from the Barremian Hammana-Mdeyrij locality (Lebanon), which are *Libanoglaris mouawadi* and *Libanoglaris chehabi*. Mockford *et al.* (2013) transferred *Libanoglaris randatae* Azar & Nel, 2004 (from the Jezzine locality in Lebanon) to the genus *Archaeatropos* based on the  $Sc'$  being curved and directed towards the wing base, as commented above. The vein  $Sc'$  is straight and reaches the costal margin, forming almost a right angle in *L. mouawadi*, which is different to the straight  $Sc'$  in *L. chehabi* that is slightly directed towards the wing base, forming an obtuse angle with the costal margin (Fig. 8). The three



**FIG. 8.** Schematic drawings of the forewings of *Libanoglaris* spp. (Psocodea, Trogiomorpha, †Archaeatropidae). The forewing of *Libanoglaris hespericus* sp. nov. has been reconstructed from the specimens AR-1-A-2019.35 (holotype) and AR-1-A-2019.69.1 (paratype). The forewings of *Libanoglaris chehabi* and *Libanoglaris mouawadi* have been redrawn from Azar & Nel (2004) and Perrichot *et al.* (2003), respectively. All images are at the same scale. Scale bar represents 0.5 mm.



specimens are assigned to a new species, *L. hespericus*, based on the diagnostic characters that differentiate them from the other two species of the genus. They are conspecific based on the venation, mainly because they share the straight distal sector of Sc that joins the wing margin at almost a right angle. Furthermore, their wings are almost glabrous, both the margin and the membrane. *Libanoglaris hespericus* is separated from the other species of the genus by a time span of *c.* 20 myr (Perrichot *et al.* 2003; Azar & Nel 2004). Interestingly, the older Lebanese species would have been distributed throughout the south-eastern margin of the Tethys Sea, while the younger *L. hespericus* would have been present in the western margin (Iberia Island). Intraspecific variability of the wing venation has been noted when comparing the holotype AR-1-A-2019.35 from Ariño with the CES.586.1 specimen from El Soplao. The length of R<sub>1</sub> (in the forewings) from the emerging of the distal part of Sc to the crossvein from R<sub>1</sub> to Rs is longer in CES.586.1 than in AR-1-A-2019.35. Furthermore, in the hind wing of AR-1-A-2019.35, Rs makes slight contact with M at a point, but they do not fuse, whereas both veins are fused for 0.23 mm in CES.586.1. Despite these differences, we prefer to putatively assign CES.586.1 to *L. hespericus* rather than to establish a new species, based on the matching characters when compared with the Ariño specimens. The morphological differences can be explained by the spatial and temporal distance between the amber localities.

*Type locality and horizon.* Level AR-1 of the Ariño amber-bearing outcrop, Teruel Province, Spain; Escucha Formation, lower Albian (Álvarez-Parra *et al.* 2021).

*Other localities.* El Soplao amber-bearing outcrop, Cantabria Autonomous Community, Spain; Las Peñasas Formation, Albian.

#### Family †EMPHERIIDAE Kolbe, 1884

*Type genus.* *Empheria* Hagen in Pictet-Baraban & Hagen, 1856.

*Included genera and species.* *Burmempheria densuschaete* Li, Wang & Yao in Li *et al.*, 2020 (Cenomanian, Myanmar); *Burmempheria raruschaetae* Li, Wang & Yao in Li *et al.*, 2020 (Cenomanian, Myanmar); *Empheria pertinens* (Enderlein, 1911) (Eocene, Baltic amber); *Empheria reticulata* Hagen in Pictet-Baraban & Hagen, 1856 (Eocene, Baltic amber); *Empherium rasnitsyni* Hakim *et al.*, 2021a (Cenomanian, Russia); *Empheropsocus arilloi* Baz & Ortuño, 2001b (Albian, Spain); *Empheropsocus margineglabrus* Baz & Ortuño, 2001b (Albian, Spain); *Eoempheria intermedia* Nel *et al.*, 2005 (Eocene, France); *Jerseyempheria grimaldii* Azar *et al.*, 2010 (Turonian, USA); *Preempheria antiqua* Baz & Ortuño, 2001b (Albian, Spain); and *Trichempheria villosa* (Hagen, 1882) (Eocene, Baltic amber).

#### Genus PREEMPHERIA Baz & Ortuño, 2001b

*Type species.* *Preempheria antiqua*; by monotypy.

*Original diagnosis.* Forewings oval. Forewing margin glabrous. Basal sector of Sc well developed, curving to meet R. Basal sector of Sc setose with the setae arranged as is typical for the family. Vein R<sub>1</sub> reunites with Rs distally with a crossvein. Origin of the first branch of M distally to the crossvein R<sub>1</sub>–Rs. A transverse vein between R and Rs + M common trunk, forming a six-angled radial cell. (Baz & Ortuño 2001b)

*Remarks.* Based on the description of the new specimen from San Just assigned to *Preempheria antiqua*, several comments can be added to the original diagnosis of the genus. Besides the characters of the forewings indicated in the original diagnosis, the forewings show closely packed linear spicules that are parallel to the wing margin, rows of setae along both sides of the veins (typical in †Empheriidae), a short Cu<sub>1</sub> that divides into Cu<sub>1a</sub> and Cu<sub>1b</sub> at the same level as that of the joining of Rs and M, a long areola postica, a setose anal region, and an absent anal vein. The hind wings are completely glabrous, with a two-branched Rs and M. Given that the original diagnosis lacks body characters, we wanted to highlight the following: the presence of three ocelli that are close together and arranged into an inverted triangle, flagellomeres that are not secondarily annulated and of a similar length, four-segmented maxillary palps with the fourth palpomere elongate and showing a round and slightly widened apex, tibiae with three distal spurs, and distal tarsomeres with two pretarsal claws without a preapical tooth and bearing one pulvillus each that is widened at the tip.

