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THE WATER MITE FAMILY ACHERONTACARIDAE COOK, 1967
NOV. STAT. AND DIAGNOSIS
OF THE SUPERFAMILY HYDROVOLZIOIDEA THOR, 1905
(ACARIFORMES, HYDRACHNIDIA)

Petr TUZOVSKIJ 1, Daniele BENFATTI 2 & Reinhard GERECKE 3
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ABSTRACT. The morphology of adults, deutonymphs and larvae of water mites of the superfamily Hydrovolzioidea is studied, taking as examples the species Hydrovolzia cancellata Walter, 1906 and Acherontacarus rutilans E. Angelier, 1951. All active stages, especially larvae, show strong differences from each other in many important character states. As a consequence, a new diagnosis of the superfamily Hydrovolzioidea is given, and the former subfamily Acherontacarinae elevated to family level. A diagnosis for all active instars of the families Hydrovolziidae and Acherontacaridae nov. stat. is proposed. New data on larval behaviour, host range, coevolution and zoogeography are provided.


INTRODUCTION.

The superfamily Hydrovolzioidea is one of the most poorly known groups of water mites. Some specialists consider it the sister group of all remaining Hydrachnidia, while BADER (1975) and SCHWOERBEL (1986b) hypothesised a closer relationship to the Halacaroida than to the true fresh water mites. The diagnosis of the superfamily given by COOK (1974), based mainly on characters of the adult stage, is now outdated due to results from recent investigations. Apart from a detailed description of the larva of Hydrovolzia gerhardi (WAINSTEIN, 1966a), there are new data on the composition of the idiosomal chaetom (TUZOVSKIJ 1987), on the presence of acetabula on coxae in deutonymphal and adult Hydrovolzia,

1. Institute for Biology of Inland Waters, Russian Academy of Sciences, RUS 152742 Borok, Nekouz District, Yaroslavl province, Russia; e-mail: tuz@ibiw.yaroslavl.ru
2. Via Cantone 61, I 46020 S.Giacomo di Segrate (MN), Italy; e-mail: daniele.benfatti@tin.it
3. Biesingerstr. 11, D 72070 Tübingen, Germany; e-mail: reinhard.gerecke@uni-tuebingen.de (address for correspondence).
and in all active stages of *Acherontacarus*, and also on
the presence of glandularia in *Acherontacarus*
(ALBERTI & BADER 1990, BENFATTI & GERECKE 1999,
BENFATTI et al. in press).

The purpose of the present paper is to review the
taxonomic significance of the recently published
information, accompanied by a detailed study on the
morphology of all active stages (larvae, deutonymphs,
adults) of water mite species in the genera
*Hydrovolzia* and *Acherontacarus*. As a result, a new
diagnosis of the superfamily Hydrovolzioidea and its
families is given. Furthermore, we employ a termino-
logical system that so far has been ignored in the
western literature (TUZOVSKIJ, 1987). As compared
with the traditional 'Western' systems based on LUN-
DBLAD, this terminology has the advantage of being
equally applicable to all free developmental stages of
water mites.

**MATERIALS AND METHODS**

The setal terminology used in this paper reflects
the segmental structure of the idiosoma and is
equally applicable for all developmental instars. In
brackets, we give the serial segment numbers (seg-
ment VII is reduced in all Acariformes — sitnikova
1978), and the corresponding 'Western' terminology
for the dorsal setae of adult Hydrovolzioidea, fol-
lowing BADER (1989). So far, no proposal has been
published for a homologization of the ventral setae in
the 'Western' system.

Fch — frontales chelicerarum (I, 'praeculare')
Fp — frontales pedipalporum (II, 'antenniforme 1')
Vi — verticales internae (III, 'antenniforme 2')
Ve — verticales externae (III, not expressed in post-
larval stages)
Oi — occipitales internae (IV, 'postoculare')
Oe — occipitales externae (IV, 'dorsoglandulare 1')
Hi — humerales internae (V, 'dorsoglandulare 2')
Hv — humerales ventralia (V, 'lateroglandulare 1')
He — humerales externae (V, 'lateroglandulare 2')
Sci — scapulares internae (VI, 'dorsoglandulare 3')
Sce — scapulares externae (VI, 'lateroglandulare 3')
Li — lumbales internae (VIII, 'dorsoglandulare 4')
Le — lumbales externae (VIII, 'lateroglandulare 4')
Si — sacrales internae (IX, 'terminoglandulare')
Se — sacrales externae (IX)
Ci — caudales internae (X)
Pi — praeanales internae (XI)
Pe — praeanales externae (XI)
Ai — anales internae (XII)
Ae — anales externae (XII)

The following abbreviations are also used:
a — acanthoid seta, e — eupathid seta, i1 — slit organ
l, s — solenidium.

**RESULTS**

3.1 Hydrovolzia Thor, 1905

The genus *Hydrovolzia*, with the first known spe-
cies *H. placophora* described almost simultaneously
by MONTI (1905) and THOR (1905), now includes 13
recognised species and one subspecies, reported from
spring and hygroscopic habitats in Asia, Europe,
Africa and N America.

