

Taxonomic Note

Cite this article: Collado G.A., Galleguillos F.F., and Hoeksema B.W. 2025. Homonymy and triple homonymy among species names of fossil *Flabellum* corals (Scleractinia: Flabellidae), with proposals for their replacement names. *Journal of Paleontology*, 1–5 <https://doi.org/10.1017/jpa.2025.10107>

Received: 24 May 2024

Revised: 05 April 2025

Accepted: 22 April 2025

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Handling Editor:

Robert Elias

Homonymy and triple homonymy among species names of fossil *Flabellum* corals (Scleractinia: Flabellidae), with proposals for their replacement names

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UUID: <http://zoobank.org/84e649ca-bbcf-4c7a-a77d-0bc7579ec402>

According to the International Code of Zoological Nomenclature (ICZN, 1999), the Principle of Homonymy (Article 52) states that when two or more taxa are distinguished from each other, they must not be denoted by the same name because this would cause confusion. Consequently, in a case of homonymy, only the senior name may be used as valid (Art. 52.2). The ICZN (1999) also indicates that if the rejected junior homonym has no known available and potentially valid synonym, it must be replaced by a new substitute name (Art. 60.3), that is, a replacement name.

Among stony corals of the order Scleractinia, homonyms are not common. This is perhaps why there has been some confusion in coral taxonomy regarding the application of replacement names. These replacement names often refer to species that were previously misidentified in the literature but are, in fact, new species (Hoeksema, 1993). An example of a *nomen novum* concerns the replacement name *Fungia curvata* Hoeksema, 1989 for the extant mushroom coral *Fungia elegans* Verrill, 1870 (now *Cycloseris curvata*) from the Indo-Pacific (Hoeksema, 1989; Gittenberger et al., 2011), junior homonym of the extinct *Fungia elegans* Bronn, 1837 (now *Stephanophyllia elegans*), from the Pliocene of Italy (Bronn, 1837; Michelin, 1841). The fact that both species were originally described in the genus *Fungia* Lamarck, 1801 (family Fungiidae) and later were moved to other genera in different families, thus forming new combination names, does not prevent them from being considered homonyms with the junior in need of replacement. Considering the rarity of documented homonyms in the taxonomy of Scleractinia, we here present a unique case involving both homonymy and triple homonymy among extinct species of a genus of deep-water corals.

The genus *Flabellum* Lesson, 1831 (Cnidaria, Anthozoa, Hexacorallia, Scleractinia, Flabellidae) comprises more than 160 distinctive extinct and recent azooxanthellate, deep-water corals (Cairns, 1995, 1999; Uhen et al., 2023; GBIF, 2024; Hoeksema and Cairns, 2024a). Its name in Latin, meaning “fan,” is derived from the flabellate shape of the corallum. A study of a putative new species of fossil corals from Chile (submitted elsewhere) has revealed previously overlooked or unresolved cases of homonymy within this genus. Three of these cases involve species names of Chilean fossils that were preoccupied by extinct species of this genus from Europe, for which three replacement names are proposed in accordance with the ICZN (1999). In addition, another case of homonymy involves one species from the United States and another one from Europe, for which a replacement name is proposed (Table 1). All cases relate to primary homonymy.

Systematic paleontology

Class **Anthozoa** Ehrenberg, 1834

Order **Scleractinia** Bourne, 1900

Family **Flabellidae** Bourne, 1905

Genus ***Flabellum*** Lesson, 1831

Type species. Flabellum pavoninum Lesson, 1831.

Flabellum philippii nom. nov.

1887 *Flabellum costatum* Philippi, p. 226, pl. 53, fig. 5. nom. preocc. (not *Flabellum costatum* Michelin, 1846 in Michelin (1840–1848), p. 271, pl. 61, fig. 10. No synonym was found to be available as a possible replacement name.

Type material. The name-bearing type is the specimen described and illustrated by Philippi (1887) (Art. 72.5.6).

