

A NEW GIANT SPECIES OF PREDATORY FAIRY SHRIMP FROM IDAHO, USA (BRANCHIOPODA: ANOSTRACA)

Authors: Rogers, D. Christopher, Quinney, Dana L., Weaver, James, and Olesen, Jørgen

Source: Journal of Crustacean Biology, 26(1) : 1-12

Published By: The Crustacean Society

URL: <https://doi.org/10.1651/C-2509.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

A NEW GIANT SPECIES OF PREDATORY FAIRY SHRIMP FROM IDAHO, USA
(BRANCHIOPODA: ANOSTRACA).

D. Christopher Rogers, Dana L. Quinney, James Weaver, and Jørgen Olesen

(DCR, correspondent) EcoAnalysts, Inc. 166 Buckeye Street, Woodland, California 95695, USA;

(DLQ, JW) State of Idaho Military Division, Gowen Field, Building 518, 4715 South Byrd Street, Boise Idaho 83705-8095, USA;

State of Idaho Military Division, Gowen Field, Building 518, 4715 South Byrd Street, Boise Idaho 83705-8095, USA;

(JO) Natural History Museum of Denmark, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark

A B S T R A C T

A previously unknown species of giant fairy shrimp is described. *Branchinecta raptor* n. sp. is highly adapted to a predatory mode of life. In both sexes, the first four pairs of thoracopods bear elongated, curved, heavily chitinized endopods, which are modified for grasping prey. Both sexes have elongated, “whip-like” cercopods nearly as long as the abdomen that are used for detecting prey. This new species appears most closely related to *B. gigas* Lynch 1937. Both species are large in size, have small eyes and sensory papillae, and share similar habitats and food preferences. However, *B. raptor* has some unusual predatory behaviors that differ from *B. gigas*. *B. raptor* is separated from all other *Branchinecta* by the unique form of the second antennae, the form of the cercopods, and the male genitalia. Large branchiopod records from Idaho are also discussed.

INTRODUCTION

In 1937, Lynch described *Branchinecta gigas*, an unusually large predatory anostracan from argillotrophic lakes in western North America, which feeds on copepods, cladocerans, anostracans, and occasionally filamentous green algae (Lynch, 1937; Fryer, 1966; White, 1967; White et al., 1969; Daborn, 1974, 1975; Broch, 1988; Belk and Ballantyne, 1988). During surveys in southern Idaho, a new species of giant predatory *Branchinecta* was discovered and is described below. This is the third species of *Branchinecta* reported as being predatory and atypically large in size.

MATERIALS AND METHODS

Animals were collected with a dip net and kept in aquaria filled with clear aged rainwater to observe their behavior. Dark grey clay from a perennial pond (in contrast to the pale tan clay of their natural environment) was added as substrate. A variety of potential prey from their habitat was provided. Behavior was also observed in culture dishes under a stereo dissection microscope.

Adults were fixed in ethyl alcohol, examined under a stereo dissection microscope and sketched by hand. The new species was compared with the original description of *Branchinecta gigas*, with material of *B. gigas* from a variety of locations and *B. ferox* (Milne Edwards, 1840).

The material for scanning electron microscopy (SEM) was dehydrated in graded series of ethanol and acetone and critical point dried following standard procedures. The SEM used was a JEOL JSM-840 situated at the Zoological Museum, University of Copenhagen.

Branchinecta gigas.—CANADA: ALBERTA: Chain Lakes, 29 May 1965, 2 males, G. White, Det. D. C. Rogers, DCR-223. USA: CALIFORNIA: Modoc County: Middle Alkali Lake, at HWY 299 causeway, March 1993, 3 males, S. Cepello, D. C. Rogers, DCR-15. Siskiyou County: Pool east of intersection of Highway 97 and Highway 161, on north side of Indian Tom Lake, 1 male, 17 March 1998, D. C. Rogers, C. LaRay, DCR-126. Pool east of intersection of Highway 97 and Highway 161, on north side of Indian Tom Lake, 27 March 1998, 8 males, 6 females, D. C. Rogers, R. E. Hill, DCR-127. Pool east of intersection of Highway 97 and Highway 161, on north side of Indian Tom Lake, 18 March 2003, 4 males, D. C. Rogers, C. LaRay.

Branchinecta ferox.—ISRAEL: El-Hadar, 1 female, 1 male, gift from D. Belk (DB-321), DCR-72.

RESULTS

Branchinecta raptor n. sp.

Material Examined.—USA: IDAHO: Ada County: Tadpole Lake, 15 km south of Boise, 5 ♀♀, 1 ♂, 11 April 1995, J. Weaver, D. Quinney, Det. D. C. Rogers. Tadpole Lake, 15 km south of Boise, 18 ♀♀, 10 ♂♂, 18 March 2004, J. Weaver, D. Quinney, Det. D. C. Rogers. Elmore County: Armadillo Lake, 16 km south of Boise, 6 ♀♀, 5 ♂♂, 18 March 2004, J. Weaver, D. Quinney, Det. D. C. Rogers. Armadillo Lake, 16 km south of Boise, 24 ♀♀, 24 ♂♂, 31 March 2004, J. Weaver, D. Quinney, Det. D. C. Rogers.

Description. Male.—Length, 66 mm measured from anterior margin of head to cercopod apices; length to 47 mm not including cercopods (Fig. 1). Head with dorsal anterior-lateral margins projecting beyond bases of compound eye peduncle (Fig. 2A). Eyes small. First antennae subequal in length to second antennal proximal antennomere; apices produced laterally, bearing sensory setae along medial and distal margins. Second antennae elongate; proximal antennomere sub-cylindrical, bearing a large pronounced basomedial pulvillus and a longitudinal, medial, elongate ridge-like pulvillus, covered with dorsally directed scales; pulvillus two-thirds the length of the antennomere (Fig. 2A). Second antennal proximal antennomere with anteriolateral surfaces covered in dense hemispherical papillae. Second antennal distal antennomere arcuate, flattened anterior-laterally, curving medially, and apically sub-acute; distomedial margin with a short row of transverse ridges (Fig. 2A).