Our knowledge of the prelude stages is rather
incomplete: deutonymphs are known for *H. placophora*
(MONTI, 1905) (WALTER, 1922; K. VIETS, 1922,
1936; BADER, 1975; BENFATTI, 1990; BENFATTI et al.,
in prep.), *H. cancellata* Walter, 1906 (BENFATTI, 1990;
BENFATTI et al., in prep.), *H. japonica* Imamura, 1961,
and *H. persica* Bader & Sepasgozarian, 1980. Larvae
have been described for *H. placophora* (WALTER,
1922; LUNDBLAD, 1930; K. VIETS, 1936; SPARING,
1959; BENFATTI et al., in prep.), *H. cancellata* (BEN-
FATTI et al. in prep.) and *H. gerhardi* (MCCULLH, 1954;
WAINESTEIN, 1966, 1980). Information on larval beha-
viour in *Hydrovolzia* is available for only three species,
in which they exclusively parasitize adult insects. For
actively searching their hosts, they leave the water and
climb on humid surfaces near the water’s edge (WAL-
TER 1922, BENFATTI et al., in prep.). As compared with
larvae of other clades of Hydrachnidia, *Hydrovolzia*
larvae are particular in their attachment sites. They
do not prefer membranous intersegmental surfaces,
but are regularly found penetrating strongly sclerified
parts of the host’s body surface, mainly leg femora
and tibiae. It is not yet known if they are really
capable of penetrating these areas with their strongly
developed chelicerae, or if they attack their hosts immediately after moulting, when they are still weakly sclerified. Larvae of *H. placophora* have often been found attached to Diptera of the family Empididae (*Clinocera, Roederioides* — new data from GERECKE coll.), as well as attached to Hemiptera (*Hebrus ruficeps*, BENFATTI et al., in prep.), Coleoptera of the families Scirtidae (*Elodes*) and Staphylinidae (*Stenus*, new data from GERECKE coll.), and even terrestrial mites (*Trombidiidae* — SARTO et al., in prep.).

*H. cancellata* has so far only been found attached to Diptera of the family Empididae (*Clinocera, Wiedemannia* - BENFATTI et al., in press and new data from GERECKE coll.; and *Kowarzia* in Sardinia, a record that still needs confirmation from rearing). *H. gerhardi* has been found attached to the hemiptera *Microvelia americana* Uhler (MITCHELL, 1954).

### 3.1.1 Hydrovolzia cancellata Walter, 1906.

Since the first description, additional morphological and ecological information on this species has been published by WALTER (1907), WALTER & MOTAS (1927), LUNDBLAD (1956), GERECKE (1991), BENFATTI (1990) and BENFATTI et al. (in prep.). It is found mainly in hygropetric (bryomadicolous sensu VAILLANT, 1955) habitats of springs and low-order streams at elevations between 150 and 2400 m, in catchments draining to the Mediterranean sea. A complete list of so far published records can be found in BENFATTI (1990) and GERECKE (1991). Detailed measurements for all instars of this species will be published by BENFATTI et al. (in prep.).

**ADULTS:** Dorsum with 2 large unpaired central shields (Fig.1), one pair of very long and slender sclerites flanking the posterior central shield, and four pairs of rather large lateral plates, each made up by a pair of sclerites separated by a narrow membranous line. Anterior central shield transverse, clearly shorter than wide, bearing 4 pairs of setae: Fch (short, thick, plumose), and Fp, Vi and Oi (thin and simple). Setae Fp and trichobothria Oi not accompanied by glandularia, setae Fch and Vi inserted at the anterior/ant eroteralateral edge of shield, each in vicinity of a glandularium placed in the soft cuticle. Posterior central shield elongate (length/width >2), with 4 pairs of setae: Oe, Hi, Sci, Li — all without glandularia; posterior dorsal shield flanked by a pair of long strip-like platelets; all lateral shields elongate, consisting of an anterior sclerite bearing a seta (He, Hv, Sce, and Le), and a posterior sclerite with a glandular opening; first pair of slit organs (i1) flanking lateral margins of anterior dorsal shield, i2 in the interspace between setae He and Sce, i3 and i4 inserted in posterior part of the narrow sclerite flanking the posterdorsal shield, i5 at caudolateral edge of idiosoma. In adult *H. placophora* (Monti), the elongate sclerite is divided in a shorter anterior part and the posterior part bearing the slit organs i3 and i4 (Fig. 2).

Coxae arranged in 4 groups (Fig. 3), bearing numerous acetabula arranged along the posterolateral margins of coxae I-II, and on lateral and medial margins of coxae III-IV; lateral margins of coxae, especially of coxae III-IV, considerably protruding over the lateral idiosomal margin; interspace between coxae 3-4 and the genital and postgenital plates with 5 pairs of setae (Si, Se, Ci, Pi, Pe), arranged on platelets with accompanying glandularia, Pi platelet more elongate, others roundish; genital flaps of males short, with 4 pairs of strong setae (Fig. 4), genital flaps of females more elongate, with 5 (4-6) pairs of setae; excretory pore opening in anterior part of a subquadratic postgenital plate; between this plate and the posterior idiosoma margin is a further elongate sclerite.

Gnathosoma (Fig. 5) with 2 pairs of short, thick setae at anterior tip of the long rostrum; chelicerae with large basal segment and relatively small, sickle-shaped claw; shape and chaetotaxy of pedipalp as shown in Figs 6-7; number of pedipalp setae generally rather constant, (P-1-5: 0, 4-5, 2-3, 4-5, 9 (s)).

Ejaculatory complex (Figs 8, 9) characterised by long brachia proximalia, extending well over the margin of the cella proximalis, and reduced brachia distalia.

Legs with 6 free segments (Fig. 10), without swimming hairs; their setae not constant in number or position — especially on terminal segments of anterior legs; terminal segments distally thickened and with well developed claw furrow flanked by 3 pairs of plumose setae; claws simple, sickle-shaped (Fig. 11).
DEUTONYMPH: Similar to adults, but differing in the absence of a gonoporus, smaller size, lower numbers of setae on legs and palps, the relative extension of some idiosoma sclerites, and the number of glandularia.

