THE HARPACTICOID AND CYCLOPOID COPEPOD FAUNA IN THE CERRADO REGION OF CENTRAL BRAZIL. 1. SPECIES COMPOSITION, HABITATS, AND ZOOGEOGRAPHY

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RESUMO: A fauna de copépodes (Harpacticoida e Cyclopoida) da região do cerrado no Brasil central. 1. A composição, os habitats e as relações zoogeográficas. Foi estudada a fauna dos copépodes (Crustacea) das ordens Harpacticoida e Cyclopoida na região do cerrado no Brasil central. Os tipos de habitats úmidos investigados incluíram o plâncton e a zona litorânea de lagos, lagoas e represas; brejos perenes; campos úmidos e solos permanentemente saturados; habitats lóticos; o interstitial arenoso; algas e musgos úmidos perto de cachoeiras e riachos; terras úmidas efêmeras; e habitats especiais como cavernas e uma lagoa térmica. Foi registrado o total de 43 espécies e subespécies de harpacticóides e 36 espécies e subespécies de ciclopóides. Entre os harpacticóides, 22 espécies ocorreram somente em um tipo de habitat, e 21 espécies foram coletadas em dois ou mais habitats distintos. Nove espécies de ciclopóides ocorreram somente na zona litorânea e/ou pelágica de águas abertas, quatro em somente um outro tipo de habitat, e os outros 23 em dois ou mais habitats distintos. A fauna de harpacticóides é diversa e altamente endêmica, com 34 espécies conhecidas somente da região; cinco espécies ocorrem em outras áreas da América do Sul, e quatro são pantropicas ou circunglobais. O grau de endemismo da fauna de ciclopóides é menor, embora ainda alta, com 10 espécies endêmicas, 19 sulamericanas, e sete pantropicais ou circunglobais. Somente uma espécie do grupo harpacticóide *Delachauxiella* e uma do gênero *Potamocaris* foram encontradas, enquanto que o gênero *Forficatocaris* é bem representado (11 espécies). A maioria das espécies ciclopóides são membros da fauna tropical e subtropical sulamericana, embora alguns gêneros, como *Mesocyclops*, têm poucos representantes no cerrado. A fauna planctônica é pouco diversificada, com somente seis espécies.

ABSTRACT: The Harpacticoid and Cyclopoid copepod fauna in the cerrado region of central Brasil. 1. Species composition, habitats, and zoogeograph. *The copepod (Crustacea) fauna of the orders Harpacticoida and Cyclopoida was studied in the cerrado region of central Brazil. Wetland types sampled included the plankton and littoral zones of open waters, perennial marshes, wet campos and perennially saturated soils, lotic habitats, the sand-interstitial, wet mosses and algae near waterfalls and streams, ephemeral wetlands, and special habitats including caves and a thermal pond. A total of 43 species and subspecies of harpacticoids and 36 species and subspecies of cyclopoids was recorded. Among harpacticoids, 22 species occurred in only a single habitat type, and 21 were collected in two or more distinct habitats. Nine species of cyclopoids occurred only in the littoral or pelagic zones of open waters, four species in only a single habitat of another type, and the other 23 in two or more distinct habitats. The harpacticoid fauna is species-rich and highly endemic, with 34 species*

known solely from the region; five species occur also in other areas of South America, and four are pantropical or circumglobal. The degree of endemism of the cyclopoid fauna is less, although still high, with ten endemic, 19 South American, and seven pantropical or circumglobal species. Only one species of the harpacticoid Delachauxiella-group and one member of the genus Potamocaris were encountered in the region, but the genus Forficatocaris is well represented with 11 species. Most cyclopoid species are members of the tropical and subtropical South American fauna, although the cerrado fauna has few representatives of certain genera such as Mesocyclops. The true plankton fauna includes only six species.

