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The misidentification of *Turdus ustulatus* Nuttall, and the names of the nightingale-thrushes (Turdidae: *Catharus*)

by Matthew R. Halley

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Summary.—An extensive review of *Turdus ustulatus* Nuttall, 1840, and *T. swainsoni* Cabanis *in* Tschudi, 1845, and comparison of John K. Townsend's extant study skins (1835–36) to freshly prepared skins of *Catharus ustulatus* (Nuttall), *C. swainsoni* (Cabanis) and *C. guttatus* (Pallas, 1811), reveals that the original description of *T. ustulatus* Nuttall, 1840, was most likely based on a single specimen (now lost) of Hermit Thrush *C. guttatus* (Pallas, 1811). The original description of *T. swainsoni* Cabanis *in* Tschudi, 1845, is also not unambiguously identifiable and the type material is untraceable. To resolve and stabilise nomenclature, (1) a petition will be filed with the International Commission of Zoological Nomenclature (ICZN) to set aside Art. 75.3.5 of the *Code* (ICZN 1999) so that a neotype of *T. ustulatus* Nuttall, 1840, can be designated; and (2) the name *C. swainsoni* (Cabanis *in* Tschudi, 1845) is herein rescued via neotypification. Finally, updated common names are proposed to standardise the English group name of the genus to 'nightingale-thrush' and reduce further confusion with respect to common names that have been applied to multiple taxa. This is the second in a series of papers concerning historical aspects of *Catharus* taxonomy and nomenclature.

The convoluted nomenclature of the nightingale-thrushes (Aves: Turdidae: *Catharus*) began with a taxonomically composite species (*Turdus minor* J. F. Gmelin, 1789) that was a source of widespread confusion until the mid-19th century. In a recent paper, I reviewed the early history of *T. minor* and demonstrated that Alexander Wilson (1766–1813), who split the composite *T. minor* into two species that were also composites (*T. solitarius* and *T. mustelinus*; Wilson, 1812), did not correctly distinguish any of the five species now recognised as breeders in eastern North America (Halley 2018). Those species are: Hermit Thrush *Catharus guttatus* (Pallas, 1811), Veery *C. fuscescens* (Stephens, 1817; for neotypification see Halley 2018), Swainson's Thrush *C. ustulatus* (Nuttall, 1840), Grey-cheeked Thrush *C. minimus* (Lafresnaye, 1848) and Bicknell's Thrush *C. bicknelli* (Ridgway, 1882). The confusion of Wilson's composites had downstream effects on the understanding of Charles Lucien Bonaparte (1803–57) and John James Audubon (1785–1851), who likewise failed to distinguish the five eastern species (Halley 2018).[1] The number of species in eastern North America was gradually resolved by Giraud (1844), Brewer (1844), Baird *et al*. (1858) and Ridgway (1882).

Here, I disentangle the taxonomic history of Western Thrush *T. ustulatus* Nuttall, 1840, which has long been recognised as the first description of the western (coastal) subspecies of Swainson's Thrush *C. u. ustulatus* (AOU 1998: 505, Mack & Yong 2000, Ruegg 2007). The Swainson's Thrush complex is comprised of two genetic clades (recognised as species

[1] Another factor, overlooked by Halley (2018), which probably exacerbated the confusion of Wilson's composite thrushes is that Sir William Jardine (1800–74) inadvertently switched the plate numbers for 'Tawney Thrush' [*sic*] and 'Hermit Thrush' in his edition of Wilson's *American ornithology* (Wilson *et al*. 1832). Audubon, who considered Jardine's work 'an enormous quantity of trash, all compilation' (Corning 1969, 2: 29), nevertheless consulted it.

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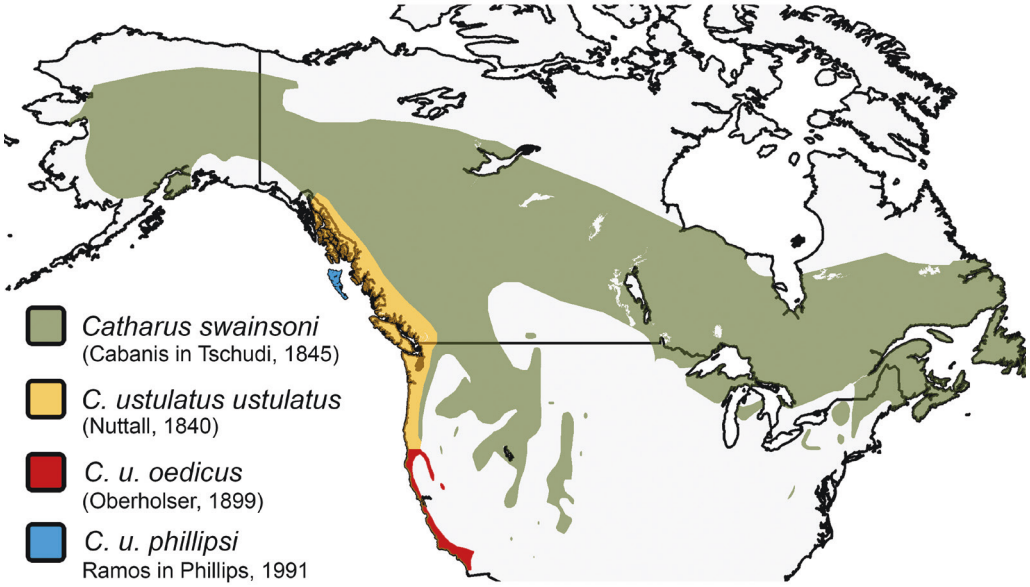


Figure 1. Map of the North American breeding ranges of *Catharus swainsoni* (Cabanis *in* Tschudi, 1845), *C. u. ustulatus* (Nuttall, 1840), *C. u. oedicus* (Oberholser, 1899) and *C. u. phillipsi* Ramos *in* Phillips, 1991. The contact zone of *C. u. ustulatus* and *C. u. oedicus* in northern California is poorly defined and requires further study (see Bond 1963: 378). Data provided by BirdLife International and *Handbook of the birds of the world Alive* (2018). Bird species distribution maps of the world. V. 2018.1. Available at http://datazone.birdlife.org/species/requestdis.

or subspecies) that were evidently geographically isolated (during the breeding season) in forested refugia during the Last Glacial Maximum (LGM). Following deglaciation, the populations expanded and came into secondary contact in the mountains of northern Washington and British Columbia, where they formed a narrow hybrid zone that persists to the present day (Ruegg & Smith 2002). Many recent authors (e.g., Mack & Yong 2000, Ruegg 2007) have classified the western (coastal) clade as *C. u. ustulatus* (Nuttall, 1840) and the eastern (inland) clade as *C. u. swainsoni* (Cabanis *in* Tschudi, 1845), although some authors have elevated the two clades to species rank (e.g, Piacentini *et al*. 2015, del Hoyo & Collar 2016). Speciation has occurred in *Catharus* multiple times despite periodic episodes of gene flow between incipient (and even non-sister) species (Bay & Ruegg 2017, Everson *et al*. 2019) and the taxa in question meet the criteria for species rank under nearly every species concept including 'relaxed' approaches to the biological species concept (BSC) that permit some gene flow between species (de Queiroz 2007). For these reasons, the two clades are herein classified as sister species: *C. ustulatus* (coastal) and *C. swainsoni* (inland). Their generalised breeding ranges are shown in Fig. 1.

History of Townsend's specimens of western thrushes

The original description of *T. ustulatus* was based on two specimens that John K. Townsend (1809–51) collected during the second Wyeth expedition (1834–37) while camped on the Columbia River near Vancouver, Washington. They were the first *Catharus* specimens from western North America to reach the eastern seaboard, and they arrived before the confusion surrounding the eastern species was resolved.

Thomas Nuttall (1786–1859), the seasoned botanist, explorer and author of *Manual of the ornithology of the United States* (1832, 1834; hereafter, *Manual*), was Townsend's companion

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and mentor on the first part of the expedition. However, the two naturalists parted ways in September 1835, which had consequences for the fate of Townsend's specimens. Nuttall sailed to the Sandwich Islands (Hawaii) and then 'around the Horn' of South America to eastern North America, where he landed in summer 1836 (Graustein 1967). Meanwhile, Townsend stayed in the Pacific Northwest for another year, and eventually returned to Philadelphia in November 1837 (Mearns & Mearns 2007).

