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Freshwater Invertebrates of Southwestern South America: Diversity, Biogeography, and Threats

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Abstract

This chapter reviews the current state of knowledge of invertebrates of rivers, lakes, and wetlands in western South America, from southern Peru to the Strait of Magellan in southern Chile. A characterization of the diverse groups of insects, mollusk crustaceans, and other smaller groups is presented, and a biogeographic analysis of them is made with emphasis on their main forcing factors, ecology, and threats in the Anthropocene. This fauna presents Gondwanic characteristics, with clear North–South latitudinal patterns, covering from the Desert of Atacama in the North, one of the most arid deserts of the world, to the rainy and cold regions of the southern end of South America. The central zone of this territory includes one of the global biodiversity “hot spots,” which currently presents serious threats associated with changes in habitat, introduction of invasive species, climate change, and overexploitation of aquatic resources.

Keywords: freshwater, invertebrates, South America, biodiversity, conservation

1. Introduction

Invertebrates represent the majority of the world’s animal species, comprising a total of 32 phyla, of which 15 are present in freshwater [1]. These organisms all lack a vertebral column, are generally small in size, and present very diverse morphologies. Some have soft bodies such as worms and planarians, while others have hard bodies such as crustaceans, insects, and mollusks. Freshwater invertebrates offer the opportunity to contemplate the enormous diversity of forms and functions existing in the animal kingdom. It’s precisely in this group of organisms where animal life is expressed without limits to particular forms or colors and is specialized to diverse forms of life. In the freshwater ecosystems of southwestern South America, there is a diverse fauna of invertebrates [2]. In this part of the world, around 1000 species of freshwater invertebrates are known. However, many scientists believe that the number of unknown species in this area could significantly increase that number. Knowledge of the diversity of these organisms is still fragmentary, despite the efforts of many researchers, especially over the last two centuries [3]. Some groups of insects, mollusks,

and crustaceans are relatively well studied, but in most other groups, much remains to be done.

Knowledge of freshwater invertebrates in this area of South America has historically lagged far behind that available for vertebrates (e.g., fish; see [4–5]). This is explained by the fact that vertebrates are easier to study than invertebrates, as they are low in diversity, large in size, and easy to identify. In addition, there are taxonomic guides for most of them. In contrast, invertebrates tend to be very diverse and small in size, and for most of them, a stereomicroscope is required for correct identification. In addition to these disadvantages, there is a lack of identification guides for most taxonomic groups.

Invertebrates play a fundamental role in the function of inland aquatic ecosystems, as they allow the transfer of energy from producers (aquatic and terrestrial vegetation) to the upper trophic levels (fish and waterfowl) [1]. In this group of animals, there are herbivorous, omnivorous, carnivorous, and detritivorous species. These feed mainly on bacteria, fungi, microalgae, vascular plants, protozoa, invertebrates, and detritus. The latter may be of autochthonous origin (remains of dead aquatic organisms) or of allochthonous origin (from the terrestrial system, such as riparian tree leaves).

Depending on their way of life, two types of invertebrates can be identified in freshwater ecosystems: planktonic (those that live suspended in the body of water) and benthic (those that live associated with the substrates at the bottom). Zooplankton is composed mainly of Protozoa, Rotifera, Cladocera, and Copepoda, and sometimes we find other elements such as the crustaceans Ostracoda and Cnidaria [1]. Benthic invertebrates are generally more diverse than zooplankton and are composed of a large number of groups of Protozoa, Porifera, Cnidaria, Platyhelminthes, Nemertea, Aschelminthes, Annelida, Mollusca (Bivalvia and Gastropoda), Arthropoda (Chelicerata, Crustacea, and Insecta), Tardigrada, and Bryozoa, among other groups of free life.

This chapter presents a characterization of the diverse groups of insects, mollusks, crustaceans, and other smaller groups from Southwestern South America and a biogeographic analysis of them, with emphasis on their main forcing factors, ecology, and anthropogenic threats.

2. The hydrographic system

In the Southwest of South America (18–55°S), five freshwater ecoregions are recognized: Atacama, Altiplano, Mediterranean, Valdivian Lakes, and Patagonia, which are defined as large areas with homogeneous hydrological and climatic conditions [6–8]. The ecoregions of the Altiplano and Patagonia are shared with Bolivia and Argentina, while the other three ecoregions are only located in Chile. The ecoregions of Atacama (18–22°S) and Altiplano (18–23°S) are characterized by having an arid climate, being four subclimates: coastal desert climate at the coast; interior desert climate at the intermediate zone; the marginal desert climate, which is located between 2000 and 3500 masl; and the steppe climate, characterized by low temperatures and wide thermal amplitude between day and night, which is located at 3500 masl. In the Mediterranean ecoregion (23–33°S), there is a typical Mediterranean climate, with long dry periods of drought and very humid winters that are concentrated in a few months. The ecoregion of the Valdivian Lakes (35–39°S) is characterized by the presence of numerous lakes, mostly oligotrophic, with a typical rainy climate temperature. Finally, the Patagonian ecoregion (42–55°S) is characterized by a dry cold temperate climate, decreasing in temperature as the latitude increases.

3. Freshwater invertebrates

The freshwater invertebrates of the Southwest of South America have numerous singularities that highlight them compared to those existing in other regions of the world [1]. Among them are the following:

- a. Very primitive fauna with ancestral Gondwanic-type relations in many of the taxonomic groups. As an example, the freshwater snails of the *Chilina* genus, which have presented their maximum evolutionary radiation in the Chilean territory and southern Argentina, correspond to one of the most primitive pulmonate gastropod groups known (Archaeopulmonata). They present evolutionary affinities with marine gastropods of the Cephalaspidea order (Opisthobranchia).

Additionally, many of the invertebrate groups have a typical Gondwanic geographic distribution. The fragmentation of the Gondwana supercontinent almost 100 million years ago (150–50 ma BP) caused geographic isolation of the ancestral biota. Each of the pieces of this giant mosaic continued to evolve in isolation but retained the signs of ancient connections. This is why, for many invertebrate groups, there is more affinity with the fauna of New Zealand than with that of the rest of South America (e.g., Brazil, northern Peru), a relationship that was already recognized by von Ihering in the late nineteenth century [9].

- b. High diversity in a small geographical area and marked endemism: As in the case of terrestrial flora and terrestrial and freshwater vertebrates, in central-southern Chile there is a biodiversity “hot spot” (35° and 43° S), of freshwater invertebrates (these are territories that host a large number of endemic species and, at the same time, have been significantly impacted by human activities). This “hot spot” has been recognized as one of the 25 most important world-wide [10] and is clearly isolated from the rest of South America by a series of geographical barriers (e.g., arid diagonal, Andean mountain range, cold and dry southern zones). This biodiversity “hot spot” of freshwater invertebrates is part of the great Archiplata region [11, 12]. However, it could also be recognized as a sub-unit, called “Chilenia” [1], following the nomenclature used by some geologists to refer to a large part of this territory [13, 14].

Within this “hot spot,” a study of the spatial pattern of species richness and indices of genetic and phylogenetic diversity of aeglids was performed [15]. Based on these indicators, they ordered the six hydrographic regions present along this territory according to their conservation priority. They concluded that the hydrographic region composed of the Tucapel (near Cañete), Imperial, and Toltén rivers is a priority for the conservation of aeglids, which can also be extended to many other invertebrate groups.

- c. With cases of extremely small geographic ranges: There are examples of species with very small geographic ranges, for example, the “Desert Snail” (*Chilina angusta*), discovered by Rodolfo Amando Philippi on his exploratory trip to the Atacama Desert (1853 and 1854), which inhabits only the Aguada de Paposo. This is a spring with a surface of ca. 30 m², located in the coastal desert north of Taltal [1].

Another example is the “Cangrejo tigre” (*Aegla conceptionensis*) that lives in the small basin of the Andalién river [1]. This crab had been considered extinct up until less than a decade ago when it was rediscovered. In the case of aeglids, there

are numerous other examples of very small geographic ranges where species are restricted to a limited portion within a given small basin [15–17]. An example of this is the case of the “Cangrejo Camaleón” (*Aegla hueicollensis*), which is found mainly in remote sectors of the Hueicolla and Pichihueicolla rivers, located in the Valdivian forest.

The best studied taxonomic groups in Southwestern South America are those of greatest relevance to the characterization of the structure and functioning of freshwater ecosystems, such as Insecta, Crustacea, Rotifera, Bivalvia, and Gastropoda [1]. Rotifera and Crustacea are well represented in lake zooplankton. Additionally, Crustacea, Insecta, Bivalvia, and Gastropoda constitute an important fraction of the zoobenthos, both lacustrine and fluvial (Table 1). Here the discussion will be limited to the large taxonomic groups present in this territory, emphasizing those most known or important in freshwater ecosystems. Most of the information has been obtained from literature regarding the Chilean territory [1–3, 15, 17–44] and southern Peru territory [3, 11, 45–48].

| Phylum (subphylum) Class (order) | Family | Genera (and number of species) |
|-------------------------------------|-----------------|---|
| Mollusca | | |
| Bivalvia (Paleoheterodonta) | Hyriidae | <i>Diplodon</i> 2 |
| | Sphaeriidae | <i>Pisidium</i> 7, <i>Sphaerium</i> 2, <i>Musculium</i> 2 |
| Gastropoda (Mesogastropoda) | Cochliopidae | <i>Potamolithus</i> 1, <i>Helobia</i> 21 |
| Gastropoda (Basommatophora) | Physidae | <i>Physa</i> 4 |
| | Planorbidae | <i>Biomphalaria</i> 7 |
| | Ancylidae | <i>Anisancylus</i> 1, <i>Uncancylus</i> 3 |
| | Chiliniidae | <i>Chilina</i> 30 |
| | Lymnaeidae | <i>Lymnaea</i> 5 |
| Arthropoda (Crustacea) | | |
| Branchiopoda (Cladocera) | Bosminidae | <i>Bosmina</i> 2, <i>Eubosmina</i> 1 |
| | Chydoridae | <i>Camptocercus</i> 3, <i>Alona</i> 6, <i>Leydigia</i> 1, <i>Alonella</i> 2, <i>Pleuroxus</i> 5, <i>Chydorus</i> 4, <i>Ephemeropus</i> 1, <i>Dunhevidia</i> 1, <i>Biapertura</i> 2 |
| | Daphnidae | <i>Daphnia</i> 7, <i>Scapholeberis</i> 2, <i>Simocephalus</i> 4, <i>Ceriodaphnia</i> 2 |
| | Macrothricidae | <i>Macrothrix</i> 4, <i>Echimisca</i> 1, <i>Cactus</i> 1, <i>Streblocerus</i> 1 |
| | Moinidae | <i>Moina</i> 1 |
| | Sididae | <i>Diaphanosoma</i> 1, <i>Latonopsis</i> 1 |
| Copepoda (Calanoidea) | Boeckellidae | <i>Boeckella</i> 17 |
| | Centropagidae | <i>Parabroteas</i> 1 |
| | Diaptomidae | <i>Tumeodiaptomus</i> 2 |
| Copepoda (Cyclopoidea) | Cyclopidae | <i>Acanthocyclops</i> 3, <i>Diacyclops</i> 2, <i>Metacyclops</i> 1, <i>Mesocyclops</i> 2, <i>Microcyclops</i> 2, <i>Tropocyclops</i> 1, <i>Eucyclops</i> 7, <i>Macrocyclops</i> 1, <i>Paracyclops</i> 3 |
| Copepoda (Harpacticoida) | Canthocamptidae | <i>Attheyella</i> 33, <i>Lofflerella</i> 5, <i>Antarctobius</i> 8, <i>Moravia</i> 2 |
| | Harpacticidae | <i>Tigriopus</i> 1 |
| Malacostraca (Decapoda) | Aegliidae | <i>Aegla</i> 20 |
| | Palaemonidae | <i>Cryphiops</i> 1 |
| | Parastacidae | <i>Parastacus</i> 2, <i>Samastacus</i> 1, <i>Virilastacus</i> 1 |
| Malacostraca (Amphipoda) | Hyalellidae | <i>Hyalella</i> 7 |

