

New challenges in anostracan research: old issues, new perspectives and hot topics

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Abstract We present a summary of responses to our call among scientists working on Anostraca to commemorate the late Professor Graziella Mura, a pioneer of modern studies on this group of animals. Colleagues from all over the world promptly answered and contributed their works among which we selected the fourteen papers published in the *Hydrobiologia* Special Volume “New Challenges in anostracan research: a tribute to Graziella Mura”. Although Anostraca are widespread globally, they are among the least known taxonomic groups. Although some biogeographical data are available for some species and higher taxa, we are still far from a clear understanding of the phylogeny, ecology and biogeography of the order. The papers collected in this Special Volume are

therefore intended to represent a step ahead to solve phylogenetic and ecological issues relative to this charming group of crustaceans.

Keywords Anostraca · Large branchiopods · Molecular taxonomy · Biogeography · Life strategies

Introduction

Anostracans, the only living representatives of the superorder Sarsostraca, belong to the most divergent taxon in the pancrustacean class Branchiopoda. Commonly known as “brine shrimps” and “fairy shrimps”, anostracans are characterized by the lack of a carapace, and the presence of stalked eyes and 11 pairs (rarely 10, 17 or 19) of scarcely differentiated thoracic appendages, the “thoracopods”. The order

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Anostraca is known from fossil records dating back to the Paleozoic Era (Gueriau et al., 2016), and has maintained its body plan, being thus a prime example of morphological conservatism. Brine and fairy shrimps are distributed worldwide but are typically limited to fishless, seasonal water bodies, where they are considered a flagship taxon. However, some anostracan taxa are also able to colonize other “extreme” habitats as high-altitude permanent ponds or hypersaline continental water bodies.

Due to their peculiar aspect and natural history, and their charming swimming behaviour, anostracans have always been objects of attention to both Natural History researchers and amateurs, and are often commercially sold as “sea monkeys” or “prehistoric pets”. Moreover, both salt and freshwater species are economically important in the fields of aquaculture and ecotoxicology (Brendonck et al., 2008), and are used for human consumption in the Americas, Africa and Asia (Dumont & Negrea, 2002).

The earliest drawings and descriptions of anostracans date back to the eighteenth century, when Petiver (1702–1709), Schlosser (in: Gautier, 1756) and Schaeffer (1766) provided descriptions and drawings of what we currently call *Chirocephalus diaphanus* (Prévost, 1803), *Artemia salina* (Linnaeus, 1758) and *Branchipus schaefferi* Fischer, 1834 (see also Rogers, 2013, for a review of older documents possibly dealing with Anostraca). Later on, Packard (1883), Daday de Deés (1910a, b) and Linder (1941) realized the first modern synopses of the world anostracan fauna, followed by checklists and comprehensive reviews on the anostracan genera and species realized by Belk & Brtek (1995, 1997), Brtek & Mura (2000) and Dumont & Negrea (2002). Since then, the discovery and description of several new taxa, and revisions of some existing ones, brought to us an updated checklist of more than 350 extant species in 10 families (Rogers, 2013), but more work is needed. In fact, as stressed by Brendonck et al. (2008), Anostraca is among the least known taxonomic groups in inland waters and, although some data are available on large-scale distributions of species and higher taxa (e.g., Brtek & Thiéry, 1995; Brtek & Mura, 2000; Brendonck et al., 2008; Stoch et al., 2016), we are still far from a clear understanding of the phylogeny, ecology and biogeography of the order, probably due to the fact that they mainly inhabit temporary ponds, a poorly studied ecosystems (e.g., Bagella et al., 2016).

This paper summarizes the outcomes of a call we launched about 1 year ago among scientists working on Anostraca to commemorate Professor Graziella Mura, a pioneer of modern studies on this group of animals, who had recently passed away (Marrone et al., 2017b). Several colleagues from around the world answered the call, and we are proud to present this Hydrobiologia Special Volume “New Challenges in Anostracan Research: A Tribute to Graziella Mura”. This volume collects their contributions and, we hope, represents a step forward to solve phylogenetic and ecological issues relative to fairy and brine shrimps.

