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Opinion

Checklist of the species of notothenioid fishes

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Abstract: We provide our perspective on the species-level taxonomy of notothenioid fishes, the dominant component of the fish fauna of Antarctica. There are 140 species in 45 genera, an increase of 15% since the previous summary in 2000. Biogeographically, 30 species are non-Antarctic, 33 are sub-Antarctic and 77 are Antarctic. The checklist is documented with footnotes that provide the rationale for our decisions. Supplementary Material provides additional details for our decisions on two species of *Pogonophryne*.

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Introduction

Once primarily of interest for their physiological adaptations for life in subzero waters, the notothenioid fishes of Antarctica are now the objects of research in other areas of biology as well as the target of an industrial fishery. They are also increasingly recognized as exemplars of marine adaptive radiation and this opens additional avenues for research in organismal biology (Bowen *et al.* 2020, Eastman 2020). Species are the vehicle of macroevolution and the entities that display components of adaptation including specialization and regression of features as well as aspects of organ system development, gene expression and population structure (Mayr & Ashlock 1991, p. 22). Biologists studying all aspects of fish biology require accurate information about the number and the scientific nomenclature of their subjects. Frequently it is difficult for those who are not specialists in a given group to grasp the taxonomic complexities related to the number, naming and validity of species. In 2000 we published a checklist of 122 species in 43 genera - the number of notothenioid species that we considered valid at that time (Eastman & Eakin 2000). The checklist was based on the 93 Antarctic species recognized in *Fishes of the Southern Ocean* (Gon & Heemstra 1990), plus the new species described after its publication, minus those placed in synonymy. We also included the non-Antarctic component of the fauna, an element absent from *Fishes of the Southern Ocean*. The checklist has apparently proven useful and has been cited 92 times, including this year, in *Scopus* (www.scopus.com), and 126 times in *Google Scholar* (www.scholar.google.com). However, the number of species has increased by 18 (15%) and we now recognize 140 species and 45 genera and believe the time is opportune for the revised checklist provided in Table I, our view of the species-level taxonomy of notothenioids.

Methods

Since the publication of our original checklist, we have monitored the literature for descriptions of new species and changes in nomenclature and rendered judgments on their validity, especially in the case of the artedidraconids where 10 new species of *Pogonophryne* have been described since 2000. The most noteworthy large-scale change since 2000 is that the South Atlantic species *Percophis brasiliensis* Quoy & Giamard 1825 has been identified as the sister lineage of notothenioids and is now included in this clade that is nested within the Perciformes (Near *et al.* 2015). Ichthyologists have different interpretations of notothenioid taxonomy and we do not attempt to accommodate these or every change in nomenclature necessitated by relationships revealed in molecular phylogenetic studies. The validity of the latter will be determined through expansion of taxonomic coverage, replication of results, and eventual adoption and usage. We retain the traditional notothenioid family names (Balushkin 2000). The species-level taxonomy presented here reflects the results of some well-substantiated molecular phylogenetic analyses including the amalgamation of the genera *Cryothenia* and *Pagothenia* into *Trematomus* (Sanchez *et al.* 2007, Kuhn & Near 2009, Dettai *et al.* 2012, Near *et al.* 2015, 2018). The polyphyly in the genus *Artedidraco* has been confirmed (Lecointre *et al.* 2011, Near *et al.* 2018), but not yet resolved with new generic names so

we retain the status quo. Next-generation DNA sequencing (RADseq) supports the monophyly of the genus *Pogonophryne* and the relationships among the species groups, but the number of species remains unsettled (Near *et al*. 2018, p. 275).

