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Species Richness and Species Turnover (Complementarity) of Rotifera in Selected Aquatic Systems of Big Bend National Park, Texas

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ABSTRACT—We documented 95 taxa of Rotifera while undertaking All Taxa Biological Inventories (ATBI) from ten aquatic systems in Big Bend National Park (Texas). Species richness varied widely among these systems: (range 8 to 46; mean (±1SD) = 18.3 ±11.0), with total occurrences in springs (40%) >ponds (22%) >tinajas (14%) >Rio Grande water (13%) >cattle tanks (11%). Approximately 59% of all species were singletons. Species Turnover Indices for all combinations of these systems indicated low relatedness: mean (±1S.D.) = 84.6 ±9.0%. When compared to published studies on worldwide sites, including subpolar, temperate, and tropical habitats, rotifers from arid regions tended to have higher inter-site variation.

The World Wildlife Fund has ranked the Chihuahuan Desert as one of the most biologically diverse ecoregions in North America, in part because of the high degree of local endemism of the freshwater biota (Dinerstein et al. 2000). Unfortunately, this desert, including its unique freshwater habitats, is at significant risk from a variety of anthropogenic activities, including industrial and recreational development, introduction of exotic species, overgrazing, atmospheric deposition of pollutants, and aquifer depletion (Anon. 2000; Olsen and Dinerstein 1998). Thus, these freshwater habitats, with their associated biota, represent an important ecological indicator for overall environmental health of the Chihuahuan Desert. Regrettably only a sparse literature exists on the aquatic fauna of its springs and ephemeral waters (e.g., Rico-Martinez and Silva-Briano 1993; Loring et al. 1988; Mackay et al. 1990; Suarez-Morales et al. 2000; Suarez and Reid 1988, 2003; Wallace et al. 2005). Lacking this important base-line information, it is difficult to make management decisions regarding spring and aquifer health. Moreover what research has been done on the springs, perennial streams (and their riparian vegetation), tanks (artificially diked ponds), *playas* (shallow ephemeral wetlands), and *huecos* and *tinajas* (small and large rock pools, respectively) focused on larger organisms (usually >1 mm), while neglecting microscopic forms, especially the small zooplankton (Bane and Lind 1978; Bowman 1981, 1985; Cole and Bane 1978; Cole and Minckley 1966, 1969; Gloyd 1958; Hamilton 2000; Hershler et al. 1999; Lind and Bane 1980; Shuster 1981). These small animals are critically important to desert aquatic communities because they comprise the food of invertebrate predators such as notonectids (Hampton and Gilbert 2001), hydra, and damselfly nymphs (Walsh 1995) as well as the first foods of many small fishes (Nogrady et al. 1993; Wallace and Snell 2001). One taxon of zooplankton that is likely to have high species richness but that has been nearly ignored in desert waters is Phylum Rotifera. Accordingly, the focus of our research is the rotiferan fauna of the rare and fragile aquatic habitats of Big Bend National Park (BBNP).

Characterization of the biodiversity of these important but incompletely inventoried water sources is essential. Species richness is an important indicator of biodiversity as recognized by the United Nations in their Convention on Biodiversity (2001 to 2005) (Sarukhán and Whyte 2005). In estimating species richness in lacustrine zooplankton, Dumont and Segers (1996) determined the degree of complementarity of faunas using Species Turnover Indices. They found high levels of species turnover across broad geographic distances. Ejsmont-Karabin (1995) used an Index of Floral Originality (IFO) to investigate how rotifer communities in quarry lakes develop over time. She found IFO values ranging from 1.0 to 0.18, with a value of 1 indicating that species found in a lake were not found in another lake. Here we apply these measures to ten selected aquatic habitats in Big Bend National Park in order to characterize their biodiversity.

STUDY SITE—Designated as a national park in 1944 and a UNESCO Biosphere Reserve in 1976, BBNP is an area of some 3200 km^2, with a sizeable elevation range (550 to 2400 m) and a low average rainfall of <25cm/yr. Despite its dry environment, over 180 springs, as well as numerous streams, huecos, tinajas, tanks, and ponds, have been recorded within the park boundaries (e.g., Anon. 1990; Bowles in litt.); Lind and Bane 1980). Much of the park has received a conservation priority designation of Highest (terrestrial) or High Priority (aquatics) (Dinerstein et al. 2000).

METHODS—*On-site sampling procedures*—Sampling took place during seven field trips (2001 to 2004), each of about four days in duration: 11–15 July 2001; 16–19 October 2001; 11–15 July 2002; 4–7 January 2003; 6–10 August 2003; 10–14 May 2004; 13–17 July 2004. The ten sites studied were visited between three and seven times and included

