

Barton and the forgotten description of *Salamandra horrida* (Amphibia, Urodela): story of a rediscovery

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Abstract

Cryptobranchus alleganiensis (Sonnini & Latreille, 1801*b*) was long considered the only species of the genus *Cryptobranchus* Leuckart, 1821. In this genus, Sabatino & Routman (2009) found eight genetic independent unities isolated from each other, which they treated as Management Units. Later, Hime (2017) recovered five strongly supported species-level lineages within this genus, corresponding more or less to the lineages of Sabatino & Routman (2009). We herein resurrect a valid nomen for one of the lineages of Hime (2017) (Ohio/Allegheny/Susquehanna lineage), the most broadly distributed of the five, which should be named *Cryptobranchus horridus* (Barton, 1807*a*). We relate the story of the rediscovery of two forgotten publications of Barton (1807*a–b*) preceding that of 1808 so far recognized as the original description of this taxon. We discuss the problem of the onymotope of *Cryptobranchus alleganiensis* and present logonomic lists for the genus *Cryptobranchus* and all the taxa described. The nucleospecies of the genus *Cryptobranchus* is *Salamandra horrida* Barton, 1807*a* which is no longer a synonym of *Salamandra alleganiensis* Sonnini & Latreille, 1801*b*. The updating of the logonymic lists revealed the forgotten designation of Barnes (1828) for the genus *Protonopsis* Le Conte, 1824, a synonym of *Cryptobranchus*. The following nomina can be allocated to three of

the five lineages identified by Hime (2017): *Cryptobranchus alleganiensis*, *Cryptobranchus horridus* and *Cryptobranchus bishopi*. Two other lineages require further studies.

Key words

CRYPTOBRANCHIDAE, *Cryptobranchus*, *Cryptobranchus horridus*, hellbender, logonymic lists, new synonymy, first revisor action, airesy, subsequent monophory, lineages.

Conventions, abbreviations and technical nomenclatural terms

In this paper, ‘the *Code*’ designates the edition currently in force of the *International Code of Zoological Nomenclature* (Anonymous 1999), and ‘the Commission’ the International Commission on Zoological Nomenclature.

Appendix 1 provides information on the technical nomenclatural terms used here, which are followed by asterisks* upon their first appearance in the text.

Introduction

The genus *Cryptobranchus* Leuckart, 1821 is one of two extant genera in the family *CRYPTOBRANCHIDAE* Fitzinger, 1826. This genus was long considered monospecific, containing one distinctive large-sized, iconic North American salamander, commonly known as the hellbender. Now in severe decline (Stuart *et al.* 2008: 636–637), hellbenders consist of two currently recognized subspecies, *C. alleganiensis alleganiensis* (Sonnini & Latreille, 1801b) and *C. alleganiensis bishopi* Grobman, 1943, the latter not being recognized by all authors.

In this genus, Sabatino & Routman (2009) found eight genetic independent unities isolated from each other by the different watersheds and treated by them as Management Units (MU): North Ozark, Ohio/Susquehanna Rivers, Tennessee River, Copper Creek, North Fork of the White River, Spring River, New River and Current River/Eleven Point River. More recently, Hime (2017: 75–76) identified in this genus five reproductively isolated species-level lineages, which no longer experience gene exchange: [1] White/Black Rivers from the Ozark drainage, itself composed of two highly distinct sublineages; [2] Kanawha River/New River; [3] Tennessee River; [4] Ohio/Allegheny/Susquehanna Rivers; and [5] Missouri/Mississippi/Green Rivers lineages. As noted by Hime (2017: 104), beside *Cryptobranchus a. alleganiensis* and *C. a. bishopi*, three lineages (*Cryptobranchus* sp. nov. 1, 2 and 3) remain unnamed. These will require additional literature review to assess whether previous authors have established available nomina* which would take precedence, and whether new nomina should be created.

Hime (2017: 104) added that “because the type locality for *Cryptobranchus alleganiensis* is described from within the Tennessee River drainage, this lineage would retain the original species epithet. The lineage from the Ozark would be elevated from *C. a. bishopi* to *C. bishopi*”. The most broadly distributed lineage of the genus corresponds to *Cryptobranchus* sp. nov. 1 of Hime (2017: 104) from the northeastern United States, north of *Cryptobranchus alleganiensis* and north and west of his *Cryptobranchus* sp. nov. 2.

One of us (JR), working on the next updated edition of his book *Les Urodèles du monde* (Raffaëlli 2013), was investigating if there were any nomina available to designate these three unnamed lineages, as recommended by Hime, who made several pertinent discoveries, which we recount herein.

Nomina for recognized taxa and story of a rediscovery

We launched a bibliographical search in order to study the descriptions and onymotopes* of taxa which have so far been considered to be synonyms or subspecies of the genus *Cryptobranchus*. According to the literature, several nomina remain in the synonymy of *Cryptobranchus alleganiensis* (Sonnini & Latreille, 1801b). Among them, the nomina *Salamandra horrida* and *Salamandra gigantea* synonymized by Harlan (1827: 320) with *Salamandra alleganiensis* Sonnini & Latreille, 1801b, are possible candidates to designate at least one of the three unnamed lineages of Hime (2017). We needed to find the publication of Barton (1808) cited as the first description of these two taxa, in particular to verify the onymotopes (type localities).

Looking for Barton (1808)

One of us (TF) attempted to find the publication of Barton¹ (1808). Unfortunately, on the internet only the reissue of Barton (1821) was easily found. This fact is not new. Barnes (1828: 69) already underlined “the difficulty of obtaining specific information from the papers of Barton, which were published in a fugitive form, and have long been out of print”.

In Barton (1821), three nomina were cited: *Salamandra horrida*, *Salamandra gigantea* and *Salamandra maxima*. These three nomina were synonymized with *Salamandra alleganiensis* Sonnini & Latreille, 1801b by Harlan (1825b: 271, 1827: 320, 1835: 87), Gray (1825: 217), Barnes (1826: 278), Holbrook (1842: 95), Duméril *et al.* (1854: 206), Smith (1877: 22), Boulenger (1882: 81), Cope (1889: 38) and Brown (1908: 127). They were considered valid by Cuvier (1816: 101, as *Salamandra gigantea*), Merrem (1820: 187, as *Molge gigantea*), Barnes (1826: 278, 1828: 69, as *Protonopsis horrida*), Wagler (1830: 209, as *Salamandra horrida* in the genus *Salamandrops*), Gray (1831: 109, as *Abranchus horridus*), Griffith & Pidgeon (1831: 410, as *Salamandra gigantia* [sic] in the genus *Menopoma*), Van der Hoeven (1833: 304, as *Menopoma giganteum*), Griffith (1835: xxxi, as *Salamandra gigantea* in the genus *Menopoma*), Tschudi (1838: 96, as *Menopoma gigantea*), Fitzinger (1843: 34, as *Salamandrops giganteus*), Gray (1850: 53, as *Protonopsis horrida*) and Schlegel (1858: 61, as *Sal. (Menopoma) gigantea*).

