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Introduction and keys to Neotropical water mites

(Acari, Hydrachnidia)

Tom Goldschmidt & Marcia M. Ramírez Sánchez

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In the Neotropical region currently 1491 species in 175 genera and 33 families of water mites (Hydrachnidia) have been recorded. According to the application of different models, the total estimate for the Neotropics is between 2100 and 5500 species (Goldschmidt 2002).

Beyond this the Neotropical water mite fauna is remarkably unique, the genus level diversity of some families is much higher in the Neotropics than in any other zoogeographical region (Di Sabatino et al. 2008).

The different water mite assemblages of various water bodies are an excellent tool for the assessment of water quality and habitat integrity (Goldschmidt 2016, Goldschmidt et al. 2016).

Water mite assemblages are interwoven in many ways with the rest of the freshwater invertebrate communities: "The parasitic larvae and predatory deutonymphs and adults of water mites have direct and almost certainly significant effects on the size and structure of insect populations in many habitats (Lanciani 1983, Proctor & Pritchard 1989, Smith 1983, 1988). Unfortunately, their impact has rarely been measured accurately because of the routine neglect of mites in ecological studies of freshwater communities (Proctor 2007). Many freshwater biologists are unfamiliar with mites and tend either to disregard them as too difficult to identify, and either ignore them or lump them together in a meaningless way when conducting community studies. Failure to include water mites must routinely result in flawed analyses of the structure and dynamics of freshwater communities" (Proctor et al. 2015, p. 646).

Therefore, with the following introduction and keys we want to give access to this important and fascinating group to the next generation of freshwater researchers especially in Central and South America.

Tom Goldschmidt (corresponding author), Sektion Arthropoda varia, Zoologische Staatssammlung, Münchhausenstr. 21, 81247 München, Germany; e-mail: tomgoldschmidt@web.de

Marcia M. Ramírez Sánchez, Profesor de Asignatura B, Facultad de Ciencias, Universidad Nacional Autónoma de México, Circuito Exterior s/n, Ciudad Universitaria, C.P. 04510, Mexico City, Mexico

We are dedicating this work to Dave Cook ∗09.08.1922 †17.01.2020, in order to honour his great contribution to water mite research. Dave was not only a great example of hard work and deep understanding but especially of passion for water mites.

Introduction

The class **Arachnida** in the subphylum **Chelicerata**, is a very old, typically terrestrial group, and together with the subphylum Myriapoda, are the oldest terrestrial animals, with a fossil record dating back to Silurian (~419 MYA) (Pisani et al. 2004). Whereas the phylogenetic relationships within the Chelicerata remain unclear, meanwhile they are – again – regarded as sister group to the **Mandibulata** (including Myriapoda and Pancrustacea (Crustacea and Hexapoda)), differentiated from them by the lack of antennae and mandibles (Giribet & Edgecomb 2019, Noah et al. 2020).

The typical Chelicerata body is divided into a **prosoma**, with six pairs of appendages (**chelicerae**, **palps** and four pairs of **walking legs**) and an **opisthosoma** originally with twelve segments, without appendages.

Within the Arachnida, the mites (subclass **Acari**) represent the highest diversity in terms of species number (more than 55 000 described (Zhang 2011) and about 1 million estimated), habitats and ecology (Krantz & Walter 2009). Acari are the only arachnids that returned to aquatic life on a grand scale. Some spiders (order **Araneae**) are bound to the edge of water bodies; however worldwide only one species is truly aquatic (Jäger 2007). Spiders are easily distinguished from mites by their clearly separated prosoma and opisthosoma and 1–4 pairs of ventral opisthosomal spinnerets, whereas mites are characterized by the fusion of prosoma and opisthosoma into an **idiosoma**, without visible primary segmentation, and the lack of opisthosomatic spinnerets.

Various mite lineages have aquatic representatives (for details see Bartsch et al. 2007, Behan-Pelletier & Eamer 2007, Proctor et al. 2015); however, only three prostigmatic groups (**Halacaroidea**, **Hydrachnidia** and **Stygothrombiae**) are exclusively aquatic. With more than 6000 described species (more than 400 genera) mites of the Subcohort **Hydrachnidia** – the "true freshwater mites" – represent the most diverse, abundant and ecologically important group in freshwater habitats (K. O. Viets 1987, Di Sabatino et al. 2008, Walter et al. 2009, Zhang et al. 2011, Watermite.org 2019).

Hydrachnidia are found in all freshwaters habitats from the bottom of large lakes to phytotelmata, and from large rivers to small spring seeps and the hyporheic interstitial of streams; some species are even found in coastal marine habitats. Rather conservative estimates of the total species number reach beyond 10 000 species worldwide (Di Sabatino et al. 2008). The Hydrachnidia, like all Parasitengonina, are differentiated by a characteristic life cycle with parasitic larvae, predatory adults and deutonymphs as well as pupae-like proto- and tritonymphs (Fig. 1F).

The huge diversity of mites and their still widely unclear phylogenetic relationships are reflected in a variety of different systematic classifications (e. g. Krantz & Walter 2009, Zhang 2011). The "true freshwater mites" are generally regarded as Subcohort Hydrachnidia within the Cohort Parasitengonina, Supercohort Anystides, Suborder Prostigmata, Order Trombidiformes, Superorder Acariformes, Subclass Acari.

In the literature, freshwater mites are referred to as "Hydracarina", "Hydrachnellae" or "Hydrachnida". The old term "Hydracarina" also included the Halacaroidea, mainly marine mites with more than 1000 species described world-wide. About 60 of these species are found in freshwater habitats (Bartsch et al. 2007, Bartsch 2008). Presently, two slightly different terms are in use: "Hydrachnidia", during the past decades has generally been accepted and is currently in use in the European literature (Bartsch et al. 2007, Di Sabatino et al. 2010, Gerecke et al. 2016); and "Hydrachnidiae" that has recently been introduced in the North American literature (Walter et al. 2009, Proctor et al. 2015, Dabert et al. 2016). As we are not favouring this recent change, we will use Hydrachnidia for the "true freshwater mites" here.

Hydrachnidia are regarded as a monophyletic group split into seven or eight superfamilies, depending upon whether Stygothrombidioidea is treated as basal within Hydrachnidia (Bartsch et al. 2007) or as their sister group (Proctor et al. 2015). Recent molecular analyses support the later, and confirmed the monophyly of the Hydrachnidia and all but one superfamily (Dabert et al. 2016). All superfamilies except Stygothrombidioidea (sensu Proctor et al. 2015) are represented in all zoogeographic regions except Antarctica, suggesting that they diverged before the separation of Pangaea in late Jurassic (~150 MYA) (Di Sabatino et al. 2008, Proctor et al. 2015), a hypothesis that is as well supported by molecular data (Dabert et al. 2016).

Besides the exclusively aquatic Halacaroidea, Hydrachnidia and Stygothrombiae, representatives of various other mite groups of the superorder Acariformes have invaded freshwater several times and are regularly found in aquatic habitats (and in freshwater samples) (Proctor et al. 2015).

Within the mainly "terrestrial groups" of the Prostigmata and the Stigmaeidae, several aquatic or semi-aquatic genera occur (*Caligohomus*, *Cheylostigmaeus*, *Eustigmaeus*, *Ledermuelleriopsis*, *Mullederia*, *Stigmaeus*) (Fan & Flechtmann 2015). However the Oribatida (order Sarcoptiformes, suborder Oribatida) has several truly aquatic taxa, even though just a marginal number of the overall vast diversity (Schatz & Behan-Pelletier 2008, Behan-Pelletier & Norton 2016).

Several groups within the Astigmatina (Cohort in Oribatida) (O'Connor 2009, Proctor et al. 2015) occur in aquatic habitats. Within the Algophagidae several species live in sap flows, water-filled tree holes, rivers and lakes (Fashing et al. 2000, O'Connor 2009). The Histiostomatidae has some species adapted for living and feeding in wet or aquatic environments. Most species within the Histiostomatidae are regarded as semi-aquatic, since they live in ephemeral water bodies; some species may as well be fully aquatic (O'Connor 2009). The chelicerae of these mites are laterally compressed and used for filtering microorganisms or organic material from the water film. There is even a unique swimming histiostomatid genus (*Creutzeria*) (Fashing et al. 1996). Though, as most "aquatic" Astigmatina live in water films or humid environments and are able to live in dry conditions as well; they are not considered truly aquatic mites (Barbosa, pers. comm.). Even though their occurrence in the Neotropics is likely, so far no information is available on Neotropical aquatic Astigmatina (Barbosa, pers. comm.).

Very few species of some Mesostigmata (superorder Parasitiformes) occur in freshwater samples, and very little is known of their biology and ecology (Proctor et al. 2015). Representatives of many families, of which none are strictly aquatic, are regularly found in freshwater habitats (Moraes, pers. comm.) – Ologamasidae (*Rhodacaroides*, *Desectophis*) (Castilho et al. 2016); Rhodacaridae (*Rhodacaropsis*) (Castilho et al. 2012); Ascidae (*Leioseius*) (Moraes et al. 2016, Santos & Moraes 2016); Blattisociidae (*Lasioseius*) (Moraes et al. 2015); Phytoseiidae (*Evansoseius*, *Macrocaudus*, *Phytoseiulus*) (Demite et al. 2016).

Despite their small body size of 0.5–2 mm, Hydrachnidia are quite striking in freshwater samples and unmistakable due to their mainly rounded-oval shape, characteristic movement and often bright colours (Figs 1A–D, 3F). Water mites are among the most abundant and diverse benthic freshwater arthropods. Consequently, the different water mite assemblages of various water bodies are an excellent tool for the assessment of water quality and habitat integrity (Young 1969, Goldschmidt 2004d, 2009b, 2016, Goldschmidt et al. 2016). In certain habitats (e.g. springs, see below) water mites provide the most specific and characteristic faunal assemblages (Goldschmidt 2004d).

However the large scale application of the information water mites could provide, in the Neotropics as in other parts of the world, is still hampered by the incomplete knowledge on the fauna and especially the lack of detailed information on the ecology of particular taxa. A further – and maybe the primarily – problem is the complete lack of tradition to use water mites in the bioassessment of water bodies (Proctor 2007, Proctor et al. 2015, Goldschmidt 2016). Nevertheless there are some scattered studies – mainly carried out by acarologists – providing valuable data on the ecology of Neotropical water mites: Böttger (1980a, 1984 – limnological studies in two mountain streams, Guatemala), Rosso de Ferradás et al. (1987 – study on the seasonality of the diversity and biomass of water mites in a reservoir, Argentina), Matveev et al. (1989) and Balseiro (1992) (water mites as cladocera predators, Argentina), Fernández (2003; structure of water mite assemblages, Argentina), Goldschmidt (2004d; ecology of water mite genera, Costa Rica), Rosso de Ferradás et al. (2004; ecology of lotic water mite species, Bolivia), Fernández & Fossati-Gaschignard (2011; habitat preferences of neotropical water mites) and Goldschmidt et al. (2016 – influence of water quality on lotic water mite assemblages, Panama).

Therefore the inclusion of water mites in general freshwater studies (ecological surveys, biomonitoring, inventories, etc.) is urgently needed in order to use the great potential of this group. The general information (on ecology, morphology, sampling, preparation and preservation techniques) and the keys presented here will provide the basis for the study of water mites in the Neotropical region, the creation of basic ecological information and the use of their bioindicator potential. For deeper insights in the fascinating evolution, phylogeny and ecology of water mites see Proctor et al. (2015) and the special literature listed there and below.

Water mites co-evolved with aquatic insects at least since the Triassic and are in different ways associated with some dominant insect groups in freshwater habitats, especially nematocerous Diptera (Fig. 1E) (Walter & Proctor 2013, Proctor et al. 2015). Their predatory-parasitic life cycle (Fig. 1F) is an important factor for their evolutionary success as well as some distributional patterns (see below). The radiation of the main water mite clades is estimated in the lower to upper Jurassic (180–155 MYA) (Dabert et al. 2016).

While water mites diversity and abundance is dramatically reduced in impacted water bodies (see Goldschmidt 2016 for an overview), in pristine habitats they can reach impressive numbers of up to 2000 specimens and 75 species (25 genera) per m² in the littoral zone of eutrophic lakes and 5000 specimens and 50 species (30 genera) per m² in stream riffles (Proctor et al. 2015). While the previous data were collected in North America, similar diversities were found in the Neotropics (Cramer 1988, Goldschmidt 2006, Fernández et al. 2009). Neotropical water mite assemblages reflect the high diversity of aquatic habitats in Central and South America. They occur in high diversities and abundances in all types of

freshwater habitats, in temperate, subtropical and tropical regions, from lowland swamps and large rivers to high mountain brooks and alpine lakes. Rosso de Ferradás & Fernández (2005) catalogued more than 900 species from South America; in the whole Neotropical region currently 1491 species in 175 genera and 33 families have been recorded. According to the application of different models, the total estimate for the Neotropics is between 2100 and 5500 species (Goldschmidt 2002). Beside the mere species number, the uniqueness of the Neotropical water mite fauna is remarkable: The genus level diversity – especially in the families Limnesiidae and Hygrobatidae – is much higher in the Neotropics than in any other zoogeographical region (Di Sabatino et al. 2008). The number of endemic families and subfamilies is by far highest (two families, twelve subfamilies) in the Neotropics (Di Sabatino et al. 2008). The diversity and complex biogeography of Neotropical water mites are response to both the heterogeneous topography and the geological history of the region. The fauna reflects as well the ecological differences between the high mountain ranges of the Andes and the lowlands of the Amazon region, as the long isolation of the South American continent and its belonging to Gondwana in the past. The southern tip of the Neotropics shows clear relationships to the Australian fauna, expressed by genera like *Corticacarus*, *Notomideopsis* (sg. in *Koenikea*), *Omartacarus* or *Momoniella*. On the other hand, *Thoracophoracarus*, *Scutobates* as well as the Eupatrellinae represent connections to the African fauna (Cook 1980, 1988, Smit & Clavier 2019, Goldschmidt & Gerecke 2003, Di Sabatino et al. 2008). Some of these southern elements are reaching far north along the Andean chain into Central or even North America. At the northern end of the Neotropics, the Central Mexican Highlands show close relationships to the Nearctic fauna, with several genera having their southernmost occurrence in this area (e. g. *Hydrovolzia*, *Thyopsella*, *Sperchonopsis*, *Testudacarus*, *Ljania*, *Chappuisides*, and *Neoacarus*). Overall Central America is both, a transitional zone between North and South America, and an independent faunal realm, representing a radiation center of northern and southern elements (e. g. *Neotyrrellia*, *Torrenticola*) (Goldschmidt 2004b, 2007). The fauna of this region includes several endemic genera and subfamilies (mainly but not only on the Greater Antilles), such as *Xenomomonia*, *Cladomomonia*, *Siboneyacarus*, *Neumanikea*, *Crocokongsbergia*, *Guanacastacarus*, *Cubanohydracarus*, Mixdeinae, Epallagopodinae (Goldschmidt 2006).

The first Neotropical water mites records date back to the end of the 19th century, when the first water mite species from Mexico (Dugès 1884) and Guatemala (Stoll 1886–1893) were described, soon followed by descriptions from Argentina (Berlese 1888), Brazil (Koenike 1890a,b, 1891, 1894) and Venezuela (Thor 1897). Since then, several researchers contributed to the water mite knowledge in the region. The largest steps are marked by publications of Lundblad (1941–1944) and K. Viets (1954a,b, 1959) on Suriname, Brazil and Paraguay, as well as Cook (1980, 1988) on Mexico, Costa Rica, Argentina and Chile (for a detailed account and references see Goldschmidt 2002).

So far no Hydrachnidia have been found on Antarctica or the sub-Antarctic islands. Pugh & Dartnall (1994) explain the absence of Hydrachnidia from these islands as a result of the low age and isolation of the habitats and because freshwater insects as potential hosts and transport media are missing rather than its ecosystem severity. Water mites are as well absent on the Malvinas (Falkland) Islands even though the freshwater fauna is closer to South America and includes several potential host insects (Chironomidae, Trichoptera, Coleoptera and Hemiptera) (Dartnall & Hollwedel 2007, Harry Smit, pers. comm.).

Hydrachnidia successfully colonized nearly every type of freshwater habitat, however many taxa are restricted to certain habitats, often resulting in the presence of characteristic water mite assemblages.

The Pontarachnidae occur primary in marine environment – mainly tropical and subtropical littoral habitats like mangroves, tidal flats, etc. (Walter 1925, Cook 1958, Pešić et al. 2008, 2012a, Chatterjee et al. 2019); however some species have been found as deep as 70 m (Pešić et al. 2012b, 2014). One species (*Litarachna brasiliensis* Smit, 2007) is known from the estuary of a river in Brazil (Smit 2007).

Standing waters are mainly inhabited by eurythermal taxa, either soft-bodied (Limnesiidae, Hygrobatidae, Pionidae) or heavily sclerotized (Arrenuroidea) (Figs 1C, 3F), most are strong swimmers, with their legs bearing long swimming setae (Figs 1C, 2F, 3F). Water mites can be found in high diversity and abundance in littoral zones with a rich growth of submerged plants, but some are as well pelagic (Riessen 1980, Gerecke et al. 1996). The very large eyes of *Centrolimnesia boopis* Gerecke & Fisher-Hartig, 1996 (from a shallow lake in the Amazonian lowland in Ecuador) are interpreted in connection with a predacious life in the pelagic zone (Gerecke et al. 1996).

Temporary pools are colonized by water mites that are either able to endure dry phases or leave the habitat as parasitic larvae (see below) (e. g. *Hydrachna*, *Eylais*) (Cramer & Costero 1985, Proctor et al. 2015).

Riffle zones of streams and rivers accommodate a very rich and diverse water mite fauna, with typical taxa often small and flattened, completely sclerotized and with strong claws (Figs 1B,I, 3I), such as *Torren-*

ticola (Goldschmidt 2007, 2009b) and the Aturidae (Cramer 1991, 1992a, 2000). However in calm pools several fast swimming, typically lentic genera (e. g. *Unionicola*, *Neumania*, *Koenikea*, *Hydrodroma*) occur as well (Goldschmidt 2004d, Goldschmidt et al. 2015). The rather untypical *Rhyncholimnochares* – large, very soft mites (Fig. 1D) – is found in protected microhabitats under large stones in the riffle zones of fast flowing streams (Goldschmidt 2004d, pers. obs.).

Water mites of more than 50 genera worldwide are adapted to a life in the hyporheic zone (interstitial) in the gravel beds of streams (Schwoerbel 1986b). The specialists in this habitat are either vermiform (e. g. *Omartacarus*, *Wandesia*) (Figs 2A, 7D) or heavily flattened and sclerotized (e. g. *Diamphidaxona*, *Neomamersa*, *Protolimnesia* (*Protolimnesella*)) (Figs 15I,J, 33H–J, 36A,B), often colourless and with the eyes reduced (Cook 1980, Fernández 1987).

Many studies in the Northern Hemisphere showed water mites as the most specific organisms in springs with the highest percentage of crenobionts, often constituting very diverse and specific assemblages (Schwoerbel 1959, Smith 1991, Gerecke & Di Sabatino 1996, Williams & Williams 1996, Gerecke et al. 1998, 2011, Cantonati et al. 2006, Stoch et al. 2011). Recently investigations in Costa Rica showed, that very specific water mite assemblages with many strict crenobionts (e. g. *Eupatrella*, *Bandakia*, *Nilotonia*, *Mamersopsides*, *Rheolimnesia*, *Fuenticola*, *Guanacastacarus*, *Stygarrenurus*) also exist in tropical springs (Goldschmidt 2004d, 2009a, 2009b). In Andean hot springs in Chile and Bolivia, *Wandesia thermalis* Viets, 1938 and *Thermacarus andinus* Martin & Schwoerbel, 2002 represent a specific warm adapted water mite fauna (Schwoerbel 1987, Martin & Schwoerbel 2002). Many undescribed species can still be expected in tropical springs.

The semi-aquatic habitats in the splash zones of streams and waterfalls are colonized by water mites as well – *Neotyrrellia*, *Tyrrellia* and *Neotorrenticola* are regularly found in these specific habitats (Goldschmidt 2004d).

Some water mite species even live in phytotelmata between the leaves of Bromeliads: *Micruracaropsis phytotelmaticola* (Viets, 1939) from Surinam (Viets 1939), *Arrenurus bromeliacearum* Orghidan, Gruia & Viña Bayés, 1977 from Cuba (Orghidan et al. 1977), *Arrenurus andrewfieldi* Orghidan & Gruia, 1983 and *A. caquetiorum* Rosso de Ferradás & Fernández, 2001 from Venezuela (Orghidan & Gruia 1987, Rosso de Ferradás & Fernández 2001), *Xystonotus phytotelmaticola* Pešić, 2015, *Bromeliacarus cardoso* Pešić, 2015 and *Protolimnesia goldschmidti* Pešić, 2016 from Brazil (Pešić et al. 2015a,b, 2016a).

Several aspects of the habitat demand of Hydrachnidia as well as their importance as bioindicators are based upon their complex life cycle (Fig. 1F), connecting them in various ways with other members of the freshwater community (e. g. Münchberg 1959, Böttger 1965a,b, 1977, 1980b, Davids 1973, Smith & Oliver 1986, Proctor et al. 2015).

Typically, the eggs are attached to the substrate in a gelatinous matrix. As exceptions, *Hydrachna* lays their eggs individually in aquatic plants' stems, Unionicolidae deposit their eggs in the tissue of sponges or mussels (Edwards & Vidrine 2013). The number of eggs produced per female varies among different taxa from very few (e. g. spring dwelling Aturidae) to several thousands (*Eylais*) (Davids 1973, Proctor et al. 2015). The hexapod larvae (Fig. 1G) are obligate ectoparasites of freshwater insects. All aquatic insect orders – with the exception of Ephemeroptera – are parasitized by certain water mite taxa, the most important hosts are nematocerous Diptera (Fig. 1E), especially Chironomidae. Besides the parasitic feeding on host fluids (the larvae form a stylostome (feeding tube) in the host tissue (Smith 2003, Davids et al. 2007), the phoretic aspect is very important. The passive transport of the larvae by their terrestrial (aerial) hosts provides an important mean of dispersal. The hosts are either located on the water surface while emerging (mainly early derivative water mite clades) or attached already as pupae or final instar larvae in the water (mainly derived clades) (Smith & Oliver 1986, Walter et al. 2009, Proctor et al. 2015). In few exceptions from this general pattern a direct development of the larvae has been observed (Smith 1998, Bohonak et al. 2004). One rare example is known of a vertebrate host: the larvae of *Thermacarus andinus* Martin & Schwoerbel, 2002, which occur in hot springs in Chile and Bolivia, are known to parasitize toads (*Bufo spinulosa*) (Martin & Schwoerbel 2002).

Engorged mite larvae detach from the host and enter the quiescent protonymph stage, which metamorphoses to the active, octopod deutonymph (Fig. 1H). This stage (similar to the adult, but sexually immature and with incomplete sclerotization) is followed by a second post-larval quiescent stage, the tritonymph that finally develops into the adult. The immobile tritonymphal stage is particularly vulnerable to poor water quality, probably due to the combination of high oxygen demand and impossibility to actively change to microhabitats with more favourable conditions. Most adults and deutonymphs are free living predators on a wide range of aquatic invertebrates – small crustaceans (Ostracoda, Cladocera, Copepoda), insect larvae and eggs (Diptera, Ephemeroptera, Trichoptera, etc.), other water mites and water mite eggs (Böttger 1970, Gliwicz & Biesiadka 1975, Gledhill 1985, Proctor & Pritchard 1989, Matveev & Martinez 1990, Balseiro

1992). Several species of Unionicolidae and few Pionidae live parasitic or commensal in mussels or sponges (Davids et al. 2007, Edwards & Vidrine 2013).

A great variety in the mode of sperm transfer – from deposition of spermatophores without contact between male and female to indirect and direct sperm transfer, mating and copulation – is realized in water mites, sometimes leading to sexual dimorphism (mainly in derived clades) (see below). The male of many different taxa, show modifications of the posterior legs either for the indirect transfer of spermatophores or the holding and positioning of females (Figs 3H, 24H, 28F, 35C,D, 46I, 52F, 54E, 56G–L, 58E).

The life span of water mites in temperate latitudes varies from a few months up to three years (Bader 1980, Davids et al. 2007). Shorter lifespan in male and phenological differences can cause strongly biased sex ratios; a strong seasonality has been documented for many species from temperate latitudes (Davids et al. 2007). K. Viets (1954a) assumed that most Neotropical species were present year round; however, we currently lack data on lifespan or phenology of tropical water mites, except for the fact that abundance and diversity is reduced in wet towards dry season (Goldschmidt et al. 2016).

Limitations

Recently, all superfamilies (except for one) were confirmed by molecular analyses (Dabert et al. 2016). In several recent revisions some critical families have been reorganized (Cook et al. 2000, Pesic et al. 2013, Smith et al. 2015). However, many families still need revision (Rosso de Ferradás & Fernández 2009). Detailed understanding of the phylogenetic relationships within the Hydrachnidia is hampered by the poor knowledge of the fauna of many regions and habitats (e. g. springs, interstitial). Nevertheless, for practical reasons in the following key we mainly applied the traditional phylogenetic system of families and superfamilies (Cook 1974, K. O. Viets 1987, Proctor et al. 2015, Smit 2020), adapted by the revisions mentioned before.

Although we are aware of the problems caused by poly- and paraphyletic families and the often still unclear phylogenetic relationships (see discussion in Smith & Cook 2016), we decided to give as well a key to families in order to facilitate the access to this large group. Therefore, we provide an artificial two-stage key; an initial key to all 33 currently known Neotropical families, and a second series of keys to the 175 genera in the respective families. In some cases subgenera are separated as well. If only one species has been described from the Neotropical area, the species name is given. However, we strongly recommend NOT using these names as determination results. The keys only lead to genera (in some cases subgenera). Species keys have been published for several genera. If such keys are available scattered in the literature, the respective references are given with the particular genus. However, readers should be cautioned that many of these keys are limited to certain regions and often not reflect the current knowledge. Users should review how many species have been described since the key appeared by checking K. O. Viets (1987) and the database for new taxa since 1987 on watermite.org (2019). Generally, it has to be emphasized that any determination to species, and especially any sensible use of species names should be done extremely carefully, and only after thoroughly consulting all relevant literature and detailed studies of the respective taxon. Because our knowledge of the Neotropical water mites fauna is far from complete, especially (but not only) in poorly studied habitats, like interstitial, springs, phytotelmata, etc., the finding of undescribed taxa (including above species level) is very likely.

A key for immature stages is not provided. However deutonymphs are mostly similar enough to adults to be identified with the adult key – despite their often being less sclerotized, bearing less setae and lacking functional genitalia (in the provisional genital field the gonopore is closed, the number of acetabula reduced). The inactive proto- and tritonymphs are very rarely found in standard collections. No key for larvae is provided, as the knowledge on Neotropical water mite larvae is limited to very few single descriptions: e. g. *Axonopsella* (Orghidan & Gruia 1981), *Mamersellides* (Cramer & Smith 1993), *Hydrachna* (Rosso de Ferradás 1996) and *Arrenurus* (Böttger 1965a,b, 1980b). The description of larvae (and their association with conspecific adults by rearing) is urgently needed, in order to provide basic information to study the life history and the parasitic association of water mites with aquatic insects. For a rough classification the key to Nearctic larvae could be consulted very carefully considering the faunistic differences and incomplete knowledge as well on North American larvae (Smith & Cook 2016).

Overall species keys currently cannot be provided as many genera are in need of revision and probably up to 75 % of the neotropical species are still undescribed (Goldschmidt 2006).

For practical reasons the Mexican fauna is included completely, even though biogeographically the Central Mexican mountain regions are generally rather considered as part of the Nearctic (several northern water mite genera included in the following key have their southernmost occurrence in Central Mexico).

Beside the already mentioned lack of knowledge on the fauna of certain regions and habitats, there is still huge research demand on all aspects of ecology, life history, morphology of larvae and their parasitic associations with insects, the role of water mites in freshwater communities, seasonality and phenology of individual taxa. The closing of all these gaps as well as the needed taxonomic revisions are severely hampered by the great shortage of trained experts and modern, well curated water mite collections (especially, but not only in the Neotropics).

Terminology and morphology

Generally water mites follow the characteristic Acari scheme: Mites (Acari) are characterized by the complete loss of the opisthosomal segmentation and the fusion of main parts of the **prosoma** and the **opisthosoma** into an **idiosoma**. The body is generally divided into the anterior **gnathosoma**, bearing the mouthparts (**pedipalps** (or **palps**), **chelicerae**) and the posterior **idiosoma**, bearing the **legs** and the **genital field** (Krantz & Walter 2009) (Fig. 1I–K).

Mite larvae bear three pairs of legs, versus four pairs in adults; deutonymphs are similar to adults, but lack a fully developed genital field and functional gonopore (Fig. 1G,H).

Although various mite groups may occur in freshwater, Hydrachnidia are clearly distinguished from all other mites by a series of paired **glandularia** (gland openings associated with sensillae that trigger the release of a defensive substance) (Fig. 2D,G). The habitus of Hydrachnidia is clearly distinct from other mites in freshwater samples: If they are completely armoured, the armour is not shiny dark or opaque smooth, like in the Oribatida (Fig. 4I), but has many pores (Fig. 3F); the idiosomal setae are never dense, or tomentose (Fig. 5A–C), or long and stiff projecting (Fig. 4I); the terminal leg segments are generally truncate (Figs 1I, 3J, 5F), not pointed or terminal rounded (Fig. 5A–E) (with exception of the forth legs of some Limnesiidae (Figs 31E, 34A,D, 35G) and Anisitsiellidae (Fig. 23K,L).

As the following keys are is only dealing with adults, the information on morphology refers exclusively to this stage. In most genera the **gnathosoma** is separated from the **idiosoma** by a membranous suture (as an exception in some Hygrobatidae (mainly *Hygrobates* (e.g. Figs 7G,H, 44F)) it is fused with the first coxae). A trunk-like protrusible tube is connecting the gnathosoma with the idiosoma in some non related genera (e.g. *Rhyncholimnochares* (Fig. 1D), *Clathrosperchon* (Fig. 3M), *Pseudotorrenticola*, *Tubophorella*, *Rhynchaturus* (Figs 34E, 49A)). The basal part of the gnathosoma – the **capitulum** – is formed by the transformed palpal coxae. The apical part of the capitulum (anterior to the palp insertions) is called **rostrum** (Fig. 1J). At the tip of the rostrum, generally flanked by two pairs of setae, is the mouth opening (Fig. 1K) with a membranous collar (forming a rather large fringe in the Eylaoidea (Figs 1L, 6L,O)). Subcutaneous sclerotized projections (variable in size and shape) at the caudal end of the gnathosoma – **gnathosomal apodemes** or **anchoral process** – function as muscle attachment sites for moving and retracting the gnathosoma. A pair of generally five-segmented palps (or pedipalps) (with various degrees of fusion in some groups), for sensing and capturing prey are inserted dorsally. The palps bear tactile sensillae, and in several genera various protrusions (Figs 1J, 15A, 22K,Q, 33L,M, 43A–C). In a number of basal groups, the fourth segment of the palp (P4) bears a dorsal protrusion extending beyond the insertion of the fifth (P5), or a large dorsal seta, forming a scissors- or pincer-like **chelate** palp (e.g. *Hydrodroma* (Fig. 7A), by far weaker developed e.g. in *Hydryphantes* (Fig. 7B)). In some advanced groups (some groups of the Arrenuroidea, e.g. *Arrenurus*) P4 is expanded ventro-distally opposing the P5 forming an **uncate** or **subchelate** palp (for grasping and holding slender appendages of prey organisms) (Figs 10K, 11G, 12E–H). The paired **chelicera** lie in longitudinal grooves between the palps on the dorsal surface of the capitulum (Fig. 1K). Generally they consist of a basal segment and a movable terminal claw. As exceptions, Hydrachnidae (*Hydrachna*) and the genus *Pontarachna* in the Pontarachnidae bear unsegmented chelicera (Figs 6K, 18D), in the Limnocharidae and Eylaidae the chelicera are medially fused.

The idiosoma of different taxa is highly variable in shape and sclerotization. Different variations of the plesiotypic soft-bodied, rounded-oval, dorsoventrally slightly flattened form (Fig. 2B,I) are found in different lineages and in adaptation to different habitats (see above). Lateral compressions (e.g. *Oxus*, *Estelloxus*, *Frontipodopsis* (Figs 8E–G, K–N, 14E)) are found as well as dorso-ventral flattening (e.g. *Neomamersa* (Fig. 15I,J)) or slight to vermiform elongation (e.g. *Omartacarus*, *Wandesia* (Figs 2A, 7D)). The latter occur mainly in interstitial habitats (see Proctor et al. 2015 for details and discussion of the evolutionary context).

Water mites of ancient clades are often bright red due to pigment granules throughout the body (most of the coloration is lost in preserved specimens). Other groups show many different colours (red, orange, yellow, green, blue) and colour patterns (e.g. Figs 1B,C, 3F), in sclerotized taxa the pigmentation is often incorporated into the plates (for further information, as well on the function of the coloration (warning, photo protection, camouflage) see Proctor et al. (2015).

The dorsal integument bears two pairs of lateral eyes (usually enclosed in a capsule on each side, incorporating a lens) (Figs 1L, 2F, 6F–I,M,P) and an unpaired median eye (or **frontal organ**, sometimes included in a **frontal plate**, reduced in the higher clades, often without pigment) (Fig. 19E,F arrows). Furthermore the dorsum bears longitudinal series of paired setae (the pre- and postocularia anterior and posterior to the lateral eyes), glandularia (six pairs of dorso-glandularia, four pairs of latero-glandularia, see below) (Fig. 2D,G), muscle-attachment plates (five pairs of dorso-centralia, four pairs of dorso-lateralia) as well as five pairs of slit organs (e. g. Fig. 19N,O) (Lundblad 1927, Bartsch et al. 2007). The integument structure and the degree of sclerotization is varying from soft and smooth (Figs 1A,D, 2A,B,H), sometimes striated, to thick leathery; sometimes bearing papillae or spines forming net-like structures (Fig. 2C,D). The dorsal plates vary between hardly visible chitinous knobs, small platelets, large plates or complete dorsal armour (e. g. Figs 1B,I, 2J, 3F, 8B,C, 9B,D,F,G, 14H,J,L, 15H,J, 19N,O). In the latter case (e. g. *Torrenticola* (Fig. 1B,I), *Arrenurus* (Figs 1C, 3F)), there is always a (sometimes narrow) stripe of soft integument – the **dorsal furrow** – between dorsal and ventral shield. All larger sclerotized areas (shields, coxae, plates) are bearing fine, regular pores facilitating gas exchange (Figs 1C, 3F).

The **coxae** (the basal leg segments) are immovably incorporated in the ventral integument forming four pairs of coxal plates: Cx-I and -II as well as Cx-III and -IV are generally fused into anterior and posterior groups (Figs 3D,E, 7C,E,H, 19A, 20F,O) . Further fusion in a complete coxal plate (or 'coxal shield' sometimes extended over the complete ventral surface) is relatively common (Figs 2H,I, 7I–K, 8E,K,M). The embayment between the antero-medial margins of the Cx-I embracing the gnathosomal base is called **gnathosomal** or **capitular bay**. In some taxa the anterior margin of the gnathosomal bay bears a sclerotized, collar-like extension, the so-called **camerostome** (Figs 2E, 3M, 9A,C). Generally between Cx-II and -III and postero-medial to the Cx-IV are two pairs of coxoglandularia (Cxgl-1, -2) (Figs 2E, 3D,E arrows), an additional pair of glandularia on the posterior coxal group in members of the family Limnesiidae is (traditionally) called **glandulae limnesiae** (e. g. Fig. 35H arrow). A similar gland is found in most Hygrobatidae (Fig. 16A–H,K,L).

The **genital field** is located posterior to the coxae or in a **genital bay** between the posterior coxal groups (e. g. Fig. 2H,I). It is including the pre- and post-genital sclerites and the genital plates flanking the gonopore (genital opening). Whereas the so called **genital plates** are immovably fused with the integument and sometimes with each other (e. g. Figs 2H, 3E), the so called **genital flaps** or **valves** are movable (e. g. Figs 2I, 3A,B,D). Originally three pairs of **acetabula** are located either in the soft integument between the gonopore and the genital flaps (and can be covered by them) (e. g. Figs 3B,D, 7E), or **on** the plates or flaps (e. g. Figs 2H, 3A, 7C,G,H, 16A–H,K,L). However, the number of acetabula can be increased (e. g. Figs 3A, 7C, 9A, 10G, 42A–E, 50H), and the plates can be fused with the ventral shield (e. g. Figs 10A, 11F, 53A–F, 56A,B, 58E,G).

The **excretory pore** (or **anal pore**) and four pairs of ventroglandularia are located posterior to the genital field (Fig. 3D). In some *Arrenurus* species the males' idiosoma is modified posteriorly, forming a **cauda** (Fig. 1C), or postero-lateral pygal lobes, in this case always bearing a posterior projection, the so called **petiole** (Fig. 3F).

The **legs** are inserted laterally on the coxae (Figs 1I, 2H,I). In most genera all legs are arranged more or less circular at the anterior end of the idiosoma, only the Hydrovolzioidea (Fig. 6B) convergently developed a morphology similar to the Halacaroidea (Fig. 5D,E) – dorsoventrally flattened, with anterior and posterior legs separated and oriented towards anterior and posterior respectively. However due to their five-segmented palps and the water mite-typical glandularia they are clearly differentiated from the Halacaroidea. The legs are six-segmented, generally ending in paired terminal claws (Figs 1I, 3I,J, 23N–R, 30I,J, 35D). In the Oxidae and some genera within the Limnesiidae and the Anisitsiellidae the claws are reduced in the posterior legs (Figs 8J, 30L, 31E, 35G).

Additional dorsal or ventral tips of the claws are called **clawlets**, the sometimes enlarged flat base is called **claw blade** (Fig. 3I). In some Hydryphantidae (*Protzia*, some *Neocalonyx*) due to fan-like lateral clawlets the claws are comb-shaped (Figs 19K,L, 20E). There is a large individual variability in the chaetotaxy of the legs in adult water mites, therefore it is not as taxonomically useful as it is in the larvae. The shape of the legs and their setation in different taxa is very variable in adaptation to the habitat and locomotion mode – e. g. long and slender with fringes of long **swimming setae** (mostly called "swimming hairs") in lentic habitats (Figs 1C, 2F, 3F, 8J, 19G, 24H, 28F, 35G); short and stocky with heavy setae for crawling in strong current or walking on muddy substrate (Fig. 3J). Some genera with direct sperm transfer show sexual dimorphism in the shape of the hind legs, with III-legs or IV-legs of male forming grasping organs to hold the female and the claws or various segments of IV-legs modified for sperm transfer (e. g. Figs 3H, 58E).

The variability of many aspects of the external morphology provides a large set of taxonomic

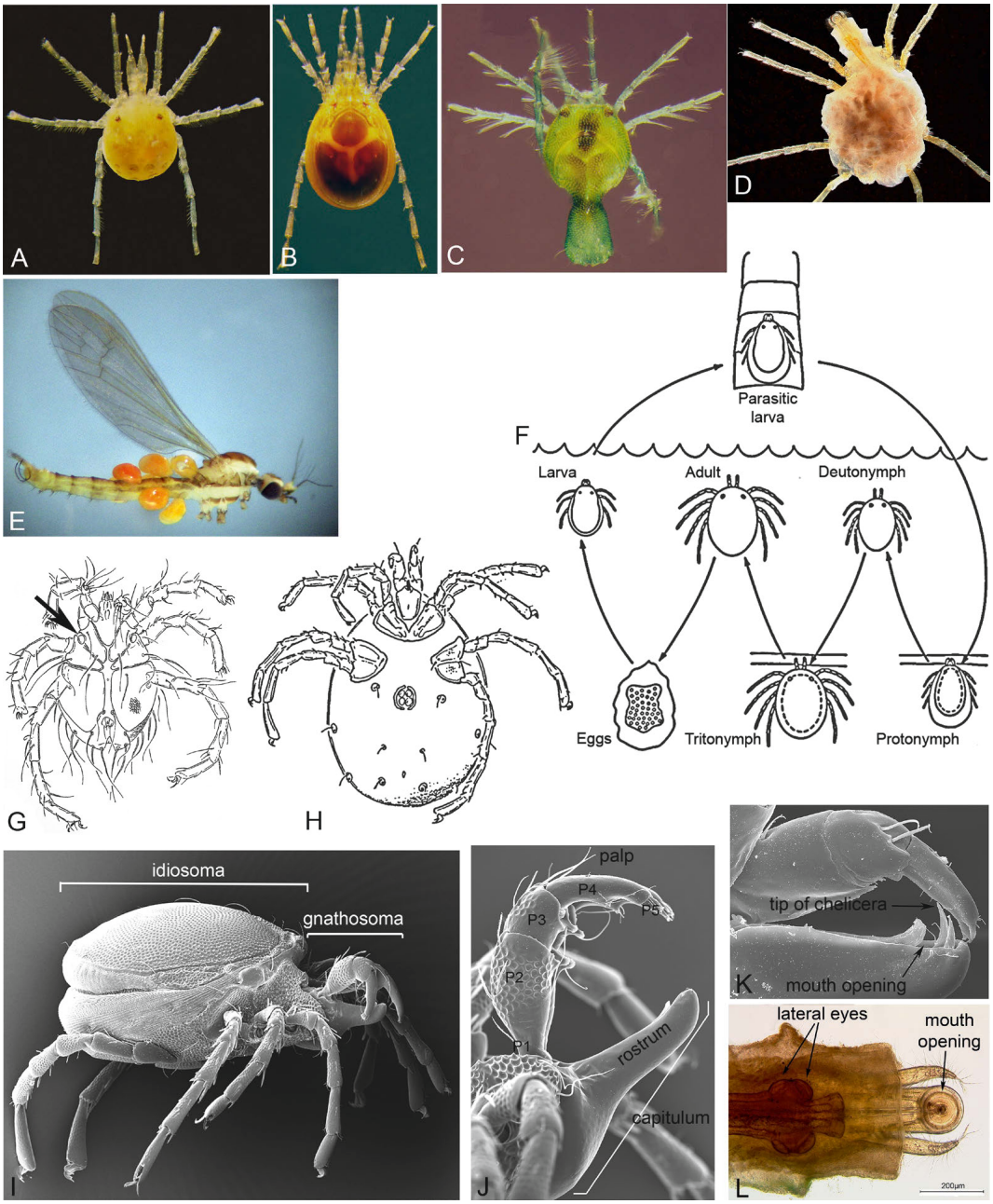


Fig. 1. **A.** *Sperchon* sp., adult, dorsal (Goldschmidt & Ramírez-Sánchez, unpublished photo). **B.** *Torrenticola* sp., adult, dorsal (Goldschmidt & Ramírez-Sánchez, unpublished photo). **C.** *Arrenurus* sp., male, dorsal (Goldschmidt & Ramírez-Sánchez, unpublished photo). **D.** *Rhyncholimnochares* sp., adult, dorsal (Goldschmidt, unpublished photo). **E.** Water mite larvae attached to a dipteran host (Limoniidae), Costa Rica (Goldschmidt, unpublished photo). **F.** General – schematic – life cycle of water mites (after Smith et al. 2010). **G.** *Sperchon* sp., larva (arrow pointing at the Claparède organ) (after Bartsch et al. 2007). **H.** *Sperchon* sp., deutonymph (after Bartsch et al. 2007). **I.** *Torrenticola pervagata*, adult, SEM (Goldschmidt 2007). **J.** *Torrenticola pervagata*, gnathosoma lateral, adult, SEM (Goldschmidt 2007). **K.** *Torrenticola guanacastensis*, adult, detail gnathosoma (palp, rostrum) (arrows pointing at chelicera tips and mouth opening), SEM (Goldschmidt 2007). **L.** *Rhyncholimnochares* sp., adult, dorsal view of anterior tip of idiosoma (eye plate, gnathosoma) (arrows pointing at lateral eyes and mouth opening) (Goldschmidt, unpublished photo).

characters. Characters relevant for the identification of water mites are mainly the arrangement of the coxae and genital flaps, the number and position of the acetabula, the shape and setation of the palps and legs as well as the degree and organization of the idiosomal sclerotization and position of glandularia. In general sexual dimorphism mainly refers to shape and setation of posterior legs (Fig. 23Q,R) and organization of genital field (e.g. Fig. 60A (male)/B (female), C/D, E/F), in different genera it varies between very strong and hardly visible (Gledhill 1985). In some genera the degree of sclerotization is not only quite variable between different species, but as well between sexes of the same species (Figs 10B/D, 14J/L, 37C/D, 43F/G).

Glossary

Acetabula or **genital acetabula** or **genital papillae:** Osmoregulatory organs with a porous surface, in adults and deutonymphs (Alberti 1977, 1979, Goldschmidt et al. 1999) (Fig. 3A,C,G); flat or convex to hemispheric, stalked in some Hydryphantidae (Figs 19C,D, 20D); plesiotypically three pairs, often proliferated (independently in all superfamilies) (Figs 3A, 7C); with few exceptions confined (and restricted) to the genital region – in the Eylaoidea free in ventral integument (Fig. 6N), in *Hydrovolzia* on the coxae (not illustrated in Fig. 6B), in *Neotyrrellia* on the genital flaps (in the normal position) and (additionally) on the Cx-IV (Goldschmidt et al. 1999, Goldschmidt 2004b) (Figs 3C, 32E, 33G); precursors in larvae – **urstigma** or **Claparède organs** (situated between Cx-I and -II) (Fig. 1G arrow).

Dorsalia: Dorsal muscle attachment sclerites (plesiotypically eleven pairs – pre- and post-frontalia, five dorsocentralia, four dorsolateralia), may be fused in various ways (Figs 2J, 19O, 20P); if all fused, forming a **dorsal shield** (e.g. Figs 1I, 3F, 9D,F).

Genital skeleton or **ejaculatory complex:** Framework of membranous chambers and sclerotized unpaired keels and paired arms, situated inside the male gonopore, assembling and expelling the spermatophores (in some genera (e.g. *Torrenticola*) providing characters for the separation of species; Barr 1972, Goldschmidt 2007) (Fig. 3K,L).

Glandularium: Defense organ comprising a goblet-shaped gland with a tiny opening surrounded by chitinous ring and associated sensory seta (Fig. 2D,G); when disturbed expelling a milky, viscous fluid (Kerfoot 1982); in *Arrenurus* caudal glandularia as well produce a glue attaching male and female during copulation; synapomorphy only in water mites (separating them from other mites); arrangement of the glandularia reflects the original segmentation of the water mite body (Wiles 1997a) – in total sixteen pairs (six pairs of **dorsoglandularia**, four pairs of **lateroglandularia**, four pairs of **coxoglandularia** (or **epimeroglandularia**) (two of them always reduced!), four pairs of **ventroglandularia**). Unfortunately there are different nomenclature systems for the description of the different idiosomal glands, in the European literature (Bartsch et al. 2007), e.g. Cxgl-1 and -2 are denominated as Cxgl-2 and -4. In order not to create more confusion, we are here following the nomenclature applied by Smith & Cook (2016). In several taxa different glandularia are reduced or shifted to different positions, furthermore there are specific terms in use for certain glandularia in certain taxa – "Cx-IV gland" in Hygrobatidae, "glandulae limnesiae" on Cx-III or -IV in most Limnesiidae (see above).

Slit organ: Mechanoreceptor, slit-shaped opening in sclerotized cuticle; incorrectly sometimes called "lyrifissures" or "lyriform organs" (however these are composed of several slits, whereas in water mites only single slits are found).

Solenidia: Chemosensory setae on the legs.

Ventralia: Ventral muscle attachment sclerites (plesiotypically four pairs around the excretory pore), may be fused in various ways, if the fusion includes the coxae then forming a **ventral shield.**

Material, collection, preparation and preservation

Sampling

Water mites frequently occur in samples collected for general ecological studies, but are often sub-estimated in density and diversity. Due to their small size and their clinging to the substrate they are easily overlooked in preserved samples or lost by using an overly coarse mesh-size for collecting or washing the samples and therefore ignored (willingly or by chance) in general limnological surveys (Proctor 2007). However, if sampled extensively, they are potentially very important indicators of ecological conditions (Goldschmidt 2016).

For a complete inventory, thoroughly sample all different microhabitats, as water mite assemblages can vary significantly among substrates and some taxa are strictly bound to certain microhabitats. Little is known about the seasonality and phenology of Neotropical water mites, however in general, much higher diversities and abundances occur in the dry season (Rosso de Ferradás et al. 1987, Goldschmidt et al. 2016).

Adult water mites are best collected using a handnet of 250 µm mesh size. To collect the often smaller interstitial species and larvae use a mesh size of 100 µm. As most species show very patchy distribution patterns and low population densities, it is generally more efficient to collect several smaller samples instead of a single large one (for details see as well Proctor el al. 2015).

Lotic habitats are best sampled by stirring up the sediment (stones, gravel, sand, coarse detritus, roots of riparian trees, moss carpets on stones, etc.) by hand, foot or spade and washing the fine detritus together with the

dislodged organisms downstream into the net. Wash the substrate (especially plant material) vigorously, as mites tend to cling to it. Brush the surface of large rocks and tree limbs in situ so that any mites will be washed into the net. Other specific methods like artificial substrates (Dewez & Wauthy 1984) or drift nets (Schmidt 1969, Martin 1999) are described elsewhere.

To sample the often very rich hyporheic fauna, dig down up to 0.5 m in riffle zones, and remove large stones to allow the current to flush out the interstitial mites. Separated samples of the hyporheic fauna can be collected either by the "Karaman-Chappuis" digging or by pumping. In the first case, a hole is dug on the bank beside the stream until the water table is reached. The water percolating into the hole should be scooped several times and passed through a net (Chappuis 1942). In the second case, the sample is pumped directly from a tube driven into the interstitial in the stream bed (Boulton et al. 1992, Scarsbrook & Halliday 2002). Scarsbrook & Halliday (2002) also reported high water mite abundance by freeze-coring.

To collect water mites in lentic habitats (including pools in larger streams) repeatedly sweep the net through beds of aquatic plants, coarse detritus, submerged plants and roots. Stir the bottom substrate by vigorously moving the net immediately above the ground; mites are then caught by moving the net through the substrate-water-mixture. If thick layers of silt and decaying leaves are present, the mites will be restricted to the oxygenated surface.

In deeper lakes water mites can be collected using plankton tow nets or underwater traps (activity traps, light traps, bait traps) (Conroy 1973, Barr 1979, Davids et al. 1994). Light traps can as well be very efficient in the riparian zone of lakes (for details and construction of traps, see Proctor et al. 2015).

In very shallow habitats such as small springs, helocrene springs, seepage areas, fens, etc. carefully gather substrate (moss, leaf litter, detritus, silt, etc.) by hand into the net. If the current is strong enough, the substrate can be stirred and washed by hand upstream of the net, so that the sample without to much substrate is washed into the net. Carpets of wet moss can be tread down and the water with the dislodged organisms scooped with a net. All these sampling methods are very "invasive" and especially in small, ecological sensitive areas like small springs therefore shall be applied very carefully and only in small parts of the habitats. Proctor et al. (2015) report as well a method of light trapping water mites in helocrene springs, as an alternative to damaging sensitive habitats.

Before sorting or transporting over longer distances, wash the samples to separate the mites from coarse organic material (disturbing the detection of mites in the sample), fine silt (blurring the sample and leading to low oxygen levels), gravel and sand (which can destroy the mites by grinding). Therefore gently stir the sample either in the pan used for sorting or a wide container to separate the heavy inorganic material from the light organic (including the organisms); then pour the water with the biotic component through a sieve of 1.5–2 mm mesh size into a finer sieve (or net) of 250 (or 100) µm mesh size. This procedure should be repeated several times until all mites and fine organic material is transferred to the sieve. The sample should then be thoroughly washed (until all fine detritus is removed). Mites inhabiting moss carpets in strong current often cling tightly to the substrate, therefore the moss should be either washed and stirred vigorously when the sample is washed through the sieve or picked apart strand by strand in a white tray with forceps to retrieve the mites.

Samples are then either transported to the laboratory alive in large containers with a small amount of water (just enough to cover the sample), or (if light conditions are favourable) sorted in the field. For sorting, place the sample gently in the centre of a white tray with enough clean water to cover it completely, and with enough space between the sample and the edge of the tray to detect the mites walking or swimming out of the debris over the white surface of the tray. It is best to sort fresh samples, because the mite's bright colours and characteristic movement when alive make them easy to spot and retrieve individually with the aid of fine soft tweezers or pipettes. However, larvae and small nymphs can only be sorted confidently under a stereoscope. Most mites will leave the sediment and start moving around at once; however some mites only start moving, when conditions in the detritus at the bottom of the tray become unfavourable (oxygen deficiency) and thus the sample should be examined with patience for some time. In the laboratory, trays are ideally checked regularly for 4–6 hrs though some mites might remain active and continue to emerge for up to 72 hrs and even after the sample had been refrigerated (Proctor et al. 2015, pers. obs.). There are as well several extraction methods for fresh (light, temperature gradients, flotation with salt solutions) as well as preserved (kerosene-flotation) samples discussed by Proctor et al. (2015).

Aquatic larvae are frequently found in underwater light traps. In contrast aerial larvae of most basal groups climb to the water's surface or riparian vegetation, in rare cases they occur in large numbers and can be collected directly with a fine brush dipped in alcohol (Proctor et al. 2015). Parasitic larvae can be picked up from adult insects (the attachment site on the host, and the host species shall always be recorded), collected by sweep netting, light traps or emergent traps. Host insects can also be kept alive until the engorged larvae detach (Böttger 1965b, 1980b, Proctor et al. 2015). Mite larvae might then be raised to deutonymphs and adults for identification. In those cases, you must supply enough adequate food (like live Ostracoda or Cladocera) for the transformation of deutonymphs to adults. Larvae can also be reared from eggs laid by fertilized females kept in micro-aquaria in the laboratory (Martin 2005, 2010, Proctor et al. 2015). In several taxa adults survive for long periods at room temperature as well without food (Proctor et al. 2015). Mites shall be placed individually (in order to be able to associate eggs and larvae with the correct adult) in small dishes with some water and substrate (e.g. sand glued to the bottom of the

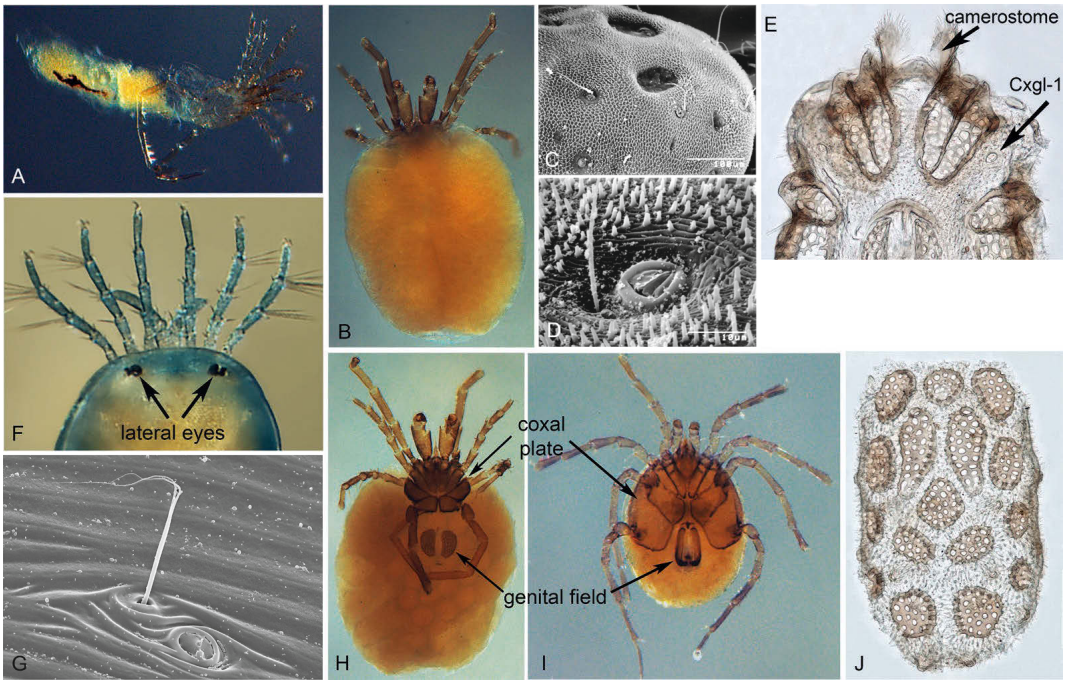


Fig. 2. A. *Omartacarus* sp., adult, ventral (Goldschmidt, unpublished photo). **B.** *Omartacarus* sp., female, dorsal (Goldschmidt, unpublished photo). **C.** *Neotyrrellia rosemariae*, male; antero-dorsal part of idiosoma, integument with chitinous tips, forming a net-structure, SEM (Goldschmidt 2004b). **D.** *Neotyrrellia rosemariae*, male; detail dorsal integument structure, glandularium, SEM (Goldschmidt 2004b). **E.** *Clathrosperchon* cf. *punctatus*, female, ventral, anterior part of idiosoma (arrows pointing at camerostome and Cxgl-1) (Goldschmidt, unpublished photo). **F.** *Albia* sp., adult, antero-dorsal part of idiosoma (arrows pointing at lateral eyes) (Radwell, unpublished photo). **G.** *Torrenticola semicolor*, adult, glandularium (gland opening and accompanying seta), SEM (Goldschmidt, unpublished photo). **H.** *Omartacarus* sp., female, ventral (arrows pointing at coxal plate and genital field) (Goldschmidt, unpublished photo). **I.** *Nilotonia* sp., female, ventral (arrows pointing at coxal plate and genital field) (Goldschmidt, unpublished photo). **J.** *Clathrosperchon* cf. *punctatus*, adult, dorsal integument (Goldschmidt, unpublished photo).

container or a fragment of the original vegetation). The containers should be covered but allow gas exchange (parafilm with small perforations can be used) (Martin 2005, 2010; for details see Proctor et al. 2015). These kind of experimental data are urgently needed because information on life cycle, host binding or prey preferences are exceedingly rare in the Neotropics.

