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Arthropod diversity in Iran: Subphylum Hexapoda Latreille, 1825, Basal Hexapod Taxa

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ABSTRACT. A comprehensive review of the literature and database records on the five lineages of basal hexapods of Iran was conducted to summarise current knowledge of their diversity and distribution within the country. A total of 379 species are currently known from Iran, belonging to 140 genera and 27 families. Collembola are the most diverse (345 species, 119 genera, 20 families), followed by Zygentoma (21 species, 10 genera, 3 families) and Archaeognatha (6 species, 5 genera, 1 family), whereas Protura (5 species, 4 genera, 2 families) and Diplura (2 species, 1 genus, 1 family) remain clearly under-sampled. Collembola have been recorded from many regions of Iran, especially the north, whereas for the other groups few or no species are known from most provinces. Most species for which Iranian habitat data are available occur only in forest environments, particularly the Hyrcanian forests. Fifty-one Collembola species (≈14.8%) and 15 non-Collembola taxa (e.g., Protura, Archaeognatha and Zygentoma) are known only from Iran and are likely endemic, indicating that the country is a regional diversity hotspot in Western Asia. Studies on basal taxa, especially Collembola, have increased the number of recorded species from 70 to 345 over the past 43 years. Nevertheless, additional research in specific environments, particularly in eastern, central, western, and southern Iran, is still needed. This quantitative overview reveals clear geographic and taxonomic gaps that future surveys must address to refine biodiversity and conservation priorities nationwide.

Keywords: Apterygota, Archaeognatha, Collembola, Diplura, Entognatha, Protura, Zygentoma

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INTRODUCTION

The Hexapoda, with over one million described species, represents the highest diversity across all animals (Stork, 2018). Monophyly of the Hexapoda is well-supported, despite early mitogenomic studies failing to recover this clade. At the base of the Hexapoda, there are five small taxa, namely Protura (coneheads), Collembola (springtails), Diplura (two-pronged bristletails), Archaeognatha (bristletails), and Zygentoma (silverfish and firebrats), which are wingless. The Collembola, Protura, and Diplura have traditionally been classified within the Entognatha, as their mouthparts are enclosed in a gnathal pouch (Staniczek & Bechly, 2007). Their relationships, however, remain contentious. The three groups of entognathous hexapods share (with many insect groups) the superficial similarities of small body size and a preference for living in soil, leaf litter, or under rocks. However, controversies about the interrelationships of these groups have raged in recent years, with the monophyly of Diplura and the relative phylogenetic positions of Diplura, Protura, and Collembola being hot spots of dispute (Hennig, 1953; Giribet et al., 2004; Luan et al., 2005; Grimaldi, 2010). Peculiar traits such as internalized mouthparts and intrinsic muscles in each antennal division have led to their separation from the class Insecta (Bitsch & Bitsch, 2004; Du et al., 2024; Machida et al., 2025) (Fig. 1). Among them, based on morphological and molecular data, it has been proposed that Diplura are more closely related to the insects than to Protura and Collembola (Bitsch & Bitsch, 2000; Misof et al., 2014). The monophyly of the insects (Insecta or Ectognatha) is also strongly supported. Within insects, the ancestrally wingless jumping bristletails (Archaeognatha) are sister to a clade composed of the wingless silverfish (Zygentoma) and the Pterygota (Delsuc et al., 2003; Sasaki et al., 2013). It is generally accepted that Archaeognatha and Zygentoma have closer phylogenetic affinities to the Insecta than to the entognathous hexapods (Hennig, 1969; Giribet et al., 2004; Letsch & Simon, 2013; Zhang, 2013; Misof et al., 2014; Blanke et al., 2014; Giribet & Edgecombe, 2019; Tihelka et al., 2021; Robla et al., 2023; Du et al., 2024; Machida et al., 2025).

Research on Iranian basal hexapod taxa, except Collembola, is surprisingly scarce. Studies on Collembola span over six decades, initiated by Gardenehire (1959) who first recorded *Sminthurus viridis* Linnaeus, 1758 as an alfalfa pest. This was followed by a similar report from Khuzestan province (Farrahbakhsh, 1961). The foundational faunistic study was conducted by Cox (1982), who documented 70 species from 30 genera and five families in central, northern, and northwestern Iran. After a research hiatus of over two decades, studies resumed with Moravvej (2003) reporting five families and 14 genera from Tehran, and Nematollahi et al. (2009) investigating Collembola in greenhouse environments in Isfahan province. While pre-2011 studies established an essential foundation for Iranian collembology, the faunal inventory remained substantially incomplete. The past decade has witnessed a significant resurgence in Iranian collembology, driven primarily by graduate research at Sari Agricultural Sciences and Natural Resources University. This period has been characterized by extensive faunistic surveys across numerous provinces and a surge in taxonomic discoveries. National checklists have documented an increase in known diversity, from 87 species in 2013 to 286 species by 2023, housed within 109 genera and 20 families (Shayanmehr et al., 2013; Mehrafrooz Mayvan et al., 2023). The order Poduromorpha dominates (47% of species), followed by Entomobryomorpha (41%). Isotomidae and Entomobryidae are the most species-rich families. This phase has been marked by prolific descriptions of new species. Between 2012 and 2024, several new species were described from Iran, mostly belonging to the two orders Entomobryomorpha and Poduromorpha. Notably, no new species from the order Neelipleona and only one species from the order Symphypleona were described during this period. A landmark synthesis by D'Haese et al. (2025) highlighted the Hyrcanian Forests as a global hotspot, documenting 250 species—approximately 70% of Iran's total Collembola fauna. Studies on Protura and Diplura, two other classes of the subphylum Hexapoda, have also been very limited in Iran. The first study on Protura in Iran was conducted by Szeptycki (1977), and since then, only another one has been carried out in recent years (Vahedi Moghadam et al., 2022). These studies resulted in the description of four new species, three of which are only known from Iran, at least until today (Szeptycki, 2007; Galli, 2022; Vahedi Moghadam et al., 2022).

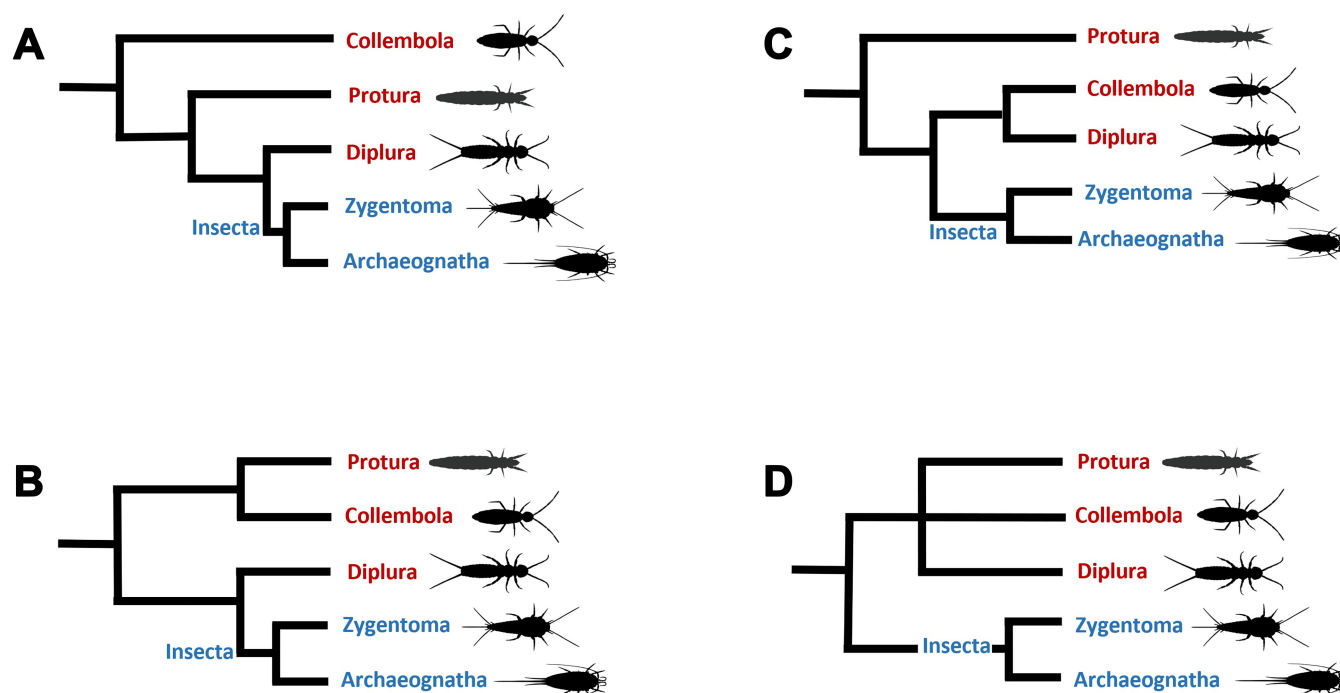


Figure 1. Four different topological hypotheses about the relationships of the early-diverging hexapod clades. **A.** Collembola + (Protura + (Diplura + Insecta)) (“Collembola-sister” hypothesis); **B.** (Collembola + Protura) + (Diplura + Insecta) (the “Elliplura” hypothesis); **C.** Protura + ((Collembola + Diplura) + Insecta) (“Protura-sister” hypothesis); **D.** unresolved polytomy corresponding to the “Entognatha” hypothesis (Du et al., 2024; Machida et al., 2025).

In contrast, research on Diplura has been even more limited, with only one study conducted by Azadbakhsh & Nozari (2016), focusing on this group in northern Iran. Initial studies on Zygentoma were conducted by only a few researchers who examined isolated specimens, including Paclt (1966), Mendes (1985), and Irish (1995). Research on this order remained dormant for nearly two decades, after which a few scattered studies were carried out, resulting in the description of four new species belonging to the genus *Ctenolepisma* Escherich, 1905 (Kahrarian et al., 2016a; Molero et al., 2018). In comparison to the order Zygentoma, research on the order Archaeognatha has been even more limited, with the first study conducted by Bitsch (1970), who reported five species. After a long gap in research, the most recent study on Archaeognatha was conducted by Molero et al. (2018), which resulted in the description of an endemic cave-dwelling species from Iran.

Iran, one of the largest countries in Southwest Asia, covers 1.64 million km² and harbors a wide range of climatic zones, ecosystems, and vegetation types that are scattered between 31 provinces (Holt et al., 2013; Asa’adi, 2017; Azizi Jalilian et al., 2020; Erfanian et al., 2021; Noori et al., 2024; Mehrafrooz Mayvan et al., 2025). Despite the vastness, climatic diversity, and ecosystems of Iran, there is limited information on arthropod diversity in this part of Asia, particularly regarding basal hexapods like Protura, Diplura, Collembola, Archaeognatha, and Zygentoma. Therefore, this article provides an overview of these hexapod taxa from Iran with the aim of filling this gap by reviewing the current state of knowledge on them in this country, emphasizing their endemic species and highlighting the critical need for further research.

