

Nepenthacarus, a new genus of Histiostomatidae (Acari: Astigmata) inhabiting the pitchers of *Nepenthes mirabilis* (Lour.) Druce in Far North Queensland, Australia

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Abstract A new genus and species, *Nepenthacarus warreni*, is described from adults, deutonymphs, protonymphs and larvae collected from the fluid-filled pitchers of *Nepenthes mirabilis* (Lour.) Druce in northern Queensland, Australia.

Key words mite, Nepentheaceae, phytotelmata, pitcher plant.

INTRODUCTION

In recent years, phytotelmata have been lauded as excellent subjects for testing community theory as they harbour arthropod communities and are natural microcosms that can be easily manipulated, provide for replication and contain relatively few species (Kitching 1971, 1983, 1987; Maguire 1971; Frank & Lounibos 1983; Kitching & Pimm 1985; Pimm & Kitching 1987; Jenkins & Kitching 1990; Kitching & Beaver 1990; Naeem 1990; Sota 1996). The arthropod communities found in the fluid-filled pitchers of members of the genus *Nepenthes* L. (Nepentheaceae) make excellent research subjects and have played a major role in phytotelm community studies.

Since Beaver (1979a,b) first described the food webs of *N. albomarginata* T. Lobb ex Lindl. and *N. ampullaria* Jack of Peninsular Malaysia, pitcher communities have been used to investigate local and regional variation in food web structure, the meaning of food web patterns, and predation and competition in patchy habitats (Beaver 1983, 1985; Kitching & Pimm 1985; Kitching & Beaver 1990; Pimm *et al.* 1991; Mogi & Yong 1992; Clarke & Kitching 1993; Kato *et al.* 1993). Although histiostomatid mite species are common inhabitants of *Nepenthes* pitchers, little is known concerning their biology. In some community studies the mite component is completely ignored and, even when their presence is acknowledged, mites are relegated to a minor role in the community. Even our knowledge concerning the systematics of *Nepenthes*-inhabiting mites is minimal. Only four species have been described: *Zwickia guentheri* (Oudemans) from *N. distillatoria* L. in Sri Lanka (Oudemans 1915); *Z. nepenthesiana* Hirst from *N. ampullaria* in Singapore (Hirst 1928); *Creutzeria tobaica* Oudemans from *N. tobaica* Dans. in Java (Oudemans 1932); and *C. seychellensis* Nesbitt from *N. pervillei* Bl. in the Seychelles (Nesbitt 1979). In community studies, mite-inhabitants have often been assigned to one of the two genera of Histiostomatidae

without actually knowing the true identity of the species involved. Other authors have simply lumped all species together by family name. As early as 1928, Hirst noted that mites found in *N. ampullaria* and *N. distillatoria* were different species and indicated a need for 'further enquiry with a view to discovering if the mites found in various species of *Nepenthes* are peculiar to them'. Such an inquiry is yet to be done. To date, over 80 species of *Nepenthes* have been described (Phillips & Lamb 1996) and many are undoubtedly inhabited by undescribed species of histiostomatid mites.

As anyone studying *Nepenthes* communities can verify, mite populations are often quite large; sheer numbers more than compensate for their lack of size. An understanding of the roles that various mite species play in *Nepenthes* communities is therefore essential for an understanding of food webs and communities dynamics. A first step in this direction is the description of the various mite species involved. This paper describes a new species of histiostomatid mite that inhabits pitchers of *N. mirabilis* (Lour.) Druce in Far North Queensland, Australia. As the species could not be assigned to any of the nominal genera in the family Histiostomatidae, a new genus is proposed.

MATERIALS AND METHODS

Fluid-filled pitchers were collected from *N. mirabilis* in the vicinity of Weipa, Queensland, placed in zip-lock bags and transported back to the laboratory at Griffith University, Brisbane. The contents of each pitcher were placed in a finger bowl and examined for mites every few days under a dissecting microscope. Specimens were cleared in Nesbitt's solution, mounted in Hoyer's medium on microscope slides (Krantz 1978; Evans 1992) and examined utilising phase-contrast and Nomarski DIC microscopy (Leitz Daplan, Ernst Leitz Wetzlar GmbH, Wetzlar, Germany.)

Measurements are given in micrometres (μm) in the following order. Females: holotype female, mean and range (in parentheses). Males: as only two males were collected, measurements for each individual are given. Immatures:

mean and range (in parentheses). Nomenclature for idiosomal setae follows Griffiths *et al.* (1990) and for leg setae Grandjean (1939).

Because of the small numbers of mites collected, only one specimen, a protonymph, was prepared for examination under a scanning electron microscope (SEM). For this procedure, the specimen was dehydrated in ethanol, dried using the critical-point procedure, affixed to a stub using double-sided sticky tape and coated with gold–palladium in a sputter coater. Scanning microscopy was performed on an AMR 1200.

Abbreviations used: ANIC, Australian National Insect Collection, CSIRO Entomology, Canberra, ACT; QM, Queensland Museum, Brisbane, Queensland; UMMZ, University of Michigan, Museum of Zoology, Ann Arbor, Michigan, USA.

TAXONOMY

Nepenthacarus gen. n.

Type species. *Nepenthacarus warreni* sp. n. by present designation.

Description. *Homeomorphic instars.* Idiosoma unsclerotised except for small, lightly sclerotised prodorsal sclerite. Idiosomal setae *se*, *c*₂, *cp*, *d*₂, *e*₁, *e*₂ and *h*₁ located on lateral margin and thereby forming a U-shaped row (Figs 3,8,15,28,30); each seta expanded laterally at base, flattened dorsoventrally and tapering to a point distally (Fig. 4). Tarsal setae *f*, *q* and *v* of tarsi I–III, with the exception of seta *f* of male tarsus I, broad, flat, rounded distally and overlapping (Fig. 5). **Adults.** Female copulatory opening terminal, between setae *h*₂. Two pairs of *ps* setae flank the anus of male; *ps* setae absent in female. Anterior coxal apodemes I directed posteromedially, joining at midline to form a V-shape in female and a Y-shaped sternum in male. Anterior coxal apodemes III of female reduced. Legs I of male only slightly enlarged in comparison to female; tibiae I of males and females similar. Tarsal solenidia ω_1 of legs I, II near base of segment. Female empodial claw I slightly longer than basal width of tarsus I, empodial claw II about half length of tarsus II, empodial claws III–IV longer than respective tarsi. With exception of tarsus II, empodial claws of male shorter than in female and never longer than respective tarsi. **Deutonymph.** Idiosoma with cuticle smooth, lightly sclerotised; gnathosomal remnant borne on anterior projection with heavily pigmented margins. Gnathosomal subcapitular remnant reduced, wider than long, without palpal remnants. Area between gnathosoma and coxal apodemes I smooth, not punctate. Coxal setae *1a* absent, *3b* small setae. Empodial claw IV absent.

Etymology. The generic name *Nepenthacarus* combines ‘*Nepenthes*’, the generic name for the pitcher plant, with ‘*acarus*’, Latin for mite.