| Phylum (subphylum) Class (order) | Family | Genera (and number of species) |
|-------------------------------------|-------------------|---|
| Malacostraca (Isopoda) | Janiridae | <i>Heterias</i> 1 |
| Arthropoda (Insecta) | | |
| Insecta (Ephemeroptera) | Ameletopsidae | <i>Chiloporter</i> 2, <i>Chaquihua</i> 2 |
| | Baetidae | <i>Americabaetis</i> 2, <i>Andesiops</i> 1, <i>Callibaetis</i> 3, <i>Deceptiviosa</i> 3, <i>Camelobaetidius</i> 1 |
| | Caenidae | <i>Caenis</i> 3 |
| | Leptophlebiidae | <i>Archethraulodes</i> 1, <i>Atalophlebia</i> 7, <i>Atalophlebioides</i> 1, <i>Dactylophlebia</i> 1, <i>Demoulinellus</i> 1, <i>Gonserellus</i> 1, <i>Hapsiphlebia</i> 1, <i>Magallanella</i> 1, <i>Massartellopsis</i> 1, <i>Meridialaris</i> 7, <i>Nousia</i> 6, <i>Penaphlebia</i> 5, <i>Rhigotopus</i> 1, <i>Secochela</i> 1, <i>Thraulodes</i> 1 |
| | Nesameletidae | <i>Metamonius</i> 2 |
| | Oligoneuriidae | <i>Murphyella</i> 1 |
| | Oniscigastridae | <i>Siphonella</i> 2 |
| Insecta (Plecoptera) | Austroperlidae | <i>Andesobius</i> 1, <i>Klapopteryx</i> 2, <i>Penturoperla</i> 1 |
| | Diamphipnoidae | <i>Diamphipnoa</i> 3, <i>Diamphipnopsis</i> 2 |
| | Eustheniidae | <i>Neuroperlopsis</i> 1, <i>Neuroperla</i> 1 |
| | Gripopterygidae | <i>Andiperla</i> 1, <i>Andiperlodes</i> 1, <i>Antarctoperla</i> 2, <i>Araucanioperla</i> 2, <i>Aubertoperla</i> 2, <i>Ceratoperla</i> 2, <i>Chilenoperla</i> 3, <i>Claudioperla</i> 1, <i>Limnoperla</i> 1, <i>Megandiperla</i> 1, <i>Notoperla</i> 2, <i>Notoperlopsis</i> 1, <i>Pelurgoperla</i> 1, <i>Plegoperla</i> 2, <i>Potamoperla</i> 1, <i>Rhitroperla</i> 2, <i>Senzilloides</i> 1, <i>Teutoperla</i> 3 |
| | Notonemouridae | <i>Austronemoura</i> 9, <i>Neofulla</i> 3, <i>Neonemoura</i> 2, <i>Udamocercia</i> 3 |
| | Perlidae | <i>Inconeuria</i> 1, <i>Kempnyella</i> 2, <i>Nigroperla</i> 1, <i>Pictetoperla</i> 2 |
| Insecta (Trichoptera) | Anomalopsychidae | <i>Anomalopsyche</i> 1, <i>Contulma</i> 1 |
| | Calamoceratidae | <i>Phylloicus</i> 1 |
| | Ecnomidae | <i>Austrotinodes</i> 12, <i>Chilocentropus</i> 1 |
| | Glossosomatidae | <i>Mastigoptila</i> 7, <i>Scotiotrichia</i> 1, <i>Tolhuaca</i> 1 |
| | Hydrobiosidae | <i>Amphichorema</i> 3, <i>Androchorema</i> 1, <i>Apatanodes</i> 2, <i>Australobiosis</i> 2, <i>Cailloma</i> 3, <i>Clavichorema</i> 7, <i>Heterochorema</i> 1, <i>Iguazu</i> 1, <i>Ischorema</i> 2, <i>Metachorema</i> 2, <i>Microchorema</i> 4, <i>Neatopsyche</i> 5, <i>Neochorema</i> 4, <i>Neopsilochorema</i> 1, <i>Nolganema</i> 1, <i>Parachorema</i> 1, <i>Pomphochorema</i> 1, <i>Pseudoradema</i> 1, <i>Rheochorema</i> 4, <i>Stenochorema</i> 1 |
| | Helicophidae | <i>Allocentrelodes</i> 2, <i>Austrocentrus</i> 3, <i>Eosericastoma</i> 2, <i>Microthremma</i> 7, <i>Pseudosericastoma</i> 1 |
| | Helicopsychidae | <i>Helicopsyche</i> 2 |
| | Hydropsychidae | <i>Smicridea</i> 15 |
| | Hydroptilidae | <i>Hydroptila</i> 1, <i>Oxyethira</i> 4, <i>Celaenotrichia</i> 1, <i>Neotrichia</i> 1, <i>Metrichia</i> 5, <i>Nothotrichia</i> 2 |
| | Kokiriidae | <i>Pangullia</i> 1 |
| | Philopotamidae | <i>Dolophilodes</i> 20 |
| | Stenopsychidae | <i>Pseudostenopsichidae</i> 3 |
| | Leptoceridae | <i>Hudsonema</i> 1, <i>Triplectides</i> 3, <i>Nectopsyche</i> 2, <i>Brachysetodes</i> 10 |
| | Limnephilidae | <i>Austrocosmoecus</i> 1, <i>Metacosmoecus</i> 1, <i>Monocosmoecus</i> 5, <i>Platycosmoecus</i> 1, <i>Verger</i> 19 |
| | Polycentropodidae | <i>Polycentropus</i> 7 |
| | Phylorheithridae | <i>Mystacopsyche</i> 2, <i>Psylopsiche</i> 3 |
| | Sericostomatidae | <i>Chiloecia</i> 1, <i>Myotrichia</i> 1, <i>Notidobiella</i> 3, <i>Parasericostoma</i> 10 |
| | Tasimiidae | <i>Charadropsyche</i> 1, <i>Trichovespula</i> 1 |

| Phylum (subphylum) Class (order) | Family | Genera (<i>and number of species</i>) |
|-------------------------------------|---------------|---|
| Insecta (Coleoptera) | Dytiscidae | <i>Rhantus</i> 4, <i>Lancetes</i> 14, <i>Leuronectes</i> 2, <i>Anisomeria</i> 1, <i>Megadytes</i> 2, <i>Laccophilus</i> 2, <i>Liodes</i> 4, <i>Laccornellus</i> 1, <i>Platynectes</i> 1, <i>Desmopachria</i> 1, <i>Agabus</i> 1 |
| | Elmidae | <i>Mycrocylloepus</i> 1, <i>Macrelmis</i> 1, <i>Austrolimnius</i> 2, <i>Austrelmis</i> 8, <i>Stenelmis</i> 1, <i>Neelmis</i> 1, <i>Hydora</i> 2 |
| | Gyrinidae | <i>Andogyrus</i> 2, <i>Gyrinus</i> 2 |
| | Haliplidae | <i>Haliplus</i> 3 |
| | Hydraenidae | <i>Ochtheosus</i> 2, <i>Gymnochthebius</i> 7, <i>Hydraenida</i> 5 |
| | Hydrophilidae | <i>Andotypus</i> 1, <i>Dactylosternum</i> 1, <i>Cylorygmus</i> 2, <i>Stethoxus</i> 2, <i>Cercyon</i> 2, <i>Dibolocelus</i> 2, <i>Enochrus</i> 5, <i>Chaetarthria</i> 1, <i>Tropisternus</i> 1, <i>Hydrochus</i> 1, <i>Berosus</i> 3, <i>Hemiosus</i> 2, <i>Anticuar</i> 1, <i>Paracymus</i> 3 |
| | Psephenidae | <i>Tychepephus</i> 1, <i>Ectopria</i> 1, <i>Eubrianax</i> 1 |

Table 1.

Synoptic vision of the most well-known families and genera of freshwater macroinvertebrates of southwestern South America (based on [1–3, 11, 15, 17–48]).

3.1 Arthropods

The most frequent groups in freshwater ecosystems are crustaceans, insects, and chelicerates. Within crustaceans is a wide diversity of organisms, ranging from complex to very simple forms such as Copepoda, Branchiopoda, and Ostracoda. Copepoda is a very important component of lake zooplankton, while the others are benthic, and frequently associated with the bottom surface [1]. Amphipods are also common components in the benthos and in some isopod areas. Regarding higher crustaceans, there are three families in Chile: Palaemonidae, Parastacidae, and Aeglidae. The two last ones host very particular commensals, such as temnocephalous and histriobdelids (see below). Insects are notably more represented in freshwater environments than crustaceans. Thus, there are several orders whose larval or nymphal stages develop in water [1]: Ephemeroptera, Plecoptera, Trichoptera, and Odonata. Adults, on the other hand, live outside of water. Almost all the other orders of insects present families adapted for aquatic life, especially in the larval state. These are Diptera (Chironomidae, Culicidae, Tipulidae, Simuliidae, Athericidae, Blephariceridae), Coleoptera (Dytiscidae, Hydrophilidae, Psephenidae), and Hemiptera (Notonectidae, Belostomatidae). Within the aquatic insects, there are different forms of feeding. Some are microphages, equipped with sophisticated filtration systems (e.g., Diptera, Trichoptera), while others are efficient carnivores, located at the terminal levels of certain food chains (e.g., Megaloptera, Odonata). Some may even prey on freshwater vertebrates (e.g., Hemiptera Belostomatidae). The number of larvae or nymphs in freshwater under natural conditions is normally high, contributing significantly to the feeding of vertebrates and invertebrates.