Preservation

Deutonymphal and adult water mites for taxonomic studies are best preserved in Koenike's solution (10 parts glycerine, 6 parts water, 3 parts acetic acid), or modified Koenike's solution (GAW) (5 parts glycerine, 4 parts water, 1 part acetic acid) (Barr 1973). For dissecting and slide mounting, specimens might be cleared in 10 % KOH (especially necessary in very dark specimens or small and difficult groups such as Aturidae). The mites should be slightly heated in 10 % KOH for some minutes, while regularly checked. As soon as the appendages become clear, transfer the specimen to glycerine, where it can be stored until mounting. Specimens preserved in alcohol (or even worse in formaline) often become hard and distorted and preparation as well as determination is much more difficult. Alcohol-fixed material can be softened again by clearing overnight in 85 % lactic acid after piercing the integument in a few places (Proctor et al. 2015). Water mite larvae can be preserved in 70 % alcohol without problems and mounted whole in Hoyer's medium (see below).

For molecular studies, the mites should be preserved in 96 % ethanol and stored dark and (as soon as possible) deep frozen. Koenike fixed material has enormous advantages for dissection, slide mounting and long term storage, as the medium does not evaporate and the mites remain flexible and suitable for dissection over decades. On the other hand, molecular techniques become increasingly accessible and important; and so far mites preserved in Koenike cannot be used for molecular analyses. Therefore, especially in areas or habitats where new taxa can be expected, a combination of both types of fixation is recommended. Ideally, if mor-

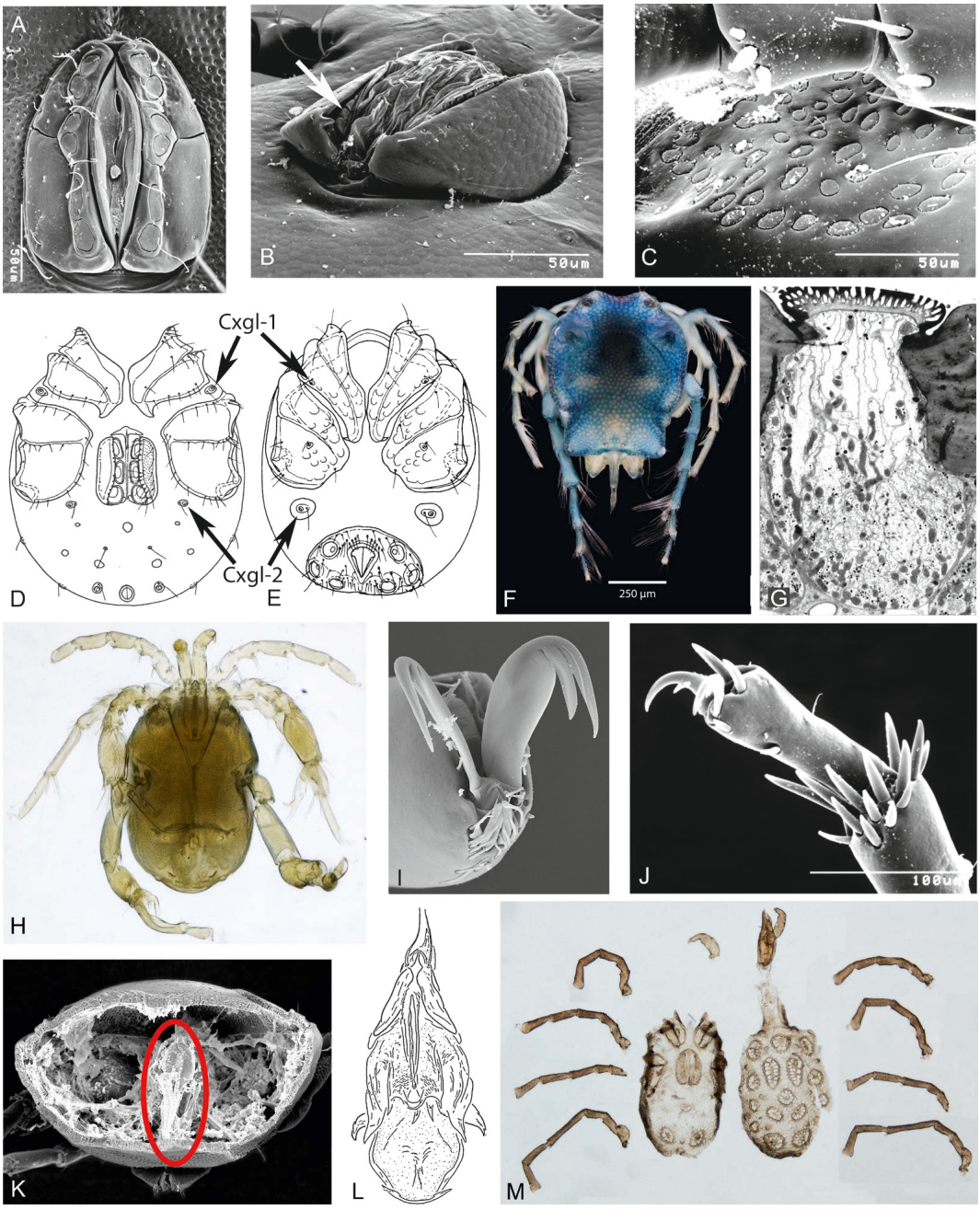


Fig. 3. **A.** *Neomamersa costarriquensis*, male, genital flaps, SEM (Goldschmidt 2004a). **B.** *Guanacastacarus mariae*, male, genital flaps, SEM (arrow pointing at acetabula under genital flap) (Goldschmidt 2004c). **C.** *Neotyrrellia rosemariae*, adult, acetabula field on Cx-IV, SEM (Goldschmidt et al. 1999). **D.** *Sperchon neotropicus*, female, ventral view (arrows pointing at Cxgl-1 and Cxgl-2) (Cook 1980). **E.** *Corticacarus coldomus*, male, ventral view (arrows pointing at Cxgl-1 and Cxgl-2) (Cook 1980). **F.** *Arrenurus* sp., male, dorsal (Montes-Ortiz, unpublished photo). **G.** *Neotyrrellia* sp., adult, cross section through an acetabulum on a genital flap, TEM (Goldschmidt et al. 1999). **H.** Aturidae (undescribed sp.), male, ventral (II-leg and IV-leg modified) (Goldschmidt, unpublished photo). **I.** *Torrenticola pervagata*, adult, terminal claws at I-leg-6, SEM (Goldschmidt 2007). **J.** *Neotyrrellia rosemariae*, male, terminal leg segments at IV-leg (Goldschmidt 2004b). **K.** *Torrenticola* sp., male, cross-section of the idiosoma, view from posterior, SEM (ellipse around genital skeleton in natural position) (Goldschmidt 2007). **L.** *Torrenticola semicolor*, male, genital skeleton, anterior view (Goldschmidt 2007). **M.** *Clathrosperchon* cf. *punctatus*, female, example of the orientation of the body parts of a slide mounted specimen (Goldschmidt, unpublished photo).

photypes could be distinguished alive, 2–3 specimens of each morphotype shall be fixed in 96 % ethanol, all the others in Koenike.

Determination, slide mounting, species description

The determination of genera is often possible without dissection. For the examination of selected character states under the light microscope, undissected mites can be placed on a concavity slide in a drop of glycerine or Koenike's.

However for the determination of unknown species and especially the description and production of types of new species, permanent preparations have to be produced. To do so, dorsal and ventral side of the idiosoma must be separated, the gnathosoma, one palp and the legs (at least of one side) must be detached. The soft body contents need to be removed (very easily in Koenike-fixed mites). For males, the sexual skeleton should be preserved and mounted together with the other body parts.

Dissection is best done in a drop of glycerine or Koenike's in a concavity slide under a stereomicroscope. First remove the legs and one palp and orient them at the edge of the liquid drop, in a way they cannot be mistaken or float around. In completely armoured specimens, dorsum and venter should then be separated by inserting a fine needle or insect pin into the dorsal furrow and 'opening the mite like a tin can'. Afterwards, push out the gnathosoma with a blunt needle. Soft skinned specimens are best cut horizontally (just dorsal to the coxae) with a fine scalpel, after the gnathosoma is removed (if it is not fused with the first coxae). If no important characters are found on the dorsal side, it might be sufficient to remove the gnathosoma and press out the content of the body by means of a blunt needle. If only small series of types are available it might be sensible to record (micro-photo, drawing) the position of smaller platelets, etc. (especially structures at the edge of the idiosoma) before dissecting.

Different mounting media are in use for permanent slides of dissected water mites. Hoyer's medium is soluble in water and has clearing effects, but is very susceptible for drying out if not sealed properly. Euparal provides high stability, but poor optical qualities. The integument of specimens mounted in PVA (recommended by Proctor et al. (2015)), can become too soft to be remounted. Probably the best medium for permanent preparations is glycerine jelly. It is easy to handle and does not bear the risk of drying out. Preparations in glycerine jelly remain in good condition over many decades. However sometimes crystallization can occur, making it difficult to see fine details. Glycerine jelly is liquified at about 50 °C and hardening by lowering the temperature. Only a small amount should be heated at a time because it will not harden anymore when heated too often. For discussion of the different media see Bartsch et al. (2007) as well as Walter & Krantz (2009).

The following instructions for slide preparation refer to glycerine jelly: First spread a thin layer of mounting medium on a cover slip; and then transfer the dissected body parts to the medium and orient them on the coverslip towards the later surface. Generally the legs and the gnathosoma with one remaining palp are oriented flat in lateral view for measurement of the segments and the second palp in medial view. If the chelicera can be removed from the gnathosoma without destruction, position one of each laterally and medially. Position the ventral and dorsal part of the idiosoma beside each other, and orient the genital skeleton in anterior view. Ideally the legs, gnathosomal appendages and other structures should be placed in a natural orientation around the idiosoma; that is with the I-leg close to the anterior end of the idiosoma, the IV-leg close to the posterior end, the mouthparts anterior to the idiosoma, and the genital skeleton posterior (Fig. 3M). If the medium hardens during the orientation of the body parts, it can be liquified by putting the coverslip back on a heating plate for few seconds. After the preparation on the coverslip is hardened, it is picked up with a small drop of liquid medium at the centre of a slide. Hardening can be accelerated by refrigeration. After completely hardening, seal the slide with a ring of lacquer reaching from the coverslip over the glycerin jelly rim to the slide surface and label the specimen. The label should include all relevant data on the location and taxonomy (a good example is given in Walter & Krantz 2009, p. 96).

List of abbreviations used in the keys

Ac-1 to -3	acetabula numbered from anterior to posterior pair
Cx-I to -IV	first to fourth coxae (anterior to posterior)
Cxgl-1, -2	coxoglandularia between Cx-II and Cx-III, posterior to Cx-IV
I-leg-6	first leg, distal segment; I- to IV-leg (anterior to posterior), each with segments 1 to 6 (trochanter, basifemur, telofemur, genu, tibia, tarsus) from proximal to distal
P1 to P5	palpal segments (proximal to distal) (trochanter, femur, genu, tibia, tarsus)
sg.	subgenera
Vgl	ventroglandularia

General key to acari in freshwater habitats

1 Three pairs of legs (Figs 1G, 4A–E). .... **larval mites** [Currently not identifiable in the Neotropics]

1' Four pairs of legs (Figs 1H, 4F–K, 5A–F). .. .. **adults** or **deutonymphs**, 2

2(1') Coxae movable (seven movable leg segments), pair of stigmata on plates dorsolaterally to III-leg or IV-leg; paired claws and unpaired pulvillus (adhesive structure between claws) at the tip of each leg; chelicera

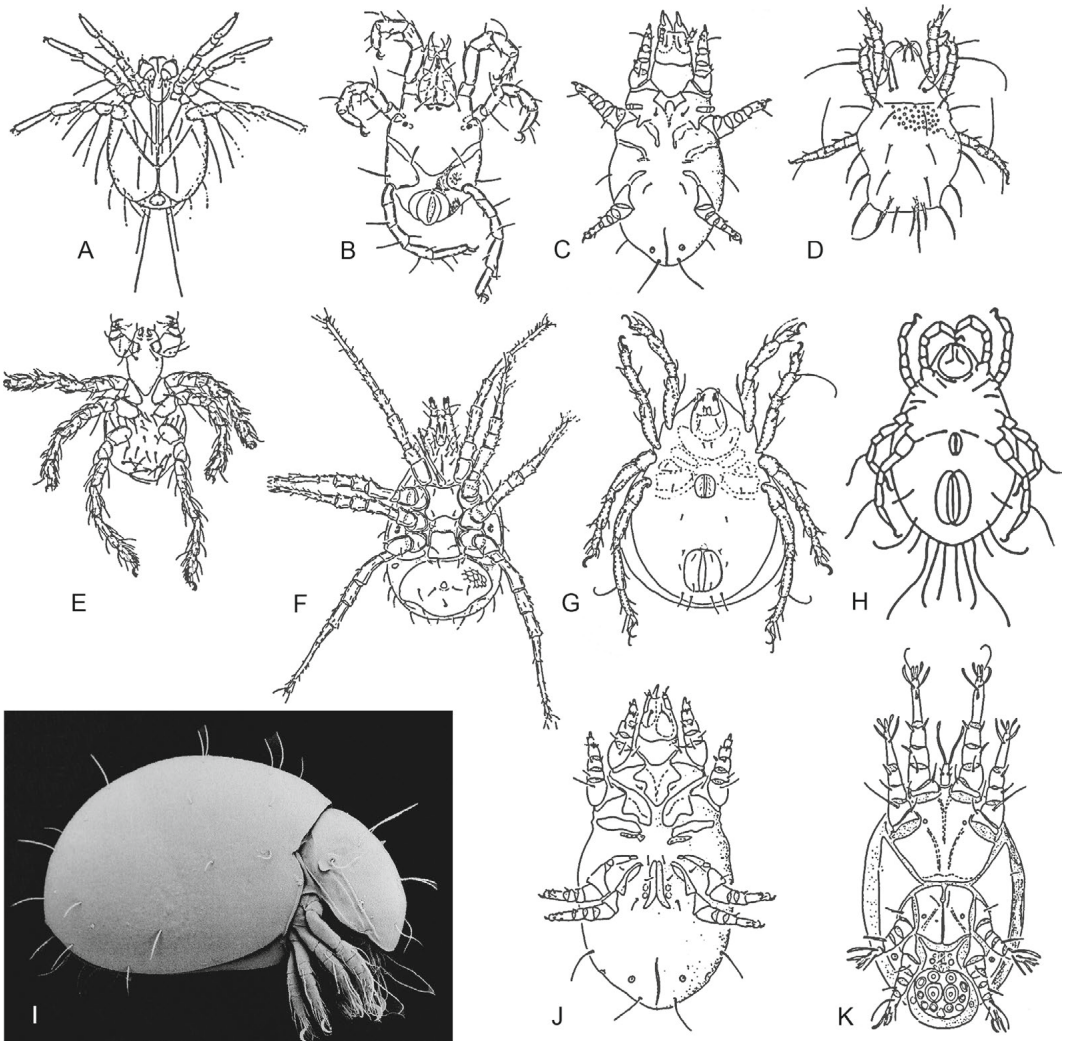


Fig. 4. A. *Arrenurus* sp. (Hydrachnidia), larva, ventral (Gerecke 1994). **B.** *Lobohalacarus weberi* (Halacaridae), larva, ventral (after Bartsch et al. 2007). **C.** *Schwiebea* sp. (Astigmata), larva, ventral (after Bartsch et al. 2007). **D.** *Hydrozetes lemnae* (Oribatida), larva, dorsal (after Bartsch et al. 2007). **E.** *Abrolophus quisquiliarus* (terrestrial Parasitengona), larva, ventral (after Bartsch et al 2007). **F.** Gamasida (Mesostigmata), adult, ventral (after Bartsch et al. 2007). **G.** *Hydrozetes lemnae* (Oribatida), adult, ventral (after Bartsch et al. 2007). **H.** Oribatida nymph. **I.** *Euphthiracarus cooki* (Oribatida), adult, lateral, SEM (Norton et al. 2003). **J.** *Schwiebea* sp. (Astigmata), adult, ventral (after Bartsch et al. 2007). **K.** *Schwiebea* sp. (Astigmata), deutonymph, ventral (after Bartsch et al. 2007).

with well developed pincers (Fig. 4F). .... **Parasitiformes**, one order: **Mesostigmata** [Not treated in the following]

2' Coxae fused to idiosoma (**six** movable leg segments), stigmata if present on anterior area of idiosoma or at gnathosoma; leg claws and chelicera variable. ..... **Acariformes**, 3

3 (2') Legs with one to three claws; prodorsum with bothridium (sensory pit with modified seta); large genital and anal openings, covered by pairs of movable flaps in adults (Fig. 4G,H); adults usually heavily sclerotized (shiny, brownish, hemispherical) (Fig. 4I); juveniles pale with cuticle smooth, wrinkled or with sclerites (Fig. 4H); usually mouthparts not visible in dorsal view (pro-

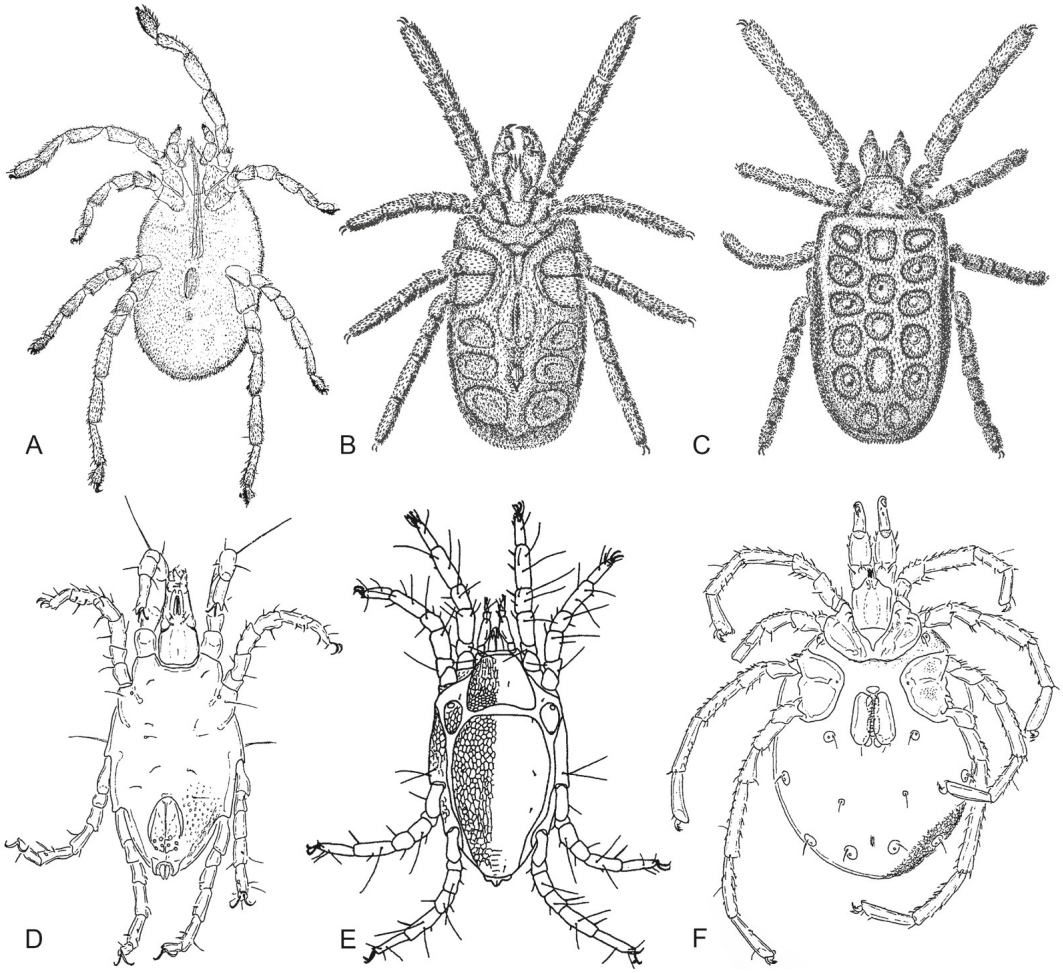


Fig. 5. A. *Abrolophus quisquiliarus* (terrestrial Parasitengona), adult, ventral (after Bartsch et al. 2007). **B.** *Trombella lusitanica* (Trombellidae, terrestrial Parasitengona), adult, ventral (after Walter et al. 2009). **C.** *Trombella lusitanica* (Trombellidae, terrestrial Parasitengona), adult, dorsal (after Walter et al. 2009). **D.** *Lobohalacarus weberi* (Halacaridae), adult, ventral (after Bartsch et al. 2007). **E.** *Porohalacarus alpinus* (Halacaridae), adult, dorsal (after Bartsch et al. 2007). **F.** *Sperchon mutilus* (Hydrachnidia), adult, ventral (after Bartsch et al. 2007).

tected by a projection of prodorsum) (Fig. 4I). ..... **Oribatida** (excluding Astigmatina)

3' Not with the described combination of characters. 4

4 (3') Legs with one claw; prodorsum without bothridium; palps minute (one or two movable segments) or reduced; adults with two pairs of genital papillae (Fig. 4J); adults weakly sclerotized; deutonymph phoretic with a well developed ventral sucker and mouthpieces reduced (Fig. 4K), I-leg and II-leg oriented anteriorly, III-leg and IV-leg posteriorly (Fig. 4J,K). .... **Oribatida**, Cohort: **Astigmatina** [Not treated in the following]

4' Typically legs with two claws; generally with different characters. ..... **Prostigmata**, 5

5 (4') Legs and idiosoma densely covered with setae; typically soft, red, never with swimming setae (Fig. 5A–C). .... **Trombidiae (terrestrial Parasitengona)**

5' Not with the described combination of characters, if soft, red, never densely hirsute. 6

6 (5') Body <1 mm long, pale yellowish, dorsoventrally flattened, rhomboid, mostly with four dorsal and four ventral plates (sometimes fused); I-leg and II-leg bases widely separated from III-leg and IV-leg bases; without swimming setae; palps four-segmented (Fig. 5D,E). .... **Halacaroidea**, one family: **Halacaridae**

6' Body shape variable; legs arranged in a subcircular pattern or gathered at idiosoma anteriormost part; sixteen pairs of glandularia; legs variable, many taxa with swimming setae; palps five-segmented (several segments fused in few taxa) (Fig. 5F). .... **Hydrachnidia, adults** (water mites in the strict sense; only these are treated in the following)

Keys to Neotropical water mites (Hydrachnidia)

Preceding comments

The diagnoses refer to Neotropical representatives of the respective taxa; for other regions, further or different characters may apply.

If only one genus is known from the Neotropical region, it is given in the family key already.

In some cases water mite families comprise a wide array of morphologies; therefore some families appear several times at different steps of the key. If the determination does not seem clear, it might be necessary to check as well the genera keys of similar families.

If not indicated differently, all character description refers to both sexes (when both are known).

As our knowledge of the neotropical water mites fauna is far from complete, the finding of undescribed taxa (as well above species level) – and combination of characters – is possible (or even likely) in any more intense study. Especially in poorly studied habitats, like interstitial, springs, phytotelmata, etc.

The data on diversity and distribution given for the individual genera are compiled from Rosso de Ferradás & Fernández (2005) (checklist South America), K. O. Viets (1987) (world catalogue), new taxa database on http://www.watermite.org/ (2019) and an unpublished database (Neotropical water mite records) of the senior author. References not included in Rosso de Ferradás & Fernández (2005) or K. O. Viets (1987) are given. Only data referring to the Neotropical diversity and distribution are given – several genera occur in other regions (Nearctic, Australis, etc.) as well. In some cases, the sole record of certain genera for certain countries is only based upon genera lists in ecological publications or rough faunal lists (e.g. Camacho et al. 1997, Goldschmidt 2004d, Goldschmidt et al. 2015, Goldschmidt et al. 2016). These references are given as well.

Revisions of systematic assignment are given for all changes after K. O. Viets (1987). In general the most recent taxonomic revisions in Smit (2020) are followed.

Habitat data are compiled from the literature and personal observation, the main habitat is given first, if just one sample site is known, the habitat is given in singular. 'Running waters' refers to streams and rivers of various size, whereas 'streams' refers to mainly small running water bodies. In most publications/samples the interstitial is not separated from stream benthos – therefore the habitat 'interstitial' is only given, if explicitly mentioned in the publication or known from ecological studies.

Key to families

1 Mostly marine (up to 70 m depth), sometimes in costal fresh water; suture line between Cx-III and -IV extending postero-medially, coxae **not** separated in anterior and posterior groups, Cx-III, -IV with two pairs of slender posterior apodemes (Figs 6A, 18A,C,E,F); Ac wheel-like, far from gonopore (Figs 6A,E, 18A,B). .... **Hygrobatoidea** (in part), **Pontarachnidae**, Koenike, 1910

1' Living in fresh water; Ac never wheel-like, mostly with Ac in, beside or near gonopore region (Fig. 3A,B,D,E), if no Ac in gonopore region, Ac very small, idiosoma very soft or flattened, coxae generally separated in anterior and posterior groups (Fig. 6B,N); Cx-IV generally without two pairs of elongated posterior apodemes, if larger apodemes present, Ac grouped beside gonopore. 2

2 (1') Ac small and inconspicuous, lying on Cx-IV; suture lines between Cx-III and -IV extending postero-laterally (Fig. 6B); dorsum with a large central plate surrounded by a mid-sized anterior platelet and several small lateral platelets (Fig. 6C); idiosoma small, dorsoventrally flattened. .... **Hydrovolzioidea**, **Hydrovolziidae** Thor, 1905, ***Hydrovolzia*** Thor, 1925
[One undescribed species. Mexico (Cramer 1988). Habitat: small stream]

2' Ac conspicuous, associated with gonopore (Fig. 3A,B,D,E) (by far most taxa) or scattered in ventral integument (Fig. 6N) (in this case, idiosoma large, soft); if Ac on Cx-IV (Fig. 3C), as well Ac on genital flaps (Figs 32E, 33G); if dorsum with large central and mid-sized anterior plate, suture lines between Cx-III and -IV **not** extending postero-laterally and Ac on genital plates or flaps. 3

3 (2') Idiosoma nearly spherical; genital field cordate, most Ac anterior to gonopore, Cx-IV wider than other coxae (Fig. 6D,H); dorsum with one large plate or one or two pairs of smaller platelets between and posterior to the eyes (Fig. 6F–H); palp chelate, P1 very long (P1 > P2), P3 longer than P4 (Fig. 6J); chelicera one-segmented, rostrum long, slender (Fig. 6K). .... **Hydrachnoidea**, **Hydrachnidae** Leach, 1815, ***Hydrachna*** Müller, 1776
[Thirteen described species. Mexico (Cramer & Costero 1985, Galicia-Alcantara 1991), Guatemala, Costa Rica, Curaçao, Aruba, Venezuela, Suriname, Brazil, Peru, Chile, Paraguay, Argentina, Uruguay. Key to South American species in Lundblad (1941). Habitat: permanent and temporary ponds, occasionally in lakes and slowly running waters]

3' Genital field generally not cordate as described, if Cx-IV wider than other coxae, palp not chelate, or, if chelate, P4 > P3, P2 > P1; chelicera 2-segmented. 4

4 (3') Eyes just about one eye-width apart, lateral eye capsules medially fused with common frontal sclerite (Fig. 6I,M,P); Ac tiny, free in ventral integument (Fig. 6N); mouth opening surrounded by large circular membranous fringe (Figs 1L, 6O,L); soft bodied, large, reddish mites. ..... **Eylaoidea**, 5

4' Eyes at least two eye-widths apart; capsules of lateral eyes, if present, not in a common frontal sclerite (e.g. Figs 2F, 8N, 9G); mouth opening without or with very small membranous fringe; wide array of colours and degree of sclerotization. 6

5 (4) Eye plate characteristically "eyeglass-shaped" (Fig. 6M,P), as wide as long or wider; Cx-III and Cx-IV scarcely fused medially (Fig. 6N); body more or less rounded. .... **Eylaidae** Leach, 1815

5' Eye plate by far longer than wide (Fig. 6I); Cx-III and Cx-IV broadly fused; body elongated. ..... **Limnocharidae** Grube, 1859

6 (4') Palp chelate, P4 dorso-distal protrusion reaching to P5 apex (Fig. 7A); genital flaps with many Ac; coxae with long setae (Fig. 7C); lateral eyes separated on respective sides, bearing lenses but not in capsules. ..... **Hydryphantoidea** (in part), **Hydrodromidae** Viets, 1936, ***Hydrodroma*** Koch, 1837
[Six described species. Mexico, Cuba, Dominican Republic, Honduras (Wiles 2005), Costa Rica, Panama (Goldschmidt et al. 2016), Venezuela, Colombia, Suriname, Ecuador (unpublished data), Brazil, Bolivia, Peru, Chile, Paraguay, Argentina. Key to South American species in Lundblad (1941, 1953). Habitat: all types of standing waters, pools in streams, streams, springs]

6' Palp not chelate (e.g. Fig. 8H) **or** if chelate with P4 dorso-distal protrusion extended only slightly beyond insertion of P5 (Fig. 7B); coxae not with many long setae; lateral eyes variable, Ac variable. 7

7 (6') Palp chelate (Fig. 7B) **or** P4 with strong dorso-distal seta (Fig. 20L,M) **and** often with idiosoma soft and elongated (Fig. 7D), **or** several Ac stalked (Figs 19C,D, 20D) (in some *Neocalonyx* from South America, Ac not stalked (Figs 19M, 20C), palp hardly visible as chelate). .... **Hydryphantoidea** (in part), **Hydryphantidae** Piersig, 1896

7' Palp not chelate, if P4 with robust dorsodistal seta, then idiosoma not elongated, Ac not stalked. 8

8 (7') Three to six pairs of Ac close together in two rows besides gonopore, **between** or **under** movable genital flaps (Fig. 7E) (if there are rows of 15–50 Ac at inner margin of genital flaps (Fig. 7F) see male of Rheolimnesiinae Goldschmidt, 2004, Hygrobatoidea, Limnesiidae Thor, 1900). ..... **Lebertioidea**, 9

8' Three to many Ac **on** immovable genital plates or movable genital flaps, or in membranous integument besides gonopore, between genital plates (fused with ventral shield) (e.g. Figs 3A, 7G–K). .... **Hygrobatoidea**, **Arrenuroidea**, **Hydryphantoidea (in part – Rhynchohydracaridae** Lundblad, 1936, **Thermacaridae** Sokolow, 1927), 13

9 (8) Dorsal and ventral shield present; dorsal shield with large central plate and two or four anterior smaller platelets (rarely fused with posterior plate, but then suture lines (in

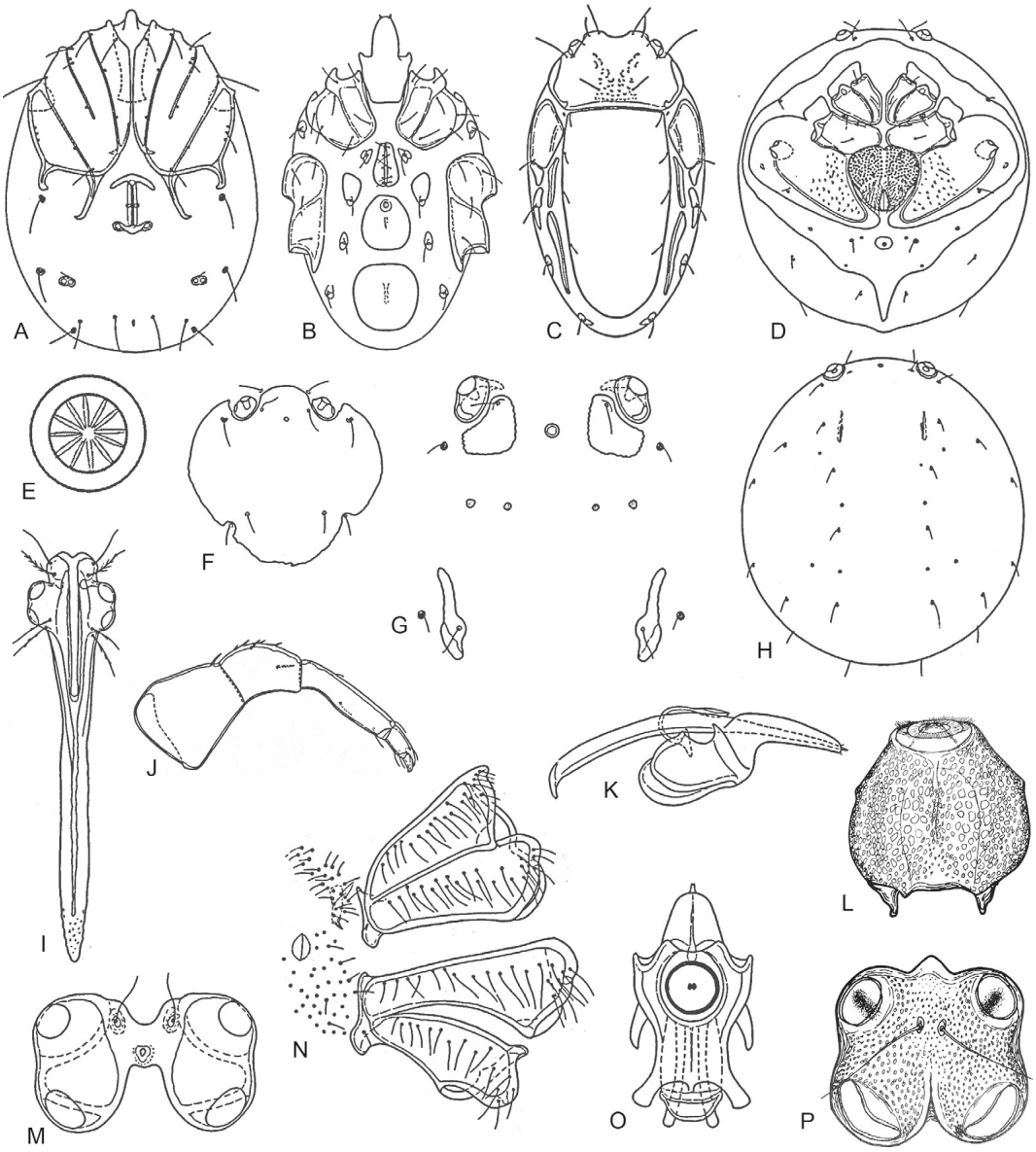


Fig. 6. A. *Pontarachna nemethi*, male, idiosoma ventral (after Walter et al. 2009). **B.** *Hydrovolzia marshallae*, female, idiosoma ventral (Cook 1974). **C.** *Hydrovolzia marshallae*, female, idiosoma dorsal (Cook 1974). **D.** *Hydrachna guanajuatensis*, male, idiosoma ventral (Cook 1980). **E.** *Pontarachna nemethi*, male, wheel-like acetabulum (after Walter et al. 2009). **F.** *Hydrachna kloomi*, male, antero-dorsal plate, eyes (Cook 1974). **G.** *Hydrachna miliaria*, female, antero-dorsal sclerites, eyes (Cook 1980). **H.** *Hydrachna rotunda*, male, idiosoma dorsal (Cook 1980). **I.** *Rhyncholimnochares expansiseta*, male, ocular plate (Cook 1980). **J.** *Hydrachna miliaria*, female, palp (Cook 1980). **K.** *Hydrachna mexicana*, female, capitulum with chelicera (Cook 1980). **L.** *Rhyncheylais connexa*, male, capitulum (Cook 1974). **M.** *Eylais* sp., deutonymph, ocular plate (Cook 1980). **N.** *Eylais multispina*, deutonymph, left coxal groups (Cook 1980). **O.** *Eylais mexicana*, male, ventral view of capitulum (Cook 1980). **P.** *Rhyncheylais connexa*, male, ocular plate (Cook 1974).

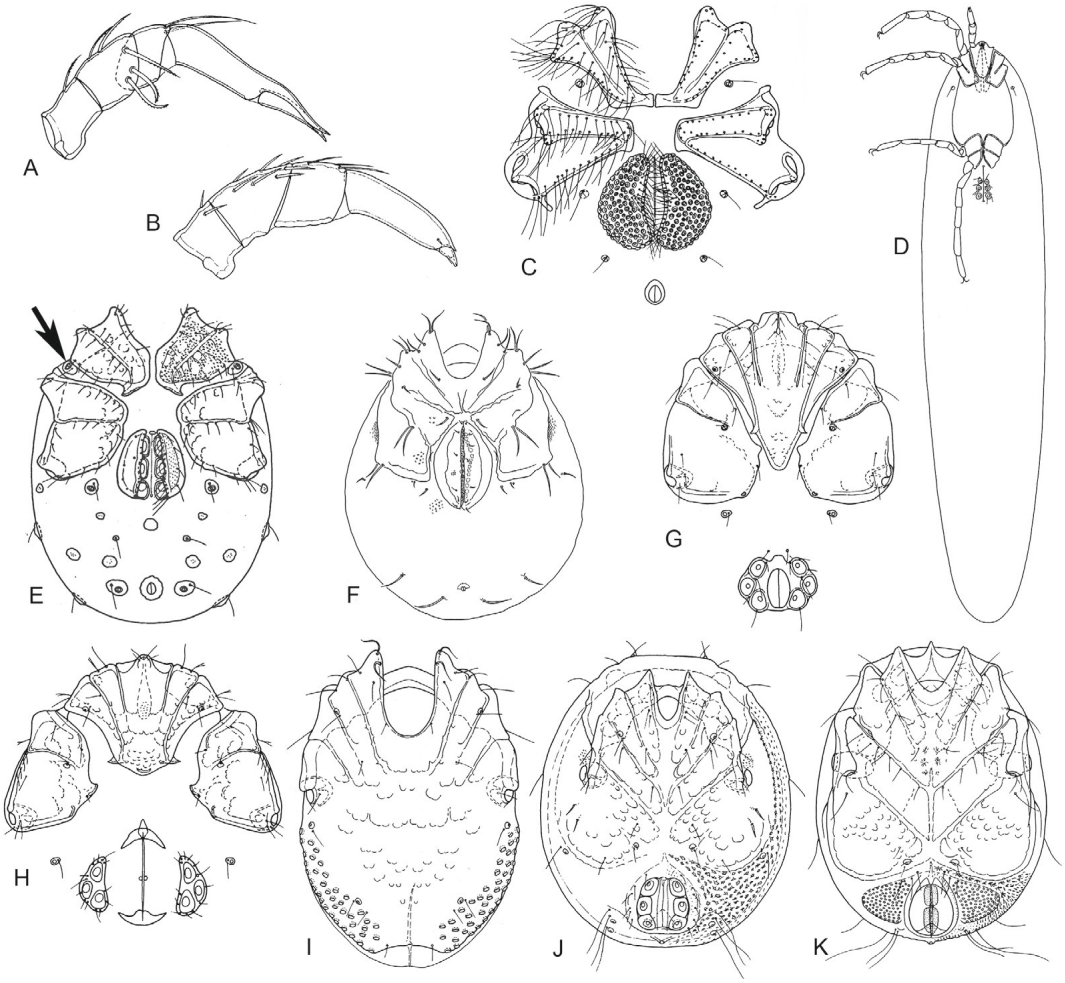


Fig. 7. A. *Hydrodroma peregrina*, female, palp (Cook 1980). **B.** *Hydryphantes jujuyensis*, female, palp (Cook 1980). **C.** *Hydrodroma peregrina*, female, coxae and genital field (Cook 1980). **D.** *Wandesia* (*Pseudowandesia*) *vermiformis*, female, idiosoma ventral (Cook 1974). **E.** *Sperchon neotropicus*, male, idiosoma ventral (arrow pointing at Cxgl-1) (Cook 1980). **F.** *Guanacastacarus mariae*, male, idiosoma ventral (Goldschmidt 2004). **G.** *Hygrobates corkelus*, male, coxae, capitulum and genital field (Cook 1980). **H.** *Hygrobates blatolus*, female, coxae, capitulum and genital field (Cook 1980). **I.** *Kongsbergia globipalpis*, female, idiosoma ventral (Cook 1980). **J.** *Mideopsis* (*Mideopsis*) *pacrodactylus*, female, idiosoma ventral (Cook 1980). **K.** *Stygarrenurus golfitensis*, female, idiosoma ventral (Cook 1980).

general) still evident) (Figs 1B,I, 8B,C); six pairs of Ac; ventral shield with characteristic Y-shaped suture from genital field to tips of Cx-I (Fig. 8A); (in *Testudacarus* (see below) central dorsal plate surrounded by small platelets, three pairs of Ac, Y-shaped suture unclear (Fig. 21B,C)). .... **Torrenticolidae** Piersig, 1902 [A key to South American species is given in Lundblad (1953)]

9' Dorsum soft or with single isolated platelets or with uniform shield; generally three pairs of Ac (in some genera largely increased); if ventral shield with Y-shaped suture (Fig. 8D,M), not with the described dorsal plates. 10

10 (9') Dorsal shield absent; laterally compressed, coxae reaching far towards dorsum; all legs inserted far anterior, fourth legs insertion not visible ventrally (Figs 8E–G,K,L, 21L);

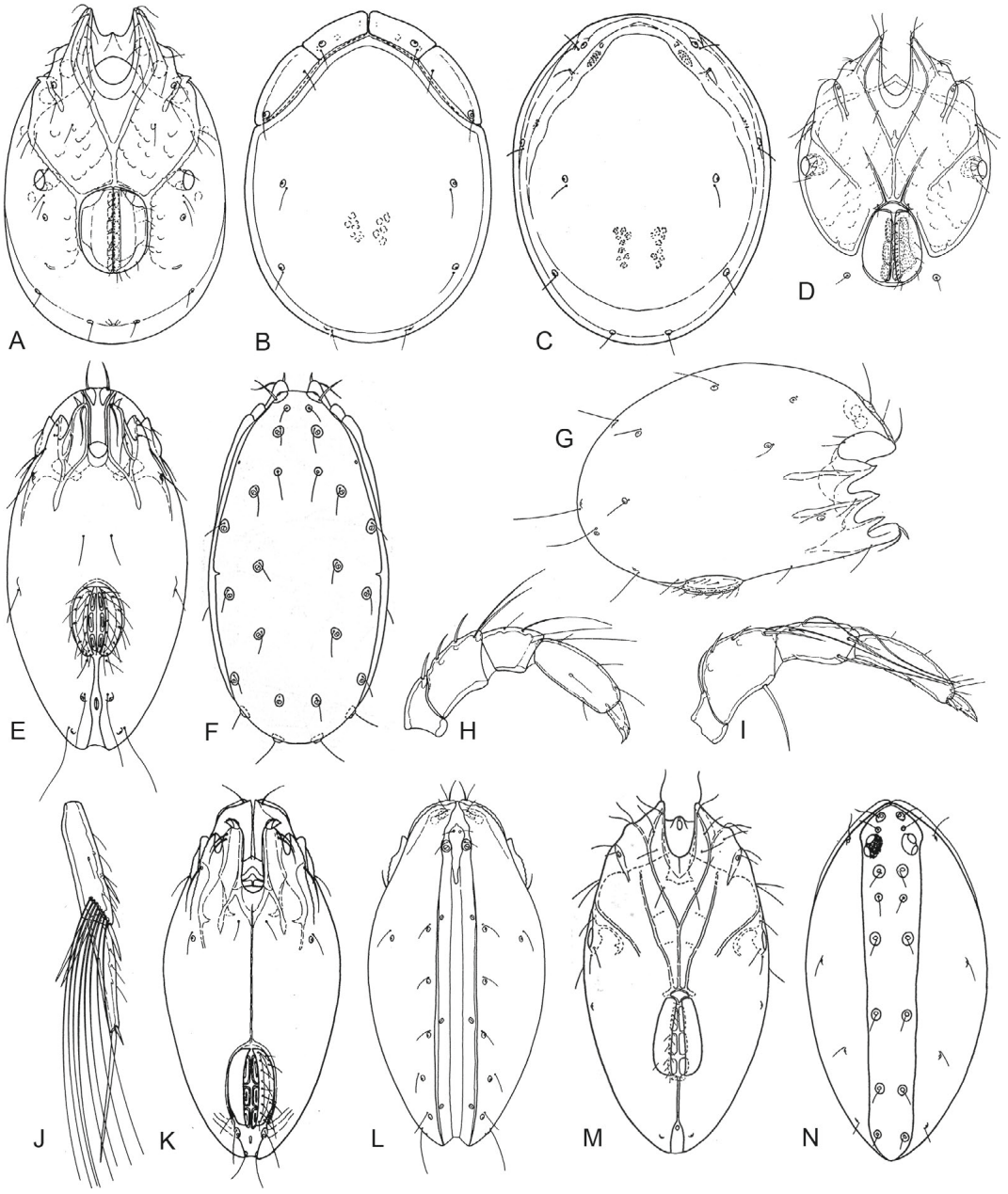


Fig. 8. A. *Torrenticola amala*, male, idiosoma ventral (Cook 1980). **B.** *Torrenticola amala*, male, idiosoma dorsal (Cook 1980). **C.** *Monatractides golfitensis*, male, idiosoma dorsal (Cook 1980). **D.** *Lebertia azteca*, female, idiosoma ventral (Cook 1980). **E.** *Oxus* (*Oxus*) *mesoamericana*, female, idiosoma ventral (Cook 1980). **F.** *Oxus* (*Oxus*) *dugesi*, male, idiosoma dorsal (Cook 1980). **G.** *Oxus* (*Oxus*) *mesoamericana*, female, idiosoma lateral (Cook 1980). **H.** *Oxus* (*Oxus*) *stolli*, female, palp (Cook 1980). **I.** *Lebertia azteca*, female, palp (Cook 1980). **J.** *Oxus* (*Oxus*) *mesoamericana*, female, IV-leg-5/-6 (Cook 1980). **K.** *Oxus* (*Flabellifrontipoda*) *neotropica*, male, idiosoma ventral (Cook 1980). **L.** *Oxus* (*Flabellifrontipoda*) *parva*, male, idiosoma dorsal (Cook 1980). **M.** *Lebertia montanus* female, idiosoma ventral (Cook 1974). **N.** *Lebertia montanus* female idiosoma dorsal (Cook 1974).

IV-leg-6 without claws (Fig. 8J); P2 and P3 without ventral protrusions or setae (Fig. 8H). ..... **Oxidae** Viets, 1926

10' Legs not shifted to anterior; if laterally compressed, not with the described combination of characters, specially not with Ac between or under movable flaps. 11

11 (10') Coxae fused, forming characteristic ventral plate with Y-shaped suture from genital field rostral to tips of Cx-I; suture between Cx-II and Cx-III incomplete (Fig. 8D,M); P2 with long disto-ventral seta; P3 with five to seven long medial setae (Fig. 8I); idiosoma soft. ... . **Lebertiidae** Thor, 1900, ***Lebertia*** Neuman, 1880
[Two described species. Mexico, Guatemala, Honduras (Wiles 2005), Costa Rica, Panama (Goldschmidt et al. 2016). Habitat: streams]
Note: The genus *Estelloxus* Habeeb, 1963, erected for a group of species with laterally compressed idiosoma and coxae extended far to the dorsal surface (Fig. 8M,N), has been synonymized with *Lebertia* by Gerecke (2009).

11' Suture between Cx-II and Cx-III complete, anterior and posterior coxal groups often well separated; P2 and P3 without setae described above; idiosoma soft or sclerotized 12

12(11') IV-leg-6 with claws; lateral eyes in capsules (Fig. 22B–E); coxae (generally) in four separated groups (Figs 7E, 22A,F), various degrees of sclerotizations may be present ventrally (including fusion of coxal groups), but never with complete ventral shield (Fig. 22E,G,H). .... **Sperchontidae** Thor, 1900

12' IV-leg-6 often without claws; lateral eyes separated, not in capsules (Fig. 24D); coxae fused, often forming complete ventral shield (Figs 9H, 23E) (**if** IV-leg-6 with claws, then with complete ventral shield). .... **Anisitsiellidae** Koenike, 1910
[Key to South American species in Lundblad (1941)]

13 (8') Many Ac on movable flaps; posterior coxae clearly longer than wide (Figs 3M, 9A,C); palps without protrusions or tubercles (Figs 3M, 9I); in most species, idiosoma covered by characteristic reticulate platelets (Figs 2J, 3M, 9A,B), or closely fitting porous platelets (Fig. 9C,D), or (in some undescribed species) platelets largely reduced to chitinous clasps or muscle attachment knobs, but with reticulate pattern under integument (in the Central American species capitulum attached to protrusible trunk-like tube (Fig. 3M)). .... **Hydryphantoidea** (in part), **Rhynchohydracaridae** Lundblad, 1936

13' Not with the described combination of characters. 14

14 (13') Complete dorsal and ventral shield (Fig. 9F,E); numerous Ac postero-lateral to genital valves, six to eleven pairs of Ac between genital valves beside gonopore, genital valves with many long setae (Fig. 9E,J); numerous setae postero-lateral to camerostome on medially fused Cx-I (Fig. 9E); P2 medio-distally with two long, bi- or trifurcate setae (Fig. 9K). .... **Thermacaridae** Sokolow, 1927 (only known from hot springs), ***Thermacarus*** Sokolow, 1927
[One described species: *T. andinus* Martin & Schwoerbel, 2002. Bolivia, Chile (Martin & Schwoerbel 2002). Habitat: thermal springs]

14' Not with the described combination of characters. 15

15 (14') Idiosoma soft and (more or less) elongated (Fig. 2A,B,H); coxae close together, but not fused, far anterior; posterior coxal groups characteristically shaped: Cx-IV small, posteriorly rounded (Figs 2H, 10G,H); Ac three pairs to numerous, on two plates in female (Figs 2H, 10G), on one plate in male (Fig. 10H,I); P4 ventrally or ventro-distally with peg-like to dentiform seta (Fig. 10M). ..... **Omartacaridae** Cook, 1963

15' Not with the described combination of characters. 16

16 (15') Ac numerous; coxal field completely separated medially, Cx-IV reduced, medial margin reduced to medial angles, not reaching midline; no glandularia on Cx-III or -IV; insertions of IV-legs with projections (Fig. 10A,C); P2 with disto-ventral projection (Fig. 10J); no swimming setae; **male**: complete dorsal and ventral shield (Fig. 10A,B); Cx-III extending far posteriorly; gonopore shifted far towards anterior to base of capitulum (Fig. 10A); **female**: without dorsal and ventral shield, dorsum with five large platelets (Fig. 10C,D); Cx-III less extended than in male; capitulum posteriorly elongated (Fig. 10C). .... **Ferradasiidae,** ***Ferradasia*** Cook, 1980

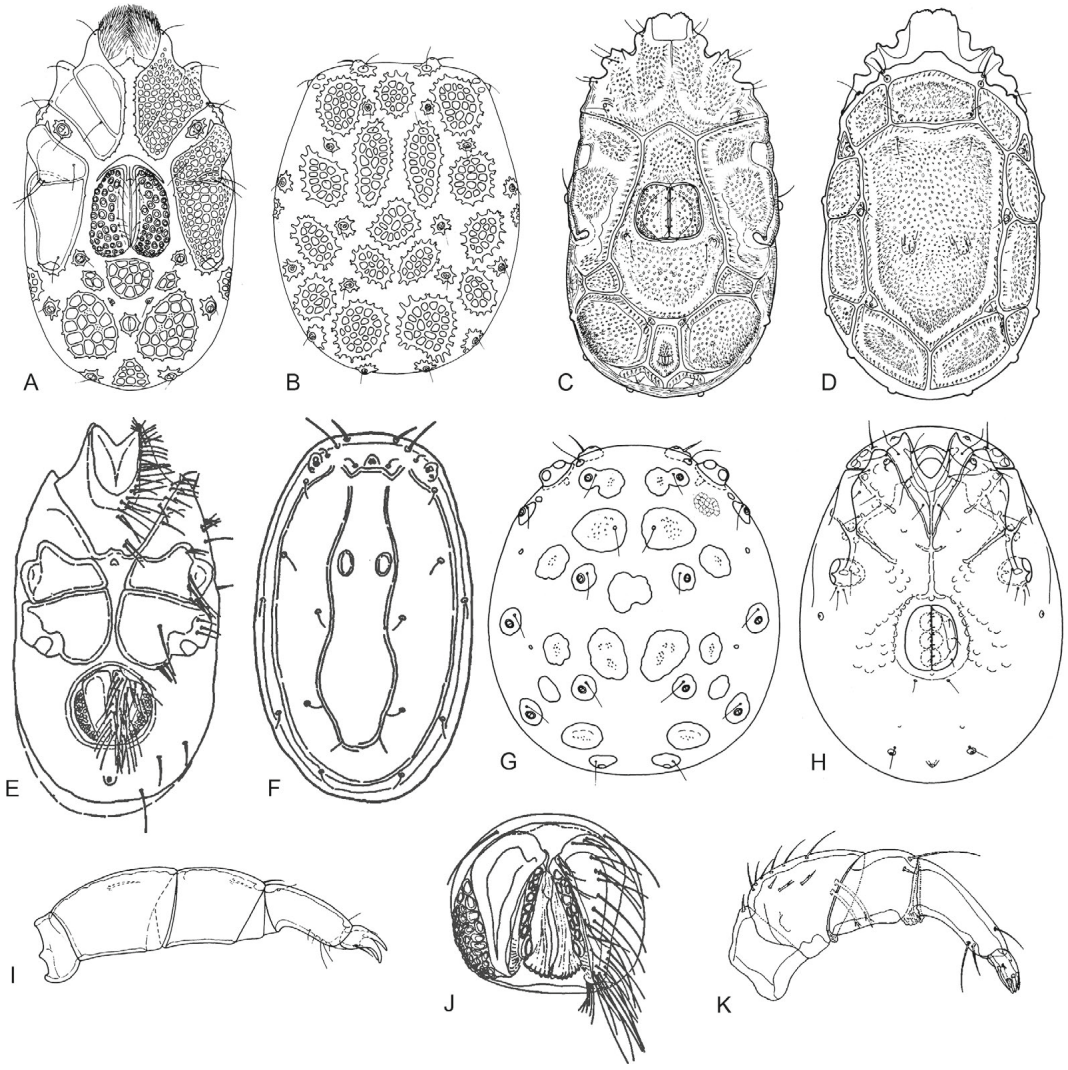


Fig. 9. A. *Clathrosperchon punctatus*, female, idiosoma ventral (Cook 1980). **B.** *Clathrosperchon punctatus*, female, idiosoma dorsal (Cook 1980). **C.** *Rhynchohydracarus testudo*, male, idiosoma ventral (Cook 1974). **D.** *Rhynchohydracarus testudo*, male, idiosoma dorsal (Cook 1974). **E.** *Thermacarus andinus*, male, idiosoma ventral (after Martin & Schwoerbel 2002). **F.** *Thermacarus andinus*, male, idiosoma dorsal (after Martin & Schwoerbel 2002). **G.** *Sperchon neotropicus*, male, idiosoma dorsal (Cook 1980). **H.** *Anisitsiellides lundbladi*, male, idiosoma ventral (Cook 1980). **I.** *Clathrosperchon punctatus*, female, palp (Cook 1980). **J.** *Thermacarus andinus*, male, genital field (genital flaps opened, setae of left side omitted) (after Martin & Schwoerbel 2002). **K.** *Thermacarus andinus*, male, palp medial (after Martin & Schwoerbel 2002).

