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## Systematics and distribution of the mountain salamanders of the genus *Paradactylodon* Risch, 1984 (Caudata: Hynobiidae)

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### Abstract

The mountain salamanders of the genus *Paradactylodon* Risch, 1984, from the family Hynobiidae, with three known species, are distributed in Iran and Afghanistan. This study addresses the challenges of classification and habitat status of these mountain salamanders based on previous research as well as our own studies. Based on morphological characteristics, the salamanders living in the mountainous regions of the Middle East (Iran and Afghanistan) have been placed in the genus *Paradactylodon*. The genus consists of three species: *Paradactylodon mustersi* (distributed in northern Afghanistan), *P. persicus* and *P. gorganensis* (distributed in northern Iran). The Hyrcanian forests represent a unique Tertiary relict ecosystem covering the northern slopes of the Alborz and Talesh (Iran, Azerbaijan), a unique biodiversity hotspot with many cryptic species that have not been fully studied yet. Since the 1970s, two species of tailed amphibians belonging to the family Hynobiidae, *Batrachuperus* (later: *Paradactylodon*), *Paradactylodon persicus* from northern and northwestern Iran and *P. gorganensis* from northeastern Iran have been documented. The Iranian stream salamander *P. persicus* was first reported from the Talesh Mountains, and the Gorganian cave salamander *P. gorganensis* was later described from the eastern Alborz Mountains. There are two distinct Iranian species of *Paradactylodon* based on morphological characteristics. Given the conservation values and the numerous threats faced by these endemic species, this taxon is listed on the IUCN Red List due to its sensitivity to habitat loss, drought, and deforestation. *Paradactylodon persicus* is listed as NT, whereas *P. gorganensis* is classified as CR.

**Keywords:** Persian salamander, *Paradactylodon persicus*, *P. gorganensis*, Systematics, Distribution, Habitat, Iran.

### Introduction

The habitat of all tailed amphibians in Iran is in mountainous areas or the edge of the Alborz and Zagros forests (Mahdipour & Rastegar-Pouyani, 2020). In the past two decades, amphibian populations have declined. There are two possible reasons for the decline of amphibians: first, destructive human activities, including the introduction of alien species, overexploitation of habitats, land use change, and increased use of pesticides and other toxic chemicals, and the second, global climate change (increased ultraviolet radiation exposure and global warming) as well as infectious diseases (Karamiani, 2021). The total number of amphibian species described by zoologists to date (Dec 2, 2025) is about 8973 species, of which: frogs or tailless amphibians (Salientia, Anura), about 7915 species; salamanders or tailed amphibians (Caudata, Urodela), about 828 species; and caecilians or limbless amphibians (Caecilians, Apoda),

