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Biogeographic Hierarchical Levels and Parasite Speciation

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1. Introduction

The historical biogeography of freshwater fish helminth parasites is linked to speciation. It is well recognized and documented that bursts of speciation are often limited to certain periods of geological time (Eldredge & Gould 1972; Gould & Eldredge; 1977, Gould, 2002; Hoberg & Brooks, 2008) and is highly dependent on the space in which it occurs (Brooks & McLennan, 2002; Hoberg & Brooks, 2008; Lieberman, 2003; Vrba, 2005). This holds for free-living organisms and parasites as well (Brooks & McLennan, 1993b; Hoberg & Brooks, 2008). Empirical evidence supports the contention that freshwater fish helminth parasites have mainly speciated allopatrically through two processes, vicariance and dispersal via host switching when the host has moved into novel areas, i.e. dispersal across pre-existing barriers (physical change *sensu* Vrba, 2005) (Brooks and McLennan, 1991, 1993b, 2002; Choudhury & Dick, 2001; Poulin, 1998). This suggests that the evolutionary biology of helminth parasites should have a strong biogeographical component, one that acts above the species level and to a lesser extent may have been driven by coevolutionary phenomena (Brooks and McLennan, 2002; Pérez-Ponce de León & Choudhury, 2005; Hoberg & Brooks, 2008). It is currently recognized that two processes, linked cyclically in time and space, have produced these patterns in parasite historical biogeography: taxon pulses (TP; Erwin, 1981; Hoberg & Brooks, 2008; 2010) and ecological fitting (EF; Janzen, 1985; Hoberg & Brooks, 2008, 2010).

TP have a strong biogeographical component. TP coupled with EF can explain several phenomena linked to parasite diversity in space and time, parasite richness across wide-ranging geographical areas, and the geography of diseases (emerging infectious diseases, EID; Brooks & Ferrao, 2005; Hoberg & Brooks, 2008). The coupling of TP and EF has scarcely been explored outside the context of recent events in parasite epidemiology (Hoberg & Brooks, 2008, 2010). The pattern that can identify the occurrence of TP in deep phylogenies has been little explored before the Cenozoic period, except for tethrabotheiidean cestodes (Hoberg & Brooks, 2008). Outbursts of speciation are probably linked to both micro- and macro- spatial and evolutionary scales; on a macroevolutionary scale TP probably are linked to punctuated events of speciation, with a predominance of peripheral isolates speciation or postdispersal speciation after an expansion phase and not especially to *in situ* speciation due to isolation and environmental heterogeneity (Hoberg & Brooks, 2008, 2010; Vrba, 2005).

EF combines both biogeographical and ecological components (Hoberg & Brooks, 2008). This purportedly common phenomenon suggests that parasite evolution might be linked to resource tracking more than to coevolutionary phenomena (Agosta & Klemens, 2008; Agosta et al., 2010; Brooks & McLennan; Brooks et al., 2006; Hoberg & Brooks, 2008). This has not only short-term implications in parasite evolution but also long-term implications that provide insight into deep phylogenies and therefore historical biogeographical analyses. A historical biogeographical pattern can reveal instances of EF in a relatively straightforward fashion; namely, a parasite with a wide-ranging distribution, but limited to few host taxa, when the host taxon is much more diverse than the parasites inhabiting it (Brooks & McLennan, 2002). The process that generates this pattern involves parasite exploitation of newly available resources without having to evolve novel capabilities for host utilization (Hoberg & Brooks, 2008).

Freshwater fish parasitic helminths have been used as examples of host-parasite interactions for nearly three decades at the micro and macroevolutionary level, and at micro and macrobiogeographical scales (Brooks & McLennan, 1993, 2002; Choudhury & Dick, 1996, 1996, 20001; Mejía-Madrid et al., 2007a,b; Pérez-Ponce de León & Choudhury, 2005; Pérez-Ponce de León et al., 2007; Rosas-Valdez et al., 2008; Choudhury, 2009). Nevertheless, the influence of TP and EF has not been addressed directly to explain pattern and process in deep phylogenies of fish parasites, in contrast to well-explored hypotheses that deal with primates (Brooks & Glen, 1982; Brooks & McLennan, 2003; Folinsbee & Brooks, 2007), Beringian mammal parasites (Hoberg & Brooks, 2008), and Palearctic parasites (Nieberding, 2004, 2005). Historical biogeography of freshwater fish helminth parasites would benefit much from such theoretical approaches.

The first aim of this chapter is to extend the phylogenetic and historical biogeographical analysis of *Rhabdochona* Railliet, 1916 species to include a more detailed account of the recent theoretical developments of TP and EF relative to freshwater fish helminths. It is entertained herein that the inclusion of such developments will help clarify to a certain extent how the deep phylogeny of a monophyletic clade of freshwater nematode parasites is related to phenomena that have not been previously considered, but are closely related to their historical biogeography. The second aim is to interpret these results across a wide spectrum of natural history data within a phylogenetic and historical biogeographical framework, including: speciation, comparison of modern distributions of hosts and parasites with fossil distribution of marine and freshwater fishes, their diversification intervals, sequential heterochrony, the spatial scale at which the phylogeny takes place, and phylogeography. Whereas it is clear that the present chapter focuses on the interpretation of hierarchical patterns in historical biogeography (Sanmartin et al., 2001), the uncertainties associated with the patterns presented here cannot be assessed at this stage of discovery.

1.1 Definition of biological terms employed

The historical biogeographical analysis employed here is based mainly on the “discovery based” protocol of van Veller & Brooks (2001), Halas et al. (2005), Hoberg, (2001), Hoberg & Brooks (2008), and Lieberman (2003). This approach is preferred in the present case because it includes all empirical information available to explain patterns of deep historical biogeography and includes no *a priori* assumptions of geological evolution or host evolution (Hoberg & Brooks, 2010). Such approach has been called phylogenetic biogeography

(Hennig, 1966; Brundin, 1981; van Veller & Brooks, 2001). Terms related to TP and EF follow Hoberg & Brooks (2008).

The historical species concept here used is the PSC1 (Phylogenetic Species Concept 1, Cracraft, 1989; Brooks & McLennan, 2002; Coyne and Orr, 2004) because where there is ecological fitting and long standing stasis, probable ancestors coexist with descendants for a considerable amount of time, during which time the process of host switching to novel resources and subsequent speciation takes place (Brooks & McLennan, 2002). Despite the fact that phylogenetic systematics has a strong gradualistic basis (Wagner & Erwin, 1995; Hennig, 1966; Wiley & Lieberman, 2011; but see Eldredge & Cracraft for a different point of view) no *a priori* considerations on the scale of evolution are entertained here, e.g., phyletic gradualism or punctuated equilibrium. Nevertheless, PSC1 is simply interpreted as pattern and the processes considered herein imply speciation promoted by physical change (Vrba, 2005).

Net diversification interval (NDI) was calculated for different parasitic nematode taxa after Stanley (1975, 1998; Coyne & Orr, 2004). These calculations employ data on numbers of extant helminth parasite species, especially those within monophyletic clades where rate of description of new species has achieved or is near stabilization. The date of calibration is taken from the most ancient fossil host related to present day clades. As siluriforms are considered the original hosts of *Rhabdochona* spp. (Moravec, 2010), the calibration point is taken to be 140 mya (Ferraris, 2007; Lundberg et al., 2007).