Freshwater Chelicerata are not as diverse as the previous two groups. There are very few aquatic spiders, and only mites (Hydracarina) are a common component in this habitat. There are some lake ecosystems, such as the Quiñenco lagoon in the Biobío Region, whose use as a source of drinking water has been limited by

the presence of high densities of Oribatida mites (*Scapheremaeus*, Galumnidae, Nothridae, Galumnoidea, Malaconothridae, Oribotuloidea) and Prostigmata (*Hygropatella*, Arrenouridae, Oxidae) [24].

Copepod, and cladoceran Crustaceans: As mentioned above, these are small fundamental organisms in lake zooplankton. The copepods are characterized by having their body divided into two regions, with the anterior region (cephalothorax) typically being elongated, with a nauplian eye and appendages. Three main groups are recognized: Calanoidea (mainly planktonic), Harpacticoidea (generally microbenthic littorals), and Cyclopoidea (littoral and only a few are typically limnetic). In contrast, cladocerans are typically planktonic organisms characterized by a thin bivalve shell (which does not cover the head) and with a reduced abdomen.

Knowledge of zooplankton in Chilean lake ecosystems has progressed significantly over recent decades [21, 42]. Southwestern South America is characterized by marked latitudinal and altitudinal gradients. In these gradients it is possible to find different types of lentic ecosystems, whose environmental diversity is clearly reflected by the composition of species of zooplanktonic crustaceans, and five zones can be recognized [42]:

- a. Northern Chile corresponds to lakes and lagoons located in the Chilean-Peruvian Altiplano, where it is possible to register endemic species of the genus *Daphnia* and *Boeckella*, among others.
- b. Central Chile brings together a series of aquatic bodies of low height and shallow depth. This area is characterized by the presence of *Diaptomus diabolicus* (synonym for *Tumeodiaptomus vivianae*). At this latitude there are also high mountain lakes of greater depth. These are characterized by the presence of species of the *Boeckella* genus, of which there are few records and taxonomic studies.
- c. Central-South Chile includes the so-called Nahuelbutan Lakes, whose zooplanktonic fauna is just beginning to be studied.
- d. Southern Chile and Chilean Patagonia include the lakes of the Magellanic region, which have a high diversity of species, especially those of the Torres del Paine area, characterized by its high endemism.

The Chilean freshwater zooplankton is composed mainly of 53 species of Cladocera and 73 species of Copepoda [42] (**Table 1**). Cladocera includes six families, of which Daphnidae and Chydoridae are the most diverse with 15 and 25 species, respectively. The Copepoda are made up of 20 species of Calanoidea, 22 of Cyclopoidea, and 49 of Harpacticoidea. The most diverse families are Cyclopidae and Canthocamptidae with 22 and 48 species, respectively. Within these taxonomic groups, the least studied are the Harpacticoidea and the Cladocera of coastal environments (e.g., Chydoridae), which require taxonomic revision.

Among the Calanoidea copepods, the genus *Boeckella* is commonly found throughout the Southern Hemisphere, in fresh and saline continental waters [42]. *Boeckella gracilipes* is one of the species with the widest geographic distribution in South America, with its presence being reported from Ecuador (Lake Mojanda) to Tierra del Fuego, although it presents morphologically differentiated populations,

probably associated with temperature [42]. Among the copepods, Calanoidea also includes the endemic species of the extreme south of South America *Parabroteas sarsi*. This is a predatory copepod, which is widely distributed in the Chilean-Argentine Patagonia, which stands out for its large size, reaching up to 8 mm, a size that places it as the largest copepod in the world. Calanoid copepods in Chilean continental waters are characterized for being the main group in zooplanktonic assemblages, being represented by the genera *Boeckella*, *Parabroteas*, and *Tumeodiaptomus* [21]. The genus *Boeckella* is represented by three species of wide geographic distribution: *B. gracilipes*, which is found between 18 and 44°S; *B. poopoensis*, found mainly in saline lakes of northern Chile (14–27°S); and *B. michaelsoni* which is found between 44 and 54°S. *Tumeodiaptomus*, represented by *T. diabolicus*, is distributed between 32 and 42°S. Finally, *Parabroteas*, with only one species, *P. sarsi*, is found in shallow lakes between 44 and 54°S. There are different species for the northern zone (*Boeckella occidentalis*, *B. gracilipes*, and *B. poopoensis*) central (*Tumeodiaptomus diabolicus*, *B. bergi*, *B. gracilipes*), and southern Chile (*T. diabolicus*, *B. michaelsoni*, and *B. gracilipes*).

In regard to Cladocera, six species of *Daphnia* (*D. pulex*, *D. ambigua*, *D. obtusa*, *D. peruviana*, *D. commutate*, and *D. sarsi*) have been recorded, of which *D. obtusa* and *D. pulex* have a cosmopolitan distribution [42]. In Chile they are located from north to south and from coast to mountain range, representing excellent indicators of water quality and with great potential to be used in toxicity tests performed in the laboratory.

Malacostraca crustaceans: In the Chilean freshwater ecosystems, they are composed of the orders Decapoda, Isopoda, and Amphipoda. They are of particular relevance in freshwater ecosystems, because they are fundamental components in the diet of large fish and water birds and also because of the great commercial importance of the different species of the families Palaemonidae and Parastacidae. Another important aspect of this group is that it is the only one in which there is evidence of species extinction.

The knowledge of Malacostraca crustaceans in Chilean freshwater ecosystems has progressed remarkably in recent decades [16, 17]. The freshwater decapods are the largest group of Malacostraca, made up of shrimp of the families Palaemonidae (one species) and Parastacidae (four species; **Figure 1(26)**), plus Anomura crabs of the family Aeglididae (19 species and 2 subspecies; **Figure 1(27)**). Peracarids are represented by seven species of Amphipoda of the *Hyaella* genus, while only one species of Isopoda has been identified (*Heterias (Fritzianira) exul*). Thus, the limnetic Malacostraca fauna in Chile is composed of 35 taxa, i.e., 33 species and 2 subspecies (**Table 1**) [17].

The geographical range occupied by the Malacostraca includes practically the entire continental territory in its latitudinal and altitudinal extension [17]. However, not all taxonomic groups are included in this range, nor is the distribution of their species continuous. On the contrary, most species have a more or less discontinuous distribution; on the one hand, they are related to the natural discontinuity of the hydrographic basins and, on the other, to the mosaic of habitats found in each basin.

The largest geographic amplitude is observed in the amphipods of the *Hyaella* genus, from Guallatire (Tarapacá) to Punta Arenas (Magallanes). In this latitudinal range, the seven *Hyaella* species are staggered in a North–South direction, with individual ranges that are very dissimilar in extension. The most widely distributed species is *H. costera*, which is recorded in sites as far away as Quebrada de Paposo (Antofagasta) and Isla Teja (Valdivia) [17]. A similar situation, of very remote limits marked by discontinuous populations, is that of *Cryphiops caementarius* (“Camarón de río del Norte”), registered between Arica and Valparaíso. Of the Parastacidae

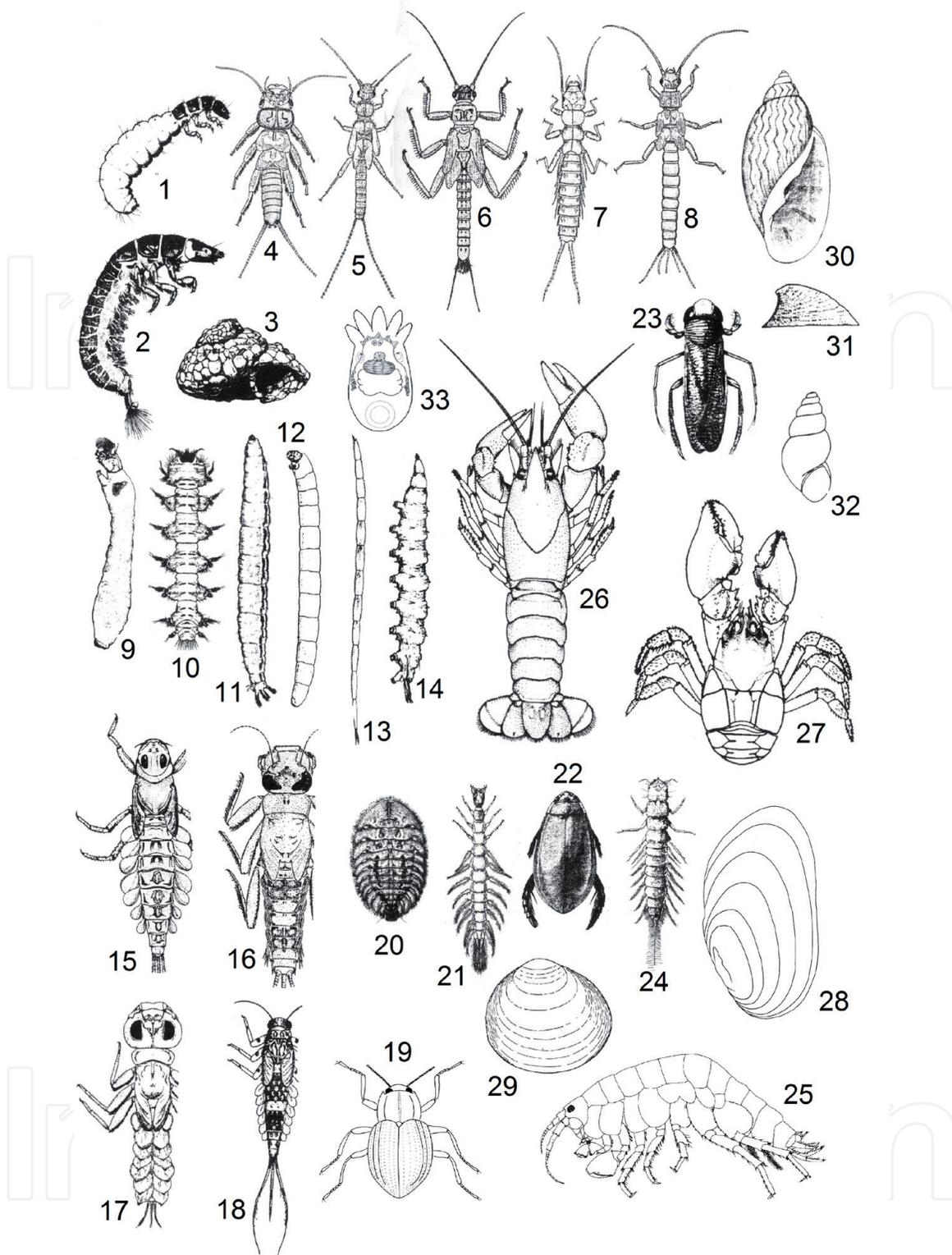


Figure 1. Some families of macroinvertebrates found in rivers of the southwest of South America (based on [1–3, 16, 34]). 1–3 Trichoptera: (1) Hydroptilidae, (2) Hydropsychidae, (3) Helicopsychidae. 4–8 Plecoptera: (4) Perlidae, (5) Notonemouridae, (6) Gripopterygidae, (7) Eustheniidae, (8) Austroperlidae. 9–14 Diptera: (9) Simuliidae, (10) Blephariceridae, (11) Tipulidae, (12) Chironomidae, (13) Ceratopogonidae, (14) Athericidae. 15–18 Ephemeroptera: (15) Siphonuridae, (16) Leptophlebiidae, (17) Ameletopsidae, (18) Baetidae. 19–22 Coleoptera: (19) Elmidae, (20) Psephenidae, (21) Gyrinidae, (22) Dytiscidae. 23 Hemiptera (Corixidae). 24 Megaloptera (Sialidae). 25–27 Crustacea: (25) Hyalellidae, (26) Parastacidae, (27) Aeglidae. 28–29 Bivalvia: (28) Hyriidae, (29) Sphaeriidae. 30–32 Gastropoda: (30) Chiliniidae, (31) Ancyliidae, (32) Cochliopidae. (33) Temnocephala.

