

Chapter 1 Introduction

“There is nothing more elegant than the form of this little crustacean; nothing more graceful than its movements. It swims almost always on its back, and by means of its fins and tail it runs in all directions . . . and deliver(s) itself up to a thousand bizarre and capricious gambols.” — Joly (on anostracans) in Baird, 1850

Anostraca or fairy shrimp are arguably the most primitive extant order of crustaceans (Belk, 1996; Martin and Davis, 2001; Rogers, 2009, 2013). Anostracans are found in seasonally astatic basins and pools, and/or saline inland aquatic habitats, on all continents (Brendonck et al., 2008; Rogers, 2009, 2013). The Anostraca (coupled with some clam shrimp, the cladocerans, copepods and ostracods) are part of the planktonic component of temporary pools, playas and salt lakes, spending most of their time in the open water column. These crustaceans are used as indicators of aquatic ecosystem health, several species are afforded protection under environmental law (Austria, Australia, Brazil, USA), and some species are economically important. As obligate aquatic macroinvertebrates, large branchiopods are important links in the aquatic food chain of ephemeral wetlands. Their presence and persistence in ephemeral wetlands (sometimes occurring in the hundreds per cubic litre of water) can serve as a biological indicators of aquatic ecosystem functions (Rogers, 1998), which ultimately reflects on land use practices and climate variations from a larger landscape perspective (De Los Rios et al., 2008).

Adult anostracans are fragile, delicate swimming animals that cannot function outside of water and are helpless in currents (Brendonck et al., 2008; Rogers, 2009, 2014a). Most anostracans

1 need their eggs to dry or desiccate preventing them from fungusing (Rogers, 2009). Typical
2 anostracan habitats include vernal pools, seasonally ponded areas within vernal swales, seasonal
3 wetlands, vlei, tundra pools, alpine pools, rock outcrop ephemeral pools (tinajas, gnammas,
4 tanks), clay pans, salt lakes, playas and alkali flats (Brendonck et al., 2008; Rogers, 2009). The
5 diapausing eggs lay dormant in or on the substrate during dry and/or frozen periods of the habitat
6 phenology, and hatch when liquid water is present. Typically, these habitats are hydrologically
7 isolated, preventing direct active dispersal by anostracans (Rogers, 2014a, b), although they
8 occasionally occur in pools that overflow one into another (e.g., Eriksen and Belk, 1999;
9 Hulsmans et al., 2007).

10
11 Taxonomically, the order Anostraca is composed of 356 species (fairy shrimp and brine shrimp),
12 separated into the suborders Artemiina and Anostracina (Table 1.) (Rogers, 2013, 2014c; Rogers
13 and Padhye, 2014). Artemiina contains two halobiont monogeneric families: Artemiidae and
14 Parartemiidae, commonly called “brine shrimp” (Weekers et al., 2002). Anostracina has six
15 primarily freshwater families commonly referred to as “fairy shrimp” (Weekers et al., 2002):
16 Branchinectidae (two genera), Thamnocephalidae, (six genera), Streptocephalidae
17 (monogeneric), Branchipodidae (six genera), Tanymastigidae (two genera), and Chirocephalidae
18 (nine genera). Male gonopodal morphology defines the anostracan genera (Rogers 2009, 2013).

19
20 The basic question proposed in this dissertation is: why do fairy shrimp live in some locations
21 and not others? Habitats occupied by anostracans occur all over the world (Table 1), on every
22 continent, and every bioregion. Yet, not all continents support all families, not all regions support
23 all genera and not all pools have all species. At least two anostracan zoogeographic patterns are

1 linked to plate tectonics; the family Chirocephalidae occurs only on landforms originally part of
2 Gondwanaland (Belk, 1995) and the thamocephalid genus *Phallocryptus* is limited to habitats
3 in ancient salt deposits on four continents that were once all clustered at the equator during the
4 Miocene (Rogers, 2003). The distribution of other taxa may also be similarly linked (Rogers and
5 Coronel, 2011). Of the more than 350 described species, more than one third of anostracans are
6 known only from their type localities, and several species have only been collected once or twice
7 (Belk and Brtek, 1995; Rogers 2013). Many species of fairy shrimp live in habitats that are lethal
8 to other fairy shrimp species, even to congeners living in immediately adjacent habitats
9 (Vanhaeke et al., 1987; Triantaphyllidis et al., 1998; Rogers, 2006a). Frequently, one finds
10 anostracans in a given habitat, and then another nearby apparently identical, potentially suitable
11 site will be uninhabited or occupied by a different congener (e.g., Dexter and Kuehnle, 1948,
12 1951).

