Diadromous fishes from Saint-Pierre and Miquelon archipelago: diagnoses, taxonomy, nomenclature and distribution

by

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Abstract. – Saint-Pierre and Miquelon is a French self-governing overseas territory near the Canadian province of Newfoundland and Labrador. Seven diadromous species occur in the rivers and ponds of this archipelago: *Anguilla rostrata* (Lesueur, 1817), *Osmerus mordax* (Mitchill, 1814), *Salmo salar* Linnaeus, 1758, *Salvelinus fontinalis* (Mitchill, 1814), *Apeltes quadracus* (Mitchill, 1815), *Gasterosteus aculeatus* Linnaeus, 1758 and *Pungitius pungitius* (Linnaeus, 1758). For each species, we review nomenclature, give all arguments delineating the taxon according to an integrative approach (morphology, molecular, time divergence, cytogenetics, life traits histories, ecology, ethology, reproductive isolation), as well as their distribution in the archipelago and their IUCN status. We highlight taxonomical issues among *O. mordax*, *S. salar* and *P. pungitius* for which a taxonomical revision is needed. We consider the genus nomen *Anguilla* Thunberg, 1795 as not available according to the International Code of Zoological Nomenclature. *Osmerus abbottii* Cope, 1870 is now a junior synonym of *O. mordax*. We handled the invalidation of the names *Salvelinus kingi*, *S. multidentatus* and *S. angustus* which are junior synonym of *S. fontinalis*. *Gasterosteus biaculeatus* Mitchill, 1815 is not available. The type locality of *Gasterosteus globiceps* Sauvage, 1874 cannot be in North America but probably France, we thus agree to consider this nomen as a junior synonym of *Pungitius laevis* (Cuvier, 1819).

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Résumé. – Les poissons diadromes de l'archipel de Saint-Pierre et Miquelon : diagnoses, taxonomie, nomenclature et distribution.

Saint-Pierre et Miquelon est un territoire Français d'outre-mer situé près de la province canadienne de Terre-Neuve et Labrador. Sept espèces diadromes sont présentes dans les rivières et les étangs de cet archipel : *Anguilla rostrata* (Lesueur, 1817), *Osmerus mordax* (Mitchill, 1814), *Salmo salar* Linnaeus, 1758, *Salvelinus fontinalis* (Mitchill, 1814), *Apeltes quadracus* (Mitchill, 1815), *Gasterosteus aculeatus* Linnaeus, 1758 et *Pungitius pungitius* (Linnaeus, 1758). Pour chaque espèce, nous abordons les aspects nomenclaturaux, donnons tous les arguments justifiant la délimitation taxonomique suivant une approche intégrative (morphologie, moléculaire, datation, cytogénétique, histoires des traits de vie, écologie, éthologie, isolement à la reproduction), ainsi que leur distribution sur l'archipel et leur statut UICN. Nous mettons en évidence les problèmes taxonomiques concernant *O. mordax*, *S. salar* et *P. pungitius* pour lesquels une révision taxonomique est nécessaire. Nous considérons le nomen du genre *Anguilla* Thunberg, 1795 comme non disponible selon le Code International de Nomenclature Zoologique. *Osmerus abbottii* Cope, 1870 est dorénavant un synonyme junior de *O. mordax*. Nous confirmons l'invalidation des noms *Salvelinus kingi*, *S. multidentatus* et *S. angustus* qui sont des synonymes juniors de *S. fontinalis*. *Gasterosteus biaculeatus* Mitchill, 1815 n'est pas disponible. La localité type de *Gasterosteus globiceps* Sauvage, 1874 ne peut être l'Amérique du Nord mais probablement la France, nous sommes ainsi d'accord pour considérer ce nomen comme synonyme junior de *Pungitius laevis* (Cuvier, 1819).

Key words
Checklist
Diadromous fishes
Nomenclature
Northwest Atlantic
Taxonomy

INTRODUCTION

North America was significantly impacted by the glaciations during the Pleistocene (French and Millar, 2014). Several glacial advancements and retreats with sea-level variations occurred in north-eastern America (Dyke and Peltier, 2000; Tarasov and Peltier, 2004). Saint-Pierre and Miquelon was formed by the retreat of the Laurentide ice sheet at the end of the last glacial period (13.7 KA) and the successive rapid crustal rebound and relative sea-level fall (Billy *et al.*, 2014, 2015, 2018). Seven diadromous species (*Anguilla rostrata*, *Osmerus mordax*, *Salmo salar*, *Salvelinus fontinalis*, *Apeltes quadracus*, *Gasterosteus aculeatus* and *Pungitius pungitius*) colonized the archipelago recently, just after the Last Glacial Period and the ice retreat (Bell and Andrews, 1997). Consequently, the timeframe for any subsequent spe-

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ciation seems limited (Smith, 1981; Bernatchez and Wilson, 1998).

Some of these species (*i.e.*, *A. rostrata*, *O. mordax*, *S. salar* and *S. fontinalis*) have high economic value either because of commercial or recreational fishing or aquaculture (Paturel, 1976; Champigneulle *et al.*, 1983; Briand *et al.*, 2021). Gasterosteids are considered as model organisms in biological research (*e.g.*, Schluter and McPhail, 1992; Huntingford and Ruiz-Gomez, 2009; Merilä, 2013). Finally, the skin of eel (*A. rostrata*) was used in traditional medicine (Street, 1959). Other anadromous species also occur within the archipelago's waters (*i.e.*, *Petromyzon marinus* Linnaeus, 1758, *Acipenser oxyrinchus* Mitchill, 1815, *Alosa pseudoharengus* (Wilson, 1811) and *Alosa sapidissima* (Wilson, 1811) but only in sea waters; they do not enter rivers to spawn (Simian *et al.*, 2022). Finally, *Oncorhynchus mykiss* (Richardson, 1836) was introduced but no population was established (formally called *Salmo gairdnerii* Richardson, 1836; Champigneulle *et al.*, 1983).

The hydrosystem is composed of 36 small coastal catchments and 81 lagoons and ponds distributed in the 242 km^2 of the archipelago's land area. Knowing where the species is occurring in an area is important. However, the taxonomy on some of these species, essential for effective conservation, may be unclear, for example that of Atlantic salmon, whose molecular, cytogenetics or live traits histories data are ambiguous (Mace, 2004; Dudgeon *et al.*, 2006).

Here we provide an annotated check-list of the native diadromous fish species occurring in Saint-Pierre and Miquelon, which complements the list of Simian *et al.* (2022) with a focus on the morphological, molecular and ecological aspects of their taxonomic delineation, (and comments on their nomenclature.

MATERIAL AND METHODS

Abbreviations used

The abbreviations used are: 5S for ribosomal RNA 5S; 12S, mitochondrial ribosomal RNA 12S; 16S, mitochondrial ribosomal RNA 16S; 18S, ribosomal RNA 18S; AFLP, amplified fragment length polymorphism; ATP5c1, mitochondrial adenosine trophosphate synthase subunit gamma; ATP6, mitochondrial adenosine trophosphate synthase F_0 subunit 6; COI, cytochrome oxidase subunit 1; COII, cytochrome oxidase subunit 2; Cyt*b*: cytochrome *b*; CR/dloop, control region; DTAM: Direction des Territoires, de l'Alimentation et de la Mer; EN, endangered; ENC1, ectodermal-neural cortex 1-like protein; FTPSPM, Fédération pour la Pêche et la Protection des Milieux Aquatiques de Saint-Pierre et Miquelon; GH, growth hormone; GH1C, intron C in growth hormone 1; GH2C, intron C in growth hormone 2; GnRH, prepro-gonadotropin releasing hormone; gylt, glycosyltransferase; HL, head length; ICZN, International Code of Zoological Nomenclature; ITS1, first internal transcribed spacer; LC, least concerned; LDH-C1, lactate deshydrogenase C1; MHC, major histocompatibility complex gene; MLL, mixed lineage leukemia-like protein; myh6, myosin heavy chain 6; NADH/ND, NADH dehydrogenase; NE, not evaluated; plagl2, pleiomorphic adenoma gene-like 2; Ptr, hypothetical protein LOC564097; RAD, restriction site associated DNA markers; RAG1, recombination activating gene 1; RAPD, random amplification of polymorphic DNA; Rh; rhodopsin retrogen; RNF213, E3 ubiquitin-protein ligase RNF213; S7, first intron of the ribosomic RNA S7; SH3PX3, similar to SH3 and PX domain containing 3 gene; SL, standard length; SNP, single-nucleotide polymorphism; SPM, Saint-Pierre and Miquelon; sreb2, super conserved receptor expressed in brain 2; tbr1, T-box brain 1; TL, total length; Trim24b, heterochromatin-binding protein TRIM24B, and zic1 for Zinc finger of the cerebellum family member 1.

List of Museums

The list of museums with relevant specimens is: ANSP, Academy of Natural Sciences of Drexel University, Philadelphia; BMNH, Natural History Museum, London; LSL, Linnean Society of London, London; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNHN, Muséum national d'Histoire naturelle, Paris; NMC, Canadian Museum of Nature, Ottawa; NMW, Naturhistorisches Museum, Vienna; NRM, Naturhistoriska riksmuseet, Stockholm; PSU, Pennsylvania State University, College Station, Pennsylvania; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt; USNM, Smithsonian Institution National Museum of Natural History, Washington D.C., and ZMB, Museum für Naturkunde, Leibniz-Institut für Evolutions und Biodiversitätsforschung, Berlin.

Species definitions have been debated for decades among biologists who proposed concept in agreement with their biological discipline (Pauly, 2002; De Queiroz, 2007). However, the choice of a species concept is is important for biological studies, conservation and management (Agapow *et al.*, 2004; Isaac *et al.*, 2004; Wiley, 2007). Here we follow the Evolutionary Species Concept (ESC) *sensu* Wiley and Mayden (2000), as have several fish taxonomists in North America and Europe (*e.g.*, Wiley, 2002; Kottelat and Freyhof, 2007). The species is then an entity composed of organisms that maintains an identity distinct from related entities through time and over space and that has its own independent evolutionary fate and historical tendencies (Simpson, 1951; Wiley, 1978; Mayden, 1997, 2002; Kottelat and Freyhof, 2007).

To delineate species, we follow an integrative approach (Dayrat, 2005; Will *et al.*, 2005; Padial *et al.*, 2009). In addition to morphological and molecular data, several other

Table I. – Worldwilde IUCN status of the seven diadromous species occurring in the Saint-Pierre and Miquelon archipelago available on the website https://www.iucnredlist.org/.

Species	Worldwide IUCN status	Reference
Anguilla rostrata	EN (A2bd)	Jacoby *et al*., 2017
Osmerus mordax	LC	NatureServe, 2013a
Salmo salar	LC	World Conservation Monitoring Centre, 1996
Apeltes quadracus	LC	NatureServe, 2019a
Gasterosteus aculeatus	LC	NatureServe, 2019b
Pungitius pungitius	LC	NatureServe, 2013b
Salvelinus fontinalis	NE	n/a

independent datasets pertaining to ecology, phylogeography, reproductive biology, cytogenetics, and life history are used to delineated species and characterize taxa (Dayrat, 2005, DeSalle *et al*., 2005; Padial *et al*., 2009, 2010; Schlick-Steiner *et al*., 2010; Pante *et al*., 2015). Then, for each species, the diagnosis will be given as well as all other biological criteria allowing the distinction from the other species belonging to the same genus.