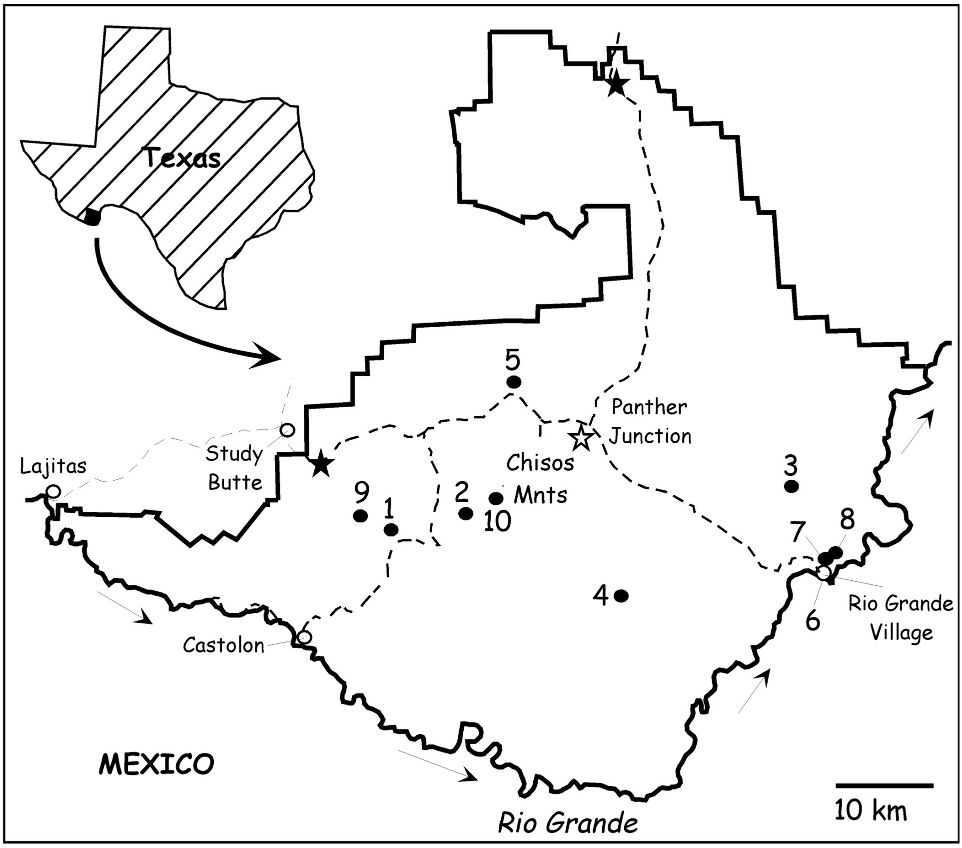

FIG. 1—Map of the study area (Big Bend National Park, TX, USA; ca. 29°15'00"N; 103°15'00"W). Dashed lines are paved roads; unimproved roads are not illustrated. Arrows indicate direction of the Rio Grande flow. Open circles are local towns; open star is the park headquarters at Panther Junction; closed stars are park entrance stations; closed circles with numbers indicate the approximate location of our sampling sites, each with one or more distinct locations, either as an aquatic complex or multiple distinct sampling sites. (n=number of visits per site). (See Appendix 1 for GPS coordinates and additional information.)

springs, former cattle tanks, tinajas, the Rio Grande, and artificially constructed ponds (Fig. 1). Some of these systems comprised multiple basins with varying degrees of inter-site connectivity. Samples were collected from planktonic, littoral, and benthic habitats using plankton nets (64 μm), grab samples (e.g., aquatic plants for sessile forms), and aspirating samplers for flocculent bottoms (e.g. Nogrady et al. 1993; Wallace and Ricci 2002). While our sampling strategy attempted to provide an All Taxa Biological Inventory (ATBI) (Dumont and Segers 1996), it is not possible to assess whether this procedure biased one habitat type over another.

All survey equipment was rinsed with distilled water and (whenever possible) dried between uses in different systems to prevent cross-sample contamination. While several samples were taken from each site, we attempted to keep the sample size to a minimum to avoid damaging the smaller, more fragile communities. Typically samples were collected in about 50 to 250 ml of source water and stored in Whirlpack® bags. GPS coordinates, water temperature, pH, DO, conductivity, total dissolved solids, oxidation reduction potential, habitat size, vegetation, general site and weather conditions, locations of obvious inflows and outflows, and a digital photographic record were recorded at nearly every site sampled (Wallace et al. 2005).

Sample Processing—All samples were stored at ca. 10 to 12°C until they were processed. Each sample was examined by at least two observers before being discarded. To avoid the possibility of cross-contaminating our samples, we used fresh Pasteur pipettes for each sample. Because most keys to the Rotifera are regional in scope and generally do not cover North American species, we were cautious with their use. Thus, species that did not match published descriptions were identified only to the level of genus. The keys used in this study were as follows: Monogononta: Berzins (1951), De Smet (1996), De Smet and Pourriot (1997), Edmondson (1959), Jose de Paggi et al. (2002), Koste (1978), Nogrady et al. (1995), Segers (1995), Stemberger (1979), Wallace and Snell (2001); Bdelloidea: Donner (1965), Ricci and Melone (2000).

Deposition of Specimens—Voucher specimens preserved in formalin (5%) and/or ethanol (70%) are deposited at the Laboratory for Environmental Biology (UTEP) and accessioned into the existing BBNP collection.

Analyses—We calculated two measures of faunal dissimilarity: Species Turnover Index (STI) (Dumont and Segers 1996) and an Index of Floral Originality (here: Index of Faunal Originality, or IFO) (Ejsmont-Karabin 1995). STI values were calculated for all combinations of the ten systems according to the following equation:

$$STIjk = \frac{SRj + SRk - 2(SHjk)}{SRj + SRk - SHjk},$$

where SR are the species richness of the jth and kth sites and SH is the number of species shared by the jth and kth sites.

IFO values were calculated for all ten systems according to the following equation.

$$IFO = \frac{\sum_{i=1}^{S} 1/M_i}{S},$$

where M_i is the number of sites in which the i^{th} species was found and S is the species richness of a site for which the IFO is being calculated.

Results—Although this report focuses on collections from ten larger systems, our overall efforts in determining an ATBI of the rotifers of BBNP thus far have yielded more than 110 species from over 25 systems as of 2004. Approximately 20 forms remain identified only to the level of genus and are not included here; these may be new to science. A species collector's curve (Dumont and Segers 1996) illustrates that we have not yet begun to approach the total species richness for the aquatic systems in BBNP (Fig. 2A).

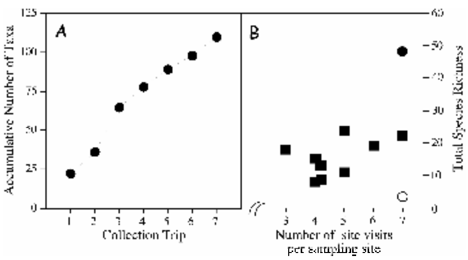

Fig. 2—Collection records. (A)Species collector's curve for all seven field trips for the entire chorographic study of the rotifers of Big Bend National Park. (B) Rotifer species richness as a function of the number of visits to the ten sampling sites. Closed symbols – this analysis; open circle – Government Spring, part of our larger study; closed circle – Cattail Spring pools. The circles represent data points illustrating that the range of species richness is not tightly related to sampling frequency.

In the systems analyzed here, we identified 95 species, all but two being members of the Class Monogononta. Of the 32 families of Eurotatoria currently recognized (Segers 2002; Jose de Paggi et al. 2002), 18 were present in our samples (Table 1). Although we did not visit each of these systems the same number of times (n=3 to 7), there appears to be no relationship between total species richness and the number of visits (Fig. 2B). In fact, of three systems visited seven times, only Cattail Spring had a remarkably high level of species richness (n = 46); Government Spring (not analyzed herein due to its unique character), on the other hand, had a very low species richness (n = 3). The mean species richness (±1 SD) for all ten systems was 18.3 ±11.0.

