

## *Gyrodactylus*

(platyhelminth: monogenean)

### Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Monogeneans are elongate to oval flatworms that are ectoparasitic on the skin and gills of fish, although a few are found in the urinary tracts of turtles, frogs, fishes and the eye of the hippopotamus. They have an anterior adhesive organ (prohaptor) and a conspicuous posterior adhesive organ (opisthaptor) armed with hooks or spines, often highly modified for attachment to specific sites. They are hermaphroditic and have direct life-cycles mostly where eggs hatch releasing a free-swimming larva (oncomiracidium) which actively seeks a new host. Monopisthocotyleans have an opisthaptor that forms a single symmetrical attachment unit lacking haptoral clamps. Gyrodactylids are unusual in that they are viviparous (produce live young); some even exhibiting hyperviviparity where subadults retained in the uterus develop their own young (cf. Russian nested dolls). Gyrodactylids are small long worms with an opisthaptor possessing a pair of large central hooks and 16 small marginal hooks. Various *Gyrodactylus* spp. are significant pests in fish ponds and heavy infestations of the gills may cause mortalities through blood loss and mucoid congestion.

### Classification:

Domain: Eukaryota (membrane-bound nucleus)  
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)  
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)  
Group: Protostomia (triploblastic, spiral cleavage)  
Subgroup: Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)  
Phylum: Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)  
Clade: Neodermata (syncytial tegument = neodermis)  
Class: Monogenea (monoxenous ectoparasites, sac-like gut, direct cycles, oncomiracidium with 3 ciliary bands)  
Order: Monopisthocotylea (posterior haptor comprising a single symmetrical attachment unit, no haptoral clamps)  
Family: Gyrodactylidae (posterior haptor, armed with hooks; viviparous, sometimes hyperviviparity)  
Genus: *Gyrodactylus* (parasitic in skin/fins/gills of fish)  
Species: various species cause respiratory signs in fish

**Parasite biodiversity and host range:** Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

Monogeneans and trematodes (flukes) have blind sac-like guts (lacking an anus) while cestodes (tapeworms) lack digestive tracts. Some 3,500 monogenean species have been described: most being ectoparasitic on the skin and gills of fish, although a few are found in the urinary tracts of turtles, frogs, fish and the eye of the hippopotamus. They have an anterior adhesive organ (prohaptor) and a conspicuous posterior adhesive organ (opisthaptor) armed with hooks, hooklets, hamuli (anchors) or clamps, often highly modified for attachment to specific sites. They are monoecious (hermaphroditic) and have direct monoxenous life-cycles mostly where eggs release free-swimming larvae (oncomiracidia with 3 ciliary bands) that actively seek new hosts (gyrodactylids are the exception as they are viviparous and produce live young). While the higher taxonomy of the Monogenea is often disputed with respect to rank, some 67 families have been resolved on the basis of morphological, biological and molecular studies. Three main groups are recognized: 28 families of Monopisthocotylea (opisthaptor with hooks, ectoparasitic on fish skin and gills, feed on epithelia); 37 families of Polyopisthocotylea (opisthaptor with clamps, ectoparasitic on fish gills, feed on blood); and 2 families of Polystomatoinea (opisthaptor with suckers, endoparasitic in tetrapods).

Order	No. families	No. spp.	DH	Characters
Class: Monogenea (= Monogenoidea) (monogenetic life-cycles, ectoparasitic mainly on fish) ~ 3,500 spp.				
Subclass: Monopisthocotylea (= Polyonchoinea) (opisthaptor with hooks, feed on fish epithelia) ~2,500 spp.				
Capsalidea	2	200	mostly marine teleosts, some elasmobranchs	2 anterior suckers, 2 pairs anchors, 14 marginal haptor hooks, some loculi
Dactylogyridea (= Monoaxonematidea)	17	1,000	freshwater and marine teleosts, coelacanth, squala	sperm with single axoneme, 12-14 haptor hooks, 2 pairs anchors, 1 transverse bar
Gyrodactylidea	5	1,500	freshwater and marine teleosts, squid, copepods	16 marginal 'hinged' haptor hooks, 1 pair anchors, dorsal and ventral bars, most viviparous (some nested polyembryony)
Monocotylidea	3	90	marine elasmobranchs	14 marginal haptor hooks, some loculi
Montchadskyellidea	1	10	marine teleosts	14 marginal haptor hooks, gut diverticulate, some endoparasitic in gut
Subclass: Polyopisthocotylea (= Heteronchoinea) (opisthaptor with clamps, most feed on blood of fish) ~1,000 spp.				
Chimaericolidea	1	5	marine holocephalans (chimaeras)	clamps, 1 pair anchors, haptor with 14 marginal hooks (each with domus)
Diclybothriidea	2	70	marine elasmobranchs, holocephalans, freshwater acipenseriform teleosts	clamps open and act as suckers, lateral sclerites absent
Mazocraeidea	34	920	numerous freshwater and marine teleost families	clamps with various structures incl. additional sclerites, hooks, spines; oral sucker a buccal organ, eggs with 2 polar filaments
Subclass: Polystomatoinea (parasitize aquatic tetrapods and lungfish)				
Polystomatidea	2	100	tetrapods (turtles, amphibians, hippopotamus), lungfish	haptor with 3 pairs suckers, egg filaments absent, some endoparasitic in tubular organs

Monopisthocotyleans have an opisthaptor that forms a single symmetrical attachment unit lacking haptor clamps. Five orders are recognized on the basis of differences in parasite morphology, development and host occurrence; including the order Gyrodactylidea characterized by worms having a posterior haptor with 16 marginal articulated ('hinged') hooks and a single pair of hamuli (anchors) with a connective dorsal bar. A total of 1,500 species belonging to 5 families (Acanthocotylidae, Anoplodiscidae, Bothitrematidae, Gyrodactylidae, Tetraonchoididae and Udonellidae) have been described from marine and freshwater bony (teleost) fishes with occasional reports on crustaceans (copepods), cephalopods (squid) and amphibians (frogs). Gyrodactylids are characterized by the possession of multiciliate 'spike' sensilla (one on each cephalic lobe), all stages lacking pigmented eyespots, and the adult male and female reproductive systems having separate openings (intromittent organ tubular and reinforced with rings, accessory sclerites or spines). Most members of the family Gyrodactylidae are not oviparous (do not lay eggs or produce oncomiracidia) but are viviparous (produce live unciliated crawling juveniles); many even exhibiting hyperviviparity (polyembryony) where subadults retained in the uterus develop their own young (cf. Russian nested dolls).

The family Gyrodactylidae was erected to accommodate only the viviparous genus *Gyrodactylus*. Subsequently, a series of subfamilies were proposed to include other genera primarily on the basis of differences in haptor morphology (e.g. Isancistrinae lacking bars and hamuli, Polyclithrinae with numerous supporting bars, and the remainder placed in the catch-all Gyrodactylinae), but these subfamilies have received little support in molecular phylogenies. Most authors continue to recognise a major division between viviparous and oviparous forms as they are profoundly different biologically. The oviparous genera are protandrous hermaphrodites that lay eggs with a sticky droplet. The eggs hatch to release unciliated crawling larvae with prominent spike sensillae. Seven genera have been described from South American catfish primarily on the basis of differences in the structure of the male reproductive system and the vitelline system; namely, *Aglaiogyrodactylus*, *Hyperopletes*, *Nothogyrodactylus*, *Ooegyrodactylus*, *Onychogyrodactylus*, *Phanerothecium* and *Phanerothecioides*. The viviparous genera exhibit little variation in internal anatomy. While some morphological differences have been observed in penis structure, the occurrence of hamuli and bars, and the presence of accessory sclerites on the haptor, molecular studies indicate that considerable variation, not reflected in morphology, occurs between and within genera. Six *Gyrodactylus* subgenera (*Gyrodactylus*, *Mesonephrotus*, *Paranephrotus*, *Metanephrotus*, *Neonephrotus*, *Limnonephrotus*) have been differentiated on the basis of type of excretory system and host occurrence, but these groupings have not been supported by molecular studies. Several genera have recently been synonymized with *Gyrodactylus* on the basis of morphological and/or molecular studies, including *Afroyrodactylus*, *Paragyrodactylus*, *Paragyrodactylodes*, *Fundulotrema* and *Metagyrodactylus*. Other gyrodactylid genera described include *Accessorius*, *Macroyrodactylus* (syn. *Neogyrodactylus*), *Mormyroyrodactylus*, *Gyrocerviceanseris*, *Scleroductus*, *Swingleus* and *Ieredactylus* from freshwater fishes, *Acanthoplacatus*, *Archigyrodactylus*, *Gyrodactylodes*, *Polyclithrum* (syn. *Micropolyclithrum*), *Citharodactylus* and *Laminiscus* (syn. *Archigyrodactylus*) from marine fishes, *Isancistrum* from cephalopods (squid) and *Gyrdicotylus* from amphibians (toads).

Some 400 *Gyrodactylus* spp. have been described from wild, captive and cultured freshwater and marine bony fish belonging to 19 different orders; namely, Anguilliformes (4 *Gyrodactylus* spp.), Clupeiformes (3), Cypriniformes (191), Characiformes (6), Siluriformes (14), Esociformes (6), Osmeriformes (2), Salmoniformes (19), Percopsiformes (2), Gadiformes (17), Mugiliformes (4), Atheriniformes (1), Beloniformes (1), Cyprinodontiformes (22), Gasterosteiformes (14), Scorpaeniformes (20), Perciformes (59), Pleuronectiformes (10) and Tetraodontiformes (3). They are absent or occur infrequently on primitive fishes (agnathans, chondrichthyans, acipenserids, sarcopterygians, neopterygians, osteoglossids), but mostly infect more recently divergent teleost fishes. Despite the broad host range for the genus, most species infect only a narrow range of hosts; many being stenoxenous (specialists) and some being euryxenous or oioxenous (generalists). Species on salmonids tend to infest more hosts than those on cyprinids, and Eurasian fish families host more species than American fish families. Heavy infestations have been found on ornamental fish in aquaria and on fish reared in aquaculture facilities.