Only rare authors cited their sources: Merrem (1820: 187, as “Burton [sic] Account on *Siren lacertina* p 28”), Gray (1825, as “Barton’s Account of *Siren Lacertina* p. 28”), Wagler (1830: 209, as “Barton account on *Siren lacertina* Philad. 1808”), Tschudi (1838: 96, as “Barton ac. ou *Siren lacert.*”), Boulenger (1882: 81, as “Barton, On *Siren lacertina*”). However, none of these authors gave any relevant date or reference for Barton’s original publication.

The nomina *Salamandra horrida*, *Salamandra gigantea* and *Salamandra maxima*, attributed to Barton (1808: 8) by Schmidt (1953: 11), Dundee (1972: 1), Nickerson & May (1973: 2) and Fouquette & Dubois (2014: 49), are cited in the synonymy of *Cryptobranchus alleganiensis*. However, in Barton (1821), these three nomina do not appear on page 8: *Salamandra horrida* on pages 5–6, *Salamandra gigantea* on page 6 and *Salamandra maxima* on page 6. Are there other differences between Barton (1808)—that we had still not seen at that point—and Barton (1821), and particularly about the

¹ Barton, Benjamin Smith (10 February 1766–19 December 1815) (Adler 2012: 393).

onymotopes cited? It was then, still searching for the original publication of Barton (1808) to verify the onymotopes of the three nomina, that we discovered two older publications of Barton.

Rediscovery of Barton (1807a and 1807b)

On the internet, we finally found the citation of *Salamandra horrida* on page 23 in a book of Barton dated 1807. The date is older than 1808, but no description of *Salamandra horrida* is available in this book, and this nomen* is therefore a gymnonym* (*nomen nudum*). But a footnote mentions: “See Second Supplement to the Philadelphia Medical and Physical Journal. Pages 196 & 197”.

We located this primary source. The entire volume was published in 1808, but the relevant part is dated July 1807 (Fig. 1). It presents a description of *Salamandra horrida* on page 197 and mention of its onymotope on page 196. This description is more complete than that cited in 1821 (and 1808 as verified later): head and body flat, mouth large with numerous teeth, up to 18 inches long in some cases, tail compressed laterally, body covered with milk-like fluid in case of aggression (Fig. 2). In this publication of Barton (1807a), the three nomina *Salamandra horrida*, *Salamandra maxima* and *Salamandra gigantea* are allelonyms* for the same taxon.

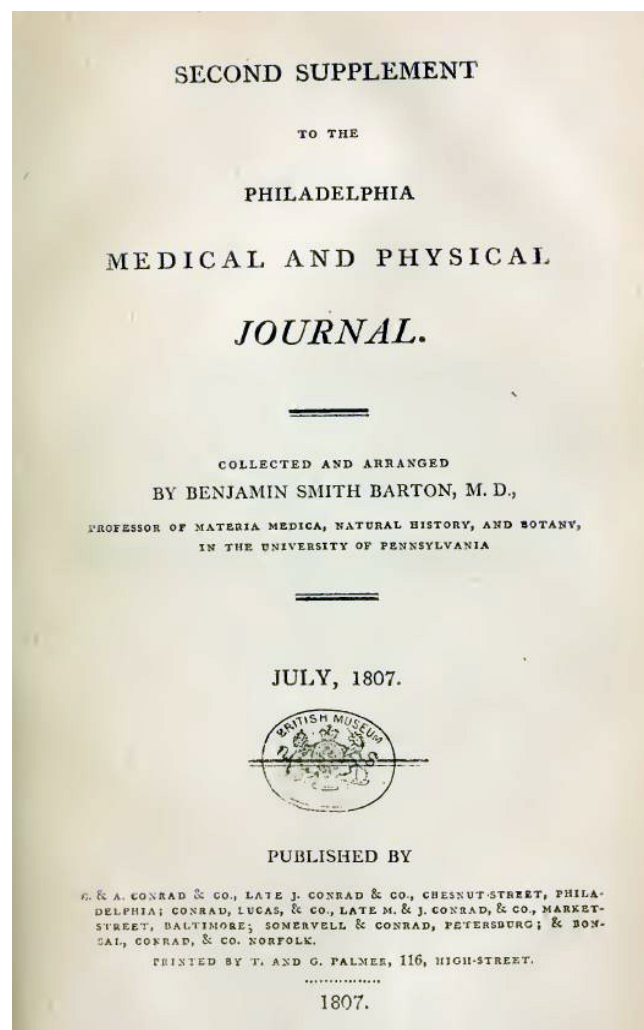


FIGURE 1. Cover page of the publication describing *Salamandra horrida* Barton, 1807a.

The *Philadelphia Medical and Physical Journal*, where the original description (Barton 1807a) was published, was edited by Barton himself (Fig. 1). This journal was published over a short period from 1805 to 1808, and comprised only three volumes. Barton (1807a: 197) wrote: “The Editor is preparing for publication, a full account of this species of *Salamandra*, to which he proposes giving the specific appellation of *S. horrida*.”

Barton (1807b: 23) cited only the nomen *Salamandra horrida*. Doing so, he acted as first revisor among the three original allelonyms (Article 24.2.4 of the *Code*).

The symprotonymotopes* of *Salamandra horrida* are: “lakes Ontario, Erie, &c., and also in the waters of the Ohio and Susquehanna [...], the waters of the Mississippi, including those which empty themselves into the Ohio”. These localities are found within the range of *Cryptobranchus* sp. nov. 1 as defined by Hime (2017: 104). So *Salamandra horrida* Barton, 1807a should be removed from the synonymy of *Cryptobranchus alleganiensis* and is the valid nomen that must be applied to this lineage from Ohio/Allegheny/Susquehanna Rivers.

We found only one other publication citing Barton (1807a), by Waite (1907: 23), in which he cited the three nomina *Salamandra horrida*, *S. maxima* and *S. gigantea*, but this publication appears to have been missed by all later authors. *Salamandra horrida* Barton, 1807a was first illustrated in Barton (1814) on the plate facing page 26 (see Fig. 2).

Finally, thanks to the help of Aaron Bauer (Villanova, USA), we obtained a copy of Barton (1808) and compared it with Barton (1821). Both publications have exactly the same content, with the exception of layout and pagination. Barton (1821) is indeed a reissue of Barton (1808) but with a different pagination.

