

= Triturus =

Triturus is a genus of newts comprising the crested and the marbled newts , which are found from Great Britain through most of continental Europe to westernmost Siberia , Anatolia , and the Caspian Sea region . Their English names refer to their appearance : marbled newts have a green ? black colour pattern , while the males of crested newts , which are dark brown with a yellow or orange underside , develop a conspicuous jagged seam on their back and tail during their breeding phase .

Crested and marbled newts live and breed in vegetation @-@ rich ponds or similar aquatic habitats for two to six months and usually spend the rest of the year in shady , protection @-@ rich land habitats close to their breeding sites . Males court females with a ritualised display , ending in the deposition of a spermatophore that is picked up by the female . After fertilisation , a female lays 200 ? 400 eggs , folding them individually into leaves of water plants . Larvae develop over two to four months before metamorphosing into land @-@ dwelling juveniles .

Historically , most European newts were included in the genus , but taxonomists have split off the alpine newt ( *Ichthyosaura* ) , the small @-@ bodied newts ( *Lissotriton* ) and the banded newts ( *Ommatotriton* ) as separate genera . The closest relatives of Triturus are the European brook newts ( *Calotriton* ) . Two species of marbled newts and seven species of crested newts are accepted , of which the Anatolian crested newt was only described in 2016 . Their ranges are largely contiguous but where they do overlap , hybridisation may take place .

Although not immediately threatened , crested and marbled newts suffer from population declines , caused mainly by habitat loss and fragmentation . Both their aquatic breeding sites and the cover @-@ rich , natural landscapes upon which they depend during their terrestrial phase are affected . All species are legally protected in Europe , and some of their habitats have been designated as special reserves .

= = Taxonomy and systematics = =

The genus name Triturus was introduced in 1815 by the polymath Constantine Samuel Rafinesque , with the northern crested newt ( *Triturus cristatus* ) as type species . That species was originally described as *Triton cristatus* by Josephus Nicolaus Laurenti in 1768 , but Linnaeus had already used the name Triton for a genus of sea snails ten years before , making a new genus name for the newts necessary .

Triturus included most European newt species until the end of the 20th century , but was substantially revised after it was shown to be polyphyletic . Three separate genera now accommodate former members of the genus : the small @-@ bodied newts ( *Lissotriton* ) , the banded newts ( *Ommatotriton* ) , and the alpine newt ( *Ichthyosaura* ) . The monophyly of the genus Triturus in the strict sense is supported by molecular data and synapomorphies such as a genetic defect causing 50 % embryo mortality ( see below , Egg deposition and development ) .

As of 2016 , the genus contains nine accepted species :

Crested newts

Marbled newts

Both the crested and the marbled newts were long considered as single species , *Triturus cristatus* and *T. marmoratus* , respectively . Substantial genetic differences between subspecies were , however , noted and eventually led to their recognition as full species , with the crested newts often collectively referred to as " *T. cristatus* superspecies " . The Balkan and the Anatolian crested newt , the most recent species formally described ( 2013 and 2016 , respectively ) , were only recognised through genetic data ; together with the Southern crested newt , they form a cryptic species complex with no morphological differences known .

= = Description = =

### == Common characteristics ==

*Triturus* is a genus of rather large @-@ bodied newts . They typically have a total length of between 10 and 16 cm ( 3 @.@ 9 and 6 @.@ 3 in ) , with some crested newts of up to 20 cm ( 8 in ) described . Size depends on sex and the environment : females are slightly larger and have a proportionally longer tail than males in most species , and the Italian crested newt seems to be larger in colder parts of its range .

Crested newts are dark brown , with black spots on the sides , and white stippling in some species . Their belly is yellow to orange with black blotches , forming a pattern characteristic for individuals . Females and juveniles of some species have a yellow line running down their back and tail . During breeding phase , crested newts change in appearance , most markedly the males . These develop a skin seam running along their back and tail ; this crest is the namesake feature of the crested newts and can be up to 1 @.@ 5 cm high and very jagged in the northern crested newt . Another feature of males at breeding time is a silvery @-@ white band along the sides of the tail .