Labrum subquadrate with lateral arcuate flange, and a posteriomedial projection (Fig. 5 E, F); posteriomedial projection apically rounded, swollen medially, and ventrally covered with dense patches of aciculate denticles directed



Fig. 1. *Branchinecta raptor* n. sp. Male is right, female left. Paratypes ZMUC CRU-4855. Scale bar is 1 cm.

anteriorly. Labrum ventral margins covered with dense patches of aciculate denticles directed anteriorly; ventral surface with long aciculate spinules directed anteriorly. Mandibles large and symmetrical, with posterior 50% of

dorsal medial margin lined with stout, chitinized spines directed anteriorly; anterior molar margins lined with stout, anteriorly directed spines; posterior-most spine five to ten times larger than other spines, directed posteriomedially,

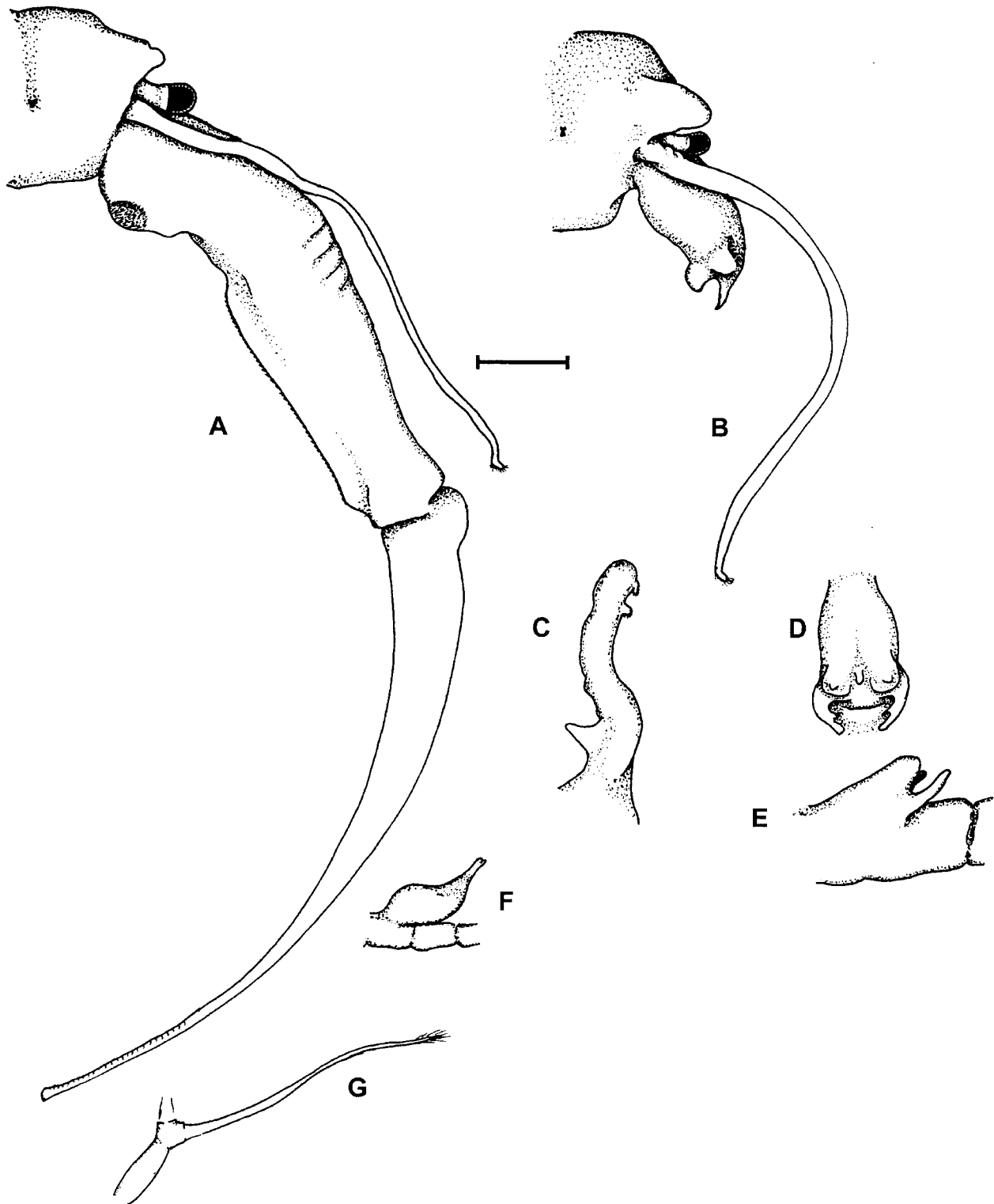


Fig. 2. *Branchinecta raptor* n. sp.: A. Male, left side of head, anterior view. B. Female, left side of head, anterior view. C. Right penis ventral view. D. Male genitalia, ventral view. E. Male genitalia, lateral view, from left side. F. Brood pouch, lateral view, from left side. G. Left cercopod, dorsal view. Scale bar: A and B = 2.5 mm; C = 0.5 mm; D and E = 4 mm; F and G = 6 mm.

densely chitinized, with apex directed anteriorly; molar surface densely denticulate (Fig. 3). Maxilla 1 large, produced ventrally, with a ventral conical palp; medial margin bearing a row of long pectinate spines, each

projecting medially, and bent anteriorly at approximately the proximal third. Maxilla 2 truncated with a short tri-ramal palp, each ramus bearing aciculate spines; medial surface densely clothed with medially directed aciculate spinules.