[One described species: *F. musicola* Cook, 1980. Argentina. Habitat: streams]

16' Not with the described combination of characters. 17

17 (16') Palp uncate, stocky (Figs 10K, 11G) (do not confuse with ventral projection at P4 (like in *Neoacarus*, and some *Mideopsis*, Fig. 27I); complete dorsal and ventral armour (Fig. 10E,F). 18

17' Palp **not uncate** (Fig. 10L), idiosoma soft or armoured. 23

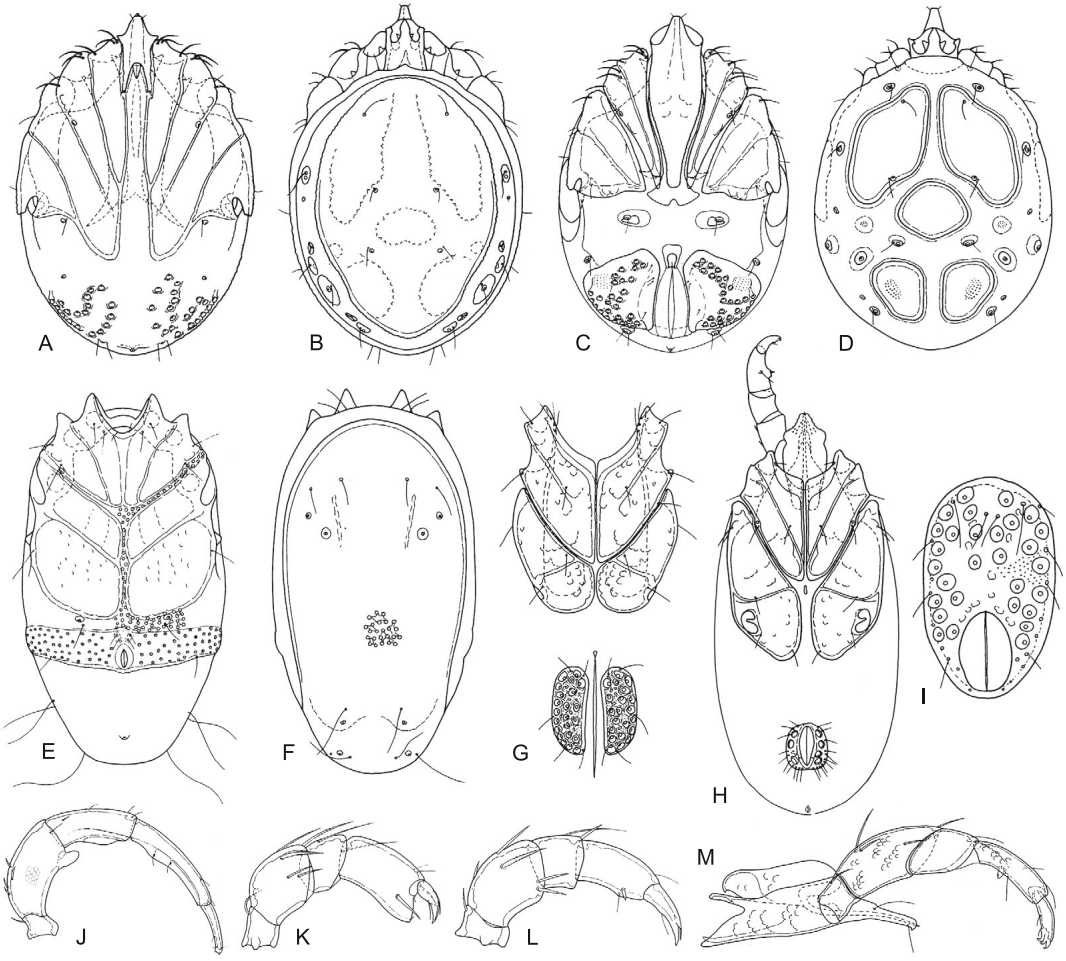


Fig. 10. A. *Ferradasia musicola*, male, idiosoma and capitulum ventral (Cook 1980). **B.** *Ferradasia musicola*, male, idiosoma dorsal (Cook 1980). **C.** *Ferradasia musicola*, female, idiosoma and capitulum ventral (Cook 1980). **D.** *Ferradasia musicola*, female, idiosoma dorsal (Cook 1980). **E.** *Arrenurus yartesus*, male, idiosoma ventral (Cook 1980). **F.** *Arrenurus yartesus*, male, idiosoma dorsal (Cook 1980). **G.** *Omartacarus motasi*, female, coxae and genital field (Cook 1980). **H.** *Maharashtracarus neotropicus*, male, idiosoma, capitulum and right palp ventral (Cook 1980). **I.** *Omartacarus motasi*, male, genital field (Cook 1980). **J.** *Ferradasia musicola*, female, palp (Cook 1980). **K.** *Arrenurus birgei*, male, palp (Cook 1980). **L.** *Micruracaropsis phytotelmaticola*, male, palp (Cook 1974). **M.** *Omartacarus* sp., deutonymph, capitulum, chelicera, right palp, lateral view (Cook 1980).

18 (17) Three to **five** pairs of Ac, **in both sexes** in membranous region besides gonopore (Fig. 11A,B,D). 19

18' Ac numerous, at least in females **not** in membranous region besides gonopore (Fig. 11F). 21

19 (18) Median margins of Cx-IV **not** reduced to median angle, but rather long; Cxgl-2 located close together, **near** suture between Cx-III and -IV (Fig. 11B); dorsal and ventral shields punctate (with small pores); dorsal shield with four pairs of glandularia (one at anterior edge of dorsal shield) (Fig. 11C). ... . **Chappuisididae (Neotropical species)**, ***Chappuisides*** Szalay, 1943
[One described species: *C. notialis* Cramer & Smith, 1991. Mexico (Cramer & Smith 1991). Habitat: streams, springs]

19' Median margins of Cx-IV reduced to median angle; Cxgl-2 incorporated in the median margins of Cx-IV, close to Cx-III; tight-

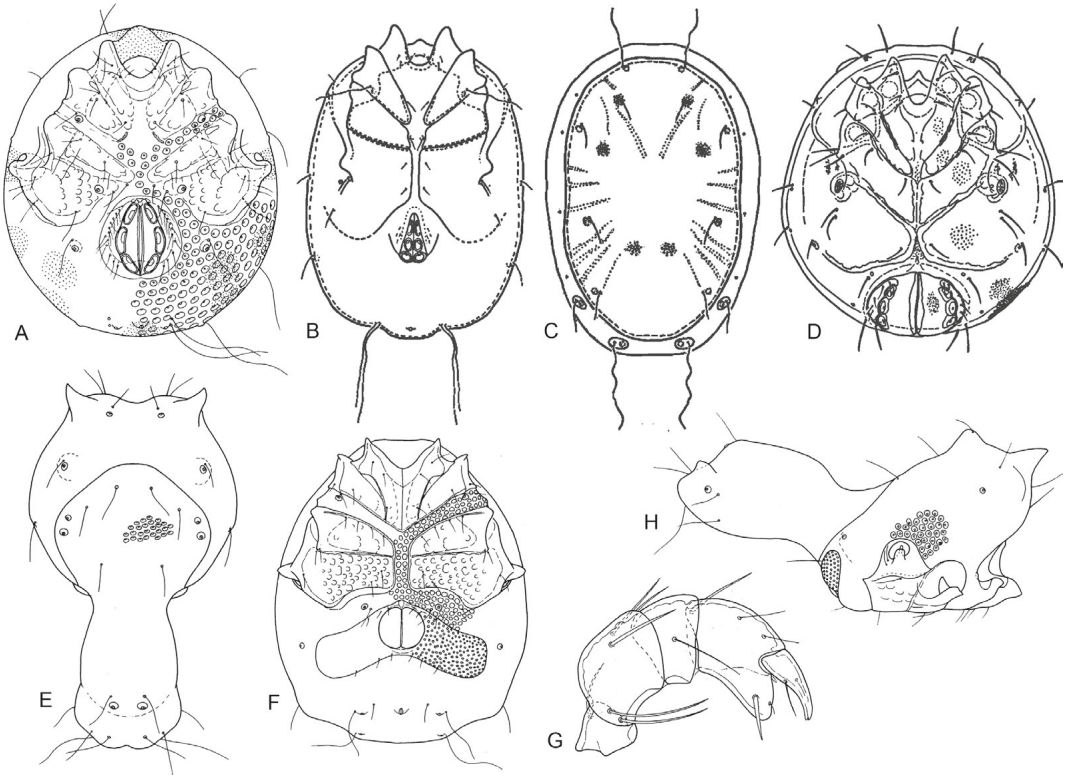


Fig. 11. **A.** *Geayia mansionensis*, female, idiosoma ventral (Cook 1980). **B.** *Chappuisides notialis*, male, idiosoma ventral (after Cramer & Smith 1991). **C.** *Chappuisides notialis*, male, idiosoma dorsal (after Cramer & Smith 1991). **D.** *Phreatomideopsis arrenuripalpis*, female, idiosoma ventral (after Schwoerbel 1986). **E.** *Arrenurus trassamus*, male, idiosoma dorsal (Cook 1980). **F.** *Arrenurus valdiviensis*, female, idiosoma ventral (Cook 1980). **G.** *Krendowskia moyara*, male, palp (Cook 1980). **H.** *Arrenurus zitavus*, male, idiosoma lateral (Cook 1980).

ly fitting dorsal and ventral shields often with large pores (Fig. 11A). 20

20 (19') Insertions of IV-legs with well developed condyles (Fig. 11A); P2 often with two long ventral setae (Fig. 11G); capitulum in some genera attached to protrusible tube, if no tube present, P2 always with two long ventral setae; dorsal and ventral shields with large pores; three to five pairs of Ac (Fig. 11A). ..... **Krendowskiidae** Viets, 1926 [A key to South American species is given in Lundblad (1943b)]

20' Insertions of IV-legs without well developed condyles (Fig. 11D); P2 without long ventral setae (Fig. 27F); capitulum not attached to protrusible tube; three pairs of Ac (Fig. 11D). ..... **Mideopsidae** Koenike, 1910 (in part), **Mideopsinae** (**in part**) (*Mideopsella*, *Phreatomideopsis*)

21 (18') Numerous Ac on laterally extended plates (Fig. 11F,H), no Ac in the membranous region besides gonopore; suture between ventral and dorsal shield in general far dorsally (except *Thoracophoracarus*); cauda of male often modified (Fig. 11E,H); medial margin of Cx-IV generally present, not reduced to medial angle (Fig. 11F). .... **Arrenuridae** Thor, 1900 (**in part**)

21' Ac numerous, **male**: several Ac in membranous region besides gonopore (Fig. 12A,I), or on heart-shaped plates (Fig. 12C); **female**: on plates flanking or partly surrounding the gonopore (Fig. 12B,D,J); dorsal furrow generally further lateral (in "normal" position) (Fig. 25F–H); no cauda in male; medial margin of Cx-IV reduced to medial angle (Fig. 12A–D), or coxae medially fused (Fig. 12I,J). 22

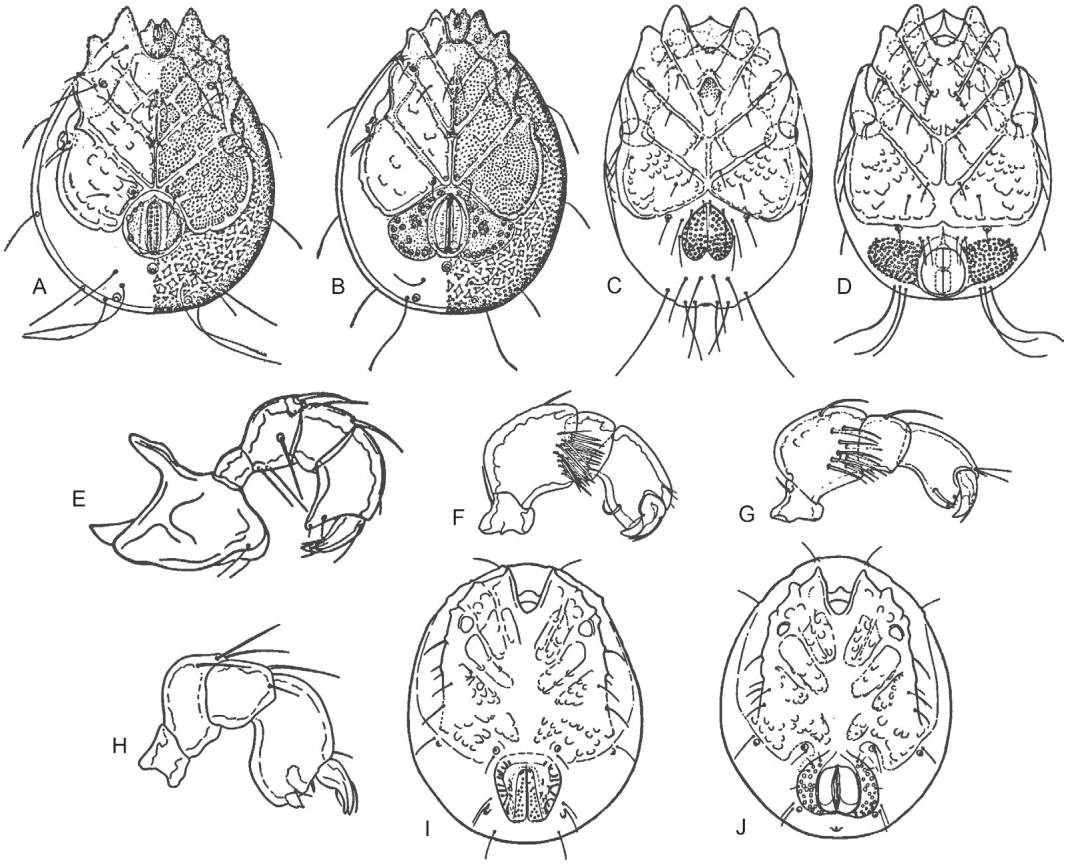


Fig. 12. **A.** *Cubanohydracarus elegans*, male, idiosoma and capitulum ventral (after Orghidan & Gruia 1980). **B.** *Cubanohydracarus elegans*, female, idiosoma and capitulum ventral (after Orghidan & Gruia 1980). **C.** *Stygarrenurus armoniensis*, male, idiosoma ventral (after Cramer & Cook 1996). **D.** *Stygarrenurus armoniensis*, female, idiosoma ventral (after Cramer & Cook 1996). **E.** *Cubanohydracarus elegans*, male, capitulum, palp lateral (after Orghidan & Gruia 1980). **F.** *Stygarrenurus golfitensis*, female, palp medial (Cook 1980). **G.** *Stygarrenurus armoniensis*, male, palp medial (after Cramer & Cook 1996). **H.** *Plaumannia arrenuripalpis*, male, palp lateral (Cook 1974). **I.** *Plaumannia arrenuripalpis*, male, idiosoma ventral (Cook 1974). **J.** *Plaumannia arrenuripalpis*, female, idiosoma ventral (Cook 1974).

22 (21') Anterior coxae projecting beyond idiosoma; median margins of Cx-IV reduced to median angle (Fig. 12A–D); P2 with two heavy ventral setae (Fig. 12E) or medio-distal patch of thickened setae (Fig. 12F,G). .... **Hungarohydracaridae** Motaş & Tanasachi, 1959

22' Anterior coxae not projecting; median margins of Cx-IV not reduced to median angle (all coxae medially fused) (Fig. 12I,J); P2 without heavy ventral setae or medio-distal patch of thickened setae, P4 with short, thick seta ventro-distally (Fig. 12H). .... **Mideopsidae** Koenike, 1910 (**in part**), **Plaumanniinae** Lundblad, 1936, ***Plaumannia*** Lundblad, 1936

[Two described species: Brazil, Paraguay. Key to species in Lundblad (1943b). Cook (1986) shifted Plaumanniinae from Athienemanniidae to Mideopsidae. Habitat: streams, springs]

23 (17') Palp not uncate (Fig. 10L), apart from this with the characters of the Arrenuridae: suture between ventral and dorsal shield far dorsally, Ac on wing-like plates, male with short cauda (Fig. 13A–C). .... **Arrenuridae** Thor, 1900 (**in part**), ***Micruracaropsis*** Viets, 1939

[One described species: *M. phytotelmaticola* (Viets, 1939). Suriname. Habitat: phytotelmata]

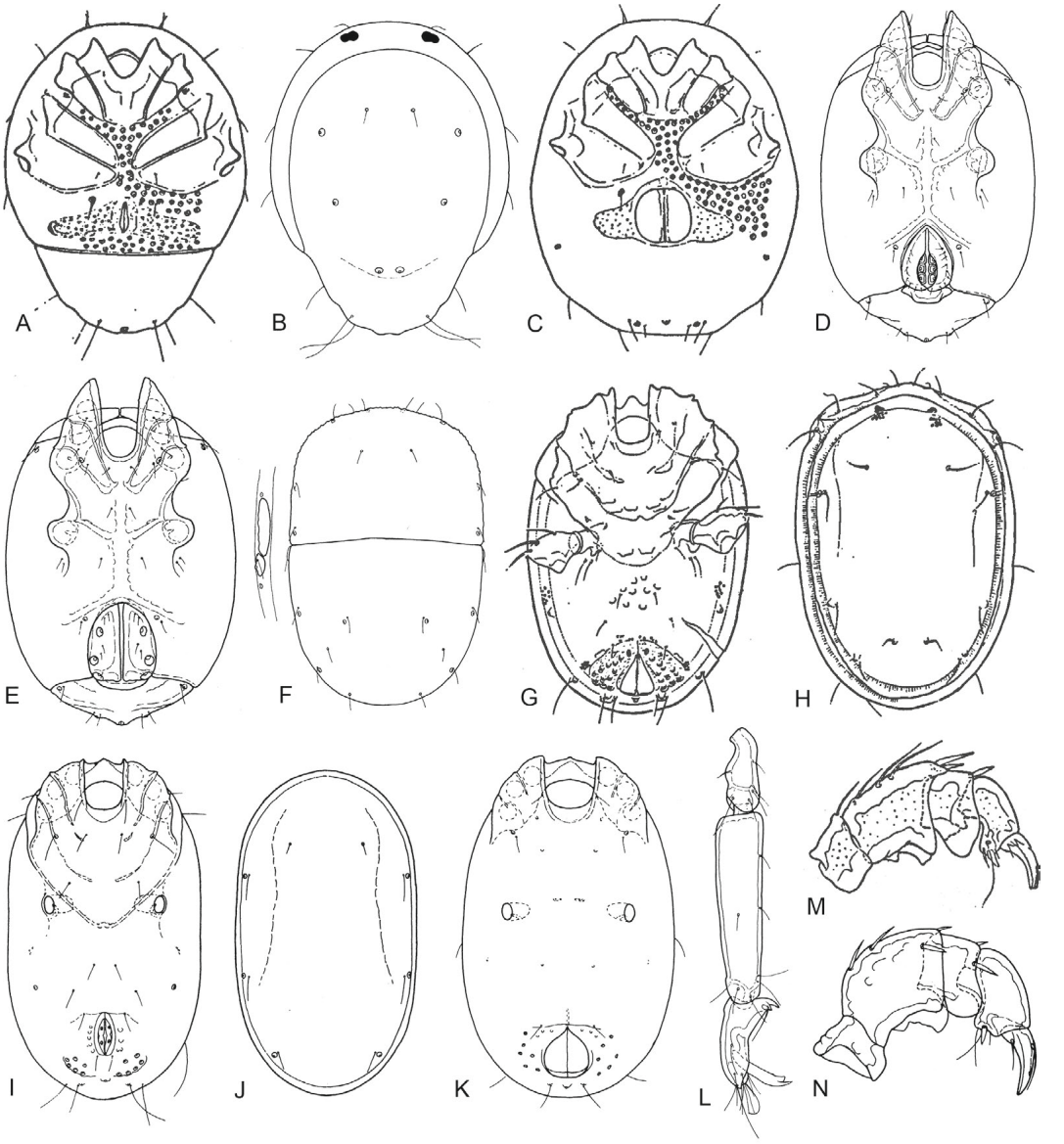


Fig. 13. A. *Micruracaropsis phytotelmaticola*, male, idiosoma ventral (after Viets 1982). **B.** *Micruracaropsis phytotelmaticola*, male, idiosoma dorsal (Cook 1974). **C.** *Micruracaropsis phytotelmaticola*, female, idiosoma ventral (after Viets 1982). **D.** *Notomomonia crassipes*, male, idiosoma ventral (Cook 1988). **E.** *Notomomonia crassipes*, female, idiosoma ventral (Cook 1988). **F.** *Notomomonia crassipes*, female, dorsal shield (Cook 1988). **G.** *Arenohydracarus pseudominimus*, female, idiosoma ventral (after Orghidan & Gruia 1983). **H.** *Arenohydracarus pseudominimus*, female, idiosoma dorsal (after Orghidan & Gruia 1983). **I.** *Arenohydracarus minimus*, male, idiosoma ventral (Cook 1980). **J.** *Arenohydracarus minimus*, male, dorsal shield (Cook 1980). **K.** *Arenohydracarus minimus*, female, idiosoma ventral (Cook 1980). **L.** *Notomomonia anchista*, female, I-leg-4/-5/-6 (Cook 1988). **M.** *Arenohydracarus pseudominimus*, female, palp (after Orghidan & Gruia 1983). **N.** *Arenohydracarus minimus*, male, palp (Cook 1980).

23' Not with the described combination of characters. 24

24 (23') I-leg-6 much shorter than I-leg-5, protrusions ventro-proximally at I-leg-6 together with claws forming characteristic grasping organ (Fig. 13L); complete dorsal and ventral shield (in most Neotropical species the dorsal shield is divided transversely) (Fig. 13F); three pairs of Ac (Fig. 13D,E). .... **Momoniidae** Viets, 1926

24' I-leg-5/6 **not** modified. 25

25 (24') With complete dorsal and ventral shield; often flattened, slightly elongated; coxae fused, no trace of median sutures, Cx-IV without posterior suture, no projections at insertions of IV-leg (Fig. 13G–K); dorsal shield with three pairs of glandularia far laterally (Fig. 13H,J); **both sexes**: Ac numerous, free in integument, flanking the gonopore (Fig. 13G,I,K), **male**: additional two pairs of Ac in the gonopore (Fig. 13I); P4 with ventro-distal bulge, but palp not truly uncate (Fig. 13M,N). .... **Arenohydracaridae** Cook, 1974, ***Arenohydracarus*** Cook, 1974

[Two described species. Mexico, Cuba (Orghidan & Gruia 1983). Habitat: streams]

25' Not with the described combination of characters. 26

26 (25') Completely armoured; three pairs of Ac in membranous region besides gonopore, no genital flaps; idiosoma more or less rounded; suture lines of coxae visible (Fig. 14A–D). 27

26' With or without complete dorsal and ventral shield; Ac **on** movable flaps or immovable genital plates besides the gonopore (e. g. Figs 32A,B,D–G, 33A,H, 35H–K, 38C,D), **if** Ac are located in the membranous region close to the gonopore, these are clearly more than five pairs and movable genital flaps are present (Figs 3B, 30C). 28

27 (26) Suture lines between Cx-III and -IV extending postero-medially to genital field, Cx-IV medially well separated from each other, extending far posterior, Cx-III and -IV forming a deep genital bay; no glandularia on coxal plates (Fig. 14A). .... **Neoacaridae** Motaş & Tanasachi, 1947, ***Neoacarus*** Halbert, 1944

[One described species: *N. adocetus* Cramer & Smith, 1991. Mexico (Cramer & Smith 1991). Habitat: rheocrene spring]

27' Genital bay very shallow; suture lines between Cx-III and -IV are meeting well anterior to the genital field (Fig. 14C). .... **Mideopsidae** Koenike, 1910 (**in part** (palp not uncate)), **Mideopsinae** Koenike, 1910 (**in part**) (*Mideopsides*, *Mideopsis*, *Neoxystonotus*, *Xystonotus*)

28 (26') Idiosoma strongly laterally compressed; Cx-IV greatly expanded, enclosing body laterally; dorsum with a median stripe of unsclerotized integument (generally bearing several small platelets); insertion of IV-leg without projection, located anterior to midlength of body (Fig. 14E); segments of IV-leg dorso-ventrally expanded, laterally flattened (Fig. 14F) ..... **Frontipodopsidae** Cook, Smith & Harvey, 2000, ***Frontipodopsis*** Walter, 1919

[Four described species. Mexico, Guatemala, Costa Rica, Panama (Camacho et al. 1997), Suriname, Ecuador (unpublished data), Brazil, Chile. Cook et al. (2000) shifted *Frontipodopsis* from Aturidae to Frontipodopsidae stat. nov. Habitat: streams]

28' Body not laterally compressed; not with the described combination of characters. 29

29 (28') I-leg-6 with claw socket at least half as long as segment (Fig. 29G); large dorsal plates surrounded by small platelets (in the few Neotropical species) (Figs 14H, 29C,F). 30

29' I-leg-6 with claw socket usually less than half as long as segment (e. g. Figs 16I,J, 17O, 24F, 38A,F, 39A,G, 47J,M, 59M); dorsum variable. 31

30 (29) Idiosoma oval to truncate anteriorly and tapering posteriorly, dorso-ventrally flattened; IV-legs inserted near midline close to each other (Fig. 29A,D); four to six pairs of Ac arranged in lines parallel to postero-lateral idiosoma margin, laterally flanking the gonopore (Fig. 29A,B,D,E). ..... **Lethaxonidae** Cook, Smith & Harvey, 2000

30' Idiosoma oval, spherical, not dorso-ventrally flattened; IV-legs inserted clearly lateral to midline (Fig. 14G); in general dorsum variable, the only so far known neotropical genus with large dorsal plate surrounded by small platelets (Fig. 14H); seven to nine pairs

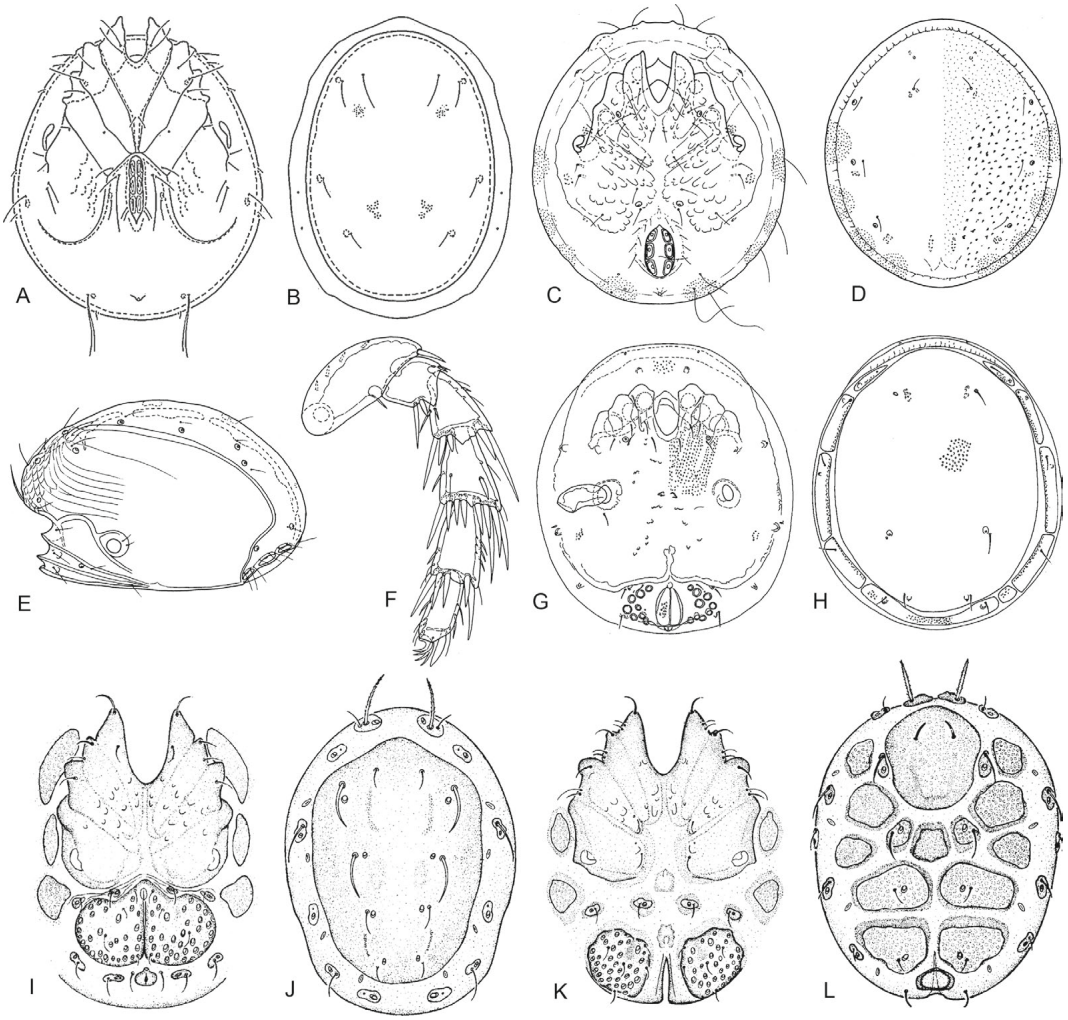


Fig. 14. A. *Neoacarus adocetus*, male, idiosoma ventral (after Cramer & Smith 1991). **B.** *Neoacarus adocetus*, male, idiosoma dorsal (after Cramer & Smith 1991). **C.** *Mideopsis sucaba*, female, idiosoma ventral (Cook 1980). **D.** *Mideopsis sucaba*, female, idiosoma dorsal (Cook 1980). **E.** *Frontipodopsis staheli*, female, idiosoma lateral (Cook 1980). **F.** *Frontipodopsis staheli*, female, IV-leg (Cook 1980). **G.** *Bromeliacarus cardoso*, female, idiosoma ventral (Pešić et al. 2015). **H.** *Bromeliacarus cardoso*, female, idiosoma dorsal (Pešić et al. 2015). **I.** *Feltria anahoffmannae*, male, idiosoma ventral (Cramer 1986). **J.** *Feltria anahoffmannae*, male, idiosoma dorsal (Cramer 1986). **K.** *Feltria anahoffmannae*, female, idiosoma ventral (Cramer 1986). **L.** *Feltria anahoffmannae*, female, idiosoma dorsal (Cramer 1986).

of Ac in half-moon shaped group around the gonopore (not parallel to lateral idiosoma margin), genital plates fused with ventral shield (Fig. 14G). .....
.. **Wettinidae** Cook, Smith & Harvey, 2000, ***Bromeliacarus*** Pešić, 2015
[One described species, only known from phytotelmata: *B. cardoso* Pešić 2015. Brazil (Pešić et al. 2015b). Habitat: phytotelmata]

31 (29') Two pairs of glandularia in transverse row between Cx-IV and genital field; Ac numerous on large plates flanking the gonopore (Fig. 14I,K); sclerotization of dorsum variable (scattered platelets to complete dorsal shield), in the Neotropical species **male**: large dorsal plate (Fig. 14J), **female**: several dorsal platelets (Fig. 14L). ..... **Feltriidae** Viets, 1926, ***Feltria*** Koenike, 1892

[Six described species. Mexico (Cramer 1986, 1988, Otero-Colina 1985). Habitat: streams]

31' Without transverse row of glandularia between coxal field and genital field. 32

32 (31') P2 with a ventral seta (hair-like (Fig. 15A,B) or peg-shaped (Fig. 15C,D), sessile or on a protrusion (Fig. 15E,F), the respective seta might be very short, sometimes difficult to see (missing in very few, rare species); Ac on movable flaps (all female, male of many genera) (Figs 3A, 15G,I, 30B,D,H, 35B,F,I,K) or immovable plates (Figs 30A, 35A,E,H,J); idiosoma soft (with or without platelets) to complete dorsal and ventral shields (Figs 15G–J, 30E,F, 31A–D, 32B–E, 33A–J). .... **Limnesiidae** Thor, 1900 [Key to South American species in Lundblad (1941)]

32' P2 without ventral seta (do not confuse with cone-shaped protrusion, that is present in several genera (Figs 43A,C, 44J,K,M)). .. 33

Note: The four remaining families – **Hygrobatidae**, **Aturidae**, **Unionicolidae** and **Pionidae** – contain a large number of genera, representing a wide variety of character states. The assignation of several genera to a certain family has been changed recently, in many cases the relationships are still unclear. Therefore, the separation of these families remains difficult and the following key should be regarded as tentative attempt rather than a final solution. If a specimen does not key out clearly, several options should be checked. Rather incomplete keys to several South American genera and species of Hygrobatidae and Unionicolidae are given in Lundblad (1942), to several South American species of Aturidae in Lundblad (1943b).

33 (32') Cx-IV bearing a pair of glandularia, mostly centrally (Fig. 16A,B,K,L) or close to the anterior margin (Fig. 16C,D), occasionally shifted far forward on an anteriorly directed loop of a coxal suture line (Fig. 16E–H). 34

33' Cx-IV without glandularia 36

34 (33) Usually soft bodied or sclerotization at least not forming complete dorsal and ventral shield. .... **Hygrobatidae** Koch, 1842 (**in part**)

34' With complete dorsal and ventral shield. 35

35 (34') All suture lines of coxae clearly visible (with few exceptions – *Diamphidaxona*, *Szalayella*, *Dubiobates*, *Scutobates* (Figs 16F,G, 36J,L, 44I)); I-leg-5 often with terminal down-curved seta (Fig. 16I,J); Ac often three pairs, on genital plates lying close to the gonopore (**male**: genital plates often fused, forming a ring around the gonopore (Fig. 16A,D–F,K); **female**: one pair of genital plates beside the gonopore (Fig. 16C,H,L)), genital plates in general separated from ventral shield (Figs 16F, 36A), with few exceptions (some *Corticacarus*, *Szalayella*, *Dubiobates* (Figs 16G,K, 36J,L)). .... **Hygrobatidae** Koch, 1842 (**in part**)

35' Suture lines of coxae at least partly obliterate; I-leg-5 never with terminal down-curved seta; genital plates often obliterate or fused with ventral shield (Fig. 17A–C). .... **Aturidae** Thor, 1900 (**in part**)

36 (33') Idiosoma soft, four clearly separated coxal groups; posterior apodemes of anterior coxae short; suture line between Cx-III and -IV incomplete; Cx-IV large, postero-medially rounded; Ac numerous (small, with two pairs of large Ac in-between), large wing- or tongue-like genital plates (Fig. 17D,E); palp with few, short setae, no projections (Fig. 17F). ..... **Pionidae** Thor, 1900 (**in part**), **Najadicolinae** Viets, 1935, ***Najadicola*** Piersig, 1897 [One described species: *N. ingens* (Koenike, 1895). Mexico (Simmons & Smith 1984). Habitat: parasites of freshwater clams]

36' Idiosoma soft or with different degrees of sclerotization, coxal groups separated (Fig. 17K–M) or fused (Fig. 17G,H); posterior apodemes of anterior coxae, and suture line between Cx-III and -IV variable (Fig. 17I,K); if Ac numerous and idiosoma soft, no large tongue-like genital plates (Fig. 17L,M); palp generally with single longer setae, with or without projections (Fig. 59P). 37

37 (36') With complete dorsal and ventral shield. 38

37' Soft bodied **or** sclerotization at least not forming complete dorsal and ventral shield. 39

38 (37) Openings for insertions of IV-legs associated with large projections, extended laterally (Fig. 17G). .... **Unionicolidae** Oudemans, 1909 (**in part**)

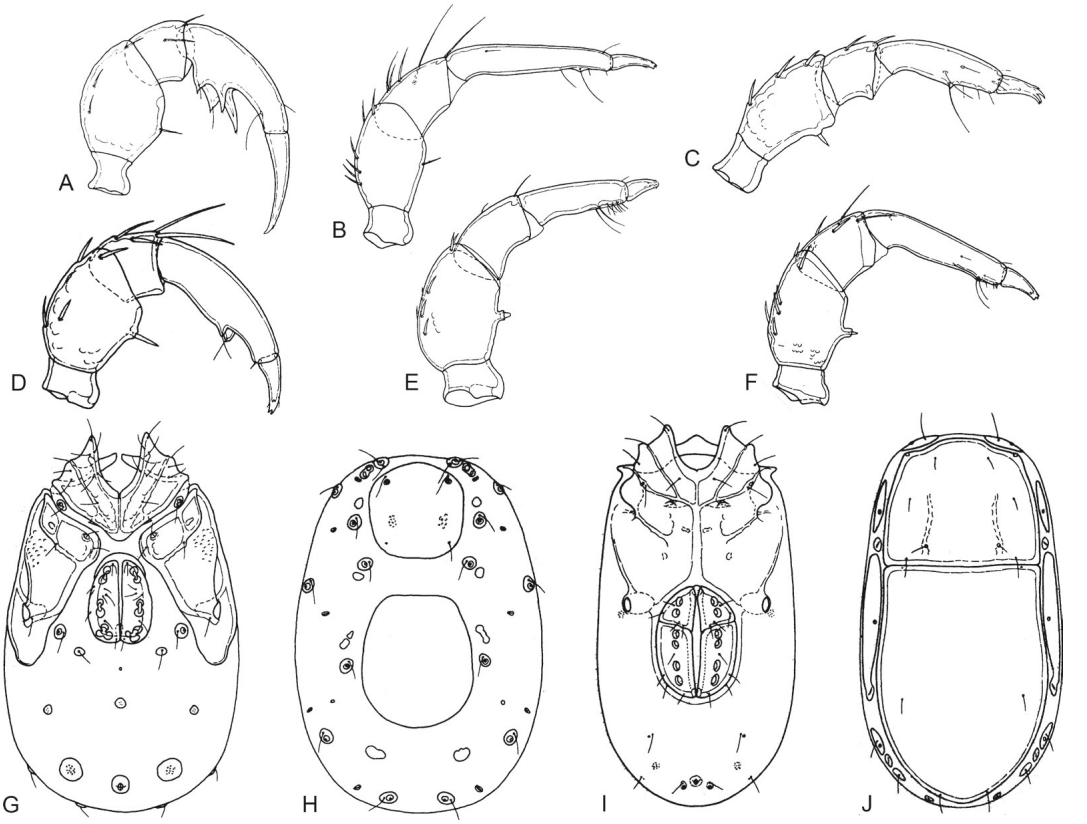


Fig. 15. **A.** *Neomamersa mexicana*, female, palp (Cook 1980). **B.** *Limnesia slanopa*, female, palp (Cook 1980). **C.** *Protolimnesia interstitialis*, female, palp (Cook 1980). **D.** *Limnesia neodentipalpis*, female, palp (Cook 1980). **E.** *Tyrrellia ovalis*, female, palp (Cook 1980). **F.** *Limnesia pauciseta*, female, palp (Cook 1980). **G.** *Protolimnesia mesoamericana*, female, idiosoma ventral (Cook 1980). **H.** *Protolimnesia mesoamericana*, female, idiosoma dorsal (Cook 1980). **I.** *Neomamersa decussa*, female, idiosoma ventral (Cook 1980). **J**. *Neomamersa decussa*, female, idiosoma dorsal (Cook 1980).

38' Openings for insertions of IV-legs with small or no projections, if large projections are present, they are directed posteriorly or postero-laterally (Fig. 17A,H). .... **Aturidae** Thor, 1900 (**in part**)

39 (37') Posterior margin of Cx-IV truncate or rounded, not forming a genital bay (Fig. 17I,K); claws simple or with clawlets; I-leg often with several long thickened setae (Fig. 17J). ... **Unionicolidae** Oudemans, 1909 (**in part**)

39' Posterior margin of Cx-IV angled or with clear protrusion, forming a genital bay (Fig. 17L,M); claws always with clawlets; I-leg not with long thickened setae as described above (Fig. 17N,O). .... **Pionidae** (**in part**)

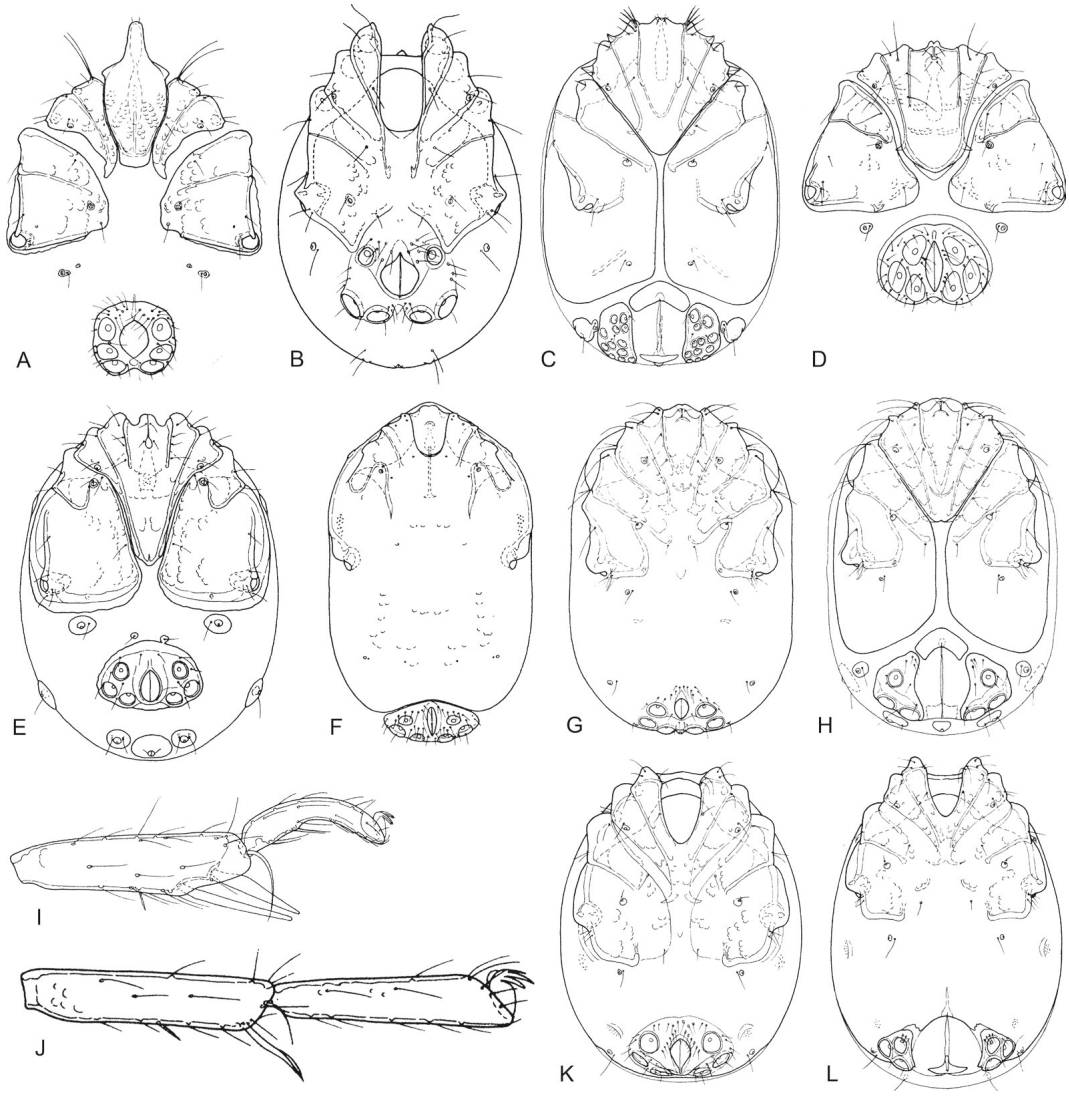


Fig. 16. **A.** *Zabobates alphus*, male, coxae, capitulum and genital field ventral (Cook 1988). **B.** *Atractidella lundbladi*, male, idiosoma ventral (Cook 1980). **C.** *Decussobates planus*, female, idiosoma and capitulum ventral (Cook 1988). **D.** *Hygrobates ampliatus*, male, coxae, capitulum and genital field ventral (Cook 1980). **E.** *Hygrobates calvotus*, male, idiosoma and capitulum ventral (Cook 1980). **F.** *Diamphidaxona mexicana*, male, idiosoma and capitulum ventral (Cook 1980). **G.** *Szalayella lundbladi*, male, idiosoma and capitulum ventral (Cook 1988). **H.** *Szalayella lundbladi*, female, idiosoma and capitulum ventral (Cook 1988). **I.** *Atractides tolas*, female, I-leg-5/-6 (Cook 1980). **J.** *Paraschizobates scutatus*, female, I-leg-5/-6 (Cook 1980). **K.** *Corticacarus penai*, male, idiosoma ventral (Cook 1988). **L.** *Corticacarus penai*, female, idiosoma ventral (Cook 1988).

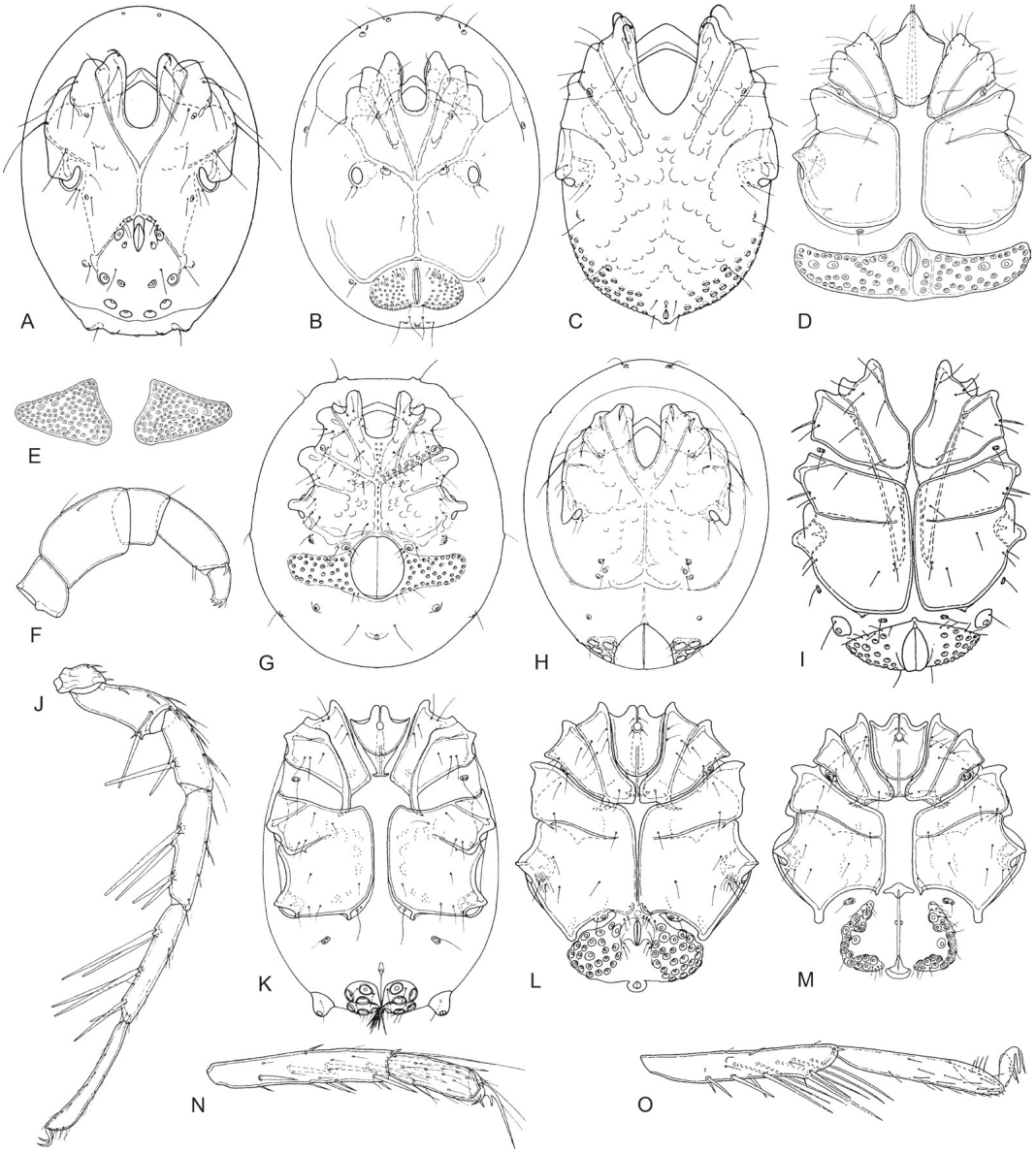


Fig. 17. A. *Axonopsella vicina*, male, idiosoma ventral (Cook 1980). **B.** *Albia lemba*, male, idiosoma ventral (Cook 1980). **C.** *Kongsbergia mexicana*, male, idiosoma ventral (Cook 1980). **D.** *Najadicola ingens*, male, coxae, capitulum and genital field ventral (Cook 1974). **E.** *Najadicola ingens*, female, genital plates (Cook 1974). **F.** *Najadicola ingens*, female, palp (Cook 1974). **G.** *Recifella mexicana*, female, idiosoma ventral (Cook 1980). **H.** *Miraxonides* (*Miraxonides*) *similis*, female, idiosoma ventral (Cook 1980). **I.** *Neumania broballa*, male, coxae and genital field ventral (Cook 1980). **J.** *Neumania conroyi*, female, I-leg (Cook 1980). **K.** *Unionicola gracilipalpis tenuis*, female, idiosoma ventral (Cook 1980). **L.** *Piona junctella*, male, coxae, capitulum and genital field ventral (Cook 1980). **M.** *Piona junctella*, female, coxae, capitulum and genital field ventral (Cook 1980). **N.** *Piona junctella*, male, III-leg-5/-6 (Cook 1980). **O.** *Piona erratica*, female, I-leg-5/-6 (Cook 1980).

Keys to genera

Key to Pontarachnidae Koenike, 1910

1 Marine; chelicera stylet-like (Fig. 18D); suture line Cx-III/-IV extending into postero-medial apodeme (Figs 6A, 18A); **male**: setae in genital region all inserted in genital sclerite (Fig. 18A). ..... ***Pontarachna*** Philippi, 1840
[One described species: *P. nemethi* Pešić, Chatterjee & Schizas, 2014. Puerto Rico (Pešić et al. 2014). Habitat: marine benthos]

1' Mainly marine, sometimes in costal fresh water; chelicera not stylet-like (in the typical shape of most water mite chelicera); suture line Cx-III/-IV not extending into postero-medial apodeme (however, posterior apodemes present) (Fig. 18C,E,F); **male**: setae in genital region on genital sclerite as well as in the surrounding integument (Fig. 18C,E). ..... ***Litarachna*** Walter, 1925
[Four marine species are recorded from the Caribbean (British West Indies, Puerto Rico (Pešić et al. 2014), Netherlands Antilles (Pešić et al. 2008)) as well as the Pacific Coast of Panama (Pešić et al. 2015c). One described species from Neotropical freshwater habitats: *L. brasiliensis* Smit, 2007. Brazil (Smit 2007). Habitat: marine benthos, mangroves, estuaries]

Key to Limnocharidae Grube, 1859

1 Capitulum trunk-like protrusible (Fig. 1D,L), palp three-segmented, or appearing two-segmented (Fig. 18G,H) .... **Rhyncholimnocharinae** Lundblad, 1936, ***Rhyncholimnochares*** Lundblad, 1936
[Twenty-one described species. Mexico, Guatemala, Costa Rica, Panama (Goldschmidt et al. 2016), Colombia, Ecuador (Tuzovskij & Gerecke 2020), Brazil, Bolivia (Fernández et al. 2009), Argentina, Chile (Tuzovskij & Gerecke 2020). Key to South American species in Lundblad (1953), Key to all species in Tuzovskij & Gerecke 2020. Habitat: streams (especially protected sites in fast flowing streams)]

1' Capitulum not trunk-like protrusible, palp four- or five-segmented (Fig. 18I,J). .... **Limnocharinae** Grube, 1859, 2

2 (1') Palp four-segmented (Fig. 18I). .... ***Neolimnochares*** Lundblad, 1937
[Six described species. Cuba, Ecuador (Tuzovskij 2008), Brazil, Paraguay. Habitat: streams, springs, hygropetric habitats]

2' Palp five-segmented (Fig. 18J). .... ***Limnochares*** Latreille, 1796
[Undescribed species. Mexico (Otero-Colina & Bassols-Batalla 1985), Costa Rica (Goldschmidt 2004d). Habitat: standing waters]

Note: Key to South American species of the family in Lundblad (1941).

Key to Eylaidae Leach, 1815

1 Capitulum attached to protrusible tube, compact (Fig. 6L); eye plate without medial bridge (Fig. 6P). .... ***Rhyncheylais*** Lundblad, 1938
[One described species: *R. connexa* Lundblad, 1938. Paraguay. Habitat: standing waters]

1' Capitulum without protrusible tube, longer than wide (Fig. 6O), eye plate with medial bridge (Fig. 6M). ..... ***Eylais*** Latreille, 1796
[Twenty described species. Mexico, Costa Rica (Goldschmidt 2004d), Colombia, Brazil, Peru, Bolivia, Chile, Paraguay, Argentina, Uruguay. Habitat: standing, slow flowing waters, springs]

Key to Hydryphantidae Piersig, 1896

1 Lateral eyes reduced or small, below the integument, but not in capsules (Fig. 19B). 2

1' Lateral eyes present, clearly visible, in capsules (Fig. 19N,O) or attached to preocular platelets (Fig. 19E,F). 4

2 (1) Body clearly elongated, coxal groups widely separated; Ac three pairs to many (Figs 7D, 19H,I); none or small dorsal plates. .... **Wandesiinae** Schwoerbel, 1961, 3

2' Body not elongated (rectangular-oval), coxal groups rather close together (Cx-I/II suture subparallel to longitudinal axis of idiosoma, Cx-III/IV suture oblique to longitudinal axis); three pairs of Ac; no dorsal plates (Fig. 19A,B). .... **Tartarothyadinae** K. Viets, 1934, ***Tartarothyas*** K. Viets, 1934
[One undescribed species. Colombia. Habitat: lake (in general springs and interstitial habitats)]

3 (2) Genital flaps absent, three pairs to many Ac (Figs 7D, 19H,I); no dorsal plates. .... ***Wandesia*** Schechtel, 1912
[Ten described species. Costa Rica (pers. obs.), Cuba (Goldschmidt & Gerecke 2003), Colombia (Pešić et al. 2010), Brazil, Bolivia, Chile, Paraguay, Argentina. Key to Neo-

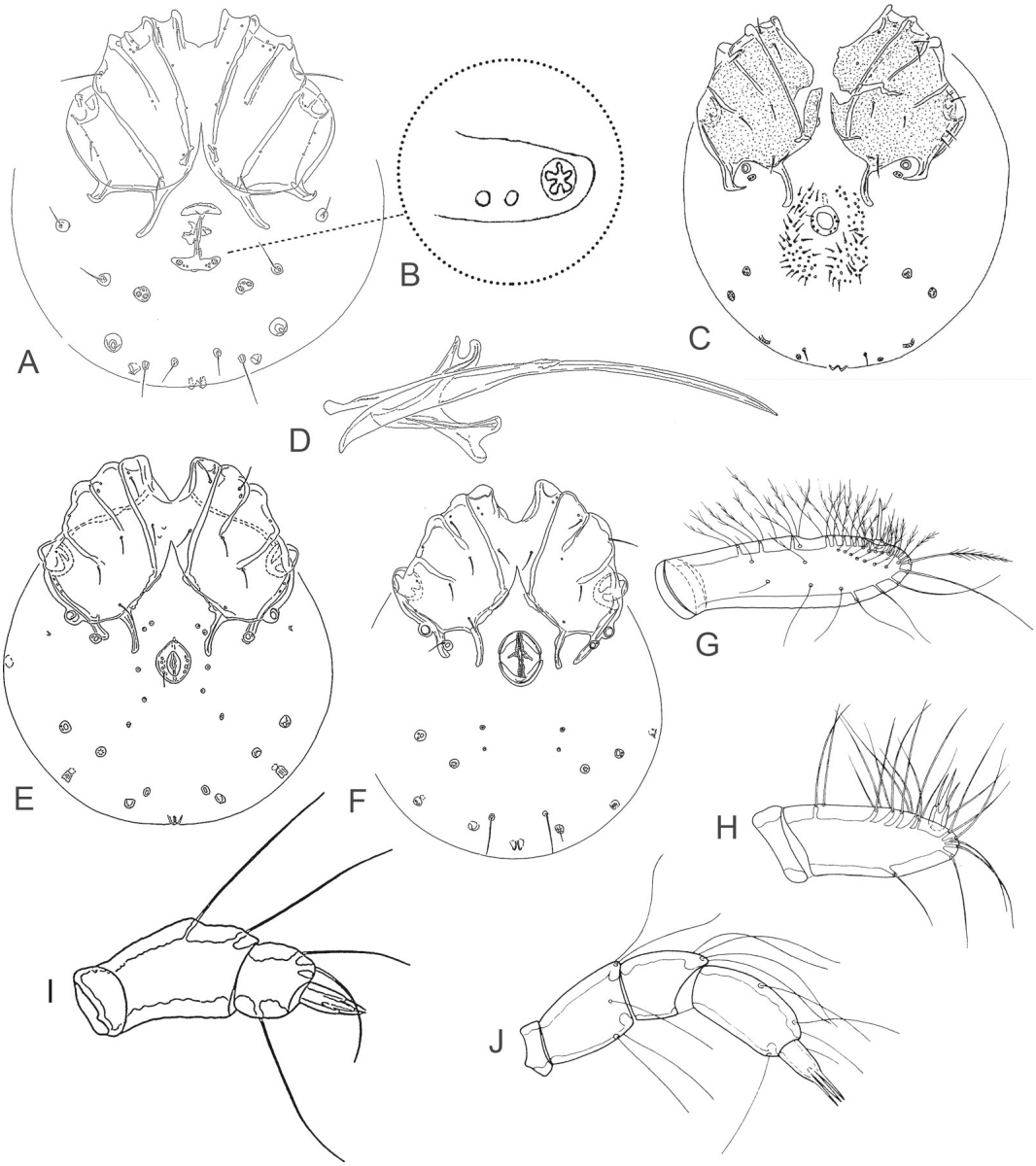


Fig. 18. **A.** *Pontarachna nemethi*, female, idiosoma ventral (genital setae omitted, just insertion illustrated) (Pešić et al. 2012). **B.** *Pontarachna nemethi*, female, wheel-like acetabulum (enlarged cutout of A) (Pešić et al. 2012). **C.** *Litarachna caribica*, male, idiosoma ventral (Pešić et al. 2008). **D.** *Pontarachna nemethi*, male, chelicera (Pešić et al. 2012). **E.** *Litarachna lopezae*, male, idiosoma ventral (genital setae omitted, just insertion illustrated) (Pešić et al. 2014). **F.** *Litarachna lopezae*, female, idiosoma ventral (Pešić et al. 2014). **G.** *Rhyncholimnochares longipalpis*, male, palp (Cook 1980). **H.** *Rhyncholimnochares mexicana*, male, palp (Cook 1980). **I.** *Neolimnochares placophora*, male, palp (after Lundblad 1941). **J.** *Limnochares crinita*, male, palp (Cook 1974).

tropical species of the subgenus *Partnuniella* in Pešić et al. (2010). Habitat: springs (one record from hot springs), interstitial, lake]

3' Three pairs of Ac partly covered by genital flaps (Fig. 19J), small medio-dorsal plate. .. .. ***Euwandesia*** Andre & Naudo, 1962

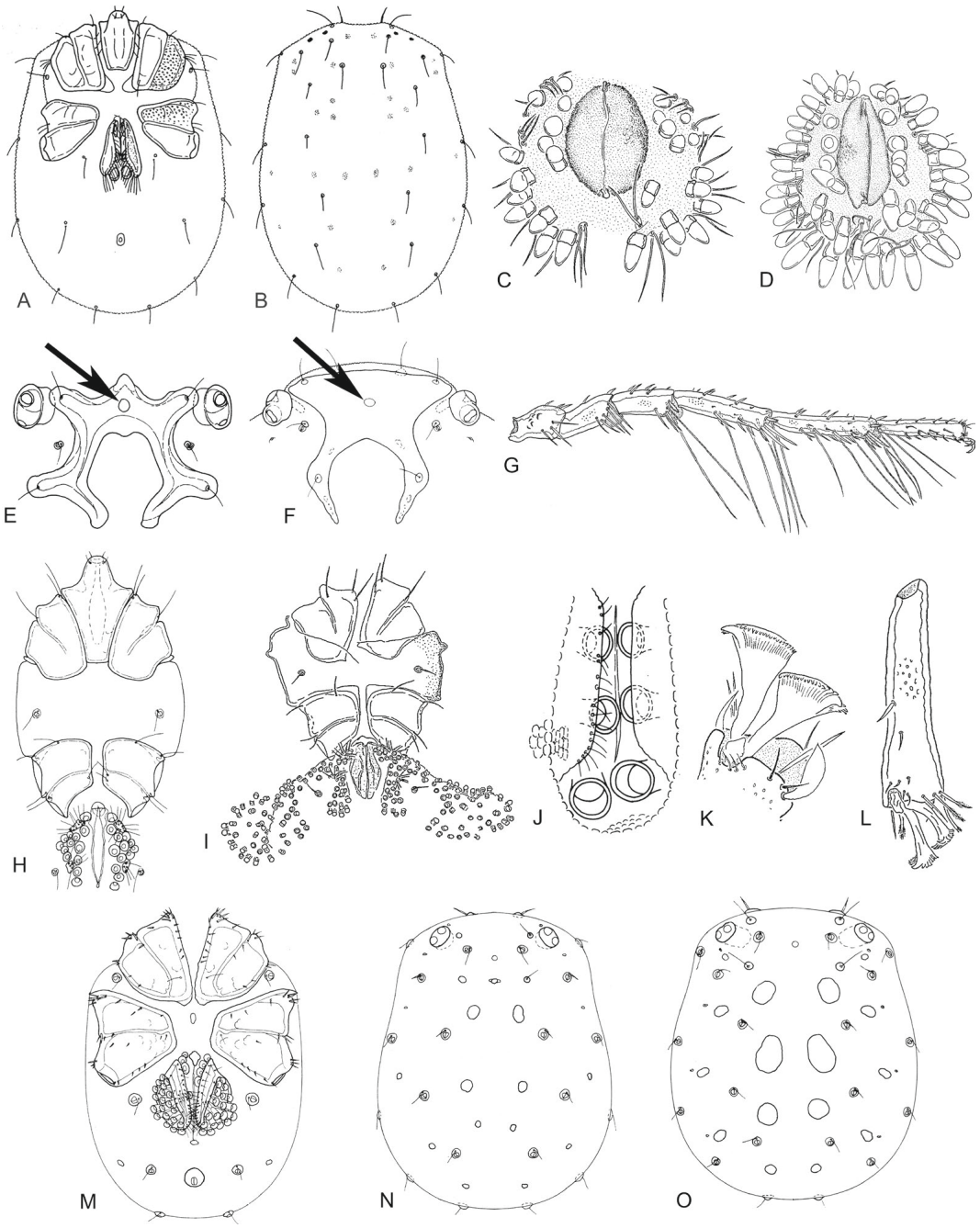


Fig. 19. **A.** *Tartarothyas romanica*, female, idiosoma ventral (Cook 1974). **B.** *Tartarothyas romanica*, female, idiosoma dorsal (Cook 1974). **C.** *Protzia salsa*, female, genital field (Goldschmidt & Gerecke 2003). **D.** *Protzia patata*, female, genital field (Goldschmidt & Gerecke 2003). **E.** *Hydryphantes ramosus ramosus*, male, frontal plate, ocular region (arrow pointing at median eye) (Cook 1980). **F.** *Hydryphantes coscaroni*, female, frontal plate, ocular region (arrow pointing at median eye) (Cook 1980). **G.** *Hydryphantes cocinero*, male, IV-leg (Goldschmidt & Gerecke 2003). **H.** *Wandesia* (*Partnuniella*) *chechoi*, female, coxae, capitulum and genital field ventral (Cook 1988). **I.** *Wandesia* (*Partnuniella*) *lehmanni*, female, coxal and genital field (after Pešić et al. 2010). **J.** *Euwandesia sensitiva*, female, genital field (Cook 1988). **K.** *Protzia salsa*, male, leg claws (Goldschmidt & Gerecke 2003). **L.** *Neocalonyx desajunos*, deutonymph, IV-leg-6 (Goldschmidt & Gerecke 2003). **M.** *Neocalonyx keldomus*, female, idiosoma ventral (Cook 1988). **N.** *Neocalonyx keldomus*, female, idiosoma dorsal (Cook 1988). **O.** *Neocalonyx placophorus*, male, idiosoma dorsal (Cook 1988).