<b><i>Gyrodactylus</i> species</b>	<b>Habitat</b>	<b>Hosts</b>	<b>Distribution</b>
<i>G. acanthorhodei</i>	freshwater	Cypriniformes: cyprinid (Russian bitterling)	Asia
<i>G. ackerti</i>	marine	Pleuronectiformes: pleuronectid (starry flounder)	Northern Pacific
<i>G. actzu</i>	freshwater	Cyprinodontiformes: poeciliid (shortfin molly)	Mexico
<i>G. adspersi</i>	marine	Labriformes: labrid (cunner)	West Atlantic
<i>G. aeglefini</i>	marine	Gadiformes: gadid (haddock)	Nort Atlantic
<i>G. afghanensis</i>	freshwater	Cypriniformes: nemacheilid (stone loach)	China
<i>G. aggregatus</i>	marine	Perciformes: embiotocid (shiner perch)	Northeast Pacific
<i>G. aideni</i>	marine	Pleuronectiformes: pleuronectid (winter flounder)	North America
<i>G. aksuensis</i>	freshwater	Cypriniformes: cyprinid (naked osman)	Asia
<i>G. alabamensis</i>	freshwater	Cypriniformes: cyprinid (bluehead chub)	North America
<i>G. albeoli</i>	freshwater	Cypriniformes: cyprinid (river shiner)	North America
<i>G. alberti</i>	freshwater	Siluriformes: clariid (North African catfish)	Africa
<i>G. albolacustris</i>	freshwater	Cypriniformes: cyprinid (Eurasian minnow)	Russia
<i>G. alburnoidesi</i>	freshwater	Cypriniformes: cyprinid (bleak)	Europe
<i>G. aldrichi</i>	freshwater	Cypriniformes: cyprinid (lake chub)	North America
<i>G. alekosi</i>	freshwater	Siluriformes: clariid (North African catfish)	Africa
<i>G. alexanderi</i>	freshwater	Gasterosteiformes: gasterosteid (three-spined stickleback)	Eurasia, North America
<i>G. alexgusevi</i>	freshwater	Gadiformes: lotid (burbot)	Eurasia, North America
<i>G. alviga</i>	marine	Pleuronectiformes: scophthalmid (turbot), pleuronectid (European flounder); Clupeiformes: engraulid (anchovy), clupeid (pontic shad); Perciformes: sparid (annular seabream, salema), mullid (red mullet), pomatomid (bluefish); Atheriniformes: atherinid (bigscale sand smelt), Gadiformes: gadid (whiting); Gobiiformes: gobiid (round goby); Ophidiiformes: ophidiid (cusk-eel); Trachiniformes: uranoscopid (stargazer); Salmoniformes: salmonid (Black Sea salmon); Rajiformes: rajid (thornback skate)	Europe
<i>G. ambystomae</i>	freshwater	Urodela: ambystomatid (long-toed salamander)	North America
<i>G. ammodyti</i>	marine	Trachiniformes: ammodytid (Pacific sand lance)	North Pacific
<i>G. amphiliusi</i>	freshwater	Siluriformes: amphiliid (loach catfish)	Africa
<i>G. anabantii</i>	freshwater	Anabantiformes: anabantid (ocellated labyrinth fish)	Africa
<i>G. anarhichatis</i>	marine	Perciformes: anarhichadid (Atlantic wolffish, spotted wolffish)	North Atlantic
<i>G. angorae</i>	freshwater	Cypriniformes: nemacheilid (Angora loach)	Middle-East
<i>G. anguillae</i>	marine, freshwater	Anguilliformes: anguillid (American eel, speckled longfin eel, Japanese eel, short-finned eel, European eel)	Atlantic, Pacific
<i>G. anisopharynx</i>	freshwater	Siluriformes: callichthyid (peppered corydoras)	South America
<i>G. antarcticus</i>	marine	Perciformes: nototheniid (dusky rockcod)	Southern Ocean
<i>G. anudarinae</i>	freshwater	Cypriniformes: cobitid (spine loach)	China
<i>G. apazapanensis</i>	freshwater	Cyprinodontiformes: poeciliid (shortfin molly, green swordtail)	Mexico
<i>G. aphredoderi</i>	freshwater	Percopsiformes: aphredoderid (pirate perch)	North America
<i>G. aphyae</i>	freshwater, marine	Salmoniformes: salmonid (Atlantic salmon),	North Atlantic

		Cypriniformes: cyprinid (Eurasian minnow)	
<i>G. aquilinus</i>	freshwater	Cypriniformes: catostomid (longnose sucker)	North America
<i>G. arcuatooides</i>	marine	Gobiiformes: gobiid (sand goby)	Europe
<i>G. arcuatus</i>	marine, freshwater	Perciformes: zoarcid (eelpout); Salmoniformes: salmonid (Atlantic salmon); Trachiniformes: ammodytid (small sandeel); Pleuronectiformes: pleuronectid (European flounder, European plaice); Cypriniformes: cyprinid (white bream); Esociformes: esocid (northern pike); Gasterosteiformes: gasterosteid (ninespine stickleback); Gobiiformes: gobiid (two-spotted goby, tubenose goby)	Europe, North America
<i>G. armatus</i>	marine	Scorpaeniformes: cottid (Pacific staghorn sculpin)	Northeast Pacific
<i>G. asiaticus</i>	freshwater	Salmoniformes: salmonid (lenok)	Asia
<i>G. asperus</i>	freshwater	Cypriniformes: cyprinid (rough shiner)	North America
<i>G. atherinae</i>	marine, freshwater	Atheriniformes: atherinid (bigscale sand smelt)	Europe
<i>G. atratuli</i>	freshwater	Cypriniformes: cyprinid (blacknose dace, longnose dace, Allegheny pearl dace), catostomid (longnose sucker)	North America
<i>G. aurorae</i>	freshwater	Anura: ranid (northern red-legged frog, tadpoles)	North America
<i>G. australis</i>	marine	Perciformes: nototheniid (crowned rockcod)	Southern Ocean
<i>G. avaloniae</i>	freshwater	Perciformes: centrarchid (pumpkinseed); Gasterosteiformes: gasterosteid (ninespine stickleback, fourspine stickleback, three-spined stickleback, blackspotted stickleback); Cyprinodontiformes: fundulid (banded killifish); Salmoniformes: salmonid (rainbow trout, brook trout); Cypriniformes: cyprinid (blacknose dace)	North America, Eurasia
<i>G. baecanthus</i>	freshwater	Cypriniformes: cyprinid (comely shiner)	North America
<i>G. baicalensis</i>	freshwater	Scorpaeniformes: cottocomephorid (bighead sculpin)	Asia
<i>G. bairdi</i>	freshwater	Scorpaeniformes: cottid (mottled sculpin, slimy sculpin)	North America
<i>G. barbatuli</i>	freshwater	Cypriniformes: nemacheilid (stone loach)	Eurasia
<i>G. barbi</i>	freshwater	Cypriniformes: cyprinid (barbel, Mediterranean barbel, Kura barbel)	Europe, Middle-East
<i>G. benedeni</i>	freshwater	Gobiiformes: gobiid (western Greece goby)	Europe
<i>G. bimaculatus</i>	freshwater	Characiformes: lebiasinid (twospot lebiasina)	South America
<i>G. bimicroforatus</i>	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
<i>G. bios</i>	freshwater	Gobiiformes: gobiid (Thessaly goby)	Europe
<i>G. birmani</i>	marine, freshwater	Salmoniformes: salmonid (Arctic char)	Eurasia, North America
<i>G. bliccensis</i>	freshwater	Cypriniformes: cyprinid (bleak, white bream)	Europe
<i>G. bodegiensis</i>	marine, freshwater	Scorpaeniformes: cottid (sharpnose sculpin)	East Pacific
<i>G. bohemicus</i>	freshwater	Salmoniformes: salmonid (rainbow trout, brook trout)	North Pacific
<i>G. bolonensis</i>	freshwater, marine	Osmeriformes: osmerid (pond smelt)	Arctic
<i>G. botnicus</i>	freshwater	Cypriniformes: cyprinid (Eurasian minnow)	Russia
<i>G. brachymystacis</i>	freshwater	Salmoniformes: salmonid (lenok)	Asia
<i>G. branchialis</i>	freshwater	Gobiiformes: gobiid (common goby)	Europe, Africa
<i>G. branchicus</i>	freshwater	Gasterosteiformes: gasterosteid (three-spined stickleback)	Eurasia
<i>G. branchius</i>	marine	Pleuronectiformes: pleuronectid (starry flounder)	North America
<i>G. bretinae</i>	freshwater	Perciformes: percid (speckled darter)	North America
<i>G. brevis</i>	freshwater	Salmoniformes: salmonid (rainbow trout), Cypriniformes: cyprinid (California roach)	North America, Asia
<i>G. bubyri</i>	marine	Gobiiformes: gobiid (Caucasian dwarf goby)	Europe
<i>G. bueni</i>	freshwater	Siluriformes: callichthyid (banded corydoras, bigfin corydoras)	South America
<i>G. bulbacanthus</i>	freshwater	Cyprinodontiformes: fundulid (Plains killifish)	North America
<i>G. bullatarudis</i>	freshwater	Cyprinodontiformes: poeciliid (molly, green swordtail, guppy, eastern mosquitofish, two-spot livebearer)	Americas, Australia

<i>G. bychowskianus</i>	freshwater	Scorpaeniformes: cottocomephorid (yellowfin Baikal sculpin)	Russia
<i>G. byrdi</i>	marine	Perciformes: nototheniid (dusky rockcod)	Southern Ocean
<i>G. caledoniensis</i>	marine	Salmoniformes: salmonid (sea trout, Atlantic salmon)	North Pacific
<i>G. californiensis</i>	marine	Gadiformes: gadid (Pacific tomcod)	Northeast Pacific
<i>G. callariatis</i>	marine	Gadiformes: gadid (Atlantic cod)	North Atlantic
<i>G. callawayensis</i>	freshwater	Cypriniformes: cyprinid (red shiner)	North America
<i>G. cameroni</i>	marine, freshwater	Gasterosteiformes: gasterosteid (fourspine stickleback)	North America
<i>G. camerunensis</i>	freshwater	Siluriformes: clariid (walking catfishes)	Africa
<i>G. campostomae</i>	freshwater	Cypriniformes: cyprinid (central stoneroller)	North America
<i>G. canadensis</i>	freshwater	Gasterosteiformes: gasterosteid (fourspine stickleback, three-spined stickleback, ninespine stickleback)	North America, Eurasia
<i>G. capoetai</i>	freshwater	Cypriniformes: cyprinid (seven khramulya)	Asia
<i>G. carassii</i>	freshwater	Cypriniformes: cyprinid (roach, rudd, gudgeon, common dace, Eurasian minnow, bleak, white bream, Crucian carp, belica, chub)	Europe
<i>G. carolinae</i>	freshwater	Characiformes: crenuchid (South American darter)	South America
<i>G. carpio</i>	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
<i>G. catesbeianae</i>	freshwater	Anura: ranid (American bullfrog, tadpoles)	North America
<i>G. centronoti</i>	marine	Perciformes: nototheniid (sharp-spined notothenia)	Southern Ocean
<i>G. cernuae</i>	freshwater	Perciformes: percoid (ruffe, European perch, pike-perch)	Europe, Asia
<i>G. charon</i>	freshwater	Gobiiformes: gobiid (Acheron spiny goby)	Europe
<i>G. chileani</i>	marine	Blenniiformes: tripterygiid (triplefin blenny)	South America
<i>G. chitandiri</i>	freshwater	Cichliformes: cichlid (redbreast tilapia, southern mouthbrooder)	Africa
<i>G. chologastris</i>	freshwater	Percopsiformes: amblyopsid (spring cavefish)	North America
<i>G. chondrostomi</i>	freshwater	Cypriniformes: cyprinid (common nase)	Europe
<i>G. cichlidarum</i>	freshwater	Cichliformes: cichlid (blackchin tilapia, mango tilapia, blue tilapia, Guinean tilapia, redbelly tilapia, banded jewelfish, jewelfish)	Eurasia, Africa
<i>G. clarii</i>	freshwater	Siluriformes: clariid (North African catfish)	Africa
<i>G. cobitis</i>	freshwater	Cypriniformes: cobitid (spined loach)	Eurasia
<i>G. colemanensis</i>	marine, freshwater	Salmoniformes: salmonid (sea trout, rainbow trout, lake trout)	Eurasia, North America
<i>G. comephori</i>	freshwater	Scorpaeniformes: comephorid (Baikal oilfish)	Russia
<i>G. commersoni</i>	marine	Scombriformes: scombrid (narrow-barred Spanish mackerel)	South-East Asia
<i>G. coriicepsi</i>	marine	Perciformes: nototheniid (black rockcod)	Southern Ocean
<i>G. corleonis</i>	marine	Syngnathiformes: syngnathid (broad-nosed pipefish)	Europe
<i>G. corti</i>	marine	Perciformes: anarhichadid (wolf-eel)	North Pacific
<i>G. corydori</i>	freshwater	Siluriformes: callichthyid (peppered corydoras)	South America
<i>G. costaricensis</i>	freshwater	Cyprinodontiformes: poeciliid (molly)	Americas
<i>G. costatae</i>	freshwater	Cypriniformes: nemacheilid (eightbarbel loach)	Asia
<i>G. cotti</i>	freshwater	Scorpaeniformes: cottid (bullhead, alpine bullhead, slimy sculpin)	Eurasia, North America
<i>G. cottinus</i>	marine	Scorpaeniformes: cottid (Arctic sculpin)	North Atlantic, North Pacific
<i>G. couesius</i>	freshwater	Cypriniformes: cyprinid (lake chub)	North America
<i>G. cranei</i>	marine	Gadiformes: gadid (Pacific tomcod)	Northeast Pacific
<i>G. crenilabri</i>	marine	Labriformes: labrid (five-spotted wrasse, East Atlantic peacock wrasse, ocellated wrasse, grey wrasse)	Mediterranean
<i>G. cryptarum</i>	marine	Gadiformes: gadid (Atlantic cod)	North Atlantic
<i>G. crysoleucas</i>	freshwater	Cypriniformes: cyprinid (golden shiner)	North America
<i>G. ctenopharyngodontis</i>	freshwater	Cypriniformes: cyprinid (grass carp)	China
<i>G. ctenopomi</i>	freshwater	Anabantiformes: anabantid (ocellated labyrinth fish)	Africa
<i>G. curemae</i>	marine	Mugiliformes: mugilid (white mullet)	West Atlantic