A collection of specimens that Townsend shipped in September 1835, which included two study skins labelled '*Turdus Wilsoni*?' and one labelled '*Turdus minor*,' reached the Academy of Natural Sciences of Philadelphia (ANSP) in July 1836, shortly before Nuttall's return. The invoice from Townsend's 1835 shipment is preserved at the American Philosophical Society (APS) Library, Philadelphia, PA (Mss.B.M843). Nuttall and Audubon examined the three western specimens of *Catharus* from Townsend's consignment at ANSP in September 1836, but neither recognised them as new species. This was a consequence of their general confusion with respect to Wilson's composites (see Halley 2018). Audubon purchased duplicates with Nuttall's approval, including (presumably) one of the two '*Turdus Wilsoni*?' specimens, which he took to London in July 1837. Audubon then remained in Europe until summer 1839, supervising the completion of *The birds of America* (1827–38) and writing the final two volumes of *Ornithological biography* (1838–39) (Fries 2006).

Meanwhile, Townsend returned to Philadelphia in November 1837 with an additional collection, approximately three times larger than the 1835 shipment (Mearns & Mearns 2007: 324). Edward Harris (1799–1863) purchased more duplicates for Audubon, and Townsend also sent many specimens directly to Audubon so that he could sell them to European collectors (see Derby List, in which one specimen of '*T. Wilsonii*' is mentioned; Mearns & Mearns 2007: 330). Thus, Audubon had access to multiple specimens of western *Catharus* from the Townsend collection in 1838, when he wrote:

> 'I have by me a female specimen of a Thrush sent me by Dr Townsend, who procured it on the Columbia River on the 19th June 1838, and which he considered as new,* but which I find to differ in no other respect from specimens of *Turdus Wilsonii* than in having some of the spots on the sides of the neck and the breast of a darker brown. This skin measures seven inches two and a half twelfths in length.' (Audubon 1839: 203–204)

An annotation (*) by Townsend in the margin of the ANSP copy of *Ornithological biography* vol. 5 (Audubon 1839: 204, ANSP Library, QL674.A915) reads: '*mistake. The specimen was marked <u>*Turdus Wilsonii*</u>? J.K.T.' (Fig. 2). This annotation was later mis-

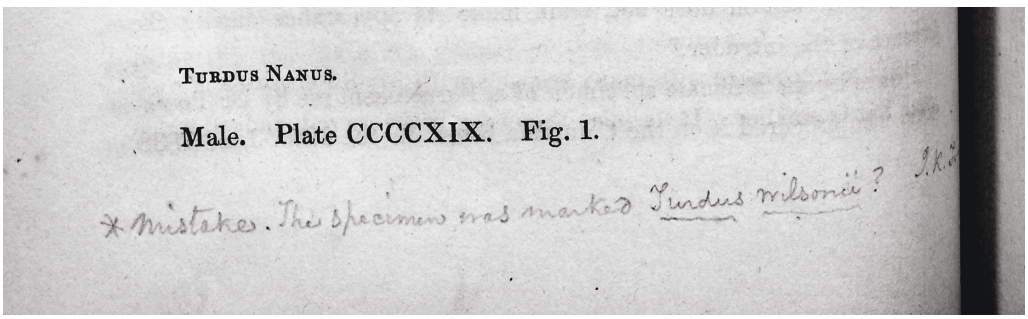


Figure 2. Annotation by John K. Townsend in the ANSP copy of *Ornithological biography*, vol. 5 (Audubon 1839: 204, ANSP Library: QL674.A915): '*mistake. The specimen was marked *Turdus Wilsonii*? J.K.T.' The image contrast has been boosted to render Townsend's faint pencil markings more visible. (Matthew R. Halley)

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transcribed by Stone (1906: 312), who inadvertently replaced Townsend's question mark with a period. Townsend included question marks on his labels and specimen invoice because he was uncertain about the identifications of some specimens ('*Turdus Wilsoni*?'), not because, as Audubon presumed, he thought they represented a new species (APS Library, Mss.B.M843).

Townsend's original data are missing from all extant specimens of *Catharus* attributed to him, except one (USNM 2040), which bears a label in Townsend's hand with the name *Merula silens* Swainson (*in* Swainson & Richardson 1831)—not *T. Wilsoni*. Therefore, the specific identity of the specimen mentioned by Audubon (1839: 203) cannot be verified. The year '1838' in Audubon's comment is a typographical error, because Townsend had already returned to Philadelphia by late 1837. Nevertheless, a handwritten '5' is easily mistaken for an '8,' and Townsend's 1835 specimen invoice included the same uncertain identification: '*Turdus Wilsoni*?' (APS Library, Mss.B.M843). For these reasons, it is plausible (but not certain) that the specimen referenced by Audubon (1839: 203–204) was the duplicate he purchased in 1836 (without Townsend's knowledge, despite Audubon's claim that Townsend 'sent' it to him), rather than one of the specimens he acquired in 1838.

Meanwhile, from 1838 to early 1840, Nuttall was in Philadelphia preparing his next major botanical work, a 200-page tome that would eventually be peer-reviewed and published by the APS (Nuttall 1841). Botany was Nuttall's primary focus and expertise; his ornithological work was not executed with the same breadth of experience or attention to detail (Graustein 1967). His *Manual* was a commercial venture that, unlike most of his botanical writings, was published without peer review and contained 'long passages without acknowledgment and with but comparatively slight verbal changes from [Alexander] Wilson' ... '[Nuttall] probably knew less about birds than has been commonly supposed' (Brewster 1906: 79–80). George Ord (1781–1866), a capable ornithologist and editor of Wilson's final (posthumous) volumes, upon the publication of the *Manual*, wrote in private correspondence: 'I know that [Nuttall] is ignorant of ornithology; and I further know that he is a sorry scoundrel' (APS Library, Mss.B.Or2).

During his residency in Philadelphia in 1838–40, or perhaps earlier, Nuttall made a cursory study of the remnants of Townsend's collection of western birds. However, by that time, relatively few of Townsend's specimens remained at ANSP; most had been dispersed among private collectors (Mearns & Mearns 2007). Townsend had shipped dozens of specimens to Audubon, to be sold in Europe, and generously supplied the cabinets of his friends including Ezra Michener (1794–1887), with whom he stayed while preparing the manuscript of his travelogue, *Narrative of a journey* (Townsend 1839).

Audubon visited Philadelphia on 10–13 February 1840, according to a letter ('I left New York on the 10th Inst. spent a few days in Philadelphia…,' Corning 1969, 2: 231), but there is no evidence that he saw Nuttall during that short trip. Nor is there evidence that Audubon knew of Nuttall's intention to describe a new species of thrush from Townsend's collection. Audubon usually stayed at Harris' home in Moorestown, NJ, when he visited the Philadelphia region (see Corning 1969), and probably spent very little time in Philadelphia itself. Meanwhile, Nuttall was busy with preparations to relocate from Philadelphia to Cambridge, Massachusetts, because he had been hired to give a series of botanical lectures for the Lowell Institute in Boston. Nuttall departed in late February 1840, approximately two weeks after Audubon passed through Philadelphia (Graustein 1967).

The publishers of Nuttall's *Manual* were based in Cambridge and they expressed interest in publishing an updated (second) edition (Nuttall 1840). Nuttall's new ornithological material included *c*.150 pages of information from his Wyeth expedition journals (now lost) and various notes concerning specimens he had examined during his residency in

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Philadelphia. There is no evidence that Nuttall took a collection of bird skins to Cambridge. The manuscript that contained the description of Western Thrush *T. ustulatus* Nuttall, 1840, was drafted rapidly, without specimens at hand, and published within four months of Nuttall's arrival in Cambridge (Graustein 1967: 350).