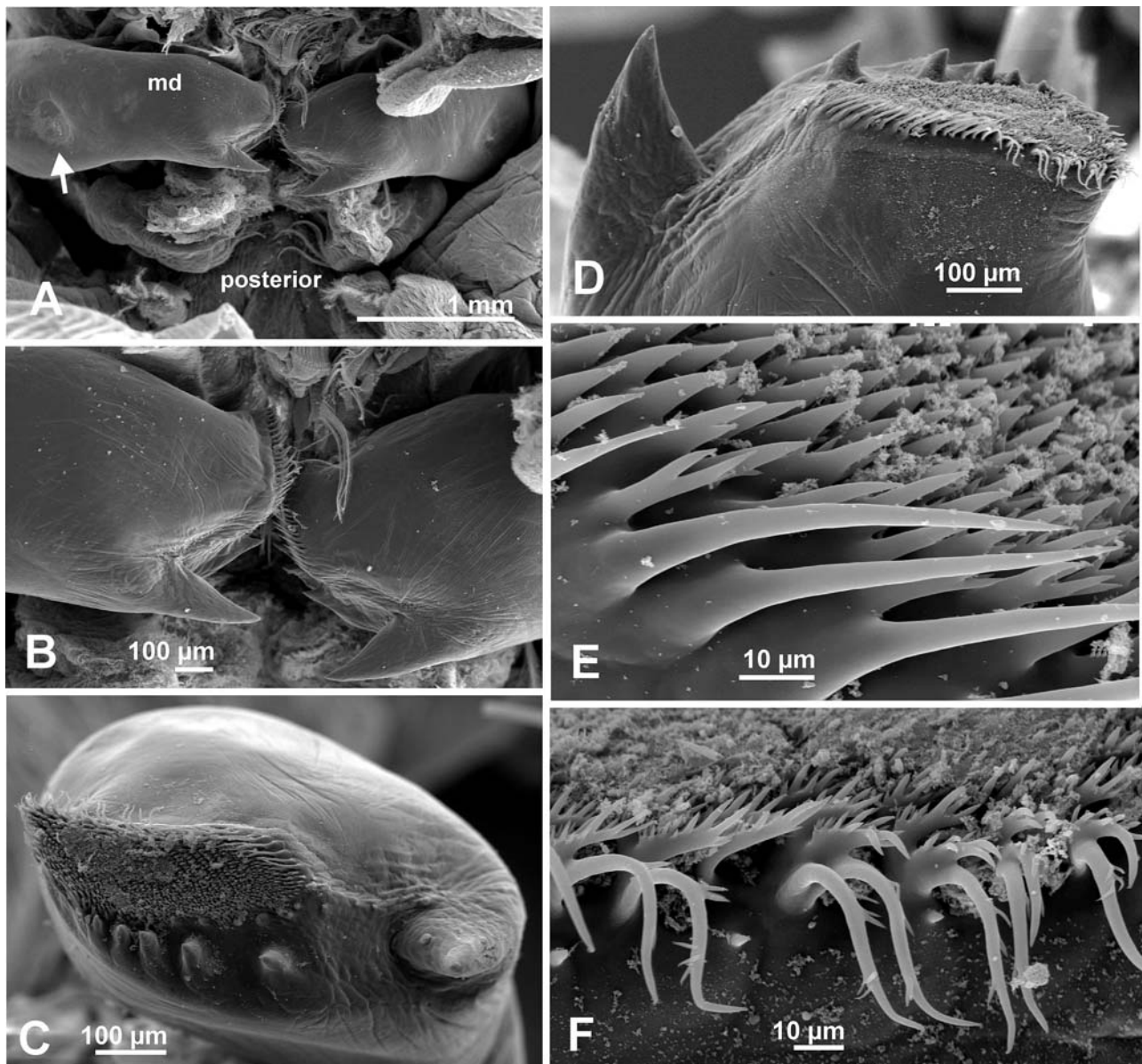


Fig. 3. *Branchinecta raptor* n. sp., mandibles: A. Left and right mandible, ventral view (female). Arrow point at 'scar' after larval mandibular palp. B. Gnathal edge of mandibles (female). C. Gnathal edge of left side mandible, apical view (male). D. Gnathal edge of left side mandible, ventral view (male). E. Marginal spines at ventral margin of gnathal edge (male). F. Branched spines at dorso-anterior margin of gnathal edge (male). (md = mandible).

Thoracopods with endopods elongate, chitinized, with stout, recurved spines along the lateral, apical and medial margins, increasing in size from posterior pairs to anterior pairs (Fig. 1, 4A, 5A). Endopods capable of bending posteriorly.

Thoracopod-one (anterior most) with endites 1, 2 and 3 covered in dense patches of aciculate denticles, with a posterior margin of long thin pectinate setae directed dorsally (Fig. 4A–D). Endites 1 and 2 slightly separated by a deep fold and a stout medial spine (Fig. 4A–D). Endite 3 with a stout, chitinized proximal posterior spine (Fig. 4A–D). Endites 4 and 5 digitiform, ending in a single long, smooth seta (Fig. 4A, B, E and F). Endite 6 lobiform, with distal margin bearing stout, smooth, aciculate spines (Fig. 4G). Endopod with medial edge margined with stout,

chitinized, recurved spines approximately four times as long as basal width, separated by a distance equal to their length; apices bent posteriorly; each spine with posterior surface bearing a ring of spinules. Endopod with apical and lateral setae stout, chitinized, aciculate and pectinate, and with a stout curved tip (Fig. 5A–D). Exopod margined with long soft setae bearing smaller setules.

Successive thoracopods similar, decreasing in size (Fig. 1).

Cercopods elongate, whip-like, nearly as long as abdomen; ventral-lateral margins with elongate sensory setae apically and sub-apically (Fig. 1, 2G). Cercopods and second antennal proximal antennomere medial and anterior surfaces densely covered with short, stout, flat topped micropapillae.