shrimp species, the one with the widest range is *Samastacus spinifrons* (“Camarón de río del Sur”), distributed without interruption between Aconcagua and Chiloé. Its presence in islands south of Chiloé, up to Taitao, is not documented, but it can

be presumed to be in at least the major islands of the archipelagos of Guaitecas and Chonos [17]. The remaining species of parastacids, of excavator habit, associated with wetlands of the Central Valley and the Coastal Mountain Range, have delimited and allopatric distributions, i.e., *Parastacus pugnax* to the north of the Toltén River and *Parastacus nicoleti* to the south of the same river. The known distribution of *Virilastacus araucanius* is clearly discontinuous, between Concepción and Hueyusca (near Osorno).

Among the Aeglidae species, *Aegla pewenchaе* stands out as having the broadest latitudinal range, followed by *Aegla papudo*. The remainder of the species have narrow latitudinal ranges, such as *Aegla concepcionensis*, which is restricted to a single hydrographic basin [17]. Another example is the distribution of *Aegla neuquensis neuquensis*, whose known distribution in Chile is restricted to one sector of the Aysén River basin [38]. Recently, the distribution of freshwater decapods in rivers and lakes in Patagonia was mapped, identifying Duque de York Island (50°75'S) as the southernmost habitat of these organisms in the world (*Aegla alacalufi*) [27].

According to the available antecedents, the highest density of Malacostraca crustacean taxa occurs between 32° and 43°S [17]. All species of parastacids, 16 of the 20 *Aegla* species and 3 of the 7 *Hyalella* species, are found exclusively in Chilean territory [17]. In Chile, *Aegla affinis* is found extraliminally. It is found in Laguna del Maule, introduced by Argentine sport fishermen from the Rio Grande basin (in the south of the Mendoza Province). On the other hand, Chilean species are generally endemic to restricted sectors of the national territory. Apart from the narrow distributional range of *Aegla concepcionensis* and *Aegla hueicollensis*, which qualifies them as extremely endemic species, there are other cases in which a species is known only from one basin or from some adjacent basins. Such is the case of *Aegla spectabilis* in the Chol Chol River basin and of *Aegla bahamondei* and *Aegla occidentalis* in the adjacent basins of the Tucapel-Paicaví and Lleu Lleu rivers, in the coastal strip of the Biobío Region [17]. On the western slope of the Cordillera de la Costa, south of Corral and up to the mouth of the river Bueno, there is *Aegla hueicollensis* distributed in a series of small individual basins isolated from each other. *Parastacus pugnax* and *Parastacus nicoleti* species, digging species associated with the coastal wetlands and the intermediate depression to the north of Temuco, are endemic in their respective dispersion areas, separated by the Toltén River basin.

The conservation status of the freshwater invertebrate species in this territory was initially established for shrimps and anomurans, based on a classification using IUCN criteria and expert opinion [49]. Subsequently, the Chilean *Aegla* species were reclassified, relying on phylogenetic and genetic diversity arguments combined with the criteria proposed by IUCN [15]. The initial proposals determined that three of the four species of parastacids (*P. nicoleti*, *P. pugnax*, and *S. spinifrons*) are “vulnerable” in much or all of their geographic range [49]. The status of *Cryphiops caementarius* was recognized as “endangered” in the Valparaíso and Metropolitan regions and “vulnerable” in the rest of its geographic range. The status of the *Aegla* species was less compromised, although *Aegla laevis laevis* and *Aegla papudo* were “endangered” in the Valparaíso and Metropolitan regions. In addition, *Aegla laevis talcahuano* was described as “vulnerable” throughout its range. The remaining *Aegla* species were classified as “insufficiently known” or “less concern” [49]. Subsequent classifications subscribed only partially to the above qualifications, establishing that *Aegla concepcionensis* and *Aegla expansa* were “extinct in the wild” and that *Aegla papudo*, *Aegla spectabilis*, and *Aegla laevis laevis* qualified as “critically endangered” [15]. More recently, in 2014 the Chilean state approved and made the classification of 24 species of freshwater decapod crustaceans official.

There are two species classified as “critically endangered,” corresponding to *Aegla affinis* and *Aegla denticulata lacustris*. In addition, there are eight “endangered” and five “vulnerable.” The remaining nine qualify in the category of “less concern.”

Of the Chilean groundwater crustaceans, relatively little is known. A synthesis has been made for the South American continent, indicating that groups such as Amphipoda (e.g., *Ingolfiella*, *Bogidiella*) and several Isopoda (e.g., *Microcerberus*), are preferably found in the Chilean-Argentine area (previously described) [11]. There are also groups of Syncarida, such as *Bathynella*, *Leptobathynella*, *Parabathynella*, *Chilibathynella*, and *Stygocaria*, registered along the territory [11].

Insects: The larval stages of Ephemeroptera, Plecoptera, and Trichoptera, as primary consumers, are a relevant component of the benthic freshwater fauna, both in abundance and in biomass. They process a significant amount of periphytic microalgae and organic matter (autochthonous and allochthonous), either by triturating large particles or filtering small ones. On the other hand, during the adult stage, in some cases they return a significant amount of energy to the terrestrial environment. Many terrestrial predators, such as spiders, insects, insectivorous birds, and bats, consume a large number of adults during the periods of emergency, nuptial flight, and oviposition. These aquatic insects are one of the most important in river trophic nets, since spawning, larvae, and adults are a fundamental part of the diet of fish and amphibians or participate in some of the stages that end in them. Due to their abundance and ubiquity, as well as the differential tolerance of different species to different degrees of pollution or environmental impact, they have been used for some time as biological indicators of water quality. In particular, Plecoptera, preferably living in fast, turbulent, cold, and highly oxygenated waters, are considered excellent indicators of water quality.

The knowledge of insects in freshwater ecosystems has progressed significantly in recent decades [1]. It is relatively easy to identify the families and genera of these invertebrates due to the existence of identification guides, for example, the book *Macroinvertebrados bentónicos sudamericanos: Sistemática y biología* [3]. However, identification at the species level of many genera is difficult and in some cases still impossible.

Ephemeroptera: These are elongated body organisms whose adult states have reticulated nervation wings. The first pair of wings is larger than the second, and when at rest, the wings are left in an upright position. Both adult aerial and aquatic nymphal states are recognized by the presence of three (or two) filiform caudal appendages (**Figure 1(15–18)**). Globally, this is a rather small group in terms of number of species. However, they are conspicuous components of freshwater benthos in their immature stages.

In Chile, a total of 57 species belonging to 7 families have been described (**Table 1**) [18]. The most diverse family is Leptophlebiidae, with 36 species belonging to 15 genera. Of the 25 genera existing in Chile, the genera *Nousia*, *Meridialaris*, and *Penaphlebia* are the most diverse, with 7 and 6 species, respectively. One of the problems with the identification of the aquatic states of Ephemeroptera is that most of the descriptions are based on the diagnostic characteristics of adults [18]. Only 40% of the species have been described at both the adult and nymph stage, 12% only in nymphs, and 47% only in adult males and/or females [18]. From the point of view of their endemism in Chilean territory, 56% of species would be exclusive to Chilean territory, 33% shared with Argentina, and 11% of them a wider distribution [18]. Below are general comments for each family based on [18]:

- a. *Baetidae*: only three of its four genera and four of the nine species can be identified by their nymphs (*Andesiops peruvianus*, *Andesiops torrens*, *Andesiops ardua*, and *Americabaetis alphus*).

- b. *Oniscigastridae*: of the two species of this group, only *Siphonella ventilans* is known to be a nymph. This species is known as the male imago and subimago but not the female.
- c. *Nesameletidae*: only the nymph of *Metamonius anceps* has been identified.
- d. *Ameletopsidae*: only one of the two genera of this family is known to have nymphs—*Chiloporter penai* and *Chiloporter eatoni*. *Chaquihua*, the other genus of this interesting Gondwanic family, characterized by having carnivorous nymphs, is practically known only by its female imagos.
- e. *Oligoneuriidae*: the *Murphyella needhami* nymph is known, which is very curious due to the absence of abdominal gills.
- f. *Caenidae*: this family has unstudied species at the nymph level and is even unidentifiable at the imago level.
- g. *Leptophlebiidae*: of the 36 species described in Chile, 14 could be recognized by their adult stage and 17 by adults and/or nymphs, and only 5 are known only in their nymph stage (*Hapsiphlebia anastomosis*, *Nousia delicata*, *Massartellopsis irarrazavali*, *Meridialaris laminata*, *Nousia maculata*, *Nousia grandis*, *Nousia minor*, *Meridialaris diguillina*, *Meridialaris biobionica*, *Penaphlebia vinosa*, *Penaphlebia chilensis*, and *Penaphlebia fulvipes*).

Plecoptera: The adult stages of these organisms have long antennae and two pairs of generally well-developed membranous wings. Both aerial and aquatic nymphal stages are recognized by the presence of two caudal appendages, which are multisegmented and variable in length (**Figure 1(4–8)**). In this territory, there are Plecoptera that can live in extreme temperature environments. For example, it has been observed that the “Dragon of Patagonia” (*Andiperla willinki*) may inhabit glacial areas, where temperatures may reach freezing point.

A total of 63 species belonging to 6 families have been identified in the territory. Gripopterygidae corresponds to the most diverse family, with 28 species included in 18 genera [39]. Like most freshwater invertebrates, the greatest diversity of the Plecoptera species is located in central-southern Chile.

