

**SARRACENIOPUS — A NEW GENUS FOR HISTIOSTOMATID MITES
INHABITING THE PITCHERS OF THE SARRACENIACEAE
(ASTIGMATA : HISTIOSTOMATIDAE)**

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ABSTRACT—A new genus, *Sarraceniopus*, is established for members of the Histiostomatidae inhabiting the pitchers of the plant family Sarraceniaceae, and a new species, *S. darlingtoniae*, is described from the pitchers of *Darlingtonia californica*. A phylogenetic analysis is presented for the genera of pitcher plant histiostomatids as well as for the species of the genus *Sarraceniopus*.

INTRODUCTION

The insectivorous pitchers of the various pitcher plant species provide a unique habitat for a number of species of arthropods (Fish and Beaver 1978). Many of these arthropod species are adapted to live exclusively in the aquatic habitat provided by the pitchers of a single species or a few closely related species of pitcher plants. Among the Acari, six species of Histiostomatidae (= Anoetidae) have been described from this habitat. In 1915, Oudemans described *Anoetus guntheri* from the pitchers of *Nepenthes distillatoria* L. collected in Sri Lanka. Later, Oudemans (1924) established the genus *Zwickia* using *A. guntheri* as the type species. In 1928, Hirst described a second species of *Zwickia*, *Z. nepenthesiana*, collected from the pitchers of *Nepenthes ampullaria* Jack in Singapore. Oudemans (1932) established another genus, *Creutzeria*, to accommodate the new species *C. tobaica* which was collected from the pitchers of *Nepenthes tobaica* Dans. in Java. Nesbitt (1954) found a new species inhabiting the pitchers of *Sarracenia purpurea* L. in Quebec, Canada, and described it as *Zwickia gibsoni*. In their revision of the family Histiostomatidae, Hughes and Jackson (1958) transferred both *Z. nepenthesiana* and *Z. gibsoni* to the genus *Anoetus*. A fifth species of pitcher plant histiostomatid, *Anoetus hughesi*, was described by Hunter and Hunter (1964) from the pitchers of *Sarracenia minor* Walt. and *S. flava* L. collected in the southeastern U.S.A. More recently, Nesbitt (1979) described *Creutzeria seychellensis* from the pitchers of *Nepenthes pervillei* Blume collected in the Seychelles.

The present paper describes a new species of histiostomatid collected from the pitchers of *Darlingtonia californica* Torr. in the northwestern U.S.A., and establishes a new genus for histiostomatid mites inhabiting North American pitcher plants (Sarraceniaceae). Because of the confusion in nomenclature and hypothesized relationships of these and other related species, a phylogenetic analysis was conducted to provide a better understanding of the phylogenetic relationships.

Sarraceniopus new genus

ADULTS—Chelicerae with fixed digits attenuate, bearing 10-30 small teeth. Palp lobate or almost cylindrical, bearing an elongate solenidion and 0-1 long eupathidial setae. Prodorsal sclerite evenly sclerotized, covering prodorsoma laterally or only dorsally, bearing setae *vi* anteriorly and *ve* on the sclerite or on its lateral edges. Hysterosoma with a single median sclerite, paired sclerites or unsclerotized. Dorsal hysterosomal chaetotaxy complete (12 pairs); para-anal chaetotaxy consisting of 3 pairs or reduced to 1 pair. Coxal apodemes well-developed; anterior apodemes of coxal fields I broadly fused into a V in females, and into a Y in males. Female ovipore transverse, located between coxal fields I-II; genital papillae ("rings") subcircular to broadly oval. Female copulatory opening dorsal, between or posterior to setae *da*. Male genital opening behind coxal fields VI. Legs exhibiting pronounced sexual dimorphism — elongate and thin in females, and much stouter in males, especially Leg II. Leg chaetotaxy complete for family; tarsal setae *e* and *f*

