
Research Article

Historical biogeography of Temnocephalida (Platyhelminthes, Rhabdocoela): testing the Gondwanan hypothesis

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Temnocephalida, a group of small epibiotic worms strictly associated with freshwater hosts, includes 179 taxa in 23 genera, classified in two major groups: Scutarielloidea, distributed in the Palearctic region, and Temnocephaloidea distributed mainly in the Australian and Neotropical regions. Based on a large-scale spatio-temporal dimension, a biogeographic hypothesis on a Gondwanan scenario was tested. The objective of this study was to describe the geographic distribution patterns of Temnocephalida in a primary biogeographic homology context. A dataset of 793 temnocephalan records, distributed in 45 hydrological basins, and assigned to different hierarchical taxonomic levels was used to construct five presence/absence matrices. We analysed the matrices using Parsimony Analysis of Endemism (PAE) and Cladistic Analysis of Distributions and Endemism (CADE). Furthermore, we constructed generalized tracks based on area clades with phylogenetic support, i.e., two or more synapomorphies. Six generalized tracks were revealed: a general clade for Eurasia, plus a complex of four hybrid zones with monophyletic relationships included in a major clade with Gondwanan affinities. The results represent the first study using biogeographic analysis to disentangle the distributional patterns of temnocephalids around the world. Based on the integration of the results obtained by biogeographic pattern-based methods, we infer that the fragmentation of Gondwana affected the diversification patterns and distribution of Temnocephalida.

Key words: CADE, diversity, endemism, freshwater river basin, PAE, Pangea, symbionts, tracks analysis

Introduction

Around the world, biogeographic patterns of flora and fauna were constructed, broken down and reconstructed in distinct occasions from the complete break-up of the supercontinent Gondwana (160–30 million years ago) to the present (Sanmartín, 2012). These patterns are the result of multiple biogeographic events (e.g., extinction, dispersal, vicariance, duplication) that occurred since the major separation between Laurasia and Gondwana, and that finally resulted in the separation of North America and Eurasia (Laurasia), and Africa, Antarctica, Australia, India, Madagascar, New Zealand and South America (Gondwana) (Sanmartín & Ronquist, 2004). Subsequently, the diversification of the biota occurred through different mechanisms. For example, in the case of animals

from the northern hemisphere (Laurasia), dispersal mediated diversification patterns are more common (Chen, Lavoué, Beheregaray, & Mayden, 2014; Opatova & Arnedo, 2014; Sanmartín, Enghoff, & Ronquist, 2001). In contrast, the southern hemisphere (Gondwana) is characterized by specific hierarchical distribution patterns between and among animals and plants (e.g., Cody, Richardson, Rull, Ellis, & Pennington, 2010; Hoorn et al., 2011; Sanmartín & Ronquist, 2004).

Freshwater organisms represent ideal biological models for testing Gondwanan distribution patterns because they are distributed in restricted geographic areas (i.e., water bodies) and most of the time do not naturally disperse over land, preventing exchange between hydrological systems (e.g., Campanella et al., 2015; Imoto et al., 2013; Sun, He, & Glenny, 2014). The freshwater symbiotic fauna is interesting and complex because it is possible to test biogeographic hypotheses that include host and symbiont patterns plus the evolution of geographic range of

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their environment (e.g., hydrological systems) (Badets *et al.*, 2011; Martínez-Aquino, Brusa, & Damborenea, 2014a; Martínez-Aquino, Ceccarelli, & Pérez-Ponce de León, 2013). However, the number of studies which infer evolutionary-biogeographic patterns influenced by the Gondwanan breakup using freshwater symbiotic organisms, is limited (Badets *et al.*, 2011; Boeger, Kritsky, & Pie, 2003; Gelder, 1999; Mayén-Estrada & Aguilar-Aguilar, 2012; Pariselle *et al.*, 2011; Verneau *et al.*, 2002).

Temnocephalida represent a plausible group of model organisms to study the diversification in freshwater systems since the supercontinent Pangaea and during and after the Gondwanan-Laurasian fragmentation period (Cannon & Joffe, 2001; Martínez-Aquino, Brusa, & Damborenea, 2014b). Temnocephalida is a group of small epibiotic worms strictly associated with freshwater hosts; they are found mainly on crustaceans, but they also occur on molluscs, insects and turtles (Damborenea & Cannon, 2001; Joffe, Cannon, & Schockaert, 1998; Martínez-Aquino *et al.*, 2014a; Sewell, 2013). Although the biogeography of Temnocephalida has been poorly studied, Cannon and Joffe (2001) described a clear geographic structure with two well-differentiated groups (superfamilies). The northern group (Scutarielloidea), extends across the southern margin of the Eurasiatic continent with the Scutariellinae to the west, from the Balkans to India, and the Caridinicolinae to the east, from Sri Lanka to Japan. The southern group (Temnocephaloidea) is much more diverse and has a Gondwanan distribution. Its members occur in Australia, Tasmania, New Guinea, New Zealand, Madagascar, the Neotropics and also India, Vietnam and China (Cannon & Joffe, 2001). Unexpectedly neither temnocephalids nor their hosts are found in Africa (Fig. 1). Presumably, Temnocephalida began to diversify when Gondwana started to break up; around 100 million years ago India separated and started moving towards Asia, at which point the divergence of the two superfamilies Scutarielloidea and Temnocephaloidea began (Cannon & Joffe, 2001). However, until now, the hypotheses that support the Gondwanan affinities of Temnocephalida have not been tested with biogeographic methods.

Phylogenies used in historical biogeography provide strong support to detect and test the patterns, process and mechanism of the geographic distribution of the biota on earth (Kidd, 2010; Ronquist & Sanmartín, 2011; Wen, Ree, Ickert-Bond, Nie, & Funk, 2013). Particularly, event-based methods and parametric biogeography incorporate phylogenetic information into their approaches (Buerki *et al.*, 2011; Ree & Smith, 2008; Sanmartín, 2012). Unfortunately, phylogenetic hypotheses do not exist for all taxonomic groups. In these cases, based on geographic information (i.e., taxonomic records), it is possible to use pattern-based methods for inferring biogeographic patterns such as primary biogeographic homology, where hypotheses of common biotic histories

are based on distributional congruence (Morrone, 2015b). Undoubtedly, after phylogenetic information, taxonomic records are the most direct empirical evidence of species distributions that support biogeographic and macroecological patterns inferred from evolutionary studies (Besnard *et al.*, 2015; Buerki & Baker, 2016; Parr, Guralnick, Cellinense, & Page, 2012). In fact, the main problem of pattern-based approaches is that they do not explicitly include phylogenetic information in their methods (Crisp, Trewick, & Cook, 2011; Livingstone, 2015; Sanmartín, 2015; Waters *et al.*, 2013). However, it is possible to combine pattern-based methods to test primary biogeographic homology using taxonomic records. For example, the developed variants of the Parsimony Analysis of Endemicity (PAE) (Morrone, 2014b and citations therein; Rosen, 1988), allow us to find area relationships based on the shared presence of taxa, and the nodes relating these areas can be represented as generalized tracks (interpreted biologically as indicating the pre-existence of ancestral biotas that were fragmented by geological (often tectonic) or climatic events) (Ferrari, Barão, & Simões, 2013; García-Barros *et al.*, 2002; Luna-Vega, Alcántara, Morrone, & Espinosa, 2000). One method derived from PAE, named Cladistic Analysis of Distributions and Endemism (CADE) (Porzecanski & Cracraft, 2005), uses data from more than one taxonomic level (e.g., genus, family, superfamily) improving and increasing the historical information contained about area relationship. Therefore, the combination of these pattern-based approaches can help to fully support the distribution patterns, on a large biogeographic scale (Morrone, 2015b; Parenti & Ebach, 2013). In terms of geographic areas, taxa can either be present in more than one, or only in one area, in which case they are considered endemic. On the other hand, microendemic taxa are restricted to small distribution areas (Nattier *et al.*, 2012).