Nepenthacarus warreni sp. n. (Figs 1–31)

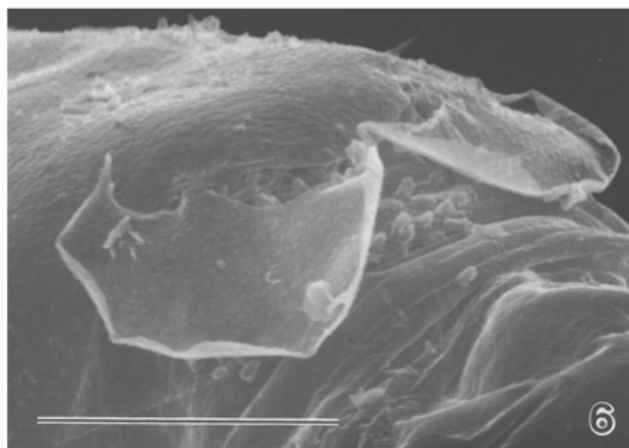
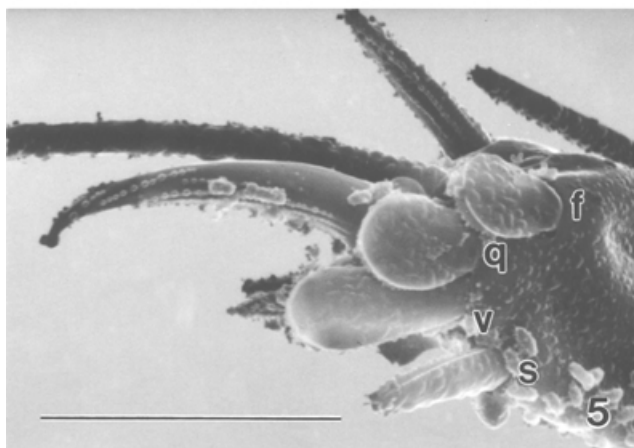
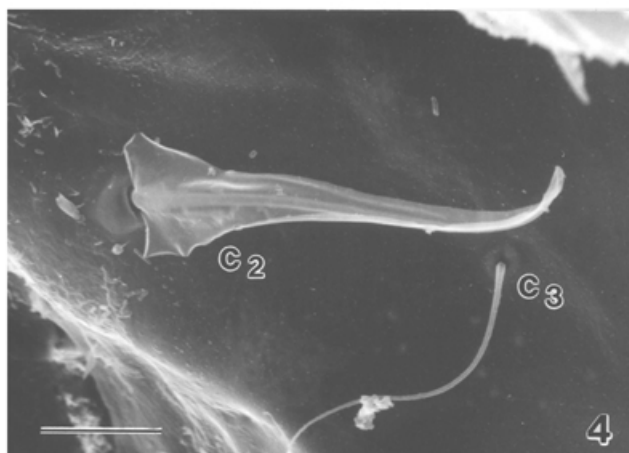
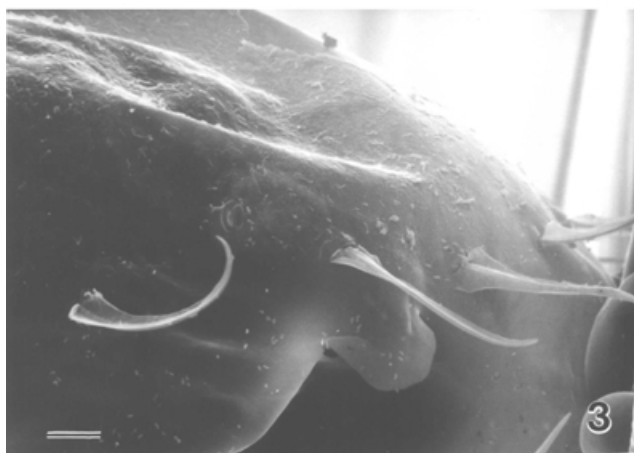
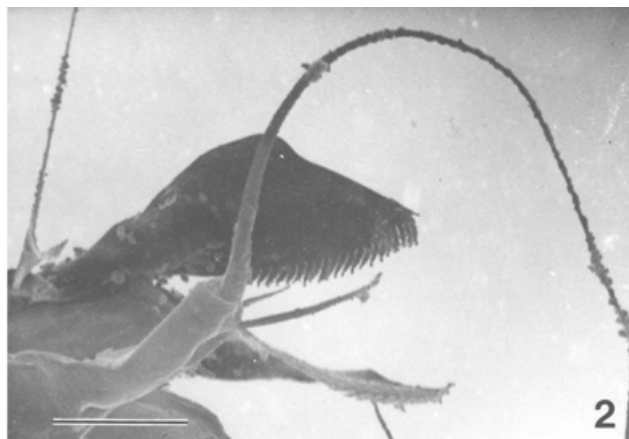
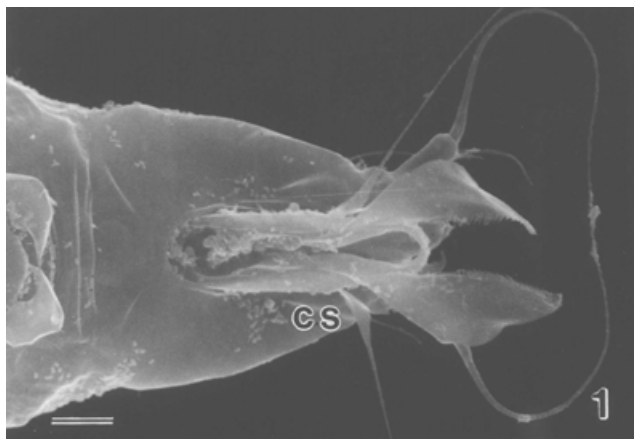
Types. *Queensland.* Holotype female, Weipa vicinity, 29.ii.94, N.J. Fashing, ex fluid-filled pitcher of *Nepenthes*

mirabilis (QM); paratypes (same data as holotype): 1 female, 1 male, 1 deutonymph, 2 protonymphs, 1 larva (QM); 1 female, 1 deutonymph, 1 protonymph, 1 larva (ANIC); 2 female, 1 male, 2 deutonymphs, 1 protonymph, 1 larva (UMMZ).

