

REVISION OF THE UNIONICOLINAE (ACARI: UNIONICOLIDAE)

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ABSTRACT — All species in the subfamily Unionicolinae Oudemans are combined into a single genus *Unionicola* Haldeman, with 18 subgenera. The genera *Unionicolopsis* Viets and *Heteratax* Lundblad are reduced in rank to subgenera. Two new subgenera (*Cookatax* and *Kovietsatax*) are erected and described for the first time. Diagnoses, hosts, list of species, distributions, and a key are provided for the subgenera. The genus *Unionicola* is considered holophyletic with the subgenus *Unionicola* as the least derived group. All other subgenera represent divergent groups displaying unique characters, but synapomorphies among subgenera permit the grouping of subgenera into separate clades. Distributions of the subgenera reflect continental drift, and molluscan parasites have ranges that coincide with their hosts. Groups of more closely related subgenera display evolutionary adaptive radiation from a subgroup of the subgenus *Unionicola*. A cladogram showing the hypothetical cladogenetic events resulting in the present subgenera in *Unionicola* is presented.

INTRODUCTION

The current classification of the Unionicolinae Oudemans does not represent the holophyletic nature of the group (Vidrine 1980). Major inconsistencies in character states that are used to define genera and subgenera (eg. acetabular plate number, acetabular number, presence or absence of sexually dimorphic legs) have been discussed (Cook 1974, Smith 1976 and Vidrine 1980). The first overall definitive classification with complete synonymies was provided by Viets (1956). The subfamily, in part, has been revised by Cook (1974), Viets (1975, 1980 and 1984) and Vidrine (1984, 1985a, b, c and d, 1986a, b, c and d). I proposed the use of the female genital field structure as a primary subgeneric criterion and leg and pedipalp structure as secondary criteria in an effort to reconcile the classification with a more probable evolutionary history of the group (Vidrine 1984). This paper employs these criteria in order to revise the subfamily and provides diagnoses, hosts, lists of species, distributions and a key to the subgenera. Also this paper provides a discussion of a more probable evolutionary history of the group.

Mites of most subgenera in *Unionicola* are known

to be parasitic on varied groups of invertebrates. Larval mites are parasitic on chironomids (Diptera) (Jones 1965 and Hevers 1975). Resting stages (protonymphs and/or tritonymphs), nymphs and/or adults are parasites of sponges (Porifera: Spongillidae), snails (Prosobranchia: Ampullarioidea: Viviparidae (Asia and North America) and Ampullariidae (Africa, Central and South America)), and mussels (Unionoida: Mutelacea and Unionacea). The Mutelacea contains two families: Mutelidae in Africa and Mycetopodidae in Mexico, South America and Africa. The Unionacea contains two families: Hyriidae in South America and Australia and Unionidae in North America including Mexico, Europe, Asia and Africa (Davis and Fuller 1981). Heard and Vail (1981) suggested that Hyriidae be reduced to a subfamily, Hyriinae, in Unionidae. The larval mussels are mostly parasitic on fish and are distributed by these hosts (Fuller 1974). All groups of hosts (sponges, snails, mussels and chironomids) may live in close proximity (Vidrine, Bouchon and Poirrier 1986). The life histories of a few mites have been studied by Mitchell (1955 and 1965), Hevers (1975), Dimock (1985), Dimock and Davids (1985) and Davids, Crowell and deGroot (1985).

RESULTS

1. Subgenus *Unionicola* Haldeman, 1842

TYPE SPECIES — *U. crassipes crassipes* (Muel-ler 1776).

DIAGNOSIS — Female genital field with 2 pairs of acetabular plates, and each plate usually similar in shape or apparently unmodified and bearing usually 2-3 acetabula (figs. 1 and 2); anterior female acetabular plates with 2, long, inner setae, posterior plates with a single, long, inner seta; all four female acetabular plates closely appressed to one another with setae forming a central mass; male genital field with a single pair of acetabular plates forming a nearly circular field that is on the venter or absolutely posterior but not extending up onto the dorsum; pedipalps subcylindrical and well-sclerotized; male and female walking legs similar and lacking obvious sexual dimorphism.

HABITAT — Most studied species are associated with Spongillidae and/or usually collected free-swimming. Occasionally transient specimens as well as encysted stages have been found in Unionidae and Mycetopodidae.

DISTRIBUTION — Worldwide (fresh-water habitats).

DISCUSSION — This subgenus contains 82 of the 187 currently accepted, named species in the genus. It is quite diverse and probably polyphyletic, yet all of the species have relatively unmodified genital fields and legs. Many species that were formerly placed in *Pentatax* because they usually possess 5 pairs of acetabula are included in this subgenus. The number of acetabula is apparently insufficient to serve as a subgeneric criterion. The lack of extensive modifications in body structures and great similarities between the type species and members of the Piontaciinae indicate that this group is the least derived in the genus. All other subgenera are apparently derived from subgroups resembling present members of this subgenus. Current status of several species is under debate (Crowell 1984, Conroy 1984 and Tuzovskii 1985), and many new species are being discovered (Cook 1986).