MATERIAL AND METHODS

The information presented in this review was compiled through an extensive survey of published literature, unpublished data (dissertations), online databases, and certain unpublished records accessible

to the authors. Relevant online databases, such as Bellinger et al. (1996–2025), served as supplementary sources to cross-verify records and obtain updated taxonomic information. Overall, a systematic approach was employed to collect and verify records of basal hexapod groups in Iran, including Protura, Diplura, Collembola, and the basal insect orders Archaeognatha and Zygentoma. Each data source was assessed primarily for its taxonomic reliability and recency of publication. Duplicate records and questionable identifications were carefully examined and excluded when necessary. The primary sources for extracting species records in this review were published faunistic studies and regional checklists focusing on the terrestrial and freshwater hexapods of Iran. These sources provided verified and up-to-date information on species presence and distribution. Notable examples include the checklists by Cox (1982), Falahati et al. (2013), Shayanmehr et al. (2013), Yoosefi Lafooraki & Shayanmehr (2015), Kahrarian et al. (2016b), Kahrarian (2017), Shayanmehr et al. (2020), Mehrafrooz Mayvan et al. (2021, 2022a, 2022b, 2023), Shayanmehr et al. (2023, 2024, 2025), and D’Haese et al. (2025), which cover various regions and habitats across the country. For Protura, records were obtained from works such as Szeptycki (2007), Galli (2022), and Vahedi Moghadam et al. (2022), whereas data on Diplura relied exclusively on faunistic surveys by Azadbakhsh & Nozari (2016). Records of Zygentoma were retrieved from Kahrarian et al. (2014), Kahrarian & Molero (2015), Kahrarian et al. (2016a), Molero et al. (2018), Vahedi Moghadam (unpublished), and Robla et al. (2023), encompassing both subterranean and epigeal habitats, while Archaeognatha species records relied solely on the study by Molero et al. (2018). High-quality photographs of Collembola species, Protura, Diplura, Archaeognatha, and Zygentoma used in this study were respectively provided by Philippe Garcelon, Dr. Stefano Zoia, Dr. Pavel Krásenský and Dr. Miquel Gaju from their collections, with their permission. Based on the review of the available resources, a summarized checklist of basal hexapod taxa in Iran was provided and endemic species were highlighted. For each parent taxon, the numbers of species, genera, subfamilies, families, superfamilies, and orders are indicated.

RESULTS

Taxonomic hierarchy

Phylum Arthropoda Gravenhorst, 1843

Subphylum Hexapoda Latreille, 1825

CLASS Collembola Lubbock, 1871 – (4 orders, 11 superfamilies, 20 families, 25 subfamilies, 119 genera, 345 species).

ORDER Entomobryomorpha Börner, 1913 – (3 superfamilies, 6 families, 12 subfamilies, 43 genera, 142 species).

Superfamily Entomobryoidea Womersley, 1934 – (3 families, 7 subfamilies, 16 genera, 63 species).

Family Entomobryidae Womersley, 1934 – (Fig. 2A) (4 subfamilies, 12 genera, 51 species).

Subfamily Entomobryinae Schäffer, 1896 – (7 genera, 28 species).

Genus *Calx* Christiansen, 1958 – (1 species).

Genus *Coecobrya* Yosii, 1956 – (2 species).

Genus *Drepanura* Schött, 1891 – (3 species).

Genus *Entomobrya* Rondani, 1861 – (18 species).

Genus *Mesentotoma* Salmon, 1942 – (2 species).

Genus *Prodrepanura* Stach, 1963 – (represented by a single unidentified species).

Genus *Sinella* Brook, 1882 – (1 species).

Subfamily Lepidocyrtinae Wahlgren, 1906 – (2 genera, 15 species).

Genus *Lepidocyrtus* Bourlet, 1839 – (7 species).

Genus *Pseudosinella* Schäffer, 1897 – (8 species).

Subfamily Seirinae Yosii, 1961 – (1 genus, 3 species).

Genus *Seira* Lubbock, 1870 – (3 species).

Subfamily Willowsiinae Yoshii & Suhardjono, 1989 – (2 genera, 5 species).

Genus *Drepanosira* Bonet, 1942 – (2 species).

Genus *Willowsia* Shoebbotham, 1917 – (3 species).

Family Orchesellidae Börner, 1906 – (Fig. 2B) (2 subfamilies, 3 genera, 9 species).

Subfamily Heteromurinae Absolon & Kseneman, 1942 – (2 genera, 6 species).

Genus *Heteromurtrella* Mari Mutt, 1979 – (represented by a single unidentified species).

Genus *Heteromurus* Wankel, 1860 – (5 species).

Subfamily Orchesellinae Börner, 1906 – (1 genus, 3 species).

Genus *Orchesella* Templeton, 1836 – (3 species).

Family Paronellidae Börner, 1906 – (Fig. 2C) (1 subfamily, 1 genus, 3 species).

Subfamily Paronellinae Börner, 1906 – (1 genus, 3 species).

Genus *Cyphoderus* Nicolet, 1842 – (3 species).

Superfamily Isotomoidea Szeptycki, 1979 – (1 family, 4 subfamilies, 22 genera, 70 species).

Family Isotomidae Schäffer, 1896 – (Fig. 2D) (4 subfamilies, 22 genera, 70 species).

Subfamily Anurophorinae Börner, 1901 – (7 genera, 27 species).

Genus *Anurophorus* Nicolet, 1842 – (4 species).

Genus *Folsomia* Willem, 1902 – (13 species).

Genus *Gnathofolsomia* Deharveng & Christian, 1984 – (represented by a single unidentified species).

Genus *Hemisotoma* Bagnall, 1949 – (4 species).

Genus *Isotomiella* Bagnall, 1939 – (2 species).

Genus *Isotomodes* Axelson, 1907 – (2 species).

Genus *Pseudanurophorus* Stach, 1922 – (represented by a single unidentified species).

Subfamily Isotominae Schäffer, 1896 – (7 genera, 28 species).

Genus *Agrenia* Börner, 1906 – (represented by a single unidentified species).

Genus *Desoria* Agassiz & Nicolet, 1841 – (6 species).

Genus *Isotoma* Bourlet, 1839 – (4 species).

Genus *Isotomurus* Börner, 1903 – (14 species).

Genus *Parisotoma* Bagnall, 1940 – (1 species).

Genus *Pseudisotoma* Handschin, 1924 – (1 species).

Genus *Vertagopus* Börner, 1906 – (1 species).

Subfamily Pachyotominae Potapov, 2001 – (1 genus, 1 species).

Genus *Pachyotoma* Bagnall, 1949 – (represented by a single unidentified species).

Subfamily Proisotominae Stach, 1947 – (7 genera, 14 species).

Genus *Bagnallella* Salmon, 1951 – (1 species).

Genus *Ballistura* Börner, 1906 – (2 species).

Genus *Ephemerotoma* Potapov, Kahrarian, Deharveng & Shayanmehr, 2015 – (1 species).

Genus *Folsomides* Stach, 1922 – (5 species).

Genus *Isotomodella* Martynova, 1968 – (1 species).

Genus *Proisotoma* Börner, 1903 – (3 species).

Genus *Scutisotoma* Bagnall, 1949 – (1 species).

Superfamily Tomoceroidea Szeptycki, 1979 – (2 families, 1 subfamily, 5 genera, 9 species).

Family Oncopoduridae Carl & Lebedinsky, 1905 – (Fig. 2E) (1 genus, 3 species).

Genus *Oncopodura* Carl & Lebedinsky, 1905 – (3 species).

Family Tomoceridae Schäffer, 1896 – (Fig. 2F) (1 subfamily, 4 genera, 6 species).

Subfamily Tomocerinae Schäffer, 1896 – (4 genera, 6 species).

Genus *Plutomurus* Yosii, 1956 – (1 species).

Genus *Pogonognathellus* Paclt, 1944 – (1 species).

Genus *Tomocerina* Yosii, 1955 – (1 species).

Genus *Tomocerus* Nicolet, 1842 – (3 species).

ORDER Poduromorpha Börner, 1913 – (4 superfamilies, 7 families, 9 subfamilies, 55 genera, 163 species).

Superfamily Hypogastruroidea Salmon, 1964 – (1 family, 11 genera, 49 species)

Family Hypogastruridae Börner, 1906 – (Fig. 2G) (11 genera, 49 species).

Genus *Acherontiella* Absolon, 1913 – (3 species).

Genus *Acheroxenylla* Ellis, 1976 – (represented by a single unidentified species).

Genus *Ceratophysella* Börner, 1932 – (12 species).

Genus *Choreutinula* Paclt, 1944 – (1 species).

Genus *Hypogastrura* Bourlet, 1839 – (14 species).

Genus *Mesachorutes* Absolon, 1900 – (represented by a single unidentified species).

Genus *Schaefferia* Absolon, 1900 – (1 species).

Genus *Schoetella* Schäffer, 1896 – (1 species).

Genus *Triacanthella* Schäffer, 1897 – (1 species).

Genus *Willemia* Börner, 1901 – (6 species).

Genus *Xenylla* Tullberg, 1869 – (8 species).

Superfamily Neanuroidea Massoud, 1967 – (2 families, 4 subfamilies, 19 genera, 52 species).

Family Brachystomellidae Stach, 1949 – (Fig. 2H) (1 genus, 2 species).

Genus *Brachystomella* Ågren, 1903 – (2 species).

Family Neanuridae Börner, 1901 – (Fig. 3A) (4 subfamilies, 18 genera, 50 species).

Subfamily Frieseinae Massoud, 1967 – (1 genus, 4 species).

Genus *Friesea* Dalla Torre, 1895 – (4 species).

Subfamily Morulininae Yosii, 1961 – (1 genus, 1 species).

Genus *Morulina* Börner, 1906 – (1 species).

Subfamily Neanurinae Börner, 1901 – (11 genera, 30 species).

Genus *Bilobella* Caroli, 1912 – (1 species).

Genus *Cryptonura* Cassagnau, 1979 – (6 species).

Genus *Deutonura* Cassagnau, 1979 – (5 species).

Genus *Endonura* Cassagnau, 1979 – (9 species).

Genus *Neanura* MacGillivray, 1893 – (3 species).

Genus *Paranura* Axelson, 1902 – (represented by a single unidentified species).

Genus *Paravietnura* Smolis & Kuznetsova, 2018 – (1 species).

Genus *Persanura* Mehrafrooz Mayvan, Shayanmehr, Smolis & Skarżyński, 2015 – (1 species).

Genus *Protanura* Börner, 1906 – (1 species).

Genus *Thaumanura* Börner, 1932 – (1 species).

Genus *Vitronura* Yosii, 1969 – (represented by a single unidentified species).

Subfamily Pseudachorutinae Börner, 1906 – (5 genera, 15 species).

Genus *Aethiopella* Handschin, 1942 – (represented by a single unidentified species).

Genus *Anurida* Laboulbène, 1865 – (2 species).

