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# A third European species of grayling (*Actinopterygii*, *Salmonidae*), endemic to the Loire River basin (France), *Thymallus ligericus* n. sp.

by

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**Abstract.** – Loire grayling was already known to belong to a distinct lineage, compared to other European population, according to molecular data (enzymatic polymorphism, mtDNA sequencing and microsatellites). In this paper, we consider this lineage as a new species, *Thymallus ligericus* n. sp., which is endemic to the Loire drainage (France). Compared with the other species, *T. ligericus* n. sp. is characterized by a more elongated body, the presence of a pointed snout and a strait or convex snout profile, a more inferior mouth with a transversal aperture and a fleshier upper lip, usually more than 50 to several hundreds black dots on the flanks, a shorter head (20.0-23.7% SL), smaller occipital and orbital depths of the head (54.8-71.7% HL and 43.5-53.4% HL, respectively) and a shorter horizontal eye diameter (22.6-26.3% HL).

**Résumé.** – Description d'une nouvelle espèce d'ombre.

L'ombre d'Auvergne est déjà connu pour appartenir à une lignée évolutive distincte par rapport aux autres populations d'ombre d'Europe d'après les données moléculaires (polymorphisme enzymatique, données mitochondriales et microsatellites). Dans cette étude, nous considérons cette lignée comme une nouvelle espèce, *Thymallus ligericus* n. sp., qui est endémique au bassin de la Loire (France). Cette espèce est caractérisée par un corps plus allongé, la présence d'un museau pointu lui conférant un profil droit ou convexe, une bouche plus infère avec une ouverture transverse et une lèvre supérieure plus charnue, généralement plus de 50 à plusieurs centaines de points noirs sur les flancs, une tête plus courte (20,0-23,7% SL), une hauteur occipitale et orbitale de la tête plus faible (respectivement 54,8-71,7% HL et 43,5-53,4 %HL) et un diamètre horizontal de l'œil plus petit (22,6-26,3% HL).

The grayling subfamily Thymallinae includes a single genus *Thymallus*. It extends across most of the boreal region, north of latitude 40°, from the east of Western Europe to North America, and includes up to 18 species (Dyldin *et al.*, 2017; Fricke *et al.*, 2019). Graylings in Europe have long been assigned to a single species, *Thymallus thymallus* (Linnaeus, 1758), until Bianco (2014) rehabilitated the historical *Thymallus aeliani* Valenciennes, 1848 as a species for grayling inhabiting the northern Adriatic basin, namely in the Po, Adige and Soca river drainages of Northern Italy and Slovenia (Susnik *et al.*, 2004; Meraner and Gandolfi, 2012; Meraner *et al.*, 2014). Persat *et al.* (1978) discussed the unusual distribution pattern of grayling in France (see also Persat and Keith, 2011). While many other native fish species or genera in France are present across the Rhine, Rhône, Seine

and Loire catchments, grayling was the only one originally absent in the Seine catchment despite the presence of suitable habitats, as proven by successful introductions in the last decades (Persat, 2011). As for its native occurrence in the Loire catchment, it is documented as early as the 16<sup>th</sup> century (Belon, 1555). Later on, Persat (1982) pointed out that the Loire grayling shows a rather peculiar colour pattern. At the population scale, Loire grayling have a much higher number of black dots on the sides than its neighbouring populations in the Rhône catchment. Additional investigations highlighted a few meristic differences, such as the number of scales on the lateral line, which tended to be slightly higher for the Loire graylings compared to those from the Rhône basin (Persat, 1996).

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The first genetic analyses on the enzymatic polymorphism on the Loire grayling also pointed out its specificity, possessing a private allele Ck-1\*87 at the *Creatine Kinase locus 1* compared to Rhine, Danube and Finnish populations (e.g. Persat, 1988; Soewardi, 1988; Bouvet *et al.*, 1990). Further investigations with the mitochondrial control region marker (CR) highlighted that Loire populations have a mean sequence divergence > 2% comparing to other European populations (Weiss *et al.*, 2002; Persat *et al.*, 2016), and microsatellites data confirmed independently that all native populations of the Loire drainage belong to a distinct evolutionary lineage (Persat *et al.*, 2016).

