DISTRIBUTION OF CAVE-DWELLING *AEGLA* SPP. (DECAPODA: ANOMURA: AEGLIDAE) FROM THE ALTO RIBEIRA KARSTIC AREA IN SOUTHEASTERN BRAZIL BASED ON GEOMORPHOLOGICAL EVIDENCE

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ABSTRACT

In this study, we assess the main ecological and evolutionary causes of the current distribution of cave dwelling species of *Aegla* from the Alto Ribeira karstic province, southeastern Brazil. Based on field surveys conducted over several years and on examination of scientific collections, we discuss herein how processes of colonization, dispersal, and vicariance could have resulted in the present pattern of distribution of these species. Given the extensive area of continuous limestone lenses interrupted by insoluble rocks, the distribution of aeglids from Alto Ribeira is limited by stratigraphic barriers, possibly due to difficulty in accessing other underground compartments and low vagility of juveniles. Sympatric speciation is unlikely, since molecular evidence does not support a strong sister-group relationship between extant troglophilic and troglobitic species with sympatric distribution in the study area. Under differing sources of evidence, we hypothesize that Pleistocene climatic fluctuations and drainage changes is the main cause of vicariance in the study area, while the fragmented nature of the limestone lenses probably hindered subsurface dispersion. Troglobites could be relicts of extinct epigean ancestrals, while the extant troglophiles did not achieve reproductive isolation after vicariance events, resulting in the present co-distribution with species less closely related.

KEY WORDS: *Aegla*, allopatric speciation, endemic troglobites, troglophiles

INTRODUCTION

One subject that has frequently been addressed by speleo-biologists is the causal factors influencing distribution and speciation patterns of troglobitic (= obligate) cave fauna. Historic and island biogeography hypotheses have supported cave fauna distribution studies, explaining biological phenomena at different spatio-temporal scales. In this regard, several authors stressed the importance of vicariance, dispersion, and ecological interactions influencing the distribution of troglobitic species (Barr, 1967, 1968; Barr and Holsinger, 1985; Christiansen and Culver, 1987; Culver et al., 2009).

Karstic areas are composed of dissolution rocks (carbonatic/limestone and quartzitic rocks), comprise caves (endokarst), and superficial landforms (dolines and towers). These features are formed by acidified water and can be connected with other subterranean habitats (hyporreic, interstitial, and superficial habitats – the Milieu Souterrain Superficiel or MSS), forming a subterranean system delimited by insoluble rocks (Karmann and Sánchez, 1979; Palmer, 2007).

We know that some cave organisms can potentially disperse via subterranean routes in continuous karst. Based on observations of distributional patterns in beetles (Carabidae:

Trechinae), Barr (1967, 1968) discussed the ecological consequences of limestone discontinuity. He hypothesized that there should be more subterranean species with smaller geographic ranges, and infrequent sympatry between closely related species in areas with interrupted limestone outcrops.

Since then, a series of studies focusing on the role of migration-extinction dynamics, besides vicariance of cave-limited species, under an island biogeographic approach (Culver et al., 1973; Culver et al., 2009) have been made. This research stressed the importance of examining the levels of migration and extinction in island-like environments because extinction destroys the history of distribution whereas migration obscures it (Culver et al., 1973; Culver, 1982).

In their classic revision, Barr and Holsinger (1985) compiled and discussed a large amount of data encompassing speciation and distribution of many terrestrial and aquatic troglobites. They discussed the vagility and size of the organisms influencing geographic expanses and demonstrated the influence of non-karst routes to aquatic species dispersion patterns as well.

More recently, Christman and Culver (2001) discussed the role that habitat availability plays in the distribution of obligate cave fauna in North America. They showed that species richness depends on the local number of caves

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allowing colonization and isolation and is also controlled by regional habitat availability because of migration, when considerable subsurface dispersion occurs. Culver and Sket (2000) and Gibert and Deharveng (2002) also discussed how fragmented habitats and restrictions to dispersal in karst areas lead to many endemic species with limited distribution and diversity being expressed regionally rather than locally.

In keeping with this conceptual framework, we take cave-dwelling aeglid decapods as a biological model to discuss dispersion and speciation patterns from an evolutionary and ecological perspective. *Aegla* Leach, 1820 is the only extant genus of Aeglidae Dana, 1852 and is endemic to subtropical and temperate South America, with meridional and septentrional limits of distribution represented by the Duque de York Island, in Chile, and Claraval County, in Brazil, respectively (Bueno et al., 2007; Oyanedel et al., 2011).