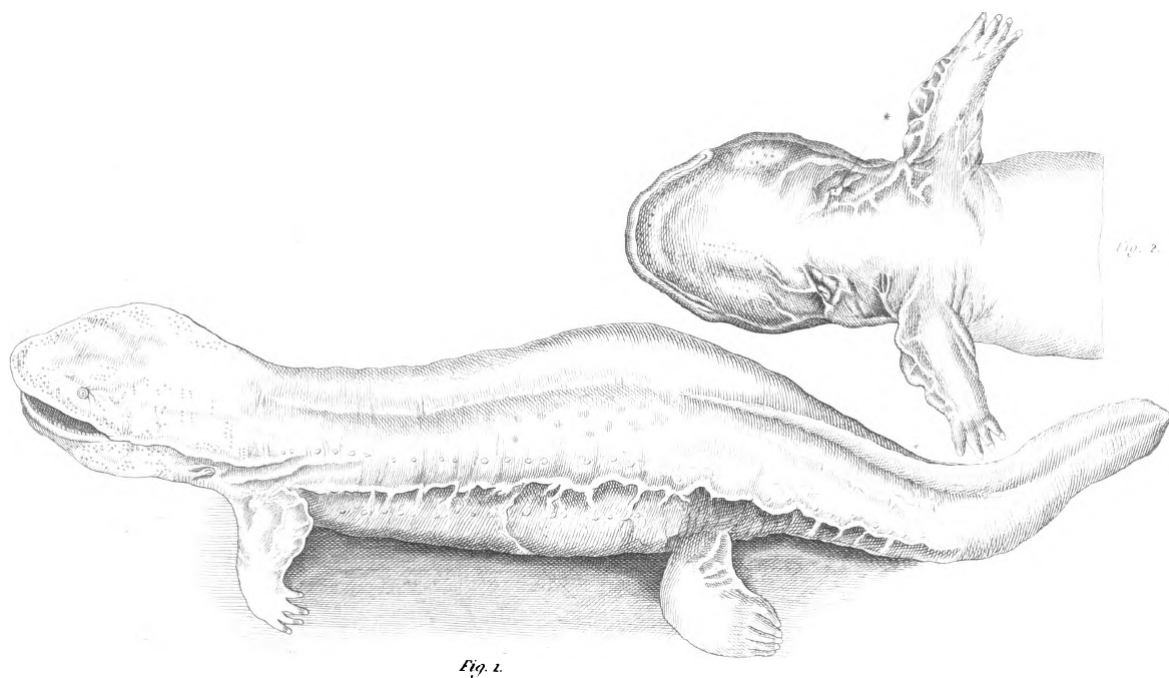


FIGURE 2. Illustration (in Barton 1814) of *Salamandra gigantea* Barton, 1807a, an invalid allelonym of *Salamandra horrida* Barton, 1807a, here considered valid as *Cryptobranchus horridus* (Barton, 1807a).

The problem of the onymotope of *Cryptobranchus alleganiensis* (Sonnini & Latreille, 1801b)

Before the description of *Salamandra alleganiensis* Sonnini & Latreille, 1801b (Fig. 3), Sonnini (*in* Sonnini & Latreille, 1801a: 253) indicated: “C’est au zèle de Michaux, savant voyageur botaniste, que l’on en doit la connoissance: il l’a trouvée en Virginie sur les monts Alléganis, et il en a remis un individu bien conservé, au Cabinet d’histoire naturelle de Paris”. [It is due to the zeal of Michaux, a learned traveler botanist, that we owe our knowledge of it: he found it in Virginia on the Allegheny mountains, and he handed over a well-preserved individual to the Cabinet d’Histoire naturelle in Paris]. This locality is therefore the holoprotonymotope* of the species.

Harper (1940: 720–721) discussed the origin of Michaux’s specimen. We quote his explanations below. Indications into square brackets ^[C1]–^[C3] refer to our comments below.

“*Salamandra alleganiensis*”

The Hellbender (now known as *Cryptobranchus alleganiensis*) was first described by Sonnini (*in* Sonnini and Latreille, Reptiles, vol. 2, p. 253, pl. 54, fig. 1, 1801) as ‘la salamander des monts Alléganis’, but no technical name was then bestowed ^[C1]. It was also described under the same common name by Bosc (Nouv. Dict. Hist. Nat., ed. 1, vol. 20, p. 48, 1803).

The first technical name, *Salamandra alleganiensis*, was proposed by Daudin (Reptiles, vol. 8, p. 231, 1803). He states that the animal was obtained by André Michaux ‘dans les monts Alléganis, en Virginie.’ However, a careful perusal of the elder Michaux’s journal (Proc. Am. Philos. Soc., vol. 26, no. 129, pp. 1–145, 1889; also in Thwaites’ Early Western Travels 1748–1846, vol. 3, pp. 25–104, 1904) reveals no mention of the species.

Fortunately the son, François André Michaux, in the course of some general observations on the Alleghany Mountains (Travels to the westward of the Alleghany Mountains, pp. 316–317, 1805, London ^[C2]), has furnished an essential clue to the type locality:

‘A species of salamander is found in the torrents, called by the inhabitants the *Alligator of the Mountains*; some of them are two feet long. The specimen described in the Nouveau Dictionnaire d’Histoire Naturelle, published by Déterville, was taken in Doe River by my father.’

On first consideration, this would appear to be the Doe River that lies in Carter County, Tennessee, and discharges into the Watauga at the present site of Elizabethton. On closer investigation, however, it becomes evident that the younger Michaux confused the names Doe and Toe and actually meant the latter river in the present case.

The elder Michaux had stopped more than once (August 16–19 and September 1–5, 1794; May 4–13, 1795; March 23–29, 1796) at Davenport’s plantation on the North Toe River. According to Price and Strother’s map of North Carolina (1808), this was situated on the west side of the river in Mitchell County, N. C., approximately a mile south of the mouth of the present Brushy Creek (Morganton quadrangle) and 4 miles ENE of the present Spruce Pine (Mount Mitchell quadrangle). Michaux had also made considerable excursions and botanical collections in this vicinity.

The son, in the course of his own travels some years later, likewise stopped here. He says (*op. cit.*, p. 309): ‘I ... arrived at the house of one Davenport, the owner of a charming plantation up on Doe River, a torrent about forty feet in breadth, and which empties itself into the Nolachucky.’ (It is the Toe River, not the Doe River, that empties into the Nolichucky.)

Since the younger Michaux was apparently consistent in misnaming the Toe River, and since the father spent considerable time on this river, we are no doubt justified in interpreting the former’s statement of the type locality as applying to the (North) Toe River. The most likely part of this river for the collection of the type specimen was probably the vicinity of Davenport’s plantation. This, then, may be considered the restricted type locality ^[C3].

Stejneger and Barbour (Check List, ed. 4, p. 4, 1939) follow Daudin quite literally in stating that the type locality is the ‘Allegheny Mountains in Virginia’. But either Daudin’s information was faulty, or his concept of the boundaries of Virginia was rather vague.”

The geographic arguments developed by Harper (1940: 720–721) are fully convincing. Thus the holoprotonymotope of *Salamandra alleganiensis* must be corrected (ergonymotope*) as: “vicinity of Davenport’s Plantation, North Toe River, 1 mile south of the mouth of the Brushy Creek and 4 miles east-northeast of the Spruce Pine Creek, Mitchell County, North Carolina, USA”. So, contrary to what Sonnini (*in* Sonnini & Latreille 1801a: 253) indicated, *Cryptobranchus alleganiensis* does not live in the Allegheny Mountains, but rather south and east of the Cumberland Mountains and in the adjacent Blue Ridge Mountains, that lie within the Tennessee River watershed, as underscored by Hime (2017: 104).