The material basis of *Turdus ustulatus* Nuttall, 1840

The scientific description of *T. ustulatus* was based on a female specimen collected by Townsend on 'the 10th of June' (1835 or 1836) on the Columbia River, presumably near Vancouver, Washington. Nuttall (1840) also described vocalisations given by multiple birds that were apparently neither collected nor clearly observed ('as soon as seen [it] flits rapidly through the thicket') and a nest found 'about the close of July [1835]…in the prairies of Wahlamet' (=Willamette River valley, Oregon). However, there is no evidence that the nest or vocalising birds were collected. Nuttall (1840) also cited Audubon's (1839: 203–204) note about the 'female specimen of a Thrush [collected]…on the 19th June [1835]' among the synonyms of *T. ustulatus*. As explained above, Audubon's specimen was likely the duplicate sold to him in 1836, which may explain Nuttall's comment that 'now' he had only one specimen for description:

> '… the only specimen from which I am now able to describe the species [*T. ustulatus*] is that of a female procured on the banks of the Columbia on the 10th of June by my friend Mr. Townsend. This neglect arose from the too hasty conclusion that it was no other than the well known Wilson's Thrush.' (Nuttall 1840: 401)

Therefore, the description of *T. ustulatus* Nuttall, 1840, was based on two female syntypes: one mentioned by Audubon (1839: 203–204) and the other described directly by Nuttall himself. Two of Townsend's study skins of *C. ustulatus* are extant: USNM 2040 (Fig. 3) and ANSP 23644 (Fig. 4). Both have been promoted as 'the only specimen' described by Nuttall (1840). However, paradoxically, neither specimen matches Nuttall's description of the dorsal plumage, which actually presents a closer match to *C. guttatus* than to *C. ustulatus*: 'Above olive-brown, a little darker on the head; the tail strongly tinged with rufous.' Just a few pages prior to his description of *T. ustulatus*, Nuttall (1840: 394–395) used those exact words to describe the dorsal plumage ('olive-brown') and tail ('strongly tinged with rufous') of Hermit Thrush *T. solitarius* Wilson, 1812; and he considered the bird in Audubon's Pl. 58 (= *C. g. faxoni* Bangs & Penard, 1921) to be an 'excellent' representation of *T. solitarius* (see Nuttall 1840: 393, and Fig. 6 in Halley 2018).

Spencer F. Baird (1823–87), who acquired USNM 2040 from Audubon, assumed incorrectly that it was Nuttall's syntype (Baird *et al*. 1858: 215). A plate (81) depicting USNM 2040 was published by Baird *et al*. (1860: VII) and claimed as 'Mr. Nuttall's type' in the introductory pages (Fig. 5). Baird also pencilled 'Type of Nuttall?' in the margin of his personal copy of Pl. 81, deposited in the Smithsonian Library (see Deignan 1961: 432). This claim was later repeated by Hellmayr (1934: 457, 'type [of *T. ustulatus*] in U. S. National Museum') and Deignan (1961: 431, 'it may be assumed that [USNM 2040] is indeed the type, and that it is a female collected on June 10, 1835, as stated in Nuttall's description').

However, one label attached to USNM 2040, written in Baird's own hand, records the sex of the bird as male ('m,' see Fig. 3) and his description of that specimen ('uniform reddish brown [dorsal plumage and tail], with a faint olivaceous tinge,' Baird *et al*. 1858) does not match Nuttall's (1840) description of the *T. ustulatus* type ('above olive-brown, a little darker on the head; the tail strongly tinged with rufous'). The illustration of USNM 2040 in Pl. 81 matches Baird *et al*.'s (1858) description, showing a more or less uniform reddish-brown

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Figure 3. USNM 2040 and its two oldest labels. The top label was apparently written by John K. Townsend: 'Silent Thrush.– / *Merula silens*. Swainson p. 186. / Columbia River. Townsend.' The bottom label was written by Spencer F. Baird: '*Turdus wilsonii* Sw. / 2040 / Columbia River / J. K. Townsend / m[ale]' (Matthew R. Halley)



Figure 4. ANSP 23644 and its label. See text for information concerning provenance. The text '♀ JKT' was purportedly copied from the base of the mount on which the bird was displayed during the mid-19th century, but the sex is recorded as male ('♂') in the ANSP specimen ledger (ANSP Archives, coll. 54, box 3). Furthermore, the red type label has been defaced and there are no data linking this specimen to Nuttall (Matthew R. Halley)

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Figure 5. Cropped lithographic image of USNM 2040 ('*Turdus ustulatus*') from Pl. 81 in Baird *et al*. (1860), ostensibly depicting 'Mr. Nuttall's type' (see Baird *et al*. 1860: VII). Produced by [J. T.] 'Bowen & Co. lith & col.' in Philadelphia, Pennsylvania. It is reproduced here courtesy of Smithsonian Libraries (QL681.B138). Portions of another image (*T. aliciae*) have been digitally removed from the upper right of this figure for clarity.

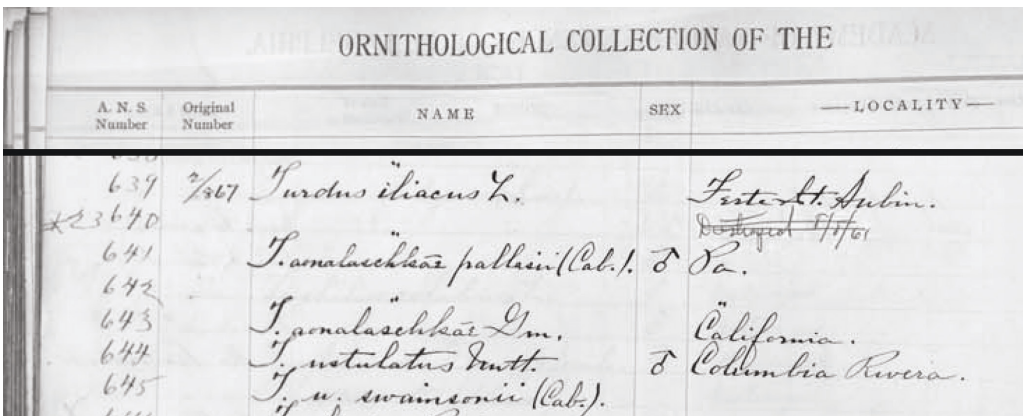


Figure 6. Digital scan of the ANSP Ornithology specimen ledger No. 3 (ANSP Archives, coll. 54, box 3), in which the sex of ANSP 23644 is recorded as male ('♂'). This contradicts the 'original' data on the defaced specimen label (see Fig. 4).

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coloration and no contrast between the back and tail (Fig. 5). There is no colour contrast in the plumage of this specimen today, after 160 years (Fig. 3). Thus, the discrepancy between Nuttall's (1840) and Baird *et al*.'s (1858) descriptions cannot be explained as a by-product of post-mortem change.

Stone (1899: 19) claimed that ANSP 23644, which is similarly coloured to USNM 2040, was Nuttall's study skin of *T. ustulatus*, but not because the skin bore a label indicating its type status or because it matched Nuttall's (1840) description. Stone merely assumed that the specimen was at ANSP because Nuttall had worked there after returning from the west, and it was the only specimen of *C. ustulatus* from Townsend's collection that could be located: '...[*T. ustulatus* was] based on a Townsend specimen in the ANSP collection which I have identified as…' (Stone 1899: 19). In an unpublished memorandum dated 1893 and entitled 'Explanations in regard to the Cataloguing of the Collection', Stone confided that 'no numbers were placed on the specimens to fix their identity' when he began his work on the ANSP bird collection in March 1888 (ANSP Archives, coll. 54, box 4). His determination of Nuttall's type of *T. ustulatus* was apparently not based on evidence, but guesswork.

The remnants of a wire armature are visible, evidence that ANSP 23644 was once mounted for display. However, there is no original label or stand, only a secondary label that bears the following information, purportedly copied from the base of the (now missing) stand: '♀ JKT.' However, Stone unambiguously recorded the sex of the bird as male ('♂') in the ANSP specimen ledger (Fig. 6, ANSP Archives, coll. 54, box 3) and some additional text was (later?) forcibly scratched off the red type label (Fig. 4). The ledger is the oldest available primary source. This begs the question whether the original sex data was scratched off the type label and replaced with false data that matched Nuttall's description. In any case, there is no provenance with ANSP 23644 that connects the specimen to Nuttall, nor does the plumage of the bird match Nuttall's (1840) description of the *T. ustulatus* syntype.

