Research Journal of Agricultural Science, 58 (3), 2026; ISSN: 2668-926X;

http://doi.org/10.59463/RJAS.2026.3.36

TRIOPS CANCRIFORMIS: A "LIVING FOSSIL" AND ITS REMARKABLE ENVIRONMENTAL ADAPTATIONS

Alexandru MURARU[1], Ștefania-Eugenia BĂLĂȘOIU[1] (ORCID: 0009-0002-8265-4026), Silvia PRUNAR[1], Florin PRUNAR[1]

[1]University of Life Sciences "King Mihai I" from Timișoara, Faculty of Agriculture, Biology

Corresponding author: muraru.alexandru.fa@usvt.ro

Abstract. *Triops cancriformis (Bosc, 1801) is a freshwater tadpole shrimp (Notostraca) often described as a "living fossil" because of its highly conserved body plan. It inhabits temporary ponds and other water bodies that dry out periodically. The aim of this paper was to document the activation of its resistant cysts, its early development and its tolerance to a change of water source under controlled laboratory conditions, and to place these observations in the context of current knowledge on the evolutionary age, biology and conservation of the species. Cysts were kept dry for three weeks and then hydrated with rainwater in transparent micro-aquaria containing fine river sand and oak (Quercus robur) leaves, under continuous LED lighting and a water temperature of 20–25 °C. Hatching of metanauplii followed hydration, and the larvae grew rapidly into adults that foraged on the substrate with their phyllopodous appendages. New cysts were deposited near the water line along the aquarium walls, consistent with reproduction in captivity, although egg viability was not tested. In a second vessel, mortality followed the addition of a small volume of dechlorinated tap water; because water chemistry was not measured, this effect could not be assigned to a specific factor. A field record from a temporary pond crossed by heavy machinery in Gorj County, Romania, is also reported. Recent phylogenetic and palaeontological studies indicate that Triassic fossils once assigned to T. cancriformis represent other taxa, so the "living fossil" label should be used with caution. Protecting temporary aquatic habitats remains essential for the persistence of this species.*

Keywords: *Triops cancriformis; living fossil; resting eggs; hatching; temporary ponds; conservation.*

INTRODUCTION

The order Notostraca, the tadpole shrimps, is a small group of freshwater branchiopod crustaceans with two living genera, *Triops* and *Lepidurus* (LONGHURST, 1955; KORN et al., 2013). Large branchiopods are typical inhabitants of temporary waters on all continents (BRENDONCK et al., 2008). *Triops cancriformis* (BOSC, 1801), the European tadpole shrimp, is native to Europe and has also been reported from south-western Asia (ZIEROLD et al., 2007; GOLZARI et al., 2009; SELLERS et al., 2017).

Notostracans are widely regarded as "living fossils" because their fossil record extends back to the Devonian and their morphology has remained highly conserved (MATHERS et al., 2013). For *T. cancriformis* the label was long linked to Triassic fossils attributed to the same species, which led to claims that it is the oldest living animal species. This view has been challenged. Molecular dating places the divergence of *T. cancriformis* at about 24–50 million years ago and led to the Upper Triassic specimens being assigned to a separate species, *Triops minor* (KORN et al., 2013), while a restudy of the Triassic material from eastern France concluded that it belongs to a notostracan genus that cannot be placed in the *Triops*idae (GEYER et al., 2024). Divergence dating of the whole order also suggests at least two global radiations, one of them recent, despite the morphological stasis (VANSCHOENWINKEL et al., 2012; MATHERS et al., 2013). The genera *Triops* and *Lepidurus* themselves date back to the Triassic–Jurassic (KORN et

al., 2013), so the species is best seen as a member of an ancient and morphologically conservative lineage rather than as an unchanged Triassic survivor.

