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Branchinecta belki n. sp. (Branchiopoda: Anostraca), a new fairy shrimp from Mexico, hybridizing with *B. packardi* Pearse under laboratory conditions

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Abstract

A new fairy shrimp, *Branchinecta belki* n.sp., endemic to the south of Coahuila state is described and figured. A total of nine species of phyllopods, including the new species, occur in ponds in the type area.

The laboratory hybridization of *B. belki* and *B. packardi* through 'no-choice' mating tests in reciprocal crosses is discussed. A mixture of characteristics of parental species is present in male F1 and F2 hybrids. This may provide a biological tool, or 'search image' (sensu Wiman, 1979a), for detecting male hybrids, should such exist, between the *Branchinecta* species of this study in nature. In addition to the reported interspecific hybridizations in *Streptocephalus* (Wiman, 1979a & 1979b) and in *Artemia* (Bowen *et al.*, 1985) under laboratory conditions, the new evidence in *Branchinecta* suggests that absence of efficient premating mechanisms may be common in Anostraca.

Introduction

Previous to this paper, Maeda-Martinez (1991) announced the presence of two undescribed species of *Branchinecta* in Mexico, one from Coahuila and one from Tlaxcala. The present paper deals with the description of the species from Coahuila, and discusses results of its ability to hybridize with *B. packardi* Pearse under laboratory conditions.

Branchinecta belki n. sp. inhabits a desertic plain inside a closed basin in the extreme east of the ancient Mayran lake. Material was collected and examined with the aim of checking the constancy of its diagnostic features. Populations were sampled by the first author during ten different occasions between 1980 to 1985. They occurred in ephemeral ponds, most of which were at the roadside of Federal Highway No. 40, approximately 10 km from El Dorado ranch, to 80 km W of Saltillo, Coahuila.

The type material consists of 20 males and 20 females collected on 25 February, 1984. Holotype male, Allotype female and 10 Paratypes of both sexes are deposited in the National Museum of Natural History, Smithsonian Institution, USA (USNM). Paratypes of both sexes are also deposited in the Institute of Animal Ecology, University of Ghent, Belgium (UG) and in the Escuela Superior de Biologia, Universidad Juarez del Estado de Durango, Mexico (UJED). The description is based of the type material and all measurements given are mean values together with the observed range. For scanning electron

micrographs, specimens and eggs (from females fixed in isopropilic alcohol 70%) of the new species, hybrids and *B. packardi*, were critical-point dried, coated with gold (9 nm, Balzers Union SCD 040) and analyzed under a JEOL JSM 840 (SEM) at 10 kV. Terminology of egg shell structures is according to Gilchrist (1978).

Branchinecta belki new species

Figs 1–8 & 14–16

Material examined. Holotype ♂, Allotype ♀ and Paratypes 5 ♂♂ & 5 ♀♀ USNM 251277, 251278 & 251279; Paratypes 5 ♂♂ & 5 ♀♀ UG 114 and 9 ♂♂ & 9 ♀♀ UJED 285 collected 25 February 1984. Paratopotypes 28 ♂♂ & 45 ♀♀ UJED 286. Additional specimens from the type locality, 66 ♂♂ & 52 ♀♀ UJED 207 collected 6 December 1980, 39 ♂♂ & 28 ♀♀ UJED 208 collected 30 January 1981, 6 ♂♂ & 5 ♀♀ UJED 205 collected 21 October 1981, 40 ♂♂ & 21 ♀♀ UJED 204 collected 2 November 1981, 20 ♂♂ & 14 ♀♀ UJED 210 collected 7 May 1982. Specimens from 2 km W of type locality 6 ♂♂ & 4 ♀♀ UJED 212 collected 6 December 1980, 32 ♂♂ & 9 ♀♀ UJED 213 collected 30 January 1981 and 25 ♂♂ & 75 ♀♀ UJED 215 collected 12 October 1981. Specimens from 5 km SE of type locality 39 ♂♂ & 27 ♀♀ UJED 211 collected 6 December 1980 and 41 ♂♂ & 67 ♀♀ UJED 203 collected 05 October 1984. Specimens from 10 km SE of type locality 21 ♂♂ & 8 ♀♀ UJED 209 collected 30 January 1981, 907 ♂♂ & 967 ♀♀ UJED 227–228 collected 11 March 1983 and 10 ♂♂ & 6 ♀♀ UJED 202 collected 11 February 1985.

