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Global diversity of crabs (Aeglidae: Anomura: Decapoda) in freshwater

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Abstract The freshwater anomuran crabs of the family Aeglidae are all restricted to southern South America occurring in Chile, Brazil, Bolivia, Uruguay, Paraguay, and Argentina. The family consists of a single genus, *Aegla*, containing 63 currently described species. There are another 5–10 known yet undescribed species to complement this diversity. The aeglids occur in freshwater lakes, streams, rivers, and in caves with freshwater. The origin of the family appears to be from marine ancestors from the Pacific invading streams in Chile about 75 mya radiating both in Chile and again on the eastern side of the Andes, particularly in Brazil. Of the 63 species, 23 or 36.5% are considered under threat and are in need of conservation action.

Keywords Conservation · Freshwater biology · Crab · Decapoda · Anomura · Aeglidae · Diversity · South America

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Freshwater Animal Diversity Assessment

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Introduction

The Aeglidae are the most abundant and widely distributed freshwater decapod "crabs" in southern South America. Unlike true brachyuran crabs, however, in aeglids the fifth pair of pereiopods is reduced in size, lacking walking capacity (Lopretto, 1978; Martin & Abele, 1988); they also possess tiny chelae with which they groom branchiae and eggs attached to the pleopods of females and the underside of the abdomen (Martin & Felgenahuer, 1986) (Fig. 1, inset). All aeglids are primarily aquatic and occur in lakes, streams, and caves, at depths of down to 320 m in Chilean lakes (Jara, 1977), and at altitudes of up to ~3,500 m in northeastern Argentinean cordilleras (Bond-Buckup & Buckup, 1994). Aeglids are the only anomuran family restricted to the Neotropical region of South America. Taxonomically, aeglids are included within the anomuran superfamily Galatheoidea, but there is some morphological evidence (e.g., gill structure and caparace sutures) and molecular