In general, most plecopteran genera include no more than two species, with the exception of *Chilenoperla*, *Diamphipnoa*, and *Teutooperla*, which have three species. From a point of view of its endemism in the Chilean territory, it covers 57% of species. The following are specific comments for each family based on [18]:

- a. *Eustheniidae*: has predatory nymphs present only in Oceania and Chile, and it is represented in Chile by two monospecific genera exclusive to our country (*Neuroperla schedingi* and *Neuroperlopsis patris*).
- b. *Diamphipnoidae*: this family of detritivorous nymphs lives exclusively in South America. Of the five Chilean species, *Diamphipnoa helgae* and *Diamphipnopsis samali* are also found in Argentina.
- c. *Austroperlidae*: this family has detritivore nymphs, whose representatives are found in South America and Australia. Of the four Chilean species, only *Klapopteryx armillata* also inhabits Argentina.
- d. *Gripopterygidae*: this is the most diversified Plecoptera family in Chile. It has mostly detritivorous nymphs, distributed in South America, Australia,

and New Zealand. Despite being a well-studied family, 55% of species with unknown or well-described nymphs persist but have only been assigned to a genera [39]. The case of *Araucanioperla* is notable, of which two species are known based on their imagos, and three different nymphs have not been assigned to any of them. In this family only the *Claudiooperla tigrina* species has been identified and is shared with Peru and Bolivia.

e. Notonemouridae: This family is distributed in South Africa, Madagascar, Australia, New Zealand, and South America, and in Chile it is the second most important with 16 species (unknown diet). According to the previously cited authors, in general immature states only allow recognition of the genera.

f. Perlidae has predatory nymphs represented in Chile by five species.

In regard to the conservation status of aquatic insect species, the only taxa officially classified in Chile correspond to *Andiperla willinki* “Dragón de la Patagonia,” which has been classified in the “endangered” category. This species is highly unique worldwide. It is a species native to Chile, found in the Aysén and Magallanes Regions and in Argentina (only one record) [40]. They are extremophilic and psychrophilic insects that live exclusively on ice in the northern, southern, and Darwin mountain ranges. Their habitat is not shared with other aquatic insects or vertebrates [31, 32]. Adults and nymphs may feed on other psychrophilic species, such as microalgae and Collembola, which also support the food web of glacial communities [31, 32]. In this way, *A. willinki* would be the top predator in these systems. This species is a potential resource for obtaining biotechnological products, especially those associated with enzymatic processes carried out under freezing conditions.

Trichoptera: correspond to insects of soft body, whose adult aerial phases have two pairs of undeveloped hairy membranous wings. The larvae are aquatic (**Figure 1(1–3)**) and build “little houses” of diverse organic materials (e.g., fragments of leaves and logs) and inorganic materials (e.g., grains of sand; **Figure 1(3)**), depending on the taxonomic group involved.

There are nearly 200 species described in Chile, with the Hydrobiosidae family being the most diversified, with 47 species belonging to 20 genera [29]. However, it is the Limnephilidae family, due to its size and abundance, which is almost emblematic in Chile, particularly distributed in the watercourses of Patagonian forests. Of the total species described, mostly based on adult states, aquatic immature states are known for only 45 of them. In other words, so far it is possible to identify only 21% of the aquatic larvae of Trichoptera up to the species level [29]. For each family, a summary is given below of the number of species per genus for which the aquatic immature states are known in relation to the total of species (immature aquatic states/known species) based on [29]:

a. Hydrobiosidae: *Cailloma* 3/3, *Neopsilochorema* 1/1, *Apatanodes* 1/2, *Neoatopsyche* 5/5, *Iguazu* 1/1, *Rheochorema* 4/4, and *Stenochorema* 1/1.

b. Glossosomatidae: *Mastigoptila* 1/7.

c. Hydroptilidae (**Figure 1(1)**): *Neotrichia* 1/1, *Celaenotrichia* 1/1, and *Metrichia* 1/5.

d. Ecnomidae: *Austrotinodes* 1/12.

- e. Limnephilidae: *Austrocosmoecus* 1/1, *Monocosmoecus* 3/5, *Platycosmoecus* 1/1, *Metacosmoecus* 1/1, and *Verger* 6/19.
- f. Leptoceridae: *Triplectides* 1/3 and *Hudsonema* 1/1.
- g. Anomalopsychidae: *Contulma* 1/1 and *Anomalopsyche* 1/1.
- h. Helicophidae: *Eosericoctoma* 1/2 and *Austrocentrus* 1/3.
- i. Sericostomatidae: *Parasericoctoma* 2/10.
- j. Tasimiidae: *Trichovespula* 1/1 and *Charadropsyche* 1/1.

In Chile, the known geographic distribution of the Trichoptera ranges from the Coquimbo Region to the Magallanes Region (30–55°S), bounded to the north by aridity, although intrusions have also been observed in the Brazilian subregion (e.g., species of the family Hydroptilidae in the Loa River) [29]. The greatest diversity of species is located in the regions of Biobío and Los Lagos (37–42°S), dominating in the Biobío Region, with a percentage that exceeds half of all species recorded in Chile [1]. On the other hand, the fundamentally endemic condition of the species, added to the fact that a group of genera has been included in exclusive families of the Australo-zelandic area (Philorheithridae, Helicophidae, Kokiriridae, Tasimiidae) and Australasian area (Stenopsychidae), has provided the foundation to distinguish and characterize the Chilean-Patagonian subregion within the Neotropical Area. Because such a distinction goes beyond the political boundaries of the territory, such endemism does not prevent species from being shared with Argentina. Only Helicophidae has presented an important diversification of genera (=5) and species (=15), among the families that have been assigned a Gondwanic origin.

Coleoptera: The adults of aquatic or aerial life are characterized by the presence of two pairs of wings, of which the previous pair has been modified as solid protective covers (elytra), the posterior pair being membranous. These insects, and mainly the larval stage, are part of the benthic macroinvertebrate fauna, participating in multiple food webs where they act as predators, detritivores, or herbivores (**Figure 1(19–22)**). From a taxonomic point of view, aquatic Coleoptera constitute a heterogeneous group that includes taxa belonging to different lineages of the Adephaga and Polyphaga suborders. In Chile, almost a hundred species belonging to seven families are known [23]. Three families of Hidradephaga are present, of which Dytiscidae presents the greatest richness at a generic and specific level with 11 genera and 34 species. Gyridae is represented by two genera and four species and Haliplidae with one genus and three species. **Table 1** summarizes the taxonomy of the group, indicating the number of known species based on [23]. Among the Dytiscidae genera, *Lancetes* is the most diversified with a total of 14 species, followed by *Rhantus* and *Liodessus* with 4 species each. The remaining genera are monospecific, except *Megadytes*, *Laccophilus*, and *Leuronectes*, each with two species. The Polyphaga are represented by four families, of which Hydrophilidae is the most diversified with 13 genera and 26 species. The Elmidae family presents seven genera, highlighting *Austrelmis* with eight species and *Austrolimnius* with two species. Hydraenidae presents only three genera, of which *Gymnochyshebius* is the most diversified with seven species. Finally, the Psephenidae family is the least diversified with three monospecific genera.

Chile does not have endemic families of aquatic Coleoptera, unlike other Mediterranean regions [23]. However, this fauna shows South American elements of tropical and Australian origin. This is the case of the *Tropisternus* genus, which is

widely distributed in the Neotropical and *Lancetes* regions with links to Australia, New Zealand, and Tasmania, as well as the genus *Tychepephus* (Psephenidae) and *Austrolimnius*, a taxa described as the dominant genus of freshwater elmids, which is also found in Central and South America. Most of the genera are not very diversified, and many of them are monotypic, a situation mainly related to the isolation of the territory since the Tertiary Period.

There are some taxa that have restricted geographic distributions, a situation that would give rise to a certain degree of endemism [23]: This is the case of the following species [1]:

- a. Hydrophilidae: *Enochrus concepcionensis* (Concepción and Biobío and Puyehue National Park)
- b. Dytiscidae: *Platynectes magellanicus* (Magallanes), *Rhantus obscuricollis* (Aysén in Chile and Neuquén in Argentina), *Rhantus antarcticus* (provinces of Concepción and Cautín), *Lancetes towianicus* (Magallanes), *Lancetes flavipes* (Magallanes), and *Lancetes kuscheli* (Province of Antofagasta)
- c. Elmidae: *Microcylloepus chilensis* (Quebrada de Camarones en Tarapacá); *Austrelmis chilensis*, *A. scissicollis*, *A. trivialis*, and *A. nyctelioides* (all three in the province of Quillota); and *Austrelmis elegans* and *A. costulata* (Tumbre, Province of Antofagasta)

In the Juan Fernández Archipelago, the fauna of Dytiscidae would be composed of only three species, all of the Colymbetinae subfamily. Of these, *Anisomeria bistrinata* and *Lancetes bäckstromi* are endemic to Masafuera Island and Masatierra, respectively. For Easter Island, *Bidessus skottsbergi* has been described as endemic, and *Rhantus signatus* was described on Mocha Island.

The following are general comments for each family based on [23]:

- a. Gyrinidae: Larvae and adults are of aquatic habits and predators; they frequent bodies of water of scarce current.
- b. Haliplidae: Their habitat consists of lentic water bodies with abundant filamentous algae and underwater plants and detritus-rich bottoms. The larvae are not swimmers and are shredders of the phytophagous regime. Adults move through water by alternating movements of mesothoracic legs.
- c. Dytiscidae: They are present in all types of freshwater ecosystems. Larvae and adults have aquatic and carnivorous habits (adults also have a great flight capacity). They are distributed throughout Chile, and the central zone reaches up to 2300 masl (they are also found in salt flats in northern Chile).
- d. Hydrophilidae: detritivorous adults (dead animals and decaying plants) and predatory larvae, of aquatic or semiaquatic habits. *Tropisternus setiger* has been reported as a predator of mosquitoes (Culicidae). The adults of the subfamily Sphaeridiinae are the only ones that are present in terrestrial habitats.
- e. Hydraenidae: They are small insects, not swimmers, and move by walking on rocks and algae in the banks of bodies of water or in the margins of clear water currents and sandy bottom. Some species are associated with mosses and most are found under boulders.

- f. Elmidae: They are aquatic in both adult and larval stages and are generally found in sandy, gravelly, or submerged bottoms among vegetation. They feed on algae and detritus and can also feed on microorganisms and small aquatic invertebrates.
- g. Psephenidae: Aquatic larvae that live attached to boulders in corrugated sectors, presenting the appearance of crustaceans. They are typical inhabitants of rithron areas that correspond to sectors of high slope, with high speeds of currents, low and stable temperatures, and high concentrations of oxygen (e.g., *Tycheapsephus felix*).