Dorsal idiosoma with 3 unpaired central shields, a pair of rather large lateral plates and 2 pairs of strip-shaped plates (Fig. 12); anterior dorsal shield as in adults with 4 pairs of setae (Fch, Fp, Vi, Oi), central dorsal shield with only 3 pairs of setae (Oe, Hi, Sci), the posterior shield without setae; internal lumbales (Li) inserted free in the membranous integument between central and posterior shield; trichobothria Fp and Oi, and setae Oe, Hi, Sci and Li without accompanying glandularia; anterior lateral shields rather large and not connected with setae Hi; the strip-shaped narrow posterolateral plate divided into two parts, the posterior of which bear i3, i4 free in the membranous integument.

The two coxal plates on each side separated by a wide membranous interspace (Fig. 13); acetabula fewer than in adults, arranged along posterolateral margins of coxae I and II, and on posteromedial margins of coxae III and IV; setae Pi and Ci without accompanying glandularia; excretory pore framed by a narrow sclerite ring, placed between a small round sclerite representing the genital field area, and a large, elongate ventrocaudal shield.
Figs 5-8. *Hydrovolzia*, adult. 5 — gnathosoma lateral view, 6 — pedipalp lateral view, 7 — tarsus of pedipalps, 8 — ejaculatory complex. 5-7 — *H. cancellata* female, 8 — *H. placophora* male.

Figs 9-11. *Hydrovolzia cancellata*, adult male. 9 — ejaculatory complex, 10 — leg I, 11 — claws of tarsus IV.

Femur and genu of pedipalps (Fig. 14) each with 2 dorsal setae nearly equal in length; tibia with 2 short and 2 long setae in the distal part; tarsus with one solenidium proximally, and 6 thick distal setae.

Legs with 6 free segments (Fig. 15); all tarsi with a well developed claw furrow; number of setae, especially on terminal segments, not strictly constant, I-L: 2-3, 3, 5, 5-6, 5-9, 19-22; II-L: 2-3, 2-3, 4-5, 5-6, 8-9, 17-19; III-L: 2, 2, 4-5, 3-4, 5-7, 11-13, IV-L: 1, 0, 4-5, 4-5, 5-9, 4-5, 7-10; IV-L-2 without any setae.

**Larva:** dorsal shield subquadrate, mediocaudally protruding in a small tip, bearing only 1 pair of setae (Fp); all other dorsal setae rather large, inserting on the membranous integument (Fig. 16); trichobothria Oi club-shaped, very different from all other body setae; 5 pairs of slit organs situated in membranous integument of dorsal idiosoma.

Coxae I and II subtrapezoidal, with pointed or rectangular mediocaudal edges, arranged closely together (Fig. 17); coxae III triangular, with anteromedial edge forming an acute angle; urstigmata numerous (11-13 pairs), aligned at anterior margin of coxae II; coxae I with 2, coxae II-III each with 1 fine seta; excretory plate weakly developed, bearing 1 pair of fine hair pores anteriorly and the opening of the excretory pore caudally.

Gnathosoma (Fig. 18) very large, but with narrow mouth opening flanked by a pair of setae; chelicerae with basal segment strongly thickened proximally and abruptly narrowed distally (Fig. 19), claw tip pointed.

Pedipalp consisting of 4 free segments (Fig. 20), setation formula (P-1-4: 0, 1, 2, 8; 4 setae on P-4 large (1 pointed, and 3 with rounded tips) and 3 elongate, solenidium short.

Legs consisting of 6 free segments, shape and seta-
tion as shown in Figs 21, 24-26; tarsi of all legs strongly narrowed distally and without claw furrow; all specialised setae (solenidia, eupathids, acanthoids) smooth, simple tactile setae comb-like (Fig. 22); general number of setae on legs (without coxae), I-L: 1, 2, 5, 6 (s), 11 (2s), 21 (s, e, ac); II-L 1, 2, 5, 6 (s), 11 (2s), 21 (s, e, ac); III-L 1, 1, 5, 4, 7, 17; empodium and ambulacrae hook-shaped, smooth (Fig. 23), empodium clearly shorter than ambulacrae.

3.1.2 Morphological peculiarities of the water mite subfamily Hydrovolziinae

Apart from *Hydrovolzia* (Monti, 1905), the subfamily Hydrovolziinae contains the two monotypic genera *Hydrovolziella* Viets, 1935, from the Ivory Coast, and *Stygovolzia* Imamura, 1957, from Japan. *Hydrovolziella* was described from a single male under the name of *Hydrovolzia lata* (Walter, 1935), but the holotype is lost. It is characterised by sexual dimorphism in the shape of IV-L and the sclerotization of the ventral surface. The male IV-L is strongly modified in shape and has only 5 free segments, whereas in females 6 segments are found (Cook, 1974: first description). In both sexes, the posterior ventral surface bears the typical pair of lateral, as well as unpaired excretory and caudal plates, but setae Pe are placed on enlarged plates anteriorly from the genital field in males, whereas they are on smaller, roundish platelets flanking the genital field in females. Furthermore, setae and glandularia Pi are fused to the posterior margin of the lateral plates in males, while in females they remain separate.

The chaetotaxy and arrangement of glandularia in *Stygovolzia uenoi* (Imamura, 1957) are not documented in a satisfactory manner, and at present it is not possible to have access to the types. In adults of that species, setae Pe are arranged on a transverse plate anterior from the genital field, while in the deutonymph they insert on small, paired sclerites. In the drawing of the dorsal idiosoma of the deutonymph,
Imamura depicts 8 pairs of setae, 4 pairs more than in adults, 3 pairs of which are without accompanying glandularia. This would be surprising, because in the ontogenesis of Hydrachnidia, there is usually no change in the number of setae in the transition from deutonymph to adult (Tuzovskij, 1987). As the position of the setae in question agrees well with the normal pattern of slit organs, it is likely that Imamura confused these two types of structures in his Fig. 3a.

