Reproductive characteristics of characid fish species (Teleostei, Characiformes) and their relationship with body size and phylogeny

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ABSTRACT. In this study, I investigated the reproductive biology of fish species from the family Characidae of the order Characiformes. I also investigated the relationship between reproductive biology and body weight and interpreted this relationship in a phylogenetic context. The results of the present study contribute to the understanding of the evolution of the reproductive strategies present in the species of this family. Most larger characid species and other characiforms exhibit a reproductive pattern that is generally characterized by a short seasonal reproductive period that lasts one to three months, between September and April. This is accompanied by total spawning, an extremely high fecundity, and, in many species, a reproductive migration. Many species with lower fecundity exhibit some form of parental care. Although reduction in body size may represent an adaptive advantage, it may also require evolutionary responses to new biological problems that arise. In terms of reproduction, smaller species have a tendency to reduce the number of oocytes that they produce. Many small characids have a reproductive pattern similar to that of larger characiforms. On the other hand they may also exhibit a range of modifications that possibly relate to the decrease in body size and the consequent reduction in fecundity. Examples of changes in the general reproductive pattern include the following: reduction in the size of mature oocytes; increase in fecundity; production of several batches of oocytes; an extended reproductive period or even continuous reproduction that allows individuals to reproduce more than once a year; high growth rates; rapid recruitment of juveniles; presence of more than one reproductive cohort that increases the sexually active population; and multiple independent development of insemination as a reproductive strategy. These changes are possibly associated with adaptive pressures that are related to the reduction in body size. In addition, such reproductive characteristics or novelties may reflect the phylogenetic history of a given species.

KEY WORDS. Neotropical, reproductive period, seasonality, fecundity, type of spawning, mode of reproduction, insemination.

RESUMO. Características da reprodução de espécies de Characidae (Teleostei: Characiformes) e suas relações com tamanho corporal e filogenia. Neste trabalho, as informações sobre reprodução de espécies de peixes da família Characidae, de Characiformes, são avaliadas considerando suas relações de tamanho corporal e interpretadas em um contexto filogenético, contribuindo para a compreensão da evolução das estratégias reprodutivas presentes nas espécies da família. A maioria das espécies de caracídeos de maior porte apresenta, assim como outros Characiformes, um padrão geral de reprodução caracterizado pelo período reprodutivo sazonal e curto, durando de um a três meses, situado entre setembro e abril; desova normalmente total; fecundidade extremamente elevada e muitas espécies apresentam migração reprodutiva. Muitas espécies que têm a fecundidade menor apresentam cuidado parental. A diminuição do tamanho corporal parece ser uma sinapomorfia dos grupos de Characidae que não apresentam o osso supraorbital. A redução no tamanho pode representar uma vantagem adaptativa em diversos aspectos, mas pode exigir respostas evolutivas a novos problemas biológicos decorrentes. Em termos de reprodução, observa-se uma tendência a que espécies de menor porte reduzam também o número de ovócitos produzidos. Muitos caracídeos de pequeno porte mantêm o padrão geral de reprodução dos Characiformes, mas muitos deles exibem diferentes modificações, possivelmente como resposta à diminuição de tamanho e consequente diminuição da fecundidade. A diminuição do tamanho dos ovócitos maduros; a produção de diversos lotes de ovócitos; o prolongamento do período reprodutivo; a presença de mais de uma coorte reprodutiva ou a reprodução contínua, permitindo que os indivíduos reproduzam mais de uma vez no ano; as altas taxas de crescimento e rápido recrutamento de jovens, aumentando a população sexualmente ativa e a inseminação dos ovários são exemplos de modificações no padrão geral de reprodução, possivelmente em resposta às pressões relacionadas à redução de tamanho corporal. Estas características reprodutivas podem refletir as relações de parentesco das espécies.

PALAVRAS-CHAVE. Neotropical, período reprodutivo, sazonalidade, fecundidade, tipo de desova.

Fish represent an estimated 47 to 51% of all vertebrate species in the world, with about 24% occurring in Neotropical freshwaters (Groombridge, 1992). Equally notable, particularly in the epicontinental waters of the Neotropics, is the immense diversity of forms, behaviors, and lifestyles that allow these organisms to inhabit these diverse environments (Vari & Malabarba, 1998). One of the most interesting features of plasticity exhibited by fish is the number of different reproductive strategies employed. One can often observe different reproductive patterns among members of a fish community that inhabit the same environment. In some cases, closely allied species exhibit different reproductive strategies, and, in others, phylogenetically distant species converge independently towards a similar strategy. Another interesting point regarding the diversity of Neotropical fish is related to the varying sizes of different species. Within some families individual species can vary from 1.5 cm to more than 1 m in length. Species of similar sizes can be found in different environments, using different food resources, and exhibiting different reproductive and phylogenetic characteristics.

This study evaluated some of the data available in the literature about reproduction in species of the family Characidae, order Characiformes. The available data were evaluated in relation to the body sizes of the species and were interpreted within a phylogenetic context to contribute to the understanding of the evolution of the different reproductive strategies found within the species of this family.

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In the order Characiformes, smaller species are concentrated in the Characidae, which is the most speciose group of this order. Relationships among family members are still controversial, but a series of recent papers, starting with MALABARBA & WEITZMAN (2003), and corroborated by CALCAGNOTTO *et al.* (2005), MIRANDE (2009, 2010) and JAVONILLO *et al.* (2010), have demonstrated that Characidae includes a series of basal taxa and a large internal clade composed of all characid species that share the synapomorphic lack of a supraorbital bone (Figs 1, 2). MIRANDE (2009, 2010) further supported this clade by the synapomorphic presence of less than 40 vertebrae (*versus* more than 40 vertebrae in more basal characid taxa), among other characters.

Although the relationships of a large number of genera remain uncertain or are controversial among the characid subgroup that includes the species lacking a supraorbital, monophyly of some ingroups have been corroborated, such as for the Aphyocharacinae, Characinae, Cheirodontinae, Rhoadsiinae, Stethaprioninae, and Tetragonopterinae (*sensu stricto*, containing only *Tetragonopterus* Cuvier, 1816) (Figs 1 and 2). The Aphyoditeinae and Heterocharacinae were newly defined by MIRANDE (2009, 2010). The Clade A proposed by

