Süßwasserfauna von Mitteleuropa 7/2–3
Reinhard Gerecke (ed.)

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Chelicerata

Acari III

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To the memory of Henk van der Hammen (1943-2002) and Kees Davids (1931-2004) who cooperated on the new edition of the Chelicerata volumes of the Brauer series, leaving drafts on Unionicolidae and Pionidae on which our corresponding chapters built up.

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8. Acari: Hydrachnidia III

By Reinhard Gerecke, Terence Gledhill, Vladimir Pešić and Harry Smit

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Contents

Introducing remarks

This volume deals with European species of two out of the eight superfamilies of true fresh water mites generally accepted worldwide, namely Hygrobatoidea and Arrenuroidea.

The remaining superfamilies were treated in preceding Chelicerata volumes of this series (7-2/1: Stygothrombioidea, Hydrovolzioidea, Eylaoidea and Hydrachnoidea – Davids et al. 2007; 7-2/2: Hydryphantoidea and Lebertioidea – Di Sabatino et al. 2010).

All taxa below subfamily level are treated in alphabetical order.

An explanation of morphological terminology and abbreviations (page 377-379 ff., Figs *9-123-125*), an illustrated key to superfamilies (page 381, Figs *9-126-129*), a glossary (page 387), and a chapter with corrections and addenda to the foregoing volumes, are found at the end of this volume.

At genus level, all keys refer to Europe as a whole. At species level, the area covered includes Central and Northern Europe extending in the West to the Southwestern margin of the Pyrenees, in the South to the Southern margin of the Alps and in the East to the Eastern state borders of Austria, Slovakia, Poland and the Baltic countries.

Superfamily Hygrobatoidea Koch, 1842

1842 Hygrobatides Koch, Übersicht des Arachnidensystems: 3(1): 7.

Diagnosis: Acetabula usually present (except for the marine Pontarachnidae and *Haloaxonopsis* Pešić, Smit & Saboori, 2012, a monotypic aturid genus known only from saline streams in southern Iran with secondarily reduced acetabula), usually disk-shaped and arranged on plates flanking the gonopore. Without movable genital flaps that can cover the gonopore. Lateral eyes not on a common eye plate, located at anterolateral idiosoma margin. Palps neither chelate nor uncate. Chelicera typically two-segmented.

Discussion: Probably a polyphyletic grouping. For detailed comments on the phylogenetic systematics in "higher" water mites (Lebertioidea + Hygrobatoidea + Arrenuroidea) see discussion of Lebertioidea in Vol. II. At the larval stage, all hygrobatoid mites are adapted for swimming and attach to their insect hosts under water. Larvae have Cx-II and -III, often also Cx-I fused on their respective sides (and occasionally medially).

Most hygrobatoid families are represented in the area covered. Exceptions are the monotypic Omartacaridae Cook, 1963 (several species adapted to interstitial life; the Americas and Australia), and Astacocrotonidae Thor, 1927 (one species found parasitic at the adult stage, on a decapod crustacean; Australia).

Key to families

1	Idiosoma laterally compressed, higher than wide (*9-1 a*); membranous integument restricted to a narrow dorsal area containing small dorsal sclerites (*9-1 b*). . . . . Frontipodopsidae (page 93)
–	Idiosoma not laterally compressed, as wide as high or wider than high (*9-1 c-d, f*). 2
2 (1)	P-2 ventrally with a single, sometimes peg-like seta located directly on the segment (*9-1 e*) or on a socket (e. g., *9-46 a-b*); all European species without dorsal and ventral shields, posteroventrally with soft integument (*9-1 c*), dorsally with one small or middle-sized plate (*9-1 d*). . . . . Limnesiidae (page 165)
–	P-2 without a single ventral seta (however, groups of setae, or various types of protrusions may be present - *9-2 c*, *9-4 c*); idiosoma sclerotization various. 3
3 (2)	Idiosoma with dorsal and ventral shields; the dorsal shield may be complete (*9-1 h*) or consist of a large central plate surrounded by small platelets (*9-1 f*); the genital field may be surrounded by a membranous area; often, suture lines between fused coxal plates partly obsolete (*9-1 g, i*) and idiosoma flattened dorsoventrally. 4
–	Idiosoma with soft integument or bearing regularly-arranged plates; if a complete dorsal shield is present, genital field and surrounding platelets remain separate from each other and from coxae, not included into a homogenous ventral shield (*9-2 a-b*); Cx-I+II and Cx-III+IV separated by membranous integument or fused to each other, but with suture lines well visible (*9-2 a-b, d, g*); idiosoma various in shape. 5
4 (3)	Dorsum with a central plate surrounded by a ring of small platelets (*9-1 f*); insertions of IV-L close to each other (separation < 50 % width of idiosoma – *9-1 g*). . . . . Lethaxonidae (page 161)
–	Dorsum with a continuous shield or with paired glandular platelets in various numbers – in the latter case, these platelets never completely surrounding a central plate (*9-2 e*); insertions of IV-L distanced from each other (separation > 50 % width of idiosoma – *9-1 i*). . . . . Aturidae (page 7)
5 (3)	Posterior margin of Cx-IV with lateral and medial long apodemes (*9-2 a*); no typical acetabula developed (marine species). . . . . .Pontarachnidae (page 225)
–	Posterior margin of Cx-IV not extending into lateral apodemes (*9-2 b, d*); medial apodemes if present short (*9-44 c*); genital field with acetabula (fresh-, rarely brackish water species). 6
6 (5)	A pair of glandularia perforating the surface of Cx-IV, Cx-I in most cases completely fused medially (*9-2 b*); legs without typical swimming setae (long, fine, arranged in rows); P-2 often with digitiform extensions, peg-like protrusions or denticulation (e. g., *9-2 c*, *9-28 d, 9-42 f, l*). . . . . Hygrobatidae (page 95)

