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NEW GYNANDROMORPH RECORDS FOR *CHIROCEPHALUS DIAPHANUS* (BRANCHIOPODA, ANOSTRACA, CHIROCEPHALIDAE)

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New Gynandromorph Records for *Chirocephalus diaphanus* (Branchiopoda, Anostraca, Chirocephalidae). Rogers, D. C., Cottarelli, V., Marrone, F. — We report and describe new *Chirocephalus diaphanus* Prévost, 1803 gynandromorphs from Tunisia and review the literature of anostracan gynandromorphy and other, possibly associated, somatic aberrations, with comments on their evolutionary significance. Our material has three specimens that are specifically deformed on the left side of the head.
Key words: fairy shrimp, sexual mosaics, somatic aberrations, Tunisia.

Introduction

Gynandromorphy (sexual mosaic) is extremely rare in Branchiopoda (Krumm, 2013) with some 43 specimens reported in the literature (table 1) across three families, four genera and ten species, out of more than 353 described species (Rogers, 2013). These gynandromorphs take one of two basic forms: axial or bilateral. Gissler (1881) described the first anostracan gynandromorph, that being a *Eubranchipus vernalis* (Verrill, 1869), which displayed axial gynandromorphy. Bowen & Hanson (1961) reported the second, an *Artemia franciscana* Kellogg, 1906, which was a bilateral gynandromorph. Although Gissler (in Packard, 1883) reported two possible gynandromorphs from one collection, all other wild collected gynandromorphs were reported as isolated individuals. Bowen et al. (1966) and Sassaman & Fugate (1997) each accumulated and examined the largest numbers of gynandromorphs through their mass culture efforts (although most of Bowen et al.'s material was generated through X-irradiation). Even then, the incidence of gynandromorphy was very low, with Sassaman & Fugate (1997) estimating a gynandromorphic frequency of 0.0020 in *Branchinecta lindahli* Packard, 1883.

Bowen & Hanson (1962) suggested that chromosomal aberrations would explain the cephalic sexual dimorphism, arguing that secondary developmental influences cause the lack of dimorphism of the remaining body; each individual cell is either male or female, and sex hormones would not suppress gonad or primary reproductive organ differentiation for either sex. Following this model, subsequent authors argue for an altered cellular genotype causing altered phenotype (Nourisson & Lenel, 1968; Cottarelli & Mura, 1972; Thiéry, 1983). Sassaman & Fugate (1997) argued that gynandromorph morphology, coupled with their relatively high frequency of occurrence, and sibship aggregation, indicate that they result from epigenetic feminizing factors rather than mutation.

We report and describe an axial gynandromorph of *Chirocephalus diaphanus* Prévost, 1803, from a collection made in a site in northern Tunisia. Interestingly, among the individuals in this site are one male, one female, and one gynandromorph, all of which bear a reduced and deformed left second antenna, plus one additional female, with a second, reduced first antenna projecting from under the left compound eye. Our gynandromorph is axial; the head is male with what appears to be a normally functioning female body.

Table 1. Records and notes on anostracan gynandromorphs. Unless otherwise stated all were spontaneous and not caused by intentional human interference