<i>G. curiosus</i>	freshwater	Cypriniformes: nemacheilid (eightbarbel loach)	Asia
<i>G. cyclopteri</i>	marine	Scorpaeniformes: cyclopterid (lumpfish)	North Atlantic
<i>G. cylindriciformis</i>	freshwater	Esociformes: umbrid (central mudminnow)	North America
<i>G. cyprini</i>	freshwater	Cypriniformes: cyprinid (freshwater bream, common carp, rudd)	Europe
<i>G. cyprinodontis</i>	freshwater	Cyprinodontiformes: cyprinodontid (Amargosa pupfish)	North America
<i>G. cytophagus</i>	freshwater	Cyprinodontiformes: poeciliid (Tanganyika lampeye, Norman's lampeye, Bitschumbi lampeye)	Africa
<i>G. dakotensis</i>	freshwater	Cypriniformes: catostomid (bigmouth buffalo, river carpsucker)	North America
<i>G. danastriae</i>	freshwater	Cypriniformes: cyprinid (Eurasian minnow)	Russia
<i>G. dechtiari</i>	freshwater	Cypriniformes: cyprinid (longnose dace, blacknose dace)	North America
<i>G. decorus</i>	freshwater	Cypriniformes: cyprinid (common roach, sunbleak)	Europe
<i>G. derjavini</i>	marine, freshwater	Salmoniformes: salmonid (Arctic char, brook trout, sea trout, rainbow trout, Atlantic salmon), Cypriniformes: cyprinid (common carp, Kura nase)	Eurasia, North America
<i>G. derjavinoidea</i>	marine	Salmoniformes: salmonid (sea trout)	Europe
<i>G. dogieli</i>	marine	Pleuronectiformes: pleuronectid (common dab)	Europe
<i>G. donghuensis</i>	freshwater	Cypriniformes: cyprinid (bitterling)	China
<i>G. dorlodoti</i>	freshwater	Gobiiformes: gobiid (western Greece goby)	Europe
<i>G. dorosomae</i>	marine	Clupeiformes: clupeid (American gizzard shad, threadfin shad)	Northwest Atlantic
<i>G. douglasadamsi</i>	freshwater	Gobiiformes: gobiid (Neretva dwarf goby)	Europe
<i>G. dubius</i>	freshwater	Cypriniformes: nemacheilid (stone loach)	Europe
<i>G. dulmaae</i>	freshwater	Cypriniformes: nemacheilid (stone loach)	Europe
<i>G. dykova</i>	freshwater	Cypriniformes: cyprinid (gudgeon)	Europe
<i>G. dzhalilovi</i>	freshwater	Cypriniformes: cyprinid (false osman)	Asia
<i>G. editus</i>	freshwater	Cypriniformes: cyprinid (false osman)	Asia
<i>G. egregius</i>	freshwater	Cypriniformes: cyprinid (Lahontan redbelly)	North America
<i>G. egusae</i>	freshwater	Anguilliformes: anguillid (Japanese eel)	Asia
<i>G. elegans</i>	freshwater	Cypriniformes: cyprinid (white-eye bream, freshwater bream)	Eurasia
<i>G. elegini</i>	marine	Gadiformes: gadid (Navaga)	Arctic
<i>G. elongatus</i>	marine	Gadiformes: gadid (Pacific tomcod)	Northeast Pacific
<i>G. emembranatus</i>	marine	Gadiformes: gadid (Atlantic cod)	North Atlantic
<i>G. ensatus</i>	freshwater	Urodela: cryptobranchid (California giant salamander, larvae)	North America
<i>G. eos</i>	freshwater	Cypriniformes: cyprinid (northern redbelly dace)	North America
<i>G. ergensi</i>	freshwater	Cichliformes: cichlid (Nile tilapia)	Africa
<i>G. errabundus</i>	marine	Labriformes: labrid (Ballan wrasse); Perciformes: zoarcid (eelpout), anarhichadid (Atlantic wolffish); Pleuronectiformes: pleuronectid (European plaice); Gadiformes: gadid (poor cod); Scorpaeniformes: cottid (longspined bullhead); Squaliformes: squalid (picked dogfish)	cosmopolitan
<i>G. esomi</i>	freshwater	Cypriniformes: cyprinid (Mekong flying barb)	Asia
<i>G. etheostomae</i>	freshwater	Perciformes: percid (mud darter, speckled darter, rainbow darter, orangethroat darter, splendid darter, Iowa darter, orangebelly darter, Johnny darter)	North America
<i>G. eucaliae</i>	freshwater	Gasterosteiformes: gasterosteid (brook stickleback)	North America
<i>G. eutheraponensis</i>	marine	Perciformes: terapontid (largescaled terapon)	Southeast Asia
<i>G. euzeti</i>	freshwater	Cypriniformes: cyprinid (spirlin)	Eurasia
<i>G. exocoeti</i>	marine	Beloniformes: exocoetid (barbel flyingfish, tropical two-wing flyingfish)	tropics
<i>G. eyipayipi</i>	marine	Syngnathiformes: syngnathid (greater pipefish)	Europe
<i>G. fairporti</i>	freshwater	Cypriniformes: cyprinid (common carp); Siluriformes: ictalurid (black bullhead)	Eurasia, North America
<i>G. fernandoi</i>	freshwater	Siluriformes: clariid (Philippine catfish)	Southeast Asia
<i>G. flavescens</i>	marine	Gobiiformes: gobiid (two-spotted goby)	Europe
<i>G. flesi</i>	marine	Perciformes: pomatomid (bluefish), carangid	cosmopolitan

		(Mediterranean horse mackerel), sparid (blotched picarel); Pleuronectiformes: pleuronectid (European flounder, European plaice); Gobiiformes: gobiid (black goby, round goby); Trachiniformes: uranoscopid (stargazer); Rajiformes: rajid (thornback ray)	
<i>G. flexibiliradix</i>	marine	Pleuronectiformes: pleuronectid (European flounder)	Europe
<i>G. fossilis</i>	freshwater	Cypriniformes: cobitid (weatherfish), nemacheilid (Angora loach)	Europe, Middle-East
<i>G. foxi</i>	marine	Mugiliformes: mugilid (flathead grey mullet)	cosmopolitan
<i>G. freemani</i>	freshwater	Perciformes: percid (American yellow perch)	North America
<i>G. fryi</i>	freshwater	Esociformes: esocid (muskellunge)	North America
<i>G. funduli</i>	marine	Cyprinodontiformes: fundulid (longnose killifish)	West Atlantic
<i>G. fuscus</i>	freshwater	Siluriformes: clariid (Hong Kong catfish)	Asia
<i>G. gambusiae</i>	freshwater	Cyprinodontiformes: poeciliid (mosquitofish)	North America
<i>G. gasterostei</i>	freshwater	Cypriniformes: cyprinid (roach, white bream, tench, chub); Perciformes: percid (European perch); Gasterosteiformes: gasterosteid (three-spined stickleback)	Eurasia, North America
<i>G. gelnari</i>	freshwater	Siluriformes: clariid (mudfish)	Africa
<i>G. gemini</i>	freshwater	Characiformes: prochilodontid (silver prochilodus)	South America
<i>G. geophagensis</i>	freshwater	Cichliformes: cichlid (pearl cichlid)	South America
<i>G. gerdi</i>	marine	Clupeiformes: clupeid (Pacific herring); Gadiformes: gadid (navaga, saffron cod)	Arctic
<i>G. glaseri</i>	freshwater	Cypriniformes: cyprinid (bleak)	Europe
<i>G. glehnii</i>	freshwater	Gobiiformes: odontobutid (Chinese sleeper)	Asia
<i>G. gloriosi</i>	freshwater	Perciformes: centrarchid (bluespotted sunfish)	North America
<i>G. gnathopogonis</i>	freshwater	Cypriniformes: cyprinid (Khanka gudgeon)	Asia
<i>G. gobiensis</i>	freshwater	Cypriniformes: cyprinid (gudgeon, Kessler's gudgeon)	Europe
<i>G. gobii</i>	freshwater	Cypriniformes: cyprinid (gudgeon, white-finned gudgeon, Siberian gudgeon, spotted steed); Salmoniformes: salmonid (rainbow trout)	Eurasia
<i>G. gobioninum</i>	freshwater	Cypriniformes: cyprinid (gudgeon, Cherskii's thicklip gudgeon, Amur whitefin gudgeon, Amur longnose gudgeon, Chinese lake gudgeon, Kessler's gudgeon, stone moroko, spotted steed)	Asia
<i>G. goerani</i>	freshwater	Perciformes: centrarchid (bluegill, rock bass, pumpkinseed)	North America
<i>G. gondae</i>	marine	Gobiiformes: gobiid (sand goby, Lozano's goby)	Europe
<i>G. gracilihamatus</i>	freshwater	Cypriniformes: cyprinid (spirlin, white bream, chub, roach, bleak)	Eurasia
<i>G. granoei</i>	freshwater	Cypriniformes: cobitid (spine loach)	China
<i>G. groenlandicus</i>	marine	Scorpaeniformes: cottid (warty sculpin, shorthorn sculpin, antlered sculpin, belligerent sculpin, Arctic sculpin); Clupeiformes: clupeid (Pacific herring); Perciformes: stichaeid (prickleback)	North Pacific, North Atlantic, Arctic
<i>G. groschafti</i>	freshwater	Siluriformes: clariid (North African catfish)	Africa
<i>G. gurleyi</i>	freshwater	Cypriniformes: cyprinid (common carp, goldfish)	Eurasia
<i>G. gussevi</i>	freshwater	Siluriformes: silurid (Soldatov's catfish, Amur catfish)	Asia
<i>G. vosdevi</i>	freshwater	Cypriniformes: nemacheilid (gray loach)	Russia
<i>G. gymneli</i>	marine	Perciformes: zoarcid (fish doctor)	Arctic
<i>G. haiteji</i>	freshwater	Scorpaeniformes: cottid (Amur sculpin)	Asia
<i>G. haplochromi</i>	freshwater	Cichliformes: cichlid (cichlids)	Africa
<i>G. harengi</i>	marine	Clupeiformes: clupeid (Atlantic herring, Pacific herring, European sprat)	Arctic, Europe
<i>G. hargisi</i>	marine	Cyprinodontiformes: cyprinodontid (sheepshead minnow)	Americas
<i>G. hellemansii</i>	freshwater	Gobiiformes: gobiid (Neretva dwarf goby)	Europe
<i>G. hemibarbi</i>	freshwater	Cypriniformes: cyprinid (barbel, Kura barbel, chub)	Europe
<i>G. hemiculteris</i>	freshwater	Cypriniformes: cyprinid (Ussuri sharpbelly)	Asia

