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Fossil record and paleobiogeography of *Steindachneria* (Pisces, Gadiformes)

2 figures, 1 plate

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Abstract

Otolith sampling provided an extensive fossil record for *Steindachneria*, an „odd" deepwater gadiform fish genus represented only by a single Recent species endemic to the Carribean realm. These otoliths constitute the ony known fossil material. They trace back the ancestry of the taxon to at least the Early Miocene and extend its past geographical range to a considerable part of the eastern Pacific coasts and to the Mediterranean. At least four taxa are recognised: *S. goederti* n. sp. from the Lower Miocene of Washington State, *S. svennielseni* n. sp. from the Upper (?) Miocene of Chile, the Recent *S. argentea* known as fossils from the Lower Pliocene (and Lower Miocene?) of Venezuela, and at least one unnamed *Steindachneria* species from the Italian Lower Miocene.

Keywords: *Steindachneria*, Gadiformes, fossil record, paleodiversity

Résumé

La récolte d'otolithes a permis de reconnaître la présence de plusieurs taxa fossiles du genre *Steindachneria*, un gadiforme d'aspect étrange, qui dans la nature actuelle n'est représenté que par une seule espèce dont la répartition est restreinte aux Caraïbes. Ces otolithes, qui constituent les seuls fossiles connus de *Steindachneria*, prouvent que le taxon existait déjà dès le Miocène inférieur et montrent que sa répartition ancienne englobait une portion considérable de la côte du Pacifique est et s'étendait jusqu'en Méditerranée. Au moins quatre taxa sont reconnus: *S. goederti* n. sp. du Miocène inférieur de l'état de Washington, *S. svennielseni* n. sp. du (?) Miocene (?) supérieur de Chili, l'actuel *S. argentea* connu à l'état fossile du Pliocene inférieur (et du Miocène inférieur?) du Venezuela et au moins une espèce de *Steindachneria* (non désigné de façon nominale) du Miocène inférieur d'Italie.

Mots-clés: *Steindachneria*, Gadiformes, présence fossile, paléodiversité

Introduction

In the Recent fauna, the genus *Steindachneria* GOODE & BEAN, 1888 is represented by a single species, *Steindachneria argentea* GOODE & BEAN, 1896 (Fig. 1) which is known only from the Gulf of Mexico and the southern Caribbean realm (Fig. 2). This macrourid-like fish is living on the outer shelf and upper slope, on soft bottoms, mainly between 400 and 500 m (COHEN et al. 1990) but was also caught as shallow as 120 m (ROBINS et al. 1986). The genus is included in the merluciids by many authors, e.g. (COHEN et al. 1990, NOLF & STEURBAUT 1989), but has also been associated with the macrourids (GOODE & BEAN 1896, FAHAY 1989) or treated as a distinct family (MARSHALL & COHEN 1973, MARKLE 1989, HOWES 1991a and b).

In my opinion, knowledge of both the fossil record and the interrelationships of gadiform taxa remain very unsatisfactory. Because the otoliths of *Steindachneria* exhibit essentially plesiomorphic features, they are not of direct help in judging the phylogenetic affinities of the taxon. However, this does not affect the goal of the present paper, which is to establish the ancient distribution and species diversity of the genus. *Steindachneria*

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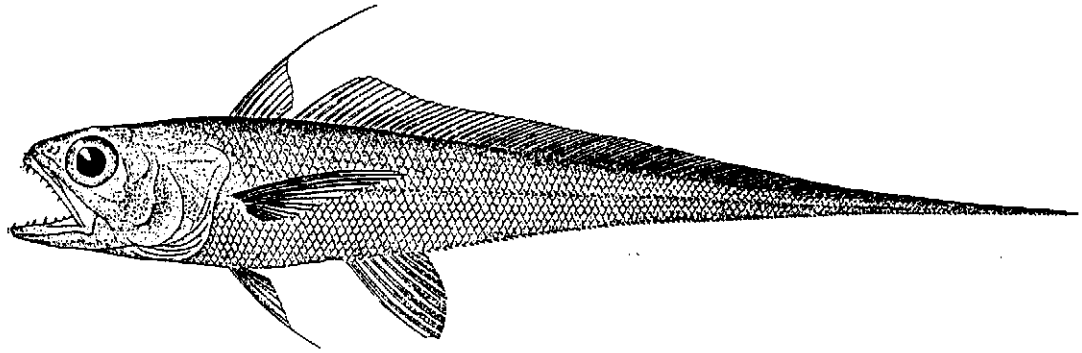

Fig. 1: *Steindachneria argentea*, after GOODE & BEAN (1896, pl. 51, fig 351). Maximal length recorded from Suriname: 27.7 cm.

otoliths exhibit excellent autapomorphic features by which they are easily distinguished them from any other gadiform clade. They are characterised by a sulcus which is very clearly divided in wide ostial and caudal portions. These are separated by a long and narrow central zone with a clear collicular crest near the crista inferior. The crista superior is always clear, and the collicula are relatively small and located mainly in the central part of the otoliths. The posterior half of the cauda is narrower than the anterior half and is slightly bent in posteroventral direction. Moreover, all *Steindachneria* species are characterised by a strong development of the anterior part of their dorsal area.