ADDITIONAL SPECIES INCLUDED — *Unionicola acutidens* (Lundblad 1936), *U. affinis* (Piersig 1906), *U. alpa* Cook 1986, *U. annulata* Lundblad 1947, *U. armata* Walter 1929, *U. augustipalpis* (Lundblad 1937), *U. bogerti* (Daday 1907), *U. brasiliensis* (Lundblad 1936), *U. chappuisi* Walter 1935, *U. conjuncta* Viets 1954, *U. crassipalpis* Walter 1915, *U. crassipes laurentiana* Crowell and Davids 1979, *U. crassipes miyazakii* Imamura 1953, *U. crassipes minor* (Soar 1900), *U. cumberlandensis*

(Rainbow 1906)?, *U. curvitaris* Lundblad 1941, *U. cyclophora* Viets 1913, *U. dadayi* Cook 1966, *U. dentifera* Cook 1966, *U. digitata* (Koenike 1898), *U. dresscheri* Besseling 1946, *U. figuralis* (Koch 1836), *U. fimbriata* Viets 1913, *U. finisbelli* Ramazzotti 1947, *U. fissipalpis* Lundblad 1942, *U. flabelliseta* Cook 1986, *U. furculopsis* Cook 1980, *U. furcula* (Lundblad 1935), *U. gracilipalpis gracilipalpis* (Viets 1908), *U. gracilipalpis tenuis* (Lundblad 1935), *U. gracilipes* (Lundblad 1936), *U. graciliseta* (Viets 1935), *U. hankoi* (Szalay 1927), *U. harpax* (Koenike 1898), *U. iheringi* (Koenike 1890), *U. inermis* Lundblad 1941, *U. inflexa* Viets 1921, *U. kantaka* Cook 1967, *U. koenikei* Viets 1913, *U. levipalpis* Besseling 1949, *U. lindrothi* Viets 1981, *U. longidens* Lundblad 1942, *U. longipes* Lundblad 1942, *U. longiseta* Walter 1915, *U. lyncea* (Koenike 1895), *U. megalopsis* Viets 1925, *U. mexicana* Cook 1980, *U. minuta* Viets 1916, *U. minutissima* Lundblad 1947, *U. necessaria* (Koenike 1906), *U. neoaffinis* Cook 1986, *U. niigata* Imamura 1954, *U. ovalis* Imamura 1954, *U. parvipora* (Lundblad 1920), *U. parvula* Lundblad 1954, *U. pectinata* (Wolcott 1898), *U. perpusilla* Viets 1954, *U. plaumanni* Lundblad 1937, *U. poirrieri* Vidrine 1984, *U. pollicigera* Viets 1921, *U. postmarginata* Viets 1925, *U. prehendens* Viets 1954, *U. procurvipes* (Koenike 1890), *U. pseudoannulata* Cook 1986, *U. pugionipalpis* Viets 1954, *U. pusuligera* Viets 1954, *U. pyriformis* (Dana and Whelpley 1836) ?, *U. retractidens* Lundblad 1937, *U. schmackeri* (Koenike 1895), *U. setifera* Cook 1967, *U. similis* (Viets 1935), *U. simplicipes* (Lundblad 1936), *U. singalensis* (Daday 1898), *U. siolii* Viets 1954, *U. tridentifera* Viets 1921, *U. tumidipalpis* (Lundblad 1936), *U. uncata* Viets 1916, *U. unidens* Lundblad 1942, *U. viciniseta* (Lundblad 1936), *U. vidrinei* Cook 1986 and *U. vietsi* Walter 1935.

2. Subgenus *Heteratax* Lundblad 1941, new combination

TYPE SPECIES — *U. falcipes* (Lundblad 1941)

DIAGNOSIS — Female indistinguishable from the subgenus *Unionicola* in genital field, leg and pedipalp morphology; male also similar to *Unionicola*, but with fourth walking leg with Ti and Ta highly modified (fig. 22).

HABITAT — One species from standing water.

DISTRIBUTION — Africa.

DISCUSSION — *Heteratax* has previously placed in a separate genus because of the unique dimorphism of the male walking legs. Sexual dimorphism in male walking legs occurs in many species in at least 5 other subgenera and is not sufficient to serve as a generic

character in this group; therefore, this group is reduced in rank to a subgenus. The similarities between females of *Unionicola* and *Heteratax* indicate the close relationship of these taxa, and *Heteratax* is considered to be a divergent clade in the genus.

3. Subgenus *Giselatax* Viets, 1975

TYPE SPECIES — *U. lundbladi* Viets 1975

DIAGNOSIS — Female and male similar to members of the subgenus *Unionicola* in genital field structure (fig. 2) and pedipalp structure (fig. 23); male with fourth walking leg sexually dimorphic, especially the Ge and Ti (fig. 21).

HABITAT — Two species are apparently free-swimming.

DISTRIBUTION — Australia.

DISCUSSION — *Giselatax* is another divergent species group with males possessing sexual dimorphism in their walking legs.

ADDITIONAL SPECIES INCLUDED — *U. aberrans* Viets 1984.

4. Subgenus *Pentatax* Thor, 1922

TYPE SPECIES — *U. bonzi* (Claparede 1869)

DIAGNOSIS — Female genital field with 2 pairs of acetabular plates closely appressed, with each plate usually bearing 2-3 acetabula (fig. 8); female anterior plates modified with an inner flap with one or 2, short, thick, spinous setae; female posterior plate apparently unmodified; setae nearly centrally located in genital field; male genital field with a single pair of acetabular plates with only small, inconspicuous setae; pedipalps subcylindrical and well-sclerotized, with the Ta usually slightly elongate and bearing obvious, but usually not large, clawlets; male and female legs similar.

HABITAT — Most studied species are parasites of Unionidae and/or Viviparidae, but several species are usually free-swimming and only employ the hosts as sites of oviposition and encystment (Vidrine, Bouchon and Poirrier 1986).

DISTRIBUTION — Europe, Asia, Africa and North America.

DISCUSSION — *Pentatax* is separated from *Unionicola* by the modified anterior acetabular plates in the female genital field. The species included are apparently a cohesive unit.

ADDITIONAL SPECIES INCLUDED — *U. aculeata* (Koenike 1890), *U. falcifera* (Daday 1907), *U. imamurai* Hevers 1978, *U. inusitata* (Koenike 1914), *U. rezvoi* Sokolow 1931, *U. setipes* Sokolow 1931, *U. thaiensis* Vidrine 1985 and *U. tricuspis* (Koenike 1895).