Heterochrony - changes in the relative time of appearance and rate of development for characters already present in ancestors (Gould, 1977) - is understood here as sequential heterochrony which conceptually incorporates timing of metamorphosis from one growth stage to another (McNamara & McKinney, 2005). Sequential heterochrony can account for the origin of certain characters of *Rhabdochona* spp. in relation to host switching and dispersal of hosts.

Finally, the phylogeography of one species of American *Rhabdochona* will be addressed in order to demonstrate that these particular nematode parasites have low speciation rates when compared to the number of species of hosts they inhabit.

2. The historical biogeography of *Rhabdochona* species: An overview

Rhabdochona species are a world-wide group of spirurid nematodes that inhabit all continents as intestinal parasites of freshwater fishes (Moravec et al., 2011). Recent molecular studies have removed them from Thelazioidea (Černotíková, et al., 2011; Nadler et al., 2007). Their outstanding morphological characters include a wide prostom, a character shared with other nematodes, several longitudinal cuticular ridges internal to the prostom that anteriorly (prorhabdion) form teeth, sessile caudal male papillae arranged in paired ventrolateral rows, eggs with different ornamental covers, and peculiarly-shaped male spicules. Some of the aforementioned characters are shared with other putatively phylogenetically related groups (Černotíková, et al., 2011; Mejía-Madrid et al., 2007a; Nadler et al., 2007), i.e., polar filaments on egg surface (*Cystidicola* spp., some species of *Spinitectus*), a wide prostom (*Megachona chamelensis* Mejía-Madrid & Pérez-Ponce de León, 2007), and caudal papillae (Physalopteridae, Cystidicolidae, and Spinitectidae). Despite the generality of most of the characters used for classifying *Rhabdochona* spp., spicular morphology

remains peculiar and possesses variation almost unique to this group of nematodes (*Spinitectus* spp. shows a similar variation). The form of this character is species specific to *Rhabdochona* spp. (Mejía-Madrid et al., 2007a; Moravec, 2010; Rasheed, 1965). Indeed, the first phylogenetic systematic analysis of this group recovered spicule form as a consistent character (Mejía-Madrid et al., 2007a). The intraspecific variability of the aforementioned character is quite limited, as a study of different spicules of North American species indicates (Mejía-Madrid, unpublished data).

Rhabdochona spp. belong to the family Rhabdochonidae. Among the 10 genera of Rhabdochonidae, 8 contain species that parasitize chondrichthyans and teleosts, and from these only 3 (*Beaninema* Caspeta-Mandujano et al., 2001; *Prosungulonema* Roytman, 1963, and *Rhabdochona*) include species that parasitize freshwater fishes (Mejía-Madrid & Pérez-Ponce de León, 2007). Nevertheless, *Rhabdochona* is the most diverse genus of this family, with 92 valid species (Moravec et al., 2011).

A phylogenetic and historical biogeographical analysis of *Rhabdochona* species is now due mainly because the systematic research on the whole genus is reaching a stage of maturity that is reflected in the stabilization of species rate discovery (Mejía-Madrid, unpublished data), and because of the quality of new descriptions and redescrptions (Sánchez-Álvarez et al., 1998; Caspeta-Mandujano & Moravec, 2000, 2001; Mejía-Madrid & Pérez-Ponce de León, 2003; Mejía-Madrid et al., 2007a; Moravec & Muzzall, 2007; Moravec et al., 2011). Such detailed morphological descriptions are essential for a clear distinction between species. Additionally, the molecular database of *Rhabdochona* spp. from Asia, Europe, and America is increasing (Černotíková et al., 2011; Mejía-Madrid & Nadler unpublished data; Wijowá et al., 2007). In the present analysis 37 out of 92 (40%) valid species have been included, mainly because this set of species is fairly well described for their main discriminant character, the male left spicule, as well as for other key characters (Mejía-Madrid et al., 2007a; Moravec, 2010; Moravec et al., 2011). The American species are completely represented in the present analyses, but I include representative species distributed worldwide, with the exception of *R. papuanensis* Moravec, Ríha & Kuchta, 2008.

The historical biogeographic analysis presented here is based on the updated matrix used for generating the phylogenetic framework of *Rhabdochona* spp. presented in Mejía-Madrid et al. (2007a) with additional character coding derived from recently redescrbed species from the Americas and Asia (Moravec & Muzzall, 2007; Moravec, 2010; Moravec, et al., 2011; Figure 1). The results presented herein represent a new phylogenetic framework for *Rhabdochona* spp., with two outstanding characteristics: the phylogeny is fairly well resolved and the degree of resolution is higher than that previously recovered.

Historical biogeographical analysis of *Rhabdochona* spp. reveals an ancient origin for the group that probably predates current continental configurations (Mejía-Madrid et al., 2007a; Moravec, 2010; Figures 2-4). Extant species distributions reflect past distributions, nevertheless these are the product not only of vicariance but also of past dispersal in a limited geographical range: however, these are difficult to distinguish from phylogenies alone (Brooks & McLennan, 2002 and references therein; Brooks & Ferrao, 2005; Wagner & Erwin, 1995). A reticulated historical biogeographical pattern is apparent when the phylogeny of *Rhabdochona* is interpreted graphically. This pattern reveals that if a) *Rhabdochona* species tend to remain relatively near their area of origin (Roy et al., 2009), closely related species in the phylogeny should inhabit neighbouring areas. This can be interpreted as vicariance and therefore b)

where species that do not conform to this pattern (e.g., exhibiting disjunct distributions, but with closely related species widely separated geographically), this can be interpreted as the product of past or relatively recent dispersal.

Furthermore, in the present case, *Rhabdochona* spp. might be interpreted as ‘ancient’ ecological relicts (Hoberg & Brooks, 2008) in that their original hosts underwent widespread extinction and survived into deep (not shallow) time through colonization and secondary radiation into a novel, but ecologically equivalent, host group, namely, the cyprinids, where they have succeeded ever since host switching from the silurids.