In this study, we explore the primary biogeographic patterns that drove the diversification of a host-symbiont association, based on the geographic structure of Temnocephalida (Cannon & Joffe, 2001). In this context, we establish the primary biogeographic homology of Temnocephalida and how it was influenced by the complex geographic scenario since the breakup of Gondwana, the possible effect of the host diversification plus the origin of hydrological system, or by a combination of the two. The aim of this study is to test the hypothesis that the current distribution of Temnocephalida is due to vicariant events that occurred during the breakup of Gondwana under two methods of primary biogeographic homology: (1) PAE, to describe the relationships between areas (basins), based on the current distribution of Temnocephalida, and their endemism; (2) CADE, to examine the influence of taxonomic-hierarchical information on historical distribution patterns of Temnocephalida. Lastly, based on the results of the phylogenetic analyses, generalized tracks were

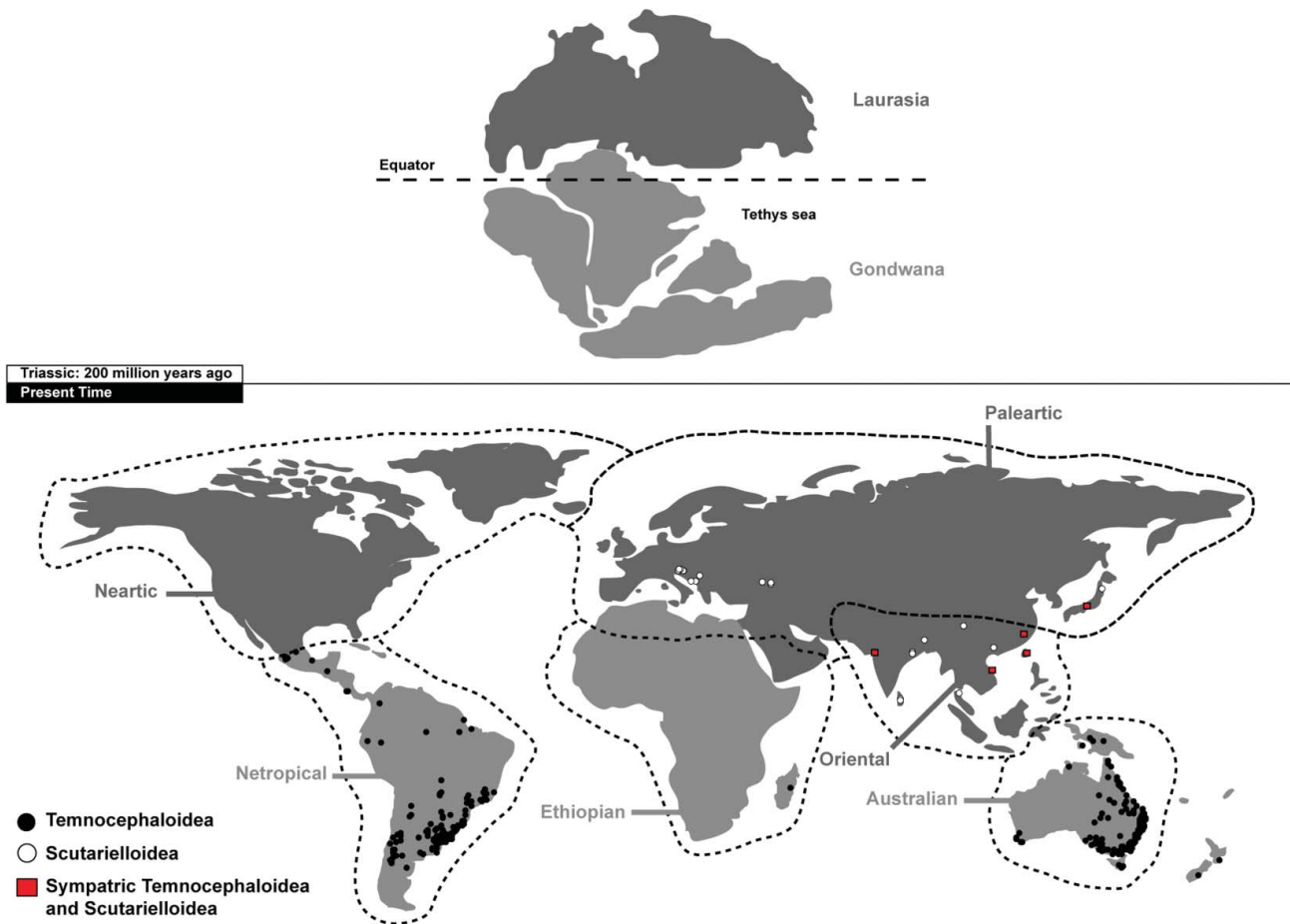


Fig. 1. Distribution patterns of Temnocephalida superfamilies and biogeographic regions (Classic zoogeographic scheme from Wallace, 1876).

built, to detect the influence of vicariant events in the distribution of Temnocephalida.

Materials and methods

Distribution dataset and areas

Taxonomic and distributional data were obtained from original records, from the Turbellarian Taxonomic Database (Tyler, Schilling, Hooge, & Bush, 2006-2016), and other available literature not included there (Arias-Pineda, Damborenea, & Castro, 2015; Kawakatsu, Wu, Kawakatsu, & Kawakatsu, 2008; Martínez-Aquino et al., 2014a; Noreña, Damborenea, Brusa, & Escobedo, 2006; Ponce de León, Berón Vera, & Volonterio, 2015; Seixas, Amato, & Amato, 2015a,b; Seixas, Amato, Amato, & Mascarenhas, 2014; Velazquez-Ocampo, 1985; Wais, 1987); from the revision of vouchers specimens deposited in the Colección Helmintológica of Museo de La Plata, Argentina (MLP-He) and the Colección Nacional de Helmintos of the Instituto de Biología, UNAM, Mexico (CNHE). Once all the distributional data were checked

and revised for possible taxonomic or distributional mistakes (e.g., inaccurate identification, synonyms, specimens lost from collections that could not be studied), we obtained an exhaustive list of the distribution of 179 taxa of Temnocephalida, classified and organized taxonomically (Appendix S1, see online supplemental material, which is available from the article's Taylor & Francis Online page at <http://dx.doi.org/10.1080/14772000.2016.1252441>). Furthermore, we complement this list with information of host plus geographic coordinates, based on specialized literature, to detect possible codivergence patterns (Appendix S2, see supplemental material online).

The areas used are those of the world's major hydrological basins map according to the Food and Agriculture Organization (FAO) of the United Nations global spatial database on water and agriculture (© FAO, 2011, derived from HydroSHED). This map provides natural geographic boundaries between areas, improving the explanatory power of analyses (e.g., Huidobro, Morrone, Villalobos, & Álvarez, 2006; Martínez-Aquino, Aguilar-Aguilar, Santa Anna del Conde-Juárez, & Contreras-Medina,

2007; Perbiche-Neves *et al.*, 2014). The areas selected for analysis were only those that had at least one record of a temnocephalid species; in total, 45 areas were used (Table S1, see supplemental material online). The distributional data were plotted on the freshwater basins map using the program DIVA-GIS 7.5 (Hijmans, Guarino, & Mathur, 2012).

To build area cladograms using parsimony (i.e., PAE and CADE), five different data matrices were built adding progressive hierarchical data: Matrix 1 contained species information only (46×179), Matrix 2 'Species + Genera' (46×202), Matrix 3 'Species + Genera + Subfamily' (46×206), Matrix 4 'Species + Genera + Subfamily + Family' (46×211), Matrix 5 'Species + Genera + Subfamily + Family + Superfamily' (46×213). Presences were coded as (1) and absences as (0). In all cases a hypothetical area with all (0) was added to root the trees (Appendices S3–S7, see supplemental material online).

Biogeographic phylogenetic analysis

Parsimony analysis of the PAE and CADE matrices was carried out in TNT (Goloboff, Farris, & Nixon, 2008), using heuristic searches with 100 random addition sequences and a TBR branch swapping algorithm. Branch support was assessed by performing bootstrap analyses with 100 pseudoreplicates (with 10 random addition sequences and TBR branch-swapping). State optimizations were visualized using WinClada (Nixon, 2002).

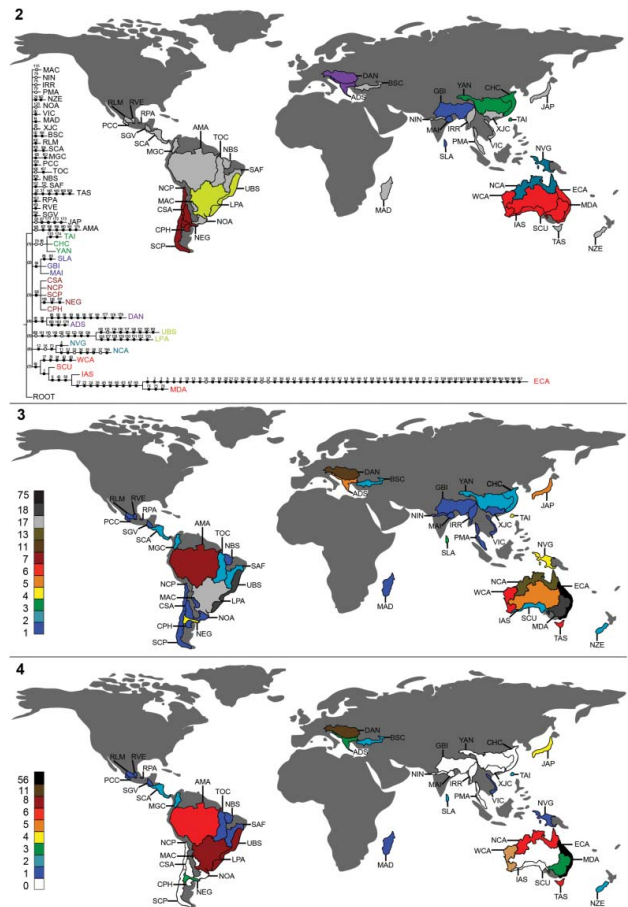
Track analysis

A variant of PAE (with progressive character elimination or PAE-PCE) was used to identify generalized tracks (e.g., Echeverry & Morrone, 2010; García-Barros *et al.*, 2002; Luna-Vega *et al.*, 2000). In PAE-PCE, generalized tracks are identified by biotic components in the resulting cladogram as the monophyletic groups of units defined by at least two taxa (= synapomorphies) (Morrone, 2014b). Similar to PAE-PCE, in this study we used CADE to detect generalized tracks. In contrast to PAE-PCE, the discovery of biotic components is achieved by an additive method of hierarchical information. Since phylogenetic information for Temnocephalida is still lacking, CADE is an appropriate method for inferring biogeographic signal (Porzecanski & Cracraft, 2005). In this context, generalized tracks were grouped by areas of the same colour of a clade (e.g., Ferrari *et al.*, 2013; see below).