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JOURNAL OF
PALEONTOLOGY
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Table 1. Summary of species found in homonymy and their proposed replacement names, with complementary information, including species samples

Original name	Type material	Registration number	Type locality	Age	References	Replacement name
<i>Flabellum costatum</i> Philippi, 1887	Unknown MNHNCL	Unknown SGO.PI.5376 ^a	Lebu, southern Chile Punta Alta de Navidad	Miocene	Philippi (1887) Covacevich and Frassinetti ^d	<i>Flabellum philippii</i>
<i>Flabellum solidum</i> Tavera Jerez, 1979	Unknown	Unknown	Navidad, central Chile	Lower Miocene	Tavera Jerez (1979)	<i>Flabellum taveri</i>
<i>Flabellum striatum</i> Gabb and Horn in Gabb, 1860	ANSP	ANSP-IP 65241 ^b ANSP-IP 708 ^c	Prairie Bluff, Alabama, USA	Cretaceous in Gabb (1860), Eocene in ANSP Eocene	Gabb (1860) Richards (1968)	<i>Flabellum rachelis</i>
<i>Flabellum striatum</i> Philippi, 1887	Unknown MHNC	Unknown MHNC 38.0083–1 to MHNC 38.0083–5 ^a	Lebu, southern Chile Ranquil Formation, southern Chile	Miocene	Philippi (1887) Volosky Medina (2021)	<i>Flabellum piri</i>

^aSamples.^bTwo syntypes figured in the original description (Gabb, 1860).^cTwo syntypes (Richards, 1968).^dSamples deposited in 1980 (unpublished).

Etymology. The species is named after the German naturalist Rodulfo Amando Philippi, the author of the original species name.

Remarks. *Flabellum costatum* Michelin, 1846 was originally described as a fossil coral specimen from the Eocene of “du Jarrier” and “de la Palarea,” France, which was deposited in the collections of Bellardi, Caillaud, Michelin, Perez, and Vandenhecke as noted by Michelin (1840–1848). The specimen was originally referred to as “*Flabellum costatum* Bellardi” (Michelin, 1846, p. 271, pl. 61; Milne Edwards and Haime, 1848, p. 266; Haime, 1852, p. 282; Milne Edwards and Haime, 1857, p. 83), taking the name from Bellardi’s unpublished manuscript notes. According to Michelin (1846, p. 271), the species “forms an intermediary between *F. appendiculatum* and *F. avicula*” and “except for its folds, it also resembles *F. cuneatum*,” referring to *Flabellum appendiculatum* (Brongniart, 1823), *Flabellum avicula* (Michelotti, 1838), and *Flabellum cuneatum* (Goldfuss, 1826). Subsequently, Milne Edwards and Haime (1848, 1857) and Haime (1852) recorded “*Flabellum costatum* Bellardi” from “La Palarea,” which was also found in the Eocene “Subapennine” formation by von Leonhard and Bronn (1856). The species has also been recorded in Italy (Piedmont, Alessandria) (Morris, 2025).

Outside of Europe, a preserved specimen of this coral was documented in Navidad, central Chile, in the GBIF database (<https://www.gbif.org/>) by Dr. Stephen D. Cairns (Orrell, 2025). In the species data of this website, *Flabellum costatum* Philippi, 1887 is qualified as an “Excluded” scientific name. *Flabellum costatum* Philippi, 1887 was originally described from Miocene Tertiary terrains in Levu (a misspelling of Lebu), south-central Chile. The main characteristics of the species include a coiled polyp with a length of 23 mm, a width of 27 mm, and a thickness of 15 mm, which is elliptical in cross section and features slightly ridged ribs on the outside that regularly alternate between larger and smaller ribs with a smooth space between them. In the original description, Philippi did not mention the fate of the type specimens or samples of the species. In later literature, the species was recorded by Tavera (1942, p. 106) from the Eocene fauna of the Arauco Formation, also in southern Chile. The same author, as Tavera Jerez (1979, p. 15, 40, 75, 98, 106, 148, 149), again recorded the species from the Eocene–Miocene terrains of Navidad, although he suggested that these samples could correspond to “*Lythomyces costellatus* Phil.” Subsequently, *Flabellum costatum* Philippi, 1887 was also recorded

in Miocene terrains of Navidad by Frassinetti and Covacevich (1982, p. 108). Covacevich and Frassinetti (unpublished) deposited samples of the species from Punta Alta de Navidad in 1980 at the Museo Nacional de Historia Natural, Santiago, Chile (MNHNCL). More recently, Volosky Medina (2021, p. 78) synonymized *Flabellum costatum* Philippi, 1887 with *Flabellum costellatus* (Philippi, 1887), originally described as *Lithomyces costellatus* Philippi, 1887 and currently accepted as *Flabellum* (*Flabellum*) *costellatum* (Philippi, 1887). In this context, we do not agree with this synonymy, considering that the descriptions and illustrations of both species are quite distinct (see Philippi, 1887; Volosky Medina, 2021). Thus, we consider *Flabellum costatum* Philippi, 1887 as a valid taxon.