Diagnosis. Male. Proximal article of antenna presenting welt and conspicuous apophysis on median side near proximal end, in superior and inferior position (Figs 1–8); Proximal article with distinctive structure on median side, consisting of prominent, spinous outgrowth generally composed of 2 or 3 protuberances, ending in variable number of spines (Figs 1–8). Around base of prominent structure, in dorsomedial position, 9–17 denticles, irregularly arranged (Figs 1–5 & 8). Proximal article also bearing at dorsal-posterior side, just in front of distal tip, a conical elevation (lateral view) covered by minute denticles (Fig. 1–5 & 8). Distal article of antenna, concave median side, curved inward; median distal part curved most (Figs 1–8); apex bifurcated with acute dorsal projection and with round ventral projection (Figs 1–8); round projection covered by rasplike surface (Figs 1 & 7), extending anteroposteriorly along three fourths of ventrolateral border of article.

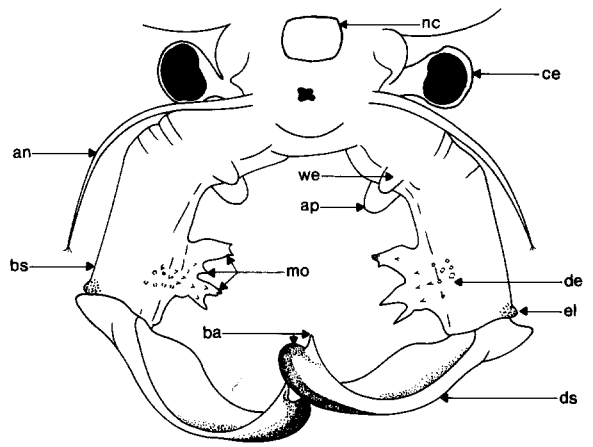


Fig. 1. Head in anterior view of *Branchinecta belki* n.sp.: an. antennule, ap. apophysis, ba. bifurcated apex (dorsal acute & ventral round projections), bs. basal article of antenna, ce. compound eye, de. denticles, ds. distal article of antenna, el. dorsal elevation, mo. median outgrowth (proximal, medial & distal protuberances), nc. nucal organ & we. welt.

Female. Antenna cylindrical, bearing median and dorsal papillose protuberance on distal half. Thoracic segments 9 to 11 and first genital segment (IX–XII trunk segments) usually with conical protuberance on both dorsolateral sides.

Description. Male: Total length from front to end of last abdominal segment (telson) between cercopods 13.3 (12.0–14.9) mm. Antennule 1.8 (1.6–2.2) mm long, filiform, with 3 subapical setae. Antenna biarticulate; proximal article 2.2 (1.8–2.4) mm long, presenting two protuberances on median side near proximal end: welt, in superior position and enlarged antero-posteriorly, and

Figs 2–4. Scanning electron micrographs (SEM). All of *Branchinecta belki* n.sp., head and both right and left basal articles of antenna in anterior view: ap. apophysis, cs. concave side of distal article, de. denticles, dp. distal protuberance, el. dorsal elevation, pp. proximal protuberance & we. welt.