Taxon	# and Type	Reference	Comments
Artemiidae			
Artemia franciscana Kellogg, 1906	3, bilateral	Bowen & Hanson, 1961; Bowen et al., 1966	From culture. Parents had been bombarded with X-rays. Histology confirms ovaries with eggs and testes with sperm.
Artemia franciscana Kellogg, 1906	1, ??	Bowen et al., 1966	Male with shell glands on testes, one second antenna intermediate between male and female. From X-irradiated egg.
Artemia franciscana Kellogg, 1906	1, subaxial	Bowen et al., 1966	Female, with one male second antenna. From X-irradiated egg.
Artemia franciscana Kellogg, 1906	1, incomplete bilateral	Bowen et al., 1966	Male with right second antenna reduced to lump. Right side testes and gonopod normal, seminal vesicle straight and vas differntia missing. Left testes with sperm, but external genitalia are mix of brood pouch and gonopod. From X-irradiated egg.
Artemia franciscana Kellogg, 1906	1, subaxial	Bowen et al., 1966	Female with one reduced and deformed male second antenna.
Artemia franciscana Kellogg, 1906	1, subaxial	Bowen et al., 1966	Head with second antenna proximally as in male, distally as in female. Body male.
Artemia franciscana Kellogg, 1906	1, incomplete bilateral	Bowen et al., 1966	Left side with male head and hybrid male/female genitalia. Right side female.
Artemia franciscana Kellogg, 1906	1, ??	Bowen et al., 1966	Left side second antennae and genitalia male/female hybrid. Right side second antenna male/female hybrid, plus brood pouch.
Artemia franciscana Kellogg, 1906	1, subaxial	Bowen et al., 1966	Male with one female second antenna.
Artemia franciscana Kellogg, 1906	1, axial	Campos-Ramos et al., 2006	Diploid male head with reduced second antennae, female body.
Artemia sp. "parthenogentic"	1, subaxial	Campos-Ramos et al., 2006	Diploid female with one male second antenna.
Artemia sp. "parthenogentic"	1, incomplete bilateral	Campos-Ramos et al., 2006	Diploid female with one deformed gonopod.
Artemia sp. "parthenogentic"	1, incomplete bilateral	Asem & Sun, 2014	Male, with right side deformed brood pouch, left side normal gonopod.
Chirocephalidae			
Chirocephalus diaphanus Prévost, 1803	1, bilateral	Nourisson & Lenel, 1968	Male left side, female right side.
Chirocephalus diaphanus Prévost, 1803	1, subaxial	Thíery, 1983	Male, with right side female second antenna.
Chirocephalus diaphanus Prévost, 1803	1, axial	This study	Male head, female body, left second antenna reduced and deformed
Chirocephalus ruffoi Cottarelli & Mura, 1984	1, subaxial	Cottarelli & Mura, 1972	Female with one reduced complete male second antenna
Eubranchipus vernalis (Verrill, 1869)	1, subaxial	Dexter, 1953	Female with one male antennal appendage.
Eubranchipus vernalis (Verrill, 1869)	1, bilateral	Gissler, 1881	Male left side, female right side.
Eubranchipus vernalis (Verrill, 1869)	2, subaxial??	Gissler, in Packard, 1883	One male, one female each with left second antenna undeveloped.

Eubranchipus serratus Forbes, 1876	1, subaxial??	Dexter, 1953	Male missing one antennal appendage.
Eubranchipus serratus Forbes, 1876	1, subaxial	Dexter, 1953	Male with one female second antenna.
Eubranchipus serratus Forbes, 1876	1, subaxial	Dexter, 1953	Female with one male antennal appendage.
Eubranchipus serratus Forbes, 1876	1, subaxial	Dexter, 1953	Female with male second antenna, appendage lacking.
Eubranchipus serratus Forbes, 1876	1, subaxial	Dexter, 1953	Female with complete male second antenna.
Branchinectidae			
Branchinecta tolli (Sars, 1897)	1, axial	Vekhov, 1989	Male head, female body
Branchinecta lindahli Packard, 1883	31, axial	Sassaman & Fugate, 1997	From Cultures. Male head, female body
Branchinecta lindahli Packard, 1883	1, incomplete bilateral	Sassaman & Fugate, 1997	Male, with one side deformed brood pouch, other side normal gonopod.
Branchinecta lindahli Packard, 1883	1, incomplete bilateral	Sassaman & Fugate, 1997	Male, with one side deformed brood pouch, other side normal gonopod.
Branchinecta lindahli Packard, 1883	1, axial	Belk, 1978	Male head, female body
Branchinecta packardi Pearse, 1912	1, axial	Sassaman & Fugate, 1997	Female head, male body
Branchinecta mackini Dexter, 1956	1, axial	Sassaman & Fugate, 1997	Male head, female body

Material and methods

The collection locality is a temporary pond close to the village of Teskraia (Gouvernorat de Bizerte, Tunisia), in the valley of the Oued Sejenane. The site has been coded as F232 in Sicilia et al. (2009), Stoch et al. (2016), Marrone et al. (2016, 2020), where other information about the site characteristics and occurring fauna can be retrieved. Crustaceans were collected by dip net on 1 January 2008 and 28 January 2009. The specimens were preserved in situ in 80 % ethyl alcohol. The preservative was replaced after 24 hours. Collected branchiopods were identified according to Cottarelli & Mura (1983), Thiéry (1987), Alonso (1996) and Korn et al. (2013); calanoid copepods were identified according to Kiefer (1978). Occurring Ostracoda were identified by Marrone et al. (2020).