Nomenclature was verified with the Eschmeyer's Catalog of Fishes (Fricke *et al*., 2021) and checked manually with taxonomic publications (McAllister, 1963; Monod, 1973; Scott and Crossmman, 1973; Smith, 1989; Paepke, 2002; Ferraris, 2003; Kottelat, 1997, 2013; Denys *et al*., 2018).

As there is no IUCN evaluation for freshwater fishes of Saint-Pierre and Miquelon, their status was taken from the (worldwide) Red List of Freshwater fishes (IUCN, 2021).

RESULTS AND DISCUSSION

The seven diadromous native fish species occurring in Saint-Pierre and Miquelon are classified in one class, four orders, four families and seven genera.

The updated list of synonyms will be available and downloadable on the French taxonomic register TAXREF (Gargominy *et al*., 2021) and from FishBase (www.fishbase.org).

Concerning their worldwilde IUCN status, one is endangered, five are least concerned and one has not been evaluated (Tab. I). However, the conservation status of diadromous species on SPM has declined for several decades (F. Urtizberea DTAM, pers. com.), so a French national IUCN evaluation is still needed for SPM.

Clade Euteleostomi
Class Actinopterygii
Super-Order Elopomorpha Greenwood, Rosen, Weitzman & Myers, 1966
Order Anguilliformes
Family Anguillidae Rafinesque, 1810
Genus *Anguilla* Garsault, 1764

Anguilla Garsault, 1764: Pl. 661 [Feminine; type species: *Muraena anguilla* Linnaeus, 1758; type by subsequent monotypy by Schrank (1798: 304, 307) according to Welter-Schultes and Klug (2009: 230)].

Anguilla Thunberg, 1795; nomen not available according to the ICZN; see below.

Anguilla Schrank, 1798: 304, 307 [Feminine; type species: *Muraena anguilla* Linnaeus, 1758; type by monotypy by Wheeler (1990: 138); on Official List of Generic Names in Zoology (ICZN, 1992: 93 Opinion 1672)].

Anguilla Shaw, 1803: 15, Pl. 1 [Feminine; type species: *Muraena anguilla* Linnaeus, 1758; type by monotypy by Cooper and Crimmen (1989: 260); *Anguilla* Shaw, 1804 from Sherborn (1922-1933: 50) is a mistake].

Terpolepis McClelland, 1844: 225 [Subgenus of *Anguilla* Schrank, 1798: 304, 307; feminine; type species: *Anguilla brevirostris* McClelland, 1844; type by subsequent designation by Blache *et al*. (1973: 220) according to Smith (1989: 32)].

Tribranchus Peters *in* Müller, 1846: 193 (Masculine; type species: *Tribranchus anguillaris* Peters, 1846, type by monotypy).

Nomenclatural note

During the second part of the 19th century, the genus nomen *Anguilla* Thunberg, 1795 appeared as "*Anguilla* Thunberg, Nouv. Mem., Stockholm" with an approximative year of description around 1795 (Agassiz, 1842-1846: 4; Gill, 1890: 159; Jordan and Davis, 1892: 666). This incertitude already intrigued Gill (1890) as he found no such nomen in the *Memoirs of the Stockholm Academy*. His doubt was also confirmed by Jordan and Davis (1892: 666), Jordan and Evermann (1917: 73) and Jordan (1963: 73). Sherborn (1922-1933: 50) affirmed that "Anguilla Thunberg 179—, Ag. Does not occur". After checking the bibliography of the publications from Carl Peter Thunberg including 584 titles (Thunberg, 1782-1827; Rookmaaker, 1994), as well as publications including lists of his works (Anonymous, 1896) and old ichthyological or zoological studies (Carus and Engelmann, 1861; Bosgoed, 1873; Brashford, 1917), the nomen *Anguilla* associated to Thunberg and around 1795 was not found. So, this genus nomen appears to be a mistake and we examined its origin. Cuvier (1817: 230) was the first to attribute the genus nomen to Thunberg: "*Anguilla* Thunb. et Shaw.". This may be due to a bad interpretation of Ahl (1789) edited by Thunberg, and then Agassiz (1842-1846: 4) mentioned "*Anguilla* Thunb. Nouv. Mem. Stock. 179." and Günther (1870: 23) "*Anguilla* (Thunberg) Cuv. Regn. Anim.". Thus, as there is no publication associated to the nomen *Anguilla* Thunberg, 1795, the condition required by the article 11.1 of the ICZN is not fulfilled. By consequence, this nomen is not available according to the ICZN. Several authors already affirmed that this nomen should not be used as valid genus, and proposed to use the nomen *Anguilla* Shaw, 1803 (Gill, 1890: 160; Jordan and Evermann, 1917: 73; Sherborn, 1922-1933: 50; Jordan, 1963: 73; Cooper and Crimmen, 1989: 260).

However, the description of Schrank (1798: 304, 307) is earlier than the one of Shaw. Wheeler (1990: 138) suggested to consider *Anguilla* Schrank, 1798 as valid nomen instead of *Anguilla* Shaw, 1803 on the Official List of Generic Names designating *Muraena anguilla* Linnaeus, 1758 as its type species (ICZN, 1992: 94).

Finally, the works of Garsault (1764), pertaining to illustrations and Garsault (1767), pertaining to their descriptions, were rediscovered by Welter-Schultes *et al.* (2008), impacting taxonomical and nomenclatural knowledges in zoology (Welter-Schultes and Klug, 2009). Since this rediscovery, the validity of several genera of zoological groups was debated, along with the concept of the genus itself (Dubois and Bour, 2010a, b, 2012; Welter-Schultes and Klug, 2011). Welter-Schultes and Klug (2009: 230) made the nomen *Anguilla* Garsault, 1764 available considering that Garsault's figure represents *Muraena anguilla* Linnaeus, 1758 currently designated as type species of *Anguilla* Schrank, 1798. Thus, *Anguilla* Schrank, 1798, as well as *Anguilla* Shaw, 1803, are junior homonym and objective junior synonym of *Anguilla* Garsault, 1764 (Welter-Schultes and Klug, 2009: 230; Kottelat, 2013: 37). However, even if the nomen *Anguilla* Schrank, 1798 has been commonly used, the nomen *Anguilla* Garsault, 1764 has been used as a valid nomen after 1900 by Kottelat (2013: 37) and further by other authors. So, the requirement of article 23.9.1.1 of the ICZN is not fulfilled, and the nomen cannot be ignored (article 23.9). *Anguilla* Garsault, 1764 must be thus considered as the valid nomen.

Anguilla rostrata **(Lesueur, 1817) – NATIVE**

Muraena rostrata Lesueur, 1817: 81 [type locality: Cayuga and Geneva lakes, New York, USA; no types known; see Smith (1989: 35) for nomenclatural discussion].

Muraena bostoniensis Lesueur, 1817: 81 (type locality: Boston Harbor, Massachutsetts, USA; no types known).

Muraena serpentina Lesueur, 1817: 81 (type locality: Harbour of Newport, Rhode Island, USA; no types known).

Muraena argentea Lesueur, 1817: 82 (type locality: Boston Harbor, Massachutsetts, USA.; no types known).

Muraena macrocephala Lesueur, 1817: 82 (type locality: Saratoga, New York; Philadelphia market, USA; no types known).

Anguilla blephura Rafinesque, 1817: 120 (type locality: Southwestern shore of Long Island, New York, USA; no types known).

Anguilla chrisypa Rafinesque, 1817: 120 (type localities: Lake George, Lake Champlain, and Hudson River above the Falls, USA; no types known).

Anguilla laticauda Rafinesque, 1818: 447 [type localities: Ohio River, Wabash River, Green River, etc., USA; no types known; spelled *laticanda* by Rafinesque (1818: 447; 1820: 245) but *laticauda* should be used (Smith, 1989: 35); may be fictional (Markle, 1997: 444)].

Anguilla aterrima Rafinesque, 1820: 245 (type localities: Tennessee River, Cumberland River, etc., USA; no types known).

Anguilla xanthomelas Rafinesque, 1820: 245 (type locality: Ohio River, USA; no types known).

Anguilla lutea Rafinesque, 1820: 246 (type localities: Cumberland, Green and Licking rivers, USA; no types known).

Anguilla tenuirostris DeKay, 1842: 310, Pl. 53 (fig. 173) (type locality: New York, USA; no types known).

Anguilla novaeorleanensis Kaup, 1856: 43, Pl. 6 (fig. 33) [type locality: New Orleans, Louisiana, USA; syntypes: MNHN-IC-B-2111 (Bauchot *et al.*, 1993: 96)].

Anguilla cubana Kaup, 1856: 44 [type locality: Cuba; holotype: MNHN-IC-B-2105 (Bauchot *et al.*, 1993: 94)].

Anguilla punctatissima, Kaup, 1856: 44 [type locality: Niagara Falls, USA and Canada; Holotype: MNHN (not found; Bauchot *et al.*, 1993: 124)].

Anguilla novaeterrae Kaup, 1856: 45, Pl. 7 (fig. 35) [type locality: Newfoundland, Canada; holotype: MNHN-IC-B-2106 (Bauchot *et al.*, 1993: 96)].

Anguilla texana Kaup, 1856: 45, Pl. 7 (fig. 36) [type locality: Texas, USA; holotype: MNHN-IC-B-2109 (Bauchot *et al.*, 1993: 97)].

Anguilla wabashensis Kaup, 1856: 46 [type locality: Wabash River, tributary of Ohio River, USA; Holotype: MNHN-IC-B-2117 (Bauchot *et al.*, 1993: 97)].

Anguilla macrops Kaup, 1856: 49, Pl. 7 (fig. 38) [No locality; Holotype: MNHN-IC-B-3154 (Bauchot *et al*., 1993: 95)].
Anguilla tyrannus Girard, 1858: 171 [type locality: Mouth of Rio Grande del Norte [Rio Bravo], Texas, USA; Holotype: USNM 857 (= USNM 43108)].
Leptocephalus grassii Eigenmann & Kennedy, 1902: 84, figs 1, 1a-b [type localities: Atlantic, Albatross station 2103, 38°47'20"N, 72°37'W, depth 0-1091 fathoms; 38°25'N, 72°40'W; syntypes: USNM 49751-49752 (Smith, 1994: 3)].

Morphological diagnosis

Anguilla rostrata is distinguished from other *Anguilla* species by the following combination of characters: plain color, long dorsal-fin, gape 25-27% HL, 103-111 vertebrae (Smith, 1989). It is therefore distinguished from *A. anguilla* (Linnaeus, 1758), its sister group species, by fewer vertebrae (110-119 for *A. anguilla*), fewer precaudal vertebrae (41-45 *vs*. 44-47), and a slightly shorter dorso-anal distance (mean 9.1% TL *vs*. 11.2% TL) (Ege, 1939; Smith, 1989).

Molecular delineation

The molecular delineation of *A. rostrata* is supported by genomic (AFLP, transcriptome, whole genome, RADseq genotyping, SNP), mitochondrial (mitogenome, mitochondrial DNA RFLP, 12S, 16S, ATP6, COI, COII, CR/dloop, Cyt*b*) and nuclear (5S, 18S, ATP5c1, C-type lectin, microsatellites, mucosal galectin, RAPD, Rh) data (*e.g*., Ishikawa *et al*., 2004; Pichiri *et al*., 2006; Gagnaire *et al*., 2009, 2012; Frankowski and Bastrop, 2010; Gong *et al*., 2013; Rehbein, 2013; Ulrik *et al*., 2014; Wielgoss *et al*., 2014; Hwang *et al*., 2015; Tsutsui *et al*., 2015, 2019; Jacobsen *et al*., 2017; Chen *et al*., 2018; Igarashi *et al*., 2018; Noh *et al*., 2018; Takeuchi *et al*., 2019; Hsu *et al*., 2020; Nikolic *et al*., 2020; Richards *et al*., 2020).