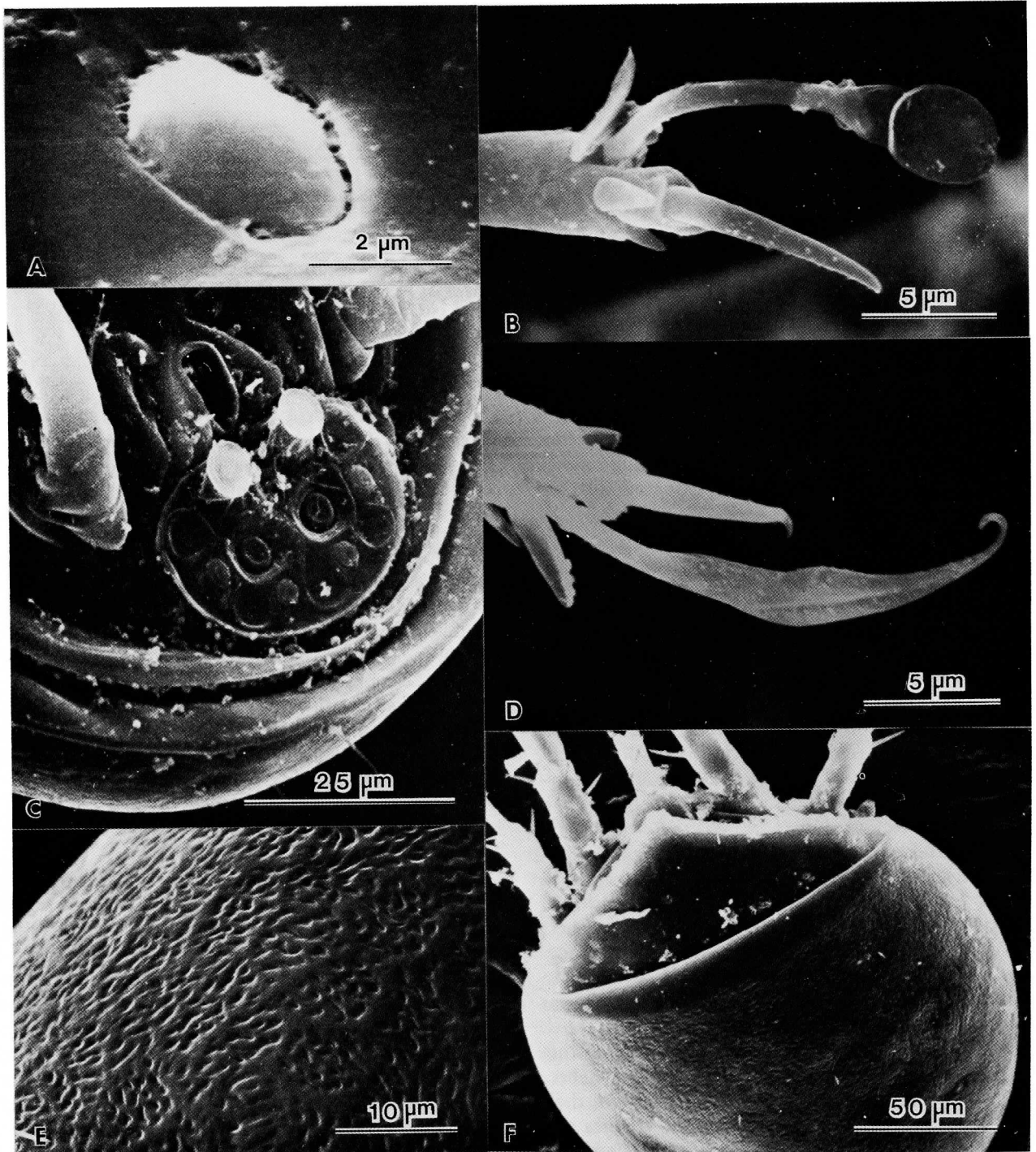


Fig. 1. *Sarraceniopus darlingtoniae* n. sp. — Scanning electron micrographs of deutonymph; A, conoidal seta *cx*₃; B, cup-like “sucker” seta of tarsus I; C, attachment organ; D, leaf-like seta of tarsus II; E, detail of hystersomal sculpturing; F, dorsal view showing smooth propodosoma and sculptured hystersoma.

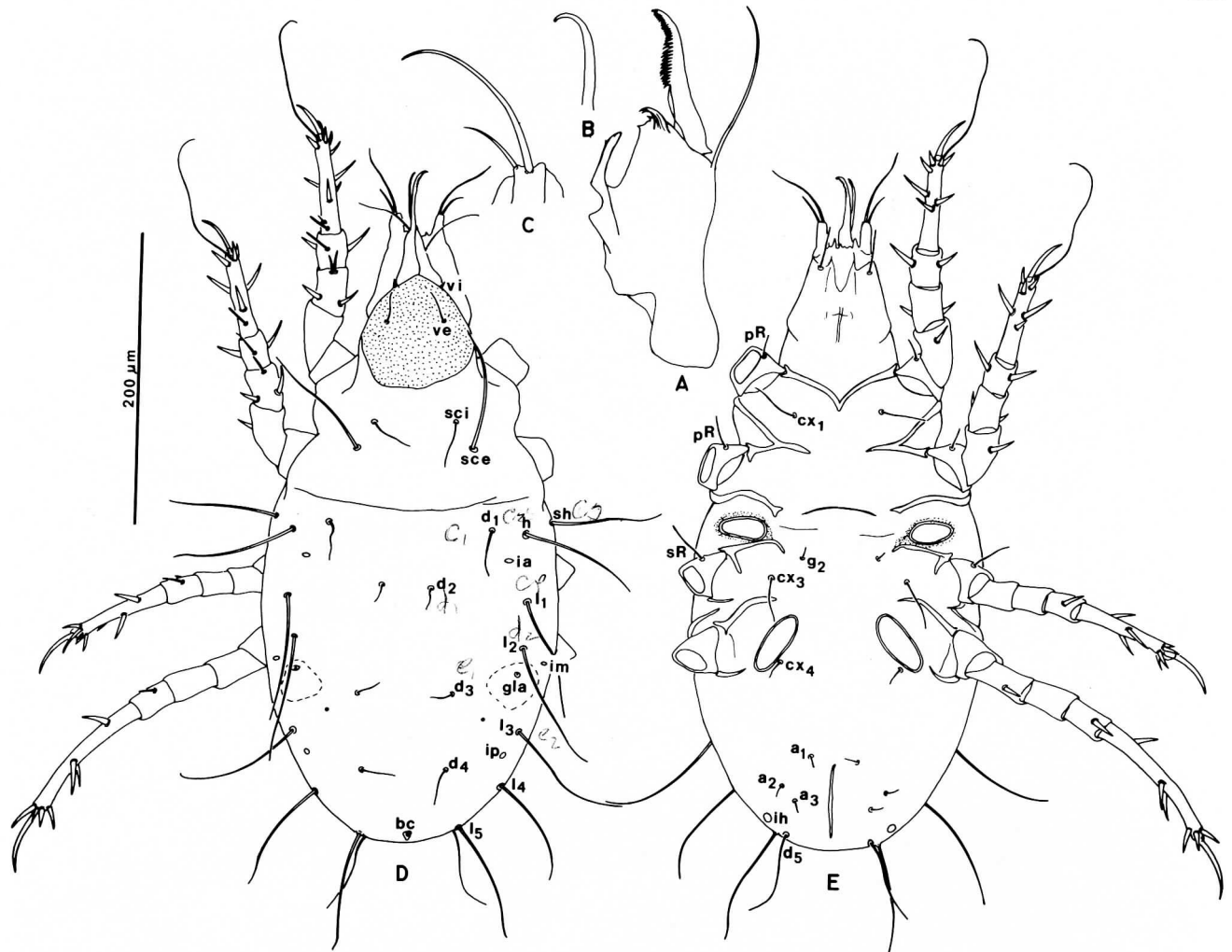


Fig. 2. *Sarraceniopus darlingtoniae* n. sp. — A, lateral view of chelicera; B, dorsal view of toothed region of chelicera; C, pedipalp; D, dorsal view of female; E, ventral view of female.

asymmetrical with *f* longer; all leg setae spiniform except *d* I-II and sometimes *f* III-IV. All empodial claws of female elongate and flattened; claws of male shorter and stouter.