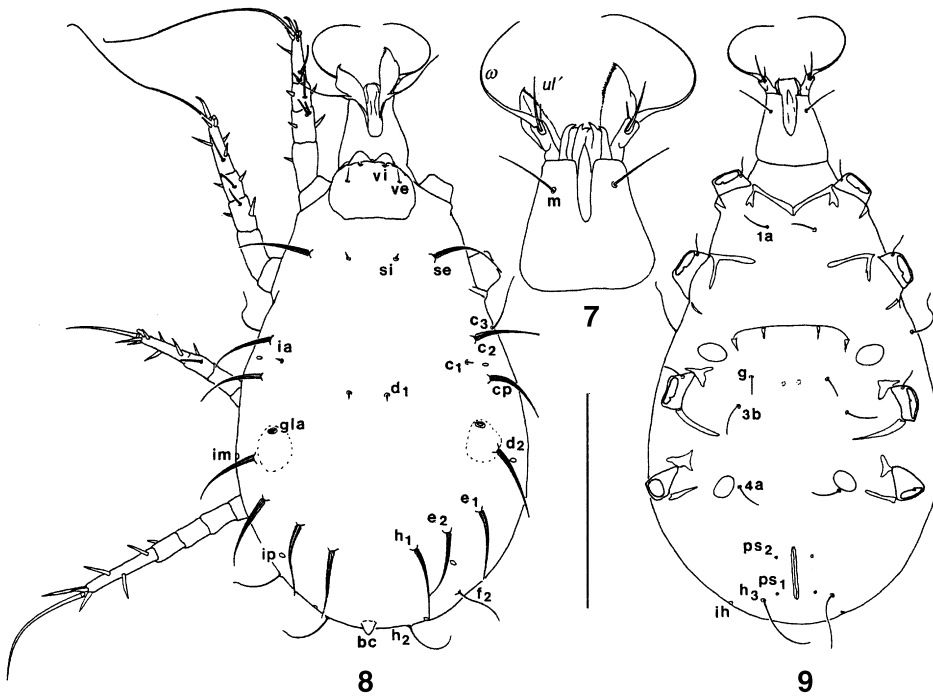
Description. **Female** (Figs 7–13). Idiosoma pyriform, widest in posterior third. Idiosomal length 471, 459 (436–476); width at level of cupule *im* 295, 292 (267–318). Gnathosoma (Figs 1,2,7). Chelicera laterally flattened; fixed digit expanded distally, arched dorsally and with numerous fine ventral serrations. Moveable digit not visible. Dorsal cheliceral seta (*cs*) extremely long, with flattened, laterally-expanded base. Palp cylindrical, bearing elongate solenidium (ω) and shorter eupathedral seta (*ul*′) distally on terminal segment; solenidium over four times as long as eupathedral seta. Solenidium reflexed outward as a result of mesial expansion at base. Terminal segment of palp bearing short seta dorsally. Venter of subcapitulum bearing pair of filiform setae (*m*). Dorsum (Fig. 8). Prodorsal sclerite very lightly sclerotised, slightly wider than long. Sejugal furrow absent. Opisthonotal gland opening (*gla*) anterior and slightly mesiad of seta *d*₂. Cupules located as follows: *ia* between setae *c*₂ and *cp*, *im* slightly posterior and laterad of seta *d*₂, and *ip* between setae *e*₂ and *f*₂. Bursa copulatrix (*bc*) at end of short projection located terminally between setae *h*₂. Dorsum bearing 15 pairs of setae. Internal vertical setae *vi* appear to arise from distal margin of prodorsal sclerite, having membranous lateral expansions forming a broad flange (Fig. 6). Setae: *ve* 11, 12 (11–13) thin and filiform, located on prodorsal sclerite; *si* 5, 4.8 (4–5); *c*₁ 5, 4.6 (4–5) and *d*₁ 3, 4.3 (3–5) short and spinelike. Setae: *se* 69, 75 (69–85), *c*₂ 66, 70 (63–76), *cp* 72, 68 (62–73), *d*₂ 62, 68 (62–74), *e*₁ 70, 69 (65–72), *e*₂ 66, 65 (61–69) and *h*₁ 66, 64 (61–68) located laterally and forming U-shaped row on dorsal margin of idiosoma; each seta expanded laterally at base, flattened dorsoventrally and tapering to a point distally. Setae: *c*₃ 52, 55 (48–62), *f*₂ 41, 46 (41–51), and *h*₂ 51, 50 (45–57) filiform. Venter (Fig. 9). Anterior coxal apodemes I bifurcate at base with dorsal branches directed posteromedially, joining at midline to form a V-shape, ventral branches directed posteriorly. Anterior coxal apodemes II bifurcate at base with dorsal branches directed medially and ventral branches directed posteriorly. Anterior coxal apodemes III and IV somewhat bifurcated with short branches. Posterior coxal apodemes I–IV directed medially. Ovipore a transverse slit located at level of setae *c*₃. A pair of small, longitudinal, genital apodemes on each side of ovipore. A pair of small structures resembling vestigial alveoli located centrally, posterior to ovipore and between setae *g*. Genital papillae oval; anterior pair laterad and slightly posterior to ovipore, posterior pair on coxal fields IV. Cupules *ih* on lateral margin of idiosoma between setae *f*₂ and *h*₂. Anus ventroterminal. Venter bearing five pairs of thin, filiform setae: *1a* 25, 23 (18–27) on coxal field I, *3b* 23, 26 (23–29) on coxal field III, *4a* 14, 17 (14–20) on coxal field IV, *g* 11, 12 (10–15) on coxal fields III posterior to genital opening, *h*₃ 75, 67 (58–75) laterad posterior margin of anus. Vestigial alveoli of setae *ps*₁ and *ps*₂ adjacent

to the anus. Legs (Figs 10–13). Legs slender. Lengths, measured from base of trochanter to tip of tarsus: I 164, 171 (164–179), II 167, 173 (164–186), III 152, 154 (148–150), IV 188, 190 (174–202). Tarsal lengths: I 47, 48 (46–49), II 52, 54 (50–59), III 50, 53 (50–56), IV 77, 78 (73–83). Setation (I–IV): tarsus 13–12–10–10; tibia 2–2–1–1, genua 2–2–0–0, femora 1–1–0–1 and trochanters 1–1–1–0. Relative position, size and shape of setae as indicated in figures. Setation (trochanters to tibiae): trochanters I–III each with a filiform

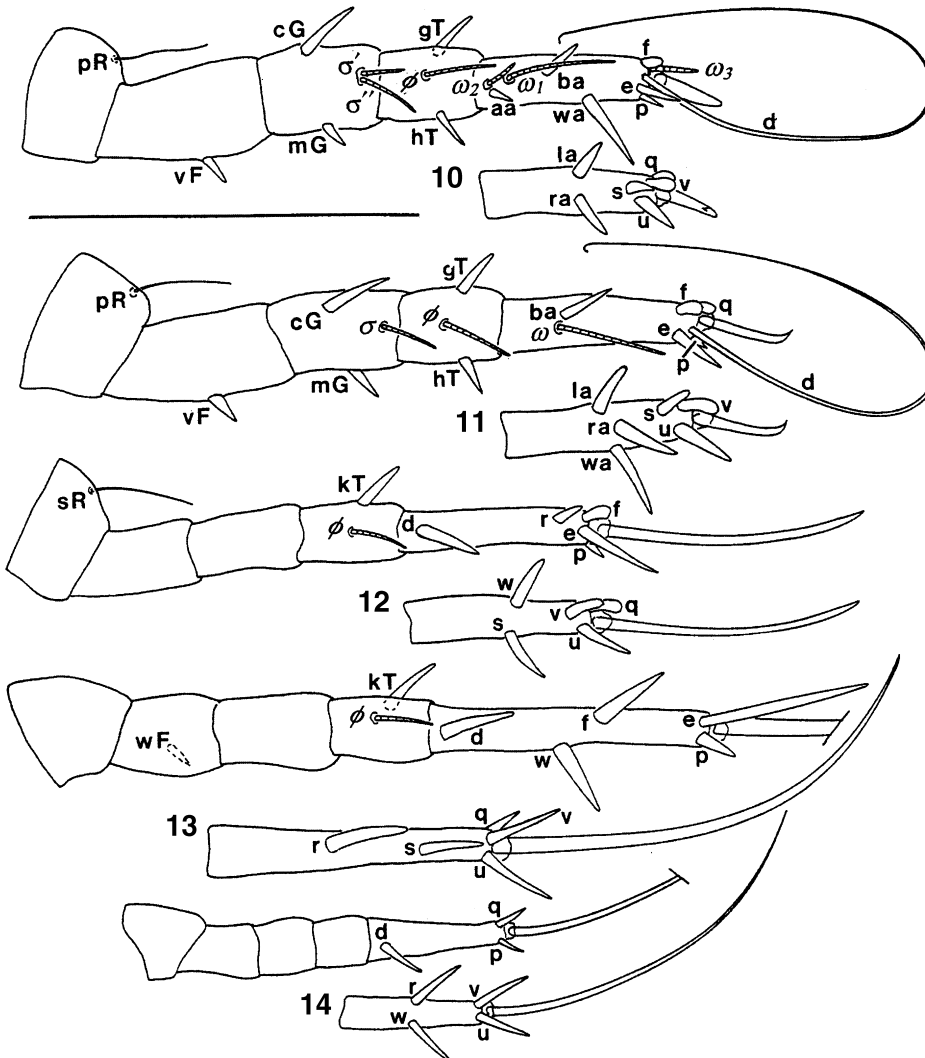
seta (*pR*, *sR*); femora I, II and IV with setae *vF*, *wF* as stout spines; genua I, II with setae *cG* and *mG* as stout spines; tibiae I, II with setae *gT* and *hT* and tibiae III, IV with setae *kT* as spines. Tarsi with the following setation: tarsus I with seta *aa* as short spine located near base of segment; setae *ba*, *la*, *ra* and *wa*, all as stout spines in centre of segment; seta *d* long, filiform, apical; setae *f*, *q* and *v* all apical, short, broad, flat, rounded distally; setae *e*, *p*, *u* and *s* all as stout apical spines. Tarsus II similar to tarsus I except lacking seta *aa*.