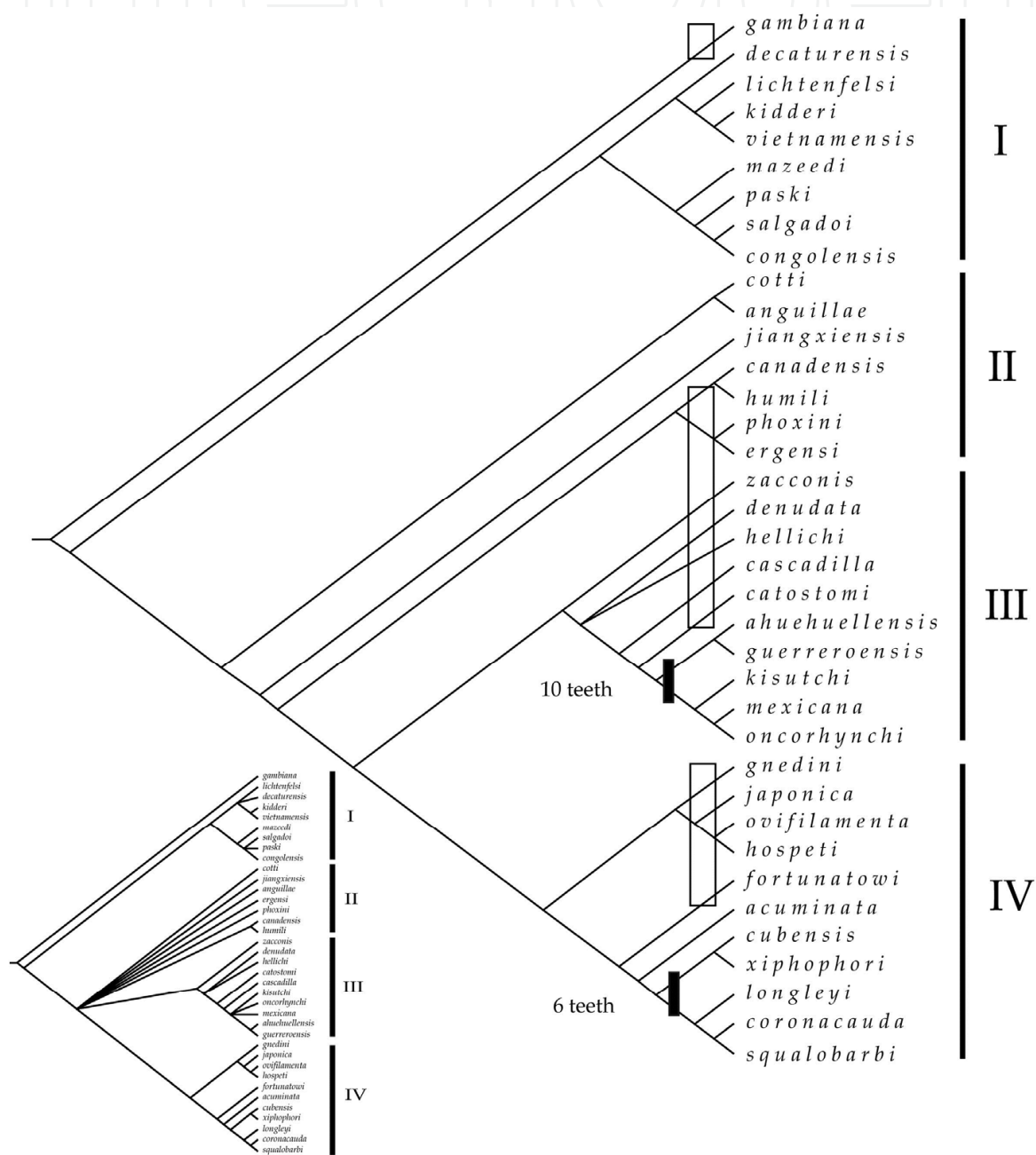


Fig. 1. Phylogeny of *Rhabdochona* species. Majority rule tree of 538 trees. Inset: strict consensus tree. Rectangles represent cypriniform hosts. Black hashmarks represent characters shared by members of clade.

The basal clade of *Rhabdochona* (Figure 1, clade I) is represented by the African *R. gambiana*, a species that parasitizes basal cyprinids from rivers in West Africa, and from the African Rift Lakes (Moravec, 1972). It is followed by an assemblage of African species that parasitize siluriform and characid fishes: *R. paski*, *R. congolensis* in several basins in South Africa and the African Rift Lakes, plus the Indian species, *R. mazeedi* specific to at least 3 families of siluroids, (Moravec, 1972, 1975, Moravec et al., 2010; Puylaert, 1973). Within this clade a species of *Rhabdochona* from *Profundulus labialis* Günther distributed in southern Mexico is consistently found, namely *R. salgadoi*. An emerging pattern of phylogenetic and historical biogeographical relationships between species of Africa and Southern Mexico is becoming apparent, including a diverse array of coexisting floristic and faunal assemblages. Those assemblages appear to have originated in other parts of the world, and exhibit extralimital affinities and origins (Lundberg et al., 2007). For example, the freshwater siluriform fish, *Lacantunia enigmatica* Rodiles-Hernández, Hendrickson, Lundberg & Humphries is endemic to Southern Mexico but is morphologically and molecularly related to the claroteids of Africa but to no other siluriform fish in North America (Lundberg et al., 2007). This distribution pattern has been recovered in phylogenies of Upper Jurassic, Cretaceous and Lower Palaeocene freshwater and marine fossil teleosts (Forey, 2010) and it seems not to be uncommon among other fossil faunas. These areas were probably not contiguous during the geological periods mentioned, but likely were passageways when environmental conditions favoured dispersal (Lundberg et al., 2007).

The sister subclade of the “African” clade just described is that of a group of species that indicate a relationship between North America and eastern Asia. To what extent this clade reflects former exchanges between the fish faunas of the Far East and eastern North America remains a matter of debate (Sanmartín et al., 2001). Modern disjunct fish distributions probably date back to the Late Mesozoic and might have resulted from a cross-Atlantic division (Sanmartín et al., 2001). In the aforementioned sister subclade three North American parasite species, *R. lichtenfelsi*, *R. decaturensis* and *R. kidderi* (the latter parasitic in cichlids and pimelodids of cenotes and caves, respectively, refugia for relict fish species) are related to an eastern Asian species (*R. vietnamensis*). All of these parasite species occur among diverse fish families where cyprinids are completely absent. The distribution of this clade is similar to the modern relict distribution of horseshoe crabs and other marine fishes. To what extent *Rhabdochona* spp. were dispersed by marine seaways will be discussed below.

Clade II is still unresolved in the strict consensus tree (Figure 1). This clade comprises a group of 5 species in a polytomy and another with two sister species (*R. canadensis* and *R. humili*) that probably were dispersed across a Northern proto-Atlantic.

Clades III and IV are fully resolved and comprise *Rhabdochona* spp. that predominantly infect cyprinids, and to a lesser extent, catostomids, silurids, poeciliids, and characids (Figures 1 and 4). Clade III comprises species that parasitize some Cypriniformes in central and eastern Asia plus Eastern Europe and predominantly salmonids from eastern Asia, Western North America and goodeids down into Central Mexico. One or several episodes of dispersal through Beringia may have left tracks in the distribution of *Rhabdochona* spp. Host switching from cyprinids to salmonids during invasion could have been the mechanism that triggered speciation within this clade for there seems to be a consistent evolutionary novelty among these species, namely, 10 teeth in prostom.

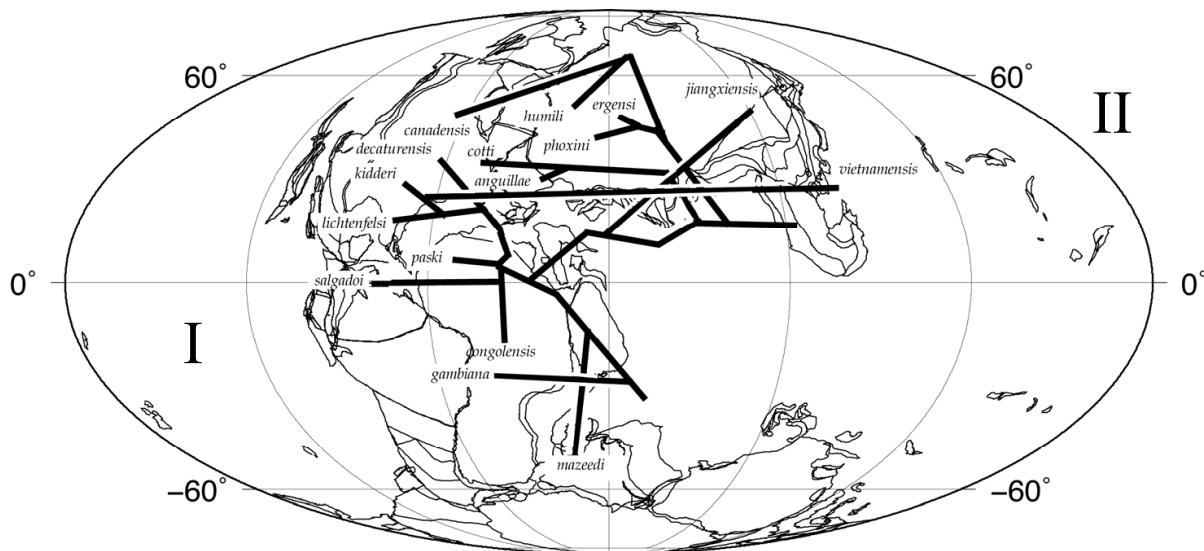


Fig. 2. Basal clades I and II of the phylogeny of *Rhabdochona* species superimposed on a world paleomap of the Lower Cretaceous c. 140 mya. Species names are approximately located in their area of distribution for clarity. Only the outline of tectonic plates is shown. Map and localities generated by <http://www.ods.de/ods/services/paleomap/paleomap.html>