DEUTONYMPH — Body ovoid. Gnathosoma longer than wide, with palpal remnants separate apically, bearing a pair of long solenidia and a pair of short setae. Gnathosoma positioned at the apex of a projection which has strongly sclerotized, pigmented lateral areas. Body sclerotized dorsally — smooth, or with an irregular pattern of sculpture. Venter with anterior coxal apodemes I-II elongate, ending freely. Posterior apodemes of coxal fields II very weak or absent. Anterior apodemes of coxal fields III curved postero-medially, continuing very weakly to eventually fuse with the anterior apodemes of coxal fields IV on each side. Posterior median apodeme very weakly developed or absent between and behind coxal fields IV. Coxal field setae *cx1* and *cx3* in the form of small conoids (Fig. 1A); *cx4* larger conoids. Posterior attachment organ small, but bearing normally developed suckers and conoidal setae (Fig. 1C). Legs rela-

tively long; each tarsus bearing a well-developed, elongate, flattened empodial claw. Tarsus I bearing a stalked, cup-like “sucker” seta (Fig. 1B); homologous seta of tarsus II leaf-like (Fig. 1D).

TYPE-SPECIES—*Zwickia gibsoni* Nesbitt, 1954, by original designation. Other included species: *Anoetus hughesi* Hunter and Hunter, 1964, and the new species described below. The generic name is a combination of *Sarracenia* and *Hypopus*, is masculine in gender, and refers to the pitcher plant family Sarraceniaceae, the pitchers of which form the habitat for all described members of the genus.

Sarraceniopus darlingtoniae new species

Relative position of setae and other structures as illustrated in figures. All measurements in microns with the mean given first and followed by the range in parentheses. All are based on a sample size of ten.

GNATHOSOMA—Fixed digit of chelicera (Figs. 2A, 2B) serrated distally, bearing 22-26 teeth which decrease in size toward the tip. Toothed region wider

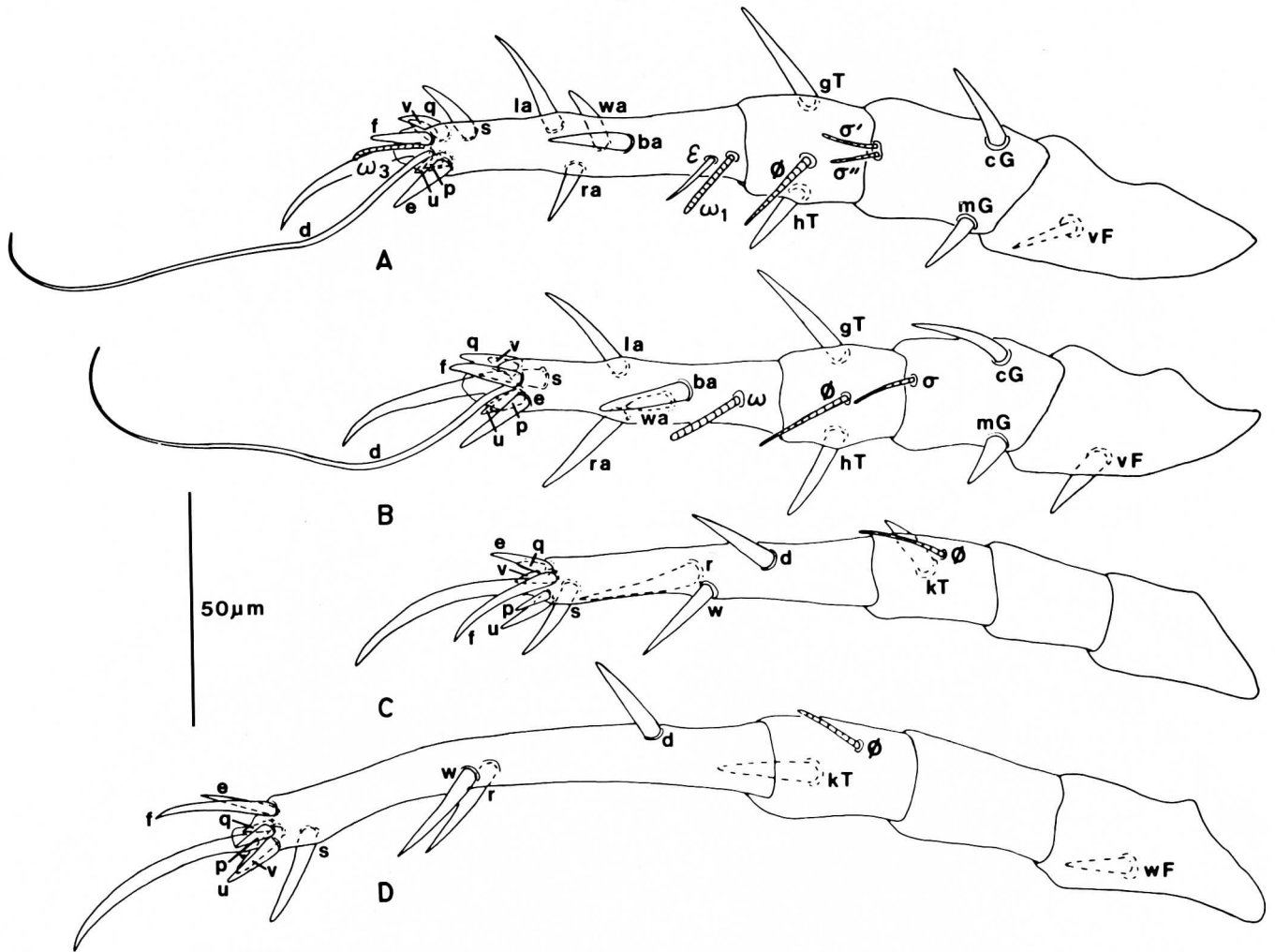


Fig. 3. *Sarraceniopus darlingtoniae* n. sp. — Legs of female; A, Leg I; B, Leg II; C, Leg III; D, Leg IV.

centrally with distal region curved mesally. Cheliceral seta approximately as long as fixed digit. Pedipalp (Fig. 2C) bearing a solenidium and eupathidial seta distally on terminal segment; solenidium over twice as long as eupathidial seta. Venter of subcapitulum bearing a pair of anteriorly directed setae (*cv*).

