

= Theodoxus fluviatilis =

Theodoxus fluviatilis , common name the river nerite , is a species of small freshwater and brackish water snail with a gill and an operculum , an aquatic gastropod mollusk in the family Neritidae , the nerites .

This widely distributed neritid snail species occurs from Europe to Central Asia . It has a thick shell with a calcified operculum . The coloration pattern on the shell is very variable . *Theodoxus fluviatilis* lives in freshwater and in brackish water , in rivers and lakes on stones . It feeds mainly by grazing on biofilms and diatoms .

Some of the populations of this species are spreading , and these can reach densities up to thousands of snails per square meter . Females lay egg capsules , each of which contains a large number of eggs , but only one snail hatches from the capsule . The snails reach sexual maturity in a year , and the total lifespan is 2 or 3 years .

= = Taxonomy = =

Theodoxus fluviatilis was originally described under the name *Nerita fluviatilis* by Carl Linnaeus in 1758 . Linnaeus ' original text (the type description) in Latin was very short , and reads as follows :

Which means in English : " *Nerita fluviatilis* , number 632 : the shell is wrinkled , there are no teeth in the aperture . It inhabits rivers in Europe . " Later , this species was moved to the genus *Theodoxus* Montfort , 1810 . *Theodoxus fluviatilis* is in fact the type species of the genus *Theodoxus* . Anistratenko and colleagues designated the lectotype for *Theodoxus fluviatilis* in 1999 (an English translation was published by Anistratenko in 2005) .

= = = Subspecies = = =

Several subspecies of *Theodoxus fluviatilis* were described and (inconsistently) recognized by various authors :

Theodoxus fluviatilis fluviatilis (Linnaeus , 1789) ? was described from a freshwater environment

Theodoxus fluviatilis fluviatilis f. *fontinalis* Brard , 1815 ? is sometimes considered as a synonym of *Theodoxus fluviatilis*

Theodoxus fluviatilis littoralis (Linnaeus , 1789) ? was described from brackish water by Linnaeus as a separate species , originally named *Nerita littoralis* . A study by Zettler (2008) proved that its status as a subspecies is unjustified , being regarded as a synonym of *Theodoxus fluviatilis* . Although these so @-@ called forms (form *fluviatilis* and form *littoralis*) differ in morphology , ecology , reproductive strategy and behaviour , they are probably just ecomorphs .

Theodoxus fluviatilis sardous (Menke , 1830)

Theodoxus fluviatilis subthermalis Issel , 1865 ? or *Theodoxus subthermalis* (Bourguignat in Issel , 1865)

Theodoxus fluviatilis thermalis (Dupuy , 1851)

Theodoxus fluviatilis transversetaeniatus A. J. Wagner , 1928

Theodoxus fluviatilis dalmaticus Sowerby ? in Lake Ohrid

Theodoxus fluviatilis euxinus (Clessin , 1885) ? has been considered to be a subspecies (see *Theodoxus euxinus*)

Bunje (2005) does not consider *Theodoxus velox* Anistratenko , 1999 to be a distinct species from *Theodoxus fluviatilis* .

= = = Cladogram = = =

A cladogram shows the phylogenetic relationships within the genus *Theodoxus* :

This cladogram shows that the sister group to clade B is clade C. They split in 5 ? 11 @.@ 5 Ma , when Lake Pannon existed . *Theodoxus* species living in brackish water include *Theodoxus fluviatilis* and *Theodoxus jordani* , but they are apparently not closely related .

= = Distribution = =

The exact type locality for this species is unknown , but it is probably the Main river in Southern Germany . Glöer (2002) considered the type locality sensu Linnaeus as " Habitat in fluviis , Upsaliae ad molendinam Ulvam & alibi " , but this would suggest a brackish water environment . The distribution of this species was considered to be European , but in reality the species occurs in the western to central Palaearctic . Its occurrence is scattered throughout Europe and in Western Asia except for the Alps and the regions immediately north of the Alps . This species does not live in Norway or Siberia . *Theodoxus fluviatilis* has the most widespread distribution of all of the species in the genus *Theodoxus* . It is in fact one of the most widely distributed species in the entire family Neritidae .

