

BRANCHINECTA BRUSHI N. SP. (BRANCHIOPODA: ANOSTRACA: BRANCHINECTIDAE) FROM A VOLCANIC CRATER IN NORTHERN CHILE (ANTOFAGASTA PROVINCE): A NEW ALTITUDE RECORD FOR CRUSTACEANS

Thomas A. Hegna and Eric A. Lazo-Wasem

(TAH, correspondence, thomas.hegna@yale.edu) Geology and Geophysics Department, Yale University, P.O. Box 208109, New Haven, Connecticut 06520-8109, U.S.A.;

(EALW) Division of Invertebrate Zoology, Peabody Museum of Natural History, Yale University, P.O. Box 208118, New Haven, Connecticut 06520-8118, U.S.A.

ABSTRACT

Branchinecta brushi is a new species of fairy shrimp described from a pool within the volcanic crater of Cerro Paniri, northern Chile. Its occurrence represents a new altitude record for anostracans (5930 m), and it shares the title for highest altitude occurrence across all of Crustacea with a cladoceran from the same pool, *Boeckella palustris*. *Branchinecta brushi* is similar to another Chilean anostracan, *B. valchetana*. However, *B. brushi* differs from *B. valchetana* in the detailed morphology of the male second antennae and gonopods. Male specimens of *B. brushi* possess a bulbous, distally spinose medial apophysis on the proximal article of its second antenna as well as short, stout, inwardly curved gonopods. Both sexes are distinguished by very short cercopods. Bringing phylogenetic order to the monogeneric family Branchinectidae will require increased levels of morphological documentation and a better understanding of intra-specific variation. Most crustaceans are not well suited to life at high altitudes; those that thrive at high elevations offer insights not only to their biological tolerances, but also to their various modes of dispersal.

KEY WORDS: Anostraca, *Branchinecta*, Chile, morphology, systematics

DOI: 10.1651/09-3236.1

INTRODUCTION

Branchinectidae has been the focus of considerable taxonomic work during the last 125 years, but studies of the in-group phylogeny of the family are essentially nonexistent. Work on the phylogeny of the family (and Anostraca in general) cannot progress unless the standards for morphological depictions are raised so that more morphological characters are brought to bear on the problem. The delimitation of new species has depended primarily on the morphology of the male second antennae (claspers) and the gonopods. While there are good reasons for believing that these characters provide key diagnostic features that reflect biological species boundaries because both are involved in mating (see Rogers, 2003), other characters provide important phylogenetic clues as well (Brendonck, 1989). As Linder (1941: 174), one of the architects of the gonopod-based classification (along with Daday de Deés) observed, "... if a firmer grip on the phylogenetic conditions in the Anostraca is to be obtained, the other parts of the body must be taken into consideration" Furthermore, alone they contribute too few characters to resolve the phylogeny of a monogeneric family with over 60 described species (Rogers, personal communication). This observation transcends the debate as to what defines an anostracan species or genus (which has been ably discussed by Belk, 1991; Brendonck and Belk, 1997; and Rogers, 2002), and instead pushes to find hierarchical structure within families or genera so that their evolutionary or biogeographic history can be unraveled (Humphries and Parenti, 1999). To make further progress on anostracan phylogeny,

we need to treat the animals holistically and move anostracan systematics toward 'tree-thinking' (Baum et al., 2005; O'Hara, 1997). Essentially, this echoes the call by Rogers (2002b) for more complete written and visual documentation of anostracans and Linder (1941) for more inclusive descriptions (Brendonck, 1989; Fugate, 1993; Rogers et al., 2006; Thiéry and Fugate, 1994). With increased sampling of the morphological characteristics of species, we could begin to unravel the biogeographic patterns of *Branchinecta* and the significance of morphological variation across Anostraca.

In addition, increased visual documentation makes the descriptions even more useful outside of the small sphere of anostracan specialists—useful for the coding of morphological characters in broad analysis or in comparative studies. A case in point: most fossil anostracans with preserved appendages have them preserved in such a manner as to make it impossible to definitively identify the limb's position—having a better understanding of the anterior-posterior pattern of size and shape change amongst these serially repeated structures will lead to a better understanding of the limb evolution in fossil species. Excellent progress on these topics has begun by several authors who have examined neglected character complexes across different species and genera (Mura, 1996; Rogers, 2002, 2002b). This contribution describes a new species of *Branchinecta* from a very unique environment. In doing so, we aim to contribute to the elevation of the standards for anostracan illustration in alpha taxonomy and to better frame the questions remaining in the phylogenetics of Branchinectidae.

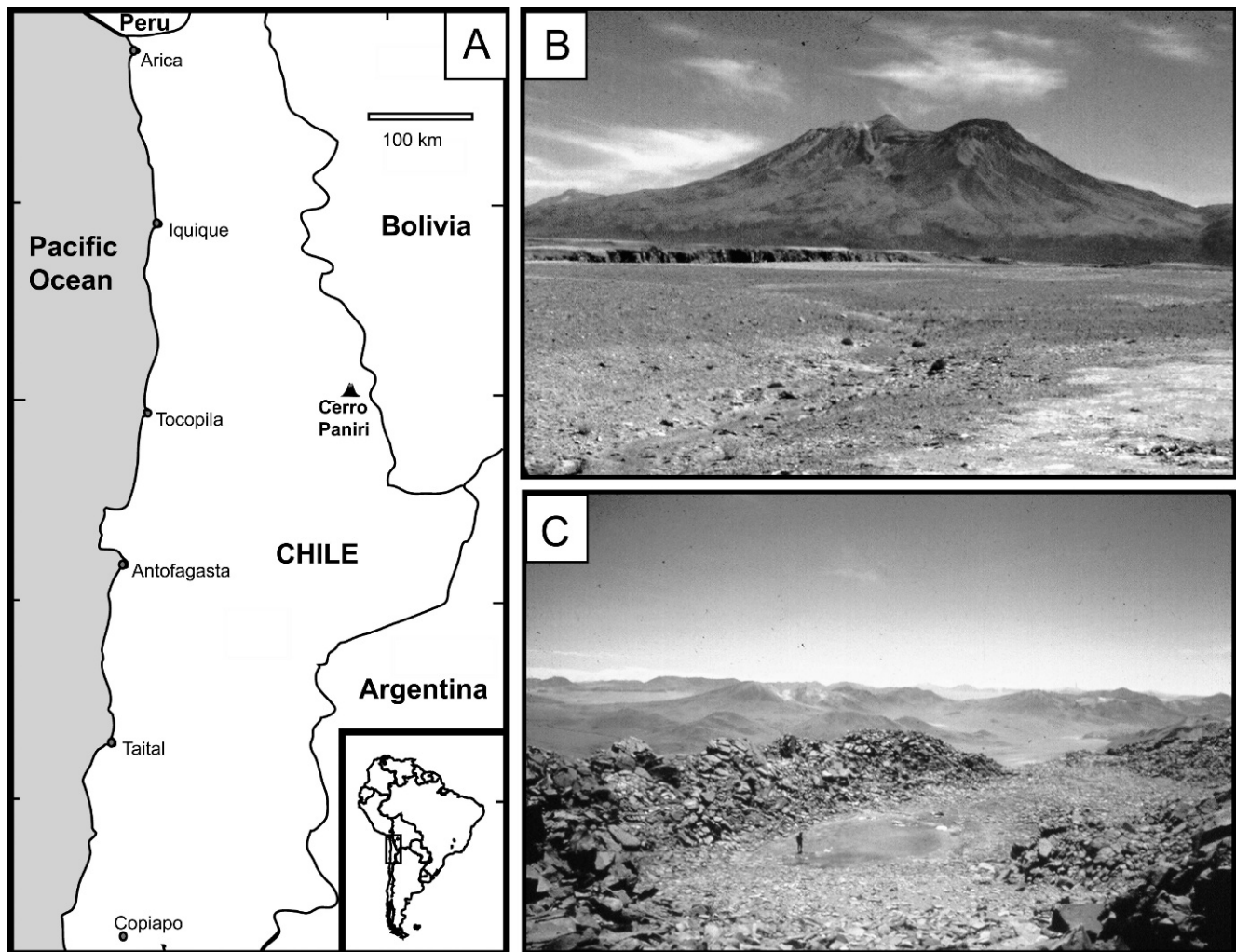


Fig. 1. A, map of western South America showing the location of Cerro Paniri. See the inset map of South America in the lower right corner for location of the illustrated area; B, Cerro Paniri; C, the branchiopod-inhabited pool in the crater of Cerro Paniri. Both B and C taken by C. F. Brush in 1988.

MATERIALS AND METHODS

Dr. Charles F. Brush collected our specimens on 13 December 1988 during a successful bid to break the world record for high altitude SCUBA diving. Collections were made in an upper pond (approximately 6 m by 12 m) near the summit of the Holocene(?) age stratovolcano, Cerro Paniri (22.08°S lat., 68.25°W long.; 5946 m or 19,508 ft above sea level), Antofagasta Province, northern Chile (Gonzalez-Ferrán, 1995). The depth of the pool was not recorded, but it was deep enough in which to SCUBA, suggesting a depth of at least two meters. Both anostracans and cladocerans were collected beneath approximately 5 cm of ice at an altitude of 5930 m (19,455 ft) some 16 m below the summit (Fig. 1).

Specimens are housed at the Yale Peabody Museum (YPM) and the United States National Museum (Smithsonian, USNM). They had been stored in 70% ethanol for nearly 20 years. Three specimens were critical point dried, gold-coated and photographed under an SEM. Cysts (eggs) and mandibles were dissected, put through HMDS (hexamethyldisilazane; see Nation, 1983), gold-coated and examined under an SEM. Additional specimens were examined by light microscopy. Imperfections in the dissected structures highlight the problems inherent in trying to describe a limited number of preserved specimens that are (for practical reasons) un-recollectable. Photos were processed digitally, and contrast was enhanced using Adobe® Photoshop. Terminology follows Linder (1941); mandibular terminology follows Brendonck (1994). The term 'cyst' is used instead of 'egg' following Dumont and Negrea (2002), who point out that the cyst is actually an encysted gastrula (dormant embryo) and not an ovum, but we acknowledge that this is a

contentious point. Criteria for species recognition follow characteristics used by other workers; however, the correspondence of these criteria to true 'biological species' is unknown. The translations of relevant portions of Daday de Deés (1910) were completed by TAH with the aid of Yahoo!'s online translation website, Babel Fish (<http://babelfish.yahoo.com/>).

SYSTEMATICS

Order Branchiopoda Latreille, 1817
Suborder Anostraca Sars, 1867
Branchinectidae Daday de Deés, 1910

Diagnosis.—Drawn from Dumont and Negrea (2002), Linder (1941), Rogers (2002), and Thiéry (1996). Anostracans with eleven pairs of thoracic limbs bearing only one pre-epipodite; second maxillae well-developed with many distal setae; narrow cercopods. Males lack a frontal appendage or clypeus; second antennae two-jointed and separated at the base; penes elongate with a non-retractable basal portion; distal portion of penes retractable, bears two denticulate protuberances. Females bear fusiform ovisacs which approximates genital segments in width.

Remarks.—Little morphological work has been conducted on the interrelationships of the major anostracan families. Daday de Deés (1910) was the first worker to provide phylogenetic trees of anostracan phylogeny. In his monograph, he illustrated two evolutionary trees: one based on genital morphology, and the other on the morphology of the male second antennae. Both are constructed as diagrams depicting ancestor-descendant relationships, with living species and extant higher taxa serving as ancestors. Both diagrams share taxonomic groups between them, but they differ in the relationship between those groups and the identity of the taxon at the root of the tree.

Daday de Deés (1910), in his first diagram (his ‘family tree’ based on pene morphology, p. 414), he created a hypothetical taxon, Protanostraca, to root the tree (not to be confused with Palaeanostraca of Hutchinson, 1930). The only characteristic that this taxon is stated to possess is many legs, a feature that Daday de Deés believed was obviously possessed by the anostracan ancestor (as well as an implied ancestral gonopod condition). His Protanostraca gave rise to two succeeding groups: Xiphophallophora, and Echinophallophora. His Xiphophallophora contains all anostracans that possess a smooth apical article on the penes (ending in a strong sabre-like spine). Likewise, his Echinophallophora contains all anostracans that have penes with a spiny surface on the apical article. Daday de Deés considered Echinophallophora to be older, based on the fact that other ‘lower animals’ also possess a spinous surface on the penis. This implicitly makes his conception of Echinophallophora both pleisiomorphic and implicitly paraphyletic. Xiphophallophora, on the other hand, roughly corresponds to a taxonomic group still in use today, Chirocephalinae (as used by Weekers et al., 2002). Even so, it does not appear that Daday de Deés intended for these terms to be used in a phylogenetic sense; rather, he used them as descriptive categories and abandoned them when discussing other characteristics.

Daday de Deés’ second ‘family tree’ uses the morphology of the male second antennae and the frontal appendages. This tree differs in another key way from his previous tree in that it begins, not from a hypothetical ancestor, but from a living taxon, Polyartemiidae. The reason for this is the fact that polyartemiids possess more than the standard complement of eleven pairs of thoracic limbs, the possession of many limbs was thought to be a basal characteristic for all arthropods (Lauterbach, 1973), as well a characteristic of other large branchiopods. This assessment was implicitly supported by both Linder (1941) and Dodson and Frey (1991) [see Remigio and Hebert (2000); note that both Linder and Dodson and Frey did not explicitly differentiate between synapomorphies and symplesiomorphies in their character evaluations and diagnostic keys, so Remigio and Hebert’s graphic reconstructions must be regarded as conjectural representations of both Linder and Dodson, and Frey’s ideas]. Recent molecular phylogenetic analysis (Remigio and Hebert, 2000; Weekers et al., 2002) and careful study of morphological features (Rogers, 2002a, 2003a) do not support the idea that Polyartemiidae is basal; rather it is well-supported as a

member of a more expansively defined Chirocephalidae diagnosed by several synapomorphies discussed by Rogers (2003a).

For Daday de Deés, the frontal appendage and second antennae proved to be a more character-rich complex. He used aspects of it to produce defining characteristics for Branchipodidae (possession of a clypeus) and an unnamed clade containing Branchinectidae, Branchipodidae, and Chirocephalidae (two articles on the second antennae). Neither of these characters (as specified by Daday de Deés) map easily onto modern published phylogenies (Weekers et al., 2002).