DESCRIPTION OF FEMALE (Figs. 2D, 2E) — Length of idiosoma 398 (356-440); width at level of coxae III, 212 (191-231). Idiosoma oval in outline and divided by sejugal furrow. Dorsal surface smooth with the exception of the sclerotized prodorsal sclerite, and bearing 16 pairs of hairlike setae: *vi* 7 (6-8), *ve* 32 (21-43), *sce* 103 (91-115), *sci* 36 (28-43), *sh* 80 (66-96), *h* 105 (87-114), *d*₁ 33 (28-43), *d*₂ 19 (14-23), *d*₃ 20 (11-26), *d*₄ 32 (27-35), *d*₅ 72 (59-85), *l*₁ 103 (93-115), *l*₂ 107 (94-115), *l*₃ 103 (94-113), *l*₄ 94 (87-101), *l*₅ 100 (87-114). Opening of bursa copulatrix located centrally on posterior margin of the idiosoma between setae *l*₅. Venter of idiosoma with seven pairs of hairlike setae: *cx*₁ 37 (33-43), *cx*₃ 43 (40-50), *cx*₄ 21 (18-28), *g*₂ 9 (6-13), *a*₁ 9 (6-14), *a*₂ 8 (4-13) and *a*₃ 10 (4-14). Ovipore a transverse slit located between the rear apo-

demes of legs II. Anal opening a longitudinal slit located at posterior margin of idiosoma. Apodemes of legs I unite to form a shallow "v". Rear apodemes of legs I and anterior apodemes of legs II unite. All other apodemes free. One pair of genital papillae located between legs II and III, and the other pair on coxal fields IV. Both pairs oval in outline.

LEGS (Fig. 3)—Relative position, size and shape of setae and solenidia as indicated in figures. Bearing a full setal compliment with the exception of tarsus I lacking seta *aa* and genu III lacking seta *nG*. All setae spinelike with the exception of seta *d* on legs I and II being long and whiplike and all trochanteral setae being hairlike. Famulus a slender spine located just in front of solenidium omega-1. **CHAETOTAXY**: Tarsus (I to IV) 12 + famulus-12-10-10, tibiae 2-2-1-1, genua 2-2-0-0, femora 1-1-0-1 and trochanters 1-1-1-0. Legs bearing a full compliment of solenidia with the exception of omega-2 lacking on tarsus I and sigma lacking on genu III. **SOLENIOTAXY**: tarsi 2-1-0-0, tibiae 1-1-1-1, and genua 2-1-0-0. Claws long and slender.

DESCRIPTION OF MALE (Fig. 4) — Idiosomal

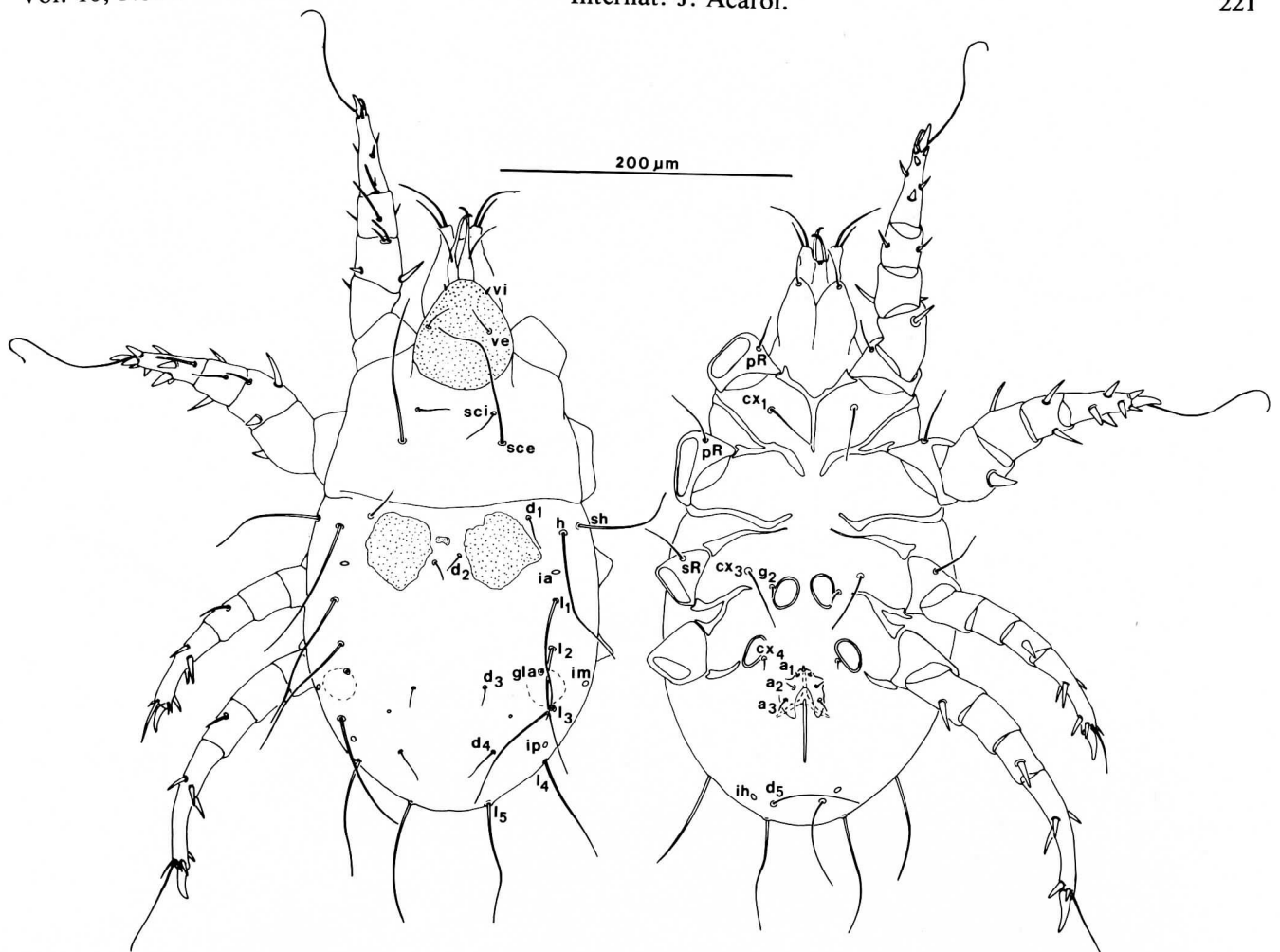


Fig. 4. *Sarraceniopus darlingtoniae* n. sp. — Dorsal and ventral view of male.

