Chapter 2
The Taxonomy, Phylogeny, and Distribution of Lampreys

Ian C. Potter, Howard S. Gill, Claude B. Renaud and Dalal Haoucher

Abstract The lampreys (Petromyzontiformes), one of the two surviving groups of agnathan (jawless) vertebrates, currently consist of 41 recognized species. This group has an antitropical distribution, with the 37 species of Northern Hemisphere lampreys assigned to the Petromyzontidae, whereas the four species of Southern Hemisphere lampreys are separated into either the Geotriidae (one species) or Mordaciidae (three species). All lamprey species have a blind and microphagous, burrowing larva (ammocoete), which spends a number of years in the soft sediment of creeks and rivers, after which it undergoes a radical metamorphosis. Eighteen lamprey species then embark on an adult parasitic phase (nine at sea and nine in fresh water) during which they increase markedly in size, whereas the other 23 species do not feed as adults and remain in fresh water. On the basis of morphology, 17 of the 23 non-parasitic species each evolved from a particular parasitic species whose descendants are still represented in the contemporary fauna. The remaining six non-parasitic species, the so-called "southern relict" species, have no obvious potential ancestral parasitic species, implying they have diverged markedly from their parasitic ancestor or that the parasitic ancestor is now extinct. Many of the main taxonomic characteristics reside in features that are associated with parasitic feeding, for example, the type and arrangement of the teeth on the suctorial disc and tongue-like piston. The phylogenetic relationships, derived by maximum parsimony analyses of morphological and anatomical data for the 18 parasitic species, were similar in most respects to those obtained by subjecting molecular data (cytochrome *b* mitochondrial DNA sequence data) for those species to Bayesian analyses. However, in contrast to the results of morphological analyses, the genera

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Eudontomyzon and *Lampetra* were not monophyletic when using molecular analyses. When non-parasitic species were included in the molecular analyses, some of the six relict non-parasitic species formed clades with parasitic species which, from their morphology, had been allocated by taxonomists to different genera. More genes, and particularly nuclear genes, should be used to help resolve the basis for these differences between the morphological and molecular phylogenies.

Keywords Evolution · Geotriidae · Mordaciidae · Morphological and molecular analyses · Paired species · Petromyzontidae

2.1 Introduction

The lampreys, together with the hagfishes, are the two sole surviving groups of agnathan (jawless) vertebrates (Janvier 1981; Hardisty 2006; see Chap. 1). The possession by these two groups of "round mouths" led to them being termed by Duméril (1806), collectively, as the Cyclostomata, a term retained as a class by Holly (1933) in his important taxonomic treatise on these animals. The implication that lampreys and hagfishes formed a monophyletic group was accepted for many years. However, detailed comparisons of their anatomy, morphology, and physiology, in conjunction with comparisons to the morphology of extinct agnathans, led to an alternative viewpoint (Hardisty 1979, 1982; Janvier 1981). The latter authors came independently to the conclusion that lampreys were more closely related to the gnathostomatous (jawed) vertebrates than to the hagfishes. Since that time, however, the majority of the numerous molecular studies undertaken on the two surviving groups of agnathans have supported the monophyly of lampreys and hagfishes (e.g., Stock and Whitt 1992; Mallatt and Sullivan 1998; Kuraku et al. 1999; Delarbre et al. 2002; Takezaki et al. 2003; Blair and Hedges 2005; Kuraku and Kuratani 2006). The question of whether or not cyclostomes are considered to constitute a monophyletic group was subsequently shown by Near (2009) to be influenced by the characters used and the types of analyses employed. A subsequent study, however, by Heimberg et al. (2010), employing microRNAs and a reanalysis of morphological characters, provided such overwhelming evidence for cyclostome monophyly that it convinced Janvier (2010) that this was indeed the case.