In his system of Hydrachnidia, K. O. Viets (1987) recognised only one genus, Hydrovolzia in the subfamily Hydrovolziinae, ranking Hydrovolziella and Stygvolzia as subgenera of Hydrovolzia. In view of our rather incomplete knowledge of developmental stages and the non-availability of type specimens, it is not possible to solve the questions concerning taxonomic rank of these taxa here and we propose to conserve Cook's system with three separate genera.

3.2 Acherontacarus K. Viets, 1932

Since the first description of this genus, with *A. halacaroides* as typus generis (Viets 1932), 8 additional species have been described from S Europe, N Africa and Gomera (Canary Islands), and two further species are in the course of being described. Smith et al. (2001) give first informations on the presence in North America; the genus *Neoacherontacarus* Bader, 1989, as well as the two subgenera *Acherontacarellus* Lundblad, 1962 and *Acherontacaropsis* Cook, 1967 are considered synonyms of *Acherontacarus* (Benfatti & Gercke 1999). Most records are from groundwater wells, interstitial habitats or rheocrenes.

Deutonymphs have been described for *A. halacaroides* (K. Viets 1933), *A. fonticulus* (K. Viets, 1934, known only from this developmental stage), *A. rutilans* E. Angelier, 1951 (E. Angelier 1954, 1959) and *A. cedro* Lundblad, 1962. Preliminary information on
larval morphology is so far available only for representatives of several, still unidentified, species and for *A. vietsi* E. Angelier, 1951 (K. Viets 1934, Benfatti & Gerecke 1999). A taxonomic revision of this genus will provide additional information on preadult morphology and determination keys for all developmental stages (Gerecke & Benfatti, in prep.).

All parasitic larvae of *Acherontacarus* so far recorded have been found on water beetles, mainly of the family Dytiscidae (several species of *Agabus* and *Deronectes*: *A. bicornis* Cook, 1974; *A. rutilans*, and an undescribed species from Italy), but in one case on *Hydraenidae* (*Hydraena: A. vietsi*). As in *Hydrovolzia*, larvae preferentially attach to strongly sclerified parts; such as leg segments and sternalia, in one case just on the dorsal elythral surface (Benfatti & Gerecke 1999; Gerecke & Benfatti, in prep.).

3.2.1 *Acherontacarus rutilans* E. Angelier, 1951

The first description of this species was based on a female and a deutonymph (E. Angelier 1951 and 1954); Santucci (1975) and Benfatti & Gerecke (1999) later published information on the morphology of the male and sexual dimorphism in this species. So far, *A. rutilans* has been recorded only from interstitial habitats and springs in Corsica and Sardinia.

**Adult:** A large part of the dorsum covered by 2 large unpaired shields, each with 4 pairs of setae; a
transverse frontal shield, about 4-5 times broader than long, and an elongate and triangular posterdorsal shield; trichobothria Fp, Oi, and all setae of posterdorsal shield (Oe, Hi, Sci, Li) without accompanying glandularia; a pair of fine, semicircular pits with medially-directed openings ('Tuberkeln' sensu BADER 1989) near the lateral margins, and a further unpaired one at the mediocaudal margin of the frontal plate; 10-12 similar structures, gradually decreasing in size, aligned along lateral margin of posterdorsal plate; frontal and posterdorsal shields flanked by 10 pairs of platelets, which alternately bear a seta (He, Hv, Sce, Li, Si) or a glandular opening; no slit organs detected.

All ventral sclerites in close contact with their neighbouring plates, forming a well-structured pattern of plates and suture lines (Fig. 28); coxae I + II and coxae III + IV fused to respective coxal plates; suture line between coxae I/II only appreciable laterally, suture line between coxae III/IV readily visible as a continuous border; acetabula arranged at lateral margins of coxae I and II, and at lateral and medial margins of coxae III and IV; genital field of males pentangular, with short flaps bearing 5, sometimes 6, setae at medial margin (Fig. 29); females with elongate genital flaps separated by a transverse suture line into a smaller anterior, and a larger posterior part, bearing 2-3 pairs of setae; setae Pe in males anterior of genital field, on a pair of trapezoidal plates flanked by smaller, subrectangular platelets with the corresponding glandular openings; in females, the platelets bearing setae Pe are subquadratic and displaced laterally by the genital flaps, which extend to the posterosmedial edges of coxae I + II plates; posteralaterally of genital field, on each side, is a longish, triangular plate bearing setae Pi and Ci, without accompanying glandularia; caudally of the genital field, a longish trapezoidal plate bearing the opening of the excretory pore and a semicircular caudal plate, both without setae; in the posterolateral edges between the mediocaudal tips of Cx-4 and the caudal shield, are setae Se and their glandularia.

Gnathosoma with long well developed rostrum (Figs 28, 31); chelicerae with a very long basal segment and short, curved claw; pedipalps consisting of 5 free segments, shape of segments and setae as
FIG. 24. Hydrovolzia cancellata, larva, leg II.

shown in Fig. 32; (P-1-5-0, 4-5, 7-8, 4-5, 11 (s); P-4 relatively short and with concave ventral margin, P-5 shortened, but with very long setae.

Ejaculatory complex (Figs 33-34) with rather short brachia distalia and massive brachia proximalia, proximal chamber well developed.

Legs with 6 free segments; all claws simple; male IV-L-4-6 modified as shown in Fig. 35.