Though the phylogenetic diagrams of Daday de Deés (1910) seemingly imply paraphyly within Branchinectidae, the monophyly of this mono-generic family has not been seriously questioned in the nearly 100 years since. However, this has never been analytically tested, as the ingroup phylogeny of the family is all but unknown. Small-scale analyses of dominantly North American species of *Branchinecta* were undertaken in two unpublished theses by Fugate (1992, morphological data and biochemical data from ten loci) and Hanner (1997, combining both molecular data and character data from Fugate, 1992). Fugate’s analysis contained twenty species of *Branchinecta* (*B. campestris* Lynch, 1960; *B. coloradensis* Packard, 1874; *B. conservatio* Eng, Belk, and Eriksen, 1990; *B. cornigera* Lynch, 1958; *B. dissimilis* Lynch, 1972; *B. ferox* Milne-Edwards, 1840 (one of the two non-North American taxa used); *B. gigas* Lynch, 1937; *B. kaibabensis* Belk and Fugate, 2000 (Fugate referred to this species as *B. sp. 4*; Hanner’s thesis used the manuscript name, *B. kaibabi*; the taxon became *B. kaibabensis* upon publication of Belk and Fugate, 2000); *B. lindahli* Packard, 1883 (Fugate’s analysis also contained another species, referred to as *B. sp. 1*, that had that exact same character codings as *B. lindahli*); *B. longiantenna* Eng, Belk, and Eriksen, 1990; *B. lynchi* Eng, Belk, and Eriksen, 1990; *B. mackini* Dexter, 1956; *B. mesovallensis* Belk and Fugate, 2000 (Fugate referred to this species as *B. sp. 3*); *B. mexicana* Maeda-Martínez, Obregón-Barboza, and Dumont, 1993 (Fugate referred to this species as *B. sp. 2*); *B. orientalis* Sars, 1901 (the other non-North American taxon used); *B. packardi* Pearse, 1912; *B. paludosa* Müller, 1788; *B. potassa* Belk, 1979; *B. sandiegonensis* Fugate, 1993; and used both *Eubranchipus vernalis* (Verrill, 1869) and *Linderiella santarosae* Thiéry and Fugate, 1994; as the outgroup). Fugate (1992) identified three clades that were consistent in all of the most parsimonious morphology trees that were also, in turn, consistent with the biochemical and joint data sets: clade 1 (*B. conservatio*, *B. cornigera*, *B. lindahli*, *B. sp. 1*, *B. longiantenna*, *B. lynchi*, *B. mesovallensis* and *B. sandiegonensis*), clade 2 (*B. campestris*, *B. mackini*, and *B. potassa*), and clade 3 (*B. coloradensis*, *B. dissimilis*, *B. ferox*, *B. kaibabensis*, *B. mexicana*, *B. orientalis*, *B. packardi*, and *B. paludosa*). However, he also noted that in some trees (Fugate did not specify which trees), *B. ferox* and *B. orientalis* were pulled out of clade 3 and formed a forth clade with *B. gigas*. This is consistent with other morphological assessments of these species (Petkovski, 1991; Rogers et al., 2006) that implicitly suggest (based on

overall morphological similarity) that they form a clade (along with *B. raptor*) of predatory fairy shrimp (though a clade with an interesting biogeographic history spanning three continents).

Hanner's taxon sampling was necessarily pared down from that done by Fugate, as Hanner collected only molecular data from each species he studied. His study did not include seven species studied by Fugate (*B. ferox*, *B. coloradensis*, *B. dissimilis*, *B. sandiegonensis*, *B. sp. 1*, *B. sp. 2*, and *E. vernalis*). Hanner not only did a phylogenetic analysis of allozyme data and 12S mitochondrial sequence data, but he also did a combined analysis of all three data sources for the same species. The morphological analysis suffered from a lack of resolution, but it did contain several features that were found in almost all his other analyses. Nearly every analysis put *B. orientalis* at the base of the tree (only the analysis of the 12S data alone put the taxon elsewhere). Hanner also found Fugate's clade 2 in all analyses, as well as a *B. kaibabensis*/*B. paludosa* sister group. Most analyses also contained elements of Fugate's clade 3. A parsimony reanalysis of Fugate's morphology dataset (with minor changes to character 12 to eliminate parsimony-uninformative character states and without any character ordering) yielded a strict consensus tree with little resolution. It only contained the following clades: *B. ferox*/*B. orientalis*; *B. kaibabensis*/*B. paludosa*; *B. mexicana*/*B. packardi*; and Fugate's clade 2. This lack of resolution implies that phylogenetic signal within the coded characters is not very strong. A majority rules (50%) consensus tree for the same data, however, showed elements of most of Fugate's three clades. The major difference was that the *B. ferox*/*B. orientalis* sister group was drawn down basal to the rest of the cladogram and *B. gigas* was a node above, but still outside of the clade containing the rest of the North American species of *Branchinecta*.

Only seven molecular phylogenetic analyses have included species of *Branchinecta* (deWaard et al., 2006; Remigio and Hebert, 2000; Richter et al., 2007; Stendrup et al., 2006; Sun et al., 2006; Weekers et al., 2002; Yang et al., 2003), and only one of these analyses included more than one species of *Branchinecta* (Weekers et al., 2002). In these analyses, five different species were used: *B. mesovallensis* and *B. lindahli* (in Weekers et al., 2002 and Sun et al., 2006); *B. occidentalis* (listed by Sun et al., 2006, but seemingly not used in their analyses); *B. packardi* (in Yang et al., 2003); and *B. paludosa* (in deWaard et al., 2006; Remigio and Hebert, 2000; Richter et al., 2007; and Stendrup et al., 2006). Consequently, it is difficult to infer anything about either the phylogenetic position of Branchinectidae within Anostraca or the in-group phylogeny of Branchinectidae (or *Branchinecta*) itself based on molecular data.

The number of anostracan taxa included varies widely between the analyses: from one (Yang et al., 2003, where *B. packardi* was the only anostracan), to twenty-seven (Weekers et al., 2002). As a result, a comparison of all of these analyses yields little regarding the phylogenetic position and relationship of Branchinectidae to other anostracans. Nearly all these molecular analyses reveal a close relationship between Chirocephalidae and Branchinectidae (deWaard et al., 2006; Remigio and Hebert, 2000; Richter et al., 2007;

and Stendrup et al., 2006; Weekers et al., 2002). However, no serious work on trying to identify morphological synapomorphies uniting the two groups has been conducted, with the closest proxy being non-evolutionary dichotomous keys (Belk, 1975; Dodson and Frey, 1991; Dumont and Negrea, 2002). Possible characters uniting Branchinectidae and Chirocephalidae (the latter including the subfamilies Branchinectellinae, Chirocephalinae, Polyartemiinae) are the lack of a medial frontal appendage, the lack of a clypeus, and penes with a short, rigid basal portion and a distal retractable portion. However, based on out-group comparisons with other branchiopods, the first two of those characters are likely symplesiomorphies and therefore not very phylogenetically useful.

Branchinecta is in need of revision (see Rogers, 2006); it contains approximately sixty species with little intraspecific phylogenetic order. The five species groups of *Branchinecta* listed by Brtek and Mura (2000) lack any sort of morphological diagnoses, and their validity is unverified at best (Rogers, 2006). Molecular phylogenies have not resolved relationships within *Branchinecta*, as the density of sampling of species is very low in all molecular analyses. Traditionally, systematics of the genus has generally relied almost exclusively on characters of the male second antennae. To resolve the in-group phylogeny, additional sampling, both morphological and molecular, is required.

Branchinecta Verrill 1869

Diagnosis.—As for family.

Branchinecta brushi, n. sp.

(Figs. 2-15)

Branchinecta valchetana Cohen, 1981; Rogers et al., 2008: p. 548.

Material Examined.—YPM 9181, holotype male (14.72 mm), collected from a small pool near the summit of Cerro Paniri (22.08°S lat., 68.25°W long.; 5946 m or 19,508 ft), Antofagasta Province, northern Chile, South America (Fig. 1; locality data the same for all subsequent specimens); YPM 24274, paratype female, (dissected; Fig. 2D, 8-10, 15); YPM 24275, paratype female (mounted ventrally for SEM; Fig. 3C, E-H, 11F-G, I-Q, 12A, C, 14D); YPM 24276, paratype female; YPM 24277, paratype male, (dissected; Fig. 2B, D; 8-10); YPM 24278, paratype male; YPM 24279, paratype lot of 5 males and 1 female; YPM 28498, paratype female (dissected; Fig. 2B); YPM 37225, paratype male (Fig. 2A); YPM 39903, paratype female (11.52 mm; Fig. 2C); YPM 42377, paratype male, (dissected); YPM 43108, paratype male (Fig. 6A-L); YPM 43109 paratype male (Fig. 6M-P); YPM 46456, paratype male (mounted ventral-up for SEM; Fig. 3A, B, D, 5, 11A-E, H, 12B, D-F, 14B-C); YPM 46457, paratype male (mounted dorsal-up for SEM; Fig. 13, 14A); USNM 1133646, lot of 2 paratype males (ex. YPM 24279).

Diagnosis.—A branchinectid with sexually dimorphic limbs, rhomboidal second maxillae, and very short and reduced cercopods (shorter than last abdominal segment);

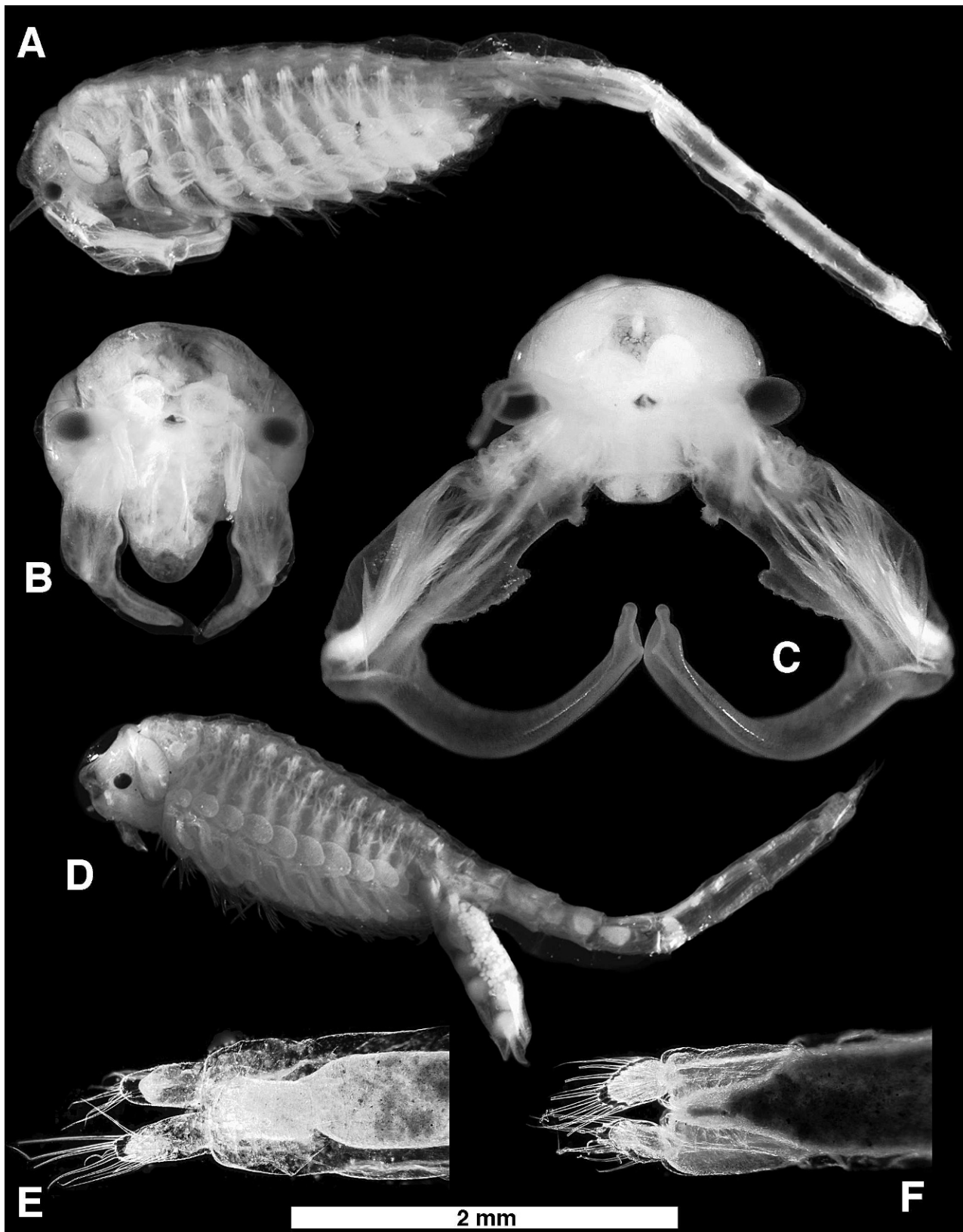


Fig. 2. *Branchinecta brushi* n. sp. The scale bar applies only to images D and E. A, male (14.72 mm long; YPM 37225), left lateral view; B, female head (1.44 mm max width across mandibles; YPM 28498); C, male head (1.84 mm max width across mandibles; YPM 24227), anterior view; D, female (11.52 mm; YPM 39903), left lateral view; E, male cercopod (YPM 24277); F, female cercopod (YPM 24274).

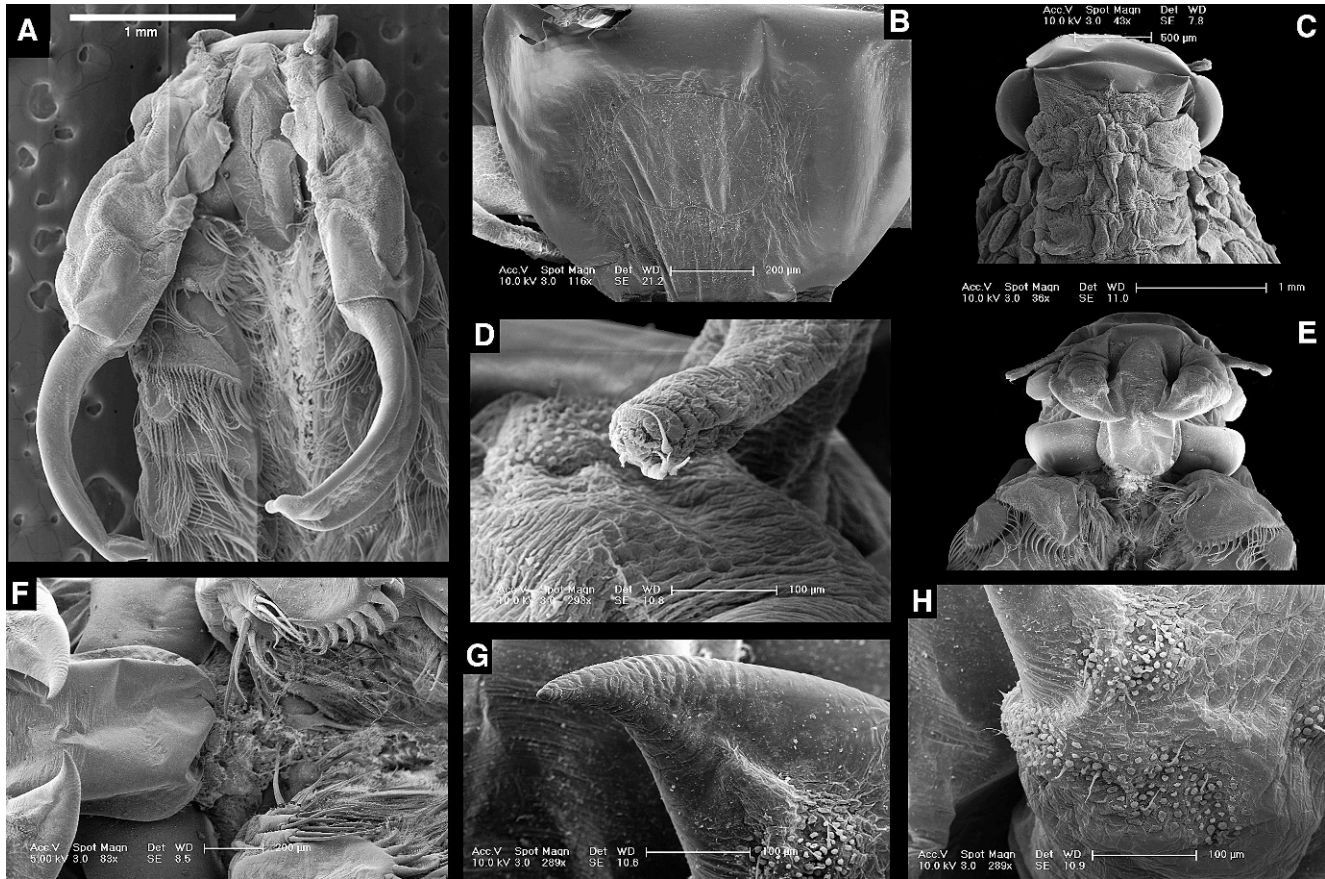


Fig. 3. SEM images of *Branchinecta brushi* n. sp. All female images are from YPM 24275. A, ventral view of an adult male (YPM 46456; constructed using Adobe® Photoshop's photomerge command); B, adult male dorsal organ (YPM 46456; dorsal side is to the top); C, dorsal view of an adult female head; D, close-up image of the tip of the first antenna of an adult male (see image A); E, ventral view of an adult female head; F, adult female labrum; G, tip of female second antenna; H, base of female second antenna.

male second antennae bearing a rounded apophysis with short conical spines situated proximally on the inner margin of the proximal article, and a triangular patch of short spines on middle part of proximal article creating an orally-facing barb; short and stout inwardly curved gonopods with short distal portion and rounded medial process, female second antennae conical with medial setae, ovisac cylindrical.