Pigmentation patterns and molecular data both support the distinctness of the Loire grayling, and led us to consider this population as a separate new species that we describe here: *Thymallus ligericus* n. sp.

## MATERIAL AND METHODS

Abbreviation used: Agence Française pour la Biodiversité (AFB), Associations Agréées de Pêche et de Protection des Milieux Aquatiques, France (AAPPMA); British Museum of Natural History, London, England (BMNH); Centre National pour la Recherche Scientifique (CNRS); Conseil Supérieur de la Pêche (CSP); Fédération Départementale des Associations Agréées de Pêche et de Protection des Milieux Aquatiques, France (FDAAPPMA); Head length (HL); Muséum national d'Histoire naturelle, Paris, France (MNHN), Office National de l'Eau et des Milieux Aquatiques, France (ONEMA); Standard length (SL); Claude Bernard Lyon 1 University Zoological Collections, Villeurbanne, France (UCBLZ); Zoologische Staatssammlung München, Germany (ZSM).

Samples were collected by electric fishing or angling between 2014 and 2018 with the collaboration of the ONEMA DR6, the FDAAPPMA 15, 42, 43, 63 and 87, and local AAPPMA. Most of the voucher specimens were euthanised by anaesthetic overdose. A few additional voucher specimens were obtained from incidental mortalities stemming from local electric fishing surveys.

Counts and measurements were taken by default from the left side according to Surre *et al.* (1986). We only added some measurements to better describe the head shape (Fig. 1): the mandible width, the chin length (from the branchiostegal membrane junction to the extremity of the mandible) and the ventral snout length (from the same point to the extremity of the snout). Measurements were taken using a digital calliper. All measurements were made point to point, never by projection. The syntype specimen of *Salmo thymallus* Linnaeus, 1758, BMNH 1853.11.12.159, which is a dry skin, was not used for comparison because its poor condition alters its head shape. All dorsal and anal-fin rays were

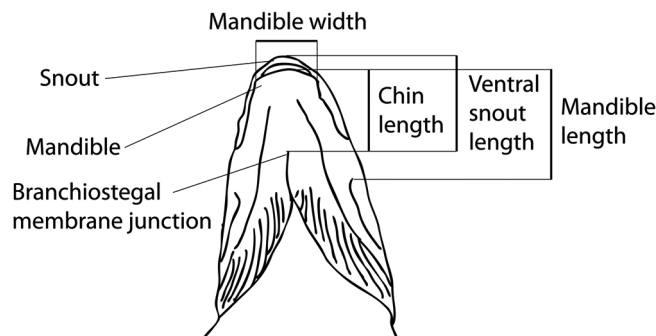


Figure 1. – The three supplementary measurements made on the ventral side of the head, in addition to those of Surre *et al.* (1986): the mandible width, the chin length (from the basibranchial junction to the extremity of the mandible) and the ventral snout length (from the same point to the extremity of the snout).

counted. Sex determination was done according to the size of the last two rays of the dorsal fin (Persat, 1977) and the aspect of the urogenital papilla. Black dots on the flanks on both sides of the lateral line were counted according to Persat (1982), both on the collection specimens and on live specimens caught in the field. During official investigations on local fish communities, black dots were also counted on live specimens before they were released back in the stream, giving us additional data.

In total, 30 morphometric parameters were measured, 7 meristic parameters were counted, and body pigmentation was observed.

### *Thymallus ligericus* n. sp. (Figs 2-6)

#### Material examined

*Holotype*. – MNHN 2018-0722, 337 mm SL ♂, France: Loire drainage, Cantal Dept., Alagnon River at La Chapelle d'Alagnon: 45°6' 21"N-2°53'48"E, 9 Sep. 2016, Persat and FDAAPPMA15 coll.