The first fossil lamprey to be described was the beautifully-preserved *Mayomyzon pieckoensis* from the upper Carboniferous (c. 280 million years ago, mya) deposits of Mazon Creek in Illinois (Bardack and Zangerl 1968, 1971). This fossil clearly possessed many of the morphological and anatomical characters of the adults of extant lampreys, such as an annular cartilage, which maintains the structural integrity of the suctorial disc, a piston cartilage, dorsolateral eyes, and seven gill apertures on either side of the body. Since the landmark discovery of *M. pieckoensis*, a further three definitive fossil lampreys have been found. The youngest of these is *Mesomyzon mengae* from the lower Cretaceous of China c. 125 mya (Chang et al. 2006), followed in age by *Hardistiella montanensis* from lower Carboniferous deposits in Montana c. 320 mya (Janvier and Lund 1983), and then *Priscomyzon riniensis*

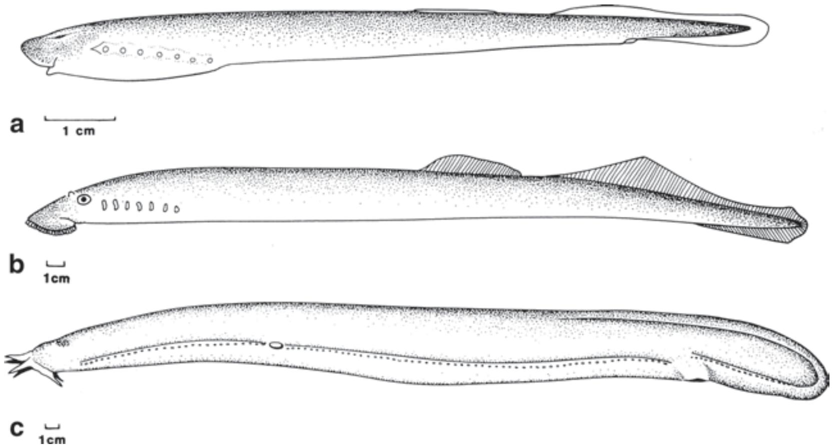

Fig. 2.1 Lateral views of **a** a larval lamprey (ammocoete), **b** an adult lamprey, and **c** a hagfish. This figure was originally published in Hardisty et al. (1989). (Reproduced by permission of The Royal Society of Edinburgh from Transactions of the Royal Society of Edinburgh: Earth Sciences volume 80 (1989), pp. 241–254)

from upper Devonian deposits in South Africa c. 360 mya (Gess et al. 2006). The first indisputable fossil hagfish to be discovered was *Myxinikela siroka,* which was found in the same geological horizon and general locality as the lamprey *M. pieckoensis*, and thus likewise dates back c. 300 mya (Bardack 1991, 1998). More recently, another hagfish fossil, *Myxineidus gononorum*, was discovered in upper Carboniferous deposits in France and is therefore also of approximately the same age as the above two fossils (Poplin et al. 2001). Germain et al. (2014) have cast doubt, however, on whether *M. gononorum* is a hagfish and provide evidence that it could be a lamprey.

Both groups of extant cyclostomes possess a similar body shape (Fig. 2.1) and typically have an antitropical distribution (Hubbs and Potter 1971; Hardisty 1979). Although lampreys are thereby essentially confined to temperate regions of the world, two species (genus *Tetrapleurodon*) are found in elevated cooler waters in a restricted sub-tropical area (Álvarez del Villar 1966). The living lampreys are represented by three families (Mordaciidae, Geotriidae, and Petromyzontidae) and 41 species (Table 2.1; Potter et al. 2014) and the hagfishes by two subfamilies (Eptatretinae and Myxininae) and approximately 60 species (Fernholm 1998). However, whereas the Mordaciidae and Geotriidae are confined to the Southern Hemisphere and the Petromyzontidae to the Northern Hemisphere, the two subfamilies of hagfishes are represented in both hemispheres.

The aim of this chapter is to provide a comprehensive list of the species, genera, subfamilies, and families of extant lampreys, providing details of the types of morphological characters used in taxonomic studies and the distributions of each species. Emphasis is also placed on outlining the schemes that have been proposed for the interrelationships of the various species, based on morphological and molecular criteria, and discussing the implications of any differences between those schemes.