Male Description.—Males with average length of 12.7 mm (range 10–16 mm, $n = 12$; though sample may be skewed toward small adults, and further biased by preservation in ethanol). Heads smoothly domed in anterior view; naupliar eye roughly diamond-shaped between first antennae (Fig. 2A, C); dorsal organ a rounded rectangle, length about 60% of width, thin border about 1% of total width, anterior edge slightly concave (Fig. 3B); eye stalk length about 1/3 maximum width of head and about 2/3 length of first antenna (Fig. 2C); base of first antenna in contact with medial-dorsal edge of base of second antenna (Fig. 3A), of uniform diameter, several short setae on tip (≈ 4 ; Fig. 3D); male labrum oblong, slightly tapered posteriorly, slight cleft present laterally equivalent to apophysis of second antennae (Figs. 3A, 4A, E, 5A).

Male second antenna comprised of two articles nearly equal in length (Fig. 2C, 3A, 4A), when fully extended nearly as long as thorax; proximal article robust and widest

medially (Fig. 2C, 3A, 4A, 5D); short wart-like apophysis near proximal article base, wider distally than proximally, short spines on tip (Fig. 4D, 5A–B); oblong raised patch (as seen laterally) with short spines present on inner edge of proximal article, about 2/3 of length of proximal article from base, entire patch projects barb-like in oral direction (as seen ventrally; Fig. 4B, 5A, E–F); distal article flattened (laterally) and curved slightly inward, scoop-like with groove along outer edge of distal article (Fig. 2C, 3A, 4A, C, 5C); in death second antennae often strongly flexed at joint between proximal and distal articles forming a 90° bend (Figs. 2C, 3A, 4A).

Mandibles asymmetrical. Left mandible bordered posterodorsally with a single row of stout spines decreasing in size to the anterior, spines point toward center of mandibular surface; transitional zone low, decreases in width to the anterior; central region accounts for the majority of mandibular surface area, filled with parallel files of rectangular platelets (long axis oriented parallel to anterior-posterior axis), each platelet is covered with low conical tubercles, tubercle length increases ventrally so that tubercles grade into flagellated processes (Fig. 6M–P). Right mandible similar save for wear facet developed dorsally between the postero-dorsal region and the central region (Fig. 6A–L).

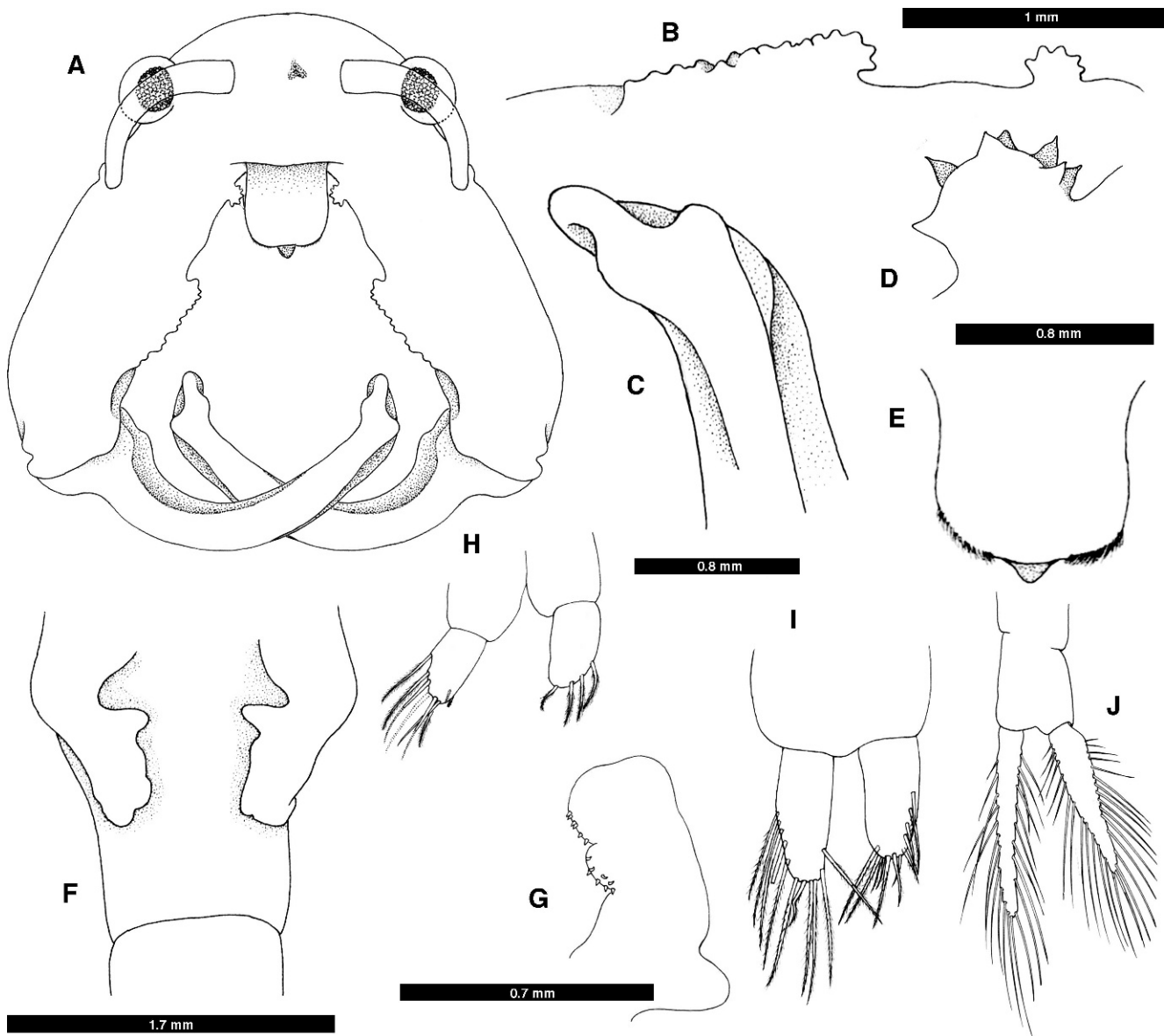


Fig. 4. Drawings of *Branchinecta brushi* n. sp. All male images drawn from YPM 42377. A, male head, anterior view; B, inner edge of the proximal portion of the male second antennae, proximal to distal axis is right to left, 1 mm scale bar above the image; C, distal tip of the male second antennae; D, proximal spiny palp-like structure from the proximal portion of the male second antennae with 0.8 mm scale bar below; E, male labrum with 0.8 mm scale bar above; F, male gonopods with 1.7 mm scale bar below; G, tip of left pene oriented with inner edge up, 0.7 mm scale bar below; H, female cercopod (YPM 39903), 0.8 mm scale bar below; I, male cercopod, with 0.8 mm scale bar to the left; J, cercopod of *Branchinecta valchetana* Cohen, 1981, redrawn from the original description.

First maxillae longer than wide, subtrapezoidal, with distal edge longest. Distal edge with uniform row of distinctive dense setae bracketed by single spine laterally, spine half as long as setae. Setae with thicker and longer basal segment, basal segment with one row of setules. End of basal setal segment branches into two portions; a long annulate plumose setae and a shorter spine-like setae (Fig. 7G).

Second maxillae subrhomboidal with longest transverse distance across from medial proximal corner to lateral distal corner. Inner edge of maxillae thicker and covered with fine short setae. At medial distal corner are two long setae, plumose distally, on distal edge near lateral distal corner are longer distally-plumose setae (Fig. 7F).

Limbs increase in size to approximately the fourth limb, decrease in size at approximately the seventh limb (Fig. 8-10). Pre-epipodite subrectangular with curved outer margin. Epipodite reniform, slightly concave side faces exopod, smooth margin, partially overlaps anterior portion of pre-epipodite (Fig. 7B, 11C-E), smaller than exopod. Exopod reniform with concave side facing epipodite, fringed with long plumose setae. Endopod large, males possess endopods with a slightly rounded apex, inner margin straight, distal margin with change in slope leading to apex, apex extends inward beyond endites (Fig. 7B), fine setae adjacent to endopod insertion increasing in size toward apex, fine setae transition into rigid conical spikes

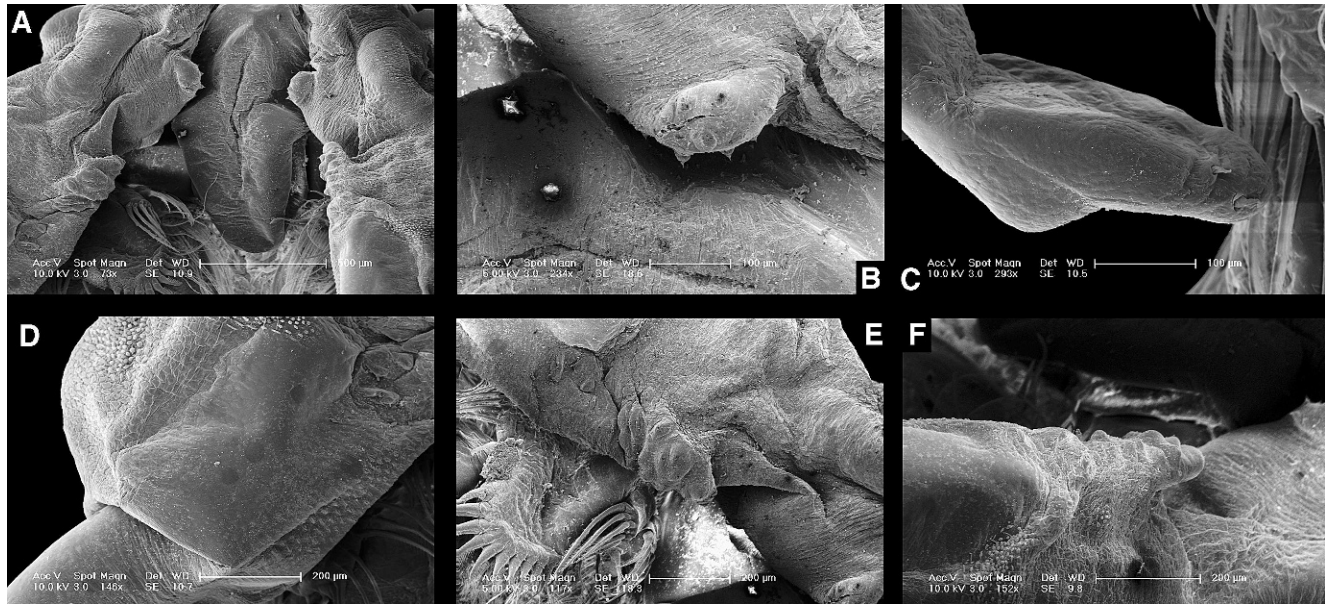


Fig. 5. Structures of male second antenna of *Branchinecta brushi* n. sp. (YPM 46456). A, labrum and armature of second antenna proximal article; B, proximal palp on the proximal article of the male second antenna (left); C, tip of male second antenna; D, junction of male second antenna proximal and distal articles; E-D, oblong spinous patch on male second antenna (left and right respectively).

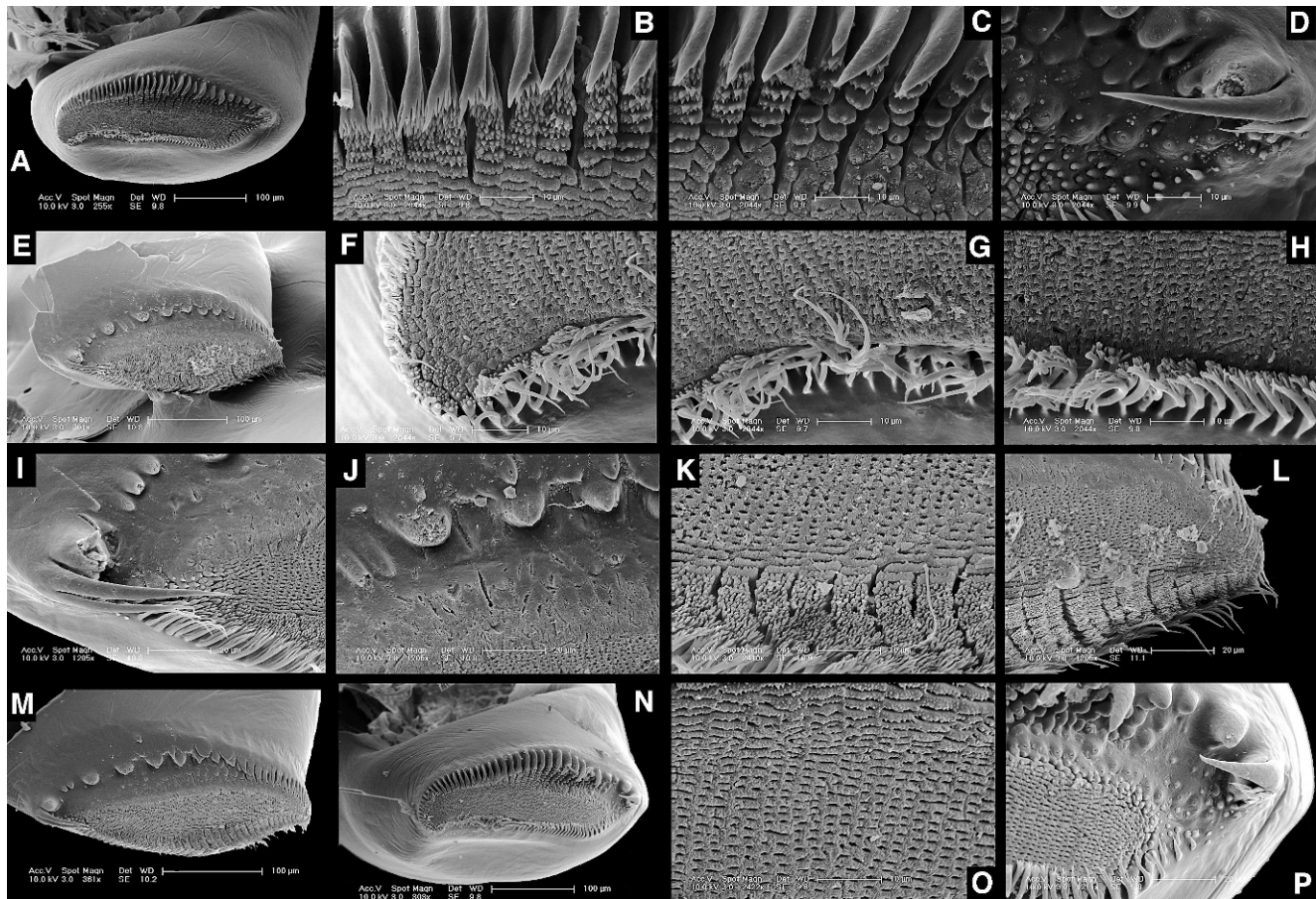


Fig. 6. Mandibular structures of *Branchinecta brushi* n. sp. A-L are from YPM 43108, and M-P are from YPM 43109. A, surface of right mandible (dorsal side up); B-D, sequential close up images along dorsal edge of right mandible (A); E, surface of left mandible (dorsal side up); F-H, sequential close up images along ventral edge of right mandible (A); I, posterior-dorsal and transitional zone of left mandible (E); J, dorsal margin of left mandible (E); K, ventral margin of left mandible (E); L, anterior edge of left mandible (E); M, surface of left mandible; N, surface of right mandible; O, central region of right mandible (N); P, posterior edge of right mandible (N).