Marbled newts owe their name to their green ? black , marbled colour pattern . In females , an orange @-@ red line runs down back and tail . The crest of male marbled newts is smaller and fleshier than that of the crested newts and not indented , but marbled newt males also have a whitish tail band at breeding time .

### == Species identification ==

Apart from the obvious colour differences between crested and marbled newts , species in the genus also have different body forms . They range from stocky with sturdy limbs in the Anatolian , Balkan and the southern crested newt as well as the marbled newts , to very slender with short legs in the Danube crested newt . These types were first noted by herpetologist Willy Wolterstorff , who used the ratio of forelimb length to distance between fore- and hindlimbs to distinguish subspecies of the crested newt ( now full species ) ; this index however sometimes leads to misidentifications . The number of rib @-@ bearing vertebrae in the skeleton was shown to be a better species indicator . It ranges from 12 in the marbled newts to 16 ? 17 in the Danube crested newt and is usually observed through radiography on dead or sedated specimens .

The two marbled newts are readily distinguished by size and colouration . In contrast , separating crested newt species based on appearance is not straightforward , but most can be determined by a combination of body form , coloration , and male crest shape . The Anatolian , Balkan , and southern crested newt however are cryptic , morphologically indistinguishable species . *Triturus* newts occupy distinct geographical regions ( see Distribution ) , but hybrid forms occur at range borders between some species and have intermediate characteristics ( see Hybridisation and introgression ) .

### == Behaviour and ecology ==

Like other newts , *Triturus* species develop in the water as larvae , and return to it each year for breeding . Adults spend one half to three quarters of the year on land , depending on the species , and thus depend on both suitable aquatic breeding sites and terrestrial habitats . After larval development in the first year , juveniles pass another year or two before reaching maturity ; in the north and at higher elevations , this can take longer . The larval and juvenile stages are the riskiest for the newts , while survival is higher in adults . Once the risky stages passed , adult newts usually attain an age of seven to nine years , although individuals of the northern crested newts have reached 17 years in the wild .

### == Aquatic phase ==

The aquatic habitats preferred by the newts are stagnant , mid- to large @-@ sized , unshaded water bodies with abundant underwater vegetation but without fish , which prey on larvae . Typical examples are larger ponds , which need not be of natural origin ; indeed , most ponds inhabited by

the northern crested newt in the UK are human @-@ made . Examples of other suitable secondary habitats are ditches , channels , gravel pit lakes , garden ponds , or ( in the Italian crested newt ) rice paddies . The Danube crested newt is more adapted to flowing water and often breeds in river margins , oxbow lakes or flooded marshland , where it frequently co @-@ occurs with fish . Other newts that can be found in syntopy with *Triturus* species include the smooth , the palmate , the Carpathian , and the alpine newt .

Adult newts begin moving to their breeding sites in spring when temperatures stay above 4 ? 5 ° C ( 39 ? 41 ° F ) . This usually occurs in March for most species , but can be much earlier in the southern parts of the distribution range . Southern marbled newts mainly breed from January to early March and may already enter ponds in autumn . The time adults spend in water differs among species and correlates with body shape : while it is only about three months in the marbled newts , it is six months in the Danube crested newt , whose slender body is best adapted to swimming . *Triturus* newts in their aquatic phase are mostly nocturnal and , compared to the smaller newts of *Lissotriton* and *Ichthyosaura* , usually prefer the deeper parts of a water body , where they hide under vegetation . As with other newts , they occasionally have to move to the surface to breathe air . The aquatic phase serves not only for reproduction , but also offers the animals more abundant prey , and immature crested newts frequently return to the water in spring even if they do not breed .

