**Appendix A**

**Taxonomic history of Pleske’s Tit** *Parus* (*Cyanistes*) *pleskii*

Hybridisation between species has always been considered a rare event in nature, and therefor commonly occurring hybrids may not have been recognised as such at the first instance. In fact, due to their common occurrence these hybrids sometimes were considered to be distinct species and got even named as such. *Parus* (*Cyanistes*) *pleskii* Cabanis, 1877, the hybrid between Blue Tit *Cyanistes caeruleus* and Azure Tit *Cyanistes cyaneus*, is a good example of this.

During the meeting of the German Ornithologists’ Club in Berlin on the 5th of February 1877, Jean Cabanis (1877a), director of the Natural History Museum of Berlin and founder of the *Journal für Ornithologie*, discussed a newly discovered species of tit of which he was made aware of by Fedor (Theodore) Dmitrievich Pleske from St. Petersburg (Fig. 1). Pleske had sent him a drawing based on a specimen in his collection, together with a full description of the bird. Pleske wrote that he had acquired this bird alive is Spring 1876 at the Bird Market in St. Petersburg. In Autumn 1876 he was offered a similar bird at the same market which was, however, paler in colour than the first. Cabanis was convinced that this was a new species, in his opinion probably the Siberian representative of the European Bluetit. Keen to be the first he named it *Parus pleskii*, in honour of its discoverer, based on Pleske’s drawing and description only, and without seeing the described specimen. He had asked Pleske to send him the actual specimen for examining, but it had not arrived before this meeting. In the March meeting, however, Cabanis (1877b) could show the attendees a specimen sent by Pleske and, in Cabanis’ opinion, the specimen confirmed that his *Parus pleskii* was a distinct species and naming it as such was correct. This specimen (Fig. 2) is still present in the Museum für Naturkunde Berlin (ZMB 23286), and was considered the type but closer examination, however, revealed that it is lacking some of the distinguishing features mentioned in the original description by Cabanis (1877a), e.g., the Lazur-blue top of the head and the clear dark throat and collar as in Bluetit, and yellow on the chest. The Berlin specimen is lacking all of these characteristics and appears to be the paler specimen acquired in Autumn 1876 by Pleske. No specimen agreeing with the type description is present in the Berlin collection (S. Frahnert *in lit*.10 March 2023), so we assume Pleske kept the bird from Spring 1876 which the original description was based on himself, and instead he sent the paler coloured specimen from Autumn 1876 to Cabanis. This specimen may be considered a paratype, but the whereabouts of the holotype are currently unknown.

Taking it that it was indeed a distinct species, Mikhail Aleksandrovich Menzbier (1882) distinguished a form of *pleskii* which, according to him, was slightly different in colour and markings from the form described by Cabanis (Fig. 3). According to Hellmayer (1901) the two forms could geographically not being distinguished, and he considered it nothing else than a ‘variety’ of *pleskii* but, nevertheless, he suggested the name *pallescens* for it. Menzbier had studied the different tit species extensively for a monograph he was intending to write, and had amassed a fair number of skin specimens of the different Palearctic species, including *pleskii.* This collection, 529 specimens in total including c. 20 *pleskii* specimens, he sold in 1901 to the then British Museum (Natural History) and some of these are used in this current research. Menzbier distinguished his *pleskii* specimens in var. A and var. B (Fig. 4). Var. B is very similar to *pleskii* as described by Cabanis, and we assumed these are F1 hybrids between Blue Tit and Azure Tit. Var. A looks more like Azure Tit and one would expect these to be back-crosses to Azure Tit instead. Our analyses, however, have shown that all of these can be considered as F1 hybrids. So, although Menzbier did not know *pleskii* was a hybrid, he was consistent in what he considered to be *pleskii* and had not accidentally included backcrosses among them. Several specimens in his collection were backcrosses but, as he believed that *pleskii* was a distinct species, he considered these to be hybrids between *pleskii* and Azure Tit instead. According to Menzbier (1884) hybrids between *pleskii* and Azure Tit were not uncommon.

Henry Dresser (1895: 125-126) too treated *Parus pleskii* a distinct and full species. Although its range was still unclear, and nothing was known respecting the breeding habits, Dresser believed that “its nest and eggs will doubtless be found to resemble those of *P. caeruleus*.” He pictured and adult male from his own collection which he had received from Pleske, and which was collected 25 Sept. 1886 at St. Petersburg (Fig. 5).