Discussion—In our study, seven species, six monogononts (*Colurella obtusa*, *Euchlanis dilatata*, *Lecane bulla*, *Lecane hamata*, *Lecane inermis*, and *Lepadella patella*) and one bdelloid (*Philodina megalotrocha*), were the most common taxa encountered, being present in ≥ 50% of the systems studied. According to the literature, all of these species have a cosmopolitian distribution therefore their presence in our samples is not surprising (Donner 1965; Koste 1978; Segers 1995). For example, *E. dilatata*, *L. bulla*, *L. hamata*, and *L. patella* have been reported from temperate and tropical waters. Although we

Table 1—Rotifera identified in this study. Sample sites are illustrated in Fig. 1. Taxa with the notation of 'cf.' indicate that minor differences were noted from published descriptions. Rotiferan classification according to Segers (2002) and Jose de Paggi et al. (2002).

Classification	Taxa identified	Sample site number
Class Eurotatoria		
Bdelloidea		
Philodinidae		
1	*Dissotrocha aculeata*	2
2	*Philodina megalotrocha*	1, 2, 3, 4, 6, 7, 8, 10
Monogononta		
(Ploima)		
Asplanchnidae		
3	*Asplanchna brightwellii*	5, 9
Brachionidae		
4	*Anuraeopsis fissa*	3
5	*Brachionus angularis*	6, 9
6	*Brachionus bidentata*	6, 7, 9
7	*Brachionus calyciflorus*	6
8	*Brachionus dimidiatus*	2, 9
9	*Brachionus durgae*	5
10	*Brachionus havanensis*	9
11	*Brachionus quadridentatus* f. *melheni*	6
12	*Brachionus urceolaris*	5, 6, 9
13	*Plationus patulus*	6, 7
14	*Platyias quadricornis*	6, 7
Dicranophoridae		
15	*Aspelta* sp.	4
16	*Dicranophorus haueri*	2
17	*Dicranophorus forcipatus*	7
18	*Wierzejskiella vagneri*	2
Epiphanidae		
19	*Epiphanes chihuahuaensis*	7, 8
Euchlanidae		
20	*Beauchampiella (=Manfredium) eudactylota*	8
21	*Euchlanis dilatata*	2, 4, 5, 6, 7, 8, 9, 10
22	*Euchlanis incisa*	2, 6
23	*Euchlanis lyra*	2
24	*Euchlanis triquetra*	2
25	*Dipleuchlanis* sp.	2, 8
26	*Tripleuchlanis plicata*	2, 6, 8

Table 1—*continued*

Classification	Taxa identified	Sample site number
Ituridae		
27	*Itura viridis*	8
Lecanidae		
28	*Lecane bifurca*	2
29	*Lecane bulla*	1, 2, 3, 4, 7, 8, 9, 10
30	*Lecane* cf. *abanica*	8
31	*Lecane closterocerca*	1, 2, 3, 8
32	*Lecane furcata*	2
33	*Lecane hamata*	2, 4, 7, 8, 10
34	*Lecane inermis*	1, 2, 3, 7, 8
35	*Lecane lateralis*	4, 6
36	*Lecane luna*	4
37	*Lecane papuana*	6, 7
38	*Lecane perpusilla*	2
39	*Lecane pyriformis*	8
40	*Lecane quadridentata*	3, 4
41	*Lecane rudescui*	2
42	*Lecane thalera*	8
Lepadellidae		
43	*Colurella colurus* f. *compressa*	7
44	*Colurella obtusa*	1, 2, 3, 4, 5, 8
45	*Colurella obtusa* f. *aperta*	1
46	*Colurella obtusa* f. *clausa*	2
47	*Colurella uncinata*	2, 4, 10
48	*Colurella uncinata* f. *bicuspidata*	2, 6, 7
49	*Lepadella ovalis*	1, 2, 3, 4, 6, 8, 10
50	*Lepadella patella*	2, 3, 4
51	*Lepadella patella* f. *oblonga*	7
52	*Lepadella pumilo*	2
53	*Lepadella* cf. *triptera*	2
54	*Squatinella mutica*	7, 8
Notommatidae		
55	*Cephalodella catellina*	5, 6
56	*Cephalodella* cf. *mira*	6
57	*Cephalodella* cf. *vitella*	2
58	*Cephalodella compacta*	2, 10
59	*Cephalodella doryphora*	10
60	*Cephalodella forficula*	2, 3, 4, 6
61	*Cephalodella gibba*	2, 4, 6, 7
62	*Cephalodella gracilis*	1, 2, 4, 10
63	*Cephalodella panarista*	2
64	*Cephalodella sterea*	2, 4, 10
65	*Cephalodella tenuiseta*	2

TABLE 1—*continued*

Classification	Taxa identified	Sample site number
66	*Cephalodella vacuna*	6
67	*Eosphora najas*	6
68	*Eosphora thoides*	6
69	*Monommata arndti*	2, 4
70	*Monommata* cf. *pseudophoxa*	6
71	*Monommata enedra*	2
72	*Taphrocampa annulosa*	1
Proalidae		
73	*Proales daphnicola*	10
74	*Proales sigmoidea*	2
Synchaetidae		
75	*Polyarthra dolichoptera*	5, 7, 9
76	*Polyarthra vulgaris*	5, 9
Trichocercidae		
77	*Trichocerca collaris*	3
78	*Trichocerca* cf. *marina*	3
79	*Trichocerca pusilla*	2, 3
80	*Trichocerca similis*	3, 8
81	*Trichocerca tenuidens*	4
82	*Trichocerca vernalis*	2
83	*Trichocerca weberi*	2
Trichotriidae		
84	*Macrochaetus sericus*	8
Monogononta (Collothecaceae)		
Collothecidae		
85	*Collotheca coronetta*	2
86	*Collotheca* cf. *paradoxa*	7
87	*Collotheca gracilipes*	2
88	*Collotheca ornata*	1
Monogononta (Flosculariaceae)		
Flosculariidae		
89	*Limnias ceratophylli*	6, 7
90	*Ptygura brachiata*	2
91	*Ptygura brevis*	2
92	*Ptygura crystallina*	2
93	*Ptygura longicornis*	2
94	*Sinantherina socialis*	9
Hexarthridae		
95	*Hexarthra cf. fennica*	3

Table 1—*continued*

Classification	Taxa identified	Sample site number
Trochosphaeridae		
96	*Filinia* cf. *longiseta*	7, 9
97	*Filinia pejleri*	7
98	*Filinia terminalis*	7, 9

were able to identify only two bdelloid species, we estimate that there were fewer than ten bdelloid species present in our samples. Given the ability of bdelloids to undergo anhydrobiosis (Ricci et al. 1987; Örstan 1995) this paucity of bdelloid taxa in our samples is surprising and warrants further investigation.

