



Two new sympatric water-mites (Acari: Hydrachnidia: Unionicolidae) from the mutelid bivalve *Aspatharia sinuata* (von Martens) in Nigeria with some data on unionicoline–bivalve relationships

TERENCE GLEDHILL† and MALCOLM F. VIDRINE‡

† *Freshwater Biological Association, Ambleside, Cumbria LA22 0LP, UK*

‡ *Louisiana State University at Eunice, Eunice, LA 70535, USA;*

e-mail: mvidrine@lsue.edu

(Accepted 22 January 2001)

Descriptions and figures of two new sympatric species of water-mites, *Unionicola blayi* and *U. planicurvata*, belonging to a new unionicoline subgenus, *Mutelicola*, found in the mutelid bivalve *Aspatharia sinuata* (von Martens, 1883) in Nigeria are presented. These are the first records of unionicoline ‘parasites’ of bivalves from Africa and the first records of unionicolines from mutelid mussels. Their occurrence in these freshwater bivalves is discussed and some data on unionicoline–bivalve relationships are also presented.

KEYWORDS: Acari, Unionicolidae, *Unionicola*, new subgenus, *Mutelicola*, new species, hosts, biogeography, Bivalvia, Muteloidea, *Aspatharia sinuata*, associations, Nigeria.

Introduction

Some water-mites, namely those from the monobasic genus *Najadicola* Piersig, 1897 (Pionidae: Najadicolinae) and polybasic genus *Unionicola* Haldeman, 1842 (Unionicolidae: Unionicolinae) are ‘parasites’ of molluscs and/or freshwater sponges during one or more stages of their life history. The majority are associated with freshwater bivalves (Unionoida) but a few are known from freshwater gastropods (Gledhill, 1985). Within the subfamily Najadicolinae Viets, 1935, transferred to the Pionidae from the Unionicolidae Oudemans, 1909 by Simmons and Smith (1984), a single species, *Najadicola ingens* (Koenike, 1895), is currently recognized and recorded from North America and South-East Asia. However, Vidrine (1996a) opined that a study of *Najadicola* from various molluscan hosts from both continents would probably reveal several species complexes. In contrast, the subfamily Unionicolinae Oudemans, 1909 (*sensu* Vidrine) now considered to consist of only one genus, *Unionicola*, with some 50 subgenera and more than 200 species is, with the exception of Antarctica, cosmopolitan in distribution.

Larvae of species in both subfamilies are now known to follow the general

pattern in the water-mites and parasitize insects, mainly chironomids—non-biting midges (Jones, 1965, 1978; Hevers, 1978, 1980; Simmons and Smith, 1984; Gledhill, 1985). Resting stages (protonymphs and tritonymphs) and the other active stages (deutonymphs and adults) are 'parasites' of freshwater sponges (Porifera: Spongillidae), the prosobranch gastropod families Viviparidae (North America and Eurasia) and Pilidae (Africa and Central and South America), but mostly freshwater bivalves (Unionoidea and Muteloidea) (North and South America, Europe, Africa, Asia and Australasia) (Vidrine, 1996a). Vidrine (1996a) presented a list of higher taxa of freshwater mussels down to genus level (classification after Bogan, 1993) and also a list of reported host mussels for *Unionicola* and *Najadicola* species of water-mites. Two mussel genera, *Elliptoideus* and *Villosa*, mentioned as hosts in the latter list, were accidentally omitted from the list of bivalve genera. No genera in the families Margaritiferidae, Mutelidae and Etheriidae (but see below) are listed by Vidrine (1996a) as being 'parasitized' by *Unionicola* or *Najadicola* species. In contrast, Vidrine (1996a) lists 57 (74%) of the 77 genera in the Unionidae; nine (69%) of the 13 genera in the Hyriidae and four (40%) of the 10 genera of the Mycetopodidae as hosts.

This paper presents descriptions and figures of the first recorded unionicoline water-mites from a mutelid host mussel. Two new sympatric species of *Unionicola*, belonging to a new subgenus and found in the mutelid bivalve *Aspatharia sinuata* (von Martens, 1883) from Nigeria, are described. Some data on their occurrence in these freshwater mussels are also presented together with some data on unionicoline-bivalve relationships.

Throughout this work, the term 'parasite' is used loosely because in only one species, *U. (Anodontinax) intermedia* (Koenike, 1882), has it been demonstrated that unionicoline mites feed upon molluscan tissues (Baker, 1977). Similarly the term 'host' is used for those molluscs (gastropods and bivalves) '...that provide(s) food or shelter for another organism' (see Lincoln *et al.*, 1982).

Bivalve classification

Whilst problems in classification of the Bivalvia still remain at subclass and ordinal level, there is some degree of consensus on groupings at superfamily level (Prezant in Morton *et al.*, 1998). Within the Order Unionoidea, two superfamilies are recognized, the Unionoidea and Muteloidea; Bogan (1993), however, recognizes the Unionoidea and Etherioidea. The Unionoidea comprises three families, the Unionidae, Hyriidae and Margaritiferidae *sensu* Vaught (1989), Bogan (1993) and Bonetto (1997) or four families by the inclusion of the Amblemidae *sensu* Prezant, p. 296 in Morton *et al.* (1998). The Muteloidea comprises three families, the Mutelidae, Mycetopodidae and Etheriidae (Vaught, 1989; Bogan, 1993 [under superfamily Etherioidea]; Prezant in Morton *et al.*, 1998) whilst Bonetto (1997) reduces the Etheriidae to subfamily rank to leave only the Mutelidae and Mycetopodidae. In this paper, the classification of Vaught (1989) is followed.

It should be noted that the use of the taxonomic category Suborder for Unionoidea and Etherioidea by Vidrine (1996a: 7 and 9, respectively) is a *lapsus* and should read Superfamily.

Unionicoline systematics

Of the 51 unionicoline subgenera, the nominate subgenus is the least derived (the most plesiomorphic) sharing the largest number of ancestral characters with

other members of the family. Other unionicoline subgenera are adjudged to be divergent from *Unionicola* s. str. in one or more characters that are considered as diagnostic subgeneric criteria (Vidrine, 1996a). Vidrine (1996a) presents 20 groupings of subgenera based on general morphology with nine subgenera occurring in one other additional group. These groups reflect the relative numbers of synapomorphies (shared derived homologous characters) and suggest membership of a single clade (a monophyletic group). Furthermore, when the synapomorphies of the bivalve-associated unionicoline and gastropod-associated unionicoline subgenera were examined separately from the free-living and sponge-associated mite subgenera, many subgenera could be grouped into four hypothetical clades and, with additional synapomorphies, into two clades. These two clades include the unionicoline 'parasites' of molluscs, both bivalve and gastropod, suggesting that these groups are derived from a single invasion by ancient unionicolid stock into molluscs, followed by extraordinary evolutionary radiation (Vidrine, 1996a). Nevertheless, further studies on the zoogeography and host associations of unionicoline mites are required in order to ascertain whether these mites are the result of single or multiple invasions (of molluscs) with concomitant diversification.

The host—*Aspatharia sinuata* (von Martens)

The family Mutelidae has a distribution covering South America, Africa and Australia with most genera and species in South America (Mandahl-Barth, 1988). Bonetto (1997), however, restricts the Mutelidae to Africa and India with only the subfamilies Mutelinae and Etheriinae occurring in Africa. Three genera, *Aspatharia* Bourguignat, 1885, *Spathopsis* Simpson, 1900 and *Mutela* Scopoli, 1777, are known from Africa. *Aspatharia sinuata* was originally described in the genus *Spatha* Lea, 1838, a genus now placed under *Mutela* (Vaught, 1989). Mandahl-Barth (1988) suggests that *A. sinuata* may be conspecific with *A. pfeifferiana* (Bernardi, 1860). However, a study on shell morphometrics, length-weight relationships and length distributions of some lotic and lentic populations of *A. sinuata* in Nigeria by Blay (1989), showed that whilst some differences occurred in the length-weight relationships and size distributions, the relative stability of the shell dimension ratios suggests that the populations examined belong to a common taxonomic unit, *A. sinuata* as proposed by Pilsbry and Bequaert (1927).

The two *Unionicola* species described below were found in samples of *A. sinuata* collected from Asa Reservoir (Ilorin, Nigeria) by Prof. John Blay. Mites were found in mussels collected between January 1983 and December 1984 and showed a monthly frequency of 90–100%. The number of mites per mussel (4.6–8.2 cm shell length) ranged from 11 to 184 ($y = 40.7x - 177.9$ where y = number of mites and x = shell length; $r = 0.92$; $n = 51$). Both species occurred sympatrically within the host mussel and most specimens were found on the ctenidia (gills), some on the inner side of the mantle lobes and a few in the region of the visceral mass (J. Blay, personal communication). Nevertheless, it is not known whether the two species are spatially separated within the host.

Taxonomic section

Preparation numbers refer to microscope preparations in the collection curated by T. Gledhill. The abbreviations used are: P.I–V, pedipalp segments 1–5 (trochanter, femur, genu, tibia and tarsus) i.e. P.III = genu; I-Leg.1–6, first leg, segments 1–6 (trochanter, basifemur, telofemur, genu, tibia and tarsus) i.e. III-Leg. 4 = genu of

third leg; Ep., epimera (pl.), epimeron (sing.); Ep.1-4, epimera 1-4, i.e. Ep.3 = third epimera.

Family UNIONICOLIDAE Oudemans, 1909
Subfamily UNIONICOLINAE Oudemans, 1909
Genus *Unionicola* Haldeman, 1842
Subgenus *Mutelicola* new subgenus

Diagnosis. With the characters of the genus. Idiosoma length 500-1000. General body form similar to species of the subgenera *Australatax* Vidrine, 1985, and *Unionicolides* Lundblad, 1937. Dorsal shield, which may be indistinct or absent in females of some species, and epimera resemble those found in Australian species of *Australatax*. Female genital field with four (two each side) acetabula-bearing plates resembling those displayed by females in *Australatax*. However, six or more pairs of acetabula are present in *Mutelicola* and only five pairs in *Australatax*. Male genital field with four (two each side) heavily sclerotized acetabula-bearing plates, five or more pairs of prominent acetabula and with a more-or-less central pair of somewhat thickened, elongate setae on each side of the gonopore. These setae, which may be separate or arise from a common base, are similar to, but different from, those of males in *Crowellatax* from New Zealand, the only other subgenus in which males have thickened setae in the central region of the genital field. However, *Crowellatax* has only two acetabula plates and five pairs of acetabula and the setae are positioned anterior to the centre of the genital field. Additionally, the acetabular plates and acetabula of *Crowellatax*, unlike those of *Mutelicola*, are only lightly sclerotized and the subgenus, with only one known species, is recorded from sponges. Male and female legs similar. Enlarged, curved distal setae present or absent on IV-Leg segments. All legs with a pair of elongate, somewhat flattened setae extending dorsally and distally over the claws. These setae resemble those found in species of the subgenera *Australatax*, *Unionicolides* and *Atacella* Lundblad, 1937.

The uniqueness of the male genital field is sufficient in the current taxonomy of *Unionicola* s. l. to warrant separation from existing subgenera. Other characters, taken as a group, serve not only to isolate *Mutelicola* morphologically, but also link it to existing subgeneric groups. Palp and leg morphology clearly ally *Mutelicola* with *Australatax* and *Unionicolides* and their cluster of subgenera including *Kovietsatax*, *Unionicolella*, *Atacella* and *Berezatax* (Vidrine, 1996a). For example, the somewhat flattened setae extending dorsally and distally over the claws are common to all these subgenera. An obvious difference where palps are used to distinguish subgenera within this group occurs in *Atacella* and *Berezatax*; both possess obviously dorsoventrally-flattened palps. Species with reduced chaetotaxy on palps and legs (presumably derived conditions) can be found in *Berezatax*, *Unionicolella*, *Unionicolides*, *Atacella* and *Australatax*, demonstrating obvious divergences within this group not yet found in *Mutelicola*. *Australatax*, *Kovietsatax* and some *Atacella* have elongated projections on the inner edges of the female genital plates; these are likewise apparent in *Mutelicola* which also has the greater number of genital acetabula; the most any of the close subgenera possess is six pairs. The enigmatic South American subgenus *Polyatacides*, also included in this group, has 10 pairs of acetabula but the male has only two genital plates and no obvious setae, the palps also have distinctly block-like segments. *Mutelicola* obviously extends the host range and geographic range of mussel-associating unionicoline mites. Thus the

morphology and chaetotaxy of the palps, legs and genital field, the morphology of the epimera, acetabula number, host range and geographic range, clearly distinguish *Mutelicola* from all other unionicoline subgenera.

Type species. *Unionicola (Mutelicola) blayi* new species.

Etymology. The subgenus name is formed from the mutelid bivalve family name Mutelidae and the suffix *cola* used adjectivally and meaning 'dwelling in'.

Descriptions of the new species

In the following descriptions, measurements of the holotypes and allotypes are given first followed in parentheses by the range, mean and *n*, where *n* is the number of measurements made and not always the number of specimens examined, i.e. when possible, measurements from both left and right palp and leg segments were always made. All measurements are given in μm and lengths of appendage segments are dorsal lengths.