Anomuran decapods are typically associated with marine habitats although some are estuarine and some are even considered terrestrial. *Aegla*, however, is unique because all known species are entirely adapted to freshwater habitats (Schmitt, 1942; Bond-Buckup and Buckup, 1994), albeit the early marine origin of Aeglidae as suggested by fossil records (Feldmann, 1984; Feldmann et al., 1998). Besides *Aegla*, complete adaptation to the freshwater habitat has also been reported in the anomuran diogenid hermit crab, *Clibanarius fonticola* McLaughlin and Murray, 1990 from Vanuatu (McLaughlin and Murray, 1990).

Over 70 species of aeglids have been described so far (see annotated checklist by McLaughlin et al. (2010), plus recent descriptions of new species by Bond-Buckup et al. (2010a, b) and Santos et al. (2009, 2010, 2012)). There is still great potential for discovering new species inhabiting yet unexplored epigean and hypogean habitats (Bueno et al., 2010).

Most species of *Aegla* are found in epigean habitats such as rivers and lakes (Bond-Buckup et al., 2008). Some species, however, are obligate (troglobites) and facultative (troglophiles) cave-dwelling species and are endemic to the karst province of the Alto Ribeira located in the Ribeira do Iguape Hydrographic Basin, southeastern Brazil (Türkay, 1972; Trajano, 1987; Bond-Buckup and Buckup, 1994; Gnaspini and Trajano, 1994; Moracchioli, 1994; Rocha and Bueno, 2004; Rocha and Bueno, 2011).

There are three troglobitic aeglid species described so far: *A. leptochela* Bond-Buckup and Buckup, 1994; *A. microphthalma* Bond-Buckup and Buckup, 1994; and *A. cavernicola* Türkay, 1972. Four additional species still await formal description (Bueno, unpublished data). Compared to epigean populations, all troglobitic aeglid species exhibit marked troglomorphic traits, such as exoskeleton depigmentation, reduced eyestalk and pigmented area of the cornea, proportionally longer walking legs and antennal flagella as compared to body size (Bond-Buckup and Buckup, 1994; Alves Jr., 2007).

Troglobitic aeglids are highly endemic and have allopatric distribution as the occurrence of each species is restricted to its respective type locality. These type localities are located within the boundaries of the Intervales State Park (PEI) and the Alto Ribeira Touristic State Park (PETAR),

in southeastern Brazil. These two parks occupy a large area (about 81 712 ha) of the karstic province characterized by discontinuous limestone lenses interrupted by non-limestone rocks (Karmann and Sánchez, 1979; São Paulo, 2006).

Besides the troglobitic species, two additional troglophilic aeglid species are also found in the PEI and in the PETAR: *Aegla schmitti* Hobbs III, 1978; and *A. marginata* Bond-Buckup and Buckup, 1994. These two species may transit freely between the epigean and hypogean environs and are able to establish self-sustained populations in both habitats. The area of occupancy (sensu IUCN, 2010) of troglophilic species is much larger than that of obligate cave-dwelling species and exceeds to a great extent the boundaries of both parks.

The purpose of the present scientific paper is to discuss the distribution of *Aegla* in the Alto Ribeira karstic area, based on geological and molecular data available in the scientific literature, and field surveys recently carried out by our team.

MATERIALS AND METHODS

The Alto Ribeira karstic area is geologically defined by the presence of metasediments and marine limestone, deposited in a Pre-Cambrian tectonically active environment. In the study area, the lithology consists of phyllites, quartzites, crystalline limestones, metaconglomerates, and metabasites (Karmann and Sánchez, 1979). Discontinuous limestone outcrops are oriented NE-SW, with a width varying from 1000 to 8000 m, but reaching up to 20 000 m of extension (Karmann and Sánchez, 1979; Genthner et al., 2003). Intercalated to the limestone lenses, the insoluble rocks mentioned above isolate different cave systems (Trajano, 1991; Bichuette, 1998).

The study area encompassed two contiguous conservation units: the Intervales State Park (PEI), and the Alto Ribeira Touristic State Park (PETAR) (Fig. 1). Only two limestone lenses cross the Intervales area, originating an extensive area of continuous limestone intercalated with insoluble rocks as phyllites and granites (Campanha, 2003). In contrast, PETAR has four limestone lenses crossing its area, where about 500 caves are found (Trajano, 1991; Bichuette, 1998; Karmann and Ferrari, 2002).