Other species present in our collections that are known to be fairly widespread include *Anuraeopsis fissa*, *Asplanchna brightwellii*, *Brachionus angularis, Brachionus bidentata, Brachionus calyciflorus, Brachionus dimidiatus, Brachionus durgae, Brachionus havanensis, Brachionus quadridentatus* f. *melheni*, *Brachionus urceolaris*, *Filinia limnetica, Filinia pejleri, Filinia novaezealandiae, Hexarthra fennica*, *Polyarthra dolichoptera,* and *Polyarthra vulgaris*. Most of the occurrences of these 16 taxa were in the stagnant waters of either a tank or a tinaja (about 61%).

Although our studies yielded these common taxa, a comparison of species composition among the ten sites revealed a relatively high level of STI and IFO values indicating that the rotifer assemblages of these ten systems were very different from one another (Table 2). The mean STI value was 84.6 ±9.0%, with >84% of the pairwise combinations having an STI of >75%. Likewise, with a mean of 0.48 ±0.09, the IFO values for these 10 systems are also rather elevated, especially that of Cattail Spring (IFO = 0.68).

We compared the mean STI values for the BBNP systems to the values from 20 other studies extracted from the literature (Fig. 3). Of these studies, the BBNP values were higher than those for subpolar (n = 3), temperate (n = 4), and tropical (n = 6) habitats. Even the STI values from seven lakes on five continents were lower than those in our 10 systems (Fig. 3; Dumont and Segers, 1996). However, the STI values from studies of sites in arid habitats were generally similar to those from the BBNP systems. A factor that may, in part, account for the higher STI values in the studies of arid waters is that many of the species encountered in these sites occurred as singletons (i.e., one species in one system).

TABLE 2—Species Turnover Indices (STI) and Indices of Faunal Originality (IFO) for 10 aquatic systems in Big Bend National Park, Texas. STI mean (± 1 S.D.) = 84.6 ±9.0%. Locations: 1. Burro Spring; 2. Cattail Spring pools; 3. Ernst Tinaja series; 4. Glenn Spring stream; 5. Paint Gap cattle tank; 6. Rio Grande river waters; 7. Rio Grande lower Pond; 8. Rio Grande upper pond; 9. Tule Tank; 10. Window Trail Tinaja series. IFO mean (± 1 S.D.) = 0.48 ± 0.09.

	1	2	3	4	5	6	7	8	9	10	IFO
1	–	85.7	66.7	76.2	94.1	93.8	85.7	73.9	95.5	76.5	**0.42**
2	.	–	84.6	76.0	96.2	87.1	86.7	81.8	94.6	81.3	**0.68**
3	.	.	–	75.0	95.2	91.4	87.5	73.1	96.2	86.4	**0.48**
4	.	.	.	–	90.9	82.4	81.3	79.3	92.6	57.9	**0.36**
5	.	.	.	.	–	89.7	92.9	92.0	68.8	94.4	**0.43**
6	.	.	.	.	.	–	72.2	89.7	87.9	90.6	**0.55**
7	.	.	.	.	.	.	–	75.8	79.3	82.1	**0.46**
8	.	.	.	.	.	.	.	–	93.3	80.0	**0.51**
9	.	.	.	.	.	.	.	.	–	90.9	**0.48**
10	.	.	.	.	.	.	.	.	.	–	**0.37**

Of the 95 species identified in our study, approximately 59% of all occurrences were as singletons. We compared this singleton rate to that from 20 other published reports for rotifers and found the singleton rate to vary widely ranging from ca. 14% in a series of floodplain lakes in India to ≥ 60% from ponds and reservoirs in Aguascalientes (Mexico). In general the highest rates of singleton occurrence were from sites in arid regions (Fig. 3), although Shiel et al. (1998) report a lower singleton rate (ca. 43%) in the ephemeral pools of the floodplain of the River Murray in southeastern Australia. While rates of singletons are higher in our data set than those found by Shiel and his colleagues in other arid regions, they are less than those found for microbes and slightly higher than those found in certain leaf-feeding insects (Mao and Colwell 2005). Elevated rates in BBNP waters may be partially explained by the fact that many samples contained low densities of rotifers, thus considerable time was spent searching for rotifer individuals. This may not be the case in samples from other regions, which have higher overall abundances.

Of the 56 singleton species, the majority (45%) were present in the pools of Cattail Spring. Collections from the two ponds collectively accounted for about 18% of singletons, whereas the tanks and tinajas together only accounted for about 16% of singletons. The Rio Grande accounted for only about 12.5% of singletons. The elevated level of singletons in Cattail Spring may be due to the relatively large size of this system, coupled with a diversity of habitats and the stable environment that it provides. Of the ten sessile species collected, nine occurred as singletons and seven were restricted to Cattail Spring. This may be due to the fact that this system has the most diverse hydrophyte community, thus providing the necessary substratum for these species. An additional six species were only present in tinajas, either of the Ernst Tinaja Series (*Anuraeopsis fissa*, *Hexarthra fennica, Trichocerca collaris,* and *Trichocerca* cf. *intermedia*) or of the Window Trail Tinaja Series (*Cephalodella doryphora* and *Proales daphnicola*). *Hexarthra fennica* is known from saline habitats (marine and inland waters (de Ridder 1960 cited by Koste 1978; Ruttner-Kolisko 1974). *Anuraeopsis fissa* is known as a warm stenotherm species (Koste 1978).