The species inhabits temporary pools, vernal ponds and flooded fields that undergo periodic drying (ZAFFAGNINI & TRENTINi, 1980; PETROV & CVETKOVIĆ, 1996). In the Banat plain, PETROV & CVETKOVIĆ (1996) found that hatching took place in March– April at 7–10 °C, that sexual maturity was reached after about one month and that the life span was about two months. Survival of the dry phase is ensured by resistant cysts (resting eggs) that enter diapause, withstand desiccation and freezing, and hatch when conditions become favorable (TAKAHASHI, 1977; BRENDONCK, 1996; ROGACKI & BRYSIEWICZ, 2021). Not all cysts hatch at once: a fraction remains dormant (TAKAHASHI, 1977; DEVÁNOVÁ et al., 2022), a bet-hedging strategy that spreads the risk across successive floods (SELLERS et al., 2017). Reproductive modes also vary geographically: southern populations are gonochoric, with similar numbers of males and females, whereas northern populations are mostly selfing hermaphrodites, and androdioecious populations also occur (ZIEROLD et al., 2007; MATHERS et al., 2015; MACHADO et al., 2017; SELLERS et al., 2017).

Because it depends on temporary water bodies, *T. cancriformis* is sensitive to habitat loss and is reported as threatened in several European countries (SELLERS et al., 2017).

Romania has one of the highest numbers of large branchiopod species in Europe (DEMETER & STOICESCU, 2008), but a national survey noted that none of them was legally protected and that most habitats were located in open agricultural landscape (DEMETER & HARTEL, 2007). Large branchiopods have been proposed as flagship taxa for the conservation of temporary ponds (DEMETER & STOICESCU, 2008).

Taxonomy and external morphology

Triops cancriformis belongs to the class Branchiopoda, order Notostraca and family *Triops*idae (LONGHURST, 1955). The body is dorsoventrally flattened and covered anteriorly by a broad, shield-like carapace, followed by a long, segmented abdomen that ends in a telson with two caudal filaments (Fig. 1). On the ventral side, numerous pairs of leaf-like (phyllopodous) thoracic appendages work together in locomotion, filter feeding and respiration, while an anterior food groove carries particles towards the mouth (Fig. 2). This arrangement allows the animal to swim and forage close to the sediment, a benthic habit with ecological consequences discussed below (ROGACKI & BRYSIEWICZ, 2021; DEVÁNOVÁ et al., 2022).



Figure 1. Adult Triops cancriformis on sandy substrate with oak leaves.



Figure 2. Ventral view of an adult showing the phyllopodous appendages.

The aim of this paper is to describe, under controlled laboratory conditions, the activation of cysts, the early development and the adult morphology and behavior of *T. cancriformis*, to record its response to a change of water source, and to report a field locality in Romania, discussing the results in the light of current knowledge on the biology, evolutionary history and conservation of the species.

MATERIAL AND METHODS

Experimental setup and environmental parameters

The experiments were carried out under controlled laboratory conditions in two transparent micro-aquaria (Vessel A and Vessel B; Fig. 3). Each vessel contained a standardized benthic substrate of fine, washed river sand (0.5–1.0 mm grain size) meant to resemble natural pond sediments. The water was rainwater collected in clean glass containers to avoid chemical contamination. Illumination was provided by a low-energy LED source, switched on continuously (24 h/day) during incubation and hatching; light is a recognized hatching cue in notostracans (Takahashi, 1977; Kuller & Gasith, 1996) and also supports phototrophic micro-organisms. Water temperature was checked daily with a calibrated thermometer and kept between 20 and 25 °C (maximum recorded value 25 °C). Dried oak (*Quercus robur*) leaves were added to release tannins and to favor the development of micro-organisms (infusoria), which served as the initial food source.

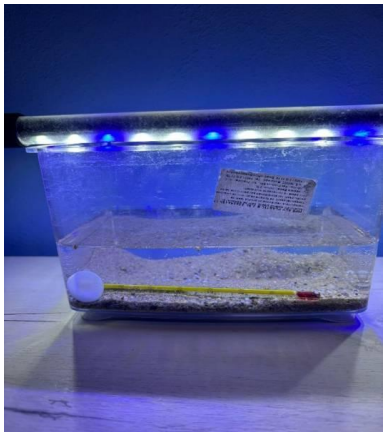


Figure 3. Laboratory micro-aquarium with sand, thermometer and LED lighting

Hydrological cycle simulation and cyst activation

To trigger hatching, the resistant cysts were first subjected to a simulated dry phase. They were stored completely desiccated, at room temperature and without contact with ambient moisture, for approximately three weeks (21 days), which reproduces the drought–flooding alternation of temporary pools; desiccation has been reported to promote subsequent hatching in *Triops* (TAKAHASHI, 1977). Inundation was started by adding rainwater directly onto the dried substrate containing the cysts. Development was followed by direct observation and documented photographically. All photographs included in this study were taken by Alexandru Muraru.