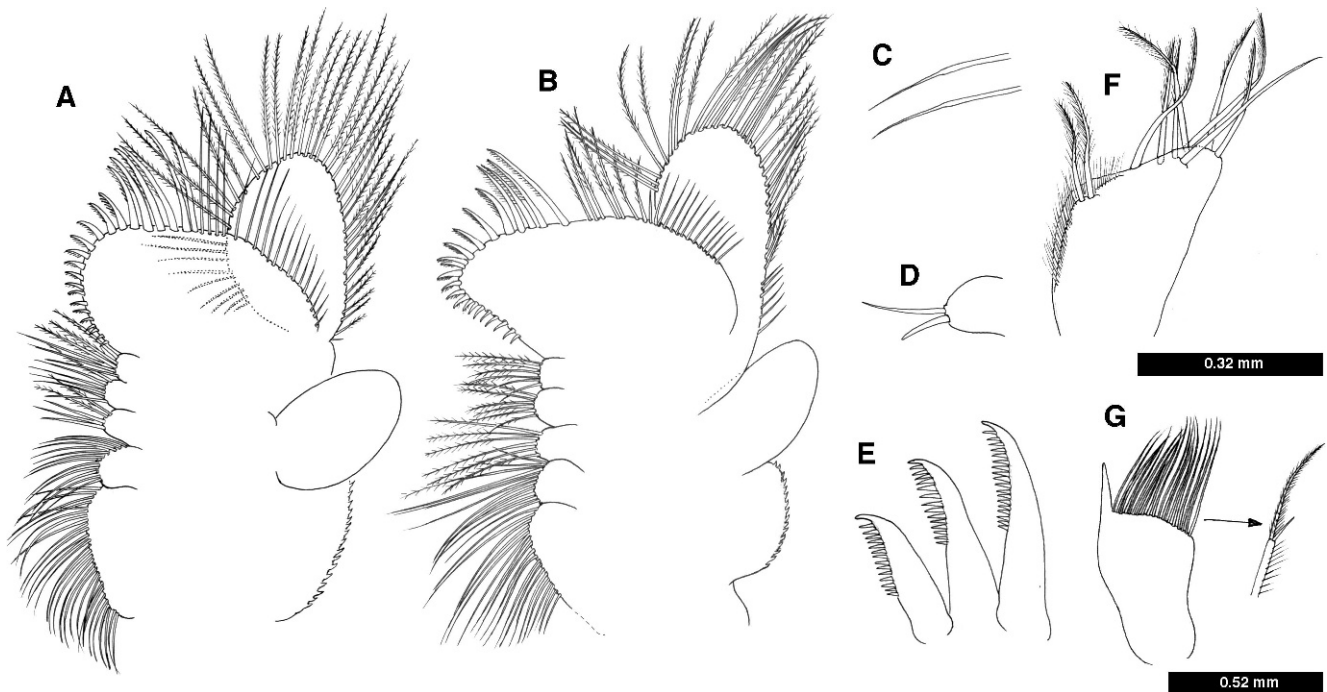


Fig. 7. *Branchinecta brushi* n. sp. limb drawings. Male limbs are from YPM 24277; female limbs from 24274. A, seventh female thoracopod; B, seventh male thoracopod; C, typical setae from proximal endites; D, generalized second endite with setae removed for clarity in order to show the single pair of spine-like setae; E, detail of comb setae from the tip of the endopod; F, second maxillae with scale bar below; G, first maxillae with scale bar below, detail of typical setae to the right.

near apex, conical spines possess two short longitudinal rows of spines near the apex of the spikes, spines decrease in size near endites (illustrated for female, see Fig. 11J-R). Endite 1 broad, as wide as endites 2-5 combined, smoothly rounded and asymmetrical, fine closely-spaced setae fringe margin, one spine-like setal element inserted amongst standard setae located midway across endite 1 (Fig. 7B, D). Endite 2 ovate with closely spaced fine setae, less than 1/3 width of endite 1. Endites 3-5 equal in size, oblong and narrower than endite 2, setae less dense but more rigid.

Penes short and stout (Fig. 4F, 12F), with slight mound between them; each penial base about 1/3 genital segment width, narrowest width across penis 2/3 that at base at a point midway between medial penal spur and base; medial penal spur short, thick and rounded (Fig. 4F, G, 12F), distal portion (post-spur) short, small tubercles present on lateral edge of tip with slight cleft immediately proximal indicating base of eversible portion (Fig. 4G, 12D-F).

Thorax and abdomen lack prominent dorsal ornamentation (the wrinkling and distortion caused by the years in ethanol made evaluation of this difficult; Fig. 2A, D), males have short paired dorsal setae encircled by short bumps (Fig. 13). These paired setae likely occur in both sexes, like those documented by Tyson and Sullivan (1980), but were only clearly observed under the SEM on a dorsally mounted male (no females were mounted dorsally). Cercopods short and reduced (Fig. 2E, F, 4H-I, 14), about half the length of last abdominal segment. Cercopod setae plumose (Fig. 14).

Differentiating Female Description.—Females with average length of 10.7 mm (9-13 mm, $n = 3$; average may be

skewed smaller due to the long period of time the material was preserved in alcohol; Fig. 2D). Eye stalk length about 1/4 maximum width of head (Fig. 2B). Base of first antenna in contact with dorsal edge of second antenna base. Labrum teardrop-shaped, wider distally, shorter than male labrum (Fig. 3E-F).

Female second antenna conical (Fig. 2B, 3E, G-H); roughly as long as labrum, consisting of only one article, short setae present on interior-medial surface.

Females have smaller, more rounded endopods, shorter, outer margin serrated with steep face of serration facing distally, teeth of serration with apex of between 40-70°, angle decreases distally (Fig. 7A, 8-10, 11F-G).

Brood pouch cylindrical, extending length of at least three abdominal segments, roughly equal in diameter to abdomen; gonopore transverse slit with protruding dorsal margin (Fig. 12A). Dorsal ornamentation present dorsally on females, but it is difficult to accurately characterize due to the long period of time the specimens have been stored in alcohol.

Reproductive cysts spherical, low ridges which that relatively large polygons, ridges moderately discrete and rounded in profile. Cyst wall with a sponge-like texture (Fig. 15).

Locality.—Cerro Paniri (22.08°S lat., 68.25°W long.; 5946 m or 19,508 ft), Antofagasta Province, northern Chile, South America (Fig. 1).

Etymology.—The specific name honors the discoverer of the specimens, the late Charles F. Brush (1923-2006), alumnus of Yale College 1945.

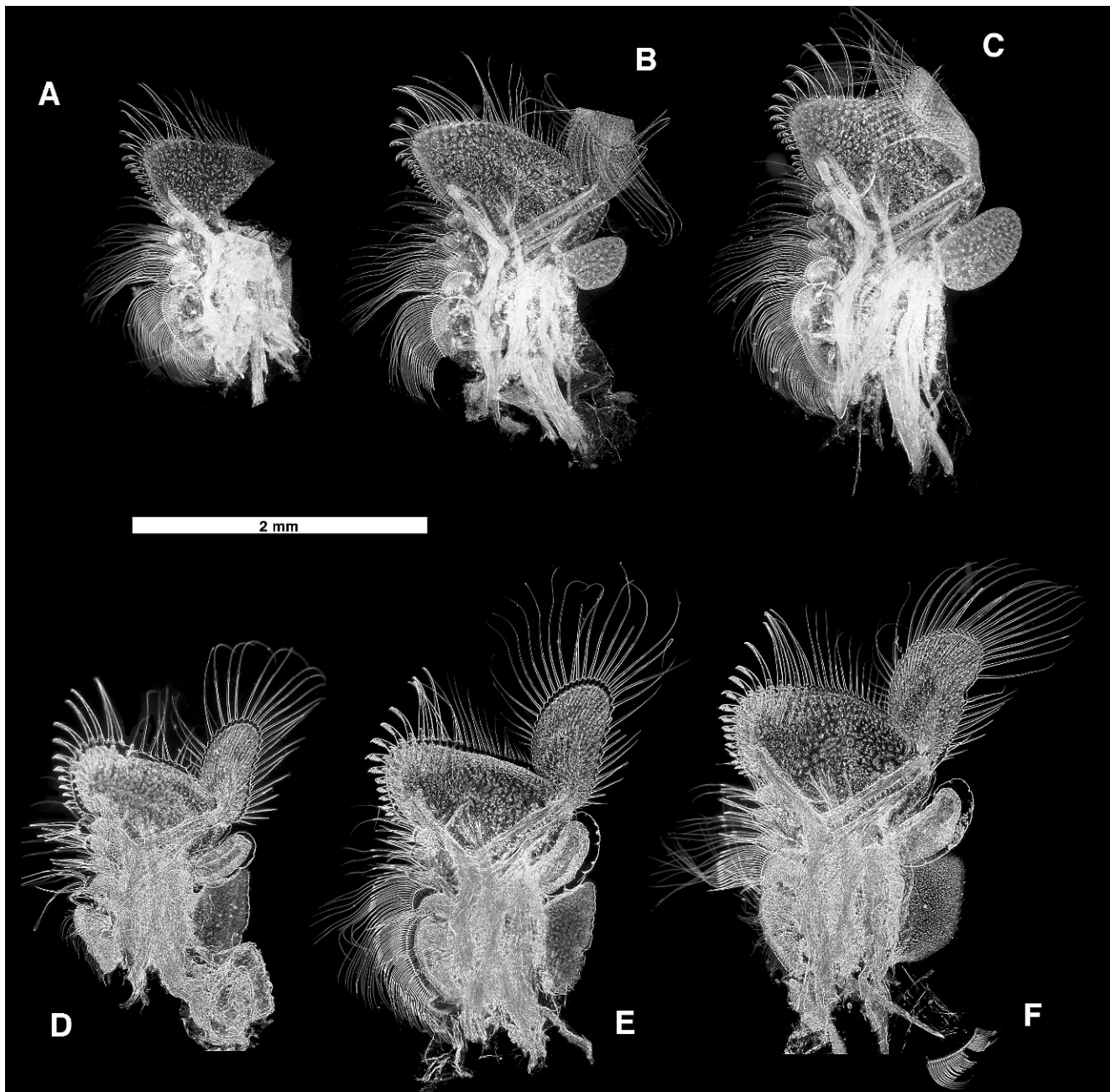


Fig. 8. *Branchinecta brushi* n. sp. Male limbs are from YPM 24277; female limbs from 24274. A-C, first through third thoracic limbs (right side of animal, except for A which is a left limb that has been flipped in photoshop) from an adult male; D-F, first through third thoracic limbs (right side of animal) from an adult female. Limbs arranged sequentially with the first limb on the left and third on the right.

Remarks.—Making comparisons on the basis of morphologic similarity, *B. brushi* is very similar to *B. valchetana* Cohen, 1981. The male antenna is comparable in both species, but it differs in the relative width of the two articles, the shape of the tip, and the shape of the apophysis on the proximal article. The palp on the basal part of the proximal article is conical in *B. valchetana* and rounded in *B. brushi*. These differences alone are traditionally considered substantial enough to warrant designation as a new species (Belk and Rogers, 2002). More substantial differences are found in the gonopods and limbs. *B. brushi* has wider gonopod bases and stouter rounded medial spurs.

The evertable portion of the gonopod is much longer in *B. valchetana*, whereas the proximal portion of the penial shaft is longer in *B. brushi* (Fig. 4F-G, 12F). In both sexes, the endopods are more rounded and less pointed, with the male *B. brushi* endopod resembling the endopod of the female (not the male) of *B. valchetana*. In *B. brushi*, endites are more regular in size and shape, and the epipod is relatively larger. In females, the second antenna is wider basally in *B. brushi* than in *B. valchetana* and the brood pouch is more cylindrical in *B. brushi*.

The medial armature of the male second antenna is often very distinct between species of *Branchinecta*. In fact,

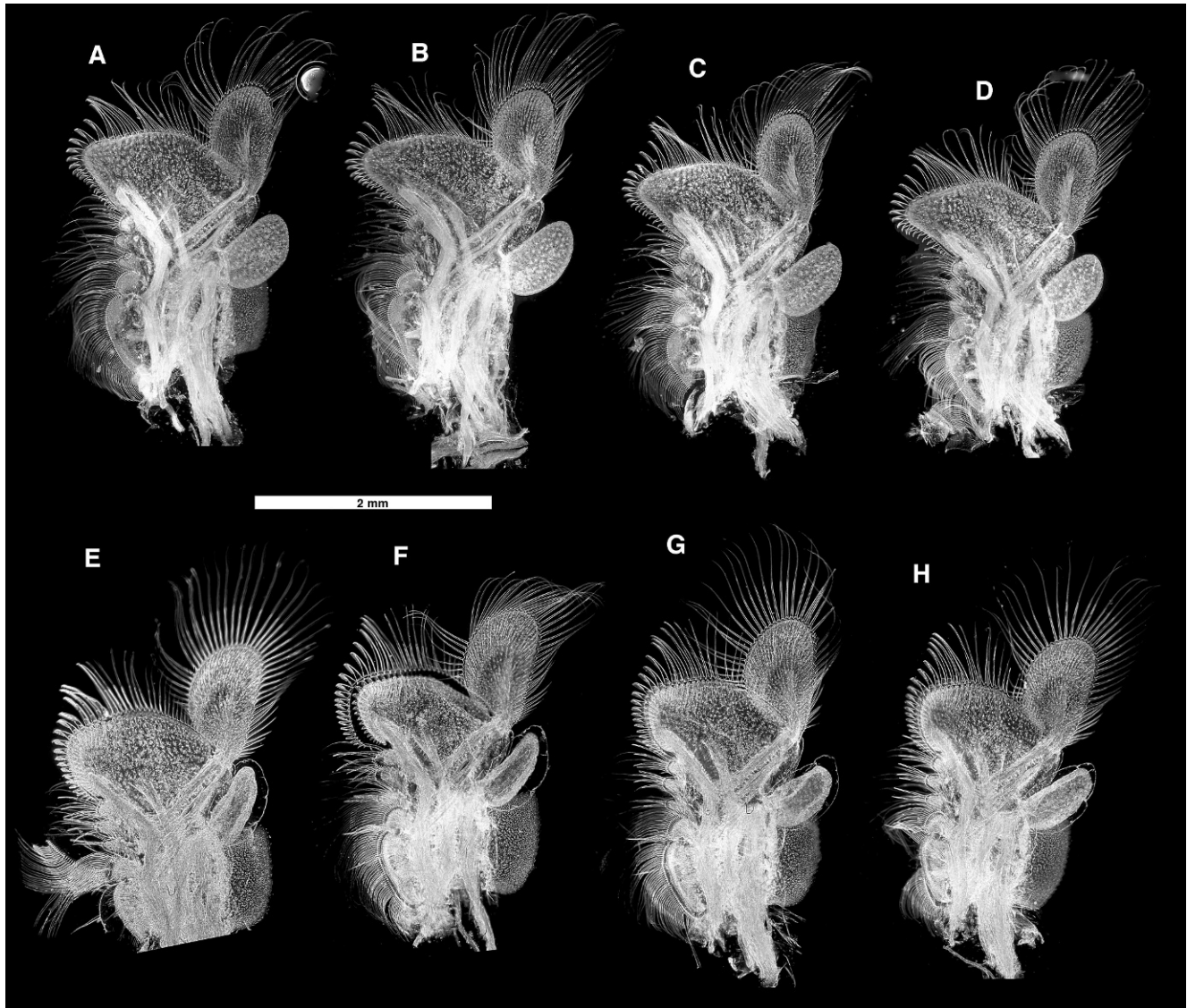


Fig. 9. Limbs from *Branchinecta brushi* n. sp. Male limbs are from YPM 24277; female limbs from 24274. A-D, male thoracic limbs (right side of animal) 4-7; E-H, female thoracic limbs 4-7 (right side of animal). Limbs arranged sequentially with the fourth limb on the left and seventh on the right.