The level of dissimilarity in faunal composition in aquatic systems separated by 100s or 1000s of km as Dumont and Segers (1996) have documented is not at all surprising, but to find such large differences when the sites are within relatively close proximity as they are in BBNP is unexpected. We hypothesize that the high percentage of singletons, which may be responsible for the relative high STI and IFO values for these ten aquatic systems in BBNP, is probably due to a confluence of factors. While the distances between these systems are not great, these habitats are, nevertheless, very isolated from one another, thus in a biogeographic sense they are islands. Moreover,

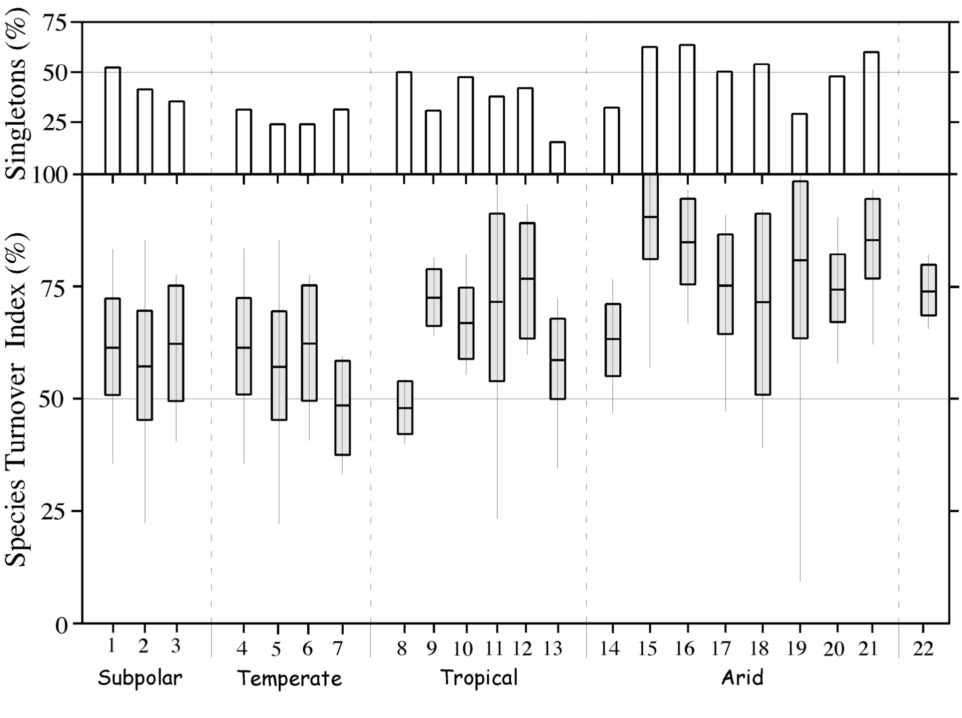

Fig. 3—Comparisons of Species Turnover Indices (STI) for selected studies. Box and whisker plots: Horizontal line = mean; Box = ±1S.D.; Whisker = range. (See Appendix 2 for a list of the works used in this analysis.)

each of these systems provides very different edaphic conditions in which only some species of rotifers can flourish. The most speciose habitats (Cattail Spring pools, the two ponds and the Rio Grande) account for about 75% of all the singletons and about 60% of all occurrences of the 95 species. We suggest that these habitats are more stable in providing both consistency in abiotic features and food web dynamics and so should be able to support a more diverse rotifer community.

While rotifers were once thought to have a cosmopolitian distribution, that view has been questioned by several authors (e.g., Dumont and Segers 1996) and it is now recognized that most species are not widely distributed. Unfortunately, we still do not understand local dispersal and habitat colonization. We do know that rotifer dispersal rates via wind, connectivity of systems through rainfall, and waterfowl are low (Jenkins and Underwood 1998) and that habitat permanence, resource availability, and colonization history (dispersal) were important in determining species richness through time in artificial freshwater pools (Jenkins 1995; Holland and Jenkins 1998).
On the other hand, Cáceres and Soluk (2002) found that rotifers are among the first metazoans to colonize newly established experimental ponds within a few weeks. Shurin (2000) also demonstrated that the ability of rotifers to successfully invade a habitat is based on the existing current biodiversity of that habitat. Despite these obstacles to colonization and population establishment, over 100 rotifer species are present in the ten relatively small, isolated habitats we examined here in BBNP.

How these species initially colonize and subsequently re-establish their populations after droughts that dry up the pools or spates that washout the community remains unknown. Although it becomes clear that diapausing eggs of monogonont rotifer species are much more drought resistant than previously thought and are able to hatch even after years of dry conditions in the desert (Walsh, unpublished observations), it is probably a combination of dispersal between habitats and emergence from the diapausing egg banks that accounts for the re-establishment of populations after drought and washout events.

Despite their unique biodiversity and abiotic conditions, desert waters have long been neglected by aquatic ecologists (Williams 1985, 1988; Erman and Erman 1995; Shiel et al. 1998). This neglect stems in part from difficulties in locating springs and their widespread distribution (Williams 1988; Shepard 1993) and the temporary nature of playas and tinajas (Williams 1985; Loring et al. 1988; Mackay et al. 1990). Our study is the first to focus solely on rotifers in a comprehensive way over a broad array of northern Chihuahuan Desert waters. As such it is a contribution to understanding the biodiversity of the microfauna of these rare waters.

The need for a substantial synoptic inventory, or ATBI, of biota components of Chihuahuan Desert aquatic systems still remains. Such efforts are especially important in light of the dramatic loss of these habitats in historic times (e.g., Brune 1981). However, such studies should not exclude important taxonomic components just because they are small and relatively difficult to collect and identify. In addition, expeditionary studies on isolated sites are usually limited to collections from a single date, and it is rare for researchers to have the opportunity to return to resample a site far from their home institution. Thus it can be difficult to accurately assess biodiversity of these habitats. In lieu of collecting living material, employing May's (1986, 1987) technique of collecting sediment samples to hatch out resting eggs under a variety of environmental conditions may help determine true levels of diversity.

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Literature Cited

Anon. 1990. *National Geographic Trails Illustrated Topographical Map to BBNP*. National Geographic Society, Washington, D.C. (ISBN 0-925873-77-2).

Anon. 2000. *The Chihuahuan Desert: An Endangered Space*. World Wildlife Fund. 1250 24th Street, NW, Washington. DC.

Bane, C.A., and O.T. Lind. 1978. The benthic invertebrate standing crop and diversity of a small desert stream in the Big Bend National Park, Texas. *Southwestern Naturalist* 23:215–226.