Figs 5–7. Scanning electron micrographs (SEM). All of *Branchinecta belki* n.sp., head and both right and left basal articles of antenna. 5. anterior view, 6 & 7 posterior view. ap. apophysis, ba. bifurcated apex, cp. most curved part of distal article, dp. distal protuberance, mp. medial protuberance, pp. proximal protuberance, rm. rudimentary mandibular palp & rs. rasp-like surface.

conspicuous apophysis in inferior position (Figs 1–8); Proximal article with most distinctive structure of species, on median side, near medial part, consisting of prominent, spinous outgrowth (Figs 1–8). Shape of this structure variable and different on two antennae of each specimen, yet generally composed of 2 or 3 protuberances (proximal, medial & distal). Tip of proximal protuberance variable and ending in 2 (Figs 3, 6 & 8), 3 or more spines (Figs 2, 4, 5 & 7); medial protuberance, when present, unicuspid (Fig. 6). Tip of distal protuberance ending in 1 (Fig. 6), 2, 3 or more spines (Figs 2–5, 7 & 8). Around base of prominent structure, in dorsomedial position, 9–17 denticles, irregularity arranged (Figs 1–5 & 8). Proximal article bearing elevation of conical shape (lateral view) at dorsal-posterior side, just in front of distal tip and covered by minute denticles (Figs 1–5 & 8).

Distal article of antenna curving inward; median distal part curved most (Figs 1–8). Length of article across arc 2.3 (1.8–2.6) mm, and composed of concave median side, ventral side, and lateral side. Apex bifurcated, with acute projection on dorsal side and with round projection on ventral side (Figs 1–8). Round projection covered by rasplike surface, extending anteroposteriorly along three fourths of ventro-lateral border of article (Figs 1 & 7).

Nuchal organ transversely oblong, 0.47 (0.44–0.52) mm along antero-posterior axis (Fig. 1). Diameter of compound eye in dorsal view and parallel to antero-posterior axis 0.50 (0.44–0.56) mm. Rudimentary mandibular palp present (Fig. 6). Maxillule with one spine on median side and 12 to 14 plumose setae. Maxilla with two median setae and 11 to 19 distal setae. Phyllopodia typical of genus; preepipodite (branchial lamina) with border serrated by cuticular papillae with incision well defined on three first pairs of phyllopodia, but less evident in other legs. Genital segments with penes typical of genus; ventro-median outgrowth of basal non-retractile part slender hook, tip of which points in dorso-posterior direction. Cercopods not including setae, 1.5 (1.4–1.7) mm long, not converging, set with plumose setae along median and lateral borders.