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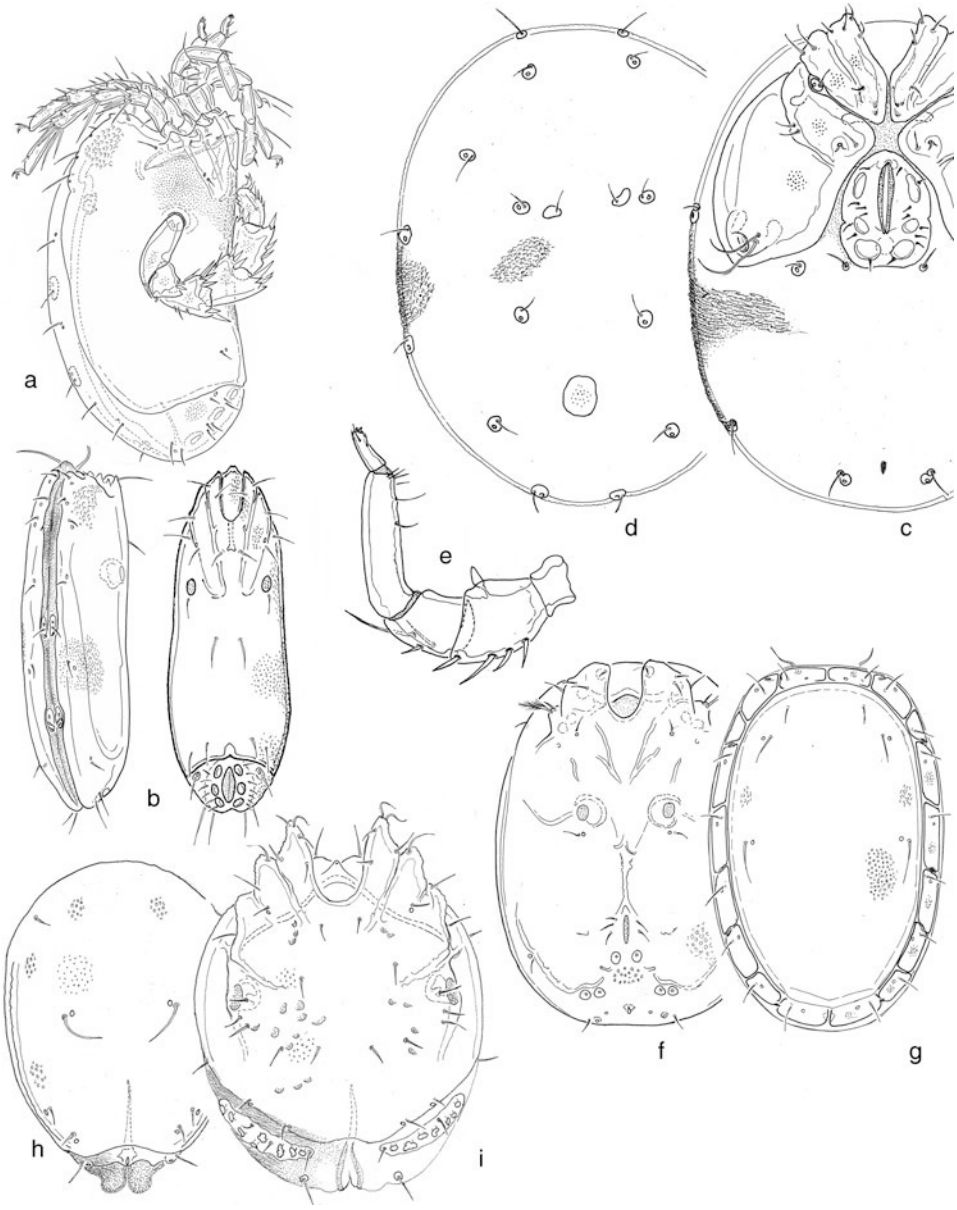
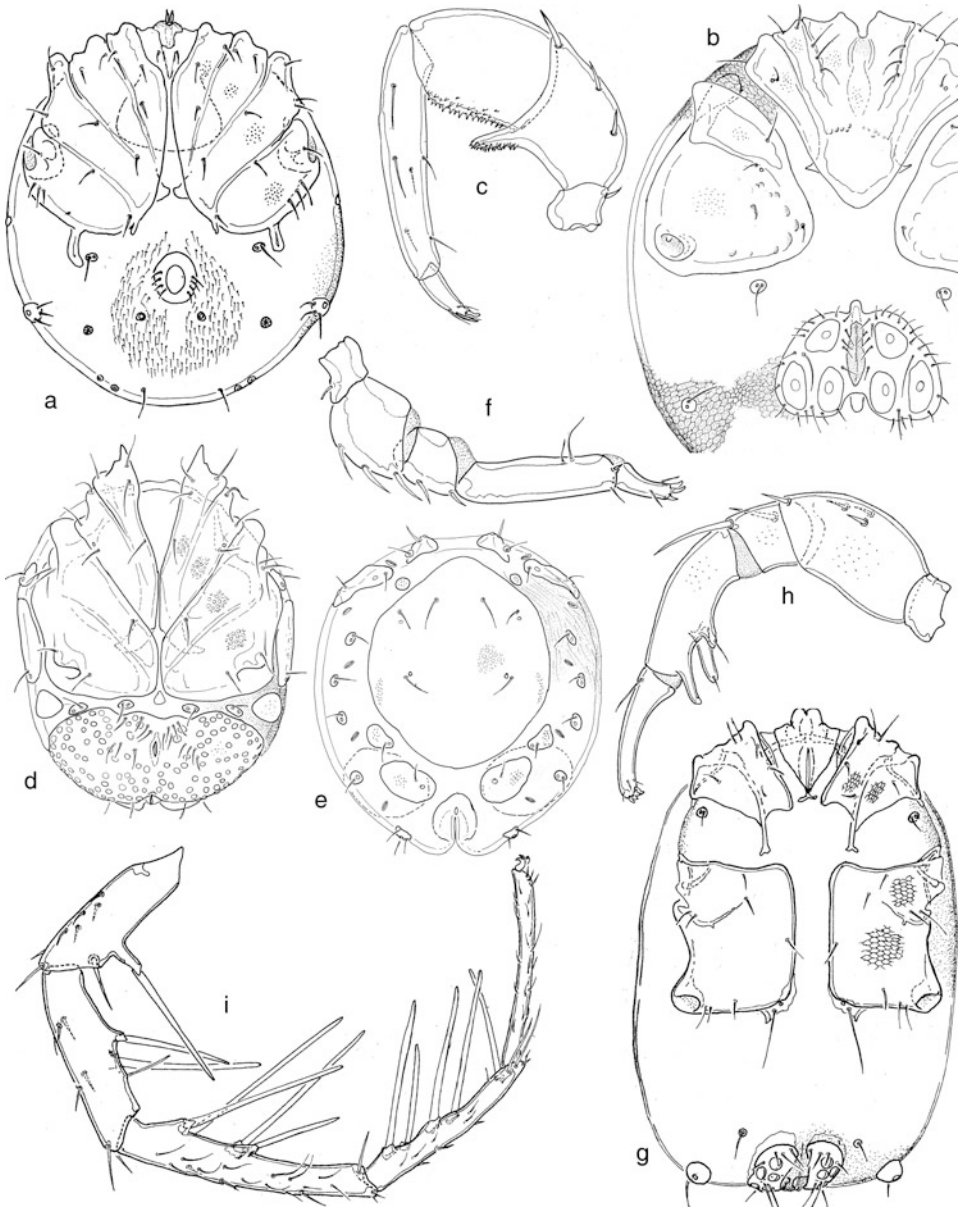


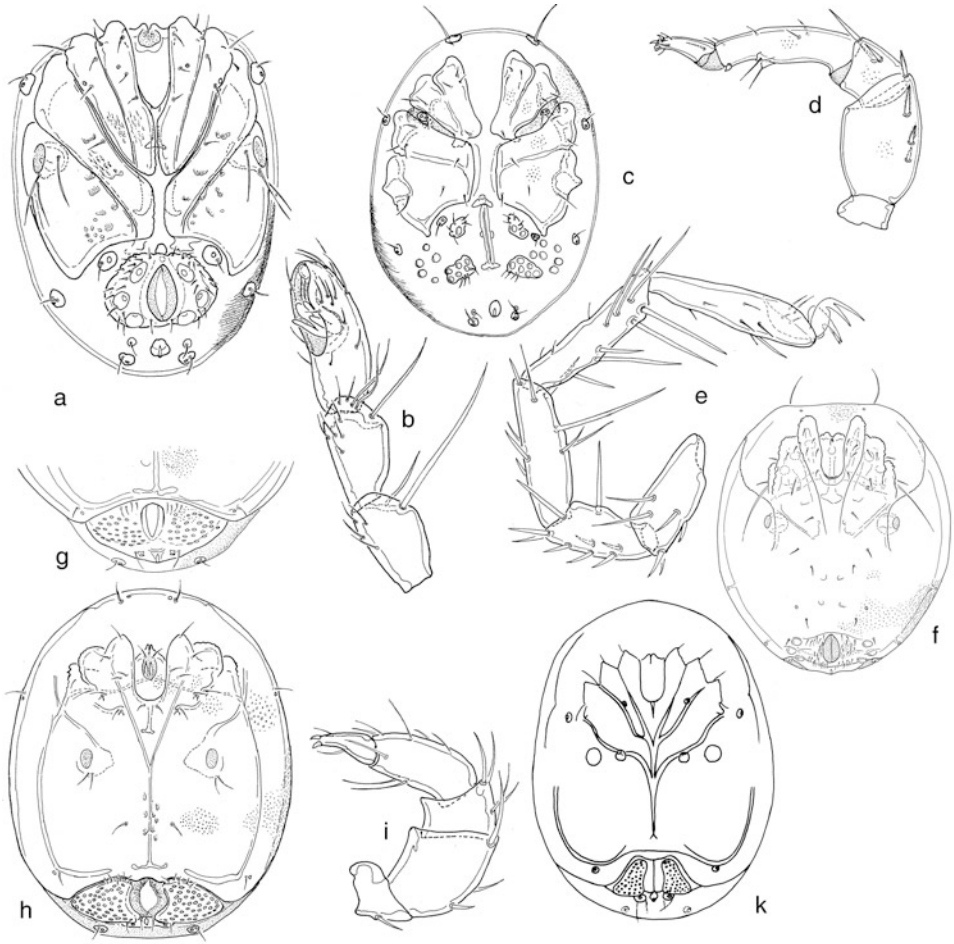
9-1: a-b, *Frontipodopsis reticulatifrons* male; a, lateral view; b, dorsal view (left) and ventral view (right); c-e, *Limnesia arevaloi* male; c, ventral view; d, dorsal view; e, palp medially; f-g, *Lethaxona pygmaea*; f, female, dorsal view; g, male, ventral view; h-i, *Aturus barbatulus* female (Gerecke 2014b); h, dorsal view; i, ventral view.

– Surface of Cx-IV not perforated by a pair of glandularia (but glandularia may be fused to the posterior margin of Cx-IV), Cx-I medially separated by membranous integument (*9-2 d, g*) or, if fused, generally with a suture marking the fusion line (rare exceptions in Feltriidae); legs with or without typical swimming setae; P-2 generally lacking ventral protrusions or denticles (exception: *Pseudofeltria*). 7



9-2: a, *Pontarachna punctulum* male, ventral view; b-c, *Hygrobates fluviatilis* male; b, ventral view; c, palp; d-f, *Feltria armata* (Gerecke 2012); d, male venter; e, female dorsum; f, female palp; g-i, *Unionicola crassipes*; g, male, ventral view; h, palp; i, I-L-4-6.

7 (6) Two pairs of glandularia arranged in a transverse (*9-21 l*) or oblique (*9-2 d*) line in the interspace between Cx-IV and genital field; dorsum with one to several larger unpaired plate(s) surrounded by minor paired platelets (*9-2 e*) or with a dorsal shield (*9-21 a, i*); P-4 generally lacking digitiform ventral protrusions or tubercles (*9-2 f*); legs without swimming setae; small, flattened, rheobiontic species. . . . . Feltriidae (page 73)



9-3: a-b, *Wettina podagrica* male; a, ventral view; b, I-L-4-6; c-e, *Piona conjugula* female; c, ventral view; d, palp; e, I-L-4-6; f, *Axonopsis inferorum* male, venter; g-i *Albia stationis*; g, male genital field; h, female venter; i, male palp; k, *Albia davidsi*, female venter (from Smit & Van der Hammen 1992).