Diptera: Correspond to insects whose adult aerial phases have two pairs of simple wings (they also have two pairs of strongly modified vestigial wings). Many of the *Diptera* groups have aquatic immature phases, with an enormous variety of shapes and adaptations to the aquatic environment (**Figure 1(9–14)**). Among the most common families in Chilean rivers and lakes, the following stand out: Chironomidae, Athericidae, Simuliidae, Ceratopogonidae, Blephariceridae, Psychodidae, Empididae, Culicidae, Tabanidae, Ephydriidae, and Tipulidae [1]. Within the *Diptera*, the Chironomidae family deserves special attention because it is one of the most important groups of insects in aquatic ecosystems (**Figure 1(12)**), due to its abundance, species richness, and wide ecological spectrum, being found in a range of natural conditions greater than any other group of insects. The bibliographic information available suggests that this group has a great taxonomic diversity in the Southwest of South America. However, the dispersion of the literature, the scarcity of specialists, and the lack of reference collections do not allow us to provide a list of the genera and number of species present. As an example of its great diversity, in a stretch of only 5 km along the middle course of the Biobío River, 18 morphospecies have been observed, belonging to the subfamilies Orthocladinae, Podonominae, Chironominae, and Tanyponidae [1]. Of these, the Orthocladinae and Chironominae families were the most represented in terms of specific wealth, with eight and seven taxa, respectively. The most common genera in this area are *Eukiefferiella*, *Thienemanniella*, *Demycryptochironomus*, *Cricotopus*, *Oliveridia*, *Pentaneura*, *Nanocladus*, *Parasmittia*, *Dicrotendipes*, *Cryptochironomus*, *Stictochironomus*, *Chironomus*, and *Parakiefferiella*.

Despite their great diversity, enormous abundance, and great ecological relevance, these small aquatic larvae are one of the least studied groups in the territory [1]. The larvae of this group of insects play an environmentally important role, as they are sensitive bioindicators of aquatic ecosystem conditions, such as temperature, pH, dissolved oxygen, and nutrients, in addition to a wide range of toxic substances. It is important to note that the effects of pollution on chironomid communities have been widely reported in the literature, showing differential taxa tolerances to specific pollution sources. As a consequence of the different tolerances to eutrophication and organic enrichment of sediments, chironomids are used to study the trophic level of aquatic ecosystems. Furthermore, the potential use of chironomids as indicators of heavy metal contamination has been reported, based on the study of deformations of their buccal structures or due to the increase in dominance of groups capable of inhabiting environments with high concentrations of metals. Additionally, the habitat preference of the different groups of chironomids can provide information on the particular eco-hydraulic characteristics of an aquatic ecosystem [1].

Chironomids have acquired particular relevance over the last decades from an ecotoxicological point of view due to malformations produced in the structures of the cephalic capsule of larvae (antennas and buccal parts and others). These morphological alterations have been observed in the genera *Chironomus*,

Procladius, and *Cryptochironomus*. Moreover, this group of insects is of great importance in paleolimnological studies, since the cephalic chitinous capsules of the larvae are preserved in lacustrine sediments, allowing them to be used in paleoenvironmental reconstitutions. Additionally, this group has been greatly relevant in biogeography studies, being used as reference elements in intercontinental faunal relations.

Other orders of common insects: There are three other orders of insects that are frequently found in freshwater ecosystems, although with less abundance and diversity than those described above. These are [1]: (a) Odonata, represented mainly by the families Lestidae, Gomphidae, Coenagrionidae, Cordulidae, Calopterygidae, Aeshnidae, Libellulidae, and Petaluridae; (b) Megaloptera, represented by the predatory families Sialidae (*Sialis*; **Figure 1(24)**), and Corydalidae (*Protochauliodes*); (c) Hemiptera, with the families Gerridae, Corixidae (**Figure 1(23)**), Notonectidae, and Belostomatidae; and (d) Lepidoptera with the family Pyralidae.

3.2 Molluscs

This group is represented by several species of the Bivalvia and Gastropoda classes, which are very common in different types of freshwater habitats.

a. *Bivalvia*: These organisms are characterized by the soft parts of their bodies (e.g., visceral mass and foot), enclosed by two calcareous shells connected dorsally by a flexible ligament. In Chile, 13 species belonging to 2 families and 4 genera have been described [28]. Numerous studies have demonstrated the important role they play in the ecosystems they integrate. For example, the large bivalves of the Hyriidae family, due to their feeding by suspension and because they are long-lived organisms, can significantly influence the abundance of phytoplankton communities, water quality, and nutrient recycling [28]. In addition, they are an important component of energy flow and nutrient cycling, as they constitute a significant portion of freshwater macrobenthic biomass. These organisms have been used as sentinel organisms and have potentially been considered as biomonitors of the health of freshwater ecosystems. The clams of the Sphaeriidae family have been less studied because of their small size, hidden way of life, and difficulty in being identified. However, since they can inhabit environments where no other bivalve can live, they can serve as biomonitors of the environmental conditions of their habitat.

The species described to date for Chile belonging to the Hyriidae family are represented only by the *Diplodon* genus, with two subgenera [28], *Diplodon* and *Australis*, each with its respective species *D. (D.) chilensis* and *D. (A.) solidulus*, and the family Sphaeriidae represented by three genera: (a) *Pisidium*, with the species *P. lebruni*, *P. observationis*, *P. chilense*, *P. meierbrooki*, *P. magellanicum*, *P. huillichum*, and *P. llanquihuense*; (b) *Sphaerium*, with species *S. forbesi* and *S. lauricochae*; and (c) *Musculium*, with the species *M. patagonicum* and *M. argentinum*.

An analysis of the geographic distribution of the species reported for Chile allows us to propose the existence of three zoogeographic areas and the postulation of four species of Sphaeriidae and one of Hyriidae as endemic species of Chile [28]: (a) High Andean region, *Sphaerium lauricochae*, *Sphaerium forbesi*, and *Pisidium meierbrooki* are species specific to this region, sharing geographical areas with Peru and Bolivia; (b) Central-southern region of Chile, characterized by *Pisidium llanquihuense*, *Pisidium huillichum*, *Pisidium chilense*, and *Musculium argentinum* (the three species of *Pisidium* have only been recorded in Chile, but not *M. lauricochae* and *Sphaerium forbesi*); and (c) Patagonian region, the species *P. magellanicum*,

P. observationis, and *Musculium patagonicum* are shared with Argentina. *Pisidium lebruni* is also a Patagonian species but is currently registered only in Chile. The authors mentioned above indicated that this biogeographic proposal is preliminary and that future studies are required for its validation. In regard to Hyriidae, endemism is at the subfamily Hyriinae level, which is endemic to South America. The species *Diplodon chilensis* is widely distributed in Argentina, but *D. solidulus* is not, a fact that allows it to be considered endemic, along with the subgenus *Australis*. However, like *Pisidium lebruni*, its presence outside Chile must be corroborated [28].

So far there are no reports of the introduction of exotic bivalve species, as is happening in Argentina with *Corbicula* and *Limnoperna* or with *Dreissena polymorpha* in the northern hemisphere [1]. The great competitive capacity of these exotic species is causing the decline of native populations, especially Hyriidae, since these are used as substrates to settle, with consequent death by asphyxia.

- b. *Gastropoda*: In the freshwater ecosystems of the extreme south of South America, there are gastropod species with a high degree of endemism, which present archaic zoogeographical relations of the Gondwanic type and constitute functionally relevant elements in the benthic communities of such ecosystems [33, 36] (e.g., Chiliniidae (**Figure 1(30)**), Cochliopidae (**Figure 1(32)**), Planorbidae, Lymnaeidae, Physidae, and Ancyliidae (**Figure 1(31)**). Chile has described 73 species belonging to six families and eight genera. However, many of these groups must be revised [36].

Although the inventory of Chilean freshwater gastropods began in the early eighteenth century and continued into the nineteenth century, it was not until the beginning and middle of the twentieth century that the number of new species described began to stabilize [36]. Subsequently, from the last half of the twentieth century until now, the number of new species described has been remarkably low. Since the compilation of freshwater gastropod mollusks from Chilean territory, the taxonomy of a few families has progressed considerably (e.g., Ancyliidae, Planorbidae), while others (e.g., Chiliniidae, Cochliopidae) still require the attention of researchers [36]. Cochliopidae species have been mostly included in the genus *Heleobia* or *Littoridina* [19]. However, it has recently become evident from penile morphology that many of the species traditionally assigned to *Littoridina* in Chile actually belong to *Heleobia* [19, 20]. According to a review of the existing literature on the group, inland water gastropod mollusks in Chile involve representatives of the subclasses Prosobranchia (one family) and Pulmonata (five families) (**Table 1**). The Pulmonata constitute the largest group, integrated by “snails” of the families Chiliniidae (30 species of the genus *Chilina*), Lymnaeidae (five species of the genus *Lymnaea*), Physidae (four species of the genus *Physa*), and Planorbidae (seven species of the genus *Biomphalaria*), plus “limpets” of the Ancyliidae family (four species of the *Anisancylus* and *Uncancylus* genera). Additionally, the prosobranchs are represented only by the family Hydrobiidae (one species of the *Potamolithus* genus and 21 species of the *Littoridina* genus (*Helobia*)).

The taxonomy of the group has been quite abandoned, so information on the species remains incomplete [36]. In this regard, a critical taxonomic review of the species of the six families described for Chile is urgent. Most of them have been described on the basis of shell characters, which, due to their strong intra- and interpopulation variability, must be validated with taxonomically more conservative characters, referring to the protoconch, radula, and the anatomy of the soft parts, i.e., penile complex and lung. Additionally, it is evident that the application of molecular taxonomy techniques is a requirement for the definitive validation of species. Preliminary studies carried out by the first author, of the penian complex

of Chilean species, suggest that several of them would be synonymous and others not yet described. In this regard, it is expected that the number of valid species described for Chile could be reduced between 10 and 20%.

The geographic range occupied by freshwater gastropods covers the entire territory, in its latitudinal extension, and from the coastal boundary (and in many cases estuarine) to the Andean highlands in the north or to the Andes Cordillera in the rest of the area. However, not all groups are included in this global range, nor is the distribution of their species continuous. On the contrary, most species have a more or less discontinuous distribution, associated on the one hand with the location of the hydrographic basins and on the other with the mosaic of habitats found within each of the basins.