length 361 (320-401); width at level of coxae III, 198 (169-241). Similar in idiosomal shape, dorsal setal pattern and cuticle texture to female, except a sclerotized patch of cuticle is found dorsally on each side between setae d_1 and d_2 . Dorsum bearing fifteen pairs of hair-like setae: vi 6 (5-6), ve 21 (15-26), sce 105 (87-114), sci 31 (21-40), sh 80 (58-92), h 107 (82-128), d_1 26 (16-39), d_2 17 (13-20), d_3 18 (13-25), d_4 28 (20-40), l_1 104 (77-113), l_2 101 (78-114), l_3 93 (74-106), l_4 85 (72-99), and l_5 89 (67-99). Venter bearing nine pairs of setae: cx_1 38 (29-49), cx_3 49 (35-53), cx_4 7 (6-9), g_2 7 (6-11), a_1 2.8 (2.4-3.4), a_2 8 (6-9), a_3 11 (7-17) and d_5 66 (45-74). Seta a_1 spinelike, all other ventral setae hairlike. Genital apparatus located centrally and just posterior to coxal fields IV. Anus a longitudinal slit "coupled" to the posterior end of the genital apparatus.

LEGS (Fig. 5) — More robust than in female, especially legs II. Similar in chaetotaxy and solenidiotaxy to female, however most spinelike setae stouter and blunter than in female. Tarsal setae f of legs III and especially legs IV more attenuate than in female. Claws of all tarsi short and stout.

DESCRIPTION OF DEUTONYMPH (Fig. 6) — Idiosomal length 262 (247-279); width at widest point 197 (183-214). Oval in outline. Idiosomal protuberance that surrounds gnathosoma bearing a longitudinal, heavy pigmented region on each side. Gnathosomal base without setae and slightly more than twice as long as wide. Palpi short, each bearing a short basal seta and a long solenidion at the apex. Dorsum of propodosoma smooth (Fig. 1F) and bearing two pair of small, hairlike setae (sci , sce). Dorsum of hysterosoma sculptured (Fig. 1E, 1F), bearing 11 pairs of small, hairlike setae. All dorsal setae of approximately equal length with the exception of d_5 which is approximately twice the length of the others. A small, oval, non-sculptured area located between setae h and l_1 which we have interpreted as cupule ia . Cupule ip is similar in texture to ia , but small, circular in outline, and located between setae l_3 and l_4 . Idiosomal venter with apodemes as illustrated and bearing five pairs of setae. Coxal setae in the form of small conoids. Setae sh and g_2 small and hairlike. Sucker plate well developed. Two pair of cupules, im and ih , located on pos-

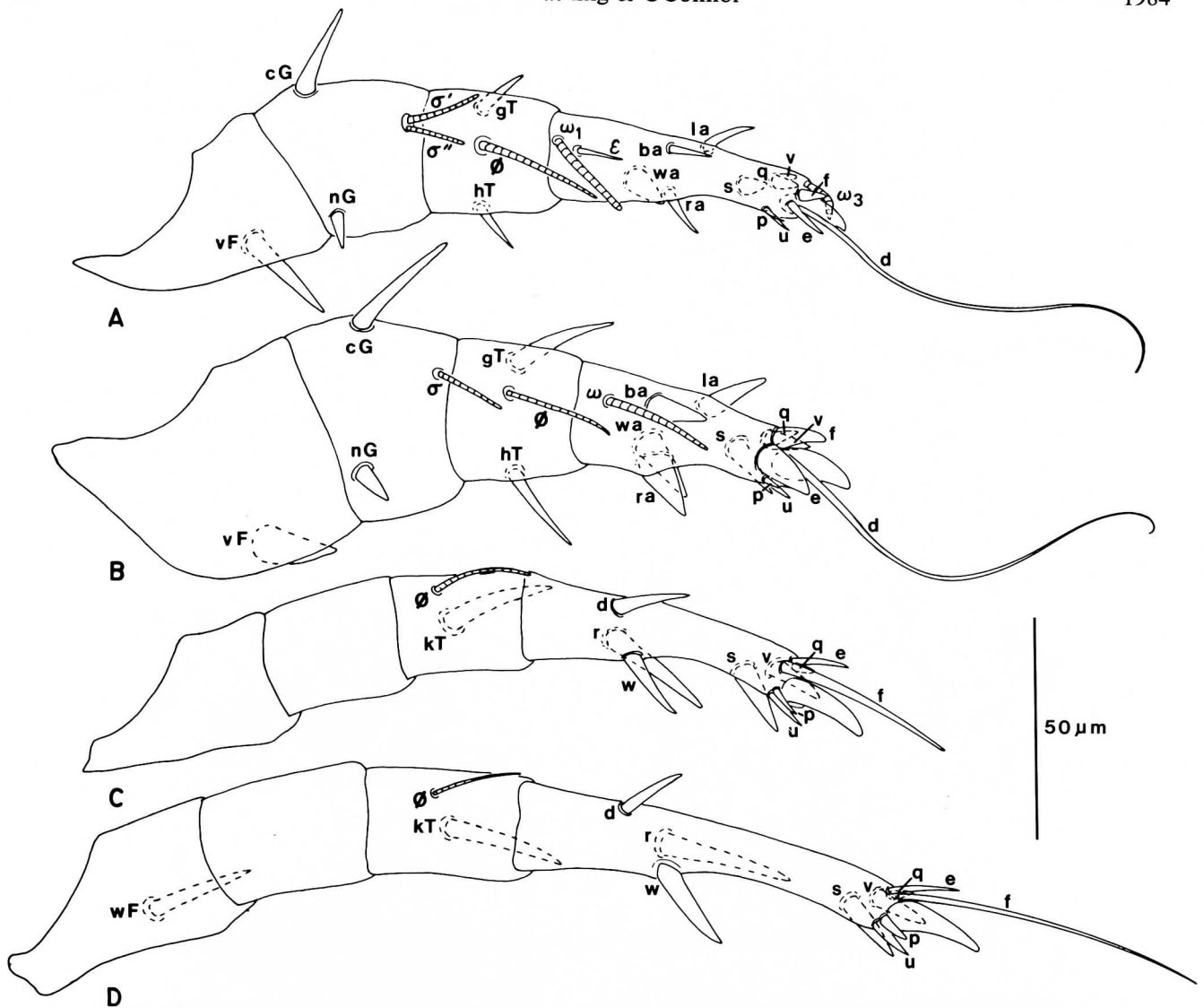


Fig. 5. *Sarraceniopus darlingtoniae* n. sp. — Legs of male; A, Leg I; B, Leg II; C, Leg III; D, Leg IV.

terior lateral margins of venter.