Genus *Israelimeria* Weiner & Kaprus', 2005 – (1 species).

Genus *Micranurida* Börner, 1901 – (1 species).

Genus *Pseudachorutes* Tullberg, 1871 – (10 species).

Superfamily Onychiuroidea – (3 families, 5 subfamilies, 24 genera, 61 species).

Family Odontellidae Massoud, 1967 – (Fig. 3B) (2 genera, 7 species).

Genus *Axenyllodes* Stach, 1949 – (3 species).

Genus *Superodontella* Stach, 1949 – (4 species).

Family Onychiuridae Lubbock, 1913 – (Fig. 3C) (2 subfamilies, 14 genera, 37 species).

Subfamily Onychiurinae Börner, 1901 – (13 genera, 36 species).

Genus *Allonychiurus* Yoshii, 1995 – (represented by a single unidentified species).

Genus *Deuteraphorura* Absolon, 1901 – (1 species).

Genus *Heteraphorura* Bagnall, 1948 – (3 species).

Genus *Hymenaphorura* Bagnall, 1948 – (1 species).

Genus *Oligaphorura* Bagnall, 1949 – (1 species).

Genus *Onychiuroides* Bagnall, 1948 – (3 species).

Genus *Onychiurus* Gervais, 1841 – (represented by a single unidentified species).

Genus *Orthonychiurus* Stach, 1954 – (3 species).

Genus *Protaphorura* Absolon, 1901 – (14 species).

Genus *Sensillonychiurus* Pomorski & Shveenkova, 2006 – (represented by a single unidentified species).

Genus *Spinonychiurus* Weiner, 1996 – (2 species).

Genus *Thalassaphorura* Bagnall, 1949 – (3 species).

Genus *Vibronychiurus* Pomorski, 1998 – (2 species).

Subfamily Tetrodontophorinae Stach, 1954 – (1 genus, 1 species).

Genus *Tetrodontophora* Reuter, 1882 – (1 species).

Family Tullbergiidae Bagnall, 1935 – (Fig. 3D) (3 subfamilies, 8 genera, 17 species).

Subfamily Austraphorurinae Deharveng, 2004 – (1 genus, 1 species).

Genus *Doutnacia* Rusek, 1974 – (1 species).

Subfamily Mesaphorurinae Dunger & Schlitt, 2011 – (4 genera, 13 species).

Genus *Mesaphorura* Börner, 1901 – (7 species).

Genus *Metaphorura* Stach, 1954 – (3 species).

Genus *Paratullbergia* Womersley, 1930 – (2 species).

Genus *Wankeliella* Rusek, 1975 – (1 species).

Subfamily Tullbergiinae Deharveng, 2004 – (3 genera, 3 species).

Genus *Fissuraphorura* Rusek, 1991 – (1 species).

Genus *Neonaphorura* Bagnall, 1935 – (1 species).

Genus *Tullbergia* Lubbock, 1876 – (1 species).

Superfamily Poduroidea – (1 family, 1 genus, 1 species).

Family Poduridae Latreille, 1804 – (Fig. 3E) (1 genus, 1 species).

Genus *Podura* Linnaeus, 1758 – (1 species).

ORDER Neelipleona Massoud, 1971 – (1 family, 1 subfamily, 2 genera, 5 species).

Family Neelidae Folsom, 1896 – (Fig. 3F) (1 subfamily, 2 genera, 5 species).

Subfamily Neelidinae Bellini, Godeiro & Zhang, 2023 – (2 genera, 5 species).

Genus *Megalothorax* Willem, 1900 – (4 species).

Genus *Neelus* Folsom, 1896 – (1 species).

ORDER Symphypleona Börner, 1901 – (4 superfamilies, 6 families, 3 subfamilies, 19 genera, 35 species).

Superfamily Dicyrtomoidea Bretfeld, 1994 – (1 family, 1 subfamily, 2 genera, 5 species).

Family Dicyrtomidae Börner, 1906 – (Fig. 3G) (1 subfamily, 2 genera, 5 species).

Subfamily Dicyrtominae Richards, 1968 – (2 genera, 5 species).

Genus *Dicyrtoma* Bourlet, 1842 – (3 species).

Genus *Dicyrtomina* Börner, 1903 – (2 species).

Superfamily Katiannoidea Bretfeld, 1994 – (2 families, 3 genera, 10 species).

Family Arrhopalitidae Stach, 1956 – (Fig. 3H) (2 genera, 3 species).

Genus *Arrhopalites* Börner, 1906 – (2 species).

Genus *Pygmarrhopalites* Vargovitsh, 2009 – (1 species).

Family Katiannidae Börner, 1913 – (Fig. 4A) (1 genus, 7 species).

Genus *Sminthurinus* Börner, 1901 – (7 species).

Superfamily Sminthuridoidea – (1 family, 3 genera, 5 species).

Family Sminthurididae Börner, 1906 – (Fig. 4B) (3 genera, 5 species).

Genus *Sminthurides* Börner, 1900 – (3 species).

Genus *Sphaeridia* Linnaniemi, 1912 – (1 species).

Genus *Stenacidia* Börner, 1906 – (1 species).

Superfamily Sminthuroidea Bretfeld, 1994 – (2 families, 2 subfamilies, 11 genera, 15 species).

Family Bourletiellidae Börner, 1913 – (Fig. 4C) (3 genera, 3 species).

Genus *Bourletiella* Banks, 1899 – (represented by a single unidentified species).

Genus *Cassagnaudiella* Ellis, 1975 – (1 species).

Genus *Heterosminthurus* Stach, 1955 – (1 species).

Family Sminthuridae Lubbock, 1862 – (Fig. 4D) (2 subfamilies, 8 genera, 12 species).

Subfamily Sminthurinae Lubbock, 1862 – (4 genera, 8 species).

Genus *Allacma* Börner, 1906 – (1 species).

Genus *Caprainea* Dallai, 1970 – (1 species).

Genus *Sminthurus* Latreille, 1804 – (5 species).

Genus *Spatulosminthurus* Betsch & Betsch-Pinot, 1983 – (represented by a single unidentified species).

Subfamily Sphyrothecinae Betsch, 1980 – (4 genera, 4 species).

Genus *Lipothrix* Börner, 1906 – (1 species).

Genus *Neosminthurus* Mills, 1934 – (represented by a single unidentified species).

Genus *Paralipothrix* Bretfeld, 1999 – (1 species).

Genus *Sphyrotheca* Börner, 1906 – (represented by a single unidentified species).

CLASS Diplura Börner, 1904 – (1 order, 1 family, 1 subfamily, 1 genus, 2 subgenera, 2 species)

ORDER Rhabdura Cook, 1896 – (1 family, 1 subfamily, 1 genus, 2 subgenera, 2 species).

Family Campodeidae Meinert, 1865 – (Fig. 5C–D) (1 subfamily, 1 genus, 2 subgenera, 2 species).

Subfamily Campodeinae Condé, 1956 – (1 genus, 2 subgenera, 2 species).

Genus *Campodea* Westwood, 1842 – (2 subgenera, 2 species).

Subgenus *Dicampa* Silvestri, 1932 – (1 species).

Subgenus *Campodea* s.str. Silvestri, 1932 – (1 species).

CLASS Protura Silvestri, 1907 – (2 orders, 2 families, 3 subfamilies, 4 genera, 5 species).

ORDER Acerentomata Yin, 1996 – (1 family, 2 subfamilies, 3 genera, 3 species).

Family Acerentomidae Silvestri, 1907 – (Fig. 5A–C) (2 subfamilies, 3 genera, 3 species).

Subfamily Berberentulinae Yin, 1983 – (2 genera, 2 species).

Genus *Acerentulus* Berlese, 1908 – (1 species).

Genus *Acerentomon* Silvestri, 1907 – (1 species).

Subfamily Acerellinae Yin, 1983 – (1 genus, 1 species).

Genus *Acerella* Berlese, 1909 – (1 species).

ORDER Eosentomata Yin, 1996 – (1 family, 1 subfamily, 1 genus, 2 species).

Family Eosentomidae Berlese, 1909 – (1 subfamily, 1 genus, 2 species).

Subfamily Eosentominae Berlese, 1909 – (1 genus, 2 species).

Genus *Eosentomon* Berlese, 1908 – (2 species).