13
14 Globally, anostracan taxa rarely co-occur in the same basin or pool. In Western Australia for
15 example, where approximately 65% of anostracan species are endemic, 19% are known to co-
16 occur with congeners (Timms, 2002). However, in the Paroo Desert of New South
17 Wales/Queensland, the co-occurrence rate is 55% (Timms and Sanders, 2002), whereas 16% of
18 North American taxa are known to co-occur (Donald, 1983). The 60 acre Jepson Prairie Preserve
19 in central California, USA, supports hundreds of occupied anostracan habitats, with four species
20 of fairy shrimp in the genus *Branchinecta* and one in the genus *Lindieriella*. None of the
21 *Branchinecta* species co-occur in the same pool, yet the *Lindieriella* can be found in all the pools.
22 The question is; why?

23

1 The first large scale research on anostracan zoogeography was published by Packard (1883) for
2 North America, and Daday de Dees (1910) for the World. These studies present significant
3 research focused on anostracan continental scale zoogeography. They are, however limited, in
4 that they only recognise less than 20 per cent of the species known today (Rogers, 2014b).

5
6 There is only one relatively recent study on anostracan zoogeography at a global or bioregional
7 (e.g.; Nearctic, Palaearctic, Afrotropical) scale: Banarescu (1990) attempted to explain the
8 zoogeography of freshwater animals. However, Banarescu's (1990) treatment of the Anostraca is
9 also limited as the author was unaware of much of the biogeographical literature of this group,
10 and some of the taxonomy used was greatly outdated at the time of publication. Five of the
11 families and subfamilies that Banarescu (1990) discusses are not recognized as valid today.
12 Furthermore, Banarescu's (1990) study describes distributions for different families and genera
13 that are sometimes at odds with the maps presented. Furthermore, the analyses are speculative
14 and based on a rudimentary understanding of higher anostracan taxonomy. For example,
15 Banarescu (1990) describes the dispersal of the genus *Branchinella* as “. . . from South and East
16 Asia . . . to North America on the one hand, to Siberia, West Asia and Europe on the other; the
17 origin of the few South American species of this genus can be clarified when their affinities . . .
18 are known.” The species that were considered *Branchinella* in 1990 are now recognized to
19 belong to six different genera and subgenera (Rogers, 2006), with *Branchinella* sensu stricto
20 limited to Australia.

21
22 Brtek and Mura (2000) have also attempted regional scale zoogeographical anostracan
23 classifications for some groups. This study provides confused biogeographic data, with no real

1 analyses (criticised in Rogers, 2006). For example, Brtek and Mura (2000) divided the genus
2 *Branchinecta* into five species groups, with the geographic distribution of each group depicted
3 on a map. These species groups are justified only by the single sentence: “One genus only:
4 *Branchinecta* Verrill, 1869 which can be divided (according to the morphology of the male
5 antenna, among other features) into five distinct species groups at least . . .”. The remainder of
6 the sentence names the species groups and gives generalized distributions for each. Nothing
7 more is provided by the authors about the Branchinectidae. There is no explanation of what
8 defines each species group, there is no indication what morphological characters of the male
9 second antenna are of significance or why, there is no indication what “other features” were
10 considered significant, there is no quantitative analyses, and no supporting citations. Instead, one
11 must use the maps to guess which species are in which species groups. Thus, it is not possible to
12 define, reconstruct, or analyze these species groups.