However, some details cited by Harper (1940: 720–721) require some comments:

^[C1] Harper (1940) did not see that the nomen (in Latin) was introduced in the fourth volume of Sonnini & Latreille (1801*b*: 406). So, he wrongly indicated that “The first technical name, *Salamandra alleganiensis*, was proposed by Daudin (Reptiles, vol. 8, p. 231, 1803).”

^[C2] Harper (1940) consulted Michaux (1805), the English translation of the French book of Michaux (1804). In the French version, there is the same mistake about Doe-river and Toe-river, as indicated in the English version by Harper (1940: 720–721). Michaux (1804: 279) wrote: “Dans les torrens on trouve une espèce de Salamandre appelée par les habitants *Alligator de montagnes*; il y en a qui ont jusqu’à deux pieds de long. C’est dans Doe-River qu’a été pris par mon père l’individu qui est décrit dans le Nouveau Dictionnaire d’Histoire naturelle publié par Déterville”.

^[C3] According to the *Code* (Article 76), an onymotope (type locality) cannot be changed (or restricted) without the designation of a lectophoront* (lectotype) or a neophoront* (neotype), but it can be corrected if it can be shown to have been wrong in the original publication.



FIGURE 3. *Cryptobranchus alleganiensis* (Sonnini & Latreille, 1801*b*), Cherokee National Forest, Tennessee, USA. © Sebastian Voitel.

Logonymic lists

Cryptobranchus Leuckart, 1821

Cryptobranchus Leuckart, 1821: 259. • Nucleospecies* by original monophory*: *Salamandra salamandroides* Leuckart, 1821: 260, neonym* of *Salamandra gigantea* Barton, 1807*a*: 197, valid as *Cryptobranchus horridus* (*Hoc loco**). • Placed on the *Official List of Generic Names in Zoology* (Anonymous 1926: 3).

Urotropis Rafinesque, 1822: 3. • Nucleospecies by original monophory: *Urotropis mucronata* Rafinesque, 1822: 3, invalid junior doxisonym* of *Salamandra horrida* Barton, 1807*a*: 197, valid as *Cryptobranchus horridus* (*Hoc loco*). • Junior isonym of *Cryptobranchus* Leuckart, 1821. Synonymy by Dundee (1972: 1).

Protonopsis Le Conte, 1824: 57. • Nucleospecies by subsequent monophory (Article 69.3) in Barnes (1828: 69): *Salamandra horrida* Barton, 1807*a*: 197, valid as *Cryptobranchus horridus* (*Hoc loco*). • The subsequent designation of the nucleospecies by Barnes (1828: 69) by subsequent monophory seems to have been overlooked by all authors since then. Junior isonym of *Cryptobranchus* Leuckart, 1821. Synonymy with *Menopoma* Harlan, 1825*b* by Guérin-Méneville (1838: 18).

Protonophis: Tschudi 1838: 68. • Ameletograph*, nothapograph*.

Protanopsis: Leuckart 1840: 19. • Ameletograph, nothapograph.

Abranchus Harlan, 1825*a*: 233 (*nec Abranchus* Boïé, 1824: 242, autoneonym* for *Abrancha* Van Hasselt, 1824: 36 [MOLLUSCA]). • Nucleospecies by original monophory: *Salamandra alleganiensis* Sonnini & Latreille, 1801*b*: 406. • Junior doxisonym of *Cryptobranchus* Leuckart, 1821. Synonymy with *Menopoma* Harlan, 1825*b* by Guérin-Méneville (1838: 18). Synonymy with *Protonopsis* Le Conte, 1824 by Gray 1850: 53.

Menopoma Harlan, 1825*b*: 270. • Neonym for *Abranchus* Harlan, 1825*a*: 233. • Junior doxisonym of *Cryptobranchus* Leuckart, 1821. Synonymy with *Cryptobranchus* Leuckart, 1821 by Eichwald (1831: 164). Synonymy with *Protonopsis* Le Conte, 1824 by Gray (1850: 53).

Menopoma: Van der Hoeven 1833: 304 [subgenus of *Amphiuma* Garden in Smith, 1821]. • Apohypse*.

Monopoma: Bonaparte 1839: [265]. • Ameletograph, nothapograph.

Pelusius Wagler, 1830: 132. • Allelonym of *Salamandrops* Wagler, 1830: 209 (Wagler 1830: 353). • Junior isonym of *Cryptobranchus* Leuckart, 1821. Synonymy by Dubois *et al.* (2021: 527, 703).

Salamandrops Wagler, 1830: 209. • Nucleospecies by original monophory: *Salamandra gigantea* Barton, 1807a: 197, valid as *Cryptobranchus horridus* (Hoc loco). • Junior isonym of *Cryptobranchus* Leuckart, 1821. • Synonymy with *Menopoma* by Guérin-Ménéville (1838: 18). Synonymy with *Protonopsis* by Gray (1850: 53).

Eurycea Rafinesque, 1832: 121 (*nec Eurycea* Rafinesque, 1822: 1 [AMPHIBIA]). • Nucleospecies by original monophory: *Urotropis mucronata* Rafinesque, 1822: 3. • Doxisonym of *Cryptobranchus* Leuckart, 1821. Synonymy with *Protonopsis* by Gray 1850: 53. Synonymy with *Cryptobranchus* Leuckart, 1821 by Dubois *et al.* (2021: 489, 703).

***Cryptobranchus alleganiensis* (Sonnini & Latreille, 1801b)**

Salamandra alleganiensis Sonnini & Latreille, 1801b: 406. • Holoprotonymotope: “Virginie sur les monts Alléganis” [Virginia (USA) on the Monts Allegheny] (Sonnini in Sonnini & Latreille, 1801a: 253). Ergonymotope by Harper (1940: 720-721): “vicinity of Davenport’s Plantation, North Toe River, 1 mile south of the mouth of the Bushy Creek and 4 miles east-northeast of the Spruce Pine Creek, Mitchell County, North Carolina, USA”. • Placed on the *Official List of Specific Names in Zoology* (Hemming 1956: 374).

Triton alleganiensis: Oppel 1811: 81. • Aponymorph*.

Salamandra alleganensis: Leuckart 1821: 257. • Aponymorph, ameletograph, nothapograph.

Triton alleghaniensis: James 1823: 5. • Aponymorph, ameletograph, nothapograph.

Salamandra alleghaniensis: Harlan 1825a: 222, 225. • Aponymorph, ameletograph, nothapograph.

Abranchus alleghaniensis: Harlan 1825a: 233. • Aponymorph, ameletograph, nothapograph.

Menopoma alleghaniensis: Harlan 1825b: 271. • Aponymorph, ameletograph, nothapograph.

Abranchus alleganensis: Gray 1825: 217. • Aponymorph, ameletograph, nothapograph.