Specimen comparisons

More than a century after Nuttall's description of *T. ustulatus*, Bent (1949: 167) aptly summarised the field marks that distinguish *C. ustulatus* and *C. guttatus* in the region where Townsend collected Nuttall's type, though it appears that he too overlooked the paradox:

> 'The russet-backed thrush [*C. ustulatus*] is not likely to be confused with any other bird on the Pacific slope except with one of the hermit thrushes, but the uniform russet-brown of its back is easily distinguished from the contrasted brown back and rufous tail of the hermits; furthermore, the haunts of the two, during the breeding season at least, are quite different.' (Bent 1949: 167)

To further investigate the identity of *T. ustulatus* Nuttall, 1840, I prepared a fresh series of adult specimens of *C. ustulatus* (n = 10) and *C. guttatus* (n = 10) from coastal Washington, west of the Cascade Mountains, and directly compared them to ANSP 23644 (*C. ustulatus*) and ANSP 16091 (*C. guttatus*), two of the four *Catharus* specimens from Townsend's collection now extant. I also prepared a series of *C. swainsoni* adults (n = 5) from eastern North America, yielding a total sample of 27 specimens for direct colour comparison (Table 1; 25 fresh, two historical). I used the rectangular (card-stock) window provided in *Color standards and color nomenclature* (Ridgway 1912) to match the capitalised colour names to the plumage just below the nape, and to the anterior and posterior portions of the tail. Most of the fresh specimens were 1–6 years old when they were scored, about the same age as the *T. ustulatus* syntype when Nuttall examined it in 1838–39. I also examined USNM 2040 (*C. ustulatus*) and compared it to other historical specimens in the USNM

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TABLE 1
Specimens used for colour comparison of *Catharus ustulatus* (*n* = 10), *C. swainsoni* (*n* = 5) and *C. guttatus* (*n* = 10). All specimens were prepared by Matthew R. Halley and deposited in the ornithology collection at the Academy of Natural Sciences of Drexel University (ANSP). Sex categories are female (F), male (M) and unknown (U). Localities are given as state abbreviation (PA = Pennsylvania; WA = Washington): county: town or site. The table is organised by species and date.

Species	ANSP No.	Sex	Date	Locality
C. ustulatus	204296	F	25 Aug 2013	WA: Skagit: Burlington
C. ustulatus	204297	F	1 Sep 2014	WA: King: Vashon
C. ustulatus	204299	U	14 Sep 2014	WA: King: Vashon
C. ustulatus	204300	M	26 Aug 2015	WA: Pierce: Gig Harbor
C. ustulatus	204301	U	27 Aug 2015	WA: Pierce: Tacoma
C. ustulatus	205164	M	10 Sep 2015	WA: Pierce: Tacoma
C. ustulatus	204295	U	13 Aug 2016	WA: Skagit: Anacortes
C. ustulatus	205165	F	28 Sep 2016	WA: Pierce: Tacoma
C. ustulatus	205167	M	2 May 2017	WA: King: Vashon
C. ustulatus	204520	M	23 May 2017	WA: King: Vashon
C. swainsoni	204304	F	20 May 2011	PA: Berks: Nolde Forest
C. swainsoni	204219	F	27 Sep 2016	PA: Montgomery: Gwynedd
C. swainsoni	204235	F	21 May 2017	PA: Luzerne: Drums
C. swainsoni	205953	M	Aug 2017	PA: Delaware: Wayne
C. swainsoni	207077	M	17 Jul 2019	PA: Warren: Allegheny National Forest
C. guttatus	204316	U	6 Nov 2003	WA: Skagit: Anacortes
C. guttatus	204314	F	7 Jan 2004	WA: King: Vashon
C. guttatus	204519	M	14 Apr 2015	WA: Skagit: Anacortes
C. guttatus	204318	F	22 Sep 2015	WA: Okanogan: Twisp
C. guttatus	204317	U	15 Oct 2015	WA: Pierce: Tacoma
C. guttatus	204518	F	6 Nov 2015	WA: King: Vashon
C. guttatus	204313	M	22 Nov 2015	WA: King: Vashon
C. guttatus	204315	M	11 Oct 2016	WA: Skagit: Anacortes
C. guttatus	204517	M	11 Jan 2017	WA: Whatcom: Bellingham
C. guttatus	205172	M	30 Apr 2017	WA: King: Seattle

bird collection, but, for logistical reasons, was unable to directly compare it to the ANSP specimens or Ridgway (1912).

The sample of recent specimens from western North America comprises, in most cases, the victims of cats and / or window collisions, salvaged by volunteers during the spring and autumn migratory periods (2003–17) and preserved (frozen) by G. Shugart and D. Paulson at the Univ. of Puget Sound. The migratory flyway west of the Cascades is utilised by 'pure' *C. ustulatus* individuals and hybrid *C. ustulatus* × *C. swainsoni* (Delmore & Irwin 2014). Breeding populations of pure *C. ustulatus* occur near Vancouver, Washington, where Townsend presumably collected Nuttall's syntypes, and extend north into the Seattle area. Vancouver is *c.*275 km south-west of the southern periphery of the hybrid zone and Seattle is *c.*70 km west. For this reason, without genotyping the birds, I cannot be certain that the sample of *C. ustulatus* study skins, from the spring and autumn migratory periods, does not contain any individuals of hybrid origin.

In the fresh *C. ustulatus* series, examined in 2018, the dorsal plumage and tails were more or less uniform Olive-Brown (Fig. 7). The dorsal plumage of ANSP 23644 was also more or less uniform Olive-Brown, though some parts of the specimen have faded in the direction of Saccardo's Umber, presumably during the years when it was mounted for

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Figure 7. Plumage colour comparison of (A) ANSP 23644, collected and prepared by John K. Townsend near Vancouver, Washington, and claimed as the 'type of Nuttall' by Stone (1899: 19), and (B–D) three relatively fresh specimens of *Catharus ustulatus*, prepared by M. R. Halley: (B) ANSP 204297, a female that died in a window collision on 1 September 2014, on Vashon Island, King County, Washington (prep. = MRH88); (C) ANSP 205167, a male that died in a window collision on 2 May 2017, also on Vashon Island (prep. = MRH146); (D) ANSP 205165, a bird of uncertain sex that died in a window collision on 28 September 2016, in Tacoma, Pierce County, Washington (prep. = MRH141). These birds died during migration in a pathway used by 'pure' individuals of *C. ustulatus* and hybrid *C. ustulatus* × *C. swainsoni* (see Delmore & Irwin 2014) (Matthew R. Halley)

display. Like fresh specimens of *C. ustulatus*, there is no obvious contrast in colour between the back and tail of ANSP 23644, nor any suggestion that there ever was such a pattern. Neither is such a contrast evident in the fresh series of *C. swainsoni*, the backs and tails of which are more or less uniform Brownish Olive. The tails of some *C. ustulatus* specimens exhibit a subtle tendency toward Sepia, but this difference would not be well characterised by Nuttall's (1840) description of a 'tail *strongly* tinged with rufous' (my italics), which was identical to his description of Hermit Thrush *T. solitarius* Wilson (see Nuttall 1840: 394–395). In conclusion, it appears that Nuttall (1840) actually described one of Townsend's fresh *C. guttatus* specimens from western Washington, as evidenced by fresh specimens from that region with Brownish Olive back plumage (below the nape) and tails that transition (anterior to posterior) from Prout's Brown to Mummy Brown (Fig. 8). However, Nuttall's (1840) and Audubon's (1839) syntypes are apparently no longer extant. Neither of the two extant specimens of *C. guttatus* (or *C. ustulatus*) from the Townsend collection are a female

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Figure 8. Plumage colour comparison of (A) a female *C. guttatus* (Pallas) collected and prepared by John K. Townsend in 'May' (1835 or 1836) on the 'Columbia River' (ANSP 16090), and (B–D) three specimens prepared by Matthew R. Halley: (B) ANSP 204316, an unsexed specimen that died in a window collision on 6 November 2003, on Salmon Beach Road, Skagit County, Washington (prep. = MRH87); (C) ANSP 204318, a female that died in a window collision on 22 September 2015, in Twisp, Okanogan County, Washington (prep. = MRH91); and (D) ANSP 204519, a male that died in a window collision on 14 April 2015, in Anacortes, Skagit County, Washington (prep. = MRH134) (Matthew R. Halley)

collected on the '10th of June' as described by Nuttall (1840), or a female collected on '19th June [1835]' as described by Audubon (1839: 203–204): MCZ 16298 is a male and ANSP 16091 was collected in 'May'.