Berzins, B. 1951. On the Collothecacean Rotatoria, with special reference to the species found in the Aneboda district, Sweden. *Arkiv för Zoologi* 1(37):565–592.

Bowman, T.E. 1981. *Thermosphaeroma milleri* and *T. smithi*, new sphaeromatid isopod crustaceans from hot springs in Chihuahua, Mexico, with review of the genus. *Journal of Crustacean Biology* 1:105–122.

Bowman, T.E. 1985. *Thermosphaeroma cavicauda* and *T. macrura*, new sphaeromatid isopods from Mexican hot springs. *Proceedings of the Biological Society of Washington* 98:1042–1047.

Brune, G. 1981. *Springs of Texas*. Vol. One. Branch Smith, Inc. Fort Worth, Texas.

Cáceres, C.E. and D.A. Soluk. 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. *Oecologia* 131:402–408.

Cole, G.A., and C.A. Bane. 1978. *Thermosphaeroma subequalum* n. gen., n. sp. (Crustacea: Isopoda) from Big Bend National Park, Texas. *Hydrobiologia* 59:223–228.

Cole, G.A., and W.L. Minckley. 1966. *Speocirolana thermydronis*, a new species of cirolanid isopod crustacean from central Coahuila, México. *Tulane Studies in Zoology* 13:17–22.

Cole, G.A., and W.L. Minckley. 1969. Occurrence of the asellid subfamily Stenasellinae (Crustacea, Isopoda) in the Western Hemisphere, with description of a new genus and species. *International Journal of Speleology* 3(3+4):317–338.

De Smet, W.H. 1988. Rotifers from Børnøya (Svalbard), with the description of *Cephalodella evabroedi* n.sp. and *Synchaeta lakowitziana artica* n. subsp. *Fauna Norvegica Series A* 9:1–18.

De Smet, W.H. 1996. Rotifera. Volume 4: The Proalidae (Monogononta). In: T. Nogrady, editor. *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*, volume 9. SPB Academic Publishing, The Hague, The Netherlands.

De Smet, W.H. 2001. Freshwater Rotifera from plankton of the Kerguelen Islands (Subantarctica). *Hydrobiologia* 446/447:261–277.

De Smet, W.H., and L. Beyens. 1995. Rotifers from the Canadian High Arctic (Devon Island, Northwest Territories). *Hydrobiologia* 313/314:29–34.

De Smet, W.H., and R. Pourriot. 1997. Rotifera. Volume 5: The Dicranophoridae (Monogononta) and: The Ituridae (Monogononta). In T. Nogrady editor. *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*, volume 12. SPB Academic Publishing, The Hague, The Netherlands.

Dinerstein, E., D. Olson, J. Atchley, C. Loucks, S. Contreras-Balderas, R. Abell, E. Inigo, E. Enkerlin, C. Williams, and G. Castilleja. 2000. *Ecoregion-based Conservation in the Chihuahuan Desert: A Biological Assessment.* World Wildlife Fund.

Donner, J. 1965. *Ordnung Bdelloidea. Bestimmungsbücher zur Bodenfauna Europas*. Akademie-Verlag, Berlin.

Dumont, H.J., and H. Segers. 1996. Estimating lacustrine zooplankton species richness and complementarity. *Hydrobiologia* 341:125–132.

Edmondson, W.T. 1959. Rotifera. In: W.T. Edmondson, editor. *Fresh-water Biology*, 2nd edition. John Wiley & Sons, Inc., New York. Pages 420–494.

Ejsmont-Karabin, J. 1995. Rotifer occurrence in relation to age, depth and trophic state of quarry lakes. *Hydrobiologia* 313/314:21–28.

Erman, N.A., and D.C. Erman. 1995. Spring permanence, Trichoptera species richness and the role of drought. *Journal of Kansas Entomological Society* 68:50–64.

Gloyd, L.K. 1958. The dragonfly fauna of the Big Bend region of Trans-Pecos Texas. *Occasional Papers, Museum of Zoology, University of Michigan* 593:1–23.

Green, J. 1985. Horizontal variations in associations of zooplankton in Lake Kariba. *Journal of Zoology, London (A)* 206:255–239.

Green, J. 1995. Association of planktonic and periphytic rotifers in a Malaysian estuary and two nearby ponds. *Hydrobiologia* 313/314:47–56.

Hamilton, D.A. 2000. A limnological comparison of two freshwater springs in the Chihuahuan Desert. Unpublished M.S. thesis, Midwestern State University, Wichita Falls, Texas.

Hampton, S. E., and J. J. Gilbert. 2001. Observations of insect predation on rotifers. *Hydrobiologia* 446/447:115–121.

Hershler, R., H.P. Liu, and M. Mulvey. 1999. Phylogenetic relationships within the aquatic snail genus *Tryonia*: implications for biogeography of the North American Southwest. *Molecular Phylogenetics and Evolution* 13:377–391.

Holland, T.A. and Jenkins, D.G. 1998. Comparison of the processes regulating zooplankton assemblages in new freshwater pools. *Hydrobiologia* 387/388:207–214.

Jenkins, D.G. 1995. Dispersal-limited zooplankton distribution and community composition in new ponds. *Hydrobiologia* 313/314:15-20.

Jenkins, D.G., and M.O. Underwood 1998. Zooplankton may not disperse readily in wind, rain, or waterfowl. *Hydrobiologia* 387/388:15–21.

Jose de Paggi, S., S. Radwan, I. Bielanska-Grajner, H. Segers, W. De Smet, E.D. Hollowday, and L. Sanoamuang. 2002. Rotifera. Volume 6: Asplanchnidae, Gastropodiae, Lindiidae, Microcodidae, Synchaetidae, Trochosphaeridae and *Filinia*. In: T. Nogrady and H. Segers, editors. *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*, volume 18. SPB Academic Publishing, The Hague, The Netherlands.

Klimowicz, H. 1967. Rotifers of astatic waters. Part II. Rotifers of small water bodies from the Mikolajki region. *Polskie Archiwum Hydrobiologii* 14:91–110.

Koste, W. 1978. *Rotatoria. Die Rädertiere Mitteleuropas*. 2 volumes. Gebrüder Borntraeger, Berlin, Stuttgart, Germany.