*Paratypes*. – MNHN 2018-0723, 327 mm SL ♀, collected together with the holotype; MNHN 2018-0724, 252 mm SL ♀, France: Loire drainage, Haute-Vienne Dept., Combade River at Masléon: 45°46' 1"N-1°33'16"E, 28 May 2015, Persat and FDAAPPMA87 coll.; MNHN 2018-0725, 252 mm SL ♀, Combade River at Masléon, same date, location, and collectors; MNHN 2018-0726, 290 mm SL ♀, Loire Dept., Lignon River at Boën-sur-Lignon: 45°45'6"N-3°59'33"E, 29 May 2015, Persat, Juglaret and Buttazzoni coll.; MNHN 2018-0727, 278 mm SL ♀, Loire Dept., Lignon River at Boën-sur-Lignon: same date, location, and collectors; MNHN 2018-0728, 300 mm SL ♂, Puy-de-Dôme Dept., Dore River at Vertolaye: 48°38'11"N-3°42'23"E, 29 May 2015, Persat, Juglaret and Buttazzoni coll.; MNHN 2019-0266, 284 mm SL ♂, Puy-de-

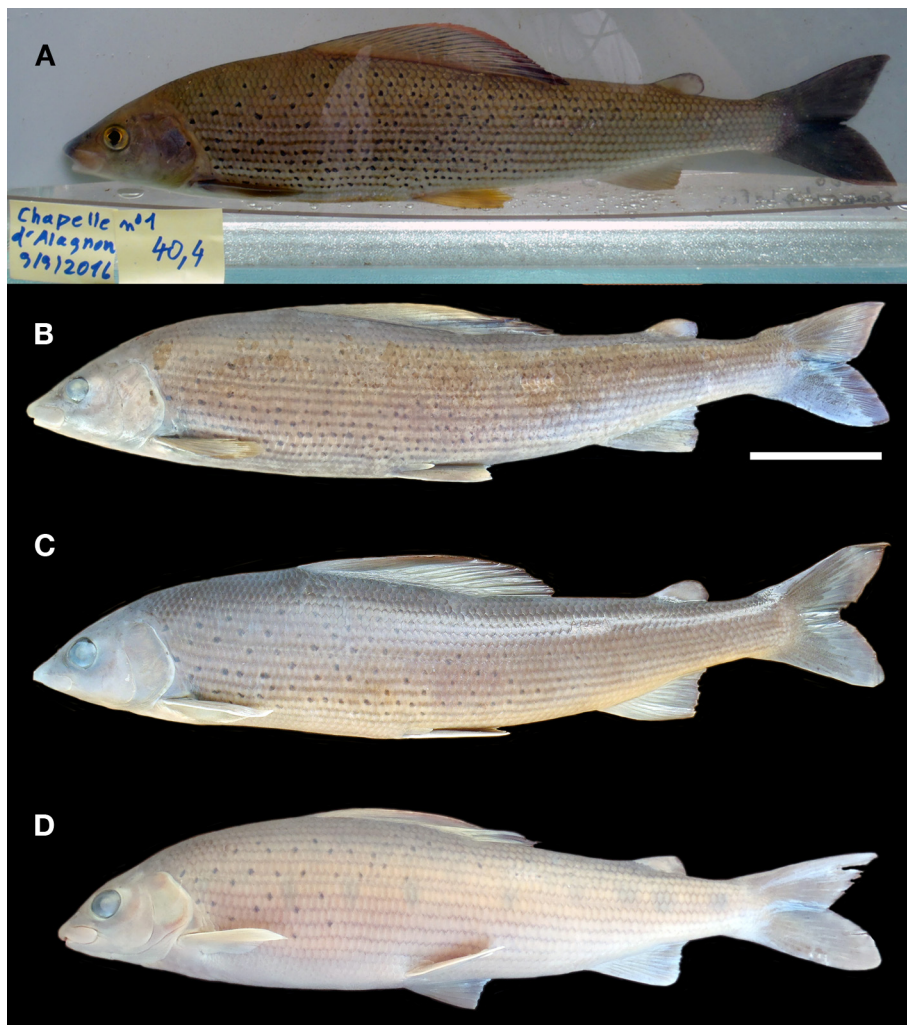


Figure 2. – Specimens of *Thymallus* spp. in lateral view. Holotype of *Thymallus ligericus* n. sp. MNHN 2018-0722, 337 mm SL ♂, Alagnon River at La Chapelle d'Alagnon, 9 Sep. 2016, Persat and FDAAPPMA15 coll., in live (A) and after preservation (B); Paratype of *Thymallus ligericus* n. sp. MNHN 2019-0267 (C), 269 mm SL ♀, Loire River at Chadron, 22 Sep. 2016, Persat and ONEMA43 coll.; UCBLZ – 2012.9.1011 (D), 292 mm TL, Rhône drainage, Ain River at Crotenay, 10 Jun. 2014, Persat and FDAAPPMA39 coll.