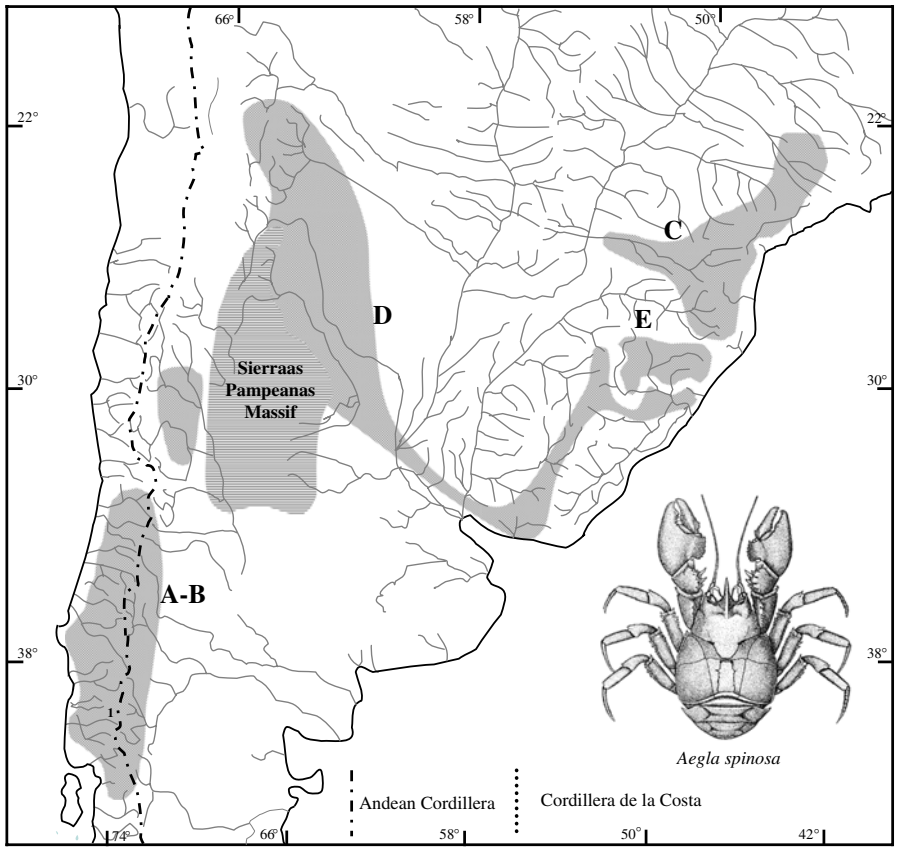

Fig. 1 Map of southern South America indicating the major river systems and distribution of the major clades (cf. Fig. 2) of species diversity in the aeglid crabs. A drawing of *Aegla spinosa* from Bond-Buckup and Buckup (1994) is shown as an inset

data that suggest the Aeglidae should be in their own superfamily (Martin & Abele, 1986; Pérez-Losada etal., 2002b; Tudge & Scheltinga, 2002). From a conservation perspective, several of the known species are very restricted in distribution, and they and their habitats are considered threatened (Pérez-Losada etal., 2002a). From an ecological perspective, aeglids are unique because they are the only anomuran family entirely restricted to freshwater habitats.

The adult size of aeglids does not surpass 60 mm carapace length (CL), and color varies according to the substrate, from greenish brown to almost black; in some lacustrine populations blue, yellow, orange, and red specimens are also sporadically found (Jara, 1989). *Aegla* are dioecious; males lack pleopods, and genital pores open on the coxa of fifth pair of pereiopods at the tip of membranous tubes; female genital pores open on the coxa of third pereopods (Martin & Abele, 1988). Spawning occurs chiefly during the autumn, but some species spawn continuously throughout the year (Bahamonde & López, 1961; Rodrigues & Hebling, 1978; Bueno & Bond-Buckup, 2000). The incubation period lasts between four and eight months, so that an adult female produces no more than one clutch of eggs per annum. Fecundity depends on the size of females, ranging between 120 eggs at 12.5 mm CL to 400 at 22.5 mm CL female in *A. laevis* (Bahamonde & López, 1961); between 115 eggs at 14.99 mm CL to 368 at 19.18 mm CL female in *A. leptodactyla* (Buckup personal observation); and between 699 eggs at 29 mm to 1043 at 33 mm CL female in *A. rostrata* (Jara, 1977). Egg size ranges between 1.00 and 1.37 mm diameter (Jara, 1977). Recruitment normally occurs once a year, in springtime (August to October) (Bahamonde & López, 1961; López 1965; Bueno & Bond-Buckup, 2000), but for *A. longirostri* and *A. castro*, it seems that two recruitment periods exist (Swiech-Ayoub & Masunari, 2001; Delevati etal., 2005). *Aegla* species lack larval stages;

Table 1 Species from the freshwater anomuran crab family Aeglidae including the countries within which they are distributed