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about 230 species (Amphibiaweb, 2025). According to Vitt and Caldwell (2014), the family Hynobiidae Cope, 1859 includes two subfamilies: Onychodactylinae and Hynobiinae (only this subfamily is distributed in Iran). The family Hynobiidae encompasses nine genera and 98 species (Amphibiaweb.org): *Batrachuperus* Boulenger, 1878 (Seven species), *Hynobius* (65 species), *Liua* (two species), *Onychodactylus* (12 species), *Pachyhynobius* (one species), *Paradactylodon* (two species), *Pseudohynobius* (six species), *Ranodon* (one species) and *Salamandrella* (two species); which are distributed in Asia, from the Ural Mountains range in Russia to Japan, mainly above latitude of 40 degrees north; growth and development in all species is indirect and with a free-living larval stage; One of the stream salamanders of the family Hynobiidae found in western Eurasia is *Paradactylodon* (Zhao & Hu, 1984), which was first reported from the mountains of western China (Dunn, 1923). Initially, this genus was considered as *Batrachuperus* Boulenger (1878), then, based on Risch (1984), it was placed in a separate genus, *Paradactylodon*, based on morphological features. But the morphological features were not convincing enough for such a decision, and therefore *Paradactylodon* was Synonymized with *Batrachuperus* by Reilly (1987). Over the past decade, genetic studies have shown that the genus *Batrachuperus* is polyphyletic (Zhang et al., 2006; Peng et al., 2010). The morphology of *Batrachuperus* salamanders (Fei et al., 1983; Zhao et al., 1988) has led to the use of DNA sequences to delimit species boundaries; Fu et al. (2001) divided *Batrachuperus* into two distinct geographical groups: (a) the eastern (Chinese) group, which specifically includes *Batrachuperus* and consists of six species; and (b) the western (Middle Eastern) group, which includes two or three species assigned to *Paradactylodon* (Fu & Zeng, 2008). Dubois and Raffaelli (2012) rejected the name *Paradactylodon* and replaced it by *Iranodon*. However, the amphibian website (Amphibiaweb.org) still uses the name *Paradactylodon* (AmphibiaWeb.org). The genus *Batrachuperus* is distributed in the western mountains of China, and along the eastern edge of the Tibetan Plateau, while the distribution of the genera *Liua* and *Pseudohynobius* is more to the east and in mountainous areas separated from the Tibetan Plateau; and the maximum altitude for mountain hynobiids is 2500 m; only the genus *Batrachuperus* can live above this altitude; Accordingly, it is assumed that *Batrachuperus* separated from other mountain hynobiids to the east, because the eastern edge of the Tibetan Plateau, after the first uplift (40 million years ago), reached about 2500 m; This inference is consistent with recent geological evidence that the Tibetan Plateau has been at an elevation of 4,000 m for at least the past 35 million years (Rowley & Currie, 2006). The *Batrachuperus* Boulenger (1878) genus is of Tibetan origin, as these salamanders are found only on the eastern edge of the Tibetan Plateau (Harrison et al., 1992; Copeland et al., 1995) and, on a time scale, the diversification of *Batrachuperus* occurred between 15 and 25 million years ago, indicating that the speciation occurred at the same time as orogeny in Tibet. This result is consistent with the geological hypothesis that rapid uplift of the Tibetan Plateau occurred 20 million years ago (Harrison et al., 1992; Copeland et al., 1995). Among the *Batrachuperus* species, the only species distributed in the Ailao-Red region (separating southern China from Indochina) in China and able to live at altitudes up to 4000 m is *B. yenyuanensis*, whose divergence time from other *Batrachuperus* species is estimated to be 24 million years ago (Tapponnier et al., 1990). The genus *Paradactylodon* is distributed in the mountainous regions of the Middle East. It consists of three species: *P. mustersi* (in Afghanistan), the *P. persicus* species, and *P. gorganensis* (in Iran); *P. persicus* was reported from the Talesh Mountains, and then *P. gorganensis* was described from Shirabad Cave, Golestan Province. These two Iranian species of *Paradactylodon* are distinct based on morphological features (Ahmadzadeh et al., 2020), but the phylogenetic relationship between the two species, investigated using two mitochondrial DNA markers, 16S and COI indicates that the hynobiid salamanders of the Talesh Mountains and Shirabad Cave, which constitute the morphological species *P. gorganensis*, are placed within *P. persicus* (Ahmadzadeh et al., 2020). Overall, both the analysis of species distribution models and the results of molecular analyses indicate that the Iranian populations of *Paradactylodon* were affected by the Quaternary glaciation. According to haplotype networks, haplotype diversity was higher in the western part of the species' range, and given the low genetic distance among all samples, it has been proposed that *Paradactylodon gorganensis* is synonymous with *Paradactylodon persicus* (Ahmadzadeh et al., 2020). Stöck et al. (2019) confirmed the existence of a *Paradactylodon persicus* from the northwest and a *Paradactylodon gorganensis* from the northeast (which should however be a subspecies of *Paradactylodon persicus*) from the Hyrcanian forests, which is in contradiction with the findings of Ahmadzadeh et al. (2020). Although the taxonomic decision of Ahmadzadeh et al. (2020) has shown that they are likely to be a single species, further studies based on the integration of mitochondrial and nuclear genes across the entire distribution area are needed. Thus, to further protect the endangered populations of *P. persicus* (sensu lato), the nomenclature of this genus has been debated for years. The *Paradactylodon* salamanders can be considered as bioindicators for "intact and healthy" riverine ecosystems of the Hyrcanian forests; However, in some cases, *P. persicus* may even survive for decades after factors such as: the animal's sensitivity to environmental changes, drought, deforestation and human habitat destruction that destroy native vegetation for a long time (Ahmadzadeh & Kami, 2009). Therefore, humans bear a great responsibility for the conservation and persistence of this species in their ecosystems and environment, for a long and continuous period, as well as the unique biodiversity of its habitats (Akhani et al., 2010). Due to its conservation values and the numerous threats faced by this endemic species, it is categorized on the IUCN Red List (Ahmadzadeh et al., 2020). *Paradactylodon persicus* is in the NT (Near Threatened) status and *P. gorganensis* is in the CR (Critically Endangered) status (Yousefi SiahKalroodi et al., 2013). This study reviews the morphological, anatomical, and molecular data of *P. persicus* and *P. gorganensis* in Ardabil, Gilan, and Golestan provinces (Iran) and *P. mustersi* in the Paghman Mountains near Kabul (Afghanistan).