Time divergence

The common ancestor between *A. rostrata* and *A. anguilla* is estimated to be ~3.4 MYA according to Jacobsen *et al*. (2014) and 1.3-2.4 MYA according to Nicolic *et al*. (2020).

Remarks

The spawning areas of *A. rostrata* and *A. anguilla* are located in a large thermal front in the northern part of the Sargasso Sea (Haro, 2014). However, there is an overlap which allows hybridization between these two species (Albert *et al*., 2006; Wielgoss *et al*., 2014; Jacobsen *et al*., 2017).

Ontology was considered as one criterion discriminating *A. rostrata* from *A. anguilla* with the first metamorphosis occurring respectively 10 to 12 months and 2 to 3 years (Schmidt, 1922). However, more recent studies demonstrated that there is no significant difference between their age of metamorphosis (respectively 156-214 days and 176-198 days; Arai *et al*., 2000; Otake, 2003).

Distribution in SPM

This species occurs in most of the freshwater systems of the archipelago (CPPMA, 2013). There are very few ponds (generally inaccessible) in which *A. rostrata* is absent.

Sub-Class Neopterygii Regan, 1923
Infra-Class Teleostei
Order Osmeriformes
Family Osmeridae Regan, 1913
Genus *Osmerus* Linnaeus, 1758

Osmerus Linnaeus, 1758: 310 [subgenus of *Salmo* Linnaeus, 1758: 308; masculine; type species: *Salmo eperlanus* Linnaeus, 1758; type by subsequent designation by ICZN (1958: Opinion 77)].
Osmerus Lacepède, 1803: 229 [Masculine; type species: *Salmo eperlanus* Linnaeus, 1758; type by subsequent designation by Bory de Saint-Vincent (1824: 205)].
Eperlanus Gaimard, 1851: Pl. (Masculine; type species: *Salmo eperlanus* Linnaeus, 1758; type by monotypy).

***Osmerus mordax* (Mitchill, 1814) – NATIVE**
Atherina mordax Mitchill, 1814: 15 [type locality: New York, USA; no types known; misspelled *A. mordas* by Zhu (1995: 13)].
Osmerus viridescens Lesueur, 1818: 230 (type locality: Boston to Newport, USA; no types known).
Osmerus sergeanti Norris, 1868: 93 [type locality: Schuylkill River below Fairmount dam, Philadelphia; Brandywine Creek, Pennsylvania, USA; syntypes: ANSP 7751-53 (Böhlke, 1984: 135); misspelled *sargenti* by Smith (1986: 241)].
Osmerus abbottii Cope, 1870: 490 [type locality: Cobessicontic Lake, Kennebec County, southwestern Maine, USA; syntypes: ANSP (not found; Böhlke, 1984: 135)].
Osmerus spectrum Cope, 1870: 490 [type locality: Wilton Pond, near the head of southwestern branch of Kennebec River, southwestern Maine, USA; neotype NMC 79-834 designated by Lanteigne and McAllister (1983: 23)].

Morphological diagnosis

Osmerus mordax differs from *O. dentex* Steindachner & Kner, 1870 by having 59-65 vertebrae (*vs*. 63-68), parietal bones not in contact with each other (*vs*. more or less contiguous, sometimes weakly at the front), and the orbito-nasal vein exits the nasal capsule usually through a cut-out of the medial edge of the lateral ethmoid or rarely below this bone through the cartilage (*vs*. through the cartilage below the lateral ethmoid or rarely cutting through the lower edge of the bone) (Kljukanov, 1969; Coad, 2018). It therefore differs from *O. eperlanus* (Linnaeus, 1758) by 13-30 pored scale on the lateral line (*vs*. 4-13) (McAllister, 1963; Scott and Crossman, 1973).

Molecular delineation

The molecular delineation of *Osmerus mordax* is supported by enzymes, mitochondrial (mitogenome, 12S, 16S, COI, Cytb) and nuclear (ITS2, S7, RAG1) data (*e.g.*, Luey *et al.*, 1982; Ilves and Taylor, 2009; Skurikhina *et al.*, 2013; Balakirev *et al.*, 2018).

Life history characteristics

Osmerus mordax differs from *O. dentex* by life history traits such as a shorter life expectancy (7 years *vs*. 15 years), an earlier age of sexual maturity (2-3 years *vs*. 6-7 years), and faster growth (von Bertalanffy growth coefficient = 0.639 *vs*. 0.11-0.24) (see Haldorson and Craig, 1984). However, these life history traits are comparable to *O. eperlanus* (Belyanina, 1969; Froese and Pauly, 2021).

Time divergence

Molecular data estimate the speciation events between *Osmerus* spp. began at the end of the Pliocene (around 3.5 Ma), and the separation of *O. mordax* and *O. dentex* at around 2.5 Ma with the opening of the Behring Strait (Taylor and Dodson, 1994).

Nomenclatural note

Osmerus abbottii Cope, 1870 has been invalidated and considered as junior synonym of *Osmerus eperlanus* by McAllister (1963: 16). But as its type locality (Cobessicontic Lake, Kennebec County, southwestern Maine, USA) occurs in North America and not in Europe, in contrast to *O. eperlanus* (Linnaeus, 1758); thus, according to molecular studies, *O. abbottii* must be considered as a junior synonym of *O. mordax*.

Taxonomy

Osmerus mordax is known to be an anadromous species, but some populations are lacustrine. Two distinct Acadian (anadromous and lacustrine populations) and Atlantic (only anadromous) evolutionary lineages have been highlighted (Baby *et al.*, 1991; Bernatchez and Martin, 1996; Bernatchez, 1997; Bradbury *et al.*, 2006, 2011; Barrette *et al.*, 2009). Two zones of secondary contact between both lineages were detected in the St. Lawrence River estuary and in southeastern Newfoundland (Bernatchez, 1997; Bradbury *et al.*, 2011). Some differences were already observed between these lineages such as morphology, behavior (benthic *vs*. pelagic), habitats, spawning places and the interval between their spawning periods (Lecomte and Dodson, 2004, 2005; Bradbury *et al.*, 2006; Coulson *et al.*, 2006; Barrette *et al.*, 2009). Bernatchez (1997), according to molecular data, found reproductive isolation between these lineages. However, Lecomte and Dodson (2004) highlighted introgression between Atlantic and lacustrine Acadian populations. The Ice Age events occurring 350,000 years ago isolated both lineages. Thus, there was an ecological speciation; populations would have then to adapt to their new environmental constraints changing morphologically reducing the gene flow between lineages (Lecomte and Dodson, 2004; Bradbury *et al.*, 2006).

In addition to that, lacustrine populations occurring in some north-eastern American lakes make some taxonomists disagree (*e.g.*, Rupp and Redmond, 1966; Lanteigne and McAllister, 1983; MacCrimmon *et al.*, 1983; Taylor and Bentzen, 1993a). In several north-eastern American lakes, two morphotypes are observed: normal and dwarf forms (Greene, 1930; Zillox and Youngs, 1958; Legault and Delisle, 1968; Delisle, 1969; Copeman, 1973, 1977; Lanteigne and McAllister, 1983; Baby *et al.*, 1991; Taylor and Bentzen, 1993a, b; Saint-Laurent *et al.*, 2003; Hopkins and Warren, 2020). In Lake Utopia (New Brunswisk, Canada), a third form, giant, is also encountered (Curry *et al.*, 2004; Shaw and Curry, 2011; Hopkins and Warren, 2020). Cope (1870) described two species of dwarf smelt *Osmerus spectrum* and *Osmerus abbottii* respectively from Wilton Pond and Cobessicontic Lake (Kennebec County, southwestern Maine, USA) according to eye diameters, head length and scales counts. They further considered these taxa as subspecies of *O. mordax* (Jordan and Evermann,1896; Jordan *et al.*, 1930), and forgotten in the following checklist published (Lanteigne and McAllister, 1983). However, considering studies comparing sympatric normal and dwarf smelt populations, Lanteigne and McAllister (1983) did a morphomeristic analysis on dwarf and normal lacustrine smelts from Wilton Pond, Utopia Land Heney Lakes, and found that dwarf smelt (or pygmy smelt) differs from *O. mordax* by higher gill raker counts, a relatively larger eye and a lower lateral scale counts in addition to a smaller maximum size. Moreover, they are planktivorous (*vs*. piscivorous for *O. mordax*), as later confirmed by Jardine and Curry (2006). Thus, Lanteigne and McAllister (1983) concluded that dwarf smelts must be considered as a distinct species, *O. spectrum*, occurring in these lakes. These results are also supported by recent studies such as a reproductive isolation between each ecotype in the Lake Utopia because the period of spawning differs in time (Taylor and Bentzen, 1993b; Shaw and Curry, 2011). Dwarf and normal morphotypes in the Lac Saint-Jean (Québec) have different life histories being respectively semelparous and iteroparous (Saint-Laurent *et al.*, 2003). However, the dwarf phenotype seems to be polyphyletic and appeared independently in each lake (Taylor and Bentzen, 1993a). Moreover, some authors considered the phenotypic dissimilarity between ecotypes insufficient to justify their taxonomic distinction and recognized only *O. mordax* as valid species (Rupp and Redmond, 1966; MacCrimmon *et al*., 1983; Robins *et al*., 1991). The rainbow smelt is then considered a species complex (Hopkins and Warren, 2020).

According to our taxonomic understanding, we consider one species of smelt *O. mordax*. However, considering the previous studies on the Acadian evolutionary lineage and the lacustrine ecotypes, a taxonomical revision may need to be undertaken. With an approach utilizing the Evolutionary Species Concept (sensu Wiley and Mayden, 2000), each case might be viewed as a newly evolved taxon, capable of being described and diagnosed (Mayden, 2002).

Remark

Bachelot de la Pylaie (1819) described in a manuscript the smelts occurring in ponds of SPM. He reported the body lengths (12-16 cm), which correspond to the 'normal' form according to Shaw and Curry (2011). So, there would not be any particular form of *O. mordax* in the archipelago. Nevertheless, there is, to our knowledge no study of this.

Distribution in SPM

Osmerus mordax occurs in bodies of water connected to the sea, such as the Savoyard Pond, the Laveuses and Cap-Noir Pond in Saint-Pierre, and in Miquelon, in the Mirande, Chapeau, Grand Etang (P. Delizarraga, pers. com.) the Grand Barachois, a large lagoon (Boulva and McLaren, 1980). It is also found in the Ollivier marshes at Langlade (D. Abraham Nature SPM, pers. com.). Nevertheless, *O. mordax*, which was previously abundant, is currently threatened in SPM because of the loss of connectivity between ponds and the sea, as well as from reductions in pond area (F. Urtizberea DTAM, pers. com.) resulting from anthropogenic landscape modification.

Order Salmoniformes
Family Salmonidae Jarocki or Schinz, 1822
Subfamily Salmoninae Jarocki or Schinz, 1822
Genus *Salmo* Linnaeus, 1758

Salmo Linnaeus, 1758: 308 [Masculine; type species: *Salmo salar* Linnaeus 1758; type by subsequent designation by Desmarest (1856: 312) according to Whitley (1939: 225; with a wrong date for Desmarest), also by Jordan and Gilbert (1883: 309); on official ICZN list (Opinion 77, Direction 56; ICZN, 1922: 73, 1956: 340)].

