SYSTEMATICS AND ECOLOGY OF *NAIADACARUS NEPENTHICOLA*, A NEW SPECIES OF ACARIDAE (ACARI : ASTIGMATA) INHABITING THE PITCHERS OF *NEPENTHES BICALCARATA* HOOK. F. IN BRUNEI DARUSSALAM

Norman J Fashing[1] and Tock Hing Chua[2]

1.Department of Biology, College of William and Mary, Williamsburg, VA 23187-8795,USA, e-mail: njfash@wm.edu; 2. Department of Biology, Universiti Brunei Darussalam, Jalan Tunku Link, Bandar Seri Begawan 2028, Negara Brunei Darussalam; Current address: Asian Institute of Medicine, Science and Technology, Amanjaya, 08000 Sungai Petani, Kedah, Malaysia; e-mail: chuath46@yahoo.com

ABSTRACT - A new species, *Naiadacarus nepenthicola*, is described from adults and deutonymphs collected in Belait District, Brunei Darussalam, from the fluid-filled pitchers of *Nepenthes bicalcarata* Hook. f.. This constitutes the first record of a member of the family Acaridae inhabiting *Nepenthes* pitchers. It is quite probably that *N. nepenthicola* feeds on decomposing leaves that fall into the pitchers as well as on decomposing insects trapped by pitchers. Dispersal is accomplished through phoresy on *Campanotus schmitzi* Staercke, an ant that nests exclusively in the hollow tendrils of *N. bicalcarata* pitchers.

Key words - Acari, Acaridae, phytotelmata, pitcher plant, mite, *Naiadacarus nepenthicola* **n. sp**., Nepentheaceae, *Campanotus schmitzi*

INTRODUCTION

Fashing (1974) established the genus *Naiadacarus* to accommodate two new species of Acaridae, *N. arboricola* and *N. oregonensis*, collected from water-filled treeholes in eastern North America and the Pacific North West of North America respectively. Fashing (1976) found that deutonymphs of *N. arboricola* disperse via phoresy on female flies of *Mallota posticata* (Fabricius) and *M. bautias* (Walker) (Diptera : Syrphidae), the larvae of which are rat-tailed maggots that also inhabit water-filled treeholes. As part of a study of the astigmatid fauna of the Huron Mountains of northern Michigan, U.S.A., OConnor (1989) collected deutonymphs phoretic on adults of vari ous syrphid fly genera. He not only collected deutonymphs of *N. arboricola*, but also collected and described two new species of *Naiadacarus*, *N. fashingi* and *N. mydophilus* from deutonymphs. Based on known host insect biologies as well as the biologies of other mite species collected on these insect hosts, OConnor (1989) hypothesized that *N. fashingi* and *N. mydophilus* inhabit wet decaying wood and/or moist treeholes rather than water-filled treeholes.

During a survey of mite inhabitants of the fluid-filled pitchers of the plant genus *Nepenthes* in Brunei Darussalam, we collected a new species of *Naiadacarus* from *Nepenthes bicalcarata* Hook. f. The present paper describes that new species and also provides notes on its biology.

MATERIALS AND METHODS

Fluid-filled pitchers were collected from *N. bicalcarata* at two localities on Labi Road, Belait District, Brunei Darussalam, and transported back to the laboratory at the Universiti Brunei Darussalam. The contents of each pitcher were placed in individual petri dishes, examined for mites under a dissecting microscope, and a random sample of mites was collected. Mite behaviors were also noted at this time. Deutonymphs were collected from ants, *Campanotus schmitzi* Staercke that were extracted from their nests in the pitcher tendrils as well as from under the pitcher peristomes. Mite specimens were cleared in Nesbitt's solution and mounted in Hoyer's medium on microscope slides (Krantz 1978; Evans 1992).

Characters were traced onto paper using a drawing tube and measurements made from the tracings. Measurements are given in micrometers (μm) in the following order: Holotype male, mean and range (in parentheses); females and deutonymphs: mean and range (in parentheses). All sample sizes equal 10. Nomenclature for idiosomal setae follows Griffiths *et al*. (1990) and for leg setae Grandjean (1939).

For observation of characters under the scanning electron microscope (SEM), live specimens were put through several baths of distilled water in an attempt to cleanse them of debris. They were then briefly submerged in distilled water near boiling point in order to force protraction of appendages. Specimens were then dehydrated in ethyl alcohol, dried using the critical point procedure, individually affixed to stubs using double-sided sticky tape, and coated with gold-palladium in a sputter coater. Microscopy was performed on an AMR 1200.

DESCRIPTION

Naiadacarus nepenthicola sp. n. (Figs 1-25)

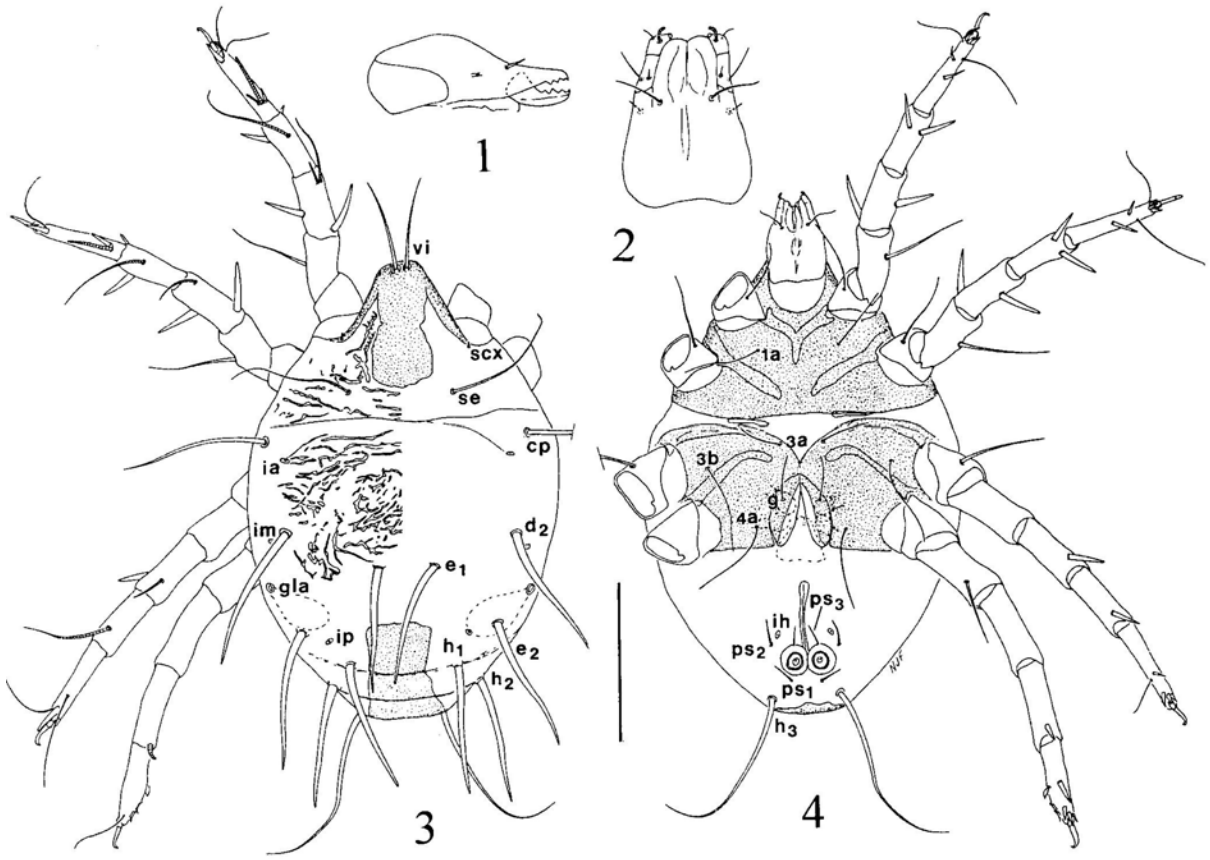
MALE (Figs 1- 8) Idiosoma ovoid, length 282, 287 (265-318); width at level of coxae III 185, 187 (174-203).