Unionicola (Mutelicola) blayi new species (figures 1–5)

Description of male (figures 1a–f, 2a–l, 3a–d). With the characters of the genus and subgenus. Body elongate and without a cauda; length excluding gnathosoma 878 (634–878, 720, $n=5$), width 598 (512–610, 563, $n=5$). Dorsum (figure 1a) with a single dorsal shield, length 498 (324–498, 385, $n=5$). Ventrally with epimera in four groups occupying *ca* half ventral surface and with anterior groups well separated from posterior groups; anterior groups with prominent posterolaterally-directed apodemes; posterior groups with a well-defined lateral cleft between Ep.3 and 4 and with more-or-less straight posterior margins to Ep.4 (figure 1b)—in some specimens the posterior margins appear straighter and more at right angles to the long axis of the body; Ep.4 with pointed lateral extensions at point of IV-Leg insertions (figure 1b); total epimeral length 504 (354–504, 409, $n=5$); median length Ep.3 + 4, 258 (198–258, 215, $n=5$); median length Ep.4, 180 (132–180, 148, $n=5$); epimeral width at Ep.3, 420 (414–450, 433, $n=4$); epimeral width at Ep.4, 468 (414–486, 461, $n=4$). Infracapitulum small, length 168 (156–192, 174, $n=5$); chelicerae short and stout, basal portion reticulate, length 192 (168–192, 186, $n=5$), cheliceral claw length (dorsal i.e. short length) 39 (36–42, 39, $n=5$). Pedipalps as in figures 1d–f, 2a–i; P.II with a proximal spine-like seta on outer lateral face and a dorsodistal spine on inner lateral face; P.III with a long ventrodistal hair-like seta on outer lateral face and a shorter pectinate seta distally on inner lateral face; P.IV with two short hair-like setae on outer lateral face and a short ventrodistal projection bearing two fine setae. P.V ventrally concave and distally multitoothed (figures 1e, 2g, i). Lengths of pedipalp segments: P.I, 18 (15–18, 18, $n=9$); P.II, 123 (108–126, 119, $n=9$); P.III, 90 (78–90, 85, $n=9$); P.IV, 132 (108–132, 124, $n=10$); P.V, 84 (66–84, 78, $n=10$). Genital field at posterior end of body, terminal and almost dorsal (holotype, male, Prep. 1360, tilted to show genital field as depicted in figure 1b). Genital field (figures 1c, 2j, k, l) comprised of two pairs of genital plates; anterior plates each with two to five or more (generally three) acetabula; setae-bearing portion of anterior genital plates may be separate from acetabula-bearing portion (figure 2j); posterior plates larger than anterior plates and each with 9–14 acetabula; gonopore slit-like and flanked on each side by two adjacently-located long setae; genital field length 123 (123–144, 134, $n=4$), genital field width 153 (123–156, 145,

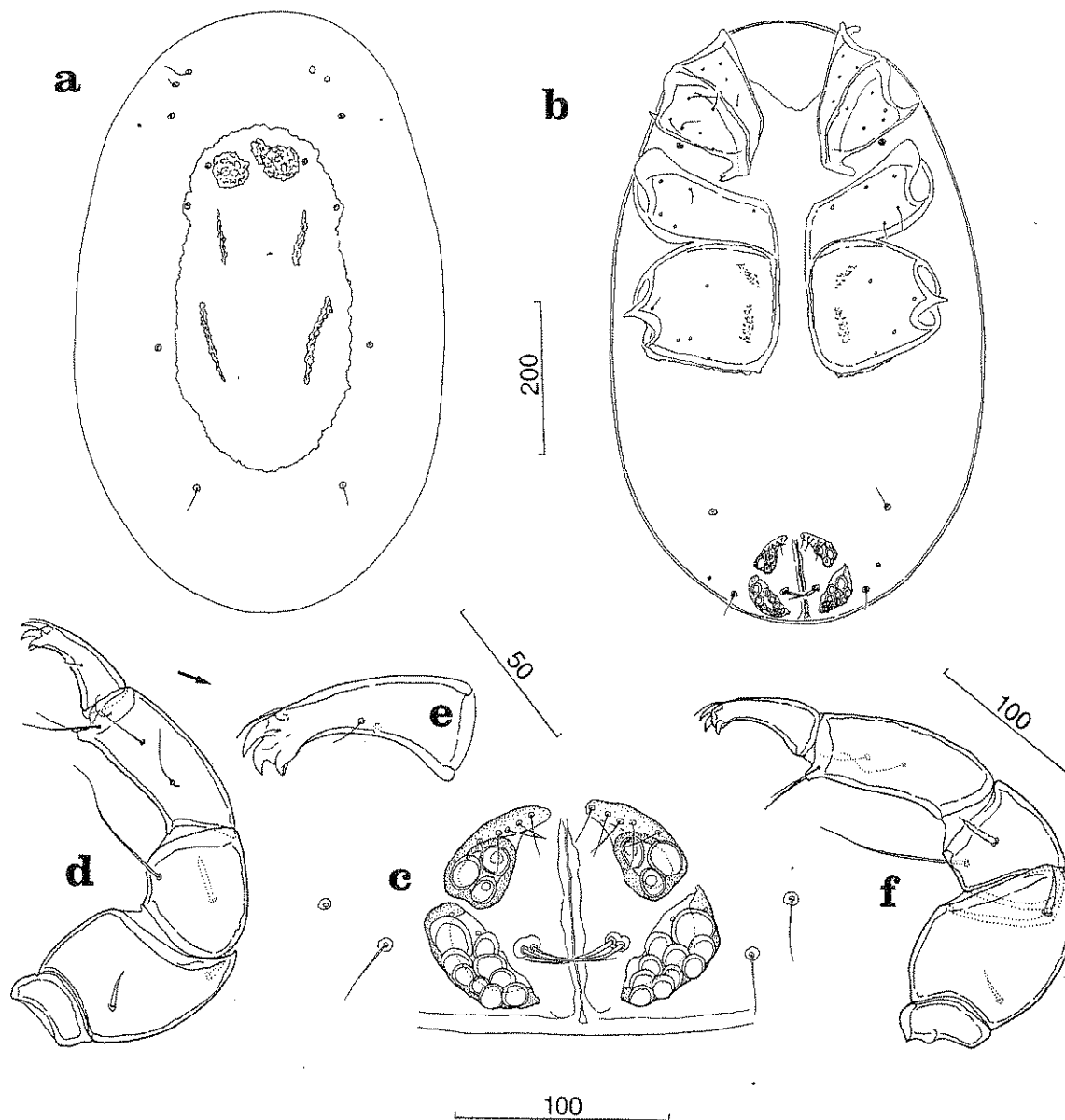


FIG. 1. - *Unionicola (Mutelicola) blayi*, male, Prep. 1360, holotype. (a) Dorsal surface; (b) ventral surface; (c) genital field; (d) left palp; (e) PV left; (f) right palp.

$n=5$). Excretory pore slit-like, free in posterior integument and dorsal to posterior genital sclerite. Morphology and chaetotaxy of legs as illustrated in figure 3a-d. I-Leg.4-5 (genu and tibia) more-or-less equal. Segment 5 (tibia) of all legs, particularly I-Leg.5, convex dorsally in lateral view, more obvious than shown in figure 3a-d. All legs, particularly III and IV, with numerous hair-like setae. Claws of all legs with two distal teeth, ventral tooth *ca* twice length of dorsal tooth and with a small pre-distal lateral accessory tooth. Lengths of leg segments: I-Leg.1-6: 66 (60-72, 67, $n=6$), 90 (72-96, 86, $n=9$), 132 (102-132, 124, $n=10$), 186 (150-192, 175, $n=10$), 186 (150-192, 174, $n=10$), 123 (90-126, 113, $n=10$); II-Leg.1-6:— (66, $n=1$), 105 (78-108, 100, $n=8$), 156 (120-156, 147, $n=9$), 210 (162-216, 200, $n=9$), 228 (174-228, 213, $n=9$), 162 (138-162, 149, $n=9$); III-Leg.1-6: 72 (66-72, 70, $n=3$), 108 (84-108, 99, $n=9$), 159 (120-162, 144, $n=9$), 213 (168-222, 201, $n=9$), 251 (180-252, 228, $n=9$), 186 (126-186, 165, $n=8$); IV-Leg.1-6: 120

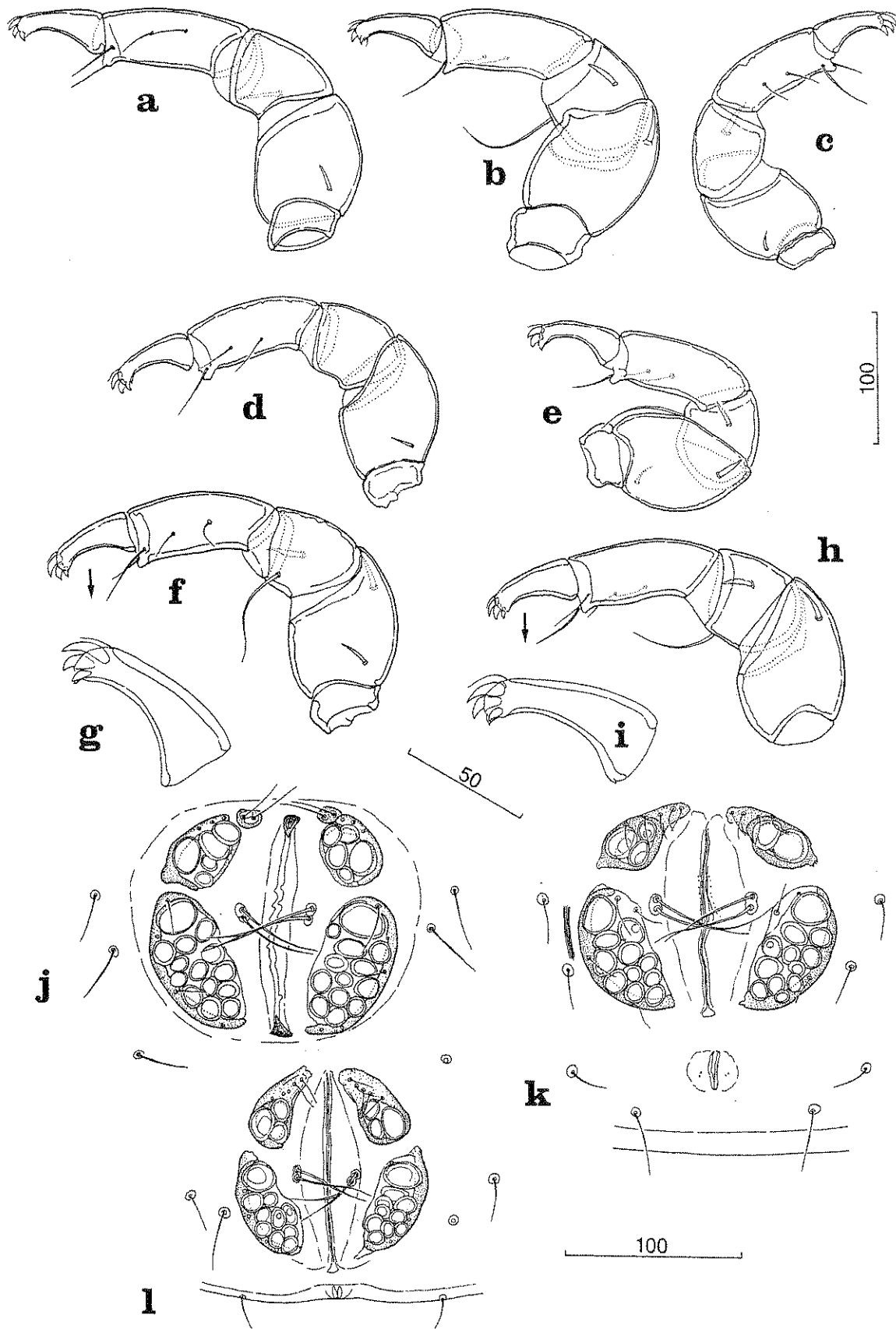


FIG. 2. *Unionicola (Mutelicola) blayi*. (a) Left palp, male, Prep. 1356; (b) right palp, male, Prep. 1356; (c) right palp, male, Prep. 1357; (d) left palp, male, Prep. 1359; (e) right palp, male, Prep. 1359; (f) left palp, male, Prep. 1358; (g) PV, left palp, male, Prep. 1358; (h) right palp, male, Prep. 1358; (i) PV, right palp, male, Prep. 1358; (j) genital field, male, Prep. 1356; (k) genital field, male, Prep. 1358; (l) genital field, male, Prep. 1357.

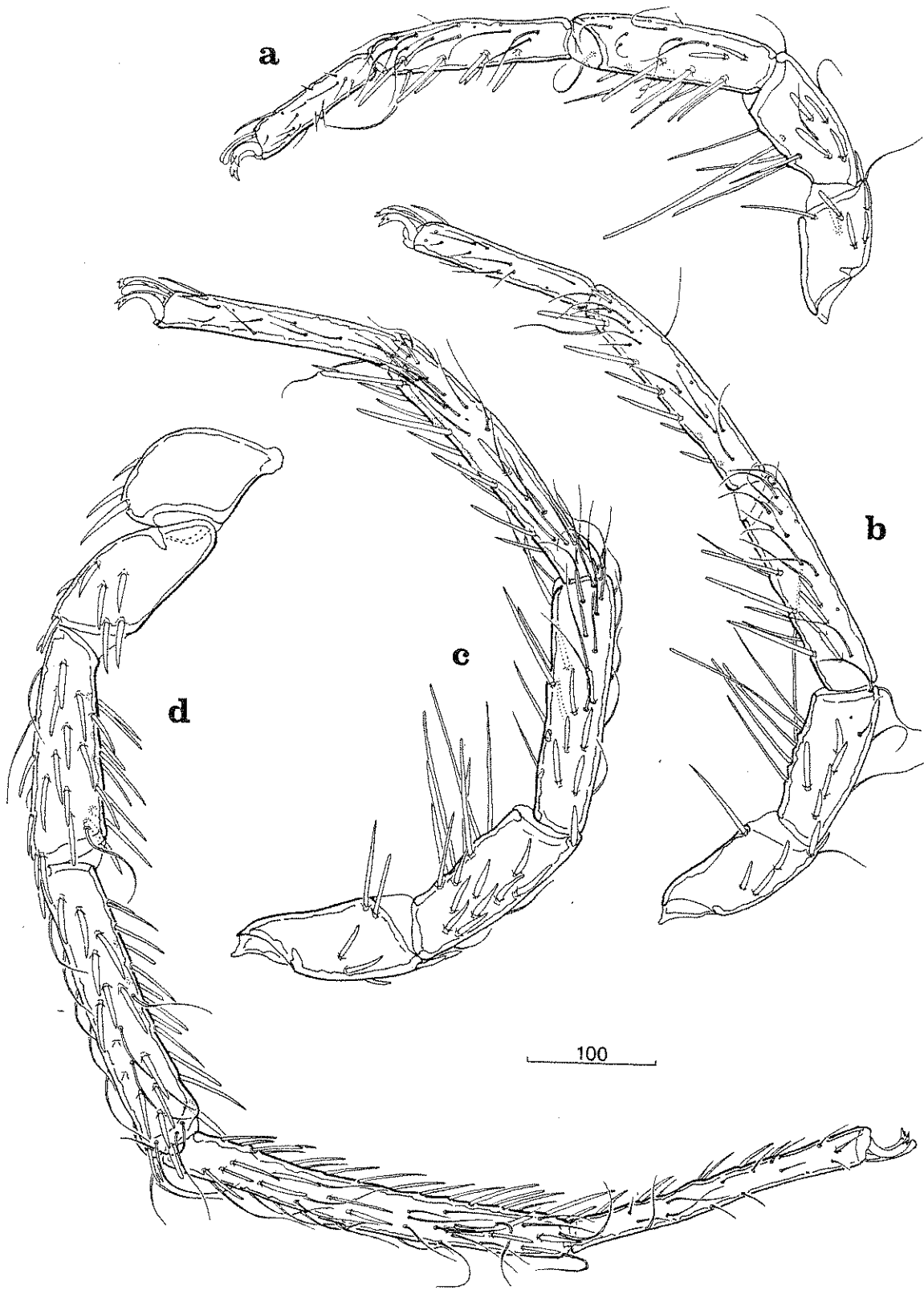


FIG. 3. *Unionicola* (*Mutelicola*) *blayi*, male, Prep. 1360, holotype. (a) I-Leg. 2-6; (b) II-Leg. 2-6; (c) III-Leg. 2-6; (d) IV-Leg. 1-6.