Data and information regarding aeglids from Alto Ribeira were obtained from examination of materials from two scientific collections: Museu de Zoologia da Universidade de São Paulo (MZUSP), and Laboratório de Estudos de Eglídeos da Universidade de São Paulo (LEEUSP). Additional materials were sampled from hypogean and epigean habitats from both State Parks (see Table 1 for details) by means of visual inspections and hand nets (Moracchioli, 1994) and baited traps randomly placed along the bottom of the rivers (Bueno et al., 2007).

RESULTS AND DISCUSSION

Influence of Geomorphology of Alto Ribeira Karstic Area on Subterranean Aeglids

A subterranean system is defined as continuous exposures of soluble rocks dissolved by acidified water. It provides a heterogeneous habitat in which the caves are only a part of the complex system of the interconnected flow pathways, storages and voids (filled or not with water) of different sizes and inhabited by hypogean invertebrates (Juberthie and Decu, 1994; Juberthie, 2000). In a continuous limestone, the interconnected subterranean system rarely imposes restrictions to dispersion of subterranean biota (Barr, 1967, 1968; Barr and Holsinger, 1985, for instance). In the interface between karstified (soluble) and non-karstified (insoluble) rocks other kinds of subterranean environments could occur, such as the micro-spaces between disaggregated sediments establishing dispersion routes for few organisms, but the great majority of the obligate subterranean cave faunas follows the delimitation of the channels in continuous cave systems (Barr and
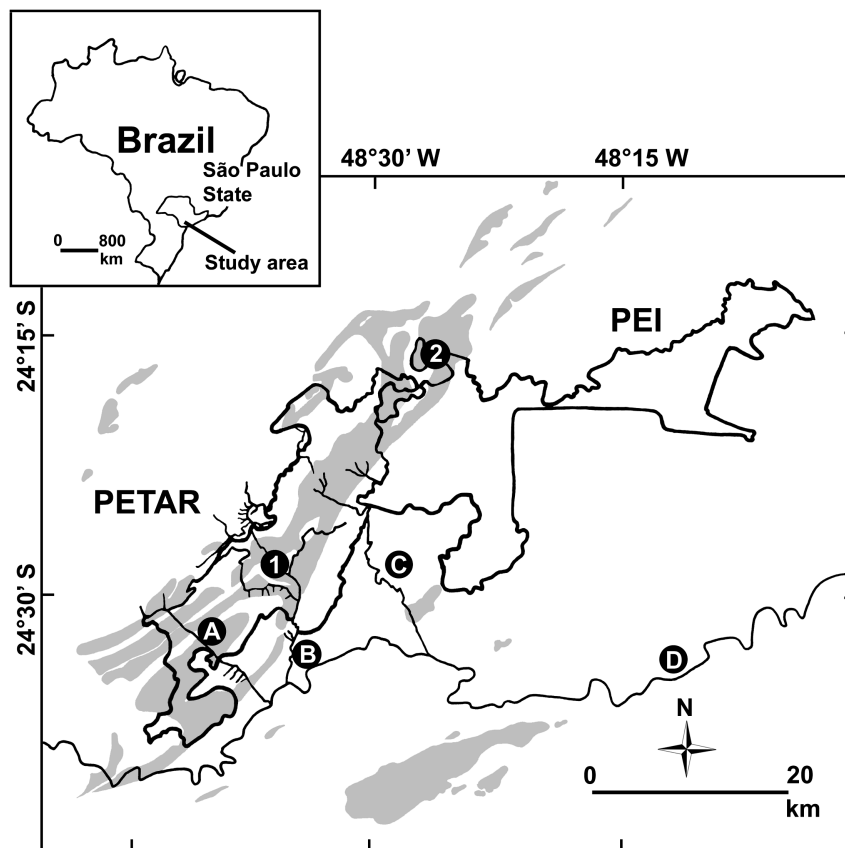
Fig. 1. Distribution of limestone lenses (in gray) and main rivers in the Alto Ribeira Touristic State Park (PETAR) and Intervales State Park (PEI). A = Betari River; B = Iporanga River; C = Pilões River; D = Ribeira River; 1 = Area amplified in Fig. 2; 2 = Area amplified in Fig. 3 (modified from Sallun and Sallun Filho, 2009).

Holsinger, 1985; Trajano, 1992). This distinction between karst and non karst routes is very important for the comprehension of dispersion patterns of subterranean biota.