Table 2.1 Classification, common names, life cycle types, and distributions of the 41 extant species of lampreys, following Potter et al. (2014) in all respects except that *hubbsi* is assigned to *Lampetra* rather than *Entosphenus*. Authorities for each taxon are given in Appendix 2.1. In the life cycle column, attention is drawn to those non-parasitic species that can unambiguously be paired with a particular parasitic species. Drainage refers to a river and its tributaries. Other frequently used common names, for example, those adopted by the American Fisheries Society (AFS; Page et al. 2013a) or Food and Agriculture Organization (FAO; see FishBase: Froese and Pauly 2013) or explanations regarding alternative or previous classifications are also provided

Classification	Common name	Life cycle type	Distribution	Comments
Family Mordaciidae (southern top-eyed lampreys)				
Genus *Mordacia* (3 species)				
Mordacia mordax	Short-headed lamprey	Anadromous; parasitic	Drainages and coastal waters of south-eastern Australia, including Tasmania	Also known as Australian lamprey, but not recommended as it is imprecise
Mordacia praecox	Precocious lamprey	Freshwater; non-parasitic derivative of *M. mordax*	Drainages of southeastern Australia	Also known as Australian brook lamprey, but not recommended as it is imprecise
Mordacia lapicida	Chilean lamprey	Anadromous; parasitic	Drainages and coastal waters of Chile	
Family Geotriidae (southern striped lamprey)				
Genus *Geotria* (1 species)				
Geotria australis	Pouched lamprey	Anadromous; parasitic	Drainages of southern Australia, New Zealand, Chile, Argentina and wide-spread in intervening oceans	
Family Petromyzontidae (Northern Hemisphere lampreys)				
Subfamily Petromyzontinae				Nelson (2006) excluded *Caspiomyzon* from this subfamily (see Sect. 2.4)
Genus *Caspiomyzon* (1 species)				
Caspiomyzon wagneri	Caspian lamprey	Anadromous; parasitic	Caspian Sea and its drainages	
Genus *Petromyzon* (1 species)				
Petromyzon marinus	Sea lamprey	Anadromous and fresh-water; parasitic	Atlantic drainages in North America from Newfoundland southwards to Florida and into the Gulf of Mexico and in Europe from Varanger Fjord southwards into the Mediterranean Sea. Widespread in the North Atlantic Ocean	

Table 2.1 (continued)

Classification	Common name	Life cycle type	Distribution	Comments
Genus *Ichthyomyzon* (6 species)				
Ichthyomyzon unicuspis	Silver lamprey	Freshwater; parasitic	Hudson Bay, Great Lakes, St. Lawrence River, and Mississippi River drainages	
Ichthyomyzon fossor	Northern brook lamprey	Freshwater; non-parasitic derivative of *I. unicuspis*	As for *I. unicuspis*	
Ichthyomyzon castaneus	Chestnut lamprey	Freshwater; parasitic	Hudson Bay, Great Lakes, St. Lawrence River, and Gulf of Mexico drainages	
Ichthyomyzon gagei	Southern brook lamprey	Freshwater; non-parasitic derivative of *I. castaneus*	Gulf of Mexico drainages	
Ichthyomyzon bdellium	Ohio lamprey	Freshwater; parasitic	Ohio River drainage	
Ichthyomyzon greeleyi	Mountain brook lamprey	Freshwater; non-parasitic derivative of *I. bdellium*	As for *I. bdellium*	
Subfamily Lampetrinae				Nelson (2006) included *Caspiomyzon* in this subfamily; Vladykov (1972) separated these five genera into subfamilies Entospheninae (*Entosphenus* and *Tetrapleurodon*), and Lampetrinae (*Lampetra*, *Lethenteron*, and *Eudontomyzon*)
Genus *Tetrapleurodon* (2 species)				Formerly synonymized with *Lampetra* (see Sect. 2.4)
Tetrapleurodon spadiceus	Mexican lamprey	Freshwater; parasitic	Celio, Duero, Zula, and Lerma rivers, and Lake Chapala, Mexico	Also known as Chapala lamprey
Tetrapleurodon geminis	Mexican brook lamprey	Freshwater; non-parasitic derivative of *T. spadiceus*	Celio and Duero rivers, and Rio Grande de Morelia drainage, Mexico	Also known as Jacona lamprey

Table 2.1 (continued)