DEUTONYMPH: very similar to adult, differing mainly by smaller size, absence of gonopore and movable genital flaps, lower number of setae on legs and pedipalps, and less extensive sclerotisation of the ventral idiosoma. Dorsum (Fig. 36) with a more variable number of marginal pits on posterodorsal shield (3-5 pairs); only anterior coxal plates adpressed to each other at medial margins, but anterior and posterior coxal plates, and all other ventral sclerites, separated from each other by extended stripes of membranous integument (Fig. 37); excretory plate pentangular, with excretory pore opening near an anteromedial incision; caudal plate with pronounced anterior angles, but equally rounded posterior margin; excretory plate flanked by a pair of elongate plates bearing setae Ci and Pi, without accompanying glandularia; setae on pedipalps fewer and more stable in number as compared to adults (Fig. 38-39), setation formula (P-1-5: 0,2,2,4,7(s); legs provided with heteromorphic (thin and thick) setae (Fig. 40), I-L-6 with an especially high number of setae.

LARVA: Dorsal shield large, covering nearly the whole idiosoma surface in unengorged specimens (Fig. 41), bearing 1 pair of setae (Fp); setae Vi and Oi on sclerite of lateral eyes; both pairs of trichobothria (Fp, Oi) shaped as usual; setae He, Hi, See, Sci, Le, Li, Se, Si, Ci and all 5 pairs of slit organs free in the membranous dorsal furrow; coxae I and II fused to form a compact sclerotized shield, with indistinct remnants of suture between coxae I/II only visible.
laterally, and with medial longitudinal suture not reaching the posterior margin (Fig. 42); coxae III separated from each other and from anterior coxal plate by a Y-shaped area of membranous integument; number of coxal setae 2, 1, 1; acetabula (= urstigmata) numerous, arranged along the lateral margins of all coxae in the same way as those of adults; excretory pore on a small triangular excretory platelet, flanked by one pair of fine setae.

Gnathosoma with very large mouth opening, directed ventrally, surrounded by 20 round vesicles which probably act together as a suction disk (Fig. 43); chelicerae very strong with basal segments very enlarged proximally, but abruptly narrowed distally, claws blunt and massive; pedipalps (Fig. 44) slender, with 4 free segments, setation formula (P-1-4) 0,1,2,11; P-3 extraordinary elongated, P-4 longish, provided with short spines and long slender setae.

Legs 6-segmented (Figs 46-48), tarsi always enlarged distally and with well expressed claw furrow; tactile setae on legs very varied in shape: smooth, plumose, thin, or thick; usual numbers of leg setae:
Figs 36-40. Acherontacarus rutilans, deutonymph. 36 — dorsal idiosoma, 37 — ventral idiosoma, 38 — pedipalp lateral view, 39 — tarsus of pedipalp, 40 — leg I.
I-L 1, 2, 4, 6, 11, 23 (s, ac); II-L 1, 2, 4, 6, 11, 23 (s, ac); III-L 1, 2, 4, 7, 13; empodium completely smooth, ambulacrae each divided distally into a dorsal and ventral branch each, dorsal branch with a ventral row of long and fine teeth (Fig. 49).

3.2.2 Morphological peculiarities of the water mite subfamily Acherontacarinae

The subfamily Acherontacarinae includes the genera *Acherontacarus* Viets, 1932 and *Bharatavolzia* Cook, 1967, the latter consisting of the subgenera *Bharatavolzia* and *Bharatavolziella*. Adults of *Bharatavolzia* are similar to *Acherontacarus* in the number and arrangement of dorsal plates, but differ in the degree of sclerotisation of the ventral surface: all ventral sclerites fuse completely, forming a continuous ventral shield; as in *Hydrovolzia*, the terminal segments of male IV-L are not sexual differentiated. Thus, *Bharatavolzia* seems to occupy an intermediate position between the Hydrovolziidae and Acherontacaridae. A more appropriate systematic assessment is not possible without research on the morphology and biology of larvae of this genus.

Among species of the genus *Acherontacarus*, there is a tendency for the glandularia to be reduced and for the plesiomorphic 10 pairs of lateral sclerites — which bear alternately setae, or glandularia He, Hv, Sc, Le, Si — to merge into 5 pairs of lateral platelets. A first step in the reduction of glandularia is found in *A. vietsi*, in which glandularia Pe are reduced.

Usually, the number of dorsal and lateral plates is the same in deutonymphs and adults of a species, but in *A. tuberculatus* deutonymphs bear 5 pairs of lateral plates, whereas 10 pairs are found in adults. Also, deutonymphs of *A. vietsi* have 5 pairs of lateral plates, but traces of a fusion line, indicating their origin from paired sclerites, are still appreciable; in adults, these plates are divided into two separate sclerites.

The degree of rapprochement of the medial margins of the anterior coxal groups varies between different species of the genus *Acherontacarus*. Usually,

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Figs 41-42. *Acherontacarus rutilans*, larva, idiosoma. 41 — dorsal side, 42 — ventral side.
in deutonymphs and adults, the anterior coxal groups are in touch along their medial margins, but do not fuse completely (A. rutilans, A. vietsi), whereas they are fused into a homogenous block in Acherontacarus dividus. The poreform organs (called 'Tuberkehn' by BADER, 1989) — deep roundish pits of uncertain homology and function arranged along the lateral margins of the dorsal shields — vary in number between species. Usually, one pair is placed on the posterolateral corners of the frontal shield; in the posterodorsal shield of A. tuberculatus, 17-19 pairs are found in deutonymphs and 23-28 in adults (BADER 1989); in A. rutilans, both deutonymphs and adult males bear 6-7 of large and 3-5 pairs of fine poreform organs; in A. vietsi, the deutonymphs bear 6-7, and the adults 6-9 pairs. In some other species, such as undescribed species from Greece, no poreform organs are found at all. Thus, the presence of poreform organs is not a common character of all Acherontacarinae. If they are present, they are found in characteristic numbers in different species. A SEM examination of their structure did not produce any
evidence for the presence of hypothesised openings (glandularia, slit organs?) at their bottom.