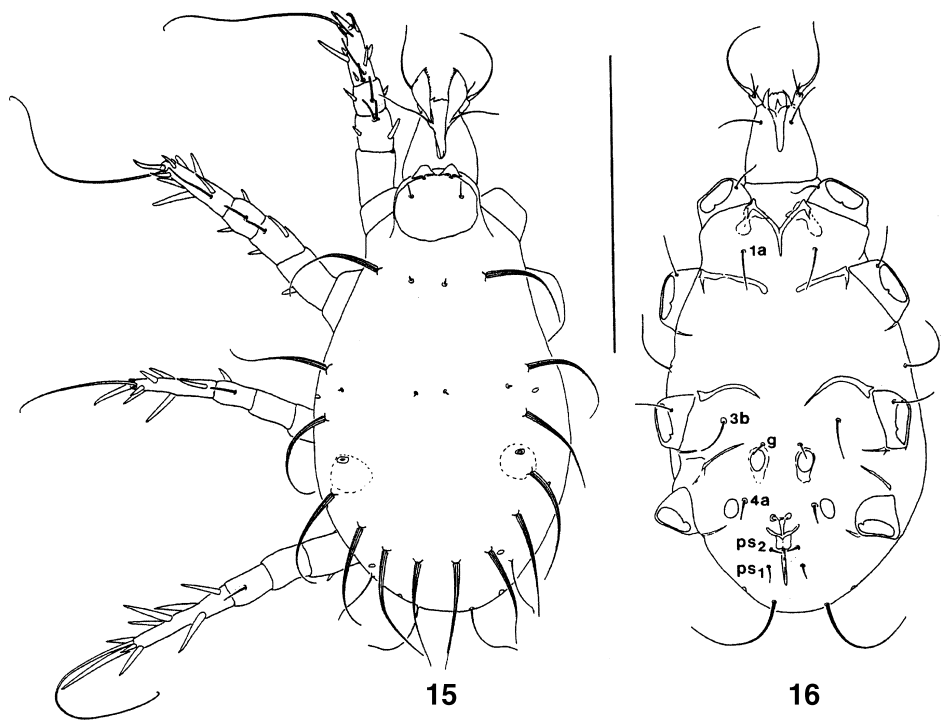
Figs 1–6. *Nepenthacarus warreni* sp. n., protonymph. (1) Gnathosoma, dorsal view. (2) Chelicerae and pedipalp, ventrolateral view. (3) Row of modified dorsal setae along lateral margin of idiosoma. (4) Modified seta (*c*₂) and normal seta (*c*₃). (5) Modified apical setae (*f*, *q*, *v*) on tarsus II. (6) Modified dorsal setae *vi*, frontal view. CS, cheliceral setae. Scale bar = 10 µm.



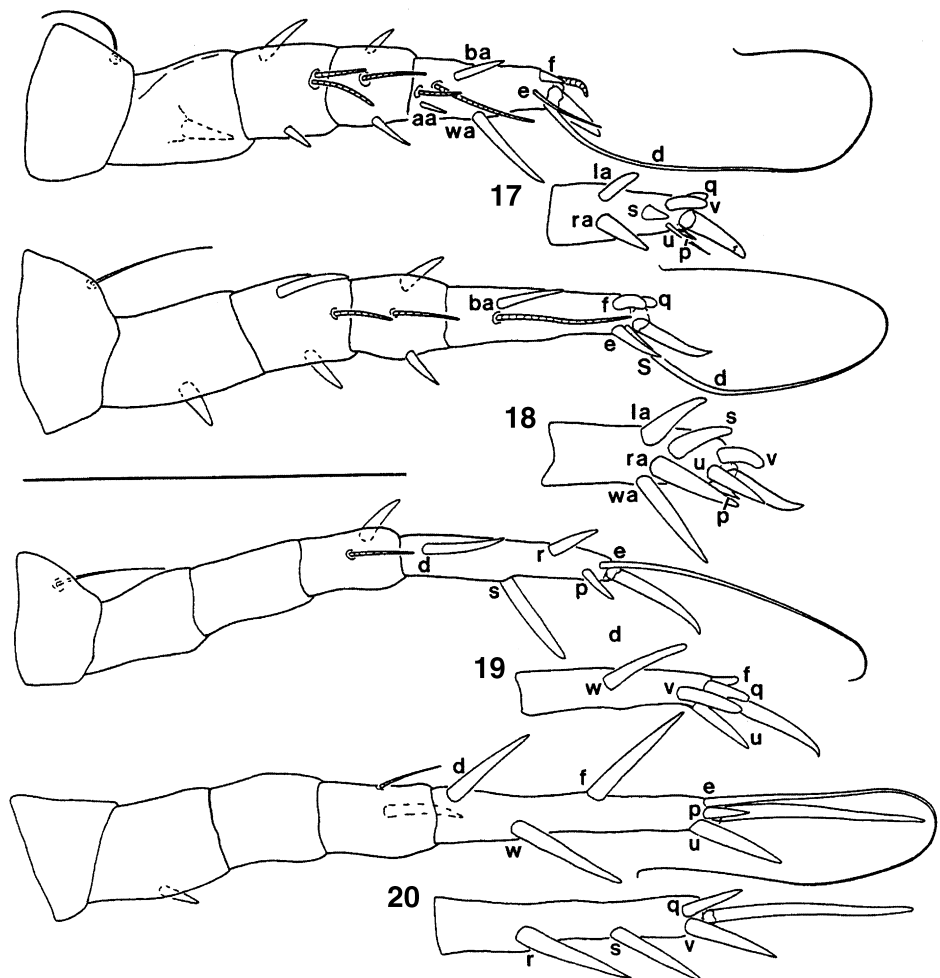
Figs 7–9. *Nepenthacarus warreni* sp. n., female. (7) Gnathosoma, ventral view. (8) Idiosoma, dorsal view. (9) Idiosoma, ventral view. Scale bar: Fig. 7 = 100 μ m; Figs 8–9 = 200 μ m.