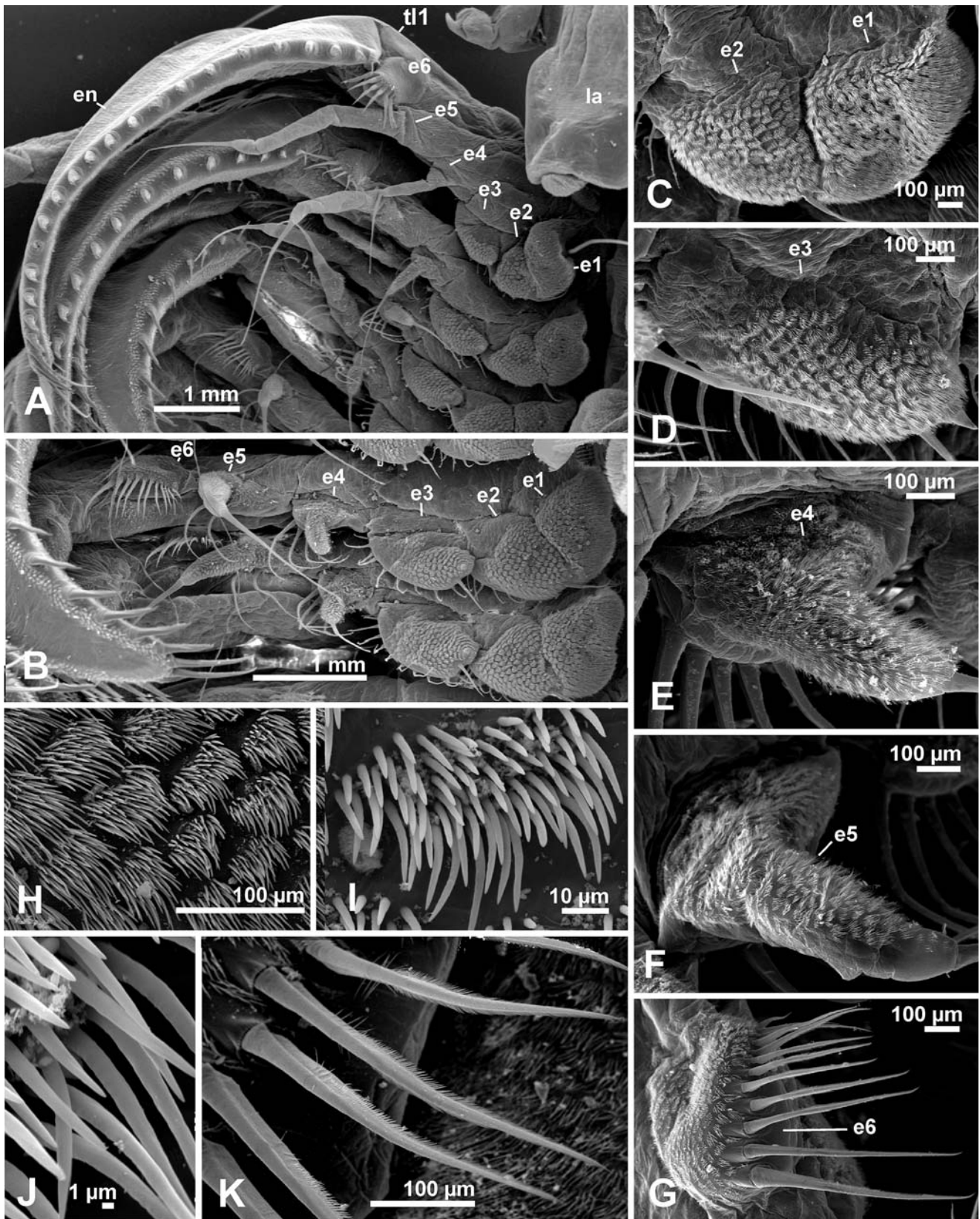


Fig. 4. *Branchinecta raptor* n. sp., trunk limbs. A. Anterior right side trunk limbs, ventral view (female). B. Trunk limb 2 and 3, endites 1-6 (female). C. Endites 1 and 2 of right trunk limb 6 (male). D. Endite 3 of right trunk limb 6 (male). E. Endite 4 of right trunk limb 6 (male). F. Endite 5 of right trunk limb 6 (male). G. Endite 6 of right trunk limb 6 (male). H. Setae groups from endite 2 of left trunk limb 2 (female). I. Close-up of previous. J. Close-up of previous. K. Setae on endite 6 of left trunk limb 2 (female). (en = endopod; e1-e6 = endites 1 to 6; tl1 = trunk limb 1).

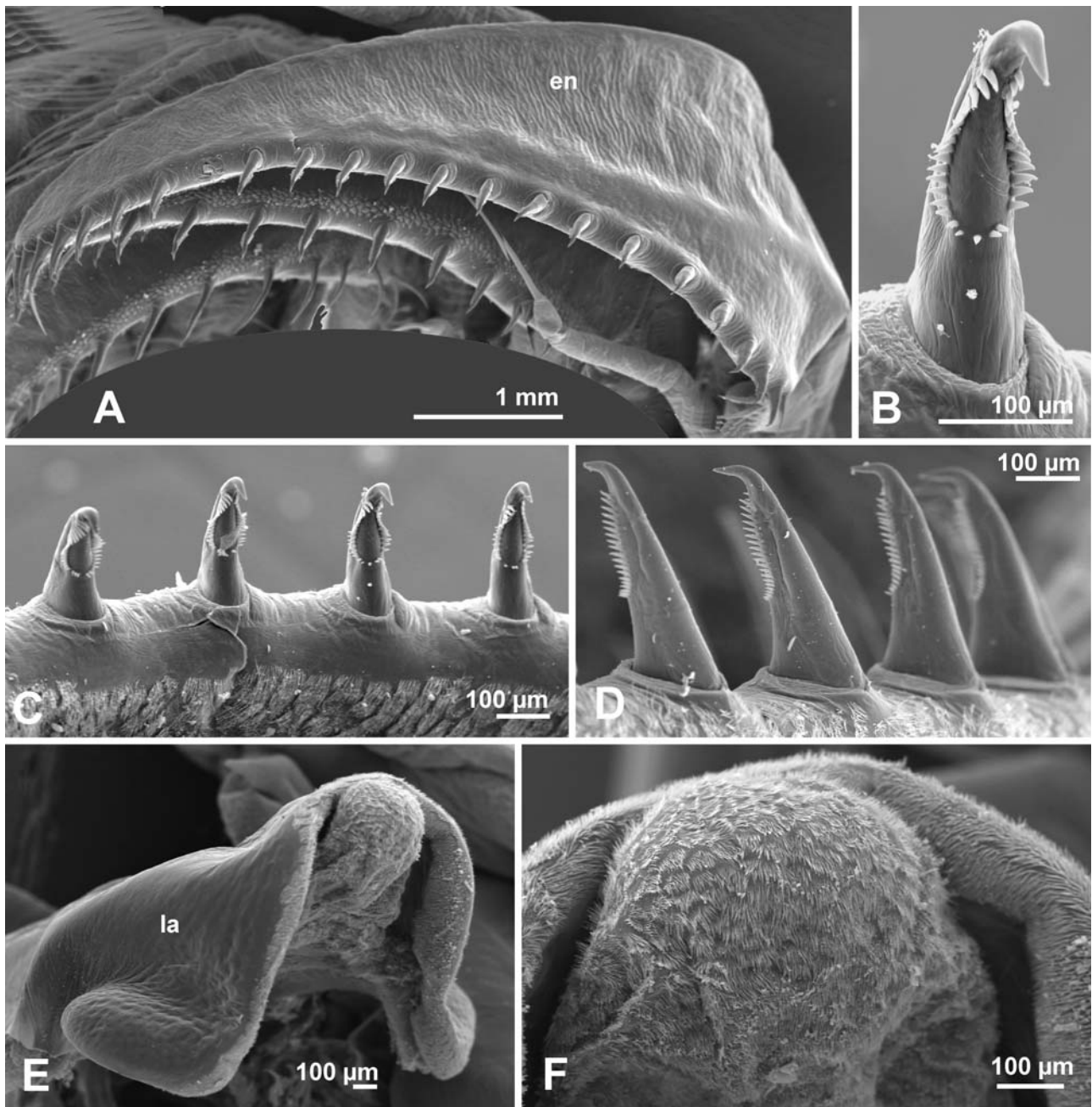


Fig. 5. *Branchinecta raptor* n. sp. A. Endopod of right trunk limbs 1 to 3 (female). B. Marginal spine of endopod (female). C. Four marginal spines of endopod (female). D. Four marginal spines of endopod (female). E. Labrum (female). F. Close-up of labrum (female). (en = endopod; la = labrum).

Thoracic genital segments swollen ventrally, bearing a ventral, sub-conical distolateral process, and a single medioventral truncate process (Fig. 2D and E). Penes short, extending to first abdominal segment. Each pene armed with an apical-lateral pair of “wart-like” mounds, covered in minute recurved denticles (Fig. 2C).

Female.—Length 80 mm from anterior margin of head to apices of cercopods; length 62 mm not including cercopods (Fig. 1). Head with dorsal anterior-lateral margins projecting beyond bases of the compound eye peduncle (Fig. 2B). Eyes small. First antennae elongate, 2–2.5 times length of second

antennae. Second antennae short, stout and apically acute; distal medial and distal anterior surfaces each with a stout, sub-hemispherical protuberance (Fig. 2B). Labrum, mandible, maxillae and maxillules as in male. Thorax with dorsum smooth. Thoracopods, abdomen and cercopods as in male. Brood pouch pyriform, with apex slightly elongated (Fig. 2F).

Cyst.—Densely covered with small spinules, 400 to 500 μm in diameter; virtually identical in size and shape to cysts of *B. gigas* (see Shepard and Hill, 2001).

Color in Life.—Like most species of *Branchinecta*, whitish and semi-translucent. Testes and ovaries pale to light blue,

which may indicate presence of artemocyanin (Peeters et al., 1994). Gut orange-brown, similar to suspended sediment in habitat where collected.