Figures 2 and 3 show distribution records of aeglids in the contiguous karstic area, based on data from previous distributional records from scientific collections (see Bond-Buckup and Buckup, 1994; Moracchioli, 1994; Rocha and Bueno, 2004) and from recent field surveys conducted by our team. Name and geographic coordinates from each location are provided in Table 1. It becomes clear that the distribution of obligate cave-dwelling aeglids from the Alto Ribeira follows the NE-SW orientation of the stratigraphic barriers and possibly is reminiscent of the colonization and speciation processes (see discussion in the next topic).

Despite the extensive area of continuous karst occurring in Intervales (Campanha, 2003), the troglobite *A. leptochela* occurs only in its type locality, the dos Paiva Cave. It seems that this species lacks the ability to disperse via subterranean channels (see Christiansen and Culver, 1987) or even that competition with the sympatric troglophile (*A. marginata*) could represent an additional restriction to distribution in other caves located in the same limestone lenses, as discussed by Barr (1967).

Ecological constraints (Barr, 1967; Christiansen and Culver, 1987) probably also had a crucial role in the distribution of all troglobitic *Aegla* from PETAR, since underground dispersion in the same limestone outcrop rarely occurs. In-

deed, while *A. microphthalma* is endemic to its type locality, *A. cavernicola* occurs in the Areias de Cima Cave (upstream) and Areias de Baixo Cave (downstream), both caves are located very close to one another in continuous limestone lenses. The latter species can migrate only a short distance via subterranean routes as shown by its distribution in both caves, but it does not occur in the Ressurgência das Areias de Água Quente Cave, located several kilometers downstream in the same cave system. The distribution of the four new species corroborates our observations, since each species was found in a specific cave; with all these caves located in the same limestone outcrop. Like all the other obligate cave species, their distribution follows the orientation of the limestone. Troglobitic *Aegla*, unlike troglophiles, does not overcome different cave systems, i.e., located in another limestone outcrop, through epigean routes (Bond-Buckup and Buckup, 1994; Moracchioli, 1994; Rocha and Bueno, 2004).

Barr (1967) and Barr and Holsinger (1985) hypothesized that interrupted limestone outcrops could act as extrinsic barriers and so the areas with this geological conformity should have a higher number of endemic species with limited distribution ranges. Our observations corroborate this predicted pattern, as the area with more limestone lenses interrupted by insoluble rocks (PETAR) has a relatively higher number of endemic species of *Aegla*, with limited range of distribution. Somewhat intriguing is that it was expected that some of these species could migrate through

Table 1. Epigean and subterranean stream reaches sampled in the present study. The cave registration number refers to the cave records (SBE 1991). Data include previous records by Bond-Buckup and Buckup (1994), Moracchioli (1994), Rocha and Bueno (2004), Maia et al. (in press), as well as site information regarding the four new troglobitic species (Bueno et al., unpublished).

Study area	Stream reaches (cave registration number)	Coordinates	Aeglid species
PETAR	Betari River	24°31′14″S; 048°41′43″W	*A. schmitti*
PETAR	Temimina I Cave (SP-060)	24°23′16.5″S; 048°34′16.5″W	*A. schmitti*
PETAR	Temimina II Cave (SP-061)	24°23′S; 048°34′W	*A. schmitti*
PETAR	Santana Cave (SP-041)	24°31′51″S; 048°42′06″W	*A. microphthalma*; *A. schmitti*
PETAR	Água Suja Cave (SP-025)	24°31′25″S; 048°42′27″W	*A. schmitti*
PETAR	Ressurgência do Córrego Seco Cave (SP-049)	24°57′85.3″S; 048°62′86.5″W	none
PETAR	Areias de Baixo Cave (SP-019)	24°35′20″S; 048°42′05″W	*A. cavernicola*
PETAR	Ressurgência das Areias de Água Quente Cave (SP-016)	24°33′51″S; 048°40′14″W	none
PETAR	Betari de Baixo Cave (SP-47)	24°34′S; 048°37′W	none
PETAR	Alambari de Baixo Cave (SP-12)	24°33′24″S; 048°39′55″W	none
PETAR	Morro do Couto Cave (SP-20)	24°31′58″S; 048°41′55″W	none
PETAR	Aranhas Cave (SP-113)	24°26′S; 048°35′W	none
PETAR	Água Sumida Cave (SP-193)	24°27′42″S; 048°36′44″W	none
PETAR	Desmoronada Cave (SP-074)	24°24′16″S; 048°32′44″W	none
PETAR	Ouro Grosso Cave (SP-054)	24°33′S; 048°41′W	none
PETAR	Lago Subterrâneo Cave	24°19′34″S; 048°29′24″W	sp. n. 1
PETAR	Ribeirãozinho III Cave (SP-138)	24°20′35″S; 048°30′33″W	sp. n. 2
PETAR	Areados IV Cave (SP-524)	24°21′41″S; 048°31′54″W	sp. n. 3
PETAR	Furo da Agulha Cave (SP-483)	24°23′23″S; 048°34′14″W	sp. n. 4
PEI	Pilões River	24°48′78″S; 048°48′30″W	none
PEI	Bocaina River	24°16′20″S; 048°27′15″W	*A. marginata*
PEI	Colorida Cave (SP-129)	24°16′13″S; 048°25′09″W	*A. marginata*
PEI	Fendão Cave (SP-239)	24°16′11″S; 048°26′55″W	*A. marginata*
PEI	Pescaria Cave (SP-10)	24°27′7.5″S; 048°33′3.5″W	none
PEI	Jane Mansfield Cave (SP-237)	24°16′S; 048°27′W	*A. marginata*
PEI	Fogo Cave (SP-236)	24°16′S; 048°26′W	none
PEI	Minotauro Cave (SP-247)	24°15′S; 048°27′W	none
PEI	Tatu Cave (SP-233)	24°16′S; 048°25′W	*A. marginata*
PEI	dos Paiva Cave (SP-042)	24°16′24″S; 48°26′32″W	*A. leptochela*; *A. marginata*
PEI	Água Luminosa Cave (SP-307)	24°17′05″S; 48°26′16″W	*A. marginata*
PEI	Barra Bonita Cave (SP-271)	24°16′03.0″S; 48°27′24.0″W	*A. marginata*