**DISCUSSION**

4.1 Morphology

During the postembryonic development, all morphological elements of the water mite body undergo deep changes, but the degree of transformations at the transition from larva to deutonymphs, and from deutonymphs to adults, differs considerably between several clades.

The quantitative structure of the body chaetom is identical in *Hydrovolzia* and *Acherontacarus*: larvae 2-2-2-2-4-4-4-2-2-2; deutonymphs and adults 2-2-2-4-6-4-4-2-4-0 — the number of setae is increased by one pair in segments IV, V and XI, but reduced by 1 pair of anal setae. As always in water mites, the larvae are devoid of glandularia. In the deutonymphal stage of *Hydrovolzia* and *Acherontacarus*, glandularia occur only at setae Fch, Vi, He, Hv, Sce, Li, Si, Se, Pe, while trichobothria Fp, Oi, as well as setae Ci and Pi, are without glandularia. In *Hydrovolzia*, the occurrence of additional glandularia is observed at setae Pi and Ci, whereas in *Acherontacarus*, as is normal for water mites, the transformation from deutonymphs to adults is not accompanied by changes of numbers of glandularia. Among Acherontacarininae, a general tendency of reduction of glandularia has been described above, but the number of body setae remains constant during postlarval development, and no species differences are found in this regard.

Apart from coxal plates, two sclerified plates are found on the idiosoma of larval Hydrovolzioidea: a dorsal shield and the anal plate. In this regard, the sclerotization of both deutonymphs and adults differs radically from larvae. In deutonymphs of *Hydrovolzia*, there are usually 3 large unpaired central shields, and 3 or 4 pairs of lateral plates of different
sizes, without setae or glandularia; on the ventral surface, a rather large posterior shield and a small genital sclerite are found, again lacking setae and glandularia. Sclerotization is more extensive in adult Hydrovolzia, occupying large parts of the body surface. Medial and posterior dorsal shields are extended; the narrow lateral platelets are frequently united, forming 1 or 2 pair of lateral plates; on the ventral surface, an additional postanal shield, and sometimes a large praegenital plate are found, the latter resulting from the fusion of the sclerites bearing setae Pe.

Obviously, the degree of changes in the integumental sclerotisation during the course of postembryonic development of Acherontacarus differs slightly from Hydrovolzia: the dorsal idiosoma of deutonymphs bears two unpaired shields and 10 pairs of lateral plates, alternately bearing setae and glandularia He, Hv, Sce, Li, Sl. No seta — or glandularia-free lateral plates are found. On the ventral surface, there are always two large shields (anal and postanal) and a pair of lateral plates bearing setae Pi and Ci. In the degree of dorsal sclerotization of Acherontacarus there is no profound difference between deutonymphs and adults; the most important distinctions concern the ventral idiosoma: all ventral plates change in size and shape and cover the whole space between the coxae and posterior end of the body in adults.

In all known larvae of Hydrovolzia, osmoregulatory organs (acetabula = urstigmata) are numerous (11-18 pairs) and placed at the anterior edge of coxae II. Similar structures are found in larvae of Acherontacarus in still higher numbers, distributed all over the lateral surface of coxae I-III (Gerecke & Benfatti 1999). In the multiplication of their acetabula, larvae of both Hydrovolzia and Acherontacarus differ from all remaining groups of Hydrachnidia, which normally bear only one, or at most two pairs of these organs. But, with regard to the (probably plesiomorphic) arrangement of acetabula at the anterior edge of coxae II, Hydrovolzia agrees with the ground plan of all other clades of Hydrachnidia. The case of Acherontacarus, where these organs are arranged in the same manner as in deutonymphs and adults, is unique within water mites, possibly an effect of developmental 'adul-tation' (Benfatti & Gerecke 1999).

In deutonymphs of Hydrovolzioidea, no traces are found of the elements typical of the genital field of water mites (flaps, plate, acetabulae, setae). On all coxae we find numerous organs which, due to their general shape and regular arrangement, can be clearly identified with the acetabula observed in the same areas in adults of Hydrovolzia (Alberti & Bader 1990) and Acherontacarus (Gerecke & Benfatti 1999). The so-called 'genital' acetabula are known to be derivatives of ventral appendages belonging to the genital segments (VIII, IX, and X); in the ground plan of mites, they are found in 3 pairs, surrounding the genital field. Physiological and ultrastructural research (Bartsch 1974e; Alberti 1977, 1979) has demonstrated their osmoregulatory function. A substantially increased number of acetabula in the final stages of ontogenesis (deutonymphs and adult), is observed as a frequent convergent tendency in nearly all families of water mites, allowing for a substantial increase of osmoregulatory surface.

The counterpart to the situation in Acherontacarus is observed in deutonymphs and adults of Pontarachnidae. Here, they are also absent from the genital region, but are found at the same site as the larval organs (urstigmata' or pectoral sticks — see Tuzovskij, 1977d, 1987) at the anterior edge of coxae II. Thus, in this case, the larval idiosomal topography has been retained by the postlarval stages. In our opinion, a single name should be used for these structures in all developmental stages: we propose to call them generally 'acetabula' — the suffix 'genital' acetabula is nonsense, at least in those taxa where these organs are arranged away from the genital area (see also Goldschmidt et al., 1999). The term 'urstigma' does not make any sense in view of our present knowledge about the function of these structures.

Adults of Hydrovolzioidea have mobile flaps which are usually short and broad in males, but long and narrow in females. These flaps bear a few setae, with males usually having 1-2 more than females.

