Distribution of limnoterrestrial Tardigrada in Georgia and the Gulf Coast states of the United States of America with ecological remarks

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ABSTRACT

This report is an effort to improve understanding of the distribution of limnoterrestrial tardigrades in Georgia and the states along the Gulf Coast of the United States of America. We collected 14 species of tardigrades from cryptogams (mosses, lichens, and liverworts) and leaf litter in a statewide survey of Louisiana and reviewed all publications and theses reporting tardigrade distributions in the Gulf Coast states. Statewide surveys have been also conducted in Alabama, Florida, and Texas, while sampling in Mississippi and Georgia has been more localized. Currently 51 species have been identified in the region: 19 in Texas, 16 in Louisiana, 10 in Mississippi, 33 in Alabama, 3 in Georgia, and 15 in Florida. These tardigrades have been collected from cryptogams (mosses, lichens, and liverworts) on trees and rocks, from soil and leaf litter, and from freshwater. Twenty species are widely distributed in the region (i.e., found in ≥ 2 non-contiguous states), while 27 have been found in only one state. Eighteen species are probably cosmopolitan. Seven species, widespread in the Gulf Coast states but unknown elsewhere in the Nearctic Region – Echiniscus kofordi, Echiniscus cavagnaroi, Parexapodibius pilatoi, Hexapodibius christenberryae, Biserovus bindae, Minibiotus fallax and a new Macrobiotus cf. hufelandi – may represent a distinctive regional fauna in cryptogams.

Key words: biogeography, Louisiana, tardigrade, southeastern U.S.A., Gulf Coast

1. INTRODUCTION

The tardigrade fauna in the states along the Gulf Coast of the United States of America continues to improve and includes both marine and limno-terrestrial (i.e., species from freshwater, cryptogams, soil, and leaf litter) species. While marine species have been collected in the Gulf of Mexico off Texas (Chitwood 1951) and Alabama (F. Romano, personal communication, 2003), and species have been reported in all the Gulf Coast states, detailed studies of the tardigrade fauna along the Gulf Coast are spotty.

Three statewide surveys have investigated tardigrades in the region: Caskey (1971) in Texas, Word (1976) in Alabama, and Meyer (2006a) in Florida. Other surveys have been limited to portions of a state. Mehlen (1969) surveyed Brazos County in Texas, Hinton & Meyer (2006) collected in 8 counties in western and southern Mississippi, Meyer (2001) collected in two Louisiana parishes (in Louisiana the parish is a unit of local government corresponding to counties in other states), while two studies (Nichols et al. 2001, Romano et al. 2001) focused on north-central Alabama. Other papers (Mathews 1938; Beasley 1968, 1988; Bernard 1977; Christenberry 1979; Christenberry & Higgins 1979; Christenberry & Mason 1979; Grigarick et al. 1983; Pilato & Binda 2003; Meyer 2006b) mention the tardigrades of the region only in passing or focus on descriptions of new species.

This study presents data on tardigrade distribution from a statewide survey of Louisiana cryptogams (mosses, lichens, and liverworts) and from leaf litter collected in Louisiana and Florida. We also reviewed the distribution of freshwater and terrestrial tardigrades in Texas, Louisiana, Mississippi, Alabama, Georgia, and Florida (Fig. 1).

2. METHODS

In the spring and summer of 2003 and 2004 we collected handfuls of mosses, lichens, and liverworts from 54 Louisiana parishes. Sampling was not quantitative. Leaf litter samples were collected from wooded areas in Calcasieu Parish, Louisiana and Citrus County, Florida. We stored samples in envelopes or paper bags. After soaking in water overnight, we examined the samples with a dissecting microscope and mounted tardigrades in Hoyer's medium or polyvinyl lactophenol. We identified tardigrades using the keys and descriptions in Ramazzotti & Maucci (1983) and Nelson & McInnes (2002), and by reference to the primary literature.

We follow the taxonomic nomenclature of Guidetti & Bertolani (2005). Comments on the global biogeography of tardigrade species are based primarily on McInnes (1994).