Species	Distribution	Habitat
Aegla abtao Schmitt, 1942	Chile	River
Aegla affinis Schmitt, 1942	Chile, Argentina	River
Aegla alacalufi Jara & López, 1981	Chile	Small streams
Aegla araucaniensis Jara, 1980	Chile	River
Aegla bahamondei Jara, 1982	Chile	River
Aegla camargoi Buckup & Rossi, 1977	Brazil	River
Aegla castro Schmitt, 1942	Brazil	River
Aegla cavernicola Turkay, 1972	Brazil	Cave
Aegla cholchol Jara & Palacios, 1999	Chile	River
Aegla concepcionensis Schmitt, 1942	Chile	Small streams
Aegla denticulata denticulate Nicolet, 1849	Chile	River
Aegla denticulata lacustris Jara, 1989	Chile	Lake
Aegla expansa Jara, 1992	Chile	Small stream
Aegla franca Schmitt, 1942	Brazil	River
Aegla franciscana Buckup & Rossi, 1977	Brazil	River
Aegla grisella Bond-Buckup & Buckup, 1994	Brazil	River
Aegla hueicollensis Jara & Palacios, 1999	Chile	River
Aegla humahuaca Schmitt, 1942	Argentina	Headwater & Lake
Aegla inconspicua Bond-Buckup & Buckup, 1994	Brazil	River
Aegla inermis Bond-Buckup & Buckup, 1994	Brazil	River
Aegla intercalata Bond-Buckup & Buckup, 1994	Argentina	River
Aegla itacolomiensis Bond-Buckup & Buckup, 1994	Brazil	River
Aegla jarai Bond-Buckup & Buckup, 1994	Brazil	River
Aegla jujuyana Schmitt, 1942	Brazil	River
Aegla laevis laevis Latreille, 1818	Chile	River
Aegla laevis talcahuano Schmitt, 1942	Chile	River
Aegla lata Bond-Buckup & Buckup, 1994	Brazil	River
Aegla leptochela Bond-Buckup & Buckup, 1994	Brazil	Cave
Aegla leptodactyla Buckup & Rossi, 1977	Brazil	River
Aegla ligulata Bond-Buckup & Buckup, 1994	Brazil	River
Aegla longirostri Bond-Buckup & Buckup, 1994	Brazil	River
Aegla manni Jara, 1980	Chile	Small streams
Aegla marginata Bond-Buckup & Buckup, 1994	Brazil	River
Aegla microphthalma Bond-Buckup & Buckup, 1994	Brazil	Cave
Aegla neuquensis Schmitt, 1942	Chile	River
Aegla odebrechtii Müller, 1876	Brazil	River
Aegla obstipa Bond-Buckup & Buckup, 1994	Brazil	River
Aegla occidentalis Jara etal., 2003	Chile	River & Lake
Aegla papudo Schmitt, 1942	Chile	River
Aegla parana Schmitt, 1942	Brazil	River
Aegla parva Bond-Buckup & Buckup, 1994	Brazil	River
Aegla paulensis Schmitt, 1942	Brazil	River
Aegla perobae Hebling & Rodrigues, 1977	Brazil	Headwater Cave
Aegla pewenchae Jara, 1994	Chile	River
Aegla plana Buckup & Rossi, 1977	Brazil	River

Table 1 continued

Species	Distribution	Habitat
Aegla platensis Schmitt, 1942	Brazil, Argentina, Paraguay, Uruguay	River
Aegla prado Schmitt, 1942	Brazil, Uruguay	Swamp & Lake
Aegla ringueleti Bond-Buckup & Buckup, 1994	Argentina	River
Aegla riolimayana Schmitt, 1942	Chile, Argentina	River
Aegla rossiana Bond-Buckup & Buckup, 1994	Brazil	River
Aegla rostrata Jara, 1977	Chile	Lake
Aegla sanlorenzo Schmitt, 1942	Argentina	River
Aegla scamosa Ringuelet, 1948	Argentina	River
Aegla schmitii Hobbs III, 1979	Brazil	River
Aegla septentrionalis Bond-Buckup & Buckup, 1994	Argentina, Bolivia	Headwater
Aegla serrana Buckup & Rossi, 1977	Brazil	River & Headwater
Aegla singularis Ringuelet, 1948	Argentina, Brazil	River
Aegla spectabilis Jara, 1986	Chile	River
Aegla spinipalma Bond-Buckup & Buckup, 1994	Brazil	River
Aegla spinosa Bond-Buckup & Buckup, 1994	Brazil	River
Aegla strinatii Turkay, 1972	Brazil	River
Aegla uruguayana Schmitt, 1942	Argentina, Uruguay, Brazil	River
Aegla violacea Bond-Buckup & Buckup, 1994	Brazil	River

offspring hatch as juvenile "crabs" of 1.13 - 1.58 mm CL (Bond-Buckup etal., 1999) that remain with the mother for 3–4 days before living independently (López etal., 2004). Population density varies widely, reaching up to 250 individuals/m^2 (Bahamonde & López, 1961) in highly productive conditions.