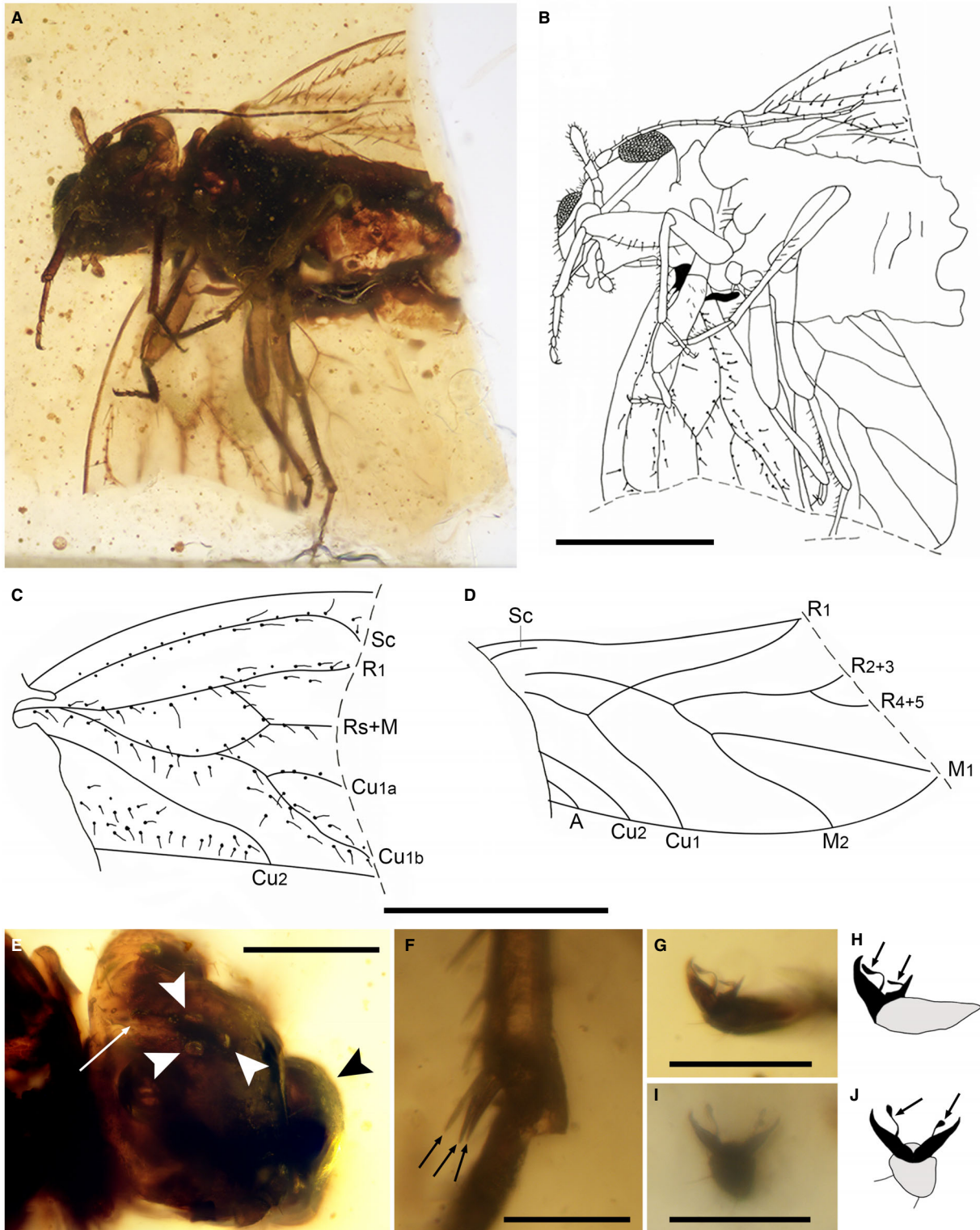
#### *Preempheria antiqua* Baz & Ortuño, 2001b

##### Figure 9

*Material.* CPT-4117; a partial specimen, sex unknown.

*Other material examined.* MCNA-8888, holotype, female. MCNA-8872, paratype, female.