Etymology.—The name ‘raptor’ is derived from the Latin *rapere*, meaning “to seize”, hence “one who seizes”, and reflects the functions of the highly modified thoracopods (especially the first pairs). ‘Raptor’ is used in English speaking countries to refer to birds of prey. This is apt in this case as well, as all currently known localities for this species occur within the Snake River Birds of Prey National Conservation Area.

Type Locality.—Tadpole Lake, 15 km south of Boise, Ada County Idaho, USA. This is a playa located within the Idaho Army National Guard Orchard Training Area south of Boise, Idaho, typical in size and topography of the ephemeral lakes of the western Snake River Plain. The playa lies at 960 m elevation, is approximately 4.6 ha (11.3 acres) in area, and 10 to 30 cm in depth. Spring rainfall is variable: combined April through June rainfall ranges from 2.5 to 10 cm (unpublished rain gauge data, 1991–2002, Idaho Army National Guard). The water is turbid, and the animals were observed at temperatures ranging between 4 and 25° C. The surrounding vegetation is dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis* Beetle and Young), winterfat (*Ceratoides lanata* [Pursh] J. T. Howell), Sandberg bluegrass (*Poa secunda* J. S. Presl.), and the non-native invasive bur-buttercup (*Ranunculus testiculatus* Crantz).

Types.—Deposited: holotype, male (USNM 1022876) and two male and four female paratypes (USNM 1022877) (collected 18 March 2004), in the National Museum of Natural History, Smithsonian Institution, Washington, D. C., USA. Deposited: two male and two female paratypes (ZMUC CRU-4855), in the Zoological Museum, University of Copenhagen, Denmark (two specimens, one male and one female, on stubs prepared for SEM); two male and three female paratypes, Los Angeles County Museum of Natural History; one male and one female paratypes, Orma J. Smith Museum of Natural History, Caldwell, Idaho.

Distribution.—To date known only from two pools (Tadpole Lake and Armadillo Lake) on the Snake River Plateau, southwestern Idaho, USA.

Habitat.—Turbid, alkaline temporary pools and alkaline playa lakes with a pH of 10.0 or higher.

Activity Period.—March through June, depending upon rainfall and temperature.

Behavior.—*B. raptor* preyed upon *Branchinecta mackini* Dexter, 1956, chironomid midges (*Chironomus* sp.), mosquito larvae (*Culiseta* sp.), cladocerans (*Daphnia* sp.), unidentified diaptomid copepods and ostracodes. *B. mackini* was consistently the prey of choice: other invertebrates were taken only when no *B. mackini* were available. Live *B. mackini* were consistently preferred to moribund animals. Dead *B. mackini* were picked from the substrate or water column, manipulated, bitten once or twice, then rejected.

Swimming behavior for *B. raptor* differs from other *Branchinecta*, in that the first two pairs of thoracopods are not used, but remain stationary and outstretched laterally. Males swim with the second antennae spread laterally, rather than parallel and directed posteriorly as in other *Branchinecta* species. Like *B. gigas*, *B. raptor* lives in highly turbid water with little light penetration, and has extremely small eyes. Prey were encountered through collision or by detecting the turbulence they created. *B. raptor* attacked dead *B. mackini* only when physical contact occurred. However, live *B. mackini* were often attacked or chased when passing in close proximity. Some *B. mackini* avoided capture by stopping all movement. *B. raptor* was then often unable to find them. Gentle expulsion of water from a pipette at a passing *B. raptor* initiated attacks on the pipette.

When another anostracan swam past, or collided with it, a *B. raptor* would immediately attack and coil around it. If the other anostracan was another *B. raptor*, the two would part quickly. On the other hand, a *B. mackini* would be bitten repeatedly, while being rapidly turned in various directions. Typically, the endopods of the first four thoracopod pairs (and the second antennae in males) were used to capture prey and pull it into the food groove. Here an enclosure surrounding the prey is made of the endopods of all the thoracopods, with those of the first four pairs bent posteriorly over the prey. The prey is grasped with the endites, which pass it to the mouth where it is bitten by the large, sharp posterior teeth of the mandibles. Large *B. mackini* were bitten, released, and recaptured several times until they stopped thrashing about (possibly to avoid injury) and then consumed or retained. Small *B. mackini* were consumed immediately upon capture or retained.

B. raptor held the prey with endites 1 and 2 and sometimes 3 of the first one or two thoracopod pairs while masticating (Fig. 6). Sometimes mastication would cease and the labrum would be moved clear of the mandibles, while the prey was repositioned by the endites.

Retention of prey was observed frequently (Fig. 7). Between one and four *B. mackini* were often carried, positioned ventral side up, head towards the anterior, between the endites of the posterior five pairs of legs, often with each stacked in the previous one’s food groove if they were particularly large. Retention behavior increased as prey availability decreased. When prey was plentiful, only one or no *B. mackini* would be carried until another was captured. As it became less abundant in the aquarium, up to four *B. mackini* would be carried at a time by a single *B. raptor*. In several instances, a *B. raptor* was consuming a *B. mackini* that began suddenly to twist and possibly attempt escape. The *B. raptor* would bite it once or twice, then, using the endopods pass it to the endites of the posterior most thoracopods, while the endites of the middle thoracopods would move another *B. mackini* to the mandibles. On one occasion, one *B. mackini* was passed to the mandibles where it was held, while the endopods and the endites switched the order of two others in the food groove. The *B. mackini* was then moved from the mandibles back to the endites. Some *B. raptor* carried one or more prey for up to 2 hours before ingesting them.



Fig. 6. *Branchinecta raptor* n. sp. Female, left; male center, showing male with out-stretched second antennae.

When prey was plentiful, *B. raptor* sometimes captured *B. mackini* with their endopods, then released them either unharmed, or would bite them once or twice and then release them, which often killed or mortally injured them.

B. raptor employed several hunting strategies. Most common was to swim randomly and encounter prey. Occasionally, particularly in cold water (temperature 4°C) a *B. raptor* would lie dorsum down on the substrate with its abdomen extended upward and its cercopods slightly splayed. When movement in the water was detected, or the cercopods were brushed, it would lunge at the potential prey.

Another hunting method is to search the substrate. *B. raptor* swam or drifted to the substrate, turned ventral side down, and literally crawled, apparently at random. The typical metachronal beat of the thoracopods was stopped and an ambulatory mode of travel was adopted. When a live, dead, or moribund *B. mackini* was encountered, it was attacked.

On two occasions, when no prey was detected, *B. raptor* swam to the substrate, turned ventral side down, and began to churn large amounts of sediment into suspension. After doing this for a few seconds it swam up to the cloud of debris and sediment, and made several passes through it, attacking larger bits of debris. Non-edible material was grasped and bitten one or more times before being discarded. It was during this behavior that chironomid midge larva and ostracodes were captured and consumed.