Lind, O.T., and C.A. Bane. 1980. Aquatic ecosystems of Big Bend National Park: Biological and chemical indicators of water quality. *Proceedings of the Second Conference on Scientific Resources in National Parks. Volume 2: Aquatic Biology*, San Francisco, CA. Pages 7–29.

LORING, S.J., W.P. MACKAY, AND W.G. WHITFORD. 1988. Ecology of small desert playas. In: J.L. Thames and C.D. Ziebell, editors. *Small Water Impoundments in Semi-arid Regions*. University of New Mexico Press, Albuquerque. Pages 89–113.

MACKAY, W.P., S.J. LORING, T.M. FROST, AND W. G. WHITFORD. 1990. Population dynamics of a playa community in the Chihuahuan Desert. *Southwestern Naturalist* 35:393–402.

MAO, C.X. AND R.K. COLWELL. 2005. Estimation of species richness: mixture models, the role of rare species, and inferential challenges. *Ecology* 86:1143–1153.

MAY, L. 1986. Rotifer sampling – a complete species list from one visit? *Hydrobiologia* 134:117–120.

MAY, L. 1987. Effect of incubation temperature on the hatching of rotifer resting eggs collected from sediments. *Hydrobiologia* 147:335–338.

MAZUELOS, N., J. TOJA, AND C. GUISANDE. 1993. Rotifers in ephemeral ponds of Doñana National Park. *Hydrobiologia* 255/256:429–434.

NOGRADY, T. 1982. Correlation of rotifer associations in a chain of lakes fed by reclaimed sewage. *Hydrobiologia* 89:277–284.

NOGRADY, T., R. POURRIOT, AND H. SEGERS. 1995. Rotifera. Volume 3: The Notommatidae and: The Scaridiidae. In: T. Nogrady, editor. *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*, volume 8. SPB Academic Publishing, The Hague, The Netherlands.

NOGRADY, T., R. L. WALLACE, AND T. W. SNELL. 1993. Rotifera. Volume 1: Biology, Ecology and Systematics. In: T. Nogrady, editor. *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*, volume 4. SPB Academic Publishing, The Hague, The Netherlands.

OLSEN, D.M. AND E. DINERSTEIN. 1998. The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conservation Biology* 12(3):502–515.

ÖRSTAN, A. 1995. A new species of bdelloid rotifer from Sonora, Mexico. *Southwestern Naturalist* 40:255–258.

RICCI, C. AND G. MELONE. 2000. Key to the identification of the genera of bdelloid rotifers. *Hydrobiologia* 418:73–80.

RICCI, C., L. VAGHI, AND M.L. MANZINI. 1987. Desiccation of rotifers (*Macrotrachela quadricornifera*): survival and reproduction. *Ecology* 68:1488–1494.

RICO-MARTÍNEZ, R. AND M. SILVA-BRIANO. 1993. Contribution to the knowledge of the Rotifera of Mexico. *Hydrobiologia* 255/256:467–474.

RUTTNER-KOLISKO, A. 1974. Planktonic Rotifers: biology and taxonomy. *Die Binnergewässer* (suppl.), 26:1–146.

SAMPAIO, E.V., O. ROCHA, T. MATSUMURA, AND J.G. TUNDISI. 2002. Composition and abundance of zooplankton in limnetic zone of seven reservoirs of the Paranapanema River, Brazil. *Brazialian Journal of Biology* 62:525–545.

SARUKHÁN, J. AND A. WHYTE, 2005. *Millennium Ecosystem Assessment. Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington, DC.

SEGERS, H. 1995. Rotifera. Volume 2: The Lecanidae (Monogononta). In: T. Nogrady, editor. *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*, volume 6. SPB Academic Publishing, The Hague, The Netherlands.

SEGERS, H. 2002. The nomenclature of the Rotifera: annotated checklist of valid family- and genus-group names. *Journal of Natural History* 36:631–640.

SEGERS, H. AND H.J. DUMONT. 1993. Rotifera from Arabia, with descriptions of two new species. *Fauna of Saudi Arabia* 13:3–26.

SEGERS, H. AND H.J. DUMONT. 1995. 102+ rotifer species (Rotifera: Monogononta) in Broa reservoir (SP., Brazil) on 26 August 1994, with the description of three new species. *Hydrobiologia* 316:183–197.

SEGERS, H., N. EMIR, AND J. MERTENS. 1992. Rotifera from north and northeast Anatolia (Turkey). *Hydrobiologia* 245:179–189.

SEGERS, H.C., S. NWADIARO, AND H.J. DUMONT. 1993. Rotifera of some lakes in the floodplain of the River Niger (Imo State, Nigeria). *Hydrobiologia* 250:63–71.

SHARMA, B.K., AND S. SHARMA. 2001. Biodiversity of Rotifera in some tropical floodplain lakes of the Brahmaputra river basin, Assam (N.E. India). *Hydrobiologia* 446/447:305–313.

SHEPARD, W. D. 1993. Desert springs - both rare and endangered. *Aquatic Conservation: Marine and Freshwater Ecosystems* 3:351–359.

SHIEL, R.J., J.D. GREEN, AND D.L. NIELSEN. 1998. Floodplain biodiversity: why are there so many species? *Hydrobiologia* 387/388:39–46.

SHURIN, J.B. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* 81:3074–3086.

SHUSTER, S. 1981. Life history characteristics of *Thermosphaeroma thermophilum*, the Socorro isopod (Crustacea: Peracarida). *Biological Bulletin* 161:291–302.

STEMBERGER, R.S. 1979. *A Guide to Rotifers of the Laurentine Great Lakes*. United States Environmental Protection Agency, Cincinnati, Ohio. (Available from National Technical Information Service, Springfield, Virginia. PB80-101280)

SUÁREZ-MORALES, E., AND J.W. REID. 1998. An updated list of the free-living freshwater copepods (Crustacea) of Mexico. *Southwestern Naturalist* 43(2):256–265.

SUÁREZ-MORALES, E., AND J.W. REID. 2003. An updated checklist of the continental copepod fauna of the Yucatan Peninsula, Mexico, with notes on its regional associations. *Crustaceana* 76(8):977–992.