– Glandularia posterior to Cx-IV not arranged in a line in the interspace between Cx-IV and genital field (*9-2 g, 9-3 a*); dorsum often with soft integument or isolated small platelets, rarely with a dorsal shield (*9-50 l*); P-4 often with digitiform protrusions or tubercles (*9-2 h*); legs of most species with swimming setae. 8

8 (7) Posterior margin of Cx-IV straight (*9-2 g*) or with knob-shaped central extensions (e. g., *9-64 d*), neither with a concave median area, nor enclosing a genital bay (*9-2 g*); basal and central segments of I-L often enlarged, with pairs of protuberances with grooved or fluted setae (*9-2 i*); in general, male legs without secondary sexual characters; claws simple, sickle-shaped, without ventral lamella. . . . . .Unionicolidae (page 229)

– Posterior margin of Cx-IV triangular or with pointed central extensions and medially concave, forming a more or less distinct genital bay (*9-3 a, c*); I-L lacking protuberances and blade-like setae (*9-3 b*); male IV-L, often also III-L, with secondary sexual characters (e. g., *9-48 c-d*); in most cases claws with clawlets and ventral lamella. 9

9 (8) I-L-6 conspicuously enlarged, with strong claws (in length about ½ I-L-6), ventral clawlet tongue-shaped, longer than pointed principal claw (*9-3 b*); Cx-IV triangular in shape, suture Cx-III/IV directed posteriorly, medial margin of Cx-III+IV formed exclusively by Cx-III (*9-3 a*); male legs without secondary sexual characters; genital field with 3 pairs of acetabula. . . . . Wettinidae (page 251)

– I-L-6 not extremely enlarged (but in some species with strongly convex ventral margin – *9-52 b*), claws normal in size and shape (*9-3 e*); Cx-III+IV various in shape, medial margin formed by Cx-III and Cx-IV (*9-3 c*) or only by Cx-III (*9-48 h*); male III-L (e. g., *9-53 f, i*) and IV-L (e. g., *9-48 c-d*) with secondary sexual characters; genital field with 3 or more pairs of acetabula. . . . . Pionidae (page 177)

Family Aturidae Thor, 1900

1900 Aturidae Thor, Arch. Math. Naturv. 23: 4.

Diagnosis: Idiosoma flattened dorso-ventrally, in genera recorded from Europe with complete ventral and dorsal shields separated by a dorsal furrow (in some extra-European genera dorsal sclerotization formed by various numbers of separate plates and platelets). Lateral eyes not in capsules, lying beneath the integument. Gnathosoma with anchoral process and separated from coxae in European genera (but without such process and fused to ventral shield in some extra-European genera); palp five-segmented, P-4 typically without a medial peg-like seta (*9-3 i* - rarely a slightly thickened or peg-like seta in this position: *9-14 g*, *9-19 n*). Legs with or without swimming setae, often exhibiting sexual dimorphism. Leg claws simple or with a clawlet, sickle-shaped. Genital field with 3 to numerous pairs of acetabula (exceptionally two, in *Haloaxonopsis* reduced to so-called wheel-like acetabula) lying on plates flanking the gonopore, these plates free or fused to the ventral shield.

Discussion: When he described and discussed in detail the taxonomic state of Aturidae as a "dumping ground […] for those higher water mite genera with heavy sclerotized bodies which do not show the characteristics used to define the remaining families", Cook (1974) expressed the hope that the family placement of the included subfamilies and genera could be ascertained on the basis of larval morphology. Since then, steps were made when Lethaxonidae and Frontipodopsidae were defined as separate families (Cook et al. 2000). Furthermore, Olomski (2012) demonstrated striking similarities in reproductive behaviour and spermatophore morphology between *Brachypoda* (Axonopsinae) and representatives of Pionidae on the one hand, and *Aturus* (Aturinae) and Arrenuridae on the other, and proposed a rearrangement, more appropriately reflecting evolutionary pathways, of taxa at present assembled in Aturidae.

However, as research during the past decades has not yet produced a convincing alternative, we follow Cook's (1974) system applying only the modifications of Cook et al. (2000). In this scenario, the family Aturidae is probably a polyphyletic taxon including a high number of genera and distributed over all continents except Antarctica. In addition to the three subfamilies present in Europe (see below), it includes Notoaturinae Besch, 1964 with a Gondwanan distribution (southern Chile, eastern Africa, Australia and New Zealand).

Key to subfamilies

1 Genital field with 3-4 pairs of acetabula (e. g., *9-3 f*, *9-14 a-b* - some extra-European genera with higher acetabula numbers characterized by strongly-developed expansions near IV-L insertions and anterior margin of Cx-I not exceeding anterior idiosoma margin); dorsum with entire shield or several plates. . . . . Axonopsinae (page 48)

– Genital field with 5 or more pairs of acetabula (*9-3 g-h* - not easily recognized in dorsal or ventral view when arranged at posterior margin: *9-1 i*); dorsal shield entire. 2

2 (1) Acetabular plates rounded, heart-shaped or triangular, located ventrally, in males fused to ventral shield, in females surrounded by soft integument; medial suture line of Cx-IV well visible; anterior margin of Cx-I not reaching idiosoma margin (*9-3 h, k*). . . . . Albiinae (page 7)

– Acetabular plates longish, located posteroventrally; Cx-IV completely fused medially, at most traces of a suture line defined; anterior margin of Cx-I extending beyond idiosoma margin (e. g., *9-1 i*). . . . . Aturinae (page 9)

Subfamily Albiinae K. Viets, 1925

1925h Albiinae K. Viets, Arch. Hydrobiol. 16: 221.

Diagnosis: Dorsal shield entire. Tips of Cx-I not extending beyond frontal idiosoma margin. Cx-IV with more or less distinct medial, posterior and lateral suture lines; no projections associated

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with IV-L insertions. Legs with or without swimming setae, without sexual dimorphism. Acetabular plates with numerous (eight or more) pairs of acetabula, lying separate from ventral shield in females, fused to ventral shield (but with well visible suture lines) in males. Palp without ventral projections.

Discussion: In the first half of the past century, Albiinae appeared to be a distinct taxonomic unit, but characters of taxa discovered since then have widely filled the gap between this subfamily and the Axonopsinae. Cook (1974) maintained the two subfamilies "mostly out of nostalgia": otherwise, following the rules of zoological nomenclature, the widely used name of Axonopsinae would have disappeared as a synonym of Albiinae. However, taxa with intermediate character states are mostly found in the southern hemisphere, while in the European fauna members of the two subfamilies are easily distinguished from each other. In addition to *Albia*, recorded from all continents except for Antarctica, only one other genus is known, *Parasitalbia* K.Viets, 1935, described from a single species at the adult stage and found parasitic on Ephemeroptera larvae in Sumatra.

Genus *Albia* Thon, 1899

1899 *Albia* Thon, Zool. Anz. 22: 100.

Type species: *Albia stationis* Thon, 1899, by monotypy.

Diagnosis: Gnathosomal bay slender, much longer than wide. Palp slender, P-4 much longer than P-3.

Remarks: Distributed worldwide except Antarctica. In addition to the subgenera represented in Europe (see below), the three subgenera *Anchistalbia* Cook, 1974 (The Americas, Asia, Africa), *Dentalbia* Cook, 1974 (Oriental region) and *Spinalbia* Cook, 1974 (Africa and Asia) are known. Larvae of *Albia* have been described for species only from outside the study area (Prasad & Cook 1972, Smith 1984).

Key to subgenera and species

1 Suture line Cx-III/IV not reaching the median line. A pair of glandularia lying near the medial end of the suture line Cx-II/III (*9-3 h*). . . . . Subgenus *Albia* (*s. str.*), only species in the area: *Albia (Albia) stationis* (page 8)

– Suture line Cx-III/IV continuous, reaching the median line. A pair of glandularia lying posterior to this line, in the European representative of the subgenus on the level of IV-L insertions (*9-3 k*). . . . . Subgenus *Albiella*, only species in the area: *Albia (Albiella) davidsi* (page 9)

Subgenus *Albia* Thon, 1899

Diagnosis: Glandularia on Cx-IV shifted far forward. Suture line Cx-III/IV developed only laterally, ending medial to IV-L insertions and not reaching the medial line. Male genital field extending to posterior end of ventral shield. Without greatly enlarged setae on coxal field or medial surface of P-2.

Remarks: Probably a monophyletic taxon; distribution Holarctic.

1. *Albia stationis* Thon, 1899 (*9-3 g-i*)

1899 *Albia stationis* Thon, Zool. Anz. 22: 101.

Description: Colour yellowish, on the dorsal surface with a whitish excretory organ in a brownish-red central area. Idiosoma elliptical in shape, tips of Cx-I far posterior to frontal margin. Gnathosoma with a long anchoral process. Palps stocky, P-4 shorter than P-2, with a pair of long setae in the centre of the ventral surface. Males: Idiosoma length/width 710/530 µm. Acetabular plates fused to an unpaired genital plate which posteriorly also includes excretory pore and a pair of glands. Females: Idiosoma length/width 840-940/620-650 µm. Acetabular plates separate, subtriangular in shape, excretory pore platelet and flanking glandularia lying free in the integument.