The present overview is based on the presence of *Steindachneria* in an eclectic series of sample sites (the whole Indian Ocean, the western Pacific and the southern Atlantic realm have never been adequately sampled for fossil otoliths), which exhibit a remarkable diversity and geographic range for a genus that today, is only known by a single species from the Carribean realm.

Locality data

Chile, Matanzas
Cliffs and foreshore exposures about 1 km north of Matanzas, at approximately 71°52'15"W 33°57'27"S.
Navidad Formation, probably Tortonian, by lateral correlation with coastal cliffs about two km north of the Rio Rapel mouth (preliminary dating of the Navidad Formation north of Rio Rapel suggests a Tortonian age, Planktonic foraminiferal Zone N 16; NIELSEN, personal communication). The mollusc association from Matanzas is described by FRASINETTI & COVACEVICH (1993), which also provide a location map of the site. The otolith association mainly consists of deep water fishes (myctophids, macrourids, ophidiids).
Sample collected by S. NIELSEN.

Chile, Punta Perro
Cliffs and foreshore exposures, see location map in FRASINETTI & COVACEVICH (1993).
Navidad Formation, probably Tortonian, by lateral correlation with coastal cliffs about two km north of the Rio Rapel mouth (see under Matanzas. Sample collected by S. NIELSEN.

Italy, (Hills of Torino), Sciolze
Casalborgone 1/25 000 quadrangle, x = 411.175, y = 94.175.
Complex of Termo Fora (turbiditic marl with molluscs), Upper Burdigalian.

Italy, (Hills of Torino), Valle Ceppi
Chieri 1/25 000 quadrangle, x = 405.250, y = 90.800
Complex of Termo Fora (green argilaceous serpentinite sand with gravel and molluscs), Upper Burdigalian. Literature: PAVIA, 1999, p. 117.

USA, Washington State, Canyon River
Grisdale 162 500/ quadrangle, 47°16'00"N, 123°31'30"W
Astoria Formation, Lower Miocene. Equivalent of locality F-117 of RAU (1966). Sample provided by J.L. GOEDERT.

Venezuela, Araya Peninsula
Cerro Barrigo, site PPP 3055.
Cubagua Formation, Cerro Negro Member, Lower Pliocene. Samples in coll. O. AGUILLERA.

Systematic account

Steindachneria argentea GOODE & BEAN, 1896
Pl. 1, Fig. 1-5

1989 *Steindachneria argentea* GOODE & BEAN, 1896 – NOLF & STEURBAUT, p.98, fig. 7i-j.
? 1998 *Steindachneria* sp. – NOLF & AGUILERA, p. 239, pl. 6, fig. 7-9.

Description: This species is characterised by otoliths which are very high anteriorly and slender strongly towards their posterior end. There is a very strong anterodorsal angle which protrudes strongly in anterior direction in most of the specimens. The rostrum is well marked, and there is a well incised excissura, which tends to become obsolete in very large specimens, e.g. Pl. 1, Fig. 1 and NOLF & STEURBAUT (1989, fig. 7i). The dorsal rim is almost straight and oblique. The outer face is smooth and nearly straight in the antero-posterior sence,