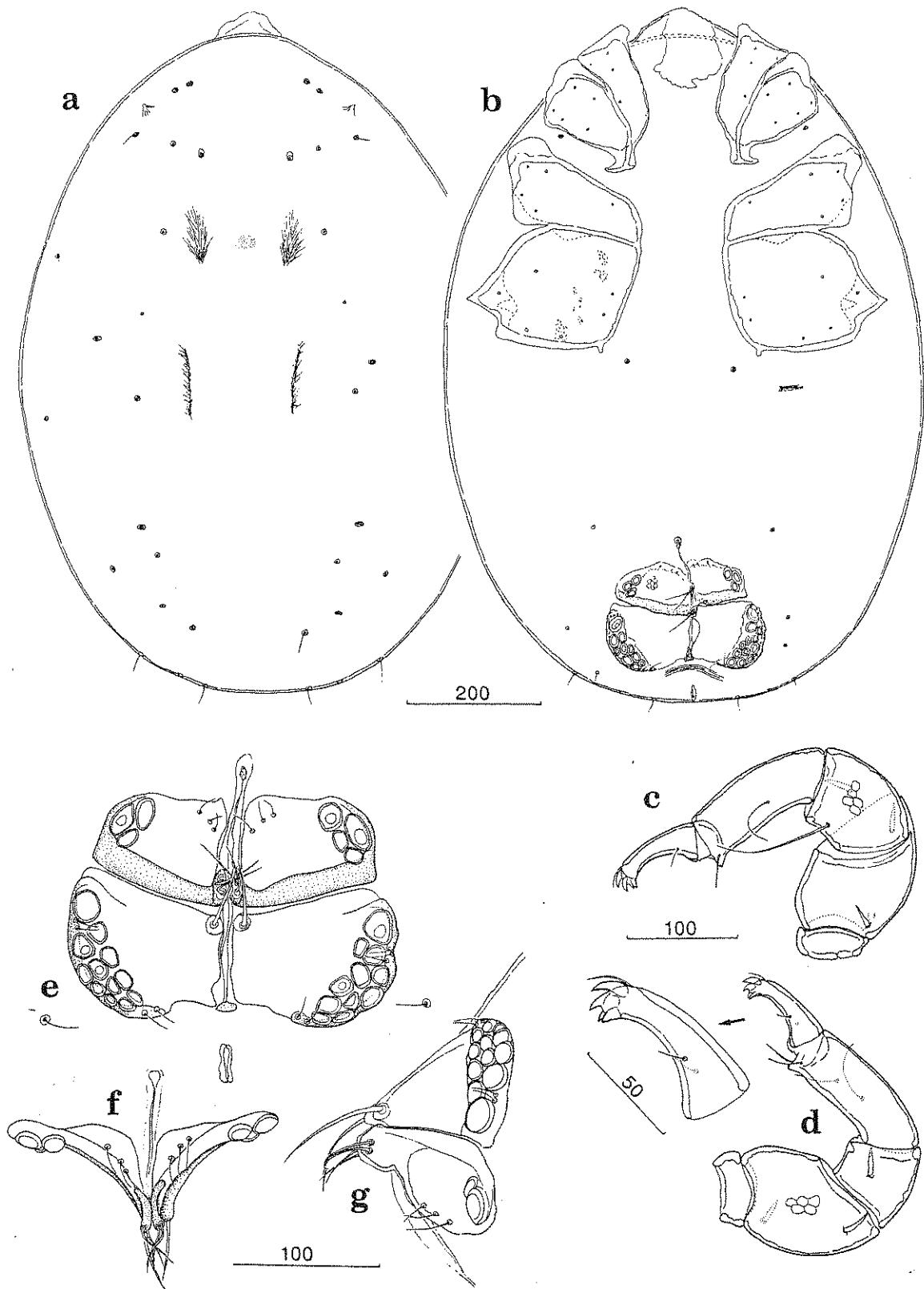


FIG. 4. *Unionicola (Mutelicola) blayi*. (a-d) female, Prep. 1361, allotype. (a) Dorsal surface; (b) ventral surface; (c) left palp; (d) right palp and PV; (e) genital field (tilted), female, Prep. 1375; (f, g) genital field female, Prep. 1375 in ventral and lateral views respectively and figured prior to final microscope preparation.

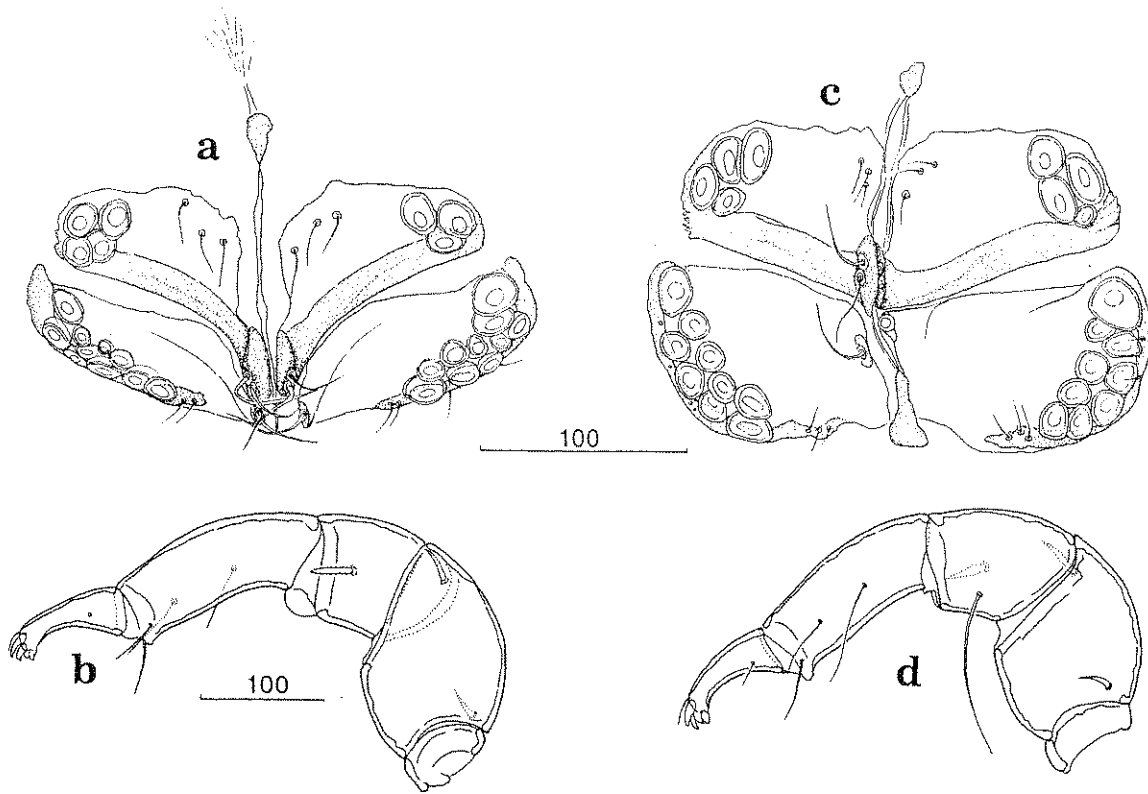


FIG. 5. *Unionicola (Mutelicola) blayi*. (a) Genital field, female, Prep. 1363; (b) right palp, female, Prep. 1363; (c) genital field (tilted), female, Prep. 1364; (d) left palp, female, Prep. 1364.

(114–138, 127, $n=4$), 114 (78–120, 105, $n=8$), 198 (150–198, 181, $n=8$), 258 (198–264, 238, $n=8$), 336 (252–342, 308, $n=7$), 252 (192–252, 228, $n=7$).

Female (figures 4a–g, 5a–d). Body rounder and larger than that of male; length, excluding gnathosoma, 1075 (1025–1171, 1110, $n=4$), width 756 (756–915, 845, $n=4$). Dorsum (figure 4a) without a dorsal shield but with two pairs of muscle attachment sites. Ventrally with epimera in four groups occupying *ca* half ventral surface (figure 4b), anterior groups well separated from each other and from posterior groups and with prominent posterolaterally-directed apodemes; lateral cleft between Ep.3 and 4 well defined; posterior margin of Ep.4 more-or-less straight as in male; Ep.4 with pointed lateral extensions at point of IV-Leg insertions; epimeral groups of each side further apart from each other than in male, this separation may be less in immature females; total epimeral length 522 (408–522, 484, $n=5$), median length Ep.3+4, 258 (240–258, 251, $n=4$), median length Ep.4, 186 (180–192, 186, $n=4$); epimeral width at Ep.3, 552 (486–634, 572, $n=5$), epimeral width at Ep.4, 658 (612–744, 679, $n=5$). Infracapitulum and chelicerae as in male, infracapitulum length 174 (162–190, 175, $n=3$), chelicera length 204 (174–204, 189, $n=2$), cheliceral claw length (dorsal, i.e. short length) 42 ($n=1$). Pedipalps (figures 4c, d, 5b, d) similar to those of male, lengths of pedipalp segments: P.I, 18 (18–24, 20, $n=8$); P.II, 132 (126–144, 135, $n=6$); P.III, 118 (102–120, 112, $n=6$); P.IV, 138 (138–162, 149, $n=6$); P.V, 87 (84–90, 89, $n=5$). Genital field (figures 4b, e, f, g; 5b, d) terminal (allotype female, Prep. 1361; female, Prep. 1375; female, Prep. 1364, tilted to show genital field as depicted in figures 4b, e, 5c, respectively); figure 4f, g depict genital field (Prep. 1375) in ventral and lateral aspects, respectively, drawn prior to final

microscope preparation. Genital field consisting of two pairs of somewhat rectangular-shaped genital plates; anterior (ventral) genital plates each with three to four laterally sited acetabula, anteromedially with three short setae and posteromedially with two long setae on a strongly sclerotized projection; posterior (dorsal) genital plates each with 9–12 laterally-sited acetabula, anteromedially, i.e. when viewed as in figures 4e, 5c, with a single long stout seta, a few short setae associated with the acetabula; gonopore slit-like; genital field length 210 (198–228, 212, $n=3$), genital field width 252 (222–270, 250, $n=5$). Excretory pore slit-like, free in posterior integument and dorsal to posterior genital sclerite. Morphology and chaetotaxy of legs as illustrated for male. Lengths of leg segments: I-Leg.1–6:—(72–78, 75, $n=2$), 93 (90–108, 103, $n=8$), 141 (138–150, 147, $n=8$), 198 (192–216, 210, $n=8$), 189 (186–216, 205, $n=8$), 120 (120–126, 122, $n=8$); II-Leg.1–6:—(72, $n=1$), 117 (114–126, 120, $n=7$), 168 (168–186, 177, $n=7$), 231 (228–264, 246, $n=7$), 249 (246–282, 265, $n=7$), 168 (162–174, 169, $n=7$); III-Leg.1–7: 78 (78–90, 84, $n=4$), 114 (108–126, 123, $n=8$), 174 (174–192, 185, $n=8$), 243 (240–276, 261, $n=7$), 264 (252–306, 290, $n=7$), 198 (186–198, 194, $n=6$); IV-Leg.1–6: 138 (138–162, 148, $n=5$), 132 (132–150, 143, $n=8$), 231 (228–252, 244, $n=8$), 303 (300–336, 319, $n=8$), 366 (366–408, 391, $n=8$), 261 (258–282, 268, $n=8$)

Material examined. Five males: holotype, Prep. 1360; paratypes, Preps 1356, 1357, 1358 and 1359; five females: allotype, Prep. 1361; paratypes, Preps 1362, 1363, 1364 and 1375. All material collected by Prof. John Blay from Asa Reservoir, Ilorin, Nigeria, no date supplied but shortly after April 1983 (personal communication).

Etymology. The species is named for Prof. John Blay Jr who collected and sent this material to T.G.