taxonomy of the genus has relied almost entirely on this complex of characters, to the neglect of the rest of the morphology. The pattern of armature in *B. brushi*, a basal apophysis and a medial patch of spines or scales on the proximal article, is shared with several other species, though each differing in expression. This group includes *B. barstowensis* Belk and Schram, 2001; *B. coloradensis*; *B. fueguina* Cohen, 2008; *B. lynchi* (see Eriksen and Belk, 1999); *B. mackini* Dexter, 1956; *B. mexicana*; *B. oterosanvicentei* Obregón-Barboza, Maeda-Martínez, García-Velazco, and Dumont, 2002; *B. packardi*; *B. pollicifera* Harding, 1940; *B. granulosa* Daday de Deés, 1910; and *B. valchetana*. However, it is premature to try and parse out intrageneric relationships based on the second antennae alone; the morphology of these other species will need to be known in comparable detail to elucidate their phylogenetic placement. *B. fueguina* has a much larger proximal apophysis than *B. brushi*. *B. mexicana* and *B. oterosanvicentei* also possess the barb-like medial spine/scale patches

on the male second antennae which is present in *B. brushi* and *B. valchetana*. However, further morphological similarity of the two Mexican species is difficult to assess, as the limb, female, and gonopod morphology of both is not illustrated. The degree of development of this medial patch on the proximal segment of the male second antennae suggests the possibility that it may be a morphological intermediary between the more simple raised spine patch of *B. coloradensis* and the medial apophysis structure on the proximal article of the male second antennae of *B. pollicifera* and *B. barstowensis*.

There are few illustrated maxillae for species of *Branchinecta*, making meaningful comparisons difficult. Illustrations of the first maxillae in species of *Branchinecta* are only available in Fryer (1983; *B. ferox*), Fugate (1993; *B. sandiegoensis*), and Sars (1896, 1897, 1901; *B. paludosa*, *B. tolli* (Sars, 1897), and *B. orientalis*, respectively). *B. brushi* possess a stout spine on the ventral side of the setae-bearing distal margin, a characteristic it shares

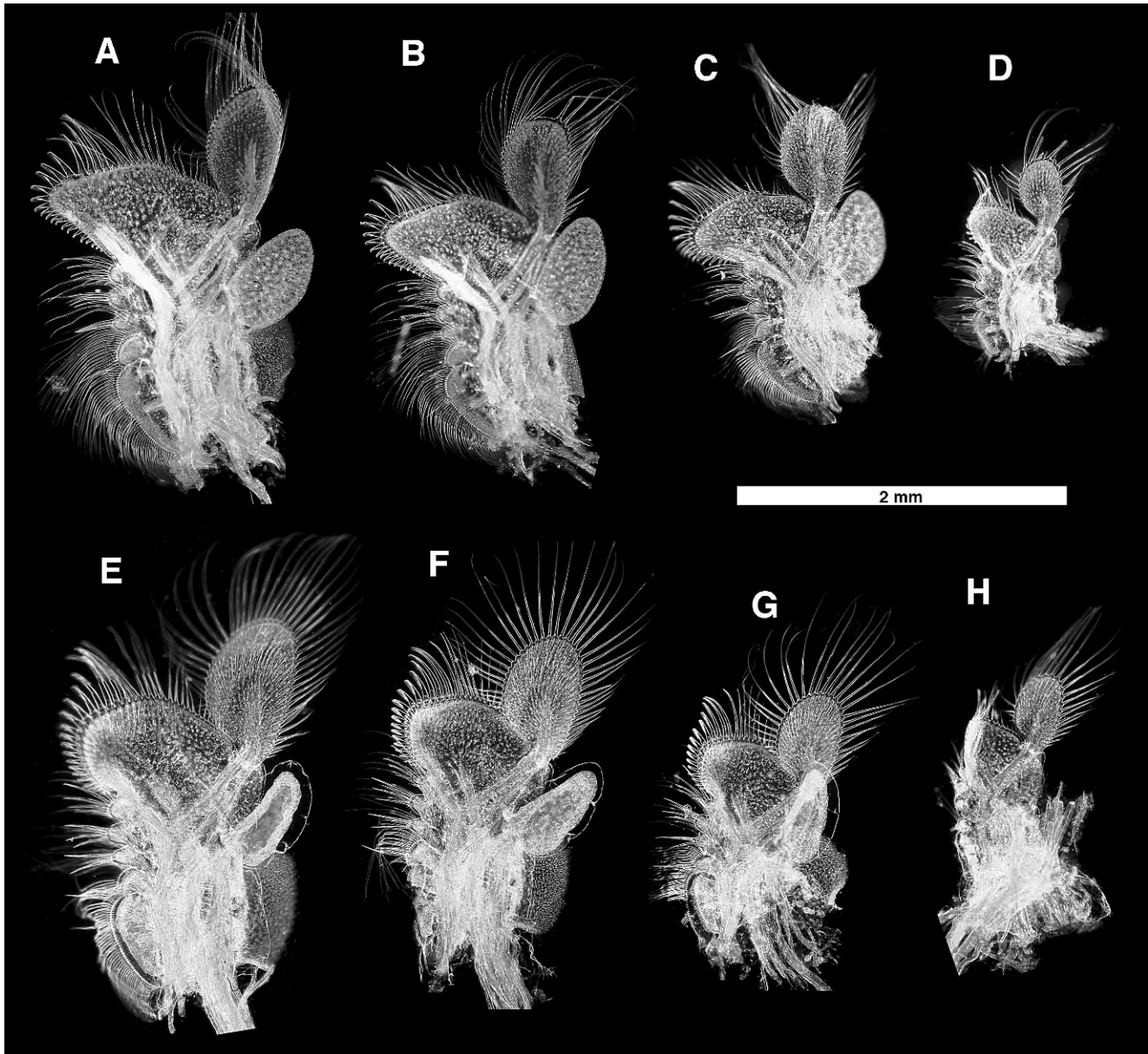


Fig. 10. Limbs from *Branchinecta brushi* n. sp. Male limbs are from YPM 24277; female limbs from 24274. A-D, male thoracic limbs (right side of animal, except for C which is a left limb that has been flipped in photoshop) 8-11; E-H, female thoracic limbs (right side of animal) 8-11. Limbs arranged sequentially with the eighth limb on the left and eleventh on the right.

with *B. ferox*, *B. orientalis*, and *B. sandiegoensis*, but this possible homology may be more apparent than real owing to the variable quality of mouthpart illustrations. From what is known, there does not seem to be a great amount of variability in the first maxillae of Branchinectidae, but extrapolating this conclusion from a mere five species is hardly a sufficient. Illustrations of second maxillae are relatively more common; *B. brushi* exhibits some interesting differences. The second maxilla of *B. brushi* is broader distally than all other known *Branchinecta* second maxillae. *B. brushi* shares a fine patch of proximal setae on the sagittal edge with *B. ferox*, *B. iheringi* Lilljeborg, 1889 (see César, 1988), and *B. sandiegoensis*. *B. valchertana* has a unique bent shape which is not found in *B.*

brushi, but shared with *B. orientalis* and *B. paludosa*. *B. sandiegoensis* has a short spine located medially near the base that has only been observed in *B. ferox*. *B. palustris* Birabén, 1946 (see Cohen, 1981) and *B. ferox* are more similar to *B. brushi* in overall shape but both have less dense distal setation. The differences observed between these few species (where the maxillae have been studied) suggest that they may be a ripe source of phylogenetically useful characters if they are investigated in more species.

Likewise, sexual morphology is hard to evaluate, as the sexual characteristics in several of the species mentioned above is not illustrated. The apical part of the gonopods of *B. brushi* are very similar to those of *B. leonensis* Cesar, 1987 and *B. somuncurensis* Cohen, 1983. The ovisac

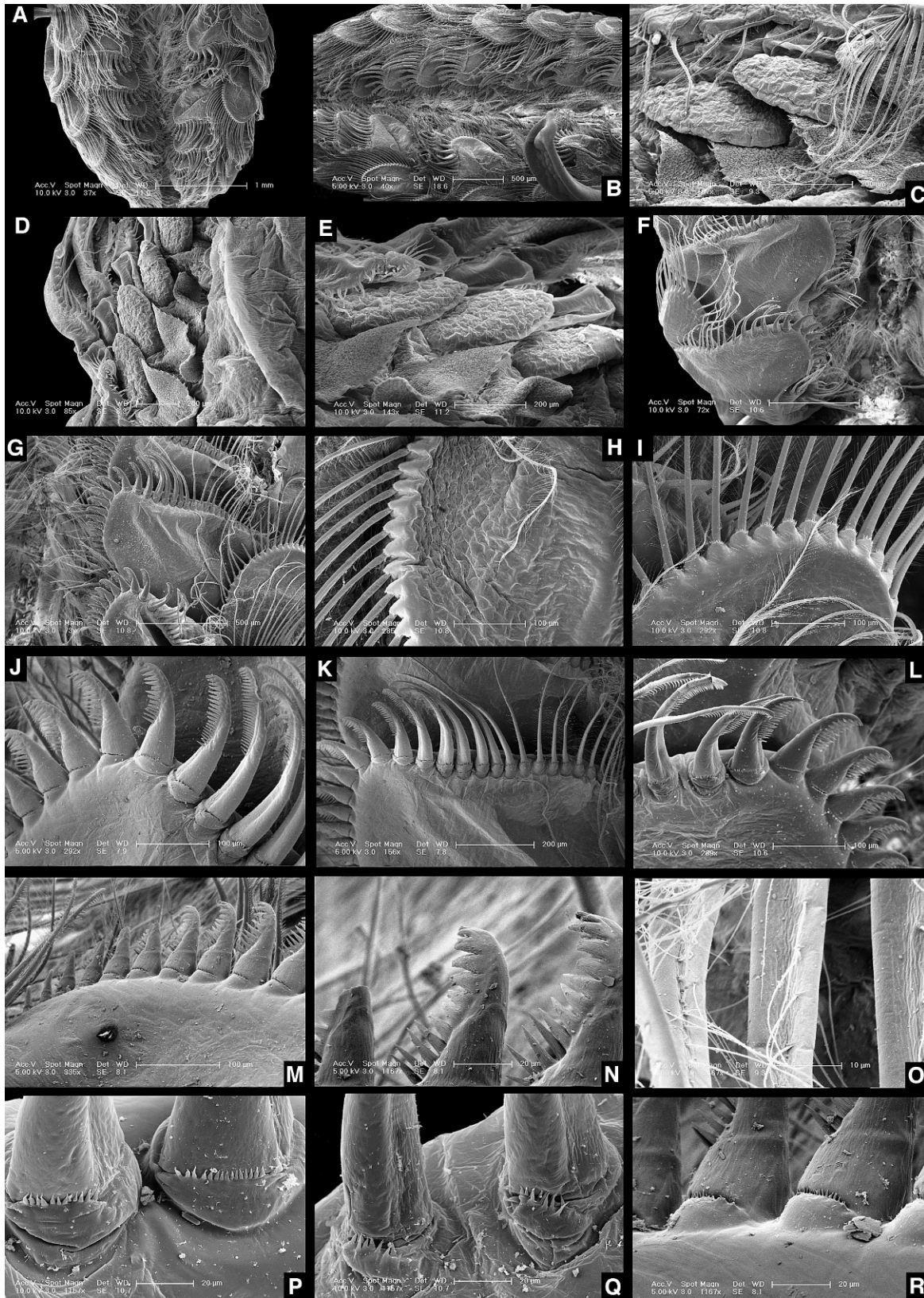


Fig. 11. SEM images of the thoracic limbs and setae of *Branchinecta brushi* n. sp. All female images from YPM 24275. A, posterior limbs from an adult male, ventral view (YPM 46456); B, middle complement of limbs from an adult male, ventral view (YPM 46456); C-E, dorsal view of epipods and preepipodites from an adult male (YPM 46457); F-G, female thoracic limbs, ventral view; H, exopod from seventh thoracic limb of adult male, ventral view (YPM 46456); I, exopod of adult female, ventral view (limb number uncertain); J, L, M, comb setae of a female endopod; K, female endopod showing comb-plumose setae transition (same lobe as in J); N, close up image of comb setae teeth (female endopod); O, close up image of plumose setae (female endopod); Q, base of plumose setae (female endopod); P, R, base of comb setae (female endopod).

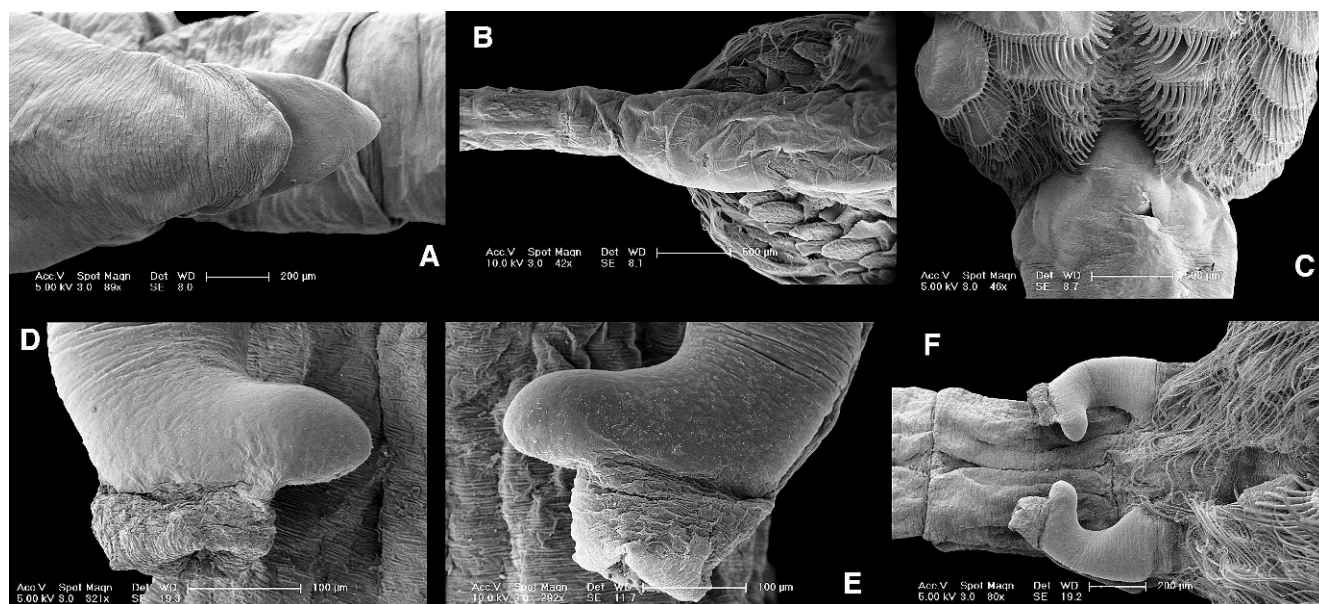


Fig. 12. SEM images of *Branchinecta brushi* n. sp. sexual morphology. A, distal tip of female ovisac (YPM 24275); B, dorsal view of male (YPM 46457); C, proximal (anterior) end of female ovisac (YPM 24275); D-E, tip of male penis (right and left respectively; YPM 46456); F, male penes (YPM 46456).