The authoritative source for fish taxonomy is *Eschmeyer's Catalog of Fishes* (www.calacademy.org), specifically the sections by Fricke *et al*. (2020a, 2020b) and Van der Laan & Fricke (2020). The existing nomenclature for notothenioids has been subjected to a recent analysis of its grammatical accuracy (Sheiko 2019) and adherence to the *International Code of Zoological Nomenclature* (www.iczn.org), and these findings have been incorporated into *Eschmeyer's Catalog*. We follow *Eschmeyer's Catalog* for the nomenclature for species, authorities and dates. We provide a reference for each of the 19 species either described or reassigned to the Notothenioidei after 2000, documentation for all other species is available in *Eschmeyer's Catalog.* Recognition of a species as a biological entity is a subjective decision, however the validity of the name applied to it is not, and the *Code* applies only to the latter. *Eschmeyer's Catalog* recognizes more species (167) than we do (140) and "assumes that all new species described in the past 10 years are valid". It is impossible for even the highly experienced ichthyologists maintaining *Eschmeyer's Catalog* to render judgment on the biological validity of each of the several hundred new species of fishes that appear in publications each year. The differences between the counts in *Eschmeyer's Catalog* and our counts are attributable to the fact that our familiarity and experience with notothenioid fauna, and knowledge of the associated literature, allows us to vet the descriptions of new species and to take a critical approach in recognizing those that show minimal morphological divergence and an undocumented amount of genetic divergence as in, for example, some recently described species of *Pogonophryne* and *Channichthys*.

Table I. Checklist of 140 notothenioid species, 30 non-Antarctic, 33 sub-Antarctic and 77 Antarctic, in 45 genera. Asterisk (*) precedes names of 19 species described after publication of Eastman & Eakin (2000) or subsequently reassigned to the Notothenioidei.

Taxa	Biogeographic distribution		
	Non-Antarctic	Sub-Antarctic	Antarctic
Perciformes			
Notothenioidei			
Percophidae (1) (Brazilian flathead)			
**Percophis brasiliensis* Quoy & Giamard 1825[a]	X		
Bovichtidae (9) (Thornfishes)			
Bovichtus angustifrons Regan 1913	X		
B. chilensis Regan 1913[b]	X		
B. diacanthus (Carmichael 1819)	X		
B. oculus Hardy 1989[c]	X		
B. psychrolutes Günther 1860	X		
B. variegatus Richardson 1846	X		
B. veneris Sauvage 1879	X		
Cottoperca trigloides (Forster 1801)[d]	X		
**Halaphritis platycephala* Last, Balushkin & Hutchins 2002	X		
Pseudaphritidae (1) (Congolli or Tupong)			
Pseudaphritis urvillii (Valenciennes 1832)	X		
Eleginopidae (1) (Patagonian blenny or Falkland Islands blenny)[e]			
Eleginops maclovinus (Cuvier 1830)	X		
«cryonotothenioids»[f]			
Nototheniidae (49) (Notothens)			
Aethotaxis mitopteryx DeWitt 1962			X
Dissostichus eleginoides Smitt 1898		X	
D. mawsoni Norman 1937			X
Gobionotothen acuta (Günther 1880)		X	
G. barsukovi Balushkin 1991[g]		X	
G. gibberifrons (Lönnberg 1905)		X	
G. marionensis (Günther 1880)		X	

(*Continued*)

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TABLE I. (*continued*).