Dôme Dept., Dore River at Vertolaye: same date, location, and collectors; MNHN 2019-0267, 269 mm SL ♀, Haute-Loire Dept., Loire River at Chadron: 44°58'7"N-3°55'11"E, 22 Sep. 2016, Persat and ONEMA43 coll.; UCBLZ – 2019.9.1009, 304 mm SL ♂, Ardèche Dept., Allier River at Laveyrune: 44°37'54"N-3°53'40"E, 22 Sep. 2016, Persat, FDAAPPMA09, FDAAPPMA43 and FDAAPPMA48 coll.; UCBLZ – 2012.9.1008, 405 mm SL ♀, Cantal Dept., Alagnon River at Ferrières-Saint-Mary: 45°10'41"N-3°53'43"E, 27 Jun. 2016, Persat and Lesbre coll.

### Diagnosis

*Thymallus ligericus* n. sp. differs from *T. thymallus* by a more elongated body (Fig. 2), the presence of a pointed snout revealing a strait or convex snout profile (Fig. 3A) (vs. a concave profile for *T. thymallus*, Fig. 3B), a more inferior mouth with a transversal aperture and a fleshier upper lip (Fig. 4A), a high number of black dots on the flanks (usually from more than 50 to several hundreds vs. less than 50 in the Rhône populations; Figs 2, 5), a shorter head length

(20.0-23.7% SL vs. 17.5-19.9% SL), smaller occipital and orbital depths of the head (respectively: 54.8-71.7% HL vs. 73.2-76.1% HL; 43.5-53.4% HL vs. 51.1-56.4% HL) and a shorter horizontal eye diameter (22.6-26.3% HL vs. 26.1-31.7% HL).

### Description

Morphometric measurements are given in table I. The holotype counts are given in brackets.

*Thymallus ligericus* n. sp. has an elongated body (Fig 2A-C) and a smaller head height (Fig. 4). The throat is usually covered by small scales. It has a pointed snout giving a strait or convex snout profile (Fig. 3A). Its mouth is clearly inferior with a transversal aperture more resembling the nose *Chondrostoma nasus* (Linnaeus, 1758) (Fig. 4A). The upper lip is fleshy. The adipose fin is usually rounded. Concerning meristic data, this species has VII-VIII 14-15 dorsal fin rays (VII-14), I 14-16 pectoral fin rays (I-15), I 9-11 pelvic fin rays (I-10), IV-V(9-11) anal fin rays (V-11), 73 + 2 to 87 + 4 lateral scales (81 + 3), 8.5-9.5 transverse dorsal scales