Habitat and Biology: In summer-warm lowland streams with dead wood and sandy substratum, e. g. outlets of lakes. Preadult stages and life cycle unknown.

Distribution: Central, eastern and southeastern Europe, England, Turkey; rare. A subspecies described from eastern Siberia.

Subgenus *Albiella* Lundblad, 1971

1971 *Albiella* Lundblad, Ark. Zool. (ser. 2) 23: 343.

Diagnosis: In setation of coxae and position of glandularia, shape of palps and formation of male genital field agreeing with *Albia s. str.*, but suture line Cx-III/IV reaching the medial line, completely developed or reduced only in its lateral part.

Remark: Probably a sister taxon of *Albia s. str.*, with the position of the coxal glandularia as a synapomorphy of both subgenera; species known from Indonesia (including New Guinea), India, Australia and Europe.

2. *Albia davidsi* Smit & Van der Hammen, 1992 (*9-3 k*)

1992 *Albia (Albiella) davidsi* Smit & Van der Hammen, Ent. Ber., Amst. 52: 114.

Description: Male unknown. Female: Colour unknown, idiosoma length/width 1085/815 µm. In posterolateral part of dorsal shield, two glandularia lying close together. Tips of coxae pointed. Glandularia at anterior margin of Cx-IV large, located halfway between medial line and IV-L insertions. Leg swimming setae numbers: II-L-5, 5; III-L-4, 4; III-L-5, 9; IV-L-4, 3; IV-L-5, 8. Acetabular plate length/width 136/126 µm. Palp slender, length: P-1, 50; P-2, 120; P-3, 91; P-4, 156; P-5, 48 µm; P-4 with 2 setae in the distal half of ventral margin and 2 dorsodistal setae. II–IV-L with swimming setae.

Habitat and Biology: A single specimen reported from a pond. Life cycle and preadult stages unknown.

Distribution: Only known from the type locality near Amsterdam, The Netherlands. As the site was intensely investigated over five years without producing further records, Smit & Van der Hammen (1992a) interpret the finding as accidental and suppose its main distribution area to be outside Europe.

Subfamily Aturinae Thor, 1900

Diagnosis: Dorsal shield entire, not divided into several platelets. Tips of Cx-I projecting well beyond idiosoma frontal margin. Genital plates with numerous (eight or more) acetabula in European taxa arranged along the posterolateral idiosoma margin.

Remarks: While the two genera known from Europe are rather distinctive in comparison with representatives of other subfamilies, several genera from other continents exhibit character combinations grading to Axonopsinae (Cook 1974), with the result that the subfamily is probably para- or polyphyletic. In addition to the genera treated here, six further genera have been described: *Subalbia* K. Viets, 1914 and *Subaturus* K. Viets, 1916 (West Africa), *Aturides* Lundblad, 1937 and *Neoaturus* Lundblad, 1941 (Neotropics), *Phreatobrachypoda* Cook, 1963 (North America) and *Bharatalbia* Cook, 1967 (India, Japan, Northern America).

Key to genera and subgenera

1 No projections associated with IV-L insertions (*9-1 i; 9-9 b*); male IV-L-5 lacking strongly thickened setae (but IV-L and often also posterior idiosoma variously modified in shape and setation - e. g., *9-4 b*, *9-6 a-e*, *g-h*); ventral margin of P-2 with (one or several) projections only in the distal part (*9-4 c*). . . . . Genus *Aturus* (page 10)

– Posteriorly-directed projections covering IV-L insertions (*9-12 d, l*); male IV-L-5 generally with strongly thickened setae (*9-4 f*); ventral margin of P-2 in most European species with projections and tubercles preferably in the proximal part (e. g., *9-4 g*). Genus *Kongsbergia* 2

2 (1) Males (females unknown): I-L modified, I-L-4 with a very long distoventral seta, I-L-5 expanded, with a heavy ventral seta (*9-4 m*). . . . . .Subgenus *Parakongsbergia* K. Viets, 1949

Not recorded from the area covered, only known from the type locality of *K.* (*Parakongsbergia*) *hansvietsi* K.Viets, 1949, in Macedonia.

– Male I-L not modified in the described manner (*9-4 h*). . . . . Subgenus *Kongsbergia* (page 34)

Genus *Aturus* Kramer, 1875

1875 *Aturus* Kramer, Arch. Naturg. 41: 309.

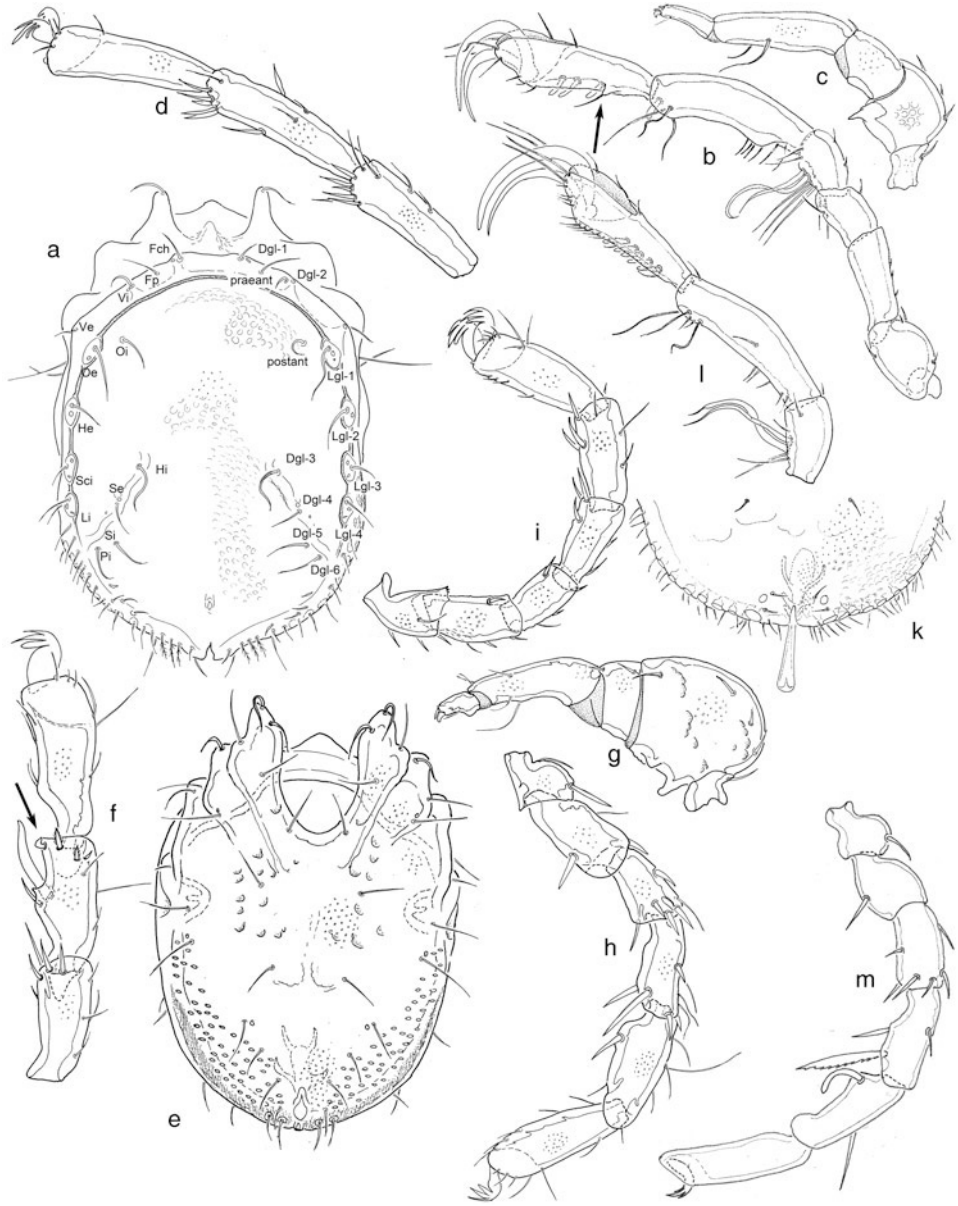
Type species: *Aturus scaber* Kramer, 1875, by original designation.

Diagnosis: Dorsal shield in males generally fused posteriorly to ventral shield, in females free, surrounded by a complete dorsal furrow; this furrow in both sexes directed dorsally, with 4-5 pairs of glandularia (Lgl-1-4, occasionally also Dgl-2). Dgl-1, often also Dgl–2, fused to frontal part of ventral shield. Postocularia, 4 pairs of glandularia and excretory pore on dorsal shield. Tips of Cx-I slightly extending beyond frontal margin; Cx-IV without glandularia, no projections or condyles associated with IV-L insertions. Legs without swimming setae. Male IV-L-4/5, occasionally also III-L, showing sexual dimorphism in shape and setation, species-specifically developed to various degrees. Acetabular plates slender, often extending beyond posterolateral idiosoma margin and bearing numerous acetabula in one or (rarely) two rows. In males, genital area often with a deep median cleft and genital field bearing variously modified setae. Palp segments shortened, P-2 with or without a short distoventral projection.