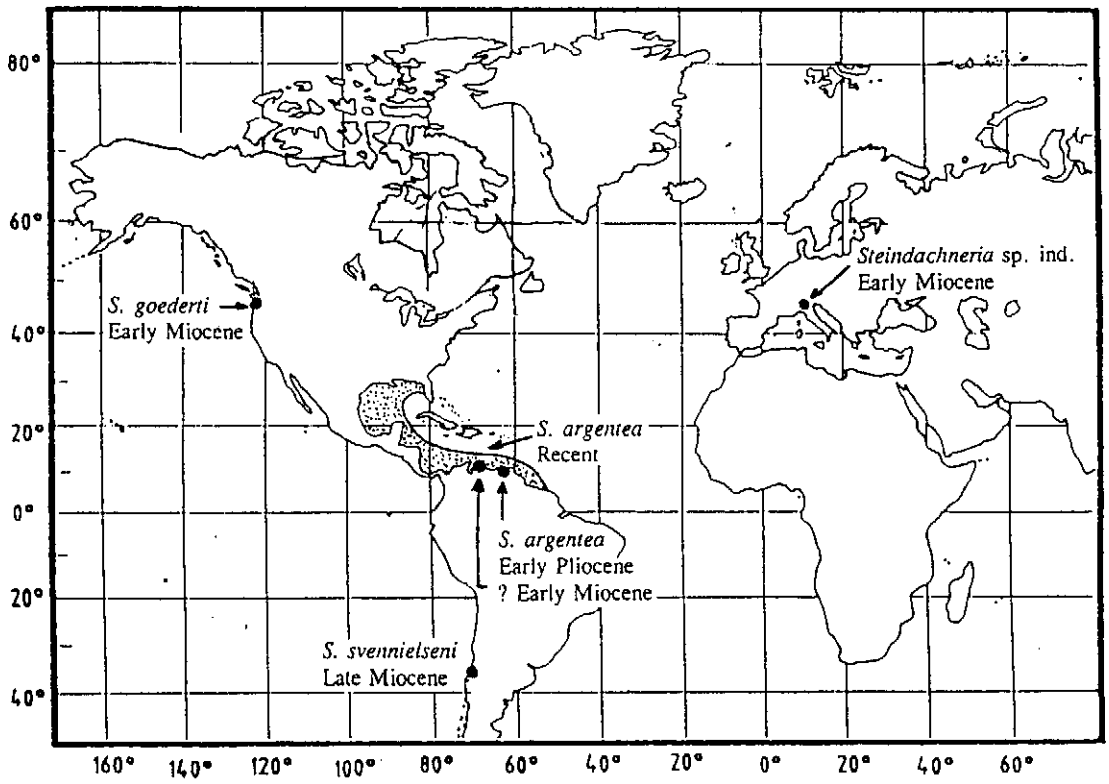

Fig. 2: Geographical distribution of fossil and Recent *Steindachneria* species.

but markedly convex in the dorso-ventral sense. The inner face is slightly convex in the the antero-posterior sense and nearly flat in the dorso-ventral sense. The otoliths show a very slight torsion along an antero-posterior axis, so that the anterior part of the dorsal area is protruding in a ventral view (Pl. 1, Fig. 1a). The sulcus corresponds to the general *Steindachneria* pattern described in the introduction.

Distribution: This Recent species from the Caribbean upper slope is known as fossil from the Lower Pliocene Cubagua Formation, Cerro Negro Member (specimens in coll. AGUILERA, University of Coro, Venezuela). Some eroded and incomplete specimens from the Lower Miocene Cantaure Formation (Venezuela) cited by NOLF & AGUILERA (1998) as *Steindachneria* sp. probably belong to the same species , or are very closely related to it.

Steindachneria goederti n. sp.

Pl. 1, Fig. 6-8

Type material: Holotype: a left otolith (Pl. 1, Fig. 6) (IRSNB P 6924); 13 paratypes of which two are figured (Pl. 1, Fig. 7-8) (IRSNB P 6925-6926).

Dimensions of holotype: Length: 9.0 mm; height: 3.8 mm; thickness: 0.9 mm.

Type locality: Astoria Formation, Lower Miocene, at Canyon Creek, Washington State, USA.

Etymology: This species is named after James L. GOEDERT, in honor of his prospecting efforts in the Washington State Tertiary.

Diagnosis: The available series of otoliths show a marked allometric growth and clear diagnostic features only appear in specimens of over 5 mm length. The allometric growth essentially affects the hight/length proportion which is 0.70 in the smallest (2.3 mm) available specimen, and 0.42 in the largest (holotype, 9.0 mm), which means that the otoliths slender very considerably during their growth. The diagnostic specimens are characterised by rather robust elongate otoliths with a high anterior and a slender posterior portion.

There is a well marked rostrum and an obtuse anterodorsal angle. The posterior rim is rounded. The ventral rim shows an obtuse but well marked anteroventral angle and is almost straight in the central part. Except in the small paratype figured Pl. 1, Fig. 8, no specimens show an excisura. The outer face is entirely smooth (only the smallest specimens show some marginal groves separating the marginal lobes) and nearly straight in the antero-posterior sense, but markedly convex in the dorso-ventral sense. The sulcus corresponds to the general *Steindachneria* pattern described in the introduction; the posterior part of the cauda is rather wide and slightly bent towards the ventral rim. The ventral area shows a clear ventral furrow near to the ventral rim.

Affinities: Otoliths of *S. goederti* are readily distinguished from those of any other fossil or Recent *Stein-*

dachneria species by their much more slender and elongate otoliths.

Steindachneria svennielseni n. sp.
Pl. 1, Fig. 9-12

Type material: Holotype: A right otolith (Pl 1, Fig. 9) (IRSNB P 6927); 5 paratypes from Matanzas of which two are figured (Pl. 1, Fig 10-11) (IRSNB P 6927-6929); 3 paratypes from Punta Perro, of which one is figured (Pl. 1, Fig 12) (IRSNB P 6930).

Dimensions of holotype: Length: 7.9 mm; height: 4.8 mm; thickness: 1.2 mm.