Gnathosoma –Chelicerae chelate (Fig.1), digits robust with interlocking teeth. Cheliceral seta spine-like and conical appendage forked. Subcapitulum, (Fig. 2) bearing a pair of filiform subcapitular setae ventrally. Each palpal tibia bears a filiform dorsal seta and filiform ventral seta, and each palpal tarsus a filiform dorsal seta, a subapical solenidion, and an apical rounded eupathidium.

Idiosomal dorsum (Fig. 3) - Propodosoma with sclerotized camerostome, consisting of heavily sclerotized cuticle contiguous with anterior margin of prodorsal sclerite, extending laterally around bases of legs, and ventrally over the coxae; remainder of dorsum sclerotized, but less so, and with sculpturing in the form of ridges on both propodosoma and opisthosoma (Fig. 20). Prodorsal sclerite over twice as long as wide, extending to level of trochanters II. Grandjean's organs absent. Sejugal furrow separating propodosoma and opisthosoma. Opisthonotal gland openings (*gla*) midway between setae d_2 and e_2. Cupules located as follows: *ia* slightly mesiad and posteriad of seta *cp*, *im* slightly posteriad and laterad of seta d_2, and *ip* midway between setae e_2 and h_1. Opisthosomal sclerite present, twice as long as wide, extending from level of cupule *ip* to seta h_3. Propodosoma bearing 3 pairs of setae: Supracoxal seta (*scx*) a small spine located dorsally above trochanter I, 3.03, 3.41 (3.03-3.79); *vi* filiform, 60, 65 (58-72); and *se* filiform, 89, 78 (70-89). Opisthosoma bearing 6 pairs of enlarged, elongate setae: *cp* 83, 85 (73-95); d_2 86, 85 (75-94); e_1 78, 86 (72-102); e_2 86, 87 (77-101); h_1 80, 83 (70-95); and h_2 68, 74 (62-83).

Idiosomal venter. (Fig. 4) - Heavily sclerotized cuticle covering propodosoma. Heavy sclerotization also surrounding bases of trochanters III and IV and extending over coxae, contiguous anteriorly. Cupule *ih* slightly mesiad and anteriad seta ps_2. Anterior coxal apodemes I directed posteromedially, joining at midline to form a Y-shape sternum. Anterior coxal apodemes II directed posteromedially; anterior coxal apodemes III directed medially; anterior apodemes IV directed anteriomedially. Small, elongate, horizontal sclerite slightly above anterior apodeme III and at its distal end. Aedeagus strongly sclerotized, located between coxal fields IV, and opening through a pair of lateral valves. Anus a longitudinal slit midway between aedeagus and terminus of idiosoma, a pair of suckers at its distal end. Venter bearing eight pairs of setae: *1a* 40, 44 (36-55) filiform, on coxal fields I; setae *3a* 25, 24 (17-33), *3b* 52, 47 (31-60) filiform, on coxal fields III; *4a* 53, 49 (39-57) filiform, on coxal fields IV and mesiad posterior genital papillae; *g* 33, 23 (20-33) filiform, on anterior end of genital valve; ps_1 17, 20 (17-24) filiform, posteriad anal sucker; ps_2 19, 20 (15-23) filiform, laterad anterior end of anal sucker; ps_3 17, 18 (15-22) arising from anterior of anal sucker; h_3 enlarged diameter 131, 120 (102-144), arising at posterior end of idiosoma.

Legs. (Fig 5-8) - Legs slender. Lengths, measured from base of trochanter to tip of tarsus: I 185, 189 (173-208); II 186, 190 (176-206); III 202, 207 (192-224); IV 215, 217 (204-230). Tarsal lengths: I 61, 62 (58-67); II 61, 63 (57-66); III 59, 60 (57-63); IV 54, 53 (43-59). Setation (I to IV): tarsus 12-12-10-10; tibia 2-2-1-1, genua 2-2-1-0, 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-II each with a thin, filiform seta (*pR*), trochanter III with a more robust filiform seta (*sR*); femora I, II and IV (*vF, wF*) each with a stout, filiform seta; genua I, II with setae *cG* and *mG* and genua III with seta *nG* stout, elongate spines; tibiae I, II with setae *gT* and *hT* and tibiae III, IV with setae *kT* stout, elongate spines. Tarsi with the following setation: tarsus I with *ba* a stout spine located near base of segment, arising from same socket as solenidia ω_1, ω_2 and famulus (ε).; *wa* an elongate ventral spine located slightly posterior to middle of segment; *la* spine-like, *ra* long and filiform, located laterally one fourth of way from distal end of segment; *e* a large dorsal, apical spine; *d* and *f* long, filiform, dorsal and apical; *q* and *p* stout, lateral, apical spines; v, *u* and *s* stout ventral apical spines. Tarsi II similar to tarsi I but with *ba* larger. Tarsi III with *w* a



