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# *Hikorocodium* Endo is not an alga but an inozoid sponge

Baba Senowbari-Daryan and J. Keith Rigby

**Abstract:** The genus *Hikorocodium*, with the type species *Hikorocodium elegantae* from the Permian of Japan, was described originally as a codiacean alga by Endo. It is not a codiacean alga but an inozoid sponge of the family Preperonidellidae. Several fossils described later by Endo and other authors as *H. elegantae* should be assigned to different inozoid sponge taxa. Specimens of *H. fertiliz*, described by Endo from the Jurassic of Japan, are also sponge fragments. The taxonomic positions of *H. transversum* Endo and *H. kuramotoi* Nakamura, as sponges or algae, remain uncertain.

**Résumé :** Le genre *Hikorocodium*, dont l'espèce type est *H. elegantae* du Permien du Japon, a été décrit à l'origine par Endo comme faisant partie des algues codiacées. Il ne s'agit toutefois pas d'algues codiacées, mais plutôt d'éponges inozoïdes de la famille des Préperonidellidés. Plusieurs fossiles décrits par la suite par Endo et d'autres auteurs comme étant *Hikorocodium elegantae* sont plutôt attribuables à différents taxons d'éponges inozoïdes. Des spécimens d'*Hikorocodium fertiliz* du Jurassique du Japon décrits par Endo sont également des fragments d'éponges. Les positions taxonomiques d'*H. transversum* Endo et *H. kuramotoi* Nakamura, plus précisément leur attribution aux éponges ou aux algues, demeurent incertaines.

[Traduit par la Rédaction]

## Introduction

Endo (1951) described a calcareous fossil from the Kitakami Mountains of northeastern Japan that he named *Hikorocodium*, and assigned it to the codiacean algae. He and other authors later described and illustrated the same or similar fossils as *Hikorocodium* several times, based on specimens from Japan, Europe, and northern Africa (see synonymy under "Systematic paleontology" later in the text). He later added two more species, *H. transversum* Endo (1957) and *H. fertiliz* Endo (1961b), to *Hikorocodium*. An additional species was described as *H. kuramotoi* by Nakamura (1994) from the Carboniferous of Japan. *H. kuramotoi* has also been reported from the Carboniferous of the Cantabrian Mountains, Spain (Mamet and Villa 2004).

Codiaceans are a nodular or blade-shaped group of calcareous algae with aragonitic skeletal mineralogy. The thallus in this group consists of a central zone (medula with siphons arranged parallel to the axis) and a peripheral zone (cortex with smaller branched utricles arranged perpendicular or oblique to the axis or to the medullar zone). Utricles of the cortex zone are clearly branched tubes or pores. However,

the internal structure of *Hikorocodium* has a reticulate structure and not "atubular pores in the peripheral part" as noted by Endo (1951, p. 126; 1961a, p. 29). The spongelike character of *Hikorocodium* was also evident to him. He observed that "The central stem may be composed of a sponge-like mass of very fine rounded thread-like filaments." (Endo 1951, p. 126). The totally different internal structures of *Hikorocodium* and codiacean algae may be the reason that neither Bassoullet et al. (1983) nor Granier and Grgasovic (2000) listed *Hikorocodium* among the codiacean or dasycladacean algae. However, skeletal characteristics of the type species, *H. elegantae* Endo, are typical of inozoid sponges. Kochansky and Herak (1960), H.W. Flügel (1963), and Vachard (in Termier et al. 1977) discussed the systematic position of *Hikorocodium*. They listed it as under "problematica" or "incertae sedis".

## Heterogeneity of fossils known as *Hikorocodium*

Endo (1951) described *H. elegantae* in detail, but unfortunately he did not give a summarized diagnosis nor designate a specimen as holotype for the genus. He summarized a diagnosis for *Hikorocodium* (Endo 1961a, p. 29), "Thallus cylindrical rather straight or somewhat undulating. It is composed of a poorly organized, pith-like, central stem and may be composed of a sponge-like mass of very fine rounded thread-like filaments. The tubular pores are given off from the central stem at about right angles or slightly ascending toward one end of the thallus." (see also Vachard, in Termier et al. 1977, p. 24).