[Two described species. Chile, Argentina (Goldschmidt & Gerecke 2003). Habitat: interstitial habitats in streams and lakes]

4(1') Characteristically shaped frontal plate with indented caudal margin, bearing pre- and post ocular setae (Fig. 19E,F), generally no further dorsalia; legs with swimming setae (Fig. 19G). .. **Hydryphantinae** Piersig, 1896, ***Hydryphantes*** Koch, 1841
[Ten described species. Mexico (Goldschmidt & Gerecke 2003), Costa Rica, Suriname, Brazil, Peru, Chile, Paraguay, Argentina, Uruguay. Key to South American species in Lundblad (1941). Habitat: various standing waters, springs, streams]

4' **If** frontal plate present, without caudal protrusions; mostly without swimming setae. 5

5(4') Many (mostly) stalked Ac (Figs 19C,D, 20D), (some species with very short stalks (Figs 19M, 20B,C)); dorsal platelets (if any) small (Fig. 19N,O); with or without swimming setae. 6

5' Three pairs of Ac, not stalked (Fig. 20G,H); often (one genus without) with regular dorsal plates; no swimming setae. 8

6(5) Leg claws with many fan-like clawlets (Fig. 19K); genital sclerites reduced to small individual platelets (Fig. 19C,D); without swimming setae. ..... **Protziinae** Koenike, 1909 (in part), ***Protzia*** Piersig, 1896
[Two described species. Mexico (Goldschmidt et al. 2015), Costa Rica (Goldschmidt & Gerecke 2003), Ecuador. Habitat: streams, springs]

6' Leg claws with or without lateral clawlets however not broad fan-like (Figs 19L, 20A,E), genital sclerites present (Fig. 20B–D), with or without swimming setae. 7

7(6') Leg claws simple (Fig. 20A); two pairs of genital plates, Ac on short stalks (Fig. 20B,C); large antero-lateral extensions at Cx-III (Fig. 20B); no swimming setae. ..... **Eupatrellinae** Viets, 1935, ***Eupatrella*** Walter, 1935
[Two described species. Costa Rica (Goldschmidt & Gerecke 2003), Panama (Goldschmidt et al. 2016), Ecuador. Habitat: springs, small streams]

7' Leg claws mostly with lateral clawlets (Figs 19L, 20E); genital sclerite D-shaped (South American species) (Fig. 20D) or elongated (Central American species) (Fig. 20F); with or without swimming setae ..... **Protziinae** Koenike, 1909 (in part), ***Neocalonyx*** Walter, 1919
[Fourteen described species. Costa Rica (Goldschmidt & Gerecke 2003), Colombia, Ecuador, Peru, Bolivia (Rosso de Ferradás & Fernández 2007), Chile, Argentina. Key to South American species in Lundblad (1953) and Cook (1988). Habitat: streams, lakes]

8(5') Dorsalia in two medial and two lateral rows (Fig. 20N); I-leg with characteristic grasping structures (I-leg-5 with ventral row of about twenty rounded peg-like setae, I-leg-6 slightly curved, folding back to segment 5) (Fig. 20K); P2 and P3 with ventral projections. ..... **Ankelothyadinae** Besch, 1964, ***Ankelothyas*** Besch, 1964
[One described species: *A. emydoides* Besch, 1964. Chile (Goldschmidt & Gerecke 2003). Habitat: stream]

8' Dorsum without dorsalia, with one medial row of dorsalia or with complete dorsal shield (but never with four rows as described above), I-leg without special structures, palp segments without ventral projections. ..... **Euthyadinae** K. Viets, 1931, 9

9(8') Dorsum without large plates, mainly soft, median eye well developed (with a chitinous ring and two pigment dots) (Fig. 20I), two pairs of genital sclerites (Fig. 20G,H). ..... ***Notopanisus*** Besch, 1964
[One described species: *N. wetzeli* Besch, 1964. Chile, Argentina (Goldschmidt & Gerecke 2003) Habitat: streams, waterfalls, interstitial habitats]

9' Dorsum with large dorsalia or complete dorsal shield. 10

10(9') Dorsum covered by complete dorsal shield (Fig. 20J). ..... ***Thyopsella*** Cook, 1965
[One described species: *T. obscura* Cook, 1980. Mexico (Goldschmidt & Gerecke 2003). Habitat: helocrene spring]

10' Dorsum covered by large but clearly separated plates. 11

11(10') Median eye reduced; idiosoma sclerites with large pores; Vgl-3 reduced (Fig. 20P,O); P4 short (Fig. 20L). ..... ***Almuerzothyas*** Goldschmidt & Gerecke, 2003
[One described species: *A. casado* Goldschmidt & Gerecke, 2003. Costa Rica (Goldschmidt & Gerecke 2003). Habitat: stream]

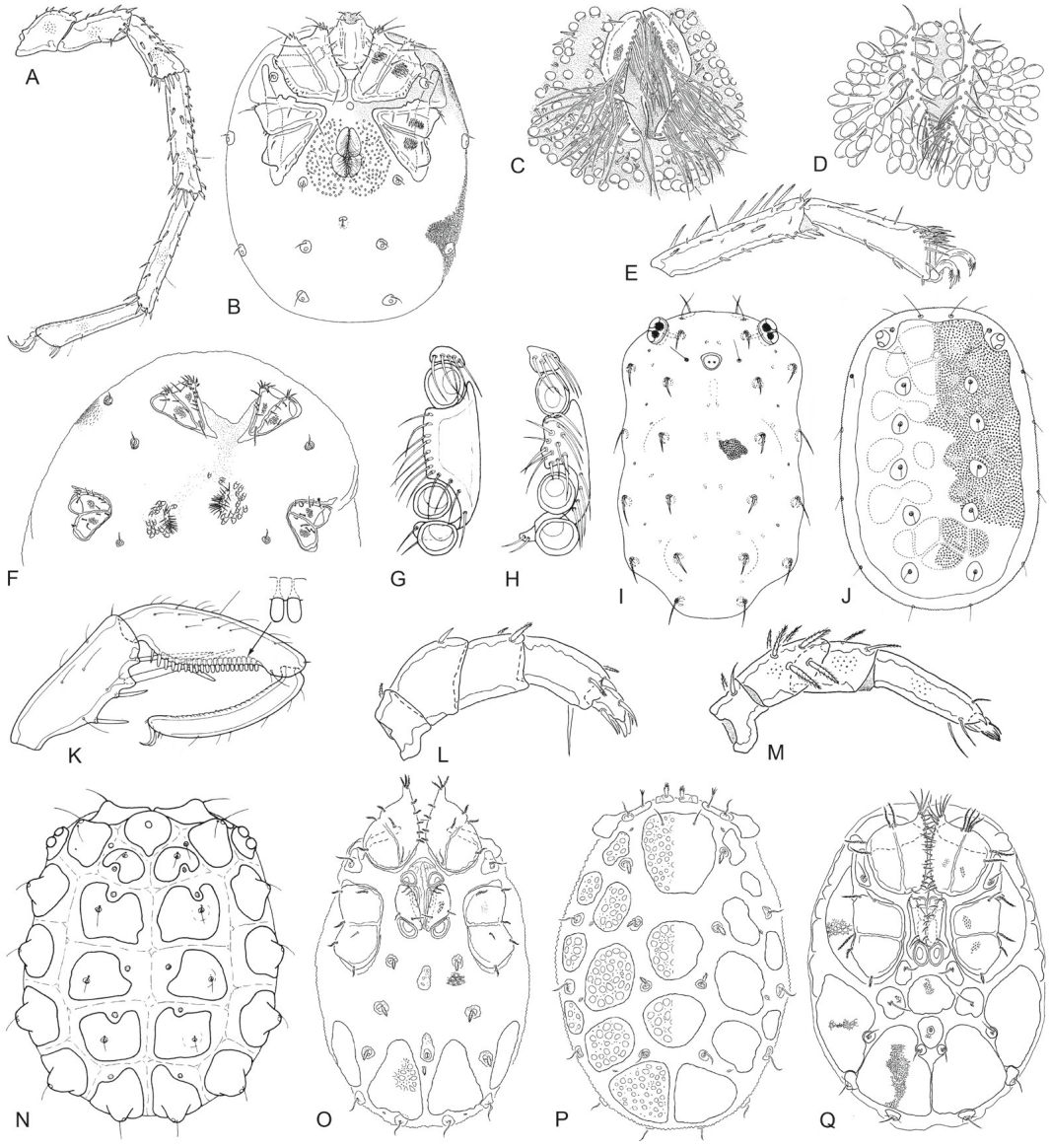


Fig. 20. **A.** *Eupatrella arroz*, male, IV-leg (Goldschmidt & Gerecke 2003). **B.** *Eupatrella arroz*, male, idiosoma and capitulum ventral (Goldschmidt & Gerecke 2003). **C.** *Eupatrella arroz*, male, genital field (Goldschmidt & Gerecke 2003). **D.** *Neocalonyx tenuirostris*, male, genital field (Goldschmidt & Gerecke 2003). **E.** *Neocalonyx pectunguis*, female, IV-leg-5/-6 (Goldschmidt & Gerecke 2003). **F.** *Neocalonyx colada*, female, anterior part of idiosoma ventral (Goldschmidt & Gerecke 2003). **G.** *Notopanisus wetzeli*, male, left genital flap and acetabula (Cook 1988). **H.** *Notopanisus wetzeli*, female, left genital flap and acetabula (Cook 1988). **I.** *Notopanisus wetzeli*, female, idiosoma dorsal (Cook 1980). **J.** *Thyopsella occidentalis*, male, idiosoma dorsal (Cook 1974). **K.** *Ankelothyas emydoides*, male, I-leg-4/-5/-6 (Cook 1988). **L.** *Almuerzothyas casado*, female, palp (Goldschmidt & Gerecke 2003). **M.** *Trichothyas compressa*, female, palp, medial view (Goldschmidt & Gerecke 2003). **N.** *Ankelothyas emydoides*, male, idiosoma dorsal (Cook 1988). **O.** *Almuerzothyas casado*, female, idiosoma ventral (Goldschmidt & Gerecke 2003). **P.** *Almuerzothyas casado*, female, idiosoma dorsal (Goldschmidt & Gerecke 2003). **Q.** *Trichothyas compressa*, female, idiosoma ventral (Goldschmidt & Gerecke 2003).

11' Median eye present but not pigmented, sclerites with regular sized pores, Vgl-3 present (Fig. 20Q); P4 longer (Fig. 20M). .... ***Trichothyas*** Viets, 1926
[One described species: *T. compressa* Viets, 1953. San Salvador, Costa Rica (Goldschmidt & Gerecke 2003). Habitat: streams, hygropetric zones]

Key to Rhynchohydracaridae Lundblad, 1936

1 Mostly dorsum and venter loosely covered by (very characteristic) reticulate plates (Figs 2J, 3M, 9A,B) (some undescribed species from Mexico, Costa Rica and Ecuador without plates, with unclear reticulate pattern under integument); Cx-I medially not fused (Figs 2E, 3M, 9A). .... **Clathrosperchontinae** Lundblad, 1936, 2
[Key to South American species in Lundblad (1941)]

1' Dorsal plates large, densely arranged, nearly completely covering the idiosoma (Fig. 9D); ventrally covered by densely arranged platelets or complete ventral shield; Cx-I medially fused (Fig. 9C). 3

2 (1) Capitulum attached to protrusible tube (Fig. 3M); palps rather compact (Fig. 21E). .... ***Clathrosperchon*** Lundblad, 1936
[Four described species. Mexico, Guatemala, Costa Rica, Panama (Valdecasas 2001), Venezuela, Colombia, Brazil, Ecuador (unpublished data), Bolivia (Fernández et al. 2009), Paraguay, Argentina. Habitat: running waters]

2' Capitulum not attached to protrusible tube; palps rather slender (Fig. 21G). .... ***Clathrosperchonella*** Lundblad, 1937
[Two described species. Brazil, Paraguay. Habitat: running waters]

3 (1') Ventrally covered by densely arranged platelets (Fig. 9C). .... **Rhynchohydracarinae** Lundblad, 1936, ***Rhynchohydracarus*** Lundblad, 1936
[Three described species. Costa Rica (Goldschmidt 2004d), Panama (Valdecasas 2001), Ecuador (unpublished data), Brazil, Paraguay. Key to South American species in Lundblad (1941). Habitat: streams, springs]

3' Ventral plates fused to ventral shield (Fig. 21A). .... **Santiagocarinae** Valdecasas, 2001, ***Santiagocarus*** Valdecasas, 2001, ***Gledhillia*** Valdecasas, 2001
[One described species each: *S. robustus* Valdecasas, 2001, *G. coibensis* Valdecasas, 2001. Panama (Valdecasas 2001). These two genera currently cannot be separated and need revision. Habitat: streams]

Key to Torrenticolidae Piersig, 1902

1 Dorsum with one **unpaired** antero-median platelet, more than five pairs of lateral platelets (Fig. 21C); three pairs of Ac (Fig. 21B). . ..... ***Testudacarus*** Walter, 1928
[Two described species (a third one still undescribed). Mexico (Cramer 1992b). Habitat: streams]

1' Dorsum with one or two **pairs** of antero-median platelets (Fig. 8B) (rarely all fused (Fig. 8C)); six pairs of Ac (Figs 8A, 21D). 2

2 (1') Palp four-segmented, P2 without ventral seta (Fig. 21H). ...***Neoatractides*** Lundblad, 1941
[Eleven described species. Mexico (Otero-Colina 1987, Cramer 1992b, Cramer & Cook 2000), Guatemala, Costa Rica, Panama (Goldschmidt et al. 2016), Colombia, Ecuador (unpublished data), Argentina. Key to South American species in Lundblad (1953). Habitat: streams, waterfalls]

2' Palp five-segmented, if seemingly four-segmented, P2 with ventral seta (Figs 1J, 21I–K). 3

3 (2') Capitulum long and narrow (Fig. 21F), attached to a protrusible tube, capitular bay shallow (Fig. 21D). .... ***Pseudotorrenticola*** Walter, 1906
[Three described species. Mexico (Cramer & Cook 2000), Guatemala, Honduras (Wiles 2005), Costa Rica (Goldschmidt 2004d), Panama (Goldschmidt et al. 2016). Habitat: streams]

3' Capitulum not attached to a protrusible tube. 4

4 (3') Capitulum with a short postero-dorsal projection; palp compact or slender, with or without ventral protrusions at P2, P3 (Fig. 21J). ..... ***Torrenticola*** Piersig, 1896
[Fifty-eight described species. Mexico (Cramer 1992b), Guatemala, Honduras (Wiles 2005), Costa Rica (Goldschmidt 2007), Panama (Goldschmidt et al. 2016), Colombia, Ecuador (unpublished data), Bolivia (Fernández et al. 2009), Argentina. Key to Neotropical species in Goldschmidt (2007) and to South American species in Lundblad (1953). Habitat: running waters, springs]

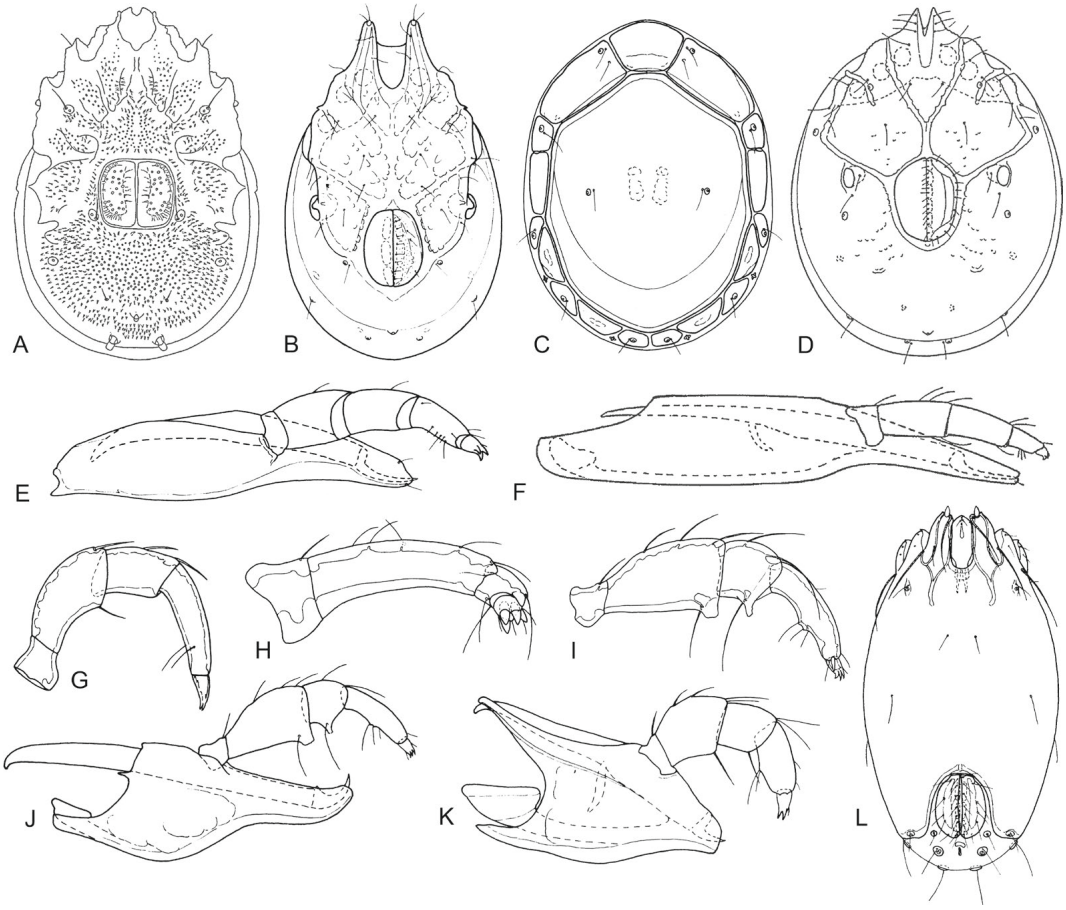


Fig. 21. A. *Santiagocarus robustus*, male, idiosoma ventral (after Valdecasas 2001). **B.** *Testudacarus americanus*, male, idiosoma ventral (Cook 1974). **C.** *Testudacarus americanus*, female, idiosoma dorsal (Cook 1974). **D.** *Pseudotorrenticola coatepecana*, male, idiosoma ventral (after Cramer & Cook 2000). **E.** *Clathrosperchon punctatus*, female, capitulum, chelicera and right palp lateral (Cook 1980). **F.** *Pseudotorrenticola coatepecana*, male, capitulum, chelicera and right palp lateral (after Cramer & Cook 2000). **G.** *Clathrosperchonella asterifera*, male, palp (Cook 1974). **H.** *Neoatractides vietsi*, female, palp (Cook 1980). **I.** *Torrenticola gennada*, female, palp (Cook 1980). **J.** *Torrenticola gennada*, female, capitulum, chelicera and right palp lateral (Cook 1980). **K.** *Monatractides veracruzensis*, male, capitulum, chelicera and right palp lateral (Cook 1980). **L.** *Oxus* (*Oxus*) *stolli*, female, idiosoma and capitulum ventral (Cook 1980).

4' Capitulum with a long postero-dorsal projection; palp compact, never with ventral protrusions at P2, P3 (Fig. 21K). .... ***Monatractides*** Viets, 1926 [Eleven described species. Mexico, Guatemala, Honduras (Wiles 2005), Costa Rica, Panama (Goldschmidt et al. 2016), Colombia, Ecuador (unpublished data). *Monatractides* has been upgraded from subgenus in Torrenticola to full generic rank by Wiles (1997b). Habitat: streams]

Key to Oxidae Viets, 1926

Note: The genus ***Flabellifrontipoda*** Lundblad, 1947 has been downgraded to subgenus within ***Frontipoda*** Koenike, 1891 by Smit (2002). Originally the species with a more circular idiosoma in cross section, and wider unsclerotized medio-dorsal strip (Fig. 8E,F) were classified as ***Oxus*** Kramer, 1877; the laterally more compressed species, with a narrower medio-dorsal unsclerotized strip (Fig. 8K,L) were classified as ***Frontipoda*** Koenike, 1891. However, as with the description of more species the differences blurred, Di Sabatino et al. (2009) synonymized

Frontipoda with ***Oxus***, and ***Flabellifrontipoda*** Lundblad, 1947 became a subgenus of ***Oxus***. Therefore all neotropical species of the family now belong to the genus ***Oxus*** – in order to sort the meanwhile rather large genus, here we are giving a key to the current subgenera.

1 Most species without a median ventral suture line (Figs 8E, 21L); leg claws simple (Fig. 22M). ..... sg. ***Oxus* s. str.** Koenike, 1891 [Twenty-one described species. Mexico, Guatemala, Costa Rica, Ecuador (unpublished data), Brazil, Peru, Chile, Paraguay, Argentina. Key to Chilean species in Cook (1988), to South American species in Lundblad (1941, 1953). Habitat: standing waters, streams]

1' Most species with a median ventral suture line (Fig. 8K); leg claws with a series of fine (difficult to see) ventral clawlets (Fig. 22N). ..... sg. ***Flabellifrontipoda*** Lundblad, 1947 [Fourteen described species. Honduras (Wiles 2005), Colombia, Bolivia (Fernández et al. 2009), Chile, Argentina. Key to Neotropical species in Cook (1988), to South American species in Lundblad (1953). Habitat: standing waters, streams]

Key to Sperchontidae Thor, 1900

1 Ventro-distal seta at P3 large; spine-like seta medio-distally at P4 (Fig. 22J); Cxgl-1 lying on Cx-II (Fig. 22G arrow). .... **Apeltosperchontinae** Cook, 1974, ***Apeltosperchon*** Besch, 1964 [One described species: *A. schmitzi* Besch, 1964. Chile. Habitat, streams]

1' No large ventro-distal seta at P3, no large seta medio-distally at P4; Cxgl-1 free (Fig. 7E arrow), or obviously secondarily fused with Cx-II (Fig. 22E arrow). .... **Sperchontinae** Thor, 1900, 2

2 (1') Glandularia raised, enlarged and with numerous papillae (Fig. 22A,B). .... ***Sperchonopsis*** Piersig, 1896 [One undescribed species. Mexico (Cramer 1988). Habitat: streams]

2' Glandularia variable, but never with numerous papillae (do no confuse with platelets (Fig. 22C,D,F)). 3

3 (2') P4 relatively long and slender, with two peg-like setae ventrally (Fig. 22O,P). .... ***Sperchon*** Kramer, 1877 [Nine described species. Mexico (Otero-Colina 1987), Guatemala, Honduras (Wiles 2005), Costa Rica (Goldschmidt 2004d), Panama (Goldschmidt et al. 2016), Colombia, Ecuador (unpublished data), Brazil, Argentina. Key to South American species in Lundblad (1953). Habitat: running waters]

3' P4 rather short, without peg-like setae (however though sometimes with ventral projections) (Fig. 22I,K,L,Q). 4

4 (3') Glands on Cx-III shifted to tips of Cx-I; Cxgl-1 on elongated triangular sclerite (laterally fused with Cx-II, medially with Cx-III) (Fig. 22F); P3 without ventral projection (Fig. 22L). .. ***Notosperchonopsis*** Besch, 1964 [Three described species. Peru, Argentina, Chile. Key to species in Cook (1988). Habitat: runnings waters, lakes, springs]

4' Glands on Cx-III lying on Cx-III close to suture with Cx-IV; Cxgl-1 on a relatively small sclerite (between Cx-II and Cx-III or fused with Cx-II) (Fig. 22E arrow, H); P3 bearing long (in one species short, but clearly visible) ventral projection (Fig. 22K,Q). ..... ***Illiesiella*** Besch, 1964 [Six described species. Chile, Argentina. Key to species in Cook (1988). Cook (1988) raised *Illiesiella* (beforehand a subgenus in *Notosperchonopsis*) to full generic rank, and synonymized the subgenus *Andinosperchon* with *Illiesiella*. Habitat: streams, waterfalls]

Key to Anisitsiellidae Koenike, 1910

1 Venter soft or with separated plates (Fig. 23A,C); dorsum with small sclerites or two larger plates (Fig. 23B,D); IV-leg without claws (Fig. 23K). .... **Nilotoniinae** Viets, 1929, ***Nilotonia*** Thor, 1905, 2

1' Venter with complete shield (Figs 9H, 23E,G); dorsum more or less completely covered by large plate (Fig. 23F,H); IV-leg with or without claws. .... **Anisitsiellinae** Koenike, 1910, 4

2 (1) Claws of legs-I-III without clawlets (Fig. 23N–P); venter and dorsum mainly soft with small sclerites (Fig. 23A,B). .... sg. ***Bolivartonia*** Orghidan & Gruia, 1983 [Three described species. Costa Rica (Goldschmidt 2004e), Venezuela. Habitat: interstitial]

2' Claws of legs-I-III with dorsal and/or ventral clawlets (Fig. 23Q); venter and dorsum mainly soft (Fig. 23I,J) or with more extensive sclerotizations (Fig. 23D,C). 3

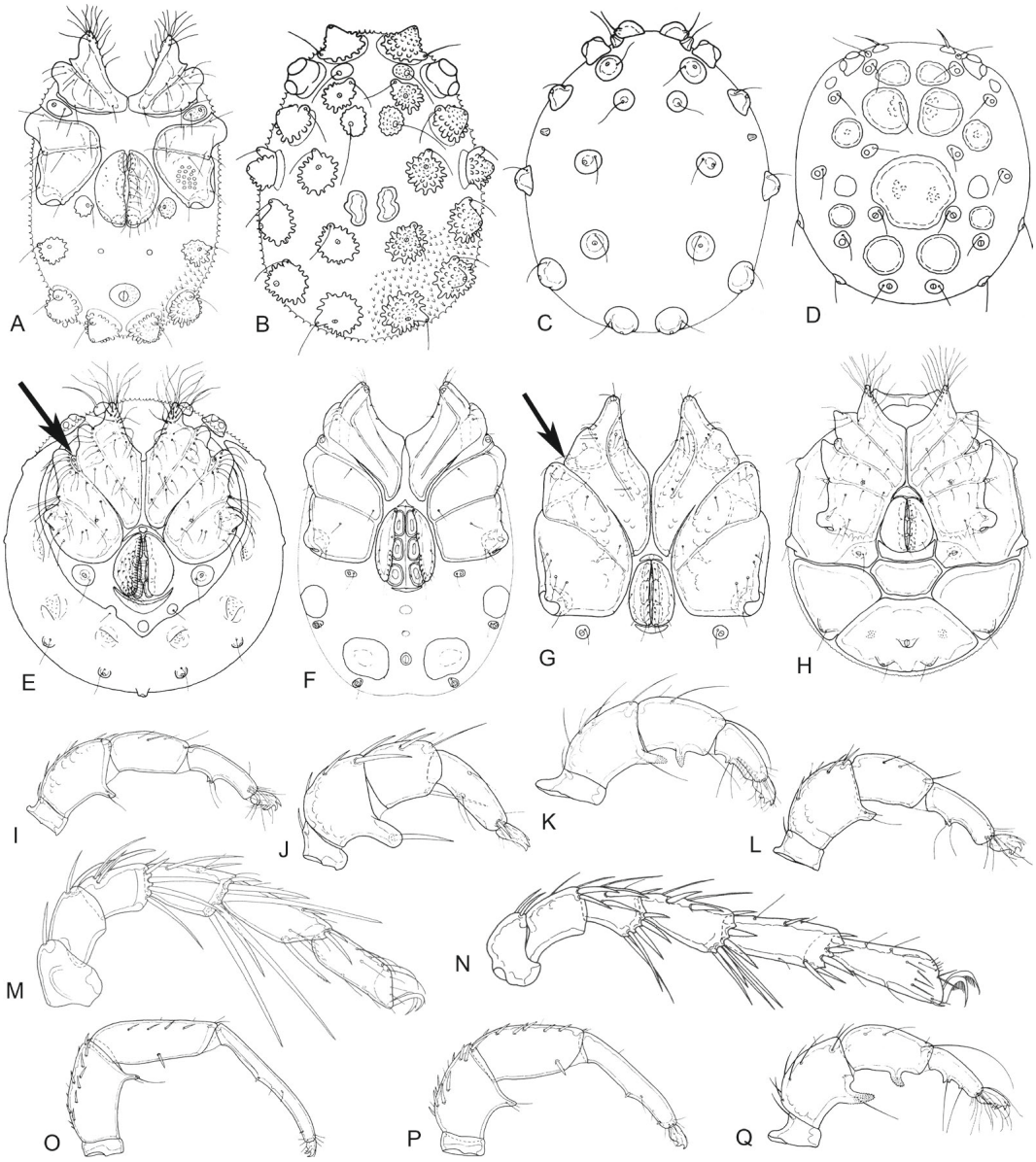


Fig. 22. A. *Sperchonopsis nova*, male, idiosoma ventral (Cook 1974). **B.** *Sperchonopsis nova*, male, idiosoma dorsal (Cook 1974). **C.** *Sperchon* (*Palpisperchon*) *crassipalpis*, male, idiosoma dorsal (Cook 1974). **D.** *Sperchon* (*Hispidosperchon*) *nilgiris*, male, idiosoma dorsal (Cook 1974). **E.** *Illiesiella cataphracta*, male, idiosoma ventral (arrow pointing at Cxgl-1) (Cook 1988). **F.** *Notosperchonopsis crassipalpis*, male, idiosoma ventral (Cook 1988). **G.** *Apeltosperchon schmitzi*, male, coxae and genital field (arrow pointing at Cxgl-1) (Cook 1988). **H.** *Illiesiella circularis*, male, idiosoma ventral (Cook 1988). **I.** *Notosperchonopsis pauciscutata neuquenensis*, female, palp (Cook 1980). **J.** *Apeltosperchon schmitzi*, male, palp (Cook 1980). **K.** *Illiesiella cataphracta*, male, palp (Cook 1988). **L.** *Notosperchonopsis pauciscutata neuquenensis*, male, palp (Cook 1988). **M.** *Oxus* (*Oxus*) *mesoamericana*, female, I-leg (Cook 1980). **N.** *Oxus* (*Flabellifrontipoda*) *neotropica*, male, I-leg (Cook 1980). **O.** *Sperchon mexicanus*, female, palp (Cook 1980). **P.** *Sperchon neotropicus*, female, palp (Cook 1980). **Q.** *Illiesiella circularis*, female, palp (Cook 1988).

3 (2') III-leg with sexual dimorphism: III-leg-6 of male enlarged (Fig. 23Q,R); venter and dorsum soft with small sclerites (Fig. 23I,J). .... sg. ***Guanacastonia*** Goldschmidt, 2004 [One described species: *N. (Guanacastonia) pablito* Goldschmidt, 2004. Costa Rica (Goldschmidt 2004e). Habitat: springs]

3' III-leg of male without sexual dimorphism; venter and dorsum with extensive secondary sclerotization (Fig. 23C,D). ....sg. ***Mamersonia*** K. Viets, 1954 [Two described species. Costa Rica (Goldschmidt 2004e), Ecuador (unpublished data), Brazil. The species described by Bader (1995) from Trinidad have meanwhile been revised and assigned to *Anisitsiella* (Smit 2019). Habitat: lakes, waterfalls]

4 (1') IV-leg-6 with claws. 5

4' IV-leg-6 without claws. 7

5 (4) Claws at IV-leg-6 tiny (Fig. 23L); P2 with blade-like protrusion (Fig. 23M). .... ***Fuenticola*** Goldschmidt, 2004 [One described species: *F. sancheziana* Goldschmidt, 2004. Costa Rica (Goldschmidt 2004e). Habitat: rheocrene spring]

5' Claws at IV-leg-6 mid-sized to large; palp variable. 6

6 (5') Dorsal plate bearing four pairs of glandularia, further four pairs of glandularia on small platelets in the membranous suture between dorsal and ventral shield (Fig. 23F); glands on Cx-III rather medial, suture line across Cx-III immediately lateral to these glands; suture between Cx-III and -IV complete (Fig. 23E). ..... ***Bandakia*** Thor, 1913 [Three described species. Mexico (Cramer & Smith 1991), Costa Rica (Goldschmidt 2004e). Habitat: springs, streams, interstitial]

6' Dorsal plate bearing six pairs of glandularia; glands on Cx-III more lateral, no suture line across Cx-III; suture between Cx-III and -IV incomplete (Fig. 23G). .... ***Sigthoriella*** Besch, 1964 [One described species: *S. hygropetrica* Besch, 1964. Chile. Habitat: mosses in hygropetric zone]

7 (4') A pair of striking glands near the anterior edge of Cx-II (close to suture with Cx-I); posterior margins of Cx-IV not or hardly visible, completely fused with ventral shield (Fig. 9H). .... ***Anisitsiellides*** Lundblad, 1941 [Five described species. Colombia, Chile, Argentina. Habitat: streams]

7' Anterior edge of Cx-II without glands (do not confuse with Cxgl-1 between Cx-II and -III), posterior margin of Cx-IV clearly visible (Fig. 24A,C,E). 8

8 (7') Posterior margin of Cx-IV sharp-pointed, closely appressed to genital field (Fig. 24E). ..... ***Rutacarus*** Lundblad, 1937 [Four described species. Panama (Valdecasas 2008a), Venezuela, Ecuador (unpublished data), Brazil, Argentina. Key to Neotropical species in Valdecasas (2008a). Habitat: streams]
Note: Most probably *Mamersopsides neotropica* Goldschmidt, 2004 from Costa Rica as well belongs to this genus (Goldschmidt 2004e).

8' Posterior margin of Cx-IV rounded or bluntly-pointed. 9

9 (8') Cx-IV closely appressed to genital field, forming deep genital bay (Fig. 24A); dorsal shield surrounded by small platelets (Fig. 24B). ..... ***Mamersella*** Viets, 1929 [One described species: *M. mesoamericana* Otero-Colina, 1987. Mexico (Otero-Colina 1987). Habitat: lakes]

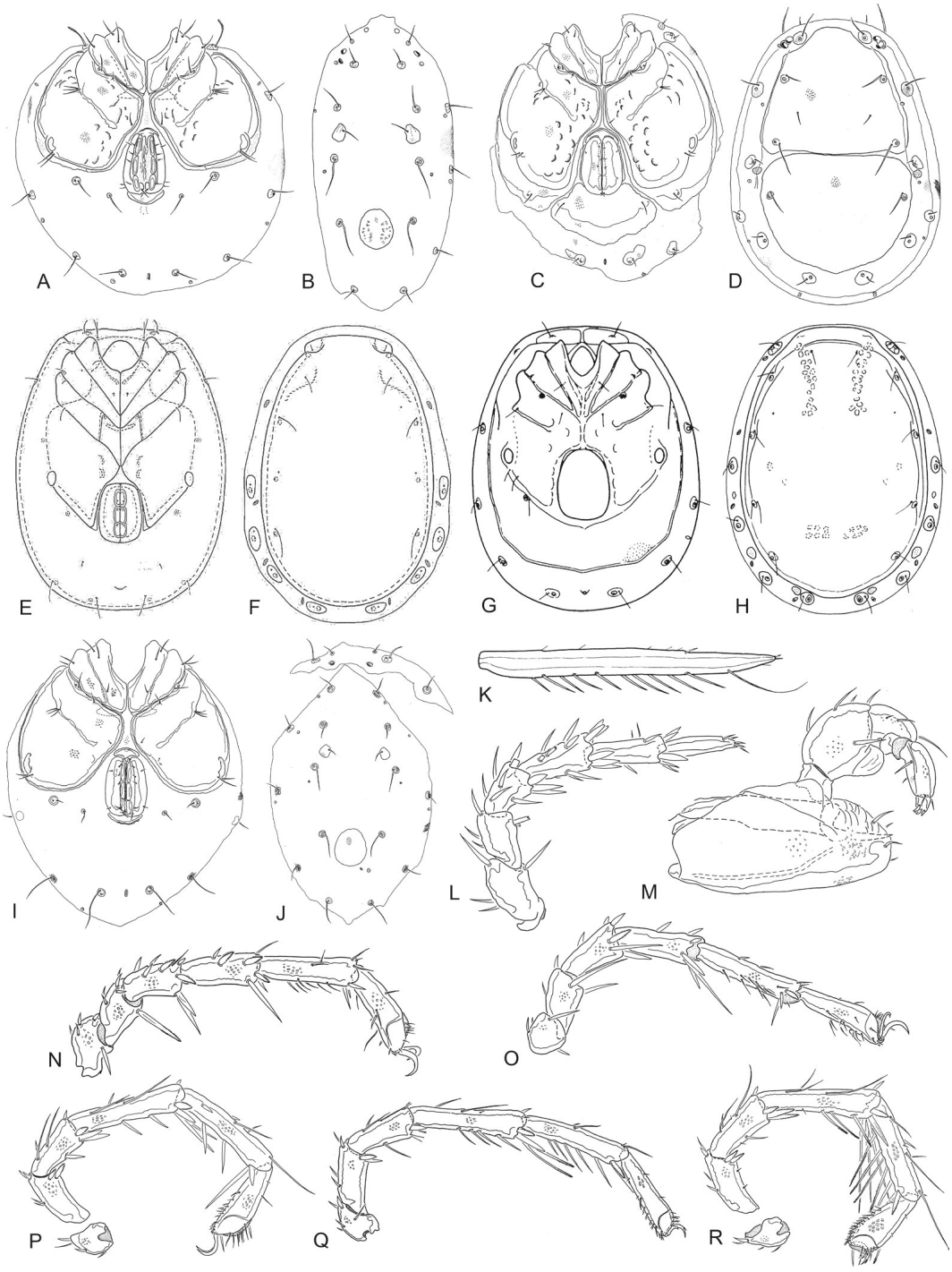
9' Cx-IV not closely appressed to genital field, genital bay shallow (Fig. 24C); large dorsal shield covering dorsum completely (Fig. 24D). ..... ***Anisitsiella*** Daday, 1905 [Two described species. Mexico (Cramer & Smith 1993), Costa Rica (Goldschmidt 2004e), Colombia, Trinidad (Smit 2019), Brazil, Paraguay, Argentina. Habitat: lakes, swamps, slow running streams]
Note: *Mamersellides* Lundblad, 1937 is regarded as a junior synonym of *Anisitsiella*; *M. ventriperforatus* is regarded as junior synonym of *A. aculeata* (Panesar 2004).

Note: Key to South American species of the family in Lundblad (1941).

Key to Omartacaridae Cook, 1963

1 Ac numerous (Fig. 10G,I). .... ***Omartacarus*** Cook, 1963 [Seven described species. Mexico, Haiti, Guatemala, Costa Rica (Goldschmidt 2004d), Panama (Goldschmidt et al. 2016), Chile, Argentina. Habitat: interstitial]

1' Three to four pairs of Ac (Fig. 10H). .... ***Maharashtracarus*** Cook, 1967 [One described species: *M. neotropicus* Cook, 1980. Mexico (Cramer 1988), Costa Rica. Habitat: interstitial]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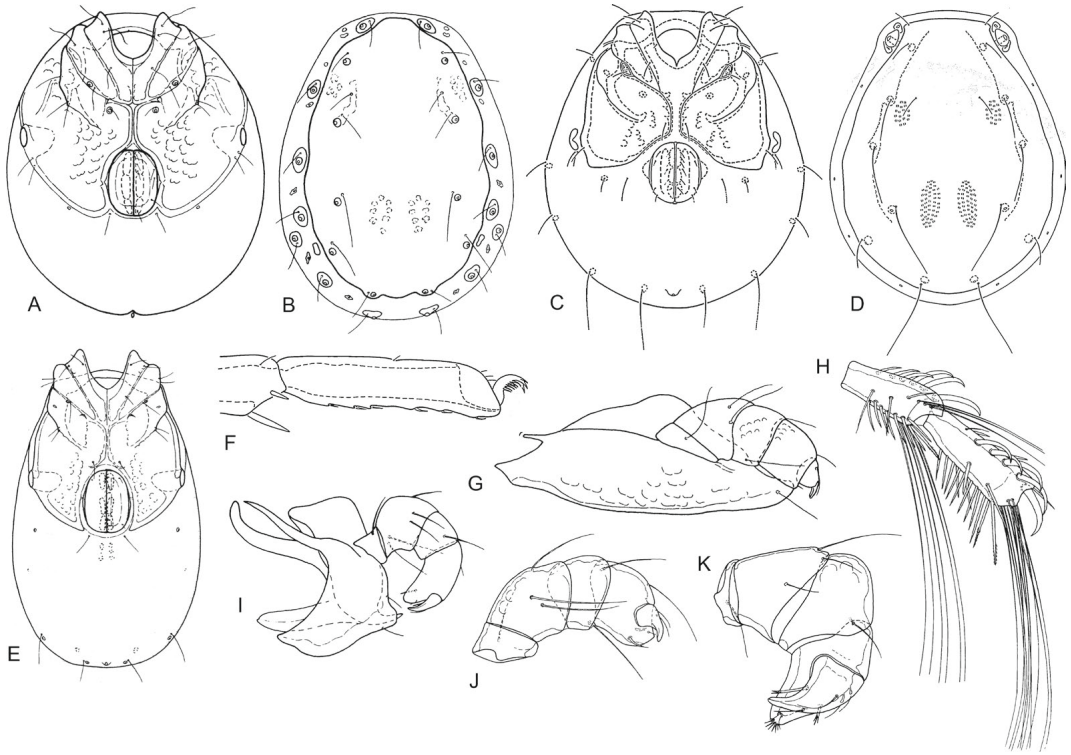


Fig. 24. A. *Mamersella* (s.s.) *maryellenae*, male, idiosoma ventral (Cook 1974). **B.** *Mamersella* (s.s.) *maryellenae*, male, idiosoma dorsal (Cook 1974). **C.** *Anisitsiella costenius*, male, idiosoma ventral (after Cramer & Smith 1993). **D.** *Anisitsiella costenius*, male, idiosoma dorsal (after Cramer & Smith 1993). **E.** *Rutacarus ferradasae*, male, idiosoma ventral (Cook 1980). **F.** *Anisitsiella costenius*, male, I-leg-6 (after Cramer & Smith 1993). **G.** *Geayia nobilis*, male, capitulum and right palp lateral (Cook 1980). **H.** *Geayia nobilis*, male, IV-leg-3/-4 (Cook 1980). **I.** *Krendowskia trodroma*, male, capitulum chelicera and right palp lateral (Cook 1980). **J.** *Geayia amacuzaca*, male, palp (Cook 1980). **K.** *Roqueella mesoamericana*, female, palp (Cook 1980).

Key to Krendowskiidae Viets, 1926

1 Capitulum short, with well developed projections, not attached to protrusible tube (Fig. 24I). ..... ***Krendowskia*** Piersig, 1895 [Fourteen described species. Mexico, Costa Rica (Goldschmidt 2004d), Brazil, Bolivia, Paraguay, Chile, Argentina. Habitat: various running and standing waters]

1' Capitulum longer, without long projections, attached to a protrusible tube (Fig. 24G). 2

2 (1') Antagonistic bristle at P4 short or long, but only slightly thickened (Fig. 24J); terminal segments of IV-leg sometimes with sexual dimorphism (Fig. 24H). .... ***Geayia*** Thor, 1897

◁ **Fig. 23. A.** *Nilotonia* (*Bolivartonia*) *panzuda*, female, idiosoma ventral (Goldschmidt 2004). **B.** *Nilotonia* (*Bolivartonia*) *panzuda*, female, idiosoma dorsal (Goldschmidt 2004). **C.** *Nilotonia* (*Mamersonia*) *cascada*, female, idiosoma ventral (Goldschmidt 2004). **D.** *Nilotonia* (*Mamersonia*) *cascada*, female, idiosoma dorsal (Goldschmidt 2004). **E.** *Bandakia mexicana*, female, idiosoma ventral (after Cramer & Smith 1991). **F.** *Bandakia mexicana*, female, idiosoma dorsal (after Cramer & Smith 1991). **G.** *Sigthoriella hygropetrica*, male, idiosoma ventral (genital flaps missing) (Cook 1974). **H.** *Anisitsiellides lundbladi*, male, idiosoma dorsal (Cook 1980). **I.** *Nilotonia* (*Guanacastonia*) *pablito*, female, idiosoma ventral (Goldschmidt 2004). **J.** *Nilotonia* (*Guanacastonia*) *pablito*, female, idiosoma dorsal (Goldschmidt 2004). **K.** *Nilotonia* (*Mamersonia*) *amazonica*, female, IV-leg-6 (Cook 1974). **L.** *Fuenticola sancheziana*, male, IV-leg (Goldschmidt 2004). **M.** *Fuenticola sancheziana*, male, capitulum, chelicera and right palp lateral (Goldschmidt 2004). **N.** *Nilotonia* (*Bolivartonia*) *panzuda*, male, I-leg (Goldschmidt 2004). **O.** *Nilotonia* (*Bolivartonia*) *panzuda*, male, II-leg (Goldschmidt 2004). **P.** *Nilotonia* (*Bolivartonia*) *panzuda*, male, III-leg (Goldschmidt 2004). **Q.** *Nilotonia* (*Guanacastonia*) *pablito*, female, III-leg (Goldschmidt 2004). **R.** *Nilotonia* (*Guanacastonia*) *pablito*, male, III-leg (Goldschmidt 2004).