Behavioural observations and nest description

The behavioural notes given by Nuttall (1840) in association with *T. ustulatus*, and his description of a nest purportedly made by that species, were not based on specimens but on Nuttall's vague recollections and (apparently) field notes from 1835. If anything, they cast more doubt on Nuttall's understanding of the species in question:

> 'At intervals, on the commencement of the breeding period, we heard their notes, bearing indeed, some resemblance to the quaint warble of the Veery or Wilson's Thrush [i.e. Wilson's composite *T. mustelinus*, see Halley 2018], though quite distinct, and easily recognizable from the notes of that Atlantic species. Its song was also more brief and interrupted, and the bird more shy and difficult of access. The warble of one of these birds which I heard at Chinhook, near the estuary of the Columbia [= Chinook,

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> Washington], on the 4th of July [1835], resembled *wit wit t'villia*, and *wit wit t'villia t'villia*, cheering the dark solitudes of evergreens where all day he remains recluse like our Wood Thrush: his recognition call is *'wit 'wit* which he utters also when surprised, and as soon as seen flits rapidly through the thicket.'

These vocalisations, at least the calls (*'wit 'wit*), seem to be a good match to *C. ustulatus*, but some calls of *C. guttatus* have been similarly described ('*quit quit*', Dellinger *et al*. 2012). The transliteration of the song (*wit wit t'villia t'villia*) is also vague and could apply also to *C. guttatus*. Wood Thrush *Hylocichla mustelina* (J. F. Gmelin, 1789), an eastern species, does not typically range west of the Rocky Mountains.

Nuttall's (1840) narrative was written as if he and Townsend distinguished *T. ustulatus* from Wilson's composite *T. mustelinus* in the field: '...we heard their notes...easily recognizable from the notes of that Atlantic species.' However, neither man recognised that there was a new species until years later. Remember that, in 1836, Nuttall did not think that either of the two specimens of '*T. Wilsonii*?' were a new species when he and Audubon examined Townsend's collection in Philadelphia, and Townsend wrote (after Nuttall's departure) on 11 April 1836: 'The Wilson's Thrush (*Turdus wilsonii*)…breeds here [near Vancouver] & is consequently, for a part of the year in full song' (see Mearns & Mearns 2007: 359). Nuttall even sanctioned the sale of one of the specimens to Audubon after coming to the 'hasty conclusion that it was no other than the well known Wilson's Thrush' (Nuttall, 1840). Furthermore, the vocalisations that Nuttall apparently transcribed in his field journal (now lost) were not uttered by the same individuals that Townsend collected, nor is there evidence that they were heard by Nuttall on the same day Townsend collected the specimens. Thus, it seems that the extent of Nuttall's first-hand knowledge of the behaviour of these secretive birds was overstated by later authors who were not personally acquainted with him:

> '[Nuttall's] ear, so quick to appreciate the characteristics of the songs of birds, which showed a close resemblance between the notes of [*T. ustulatus*] and that of Wilson's Thrush (*T. fuscescens*), enabled him to detect very distinct and easily recognizable differences.' (Baird *et al*. 1874: 17)

The nest described by Nuttall (1840) seems unlikely to have been made by *C. guttatus* or *C. ustulatus*, or indeed any *Catharus* species. Mud has often been mentioned as a structural material in historical literature of *C. ustulatus*, but has not been observed in *C. ustulatus* nests by modern researchers (Mack & Yong 2000). Published references to mud are probably a consequence of Nuttall's (1840) original composite description of *T. ustulatus*: 'lined with dry leaves and some mud, externally of coarse grass.' Heckscher *et al*. (2014), by dissecting a sample of nests of *C. fuscescens*, recently debunked similar claims about the ostensible use of mud in nest construction; the natural desiccation process of wet leaves stabilises nest structures in lieu of mud. There is no evidence that Nuttall (1840) collected or dissected the nest he described.

Green moss typically replaces grass as a structural material in *C. ustulatus* nests (Mack & Yong 2000), but Nuttall (1840), an expert botanist, made no mention of moss in his description. Furthermore, the location of the nest on the 'prairies of Wahlamet' (= meadows in Willamette River valley, Oregon) is peculiar breeding habitat for *C. ustulatus*. Rathbun *in* Bent (1949) reported that in western Washington, '[*C. ustulatus*] nests from June 10 up to the middle of July…well within the forest, and a favorite location is among the low growth

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along the forest's edge, particularly in the proximity of water.' In short, the nest described by Nuttall was probably not made by any *Catharus* species.

Nomenclatural consequences

The name *ustulatus* (Nuttall, 1840) has been in universal use in global ornithological literature for more than 150 years. However, the original description of *T. ustulatus* Nuttall, 1840, was likely based on a (syntype) specimen of Hermit Thrush *C. guttatus* (Pallas, 1811), a different species than that to which the name *ustulatus* has traditionally been applied. The identity of a second syntype, mentioned by Audubon (1839: 203–204) and cited by Nuttall (1840: 400) among the synonyms of *T. ustulatus*, is not identifiable (see above). The two extant specimens of *C. ustulatus* attributed to the Townsend collection (USNM 2040, ANSP 23644) have both been claimed as types, but this status can be ruled out on the basis of collection dates and sex data that conflict with the accounts of Nuttall (1840) and Audubon (1839). Furthermore, they do not match Nuttall's (1840) description of the colours of the dorsal plumage and tail.

Neotypification is reserved for circumstances in which 'an author considers that a name-bearing type is necessary to define the nominal taxon objectively' (Art. 75.1). However, this is not a straightforward case because the only syntype for which an adequate description exists (in Nuttall 1840) is a closer match to *C. guttatus* than *C. ustulatus*, and a neotype must be 'consistent with what is known of the former name-bearing type from the original description and from other sources' (Art. 75.3.5). Accordingly, traditional nomenclature can be preserved and stabilised via neotypification only if the ICZN uses its plenary power to set aside Art. 75.3.5. A petition of this kind will soon be submitted to the *Bulletin of Zoological Nomenclature* for consideration by the Commission.

The material basis of *T. swainsoni* Cabanis *in* Tschudi, 1845

As a replacement name, *T. swainsoni* Cabanis *in* Tschudi, 1845, is typified by the original material in Swainson & Richardson's (1831) circumscription of *Merula Wilsonii* (i.e., not including the type material of the synonyms, see ICZN 1999, Art. 72.7). Their original material included several 'northern specimens' of unspecified provenance, a male collected in May 1827 at Carlton House National Historic Site of Canada, Saskatchewan, and 'no less than five others, killed last year in New Jersey, and now in our museum' (Swainson & Richardson 1831: 183). Therefore, *T. swainsoni* Cabanis *in* Tschudi, 1845, was based on a series of syntypes (Art. 72.1.1) collected at geographically distant localities, and of unknown breeding origin because they were collected during the migratory period.