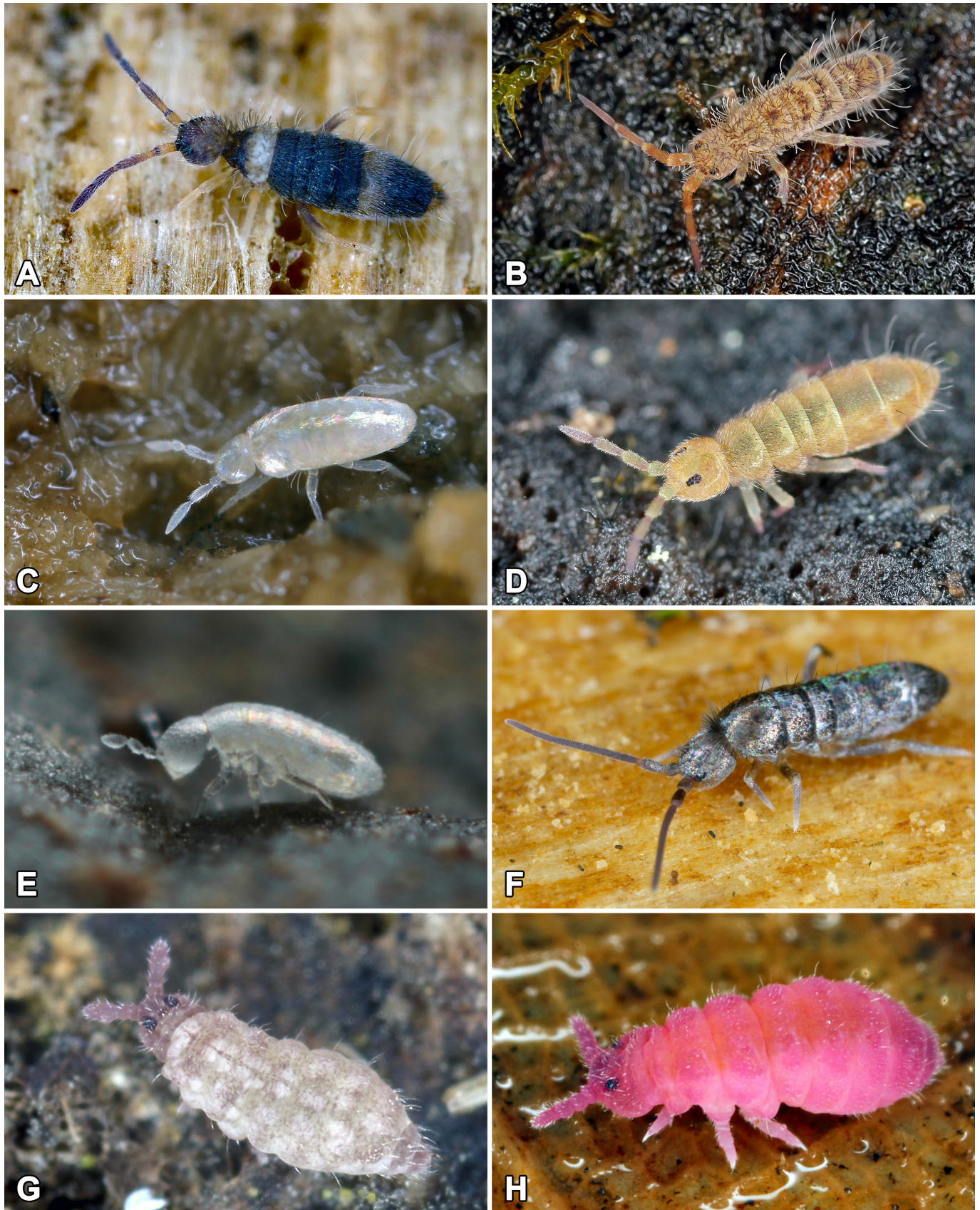


Figure 2. Class Collembola. **A.** Entomobryidae: *Entomobrya albocincta* (Templeton, 1835); **B.** Orchesellidae: *Orchesella cincta* (Linnaeus, 1758); **C.** Paronellidae: *Cyphoderus albinus* Nicolet, 1842; **D.** Isotomidae: *Isotomurus graminis* Fjellberg, 2007; **E.** Oncopoduridae: *Oncopodura* sp.; **F.** Tomoceridae: *Tomocerus minor* (Lubbock, 1862); **G.** Hypogastruridae: *Ceratophysella armata* (Nicolet, 1842); **H.** Brachystomellidae: *Brachystomella parvula* (Schäffer, 1896). Photos by Philippe Garcelon.

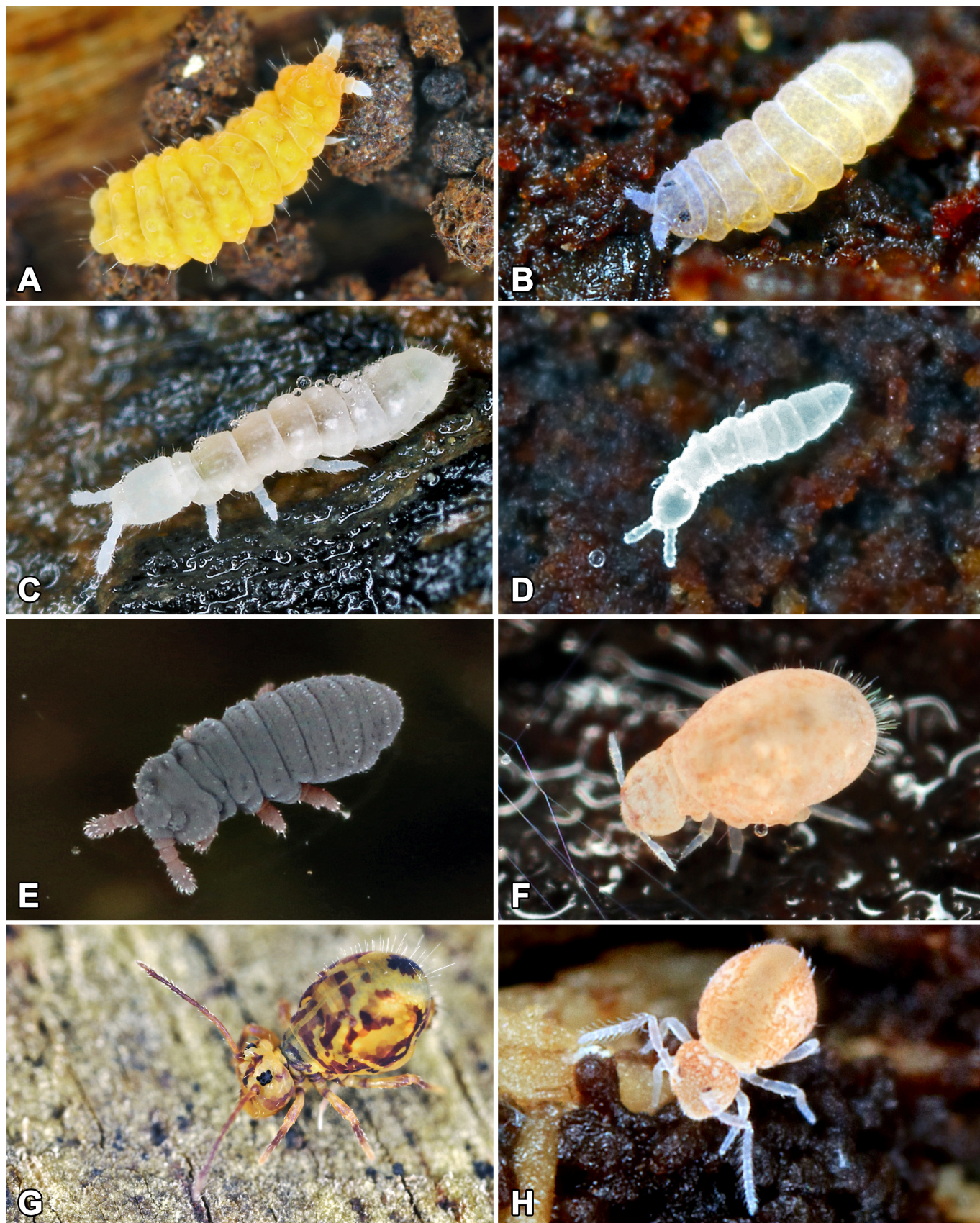


Figure 3. Class Collembola. **A.** Neanuridae: *Bilobella aurantiaca* (Caroli, 1912); **B.** Odontellidae: *Superodontella lamellifera* (Axelson, 1903); **C.** Onychiuridae: *Protaphorura* sp.; **D.** Tullbergiidae: *Mesaphorura* sp.; **E.** Poduridae: *Podura aquatica* Linnaeus, 1758; **F.** Neelidae: *Neelus murinus* Folsom, 1896; **G.** Dicyrtomidae: *Dicyrtomina ornata* (Nicolet, 1842); **H.** Arrhopalitidae: *Pygmarrhopalites principalis* (Stach, 1945). Photos by Philippe Garcelon.



Figure 4. Class Collembola. **A.** Katiannidae: *Sminthurinus signatus* (Krausbauer, 1898); **B.** Sminthurididae: *Sminthurides aquaticus* (Bourlet, 1842); **C.** Bourletiellidae: *Bourletiella arvalis* (Fitch, 1863); **D.** Sminthurididae: *Allacma fusca* (Linnaeus, 1758). Photos by Philippe Garcelon.

CLASS Insecta Linnaeus, 1758 – (2 Apterygota orders, 4 families, 7 subfamilies, 15 genera, 27 species).

ORDER Archaeognatha Börner, 1904 – (1 family, 1 subfamily, 5 genera, 6 species).

Family Machilidae Grassi, 1888 – (Fig. 6D–F) (1 subfamily, 5 genera, 6 species).

Subfamily Machilinae Grassi, 1888 – (5 genera, 6 species).

Genus Haslundiella Janetschek, 1954 – (1 species).

Genus Lepismachilis Verhoeff, 1910 – (Fig. 6E) (2 species).

Genus Machilanus Silvestri, 1934 – (1 species).

Genus Silvestrichilis Wygodzinsky, 1950 (Fig. 6D) (1 species).

Genus Trigoniphthalmus Verhoeff, 1910 – (Fig. 6F) (1 species).

ORDER Zygentoma Börner, 1904 – (Fig. 6A–C) (3 families, 6 subfamilies, 10 genera, 2 subgenera, 21 species).

Family Lepismatidae Latreille, 1802 – (4 subfamilies, 7 genera, 17 species).

Subfamily Acrotelsatinae Mendes, 1991 – (2 genera, 2 species).

Genus Acrotelsa Escherich, 1905 – (1 species).

Genus Lepismina Gervais, 1844 – (1 species).

Subfamily Ctenolepismatinae Mendes, 1991 – (3 genera, 11 species).

Genus Ctenolepisma Escherich, 1905 – (Fig. 6B) (6 species).

Genus Sceletolepisma Wygodzinsky, 1955 – (3 species).

Genus Thermobia Bergroth, 1890 – (2 species).

Subfamily Heterolepismatinae Mendes, 1991 – (1 genus, 1 species).

Genus *Allacrotelsa* Silvestri, 1935 – (Fig. 6C) (1 species).

Subfamily Lepismatinae Latreille, 1802 – (1 genus, 3 species).

Genus *Neoasterolepisma* Mendes, 1988 – (Fig. 6A) (3 species).

Family Nicoletiidae Escherich, 1905 – (2 subfamilies, 2 genera, 2 subgenera, 3 species).

Subfamily Atelurinae Escherich, 1905 – (1 genus, 1 species).

Genus *Persiatelurina* Molero, Tahami, Gaju & Sadeghi, 2018 – (1 species).

Subfamily Coletiniinae Mendes, 1988 – (1 genus, 2 subgenera, 2 species).

Genus *Lepidospora* Escherich, 1905 – (2 subgenera, 2 species).

Subgenus *Brinckiletinia* Molero, Tahami, Gaju & Sadeghi, 2018 – (1 species).

Subgenus *Brinckina* Wygodzinsky, 1955 – (1 species).

Family Protrinemuridae Mendes, 1988 – (1 genus, 1 species).

Genus *Trinemophora* Schaeffer, 1897 – (represented by a single unidentified species).



Figure 5. A–B. Class Protura Silvestri, 1907; two photos of an *Acerentomon* species; **A.** Specimen on a leaf in the litter; **B.** Specimen in the soil; C–D. Class Diplura Börner, 1904; Campodeidae; **C.** A campodeid dipluran in the background (together with a specimen of *Acerentomon* - proturan). Photos by Stefano Zoia; **D.** A *Campodea* sp. in forest stone rubble. Photo by Pavel Krásenský.

