Checklist of freshwater symbiotic temnocephalans (Platyhelminthes, Rhabditophora, Temnocephalida) from the Neotropics

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Abstract

Based on published records and original data derived from our research, we have generated a checklist of symbiotic temnocephalan fauna from 57 taxa of freshwater invertebrate and vertebrate hosts from 16 families included in four classes from the Neotropics. The checklist contains 38 nominal species from 3 genera belonging to the Temnocephalida families Diceratocephalidae, Didymorchidae and Temnocephalidae. All taxa (35) of the genus Temnocephala are endemic to the Neotropics and 14 (40%) are considered micro-endemic (i.e. only one record each from a single locality). While only one species and one variety of Didymorchis are known from the Neotropics; there are also two putative undescribed species of this genus. Only Diceratocephala boschmai (Diceratocephalidae) is reported as an introduced species from Uruguay. Host specificity to a particular group of invertebrates and vertebrates is the first evidence for the ecological and evolutionary associations that will be analyzed in future studies.

Key Words

Temnocephala
Didymorchis
Diceratocephala
Malacostraca
Insecta
Gastropoda
Chelonia
taxonomy
inventory

Introduction

Temnocephalida (Platyhelminthes, Rhabditophora) is the most diverse group of symbiotic turbellarians typically associated with crustaceans, with 122 valid species and 24 genera described in the world (Tyler et al. 2006–2012). Recently, Temnocephalida was confirmed as a monophyletic group included in Lymnophloplanida, which in turn makes up part of the Dalytophloplanida clade, a major group of Rhabdocoela (Van Steenkiste et al. 2013). Within the Temnocephalida, the family Temnocephalidae Monticelli, 1899, is the most diverse, distributed in the Australian region with high species richness, but low host diversity, and in the Neotropics with an apparently lower number of temnocephalan species, but a greater diversity of host taxa (Damborenea and Brusa 2009, Sewell 2013). In fact, in the Neotropics, 32 species belonging to the genus Temnocephala and four taxa belonging to Didymorchis, endemic to this region and associated with crustaceans, mollusks, insects and chelonians have been described (Damborenea and Cannon 2001b, Garcés et al. 2013 and cited therein).

The inventory work of the temnocephalan fauna in the Neotropics began in the 18th century, when the first species of Temnocephalida was described, Temnocephala chilensis (Moquin-Tandon 1846), associated with anomuran crabs, Aegla laevis (Latreille), from Chile (Damborenea and Cannon 2001a). Since then, more than 50 studies have been published regarding aspects of the temnocephalan fauna in the Neotropics, including descriptions of new species, analyses of temnocephalan symbiotic community structure of particular host species, and studies with phylogenetic and biogeographic inferences (e.g. Damborenea 1998, Volunterio 2007a, 2007b).
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Surface) and internal structures (e.g. branchial cavity) were examined for temnocephalans; external (e.g. carapace and claw surface) and internal structures (e.g. branchial cavity) were analyzed separately in Petri dishes with 0.65% saline solution, under a stereomicroscope. Gills from each decapod were also obtained and placed in tap water to search for temnocephalans. In the case of mollusk hosts, their mantle cavity was opened after sacrificing. Temnocephalan collections from live turtles were carried out by the catch-and-release method (e.g. FAO 2012); therefore, the live turtles were identified directly in the field (L. Alcalde, personal communication). Temnocephalans were fixed with hot (steaming) 4% formalin or hot (steaming) distilled water. In some cases, specimens from the same host and with the same external aspect were fixed in 100% ethanol in the field for future molecular studies. All temnocephalans were processed following standard procedures (Sewell 2013). Species identification was achieved using specialized literature, and voucher specimens of some temnocephalans were deposited at the Colección Helmintológica de Museo de La Plata, Argentina (MLP-He) and the Colección Nacional de Helmintos (CNHE), Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), Mexico City, Mexico, as follows: symbionts of Malacostraca (CNHE: 9276-9277; MLP-He: 6148-6155, 6218, 6641, 6763, 6768, 6770, 7153); symbionts of Gastropoda (MLP-He: 3050-3052, 6622, 6764-6767, 6769) and symbionts of Chelonia (MLP-He: 6642-6643).

Results

In total, 60 papers have been published establishing host and locality records of the freshwater temnocephalan fauna in the Neotropics. The analysis of all available information (bibliographic and new original data) allowed us to establish a list of 38 symbiotic temnocephalan taxa in invertebrates and vertebrates in the Neotropical region, which are contained in four groups of hosts. Malacostraca (Decapoda): 4 taxa of Didymorchis associated with 3 taxa of crabs, 17 species of Temnocephala associated with 32 taxa of decapod crustaceans and only one species of Dietceratocephala associated with one species of decapod crustacean; Gastropoda (Caenogastropoda): 5 species of Temnocephala associated with 5 taxa of freshwater snail hosts; Insecta: 1, 2, 2 and 1 taxa of Temnocephala associated with 1, 5, 3 and 1 taxa hosts of Trichoptera, Hemiptera, Megaloptera and Plecoptera, respectively; Chelonia (Testudines): 4 taxa of Temnocephala associated with 7 species of freshwater turtle hosts.