Clade IV is represented by species that are distributed from central Asia to eastern Europe (*R. fortunatowi*, *R. gnedini*) and North America (*R. ovifilamenta*), South America, Mexico (*R. acuminata*), Cuba (*R. cubensis*), and the southern United States (*R. longleyi*, inhabitant of cave-dwelling blind catfishes). This series of dispersal events probably was limited to the western and northern Tethys, because there are only two or three species of *Rhabdochona* in South America, where the diversity of freshwater fishes is the largest in the world mainly because of the extension and complexity of the geological history of this sub-continent (Brooks, 1992; Lundberg et al., 1998). Additionally, the distribution of Clade IV seems to follow the tracks of *Spinitectus* spp. (Choudhury & Dick, 2001) and proteocephalid distributions in the modern Holarctic and Palaearctic biogeographic zones (Brooks, 1978; de Chambrier, 2004; Rego et al., 1998). The latter northern helminth faunas are well represented in South America, whereas *Rhabdochona* spp. are almost entirely absent. It is probable that the presence of cyprinids by the end of the Mesozoic Era set the stage for dispersal of *Rhabdochona* spp. in the Tertiary.

The main fish families of each species of *Rhabdochona* analyzed (Figure 4) reveal an apparent history of host-switching, but with an underlying structure: all groups from clade II onwards comprise basal clades where nematodes predominantly parasitize cyprinids (Figure 1), except Clade III that involves a clear salmonid host component and a subclade in IV that includes *cubensis*, *xiphophori*, *longleyi*, and *squalobarbi* and in which teeth number (6) predominates in parasites that inhabit non-cyprinid hosts.

A general comparison was undertaken between the parasite host area phylogeny of *Rhabdochona* spp. (Figure 4) and phylogenies of proteocephalids (de Chambrier et al., 2004; Rego et al., 1998), *Spinitectus* spp. (Choudhury & Dick, 2001), fossil teleosts (both freshwater and marine; Forey, 2010), and Cyprinodontiformes (Parenti, 1981). Discovery based-methods were employed to generate general and particular area hypothesis (BPA and PACT 2.0 software; Wojcicki & Brooks, 2005). Several attempts were made to compare different trees, but as areas recorded for helminth parasites are so distinct (despite the fact that area names

were adjusted in each case), only a single area cladogram could be recovered from the PACT analysis between *Rhabdochona* and Cyprinodontiformes. On the other hand, a single cladogram for fossil fishes (Forey, 2010) emerged and was therefore compared in broad terms with the area cladogram of *Rhabdochona* spp.

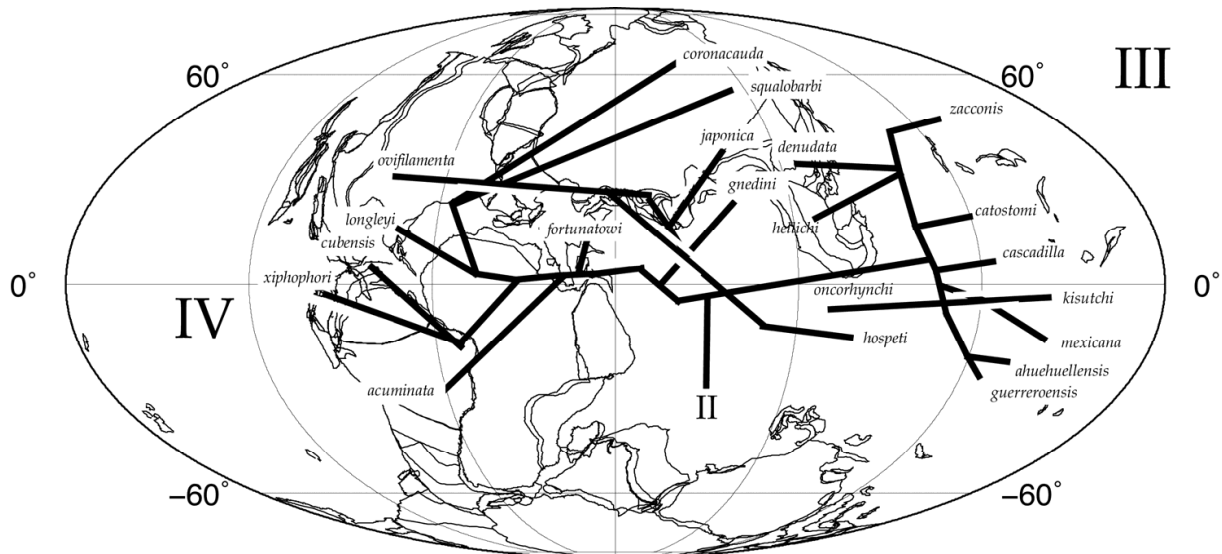


Fig. 3. Clades III and IV of the phylogeny of *Rhabdochona* species superimposed on a world paleomap of the Lower Cretaceous c. 140 mya. Species names are approximately located in their area of distribution for clarity. Only the outline of tectonic plates is shown. Map and localities generated by <http://www.odsn.de/odsn/services/paleomap/paleomap.html>

The PACT tree of Cyprinodontiformes and *Rhabdochona* spp. recovers a series of postdispersal speciation origins for species within clades I and II (Figure 5). This pattern can be inferred as well as when the areas are inspected on the 140 mya map (Figures 2 and 3). Most of the areas are not neighbouring but certainly are coastal marine tracks of southern, western and northern Tethys. It must be noted that there is a time gap between the origin of Old World aplocheiloids and New World aplocheiloids. In between, clades I and II of *Rhabdochona* spp. diversified before Africa and South America separated. So probably later on, geologically speaking, *Rhabdochona* spp. dispersed into western Tethys, where most probably *R. salgadoi* originated.