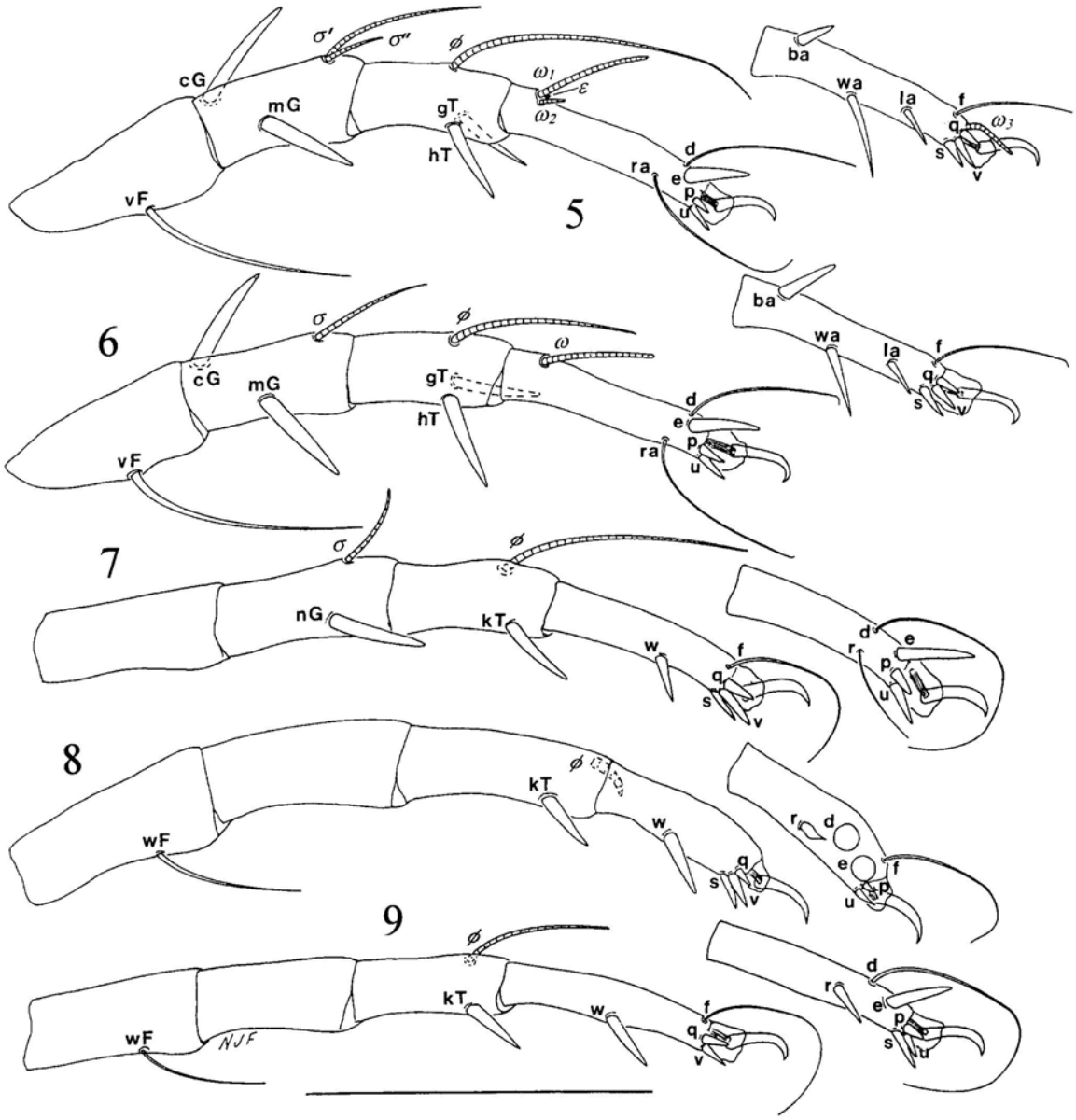
Figs. 1-4. *Naiadacarus nepenthicoloa* n. sp. Male – 1. chelicera, lateral view, 2. gnathosoma, ventral view, 3. dorsum, 4. venter. Scale bar: 200 μm (Figs. 1, 2), 100 μm (Figs. 3, 4)..

centrally located ventral spine; *d* dorsal and r lateral, both long, filiform and located one forth of way from distal end of segment; *f* dorsal, apical, long and filiform; e an enlarged, dorsal, apical spine; *p*, *q*, *s*, *u* and *v* similar to tarsi I and II. Tarsi IV (Fig. 23) similar to tarsi III except enlarged and with setae *r* a short, broad, flattened, pointed seta, and setae *d* and *e* lateral and in the form of suckers. Solenidia (I to IV): tarsi 3-1-0-0, tibiae 1-1-1-1, genua 2-1-1-0. Genua with solenidia σ originating one-fifth of way from apical end; solenidion σ″ one-third length of σ′. Tibiae I-IV with solenidion ϕ originating approximately one-quarter to one-third of way from apical end, and on tibia IV being short, robust and arching ventrally. Tarsus I with solenidion ω_2 and ω_1 originating near base and from the same socket; solenidion ω_3 apical, enlarged and arching ventrally. Famulus (ε) small, located between ω_1 and *ba* (Fig. 22). Pretarsi with small, membranous ambulacra containing robust, curved claw and sclerotized condylophores.

FEMALE (Figs. 9-11) - Gnathosoma and general features of idiosoma, including shape, similar to male; idiosomal length 312 (294-324); idiosomal width at level of coxae III 222 (209-229).

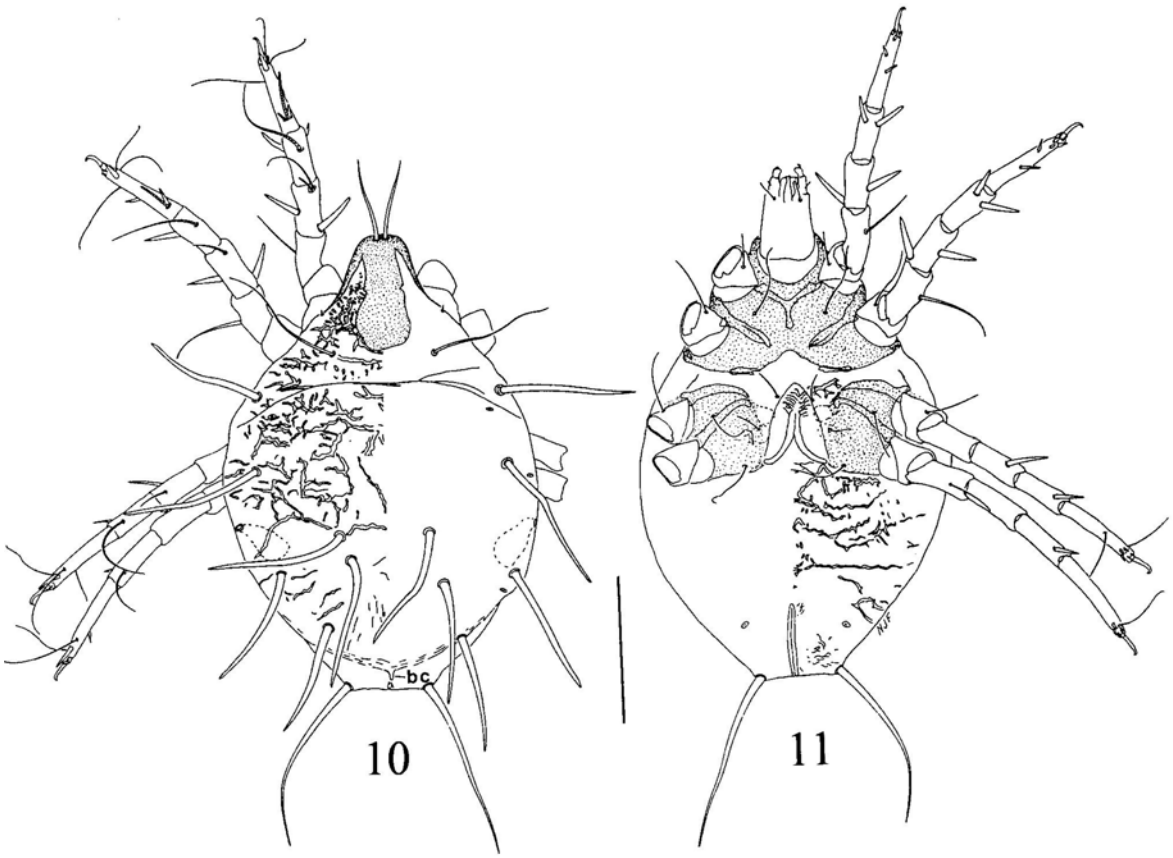
Idiosomal dorsum (Fig.10) - Cuticular sclerotization and sculpturing similar to male, except opisthosomal shield absent. Setae similar in shape and location to male except h_3 terminal: scx 3.26 (2.27-3.79), *vi* 67 (55-76), *se* 87 (71-96), *cp* 89 (70-99), d_2 93 (82-104), e_1 91 (83-100), e_2 91 (79-100) and h_1 85 (76-97) , h_2 81 (67-92), and h_3 120 (111-139). Bursa copulatrix (bc) at end of short tube located just above anus (Fig. 22).