The results of this study are presented in the Table 1 which shows the symbiont-host list, where temnocephalans are organized by taxonomic groups and ordered alphabetically by family name. Then species within each family are listed alphabetically followed by authority name and date. The next category is the host species in which the temnocephalids were found, followed by the locality, and the bibliographic reference from which the information was obtained, except for those records established in the present work. In the temnocephalan species found in more than one host species, the latter are listed alphabetically, and host...
Table 1. Freshwater symbiotic Temnocephalida list from Neotropics. AR = Argentina; BR = Brazil; CL = Chile; CO = Colombia; CR = Costa Rica; MX = Mexico; PY = Paraguay; PE = Peru; UY = Uruguay. NR = Coordinates not reported. *Coordinates not presented in the original work, but obtained for this study using Google Earth (https://earth.google.com/).

| Symbiotic species | Host | Locality | Geographical coordinates | Reference |
|-------------------|------|----------|--------------------------|-----------|
| Temnocephalidae Blanchard, 1849 | | | | |
| Family Didymorchiidae Breslau and Reisinger, 1933 | | | | |
| Didymorchis haswelli Mañé Garzon, 1960 | Parastacus saffordi | Aigua, Lavalleja, UY | 34°12'08"S; 54°46'16"W* | Mañé-Garzon (1960) |
| Didymorchis haswelli var. australis Dioni, 1972 | Parastacus sp. | Nahuel Huapi National Park, Rio Negro, AR | 41°02'35"S; 71°19'51.5"W* | Dambiorenea and Cannon (2001a) |
| Didymorchis sp. 1 | Aegla neaniquensis | Nahuel Huapi Lake, Bariloche, Rio Negro, AR | 41°07'54.3"S; 71°19'51.5"W | Dambiorenea and Cannon (2001a) |
| Didymorchis sp. 2 | Aegla neaniquensis | Nahuel Huapi Lake, Bariloche, Rio Negro, AR | 41°07'54.3"S; 71°19'51.5"W | Dambiorenea and Cannon (2001a) |
| Remarks. Dioni (1972) recorded Didymorchis haswelli var. australis for Southwest of Argentina. Dambiorenea and Cannon (2001a) recorded Didymorchis sp. 1 and Didymorchis sp. 2 for the same area. These species will be described elsewhere. |
| Family Diceratoccephalidae Joffe, Cannon and Schockaert, 1998 | | | | |
| Diceratoccephala boschmai Baer, 1953 | Cherax quadricarinatus | Piriápolis, Maldonado, UY | 34°58' S; 56°18'W | Volonterio (2009b) |
| Family Temnocephalidae Monticelli, 1899 | | | | |
| Aegla castro | Curitiba, BR | | 25°25'0"S; 49°15'0"W* | Pérez González (1949) |
| Aegla franca | Itatinga, São Paulo, BR | | 23°09'53"S; 48°37'4"W | Own findings |
| Aegla humahuaca | La Chacra, Antúgalá, Catamarca, AR | | 27°43'04"S; 55°54'15"W* | Dioni (1967c) |
| Aegla laevis | Cochuna River, Tucumán, AR | | 27°21'49"S; 65°50'28"W | Dioni (1967c) |
| Aegla platensis | Colondo Stream (Route 6 km 35), Canelones, UY | | 34°39' S; 56°04'W | Volonterio (2007b) |
| Aegla plasenitis | Martin Garcia Island, Rio de la Plata, AR | | 34°09' S; 58°15'W | Dambiorenea et al. (1997) |
| Aegla uruguayana | Route 8 km 238, Lavalleja, UY | | 33°36' S; 56°35'W | Volonterio (2007b) |
| Isla Paulino, Berisso, Rio de la Plata, Buenos Aires, AR | Isla Paulino, Berisso, Rio de la Plata, Buenos Aires, AR | | 34°49'41"S; 57°52'28"W | Dambiorenea et al. (1997) |
| Sangrador del Suro, Federación, Entre Ríos, AR | Sangrador del Suro, Federación, Entre Ríos, AR | | 31°00' S; 57°53'W | Dioni (1967b) |
| Aguas Blancas, Maldonado, UY | Aguas Blancas, Maldonado, UY | | 34°31'0"S; 55°27'0"W* | Dioni (1967b) |
| Aegla sp. | Isla Paulino, Berisso, Rio de la Plata, Buenos Aires, AR | | 34°49'41"S; 57°52'23"W | Own findings |
| Cebollati River, Lavalleja, UY | Cebollati River, Lavalleja, UY | | 33°9'21"S; 55°38'18"W* | Dioni (1967b) |
| Dom Pedro Stream, Rio Grande do Sul, BR | Dom Pedro Stream, Rio Grande do Sul, BR | | 29°21'51"S; 49°51'12"W* | Dioni (1967b) |
| Santa Lucia River, Montevideo, UY | Santa Lucia River, Montevideo, UY | | 34°12'30"S; 56°21'30" | Dioni (1967b) |
| Sauce Lagoon, Maldonado, UY | Sauce Lagoon, Maldonado, UY | | 34°49'31"S; 55°3'37"W* | Dioni (1967b) |
| Temnocephalidae asenos Monticelli, 1899 | | | | |
| Aegla sp. | Cerros do Jarau, Quaraí, Rio Grande do Sul, BR | | 30°11'23"S; 56°29'54"W* | Dioni (1967b) |
| Negro River, Paso de Los Toros, Tacuarembó, UY | Negro River, Paso de Los Toros, Tacuarembó, UY | | 32°49'5"S; 56°03'23"W* | Dioni (1967b) |
| Vila Jardim, Porto Alegre, Rio Grande do Sul, BR | Vila Jardim, Porto Alegre, Rio Grande do Sul, BR | | 30°15'21"S; 51°09'21"W* | Dioni (1967b) |
| Temnocephalidae brenesi Jennings, 1968 | | | | |
| Macrobranchium americanum | Barranca River (East), Punta Arenas, CR | | 9°57'3'2"N; 84°48'1.5"W* | Jennings (1968) |
| Viulla River and tributaries, Alajuela, CR | Viulla River and tributaries, Alajuela, CR | | 9°55'50"N; 84°15'59"W* | Jennings (1968) |
| Symbiotic species          | Host           | Locality                     | Geographical coordinates       | Reference                  |
|---------------------------|----------------|------------------------------|--------------------------------|---------------------------|
| Temnocephala brevicornis  | Monticelli, 1889 | Viamão, Rio Grande do Sul, BR | 30°04'56.64"S; 51°01'11.81"W | Ferreira Yuki et al. (1993) |
| Temnocephala caddisflyi   | Amato, Amato and Seixas, 2011 | Córrego das Pedras, Serra do Cipó National Park, Jaboticatubas, BR | 8°22'10"S; 43°35'53"W | Amato et al. (2011) |
| Aegla abaho                | Limay River, Neuquén, AR | 38°59'31"S; 68°03'51"W | Own findings                  | Damborenea (1992) |
| Aegla affinis              | Telsen Stream, Chubut, AR | 42°38'35.2"S; 66°52'18.0"W | Own findings                  | Dioni (1967c) |
| Aegla jaguyana             | Chico River, Jujuy, AR | 24°11'4"S; 65°17'4"W | Own findings                  | Dioni (1967c) |
| Aegla laurensis            | Talca River, CL | 35°25'53.51"S; 71°38'18.57"W | Own findings                  | Dioni (1967c) |
| Aegla neaqoenuisis         | Cuvonco Stream, Neuquén, AR | 38°47.603'S; 70°11.402'W | Own findings                  | Damborenea (1992) |
| Aegla rosilimayana         | Nahuel Huapi Lake, Río Negro, AR | 41°02'35"S; 71°20'56"W | Own findings                  | Dioni (1967c) |
| Temnocephala chilensis     | (Moquin-Tandon, 1846) | El Carrizal, Luján de Cuyo, Mendoza, AR | 33°20'03"S; 68°43'44"W | Dioni (1967c) |
| Aegla scamosa              | Limay River, Neuquén, AR | 38°59'31"S; 68°03'51"W | Own findings                  | Damborenea (1992) |
| Mendoza River, Potrerillos, Mendoza, AR | 38°04'04.7"S; 70°36'42"W | Own findings                  | Dioni (1967c) |
| Nirco Stream, Neuquén, AR | 37°29'08.5"S; 70°45'20"W | Damborenea (1992) |
| Posadas Misiones, AR       | 27°22'10"S; 75°54'24"W | Dioni (1967c) (+) |
| Valparaiso, Santiago, CL   | 33°30'45"S; 70°40'35"W | Dioni (1967c) |
| Zapala, Neuquén, AR        | 38°54'02.3"S; 70°40'15"W | Own findings                  | Dioni (1967c) |
| Chos-Malal, Neuquén, AR    | 37°22'41.5"S; 71°01'15.5"W | Own findings                  | Dioni (1967c) |
| Aegla sp.                  | Diamante River, San Rafael, Mendoza, AR | 34°36'49.7"S; 68°36'04.1"W | Own findings                  | Dioni (1967c) |
| Grande River, Route 40, Mendoza, AR | 35°5.525"S; 69°48.468"W | Own findings                  | Dioni (1967c) |
| Lacar Lake, Neuquén, AR    | 40°10'10"S; 71°30'32.2"W | Own findings                  | Dioni (1967c) |