Taxa	Biogeographic distribution		
	Non-Antarctic	Sub-Antarctic	Antarctic
Gvozdarus svetovidovi Balushkin 1989[h]			X
Indonotothenia cyanobrancha (Richardson 1844)		X	
Lepidonotothen squamifrons (Günther 1880)			X
Notothenia angustata Hutton 1875	X		
N. coriiceps Richardson 1844		X	
N. microlepidota Hutton 1875	X		
N. rossii Richardson 1844		X	
Nototheniops larseni (Lönnberg 1905)		X	
N. mizops (Günther 1880)		X	
N. nudifrons (Lönnberg 1905)[i]		X	
Paranotothenia dewitti Balushkin 1990			X
P. magellanica (Forster 1801)		X	
Patagonotothen brevicauda (Lönnberg 1905)[j]	X		
P. cornucola (Richardson 1844)	X		
P. elegans (Günther 1880)	X		
P. guntheri (Norman 1937)		X	
P. jordani (Thompson 1916)	X		
P. kreffti Balushkin & Stehmann 1993	X		
P. longipes (Steindachner 1875)	X		
P. ramsayi (Regan 1913)	X		
P. sima (Richardson 1845)	X		
P. squamiceps (Peters 1877)	X		
P. tessellata (Richardson 1845)	X		
P. thompsoni Balushkin 1993	X		
P. trigramma (Regan 1913)	X		
P. wiltoni (Regan 1913)	X		
Pleuragramma antarcticum Boulenger 1902[k]			X
**Trematomus amphitreta* (Cziko & Cheng 2006)			X
T. bernacchii Boulenger 1902			X
T. borchgrevinki Boulenger 1902			X
T. brachysoma Pappenheim 1912			X
T. eulepidotus Regan 1914			X
T. hansoni Boulenger 1902			X
T. lepidorhinus (Pappenheim 1911)[l]			X
T. loennbergii Regan 1913[l]			X
T. newnesi Boulenger 1902			X
T. nicolai (Boulenger 1902)			X
T. peninsulae (Daniels 1981)			X
T. pennellii Regan 1914			X
T. scotti (Boulenger 1907)			X
T. tokarevi Andriashev 1978			X
T. vicarius Lönnberg 1905		X	
Harpagiferidae (11) (Spiny plunderfishes)[m]			
**Harpagifer andriashevi* Prirodina 2000		X	
H. antarcticus Nybelin 1947		X	
H. bispinis (Forster 1801)	X		
**H. crozetensis* Prirodina 2004		X	
H. georgianus Nybelin 1947		X	
H. kerguelensis Nybelin 1947		X	
**H. macquariensis* Prirodina 2000		X	
**H. nybelini* Prirodina 2002		X	
H. palliolatus Richardson 1845	X		
**H. permitini* Neelov & Prirodina 2006		X	

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TABLE I. (*continued*).

Taxa	Biogeographic distribution		
	Non-Antarctic	Sub-Antarctic	Antarctic
H. spinosus Hureau, Louis, Tomo & Ozouf 1980		X	
Artedidraconidae (36) (Barbeled plunderfishes)			
Artedidraco glareobarbatus Eastman & Eakin 1999			X
**A. longibarbatus* Eakin, Riginella & La Mesa 2015			X
A. lonnbergi Roule 1913[n]			X
A. mirus Lönnberg 1905		X	
A. orianae Regan 1914			X
A. shackletoni Waite 1911			X
A. skottsbergi Lönnberg 1905			X
Dolloidraco longedorsalis Roule 1913			X
Histiodraco velifer (Regan 1914)			X
Pogonophryne albipinna Eakin 1981[o]			X
P. barsukovi Andriashev 1967			X
**P. bellingshausenensis* Eakin, Eastman & Matallanas 2008			X
**P. brevibarbata* Balushkin, Petrov & Prutko 2010			X
P. cerebropogon Eakin and Eastman 1998			X
P. dewitti Eakin 1988			X
P. eakini Balushkin 1999			X
**P. favosa* Balushkin & Korolkova 2013			X
P. fusca Balushkin & Eakin 1998			X
P. immaculata Eakin 1981			X
P. lanceobarbata Eakin 1987			X
P. macropogon Eakin 1981			X
**P. maculiventrata* Spodareva & Balushkin 2014			X
P. marmorata Norman 1938			X
P. mentella Andriashev 1967			X
**P. neyelovi* Shandikov & Eakin 2013			X
P. orangiensis Eakin & Balushkin 1998			X
**P. pavlovi* Balushkin 2013			X
P. permitini Andriashev 1967			X
P. platypogon Eakin 1988			X
**P. sarmentifera* Balushkin & Spodareva 2013			X
P. scotti Regan 1914			X
**P. skorai* Balushkin & Spodareva 2013			X
**P. stewarti* Eakin, Eastman & Near 2009			X
P. squamibarbata Eakin & Balushkin 2000			X
**P. tronio* Shandikov, Eakin & Usachev 2013			X
P. ventrimaculata Eakin, 1987			X
Bathydraconidae (16) (Antarctic dragonfishes)			
Acanthodraco dewitti Skóra 1995			X
Akarotaxis nudiceps (Waite 1916)			X
Bathydraco antarcticus Günther 1878		X	
B. joannae DeWitt 1985		X	
B. macrolepis Boulenger 1907			X
B. marri Norman 1938			X
B. scotiae Dollo 1906			X
Cygnodraco mawsoni Waite 1916			X
Gerlachea australis Dollo 1900			X
Gymnodraco acuticeps Boulenger 1902			X
Parachaenichthys charcoti (Vaillant 1906)		X	

(*Continued*)

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TABLE I. (*continued*).