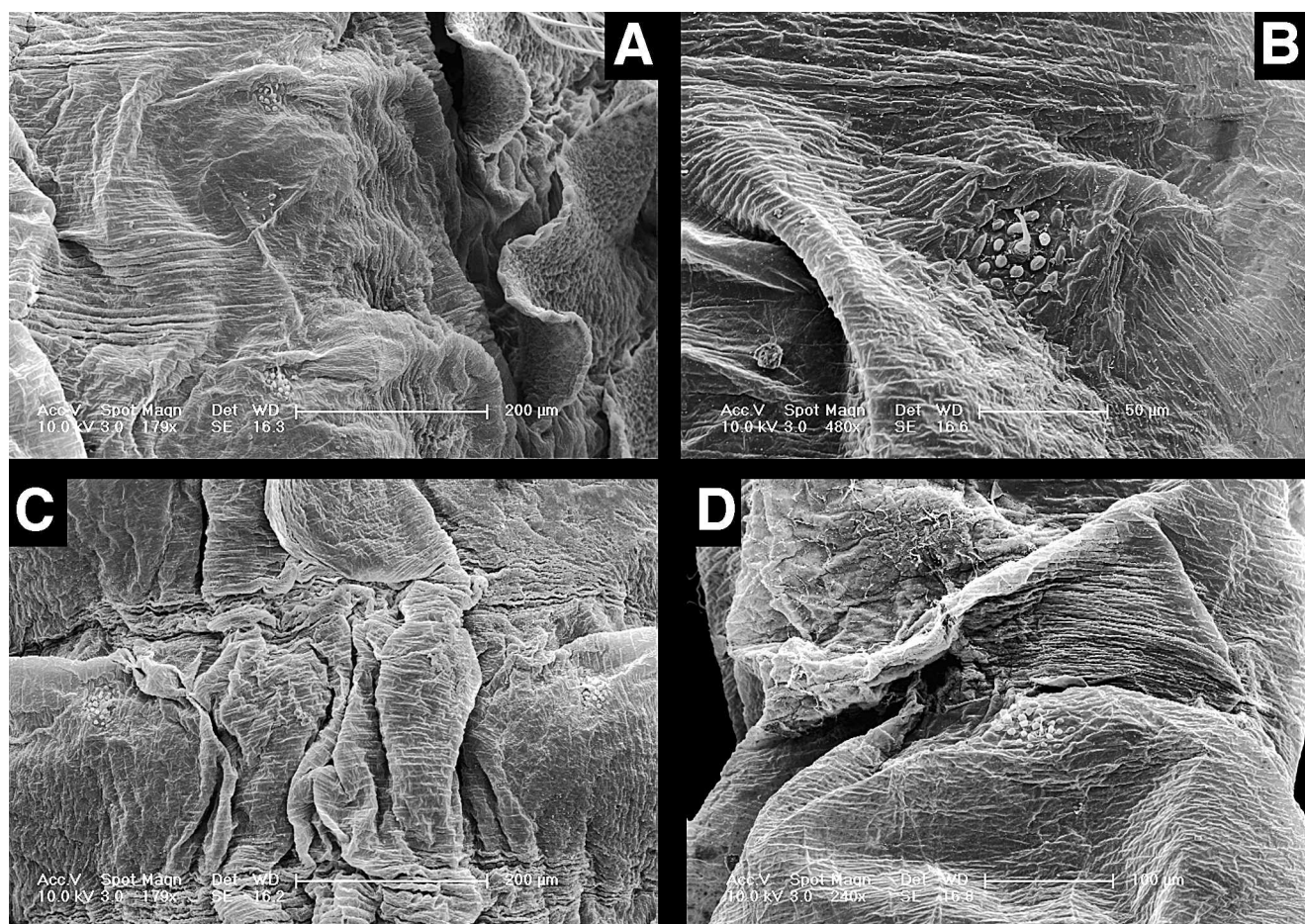


Fig. 13. Dorsal sensory (?) structures on the thorax of *Branchinecta brushi* n. sp (YPM 46457; male). A, round structures next to thoracic limbs; B and D, single sensory rosette with lone central seta; C, paired rosettes on single thoracic segment.

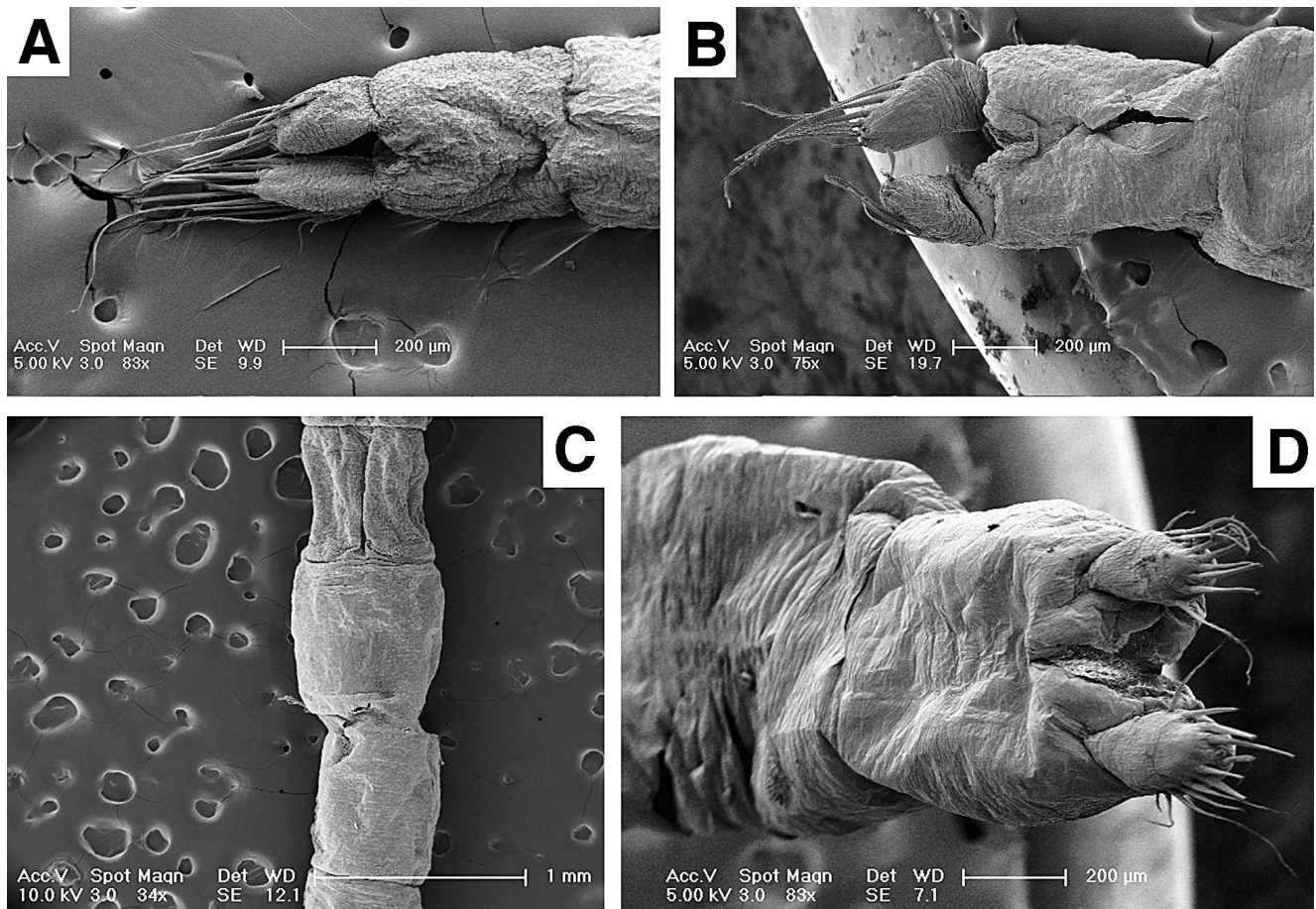


Fig. 14. SEM images of *Branchinecta brushi* n. sp. tails. A, dorsal view of male tail (YPM 46457); B, ventral view of male tail (YPM 46456); C, ventral view of male abdomen (YPM 46456); D, ventral view of female tail (YPM 24275).

morphology of *B. brushi* is similar to that of *B. palustris* Birabén, 1946 and *B. rocaensis* Cohen, 1982. It is also similar in proportion to that of *B. leonensis*, but far shorter.

The cercopods are very short in both sexes of *B. brushi*, shorter than in any other species (compare *B. brushi* (Fig. 4H-I) with *B. valcheta* (Fig. 4J)). Though this is perhaps the most distinctive characteristic of the new species, it is also somewhat problematic. Shantz (1905) documented short cercopods in *B. coloradensis*. This shortening of the cercopods was attributed to disease in some cases, and resorption (absorption sensu Shantz, 1905), and Shantz characterized the diseased cercopods as distally blackened and with asymmetry of affected areas. Resorption, on the other hand, was attributed in cases where the cercopods were shortened (always asymmetrically in illustrated examples) without any distal blackening. No asymmetry was observed in *B. brushi*, and therefore there is no evidence that the short cercopods of *B. brushi* are a result of either disease or resorption. Therefore, short cercopods seem to be a real biological feature unique to *B. brushi*.

The degree of eco-phenotypy at high altitudes remains to be addressed and may have significant taxonomic implications. Given modern morphological standards, *B. brushi* qualifies as a distinct species. To what degree its distinctiveness is due to eco-phenotypy is an open question. How lower levels of oxygen coupled with colder

temperatures affect the growth of fairy shrimp is essentially unknown. What is known, however, is that some fairy shrimp are able to withstand conditions of extreme temperature (both hot and cold) and high elevation. Studies on the Antarctic species of *Branchinecta*, *B. gaini* Daday de Deés, 1910 have focused on the physiological innovations needed to survive in extreme, low temperature environments (Hawes et al., 2008; Peck, 2004; Pocięcha, 2007) and implicitly suggesting that survival in extreme environments depends on physiological, not morphological, innovations. This is further borne out by the mortality of *B. gaini* correlated to increases in temperature (Peck, 2004) and salinity (Hawes et al., 2008). Therefore, facile attribution of morphological variation to 'eco-phenotypic' causes is both unlikely and unsatisfactory as an explanation.

ECOLOGY OF ALTITUDE

Crustaceans are not normally associated with high altitudes ('high' altitudes are herein considered anything above about 3000 m or 10,000 ft). Their need of aquatic (or humid) environments almost necessitates that they be restricted to lower altitudes. High-altitude occurrences of crustaceans are restricted to species that can produce reproductive cysts that lie dormant during the coldest months of the year when the water is frozen. This not only

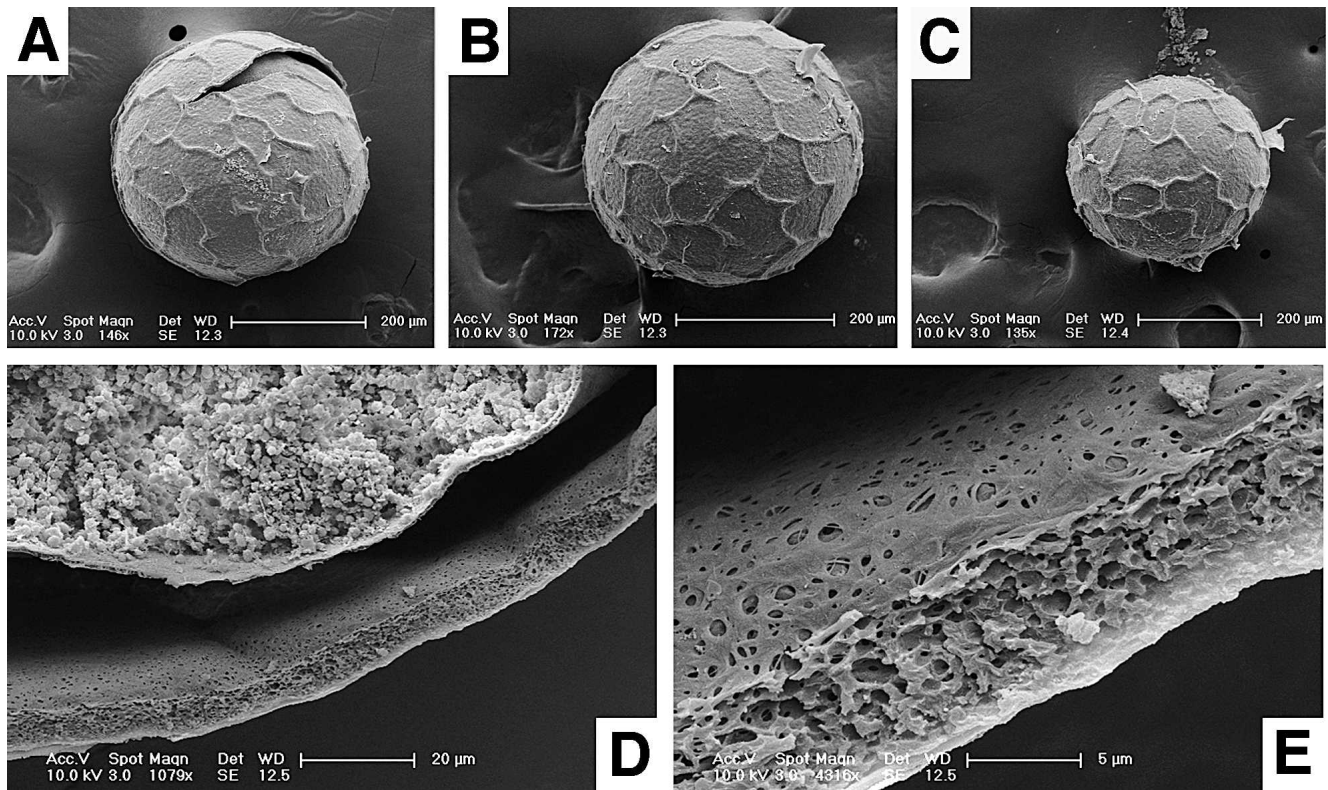


Fig. 15. Cyst morphology of *Branchinecta brushi* n. sp. A-C, cysts; D-E, cyst wall of the cyst in image A. Cysts dissected from YPM 24274.

allows them to cope with the cold, but also enables easier dispersal by birds or other agents. Crustaceans which are better adapted to more terrestrial lifestyles, such as isopods, are direct developers, and are thereby often less efficient in their dispersal. Other crustaceans with significant terrestrial portions to their lifecycles are tied to water sources for their reproduction, and do not produce easily dispersed cysts.

Several authors have discussed high-altitude occurrences of crustaceans and their ecology (Dodd, 1917; Manca and Mura, 1997). Common to all of these occurrences is the nature of the water body; they are always small seasonal bodies of water with presumably little to no open drainage to lower altitudes. Often the pools are frozen for a portion of the year. Such an environment supports a depauperate fauna, often only accompanied by other crustaceans with a similar reproductive mode. The limnological literature is full of high-altitude lake surveys that explore the ecology in more detail (Elías-Gutiérrez, 1995; Hurlbert et al., 1986; James and Hubback, 1969; Löffler, 1964, 1969; Raina and Vass, 1993; Reed and Olive, 1958; Valdivia Villar, 1988). Predation is likely minimal when compared to lower altitude ephemeral water bodies, but no comparative studies of this have been conducted.