This species is threatened mainly by river engineering and water pollution in densely populated regions . The species ' population trend is overall stable , but is declining in some areas (Germany) , while in other areas it is expanding (for example in the Danube river) . In the Rhine river during the 1970s , *Theodoxus fluviatilis* came close to local extinction because of water pollution . Subsequently , the water quality improved for more than two decades , leading to a recovery . Even so , the species became extinct in the Rhine for an unknown reason in the late 1990s . Since 2006 , *Theodoxus fluviatilis* recolonized the Rhine , probably via ship transport through the Main @-@ Danube Canal . An analysis based on cytochrome @-@ c oxidase I (COI) gene has shown that the recolonization probably originated in the Danube .

= = = Europe = = =

The species occurs widely in Western Europe , and it is also widespread in the north of Ireland , living in 10 % of Irish streams and rivers . It lives in Great Britain , including the isle of Orkney , as well as in the Netherlands , Belgium , Luxembourg , Liechtenstein , and Monaco . It also is found in France and Switzerland , where it is considered to be critically endangered . More to the south , it occurs in Spain and Portugal , although the species is restricted to karst springs in Central Portugal .

In central Europe , this species lives as neozoon in the Austrian Danube , where it was first recorded in Tulln , Lower Austria in 2001 . In the Czech Republic , it is now extinct in Bohemia ; the only findings were in the Elbe river near Litom??ice in 1917 , and the most recent findings of empty shells took place in 1943 . *Theodoxus fluviatilis* also occurs in Poland , in Slovakia where it is non @-@ indigenous since 2002 , and in Hungary . Zettler (2008) provided a detailed bibliography of the distribution of *T. fluviatilis* in Germany . The indigenous distribution of *T. fluviatilis* included all of the large rivers : Rhine , Main , Moselle , Neckar , Weser , Elbe and Oder . However , this species is now highly endangered in Germany (Stark gefährdet) .

In Northern Europe , this species is found in Denmark , in Sweden as far north as 58 ° N. It can also be found on the coasts of Finland , in the Åland Islands , and is known to be found alive there since 1994 . No other *Theodoxus* species reaches the Baltic Sea . It has the northernmost distribution of the genus *Theodoxus* and it is also the northernmost species of all Neritidae . In Eastern Europe this snail occurs in Estonia , Lithuania , and Latvia , as well as Belarus , and in Russia from western Russia to Caucasus . Since 1997 it has been found in the Gulf of Odessa , Ukraine . In Ukraine and in Crimea it is non @-@ indigenous , and was first recorded in the area in 1955 . It also occurs in Moldova . In Southern Europe , *Theodoxus fluviatilis* lives in Albania , Bosnia and Herzegovina , Romania , Bulgaria , Slovenia , and Croatia . In Macedonia and Albania it occurs in Lake Ohrid (which spans the border of the two countries) as the subspecies *Theodoxus fluviatilis dalmaticus* . It is found on the mainland of Greece and also on Crete . It is known to occur in the mainland of Italy and also in Sardinia . It occurs in Montenegro , and in Serbia .

= = = Asia and Africa = = =

In Asia , *Theodoxus fluviatilis* is found in Turkey . It can also be found in Iran , in the provinces of Kerman , Gilan , Mazandaran , Fars , Hormozgan , Lorestan and Khorasan . However , until 2012 , all the records from Iran were listed as *Theodoxus doriae* . In Africa this species occurs in Algeria , and possibly (or probably) in Morocco , where there are records which some authors consider to be reliable . However , instead of one species , *Theodoxus fluviatilis* , Brown (1994) recognized three species in northwestern Africa : *Theodoxus numidicus* , *Theodoxus maresi* , *Theodoxus meridionalis* .