After establishing that the species described by Michelin, the senior homonym, has been employed as a valid name post-1899 (Art. 23.9.1.1), and confirming that Philippi’s name, the junior homonym, is valid and has been cited in fewer than 25 works (Art. 23.9.1.1), the next step is to ascertain whether they denote distinct entities (thus homonymous) or refer to the same species, with *Flabellum costatum* Philippi, 1887 as junior synonym. In the original description of this species (in Spanish and in German), the author described this coral on the basis of an incomplete specimen illustrated in calicular and lateral view. The fossil was characterized as cuneiform in shape, elliptical (in cross section), and showing 19 ribs, somewhat keeled, alternating between major and minor in a regular pattern, with smooth spaces between them. The cuneiform shape is consistent with the external appearance described (in French) by Michelin (1846) for his *Flabellum costatum*. However, Michelin also described the polyp with an ovate–oblong star, having longitudinal lines, rounded, interrupted, raised on both sides; few and unequal lobes; and edges with appendages. The slightly keeled ribs differentiate Philippi’s species from Michelin’s species, in addition to the fact that the former lacks appendages on the edges. Furthermore, the species were found on different continents.

Flabellum taveri nom. nov.

1979 *Flabellum solidum* Tavera Jerez, p. 15, 54, 75, 98 (description), 108, 139, 144, 147, 165, pl. 21, fig. 86. nom. preocc. (not *Flabellum solidum* Seguenza, 1864, p. 484, 557, pl. 10, fig. 6). No synonym was found to be available as a possible replacement name.

Type material. The name-bearing type is the specimen described and illustrated by Tavera Jerez (1979) (Art. 72.5.6).

Etymology. The species is named in honor of the pioneering Chilean paleontologist Juan Tavera Jerez.

Remarks. *Flabellum solidum* Seguenza, 1864 was originally described as a fossil from Miocene marls of Rometta, Italy, on the basis of an incomplete specimen, well illustrated, deposited in the author's collection. In the original description, Seguenza (1864) noticed some resemblance with *Flabellum messanense* Seguenza, 1864, described in the same work, and therefore he did not establish *Flabellum solidum* without any doubt. However, in a subsequent work, alluding to another Italian species of the genus, Seguenza (1875, p. 29) explicitly recognized the species as valid. Thus, although in the World List of Scleractinia of the World Register of Marine Species (WoRMS) database the species is currently listed as a *taxon inquirendum* (Hoeksema and Cairns, 2024b), we consider the species as valid.

Flabellum solidum Tavera Jerez, 1979 was originally described as a fossil from lower Miocene terrains of Navidad, central Chile. The main characteristics of the polyp include a length of 38.5 mm, a maximum diameter of 11 mm, and a thickness of 10 mm, soft and irregularly spaced transverse wrinkles on the surface, a tectura with fine, low-relief crest, along with other finer ones, and about 23 first-order septa plus one interstitial. Although the species has not been subsequently cited, Tavera Jerez (1979, p. 54) noted in the original description (in Spanish) that this coral was “frequent and characteristic,” collecting several specimens at different sites along a 35 to 40 km coastline. Considering its presence on a different continent, its “abundance” and the observable characteristics in two well-photographed specimens of the species, we conclude that *Flabellum solidum* Tavera Jerez, 1979 is distinct from *Flabellum solidum* Seguenza, 1864.

***Flabellum rachelis* nom. nov.**

1860 *Flabellum striatum* Gabb and Horn in Gabb, p. 399, pl. 69, figs. 10, 11. nom. preocc. (not *Flabellum striatum* Keferstein, 1859, p. 362, pl. 14, fig. 4). No synonym was found to be available as a possible replacement name.

Type material. Syntypes, Academy of Natural Sciences of Philadelphia (ANSP).

Etymology. The species is named in honor of the American marine biologist and conservationist Rachel Carson.