subterranean routes in the same limestone outcrop. The reason why they are restricted only to their type locality still needs to be investigated, but could be related to inability to access these subterranean routes.

As observed by Barr (1968), the dispersal of troglophiles is not dependent upon underground channels through the limestone and, thus, their geographic distribution is not necessarily controlled by the extent of karst regions. Without the restrictions imposed by limestone discontinuity, migrations of troglophiles should occur among caves as well as epigean routes in the same biospeological system. In this case, as discussed by Barr (1967) and Barr and Holsinger (1985), these species are frequently widely distributed. Corroborating this statement, we confirmed a wide range of the troglophile *A. marginata* in epigean, as well as in subterranean stream reaches in Intervales (Bond-Buckup and Buckup, 1994), where all caves surveyed (Table 1) are located in the same limestone belt (see geological map from Pellegatti-Franco, 1997). This indicates that both routes can be used for dispersal by this troglophile as shown by several localities where the occurrence of this species has been reported.

Contrasting with the wide range of *A. marginata*, *A. schmitti* occurs only in superficial rivers and in a few caves

from PETAR, all of them located in different limestone lenses. This difference between the distributions of the two troglophiles is possibly due to different degrees of specialization to subterranean environment and also to the PETAR geomorphologic unit. Unlike Intervales, PETAR comprises four different limestone belts intercalated with insoluble rocks and each cave with *A. schmitti* record is located in a different belt of limestone outcrops, inaccessible via underground routes (Trajano, 1991; Bichuette, 1998; Genthner et al., 2003). This truncated and non-linear pattern suggests that colonization of the subterranean domain by this species occurs only through epigean source populations.

Hypotheses about Colonization of Subterranean Realms and Speciation of Troglobitic *Aegla*