Figs 10–14. *Nepenthacarus warreni* sp. n. (10) Female, leg I. (11) Female, leg II. (12) Female, leg III. (13) Female, leg IV. (14) Protonymph, leg IV. Scale bar = 100 μ m.



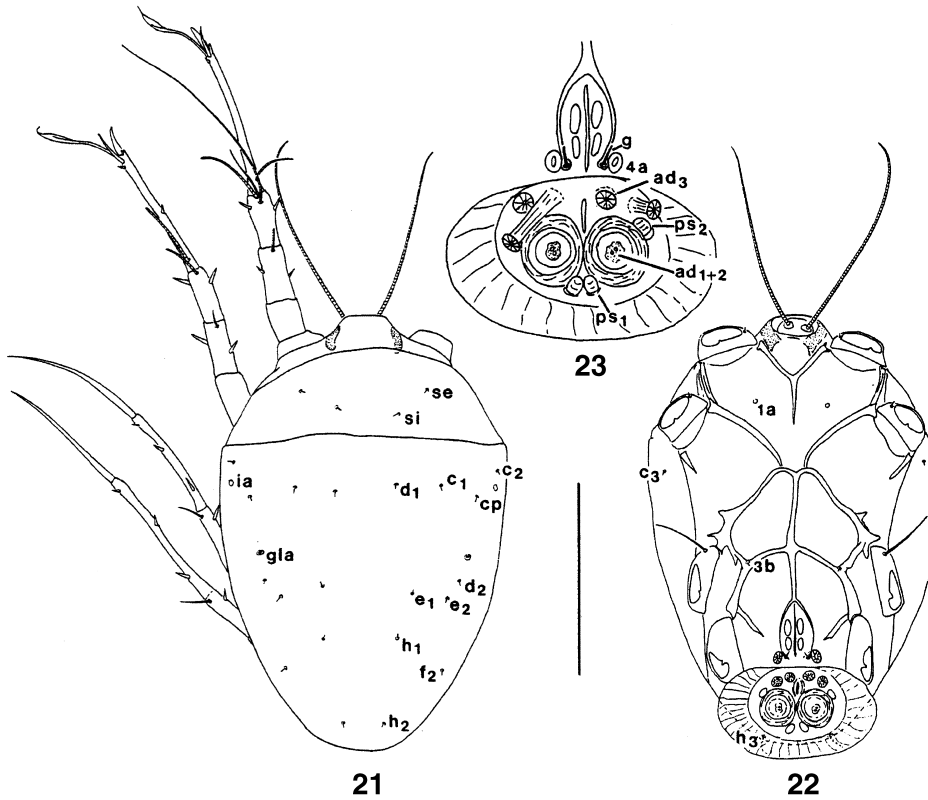
Figs 15–16. *Nepenthacarus warreni* sp. n., male. (15) Idiosoma, dorsal view. (16) Idiosoma, ventral view. Scale bar = 200 μ m.



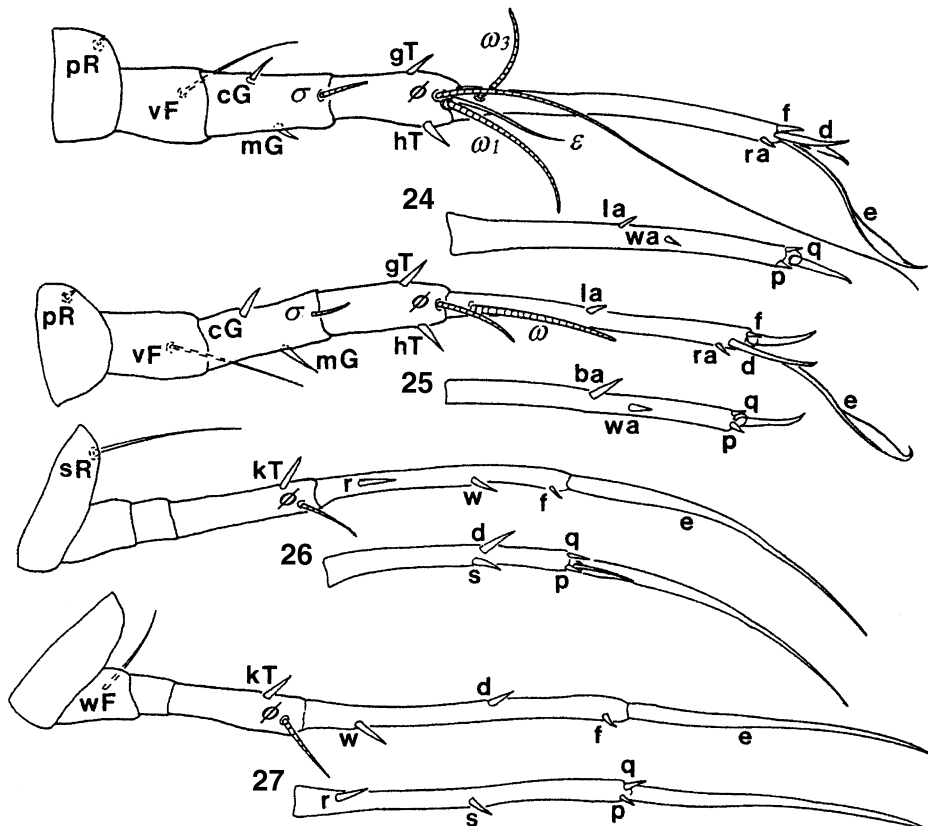
Figs 17–20. *Nepenthacarus warreni* sp. n., male. (17) Leg I. (18) Leg II. (19) Leg III. (20) Leg IV. Scale bar = 100 μ m.

Tarsus III with seta *d* as stout basal spine; setae *w* and *s* as stout spines slightly anterior to middle of segment; seta *r* as stout spine near apex of segment; setae *f*, *q*, *v*, *p* and *u*, similar

to tarsi I and II; seta *e* 24, 26 (24–28) long, apical spine. Tarsus IV similar to tarsus III except setae *r* and *f* as spines located further back on segment; setae *q* and *v* as spines; seta *e*



Figs 21–23. *Nepenthacarus warreni* sp. n., deutonymph. (21) Idiosoma, dorsal view. (22) Idiosoma, ventral view. (23) Attachment organ, ventral view. Scale bar: Figs 21–22 = 100 μm; Fig. 23 = 60 μm.