The "type material" of *H. elegantae* described by Endo includes three specimens he illustrated (Endo 1951, pl. 10, figs. 1–3). Figures 1 and 2 illustrate specimens with longitudinal sections that exhibit a relatively wide axial canal (called "central stem" by Endo) surrounded by an irregularly

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**Fig. 1.** Various species of *Hikorocodium* that have been figured by previous authors. (A–C) *Hikorocodium elegantae* Endo. Original illustrations by Endo (1953, pl. 10, figs. 1–3). Explanations and magnification of all three figures as given by him,  $\times 3$ . (Endo 1951, p. 128) (A, B) “Longitudinal sections showing undulated outlines, rounded protuberances, and branched, anastomosing, tubular pores which end blindly near the outer surface.” (C) “A cross-section of a specimen showing a just-dividing point of bifurcating central stem, coated with dark layers of some kind of sponge.” (D, E) *Hikorocodium elegantae* Endo. Both figures were illustrated by Endo (1957, pl. 42, figs. 5, 6). Explanations and magnifications are as given by him (Endo 1951, p. 128). (D) “Well preserved cross-section showing anastomosing tubular pores,  $\times 15$ .” (E) “Longitudinal section,  $\times 10$ .” (F) *Hikorocodium elegantae* Endo. Only one specimen was figured by Endo and Horiguchi (1957, pl. 14, fig. 3). The explanation and magnification, according to the authors (Endo 1957, p. 301) are, “A tangential section, showing characteristic anastomosing branched tubular pores,  $\times 25$ .” (G) *Hikorocodium* sp., illustrated by Wray, (1977, fig. 87, p. 85.) with the explanation, “Longitudinal and transverse section. Permian, Tunisia. Transmitted light, thin section.” (H) *Hikorocodium elegantae* Endo, illustrated by Flügel (1980, pl. 2, fig. 7, p. 56). The explanation and magnification of the transverse section, according to the author are, “Querschnitt,  $\times 15$ .”

arranged, loose fibrous structure characteristic of sponges. The endowall (wall of the axial canal) is not distinct. The third specimen, illustrated as fig. 3, is a cross-section that exhibits two axial canals surrounded by relatively coarse and densely packed fibrous structure. The axial canals are separated from one another by a thin wall and each canal has a distinct wall. Endo explained this figure as “a specimen of cross-section showing the division point of bifurcating central stem, coated with dark layers of some kind of sponge” (Endo 1951, p. 129).

In our opinion, the specimens illustrated in figs. 1 and 2 by Endo (1951) are of the same species, but the specimen shown in fig. 3 does not belong to this species. Therefore, two different sponge species were assigned to *H. elegantae* by Endo (1951).

Endo did not designate a holotype for *H. elegantae*. However, he noted (Endo 1951, p. 127) “Genotypes: L.E.S., Saitama Univ., Slides No. 41, 59, 60, Specimen, 10769”. Because the description of *H. elegantae* by Endo (1951) was based mainly on the longitudinal sections of specimens illustrated in figs. 1 and 2, we designate the specimen shown in fig. 2 as the “lectotype” (Fig. 1B) and that in fig. 1 as a “paralectotype” (Fig. 1A) for *H. elegantae*. Figure 3 in Endo (1951) represents an inozoid sponge with two axial spongocoels (Fig. 1C), a feature characteristic of the genera *Bisiphonella* Wu (1991); *Bicoelia* Rigby, Senowbari-Daryan, and Liu (1998); or *Imperatoria* de Gregorio (1930). However, these three genera cannot be distinguished in transverse sections (see Rigby and Senowbari-Daryan 1996, p. 81; Rigby et al. 1998).

Endo (1953, pl. 12, fig. 8, p. 124) later described and illustrated another example of *H. elegantae* from the Lower Permian of the Iwaizaki Limestone, from about 80 km northeast of Sendai. This poorly preserved specimen also seems to be a sponge, like the type material of Endo (1951), and could be assigned to *H. elegantae* Endo.