We made direct comparisons between our specimens and other *Chirocephalus* material as well as original descriptions. We prepared a detailed description of the gynandromorph and the other aberrant specimens where they physically deviated from the typical specimens in our collections.

Comparative material

Chirocephalus diaphanus **Algeria**: reared from culture derived from pool at University of Sciences and Technology Houari Boumediene (USTHB), 15 km south of Algiers (36°42'41" N 03°10'54" E); 2005; L. Beladjal; DCR-349. **Italy**: **Rome**: Casal Palocco: 14 December 1966; G. Mura; DCR 346.

Results

Both in January 2008 and 2009, *Chirocephalus diaphanus* was abundant, and it co-occurred with other crustaceans typical of Tunisian temporary water bodies, including the notostracan *Lepidurus lubbocki* Brauer, 1873 and the spinicaudatan *Cyzicus tetracerus* Krynicki, (1830) (see table 2). The only vertebrate predators occurring in the water body were the larvae and adults of the Algerian ribbed newt *Pleurodeles nebulosus* (Guichenot, 1850); conversely, several unidentified invertebrate predators belonging to the Heteroptera, Odonata, and Coleoptera were present.

Overall, 66 individuals of *C. diaphanus* (37 immature specimens, 12 males, 13 females, 1 gynandromorph and 3 aberrant individuals, see below) were collected on 1 January 2008, and 34 individuals (16 males and 18 females) on 28 January 2009. At the sampling dates, water electric conductivity was 270 and 293 microS/cm, respectively, and water temperature 16.2 and 14.6 °C.

Interestingly, in the January 2008 collection are one *C. diaphanus* male, one female, and one gynandromorph, all of which bear a reduced and deformed left second antenna,

Table 2. List of the crustaceans occurring in the temporary pond F232

BRANCHIOPODA	
Anostraca	
Chirocephalus diaphanus Prévost, 1803	
Notostraca	
Lepidurus lubbocki Brauer, 1873	
Spinicaudata	
Cyzicus tetracerus (Krynicki, 1830)	
Anomopoda	
Daphnia (*Ctenodaphnia*) *atkinsoni* Baird, 1859	
Coronatella (*Ephemeralona*) *elegans* (Kurz, 1875)	
Ceriodaphnia smirnovi Alonso, Neretina & Ventura, 2021	
COPEPODA	
Calanoida	
Arctodiaptomus wierzejskii (Richard, 1888)	
Cyclopoida	
Unidentified copepodids	
OSTRACODA	
Podocopa	
Cypridopsis cf. *elongata* (Kaufmann, 1900	
Eucypris virens complex (Jurine, 1820)	
Isocypris beauchampi (Paris, 1920)	
Potamocypris arcuata (Sars, 1903)	

plus one additional female, with a second, reduced first antenna projecting from under the left compound eye. These specimens are described below. The remaining anostracan specimens appear to have normal morphology. Specimens are now deposited in the authors' collections at the University of Kansas (USA).

Gynandromorph

The specimen is an axial gynandromorph, with a seemingly normal female thorax and abdomen (fig. 1, B) and a male head with various morphological deformities (fig. 1, A). The head has deformed male morphology. First antennae as typical. Right second antenna with antennal appendage and apophysis absent; proximal antennomere inerm, articulation with distal antennomere obscure; distal antennomere ~ 0.7x proximal antennomere, proximal branch absent, distal fourth recurved posteriolaterally, apex cleft. Left second antenna with antennal appendage present, posterior lobe less than 0.5x anterior lobe length when uncurled, margined with hamulate, aciculate spines; anterior lobe as typical, but smaller than is typical; proximal antennomere with two anterior subapical papillae, otherwise antennomere and apophysis as typical; distal antennomere ~ 0.9x proximal antennomere, proximal branch fused with antennomere, minute spiniform projection on posteriobasal side; distal antennomere with longitudinal medial tumidity just distad of proximal bend; antennomere with a second medial tumidity in distal fourth just before apex; apex rounded, bent at 90° anteriorly. Compound eyes, labrum, and mouthparts as typical.