Trutta Garsault, 1764: Pl. 665 [Feminine; type species: *Salmo trutta* Linnaeus, 1758; type by subsequent monotypy or subsequent designation or possibly absolute tautonymy according to Welter-Schultes and Klug (2009: 236); attributed to E.L. Geoffroy with the date 1764 by Bogutskaya and Naseka (2004: 156)].

Fario Valenciennes *in* Cuvier & Valenciennes, 1848: 277 [Masculine; type species: *Fario argenteus* Valenciennes *in* Cuvier & Valenciennes, 1848; type by subsequent designation by Berg (1916: 34)].

Salar Valenciennes *in* Cuvier & Valenciennes, 1848: 314 [Masculine; type species: *Salar ausonii* Valenciennes *in* Cuvier & Valenciennes, 1848; type by subsequent designation by Berg (1916: 34)].

Salmothymus Berg, 1908: 502, 503 (Masculine; type species: *Salar obtusirostris* Heckel, 1851; type by monotypy).

Acantholingua Hadžišče, 1960: 47 (Subgenus of *Salmothymus* Berg, 1908: 502, 503; Feminine; type species: *Salmo ohridanus* Steindachner, 1892; type by monotypy).

Platysalmo Behnke, 1968: 2 (Subgenus of *Salmo* Linnaeus, 1758: 308; Masculine; type species: *Salmo (Platysalmo) platycephalus* Behnke, 1968; type by monotypy).

***Salmo salar* Linnaeus, 1758 – NATIVE**

Salmo salar Linnaeus, 1758: 308 (type locality: European seas and rivers; no types known).

Salmo nobilis Olafsen, 1772: 65 (type localities: Sweden, Heller-Aa, Kortolfstade-Aa and Lar-Aa, Iceland; no types known).

Salmo goedenii Bloch, 1784: 155, Pl. 102 [type locality: Baltic Sea in Rügenwalde, Hinterpommern (now Darłowo), north-western Poland; holotype: ZMB 3710 (Paepke, 1999: 124)].

Salmo strom Bonnaterre (ex Müller), 1788: 168 (type locality: Norway; no types known).

Salmo fario var. *samulus* Walbaum, 1792: 61 (type locality: Great Britain; no types known).

Salmo salmulus Walbaum, 1792: 65 [type locality: Rivers Wye, upper Severn and tributaries, north of England and Wales, UK; syntypes: whereabouts unknown; objective synonym of *Salmo fario* var. *samulus* Walbaum, 1792: 61 as both are based in part on Pennant (1769: 253; 1776: 303 pl. 59)].

Salmo caerulescens Schmidt, 1795: 65 (*nomen nudum*; type locality : river Moldau now river Vltava, Czech Republic).

Salmo punctatus Bloch & Schneider, 1801: 419 (type locality: Osefjord, branch of Ejdfjord, Hardangerfjord, Søndmør Region, Bergen, Norway; no types known).

Salmo renatus Lacepède, 1803: 157, 224 (type locality : River Moselle, France; no types known).

Salmo rilla Lacepède, 1803: 157, 224, Pl. 5 (fig. 3) (type locality: Rille River, a tributary of the Seine River, France; no types known).

Salmo nobilis Pallas, 1814: 342 (type localities: Baltic Sea, Caspian Sea, northern Russia and Siberia, Russia; no types known; junior homonym of *Salmo nobilis* Olafsen 1772: 65).

Salmo hamatus Cuvier, 1829: 303 (type locality: Europe; possible syntypes: MNHN-IC-0000-0777, MNHN-IC-

A-1064, MNHN-IC-A-8841, MNHN-IC-A-8553 (Bertin, 1940: 301-302)].

Salmo ocla Nilsson, 1832: 4 (type locality: Älvkarleby on Dalälfven River, north of Uppsala, Sweden; no types known).

Salmo salmo Valenciennes *in* Cuvier & Valenciennes, 1848: 169, Pl. 614 [type localities: Dieppe, Fecamp, Abbeville, Manche, North Sea, Belgium, Netherlands, England, Berlin; syntypes: MNHN-IC-A-8552, MNHN-IC-A-8559 (Bertin, 1940: 301].

Salmo sebago Girard, 1853: 380 (type locality: Lake Sebago, southern Maine, USA; no types known).

Salmo gloverii Girard, 1854: 86 (type locality: Upper affluent of Union River, Maine, USA; syntypes: USNM 3586).

Salmo salar var. *lacustris* Hardin, 1862: 382 (type locality: Lake Vänern, Sweden; syntypes: whereabouts unknown; junior homonym of *Salmo lacustris* Linnaeus, 1758: 309).

Trutta salar relicta Malmgren, 1863: 59 [type locality: Lake Ladoga at Keksgolm, Finland (now Priozersk in Russia); syntypes: whereabouts unknown].

Salmo gracilis Couch, 1865: 216, Pl. 216 (type locality: Fowey harbour, UK; holotype: BMNH; junior homonym of *Salmo gracilis* Valenciennes in Cuvier & Valenciennes, 1848: 265).

Salmo hardinii Günther, 1866: 107 (type locality: Lake Vänern, Sweden; syntypes: BMNH 1864.11.9.14).

Salmo brevipes Smitt, 1882: 32 (type locality: Arkhangelsk, Russia; syntypes: NRM 24881).

Salmo salar tasmanicus Johnston, 1889: xvi (type locality: Tasmania, Australia; no types known).

Salmo salar ouananiche Jordan & Evermann (ex McCarthy), 1896: 487 (type locality: Saguenay River, outlet of Lake St. John, Canada; no types known).

Salmo salar infraspecies *biennis* Berg, 1912: 137 (infrasubspecific, nomen not available).

Salmo salar brevipes natio relictus Berg, 1932 (infrasubspecific, nomen not available).

Salmo salar saimensis Seppovaara, 1962: 78 (type locality: Iso-Saimaa, Finland; syntypes: whereabouts unknown).

Salmo salar americanus Payne, Child & Forrest, 1971: 251 (*nomen nudum*; type locality: North America; no types known; junior homonym of *Salmo americanus* Bloch & Schneider 1801: 410).

Salmo salar europaeus Payne, Child & Forrest, 1971: 251 (*nomen nudum*; type locality: Europe; no types known).

Morphological diagnosis

Salmo salar is distinguished from other *Salmo* species by 10-13 scales between the adipose base and the lateral line (*vs*. 13-16 scales), 17-24 gill rakers (*vs*. 14-16), a caudal fin deeply forked in specimens smaller than 200 mm SL (*vs*. caudal emarginate), hyaline or grey adipose margins (*vs*. orange or red) and the posterior part of vomer toothless (*vs*. posterior part of vomer toothed) (Kottelat and Freyhof, 2007).

Molecular delineation

The molecular delineation of *S. salar* is supported by genomic (AFLP, whole genome, RADseq genotyping, RAPD and SNP), mitochondrial (mitogenome, mitochondrial DNA RFLP, 12S, ATPase6, COI, COII, CR/dloop, Cyt*b*, NADH1/ND-1, ND-3/4; ND-5/6, Pro tRNA) and nuclear (5S, GH, GH2C, GnRH, histone-3 coding gene, ITS1, LDH-C1, MHC, microsatellites, minisatellites, RFLP, transferrin gene) data (*e.g*., Goodier and Davidson, 1993, 1998; Gross and Nilsson, 1995; Gross *et al*., 1996; Nielsen *et al*., 1998; Phillips *et al*., 2000; Grimholt *et al*., 2002; Presa *et al*., 2002; Woram *et al*., 2003; Crespi and Fulton, 2004; Campos *et al*., 2006; Ryynänen and Primmer, 2006; Castillo *et al*., 2008; Snoj *et al*., 2008; Davidson *et al*., 2010; Pustovrh *et al*., 2011; Shedko *et al*., 2012, 2013; Karlsson *et al*., 2013; Shubina *et al*., 2013; Horreo, 2017; Lecaudey *et al*., 2018).

Cytogenetics

The analysis of the genome of *S. salar* revealed extensive chromosomal rearrangements with fusion and fission events, comparing to the brown trout *S. trutta* Linnaeus, 1758 which as the ancestral chromosome structure (Leitwein *et al*., 2017).

Time divergence

S. salar is located on a phylogenetic tree as sister to all other *Salmo* species (*e.g*., Lecaudey *et al*., 2018; Tougard *et al*., 2018). Their common ancestor is estimated ~4-11 MYA for Shedko *et al*. (2012) as well as for Campbell *et al*. (2013), and 14.2-17.0 for Horreo (2017) and Lecaudey *et al*. (2018).

Taxonomy

The Atlantic salmon, *S. salar,* has a native distribution from north-eastern America (Québec, Connecticut, New York) to Atlantic coasts of western Europe to the Baltic, Barents and White Sea basins (Kotttelat and Freyhof, 2007; Page and Burr, 2011). Molecular data distinguishes two major evolutionary lineages within this taxon, *i.e*., North American and European lineages (Payne *et al*., 1971; Ståhl, 1987; Bermingham *et al*., 1991; Birt *et al*., 1991; Cutler *et al*., 1991; McConnell *et al*., 1995; Taggart *et al*., 1995; Bourke *et al*., 1997; Kauppi *et al*., 1997; King *et al*., 2001, 2007; Bourret *et al*., 2013; Rougemont and Bernatchez, 2018; Lehnert *et al*., 2020). Both lineages would have diverged during the mid-Pleistocene: 600,000-700,000 years ago according to King *et al*. (2007) and 2.58 MYA to 11,000 years ago according to Rougemont and Bernatchez (2018), even if secondary contacts occurred (Rougemont and Bernatchez, 2018;

Lehnert *et al.*, 2019). Moreover, cytogenetic studies demonstrated differences in chromosome numbers between North American (2N = 54) and European (2N = 58) lineages due to chromosomal rearrangements (Hartley, 1987; Phillips and Rab, 2001; Lubieniecki *et al.*, 2010; Brenna-Hansen *et al.*, 2012). Genomic data highlighted a divergence between both lineages (Lehnert *et al.*, 2020), which would explain some reproductive incompatibilities (Cauwelier *et al.*, 2012) without implying a reproductive barrier (O'Reilly *et al.*, 2006; Pedersen *et al.*, 2017; Rougemont and Bernatchez, 2018; Lehnert *et al.*, 2019). Other studies highlighted differences of life history such as temperature preferences, traits associated with domestication and age at first maturity (Jeffery *et al.*, 2017; López *et al.*, 2018; Boulding *et al.*, 2019). Finally, morphometrical studies distinguish North American from European populations, but with no diagnosis and an overlap of meristic characters (MacCrimmon and Claytor, 1986; Luther, 1989). Shape analyses on scales and otoliths also support discriminating two lineages (Reddin, 1986; de Pontual and Prouzet, 1987; Friedland and Reddin, 1994). There are then several evidences suggesting to consider these two lineages as distinct taxa (Payne *et al.*, 1971; Kottelat, 1997; Lehnert *et al.*, 2020). Thus, as the type locality of *S. salar* is "European seas and rivers" (translated from Latin; Linnaeus, 1758: 308), the North American populations of Atlantic salmon cannot belong to *S. salar*. Thus, a taxonomic revision is required to identify morphological characters to reliable diagnose this lineage. However, as the Atlantic salmon is subject to protective measures in North America with major conservation issues (*e.g.*, Gibson, 2017; Dadswell *et al.*, 2022), it would be irresponsible to call the North American lineage *Salmo* sp. because a taxon needs to be named to be clearly mentioned in the legislative texts and then to be protected (Denys, 2021). Pending the taxonomic revision, the North American lineage should be still named as *S. salar* but it needs to be distinct from the European populations and considered as an Evolutionary Significant Unit (ESU; see Mayden and Wood, 1995) when considering the spatial distribution of genetic diversity), or an Operational Conservation Unit (OCU; Dodson *et al.*, 1998) to reflect ESUs and their interaction with socio-economic issues.