The phylogenetic relationship among extant aeglids is based on molecular data and biogeography published by Pérez-Losada et al. (2004), and updated modifications in subsequent works (Pérez-Losada et al., 2009; Bond-Buckup et al., 2010b; Santos et al., 2010). In these papers, the troglobitic species *A. cavernicola* and *A. leptochela* are more related respectively to the troglophilic species *Aegla strinatti* Türkay, 1972 (from Jacupiranga State Park) and *A. marginata*, then to each other. Even the clade *A. cavernicola/A. strinatii* is
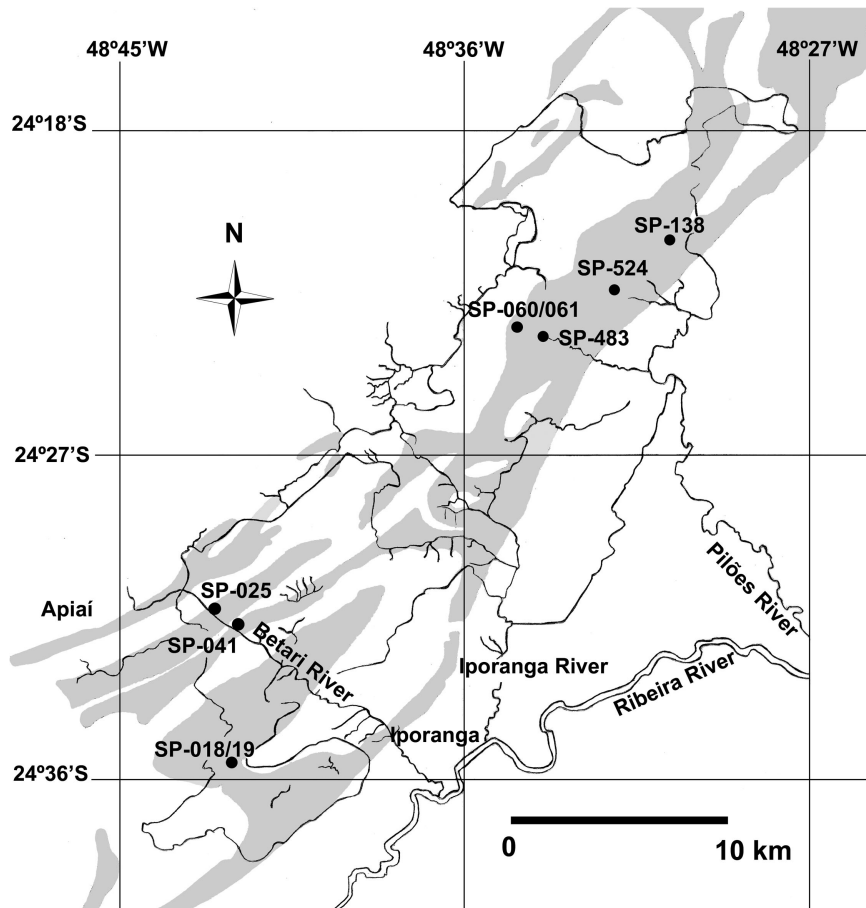
Fig. 2.   Caves and rivers in the Alto Ribeira Tourist State Park (PETAR), where we obtained individuals of *Aegla*. The limestone lenses are highlighted and the cave registration number refers to the cave records (SBE, 1991) where aeglid specimens were collected. SP-018 = Areias de Cima Cave; SP-019 = Areias de Baixo Cave; SP-025 = Água Suja Cave; SP-041 = Santana Cave; SP-060 = Temimina I Cave; SP-061 = Temimina II Cave. Three new troglobitic aeglid awaiting full description and sampled from recently discovered/explored caves are also indicated: sp. n. 2 from Ribeirãozinho III Cave (SP-138); sp. n. 3 from Areado IV Cave (SP-524) and sp. n. 4 from Furo da Agulha Cave (SP-483) (modified from Bichuette, 1998 and Campanha, 2003).

indicated as showing more of a phylogenetic affinity to the clade formed by the epigean species *Aegla parana* Schmitt, 1942 and *A. schmitti* than to the troglobite *A. leptochela*.

According to Pérez-Losada et al. (2004), the troglobite *A. leptochela* is closely related to the troglophile *A. marginata* and both populations co-exist inside dos Paiva Cave. Oddly, the clade *A. leptochela*/*A. marginata* is depicted in the clado-gram as being more related to aeglids from a different hydro-graphic basin (clade E in Pérez-Losada et al., 2004, which includes species from Rio Grande do Sul, the southernmost state of Brazil) than to any other aeglid species from the karstic province of the Alto Ribeira. In later trees, modi-fied from Pérez-Losada et al. (2004), *A. leptochela* has been depicted as sister-taxon of *A. muelleri* Bond-Buckup et al., 2010b from the hydrographic basin (Itajaí Basin) in the state of Santa Catarina, but still maintained in a separate clade from the one that contains the species from the Alto Ribeira (Bond-Buckup et al., 2010b, Santos et al., 2012). So far, *A. microphthalma* and the four new troglobitic species have not yet been included in any phylogenetic study.