Remarks: In view of the enormous variety of character combinations in *Aturus*, Mitchell (1954c) proposed to organize species groups, no subgenera are presently accepted. For a survey on numbering and terminology of idiosoma glandularia and setae see *9-4 a*. The numbers given to dorsoglandularia follow Smith et al. (2010) and differ from the scheme of Bader (e. g., 1994) who named Dgl-1 and -2 as “Prae- and Postantenniformia” and designated as “Dgl-1” what here is named “Dgl-3” (for more details see Vol. I, pp. 244-250).

As male legs showing sexual dimorphism are of particular importance for taxonomy in the genus, we introduce a series of terms. In normal position when crawling, the anterior side of legs is generally turned to the observer in ventral view, the posterior side in dorsal view; however, the position of IV-L is rather flexible, and single segments may also be rotated against each other. The following types of setae may be found: “sword setae” - much enlarged and flattened; “blade setae” – enlarged, denticulate at least on one side; “bi-” or “trifurcated setae” - apically with 2, or 3 tips; “denticulate setae” - with numerous tips, long; “elk-horn setae” – with numerous tips, short; “whip setae” – long, distally hair-like, narrowed and spiralling.

Sex-specific modifications in the male III-IV-L are observed as follows: III-L-4/5 generally little modified; III-L-4 may bear a long, thickened posterodistal seta; III-L-5 with a group of 1-3 setae in the centre on posterior and ventral surface (“central setae”) and several setae at distal margin (“distal setae”, occasionally including 1-2 whip setae); between these two groups a row of “ventral setae” may be present. IV-L-4 again with a group of “central setae” and a group of “distal setae”, but both groups in many cases making part of one dense field of variously modified “distoventral” setae. Among them, in most species, a pair of sword setae at anterior distal margin. IV-L-5 ventrally with a group of variously modified “proximal setae” – these setae strongly overlapping with IV-L-5



9-4: a-d, *Aturus scaber*, a-c, male; a, dorsum, with explanation of the numbering system for glandularia; b, IV-L (arrow: proximoventral extension); c, palp; d, female IV-L-4-6; e-h, *Kongsbergia materna*, male; e, venter; f, IV-L-4-6 (arrow: distoventral seta); g, palp; h, I-L-4-6; i, *Kongsbergia pectinigera* female IV-L-4-6; k-l, *Aturus rotundus*, male; k, posterior idiosoma margin; l, IV-L-4-6; m, *Kongsbergia* (*Parakongsbergia*) *hansvietsi*, male, I-L-4-6. (a-l, Gerecke 2014b, m after K.Viets, 1949c).

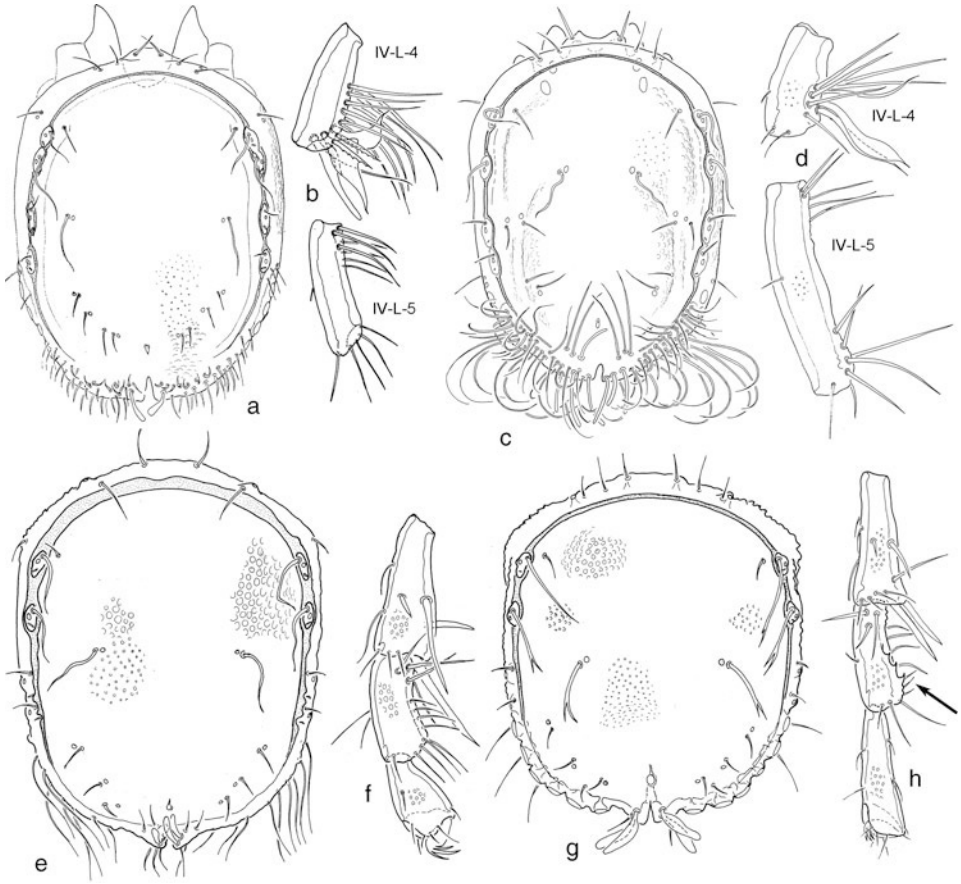
distoventral setae, together obviously forming a functional unit; furthermore, the proximoventral margin in most cases with a row of simple, long setae ("ventral line setae"), distal margin with a group of "distal setae" rather various in length, often including a whip seta.

The genital field is characterized in both sexes by a pair of transverse acetabular plates extending between gonopore and IV-L insertions, but males of most species show strong modifications involving the posterior margins of dorsal and ventral shields as described in single species sections. In females, the gonopore is surrounded by a membranous area (sometimes forming darker and more sclerotized gonopore lips) and extends from the posterior ventral shield margin to the excretory pore area on the dorsum. In most cases, the female excretory pore (surrounded by a fine transverse sclerotized platelet) and the flanking Dgl-6 are embedded in an area of porose secondary sclerotization extending at posterior dorsal shield margin. Female acetabular plates lie in a similar area of secondary sclerotization which covers the posteroventral idiosoma, and 2 pairs of Vgl are positioned anterior to acetabular plates, in the area of secondary sclerite or fused to the posterior margin of primary sclerotization.

In *Aturus*, there are only a few criteria that allow judgement on whether females and males represent the same or different species: general coincidence in colour, dimensions of sclerotized parts and numbers of acetabula may be helpful in certain occasions. As the morphology of the gnathosoma and its appendages is highly uniform in all species, this aspect will be addressed in the species treatment only in exceptional cases. Palps have mostly the same shape in both sexes of all species treated here, with a slender P-1 bearing one dorsal seta, and a thickened P-2 nearly as long as high, with strongly convex dorsal, and straight ventral margins, with 4-5 dorsal and dorsodistal setae and a pointed ventrodistal projection. As the insertion of this projection is slightly shifted laterally, depending on palp inclination it may appear more or less prominent, and its shape and relative length is therefore not useful for species assignment - P-2 height measurements are given here excluding this projection. P-3 is always short and curved (with convex dorsal and concave ventral margins) and with 2-3 dorsodistal setae; P-4 is rather long and slender, with a pair of ventral setae in the centre or distal half, a longer lateral one, and a shorter medial one; P-5 is slender, distally strongly narrowed and with 3 variously modified claws.

In view of the low morphological congruence between sexes, females were in many cases attributed with males due to co-occurrence. Consequently, there are still open questions and also several of the frequently recorded European species are only known in the male sex. In addition to the relative distance of dorsal glandularia (separation ratio Dgl-3-4/4-5), character states of potential taxonomic value in females are found in first line in the posteroventral idiosoma: Here, acetabular plates extend in parallel to the coxal plate margin as strips from the gonopore (in terminal position) to the posterolateral idiosoma edge. In juveniles, they lie free in the membranous integument, in mature females an area of secondary sclerotization develops. In most cases, the border line between primary and secondary sclerotization is well visible due to the finer porosity characterizing the latter. The position of a pair of glandularia (lateral and medial Vgl) located between ventral shield and acetabular plates is obviously of systematic significance - with the restriction that the situation changes with age, and the species attribution may be completely impossible in juveniles: Species-specifically, Vgl may be positioned in primary or secondary sclerotization, or on the separating border line. Further species-specific character states are found in number and arrangement of acetabula and accompanying setae. In this treatment, following Gerecke (2014b), we give morphological details for females based on populations from remote areas or extreme habitats where the isolated presence of one single species is highly probable. On the other hand, a consequence is that diagnostic features are often based on low specimen numbers and need confirmation from future variability studies. In many cases, the female key does not allow species identification in the absence of males, but it will be useful if information on the probable presence/absence of *Aturus* species is sufficiently known from collections of males in an investigated habitat, or an explored area.