On the idiosoma surface of larvae of Hydrovolzia and Acherontacarus there are 5 pairs of slit organs, the typical number for all larvae of water mites (Tuzovskij 1984, 1987). The low number of only 3 pairs in larvae of Hydrovolzia gerhardi (as published by Wainstein 1980) probably is due to incorrect observation rather than a real morphological difference. As in the majority of Hydrachnidia, the num-

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number of slit organs in Hydrovolzia is constant through all free ontogenetic stages, whereas Acherontacarus lacks them completely in the deutonymphal and adult stages. The same developmental change is observed in Eyalis and Limnocharis in which slit organs are again found only in the larvae (Tuzovskii, 1984, 1987).

The shape of the hypostomal plate is different in larvae of Hydrovolzia and Acherontacarus. In Hydrovolzia it is enlarged and bears a small mouth cavity in terminal position, whereas in Acherontacarus it is elongate, with a large mouth cavity, opening ventrally and surrounded by a ring of sucker-like vesicles. In both genera, the basal segment of the larval chelicera is strongly thickened proximally, and abruptly narrowed proximally from the claw insertion.

In deutonymphs and adults of Hydrovolzia and Acherontacarus, the gnathosoma is similar in shape. In dorsal view, it has a rather large basal part and is abruptly narrowed into an elongated rostrum at the level of the pedipalp insertions. The chelicerae of these stages have long basal segments with nearly parallel dorsal and ventral margins, and short, strong claws.

Pedipalps of larvae of Hydrovolzia and Acherontacarus consist of 4 segments, but differ in the shape of segments 2-4; the number of setae is identical on segments 1-3, while the terminal segment bears 8 setae in Hydrovolzia, but 11 in Acherontacarus. Pedipalps of deutonymphs and adults are 5-segmented and more similar. However, deutonymphs and adults of Hydrovolzia have a long pedipalp tarsus with short distal setae, while this segment in Acherontacarus, on the contrary, is short, with long setae. Regarding the pedipalp, in both genera the transition from deutonymphs to adults is accompanied by an increase in the size and number of setae only.

The most impressive differences between larvae of Hydrovolzia and Acherontacarus are observed in leg morphology. The legs of Hydrovolzia larvae have all tactile setae homeomorphic; their tarsi are strongly narrowed distally and lack a claw furrow, and their claws are simple and smooth. Those of Acherontacarus larvae, on the other hand, are armed with heteromorphical tactile setae; their tarsi are continuously thickened distally and have a well developed claw furrow, and their ambulacrae are divided into 2 branches, with the dorsal one bearing a row of ventral denticles similar to those found in Stygothrombium. Thus, during ontogenesis in Hydrovolzia, all leg tarsi change profoundly from the distally narrowed larval shape to the condition typical for adults, with distally diverging dorsal and ventral margins, a claw furrow, and tactile leg setae becoming heteromorphic. On the contrary, in Acherontacarus the general structure of legs does not change at all during ontogenesis — there is only an increase in the size and number of setae. From their general structure (shape and setation of segments), the larval legs of Hydrovolzia are rather similar to mite larvae that conduct a terrestrial life (Hydryphantoidea, Limnochariidae, Piersigidae, Eylaidae), whereas the larval legs of Acherontacarus resemble those of larvae adapted to longer stays in submerged environments (Hydrachnoidea, Hygroboidea).

4.2 Biology

Our observations on larval morphology agree with the available data on microhabitat preference and parasitism in both genera. Larvae of Acherontacarus are generally found in large numbers in samples taken from submerged sediments, and all available data on parasitism refer to hosts that pass large parts of their life submerged (exclusively aquatic beetles, including wingless species of the genus Deronectes, Gerecke & Benfatti 1999). Furthermore, unlike most other water mite larvae parasitic on Coleoptera, they were never found in the subelytral air chamber, but always attached to body parts of the host which are completely exposed to the water (ventral thorax, leg segments, dorsal surface of elytra). Within aquatic mites, this type of attachment site selection was so far only known from the superfamily Hydrachnoidea, where we also encounter similarities concerning the larval mouth apparatus. As to Hydrovolzia, the fact that most records of the larval stage refer to specimens detached from host insects indicates that the phase of submerged larval life is relatively short in this genus. From the host range (ripicolous Diptera, Coleoptera and Heteroptera with a predominantly terrestrial way of life) we can deduce that Hydrovolzia is much more adapted to terrestrial life during the larval stage than Acherontacarus.
4.3 Geographical distribution

Records of Hydrovolzioidea are scattered over large parts of the northern hemisphere, but are still patchy outside Europe, with many taxa known from only a single locality. For the better studied European fauna, we can give a preliminary zoogeographical interpretation. It is remarkable that *Hydrovolzia* is represented by only two species, both with very extended distribution areas, while in *Acherontacarus* a higher number of species is known, each of them with a more restricted distribution. This difference could be explained by the above mentioned characteristics of host preference. One could admit that the less specialised host selection of *Hydrovolzia* allows for a much more extended range of areas that can be reached by phoresy, while *Acherontacarus* has lower colonisation possibilities due to its preference for less motile hosts. It would be very interesting to check this hypothesis, as well as possible parasite-induced effects on the hosts, in a co-operative investigation on the coevolution between water mites and insects.

4.4 The taxonomic rank of the main groups in Hydrovolzioidea

From our review of the morphology of larvae, deutonymphs and adults, as well as from the peculiarities in postembryonic development and biology of *Acherontacarus* and *Hydrovolzia*, the results provide striking evidence that these two taxa — at first view so similar in the adult stage — represent two groups of mites that have separated very early in the course of phylogeny. In the larval stage, the differences found between these two genera even surpass the level of differences we are accustomed to seeing, for example, between families of Hydryphantoidea, Hygrobatoiidea and other groups of water mites. The former subfamily Acherontacarinae should therefore be elevated to family rank. At this point, an extended and corrected diagnosis of the superfamily Hydrovolzioidea sensu Cook 1974, and of the two families Hydrovolziidae and Acherontacaridae, becomes necessary.