Idiosomal venter (Fig. 11) - Sclerotization and apodemes similar to male, except strongly sclerotized areas covering coxal fields III and IV not contiguous. Venter bearing five pairs of thin, filiform setae: *1a* 49 (39-58) on coxal field I, 3a 25 (17-36) at anterior end of ovipore, *3b* 46 (39-50) on coxal field III, and *4a* 45 (40-55) and *g* 20 (15-27) on coxal field IV. Genital apparatus located centrally between coxal fields III and IV. Anus a longitudinal slit at posterior end of idiosoma.



Figs 5-9. *Naiadacarus nepenthicola*, sp. n. - 5. male, leg I, 6. male, leg II, 7. male, leg III, 8. male, leg IV, 9. female, leg IV. Scale bar = 100 μm

Legs (Fig. 9) - Legs similar to male except slightly shorter and more slender, especially legs III, IV and tarsus IV (Fig. 9). Lengths, from base of trochanter to tip of tarsus: I 180 (173-194), II 182 (171-197), III 188 (176-209), IV 205 (191-226). Tarsal lengths: I 61 (55-70), II 62 (56-67), III 60 (55-65), IV 66 (61-73). Similar in chaetotaxy and solenidotaxy to male with the following exceptions: most tarsal setae less robust; setae *d* and *e* tarsus IV spines rather than suckers; solenidion ω_3 tarsus I less robust, not arched ventrally; solenidion ϕ tibia IV long and slender, not arched ventrally. Legs more slender than male, especially tarsus IV (Fig. 9).



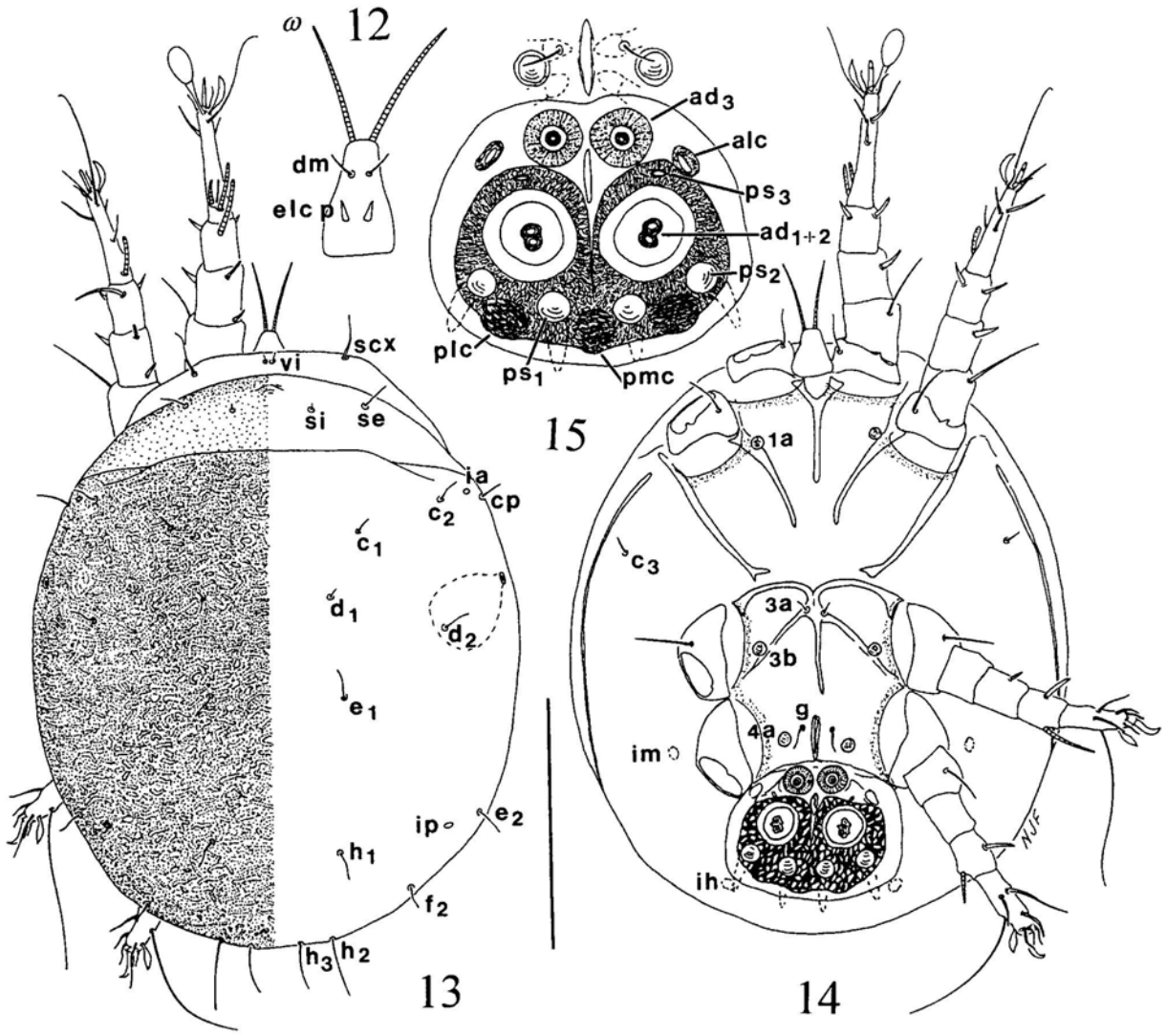
Figs 10-11. *Naiadacarus nepenthicola*, sp. n., female - 10. dorsum, 11. Venter. Scale bar = 100 μm.