5. Subgenus *Anodontinatax* Vidrine, 1986a

TYPE SPECIES — *U. intermedia* (Koenike 1882)

DIAGNOSIS — Female genital field with 2 pairs of acetabular plates that are similar to the fields of *Pentatax* and *Vietsatax* (fig. 9); male genital field similar to *Pentatax*: pedipalps similar to *Pentatax*; male fourth walking legs sexually dimorphic with groups of serrated setae on the distal Ge and mesial Ti; all walking legs with deeply bifid tarsal claws with dorsal prong longer than ventral prong.

HABITAT — All are parasites of Unionidae, but the males are usually collected free-swimming.

DISTRIBUTION — North America, Asia and Europe.

DISCUSSION — *Anodontinatax* is intermediate in morphology between the subgenera *Pentatax* and *Vietsatax*. All three groups are considered as mantle mites, since they oviposit in the mantle epithelia of their hosts, and this may account for some convergence. While the females of the three subgenera are difficult to separate, the males are readily separated by leg morphology.

ADDITIONAL SPECIES INCLUDED — *U. belli* Vidrine 1986, *U. clarki* Vidrine 1986, *U. mitchelli* Conroy 1982, *U. smithae* Vidrine 1986 and *U. wolcotti* (Piersig 1900).

6. Subgenus *Vietsatax* Uchida and Imamura, 1938 (in Imamura 1938)

TYPE SPECIES — *U. parasitica* (Uchida and Imamura 1938)

DIAGNOSIS — Female genital field similar to *Pentatax* (fig. 10); male genital field elongate and extending up onto the dorsum (figs. 25 and 26); male fourth walking leg sexually dimorphic with many rows of heavy setae; all tarsal claws of walking legs deeply bifid with the dorsal prong longer than the ventral prong.

HABITAT — A single species parasitizing Unionidae, but the males are usually collected free-swimming.

DISTRIBUTION — Asia (Japan).

DISCUSSION — *Vietsatax* is apparently part of a subgroup of mites with *Anodontinatax* and *Pentatax*. *Vietsatax* is very distinctive with the male genital field morphology.

7. Subgenus *Polyatax* Viets, 1933

TYPE SPECIES — *U. japonensis* Viets 1933

DIAGNOSIS — Genital acetabula 3 to many

pairs; female genital field with 2 pairs of acetabular plates (figs. 12 and 13); female anterior plates with an elongate, inner flap that is heavily sclerotized and bears one or 2, short, thick, spinous, setae; female posterior plate usually unmodified; pedipalp subcylindrical and well-sclerotized with Ta usually nearly quadrate in outline with large, obvious clawlets; most species with obvious dorsal plates; male genital field as in *Pentatax*; male fourth walking leg modified in some species; tarsal claws of walking legs deeply bifid in some species.

HABITAT — Parasites of Unionidae, Viviparidae and Ampullariidae.

DISTRIBUTION — Africa, Asia and North America.

DISCUSSION — *Polyatax* resembles members of *Pentatax* and *Anodontinatax*, but the female genital fields are more modified, and the males have distinctive types of sexual dimorphism in their walking legs, if any occurs. Studied species of *Polyatax* oviposit in mantle and foot epithelia of their hosts as do *Pentatax* and *Anodontinatax*, but *Polyatax* apparently resembles *Fulleratax*, *Parasitatax* and *Ampullariatax* in leg and pedipalp chaetotaxy. African *Polyatax* from ampullariid snails are divergent in male leg sexual dimorphism (Bader 1978 and Gledhill 1985).

ADDITIONAL SPECIES INCLUDED — *U. abnormipes* (Wolcott 1898), *U. australindistincta* Vidrine 1985, *U. campelomaicola* Marshall 1935, *U. causeyae* Vidrine 1985, *U. curtialpis* Bader 1978, *U. dobsoni* Vidrine 1985, *U. heardi* Vidrine 1985, *U. hensleyi* Vidrine 1985, *U. indistincta* (Wolcott 1898), *U. macani* Gledhill 1985, *U. megachela* Vidrine 1985, *U. neokoeningi* Viets 1957, *U. serrata* (Wolcott 1898), *U. scutigera* Viets 1926 and *U. viviparaicola* Vidrine 1985.

8. Subgenus *Parasitatax* Viets, 1949

TYPE SPECIES — *U. ypsilophora* (Bonz 1783)

DIAGNOSIS — Genital acetabula many pairs; female genital field with a single pair of acetabular plates (fig. 14); male genital field with a single pair of acetabular plates; pedipalps variable, but usually large; male and female legs similar.

HABITAT — Parasites of Unionidae.

DISTRIBUTION — Europe, Asia and North America.

DISCUSSION — *Parasitatax* females have uniquely divergent genital fields, but some characters are shared with *Polyatax*, *Fulleratax* and *Ampullariatax*. Whereas nymphs of other subgenera usually only have 2 pairs of acetabula, nymphs of *U. serrata*, *U. thienemanni* and *U. uchidai* have more pairs. *U. tumidoides* has pedipalps similar to *Fulleratax*, while *U. yp-*

silophora has pedipalps similar to *Ampullariatax*. The *Parasitatax* oviposit in the blade of the demibranchs of their hosts.

ADDITIONAL SPECIES INCLUDED — *U. arcuata* (Wolcott 1898), *U. arcuatoides* Vidrine 1986, *U. bishopi* Vidrine 1986, *U. brandti* Vidrine 1985, *U. cooki* Vidrine 1986, *U. dimocki* Vidrine 1986, *U. diversipes* (Viets 1926), *U. formosa* (Dana and Whelpley 1836), *U. thienemanni* Viets 1957, *U. tumida* (Wolcott 1898), *U. tumidoides* Vidrine 1986 and *U. uchidai* Imamura 1953.