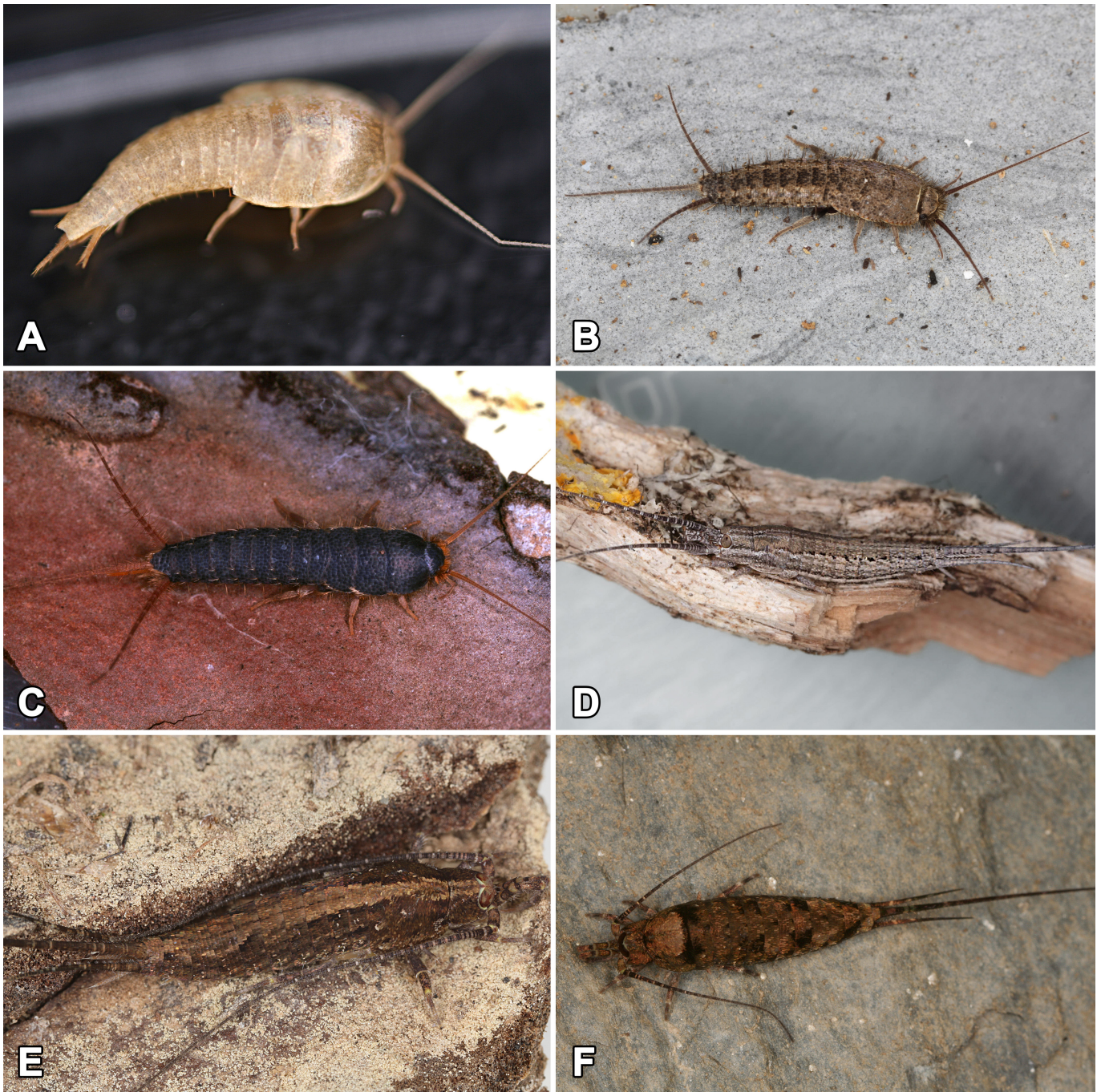


Figure 6. A–C. Order Zygentoma Börner, 1904; **A.** *Neoasterolepisma* sp.; **B.** *Ctenolepisma ciliatum* (Dufour, 1831); **C.** *Allacrotelsa kraepelini* Escherich, 1905; D–F. Order Archaeognatha Börner, 1904; **D.** *Silvestrichilis* sp.; **E.** *Lepismachilis* sp.; **F.** *Trigoniphthalmus* sp. specimens. Photos by Miquel Gaju.

DISCUSSION

The study of basal hexapods in Iran reveals a fascinating yet incompletely understood picture of the region's biodiversity. Compared to global research efforts (Stork, 2018; Sendra et al., 2021; Galli, 2022; Bellinger et al., 1996–2025), the taxonomic and ecological studies conducted in Iran are still limited despite Iran's vast geographic heterogeneity and complex biogeographic history. While countries with longer histories of entomological exploration (particularly those in Europe, North America, and parts of East Asia) boast comprehensive faunal inventories and extensive taxonomic revisions (Bellinger et al., 1996–2025), Iran's fauna is still being documented and described, often with new species and even

genera being discovered. Through a detailed literature survey encompassing recent taxonomic revisions and checklists, we explored the extent of current knowledge on Iran's basal hexapods. Duplicate records and questionable identifications were carefully examined and excluded when necessary (Table 1). In total, 379 species belonging to 140 genera and 27 families of basal hexapods have been documented from Iran. Among these, springtails are the most species-rich group, with 345 recorded species across 119 genera and 20 families. In contrast to Collembola, Diplura represents the least diverse group in Iran, with only two species belonging to one genus and one family. Meanwhile, Protura includes five species belonging to four genera and two families. Within the basal apterous insects, six species of jumping bristletails (Archaeognatha) have been identified, spanning five genera and one family. Finally, Zygentoma comprises 21 species placed in 10 genera and three families.

Globally, approximately 12,495 species are currently known from these five groups combined, including about 9,600 species of Collembola, 976 of Diplura, 831 of Protura, 514 of Archaeognatha, and 574 of Zygentoma (Zhang, 2013; Stork, 2018; Sendra et al., 2021; Galli, 2022; Bellinger et al., 1996–2025). In comparison, the Iranian fauna accounts for a relatively small portion of this global diversity (3.8%). Nevertheless, it provides an essential regional benchmark for future faunistic and taxonomic research on these poorly studied groups. Diplura research is exceptionally scarce, with only one study conducted in northern Iran (Azadbakhsh & Nozari, 2016). The two documented species to date, *Campodea* (*Dicampa*) *sprovieri* Silvestri, 1932 and *C. (Campodea) fragilis* Meinert, 1865, were collected from Mazandaran province and exhibit a primarily Mediterranean-Anatolian distribution pattern, with no evidence currently supporting their endemism. Their presence likely reflects the broader biogeographic continuity between the Eastern Mediterranean and Western Asia. Also, Protura in Iran are currently represented by only five species. Studies on Protura began with Szeptycki (1977), followed by recent research describing four new species (Szeptycki, 2007; Galli, 2022; Vahedi Moghadam et al., 2022). Interestingly, three of these species (*Acerentulus iranicus* Vahedi Moghadam, Shayanmehr, Mohammadi Sharif & Galli, 2022, *Eosentomon iranicum* Szeptycki, 1977, and *E. boguslavi* Szeptycki, 1977) are known only from Iran, suggesting a potentially unique proturan assemblage in the Hyrcanian Forests zone. *Acerentomon dominiaki* Szeptycki, 1977 is shared with Turkey and *Acerella muscorum* (Ionesco, 1930) is also distributed in Israel, and in Western, Central, and Eastern Europe, indicating some regional continuity within the Palearctic fauna. Despite their minute size and cryptic life habits, the discovery of three potentially endemic species within a single province highlights both the biogeographic uniqueness and the substantial sampling gaps for this class in Iran.

Within the basal insects, Archaeognatha remains a genuinely elusive component of Iran's insect fauna, with only six species identified, spanning five genera and one family. More than 200 species are known from the Western Palearctic region alone, and approximately 450–500 species are described globally (Sturm & Machida, 2001; Barnard, 2011). This group has received the least attention and there are only two published studies to date on the Iranian fauna: the first by Bitsch (1970) and the most recent describing an endemic cave species (Molero et al., 2018). Four taxa (*Haslundiella iranica* Gaju, Molero, Tahami & Sadeghi, 2018, *Lepismachilis (Lepismachilis) dominiaki* Mendes, 1985, *Machilanus spinosissimus* Mendes, 1981 and *Silvestrichilis wittmeri* Bitsch, 1970) appear to be strictly Iranian endemics, each known from a single or very few localities scattered across different biogeographic zones. The remaining species, *L. (L.) hobertandti* Wygodzinsky, 1952, has been recorded in both Iran and neighbouring Turkey, hinting at a wider Anatolian-Hyrcanian distribution corridor. The conspicuous temporal gap between the older records and the discovery of *H. iranica* underscores how little targeted collecting has been undertaken during the last half-century, especially in subterranean and rocky montane habitats where these relict insects often hide. The order Zygentoma constitutes the best-documented lineage among Iran's basal insects, with 21 species placed in 10 genera and three families. Among the non-Collembola groups, Zygentoma shows the highest species diversity in Iran until 2025. Early studies were sporadic, but recent research has led to the description of eight endemic species (≈38% of the fauna), several of which inhabit strictly subterranean ecosystems such as karstic cave networks and deep soil crevices, whereas others are restricted to single oases, humid forest-floor refugia, or the slopes along the Alborz and Zagros ranges (Kahrarian et al., 2016a; Molero et al., 2018; Tahami et al., 2018).

Table 1. Recorded basal hexapod taxa from Iran, with notes on identification status, distribution, and taxonomic updates.