#### Systematic account:

##### *Paradactylodon* Risch, 1984

##### Diagnostic characters:

The species of the genus *Paradactylodon* Risch, 1984 have a large, broad head that gradually tapers toward the neck and has palatal blade-like teeth arranged in two arcuate rows; these short teeth do not extend forward of the nostrils and are barely distinguishable from each other in the middle. The fore and hind limbs have four clawless digits. They have a broad tail that is compressed laterally and have a dorsal crest in the upper part that extends along the entire length of the tail. This apparent structure of the tail helps the animal in swimming. It has smooth skin with numerous pores that play a role in the animal's skin respiration. The dorsal area is dark



or light brown and sometimes yellowish, but the color of the lower body and sides is lighter and often pinkish or yellow. Also, irregular light yellowish, pinkish or orange lines or spots are seen in most specimens. This coloring is uniform throughout the body. They have black, large and prominent eyes. The body length from the tip of the snout to the end of the tail reaches a maximum of 200 mm in adult specimens, in which the tail length is longer than the length of the head and body. The total body length in some specimens reaches 22.6 cm (Ahmadzadeh & Kami, 2009). The tail length in some specimens is as long as the head and body combined, the body background color in living specimens is yellowish gray or deep purple with a metallic sheen with faint yellow spots, the vertebral lines in the dorsal region are clearly defined. In part of the body and in the tail region, it has blackish brown spots and the body color in the abdominal region is somewhat lighter and clearer. In young specimens, the skin is completely smooth. In larger specimens, the skin of the body is rougher and has fewer yellow spots in comparison with younger specimens. The lips lack a labial margin and often have a groove behind the eye area and on the posterior margin of the eye. The throat groove is well developed. The tail length in adult specimens is smaller than the total length of the head and body, or in some specimens, larger. They have four fingers on the forelimbs and four fingers on the hindlimbs, all of which are pale, thick, and circular, have approximately 13 to 14 lateral grooves, and the cloacal slit is longitudinally located (Yousefi Siahkalroodi et al., 2013).

### Species account

#### Afghan mountain salamander, *Paradactylodon mustersi* (Smith 1940)

The species *Paradactylodon mustersi* was described by Smith in 1940 from the Paghman Mountains near Kabul, Afghanistan. The total body length is 119–215 mm and there are 14 costal grooves extending towards the tail. The snout is broadly rounded and the limbs are well developed. The tail is slightly shorter than the body and the body color is dark olive-brown to yellowish-olive (Figure 1) and is vaguely speckled with small pigment spots (Reilly, 1983). This species is considered to be endangered by the IUCN and is also listed as the most evolutionary distinct and globally threatened species. One of the locations and habitats where this species is distributed in Afghanistan is the Paghman region of Kabul province, in mountainous and highland areas at an altitude of about 2600 m above sea level and in a stream approximately 4.5 km long (Figure 2, A & B). Knowledge remains very limited about the distribution, morphology, ecology and current threats of this (enigmatic) amphibian. The distribution of this species (*P. mustersi*) in Afghanistan is shown in (Figure 3) in red and numbers 1 to 4, and the distribution of Iranian salamander in Iran is shown in green and numbers 5 to 8 (Ayobi et al., 2022).



Figure 1. *Paradactylodon mustersi* (Ayobi et al., 2022)



Figure 2. Habitat of *Paradactylodon mustersi*; A, B. Paghman area, Kabul Province (Ayobi et al., 2022)



**Figure 3.** Distribution map of *Paradactylodon* species: Distribution location of *Paradactylodon mustersi* in Afghanistan: 1. Paghman area, Kabul Province; 2. Raku', border of Wardak and Kabul provinces; 3. offsprings of Paghman stream, Parwan Province; 4. Sanglakh, Wardak Province; and distribution location of *Paradactylodon persicus* in Iran: 5. Guilan province 6. Ardabil province 7. Mazandaran province 8. Golestan province.

**Iranian Stream Salamander, *Paradactylodon persicus* (Eiselt & Steiner, 1970)**

This species inhabits cold streams and small pools among dense Hyrcanian forests. The maximum water temperature in the streams is 13-15°C and these salamanders live at an altitude of 800 to 1200 m (Figure 4, A & B).