Taxa	Biogeographic distribution		
	Non-Antarctic	Sub-Antarctic	Antarctic
P. georgianus (Fischer 1885)		X	
Prionodraco evansii Regan 1914			X
Psilodraco breviceps Norman 1937		X	
Racovitzia glacialis Dollo 1900			X
Vomeridens infuscipinnis (DeWitt 1964)			X
Channichthyidae (16) (Icefishes)			
Chaenocephalus aceratus (Lönnberg 1906)		X	
Chaenodraco wilsoni Regan 1914			X
Champsocephalus esox (Günther 1861)	X		
C. gunnari Lönnberg 1905		X	
Channichthys rhinoceratus Richardson 1844[p]		X	
Chionobathyscus dewitti Andriashev & Neelov 1978			X
Chionodraco hamatus (Lönnberg 1905)			X
C. myersi DeWitt & Tyler 1960			X
C. rastrospinosus DeWitt & Hureau 1980			X
Dacodraco hunteri Waite 1916			X
Neopagetopsis ionah Nybelin 1947			X
Pagetodes antarcticus (Dollo 1900)[q]			X
P. atkinsoni (Regan 1914)[q]			X
Pagetopsis macropterus (Boulenger 1907)			X
P. maculata Barsukov & Permitin 1958[r]			X
Pseudochaenichthys georgianus Norman 1937		X	

[a]Through the use of DNA sequences from 10 nuclear genes, previously never employed in phylogenetic analyses, *Percophis brasiliensis* was resolved, with strong support, as the sister lineage of notothenioids (Near *et al*. 2015). The support from morphology is minimal but not conflicting. Given the absence of any persuasive prior or alternative hypotheses for a sister group, this is definitely an advance.

[b]Bravo *et al*. (1999) have placed *Bovichtus elongatus* and *B. argentinus* in the synonymy of *Bovichtus chilensis*. This paper appeared too late to be included in our 2000 list.

[c]Although Balushkin (2016) has placed *Bovichtus oculus* in the synonymy of *B. psychrolutes,* Stewart (2015) continues to recognize *B. oculus* as valid, as do we. *Bovichtus oculus* is known from the holotype in the Museum of New Zealand Te Papa Tongarewa (NMNZ P. 018510), and from two other specimens in the same collection tentatively identified as *B. oculus*. Although Balushkin (2016, pp. 632 and 637) indicates that he examined a radiograph of this holotype and measured its eye diameter, it is doubtful that the specimen he examined was the holotype. Records held by the NMNZ provide no evidence that the specimen was ever radiographed or that it was ever sent out on loan. *Bovichtus oculus* has eyes with a horizontal eye diameter < 9.0 times in SL, the most important character in distinguishing it from other species of bovichtids including *B. psychrolutes* (Hardy 1988). Balushkin reports that in his radiograph this value was 9.2–9.4 times in SL, not the 8.2 in SL reported by Hardy in his table 1. He also states that his measurements place the holotype in the range of eye diameters for *B. psychrolutes* and therefore that it is this latter species. However, re-measurement of the NMNZ type specimen of *B. oculus* using two different calipers showed that the eye was a little smaller than recorded by Hardy, but still < 9 times in SL. The actual measurements were: bony eye diameter = 13.04 mm; SL = 109.15 mm = 8.37 in SL or 11.94% of SL (Andrew Stewart, Collection Manager, Fishes, NMNZ, personal communication to J.T. Eastman, 12 December 2016.) Given this information, we continue to recognize *B. oculus* as a valid species. It should also be noted that, based on information in *Eschmeyer's Catalog of Fishes*, the correct date for this species is 1989, not 1988 as indicated in our 2000 list, because the article was not published until 1989.

[d]We follow Balushkin (1992, 2000) in considering *Cottoperca gobio* (Günther 1861) as a junior synonym of *C. trigloides* (Forster 1801). Some South American ichthyologists continue to recognize the South American population as *Cottoperca gobio* (Günther 1861).