[Twenty-one described species. Mexico, Costa Rica, Venezuela, Ecuador (unpublished data), Brazil, Paraguay, Argentina. Habitat: various running and standing waters]

2' Antagonistic bristle at P4 short and thickened, pectinate (Fig. 24K); IV-leg without sexual dimorphism. ..... ***Roqueella*** Lundblad, 1930 [Eleven described species. Costa Rica, Brazil, Peru. Habitat: streams]

Key to Arrenuridae Thor, 1900

1 Palp not uncate (Fig. 10L). ..... ***Micruracaropsis*** Viets, 1939 [One described species: *M. phytotelmaticola* (Viets, 1939). Suriname. Habitat: phytotelmata]

1' Palp uncate (Fig. 25I). 2

2 (1') With dorsal furrow (Figs 10F, 11E, 25E). ..... ***Arrenurus*** Dugès, 1834 [Two hundred and twelve described species. Mexico (Cramer & Cook 1992a, 1992b; Rivas-Lechuga & Cramer-Hemkes 1998; Ramírez-Sánchez & Rivas 2013), Cuba, Haiti, Dominican Republic, Guatemala, Costa Rica, Panama (Goldschmidt et al. 2016), Venezuela, Colombia, Guyana, Suriname, Ecuador, Brazil, Peru, Bolivia, Chile, Paraguay, Argentina (Rosso de Ferradás 2006), Uruguay. Key to South American species in Lundblad (1944); key to males of eleven species of the subgenus *Megaluracarus* from Brazil in Viets (1936). Cramer & Cook (1992a) downgraded *Dadayella* to a subgenus in *Arrenurus*. Habitat: temporary and permanent standing waters (lakes, pools, ponds, ditches, marshes), slow flowing streams, springs]

2' Without dorsal furrow (Fig. 25B,D). 3

3 (2') **Male**: cauda indistinctly set off; all Ac on wing-like plates beside the gonopore (Fig. 25A,B) (female unknown). ..... ***Thoracophoracarus*** Viets, 1914 [One described species: *T. simplex* Cook, 1988 Chile, Paraguay (Rosso de Ferradás & Böttger 1997). Habitat: streams, ponds]

3' **Male**: cauda distinctly set off; a pair of acetabula lying free in soft integument of the male gonopore (Fig. 25C,D,K). ..... ***Xenthoracaphorus*** Cook, 1988 [One described species: *X. chilensis* Cook, 1988. Chile. Smit (2020) is rising *Xenthoracaphorus* (originally described as sg. in *Thoracophoracarus*) to the rank of a full genus, based upon the Ac lying in the gonopore – a character unique within the Arrenuridae. Habitat: streams]

Key to Hungarohydracaridae Motaş & Tanasachi, 1959

1 U-shaped **ridge** on dorsal shield (Fig. 25F,G); **male**: Ac on heart-shaped plates (Fig. 12C); **female**: Ac on wing-like plates lateral to gonopore (Figs 7K, 12D); P2 with disto-medial patch of thickened setae (Fig. 12F,G). .. .. ***Stygarrenurus*** Cook, 1980 [Two described species. Mexico (Cramer & Cook 1996), Costa Rica, Panama (Goldschmidt et al. 2016). Cramer & Cook (1996) transferred *Stygarrenurus* from Arrenuridae to Hungarohydracaridae. Habitat: interstitial, streams, springs]

1' No **dorsal** ridge (Fig. 25H); **male**: Ac in two dense rows beside the gonopore as well as some on genital plates (Figs 12A, 25J); **female**: Ac on wing-like plates lateral and slightly anterior to gonopore (Fig. 12B); P2 with two heavy ventral setae, no disto-medial patch of thickened setae (Fig. 12E). ..... ***Cubanohydracarus*** Orghidan & Gruia, 1980 [One described species: *C. elegans* Orghidan & Gruia, 1980. Cuba. One undescribed species. Costa Rica (Goldschmidt 2004d). Habitat: interstitial, streams]

Key to Momoniidae Viets, 1926

1 Dorsal **shield** complete (Fig. 26A). 2

1' Dorsal shield **separated** in two parts (Fig. 13F). 3

2 (1) P4 ventrally and ventro-laterally with large projections and a heavy seta, P3 with ventral or ventro-lateral projection (Fig. 26B,C). .... ***Cladomomonia*** Orghidan & Gruia, 1980 [One described species: *C. mirifica* Orghidan & Gruia, 1980. Cuba. Habitat: interstitial]

2' P4 ventral with two heavy setae on small protrusions (no large projections), P3 ventrally smooth (Fig. 26D) (description based on nymphs, adults unknown). ..... ***Momoniella*** Viets, 1929 [One described species: *M. sudamericana* Cook, 1988. Chile. Habitat: streams]

3 (1') Separate plate (or pair of platelets) posterior to genital field (Fig. 26E,F); **male**: three pairs

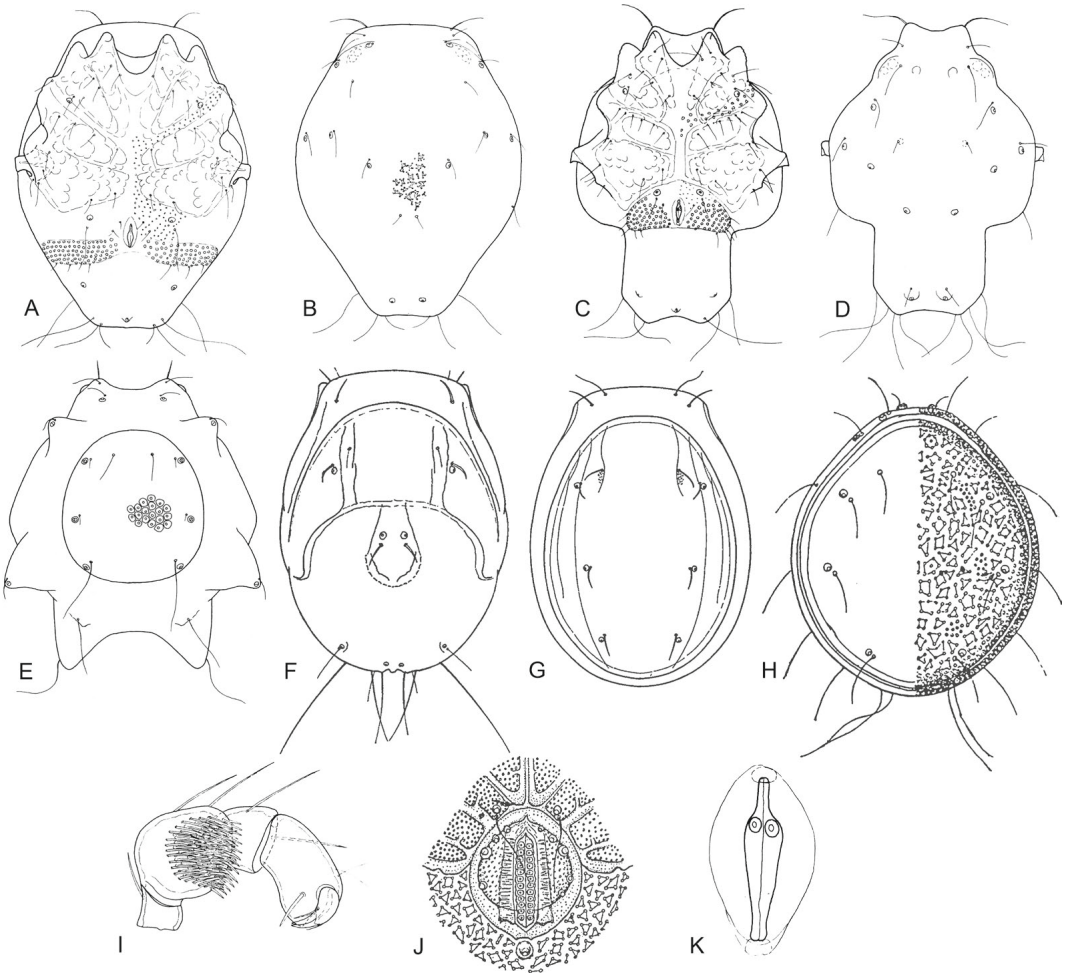


Fig. 25. **A**. *Thoracophoracarus simplex*, male, idiosoma ventral (Cook 1988). **B.** *Thoracophoracarus simplex*, male, idiosoma dorsal (Cook 1988). **C**. *Xenthoracaphorus chilensis*, male, idiosoma ventral (Cook 1988). **D.** *Xenthoracaphorus chilensis*, male, idiosoma dorsal (Cook 1988). **E.** *Arrenurus valencius*, female, idiosoma dorsal (Cook 1980). **F.** *Stygarrenurus armoniensis*, male, idiosoma dorsal (after Cramer & Cook 1996). **G.** *Stygarrenurus armoniensis*, female, idiosoma dorsal (after Cramer & Cook 1996). **H.** *Cubanohydracarus elegans*, male, idiosoma dorsal (after Orghidan & Gruia 1980). **I.** *Arrenurus neoexpansus*, male, palp (Cook 1980). **J.** *Cubanohydracarus elegans*, male, genital field (after Orghidan & Gruia 1980). **K**. *Xenthoracaphorus chilensis*, male, gonopore region (Cook 1988).

of Ac in parallel rows in the gonopore (Figs 26E, 13D); **female**: three pairs of Ac on large genital flaps (Figs 26F, 13E). .... ***Notomomonia*** Cook, 1988 [Three described species. Chile (Cook 1988). Habitat: streams]

3' **No** separate platelets posterior to genital field (Fig. 26G,H); **male**: Ac fused with ventral shield beside to the gonopore (Fig. 26G); **female**: Ac on small genital plates (Fig. 26H). .... ***Xenomomonia*** Orghidan & Gruia, 1977 [One described species: *X. subcentrata* Orghidan & Gruia, 1977. Cuba, Haiti (Cook 1981). Habitat: interstitial]

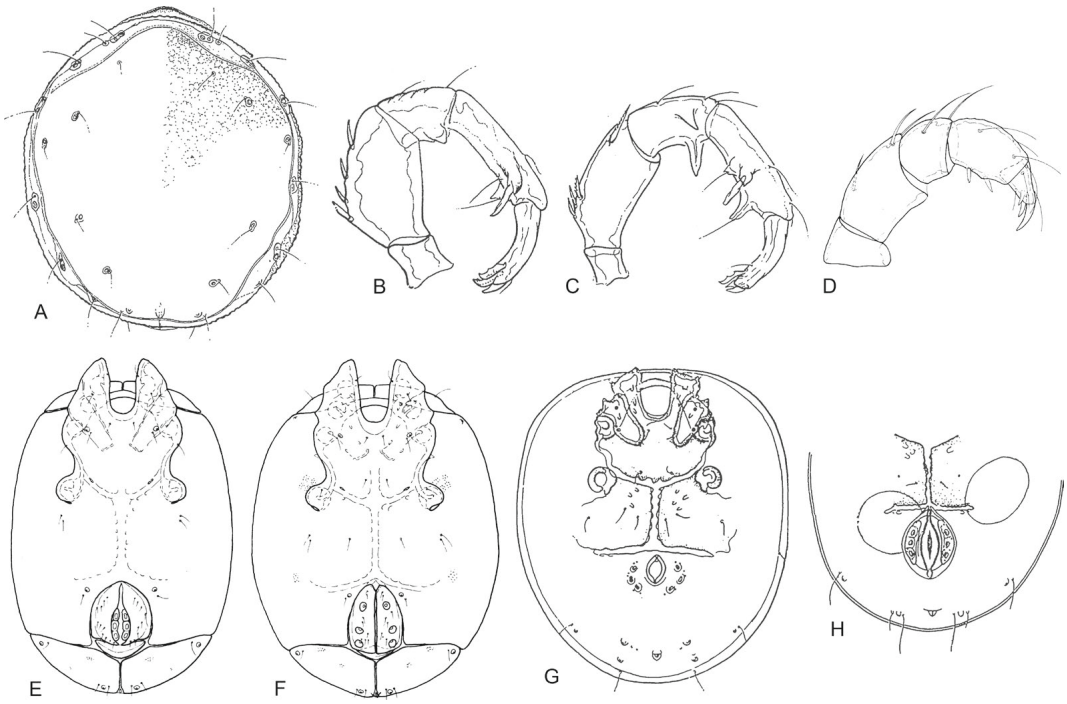


Fig. 26. A. *Cladomomonia mirificata*, female, idiosoma dorsal (after Orghidan & Gruia 1983). **B.** *Cladomomonia mirificata*, male, palp (after Orghidan & Gruia 1983). **C.** *Cladomomonia mirificata*, female, palp (after Orghidan & Gruia 1983). **D.** *Momoniella sudamericana*, deutonymph, palp (Cook 1988). **E.** *Notomomonia alza*, male, idiosoma ventral (Cook 1988). **F.** *Notomomonia alza*, female, idiosoma ventral (Cook 1988). **G.** *Xenomomonia subcentrata*, male, idiosoma ventral (after Orghidan et al. 1977). **H.** *Xenomomonia subcentrata*, female, caudal end of idiosoma ventral (after Orghidan et al. 1977).

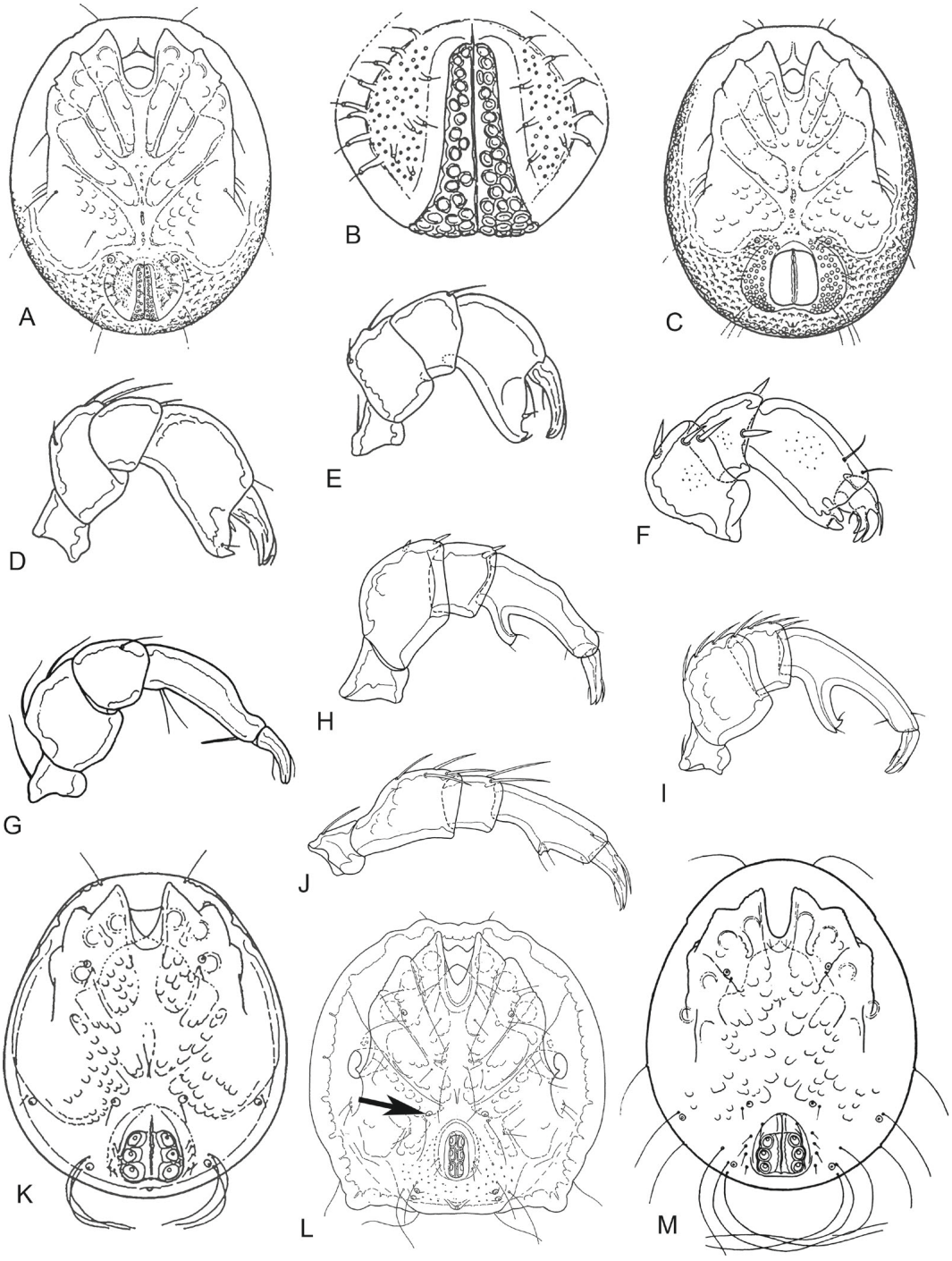
Key to Mideopsidae Koenike, 1910

Pešić et al. (2013) synonymized Mideopsellinae Lundblad, 1937 and Phreatomideopsinae Schwoerbel, 1986 with Mideopsidae Koenike, 1910; the subgenera *Mideopsides* Lundblad, 1943, *Neoxystonotus* Lundblad, 1927 and *Xystonotus* Wolcott, 1900 are redefined and proposed as distinct genera.

1 Three pairs of Ac (in Neotropical species!) (Figs 27K–M, 28A–D); palp uncate or not uncate (Fig. 27E–J). .... **Mideopsinae** Koenike, 1910, 2

1' Ac numerous (Fig. 27A–C); palp uncate (Fig. 27D). .... **Plaumanniinae** Lundblad, 1936, ***Plaumannia*** Lundblad, 1936
[Two described species. Brazil, Paraguay. Key to species in Lundblad (1943b). Habitat: streams, springs]

Fig. 27. A. *Plaumannia crenophila*, male, idiosoma ventral (after Lundblad 1943). **B.** *Plaumannia crenophila*, male, genital field (after Lundblad 1943). **C.** *Plaumannia crenophila*, female, idiosoma ventral (after Lundblad 1943). **D.** *Plaumannia crenophila*, male, palp (after Lundblad 1943). **E.** *Mideopsella forficipalpis*, male, palp (after Lundblad 1943). **F.** *Phreatomideopsis arrenuripalpis*, female, palp (P-1 missing) (Pešić et al. 2013). **G.** *Mideopsides gibberipalpis*, female, palp (Pešić et al. 2013). **H.** *Neoxystonotus reelfootensis*, male, palp (Pešić et al. 2013). **I.** *Mideopsis barri*, female, palp (Pešić et al. 2013). **J.** *Mideopsis fibrosa*, female, palp (Pešić et al. 2013). **K.** *Mideopsella forficipalpis*, female, idiosoma ventral (after Lundblad 1943). **L.** *Neoxystonotus reelfootensis*, male, idiosoma ventral (arrow pointing at Cxgl-2) (Pešić et al. 2013). **M.** *Mideopsides gibberipalpis*, female, idiosoma ventral (Pešić et al. 2013). ▷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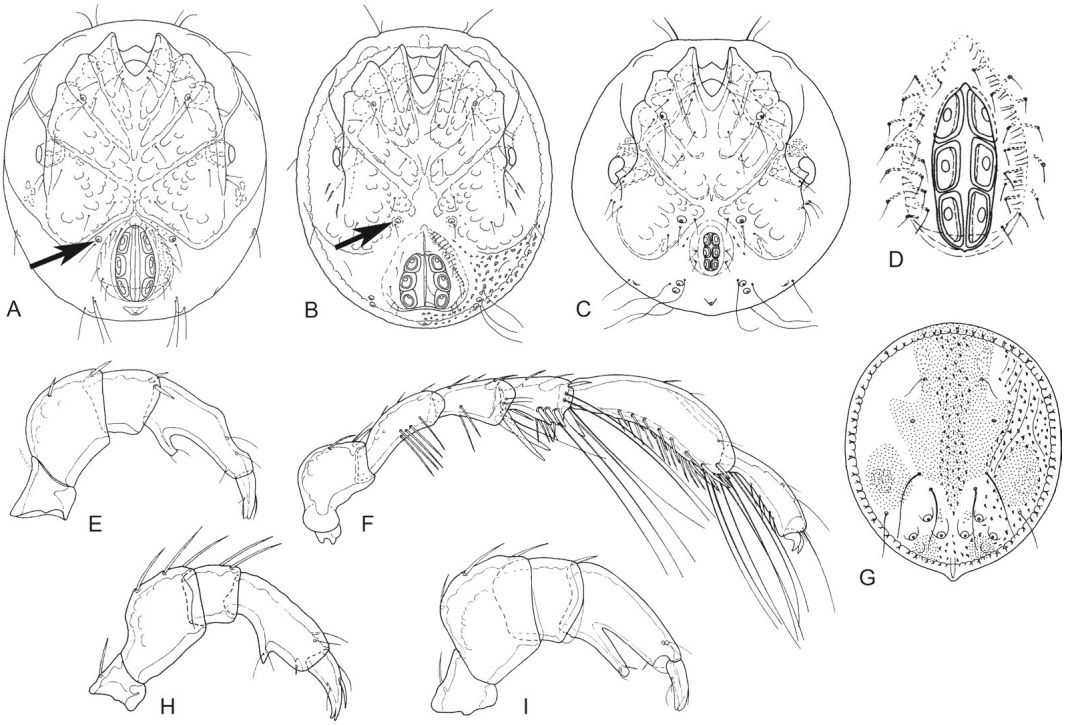


Fig. 28. A. *Xystonotus mexicana*, female, idiosoma ventral (arrow pointing at Cxgl-2) (Cook 1980). **B.** *Mideopsis longidens*, female, idiosoma ventral (arrow pointing at Cxgl-2) (Cook 1980). **C.** *Neoxystonotus nobilis*, male, idiosoma ventral (Cook 1980). **D.** *Mideopsis sucaba*, male, genital field (Cook 1980). **E.** *Neoxystonotus nobilis*, male, palp (Cook 1980). **F.** *Neoxystonotus nobilis*, male, IV-leg (Cook 1980). **G.** *Neoxystonotus nobilis*, male, dorsal shield (Cook 1980). **H.** *Mideopsis sucaba*, female, palp (Cook 1980). **I.** *Mideopsis choconensis*, male, palp (Cook 1988).

2 (1) Palp uncate (distal end of P4 much higher than the dorsally inserted proximal end of P5, forming a grasping appendage) (Fig. 27E,F). 3

2' Palp not uncate (distal end of P4 only slightly, if at all, higher than proximal end of P5) (Fig. 27G–J), do not confuse with basal protrusion at P4 (Figs 27H,I, 28E,H,I). 4

3 (2) Ventrodistal projection at P4 long, P5 slender (Fig. 27E); Ac in rows close to gonopore (Fig. 27K). ..... ***Mideopsella*** Lundblad, 1927 [One described species: *M. forficipalpis* Lundblad, 1937. Brazil, Paraguay. Habitat: streams]

3' Ventrodistal projection at P4 short, P5 stocky (Fig. 27F); Ac in rows rather distant from gonopore (Fig. 11D). .... ***Phreatomideopsis*** Schwoerbel, 1986 [One described species: *P. arrenuripalpis* Schwoerbel, 1986. Chile. Habitat: interstitial]

4 (2') Ridges (continuations of suture lines between Cx-III and -IV) extending antero-laterally from region of insertion of IV-leg (Fig. 27L); P4 with two ventral setae (usually) near middle of segment on a (small or large) projection (Fig. 27J). 5

4' No ridges extending antero-laterally from region of insertion of IV-leg (Fig. 27M); P4 with two ventral setae at the proximal end of segment (Fig. 27G). .... ***Mideopsides*** Lundblad, 1943 [Five described species. Mexico, Guatemala, Costa Rica, Suriname, Brazil, Peru. Habitat: running waters]

5 (4) Cxgl-2 located at same level or slightly anterior to first pair of Ac (Fig. 28A arrow); Cx-IV without projections partially covering insertions of IV-leg (Fig. 28A); swimming setae typically absent. .... ***Xystonotus*** Wolcott, 1900 [Two described species. Mexico, Brazil (Pešić et al. 2015a). Habitat: streams, springs, phytotelmata]

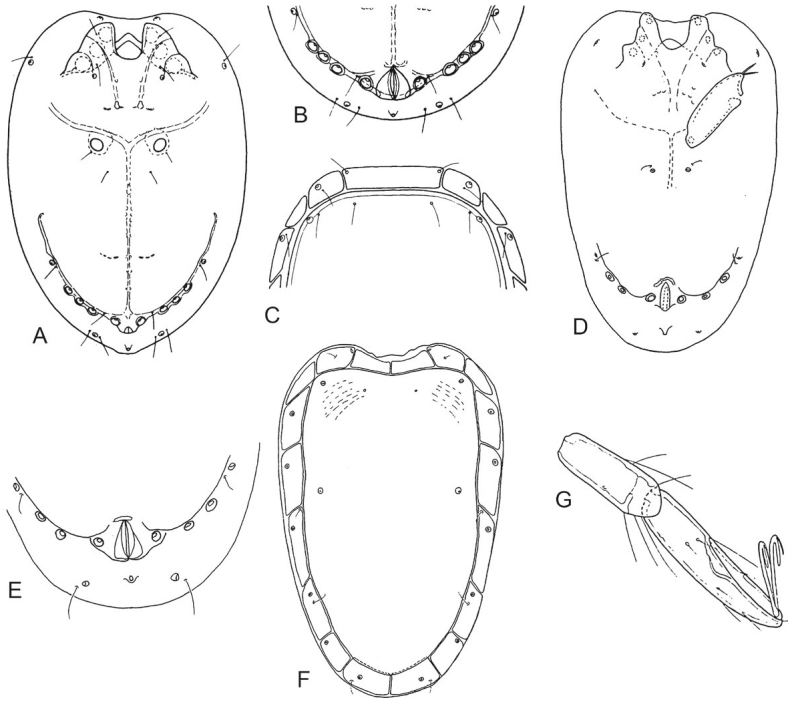


Fig. 29. A. *Lethaxonella argentinensis*, male, idiosoma ventral (Cook 1980). **B.** *Lethaxonella argentinensis*, female, caudal end of idiosoma ventral (Cook 1980). **C.** *Lethaxonella argentinensis*, female, anterior end of idiosoma dorsal (Cook 1980). **D.** *Transitia carlosi*, male, idiosoma ventral (Valdecasas 2010). **E.** *Transitia carlosi*, female, caudal end of idiosoma ventral (Valdecasas 2010). **F.** *Transitia carlosi*, male, idiosoma dorsal (Valdecasas 2010). **G.** *Lethaxonella argentinensis*, male, I-leg-5/ -6 (Cook 1980).

5' Cxgl-2 located well anterior to genital field (Figs 27L arrow, 28B arrow); Cx-IV with short (in some species hardly visible) projections partially covering insertions of IV-leg (Figs 27L, 28B); swimming setae present (Fig. 28F). 6

6 (5') Gonopore flanked by two or three pairs of short setae (Fig. 28C); P4 with a well developed ventral projection (Fig. 28E); **male**: IV-leg with sexual dimorphism (with a pronounced elongation and curvature of IV-leg-5 (Fig. 28F)); dorsal shield with second and third pair of dorso-glandularia often grouped together medially at posterior end (Fig. 28G). .... ***Neoxystonotus*** Lundblad, 1927 [Fourteen described species. Mexico, Costa Rica, Cuba, Brazil, Peru, Paraguay. Habitat: standing waters, running waters]

6' Gonopore flanked by six to numerous pairs of short setae (Fig. 28D); P4 with ventral projections varying from slightly (Fig. 28H) to well developed (Fig. 28I); no sexual dimorphism of either the legs or position of the dorsal glandularia. .... ***Mideopsis*** Neuman, 1880 [Twenty species described. Mexico, Costa Rica, Panama (Goldschmidt et al. 2016), Suriname, Ecuador (unpublished data), Brazil, Chile, Paraguay, Argentina. Key to South American species in Lundblad (1943b, 1953). Habitat: running waters, standing waters]

Key to Lethaxonidae Cook, Smith & Harvey, 2000

1 Ac four (up to six in Nearctic species) pairs (Fig. 29A,B); **female**: antero-medial dorsal platelets fused (Fig. 29C); gonopore between or slightly anterior to Ac (Fig. 29B); **male**: antero-medial dorsal platelets separated; gonopore posterior to Ac (Fig. 29A). .... ***Lethaxonella*** Cook, 1963 [One species described: *L. argentinensis* Cook, 1980. Argentina. Cook et al. (2000) shifted *Lethaxonella* from Axonopsinae to Lethaxonidae. Habitat: stream]

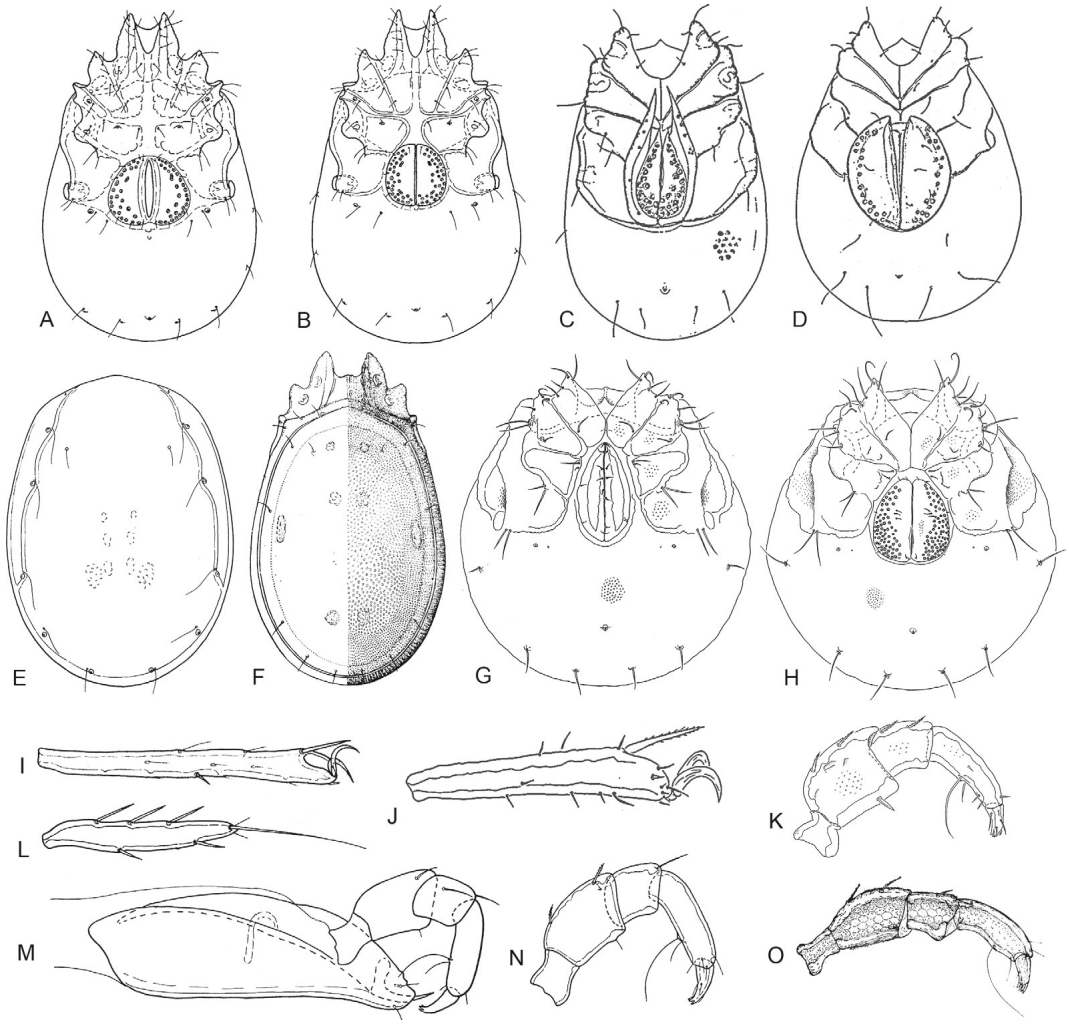


Fig. 30. A. *Tubomixdea voldroguea*, male, idiosoma ventral (Cook 1981). **B.** *Tubomixdea voldroguea*, female, idiosoma ventral (Cook 1981). **C.** *Siboneyacarus sordidus*, male, idiosoma ventral (after Orghidan et al. 1977). **D.** *Siboneyacarus sordidus*, female, idiosoma ventral (after Orghidan et al. 1977). **E.** *Tubomixdea voldruguea*, female, idiosoma dorsal (Cook 1981). **F.** *Mixdea composita*, male, idiosoma dorsal (after Orghidan & Gruia 1980). **G.** *Rheolimnesia costarricense*, male, idiosoma ventral (Goldschmidt 2004). **H.** *Rheolimnesia costarricense*, female, idiosoma ventral (Goldschmidt 2004). **I.** *Protolimnesia interstitialis*, female, IV-leg-6 (Cook 1980). **J.** *Rheolimnesia costarricense*, male, IV-leg-6 (Goldschmidt 2004). **K.** *Rheolimnesia costarricense*, male, palp (Goldschmidt 2004). **L.** *Neomamersa decussa*, male, IV-leg-6 (Cook 1980). **M.** *Tubomixdea voldruguea*, female, gnathosoma (Cook 1981). **N.** *Tubomixdea voldroguea*, male, palp (Cook 1981). **O.** *Mixdea composita*, male, palp (after Orghidan & Gruia 1980).

1' Ac three pairs (Fig. 29D,E); **both sexes**: antero-medial dorsal platelets separated (Fig. 29F); gonopore between Ac (Fig. 29D,E). .. .. ***Transitia*** Valdecasas, 2010 [One species described: *T. carlosi* Valdecasas, 2010. Panama (Valdecasas 2010). Habitat: interstitial]

Key to Limnesiidae Thor, 1900

1 IV-leg-6 with terminal claws (Fig. 30I,J). . 2

1' IV-leg-6 without terminal claws (Fig. 30L). 14

2 (1) Complete dorsal and ventral armour; many Ac (Fig. 30A–H). 3

2' Degree of sclerotization very variable (Fig. 31C,D,O), but never with complete armour (**male**: often with large dorsal plates, **female**: with several platelets); Ac three pairs to many (Figs 31B,F–H,N, 32A,B,D–G). 7

3 (2) Ac **on** genital plates (male) or flaps (female) in both sexes; glandula limnesiae present on Cx-III (Fig. 30A,B); P2 seta short and hair-like (Fig. 30N) (two species from Haiti) or absent (one species from Cuba); capitulum attached to protrusible tube (two species from Haiti) or without protrusible tube (one species from Cuba). .... **Mixdeinae** Orghidan & Gruia, 1980, 4

3' **Female**: Ac **on** genital flaps (Fig. 30D,H), **male**: Ac **between** genital flaps (Figs 3B, 30C,G); glandula limnesiae missing (Fig. 30 C,D,G,H); P2 seta heavy, peg-like (Fig. 30K); capitulum without a tube. .... **Rheolimnesiinae** Goldschmidt, 2004, 5

Note: The genus *Guanacastacarus* Goldschmidt, 2004 lacks terminal claws at IV-leg-6, however the general characters are very typical for the Rheolimnesiinae (thus, the other members of the subfamily bear terminal claws at IV-leg-6), so it is keyed out in both branches of this key – check as well under "1' IV-leg-6 without terminal claws".

4 (3') Gnathosoma attached to protrusible tube (Fig. 30M); dorsal shield with 4–5 pairs of glandularia (Fig. 30E); P2 seta short hair-like (Fig. 30N). ..... ***Tubomixdea*** Cook, 1981
[Two described species. Haiti. Habitat: interstitial]
Note: *Tubomixdea*, originally described as a subgenus of *Mixdea*, is raised to a separate genus by Smit (2020).

4' Gnathosoma without a protrusible tube; dorsal shield without glandularia (Fig. 30F); P2 seta absent (Fig. 30O). .... ***Mixdea*** Orghidan & Gruia, 1980
[One described species: *M. composita* Orghidan & Gruia, 1980. Cuba. Habitat: interstitial]

5 (3') **Male**: Ac on genital flaps (these lie between additional movable flaps) (Fig. 30C), **female**: Ac laterally on movable genital flaps (Fig. 30D); Cx-I, -II and -III meeting medially anterior to (partly under) genital field (Fig. 30C,D). .... ***Siboneyacarus*** Orghidan & Gruia, 1977
[One described species: *S. sordidus* Orghidan & Gruia, 1977. Cuba. Habitat: cave]

5' **Male**: Ac in soft integument under genital flaps (Figs 3B, 7F, 30G), **female**: Ac on movable genital flaps (Figs 30H, 31A); just Cx-I meeting medially (in some species fused) anterior to genital field (Figs 7F, 30G,H, 31A). 6

6 (4') Capitular bay triangular; Ac not in groups (Fig. 30H); IV-leg-6 with claws (Fig. 30J). .... ***Rheolimnesia*** Lundblad, 1953
[Four described species. Costa Rica (Goldschmidt 2004c), Colombia, Venezuela, Ecuador. Habitat: streams, springs, spring brooks, interstitial]

6' Capitular bay rounded; Ac in three groups (Figs 7F (not very clear in male), 31A); IV-leg-6 without claws (Fig. 31E) (see comment above). .... ***Guanacastacarus*** Goldschmidt, 2004
[One described species: *G. mariae* Goldschmidt, 2004. Costa Rica (Goldschmidt 2004c). Habitat: spring]

7 (2') Dorsum and venter with variable degree of sclerotization (several species with large dorsal and large postero-ventral plates, but never with complete dorsal and ventral armour) (Fig. 31B–D,F), coxae separated in four (closely approached) groups (Fig. 31B,F); three or six pairs of Ac, genital flaps movable in **both sexes**, divided into anterior and posterior (in some male as well middle) sclerites (Fig. 31B,F–H); P2 seta hair-like, occasionally absent (Fig. 31I,J). .... **Mixolimnesiinae** Cook, 1988, ***Mixolimnesia*** Cook, 1988
[Eight described species. Chile, Argentina. Habitat: interstitial, streams]

7' Not with the described combination of characters. 8

8 (7') P4 ventrally with five or more long tubercles, large medial seta; P5 elongated, pointed (Fig. 31K,M); three pairs of Ac (Fig. 31N); dorsum with three mid-sized to large plates (no complete dorsal shield, venter soft) (Fig. 31O); IV-leg-6 with small terminal claws (Fig. 31L). .... **Kawamuracarinae** Viets, 1943, ***Kawamuracarus*** Uchida, 1937 (**in part**)
[Three described species. Mexico (Cramer 1987), Costa Rica (pers. obs.). Habitat: interstitial]
Note: In the genus *Kawamuracarus* two species bear very small claws at IV-leg-6 and one species lacks claws at IV-leg-6. The genus

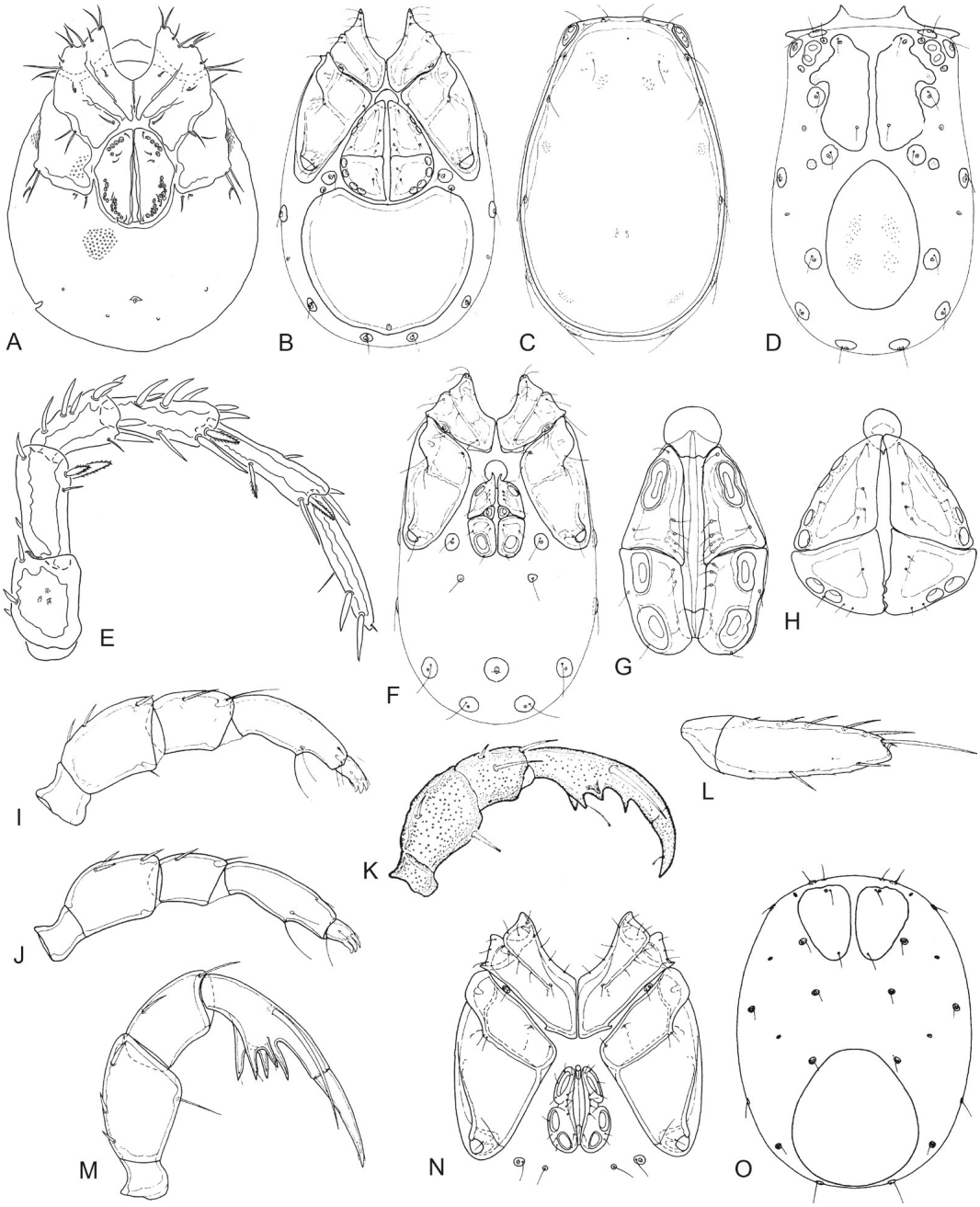


Fig. 31. **A.** *Guanacastacarus mariae*, female, idiosoma ventral (Goldschmidt 2004). **B.** *Mixolimnesia magnifica*, female, idiosoma ventral (Cook 1988). **C.** *Mixolimnesia magnifica*, male, idiosoma dorsal (Cook 1988). **D.** *Mixolimnesia ribagai*, male, idiosoma dorsal (Cook 1988). **E.** *Guanacastacarus mariae*, male, IV-leg (Goldschmidt 2004). **F.** *Mixolimnesia pallida*, male, idiosoma ventral (Cook 1988). **G.** *Mixolimnesia pallida*, female, genital field (Cook 1988). **H.** *Mixolimnesia magnifica*, male, genital field (Cook 1988). **I.** *Mixolimnesia pallida*, male, palp (Cook 1988). **J.** *Mixolimnesia lemba*, male, palp (Cook 1988). **K.** *Kawamuracarus iansmithi*, nymph, palp (Cramer 1987). **L.** *Kawamuracarus expansipes*, male, IV-leg-6 (Cook 1980). **M.** *Kawamuracarus expansipes*, male, palp (Cook 1980). **N.** *Kawamuracarus expansipes*, male, coxae and genital field (Cook 1980). **O.** *Kawamuracarus expansipes*, male, idiosoma dorsal (Cook 1980).

is therefore keyed out in both branches of this key (check as well under "1' IV-leg-6 without terminal claws").

8' P4 without long tubercles, not with the described combination of characters (palps, Ac and sclerotization). 9

9 (8') Ac numerous, arranged in three groups on each side (one large posterior group, two small anterior groups), **male**: grouping always distinct (Fig. 32A), **female**: often not very clear (Fig. 32D); Cx-I medially separated, in some species far separated by capitulum (Fig. 32A,D); **male**: large dorsal plate, female: several dorsal platelets. .... **Neotorrenticolinae** Lundblad, 1936, *Neotorrenticola* Lundblad, 1936
[Nine described species. Mexico (Cramer 1987), Costa Rica (Springer & Gerecke 1992), Venezuela, Colombia, Brazil, Ecuador (unpublished data), Peru, Paraguay. Key to South American species in Lundblad (1953). Habitat: streams, hygropetric]

9' Three pairs to many Ac (however never in three groups as described) (Fig. 32B,E–G); Cx-I medially closely approached or fused (Fig. 32B,E); **if** dorsum is nearly covered, then more than one dorsal plate is present (Fig. 33F). 10

10 (9') Three pairs of Ac (in some species lobed, deeply constricted) (Figs 32F,G, 33A); integument not papillate; lateral eyes **under** the integument (Figs 15H, 33F). .... **Protolimnesiinae** Viets, 1940, 11

10' Three pairs to many Ac (Fig. 32B,E); integument papillate (Fig. 2C,D); lateral eyes in the integument (Fig. 32C,I). .... **Tyrrelliinae** Koenike, 1910, 13

11 (10) IV-leg-1 over twice as long as IV-leg-2 (Fig. 32H); Cx-I to -III small, Cx-IV greatly extended (by far beyond genital field, nearly reaching posterior margin of body) (Fig. 32J); Ac greatly elongated (Fig. 32G). .... ***Limnesides*** Lundblad, 1936
[One described species: *L. epimeratus* Lundblad, 1936. Brazil. Habitat: streams]

11' IV-leg-1 shorter or only slightly longer than IV-leg-2 (Fig. 33B); Cx-IV not or only moderately extended beyond genital field; Ac rounded or lobed (Figs 32F, 33A,B,D,E). 12

12 (11') Cx-I medially fused; genital field large, three pairs of rounded Ac, Ac-2 and -3 close together at posterior end (distance between Ac-1 and Ac-2 more than twice the diameter of Ac); one large ventral plate posteriorly attached to genital field (Fig. 33B); dorsum with large posterior plate and short, crescent-shaped anterior platelet, both without glandularia (Fig. 33C). .... ***Crenolimnesia*** Lundblad, 1938
[One species described: *C. placophora* Lundblad, 1938. Brazil. Habitat: springs]

12' Cx-I medially fused or separated; three pairs of rounded Ac (in two subgenera) (Fig. 33A,D) or lobed to deeply constricted (in one subgenus) Ac (Figs 32F, 33E), distance between Ac-1 and Ac-2 less or hardly more than one diameter of Ac; sclerotization of venter and dorsum variable, but if a large postero-ventral plate is present, not as close to genital field as described above (Fig. 33A,D,E); dorsum with small platelets (in two subgenera) or two large plates (anterior plate bearing two pairs of glandularia) (in one subgenus) (Fig. 33F). .... ***Protolimnesia*** Lundblad, 1927
[Three subgenera: *Protolimnesia* s. str., seven described species: Costa Rica (Goldschmidt 2004c), Panama (Camacho et al. 1997), Brazil (Pešić et al. 2016a), Peru, Bolivia (Pešić et al. 2016b), Argentina; *Protolimnesella*, five described species: Ecuador, Argentina, Costa Rica (Goldschmidt, 2004c); *Voldruguella*, one described species: *V. hispaniolae* Cook, 1981: Haiti. Key to species in Goldschmidt (2004c). Habitat: streams, interstitial]

13 (10') Three pairs to many Ac on genital flaps, many Ac on lateral field on Cx-IV (Figs 3C, 32E, 33G). ..... ***Neotyrrellia*** Lundblad, 1938
[Nine described species. Costa Rica (Goldschmidt 2004b), St. Vincent, Colombia, Brazil, Paraguay, Argentina, Chile (Goldschmidt 2004b). Keys to South American species in Lundblad (1953). Habitat: streams, springs, hygropetric]

13' Three pairs of Ac on genital flaps, no Ac on Cx-IV (Fig. 32B). ... ***Tyrrellia*** Koenike, 1895
[Nine described species. Mexico, El Salvador, Costa Rica (Goldschmidt 2004b), Brazil, Chile, Paraguay, Argentina. Key to South American species in Lundblad (1953). Habitat: springs, streams, hygropetric, swamps]

14 (1') Dorsal shield formed by two large plates (Figs 15J, 33J), covering dorsum almost completely (except of a fine dorsal furrow bearing several small platelets in most species);

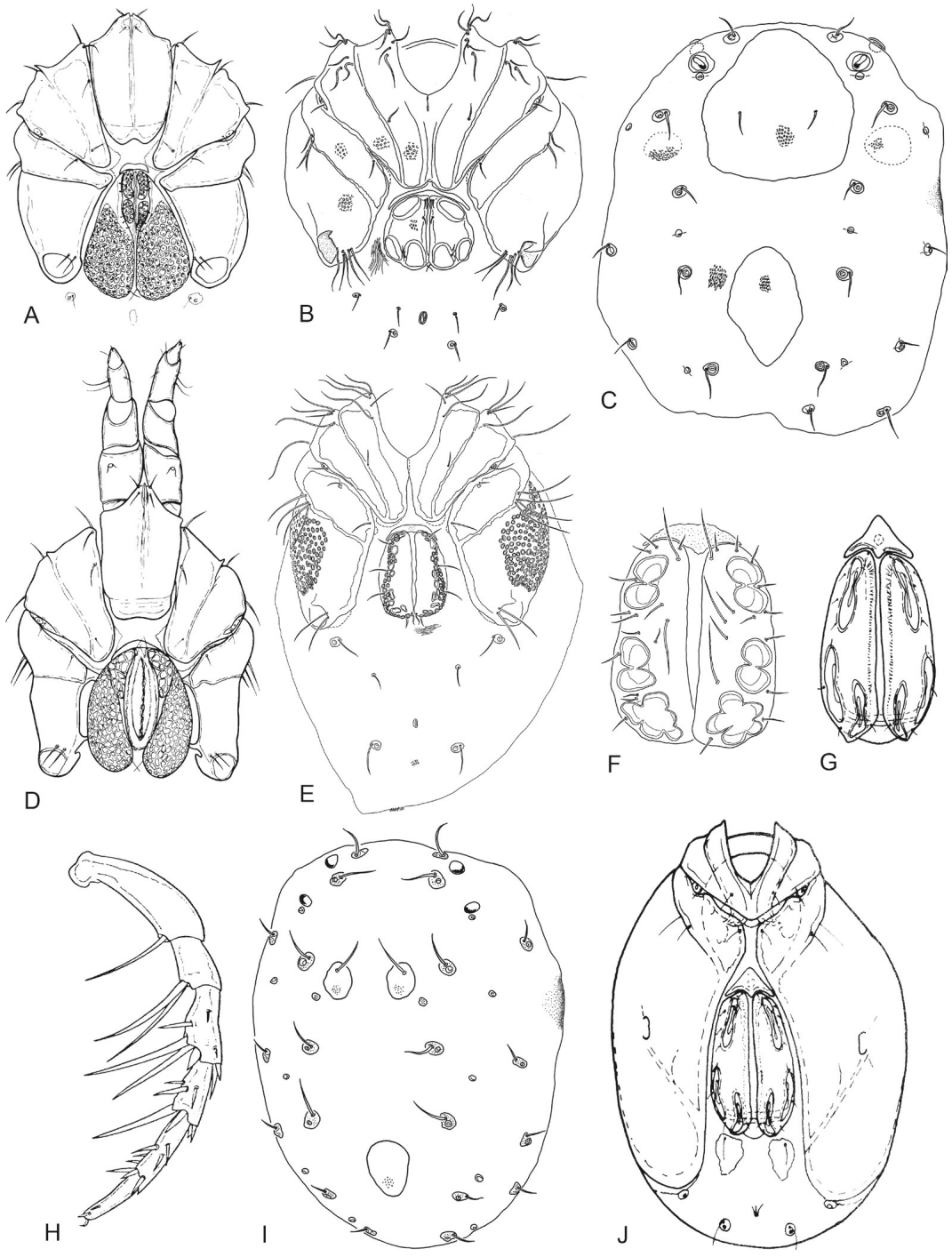


Fig. 32. **A.** *Neotorrenticola violacea*, male, coxae, capitulum and genital field (Cook 1974). **B.** *Tyrrellia circularis*, male, coxae and genital field (Goldschmidt 2004). **C.** *Tyrrellia circularis*, male, idiosoma dorsal (Goldschmidt 2004). **D.** *Neotorrenticola violacea*, female, coxae, gnathosoma and genital field (Cook 1974). **E.** *Neotyrrellia reticulata*, female, idiosoma ventral (Goldschmidt 2004). **F.** *Protolimnesia lobata*, female, genital field (Goldschmidt 2004). **G.** *Limnesides epimeratus*, female, genital field (Cook 1974). **H.** *Limnesides epimeratus*, female, IV-leg (after Lundblad 1941). **I.** *Neotyrrellia triacetabulata*, nymph, idiosoma dorsal (Goldschmidt 2004). **J.** *Limnesides epimeratus*, female, idiosoma ventral (Cook 1974).

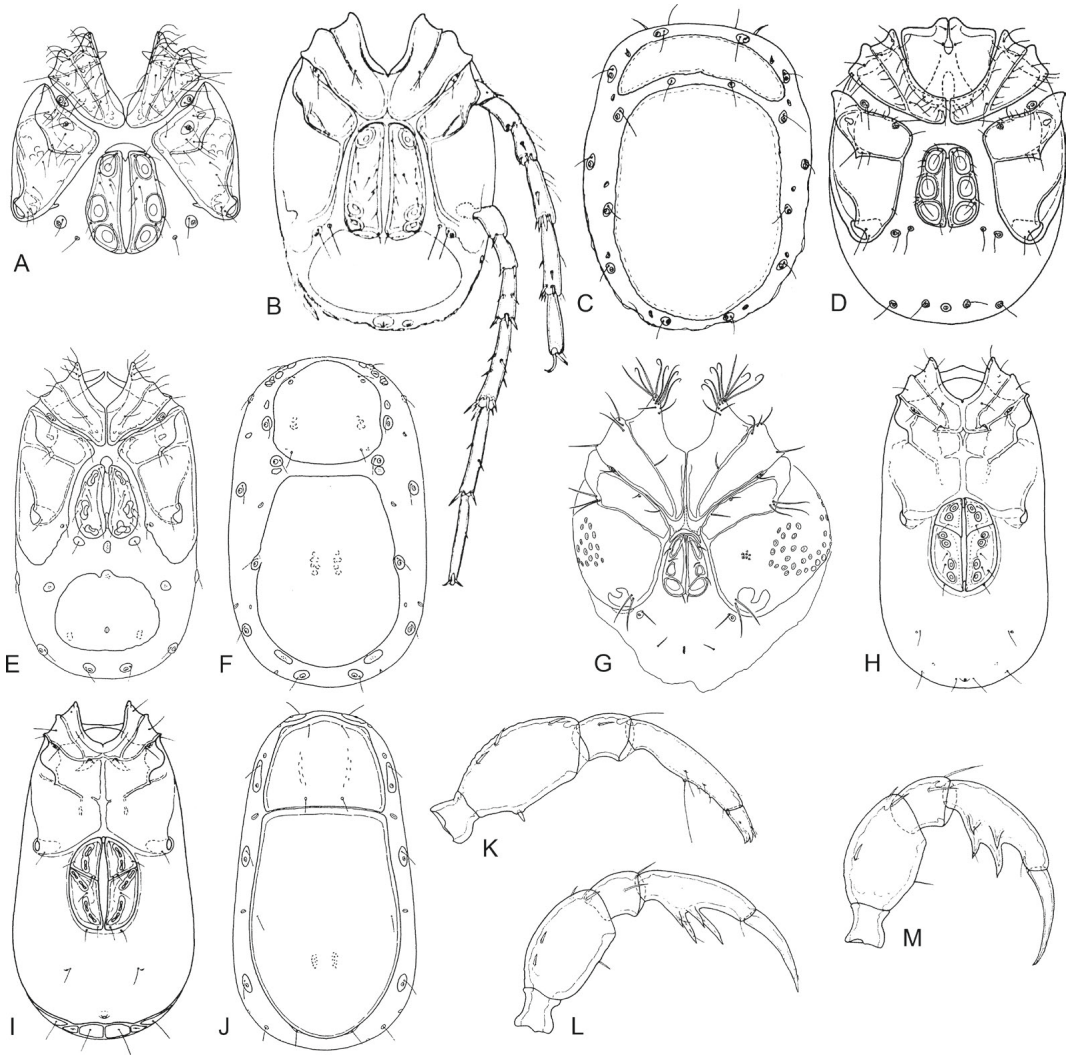


Fig. 33. A. *Protolimnesia setifera*, female, coxae and genital field (Cook 1980). **B.** *Crenolimnesia placophora*, female, idiosoma ventral (III- and IV-leg attached) (Cook 1974). **C.** *Crenolimnesia placophora*, female, idiosoma dorsal (Cook 1974). **D.** *Protolimnesia hispaniolae*, female, idiosoma and capitulum ventral (Cook 1981). **E.** *Protolimnesia sorpresa*, male, idiosoma ventral (Cook 1980). **F.** *Protolimnesia sorpresa*, male, idiosoma dorsal (Cook 1980). **G.** *Neotyrrellia triacetabulata*, male, idiosoma ventral (Goldschmidt 2004). **H.** *Neomamersa willinki*, female, idiosoma ventral (Cook 1980). **I.** *Meramecia mexicana*, female, idiosoma ventral (Cook 1980). **J.** *Meramecia diamphida*, female, idiosoma dorsal (Cook 1980). **K.** *Meramecia diamphida*, female, palp (Cook 1980). **L.** *Neomamersa willinki*, male, palp (Cook 1980). **M.** *Neomamersa faceta*, female, palp (Cook 1980).

three pairs to many Ac (always in three more or less clearly visible groups); **in both sexes**: movable genital flaps separated in anterior and posterior (sometimes as well central, or medial) sclerites (Figs 15I, 33H,I); legs without swimming setae. .... **Neomamersinae** Lundblad, 1953, 15

14' Without the described combination of characters, if dorsum covered by two large plates, genital field not as described. 16

15 (14) Small platelets at posterior end of ventral shield (Fig. 33I); P4 without ventral tubercles, P5 compact (Fig. 33K). .... ***Meramecia*** Cook, 1963

[Three described species. Mexico, Costa Rica (Goldschmidt 2004a), Brazil (unpublished data), Argentina. Habitat: interstitial]

15' No small platelets at posterior end of ventral shield (see above) (Fig. 33H); P4 with large ventral tubercles, P5 long and slender (Fig. 33L,M). ..... ***Neomamersa*** Lundblad, 1953
[Sixteen described species. Mexico (Cramer 1987), Haiti, Cuba, Costa Rica (Goldschmidt 2004a), Panama (Goldschmidt et al. 2016), Venezuela, Colombia, Ecuador (unpublished data), Chile, Argentina. Habitat: interstitial]

16 (14) P4 ventrally with five or more long tubercles, large medial seta; P5 elongated, pointed (Fig. 31K,M); three pairs of Ac; dorsum with three mid-sized to large plates (no complete dorsal shield), venter soft (Fig. 31N,O) (see comment above – two species with small, one species without claws). ..... **Kawamuracarinae** Viets, 1943, ***Kawamuracarus*** Uchida, 1937 (in part)
[Three described species. Mexico (Cramer 1987), Costa Rica (pers. obs.). Habitat: interstitial]

16' P4 without long tubercles, not with the described combination of characters. 17

17 (16') Idiosoma elongated, posterior end swollen, coxae far anterior (Fig. 34A); three pairs of Ac (Fig. 34B,C); legs without swimming setae. ..... **Psammolimnesiinae** Cook, 1974, ***Psammolimnesia*** Cook, 1974
[Two described species. Mexico, Costa Rica, Brazil (unpublished data). Habitat: interstitial]

17' Idiosoma rounded-oval, not elongated or posteriorly swollen. 18

18 (17') **Both sexes** with movable genital flaps, **male**: Ac in single rows of fifteen to eighteen pairs under genital flaps (Figs 3B, 7F), **female**: Ac in three groups of five to eight on genital flaps (Fig. 31A); capitular bay and genital bay rather deep (Figs 7F, 31A); legs without swimming setae (Fig. 31E); complete ventral and dorsal shield. ..... ***Guanacastacarus*** Goldschmidt, 2004
[One described species: *G. mariae* Goldschmidt, 2004. Costa Rica (Goldschmidt 2004c). Habitat: spring]

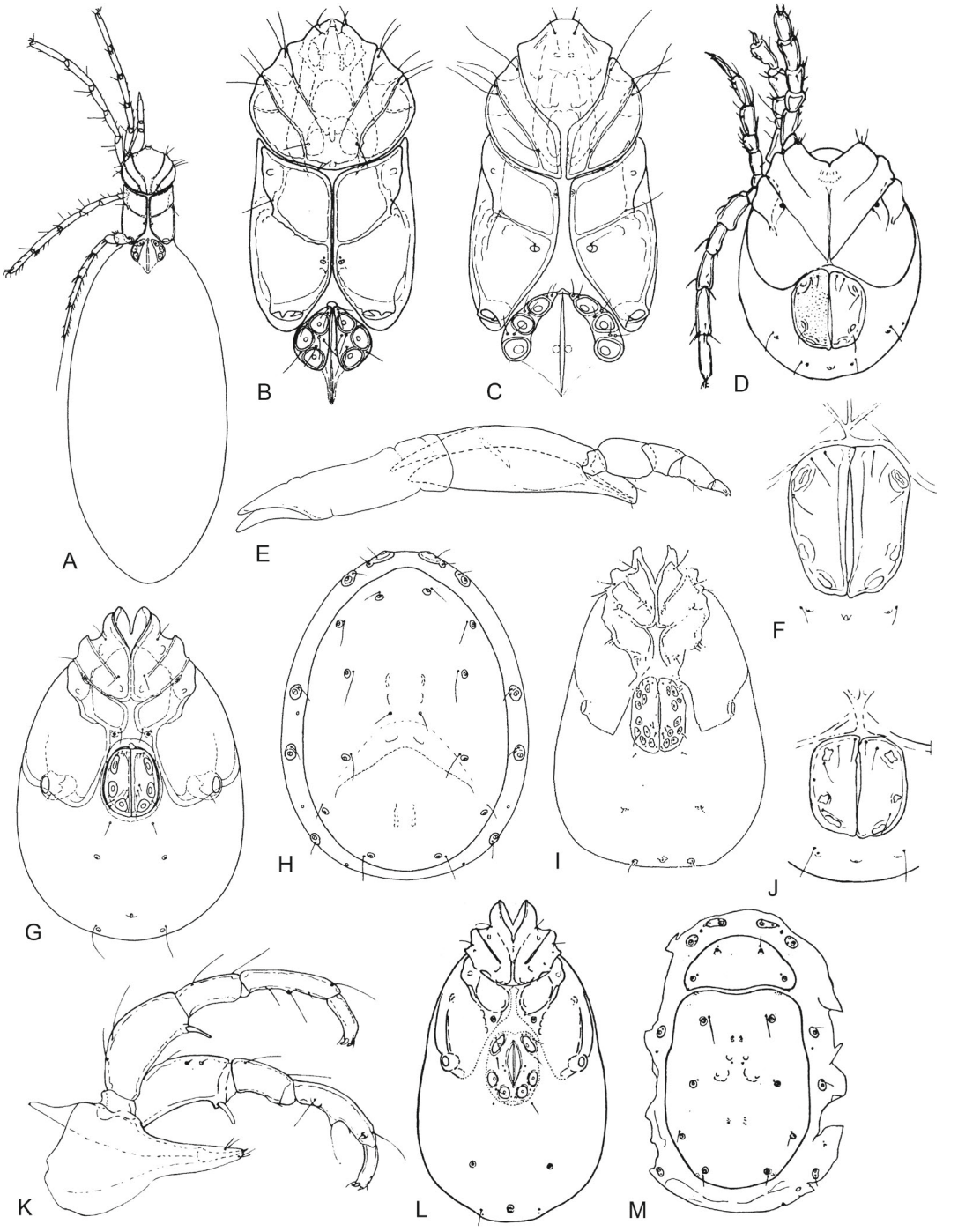
18' Not with the described combination of characters; **both sexes**: three pairs to many Ac on flaps or plates; if complete dorsal and ventral shield present, genital bay shallow; legs with or without swimming setae. ... 19

19 (18') **Both sexes**: movable genital flaps; capitular bay and genital bay shallow (Fig. 34D,F,J); P4 medio-distal with peg-like seta (Fig. 34K); legs without swimming setae; complete ventral and dorsal shield. ..... **Epallagopodinae** K. Viets, 1953, ***Epallagopus*** K. Viets, 1953
[One described species: *E. tecticoxalis* K. Viets, 1953. El Salvador. Habitat: hygropetric]

19' **Female**: movable genital flaps (Figs 34G, 35B,F,I,K), **male**: immovable genital plate (Figs 34L, 35A,E,H,J); P4 without medial peg-like seta (Fig. 15B,D,F); legs with or without swimming setae; degree of sclerotization variable. ..... **Limnesiinae** Thor, 1900, 20

20 (19') Complete ventral shield, dorsum completely armoured (one large shield, or separated in one large posterior and one smaller anterior plates) (Fig. 34G,H,L,M); three pairs to many Ac (Fig. 34G,I,L); capitulum large, elongated, attached to a protrusible tube (Fig. 34E); P2 seta hair-like (two species) or absent (one species); legs without swimming setae. ..... ***Tubophorella*** K. O. Viets, 1978
[Three described species. Guatemala, Costa Rica, Panama (unpublished data), Brazil (unpublished data), Argentina. Habitat: streams]

Fig. 34. A. *Psammolimnesia mexicana*, female, idiosoma (with right legs) and capitulum (with right palp) ventral (Cook 1980). **B.** *Psammolimnesia mexicana*, male, coxae, capitulum, genital field (Cook 1980). **C.** *Psammolimnesia costarriquena*, male, coxae, capitulum, genital field (Cook 1980). **D.** *Epallagopalpus tecticoxalis*, female, idiosoma ventral (with right legs – note that IV-leg is folded to anterior, lying between II- and III-leg) (Cook 1974). **E.** *Tubophorella vietsi*, female, capitulum (with protrusible tube), chelicera and right palp lateral (Cook 1980). **F.** *Epallagopalpus tecticoxalis*, female, genital field (Cook 1974). **G.** *Tubophorella vietsi*, female, idiosoma ventral (Cook 1980). **H.** *Tubophorella vietsi*, female, idiosoma dorsal (Cook 1980). **I.** *Tubophorella multiacetabulata*, female, idiosoma ventral (after Fernández 1992). **J.** *Epallagopalpus tecticoxalis*, male, caudal end of idiosoma with genital field (Cook 1974). **K.** *Epallagopalpus tecticoxalis*, female, gnathosoma lateral (Cook 1974). **L.** *Tubophorella scutata*, male, idiosoma ventral (Viets 1977). **M.** *Tubophorella scutata*, male, idiosoma dorsal (Viets 1977). ▷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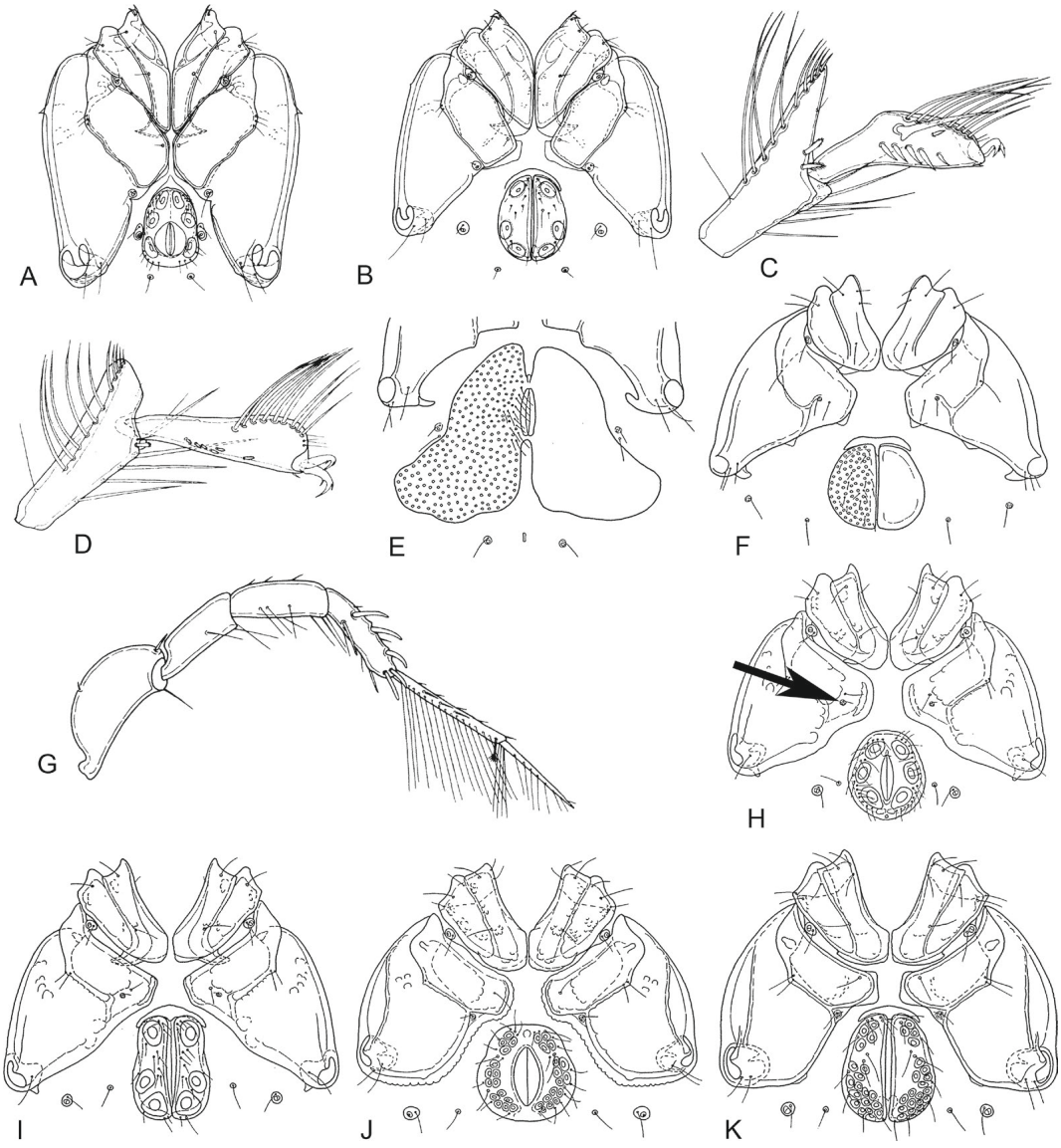

Fig. 35. **A.** *Centrolimnesia motasi*, male, coxae and genital field (Cook 1980). **B.** *Centrolimnesia motasi*, female, coxae and genital field (Cook 1980). **C.** *Centrolimnesia motasi*, male, III-leg-5/-6 (Cook 1980). **D.** *Centrolimnesia bondi*, male, III-leg-5/-6 (Cook 1980). **E.** *Acantholimnesia millepora*, male, genital field (Cook 1974). **F.** *Acantholimnesia millepora*, female, coxae and genital field (Cook 1974). **G.** *Acantholimnesia millepora*, male, IV-leg (Cook 1974). **H.** *Limnesia minuscula*, male, coxae (arrow pointing at glandula limnesiae on Cx-III/-IV) and genital field (Cook 1980). **I.** *Limnesia minuscula*, female, coxae and genital field (Cook 1980). **J.** *Limnesia mexicana*, male, coxae and genital field (Cook 1980). **K.** *Limnesia mexicana*, female, coxae and genital field (Cook 1980).