#### = = = Terrestrial phase = = =

During their terrestrial phase , crested and marbled newts depend on a landscape that offers cover , invertebrate prey and humidity . The precise requirements of most species are still poorly known , as the newts are much more difficult to detect and observe on land . Deciduous woodlands or groves are in general preferred , but conifer woods are also accepted , especially in the far northern and southern ranges . The southern marbled newt is typically found in Mediterranean oak forests . In the absence of forests , other cover @-@ rich habitats , as for example hedgerows , scrub , swampy meadows , or quarries , can be inhabited . Within such habitats , the newts use hiding places such as logs , bark , planks , stone walls , or small mammal burrows ; several individuals may occupy such refuges at the same time . Since the newts in general stay very close to their aquatic breeding sites , the quality of the surrounding terrestrial habitat largely determines whether an otherwise suitable water body will be colonised .

Juveniles often disperse to new breeding sites , while the adults in general move back to the same breeding sites each year . The newts do not migrate very far : they may cover around 100 metres ( 110 yd ) in one night and rarely disperse much farther than one kilometre ( 0 @.@ 62 mi ) . For orientation , the newts likely use a combination of cues including odour and the calls of other amphibians , and orientation by the night sky has been demonstrated in the marbled newt . Activity is highest on wet nights ; the newts usually stay hidden during daytime . There is often an increase in activity in late summer and autumn , when the newts likely move closer to their breeding sites . Over most of their range , they hibernate in winter , using mainly subterranean hiding places , where many individuals will often congregate . In their southern range , they may instead sometimes aestivate during the dry months of summer .

#### = = = Diet and predators = = =

Like other newts , *Triturus* species are carnivorous and feed mainly on invertebrates . During the land phase , prey include earthworms and other annelids , different insects , woodlice , and snails and slugs . During the breeding season , they prey on various aquatic invertebrates , and also tadpoles of other amphibians such as the common frog or common toad , and smaller newts . Larvae , depending on their size , eat small invertebrates and tadpoles , and also smaller larvae of their own species .

The larvae are themselves eaten by various animals such as carnivorous invertebrates and water birds , and are especially vulnerable to predatory fish . Adults generally avoid predators through their

hidden lifestyle but are sometimes eaten by herons and other birds , snakes such as the grass snake , and mammals such as shrews , badgers and hedgehogs . They secrete the poison tetrodotoxin from their skin , albeit much less than for example the North American Pacific newts ( *Taricha* ) . The bright yellow or orange underside of crested newts is a warning coloration which can be presented in case of perceived danger . In such a posture , the newts typically roll up and secrete a milky substance .

= = Reproduction = =

= = = Courtship = = =

A complex courting ritual performed underwater characterises the crested and marbled newts . Males are territorial and use leks , or courtship arenas , small patches of clear ground where they display and attract females . When they encounter other males , they use the same postures as described below for courting to impress their counterpart . Occasionally , they even bite each other ; marbled newts seem more aggressive than crested newts . Males also frequently disturb the courting of other males and try to guide the female away from their rival . Pheromones are used to attract females , and once a male has found one he will pursue her and position himself in front of her . After this first orientation phase , courtship proceeds with display and spermatophore transfer .

Courtship display serves to emphasise the male 's body and crest size and to waft pheromones towards the female . A position characteristic for the large *Triturus* species is the " cat buckle " , where the male 's body is kinked and often rests only on the forelegs ( " hand stand " ) . He will also lean towards the female ( " lean @-@ in " ) , rock his body , and flap his tail towards her , sometimes lashing it violently ( " whiplash " ) . If the female shows interest , the ritual enters the third phase , where the male creeps away from her , his tail quivering . When the female touches his tail with her snout , he deposits a packet of sperm ( a spermatophore ) on the ground . The ritual ends with the male guiding the female over the spermatophore , which she then takes up with her cloaca . In the southern marbled newt , courtship is somewhat different from the larger species in that it does not seem to involve male " cat buckles " and " whiplashes " , but instead slower tail fanning and undulating of the tail tip ( presumably to mimic a prey animal and lure the female ) .