<i>G. hemivicinus</i>	freshwater	Cypriniformes: cyprinid (common marinka)	Asia
<i>G. heterodactylus</i>	freshwater	Perciformes: elassomatid (banded pygmy sunfish)	North America
<i>G. hildae</i>	freshwater	Cichliformes: cichlid (Nile tilapia)	Africa
<i>G. hoffmani</i>	freshwater	Cypriniformes: cyprinid (fathead minnow)	Americas
<i>G. honghuensis</i>	freshwater	Cypriniformes: cyprinid (humpback)	Asia
<i>G. hrabei</i>	freshwater	Scorpaeniformes: cottid (bullhead, Alpine bullhead)	Eurasia
<i>G. hronosus</i>	freshwater	Cypriniformes: cyprinid (spiralin, bleak)	Eurasia
<i>G. hunanensis</i>	freshwater	Cypriniformes: cyprinid (predatory carp)	Asia
<i>G. hyderabadensis</i>	freshwater	Anabantiformes: channid (snakehead)	India
<i>G. hypophthalmichthydis</i>	freshwater	Cypriniformes: cyprinid (silver carp)	Asia
<i>G. ibragimovi</i>	freshwater	Cypriniformes: cyprinid (seven khramulya)	Asia
<i>G. ictaluri</i>	freshwater	Siluriformes: ictalurid (Channel catfish)	North America
<i>G. ihkahuili</i>	freshwater	Cyprinodontiformes: poeciliid (shortfin molly)	Mexico
<i>G. illigatus</i>	freshwater	Cypriniformes: cyprinid (silverband shiner)	North America
<i>G. imperialis</i>	marine	Gobiiformes: gobiid (longjaw mudsucker)	North America
<i>G. incognitus</i>	freshwater	Cypriniformes: nemacheilid (spotted thicklip loach)	Russia
<i>G. inesperatus</i>	freshwater	Characiformes: crenuchid (South American darter)	South America
<i>G. iumuri</i>	freshwater	Cyprinodontiformes: goodeid (blackfin goodea)	Mexico
<i>G. ivindoensis</i>	freshwater	Cypriniformes: cyprinid (barbel)	Europe
<i>G. jalalii</i>	freshwater	Cichliformes: cichlid (Iranian mouthbrooder)	Middle-East
<i>G. japonicus</i>	marine	Osmeriformes: plecoglossid (Ayu sweetfish)	Northwest Pacific
<i>G. jarocho</i>	freshwater	Cyprinodontiformes: poeciliid (green swordtail)	Mexico
<i>G. jennyae</i>	freshwater	Anura: ranid (American bullfrog, tadpoles)	North America
<i>G. jiroveci</i> (syn. <i>papernai</i> )	freshwater	Cypriniformes: cyprinid (gudgeon), nemacheilid (stone loach)	Eurasia
<i>G. joi</i>	marine	Anguilliformes: anguillid (Japanese eel)	Asia
<i>G. jussii</i>	freshwater	Cypriniformes: cyprinid (Eurasian minnow)	Eurasia
<i>G. kafirniganensis</i>	freshwater	Cypriniformes: cyprinid (common marinka)	Asia
<i>G. karabekovi</i>	freshwater	Cypriniformes: cyprinid (naked osman)	Asia
<i>G. karatagensis</i>	freshwater	Cypriniformes: nemacheilid (Tibetan stone loach)	Asia
<i>G. katamba</i>	freshwater	Cyprinodontiformes: goodeid (blackfin goodea)	Mexico
<i>G. katharineri</i>	freshwater	Cypriniformes: cyprinid (common carp, Crucian carp, bighead carp, silver carp, goldfish, barbel, Mediterranean barbel, Balkan barbel, seven khramulya, gudgeon, bleak)	Eurasia
<i>G. kearni</i>	freshwater	Cypriniformes: cyprinid (chub)	Eurasia
<i>G. kessleri</i>	freshwater	Cypriniformes: nemacheilid (spotted thicklip loach)	Russia
<i>G. kherulensis</i>	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
<i>G. kobayashii</i>	freshwater	Cypriniformes: cyprinid (goldfish)	Asia
<i>G. konovalovi</i>	freshwater	Cypriniformes: cyprinid (Amur minnow)	Asia
<i>G. kottelati</i>	freshwater	Cypriniformes: cyprinid (Mekong flying barb)	Asia
<i>G. kutikovana</i>	marine	Gadiformes: gadid (Polar cod)	Arctic
<i>G. kyogae</i>	freshwater	Cypriniformes: cyprinid (Neumayer's barb, threespot barb)	Africa
<i>G. lacusgrandis</i>	freshwater	Scorpaeniformes: cottid (mottled sculpin)	North America
<i>G. lacustricolae</i>	freshwater	Cypriniformes: catostomid (Lake chubsucker)	North America
<i>G. lacustris</i>	freshwater	Cypriniformes: cyprinid (fathead minnow)	Americas
<i>G. laevis</i>	freshwater	Cypriniformes: cyprinid (belica, chub, bleak, Eurasian minnow, roach, bitterling, freshwater bream, white bream, zope, rudd, Dalmatian nase)	Eurasia
<i>G. laevisoides</i>	freshwater	Cypriniformes: cyprinid (redbelly dace)	North America
<i>G. lagowskii</i>	freshwater	Cypriniformes: cyprinid (Amur minnow)	Asia
<i>G. lambanus</i>	freshwater	Cypriniformes: cyprinid (longnose shiner)	North America
<i>G. lamberti</i>	freshwater	Cypriniformes: cyprinid (chub)	Eurasia
<i>G. lamothei</i>	freshwater	Cyprinodontiformes: goodeid (blackfin goodea, dark-edged splitfin)	Mexico
<i>G. laruei</i>	freshwater	Cypriniformes: cyprinid (central stoneroller)	North America
<i>G. lateolabrax</i>	marine	Perciformes: lateolabracid (Japanese seabass)	West Pacific
<i>G. latus</i>	freshwater	Cypriniformes: nemacheilid (eightbarbel loach), cobitid (spined loach)	Eurasia
<i>G. lavareti</i>	freshwater	Salmoniformes: salmonid (rainbow trout, European)	Eurasia, North

		whitefish, broad whitefish)	America
<i>G. lebiasinus</i>	freshwater	Characiformes: lebiasinid (twospot lebiasina)	South America
<i>G. lefua</i>	freshwater	Cypriniformes: nemacheilid (eightbarbel loach)	Asia
<i>G. lenoki</i>	marine, freshwater	Salmoniformes: salmonid (Atlantic salmon, lenok)	North Atlantic, Asia
<i>G. leopardinus</i>	marine	Gobiiformes: gobiid (marbled goby)	Mediterranean
<i>G. leptorhynchi</i>	freshwater	Syngnathiformes: syngnathid (Bay pipefish)	North America
<i>G. leucisci</i>	freshwater	Cypriniformes: cyprinid (chub, common dace, roach)	Eurasia
<i>G. lhkahuili</i>	freshwater	Cyprinodontiformes: poeciliid (shortfin molly)	Mexico
<i>G. lichuanensis</i>	freshwater	Cypriniformes: cyprinid (Amur minnow)	Asia
<i>G. limi</i>	freshwater	Esociformes: umbrid (central mudminnow)	North America
<i>G. limneus</i>	freshwater	Cypriniformes: cyprinid (Eurasia minnow)	Eurasia
<i>G. lineadactylus</i>	freshwater	Perciformes: centrarchid (black crappie)	North America
<i>G. lingulatus</i>	freshwater	Cypriniformes: catostomid (Alabama hog sucker)	North America
<i>G. llewellyni</i>	freshwater	Cypriniformes: cyprinid (Eurasian minnow, Czekanowski's minnow, Altai osman)	Eurasia
<i>G. lomi</i>	freshwater	Cypriniformes: cyprinid (chub)	Eurasia
<i>G. longidactylus</i>	marine	Gobiiformes: gobiid (Lozano's goby)	Northeast Atlantic
<i>G. longihamus</i>	freshwater	Cypriniformes: cyprinid (naked osman)	Asia
<i>G. longipes</i>	marine	Perciformes: sparid (gilthead seabream)	Mediterranean
<i>G. longiradix</i>	freshwater	Perciformes: percid (ruffe, European perch, pike-perch)	Eurasia
<i>G. longoacuminatus</i>	freshwater	Cypriniformes: cyprinid (common carp, Crucian carp, Prussian carp)	Eurasia
<i>G. lotae</i>	freshwater	Gadiformes: lotid (burbot)	Eurasia, North America
<i>G. lucii</i>	freshwater	Esociformes: esocid (northern pike); Perciformes: percid (European perch, pike-perch); Anguilliformes: anguillid (European eel)	North America, Eurasia
<i>G. luciopercae</i>	freshwater	Perciformes: percid (European perch, ruffe, Volga pike-perch, Danube streber)	Eurasia
<i>G. luckyi</i>	freshwater	Cypriniformes: nemacheilid (spotted thicklip loach)	Russia
<i>G. lythruri</i>	freshwater	Cypriniformes: cyprinid (blacktip shiner)	North America
<i>G. macracanthus</i>	freshwater	Cypriniformes: cobitid (pond loach)	Asia
<i>G. macrochiri</i>	freshwater	Perciformes: centrarchid (green sunfish, spotted sunfish, orangespotted sunfish, bluegill, largemouth black bass, warmouth, pumpkinseed); Scorpaeniformes: cottid (mottled sculpin)	North America
<i>G. macrocornis</i>	freshwater	Cypriniformes: cyprinid (common nase)	Europe
<i>G. macronychus</i>	marine, freshwater	Salmoniformes: salmonid (sea trout); Cypriniformes: cyprinid (Eurasian minnow)	Europe
<i>G. maculatus</i>	freshwater	Anabantiformes: channid (blotched snakehead)	Asia
<i>G. maculosi</i>	marine	Scorpaeniformes: cottid (tidepool sculpin)	North Pacific
<i>G. magniclypeus</i>	freshwater	Cypriniformes: catostomid (blacktip jumprock)	North America
<i>G. magnificus</i>	freshwater	Cypriniformes: cyprinid (roach, Eurasian minnow); Salmoniformes: salmonid (European whitefish)	Eurasia
<i>G. magnus</i>	freshwater	Salmoniformes: salmonid (Arctic grayling)	North America
<i>G. major</i>	freshwater	Siluriformes: callichthyid (banded corydoras, bigfin corydoras)	South America
<i>G. malalai</i>	freshwater	Cichliformes: cichlid (Nile tilapia)	Africa
<i>G. malmbergensis</i>	freshwater	Cypriniformes: cyprinid (Eurasian minnow)	Eurasia
<i>G. malmbergi</i>	freshwater	Cypriniformes: cyprinid (barbel, Mediterranean barbel)	Europe
<i>G. mantschuricus</i>	freshwater	Cypriniformes: cyprinid (lake minnow)	Eurasia
<i>G. margaritae</i>	freshwater	Cypriniformes: cyprinid (Allegheny pearl dace)	North America
<i>G. mariannae</i>	freshwater	Scorpaeniformes: cottid (Alpine bullhead)	Eurasia
<i>G. marinus</i>	marine	Gadiformes: gadid (Alaska pollock, Atlantic cod)	North Pacific
<i>G. marjami</i>	freshwater	Cypriniformes: cyprinid (common marinka)	Asia
<i>G. markakulensis</i>	freshwater	Cypriniformes: cyprinid (gudgeon, Danubian longbarbel gudgeon, white-finned gudgeon, Amur whitefin gudgeon)	Eurasia