Results

Analysis 1, PAE

The PAE yielded 42 trees (MPT) of 192 steps, CI = 0.93, and RI = 0.78 (Fig. 2; the species supporting the branch



Figs. 2–4. 2. Biogeographic relationships between hydrological freshwater basins for Temnocephalida species, as inferred by parsimony analyses of endemism (PAE). 3. Geographic distribution of species richness of Temnocephalida across hydrological basins, coloured bar and numbers correspond to number of species in each freshwater basin. 4. Geographic distribution of endemics species of Temnocephalida across hydrological basins, coloured bar and numbers correspond to number of endemic species in each freshwater basin.

of each clade in the cladogram are detailed in Table 1). Seven monophyletic groups with no clear relationships were distinguished within the cladogram. However, it is possible to discover three clades corresponding to separate geographic areas; e.g., Clade 1 (TAI, CHC, YAN) and Clade 2 (MAI, SLA, GBI) in the Oriental region, and Clade 6 in the Australian region (NVG, NCA). On the other hand, adjacent geographic areas were discovered for Clade 3 (NCP, CSA, NEG, CPH, SCP), and Clade 5 (UBS, LPA) in the Neotropical region; Clade 7 (WCA (SCU (IAS (ECA, MDA)))) in the Australian region, and Clade 4 (DAN, ADS) in the Palaearctic region. Lastly, 23 areas (i.e., IRR, PMA, NZE, TAS, VIC, MAD, XJC, BSC, RLM, SCA, MGC, PCC, TOC, NBS, SAF, NOA, RPA, RVE, SGV, MAC, AMA, NIN, and JAP), did not show phylogenetic affinities (Fig. 2).

Table 1. Description of the taxa defining nodes in the cladogram inferred by Parsimony Analyses of Endemism (PAE). * = Species supporting more than one clade (homoplasies).

Clade	Taxa
1	<i>Temnosewellia semperi</i> *, <i>Scutariella japonica</i> *
2	<i>Paracaridinicola indica</i>
3	<i>Temnocephala chilensis</i>
4	<i>Troglocaridicola capreolaria</i> , <i>Troglocaridicola cestoidaria</i>
5	<i>Temnocephala lutzii</i> *, <i>Temnocephala brevicornis</i> , <i>Temnocephala axenos</i> *, <i>Temnocephala haswelli</i> , <i>Temnocephala iheringi</i> *, <i>Temnocephala pereirai</i> , <i>Temnocephala talicei</i> , <i>Temnocephala mertoni</i> , <i>Didymorchis haswelli</i>
6	<i>Diceratocephala boschmai</i> , <i>Notodactylus handschini</i> *, <i>Temnosewellia rouxii</i>
7	<i>Temnosewellia minor</i> , <i>Craspedella simulator</i> , <i>Craspedella spenceri</i> , <i>Temnosewellia dendyi</i> , <i>Temnosewellia queenslandensis</i> , <i>Temnohaswellia simulator</i> , <i>Temnohaswellia comes</i> , <i>Temnohaswellia verruca</i> , <i>Temnohaswellia alpina</i> , <i>Temnosewellia acirra</i> , <i>Temnosewellia gingrina</i> , <i>Temnosewellia fasciata</i> , <i>Temnosewellia fax</i> , <i>Temnosewellia muscalingulata</i> , <i>Temnosewellia acicularis</i>

Biogeographic relationships were found using PAE for seven monophyletic groups (i.e., clades) based on one or more synapomorphies (Table 1). Clade 1 is supported by two homoplastic characters (*Temnosewellia semperi* and *Scutariella japonica*); and only TAI includes two additional species from *Temnosewellia* sp. 3 and *Temnosewellia* sp. 7 (Fig. 2). Clade 2 is supported by a synapomorphic character: *Paracaridinicola indica*. In this clade, only Sri Lanka (SLA) of the Oriental region, includes two autapomorphic taxa of the family Scutariellidae: *Monodiscus macbridei* and *M. parvus* (Fig. 2). Clade 3 is supported by a synapomorphy: *Temnocephala chilensis* (Fig. 2), that is the only species recorded in the Colorado South America, North and South Chile Pacific Coast, Negro River and Central Patagonia Highlands (CSA, NCP, SCP, NEG, CPH). Only one area of Clade 3 (Negro River Basin (NEG)), has three endemic taxa of the family Didymorchiidae; *Didymorchis haswelli australis*, *Didymorchis* sp. A and *Didymorchis* sp. B (Fig. 2). Clade 4 is located in the Eurasian region and is supported by two synapomorphies: *Troglocaridicola capreolaria* and *Tc. cestoidaria* (Fig. 2). All taxa included that pertain to both areas of Clade 4 are endemics; e.g., the Adriatic Sea area (ADS) shows three autapomorphies, while Danube (DAN) shows eleven autapomorphies (Fig. 2). Clade 5 is highly supported by six synapomorphies of the Temnocephaloidea; *Temnocephala brevicornis*, *T. haswelli*, *T. pereirai*, *T. talicei*, *T. mertoni*, and *Didymorchis haswelli*. Geographically, this clade is located in the Neotropical region (Fig. 2). Clade 6 is supported by two synapomorphies: *Diceratocephala boschmai* (Diceratocephalidae), and *Temnosewellia rouxii* (Temnocephalidae) (Fig. 2). Clade 7 is supported by one synapomorphy, *Temnosewellia minor* (Temnocephalidae). West Coast Australia (WCA) and South Coast Australia (SCU) are associated with the areas (IAS (ECA, MDA)), but only based on one synapomorphy. In contrast with WCA, IAS and SCU do not include any endemic species. Furthermore, ECA and MDA are the areas with the greatest number of endemic

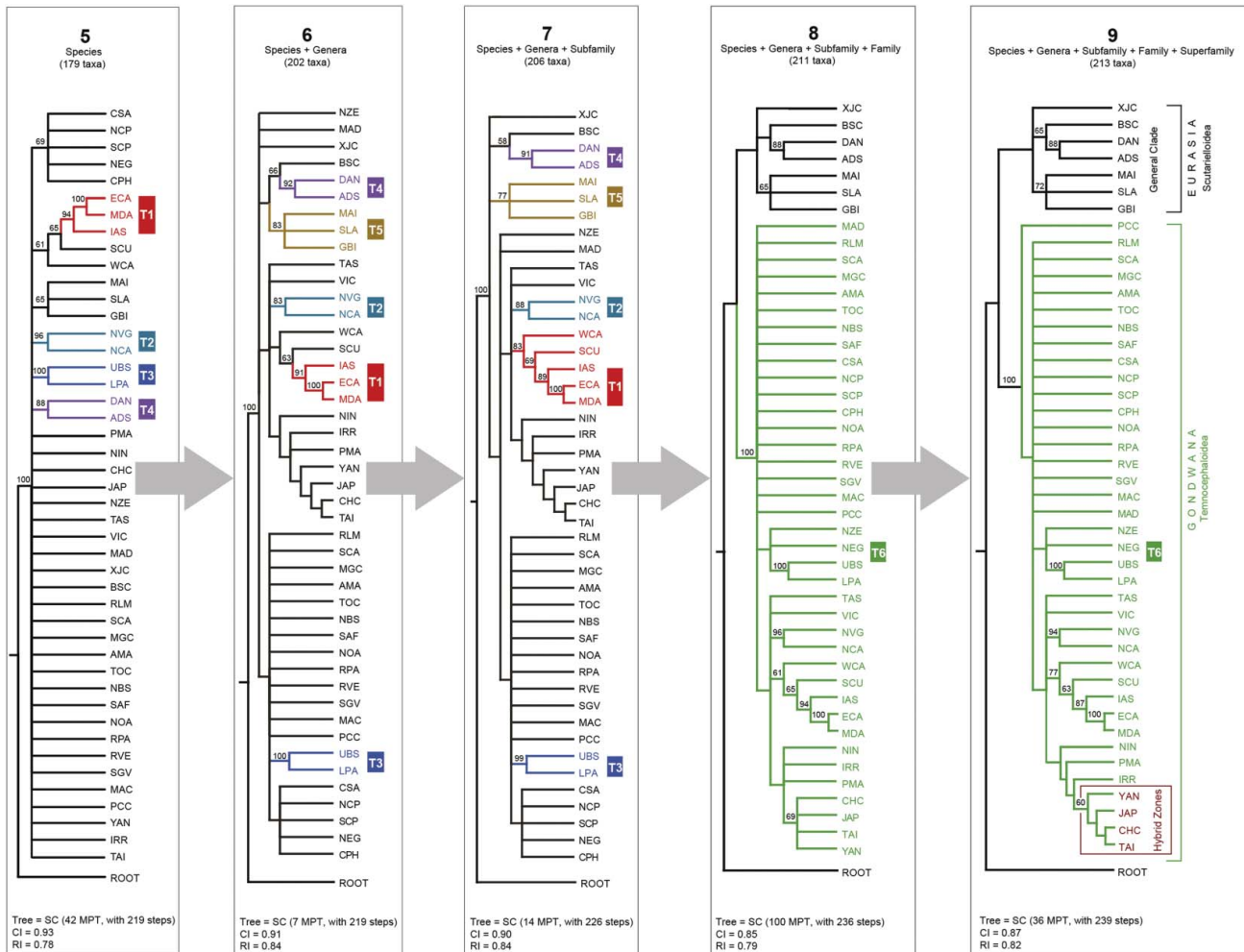
species and richness with regards to Temnocephalida (see below).