When compared to the fossil fish PACT tree (Figure 6), *Rhabdochona* spp. can only be compared in very broad terms. The reticulated pattern of areas of fossil fishes is in itself complex. Two episodes of widespread dispersal and probably postdispersal speciation can be inferred: the aforementioned clade I and part of clade IV. While nematode species may conform to a Sea of Tethys distribution, the phylogeny on its own cannot account by itself for a general explanation of a taxon pulse or pulses that took place probably 140 mya. Despite the fact that cyprinodontiforms are freshwater fishes (although some inhabit brackish waters) and therefore have been interpreted as having evolved by vicariance (Parenti, 1981 only invoked vicariance for the present distribution of cyprinodontiforms) the PACT tree could recover postdispersal speciation in the nematode parasites. This indicates that *Rhabdochona* spp. within clade I probably speciated in eastern Africa freshwater drainages of Gondwana and some species reached western Africa later by dispersal when the Congo basin flowed west (Stankiewicz & de Wit, 2006). A reticulated biogeographic

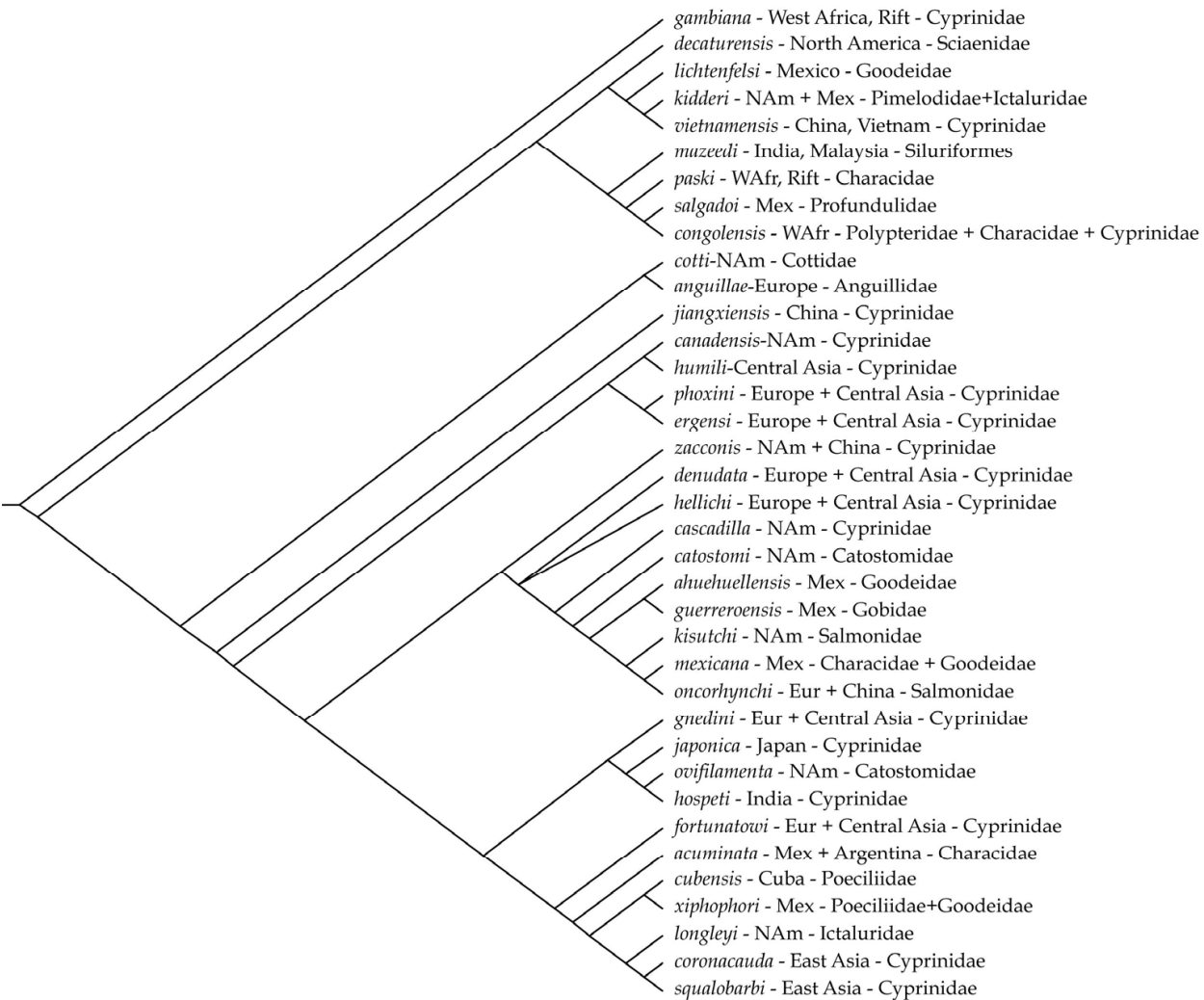


Fig. 4. Parasite-host area cladogram of *Rhabdochona* species.

pattern of fossil fishes distribution might indicate that freshwater and marine dispersion throughout the western Tethys took hold once Laurasia and Gondwana drifted apart (Forey, 2010). *Rhabdochona* spp. seems to have been influenced by this wide-ranging dispersal routes that included South America, Cuba, North America, and all the way to eastern Asia (i.e., the northern Tethys sea and freshwater drainages that flowed into it). Therefore, it seems that *Rhabdochona* was originally a freshwater parasite that has had a deep history of marine dispersion.

Two hypotheses emerge from the historical biogeography pattern seen in *Rhabdochona* spp. First, the original hosts of *Rhabdochona* species were not cyprinids, but some other group of teleosts, probably silurids as mentioned above. The gap seen in host trends between clades I and part of II can be explained by the fact that the other hosts that might have been parasitized by these nematodes probably became extinct by the end of the Cretaceous, along many other groups of vertebrates and plants.

Second, cyprinids, already present in the Cretaceous were already parasitized with *Rhabdochona* through host switching from siluriforms. As cyprinids began to diversify in the early Tertiary, *Rhabdochona* remained in the areas they once inhabited, probably infecting a