20' Sclerotization variable; capitulum without protrusible tube; legs with or without swimming setae. 21

Note: The female of the following three genera cannot be separated confidently, therefore the key only refers to male (however some figures are given for females as well).

21 (20') Three pairs of Ac (Fig. 35A,B); III-leg-5/-6 with sexual dimorphism (Fig. 35C,D). .... ***Centrolimnesia*** Lundblad, 1935 [Eleven described species. Mexico, Haiti, Costa Rica, Panama, Colombia, Suriname, Ecuador, Brazil, Paraguay. Key to males of South American species in K. Viets (1954a). Habitat: standing waters, slow flowing streams]

21' III-leg without sexual dimorphism **or**, if a weak sexual dimorphism of III-leg is present then more than three pairs of Ac. 22

22 (21') Many Ac; male genital field extending far laterally (Fig. 35E,F); IV-leg-5/-6 very long and slender (Fig. 35G). .... ***Acantholimnesia*** Viets, 1954 [One described species: ***A. millepora*** Viets, 1954. Brazil. Habitat: flooded forests, rivers]

22' Three pairs to many Ac; genital field less extended (Fig. 35H–K); IV-leg without sexual dimorphism. ..... ***Limnesia*** Koch, 1836 [Ninety-six described species. Mexico, Cuba, Haiti, Dominican Republic, Guatemala, Costa Rica, Panama, Venezuela, St. Vincent, Curaçao, Bonaire, Colombia, Suriname, Ecuador, Brazil, Peru, Bolivia, Chile, Paraguay, Argentina, Uruguay. Key to South American species in Lundblad (1953). Habitat: all types of fresh and brackish waters]

Key to Hygrobatidae Koch, 1842

Preceding comments

The separation of the genera of Hygrobatidae is sometimes problematic because of a large variation (between and within genera) in:

– the degree of sclerotization (often strong sexual dimorphism)
– the morpholgy of the palps (serration, projections, tubercles of P2 and P3).

A sexual dimorphism can often be observed in characters that generally separate among the different genera as well (fusion of capitulum, shape of palp, degree of sclerotization, etc.).

The assignment of some genera to the family **Hygrobatidae** or **Aturidae** is not very clear and several genera have recently been shifted from the Aturidae to the Hygrobatidae. In case of doubt, both genera keys should be tried.

Within the Hygrobatidae we refrain from the assignment of subfamilies as a complete revision of the family would be necessary (but this is far beyond the scope of this key).

The subfamily **Rhynchaturinae** Schwoerbel, 1986, has been erected in order to accommodate the genus *Rhynchaturus* Besch, 1964 (originally assigned to the Aturidae). The diagnosis (dorsal plates, capitulum free in capitular bay, I-leg-2 without modified setae, I-leg-1 not modified, 3–4 pairs of Ac) though is not very distinctive. In the comprehensive work on water mites from Chile (1988), Cook (p. 123) upgraded *Brevaturus* (described as subgenus of *Rhynchaturus* by Schwoerbel (1986a) to genus level and downgraded *Paraspidiobates* (described as genus by Schwoerbel (1986a)) as subgenus in *Brevaturus*. Furthermore he included the genera *Aciculacarus* Hopkins, 1975 from New Zealand and *Rhynchaustrobates* Cook, 1986 from Australia into the "*Rhynchaturus*-like" genera. As the assignation of all hygrobatid genera to distinct subfamilies is currently not possible, Cook (1988) intentionally did not use the subfamily designation "Rhynchaturinae" (Dave Cook, pers. comm.). In their checklist of water mites from South America, Rosso de Ferradás & Fernández (2005) are listing as well the genera *Andesobates* Smit, 2002 and *Szalayella* Lundblad, 1953 under the Rhynchaturinae; all remaining hygrobatid genera – including *Brevaturus* Schwoerbel, 1986 – are listed under the Hygrobatinae. *Rhynchaturus* Besch, 1964 originally described as genus in Notoaturinae (Besch 1964), has been transferred to Axonopsinae by Cook (1974) and later to the Hygrobatidae by Schwoerbel (1986).

A key to South American genera of Hygrobatidae is available in Lundblad (1942).

1 Complete ventral shield in both sexes (Figs 16F, 36A); dorsum covered by two large, closely fitting plates (Fig. 36B); medial coxal suture lines and posterior suture line of Cx-IV obliterated; glandularium on Cx-IV shifted far anterior in a looped suture; capitulum separated from coxal field; genital field separated or fused with ventral shield; three pairs of Ac (Figs 16F, 36A); generally small, unpigmented, dorso-ventrally flattened dwellers of interstitial habitats. .... ***Diamphidaxona*** Cook, 1963 [Nine described species. Mexico, Cuba, Guatemala, Costa Rica (Goldschmidt 2004d), Panama (Goldschmidt et al. 2016), Venezuela, Argentina. Habitat: interstitial]

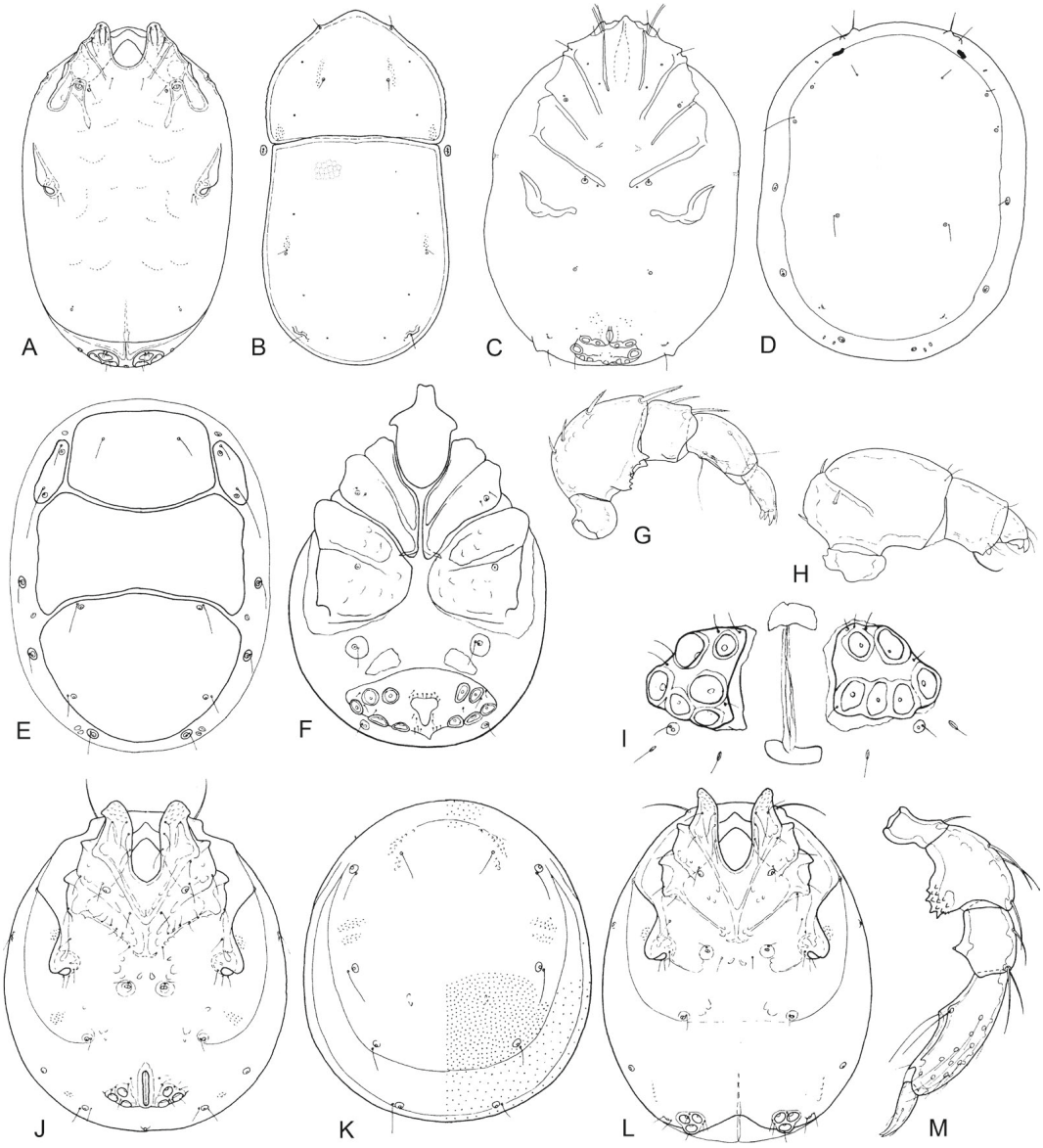

Fig. 36. **A.** *Diamphidaxona yungasa*, female, idiosoma ventral (Cook 1980). **B.** *Diamphidaxona yungasa*, female, dorsal shield (Cook 1980). **C.** *Decussobates minutipalpis*, male, idiosoma ventral (Smit 2018). **D.** *Decussobates minutipalpis*, male, idiosoma dorsal (Smit 2018). **E.** *Decussobates planus*, female, idiosoma dorsal (Cook 1988). **F.** *Neocorticacarus validipalpis*, male, idiosoma and capitulum ventral (Cook 1974). **G.** *Decussobates planus*, female, palp (Cook 1988). **H.** *Neocorticacarus validipalpis*, female, palp (Cook 1974). **I.** *Neocorticacarus validipalpis*, female, genital field (Cook 1974). **J.** *Dubiobates penai*, male, idiosoma ventral (Cook 1988). **K.** *Dubiobates penai*, male, dorsal shield (Cook 1988). **L.** *Dubiobates penai*, female, idiosoma ventral (Cook 1988). **M.** *Dubiobates penai*, male, palp (Cook 1988).

1' Not with the described combination of characters; if dorsal shield complete, not formed by two large plates. 2

2(1') **Female**: dorsum with three large medial plates, anterior one flanked by a pair of narrow platelets, each bearing two glandularia (Fig. 36E); coxae in three groups, Cx-IV with secondary sclerotization extending far posterior and postero-lateral; Ac numerous (Fig. 16C); **male**: dorsum with single large plate (Fig. 36D); coxae fused with ventral plate; Ac posterior to gonopore; in both sexes capitulum fused with Cx-I; palp stocky, P2 ventrally with serrate ridge (Fig. 36G). .. .. ***Decussobates*** Cook, 1988
[Three described species. Chile, Argentina (Smit 2018). Habitat: streams]

2' Not with the described combination of characters. 3

3(2') Palp very short and stocky, P2 and P3 partially fused (Fig. 36H); five to six pairs of Ac (Fig. 36F,I). .... ***Neocorticacarus*** Lundblad, 1953
[One described species: *N. validipalpis* Lundblad, 1953. Colombia. Habitat: stream]

3' Palp segments usually more slender, P2 and P3 without tendencies of fusion. 4

4(3') Dorsal and ventral shield complete (Fig. 36J–L); glands of the Cx-IV more or less medial, far posterior (between or posterior to insertion of IV-legs); capitulum not fused with coxae; three pairs of Ac, genital field terminal or subterminal, fused with ventral shield (Fig. 36J,L); P2 with ventral papillae; **male**: P4 medial with numerous short setae (Fig. 36M), **female**: P4 without the respective setae. ..... ***Dubiobates*** Cook, 1988
[Ten described species. Chile. Key to species in Cook (1988). Habitat: streams]
Note: For a discussion of the similarities of *Dubiobates* with the Aturidae (Axonopsinae), see Cook (1988, p. 143).

4' Not with the described combination of characters. 5

5(4') Dorsal and ventral shield complete; dorsal shield with four pairs of large, heart-shaped glandularia in posterior half and four pairs of "normal" glandularia; glands of the Cx-IV shifted far rostral, near Cxgl-1; three pairs of Ac (Fig. 37A,B). .... ***Actinacarus*** Lundblad, 1953
[Two described species. Costa Rica (pers. obs.), Colombia. Habitat: streams]

5' Without large heart-shaped, dorsal glandularia; not with the described combination of characters. 6

6(5') Capitulum fused with Cx-I, genital field terminal to subterminal, posterior suture line of Cx-IV looped towards rostral around glands of the Cx-IV; three or four pairs of Ac (Fig. 16G,H); **male**: with complete ventral shield and one large dorsal plate (Figs 16G, 37C); **female**: three coxal groups very close to each other, Cx-IV with large secondary sclerotization posterior, dorsum with three large characteristic plates and two pairs of small platelets beside and posterior to the posterior large plate (Figs 16H, 37D); P2 with ventro-distal projection (Fig. 37E). .... ***Szalayella*** Lundblad, 1953
[Three described species. Costa Rica (Goldschmidt 2004d), Colombia, Chile, Argentina. Habitat: streams]

6' Not with the described combination of characters. 7

7(6') Idiosoma and coxal field elongated; Cx-I medially very close but clearly separated; capitulum free; Cx-IV far extended to posterior; glands of the Cx-IV far anterior; genital field subterminal (Fig. 37F,G); dorsum bearing two large plates with two pairs of glandularia each; one pair of small platelets in soft integument between large plates, five pairs of glandularia platelets surrounding large plates (Fig. 37H). .... ***Camposea*** Schwoerbel, 1986
[One described species: *C. phreaticola* Schwoerbel, 1986. Chile. Habitat: streams, interstitial]

7' Not with the described combination of characters. 8

8(7') P4 medially with one **thickened medial seta** centrally (Fig. 38B) or a peg-like seta more distally (Fig. 38E), if heavy seta shifted somewhat ventrally, there is **no** well developed ventral projection on P2 (Fig. 38G), **or**, if no thickened seta on medial surface of P4, I-leg-5 with **two** heavy setae ventro-distally and **I-leg-6 bowed** (Fig. 38A). 9

8' P4 medially without a thickened seta (either without thickened seta, **or** this is in ventral position), **if** heavy seta shifted somewhat medially, there is a **well developed ventral projection on P2** (Figs 43A,C, 44J,K,M). 19

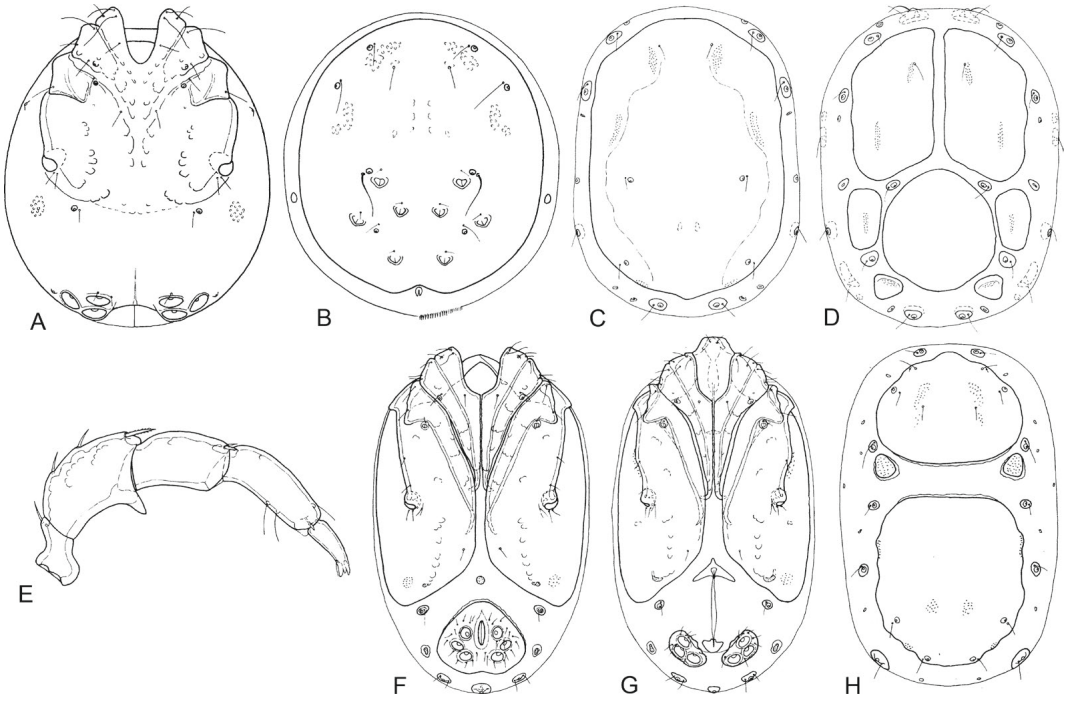

Fig. 37. A. *Actinacarus cardioporus*, female, idiosoma ventral (Cook 1974). **B.** *Actinacarus cardioporus*, female, idiosoma dorsal (Cook 1974). **C.** *Szalayella lundbladi*, male, idiosoma dorsal (Cook 1988). **D.** *Szalayella lundbladi*, female, idiosoma dorsal (Cook 1988). **E.** *Szalayella lundbladi*, male, palp (Cook 1988). **F.** *Camposea phreaticola*, male, idiosoma ventral (Cook 1988). **G.** *Camposea phreaticola*, female, idiosoma and capitulum ventral (Cook 1988). **H.** *Camposea phreaticola*, female, idiosoma dorsal (Cook 1988).

9 (8) Three to (rarely) four pairs of Ac. 10

9' Six or more pairs of Ac. 16

10 (9) P4 with heavy medial seta (Fig. 38G), **I-leg-6 straight**, I-leg-5 distally with **single heavy seta** which is expanded and pointed distally (Fig. 38F); **male**: Cx-I fused medially, capitulum lightly fused (Fig. 38C); **female**: Cx-I separated, capitulum free with long posterior process (Fig. 38D). .... ***Paraschizobates*** Lundblad, 1937 [Three described species. Mexico, Costa Rica, Panama (Goldschmidt et al. 2016), Colombia, Suriname, Brazil, Paraguay. Habitat: streams]

10' I-leg-5 distally variable, but **not** with single heavy seta as described. 11

11 (10') I-leg-5 distally with two modified, large setae; I-leg-6 slightly to heavily bowed (Figs 38A, 39A,B,G). 12

11' If I-leg-5 distally with two large setae, I-leg-6 **not** bowed. 13

12 (11) I-leg-5 disto-ventrally with **two heavy setae**, **one** more or less **straight** located ventrally, **one curved** located more dorsal near middle of distal end; **I-leg-6 bowed** (Fig. 39A,B); P4 dorsally with one or two single setae (Fig. 39E,F); **male**: Cx-I fused medially, capitulum fused with Cx-I (Fig. 39C), **female**: Cx-I separated, capitulum free with long posterior process (Fig. 39D); soft integument. ..... ***Megapella*** Lundblad, 1936 [Two described species. Panama (Goldschmidt et al. 2016), Brazil, Paraguay. Habitat: running waters, springs]

12' I-leg-5 disto-ventrally with **two relatively straight heavy** setae and one terminal curved seta, I-leg-6 usually bowed (but more or less straight in some species) (Figs 38A, 39G); P4 dorsally hirsute with many fine setae (Fig. 39H,I); Cx-I fused medially, capitulum typically separated from coxae (occasionally lightly joined by a very narrow bridge) (Fig. 39J,K); great variability in sclerotization degree. ..... ***Atractides*** Koch, 1837

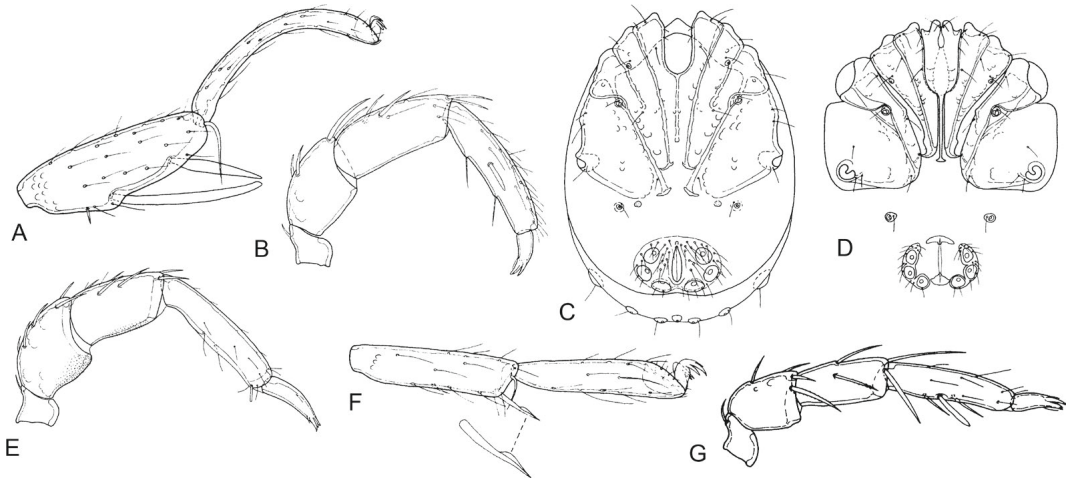

Fig. 38. A. *Atractides tanutus*, female, I-leg-5/-6 (Cook 1980). **B.** *Atractides toldomus*, female, palp medial (Cook 1980). **C.** *Paraschizobates scutatus*, male, idiosoma ventral (Cook 1980). **D.** *Paraschizobates scutatus*, female, coxae, capitulum and genital field (Cook 1980). **E.** *Hygrobatella* (*Schwoerbelobatella*) *multiacetabulata*, female, palp medial (Cook 1980). **F.** *Paraschizobates scutatus*, male, I-leg-5/-6 (Cook 1980). **G.** *Paraschizobates scutatus*, female, palp medial (Cook 1980).

[Thirty-three described species. Mexico (Otero-Colina 1987), Cuba, Guatemala, Honduras (Wiles 2005), Costa Rica, Panama (Goldschmidt et al. 2016), Colombia, Brazil, Ecuador (unpublished data), Peru, Bolivia (Fernández et al. 2009), Paraguay, Argentina. Habitat: running waters, springs, interstitial]

13 (11') Cx-I medially far separated by broad capitulum (in one genus, **male**: capitulum and coxal field fused with ventral shield); capitulum posteriorly slightly tapering (Fig. 40A,B,I) or with anchoral process (Fig. 40C,J); suture line Cx-III/IV extending abruptly antero-medially at glandularium of Cx-IV, Cx-IV without posterior processes (Fig. 40A–C,I,J); P2 and P3 without ventral projection, but with denticles, P4 with small peg-like seta near distal end of medial surface (Fig. 38E). 14

13' Cx-I medially separated but very close; capitulum posterior greatly tapering, posterior process long and slender (Fig. 40D), short (Fig. 40E) or reduced, but with capitulum posterior pointed (Fig. 40F); suture line Cx-III/IV straight, not extending abruptly antero-medially at glandularium of Cx-IV, Cx-IV posterior generally with well developed processes, muscle scars as well extending anterior towards glandularium of Cx-IV (Fig. 40D–F), in some species only weakly developed (Fig. 40G,H); P2 and P3 without ventral projection or denticles, P4 with (slightly) enlarged or peg-like medial seta either central or ventro-distal (Fig. 46F–H). 15

14 (13) Genital field centrally, rather close to coxal field; capitulum with more or less developed anchoral process; soft bodied; capitulum free (Fig. 40B,C,I,J). .... ***Hygrobatella*** Viets, 1926 (**in part**), subgenus ***Hygrobatella*** Viets, 1926
[Fourteen described species. Costa Rica (Goldschmidt 2004d), Colombia, Peru, Bolivia, Chile, Argentina. Key to South American species in Lundblad (1953). Habitat: streams, lakes, spring]

14' Genital field terminal or subterminal; capitulum short, never with anchoral process; **male**: with complete dorsal and ventral shield; capitulum fused with coxal field (Fig. 41A,B); **female**: soft bodied; capitulum free (Fig. 41C,D). .... ***Tetrahygrobatella*** Lundblad, 1953
[Three described species. Bolivia, Chile, Argentina. Habitat: running waters]

15 (13') Capitulum posterior with either short (Fig. 40E) or long and slender (Figs 40D,G,H, 41E) process. .... ***Australiobates*** Lundblad, 1941 (in part)

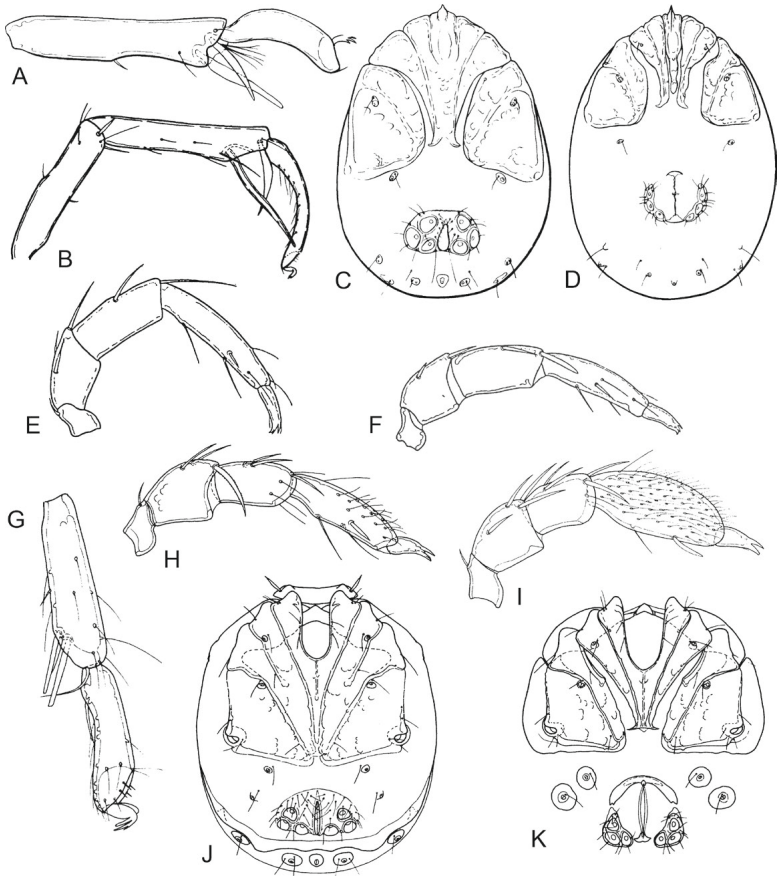

Fig. 39. A. *Megapella* (*Megapodellides*) *flabellum*, female, I-leg-5/-6 (Cook 1974). **B.** *Megapella* (*Megapella*) *longimaxillaris*, female, I-leg-4/-5/-6 (Cook 1974). **C.** *Megapella* (*Megapella*) *longimaxillaris*, male, idiosoma and capitulum ventral (Cook 1974). **D.** *Megapella* (*Megapella*) *longimaxillaris*, female, idiosoma and capitulum ventral (Cook 1974). **E.** *Megapella* (*Megapella*) *longimaxillaris*, female, palp (after Lundblad 1942). **F.** *Megapella* (*Megapodellides*) *flabellum*, female, palp (after Lundblad 1942). **G.** *Atractides tucabus*, female, I-leg-5/-6 (Cook 1980). **H.** *Atractides* sp., female, palp medial (Cook 1980). **I.** *Atractides travus*, male, palp medial (Cook 1980). **J.** *Atractides tucabus*, male, idiosoma ventral (Cook 1980). **K.** *Atractides tucabus*, female, coxae and genital field (Cook 1980).

[Two subgenera: *Australiobates* s.str. – five described species. Chile, Argentina; *Lundbladobates* – two described species. Chile, Argentina. Habitat: running waters]
Note: Some species without large medial seta at P4 are keyed below (28').

15' Capitulum posterior pointed, process reduced (Fig. 40F). .... ***Australiobatella*** Lundblad, 1953
[One described species: *A. vietsi* Lundblad, 1953. Colombia. Habitat: stream]

16 (9') Six to thirteen pairs of Ac; moderate to strong sexual dimorphism in the shape of IV-leg (see below); **male**: genital field heart-shaped, with posterior spout-like projection (Figs 41H,J, 42A); large dorsal plate; **female**: genital plates crescent-shaped; dorsum soft (Figs 41I, 42B). 17

16' More than thirty pairs of Ac on wing-like plates extending slightly to heavily towards posterior (Fig. 41F,G); dorsum soft with small platelets in both sexes. 18

17 (16) Six pairs of Ac; capitulum free; **male**: Cx-I-IV fused on respective sides (Fig. 41H); **female**: four coxal groups (Fig. 41I); strong sexual dimorphism in the shape of IV-leg (Fig. 41K); slight dimorphism in palps (Fig. 41L,M). ... . ***Dodecabates*** Viets, 1926

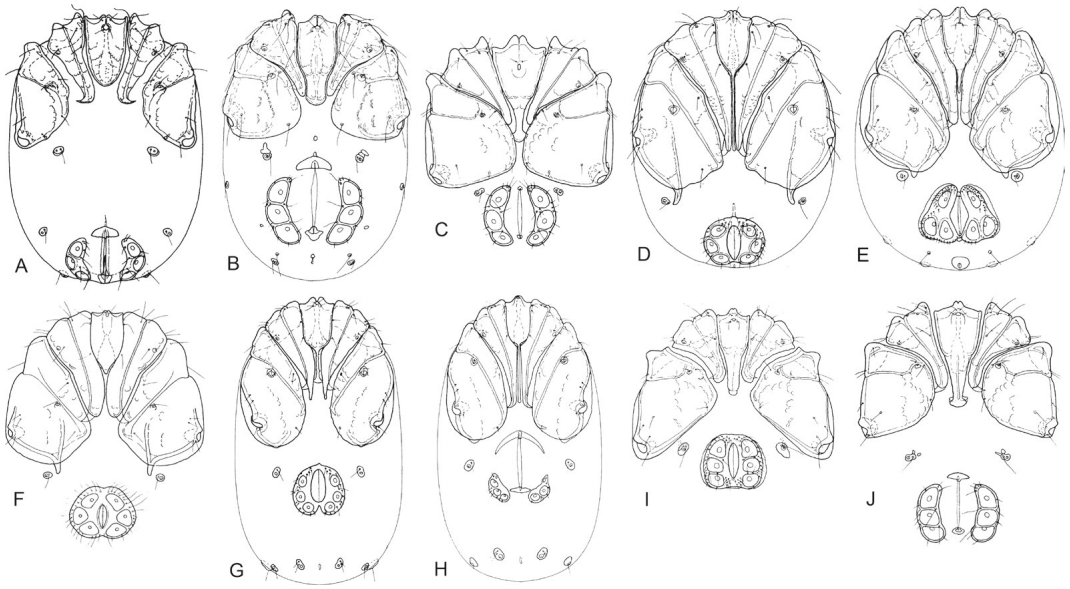

Fig. 40. A. *Tetrahygrobatella chilensis*, female, idiosoma and capitulum ventral (Cook 1980). **B.** *Hygrobatella* (*Hygrobatella*) *chillanensis*, female, idiosoma and capitulum ventral (Cook 1988). **C.** *Hygrobatella (Hygrobatella) karinae*, female, coxae, capitulum and genital field (Cook 1988). **D.** *Australiobates* (*Australiobates*) *cekalovici*, male, idiosoma and capitulum ventral (Cook 1988). **E.** *Australiobates* (*Lundbladobates*) *klaasseni*, male, idiosoma and capitulum ventral (Cook 1988). **F.** *Australiobatella vietsi*, male, coxae, capitulum and genital field (Cook 1974). **G.** *Australiobates* (*Australiobates*) *litatus*, male, idiosoma and capitulum ventral (Cook 1988). **H.** *Australiobates* (*Australiobates*) *vantermus*, female, idiosoma and capitulum ventral (Cook 1988). **I.** *Hygrobatella (Hygrobatella) valdiviensis*, male, coxae, capitulum and genital field (Cook 1988). **J.** *Hygrobatella (Hygrobatella) puberula puberula*, female, coxae, capitulum and genital field (Cook 1988).

[One described species: *D. dodecaporus* (Nordenskiöld, 1904). Chile, Argentina. Probably *Hygrobatulus linguliger* Viets, 1953 from Peru (only known in female) as well belongs to this genus. Habitat: running waters]

Note: For a discussion of the taxonomic problems within the *Hygrobatella*-like mites, see Cook (1980, pp. 161–162).

17' Thirteen pairs of Ac; **male**: capitulum fused with Cx-I, coxal field fused to ventral shield (Fig. 42A); **female**: capitulum free, four coxal groups (Fig. 42B); moderate sexual dimorphism in the shape of IV-leg (Fig. 42H); strong sexual dimorphism in palps (**male**: P2 with large ventral protrusion (Fig. 42F); **female**: P2 and P3 without ventral projection, but with small denticles (Fig. 42I). .... ***Polyhygrobatella*** Lundblad, 1953
[One described species: *P. polygramma* (Lundblad, 1953). Colombia. Habitat: river]

18 (16') Genital plates mainly beside gonopore, slightly extended towards posterior; capitulum free (Fig. 41F,G); P2, P3 ventrally serrated, without projections (Fig. 38E). .... ***Hygrobatella*** Viets, 1926 (**in part**), sg. ***Schwoerbelobatella*** Rosso de Ferradás, Fernández & Rocabado, 2004
[Two described species. Colombia, Bolivia, Argentina. Habitat: streams]

18' Genital plates drop-shaped, extended far posteriorly (Fig. 42D,E); **male**: capitulum fused with complete ventral shield (Fig. 42D); P2 ventrally with large projection, P3 ventrally with small projection, both without denticles (Fig. 42G); **female**: capitulum free, no ventral shield (Fig. 42E); P2 ventrally with small projection, P3 ventrally convex, without projection, both with denticles (Fig. 42J). ..... ***Crenohygrobates*** Lundblad, 1938
[One described species: *C. multiporus* Lundblad, 1938. Brazil. Habitat: streams, spring]

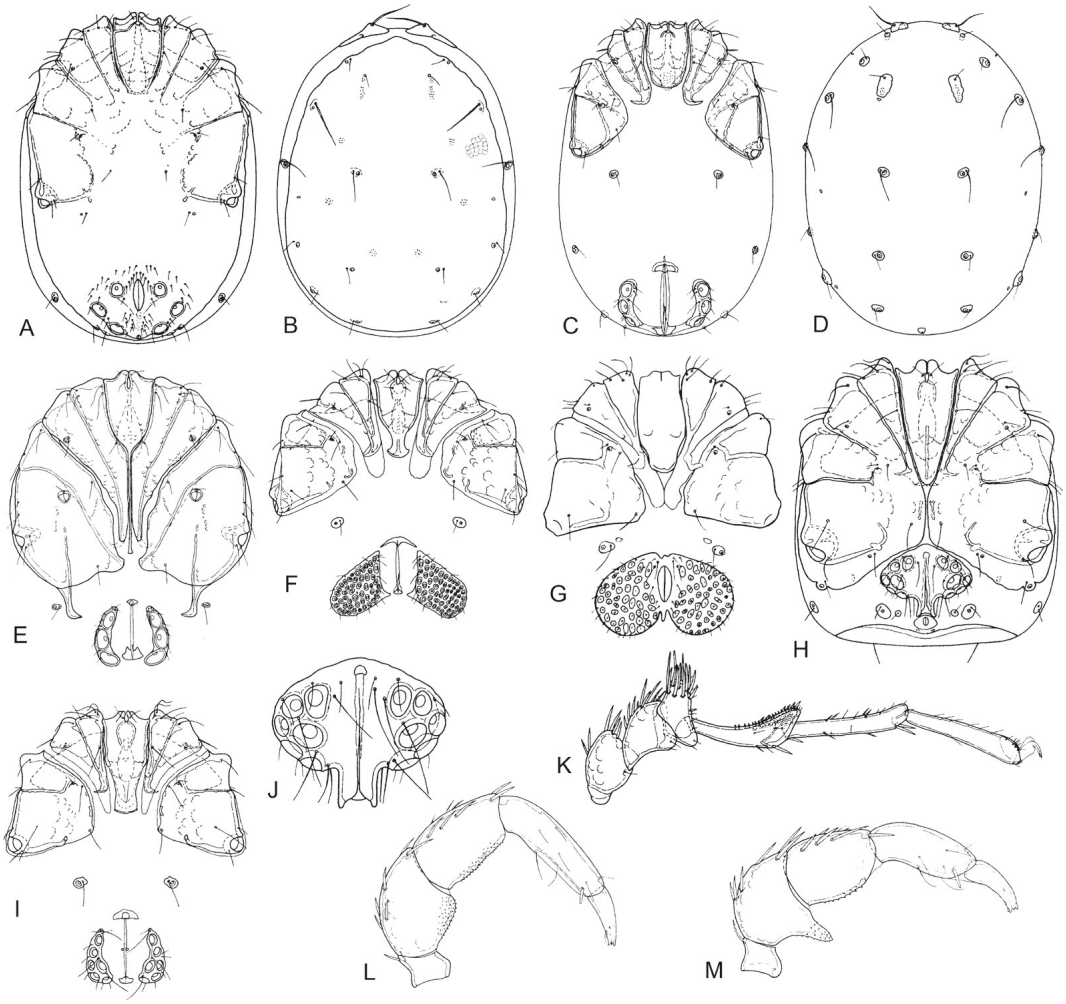

Fig. 41. A. *Tetrahygrobatella bovala*, male, idiosoma and capitulum ventral (Cook 1980). **B.** *Tetrahygrobatella bovala*, male, idiosoma dorsal (Cook 1980). **C.** *Tetrahygrobatella bovala*, female, idiosoma and capitulum ventral (Cook 1980). **D.** *Tetrahygrobatella bovala*, female, idiosoma dorsal (Cook 1980). **E.** *Australiobates* (*Australiobates*) *cekalovici*, female, coxae, capitulum and genital field (Cook 1988). **F.** *Hygrobatella* (*Schwoerbelobatella*) *multiacetabulata*, female, coxae, capitulum and genital field (Cook 1980). **G.** *Hygrobatella* (*Schwoerbelobatella*) *polygramma*, male, coxae, capitulum and genital field (Cook 1974). **H.** *Dodecabates dodecaporus*, male, idiosoma and capitulum ventral (Cook 1980). **I.** *Dodecabates dodecaporus*, female, coxae, capitulum and genital field (Cook 1980). **J.** *Dodecabates dodecaporus*, male, genital field (Cook 1980). **K.** *Dodecabates dodecaporus*, male, IV-leg (Cook 1980). **L.** *Dodecabates dodecaporus*, female, palp medial (Cook 1980). **M.** *Dodecabates dodecaporus*, male, palp medial (Cook 1980).

19 (8') Ac numerous (>25); suture line between Cx-III and Cx-IV incomplete (Fig. 42C); P2 with long, distally serrate ventral projection, P3 with serrate ventral lamella (Fig. 42K). .. .. ***Kyphohygrobatella*** Lundblad, 1936 [One described species (only male): *K. serratipalpis* Lundblad, 1936. Brazil. Habitat: stream]

19' Ac three pairs (in some species of *Corticacarus* up to eight pairs of Ac); not with the described combination of characters. 20

20 (19') P3 with well developed ventral projection, P2 with or without projection; capitulum not fused with coxae, long rostrum (Fig. 43A–C); Cx-I fused medially (posterior to capitulum); **male**: dorsal and ventral shield (Fig. 43D,G);

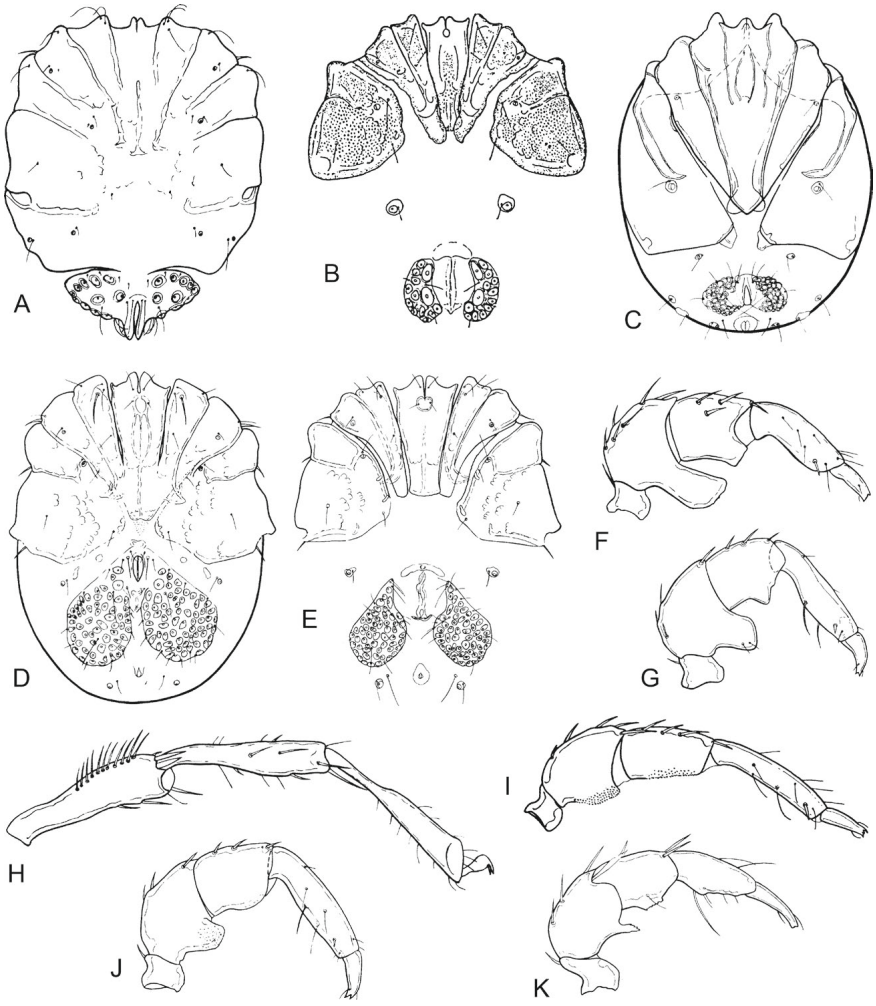

Fig. 42. A. *Polyhygrobatella polypora*, male, coxae, capitulum and genital field (Cook 1974). **B.** *Polyhygrobatella polypora*, female, coxae, capitulum and genital field (after Lundblad 1953). **C.** *Kyphohygrobatella serratipalpis*, male, idiosoma and capitulum ventral (Cook 1974). **D.** *Crenohygrobates multiporus*, male, idiosoma and capitulum ventral (Cook 1974). **E.** *Crenohygrobates multiporus*, female, coxae, capitulum and genital field (Cook 1974). **F.** *Polyhygrobatella polypora*, male, palp (Cook 1974). **G.** *Crenohygrobates multiporus*, male, palp (Cook 1974). **H.** *Polyhygrobatella polypora*, male, IV-leg-4/-5/-6 (Cook 1974). **I.** *Polyhygrobatella polypora*, female, palp (Cook 1974). **J.** *Crenohygrobates multiporus*, female, palp (Cook 1974). **K.** *Kyphohygrobatella serratipalpis*, male, palp (Cook 1974).

female: soft bodied, dorsum with small anterior plate or pair of platelets (Fig. 43E,F). .... ***Atractidella*** Lundblad, 1936 [Fourteen described species. Mexico, Honduras (Wiles 2005), Costa Rica, Panama (Goldschmidt et al. 2016), Colombia, Venezuela, Brazil, Peru, Paraguay, Argentina. Key to South American species in Lundblad (1953). Habitat: streams]

20' P3 usually without ventral projection; **if** there is a ventral projection on P3 the capitulum is broadly fused with coxae. 21

21 (20') Capitulum large, free, with long, downcurved rostrum (Fig. 43I); P4 very long and slender (Fig. 43H); dorsum with series of mid-sized platelets (Fig. 43K); venter with row of six platelets between coxal field and genital field (Fig. 43J). .... ***Motasia*** Lundblad, 1953

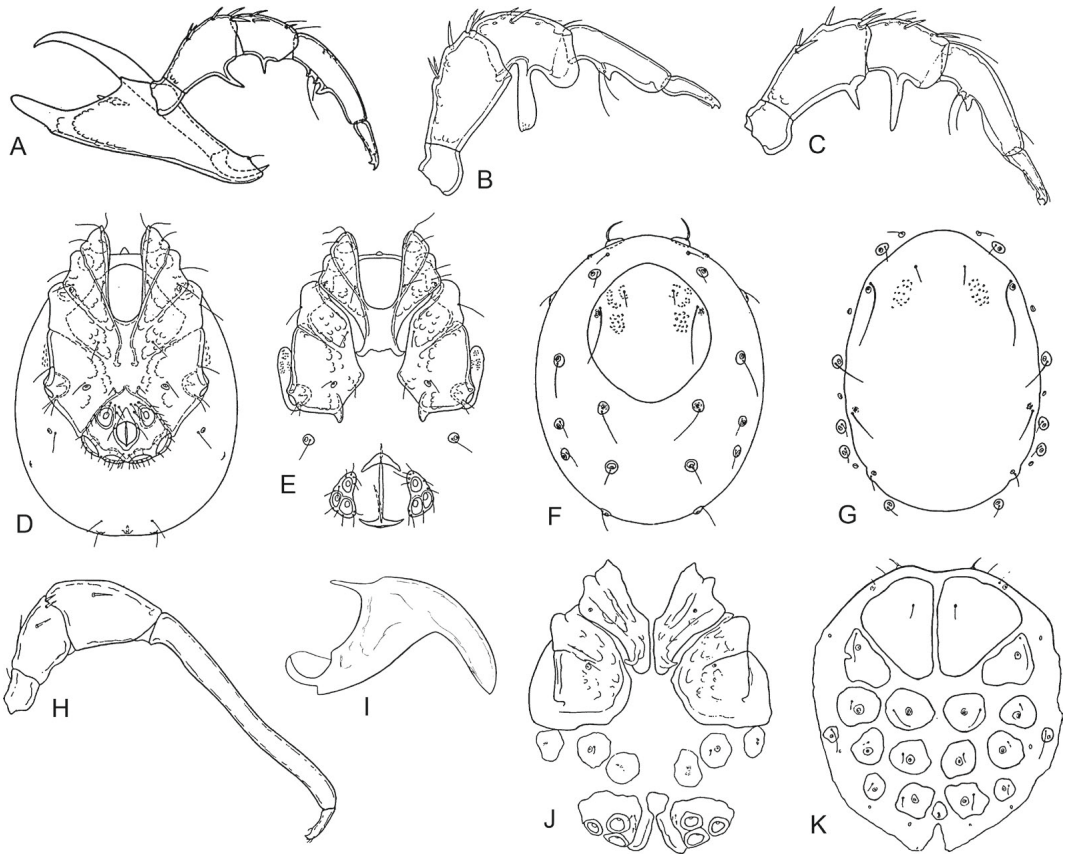

Fig. 43. A. *Atractidella mesoamericana*, female, capitulum, chelicera and right palp lateral (Cook 1980). **B.** *Atractidella obtusidens*, male, palp (Cook 1980). **C.** *Atractidella porophora*, male, palp (Cook 1980). **D.** *Atractidella obtusidens*, male, idiosoma ventral (Cook 1980). **E.** *Atractidella obtusidens*, female, coxae and genital field (Cook 1980). **F.** *Atractidella mesoamericana*, female, idiosoma dorsal (Cook 1980). **G.** *Atractidella mesoamericana*, male, idiosoma dorsal (Cook 1980). **H.** *Motasia placoderma*, female, palp (Cook 1974). **I.** *Motasia placoderma*, female, capitulum lateral (Cook 1974). **J.** *Motasia placoderma*, female, coxae and genital field (Cook 1974). **K.** *Motasia placoderma*, female, idiosoma dorsal (Cook 1974).