Unionicola (Mutelicola) planicurvata new species
(figures 6–10)

Description of male (figures 6a–k, 7a–h, 8a, b). With the characters of the genus and subgenus. Body elongate, tapering posteriorly, without a cauda; length excluding gnathosoma 780 (780–854, 817, $n=2$), width 440 ($n=1$). Dorsum (figure 6a) with a single dorsal shield, length 540 (540–588, 564, $n=2$), width 372 ($n=1$). Ventrally with epimera in four groups occupying slightly more than half ventral surface, *ca* the same size as dorsal shield. Anterior groups with prominent posterior apodemes extending beneath anterior margins of Ep.3 before becoming more laterally directed. Posterior groups with a well-defined lateral cleft between Ep.3 and 4 and with well-rounded posterior margins to Ep.4; Ep.4 with pointed lateral extensions at point of IV-Leg insertions (figure 6b). Total epimeral length 488 (488–540, 514, $n=2$); median length Ep.3 + 4, 324 ($n=1$); median length Ep.4, 240 ($n=1$); epimeral width at Ep.3, 396 ($n=1$); epimeral width at Ep.4, 426 ($n=1$). Infracapitulum small, length 156 (144–156, 148, $n=3$); chelicerae short and stout, length, (162, $n=1$), cheliceral claw length (dorsal, i.e. short length), (42, $n=1$). Pedipalps as in figure 6d, e, h–k; P.II with a proximal spine-like seta on outer lateral face and a dorsodistal spine on inner lateral face; P.III with a long hair-like seta on outer lateral face and a shorter, stout seta distally on inner lateral face; P.IV with two to three short hair-like setae on outer lateral face and with a short ventrodistal projection bearing two fine setae; P.V ventrally strongly concave and distally multitoothed (figure 6h–k). Lengths of palp segments: P.I, 13 (12–15, 14, $n=4$); P.II, 95 (84–105, 95, $n=5$); P.III, 55 (51–63, 59, $n=5$); P.IV, 97 (96–105, 99, $n=5$); P.V, 66 (60–69, 64, $n=5$). Genital

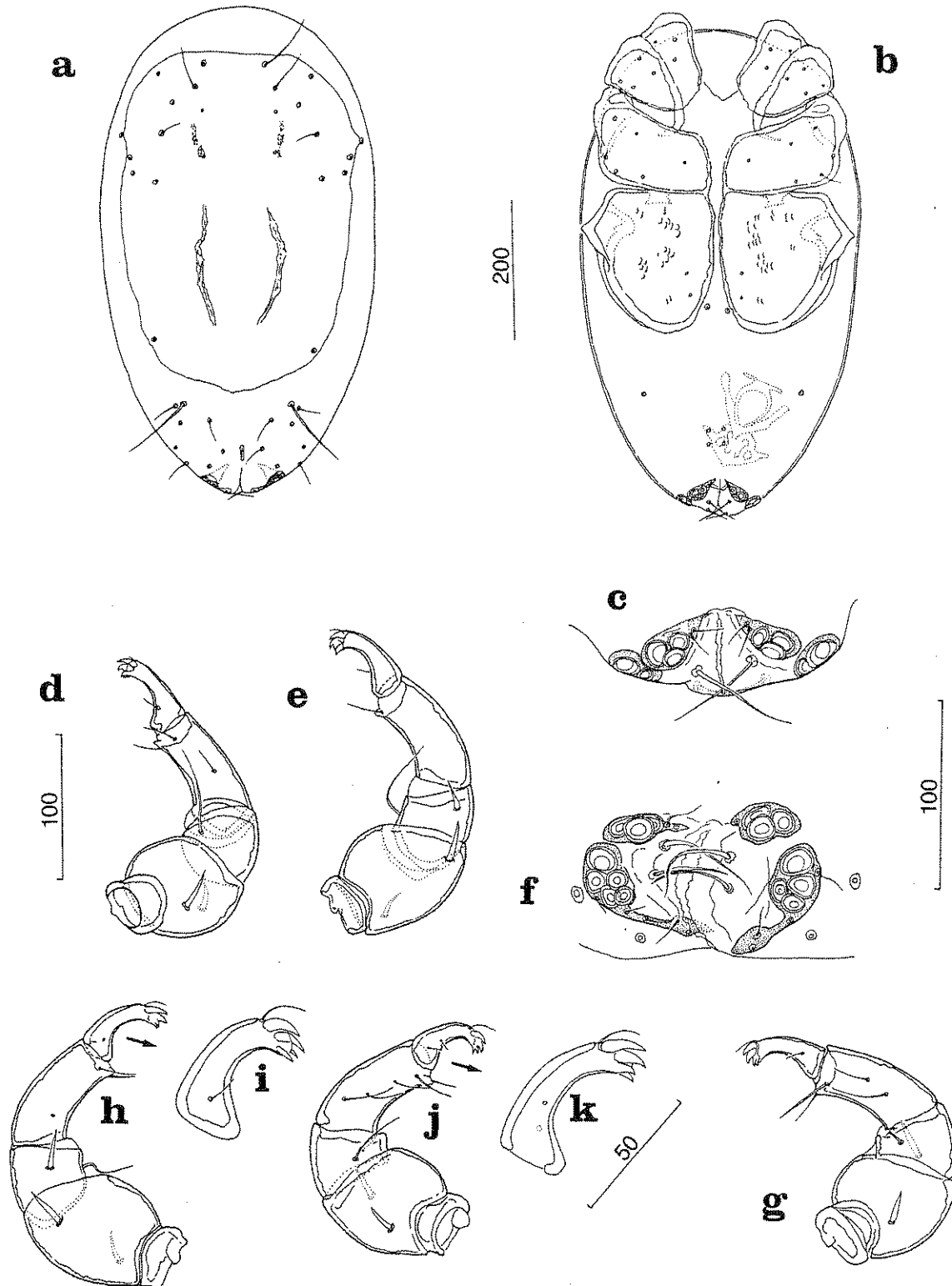


FIG. 6. *Unionicola (Mutelicola) planicurvata*. (a–e) male, Prep. 1366, holotype. (a) Dorsal surface; (b) ventral surface; (c) genital field; (d) left palp; (e) right palp; (f) genital field (posterior view) male, Prep. 1367; (g) left palp, male, Prep. 1367; (h) left palp, male, Prep. 1365; (i) PV left palp, male, Prep. 1365; (j) right palp, male, Prep. 1365; (k) PV right palp, male, Prep. 1365.

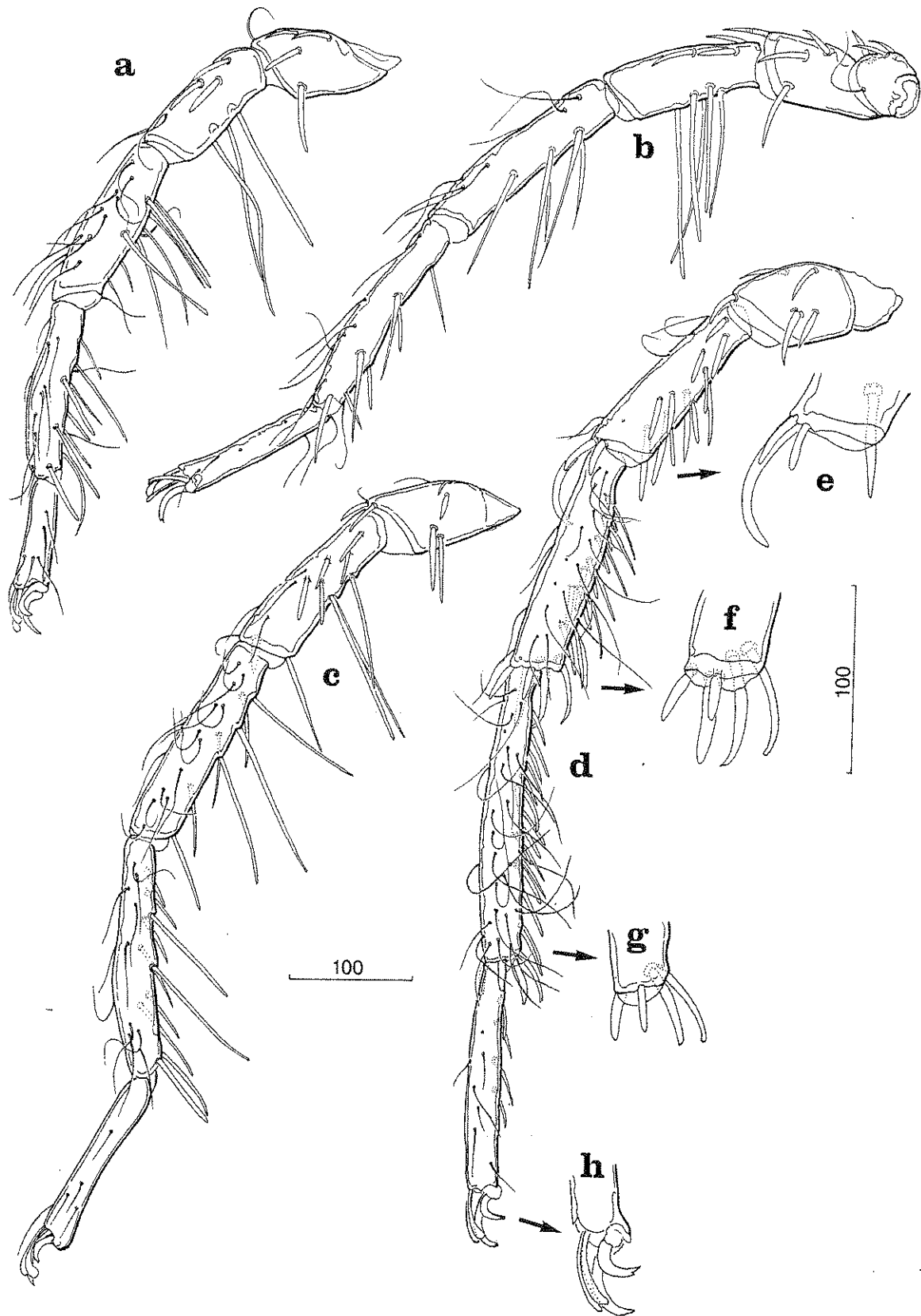


FIG. 7. *Unionicola (Mutelicola) planicurvata* male, Prep. 1366, holotype. (a) I-Leg.2-6 right; (b) II-Leg.1-6 right; (c) III-Leg.2-6 right; (d) IV-Leg.2-6 right; (e) IV-Leg.3, distal setae; (f) IV-Leg.4, distal setae; (g) IV-Leg.5, distal setae; (h) IV-Leg.6, terminal claws.

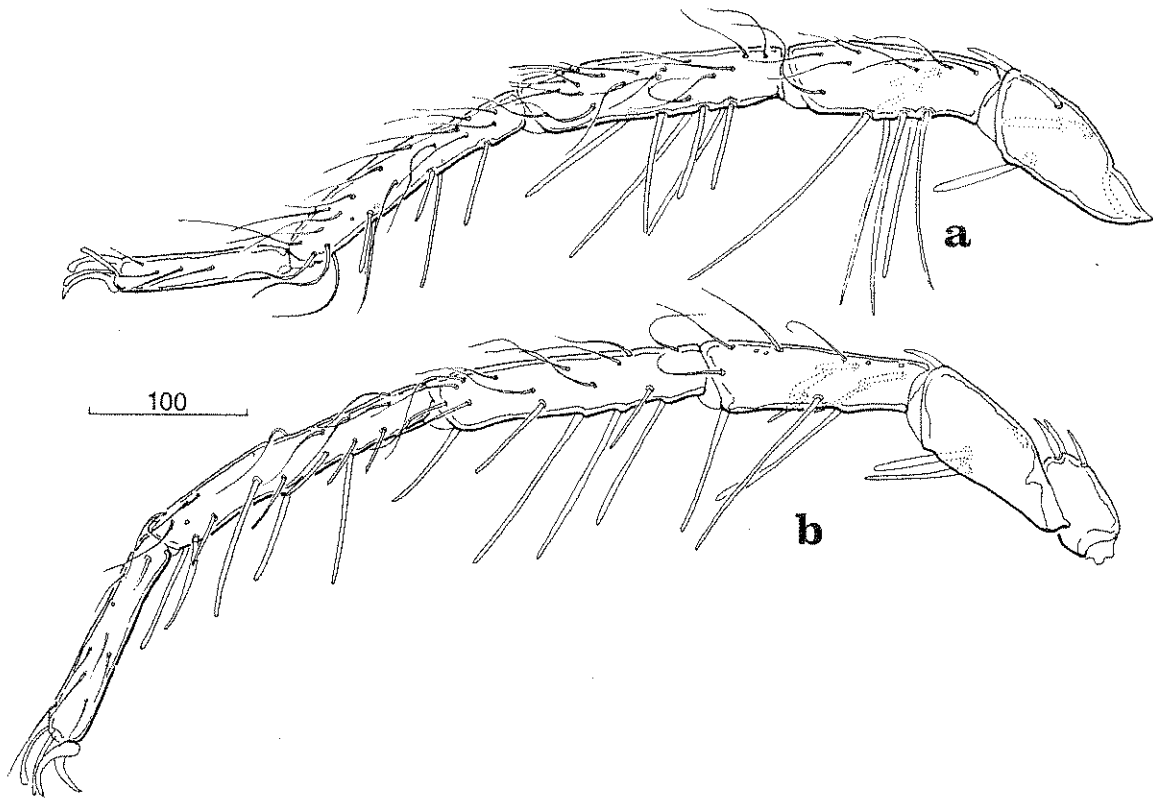


FIG. 8. *Unionicola (Mutelicola) planicurvata* male, Prep. 1366, holotype. (a) II-Leg.2-6, left; (b) III-Leg.1-6, left.

field at posterior of body, terminal and extending on to dorsum (figure 6a, b); figure 6f shows genital field of Prep. 1367 in posterior view. Genital field (figure 6c, f) comprised of two pairs of genital plates; anterior plates each with three acetabula, setae-bearing portion of anterior genital plate may or may not be extended and bears two short, fine setae; posterior plates larger than anterior plates, each with four to five acetabula and with posterior dorsally-directed setae-bearing extensions bearing three to four setae; gonopore slit-like and flanked on either side by two well-separated long setae (figure 6f); genital field length, (90, $n=1$), genital field width, 135 (135-141, 138, $n=2$). Excretory pore slit-like and free in dorsal integument (figure 6a). Morphology and chaetotaxy of legs as illustrated in figures 7a-h, 8a, b. All legs, particularly III and IV-Legs, with numerous hair-like setae. IV-Leg.3-5 distally with stout curved setae (figure 7e-g). Claws of all legs with barely discernible terminal teeth. Lengths of leg segments: I-Leg.1-6:—(78, $n=1$), 84 (72-84, 81, $n=4$), 126 (120-126, 123, $n=4$), 162 (162-168, 163, $n=4$), 159 (156-162, 159, $n=3$), 96 (84-114, 99, $n=4$); II-Leg.1-6: 60 ($n=1$), 93 (90-102, 96, $n=6$), 150 (150, $n=6$), 192 (192-198, 194, $n=6$), 195 (192-210, 201, $n=6$), 129 (120-132, 123, $n=6$); III-Leg.1-6: 72 (72, $n=3$), 102 (102, $n=6$), 162 (156-168, 163, $n=6$), 197 (195-210, 200, $n=5$), 216 (216-240, 228, $n=6$), 156 (150-162, 156, $n=5$); IV-Leg.1-6:—(96-132, 120, $n=3$), 114 (114-126, 120, $n=4$), 180 (174-180, 178, $n=4$), 210 (210-216, 213, $n=4$), 258 (258-270, 265, $n=4$), 198 (198-216, 207, $n=4$).