9. Subgenus *Fulleratax* Vidrine, 1984

TYPE SPECIES — *U. robacki* Vidrine 1984

DIAGNOSIS — Genital acetabula many pairs; female genital field with 2 pairs of acetabular plates, each bearing an elongate, inner flap with relatively long, hairlike setae (fig. 15); male genital field with a single pair of acetabular plates fused anteriorly and posteriorly by secondary sclerotization; pedipalps subcylindrical and well-sclerotized with Ta elongate and bearing a single large clawlet; one species with first walking legs sexually dimorphic; all tarsal claws of walking legs serrated dorsally.

HABITAT — Parasites of Unionidae.

DISTRIBUTION — Asia (Thailand and Laos).

DISCUSSION — *Fulleratax* females have unique genital fields, but otherwise resemble female *Polyatax* and *Parasitatax*. *Fulleratax* has species with unique leg chaetotaxy.

ADDITIONAL SPECIES INCLUDED — *U. davisi* Vidrine 1984.

10. Subgenus *Ampullariatax* Vidrine, 1985c

TYPE SPECIES — *U. ampullariae* (Koenike 1890)

DIAGNOSIS — Genital acetabula many pairs; female genital field with 2 pairs of acetabular plates (fig. 11); all 4 female plates similar with more than 10 acetabula and an inner, small flap with short, hairlike setae; male genital field with a single pair of acetabular plates; pedipalps subcylindrical and well-sclerotized with Ta relatively short and bearing small clawlets; pedipalp Ta tapered distally; male and female legs similar.

HABITAT — Parasites of Ampullariidae.

DISTRIBUTION — Central and South America.

DISCUSSION — *Ampullariatax* has distinctive female genital fields. The males are apparently similar to males of *Polyatax* and *Parasitatax*.

ADDITIONAL SPECIES INCLUDED — *U. thompsoni* Cook 1974.

11. Subgenus *Bassatax* Cook, 1966

TYPE SPECIES — *U. separata* Cook 1966

DIAGNOSIS — Genital acetabula usually 5 pairs; female genital field with 2 pairs of acetabular plates that are widely separated and only possess fine, hair-like setae (fig. 5); male morphology is similar to *Unionicola*; distal tubercle on Ti of pedipalp; pedipalps subcylindrical and well-sclerotized; posterior coxal group with an incomplete suture.

HABITAT — Free-swimming in streams.

DISTRIBUTION — Africa.

DISCUSSION — Only a single species is known in this subgenus. *Bassatax* females have genital fields that are similar to female genital fields of *Unionicolopsis*.

12. Subgenus *Unionicolopsis* Viets, 1980,
new combination

TYPE SPECIES — *U. opimipalpis* Viets 1980

DIAGNOSIS — Genital acetabula 5-7 pairs; female genital field with 2 pairs of acetabular plates that are widely separated and only possess fine, hair-like setae (fig. 6); no distal tubercle on Ti of pedipalp; pedipalps subcylindrical and well-sclerotized; posterior coxal group with complete suture.

HABITAT — Parasites of Hyriidae.

DISTRIBUTION — Australia.

DISCUSSION — Only females of this taxon are known. Female genital fields are similar to female fields of *Bassatax*. This taxon was previously considered a genus, but the similarities with *Bassatax* indicate that it should be reduced to a subgenus.

13. Subgenus *Unionicolides* Lundblad, 1937

TYPE SPECIES — *U. sica* Lundblad 1937

DIAGNOSIS — Genital acetabula usually 4-6 pairs; female genital field with a single pair of acetabular plates (fig. 16); each plate with at least one seta on the inner margin resulting in a central complex of setae in the genital field; male genital field similar to *Unionicola*; pedipalps subcylindrical and well-sclerotized; male and female legs similar, except for minor chaetotaxic differences in the first walking legs of some species.

HABITAT — Parasites of Hyriidae, Unionidae, and Mycetopodidae.

DISTRIBUTION — North and South America.

DISCUSSION — *Unionicolides* is similar to *Berezatax*, *Atacella* and *Australatax* (Vidrine 1985a). These subgenera are apparently derived from ancestral groups that might have resembled some recent South

American members of the *Unionicola*, eg. *U. procurvipes* and *U. brasiliensis*.

ADDITIONAL SPECIES INCLUDED — *U. amandita* Mitchell and Wilson 1965, *U. bakeri* Vidrine 1986, *U. bonariensis* Mauri and Alzuet 1972, *U. burchi* Vidrine 1986, *U. calnani* Vidrine 1986, *U. conroyi* Vidrine 1986, *U. fossulata* (Koenike 1895), *U. fulleri* Vidrine 1986, *U. hoesei* Vidrine 1986, *U. lasallei* Vidrine 1986, *U. pachyscelus* Lundblad 1941, *U. poundsi* Vidrine 1986, *U. sakantaka* Mitchell and Wilson 1965, *U. scutella* Vidrine 1986, *U. stansberyi* Vidrine 1986, *U. stricta* (Wolcott 1898), *U. tupara* Mitchell and Wilson 1965, *U. vamana* Mitchell and Wilson 1965 and *U. vikitra* Mitchell and Wilson 1965.

14. Subgenus *Berezatax* Vidrine, 1985a

TYPE SPECIES — *U. berezai* Vidrine 1985a

DIAGNOSIS — Genital acetabula 4-6 pairs; female genital field with a single pair of acetabular plates (fig. 17); each plate with at least one seta on the inner margin resulting in a central complex of setae in the genital field; male genital field similar to *Unionicola*; pedipalps dorsoventrally flattened and weakly sclerotized ventrally (fig. 24); male and female legs similar.