SUÁREZ-MORALES, E., M. SILVA-BRIANO, AND M. ELÍAS-GUTIÉRREZ. 2000. Redescription and taxonomic validity of *Leptodiaptomus cuauhtemoci* (Osorio-Tafall, 1941) (Copepoda, Calanoida), with notes on its known distribution. *Journal of Limnology* 59(1):5–14.

VOGEL, A.H., R.R. PETERSEN, AND V.J. KELLY. 2000. Zooplankton colonization of two new lakes, Mt. St. Helens, Washington, U.S.A. *Verhandlungen Internationale Vereinigung Limnologie* 27:785–790.

WALLACE, R.L. AND C. RICCI. 2002. Rotifera. In: S. D. Rundle, A. L. Robertson, and J. M. Schmid-Araya, editors. *Freshwater Meiofauna: Biology and Ecology*. Backhuys Publishers, Leiden, The Netherlands. Pages 15–44.

WALLACE, R.L. AND T.W. SNELL. 2001. Rotifera. In: J. Thorp and A. Covich, editors. *Ecology and Classifications of North American Freshwater Invertebrates*, 2nd edition. Academic Press, New York. Pages 195–254.

WALLACE, R.L., E.J. WALSH, M.L. BONILLA, AND P. L. STARKWEATHER. 2005. Life on the edge: Rotifers from springs and ephemeral waters in the Chihuahuan Desert, Big Bend National Park (Texas, U.S.A.). *Hydrobiologia* 546:147–157.

WALSH, E.J. 1995. Habitat-specific predation susceptibilities of a littoral rotifer to two invertebrate predators. *Hydrobiologia* 313/314:205–211.

WILLIAMS, W.D. 1985. Biotic adaptations to temporary lentic waters, with special reference to those in semi-arid and arid regions. *Hydrobiologia* 125:85–110.

WILLIAMS, W. D. 1988. Limnological imbalances: an antipodean viewpoint. *Freshwater Biology* 20:407–420.

Appendix 1: Location of study sites.

1. Burro Spring (spring/seep and stream complex; *n* = 4) [29°14.250'N; 103°25.550'W]
2. Cattail Spring Pools (spring with a stepping-stone pattern of pools; *n* = 7) [29°16.391'N; 103°20.133'W]

3. Ernst Tinaja (ephemeral stream with a stepping-stone pattern of tinajas; *n* = 5) [29°15.359–15.412'N; 103°00.605–00.712'W]

4. Glenn Spring (spring/stream complex; *n* = 3) [29°.10.465–10.525'N; 103°09.400–10.500'W]

5. Paint Gap Cattle Tank (tank; *n* = 4) [29°23.276'N; 103°18.149'W]

6. Rio Grande (river + a pond and canal fed from the river; *n* = 5)

7. Rio Grande Village Lower Pond (pond; *n* = 7) [29°10.717'N; 102°57.226'W]

8. Rio Grande Village Upper Pond (pond, *n* = 6) [29°10.711'N; 102°57.197'W]

9. Tule Cattle Tank (tank; *n* = 5) [29°14.525'N; 103°26.550'W]

10. Window Trail (ephemeral stream with a stepping-stone pattern of tinajas; *n* = 5) [29°16.800'N; 103°19.785–19.835'W]

Appendix 2—Works used in the analysis of STI values for water bodies worldwide.

Subpolar regions

1. Selected sites on Kerguelen Island (Subantarctic) (sites, *n* = 7; total taxa, *n* = 32) [De Smet, 2001]

2. Sites on Devon Island (N.W.T., Canada) (sites, *n* = 9; total taxa, *n* = 70) [De Smet and Beyens, 1995]

3. Pools on Bear Island (Børnøya) (sites, *n* = 6; total taxa, *n* = 49) [De Smet, 1988]

Temperate zone

4. Abandoned quarries in Poland (sites, *n* = 15; total taxa, *n* = 77) [Ejsmont-Karabin, 1995]

5. Small astatic pools and ponds in Poland (sites, *n* = 16; total taxa, *n* = 123) [Klimowicz, 1967]

6. Paternoster lakes fed by reclaimed sewage in Santee (California, USA) (sites *n* = 7, total taxa, *n* = 50) [Nogrady, 1982]

7. Recently formed lakes near Mount St. Helens (Washington State, USA) (sites, *n* = 3; total taxa, *n* = 15) [Vogel et al., 2000]

APPENDIX 2—*continued*

Tropical zone
8. Lake Kariba in Zimbabwe (sites, *n* = 3; total taxa, *n* = 30) [Green, 1985]

9. Malaysian estuary (sites, *n* = 5; total taxa, *n* = 62) [Green, 1995]

10. Reservoirs, Paranapanema River in Brazil (sites, *n* = 7; total taxa, *n* = 66) [Sampaio et al., 2002]

11. Broa Reservior in Brazil (sites, *n* = 12; total taxa, *n* = 104) [Segers and Dumont, 1995]

12. Floodplain lakes of the River Niger in Nigeria (sites, *n* = 6; total taxa, *n* = 213) [Segers et al., 1993]

13. Floodplain lakes of the Brahmaputra River in India (sites, *n* = 7; total taxa 118) [Sharma and Sharma, 2001]

Arid regions
14. Selected ephemeral Ponds, Donana National Park in Spain (sites, *n* = 5; total taxa, *n* = 22) [Mazuelos et al., 1993]

15. Ponds, Aquascalientes in México (sites, *n* = 8; total taxa, *n* = 38) [Rico-Martínez and Silva-Briano, 1993]

16. Reservoirs, Aquascalientes in México (sites, *n* = 5; total taxa, *n* = 43) [op. cit.]

17. Selected sites in Oman (sites, *n* = 9; total taxa, *n* = 66) [Segers and Dumont, 1993]
18. Selected sites in Saudi Arabia (sites, *n* = 4; total taxa, *n* = 30) [op. cit.]

19. Selected sites in Yemen (sites, *n* = 12; total taxa, *n* = 62) [op. cit.]

20. Selected sites in Turkey (sites, *n* = 8; total taxa, *n* = 97) [Segers et al., 1992]

21. Big Bend National Park (sites, *n* = 10; total taxa, *n* = 101) [this study]

Lakes World-wide
22. Africa, Australia, Europe, North America, South America (sites, *n* = 7; taxa, species richness, range = 100–210) [Dumont and Segers, 1996]