== Prehistoric biogeography ==

Shells of *Theodoxus fluviatilis* have been found in an Upper Paleolithic archaeological site in the cave Caldeirão , Pedreira (Tomar) , Tomar Municipality , Portugal , and also in a site from about 6000 years B.P. of Litorina age on the Åland Islands . Shells from the Late Neolithic have been found in Divoká ?árka , Czech Republic . Bunje (2005) hypothesized that the ancestral range of *Theodoxus fluviatilis* was the Ponto @-@ Pannonian region (southern Ukraine , Romania and Hungary) . Bunje suggested that the species first colonized northern Italy , Greece and Turkey ; in the second phase it colonized Spain , France and Germany ; and finally in the Holocene it colonized the British Isles , Sweden and the Baltic Sea . In 2002 , German malacologist Peter Glöer summarized the distribution of this species during the Pleistocene and Holocene epochs .

== Description ==

The shell of *Theodoxus fluviatilis* is somewhat depressed (with an usually low spire) , strongly calcified , and has 3 ? 3 @.@ 5 whorls (including the protoconch) . Larger specimens are usually eroded . The width of an adult shell is usually 5 ? 9 mm , but can reach up to 11 ? 13 mm . The height of the shell is 4 ? 6 @.@ 5 mm , or up to 7 mm . These mean values vary among populations depending on the environment : the maximum width of the shell of brackish water populations is 9 @.@ 3 mm . Brackish water shells are somewhat shorter , reaching up to 5 @.@ 8 mm , and the maximum weight of the shell is 124 mg . In freshwater populations , the maximum recorded shell width is 13 @.@ 1 mm , and maximum height is 9 @.@ 3 mm . The maximum weight of freshwater shells is 343 mg .

The exterior of the shell is basically whitish or yellowish , with a net @-@ like dark reddish or violet pattern . This pattern is very variable (depending on environmental factors) , sometimes partly presenting bands , and even occasionally being evenly dark . The shell is very variable in color and color patterns , showing great polymorphism . Shell coloration and patterns are very plastic in all species of the genus *Theodoxus* and these qualities may be influenced by factors like ionic composition of water , type of substratum and nutrition of individuals in various habitats . Zettler and colleagues (2004) showed that in the outer coastal waters of the Baltic Sea , the nearly black and often corroded shell form of *Theodoxus fluviatilis* is predominant , whereas in the inner (sheltered) parts of coastal waters , yellowish @-@ green forms prevail . Glöer and Pe?i? (2015) observed that specimens from a darker stony substrate were black or dark brown . Shells of specimens of *Theodoxus fluviatilis* from Northern Europe are ornamented with a pattern of white , drop @-@ like spots on a dark or red background . Specimens from South France and Spain are ornamented with a pattern of zigzag stripes , while specimens from the Balkans show all possible combinations of white drop @-@ like spots and zigzag stripes . Animals from lacustrine habitats show dark or light bands on the shell .

Images showing variability in the color patterns of shells of *Theodoxus fluviatilis* :

The shell shape of *Theodoxus fluviatilis* is similar to that of *Theodoxus transversalis* . The shell shape of *Theodoxus danubialis* is more spherical . The shape of the aperture of *Theodoxus prevostianus* is usually descending . However , all of these species display a large morphological plasticity , which makes them difficult to differentiate . The overall outline of the shell is still used for species identification in recent malacological literature . Though the coloration and patterns of the shells cannot be relied upon to identify specimens , opercular characters can be used for a proper

identification of *Theodoxus fluviatilis* . The calcified operculum of *T. fluviatilis* is D @-@ shaped , light reddish with a red margin , bearing a broad rib (also called a ridge) on its inner surface . The columellar muscle is attached to the rib . The rib is long and thin , attenuated at the base , while the callus is thin ; a peg is lacking . The characteristic features of the operculum are already visible in juveniles . There is sexual dimorphism on the border of the rib shield of the operculum , which is straight in females , but curved in males .

Aberrations in the shape of operculum have been observed . In a specimen from Vouvant in France , and another from a spring near Bar in Montenegro , a double rib was present , but the rib shield was reduced ; in a specimen from Ohrid Lake , only the rib shield was reduced . *Theodoxus fluviatilis* can be distinguished from the other three mentioned species by having a rib pit , which is formed by the rib and the rib shield . The rib shield , and consequently a rib pit , are lacking in *Theodoxus transversalis* , *Theodoxus danubialis* and *Theodoxus prevostianus* . These three species differs in having , in addition to a rib , a peg , which is absent in *T. fluviatilis* . The visible soft parts of the animal are light yellow with a black head . The tentacles are greyish and long . The eyes are large and black ; the foot is whitish .