Female (figures 9a-e, 10a-g). Body larger and rounder than that of male; length, excluding gnathosoma 976 (830-976, 927, $n=3$), width 646 (622-646, 638, $n=3$). Dorsum (figure 9a) with a dorsal shield, length 396 (396-492, 456, $n=3$), width 264

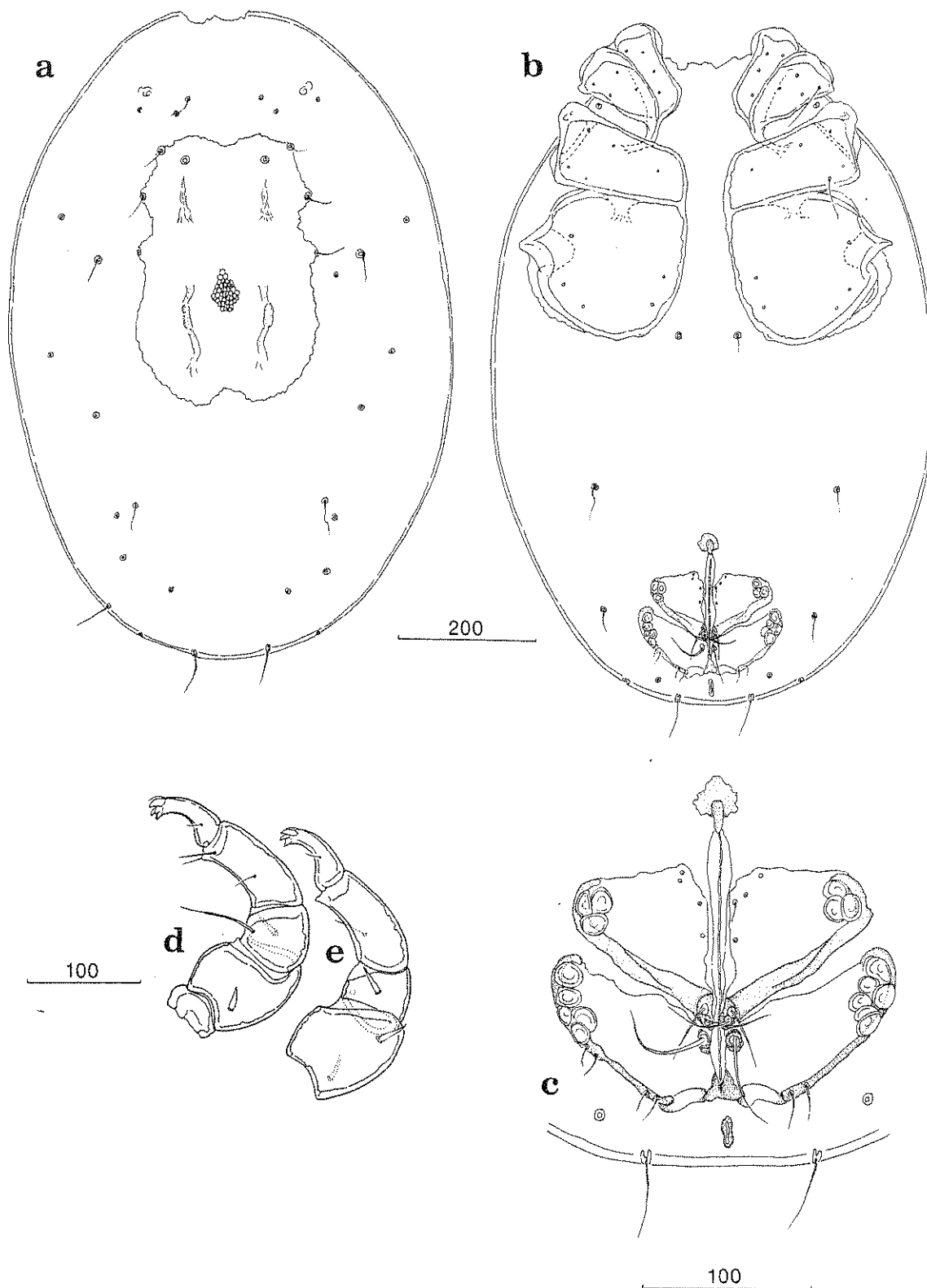


FIG. 9. *Unionicola (Mutelicola) planicurvata* female, Prep. 1369, allotype. (a) Dorsal surface; (b) ventral surface; (c) genital field; (d) left palp; (e) right palp.

(264–318, 298, $n=3$). Ventrally with epimera in four groups, similar to those of male but with posterior groups more separated (figure 9b); total epimeral length 462 (462–558, 500, $n=3$), median length Ep.3+4, 294 (294–318, 306, $n=3$), median length Ep.4, 210 (210–234, 220, $n=3$); epimeral width at Ep.3, 426 (426–486, 458,

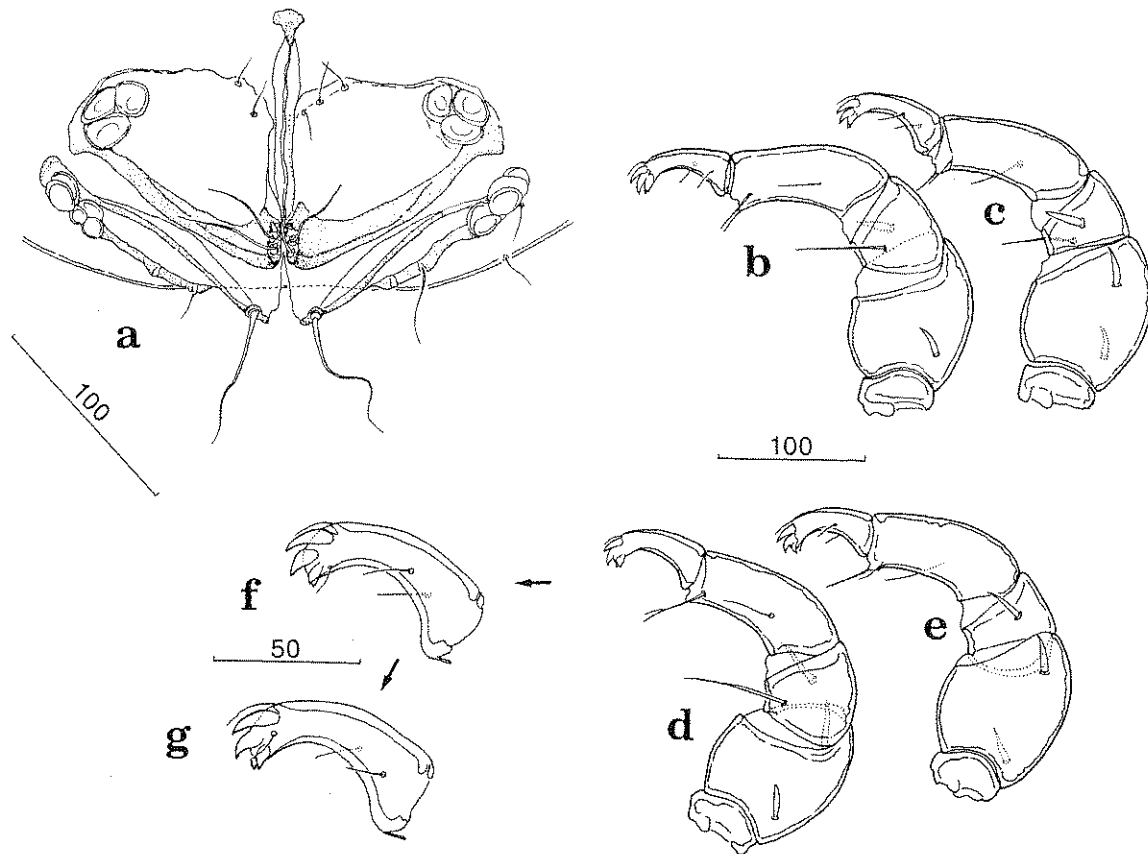


FIG. 10. *Unionicola (Mutelicola) planicurvata*. (a) Genital field, female, Prep. 1370; (b) left palp, female, Prep. 1370; (c) right palp, female, Prep. 1370; (d) left palp, female, Prep. 1368; (e) right palp, female, Prep. 1368; (f) PV of left palp, inner lateral face, female, Prep. 1368; (g) PV of left palp, outer lateral face, female, Prep. 1368.

$n=3$), epimeral width at Ep.4, 528 (528–576, 556, $n=3$). Infracapitulum and chelicerae similar to those of male, infracapitulum length 147 (147–159, 154, $n=3$), chelicera length 144 (144–156, 150, $n=2$), cheliceral claw length (dorsal, i.e. short length) 36 (–, 36, $n=2$). Pedipalps (figures 9d, e, 10b–g) similar to those of male, lengths of pedipalp segments: P.I, 12 (12–15, 13, $n=5$); P.II, 98 (96–111, 105, $n=6$); P.III, 63 (57–69, 65, $n=6$); P.IV, 99 (99–108, 105, $n=6$); P.V, 60 (60–69, 66, $n=6$). Genital field more-or-less terminal (allotype female, Prep. 1369, tilted to show genital field as depicted in figure 9b, c); figure 10a illustrates genital field in ventral aspect. Genital field consisting of two pairs of somewhat triangular wing-like genital plates; anterior plates each with two to five, generally three, lateral acetabula, two to four short, fine setae on inner margin and posteromedially with two long setae on a strongly sclerotized projection (figures 9c, 10a); posterior genital plates each with five to eight lateral acetabula, sclerotized setae-bearing (two to four) posterior extensions long and narrow (figure 9c) and anteromedially with a single stout seta (figures 9c, 10a); gonopore slit-like; genital field length 192 (150–192, 171, $n=2$), genital field width 204 (204–240, 224, $n=3$). Excretory pore slit-like and free in integument. Morphology and chaetotaxy of legs similar to those of male; IV-Leg.3–5 also as male with distal stout curved setae. Lengths of leg segments: I-Leg.1–6: 60 (60–66, 63, $n=2$), 78 (78–84, 80, $n=3$), 120 (120–126, 122, $n=3$), 156 (156–174, 162, $n=3$), 144 (144–168, 152, $n=3$), 90 (90–102, 94, $n=3$); II-Leg.1–6: 60 (60–69, 65, $n=3$), 90 (90–102, 97, $n=5$), 144 (144–156, 151, $n=6$), 186 (186–198, 194,

$n=6$), 192 (192–210, 202, $n=6$), 123 (120–138, 128, $n=6$); III-Leg.1–6: 72 (72–78, 73, $n=5$), 102 (102–108, 103, $n=6$), 153 (150–162, 159, $n=6$), 192 (192–204, 200, $n=6$), 216 (216–234, 228, $n=6$), 153 (144–156, 151, $n=5$); IV-Leg.1–6: 126 (108–126, 121, $n=4$), 114 (114–132, 124, $n=6$), 168 (168–186, 177, $n=6$), 210 (210–234, 223, $n=6$), 252 (252–282, 270, $n=6$), 198 (198–216, 205, $n=6$).

Material examined. Three males: holotype, Prep. 1366; paratypes, Preps 1365 and 1367; three females: allotype, Prep. 1369; paratypes Preps 1368 and 1370. Several unmounted specimens preserved in Koenike's Fluid. All material collected by Prof. John Blay from Asa Reservoir, Ilorin, Nigeria.

Etymology. The specific epithet is formed from the latin words *plane* meaning distinctly and *curvatus* meaning curved. The name alludes to the strongly curved pedipalp tarsus (P.V).

Deposition of material. The holotypes and allotypes of *Unionicola blayi* and *Unionicola planicurvata* will be deposited in The Natural History Museum, London. Paratypes and material preserved in Koenike's will be retained in the collection held by T.G.

Separation of U. blayi and U. planicurvata. Whilst closely related, the two species are readily separated; the main characters are found in the shape of the posterior margins of Ep.I: straight in *U. blayi* and rounded in *U. planicurvata*; the curvature of the pedipalp tarsus (P.V): strongly curved in *U. planicurvata*; the form of the setae-bearing extensions to the posterior pair of genital plates: long and narrow in *U. planicurvata* and more-or-less absent or short in the female of *U. blayi* and the presence, in *U. planicurvata*, of the stout, curved, distal setae on the telofemur, genu and tibia of the fourth leg (IV-Leg.3–5) which are absent in *U. blayi*.