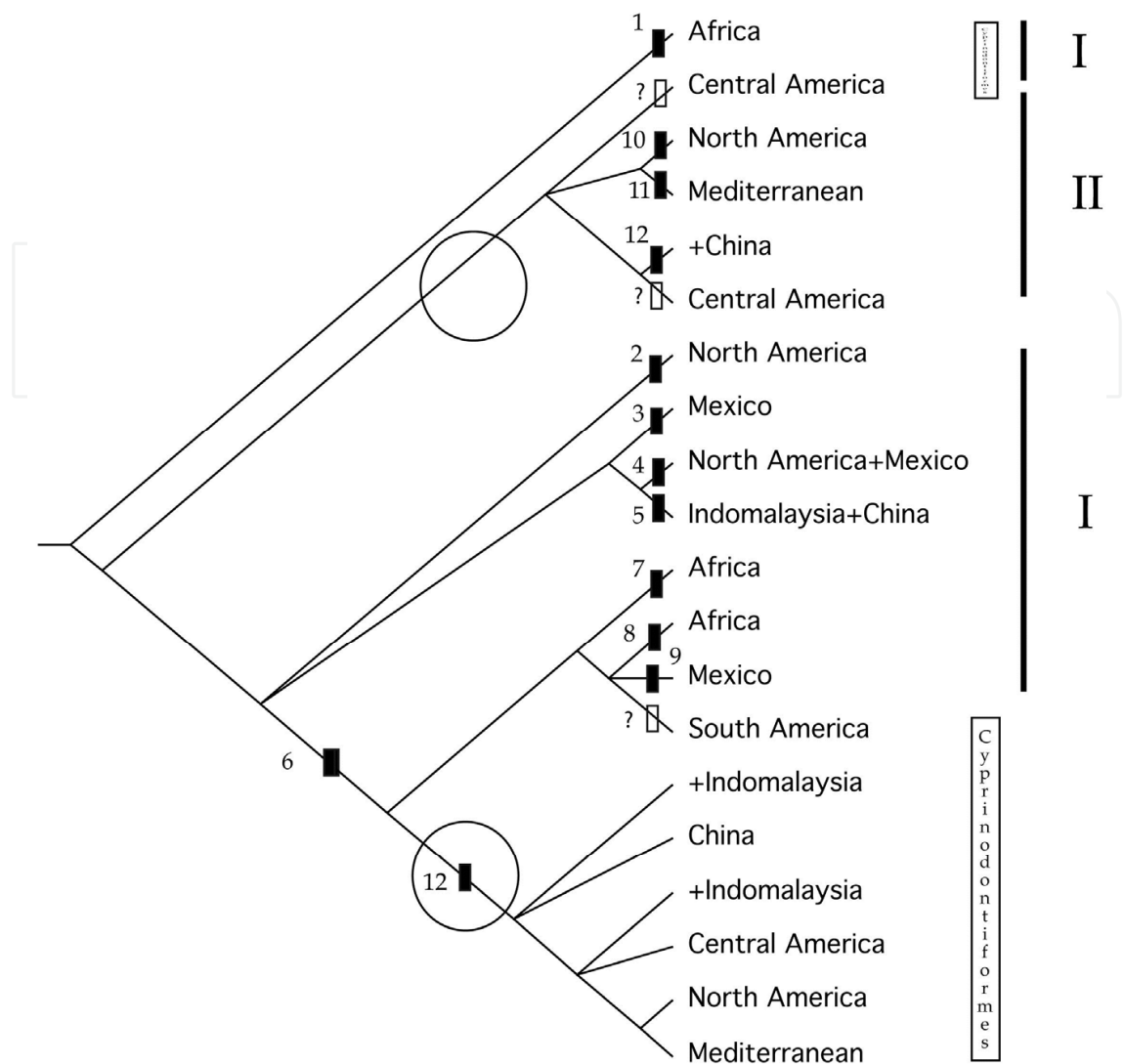


Fig. 5. PACT generated tree from *Rhabdochona* spp. and Cyprinodontiformes area cladograms (data of fishes from Parenti, 1981). Hashmark numbers indicate *Rhabdochona* species: 1=*gambiana*; 2=*decatuensis*; 3=*lichtenfelsi*; 4=*kidderi*; 5=*vietnamensis*; 6=*mazeedi*; 7=*paski*; 8=*salgadoi*; 9=*congolensis*; 10=*cotti*; 11=*anguillae*; 12=*jiangxiensis*. Circles indicate redundant area clades. ?=no response to dispersal/vicariance.

wider range of hosts, but remained in the cyprinids that finally dispersed them to other drainages (ecological relicts). Nevertheless, there seems to be no empirical evidence of cyprinids dispersing through marine waters in the present or past (Cavender et al., 1998; Chen et al., 2008; Hurley et al., 2007; Peng et al., 2006). So, other hosts, probably diadromous fishes, helped disperse *Rhabdochona* spp. in what seems an ancient TP that took place when the major landmasses of Laurasia and Gondwana separated. In this case *Rhabdochona* spp. might have only been sea dispersed but remained in freshwater hosts, as in the case of the diadromous salmonid species, in which marine hosts serve only as dispersal agents, but the parasites only develop in freshwater in appropriate intermediate hosts, i.e., ephemeropterans.

During the Tertiary, *Rhabdochona* could have been dispersed by diadromous salmonids from eastern Asia to western North America during the formation of one of the Beringian land

bridges (Hoberg & Brooks, 2008). Similarly, ancestral acipenserids were diadromous and dispersion of their helminths to North America from Eurasia explains their present distribution (Choudhury & Dick, 2001). In Mexico, although salmonids are mainly restricted to Northwestern Mexico (Miller & Smith, 2005), fossils of these fishes dated from the Late Pleistocene have been found further south and near modern Lake Chapala (Cavender & Miller, 1982; Miller & Smith, 1986; Miller, 2005) and most probably left parasites that evolved in Mesa Central of Mexico and speciated through host switching into species like *R. mexicana*, *R. ahuehuellensis*, and *R. guerreroensis*.

2.1 Taxon pulses as inferred from the phylogeny of *Rhabdochona* species

Taxon pulse patterns seem to conform to long-term biogeographical phenomena (Erwin, 1988; Halas et al., 2005; Marshall & Liebherr, 2000; Brooks & Ferrao, 2005). Clade by clade, *Rhabdochona* species reflect various episodes of TP in the Mesozoic and Cenozoic eras (Figures 2-6). *Rhabdochona* species seem to have had a long history of expansion when it originated in southern Tethys coasts or rivers (Figure 3). It can be inferred that much speciation could have occurred around 140 mya, but many of its representatives have become extinct. The historical biogeographical relationships between African, Asian, Mesoamerican, North American, and European species in these basal clades might indicate that species of *Rhabdochona* are a relict group of nematode parasites of extinct fishes (ecological relicts *sensu* Hoberg & Brooks, 2008). The alternative view is that few species originated ever since, and *Rhabdochona* as a genus has never been really species rich, if compared with closely related groups, like ascarids (Ascaridida) or filarids (Chabaud, 1975; Nadler et al., 2007).

Rhabdochona spp. represents a case where TP probably is the pattern that best explains early postdispersal speciation events during the Cretaceous. If this nematode group evolved as parasites of long extinct teleost fishes, probably ancient silurids, and developed broad ranges (i.e., *R. denudata*) with cyprinid dispersal by EF, it can be inferred that they evolved by host-switching (Mejía-Madrid et al., 2007a). There might be no other more parsimonious explanation as to why *Rhabdochona* spp. represent an ancient nematode stock predating their modern hosts.

Clade III shows a most recent history of TP, i.e., dispersal across Beringia that probably dates back to the last glaciation. Salmonid fishes inhabited naturally Central Mexico most probably during the Pliocene, just before the recorded draught that originated the modern Sonoran Desert (Miller & Smith, 1986). Remnants of these former freshwater fauna include *Oncorhynchus chrysoleucas* from Northwestern Mexico. Fossils from salmonids have been found in former Lake Chapala in western Mexico. So, most probably there is strong evidence that *Rhabdochona* spp. that parasitize freshwater fishes of Central Mexico related to species of salmonids that range from eastern Asia to North America, are probably a consequence of dispersal along a broad front during an episode of expansion from eastern Asia to North America (Mejía-Madrid et al., 2007a). The similarity in their morphology, especially the presence of a closely similar left spicule form in males, makes them a good candidate for a pattern of a recent episode of TP just before habitat fragmentation due to the desertification of southern North America that left as evidence of a once humid and freshwater landscape nematodes that parasitize modern freshwater fish faunas. This pattern represents a contraction of once widespread taxa, such as goodeid fishes (Domínguez &

fishes or their ancestors by EF once their original hosts become extinct at different periods during the Cretaceous. This is exemplified by *R. anguilla*, which is a parasite specific to European freshwater eels. Freshwater eels seem to have originated in the Far East (Bastrop et al., 2000; Tsukamoto et al., 2002) and then dispersed through the Indian Ocean to the rest of Asia and into Europe. *Rhabdochona anguilla* is not present in Asian eels. The aforementioned then was a former parasite of another teleost, because it appears to be the sister species of *R. cotti*, a parasite of eastern North American Cottidae, a fish family with mostly marine representatives.

3. Speciation and stasis of *Rhabdochona* species

Parasites leave few fossils and lack a substantial fossil record when compared to free-living, hard skeleton species. So, diversification or speciation times of parasites based on modern species numbers are outstanding. A molecular clock approach has rarely been used in the case of nematodes, either free-living or parasitic as dates of divergence vary from taxon to taxon (Kiontke & Fitch, 2005). In order to explain how species diversity affects the historical biogeography of *Rhabdochona* spp., speciation intervals (as indicated above) were calculated to address: a) speciation periods and therefore, stasis times of *Rhabdochona* spp. and b) the depauperate condition of *Rhabdochona* compared to the number of potential extant hosts into which they could have diversified. A calculation of this type is more reliable when a fossil record exists, but such a record does not exist for nematodes (Poinar, 1984). I propose that a calculation of NDI (see Coyne & Orr, 2004) can indicate a first approximation of the rates and intervals of diversification of certain parasite clades. NDI values were calculated for monophyletic parasite clades. Some taxa of Platyhelminthes are used to compare the NDI of different groups of parasites not related to nematodes (Table 1).