DEUTONYMPH (Figs 12-19) - Body broadly oval, almost round, and widest at level of coxae III; idiosomal length 193 (180-208); width 154 (141-164).

Gnathosoma (Fig. 12) - Gnathosoma with subcapitular remnant relatively long 18 (16-20), broad at base, and tapering toward apex. Palpal remnants absent; palpal solenidia (ω) 22 (19-24) arising directly from subcapitu lum. Dorsal subcapitular setae variable in presence; when present, palpal setae (*dm*) filiform, sometimes spine-like, and supracoxal setae (*elc p*) spine-like.

Idiosomal dorsum(Fig. 13) - Internal vertical setae (*vi*) filiform 3.45 (2.27-4.55), located anterior to apex of propodosoma; external vertical setae (*se*) absent. Supracoxal setae (*scx*) filiform 16 (14-21). Propodosomal and hysterosomal sclerites separated by well developed sejugal furrow; hysterosomal sclerite ornamentation (Fig. 24) in the form of small protuberances irregularly separated by sinuous grooves; propodosomal sclerite without sculpturing but with a small central protuberance near apex. Propodosoma bearing two pairs of short, filiform setae: *si* 2.80 (2.27-3.03), *se* 9 (8-12). Hysterosomal sclerite bearing 11 pairs of short, filiorm setae: c_1 3.3 (2.3-4.6), c_2 3.4 (3.0-3.8), *cp* 8.5 (6.8-9.8), d_1 3.20 (2.3-3.8), d_2 7.5 (5.3-9.8), e_1 8.6 (6.8-9.8), e_2 8.3 (6.8-10.6), f_2 3.7 (2.3-4.6), h_1 8.5 (7.6-10.6), h_2 20 (18-23), h_3 11.6 (9.1-14.4). Opisthosomal gland openings located laterally between setae *cp* and d_2. Cupules *ia* located laterally between setae c_2 and *cp*, and cupules *ip* between setae e_2 and h_1.

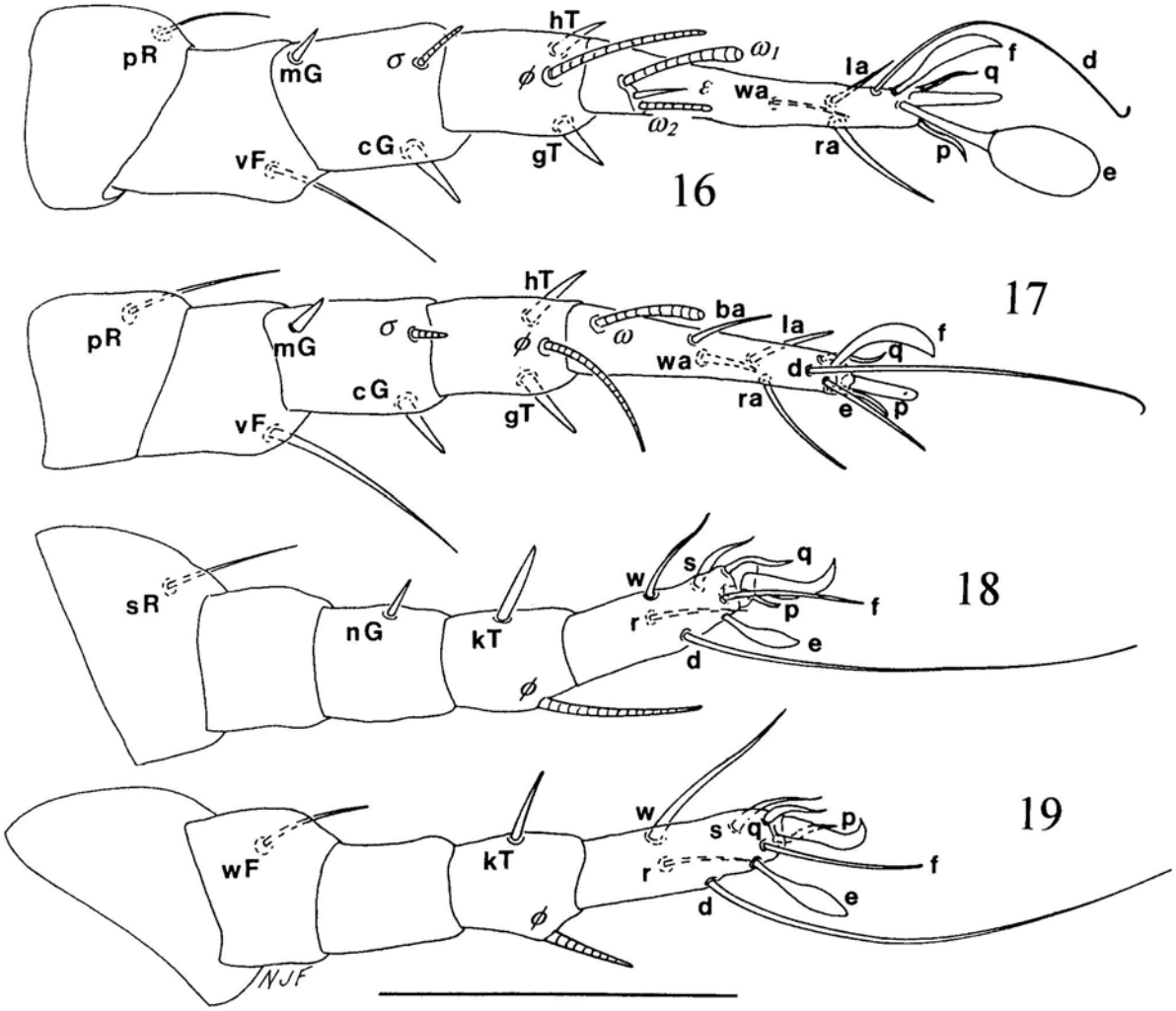
Idiosomal venter (Fig. 14) - Anterior apodemes of coxal fields I fused to form Y-shaped sternum. Anterior and posterior apodemes of coxal fields II curved medially. Anterior apodemes III directed mesially, fused with each other and with anterior apodemes of coxal fields IV. Posterior medial apodeme well developed, extending from anterior apodemes IV to just anterior to genital opening. Setae c_3 very short 2.65 (2.27-3.79), filiform, positioned on lateral margin of ventral sclerite between legs II and III. Setae of coxal fields I (*1a*), III (*3b*) and IV (*4a*) in the form of small conoids; setae *3a* short 5.00 (3.03-6.06), filiform. Genital opening between coxae IV; setae *g* short 6.0 (4.6-6.8), filiform, laterad to genital opening. Genital papillae relatively large, two segmented. Attachment organ



Figs 12-15. *Naiadacarus nepenthicola*, sp. n., deutonymph - 12. Gnathosoma, dorsal view, 13. Dorsum, 14. Venter. 15. Attachment organ. Scale bar: 100 μm (Figs. 13-14), 200 μm (Figs. 12, 15).