The current understanding of the phylogenetic relation-ship of *Aegla* provides support to a coherent interpretation of the possible route of colonization and speciation of troglo-bitic aeglids according to the Adaptative Zone Model, pro-posed by Stoch (1995) to explain historical determinants of species diversity in hypogean habitats. In this model, the di-versity and distributional pattern of troglobitic aeglids in the karst province are coherent with the multiple colonization events, and would involve the following sequence of steps: colonization (exploitation of resources and occupation of empty niches) of subterranean domain by epigean species; speciation leading to the formation of true troglobitic popu-lation through genetic isolation of colonizers from epigean population; no radiation would occur (see Stoch, 1995, for details of each step). The adequacy of the multiple colo-nization events model to explain the diversity of troglobitic aeglids and yet remaining coherent to the current phyloge-netic view of *Aegla* do imply that successful colonization of hypogean habitats occurred independently, not necessarily simultaneous in time, from epigean populations, and led to the establishment of highly endemic troglobitic populations, with each species completely isolated from one another. As-suming that all surface ancestors of a troglobite are extinct, then the phylogenetic trees of extant species resulting from a vicariant or dispersal model of allopatric speciation are identical (see Culver et al., 2009). Further considerations,
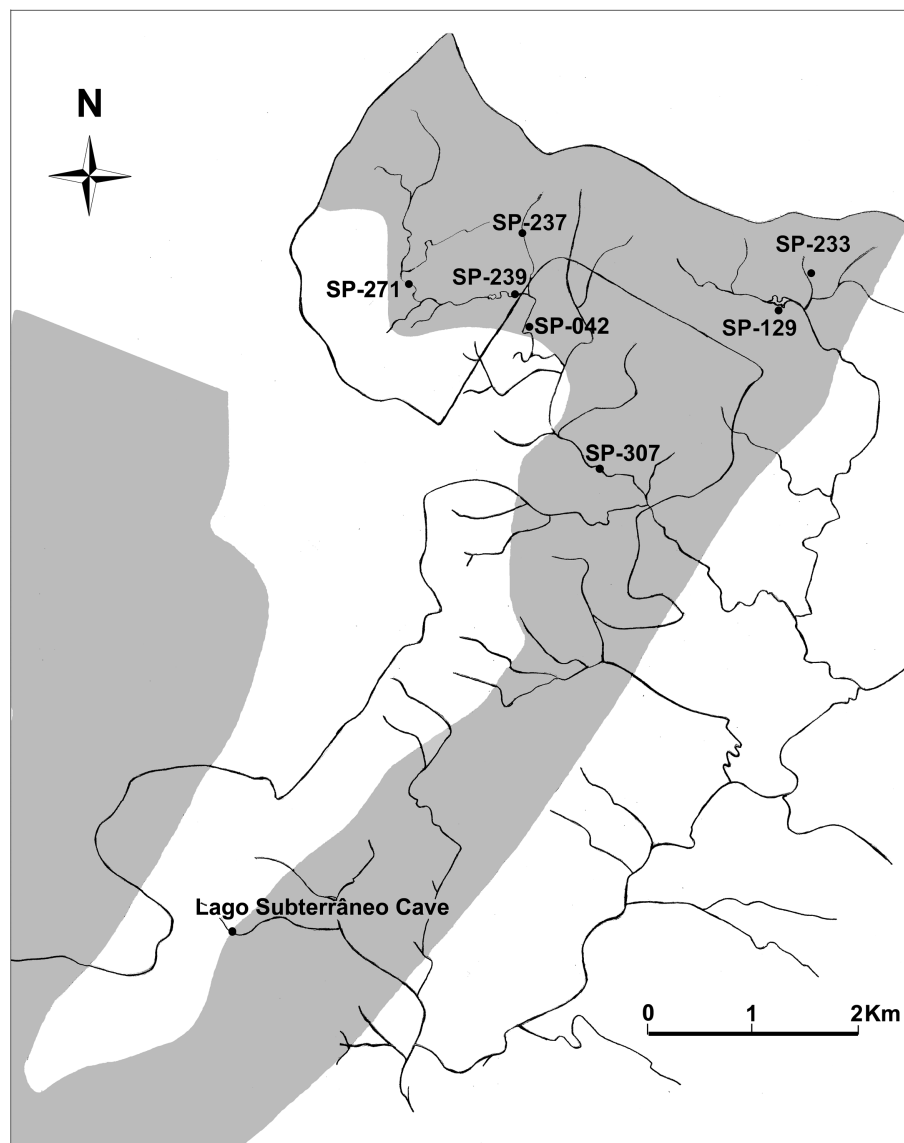
Fig. 3.   Caves and rivers in the Intervales State Park (PEI), where we collected *Aegla*. The limestone lenses are highlighted and the cave registration number refers to the cave records (SBE 1991) where aeglid specimens were collected. SP-271 = Barra Bonita Cave; SP-239 = Fendão Cave; SP-237 = Jane Mansfield Cave; SP-042 = Paiva Cave; SP-129 = Colorida Cave; SP-233 = Tatu Cave; SP-307 = Água Luminosa Cave. The type locality of, as yet undescribed species, *Aegla* sp. n. 1 (Lago Subterrâneo Cave, unregistered) is also indicated (modified from Pellegatti-Franco, 1997).

therefore, should be viewed with caution. Nevertheless, we discuss the most probable scenario.