LEGS (Fig. 6) — Relative position, size and shape of setae and solenidia as illustrated. Tarsi long and slender. **CHAETOTAXY**: tarsi 8 + famulus-9-8-8, tibiae 2-2-1-1, genua 2-2-0-0, femura 1-1-0-1, and trochanters 0-0-1-0. **SOLENIOTAXY**: tarsi 2-1-0-0, tibiae 1-1-1-1, and genua 1-1-0-0.

The specific name refers to the pitcher plant genus *Darlingtonia*, the habitat in which the new species is found.

TYPE LOCALITY—The holotype and most of the paratypes were taken from the pitchers of *Darlingtonia californica* collected at Darlingtonia Wayside, Lane County, Oregon.

LOCATION OF TYPES—The holotype (female), male, female and deutonymphal paratypes will be deposited in the National Museum of Natural History, Washington, D.C. Paratypes will be deposited with

the following: Museum of Zoology, The University of Michigan, Ann Arbor; The Acarology Laboratory, Ohio State University, Columbus; Canadian National Collection, Ottawa; British Museum (Natural History), London; and L'Institut Royal des Sciences Naturelles, Brussels.

DISCUSSION

SYSTEMATIC POSITION OF THE GENUS *SARRACENIOPUS* — Much confusion has existed regarding the relationships of the mites here placed in the genus *Sarraceniopus*, and with the histiostomatid mites associated with pitcher plants in general. Nesbitt (1954), in describing the first species from the Sarraceniaceae, placed the species *gibsoni* in the genus *Zwickia*. At that time the genus contained the species *Z. guentheri* (Oudemans) and *Z. nepenthesiana* Hirst,

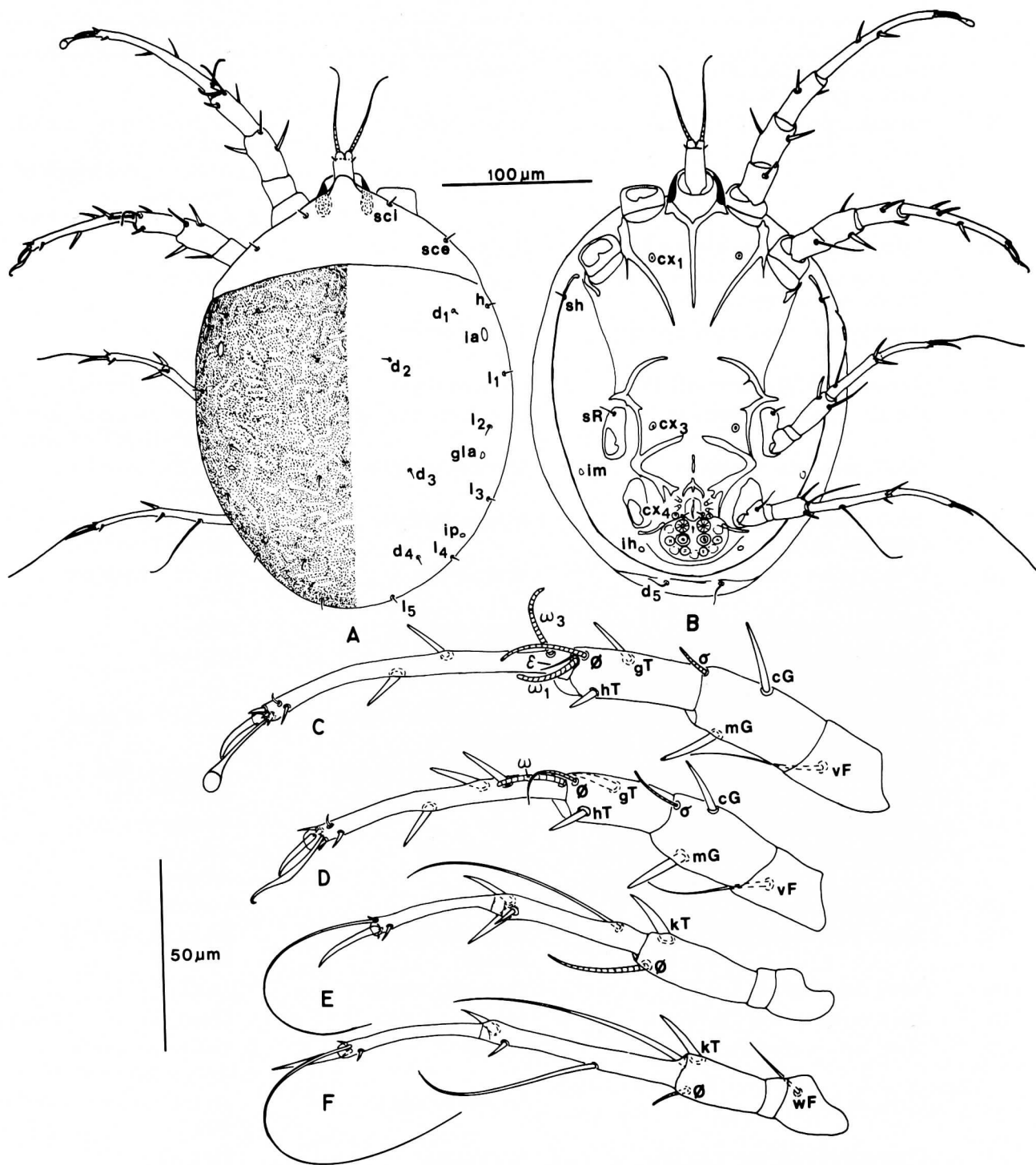


Fig. 6. *Sarraceniopus darlingtoniae* n. sp. — Deutonymph; A, dorsal view; B, ventral view; C, Leg I; D, Leg II; E, Leg III; F, Leg IV.

TABLE 1. Characters used in hypothesizing relationships among taxa discussed in the text (Figs. 7 and 8).