**SUPERFAMILY HYDROVOLZIOIDEA**

**ADULTS:** Idiosoma flattened, normally not more than 1000 μm in length; colour red, orange or yellow or colourless; dorsum with 2 unpaired central shields: a short and broad anterior shield with 4 setae, and a long posterior one, with 4 pairs of setae; integument surrounding the central shields with 2-11 pairs of small platelets; body chaetom formula: 2-2-4-4-6-4-4-2-4-0; idiosoma setae and glandularia placed on separate sclerites or plates, trichobothria Fp, Oi, and also setae Oe, Hi, Sc, Li, lacking glandularia, secondary reduction of further glandularia and idiosoma setae possible; gonopore flanked by movable flaps; no acetabula in the genital field, but analogous organs arranged on lateral and caudal surfaces of all coxae; lateral margins of all coxae, but especially of coxae IV, extending over the level of the lateral idiosoma margin; genital field and excretory pore sclerite arranged close to each other in the interspace between the posterior margin of coxal plate I + II and the medial margin of coxal plate III + IV; sclerotization of the ventral idiosoma surface strongly variable, ranging from 4-8 plates to the formation of a continuous ventral shield that also includes the coxae; slit organs present in 5 pairs or lacking; pedipalps 5-segmented, not chelate; gnathosoma with well-developed rostrum; chelicerae not fused, consisting of a large basal segment and a short, crescent-shaped claw; legs without swimming hairs, IV-L sometimes with sexual dimorphism.

**DEUTONYMPH:** similar to adults; differences are found in generally smaller size, lack of an external genital organ, smaller degree of idiosoma sclerotisation, and setae Fp, Oi, Oe, Hi, Sc, Li, Ci, Pi lacking accompanying glandularia.

**LARVA:** Idiosoma with a more or less extended dorsal shield bearing 1-2 pairs of setae; body chaetom formula: 2-2-2-2-4-4-4-2-2-2; trichobothria simple or clavate; all coxae separate or coxae I + II fused to form a single coxal plate; number of coxal setae: 2-1-1; more than 5 pairs of acetabula, either arranged in a line along the anterior edges of coxae II, or incorporated into the lateral sclerotization of
all coxae; 5 pairs of slit organs; pedipalps with 4 free segments (tibia and tarsus fused).

**Family Hydrovolziidae Thor, 1905**

**Adults:** Dorsum with 1 or 2 pairs of narrow, longish plates arranged laterally from the central shields; setae Fp, Oi, Oe, Hi, Sci, Li without accompanying glandularia; 5 pairs of slit organs present, i3 and i4 placed on the pair of (sometimes fused) narrow plates flanking the posterodorsal shield; no poreform pits on lateral margins of dorsal shields; coxae arranged in 4 groups, suture line between coxae I and II usually well developed; sclerotization of ventral surface incomplete, with well developed stripes of soft integument between coxal plates, and surrounding genital field and other plates and shields; distal segments of male IV-L with or without secondary sexual differences.

**Deutonymphs:** Similar to adults; generally differing in smaller size, absence of genital field, reduced number of setae on pedipalps and legs, and of glandularia (setae Ci, Pi lacking glandularia); dorsum with three unpaired central shields, anterior, medial, and posterior shield, bearing 4, 3, 0 setae respectively; all lateral plates lacking setae and glandularia; ventrally, in general only the postanal shield well developed.

**Larva:** Dorsal shield reduced in size, not covering more than 50% of the idiosoma surface; setae Oi enlarged, clavate; eye capsules free, not fused with any of the surrounding sclerites; all coxae separate; numerous acetabula arranged in a line at the anterior margin of coxae II; pedipalp tarsus bearing 4 large setae; legs with homeomorphic tactile setae, tarsi distally narrowed and without claw furrow; empodium and ambulacrae large and smooth, not bifurcate distally.


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**Family Acherontacaridae**

**Adults:** dorsum with two central shields surrounded by 5 or 10 pairs of platelets (not counting an additional small, unpaired plate sometimes present at the posterior end of the idiosoma), alternately bearing setae and accompanying glandularia; setae Fp, Oi, Oe, Hi, Sci, Li, Ci, Pi always without glandularia — further glandularia can be secondarily reduced in some species; no slit organs visible; dorsocentral shields frequently with poreform pits arranged at their margins in species-specific numbers; coxae in 4 groups, closely approached to each other, and forming, together with the lateral plates, genital sclerites, anal, and postanal plates, a continuous shield covering the whole ventral idiosoma surface; suture line separating coxae I + II visible only in its lateral part; distal segments of male IV-L with secondary sexual differences.

**Deutonymph:** similar to adults, but generally smaller in size, without genital field, with fewer setae on pedipalps and legs; ventral idiosoma not completely covered by sclerotisation, anterior and posterior coxal groups and plates of the posterior ventrum separated by large interspaces of membranous integument; anal plate minute, round, postanal plate large, setae Ci and Pi on small round sclerites free in the membranous integument.

**Larva:** dorsal shield large, covering more than 50% of the idiosoma; eye capsules fused with the sclerites bearing setae Vi and Oi; both pairs of trichobothria hair-shaped as usual; coxae I + II fused to form a single coxal plate, separated from coxae III by membranous integument; acetabula rather numerous, imbedded in the lateral margins of all coxae; pedipalp tarsus with normally-shaped setae various in length; all legs with heteromorphic tactile setae; tarsi of all legs equally thickened from the base to the tip, with a claw furrow; empodium smooth, ambulacrae distally bifurcated, dorsal branch bearing a row of strong ventral denticles.

**Included taxa:** Acherontacarus K.Viets, 1932 (syn.: Acherontacarellus Lundblad, 1962, Acheronta-

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