Remarks. Caballero y Caballero and Cerecedo (1951) mentioned Temnocephala brevicornis being a comensal of Pseudothelphusa sp. (Crustacea) from El Salvador and Venezuela; however, this association has to be considered with caution because of the probable misidentification of the specimens.
| Symbiotic species | Host | Locality | Geographical coordinates | Reference |
|-------------------|------|----------|--------------------------|-----------|
| *Parastacus* sp. | Meliquina River, flows into Meliquina Lake, Neuquén, AR | 40°23'00.7"S; 71°15'9.16"W | Own findings |
| | Nahuel Huapi Lake, Río Negro, AR | 41°02'25.6"S; 71°21'06.7"W | Dioni (1967a), Dioni (1972) |
| | Near Santiago city, CL | 33°20'08"S; 70°39'31"W | Moquin-Tandon (1846) |
| | Parana River, Rosario, Santa Fe, AR | 32°57'03"S; 60°37'07"W | Dioni (1967c) (+) |
| | Uspallata, Mendoza, AR | 32°59'14"S; 69°22'20"W | Dioni (1967c) |
| | Nahuel Huapi Lake, Río Negro, AR | 41°02'25.6"S; 71°21'06.7"W | Dioni (1992) |
| | Tumbos, Tachahuanos, CL | NR | Wickel (1905) |
| *Samastacus* sp. | Limay River, Rincón de Creide, Neuquén, AR | 40°47'14.5"S; 71°07'08.4"W | Own findings |