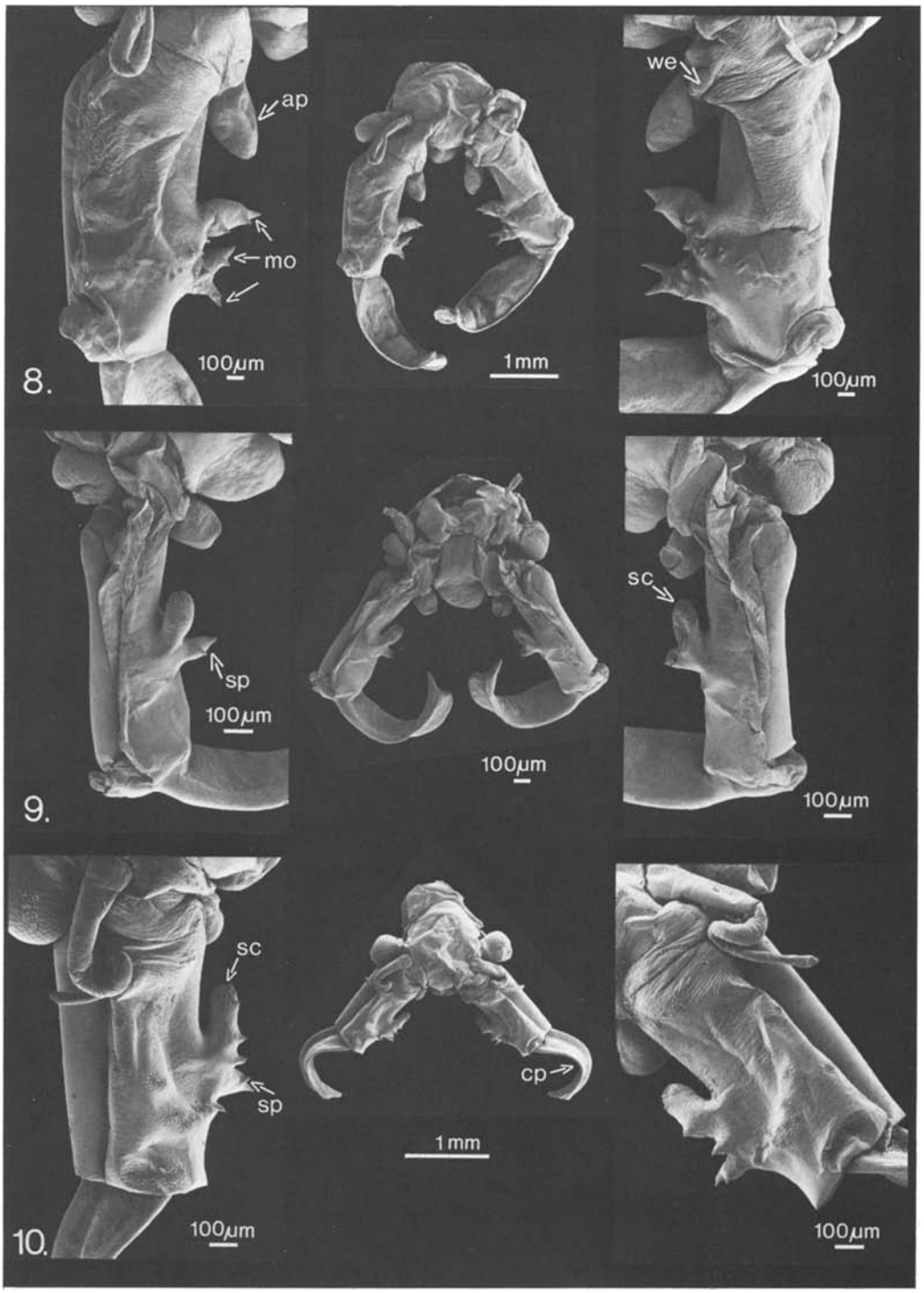
Female: Total length (from front to end of last abdominal segment (telson)) between cercopods 13.1 (10.6–14.0) mm. Antennule 1.4 (0.9–1.6) mm long, filiform, with 3 subapical setae. Antenna 1.5 (1.2–1.6) mm long, cylindrical, bearing two papillose protuberances on distal half: one on median side and one on dorsal side just at base of distal, sharp part of antenna. Nuchal organ transversely oblong, 0.51 (0.48–0.56) mm along antero-posterior axis. Diameter of compound eye in dorsal view and parallel to the antero-posterior axis 0.34 (0.28–0.40) mm. Rudimentary mandibular palp present. Thoracic segments 9 to 11 and first genital segment (IX–XII trunk segments) with conical protuberance on both dorsolateral sides. These conical protuberances, or lobes, increase in size in antero-posterior direction. Ten percent of females present lobes on thoracic segments 10 to 11 and on the first genital segment.

Ovisac fusiform, tip ending under abdominal segments 6 or 7. Number of eggs (also called resistant eggs, dormant embryos or cysts) in ovisac 36 to 117 ($n = 10$); spherical eggs 0.26 (0.16–0.32) mm in diameter; outer surface wrinkled with ridges forming polygonal areas (Fig. 14 & 15); tertiary shell consisting of two alveolar layers: outer cortex and inner alveolar layer with subcortical space between them (Fig. 16).

Cercopods not including setae, 1.3 (1.1–1.5) mm long; not converging, and with plumose setae along median and lateral borders.