Cryptobranchus alleghaniensis: Van der Hoeven 1838: 384. • Aponymorph, ameletograph, nothapograph.

Salamandra alleghaniensis: Tschudi 1838: 96. • Aponymorph, ameletograph, nothapograph.

Menopoma allegheniense: Knauer 1878: 96; Davis & Rice 1883: 26. • Aponymorph, ameletograph, nothapograph.

Cryptobranchus alleganiensis: Morse 1901: 114. • Aponymorph, eunymorph*.

Cryptobranchus alleganiensis alleganiensis: Schmidt 1953: 11. • Aponymorph.

Salamandrops alleghaniensis: Fouquette & Dubois 2014: 48. • Aponymorph, ameletograph, nothapograph. •

Wagler (1830) did not write this combination, as sometimes stated (Fouquette & Dubois 2014: 48).

Menopoma fusca Holbrook, 1842: 99. • Symprotonymotope: “waters of the mountainous regions of North Carolina and Georgia” and “waters of French Broad, [...] of Ashville, Buncomb county, North Carolina”. • Synonymy following Dundee (1972: 1).

Protonopsis fusca: Gray 1850: 54. • Aponymorph.

Menopoma fuscum: Boulenger 1882: 82; Yarrow, 1882: 20. • Aponymorph. • Relative dates of publication unknown: the preface in Boulenger (1882: iii) is dated 26 November 1882; the advertisement in Yarrow (1882: ii) is dated November 1882.

Cryptobranchus fuscus: Cope 1889: 43. • Aponymorph.

Cryptobranchus terassodactylos Wellborn, 1936: 63. • Holoprotonymotope: “Nordamerika” [North America]. • Synonymy by Stejneger & Barbour (1939: 3) without explanation. Provisional synonymy following Grobman (1943: 5) and Bauer *et al.* (1993: 290), pending onymophoront* review. • The restriction of the onymotope by Schmidt (1953: 11) is invalid, as already noticed by Fouquette & Dubois (2014: 50). The onymophoront of *Cryptobranchus terassodactylos* have 4 toes like species of the genus *Necturus* Rafinesque, 1819 and not 5 toes like all species of the genus *Cryptobranchus*. But the presence of tubercles on the head, a fleshy skin fold on each flank and the total length (523 mm) show that the holophoront represents obviously an atypical specimen of the genus *Cryptobranchus*, as already noted by Grobman (1943: 5).

Cryptobranchus terassodactylus: Schmidt 1953: 11. • Aponymorph, ameletograph, nothapograph.

***Cryptobranchus horridus* (Barton, 1807a)**

Salamandra horrida Barton, 1807a: 197. • Symprotonymotope: “lakes Ontario, Erie, &c., and also in the waters of the Ohio and Susquehanna [...] the waters of the Mississippi, including those which empty themselves into the Ohio” (Barton, 1807a: 196). • Lectallelonym* (Barton, 1807b: 23).

- Protonopsis horrida*: Barnes 1826: 278. • Aponymorph. • Le Conte (1824) did not write this combination, as sometimes stated (Barnes 1826: 278).
- Abranchus horridus*: Gray 1831: 109. • Aponymorph.
- Protonophis horrida*: Duméril, Bibron & Duméril 1854: 207. • Aponymorph, ameletograph, nothapograph.
- Cryptobranchus* sp. nov. 1: Hime 2017: 104.
- Salamandra gigantea* Barton, 1807a: 197. • Symprotonymotope: “lakes Ontario, Erie, &c., and also in the waters of the Ohio and Susquehanna [...] the waters of the Mississippi, including those which empty themselves into the Ohio.” (Barton, 1807a: 196). • Leipallelonym* (Barton, 1807b: 23).
- Molge gigantea*: Merrem 1820: 187. • Aponymorph.
- Salamandra gigantia*: Griffith & Pidgeon 1831: 410. • Ameletograph, nothapograph.
- Amphiuma (Menopoma) giganteum*: Van der Hoeven 1833: 304. • Aponymorph.
- Menopoma gigantea*: Tschudi 1838: 96. • Aponymorph.
- Salamandrops giganteus*: Fitzinger 1843: 34. • Aponymorph.
- Sal[amandra] (Menopoma) gigantea*: Schlegel 1858: 61. • Aponymorph.
- Salamandrops gigantea*: Cope 1889: 39. • Aponymorph. • Wagler (1830) did not write this combination, as sometimes stated (e.g., Cope 1889: 39, Dundee 1972: 1).
- Cryptobranchus gigantesque*: Grobman 1943: 5. • Aponymorph, ameletograph, nothapograph.
- Salamandra maxima* Barton, 1807a: 197. • Symprotonymotope: “lakes Ontario, Erie, &c., and also in the waters of the Ohio and Susquehanna [...] the waters of the Mississippi, including those which empty themselves into the Ohio.” (Barton, 1807a: 196). • Leipallelonym (Barton, 1807b: 23).
- Cryptobranchus salamandroides* Leuckart, 1821: 260. • Neonym for *Salamandra gigantea* Barton, 1807a. • **New synonymy**, previously in the synonymy of *Cryptobranchus alleganiensis* (Sonnini & Latreille, 1801b). • Leuckart (1821: 257) cited only Barton “1812” [in fact 1814]. He seems not to have been aware of the previous description of Barton (1807a).
- Urotropis mucronata* Rafinesque, 1822: 3. • Holoprotonymotope: “Kentucky river”. • **New synonymy**, previously in the synonymy of *Cryptobranchus alleganiensis* (Sonnini & Latreille, 1801b).
- Eurycea mucronata*: Rafinesque 1832: 121. • Aponymorph.
- Cryptobranchus guildayi* Holman, 1977: 159. • Holoprotonymotope: “Cumberland Cave, Allegany County, Maryland”. • **New synonymy**, previously in the synonymy of *Cryptobranchus alleganiensis* (Sonnini & Latreille, 1801b).

***Cryptobranchus bishopi* Grobman, 1943**

- Cryptobranchus bishopi* Grobman, 1943: 6. • Holoprotonymotope: “Current River at Big Spring Park, Carter County, Missouri”.
- Cryptobranchus alleganiensis bishopi*: Schmidt 1953: 12. • Aponymorph.
- Cryptobranchus bishopi*: Collins 1991: 43. • Eunymorph.

***Cryptobranchus* sp. nov. 2: Hime 2017**

No available nomen is known for this taxon.

***Cryptobranchus* sp. nov. 3: Hime 2017**

No available nomen is known for this taxon.