Unionicoline mite associations with Mollusca

One hundred and fifteen *Unionicola* species in 29 subgenera are known to be associated with 212 molluscan taxa from 79 genera. Of these unionicolines, 110 are parasites of 200 species of freshwater unionoid bivalve molluscs from 71 genera [data collated from Vidrine (1996a) who followed the bivalve classification of Bogan (1993)]. *Unionicola* (s. str.) *laurentiana* Crowell and Davids, 1979, with 17 reported unionoid hosts is also associated with the non-unionoid bivalve *Sphaerium simile* Say (Corbiculacea: Sphaeriidae) whilst five other unionicolines, *Unionicola* (*Pentatax*) *aculeata* (Koenike, 1890), *U.* (*Polyatax*) *campelomaicola* Marshall, 1935, *U.* (*Polyatax*) *dobsoni* Vidrine, 1985, *U.* (*Polyatax*) *viviparaicola* Vidrine, 1985, and *U.* (*Imamuratax*) *scutigera* Viets, 1926, are associated with both unionoid bivalves and freshwater prosobranch gastropods. Nevertheless, whilst associated with 73 unionoid bivalves *U. aculeata* has only been recorded from two gastropods, *Campeloma decisum* Say (Vidrine, 1996a) and *Viviparus viviparus* (Linn.) (Böttger, 1972; Gledhill, 1985, Vidrine, 1996a). On the other hand, *U. campelomaicola* is associated with only two unionoid bivalves, *Obovaria jacksoniana* (Frierson) and *Utterbackiana peggyae* (Johnson) and the gastropod *C. decisum*; *U. dobsoni* with the bivalve *U. peggyae* and the gastropod *Campeloma geniculum* (Conrad); *U. viviparaicola* with the bivalve *Anodonta suborbiculata* (Say) and the gastropod *Viviparus subpurpureus* (Say) and *U. scutigera* with a *Lamellidens* sp. and *Lamellidens marginalis* (Lamarck) (Viets, 1957; Majumder and Pal, 1987, 1988, 1990) and the gastropod *Viviparus japonicus* von Martens (= *Cipangulopaludina japonica* (von Martens)) (Viets and Plate, 1954; Gledhill, 1985; Vidrine, 1996a). With reference to *U. aculeata*, it is questionable whether non-European specimens are conspecific with *U. aculeata*

sensu Koenike. In known contrast to the many unionicoline–bivalve associations, only five unionicolines are so far known to be associated only with gastropod molluscs: *U. (Polyatax) japonensis* Viets, 1933 with the viviparid gastropods *Cipangulopaludina chinensis malleata* (Reeve) and *C. japonica*; *U. (Ampullariatax) ampullariae* (Koenike, 1890) with *Ampullaria canaliculata* Lamarck and *A. insularum* d'Orbigny, 1835; *U. (Ampullariatax) thompsoni* Cook, 1974 with a *Pomacea* sp. and *U. (Baderatax) curtialpis* Bader, 1978, and *U. (B.) macani* Gledhill, 1985 with *Pila cecillei* Philippi and *Lanistes ovum* Peters, respectively.

Are there some common features amongst those molluscs suitable as hosts or, some common characteristics that render non-parasitized molluscan taxa unsuitable for unionicoline mites? All known bivalve hosts to unionicolines possess gills and amongst the great variety of aquatic gastropod molluscs only gilled (prosobranch) snails appear to be parasitized. Thus, gills are possibly important to associating unionicolines. Dimock and LaRochelle (1980) showed that unionicolines locate hosts in part by chemosensory activity. Other species within the genus use sponges as oviposition sites. Mites have not been recovered from the unionoid genera *Margaritifera* and *Cumberlandia* (= syn. to *Margaritifera sensu* Vaught, 1989) despite many thousands of specimens from North America and Europe being examined (D. Smith, personal communication). Thus there are some mussel taxa that for some reason(s) are not parasitized. Unfortunately, the full answers to these questions remain unanswered but a number of factors appear to impact mite–mussel relationships amongst which are intriguing potential co-evolutionary ones.

Unionicoline mite associations with unionoid bivalves

Fifty-five (41%) of the 135 genera in the Unionoidea *sensu* Vaught (1989) and five (26%) of the 19 genera in the Muteloidea *sensu* Vaught (1989) are known hosts to unionicoline mites. Most bivalve hosts occur in the Unionidae with 50 (42%) of the 119 genera parasitized. The subfamilies Anodontinae and Amblesinae have similar percentages of host genera with 56% (10 of 18 genera) and 58% (35 of 60 genera), respectively, whilst the Unioninae only has 12% (five of 41 genera). Of the three subfamilies in the Hyriidae, only five (36%) of the 14 genera in the Hyriinae have associations with unionicoline mites. In the Muteloidea, 17% of host genera occur in the Mutelidae, 33% in the Mycetopodidae and 25% in the Etheriidae (one of six, three of nine and one of four genera, respectively).

Table 1 shows the unionoid genera which act as hosts and the respective unionicoline mite subgenera associated with them, together with data on the numbers involved at species level for both mites and bivalves (bivalve classification after Vaught (1989)). The number of unionicoline mite subgenera with known associations with each of the 60 genera of unionoid bivalves ranges from 1 to 14 (mean = 4). Only the bivalve genera *Anodonta* and *Lampsilis* are associated with more than 10 unionicoline subgenera, 14 and 11 respectively. Currently 15 *Anodonta* spp. and 24 *Lampsilis* spp. are known to be associated with 35 and 18 *Unionicola* spp., respectively. Of known bivalve hosts, 25% are associated with only one unionicoline subgenus, and 80% of these are host to only one mite species. Twenty-seven (53%) of the 51 unionicoline subgenera are associated with unionoid bivalves and, of these, five (*Clarkatax*, *Neoatax*, *Parasitatax*, *Pentatax* and *Unionicolides*) are associated with more than 20 bivalve genera, the last two parasitizing 35 and 44 bivalve genera involving eight and 28 unionicoline spp. In contrast, *Clarkatax*, with only one species, is associated with 51 bivalve species in 23 genera. Of the 27 unionicoline

subgenera associated with bivalves, 11 (41%) involve only one mite species and of these subgenera, only in *Lundbladatax*, *Majumderatax* and *Wolcottatax* are there more than one currently known species (three, two and two, respectively). (The records of *U. (Wolcottatax) arcuatoides* Vidrine, 1986, from 'freshwater mussels' in Japan and Asia (Imamura, 1953; Vidrine, 1996a) have been ignored in this account.)

In 19 (70%) of the 27 bivalve-associated unionicoline subgenera, all known species are involved. Of the eight (30%) remaining subgenera only *Unionicola* s. str., with two (5%) of its 42 species, has less than 33% of species with bivalve associations. However, 11 (26%) of *Unionicola* s. str. species are known to be associated with freshwater sponges (Spongillidae).

The number of bivalve taxa associated with each unionicoline species ranges from 1 to 73 (mean = 6). Four unionicoline species in four subgenera are recorded from more than 50 bivalve host species: *U. (Clarkatax) serrata* (Wolcott, 1898)—51; *U. (Neoatax) abnormipes* (Wolcott, 1898)—55; *U. (Pentatax) aculeata* (Koenike, 1890)—73 and *U. (Unionicolides) hosei* Vidrine, 1986—63. Four species in three subgenera are known from 20 to 50 bivalve hosts: *U. (Breaudatax) megachela* Vidrine, 1985—24; *U. (Parasitatax) formosa* (Dana and Whelpley, 1836)—23; *U. (Unionicolides) fossulata* (Koenike, 1895)—32 and *U. (Unionicolides) vamana* Mitchell and Wilson, 1965—21 hosts. Eleven species are recorded from 10 to 20 host bivalves: *U. (Anodontinatax) wolcotti* (Piersig, 1900)—15; *U. (Neoatax) australindistincta* Vidrine, 1985—13; *U. (Neoatax) causeyae* Vidrine, 1985—15; *U. (Parasitatax) dimocki* Vidrine, 1986—11; *U. (Unionicola) laurentiana* Crowell and Davids, 1979—17; *U. (Unionicolides) fulleri* Vidrine, 1986—10; *U. (Unionicolides) sakantaka* Mitchell and Wilson, 1965—17; *U. (Unionicolides) stricta* (Wolcott, 1898)—13; *U. (Unionicolides) tupara* Mitchell and Wilson, 1965—18; *U. (Unionicolides) vikitra* Mitchell and Wilson, 1965—14 and *U. (Wolcottatax) arcuata* (Wolcott, 1898)—13 hosts. The remaining 91 bivalve-associated *Unionicola* s. l. species are recorded from one to nine bivalve host species with 51 (56%) of these known only from one host species.

Only nine (5%) of the 199 bivalve species (*sensu* Vidrine, 1996a), which are known hosts to unionicoline mites, are associated with 10 or more (10–19) *Unionicola* s. l. species: Anodontinae—*Anodonta (Pyganodon) grandis* (Say, 1829)—19; *A. (Utterbackiana) imbecilis* (Say, 1829)—10 and *Strophitus undulatus* (Say, 1817)—10; Ambleminae: Amblemini—*Amblema plicata plicata* (Say, 1817)—11; *Quadrula pustulosa pustulosa* (Lea, 1831)—10; *Tritogonia verrucosa* (Rafinesque, 1820)—12 and *Villosa lienosa* (Conrad, 1834)—12; Lampsilini—*Lampsilis teres* (Rafinesque, 1820)—12 and *Leptodea fragilis* (Rafinesque, 1820)—10. Of the remaining host species 61 (31%) are associated with only one *Unionicola* s. l. species.

This discussion simplifies details of mite–mussel associations in that many species of *Unionicola* are preferentially distributed among their reported hosts. The best examples of these preferences showed that mites of a species are usually 'residents' in a specific host species or group of host species (often closely related and representing a phylogenetic clade). However, these same mites are also 'incidentally' or 'accidentally' found in other hosts in the habitat. In contrast to the 'residents', 'incidental' mites were considered as 'vagrants' when found in moths and butterflies (Treat, 1975). Other mites, found in hosts for only brief periods of their life-history, were treated as transients. Mite–mollusc associations displayed similar phenomena, e.g. see host association data for North American *Unionicola* species in Vidrine (1996b, 1996c, 1996d). Thus co-evolutionary studies necessarily require the

Table 1. Unionoid host genera and the unionicoline mite subgenera associated with them together with data on the numbers involved at species level for both mites and bivalves.

Mite-associated unionoid bivalve genera and subgenera	Number of unionicoline subgenera associated with each bivalve genus	Number of unionicoline mite species associated with each bivalve genus	Number of bivalve host species
Order UNIONOIDA			
Superfamily UNIONOIDEA			
Family UNIONIDAE			
Subfamily UNIONINAE			
Genus <i>Utio</i> Philipsson, 1788	•	3	7
<i>Chamberlainia</i> Simpson, 1900		1	1
<i>Hyriopsis</i> Conrad, 1853		3	3
<i>Nephronaias</i> Crosse and Fischer, 1844	•	3	6
<i>Anodontina</i> Vidrine, 1986			
<i>Atacella</i> Lundblad, 1937			
<i>Australatax</i> Vidrine, 1985			
<i>Berezatax</i> Vidrine, 1985			
<i>Breaudatax</i> Vidrine, 1994			
<i>Causeyatax</i> Vidrine, 1994			
<i>Clarkatax</i> Vidrine, 1994			
<i>Dimockatax</i> Vidrine, 1992			
<i>Ferradasatax</i> Vidrine, 1988			
<i>Fulleratax</i> Vidrine, 1984	•		
<i>Imamuraatax</i> Vidrine, 1994			
<i>Kovietatax</i> Vidrine, 1986			
<i>Lundbladatax</i> Vidrine, 1988			
<i>Majumderatax</i> Vidrine, 1993			
<i>Mutlicola</i> subgen. nov.			
<i>Neolatax</i> Lundblad, 1941	•		
<i>Parashitatax</i> Viets, 1949	•		
<i>Pentatax</i> Thor, 1922	•		
<i>Polyataxides</i> Lundblad, 1941			
<i>Polyatax</i> Viets, 1933			
<i>Prasadatax</i> Vidrine, 1992			
<i>Unionicola</i> Haldeman, 1842			
<i>Unionicolella</i> Lundblad, 1941			
<i>Unionicolides</i> Lundblad, 1937			
<i>Unionicolopsis</i> K.O. Viets, 1980			
<i>Vietsatax</i> Uchida and Imamura, 1938			
<i>Wolcottatax</i> Vidrine, 1992			

<i>Elliptio</i> Rafinesque, 1819	• • •	• • •	• • •	• • •	6	12	15
<i>Fusconaiia</i> Simpson, 1900	• • •	• • •	• • •	• • •	6	14	9
<i>Hemistena</i> Rafinesque, 1820				•	1	1	1
<i>Plethobasus</i> Simpson, 1900				•	1	1	1
<i>Unimerus</i> Conrad, 1853	•	• • • • •	• • • • •	• • • • •	7	11	3
Tribe Lampsilini							
<i>Lampsilis</i> Rafinesque, 1820	• • • • •	• • • • •	• • • • •	• • • • •	11	18	24
Subgenus							
<i>Disconaias</i> Fischer and Crosse, 1894	• • • • •	• • • • •	• • • • •	• • • • •	(6)	(7)	(3)
<i>Venustaconcha</i> Thiele, 1934	• • • • •	• • • • •	• • • • •	• • • • •	(2)	(2)	(1)
<i>Actinonaias</i> Crosse and Fischer, 1893	• • • • •	• • • • •	• • • • •	• • • • •	5	8	3
<i>Carunculina</i> Simpson, 1894 ³	• • • • •	• • • • •	• • • • •	• • • • •	8	15	3
<i>Cyprogenia</i> Agassiz, 1852	• • • • •	• • • • •	• • • • •	• • • • •	2	2	1
<i>Cyrtionaias</i> Crosse and Fischer, 1894	• • • • •	• • • • •	• • • • •	• • • • •	4	6	1
<i>Ellipsaria</i> Rafinesque, 1820	• • • • •	• • • • •	• • • • •	• • • • •	2	2	1
<i>Frieronia</i> Ortmann, 1912	• • • • •	• • • • •	• • • • •	• • • • •	4	4	3
<i>Glebula</i> Conrad, 1853	• • • • •	• • • • •	• • • • •	• • • • •	3	3	1

identification of the three ecological relationships, i.e. residents, vagrants and transients (Treat, 1975). Additionally, on the matter of reported mite–mussel associations, the literature is replete with misidentifications, not only of unionicoline mites but also of their mussel hosts. The unravelling of historical records therefore requires some knowledge of the species authors' skills, mites, hosts and biogeography in order to assess the credibility of each published record (Vidrine, 1996d).