INTRODUCTION

The aquatic microcrustacean fauna of the cerrado (savana) region in central Brazil is incompletely know. Taxonomic and ecological inderstanding of benthic and planktonic copepod and cladoceran communities is essential for comprehension of the functioning of aquatic systems, since these numerous and ubiquitous microcrustaceans play a central role as primary and secondary consumers in food webs and are an essential component of the food of many fishes. Knowledge of the distribution of species and genera, especially of benthic species which may be less vagile than planktonic forms, is likely to provide valuable insight into biogeographical questions. The cerrado facies includes a rich array of wetland habitats (Bastos & Lourenço, 1983), some of these supporting highly diverse copepod communities (Reid, 1984). The area is of great biogeographical interest because of its location on the Brazilian Shield, between the Amazon forests to the north, the lower Paraná valley to the south and west,
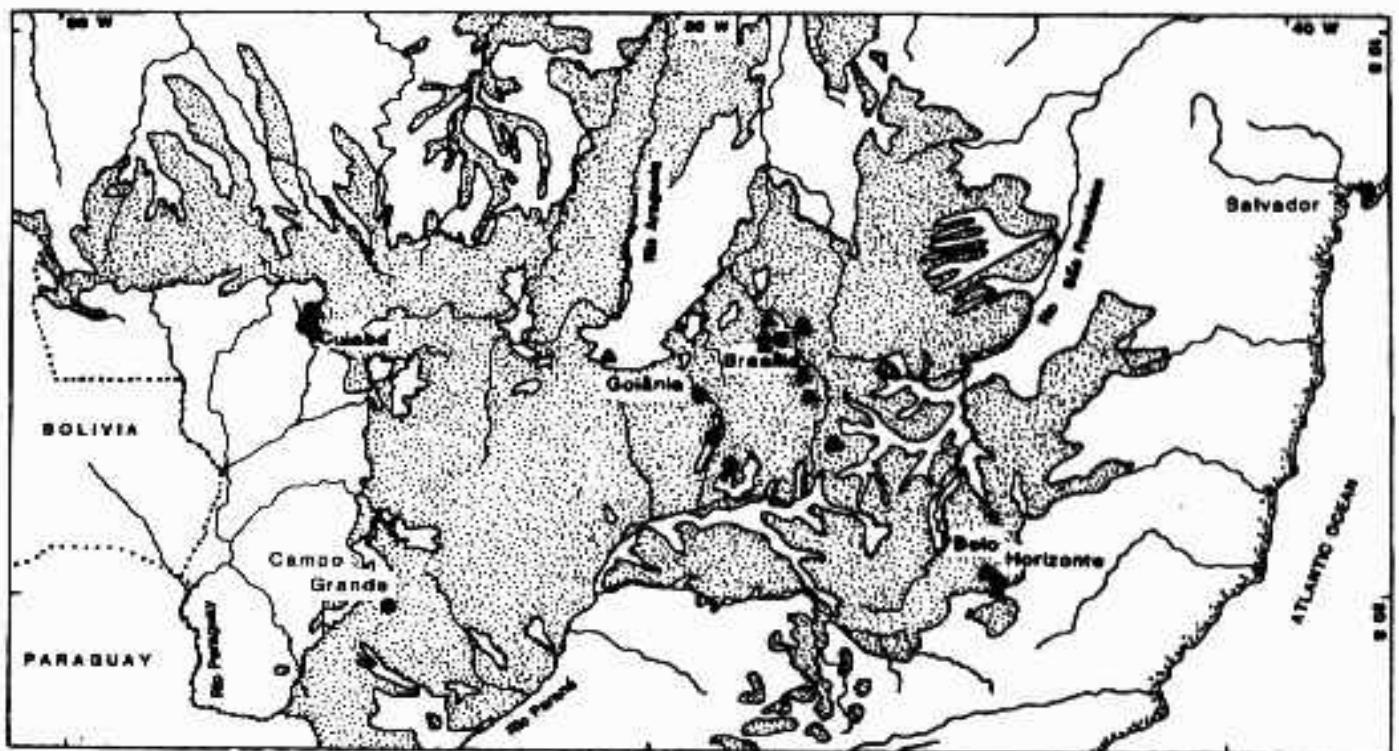

Figura 1 – Principal localities (triangles) investigated in the cerrado region (shaded) of central Brazil.

and coastal Brazil to the east, including parts of the drainage basins of the three major interior river systems of South America, the Paraná, Amazon and São Francisco. The few taxonomic publications on the harpacticoid and cyclopoid copepods of the region have treated so far only a few taxa or the communities of certain habitats and limited areas (Matsumura-Tundisi, 1986, Matsumura-Tundisi & Rocha, 1983, Reid, 1982, 1984, 1985, 1987a, c, 1988a, 1989, 1990b,c, 1991a, b; Reid & José, 1987, Reid & Saunders, 1987, Reid *et al.*, 1988, Rocha & Matsumura-Tunsidi, 1976). This article summarizes these reports as well as unpublished results of collections made mostly during 1978-1982 from open-water and wetland habitats of the cerrado, and discusses species composition, habitat preferences of species and genera, and biogeographical relationships of selected taxa.

AREA OF STUDY

The geographical area investigated includes parts of the States of Bahia, Goiás, Mato Grosso, Minas Gerais, and the Distrito Federal, and covers the central cerrado region from Cuiabá in the west to central Bahia and Belo Horizonte in the east (fig. 1). The climate is humid tropical; annual rainfall is about 1500mm, but varies greatly across the region and annually; and the dry season is pronounced, lasting four to six months in most areas (Reis, 1971). Predominant soils are acidic red and yellow laterite clays, grading to variable hydromorphic soils in poorly drained areas (Ranzani, 1971). Water tends to be acid and most lakes and ponds extremely oligotrophic except when influenced by human settlement and agricultural activities. Most samples were taken from the Distrito Federal and neighboring parts of Goiás, many in protected areas such as the Águas Emendadas Biological Reserve, the Distrito Federal National Park, and the Fazenda Água Limpa, the experimental farm of the University of Brasília, all in the Distrito Federal. Most individual localities are listed in the succeeding article (Reid, 1993) and will be described more fully elsewhere.