Swainson's collection was sold to the Univ. of Cambridge (UK) in 1840, but there is no trace of the specimens mentioned in his *M. Wilsonii* account (Swainson & Richardson 1831: 183, Parkinson 1988). Three specimens of *C. swainsoni* are extant in the collection, but none have collection dates (UMZC No 27/Tur/6/j/5–7) and two were collected by Ward in 'Pennsylvania.' Because no other extant material from Swainson's collection is known, the type material of *T. swainsoni* Cabanis *in* Tschudi, 1845, is presumed to be lost or destroyed. Therefore, the text description of the Carlton House specimen is the only available evidence for determination of the identity of *T. swainsoni*:

> 'Colour of the whole dorsal aspect a uniform deep hair-brown, inclining slightly to oil-green. The cheeks and the spaces between the eyes and nostrils are pale yellowish-brown, obscurely spotted with hair-brown. The *under plumage* is mostly white, tinged on the sides of the throat with yellowish-brown, and faintly clouded and blotched on

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the flanks with hair-brown. The throat and breast are marked with broad, triangular, blackish-brown spots on the tips of the feathers. *Bill* dark umber-brown, pale at the base of the lower mandible. *Legs* pale yellowish-brown.' (Swainson & Richardson 1831: 183)

The above description is insufficient to distinguish between *C. swainsoni* (Cabanis *in* Tschudi, 1845) and *C. minimus aliciae* (Baird *et al*., 1858), which both occur during the spring migration in Saskatchewan. The latter species was not yet known when Swainson & Richardson (1831) made their description, nor when Cabanis (*in* Tschudi, 1845) published the replacement name *T. swainsoni*. Morphometric values given by Swainson & Richardson (1831) are insufficient to distinguish between these two closely related taxa. The coloration of the dorsal plumage of *C. swainsoni* and *C. m. aliciae* is practically identical and approximately one-quarter of *C. m. aliciae* males have 'medium buff' on the throat (Ouellet 1993) that may extend onto the cheeks and lores like *C. swainsoni* (e.g., ANSP 203886, 204425). The bird described by Swainson & Richardson (1831) had '*pale* yellowish brown' lores (my italics), which does not exclude *C. m. aliciae* from consideration. Coues (1878: 36), who distinguished *T. aliciae* from *T. swainsoni* on the basis of 'the *distinct* yellowish orbital ring and lores [my italics] of *swainsoni* not being seen', conceded that these characters are 'faintly indicated' in some specimens of *C. m. aliciae*. No mention of the eye-ring was made in Swainson and Richardson's (1831) description. Furthermore, Richardson's remark that the eggs of *M. Wilsonii* are 'without spots' matches *C. m. aliciae* but not *C. swainsoni*, adding further uncertainty (Bent 1949).

Neotypification of *T. swainsoni* Cabanis *in* Tschudi, 1845

The name *T. swainsoni* Cabanis *in* Tschudi, 1845, has been in universal use for the eastern (inland) taxon for more than 150 years. However, it is not unambiguously identifiable because none of its syntypes are extant and the attributes of the specimens described by Swainson & Richardson (1831), to which Cabanis (*in* Tschudi 1845) applied the replacement name *T. swainsoni*, are shared by more than one species.

To fix the taxonomic identity of *Merula Wilsonii* Swainson & Richardson, 1831 (excluding synonyms), and its replacement names including *T. swainsoni* Cabanis *in* Tschudi, 1845, an adult male (ANSP 207077) in the collection of the Academy of Natural Sciences of Drexel University, Philadelphia, PA, is hereby designated as its neotype (Fig. 9). This action stabilises traditional nomenclature and prevents destabilising confusion arising from alternative identifications. It fulfills the requirements for neotype designation in the *Code* (ICZN 1999) by clarifying the taxonomic application (status) of the name, as explained above (Art. 75.3.1), describing, illustrating and referencing the defining characters of *C. swainsoni* and its neotype (Art. 75.3.2), providing data sufficient to ensure recognition of the specimen designated (Art. 75.3.3), providing grounds for believing that all original type material has been lost and is untraceable (Art. 75.3.4), showing that traits of the neotype are included in the original description (Art. 75.3.5), choosing a neotype collected in the Mid-Atlantic region of North America, where some of Swainson & Richardson's (1831) syntypes originated (Art. 75.3.6), and recording that the neotype is preserved as the property of a recognised scientific institution (Art. 75.3.7). The choice of a specimen from its breeding grounds provides more stability than selecting a migrant individual with an unknown breeding locality.

ANSP 207077 is an adult male collected by M. R. Halley on 17 July 2019 on the west branch of Tionesta Creek, Allegheny National Forest, Warren County, Pennsylvania (41°69′03.79″N, 79°23′98.00″W, 550 m elevation). The bird was on its breeding territory near Heart's Content, an old-growth stand of eastern hemlock *Tsuga canadensis* and eastern

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Figure 9. ANSP 207077, the neotype of *M. Wilsonii* Swainson & Richardson, 1831, and its replacement names including *T. swainsoni* Cabanis *in* Tschudi, 1845; see text for detail of the specimen's provenance (Matthew R. Halley)

white pine *Pinus strobus*. For more detail concerning the vegetative history of the area see Lutz (1930) and Rooney & Dress (1996). An audio recording was made of the singing bird with a Sennheiser ME66/K6 condenser microphone and Sony Zoom H1 recorder (.wav format, 24 bit, 96 kHz). Speaker playback of the recording was used to lure the bird into a mist-net. A compressed audio file (.mp3) was uploaded to xeno-canto.org (XC 489007) and an uncompressed file (.wav) was deposited in the Macaulay Library of Natural Sounds (Cornell University, Ithaca, NY) (ML 170463711, eBird checklist S58570739).

Approximately 50 µL of blood was drawn via brachial venipuncture into a microhematocrit capillary tube. Fresh blood was applied to a FTA card, and smeared onto a glass slide which was immediately fixed in pure methanol. The bird was euthanised in the field via cardiac compression, then transported on dry ice to ANSP, where it was prepared as a study skin and spread wing (Fig. 9, prep. = MRH214). The wingspan of the fresh (pliable) specimen measured 293 mm before removing the skin. An immature (unscleratised) feather louse with sternal asters (*Myrsidea* sp., identified by J. Gausas) was removed from ANSP 207077 and preserved in 95% EtOH. Samples of the heart, liver and muscle tissue of ANSP 207077 were frozen (-80° F) and archived (ANSP tissue = 35982). The syrinx was excised and initially preserved in 95% EtOH, then transferred to 10% neutral buffer formalin. Prior to preparation, the bird weighed 29.8 g with a stomach full of black insect parts and some seeds. It had enlarged, cream-coloured testes (10 × 6 and 9 × 6 mm) and enlarged seminal vesicles. No fat or moult was noted. There was no bursa and the skull was 100% pneumatised.

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Diagnosis.—*C. swainsoni* is distinguished from other *Catharus* species by the combination of a buffy eye-ring, which is bold and spectacle-like, and uniform brownish-olive dorsal plumage and tail. In contrast to the similar *C. m. aliciae* (Baird *et al*., 1858), which also has Brownish Olive dorsal plumage and tail, the eye-ring of *C. swainsoni* is 'full and distinct,' the breast spots are 'larger and less distinct' and there is a 'lack of emargination on p6' (Pyle 1997: 397).

Through neotypification, the name *C. swainsoni* (Cabanis *in* Tschudi, 1845) is now restricted to the inland species to which the names *C. u. swainsoni* and *C. swainsoni* have been formerly applied (e.g., Ruegg 2007, del Hoyo & Collar 2016). For clarity of reference, the synonyms, nomenclatural combinations and principal citations of *C. swainsoni* (Cabanis *in* Tschudi, 1845), *C. u. ustulatus* (Nuttall, 1840), *C. u. oedicus* (Oberholser, 1899) and *C. guttatus* (Pallas, 1811) are provided in the Appendix.

English common names

Molecular phylogenetic studies have unanimously demonstrated that the resident (non-migratory) *Catharus* species, which have been traditionally called 'nightingale-thrushes,' do not form a monophyletic group (Outlaw *et al*. 2003, Klicka *et al*. 2005, Winker & Pruett 2006, Voelker *et al*. 2013, Everson *et al*. 2019). Therefore, the common name 'nightingale-thrush' is appropriately applied to all species in *Catharus* and continued use of 'thrush' for the migratory species alone perpetuates historical misconceptions about phylogenetic relationships.