HABITAT — Parasites of Unionidae.

DISTRIBUTION — North America (southern United States and Mexico).

DISCUSSION — *Berezatax* is morphologically intermediate between *Unionicolides* and *Atacella*. *Berezatax* has female genital fields similar to *Unionicolides* and pedipalps similar to *Atacella*.

ADDITIONAL SPECIES INCLUDED — *U. acylindrotarsa* Vidrine 1985 and *U. latipalpa* Vidrine 1985.

15. Subgenus *Atacella* Lundblad, 1937

TYPE SPECIES — *U. clathrata* (Lundblad 1937)

DIAGNOSIS — Genital acetabula 5-10 pairs; female genital field with one or 2 pairs of acetabular plates (figs. 19 and 20); setae not centrally located in female genital field, but usually displaced posteriorly; pedipalps dorsoventrally flattened and weakly sclerotized ventrally; male genital field similar to *Unionicola*; male and female legs similar, except for a single species with fourth walking leg with Ge, Ti and Ta modified.

HABITAT — Parasites of Hyriidae and Mycetopodidae.

DISTRIBUTION — North America (Mexico), Central America and South America.

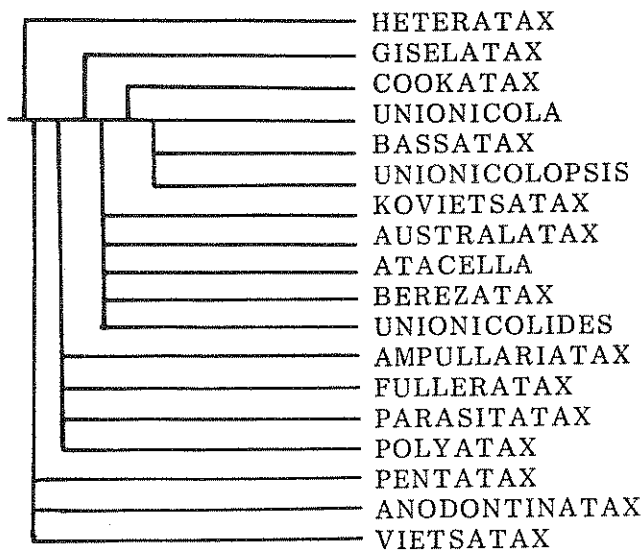


Fig. 1. Cladogram illustrating the hypothetical cladogenetic events resulting in the divergence of subgenera in the genus *Unionicola*.

DISCUSSION — *Atacella* has females with the unique combination of dorsoventrally flattened pedipalps and unique genital fields. The genital fields of several females are similar to those of *Australatatax*.

ADDITIONAL SPECIES INCLUDED — *U. crassiparma* Vidrine 1985, *U. entrrianensis* (Rosso de Ferradas 1976), *U. fissipes* (Koenike 1891), *U. granadosi* Hoffman and Cramer 1979, *U. gigantea* (Caches and Mane-Garzon 1973), *U. nelsoni* Vidrine 1985, *U. neoperforata* Vidrine 1985, *U. parmaphora* Vidrine 1985, *U. perforata* (Koenike 1890), *U. petita* Vidrine 1985, *U. prominens* (Koenike 1914), *U. quadriplaca* Vidrine 1985, *U. recta* Vidrine 1985, *U. redfordi* Vidrine 1985, *U. rosewateri* Vidrine 1985, *U. rugosa* (Koenike 1890), *U. schubarti* (Viets 1954) and *U. subrecta* (Caches and Mane-Garzon 1973).

16. Subgenus *Australatatax* Vidrine, 1985a

TYPE SPECIES — *U. sinuata* Lundblad 1938

DIAGNOSIS — Genital acetabula 5 pairs; female genital field with 2 pairs of acetabular plates (fig. 18); each plate bearing an elongate, posteriorly projecting flap with relatively small, hairlike setae; male genital field similar to *Unionicola*; pedipalps subcylindrical and well-sclerotized; male and female legs similar.

HABITAT — Parasites of Hyriidae and Mycetopodidae.

DISTRIBUTION — Southern South America and Australia.

DISCUSSION — *Australatatax* is morphologically intermediate between *Unionicolides* and *Atacella*. Females of *Australatatax* have pedipalps similar to *Unionicolides* and genital fields similar to *Atacella*.

ADDITIONAL SPECIES INCLUDED — *U. assimilis* Viets 1980, *U. clipeata* Viets 1980, *U. conjunctella* Viets 1980, *U. ligulifera* Viets 1980, *U. procursa* Viets 1980 and *U. scutata* Viets 1980.

17. Subgenus *Kovietsatatax* new subgenus

TYPE SPECIES — *U. cirrosa* (Koenike 1914)

DIAGNOSIS — Genital acetabula 5-6 pairs; female genital field with 2 pairs of acetabular plates (fig. 7); each plate with a small, flaplike projection extending to the center of the genital field and bearing a single, very short, stout setae; male genital field similar to *Unionicola*; pedipalps subcylindrical and well-sclerotized; male and female legs similar.

HABITAT — Parasites of Hyriidae.

DISTRIBUTION — Australia.

DISCUSSION — *Kovietsatatax* possess similar leg, pedipalp and general body morphology with the *Australatatax*. The female genital fields are similar, yet quite distinct, to those of *Unionicolopsis* and *Bassatatax*.

ADDITIONAL SPECIES INCLUDED — *U. walkeri* Viets 1980.