In theory, branchiopod colonization only takes a single cyst or ephippium (Dumont and Negrea, 2002), i.e., one visit by a bird, or one fortunate gust of wind. However, for the colony to survive, reproduction must take place; and since most species of anostracans are sexual, there needs to be at least two cysts for the initial colonization to succeed. High altitude occurrences are more likely due to birds, as wind dispersal seems to operate only over short ranges

(Brendonck and Riddoch, 1999) and would be most likely to succeed with parthenogenetic branchiopods (Dumont and Negrea, 2002). Hulsmans et al. (2007) experimentally determined that a fifty-meter separation between habitats acts as a barrier to gene flow (and possibly dispersal) for branchiopod populations. However, as Graham and Wirth (2008) note, cysts can be transported by relatively low wind speeds, and it is possible for them to be transported significant distances by higher wind speeds.

Branchiopod reproductive cysts can survive passage through bird digestive tracts (Mathias, 1937; Procter, 1964) and any bird preying on fairy shrimp would likely have consumed many females bearing cysts. Therefore, bird-mediated colonization of Cerro Paniri appears a likely possibility. It is unknown if Cerro Paniri lies directly on any bird migration routes. *B. brushi* is a sexual population, and it seems much more likely to postulate a visit by a bird than two reproductive cysts being blow up a mountain and landing in a pool during the same season. This discussion on the original mode of delivery for *B. brushi* mirrors that for another high altitude occurring species, *B. coloradensis*. Behre (1931) suggested glaciation as an isolating mechanism for speciation, Creaser (1931) suggested animal-mediated dispersal, and Gordon (1931) advocated wind dispersal. *B. coloradensis* was originally vaguely characterized as a high altitude specialist (Packard, 1874; Behre, 1931), but their eventual discovery at lower altitudes (Gordon, 1932; Lynch, 1964) gives caution to over-interpreting the distribution data at hand.

Geology provides a maximum age constraint for the population as the volcano has erupted within the last

Table 1. Altitude records for various crustacean taxa. YPM indicates unpublished material in the Yale Peabody Museum Invertebrate Zoology collection.

Species	Group	Elevation	Locality	Reference
<i>Branchinecta brushi</i>	Anostraca	5930 m	Cerro Paniri, Chile	Herein
<i>Boeckella palustris</i>	Cladocera	5930 m	Cerro Paniri, Chile	YPM 9204
<i>Daphniopsis chilensis</i>	Cladocera	5883 m	Licancebur Volcano, Chile	Hann, 1986
<i>Daphnia tibetana</i>	Cladocera	5460 m	Nepal	Manca et al., 1994
<i>Daphnia tibetana</i>	Cladocera	5460 m	Nepal	Manca et al., 1994
<i>Daphnia longispina</i>	Cladocera	5400 m	Nepal	Manca et al., 1994
<i>Gammarus pulex</i>	Amphipoda	5334 m	India	Uéno, 1934
<i>Arctodiaptomus (S.) altissimus</i>	Copepoda	5297 m	Ladak, India	Hutchinson, 1937
<i>Branchinecta orientalis</i>	Anostraca	5217 m	North India	Bond, 1934
<i>Ilyocryptus denticulatus</i>	Cladocera	5140 m	Chile-Peru	Kotov and Štifter, 2005
<i>Daphnia carinata</i>	Cladocera	4875 m	Ladak, India	Brehm and Woltereck, 1939
<i>Arctodiaptomus (S.) altissimus</i>	Copepoda	4875 m	Ladak, India	Hutchinson, 1937
<i>Cyclops ladakanus</i>	Copepoda	4875 m	Ladak, India	Hutchinson, 1937
<i>Branchinecta orientalis</i>	Anostraca	4830 m	Himalayas	Manca and Mura, 1997
<i>Gammarus pulex</i>	Amphipoda	4755 m	Killik Pass, Central Asia	Tattersal, 1914
<i>Protracheoniscus (P.) nivalis</i>	Isopoda	4725 m	Ladak, India	Verhoeff, 1936
<i>Eurycerus</i> sp.	Cladocera	4700 m	Nepal	Dumont and van de Velde, 1977
<i>Simocephalus vetulus elisabethae</i>	Cladocera	4600 m	Nepal	Dumont and van de Velde, 1977
Unidentified ostracodes	Ostracoda	4336 m	Cushol, India	YPM 47839
<i>Ilyocryptus nevadensis</i>	Cladocera	4120 m	Volcano Nevado de Toluca, Mexico	Cervantes Martínez et al., 2000
<i>Branchinecta shantzi</i>	Anostraca	3810 m	Colorado	YPM 8192
<i>Branchinecta coloradensis</i>	Anostraca	3800 m	Colorado	Packard, 1874
<i>Scleropactes pululahua</i>	Isopoda	3500 m	Ecuador	Schmidt, 2007
<i>Sphaeroniscus pilosus</i>	Isopoda	3500 m	Columbia	Schmidt, 2007
<i>Colomboscia</i> sp.	Isopoda	3400-3650 m	Columbia	Schmidt, 2007
<i>Porcellionides pruinosus</i>	Isopoda	3380-3450 m	Nepal	Schmalfuss, 1983

11,550 years (Holocene; Gonzalez-Ferran, 1995). This does not imply a maximum age for the species, as *B. brushi* could occur elsewhere in the Andes and have been transported to Cerro Paniri after it had ceased being volcanically active. Mountain isolation would seem to provide a perfect predator-free habitat for *B. brushi* to adapt to local conditions with infrequent outside contributions to the gene pool. This is in contrast to typical branchiopod populations, where the passive mode of distribution and the reliance on ephemeral bodies of water are thought to prevent much local adaptation (Graham and Wirth, 2008; Williams and Busby, 1991).

This occurrence of *B. brushi* is not only the highest known occurrence of branchiopods, but of crustaceans in general. Other high altitude records for anostracans and other crustaceans are shown in table 1. Bond (1934), describing specimens from the Yale North India Expedition, documented *B. orientalis* Sars, 1901 from several localities in northern India, the highest of which being 5217 m. One of Bond's *B. orientalis* samples (Cushol, 4336 m) contains some unidentified ostracodes, possibly representing the highest known occurrence of ostracodes. Manca and Mura (1997), also working in the Himalayas, documented *B. orientalis* at 4830 m. Packard (1874) cited specimens of *B. coloradensis* from 3800 m, and specimens labeled as *B. shantzi* in the Yale Peabody Museum Invertebrate Zoology collections were collected at altitudes of 3810 m. The record mentioned by Linder (1941) of *B. paludosa* Müller, 1788, occurring at 97,000 ft is almost certainly a topographical error for 9700 ft (2956 m).

Cladocerans also occur at high altitudes. The highest record is also from Cerro Paniri: *Boeckella palustris* Harding, 1955 (5930 m). *Daphniopsis chilensis* Hann, 1986 is another high-altitude Andean species from

Licancabur Volcano (5883 m), Chile. Like *B. brushi*, it is apparently endemic to this high Andean lake in a volcanic crater (as is *Ilyocryptus nevadensis* Cervantes Martínez, Gutiérrez-Aguirre and Elías-Gutiérrez, 2000, from Volcano Nevado de Toluca (4120 m), Mexico). Other high-altitude occurrences of cladocerans are known from the Himalayas (Brehm and Woltereck, 1939; Dumont and van de Velde, 1977; Manca et al., 1994) and from the Andes (Kotov and Štifter, 2005).

Several other arthropod taxa are also recorded at relatively high altitudes. The highest of these is the amphipod *Gammarus pulex* Linné, 1758 described by Uéno (1934) from material collected on the Yale North India Expedition in Tibet at 5334 m. This is higher than another occurrence of *G. pulex* cited by Tattersal (1914) of 15,600 ft (4755 m). Isopods could be expected to occur at lower altitudes. The highest known occurrence of isopods is *Protracheoniscus (Protracheoniscus) nivalis* Verhoeff, 1936 from an elevation of 4725 m in north India. Schmidt (2007) documented several high altitude isopods from South America: *Colomboscia* sp. at between 3400-3650 m (Colombia) and both *Scleropactes pululahua* Schmidt, 2007 and *Sphaeroniscus pilosus* Vandel, 1972 at 3500 m (from Ecuador and Colombia respectively). Schmalfuss (1983) found *Porcellionides pruinosus* (Brandt, 1833) at between 3380-3450 m in Nepal. Maxillopodan crustaceans are seemingly less well known at higher altitudes. The ostracodes mentioned above at 4336 m in north India seem to be the highest representative of their kind. Copepods have been documented in several Himalayan lakes at high altitudes, the highest of which being 5297 m (Hutchinson, 1937).

Crustaceans are not well suited to high altitudes. Their life cycles require liquid water and they cannot traverse

long distances on their own. However, a dormant cyst can much more easily travel distances that cannot be traveled by an adult. The isolated mountain top pools, like the one home to the only known population of *B. brushii*, should provide a natural laboratory to study not only dispersal, but also gene flow and morphological differentiation in response to a harsh mountain climate.

ACKNOWLEDGEMENTS

The late Denton Belk first suggested to one of us (EALW) the specimens represented a new species and went so far as to segregate the holotype. Subsequent in-put was provided by D. C. Rogers. G. D. F. Wilson helped with isopod references, as did A. A. Kotov with cladoceran references. Helpful comments were provided D. E. G. Briggs and two anonymous reviewers as well as the associate editor, D. C. Rogers. Errors remain our own.

REFERENCES

- Baum, D. A., S. D. Smith, and S. S. S. Donovan. 2005. The tree-thinking challenge. *Science* 310: 979-980.
- Behre, C. H. 1931. *Branchinecta* at Leadville, Colorado. *Science* 73(1887): 235-236.
- Belk, D. 1975. Key to the Anostraca (fairy shrimps) of North America. *Southwestern Naturalist* 20(1): 91-103.
- . 1979. *Branchinecta potassa* new species (Crustacea: Anostraca), a new fairy shrimp from Nebraska, U.S.A. *Southwestern Naturalist* 24(1): 93-96.
- . 1991. Anostracan mating behavior: a case of scramble-competition polygyny, pp. 111-125. In: R. T. Bauer and J. W. Martin (eds.), *Crustacean Sexual Biology*. Columbia University Press, New York. 351 pp.
- , and M. Fugate. 2000. Two new *Branchinecta* (Crustacea: Anostraca) from the southwestern United States. *The Southwestern Naturalist* 45: 111-117.
- , and D. C. Rogers. 2002. A confusing trio of *Branchinecta* (Crustacea: Anostraca) from the western North America with a description of a new species. *Hydrobiologia* 486: 49-55.
- , and F. R. Schram. 2001. A new species of anostracan from the Miocene of California. *Journal of Crustacean Biology* 21: 49-55.
- Birabén, M. 1946. Sobre tres nuevas especies de *Branchinecta* de la Patagonia (Phyllopora). *Notas del Museo de la Plata Zoología* 11(94): 128-139.
- Bond, R. M. 1934. Report on the phyllopod Crustacea (Anostraca, Notostraca, and Conchostraca) including a revision of the Anostraca of the Indian Empire. *Memoirs of the Connecticut Academy of Arts and Sciences* 10(5): 29-62.
- Brandt, J. F. 1833. *Conspectus monographiae crustaceorum oniscodorum latreillii*. *Bulletin de la Société Impériale des Naturalistes de Moscou* 6: 171-193.
- Brehm, V., and R. Woltereck. 1939. Die Daphniden der Yale-Northindia-Expedition. *Internationale Revue der gesamten Hydrobiologie* 39: 1-19.
- Brendonck, L. 1989. Redescription of the fairy shrimp *Streptocephalus proboscideus* (Frauenfeld, 1873) (Crustacea, Anostraca). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie* 59: 49-58.
- . 1994. Molar surface morphology in *Streptocephalus coomansi* (Crustacea: Branchiopoda: Anostraca). *Journal of Morphology* 219: 165-172.
- , and B. Riddoch. 1999. Wind-borne short-range egg dispersal in anostracans (Crustacea : Branchiopoda). *Biological Journal of the Linnean Society* 67: 87-95.
- Brtek, J., and G. Mura. 2000. Revised key to families and genera of the Anostraca with notes on their geographical distribution. *Crustaceana* 73: 1037-1088.
- Cervantes-Martínez, A., M. Gutiérrez-Aguirre, and M. Elías-Gutiérrez. 2000. Description of *Ilyocryptus nevadensis* (Branchiopoda, Anomopoda), a new species from a high altitude crater lake in the volcano Nevado de Toluca, Mexico. *Crustaceana* 73: 311-321.
- César, I. I. 1987. *Branchinecta santacrucensis* sp. nov. (Crustacea: Anostraca) de la Patagonia. *Neotropica* 33(90): 75-82.
- . 1987. *Branchinecta leonensis* sp. nov. (Crustacea: Anostraca) de la provincia de Santa Cruz, Republica Argentina. *Notas del Museo de la Plata Zoología* 21(206): 77-86.
- . 1988. Primer registro de *Branchinecta iheringi* Lilljeborg 1889 (Crustacea: Anostraca) para la Argentina. *Revista de la Asociación de Ciencias Naturales del Litoral* 19: 101-111.
- Cohen, R. G. 1981. Notas sobre anostracos neotropicales (Crustacea). I. *Branchinecta valchetana* sp. nov. y redescrpcion de *Branchinecta palustris* Birabén, 1946. *Physis. Sección B: Los Aguas Continentales y sus Organismos* 40(98): 1-13.
- . 1983. Notas sobre anostracos neotropicales (Crustacea). III. *Branchinecta somuncurensis* y *Branchinecta prima* spp. nov. *Physis. Sección B: Los Aguas Continentales y sus Organismos* 41(101): 69-80.
- . 2008. A new species of *Branchinecta* (Crustacea: Branchiopoda: Anostraca) from the Argentinian Tierra del Fuego. *Zootaxa* 1884: 60-68.
- Creaser, E. P. 1931. North American phyllopods. *Science* 74: 267-268.
- Daday de Deés, E. 1910. *Monographie systématique des Phyllopodes Anostracés*. *Annales des Sciences Naturelles Zoologie, Neuvième Série* 11: 91-489.
- DeWaard, J. R., V. Sacherova, M. E. A. Crestescu, E. A. Remigio, T. J. Crease, and P. D. N. Hebert. 2006. Probing the relationships of the branchiopod crustaceans. *Molecular Phylogenetics and Evolution* 39: 491-502.
- Dexter, R. W. 1956. A new fairy shrimp from western United States, with notes on other North American species. *Journal of the Washington Academy of Sciences* 46: 159-165.
- Dodds, G. S. 1917. Altitudinal distribution of Entomostraca of Colorado. *Proceedings of the United States National Museum* 54: 59-87.
- Dodson, S. I., and D. G. Frey. 1991. Cladocera and other Branchiopoda, pp. 723-786. In: J. H. Thorp and A. P. Covich (eds.), *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press Inc, San Diego.
- Dumont, H. J., and I. Van de Velde. 1977. Report on a collection of Cladocera and Copepoda from Nepal. *Hydrobiologia* 53: 55-65.
- , and S. V. Negrea. 2002. Branchiopoda. Guides to the Identification of the Microinvertebrates of the Continental Waters of the World. Backhuys Publishers, Leiden.
- Elías-Gutiérrez, M. 1995. Notas sobre los cladóceros de embalses a gran altitud en el Estado de México, México. *Anales de la Escuela Nacional de Ciencias Biológicas* 40: 197-214.
- Eng, L. L., D. Belk, and C. H. Eriksen. 1990. Californian Anostraca: distribution, habitat, and status. *Journal of Crustacean Biology* 10: 247-277.
- Eriksen, C. H., and D. Belk. 1999. Fairy Shrimps of California's Puddles, Pools, and Playas. Mad River Press, Eureka, California.
- Fryer, G. 1983. Functional ontogenetic changes in *Branchinecta ferox* (Milne-Edwards) (Crustacea: Anostraca). *Philosophical Transactions of the Royal Society of London B Biological Sciences* 303: 229-343.
- Fugate, M. L. 1992. Speciation in the fairy shrimp genus *Branchinecta* (Crustacea: Anostraca) from North America. Ph. D. dissertation, University of California, Riverside.
- . 1993. *Branchinecta sandiegonensis*, a new species of fairy shrimp (Crustacea: Anostraca) from western North America. *Proceedings of the Biological Society of Washington* 106: 296-304.
- Gonzalez-Ferrán, O. 1995. Volcanes de Chile. Instituto Geografico Militar, Santiago. 635 pp.
- Gordon, K. 1932. *Branchinecta coloradensis* in Colorado. *Science* 75: 287-288.
- Graham, T. B., and D. Wirth. 2008. Dispersal of large branchiopod cysts: potential movement by wind from potholes on the Colorado Plateau. *Hydrobiologia* 600: 17-27.
- Hann, B. J. 1986. Revision of the genus *Daphniopsis* Sars, 1903 (Cladocera: Daphniidae) and a description of *Daphniopsis chilensis*, new species, from South America. *Journal of Crustacean Biology* 6: 246-263.
- Hanner, R. H. 1997. Taxonomic problems with phylogenetic solutions derived from the integration of biochemical, morphological and molecular data. Ph. D. dissertation, University of Oregon.
- Harding, J. P. 1940. VIII. Crustacea: Anostraca and Conchostraca. *Transactions of the Linnean Society of London* (3)1: 149-153.
- . 1955. Percy Sladen Trust expedition. XIX. Crustacea: Cladocera. *Transactions of the Linnean Society of London* (3)1: 329-354.