**Remarks.** Taking into account the known distribution of *T. chilensis*, the citations marked with (+) are considered doubtful.
| Symbiotic species | Host | Locality | Geographical coordinates | Reference |
|------------------|------|----------|--------------------------|-----------|
| Temporal body water, Route 14, Entre Ríos, AR | 33°21'11"S, 58°48'41"W | Own findings |
| Bird Observatory, Rocha, UY | 33°54'S, 53°40'W | Volontero (2007a) |
| Bridge over Andreeoni channel, Rocha, UY | 33°54'S, 53°40'W | Volontero (2007a) |
| Bridge over athena, Rocha, UY | 33°51'S, 53°55'W | Volontero (2007a) |
| Bridge over the Averías Stream, Rocha, UY | 33°53'S, 53°51'W | Volontero (2007a) |
| Cacheo River, Barragem do Centro, Barra do Ouro, Maquiné, Rio Grande do Sul, BR | 29°34'15"S, 50°16'51"W | Seixas et al. (2010a) |
| Cañada 1, Soriano, UY | 33°12'S, 57°27'W | Volontero (2007a) |
| Cañada del Cerbo, Colonia, UY | 34°40'S, 56°03'W | Volontero (2007a) |
| Channels around rice, Arrozeira, Eldorado do Sul, Rio Grande do Sul, BR | 30°13'36"S, 51°22'42"W | Seixas et al. (2010a) |
| Chaculé Stream, Buenos Aires, AR | 36°48'53"S, 59°08'05"W | Martín et al. (2005) |
| Chascó Stream, near Los Chilenos Lake, Buenos Aires, AR | 38°09'59"S, 62°36'02"W | Martín et al. (2005) |
| Colonia city, near the wall, Colonia, UY | 34°28'S, 57°50'W | Volontero (2007a) |
| Delta Flora Stream, Buenos Aires, AR | 34°50'57"S, 57°52'20"W | Damborenea (1992) |
| El Fuerte reservoir at Tandil city, Buenos Aires, AR | 37°25'41"S, 59°07'45"W | Martín et al. (2006) |
| El Pescado stream, near the Río de la Plata estuary, Buenos Aires, AR | 34°57'S, 57°46'W | Damborenea et al. (2006) |
| Kakel Huinca reservoir, Route 2, Buenos Aires, AR | 36°47'36"S, 57°46'29"W | Martín et al. (2005) |
| Fazenda Sossego, Santa Vitória do Palmar, Rio Grande do Sul, BR | 33°10'13"S, 53°26'28"W | Seixas et al. (2010a) |
| Indio Muerta Stream, Rocha, UY | 33°46'S, 54°05'W | Volontero (2007a) |
| Juncal Stream, Flores, UY | 33°29'S, 56°58'W | Volontero (2007a) |
| La Lancha Stream, Soriano, UY | 33°37'S, 57°58'W | Volontero (2007a) |
| Langueyu Stream, Buenos Aires, AR | 36°47'24"S, 58°26'42"W | Martín et al. (2005) |
| Los Chilenos lake, Fishing Club Tornquist, Buenos Aires, AR | 38°02'37"S, 62°31'01"W | Martín et al. (2005) |
| Los Padres lake, Buenos Aires, AR | 37°56'06"S, 57°43'54"W | Martín et al. (2005) |
| Los Talas, Berisso, Buenos Aires, AR | 34°55'00"S, 57°49'57"W | Damborenea (1992) |
| Los Talas lagoon, near the Río de la Plata estuary, Buenos Aires, AR | 34°57'S, 57°46'W | Damborenea et al. (2006) |
| Martín García Island, Río de la Plata, AR | 34°10'45"S, 58°15'08"W | Own findings |
| Miguelse Stream, Punta Lara, Ensenada, Buenos Aires, AR | 34°40'00"S, 57°59'22"W | Damborenea (1992) |
| Paraná Medio, AR | 30°02'23"S, 51°25'49"W | Di Persia and Radici de Cura (1973) |
| Paso de la Cruz, tributary of Bequelló Stream, Soriano, UY | 33°13'S, 57°55'W | Volontero (2007a) |
| Paso de Las Piedras reservoir, Buenos Aires, AR | 38°24'32"S, 61°44'37"W | Martín et al. (2005) |
| Ponta de Cereola, Barra do Ribeiro, Rio Grande do Sul, BR | 30°15'51"S, 51°16'49"W | Seixas et al. (2010a) |
| Praia Florida, Guaiba, Rio Grande do Sul, BR | 30°15'54"S, 51°12'25"W | Seixas et al. (2010a) |
| Punta Indio, Buenos Aires, AR | 35°19'S, 57°13'W | Damborenea (1992) |
| Jacuí River, at Iha da Piratá, Porto Alegre, Rio Grande do Sul, BR | 30°22'23"S, 51°25'40"W | Seixas et al. (2010a) |
| Route 4 near Los Charras, Entre Ríos, AR | 31°21'11"S, 58°6'16"W | Own findings |
| San Pedro Stream, Colonia, UY | 34°18'S, 57°52'W | Volontero (2007a) |
| Sarandi Chico Stream, Flores, UY | 33°37'S, 56°51'W | Volontero (2007a) |
| Sarandi del Consejo Stream, Rocha, UY | 34°15'S, 53°59'W | Volontero (2007a) |
| Symbiotic species | Host | Locality | Geographical coordinates | Reference |
|-------------------|------|----------|--------------------------|-----------|
| **Pomacea lineata** | Sauce Stream, Canelones, UY | 34°38'S; 56°3'W | Volonterio (2007a) |
| | Sava Chube, Guaiaba Lake, Porto Alegre, Rio Grande do Sul, BR | 30°06'09"S; 51°15'57.5"W | Seixas et al. (2010a) |
| | Sauce Stream, La Plata, Buenos Aires, AR | 34°55'2.1"S; 57°54'31.58"W | Own findings |
| | Stream 1, Rocha, UY | 33°26'S; 53°52"W | Volonterio (2007a) |
| | Stream 2, Rocha, UY | 33°24'S; 53°51"W | Volonterio (2007a) |
| | Stream near Route 11, Magdalena, AR | 34°57'51.53"S; 57°40'09.1"W | Own findings |
| | Zapata Stream, Magdalena, AR | 34°59'18"S; 57°43'00"W* | Damborenea (1992) |
| **Pomella megalotoma** | Gaiizardo, Mato Grosso do Sul, BR | 20°51'S; 56°45"W* | Pereira and Cuocolo (1941) |
| | Salobra, Mato Grosso do Sul, BR | 20°10'S; 56°31"W* | Pereira and Cuocolo (1941) |
| **Pomacea sp.** | Martin Garcia Island, Rio de la Plata, AR | 34°10'45"S; 58°15'08"W | Damborenea et al. (1997) |
| **Trichodactylus sp.** | Jaquiá, São Paulo, BR | 24°41'22"S, 47°38'57"W | Pereira and Cuocolo (1941) |
| **Trichodactylus longivaginatus** | Peixe-Boi River, Peixe-Boi, Pará, BR | 1°07'17"S; 47°18'48"W | Seixas et al. (2011) |
| **Sylvioarcus pictus** | Amapá River, Cachoeira Grande, BR | 2°09'S; 50°55"W* | Damborenea (1994) |
| **Telphusa sp.** | São Paulo, UY | 34°15'S; 56°45"W* | Dioni (1978) |
| **Trichodactylus flavialis** | Rio das Trutas, head waters of Rio das Antas, São José dos Ausentes, Rio Grande do Sul, BR | 28°47'00"S; 57°54'53"W | Damborenea (2005) |
| **Trichodactylus parolus** | Arrozeira Stream, Maquiné, Rio Grande do Sul, BR | 29°32'29"S; 50°13'49"W | Amato et al. (2005) |
| | Boticario Stream, Route 14, km 3, Soriano, UY | 33°15'S; 57°55"W | Volonterio (2007a) |
| | Rio do Conte Stream, Guaiaba, BR | 30°09'S; 51°22'42"W | Amato et al. (2005) |
| **Temnocephala longivaginata** | Colorado Stream, Canelones, UY | 34°41' S; 56°04'W | Volonterio (2007b) |
| | Molles Stream, Lavalleja, UY | 33°36'S; 54°35"W | Volonterio (2007b) |
| **Procambarus digueti** | Caneuara Lake, Micoaan, MX | 19°54'12"N; 102°12'37"W | Lamothe-Argumedo (1968), Own findings |
| | Chapada Lake, Jalicó, MX | 20°15'N; 103°00'W | Lamothe-Argumedo (1980) |
| **Pseudothelphusa jouyi** | Caneuara Lake, Micoaan, MX | 19°54'12"N; 102°12'37"W | Lamothe-Argumedo (1968), Own findings |