Classification	Common name	Life cycle type	Distribution	Comments
Genus *Entosphenus* (6 species)				Formerly synonymized with *Lampetra* (see Sect. 2.4)
Entosphenus tridentatus	Pacific lamprey	Anadromous and freshwater; parasitic	Drainages of western Canada, USA and Mexico, and Japan. Widespread in the North Pacific Ocean	
Entosphenus minimus	Miller Lake lamprey	Freshwater; parasitic	Upper Klamath River drainage, Oregon	
Entosphenus similis	Klamath lamprey	Freshwater; parasitic	Klamath River drainage, Oregon and California	
Entosphenus macrostomus	Vancouver lamprey	Freshwater; parasitic	Lake Cowichan drainage, Vancouver Island, British Columbia	Cowichan lamprey more precise than Vancouver lamprey (see Beamish and Wade 2008)
Entosphenus folletti	Northern California brook lamprey	Freshwater; non-parasitic	Klamath River drainage, California	Formerly considered by AFS to be synonymous with *En. lethophagus* (Robins et al. 1980), but recognized as distinct on recent list (Page et al. 2013a) Appears to be recent non-parasitic derivative but not clear whether *En. tridentatus* or *En. similis* is the ancestor (see Sect. 2.2)
Entosphenus lethophagus	Pit-Klamath brook lamprey	Freshwater; non-parasitic	Klamath River drainage, Oregon, and Pit River, California	Appears to be recent non-parasitic derivative but not clear whether *En. tridentatus* or *En. similis* is the ancestor (see Sect. 2.2)
Genus *Lethenteron* (6 species)				Formerly synonymized with *Lampetra* (see Sect. 2.4)
Lethenteron camtschaticum	Arctic lamprey	Anadromous and freshwater; parasitic	Drainages of Arctic and North Pacific oceans	Formerly known as *Lethenteron japonicum* (see Renaud et al. 2009b)
Lethenteron alaskense	Alaskan brook lamprey	Freshwater; non-parasitic derivative of *Le. camtschaticum*	Drainages of Brooks and Chatanika rivers, Alaska, and Mackenzie River, Canada	

Table 2.1 (continued)

Classification	Common name	Life cycle type	Distribution	Comments
Lethenteron appendix	American brook lamprey	Freshwater; non-parasitic derivative of *Le. camtschaticum*	Great Lakes drainages and eastern USA, St. Lawrence, and Mississippi river drainages	
Lethenteron reissneri	Far Eastern brook lamprey	Freshwater; non-parasitic derivative of *Le. camtschaticum*	Drainages of Amur River, Sakhalin Island and Kamchatka Peninsula, Russia and in South Korea and Japan	
Lethenteron kessleri	Siberian brook lamprey	Freshwater; non-parasitic derivative of *Le. camtschaticum*	Drainages between Ob and Anadyr rivers, and of Sakhalin Island, Russia and Hokkaido Island, Japan	Also known as Siberian lamprey, but "brook" lamprey makes clear that this species is non-parasitic
Lethenteron ninae	Western Transcaucasian brook lamprey	Freshwater; non-parasitic	Drainages of the Black Sea	
Genus *Eudontomyzon* (6 species)				Formerly synonymized with *Lampetra* (see Sect. 2.4)
Eudontomyzon danfordi	Carpathian lamprey	Freshwater; parasitic	Danube River drainage	
Eudontomyzon mariae	Ukrainian brook lamprey	Freshwater; non-parasitic derivative of *Eu. danfordi*	Drainages of Baltic, Azov, Black, Adriatic, and Aegean seas	
Eudontomyzon stankokaramani	Drin brook lamprey	Freshwater; non-parasitic derivative of *Eu. danfordi*	Drainages of Adriatic Sea	Synonymized with *Eu. mariae* in Renaud (2011)
Eudontomyzon morii	Korean lamprey	Freshwater; parasitic	Yalu River drainage, China and North Korea	
Eudontomyzon *hellenicus*	Macedonia brook lamprey	Freshwater; non-parasitic	Strymon River drainage, Greece	Also known as Greek brook lamprey, but Macedonia brook lamprey distinguishes this species from the more recently-described *Eu. graecus*
Eudontomyzon graecus	Epirus brook lamprey	Freshwater; non-parasitic	Loúros River drainage, Greece	

Table 2.1 (continued)