Some Atlantic salmon populations are landlocked in lakes in North America as well as north-eastern Europe (Berg, 1948; Scott and Crossman, 1973; Berg, 1985). These non-anadromous populations have smaller sizes and a lower fecundity, with some variabilities between them (Hutchings *et al.*, 2019). Girard (1853) as well as Jordan and Evermann (1896) who followed McCarthy (1894) described new taxa of landlocked salmon: respectively *Salmo sebago* from the Lake Sebago (southern Maine, USA) and *Salmo salar ouananiche* from the Saguenay River (Québec, Canada). These populations were trapped by the ice rising during the last maximum ice age around 10,000 years ago and independently lost their anadromous behaviour (Bourret *et al.*, 2013; Lumme *et al.*, 2015; Kjærner-Semb *et al.*, 2020). It is also true in a smaller scale with the Lake Saint-Jean where a double origin of landlocked populations was highlighted (Tessier and Bernatchez, 2000). Perrier *et al.* (2013) found no common signature of freshwater life between these last populations and the one from Lake Musquaro. Moreover, anadromous and landlocked species are not distinguishable based on morphometry (Claytor and MacCrimmon, 1988). Thus, given our state of knowledge, we consider landlocked populations belonging to the same species as anadromous populations.

Remark

Kottelat (1997: 140) hypothetized that the nomen *Salmo omiscomaycus* Walbaum (ex Pennant), 1792: 65 would correspond to *S. salar* expecting to find the old nomen corresponding to the North American lineage. But Kendall (1912: 51) classified it among the genus *Percopsis* (Percopsidae). This classification *Percopsis omiscomaycus* is still valid (Fricke *et al.*, 2021).

Distribution in SPM

The presence of Atlantic salmon in Saint-Pierre and Miquelon is anecdotal and its fishery in freshwaters is strictly forbidden (CPPMA, 2013). Old references mentioned this species at Langlade and Miquelon; also, during the 1960s, fishers reported that the Dolisie stream at Langlade had an abundance of salmon. Nowadays, this species may occur only in small number in the Belle-Rivière River. Studies revealed that some parr are caught every year in its tributary, the Fourche Gauche stream, which is connected to several ponds. But, while no adult specimen has been recently observed, it has been established that there may be a residual landlocked population living upstream. Fishers' testimonies from the 1950s mentioned many captures of *peel salmons* (corresponding to landlocked salmons in Newfoundland) support this hypothesis (CPPMA, 2013; R. Langlois FTP-SPM, pers. com.).

Genus *Salvelinus* Richardson, 1836

Salvelinus Richardson (ex Nilsson), 1836: 169 [subgenus of *Salmo* Linnaeus, 1758: 308; masculine; type species: *Salmo salvelinus* Linnaeus, 1758; type by absolute tautonymy; see Eschmeyer (1990: Appendix A)].

Baione DeKay, 1842: 244 (Feminine; type species: *Baione fontinalis* DeKay, 1842; type by monotypy).

Umbla Rapp, 1854: 171 (Feminine; type species: *Salmo umbla* Linnaeus, 1758; type by absolute tautonymy).

Cristivomer Gill & Jordan *in* Jordan, 1878: 356, 359 [Masculine; type species: *Salmo namaycush* Walbaum, 1792;

type by subsequent designation in Jordan and Gilbert (1883: 317)].

***Salvelinus fontinalis* (Mitchill, 1814) – NATIVE** (Fig. 1)

Salmo fontinalis Mitchill, 1814: 12 [type locality: Connetquot River, Connetquot River State Park, Long Island, New York, USA, 40°47.1714'N, 73°10.1134'W; neotype: PSU 11387 (Fig. 1) designated by Stauffer and King (2014: 561)].

Salmo alleganiensis Rafinesque, 1820: 176 (type localities: Alleghany and Monongahela rivers, USA; no types known)/

Salmo canadensis Griffith & Smith, 1834: 474, Pl. 41 (type locality: Canada; no types preserved).

Salmo erythrogaster DeKay, 1842: 236, Pl. 39 (fig. 136) (type localities: Indian Lake, Hamilton County; Lake Janet, St. Lawrence County; Franklin County; and Essex County, New York; Silver Lake, Pennsylvania, USA; no types known).

Baione fontinalis DeKay, 1842: 244, Pl. 20 (fig. 58) (type locality: Spring in Rockland County, New York, USA; syntypes: New York State coll. (whereabouts unknown); independent of *Salmo fontinalis* Mitchill 1814 which DeKay treats on p. 235).

Salmo immaculatus Storer, 1850: 264 [type locality: Brook flowing into Red Bay, Labrador, Canada; holotype: ?MCZ 32955 according to Fricke *et al.* (2021)].

Salmo hudsonicus Suckley, 1861: 310 (type locality: Hudson Bay and tributaries, New York, USA; Labrador and Newfoundland, Canada; syntypes: USNM 3594).

Salvelinus timagamiensis Henn & Rinckenbach, 1925: 131, Pls 8-9 (figs 1-3) [Type locality: White Pine Lake, Gamble Township, Timagami Forest Reserve, Ontario, Canada; holotype: FMNH 70514 (ex CM 7969); paratypes: FMNH 70515 (Ibarra and Stewart, 1987: 77)].

Salvelinus kingi Stauffer, 2020:5, Figs 3, 4b, 6b) (Type locality: Cosby Creek, Pigeon / French Broad drainage, Great Smoky Mountains National Park, Haywood County, Tennessee State, USA, 35°44'53"N, 83°12'01"W; holotype: PSU 13088; paratypes: PSU 11392).

Salvelinus angustus Stauffer, 2020: 7, Figs 3c, 4c, 5 (type locality: Little Greenbrier Creek, Pigeon / French Broad drainage, Great Smoky Mountains National Park, Haywood County, Tennessee State, USA, 35°44'16"N, 83°16'40"W; holotype: PSU 13087; paratypes: PSU 11393).

Salvelinus multidentatus Stauffer, 2020: 8, Figs 4d, 6d, 7 (type locality: Indian Camp Creek, Pigeon / French Broad drainage, Great Smoky Mountains National Park, Haywood County, Tennessee State, USA, 35°45'56"N, 83°15'14"W; holotype: PSU 13089; paratypes: PSU 11391).

Figure 1. – *Salvelinus fontinalis* (Mitchill, 1814): neotype PSU 11387, Connetquot River, Connetquot River State Park, Long Island, New York, USA, 40°47.1714'N, 73°10.1134'W; credit photo J.R. Stauffer Jr. PSU.

Morphological diagnosis

Salvelinus fontinalis differs from other *Salvelinus* species by having the caudal fin straight to slightly emarginate (*vs*. forked); dorsal and caudal fins with distinct, dark, wavy lines or blotches (*vs*. without dark, wavy lines on dorsal and caudal fins), lower fins with pure white leading edges usually followed by black (*vs*. lower fins with pure white leading edges, but not usually followed by black), back usually with vermiculations (*vs*. back usually with spots), sides with pink or red spots, many of which have blue borders (*vs*. sides with white, creamy, pink, or reddish spots, not extending onto fins), young with 8-10 regularly arranged parr marks on sides (*vs*. parr marks vague or irregular, not well defined) (Scott and Crossman, 1973).

Molecular delineation

The molecular delineation of *Salvelinus fontinalis* is supported by genomic (RADseq genotyping), mitochondrial (mitochondrial DNA RFLP, 12S, 16S, ATPase6, COI, COIII, Cyt*b*, CR/dloop) and nuclear (GH1C, ITS1, ITS2, microsatellites, RAG1) data (*e.g.*, Vitic and Strobed, 1996; Angers and Bernatchez, 1998; Crespi and Fulton, 2004; Crête-Lafrenière *et al.*, 2012; Moore *et al.*, 2015; Lecaudey *et al.*, 2018; Gehri *et al.*, 2021; Osinov *et al.*, 2021).

Time divergence

Salvelinus fontinalis is the sister species to *S. namaycush* (Walbaum, 1792) and their common ancestor is estimated at around 8 MYA (Lecaudey *et al.*, 2018).

Taxonomy

There is remarkable phenotypic plasticity within populations of *S. fontinalis* (McGlade and MacCrimmon, 1979; Stauffer and King, 2014; Kazyak *et al.*, 2015, 2022; Weathers *et al.*, 2019; Stauffer, 2020; White *et al.*, 2021), including the differentiation between juveniles anadromous and resident fish (Morinville and Rasmussen, 2008). There is genetic structure especially by drainages and lakes (Gyllensten, 1985; Ferguson *et al.*, 1991; Perkins *et al.*, 1993; Ward *et al.*, 1994; Danzmann and Ihssen, 1995; Angers and Bernatchez, 1998; Castric *et al.*, 2001; Ferchaud *et al.*, 2020; Kazyak *et* *al.*, 2022). Danzmann *et al.* (1998) delimited at least three evolutionary lineages (Mississippian, Atlantic and Acadian lineages) due to allopatric events during the last Ice Age. However, some studies highlighted the absence of correlation between morphological and molecular data (Kazyak *et al.*, 2015; Weathers *et al.*, 2019; White *et al.*, 2021). Stauffer (2020) observed three brook trout populations from the Great Smokey Mountains National Park (Tennessee). He noticed distinct morphological characters from each of the Smokey Mountain populations in comparison to the population from which the neotype of *S. fontinalis* belongs. He concluded that each population belonged to distinct species: *S. kingi* Stauffer, 2020, *S. multidentatus* Stauffer, 2020 and *S. angustus* Stauffer, 2020. However, White *et al.* (2021) analysed more samples from the same area and other locations, and they concluded that the morphological differences observed by Stauffer (2020) are only phenotypic plasticity considered these three new species are not valid (White *et al.*, 2021).

Nomenclatural note

White *et al.* (2021: 743) considered the three new species described by Stauffer (2020) as invalid and synonyms of *S. fontinalis*. However, none of these names are mentioned in the manuscript, which makes these potential synonymizations ambiguous. The nomenclatural change is, in consequence, not valid. Here, we consider *S. kingi*, *S. multidentatus* and *S. angustus* as junior synonyms of *S. fontinalis*.

Distribution in SPM

S. fontinalis, or brook trout, occurs in the main rivers and some ponds of the archipelago (Briand *et al.*, 2021; Viana *et al.*, 2022). Nevertheless, its population of the archipelago declined due to the fishing pressure and the presence of obstacles preventing the migration within streams. They are also infected by three parasites which were introduced (Briand *et al.*, 2021): the copepod *Salmincola edwardsii* (Olsson, 1869), the cestode *Eubothrium salvenili* (Schrank, 1790) Nybelin, 1922 and the digenea *Posthodiplostomum cuticola* (von Nordmann, 1832) Dubois, 1936.