13
14 There are few regional zoogeography studies on the Anostraca. Røen (1962) provides much
15 generalised biogeographic information for Greenland anostracans. Thiéry (1987) details the
16 biogeography of the large branchiopod crustaceans of Morocco, focusing on climate, water
17 chemistry, vegetation and large scale geology as relates to habitat distribution. Vekhoff (1990,
18 1993, 1997) discusses anostracan zoogeography as related to the larger bioregions of Russia
19 (discussed in Rogers, 2014b). Belk (1977) discussed the regional biogeography of Arizona
20 (discussed in Rogers, 2014b). Eng et al. (1990) and Eriksen and Belk (1999) give general
21 descriptions of anostracan distribution in California from the perspective of the individual
22 species. Maeda-Martínez (1991) and Maeda-Martínez et al. (2002) discuss the biogeography of
23 the Mexican Anostraca as relating to desert type. Hammer (1994) presents the biogeography of

1 the Anostraca of the southern portion of Africa in great detail as related to climate. Brendonck
2 and Riddoch (1997) provide an assessment of the distribution of anostracans in Botswana as
3 generally related to climate and geographic regions. Lang and Rogers (2002) demonstrate
4 distribution of Anostraca in New Mexico as related to desert type and Samchyshyna et al. (2008)
5 discusses anostracan distribution as relating to Holarctic glaciation. Pinceel et al. (2013a, b)
6 relate Australian anostracan genetic differentiation to historic climate change using molecular
7 clocks. All these studies focus on climate as a primary driver of anostracan distribution. Climate
8 is very important to anostracans: climate that facilitates a dry season is vital to most species.
9 However, climate is very difficult to quantify. Furthermore, topographical variations create
10 localised microclimates conducive to organisms in areas that would otherwise be unable to
11 support them (Tyler et al., 1996).

12
13 At a smaller scale, Maynard and Romney (1975) discuss the biogeography of Anostraca in
14 northeastern Utah. Belk (1991) explored ecological reasons as to why only one of two locally
15 common congeners occurs in a single rock pool. Timms and Sanders (2002) relate the anostracan
16 biogeography of the Paroo Desert in New South Wales and Queensland, Australia to water
17 chemistry.

18
19 Detailed research on the zoogeography or biogeography of specific taxa is limited. Browne and
20 MacDonald (1982), Vanhaecke et al. (1987), and Triantaphyllidis et al. (1998) discuss the
21 biogeography of the genus *Artemia* at a global scale. Belk (1995) examines the distribution of the
22 genus *Eubranchipus* and discusses the possibility of this genus being Laurasian in origin. Belk
23 (2000) and Rogers (2006a) describe the distribution of sister taxa occurring on opposite sides of

1 the North American Continental Divide, yet occupying the same habitat types and latitudes.
2 Rogers (2003) discusses the biogeography of the genus *Phallocryptus* in relation to plate
3 tectonics. Rogers and Coronel (2011) examined *Archaebranchinecta* biogeography and its
4 association to continental drift. Daniels et al. (2004) discuss radiation of the genus
5 *Streptocephalus* from a molecular standpoint, where they found that all New World species were
6 derived from a single African ancestor. However, all these studies have unexplained variances,
7 outliers, and deviations from their proposed biogeographical interpretations. Some studies go so
8 far as to ignore records or data that were deemed “extreme” or “not characteristic of the species”
9 (e.g., Eng et al., 1990).

10
11 Anostracan biogeography as a whole is not well understood because of the tremendous age of the
12 group (Harvey et al., 2012), the numerous instances of disjunct distributions in genera (e.g.: Belk
13 and Brtek, 1995; Rogers, 2002, 2003; Daniels et al., 2004) and species (e.g.: Belk, 1996; Creaser,
14 1930; Rogers, 2006b), as well as attempts to characterise anostracan habitat using qualitative
15 climatic parameters and by water chemistry parameters. Studies using water chemistry rarely if
16 ever find consistent associations with anostracan distribution, and often the results conflict with
17 other studies on the same species or even the same site (e.g., Eng et al., 1990). The very astatic
18 nature of anostracan habitat by definition requires that water chemistry parameters are highly
19 variable, even on a 24 hour cycle. As a given basin dries, dissolved salts and organic materials
20 become concentrated, whereas replenishing precipitation dilutes these same components.
21 Hydrophytic plants photosynthesizing during daylight hours will remove CO₂ from the water
22 column, thus raising the pH (Rogers, 2009). However at night, the same plants are respiring,
23 reducing the dissolved oxygen levels and increasing the CO₂ (and thereby, the HCO₃) in the

1 water causing pH to fall (Rogers, 2009). Rainfall and increased wave action from wind will also
2 lower the pH (Rogers 2009). Thus, standard water quality parameters are of limited use in
3 defining habitat preferences for specific taxa. They may define “windows” of hydrochemical
4 conditions suitable to a given species life stage as the geochemical components are diluted or
5 concentrated by fluctuating hydroperiods. Water quality measurements are, on the whole, little
6 more than “snapshots” in time, demonstrating the parameters of the moment.

