

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

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 pereopods 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

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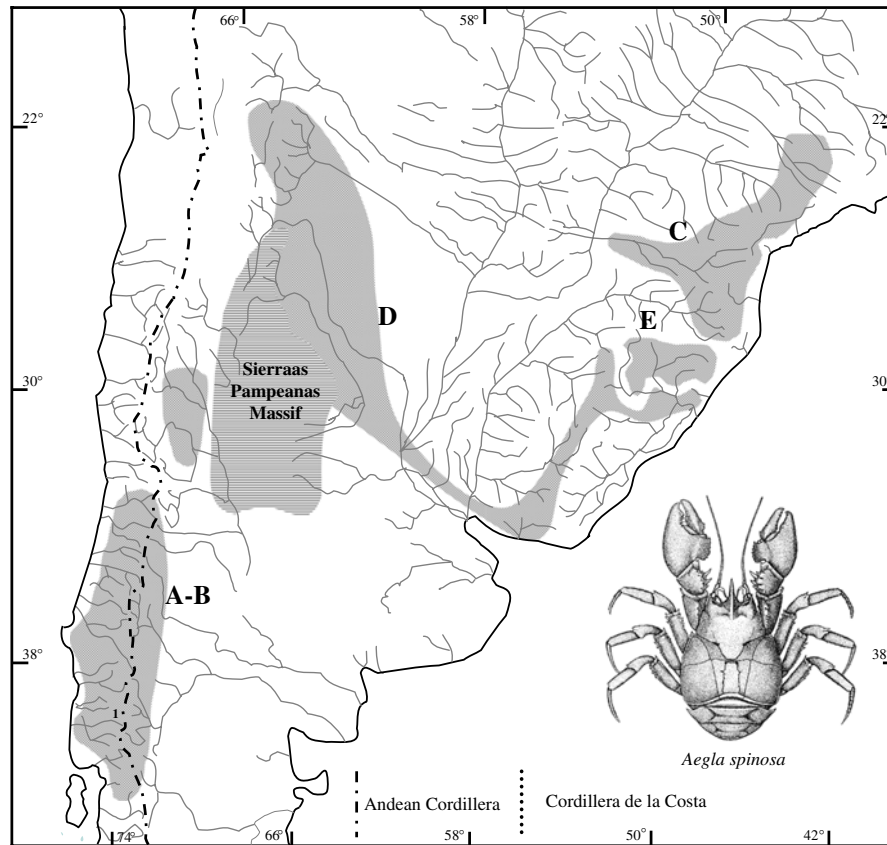


Fig. 1 Map of southern South America indicating the major river systems and distribution of the major clades (cf. Fig. 2) of species diversity in the aeglid crabs. A drawing of *Aegla spinosa* from Bond-Buckup and Buckup (1994) is shown as an inset

data that suggest the Aegliidae should be in their own superfamily (Martin & Abele, 1986; Pérez-Losada et al., 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 et al., 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 pereopods 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 et al., 2005). *Aegla* species lack larval stages;

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

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

Table 1 continued

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

offspring hatch as juvenile “crabs” of 1.13 - 1.58 mm CL (Bond-Buckup et al., 1999) that remain with the mother for 3–4 days before living independently (López et al., 2004). Population density varies widely, reaching up to 250 individuals/m² (Bahamonde & López, 1961) in highly productive conditions.

The ecological role of *Aegla* species has not been assessed but their omnivorous diet includes periphyton, decaying allochthonous 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 Aegliidae 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 et al., 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 et al., 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 et al., 2004 for more detailed discussions on the phylogenetic relationships among all the aeglid species).