MATERIAL E METHODS

Specimens were taken by plankton net in open waters and among macrophytes. Bottom samples were taken by Ekman grab in deeper waters, or by hand in nearshore and semiterrestrial localities. Specimens were preserved in 5% formalin and later studied by the methods described in preceding articles (Reid, 1982; Reid & José, 1987).

RESULTS AND DISCUSSION

1. Species composition and habitat relationships

The copepod species together with the range of habitats occupied and general geographical distribution of each are listed in tab. I. Since taxonomic descriptions of 35 species are in progress, each is indicated by letter rather than by name in the present article. Habitats are classified generally by presence or absence and permanency of open water, and by type of substrate. Categories correspond in general to those used by Lewis (1984) for a similar classification of the

Table I – Species of harpacticoid and cyclopoid copepods from the cerrado region of central Brasil. Habitat type: A, Open waters; B, Littoral-benthic; C, Perennial marshes; D, Wet campos; E, Lotic; F, Sand-Interstitial; G, Dripping Moss; H, Ephemeral; I, Special Distribution: 1, circumglobal or pantropical; 2, South American-neotropical; 3, Cerrado. River drainage basin: 1, Paraná; 2, Amazon; 3, São Francisco.

SPECIES	HABITATS	DISTR.	BASIN
Order Harpacticoida			
Family Canthocamptidae			
Attheyella s. l. *jureiae* POR & HADEL, 1986	B C D E · · H	2	1 2 3
Attheyella (Chappuisiella) fuhrmanni (THIÉBAUD, 1914)	B C	2	1 · 3
Attheyella (Chappuisiella) a	B · D E	3	1
Attheyella (Chappuisiella) b	B C D	3	1 · 3
Attheyella (Chappuisiella) c	I	3	2
Attheyella (Chappuisiella) d	A B · D E · G	3	1 2 3
Attheyella (Chappuisiella) e	H	3	2
Attheyella (Chappuisiella) f	D	3	1
Attheyella (Chappuisiella) g	C · G	3	1
Attheyella (Chappuisiella) h	B	3	1
Attheyella (Chappuisiella) i	D E	3	1 · 3
Attheyella (Chappuisiella) j	B · E	3	1 2 3
Attheyella (Chappuisiella) k	G	3	1
Attheyella (Delachauxiella) a	D	3	1
Canthocamptus s. l. *a*	D	3	1
Elaphoidella bidens (SCHMELL, 1894), incl. *E. bidens coronata* (SARS, 1904)	A B C · E	1	1 · 3
Elaphoidella bidens a	A B C	2	1 · 3
Elaphoidella grandidieri (GUERNE & RICHARD, 1893)	B C D E · · H	1	· 2 3
Elaphoidella parajokobii REID & JOSÉ, 1987	G · I	3	1 2
Elaphoidella pintoae REID & JOSÉ, 1987	I	3	2
Elaphoidella schubarti CHAPPUIS, 1936	D · G	2	1 2
Elaphoidella suarezi REID, 1987	A B C · E · G	2	1 · 3
Elaphoidella a	G	3	1
Epactophanes richardi MRÁZEK, 1893	D E · G	1	1
Family Parastenocarididae			
Forficatocaris schadeni REID, 1982	B · D E	3	1
Forficatocaris a	D · · H	3	1
Forficatocaris b	D · · H	3	1
Forficatocaris c	D	3	1
Forficatocaris d	D	3	1
Forficatocaris e	D	3	1
Forficatocaris f	D · G	3	1
Forficatocaris g	D	3	1
Forficatocaris h	B	3	· · 3
Forficatocaris j	B	3	1
Forficatocaris k	D	3	1
Parastenocaris a	D · · H	3	1
Parastenocaris b	D	3	1
Parastenocaris c	D · · H	3	1
Parastenocaris d	D	3	1
Parastenocaris e	D	3	1
Potamocaris cuiabaensis REID, 1991b	F	3	1
Parastenocarididade n.g.a.	D	3	1
Family Phyllognathopodidae			
Phyllognathopus viguieri (MAUPAS, 1892)	G	1	1

Table I – Continued.