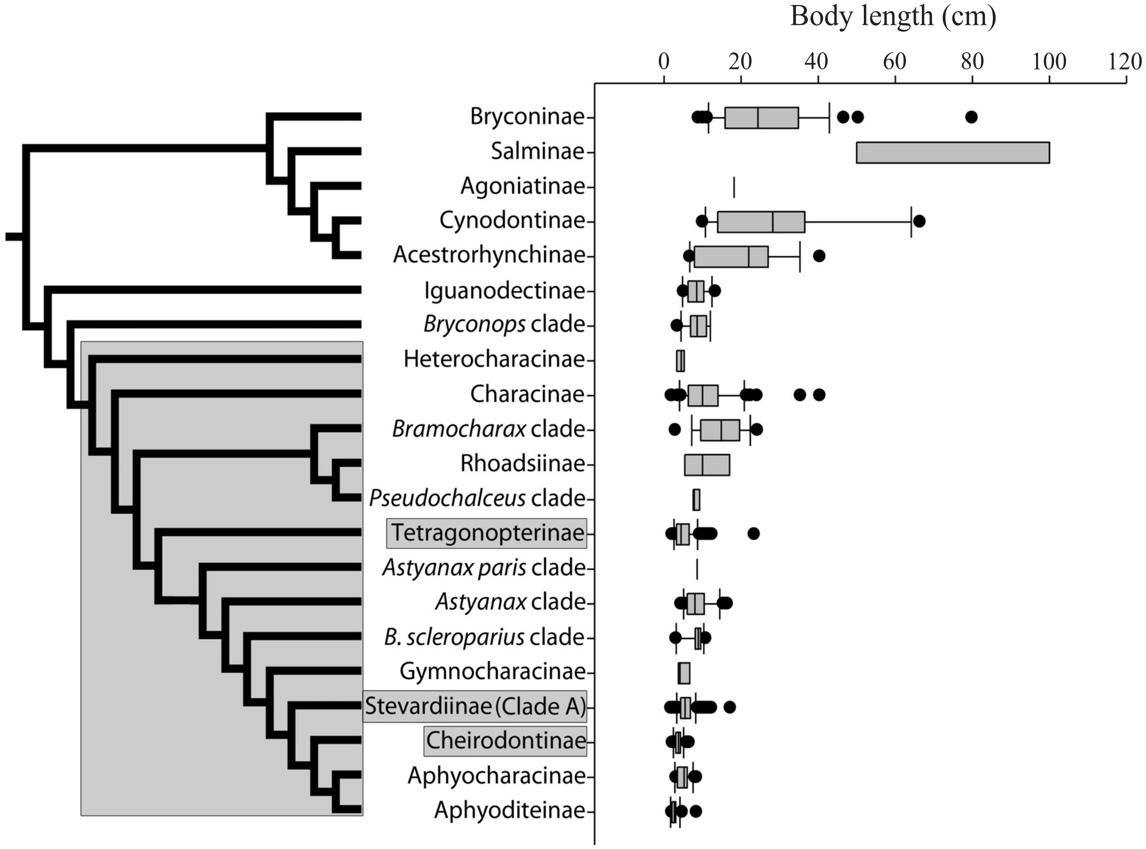


Figure 1. Comparative plots of the body size for the species in each monophyletic group resulting in the phylogeny of Mirande (2010) expressed by Tukey box plots based on percentiles. Shaded portion of the cladogram represents those lineages sharing the lack of a supraorbital bone. Shaded terminals represent those taxa that show both inseminating and externally fertilized species. Body length data extracted from Reis *et al.* (2003). Genera belonging to each terminal extracted from Mirande (2010), as follows: Acestrorhynchinae (n = 15; *Acestrorhynchus*), Agoniatinae (n = 2; *Agoniates*), Aphyocharacinae (n = 20; *Aphyocharax, Inpaichthys* Géry & Junk, *Leptagoniates*, *Paragoniates*, *Phenagoniates*, *Prionobrama*, *Rachoviscus*, and *Xenagoniates*), Aphyoditeinae (n = 21; *Aphyocharacidium*, *Aphyodite*, *Axelrodia*, *Leptobrycon*, *Microschemobrycon*, *Oxybrycon*, *Parecbasis*, and *Tyttobrycon*), *Astyanax* clade (n = 31; *Astyanax*, *Ctenobrycon*, *Markiana*, *Psellogrammus*, *Hyphessobrycon*), *Astyanax paris* clade (n = 1), *Bramocharax* clade (n = 18; *Bramocharax* and *Oligosarcus*), *Bryconamericus scleroparius* clade (n = 10; *Bryconamericus brevirostris*, *B. emperador*, *B. guaytarae*, *B. loisae*, *B. multiradiatus*, *B. peruanus*, *B. scleroparius*, *B. simus*, *B. terrabensis*, *B. zeteki*), Bryconinae (n = 56; *Brycon*, *Chilobrycon*, *Henochilus*, *Lignobrycon*, and *Triportheus*), *Bryconops* clade (n = 13; *Bryconops*), Characinae (n = 71; *Acanthocharax*, *Acestrocephalus*, *Bryconexodon*, *Charax*, *Cynopotamus*, *Exodon*, *Galeocharax*, *Phenacogaster*, *Priocharax*, *Roeboexodon*, and *Roeboides*), Cheirodontinae (n = 48; *Acinocheirodon*, *Amazonspinther*, *Aphyocheirodon*, *Cheirodon*, *Cheirodontops*, *Compsura*, *Heterocheirodon*, *Kolpotocheirodon*, *Macropsobrycon*, †*Megacheirodon*, *Nanocheirodon*, *Odontostilbe*, *Prodontocharax*, *Pseudocheirodon*, *Saccoderma*, *Serrapinnus*, and *Spintherobolus*), Cynodontinae (n = 14; *Cynodon*, *Gilbertolus*, *Hydrolycus*, *Rhaphiodon*, and *Roestes*), Gymnocharacinae (n = 4; *Coptobrycon*, *Grundulus*, *Gymnocharacinus*, and *Nematobrycon*), Heterocharacinae (n = 6; *Gnathocharax*, *Heterocharax*, *Hoplocharax*, and *Lonchogenys*), Iguanodectinae (n = 11; *Iguanodectes* and *Piabucus*), *Pseudochalceus* clade (n = 4; *Hollandichthys* and *Pseudochalceus*), Rhoadsiinae (n = 7; *Carlana*, *Nematocharax*, *Parastremma*, and *Rhoadsia*), Salmininae (n = 3; *Salminus*), Stevardiinae (n = 214; *Acrobrycon*, *Argopleura*, *Attonitus*, *Aulixidens*, *Boehlkea*, *Bryconacidnus*, *Bryconadenos*, *Bryconamericus*, *Caiapobrycon*, *Ceratobranchia*, *Chrysobrycon*, *Corynopoma*, *Creagrutus*, *Cyanocharax*, *Diapoma*, *Gephyrocharax*, *Glandulocauda*, *Hemibrycon*, *Hypobrycon*, *Hysteronotus*, *Iotabrycon*, *Knodus*, *Landonia*, *Lophiobrycon*, *Microgenys*, *Mimagoniates*, *Monotocheirodon*, *Nantis*, *Odontostoechus*, *Othonocheirodus*, *Phallobrycon*, *Phenacobrycon*, *Piabarchus*, *Piabina*, *Planaltina*, *Pseudocorynopoma*, *Pterobrycon*, *Ptychocharax*, *Rhinobrycon*, *Rhinopetitia*, *Scopaeocharax*, *Tyttocharax*, and *Xenurobrycon*), Tetragonopterinae (n = 252; *Bario*, *Brachychalcinus*, *Deuterodon*, *Gymnocorymbus*, *Hasemania*, *Hemigrammus*, *Hyphessobrycon*, *Jupiaba*, *Moenkhausia*, *Myxiops*, *Paracheirodon*, *Orthospinus*, *Petitella*, *Poptella*, *Pristella*, *Probolodus*, *Stethaprion*, *Stichonodon*, *Tetragonopterus*, and *Thayeria*).

Malabarba & Weitzman (2003) to include the Glandulocaudinae, the Stevardiinae and several characid genera sharing four teeth in the inner series of the premaxilla and 2 unbranched plus 8 branched dorsal fin rays, was further supported by Calcagnotto *et al.* (2005) and Javonillo *et al.* (2010), and later redefined and renamed as the Stevardiinae by Mirande (2009, 2010). Throughout this paper I will continue to refer the lineage Clade A, which includes the tribes Corynopomini, Diapomini, Glandulocaudini, Stevardiini, and Xenurobryconini, and the genera *Attonitus* Vari & Ortega, 2000, *Auxilidens* Böhlke, 1952, *Boehlkea* Géry, 1966, *Bryconacidnus* Myers, 1929, *Bryconadenos* Weitzman, Menezes, Evers & Burns, 2005, *Bryconamericus* Eigenmann, 1907, *Caiapobrycon* Malabarba & Vari, 2000, *Ceratobranchia* Eigenmann, 1914, *Creagrutus* Günther, 1864, *Cyanocharax* Malabarba & Weitzman, 2003, *Hemibrycon* Günther, 1864, *Hypobrycon* Malabarba & Malabarba, 1994, *Microgenys* Eigenmann, 1913, *Monotocheirodon* Eigenmann & Pearson, 1924, *Nantis* Mirande, Aguilera & Azpelicueta, 2006, *Odontostoechus* Gomes, 1947, *Othonocheirodus* Myers, 1927, *Phallobrycon* Menezes, Ferreira & Netto-Ferreira, 2009, *Piabarchus* Myers, 1928, *Piabina* Reinhardt, 1867, *Rhinobrycon* Myers, 1944, and *Rhinopetitia* Géry, 1964. I have included the species of the Serrasalminae in the comparisons, regardless the fact they have been alternately referred as a subfamily (Serrasalminae – Javonillo *et al.*, 2010) or as a different family from the Characidae (Serrasalmidae – Mirande, 2010).