Classification	Common name	Life cycle type	Distribution	Comments
Genus *Lampetra* (9 species)				
Lampetra ayresii	Western river lamprey	Anadromous and possibly freshwater; parasitic	Drainages of North American Pacific Coast	Western river lamprey proposed as common name by Renaud et al. (2009b) and adopted by AFS, but also commonly referred to as river lamprey
Lampetra pacifica	Pacific brook lamprey	Freshwater; non-parasitic derivative of *La. ayresii*	Drainages of Columbia River, Oregon and Sacramento-San Joaquin rivers, California (but see Sect. 2.5)	Formerly considered by AFS to be synonymous with *La. richardsoni* (Robins et al. 1991), but recognized as distinct on recent list (Page et al. 2013a)
Lampetra richardsoni	Western brook lamprey	Freshwater; non-parasitic derivative of *La. ayresii*	Drainages of Pacific Ocean, British Columbia, Washington, Oregon and Alaska	
Lampetra hubbsi	Kern brook lamprey	Freshwater; non-parasitic	Friant-Kern Canal and Merced River, California	Formerly referred to *Entosphenus* (see Sect. 2.4.2)
Lampetra aepyptera	Least brook lamprey	Freshwater; non-parasitic	Drainages of northwestern Atlantic Ocean and Gulf of Mexico, USA	
Lampetra fluviatilis	European river lamprey	Anadromous and fresh-water; parasitic	Drainages of northeastern Atlantic Ocean	
Lampetra planeri	European brook lamprey	Freshwater; non-parasitic derivative of *La. fluviatilis*	As for *La. fluviatilis,* plus Danube and Volga river drainages	
Lampetra lanceolata	Turkish brook lamprey	Freshwater; non-parasitic derivative of *La. fluviatilis*	Iyidere River, Turkey	
Lampetra zanandreai	Po brook lamprey	Freshwater; non-parasitic	Drainages of the Adriatic Sea	Also known as Lombardy brook lamprey Sometimes referred to *Lethenteron* (see Sect. 2.4.2)

2.2 Life Cycles and "Paired Species"

The ability to describe accurately a species of lamprey and thereby facilitate its allocation to the appropriate genus and family requires both a thorough understanding of the features that characterize the divergent larval and adult stages and recognition that, in some species, the morphology changes markedly during adult life. It should also be recognized that the types of life cycle vary amongst lampreys, with some containing a parasitic adult phase whereas others do not feed after the completion of larval life (see later).

The life cycle of all lamprey species contains a protracted larval phase that is spent in fresh water (Hardisty and Potter 1971a; Potter 1980a; see Chap. 3). The larva, termed an ammocoete, has a worm-like body shape and is blind and toothless (Fig. 2.1a). The ammocoete spends most of its time burrowed in the soft substrata in the slower-flowing regions of streams and rivers, feeding on the detritus and microorganisms (e.g., diatoms) that it extracts from the water overlying its burrow (Moore and Mallatt 1980; Yap and Bowen 2003). After typically between 3 and 7 years, the ammocoete undergoes a radical metamorphosis, which leads to the development of functional eyes, a suctorial disc and protrusible tongue-like piston (both of which are armed with teeth), and enlargement of the dorsal fins (Figs. 2.1b, 2.2, and 2.3; Hardisty and Potter 1971b; Potter 1980a; Youson 1980; see Chap. 4), with metamorphosis typically occurring at body lengths of 80–200 mm (Hardisty and Potter 1971a).

Following the completion of the larval phase, the life cycle of the lamprey diverges in one of two main directions. One course leads to the development, during metamorphosis, of a sexually immature young adult (Fig. 2.1b) that embarks on a parasitic feeding phase (Renaud et al. 2009a; Renaud and Cochran in press). The young adults of nine of these eighteen parasitic species feed at sea following a downstream migration. When fully grown they cease feeding and return to rivers, but not necessarily their natal systems, where they become sexually mature, spawn and die (Table 2.1; Hardisty and Potter 1971b; Potter et al. 2014; see Chap. 5). Five of these nine anadromous species have given rise to freshwater-resident or landlocked forms, whose immature adults feed in lakes or in the wider regions of large rivers (Table 2.1; Applegate 1950; Nursall and Buchwald 1972; see Docker and Potter in press). The remaining nine parasitic species are confined to fresh water and have essentially the same life cycle as the landlocked forms of anadromous species (Table 2.1; Hubbs and Trautman 1937; Chappuis 1939; Álvarez del Villar 1966; Renaud and Cochran in press). The maximum total length attained by parasitic species varies markedly, ranging from 145 mm in the freshwater Miller Lake lamprey *Entosphenus minimus* to 310–490 mm in small anadromous species, such as the western and European river lampreys (*Lampetra ayresii* and *La. fluviatilis*, respectively) to between 780 and 1,200 mm in the large anadromous pouched lamprey *Geotria australis*, Pacific lamprey *Entosphenus tridentatus*, and sea lamprey *Petromyzon marinus* (Oliva 1953; Vladykov and Follett 1958; Hardisty and Potter 1971b; Potter et al. 1983; Hardisty 1986; Lorion et al. 2000).