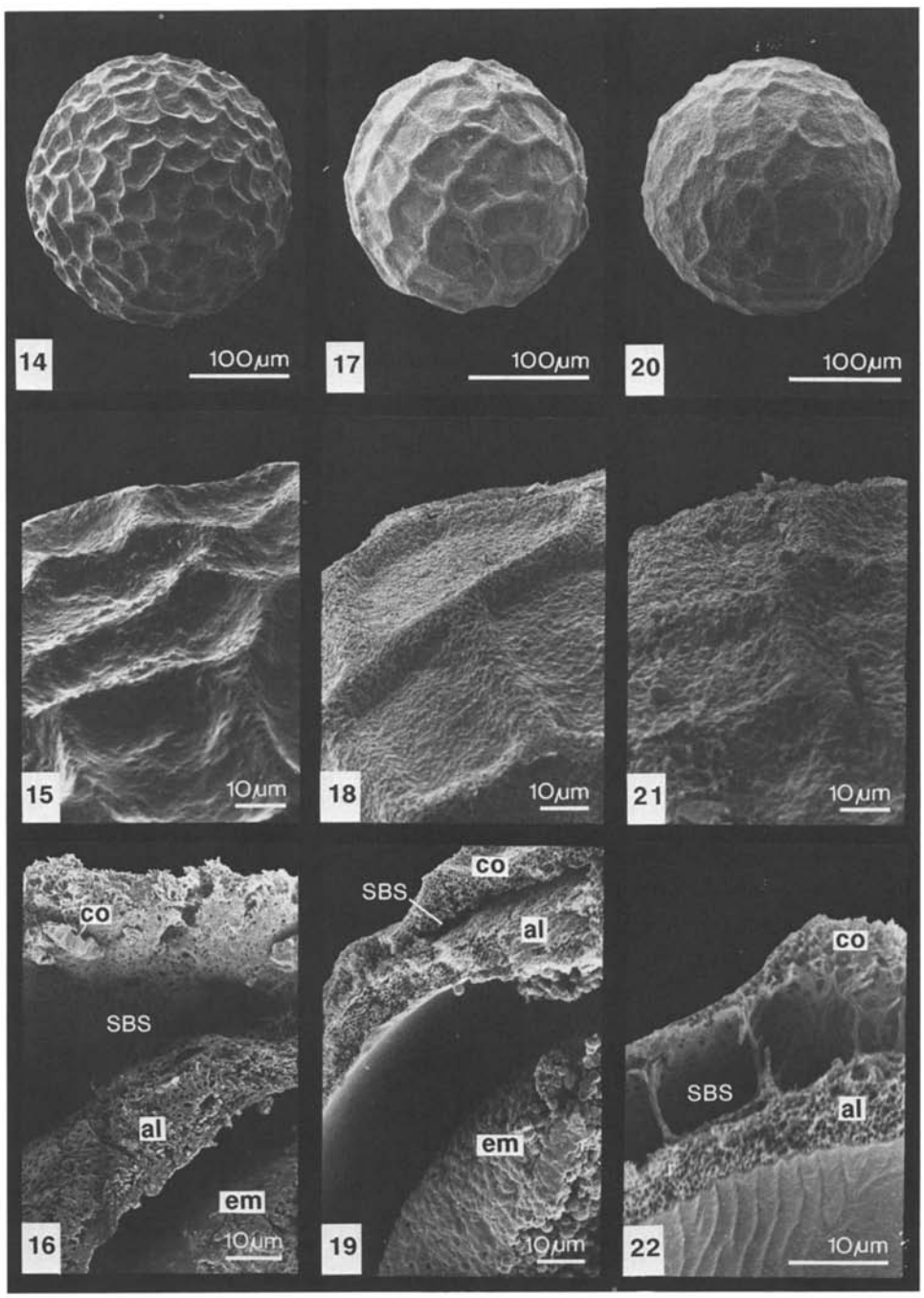
Differential diagnosis

Accepting the morphology of both articles of the antenna in the male as the principal diagnostic characteristic, *Branchinecta belki* n.sp. differs from all North America species so far described. It is related to *B. packardi* due to the presence in the males of a welt and of one apophysis near the base of the proximal article, on the median side (Lynch, 1964) (Fig. 11). In females, the conical dorsolateral processes or lobes on trunk segments IX to XII are present as well (Lynch, loc. cit.). Nonetheless, two important differential features occur: First, the process on the median side of the



Figs 8–10. Scanning electron micrographs (SEM). Head and both right and left basal articles of antenna in anterior view of: 8. *Branchinecta belki* n.sp., 9. F1 hybrid *B. belki* ♂ × *B. packardi* ♀, 10. F2 hybrid *B. belki* ♂ × *B. packardi* ♀. ap. apophysis, cp. most curved part of distal article, mo. median outgrowth, sc. scales, sp. spinous protuberance & we. welt.