Specimens described and illustrated as *H. elegantae* by Endo (1954b, pl. 19, figs. 1–3, p. 218) seem to be a different form. The specimens shown in figs. 1 and 3 differ markedly from the type material of Endo (1951) and also from another specimen he later illustrated (Endo 1954b, fig. 2). All three of these specimens are sponges, however, and are not algae.

Endo (1957, pl. 42, figs. 5, 6, p. 297) described and illustrated two additional specimens as *Hikorocodium elegantae* (Figs. 1D, 1E). These specimens, particularly the one shown in cross-section in Endo’s figure 6, have an axial canal surrounded by a coarse fibrous skeletal structure. These speci-

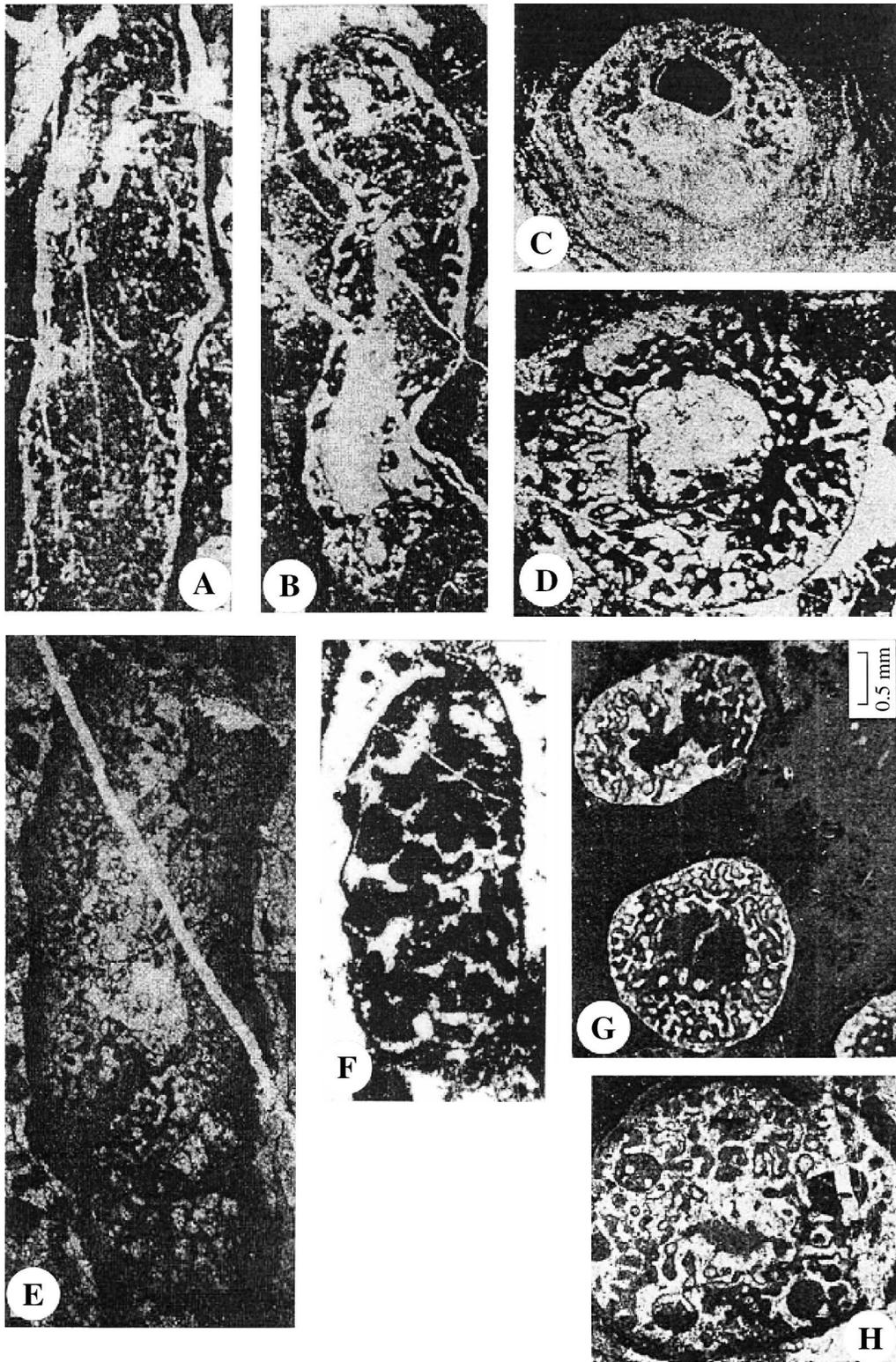
mens are also inozoid sponges. Such sponges are known from the Carboniferous and Permian, and were described as *Maeandrostia* by Girty (1908) (see Finks and Rigby 2004, p. 644). Wray (1977, fig. 87, p. 84) described and illustrated as *Hikorocodium* two transverse sections of sponges from the Upper Permian of Tunisia that could be *Maeandrostia* (Fig. 1G).