The genus is represented with a high number of species in the Holarctic; in addition, species are recorded from East Africa, India, Java, Borneo, Mexico and Columbia, they are found exclusively in surface or interstitial habitats of streams.



9-5: *Aturus* males; a-b, *A. karamani*; a, dorsal view; b, IV-L-4/5; c-d, *A. barbatulus* (Gerecke 2014b); c, dorsal view; d, IV-L-4/5; e-f, *A. brachypus*; e, dorsal view; f, IV-L-4-6; g-h, *A. paucisetus* (Gerecke 2014b); g, dorsal view; h, IV-L-4-6 (arrow: distoventral teeth).

Key to species

Attribution of sexes generally based only on coexistence, in most of the rare species questionable and in need of revision; variability of characters used for discrimination of females little known. Excluded as a *species incerta* (Gerecke 2014b): *Aturus elongatus* Walter, 1927.

1 IV-L-4-6 variously modified as a grasping organ, in particular IV-L-4 bearing characteristically modified setae (e. g., *9-4 b*, *9-5 b, d*). Posterior idiosoma margin often flattened and truncate, frequently bearing variously modified (hair-, spatula-, nail-, peg-like) setae (e. g., *9-5 c*, *9-6 a-e*): Males. 2

– IV-L-4-6 not modified as grasping organ, not bearing modified setae (*9-4 d*). Posterior idiosoma margin rounded or forming an obtuse angle (*9-1 i*, *9-9*), without modified setae: Females (not included: the unknown females of the four "*p*-species" *A. prenanti, A. processiger, A. protzi* and *A. pulchellus*). 21

2 (1) IV-L-6 with strongly enlarged claws (about 1/2 L IV-L-6) and a row of short and stout ventral setae. IV-L-4 extremely shortened (*9-4 b, l*). Insertions of IV-L at lateral idiosoma margin. Posterior idiosoma margin with short and stout setae only (*9-4 a, k*). 3

– IV-L-6 with shorter claws (≪ 1/2 L IV-L-6), without short, stout ventral setae. IV-L-4 relatively longer (9-5 *b*, *d*, *f*, *h*). Insertions of IV-L slightly set off from lateral idiosoma margin. Posterior idiosoma margin often with variously modified setae (9-5 *c*, 9-6 *a, c-e*). 4

3 (2) Anterior surface of IV-L-5 proximally with a blunt triangular extension; IV-L-6 anterior surface proximally with a small tubercle bearing a fine hair-like seta (9-4 *b*, arrow), ventral surface with 3-4 setae. . . . . *Aturus scaber* (page 32)

– Anterior surface of IV-L-5 without a proximal extension; IV-L-6 without a seta-bearing tubercle, bearing 5-6 ventral setae (9-4 *l*). . . . . *Aturus rotundus* (page 31)

4 (2) Posterior end of idiosoma with 2-3 pairs of slender, tube- or club-shaped setae flanking the gonopore (9-5 *c, e, g*), or without specialized setae. Setation at posterior idiosoma margin various, but never with groups of basally thickened, strongly elongated setae. Setae of Lgl and Dgl fine, not bifurcated or only finely split into two tips at their very end. III-L-5 without higher numbers of long setae. Slender species. 5

– Posterior end of idiosoma with one, more rarely two pair(s) of strongly enlarged, spatula- or balloon-shaped setae flanking the gonopore (9-6 *c-e*). Setation at posterior idiosoma may include groups of basally thickened, strongly elongated setae. Setae of Lgl and Dgl may be thickened and deeply bifurcated (9-6 *a*, 9-7 *a-b*). III-L-5 may have numerous (> 10) long setae. Species often more compact in idiosoma shape. 8

5 (4) Posterior idiosoma margin with a row of short and stout, slightly curved setae. A pair of short, club-shaped setae flanking the gonopore (9-5 *a*). . . . . *Aturus karamani* (page 26)

– Setae at posterior idiosoma margin longer and finer. Gonopore flanked by 2-3 pairs of modified setae (9-5 *c, e, g*). 6

6 (5) Posterior idiosoma margin with dense setation extending to dorsal surface. Specialized setae flanking gonopore long and slender (9-5 *c*). IV-L-5 long and slender, with an extended setae-free central part (9-5 *d*). . . . . *Aturus barbatulus* (page 21)

– Posterior idiosoma margin with scattered setae, not extending to dorsal surface. Specialized setae flanking gonopore shorter, club-shaped (9-5 *e, g*). IV-L-5 short and stout, with setae all over the ventral surface (9-5 *f, h*). 7

7 (6) All dorsal setae simple. A group of longer setae at posterolateral idiosoma margin (9-5 *e*). IV-L shortened and stout. IV-L-5 without ventral extensions. IV-L-6 strongly thickened (L/H < 2.0), shorter than IV-L-5 (9-5 *f*). . . . . *Aturus brachypus* (page 21)

– Setae Dgl-3 and Lgl-1-2 bifurcate. Posterolateral idiosoma with very few, scattered, short setae (9-5 *g*). IV-L more slender. IV-L-5 with teeth-like, proximally-directed extensions on ventral side (9-5 *h*, arrow). IV-L-6 L/H ≫ 2.0, as long as or longer than IV-L-5 (9-5 *h*). . . . . *Aturus paucisetus* (page 28)

8 (4) Setae Dgl-3-5 all bifurcated, arranged in a transverse line in the centre of dorsal shield; Lgl-1-4 all with very short and simple setae, located at equal distances in the dorsal furrow (9-6 *a*). . . . . *Aturus prenanti* (page 29)

– Setae Dgl-3-5 arranged in a different way, at least setae Dgl-5 not bifurcated (9-6 *b-f*). Lgl-1-2 with longer, often thickened or bifurcated setae, Lgl not arranged at equal distance, some of them may be fused to margin of ventral shield (9-6 *b*). 9

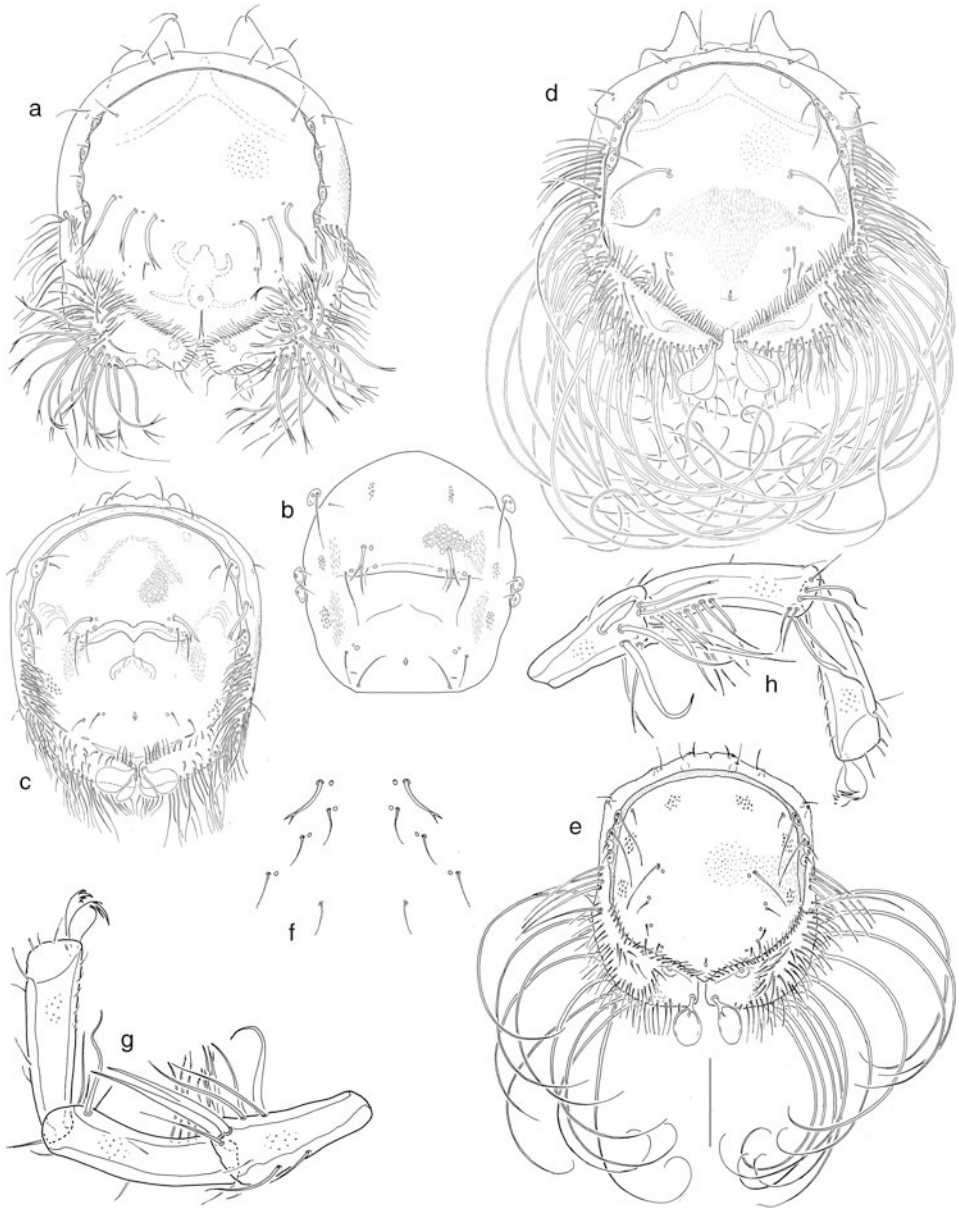
9 (8) Dorsal shield with a strong transverse sclerotized bar on its central surface. Lgl-2 fused to the upwardly-bent ventral shield (9-6 *b-c*). 10