**Figure 4.** A, B; Habitat of *Paradactylodon persicus* (Gilvan, Khalkhal, Ardabil Province) (Photo: Ghsemi Kassari)

The distribution area is in the Talesh and Alborz Mountains regions in the provinces of Guilan, Mazandaran, Ardabil and Golestan. This species lives exceptionally in humid areas (Figure 5), which represents a rare and endangered fauna of Iran (Ahmadzadeh & Kami, 2009; Yousefi SiahKalroodi et al., 2013).



**Figure 5.** *Paradactylodon persicus* (Gilvan, Khalkhal, Ardabil Province) (Photo: Ghsemi Kassari)

The known locations for the distribution of *P. persicus* are one in the village of Vissar in southeast Chalus in Mazandaran Province and the other in the village of Deilmedeh in southeast Khalkhal on the Khalkhal-Asalem road in Ardabil Province. Information on the taxonomy, biology, and ecology of *P. persicus* is limited to a few articles (Baloutch & Kami, 1995; Kami & Vakilpour, 1996; Kami, 1999; Stöck, 1999) and even less information is available on the current status of the habitats of these two locations (Kami, 2004; Ebrahimi et al., 2004). Ebrahimi et al. (2004) believed that *P. persicus* probably mates in spring and lays its eggs, which are in two jelly cylinders, in the water, while studies on *P. gorganensis* showed (Figure 6) that in September, the gonads were active and spermatozoa were seen in them, while in tissue sections prepared from the testes in May, June and July, no sperm was seen and only the lobules were filled with spermatogonia (Rezapour et al., 2009). This species is classified as Near Threatened (NT) in the IUCN Red List (IUCN 2007) and is a protected and protected species under national laws (Ahmadzadeh & Kami, 2009).



**Figure 6.** *Paradactylodon gorganensis*. Eggs embedded in two jelly masses (Ebrahimi et al., 2004)

**Gorgan's cave salamander, *Paradactylodon gorganensis* (Clergue-Gazeau & Thorn, 1979)**

The second nominal taxon, *Batrachuperus gorganensis* (Clergue-Gazeau & Thorn, 1979), was described from a single adult male type discovered in a cave at the eastern edge of the Hyrcanian corridor (Clergue-Gazeau & Farcy, 1978). Stöck (1999) compared themorphological characteristics of topotype specimens (specimens collected from the type locality) of larval and immature *P. persicus* and *P. gorganensis* and concluded that the separation of *P. gorganensis* as a subspecies of *P. persicus* is logical; but as a species, further investigation is required, as *P. persicus* and *P. gorganensis* are morphologically different. Although Kami (2004) accepted this view,

Ebrahimi et al. (2004) and Frost (2011) considered *P. gorganensis* as a distinct species. Stöck et al. (2019) examined the genetic structure of *P. persicus* and *P. gorganensis* and proposed them as a single species. The Gorgan cave salamander (*P. gorganensis*) has a two-stage life cycle. The aquatic larvae of these salamanders develop into adults during metamorphosis. The larvae have external gills, pairs of gill slits, and a fin-like tail, which are lost during metamorphosis, and their larval stage lasts 2-3 years (Figure 7). During the mating phase, the female produces a pair of gelatinous sacs, each containing 35-70 eggs, which the male encloses and fertilizes externally. There is no obvious difference between male and female specimens in terms of morphology. Adult specimens are found inside the cave and larvae are found in the streams surrounding the cave. Histological studies on *P. gorganensis* have shown that the gonads are active in September, sperm clusters are seen in them, and the reproductive season is September (Rezapour et al., 2009).



**Figure 7.** Adult specimen of *Paradactylodon gorganensis* (Shirabad Cave, Golestan Province) (Photo: Ghsemi Kassari).

This amphibian has a small territory and a specific habitat that only includes a cave, and currently the population is very small and any minor changes in the habitat, hunting or neglectation in its conservation will lead to the complete extinction of this species (Figure 8, A & B). According to national laws, the Gorgani cave salamander is a protected cave species (Yousefi SiahKalroodi et al., 2013).



**Figure 8.** A, B; Habitat of *Paradactylodongorganensis* (Shirabad Cave, Gorgan, Golestan Province) (Photo: Ghsemi Kassari).