*Description.* Specimen covered by fine hairs and with head, thorax, proximal parts of wings and half of abdomen preserved (Fig. 9A, B). Macropterous with visible venation (Fig. 9C, D). Head 0.53 mm wide with two prominent compound eyes that are globular in shape, 0.17 mm in diameter and separated by 0.22 mm; vertex broad and covered by fine hairs, showing epicranial suture, with three ocelli close together and arranged into an inverted triangle (Fig. 9E); left antenna partially preserved with scape, pedicel and 16 flagellomeres preserved, lacking the distal ones, each *c.* 0.07 mm long and with a pair of distal fine hairs, without secondary annulations; right antenna with only scape, pedicel and five flagellomeres preserved; gibbous clypeus; maxillary palps four-segmented and covered by fine hairs, fourth palpomere with round and slightly widened apex, length of maxillary palpomeres: I 0.06 mm, II 0.04 mm, III 0.05 mm, IV 0.13 mm, a short conical sensillum is not visible on second palpomere; a thick elongate structure possibly corresponding to lacinia and galea can also be observed; labial palps two-segmented with a wide and round apex and covered by fine hairs, length of labial palpomeres: I 0.03 mm, II 0.04 mm. The



**FIG. 9.** New studied specimen of *Preempheria antiqua* Baz & Ortuño, 2001b (Psocodea, Trogiomorpha, †Empheriidae) from the upper Albian amber of San Just (Teruel Province, Spain), CPT-4117, sex unknown. A–B, photograph and drawing of the habitus. C–D, forewing and hind wing, respectively, both images are at the same scale. E, dorsal view of the head, with the epicranial suture indicated by an arrow, the ocelli indicated by white arrowheads, and the clypeus indicated by a black arrowhead. F, distal part of the tibia of the left hind leg, with the spurs indicated by arrows. G–J, details of the pretarsal claws bearing one pulvillus each, with the pulvilli indicated by arrows, G and H are from the right foreleg, while I and J are from the right midleg. Scale bars represent: 0.5 mm (A–D); 0.2 mm (E); 0.05 mm (F–J).



thorax is obscure and the wings are incomplete, but the legs are completely preserved, except for the distal part of the right hind leg. Forewings hyaline, 0.63 mm wide and with a glabrous margin (Fig. 9C); closely packed linear spicules parallel to the wing margin described by Baz & Ortuño (2001b) are clearly visible; setae are visible as rows along both sides of the veins; the basal sector of Sc is long and distally curved and directed towards R<sub>1</sub>, although the joining is not preserved; Rs oblique, joining M at 0.58 mm from the wing base; Cu<sub>1</sub> short and dividing into Cu<sub>1a</sub> and Cu<sub>1b</sub> at the same level as that of the joining of Rs and M, Cu<sub>1b</sub> shows a slightly sigmoidal path, areola postica is long; Cu<sub>2</sub> reaches the margin at 0.66 mm from the wing base; anal vein is not present, although the anal region is setose, a row of setae is directed towards Cu<sub>2</sub>. Hind wings hyaline, 0.46 mm wide and completely glabrous, without setae (Fig. 9D); Sc short; R<sub>1</sub> showing a slightly sigmoidal path; basi-radial cell three-angled, triangular in shape; Rs and M two-branched; Cu<sub>1</sub>, Cu<sub>2</sub> and A all present. Legs covered by fine hairs, thick femora, thin tibiae, and three-segmented tarsi; tibiae with two distal spurs, although three distal spurs can be seen in the tibia of the left hind leg (Fig. 9F); length of tarsomeres from proximal to distal: 0.13 mm, 0.04 mm, 0.05 mm; distal tarsomeres with two pretarsal claws, without a preapical tooth and bearing one pulvillus each that is widened at the tip (Fig. 9G–J). Abdomen is incomplete and genitalia are not preserved.

*Remarks.* Despite being incomplete the CPT-4117 specimen is assigned to a species. The short and broad head, flagellomeres that are not secondarily annulated, the two-segmented labial palps (with a minute basal segment and a rounded distal segment) and the three-segmented tarsi were used to assign the specimen to Atropetae belonging to Trogiomorpha (Smithers 1972; Mockford 1993). The presence of more than 18 flagellomeres and a sensillum on the second palpomere could not be determined due to preservation. Baz & Ortuño (2001b) stated that the following characters defined the †Empheriidae family: wings rounded at the apex, a forewing with a well-developed Sc whose basal sector joins with R, crossvein R<sub>1</sub>–Rs, the forking of Cu close to the wing base, a long areola postica, setae arranged along both sides of the veins and a glabrous hind wing. The observable characters in CPT-4117 corresponded to those of †Empheriidae. Furthermore, an important character that differentiates †Empheriidae from †Archaeatropidae is the nodule corresponding to the joint between Cu<sub>2</sub> and A (Baz & Ortuño 2000), which is absent in †Empheriidae and in CPT-4117. Considering the empheriid species, CPT-4117 belongs to *Preempheria antiqua* based on the preserved characters. The previously described *P. antiqua* specimen from the upper Albian Peñacerrada I amber-bearing outcrop has three distal spurs on the tibiae (Baz & Ortuño 2001b), but CPT-4117 has two distal spurs on the tibiae, except for one leg that has three, possibly due to a preservation artefact. Furthermore, the proximal tarsomere of CPT-4117 measures c. 0.13 mm, which is different to the length of 0.28 mm observed in the specimens from Peñacerrada I (Baz & Ortuño 2001b). These two characters constitute minor differences that would not justify the description of a new species. Although Baz & Ortuño (2001b) did not indicate it, the diagnosis of *P. antiqua* is the same as that of the