- Hawes, T. C., M. R. Worland, and J. S. Bale. 2008. Physiological constraints on the life cycle and distribution of the Antarctic fairy shrimp *Branchinecta gaini*. *Polar Biology* 31: 1531-1538.
- Hulsmans, A., K. Moreau, L. De Meester, B. J. Riddoch, and L. Brendonck. 2007. Direct and indirect measures of dispersal in the fairy shrimp *Branchiopodopsis wolfi* indicate a small-scale isolation-by-distance pattern. *Limnology and Oceanography* 52: 676-684.
- Humphries, C. J. and L. R. Parenti. 1999. *Cladistic Biogeography*. Oxford University Press, Oxford.
- Hurlbert, S. H., W. Loayza, and T. Moreno. 1986. Fish-flamingo-plankton interactions in the Peruvian Andes. *Limnology and Oceanography* 31: 457-468.
- Hutchinson, G. E. 1930. Restudy of some Burgess Shale Fossils. *Proceedings of the United States National Museum* 78(11): 1-24.
- . 1937. Limnological studies in Indian Tibet. *Internationale Revue der Gesamten Hydrobiologie* 35: 134-177.
- James, A., and J. Hubbick. 1969. Studies on some high-altitude lakes in the Hindu Kush. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 17: 362-372.
- Kotov, A. A., and P. Stifter. 2005. Notes on the genus *Ilyocryptus* Sars, 1862 (Cladocera: Anomopoda: Ilyocryptidae). 6. South American *I. denticulatus denticulatus* Delachaux, 1919 and *I. denticulatus freyi* subsp.n. *Arthropoda Selecta* 14: 207-218.
- Latreille, P. A. 1817. *Les Crustacés, les Arachnides, les Insectes*. Base à l'Histoire Naturelle des Animaux et d'Introduction à l'Anatomie Comparée, v. 3. Deterville, Paris.
- Lauterbach, K.-E. 1973. Schlüsselereignisse in der Evolution der Stammgruppe der Euarthropoda. *Zoologische Beiträge (N.F.)* 19: 251-299.
- Lilljeborg, W. 1889. Diagnosen zweier phyllopoden-arten aus Süd-Brasilien. *Abhandlungen Herausgegeben von Naturwissenschaftlichen vereine zu Bremen* 10: 424.
- Linder, F. 1941. Contribution to the morphology and the taxonomy of the Branchiopoda Anostraca. *Zoologiska Bidrag Från Uppsala* 20: 101-303.
- Linné, C. 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. Holmiae. 824 pp.
- Löffler, H. 1964. The limnology of tropical high-mountain lakes. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 15: 176-193.
- . 1969. High altitude lakes in Mt. Everest region. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 17: 373-385.
- Lynch, J. E. 1937. A giant new species of fairy shrimp of the genus *Branchinecta* from the state of Washington. *Proceedings of the United States National Museum* 84(3025): 555-562.
- . 1958. *Branchinecta cornigera*, a new species of anostracan phyllopod from the state of Washington. *Proceedings of the United States National Museum* 108(3392): 25-37.
- . 1960. The fairy shrimp *Branchinecta campestris* from northwestern United States (Crustacea: Phyllopoda). *Proceedings of the United States National Museum* 112(3447): 549-561.
- . 1964. Packard's and Pearse's species of *Branchinecta*: analysis of a nomenclatural involvement. *American Midland Naturalist* 71: 466-488.
- . 1972. *Branchinecta dissimilis* n. sp., a new species of fairy shrimp, with a discussion of specific characters in the genus. *Transactions of the American Microscopical Society* 91: 240-243.
- Maeda-Martínez, A. M., H. Obregón-Barboza, and H. J. Dumont. 1993. *Branchinecta mexicana*, new species (Branchiopoda: Anostraca), a fairy shrimp from central Mexico. *Journal of Crustacean Biology* 13: 585-593.
- Manca, M., and G. Mura. 1997. On *Branchinecta orientalis* Sars (Anostraca) in the Himalayas. *Hydrobiologia* 356: 111-116.
- , P. Cammarano, and T. Spagnuolo. 1994. Notes on Cladocera and Copepoda from high altitude lakes in the Mount Everest Region (Nepal). *Hydrobiologia* 287: 225-231.
- Mathias, P. 1937. Biologie des crustacés phyllopoies. *Actualités Scientifiques et Industrielles* 447: 1-106.
- Milne Edwards, H. 1840. *Histoire naturelle des Crustacés, Comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux*. Librairie Encyclopédique de Roret, Paris.
- Muller, O. F. 1788. *Zoologia Danica Sev Animalium Daniae et Norvegiae Rariorum ac Minus Notorum Descriptiones et Historia*. Vol. 2. N. Mölleri et Fillii. Havniae.
- Mura, G. 1996. Pattern of mandibular morphology in Anostraca with some taxonomic remarks. *Crustaceana* 69: 129-154.
- Nation, J. L. 1983. A new method using hexamethyldisilazane for preparation of soft insect tissues for scanning electron microscopy. *Stain Technology* 58: 347-351.
- O'Hara, R. J. 1997. Population thinking and tree thinking in systematics. *Zoologica Scripta* 26(4): 323-329.
- Obregón-Barboza, H., A. M. Maeda-Martínez, H. García-Velazco, and H. J. Dumont. 2002. *Branchinecta oterosanvicentei* n. sp. (Branchiopoda: Anostraca), a new fairy shrimp from the Chihuahuan Desert, with a proposal for the conservation of the Branchinectidae of Mexico. *Hydrobiologia* 467: 45-56.
- Packard, Jr., A. S. 1874. Synopsis of the fresh-water phyllopod crustacea of North America. *Annual Report of The United States Geological and Geographical Survey of the Territories* 1874: 614-622.
- . 1883. A monograph of the phyllopod Crustacea of North America, with remarks on the Order Phyllocarida. Twelfth Annual Report of the United States Geological and Geographical Survey of the Territory for 1878 1(2): 295-592.
- Pearse, A. S. 1912. Notes on phyllopod crustacea. *Report of the Michigan Academy of Science* 14: 191-197.
- Peck, L. S. 2004. Physiological flexibility: the key to success and survival for Antarctic fairy shrimps in highly fluctuating extreme environments. *Freshwater Biology* 49: 1195-1205.
- Petkovski, S. 1991. On the presence of the genus *Branchinecta* Verrill, 1869 (Crustacea, Anostraca) in Yugoslavia. *Hydrobiologia* 226: 17-27.
- Pociecha, A. 2007. Effect of temperature on the respiration of an Antarctic freshwater anostracan, *Branchinecta gaini* Daday 1910, in field experiments. *Polar Biology* 30: 731-734.
- Procter, V. W. 1964. Viability of crustacean eggs recovered from ducks. *Ecology* 45: 656-658.
- Raina, H. S., and K. K. Vass. 1993. Distribution and species composition of zooplankton in Himalayan ecosystems. *Internationale Revue der Gesamten Hydrobiologie* 78: 295-307.
- Reed, E. B., and J. R. Olive. 1958. Altitudinal distribution of some Entomostraca in Colorado. *Ecology* 39: 66-74.
- Remigio, E. A., and P. D. N. Hebert. 2000. Affinities among anostracan (Crustacea: Branchiopoda) families inferred from phylogenetic analyses of multiple gene sequences. *Molecular Phylogenetics and Evolution* 17: 117-128.
- Richter, S., J. Olesen, and W. C. Wheeler. 2007. Phylogeny of Branchiopoda (Crustacea) based on a combined analysis of morphological data and six molecular loci. *Cladistics* 23: 301-336.
- Rogers, D. C. 2002. The amphialax morphology of selected Anostraca. *Hydrobiologia* 486: 1-18.
- . 2002a. A morphological re-evaluation of the anostracan families Linderiellidae and Polyartemiidae, with a redescription of the linderiellid *Dexteria floridana* (Dexter 1956) (Crustacea: Branchiopoda). *Hydrobiologia* 486: 57-61.
- . 2002b. Female-based characters for anostracan (Crustacean: Branchiopoda) identification: A key for species of California and Oregon, USA. *Hydrobiologia* 486: 125-132.
- . 2003. Revision of the thamocephalid genus *Phallocryptus* (Crustacea; Branchiopoda; Anostraca). *Zootaxa* 257: 1-14.
- . 2003a. The development of the male second antenna in *Polyartemiella hazeni* (Murdoch, 1884) with a morphological definition of the Chirocephalidae (Crustacea: Anostraca). *Zootaxa* 251: 1-12.
- . 2006. Three new species of *Branchinecta* (Crustacea: Branchiopoda: Anostraca) from the Nearctic. *Zootaxa* 1126: 35-51.
- , P. De los Ríos, and O. Zúñiga. 2008. Fairy shrimp (Branchiopoda: Anostraca) of Chile [Camarón Duende (Branchiopoda: Anostraca) en Chile]. *Journal of Crustacean Biology* 28(3): 543-550.
- , D. L. Quinney, J. Weaver, and J. Olesen. 2006. A new giant species of predatory fairy shrimp from Idaho, USA (Branchiopoda: Anostraca). *Journal of Crustacean Biology* 26: 1-12.
- Sars, G. O. 1867. *Histoire naturelle des Crustacés d'eau douce de Norvège 1: Les Malacostracés*. Johnsen, Christiania.
- . 1896. Beskrivelse af de hidtil kjendte norske Arter af Underordenene Phyllocarida og Phyllopoda [Descriptions of the Norwegian species at present known belonging to the suborders Phyllocarida and Phyllopoda]. *Fauna Norvegiae* 1: 1-140.
- . 1897. *The Phyllopoda of the Jana-Expedition*. *Annuaire du Musée Zoologique de L'Académie Impériale des Sciences de Saint-Petersbourg* 2: 463-493.

- . 1901. On the crustacean fauna of central Asia. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de Saint-Petersbourg* 6: 130-164.
- Schmalzfuss, H. 1983. Terrestrial isopods from Nepal (Crustacea: Isopoda: Oniscoidea). *Senckenbergiana Biologica* 63(5/6): 373-392.
- Schmidt, C. 2007. Revision of the neotropical Scleropactidae (Crustacea: Oniscoidea). *Zoological Journal of the Linnean Society* 151(Suppl. 1): 1-339.
- Shantz, H. L. 1905. Notes on the North American species of *Branchinecta* and their habitats. *Biological Bulletin of the Marine Biological Laboratory* 9: 259-263.
- Stenderup, J. T., J. Olesen, and H. Glenner. 2006. Molecular phylogeny of the Branchiopoda (Crustacea) – Multiple approaches suggest a 'diplostracan' ancestry of the Notostraca. *Molecular Phylogenetics and Evolution* 41: 182-194.
- Sun, X., Q. Yang, and Y. Shen. 2006. Jurassic radiation of large Branchiopoda (Arthropoda: Crustacea) using secondary structure-based phylogeny and relaxed molecular clocks. *Progress in Natural Science* 16: 292-302.
- Tattersall, W. M. 1914. Notes on some amphipods collected on the Pamirs at an altitude of 15,600 feet. *Records of the Indian Museum* 10: 213-215.
- Thiéry, A. 1996. Branchiopodes I. Ordres des Anostracés, Notostracés, Spinicaudata et Laevicaudata, pp. 287-351. In, P.-P. Grassé (ed.), *Traité de Zoologie, Tome VII, Crustacés, Fascicule 2*. Masson, Paris.
- , and M. Fugate. 1994. A new American fairy shrimp, *Linderiella santarosae* (Crustacea: Anostraca: Linderiellidae), from vernal pools of California, USA. *Proceedings of the Biological Society of Washington* 107: 641-656.
- Tyson, G. E., and M. L. Sullivan. 1980. Scanning electron microscopy of cuticular sensilla of *Artemia*: setae of the adult trunk segments, pp. 99-106. In, G. Persoone, P. Sorgeloos, O. Roels, and E. Jaspers. (eds.), *The Brine Shrimp Artemia*, vol. 1. Universa Press, Wetteren, Belgium.
- Uéno, M. 1934. Report on amphipod Crustacea of the genus *Gammarus*. *Memoirs of the Connecticut Academy of Arts and Sciences* 10: 63-75.
- Valdivia Villar, R. S. 1988. Lista de Cladóceros dulceacuícolas del Perú. *Amazoniana* 10: 283-297.
- Vandel, A. 1972. Les isopodes terrestres de la Colombie. *Studies on the Neotropical Fauna* 7: 147-172.
- Verhoeff, K. W. 1936. Ueber einen land-isopoden aus ladak. *Memoirs of the Connecticut Academy of Arts and Sciences* 10: 187-190.
- Verrill, A. E. 1869. Contribution to Zoölogy from the Museum of Yale College. No. III.—Descriptions of some new American phyllopod Crustacea. *American Journal of Science and Arts* 48: 244-254.
- Weekers, P. H. H., G. Murugan, J. R. Vanfleteren, D. Belk, and H. J. Dumont. 2002. Phylogenetic analysis of anostracans (Branchiopoda: Anostraca) inferred from nuclear 18S ribosomal DNA (18S rDNA) sequences. *Molecular Phylogenetics and Evolution* 25: 535-544.
- Williams, W. D., and J. R. Busby. 1991. The geographical distribution of *Triops australiensis* (Crustacea: Notostraca) in Australia: a biogeoclimatic analysis. *Hydrobiologia* 212: 235-240.
- Yang, Q., X. Sun, P. Wu, and K.-Y. Zhang. 2003. Arthropod phylogenetic chronology. *Journal of Genetics and Molecular Biology* 14(3): 145-158.

RECEIVED: 11 February 2009.

ACCEPTED: 8 October 2009.