Thorax generally as typical for female (fig. 1, B). Eggs subspherical, with tertiary envelope not fully formed, likely due to timing of preservation and not any abnormality. Diameter approximately 240 μm. Apparently normal in all respects. Cercopods were damaged as if by a predator.

Aberrant female 1

This female bears a second, reduced first antenna on the right side of the head (fig. 1, D). This additional first antenna originates on the head, below the eyestalk, and is separated from the original first antenna by a distance equal to three times its basal width. The accessory first antenna is approximately 0.3x the length of the natural first antenna. The remainder of the specimen appears to be normal morphologically.

Aberrant female 2

This female appears normal in all respects except for the second antennae, which are deformed (fig. 1, E). A normal female second antenna is presented in figure 1, D. The right antenna is only deformed apically, with the last 20 % of the conical structure constricted basally, cylindrical for most of its length, and the apex slightly hooked posteriorly. The structure is of a generally normal length.

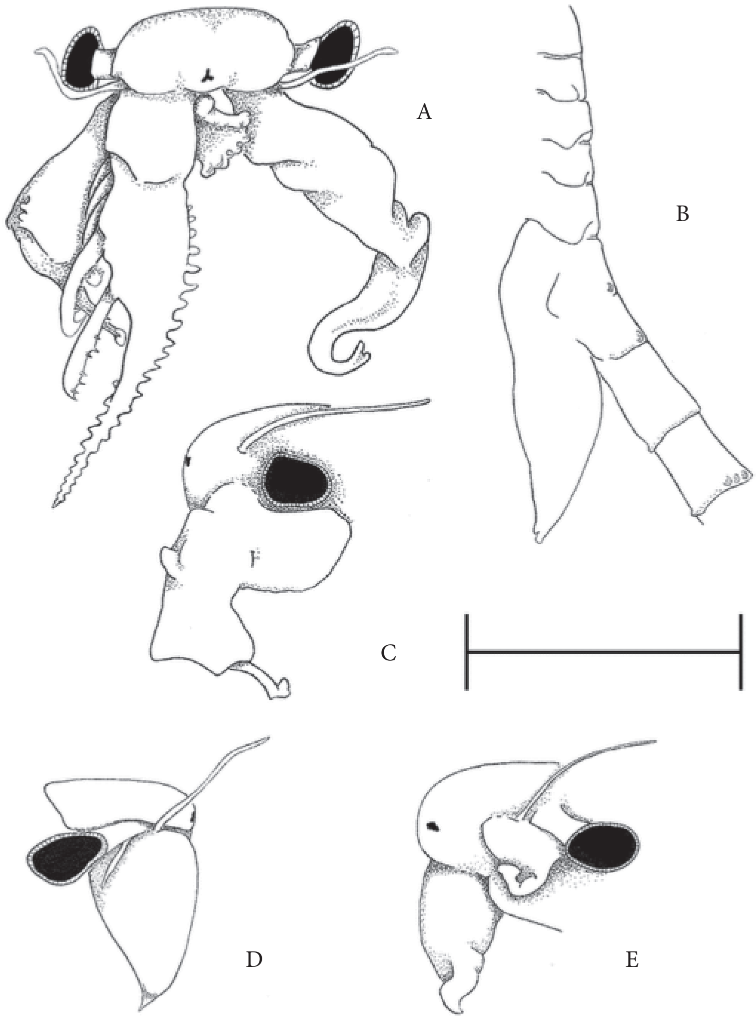

Fig. 1. *Chirocephalus diaphanus* Prévost, 1803: A — gynandromorph head, anterior view; B — gynandromorph brood pouch and abdomen, left lateral view; C — male head with deformed second antennae, left lateral view (right second antenna not depicted); D — female head with aberrant extra second antenna, right lateral view; E — female head with deformed second antennae, left oblique anteriolateral view. Scale bar: A, C = 4.5 mm; B = 4 mm. D, E = 5 mm.