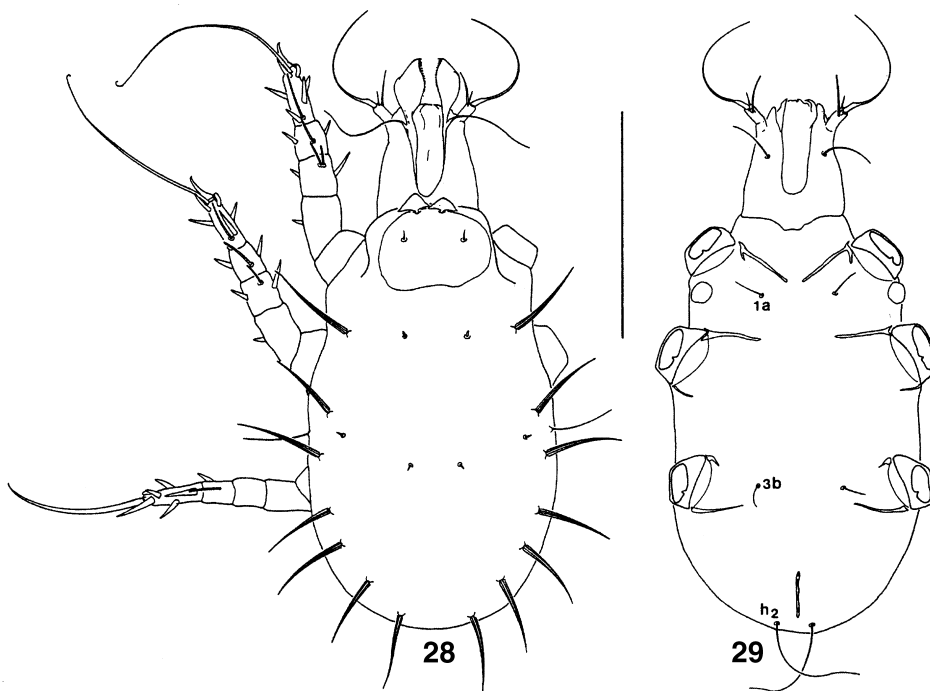


Figs 24–27. *Nepenthacarus warreni* sp. n., deutonymph. (24) Leg I. (25) Leg II. (26) Leg III. (27) Leg IV. Scale bar = 100 μm.

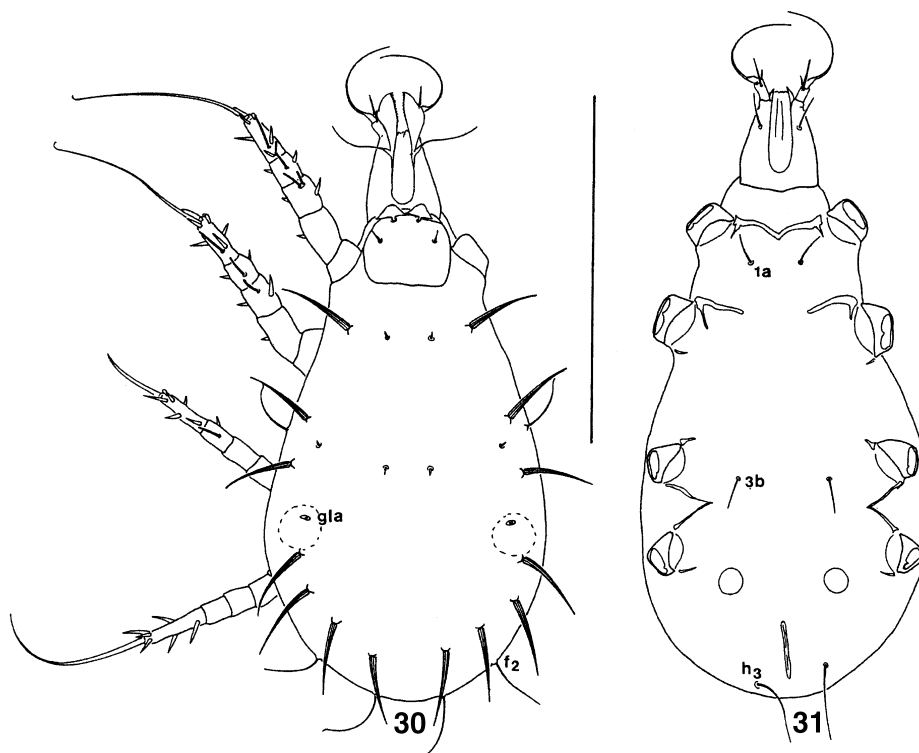
43, 46 (41–52) much longer. Solenidia I to IV: tarsi 3-1-0-0, tibiae 1-1-1-1, genua 2-1-0-0. Genu with solenidia σ originating one-fifth of way from apical end, solenidium σ' two-thirds length of σ'' . Tibiae I–IV with solenidium ϕ originating approximately midway along segment. Tarsus I with solenidium ω_2 originating near base of segment just posterior to ω_1 ; solenidium ω_3 apical. Famulus (ϵ) absent. Pretarsi with small, membranous ambulacra. Claw I 19, 20 (17–22) stout, curved

ventrally, 35% of tarsal length. Claw II 24, 26 (22–29) slightly curved, 48% of tarsal length. Claw III 73, 73 (66–78) long, 138% of tarsal length. Claw IV 118, 124 (117–135) long, 159% of tarsal length. **Male** (Figs 15–20). Idiosomal shape similar to female; length 294, 280, width at level of opening to opisthosomal gland (*gla*) 173, 161. Gnathosoma and general features of idiosoma similar to female. Dorsum (Fig. 15). Dorsum bearing 15 pairs of setae with shapes and

Figs 28–29. *Nepenthacarus warreni* sp. n., larva. (28) Idiosoma, dorsal view. (29) Idiosoma, ventral view. Scale bar = 100 μ m.



Figs 30–31. *Nepenthacarus warreni* sp. n., protonymph. (30) Idiosoma, dorsal view. (31) Idiosoma, ventral view. Scale bar = 200 μ m.



locations similar to female. Setae *vi*; *ve* 10; *si* 5, 5; *c*₁ 4, 4; *d*₁ 5, 4; *se* 117, 91; *c*₂ 76, 69; *cp* 61, 73; *d*₂ 87, 67; *e*₁ 80, 70; *e*₂ 80, 66; *h*₁ 80, 71; *c*₃ 48, 41; *f*₂ 38, 46; *h*₂ 60, 45. Location of cupules and opisthosomal glands as in female. Venter (Fig. 16). Anterior coxal apodemes I bifurcate at base with dorsal branches directed posteriomediaally, joining at midline to form Y-shaped sternum, ventral branches directed posteriorly. Anterior coxal apodemes II bifurcate at base with dorsal branches directed medially and ventral branches directed posteriorly. Anterior coxal apodemes III and IV and posterior coxal apodemes II, III and IV, directed medially. Genital apparatus located centrally and just posterior to coxal fields IV. Anus a longitudinal slit 'coupled' to posterior end of genital apparatus. Two pairs of oval genital papillae; anterior pair between coxal fields III and IV, posterior pair on coxal fields IV. Venter bearing seven pairs of setae: *1a* 28, 20 filiform, on coxal field I; *3b* 22, 23 filiform, on coxal field III; *4a* 13, 11 filiform, on coxal field IV and mesiad to posterior genital papilla; *g* 10, 7 filiform, anterior to anterior genital papilla; *ps*₁ 8, 11 and *ps*₂ 8, 8 filiform, adjacent to anal slit; and *h*₃ 101, 89 similar to enlarged dorsal setae, except thinner and located on posterior margin of idiosoma. Legs (Figs 17–20). More robust than in female. Lengths, from base of trochanter to tip of tarsus: I 138, 132; II 168, 162; III 153, 153; IV 171, 177. Tarsal lengths: I 31, 35; II 48, 48; III 48, 48; IV 69, 67. Similar in leg chaetotaxy and solenidotaxy to female with the following exceptions: most tarsal setae more robust; setae *e* and *u* on tarsus I filiform; seta *e* 77, 89 on tarsus III and seta *e* 108, 136 on tarsus IV long and tapering; solenidia ω_3 more robust and arched ventrally. Empodial claws shorter than in female: claw I 17, 18, 13% of tarsal length; claw II 24, 26, 52% of tarsal length; claw III 31, 34, 68% of tarsal length; claw IV 53, 73, 93% of tarsal length.