Systematics and phylogeny

Sound taxonomic identification is the fundamental premise for any ecological, biogeographical and phylogenetic analysis. Traditionally, anostracan systematics and phylogeny was mostly based on the morphology of male second antennae, and on some other autoapomorphic characters possibly present. However, the description and analysis of morphological autoapomorphies are more useful for identification purposes than phylogenetic inferences, which remain poorly resolved or questionable for several taxa. Attempts were also made using resting egg morphology in anostracan systematics, as well as to isolate monophyletic species-groups within species-rich genera (e.g., Mura, 1991, 1992; Brendonck & Coomans, 1994a, b; Mura et al., 2002), however convergent morphologies in distantly related taxa sometimes frustrated these attempts (Mura, 2001). From the beginning of the twenty-first century onwards, morphological analyses began to be coupled with molecular phylogenies. Such integrative approaches often revealed previously obscured relationships among genera and families (Remigio & Hebert, 2000; Weekers et al., 2002) and at the intra-generic or intraspecific levels (e.g., Ketmaier et al., 2003; Reniers et al., 2013; Gandolfi et al., 2015). This is also demonstrated in two contributions in this volume: Cottarelli et al. (2017), using mtDNA sequences and morphology to define a new *Chirocephalus* species collected in Turkey, questions the validity of the traditionally accepted species-groups within the genus, and; Kappas et al. (2017) rejects the subspecific differentiation of eastern versus western *Streptocephalus torvicornis* (Waga, 1842) populations

based on a morphological re-analysis of both adults and eggs and on mtDNA sequences.

In fact, as stressed by Milicic et al. (2017), the comparison between the morphological and molecular diversity patterns in anostracans encompasses a wide range of cases, from a high genetic diversity between morphologically identical populations (which is suggestive of phenomena of cryptic or incipient speciation, e.g., *Branchipus* spp. in Gandolfi et al., 2015; *Branchinecta ferox* (Milne-Edwards, 1840) in Rodríguez-Flores et al., 2017, but see also Aguilar et al., 2017 for a plea for caution when attributing species rank to divergent clades) to a pronounced morphological diversity not paralleled by an analogous molecular diversification (which is suggestive of phenomena of morphological plasticity, e.g., Zofkova & Timms, 2009).

The decoupling of the morphology- and molecular-based phylogenies is rather puzzling and sometimes disappointing, but it should stimulate the reassessment of the phylogenetic significance of some traditionally used characters.

Moreover, the suitability of mitochondrial and nuclear markers with different evolutionary rates at different evolutionary scales needs to be critically assessed. In fact, an increasing body of evidence points out the large risks linked with the acritical use of “standard” molecular markers, as the “barcode fragment” of the cytochrome C oxidase subunit I, for investigating the molecular diversity patterns at different levels. The widespread presence of heteroplasmy, pseudogenes and saturation phenomena might, in fact, prevent a sound picture of the phylogeny of the studied taxa (Gandolfi et al., 2015; Lindholm et al., 2016) or might prevent the use of some markers for investigating the molecular diversity patterns (Kappas et al., 2017). It should be remembered that, as pointed out by Fontaneto et al. (2015), Aguilar et al. (2017) and Rodríguez-Flores et al. (2017), DNA taxonomy just provides “primary species hypotheses”, which should desirably be complemented by other evidence based on morphology, distribution, and ecology in order to be validated.

Ecology, biogeography and conservation

Since the seminal paper “Homage to Santa Rosalia” was published almost 60 years ago, understanding how environmental factors influence species

distribution patterns is a central ecological research theme (Hutchinson, 1959; Naselli-Flores & Rossetti, 2010). Although it is widely accepted that different spatial and temporal scales govern species distribution and their coexistence in natural environments (e.g., Stoch et al., 2016; Marrone et al., 2017a), the discussion about biogeographical patterns in organisms subjected to passive dispersal is still open. As regards anostracans, dispersal is more clearly understood regarding mechanisms (reviewed in Rogers, 2014), although dispersal patterns are more stochastic (Daniels, et al., 2004; Rogers, 2015). In this volume, Rodríguez-Flores et al. (2017) show the identity of Spanish and Hungarian *Branchinecta orientalis* (G. O. Sars, 1901) populations, which is likely to be ascribed to the recent colonization of the Iberian Peninsula by long-range-dispersed *B. orientalis* propagules originating from central Europe; Kappas et al. (2017), by investigating the phylogeography of *Streptocephalus torvicornis* across its circum-Mediterranean and Eurasian distribution, found patterns of extensive genetic and morphological homogeneity pointing to unhindered gene flow and widespread connectivity among populations; Aguilar et al. (2017) observed quite a high degree of haplotype endemism in *Branchinecta lindhali* Packard, 1883 coupled with little geographic structure for the shared haplotypes, which they attribute to the stochastic nature of dispersal and colonization for this species.

One of the explanations offered by Kappas et al. (2017) to interpret the peculiar pattern observed in *S. torvicornis* resides in the outbreeding vigour opportunity given to secondary immigrants in an already colonized environment, which may increase their frequency and chances of a permanent establishment. This hypothesis is partially contradicted by the results shown by Thanakiattiwibun et al. (2017) who, in a lab experiment, found no differences in the reproductive success of inbreeding and crossbreeding populations of *Streptocephalus sirindhornae* Sanoamuang, Murugan, Weekers, & Dumont, 2000.