Unionicoline biogeography

Table 2 summarizes the known distribution of unionicoline mite subgenera. North America, with 19 subgenera, of which 14 are associated with bivalves, has the most and also 'the richest and most diverse unionacean (bivalve) fauna in the world including, conservatively, 227 species in 46 genera' (McMahon, 1991). Europe, with only five subgenera, has the least but also has an impoverished unionoid fauna. Clearly *Unionicola s. str.* is the only subgenus with a cosmopolitan distribution, other subgenera are known from only one, two or three continents with more than half (63%) currently known from one continent only. Ten subgenera (20%) with 113 species (54%) have been recorded from both hemispheres, 28 subgenera (55%) are recorded from the northern (Laurasian) continents of which 18 (35%) with 52 species (25%) are known only from that region. Whilst 33 subgenera (65%) are known from the southern (Gondwanan) continents, 23 (45%), with 44 species (21%) appear to be so far restricted to a southern distribution. Nevertheless, distribution of water-mites relative to continental drift events, especially in the southern hemisphere, are poorly understood (Cook, 1984). Vidrine (1996a) considered 18 subgenera (closed circles in table 2) as northern and 23 (open circles) as southern subgenera. Nevertheless, the distribution patterns suggested in table 2 should be treated with caution, for example, *Ampullariatax*, a parasite of gastropod snails (*Pilidae*) is recorded from both North and South America yet considered as a distinctly southern subgenus by Vidrine (1996a) for it only extends northwards into Central America. Similarly, the subgenus *Atacella*, also recorded from North and South America, is another distinctly southern taxon, only reaching northwards into Mexico. *Unionicolides* reaches its greatest diversity in North American mussels that invaded the continent following recent glaciations but probably arrived from the southern part of its range, its close relatives *Ferradasatax* and *Unionicolella* being restricted to the southern continent; *Pentatax* is another northern subgenus but its close relatives *Majumderatax* (Asia and Europe) and *Heversatax* (India and Africa) have a more southerly distribution (Vidrine, 1996a).

In general, most unionicoline water-mite parasites have distribution ranges that coincide with the geographic range of their specific unionoid hosts. Does this mean that wherever a potential host occurs the associated mite(s) is (are) also present? Also, are there extended areas with unparasitized potential hosts? In the USA extensive sampling (see Vidrine, 1996b, 1996c, 1996d) has demonstrated that host-specificity ranges amongst *Unionicola* species vary widely from monophagy to polyphagy. Unionicolines with narrow host ranges (showing a tendency towards monophagy) are found in specific mussel hosts across the geographic range of that host or group of hosts. This pattern of host–parasite co-distribution is evident for many species in North America where the same species of mite may be found from the same host from Canada to the southern USA. In other cases, where a number of mussel species of the same genus occur in different faunal zones, it is common to find the same unionicoline species in all zones but occupying different host species

Table 2. Continental distribution of unionicoline subgenera, the number of species in each subgenus and indications of their known life-mode.

	Number of species	Life mode	Asia	Europe	North America	South America	Africa	Australia and New Zealand
<i>Ampullariatax</i>	2	G			×	×		
<i>Armatax</i>	4	F	×				×	
<i>Atacella</i>	18	B			×	×		
<i>Bakeratax</i>	5	F	×				×	
<i>Heversatax</i>	4	F	×				×	
<i>Laselleatax</i>	3	F			×	×		
<i>Lundbladatax</i>	3	B, F, S			×	×		
<i>Unionicola</i> s.str	42	B, F, S	×	×	×	×	×	×
<i>Unionicolides</i>	29	B			×	×		
<i>Wilsonatax</i>	3	F			×	×		
<i>Anodontinatax</i>	6	B	•	•	•			
<i>Berezatax</i>	3	B			•			
<i>Breaudatax</i>	1	B			•			
<i>Causeyatax</i>	1	B			•			
<i>Clarkatax</i>	1	B			•			
<i>Conroyatax</i>	1	F	•					
<i>Dimockatax</i>	4	B	•		•			
<i>Everittatax</i>	1	F			•			
<i>Fulleratax</i>	2	B	•					
<i>Imamuratax</i>	3	B	•					
<i>Majumderatax</i>	2	B, F	•	•				
<i>Neoatax</i>	4	B			•			
<i>Parasitatax</i>	6	B	•	•	•			
<i>Pentatax</i>	8	B, F, G	•	•	•			
<i>Polyatax</i>	4	B, G	•		•			
<i>Prasadatax</i>	2	B	•					
<i>Vietsatax</i>	1	B	•					
<i>Wolcottatax</i>	2	B	•		•			
<i>Australatax</i>	7	B				○		○
<i>Australionicola</i>	1	F						○
<i>Baderatax</i>	2	G					○	
<i>Bassatax</i>	1	F					○	
<i>Cookatax</i>	1	F					○	
<i>Crameratax</i>	3	F				○		
<i>Crowellatax</i>	1	S						○
<i>Curryatax</i>	1	F				○		
<i>Dauidsatax</i>	1	F					○	
<i>Downesatax</i>	1	F						○
<i>Edwardsatax</i>	2	F						○
<i>Ferradasatax</i>	1	B				○		
<i>Giselatax</i>	2	F						○
<i>Gledhillatax</i>	4	F				○		
<i>Heteratax</i>	1	F					○	
<i>Kovietsatax</i>	2	B						○
<i>Mitchellatax</i>	4	F				○		○
<i>Mutelicola</i> s-g.nov	2	B					○	
<i>Polyatacides</i>	1	B				○		
<i>Poundsatax</i>	1	F				○		
<i>Smithatax</i>	3	F						○
<i>Unionicolella</i>	1	B				○		
<i>Unionicolopsis</i>	1	B						○
Totals	209		16	5	19	16	10	11

B, Bivalve associated; G, gastropod associated; S, sponge associated; F, free-living.
 × = Subgenera present in northern and southern hemisphere; • = northern subgenera;
 ○ = southern subgenera.

as the zones change. For those unionicoline species with a tendency towards polyphagy and parasitizing a large number of hosts (often not closely related), their geographic distribution may be much broader and less easily defined. In answer to the second question, there are locations where no, or very few, mites were found despite the presence of large mussel beds with 20 or more mussel species. At some of these locations it was noted that intensive agricultural runoff may carry insecticides and/or other chemicals that are lethal to the chironomid hosts (of unionicoline larvae) and/or the adult mites themselves. Within the same drainage system, a stream not impacted by such runoffs may harbour mussels with mites, in some cases the same mussel species found unparasitized in a previous bed, but here harbouring a dozen or more different unionicolines. Thus, environmental impacts may cause extended areas with unparasitized potential hosts. Also many rare mussel species, and several mussel genera, listed as federally rare and/or endangered over the last 30 years, have not been found parasitized by unionicoline mites. It is suspected that host population levels are below a minimum needed to maintain a host-specific mite species and/or a diverse community of parasitic unionicolines. Thus these scenarios indicate that a variety of factors affect the existing data, and generalizations regarding those may be suspect.

Concluding remarks

A mussel is generally a member of a community of mussels and an individual mussel may contain a community of mites. Mitchell (1955, 1965) made this clear when he showed that *Lampsilis siliquoidea* (Barnes, 1823) may hold up to four species of *Unionicola s. l.* and a *Najadicola* species. Each species was spatio-temporally separated from the others with females selectively using various portions of gills, mantle, foot, inner gill chambers etc. as oviposition sites; different species maintained different seasonal cycles of host infestation and some species controlled population sizes at various levels.

Discussions of mites and mussels necessarily extend into the area of community ecology since these are truly communities of mites and mussels. The mites are interacting and possibly excluding one another from hosts; additionally, mites may be excluded from potential hosts by other organisms, e.g. chironomid larvae (Roback *et al.*, 1980). Such interactions, when compounded by the larval requirement of *Unionicola s. l.* species for a chironomid host, lead into the realm of parasitology where different hosts are required for different stages of a life-cycle. This is further enhanced by the fact that mussels at the larval stage require a fish host for further development. Such obligatory relationships (mussel to fish, mite to chironomid, mite to mussel) clearly show the vulnerability of any mite to mussel co-existence over time.

Because unionoid bivalves, which according to Bauer (1992) are long-lived (30–130 years), have this parasitic stage on freshwater fishes, they are not only threatened by unfavourable environmental perturbations that affect them directly, e.g. the effects of siltation, but also those affecting their host fish species. Bogan (1993) discusses bivalve extinctions and their causes world-wide and expresses concern about their loss. Of North America, which has the most diverse unionoid fauna in the world, Bogan states: '19 taxa are presumed extinct, 44 species listed or proposed as federally endangered. A number of these endangered species are functionally extinct (individuals of a species surviving but not reproducing)'. Impoundment and inundation of riffle habitats in major rivers, with the loss of

obligate fish hosts together with increased siltation and various industrial and domestic pollution, are blamed for the rapid decline in these bivalves (Bogan, 1993).

Surely disturbances to freshwater habitats which affect unionoid bivalves will have a knock-on effect on those unionicoline mites associated with them. Those unionicoline species in subgenera that appear to be more catholic in their choice of bivalve hosts may fare better than those which, so far as is currently known, are associated with only one bivalve host species. In places where degradation or destruction of freshwater habitats due to economic and other pressures are possible, and to further understanding of mollusc-mite relationships, there is an urgent need for sampling of unionoid bivalves and prosobranch gastropods for their associated (parasitizing) unionicoline mites. This is particularly important for geographic areas which have not been, or have been inadequately, searched, for example Africa and Asia. There are sure to be some surprises.

Although 'host-induced morphology' may be a plausible hypothesis explaining some host-parasite relationships amongst species of *Unionicola* inhabiting molluscs (Downes, 1990), recent evidence all but dismissed it (Edwards and Labhart, 2000). Also, studies by Edwards and Dimock (1988) and Edwards and Vidrine (1994) separated previously considered morphologically identical mites into separate species *vis-à-vis* behavioural and biochemical data. Such analyses regarding mite systematics are currently being expanded with DNA studies by Edwards (personal communication).

In terms of general morphology, *Mutelicola* resembles two subgenera of closely related unionicolines (*Australatax* and *Unionicolides*) occurring in mussels in Australia and South America. Mites belonging to these subgenera are gill-mites, using the gills as oviposition sites in host mussels including members of the Unionidae, Hyriidae and Mycetopodidae. Similarly, most specimens of the two new unionicolines described above occurred in the gills of their mutelid host, *Aspatharia sinuata*.

The discovery of these two new species, *Unionicola blayi* and *U. planicurvata*, is significant in several ways: they provide the first record of unionicoline mussel mites from Africa; the first record of unionicoline mites from mutelid bivalves and, whilst these two species fit into currently known subgeneric complexes, they clearly represent a new and previously undescribed group. Biogeographically these new species fill a gap in Gondwanaland unionicoline distribution and the new subgenus extends the diversity of unionicoline genital field morphology.

Acknowledgements

The writers thank Prof. John Blay for sending this important material for study, Sarah Gee for formatting the tables and the reviewers of the manuscript for their valuable comments. Dr Fred Naggs, Natural History Museum, London, kindly provided T.G. with information on bivalve systematics. T.G. also thanks the Council of the Freshwater Biological Association for continued support and encouragement, and his colleague, Prof. Malcolm Elliott, for reading the manuscript.

References

- BAKER, R. A., 1977, Nutrition of the mite *Unionicola intermedia* Koenike and its relationship to the inflammatory response induced in its host *Anodonta anatina* L., *Parasitology*, **75**, 301-308.