<i>G. markevitschi</i>	freshwater	Cypriniformes: cyprinid (barbel, Mediterranean barbel); Perciformes: percid (ruffe)	Europe
<i>G. masu</i>	marine, freshwater	Salmoniformes: salmonid (masu salmon, sockeye salmon, rainbow trout, Japanese amago)	Northwest Pacific, North America, Asia
<i>G. matovi</i>	freshwater	Cypriniformes: cobitid (spined loach)	Eurasia
<i>G. medaka</i>	freshwater	Beloniformes: adrianchthyid (medaka)	Japan
<i>G. mediotorus</i>	freshwater	Cypriniformes: cyprinid (spottail shiner)	North America
<i>G. medius</i>	freshwater	Cypriniformes: cyprinid (roho labeo, common carp, Crucian carp, freshwater bream, goldfish), cobitid (weatherfish)	Eurasia, Indo-China
<i>G. meelkopae</i>	freshwater	Gobiiformes: gobiid (Trichonis dwarf goby)	Europe
<i>G. megacanthus</i>	freshwater	Cyprinodontiformes: fundulid (Bayou topminnow, blackspotted topminnow)	North America
<i>G. menschikowi</i>	freshwater	Cypriniformes: nemacheilid (stone loach)	Eurasia
<i>G. mexicanus</i>	freshwater	Cyprinodontiformes: goodeid (blackfin goodea, olive skiffia)	Mexico
<i>G. micracanthus</i>	freshwater	Cypriniformes: cobitid (pond loach)	Asia
<i>G. microalestis</i>	freshwater	Characiformes: alestid (sharptooth tetra)	Africa
<i>G. microanchoratus</i>	marine	Perciformes: anarhichadid (Atlantic wolffish)	Northeast Atlantic
<i>G. microdactylus</i>	freshwater	Cyprinodontiformes: poeciliid (shortfin molly)	Mexico
<i>G. micropogonus</i>	marine	Perciformes: sciaenid (Atlantic croaker)	West Atlantic
<i>G. micropsi</i>	marine	Gobiiformes: gobiid (common goby, Lozano's goby, sand goby)	East Atlantic
<i>G. micropteri</i>	freshwater	Perciformes: centrarchid (smallmouth bass)	North America
<i>G. mikailovi</i>	freshwater	Cypriniformes: cyprinid (seven khramulya)	Asia
<i>G. milleri</i>	freshwater	Cyprinodontiformes: poeciliid (cauca molly)	South America
<i>G. minimus</i>	freshwater	Cypriniformes: cyprinid (Eurasian minnow)	Eurasia
<i>G. minytremae</i>	freshwater	Cypriniformes: catostomid (spotted sucker)	North America
<i>G. mirabilis</i>	marine, freshwater	Scorpaeniformes: cottid (prickly sculpin)	North America
<i>G. misgurni</i>	freshwater	Cypriniformes: cobitid (weatherfish, pond loach)	Eurasia
<i>G. mizellei</i>	freshwater	Siluriformes: bagrid (striped dwarf catfish); Perciformes: percid (sauger, walleye)	Indo-China, North America
<i>G. mobilensis</i>	marine, freshwater	Cyprinodontiformes: cyprinodontid (sheepshead minnow)	Americas
<i>G. molnari</i>	freshwater	Cypriniformes: cobitid (spined loach)	Eurasia
<i>G. mongolicus</i>	freshwater	Cypriniformes: cyprinid (Altai osman, dwarf Altai osman)	Asia
<i>G. monstrosus</i>	freshwater	Cypriniformes: cobitid (spined loach, pond loach), nemacheilid (eightbarbel loach)	Eurasia
<i>G. montanus</i>	freshwater	Cypriniformes: cyprinid (Eurasian minnow, common marinka)	Eurasia
<i>G. montealbani</i>	freshwater	Cyprinodontiformes: profundulid (killifish)	Mexico
<i>G. moravecii</i>	freshwater	Cypriniformes: nemacheilid (Sistan loach)	Asia
<i>G. mugelus</i>	marine, freshwater	Mugiliformes: mugilid (flathead grey mullet)	cosmopolitan
<i>G. mugili</i>	marine	Mugiliformes: mugilid (so-iuy mullet)	Asia
<i>G. mutabilis</i>	freshwater	Cypriniformes: cyprinid (seven khramulya)	Asia
<i>G. nagibinae</i>	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
<i>G. nainum</i>	marine	Scorpaeniformes: cottid (fourhorn sculpin)	Arctic
<i>G. nannus</i>	freshwater	Atheriniformes: atherinopsid (inland silverside)	North America
<i>G. narzikulovi</i>	freshwater	Cypriniformes: cyprinid (false osman, marinka)	Asia
<i>G. nataliae</i>	freshwater	Cypriniformes: cyprinid (bigeye chub)	North America
<i>G. navarroensis</i>	freshwater	Cypriniformes: cyprinid (California roach)	North America
<i>G. nebraskensis</i>	freshwater	Cypriniformes: cyprinid (northern redbelly dace)	North America
<i>G. nebulosus</i>	freshwater	Siluriformes: ictalurid (brown bullhead, Channel catfish)	North America
<i>G. neili</i>	freshwater	Esociformes: esocid (chain pickerel)	North America
<i>G. nemacheili</i>	freshwater	Cypriniformes: nemacheilid (stone loach, gray loach, Tibetan stone loach, spotted thicklip loach)	Eurasia
<i>G. neonephrotus</i>	freshwater	Siluriformes: heteropneustid (stinging catfish)	Asia
<i>G. neotropicalis</i>	freshwater	Characiformes: characid (banded astyanax)	Americas
<i>G. neretum</i>	marine	Syngnathiformes: syngnathid (Gulf pipefish)	West Atlantic

<i>G. nerkae</i>	marine, freshwater	Salmoniformes: salmonid (sockeye salmon, brook trout)	North Pacific
<i>G. nevadensis</i>	freshwater	Cyprinodontiformes: cyprinodontid (Amargosa pupfish)	North America
<i>G. nigratae</i>	freshwater	Siluriformes: mochokid (false upsidedown catfish)	Africa
<i>G. nigrum</i>	freshwater	Perciformes: percid (Johnny darter)	North America
<i>G. niloticus</i>	freshwater	Cichliformes: cichlid (Nile tilapia)	Africa
<i>G. nipponensis</i>	freshwater	Anguilliformes: anguillid (Japanese eel)	Asia
<i>G. nordmanni</i>	freshwater	Cypriniformes: cyprinid (Altai osman)	Asia
<i>G. notatae</i>	marine	Atheriniiformes: atheriniid (Atlantic silverside)	Atlantic
<i>G. nudifronsi</i>	marine	Perciformes: nototheniid (gaudy notothen)	Southern Ocean
<i>G. nyanzae</i>	freshwater	Cichliformes: cichlid (Victoria tilapia)	Africa
<i>G. nyongensis</i>	freshwater	Siluriformes: clariid (catfishes)	Africa
<i>G. occupatus</i>	freshwater	Cichliformes: cichlid (southern mouthbrooder, Nile tilapia, dwarf bream)	Africa
<i>G. olsoni</i>	marine	Gobiiformes: gobiid (longjaw mudsucker)	East Pacific
<i>G. onegensis</i>	freshwater	Scorpaeniformes: cottid (bullhead)	Europe
<i>G. ophiocephali</i>	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
<i>G. orecchiaie</i>	marine	Perciformes: sparid (gilthead seabream)	Europe
<i>G. oreoleucisci</i>	freshwater	Cypriniformes: cyprinid (Altai osman, dwarf Altai osman)	Asia
<i>G. osmeri</i>	marine	Osmeriformes: osmerid (European smelt)	North Atlantic
<i>G. osoblahensis</i>	freshwater	Cypriniformes: cyprinid (common carp, common dace, chub)	Eurasia
<i>G. ostendicus</i>	freshwater	Gobiiformes: gobiid (common goby)	Europe
<i>G. ouluensis</i>	freshwater	Cypriniformes: cyprinid (roach)	Europe
<i>G. oxycephali</i>	freshwater	Cypriniformes: cyprinid (Chinese minnow)	Asia
<i>G. pacificus</i>	marine	Gadiformes: gadid (Pacific tomcod)	East Pacific
<i>G. pakan</i>	freshwater	Characiformes: characid (banded tetra)	Mexico
<i>G. pannonicus</i>	freshwater	Cypriniformes: cyprinid (barbel, Eurasian minnow)	Europe
<i>G. parabotia</i>	freshwater	Cypriniformes: cobitid (loach)	Asia
<i>G. paraminimus</i>	freshwater	Cypriniformes: cyprinid (common nase)	Europe
<i>G. paranemacheili</i>	freshwater	Cypriniformes: nemacheilid (spotted thicklip loach, gray loach)	Asia
<i>G. parasiluri</i>	freshwater	Siluriformes: silurid (Amur catfish)	Asia
<i>G. pardalidis</i>	marine, freshwater	Tetraodontiformes: tetraodontid (finepatterned puffer)	Northwest Pacific
<i>G. parisellei</i>	freshwater	Cichliformes: cichlid (Nile tilapia, southern mouthbrooder)	Africa
<i>G. parvae</i>	freshwater	Cypriniformes: cyprinid (stone moroko)	Asia
<i>G. parvicirrus</i>	freshwater	Cypriniformes: cyprinid (emerald shiner)	North America
<i>G. parvus</i>	freshwater	Cypriniformes: nemacheilid (gray loach, Tibetan stone loach, plain thicklip loach, spotted thicklip loach), cyprinid (Seven River's minnow)	Asia
<i>G. patersoni</i>	marine	Atheriniiformes: atherinid (Atlantic silverside)	Atlantic
<i>G. pavlovskyi</i>	freshwater	Cypriniformes: nemacheilid (stone loach)	Eurasia
<i>G. percotti</i>	freshwater	Gobiiformes: odontobutid (Amur sleeper)	Asia
<i>G. percinae</i>	freshwater	Perciformes: percid (blackbanded darter)	North America
<i>G. percunuri</i>	freshwater	Cypriniformes: cyprinid (lake minnow)	Eurasia
<i>G. perforatus</i>	marine	Gobiiformes: gobiid (arrow goby)	East Pacific
<i>G. perlucidus</i>	marine	Perciformes: zoarcid (eelpout)	Northeast Atlantic
<i>G. pewzowi</i>	freshwater	Cypriniformes: cyprinid (Altai osman, dwarf Altai osman)	Asia
<i>G. pharyngicus</i>	marine	Gadiformes: gadid (haddock, Atlantic cod)	Northeast Atlantic, Arctic
<i>G. phoxini</i>	freshwater, marine	Cypriniformes: cyprinid (Eurasian minnow, lake minnow); Salmoniformes: salmonid (Atlantic salmon)	Eurasia, North Atlantic
<i>G. pictae</i>	freshwater	Cyprinodontiformes: poeciliid (scarlet livebearer)	Central America
<i>G. pimelodellus</i>	freshwater	Siluriformes: heptapterid (three-barbeled catfish)	South America
<i>G. pisculentus</i>	marine	Syngnathiformes: syngnathid (northern pipefish)	Europe