The equation employed is:

$$t/\ln N_t = \text{NDI} \quad (1)$$

where t is the age of the parasite taxon (calibrated from its putative original hosts), N_t , the number of extant species (Coyne & Orr, 2004; Gould, 2002; Stanley, 1975, 1998). When compared to other invertebrate species where a fossil record exists, metazoan parasites score near or higher than their free-living relatives in their diversification intervals (Coyne and Orr, 2004; Stanley, 1998). This would mean that nematode and plathyhelminth parasites have longer diversification intervals than their hosts, in general. NDI calculations are dependant on the number of species described or estimated and cannot incorporate extinct species.

In terms of historical biogeography, ecological fitting can be explained in terms of long diversity intervals, e.g., long periods intervening between one diversification event from another, where speciation is probably low and is replaced by resource tracking. This may mean that *Rhabdochona* spp., have been around since the Cretaceous parasitizing different groups of fishes mainly by EF. Such data, when compared to that of their hosts, can only indicate that long diversification intervals are a common feature in metazoan parasites, and may be interpreted as longer stasis periods as compared to that of their fish or other vertebrate hosts.

Monophyletic clade ¹ Helminth parasites	Number of extant species	t (ranges in millions of years) ³	NDI	Host calibration	References on host origin/ parasite clade
Monogenea ²	4998	466	54.7	Origin of Agnatha	our estimates
		460.5	54.0		
Digenea	11846	416	44.3	Origin of Placodermi	Brooks & McLennan, 1993
		411	43.8		
Eucestoda	3851	350	42.4	Origin of Vertebrata	Hoberg et al., 1999
		420	50.8		
Ascaridoidea	818	306.5	45.7	Oldest reptile fossils	our estimates
		311.7	46.4		
Oxyuroidea	725	416	63.1	First terrestrial arthropods	
Dracunculoidea (Moravec, 2006)	160	306.5	60.3	Oldest reptile fossils	
		311.7	61.4		
Camallanidae	348	306.5	52.3	Oldest reptile fossils	
		311.7	53.2		
Physalopteroidea	291	374.5	66.0	First tetrapods	
Trichostrongylidae	130	374.5	76.9		
<i>Rhabdochona</i> (Moravec, 2011)	92	140	30.9	Silurids	
Fish hosts ⁴					
Cyprinidae	23000	48.6	4.8	-	our estimates/Stanley 1998
		55.8	5.5/5.6		
Siluridae	104	11.6	2.49		our estimates
		5.3	1.1		
Siluriformes	3000	99.6	12.4		
		65.5	8.1		
Ictaluridae	-	-	13.2		Stanley 1998
<i>Gambusia</i>	-	-	1.6		Stanley 1998
Salmonidae ⁴	225	48.6	8.9		our estimates
		40.8	7.4		

Table 1. Net diversification rates (NDI) of some metazoan parasite clades (helminths) and some common hosts of *Rhabdochona*. ¹Clades as they appear in phylogenies regardless of hierarchical nomenclature. ²Parasite species counts according to <http://insects.tamu.edu/research/collection/hallan/0SYNOPT1.htm> unless otherwise stated. ³After *The Fossil Record 2* (Benton, 1993) except for Siluridae. ⁴<http://www.fishbase.org>. See text for explanation.

From the foregoing data, it may be inferred that parasites do not have time lags in their speciation as compared to their hosts (Brooks, 1981; Brooks & McLennan, 1993; Manter, 1963; Choudhury et al., 2002). As invertebrates, metazoan parasite species have longer stasis periods, as seen through NDI, than their vertebrate hosts. EF appears to have been the structuring force behind parasite colonization/dispersal. This helps explain why not every freshwater fish has a *Rhabdochona* species, and why there are only 8000 species of Digenea, while there are more than 40,000 species of potential vertebrate hosts to be infected (Hugot et al., 2001). A similar observation was inferred from gyrodactylid phylogenies (Simková et al., 2006; Zietara, & Lumme, 2002).

Additionally, nematode parasites may not speciate along with their vertebrate hosts because they have longer stasis periods than do their hosts. Nematode parasite survival strategy involves moving among host species via EF without speciating. Parasite speciation might take place when parasites switch host families. This might be the real reason why Fahrenholz's and Manter's rules (co-speciation of parasites and hosts and parasite evolution lags behind host evolution, respectively) are not supported among these parasites and why research programs based on cospeciation are unlikely to succeed.

A consequence of EF is the coexistence of ancestral and descendant species in space and in time (Brooks & McLennan, 2002). The PSC1 concept includes survival or coexistence of ancestors along with their descendant species. It seems that this is not uncommon in the paleontological record, although it has rarely been acknowledged among extant species (Wagner & Erwin, 1995). In the case of relatively recent episodes of putative speciation events in *Rhabdochona* spp. one example involves a pair of sister species in clade III: *R. ahuehuellensis* and *R. guerreroensis*. The former species possesses no autapomorphies and its characters are shared with its putative ancestor (node), i.e., *R. ahuehuellensis* seems to be ancestral to *R. guerreroensis*.

EF also supports the hypothesis that parasite faunas in freshwater fishes are largely circumscribed to higher levels of monophyletic host taxa (Pérez-Ponce de León and Choudhury, 2005). Such a pattern has previously been noted in the monogeneans (Zietara & Lumme, 2002). This indicates that there is little coevolutionary pattern at the species level, and speciation takes place at the parasite-species/host-family level, coupled with long-distance postdispersal speciation. Thus, a higher level of host and geographic expansion can be discerned in *Rhabdochona* and probably other freshwater fish helminth parasites that promotes speciation at the family (clade) level of hosts, when hosts move into new habitats at macrobiogeographical scales, but not at lower levels.

4. The phylogeography of *Rhabdochona lichtenfelsi*

The phylogeography of the American species, *R. lichtenfelsi* (Mejía-Madrid et al., 2007b) revealed low divergence between the distinct subclades identified in its range, despite the fact that this species has colonized at least 15 different goodeine host species in 10 genera during the past million years. It even inhabits geographically distant freshwater drainages in Central Mexico. The haplotypes of this nematode species were explored in 3 different genera of goodeines and could not be differentiated among them (Mejía-Madrid et al., 2007b). Recent colonization and expansion of their hosts enabled *R. lichtenfelsi* to invade new drainages north of its ancient distribution, revealing dispersal/colonization within the last

million years. Despite this dispersal phenomenon, *R. lichtenfelsi* has not responded to vicariance, in contrast to their goodeine hosts, which have radiated to nearly 40 genera in the past 16 my (Doadrio & Domínguez, 2004; Webb et al., 2004).