Remarks. *Flabellum striatum* Keferstein, 1859 was originally described as a fossil of an extinct species from the upper Oligocene of Crefeld and Neuss, Germany. The main characteristics of the species include a nearly conical polyp with an angle at the tip of 75–80°, elliptical in shape, with an axial ratio of 100:210 and a rough tectura. The septa are organized into six non-uniform systems, with a total of 24 septa (1, 2, 3 cycles) extending to the spiral formed by their thickened edges, in addition to 24 septa of the fourth cycle, which are approximately one-third wider, and a fifth cycle of septa in all chambers that are very fine and narrow. The largest individual from the original description has a calyx length of 12 mm and a height of 13 mm. In his paper, Keferstein (1859) did not mention the fate of the type specimens or samples of the species. Shortly after, it was recognized and illustrated by Roemer (1863, p. 40). De Gruyter (1944) subsequently reported the species from the late

Oligocene terrains of the Netherlands. The species has also been recorded in limestones of southwestern France (Chaix et al., 1999; Chaix and Cahuzac, 2001) and clayey–sandy strata of the Langhian (middle Miocene) of Lăpușiu de Sus site (southwest Romania) (Chaix et al., 2018). Concerning websites, *Flabellum striatum* Keferstein, 1859 is currently recognized as valid in the World List of Scleractinia of the WoRMS database (Hoeksema and Cairns, 2024c), Mineralienatlas - Fossilienatlas database (<https://www.mineralienatlas.de>), and Paleobiology Database (Uhen et al., 2023). In appearance, the species resembles *Flabellum thouarsii* Milne Edwards and Haime, 1848 (Keferstein, 1859).

Flabellum striatum Gabb and Horn in Gabb, 1860 was originally described as a fossil species from the Rotten limestone of the Cretaceous Period in Prairie Bluff, Alabama, USA, using two specimens figured by Gabb and Horn, which are deposited in the ANSP. The species was described as thick wedge-shaped, with acute angles, thin laminae, finely crenate slightly undulating edges, coarsely granulous sides, regular striations, and granules finer toward the edge. After the first description, the species was recorded by Vaughan (1900, p. 196), who wrote “The figures given by Gabb are worthless and the description is entirely insufficient for specific identification. The types sent to me from the Academy of Natural Sciences of Philadelphia are only internal casts, and are not sufficient for specific characterization, so the species lapses.” Nevertheless, the species was recognized shortly after by Johnson (1905) after reviewing the material deposited in the ANSP, later cited by Richards (1968) as cotypes, validating the species. More recently, Groves and Squires (2018) cited the species and recognized it as a junior homonym of *Flabellum striatum* Keferstein, 1859, which was not further resolved. *Flabellum striatum* Gabb and Horn in Gabb, 1860 is also cited in the GBIF (2023) and WoRMS databases (Hoeksema and Cairns, 2024d). Considering the various citations, we conclude that this species is not a *nomen dubium*.

***Flabellum pirii* nom. nov.**

1887 *Flabellum striatum* Philippi, p. 226, pl. 53, fig. 6. nom. preocc. (not *Flabellum striatum* Keferstein, 1859, pl. 14, fig. 4). No synonym was found to be available as a possible replacement name.

Type material. The name-bearing type is the specimen described and illustrated by Philippi (1887) (Art. 72.5.6).

Etymology. The species is named after the Ottoman cartographer Piri Reis.

Remarks. *Flabellum striatum* Philippi, 1887 was originally described from Miocene Tertiary terrains of Levu (a misspelling of Lebu), south-central Chile, without reference to the type material. The main characteristics of the species include a coiled polyp that is elliptical in cross section, densely and deeply striated, and slightly rough. It has thin lamellae extending from the center to the circumference, spaced 3 mm apart, and an exterior surface that is also deeply striated and rough. The height is approximately 23 mm, the width is approximately 25 mm, and the thickness is 16 mm. Tavera (1942, p. 603, 605) recorded this species from the Tertiary of Arauco (Miocene), south-central Chile. Recently, it was also recorded by Volosky Medina (2021, p. 77), who deposited samples from the Ranquil Formation, south-central Chile, at the Museo de Historia Natural de Concepción (MHNC). Thus, we consider the species as valid.

Taking into account the original descriptions of *Flabellum striatum* by their authors, the differences observed in the drawings or photographs of the species, and the different continents or subcontinents where they were described (Keferstein, 1859; Gabb and Horn in Gabb, 1860; Philippi, 1887; Chaix et al., 1999; Chaix and Cahuzac, 2001; Volosky Medina, 2021), we consider the three species named as *Flabellum striatum* to be distinct from each other. Thus, replacement names are justified.

Acknowledgments. We thank D. Volosky for valuable suggestions. We also thank those who assisted in locating type specimens: A. Martínez-Melo and J. Sessa, both from the ANSP, and I. Araya from the MNHNCL. We also thank the editor and two anonymous reviewers for their valuable comments on the original manuscript.

Competing interests. The authors declare that they have no competing interests.

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