There were a total of 158 helminth taxa restricted to a single analysed hydrological basin, which represent autapomorphies. In total, 29 areas present autapomorphies, with intervals of 1 (e.g., VIC, MAD, RLM, PCC, TOC, NBS, SAF, RPA, RVE, SGV, NVG) to 56 microendemic taxa (e.g., ECA) (Fig. 2). On the other hand, 16 areas did not show any endemic taxa (e.g., MAC, NIN, IRR, PMA, NOA, XJC, CHC, YAI, GBI, MAI, CSA, NCP, SCP, CPH, SCU, IAS); eight areas only show homoplastic characters (e.g., MAC, NIN, IRR, PMA, NOA, XJC, CHC, YAI), while eight areas only included one to four synapomorphies (e.g., GBI, MAI, CSA, NCP, SCP, CPH, SCU, IAS).

The observed species richness by area is relatively similar to the pattern of endemic species richness by area detected by PAE. A pattern of few species per area is observed. For example, 39 areas contain a range of 1–7 species, five areas contain a range of 11–18 species and only one area contains the maximum number of species richness (59 taxa). Similarly, 27 areas contain a range of 1–8 endemic species, one area contains 11 endemic species and only one area contains the maximum number of endemic species (56 taxa). In general, 50% of analysed areas only contain a single record (i.e., 20 of 45 areas), and 20 areas contain records of one to three endemic species. Also, eight areas do not contain any endemic taxa (e.g., MAC, NIN, IRR, PMA, NOA, XJC, CHC, YAN), while 20 areas only contain one record of temnocephalan (e.g., MAC, NIN, IRR, PMA, NOA, VIC, MAD, XJC, RLM, PCC, NBS, RPA, RVE, SGV, GBI, MAI, CSA, NCP, SCP, CPH). Only one area (ECA) contains both high species richness and endemism (Figs 3–4).

Analysis 2, CADE linked generalized track

In this study, the CADE analyses were used to detect generalized tracks based on two or more synapomorphies per node, for five runs (Appendices S8–S12, see supplemental



Figs. 5–9. Results of the cladistic analysis of distributions and endemism (CADE) detecting the influence of hierarchical information on tree topology and discovering generalized tracks. Five datasets were used, including: **5.** Species. **6.** Species + Genera. **7.** Species + Genera + Subfamily. **8.** Species + Genera + Subfamily + Family. **9.** Species + Genera + Subfamily + Family + Superfamily. A comparison of trees obtained, using hierarchical information from species to subfamily, shows that four generalized equal tracks are discovered (5–7). On the other hand, using hierarchical information from family to superfamily, a generalized track and a general clade are detected (8–9). Based on conservative position, because the results obtained from run 1 to 3 and 4 to 5 of CADE are relatively similar, the integrative of the biogeographic patterns detected in this study correspond to 7 and 9 figures. For more details see the discussion on the text. Numbers above branches show bootstrap support $\geq 60\%$, SC = consensus trees, MPT = most parsimonious tree, CI = consistent index, RI = retention index.

material online). In the first run (Matrix 1; Appendix S3, see supplemental material online), four generalized tracks were identified (Fig. 5). The species that were diagnostic for the generalized tracks are shown in Table 2. Generalized Track 1 included the East Coast Australia (ECA), Murray Darling River Basin (MDA), and the Interior Australia (IAS). Generalized Track 2 included the North Coast Australia (NCA) to the Irian Jaya Coast, New Guinea (NVG). Generalized Track 3 included the South Atlantic Coast of Uruguay-Brazil (UBS) to the La Plata River Basin (LPA). Generalized Track 4 included the Danube River Basin (DAN) and Adriatic Sea River Basin (ADS). The second run of CADE (Matrix 2; Appendix S4, see supplemental material online) produced 7 equally

MPT. The Generalized Track 5 identified included Mahandi India (MAI), Sri Lanka (SLA), and Ganges Brahmaputra India (GBI). On the other hand, the four generalized tracks obtained in the first run were identified (Fig. 6). The third run of CADE (Matrix 3; Appendix S5, see supplemental material online) produced 14 equally MPT. 'Track 1' was identified including five river basins; the previously mentioned IAS, ECA and MDA, plus West Coast Australia (WCA) and South Coast Australia (SCU) (Fig. 7). The fourth run of CADE (Matrix 4; Appendix S6, see supplemental material online) produced 100 equally MPT. The Generalized Track 6 was identified, which included 30 river basins extending across three Gondwanan regions: the Neotropical region (20 river

Table 2. Taxonomic composition of Generalized tracks (GT) 1, 2, 3, 4 and 5 retrieved by cladistics analysis of distributions and endemism (CADE) using freshwater river basin (FRB) as analytical units, under the Matrix 1, 2 and 3 datasets from Temnocephalida (Appendices S3-S5). The asterisks (*) correspond to homoplasies. See text for more details.

GT	FRB	Taxonomic composition
1	East Coast Australia, Murray Darling Australia, Interior Australia	<p>Species.- <i>Achenella cougal</i>, <i>A. sathonata</i>, <i>Achenella</i> sp., <i>Actinodactylella blanchardi</i>, <i>Craspedella bribiensis</i>, <i>C. cooranensis</i>, <i>C. gracilis</i>, <i>C. joffei</i>, <i>C. shorti</i>, <i>C. spenceri</i>, <i>C. yaba</i>, <i>Craspedella</i> sp. 1, <i>Gelasinella powellorum</i>, <i>Heptacraspedella peratus</i>, <i>Notodactylus handschini</i>*, <i>Temnohaswellia alpina</i>, <i>Th. breviumbella</i>, <i>Th. capricornia</i>, <i>Th. comes</i>, <i>Th. cornu</i>, <i>Th. crotalum</i>, <i>Th. munifica</i>, <i>Th. pearsoni</i>, <i>Th. simulator</i>, <i>Th. subulata</i>, <i>Th. umbella</i>, <i>Th. verruca</i>, <i>Temnohaswellia</i> sp., <i>Temnosewellia acicularis</i>, <i>Ts. acirra</i>, <i>Ts. alba</i>*, <i>Ts. albata</i>*, <i>Ts. apiculus</i>, <i>Ts. arga</i>, <i>Ts. argeta</i>, <i>Ts. aspinosa</i>, <i>Ts. aspra</i>, <i>Ts. athertonensis</i>, <i>Ts. bacrio</i>, <i>Ts. bacroniculus</i>, <i>Ts. batiola</i>, <i>Ts. belone</i>, <i>Ts. butlerae</i>, <i>Ts. caeca</i>, <i>Ts. caliculus</i>, <i>Ts. cestus</i>, <i>Ts. christineae</i>, <i>Ts. comythus</i>, <i>Ts. coughrani</i>, <i>Ts. cypellum</i>, <i>Ts. dendyi</i>, <i>Ts. engaei</i>, <i>Ts. fasciata</i>, <i>Ts. fax</i>, <i>Ts. flammula</i>, <i>Ts. geonoma</i>, <i>Ts. gingrina</i>, <i>Ts. gracilis</i>, <i>Ts. improcera</i>, <i>Ts. keras</i>, <i>Ts. maculata</i>, <i>Ts. magna</i>, <i>Ts. maxima</i>, <i>Ts. minima</i>, <i>Ts. minuta</i>, <i>Ts. muscalingulata</i>, <i>Ts. possibilitas</i>, <i>Ts. queenslandensis</i>, <i>Ts. unguiculus</i>, <i>Temnosewellia</i> sp. 1, <i>Temnosewellia</i> sp. 2, <i>Didymorchis astacopsidis</i>, <i>Didymorchis cherapsis</i>, <i>Didymorchis</i> sp. 1, <i>Didymorchis</i> sp. 2.</p> <p>Genera.- <i>Achenella</i>, <i>Actinodactylella</i>, <i>Craspedella</i>, <i>Didymorchis</i>, <i>Gelasinella</i>, <i>Heptacraspedella</i>, <i>Notodactylus</i>, <i>Temnohaswellia</i>, <i>Temnosewellia</i>.</p> <p>Subfamilies.- Temnocephalinae, Craspedellinae.</p>
2	North Coast Australia, Irian Jaya Coast	<p>Species.- <i>Craniocephala biroi</i>, <i>Craspedella pedum</i>, <i>Decadidymus gulosus</i>, <i>Diceratocephala boschmai</i>, <i>Notodactylus handschini</i>*, <i>Temnosewellia phantasmella</i>, <i>T. aphyodes</i>, <i>T. argilla</i>, <i>T. neqae</i>, <i>T. rouxii</i>, <i>T. alba</i>*, <i>T. albata</i>*.</p> <p>Genera.- <i>Craniocephala</i>, <i>Craspedella</i>, <i>Decadidymus</i>, <i>Diceratocephala</i>, <i>Notodactylus</i>, <i>Temnosewellia</i>.</p> <p>Subfamilies.- Temnocephalinae, Craspedellinae.</p>
3	Uruguay Brazil South Atlantic Coast, La Plata	<p>Species.- <i>Didymorchis haswelli</i>, <i>Temnocephala axenos</i>*, <i>T. brevicornis</i>, <i>T. cuocoloi</i>, <i>T. curvicirri</i>*, <i>T. cyanoglandula</i>, <i>T. decarloi</i>, <i>T. digitata</i>, <i>T. haswelli</i>, <i>T. iheringi</i>*, <i>T. lamothei</i>, <i>T. lanei</i>, <i>T. lutzii</i>*, <i>T. mertoni</i>, <i>T. microdactyla</i>, <i>T. minutocirrus</i>, <i>T. pereirai</i>, <i>T. pignalberiae</i>, <i>T. rochensis</i>, <i>T. santafesina</i>, <i>T. stoneflyi</i>, <i>T. talcei</i>, <i>T. trapeziformis</i>, <i>T. travassosfilhoi</i>, <i>Temnocephala</i> sp. 1, <i>Temnocephala</i> sp. 3.</p> <p>Genera.- <i>Didymorchis</i>, <i>Temnocephala</i>.</p> <p>Subfamilies.- Temnocephalinae.</p>
4	Danube, Adriatic Sea	<p>Species.- <i>Bubalocerus pretneri</i>, <i>B. sketi</i>, <i>Scutariella stammeri</i>, <i>S. didactyla</i>, <i>S. maxima</i>, <i>Stygoditycola hadzii</i>, <i>Subtelsonia perianalis</i>, <i>Troglocaridicola capreolaria</i>, <i>Tc. cestoidaria</i>, <i>Tc. cervaria</i>, <i>Tc. istriana</i>, <i>Tc. krkensis</i>, <i>Tc. longipenis</i>.</p> <p>Genera.- <i>Bubalocerus</i>, <i>Scutariella</i>, <i>Stygoditycola</i>, <i>Subtelsonia</i>, <i>Troglocaridicola</i>.</p> <p>Subfamilies.- Scutariellinae.</p>
5	Mahandi India, Sri Lanka, Ganges Bramaputra India	<p>Species.- <i>Paracaridinicola indica</i>, <i>Monodiscus parvus</i>, <i>M. macbridei</i>.</p> <p>Genera.- <i>Paracaridinicola</i>, <i>Monodiscus</i>.</p> <p>Subfamilies.- Caridinicolinae.</p>