Anostracans are widespread in temporary water bodies in the temperate, sub-tropical and tropical zones of the world. These aquatic ecosystems, being scattered on the dryland as islands in the ocean, show several “insular” spatial features. Moreover, temporary water bodies add a further temporal dimension to their insularity, by alternating flooded and dry phases (Incagnone et al., 2015). Both Monopolization

Hypothesis and the Theory of Island Biogeography offer conceptual tools to create a theoretical framework to investigate species distribution patterns (for more details, see: De Meester et al., 2002; Rogers, 2015).

Several papers in the present volume analysed the distribution patterns of Anostraca and other “large branchiopod” (Notostraca and Spinicaudata) species at various spatial scales and contributed to define the importance of landscape metrics for all the issues related to biodiversity analysis and conservation. In particular, Sala et al. (2017) gathered historical and recent data on species distribution and evaluated the effect of several landscape characteristics (including anthropization) on large branchiopods’ distribution in the Iberian Peninsula. These authors provide details on (i) the spatial scale at which landscape use can influence the presence of these organisms in the region, and (ii) the impacts caused by the extent of anthropic land use. As also shown by García-de-Lomas et al. (2017), traditional, non-intensive agricultural practices are still compatible with the existence of highly biodiverse temporary ponds. Conversely, land-use changes and water demands impact these environments as well as their associated biological communities and significantly contribute to extinction risks.

Anthropogenic pressure effects may explain the relatively low species numbers recorded by Padhye et al. (2017) in a large-scale study on Anostraca distribution on the Indian Subcontinent. Although the study area shows a very broad range of physical variables, such as altitude, temperature and precipitation, only 19 species (40% of which are endemic) were recorded after an extensive literature survey. An additional reason for such rather low species diversity pointed out by the authors could be the lack of both surveys and specialists in several parts of this quite large area.

Kneitel et al. (2017) discuss that many large branchiopods exhibit high endemism levels and many are threatened or endangered; therefore there is an urgent need to better understand how ecological factors related to habitat periodicity influence life strategies. These authors examined the effects of hydroperiod stability, plant thatch and nutrient runoff on the emergence and density of four vernal pool endemic species (two anostracans, one notostracan and one spinicaudatan) in California (USA).

Hydroperiod stability effected anostracans and notostracans but this was moulded by life history, as anostracans tended to hatch more quickly and had shorter life cycles than the other studied large branchiopods. These results are consistent with those shown by Pinceel et al. (2017) and by Beladjal & Mertens (2017), who investigated anostracan reproductive strategies with regard to the “habitat uncertainty” typical of temporary environments. In particular, anostracans show a high degree of adaptation to the unpredictability of the hydroperiod in temporary waters which includes a temporally differentiated egg hatching, different dimensions of embryos at different inundation times, production of variably sized offspring within each clutch and production of larger clutches of smaller eggs from parents inhabiting more uncertain habitats.

Reproductive strategies, including mate searching, are also responsible for patchy distribution in syntopically occurring species. When anostracan species occur syntopically and synchronically, it can be difficult to investigate population dynamics and coexistence patterns in naupliar and larval stages due to a lack of taxonomic characters during these early stages. Zarattini et al. (2017) proposed a set of six discriminant functions based on selected morphological descriptors which allow individuals of the same larval stage to be differentiated according to species. The results offer the opportunity to investigate fundamental aspects related to the mechanism of local adaptations in anostracans by following population dynamics from hatching.

Conclusions

During the twentieth century, renowned scientists as E. Daday de Deés, F. Linder, J. Brtek, D. Belk and G. Mura built the foundations of modern anostracan taxonomy and biogeography. By standing on the shoulders of these giants, and taking advantage of the modern laboratory and analytical techniques, the anostracan workers of the twenty-first century are experiencing an exciting phase of discoveries, and are producing significant progress in several aspects of anostracan sciences. Today, both systematics and biogeography are embedded in a clearer phylogenetic frame, and ecological studies have passed from an old-fashioned descriptive approach to the investigation of

mechanisms underlying the presence, phenology and distribution of species and communities. The ever-increasing amount of molecular data pave the way for a critical (re)appraisal of taxonomic and phylogenetic value of morphological characters, and allow us to develop sounder taxonomic revisions. However, molecular tools are not sufficient in and of themselves: the above-mentioned caveat on the use of molecular markers must be considered, to avoid the incorrect use of these mighty tools. Moreover, these organisms are mostly linked with seasonally flooded wetlands and fishless high-mountain and high-latitude ponds (e.g., Jeppesen et al., 2017), which are fragile ecosystems, impacted and largely impaired globally. It is therefore necessary to continue increasing our knowledge on the identity, ecology and distribution of anostracans, in order to plan effective and sound conservation actions. This is beyond doubt the biggest challenge for modern “anostracan” scientists.

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