Order Gasterosteiformes
Family Gasterosteidae Bonaparte, 1831
Genus *Apeltes* DeKay, 1842

Apeltes DeKay, 1842: 67 (Masculine; type species: *Gasterosteus quadracus* Mitchill, 1815; type by original designation)

***Apeltes quadracus* (Mitchill, 1815) – NATIVE** (Fig. 2)

Gasterosteus quadracus Mitchill, 1815: 430, Pl. 1 [type locality: New York, USA; no types known but a drawning is available (Fig. 2A); misspelled *quadratus* by Linsley (1844: 61)].

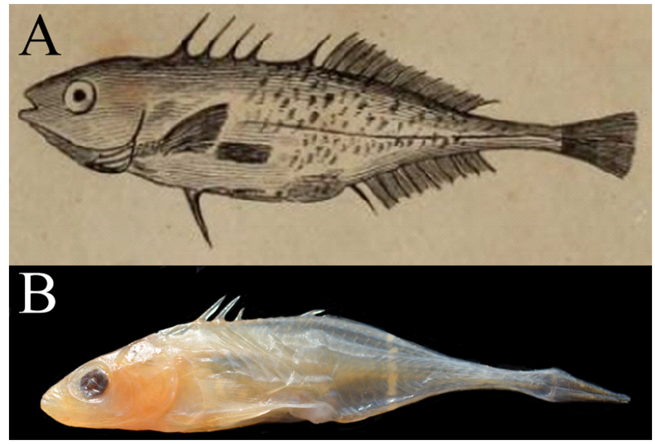

Figure 2. – *Apeltes quadracus* (Mitchill, 1815): drawning of an individual from New York, USA given by Mitchill (1815: 430, Pl. 1) with its species description (**A**); MNHN-IC-2022-0021, 26.9 mm SL, Saint-Pierre and Miquelon, Saint-Pierre Island, Airport Pond (**B**).

Gasterosteus apeltes Cuvier *in* Cuvier & Valenciennes, 1829: 505 [type locality: Philadelphia; syntypes: MNHN-IC-0000-4062 (Bertin and Estève, 1950: 40)].

Gasterosteus millepunctatus Ayres, 1843: 294, Pl. 12 (fig. 3) (type locality: New York and Connecticut, USA; no types known).

Morphological diagnosis

Apeltes quadracus is distinguished from other gasterosteids by IV (rarely V) dorsal spines (*vs.* III or more than IV dorsal spines) and by the absence of bony plate on the body (*vs.* lateral bony plate present or absent) (Scott and Crossman, 1973).

Molecular delineation

Its molecular delineation is supported by genomic (whole genome, RADseq genotyping), mitochondrial (mitogenome, 12S, 16S, COI, ATPase 6, Cyt*b*, CR/dloop) and nuclear (RAG1, MLL, zic1, myh6, Ptr, tbr1, ENC1, gylt, SH3PX3, plagl2, and sreb2) data (*e.g.*, Mattern, 2004; Kawahara *et al.*, 2009; Guo *et al.*, 2019; Liu *et al.*, 2021; Maduna *et al.*, 2022).

Cytogenetics

Apeltes quadracus differs from other gasterosteids by its sexual chromosomes having a ZW genetic sex determination system (*vs.* XY) (Chen and Reisman, 1970; Ross *et al.*, 2009). However, some populations may have heteromorphic sex chromosomes, providing evidence for sex chromosome diversity in this species (Urton *et al.*, 2011).

Distribution

This species occurs only in lagoons and ponds in contact with marine waters.

Genus *Gasterosteus* Linnaeus, 1758

Gasterosteus Linnaeus, 1758: 295 [Masculine; type species: *Gasterosteus aculeatus* Linnaeus, 1758; type by subsequent designation by Jordan and Gilbert (1883: 393); on official ICZN list (Opinion 77, Direction 56; ICZN, 1922: 73, 1956: 340); misspellings include *Gastrosteus*, *Gasterostius* (Nau, 1787: 108) and *Garterosteus* (Griffith and Smith, 1834: 189)].

Obolarius Tilesius (ex Steller), 1811: 225 (Masculine; type species: *Obolarius aculeatus* Tilesius, 1811).

Gasteracanthus Pallas, 1814: 228 (Masculine; type species: *Gasteracanthus cataphractus* Pallas, 1814; type by subsequent designation).

Leiurus Swainson, 1839: 175, 242 [subgenus of *Gasterosteus* 1758: 295; masculine; type species: *Gasterosteus aculeatus* Linnaeus, 1758; type by subsequent designation by Swain (1883: 276)].

Gladiunculus Jordan & Evermann, 1927: 504 (subgenus of *Gasterosteus* 1758: 295; masculine; type species: *Gasterosteus gladiunculus* Kendall, 1896; type by monotypy and by absolute tautonymy).

Gasterosteus aculeatus Linnaeus, 1758 – NATIVE (Fig. 3)

Gasterosteus aculeatus Linnaeus, 1758: 295 [type locality: Europe; syntypes: LSL 29-31 (Wheeler, 1985: 43; Fig. 3A)].

Gasterosteus bispinosus Walbaum, 1792: 450 (type locality: New York, USA; no types known).

Gasterosteus teraculeatus Lacepède, 1801: 295, 296 (unneeded new nomen for *Gasterosteus aculeatus* Linnaeus, 1758: 295).

Gasterosteus biaculeatus Shaw, 1803: 608 (type locality: New York, USA; unneeded new name for *Gasterosteus bispinosus* Walbaum, 1792: 450).

Gasteracanthus cataphractus Pallas, 1814: 229 (type locality: Kamchatka, Russia; no types known).

Gasterosteus gymnurus Cuvier (ex Willughby), 1829: 170 [type locality: England and northward France; no types known; based on *Pisciculus aculeatus* of Willughby (1686: 341)].

Gasterosteus leiurus Cuvier *in* Cuvier & Valenciennes, 1829: 481, 487, Pl. 98 (fig. 4) [type localities: France; Germany; syntypes: MNHN-IC-0000-7088, MNHN-IC-0000-7151 (Monod, 1973: 281)].

Gasterosteus trachurus Cuvier *in* Cuvier & Valenciennes, 1829: 481, 487, Pl. 98 (fig. 1) (type localities: France, Germany; syntypes: ?NMW 6918).

Gasterosteus semiarmatus Cuvier *in* Cuvier & Valenciennes, 1829: 493 [type localities: Le Havre and River Braie near Abbeville, France; Syntypes: MNHN-IC-0000-2347, MNHN-IC-0000-2348 and MNHN-IC-0000-7078 (Bertin and Estève, 1950: 34-35)].

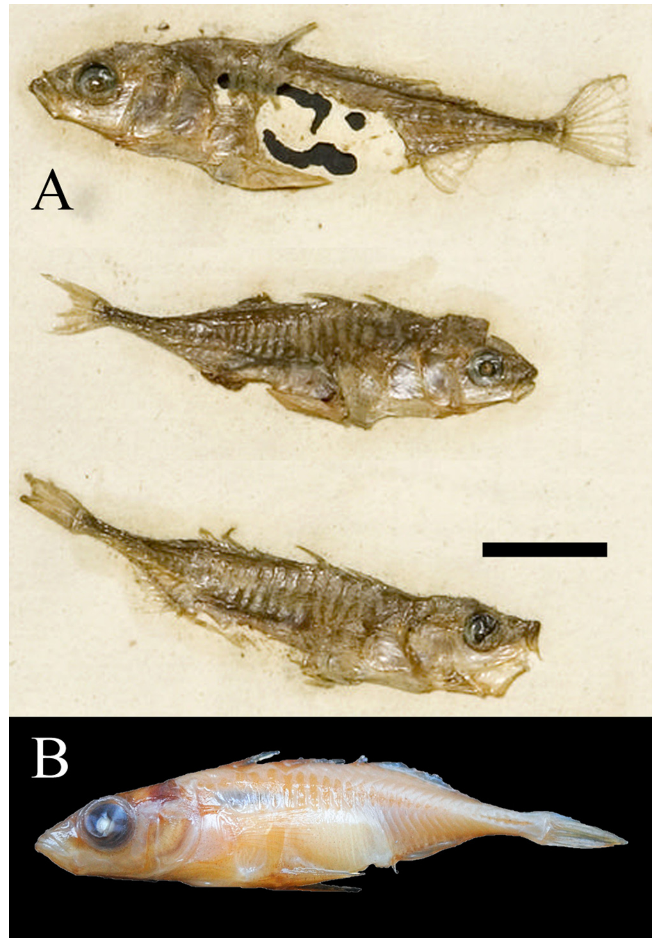

Figure 3. – *Gasterosteus aculeatus* Linnaeus, 1758: syntypes LSL 29-31; scale bar = 1cm; with the permission of the Linnean Society of London (**A**); MNHN-IC-2022-0022, 33.7 mm SL, Saint-Pierre and Miquelon (**B**).

Gasterosteus semiloricatus Cuvier *in* Cuvier & Valenciennes, 1829: 494 [type localities: Somme River, around Paris, Oise, La Rochelle, Normandy, Caen, Hable d'Ault, Le Treport, Berlin; syntypes: whereabouts unknown; the lot of specimens MNHN-IC-0000-2347 was considered as syntypes of *G. semiloricatus* according to Bertin (1925: 154), however, as they came from Le Havre so one of the type locality of *G. semiarmatus* and confirmed as well by Monod (1973: 281), this designation might be a mistake].

Gasterosteus argyropomus Cuvier *in* Cuvier & Valenciennes, 1829: 498 [type locality: Florence, Italy; syntypes: MNHN-IC-0000-0677 (Bertin and Estève, 1950: 35)].

Gasterosteus brachycentrus Cuvier *in* Cuvier & Valenciennes, 1829: 499, Pl. 98 (fig. 2) [type locality: Florence, Italy; syntypes: MNHN-IC-0000-0694 and MNHN-IC-0000-7097 (Bertin and Estève 1950: 35), SMF 1181].

Gasterosteus tetracanthus Cuvier *in* Cuvier & Valenciennes, 1829: 499 [type locality: Florence, Italy; holotype: MNHN-IC-0000-1821 (Bertin and Estève, 1950: 35)].

Gasterosteus obolarius Cuvier *in* Cuvier & Valenciennes, 1829: 500 (type locality: Kamchatka, Russia; no types known).

Gasterosteus noveboracensis Cuvier *in* Cuvier & Valenciennes, 1829: 502, Pl. 98 (fig. 3) (type locality: New York, USA; holotype: MNHN-IC-0000-7074 (Bertin and Estève, 1950: 35)].

Gasterosteus niger Cuvier *in* Cuvier & Valenciennes 1829: 503 [type locality: Newfoundland, eastern Canada; syntypes: MNHN-IC-0000-3057 (Bertin and Estève, 1950: 36); the nomen *Gasterosteus niger* Cuvier, 1829: 170 is erroneous].

Gasterosteus spinulosus Yarrell (ex Jenyns), 1835: 350 (type locality: Edinburgh, Scotland; no types known).

Gasterosteus loricatus Reinhardt, 1837: 114, 193 (type locality: Greenland; no types known).

Gasterosteus dimidiatus Reinhardt, 1837: 114, 137, 193 (type locality: Greenland; syntypes: whereabouts unknown).

Gasterosteus ponticus Nordmann, 1840: 380, 613, Pl. 3 (fig. 11) [type locality: Tauria (Crimea), Black Sea; syntypes: MNHN-IC-0000-7098 (Bertin and Estève 1950: 363), NMW 77244].