SPECIES	HABITATS	DISTR.	BASIN
Order Cyclopoida			
Ectocyclops herbsti DUSSART, 1984	A B C D E G H	2	1 2 3
Eucyclops agilis (KOCH, 1838)	A B C E	1	1 3
Eucyclops ensifer KIEFER, 1936	B	2	1
Eucyclops cf. *leptacanthus* KIEFFER, 1956	B C I	2	1
Eucyclops solitarius HERBST, 1959	E	2	1
Eucyclops a	B C	3	1 3
Macrocyclops albidus (JURINE, 1820)	B	1	1
Macrocyclops albidus principalis HERBST, 1962	E H	2	2
Macrocyclops cf. *fuscus* (JURINE, 1820)	B	1	1
Mesocyclops aspericornis (DADAY, 1906)	B	1	1 3
Mesocyclops longisetus (THIÉBAUD, 1914)	A B C	2	1 2 3
Mesocyclops meridianus (KIEFER, 1926)	B	2	3
Metacyclops campestris REID, 1987	C D	3	1
Metacyclops laticornis (LOWNDES, 1934)	B C	2	3
Metacyclops mendocinus (WIERZEJSKI, 1892)	A	2	1 3
Metacyclops a	I	3	2
Microcyclops alius (KIEFER, 1935)	B C E	2	1 3
Microcyclops anceps (RICHARD, 1897)	B C E I	2	1 2 3
Microcyclops cf. *ceibaensis* (MARSH, 1919)	C	2	2
Microcyclops finitimus DUSSART, 1984	A B C E	2	1 2 3
Microcyclops a	I	3	1
Muscocyclops bidentatus REID, 1987	D	3	1
Muscocyclops therasiae REID, 1987	C D	3	1
Neutrocyclops brevifurca (LOWNDES, 1934)	B	2	1 3
Paracyclops carectum REID, 1987	A B C D	3	1 3
Paracyclops fimbriatus chiltoni (THOMSON, 1882)	B C D E G H I	1	1 2 3
Ponticyclops boscoi REID, 1987	E	3	1
Thermocyclops decipiens (KIEFER, 1929)	A B	1	1
Thermocyclops inversus KIEFER, 1936	A B	2	3
Thermocyclops minutus (LOWNDES, 1934)	A B	2	3
Thermocyclops tenuis (MARSH, 1910)	A H	2	2
Tropocyclops federensis REID, 1991a	B	3	1
Tropocyclops nananae REID, 1991a	B C	3	1
Tropocyclops prasinus (FISCHER, 1860)	A I	1	1
Tropocyclops prasinus meridionalis (KIEFER, 1931)	A B D	2	1 2 3
Tropocyclops schubarti (KIEFER, 1935)	B C E H	2	1 2

harpacticoids of New Zealand, but additional distinctions have been made between the pelagic and littoral zones of open water to better characterize the cyclopoid species; and between perennial marshes with standing water and wet campo marshes and saturated soils with seasonally fluctuating groundwater levels. Lewis (1984) included no category for lotic habitats, except for that of water flowing slowly through and over dripping wet mosses. Some temperate zone habitat types such as *Sphagnum* bogs do not occur in the cerrado, and terrestrial moss, which does occur in scattered rochy areas, was not found to harbor copepods, probably because of lack of moisture during the long cerrado dry season.

A. OPEN WATERS. – This habitat type includes the pelagic zone of lakes, ponds, and reservoirs, such as Lago Paranoá, Lagoa Bonita (Mestre d'Armas), Lagoas da Península Norte, Represas Santa Maria and Santo Antônio do Descoberto (Distrito Federal), and Lagoa Formosa (Goiás). Several types of artificial water such as cattle ponds, tanks, and shallow dug wells are included. *Tropocyclops prasinus meridionalis* occurred in a wide range of such habitats, although usually not in eutrophic or polluted waters. In some highly productive waters, *Thermocyclops decipiens* was the dominant crustacean plankter (Reid, 1988a, 1989). Several species of cyclopoids and harpacticoids were collected in plankton as strays from the littoral zone.

B. LITTORAL-BENTHIC. – This category includes the littoral and benthic zones of water bodies with significant open areas, whether or not macrophytes were present. Several species such as *Attheyella h*, *Attheyella j*, *Neutrocyclops brevifurca*, and *Tropocyclops federensis* were collected in the littoral of small ponds with extensive macrophyte stands, but never from perennial marshes.

C. PERENNIAL MARSHES. – These habitats include "veredas", which are marshes dominated by dense stands of Cyperaceae and often buriti palms (Bastos & Lourenço, 1983); cattail and *Pontederia* marshes, in fact every type of perennial wetland without significant open water, developed on flat ground. Examples are perennial marshes near the Córregos Cabeça do Veado and Córrego do Acampamento, and the Campo de Vereda Grande in the Águas Emendadas Biological Reserve. No species was found to inhabit marshes exclusively, but several such as the harpacticoids *Attheyella b*, *Elaphoidella bidens*, and *Elaphoidella bidens a* and the cyclopoids *Eucyclops a*, *Mesocyclops longisetus*, *Metacyclops laticornis*, and *Tropocyclops nananae* occured predominantly in shallow perennial waters including marshes and the littoral of small ponds (Category B).