Remarks. Dioni (1972) mentioned *T. mexicana* on *Aegla* sp. and *Parastacus* sp. from Nahuel Huapi Lake, Rio Negro, AR 41°02'35"S; 71°28'06"W.
| Symbiotic species                  | Host               | Locality                          | Geographical coordinates | Reference               |
|-----------------------------------|--------------------|-----------------------------------|--------------------------|-------------------------|
| **Temnocephala microdactyla**      | Dilocarcinus pagei | Guadalupe Lagoon, Santa Fe, AR    | 31°39'S; 60°42'W         | Domí (1967d)            |
| Monticelli, 1903                  |                    | Mato Grosso, BR                    | NR                       | Monticelli (1903)       |
| Monticelli, 1903                  |                    | Piedras Blancas, Guadalupe Lagoon, Santa Fe, AR | 31°39'S; 60°42'W | Damborenea (1992) |
| **Syntocrinus australis**         | Piedras Blancas    | Guadalupe Lagoon, Santa Fe, AR    | 31°39'S; 60°42'W         | Damborenea (1992)       |
| **Syntocrinus pictus**            | Diodocarpus, Mato Grosso, BR | 20°32'9"S; 56°44'54"W* | Pereira and Cuocolo (1941) |                        |
| **Temnocephala minutissimus**      | Cryptocrinus granulosus | Forqueta Stream, Barra do Ouro, Maqui, Rio Grande do Sul, BR | 29°32'19"S; 50°14'47"W | Amato et al. (2007)     |
| Amato et al., 2007                |                    | Girapu Stream, Barra do Ouro, Maqui, Rio Grande do Sul, BR | 29°33'23"S; 50°14'38"W | Amato et al. (2007)     |
| **Temnocephala peronii**           | Hydromedusa tectifera | Barra de Carrasco, Canelones, UY | 34°52'S; 56°02'W       | Volontorio (2010)       |
| Volontorio, 2010                  |                    | Colorado Stream, Canelones, UY    | 34°38'S; 56°03'W        | Volontorio (2010)       |
| **Temnocephala peruensis**         | Hypobocera henrici | Namparicem and Kumpiunse, Marindon River, Imaza, Bagua, PI | 4°59'34"S; 78°23'58"W* | Ibáñez Herera and Jarab (2003) |
| Ibáñez Herera and Jarab, 2003     |                    | Crowdus Stream, Ecological Station, Belen, São Paulo, BR | 20°56'58"S; 48°25'43"W | Amato et al. (2010)     |
| **Temnocephala pignalberiae**      | Dilocarcinus pagei | Guadalupe Lake, Piedras Blancas, Santa Fe, AR | 31°39'S; 60°42'W* | Damborenea (1992) |
| Pignalberi, 1967                  |                    | Los Espejos Lagoon, Santa Fe, AR  | NR                      | Domí (1967d)            |
| Domí (1967d)                      |                    | Madejón Don Felipe, Santa Fe, AR  | NR                      | Domí (1967d)            |
| Domí (1967d)                      |                    | Piedras Blancas, Guadalupe Lagoon, Santa Fe, AR | 31°39'S; 60°42'W* | Damborenea (1992) |
| **Trichodactylus panoplus**       | Sylviocarcinus australis | Guadalupe Lake, Santa Fe, AR      | 31°33'46"S; 60°32'0"W* | Domí (1967d)            |
| Damborenea (1992)                 |                    | Madejón Don Felipe, Santa Fe, AR  | 31°40'11"S; 60°44'35"W* | Domí (1967d)            |
| **Trichodactylus sp**             |                    | Piedras Blancas, Guadalupe Lagoon, Santa Fe, AR | 31°39'S; 60°42'W* | Damborenea (1992) |
| Volontorio, 2007a                 |                    | Boticario Stream (Route 14, km 3), Soriano, UY | 33°13'S; 57°55'W      | Volontorio (2007a)      |
| **Temnocephala rochensis**         |                    | Madejón Don Felipe, Santa Fe, AR  | NR                      | Domí (1967d)            |
| Ponce de León, 1979               |                    | Madejón Don Felipe, Santa Fe, AR  | NR                      | Domí (1967d)            |
| Domí (1979)                       |                    | Madejón Don Felipe, Santa Fe, AR  | NR                      | Domí (1979)             |
| Bird Observatory (Route 14, km 487), Rocha, UY | 33°54'S; 55°40'W | Seias et al. (2010b)              |
| Cebollati River (Route 15, km 195), UY | 33°14'S; 55°47'W | Volontorio (2007a)               |
| Channel on the road to São Lorenço do Sul, BR | 31°20'14"S; 52°03'10"W | Seias et al. (2010b) |
| Juncaial Stream, Fazenda da Invernada, BR | 32°27'08"S; 55°15'44.6"W | Seias et al. (2010b) |
| Fazenda Sossego, 30 km west of Santa Vitoria do Palmar, BR | 33°16'13"S; 53°26'28"W | Seias et al. (2010b) |
| Negro Lake, Rocha, UY              | 34°01'S; 53°38'W    | Ponce de León (1979)              |                         |                         |
| **Pomacea canaliculata**           |                    | Pond at Fazenda da Invernada, BR  | 32°27'41"S; 53°15'14"W | Seias et al. (2010b)     |