7
8 The Anostraca appear to defy any simple explanation of their zoogeography at any scale. The
9 seasonally astatic wetlands on which they depend are habitat patches embedded within larger
10 geomorphic landscapes. Indeed, they are islands of aquatic habitat in a terrestrial landscape, or
11 sea of land, with varying degrees of isolation from other seasonally astatic wetlands or other
12 inland aquatic habitats. These habitats are also islands in time, in that these habitats may
13 inundate once annually, semi-annually, or even once per decade (Ebert and Balko, 1984;
14 Williams and Campbell, 1987; Williams, 2001). In an extreme example, Lake Torrens, Australia,
15 has filled once in recorded human history, and when it did it was replete with anostracans
16 (Williams et al., 1998). Conversely there are aquatic habitats that only dry out once per year,
17 every few years, or even once per century (Williams, 1987) and support anostracans upon
18 reinundation. Furthermore, seasonally astatic habitats tend to be short lived geologically existing
19 at most 10,000 to 20,000 years (Williams and Campbell, 1987; Williams, 1987). Thus, an
20 essential objective of this dissertation is to explore whether anostracan biogeography can be
21 explained in terms of island biogeography (sensu MacArthur and Wilson, 1963, 1967) and the
22 Monopolisation Hypothesis of De Meester et al. (2002).

23

1 Island biogeography theory states that insular biogeographic patterns result from predictable
2 variation among the rates and capacities of the fundamental processes of immigration, evolution
3 and extinction among islands and among species (MacArthur and Wilson, 1967; Lomolino et al.,
4 2010). Overly simplified, Immigration rate should decline as a function of isolation, and
5 extinction rate should decline as a function of area (see Figure 1 in Chapter 8).

6
7 The Monopolization Hypothesis states that rapid adaptation and growth of founder populations
8 colonising unoccupied wetland habitat will impede gene flow, allowing the founding colony
9 lineage to monopolize resources and exclude other conspecific lineages (DeMeester et al., 2002).

10 Applying the Monopolization Hypothesis to anostracan biogeography, it would seem that
11 immigration, evolution and extinction would affect habitat monopolization by a given lineage.

12
13 Seven specific questions are put forward to address the objectives of this thesis concerned with
14 anostracan biogeography and island biogeography and the Monopolisation Hypothesis. These
15 are:

- 16 1. Does dispersal type affect habitat monopolization?
- 17 2. Does the egg bank support resource monopolization?
- 18 3. Do anostracan lineages adapt to the local conditions in the specific basin monopolized?
- 19 4. Do anostracans adapt at a regional scale?
- 20 5. Does resource monopolization work at different scales?
- 21 6. Do species evolve anagenically, cladogenically or both?
- 22 7. Can the seemingly random distribution of anostracans be explained using island
23 biogeographic theory?

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To this end, six studies are undertaken; the results of which are outlined in the following chapters.

Chapter 2 explores local adaptation to temperature across the geographical range of a broadly distributed anostracan species (Rogers, 2014d). In this study I show that local adaptation to local conditions may drive clinal variation and isolation. This chapter is in press in *The Journal of Limnology*.

Chapter 3 examines the role of dispersal in anostracan biogeography (Rogers, 2014a). Herein, I demonstrate that eggs that pass through digestive tracts of birds hatch in significantly larger fractions than eggs dispersed by other vectors and eggs from resident habitat egg banks. Predator dispersed eggs would have a greater chance of reaching suitable habitat than eggs that are randomly dispersed (such as by wind). This larger hatching fraction would amplify the priority effects of habitat monopolisation should the eggs be deposited in unoccupied habitat. This strengthens the priority effect of a colonising population, in that the first generations would hatch at a higher fraction than subsequent generations, allowing the founding population to more rapidly monopolize habitat resources than randomly dispersed eggs, and establish an egg bank that could resist additional colonial events. Habitat monopolisation through rapid population growth coupled with rapid adaptation and the buffering effect of the constantly mixing and staggered egg bank creates a tight, coadapted gene pool that resists change. This greatly increased inbreeding potential within the founder colony minimizes phenotypic variation and maintains existing successful phenotypes, further resisting new genetic input from outside the

1 habitat. Therefore, anostracan speciation must occur allopatrically via colonisation of new or
2 recently unoccupied habitats. This chapter was published in *The Journal of Crustacean Biology*,
3 34(2): 135-143, 2014.