<i>G. planensis</i>	freshwater	Cypriniformes: cyprinid (bigmouth shiner)	North America
<i>G. plecoglossi</i>	marine	Osmeriformes: plecoglossid (Ayu sweetfish)	Northwest Pacific
<i>G. pleuronecti</i>	marine	Pleuronectiformes: pleuronectid (winter flounder)	West Atlantic
<i>G. plotosi</i>	marine	Siluriformes: plotosid (striped eel catfish)	Indo-Pacific
<i>G. plumbeae</i>	freshwater	Cypriniformes: cyprinid (lake chub)	North America
<i>G. poeciliae</i>	freshwater	Cyprinodontiformes: poeciliid (cauca molly, guppy)	South America, Central America
<i>G. pomeraniae</i>	freshwater	Cypriniformes: cyprinid (roach)	Europe
<i>G. presidencyus</i>	freshwater	Anabantiformes: channid (snakehead)	India
<i>G. procerus</i>	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
<i>G. prolongis</i>	marine, freshwater	Cyprinodontiformes: fundulid (mummichog, banded killifish, Gulf killifish); Cyprinodontiformes: cyprinodontid (sheepshead minnow)	West Atlantic, Americas
<i>G. prostaе</i>	freshwater	Cypriniformes: cyprinid (roach, ide, chub, belica, freshwater bream, white bream, vimba bream, zope, common dace, Eurasian minnow)	Eurasia
<i>G. proterorhini</i>	marine	Gobiiformes: gobiid (giant goby, round goby, black goby, tubenose goby)	Europe, Mediterranean
<i>G. protruberus</i>	freshwater	Cypriniformes: cyprinid (skygazer shiner)	North America
<i>G. proximus</i>	marine	Scorpaeniformes: agonid (tubenose poacher)	North Pacific
<i>G. pseudobullatarudis</i>	freshwater	Cyprinodontiformes: poeciliid (green swordtail, porthole livebearer, shortfin molly)	Mexico
<i>G. pseudonemacheili</i>	freshwater	Cypriniformes: nemacheilid (gray loach, spotted thicklip loach)	Russia
<i>G. pterygialis</i>	marine	Gadiformes: gadid (saithe, Atlantic cod); Clupeiformes: clupeid (Pacific herring)	East Atlantic, Arctic
<i>G. pungitii</i>	marine, freshwater	Gasterosteiformes: gasterosteid (ninespine stickleback)	Eurasia, North America
<i>G. quadratidigitus</i>	marine	Gobiiformes: gobiid (leopard-spotted goby)	East Atlantic
<i>G. rachelae</i>	freshwater	Cypriniformes: cyprinid (shiner)	North America
<i>G. rafinesqueii</i>	freshwater	Perciformes: percid (Kentucky darter)	North America
<i>G. raipurensis</i>	freshwater	Abantiformes: channid (snakehead, spotted snakehead)	Asia
<i>G. rarus</i>	marine, freshwater	Gasterosteiformes: gasterosteid (ninespine stickleback)	Eurasia, North America
<i>G. rasini</i>	freshwater	Cyprinodontiformes: poeciliid (green swordtail)	Europe
<i>G. recurvensis</i>	freshwater	Cyprinodontiformes: aplocheilid (green panchax, blue panchax)	Asia, India
<i>G. rhigophilae</i>	marine	Perciformes: zoarcid (eelpout)	Southern Ocean
<i>G. rhinichthius</i>	freshwater	Cypriniformes: cyprinid (speckled dace)	North America
<i>G. rhinogobius</i>	freshwater	Gobiiformes: gobiid (goby)	Asia
<i>G. rhodei</i>	freshwater	Cypriniformes: cyprinid (bitterling, Russian bitterling, European bitterling, Chinese bitterling, giant Chinese bitterling)	Eurasia
<i>G. richardsonius</i>	freshwater	Cypriniformes: cyprinid (Lahontan redbelly)	North America
<i>G. rivularae</i>	freshwater	Cypriniformes: cyprinid (Chinese false gudgeon)	Asia
<i>G. robustus</i>	marine, freshwater	Clupeiformes: clupeid (Pacific herring); Pleuronectiformes: pleuronectid (European flounder, starry flounder)	Palaearctic
<i>G. roгатensis</i>	freshwater	Scorpaeniformes: cottid (bullhead)	Europe
<i>G. rogersi</i>	marine	Gadiformes: gadid (Pacific tomcod)	East Pacific
<i>G. rubripedis</i>	marine	Tetraodontiformes: tetraodontid (Japanese pufferfish)	Asia
<i>G. rugiensis</i>	marine, freshwater	Gobiiformes: gobiid (common goby, sand goby)	East Atlantic
<i>G. rugiensoides</i>	marine	Gobiiformes: gobiid (Lozano's goby, sand goby, painted goby)	Northeast Atlantic
<i>G. rutilensis</i>	freshwater	Cypriniformes: cyprinid (roach)	Europe
<i>G. rysavyi</i>	freshwater	Siluriformes: clariid (North African catfish)	Africa
<i>G. salaris</i>	freshwater, marine	Salmoniformes: salmonid (Atlantic salmon, sea trout, Arctic char, grayling, European whitefish, Adriatic trout, lake trout, brook trout, rainbow trout); Gasterosteiformes: gasterosteid (three-spined	Eurasia, North America

		stickleback, ninespine stickleback); Cypriniformes: cyprinid (Eurasian minnow)	
<i>G. salinae</i>	freshwater	Cyprinodontiformes: cyprinodontid (European toothcarp)	Europe
<i>G. salmonis</i>	marine, freshwater	Salmoniformes: salmonid (cutthroat trout, sea trout, golden trout, rainbow trout, brook trout, Atlantic salmon, coho salmon)	Pacific, Atlantic, North America
<i>G. salvelini</i>	marine, freshwater	Salmoniformes: salmonid (Arctic char)	Arctic
<i>G. samirae</i>	freshwater	Siluriformes: callichthyid (peppered corydoras)	South America
<i>G. saratogensis</i>	freshwater	Cyprinodontiformes: cyprinodontid (Amargosa pupfish)	North America
<i>G. scardiniensis</i>	freshwater	Cypriniformes: cyprinid (rudd, chub)	Eurasia
<i>G. schmidti</i>	freshwater	Perciformes: percid (walleye)	North America
<i>G. scleromystaci</i>	freshwater	Siluriformes: callichthyid (banded corydoras, bigfin corydoras)	South America
<i>G. sculpinus</i>	marine	Scorpaeniformes: cottid (Pacific staghorn sculpin)	East Pacific
<i>G. sedelnikowi</i>	freshwater	Cypriniformes: nemacheilid (stone loach)	Eurasia
<i>G. seravschani</i>	freshwater	Cypriniformes: cyprinid (common marinka)	Asia
<i>G. sergeji</i>	freshwater	Cypriniformes: cyprinid (Amur ide)	Asia
<i>G. shariffi</i>	freshwater	Cichliformes: cichlid (Nile tilapia)	Africa
<i>G. shorti</i>	marine, freshwater	Syngnathiformes: syngnathid (Gulf pipefish)	West Atlantic
<i>G. shulmani</i>	freshwater	Cypriniformes: cyprinid (common carp, Prussian carp, silver carp, crucian carp)	Eurasia
<i>G. sibiricus</i>	freshwater	Cypriniformes: cobitid (spine loach)	Asia
<i>G. slendrus</i>	freshwater	Characiformes: lebiasinid (twospot lebiasina)	South America
<i>G. slovacicus</i>	freshwater	Esociformes: umbrid (mudminnow)	Europe
<i>G. sommervilleae</i>	freshwater	Cypriniformes: cyprinid (freshwater bream)	Eurasia
<i>G. somnaensis</i>	freshwater, marine	Cypriniformes: cyprinid (Eurasian minnow); Salmoniformes: salmonid (chum salmon)	Eurasia
<i>G. spathulatus</i>	freshwater	Cypriniformes: catostomid (longnose sucker)	North America
<i>G. sphinx</i>	marine	Blenniformes: blenniid (sphinx blenny)	East Atlantic
<i>G. sprostonae</i>	freshwater	Cypriniformes: cyprinid (common carp, Prussian carp, redfin)	Eurasia
<i>G. squaliobarbi</i>	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
<i>G. stableri</i>	freshwater	Cyprinodontiformes: fundulid (Plains killifish)	North America
<i>G. stankowici</i>	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
<i>G. stegurus</i>	freshwater	Cyprinodontiformes: fundulid (banded killifish)	North America
<i>G. stellatus</i>	marine	Pleuronectiformes: pleuronectid (English sole, starry flounder), paralichthyid (speckled sanddab)	Pacific
<i>G. stephanus</i>	freshwater, marine	Cyprinodontiformes: fundulid (Gulf killifish, mummichog); Gasterosteiformes: gasterosteid (ninespine stickleback)	Palaearctic
<i>G. strelkovi</i>	freshwater	Cypriniformes: cobitid (weatherfish, pond loach)	Eurasia
<i>G. stunkardi</i>	freshwater	Cypriniformes: cyprinid (blacknose dace, longnose dace), catostomid (Sacramento sucker); Perciformes: percid (Johnny darter); Anura: ranid (American bullfrog, tadpoles)	North America
<i>G. sturmbaueri</i>	freshwater	Cichliformes: cichlid (southern mouthbrooder)	Africa
<i>G. superbus</i>	freshwater	Siluriformes: callichthyid (peppered corydoras)	South America
<i>G. syngnathi</i>	marine	Syngnathiformes: syngnathid (Nilsson's pipefish)	Northeast Atlantic
<i>G. synodonti</i>	freshwater	Siluriformes: mochokid (false upsidedown catfish)	Africa
<i>G. szanagai</i>	freshwater	Scorpaeniformes: cottid (alpine bullhead)	Eurasia
<i>G. taimeni</i>	freshwater	Salmoniformes: salmonid (taimen)	Eurasia
<i>G. takoke</i>	freshwater	Cyprinodontiformes: poeciliid (two-spot livebearer, porthole livebearer)	Mexico
<i>G. teken</i>	freshwater	Characiformes: characid (banded tetra)	Mexico
<i>G. tenesseensis</i>	freshwater	Cypriniformes: cyprinid (southern redbelly dace)	North America
<i>G. tepari</i>	freshwater	Cyprinodontiformes: goodeid (blackfin goodea)	Mexico
<i>G. teuchis</i>	marine, freshwater	Salmoniformes: salmonid (rainbow trout, Atlantic salmon, sea trout)	North America, Europe
<i>G. thlapi</i>	freshwater	Cichliformes: cichlid (southern mouthbrooder)	Africa