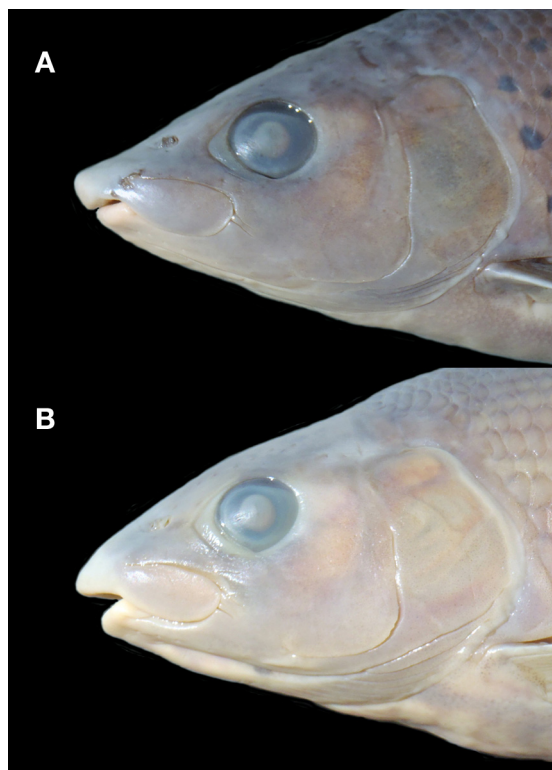


Figure 3. – Head profiles of *Thymallus* spp. **A:** Paratype of *Thymallus ligericus* n. sp. MNHN 2018-0728, 300 mm SL ♂, Dore River at Vertolaye, 29 May 2015, Persat, Juglaret and Buttazzoni coll.; **B:** *Thymallus thymallus* UCBLZ – 2012.9.1010, 376 mm TL, Rhône drainage, Ain River at Crotenay, 10 Jun. 2014, Persat and FDAAPPMA39 coll.

and 8.5-9.5 transverse pelvic scales. According to Knizhin (unpubl. data), who observed 7 specimens from the Loire catchment, this species has (15)18(19) pyloric caeca.

#### Colouration in life

In adults, overall body colour is usually darker than that of the Rhone or Rhine *T. thymallus*, but this might depend on the substrate. They can take on a blue metallic sheen in the darkest individuals. The sides are highly spotted by usually more than 50 and up to hundreds of black dots (270 in the holotype) (Figs 2A-C, 5), sometimes extending up to the head, with the exception of the uppermost section of the Allier River where the population is less spotted. In some populations, dots might be coalescent forming a kind of short horizontal lines. The lateral large faint wine-red patch in the centre of the side above the pectoral fins, common in many European populations, is often not visible when present because of the dark background colour of the body. Paired and anal fins have a rather dark green-brown colour. The pectoral fin does not develop the patchy colouration pattern usually visible in the largest *T. thymallus* of the Rhine and sometimes Rhone catchments. Caudal fin is dark-greenish, sometimes turning to dark purple, with a blue iridescent shine in large

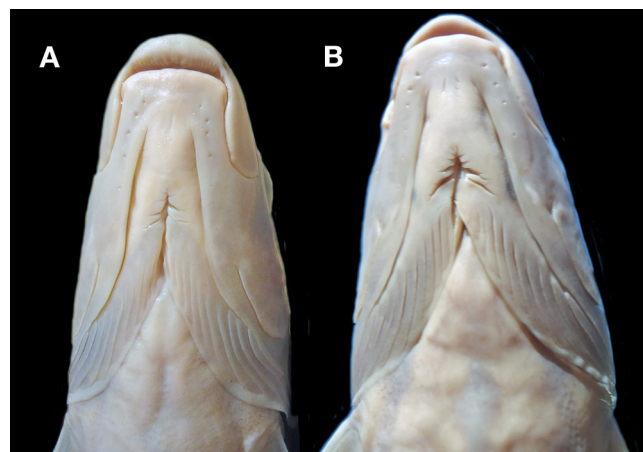


Figure 4. – Mouth in ventral view of *Thymallus* spp. **A:** Holotype of *Thymallus ligericus* n. sp. MNHN 2018-0722, 337 mm SL ♂, Alagnon River at La Chapelle d'Alagnon, 9 Sep. 2016, Persat and FDAAPPMA15 coll.; **B:** *Thymallus thymallus* UCBLZ 2012.9.1010, 376 mm TL, Rhône drainage, Ain River at Crotenay, 10 Jun. 2014, Persat and FDAAPPMA39 coll.

individuals. The large dorsal fin of the adults, especially in the males, is a bit less extended and less coloured than in the Rhône or Rhine populations of *T. thymallus*. The fin rays are contrastingly lighter than the inter ray membrane. The outer margin of the dorsal fin is often underlined by a thin pink line (Fig. 6). Towards the posterior part of the dorsal fin, the edge line takes a brown colour that extends more and deeper between the last dorsal fin rays. A checked pattern of alternatively dark grey and brown-reddish blotches covers most of the surface of the fin. This checked pattern is completed on its outer and posterior part by an alignment of increasingly clear blotches showing the same blue iridescent shine as the caudal fin. For large individuals, this blue colour part of the dorsal fin is visible from the riverbank.