[One described species (only female): *M. placoderma* Lundblad, 1953. Colombia. Habitat: streams]

21' Not with the described combination of characters; especially not with down-curved rostrum. 22

22 (21') Without dorsalia or ventralia; coxal field in four groups, Cx-I, -II rather small, far separated by large capitulum; tips of Cx-I with long setae; glands on Cx-IV medial, well posterior to suture line between Cx-III and -IV; capitulum free, with large rostrum (Figs 16A, 44E); P2 with long ventral projection, P2 and P3 ventral fine denticulate, P4 ventral with conspicuous tubercles and ridges (Fig. 44J,K,M). .... ***Zabobates*** Cook, 1988
[Three described species. Chile. Habitat: streams]

22' Not with the described combination of characters; capitulum considerably smaller. 23

23 (22') Gland on Cx-IV shifted towards anterior, forming a loop of suture line between Cx-III and -IV (Fig. 44A,C); P2, P3 ventral slightly denticulate, P4 ventrally with setal tubercle, without peg-like seta (Fig. 44N); **male**: dorsum with three large plates (two anterior,

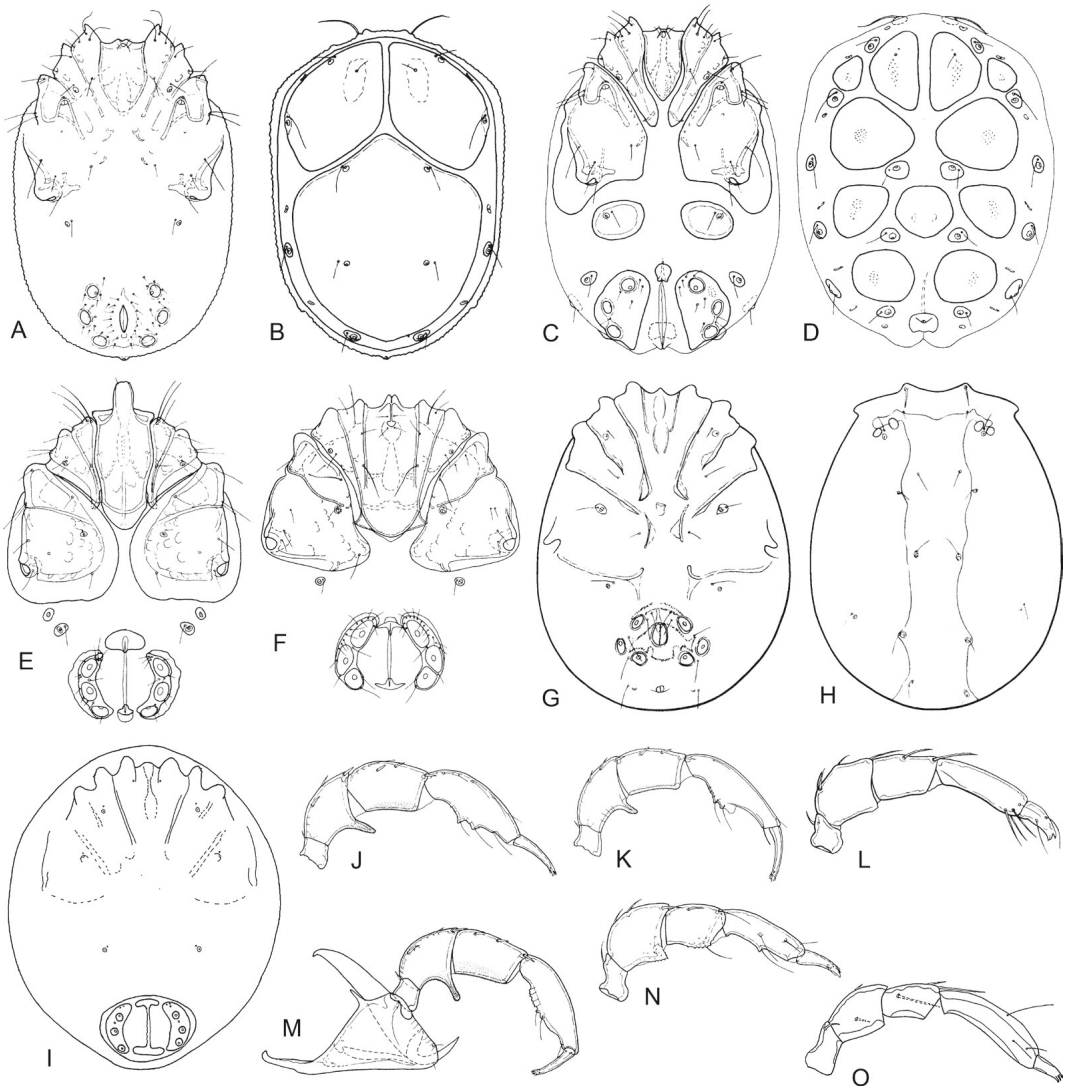

Fig. 44. **A.** *Callumobates kurtvietsi*, male, idiosoma and capitulum ventral (Cook 1988). **B.** *Callumobates kurtvietsi*, male, idiosoma dorsal (Cook 1988). **C.** *Callumobates kurtvietsi*, female, idiosoma and capitulum ventral (Cook 1988). **D.** *Callumobates kurtvietsi*, female, idiosoma dorsal (Cook 1988). **E.** *Zabobates facetus*, female, coxae, capitulum and genital field (Cook 1988). **F.** *Hygrobates ampliatus*, female, coxae, capitulum and genital field (Cook 1980). **G.** *Thoracohygrobates cancellatus*, male, idiosoma and capitulum ventral (Cook 1974). **H.** *Thoracohygrobates cancellatus*, male, idiosoma dorsal (Cook 1974). **I.** *Scutobates guianaensis*, female, idiosoma ventral (after Smit & Clavier 2019). **J.** *Zabobates alphus*, female, palp (Cook 1988). **K.** *Zabobates facetus*, female, palp (Cook 1988). **L.** *Thoracohygrobates cancellatus*, male, palp (Cook 1974). **M.** *Zabobates gledhilli*, female, capitulum, chelicera and palp lateral (Cook 1988). **N.** *Callumobates kurtvietsi*, female, palp (Cook 1988). **O.** *Scutobates guianaensis*, female, palp (after Smit & Clavier 2019).

one posterior) (Fig. 44B); complete ventral shield, capitulum fused with coxae (suture line still visible) (Fig. 44A); **female**: dorsum with series of mid-sized platelets (Fig. 44D); four coxal groups, capitulum free; a pair of mid-sized platelets between coxal field and genital field, Ac on large plates (Fig. 44C). . ..... ***Callumobates*** Cook, 1988 [One described species: *C. kurtvietsi* Cook, 1988. Chile. Habitat: stream]

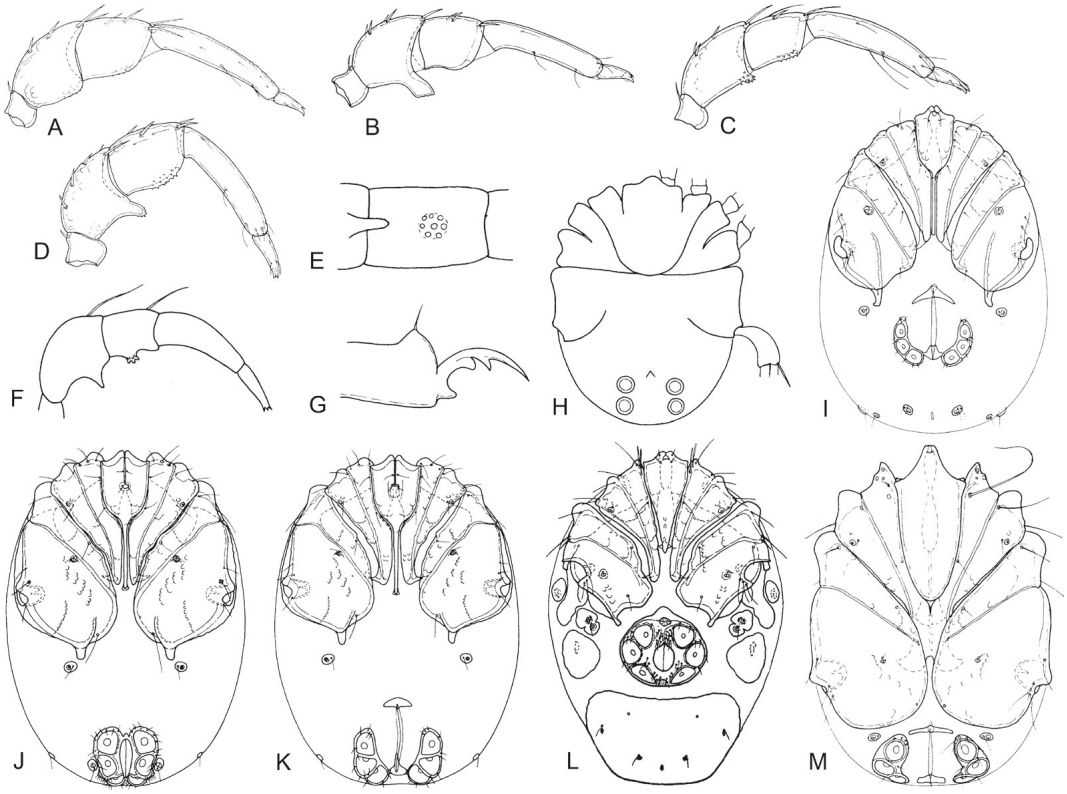

Fig. 45. **A.** *Hygrobates amplipalpis*, male, palp (Cook 1980). **B.** *Hygrobates blatolus*, male, palp (Cook 1980). **C.** *Hygrobates mexicanus*, female, palp (Cook 1980). **D.** *Hygrobates clevamus*, female, palp (Cook 1980). **E.** *Kyphohygrobates verrucifer*, deutonymph, detail P2, P3 ventral (Cook 1974). **F.** *Kyphohygrobates verrucifer*, deutonymph, palp (Cook 1974). **G.** *Kyphohygrobates verrucifer*, deutonymph, IV-leg-6 distal claw (Cook 1974). **H.** *Kyphohygrobates verrucifer*, deutonymph, idiosoma ventral (Cook 1974). **I.** *Australiobates* (*Australiobates*) *gomorus*, female, idiosoma and capitulum ventral (Cook 1988). **J.** *Schizobates disjunctus*, male, idiosoma and capitulum ventral (Cook 1988). **K.** *Schizobates disjunctus*, female, idiosoma and capitulum ventral (Cook 1988). **L.** *Osornobates gennadus*, male, idiosoma and capitulum ventral (Cook 1988). **M.** *Mapuchacarus condiscipulorum*, female, idiosoma and capitulum ventral (Cook 1988).

23' Not with the described combination of characters; **if** suture line between Cx-III and -IV looped around gland, complete dorsal and ventral shield present in both sexes (*Aspidiobates*, see below) or both sexes soft bodied (very few *Hygrobates*, see below). 24

24 (23') Capitulum fused with Cx-I, forming three coxal groups (Figs 44F, 16D) or complete ventral shield (Fig. 44G). 25

24' Capitulum **not** fused with coxae. 28

25 (24) Idiosoma completely sclerotized except a small area surrounding the genital field (Fig. 44I), dorsal furrow absent; P2 and P3 without denticles (Fig. 44O); legs without swimming setae. ..... ***Scutobates*** Cook, 1966
[One described species: *S. guianaensis* Smit & Clavier 2019. French Guiana (Smit & Clavier 2019). Habitat: lake]

25' Sclerotization, if present, less extended, if a ventral shield is present, the genital field is fused. 26

26 (25') Large ventral shield extended far to dorsum, leaving only medial stripe of soft integument free (Fig. 44G,H); all legs with swimming setae; palp without ventral projections or denticles, P4 ventro-distal with three long setae far distally (Fig. 44L). ..... ***Thoracohygrobates*** Lundblad, 1936
[One described species: *T. cancellatus* Lundblad, 1936. Brazil. Habitat: stream]

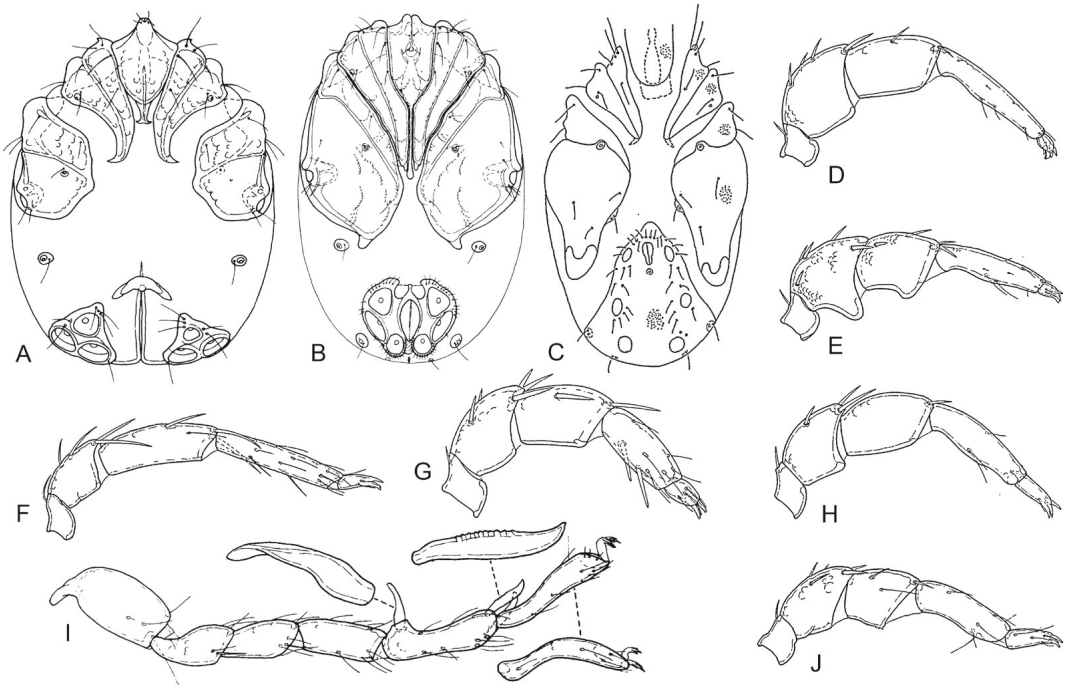

Fig. 46. A. *Corticacarus baderi*, female, idiosoma and capitulum ventral (Cook 1980). **B.** *Schizobates critus*, male, idiosoma and capitulum ventral (Cook 1988). **C.** *Andesobates magellanica*, male, idiosoma ventral (Tuzovskij & Stolbov 2016). **D.** *Schizobates similis*, male, palp (Cook 1988). **E.** *Schizobates clanopus*, female, palp (Cook 1988). **F.** *Australiobates* (*Australiobates*) *cekalovici*, female, palp (Cook 1988). **G.** *Australiobates* (*Australiobates*) *curtipalpis*, female, palp (Cook 1988). **H.** *Australiobates* (*Australiobates*) *litatus*, male, palp (Cook 1988). **I.** *Osornobates gennadus*, male, IV-leg (Cook 1988). **J.** *Osornobates gennadus*, male, palp (Cook 1988).

26' Sclerotization, if present, mostly less extended (if extended up to dorsum, palp not as described); palp variable, often with ventral projection at P2 and/or P2, P3 often ventrally denticulate (Fig. 45A,D). 27

27(26') P2 with ventral projection, P3 with large papillae on a shallow ventral tubercle (Fig. 45E,F); IV-leg-6 dorso-distally raised (Fig. 45G); transversal suture line between Cx-IV and the other coxae (Fig. 45H). .... ***Kyphohygrobates*** Viets, 1935 [One described species: *K. verrucifer* (Daday, 1905). Paraguay. The genus is only based on a single deutonymph, documented only by very diagrammatic drawings (see Cook 1974, p. 430). Habitat: stream]

27' Not with the described combination of characters; P2 often with ventral projection (variable in size and shape), P3 often with ventral denticles (variable in size and shape, but not confined to a tubercle, as described above) (Fig. 45A–D); coxae without transversal suture (Figs 7G,H, 16D,E, 44F). .... ***Hygrobates*** Koch, 1837 [Thirty-seven described species. Mexico, Guatemala, Honduras (Wiles 2005), Costa Rica, Panama (Goldschmidt et al. 2016), St. Vincent, Trinidad and Tobago (Bader 1988), Colombia, Venezuela, Suriname, Ecuador (Cook et al. 2000), Brazil, Peru, Bolivia (Fernández et al. 2009), Paraguay, Argentina, Uruguay. Key to South American species in Lundblad (1953). Habitat: running waters, standing waters, springs]

28(24') Capitulum with long, slender posterior process (Figs 40H, 45I–K). 29

28' Capitulum without, or with short posterior process (Figs 45L,M, 46A). 30

29(28) P4 ventral bearing two hair-like setae; P5 short in relation to P4 (Fig. 46D,E); **male**: one pair of glandularia close to Cx-IV, a second pair closely flanking the genital field (Figs 45J,K, 46B). ..... ***Schizobates*** Thor, 1927

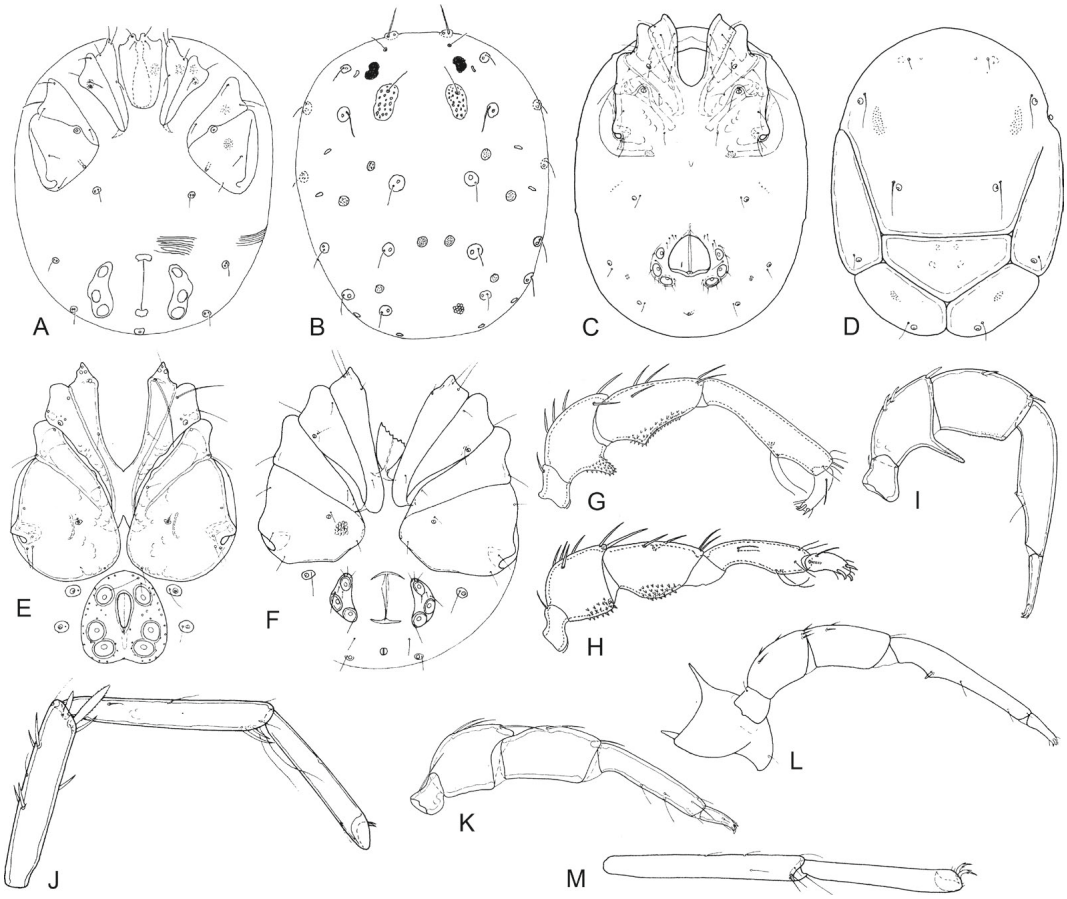

Fig. 47. A. *Andesobates magellanica*, female, idiosoma and capitulum ventral (Tuzovskij & Stolbov 2016). **B.** *Andesobates magellanica*, female, idiosoma dorsal (Tuzovskij & Stolbov 2016). **C.** *Aspidiobates harveyi*, female, idiosoma ventral (Cook 1988). **D.** *Aspidiobates harveyi*, female, idiosoma dorsal (Cook 1988). **E.** *Mapuchacarus condiscipulorum*, male, coxae and genital field (Cook 1988). **F.** *Stylohygrobates longipalpis*, female, idiosoma ventral (Cook 1974). **G.** *Andesobates magellanica*, male, palp lateral (Tuzovskij & Stolbov 2016). **H.** *Andesobates magellanica*, female, palp lateral (Tuzovskij & Stolbov 2016). **I.** *Mapuchacarus condiscipulorum*, male, palp (Cook 1988). **J.** *Mapuchacarus condiscipulorum*, male, I-leg-4/-5/-6 (Cook 1988). **K.** *Aspidiobates harveyi*, female, palp (Cook 1988). **L.** *Stylohygrobates longipalpis*, female, capitulum and right palp lateral (Cook 1974). **M.** *Stylohygrobates longipalpis*, female, I-leg-5/-6 (Cook 1974).

[Five described species. Chile, Argentina. Habitat: standing waters, streams]

29' P4 ventral setae thickened in some species; P5 elongated relative to P4 (Fig. 46F–H); **male**: one pair of glandularia between Cx-IV and the genital field, a second pair far posterior to the genital field (Fig. 40G). .... ***Australiobates*** Lundblad, 1941 (in part), sg. ***Australiobates*** Lundblad, 1941
[Five described species. Chile, Argentina. Habitat: running waters]
Note: Some species with large medial seta at P4 are keyed above (15).

30 (28') Dorsum and venter with extensive sclerotization but without complete dorsal or ventral shield, posterior end of idiosoma sclerotized; four coxal groups; capitulum free, triangular, posteriorly pointed; Cx-IV with large postero-lateral projections; gland on Cx-IV centrally located (Fig. 45L); P3 disto-ventrally with small denticles (Fig. 46J); IV-leg-5 with two enlarged setae (Fig. 46I). .... ***Osornobates*** Cook, 1988
[One described species (only male): *O. gennadus* Cook, 1988. Chile. Habitat: stream]

30' Not with the described combination of characters. 31

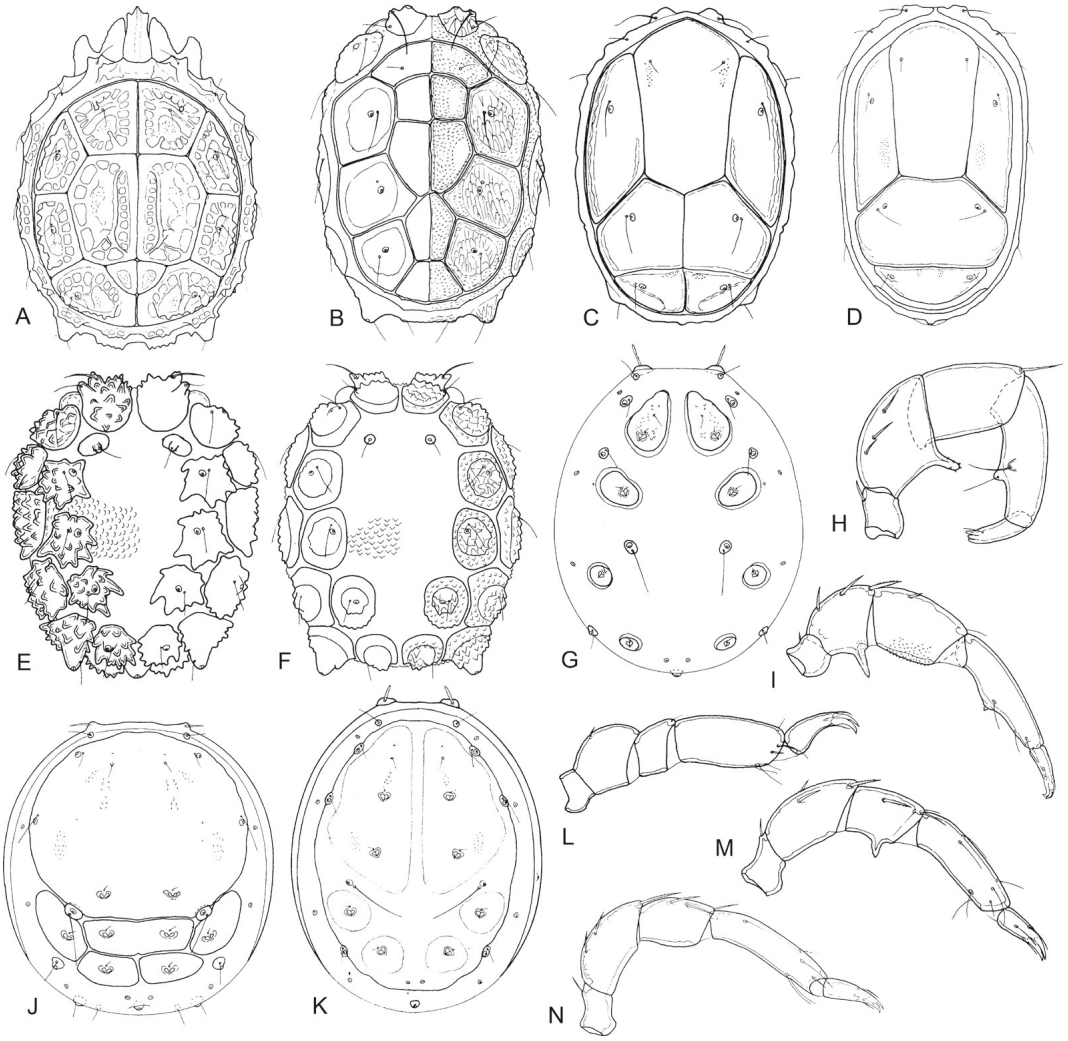

Fig. 48. A. *Rhynchaturus tricornis*, female, idiosoma and capitulum dorsal (Cook 1988). **B.** *Brevaturus geometricus*, male, idiosoma dorsal (Cook 1988). **C.** *Brevaturus lembus*, male, idiosoma dorsal (Cook 1988). **D.** *Brevaturus similis*, female, idiosoma dorsal (Cook 1988). **E.** *Brevaturus stellatus*, male, idiosoma dorsal (Cook 1988). **F.** *Brevaturus schwoerbeli*, male, idiosoma dorsal (Cook 1988). **G.** *Corticacarus dividus*, female, idiosoma dorsal (Cook 1988). **H.** *Eocorticacarus siolii*, male, palp (Cook 1974). **I.** *Corticacarus dividus*, male, palp (Cook 1988). **J.** *Corticacarus exilis*, female, idiosoma dorsal (Cook 1988). **K.** *Corticacarus anchistus*, male, idiosoma dorsal (Cook 1988). **L.** *Rhynchaturus projectus*, male, palp (Cook 1988). **M.** *Brevaturus chilensis*, female, palp (Cook 1988). **N.** *Brevaturus triangularis*, male, palp (Cook 1988).

31 (30') **Male**: idiosoma elongated-oval, Cx-IV elongate; genital field enlarged, triangular; IV-legs inserted at posterior end of Cx-IV; a pair of glandularia at medial margin of Cx-IV, a second pair of glandularia postero-laterally fused with genital plate (Fig. 46C); dorsum with large plate; P2 with ventral projection, P2, P3 ventrally denticulate (Fig. 47G); **female**: dorsum soft with several small platelets (Fig. 47B); venter similar to the *Hygrobatella*-like mites (Fig. 47A), P2, P3 ventrally denticulate, without projection (Fig. 47H). . ..... ***Andesobates*** Smit, 2002
[Two described species. Chile (Tuzovskij & Stolbov 2016a), Argentina. Habitat: streams]
Note: The genus *Paratetrahygrobatella* Tu-

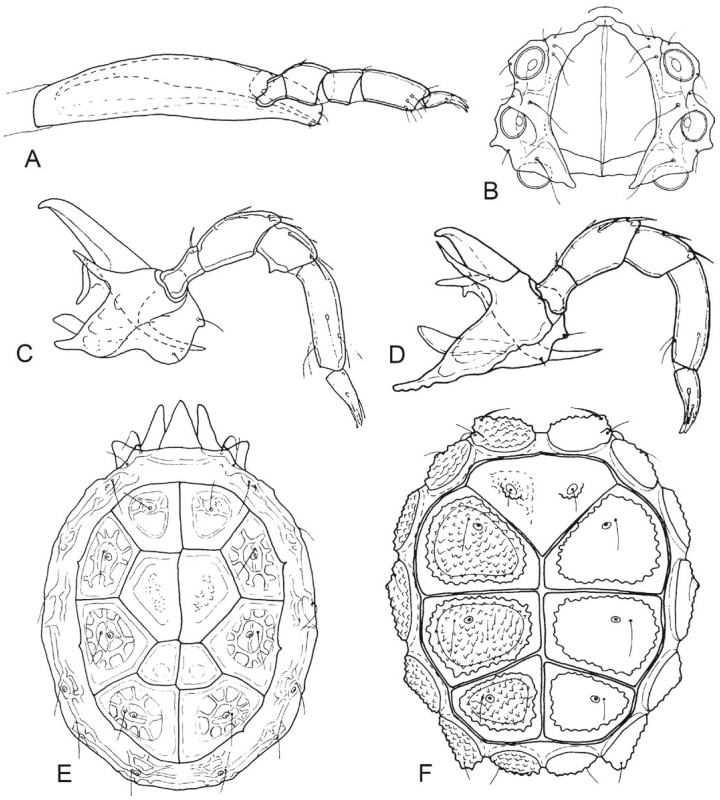

Fig. 49. A. *Rhynchaturus octoporus*, male, capitulum, chelicera and right palp lateral (Cook 1988). **B.** *Rhynchaturus circularis*, female, genital field (Cook 1988). **C.** *Brevaturus stellatus*, female, capitulum, chelicera and right palp lateral (Cook 1988). **D.** *Brevaturus schwoerbeli*, female, capitulum, chelicera and right palp lateral (Cook 1988). **E.** *Rhynchaturus hexaporus*, female, idiosoma dorsal (Cook 1988). **F.** *Brevaturus triangularis*, male, idiosoma dorsal (Cook 1988).

zovskij & Stolbov, 2016 matches the description of *Andesobates*. The large dorsal plate in males was not mentioned by Smit (2002) but is present, therefore *Paratetrahygrobatella* is synonymized with *Andesobates* (Smit 2020).

31' If genital field enlarged, not triangular, Cx-IV rather rounded than elongated. 32

32 (31') Coxal field and genital field fused to complete ventral shield; capitulum free; gland on Cx-IV shifted towards anterior end, suture line between Cx-III and -IV forming a loop around it (Fig. 47C); dorsum densely covered by a large anterior plate and five closely fitting posterior and postero-lateral plates (Fig. 47D); palp without ventral projections or denticles (Fig. 47K). .... ***Aspidiobates*** Lundblad, 1941 [One described species (only female): *A. harveyi* Cook, 1988. Chile. Habitat: stream]

32' Not with the described combination of characters; **if** complete ventral shield is present, suture line between Cx-III and -IV **not** forming a loop. 33

33 (32') Dorsum and venter soft in both sexes. ... 34

33' Sclerotization variable, at least some larger dorsal plates present (at least in male) (Fig. 48A–F). 35

34 (33) Cx-I medially fused posterior to free capitulum; apodemes of first coxal group relatively long (Figs 45M, 47E); P2 **with** a long ventral projection, P4 with short peg-like seta (Fig. 47I); legs with some swimming setae (Fig. 47J). .... ***Mapuchacarus*** Besch, 1964 [Two described species. Costa Rica (Goldschmidt 2004d), Chile. Habitat: streams]

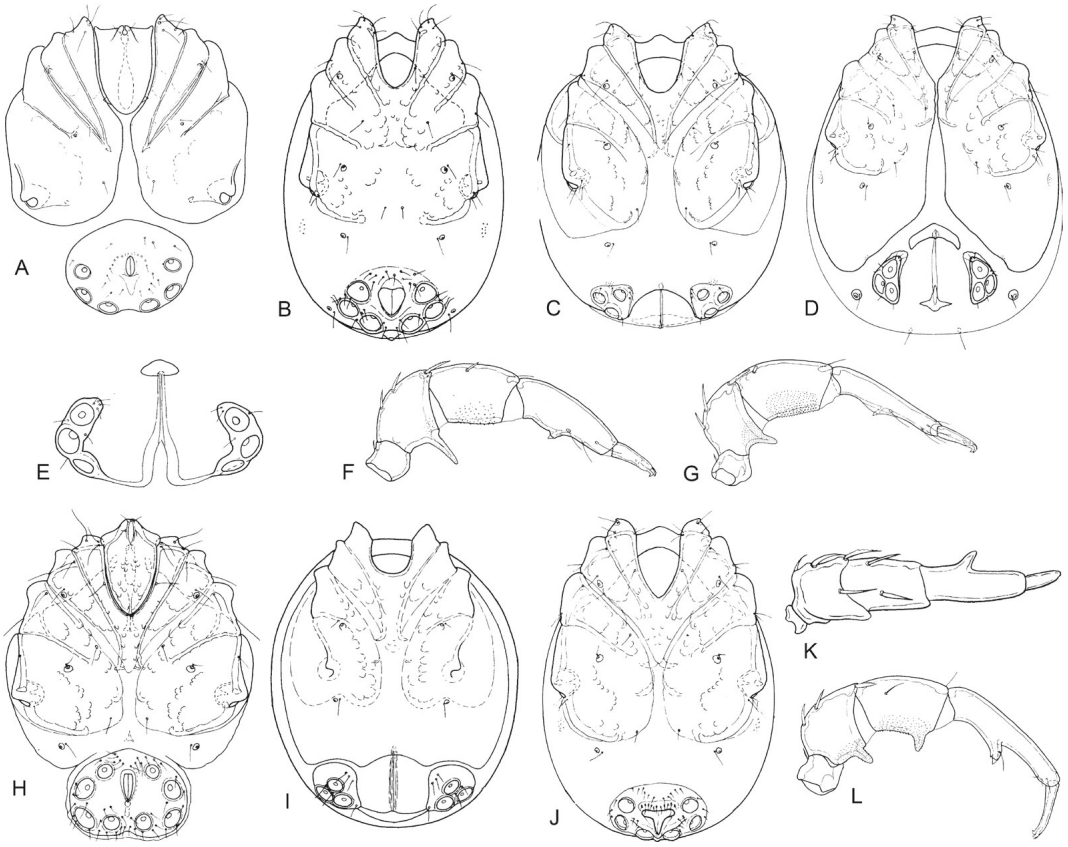

Fig. 50. A. *Eocorticacarus siolii*, male, coxae, capitulum and genital field (Cook 1974). **B.** *Corticacarus argentinensis*, male, idiosoma ventral (Cook 1988). **C.** *Corticacarus umadus*, female, idiosoma ventral (Cook 1988). **D.** *Corticacarus dividus*, female, idiosoma ventral (Cook 1988). **E.** *Eocorticacarus siolii*, female, genital field (Cook 1974). **F.** *Corticacarus argentinensis*, male, palp (Cook 1988). **G.** *Corticacarus umadus*, female, palp (Cook 1988). **H.** *Corticacarus nilsoni*, male, coxae, capitulum and genital field (Cook 1988). **I.** *Subcorticacarus digitatus*, female, idiosoma ventral (Cook 1974). **J.** *Corticacarus brundini*, male, idiosoma ventral (Cook 1988). **K.** *Subcorticacarus digitatus*, female, palp dorsal (Cook 1974). **L.** *Corticacarus schwoerbeli*, male, palp (Cook 1988).

34' Cx-I medially separated; apodemes of first coxal group short (Fig. 47F); P2 **without** a ventral projection, P4 with short peg-like seta (Fig. 47L); legs without swimming setae (Fig. 47M). ..... ***Stylohygrobates*** Viets, 1935 [One described species (only female): *S. longipalpis* K. Viets, 1935. Costa Rica (Goldschmidt 2004d), Brazil. Habitat: standing waters (ditches)]

35 (33') Dorsum and venter covered by closely fitting plates and platelets (Fig. 48A–D) **or**, **if** there are larger areas of soft integument between the sclerites, these bearing large papillae (Fig. 48E,F); P2 and P4 ventrally smooth, without projections or peg-like setae (Fig. 48L–N). 36

35' Sclerotization of dorsum and venter variable (single platelets to complete armour); sclerites not with large papillae (Fig. 48G,J,K); P2 with ventral projection; P4 with peg-like seta or setal tubercles (Fig. 48H,I). 37

36 (35) Gnathosoma long, attached to a protrusible tube (Fig. 49A); dorsum in **all** species covered by closely fitting platelets (always arranged in pairs, separated in medial axis) (Fig. 49E). ..... ***Rhynchaturus*** Besch, 1964 [Eight described species. Chile, Argentina. Key to Chilean species in Schwoerbel (1986a) and Cook (1988). Habitat: streams]

36' Gnathosoma short, without protrusible tube (Fig. 49C,D); dorsum covered by closely fitting platelets arranged in pairs, separated

in medial axis in **some** species (Fig. 48B), with single central plates (Fig. 48C–D) or anterior single plate with pairs of posterior plates (Fig. 49F) in other species, **or** dorsal sclerites leaving larger areas of soft integument free, these sclerites bearing large papillae (Fig. 48E,F). .... ***Brevaturus*** Schwoerbel, 1986 [Ten described species. Chile. Key to species in Cook (1988). Habitat: streams]

37 (35') Coxal groups separated medially, but fused on their respective sides; glands on Cx-IV far anterior, appearing to lie on Cx-III; three pairs of Ac (Fig. 50A); **male**: large genital plate, gonopore oval (Fig. 50A); **female**: Ac forming two arcs (Fig. 50E); P2 with ventral projection, P4 with ventral tubercles bearing hair-like setae (but no peg-like setae) (Fig. 48H). ..... ***Eocorticacarus*** Besch, 1964 [One described species: *E. siolii* Besch, 1964. Peru. Habitat: spring]

37' Coxal groups fused medially in general (separated in some species); glands on Cx-IV anterior, near suture between Cx-III and -IV or centrally; three to eight pairs of Ac (Fig. 50B–D,H–J); **male**: large genital plate, gonopore oval to triangular or heart-shaped (Fig. 50B,H,J); **female**: Ac forming a triangle (Fig. 50C,D,I); P2 with a ventral projection, P4 ventrally with peg-like seta (Fig. 50F,G) or with a lateral tubercle (Fig. 50K). 38

38 (37') Glands on Cx-IV anterior, close to suture line between Cx-III and Cx-IV; insertion of IV-leg far medial, well developed ridge on each side extending from insertion of IV-leg anterolaterally (Fig. 50I); P4 with a lateral tubercle (Fig. 50K). .... ***Subcorticacarus*** Lundblad, 1937 [Two described species (only female). Brazil. Habitat: streams]

38' Glands on Cx-IV (in most species) more centrally, posterior to suture line between Cx-III and Cx-IV; insertion of IV-leg more lateral (Fig. 50B–D,H,J); P4 with or without a ventral tubercle (no lateral tubercle) (Fig. 50G,L). ..... ***Corticacarus*** Lundblad, 1936 [Sixty-four described species. Mexico, Guatemala, Costa Rica, Panama (Goldschmidt et al. 2016), St. Vincent, Colombia, Ecuador (unpublished data), Chile (Tuzovskij 2016, Tuzovskij & Stolbov 2016b), Brazil, Peru, Bolivia (Fernández et al. 2009), Paraguay, Argentina. Key to South American species in Lundblad (1953), and to Chilean species in Cook (1988). Habitat: streams, springs]

Key to Aturidae Thor, 1900

Preceding comments

The Aturidae is a large and difficult group that needs a critical revision. Therefore in this family keys to subgenera are included as well. A key to subfamilies is preceding the genera key.

In unclear cases both alternative branches of the key should be checked carefully.

In this family, some genera so far just published from North America are included as well, as their occurrence in the Neotropics can be expected, or they have already been found in unpublished material from the Neotropics.

A key to (some) South American species of Aturidae is available in Lundblad (1943b).

Most specimens in this family are very small, therefore some characters are only visible under the microscope. In some cases, when specimens are relatively clear, this might as well be possible without mounting. However in this group clearing and slide-mounting of representative specimens is often indispensable.

Key to subfamilies

1 Dorsal shield composed of several closely fitting platelets (Fig. 51B,D–F); anterior coxae projecting slightly to far beyond anterior idiosoma margin; four to many pairs of Ac (Fig. 51A,C). .... **Notoaturinae** Besch, 1964, 4

1' Dorsal shield complete (eventually with some small additional platelets in dorsal furrow) (Fig. 52A,J); anterior coxae may or may not project beyond anterior idiosoma margin; three to many pairs of Ac (Fig. 51G–L). ... 2

2 (1') At least ten pairs of Ac, genital plates (separated from ventral shield) flanking gonopore; coxal field with suture lines between Cx-I and -II and between Cx-III and -IV distinct, all extending to midline, meeting at level of insertions of IV-leg, Cx-IV at insertions of IV-leg without projections, anterior margin of Cx-I far from anterior idiosoma margin (Fig. 51G). ..... **Albiinae** Viets, 1915 (in the Neotropics only genus ***Albia*** Thon, 1899, sg. ***Albiella*** Lundblad, 1971) [Four described species. Mexico, Costa Rica, Panama (Camacho et al. 1997), Brazil, Paraguay, Argentina. Habitat: streams, standing waters]

2' Three to many pairs of Ac, genital plates fused with ventral shield; coxal field not as

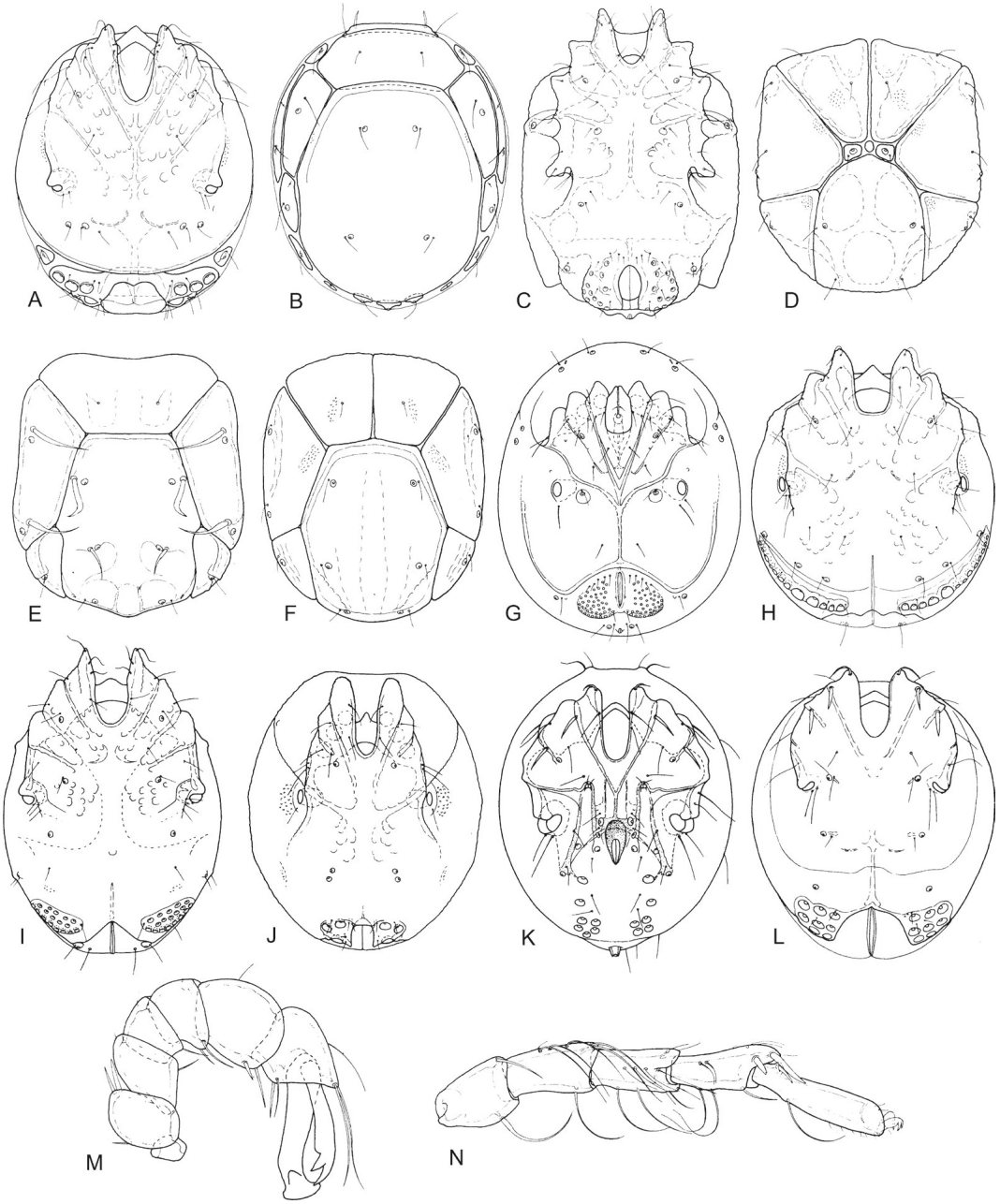

Fig. 51. A. *Notaxona ochiepus*, female, idiosoma ventral (Cook 1988). **B.** *Notaxona ochiepus*, female, idiosoma dorsal (Cook 1988). **C.** *Notoaturus leptoglyphus*, female, idiosoma ventral (Cook 1988). **D.** *Notoaturus leptoglyphus*, female, idiosoma dorsal (Cook 1988). **E.** *Noesaturus otendus*, male, idiosoma dorsal (Cook 1988). **F.** *Noesaturus otendus*, female, idiosoma dorsal (Cook 1988). **G.** *Albia iantha*, male, idiosoma and capitulum ventral (Cook 1980). **H.** *Aturus kronestedti*, female, idiosoma ventral (Cook 1988). **I.** *Neoaturus kurtvietsi*, female, idiosoma ventral (Cook 1980). **J.** *Brachypodopsis* (*Brachypodopsis*) *cemoba*, female, idiosoma ventral (Cook 1980). **K.** *Miraxona expansipes*, male, idiosoma ventral (Cook 1980). **L.** *Neoalbia* (*Neoalbiella*) *octopora*, female, idiosoma ventral (Cook 1974). **M.** *Notaxona ochiepus*, male, IV-leg (Cook 1988). **N.** *Noesaturus otendus*, male, IV-leg (Cook 1988).

above, insertions of IV-leg with or without projections. 3

3 (2') Ac numerous (eight or more pairs), arranged in transversal fields parallel to posterior margin of idiosoma; anterior coxae well projecting beyond anterior end of body (Figs 17C, 51H,I). ... **Aturinae** Thor, 1900, 6

3' Three or four pairs of Ac, if more, not arranged in transversal fields and anterior coxae projecting only slightly (e.g. some species of *Miraxona*, *Neoalbia*, *Polyaxonopsella*) or not at all beyond anterior end of body (Fig. 51J–L). .... **Axonopsinae** Viets, 1929, 10

Key to genera and subgenera

Notoaturinae Besch, 1964

4 (1) One large posterior, several smaller antero-lateral platelets (diminishing towards posterior) (Fig. 51B); four pairs of Ac; anterior coxae only slightly projecting beyond anterior end of body (Fig. 51A); sexual dimorphism in leg-IV (**male**: all segments shortened and expanded, claws greatly elongated) (Fig. 51M). ..... ***Notaxona*** Besch, 1964
[One described species: *N. ochiepus* Besch, 1964. Chile. Habitat: streams]

4' Dorsal shield variable, but not as described (Fig. 51D–F); anterior coxae by far projecting beyond anterior end of body, Ac numerous (Fig. 51C). 5

5 (4') Dorsal shield with large paired antero-medial plates, centrally with a pair of small sclerites bearing glandularia (fused to a single sclerite in one species); associated setae of dorsal glandularia not thickened (Fig. 51D); no sexual dimorphism in leg-IV. ..... ***Notoaturus*** Besch, 1964
[Four described species. Chile. Habitat: streams]

5' **Male**: dorsal shield with single antero-medial plate; associated setae of antero-lateral and first two postero-medial dorsal glandularia greatly thickened (Fig. 51E); **female**: paired antero-medial plates; dorsum without small central platelets (Fig. 51F); sexual dimorphism in IV-leg (**male**: thickened segments, elongated setae at IV-leg-3 and -4; modified setae at IV-leg-5 and -6) (Fig. 51N). ..... ***Noesaturus*** Cook, 1988
[Four described species. Chile. Habitat: streams]

Aturinae Thor, 1900

6 (3) Dorsal shield with seven pairs of large glandularia, six of these characteristically grouped together in posterior half (Fig. 52A). .... ***Aturides*** Lundblad, 1937
[Three described species. Mexico, Costa Rica, Brazil. Habitat: streams]

6' Glandularia on dorsal shield not grouped as described above. 7

7 (6') Coxae at insertions of IV-leg without projections; Ac in a single row along (in some species **at**) postero-lateral edge of ventral shield (Fig. 51H); IV-leg-5 of male bearing several long, thick setae. .... ***Aturus*** Kramer, 1875
[Nine described species. Mexico, Guatemala, Costa Rica (Goldschmidt 2004d), Colombia, Chile. Habitat: streams, interstitial]

7' Coxae at insertions of IV-leg with well developed projections; Ac mostly in several rows (Figs 7I, 17C, 51I) (in *Kongsbergia* (*Crocokongsbergia*) *cooki* a single row of Ac is curved far anterior to posterior edge of idiosoma, coxae characteristically different (see below) (Fig. 52B,G)). 8

8 (7') Projections at insertions of IV-leg do not extend to lateral edge of ventral shield; Ac in several rows (mostly forming well-defined elongated oval fields) flanking the gonopore; two pairs of large glandularia (antero- and postero-medial to insertion of IV-leg (Fig. 51I)); IV-leg without strong sexual dimorphism (male without large, blade-like seta). ..... ***Neoaturus*** Lundblad, 1941
[Nine described species. Mexico, Costa Rica, Colombia, Surinam, Brazil, Ecuador (unpublished data), Argentina. Key to South American species in Lundblad (1953). Habitat: running waters]

8' Projections at insertions of IV-leg generally extend to lateral edge of ventral shield (Figs 17C, 52B); Ac in one or several rows along postero-lateral edge of ventral shield (irregular, not forming clearly delimited fields); no glandularia medial to insertion of IV-leg (Fig. 17C); **male**: IV-leg-5 bearing large, blade-like (often curved) seta (Fig. 52B,E,F). ..... ***Kongsbergia*** Thor, 1899, 9

9 (8') **Male**: first coxae distally with hook-like recurved process (Fig. 52D); **female**: gonopore elongated (Fig. 52G); **both sexes**: projection at insertion of IV-leg extending far laterally (beyond lateral outline of body); Ac in one

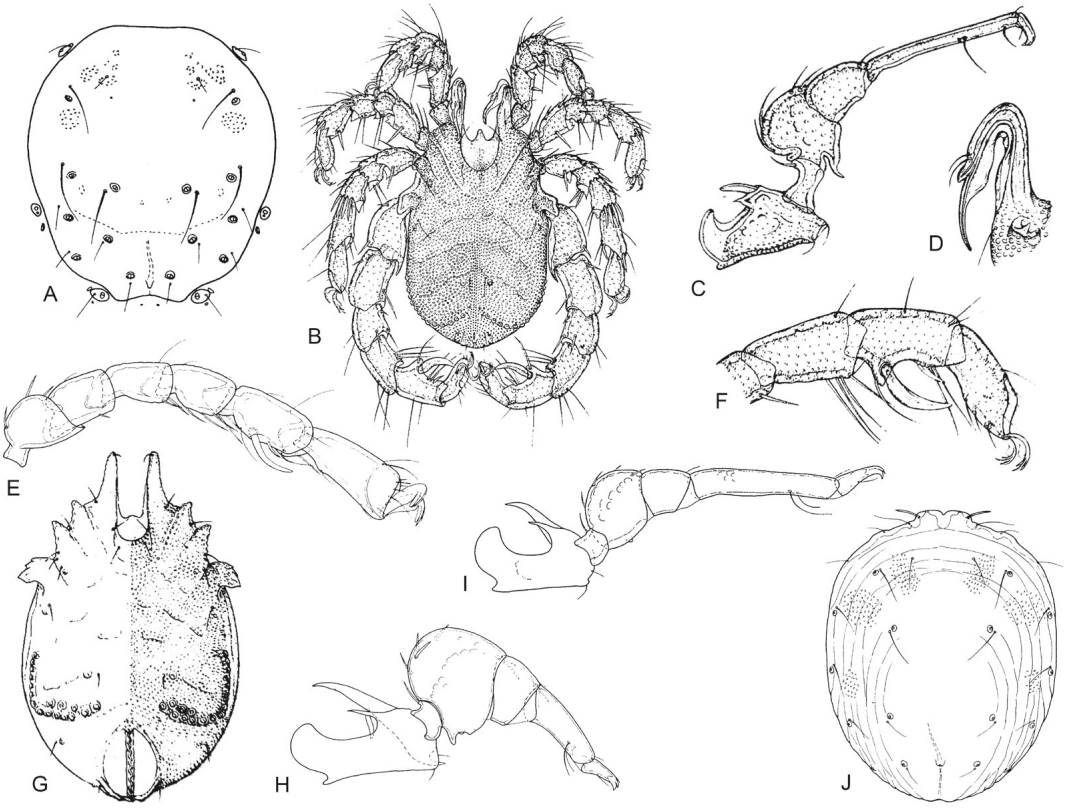

Fig. 52. A. *Aturides aldomus*, female, dorsal shield (Cook 1980). **B.** *Kongsbergia* (*Crocokongsbergia*) *cooki*, male, idiosoma (with all legs) ventral (after Orghidan & Gruia 1983). **C.** *Kongsbergia* (*Crocokongsbergia*) *cooki*, male, capitulum and right palp lateral (after Orghidan & Gruia 1983). **D.** *Kongsbergia* (*Crocokongsbergia*) *cooki*, male, detail antero-medial tip of Cx-I (after Orghidan & Gruia 1983). **E.** *Kongsbergia mexicana*, male, IV-leg (Cook 1980). **F.** *Kongsbergia* (*Crocokongsbergia) cooki*, male, IV-leg-4/-5/-6 (after Orghidan & Gruia 1983). **G.** *Kongsbergia* (*Crocokongsbergia*) *athleta*, female, idiosoma ventral (after Orghidan & Gruia 1983). **H.** *Kongsbergia globipalpis*, male, capitulum, chelicera and right palp lateral (Cook 1980). **I.** *Kongsbergia globipalpis*, female, capitulum, chelicera and right palp lateral (Cook 1980). **J.** *Kongsbergia globipalpis*, female, dorsal shield (Cook 1980).

or two rows, posterior curved towards antero-medial (Fig. 52B,G); P4 very slender, P2 with pointed posteriorly directed ventral projection (Fig. 52C); dorsal shield smooth. .. sg. ***Crocokongsbergia*** Orghidan & Gruia, 1980

[Two described species. Cuba. Habitat: streams]

9' **Male**: first coxae without distal hook-like process; **female**: gonopore smaller (Fig. 7I); **both sexes**: projection at insertion of IV-leg laterally only slightly extending beyond lateral outline of body (Figs 7I, 17C); P4 generally less elongated (exception: *K. suturata*), ventral projection at P2 generally not directed to posterior (Fig. 52I) (exception male of *K. globipalpis* (Fig. 52H)); Ac in several rows, posterior not curved towards medial (Fig. 7I); dorsal shield sculptured (Fig. 52J). ..... sg. ***Kongsbergia*** Thor, 1899

[Eight described species. Mexico, Guatemala, Costa Rica (Goldschmidt 2004d), Colombia, Ecuador (unpublished data), Argentina. Habitat: streams, interstitial]

Axonopsinae Viets, 1929

10 (3') Insertions of IV-leg **with** well developed posterior directed projections (Figs 17A,H, 51K). 11

10' Insertions of IV-leg **without** well developed projections (Fig. 51J). 32

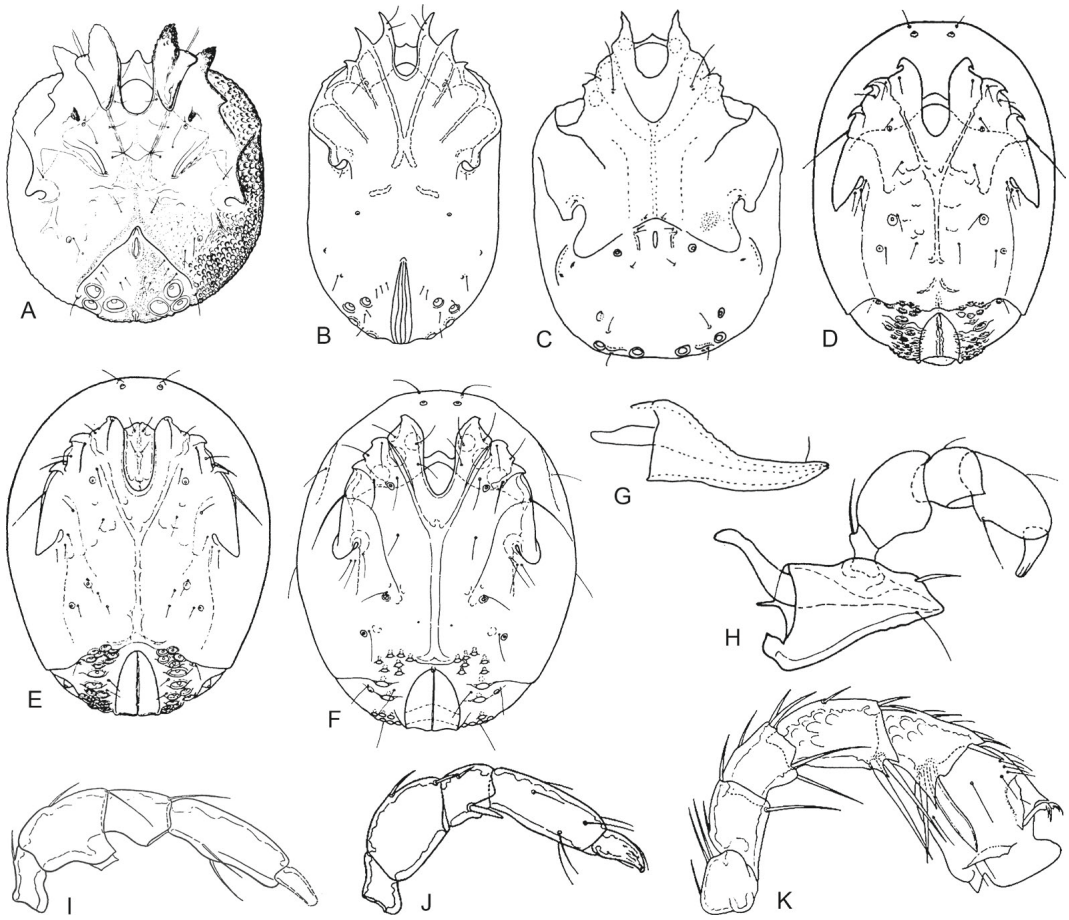

Fig. 53. **A.** *Neoaxonopsis odontogaster*, male, idiosoma ventral (Cook 1974). **B.** *Adelaxonopsella pallida*, female, idiosoma ventral (Cook 1980). **C.** *Vagabundia sci*, male, idiosoma ventral (Valdecasas 2008). **D.** *Neoaxona* (*Neoaxona*) *oblonga*, female, idiosoma ventral (after Lundblad 1943). **E.** *Neoaxona* (*Neoaxona*) *plaumanni*, female, idiosoma and capitulum ventral (after Lundblad 1943). **F.** *Neoaxona* (*Lamellaxona*) *mexicana*, female, idiosoma ventral (Cook 1980). **G.** *Vagabundia sci*, male, capitulum lateral (Valdecasas 2008). **H.** *Adelaxonopsella pallida*, female, capitulum, chelicera and right palp lateral (Cook 1980). **I.** *Neoaxonopsis odontogaster*, female, palp (Cook 1974). **J.** *Neoaxona* (*Neoaxona*) *oblonga*, male, palp (after Lundblad 1943). **K.** *Neoaxona* (*Lamellaxona*) *abnormipes*, male, II-leg (after Lundblad 1943).