3. RESULTS

Our samples from Louisiana contained 14 species (Tab. 1), including seven not found by Meyer (2001). Authors and years of all species discussed in this paper are in table 2. Leaf litter from Calcasieu Parish, Louisiana contained Milnesium tardigradum, Diphascon (Diphascon) pingue, Itaquascon umbellinae and
Minibiotus intermedius. Other tardigrade species were present in the Louisiana material; unfortunately, their identification has been precluded by damage to McNeese State University inflicted by Hurricane Rita in September, 2005. *Milnesium tardigradum, D. (D.) pingue* and *Macrobiotus richtersi* were present in leaf litter in Citrus County, Florida.

The most common species in Louisiana cryptogams were *M. tardigradum* and *M. intermedius*. *Milnesium tardigradum* was also ubiquitous in Texas, Alabama, and Florida. Although *M. intermedius* is very common in Alabama and Florida, Caskey (1971) only found it in the easternmost counties of Texas.

4. DISCUSSION

Pilato & Binda (2001) described tardigrade species found in five or more biogeographical regions as probably cosmopolitan. By this criterion, 18 of the Gulf Coast species are cosmopolitan or probably cosmopolitan (Tab. 2). In contrast, eleven species have only been found in the Nearctic region (Tab. 2). Twenty species are widely distributed in the region, i.e., they are found in two or more non-contiguous states. The distribution of four species – *Parhexapodibius pilatoi, Hexapodibius christenberryae, Biserovus bindae* and a new species of *Macrobiotus* of the *hufelandi* group – is limited to the Gulf Coast states. These species, and probably also *Echiniscus cavagnaroi, Echiniscus kofordi*, and *Minibiotus fallax*, may constitute a distinctive regional fauna within the Nearctic realm. Although the two *Echiniscus* have been found in the Neotropical Region and in the Galapagos Islands, and *M. fallax* was described in Australia, the known distribution in the Nearctic Region of these three species is limited to the Gulf Coast states, where they are frequently encountered in mosses and lichens.

The distribution of two species within the region is not certain. Grigarick et al. (1983) noted that Christenberry found *Echiniscus perarmatus* in the "southeastern United States," and Pilato & Binda (2003) described *H. christenberryae* from material of uncertain provenance in Christenberry’s collection. Christenberry’s three publications (Christenberry 1979; Christenberry & Higgins 1979; Christenberry & Mason 1979) include material from Alabama, Florida, and Georgia. Because her work focused primarily on Alabama, the two species are assigned to that state in table 2. The number of species reported is therefore 19 in Texas, 16 in Louisiana, 10 in Mississippi, 33 in Alabama, 3 in Georgia, and 15 in Florida.

Fifty-one species of tardigrade have been identified in the Gulf Coast states in this paper and other literature (Tab. 2). Published lists also include 15 unidentified species (i.e., identified only to genus or species complex) in the region. We include in table 2 only one of these, a widely-distributed new species in the *hufelandi* group with a distinctive egg that will be described elsewhere.

Word (1976) collected *Thulinius augusti* from two small ponds in Lee County, Alabama. We have collected *Pseudobiota* sp. from the Ouiskachitto River in Louisiana. These are the only records of freshwater tardigrades in the Gulf Coast states.
Tab. 1. Tardigrade species found in Louisiana cryptogams and leaf litter in 2003 and 2004. Sub = substrate, C = mixed cryptogams, L = lichen, Lv = liverwort, M = moss, LL = leaf litter, Ec = Echiniscus cavagnaroi, Ek = Echiniscus kofordi, Ev = Echiniscus virginicus, Mt = Milnesium tardigradum, Df = Doryphoribius flavus, Ro = Ramazzottius oberhaeueri, Dp = Diphascon (Diphascon) pingue, Ma = Macrobiotus areolatus, Mc = Macrobiotus echinogenitus, Mo = Macrobiotus occidentalis, Mfa = Minibiotus fallax, Mfu = Minibiotus furcatus, Mi = Minibiotus intermedius, Iu = Itaquascon umbellinae.