genus *Preempheria*. The genus *Empheropsocus* could be related to *Preempheria* based on the absence of the A vein, which is an apomorphic character for both according to Mockford *et al.* (2013). The presence of a short vein from the basal sector of Sc directed towards the wing margin or to the distal sector of Sc in *Empheropsocus* and its absence in *Preempheria* is a key character for the differentiation of the two genera (Baz & Ortuño 2001b). The genus *Burmempheria* resembles *Empheropsocus* in that both show a short vein emerging from the basal sector of Sc. However, Li *et al.* (2020) indicated several additional characters that differentiate them. Therefore, *Empheropsocus* and *Preempheria* may form a subgroup in †Empheriidae that is characterized by the absence of the A vein as a putative synapomorphy (Mockford *et al.* 2013), which would be related to *Burmempheria*. The genus *Jerseyempheria* has a setose forewing margin, the presence of the A vein in the forewing, and a hind wing in which the M<sub>1</sub> and M<sub>2</sub> emerge from different branches of Rs + M, not forking from an M common trunk (Azar *et al.* 2010). Cretaceous empheriids have a forewing with a basal R<sub>s</sub>–M vein and a hind wing with a closed cell, differing from Cenozoic empheriids (Mockford *et al.* 2013).

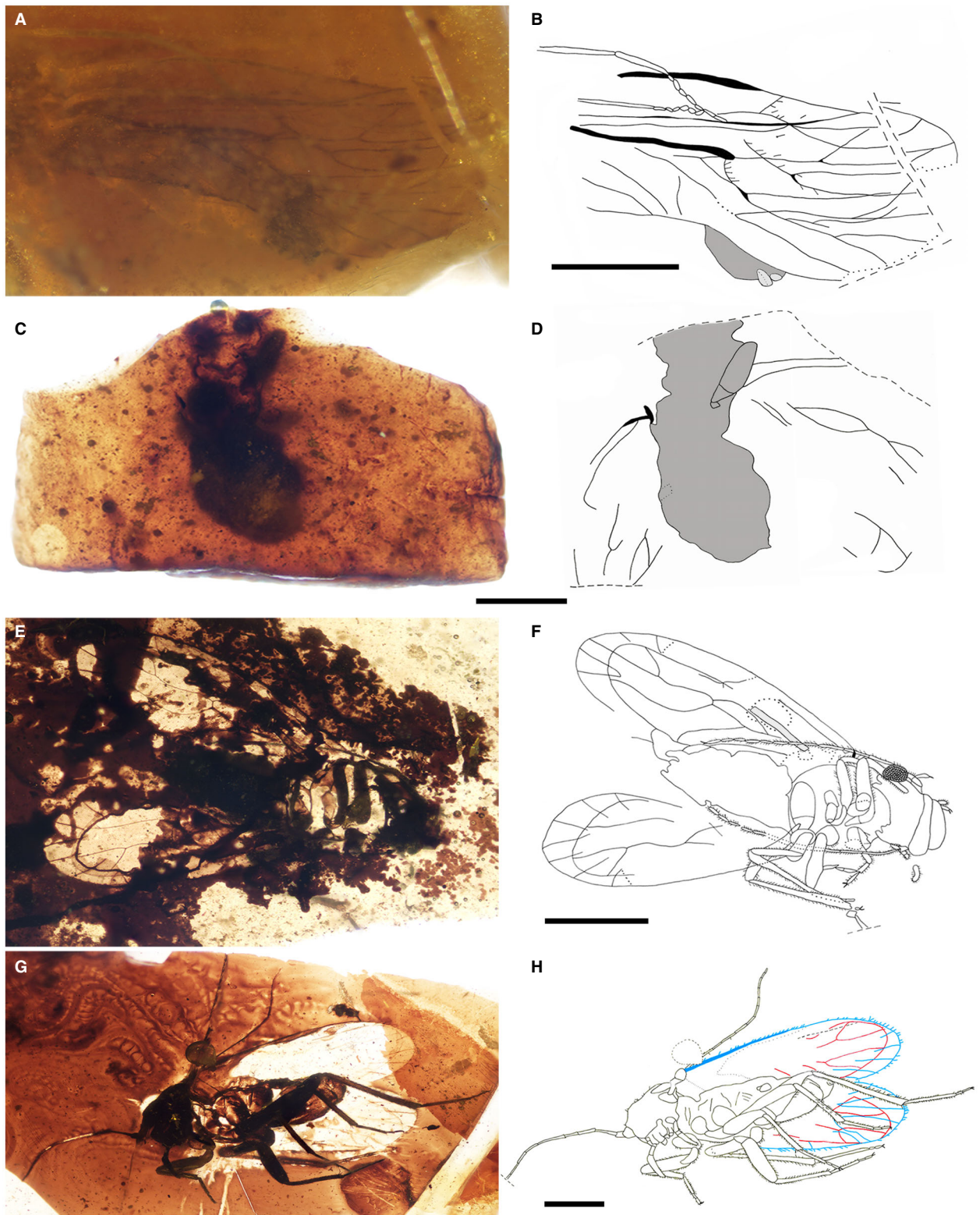
#### Indeterminate material

Four additional psocodean specimens were studied (Fig. 10), although they lack diagnostic characters to assign them to a group.

*AR-1-A-2018.3.2.* Wing remains of a psocid specimen (Fig. 10A, B). Antenna and abdomen poorly preserved. Genitalia can be seen in the distal part of the abdomen but they are obscure. Forewings and hind wings overlap, therefore their respective veins cannot be clearly resolved. A long pterostigma bounded by an oblique distal sector of Sc and an R<sub>1</sub> with a curved path seems to be similar to that of some Manicapsocidae (Troctomorpha) specimens.