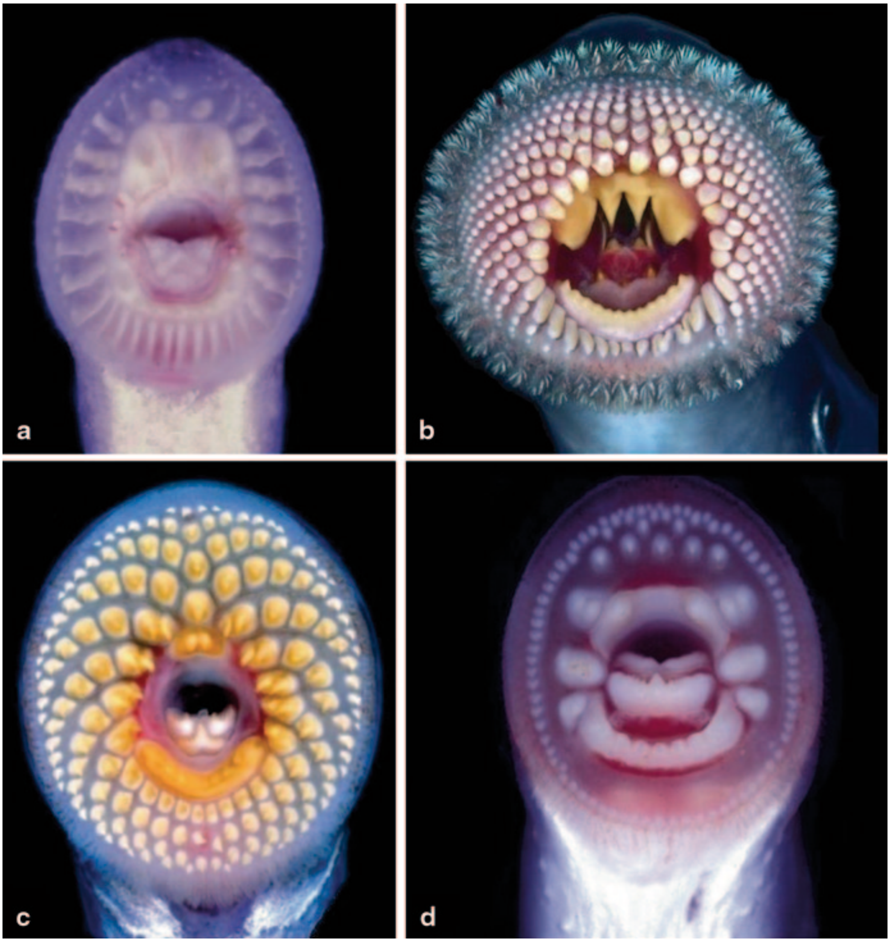

Fig. 2.2 The suctorial disc and dentition of **a** a fully-metamorphosed *Mordacia mordax*, **b** an early upstream migrant of *Geotria australis*, **c** a young feeding adult of anadromous *Petromyzon marinus*, and **d** a recently-metamorphosed *Lampetra fluviatilis*. (Photos b–d: David Bird)

The second main direction exhibited by the lamprey life cycle involves a shifting in the timing of sexual maturation relative to metamorphosis, such that it commences during the transition from the ammocoete to the adult rather than after the completion of a parasitic phase as with the species above. The parasitic phase thus becomes eliminated and spawning takes place soon after the completion of metamorphosis (Hardisty 2006; Docker 2009). Consequently, these non-parasitic species breed at a length no greater than that of their longest ammocoetes. As most of these non-parasitic species are morphologically similar to a particular parasitic species in all aspects other than body size, it has been assumed that each evolved from that parasitic species (Potter 1980b; Docker 2009). On this basis, 15 of the 23 non-parasitic species listed in Table 2.1 can be "paired" with a congeneric parasitic species (in some cases, with a single parasitic "stem" species giving rise http://www.springer.com/978-94-017-9305-6

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