D. WET CAMPOS AND MOIST ORGANIC SOILS. – Wet campo (campo úmido) marshes are a usual feature in the cerrado along the uphill margins of gallery forests (Bastos & Lourenço, 1983; Reid, 1982, 1984, 1987a). In these perennial flush marshes, slowness of decomposition of organic matter permits development of highly organic, well-oxygenated soils which are a hospitable habitat for diverse meiofaunal communities. Although soils in uphill areas of a wet campo may dry considerably with lowering of the water table during the dry season, many species of copepods are able to persist during this period. Most wet campos not located in protected reserves have undergone disturbance by man to some extent, many having been drained for truck farming. Saturated or nearly-saturated organic lakeshore soils provide conditions similar to those in wet campos, and harbor similar although less species-rich faunas characterized by the presence of many species of the parastenocaridid genera *Forficatocaris* and *Parastenocaris* and an undescribed genus of Parastenocarididae, and the cyclopoid genus *Muscocyclops*. Several species of canthocamptids, both species of *Paracyclops*, and *Ectocyclops herbsti* are also prominent faunal components.

E. LOTIC HABITATS. – Bottom sediments and drift in small streams and below perennial springs yielded a number of species. Best-studied localities included the Olho d'Água da Onça on the Fazenda Água Limpa and the Ribeirão do Torto, and several small streams in the basin of the Rio São Bartolomeu, Distrito Federal. Principal faunal components are *Ectocyclops herbsti*, *Microcyclops anceps*, *Paracyclops fimbriatus chiltoni* and the rare endemic species *Ponticyclops boscoi*, known only from a small stream in a wet campo.

F. SAND-INTERSTITIAL HABITATS. – Sandy beaches and bottoms are a well known habitat of interstitial copepods. Since the soil in large areas of the cerrado is composed primarily of laterite clays, lakes, reservoirs and the smallest streams tend to lack significant accumulations of sand, and bottom sediments are usually composed of hard clay or silty organic deposits. The upper layers of small sandbanks in several larger cerrado streams were sampled without finding any interstitial species, possibly because the sand interstices were filled by fine silts (R. Whitman, personal communication). A sandy beach of the third-order stream Rio Coxipó in Cuiabá yielded the new species *Potamocaris cuiabaensis*.

G. DRIPPING MOSS, SPLASH AND SPRAY ZONES. – Mosses and algae near streams and in the splash and spray zones of waterfalls form a semi-interstitial, perennially wet habitat. Mosses near several waterfalls, such as the Cachoeira da Itiquira (Goiás) and several in the Chapada dos Guimarães (Mato Grosso), as well as along streams consistently contained *Ectocyclops herbsti*, sometimes *Paracyclops fimbriatus chiltoni*, and usually a few species of harpacticoids, particularly *Attheyella d* and *Attheyella g* and several species of *Elaphoidella*. In contrast to New Zealand, where Lewis (1984) reported that several species of harpacticoids occur exclusively or primarily in such habitats, in the Brazilian cerrado only two species, *Elaphoidella a* and *Phyllognathopus viguieri*, were limited to dripping moss.

H. EPHEMERAL WETLANDS. – Ephemeral habitats prospected in the cerrado included small temporary puddles filled during the rainy season. Puddles yielded several species of harpacticoids, as well as the only record of *Thermocyclops tenuis* in the central cerrado region. *Tropocyclops schubarti* was numerous in small forest pools in Mato Grosso. Also during the rainy season, cerrado clays may become temporarily saturated, sometimes with surface water present, although there is usually little or no surface organic matter beyond thin films of algae. A few species such as *Forficatocaris a*, *Forficatocaris b*, and *Parastenocaris a* were collected on such soils in the Fazenda Água Limpa, to which they had probably migrated from a nearby wet campo where they are numerous.

Also included in category H are moist but not saturated organic soils. As Lewis (1984) observed, many species of harpacticoids and cyclopoids are known to inhabit the thin surface film of moisture on damp leaf litter and soils. In the cerrado, however, organic matter which might retain such a film does not accumulate except to a slight extent in gallery forests, and even there, leaves decompose quickly. Samples of soil and litter from gallery forests did not yield copepods except from permanently saturated soil directly downhill from wet campos, which contained more or less the same species as in the campos proper. A very few species of harpacticoids were found in the damp but not saturated soil of a murundu (hummock) in the Campo Úmido da Onça on the Fazenda Água Limpa (Reid, 1984). Leaf litter in parts of Brazil which are more humid than the central cerrado does harbor copepods, and collections from litter in the State of São Paulo have yielded several species (Rocha & Bjornberg, 1987, 1988; Rocha & Reid, unpublished records).

I. SPECIAL HABITATS. – Lagoa Pirapitinga, a thermal pond in southern Goiás fed by hot springs, yielded a previously undescribed species of *Microcyclops*. Streams and pools in caves in Goiás also harbor several species of cyclopoids and harpacticoids (Reid & José, 1987; Reid, unpublished). *Elaphoidella pintoae* and *Metacyclops a* have been found only in caves, although

other species such as *Elaphoidella parajakobii* and *Eucyclops* cf. *leptacanthus* were collected in surface wetlands as well.