Species name	Class	Sources	Location	Remarks
<i>Acheroxenylla</i> sp.	Collembola	Abdolzadeh et al. (2019)	Kerman	Needs further identification
<i>Aethiopella</i> sp.	Collembola	Yahyapour et al. (2020)	Mazandaran	Needs further identification
<i>Agrenia</i> sp.	Collembola	Mehrafrooz Mayvan et al. (2022a)	North Khorasan	Needs further identification
<i>Allonychiurus</i> sp.	Collembola	Hosseini et al. (2016)	Golestan	Needs further identification
<i>Anurida sensillata</i> Gisin, 1953	Collembola	Cox (1982)	Northern and northeastern Iran	Generic name updated to <i>Micranurida sensillata</i> (Gisin, 1953)
<i>Bourletiella</i> sp.	Collembola	Mehrafrooz Mayvan et al. (2021)	North Khorasan	Needs further identification
<i>Ceratophysella</i> cf. <i>borealis</i> Martynova, 1977	Collembola	Moradi et al. (2018, 2019)	Lorestan	Identification uncertain
<i>Cyphoderus ambigua</i> Cox, 1982	Collembola	Cox (1982)	Mazandaran; Gilan	Generic name changed to <i>Oncopodura ambigua</i> Christiansen, 1957
<i>Entomobrya dollfusi</i> Denis, 1924	Collembola	Yahyapour, 2012	Mazandaran	Generic name updated to <i>Mesentotoma dollfus</i> (Denis, 1924)
<i>Folsomia multisetata</i> Stach, 1947	Collembola	Cox (1982)	Northern and northwestern Iran	Generic name updated to <i>Folsomia penicula</i> Bagnall, 1939
<i>Gnathofolsomia</i> sp.	Collembola	Amiri & Kahrarian, (2015)	Kermanshah	Needs further identification
<i>Heteromurtrella</i> sp.	Collembola	Mehrafrooz Mayvan et al. (2022a)	North Khorasan	Needs further identification
<i>Hymenaphorura prox. sibirica</i> (Tullberg, 1876)	Collembola	Cox (1982)	Northern and central Iran	Identification uncertain
<i>Hypogastrura</i> cf. <i>distincta</i> (Axelson, 1902)	Collembola	Qazi & Shayanmehr (2016)	Tehran	Identification uncertain
<i>Hypogastrura</i> cf. <i>rangkuli</i> Martynova, 1975	Collembola	Qazi & Shayanmehr (2016)	Tehran	Identification uncertain
<i>Hypogastrura ripperi</i> Gisin, 1952	Collembola	Qazi & Shayanmehr (2016)	Tehran	Considered a junior synonym of <i>Hypogastrura serrata</i> (Ågren, 1904)
<i>Hypogastrura</i> cf. <i>tullbergi</i> (Schäffer, 1900)	Collembola	Cox (1982)	Mazandaran, Gilan	Identification uncertain
<i>Isotoma notabilis</i> Schäffer, 1896	Collembola	Cox (1982)	Northwestern and central Iran	Generic name updated to <i>Parisotoma notabilis</i> (Schäffer, 1896)
<i>Isotoma</i> cf. <i>riparia</i> (Nicolet, 1842)	Collembola	Alijani-Ardeshtir et al. (2017)	Mazandaran	Identification uncertain
<i>Isotomina orientalis</i> Stach, 1947	Collembola	Cox (1982)	Northern and central Iran	Generic name updated to <i>Hemisotoma orientalis</i> (Stach, 1947)
<i>Isotomina pontica</i> Stach, 1947	Collembola	Cox (1982)	Northern and central Iran	Generic name updated to <i>Hemisotoma pontica</i> (Stach, 1947)
<i>Isotomurus</i> cf. <i>balteatus</i> (Reuter, 1876)	Collembola	Hosseini et al. (2016)	Golestan	Identification uncertain
<i>Mesachorutes</i> sp.	Collembola	Mehrafrooz Mayvan et al. (2022b)	North Khorasan	Needs further identification
<i>Micraphorura absoloni</i> (Börner, 1901)	Collembola	Arbea & Kahrarian (2017)	Kermanshah	Considered a junior synonym of <i>Oligaphorura absoloni</i> (Börner, 1901)
<i>Neanura aurantiaca</i> Caroli, 1910	Collembola	Cox (1982)	Northern and central Iran	Generic name updated to <i>Bilobella aurantiaca</i> (Caroli, 1912)
<i>Neanura echinata</i> (Kos, 1940)	Collembola	Cox (1982)	Northern and central Iran	Generic name updated to <i>Thaumanura echinata</i> (Kos, 1940)
<i>Neonaphorura</i> sp.	Collembola	Shayanmehr & Yoosefi Lafooraki (2024)	Gilan	Needs further identification
<i>Neosminthurus</i> sp.	Collembola	Khanahmadi (2018)	Golestan	Needs further identification
<i>Onychiurus pseudogranulosus</i> Gisin, 1951	Collembola	Cox (1982)	Northern and central Iran	Generic name updated to <i>Onychiuroides pseudogranulosus</i> (Gisin, 1951)
<i>Orthonychiurus</i> cf. <i>rectopapillatus</i> (Stach, 1933)	Collembola	Cox (1982)	Northern and central Iran	Identification uncertain
<i>Onychiurus rectopapillatus</i> Stach, 1933	Collembola	Cox (1982)	Northern and central Iran	Generic name updated to <i>Orthonychiurus rectopapillatus</i> (Stach, 1933)
<i>Onychiurus</i> sp.	Collembola	Alijani-Ardeshtir et al. (2017)	Mazandaran	Needs further identification
<i>Onychiuroides</i> cf. <i>granulosus</i> (Stach, 1930)	Collembola	Cox (1982)	Northern and central Iran	Identification uncertain
<i>Paranura</i> sp.	Collembola	D'Haese et al. (2025)	Mazandaran	Needs further identification
<i>Paratullbergia callipygos</i> (Börner, 1902)	Collembola	Cox (1982)	Northern and central Iran	Generic name updated to <i>Paratullbergia callipygos</i> (Börner, 1902)
<i>Prodrepnura</i> sp.	Collembola	Kahrarian et al. (2012)	Kermanshah	Needs further identification
<i>Proisotoma schoetti</i> (Dalla Torre, 1895)	Collembola	Cox (1982)	Gilan	Considered a junior synonym of <i>Ballistura schoetti</i> (Dalla Torre, 1895)
<i>Protaphorura</i> cf. <i>quadriocellata</i> (Gisin, 1947)	Collembola	Cox (1982)	Northern and central Iran	Identification uncertain
<i>Protaphorura</i> cf. <i>salsa</i> Kaprus', Pašnik & Weiner, 2014	Collembola	Hosseini et al. (2016)	Golestan	Identification uncertain

Species name	Class	Sources	Location	Remarks
<i>Pseudanurophorus</i> sp.	Collembola	D'Haese et al. (2025)	Mazandaran	Needs further identification
<i>Pseudosinella</i> cf. <i>decipiens</i> Denis, 1924	Collembola	Shayanmehr et al. (2024)	Mazandaran	Needs further identification
<i>Pseudosinella</i> sp.01	Collembola	D'Haese et al. (2025)	Mazandaran	Needs further identification
<i>Sensillonychiurus</i> sp.	Collembola	Khanahmadi (2018)	Golestan	Identification uncertain
<i>Sminthurus marginatus</i> Schött, 1893	Collembola	Kahrarian et al., 2012	Kermanshah	Generic name changed to <i>Caprainea marginata</i> (Schött, 1893)
<i>Spatulosminthurus</i> sp.	Collembola	Shayanmehr et al. (2024); D'Haese et al. (2025)	Mazandaran	Needs further identification
<i>Sphyrothea</i> sp.	Collembola	Ghasemi Cherati, 2017	Mazandaran	Needs further identification
<i>Tullbergia krausbaueri</i> Greenslade, 1992	Collembola	Cox (1982)	Northern and central Iran	Generic name combination updated to <i>Mesaphorura krausbaueri</i> Börner, 1901
<i>Vitronura</i> sp.	Collembola	Yoosefi Lafooraki (2014)	Mazandaran	Needs further identification
<i>Willemia aspinata</i> Stach, 1949	Collembola	Daghighi, 2012	Gilan	Considered a junior synonym of <i>Willemia denisi</i> Mills, 1932
<i>Acerentomon</i> sp.	Protura	Vahedi Moghadam et al. (2022)	Mazandaran	Needs further identification
<i>Ctenolepisma ciliata</i> Dufour, 1831	Zygentoma	Kahrarian et al. (2014)	Kermanshah	Species name updated to <i>Ctenolepisma ciliatum</i> (Dufour, 1831)
<i>Ctenolepisma</i> (<i>Sceletolepisma</i>) <i>kermanshanum</i> Molero, Kahrarian & Gaju, 2016	Zygentoma	Kahrarian et al. (2016a)	Kermanshah	Generic name updated to <i>Sceletolepisma kermanshanum</i> Molero, Kahrarian & Gaju, 2016
<i>Ctenolepisma</i> (<i>Sceletolepisma</i>) <i>sagartianum</i> Molero, Kahrarian & Gaju, 2016	Zygentoma	Kahrarian et al. (2016a)	Kermanshah	Generic name updated to <i>Sceletolepisma sagartianum</i> Molero, Kahrarian & Gaju, 2016
<i>Ctenolepisma</i> (<i>Sceletolepisma</i>) <i>targionii</i> (Grassi & Rovelli, 1889)	Zygentoma	Molero et al. (2024)	Fars	Generic name updated to <i>Sceletolepisma villosum</i> (Fabricius, 1775)
<i>Ctenolepisma mauritanicum</i> (Lucas, 1846)	Zygentoma	Kahrarian et al. (2016a)	Kermanshah	The status of <i>C. mauritanicum</i> is doubtful
<i>Lepidospora</i> (<i>Brinckina</i>) sp.	Zygentoma	Tahami et al. (2018)	Fars	Needs further identification
<i>Trinemophora</i> sp.	Zygentoma	Kahrarian & Molero-Baltanás (2015)	Kermanshah	Needs further identification

The fauna of basal hexapods in Iran exhibits a complex mosaic of widely distributed and cosmopolitan taxa coexisting with rare, regionally restricted, and endemic species. Among Collembola, several exotic species such as *Brachystomella parvula* (Schäffer, 1896), *Ceratophysella engadinensis* (Gisin, 1949), *C. gibbosa* (Bagnall, 1940), *Folsomia candida* (Willem, 1902), *Folsomides parvulus* Stach, 1922, *Hemisotoma thermophila* (Axelson, 1900), *Heteromurus nitidus* (Templeton, 1836), *Hypogastrura manubrialis* (Tullberg, 1869), *H. vernalis* (Carl, 1901), *Mesaphorura krausbaueri* Börner, 1901, *Neelus murinus* Folsom, 1896, *Parisotoma notabilis* (Schäffer, 1896), *Proisotoma minuta* (Tullberg, 1871), and *Sminthurus viridis* Linnaeus, 1758 have a global distribution and dominate a wide range of habitats, from temperate forests and grasslands to mountainous regions. Many of these species have also been recorded from various provinces and ecosystems across Iran, highlighting their ecological adaptability and cosmopolitan nature. Endemic species represent an essential component of Iran's Collembola fauna, offering unique insights into the evolutionary processes that have occurred in the region's diverse and often isolated habitats. To date, 51 species (14.8%) of Collembola have been identified as endemic to Iran (Table 2). The first endemic springtails described from Iran were *Cryptonura persica* Smolis, Falahati & Skarżyński, 2012 and *C. maxima* Smolis, Falahati & Skarżyński, 2012, both discovered in the Alborz Mountain in Golestan province, which marked the beginning of a series of faunistic discoveries revealing the country's hidden biodiversity. These species are often associated with ecologically specialized or geographically restricted habitats, such as forest soils, highland grasslands, or karstic cave systems, and are currently known only from Iran. Some species exhibit a narrowly restricted distribution pattern, having been reported exclusively from Iran after their original description from their type localities. For instance, species like *Acherontiella bougisi* Cassagnau & Delamare Deboutteville, 1955, *Calx kailashi* Mandal, 2018, *Entomobrya indica* (Baijal, 1955), and *Drepanosira hussi* Neuherz, 1976 were originally described from India and *E. mesopotamica* Rusek, 1981, *Pseudosinella baghdadica* Rusek, 1981 and *Isotomiella gracilimucronata* Rusek, 1981 were described from Iraq but have since been recorded solely within Iran. A total of 31 such species have been recorded, accounting for approximately 8% of all Collembola species known from the country.

Table 2. Endemic species of basal hexapods, recorded from Iran.