Number	Character	Ancestral State	Derived State(s)
1.	Deutonymph, pigmented projection bearing gnathosoma	Absent	Present
2.	Female, empodial claws II-IV	Short, stout	b. Slightly longer than basal width of tarsus c. About ½ the length of the tarsus d. Longer than the tarsus
3.	Deutonymph, empodial claw IV	Present	Absent
4.	Deutonymph, area between gnathosoma and coxal apodemes I	Smooth	Punctate
5.	Deutonymph, coxal setae I & III	Small conoids	b. small setae c. absent
6.	Deutonymph, apodemes III-IV	Fused medially	Separated medially
7.	Female, copulatory opening	Dorsal, between setae d ₃	b. Dorsal, between setae d ₄ c. Terminal, behind setae d ₅
8.	Adult, prodorsal sclerite	Strongly sclerotized	b. Weakly sclerotized c. Absent
9.	Adult, sexual dimorphism of empodial claws	No dimorphism	Male with all claws stouter than female
10.	Deutonymph, posterior coxal apodeme II	Well-developed	Weakly developed or absent
11.	Female, coxal apodemes I	Fused medially	Separated
12.	Female, coxal apodemes III	Well-developed	Reduced
13.	Adult, tarsal solenidia omega-1, I-II	Basal	Apical
14.	Male, legs I	As female or slightly enlarged	Strongly enlarged
15.	Male, tibia I	As female or slightly enlarged	Enlarged, with a modified seta
16.	Adult, setae f & q, tarsi II-IV	Short	Greatly elongate
17.	Female, anal setae	Three pairs	b. One pair c. Absent
18.	Adult, palp shape	Lobate	Cylindrical
19.	Adult, palp eupathidial seta pp ₂	Well-developed, directed laterally	Reduced, directed medially
20.	Adult, leg setae	Generally slender	Stout
21.	Male, tarsal setae f III-IV	Short	Elongate
22.	Male, hysterosomal sclerotization	Absent	b. One large sclerite c. Two smaller sclerites
23.	Male, legs II	Similar to legs I	At least twice as stout as legs I
24.	Deutonymph, dorsal sclerites	Sculptured	Smooth
25.	Adult, prodorsal sclerite	Wide	Narrow
26.	Adult, sexual dimorphism in dorsal setal lengths	No dimorphism	Male setae much longer
27.	Female, hysterosomal sclerotization	Absent	One large sclerite
28.	Adult, tarsal solenidion omega-2 I	Present	Absent

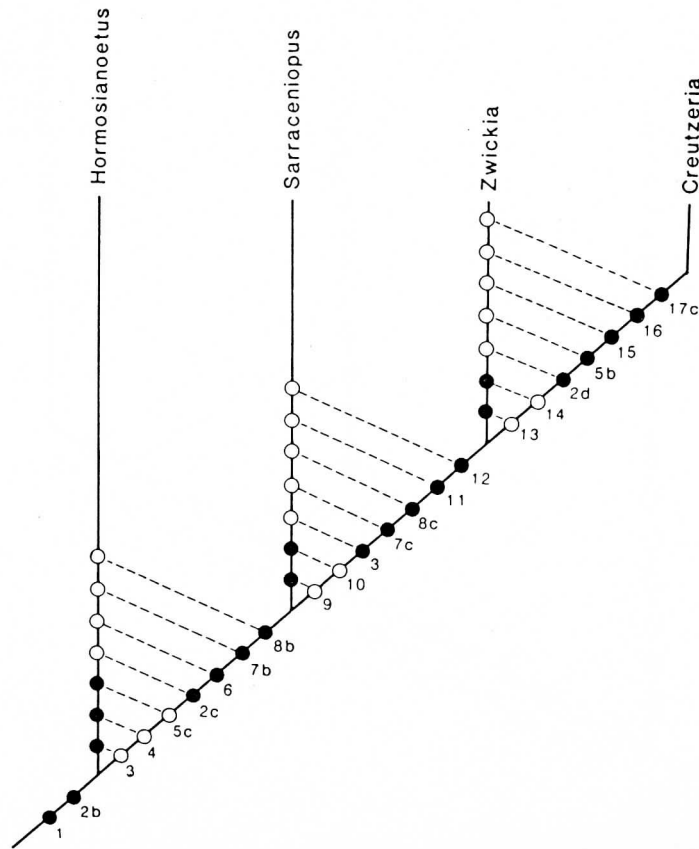


Fig. 7. Hypothesized phylogenetic relationships among genera of Histiostomatidae inhabiting phytotelmata. Numbers correspond to characters in table 1; derived character states indicated by dark circles, ancestral states by open circles; letters indicate different derived states of same character.

both associated with the Old World pitcher plants of the family Nepenthaceae. Nesbitt gave no specific reasons for such placement and listed no character states supporting it, although a number of similarities among the three species are apparent from his description and figures. Hughes and Jackson (1958) removed *Z. gibsoni* and *Z. nepenthesiana* from the genus *Zwickia* and placed both species in the genus *Anoetus* along with other species with reduced coxal setae in the deutonymph. Hunter and Hunter (1964) retained this generic arrangement in describing *Anoetus hughesi*, the second species from the Sarraceniaceae. Mahunka (1974) restricted the concept of the genus *Anoetus* to species associated with halictid bees, a concept with which we are in agreement on the basis of a number of uniquely derived character states in *Anoetus*. He did not, however, discuss the systematic position of *Anoetus* species excluded from this concept.

We hypothesize that the three species here included in the genus *Sarraceniopus*, *S. gibsoni* (Nesbitt) New Combination, *S. hughesi* (Hunter and Hunter) New Combination, and *S. darlingtoniae* New Species, form a monophyletic group. These three species share a

number of derived character states included in the above generic definition, notably the type of sexual dimorphism of the adult empodial claws and the reduction of the posterior apodemes of coxal fields II in the deutonymph, both synapomorphies unique to these species.