2. Geographical distribution of species within the cerrado region

Many connections between the Paraná, Amazon and São Francisco drainage basins now exist or have occurred in the past. The Águas Emendadas Biological Reserve protects an area where the Paraná and Amazon Rivers connect through a series of veredas. Although most collections in wet campos were made in the Paraná basin, several examples of other habitats were collected in each basin. As might be expected, common eurytopic species such as *Attheyella jureiae, Attheyella d, Attheyella j, Ectocyclops herbsti* (= *Ectocyclops rubescens* of Matsumura-Tundisi & Rocha, 1983), *Microcyclops anceps, Microcyclops finitimus, Paracyclops fimbriatus chiltoni*, and *Tropocyclops prasinus meridionalis* occurred in all three basins. *Mesocyclops longisetus* was also widespread in the littoral zone of lakes and ponds and in perennial marshes.

Several relatively common, eurytopic species were collected in the Paraná and São Francisco basins but not in the Amazon: the cerrado endemics *Attheyella b, Attheyella i, Elaphoidella bidens a,* and *Paracyclops carectum*; and the more widespread species *Elaphoidella bidens, Elaphoidella suarezi, Eucyclops agilis,* and *Microcyclops alius*. Records of *E. bidens* in South America include warm lowlands of Brazil (São Paulo and Rio Grande do Sul), Paraguay, Venezuela, and northern Argentina. The cosmopolitan *Eucyclops agilis* (= *E. serrulatus* Fischer) has been reported several times from southern Brazil and most other parts of South America, but never yet from the Amazon basin (Reid, 1985). The reported range of *M. alius* includes the equatorial Andes, Central America and Uruguay, so the records from the cerrado represent a significant range extension.

Only *Elaphoidella grandidieri* was collected from the Amazon and São Francisco basins but not from the Paraná.

Macrocyclops albidus principalis was found only in Amazon basin collections, and in fact seems to be confined to the Amazon and Orinoco systems (Reid, 1985). Most of the few other species collected only from the cerrado Amazon basin inhabit caves (tab. I).

Species collected only in the São Francisco basin were *Forficatocaris h, Mesocyclops meridianus, Metacyclops laticornis, Thermocyclops inversus* and *Thermocyclops minutus*. At least in the case of the cyclopoids, this impression of exclusivity is probably only a result of their comparative rarity in cerrado waters, since all have previously been collected in other continental drainage basins (Reid, 1985, 1989).

The find of *Potamocaris cuiabaensis*, a representative of a neotropical genus previously known only from Argentina and southeastern Brazil, in Cuiabá on the western edge of the cerrado, constitutes the northernmost known record of this genus and extends its known range nearly to the northern limit of the Paraná drainage basin (Reid, 1991b).

From present collection data it seems possible, therefore, to make a distinction between the Amazonian fauna on the one hand, and the Paraná and São Francisco faunas on the other. This is rather surprising in view of existing and former physical connections and the similarity in environmental conditions between large contiguous parts of the basins.

A second interesting aspect is an apparent distinction between the faunas of the northern Paraná basin at the Chapada dos Guimarães near Cuiabá, and the central and eastern cerrado areas of the same basin. The species *Attheyella e, g* and *k* and *Forticatocaris e, f* and *g* occurred

only in the western region, with similar but distinct species occurring in comparable habitats to the east. An analogous faunal break is seen in the genus *Muscocyclops*, in which western species are more closely related to Amazonian species than to those of the eastern Paraná and the Atlantic coast (Rocha & Bjornberg, personal communication). Possibly the Pantanal forms a barrier to the movement of more stenotopic and substrate-bound copepods.

3. Zoogeographical relationships of the cerrado fauna

The harpacticoid fauna of the cerrado is highly endemic, as predicted by Noodt (1969): only nine of 43 species have been collected elsewhere. Taxonomic questions complicate this interpretation, particularly in the case of the Canthocamptidae, a family with many inadequately described species. It seems more prudent to erect new taxa rather than doubtfully unite cerrado forms with incompletely known species, realizing that better knowledge of within-species variation will probably result in eventual synomyzation of some of the new taxa. A second problem is the lack of thorough collecting in organic-soil and wet campo habitats except in the central cerrado. Nevertheless it is clear that few species of canthocamptids and no species of parastenocaridids have been found in other areas of South America, even in the relativelly well-prospected central Amazon and upper Paraná valleys.

Among the four circumglobal or pantropical species of harpacticoids, *Elaphoidella bidens* was common and sometimes numerous, especially among macrophytes in perennial marshes and larger bodies of water, and also occurred in a few slowly moving streams. *Epactophanes richardi* was also common and often numerous in wet campo soil and associated springs and rivulets, and was found once in wet mosses bordering a stream. *Phyllognathopus viguieri*, a species nearly ubiquitous in moist soils in the temperate zone and more humid tropics, was found only once, in damp moss near a stream, but surprisingly never in the wet campo or saturated-soil habitat, nor did it ever occur together with *E. richardi*. *Elaphoidella grandidieri* is a pan-tropical, eurytopic species with a single possible previous record from continental South America (from São Paulo, as *Canthocamptus laciniatus*, by Douwe, 1911); my records of this species include the central Amazon basin, coastal Pernambuco and Sergipe, and Belo Horizonte, but my only record from the central cerrado region is from the Rio Paraim, Goiás, and affluent of the Amazon.