Gasterosteus biarmatus Nordmann, 1840: 381 (type locality: Lagoons near Tarkanckut, Crimea; no types known).

Gasterosteus biaculeatus DeKay, 1842 (ex Mitchill): 64, Pl. 3 (fig. 9) (type locality: New York, USA; no types known; junior homonym of *Gasterosteus biaculeatus* Shaw, 1803: 608).

Gasterosteus neoboracensis DeKay, 1842: 66, Pl. 6 (fig. 17) (type locality: New York, USA; no types known).

Gasterosteus nemausensis Crespon, 1844: 283 (type locality: Nîmes, France; no types known) .

Gasterosteus quadrispinosa Crespon, 1844: 283 (type locality: Vistre River and ditches around Nîmes, France; syntypes: whereabouts unknown).

Gasterosteus cuvieri Girard *in* Storer, 1850: 254, Pl. 7 (fig. 1) (type localities: Bras d'Or and Red Bay, Labrador, Canada; no types known).

Gasterosteus microcephalus Girard, 1854: 133 [type locality: Tule Lake, San Joaquin Valley, California, USA; syntypes: ANSP 14275-87, ANSP 14288-89 (missing), MNHN-IC-0000-0302, UMMZ 146720 (Bertin and Estève 1950: 36; Böhlke, 1984: 103)].

Gasterosteus williamsoni Girard, 1854: 133 [type locality: upper part of Santa Clara River, Soledad Canyon, Los Angeles County, California, USA (Miller, 1960); syntypes: MNHN-IC-0000-0303 (Bertin and Estève, 1950: 36), USNM 340].

Gasterosteus plebeius Girard, 1854: 147 [type locality: salt marshes about Presidio, California, USA; Syntypes: FMNH 6038, MCZ 6706, MNHN-IC-0000-0298 (Bertin and Estève 1950: 36-37)].

Gasterosteus inopinatus Girard, 1854: 147 [type locality: a fresh water lagoon about 1 mile back of Presidio, California, USA; syntypes: MCZ 6701, MNHN-IC-0000-0300 (Bertin and Estève, 1950: 37)].

Gasterosteus serratus Ayres, 1855: [2] col. 6 [type locality: San Francisco, California, USA; holotype: apparently lost even if Monod (1973: 282) lists a syntype at MNHN].

Gasterosteus dekayi Ayres, 1855: 48 (objective synonym of *Gasterosteus biaculeatus* DeKay ; junior homonym of *Gasterosteus dekayi* Agassiz, 1850).

Gasterosteus insculptus Richardson, 1855: 356, Pl. 25 (type locality: Northumberland Sound, western Greenland; holotype: ? BMNH).

Gasterosteus pugetti Girard, 1856: 135 (type locality: Fort Steilacoom, Puget Sound, Washington, USA; no types known).

Gasterosteus intermedius Girard, 1856: 135 (type locality: Cape Flattery, Washington, USA; no types known).

Gasterosteus elegans Blanchard, 1866: 234, Fig. 37 [type locality: between Cadillac and Langon, Gironde, southwestern France; syntypes: MNHN-IC-0000-6673 (Bertin and Estève 1950: 38)].

Gasterosteus neustrianus Blanchard, 1866: 220, Fig. 28 [type locality: Brooks in Harfleur and Gournay, France; syntype: MNHN-IC-0000-7114 (Bertin and Estève, 1950: 37)].

Gasterosteus bailloni Blanchard, 1866: 231, Fig. 34 [type locality: Abbeville, France; syntypes: MNHN-IC-0000-7151, MNHN-IC-0000-7153 (Bertin and Estève, 1950: 37)].

Gasterosteus argentatissimus Blanchard, 1866: 232, Figs. 35-36 [type locality: Brooks near Avignon, France; syntypes: BMNH 1883.7.4.5-10, MNHN-IC-0000-6675, MNHN-IC-0000-6678 (Bertin and Estève, 1950: 38), USNM 21140].

Gasterosteus algeriensis Sauvage, 1874: 17 [type locality: Algeria; syntypes: MNHN-IC-0000-5123 (Bertin and Estève, 1950: 38)].

Gasterosteus suppositus Sauvage, 1874: 11 (type locality: New York, USA; based on *Gasterosteus noveboracensis* Dekay, 1842: 66)

Gasterosteus texanus Sauvage, 1874: 15, Pl. 1 (fig. 5-5a) [type locality: Texas, USA; holotype: MNHN-IC-0000-7076 (Bertin and Estève, 1950: 38)].

Gasterosteus atkinsii Bean, 1879: 67 [type locality: Schoodic Lakes, Maine, USA; Syntypes: USNM 2249; misspelled *atkinsi* (Froese and Pauly, 2021)].

Gastrosteus hologymnus Regan, 1909: 436 (type locality: Rome, Italy; syntypes: BMNH 1852.8.17.19-22; original genus should have been *Gasterosteus*).

Gasterosteus santaeannae Regan, 1909: 437 (type locality: Colton, Santa Ana River, California, USA; syntypes: BMNH 1894.2.22.15-17).

Gasterosteus williamsoni japonicus Franz, 1910: 19, Pl. 3 (fig. 10) [type locality: Misaki, Japan; syntypes: ZSM destroyed in World War II (Neumann 2006: 275)].

Gasterosteus aculeatus var. *messinicus* Stephanidis, 1971: 202, Fig. 10 (not available, infrasubspecific; type locality: Pamissos River near Messini, Greece).

Morphological diagnosis

Gasterosteus aculeatus is distinguished from *G. wheatlandi* Putnam, 1867 in having pelvic fins with one spine with one well-developed pointed cusp at the base (*vs.* two cusps), one pelvic soft fin rays (*vs.* two pelvic soft fin ray), and no particular pigmentation along the sides (*vs.* presence of many black spots) (Scott and Crossman, 1973). It is distinguished from *G. nipponicus* Higushi, Sakai & Goto, 2014 by the lateral plates incomplete or complete becoming gradually smaller from the trunk to the caudal peduncle (*vs.* strictly complete abruptly smaller from just above the anus), depth of the plate just above the anus is > 60% of that of the deepest plate (*vs.* < 60%), and caudal keels bony and thick (*vs.* thin and membranous) (Higuchi *et al.*, 2014).

Molecular delineation

The molecular delineation of *G. aculeatus* is supported by genomic (AFLP, whole genome, RADsequencing, SNP), mitochondrial (mitochondrial DNA RFLP, mitogenome, Cyt*b*, ND5/6) and nuclear (allozymes, Trim24b) data (*e.g.*, Halglund *et al.*, 1992; Higuchi and Goto, 1996; Yamada *et al.*, 2001; Takahashi *et al.*, 2016; Ravinet *et al.*, 2018; Fang *et al.*, 2018, 2020; Yoshida *et al.*, 2018; Kakioka *et al.*, 2020; Dahms *et al.*, 2021; Liu *et al.*, 2021).

Time divergence

Gasterosteus aculeatus is sister to *G. nipponicus* and their common ancestor is estimated at around 0.68 to 1 MYA (Ravinet *et al.*, 2018; Kakioka *et al.*, 2020).

Ecology

Gasterosteus aculeatus is an anadromous species breeding in freshwaters with numerous non-anadromous populations spending their total life cycle in brackish and fresh waters (Bell and Foster, 1994), whereas *G. wheatlandi* breeds only in brackish waters (McInerney, 1969). *Gasterosteus nipponicus* is mainly anadromous species but also has some brackish-resident populations (Higuchi and Goto, 1996; Arai *et al.*, 2003a, b, 2020; Higuchi *et al.*, 2014) without freshwater-resident populations (Arai *et al.*, 2020) due to the absence of tolerance to freshwaters (Ishikawa *et al.*, 2016).

Reproductive isolation

The reproductive isolation between *G. aculeatus* and *G. wheatlandi* is well documented (Rowland, 1970; Buth and Haglund, 1994; Baube, 2008). The hybridization between *G. aculeatus* and *G. nipponicus* is considered rare (Higuchi and Goto, 1996), even if some introgression has been noted (Yamada *et al.*, 2001; Ravinet *et al.*, 2018; Kakioka *et al.*, 2020). Mating of male *G. aculeatus* and female *G. nipponicus* results in sterile male offspring lacking normal sperm because the spermatocytes disappear during spermatogenesis (Kitano *et al.*, 2007).

Cytogenetics

Gasterosteus spp. are characterized by fusions between sex chromosomes (chromosome 19) and autosomes creating neo-Y chromosomes (Kitano *et al.*, 2009; Ross *et al.*, 2009; Yoshida *et al.*, 2014; Sardell *et al.*, 2021). However, *G. aculeatus* is the only species of this genus for which there is no fusion between the chromosome 19 Y and any autosome (*vs.* chromosome 19 fused with the autosome 9 for *G. nipponicus* and with autosome 12 for *G. wheatlandi*).

Ethology

Male courtship behaviour of *G. aculeatus* is characterized by a zigzag approach, (*vs.* a dancing approach fo *G. wheatlandi* and a rolling approach for *G. nipponicus*) (Ishikawa and Mori, 2000; Ishikawa *et al.*, 2006; Kitano *et al.*, 2007, 2008; Baube, 2008).

Life history traits

Gasterosteus aculeatus lays larger eggs than *G. nipponicus* (1.69 mm ± 0.054 *vs.* 1.36 mm ± 0.050) (Kume, 2011).

Taxonomy

Gasterosteus aculeatus is distributed in all the Holarctic area: North America, Europe, North Africa and Eastern Asia (*e.g.*, Scott and Crossman, 1973; Masuda *et al.*, 1984; Arnoult, 1986; Kottelat and Freyhof, 2007). It has strong polymorphism, especially regarding to plate morphs within every continent (*i.e.,* the number of bony plates on the flanks covering it totally "*trachurus*" meaning "rough until the tail" in Greek, partially "*semiarmatus*" meaning "semi armed" in Latin) or not "*leiurus*" or "*hologymnurus*" meaning respectively "smooth" in Latin and "totally naked" from Greek) (*e.g.*, Bertin, 1925; Münzing, 1963; Bakker and Sevenster, 1988; Barrett, 2010). Forty-seven species and subspecies were described all over the world based on plate polymorphisms; however, these phenotypes do not follow any phylogenetic or any geographical patterns (Denys *et al.*, 2015; Fang *et al.*, 2020; Roberts Kingman *et al.*, 2021).

Lateral plate number is controlled by the ectodysplasin-A Eda gene, with a stronger expression in adults than juveniles as well as in populations living in marine waters which are fully plated, whereas freshwater populations are less shielded (see Barrett, 2010). There is indeed a coastal-inland gradient with a positive relationship between salinity and plate numbers (Raeymaekers *et al.*, 2007), activating firstly the anterior plates development, followed by posterior plates and finally middle plates (Bell, 2001). Freshwater populations are adapted to their environment by plate reduction (*e.g.*, Le Rouzic *et al.*, 2011) allowing escape capacity into vegetations whereas marine populations would need to have defensive structures against predators (Barrett, 2010; Wasserman *et al.*, 2021; Yanos *et al.*, 2021). Marine, fully-plated threespine sticklebacks colonized freshwaters basins many times based on allelic substitution in the Eda gene (Leinonen *et al.*, 2012; Fang *et al.*, 2020; Kakioka *et al.*, 2020), and with the absence of marine predators, the plateless phenotype increases in frequency after only a few generations (Roberts Kingman *et al.*, 2021).