*AR-1-A-2019.42.* This specimen is poorly preserved because it has only partial body remains and some blurred veins in wings with poorly defined margins (Fig. 10C, D). It could belong to †Archaeatropidae based on the basal sector of Sc being tentatively directed to R<sub>1</sub>, but the latter is not preserved. The assignment to †Archaeatropidae is uncertain.

*SJNB2012-12-06.* Body 1.38 mm long, poorly preserved (Fig. 10E, F). Left prominent compound eye is visible; the postclypeus is bulging; antennae with at least 11 flagellomeres, hardly differentiable, lacking secondary annulations and covered by long, fine hairs; four-segmented maxillary palpus covered by fine hairs, a sensillum in the second maxillary palpomere seems to be absent. Forewings hyaline, 1.35 mm long and 0.45 mm wide; wing margin and membrane glabrous; a long basal section of Sc is tentatively visible in the left forewing; distal section of Sc might be present in both forewings, emerging from R<sub>1</sub> near the wing margin and forming a triangular pterostigma, although it is unclear whether it is a preservation artefact; the most distal parts of R<sub>1</sub>, R<sub>2+3</sub>, R<sub>4+5</sub>, M<sub>1</sub>, M<sub>2</sub>, M<sub>3</sub> and Cu<sub>1a</sub> are preserved. Hind wings hyaline and glabrous, 1.18 mm long and 0.35 mm wide; basi-radial



**FIG. 10.** Habitus of undetermined psocid (Psocodea) specimens from the lower Albian amber of Ariño and the upper Albian amber of San Just (both in Teruel Province, Spain). A–B, specimen AR-1-A-2018.3.2, similar to some Manicapsocidae (Troctomorpha) specimens. C–D, specimen AR-1-A-2019.42 putatively belonging to †Archaeatropidae. E–F, specimen SJNB2012-12-06 in dorsal view. G–H, specimen MAP-7822 in ventral view, with the forewings shown in blue and the hind wings in red. Scale bars represent: 0.5 mm.

cell four-angled;  $R_1$  not visible;  $R_s$  two-branched;  $M$  not branched, showing a sigmoidal path;  $Cu_1$  curved. Legs with preserved coxae, trochanters, femora, tibiae and tarsi and covered by fine hairs; tibiae with ctenidiobothria and two distal spurs; tarsi three-segmented; distal tarsomere with two pretarsal claws bearing one preapical tooth each. Abdomen obscure, the two external valvulae covered by setae of the female genitalia are visible.

*MAP-7822*. Body 1.75 mm long (Fig. 10G, H). Head covered by fine hairs; two prominent compound eyes; ocelli not visible; antennae with at least 12 flagellomeres lacking secondary annulations and fine hairs; mouthparts partly visible; maxillary palps four-segmented and covered by fine hairs, length of maxillary palpomeres: I 0.06 mm, II 0.09 mm, III 0.02 mm, IV 0.19 mm, distal maxillary palpomere thick and long and with a pointed apex, a sensillum in second maxillary palpomere seems to be absent. Forewing 1.81 mm long and 0.52 mm wide; forewing margin setose; right forewing might be presenting the distal sections of  $Sc$  and  $R_1$ ; distal sections of  $R_{2+3}$ ,  $R_{4+5}$ ,  $M_1$ ,  $M_2$  and  $M_3$  visible in both forewings. Hind wings hyaline and glabrous, 0.42 mm wide;  $R_s$  and  $M$  two-branched. Five legs completely preserved, covered by fine hairs; three distal spurs in tibiae (only two visible in some tibiae) and two distal spurs in proximal tarsomeres; tarsi three-segmented; proximal tarsomere with ctenidiobothria; two pretarsal claws with one preapical tooth each. Genitalia poorly preserved.

## DISCUSSION

The fossil record of Psocodea from the Iberian Peninsula has been little studied and is represented only in Cretaceous amber and Miocene compression rock to date. Including the new addition described in this paper, the psocid record of Spanish amber consists of six species in five genera from five amber-bearing outcrops along the Basque–Cantabrian Basin and the Maestrazgo Basin. In addition to the new †Archaeatropidae and †Empheriidae specimens, there are several specimens of Trogiomorpha and Troctomorpha in Spanish amber that are currently under investigation (SÁ-P, pers. obs.) The only known compression fossil of a psocid from the Iberian Peninsula corresponds to an isolated forewing assigned to cf. *Mesopsocus* sp. (Psocomorpha: Mesopsocidae) that was found in the Lower Miocene laminated dolostones of the Ribesalbes–Alcora Basin from the La Rinconada outcrop (Peñalver *et al.* 1996). Cretaceous psocids from compression sites are virtually unknown and only a few finds have been reported, for example, two undetermined barklice from the Turonian Orapa site in Botswana (Brothers & Rasnitsyn 2003). Furthermore, some putative psocids from compression sites have been found to belong to closely related groups such as †Permopsocida and †Lophioneurida, as in the case of *Undacypha una* (Jell & Duncan 1986) from the Lower Cretaceous Koonwarra site

in Australia that was most recently assigned to Lophioneurida (Ansorge 1996). Interestingly, the different preservation of psocids in amber and compression sites could be influenced by taphonomic bias (Martínez-Delclòs *et al.* 2004). Compression outcrops usually preserve large insect fossils, while amber preserves insects that were a few millimetres in size (Martínez-Delclòs *et al.* 2004). Additionally, the record of insects in compression sites depends on their buoyancy and the presence of predators and scavengers (Martínez-Delclòs *et al.* 2004). A detailed examination of the slabs could eventually increase the known fossil record of psocids, if there were not palaeoenvironmental constraints. Nevertheless, the three-dimensional preservation of insects in amber highlights the possibility of gaining further knowledge on Cretaceous and Cenozoic psocids.