Deutonymph (Figs 21–27). Body broadly ovoid; idiosomal length 234 (213–254); width 156 (139–171). Gnathosoma with subcapitular remnant extremely reduced and without setae; palpal remnants absent; long palpal solenidia 105 (89–121) arising directly from subcapitulum. Dorsum (Fig. 21). Short idiosomal protuberance surrounding gnathosoma and bearing a longitudinal heavily pigmented region on each side. Propodosomal and hysterosomal sclerites separated by well-developed sejugal furrow. Propodosomal sclerite with two pairs and hysterosomal sclerite with 10 pairs of very short filiform setae. Opisthosomal gland opening located laterally and anterior to seta *d*₂. Cupules *ia* located laterally and slightly posterior to setae *c*₂; other cupules not observed. Venter (Fig. 22). Anterior apodemes of coxal fields I fused to form Y-shaped sternum; anterior apodemes of coxal fields II curved medially, joining with anterior apodemes III. Anterior apodemes III directed anteriorly and mesially, fused with each other and with anterior apodemes of coxal fields II; posterior projection at base of anterior apodemes III fused midway with anterior apodemes IV; coxal fields III completely enclosed. Medial apodeme well developed, extending posteriomediaally from anterior apodemes III to slightly anterior of genital opening, bifurcating with branches extending laterally and parallel to genital

opening and surrounding genital seta (*g*). Seta *c*₃ very short, filiform, positioned on hysterosomal sclerite slightly posterior and laterad of trochanter II. Seta *h*₃ filiform, approximately four times longer than dorsal idiosomal setae and located on posterior idiosomal margin under fringe of attachment organ. Setae of coxal fields I (*1a*) absent, their positions represented by vestigial alveoli. Setae of coxal fields III (*3b*) short, filiform, located at junctions of posterior branches of anterior apodemes III with anterior apodemes IV. Setae *3a* absent. Setae of coxal fields IV (*4a*) sucker-like. Genital opening between coxae IV; setae *g* short, filiform, adjacent to posterior end of genital opening. Genital papillae narrowly oval, anterior pair larger than posterior pair. Attachment organ (Fig. 23) well developed with large, membrane-like outer fringe. Anterior suckers (*ad*₃) stalked with spokes radiating from centre. Median suckers large, consisting of a marginal ring surrounding an inner core containing paired vestigial alveoli (*ad*₁₊₂). Setae *ps*₂ conoidal, situated anterio-laterally to median suckers; setae *ps*₁ conoidal, situated medially and posteriorly to median suckers. Anterior lateral cuticular suckers stalked with spokes radiating from centre; similar in appearance to *ad*₃. Posterior median and posterior lateral cuticular suckers not present. Anus located between anterior and median suckers. Legs (Figs 24–27). Legs slender, elongate. Femur and genu of legs I, II as well as genu and tibia of legs III, IV appear to be fused. Legs I 177 (162–196) and II 168 (157–177) longer than legs III 125 (116–135) and IV 140 (127–154). Tarsal lengths: I 51 (48–54), II 50 (48–52), III 33 (32–34), IV 37 (34–39). Setation (I–IV): tarsus 8-9-8-8, tibiae 2-2-1-1; genua 2-2-0-0, femora 1-1-0-1, trochanters 1-1-1-0. Setation (trochanters to tibiae): trochanters I, II each with short spinelike seta (*pR*), trochanter III with long filiform seta (*sR*); femora I, II, IV each with long filiform setae (*vF*, *wF*), *vF* longer than *wF*; genua I, II with setae *cG* and *mG* as stout spines; tibiae I, II with setae *gT* and *hT* and tibiae III, IV with setae *kT* as stout spines. Tarsi with the following setae present: tarsus I with setae *la*, *wa*, spinelike, in middle of segment; *ra*, *f*, *p* and *q* spinelike, near apex of tarsus; *d* apical, flat, tapering to a thin point, approximately as long as claw; *e* apical, long, foliate distally. Tarsus II with setae similar to tarsus I except spinelike seta *ba* present in middle of segment. Tarsus III with spinelike seta *r* at base of segment; spinelike setae *d*, *s* and *w* slightly anterior to middle of segment; setae *f*, *p* and *q* apical, spinelike; seta *e* large, elongate apical spines tapering to a point distally. Tarsus IV similar to tarsus III except setae *w*, basal. Solenidia (I–IV): tarsus 2-1-0-0, tibia 1-1-1-1, genu 1-1-0-0. Solenidia (σ) genua I, II short, located at apex of segment. Solenidium (ϕ) tibia I extremely long, 114 (103–123), tapering distally; solenidia (ϕ) much shorter on tibiae II–IV; all located near apex of segment. Solenidium (ω_1) tarsus I tapering distally, arising from base of segment and in notch of tibia apex; (ω_1) slightly more anterior on tarsus II. Solenidium (ω_3) tarsus I tapering distally, near base of segment. Famulus (ϵ) elongate, tapering, filiform located adjacent to solenidium ω_1 on tarsus I. Pretarsi I, II consisting of short membranous ambulacra with long, slightly curved,

empodial claws; pretarsus III consisting of short membranous ambulacrum with slender, curved empodial claw; pretarsus IV, including ambulacrum and empodial claw, absent.

Egg. One egg observed within female body; smooth, unsculptured chorion; length 172, width 89. **Larva** (Figs 28,29). Idiosomal length 196 (181–205); width 110 (99–117). Gnathosoma similar to female. Opisthosomal glands absent, cupules not observed. Dorsum (Fig. 28). Bearing 13 pairs of setae with shapes and locations similar to female: *vi*; *ve* 4 (4–4); *si* 3 (3–3); *se* 39 (37–40); *c*₁ 3 (2–4); *c*₂ 37 (34–39); *c*₃ 27 (26–28); *cp* 33 (32–35); *d*₁ 3 (2–3); *d*₂ 32 (31–32); *e*₁ 29 (29–30); *e*₂ 30 (27–32); *h*₁ 29 (26–30). Venter (Fig. 29). Anterior coxal apodemes I free; directed medially. Anterior and posterior coxal apodemes II, III directed medially. Claparede's organ, small circular ring located laterally on coxal field I. Venter bearing three pairs of filiform setae: *Ia* 12 (10–15), located on coxal field I; *3b* 11 (10–12), located on coxal field III; and *h*₂ 43 (39–46), located on posterior margin of idiosoma behind anus. Legs. Lengths (base of trochanter to tip of tarsus): I 84 (81–86); II 84 (83–86); III 71 (68–73). Tarsal lengths: I 23 (23–23); II 22 (20–25); III 21 (20–21). Leg chaetotaxy and solenidiotaxy similar to female except trochanter setae I–III and solenidia (ω_2 and ω_3) absent. Empodial claws similar to female. Claw I 12 (11–12); 52% of tarsal length. Claw II 12 (11–13); 54% of tarsal length. Claw III 61 (60–62); 290% of tarsal length.