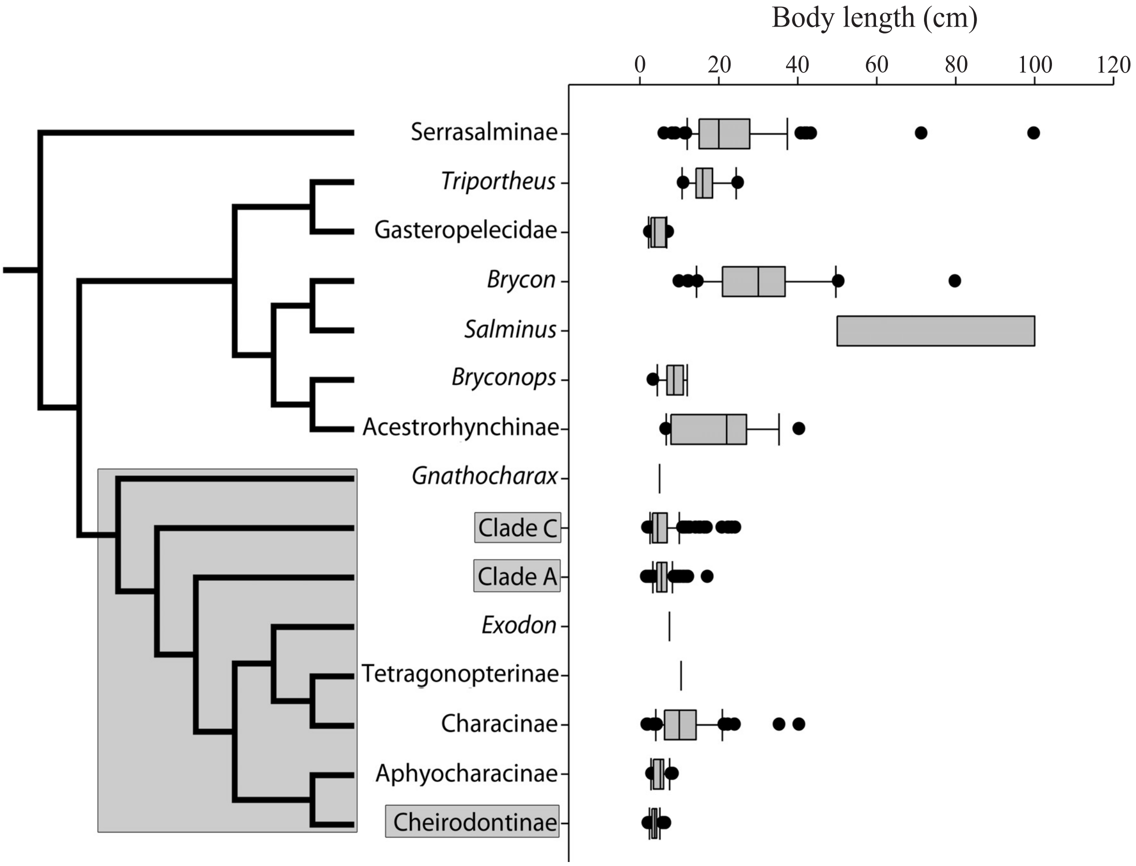


Figure 2. Comparative plots of the body size for the species in each monophyletic group resulting in the phylogeny of Javonillo *et al.* (2010) expressed by Tukey box plots based on percentiles. Shaded portion of the cladogram represents those lineages sharing the lack of a supraorbital bone. Shaded terminals represent those taxa that show both inseminating and externally fertilized species. Body length data extracted from Reis *et al.* (2003). Genera belonging to each terminal, as follows: Acestrorhynchinae (n = 15; *Acestrorhynchus*), Aphyocharacinae (n = 20; *Aphyocharax*, *Inpaichthys*, *Leptagoniates*, *Paragoniates*, *Phenagoniates*, *Prionobrama*, *Rachoviscus*, and *Xenagoniates*), *Brycon* clade (n = 40), *Bryconops* clade (n = 13), Characinae (n = 70; *Acanthocharax*, *Acestrocephalus*, *Bryconexodon*, *Charax*, *Cynopotamus*, *Galeocharax*, *Phenacogaster*, *Priocharax*, *Roeboexodon*, and *Roeboides*), Cheirodontinae (n = 48; *Acinocheirodon*, *Amazonspinther*, *Aphyocheirodon*, *Cheirodon*, *Cheirodontops*, *Compsura*, *Heterocheirodon*, *Kolpotocheirodon*, *Macropsobrycon*, †*Megacheirodon*, *Nanocheirodon*, *Odontostilbe*, *Prodontocharax*, *Pseudocheirodon*, *Saccoderma*, *Serrapinnus*, and *Spintherobolus*), Clade C (n = 278; *Astyanax*, *Ctenobrycon*, *Gymnocorymbus*, *Hasemania*, *Hemigrammus*, *Hollandichthys*, *Hyphessobrycon*, *Inpaichthys*, *Jupiaba*, *Macropsobrycon*, *Moenkhausia*, *Nematobrycon*, *Oligosarcus*, *Paracheirodon*, *Poptella*, *Pristella*, *Rachoviscus*, *Thayeria*.), *Exodon* clade (n = 1), Gasteropelecidae (n = 11; *Carnegiella*, *Engraulisoma*, *Gasteropelecus*, and *Thoracocharax*), *Gnathocharax* clade (n = 1), *Salminus* clade (n = 3), Serrasalminae (n = 68; *Acnodon*, *Catoprion*, *Colossoma*, *Metynnis*, *Mylesinus*, *Myleus*, *Mylossoma*, *Ossubtus*, *Piaractus*, *Pristobrycon*, *Pygocentrus*, *Pygopristis*, *Serrasalmus*, *Tometes*, and *Utiaritichthys*), Stevardiinae (n = 214; *Acrobrycon*, *Argopleura*, *Attonitus*, *Aulixidens*, *Boehlkea*, *Bryconacidnus*, *Bryconadenos*, *Bryconamericus*, *Caiapobrycon*, *Ceratobranchia*, *Chrysobrycon*, *Corynopoma*, *Creagrutus*, *Cyanocharax*, *Diapoma*, *Gephyrocharax*, *Glandulocauda*, *Hemibrycon*, *Hypobrycon*, *Hysteronotus*, *Iotabrycon*, *Knodus*, *Landonia*, *Lophiobrycon*, *Microgenys*, *Mimagoniates*, *Monotocheirodon*, *Nantis*, *Odontostoechus*, *Othonocheirodus*, *Phallobrycon*, *Phenacobrycon*, *Piabarchus*, *Piabina*, *Planaltina*, *Pseudocorynopoma*, *Pterobrycon*, *Ptychocharax*, *Rhinobrycon*, *Rhinopetitia*, *Scopaeocharax*, *Tyttocharax*, and *Xenurobrycon*), Tetragonopterinae (n = 2; *Tetragonopterus*), and *Triportheus* clade (n = 13).

Reproductive patterns among characid fishes will be discussed following the classifications proposed above. Most characids are externally fertilized, but 69 species are known to be inseminating, as listed by JAVONILLO *et al.* (2010). These include all species of the tribes Corynopomini, Diapomini, Glandulocaudini, Stevardiini, and Xenurobryconini (Clade A), all species of the tribe Compsurini (Cheirodontinae), and a several species of uncertain affinities (Figs 1, 2).