== Radula ==

Theodoxus fluviatilis , like all other species in the family Neritidae , has a radula which is of the rhipidoglossan type (a radula with many small marginal teeth which help " brush " food particles into the gullet) . Zettler and colleagues (2004) and Zettler (2008) made SEM micrographs of the radula of this species .

== Reproductive system ==

Theodoxus fluviatilis has separate sexes (i.e. these snails are dioecious) . The diploid number of chromosomes ($2n$) is 25 in males and 26 in females . There is XO sex @-@ determination system in Neritidae , and it was confirmed for this species too .

Females have two openings located under the edge of the mantle in the mantle cavity : the opening of the vagina and an opening for laying eggs . The vagina accepts the sperm during copulation . The vagina is connected to the bursa copulatrix and to the spermatheca (for storing sperm) . The other opening is for laying eggs . Egg cells originate in the ovary . Egg cells travel through the oviduct to the fertilization chamber , where fertilization occur . Eggs then develop in the glandular uterus . A capsule is formed in the diverticulum next to the uterus . The eggs are then laid .

In males , the semen is forming in the testis . The sperm structure of *Theodoxus fluviatilis* was examined by Gustaf Retzius . Then semen travels through the prostate , where it mixes with prostatic fluid . Finally it goes through the vas deferens to the penis . The penis is located on the inner side of the right tentacle . The following illustrations show the reproductive system in the female and in the male :

== Various organ systems ==

Circulatory system : The osmotic pressure of the hemolymph of *Theodoxus fluviatilis* is 95 mOsm . That is much lower value than in marine snails in the subfamily Neritinae . The osmotic pressure and the composition of ions of the hemolymph of the subfamily Neritinae (where does the *Theodoxus* belong to) is similar to the hemolymph of the land snail family Heliciniidae .

== Ecology ==

== Habitat ==

Theodoxus fluviatilis prefers lowland habitats (in Switzerland it occurs up to 275 m a.s.l.) and

calcium @-@ rich waters . This small snail inhabits the central and lower parts of rivers (up to 13 m deep) , including in brackish water in tidal rivers of estuaries . It sometimes lives in lakes on unvegetated bottoms . Rarely , it lives in springs (rheocrenes) , in ground water , and in caves . For example , in the Åland Islands , *Theodoxus fluviatilis* was found living in lakes with a pH of 7 @.@ 8 ? 8 @.@ 9 . In streams and rivers in Ireland , the species lived in water with a pH of 7 @.@ 0 ? 8 @.@ 4 .

The species easily attaches itself to stones , which allows it to live in fast @-@ running waters and in wave zone in lakes . The ability of *Theodoxus fluviatilis* to live in freshwater and also in brackish water demonstrates the phenotypic plasticity of this species . This small snail can live in up to 60 m depth in coastal waters . Brackish water populations can live in salinities of up to 15 % in the Baltic Sea or up to 18 % in the Baltic Sea and in Black Sea . Populations from brackish water can tolerate higher salinity than populations from freshwater . Brackish water populations have much higher accumulation of ninhydrin @-@ positive substances in the foot .

This species lives on hard benthic substrates , typically rocks . It lives on pebbles , sometimes on boulders , and rarely on dead wood . It tolerates mild organic pollution , low oxygen content (down to below 2 mg / liter) but it does not tolerate long periods of droughts , or ice . It lives in mesotrophic waters , and sometimes in oligotrophic waters .

Theodoxus fluviatilis serves an indicator species for river monitoring (in Germany) ; however the spreading populations also have a high tolerance for degraded habitats . *Theodoxus fluviatilis* has a large phenotypic plasticity : it was found living on stones and on dead wood in freshwater environments ; whereas it lives on stones and on *Fucus vesiculosus* , *Potamogeton* spp. and *Zostera marina* in brackish water in the Baltic Sea . The species can also be found on aggregates of *Mytilus* .