Comparative water quality trial (Vessel A vs. Vessel B)

Two vessels were used to observe development and mortality under different water conditions (Table 1). Vessel A (control) was maintained exclusively with rainwater under the

standardized conditions described above. Vessel B (treatment) followed identical initial rearing conditions; after rapid initial growth, a minor volume fraction of dechlorinated tap water was introduced to observe short-term tolerance. Mortality in Vessel B after the water substitution was recorded. No chemical assays were performed, so a causal attribution to tap-water parameters is not possible; sudden osmotic change, accumulated nitrogenous waste and small temperature fluctuations were considered potential confounding factors that require controlled multifactorial testing. The study is descriptive: observations were qualitative, the vessels were not replicated and no statistical tests were applied.

Table 1

Experimental design of the two vessels

Parameter	Vessel A	Vessel B
Substrate	River sand, 0.5–1.0 mm	Same as A
Water	Rainwater only	Rainwater; small addition of dechlorinated tap water
Lighting	Continuous LED, 24 h/day	Same as A
Temperature	20–25 °C	Same as A
Organic material	Dried Quercus robur leaves	Same as A
Cyst treatment	21 days dry, then rainwater	Same as A

Field observation

The species was also recorded at Dănești Commune, Gorj County, Romania, at the edge of a deciduous forest dominated by oak, in a temporary pond crossed by heavy machinery, where the water was rather muddy. Other small invertebrates were present in the same pond. The record was uploaded by the authors to the iNaturalist platform, where the exact location is available.

RESULTS AND DISCUSSION

Cyst activation and early development

Hydration of the dried substrate with rainwater was followed by hatching in Vessel A. The newly hatched larvae (metanauplii) swam actively, often close to the air– water interface (Fig. 4), and high-magnification observation of a newly hatched larva showed the rapid onset of growth that follows cyst activation (Fig. 5). Hatching occurred at 20–25 °C under continuous light after a 21-day dry phase, that is, under a combination of recognized hatching cues: desiccation followed by rehydration, light and warm water (TAKAHASHI, 1977; BRENDONCK, 1996; KULLER & GASITH, 1996). The temperature used here lies at the warm end of the values reported for natural populations. *T. cancriformis* is more thermophilic than *Lepidurus*, with an optimum for hatching 8–12 °C higher (KULLER & GASITH, 1996), yet in the Banat plain hatching in the field took place at 7–10 °C (PETROV & CVETKOVIĆ, 1996), and eggs of the Arctic *Lepidurus arcticus* hatched at 5 and 10 °C but not at 15 or 25 °C (PASQUALI et al., 2019). Thermal requirements therefore differ among populations and species, and our laboratory range should be regarded as permissive rather than obligatory for the material studied.

Hatching is rarely synchronous. In other *Triops* species it is heterogeneous and many eggs remain dormant (TAKAHASHi, 1977), and the presence of adults can increase the proportion of eggs that hatch (DEVÁNOVÁ et al., 2022). Since hatchlings were not counted, hatching rate and timing could not be quantified in this study. Rapid growth, in contrast, is consistent with the short life cycle of the species: maturity within about one month in the field (PETROV & CVETKOVIĆ, 1996) and the onset of oviposition 10 days after submergence in two other *Triops* species (TAKAHASHI, 1977).



Figure 4. Early developmental stages in Vessel A.



Figure 5. Enlarged view of newly hatched larvae; stage identification requires confirmation.