Body size reduction in Characidae

Neotropical freshwater fishes, one of the most diverse groups of vertebrates on the planet, is dominated by the orders Siluriformes and Characiformes, which represent approximately 47% and 37%, respectively, of the total number of freshwater species found in the Neotropics (REIS *et al.*, 2003). According to CASTRO (1999), approximately 50% of all Neotropical freshwater species of Characiformes and Siluriformes exhibit small body size, and many authors claim that smaller fish show reduced features such as a reduced number of scales, infraorbital bones, and fin rays (MYERS, 1958; FINK, 1981; WEITZMAN & VARI, 1988). CASTRO (1999) also reports that pedomorphosis (retention of characters of juveniles in adults) and progenesis (early gonadal maturation that truncates the ontogenetic process and produces an adult that resembles the larval or juvenile stage in general appearance and dimensions) are heterochronic processes related to reduction of body size, and that heterochronic events are the main evolutionary processes responsible for faunal size reduction.

In reference to the fish fauna in South American streams, which are dominated by the small species of the orders Characiformes and Siluriformes, CASTRO (1999) argues that the environments of these streams have exerted a series of selective pressures that favored the reduction in size of fish species. CASTRO (1999) also argues that this reduction has allowed for the best use of these environments. In addition, the author hypothesizes that numerous vicariant events in these environments, associated with the low displacement capacity of these fish, promoted events of allopatric speciation that were responsible for the radiation of these species into streams. However, his hypothesis lacks examples and phylogenetic support.

In the order Characiformes, the smaller species are concentrated in the family Characidae, which is the most speciose group of this order. Considering the total length measurements for all species provided by REIS *et al.* (2003), the following patterns of distribution of total length are observed in Characidae. There is a series of basal lineages, all sharing the plesiomorphic presence of a supraorbital bone, that consist of the largest species of the family, such as those in the genera *Salminus* Agassiz, 1829, *Brycon* Müller & Troschel, 1844, *Triportheus* Cope, 1872 and the family Serrasalminae, with body lengths similar to most other characiform families (*e.g.*, Erythrinidae, Curimatidae, Prochilodontidae, and Anostomidae) and reaching up to 1 m in length, and with about 82% exceeding 120 mm in body length. There is also a large internal clade, however, including all species sharing the apomorphic lack of a supraorbital and less than 40 vertebrae, that includes most of the small species of the family, with more than 82% reaching a maximum of 120 mm in length, and only about 17% exceeding this length. These include the Aphyocharacinae, Aphyoditeinae, Characinae, Cheirodontinae, Heterocharacinae, Rhoadsiinae, Stethaprioninae, Stevardiinae (*sensu* MIRANDE, 2010), and Tetragonopterinae (*sensu stricto*, containing only *Tetragonopterus*). Thus, this framework allows us also to formulate the hypothesis that there was one significant event of body size reduction (miniaturization) in the common ancestor of all species sharing the apomorphic lack of a supraorbital and less than 40 vertebrae. According the phylogeny of Mirande (2010), this general body size reduction may have occurred in a common ancestor including *Bryconops* Kner, 1858 and the Iguanodectinae (Fig. 1), but according to the tree topology of Javonillo *et al.* (2010) the body size reduction in *Bryconops* occurred separately from the groups mentioned above (Fig. 2).

Although a number of these groups and small species are found in small streams and rapids, many are also found in open areas of larger rivers, backwaters, freshwater beaches, and lakes. Therefore, body size reduction may also represent an adaptation to lentic environments, with physical and ecological characteristics different from those typical of small streams, in such a way that we cannot unambiguously associate body size reduction with an adaptation to stream environments, as suggested by CASTRO (1999). Although the characteristics of the small stream environments seem more conducive to speciation and vicariant events, only studies of biogeography, the phylogenetic relationships of these species, and the geological history of the waterways where they occur will help identify which scenario produced the common ancestor(s) of the small characid species.

Relationships between the reduction in body size and the biological characteristics of small fishes

If we assume that a reduced body size is a homologous evolutionary novelty that is shared by most of the small sized characid species, one may pose the following question: what would be the adaptive advantages of a reduced body size for these fish, and what are the secondary or collateral implications of this characteristic?

One point raised by CASTRO (1999) and MOYLE & CECH JR (1996) is that smaller species reach sexual maturity more rapidly. CASTRO (1999) also states that variable and ephemeral environmental conditions, such as those found in streams, tend to favor the adaptive success of r-strategist species, which are opportunists that are characterized by their small size, short lifespan, high growth rate, early sexual maturity, elevated natural mortality and fecundity, and the ability to quickly occupy new habitats or reoccupy habitats whose fish populations were reduced or eliminated by regular or random abiotic environmental fluctuations. Although some studies can corroborate the existence of this pattern, the high diversity of the reproductive strategies that are adopted by different characid species and fish in general suggest that there could be other, more complex, patterns that have not yet been explored. It is indisputable, however, that in any type of environment, the smaller fish are able to occupy niches that are not available to the larger fish and that a reduced size could represent an adaptive solution for some species.

Reproductive biology of small characids

In recent years, several studies on the reproduction of small characids have been conducted in different drainage basins in the state of Rio Grande do Sul, Brazil (Gelain *et al.*, 1999; Azevedo, 2000; Azevedo *et al.*, 2000; Oliveira *et al.*, 2002; Azevedo, 2004; Lampert *et al.*, 2004, 2007; Gonçalves *et al.*, 2005; Oliveira *et al.*, 2010; Azevedo *et al.*, 2010). These studies, in addition to the information synthesized by Vazzoler & Menezes (1992) and Vazzoler (1996), and those presented by Kramer (1978), Winemiller (1989) and Meni & Almirón (1994) provide a set of reproductive data for a large number of characid species. Many of these species were of a smaller size and were residing in different environments. Despite the limited amount information, these data allow us to draw a general conclusion about the evolution of characid reproductive traits, the involved phylogenetic aspects, and the relationship between these characteristics and a reduced body size.

Vazzoler & Menezes (1992) analyzed the data that were available in the literature about the reproduction of South American characiform species. In this study they evaluated the following reproductive tactics: spawning period, fecundity, type of spawning, and rate of first gonadal maturation. The species were separated according to the large basins in which they were studied and according to the respective reproductive strategies.

Analyzing the data reported by Vazzoler & Menezes (1992), I observed that all characid species reproduced seasonally during the spring and summer, independent of size, reproductive strategy, and location, with variations in reproductive period lengths. The establishment of the reproductive period of these characiform species during the spring and summer months was attributed to both the increase in temperature and level of rainfall. In both cases, the climatic and environmental conditions during this time period favored the development of larvae. However, correlations between the reproductive characteristics and body size or phylogenetic relationships were not discussed in this work.

Winemiller (1989) provided data on the life history and reproduction of roughly 72 freshwater fish species from various drainages in Venezuela, including 24 characid species, characterizing three reproductive strategies: equilibrium, opportunistic and seasonal. In the equilibrium strategy, generation time is intermediate or long, there is a large investment in individual offspring, maturation is delayed, reproduction is aseasonal and breeding prolonged. According Winemiller (1989), to some extent these life history traits agree with the relative “K-strategy” as originally proposed by Pianka (1970). The seasonal strategy is characterized by reproduction that is cyclical and annual, with a relatively long generation time that usually coincides with the reproductive cycle and with large clutches and low levels of care for the offspring. The opportunistic strategy is characterized by a short generation time, low fecundity, and minimum offspring care. According to the author, the latter strategy is associated with small species that exhibit high rates of reproduction despite the apparent high mortality rate of young adults as a result of unfavorable conditions and predation during the dry season. The opportunistic and seasonal strategies share many of the characteristics of a typical r-strategist (Pianka, 1970).

Most characids studied by Winemiller (1989) exhibited seasonal reproductive strategies with a reproductive period that lasted from one to three months for the large species and from one to six months for the smaller species. Some small characids species used an opportunistic reproductive strategy, with the reproductive period varying between 10 and 12 months. Other small species used reproductive strategies exhibiting opportunistic/seasonal characteristics, with reproductive periods lasting between five and eight months.