[e]The spelling of this name has gone back and forth between Eleginopidae/Eleginopsidae. Sheiko (2019) recently resolved this matter by determining that the correct stem is *Eleginop*-, not *Eleginops*-, and therefore the correct name for the family is Eleginopidae.

[f]Although Cryonotothenioidea bears the suffix of a superfamily, Near *et al*. (2015, 2018) have employed this and several other rank-free names for various notothenioid clades. Although rank-free names do not comply with the *International Code of Zoological Nomenclature* (Sheiko 2019), cryonotothenioids

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TABLE I. (*continued*).

has begun to appear in the literature as a convenient way of referring to the clade that radiated in Antarctica and that encompasses 91% (128/140) of notothenioid species. We think it is acceptable to use it informally with the understanding that it is a non-*Code* compliant, colloquial name for the five families of the Antarctic clade. Use of left («) and right (») guillemets or double chevrons (as «cryonotothenioids») indicates that the name is non-*Code* compliant (Sheiko 2019).

[g]Duhamel *et al*. (2005, pp. 327 and 334) are not convinced that there is sufficient evidence to prove that *Gobionotothen barsukovi* is distinct from *G. acuta*. Although Balushkin (2014) has supplemented his original description (Balushkin 1991) of *G. barsukovi* with meristic data from additional specimens, there are no genetic data and we also remain skeptical about the validity of this species. A recent molecular phylogenetic study supported the validity of *G. acuta* and *G. marionensis*, but did not include specimens of *G. barsukovi* (Miya *et al*. 2016).

[h]Voskoboinikova & Kellermann (1993) have described another species of *Gvozdarus, G. balushkini,* from the Weddell Sea based on a single 30 mm SL specimen. This seems premature to us given the dearth of information about *G. svetovidovi*, a species known from only two specimens.

[i]Using a combination of morphological and molecular genetic data, Dornburg *et al*. (2016a) determined that *Lepidonotothen nudifrons* consists of two cryptic species: *L. nudifrons* around South Georgia and the South Sandwich Islands, and *L.* cf. *nudifrons* in the area of the Antarctic Peninsula. Obviously, the cryptic species will not be recognized until it has been formally described and named. The genus of these species is now *Nototheniops*.

[j]*Patagonotothen* supposedly contains cryptic species that have not been named (Ceballos *et al*. 2019).

[k]The correct name is now back to *Pleuragramma antarcticum,* not *P. antarctica* (Sheiko 2019).

[l]Until recently, there had never been any question about the validity of the sister species *Trematomus lepidorhinus* and *T. loennbergii*. However there have been reports of investigators being unable to distinguish specimens of these species morphologically or through the use of mitochondrial COI gene barcodes or nuclear gene DNA sequences (Lautrédou *et al*. 2010, 2012, Causse *et al*. 2011, Dettai *et al*. 2011a, 2011b, Smith *et al.* 2012). However, these species are distinguished by next-generation DNA sequencing (RADseq) (Near *et al*. 2018). Karyological studies also support the existence of two species (Ghigliotti *et al*. 2015), as does morphological divergence of the sense organs and brains, and their preferred habitat depths (Eastman & La Mesa 2021). Therefore we continue to recognize these two species as valid and suggest that the difficulty in identifying at least some of the Indian Ocean specimens is attributable to phenotypic plasticity in the dimensions of the head in *T. lepidorhinus* (Eastman & La Mesa 2021).

[m]Since 2000 five new species of *Harpagifer* have been described on the basis of being either the "soft" littoral form or deeper-dwelling "spiny" form at a given island (Prirodina 2004). The primary morphological difference between the species in each pair is in the degree of head spination, especially the extent of development of the supraorbital ridge and its protuberances. Duhamel et al. (2005, p. 328, 358) question the validity of *Harpagifer andriashevi* Prirodina 2000, *H. nybelini* Prirodina 2002, *H. crozetensis* Prirodina 2004 and *H. macquariensis* Prirodina 2000. Although it was described after the publication of their book, *Harpagifer permitini* Neyelov & Prirodina 2006 should probably added to this group. Duhamel *et al*. (2005) consider the species in this genus to be "extremely polymorphic" and caution that, based on their samples from the MNHN collections, meristic data do not discriminate the species. They also state that the diagnoses of the species of *Harpagifer* are also heavily reliant on the degree of development of the supraorbital protuberance, a highly subjective character showing intermediate degrees of development in species from coastal areas. This situation would obviously benefit from the perspective that molecular genetic data could provide.