Paleontological and geological evidence shows that the Alto Ribeira karstic area was under the influence of Pleistocene climatic changes which may have provoked alterations in groundwater level and, consequently, isolation of troglophilic populations in subterranean environments (Ab'Saber, 1977; Trajano and Britski, 1992; Ledru, 1993; Cruz et al., 2005). Associated with this, it seems that a gradual increase in the subterranean drainage capacity of limestones has occurred, resulting from chemical dissolution, and, consequently, successive drainage alterations (Karmann, 1994). While these events possibly isolated subterranean populations, the insoluble rocks that uplifted between formerly connected systems (Trajano, 1991, 1995) could have acted as barriers to subterranean dispersal.

Considering the geological and molecular evidence mentioned above, we suggest that an independent colonization of subterranean domain occurred by different epigean ancestors, followed by vicariance and speciation. Thus, the troglobites would be relicts of extinct epigean ancestors, while the extant troglophilic species did not achieve reproductive isolation after the vicariance events, resulting in their present distribution with species not closely related to them, as hypothesized by Barr (1967, 1968) when discussing the ecological consequences of limestone discontinuity.

In his paper about a globalized world of globalized biota, Schram (2008) rightfully pointed out that life forms that suffer minimal effects from globalization (marginal fauna from quite inaccessible environments) constitute the best material for biogeographic and evolutionary studies. In this context, candidate taxa should meet four criteria

(Schram, 2008): (1) be of a demonstrated ancient lineage, (2) be ecological generalists, (3) live in cryptic habitats, and (4) have limited abilities to disperse.

The taxon *Aegla* does meet at least three of these criteria. The point of origin and dispersion routes of freshwater aeglids through paleohydrograhic basins of continental South America has recently been well established and dated (Perez-Losada et al., 2004). The east-northward dispersion route through the Paraná river paleobasin are among the latest chapter in the evolutionary history of freshwater aeglids, having taking place at approximately 25 my, identified as clade C in Pérez-Losada et al. (2004). Presently, the hydrographic area known as the Upper Paraná Basin includes all species from the southeastern region of Brazil. This region is of particular interest because it contains the only known representatives of true cave-dwelling aeglids. Several species from epigean habitats as well as all troglobitic species are highly endemic (Türkay, 1972; Hebling and Rodrigues, 1977; Bond-Buckup and Buckup, 1994; Bueno et al., 2007), the latter group being reported from their respective type locality only. Both epigean and hypogean populations of aeglids show limited potential for dispersion. Average fecundity is usually low and the post-embryonic development is epimorphic, that is, the hatching form is a benthic juvenile (Bond-Buckup et al., 1996, 1999; Bueno and Bond-Buckup, 1996; Francisco et al., 2007; Teodósio and Masunari, 2007; Moraes and Bueno, 2013). Newly hatched juveniles remain under maternal care for a few days before venturing in the surroundings on their own (Bahamonde and López, 1961; Rodrigues and Hebling, 1978; Bueno and Bond-Buckup, 1996; Bond-Buckup et al., 1999; Swiech-Ayoub and Masunari, 2001; López-Greco et al., 2004; Francisco et al., 2007). Dispersion is limited because recruits tend to remain in the same area inhabited by the parental cohorts.

CONCLUSIONS

In this paper we have tried to demonstrate that the current distribution of aeglids in the karstic province of the Alto Ribeira can be a consequence of multiple colonization events influenced by the geomorphology of the area as well as by the limited potential for dispersion of these species. The study area, known as the only which harbors troglobitic aeglids, is thus favorable to troglobite occurrence, as a consequence of the fragmented nature of the limestone. This potential is confirmed by the four recently discovered troglobites. Given the extensive area of continuous limestone lenses intercalated with insoluble rocks and the large number of caves yet to be fully explored, one can see the high potential for new species findings that the Alto Ribeira area can provide.

We are aware that this issue is pretty complex and that some hypotheses discussed here still needs to be validated by further field explorations and molecular studies. As new information on the geological formation of the Alto Ribeira becomes available and new troglobitic aeglid species are described and validated, future studies should provide further insights regarding the distributional pattern and speciation mechanisms of aeglids, or other aquatic organism such as cave-dwelling fish.

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