Conclusion

The valid nomen of the Ohio River lineage, recovered as *Cryptobranchus* sp. nov. 1 by Hime (2017: 104), is *Cryptobranchus horridus* (Barton, 1807a). The nomen *Salamandra horrida* had been cited twice before what has long been considered the original publication of Barton (1808). The original description of the hellbender in Barton (1807a) mentioned three allelonyms for the nomen

of this species: *Salamandra horrida*, *Salamandra gigantea* and *Salamandra maxima*. Barton (1807b) acted as first reviser in choosing *Salamandra horrida* among them. So only this latter nomen should be used as valid to designate the Ohio River lineage. *Cryptobranchus horridus* (Barton, 1807a) could be known under the vernacular name ‘Ohio River hellbender’ (or in French ‘Ménopome de l’Ohio River’), while *Cryptobranchus alleganiensis* (Sonnini & Latreille, 1801b) could be called ‘Tennessee River hellbender’ (or ‘Ménopome de la Tennessee River’) and *Cryptobranchus bishopi* Grobman, 1943, ‘Ozark hellbender’ (or ‘Ménopome de l’Ozark’).

We discussed above the problem of the onymotope of *Cryptobranchus alleganiensis*, in agreement with the conclusions provided by Harper (1940: 720–721) citing the original discovery of the specimen by Michaux (1805). We report that the original book was actually first published in French by Michaux (1804). By removing the nomen *Salamandra horrida* Barton, 1807a from the synonymy of *Cryptobranchus alleganiensis*, *Salamandra salamandroides* Leuckart, 1821 becomes a junior synonym of *Cryptobranchus horridus* Barton, 1807a, the valid nomen of the nucleospecies of the genus *Cryptobranchus* Leuckart, 1821.

We present (above) the logonymic lists* of the genus *Cryptobranchus* and of the species *C. alleganiensis*, *C. horridus* and *C. bishopi*. Several synonyms of *C. alleganiensis*, until now considered the only species of its genus, should now be attributed to *C. horridus*. The nucleospecies of the genus *Protonopsis* Le Conte, 1824 is *Salamandra horrida* Barton, 1807a by subsequent monophory in Barnes (1828: 69). This fact seems to have been overlooked by all authors since then. Pending onymophoront review or precision on the onymotope, the synonymy of *Cryptobranchus terrassodactylos* Wellborn, 1936 with *C. alleganiensis* remains tentative. Among the five species level lineages identified by Hime (2017), two remain to be described and named: *Cryptobranchus* sp. nov. 2 and *Cryptobranchus* sp. nov. 3.

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Appendix 1. Glossary of technical nomenclatural terms

Each term is presented with the following information:

Term. • Etymology of term (G: Greek, L: Latin). • Short definition. • Antonym, if relevant. • Reference. • Equivalent term used in the *Code*, if available.

Hoc loco: Here, in the present work.

Airesy. • G: αἵρεσις (*airesis*), ‘choice, election’. • Any nomenclatural act of resolution of uncertainties, ambiguities and conflicts which may have remained after the original publication of a nomen: e.g., designation of a single specimen or nominal taxon as onomatophore* of a nomen introduced without this information or relative precedence between two nomina published at the same date. Airesies consist either in choices between several possibilities or in the brand new introduction of missing information: e.g. listing subsequently included specimens or nominal taxa in a nominal taxon which until then missed them. Choices made in airesies are left to the freedom of individual authors, but in some cases the *Code* contains Recommendations in this respect (e.g., the Recommendations of Article 74 concerning the designations of lectotypes). Once published, an airesy is irreversible and cannot be modified by individual authors but only by the Commission acting under its Plenary Power. • Dubois 2013: 3, 6. • *Code*: first reviser action.

Allelonym. • G: ἀλλήλων (*allelon*), ‘the one... the other...’; ὄνομα (*onoma*), ‘name’. • One of two (or several) synonymous nomina used both (or all) as valid for the same taxon (having the same content) in the same publication. • Dubois 2006: 183, 2011: 41. • *Code*: no term.

Alloneonym. • G: ἄλλος (*allos*), ‘other’; νέος (*neos*), ‘new’; ὄνομα (*onoma*), ‘name’. • Neonym having a partially or totally different etymology from its archaeonym*, i.e., not directly derived from it through unjustified emendation. • Antonym: autoneonym. • Dubois 2000: 52. • *Code*: new replacement name, *nomen novum*.

Ameletograph. • G: ἀμελής (*ameles*), ‘inattentive, careless’; γράφω (*grapho*), ‘I write’. • Spelling of a nomen used inadvertently in a publication by an author, scriptor*, editor, printer or publisher. • Antonym: meletograph*. • Dubois 2000: 54 (as ‘ameletonym’), 2010: 7. • *Code*: no term.

Anoplonym. • G: ἄνοπλος (*anoplos*), ‘unarmed’; ὄνομα (*onoma*), ‘name’. • Published but nomenclaturally unavailable nomen according to the Rules of the *Code*. • Antonyms: exoplonym*, hoplonym*. • Dubois 2000: 50. • *Code*: unavailable name.

Apograph. • G: ἀπό (*apo*), ‘away from, far from’; γράφω (*grapho*), ‘I write’. • A category of aponym*: any subsequent paragraph* of a hoplonym. • Antonym: protograph*. • Dubois 2010: 6. • *Code*: subsequent spelling.

Apohypse. • G: ἀπό (*apo*), ‘away from, far from’; ὑψος (*hypsos*), ‘height’. • A category of aponym: any subsequent parohypse* of a nomen. • Antonym: protohypse*. • Dubois 2010: 6. • *Code*: no term.

Aponym. • G: ἀπό (*apo*), ‘away from, far from’; ὄνομα (*onoma*), ‘name’. • Any subsequent paronym* of a protonym*, modified in spelling, rank and/or, if relevant, onymorph*. • Antonym: protonym. • Dubois 2000: 51. • *Code*: no term.

Aponymorph. • G: ἀπό (*apo*), ‘away from, far from’; ὄνομα (*onoma*), ‘name’; μορφή (*morphe*), ‘form, shape’. • A category of aponym: any subsequent paronymorph* of a nomen. • Antonym: protonymorph*. • Dubois 2010: 6. • *Code*: no term.

Archaeonym. • G: ἀρχαῖος (*arkhaios*), ‘ancient’; ὄνομα (*onoma*), ‘name’. • Original nomen that has been replaced by a neonym. • Dubois 2005a: 88, 2006: 169. • *Code*: no term.

Autoneonym. • G: αὐτός (*autos*), ‘same’; νέος (*neos*), ‘new’; ὄνομα (*onoma*), ‘name’. • Neonym having the same etymology as its archaeonym, i.e., directly derived from it through unjustified emendation. • Antonym: alloneonym*. • Dubois 2000: 52. • *Code*: unjustified emendation.