basins), the Ethiopian region (1 river basin), and the Australian region (9 river basins). Furthermore, the Generalized Track 6 also included seven river basins located in the Oriental region (Narmada India [NIN], Irrawady [IRR], Peninsula Malaysia [PMA], China Coast [CHC], Japan [JAP], Yangtze [YAN], and Taiwan [TAI]) (Fig. 8). Furthermore, a general clade was identified in Eurasia, which included seven river basins; the Mahandi [MAI], Sri Lanka [SLA], the Ganges Bramaputra India [GBI], the Black Sea South Coast [BSC], the Danube [DAN], the Adriatic Sea [ADS], and the Xun Jiang [XJC]. The fifth run of CADE (Matrix 5) produced 36 equally MPT. The Generalized Track 6 identified from the fourth run of CADE, plus General clade in Eurasia, was also found (Fig. 9). The species and areas identified by the Generalized Track 6 and General clade are shown in Table 3. The results obtained by the CADE analyses show that when hierarchical information is included, few differences

between distribution patterns (e.g., generalized track) are discovered (Figs 5–9). Finally, only the total-evidence matrix (i.e., Matrix 5; Appendix S7, see supplemental material online) yielded the general resolution in the strict consensus tree, where the fragmentation pattern of Gondwana was recovered (Fig. 9).

Discussion

PAE: Describing the patterns of geographic distribution of Temnocephalida

The strict consensus tree obtained by PAE represents a hypothesis of relationships between different river basins of the world, with special emphasis on basins with Gondwanan and Eurasian affinities (Fig. 2). Consensus tree topologies show area groups (clades) involving different biogeographic provinces and regions. Today, a reasonable

Table 3. Taxonomic composition of Generalized Track (GT) 6 and General clade (Gc) recovered in cladistics analysis of distributions and endemism (CADE) under the Matrix 5 datasets for Temnocephalida (Appendix S6 and Appendix 7). The asterisk (*) in the freshwater river basin (FRB) and taxa correspond to complex area and taxa from hybrid areas discovering in this study. See text for more details.

GT	FRB	Taxonomic composition
6	Cutzamala, Southern Central America, Magdalena, Amazon, Tocantins, North Brazil South Atlantic Coast, Sao Francisco, Colorado South America, North Chile Pacific Coast, South Chile Pacific Coast, Central Patagonia Highlands, North Argentina, Papaloapan, Río Verde, Grijalba, Mar Chiquita, Lerma, Madagascar, Negro, New Zealand, Uruguay Brazil South Atlantic Coast, La Plata, Tasmania, Vietnam Coast, Irian Jaya Coast, North Coast Australia, Narmada India*, China Coast, Japan*, Taiwan*, West Coast Australia, South Coast Australia, Interior Australia, East Coast Australia, Murray Darling Australia, Yangtze*, Irriwady, Peninsula Malaysia	<p>Species.- <i>Scutariella japonica</i>*, <i>Actinodactylella blanchardi</i>, <i>Achenella cougal</i>, <i>A. sathonata</i>, <i>Achenella</i> sp., <i>Craniocephala biroii</i>, <i>Craspedella gracilis</i>, <i>C. shorti</i>, <i>C. spenceri</i>, <i>C. yabba</i>, <i>C. simulator</i>, <i>C. pedum</i>, <i>Craspedella</i> sp., <i>Dactylocephala madagascariensis</i>, <i>Didymorchis astacopsidis</i>, <i>D. cherapsis</i>, <i>D. haswelli</i>, <i>D. haswelli australis</i>, <i>D. paraneprophis</i>, <i>Didymorchis</i> sp. A, <i>Didymorchis</i> sp. B, <i>Didymorchis</i> sp. 2, <i>Didymorchis</i> sp. 3, <i>Diceratocephala boschmai</i>, <i>Decadidymus gulosus</i>, <i>Gelasinella powellorum</i>, <i>Heptacraspedella peratus</i>, <i>Notodactylus handschini</i>, <i>Temnocephala mexicana</i>, <i>T. costarricensis</i>, <i>T. brenesi</i>, <i>T. colombiensis</i>, <i>T. lutzi</i>, <i>T. peruensis</i>, <i>T. kingsleyae</i>, <i>T. longivaginata</i>, <i>T. caddisfly</i>, <i>T. curvicirri</i>, <i>T. axenos</i>, <i>T. iheringi</i>, <i>T. chilensis</i>, <i>T. mertoni</i>, <i>T. haswelli</i>, <i>T. icononcensis</i>, <i>T. pereirai</i>, <i>T. talicei</i>, <i>T. brevicornis</i>, <i>T. lanei</i>, <i>T. trapeziformis</i>, <i>T. cyanoglandula</i>, <i>T. minutocirrus</i>, <i>T. stoneflyi</i>, <i>T. rochensis</i>, <i>T. pignalberiae</i>, <i>T. microdactyla</i>, <i>T. travassosfilhoi</i>, <i>T. lamothei</i>, <i>T. santafesina</i>, <i>T. decarloi</i>, <i>T. digitata</i>, <i>T. cuocoloi</i>, <i>T. euryhalina</i>, <i>T. icononcensis</i>, <i>Temnocephala</i> sp. 1, <i>Temnocephala</i> sp. 3, <i>Temnocephala</i> sp. 4, <i>Temnocephala</i> sp. 5, <i>Temnocephala</i> sp. 6, <i>Temnocephala</i> sp. 7, <i>Temnocephala</i> sp. 8, <i>Temnocephala</i> sp. 9, <i>Temnocephala</i> sp. 10, <i>Temnohaswellia alpina</i>, <i>Th. brevumbella</i>, <i>Th. capricornia</i>, <i>Th. comes</i>, <i>Th. cornu</i>, <i>Th. crotalum</i>, <i>Th. munifica</i>, <i>Th. pearsoni</i>, <i>Th. simulator</i>, <i>Th. subulata</i>, <i>Th. umbella</i>, <i>Th. verruca</i>, <i>Th. novaezealandiae</i>, <i>Temnohaswellia</i> sp., <i>Temnomonticellia aurantica</i>, <i>Tm. fulva</i>, <i>Tm. tasmanica</i>, <i>Tm. pygmea</i>, <i>Tm. quadricornis</i>, <i>Temnosewellia minor</i>, <i>Ts. punctata</i>, <i>Ts. chaeropsis</i>, <i>Ts. semperi</i>*, <i>Ts. cf. semperi</i>*, <i>Ts. vietnamensis</i>, <i>Ts. phantasmella</i>, <i>Ts. aphyodes</i>, <i>Ts. argilla</i>, <i>Ts. neqae</i>, <i>Ts. rouxii</i>, <i>Ts. alba</i>, <i>Ts. albata</i>, <i>Ts. acicularis</i>, <i>Ts. acirra</i>, <i>Ts. apiculus</i>, <i>Ts. arga</i>, <i>Ts. argeta</i>, <i>Ts. aspinosa</i>, <i>Ts. aspra</i>, <i>Ts. athertonensis</i>, <i>Ts. bacrio</i>, <i>Ts. bacrioniculus</i>, <i>Ts. batiola</i>, <i>Ts. belone</i>, <i>Ts. butlerae</i>, <i>Ts. caeca</i>, <i>Ts. caliculus</i>, <i>Ts. cestus</i>, <i>Ts. christineae</i>, <i>Ts. cita</i>, <i>Ts. comythus</i>, <i>Ts. coughrani</i>, <i>Ts. cypellum</i>, <i>Ts. dendyi</i>, <i>Ts. engaei</i>, <i>Ts. fasciata</i>, <i>Ts. fax</i>, <i>Ts. flammula</i>, <i>Ts. geonoma</i>, <i>Ts. gingrina</i>, <i>Ts. gracilis</i>, <i>Ts. improcera</i>, <i>Ts. keras</i>, <i>Ts. maculata</i>, <i>Ts. magna</i>, <i>Ts. maxima</i>, <i>Ts. minima</i>, <i>Ts. minuta</i>, <i>Ts. muscalingulata</i>, <i>Ts. possibilitas</i>, <i>Ts. queenslandensis</i>, <i>Ts. unguiculus</i>, <i>Temnosewellia</i> sp. 1, <i>Temnosewellia</i> sp. 2, <i>Temnosewellia</i> sp. 3*, <i>Temnosewellia</i> sp. 4*, <i>Temnosewellia</i> sp. 5*, <i>Temnosewellia</i> sp. 6*, <i>Temnosewellia</i> sp. 7*, <i>Temnosewellia</i> sp. 8, <i>Zygopella pista</i>, <i>Z. stenota</i>, <i>Zygopella deimata</i>.</p> <p>Genera.- <i>Actinodactylella</i>, <i>Decadidymus</i>, <i>Diceratocephala</i>, <i>Didymorchis</i>, <i>Scutariella</i>*, <i>Achenella</i>, <i>Craniocephala</i>*, <i>Craspedella</i>, <i>Dactylocephala</i>, <i>Gelasinella</i>, <i>Heptacraspedella</i>, <i>Notodactylus</i>, <i>Temnocephala</i>*, <i>Temnohaswellia</i>, <i>Temnomonticellia</i>, <i>Temnosewellia</i>*, <i>Zygopella</i>.</p> <p>Sufamilies.- Craspedellinae, Scutariellinae*, Temnocephalinae.</p> <p>Families.- Scutariellidae*, Actinodactylellidae, Didymorchidae, Diceratocephalidae, Temnocephalidae*.</p> <p>Superfamilies.- Scutarielloidea*, Temnocephaloidea*.</p>
Gc	Mahandi India, Sri Lanka, Ganges Bramaputra India, Black Sea South Coast, Danube, Adriatic Sea, Xun Jiang	<p>Species.- <i>Bubalocerus pretneri</i>, <i>B. sketi</i>, <i>B. undulatus</i>, <i>Caridinicola sinica</i>, <i>Monodiscus macbridei</i>, <i>M. parvus</i>, <i>Paracaridinicola indica</i>, <i>Stygodyticola hadzii</i>, <i>Scutariella japonica</i>*, <i>S. maxima</i>, <i>S. stammeri</i>, <i>S. didactyla</i>, <i>S. georgica</i>, <i>Subtelsonia perianalis</i>, <i>Troglocaridicola capreolaria</i>, <i>Tc. longipenis</i>, <i>Tc. maxima</i>, <i>Tc. istriana</i>, <i>Tc. cestoidaria</i>, <i>Tc. kirkensis</i>, <i>Tc. spelaeocaridicola</i>, <i>Tc. mrazeki</i>.</p> <p>Genera.- <i>Scutariella</i>, <i>Bubalocerus</i>, <i>Caridinicola</i>, <i>Monodiscus</i>, <i>Stygodyticola</i>, <i>Subtelsonia</i>, <i>Troglocaridicola</i>.</p> <p>Subfamily.- Caridinicolinae.</p> <p>Family.- Scutariellidae.</p> <p>Superfamily.- Scutarielloidea.</p>