<i>G. thymalli</i>	freshwater	Salmoniformes: salmonid (grayling, Arctic grayling)	Europe, North America
<i>G. thysi</i>	freshwater	Cichliformes: cichlid (southern mouthbrooder)	Africa
<i>G. tibetanus</i>	freshwater	Cypriniformes: nemacheilid (Tibetan stone loach)	Asia
<i>G. tincae</i>	freshwater	Cypriniformes: cyprinid (tench)	Eurasia
<i>G. tokobaevi</i>	freshwater	Cypriniformes: cyprinid (naked osman)	Asia
<i>G. tomahuac</i>	freshwater	Cyprinodontiformes: goodeid (blackfin goodea)	Central America
<i>G. tominagai</i>	marine, freshwater	Osmeriformes: plecoglossid (Ayu sweetfish)	Northwest Pacific
<i>G. tonii</i>	freshwater	Cypriniformes: nemacheilid (stone loach)	Eurasia
<i>G. trairae</i>	freshwater	Characiformes: erythrinid (wolf fish)	South America
<i>G. transvaalensis</i>	freshwater	Siluriformes: clariid (North African catfish)	Africa
<i>G. trematoclitrus</i>	freshwater	Cyprinodontiformes: fundulid (bluefin killifish)	North America
<i>G. trematomi</i>	marine	Perciformes: nototheniid (dusky rockcod)	Southern Ocean
<i>G. truttiae</i>	freshwater, marine	Salmoniformes: salmonid (sea trout, rainbow trout, brook trout, grayling, Atlantic salmon)	North America, Europe
<i>G. tularosae</i>	freshwater	Cyprinodontiformes: cyprinodontid (White Sands pupfish)	North America
<i>G. tulensis</i>	freshwater	Cypriniformes: cyprinid (ide, Siberian dace)	Eurasia
<i>G. turkanaensis</i>	freshwater	Siluriformes: clariid (African sharptooth catfish)	Africa
<i>G. turnbulli</i>	freshwater	Cyprinodontiformes: poeciliid (guppy, livebearer)	Europe, South America
<i>G. ulinganisus</i>	freshwater	Cichliformes: cichlid (Mozambique tilapia)	Africa
<i>G. umbrae</i>	freshwater	Esociformes: umbrid (mudminnow)	Europe
<i>G. unami</i>	freshwater	Cyprinodontiformes: poeciliid (porthole livebearer)	Mexico
<i>G. unicopula</i>	marine	Pleuronectiformes: pleuronectid (Arctic flounder, starry flounder, European plaice)	Arctic
<i>G. unipons</i>	marine	Pleuronectiformes: pleuronectid (European plaice)	Europe
<i>G. vancleavei</i>	marine	Scorpaeniformes: hexagrammid (rock greenling)	East Pacific
<i>G. variabilis</i>	freshwater	Cypriniformes: cyprinid (golden shiner)	North America
<i>G. varicorhini</i>	freshwater	Cypriniformes: cyprinid (seven khramulya)	Asia
<i>G. vicinoides</i>	freshwater	Cypriniformes: cyprinid (common marinka)	Asia
<i>G. vicinus</i>	freshwater	Cypriniformes: cyprinid (Eurasian minnow, common marinka)	Eurasia
<i>G. vimbi</i>	freshwater	Cypriniformes: cyprinid (gudgeon, rudd, Tiber rudd, roach, chub, freshwater bream, vimba bream, white bream, white-eye bream, common carp, crucian carp, Mediterranean barbel, pigo, common dace, bleak)	Eurasia
<i>G. viriosus</i>	freshwater	Cypriniformes: catostomid (northern hog sucker, Alabama hog sucker)	North America
<i>G. wardi</i>	freshwater	Cypriniformes: catostomid (longnose sucker, Sacramento sucker)	North America
<i>G. wellborni</i>	freshwater	Cypriniformes: cyprinid (golden shiner)	North America
<i>G. wilkesi</i>	marine	Perciformes: nototheniid (striped rockcod, emerald rockcod)	Southern Ocean
<i>G. wuchangensis</i>	freshwater	Cypriniformes: cyprinid (Chinese bitterling)	China
<i>G. xalapensis</i>	freshwater	Cyprinodontiformes: poeciliid (two-spot livebearer)	Mexico
<i>G. xiamenensis</i>	marine	Mugiliformes: mugilid (largescale mullet)	Indian Ocean, Pacific
<i>G. xtachuna</i>	freshwater	Cyprinodontiformes: poeciliid (porthole livebearer, two-spot livebearer, shortfin molly)	Mexico
<i>G. xymus</i>	marine	Gerreiformes: gerreid (common silverbelly)	Australia
<i>G. yacatli</i>	freshwater	Cichliformes: cichlid (Nile tilapia)	Africa
<i>G. yukhimenkoi</i>	freshwater	Cypriniformes: cobitid (spine loach)	China
<i>G. zapoteco</i>	freshwater	Cyprinodontiformes: profundulid (killifish)	Mexico
<i>G. zhukovi</i>	marine	Mugiliformes: mugilid (so-iuy mullet)	Asia
<i>G. zimbae</i>	freshwater	Cichliformes: cichlid (southern mouthbrooder)	Africa

**Parasite morphology:** *Gyrodactylus* spp. are unique parasites because they effectively have only adult stages in their developmental cycles. The worms are viviparous and produce live unciliated young whereas all other monogeneans are oviparous and produce eggs containing ciliated oncomiracidia. In addition, many *Gyrodactylus* spp. exhibit hyperviviparity (polyembryony) where unborn individuals (subadults retained in the uterus) develop their own young (cf. Russian nested dolls). The adults are hermaphroditic and contain an ovovitellarium which is a fused mass of ova and vitelline cells (vitellaria are not distinct). In gravid worms, body organs are usually compressed by the extensive volume of developing embryos curled within the uterus. Indeed, the internal anatomy of viviparous gyrodactylids has often been misinterpreted because they lack many structures present in oviparous monogeneans. Most gyrodactylid species do not possess a vagina but have a birth pore. Adults have small fusiform bodies < 1 mm in length often curved with the dorsal surface convex. They have a syncytial tegument characteristic of monogeneans and there are three body regions: cephalic (anterior to pharynx), trunk (body) and peduncle (tapered end of body). Although usually transparent and colourless, worms may vary in colour (grey, yellow, brown, black, pink, red) depending on ingested food. All worms possess a prominent posterior attachment organ (opisthaptor) apparent as a circular-semicircular disc bearing 16 small marginal hooks (often appearing as radial pins) and a central pair of large ventrally-orientated hamuli (appearing as fish-hooks) linked by separate dorsal and ventral bars. Adults also have two conspicuous anterior cephalic processes (bilobed head) bearing adhesive glands and spike sensilla involved in attachment and sensation.

**Site of infection:** Gyrodactylids are commonly known as skin flukes as they usually infect the skin and fins of their fish hosts, but some species may also infect the gills. Several studies have shown many species to exhibit pronounced tissue tropism (site specificity), but it appears to be highly variable depending on environmental conditions, host age and condition, and stage of parasite development. Many gyrodactylid species apparently undergo characteristic migrations between sites as they mature e.g. juvenile *G. salaris* attach preferentially to the dorsal fin but migrate to the pectoral and anal fins as they mature. However, worms are less selective when infection densities are high and they may attach to any area of open skin. Other species have been shown to develop in infection foci ('hot-spots') when newborn worms attach alongside their mothers using their posterior attachment organ (opisthaptor). Worms have also been observed moving freely over their hosts in an 'inch-worm' or 'caterpillar'-like fashion involving alternate attachment of their posterior and anterior attachment organs.

**Pathogenesis:** Following attachment to the external surfaces of fish, gyrodactylid worms feed on host epithelial cells and mucus and may cause significant damage to the skin, fins and even gills of the host. Even low levels of infections may cause disease (known as gyrodactylosis) which has been associated with morbidity and mortality in wide variety of fish species. Clinical signs include skin pallor (due to excessive mucus production and epithelial hyperplasia), mottling, necrosis, ulceration, focal haemorrhagic lesions, erosion, desquamation, loss of scales, fin erosion, fin clamping, restlessness, lethargy, anorexia, flashing behaviours and secondary bacterial and fungal infections are common. Infection of the gills may result in lamellar hyperplasia, excessive mucus production, rapid respiratory movements and severe distress. Mortalities are often attributed to a combination of problems associated with secondary infections and osmotic problems due to puncture wounds. Some infections have been observed to decline spontaneously over time, this being attributed to the development of host protective immune responses, but considerable heterogeneity was found within and between host populations. Gyrodactylid infections do present significant problems to the aquarium trade and they have caused significant economic losses in aquaculture (esp. salmonids, cod, flatfish, wolf fish, eels and cyprinids), with increasing drug resistance reported in farmed fish.

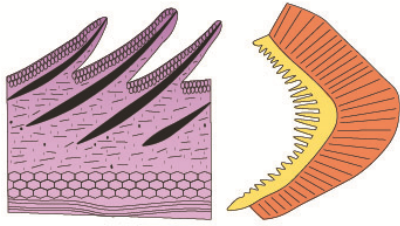
**Developmental cycle and mode of transmission:** Gyrodactylids are transmitted horizontally and directly between hosts when worms move from fish-to-fish by direct physical contact, or by being dislodged and then contaminating the immediate aquatic environment. Infections are, therefore, more easily transmitted between gregarious hosts or those kept in crowded or confined conditions. This direct mode of transmission is rare in that no specific transmissive stage is involved as the parasites reproduce *in situ* on their hosts. They also exhibit accelerated reproductive development (progenesis) and bear live young (viviparity). Gyrodactylids give birth to fully grown young which already contain second-generation (F1) embryos which in turn develop third-generation (F2) embryos. This 'Russian nested doll' succession of embryos occurs through a process of polyembryology. Viviparous gyrodactylids are protogynous hermaphrodites, in that the female system matures first although it remains structurally simple characterised by syncytial structures. Worms do not develop extensive internal organ systems but retain extensive syncytial layers in which metabolic functions take place. Newborn worms give birth at least twice before the male reproductive system develops and insemination occurs. Daughters are usually created asexually from a ball of germ cells, while subsequent daughters develop from eggs released from an oocyte before self-fertilization. Unlike other helminths, the eggs do not have eggshells normally created by vitelline cells. Cross-fertilization has been observed for some species when one individual pierces the body of another and injects sperm to fertilize developing embryos thus creating genetically different offspring. In addition to asexual and sexual development, some species have recently been reported to undergo parthenogenesis. Irrespective, all newborn worms immediately function as adults, attach and begin feeding on mucus and epithelial cells. Generation times are typically quite short (1-5 days), as are the lifespans of adults (6-15 days). Various patterns of infection have been reported: some being seasonal and apparently

associated with decreased host activity in winter; others with host migrations and increased activity around breeding; and several being sporadic and seemingly influenced by parasite population density (asexual reproduction when population density is low and sexual reproduction when population density is high). The processes of progenesis, polyembryology and hyperviviparity, combined with rapid generation times, means parasite populations can potentially grow exponentially on hosts leading to outbreaks, particularly in aquaria or intensive culture.