Distinct signs of stress were apparent after 2.5 hours without food (listing, difficulty in swimming, remaining on the bottom, periodic interruptions in the metachronal beat of the thoracopods), and individuals were dying 3.5 hours after all live prey and recently (less than one hour) dead items were consumed. At no time was the “C” shaped hunting behavior reported for *B. gigas* (White et al., 1969) observed in *B. raptor*, nor was it observed to scrape substrates for periphyton and micrometazoa, or to ingest filamentous green algae.

IUCN Red List Status.—*Branchinecta raptor* meets the International Union for the Conservation of Nature and Natural Resources (IUCN) red list criteria for designation as a VU D2 species (IUCN, 2000). That is to say, this taxon is vulnerable due to the population being very small and restricted, and thus prone to the effects of human activities or stochastic events within a short period of time.

DISCUSSION

Affinities of *Branchinecta raptor*

B. raptor is readily separated from all other *Branchinecta* species by the form of the second antennae, the first pairs of thoracopods, the cercopods, by the female first antennae being 2 to 2.5 times longer than the second antennae, and by the male genitalia. It is most similar to *B. gigas* and *B. ferox*.



Fig. 7. *Branchinecta raptor* n. sp. female each carrying one *Branchinecta mackini* in anterior thoracopod endites, with a second carried in the posterior thoracopod endites.

B. raptor shares the form of the head, small eyes, extensive coverings of micropapillae (Boudrias and Pires, 2002), and similar cyst morphology with *B. gigas*. In *B. raptor*, the male second antennal distal antennomere is flattened anteroposteriorly and is nearly twice as long as the proximal antennomere, whereas in *B. gigas* it is flattened laterally and subequal in length to the proximal antennomere.

B. raptor shares with *B. ferox* the form of the male second antennal proximal antennomere and the form of the penes. It is separated from *B. ferox* by the male second antennal distal antennomere being nearly twice as long as the proximal antennomere, and by the large spiny pulvillus. *B. raptor* appears to be closely related to *B. gigas*, being of similar size, having small eyes, similar head shape, sensory micropapillae, habitat, number of endites, and food preferences.

All three species have similar mouthparts, but the posterior and dorsal biting mandibular teeth of *B. raptor* are far larger than in the other two species (Fryer 1966, 1983).

Feeding of *Branchinecta raptor*

The modifications of the thoracopods allow *B. raptor* to manipulate prey with a high degree of dexterity, and to reach in several different directions for prey items adjacent to the body. The chitinized pads of endites 1, 2 and 3 grip

large prey items tightly (Fig. 4). Their surface is covered with a dense layer of small, robust setae, all pointing towards the midline of the animal (food groove), which will tend to keep prey from escaping or accidentally moving away from the feeding area. Considering the size and shape of these endites, *B. raptor* may possibly capture and consume amphibian larvae, but this has not been observed or tested.

One of us (DCR), collecting *B. gigas* in northeastern California observed the dexterity of this species. A large female lay in his hands, and one of its thoracopods brushed a *B. mackini* that was lying nearby. It reached for the animal with the endopod of the second and third thoracopods, and quickly pulled it to the food groove. The *B. mackini* lay with its head towards the mouth of the *B. gigas* female, and its body lying in the food groove. The *B. gigas* then lifted the *B. mackini* with its endopods, turned it around, and began pushing it, abdomen first, into its rolling jaws. This was accomplished entirely out of the water.

B. raptor utilizes a larger repertoire of hunting behaviors than has been observed in other predatory anostracans. At no time was the "C" shaped hunting behavior of *B. gigas* observed (White et al., 1969). The fact that this animal actively hunted live prey using a variety of methods is unique among the Branchiopoda. Active selection and rejection of food is unknown in the Anostraca, which typically consume whatever particles can fit through the

mouth including styrene or glass beads (see review of feeding in the Anostraca in Brendonck, 1993a, b). Even *B. gigas*, which actively predaes on other metazoans, does not show this selectivity, and will accept dead and moribund food and any metazoan that it encounters (Fryer, 1983; unpublished data).

B. raptor was not observed to scrape substrates for periphyton and micrometazoa, or to consume filamentous algae as do other predatory taxa (Fryer, 1966; Belk and Ballantyne, 1988 for *B. gigas*; Fryer, 1983 for *B. ferox*) even when starved. Fryer (1983) showed that predatory *Branchinecta* species begin as filter feeders (like other Anostraca) in the earlier instars, move to substrate scraping in later instars, then adopt a predatory mode of feeding in the larger instars. No earlier instars of *B. raptor* have been found, so it is not known if this pattern is followed here. The gut was always filled with the orange clay and sediment particles suspended in their natural habitat. However, the few setae of the medial margin of the thoracopods are insufficient to filter suspended sediment and move it towards the mouth. In aquaria with clear water and dark grey clay sediment, their gut never reflected the colour of the grey sediment in the tank, even after being starved. Therefore it is assumed that these particles are ingested during predatory feeding, and normal oral and anal intake of water rather than from sediment scraping, at least as adults. The particulate matter in the gut may be present from filter feeding or scraping during immature stages, or more likely from the gut of the filter feeding *B. mackini* that they ingest. The high salinity of their habitat causes the substrate to be highly viscous, and therefore difficult to pass through the gut.

B. raptor adults are obligate carnivores, consuming only live or moribund prey, and consume recently dead prey only when starving.

Evolutionary Significance of Feeding Structures in *Branchinecta raptor*

The morphology of *Branchinecta raptor* is a combination of primitive anostracan features and highly modified structures. Clearly primitive is the number of six distinct thoracopodal endites, in contrast to only five in most other anostracans, where the proximal endite is a fusion product of two smaller endites present in early development (see Olesen, 2003; Møller et al., 2004). *B. gigas* also has six endites (Fryer, 1966). Modified features include all the adaptations to a predatory lifestyle, which probably evolved secondarily within the Anostraca. Most notably, the thoracopods have various modifications (Fig. 4 and 5A–D), including the enlarged and strongly chitinized endopods bearing a highly modified type of spines. Further predatory adaptations include the widely separated thoracopods, the absence of filtering or scraping setae, and modified endites. The function of endites 1–3 is probably to manipulate and immobilize prey while endites 4 and 5 are probably sensory.