A specimen from the Carboniferous of the Hida Massif, Japan, was described and illustrated as *Hikorocodium elegantae* by Endo and Horiguchi (1957, pl. 14, fig. 3, p. 176) (Fig. 1F). It also seems to be different from the type specimens illustrated by Endo (1951). The structure of this later specimen is comparable with that of the sponge described as *Vermispongia spiniformis* Wu 1991 (= *Vermispongiella spiniformis* Finks and Rigby 2004, p. 607) from the Permian of China.

In addition, Endo (1961c, pl. 7, p. 135) described and illustrated a specimen as *H. elegantae* from the Permian of Honshû Island, Japan. This specimen is differentiated from all other specimens described by Endo in earlier publications by its large axial canal and five (six?) collateral vertical canals located near the periphery of the skeleton. This specimen belongs to the preperonidelliid inozoid sponge genus *Heptatubispongia*, and the same sponge species was described as *H. symmetrica* by Rigby and Senowbari-Daryan (1996) from the Upper Permian of Tunisia and by Senowbari-Daryan et al. (2005) from the Permian of Iran.

Two specimens of sponges from the Lower Permian of the Kitakami Mountains, northeastern Japan, were described and illustrated as *H. elegantae* by Horiguchi (1958, pl. 27, fig. 3; pl. 28, fig. 7; pp. 137–138; see later in the text under “Systematic paleontology” for an explanation of plate and figure numbering). Figure 3 in plate 27 illustrates transverse section of a sponge with an axial spongocoel surrounded by skeletal fibers without exhalant or inhalant canals, and it may be a *Preperonidella*. The oblique transverse section of the specimen illustrated by fig. 7 in plate 28 clearly shows a large axial spongocoel and nine (or 10?) collateral peripheral canals that are characteristic features of *Heptatubispongia symmetrica* Rigby and Senowbari-Daryan (1996).

Kochansky and Herak (1960, pl. 10, figs. 9–13, p. 90) described and illustrated different sponges from the Permian of several localities in the former Yugoslavia as *Hikorocodium elegantae* Endo. For example, the specimen shown in their fig. 13 has two axial canals, like the specimen illustrated by Endo (1951, pl. 10, fig. 3), and should be assigned to *Bisiphonella* Wu (1991) or to *Bicoelia* Rigby, Senowbari-



Daryan, and Liu (1998). None of the specimens illustrated by Kochansky and Herak are comparable to other specimens illustrated by Endo (1951, pl. 10, figs. 1, 2). Kochansky and Herak (1960, p. 90) interpreted *Hikorocodium* as a problematic organism. They wrote that "In our slides from various localities we find numerous specimens which are identical with those published by Endo (1954a, 1957), Endo and

Horiguchi (1957), and Horiguchi (1958) as *Hikorocodium elegans*. However, it is necessary to note that in our opinion the organization can not be regarded as doubtlessly typical dasycladacean. A slight general similarity with Hydrozoa was the reason that some of our specimens were first published as 'cf. *Carterina* sp.' or 'Stromatoporidae gen. et sp. indet.'."

H.W. Flügel (1963) described sponge-like fossils from the Permian of Dizdere bei Julfa, Iran, and from Ala Dag, Taurus Mountains, Turkey, as *Hikorocodium elegantae* Endo, and attributed them to problematic organisms. He noted that *Hikorocodium* could be a sponge.