**Differential diagnosis:** Whole parasites can be detected microscopically in wet mounts made from skin scrapings or gill snips. The genus *Dactylogyrus* can be differentiated by the characteristic arrangement of hooks on the haptor and the presence of developing embryos within the body, but their specific identification is difficult as the worms have simple anatomical features. Many species have been identified simply on the basis of host occurrence.

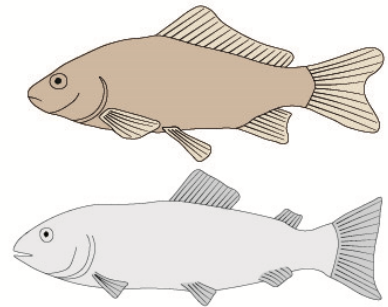
**Treatment and control:** Early diagnosis and treatment is essential because parasite numbers may increase exponentially over a short period (often days). Standard treatments involve bathing freshwater fish in saltwater, bathing marine fish in freshwater, or bathing either in dilute formalin or potassium permanganate solutions. Some success has been reported treating ornamental fish with trichlorfon or praziquantel. Control in the aquarium trade is best facilitated by screening exports and imports and using quarantine procedures to minimize parasite translocations. The species *G. salaris* has wrought havoc in Europe by causing epidemics in salmon aquaculture as well as endangering wild salmon stocks in rivers. Rotenone poisoning of entire river systems was used for many years, largely unsuccessfully, and recent efforts involving heavy metal (aluminium) dosing are similarly unequivocal.

# Gyrodactylus

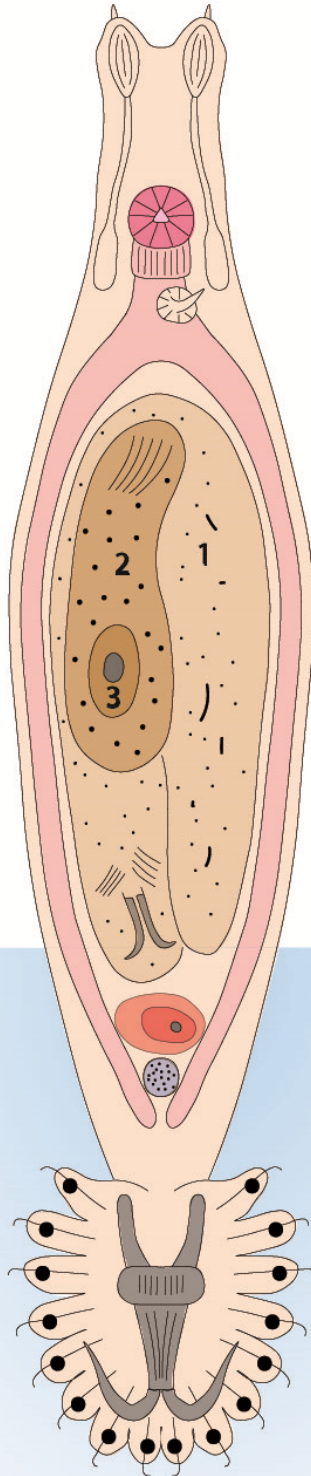


skin, sometimes gills  
(traumatic damage,  
inflammation, necrosis)

aquatic cycle

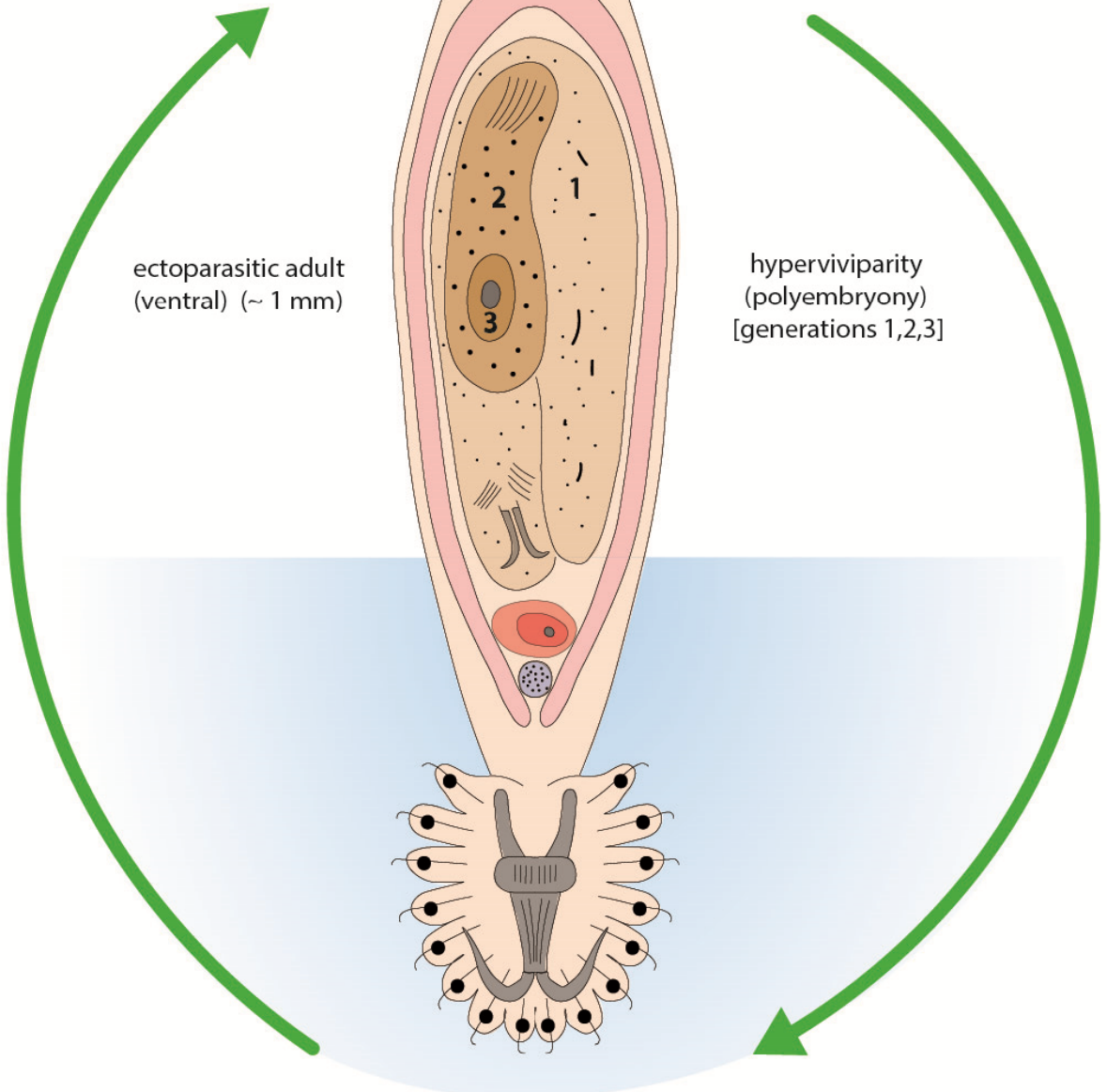


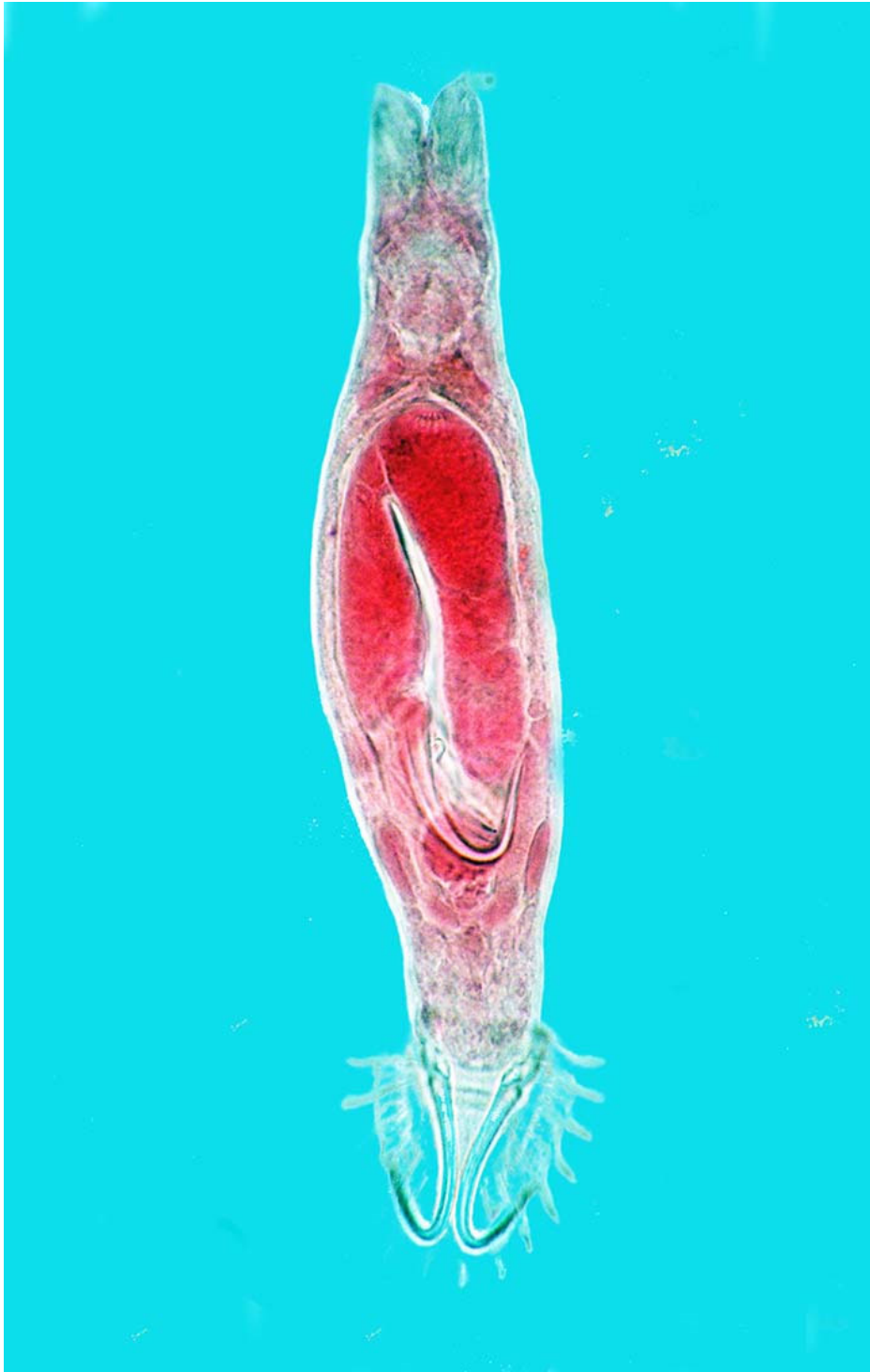
Definitive Hosts  
(fish, esp. cyprinids  
and salmonids)



ectoparasitic adult  
(ventral) (~ 1 mm)

hyperviviparity  
(polyembryony)  
[generations 1,2,3]





*Gyrodactylus* adult worm