The monophyly of Trogiomorpha is well supported by molecular data and anatomical autapomorphies (Yoshizawa *et al.* 2006; Johnson *et al.* 2018; Yoshizawa & Lienhard 2020). It is considered to be the most basal group within Psocodea because it retains plesiomorphic characters (Smithers 1972; Mockford 1993; Lienhard 1998; De Moya *et al.* 2021). The family †Cormopsocidae has been tentatively included in the suborder Trogiomorpha, although it may be phylogenetically located outside this group, basally to Psocodea, given that the female characters have not been described (Yoshizawa & Lienhard 2020). Despite this, the description of additional cormopsocid specimens supports its inclusion in Trogiomorpha (Hakim *et al.* 2021b; Wang *et al.* 2021). The families †Archaeatropidae and †Empheriidae have been placed basally to Atropetae (Yoshizawa & Lienhard 2020), retaining plesiomorphic characters that are also present in †Cormopsocidae and Prionoglarididae, such as the presence of a strongly curved  $Sc$  vein that makes contact with  $R_1$  and the crossvein from  $R_1$  to  $R_s$  in the forewings. To date, the relationships of Trogiomorpha indicated by Yoshizawa & Lienhard (2020) within Trogiomorpha seem to be plausible and can be summarized as follows: [Cormopsocidae (Prionoglaridetae [Psyllipsocetae (Atropetae)])].

Hagen (*in* Pictet-Baraban & Hagen 1856) described the genus *Empheria* as clearly lacking a nodulus. Kolbe (1883, p. 190) proposed the group ‘Empheriini’ without a diagnosis, while Kolbe (1884, p. 37) proposed the first diagnosis for the family. Enderlein (1911, p. 285) proposed the diagnosis for †Empheriidae as follows (translation from German), with these two characters possibly crucial in distinguishing between †Empheriidae and †Archaeatropidae: ‘no nodulus and an absent maxillary palpus sensillum’. †Archaeatropidae specimens have a sensillum on the second maxillary palpomere, except for the genus *Proprionoglaris* (Perrichot *et al.* 2003). Unfortunately Li *et al.* (2020) indicated nothing about the presence versus absence of this structure in *Burmempheria*. Li *et al.* (2020,