Taxa	References
CLASS COLLEMBOLA	
<i>Acherontiella nezamdoosti</i> Mehrafrooz Mayvan & Kováč, 2025	Mehrafrooz Mayvan & Kováč (2025)
<i>Acherontiella palaciosi</i> Mehrafrooz Mayvan & Kováč, 2025	Mehrafrooz Mayvan & Kováč (2025)
<i>Arrhopalites persicus</i> Vargovitsh & Kahrarian, 2020	Vargovitsh & Kahrarian (2020)
<i>Cryptonura abmalensis</i> Arbea, Yahyapour & Shayanmeh, 2022	Yahyapour et al. (2022b)
<i>Cryptonura dohezarensis</i> Arbea, Yahyapour & Shayanmeh, 2022	Yahyapour et al. (2022b)
<i>Cryptonura maxima</i> Smolis, Falahati & Skarżyński, 2012	Smolis et al. (2012)
<i>Cryptonura persica</i> Smolis, Falahati & Skarżyński, 2012	Smolis et al. (2012)
<i>Cryptonura sariensis</i> Arbea, Yahyapour & Shayanmeh, 2022	Yahyapour et al. (2022b)
<i>Deuteraphorura dashtenazensis</i> Arbea, Yahyapour & Shayanmeh, 2020	Yahyapour et al. (2020)
<i>Deutonura breviseta</i> Smolis & Skarżyński, 2020	Smolis & Skarżyński (2020)
<i>Deutonura iranica</i> Smolis & Skarżyński, 2020	Smolis & Skarżyński (2020)
<i>Deutonura persica</i> Smolis, Shayanmeh & Yoosefi Lafooraki, 2018	Smolis et al. (2018)
<i>Deutonura sengleti</i> Smolis & Skarżyński, 2020	Smolis & Skarżyński (2020)
<i>Endonura agnieszkae</i> Smolis & Skarżyński, 2020	Smolis & Skarżyński (2020)
<i>Endonura annae</i> Smolis & Skarżyński, 2020	Smolis & Skarżyński (2020)
<i>Endonura ceratolabralis</i> Smolis, Kahrarian, Piwnik & Skarżyński, 2016	Smolis et al. (2016)
<i>Endonura dictaeta</i> Smolis, Kahrarian, Piwnik & Skarżyński, 2016	Smolis et al. (2016)
<i>Endonura longirostris</i> Smolis, Shayanmeh, Kuznetsova & Lafooraki, 2017	Smolis et al. (2017)
<i>Endonura paracentaura</i> Smolis, Shayanmeh, Kuznetsova & Lafooraki, 2017	Smolis et al. (2017)
<i>Endonura persica</i> Smolis, Kahrarian, Piwnik & Skarżyński, 2016	Smolis et al. (2016)
<i>Endonura schwendingeri</i> Smolis & Skarżyński, 2020	Smolis & Skarżyński (2020)
<i>Ephemerotoma skarzynskii</i> Potapov, Kahrarian, Deharveng & Shayanmeh, 2015	Potapov et al. (2015)
<i>Folsomides halshinicus</i> Arbea & Kahrarian, 2015	Arbea & Kahrarian (2015a)
<i>Folsomides subviusus</i> Arbea & Kahrarian, 2015	Arbea & Kahrarian (2015a)
<i>Heteraphorura iranica</i> Kaprus', Shayanmeh & Kahrarian, 2017	Kaprus' et al. (2017)
<i>Heteraphorura kaprusi</i> Arbea, Yahyapour & Shayanmeh, 2020	Yahyapour et al. (2020)
<i>Hypogastrura persica</i> Kahrarian, Vafaei-Shoushtari, Skarżyński & Konikiewicz, 2013	Kahrarian et al. (2013)
<i>Isotoma iranica</i> Arbea & Kahrarian, 2015	Arbea & Kahrarian (2015b)
<i>Isotomodes golestani</i> Yoosefi Lafooraki, Hajizadeh, Shayanmeh & Hosseini, 2020	Yoosefi Lafooraki et al. (2020b)
<i>Isotomodes korkorensis</i> Arbea & Kahrarian, 2015	Arbea & Kahrarian (2015b)
<i>Isotomurus hyrcanicus</i> Yoosefi Lafooraki & Shayanmeh, 2023	Yoosefi Lafooraki et al. (2023)
<i>Isotomurus katule</i> Yoosefi Lafooraki & Shayanmeh, 2023	Yoosefi Lafooraki et al. (2023)
<i>Isotomurus potapovi</i> Yoosefi Lafooraki & Shayanmeh, 2023	Yoosefi Lafooraki et al. (2023)
<i>Isotomurus matanicus</i> Shayanmeh, Yoosefi & Zamani, 2024	Zamani Khormandchali et al. (2024)
<i>Israelimeria persica</i> Alijani, Shayanmeh, Skarżyński, Piwnik & Smolis, 2015	Alijani et al. (2015)
<i>Neanura deharvengi</i> Smolis, Shayanmeh & Lafooraki, 2018	Smolis et al. (2018)
<i>Neanura persica</i> Arbea, Yahyapour & Shayanmeh, 2022	Yahyapour et al. (2022b)
<i>Oncopodura moghanensis</i> Mehrafrooz Mayvan & Kováč, 2024	Mehrafrooz Mayvan et al. (2024)
<i>Onychiurides mazandaranensis</i> Arbea, Yahyapour & Shayanmeh, 2020	Yahyapour et al. (2020)
<i>Paravielnura rostrata</i> Smolis & Skarżyński, 2020	Smolis & Skarżyński (2020)
<i>Persanura hyrcanica</i> Mehrafrooz Mayvan, Shayanmeh, Smolis & Skarżyński, 2015	Mehrafrooz Mayvan et al. (2015b)
<i>Plutomurus danielensis</i> Barjadze, Kováč & Mehrafrooz Mayvan, 2024	Barjadze et al. (2024)
<i>Protaphorura golestanica</i> Kaprus', Shayanmeh & Kahrarian, 2017	Kaprus' et al. (2017)
<i>Protaphorura hyrcanica</i> Arbea, Yahyapour & Shayanmeh, 2020	Yahyapour et al. (2020)
<i>Protaphorura iranica</i> Arbea, Yahyapour & Shayanmeh, 2020	Yahyapour et al. (2020)
<i>Protaphorura persica</i> Arbea & Kahrarian, 2017	Arbea & Kahrarian (2017)
<i>Pseudachorutes hyrcanicus</i> Kaprus', Shayanmeh & Yahyapour, 2022	Shayanmeh et al. (2022)
<i>Pseudachorutes kurdistanicus</i> Kaprus', Shayanmeh & Ghobari, 2022	Shayanmeh et al. (2022)
<i>Schaefferia greensladeae</i> Mehrafrooz Mayvan & Kováč, 2025	Kováč et al. (2025)
<i>Spinonychurus persicus</i> Kaprus', Shayanmeh & Kahrarian, 2017	Kaprus' et al. (2017)
<i>Vertagopus persicus</i> Potapov, Yoosefi & Shayanmeh, 2020	Yoosefi Lafooraki et al. (2020a)
CLASS PROTURA	
<i>Acerentulus iranicus</i> Vahedi Moghadam, Shayanmeh, Mohammadi Sharif & Galli, 2022	Vahedi Moghadam et al. (2022)
<i>Eosentomon iranikum</i> Szeptycki, 1977	Szeptycki (1977)
<i>Eosentomon boguslavi</i> Szeptycki, 1977	Szeptycki (1977)
CLASS INSECTA - Order Archaeognatha	
<i>Haslundiella iranica</i> Gaju, Molero, Tahami & Sadeghi, 2018	Molero et al. (2018)
<i>Lepismachilis (Lepismachilis) dominiaki</i> Mendes, 1985	Mendes (1985)
<i>Machilanus spinosissimus</i> Mendes, 1981	Molero et al. (2018)
<i>Silvestrichilis wittmeri</i> Bitsch, 1970	Bitsch (1970)
CLASS INSECTA - Order Zygentoma	
<i>Ctenolepisma iranikum</i> Molero, Kahrarian & Gaju, 2016	Kahrarian et al. (2016a)
<i>Ctenolepisma subterraneum</i> Molero, Tahami, Sadeghi & Gaju, 2018	Molero et al. (2018)
<i>Lepidospora (Brinckileptina) malousjanica</i> Molero, Tahami, Gaju & Sadeghi, 2018	Tahami et al. (2018)
<i>Lepidospora (Brinckina) montaziana</i> Molero, Tahami, Sadeghi & Gaju, 2018	Molero et al. (2018)
<i>Lepismina persica</i> Escherich, 1905	Escherich, 1905
<i>Persiatelurina farsiana</i> Molero, Tahami, Gaju & Sadeghi, 2018	Tahami et al. (2018)
<i>Sceletolepisma kermanshanum</i> Molero, Kahrarian & Gaju, 2016	Kahrarian et al. (2016a)
<i>Sceletolepisma sagartianum</i> Molero, Kahrarian & Gaju, 2016	Kahrarian et al. (2016a)

The discovery of several endemic or narrowly distributed species among these taxa underscores Iran's role as a possible center of microendemism within the Western Palaearctic. Accordingly, within Western Asia, Iran has been the most extensively studied country regarding springtails, and it currently holds the highest number of endemic Collembola species in the region.

The distribution of Collembola in Iran spans 23 provinces (Fig. 7), leaving significant gaps in Bushehr, Hormozgan, Sistan and Baluchestan, Yazd, Chaharmahal and Bakhtiari, Qazvin, Qom, and Ardabil provinces. The highest species richness is documented in northern provinces, notably Mazandaran (188 species) and Gilan (86 species), with western Kermanshah (89 species) also exhibiting notable diversity. Semnan province (four species), South and Razavi Khorasan (three species) and Alborz and Fars (one species) were less studied. Sampling efforts have predominantly focused on soil and litter habitats within the Hyrcanian Forest belt, resulting in spatial and ecological sampling biases. Consequently, many habitats, especially in central and southern regions, remain underexplored, suggesting the potential for undiscovered diversity in these basal hexapods. Unlike the relatively comprehensive and geographically widespread records of Collembola in Iran, the other basal hexapod groups remain markedly underrepresented. Diplura (Fig. 8), with only three records from Mazandaran and a single record from Alborz, exemplifies this scarcity. Knowledge about Protura (Fig. 9) is similarly limited, with all records restricted to Mazandaran, indicating a narrow sampling focus. Archaeognatha (Fig. 10) exhibits a somewhat broader, yet still sparse distribution, with records from Mazandaran, East and West Azerbaijan, Gilan, and Kerman provinces, reflecting patchy knowledge of its range. Zygentoma (Fig. 11) shows a more localized pattern, predominantly recorded in western provinces such as Kermanshah (13 records) and Fars (seven records). The notably high number of 15 species recorded in Kermanshah likely reflects both the region's diverse habitats and more intensive sampling efforts there, suggesting that other provinces, currently under-sampled, may harbor equal or even greater Zygentoma diversity.



Figure 7. Map of Iran illustrating the number of recorded Collembola species across the provinces.



Figure 8. Map of Iran illustrating the number of recorded Diplura species across the provinces.



Figure 9. Map of Iran illustrating the number of recorded Protura species across the provinces.



Figure 10. Map of Iran illustrating the number of recorded Archaeognatha species across the provinces.