11 (10) Three pairs of Ac (Fig. 53A); P2 (in both sexes) with well developed, broad disto-ventral projection (Fig. 53I). .... ***Neoaxonopsis*** Lundblad, 1938 [One described species: *N. odontogaster* Lundblad, 1938. Brazil. Habitat: stream]

11' Four to many pairs of Ac; P2 without or with a very small ventral projection. 12

12 (11') First coxae by far projecting beyond anterior margin of idiosoma; tips of Cx-I sharp pointed (Fig. 53B,C); **female**: gonopore very long and narrow (at least in one of the two genera, in the second one the female is unknown) (Fig. 53B). 13

12' First coxae not or only slightly projecting beyond anterior margin of idiosoma; tips of Cx-I rounded or bluntly pointed (Figs 53F, 54A,D,H); **female**: gonopore relatively wide. 14

13 (12) Tips of Cx-II and -III sharp pointed; posterior margin of Cx-IV obliterate (Fig. 53B); rostrum short, pointed (Fig. 53H). .... ***Adelaxonopsella*** Cook, 1974

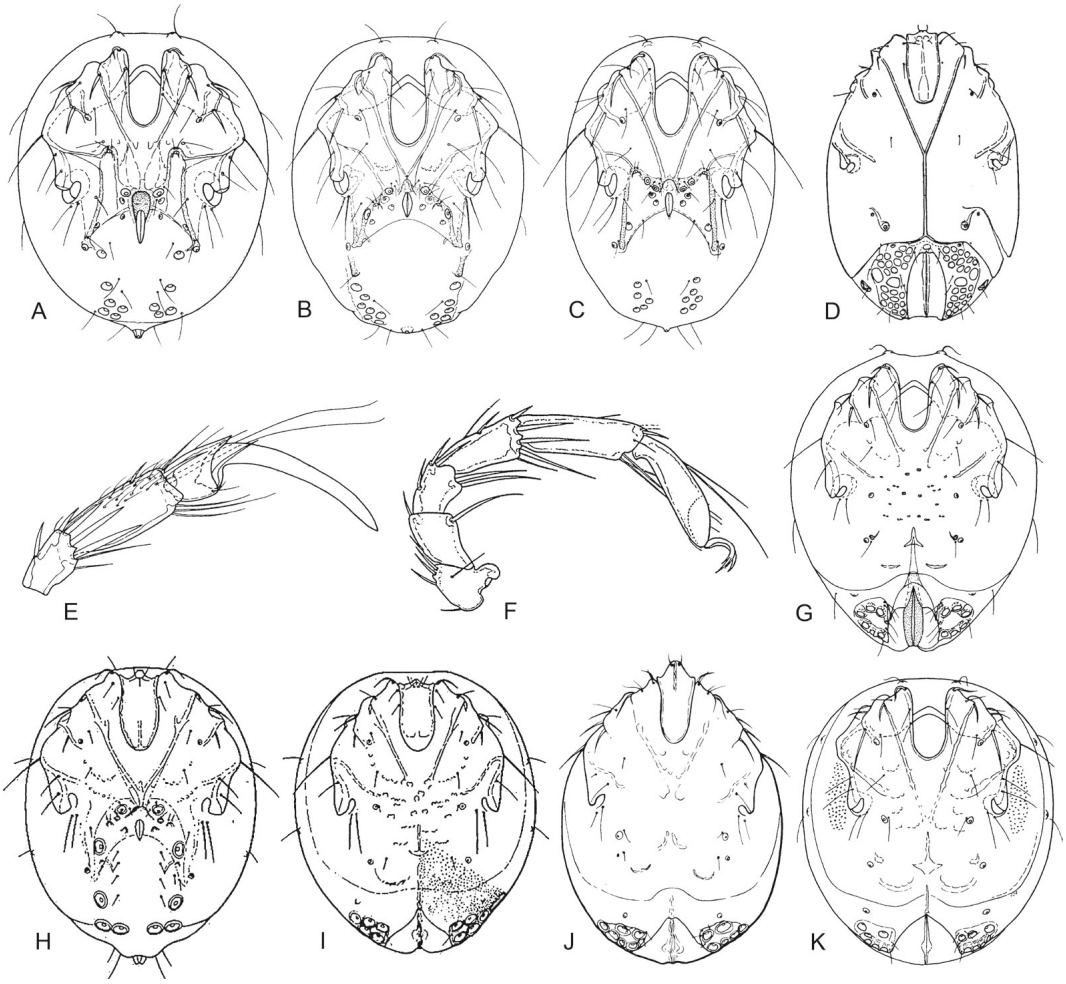

Fig. 54. A. *Miraxona* (*Miraxona*) *mexicana*, male, idiosoma ventral (Cook 1980). **B.** *Submiraxona* (*Submiraxona*) *bella*, male, idiosoma ventral (Cook 1980). **C.** *Submiraxona* (*Submiraxona*) *stolli*, male, idiosoma ventral (Cook 1980). **D.** *Polyaxonopsella anomala*, female, idiosoma and capitulum ventral (Viets 1977). **E.** *Miraxona* (*Miraxona*) *mexicana*, male, II-leg-4/-5/-6 (Cook 1980). **F.** *Miraxona* (*Miraxonella*) *complicata*, male, II-leg (after Lundblad 1943). **G.** *Miraxona* (*Miraxona*) *mexicana*, female, idiosoma ventral (Cook 1980). **H.** *Submiraxona* (*Pentalbia*) *walteri*, male, idiosoma and capitulum ventral (after Lundblad 1943). **I.** *Submiraxona* (*Pentalbia*) *walteri*, female, idiosoma and capitulum ventral (after Lundblad 1943). **J.** *Neoalbia* (*Neoalbia*) *violacea*, female, idiosoma and capitulum ventral (Cook 1974). **K.** *Submiraxona* (*Submiraxona*) *bella*, female, idiosoma ventral (Cook 1980).

[One described species (only female): *A. pallida* Cook, 1974. Mexico. Habitat: interstitial]

13' Tips of Cx-II and -III rounded; posterior margin of Cx-IV clearly visible (Fig. 53C); rostrum long, pointed (Fig. 53G). ..... ***Vagabundia*** Valdecasas, 2008
[One described species (only male): *V. sci* Valdecasas, 2008. Panama (Valdecasas 2008b). Habitat: stream]

14(12') Ac numerous (at least more than four pairs; do not confuse with glandularia in the genital region!) (Figs 53F, 54A,B). 15

14' Four pairs of Ac (Figs 55A,B, 56A–D). ..... **'*Axonopsella*-like mites'**, 23

15(14) Cx-I-III distally with hook-like recurved processes (Fig. 53D–F); P3 in male with a heavy ventral seta (Fig. 53J). ..... ***Neoaxona*** Lundblad, 1936, 16

15' First coxae distally short, rounded, not with hook-like recurved processes (Fig. 54A–C); palps of both sexes without heavy seta on ventral side of P3. ..... **'multiacetabulate *Axonopsella*-like mites'**, 17

16 (15) Transverse ridge into Ac area points to anterior end of acetabular field; projections at insertions of IV-leg more or less pointed in both sexes (Fig. 53D,E); terminal segments of male II-leg not modified. .... sg. ***Neoaxona*** Lundblad, 1936 [Three species described. Suriname, Brazil. Key to South American species in Lundblad (1953). Habitat: stream]

16' Transverse ridge into Ac area points to centre of acetabular field (to anterior pair of enlarged Ac); projections at insertions of IV-leg more or less rounded in both sexes (Fig. 53F); **male**: terminal segments of II-leg highly modified (Fig. 53K). .... sg. ***Lamellaxona*** Lundblad, 1936 [Two species described. Mexico, Brazil, Paraguay. Key to South American species in Lundblad (1953). Habitat: streams]

'*Axonopsella*-like mites'

The group of multiacetabulate '*Axonopsella*-like' mites comprises the genera *Neoalbia* and *Polyaxonopsella* (both of them so far only known in the female sex), as well as *Miraxona* and *Submiraxona* (known in both sexes). As males and females in these genera are morphologically very different, the following steps of the key are separated for male and female.

17 (15') Gonopore completely surrounded by sclerotization (e.g. Fig. 54A–C,H). ..... **male**, 18

17' Gonopore open posteriorly (e.g. Fig. 54D,G, I–K). ..... **female**, 21

Key to males

18 (17) Deep genital pit slightly anterior to gonopore; posterior suture line of Cx-IV extending anteriorly, forming a U-shaped loop (reaching far anterior to insertion of IV-leg, with a glandularium at anterior end of this loop) (Fig. 54A). .... ***Miraxon***a Lundblad, 1936, 19

18' Large apodeme at anterior end of genital field (do not confuse with genital pit in *Miraxona*); U-shaped loop absent or short (not surpassing insertion of IV-leg) (Fig. 54B,C). ..... ***Submiraxona*** Lundblad, 1937, 20

19 (18) II-leg-5 and claws greatly enlarged (Fig. 54E). ..... sg. ***Miraxona*** Lundblad, 1936 [Three described species. Mexico, Ecuador (unpublished data), Brazil. Habitat: streams]

19' II-leg-5 and claws not greatly enlarged (Fig. 54F). .... sg. ***Miraxonella*** Lundblad, 1936 [One described species: *M. complicata* Lundblad, 1936. Brazil. Habitat: streams]

20 (18') Five pairs of Ac (Fig. 54H). .... sg. ***Pentalbia*** Lundblad, 1937 [One described species: *S. walteri* (Lundblad, 1937). Brazil. Habitat: running waters]

20' More than five pairs of Ac (Fig. 54B,C). .... sg. ***Submiraxona*** Lundblad, 1937 [Five described species. Mexico, Costa Rica, Brazil, Argentina. Habitat: running waters]

Key to females

21 (17') Median suture of Cx-IV well developed (Fig. 54D). .... ***Polyaxonopsella*** Lundblad, 1943 [Four described species (only female). Guatemala, Colombia, Venezuela, Paraguay. Habitat: streams, interstitial]

21' Median suture of Cx-IV obliterated (incomplete to absent) (Fig. 54G,I–K). 22

22 (21') Five pairs of Ac (Fig. 54I). ..... ***Submiraxona***, sg. ***Pentalbia*** Lundblad, 1937 [One described species: *S. walteri* (Lundblad, 1937). Brazil. Habitat: running waters]

22' More than five pairs of Ac (mostly six or eight) (Figs 51L, 54G,J,K). .... ***Neoalbia*** Lundblad, 1936; ***Miraxona*** Lundblad, 1936; ***Submiraxona*** sg. ***Submiraxona*** Lundblad, 1937 [***Neoalbia*** – two subgenera: ***Neoalbia*** Lundblad, 1936 – one described species (only female): *N. violacea* Lundblad, 1936; Brazil; ***Neoalbiella*** Viets, 1954 – two described species (only female). Brazil. Habitat: streams] [***Miraxona*** – two subgenera: ***Miraxona*** Lundblad, 1936 – three described species. Mexico, Brazil; ***Miraxonella*** Lundblad, 1936 – one described species: *M. complicata* Lundblad, 1936; Brazil. Habitat: streams] [***Submiraxona*** – one subgenus: ***Submiraxona*** Lundblad, 1937 – five described species. Mexico, Costa Rica, Brazil, Argentina. Habitat: running waters]
Note: These genera can not be separated based on female morphology only.

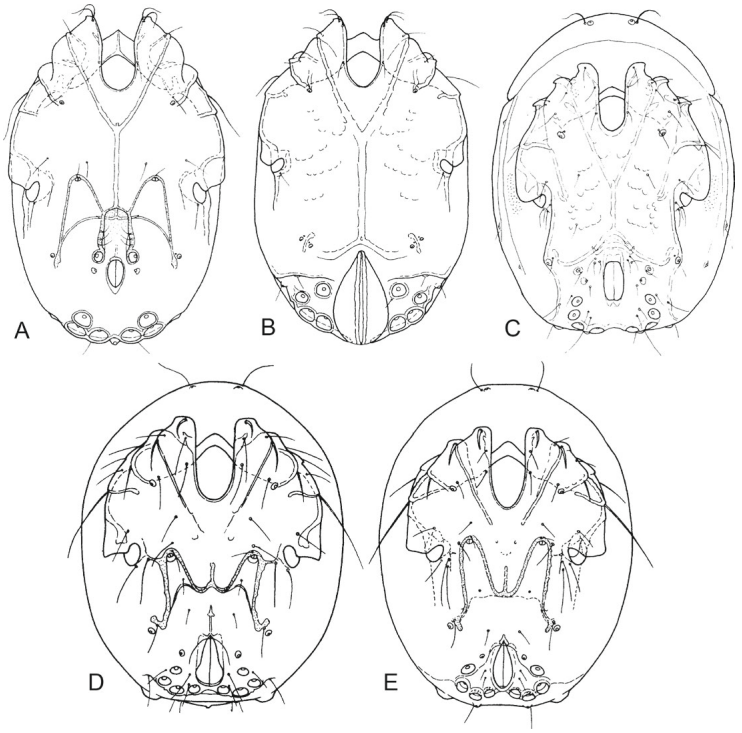

Fig. 55. A. *Stygalbiella tucumanensis*, male, idiosoma ventral (Cook 1980). **B.** *Stygalbiella tucumanensis*, female, idiosoma ventral (Cook 1980). **C.** *Miraxonides* (*Eomiraxonides*) *primitivus*, male, idiosoma ventral (Cook 1988). **D.** *Miraxonides* (*Miraxonides*) *similis*, male, idiosoma ventral (Cook 1980). **E.** *Miraxonides* (*Miraxonides*) *karlvietsi*, male, idiosoma ventral (Cook 1980).

Note: The following key to the four-acetabulate '*Axonopsella*-like' mites again applies to both, male and female.

23 (14') Anterior coxae projecting well beyond anterior margin of the idiosoma (Fig. 55A,B). ... . ***Stygalbiella*** Cook, 1974
[Three described species. Mexico, Guatemala, Argentina. Habitat: running waters]

23' Anterior coxae not reaching (or at least not projecting beyond) anterior margin of the idiosoma (Figs 55C–E, 56A–E). 24

24 (23') **Male**: all four pairs of Ac close together on their respective side; gonopore near or slightly shifted from posterior end of ventral shield; posterior suture line of Cx-IV with U-shaped loop (long or short!) and a glandularium at the anterior end of this loop (except in the sg. *Eomiraxonides*) (Fig. 55D,E). ..... ***Miraxonides*** Lundblad, 1938, 25

24' **Male**: gonopore shifted from posterior end of ventral shield close to posterior margin of Cx-IV; Ac-1 beside gonopore, well anterior to Ac-3 and Ac-4; posterior suture line of Cx-IV never with U-shaped loop (Fig. 56A–C). ..... ***Axonopsella*** Lundblad, 1930, 26

25 (24) **Male**: gonopore near posterior end of ventral shield; posterior suture line of Cx-IV with U-shaped loop (long or short!) and a glandularium at the anterior end of this loop (Fig. 55D,E). .... sg. ***Miraxonides*** Lundblad, 1938, sg. ***Miraxonidella*** Cook, 1980
[Four described species. Mexico, Costa Rica, Brazil, Argentina. Habitat: streams, standing waters, springs]

25' **Male**: gonopore **slightly** shifted from posterior end of ventral shield; posterior suture line of Cx-IV without U-shaped loop (Fig. 55C). .... sg. ***Eomiraxonides*** Cook, 1988
[One described species: *M. (E.) primitivus* Cook, 1988. Chile. Habitat: streams]

Note: Most subgenera of *Axonopsella* can just be separated based on males morphology, as the subgenus definitions are based upon sexual dimorphism of male legs, however in some subgenera female provide differentiating characters as well. The separation of the subgenera ***Paraxonopsella*** vs ***Neoaxonopsella*** (see below) is rather inaccurate, as the species ***Axonopsella (Paraxonopsella) hamata*** and ***Axonopsella (Neoaxonopsella) trifida*** represent intermediate character stages. The subgenus ***Axonopsella*** is a "dumping ground" for species with no male known, and no special characters – though it is mainly characterized by the following features: Anterior coxae not projecting beyond idiosoma; four pairs of Ac; posterior suture line of Cx-IV not forming a U-shaped loop and no postero-dorsal glandularia tubercles. [sg. ***Axonopsella***. Ten species. Mexico, Guatemala, Costa Rica, Panama (Camacho et al. 1997), Colombia, Venezuela, Brazil, Ecuador (unpublished data), Argentina, Chile. Key to South American species of *Axonopsella* in Lundblad (1953). Habitat: running waters]

26 (24') Rostrum very long and broad (Fig. 56F). ... sg. ***Rostaxonopsella*** Orghidan & Gruia, 1987
[One described species: *A. (R.) nana* Orghidan & Gruia, 1987. Costa Rica (pers. obs.), Venezuela. Habitat: interstitial]

26' Rostrum small, short. 27

27 (26') Idiosoma elongated-oval; **male**: lateral ridge between genital field and insertion of IV-leg (Fig. 56B,C arrows); genital field separated from ventral shield by complete suture line (Fig. 56B,C); **female**: antero-lateral ridge extending anteriorly from insertion of IV-leg; Cx-IV glandularia very large, close to insertion of IV-leg (Fig. 56D). .... sg. ***Coaxonopsella*** Cook, 1980
[One described species: *A. (C.) jujuyensis* Cook, 1980. Argentina. Habitat: stream]

27' Idiosoma elongated-oval or rounded, but not as described above; no postero-lateral ridge; suture line around genital field incomplete. 28

28 (27') **Male**: IV-leg-4 with two very short, heavy setae on ventral projection (Fig. 56I); **female**: dorsal and ventral shields posteriorly fused. ..... sg. ***Chilaxonopsella*** Cook, 1988
[Four described species. Chile. Habitat: streams]

28' **Male**: IV-leg-4 with single large (mostly hooked) seta on ventral projection; **female**: dorsal and ventral shields posteriorly separated. 29

29 (28') **Female**: Ac on genital plates, separated from ventral shield; genital area not cone-shaped, but anteriorly widened (Fig. 56E). .... sg. ***Humboldtaxonopsella*** Orghidan & Gruia, 1981
[One described species (only female): *A. (H.) linaresi* Orghidan & Gruia, 1981. Venezuela. Habitat: interstitial]

29' **Female**: genital plates completely fused with ventral shield; genital area more or less cone-shaped. 30

30 (29') Claws of II-leg with slight sexual dimorphism (Fig. 56G). .... sg. ***Neoaxonopsella*** Lundblad, 1937
[Ten described species. Mexico, Cuba, Costa Rica, Venezuela, Brazil, Argentina. Habitat: streams, interstitial]

30' II-leg (claws and/or terminal segments) with pronounced sexual dimorphism. 31

31 (30') **Male**: II-leg-5 large, II-leg-6 very short with long swimming setae, claws strongly transformed (one straight with dorsal tooth, one large, tube-like) (Fig. 56H); IV-leg-4 short, ventro-distal projection with three short and heavy setae (Fig. 56J). ..... sg. ***Luciaxonopsella*** Rosso de Ferradás, 1995
[One described species (only male): *A. (L.) misionum* Rosso de Ferradás, 1995. Argentina. Habitat: stream]

31' **Male**: II-leg-6 one claw normal, one claw heavily prolonged or widened (Fig. 56K,L). ..... sg. ***Paraxonopsella*** Lundblad, 1937
[Three described species. Brazil, Argentina. Habitat: streams]

32 (10') Postero-medial margin of Cx-IV complete, with characteristic indentation, partly surrounding a pair of glandularia (Fig. 57M,N). ..... ***Ljania*** Thor, 1898
[One undescribed species. Mexico (Cramer 1988). Habitat: streams]

32' Postero-medial margin of Cx-IV if complete, without such an indentation. 33

33 (32') Well developed antero-lateral ridge extending from medial or slightly anterior (in one genus well anterior) to insertion of IV-leg to antero-lateral sides of body (Fig. 57C,G, H,K). 34

33' Without such antero-lateral ridge (Fig. 57I,J). ..... **'*Axonopsalbia*-like mites'**, 39

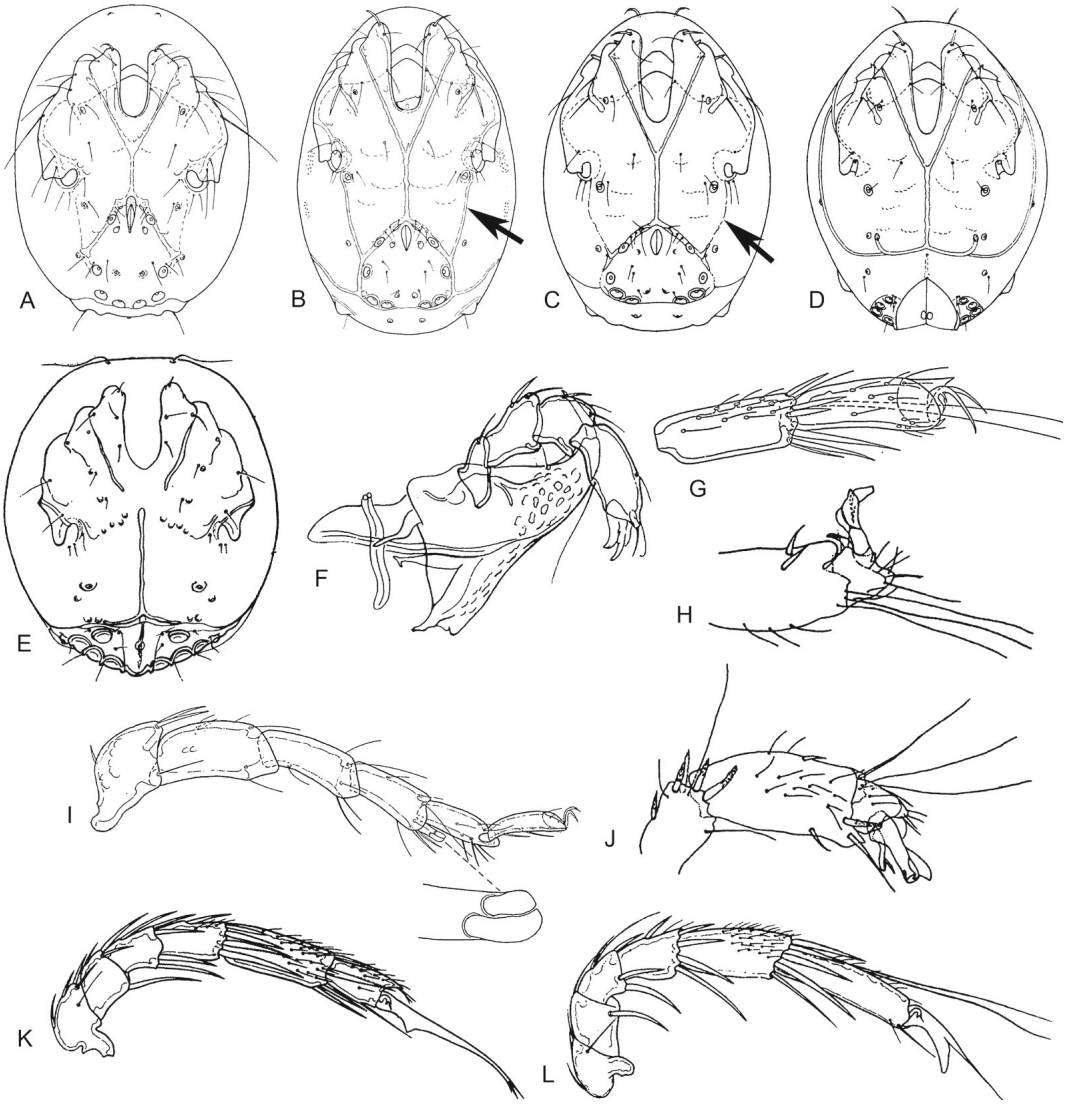

Fig. 56. A. *Axonopsella* (*Neoaxonopsella*) *nayaritensis*, male, idiosoma ventral (Cook 1980). **B.** *Axonopsella* (*Coaxonopsella*) *jujuyensis*, male, idiosoma ventral (arrow pointing at lateral ridge between genital field and insertion of IV-leg) (Cook 1980). **C.** *Axonopsella* (*Coaxonopsella*) *bakeri*, male, idiosoma ventral (arrow pointing at lateral ridge between genital field and insertion of IV-leg) (after Smith & Cook 1998). **D.** *Axonopsella* (*Coaxonopsella*) *bakeri*, female, idiosoma ventral (after Smith & Cook 1998). **E.** *Axonopsella* (*Humboldtaxonopsella*) *linaresi*, female, idiosoma ventral (after Orghidan & Gruia 1981). **F.** *Axonopsella* (*Rostaxonopsella*) *nana*, female, capitulum, chelicera and right palp lateral (after Orghidan & Gruia 1987). **G.** *Axonopsella* (*Neoaxonopsella*) *argentinensis*, male, II-leg-5/-6 (Cook 1980). **H.** *Axonopsella* (*Luciaxonopsella*) *misionum*, male, II-leg-5, -6 (after Rosso de Ferradás 1995). **I.** *Axonopsella (Chilaxonopsella*) *tanda*, male, IV-leg lateral (enlarged detail of setae at IV-leg-4) (Cook 1988). **J.** *Axonopsella* (*Luciaxonopsella*) *misionum*, male, IV-leg-4/-5/-6 (after Rosso de Ferradás 1995). **K.** *Axonopsella* (*Paraxonopsella*) *filunguis*, male, II-leg (after Lundblad 1943). **L.** *Axonopsella* (*Paraxonopsella*) *bifida*, male, II-leg (after Lundblad 1943).

34 (33) Excretory pore on a separate platelet at posterior end of dorsal shield (Fig. 57L); **female**: Ac plates separated from ventral shield (Fig. 57K). ..... ***Woolastookia*** Habeeb, 1954 [One described species: *W. gretae* Viets, 1978. Mexico, Guatemala. Habitat: streams]

34' Excretory pore not on separate platelet; **female**: Ac plates fused with ventral shield. . ..... **'*Axonopsis*-like mites'**, 35

'*Axonopsis*-like mites'

35 (34') Lateral ridge beginning well anterior to insertion of IV-leg (Fig. 57C); segments of IV-leg expanded and flattened; IV-leg-3 noticeably smaller and greatly expanded at distal end (Fig. 57A). .... ***Erebaxonopsis*** Motas & Tanasachi, 1947 [Two undescribed species. Cuba (pers. obs.), Panama (Camacho et al. 1997). Habitat: streams]

35' Lateral ridge beginning near insertion of IV-leg; segments of IV-leg not greatly expanded and flattened; IV-leg-3 not noticeably smaller and not greatly expanded at distal end. 36

Note: The following genera were originally considered subgenera of *Axonopsis*, but were raised to full generic rank by Smith et al. (2015). The authors are proposing a very restricted concept of *Axonopsis* s.str., not including any of the so far described neotropical species (Smith et al. 2015).

36 (35') Capitulum with very long posterior apodeme; P5 as long as P4 (Fig. 57E). .... ***Vicinaxonopsis*** Cook, 1974 [Three described species. Cuba. Habitat: streams, interstitial]

36' Capitular apodeme not greatly elongated; P5 much shorter than P4. 37

37 (36') Palp very robust (especially P2, P3, P4 short, with ventral extensions) (Fig. 57D,F); all leg segments short, with flat extensions (Fig. 57B,D). .... ***Cubaxonopsis*** Orghidan & Gruia, 1981 [Three described species. Cuba. Habitat: interstitial]

37' Palp and legs not especially extended. ... 38

38 (37') Usually two pairs of glandularia between genital field and insertion of IV-legs; dorsal and ventral shield slightly fused anteriorly; male without tendency to cauda development (Fig. 57G). .... ***Brachypodopsis*** Piersig, 1903 [Nine described species. Mexico, Cuba, Guatemala, Costa Rica, Colombia, Argentina. Habitat: streams]

38' One pair of glandularia between genital field and insertion of IV-legs; dorsal and ventral shield broadly fused anteriorly; male with tendency to cauda development (Fig. 57H). ..... ***Paraxonopsis*** Motas & Tanasachi, 1947 [One described species: *P. stolli* K. O. Viets, 1978. Guatemala. One undescribed species: Panama (unpublished data). Habitat: streams]

'*Axonopsalbia*-like mites'

39 (33') Four pairs of Ac; first coxae not reaching anterior margin of body (Fig. 57I). ....***Axonopsalbia*** Viets, 1914 [One described species (only female): *A. gila* Viets, 1978. Guatemala. One undescribed species. Costa Rica (Goldschmidt 2004). Habitat: streams]

39' Three pairs of Ac; first coxae extending slightly beyond anterior margin of body (Fig. 57J). ..... ***Albaxona*** Szalay, 1944 [One undescribed species: Costa Rica (Goldschmidt 2004d). Habitat: streams]

Key to Unionicolidae Oudemans, 1909

1 Idiosoma mostly soft; suture between Cx-III and Cx-IV mostly incomplete, **if** suture complete, then only five or six pairs of Ac, **or** mites collected from clams (Figs 58A, 17K); genital field in general as wide as long (Fig. 58I,K), **female**: generally with two pairs of genital plates (in rare cases might be fused to one pair) appressed medially and with heavy setae between them (Figs 17K, 58K). ..... **Unionicolinae** Oudemans, 1909, ***Unionicola*** Haldeman, 1842 [Highly variable genus: twenty-one Neotropical subgenera, sixty-four described species. Mexico, Dominican Republic, Guatemala, Honduras, Costa Rica, Panama, Colombia, Suriname, Ecuador (unpublished data), Brazil, Paraguay, Chile, Argentina, Uruguay. Habitat: standing waters, running waters]
Note: The splitting of the genus into such a high number of subgenera, all kept within one genus, is not accepted by all authors. However it's soundly based upon molecular phylogenetic studies. See Edwards & Vidrine (2013) for an overview. The authors as well

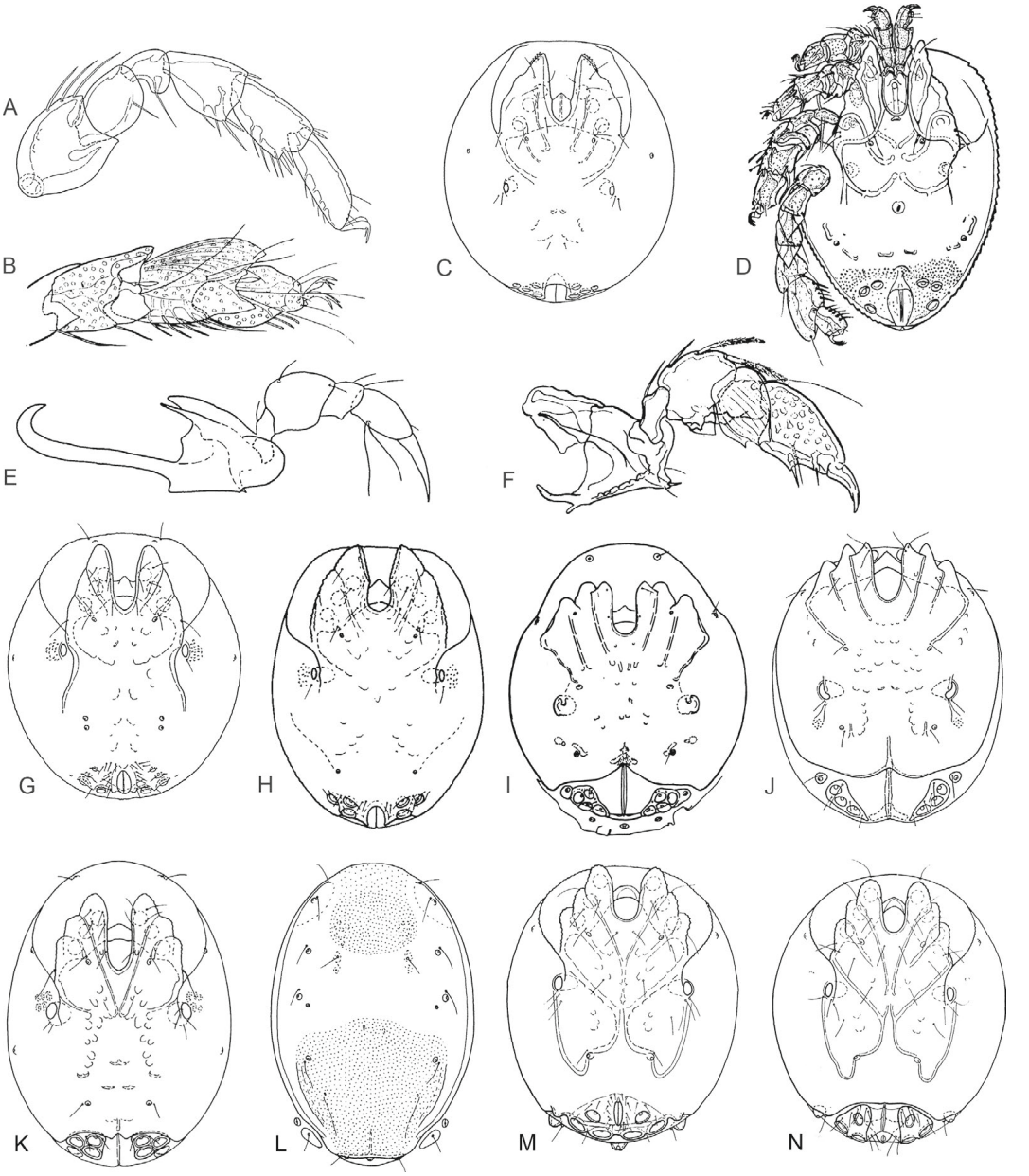

Fig. 57. **A.** *Erebaxonopsis nearctica*, male, IV-leg (Cook 1974). **B.** *Cubaxonopsis* (*Cubaxonopsis*) *robustipalpis*, female, IV-leg-4/ -5/ -6 (after Orghidan & Gruia 1981). **C.** *Erebaxonopsis nearctica*, female, idiosoma ventral (Cook 1974). **D.** *Cubaxonopsis* (*Cubaxonopsis*) *robustipalpis*, female, idiosoma (with right legs) and gnathosoma ventral (after Orghidan & Gruia 1981). **E.** *Vicinaxonopsis californica*, female, capitulum, chelicera and left palp lateral (Cook 1974). **F.** *Cubaxonopsis* (*Cubaxonopsis*) *robustipalpis*, female, capitulum, chelicera and right palp lateral (after Orghidan & Gruia 1981). **G.** *Brachypodopsis* (*Brachypodopsis*) *mesoamericana*, male, idiosoma ventral (Cook 1980). **H.** *Paraxonopsis* (*Paraxonopsis*) *pumila*, female, idiosoma ventral (Cook 1974a). **I.** *Axonopsalbia gila*, female, idiosoma ventral (Viets 1977). **J.** *Albaxona nearctica*, female, idiosoma ventral (Cook 1974). **K.** *Woolastookia gretae*, female, idiosoma ventral (Cook 1980). **L.** *Woolastookia gretae*, female, idiosoma dorsal (Cook 1980). **M.** *Ljania michiganensis*, male, idiosoma ventral (Cook 1974). **N.** *Ljania michiganensis*, female, idiosoma ventral (Cook 1974).

downgraded *Atacella* Lundblad, 1937 as a subgenus in *Unionicola* Haldeman, 1842 (Edwards & Vidrine 2013).

1' Integument soft or with different degrees of sclerotization; suture between Cx-III and Cx-IV mostly complete, **if** soft and suture between Cx-III and Cx-IV incomplete, then ten or more pairs of Ac; genital field mostly wider than long (Figs 17I, 58E,M, 59H); **female**: in general only with one pair of genital plates, never with heavy setae between genital plates (Figs 17I, 58B,C,G,J, 59A). ... . **Pionatacinae** Viets, 1916, 2

2(1') Dorsal and ventral shield always complete in both sexes; many Ac on wing-like plates beside the gonopore (Fig. 58E–H). 3

2' Soft to sclerotized, however mostly not with complete dorsal and ventral shield, **or** with a wide area of soft integument between dorsal and ventral shield, **or** Ac **not** on wing-like plates beside the gonopore (on four plates, or rather irregularly scattered) (Fig. 58C,J,L,M). 5

Note: As some of the following genera (*Neumanikea*, *Koenikea*, *Recifella*, as well as some species of *Neumania*) are rather similar and difficult to separate, and distinctive characters sometimes difficult to see, all described features should be checked carefully. Species of the genus *Koenikea* sg. *Notomideopsis* provide "primitive "characters, making them similar to heavy sclerotized *Neumania* as well as *Neumanikea* – such as long posterior apodemes of the anterior coxal group, and long, heavy setae at the first leg (and often the second as well) (Cook 1980, p. 206).

3(2) Dorsal furrow complete (dorsal and ventral shield always completely separated), dorsal shield laterally bearing five to six pairs of glandularia (Fig. 59B,D,E); Cx-I/-II with long posterior apodemes (reaching to Cx-IV) (Fig. 59A,C); I-leg with long heavy setae (Fig. 59M); **male**: dorsal shield with short cauda, posteriorly bearing several oval depressions or latero-caudal prolongations (Fig. 59D,E). .... ***Neumanikea*** Orghidan & Gruia, 1980 [Two described species. Cuba, Brazil (unpublished data). Habitat: running waters, cave]

3' Not with the described combination of characters. 4

4(3') Dorsal furrow complete; dorsal shield with six (rarely five) pairs of glandularia; postocularia fused with dorsal shield; dorsal plate mostly round, rough, often depressed towards the edge, idiosoma overall dorsoventrally flattened (Fig. 59G,I); one pair of glandularia in-between the Ac; posterior apodemes of Cx-I/-II rather long (Fig. 59 F,H). ..... ***Koenikea*** Wolcott, 1900 [One hundred and eleven described species. Mexico, Dominican Republic, Guatemala, Costa Rica, Panama, Colombia, Suriname, Ecuador (unpublished data), Brazil, Peru, Chile, Paraguay, Argentina. Key to South American species in Lundblad (1943a). Habitat: running waters, standing waters, springs]

4' Dorsal shield with three (apparently four in male with fused dorsal and ventral shield) pairs of glandularia; postocularia free in dorsal furrow or fused with ventral shield; dorsal plate mostly oval, smooth, often slightly arched (Fig. 58F,H); no glandularia in-between Ac; posterior apodemes of Cx-I/-II always short; Cx-III often with projections at insertions of III-leg (Fig. 58E,G); **most male**: dorsal and ventral shield fused posteriorly, male IV-leg with sexual dimorphism (Fig. 58E,F); **female** (and **some male**): dorsal furrow complete (Fig. 58H). .... ***Recifella*** Viets, 1935 [Thirty-three described species. Mexico (Cramer & Cook 1998), Guatemala, Honduras (Wiles 2005), Costa Rica, Suriname, Brazil, Paraguay. Habitat: running waters, standing waters, springs]

5(2') Idiosoma soft or with complete dorsal and ventral shield (Fig. 58D); coxae fused into single unit, anterior coxal group without posterior apodemes (Fig. 58C); **female**: genital field with two pairs of genital plates (in one species known from Central America, anterior pair fused with ventral shield) (Fig. 58J). ..... ***Amazonella*** Lundblad, 1930 [Four described species. Costa Rica. Suriname, Brazil, Paraguay. Habitat: running waters, standing waters]

5' Idiosoma soft or with various degrees of sclerotization; coxae **not** fused into single unit, **if** fused, with extensive sclerotization of integument and anterior coxal group with posterior apodemes (Fig. 58M); **female**: genital field with one pair of genital plates, or if with two pairs, either the anterior or the posterior one fused (Fig. 58B). 6

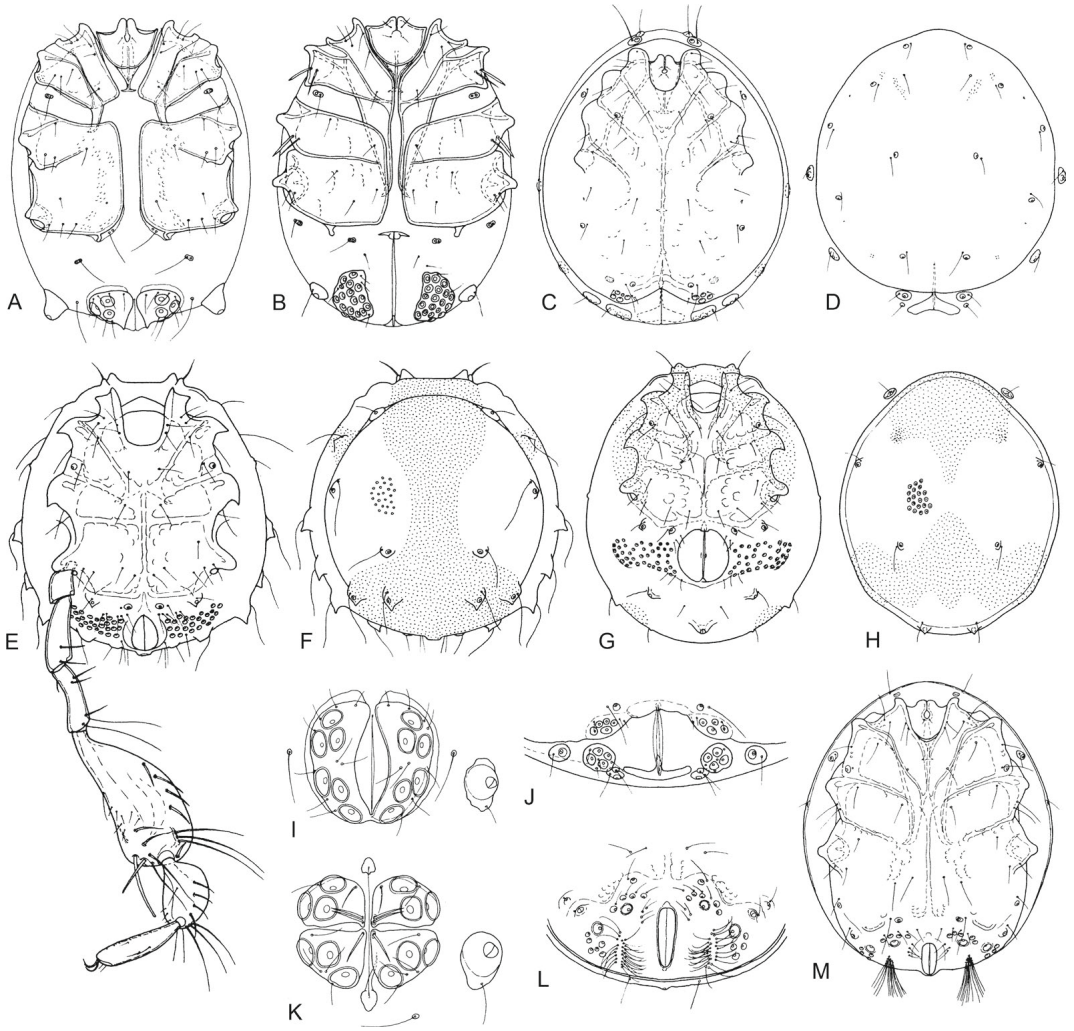

Fig. 58. A. *Unionicola gracilipalpis tenuis*, male, idiosoma and capitulum ventral (Cook 1980). **B.** *Neumania broballa*, female, idiosoma and capitulum ventral (Cook 1980). **C.** *Amazonella mesoamericana*, female, idiosoma and capitulum ventral (Cook 1980). **D.** *Amazonella mesoamericana*, female, idiosoma dorsal (Cook 1980). **E.** *Recifella bella*, male, idiosoma ventral (with IV-leg) (Cook 1980). **F.** *Recifella bella*, male, idiosoma dorsal (Cook 1980). **G.** *Recifella bella*, female, idiosoma ventral (Cook 1980). **H.** *Recifella bella*, female, dorsal shield (Cook 1980). **I.** *Unionicola gracilipalpis tenuis*, male, genital field (Cook 1980). **J.** *Amazonella mesoamericana*, female, genital field and ventro-caudal end of idiosoma (Cook 1980). **K.** *Unionicola gracilipalpis tenuis*, female, genital field (Cook 1980). **L.** *Neumania nodanda*, male, genital field and ventro-caudal end of idiosoma (Cook 1980). **M.** *Neumania nodanda*, male, idiosoma and capitulum ventral (Cook 1980).

6 (5') Idiosoma soft; anterior coxal group with short posterior apodemes (Fig. 59J,K); palp stocky, P4 with large medial tubercle, P3 with short distal seta (Fig. 59N); rostrum elongated (Fig. 59O). ..... ***Schadeella*** Lundblad, 1938 [Two described species. Cuba, Costa Rica (Goldschmidt 2004d), Brazil, Paraguay. Habitat: standing waters, streams]

6' Idiosoma soft or with various degrees of sclerotization; anterior coxal group with long posterior apodemes (Figs 58M, 59L); palp slender, P4 without large medial tubercle, P3 with one or several long distal setae (Fig. 59P); rostrum short. .... ***Neumania*** Lebert, 1879

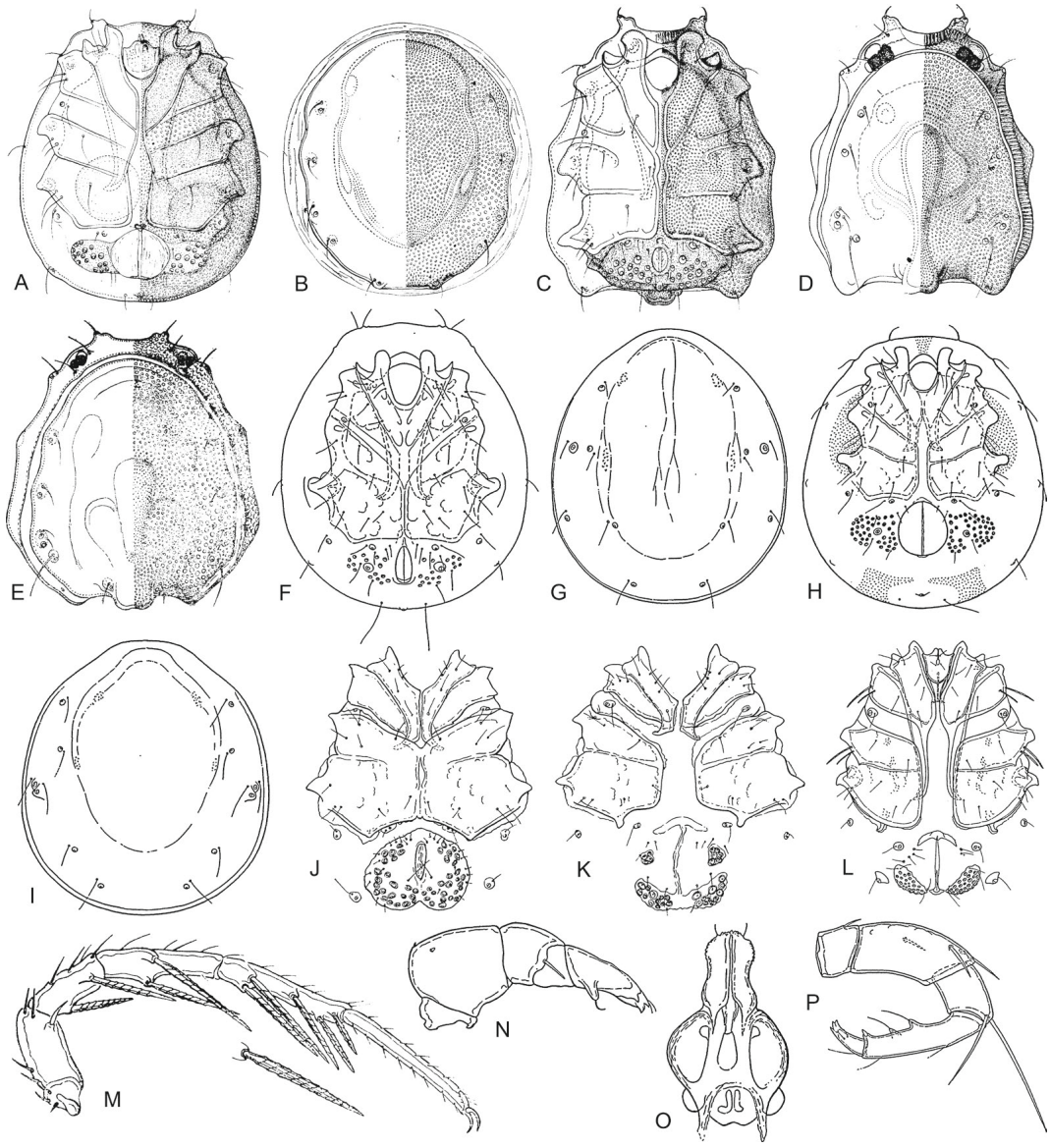

Fig. 59. A. *Neumanikea coenotica*, female, idiosoma and capitulum ventral (after Orghidan & Gruia 1980). **B.** *Neumanikea coenotica*, female, idiosoma dorsal (after Orghidan & Gruia 1980). **C.** *Neumanikea guantanamense*, male, idiosoma ventral (after Orghidan & Gruia 1980). **D.** *Neumanikea guantanamense*, male, idiosoma dorsal (after Orghidan & Gruia 1980). **E.** *Neumanikea coenotica*, male, idiosoma dorsal (after Orghidan & Gruia 1980). **F.** *Koenikea veracruzensis*, male, idiosoma ventral (Cook 1980). **G.** *Koenikea veracruzensis*, male, dorsal shield (Cook 1980). **H.** *Koenikea paragrossa*, female, idiosoma ventral (Cook 1980). **I.** *Koenikea toloma*, female, dorsal shield (Cook 1980). **J.** *Schadeella crassipalpis*, male, coxae and genital field (Cook 1974). **K.** *Schadeella crassipalpis*, female, coxae and genital field. (Cook 1974). **L.** *Neumania alticola*, female, coxae, capitulum and genital field (Cook 1980). **M.** *Neumanikea coenotica*, male, I-leg (after Orghidan & Gruia 1980). **N.** *Schadeella crassipalpis*, female, palp medial (Cook 1974). **O.** *Schadeella crassipalpis*, female, capitulum dorsal (Cook 1974). **P.** *Neumania alticola*, female, palp (Cook 1980).

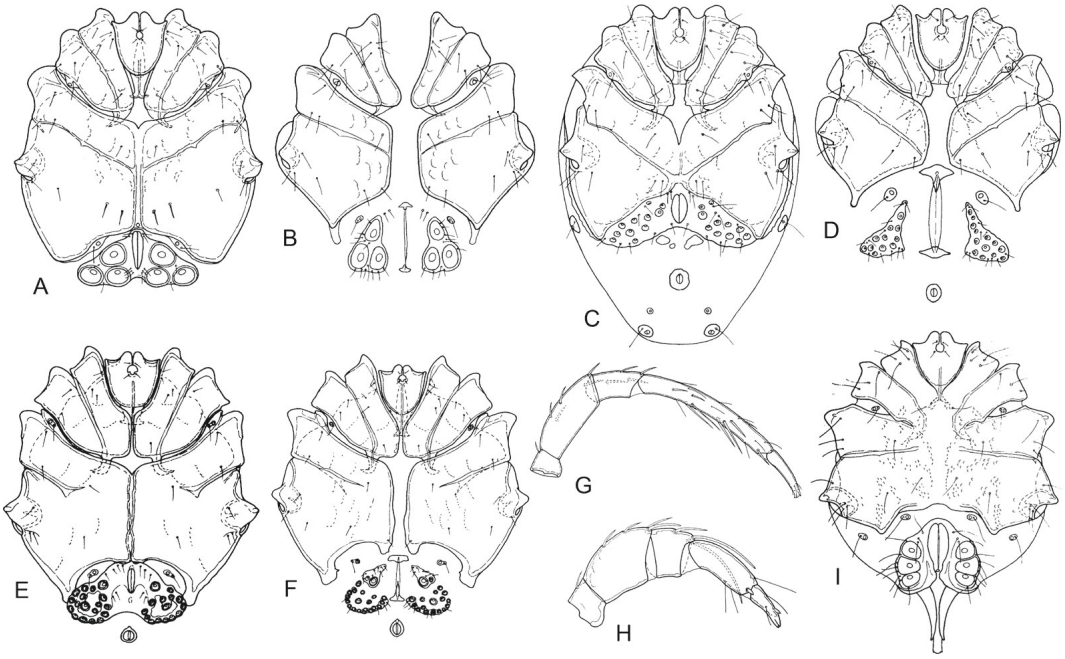

Fig. 60. A. *Pionopsis paludis*, male, coxae, capitulum and genital field (Cook 1974). **B.** *Pionopsis paludis*, female, coxae and genital field (Cook 1974). **C.** *Forelia floridensis*, male, idiosoma and capitulum ventral (Cook 1974). **D.** *Forelia floridensis*, female, coxae, capitulum and genital field (Cook 1974). **E.** *Piona setipes*, male, coxae, capitulum and genital field (Cook 1980). **F.** *Piona setipes*, female, coxae, capitulum and genital field (Cook 1980). **G.** *Hydrochoreutes intermedius*, male, palp (Cook 1974). **H.** *Pionopsis* (*Neotiphys*) *drepaniseta*, female, palp (Cook 1974). **I.** *Hydrochoreutes intermedius*, male, idiosoma ventral (Cook 1974).

[Twenty-four described species. Mexico, Cuba, Guatemala, Costa Rica (Goldschmidt 2004d), Panama, Ecuador (unpublished data), Brazil, Paraguay, Argentina. Habitat: standing waters, running waters, springs]

Note: A key to South American species of Unionicolidae is available in Lundblad (1942).

Key to Pionidae Thor, 1900

1 Generally three pairs of Ac (Fig. 60A,B). ..... **Tiphyinae** Oudemans, 1941, 2

1' Mostly with seven or more pairs of Ac. 3

2 (1') Palp extremely long and slender, P4 bearing numerous thickened setae (Fig. 60G); **male**: idiosoma with petiolus (Fig. 60I). ..... ***Hydrochoreutes*** Koch, 1837
[One (doubtful, as in general with palaeacrtic distribution) described species: *H. krameri* Piersig, 1896. Chile, Argentina. Habitat: standing waters]

2' Palp more compact, if long, P4 without numerous thickened setae (Fig. 60H); male: idiosoma without petiolus. ..... ***Pionopsis*** Piersig, 1894
[One undescribed species. Costa Rica (Goldschmidt 2004d). Habitat: standing permanent and temporary waters, pools of streams]

3 (1') Median margins of Cx-IV reduced to median angles, suture between Cx-III and Cx-IV complete; capitulum posterior with well developed anchoral process (Fig. 60C,D). .. **Foreliinae** Thor, 1923, ***Forelia*** Haller, 1882
[One described species: *F. mesoamericana* Otero-Colina, 1987. Mexico (Otero-Colina 1987). Habitat: standing waters, slow flowing streams]

3' Median margins of Cx-IV well developed, suture between Cx-III and Cx-IV often incomplete; capitulum posterior with or without anchoral process. 4

4 (3') Cx-IV postero-medially rounded, suture between Cx-III and Cx-IV incomplete; capitulum posterior without anchoral process;

many Ac on large tongue-shaped plates, extending far laterally from gonopore (Fig. 17D,E). ..... **Najadicolinae** Viets, 1935, ***Najadicola*** Piersig, 1897

[One described species: *N. ingens* (Koenike, 1895). Mexico (Simmons & Smith 1984). The Najadicolinae were shifted from Unionicolidae to Pionidae by Simmons & Smith (1984). Habitat: freshwaters clams (parasites)]

4' Cx-IV postero-medially angled, suture between Cx-III and Cx-IV complete or incomplete; anchoral process of capitulum well developed; Ac numerous (however generally less than in *Najadicola*), on irregular oval to drop-shaped or arc-shaped plates (Figs 17L,M, 60E,F). .... **Pioninae** Thor, 1900, ***Piona*** Koch, 1842

[Forty-five described species. Mexico (Marín-Hernández & Cramer-Hemkes 2009), Cuba, Guatemala, Costa Rica, Panama, Venezuela, Colombia, Suriname, Brazil, Paraguay, Chile, Argentina, Uruguay. Key to South American species in Lundblad (1943b). Habitat: standing waters, slow flowing streams, temporary waters]

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