– No transverse sclerotization in the centre of dorsal shield (a sclerotized bar may be present in the dorsocaudal area, 9-7 *b*). Lgl-2 in the dorsal furrow or fused to ventral shield. 11

10 (9) Dorsocentral sclerite bar medially straight, in its lateral parts bent anteriorly (9-6 *b*). . . . . *Aturus asserculatus* (page 20)

– Dorsocentral sclerite bar moustache-shaped, medially with a distinct, posteriorly-directed tip (9-6 *c*). . . . . *Aturus gallicus* (page 25)

11 (9) Suture line between dorsal shield and the dorsally-bent ventral shield marked by a straight or slightly curved line of densely-arranged, anteriorly-directed short setae. Posterolateral idiosoma margin with a row of "onion-like" (basally inflated), extremely elongated (length ≥ idiosoma width) and elegantly curved setae (9-6 *d-e*). 12



9-6: *Aturus* males, a-e, dorsal view; a, *A. prenanti*; b, *A. asserculatus* (only dorsal plate and Lgl); c, *A. gallicus*; d, *A. crinitus*; e, *A. villosus*; f, *A. brteki*, arrangement of dorsal setae (after Láska 1959a); g-h, IV-L-4-5; g, *A. gallicus*; h, *A. asserculatus*. (a-d, g-h: Gerecke 2014b).

– Short setae in the transition area between dorsal shield and the dorsally-bent ventral shield arranged in patches or circles (*9-7 b-e*). "Onion-like" setae at posterolateral idiosoma margin shorter than idiosoma width and not strongly curved, or completely absent. 18

12 (11) All dorsal setae (Lgl and Dgl) simple, not bifurcated (*9-6 d-e*). Dorsal shield anterior to excretory pore with a dense cover of fine, hair-like extensions. A pair of round grooves on ventral side flanking anterior end of gonopore, visible by transparency also in dorsal view. 13

9-7: *Aturus* males, a-b, dorsal view; a, *A. comatus*; b, *A. spatulifer*; c, *A. pulchellus*, seta Dgl-3; d, *A. protzi*, IV-L-4/5; e-f, *A. fontinalis*; e, dorsum; f, IV-L-4-5; g-h, *A. processiger*; g, dorsum; h, IV-L-4-5. (b, d, g-h: Gerecke 2014b, d: after Biesiadka 1975).

– At least Dgl-3, often also Lgl-1 and -2 bifurcated (*9-7 b-c, e, g*). Dorsal shield surface with or without hair-like extensions. Ventral grooves at anterior end of gonopore present or absent (similar grooves may also be visible on dorsal side!). 14

13 (12) Posterolateral idiosoma margin with more than 15 pairs of long "onion-setae" (*9-6 d*). IV-L with more slender terminal segments similar in length. . . . . *Aturus crinitus* (page 23)

– Posterolateral idiosoma margin with less than 15 pairs of long "onion-setae" (9-6e). IV-L with stouter terminal segments decreasing in length. . . . . *Aturus villosus* (page 34)

14 (12) Posteromedial part of dorsal shield with a pair of grooves flanking the excretory pore (specimens with little developed medial ridge between the grooves show an unpaired, inversely U-shaped deepening anterior to the inflated terminal setae - 9-7b). Dorsal shield anterior to excretory pore with a dense cover of fine, hair-like extensions. . . . . *Aturus spatulifer* (page 33)

– Posteromedial part of dorsal shield without paired grooves (9-7a, g). If an unpaired depression is developed, posteromedial margin not setose. The area anterior to excretory pore not covered by hair-like extensions. 15

15 (14) Posterior idiosoma subrectangular - lateral margins strongly rounded, posteromedial margin nearly straight. Medial margins flanking gonopore protruding, with a group of hair-setae (9-7g). . . . . *Aturus processiger* (page 30)

– Posterior idiosoma margin equally rounded, without a straight posteromedial part and without protruding margins flanking gonopore, numerous fine setae all over posterior margin (9-7a). 16

16 (15) Setae Dgl-3 trifurcated (9-7c). Lgl probably as in 9-7b (only Lgl-1 free in the dorsal furrow; Lgl-2, probably also Lgl-3-4, fused to border of ventral shield; Lgl-1-2 bearing strong, bifurcated setae). A little documented species. . . . . *Aturus pulchellus* (page 31)

– Setae Dgl-3 bifurcated. Position and setation of Lgl various. 17

17 (16) Dgl-4-6 arranged in a caudally diverging line (9-6f: Dgl-6 closer to each other than Dgl-5). Setae Dgl-3 and Lgl-1 finely bifurcate, Lgl-2, Dgl-4 and Dgl-5 simple (position of Lgl-2-4 not described, probably fused to border of ventral shield). 8 pairs of "onion setae". III-L-5 with numerous long ventral setae. IV-L-4/5 ventrodistally without particularly modified bifurcate setae. . . . . *Aturus brteki* (page 22)

– Dgl-4-6 in a medially-directed triangle (Dgl-5 closer to each other than Dgl-6). Dgl-3-5 and Lgl-2 bifurcated; 12-14 pairs of "onion setae" (9-7a). III-L-5 with 2-3 short ventral setae. IV-L-4 distoventrally, in addition to a pair of sword setae, with a distally flattened and curved in the centre finely bifurcated seta; IV-L-5 distoventrally with 2 asymmetrically bifurcated setae (9-8d). . . . . *Aturus comatus* (page 22)

18 (11) III-L-5 with 2 backwards-curved whip setae in anterodistal position. Lgl-2 in touch with Lgl-3 (9-7e, 9-8a). 19

– III-L-5 with one backwards-curved whip seta in anterodistal position. Lgl-2 distanced from Lgl-3 (9-8b). 20

19 (18) Setae Lgl-1 heavy, bifurcated. Setae Dgl-3 may be trifurcate. Dgl-5 further apart from each other than Dgl-3 and -4 (9-8a). Onion setae at posterior idiosoma margin very dense and numerous. Only 1-2 setae on III-L-5 directed dorsally. . . . . *Aturus intermedius* (page 26)

– Setae Lgl-1 fine, simple. Setae Dgl-3 bifurcate. Dgl-4 further apart from each other than Dgl-3 and -5 (9-7e). Onion setae at posterior idiosoma margin more scattered. Several setae on III-L-5 directed dorsally. . . . . *Aturus fontinalis* (page 24)

20 (18) Setae Lgl-1 strong and bifurcate, Dgl-5 further apart from each other than Dgl-3 and –4 (as in 9-8a). III-L-5 with more than 20 long setae (9-8f). IV-L-5 with elk-horn-like proximal setae (9-7d). . . . . *Aturus protzi* (page 30)

– Dgl-5 closer to each other than Dgl-3 and –4 (9-8b). III-L-5 with less than 15 long setae (as in 9-8e). Setae Lgl-1 fine and simple. . . . . *Aturus natangensis* (page 27)

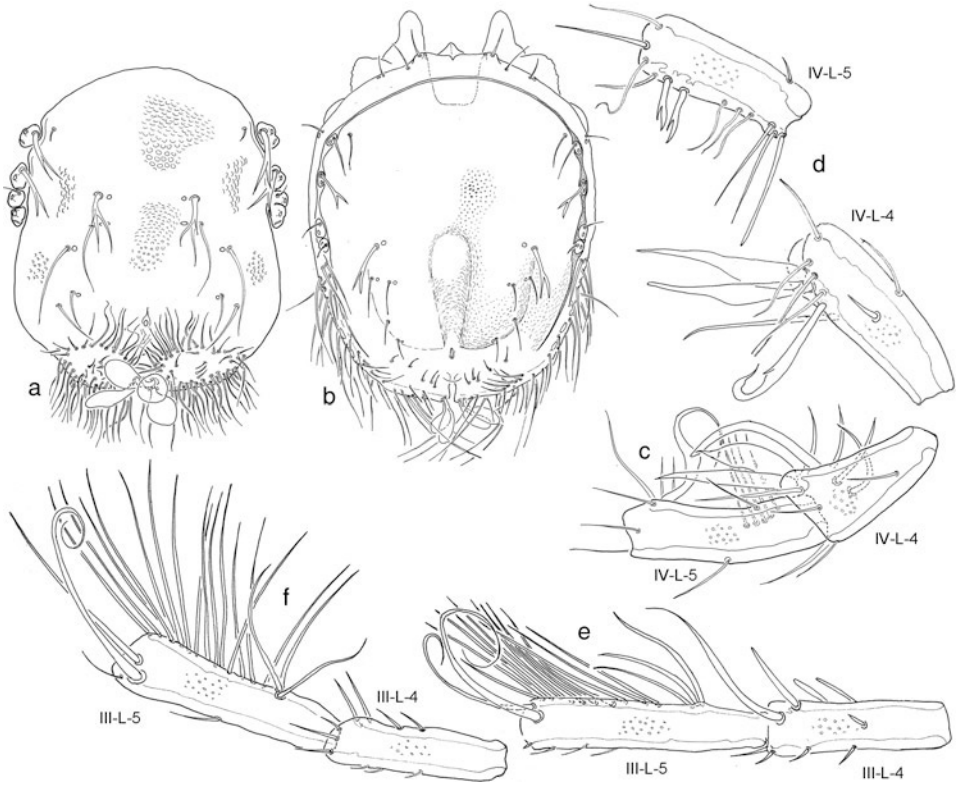
21 (1) Gonopore area in dorsal view with a pair of subtriangular porose platelets extending beyond posterior idiosoma margin and covering the genital membrane (9-9a, c), in ventral view, a deep, inversely U-shaped bay embraces a further pair of subtriangular porose platelets (9-9b). 22