Kramer (1978) studied the reproductive characteristics of six characid species in Panama and discussed the influence of seasonality on the time and duration of the breeding and spawning periods. He presents five hypotheses to explain which factors determine the time and duration of the breeding period: 1) the reproductive period is controlled by the availability of food for the young and adults; 2) the reproductive period is controlled by interspecific competition among the young for food; 3) the reproductive period is controlled by competition for breeding locations; 4) the reproductive period is a mechanism of reproductive isolation; and 5) the reproductive period is not related to local conditions but was related to the evolution of previously primitive reproductive specializations and to those specialization that limit a species to spawning under particular conditions.

In terms of the last hypothesis, Kramer (1978) argues that the seasonality of reproduction may be a characteristic with a strong phylogenetic inertia. He also states that body size may be another factor that is involved in reproduction, and that there is a tendency for smaller species to have long reproductive periods. According to the author, smaller species, which do not have proportionally reduced ova [oocyte size] must have reduced fecundity unless able to produce multiple clutches within a season.

Menni & Almirón (1994) evaluated the reproductive period of fourteen fish species in Argentina, eight of which were characids. The authors also identified three distinct species groups that were based on the duration of spawning or according to the presence of spawning specimens: 1) species that spawned throughout most or all of the year; 2) species that did not spawn during the winter, avoiding temperatures lower than 20ºC, and 3) species with short spawning periods that were restricted to the last months of the winter or spring, spawning during the time when the temperature varied between minimum and maximum values. In all three groups, small characid species were present.

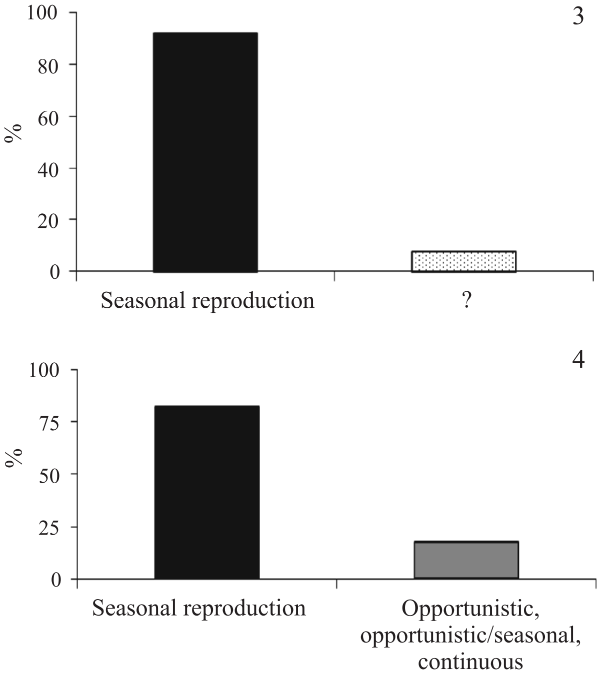
Studies conducted on the reproduction of small characids in southern Brazil evaluated reproductive characteristics, such as the timing and duration of the reproductive period, absolute and relative fecundity, spawning mode and diameter of mature oocytes. These studies included species of inseminating characids distributed in different groups within the family. In some cases, it was possible to establish correlations between certain reproductive characteristics and phylogenetic relationships of these same species. Some results for species of Cheirodontinae in northeastern Brazil are also informative.

Based on the data compiled here (Tab. I), it is possible to detect some general patterns in characid reproduction. More than 90% of the characid species that have the supraorbital bone, which are named the “large species,” reproduce seasonally (Fig. 3). For the species lacking a supraorbital bone, which are named the “small species,” over 80% reproduce seasonally, and approximately 18% show some variation of this pattern (Fig. 4). Over 50% of the large species have a reproductive period that is restricted to one, two, or three months, approximately 30% reproduce for four to six months, and only about 8% prolong reproduction for up to seven or eight months (Fig. 5). For the small species, just over 15% restrict reproduction to three months, more than 50% reproduce in four to six months, and more than 20% extend the reproductive period beyond six months. Approximately 13% of the small species reproduce for ten to twelve months (Fig. 6). For the large species, roughly 70% reproduce between the months of September and April, and only 8% also reproduce in other months (Fig. 7). For the small species, about 36% reproduce between September and April, and 33.3% are found to reproduce in other months (Fig. 8).

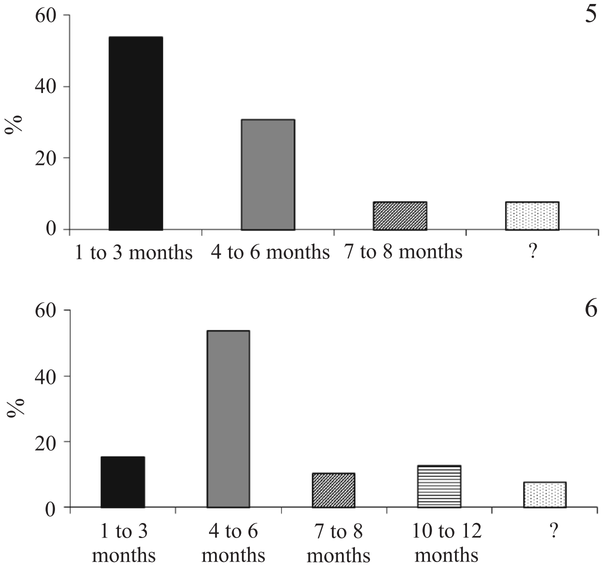
The absolute fecundity of the large species varies from 100 to 500,000 oocytes, and that of small species varies from 94 to 10,000 oocytes. Approximately 27% of the large species produce more than 5,000 oocytes, 19% produce between 2,500 and 5,000 oocytes, and only two species produce between 100 and 400 oocytes (Fig. 9). For the small species, only 11% produce more than 5,000 oocytes, and the same percentage produces 1,000 to 5,000 oocytes. Approximately 21% of these species produce 500 to 1,000 oocytes, and more than 36% produce from 90 to 500 oocytes (Fig. 10).

Of the large species that produce an extremely high number of oocytes (more than 5,000), more than 57% of these do not provide offspring care (Fig. 11), and more than 42% migrate (Fig. 12). Of the smaller species that produce up to 500 oocytes, 50% are inseminated (Fig. 13), and within those that produce up to 1,000 oocytes, more than 43% break up spawning events or have more than one courtship during the breeding period (Fig. 14).

The four smaller species that produce between 3,000 and 9,500 oocytes are above 80 mm in standard length. The other species, which produce a maximum of approximately 1,000 oocytes, are between 28 and 69 mm in length. There is a statistically significant positive correlation between absolute fecundity and body size ($r_{Pearson}$)=0,7074; p<0,0001) (Fig. 15). Moreover, there is also a significant negative correlation between relative fecundity and body size ($r_{Pearson}$)=-0,6280; p<0,0162) (Fig. 16). These data indicate that, whereas larger species may increase the absolute number of oocytes produced, the relative fecundity, which represents the average number of oocytes per gram of body weight, actually decreases as body size increases, suggesting that the smaller species may actually spend more energy on individual oocyte production. Available oocyte diameter measurements for 15 species show a significant correlation between oocyte diameter and body size ($r_{Pearson}$)=0,6484; p<0,0121) (Fig. 17).



Figures 3, 4. Relative frequencies (%) of species showing seasonal, opportunistic or continuous reproductive strategies in large (3) and small size (4) characid species. Source data given in Table I. “?” means unknown.



Figures 5, 6. Relative frequencies (%) of species showing different reproductive period lengths (months) in large (5) and small size (6) characid species. Source data given in Table I. “?” means unknown.

Table I. Summary of published data about reproductive traits and life history of characid species. Maximum length was extracted from the reference given for each species or from Reis *et al.* (2003). The data from Vazzoler & Menezes (1992) were compiled from several publications by those authors.