Another adaptation for a predatory lifestyle concerns the mandible (Fig. 3). The gnathal edge of the mandible is composed of an anterior molar process and a posterior large tooth. Comparable morphology is seen also in *B. gigas* and *B. ferox*, but the posterior tooth is much larger in *B. raptor*. A division into a molar part (pars molaris) and a cutting or biting part (pars incisivus) of the mandibular gnathal edge is

common within the Crustacea but rare within the Branchiopoda. Richter et al. (2004) interpreted the fact that the pars molaris largely forms the entire gnathal edge as an apomorphy of the Branchiopoda. In contrast, Manton (1977, p. 74) considered mandibles of *Chirocephalus* (Anostraca) very close to a simple, hypothetical crustacean mandible from which she derived an incisor-bearing mandible of *Anaspides* (Malacostraca). In Manton's (1977) view the change from a '*Chirocephalus*'-morphology to an '*Anaspides*'-morphology involved a shift in the axis of swing of the mandible, so that it no longer lies in the transverse plane. Among other things, this results in the posterior corner of the mandible — the pars incisivus — in *Anaspides* being directed ventrally as well as posteriorly, sometimes forming a cutting edge in the proximity the posterior margin of the labrum; an arrangement commonly observed within the Malacostraca. Given the presumed phylogenetic position of *Branchinecta* as an early off-shoot within the Anostraca (and thereby of the Branchiopoda), we speculate whether the robust posteriomedial tooth at the mandible's gnathal edge in *B. raptor* and other species of the genus could be a precursor to the well-developed pars incisivus seen in many malacostracans. On the other hand, the uniquely distinct mandibular tooth may more likely be interpreted as an adaptation to the predatory lifestyle employed by *B. raptor* and certain other congeneric species. Richter (2004) showed a more 'normal' mandibular gnathal edge of *Branchinella lyrifera* Linder, 1941 (Thamnocephalidae), which is a filter feeding anostracan. Except for the missing posterior tooth in *Branchinella lyrifera*, the gnathal edge of its right mandible is rather similar to those of *B. raptor* [compare Richter's (2004) Fig. 2A with our Fig. 3]. Most significant is the presence of a row of dorsal spines along the posteriodorsal part of the pars molaris, not seen in any of the other branchiopod mandibles studied by Richter (2004). It is likely that the most posterior spine on the gnathal edge of a 'normal' anostracan mandible during evolution has been modified to the extraordinary large posterior tooth in predatory species of *Branchinecta*.

LARGE BRANCHIOPOD CRUSTACEA IN IDAHO

Western North America has been extensively surveyed for large branchiopod crustaceans (Anostraca, Notostraca, Laevicaudata, and Spinicaudata) (Dodds, 1915; Lynch, 1937; Mackin, 1938; Tasch and Shaffer, 1964; Maynard and Romney, 1975; Belk 1977, 1992; Eng et al. 1990; Maeda-Martínez, 1991; Maeda-Martínez et al., 1997a; Maeda-Martínez et al., 1997b; Hill et al., 1997; Rogers 2001), and new species are still being found (Fugate, 1993; Belk and Fugate, 2000; Rogers 2001; Rogers and Fugate 2001; Belk and Rogers, 2002; Obregón-Barboza et al., 2002; this study). Many areas are still not entirely surveyed or are only now being explored. No species were listed from the state of Idaho in the USA in Belk's (1975) work on the Anostraca of North America. To date, the only reports of large branchiopods in Idaho have been in the anthropological literature (as potential aboriginal food resources in Henrikson et al., 1998 and Plew and Weaver, 2001), the notostracan species *Lepidurus bilobatus* Packard, 1883 and *L. couesii* Packard, 1875 (Rogers, 2001), the anostracan *Branchinecta coloradensis* Packard, 1874 (Belk and Rogers

2002), and a grey literature reference that reports *Branchinecta paludosa* (Müller, 1788) (Rabe, 2001). Unfortunately, the *B. paludosa* material collected by Rabe was discarded and never verified (Rabe, personal communication). It is entirely likely that Rabe found this species during the course of his investigations, as this taxon occurs in adjacent states and provinces (Saunders et al., 1993; Stern and Belk, 1999) and its presence in Idaho would be expected.

In the Idaho National Guard Orchard Training Area, south of Boise, Idaho, where we found *Branchinecta raptor* and *B. mackini*, we also encountered *B. hiberna* Rogers and Fugate, 2001, *B. lindahli* Packard, 1883, *B. coloradensis*, and the tadpole shrimp *Lepidurus bilobatus* Packard, 1883.

Branchinecta hiberna has previously been reported from Great Basin Desert regions of central Oregon, northeastern California and adjacent Nevada (Rogers and Fugate, 2001) and the new records represent a significant range extension. All our Idaho *B. hiberna* co-occurred with *B. coloradensis* or *B. lindahli*. As was reported by Rogers and Fugate (2001) the *B. hiberna* were maturing long before their congeners, and disappearing before *B. coloradensis* or *B. lindahli* reached sexual maturity. Both species are widespread at the Orchard Training Area.

Branchinecta coloradensis populations at this site were similar to those from the southern Cascade Mountains of California, in that the apophyses are either lacking, or are extremely reduced (Belk and Rogers, 2002).

Both *B. lindahli* and *B. coloradensis* are widespread in western North America, and their presence in Idaho would be expected (Belk, 1975). *B. mackini* also has not previously been reported from Idaho.

Lepidurus bilobatus, previously reported from this region of Idaho (Rogers, 2001), has a sporadic distribution across western North America, which may only be an artifact of collecting.

One of us (DCR) collected the anostracan *Eubbranchipus serratus* Forbes, 1876, from Latah County in northern Idaho, from a pool south of Princeton, on 26 April 2004. Furthermore, the collections of the late Denton Belk contained the following large branchiopod crustacean records from Idaho:

Eubbranchipus serratus: Comas County: Macon Flat Pond 2 & 3, 29 April 1998, L. S. Henrikson, DB (Denton Belk collection number) 1324 & 1325.

Lynceus brachyurus Müller, 1776 Comas County: Macon Flat Pond 3, 29 April 1998, L. S. Henrikson, DB1325. Minidoka County: "The Bowl" at Lava Point, 29 April 1998, L. S. Henrikson, DB 1327. Playa east of "The Bowl" at Lava Point, 29 April 1998, L. S. Henrikson, DB 1328. Sparrow Lake, 29 April 1998, L. S. Henrikson, DB 1329.

ACKNOWLEDGEMENTS

We thank Tim Messick for his kindness and generosity in scanning and manipulating the figures, Geert Brovad (ZMUC) for producing fig. 1, and Brian Timms and Brenda Hann for useful comments on an early draft of this paper. Special thanks go to L. Evans, M. McHenry and S. Quinney for all their help and hard work. We are also grateful to G. Fryer for numerous helpful comments on our early drafts.

REFERENCES

Belk, D. 1975. Key to the Anostraca (fairy shrimps) of North America. *The Southwestern Naturalist* 20: 91-103.