#### Key to the identification of species of the genus *Paradactylodon* in Iran

- A. Body with irregular yellow spots; tail as long as head and body, sometimes larger and rarely smaller..... *Paradactylodon persicus*  
 B. Body without yellow spots, tail longer than head and body.....*Paradactylodon gorganensis*

## Discussion

The genus *Paradactylodon* is distributed in the mountainous regions of the Middle East and consists of three species: *Paradactylodon mustersi* (in Afghanistan), *Paradactylodon persicus*, and *Paradactylodon gorganensis* (in Iran) (Zivari & Kami, 2017). The distinction of the two Iranian salamander species (*Paradactylodon*) is based on morphological features, but there is some debate about their taxonomic status. Analysis of species distribution models (SDM) and molecular analyses indicate that the Iranian populations of *Paradactylodon* indicates higher haplotype diversity in the western part of the species' range. Given the low genetic distance between the two species, it has been suggested that *P. gorganensis* synonymous with *P. persicus* (Ahmadzadeh et al., 2020). Further, Stöck et al. (2019) examined the genetic structure of the western (*P. persicus*) and eastern (*P. gorganensis*) taxa and proposed them as a single species. Molecular data and morphological studies have not been conducted across the Hyrcanian Corridor, therefore, there is insufficient evidence to confirm or reject the accepted taxonomic status of *P. gorganensis*. The results of the studies and investigation of the phylogenetic relationships between Iranian specimens of *Paradactylodon persicus* and their potential distribution range showed that *P. persicus* is in fact a single species and forms a main clade with some regional subclades based on COI and concatenated gene trees. The mtDNA markers showed a small genetic distance between the two species (about 2% for COI and less than 0.6% for 16S) (Ahmadzadeh et al., 2020). Findings from SDM analysis provided evidence that climatic fluctuations during the Pleistocene caused a significant reduction in the range of suitable habitat for *P. persicus* and forced the species to move to lower elevations, so that *P. persicus* was previously thought to have two distinct species: *P. persicus*, which is distributed in the northwest, and *P. gorganensis*, which is distributed in the northeast of Iran (Schmidtler & Schmidtler, 1971; Ebrahimi et al., 2004; Frost, 2011). Stöck (1999) believed that these two species are distinct only at the subspecies level and not at the species level. Furthermore, using molecular tools, based on only three specimens of *P. persicus* from the eastern, central and western Alborz and using the complete mtDNA genome, only minor genetic differences (about 2%) were observed among these specimens. They also examined more specimens (18 specimens) with the Cyt b gene and showed that the two species *P. persicus* and *P. gorganensis* are closely related to each other with some intraspecific variation. According to the results of Stöck et al. (2019), it is concluded that *P. persicus* and *P. gorganensis* are not separate species; Therefore, it is suggested that the nomenclature of *P. persicus* be considered with priority over *P. gorganensis*, but its validity requires further research using other genes. According to studies, the *Ranadon-Paradactylodon* species diverged about 35 million years ago and the *Paradactylodon* species about 22.7 million years ago, and the diversification of *P. persicus* (Iranian species) occurred earlier than *Paradactylodon mustersi* (Afghan species). The diversification of lineages in the Iranian clade occurred in the late Pliocene (2.87 million years ago) (Ahmadzadeh et al., 2020). According to Ahmadzadeh and Kami (2009) the Hynobiid salamander populations are exposed to many environmental threats such as: land use change, habitat loss, severe drought, and deforestation. In order to genetically investigate two different phenotypes of the Gorgani cave salamander, after sampling two different phenotypes and based on molecular studies and DNA extraction from 10 salamanders, the mitochondrial (D-loop gene) was used. After amplifying the 504 base pair locus by PCR, all samples were sequenced. The results of this study indicated that all the sequencing patterns of the D-loop region between the two phenotypes studied were similar to each other. Due to the lack of different patterns, it can be concluded that the locus under study in the two phenotypes of the species under study has a haplotype, and the appearance of the matter indicates that there is no difference in the mentioned populations and the genetic similarity of the two mentioned phenotypes to each other (Yousefi Siahkalroodi et al., 2015). Of the two Hynobiid salamander species found in Iran, *Paradactylodon persicus* (Iranian stream salamander) is considered a Near Threatened (NT) species and is distributed in certain locations of the Hyrcanian forests in four northern provinces of Iran, and *Paradactylodon gorganensis* (Gorganian cave salamander) is restricted to Shirabad Cave and its surrounding streams 60 km east of Gorgan, east of the Alborz mountain range in Golestan province, and is listed as a Critically Endangered (CR) species on the IUCN Red List. Hynobiids found in Iran are stream salamanders and usually live in mountain streams with cold water and fast currents. According to studies conducted by Ebrahimi et al. (2004), *Paradactylodon persicus* are not active during the day and are often found under rocks in the water during daylight hours and may be active only at night, while *Paradactylodon gorganensis* is active at all times of the year in Shirabad Cave. So far, no researchers have been able to determine the exact reproductive time of these two species (Rezapour et al., 2009).

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