dataset for Temnocephalida of the world is available (e.g., Martínez-Aquino *et al.*, 2014a; Sewel, 2013; Tyler *et al.*, 2006-2016; Appendix S2, see supplemental material online). However, the dataset for Temnocephalida is incomplete because many hydrological systems have only been partially explored or not explored at all. For example, the results obtained by PAE show that 50% of the analysed areas in this study only have one record of temnocephalans (Fig. 3). In this context, the results obtained here are likely to be modified or supported by new data in future studies. Despite these limitations, the dataset constructed in this study is the most complete reference for

Temnocephalida in each hydrological basin of the world. It is important to mention that the anthropogenic spread of Temnocephalida species recorded in several river basins was not considered; e.g., *Diceratocephala boschmai*, *Temnosewellia minor*, *T. rouxi* (Chivavaya, 2013; Du Preez & Smit, 2013; Martínez-Aquino *et al.*, 2014a; Niwa & Ohtaka, 2006; Saoud & Ghanawi, 2013; Sewell, Cannon, & Blair, 2006; Volonterio, 2009). This means that the distribution patterns detected by PAE are not influenced by introduced species.

Based on PAE it is possible to find primary biogeographic homology between two areas or more (Morrone,

2014b). In the case of the results obtained for Temnocephalida by PAE, several groups are defined by only one synapomorphy; however, some are polytomies (e.g., Clades 1, 2 and 3; Fig. 2). In these cases, it is difficult to support the patterns detected. Therefore, we decided to carry out biogeographic inferences of Temnocephalida using a PAE derivative (i.e., CADE), detecting area clades based on two or more synapomorphies to support the distributional patterns through generalized tracks (see next section).

CADE: Hierarchical-taxonomic information and their effect on detecting generalized tracks

Generalized tracks represent ancestral biotic components that became fragmented by tectonic or other geological events; however, it is also possible to hypothesize dispersal events based on generalized tracks (Morrone, 2015b). In this study, each CADE run is considered an independent analysis (Figs. 5–9). The generalized tracks obtained in the CADE analyses using Matrix 1, 2 and 3, are similar with the exception of Generalized Track 1 and 5 (Figs. 5–7). For this reason, the generalized tracks are interpreted with the same distributional patterns using three taxonomic levels; i.e., species, genera, and subfamily. On the other hand, the Generalized Track 6 and the General clade was discovered using a dataset that included higher taxonomic levels; i.e., family, superfamily (Appendices S6 and S7, see supplemental material online). Particularly, the General clade includes the Generalized Tracks 4 and 5 starting from the fourth run of the CADE (Fig. 8), and finally was inclusive of all the areas distributed on Eurasia (Fig. 9). Meanwhile the Generalized Track 6 included the Generalized Tracks 1, 2 and 3 (Fig. 9).

Based on the integration of the generalized tracks obtained by CADE runs, we detected grouping of the Gondwanan hydrological systems. The identification, quantification and measure of the generalized tracks allows the detection of complex or composite areas (Dos Santos, Cuezco, Reynaga, & Domínguez, 2012; Ferrari et al., 2013; Morrone, 2015b; Page, 1987). The interpretation of the generalized tracks is supported by the included biota (symbionts plus their hosts). In this sense, in the next section we show the results obtained for each generalized track, and if possible, a brief discussion of its biogeographic complexity is included.

Generalized Track 1

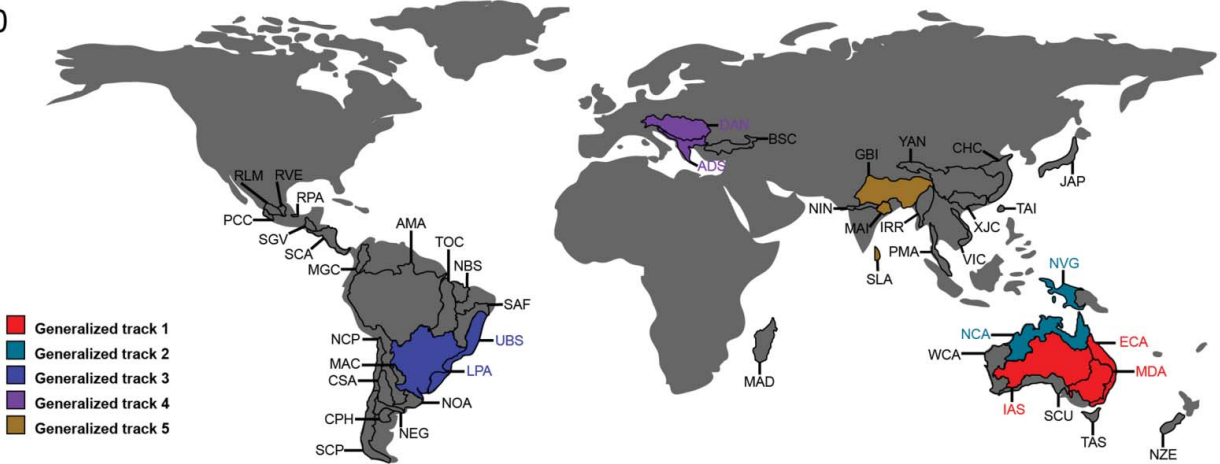
It is the most complex biotic component in terms of species richness of temnocephalids; e.g., 75 species with 72 endemic species; with 43 species of *Temnosewellia*