= = = Egg deposition and development = = =

Females usually engage with several males over a breeding season . The eggs are fertilised internally in the oviduct . The female deposits them individually on leaves of aquatic plants , such as water cress or floating sweetgrass , usually close to the surface , and , using her hindlegs , folds the leaf around the eggs as protection from predators and radiation . In the absence of suitable plants , the eggs may also be deposited on leaf litter , stones , or even plastic bags . In the northern crested newt , a female takes around five minutes for the deposition of one egg . Crested newt females usually lay around 200 eggs per season , while the marbled newt ( *T. marmoratus* ) can lay up to 400 . *Triturus* embryos are usually light @-@ coloured , 1 @.@ 8 ? 2 mm in diameter with a 6 mm jelly capsule , which distinguishes them from eggs of other co @-@ existing newt species that are smaller and darker @-@ coloured . A genetic particularity in the genus causes 50 % of the embryos to die : their development is arrested when they do not possess two different variants of chromosome 1 ( i.e. , when they are homozygous for that chromosome ) .

Larvae hatch after two to five weeks , depending largely on temperature . In the first days after hatching , they live on their remaining embryonic yolk supply and are not able to swim , but attach to plants or the egg capsule with two balancers , adhesive organs on their head . After this period , they begin to ingest small invertebrates , and actively forage about ten days after hatching . As in all salamanders and newts , forelimbs ? already present as stumps at hatching ? develop first , followed later by the backlegs . Unlike smaller newts , *Triturus* larvae are mostly nektonic , swimming freely in the water column . Just before the transition to land , the larvae resorb their

external gills ; they can at this stage reach a size of 7 centimetres ( 2 @. @ 8 in ) in the larger species . Metamorphosis takes place two to four months after hatching , but the duration of all stages of larval development varies with temperature . Survival of larvae from hatching to metamorphosis has been estimated at a mean of roughly 4 % for the northern crested newt , which is comparable to other newts . In unfavourable conditions , larvae may delay their development and overwinter in water , although this seems to be less common than in the small @-@ bodied newts . Paedomorphic adults , retaining their gills and staying aquatic , have occasionally been observed in several crested newt species .

#### = = Distribution = =

Crested and marbled newts are found in Eurasia , from Great Britain and the Iberian Peninsula in the west to West Siberia and the southern Caspian Sea region in the east , and reach north to central Fennoscandia . Overall , the species have contiguous , parapatric ranges ; only the northern crested newt and the marbled newt occur sympatrically in western France , and the southern crested newt has a disjunct , allopatric distribution in Crimea , the Caucasus , and south of the Caspian Sea .

The northern crested newt is the most widespread species , while the others are confined to smaller regions , e.g. the southwestern Iberian Peninsula in the southern marbled newt , and the Danube basin and some of its tributaries in the Danube crested newt . The Italian crested newt ( *T. carnifex* ) has been introduced outside its native range in some European countries and the Azores . In the northern Balkans , four species of crested newt occur in close vicinity , and may sometimes even co @-@ exist .

*Triturus* species usually live at low elevation ; the Danube crested newt for example is confined to lowlands up to 300 m ( 980 ft ) above sea level . However , they do occur at higher altitudes towards the south of their range : the Italian crested newt is found up to 1 @, @ 800 m ( 5 @, @ 900 ft ) in the Apennine Mountains , the southern crested newt up to 2 @, @ 000 m ( 6 @, @ 600 ft ) in the southern Caucasus , and the marbled newt up to around 2 @, @ 100 m ( 6 @, @ 900 ft ) in central Spain .