A few other species of Canthocamptidae found in the cerrado occur elsewhere in South America. The most widespread of these is *Attheyella fuhrmanni*, which has been reported from many localities in South America and also Costa Rica. Surprisingly though, *A. fuhrmanni* appears to be absent from the central cerrado region. My records of this species include two localities near Belo Horizonte, and otherwise outside the cerrado region in southern São Paulo, Pernambuco, and Rio de Janeiro (Reid, unpublished); the species has also been recorded from the southern cerrado in São Paulo State (Matsumura-Tundisi & Rocha, 1983; Rocha & Matsumura-Tundisi, 1976). In the central cerrado region, the primary niche of this species, the littoral-benthic zone of lakes and ponds, seems to be preoccupied by the morphologically similar *Attheyella j. Attheyella jureiae* is common, often numerous, and even more eurytopic than indicated in Tab. I, having been reported from bromeliads by Por & Hadel (1986). The known range of this species extends from Mato Grosso to the coast of São Paulo State (Reid, 1990b). *Elaphoidella schubarti* was previously known only from coastal Pernambuco; these collections have extended its known range to the Distrito Federal (Paraná basin) and to central Amazonia (Reid, unpublished). This is a stenotopic species, found

originally in wet moss near a spring, and recently in wet moss at Manaus (Rocha & Reid, unpublished data); in the cerrado it occurs only in wet campo soils. *Elaphoidella bidens a*, a previously undescribed member of the *bidens*-group, occurred in several waterbodies in the Paraná and São Francisco basins, often together with *E. bidens*; I have additional records from the Pantanal and coastal Pernambuco. *Elaphoidella suarezi*, known previously from artificial containers and small waterbodies in Colombia (Reid, 1987b, 1988b), is eurytopic in the cerrado region and was collected also in Lago do Abaeté on the coast of Bahia (Reid, unpublished).

At the genus level, the cerrado canthocamptid fauna has close affinities to neighboring South American faunas. Most members of this family belong to the species-rich *Chappuisiella*-group of *Attheyella*, which occurs over the whole continent as well as in New Zealand, Australia, Antarctica, and parts of Indonesia. The many previously undescribed species show close relationships, unsurprisingly, with species from neighboring regions to the north and south. The *Delachauxiella*-group has a similar Gondwanaland distribution extending to New Zealand and Australia, but in South America is largely confined to the southern part of the continent and to the Andes, with two or three species known from the southern Paraná basin in Argentina and Paraguay. The single *Delachauxiella*-group species from the cerrado was found only in one wet campo located near the northern extension of the Paraná basin. Possibly the stable environment afforded by the wet campo has permitted colonization of this habitad by a basically temperate-zone species. The species designated *Canthocamptus* s. 1. *a* in tab. I rather enigmatically presents a similar problem of distribution as *Attheyella* (*Delachauxiella*) *a*. It is known from only a single female specimen in the wet campo, and without knowledge of the male cannot be ascribed with certainty to genus. It is most closely related to the genus *Bryocamptus*, which is basically holarctic with a few representatives in New Zealand and tropical Asia. Although Lewis (1986) suggested that chance dispersal might account for the presence of *Bryocamptus* in New Zealand, it seems improbable for this to have occurred in a nearly untouched marsh in the middle of South America. Further collecting will be necessary to establish the generic relationships of this interesting form and throw light on the question of whether it might be a relict species afforded refuge in the wet campo.

The genus *Elaphoidella* is well-represented in the neotropics, with about 22 species and subspecies known from northern South America, 18 of which are endemic to the continent. The genus is distributed almost in mirror-image to the *Delachauxiella*-group, since its southernmost records are of *E. bidens* in Paraguay and northern Argentina. The *bidens*-group in particular has undergone considerable radiation, since besides the ubiquitous *E. bidens* s. str., its *coronata*- and *coronata* f. *subtropica*- forms and *E. bidens a*, a third subspecies *E. bidens subterranea* was described by Nogueira (1959) from Paraná (her *E. bidens paranaensis* being indistinguishable from *E. bidens* s. str.). However in the cerrado, both species richness and degree of endemism of *Elaphoidella* are lower than in the genus *Attheyella* (tab. I).

A striking aspect of the parastenocaridid harpacticoid assemblage is the large number of species of the genus *Forficatocaris*. The cerrado region is in the center of the known geographical range of this genus, which extends from the Peruvian Amazon to Paraguay and the southeast Atlantic coast of Brazil (Reid, 1982). Of the 21 species now described or with descriptions in preparation, 11 occur in the cerrado. Most known species have been described from the sand-interstitial of streams, but obviously the wet campo and other moist organic soils afford suitable habitad. A few specimens (*Forficatocaris h, j*) were collected from organic

lake bottom sediments or the roots of floating macrophytes, but the preferred habitad of these species is probably the organic sediments of the lakeshore. Others (*Forficatocaris a, b*) were collected from water overlying cerrado clay soils during the rainy season, but it seems likely that they had come there from an adjacent wet campo downhill.