- Class-series.** • In the nomenclatural hierarchy, the nominal-series* ranked above the family-series*, which is not fully regulated by the *Code*. It includes nomina of taxa at the ranks of phylum, class, order, and any additional ranks that may be required. • Dubois 2000: 40. • *Code*: no term.
- Doxisonym.** • G: δόξα (*doxa*), ‘opinion’; ἴσος (*isos*), ‘equal’; ὄνομα (*onoma*), ‘name’. • A category of synonym: any of two or more nomina based on different onomatophores but considered, for subjective (taxonomic) reasons, to denote the same taxon, whose inclusive extension includes both their onomatophores. • Dubois 2000: 57. • *Code*: subjective synonym.
- Ergonymotope.** • G: ἔργον (*ergon*), ‘work, action’; ὄνομα (*onoma*), ‘name’; τόπος (*topos*), ‘place’. • Current and correct place(s) of collection of the onymophoront(s) of a species-series* nomen. • Frétey *et al.* 2018: 39. • *Code*: type locality.
- Ergotaxonomy.** • G: ἔργον (*ergon*), ‘work, action’; τάξις (*taxis*), ‘order, arrangement’; νόμος (*nomos*), ‘law, rule’. • Any classification considered valid in a certain work by a given author. • Dubois 2005b: 406. • *Code*: no term.
- Eugraph.** • G: εὖ (*eu*), ‘well, easily’; γράφω (*grapho*), ‘I write’. • Correct spelling of a nomen for a given taxon in a given ergotaxonomy*. • Antonym: nothograph*. • Dubois 2010: 7. • *Code*: correct original spelling, justified emendation, mandatory change.
- Eunymorph.** • G: εὖ (*eu*), ‘well, easily’; ὄνομα (*onoma*), ‘name’; μορφή (*morphe*), ‘form, shape’. • Correct onymorph of a nomen for a given taxon in a given *ergotaxonomy*. • Dubois 2010: 7. • *Code*: no term.
- Exoplonym.** • G: ἐξοπλος (*exoplos*), ‘disarmed’; ὄνομα (*onoma*), ‘name’. • Hoplonym permanently invalidated, either as a result of the Rules of the *Code* or of a specific action of the Commission under its Plenary Power. • Dubois 2000: 51. • *Code*: no term.
- Family-series.** • In the nomenclatural hierarchy, the highest-ranking nominal-series fully regulated by the *Code*. It includes nomina of taxa at the ranks of family, subfamily, tribe, subtribe, superfamily, and any additional ranks that may be required. • Dubois 2000: 40. • *Code*: family group [English text]; niveau famille [French text].
- Genus-series.** • In the nomenclatural hierarchy, the nominal-series ranked between the species-series and the family-series. It includes taxa at the ranks of genus and subgenus. • Dubois 2000: 40. • *Code*: genus group [English text]; niveau genre [French text].
- Gymnonym.** • G: γυμνός (*gymnos*), ‘naked’; ὄνομα (*onoma*), ‘name’. • A particular case of anoplonym: published but nomenclaturally unavailable nomen according to the *Code*, for failing to comply with the provisions of Articles 12 or 13 (i.e., missing a diagnosis or description, and in some cases an onomatophore). • Dubois 2000: 49–50. • *Code*: *nomen nudum*.
- Holoprotonymotope.** • G: ὅλος (*holos*), ‘whole, complete’; πρῶτος (*protos*), ‘first, earliest’; ὄνομα (*onoma*), ‘name’; τόπος (*topos*), ‘place’. • Single original place of collection of the onymophoront(s) of a species-series nomen. • Frétey *et al.* 2018: 38. • *Code*: type locality.
- Hoplonym.** • G: ὅπλον (*hoplon*), ‘tool, arm, weapon’; ὄνομα (*onoma*), ‘name’. • Nomenclaturally available nomen according to the Rules of the *Code*. • Dubois 2000: 50. • *Code*: available name.
- Isonym.** • G: ἴσος (*isos*), ‘equal’; ὄνομα (*onoma*), ‘name’. • A category of synonym: any of two or more nomina of the same nominal-series based on the same onomatophore. • Dubois 2000: 57. • *Code*: objective synonym.
- Lectallelonym.** • G:λεκτός (*lektos*), ‘chosen, picked out’; ἀλλήλων (*allelon*), ‘the one... the other...’; ὄνομα (*onoma*), ‘name’. • One among two allelonyms which was clearly given precedence relative to the other one through airesy in a subsequent publication. • Antonym: leipallelonym. • *Hoc loco* (Dubois, personal communication). • *Code*: no term.
- Lectophoront.** • G:λεκτός (*lektos*), ‘chosen, picked out’; φέρω (*phero*), ‘I bear’; ὄν, ὄντος (*on,ontos*), ‘being, individual’. • Single specimen subsequently designated among a series of symphoronts* for designation as onymophoront of a species-series nomen. • Dubois 2005b: 403. • *Code*: lectotype.
- Leipallelonym.** • G:λείπω (*leipo*), ‘I leave, I abandon’; ἀλλήλων (*allelon*), ‘the one... the other...’; ὄνομα (*onoma*), ‘name’. • One among two allelonyms which was clearly given subservience relative to the other one through airesy in a subsequent publication. • Antonym: lectallelonym. • *Hoc loco* (Dubois, personal communication). • *Code*: no term.
- Logonymic list.** • G:λόγος (*logos*), ‘speech, discourse’; ὄνομα (*onoma*), ‘name’. • Any list of nomina, including synonyms, aponyms and/or nomen uses or citations. • Dubois 2000: 59 (as ‘logonymy’); Dubois & Aesch 2019: 106. • *Code*: no term.
- Meletograph.** • G:μελέτη (*melete*), ‘attention, care’; γράφω (*grapho*), ‘I write’. • Spelling of a nomen used voluntarily in a publication by an author, scriptor, editor, printer or publisher. • Antonym: ameletograph. • Dubois 2000: 54 (as ‘meletonym’), 2010: 7. • *Code*: no term.
- Monophory.** • G:μόνος (*monos*), ‘single, unique’; φέρω (*phero*), ‘I bear’. • Qualification of a nomen created with and supported by an onomatophore composed of a single specimen (in the species-series) or taxomen* (in the three other nominal-series). • Dubois 2005b: 404. • *Code*: monotypy.
- Neonym.** • G:νέος (*neos*), ‘new’; ὄνομα (*onoma*), ‘name’. • Nomen established expressly to replace an already established nomen (its archaeonym) and having the same onomatophore. • Antonym: poieonym*. • Dubois 2000: 52. • *Code*: new replacement name, *nomen novum*.
- Neophoront.** • G:νέος (*neos*), ‘new’; φέρω (*phero* φέρω (*phero*), ‘I bear’; ὄν, ὄντος (*on,ontos*), ‘being, individual’. • Single