associated mainly with the freshwater crayfish *Euastacus* (Parastacidae) (Table 2). Similar to Clade 7 (WCA, (SCU (IAS (ECA, MDA)))) identified by PAE, the Generalized Track 1 is located across Australia (Fig. 10), but only includes the areas West Coast Australia (WCA) and South Coast Australia (SCU), when taxonomic hierarchical information is included (i.e., Species + Genera + Subfamily; Fig. 7). For this reason, we consider that this biogeographic relationship is weak. WCA River Basin is considered a separate hydrological system to Central and East Australia, and as such is suggested to be an independent area of freshwater endemism (e.g., Davies & Stewart, 2013; Morgan et al., 2014; Morrongiello et al., 2011). In this study, this idea is supported because WCA includes five endemic taxa (e.g., *Temnosewellia punctata*, *Ts. chaeropsis*, *Zygopella pista*, *Z. stenota* and *Z. deimata*), associated with *Cherax* host species with a distribution restricted to Western Australia (Horwitz & Adams, 2000; Morgan et al., 2014; Munasinghe, Burrige, & Austin, 2004; Unmack, Allen, & Johnson, 2013). On the other hand, using distinct freshwater groups, a similar delimitation of areas of endemism occurred in South Coast Australia (SCU) (Buhlmann et al., 2009; Unmack, 2001; Unmack, Hammer, Adams, & Dowling, 2011; Whiting, Lawler, Horwitz, & Crandall, 2000). For these reasons, CADE did not detect WCA and SCU as part of the Generalized Track 1 in the first and second runs. Generalized Track 1 supports the hypothesis that Central and Eastern Australia are diversity hotspots for freshwater biota (Bentley, Schmidt, & Hughes, 2010; Hammer, Unmack, Adams, Raakik, & Johnson, 2014; Hodges, Donnellan, & Georges, 2014). For example, based on Temnocephalida taxa (e.g., *Achenella* spp., *Craspedella* spp., *Didymorchis* spp., *Temnohaswellia* spp., *Temnosewellia* spp.) (Table 2), the fact that the East Coast Australia (ECA) river basin must be considered an area of high conservation priority is supported (Beatty, Morgan, Rashnavadi, & Lymbery, 2011; Davies & Stewart, 2013; Morgan et al., 2014) (Fig. 4).

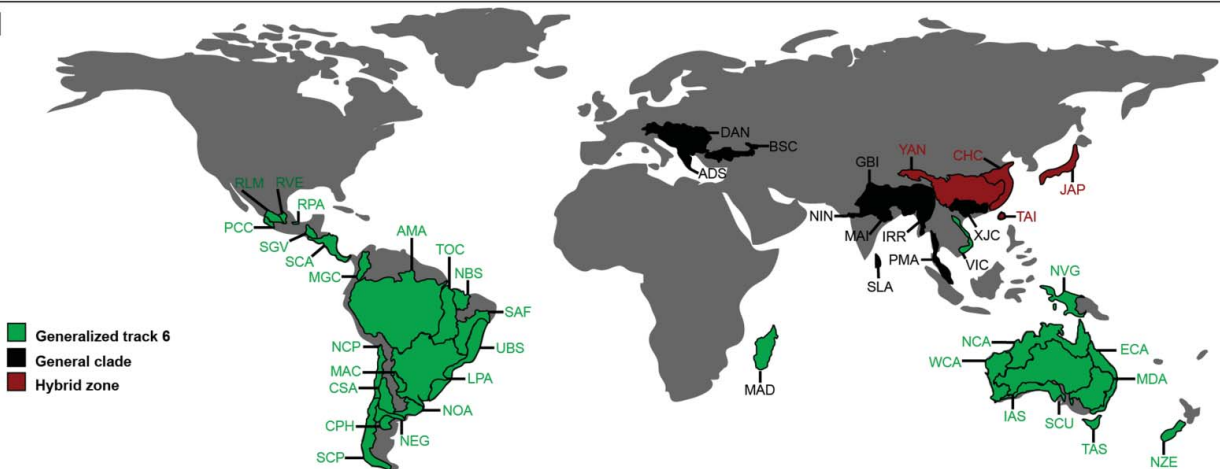
Generalized Track 2

The biotic composition that forms the structure of this track responds to a classic event of vicariance between the North Coast Australia (NCA) and Irian Jaya Coast, New Guinea (NVG) (e.g., Jordan & Hubbs, 1919; Mayr, 1944; Wallace, 1860). This track includes three endemic genera (*Craniocephala*, *Decadidymus*, and *Diceratocephala*), from two families (Temnocephalidae and Diceratocephalidae), plus five endemic species of the genera *Temnosewellia* (Table 2). Geographically, the Generalized Track 1 and the Generalized Track 2 are close (Fig. 10), but they only share three taxa, which in the case of Generalized Track 1 are located exclusively in the ECA River Basin;

10



11



Figs. 10–11. Geographic location of Generalized tracks recovered in the cladistic analysis of distributions and endemism (CADE) to Temnocephalida. **10.** Generalized tracks 1–5, under the integration and interpretation of the results of the matrix 1–3 datasets. **11.** Generalized track 6, General clade, and Hybrid zones, under the integration and interpretation of the results of the matrix 4–5 datasets (Appendices S6 and S7, see supplemental material online). Numbers of generalized tracks correspond with the clades detected by CADE in the Figs 5–9. Species composition to each generalized track, General clade and Hybrid zone is mentioned in Tables 2 and 3.

i.e., *Notodactylus handschini*, *Temnosewellia albata*, and *Ts. alba* (Appendix S8). In this context, the biota of the Generalized Track 1 and Generalized Track 2 support independent distribution patterns (e.g., Hammer *et al.*, 2014; Morgan, Roberts, & Keogh, 2007; Unmack *et al.*, 2011). The distribution pattern of the Temnocephalida of Generalized Track 1 was influenced by dispersion plus vicariance events during the evolutionary history of their crab hosts (e.g., Gecarcinucidae, Potamidae, and Potamonautidae), and shrimp hosts (e.g., Parastaciade) (Klaus, Yeo, & Ah Yong, 2011; Munasinghe *et al.*, 2004; Shull *et al.*, 2005; Toon *et al.*, 2010; Whiting *et al.*, 2000). The Generalized Track 2 is congruent with the vicariant distribution patterns of other freshwater biota; e.g., fishes, crayfishes, lobsters (Bracken-Grissom *et al.*, 2014; Cook, Unmack, Huey, & Hughes, 2014; Georges *et al.*, 2014; Kadarusman, Hadiaty, Sudarto, & Pouyaud, 2012; Sparks & Smith, 2004; Unmack *et al.*, 2013).

Generalized Track 3

This track is well supported by six synapomorphies (Appendix S8). The ancestral connection between Uruguay-Brazil South Atlantic Coast (UBS) and La Plata River Basin (LPA) can be explained by several marine transgressions in the past; e.g., Miocene–Quaternary Periods (23–5.3 Mya), in the case of the hosts *Aegla*, a particular endemic group of freshwater anomurans (Aeglidae) from South America with multiple temnocephalan symbionts (Collins, Giri, & Williner, 2011; Giri & Collins, 2014; Martínez-Aquino *et al.*, 2014a; Noreña, Damborenea, & Brusa, 2005). Also, there is a known ancestral connection between both basins (UBS, LAP) supported by freshwater fauna (Arzamendia & Giraud, 2009; Cuhna-Ribeiro, 2006; López, Menni, Donato, & Miquelarena, 2008). Furthermore, the UBS and the LAP River Basins contain a considerable degree of endemic

Temnocephalida (eight endemic species each; Appendix S8, see supplemental material online). In this context, it is also possible to consider each basin as a separate area of endemism (e.g., Arzamendia, Giraud, & Bellini, 2015; Dos Santos, Emmerich, Molineri, Nieto, & Domínguez, 2015; Ferretti, González, & Pérez-Miles, 2012; Morrone, 2014a).