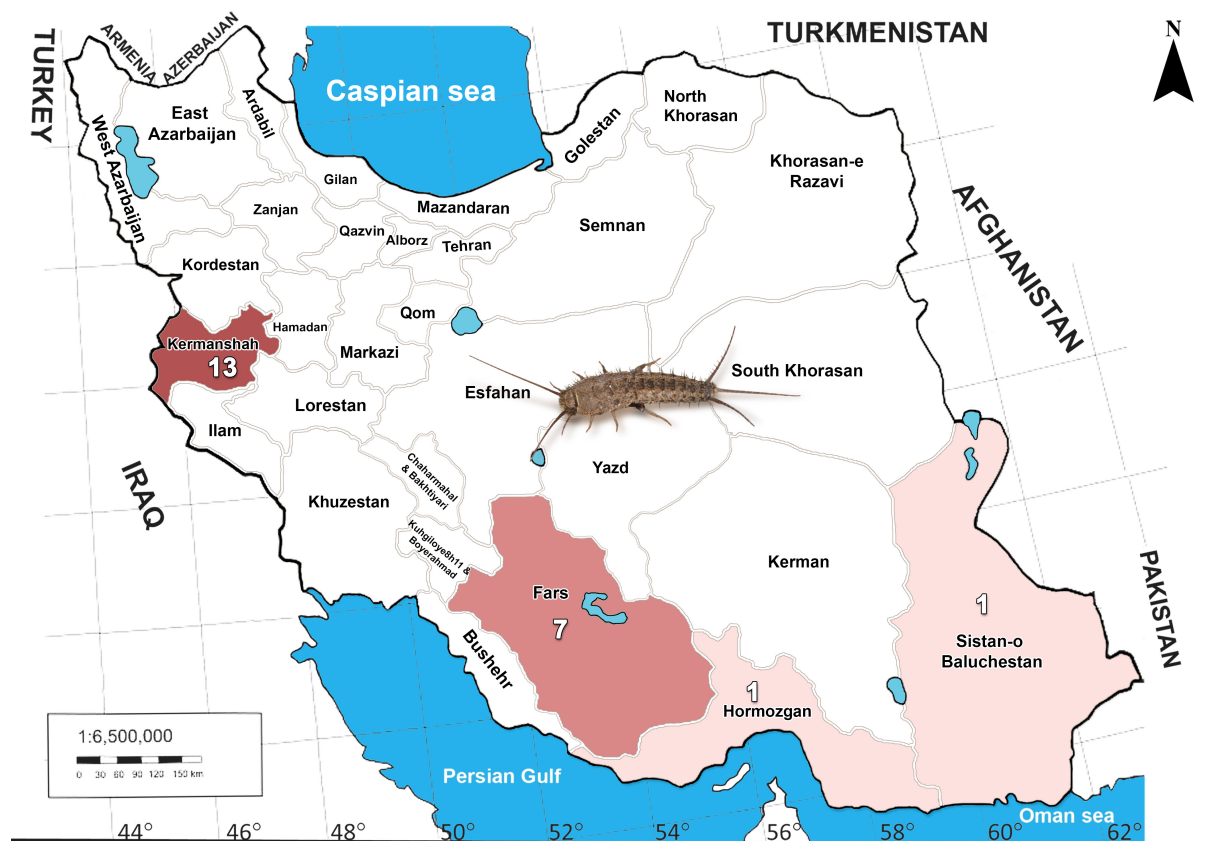


Figure 11. Map of Iran illustrating the number of recorded Zygentoma species across the provinces.

In general, most published records of basal Hexapoda are confined to the Hyrcanian forests of northern Iran and a handful of sites in the west, chiefly Kermanshah province, while much of the rest of the country remains largely unsampled. Moreover, most of these primitive hexapods have been collected from forest soils, while studies on other ecosystems remain scarce. Targeted collecting in these climatically and edaphically contrasting regions is expected to reveal many additional records—quite probably including further endemic lineages—thus testing whether the pronounced northern micro-endemism is replicated elsewhere. Endemic species and endemic areas therefore deserve particular attention when biodiversity fluctuations caused by reforestation are studied. This could lead to reassessment of the potential effects of artificial reforestation on the biodiversity of temperate forests. There is a general need for systematic inventory and protection of forests with endemic soil biota (Deharveng, 1996).

Preliminary ecological studies already show a strong link between habitat integrity and species richness. For example, old-growth Hyrcanian plots with minimal disturbance harbour the densest and most diverse springtail communities. A number of studies examining the impact of human activities on changes in diversity, and population density of Collembola have shown that areas with less human disturbance tend to have higher diversity and density of these basal hexapods (Mehrafrooz Mayvan et al., 2015a; Ramezani & Mossadegh, 2016; Moradi et al., 2019; Mehrafrooz Mayvan et al., 2022b; Yahyapour et al., 2022a; Saberi Pour et al., 2023; Tully et al., 2025). Although quantitative monitoring remains scarce, the available evidence highlights the vulnerability of these low-dispersal, soil-dwelling arthropods to forest disturbance, pesticide drift, and broader agricultural intensification. A major gap in the study of Iran's basal hexapods is the lack of an integrated morphological-molecular approach to their identification and classification. Molecular methods as identification tools have rarely been applied to the taxonomy of Collembola in Iran, while most identifications still rely on traditional morphology. Pioneering work on *Isotomurus* in the Hyrcanian forests demonstrated the utility of COI gene sequencing, thereby correcting previous misidentifications of *I. palustris* (Müller, 1776) and revealing new species (Yoosefi Lafooraki et al., 2023). More recently, a pivotal study on *Ceratophysella* (Hypogastruridae) provided a phylogenetic analysis, enabling clear species discrimination and recording two new species for Iran (Salimi et al., 2025). In stark contrast, no molecular studies have been conducted on the other four basal hexapod groups—Diplura, Protura, Archaeognatha, and Zygentoma—in Iran, leaving their genetic diversity and phylogenetic relationships entirely unexplored. This overwhelming reliance on morphology for these groups underscores the critical need for future research to adopt a combined taxonomic approach.

In sum, Iran's basal hexapod fauna is both taxonomically rich and conspicuously undersampled. The pronounced concentration of records in the Hyrcanian forests, the high proportion of local endemics, and the clear sensitivity of soil assemblages to disturbance all point to vast, still-hidden diversity in the country's arid, montane, and subterranean landscapes. Systematic surveys paired with integrative taxonomy and long-term ecological monitoring beyond the northern part of the country are therefore essential not only to refine regional checklists, but also to secure baseline data for conservation. Filling these research gaps will not only provide a more complete picture of Iran's basal hexapod diversity but also lay the essential groundwork for future ecological studies and nationwide conservation planning.

AUTHORS' CONTRIBUTION

The authors confirm their contribution in the paper as follows: M. Shayanmehr, M. Mehrafrooz Mayvan & E. Yoosefi Lafooraki: designing the study, collecting the resources, writing the manuscript. M. Kahrarian, E. Yahyapour, E. Daghighi, R. Jordana, J. Arbea, M. Potapov, C. D'Haese, T. Tully, D. Skarżyński, A. Smolis, N. Gioia Cipola and L. Kováč: collecting the resources for Collembola, writing and reviewing the manuscript. L. Galli, A. Sendra & R. Molero: designing the study, collecting the resources on Protura, Diplura and two orders of insects (Archaeognatha and Zygentoma) respectively, writing the manuscript and taking the photographs. All authors have read and approved the final version of the manuscript.

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AVAILABILITY OF DATA AND MATERIAL

All source data used in this study are cited in the Materials and Methods section.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This study only included arthropod material, and all required ethical guidelines for the treatment and use of animals were strictly adhered to in accordance with international, national, and institutional regulations. No human participants were involved in any studies conducted by the authors for this article.

CONSENT FOR PUBLICATION

Not applicable.

CONFLICT OF INTERESTS

The authors declare that there is no conflict of interest regarding the publication of this paper.

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تنوع بندپایان در ایران: زیرشاخه شش‌پایان (Hexapoda Latreille, 1825)، گروه‌های پایه‌ای

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چکیده: مرور جامع منابع و اطلاعات ثبت شده در پایگاه داده‌ها در مورد پنج تبار پایه‌ای شش‌پایان ایران انجام شد تا دانش فعلی در مورد تنوع و حوزه انتشار آن‌ها در کشور گردآوری شود. در حال حاضر، ۳۷۹ گونه از ایران شناخته شده است که به ۱۴۰ جنس و ۲۷ خانواده تعلق دارند. دم‌فنی‌ها (Collembola) با بیشترین تنوع (۳۴۵ گونه، ۱۱۹ جنس، ۲۰ خانواده)، و پس از آن نقره‌ماهیان (Zygentoma) (۲۱ گونه، ۱۰ جنس، ۳ خانواده) و دم‌فرچه‌ای‌ها (Archaeognatha) (۶ گونه، ۵ جنس، ۱ خانواده) قرار دارند. در حالی که سرمخروطی‌ها (Protura) (۵ گونه، ۴ جنس، ۲ خانواده) و دو دُمی‌ها (Diplura) (۲ گونه، ۱ جنس، ۱ خانواده) مشخصاً کمتر مورد مطالعه قرار گرفته‌اند. انتشار دم‌فنی‌ها در مناطق متعددی از ایران، به ویژه شمال کشور، ثبت شده است، در حالی که برای گروه‌های دیگر، تعداد کم یا هیچ گونه‌ای از اکثر استان‌ها شناخته نشده است. بیشتر گونه‌هایی که اطلاعات زیستگاهی آنها در ایران ثبت شده، تنها در محیط‌های جنگلی، به ویژه جنگل‌های هیرکانی یافت می‌شوند. پنجاه و یک گونه از دم‌فنی‌ها (۱۴٫۸٪) و ۱۵ آرایه از دیگر گروه‌ها (مانند سرمخروطی‌ها، دم‌فرچه‌ای‌ها و نقره‌ماهیان) تنها از ایران شناخته شده‌اند و احتمالاً بومی هستند که نشان می‌دهد این کشور یک نقطه پرتنوع منطقه‌ای در غرب آسیا است. مطالعات روی تبارهای پایه‌ای شش‌پایان، به ویژه دم‌فنی‌ها، تعداد گونه‌های ثبت شده را در طی ۴۳ سال گذشته از ۷۰ به ۳۴۵ افزایش داده است. با این حال هنوز هم، انجام تحقیقات بیشتر در محیط‌های خاص، به ویژه در شرق، مرکز، غرب و جنوب ایران هنوز ضروری است. تحلیل عددی این مقاله، شکاف‌های جغرافیایی و تاکسونومیک واضحی را نشان می‌دهد که در مطالعات آینده باید به آن‌ها پرداخته و اولویت‌های تنوع زیستی و حفاظت در سطح ملی را بر اساس آنها اصلاح کنند.

واژگان کلیدی: بی‌بالان، دم‌فرچه‌ای‌ها، دم‌فنی‌ها، دو دُمی‌ها، دهان درونیان، سرمخروطی‌ها، نقره‌ماهیان