According to mitochondrial and genomic data, several evolutionary lineages (*e.g.*, Pacific, Northern Atlantic and Mediterranean) have been highlighted with several trans-oceanic migrations occurring during the different ice ages of the Pleistocene (45,000 to 260,000 years ago) (Ortí *et al.*, 1994; Mäkinen and Merilä, 2008; Fang *et al.*, 2018). Globally, we have no reason to consider these evolutionary lineages as distinct taxa than *G. aculeatus*, except maybe the Mediterranean lineage (see Lucek and Seehausen, 2015). Nevertheless, several cases of ecological speciation with reproductive isolation between sympatric populations have been highlighted in several lakes of North America and in Lake Constance in Switzerland (*e.g.*, Rundle and Schluter; 2004; Gelmond *et al.*, 2009; Marques *et al.*, 2019). Moreover, there is a high variability of breeding period between these lineages and between ecotypes (Ishikawa and Kitano, 2020). So, the existence of a species recently speciated cannot be excluded.

Nomenclatural note

The nomen *Gasterosteus biaculeatus* Mitchill, 1815 has been considered available by several references (Monod, 1973: 281; Smith, 1986: 277). However, the text given by Mitchill (1815: 430) does not appear to be an original description but an identification of *Gasterosteus biaculeatus* Shaw, 1803. This nomen is then not available.

Franz (1910: 19) described a susbspecies of stickleback *Gasterosteus williamsoni japonicus* from Misaki (South Japan) where *G. aculeatus* and *G. nipponicus* may co-occur. The description and the drawing of this taxon highlights the presence of bony plate to the second dorsal-spine. Thus, this nomen corresponds to the freshwater phenotype of *G. aculeatus*, being then its junior synonym.

Remark

Gasterosteus islandicus Sauvage, 1874 is currently valid according to morphological data (Kottelat, 1997; Kottelat and Freyhof, 2007). However, mitochondrial data do not allow its discrimination from *G. aculeatus* (Denys *et al.*, 2015). A taxonomical revision is needed to determine if this species is valid or if it should be considered as junior synonym of *G. aculeatus*.

Distribution

This species occurs only in lagoons and ponds in contact with marine waters.

IUCN status

LC (NatureServe, 2019b).

Genus *Pungitius* Coste, 1848

Pungitius Coste, 1848: 588 (Masculine; type species: *Gasterosteus pungitius* Linnaeus, 1758; type by subsequent designation or tautonymy).

Pygosteus Gill (ex Brevoort), 1861: 39 [Masculine; type species: *Gasterosteus occidentalis* Cuvier, 1829; type by subsequent designation by Jordan and Gilbert (1877: 93)].

Gasterostea Sauvage, 1874: 7, 29 [subgenus of *Gasterosteus*, 1758: 295; feminine; type species: *Gasterosteus pungitius* Linnaeus, 1758; type by subsequent designation by Jordan (1919: 377); objective synonym of *Pungitius* Coste, 1848].

***Pungitius pungitius* (Linnaeus, 1758) – NATIVE** (Fig. 4)

Gasterosteus pungitius Linnaeus, 1758: 296 [type locality: Europe; syntypes: LSL 34-35 (Wheeler, 1985: 44) (Fig. 4A)].

Gasterosteus occidentalis Cuvier *in* Cuvier & Valenciennes, 1829: 509 [type locality: Newfoundland; holotype: MNHN-IC-0000-7112 (Bertin and Estève, 1950: 39)].

Gasterosteus concinnus Richardson, 1836: 57 [type locality: Saskatchewan (53°N) to Great Bear Lake (65°N), Canada; syntypes: whereabouts unknown].

Gasterosteus mainensis Storer, 1837: 465 (type locality: Kennebeck County, Maine, USA; no types known).

Gasterosteus nebulosus Agassiz, 1850: 310, Pl. 4 (fig. 2) (type locality: Mouth of Pic River, Lake Superior; syntypes: MCZ 6696, ?MCZ 58765, USNM 120414).

Gasterosteus dekayi Agassiz, 1850: 311 (type locality: New York and Massachusetts, USA; no types known).

Gasterosteus burgundianus Blanchard, 1866: 240, Fig. 40 [type locality: Dijon, Côte d'Or, France; syntypes: MNHN-IC-0000-7109; Bertin and Estève (1950: 39) mentioned MNHN-IC-0000-7103 as syntypes by error).

Figure 4. – *Pungitius pungitius* (Linnaeus, 1758): syntypes LSL 34 and 35; scale bar = 1cm; with the permission of the Linnean Society of London (**A**); MNHN-IC-2022-0020, 32.7 mm SL, Saint-Pierre and Miquelon, Saint-Pierre Island, Milieu Pond (**B**).

Gasterosteus (Gasterostea) blanchardi Sauvage, 1874: 32, Pl. 1 (fig. 16-16a) [type locality: New York, USA; syntypes: MNHN-IC-0000-7111, MNHN-IC-0000-9383 to 9385 (Bertin and Estève, 1950: 40), USNM 21139].

Gasterosteus pungitius brachypoda Bean, 1879: 129 [type locality: Oosooadlin Mountain, Cumberland Gulf, Greenland, elevation 1500 feet; syntypes: NMC 58-13, USNM 21738, USNM 21766, USNM 21768, USNM 21771, USNM 21773, USNM 21773a, USNM 21773c, USNM 21773d (McAllister, 1965: 10)].

Pygosteus pungitius forma *trachura* Bertin, 1925: 122 (not available, infrasubspecific).

Pygosteus pungitius forma *semiarmata* Bertin, 1925: 122 (not available, infrasubspecific).

Pygosteus pungitius forma *carinata* Bertin, 1925: 122 (not available, infrasubspecific).

Morphological diagnosis

Pungitius pungitius is distinguished from other *Pungitius* species by the presence of a keel constituted by lateral plates on the caudal peduncle only and reaching the last anal fin ray (4-12 lateral plates, *vs*. 0-5 or more than 28) except in northern France where a hybrid zone between *P. pungitius* and *P. laevis* was highlighted and populations can have no keel (Denys *et al*., 2018; Matsumoto *et al*., 2021). It is further distinguished from *P. hellenicus* Stephanidis, 1971 and *P. tymensis* by having 8-11 dorsal fin spines (*vs*. II-VI and X-XIII, respectively) (Keivany *et al*., 1997; Shedko *et al*., 2005). It is also therefore distinguished from the two other French species *P. laevis* (Cuvier, 1829) and *P. vulgaris* (Mauduyt, 1848), by a flat head with a straight or slightly concave snout (*vs*. concave, straight or slightly convex), typically 9-10 dorsal spines (*vs*. typically VIII-IX), typically 10-11 dorsal soft rays (*vs*. 9-10), typically 9-10 anal soft rays (*vs*. 8-9), 0-12 scutes on the caudal peduncle (*vs*. 0-4) with the lateral plates keel reaching the last anal fin ray, a longer post-dorsal length (11.7%-20.6% of the standard length SL, *vs*. 9.2%-16.2% and 11.1%-15.6% for, respectively, *P. laevis* and *P. vulgaris*), a longer caudal peduncle length (13.3%-20.0% SL, *vs*. 10.1%-17.8% and 12.7%-16.9%, Fig. 4), the smallest ratio caudal peduncle depth/length (11.8%-21.9% *vs*. 15.7%-34.5% and 19.1%-27.2%), and longer pelvic fin lengths (7.3%-14.4% SL, *vs*. 5.3%-10.6% and 5.6%-9.6%) (Denys *et al*., 2018).

Molecular delineation

The molecular delineation of *Pungitius pungitius* is supported by genomic (RADsequencing, SNP), mitochondrial (mitogenome, COI, ATPase 6, Cyt*b*) and nuclear (myh6, plagl2, RNF213, SH3PX3, sreb2) data (Wang *et al*., 2015, 2017, 2021; Guo *et al*., 2016, 2019; Denys *et al*., 2018).

Time divergence

Wang *et al*. (2015) did a first estimation of the divergence between *P. pungitius* and its closest sister species, *P. vulgaris* which is endemic in France as 1.38 MYA (0.88-1.95 MYA) according to mitochondrial data. However, Denys *et al*. (2018) pointed out that this estimation does not correspond to biogeographical data because the distribution areas of *P. vulgaris* and *P. laevis* look like the hydrographic areas of France during the early Pliocene, so it may be underestimated. Later, another analysis of mitochondrial and genomic data estimated the divergence at 3.48 MYA (2.48-4.68 MYA) (Wang *et al*., 2021).

Taxonomy

According to osteological data, Keivany and Nelson (2000) distinguished European and North American *P. pungitius* as two subspecies: *Pungitius pungitius pungitius* and *P. p. occidentalis* (Cuvier, 1819). Guo *et al*. (2019) support this distinction with molecular data (RADsequencing) highlighting a divergence > 3% between these lineages and consider the North American populations as a separate species *P. occidentalis*. Moreover, Teacher *et al*. (2011) estimated the splitting between North American and European populations at 1.62 MYA. However, the molecular delineation is not evident as North American populations do not form a monophyletic clade (Aldenhoven *et al*., 2010; Takahashi *et al*., 2016; Guo *et al*. 2019). However, it would be interesting to revise the North American *Pungitius* comparing them with the European populations.

Remark

The two syntypes of *Gasterosteus globiceps* MNHN-IC-0000-4081 (34.8-48.2 mm SL) from North America according to Sauvage (1874: 35), have provoked interrogations about the valid nomen to which it is synonymized. This nomen was considered first as a junior synonym of *Culaea inconstans* (Kirtland, 1840) (Eigenmann, 1886: 238; Jordan *et al*., 1930: 238), *P. pungitius* (Monod, 1973: 284; Paepke, 2002: 277), *P. pungitius occidentalis* (Cuvier, 1829) (Keivany and Nelson 2000: 118) and potentially *P. laevis* (Kottelat, 1997: 166) according to Berg (1932: 169) and Münzing (1969: 217). The morphomeristic analysis of the two syntypes following Denys *et al*. (2018) do not correspond to the redescription of *P. pungitius* with a longer predorsal, preanal and anal fin base lengths (respectively 34.5-37.1% SL *vs*. 24.0-35.5% SL, 66.8-68.8% SL *vs*. 51.1-65.0% SL, and 27.4-30.1% SL *vs*. 19.7-27.7% SL) as well as a shorter postdorsal and caudal peduncle lengths (respectively 4.5-5.9% SL *vs*. 11.7-20.6% SL, and 7.3-7.5% SL *vs*. 13.9-20.0% SL). However, the ratio depth/length of the caudal peduncle (36.5-46.7%) seems to be close to the one of the holotype of *Gasterosteus breviceps* Blanchard, 1866 (junior synonym of *P. laevis*) MNHN-IC-0000-7110 (34.5%) caught in Normandy (Denys *et al*., 2018). These two syntypes were collected by the French naturalist Lesueur (1778-1846) who was known for his expeditions in Austral Lands and North America, before being the director of the Museum of Natural History of Le Havre in Normandy in 1845 (Baglione and Crémière, 2016). The MNHN register (available via this link https://science.mnhn.fr/catalogue/cat-ichtyo-1-6649/page/85) indicates only the mention “from the collections of Lesueur” with no mention of any locality. So, it is very possible that the specimens came from Normandy and labelled erroneously from North America. Thus, we agree with Kottelat (1997: 166) concluding that *G. globiceps* should be considered as a junior synonym of *P. laevis*.

Distribution

The ninespine stickleback *P. pungitius* occurs only in lagoons and ponds connected to marine waters.

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