The genus *Temnocephala* is an endemic component of the Neotropical region, with a great diversity of hosts: the decapods are the most species-rich host of temnocephalans (28), followed by the snails (seven taxa) and insects (five species) (Arias-Pineda et al., 2015; Martínez-Aquino et al., 2014a; Seixas et al., 2015a, b). The evolutionary history of *Temnocephala*'s host groups has been inferred for neotropical freshwater river basins in several studies (e.g., Hayes, Cowie, & Thiengo, 2009; Liu, Wang, Shih, Ren, & Yang, 2012; Morrone, Mazzucconi, & Bachmann, 2004; Noonan, 2000). Particularly, the distribution patterns of *Temnocephala* in the Neotropical region is explained based on their associations with crustacean groups, being the taxa with the most temnocephalans for America; e.g., 17 taxa of *Temnocephala* are associated with three families of freshwater crab hosts (Aegliidae, Pseudothelphusidae, and Trichodactylidae), while five *Temnocephala* species are associated with eight taxa of freshwater shrimps included in three families (Cambariade, Palaemonidae, and Parastacidae) (Cannon & Joffe, 2001; Lamothe-Argumedo, 1968; Martínez-Aquino et al., 2014a; Riek, 1972). Cannon and Joffe (2001) mentioned that *Temnocephala* have migrated as far as the north of the Neotropical region (Mexico), based on the association with parastacid crayfish. The Generalized Track 3 obtained in this study does not support this hypothesis. However, it is possible that the extension of the distributional area of *Temnocephala* in the Neotropical region was caused by the contraction-expansion events undergone by crustacean migrations of the Most Recent Common Ancestor (MRCA) of each host group; e.g., crayfish (Álvarez, Villalobos, Armendáriz, & Hernández, 2012; Collins et al., 2011; Cumberlidge, Alvarez, & Villalobos, 2014; Feldmann & Schweitzer, 2006; Giri & Collins, 2014; Pérez-Losada, Bond-Buckup, Jara, & Crandall, 2004). In this context, testing a geographic range evolution model of dispersal, combined with host-switching events, can support or reject this hypothesis (Hoyal Cuthill et al., 2016; Martínez-Aquino, 2016; Ree & Smith, 2008). On the other hand, this hypothesis can also be supported by the discovery of new records of *Temnocephala* associated with crustaceans distributed in Central and South America, such as pseudothelphusid crabs from Mexico, Ecuador, and Colombia (Arias-Pineda et al., 2015; present work). Furthermore, several distributional patterns between biota of freshwater river basins from Central and South America can also support these inferences (Hayes et al., 2015; Mayén-Estrada & Aguilar-Aguilar, 2012;

Mercado-Salas, Pozo, Morrone, & Suárez-Morales, 2012; Van Damme & Sinev, 2013).

Generalized Track 4

This is the most interesting biotic component because of its geographic location (South-east Europe), ecological characteristics (freshwater subterranean environments), and degree of endemism; e.g., four endemic genera and a total of 11 endemic species of Scutariellidae (Table 2; Fig. 10). It is important to mention that the Black Sea South Coast River Basin (BSC) is found close to this track, but does not form part of it, even though the basin includes two genera distributed in the areas Danube (DAN) and Adriatic Sea (ADS) (*Scutariella* and *Troglocaridicola*; Figs S1–3). This may be due to the fact that the species included in BSC (*S. georgica* and *T. mrazeki*), are considered microendemic species (Gottsetein-Matočec, 2002; Sket, 1999; Sket & Stoch, 2014). Therefore, the CADE analyses did not detect biogeographic homology between DAN + ADS and BSC. However, Altermatt et al. (2014), Gottsetein-Matočec (2002), and Sendra and Rebolera (2012) mentioned that the temnocephalids and their hosts are a poorly surveyed group in this European region. Particularly, the crustacean hosts (*Troglocaris*) can elucidate information on European temnocephalids because they show phylogenetic and biogeographic structure for the same distribution patterns inferred in the Generalized Track 4 (Jugovic, Jalžić, Prevorčnik, & Sket, 2012; Jugovic, Prevorčnik, Blejec, & Sket, 2011; Sket & Zakšek, 2009; Zakšek, Sket, & Trontelj, 2007; Zakšek, Sket, Gottstein, & Franjevic, 2009).

Generalized Track 5

The relationships detected between areas (MAI, SLA, GBI) in this track support a vicariant event for freshwater biota (i.e., potamid crabs) from the oriental mainland and the Sri Lanka River Basin (Shih & Ng, 2011; Shih, Yeo, & Ng, 2009; Shih, Zhou, Chen, Chien, & Ng, 2011). Furthermore, SLA presents an endemic scutariellid genus that includes two endemic species (*Monodiscus mcbridei* and *M. parvus*), suggesting that the fragmentation has been a factor for speciation (Beenaerts et al., 2010; Bossuyt et al., 2004).

Generalized Track 6

Biogeographic patterns of the Generalized Track 6 were discovered from Matrix 4 and 5 (Appendices S6 and S7, see supplemental material online). We interpret the results of the Generalized Track 6 based on the total matrix (Matrix 5). A Gondwanan pattern is apparent for Temnocephaloidea, congruent with major vicariant events; e.g., the fragmentation of Madagascar, southern Africa, and

analyses with molecular clock dating (Ceccarelli et al., 2016; Ronquist et al., 2012; Yang & Rannala, 2012).

Based on the distribution of Scutarielloidea, congruence with major vicariant events can be recognized. The geographic location of the areas included in the General clade, plus the areas that are included in the hybrid zones support the hypothesis that the MRCA of Scutarielloidea was located in India (Fig. 12). The biological radiation of Scutarielloidea was probably associated with major geological events; e.g., the collision of the Indian plate with Asia (100 Mya), and the separation of Sri Lanka (SLA) from India (70 Mya). This hypothesis can be tested and contrasted together with the ancestral symbiont host groups; e.g., freshwater crabs of the family Potamidae (Shih et al., 2009; Shih et al., 2011). Furthermore, the distribution of scutariellids from North India (NIN) to Yangtze (YAN) and West China (CHC) (Fig. 11), may be explained by their expansion with their ancestral hosts after the contact of the Indian Plate with Asia (Cumberlidge et al., 2011; Shih & Ng, 2011; Shih et al., 2009). Finally, the extension of scutariellids from CHC to Japan (JAP) and Taiwan (TAI), may have been caused by dispersal events of their hosts (e.g., Potamidae), via land-bridges as postulated for the East Asian Islands (Shih & Ng, 2011 and citations therein) (Fig. 13).

In the case of the European temnocephalids, the geographic disjunction based on biogeographic homology is difficult to explain because central Europe did not exist in Gondwanan times (Plant, Whittaker, Demetriades, De Vivo, & Lexa, 2003; Sanmartín, Enghoff, & Ronquist, 2001). Also, it is difficult to explain an event of long-distance dispersal from India to central Europe, because the host(s) (e.g., cave shrimps of the genus *Troglocaris*) must have crossed multiple geographic barriers during the fusion of India with Eurasia, e.g., mountain chains or seas. In contrast with the theory mentioned by Cannon and Joffe (2001) with respect to the inference of the age of origin of Scutarielloidea (≈ 100 Ma), different authors mentioned that the age of their troglobite crustacean hosts is relatively recent (5.3–3.7 Mya), and that their origin was influenced by marine introgression events (Zakšek et al., 2007). In this context, the origin of the European temnocephalids has not yet been unambiguously defined. More interestingly, based on the evolution of their hosts, it is important to test the monophyly of Scutarielloidea, since the European taxa may be paraphyletic.

The results in this study were obtained based on PAE approaches. In fact, PAE has been criticized for four main failures. (1) It will only recover correct historical relationships when species undergo a particular combination of vicariance and non-response to vicariance. (2) It does not use any phylogenetic information. (3) Areas may be grouped together by shared absences, but character change is not examined. (4) It is susceptible to being

misled by shared episodes of post-speciation dispersal (e.g., Brooks & van Veller, 2003; Porzecanski & Cracraft, 2005). However, other authors defend PAE based on the fact that criticisms of this method usually stem from three issues. (1) Misunderstanding of the method's theoretical basis. (2) In a 'cladistic biogeographic context', the critics' arguments are circular because they refer to biogeographic analyses based on phylogenetic hypotheses. (3) PAE is an efficient tool for identifying areas of endemism. Readers interested in a more detailed discussion of the pros and cons of PAE and its techniques might consult Morrone (2014b and citations therein). In this study, despite being aware of the method's limitations we use PAE for the purpose of pattern retrieval to infer primary biogeographic homology (Morrone, 2015b) in the absence of phylogenetic information for the taxa. We consider PAE to be an effective and rigorous method to detect similarities between areas expressed in the shared presence of taxa (such as other statistical methods, e.g. UPGMA, Ward, Bray–Curtis and Jaccard; see Aguilar-Medrano, Reyes-Bonilla, & Polly, 2015; Bradshaw, Colville, & Linder, 2015), while implementing the parsimony algorithm to test historical reconstruction hypotheses.

Conclusions

In this study we tested several biogeographic patterns under the influence of Gondwanan fragmentation and found areas with high endemism and species richness (e.g., East Coast Australia [ECA]), that can be key to understanding the diversification processes of Temnocephalida. Also, we detected primary biogeographic homology using hierarchical-taxonomic information: six generalized tracks, four hybrid zones, and one General clade. Based on the integration of the results obtained by pattern-based biogeographic methods, all the Gondwanan hydrological systems were grouped in accordance with previous proposals based on other animal taxa (e.g., Morrone, 2015a; Sanmartín & Ronquist, 2004). Based on the distribution patterns, we infer the geological effect on the deep diversification of Temnocephalida and contrast their distribution with the evolutionary history of some of their hosts (Fig. 5). On the other hand, this study shows evidence in contrast with previous hypotheses presented as an explanation for the distribution of Temnocephalida, e.g., Scutarielloidea (Cannon & Joffe, 2001). The present study demonstrates the utility of the pattern-based biogeographic tools, using taxonomic records to detect primary biogeographic homology at several hierarchical-taxonomic levels. A more accurate biogeographic analysis should be undertaken in the future by considering a phylogenetic hypothesis based on molecular data and incorporating information of their hosts, fossils, and geological evidence; i.e., parametric biogeography (Drinkwater,

Qiao, & Charleston, 2016; Klompmaker & Boxshall, 2015; Martínez-Aquino, 2016).

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Supplemental data

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