Adult morphology, behavior and reproduction

Adults kept on fine sand with submerged oak leaves foraged on the substrate (Fig. 1), and in the culture many individuals swam and foraged near the bottom at the same time (Fig. 6). The ventral view (Fig. 2) shows the numerous phyllopodous appendages that, in the living animal, beat together for locomotion, filter feeding and gas exchange. This anatomy is linked to a benthic way of life in which the sediment is constantly disturbed, and tadpole shrimps are regarded as keystone species of temporary waters (ROGACKI & BRYSIEWICZ, 2021). Adults are mainly benthic feeders and may prey on resting eggs (DEVÁNOVÁ et al., 2022), so dense cultures like ours could be used to test adult–cyst interactions.

Experimental evidence supports a functional role beyond substrate foraging. WATERKEYN et al. (2016) used 400-L mesocosms with densities of 0, 5, 25 and 100 individuals m^{-2}. After 13 weeks, the two highest density treatments altered community composition and water quality through bioturbation, supporting the interpretation of *T. cancriformis* as an ecosystem engineer. These literature results provide ecological context, but no equivalent effects were measured in the present cultures.

Cysts were deposited near the water line along the inner walls of the aquarium (Fig. 7), consistent with reproduction in captivity; however, viability of these newly produced eggs was not tested. Resting eggs of notostracans are reported to float and to be exposed to light and warm surface water, which favors their development (KULLER & GASITH, 1996), so the position of the cysts at the water line may not be accidental, although this was not tested. Cyst morphology has been described for Polish populations of this and other large branchiopods (CZYŻ et al., 2016) and could be used to compare cysts from the aquarium with field material.

The sex ratio of the culture was not determined. This matters because the reproductive mode ranges from gonochoric to selfing hermaphroditic or androdioecious across Europe (ZIEROLD et al., 2007; MATHERS et al., 2015; MACHADO et al., 2017), and bisexual populations with 15–40 % males were described in the Banat plain (PETROV & CVETKOVIĆ, 1996). Sexing adults would provide an initial description of the sex ratio; distinguishing females from self-fertilising hermaphrodites would require additional reproductive or genetic evidence.



Figure 6. Dense laboratory culture of Triops cancriformis.



Figure 7. Putative resting eggs accumulated near the water line.

Response to a change of water source

Vessel A, kept exclusively with rainwater, was the reference for normal development. In Vessel B, mortality was recorded after a minor fraction of dechlorinated tap water was added to the rapidly growing animals. Because pH, conductivity, hardness, residual disinfectants, nitrogenous wastes and temperature were not measured, the mortality cannot be attributed to tap water as such. Several explanations remain plausible and are not mutually exclusive: a sudden osmotic or ionic shock when soft rainwater was mixed with more mineralized tap water; residual disinfectant, since dechlorination does not necessarily remove all such compounds; a pH shift, because survival of *Triops longicaudatus* larvae depends strongly on pH (HAMASAKI & OHBAYASHI, 2000); accumulation of nitrogenous waste in a densely stocked vessel; or temperature changes during water replacement.

Natural populations can tolerate quite different water chemistry: ponds with *T. cancriformis* in Iran had conductivities of 450–860 µS cm^{-1} and a pH of 7.5–8.5 (GOLZARI et al., 2009). This suggests that mineralized water is not necessarily lethal and that the speed of change may matter more than the final values. As Vessel B was not replicated and no measurements were taken, this remains a hypothesis. A proper test would use replicated vessels, gradual acclimation, a graded series of tap water– rainwater mixtures and measurements of the parameters listed above.

Field record and habitat

The population at Dănești occupied a muddy temporary pond crossed by heavy machinery, at the edge of an oak-dominated forest. Similar disturbed or human- made habitats are known elsewhere: in Portugal the species was first found in rice paddies and was later seen mainly in flooded tracks left by trucks and heavy machinery (MACHADO et al., 2017), and in Poland it occurs in extensive carp ponds (CUKIER et al., 2023). Such sites show that *T. cancriformis* can use small, disturbed water bodies, but they are also vulnerable, because ruts and tracks are ephemeral and may be levelled or filled. Machinery and farm animals can also carry sediment with cysts between water bodies, a plausible mechanism for short-range dispersal

(ADAMS et al., 2014). The oak leaf litter used in our cultures resembles the oak forest edge of the Dănești pond, but our data do not allow any causal link between leaf litter and the occurrence of the species.