One of the problems facing the analysis of the geographic distribution patterns of freshwater gastropod species is the scarcity of sampling and lack of data specific to the collection site. In fact, most of the published records correspond to the “type location” [36]. Another obvious problem is that several species have imprecise localities. At the supra-specific level, the Cochliopidae, Physidae, and Lymnaeidae families are the most widely distributed in Chile, from the basins of the extreme north of the Atacama Desert to the Magellanic Region. On the contrary, Chilinae species are mainly distributed between Valparaíso and Tierra del Fuego. An exception within this Family is the *Chilina angusta*, which has a different distribution compared to the rest of the family, living in springs of the Quebrada de Paposos on the coast of the Atacama Desert (25°S). Most species of the Planorbidae family are restricted to northern and central Chile (e.g., *Biomphalaria atacamensis*, *B. termala*, *B. montana*, *B. Schmiererianus*, *B. costata*, and *B. aymara* [34]). Only one species of Planorbidae extends in central and southern Chile to the Puelo River (*B. chilensis*). The Ancyliidae family is the one with the most restricted geographic distribution in Chile, covering from Valparaíso to Chiloé, being a very abundant group in the stony coastal rivers of the VIII Region. According to the available antecedents, the highest density of freshwater gastropod taxa is located between regions VII and X, the latter being the one that concentrates the greatest diversity of species. To the south of Chiloé and to the north of the Choapa River, the number of species clearly tends to decrease. Of the total of 72 species described for Chile, 91.7% are endemic to the country [36]. In this regard, all the species of the families Cochliopidae, Chilinae, Physidae, and Planorbidae are endemic. Of the Lymnaeidae family, only *Lymnaea lebruni* is endemic, having only been cited for Punta Arenas. In the case of Ancyliidae, only *Uncancylus foncki* is endemic, having been cited for the Maullín River and Llanquihue Lake.

As for most Chilean freshwater invertebrates, the proposal of conservation categories for gastropod species is a difficult task given the lack of information [36]. On the other hand, no specific criteria and parameters have yet been developed for the classification of freshwater mollusks in the different conservation categories proposed by the World Conservation Union (IUCN) and established in Article 37 of Law No. 19,300 on the General Bases of the Environment (Chile). As a result, there is no general picture of the conservation status of Chilean species. Valdovinos et al. [37] tentatively proposed a classification of freshwater mollusks of the Chilean Coastal Range, mainly between 36° 50'S and 39° 26'S (following the IUCN “B criterion” (1994), which classifies a species as threatened when its geographical distribution is very restricted, and there are other factors that allow us to suspect that it is endangered. According to these authors, their proposal should be considered with caution as it is based on fragmentary information and general observations made by the author over the last 20 years. They considered all the representatives of the Chilinae family within the “vulnerable” category, since, although their species still have relatively high occupation areas, it is evident that there is a continuous

decline in the availability of their habitats. In contrast, given their large areas of occupation, along with their high dispersal and colonization capacity, and their abundance in different habitat types, the following species were considered to be at a “lower risk”: *Physa chilensis*, *Lymnaea viator*, *Littoridina cumingi*, and *Biomphalaria chilensis*. Due to the scarcity of information, species such as *Littoridina pachispira* were classified within the category of “insufficient data.” Following the same criteria, apart from these species from southern Chile, the *Chilina angusta* species from the Quebrada de Paposo (Taltal) should be considered “critically endangered.” Regarding the conservation status of mollusk species, the only taxa officially classified are *Biomphalaria costata* and *Heleobia atacamensis*, both classified as “critically endangered,” and *Heleobia chimbaensis*, considered “vulnerable.”

The exotic freshwater mollusks present in Chile have been analyzed on the basis of specimens collected in wetlands and in commercial aquariums or intercepted in customs barriers, as well as bibliographical references. A total of seven species belonging to six genera were recorded, i.e., *Melanoides maculata*, *Thiara (Melanoides) tuberculata*, *Helobia* sp., *Pomacea bridgesii*, *Physella venustula*, *Physa* sp., and *Biomphalaria* sp. (*M. maculata* was collected in the Lluta River and classified as a cryptogenic species).

3.3 Other invertebrate groups

Protozoa (several phyla): Within the protozoa of free life, only the Sarcomastigophora and Ciliophora are normally found in freshwater. The first group is mainly represented by heliozoa, amoebas, and various flagellates and the second, by planktonic ciliates such as *Ophrydium* and *Stentor* and benthic ciliates such as suctors and hypotrichs. A review has been made of the ciliates present in lake ecosystems of central and southern Chile [43]. The ecological importance of the species of the orders Prostomatida (*Urotricha* spp. and *Balanion planctonicum*) and Haptorida (*Lacrymaria* sp., *Askenasia* spp.), Peritrichida (*Ophrydium nau-manni*, *Vorticella* sp., *Vaginicola* sp.), Heterotrichidae (*Stentor araucanus*, *Stentor amethystinus*), Oligotrichida (*Strobilidium viride*, *Strombidium* spp., *Halteria* spp., *Strobilidium* spp.), and Scuticociliatida (*Uronema* spp., *Cyclidium* spp.). The taxonomic knowledge of this group of typed amoebas has progressed substantially in recent decades, with a large number of species having been described, especially in freshwater ecosystems in central and southern Chile [44]. In addition, a complete taxonomic listing of Chilean tecamebas (sensu lato) was recently published [22]. The authors point out that the known diversity includes 416 taxa (64 genera and 352 taxa), 24 of which were reported for the first time.

Porifera: The members of the Spongillidae family are the only freshwater organisms. Species diversity is proportionally low relative to other groups of invertebrates. However, they are usually very abundant in the benthos of some lakes (e.g., Lake Lleu Lleu). Some species live in shady habitats, but those of the *Spongilla* genus, due to their association with zooxanthellae, live in illuminated areas. As an adaptation to the highly variable conditions of abiotic factors in freshwater, these sponges lack larvae and produce resistance structures.

Cnidaria: Like porifers, Cnidaria are poorly represented in Chile’s freshwater ecosystems. In some lacustrine systems of central Chile, which show clear eutrophication symptoms (e.g., Laguna Grande de San Pedro and Lago Lanalhue, Biobío Region), the presence of the invasive jellyfish *Craspedacusta sowerbii* from Asia has been recorded [1]. This organism is an active predator of zooplankton, which can alter the planktonic communities of the ecosystems it invades. This small jellyfish is shaped like a bell, has between 50 and 500 tentacles, and does not usually exceed 25 millimeters in length. Some of its tentacles are long and allow it to maintain its

position in the water while favoring movement, while the others are short and have a food function. It is in the latter where the nematocysts are housed, which include small harpoon-shaped cells (cnidocytes) that shoot when they come into contact with prey. As far as coloring is concerned, the hydromedusa is translucent, although with certain whitish or greenish tones. In addition to these jellyfish, the polyps also include *Hydra*, which are organisms that can become very abundant in palustrine systems.

Platyhelminthes: Of the six classes of this group, only Turbellaria and Temnocephala are found in freshwater ecosystems, as free living organisms or commensals (other groups are parasites; see below) [1]. The first group is composed of the genera *Dugesia* (*D. anceps*, *D. rincona*, *D. chillia*, *D. titicacana*, *D. sanchezi*, and *D. dimprpha*) and *Curtisia* (*C. michaelsoni*), benthic organisms still imperfectly known in the area. The Temnocephala are a very interesting group that live as ectocommensals on the Parastacidae and Aeglidae crustaceans. Temnocephala were originally discovered in Chile and have a clear Gondwana-type distribution, restricted to the southern continents. The most common species of this group found in central-southern Chile are *Temnocephala chilensis* and *T. tumbesiana*.

Nemertea: Only a few nemertines have been found in freshwater worldwide. Most South American freshwater nemertes belong to the genus hoplonemertes, *Prosoma* (e.g., Venezuela, Brazil, and Argentina) [1]. The other type of South American nemerte is the heteronemerte, *Siolineus turbidus*, found in Brazil. In Chile, bdelonemertean *Malacobdella auriculae* has been described as an ectoparasite of a pulmonary gastropod [30]. These authors described a new genus and species for Chile, *Koinoporus mapochi*, which has been recorded in central Chile (Melipilla, Talagante, San Javier, Angostura de Paine, Pelarco, and Concepción). This species lives in low velocity waters, in both lotic and lentic ecosystems, associated with areas containing abundant aquatic macrophytes such as *Hydrocotyle ranunculoides*.

Aschelminthes: The Rotifera, Nematomorpha, Nematoda, and Gastrotricha are very common groups in freshwater environments of Southeastern South America [1]. Rotifers are an important part of lake zooplankton, although many are benthic. Nematodes are a very diverse group, but little is known about their taxonomy, despite being very common in practically all types of freshwater environments. Gastrotriches are a group of organisms that in freshwater ecosystems are apparently not very diverse and are frequently associated with muddy bottoms and the roots of aquatic plants (e.g., *Ichthydium*, *Polymerurus*, *Lepidodermella*, *Chaetonotus*, *Heterolepidoderma*, and *Aspidiophorus*). Nematomorpha are quite common in seasonal pools, which are represented by *Gordius paranensis*, *Gordius chilensis*, and *Beatogordius latastei*.

Annelida: Of this group of segmented worms, oligochaetes are undoubtedly the most common in freshwater ecosystems, especially in the low-moving water environments of lakes and rivers [1]. In benthic environments with a high organic load, Oligochaeta Tubificidae (*Tubifex*, *Limnodrilus*, *Potamothrix*, *Bothrioneurum*, *Epirodrius*, *Isochaetides*) are usually abundant, while in less extreme environments, Naididae (*Nais*, *Chaetogaster*, *Schmardaella*, *Paranais*, *Pristinilla*, *Dero*, *Pristina*) and Lumbriculidae (*Lumbriculus*) are frequent [1]. Not much is known about this group in the area, and its scarce knowledge has been derived fundamentally from studies carried out by Argentine researchers. Other common annelids, especially in marshy environments, are the Hirudinea or “leeches” of which *Mesobdella gemmata* is perhaps one of the most common in central-southern Chile.

Another quite frequent group, especially in the soft bottoms of the estuary of some rivers, is the Archiannelida (e.g., Biobío River). Within this group, those belonging to the Histriobdellidae family are of great evolutionary and biogeographic importance, as they are commensals of decapod crustaceans (they live in

their gill chambers) and because of their typical Gondwanic distribution (e.g., Madagascar, Tasmania, New Zealand, and the southern tip of South America). This is a group, represented in Chile by two species of the *Stratiodrillus* genus, which have highly specialized hosts [41].

For example, *Stratiodrillus aeglaphilus* inhabits the “crab” *Aegla laevis* (e.g., Río Maipo, in central Chile), and *S. pugnaxi* inhabits the “Camarón de Vega” *Parastacus pugnax* (e.g., Reumén, southern Chile).

Tardigrada: These small invertebrates are present in almost all types of freshwater environments, forming part of the benthos located on submerged plants and also in humid areas outside the water, for example, among mosses [1].

Bryozoa: The six species of Phylactolaemata bryozoans present in Chilean freshwater ecosystems belong to the cosmopolitan genera, *Fredericella* (*F. sultana*) and *Plumatella* (*P. repens*, *P. mukaii*, *P. patagonica*, *P. casmiana*). Although many authors acknowledge that freshwater bryozoans are common and abundant organisms in all freshwater bodies around the world (e.g., lakes, rivers, temporary pools), the development of knowledge regarding these organisms in Latin America is scarce and far from being a line of research that has persisted over time [26].