The number of species of *Parastenocaris* so far collected in the cerrado region (5) is low compared to the 13 species known from the Amazon basin, and to the 14 known from the southern Paraná basin, most of the latter collected from sand-interstitial sediments. This genus seems to have been less successful than *Forficatocaris* in organic-soil habitats. Among the factors leading to the relative success of species of *Forficatocaris* is their relative large size, about 0.5mm long; other parastenocaridids found in organic soils are all much smaller, about 0.3mm in length. The reproductive capacity of species of *Forficatocaris* may be higher since females have been observed to carry as many as five egg sacs with two eggs each. Also, the genus *Forficatocaris* possesses the highest degree of development of sexual dimorphism and modified appendages in the family, which may increase efficiency of intersex recognition and reproduction in an environment with low densities of individuals and consequent reduced likelihood of encounters between sexes (Reid, 1984).

The cyclopoid fauna shows less endemism, which may be related to the lower proportion of stenotopic species than in the harpacticoid fauna. 22 of 43 or about 50% of the harpacticoid species were found in only one type of habitat, and actually the proportion is much higher if benthic species straying into the plankton are discounted. For the cyclopoids, 10 of 36 or less than 1/3 of the species occurred in a single habitat. However, the proportion of cerrado endemics (10 of 35) seems to be high relative to other parts of the world. Most endemic species inhabit mainly wet campos and small bodies of water (*Eucyclops a, Metacyclops campestris, Muscocyclops bidentatus, Muscocyclops therasiae, Paracyclops carectum,* and *Ponticyclops boscoi*) and special habitats (*Metacyclops a* and *Microcyclops a*). The circumglobal *Paracyclops fimbriatus chiltoni* and the tropical South American *Ectocyclops herbsti* are nearly ubiquitous and common in all types of waters.

Interesting aspects of the cyclopoid copepod fauna have less to do with the species that are present than with species that are absent or occur only sporadically. Members of the genus *Eucyclops*, although represented by several species, are not common as in temperate waters. *Eucyclops ensifer*, reported by Matsumura-Tundisi & Rocha (1983) from Broa Reservoir, São Paulo, was not collected further north. The genus *Mesocyclops* is represented by six species in Brazil (Reid, 1985), but in the cerrado region only three species were collected. Of these, *M. longisetus* is common but *M. aspericornis* and *M. meridianus* occurred only sporadically. *M. aspericornis*, although pantropical, is usually found in cryptic habitats such as very small waterbodies, shallow wells, and phytotelmata, and may be a fugitive species (Reid & Saunders, 1986). *M. meridianus* was originally described from Paraguay and has been recorded many times in tropical South America, so the fact that in the central cerrado it was found only in the São Francisco basin is surprising. *Neutrocyclops brevifurca* is rare, with only two records in the central cerrado and one on the southern border (as *Cryptocyclops brevifurca* of Matsumura-Tundisi & Rocha, 1983). This seems to be the usual case for this species, since throughout its broad range through tropical South America east of the Andes, the Antilles, and Central America (Reid, 1985, 1988b), individual records are few. *Tropocyclops schubarti* was not common in the littoral of open waters; its preferred habitat seems to be small pools, sometimes ephemeral, and backwaters of small streams (Reid, 1991a).

As in other parts of the tropics, the true planktonic fauna is species-poor. Of the species indicated under habitat type A in tab. I, only *Tropocyclops prasinus meridionalis*, *Metacyclops mendocinus*, and the four species of *Thermocyclops* should be considered true plankters. *T. prasinus meridionalis* is extremely common in all water types, particularly in oligotrophic waters (Reid, 1993). Other species of *Tropocyclops* occurred mainly in the littoral zone of open waters, in perennial marshes, and in ephemeral puddles. *M. mendocinus*, often found in São Paulo reservoirs (Reid, 1985) was collected only twice, both times in eutrophic waters, Lagoa do Jaburu and Represa da Pampulha. Of the *Thermocyclops* species only *T. decipiens* is a common member of the plankton in the central cerrado, while *T. minutus* and *T. tenuis* occurred in only a few waters (Reid, 1989). *T. inversus* was not collected throughout the cerrado region, but only at its eastern edge in a few ponds in Belo Horizonte (Reid, 1989; Reid et al., 1988).

The cerrado copepod species assemblage as a whole, expect for a few truly pantropical or circumglobal species, reinforces earlier impressions (Löffler, 1981; Noodt, 1969) of the endemicity of the South American fauna. As with many other groups, the lack of any clear relationships to the African copepod fauna suggests that the ages of the major species-groups predate continental separations (Laurent, 1973; Löffler, 1981). The relatively high endemism of the cerrado fauna cannot be used to argue that the Brazilian Shield may have served as a historical faunal refuge, since special local conditions may well have permitted the evolution of many endemic species (Weitzman & Weitzman, 1982).

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