(Fig. 15) well developed with membrane-like outer fringe. Anterior suckers (ad_3) with spokes radiating from center. Median suckers large, consisting of a marginal ring surrounding an inner core containing paired vestigial alveoli (ad_{1+2}). Setae ps_2 conoidal, situated posterior and lateral to median suckers; setae ps_1 conoidal, situated medially and posterior to median suckers. Setae ps_3 represented by small alveoli anterior to median suckers. Anterior lateral cuticular suckers (*alc*) small; posterior median (*pmc*) and posterior lateral (*plc*) cuticular suckers well developed. Median suckers, ps_1, ps_2, ps_3, *plc* and *pmc* surrounded by cuticle with a reticulated pattern. Anus located between anterior and median suckers.

Legs (Figs 16-19) - Legs elongate with all segments free. Legs I 92 (86-97) and II 83 (77-87) longer than legs III 63 (58-68) and IV 64 (61-69). Tarsal lengths: I 38 (36-39), II 34 (32-35), III 24 (22-27), IV 25 (23-27). Setation (I-IV): tarsus 8-9-8-8, tibiae 2-2-1-1; genua 2-2-1-0, femora 1-1-0-1, trochanters 1-1-1-0. Setation, trochanters to tibiae: trochanters I-III each with filiform seta (*pR , sR*); femora I, II, IV each with long filiform seta (*vF, wF*), *vF* longer than *wF*; genua I, II with setae *cG* and *mG* and genu III with seta *nG* spine-like; tibiae I, II with setae *gT* and *hT* and tibiae III, IV with setae *kT* spine-like. Tarsi with the following setae present: tarsus I with setae *la, ra*, somewhat spine-like; seta wa filiform; setae *p* and *q* flat-

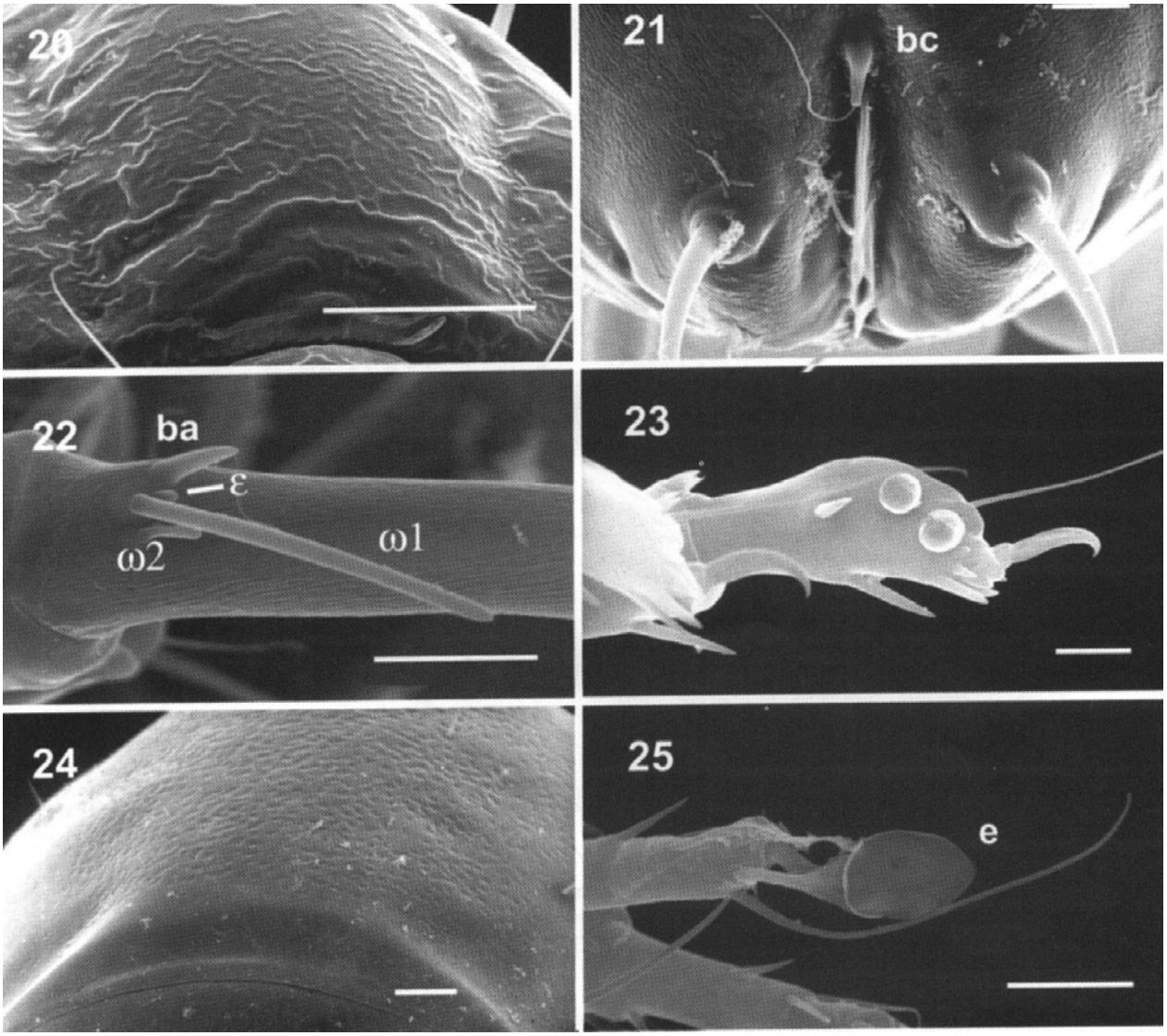


Figs 16-19. *Naiadacarus nepenthicola*, sp. n., deutonymph - 16. leg I, 17. leg II, 18 leg III, 19. leg IV. Scale bar = 100 μm.

tened; seta *f* enlarged, foliate; seta *d* long, filiform; seta *e* spoon-shaped (Fig. 25). Tarsus II with setae similar to tarsus I except seta *wa* slightly spine-like, seta *e* filiform, and the addition of slightly spine-like setae *ba* to middle of segment. Tarsi III with setae *r*, *w* and *s* slender, somewhat spine-like; seta *d* long, filiform; seta *f* filiform; setae *p* and *q* similar to legs I-II; seta *e* enlarged with bulbous apex. Tarsi IV similar to tarsi III except setae *w* longer. Solenidia (I-IV): tarsi 2-1-0-0, tibiae 1-1-1-1 and genua 1-1-0-0. Solenidion σ genu I 7.42 (6.06-9.09), genu II 4.55 (3.79-6.06) , each located at apex of segment. Solenidion ϕ tibia I 38 (33-43), tibia II 18.2 (15.2-21.2), tibia III 16.9 (13.6-23.5), tibia IV 8.8 (7.6-11.4). Solenidion ω_1 tarsus I 14.8 (12.9-16.7) slightly enlarged apically, ω_2 8.8 (6.8-10.6); solenidion ω tarsus II 13.8 (12.1-17.4). Elongate, tapering, filiform famulus (ε) located between solenidia ω_1 and ω_2. Pretarsi consisting of hooked empodial claws arising from apices of tarsi.