| Ponce de León, 1979               |                    | Route 15, km 202, Pond, UY        | 33°13'S; 53°48'W        | Volontorio (2007a)      |
| Seias et al. (2010b)              |                    | Route 14, km 446, India Muerta stream, UY | 33°46'S; 54°05'W | Volontorio (2007a)      |
| Seias et al. (2010b)              |                    | Route 14, km 469, Bridge on the Averias Stream, UY | 33°53'S; 53°51'W | Volontorio (2007a)      |
| Seias et al. (2010b)              |                    | Sarandi del Correjo Stream (Route 9 km 251), UY | 34°15'S; 53°59'W | Volontorio (2007a)      |
| Seias et al. (2010b)              |                    | Side way ditch on the road to Fazenda São João 2, Jaguará, BR | 32°35'29.7"S; 53°14'04.5"W | Seias et al. (2010b)     |
| Seias et al. (2010b)              |                    | Side way pond, Interstate Road 116 (km 12), BR | 32°28'21"S; 53°17'20"W | Seias et al. (2010b)     |
| Seias et al. (2010b)              |                    | Route 15, km 195, Stream, Rocha, UY | 33°26'S; 53°52'W | Volontorio (2007a)      |
| Symbiotic species | Host | Locality | Geographical coordinates | Reference |
|-------------------|------|----------|--------------------------|-----------|
| *Temnocephala santafesina* Dioni, 1967 | *Dilocarcinus pagei* | Los Espejos Lagoon, Santa Fe, AR | NR | Dioni (1967d) |
| | | Madejón Don Felipe, Santa Fe, AR | NR | Dioni (1967d) |
| | | Piedras Blancas, Guadalapue Lagoon, Santa Fe, AR | 31°39'S; 60°42'2W* | Damborenea (1992) |
| *Temnocephala* sp. | Corydalus sp. | Cerrado formation municipality, BR | 19°57'16"S; 40°52'25"W | Trivinho-Strixino et al. (2012) |
| | Proshcladiodes sp. | Cerrado formation municipality, BR | 19°57'16"S; 40°52'25"W | Trivinho-Strixino et al. (2012) |
| *Temnocephala* sp. | Kempyna reticulata | Rivers of Estação Botânica de Santa Lúcia, Santa Teresa, Espirito Santo, BR | 19°57'10"S; 40°32'25"W* | Aveldino-Capistrano et al. (2013) |
| *Temnocephala* sp. | *Hydromedusa tectifera* | Palma, Encruzilhada do Sul, BR | 30°34'-30°43'S; 52°30'-52°51'W* | Soares et al. (2007) |
| *Temnocephala talicei* Dioni, 1967 | Aegla platensis | Anchorena Stream, Martinez, Buenos Aires, AR | 34°29'20"S; 58°28'35"W* | Damborenea (1992) |
| | | Lavalleja (Route 8, km 238), UY | 33°36'S; 54°35'W | Volonterio (2007a) |
| | | Martin García Island, Rio de la Plata, Buenos Aires, AR | 34°10'45"S; 58°15'08"W* | Damborenea et al. (1997) |
| | | Villa Rica, PY | 25°46'50"S; 56°29'55"W* | Dioni (1968) |
| *Temnocephala* sp. | Aegla prado | El Prado Botanic Garden, Montevideo, UY | 34°49"S; 56°12"W | Volonterio (2009b) |
| | | Martin García Island, Rio de la Plata, Buenos Aires, AR | 34°10'45"S; 58°15'08"W* | Damborenea et al. (1997) |
| | | Moller Stream (Route 8, km 238), Lavalleja, UY | 33°36'S; 56°35'W | Volonterio (2006b) |
| | | Olivos, Buenos Aires, AR | 33°30'S; 63°10"W* | Damborenea (1992) |
| | | Paulino Island, Rio de la Plata, Buenos Aires, AR | 34°50'08"S; 57°52'44"W | Damborenea (1992) |
| | | Lunearejo Stream, Rivera, UY | 31°15'00"S; 55°50'00"W* | Dioni (1967b) |
| | | De Doll Stream, Route 11, Entre Ríos, AR | 32°18'37"S; 60°25'54"W | Own findings |
| | | Tres Islas, Cerro Largo, UY | 32°34'40"S; 53°38'00"W* | Dioni (1967b) |
| *Temnocephala tupeziiformis* Amato, Amato and Sebeca, 2006 | Aegla uruguayana | Lunarejo Stream, Rivera, UY | 31°15'00"S; 55°50'00"W* | Dioni (1967b) |
| | | De Doll Stream, Route 11, Entre Ríos, AR | 32°18'37"S; 60°25'54"W | Own findings |
| | | Tres Islas, Cerro Largo, UY | 32°34'40"S; 53°38'00"W* | Dioni (1967b) |
| *Temnocephala* sp. | Aegla sp. | Agua Parada Stream, Maquiné River Basin, Maquiné, Rio Grande do Sul, BR | 29°66'20"S; 50°21'15"W | Amato et al. (2006) |
| | | Carvão Stream, Maquiné River Basin, Maquiné, Rio Grande do Sul, BR | 29°32'29"S; 50°13'49"W | Amato et al. (2006) |
| | | Forqueta Stream, Maquiné River Basin, Maquiné, Rio Grande do Sul, BR | 29°32'17"S; 50°14'44"W | Amato et al. (2006) |
| | | Vale das Trutas head waters of Rio das Antas, Taquari-Antas basin, São Jose dos Ausentes, Rio Grande do Sul, BR | 28°47'00"S; 49°50'53"W | Amato et al. (2006) |
| *Temnocephala travassosfilhoi* Pereira and Cioccola, 1941 | Trichodactylus flaviosialis | San Bernardo, São Paulo, BR | 22°00'00"S; 49°10'00"W | Pereira and Cioccola (1941) |
species for which more than one locality was recorded, are listed together. Furthermore, a host-symbiont list (See Appendix 1) is taxonomically and alphabetically organized.