4

5 Chapter 4 defines anostracan bioregions for North America quantitatively using Jaccard's
6 Coefficient of Community Similarity, and qualitatively defined using climate data (Rogers,
7 2014b). Furthermore I use Fager's Index of Recurring Species Groups to quantify species
8 assemblages. In this chapter I present nine quantitative North American anostracan bioregions,
9 and show that the average Fager's Index for each bioregion, as well as the percentage of taxa co-
10 occurring, generally decreases with the length of time the region has been available for
11 colonisation. A general relationship between anostracan diversity, endemism, precipitation and
12 precipitation reliability is shown. The more arid and unreliable precipitation patterns are, the
13 more seasonally astatic wetlands will be present and more of them will be isolated, thus
14 increasing potential endemism. The strong Fager's Index/colonisation time availability
15 relationship suggests that the Monopolization Hypothesis of De Meester et al. may function at
16 larger landscape scales for species and species groups, and suggests that the majority of
17 anostracan species may specialise to habitat conditions in their respective bioregions. The lower
18 average Fager's index, the increased percentage of endemic and insular taxa, and the generally
19 decreasing percentage of co-occurring taxa with younger landscapes supports the idea that
20 anostracans evolve allopatrically. However, it may be that speciation occurs allopatrically via
21 founder effects in new habitats, and also in established populations through a given population's
22 rapid local adaptation to its particular habitat over time. Thus the monopolization of a given

1 habitat by a founder population may drive speciation in two ways. This chapter was published in
2 *Zootaxa*, 3838 (3): 251-275.

3
4 Chapter 5 examines North American anostracan species distribution as related to geochemistry
5 (Rogers, 2014e). This study used geochemistry to demonstrate specific relationships between
6 percent geochemical components, salinity and dominant salt cations parameters and the
7 distributions of all 63 US species and species assemblages. The tolerance values for the species
8 for each bioregion were statistically significant, further supporting the nine North American
9 anostracan bioregions defined in Chapter 4. Thus, the North American anostracan bioregions are
10 each unique not only in terms of anostracan fauna, species assemblages, climate, and
11 geomorphology, but also geochemistry. Furthermore, the geochemical ranges for the different
12 species were shown to impose a strong filter for egg banks as well as active stages. Large
13 dichotomies between the geochemical tolerance values within each of three species across more
14 than one bioregion allowed me to descry cryptic species, each with their own geochemical
15 tolerance ranges. Because anostracan habitats are almost entirely endorheic basins, geochemical
16 concentrations should increase perceptibly over many centuries time. This would necessarily
17 drive the anostracan population in a given basin to adapt to the changing habitat or become
18 extinct. This type of localised adaptation would reinforce the strong priority effects of habitat
19 monopolization. This study also demonstrates that standard water chemistry cannot be used to
20 define anostracan habitat for individual species. This chapter was published in *Zootaxa* 3856
21 (1):1-49.

22

1 Chapter 6 applies the methods of Chapters 4 and 5 to Australia (Rogers and Timms, 2014). This
2 chapter uses the collection data of Dr. Brian V. Timms (University of New South Wales,
3 Sydney, Australia). Three anostracan bioregions are presented for the Australian continent. The
4 bioregion characteristics and faunal compositions are compared with those in North America.
5 Australia and North America are reasonably comparable in that both continents have roughly the
6 same number of species (62 in Australia, 68 in North America). However, Australia has far
7 lower numbers of higher level taxa, with only five genera, each in its own family (verses North
8 America with 11 genera). The Australian Continent is dominated by two primary genera:
9 *Branchinella* in fresh to hyposaline habitats, and; *Parartemia* in hypersaline habitats. Because of
10 the lack of geological upheaval driving rapid local extinctions and creating new colonisation
11 opportunities, these two genera have monopolised these two habitat types in Australia. In this
12 study I argue that that the Monopolisation Hypothesis functions at continental scales. This
13 chapter is published in Zootaxa 3881(5): 453-487.