TAXONS	Maximum length of species (mm)	Size difference (♂/♀)	Reproductive seasonality	Time of year	Length reproduction (months)	Total fecundity (nº oocytes)	Relative fecundity (nº oocytes/mg body weight)	Spawning	Size of mature oocytes (mm)	Length of 1ª maturation	Parental care, migration, fecundation	Data source
SPECIES WITH SUPRAORBITAL BONE												
Brycon cephalus (Günther, 1869)	220		seasonal	December and January	2	36,700–309,290		total		306-325	migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
B. henni Eigenmann, 1913	350		seasonal	February and November	2							Vazzoler & Menezes, 1992; Vazzoler, 1996
B. **cf.** *melanopterus* (Cope, 1872)	300		seasonal	December and January	2						non-migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
B. orbignianus (Valenciennes, 1850)	625		seasonal	December and January	2			total	1.5	251	migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
B. petrosus Meek & Hildebrand, 1913	156	females larger	seasonal	February and March	2			apparently total	1.6-1.9			Kramer, 1978
B. whitei Myers & Weitzman, 1960	313		seasonal		1	171,545		apparently total				Winemiller, 1989
Colossoma macropomum (Cuvier, 1818)	995					500,000						Vazzoler & Menezes, 1992; Vazzoler, 1996
Milossoma aureum (Agassiz, 1829)	200		seasonal	November and December	2						migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
M. duriventris (Cuvier, 1818)	250		seasonal	November to March	5	25,500–100,000		total		156	migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
Myleus pacu (Jardine 1841)			seasonal	November to March	5					130	migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
Piaractus brachypomus (Cuvier, 1818)	710					400,000						Vazzoler & Menezes, 1992; Vazzoler, 1996
P. mesopotamicus (Holmberg, 1887)	405		seasonal	October to December	3	60,000 – 427,000		apparently multiple			non-migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
Pygocentrus notatus = *Pygocentrus cariba* (Humboldt 1821)	248		seasonal		3	4,303		apparently multiple				Winemiller, 1989
Salminus brevidens = *S. brasiliensis* (Cuvier, 1816)	1000		seasonal	November to February	4	100						Vazzoler & Menezes, 1992; Vazzoler, 1996
S. hilarii Valenciennes, 1850	500		seasonal	December and January	2	52,000		total		210-230	migratory, without parental care	
S. maxilosus = *S. brasiliensis* (Cuvier, 1816)	776		seasonal	October to January	4	2,600		total	1.3	320-411	migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
Serrasalmus irritans Peters, 1877	147		seasonal		3	3,048		apparently multiple				Winemiller, 1989
S. marginatus = Valenciennes, 1837	221		seasonal	September to April	8					98-116	non-migratory, with parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996

Tab. I (cont.)

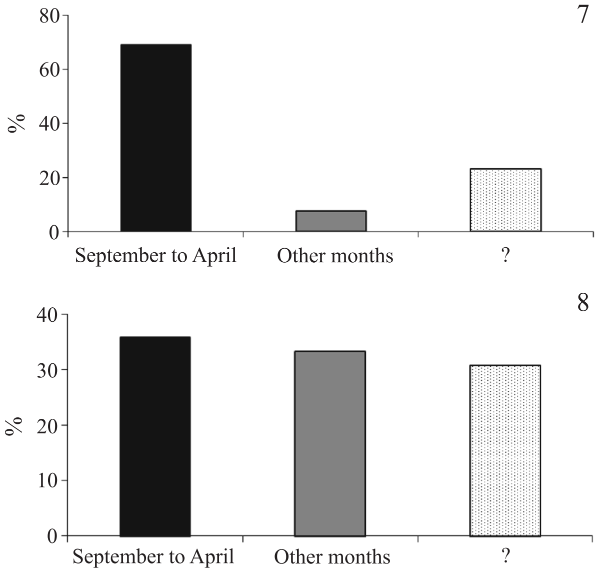
S. medinai Ramírez, 1965	140		seasonal		3	3,048		apparently multiple				Winemiller, 1989
S. nattereri = *Pygocentrus nattereri* Kner, 1858	333		seasonal	November to April	6						non-migratory, with parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
S. rhombeus (Linnaeus, 1766)	195		seasonal		3	4,303		apparently multiple				Winemiller, 1989
S. serrulatus Valenciennes, 1850	190		seasonal	January to June	6			multiple		124-127	non-migratory, with parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
S. spilopleura Kner, 1858	210		seasonal	October to April	7					108-138	non-migratory, with parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
Triportheus albus Cope, 1872	151		seasonal	December	1					120	migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
T. angulatus (Spix & Agassiz, 1829)	163		seasonal	November to March	5	400						Vazzoler & Menezes, 1992; Vazzoler, 1996
T. elongatus (Günther, 1864)	242		seasonal	September to January	5					150	migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
Triportheus sp.	120		seasonal		2	3,175		apparently total				Winemiller, 1989
SPECIES WITHOUT SUPRAORBITAL BONE												
Aphyocharax alburnus (Günther, 1869)	37		seasonal		3	617		apparently multiple				Winemiller, 1989
A. anisitsi Eigenmann & Kennedy, 1903	32.31	females larger	seasonal	September and February	6	344.8	0.68					Gonçalves *et al.*, 2005
A. difficilis = *A. dentatus* Eigenmann & Kennedy, 1903	69		seasonal January	October to	4						non-migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
A. nasutus = *Aphyocharax dentatus* Eigenmann & Kennedy 1903	46								17			Vazzoler & Menezes, 1992; Vazzoler, 1996
Astyanax bimaculatus (Linnaeus, 1758)	195		seasonal March	September to	7 3,200	300–		multiple	0.77	60-78	non-migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
A. bimaculatus	91		seasonal		2	4,287						Vazzoler & Menezes, 1992; Vazzoler, 1996
A. eigenmanniorum (Cope, 1894)	66.3	females larger	seasonal	spring, much of the summer and autumn								Menni & Almirón, 1994
A. fasciatus (Cuvier, 1819)	132		seasonal	November to April	6	600–10,000		total	0.78	52	non-migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
A fasciatus	85	females larger	seasonal	October and December to May	about 7							Menni & Almirón, 1994
A. integer Myers, 1930	92		seasonal		1	8,400		apparently multiple				Winemiller, 1989
A. metae Eigenmann, 1914						300						Vazzoler & Menezes, 1992
A. metae	106		seasonal		1	9,528						Winemiller, 1989
A. schubarti Britski, 1964	106		seasonal	November to May	7	600–7,800		total		41	non-migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
A. superbus Myers, 1942	64		seasonal		1	800		apparently multiple				Winemiller, 1989
Charax gibbosus (Linnaeus, 1758)	1125		seasonal		6	280		apparently multiple				Winemiller, 1989

Tab. I (cont.)