The decapods are the most species-rich host group with temnocephalans (27), followed by the insects (5 taxa) and snails (5 species). Of the 38 taxa of Temnocephalidae listed in this work, all appear to be specific to particular host groups, while at least only one species of the family Diceratocephalidae have successfully associated with hosts after their anthropogenic introduction, i.e. Diceratocephala boschmai. The most widely distributed species are T. axenos, T. chilensis and T. iheringi, which are present in 9 and 10 crab host species and 5 snail host species, along 20, 25 and 49 localities, respectively.

In terms of hosts, Hydromedusa tectifera (a turtle) is the host with the highest temnocephalan species richness with 4 taxa, followed by Aegla neuquensis, A. platensis, Dilocarcinus pagei (decapod crabs) and Pomacea canaliculata (snail), all with 3 species; meanwhile, 49 host taxa show only one record of temnocephalid taxa for one locality.

The species accumulation curve for Neotropic temnocephalans plotted against the total number of species (Figure 1) shows irregular growth over 15 decades of studies in Temnocephalida (each decade divided into two periods of five years). This graph shows that the asymptote has not been reached yet and, if the systematic studies of the group are continued, a significant increase in the number of species in the Neotropical region can be expected. This graphic also reflects two important periods of research. The first shows the initial prospecting for temnocephalid species in the Neotropical region, between 1890 and the beginnings of the 20th century. The second period, beginning around 1970, shows an increase in the research on temnocephalans from different host species, with some stationary periods.

Discussion

The genus Temnocephala is an endemic component of the Neotropical region (Damborenea and Cannon 2001a). At the moment, it includes 35 taxa, of which 14 (40%) are considered microendemic (only one record for locality) (Table 1). In total, 57 host taxa are associated with one or more temnocephalan taxa, which belong to seven orders and 14 families within four classes. It is worth pointing out that each major group of hosts is characterized by a particular assemblage of temnocephalan species, with host specificity at family level. For example, 17 taxa of Temnocephala are associated with three families of freshwater crab hosts (Aeglidae, Pseudothelphusidae and Trichodactylidae), while five Temnocephala species are associated with 8 taxa of freshwater shrimps included in three families (Cambariade, Palaemonidae and Parastaciade). Information about the natural history of this endemic genus is key to understanding the role of different factors that shaped its diversification patterns across several hydrological basins in the Neotropics and the possible implications of codivergence with host groups (see below) (e.g. Thompson 2005, Martínez-Aquino et al. 2014b).