The ecological role of *Aegla* species has not been assessed but their omnivorous diet includes periphyton, decaying allochtonous vegetable matter, aquatic invertebrates (Bahamonde & López, 1961; Burns, 1972; Lara & Moreno, 1995, Castro-Souza & Bond-Buckup, 2004), and fine particulate organic matter (Isler, 1988). Additionally, they constitute a relevant dietary item for the non-native rainbow trout (*Oncorhynchus mykiss*) in Chile and South Brazil and brown trout (*Salmo trutta fario*) in Chile (Burns, 1972; Arenas, 1978; Buckup, personal observation), and for the Chilean and Brazilian species of river otter (*Lontra provocax*) (Medina, 1998).

Species diversity

The present Aeglidae belong to a single genus, *Aegla* Leach, 1820, consisting of 63 described species (Bond-Buckup & Buckup, 1994; Bond-Buckup, 2003) (Table 1); including, newly described species based on recent molecular phylogenetic analyses (Jara etal., 2003). By our count, there are at least six additional species waiting to be described. Of these species, 57 are found mainly in rivers, only two in lakes, and four in cave habitats.

Phylogeny and historical processes

Ortmann (1902) proposed that aeglid species from Chile represented the more primitive forms of the genus. However, Schmitt (1942) hypothesized that *Aegla* from the Atlantic side of South America were more primitive, and species ranging in the Chilean streams were more derived. Recent estimates of phylogenetic relationships based on a variety of molecular data support the Pacific origin hypothesis (Pérez-Losada etal., 2004) (Fig. 2) and suggest that the group, as a whole originated around 75 mya. The western *Aegla* species radiated, approximately, 40–45 mya (clades A and B—Fig. 2), but the speciation of the central and eastern taxa took place later, around 23–35 mya (clades C-E in Fig. 2) (see Pérez-Losada etal., 2004 for more detailed discussions on the phylogenetic relationships among all the aeglid species).