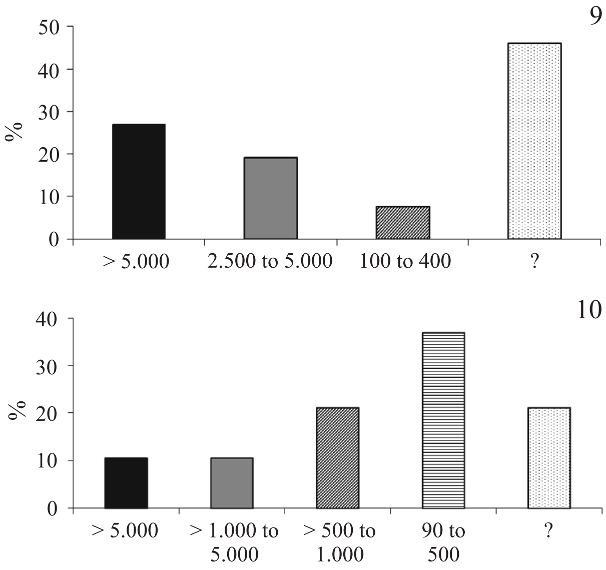
C. stenopterus (Cope, 1894)	103.2	females larger	seasonal	Spring and summer							Menni & Almirón, 1994
Ctenobrycon spilurus (Valenciennes, 1850)	580		seasonal		2 to 3	755		apparently multiple			Winemiller, 1989
Galeocharax knerii (Steindachner, 1879)	240		seasonal	December to February	3				1.1	96		Vazzoler & Menezes, 1992; Vazzoler, 1996
Hemigrammus sp.	33		opportunistic/ seasonal		7 to 8	282		apparently multiple				Winemiller, 1989
Hyphessobrycon meridionalis Ringuelet, Miquelarena & Menni, 1978	56	females larger	seasonal	September to December	4							Kramer, 1978
H. panamensis Durbin, 1908	41	females larger	seasonal	November to April	6				0.7-0.8			Kramer, 1978
Markiana geayi (Pellegrin, 1908)	104						400					Vazzoler & Menezes, 1992; Vazzoler, 1996
M. geayi	933		seasonal		2	3,398		apparently total				Winemiller, 1989
Moenkhausia intermedia Eigenmann, 1908	880		seasonal	November to June	8			multiple	0.7	55	non-migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
Myloplus asterias (Müller & Troschel, 1844)	?		seasonal	October and November	2						non-migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
Oligosarcus jenynsii (Günther, 1864)	2222		seasonal	November to January and March and April	6					145	non-migratory, with parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996; Menni & Almirón, 1994
Piabucina panamensis Gill, 1877	141	males larger	seasonal	rainy season				apparently total	1.2-1.5			Kramer, 1978
Pristella maxillaris (Ulrey, 1894)	45					100						Vazzoler & Menezes, 1992; Vazzoler, 1996
Roeboides guatemalensis (Günther, 1864)	130		non-seasonal	every months	12				0.85-1.0			Kramer, 1978
R. dayi (Steindachner, 1878)	109		opportunistic		7 to 12	280		apparently multiple				Winemiller, 1989
R. paranensis Pignalberi, 1975	95		sazonal	October to March	6			multiple	0.9	37		Vazzoler & Menezes, 1992; Vazzoler, 1996
Tetragonopterus argenteus (Cuvier, 1816)	83		seasonal		1 to 2	3,398		apparently total				Winemiller, 1989
CHEIRODONTINAE												
Cheirodon ibicuhiensis Eigenmann, 1915	44.6	females larger	seasonal	spring and summer	6	513	0.5	multiple				Oliveira *et al.* 2002
Cheirodon interruptus (Jenyns, 1842)	61.4	males larger	seasonal	late winter, spring and summer	8	400						Vazzoler & Menezes, 1992; Vazzoler, 1996
Cheirodon piaba = *Serrapinnus piaba* (Lütken, 1875)		seasonal	October to January	4	500						non-migratory, without parental care	Vazzoler & Menezes, 1992; Vazzoler, 1996
Cheirodontops geayi Schultz, 1944	28		seasonal		2	1,108		apparently total				Vazzoler & Menezes, 1992; Vazzoler, 1996
Odontostilbe pequira (Steindachner, 1882)	44.97	females larger	seasonal	September and October, January and February	4	722	0.71					Oliveira *et al.*, 2010

Tab. I (cont.)

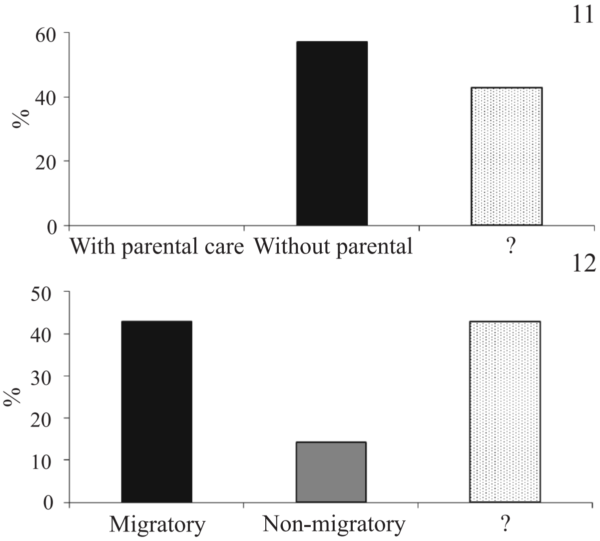
O. pulcher = *Odontostilbe pulchra* (Gill, 1858)	36		seasonal		5	1,108		apparently multiple				Winemiller, 1989
Serrapinnus calliurus (Boulenger, 1900)	46	females larger	seasonal	spring and summer	4	406	0.631	multiple				Gelain *et al.*, 1999
Serrapinus piaba (Lütken, 1875)	30.18	females larger	seasonal (♀)/ continuous (♂)	January to April (♀) and every months (♂)	4 (♀) and 12(♂)	441	0.74					Silvano *et al.*, 2003
COMPSURINI												
Compsura heterura Eigenmann, 1915	34.14	females larger	seasonal	January to April	4	434	0.55				inseminating	Oliveira *et al.*, 2010
Macropsobrycon uruguayanae Eigenmann, 1915	34.04	females larger	non-seasonal	continuous every months		191.08	0.539	total	0.6711	24	inseminating	Azevedo *et al.*, 2010
CLADE A												
B. beta Eigenmann, 1914	44		opportunistic	every months	12	796		apparently multiple				Winemiller, 1989
B. deuterodonoides Eigenmann, 1914	39		seasonal		6	243		apparently multiple				Winemiller, 1989
B. emperador (Eigenmann & Ogle, 1907)	76	males larger	seasonal	dry season					1.2-1.5			Kramer, 1978
B. iheringii (Boulenger, 1887)	54.58	females larger	seasonal	September to January	5	933.71	0.36					Lampert *et al.*, 2007
Bryconamericus stramineus Eigenmann, 1908	66.3	females larger	seasonal	October to February	5	371.3	0.35					Lampert *et al.*, 2007
Creagrutus sp.	28		opportunistic/ seasonal		6	94		apparently multiple				Winemiller, 1989
GLANDULOCAUDINAE												
M. microlepis (Steindachner, 1876)	40.2	males larger	seasonal	autumn and winter	4	109.33	0.27				inseminating	Azevedo, 2004
Mimagoniates rheocharis Menezes & Weitzman, 1990	54.85	males larger	non-seasonal	every months	continuous	421.05	0.356				inseminating	Azevedo, 2004
STEVARDIINAE												
Corynopoma riisei Gill, 1858	43		opportunistic	almost every year	about 10	135		apparently multiple			inseminating	Winemiller, 1989
Diapoma speculiferum Cope, 1894	48.7	females larger	seasonal	spring and summer	4	491.1	0.4101				inseminating	Azevedo *et al.*, 2000
D. terofali (Géry, 1964)	52.6	males larger	seasonal	spring and summer	4	322.63	0.565	total	0.8375	26-36.5	inseminating	Azevedo, 2004
D. terofali	67.5	females larger	seasonal	August to November	4						inseminating	Menni & Almirón, 1994
Gephyrocharax atracaudata Meek & Hildebrand, 1912	53	males larger	non-seasonal	every months	12				0.7-0.8		inseminating	Kramer, 1978
G. valencia Eigenmann, 1920	37		opportunistic/ seasonal		5	734		apparently multiple			inseminating	Winemiller, 1989
Pseudocorynopoma doriae Perugia, 1891	68.9		seasonal	cold months	about 6	980	0.3412				inseminating	Filipe Melo, comm. pes.; Carlos Machado, comm. pes.
P. doriae			seasonal	late winter spring and early autumn	about 6	1286.42	0.507				inseminating	Ferris *et al.*, 2007



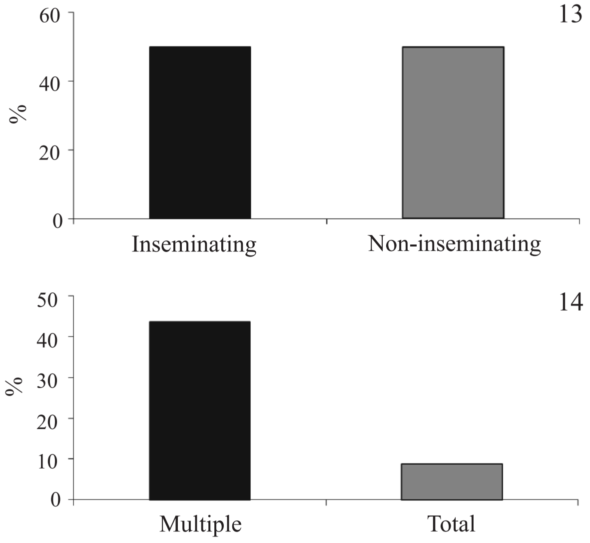
Figures 7, 8. Relative frequencies (%) of species with the reproductive period lasting between September and April, and of species showing reproductive activity outside this period, in large (7) and small size (8) characid species. Source data given in Table I. "?" means unknown.