In this inventory, only Dicerotocephala boschmai was detected as an introduced species because of translocation together with their crustacean hosts, the invasive redclaw Cherax quadricarinatus in Uruguay (Volonterio 2009a), due to human activities such as aquaculture and breeding of ornamental species (Lodge et al. 2012, Saoud and Ghanawi 2013). According to several authors, D. boschmai causes a detrimental economic impact because of an aesthetic effect of the eggs on the body surface of the C. quadricarinatus (Herbert 1987, Volonterio 2009a). However, it is more important to mention the detrimental biological and ecological impact of these introduced species.
To date, the values of ecological infection parameters (e.g. prevalence and abundance; see Bush et al. 1997) are unknown not only locally but globally. These parameters are required to measure the effect of this symbiotic association – both introduced species, *C. quadricarinatus* and *D. boschmai* – to detect the extent of the spread of *D. boschmai* to other crustacean taxa, especially endemic crabs in their natural ecosystems (Jones and Lester 1993, Chivavaya 2013, du Preez and Smit 2013). Furthermore, the introduced populations of *D. boschmai* in natural hydrological systems in Uruguay represent a serious problem of displacement to the endemic populations of Neotropical *Temnocephala* species because of interspecific competition between symbiotic organisms (Gelder 1999, Sicard et al. 2006, Witte et al. 2008, Tsuchida et al. 2011, Ohtaka et al. 2012). In this context, the data generated in this checklist can be used to support conservation strategies for freshwater biodiversity (Cardoso et al. 2011a, b, Stendera et al. 2012, Collen et al. 2013).

One hundred sixty eight years have passed since the first description and record of a temnocephalan from the Neotropics (Damborenea and Cannon 2001a), and, currently, ±236 records of temnocephalans have been published. However, considering the number of described species and the time passed, it can be stated that most of the diversity of *Temnocephala* remains yet to be described. There is also a significant number of potential hosts that have not been studied with regards to symbiotic temnocephalans. On the other hand, Schoackaert et al. (2008) mentioned that the few species recorded in South America were mostly recorded up to about 1970. Based on the species accumulation curve (Figure 1), this study shows clearly the increase in knowledge about the biodiversity of the temnocephalan fauna in recent times, but based on all of the information compiled for Neotropical temnocephalans, we show the necessity to continue inventory work. The Neotropic temnocephalan fauna contains 31% of Temnocephalida taxa described at the moment, representing 37 taxa allocated to two genera.

Figure 2. Map of Latin America indicating the countries where freshwater invertebrate and vertebrate hosts, of four classes, have been studied for neotropic symbiotic temnocephalans. Countries with major to 10 species records in dark grey and minor to 2 in low grey. The numbers in circles indicate the total temnocephalan taxa recorded. Map produced by http://www.naturalearthdata.com/, and modified in DIVA-GIS 7.5 (Hijmans et al. 2012) (freely available through www.diva-gis.org).
This checklist presents data on almost all the extant species of temnocephalans along their distributional ranges in 11 Neotropical countries, which represents 35% of the total political territories (i.e. countries) in the Neotropics (Figure 2). Argentina, Brazil and Uruguay are the countries with the most records of temnocephalans and with the most endemic species of Temnocephala, which are represented by 6, 9 and 4 species, respectively, while Colombia, Costa Rica, Mexico and Peru hold 1, 2, 1 and 1 endemic species, respectively. The relatively high number of records in Argentina, Brazil and Uruguay can imply that in these countries there are more research groups working with turbellarians compared to other Neotropical countries (e.g. Damborenea and Brusa 2008, Volonterio 2010, Amato et al. 2011). Therefore, the values of endemism for these particular countries are subjective – a function of the research effort – and it is probable that the endemism may be increased/decreased in future studies from different Neotropical countries. With regards to its exclusively Neotropical distribution, morphological evidence (mosaic syncytial plates) (e.g. Cannon and Joffé 2001, Damborena and Cannon 2001b), plus the recorded host specificities shown in this study (Appendix 1), allow for the inference that the biological radiation of Temnocephala may be the result of a complex combination of ancestral allopatric speciation processes (as a result of the separation of South America and Australia), plus the diversification of their host groups (e.g. Parastacidae) in South (and subsequent radiation in Central) America. For example, the species of Temnocephala associated with mollusks appear to be a morphologically homogeneous group with a phylogenetic structure (Volonterio 2007a, Damborena and Brusa 2008). On the other hand, the almost exclusive distribution in the Southern Hemisphere of the family to which Temnocephala belongs (Temnocephalidae) is noteworthy and alludes to a Gondwanian origin (Gelder 1999, Cannon and Joffé 2001). However, a reliable molecular clock of the Temnocephalida is required to support or reject this hypothesis. Future studies combining research programs in integrative taxonomy (Schlick-Steiner et al. 2010, Ceccarelli et al. 2012, Fujita et al. 2012) with approaches of historical association (e.g. genes, organism and areas; see Page and Charleston 1998) will decipher the evolutionary history of Temnocephala.

At least 60 papers have been published dealing with the records of Neotropical symbiotic temnocephalans; however, the scarcity of studies in many countries is clear, and needs to be rectified. For example, some countries comprising complex geographic areas (i.e. Mexican Transition Zone, South American Transition Zone) only have one record of these turbellarians, and the diversity of the four major host groups is also unknown (Martínez-Aquino et al. 2014a). Therefore, we contend that future survey work should be strategic, aimed at enhancing the biodiversity inventory, combining identification of the host spectrum with choice of appropriate drainages based on biogeographic, faunistic, and hydrologic data and on lessons from other freshwater symbiotic Platyhelminthes (e.g. Pérez-Ponce de León and Choudhury 2010, Martínez-Aquino et al. 2014c).

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Supplementary material

Appendix 1. Host-symbiont temnocephalans list from Neotropics
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Data type: Microsoft Excel file (xls)
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