The left second antenna appears atrophied and is approximately 0.24x the length of the right second antenna. The distal portion is greatly reduced, curling anteriorly back to the antenna base, with the apex expanded and truncated. The odd expanded apex is somewhat suggestive of the apex of the male second antenna (fig. 1, A, right second antenna), and may be an indication of at least partial gynandromorphy.

Aberrant male

One male has an aberrant left second antenna (fig. 1, C), but otherwise appears normal. The left second antenna proximal antennomere length is 0.5x the right proximal antennomere and is deeply concave on the posterior side. The antennal appendage is reduced to a small, angular projection in the middle of the anterior face. The distal antennomere is reduced to approximately 0.2x the length of the right distal antennomere and is directed obliquely posteriorly. The distal antennomere apex is bent posteriorly nearly 180° and is distally rounded.

Discussion

Anostracan gynandromorphs are reported as either axial (or subaxial) or bilateral. Axial gynandromorphs have the head one gender and the body the other gender. Subaxial specimens have only one half of the head or the genitalia with the morphology the opposite gender of the remaining body.

Bilateral gynandromorphs are highly variable, with one of three conditions: 1) only one side of the head (and corresponding antennae) male, the other side female; 2) with one half the genitalia male, the other half and the head female, and; 3) with one entire side of the body male and the other female. Bilateral gynandromorphs are much rarer, comprising only six (14 %) of the 44 specimens to date.

Sassaman & Fugate (1997) developed an empirical model to explain axial gynandromorphy in the anostracan genus *Branchinecta*. Sassaman & Fugate (1997) argued that since during development the cellular determination of the thoracic segments and their appendages occurs after the anterior cephalic appendages, the sequential expression of gender on successive limbs of the adult reflects the temporal history of the developing larva. Thus, some individuals of affected clutches undergo normal development, while others are phenotypically transformed from their genotypic sex to the alternate condition, and the very rare gynandromorphs are where transformation occurred after cellular determination of cephalic segmentation (Sassaman & Fugate, 1997). As our gynandromorph specimen is axial, this model would seem to be the best explanation for its origin.

Whatever the cause, the effect seems to be uniform in our material, primarily causing the left second antenna to be reduced and deformed in one male, one female and one gynander. It remains to be seen if the cause of the deformity is also the cause of the gynandromorphy. Regardless, the fact that these three, plus the one female with an extra second antenna, were all collected together, also demonstrates a sibship aggregation that shared in the original cause. Additional collections from the same site coupled with an assessment of the health and quality of the habitat as well as the surrounding land watershed, may yield more insights.

Interestingly enough, among the four reports of *Chirocephalus* gynandromorphs known to date, three pertain Maghrebian populations of *Chirocephalus diaphanus* s. l. (i. e., Nourisson & Lenel, 1968; Thiéry, 1983; Present work), and the fourth one to *Chirocephalus ruffoi* Cottarelli & Mura, 1984 (Cottarelli & Mura, 1972, sub *Chirocephalus diaphanus*) from southern Italy, thus suggesting a possible latitudinal gradient in the incidence of gynandromorphism in this genus. This might be due to environmental factors exerting some epigenetic effects during the development of these anostracans, or it might be rather due to a different predisposition of different *Chirocephalus* taxa to gynandromorphism. In fact, the taxonomy of the *diaphanus*-group of the genus *Chirocephalus* is to date unsettled (cf. Reniers et al., 2013; Boumendjel et al., 2018; Marrone et al., 2019), and it is possible that the populations currently ascribed to *C. diaphanus* in the circum-Mediterranean area might belong to several different species. An integrative approach to the revision of this entire genus is urgently needed (Rogers, 2005, 2006, 2013; Rogers & Soufi, 2013).

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