[n]This is a recent change in the spelling of the name of this species. It incorporates the corrections of Koerber (2009) with respect to the use of diacritical vowels and diphthongs in the scientific names of certain notothenioid species dedicated to the Swedish zoologist Einar Lönnberg. Koerber's corrections are accepted and included in *Eschmeyer's Catalog of Fishes*.

[o]We view two additional species of *Pogonophryne*, *P. minor* Balushkin & Spodareva 2013a and *P. pallida* Balushkin & Spodareva 2015, as doubtful and they are not included in the list. See Eakin's critiques in Supplemental material 1 concerning these two species.

[p]There are widely differing opinions about the number of species of *Channichthys*, a genus endemic to the Kerguelen Plateau. Iwami & Kock (1990) and Kock (2005) recognize only *C. rhinoceratus.* Balushkin (2000) recognizes four species. Duhamel *et al*. (2005) recognize *C. rhinoceratus, C. velifer* and suggest the existence of a single undescribed species. In considering the species level taxonomy of *Channichthys*, Duhamel *et al*. (2005) state that (page 368, French to English translation using Google Translate, with [bracketed material] added by us):

"The systematics and biology of *Channichthys* require a complete overhaul because the original descriptions were very imprecise. Following the original description of *C. rhinoceratus* from the coastal region, another species, *C. rugosus*, [*Channichthys rugosus* Regan 1913, based on a single 400 mm specimen, with no drawing provided] was minimally described from the same area and then later placed in synonymy. The specimens subsequently captured on the plateau have led to the description of a profusion of new species that need to be reexamined to draw conclusions on their status and to correctly redefine *C. rhinoceratus* (as well as other species, valid nor not). In addition, the measurements carried out on individuals greatly depend on the condition of the specimen at the time of death (often gaping opercula and mouth open …) and only meristic characters can then be used. The report of *C. rhinoceratus* at Marion from an otolith in a gentoo penguin (*P. papua*) [stomach presumably?] has never been validated by the capture of other complete specimens. The initial descriptions of the larvae of *C. rhinoceratus* and *C. velifer*, then those of *C. rhinoceratus* and *C. rugosus*, add to the confusion because no series is complete and valid."

Adding to the uncertainty about the number of species of *Channichthys*, Shandikov (2011) described *Channichthys richardsoni* and implied that, based on his previous work, there are a total of nine species of *Channichthys* around Kerguelen. *Eschmeyer's Catalog of Fishes* also indicates that there are nine valid names for species of *Channichthys*. Therefore, given the confusion over the number of species and the possible existence of phenotypic plasticity in *C. rhinoceratus*, we think it is best to maintain a conservative approach by recognizing only *C. rhinoceratus* until a comprehensive analysis, including genetic data, lends some clarity to this situation.

[q]These two species were formerly in the genus *Cryodraco.* Sheiko (2019, p. 66) has determined that, according to the Principle of Priority, the name *Pagetodes* Richardson 1844 stands as the valid senior isonym of *Cryodraco* Dollo, 1900. Dornburg *et al.* (2016b) provide molecular data in support of previous morphological data (La Mesa *et al*. 2002) documenting the validity of the two species of *Pagetodes* (formerly *Cryodraco*).

[r]Sheiko (2019) has determined that the correct spelling is *Pagetopsis maculata*, not *P. maculatus.*

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Author contributions

Both authors participated in the analysis, writing and final approval of this paper. Richard Eakin was primarily responsible for our decisions regarding the validity and recognition of the species of Artedidraconidae.

Supplemental material

Supplemental Material provides Richard Eakin's rationale for excluding *Pogonophryne minor* Balushkin & Spodareva 2013 and *P. pallida* Balushkin & Spodareva 2015 from the checklist by placing them in synonymy. This material is found at https://doi.org/10.1017/S0954102020000632.

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