Parasitic invertebrate metazoa: Until now mainly free life forms have been studied, but there are many other species of parasitic invertebrates associated with freshwater organisms, at least for some part of their life cycle. In the case of metazoa parasites of aquatic and semiaquatic organisms, there are approximately 60 taxa described in Chile [25]. 47% of them have been identified at the species level and 53% as a genus or family. These parasites are composed of five phyla (Arthropoda, Nematoda, Acanthocephala, Platyhelminthes, and Myxozoa), between 1 and 3 classes per phylum, with a total of 8 classes, 19 orders, and 31 families. Phylum Platyhelminthes is the most diverse and is composed of 3 classes, 11 orders, and 19 families. Within this group, Digenea has the highest number of species. Like most of the Chilean freshwater invertebrate groups, the greatest diversity is found in central-southern Chile. The study of the ecological aspects of the digenees present in freshwater organisms of our country is of great importance, because many of them negatively affect man (e.g., *Fasciola hepatica*, which affects livestock, and *Furcocercaria*, which produce swimmer itch) [1]. Swimmer itch is caused by exposure to cercarias that have birds or mammals as definite hosts. In the summer of 2004, public alarm was generated when this parasitic disease was registered for the first time in central-southern Chile. It was found that the culprit was *Trichobilharzia* sp., whose intermediate host was the freshwater snail *Chilina dombeyana* [35]. This is clearly an emerging phenomenon, which is expected to intensify with increased eutrophication of ecosystems and climate change.

4. Threats to the biodiversity

As mentioned above, in central-southern Chile there is a biodiversity “hot spot” of global interest, which includes benthic freshwater invertebrates. Given the climatic, geographic, and hydrological conditions of this territory, located approximately between 35° and 43° S, this zone also corresponds to a “hot spot” of economic activities which place a lot of pressure on aquatic biodiversity [1]. Paradoxically, the Biobío Region, which corresponds to the heart of this territory for its valuable heritage of freshwater fauna (fish and invertebrates), is one of the most intervened and unprotected in the country. For example, in the region’s

36,929.3 km² of territory, only 843.6 km² correspond to “protected wild areas” (2.28%), which are outside areas of interest for the conservation of freshwater biota [1]. The most intense impact within this zone is concentrated in the middle and lower parts of watersheds, particularly in areas formerly occupied by coastal forests, whose importance has already been mentioned [50]. At present, these forests have consisted in a high proportion of pine and eucalyptus plantations, which support cellulose production at a global scale.

There are numerous factors that put freshwater invertebrate communities at risk (as well as fish), many of which work together to enhance the effects on biota [17]. In this regard, the following factors are of particular importance:

- a. Loss and degradation of freshwater habitats: Important “pharaonic works” carried out in northern and central Chile, such as the construction of hydroelectric power plants (reservoir or run-of-river), irrigation works (ponds and canals), and mining operations, are currently endangering the survival of many freshwater invertebrate species, especially those with benthic habits. For example, there has been a notable loss of diversity and local extinctions (e.g., *Chilina dombeyana*) in lakes regulated by hydroelectric generation activities (e.g., Laja Lake). Massive local extinctions of *Aegla pewencha* have also been observed, associated to the strong hourly changes in the level of the Biobío River, product of the activity of the plants of the Biobío [1]. Similarly, the “minimum ecological flows” considered in many hydroelectric and irrigation projects are insufficient for the conservation of potentially threatened macroinvertebrate species. For example, the Maipo River basin is fragmented by 10 hydroelectric plants (Queltehues, Alfalfal, Carena, Maitenes, Puntilla, El Volcán, Los Bajos-Caemsa, Los Morros, La Florida, Planchada-La Ermita), the Maule River by eight plants (Loma Alta, Cipreses, Curillinque, Pehuenche, Isla, Colbún, Machicura, San Ignacio), and the Biobío River by nine plants (El Toro, Abanico, Mampil, Pangué, Antuco, Peuchén, Ralco, Rucúe, and Angostura).

As mentioned above, not only the “pharaonic works” are a serious threat to the conservation of Chile’s freshwater invertebrates. Deforestation of native forest basins and its transformation into areas dedicated to forestry, agriculture, and urbanization are generating alterations of great magnitude to freshwater ecosystems of central-southern Chile. Although many aspects of the patterns and processes that occur in riparian environments have been studied in recent years, little is known about the effect of vegetation type on Chilean fluvial communities [1]. However, replacement of native forest with introduced species and deforestation are common practices in many regions. Currently, in forested areas of central Chile, deciduous native components are being replaced on a large scale by pine and eucalyptus, suggesting that this process has an important impact on freshwater invertebrates and hence on the energetic characteristics of river communities. This situation reaches its greatest impact in the Chilean regions Maule, BioBío, and Araucanía, extending progressively towards the south. Within these territories, the areas of the coastal mountain range have been almost completely destroyed and are now occupied by forest plantations of exotic species.

There are numerous other factors that cause the degradation of aquatic habitats; among them it is necessary to highlight the erosion of basins, which produces high sedimentations in lakes and rivers [1]. In this regard, it is estimated that 70% of rivers in central Chile are affected by this process (e.g., rivers Aconcagua, Cachapoal, Maipo, and many others). The effect of large sediment loads on rivers is multiple. However, its effect on photosynthesis and the development of microalgae limits the

penetration of light and the filling of microhabitats that are occupied by benthic invertebrates. Another direct effect on aquatic habitats is the extraction of aggregates directly in river beds.

b. Invasive species: The introduction of exotic fish species produces significant negative effects on Chilean freshwater invertebrate populations, the magnitude of which is just beginning to be discovered. Among the most common species are “rainbow trout” (*Oncorhynchus mykiss*) and “brown trout” (*Salmo trutta*), which actively prey on benthic macroinvertebrates in the upper and middle part of rivers, juvenile states especially on Chironomidae diptera; intermediate states on Ephemeroptera, Plecoptera, and Trichoptera; and adult stages on Aeglidae crustaceans. It is very probable that one of the main causes of the extinction of local Aeglidae populations is associated with predation by these two trout species. In the lower part of rivers and in many mesotrophic and eutrophic lakes, the “carp” (*Cyprinus carpio*) and the “mosquito fish” (*Gambusia holbrooki*) have relevant effects on invertebrate communities, either by resuspending sediment produced by the former (which affects suspended species such as the mussel *Diplodon chilensis*) or by predation of planktonic and benthic organisms, which produces the latter. Another species, the “chanchito” (*Cichlasoma facetum*), which is very common in lakes of central Chile (e.g., in the area of Concepción), is extremely voracious and generates large modifications in invertebrate populations. As previously mentioned, in the zooplankton of lentic ecosystems located in central Chile, with clear symptoms of eutrophication, it is possible to find the hydromedusa *Craspedacusta sowerbi*, originating from Asia. This organism is an active predator of zooplankton, which can alter the planktonic communities of the ecosystems it invades.

There are also other invasive benthic invertebrates, such as the mollusks mentioned above. Exotic freshwater mollusks are reported in local wetlands, particularly *Melanoides maculata* and *Physella venustula* [1]. Species of the genera *Helobia* and *Physa* have also been recorded. However, they have been classified as cryptogenic, species not defined as native or exotic, since *Physa* is a genus widely distributed in the Pacific basin of North and Central America and its current taxonomic knowledge in South America is limited. The main pathways of voluntary and involuntary introduction of exotic freshwater molluscs are trade. Given the increase in inter-regional trade, appropriate ecological and taxonomic data must be collected to evaluate their eventual establishment in local ecosystems. In addition, the advance of the invasive diatom *Didymosphenia geminata* known as “didymo” has recently been recorded. This is a highly invasive algae with a high capacity to affect aquatic ecosystems into which it is introduced. This microalgae is present from the Biobío River basin to the Patagonian ecosystems, where it is generating important changes to fluvial benthic macroinvertebrates that are only now beginning to be studied.

c. Aquatic pollution: Pollution of rivers and lakes is one of the most visible threats affecting the survival of the area’s freshwater invertebrates. The nature of the compounds that affect aquatic biota varies from one basin to another, depending on the productive activities developed there and the presence of human settlements. For example, in sectors with a high population density, the main factors are associated with nutrients and organic matter (e.g., the Aconcagua and Maipo River basins, among others); in areas with strong mining activity, the main factors are metals and pH (e.g., acid drains in northern and central Chile); in agricultural areas, fertilizers and pesticides (e.g., central-southern Chile); and in areas with cellulose and paper industries, a large diversity

of persistent organic compounds (e.g., Biobío River basin [51]). A relevant aspect in Chile regarding this disturbance factor is the absence of a policy that regulates the quality of surface waters of rivers and lakes. It is evident that the almost total absence of this regulation has a negative impact on aquatic biota, as it does not set limits regarding the concentration and pollutant loads contributed to these systems, either from specific or diffuse sources.

d. Overexploitation: With the exception of “Camarón de río del norte” (*Cryphiops caementarius*), present in the rivers of northern Chile, and the species “Camarón de vega” (*Parastacus pugnax*) and “Camarón de río del Sur” (*Samastacus spinifrons*), present in central-southern Chile, there are no other species that are strongly affected by overexploitation [1].

e. Global climate change: The effect of global climate change is the least predictable of the five factors considered. This lack of prediction is associated with the uncertainty of future climate scenarios and the difficulty of anticipating their ecological consequences [52]. However, it is predicted that changes in water availability and thermal regime will be more serious at medium and high latitudes, where important changes in the latitudinal and altitudinal distribution of species will occur. The biota of these areas is particularly vulnerable due to their thermal regime (many species associated with low water temperatures, e.g., Plecoptera) and the lack of adequate escape routes to more suitable habitats. It is evident that the most vulnerable species to extinction within freshwater invertebrates are those of large size (>10 mm), without the capacity to fly, stenohalines, and with narrow geographical distribution ranges, such as many crustaceans (e.g., Aeglidae) and mollusks (e.g., Chiliniidae).

5. Conclusions

The invertebrates of rivers, lakes, and wetlands of the Southwest of South America are one of the oldest testimonies of the great climatic changes suffered by the landscape, especially during the Tertiary and Quaternary periods. In particular, the freshwater ecosystems of the mountainous territories and plains, ranging from the Maule to the Aysén Regions of Chile, which were once covered by forests in virtually all their extension. Today, many invertebrate species in the northern and central parts of this territory are threatened, particularly those with small populations and low dispersal capacity, such as mollusks and decapod crustaceans. In this territory of high diversity and endemism, the rivers are severely fragmented as a result of the presence of hydroelectric plants and irrigation infrastructures. In addition, water quality shows a progressive deterioration, associated with strong industrial and urban growth. Also, deforestation and substitution of native forest for pine and eucalyptus plantations, especially in the central valley and the coastal mountain range, are generating profound changes in this group of invertebrates. However, in these zones it is still possible to find small remnants of rivers associated with native vegetation, although markedly isolated from each other. These remnants of great past climatic and geological changes are today highly threatened.

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