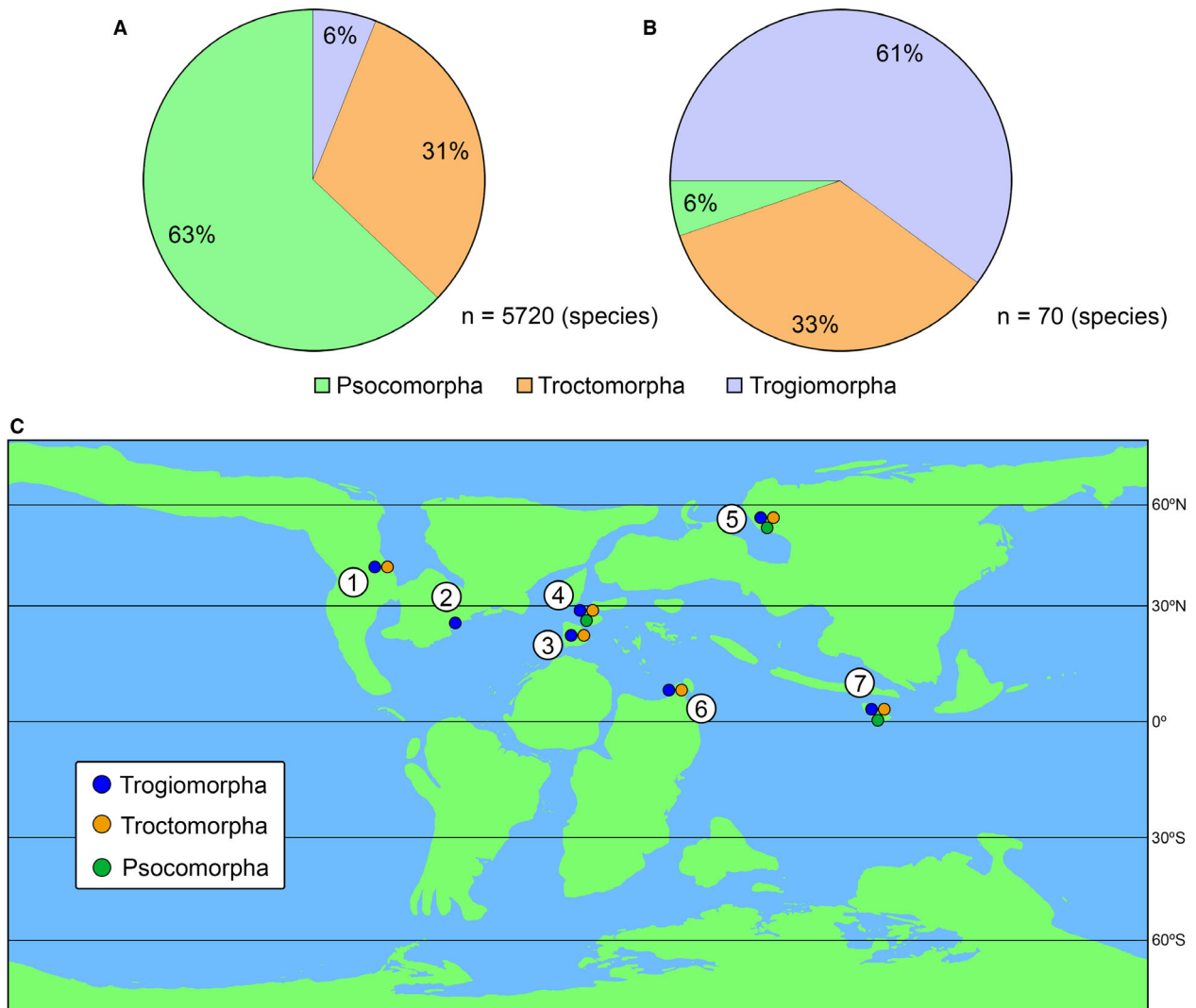


p. 6) minimized the importance of the nodulus for family diagnoses: ‘among the recent research, nodulus in forewing is an unstable character (Wang *et al.* 2019)’. However, Wang *et al.* (2019, p. 4) noticed this intrafamilial diversity in the two trogiomorphan families Lepidopsocidae and Psyllipsocidae only. We can add that the most basal trogiomorphan family †Cormopsocidae has no nodulus (Yoshizawa & Lienhard 2020; Hakim *et al.* 2021b), while the prionoglaridid genus *Siamoglaris* has one and *Sensitibilla* has none. Thus, the nodulus seems to be an unstable structure among trogiomorphans. Interestingly, despite the absence of the nodulus, an in-flight wing-coupling structure is present in *Cormopsocus groehni*, *Cormopsocus neli* and *Stimulopsocus* in the form of 12–14 separate and almost straight spines (Yoshizawa & Lienhard 2020; Hakim *et al.* 2021b; Liang & Liu 2022). The presence or absence of a sensillum on the second maxillary palpomere is more difficult to demonstrate for fossil taxa. For instance, Yoshizawa & Lienhard (2020) and Hakim *et al.* (2021b) said nothing about this structure for †Cormopsocidae, although it is clearly absent in *Cormopsocus baleoi* and *Stimulopsocus* (Hakim *et al.* 2021c; Liang & Liu 2022), while a sensillum on the fourth maxillary palpomere is present in *Longiglabeilus* (Wang *et al.* 2021). As a result, the boundaries between †Archaeatropidae and †Empheriidae remain vague. †Archaeatropidae may be a junior synonym of †Empheriidae (Li *et al.* 2020). However, only a phylogenetic analysis including both extant and fossil taxa as well as morphological and molecular characters will help to solve this problem.

Today, the most diverse psocid suborder (excluding parasitic lice) is Psocomorpha, comprising 63% of psocid species, while Troctomorpha and Trogiomorpha contain 31% and 6% of psocid species, respectively (Yoshizawa *et al.* 2006; Zhang 2011; Yoshizawa & Johnson 2014) (Fig. 11A). Interestingly, current information about Cretaceous psocids shows the following relative diversity of the species for each suborder: 6%, Psocomorpha; 33%, Troctomorpha; and 61%, Trogiomorpha (Álvarez-Parra *et al.* 2020a, table 1; plus the new additions) (Fig. 11B). This different diversity might be explained by palaeobiological or evolutionary constraints. Furthermore, Trogiomorpha had a global distribution during the Cretaceous, while Psocomorpha has been found only in Eurasia (Fig. 11C) from French, Burmese and Taimyr ambers (Vishniakova 1975; Azar *et al.* 2015; Yoshizawa & Yamamoto 2021). Given that Trogiomorpha is the most basal suborder in Psocodea (De Moya *et al.* 2021), a preliminary diversification of this group during the Cretaceous could have occurred, which is supported by the fossil record (Fig. 11B). Later, the diversification of Psocomorpha probably occurred during the Cenozoic. Although some trogiomorphan species are cosmopolitan, most usually live in

marginal habitats, such as ground litter in forests, caves and domestic environments (New 1987; Baz & Ortuño 2000). Therefore, the extant representatives may represent a relict group that evolved from generalist taxa into dwellers of marginal habitats to avoid competing with the more modern psocomorphans. This hypothesis was also stated by Thornton (1962) for cave barklice (Psyllipsocidae). Psyllipsocids are interesting because they include the only known extant psocid genus dating back to the Cretaceous (Álvarez-Parra *et al.* 2020a; Jouault *et al.* 2021; Liang & Liu 2021), showing a high grade of evolutionary stasis or bradytely that is typical of inhabitants of marginal environments (Peris & Háva 2016; Sánchez-García & Engel 2017; Arillo *et al.* 2022). †Cormopsocidae, †Archaeatropidae and †Empheriidae could have been generalists given their high diversity during the Cretaceous, but they probably began to decrease in abundance or became extinct when psocomorphans thrived due to niche competition. Troctomorphan have a similar relative diversity today as they did during the Cretaceous (Fig. 11A, B).