– If gonopore (rarely) flanked by paired structures at posterior idiosoma margin, these are membranous or little sclerotized without porosity and not shaped as platelets (9-9d-g). 23

22 (21) Idiosoma inversely egg-shaped, posterior margin slightly projecting (9-9a-b). . . . . *Aturus scaber* (page 32)

– Idiosoma more rounded (9-9c). . . . . *Aturus rotundus* (page 31)

23 (21) Less than 8 pairs of acetabula (9-9g - in specimens with 8-10 pairs of acetabula check both alternatives). 24



9-8: *Aturus* males; a-b, dorsal view; a, *A. intermedius*; b, *A. natangensis*; c-d, IV-L-4-5; c, *A. intermedius*; d, *A. comatus;* e-f, III-L-4-5; e, *A. intermedius*; f, *A. protzi*. (a-c, e-f: Gerecke 2014b).

– 8 or more pairs of acetabula (e. g., *9-9 e-f*) 28

24 (23) Lgl-1/2 lying close to each other (separation < glandular diameter, *9-9 m*). . . . . .*Aturus karamani* (page 26)

– Separation Lgl-1-2 similar to separation between other Lgl (separation > glandular diameter, *9-9 l*). . .25

25 (24) Dgl-4 very far from Dgl-3 (separation ratio Dgl-3-4/4-5 > 3.0, as in *9-9 m*). Length P-4 > 70 µm. Colour dark red. 26

– Dgl-4 closer to Dgl-3 (as in *9-9 d*). At least one Vgl in secondary sclerotization. Length P-3 < 70 µm. Frontal dorsal shield with a bowed line of stronger sclerotization (*9-9 l*, arrow). Colour various. 27

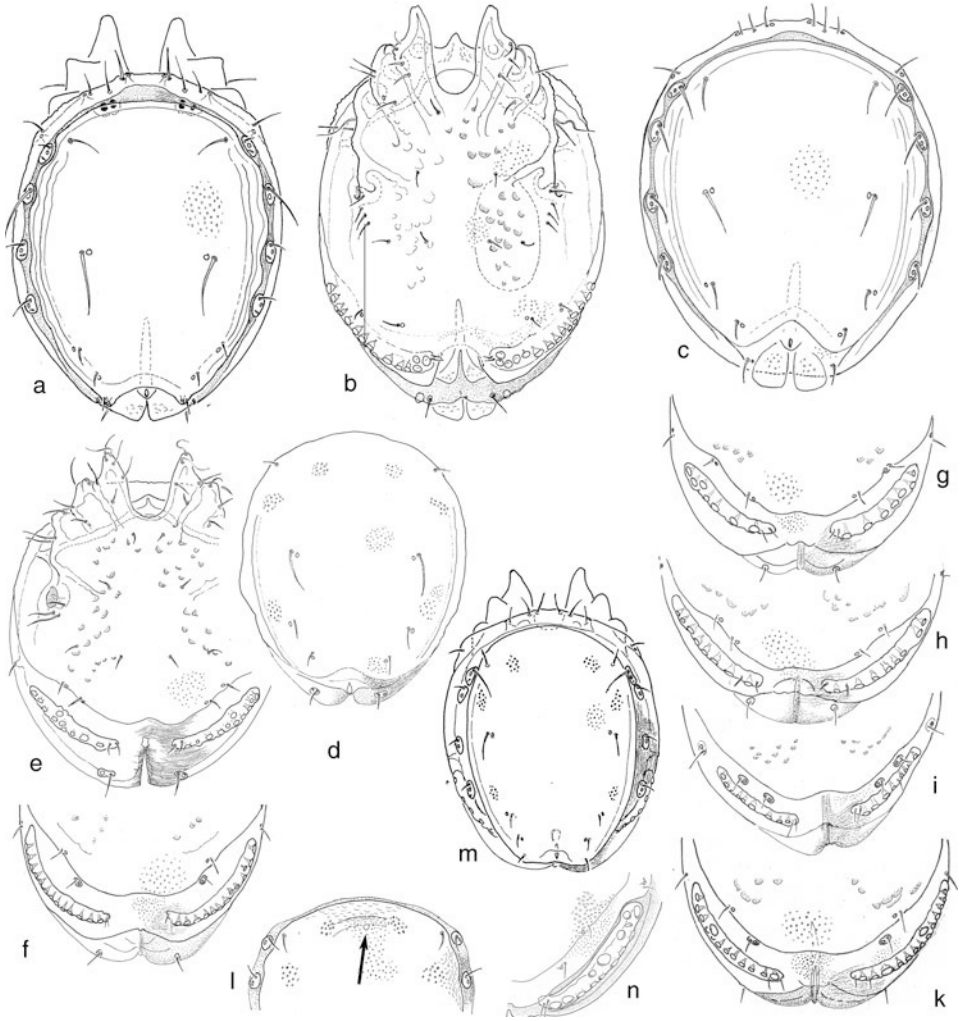
26 (25) In mature specimens both Vgl in primary, otherwise the lateral Vgl in secondary sclerotization (e. g., in *9-9 g* left hand); in the area of lateral Vgl, posterior margin of primary sclerite concave (*9-9 g*). . . . . *Aturus spatulifer* (page 33)

– Vgl on the border primary/secondary sclerotization; in the area of lateral Vgl, posterior margin of primary sclerite straight to convex (*9-1 i*). . . . . .*Aturus barbatulus* (see also 34; page 21)

27 (25) Bowed frontal line embracing a frontal eye-like structure (*9-9 l*, arrow). Dgl-4 closer to Dgl-3 (separation ratio Dgl-3-4/4-5 < 2.5). . . . . .*Aturus paucisetus* (page 28)

– No frontal-eye-like structure reported. Dgl-4 apart from Dgl-3 (separation ratio Dgl-3-4/4-5 > 2.5). . . . . .*Aturus brachypus* (page 21)

28 (23) Both Vgl in area of primary sclerotization; posterolateral margin of primary sclerotization straight to concave (*9-9 h*). Most medial acetabula located between 2 setae. Dgl-4 close to Dgl-3 (separation ratio Dgl-3-4/4-5 about 2.0). Variability poorly documented, known from two female specimens only. . . . . *Aturus comatus* (page 22)



9-9: *Aturus* females; a-b, *A. scaber*; a, dorsal view; b, ventral view; c, *A. rotundus* dorsal view; d-e, *A. crinitus*, specimen from Sicily; d, dorsal shield; e, ventral view; f-k, posterior venter; f, *A. crinitus*, specimen from Germany; g, *A. spatulifer*; h, *A.comatus*; i, *A. natangensis*; k, *A. villosus*; l, *A. paucisetus*, frontal area (arrow: frontal eye-like structure); m, *A. karamani* dorsum; n, *A. prenanti*, right acetabular plate. (a-b, d-e, n: Gerecke 2014b; c: after K.Viets 1936d; m: from K. Viets 1936b).

– If most medial acetabula located between 2 setae, medial Vgl in secondary sclerotization (*9-9k*). Otherwise, medial acetabula located lateral to 2 medial setae (e. g., *9-9g, i*). Position of Vgl and Dgl-3-5 various. 29

29 (28) Dgl-4 rather close to Dgl-3 (separation ratio Dgl-3-4/4-5 < 2.0). 30

– Dgl-4 further apart from Dgl-3 (ratio Dgl-3-4/4-5 > 2.0). 32

30 (29) At least one (in Mediterranean populations both) Vgl in the primary sclerotization (*9-9e-f*). Here could key out *A. prenanti*, possibly differing in a higher acetabula number of 13-15 pairs (*9-9n*), see under that species for details. . . . . *Aturus crinitus* (page 23)

– Vgl in secondary (as in *9-9i*), or at the posterior border of primary, sclerotization (as in *9-1i*). 31