Protonymph (Figs 30,31). Idiosomal length 267 (240–300); width 147 (132–166). Gnathosoma similar to female. Opisthosomal gland opening between setae *cp* and *d*₂; cupules not observed. Dorsum (Fig. 30). Bearing 15 pairs of setae with shapes and locations similar to female: *vi*; *ve* 8 (5–11); *si* 4 (3–5); *se* 47 (45–53); *c*₁ 4 (2–5); *c*₂ 42 (37–46); *c*₃ 30 (29–32); *cp* 36 (32–46); *d*₁ 3 (2–4); *d*₂ 42 (39–43); *e*₁ 41 (36–45); *e*₂ 40 (36–43); *f*₂ 24 (21–26); *h*₁ 38 (34–42); *h*₂ 34 (34–46). Venter (Fig. 31). Anterior coxal apodemes I, II similar to female. Posterior coxal apodeme III join with anterior coxal apodeme IV. One pair of small, round genital papillae located slightly posterior to coxal fields IV. Venter bearing three pairs of filiform setae: *Ia* 15 (14–17), located on coxal field I; *3b* 16 (15–17), located on coxal field III; and *h*₃ 43 (38–52), located on idiosomal margin posterior to anus. Legs. Lengths (base of trochanter to tip of tarsus): I 108 (105–114); II 111 (107–117); III 91 (88–97); IV 94 (91–97). Tarsal lengths: I 29 (27–30); II 30 (28–32); III 27 (27–28); IV 34 (33–36). Legs I–III similar to larva with same chaetotaxy and solenidiotaxy, except solenidium (ω_2) present on tarsus I. Legs IV present (Fig. 14), chaetotaxy similar to female except setae *s*, *e* and *f* absent. Empodial claws similar to female except longer in respect to tarsi. Claw I 14 (13–14), 48% of tarsal length. Claw II 16 (14–18), 53% of tarsal length. Claw III 46 (43–49), 170% of tarsal length. Claw IV 104 (92–119), 305% of tarsal length. **Tritonymph**. Unknown.

Etymology. The species is named in honor of Paul Warren who was a resident of Weipa during my visits to northern Queensland. He kindly volunteered his time to help locate and collect pitchers. Without his help, this study could not have been done.

Taxonomic remarks. Fashing and OConnor (1984) proposed a monophyletic lineage within the family Histiotomatidae, subfamily Histiotomatinae, characterised by the presence, in the deutonymph, of a ventral, apical, idiosomal projection that bears the gnathosomal remnant and has strongly sclerotised and pigmented lateral margins. Adults of this lineage are characterised by enlarged empodial claws and the non-deutonymphal instars of all known taxa inhabit phytotelmata. Currently, the nominate genera *Hormosianotus* Fain, *Sarraceniopus* Fashing and OConnor, *Zwickia* Oudemans and *Creutzeria* Oudemans belong to this lineage (Fashing & OConnor 1984) and *Nepenthacarus* can now be added to the list. *Nepenthacarus* is most closely allied with the genera *Zwickia* and *Creutzeria*. All three inhabit the fluid-filled pitchers of *Nepenthes* and are characterised by the reduction of female coxal apodemes III, the terminal position of the female copulatory opening and the absence of deutonymph empodial claws IV. *Nepenthacarus* and *Creutzeria* share in common the basal location of tarsus I solenidium ω_1 (apical in *Zwickia*), the fusion of female coxal apodemes I (separated in *Zwickia*), the absence of *ps* setae in the female (three pairs in *Zwickia*), empodial claws III–IV longer than tarsi in the female (shorter in *Zwickia*) and leg I of the male only slightly enlarged or similar in comparison to the female (greatly enlarged in *Zwickia*). *Nepenthacarus* differs from *Creutzeria* in the following characters: weakly sclerotised adult prodorsal sclerite (absent in *Creutzeria*); short tarsal setae *f* and *q* on legs II–IV in adult (greatly elongated in *Creutzeria*); female empodial claw II shorter than tarsus (longer in *Creutzeria*); tibia I of male similar in comparison with female (enlarged and with modified seta in *Creutzeria*); absence of seta on coxa I of deutonymph (small seta or conoid on coxa I in *Creutzeria*). In addition, *Nepenthacarus* moves about by walking (skating) on the water surface and *Creutzeria* by swimming under the water.

Biology. *Nepenthacarus warreni* appears to be a relatively rare inhabitant of *N. mirabilis* pitchers in the Weipa vicinity, being recovered from only one of the 39 pitchers examined. All specimens were collected from the water surface and recent observations on undescribed species of the genus in both Thailand and Brunei reveal that water surface is their normal habitat. The occasional individual found submerged probably results from accidental immersion while pouring the fluid from the pitcher into a dish for observation. Small size, coupled with morphological adaptations, allow them to take advantage of water surface tension and occupy this niche. Analogous to water striders (Gerridae), the legs, held widely apart, are strategically positioned for life on the water surface. The U-shaped row of setae surrounding the lateral margin of the idiosoma (Figs 3,8,15,28,30) are expanded laterally and flattened dorsoventrally (Fig. 4) to increase surface area. Located at approximately water level, they function as 'floats'. Backward movements of legs I, II, and especially III propel individuals forward. The elongate, flattened claws on tarsi III quite likely aid in this function. When skating across the water, legs IV trail behind and probably act as rudders for steering. Observations in south-east Asia

indicate that individuals often crawl about on debris or arthropod parts floating on the water surface, a feat facilitated by the short claws on the tarsi of legs I and II.

The gnathosoma has the typical histiostomatid morphology with non-chelate, serrated chelicerae and pedipalps each bearing a very long, flagella-like terminal seta. It has been demonstrated in other species with similar gnathal modifications (Hughes 1953; Fashing 1994) that the long, terminal pedipalpal setae beat in a manner that creates a vortex in the fluid medium, thereby drawing small particulate matter and microorganisms toward the anterior region of the subcapitulum. Here the food is raked into the gnathosoma by alternate protraction and retraction of the serrated chelicerae. The surface film is rich in microorganisms and fine particulate matter, and *N. warreni* undoubtedly exploits this resource. This mode of feeding classifies *N. warreni* as a filtering collector (Cummins & Klug 1979). In south-east Asia, *Nepenthacarus* was often observed moving about on debris and decomposing insect parts floating on the water surface. Such substrates are often richly covered with microbes as well as fine particulate matter. The whip-like pedipalpal setae can be used to stir up this material and the chelicerae once again used to rake it into the gnathosoma ('gathering collector' [Cummins & Klug 1979]). *N. warreni* therefore probably functions as a filtering collector as well as a gathering collector in the pitcher plant community. Bongers *et al.* (1985) stressed the need for a knowledge of ontogenetic transformations in histiostomatid taxa as, once such data are known for sufficient taxa, they might prove useful in ascertaining character state polarities or phylogenetic relationships. Although tritonymphs of *N. warreni* were not seen, the other ontogenetic stages are described and at least partially corroborate an ontogeny that appears unique to the family Histiostomatidae. Opisthosomal glands are absent in the larva and tritonymph but are present in the protonymph and adult (Hughes & Jackson 1958; Fashing 1973; Bongers *et al.* 1985). As the tritonymphal instar of *N. warreni* was not seen, the absence of opisthosomal glands in this instar can only be surmised.

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