| Parish            | Sub | Ec | Ek | Ev | Mt | Df | Ro | Dp | Ma | Me | Mo | Mfa | Mfu | Mi | Iu |
|-------------------|-----|----|----|----|----|----|----|----|----|----|----|-----|-----|----|----|
| Acadia            | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Allen             | L   | x  | x  |    |    |    |    |    |    |    |    |     |     |    |    |
| Ascension         | C   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Assumption        | L   | x  | x  | x  |    |    |    |    |    |    |    |     |     |    |    |
| Avoyelles         | L   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Beauregard        | M   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Beauregard        | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Bossier           | M   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Caddo             | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Calcasieu         | Lv  |    | x  | x  |    |    |    |    |    |    |    |     |     |    |    |
| Calcasieu         | LL  | x  | x  | x  | x  |    |    |    |    |    |    |     |     |    |    |
| Caldwell          | L   | x  | x  | x  | x  |    |    |    |    |    |    |     |     |    |    |
| Cameron           | M   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Catahoula         | M   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Claiborne         | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Concordia          | M   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| De Soto           | L   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| East Baton Rouge  | M   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| East Feliciana    | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Evangeline        | M   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Grant             | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Iberia            | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Iberville         | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Jefferson Davis   | M   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Lafayette         | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Lafourche         | C   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| LaSalle           | M   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| LaSalle           | L   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Lincoln           | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Livingston        | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Morehouse         | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Orleans           | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Ouachita          | C   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Plaquemines       | M   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Rapides           | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Richland          | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Sabine            | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| St. Bernard       | M   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| St. Bernard       | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| St. Charles       | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| St. Helena        | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| St. John the Baptist | L  |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| St. Landry        | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| St. Martin        | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| St. Tammany       | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Tangipahoa        | L   | x  | x  | x  |    |    |    |    |    |    |    |     |     |    |    |
| Tensas            | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Union             | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Vermilion         | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Vernon            | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Washington        | L   | x  | x  |    |    |    |    |    |    |    |    |     |     |    |    |
| Webster           | L   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| West Feliciana    | L   | x  |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Winn              | M   |    |    |    |    |    |    |    |    |    |    |     |     |    |    |
| Species                      | Range          | State          | Habitat |
|------------------------------|----------------|----------------|---------|
| Echiniscus arctomys          | x              | TX             | cr      |
| Ehrenberg, 1853              |                | LA             |         |
| Echiniscus banus             | x              | MS             |         |
| Caskey, 1971                 |                | AL             |         |
| Echiniscus cavagneroi        | x              | GA             |         |
| Schuster & Grigarick, 1966   |                | FL             |         |
| Echiniscus kofordi           | x              |                 |         |
| Schuster & Grigarick, 1966   | x              |                 |         |
| Echiniscus mauceri           | x              |                 |         |
| Ramazzotti, 1956             | x              |                 |         |
| Echiniscus perarmatus        | x              |                 |         |
| Murray, 1907                 |                |                 |         |
| Echiniscus tamus             | x              |                 |         |
| Mehelen, 1969                |                |                 |         |
| Echiniscus virgincus         | x              |                 |         |
| Riggin, 1962                 |                |                 |         |
| Echiniscus viridissimus      | x              |                 |         |
| Pétrefi, 1956                |                |                 |         |
| Milnesium tardigradum        | x              |                 |         |
| Doyère, 1840                 |                |                 |         |
| Pseudechiniscus brevimontanus| x              |                 |         |
| Kendall-Fite & Nelson, 1996  |                |                 |         |
| Pseudechiniscus ramazzottii  | x              |                 |         |
| Maucci, 1952                 |                |                 |         |
| Pseudechiniscus suillus      | x              |                 |         |