H.W. Flügel (1963, p. 92) synonymized the fossils described as “*Carta* sp. n. sp. A and n. sp. B” (Hydrozoa) by E. Flügel (1959) from the Permian of Slovenia and Crna Gera, Montenegro. E. Flügel (1959, fig. 1) illustrated only the species “*Carta* sp. n. sp. A”. There is no illustration of “*Carta* sp. n. sp. B” from the Crna Potok locality, Montenegro.

The cross-section of “*Carta* sp. n. sp. A” illustrated by E. Flügel (1959) in fig. 1 shows an axial cavity. Apparently E. Flügel (1959, p. 90) interpreted this cavity as a “Fremdkörper” (extraneous object). The skeletal structure of his “*Carta*” is totally different from *Hikorocodium*. The taxonomic position of E. Flügel’s *Carta* sp. n. sp. A and B as hydrozoans or sponges is doubtful.

*Hikorocodium* was listed as a genus of “uncertain affinities” by Johnson (1964). He reillustrated (Johnson 1964, pl. 45, fig. 1) an enlarged view Endo’s original material (Endo 1951, pl. 10, fig. 1). He gave Endo’s original description of the genus and type species (Johnson 1964, p. 38) and noted that “The description and original illustration do strongly suggest a rather poorly preserved green alga.” (Johnson 1964, p. 39). However, later descriptions (Endo 1953, pl. 12, fig. 8, p. 124; pl. 4, fig. 3, p. 176; Endo 1957, pl. 42, figs. 5–7, p. 297–298) add little information, whereas the illustrations progressively show specimens that look less and less like algal material, ending with Endo’s 1957 illustration of Permian specimens and Endo’s 1961c Jurassic paper where the illustrations really suggest stromatoporoids.

Kochansky-Devidé (1970, pl. 26, fig. 5, p. 220) described and illustrated a specimen as *Hikorocodium elegantae* Endo that exhibits two spongocoels. This inozoid specimen belongs to either *Bicoelia* Rigby, Senowbari-Daryan, and Liu (1998) or *Bisiphonella* Wu (1991).

Homann (1972, pl. 2, fig. 15, p. 181) described and illustrated a specimen, from the Carnic Alps, Austria, as *Hikorocodium elegantae* Endo. It is not possible to be certain about skeletal details and classification of the specimen based on his illustration.

The specimen illustrated by E. Flügel (1980, pl. 2, fig. 7) as *Hikorocodium elegantae* Endo, from the lower Permian (Troglkofel beds) of the Carnic Alps, shows the large axial and small collateral canals (Fig. 1H) typical of *Heptatubispongia symmetrica* Rigby and Senowbari-Daryan 1996.

Nakazawa (2002, pl. 29, fig. 5) illustrated several specimens that were considered by him to be *Hikorocodium*. According to his description, “This incertae sedis has a tube form with inner pores.” (Nakazawa 2002, p. 198) and in his photographs these specimens may be algae but are not *Hikorocodium* comparable to the type material of Endo (1951).

In summary, *Hikorocodium* was not accepted as a certain alga and was listed as a problematic alga by algal specialists (e.g., Kochansky and Herak 1960; H.W. Flügel 1963; Johnson 1964; Kochansky-Devidé 1970; Vachard, in Termier et al. 1977). Some fossils that were described in the literature as *Hikorocodium elegantae* Endo should be assigned taxonomically to several different sponge genera. They are clas-

sified within the hypercalcified Demospongea in the following section.

A small specimen of questionable taxonomy, but referred to as *Hikorocodium?* sp., was described and figured by Rigby, Fan, and Han (1995) from the Upper Permian of western Hubei Province, China. They concluded that the silicified specimens they had were not suitable for detailed comparisons with other forms of the genus, but suggested that the genus should be re-examined by researchers with better material to make a taxonomic evaluation of the genus.

## Systematic paleontology

- Class Demospongea Sollas, 1875
- Subclass Ceractinomorpha Lévi, 1953
- Order Agelasida Verrill, 1907
- Family Preperonidellidae Finks and Rigby, 2004
- Subfamily Preperonidellinae Finks and Rigby, 2004
- Genus *Hikorocodium* Endo, 1951

TYPE SPECIES: *Hikorocodium elegantae* Endo, 1951.