#### Colouration in preservation

Fixed in formalin, then preserved in 70° ethanol, most of the colours, except the black dots, turn to grey. The checked pattern and colours of the dorsal fin, as well as the faint wine-red become faded but persist, for at least several years.

#### Etymology

*Ligericus* is a Latin adjective meaning “from the Loire drainage”.

#### Vernacular name

Loire grayling (English), Ombre d'Auvergne, Ombre de la Loire (French).

#### Distribution and habitat

The Loire grayling lives in medium to large foothill, canyon and plateau rivers of the mountainous part of the Loire catchment, i.e. in the Upper Vienne, Upper Loire and Upper

Table I. – Morphometric data for the holotype and means and extreme values for the 10 paratypes of *Thymallus ligericus* n. sp.

	Holo-type	With paratypes (n = 11)
Standard length (SL)	337	300 (252-405)
in % SL		
Head length	20.7	22.0 (20-23.7)
Body depth	20.7	22.1 (20.7-24.1)
Caudal peduncle depth	7.2	7.7 (7.2-8.3)
Predorsal length	35.4	36.7 (34.4-38.9)
Dorsal adipose distance	23.8	21.9 (19.0-23.8)
Post-adipose length	16.2	15.4 (14.4-16.6)
Prepectoral length	19.0	20.9 (19.0-22.7)
Prepelvic length	47.7	49.6 (47.7-51.4)
Pre-anal length	74.5	75.5 (72.8-79.2)
Pectoral-pelvic distance	26.9	27.4 (26.4-28.2)
Pelvic-anal distance	25.4	24.3 (22.5-25.9)
Caudal peduncle length	15.6	15.9 (15.1-16.8)
First dorsal fin branched length	13.9	15.3 (13.9-17.5)
Penultimate dorsal fin branched ray length	14.2	13.8 (11.5-16.2)
Pectoral fin length	14.6	15.4 (13.8-16.8)
Pelvic fin length	15.8	15.9 (14-17.6)
Anal fin length	13.8	14.5 (13.6-15.6)
Adipose fin length	8.8	8.3 (7.6-9.3)
in % HL		
Occipital depth of head	64.8	66.0 (54.8-71.7)
Orbital depth of head	46.9	48.8 (43.5-53.4)
Inter-orbital width	27.0	27.2 (24.5-30.0)
Horizontal eye diameter	23.9	24.7 (22.6-26.3)
Snout length	30.9	31.3 (28.8-35.0)
Mandible length	43.8	42.1 (40.8-44.4)
Maxillary length	21.0	22.0 (20.5-25.4)
Maxillary width	12.7	11.9 (10.6-13.1)
Mandible width	24.3	23.1 (19.9-26.1)
Chin length	27.2	29.2 (25.3-32.1)
Ventral snout length	35.5	36.9 (32.1-39.6)

Allier districts, where it cohabits with brown trout *Salmo trutta* Linnaeus, 1758, and Atlantic salmon *Salmo salar* Linnaeus, 1758, in the Allier branch. It is able to colonise rather small rivers with mean discharges of ca. 1 m<sup>3</sup>/s when protected from overfishing. It is able to swallow and digest caddisfly larvae with their gravel cases, a common prey in the Loire catchment (Persat, 1976). Only one known population, from the Besbre River, seems to have been driven to extinction, but all populations are potentially threatened by climatic change as droughts result in exceedingly high temperatures and too low water velocities. Up to now, stocking attempts appear to regularly fail in sustaining local native populations (Persat *et al.*, 2016), suggesting that wild stocks are more competitive than introduced ones. However, some