| (Ehrenberg, 1853)            |                |                 |         |
| Milnesia                     | x              |                 |         |
| tardigradum                  |                |                 |         |
| Doyère, 1840                 |                |                 |         |
| Haplohexapodibius seductor   | x              |                 |         |
| Pilato & Beasley, 1987       |                |                 |         |
| Hexapodibius christenberneyae| x              |                 |         |
| Pilato & Binda, 2003         |                |                 |         |
| Parhexapodibius pilatoi      | x              |                 |         |
| (Bernard, 1977)              |                |                 |         |
| Dorophoribius flavus         | x              |                 |         |
| (Iharos, 1966)               |                |                 |         |
| Hypsibius calcaratus         | x              |                 |         |
| Bartoš, 1935                 |                |                 |         |
| Hypsibius convergens         | x              |                 |         |
| Urbanowicz, 1925             |                |                 |         |
| Hypsibius djuardini          | x              |                 |         |
| Doyère, 1840                 |                |                 |         |
| Hypsibius macrocalcaratus    | x              |                 |         |
| Beasley, 1988                |                |                 |         |
| Hypsibius pallidus           | x              |                 |         |
| Thulin, 1911                 |                |                 |         |
| Isolyphsibius schaudinni      | x              |                 |         |
| (Richters, 1909)             |                |                 |         |
| Ramazzottius baumanni        | x              |                 |         |
| Ramazzotti, 1962             |                |                 |         |
| Ramazzottius oberhaeuseri    | x              |                 |         |
| Doyère, 1840                 |                |                 |         |
| Thalnias augusti             | x              |                 |         |
| (Murray, 1907)               |                |                 |         |
| Diphascon (Diphascon) iltisi  | x              |                 |         |
| (Schuster & Grigarick, 1965) |                |                 |         |
| Diphascon (Diphascon) oculatum| x             |                 |         |
| Murray, 1906                 |                |                 |         |
| Diphascon (Diphascon) pingue | x              |                 |         |
| Marcus, 1936                 |                |                 |         |
| Diphascon (Diphascon) rugosum| x              |                 |         |
| Bartoš, 1933                 |                |                 |         |
| Diphascon (Adropion) scoticum| x              |                 |         |
| Murray, 1905                 |                |                 |         |
| Astatumen bartosi            | x              |                 |         |
| Weglarcka, 1959              |                |                 |         |
| Astatumen trinacrae          | x              |                 |         |
| Arcidiacono, 1962            |                |                 |         |
| Itaquascon umbellinae         | x              |                 |         |
| De Barros, 1939              |                |                 |         |
| Piatricista angastata        | x              |                 |         |
| Murray, 1905                 |                |                 |         |
| Biserovus bindae             | x              |                 |         |
| Christenberry & Higgins, 1979|                |                 |         |
| Macrobiotus areolatus        | x              |                 |         |
| Murray, 1907                 |                |                 |         |
| Macrobiotus echinogenitus    | x              |                 |         |
| Richters, 1904               |                |                 |         |
| Macrobiotus harmsworthi      | x              |                 |         |
| Murray, 1907                 |                |                 |         |
| Macrobiotus hufelandii       | x              |                 |         |
| Schultze, 1834               |                |                 |         |
| Macrobiotus n. sp.           | x              |                 |         |
| Macrobiotus islandicus       | x              |                 |         |
| Richters, 1904               |                |                 |         |
| Macrobiotus occidentalis     | x              |                 |         |
| Murray, 1910                 |                |                 |         |
| Macrobiotus ovovillosus      | x              |                 |         |
| Baumann, 1960                |                |                 |         |
| Macrobiotus richtersi        | x              |                 |         |
| Murray, 1911                 |                |                 |         |
| Macrobiotus tonolli          | x              |                 |         |
| Ramazzotti, 1956             |                |                 |         |
| Minibiota fallax Pilato      | x              |                 |         |
| Claiston & Binda, 1989       |                |                 |         |
| Minibiota fuscatus           | x              |                 |         |
| (Ehrenberg, 1859)            |                |                 |         |
| Minibiota intermedius        | x              |                 |         |
| Plate, 1889                  |                |                 |         |
| Minibiota pustulatus          | x              |                 |         |
| Ramazzotti, 1959             |                |                 |         |
Most collections of terrestrial tardigrades have been from cryptogams (Tabs 1 and 2) on trees or rocks. Some reports identify collected cryptogams as moss, lichen, or liverworts, but the species of substrate is very rarely reported. Only Bernard (1977) and the present study have reported the presence of tardigrades in leaf litter in the Gulf Coast states. Other possible substrates have not been investigated.

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