The "living fossil" concept

Our observations of a broad carapace, serial phyllopods and fast development in ephemeral water illustrate why notostracans are called living fossils, but the label needs qualification. The conserved body plan hides considerable genetic diversification: *Triops* appeared polyphyletic in mitochondrial analyses and *T. cancriformis* differs strongly from its congeners (MANTOVANI et al., 2004), the order underwent at least two global radiations, one of them recent (MATHERS et al., 2013), and *T. cancriformis* itself diverged only about 24–50 million years ago (KORN et al., 2013). Triassic specimens formerly assigned to the species have been reassigned to other taxa (KORN et al., 2013; GEYER et al., 2024). We therefore use the term in quotation marks, for a morphologically conservative lineage of ancient origin rather than an unchanged species.

Conservation implications and limitations

Temporary ponds are lost through drainage, land-use change and agricultural intensification (DEMETER & HARTEL, 2007; SELLERS et al., 2017). If a pond dries before the animals reproduce, recruitment fails; however, because the cyst bank survives drought, a site can become productive again when flooding resumes, so egg banks, and not only visible adults, must be assessed. Net sampling is poorly suited to a species that is active only briefly, and methods based on sugar flotation of eggs and DNA barcoding of isolated eggs detected viable egg banks more effectively than conventional approaches (SELLERS et al., 2017). The effects of agrochemicals must be assessed substance by substance: chronic exposure to chlortetracycline at ecologically relevant concentrations had no apparent effect on *Triops* spp. in one experiment (O'NEILL & STREIT, 2024), which cannot be generalized to pesticides or fertilizers. Because hatching depends on temperature and light (KULLER & GASITH, 1996; PASQUALI et al., 2019), climate change may alter the timing of hatching relative to the length of flooding. Protection of the water bodies themselves, maintenance of their hydrological regime, reduction of agricultural contamination and periodic monitoring of egg banks are therefore essential; cyst-bank storage and translocation have been suggested for threatened British populations (ADAMS et al., 2014) but require case-by-case evaluation. Recording localities such as Dănești is a first step, since further regional data are needed for national assessments (DEMETER & STOICESCU, 2008), as shown by regional studies in western Poland (GOŁDYN et al., 2012).

For monitoring, absence of adults or failure to obtain hatchlings should not automatically be interpreted as local extinction. SELLERS et al. (2017) combined sugar flotation with species-specific mitochondrial DNA assays and detected viable egg banks in six ponds at Caerlaverock. Their use of different DNA fragment lengths helped distinguish viable from degraded eggs. This supports combining repeated field observations with sediment-based monitoring at the Dănești locality rather than relying on a single visit.

The main limitations of this study are the absence of replication, the lack of quantitative data on hatching, survival and growth, and the lack of water chemistry measurements. The results should therefore be read as descriptive observations that suggest hypotheses for experimental testing, not as evidence of causal effects.

CONCLUSIONS

Under the conditions tested, hydration of cysts after a 21-day dry phase, with rainwater, continuous light and a water temperature of 20–25 °C, led to hatching and rapid growth, and new putative cysts were observed near the water line, consistent with reproduction; their viability requires confirmation.

Adults showed benthic foraging behavior and a ventral phyllopodous anatomy that serves locomotion, filter feeding and respiration at the same time.

Mortality in Vessel B after the addition of dechlorinated tap water was recorded, but without chemical data it cannot be attributed to tap water itself; replicated experiments with measured water parameters and gradual acclimation are needed.

The record from Dănești adds a locality from a disturbed temporary pond in Romania and supports the need to protect temporary water bodies. The expression "living fossil" should be applied to *T. cancriformis* with caution, because Triassic fossils once assigned to it belong to other taxa.

Future work should quantify hatching and survival, determine the sex ratio and reproductive mode, confirm the lineage with molecular markers and test experimentally the effect of water chemistry and agrochemicals.

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