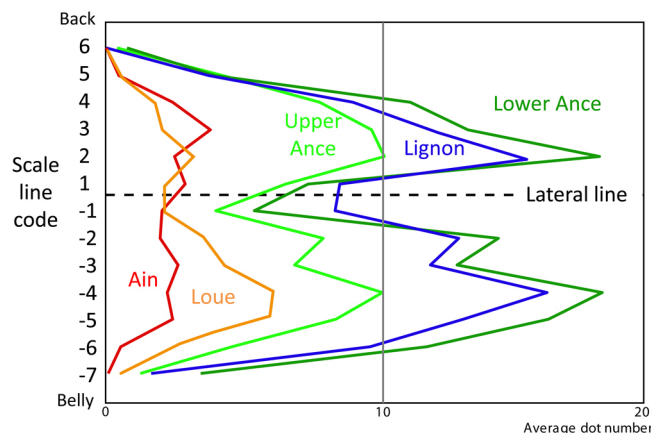


Figure 5. – Average dot numbers on each scale row on the flank for populations of *Thymallus ligericus* n. sp. from the Upper Ance (47 specimens), Lower Ance (7 specimens) and Lignon Rivers (16 specimens) in the Loire drainage as well as for *Thymallus thymallus* populations from the Ain (176 specimens) and Loue rivers (35 specimens) in the Rhône drainage.



Figure 6. – Dorsal fin on a live paratype of *Thymallus ligericus* n. sp. MNHN 2018-0726, 290 mm SL ♀, Lignon River at Boën-sur-Lignon, 29 May 2015, Persat, Juglaret and Buttazzoni coll.

Loire grayling populations have been successfully introduced elsewhere, such as in the Corrèze River of the Dordogne catchment, based on stocks reared at the Puy-de-Dôme federal fish farm of Besse-en-Chandesse (M. Mestas, pers. comm.).

### Comparative material

*Thymallus thymallus* (Linnaeus, 1758): BMNH 1979.6.22.191-192, 2 specimens, England: Thames drainage, Lambourn River at Lambourn, 1976, Bellamy coll.; BMNH 1979.6.22.226-238, 4, Kennet River, 1973, Bellamy coll.; BMNH 2018.9.4.14, 1, River Holme at Lockwood, Huddersfield, 15 Sep. 2017, Beer coll.; MNHN 1959-0546, 1, France: Rhône drainage at Nant-de-Sion, Spillmann coll.; MNHN B-2478, 2, Rhône drainage, de Candolle coll.; MNHN B-2479, 1, Rhône drainage, Blanchard coll.; MNHN B-2480, 3, Rhône drainage, Dept. Isère at Saint-Laurent-du-Pont, Galbert coll.; UCBLZ – 2012.9.1012, 2, Rhône drainage, Ain River at Crotenay, 11 Jun. 2014, Persat and FDAAPPMA39

coll.; UCBLZ – 2012.9.1013, 1, Rhône drainage, Ain River at Marigny, 19 Jul. 2016, Persat and FDAAPPMA39 coll.; UCBLZ – 2012.9.1014, 1, Rhône drainage, Bourne River at Saint Thomas en Royans, 19 Oct. 2010, Persat and Mallet coll.; ZSM-Pis-032234/537416/389004, 1, Germany: Danube drainage, Inn River at Wasserburg, below dam, downriver to “Am Griess”, 48.058N 12.220E, 10 Nov. 2004; ZSM-Pis-036238/541401/392989, 1, Elbe drainage, Sächsische Saale stream North of Förbau, East of Münchberg, 50.212N 11.917E, 26 Sep. 2007.