#### = = Evolution = =

Molecular phylogenetic data helped clarify relationships within the genus *Triturus* . A 2011 phylogeny based on complete mitochondrial DNA resolved all divergences with high statistical support . The crested and the marbled newts are sister groups , and within the crested newts , the Balkan ? Asian group with *T. anatolicus* , *T. karelinii* and *T. ivanbureschi* is sister to the remaining species , results consistent with other studies . The mitochondrial analysis also supports the northern ( *T. cristatus* ) and the Danube crested newt ( *T. dobrogicus* ) , as well as the Italian ( *T. carnifex* ) and the Macedonian crested newt ( *T. macedonicus* ) , respectively , as sister species , but analysis of nuclear DNA gave some conflicting results regarding those divergences .

A 24 @-@ million @-@ year @-@ old fossil belonging to *Triturus* , perhaps a marbled newt , shows that the genus already existed at that time and contradicts the earlier estimate of 8 @. @ 3 million years ago ( mya ) for the split between the crested and marbled newts and their sister genus , the European brook newts ( *Calotriton* ) . An age calibration study based on this and other fossils places that divergence much earlier , at around 39 mya in the Eocene , with an uncertainty range of 47 to 34 mya . Based on this estimation , authors have investigated diversification within the genus and related it to paleogeography : The crested and marbled newts split between 30 and 24 mya , and the two species of marbled newts have been separated for 4 @. @ 7 ? 6 @. @ 8 million years .

The crested newts are believed to have originated in the Balkans and radiated in a brief time interval between 11 @. @ 5 and 8 mya : First , the Balkan ? Asian group ( the Anatolian , Balkan and southern crested newt ) branched off from the other crested newts , probably in a vicariance event caused by the separation of the Balkan and Anatolian land masses . The origin of current @-@ day species is not fully understood so far , but one hypothesis suggests that ecological differences ,

notably in the adaptation to an aquatic lifestyle , may have evolved between populations and led to parapatric speciation . Alternatively , the complex geological history of the Balkan peninsula may have further separated populations there , with subsequent allopatric speciation and the spread of species into their current ranges .

#### = = = Glacial refugia and recolonisation = = =

At the onset of the Quaternary glacial cycles , around 2 @. @ 6 mya , the extant *Triturus* species had already emerged . They were thus affected by the cycles of expansion and retreat of cold , inhospitable regions , which shaped their distribution . A study using environmental niche modelling and phylogeography showed that during the Last Glacial Maximum , around 21 @, @ 000 years ago , crested and marbled newts likely survived in warmer refugia mainly in southern Europe . From there , they recolonised the northern parts after glacial retreat . The study also showed that species range boundaries shifted , with some species replacing others during recolonisation , for example the southern marbled newt which expanded northwards and replaced the marbled newt . Today 's most widespread species , the northern crested newt , was likely confined to a small refugial region in the Carpathian Basin during the last glaciation , and from there expanded its range north- , east- and westwards when the climate rewarmmed .

#### = = = Hybridisation and introgression = = =

The northern crested newt and the marbled newt are the only species in the genus with a considerable range overlap ( in western France ) . In that area , they have patchy , mosaic @-@ like distributions and in general prefer different habitats . When they do occur in the same breeding ponds , they can form hybrids , which have intermediate characteristics . Individuals resulting from the cross of a crested newt male with a marbled newt female had mistakenly been described as distinct species *Triton blasii* de l 'Isle 1862 , and the reverse hybrids as *Triton trouessarti* Peracca 1886 . The first type is much rarer due to increased mortality of the larvae and consists only of males , while in the second , males have lower survival rates than females . Overall , viability is reduced in these hybrids and they rarely backcross with their parent species . Hybrids made up 3 ? 7 % of the adult populations in different studies .