Recently, the American Ornithological Society North American Classification Committee addressed a similar problem in hummingbirds by voting to 'standardize the English group name of all species of *Lampornis* to Mountain-gem and reduce the prevalence of the English group name 'hummingbird' across the family, thereby strengthening the association of these species with other species of *Lampornis* and emphasizing their distinctness relative to other species in the Trochilidae' (Chesser *et al*. 2019: 7). Following that example, I propose that the common names of the migratory species of *Catharus* be revised to 'strengthen

TABLE 2
Scientific and English common names of species in the genus *Catharus*, known collectively as nightingale-thrushes. Current names follow Clement (2000) with updates by Halley *et al*. (2017). The ordering of species according to phylogenetic clades (A–C) follows Voelker *et al*. (2013) and Everson *et al*. (2019). Novel proposed names are shown in bold.

Clade	Scientific name	Current name(s)	Proposed name
A	*C. aurantiirostris*	Orange-billed Nightingale-Thrush	Orange-billed Nightingale-Thrush
	C. mexicanus	Black-headed Nightingale-Thrush	Black-headed Nightingale-Thrush
	C. fuscater	Slaty-backed Nightingale-Thrush	Slaty-backed Nightingale-Thrush
	C. dryas	Gould's Nightingale-Thrush	Gould's Nightingale-Thrush
	C. maculatus	Sclater's Nightingale-Thrush	Sclater's Nightingale-Thrush
B	*C. minimus*	Grey-cheeked Thrush	**Grey-cheeked Nightingale-Thrush**
	C. bicknelli	Bicknell's Thrush	**Bicknell's Nightingale-Thrush**
	C. fuscescens	Veery / Wilson's or Tawny Thrush	**Veery Nightingale-Thrush**
	C. swainsoni	(Olive-backed) Swainson's Thrush	**Boreal Nightingale-Thrush**
	C. ustulatus	(Russet-backed) Swainson's Thrush	**Pacific Nightingale-Thrush**
C	*C. guttatus*	Hermit Thrush	**Hermit Nightingale-Thrush**
	C. occidentalis	Russet Nightingale-Thrush	Russet Nightingale-Thrush
	C. gracilirostris	Black-billed Nightingale-Thrush	Black-billed Nightingale-Thrush
	C. frantzii	Ruddy-capped Nightingale-Thrush	Ruddy-capped Nightingale-Thrush

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the association' of these species with the other (non-migratory) species in the genus. This action will highlight the distinctness of *Catharus* relative to other genera in the Turdidae and 'reduce the prevalence' of the vague English group name 'thrush' across the family. Proposed names are listed in Table 2 and discussed below.

The common names Boreal Nightingale-Thrush (*C. swainsoni*) and Pacific Nightingale-Thrush (*C. ustulatus*) are ecologically and geographically appropriate and will reduce confusion with past uses of 'Swainson's Thrush', which was formerly applied to both species. Use of the adjective 'Russet-backed' for *C. ustulatus* is problematic because the similarly named Russet Nightingale-Thrush *C. occidentalis* occurs sympatrically with *C. ustulatus* in southern Mexico for most of the year. The fact that two other *Catharus* species have widespread breeding ranges that include boreal forest (*C. guttatus*, *C. minimus*) should not raise objection to the use of 'Boreal Nightingale-Thrush' for *C. swainsoni* alone; consider the similar case of Boreal Chickadee *Poecile hudsonicus* and Black-capped Chickadee *Poecile atricapillus*, which breed sympatrically in boreal habitats.

In phylogenetic analyses, *C. guttatus* has been reconstructed as the sister species of *C. occidentalis*, and this pair is more closely related to Ruddy-capped Nightingale-Thrush *C. frantzii* and Black-billed Nightingale-Thrush *C. gracilirostris* (also sister species) than to any of the long-distance migratory species (Voelker *et al*. 2013, Everson *et al*. 2019). The common name Hermit Nightingale-Thrush *C. guttatus* (Pallas) will strengthen the association of these closely related species (Table 2). For the same reasons, I propose the common names Veery Nightingale-Thrush *C. fuscescens* (Stephens), Grey-cheeked Nightingale-Thrush *C. minimus* (Lafresnaye) and Bicknell's Nightingale-Thrush *C. bicknelli* (Ridgway).

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Appendix

Synonyms and taxonomic combinations of *C. swainsoni* (Cabanis *in* Tschudi), *C. u. ustulatus* (Nuttall), *C. u. oedicus* (Oberholser) and *C. guttatus* (Pallas), and their principal citations. For clarity, references to composite taxa published prior to 1840 are excluded, including *T. minor* J. F. Gmelin, 1789, and Wilson's (1812) secondary composites (reviewed by Halley 2018). Accordingly, the following synonymy of *C. swainsoni* begins with Giraud (1844) and Brewer (1844). The name *T. aonalaschkae* J. F. Gmelin, 1789, is included in the synonymy of *C. guttatus* to clarify the resurgent use of that name in the late 19th century; it was deemed unidentifiable (AOU 1902: 215). Due to a lack of available material for comparison, subspecies within the *C.*

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swainsoni and *C. guttatus* complexes are listed among the synonyms of those complexes. The subspecies *C. u. phillipsi* Ramos *in* Phillips, 1991, is omitted for the same reason.

Catharus swainsoni (Cabanis *in* Tschudi)[2]
Boreal Nightingale-Thrush

Turdus olivaceus Giraud 1844: 91 (junior homonym of *T. olivaceus* Linnaeus, 1766).
Merula olivacea Brewer 1844: 191 (idem).
Turdus swainsoni Cabanis *in* Tschudi 1845: 28; Sclater 1859: 326; Cooper 1870: 6; Coues 1872: 73; Baird *et al*. 1874: 14; Coues 1878: 34; Salvin & Godman 1879: 10; Seebohm 1881: 201; Taczanowski 1884: 487; Seebohm 1902: 179.
Turdus swainsonii Cabanis 1847: 205; Baird *et al*. 1858: 216; Baird 1864: 19; Allen 1864: 56; Ridgway 1869: 128; Maynard 1881: 6.
Turdus ustulatus swainsoni Beckham 1887: 125.
Turdus ustulatus swainsonii White 1893: 229; AOU 1889: 67; Fisher 1893: 145; AOU 1895: 318.
Hylocichla ustulata almae Oberholser 1898: 304; Dickey & van Rossem 1938: 457; Wetmore 1943: 305; AOU 1944: 457; Rand & Traylor 1954: 230; Bond 1963: 380.
Hylocichla ustulata swainsonii Bangs 1902: 49; Ridgway 1907: 55.
Hylocichla ustulata swainsoni AOU 1910: 361; Osgood, 1909: 43; AOU 1931: 259; Hellmayr 1934: 457; Dickey & van Rossem 1938: 456; Rand & Traylor 1954: 230; Bond 1963: 379.
Hylocichla ustulata clarescens Burleigh & Peters 1948: 118.
Hylocichla ustulata incana Godfrey '1951' [= 1952]: 173.
Catharus ustulatus Ripley 1964: 171; AOU 1983: 556 (in part), 1998: 505 (in part); Chesser *et al*. 2018 (in part).
Catharus ustulatus almae Ripley, 1964: 171; Clement, 2000: 313.
Catharus ustulatus swainsoni Ripley 1964: 172; Ramos *in* Phillips 1991: 89; Clement 2000: 314; Gill & Donsker 2019.
Catharus ustulatus appalachiensis Ramos *in* Phillips 1991: 90.
Catharus ustulatus incanus Ramos *in* Phillips 1991: 91.
Catharus swainsoni Piacentini *et al*. 2015; del Hoyo & Collar 2016.

Catharus ustulatus ustulatus (Nuttall)
(Northern) Pacific Nightingale-Thrush

Turdus ustulatus Nuttall, 1840: 400 (misidentified, neotypification pending); Baird *et al*. 1858: 215; Sclater 1859: 326; Baird 1864: 18; Ridgway 1869: 127; Cooper 1870: 5; Salvin & Godman 1879: 11 (in part); Seebohm 1881: 202 (in part); AOU 1889: 67 (in part), 1895: 318 (in part); Stone 1899: 19; Seebohm 1902: 175 (in part).
Turdus swainsoni* var. *ustulatus Coues 1872: 73 (in part); Baird *et al*. 1874: 16 (in part); Coues 1878: 35 (in part).
Hylocichla ustulata Brewster 1902: 210.
Hylocichla ustulata ustulata Grinnell 1902: 73 (in part); Ridgway 1907: 52 (in part); AOU 1910: 361 (in part), 1931: 259 (in part); Hellmayr 1934: 456 (in part); AOU 1957: 438 (in part); Deignan 1961: 431; Bond 1963: 378.
Catharus ustulatus ustulatus Ripley 1964: 172; Ramos *in* Phillips 1991: 91; Clement 2000: 313 (in part); Mack & Yong 2000.
Catharus ustulatus AOU 1983: 556 (in part), 1998: 505 (in part).