18. Subgenus *Cookatatax* new subgenus

TYPE SPECIES — *U. latilaminata* (Viets 1911)

DIAGNOSIS — Genital acetabula 5 pairs; female genital field with 2 pairs of acetabular plates (fig. 4); anterior plates with 2 acetabula and 6 thickened hair-like setae projecting posteriorly; posterior plates with 3 acetabula and 2 thickened setae; male genital field similar to *Unionicola*; pedipalps and legs similar to *Unionicola*.

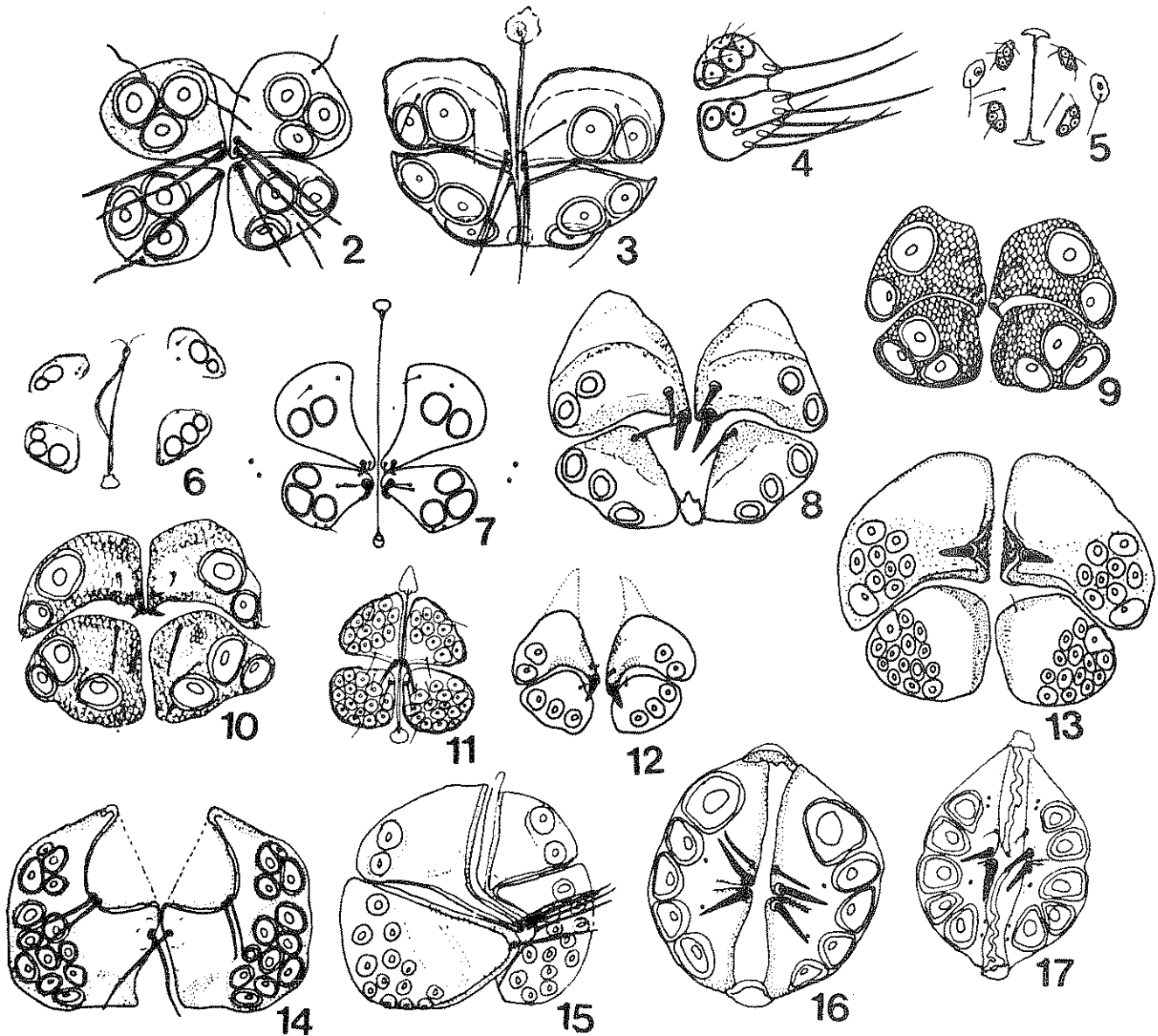
HABITAT — A single species collected free-swimming.

DISTRIBUTION — Africa.

DISCUSSION — *Cookatatax* represents a species that possesses female genital fields that are very divergent.