EMENDED DIAGNOSIS: Cylindrical inozoid sponges with a relatively wide axial spongocoel equal to approximately 40% of whole sponge diameter. Sponge skeleton composed of loose irregular or reticular fibrous elements. A cortex (outer wall of sponge) well developed and pierced by openings of different size. Endowall (wall of spongocoel) is not distinct.

1951 *Hikorocodium elegantae* n. sp.- Endo, pl. 10, figs. 1, 2, pp. 126–127 (non fig. 3, which is an inozoid sponge attributed to *Bicoelia*).

? 1953 *Hikorocodium elegantae* Endo.- Endo, pl. 12, fig. 8, p. 124.

1954a *Hikorocodium elegantae* Endo.- Endo, pl. 14, fig. 6, pp. 201–202.

1954b *Hikorocodium elegantae* Endo.- Endo, pl. 19, fig. 2, pp. 218–219 (non figs. 1, 3; these species are also sponges but gen. et sp. indet.).

? 1957 *Hikorocodium elegantae* Endo.- Endo, pl. 42, fig. 5, pp. 297–298.

non 1957 *Hikorocodium elegantae* Endo.- Endo, pl. 42, fig. 6, pp. 297–298 (it is a *Maeandrostia*).

non 1957 *Hikorocodium elegantae* Endo.- Endo and Horiguchi, pl. 14, fig. 3, p. 176 (may be *Vermispongiella* Finks and Rigby 2004, p. 607, *pro Vermispongia* Wu 1991).

non 1958 *Hikorocodium elegantae* Endo.- Horiguchi, pl. 27, fig. 3, pp. 137–138 (not pl. 28, fig. 7).

non 1960 *Hikorocodium elegantae* Endo.- Kochansky and Herak, pl. 9, figs. 9–13, p. 90 (different sponges with one or two spongocoels).

non 1961c *Hikorocodium elegantae* Endo.- Endo, pl. 4, fig. 7, p. 135 (see *Heptatubispongia*).

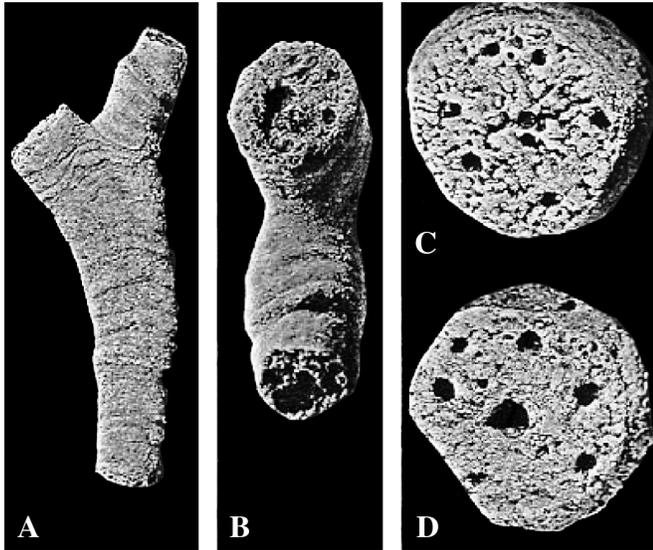
? 1963 *Hikorocodium elegantae* Endo.- H. W. Flügel, pl. 2, fig. 2, p. 92.

non 1970 *Hikorocodium elegantae* Endo.- Kochansky-Devidé, pl. 26, fig. 5, p. 220 (sponges with two spongocoels).

? 1972 *Hikorocodium elegantae* Endo.- Homann, pl. 2, fig. 15, pp. 181–183.

non 1977 *Hikorocodium* Endo.- Wray, fig. 87, p. 84 (may be *Maeandrostia*).

**Fig. 2.** *Heptatubispongia symmetrica* Rigby and Senowbari-Daryan 1996, holotype from the Upper Permian of Djebel Tebaga, Tunisia, USNM 463724. (A) Side view of branched holotype with weakly annulate growth lines,  $\times 2$ . (B) Summit view, with left branch as shown in Fig. A as upper branch, with minor axial canals and symmetrically distributed vertical canals near the periphery,  $\times 4$ . (C) Base of sponge with typical ring of exhalant canals near the periphery and radial canals around the central spongocoel,  $\times 8$ . (D) Summit of right branch with characteristic canal pattern,  $\times 5$  (from Rigby and Senowbari-Daryan 1996, pl. 33, figs. 9–12).