14
15 Chapter 7 describes and defines two cryptic species identified in Chapter 5 (Rogers, 2014c). In
16 the past many geographically widespread anostracans have been shown to be composed of two
17 or more cryptic species, but always based on a closer examination of their morphology. In the
18 present case, geochemical components of the dry habitat substrate indicated that populations of
19 two different species were different between different anostracan bioregions. In this chapter I
20 argue that generalist anostracan species occurring in basins across more than one bioregion, are
21 under ecological pressures unique to each bioregion. These different pressures would drive
22 divergence, and ultimately speciation, generating populations that are adapted and specialized to
23 their specific bioregion. Thus, localised ecological pressures will drive localised anostracan

1 adaptation, further reinforcing the population's monopolization of the habitat. This chapter is
2 published in *The Journal of Crustacean Biology* 34(6): 862-874.

3
4 Chapter 8 presents a conceptual framework for understanding and interpreting anostracan
5 biogeographical patterns (Rogers, 2014f). In this chapter I argue that anostracan biogeography is
6 structured along the fundamental biogeographic processes of immigration, evolution and
7 extinction, and patterns of endemism, distribution and disjunction only make sense when
8 examined in the light of island biogeography theory. This chapter is in review in *The Journal of*
9 *Crustacean Biology*.

10
11 Following these Chapters is an appendix that presents a catalogue of the Anostraca of the world
12 (Rogers, 2013). This catalogue was important to the larger study in that it was necessary to
13 accurately descry the numbers of genera, species, and species within each genus. This appendix
14 was published in *The Raffles Bulletin of Zoology*, 61(2): 525-546, 2013.

15
16 “Probably (no one would be) seriously inconvenienced if the fairy shrimps were
17 to suddenly disappear from the face of the earth; I suppose few would even know the
18 difference. Among these, however, would certainly be numbered those biologists who
19 have found the study of these interesting though much neglected animals a rewarding
20 activity.” — Walter G. Moore, 1959

21

22

1 Table 1. Extant Anostracan families and genera (from Rogers, 2013).

CLASS BRANCHIOPODA
SUBCLASS SARSOSTRACA

Order Anostraca

Suborder Artemiina

Family	Artemiidae	<i>Artemia</i>	7 species, all continents except Antarctica
	Parartemiidae	<i>Parartemia</i>	18 species, Australia

Suborder Anostrocina

Family	Branchinectidae	<i>Branchinecta</i>	49 species, Americas, Eurasia, Antarctica
		<i>Archaebranchinecta</i>	1 species, Americas
	Thamnocephalidae	<i>Thamnocephalus</i>	4 species, Americas
		<i>Carinophallus</i>	1 species, Eurasia, Africa
		<i>Phallocryptus</i>	4 species, Americas, Africa, Eurasia
		<i>Spiralifrons</i>	1 species, South America
		<i>Dendrocephalus</i>	18 species, Americas
		<i>Branchinella</i>	47 species, Australia, Eurasia, Africa
		New Genus 1	1 species, South America
	Streptocephalidae	<i>Streptocephalus</i>	64 species, Africa, North America, Eurasia, Australia
	Branchipodidae	<i>Australbranchipus</i>	2 species, Australia
		<i>Branchipus</i>	5 species, Eurasia, Africa
		<i>Branchipodopsis</i>	21 species, Africa, Eurasia
		<i>Metabbranchipus</i>	3 species, Africa
		<i>Pumilibranchipus</i>	1 species, Africa
		<i>Rhinobbranchipus</i>	1 species, Africa
	Tanymastigidae	<i>Tanymastix</i>	4 species, Eurasia, Africa
		<i>Tanymastigites</i>	5 species, Africa
	Chirocephalidae	<i>Branchinectella</i>	1 species, Eurasia, Africa
		<i>Artemiopsis</i>	3 species, Arctic
		<i>Parartemiopsis</i>	1 species, Eurasia
		<i>Chirocephalus</i>	53 species, Eurasia
		<i>Eubbranchipus</i>	18 species, North America, Eurasia
		<i>Dexteria</i>	1 species, North America
		<i>Linderiella</i>	5 species, North America, Eurasia, Africa
		<i>Polyartemia</i>	1 species, Eurasia
		<i>Polyartemiella</i>	2 species, North America

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