Taxonomic determination of fossil psocid immatures is challenging because the diagnostic characters are based on winged adult specimens (Kiesmüller *et al.* 2021). Furthermore, psocid nymphs are poorly known in the fossil record to date. However, the outstanding preservation of SJNB2012-12-02 enabled us to assign the specimen to †Archaeatropidae. It provides insights into the growth of psocid nymphs and the development of the wings, which are visible in the specimen. Kiesmüller *et al.* (2021) and Xu *et al.* (2022) described a debris-carrying behaviour in psocid nymphs from Burmese amber. This type of behaviour is also observed in extant immatures from diverse psocid families and has been linked to camouflage (Kiesmüller *et al.* 2021). The debris-carrying larval habit has also been reported in Cretaceous specimens of other insect groups (Pérez-de la Fuente *et al.* 2012, 2018). Therefore, it is assumed that psocid nymphs, inhabiting the ground litter or tree bark, developed this defensive strategy in response to predatory pressure (Kiesmüller *et al.* 2021). There is no evidence of debris-carrying behaviour in SJNB2012-12-02, suggesting three hypotheses: (1) debris-carrying behaviour and the related camouflage in psocids were restricted to the Burmese amber palaeoenvironment or were not globally distributed; (2) debris-carrying behaviour was not widely distributed phylogenetically in psocids; or (3) the lack of debris-carrying behaviour in SJNB2012-12-02 can be explained by a finding bias and it is also probable that it was present worldwide during the Cretaceous. Hypothesis 1 is plausible because psocid nymphs from French and Taimyr ambers do not show debris-carrying behaviour (Vishniakova 1975; Azar *et al.* 2015). Hypothesis 2 is also plausible. The diverse morphologies of psocid nymphs showing debris-carrying behaviour suggest that this could have



**FIG. 11.** Past and recent diversity and global palaeodistribution of the psocid (Psocodea) suborders. A–B, relative diversity of each of the psocid suborders today (A) and during the Cretaceous (B). C, Late Cretaceous global palaeogeographical reconstruction showing the presence of the described species of each psocid suborder in the amber sites: 1, Canadian amber (Cedar Lake and Pipestone Creek; Campanian); 2, Raritan amber (Sayreville; Turonian); 3, Spanish amber (Ariño, Arroyo de la Pascueta, El Soplao, Peñacerrada I and San Just; Albian); 4, French amber (Archingeay-Les Nouillers and La Garnache; Albian–Santonian); 5, Taimyr amber (Nizhnyaya Agapa, Timmerdyakh-Khaya and Yantardakh; Cenomanian–Santonian); 6, Lebanese amber (Bcharreh, Falougha, Hammana-Mdeyrij and Jezzine; Barremian); 7, Burmese amber (Hkamti and Tanai; Albian–Cenomanian). Undescribed psocids have been identified in Aptian Congolese amber (Bouju & Perrichot 2020) and Campanian Tilin (Myanmar) amber (Zheng *et al.* 2018). Parasitic lice (Phthiraptera) are excluded in A. Data for A and B were obtained from Yoshizawa *et al.* (2006), Zhang (2011), Yoshizawa & Johnson (2014) and Álvarez-Parra *et al.* (2020a), with the addition of the new species. Map modified from Scotese (2001).

been present in several families (Kiesmüller *et al.* 2021), but the family of the studied nymph (†Archaeatropidae) might not have shown this type of behaviour. Hypothesis 3, involving a finding bias, cannot be discarded either. It is possible that this behaviour was determined by both phylogenetical restrictions and environmental conditions.

## CONCLUSION

Psocids were a widely distributed and diverse group of insects during the Cretaceous. The suborder Trogiomorpha comprises most of the described species from this period to date. The new specimens studied in this paper provide interesting data about the distribution



of the previously known species on the Iberia Island, as well as additional anatomical information and details about the development and growth of immature psocids based on the discovery of a well-preserved psocid nymph. A new species belonging to †Archaeatropidae is described and assigned to a genus previously known to occur only in northern Gondwana. Trogiomorpha is the most basal suborder within Psocodea. The phylogenetic placement of the extinct families †Archaeatropidae and †Empheriidae seems to be basal to the rest of the families within the infraorder Atropetae, although a phylogenetic analysis is needed to better understand their relationships with the other families. Furthermore, †Archaeatropidae could be a junior synonym of †Empheriidae based on recent findings. Trogiomorpha was the most diverse psocid suborder during the Cretaceous, unlike today when it is less diverse. Therefore, it is possible that the diversification of this basal group occurred during the Cretaceous, before the diversification of psocomorphans. Psocomorphans could have ecologically competed with trogiomorphans, relegating the latter to marginal habitats. It is also possible that palaeoenvironmental conditions could explain the different diversities of these groups. The study of Cenozoic psocids would provide interesting information about the evolutionary trends and niche competition in the history of Psocodea. Psocid nymphs showed debris-carrying behaviour, at least in the Burmese amber palaeoenvironment, although it is possible that this type of behaviour was not widely distributed, geographically or phylogenetically, among psocid immatures. This topic might be traced only in the amber record with further investigations.

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## DATA ARCHIVING STATEMENT

This published work and the nomenclatural act it contains, have been registered in ZooBank: <http://zoobank.org/References/0ABCDC39-0D0F-4268-A53E-1D97D328DE89>

*Editor.* Conrad Labandeira

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