5. Geomorphological scaling effects in the phylogeny of *Rhabdochona*

Aquatic habitat areas involved in broad historical biogeographical interpretations change at very different scales. These spatial scales actually represent disparate orders of magnitude. Historical biogeography comprises two levels of spatial variation: a macroscale involving areas that range from 10^1 to 10^7 km², and a microscale involving magnitudes from 10^{-8} to 10^1 km². The degree of magnitude of differences between areas is related to the hierarchical level of evolution addressed in historical biogeographical analyses. Vicariance is a phenomenon that involves the physical separation of landmasses at continental spatial scales, but not necessarily in the same geological time scales (Cavin et al., 2008; Forey, 2010), or that take place simultaneously at scales above 10 km². These include minor to major tectonic units ranging from continent and ocean basin building or to origination of fault blocks, volcanoes, troughs, sedimentary sub-basins, or individual mountain ranges. By microscale I refer to scenarios that some proponents of the BSC had in mind, involving large-scale erosional or depositional units, like the development of river deltas, major valleys, or piedmonts within major landmasses. The test for the role of different historical biogeographical scenarios includes the duration of these various vicariance-dispersal phenomena within the range of geomorphological microscale or macroscale events.

Metazoan parasites undergo various forms of speciation according to the geomorphological scale in which the taxa radiate. But which spatial scales have been involved in the events leading to the crown group of *Rhabdochona*? *Rhabdochona* spp. might speciate only when hosts diverge or disperse after invading new habitats, i.e., when long-distance host dispersal occurs. Therefore, active speciation by peripheral isolates or postdispersal speciation might have structured the present phylogenetic relationships within this genus. The basal clades of *Rhabdochona* spp. (I and II) might conform to postdispersal speciation along considerable distances. Yet, as this dispersal was taking place, landmasses were actively separating by the Upper Cretaceous that probably enhanced speciation probability during the early phases of the evolution of *Rhabdochona* spp. This seemingly occurred when marine and freshwater teleosts began to diversify (Forey, 2010). So, *Rhabdochona* historical biogeography has tracked the breakup of Pangea as well as the radiation of their original host families.

The origination of some clades of *Rhabdochona*, namely the crown clades III and IV (Figures 1 and 4), is related to macrobiogeographical spatial scale events and wide-ranging changes in host habitat, due to dispersal and probably host-switching, along with further host range extension, as well as heterochronic macroevolutionary events that involved a change in the timing of maturation (paedomorphosis), as described below.

6. Heterochrony and evolutionary novelties in *Rhabdochona* species

Clade IV of the phylogeny (Figure 1) includes another diverse array of species of *Rhabdochona* that parasitize mainly cyprinids and to a lesser extent characids, poeciliids, and catostomids. Curiously enough, a crown group that comprises Mexican, Cuban, and South

American species that possess 6 teeth in their prostom, appear to be closely related to a sister pair comprised of *R. coronacauda* and *R. squalobarbi* (which possess lateral body alae, a character regarded as plesiomorphic by Moravec, 2010) from Europe and the Far East. The basal species of this group is represented by *R. fortunatowi*, a species whose males possess a left spicule that is very characteristic of a group that comprises the Afghan species, *R. tigridis* (not included in this analysis), *R. acuminata* from South America, and *R. xiphophori* from Mexico.

The other clade that suggests speciation events involving change of hosts and location is that of the clade involving the salmonid species of *Rhabdochona*. This clade has undergone a change in tooth number from 14 to 10, and host switching from cyprinids to salmonids.

Rhabdochona phylogeny thus reveals an interesting pattern of speciation by heterochrony. The life cycle of *Rhabdochona* involves a 4th larval stage characterized by the presence of 6 teeth in the stoma and simple deirids (Moravec, 2010 and references therein). When this 4th stage moults into an adult, they exhibit a duplication of lateral teeth seen in many “14 tooth species” and the dorsal-ventral teeth multiply as well. The phylogeny of *Rhabdochona* recovers an entire clade that possesses these larval characteristics. These apomorphies probably owe their appearance to paedomorphosis. This heterochronic event is seemingly coupled to the acquisition of hosts in several fish families different from cyprinids. Furthermore, this pattern is in accordance with a change in the environmental or geomorphologic conditions that probably accompanied these speciation events, related to the aforementioned TP event. Additionally, the common presence of homoplastic characters in *Rhabdochona* phylogeny suggests reversals originating through heterochronic events, which enabled these nematode parasites to disperse/colonize to new host families. Therefore, heterochrony (Brooks & McLennan, 1993a; Gould, 1977) is probably one of the mechanisms underlying speciation of *Rhabdochona* spp., coupled with colonization of new host families after these hosts dispersed distances greater than a radius of 10² km² or more.

The ontogenetic age structure of metazoan parasites has scarcely been studied in macroevolutionary terms (Brooks & McLennan, 1993a). Developmental constraints might be one of the causes of conservatism in living fossils (Avise et al., 1994). *Rhabdochona* spp. cannot qualify as living fossils, although some authors have stated that absence of a record is not evidence that a form, a lineage, or a molecule is not or has not been persistent (Liow, 2006). However, these taxa may qualify as an extremely conservative group (Hoberg & Brooks, 2008) in which few morphological changes have allowed species within this nematode genus to disperse through its hosts to multiple continents after the breakup of Pangea, and later due to TP. It is probable that some species of *Rhabdochona* have remained in stasis for nearly 31 my.

7. Conclusions

A combination of events promoted by TP, host switching and postdispersal speciation has resulted in the modern distribution of *Rhabdochona* spp. Ecological fitting helps explain why in past expansion phases of these parasites into new hosts no apparent speciation has occurred. *Rhabdochona* represents a group of species that has remained relatively unchanged as it has invaded new fish hosts, as inferred from morphology, life cycle, and host habitat preference analyses.

EF has played a major role in the evolution of freshwater fish helminth host parasite systems by maintaining parasite species stasis while they track plesiomorphic resources (Agosta et al., 2010; Brooks & McLennan, 2002; Brooks & Ferrao, 2005; Brooks et al., 2006). This might explain why parasite adaptive radiation is not as extensive as has been previously believed (Brooks & McLennan, 1993). Nematode parasite radiations probably have been driven more by speciation via TP and punctuated phenomena than by phyletic gradualism. Vertebrate nematode parasites likely have longer periods of stasis than do their hosts. Therefore, the effect of stasis via EF results in an apparent “lag” pattern in parasite evolution, as compared to evolution of their hosts. Lastly, heterochrony probably is a primary mechanism in nematode parasite postdispersal speciation, when coupled with long distance dispersal of their hosts.

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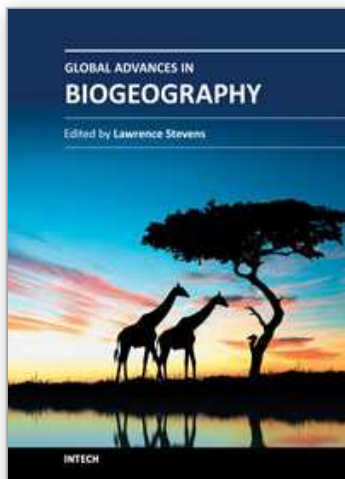
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Global Advances in Biogeography brings together the work of more than 30 scientific authorities on biogeography from around the world. The book focuses on spatial and temporal variation of biological assemblages in relation to landscape complexity and environmental change. Global Advances embraces four themes: biogeographic theory and tests of concepts, the regional biogeography of individual taxa, the biogeography of complex landscapes, and the deep-time evolutionary biogeography of macrotaxa. In addition, the book provides a trove of new information about unusual landscapes, the natural history of a wide array of poorly known plant and animal species, and global conservation issues. This book is well illustrated with numerous maps, graphics, and photographs, and contains much new basic biogeographical information that is not available elsewhere. It will serve as an invaluable reference for professionals and members of the public interested in global biogeography, evolution, taxonomy, and conservation.

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