Figures 9, 10. Relative frequencies (%) of species per absolute fecundity classes in large (7) and small size (8) characid species. Source data given in Table I. "?" means unknown.



Figures 11, 12. Relative frequencies (%) of parental care (11) and migratory behavior (12) in large size characid species with high fecundity (more than 5,000 oocytes). Source data given in Table I. "?" means unknown.



Figures 13, 14. Relative frequencies (%) of insemination and external fertilization in species with absolute fecundity up to 500 oocytes (13) and of species showing complete or partial spawning with absolute fecundity up to 1000 oocytes (14). Source data given in Table I. "?" means unknown.

In one of these species, however, the average diameter of the oocytes is the largest observed, regardless of its small body size (Fig. 17 - *B. emperador* (Eigenmann & Ogle, 1907)). This particular case suggests that this species compensates the low oocyte production by increasing the diameter of the oocytes.

Interpretations of the patterns of reproduction of characid species

In spite of the fact that these data represent a very limited number of characid species, and that possible errors in data analysis or species identification by the researchers may have occurred, it is still possible to formulate some initial hypotheses about the reproductive characteristics of the family Characidae that can be further tested as more data are accumulated in the future.

1) Characid species sharing a supraorbital bone tend to be larger than those without a supraorbital bone. A larger size is also observed in the majority of the species from the other characiform families.

2) Most of the species with a supraorbital bone have a general reproductive pattern that is characterized by a short seasonal reproductive season that lasts from one to three months and that rarely exceeds six months. Reproduction in these species normally occurs between September and April. Spawning in these species is generally complete, their absolute fecundity can be

extremely high, and several species are migratory. Many species with lower fecundity present some form of parental care, providing a higher chance for egg and larval survival.

3) There may have been a single event of body size reduction (miniaturization) in the common ancestor of all characid species that share the apomorphic lack of a supraorbital and less than 40 vertebrae. Body size reduction may have independently appeared in other lineages of Characiformes, as for example the Crenuchidae, Gasteropelecidae, and Lebiasinidae. Size reduction possibly represented an adaptive advantage in several aspects related to the occupation of new environments and niches, but can, moreover, have required new evolutionary responses to new biological problems arising.

4) In terms of reproduction, the most direct consequence of a reduced body size is the reduction of the absolute number of oocytes produced by smaller species.

5) Many small characid species retain some or most of the reproductive traits of the larger species, with a seasonal reproductive period between September and April, a relatively high fecundity, and total spawning. However, many of these species, especially those belonging to Clade A (*sensu* Malabarba & Weitzman, 2003), exhibit changes in this reproductive pattern, such as extended reproductive period, reproducing during the colder months, reduced fecundity, and multiple spawning. These changes are possibly in response to a decrease in size and subsequent decrease in fecundity.

6) The following changes in the general reproductive patterns of characiforms are found in small species and may constitute novelties in response to environmental pressures that are related to the reduction of body size and fecundity: size reduction of mature oocytes (increasing fecundity) or an increase in the size of the oocytes (maximizing offspring survival), multiple spawning to produce several batches of oocytes in one breeding season, extended reproductive periods, the presence of more than one reproductive cohort during the year or continuous reproduction, high growth and recruitment rates (quickly increasing sexually active population), the insemination and all of the morphological, physiological, and behavioral adaptations known to exist for inseminating species (see Burns & Weitzman, 2005). Similar selective pressures may lead to the emergence of these independent adaptations in different lineages of small characids and at different times in evolutionary history.

Some specific trends are observed in Clade A species, particularly in the inseminating species. The majority of species belonging to Clade A, and particularly the inseminating species, have lower relative fecundity values than other characid species (data available only to small size species, Fig. 16). Among small size species, lower relative fecundity values may be associated with the presence and efficiency of insemination. In the same manner, some species considered to be highly adapted to the mode of insemination, such as the genera *Mimagoniates* Regan, 1907 and *Pseudocorynopoma* Perugia, 1891, are able to reproduce during a major part of the year or during months outside of spring and summer (Tab. I), which may represent an adaptation related to the efficiency of insemination. Protracted reproduction may also have arisen independently in other inseminating characid lineages.

Large species have oocytes with diameters that are larger than those of smaller species (Fig. 17). Among the smaller species, however, the oocyte diameter varies very little. For example, *Diapoma terofali* (Géry, 1964) (Stevardiinae) engages in insemination and has low absolute fecundity, but the diameter of the oocytes is very similar to that of the other small species that are externally fertilizing and with higher fecundity (Azevedo, 2004). However, the inseminating cheirodontine, *Macropsobrycon uruguayanae* Eigenmann, 1915, has a reduced oocyte diameter and a high relative fecundity (Azevedo *et al.*, 2010). The decrease in oocyte size in *M. uruguayanae* does not seem to be present in the inseminating Stevardiinae species, suggesting that the reproductive traits of both groups have evolved under different selective pressures. This finding supports the hypothesis that insemination has independent origins in both groups (Burns *et al.*, 1995, 1997, 1998; Azevedo, 2004; Weitzman *et al.*, 2005).

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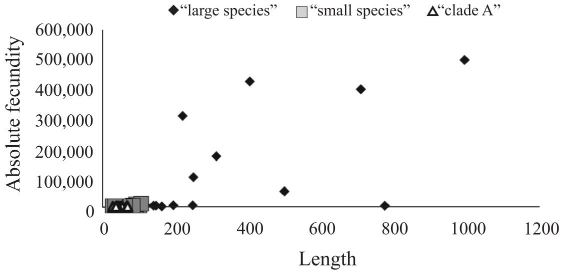

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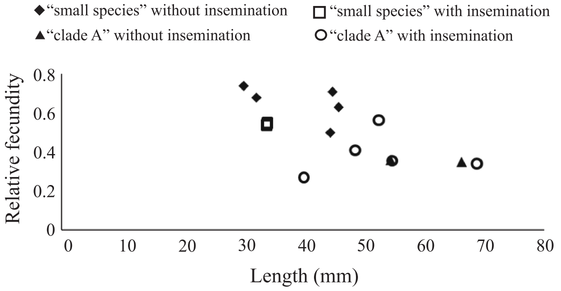

Figures 15, 16. Scatter plot of absolute fecundity (15) and relative fecundity (16) versus body length in small characid species. Source data given in Table I. "?" means unknown.

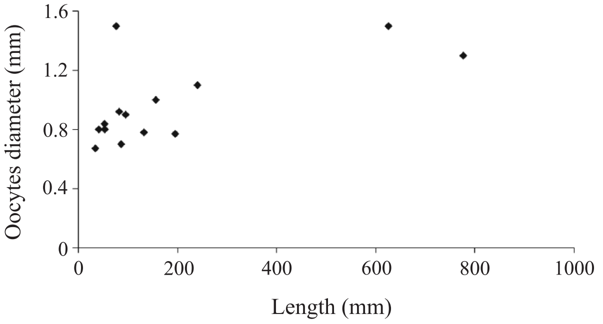

Figure 17. Scatter plot of oocyte diameter versus body length in characid species. Source data given in Table I. "?" means unknown.

Although the information from the literature that was compiled in this study represent an advance in studies on reproductive strategies of characid species, the available data are extremely fragmented and represent only some aspects of reproduction for a limited number of species. Further research aiming to test the hypotheses and trends reported in the present study are required. The reproductive patterns related to body size and phylogeny of the groups and species of this family show that this type of information is potentially useful in systematic terms and may reflect the relationships among these groups.

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