This species , together with the isopod *Saduria entomon* , have been found to be a dominant part of the fauna biomass in the central and northern Baltic Sea . Brackish water populations can reach densities up to 200 ? 1000 snails per m² . *Theodoxus fluviatilis dalmaticus* in Lake Ohrid can reach population densities up to 6412 snails per m² . The species was found in population densities of up to 9000 snails per m² in a spring of the Anços river in Central Portugal , where there is a stable temperature of 15 @.@ 3 ? 16 @.@ 6 ° C , which allows continuous reproduction in *Theodoxus fluviatilis* . At Gabčíkovo port , in September 2003 , a density of 34 @,@ 932 juvenile snails per m² was recorded .

=== Feeding habits ===

Theodoxus fluviatilis feeds mainly on diatoms living on stones , scraping biofilms and also consuming detritus . It can also consume Cyanobacteria and green algae as a poor @-@ quality food supply . Cyanobacteria contain toxins and indigestible mucopolysaccharides , and green algae have cellulose in their cell walls (*Theodoxus* species have no cellulase enzymes to digest cellulose) . They also graze on zygotes and germlings of brown alga *Fucus vesiculosus* , when the alga is small up to 1 mm . Peters and Traunspurger (2012) studied the effect of the grazing of *Theodoxus fluviatilis* on epilithic meiofauna and algae .

=== Life cycle ===

Theodoxus fluviatilis is gonochoristic , which means that each individual animal is distinctly male or female , and cross @-@ fertilization can occur . The sex ratio is 1 : 1 . The structure of the flagellum of the spermatozoon is unique : the flagellum is divided into two parts .

T. fluviatilis eggs are usually laid in from mid @-@ April to October , in temperatures above 10 ° C. Eggs are laid in egg capsules deposited on stones and sometimes on shells of conspecific individuals . Females usually lay a cluster containing 4 ? 5 capsules . A single female will usually lay about 40 capsules during summer , and about 20 capsules during autumn . Fresh capsules are white , but older capsules become yellow or brown and may bear an epiphytic outer layer . The capsules are around 1 mm in diameter (0 @.@ 9 ? 1 @.@ 1 mm) , but in brackish water they are

usually smaller (about 0.8 mm). Empty (sterile) small capsules (0.5 - 0.8 mm in diameter) can also be laid . The number of eggs per egg capsule changes depending on the environment . There are 100 - 200 eggs in each capsule in freshwater , as opposed to 55 - 80 eggs in each capsule in brackish water . Usually , only one egg develops , with the remaining eggs serving as nutrition for the embryo , which results in a single juvenile snail hatching from each capsule .

Juveniles with a shell length of 0.5 - 1 mm hatch after 30 days (in 25 ° C) , or after 65 days (in 20 ° C) . The ash-free dry weight of newly hatched snails is 0.012 mg . The protoconch has one whorl . Capsules laid in spring hatch after 2 - 3 months , in August - September . Capsules from late summer overwinter because embryonic development ceases in temperatures below 10 ° C , thus these capsules hatch in spring after 7 - 8 months . The shell grows mainly from May to August ; there is no shell growth in winter . The snails reach sexual maturity in less than 1 year , when the shell length is 5 - 7 mm .

The life span of *T. fluviatilis* is 2 - 3 years . The age of a few snails was estimated to be 3 - 5 years . The mortality rate is low in summer . However , it is higher in winter because ice and storms can dislocate the substrate , which can result in mechanical damage to the snails .

== Parasites and predators ==

Parasites of *Theodoxus fluviatilis* include several species of trematodes . The snail serves as first intermediate host to *Plagioporus skrjabini* and as second intermediate host to *Cotylurus cornutus* . *Asymphylogaster demeli* is also found in this small snail , as is *Notocotylus zduni* . This small snail is also parasitized by several species of ciliates . It is the main host for the ciliate *Trichodina baltica* ; the snails are usually 100 % infected in the mantle cavity . Another ciliate found in the mantle cavity is a species of *Scyphidia* . Two other parasitic ciliate species found in this snail are *Protopharynx mazurica* , and *Hypocotylus quatuor* . Predators of *Theodoxus fluviatilis* include the common roach (a freshwater fish) , *Rutilus rutilus* . *Theodoxus fluviatilis* is also the prey of some birds .