Figs 11–13. Scanning electron micrographs (SEM). Head and both right and left basal articles of antenna in anterior view of: 11. *Branchinecta packardi* Pearse, 12. F1 hybrid *B. packardi* ♂ × *B. belki* ♀, 13. F2 hydrid *B. packardi* ♂ × *B. belki* ♀. ap. apophysis, cp. most curved part of distal article, pe. peg-like protuberance, sc. scales, sp. spinous protuberance, ss. semitubular spur & we. welt.



Figs 14–22. Scanning electron micrographs (SEM) of cyst of: 14–16. *Branchinecta belki* n. sp.; 17–19. F1 hybrid *B. packardi* ♂ × *B. belki* ♀. 20–22. *B. packardi*. 14, 17 & 20. whole egg; 15, 18 & 21. enlarged detail of external surface; 16, 19 & 22. shell detail of cracked egg; co: outer cortex; sbs: subcortical space; al: inner alveolar layer; em: embryonic cells.

basal antennal article in *B. belki* consists of a prominent spinous outgrowth (Fig. 1), while in *B. packardi* it is a peg-like protuberance with tip directed postero-dorsally (Lynch, op. cit.). This structure was mentioned as a 'spiny process' (Pearse, 1912) as well as a protuberance 'bearing

cuticular denticles and sensory hairs' (Lynch, op. cit.). However, our observations by SEM reveal only scales on the surface covering the peg-like process from base to tip (Fig. 11). These scales were not found on the spinous outgrowth of *B. belki*. Second, the apex of the distal antennal article of *B. packardi* ends in a semitubular medially projecting spur, and the posterior border is short, not turning medially (Lynch, op. cit.) (Fig. 11); in *B. belki* the apex is bifurcated, with an acute projection on its anterior border, and with a round projection on its posterior border (Figs 1, 5–7).

By the external ornamentation of its cysts, *B. belki* may be joined to the congeneric group of North American species characterized by ridges forming a polygonal pattern with large areas (Mura, 1991). It shows most similarity with *B. paludosa* Müller and *B. packardi*.

Branchinecta belki resembles some species from South America, particularly *B. granulosa* Daday (1910a), *B. gaini* Daday (1910b), *B. vuriloche* Cohen (1985), and *B. santacrucensis* César (1987). All these species have a median spinose or verruciform tubercle near the base of the proximal article. Instead of that, *B. belki* bears a welt and a conspicuous apophysis. On the same side, but more distally, the mentioned species present a process: in *B. granulosa* it is an aculeiform dentate outgrowth (Daday, 1910a); in *B. gaini* it is composed of numerous spines, giving it a denticulate appearance (Linder, 1941), rather similar to that present in *B. vuriloche* (Cohen, 1985) and *B. santacrucensis*, but where the spines are more scattered (Cesar, 1987). In *B. belki*, the outgrowth consists of two or three prominent and spinous processes. The distal article of *B. belki* also lacks the spinose tubercle which sits near to tip of the article in *B. granulosa* (Daday, 1910). In *B. gaini* and *B. vuriloche*, the apex of this article ends in an acute projection (Daday, 1910b, Linder, 1941 & Cohen, 1985), and in *S. santacrucensis* it terminates in three lobulate tips (Cesar, 1987). In *B. belki* the apex is bifurcated, with an acute projection on the anterior border, and with a round projection on the posterior border.

Type locality

An ephemeral pond on the south side of a bridge of Federal highway No. 40, approximately 0.5 km W of El Dorado Ranch, Coahuila, 25° 39′ N, 101° 35′ W, altitude c. 1130 meters above sea level, 80 km W of Saltillo, Coahuila, Mexico.