Ernst Hartert (1903: 351-352) mentioned that the species status of *pleskii* was questioned by some. He did not mention names, but he probably referred to Lorenz (see below) who had stated that it was a hybrid. In Hartert’s opinion that could not be the case based on the high number of specimens recorded and collected. He agreed with Menzbier (1884) that *pleskii* not uncommonly ‘hybridised’ with Azure Tit and probably also, but rarely, with Blue Tit. Given that *pleskii* was more similar in colour and size to Blue Tit, Hartert considered it to be a subspecies of the latter; *Parus caeruleus pleskii*. The breeding grounds of *pleskii* were still unknown but, so reasoned Hartert, as *pleskii* hybridised more with *cyanus* than with *caeruleus*, the breeding grounds must be within those of *cyanus* and most likely only bordering with *caeruleus*.

Fedor (Theodore) Lorenz (1895) was probably the first to recognise *pleskii* as actually being a hybrid between Blue Tit and Azure Tit but, as shown above, his opinion was not shared at the time. After Lorenz others also started to question the status of *pleskii*. Petr Petrovich Suschkin (1910), for example, questioned whether *pleskii* could be considered a rare and ancient species or merely a hybrid, and he argued in favour for it most likely to be a hybrid. It was Pleske (1912) himself who finally gathered the evidence to show that the ‘species’ named after him was in fact a hybrid. One of the strong points of evidence he presented was based on hybrids bred in captivity between Blue Tit and Azure Tit. The breeder, Mr. Ernst H. Zollikofer from St. Gallen in Switzerland, had informed Pleske that he in two successive years —1909 and 1910—had bred offspring from the same *cyaneus* female with two different *caeruleus* males, and that the offspring agreed fully with *pleskii*. Remarkably, the hybrids of both males were slightly different and resembled the two different forms—Var. A and Var. B— reported by Menzbier. The birds hatched in 1910 had some clear Blue Titcharacteristics like a full throat patch, collar and chest stripe, blue head, no white on the primary tips and hardly any white in the tail feathers. These birds resembled *pleskii* as described by Cabanis and Menzbier’s Var. B. The birds hatched in 1909, and being from a different Blue Tit male, looked more like Azure Tit with a paler head, hardly or no throat patch, and whiter in the primaries and tail feathers and resembled Menzbier’s Var. A. All in all, with the facts available at that time Pleske ‘proofed’ perfectly that *pleskii* was not a rare and ancient species but a hybrid instead. That fact was accepted in the ornithological community ever since, but more questions arose. The breeding results by Zollikofer (reported by Pleske 1912) showed, for example, that hybrid offspring resulting from the same parent combination (in this case *caeruleus* father and *cyaneus* mother) can look differently. In Zollikofer’s case the difference suggests that one of the Blue Tit fathers may have had a hybrid history himself.

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**Fig. 1** Plate of *Parus pleskii* Cabanis, 1877 what was published with the original description of the ‘species’ (Cabanis 1877a). Characteristics like the Lazur-blue top of the head and the clear dark throat and collar, and yellow on the chest as mentioned in the description are clearly figured in this plate. Photo: © Hein van Grouw, Natural History Museum, Tring.





**Fig. 2** Paratype of *Parus pleskii* Cabanis 1877, ZMB 23286. This specimen collected in Autumn 1876 does not agree with the type description, what was based on a single specimen collected in Spring 1876, but it is mentioned in the further discussion (Cabanis 1877a). Photo: © C. Radke/Museum fur Naturkunde, Berlin.



**Fig. 3** Plate of *Parus pleskii, Var*. in Menzbier 1882. Menzbier had noticed that besides the form described by Cabanis, another, paler, form of *pleskii* existed as well. In fact, Pleske’s second bird (Fig.2) was also this paler form. Photo: © Hein van Grouw, Natural History Museum, Tring.



**Fig. 4** Two *Parus pleskii* specimens from Menzbier’s collection to demonstrate the two different variations within the ‘species’. Left ‘Var. a’, the paler form, what looks more like Azure Tit(NHMUK 1901.5.4.305 and right ‘Var. b’, the form described by Cabanis and looks more like Bluetit(NHMUK 1901.5.4.309). Based on our analyses, both specimens can be considered F1 hybrids. Photo: © Jonathan Jackson, Natural History Museum, London.



**Fig. 5** Plate of *Parus pleskii* in Dresser 1895-96. The drawing is based on a specimen collected 25 Sept. 1886 at St. Petersburg and which Dresser had received from Pleske. The specimen represents *pleskii* as described by Cabanis (= Menzbier’s var. a). Photo: © Hein van Grouw, Natural History Museum, Tring.