- BAUER, G., 1992, Variation in the life span and size of the freshwater pearl mussel, *Journal of Animal Ecology*, **61**, 425–436.
- BLAY, J., 1989, Morphometry, length–weight relationships and length distributions of five populations of the freshwater bivalve *Aspatharia sinuata* (Unionacea, Mutelidae) in Nigeria, *Malacologia*, **30**, 365–372.
- BOGAN, A. E., 1993, Freshwater bivalve extinctions (Mollusca: Unionoida): a search for causes, *American Zoologist*, **33**, 599–609.
- BONETTO, A. A., 1997, “Freshwater oysters” (Muteloidea: Mutelidae). Their taxonomy and geographical distribution in the whole of the naiads of the world, *Biociencias, Porto Alegre*, **5**, 113–142.
- BÖTTGER, K., 1972, Wassermilben in der Mantelhöhle von Süßwasserschnecken [Water mites in the mantle cavity of freshwater snails], *Zoologischer Anzeiger*, **189**, 233–235.
- COOK, D. R., 1984, Preliminary review of the relationships of the water mite faunas of South America, Australia and New Zealand, in D. A. Griffiths and C. E. Bowman (eds) *Acarology VI*, Vol. 2 (Chichester: Ellis Horwood), pp. 959–964.
- DIMOCK, R. V. Jr and LAROCHELLE, P. B., 1980, Chemically mediated host recognition: a behavioural basis for the specificity of water mite symbioses, *American Zoologist*, **26**, 922.
- DOWNES, B. J., 1990, Host-induced morphology in mites: implications for host–parasite coevolution, *Systematic Zoology*, **39**, 162–168.
- EDWARDS, D. D. and DIMOCK, R. V. JR, 1988, A comparison of the population dynamics of *Unionicola formosa* from two anodontine bivalves in a North Carolina farm pond, *Journal of the Elisha Mitchell Scientific Society*, **104**, 1–6.
- EDWARDS, D. D. and LABHART, M., 2000, Genetic differences among host-associated populations of water mites (Acari: Unionicolidae: *Unionicola*): allozyme variation supports morphological differentiation, *Journal of Parasitology*, **86**, 1008–1011.
- EDWARDS, D. D. and VIDRINE, M. F., 1994, A new species in the water mite subgenus *Parasitotax* (Acari: Unionicolidae: *Unionicola*) from the North American freshwater mussel, *Utterbackia imbecilis* (Bivalvia: Unionidae), *Journal of the Elisha Mitchell Scientific Society*, **110**, 1–6.
- GLEDHILL, T., 1985, A new species of water-mite, *Unionicola* (*Pentatax*) *macani* (Unionicolidae, Hydrachnellae, Acari), from the mantle cavity of the prosobranch mollusc *Lanistes ovum* Peters in Nigeria, with remarks on some aspects of host/parasite relationships between unionicolids and molluscs, *Archiv für Hydrobiologie*, **104**, 77–92.
- HEVERS, J., 1978, Interspezifische Beziehungen zwischen *Unionicola*—Larven (Hydrachnellae, Acari) und Chironomidae (Diptera, Insecta), *Verhandlungen Gesellschaft für Ökologie*, **7**, 211–217.
- HEVERS, J., 1980, Biologisch—ökologische Untersuchungen zum Entwicklungszyklus der in Deutschland auftretenden *Unionicola*—Arten (Hydrachnellae, Acari), *Archiv für Hydrobiologie*, Suppl. **57**, 324–373.
- IMAMURA, T., 1953, Some stenophilous water-mites from Hyogo Prefecture, *Journal of the Faculty of Science, Hokkaido University*, **11**, 261–276.
- JONES, R. K. H., 1965, Parasitism by larvae of *Unionicola intermedia* Koenike, and another *Unionicola* sp. (Acarina, Pionae), on Chironomids, *Nature, London*, **207**, 317–318.
- JONES, R. K. H., 1978, Parasitism by *Unionicola* spp. larvae on Chironomids, *Hydrobiologia*, **60**, 81–87.
- LINCOLN, R. J., BOXSHALL, G. A. and CLARK, P. F., 1982, *A Dictionary of Ecology, Evolution and Systematics* (Cambridge: Cambridge University Press), 298 pp.
- MAJUMDER, M. Z. R. and PAL, S. G., 1987, Larval development of a *Unionicola* sp., a freshwater mite of a freshwater bivalve (*Lamellidens marginalis*) from Bengal, in S. Palanichamy (ed.) *Proceedings of the Fifth Indian Symposium of Invertebrate Reproduction*, pp. 158–170.
- MAJUMDER, M. Z. R. and PAL, S. G., 1988, Adaptations of *Unionicola* sp. A freshwater mite on *Lamellidens marginalis* from Bengal, *Bicovas*, **1**, 191–202.
- MAJUMDER, M. Z. R. and PAL, S. G., 1990, Egg laying behaviour of *Unionicola* sp. in freshwater bivalve host, in H. Patel (ed.) *Proceedings of the National Symposium of Animal Behaviour in The Behaviour* (Bhavnagar: Institute of Science), pp. 83–88.
- MANDAHL-BARTH, G., 1988, Studies on African freshwater bivalves, in T. K. Kristenson and E. Svenningsen (eds) *Publication of Danish Bilharziasis Laboratory*, pp. 1–161.

- McMAHON, R. F., 1991, Mollusca: Bivalvia, in J. H. Thorp and A. P. Covich (eds) *Ecology and Classification of North American Freshwater Invertebrates* (New York: Academic Press), pp. 315-399.
- MITCHELL, R., 1955, Anatomy, life history, and evolution of the mites parasitizing freshwater mussels, *Miscellaneous Publications, Museum of Zoology, University of Michigan*, No. 89, 28 pp. + 6 figures.
- MITCHELL, R., 1965, Population regulation of a water mite parasitic on unionid mussels, *Journal of Parasitology*, **51**, 990-996.
- MORTON, B., PREZANT, R. S. and WILSON, B., 1998, Class Bivalvia, in P. L. Beesley, G. J. B. Ross and A. Wells (eds) *Mollusca; The Southern Synthesis, Fauna of Australia*, Vol. 5 (Melbourne: CSIRO Publishing), Part A, pp. 195-234.
- PILSBRY, H. A. and BEQUAERT, J., 1927, The aquatic Mollusca of the Belgian Congo, with a geographical and ecological account of Congo malacology, *Bulletin of the American Museum of Natural History*, **53**, 69-602.
- ROBACK, S. S., BEREZA, D. J. and VIDRINE, M. F., 1980, Description of an *Ablabesmyia* (Diptera: Chironomidae: Tanypodinae) symbiont of unionid fresh-water mussels (Mollusca: Bivalvia: Unionacea), with notes on its biology and zoogeography, *Transactions of the American Entomological Society*, **105**, 577-620.
- SIMMONS, T. W. and SMITH, I., 1984, Morphology of larvae, deutonymphs and adults of the water mite *Najadicola ingens* (Prostigmata: Parasitengona: Hygrobatoidae) with remarks on phylogenetic relationships and revision of taxonomic placement of Najadicolinae, *Canadian Entomologist*, **116**, 691-701.
- TREAT, A. E., 1975, *Mites of Moths and Butterflies* (Ithaca, NY: Cornell University Press), 362 pp.
- VAUGHT, K. C., 1989, *A Classification of the Living Mollusca* (Melbourne, FL: American Malacologists), 195 pp.
- VIDRINE, M. F., 1996a, *Najadicola and Unionicola: I. Diagnoses of Genera and Subgenera, II. Key, III. List of Reported Hosts* (Eunice, LA: Gail Q. Vidrine Collectibles), pp. i-vi, 1-182.
- VIDRINE, M. F., 1996b, *North American Najadicola and Unionicola: Collections and Communities* (Eunice, LA: Gail Q. Vidrine Collectibles), pp. i-vi, 1-259.
- VIDRINE, M. F., 1996c, *North American Najadicola and Unionicola: Systematics and Coevolution* (Eunice, LA: Gail Q. Vidrine Collectibles), pp. i-vi, 1-145.
- VIDRINE, M. F., 1996d, *North American Najadicola and Unionicola: Diagnoses and Distributions* (Eunice, LA: Gail Q. Vidrine Collectibles), pp. i-vi, 1-355.
- VIETS, K., 1957, Neue Wassermilben (Hydrachnellae, Acari) von Borneo, Indonesia, *Abhandlungen hrsg. vom Naturwissenschaftlichen Verein zu Bremen*, **35**, 8-23.
- VIETS, K. and PLATE, H. P., 1954, Die ökologischen (parasitologischen) Beziehungen zwischen Wassermilben (Hydrachnellae, Acari) und Süßwasser-Mollusken, *Zeitschrift für angewandte Entomologie* **35**, 459-494.

Mite-associate unionoid bivalve genera and subgenera	Bivalve-associated unionoid subgenera																	Number of unionoid mite subgenera associated with each bivalve genus	Number of unionoid mite species associated with each bivalve genus	Number of bivalve host species								
	<i>Anodonta</i> Vidrine, 1986	<i>Ascoris</i> Lundblad, 1977	<i>Austrotas</i> Vidrine, 1985	<i>Bercasus</i> Vidrine, 1985	<i>Brecaudatus</i> Vidrine, 1994	<i>Caucygnatus</i> Vidrine, 1994	<i>Clatias</i> Vidrine, 1994	<i>Dinocki</i> de Vidrine, 1992	<i>Ferriatas</i> Vidrine, 1988	<i>Fulcratus</i> Vidrine, 1984	<i>Inauratus</i> Vidrine, 1994	<i>Kovrasius</i> Vidrine, 1986	<i>Lundbladatus</i> Vidrine, 1988	<i>Rajundratras</i> Vidrine, 1993	<i>Allochis</i> subgen. nov.	<i>Neosar</i> Lundblad, 1941	<i>Parasaratus</i> Viets, 1949				<i>Penina</i> Thor, 1922	<i>Polypratus</i> Lundblad, 1941	<i>Polyprax</i> Viets, 1953	<i>Prasidatus</i> Vidrine, 1992	<i>Unioscolia</i> Haldeman, 1842	<i>Unioscolia</i> Lundblad, 1941	<i>Unioscolia</i> Lundblad, 1927	<i>Unioscolia</i> K. C. Viets, 1980
Order UNIONIDA																												
Superfamily UNIONOIDEA																												
Family UNIONIDAE																												
Subfamily UNIONINAE																												
Genus <i>Uta</i> Phillipson, 1788																												
<i>Chamberlania</i> Simpson, 1900																												
<i>Thylopsis</i> Conrad, 1853																												
<i>Nephrosia</i> Crosse & Fischer, 1844																												
Subgenus <i>Elliptoides</i> Frierson, 1927																												
<i>Sphenonius</i> Crosse & Fischer, 1894 ¹																												
<i>Physius</i> Simpson, 1900																												
Subfamily ANODONTINAE																												
Genus <i>Anodonta</i> Lamarck, 1799																												
Subgenus <i>Proanodonta</i> Crosse & Fischer, 1984																												
<i>Utterbackiana</i> Frierson, 1927 ²																												
<i>Alasmodonta</i> Say, 1818																												
<i>Arcidens</i> Simpson, 1900																												
<i>Arkansas</i> Ortmann & Walker, 1912																												
<i>Ameloides</i> Baker, 1898																												
<i>Cristaria</i> Schumacher, 1817																												
<i>Lasmigona</i> Rafinesque, 1831																												
<i>Pilbryococha</i> Simpson, 1900																												
<i>Pseudanodonta</i> Bourguignat, 1876																												
<i>Sirophus</i> Rafinesque, 1820																												
Subfamily AMBLEMENINAE																												
Tribe Amblemini																												
Genus <i>Amblema</i> Rafinesque, 1820																												
<i>Cyclonatus</i> Pilbry, 1922																												
<i>Ensodens</i> Frierson, 1911																												
Subgenus <i>Unandra</i> Maas, 1912																												
<i>Lamellidens</i> Simpson, 1900																												
<i>Megalonatus</i> Utterback, 1915																												
<i>Plecomerus</i> Conrad, 1853																												
<i>Poponatus</i> Frierson, 1927																												
<i>Pseudodon</i> Gould, (1844-1845)																												
<i>Quadrula</i> Rafinesque, 1820																												
<i>Quincuncina</i> Ortmann, 1922																												
<i>Trapezoides</i> Simpson, 1900																												
<i>Tritogonia</i> Agassiz, 1852																												
Tribe Pleurobentini																												
<i>Pleurobema</i> Rafinesque, 1819																												
<i>Elliptio</i> Rafinesque, 1819																												
<i>Fusconia</i> Simpson, 1900																												
<i>Henistena</i> Rafinesque, 1820																												
<i>Plethobasus</i> Simpson, 1900																												
<i>Unionites</i> Conrad, 1853																												
Tribe Lampsilini																												
<i>Lampsilis</i> Rafinesque, 1820																												
Subgenus <i>Disconus</i> Fischer & Crosse, 1894																												
<i>Temistacochoa</i> Thiele, 1934																												
<i>Actinonatus</i> Crosse & Fischer, 1893																												
<i>Cornuculina</i> Simpson, 1894 ³																												
<i>Cyprigenia</i> Agassiz, 1852																												
<i>Cyrtionatus</i> Crosse & Fischer, 1894																												
<i>Elliptaria</i> Rafinesque, 1820																												
<i>Friersonia</i> Ortmann, 1912																												
<i>Glebia</i> Conrad, 1853																												
<i>Leptodea</i> Rafinesque, 1820																												
<i>Ligumia</i> Swainson, 1840																												
<i>Medionidus</i> Simpson, 1900																												
<i>Obliquaria</i> Rafinesque, 1820																												
<i>Obovaria</i> Rafinesque, 1819																												
<i>Patanilus</i> Rafinesque, 1818																												
<i>Psychobanchus</i> Simpson, 1900																												
<i>Truncilla</i> Rafinesque, 1819																												
<i>Villosa</i> Frierson, 1927																												
Family HYRHDAE																												
Subfamily HYRHIINAE																												
Genus <i>Prisona</i> Schumacher, 1817 ⁴																												
<i>Castalia</i> Lamarck, 1819																												
<i>Castalina</i> Thuring, 1891																												
<i>Dipodon</i> Spix, 1827																												
<i>Hyrcella</i> Swainson, 1840																												
Subgenus <i>Telesteno</i> Uehida, 1934 ⁵																												
Superfamily MUTELOIDEA																												
Family MUTELOIDAE																												
Genus <i>Apsatharia</i> Bourguignat, 1885																												
Family MYCTOPODIDAE																												
Subfamily MYCTOPODINAE																												
Genus <i>Myctopoda</i> Orbigny, 1835																												
Subfamily ANODONTINAE																												
Genus <i>Anodontes</i> Bruguere, 1792																												
Subfamily MONOCONDYLAENAE																												
Genus <i>Monocondylaea</i> Orbigny, 1835																												
Family ETHERIDAE																												
Genus <i>Acastaea</i> Orbigny, 1851																												
Number of mite-associate bivalve genera and subgenera	14	7	3	9	16	5	26	9	1	3	2	2	2	1	1	23	23	35	1	3	6	15	1	44	2	1	7	
Number of bivalve-associated mite species per unionoid subgenus	6	18	7	3	1	1	4	1	3	2	2	1	1	2	4	5	8	1	3	2	2	1	28	1	1	1		

1 = *Barynotis* Crosse & Fischer, 1894 sensu Vidrine (1996)
 2 = *Utterbackia* sensu Vidrine (1996)
 3 = *Taxalastina* Rafinesque, 1831 sensu Vidrine (1996)
 4 = *Hyria* sensu Vidrine (1996) = *Prisona* sensu Vaught (1989)
 5 = *Telesteno*, listed at genus level by Vidrine (1996)

Table 1. Unionoid host genera and the unionoid mite subgenera associated with them together with data on the numbers involved at species level for both mites and bivalves.