Etymology

The species is named in honor of Dr. Denton Belk, who has worked intensely on furthering the knowledge of the phyllopods and has offered constant friendly stimulation and advice to the first author.

Associated phyllopods

A total of nine species of phyllopods occur in the ponds of the type area. *Branchinecta belki* n. sp. was either found alone, or coexisted, during the cold months of the year (October–May) with *B.* cf. *lindahli* Packard, *Streptocephalus mackini* Moore, *S. texanus* Packard, and *Triops longicaudatus* (LeConte). During the warm months (July–September), the communities of phyllopods amounted to seven species: *S. mackini*, *S. texanus*, *Thamnocephalus platyurus* Packard, *T. longicaudatus*, *Caenestheriella setosa* (Pearse), *Eocyzicus digueti* (Richard), and *Leptestheria compleximanus* (Packard).

Laboratory hybrids

In naturally coexisting *B. belki* and *B.* cf. *lindahli*, no hybrids could be detected, in spite of the ease in separating males and females of both species (in *B.* cf. *lindahli* the antenna of the male presents a pulvillus near the base of the proximal article on the median side, and no apophysis like in *B. belki*; the dorsolateral lobes of females are different in shape as well as in position).

Branchinecta packardi, a species related to *B. belki* see differential diagnosis) has a wide dis-

tribution in Canada, USA (Belk, 1975), and localities in Mexico in the states of San Luis Potosi (Strenth & Littleton, 1990), Coahuila, Durango and Zacatecas (Maeda-Martinez, 1991). The nearest known to the type locality of *B. belki*, is only about 50 km away (a roadside ephemeral pond, kilometer No. 132 W Saltillo, Coahuila, Federal Highway No. 40). Since both localities are in the same semiarid plain in the ancient Laguna de Mayran basin, without geographical barriers, it is probable that these species have been or will be in contact with each other. Because of this potential contact between related species, currently believed to be allopatric, and considering the successful hybridization between streptocephalids and the ease of detecting natural hybrids (Wiman, 1979a & 1979b), a laboratory study of hybridization between *B. belki* and *B. packardi* through 'no-choice' mating tests (backcrosses were not attempted) was carried out. Preliminary results are presented.

Cysts of *B. packardi* were obtained from dry mud collected at of a roadside ephemeral pond in La Popular, State highway No. B-7, 12.5 km N of Gomez Palacio, Durango. Cysts of *B. belki* were collected from the type locality. Both species were cultured separately according to the argillotrophic method (Maeda-Martinez, 1991). Before the animals reached maturity, 20 males from *B. belki* and 20 females from *B. packardi* were removed and put together in an aquarium. In another aquarium the reciprocal cross using the same quantity of specimens, was carried out. The rest of the animals were left in their respective aquaria for corroboration of parental species. The production of cysts in both crosses, demonstrated that successful fertilization was possible. Cysts were collected, dried at room temperature, and submitted thirty days later to hatching. F1 hydrid nauplii were removed to a new aquarium where, after 5 days, they reached maturity and crossed among themselves. From the F1 hybrid cultures the next material was fixed: F1 *B. belki* ♂ × *B. packardi* ♀, 7 ♂♂ (7.5 (6.7–8.3) mm length) and 2 ♀♀ (6.5 & 7.6 mm length); F1 *B. packardi* ♂ × *B. belki* ♀, 5 ♂♂ (8.2 (6.2–10.2) mm length) and 7 ♀♀ (7.8 (7.2–8.5) mm length). The production of cysts in both cultures of adult F1 hybrids, demonstrated again successful fertilization. They were collected and submitted again to the same procedure, resulting in F2 hybrid nauplii. These animals were moved to a new aquarium, where they reached maturity after 5 days and crossed between themselves. From the F2 hybrid cultures, the next material was fixed: F2 *B. belki* ♂ × *B. packardi* ♀, 7 ♂♂ (6.4 (5.0–7.2) mm length) and 3 ♀♀ (7.6 (6.8–8.3) mm length); F2 *B. packardi* ♂ × *B. belki* ♀, 12 ♂♂ (5.8 (4.3–7.8) mm length) and 1 ♀ of 7.3 mm length. Eggs were present in the ovisac of females in both cultures of adult F2 hybrids, but their viability was not tested any further.