DISCUSSION

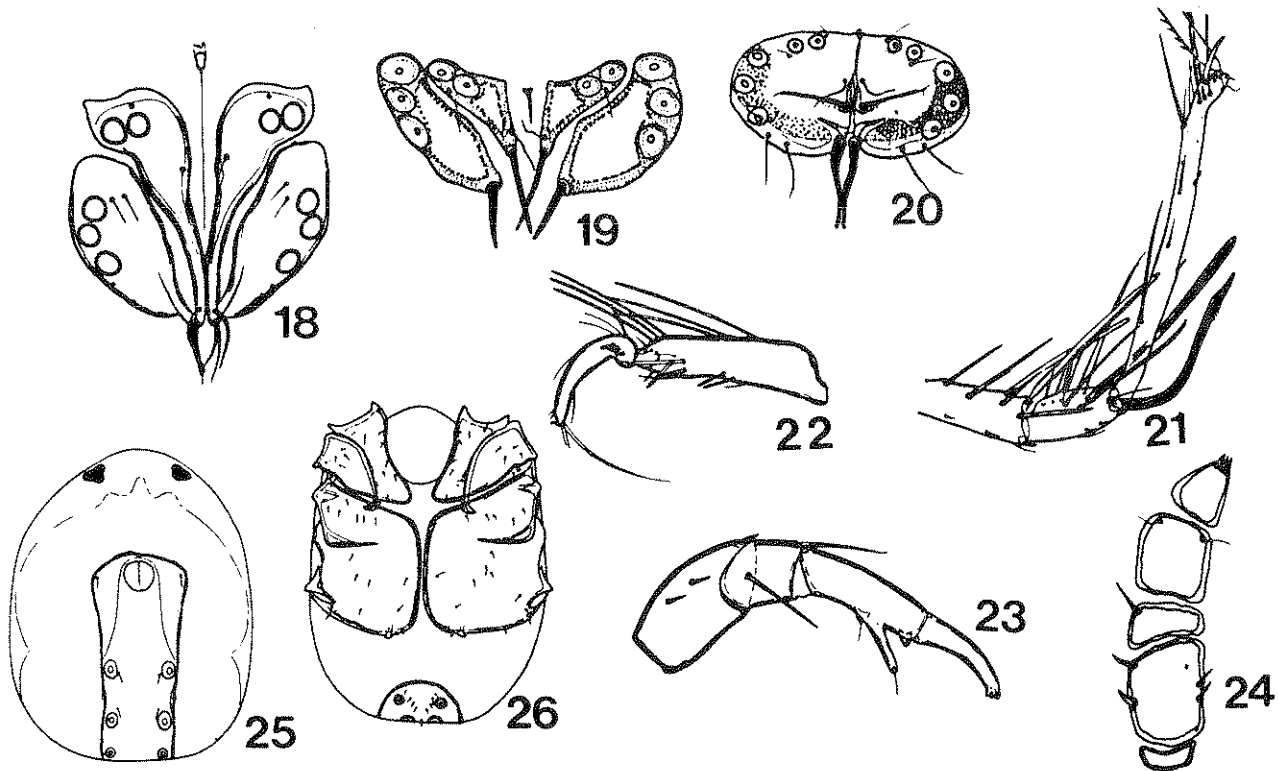
All of the species in the subfamily Unionicolinae are combined into a single genus, *Unionicola*, which contains 18 subgenera. The subgenus *Unionicola* is the



Figs. 2-17. Female genital fields: 2. *Unionicola (Unionicola) poirrieri* Vidrine, 3. *U. (Giselatax) lundbladi* Viets — redrawn after Viets 1975, 4. *U. (Cookatax) latilaminata* Viets lateral view — redrawn after Cook 1974, 5. *U. (Bassatax) separata* Cook — redrawn after Cook 1974, 6. *U. (Unionicolopsis) opimipalpis* Viets — redrawn after Viets 1980, 7. *U. (Kovietsatax) walkeri* Viets — redrawn after Viets 1980, 8. *U. (Pentatax) thaiensis* Vidrine, 9. *U. (Anodontinatax) smithae* Vidrine, 10. *U. (Vietsatax) parasitica* (Uchida and Imamura), 11. *U. (Ampullariatax) thompsoni* Cook — redrawn after Cook 1974, 12. *U. (Polyatax) megachela* Vidrine, 13. *U. heardi* Vidrine, 14. *U. (Parasitatax) brandti* Vidrine, 15. *U. (Fulleratax) robacki* Vidrine, 16. *U. (Unionicolides) conroyi* Vidrine, 17. *U. (Berezatax) berezai* Vidrine.

least derived and possesses the largest number of pleisomorphic characters with other members of the *Unionicolidae*. Other subgenera are divergent from *Unionicola* stock in one or more major characters that are considered as subgeneric criteria.

Whereas *Heteratax*, *Giselatax* and *Cookatax* appear to represent distinct clades, other subgenera may be grouped because of synapomorphies into four hypothetical clades: 1. *Bassatax* and *Unionicolopsis*; 2. *Kovietsatax*, *Australatax*, *Atacella*, *Berezatax* and



Figs. 18-26. Female genital fields: 18. *U. (Australatax) procrusa* Viets — redrawn after Viets 1980, 19. *U. (Atacella) nelsoni* Vidrine, 20. *U. (Atacella) neoperforata* Vidrine. Additional figures include: 21. *U. (Giselatax) lundbladi* male fourth walking leg Ge and Ti — redrawn after Viets 1975, 22. *U. (Heteratax) falcipes* Lundblad fourth walking leg Ti and Ta, 23. *U. (Giselatax) lundbladi* pedipalp — redrawn after Viets 1975, 24 *U. (Berezatax) acylindrotarsa* Vidrine pedipalp, 25. *U. (Vietsatax) parasitica* male dorsum, and 26. *U. (Vietsatax) parasitica* male venter — redrawn after Cook 1974.

Unionicolides; 3. *Ampullariatax*, *Fulleratax*, *Parasitatax* and *Polyatax*; and 4. *Pentatax*, *Anodontinatax* and *Vietsatax*. A cladogram (fig. 1) shows the hypothetical cladogenetic events resulting in the evolution of the subgenera in *Unionicola*. Additional synapomorphies suggest that the *Bassatax* and *Kovietsatax* groups may represent a single large clade, while the *Ampullariatax* and *Pentatax* groups may represent another large clade. These two large clades would include the molluscan parasites, and one might assume that both groups are derived from a single invasion of ancient stock into mollusks followed by massive evolutionary adaptive radiation. In order to determine whether all these molluscan parasites are a result of a single or multiple invasions with attendant diversification, more studies on the zoogeography and host associations of the mites are required.