? 1977 *Hikorocodium elegantae* Endo.- Vachard (in Termier et al.), p. 24 (no illustration).

non 1980 *Hikorocodium elegantae* Endo.- E. Flügel, pl. 56, fig. 7 (see *Heptatubispongia*).

non 2002 *Hikorocodium* Nakazawa, pl. 29, fig. 5 (may be an alga but not *Hikorocodium* comparable with type material of Endo 1951).

**DISCUSSION:** The diagnosis presented earlier in the text is based on two longitudinal specimens illustrated by Endo (1951, pl. 10, figs. 1, 2) (Figs. 1A, 1B).

Endo (1957, pl. 42, fig. 7; pl. 43, figs. 1–3; p. 298).

A third species of *Hikorocodium*, *H. fertiliz*, was described and illustrated by Endo (1961b, pl. 10, fig. 1; pl. 14, fig. 5; pl. 17, fig. 5; pp. 66–67) from Upper Jurassic limestone, Fukushima-ken in Endo (1961b, p. 66) or Tokushima-ken in Endo (1961b, p. 72), Japan. Endo designated “Slide No. 684” (1961b, p. 66) as the holotype of *H. fertiliz* and illustrated it in fig. 5 of plate 17 (Endo 1961b). According to Endo, an enlargement of that holotype was illustrated in fig. 1 of plate 10 (Endo 1961b; the same enlargement was reillustrated by Johnson 1964, pl. 45, fig. 1), but this figured material does not correspond to any part of the holotype. Both specimens of *H. fertiliz* illustrated by Endo are fragments of undetermined sponges and should be excluded from the algae.

Finally, the fourth species was described as *Hikorocodium kuramotoi* by Nakamura (1994) from the Carboniferous of Japan. The systematic position of this species is uncertain.

Subfamily Heptatubispongiinae Rigby and Senowbari-Daryan, 1996

Genus *Heptatubispongia* Rigby and Senowbari-Daryan, 1996

**TYPE SPECIES:** *Heptatubispongia symmetrica* Rigby and Senowbari-Daryan, 1996.

**ORIGINAL DIAGNOSIS:** “Cylindrical to branched sponge with relatively large axial canal or spongocoel, and usually seven but in some specimens with as few as six or as many as eight or more collateral vertical canals located near periphery of sponge. Outer surface bears a few ostia. Internal structure characterized by relatively coarse reticulate fibers. Growth lines prominent on exterior.” (Rigby and Senowbari-Daryan 1996, p. 83).

1958 *Hikorocodium elegantae* Endo.- Horiguchi, pl. 28, fig. 7 (non pl. 27, fig. 3).

1961c *Hikorocodium elegantae* Endo.- Endo, pl. 4, fig. 7, p. 135.

1977 *Graminospongia girtyi* (Parona).- Termier and Termier, pl. 8, fig. 1.

1980 *Hikorocodium elegantae* Endo.- E. Flügel, pl. 56, fig. 7.

1996 *Heptatubispongia symmetrica* n. sp.- Rigby and Senowbari-Daryan, pl. 33, figs. 9–16, pl. 49, fig. 9, pp. 83–84.

2005 *Heptatubispongia symmetrica* Rigby and Senowbari-Daryan.- Senowbari-Daryan, Rashidi and Hamedani, figs. 11.1–11.5, 13.1H and 2H (synonymy), p. 395.

**OCCURRENCE:** *Heptatubispongia symmetrica* (Figs. 2A–2D) is an abundant preperonidelliid inozoid sponge, occurring in Permian deposits of Tunisia (Rigby and Senowbari-Daryan 1996), the Carnic Alps of Austria (Flügel 1980), Japan (Horiguchi 1958, Endo 1961c), Sicily (material of Senowbari-Daryan, see Senowbari-Daryan and Di Stefano 1988) and in Iran (Senowbari-Daryan et al. 2005).

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