Other *Triturus* species only meet at narrow zones on their range borders . Hybridisation does occur in several of these contact zones , as shown by genetic data and intermediate forms , but is rare , supporting overall reproductive isolation . Backcrossing and introgression do however occur as shown by mitochondrial DNA analysis . In a case study in the Netherlands , genes of the introduced Italian crested newt were found to introgress into the gene pool of the native northern crested newt . The two marbled newt species can be found in proximity in a narrow area in central Portugal and Spain , but they usually breed in separate ponds , and individuals in that area could be clearly identified as one of the two species . Nevertheless , there is introgression , occurring in both directions at some parts of the contact zone , and only in the direction of the southern marbled newt where that species had historically replaced the marbled newt ( see also above , Glacial refugia and recolonisation ) .

#### = = Threats and conservation = =

Most of the crested and marbled newts are listed as species of " least concern " by the International Union for the Conservation of Nature , but population declines have been registered in all assessed species . The Danube crested newt and the southern marbled newt are considered " near threatened " because populations have declined significantly . Populations have been affected more heavily in some countries and species are listed in some national red lists . The Anatolian , Balkan and the Macedonian crested newt , recognised only recently , have not yet been evaluated separately for conservation status .

## === Reasons for decline ===

The major threat for crested and marbled newts is habitat loss . This concerns especially breeding sites , which are lost through the upscaling and intensification of agriculture , drainage , urban sprawl , and artificial flooding regimes ( affecting in particular the Danube crested newt ) . Especially in the southern ranges , exploitation of groundwater and decreasing spring rain , possibly caused by global warming , threaten breeding ponds . Aquatic habitats are also degraded through pollution with agricultural pesticides and fertiliser . Introduction of crayfish and predatory fish threatens larval development ; the Chinese sleeper has been a major concern in Eastern Europe . Exotic plants can also degrade habitats : the swamp stonecrop replaces natural vegetation and overshadows waterbodies in the United Kingdom , and its hard leaves are unsuitable for egg @-@ laying to crested newts .

Land habitats , equally important for newt populations , are lost through the replacement of natural forests by plantations or clear @-@ cutting ( especially in the northern range ) , and the conversion of structure @-@ rich landscapes into uniform farmland . Their limited dispersal makes the newts especially vulnerable to fragmentation , i.e. the loss of connections for exchange between suitable habitats . High concentrations of road salt have been found to be lethal to crested newts .

Other threats include illegal collection for pet trade , which concerns mainly the southern crested newt , and the northern crested newt in its eastern range . The possibility of hybridisation , especially in the crested newts , means that native species can be genetically polluted through the introduction of close species , as it is the case with the Italian crested newt introduced in the range of the northern crested newt . Warmer and wetter winters due to global warming may increase newt mortality by disturbing their hibernation and forcing them to expend more energy . Finally , the genus is potentially susceptible to the highly pathogenic fungus *Batrachochytrium salamandrivorans* , introduced to Europe from Asia .

## === Conservation measures ===

The crested newts are listed in Berne Convention Appendix II as " strictly protected " , and the marbled newts in Appendix III as " protected " . They are also included in Annex II ( species requiring designation of special areas of conservation ; crested newts ) and IV ( species in need of strict protection ; all species ) of the EU habitats and species directive . As required by these frameworks , their capture , disturbance , killing or trade , as well as the destruction of their habitats , are prohibited in most European countries . The EU habitats directive is also the basis for the Natura 2000 protected areas , several of which have been designated for the crested newts .

Habitat protection and management is seen as the most important element for the conservation of *Triturus* newts . This includes preservation of natural water bodies , reduction of fertiliser and pesticide use , control or eradication of introduced predatory fish , and the connection of habitats through sufficiently wide corridors of uncultivated land . A network of aquatic habitats in proximity is important to sustain populations , and the creation of new breeding ponds is in general very effective as they are rapidly colonised when other habitats are nearby . In some cases , entire populations have been moved when threatened by development projects , but such translocations need to be carefully planned to be successful . Strict protection of the northern crested newt in the United Kingdom has created conflicts with local development projects ; at the same time , the charismatic crested newts are seen as flagship species , whose conservation also benefits a range of other amphibians .