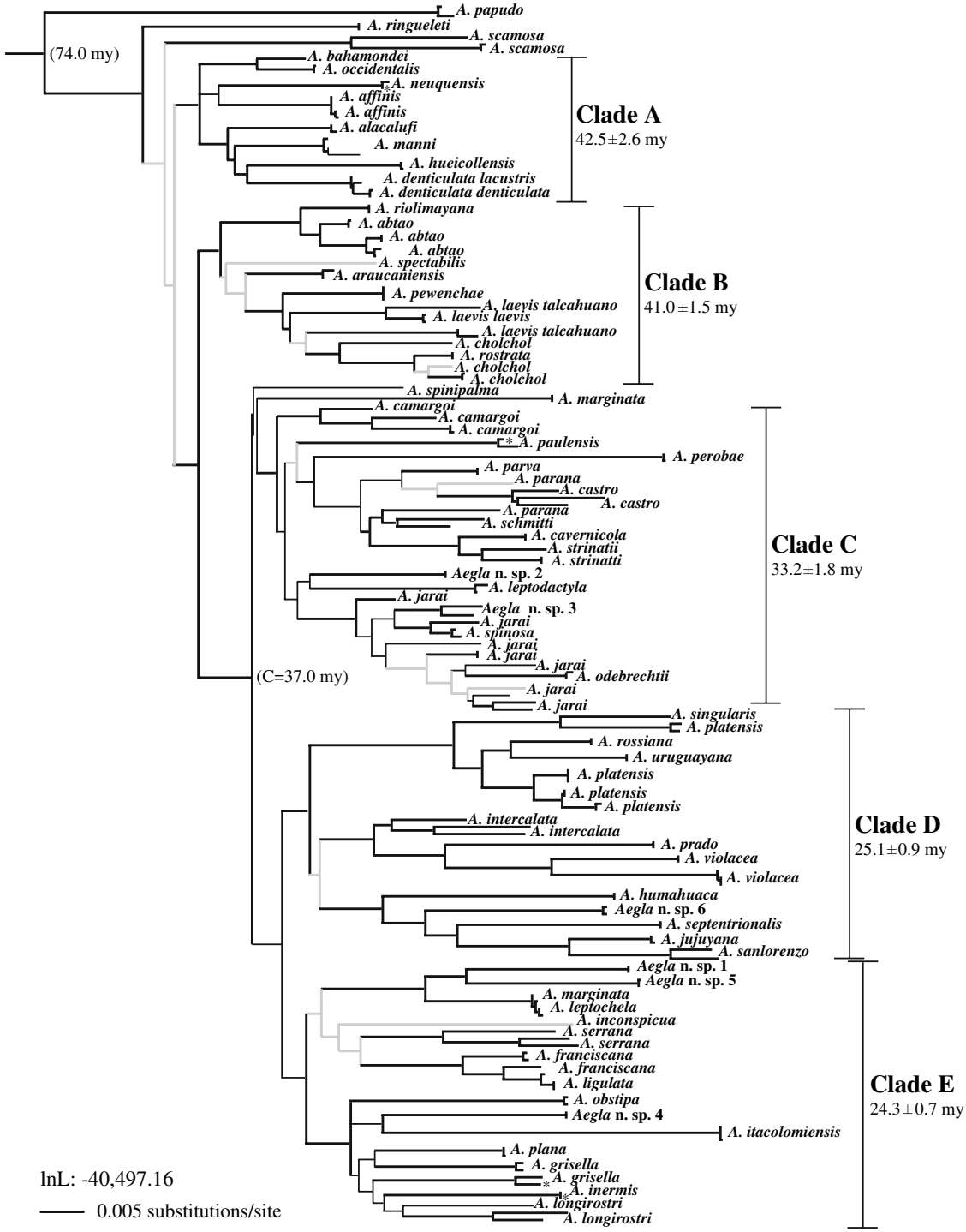

Fig. 2 Bayesian and maximum likelihood estimate of phylogenetic relationships among the aeglid species using the GTR+Γ+I model of evolution. Clade support is graphically indicated as follows: ━ bp ≥ 70% and pP ≥ 0.95, ▬ 50% ≤ bp < 70% and/or 0.75 ≤ pP < 0.95, and — bp < 50% and/or pP < 0.75. Branch lengths are shown proportional to the amount of change along the branches in the maximum likelihood tree with estimated divergence dates shown for the root and major clades (see Pérez-Losada etal., 2004, for details)

Present distribution and areas of endemicity

The aeglids are distributed in southern South America (Fig. 1) including Chile, Brazil, Argentina, Uruguay, Bolivia, and Paraguay. Thus, all 63 species are contained within the Neotropical region. There are 16 species endemic to Chile, seven species endemic to Argentina and 36 species endemic to southern Brazil (Bond-Buckup etal. 2003). They occur in all the main rivers of southern South America, except the most southern Patagonian drainages.

Human related issues

Most *Aegla* species have very narrow distributional areas and are therefore of significant conservation concern. Of the 63 species currently recognized in the genus, using the IUCN Red List criteria (IUCN, 2001), we recognize 23 species or 36.5 % as under threat or endangered, mainly due to their narrow distributions and the rapid degradation of the freshwater habitats they occupy.

In Chile, aeglids are recognized as an important food item for exotic salmonid species (*Salmo trutta fario* and *Oncorhynchus mykiss*) which support a fast-growing fly-fishing sport industry, especially in the Llanquihue Lake region and South Brazilian Highlands. On the negative side, the fast-growing fruit and wine producing industries in Central Chile constitute a threat for conservation of aeglids, and benthic river fauna in general, due to the widespread use of biocides, which likely accumulate and have an impact in rivers and streams. Threats for conservation of aeglids also derive from silvicultural practices related to the establishment of extensive plantations of pine and *Eucalyptus*, mainly along the Coastal Cordillera and south Brazil. Additionally, it must be pointed out that the exaggerated use of pesticides in the widespread apple tree and potatoes cultivation and mainly, the hog raising activities along the majority of the South Brazilian Rivers, are an important menace to the native populations of aeglids, particularly in the states of Santa Catarina and Rio Grande do Sul, in Brazil.

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