- specimen designated as onymophoront of a species-series nomen when the original or subsequent onymophoront(s) is/are considered to have been lost or destroyed. • Dubois 2005b: 403. • *Code*: neotype.
- Nomen** (plural **nomina**). • L: *nomen*, ‘name’. • Scientific name as defined and regulated by the *Code*. • Dubois 2000: 39. • *Code*: scientific name.
- Nominal-series**. • Any of the series of coordinated nomina interacting for priority and validity regarding synonymy, homonymy and nomenclatural acts: the species-series, genus-series*, family-series and class-series*. • Dubois 2000: 40. • *Code*: group of names [English text]; niveau nomenclatural [French text].
- Nothapograph**. • G: νόθος (*nothos*), ‘wrong, illegitimate’; ἀπό (*apo*), ‘away from, far from’; γράφω (*grapho*), ‘I write’. • A category of apograph*: Subsequent nothograph for a given taxon at a given rank in a given ergotaxonomy. • Frétey & Dubois 2019: 33. • *Code*: incorrect original spelling.
- Nothograph**. • G: νόθος (*nothos*), ‘wrong, illegitimate’; γράφω (*grapho*), ‘I write’. • Incorrect spelling of a nomen for a given taxon in a given ergotaxonomy. • Antonym: eugraph*. • Dubois 2010: 29. • *Code*: incorrect spelling.
- Nucleospecies**. • L: *nucleus* (from *nux*, ‘nut’), ‘nucleus, core, stone’; *species*, ‘idea, kind, species’. • Specific taxomen serving as onomatophore of a genus-series nomen. • Dubois 2005b: 404. • *Code*: type species.
- Onomatophore**. • G: ὄνομα (*onoma*), ‘name’; φέρω (*phero*), ‘I bear, I carry’. • Objective reference determining the taxonomic allocation of a nomen. In the species-series, onomatophores are specimens (see onymophoront); in the other nominal-series, they are taxomina. • Simpson 1940: 421. • *Code*: type, name-bearing type.
- Onymophoront**. • G: ὄνομα (*onoma*), ‘name’; φέρω (*phero*), ‘I bear’; ὄν, ὄντος (*on,ontos*), ‘being, individual’. • Specimen(s) serving as onomatophore of a nomen of the species-series. • Dubois 2005b: 403. • *Code*: type specimen.
- Onymotope**. • G: ὄνομα (*onoma*), ‘name’; τόπος (*topos*), ‘place’. • Place of collection of the onymophoront(s) of a species-series nomen. • Dubois 2005b: 404. • *Code*: type locality.
- Onymorph**. • G: ὄνομα (*onoma*), ‘name’; μορφή (*morphe*), ‘form, shape’. • Any particular association between genus-series substantive(s) and species-series epithet(s). • Smith & Pérez-Higareda 1986: 422. • *Code*: no term.
- Parograph**. • G: παρά (*para*), ‘near, beside, along’; γράφω (*grapho*), ‘I write’. • A category of paronym: any spelling, either original (protograph) or subsequent (apograph), ever used in the literature for a nomen. • Dubois 2010: 6. • *Code*: no term.
- Parohypse**. • G: παρά (*para*), ‘near, beside, along’; ὑψος (*hypsos*), ‘height’. • A category of paronym: any of the avatars, either original (protohypse) or subsequent (apohypse), of the rank of a nomen. • Dubois 2010: 6. • *Code*: no term.
- Paronym**. • G: παρά (*para*), ‘near, beside, along’; ὄνομα (*onoma*), ‘name’. • Any of the avatars of a nomen, either original (protonym) or subsequent (aponym), and concerning its spelling, rank and/or, if relevant, onymorph. • Dubois 2000: 53. • *Code*: no term.
- Paronymorph**. • G: παρά (*para*), ‘near, beside, along’; ὄνομα (*onoma*), ‘name’; μορφή (*morphe*), ‘form, shape’. • A category of paronym: any of the avatars, either original (protonymorph) or subsequent (aponymorph), of the onymorph of a nomen. • Dubois 2010: 6. • *Code*: no term.
- Poieonym**. • G: ποιέω (*poieo*), ‘to create’ and ὄνομα (*onoma*), ‘name’. • Brand new nomen, not proposed to replace an existing one. • Antonym: neonym. • Dubois 2017: 12. • *Code*: no term.
- Protograph**. • G: πρῶτος (*protos*), ‘first, earliest’; γράφω (*grapho*), ‘I write’. • A category of protonym: original parograph of a nomen in the publication where it was originally introduced. • Antonym: apograph. • Dubois 2010: 6. • *Code*: original spelling.
- Protohypse**. • G: πρῶτος (*protos*), ‘first, earliest’; ὑψος (*hypsos*), ‘height’. • A category of protonym: original rank of a nomen. • Antonym: apohypse. • Dubois 2010: 6. • *Code*: no term.
- Protonym**. • G: πρῶτος (*protos*), ‘first, earliest’; ὄνομα (*onoma*), ‘name’. • Original spelling, rank and/or, if relevant, onymorph of a nomen. • Antonym: aponym. • Dubois 2000: 51. • *Code*: no term.
- Protonymorph**. • G: πρῶτος (*protos*), ‘first, earliest’; ὄνομα (*onoma*), ‘name’; μορφή (*morphe*), ‘form, shape’. • A category of protonym: original onymorph of a nomen. • Antonym: aponymorph. • Dubois 2010: 6. • *Code*: no term.
- Protonymotope**. • G: πρῶτος (*protos*), ‘first, earliest’; ὄνομα (*onoma*), ‘name’; τόπος (*topos*), ‘place’. • Original place(s) of collection of the onymophoront(s) of a species-series nomen as it is presented in the original publication. Two categories: holoprotonymotope and symprotonymotope. • Frétey *et al.* 2018: 38. • *Code*: type locality.
- Scriptor** (plural **scriptores**). • L: *scriptor*, ‘writer, author’. • In the context of zoological nomenclature, name(s) of the person(s) to whom the first use of an aponym is credited, i.e., whose name(s) appear(s) as signatory of the work where this aponym first appeared itself—not established through subsequent investigation (see Dubois 2008a). • Dubois 2000: 42 (as ‘first-user’), 2013: 3 (as ‘primoscriptor’), 2015: 15. • *Code*: no term.
- Species-series**. • In the nomenclatural hierarchy, the lowest-ranking nominal-series which is fully regulated by the *Code*, ranked below the genus-series. It includes nomina of taxa at the ranks of species, subspecies, species aggregate and subspecies aggregate. • Dubois 2000: 40. • *Code*: species group [English text]; niveau espèce [French text].
- Symphoront**. • G: σύν (*syn*), ‘together’; φέρω (*phero*), ‘I bear’; ὄν, ὄντος (*on,ontos*), ‘being, individual’. • One of several specimens originally used collectively as onomatophore of a species-series nomen. • Dubois 2005b: 403. • *Code*: syntype.
- Symprotonymotope**. • G: σύν (*syn*), ‘together’; πρῶτος (*protos*), ‘first, earliest’; ὄνομα (*onoma*), ‘name’; τόπος (*topos*),

‘place’. • Any one of several original places of collection of the onymophoronts of a species-series nomen. • Frétey *et al.* 2018: 39. • *Code*: type locality.

Taxomen (plural **taxomina**). • G: τάξις (*taxis*), ‘order, arrangement’; L: *nomen*, ‘name’. • The permanent association between a nomen (hoplonym) and an onomatophore, allowing objective, non-ambiguous and stable allocation of nomina to taxa. • Dubois 2000: 40. • *Code*: nominal taxon.

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