- . 1977. Zoogeography of the Arizona fairy shrimps (Crustacea: Anostraca). *Arizona Academy of Science* 12: 70-78.
- . 1992. Observations on the clam shrimps of Arizona. *Journal of the Arizona-Nevada Academy of Science* 26: 132-138.
- , and R. Ballantyne. 1988. Filamentous algae an additional food for the predatory anostracan *Branchinecta gigas*. *Journal of Crustacean Biology* 16: 552-555.
- , and M. L. 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.
- Boudrias, M., and J. Pires. 2002. Unusual sensory setae of the raptorial *Branchinecta gigas* (Branchiopoda: Anostraca). *Hydrobiologia* 486: 19-27.
- Brandonck, L. 1993a. Feeding in the fairy shrimp *Streptocephalus probiscideus* (Frauenfeld) (Branchiopoda: Anostraca). I. Aspects of the feeding biology. *Journal of Crustacean Biology* 13: 235-244.
- . 1993b. Feeding in the fairy shrimp *Streptocephalus probiscideus* (Frauenfeld) (Branchiopoda: Anostraca). II. Influence of environmental conditions on feeding rate. *Journal of Crustacean Biology* 13: 245-254.
- Broch, E. S. 1988. Osmoregulatory patterns of adaptation to inland astatic waters by two species of fairy shrimps, *Branchinecta gigas* Lynch and *Branchinecta mackini* Dexter. *Journal of Crustacean Biology* 8: 383-391.
- Cannon, H. G., and S. M. Manton. 1927. On the feeding mechanism of a mysid crustacean, *Hemimysis lamornae*. *Transactions of the Royal Society of Edinburgh* 55: 219-253.
- Daborn, G. R. 1974. Length-weight allometric relationships in four crustaceans from Alberta lakes and ponds. *Canadian Journal of Zoology* 52: 1303-1310.
- . 1975. Life history and energy relations of the giant fairy shrimp *Branchinecta gigas* Lynch 1937 (Crustacea: Anostraca). *Ecology* 56: 1025-1039.
- Dodds, G. S. 1915. A key to the entomostraca of Colorado. *University of Colorado Bulletin* 15: 265-298.
- Eng, L. L., D. Belk, and C. Eriksen. 1990. California Anostraca: distribution, habitat, and status. *Journal of Crustacean Biology* 10: 247-277.
- Fryer, G. 1966. *Branchinecta gigas* Lynch, a non-filter-feeding raptorial anostracan, with notes on the feeding habits of certain other anostracans. *Proceedings of the Linnean Society of London* 177: 19-34.
- . 1983. Functional ontogenetic changes in *Branchinecta ferox* (Milne-Edwards) (Crustacea: Anostraca). *Philosophical Transactions of the Royal Society of London* 303: 229-343.
- Fugate, M. L. 1993. *Branchinecta sandiegoensis*, a new species of fairy shrimp (Crustacea: Anostraca) from western North America. *Proceedings of the Biological Society of Washington* 106: 296-304.
- Henrikson, L. S., R. M. Yohe II, M. E. Newman, and M. Druss. 1998. Freshwater crustaceans as an aboriginal food resource in the northern Great Basin. *Journal of California and Great Basin Anthropology* 20: 72-87.
- Hill, R. E., D. C. Rogers, B. D. Quelvog, and S. P. Gallagher. 1997. New records and observations on the Anostracan genus *Eubbranchipus* in California. *Hydrobiologia* 359: 75-81.
- 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: 555-566.
- Mackin, J. G. 1938. Key to the species of Phyllopoda in Oklahoma and neighboring states. *Proceedings of the Oklahoma Academy of Science* 19: 44-47.
- Maeda-Martínez, A. M. 1991. Distribution of species of Anostraca, Notostraca, Spinicaudata and Laevicaudata in México. *Hydrobiologia* 212: 209-212.
- , D. Belk, H. Obregón-Barboza, and H. J. Dumont. 1997a. Large branchiopod assemblages common to México and the United States. *Hydrobiologia* 359: 45-62.
- , H. Obregón-Barboza, and H. García-Velazco. 1997b. New records of large branchiopods (Branchiopoda: Anostraca, Notostraca, and Spinicaudata) in México. *Hydrobiologia* 359: 63-68.
- Manton, S. M. 1977. *The Arthropoda: their habits, functional morphology and evolution*. Oxford University Press, Clarendon, London and New York.
- Maynard, S. D. S., and S. V. Romney. 1975. The occurrence of four new anostracan (Crustacea) phyllopods in Utah, multispecies records, and

- some notes on their ecology. *Proceedings of the Utah Academy of Science, Arts and Letters* 52: 6-11.
- Møller, O. S., J. Olesen, and J. T. Høeg. 2004. On the larval development of *Eubranchipus grubii* (Crustacea, Branchiopoda, Anostraca), with notes on the basal phylogeny of the Branchiopoda. *Zoomorphology* 123: 107-123.
- Olesen, J. 2003. On the ontogeny of the Branchiopoda (Crustacea): contribution of development to phylogeny and classification. pp. 217-269 In, G. Scholtz, ed. *Crustacean Issues 15, Evolutionary Developmental Biology of Crustacea*. Balkema, Lisse.
- Obregón-Barboza, H., A. 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.
- Peeters, K., L. Brendonck, and L. Moens. 1994. The occurrence of artemocyanin in Branchiopoda (Crustacea). *Comparative Biochemistry and Physiology* 109: 773-779.
- Plew, M. G., and J. Weaver. 2001. Implications of an experimental freshwater shrimp harvest. *Northwest Anthropological Research Notes* 35: 21-26.
- Rabe, F. W. 2001. High mountain lake research natural areas in Idaho. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station General Technical Report RMRS-GTR-77.
- Richter, S. 2004. A comparison of the mandibular gnathal edges in branchiopod crustaceans: implications for the phylogenetic position of the Laevicaudata. *Zoomorphology* 123: 31-44.
- Rogers, D. C. 2001. Revision of the North American *Lepidurus* (Notostraca:Crustacea) with a description of a new species previously confused with two other species. *Journal of Crustacean Biology* 21: 994-1006.
- , and M. L. Fugate. 2001. *Branchinecta hiberna*, a new species of fairy shrimp (Crustacea: Anostraca) from western North America. *Western North American Naturalist* 61(1): 11-18.
- Saunders, J. F., D. Belk, and R. Dufford. 1993. Persistence of *Branchinecta paludosa* (Anostraca) in southern Wyoming, with notes on zoogeography. *Journal of Crustacean Biology* 13: 184-189.
- Shepard, W. D., and R. E. Hill. 2001. Anostracan cysts found in California lakes. *Hydrobiologia* 466: 149-158.
- Stern, S., and D. Belk. 1999. Confirmation of *Branchinecta paludosa* (Crustacea, Anostraca) in Utah. *The Southwestern Naturalist* 44: 212-213.
- Tasch, P., and B. L. Shaffer. 1964. Conchostracans: living and fossil from Chihuahua and Sonora, México. *Science* 143: 806-807.
- White, G. E. 1967. The biology of *Branchinecta mackini* and *Branchinecta gigas* (Crustacea: Anostraca). M. S. thesis. University of Calgary. Calgary, Alberta, Canada. 88 pages.
- , B. Fabris, and R. Hartland-Rowe. 1969. The method of prey capture by *Branchinecta gigas* Lynch, 1937 (Anostraca). *Crustaceana* 16: 158-160.

RECEIVED: 19 April 2004.

ACCEPTED: 30 August 2005.