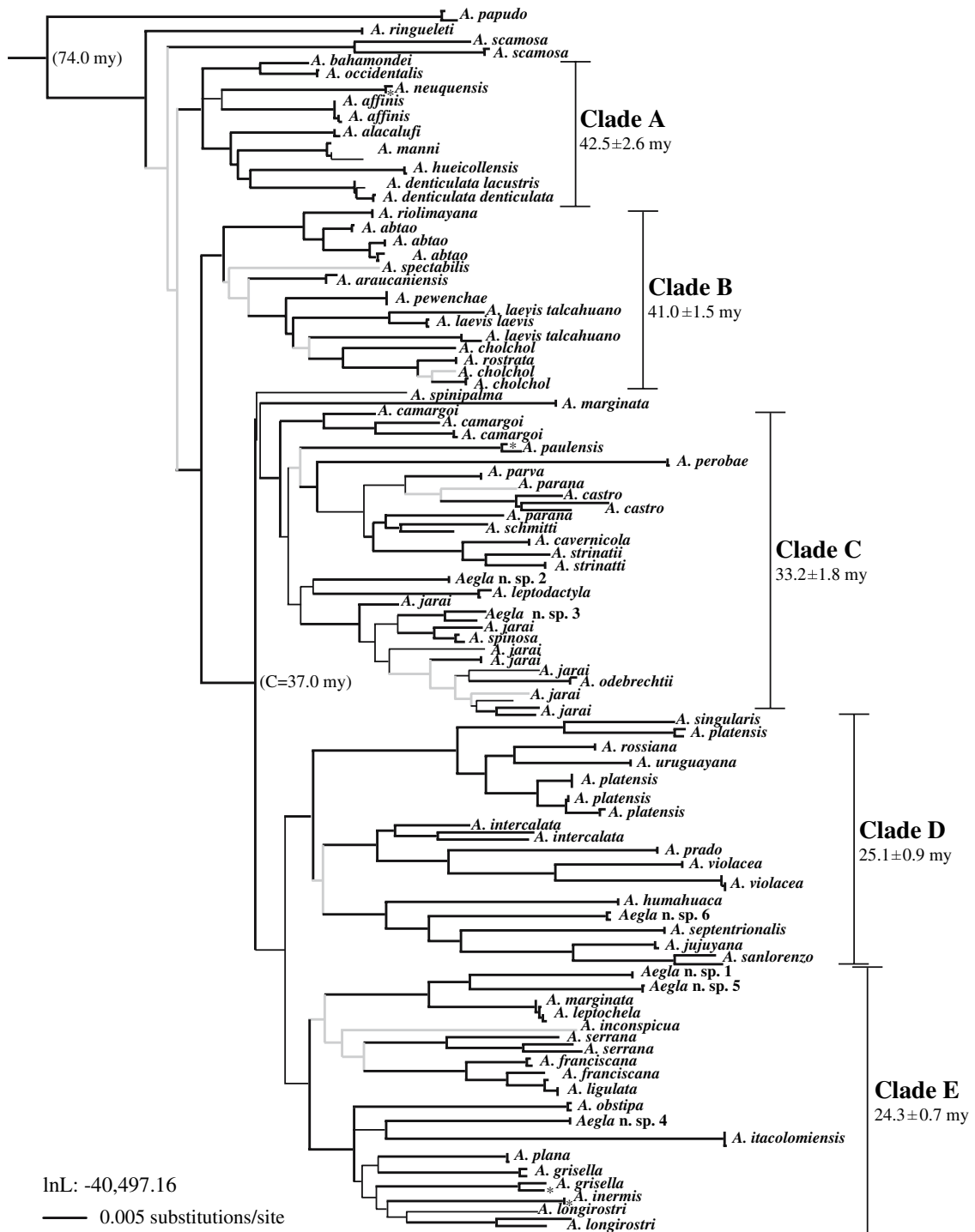


Fig. 2 Bayesian and maximum likelihood estimate of phylogenetic relationships among the aeglid species using the GTR+ Γ +I model of evolution. Clade support is graphically indicated as follows: \blacksquare bp \geq 70% and $pP \geq 0.95$, \blacksquare 50% \leq bp < 70% and/or 0.75 \leq pP < 0.95,

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 et al., 2004, for details)

Present distribution and areas of endemism

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 et al. 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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