We hypothesize that the genus *Sarraceniopus* belongs to a monophyletic lineage within the family Histiostomatidae, subfamily Histiostomatinae, which may be characterized by the presence of a ventral projection of the idiosoma of the deutonymph which bears the gnathosomal remnant apically and which has strongly sclerotized, pigmented lateral margins. Adults of this lineage are all characterized by the enlargement of the empodial claws, possibly an adaptation to the aquatic environments in which all species are found. The group is ecologically homogeneous, with non-deutonymphal instars of all known taxa inhabiting phytotelmata (water-filled plant cavities). We include four nominate genera in this group. *Hormosianoetus* is known from two species: *H. aeschlimanni* Fain, described only from deutonymphs collected from a *Drosophila* culture in Switzerland (Fain 1980), and *H.*

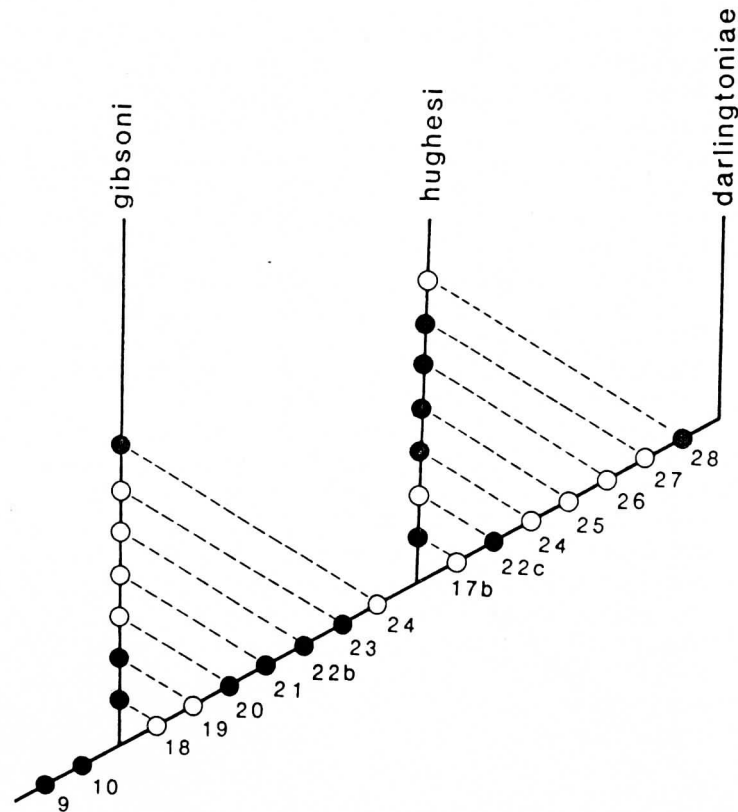


Fig. 8. Hypothesized phylogenetic relationships among species of *Sarraceniopus*. Numbers correspond to characters in table 1; derived character states indicated by dark circles, ancestral states by open circles; letters indicate different derived states of same character.

mallotae (Fashing), an inhabitant of water-filled tree-holes in the United States and known from all instars (Fashing 1973). The genus *Zwickia* is here restricted to the type-species, *Z. guentheri*, from *Nepenthes* pitchers in Southeast Asia. *Creutzeria*, with the included species *C. tobaica* and *C. seychellensis*, is also restricted to *Nepenthes* pitchers in Asia, the Seychelles and New Guinea. *Sarraceniopus* forms the fourth named genus in the group. The species "*Anoetus*" *colocasiae* Vitzthum, described from adults collected from a species of Araceae, may also belong to this group but requires redescription. We have seen additional undescribed representatives of this lineage which inhabit water-filled *Heliconia* (Musaceae) bracts in the Neotropics, as well as additional generic entities collected from other *Nepenthes* species.

In order to hypothesize the relationship of the genus *Sarraceniopus* to the related taxa mentioned above, we have conducted a phylogenetic analysis of this group using 28 morphological characters (21 adult characters and 7 deutonymphal characters). Character states were polarized into ancestral and derived states using the outgroup method of analysis. The outgroup

in this study was the large (and possibly paraphyletic) genus *Histiostoma*. Characters and their states are listed in Table 1, with the results of the generic analysis presented as a cladogram (Fig. 7).

The first conclusion of this analysis is that the two presently named genera associated with Old World Nepenthaceae form a monophyletic group characterized by the loss of the empodial claw from tarsus IV in the deutonymph (3b), the terminal position of the female copulatory opening (7c), the loss of the adult prodorsal sclerite (8c), the lack of fusion of apodemes I in the female (11b) and the reduction of apodemes III in the female (12b). As mentioned above, additional unnamed taxa collected from *Nepenthes* pitchers belong to this restricted lineage and are presently under study (OConnor, in prep.).

The genus *Sarraceniopus* is hypothesized to be the sister-group of the *Nepenthes*-associates. Derived character states shared by all three genera include the elongation of the empodial claws of the female so that they are at least half the length of the tarsus (2c), the separation of the posterior apodemes of the deutonymph along the midline such that the apodemes of

coxal fields III no longer fuse with each other but to the apodemes of coxal fields IV (6b), the posterior migration of the female copulatory opening to a position behind setae *d4* (7b), and the reduction in the sclerotization of the adult prodorsal sclerite (8b).

We hypothesize the genus *Hormosianoetus* to be the earliest derivative genus in this lineage. Adults of this genus retain all ancestral character states in the lineage, with the monophyly of the genus based only on derived character states of the deutonymphs. Besides being the least modified morphologically, this genus has the widest known geographical distribution, with species known from the Palaearctic, Nearctic and Neotropical (unnamed species) regions.

One conclusion which might be drawn from the cladogram of generic relationships (Fig. 7) is that the sister-group relationship between *Sarraceniopus* on one hand and the *Nepenthes*-associated lineage on the other, reflects the colonization of an ancestral pitcher plant by an ancestral mite. Phylogenetic relationships of the two plant families, however, indicate that the two are not closely related and that the insectivorous "pitchers" have evolved independently in each group. It seems probable that additional collecting in phytotelmata in the Asian tropics will yield new taxa more closely related to the *Nepenthes* associated lineage.

SYSTEMATIC RELATIONSHIPS WITHIN THE GENUS *SARRACENIOPUS*—Each of the three species of *Sarraceniopus* exhibits autapomorphic character states allowing relatively easy diagnoses of the species, at least in the adult instar. Using characters from Table 1, we hypothesize that *S. hyghesi* and *S. darlingtoniae* share a more recent common ancestor than either shares with *S. gibsoni*. Derived character states shared by *S. hughesi* and *S. darlingtoniae* which support this hypothesis include the enlargement of the adult leg setae (20b), elongation of seta *f* on tarsi III-IV of the male (21b), development of sclerotization on the male hysterosoma (22b), and enlargement of legs II of the male (23b). The distribution of character states within the genus is illustrated by the cladogram presented in Figure 8.

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