Catharus ustulatus oedicus (Oberholser)
(Southern) Pacific Nightingale-Thrush

Turdus ustulatus Salvin & Godman 1879: 11 (in part); Seebohm 1881: 202 (in part); AOU 1889: 67 (in part), 1895: 318 (in part); Seebohm 1902: 175 (in part).
Turdus swainsoni* var. *ustulatus Coues 1872: 73 (in part); Baird *et al*. 1874: 16 (in part); Coues 1878: 35 (in part).
Hylocichla ustulata œdica Oberholser 1899: 23; Brewster 1902: 211; Deignan 1961: 432; Bond 1963: 378.
Hylocichla ustulata ustulata Grinnell 1902: 73 (in part); Ridgway 1907: 52 (in part); AOU 1910: 361 (in part), 1931: 259 (in part); Hellmayr 1934: 456 (in part); AOU 1957: 438 (in part); Bond 1963: 378.
Catharus ustulatus oedicus Ripley 1964: 172; Ramos *in* Phillips 1991: 92; Clement 2000: 313 (in part); Mack & Yong 2000; Gill & Donsker 2019.
Catharus ustulatus AOU 1983: 556 (in part), 1998: 505 (in part).

[2] Jean Louis Cabanis (1816–1906) wrote the ornithological portions of Tschudi's (1845) *Untersuchungen über die Fauna Peruana*, including the following passage: '*T. Swainsoni* Cab. MSS. *Merula Wilsoni* Swains. (nec Bonap.) Faun. Bor. Amer. II. p. 182 excl. Synon.' Authorship of the name *T. swainsoni* has often been misattributed to Tschudi (e.g., AOU 1998: 505; see Cabanis 1847, and Sclater 1859: 326).

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Catharus guttatus (Pallas)
Hermit Nightingale-Thrush

Turdus aonalaschkae J. F. Gmelin 1789: 808 (based on young bird, unidentifiable; see AOU 1902: 315); Ridgway 1880: 1; Seebohm 1881: 200; AOU 1889: 67; Fisher 1893: 145; AOU 1895: 318; Seebohm 1902: 193.
Muscicapa guttata Pallas '1826' [=1811]: 465.
Turdus nanus Audubon 1839: 201; Townsend 1839: 153; Nuttall 1840: 396; Baird *et al*. 1858: 213; Sclater 1859: 325; Baird 1864: 15; Ridgway 1869: 129; Cooper 1870: 4.
Turdus guttatus Cabanis *in* Tschudi 1845: 187.
Turdus pallasii Cabanis 1847: 205; Baird *et al*. 1858: 212; Sclater 1859: 325; Baird 1864: 14; Allen 1864: 56; Coues 1872: 72; Maynard 1881: 8.
Turdus silens Sclater 1859: 325.
Turdus audubonii Baird, 1864: 16; Salvin & Godman 1879: 14; Seebohm 1881: 198, 1898: 197.
Turdus pallasi Ridgway 1869: 128; Baird *et al*. 1874: 18; Coues 1878: 20; Henshaw 1879; Salvin & Godman 1879: 13; Seebohm 1881: 199, 1898: 185.
Turdus audubonii Ridgway 1869: 129.
Turdus pallasii audubonii Coues 1872: 72.
Turdus pallasii nanus Coues 1872: 72.
Turdus pallasi* var. *nanus Baird *et al*. 1874: 20.
Turdus pallasi* var. *audubonii Baird *et al*. 1874: 21.
Turdus aonalaschkae pallasi Ridgway 1880: 1.
Turdus aonalaschkae audubonii Ridgway 1880: 1; Beckham 1887: 124; AOU 1889: 67; Fisher 1893: 146; AOU 1895: 319.
Turdus aonalaschkae pallasii AOU 1889: 67, 1895: 319.
Turdus sequoiensis Belding 1889: 18.
Hylocichla guttata sequoiensis Ridgway 1907: 44; AOU 1910: 362, 1931: 258; Hellmayr 1934: 455.
Hylocichla aonalaschkae verecunda Osgood 1901: 183; Grinnell 1902: 73.
Hylocichla aonalaschkae aonalaschkae Grinnell 1902: 73.
Hylocichla aonalaschkae slevini Grinnell 1902: 73.
Hylocichla aonalaschkae sequoiensis Grinnell 1902: 73.
Hylocichla guttata Brewster 1902: 211; AOU 1957: 436.
Hylocichla guttata nana Brewster 1902: 212; Ridgway 1907: 42; Bangs 1930: 331; Hellmayr 1934: 454.
Hylocichla guttata audubonii Brewster 1902: 212; Ridgway 1907: 46; AOU 1910: 362, 1931: 258; Hellmayr 1934: 455.
Hylocichla guttata guttata Ridgway 1907: 39; AOU 1910: 361, 1931: 258; Hellmayr 1934: 453.
Hylocichla guttata slevini Ridgway 1907: 44; AOU 1910: 362, 1931: 258; Hellmayr 1934: 454.
Hylocichla guttata pallasii Ridgway 1907: 48.
Hylocichla guttata pallasi AOU 1910: 362.
Hylocichla guttata nanus AOU 1910: 362, 1931: 258.
Hylocichla guttata polionota Grinnell 1918: 89; AOU 1931: 258; Hellmayr 1934: 455.
Hylocichla guttata faxoni Bangs & Penard 1921: 433; Bangs 1930: 332; AOU 1931: 259; Hellmayr 1934: 456.
Hylocichla guttata vaccinia Cumming 1933: 79.
Hylocichla guttata crymophila Burleigh & Peters 1948: 117.
Hylocichla guttata euboria Oberholser 1956: 69.
Catharus guttatus Phillips '1961' [=1962]; Ripley 1964; AOU 1983: 556, 1998: 505; Chesser *et al*. 2018; Gill & Donsker 2019.
Catharus guttatus munroi Phillips '1961' [=1962]: 351, 1991: 80.
Catharus guttatus guttatus Phillips '1961' [=1962]: 353; Ripley 1964: 173; Aldrich 1968: 14; AOU 1973: 416; Phillips 1991: 81.
Catharus guttatus verecundus Phillips '1961' [=1962]: 354, 1991: 80.
Catharus guttatus slevini Phillips '1961' [=1962]: 355; Ripley 1964: 174; Aldrich 1968: 20; Phillips 1991: 84.
Catharus guttatus oromelus Phillips '1961' [=1962]: 356; Aldrich 1968: 23; Phillips 1991: 82.
Catharus guttatus jewetti Phillips '1961' [=1962]: 356, 1991: 83.
Catharus guttatus auduboni Phillips '1961' [=1962]: 359; Ripley 1964: 174; Aldrich 1968: 22; Phillips 1991: 86.
Catharus guttatus sequoiensis Phillips '1961' [=1962]: 360; Ripley 1964: 174; Aldrich 1968: 22; Phillips 1991: 84.
Catharus guttatus osgoodi Phillips 1991: 81.
Catharus guttatus vaccinius Aldrich 1968: 20; Phillips 1991: 82.
Catharus guttatus nanus Ripley 1964: 173; Aldrich, 1968: 18; Phillips 1991: 77.
Catharus guttatus polionotus Ripley 1964: 174; Phillips 1991: 85.
Catharus guttatus faxoni Ripley 1964: 175; Aldrich 1968: 26.
Catharus guttatus crymophilus Ripley 1964: 175; Aldrich 1968: 14.
Catharus guttatus euborius Aldrich 1968: 25; Phillips 1991: 77.

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