ETYMOLOGY - The name *nepenthicola* is compounded from the pitcher plant genus *Nepenthes* and the Latin word -*cola*, meaning dweller.

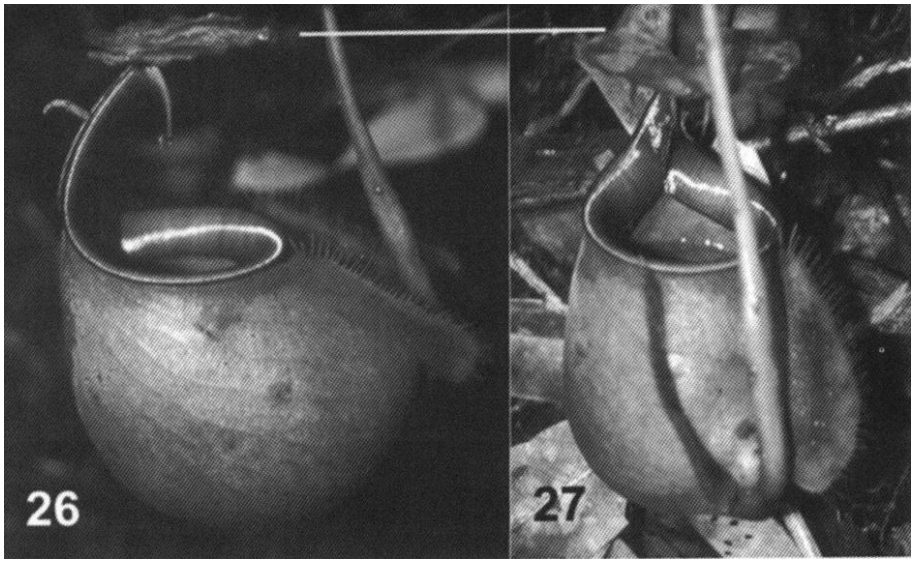
TYPES - Holotype male, N. J. Fashing and T. H. Chua, ex fluid-filled pitcher of *Nepenthes bicalcarata,* Brunei Darussalam, Belait District, deposited in Brunei Natural History Museum, Bandar Seri Begawan 2028, Brunei Darussalam. Paratypes, same data as holotype, deposited in Brunei Natural History Museum, Biology



Figs 20-25. *Naiadacarus nepenthicola*, sp. n. - 20. Cuticular sculpturing on dorsum, female, 21. Bursa copulatrix, female; 22. Base of tarsus I, dorsal view, female. 23. Lateral view of tarsus IV, male, 24. Cuticular sculpturing on dorsum, deutonymph, 25. Tarsal apex, dorsal view, deutonymph. Scale bar = 10μm.

Department Museum of Universiti Brunei Darussalam, Raffles Museum of Biodiversity Research, Singapore, The Natural History Museum, London, University of Michigan, Museum of Zoology, Ann Arbor, Michigan, U.S.A.

REMARKS - The new species exhibits the characteristics of the genus *Naiadacarus* as described by Fashing (1975) and modified by OConnor (1989). An exception is the presence of seta *n*G on genu III, a character lacking in other described members of the genus. Fashing (1973) reported that non-deutonymphal instars of *N. arboricola* lack supracoxal setae. As part of the current study, we examined *N. arboricola* for comparision with *N. nepenthecola* .On close examination with the SEM, we found that *N. arboricola* actually has very small supracoxal setae, thereby establishing that all described members of the genus possess this character.



Figs 26-27. *Nepenthes bicalcarata* ground pitcher – 26. Lateral view; 27. Rear views. Scale bar = 5 cm

Whereas *N. arboricola* is know from both adults and deutonymphs, *N. oregonensis* is known only from adults, and *N. fashingi* and *N. mydophilus* only from deutonymphs. Among adult characters that separate *N. nepenthicola* from *N. arboricola* and *N. oregonensis* are the following: smaller body size; heavier idiosomal sclerotization; presence of cuticular sculpturing in the form of "ridges"; presence of camerostome; dorsal idiosomal setae more robust and larger in basal diameter; presence of genual seta nG III; and longer and more robust tarsal setae *e*. In males, leg III only slightly enlarged in comparison to female and with seta *w*, claw and ambulacrum similar to female. In addition, males with tarsus IV "inflated" and seta *r* lanceolate. Among deutonymphal characters that separate *N. nepenthicola* from *N. arboricola*, *N. fashingi* and *N. mydophilis* are the following: presence of seta *nG* on genu III; absence of solenidion ω_3 on tarsus I; setae *1a* and *3a* in the form of rounded conoids; shorter legs in relation to idiosomal length; shorter gnathosomal solenidion and shorter solenidia ϕ on legs II and III.

BIOLOGY - Of the nine aerial and ground *N. bicalcarata* pitchers we examined, eight contained populations of *N. nepenthicola*. *Nepenthes ampullaria* is nearly always found growing near *N. bicalcarata* (Clarke 1997), and was the only other *Nepenthes* species in the forest at our collection sites. Eleven pitchers of *N. ampullaria* collected from plants in close proximity to *N. bicalcarata* were examined, and, although species representing three genera of the mite family Histiostomatidae were recovered, *N. nepenthicola* was not. In addition, *N. nepenthicola* was not found in our examination of 20 pitchers of *N. ampullaria* collected from other localities, nor from 17 pitchers of *N. mirabilis*, 25 pitchers of *N. albomarginata*, 30 pitchers of *N. rafflesiana*, and 38 pitchers of *N. gracilis*. *Naiadacarus nepenthicola* appears to be restricted to the pitchers of *N. bicalcarata*.

Nepenthes bicalcarata is a forest inhabitant, mainly found in, or on the periphery of, undisturbed peat swamp forest (Clarke 1997; Philipps and Lamb, 1996). Although the pitchers we collected were smaller, pitchers have been recorded as large as 15 cm in diameter (Phillipps and Lamb 1996) and with a capacity exceeding one liter in lower pitchers (Clarke 1997). The pitcher's lid is comparatively high above its relatively large mouth (Figs. 26,27), and leaves and leaf fragments easily fall into a pitcher from surrounding trees and shrubs.