All fixed male F1 and F2 hybrids present an antenna with a morphology intermediate to their parental species. They can therefore easily be distinguished. The male F1 hybrids from both crosses are characterized by a deformity in the peg-like protuberance (Figs 9 & 12), normally acute at the tip and covered with scales from base to tip in *B. packardi* (Fig. 11). In F1 hybrids, this peg-like protuberance is rounded at the tip. Scales, if present, are only located around the tip. The base of the protuberance presents spinous processes (Figs 9 & 12) corresponding to those characteristic of *B. belki* (Figs 1–8). male F2 hybrids present similar structures to F1 hybrids, but a larger deformity occurred. For instance, in the specimen of Fig. 10, the spinous processes are more numerous than in F1 hybrids and, in the specimen of Fig. 13, the peglike protuberance is lacking and only prominent spinous processes are present. The tip of the distal antennal article in both F1 and F2 hybrids can be similar to one or the other of the parental species. For example, the F1 hybrid specimen of Fig. 9 (*B. belki* ♂ × *B. packardi* ♀) and the F2 hybrid specimen of Fig. 13 (*B. packardi* ♂ × *B. belki* ♀) show a tip similar to that of *B. belki*, because they bear an acute projection and a rounded projection. Instead of this, in the F1 hybrid specimen of Fig. 12 (*B. packardi* ♂ × *B. belki* ♀) and in the F2 hybrid specimen of Fig. 10 (*B. belki* ♂ × *B. packardi* ♀) the tip of the distal article is similar to the semitubular spine found in *B. packardi* (Fig. 11).

This mixture of characteristics from parental species is also evident in F1 and F2 hybrids in a tendency towards a semicircular shape of the distal article (Figs 9, 10, 12 & 13).

In *B. packardi*, the curved part is on the proximal half of the article (Fig. 11), while in *B. belki* the curved part is on the apical half of the article (Fig. 7).

The phenotype of laboratory female hybrids looks morphologically indistinct, and is thus useless for detection of hybrids in the wild. We failed to find any important feature to distinguish the female hybrids from either parental species. However, the external ornamentation of cysts from one female hybrid (Fig. 17), looks different from those of both *B. belki* (Fig. 14) and *B. packardi* (Gilchrist, 1978 & Mura, 1991) (Fig. 20). The ridges of the polygonal areas in the hybrid eggs are thicker at their base and finish rounded, giving them an appearance of cordons. As in the parental species (Gilchrist, loc. cit.) (Figs 16 & 22), the shell of the hybrid cysts is composed of an outer cortex, and inner alveolar layer, and a subcortical space (Fig. 19).

Our results are in accordance with the results of Mayr's (1963) review, that F1 hybrids are generally intermediate between parental species, and that F2 hybrids, when they occur, present an increased variability. The incomplete sexual isolation between morphologically distinct species of the anostracan genus *Streptocephalus* has been discussed and demonstrated before, and even included hybrids among an African and an American species (Wiman, 1979a & 1979b). Also, in *Artemia*, under carefully controlled laboratory conditions, fertile F1 and viable F2 adults have been obtained in reciprocal crosses between *A. monica* Verrill and *A. franciscana* Kellogg (Bowen *et al.*, 1985). Our evidence of interspecific hybridization capacity in *Branchinecta* suggests that the absence of efficient premating mechanisms may be common in Anostraca. This may result because speciation in anostracans has probably followed a primarily geographical speciation pattern. Wiman (1979b) therefore proposed that, in 'closely related species that remain allopatric, efficient premating isolating mechanisms may not develop'. It remains necessary to evaluate a possible genetic incompatibility among hybrids and parental specimens, because this may lead to severe or lethal physiological and morphological disturbances (Mayr, 1963). In our hybrids of *Branchinecta*, this could be in the form of an excessive curvature of the distal article of the male antenna thus limiting successful mating.

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