Distributions of water mites in respect to events dealing with continental drift, especially in the southern hemisphere, are poorly understood (Cook

1984). Zoogeographically, southern (Gondwana) elements include the subgenera *Unionicola*, *Heteratax*, *Giselatax*, *Cookatax*, *Bassatax*, *Unionicolopsis*, *Pentatax*, *Unionicolides*, *Atacella*, *Australatax*, *Kovietsatax*, *Polyatax* and *Ampullariatax*. Northern (Laurasia) elements include subgenera *Unionicola*, *Pentatax*, *Anodontinatax*, *Vietsatax*, *Polyatax*, *Parasitatax*, *Fulleratax*, *Berezatax*, *Atacella* and *Unionicolides*. Whereas *Unionicola* is cosmopolitan, the other subgenera are apparently restricted to a single hemisphere with a few, possibly explainable, exceptions. *Pentatax* is essentially restricted to the northern hemisphere, but a single species occurs in Africa. *Atacella*, a diverse southern group, follows its host group into Mexico. *Unionicolides* reaches its greatest known diversity in North America in mussels that invaded the continent following recent glaciations, but it apparently originated in the southern portion of its range. Divergent African *Polyatax* possibly followed their host group, while the remaining members of this

subgenus are restricted to the northern hemisphere. In general, most molluscan parasites have ranges that coincide with their specific host groups.

The evolution of the Unionicolinae is apparently closely tied to the evolution of their host groups (Vidrine 1980). Information on the associations and natural histories of the mites is restricted to a few species in North America and Europe. Other areas of the world, especially South America, Africa and Asia, contain many subgenera that are scantily known. Further investigation of the coevolution of these mites and their hosts is needed in order to understand the evolution of *Unionicola*.

The subgenera in this paper are based upon morphological characters, but the distributions and apparent host-specificities appear to support the proposed systematic scheme. The origin of the molluscan, especially mussel, parasites appears to antedate the final break-up of Pangaea, since the mites apparently fall into two large groups with each group reaching its greatest diversity in one of the two hemispheres. With current morphological, zoogeographic and host preference data, the systematic scheme presented here is apparently representative of a more probable evolutionary history of the Unionicolinae.

The following artificial key is provided for identification of the known subgenera in the genus *Unionicola*. Most subgenera can readily be identified using adult females, but in some instances where females are essentially identical, males will be required.

KEY TO THE SUBGENERA OF *UNIONICOLA*

1. Females with acetabular plates not closely appressed to one another and not bearing short, thick or elongate setae (figs. 5 and 6) 2
 - Females not as above 3
2. Females with a complete suture between posterior coxae and without a distal tubercle on pedipalp Ti *Unionicolopsis*
 - Females without a complete suture between posterior coxae and with a distal tubercle on pedipalp Ti *Bassatax*
3. With dorsoventrally flattened pedipalps (fig. 24) 4
 - With subcylindrical well-sclerotized pedipalps (fig. 23) 5
4. Female genital field with central group of setae (fig. 17) *Berezatax*
 - Female genital field with group of setae posterior to the center of the field (figs. 19 and 20) *Atacella*
5. Females with one pair of acetabular plates 6
 - Females with two pairs of acetabular plates 7
6. With 4-6 pairs of acetabula (fig. 16) *Unionicolides*
 - With more than 6 pairs of acetabula (fig. 14) *Parasitatax*
7. Female with similar anterior and posterior acetabular plates and each plate bearing only hairlike setae and no sexual dimorphism in male legs . . . 8
 - Female with obviously different anterior and posterior acetabular plates or short, thick setae on acetabular plates or obvious sexual dimorphism in male legs 9
8. With 3-7 pairs of acetabula (fig. 2) *Unionicola*
 - With more than 7 pairs of acetabula (fig. 11) *Ampullariatax*
9. Female genital field with more than 3 pairs of long, posteriorly protruding, thick setae (fig. 4) *Cookatax*
 - Female genital field not so 10
10. Female genital field with all 4 acetabular plates bearing very elongate inner flaps with hairlike setae 11
 - Female genital field not so 12
11. With 4-6 pairs of acetabula (fig. 18) *Australatax*
 - With more than 6 pairs of acetabula (fig. 15) *Fulleratax*
12. Female genital field with 3 pairs of long, hairlike setae (fig. 3) and no short, stout setae 13
 - Female genital field with short, stout setae 14
13. Male fourth walking leg dimorphic (fig. 22) *Heteratax*
 - Male fourth walking leg dimorphic (fig. 21) *Giselatax*
14. All 4 female acetabular plates with short, stout setae and plates nearly equal in size and shape (fig. 7) *Kovietsatax*
 - Only anterior female acetabular plates with short, stout setae, and anterior and posterior plates different (figs. 8, 9, 10, 12 and 13) 15
15. Male genital field extending up onto dorsum (figs. 25 and 26) *Vietsatax*
 - Male genital field nearly circular in outline and on venter only 16
16. Male fourth walking leg Ge with a distal cluster of serrated setae and all tarsal claws of walking legs deeply bifid with the dorsal prong longer than the ventral prong *Anodontinatax*
 - Male fourth walking leg, if modified, without Ge with distal cluster of serrated setae and tarsal claws not as above 17
17. Female genital field with 4-6 pairs of acetabula (fig. 8) and male fourth walking leg similar to female and pedipalp Ta elongate with obvious but small clawlets and dorsal plates not obvious *Pentatax*

- Female genital field with more than 6 acetabular pairs (figs. 12 and 13) and/or male fourth walking leg dimorphic and/or pedipalp Ta nearly quadrate in outline with relatively large clawlets and/or obvious dorsal plates *Polyatax*

ACKNOWLEDGEMENTS

Daniel J. Bereza, Samuel L.H. Fuller, H. Dickson Hoese and the late Nell B. Causey provided valuable assistance in the many years of my studies. John C. Conroy and Ian M. Smith read the original manuscript. My wife, Gail, has provided her usual support during this work. Colin Fake and the Drafting Department of Sowela Technological Institute, Lake Charles, Louisiana, are also acknowledged.

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