From biological as well as morphological studies, Fashing (1994, 1998) determined that *N. arboricola*, a congener that inhabits water-filled treeholes, is a "shredder" (Cummins and Klug 1979) that trophic instars feed by biting chunks out of decomposing leaves, thereby ingesting leaf mesophyll and the associated microbes. It is therefore not surprising that adults and non-deutonymphal immature instars of *N. nepenthicola* are quite often found associated with decomposing leaves in the bottom of the pitchers. Possessing cheliceral morphology very similar to that of *N. arboricola*, it is quite probable that decomposing leaves form at least part of the diet of *N. nepenthicola*. Although decomposing insects are only occasionally found in water-filled treeholes, when present such insects are frequented as food sources by adult as well as later immature instars of *N. arboricola* (Fashing 1975). Decomposing arthropods are, of course, very common in *Nepenthes* pitchers, and *N. nepenthicola* individuals were often observed moving about on them. It is probable that decomposing arthropods and their associated microbes also form a part of the diet of *N. nepenthicola*.

Nepenthes bicalcarata is unique in the genus *Nepenthes* in that it not only attracts and traps various species of ants, but also has a mutualistic relationship with the ant *Campanotus schmitzi*. *Campanotus schmitzi* ants are only found in association with *N. bicalcarata* plants where they prey on mosquito larvae and scavenge dead insects in the pitchers, as well as imbibes nectar from the enlarged nectaries located in the pitcher peristome. (Clarke, 1997; Beattie, 1991; Booth, personal communication). Imagines are found roaming about on the plant as well as resting under the pitcher peristome, and the queens, their attendants and brood are found in the hollow tendrils of the pitchers. (Clarke and Kitching, 1995). In return for food and domatia, *C. schmitizi* ants protect *N. bicalcarata* from phytophagous insects (Booth, personal communication). *Campanotus schmitizi* ants provide an additional benefit by removing large captured insects from pitchers, thereby significantly reducing the rates of putrefication and ammonia accumulation (Clarke and Kitching, 1995; Clarke, 1997). The presence of pitcher infauna is thought to be beneficial to the plant, and excessive levels putrefication and ammonia often kill infauna and sometimes even pitchers (Clarke and Kitching, 1995; Clarke, 1997).

Although deutonymphs of *N. nepenthicola* were occasionally found moving about on dead insects or debris in the pitcher fluid, they were commonly found attached to imagines of *C. schmitzi*, especially workers collected from under the peristome. Workers are known to move among pitchers on the host plant, and also between individual plants that are in direct contact with one another (Clarke and Kitching 1995). Clarke and Kitching (1995) found that plants of *N. bicalcarata* occur in large indistinct aggregations, implying that there is a high degree of contact between individual plants. *Campanotus schmitzi* ants are therefore ideal phoretic hosts for *N. nepenthicola* dispersal; it is highly probable that worker ants carry deutonymphs between pitchers on individual plants and between plants in contact with one another, and that queen ants carry deutonymphs between *N. bicalacarata* populations. To date, flies of the family Syrphidae are the only known dispersal agents for other species of *Naiadacarus* (Fashing 1976, OConnor 1989). The possibility exists that *N. nepenthicola* is also phoretic on a syprhid fly host since larvae of a species of *Nepenthosyrphus* have been found to inhabit *N. bicalcarata* pitchers (Clarke and Kitching 1993). However *Nepenthosyrpus* species are relatively rare pitcher inhabitants (Clarke and Kitching 1993) and it's therefore doubtful they play a major role, if any, in the dispersal of *N. nepenthicola*.

ACKNOWLEDGEMENTS

We are indebted to the following persons, all of whom were at the Universiti Brunei Darussalam when the field work was underway: Mr. Samhan Nyawa (present employer: Brunei Museums) for help in locating *Nepenthes* sites and collecting pitchers, Drs. David Edwards, Dean of Sciences, and Kamariah Abu Salim, Head, Biology Department, for providing logistic support as well as laboratory space and equipment for NJF, and Dr. Webber Booth for help in locating collection sites for *Nepenthes* species, especially *N. albomarginata*, and also for providing valuable information on the mutualistic relationship of *N. bicalcarata* and *C. schmitzi*. NJF is indebted to the Brunei Research Council for permission to conduct research in Brunei Darussalam, and to the College of William and Mary, VA, USA, for a Faculty Semester Research Assignment Grant in support of this research.

REFERENCES

Beattie, A. J. 1991. Problems outstanding in ant-plant interaction research. Chapater 37. *In* C. R. Huxley and D. F. Cutler (Eds). Ant-Plant Interactions. Oxford University Press., Oxford.

Clarke, C. M. 1997. Nepenthes of Borneo. Natural History Publications (Borneo), Kota Kinabalu, Sabah, 207 pp.

Clarke, C. M., and R. L. Kitching. 1993. The metazoan food webs from six Bornean *Nepenthes* species. Ecolog. Entomol. 18: 7-16

Clarke, C.M., and R.L. Kitching. 1995. Swimming ants and pitcher plants: a unique ant-plant interaction from Borneo. Jour. Trop. Ecol. 11: 589-602.

Cummins, K.W., and M.J. Klug. 1979. Feeding ecology of stream invertebrates. Ann. Rev. Ecol. Syst. 10: 147-172.

Evans GO. 1992. Principles of Acarology. CAB International, Oxford.

Fashing, N.J. 1974. A new subfamily of Acaridae, the Naiadacarinae, from water-filled treeholes (Acarina: Acaridae). Acarologia 14: 166-181.

Fashing, N. J. 1994. Life history patterns of astigmatid inhabitants of water-filled treeholes. pp. 160-185. *In*: M. A. Houck (ed.). Mites, ecological and evolutionary analyses of life-history patterns. Chapman and Hall. New York.

Fashing, N. J. 1976. The evolutionary modification of dispersal in *Naiadacarus arboricola*, a mite restricted to water-filled treeholes (Acarina : Acaridae). Amer. Midland Nat. 95: 337-336.

Fashing, N.J. 1975. Life history and general biology of *Naiadacarus arboricola* Fashing, a mite inhabiting water-filled treeholes. Jour. of Nat. Hist. 9: 413-424.

Fashing, N. J. 1998. Functional morphology as an aid in determining trophic behavior:the placement of astigmatic mites in food webs of water-filled tree-hole communities. Exper. Appl. Acarol. 22: 435-453.

Grandjean F. 1939. La chaetotaxie des pattes chez les Acaridiae. *Bull. Soc. Zool. France* 64, 50-60.

Griffiths, D.A., W.T. Atyeo, R.A. Norton and C.A. Lynch 1990. The idiosomal chaetotaxy of astigmatid mites. *Jour. Zool. (London)* 220, 1-32.

Krantz GW. 1978. A Manual of Acarology, Second Edition. Oregon State University Book Stores, Oregon.

OConnor, B.M. 1989. Systematics, ecology and host associations of *Naiadacarus* (Acari: Acaridae) in the Great Lakes region. Great Lakes Entomol. 22: 79-94.

Phillipps, A., and A. Lamb. 1996. Pitcher-plants of Borneo. Natural History Publications (Borneo), Kota Kinabalu. 171 pp.

*****