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## REFERENCES

- BELON P., 1555. – La Nature et Diversité des Poissons avec leurs pourtraicts representez au plus pres du naturel. 448 p. Charles Etienne, Paris.
- BIANCO P.G., 2014. – An update on the status of native and exotic freshwater fishes of Italy. *J. Appl. Ichthyol.*, 30: 62-77.
- BOUVET Y., SOEWARDI K. & PATTEE E., 1990. – Genetic divergence within natural populations of grayling (*Thymallus thymallus*) from two French river systems. *Archiv Hydrobiol.*, 119(1): 89-101.
- DYLDIN Y.V., HANEL L., ROMANOV V.I. & PLESNÍK J., 2017. – A review of the genus *Thymallus* (Pisces: Salmoniformes, Salmonidae, Thymallinae) with taxonomic notes. *Bull. Lamprol.*, 8: 103-126.
- FRICKE R., ESCHMEYER W.N. & VAN DER LAAN R., 2019. – Eschmeyer's Catalog of fishes: genera, species, references. Electronic version accessed 3 Sep. 2019. <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>
- MERANER A. & GANDOLFI A., 2012. – Phylogeography of European grayling, *Thymallus thymallus* (Actinopterygii, Salmonidae), within the Northern Adriatic basin: evidence for native and exotic mitochondrial DNA lineages. *Hydrobiologia*, 693: 205-221.
- MERANER A., CORNETTI L. & GANDOLFI A., 2014. – Defining conservation units in a stocking-induced genetic melting pot: unraveling native and multiple exotic genetic imprints of recent and historical secondary contact in Adriatic grayling. *Ecol. Evol.*, 4(8): 1313-1327.
- PERSAT H., 1976. – Écologie de l'Ombre commun, *Thymallus thymallus* (L., 1758) (Poissons Salmonidés). PhD Thesis, 69 p., Univ. Lyon 1, France.
- PERSAT H., 1977. – Écologie de l'Ombre commun. *Bull. Fr. Pêche Piscic.*, 266: 11-20.
- PERSAT H., 1982. – Photographic identification of individual grayling, *Thymallus thymallus* based on the disposition of black dots and scales. *Freshw. Biol.*, 12: 97-101.
- PERSAT H., 1988. – De la biologie des populations de l'Ombre commun *Thymallus thymallus* L., 1758 à la dynamique des communautés dans un hydrosystème fluvial aménagé, le Haut-Rhône français. Éléments pour un changement d'échelles. State Thesis, 223 p. Univ. Lyon 1, France.
- PERSAT H., 1996. – Threatened populations and conservation in the European grayling, *Thymallus thymallus* (L. 1758). In: Conservation of Endangered Freshwater Fish in Europe (Kirchhofer A. & Hefti D., eds), pp. 233-247. Birkhäuser Verlag, Basel.
- PERSAT H., 2011. – L'ombre commun. In: Les Poissons d'eau douce de France (Keith P., Persat H., Feuteun E. & Allardi J., eds), pp. 413-415. MNHN, Paris & Biotope Edition, Mèze.
- PERSAT H. & KEITH P., 2011. – Biogéographie et historique de la mise en place des peuplements ichtyologiques de France métropolitaine. In: In: Les Poissons d'eau douce de France (Keith P., Persat H., Feuteun E. & Allardi J., eds), pp. 37-93. MNHN, Paris & Biotope Edition, Mèze.
- PERSAT H., PATTEE E. & ROUX A.L., 1978. – Origine et caractéristiques de la distribution de l'Ombre commun, *Thymallus thymallus* (L. 1758), en Europe et en France. *Verh. Int. Verein. Limnol.*, 20: 2117-2121.
- PERSAT H., MATTERS DORFER K., CHARLAT S., SCHENEKAR T. & WEISS S., 2016. – Genetic integrity of the European grayling (*Thymallus thymallus*) populations within the Vienne River drainage basin after five decades of stockings. *Cybium*, 40(1): 7-20.
- SURRE C., PERSAT H., GAILLARD J.M., 1986. – A biometric study of three populations of the European grayling, *Thymallus thymallus* (L.) from the French Jura mountains. *Can. J. Zool.*, 64(11): 2430-2438.
- SOEWARDI K., 1988. – Caractérisation des populations de *Thymallus thymallus* L. (Poissons Salmonidés) et de *Rutilus rutilus* L. (Poissons Cyprinidés) dans le réseau fluvial du Rhône. Approche par l'étude du polymorphisme enzymatique. PhD Thesis, 125 p. Univ. Lyon-1, France.
- SUŠNIK S., BERREBI P., DOVČ P., HANSEN, M.M. & SNOJ A., 2004. – Genetic introgression between wild and stocked salmonids and the prospects for using molecular markers in population rehabilitation: the case of the Adriatic grayling (*Thymallus thymallus* L., 1758). *Heredity*, 93: 273-282.
- WEISS S., PERSAT H., EPPE R., SCHLÖTTERER C. & UIBLEIN F., 2002. – Complex pattern of colonization and refugia revealed for European grayling *Thymallus thymallus*, based on complete sequencing of the mtDNA control region. *Mol. Ecol.*, 11: 1393-1407.