Type locality: Navidad Formation (? Tortonian), cliff exposures 1 km N of Matanzas, Chile.

Etymology: This species is named in honour of Sven NIELSEN, who collected the fossils and brought them to my attention.

Diagnosis: This species is characterised by rather robust subtriangular shaped otoliths with a salient rostrum. The anterior part of the dorsal area is well developed but does not extend in the anterior sense. The central part of the dorsal rim is slightly concave. None of the species show a clear excissura. The outer face is merely smooth, with some radial groves separating the marginal lobes. The inner face is very slightly convex in the antero posterior sense and nearly flat in the dorsoventral sense. The sulcus corresponds to the general *Steindachneria* pattern described in the introduction; larger specimens show a considerable widening of the ostium and the cauda in the sulcus areas occupied by the collicula. The ventral area shows a clear ventral furrow.

Affinities: Otoliths of *S. svennielseni* ressemble most closely to those of the Recent *S. argentea* but differ from them by their less developed anterodorsal area which does not extends anteriorly, by their slightly concave center of the dorsal rim, by their salient rostrum, and by the absense of an excissura.

Steindachneria sp. ind.
Pl. 1, Fig. 13-14

Material: Five poorly preserved otoliths from the Upper Burdigalian Complex of Termo Fora in the hills of Torino, three from Vale Ceppi and two from Sciolze belong to the genus *Steindachneria*; an other large but poorly preserved specimen from the old collection CANTAMESSA (n° 11568) in the Geological Museum of the University of Torino may also belong to the same genus.

Although none of the specimens are perfect enough to desserve an unambiguous identification at species level, they can perfectly be recognised as *Steindachneria* otoliths. The specimen of Pl. 1, Fig. 13 especially shows the typical *Steindachneria* sulcus pattern, the flat inner face, and the outer face that is flat in the antero-posterior sense but markedly convex in the dorso-ventral sense. The quality of the available material does not allow to conclude if all those specimens belong to a single species. The specimen from Valle Ceppi figured on Pl. 1, Fig. 14 shows markedly more elongate collicula.

Conclusions

In the present day fauna, *Steindachneria* is an "odd" gadiform fish of uncertain relationships with a restricted geographical range (Fig. 2). Data resulting from the otoliths trace back its ancestry to at least the Early Miocene and extend its past geographical range to a considerable part of the eastern Pacific realm and to the Mediterranean. The past presence of the genus in the eastern Pacific is not a totally unexpected fact since the isthmian barrier of Panama has only existed since the end of the Pliocene and because the taxon is not really a rare fish on the Recent Caribbean upper slope. The presence of two species and several specimens in a very restricted number of small samples from the eastern Pacific Miocene suggests that the taxon was abundant there at that time. One presumes that *Steindachneria* became extinct in the eastern Pacific after the closure of the Isthmus of Panama because John FITCH never mentionned any specimens in his many reports on Californian Pleistocene otoliths, but it is true that California is only a restricted sampling area for the eastern Pacific. An alternative interpretation could be that the Pleistocene climate was already too cold for finding the taxon so far north. The presence of *S. argentea* in the Venezuelan Pliocene (and probably also in the Early Miocene) is not unexpected: the species is still living there today.

The Mediterranean occurrence of *Steindachneria* is only documented by very rare, poorly preserved specimens, but there is no doubt about their generic identification. Moreover, this Mediterranean occurrence represents a peculiar interest because there is no area in the world where the (otolith-based) fossil record of deep-sea fishes is so well documented from Early Oligocene till present. (see NOLF, 1995, NOLF et al. 1998, GIRONE 2000). *Steindachneria* is only recorded there from Late Burdigalian (Early Miocene) strata, although rather diversified Oligocene deepwater faunas have been sampled from the Mediterranean and the Paratethys (Pizzo Corno site, Arenarie de Ranzano, Pouzdrany Beds, Kiscell Clay). The taxon seems to have disappeared from the Mediterranean at the end of the Late Miocene: it was not recorded from the Langhian of the Paratethys, or from the Italian Tortonian and Zanclean or the South Italian Pleistocene, all deposits that provided the most diversified deep-sea otolith associations known in the world.

For all other areas in the world, no significant deepwater otolith associations have yet been collected, except for some New Zealandian Cenozoic sites (SCHWARZHANS 1980, GRENFELL 1984) and the somewhat

shallower Oligo-Miocene Paleocanyon of Saubrigues in Aquitaine, SW France (NOLF & BRZOBOHATY in press), where *Steindachneria* was not recorded. However, such negative data does not provide any relevant information. The important conclusion is that during the Miocene, the present-day Caribbean endemic fish genus *Steindachneria* had a widespread geographical range, covering much of the eastern Pacific coast, the Caribbean realm and eastward to the Mediterranean.

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Plate 1

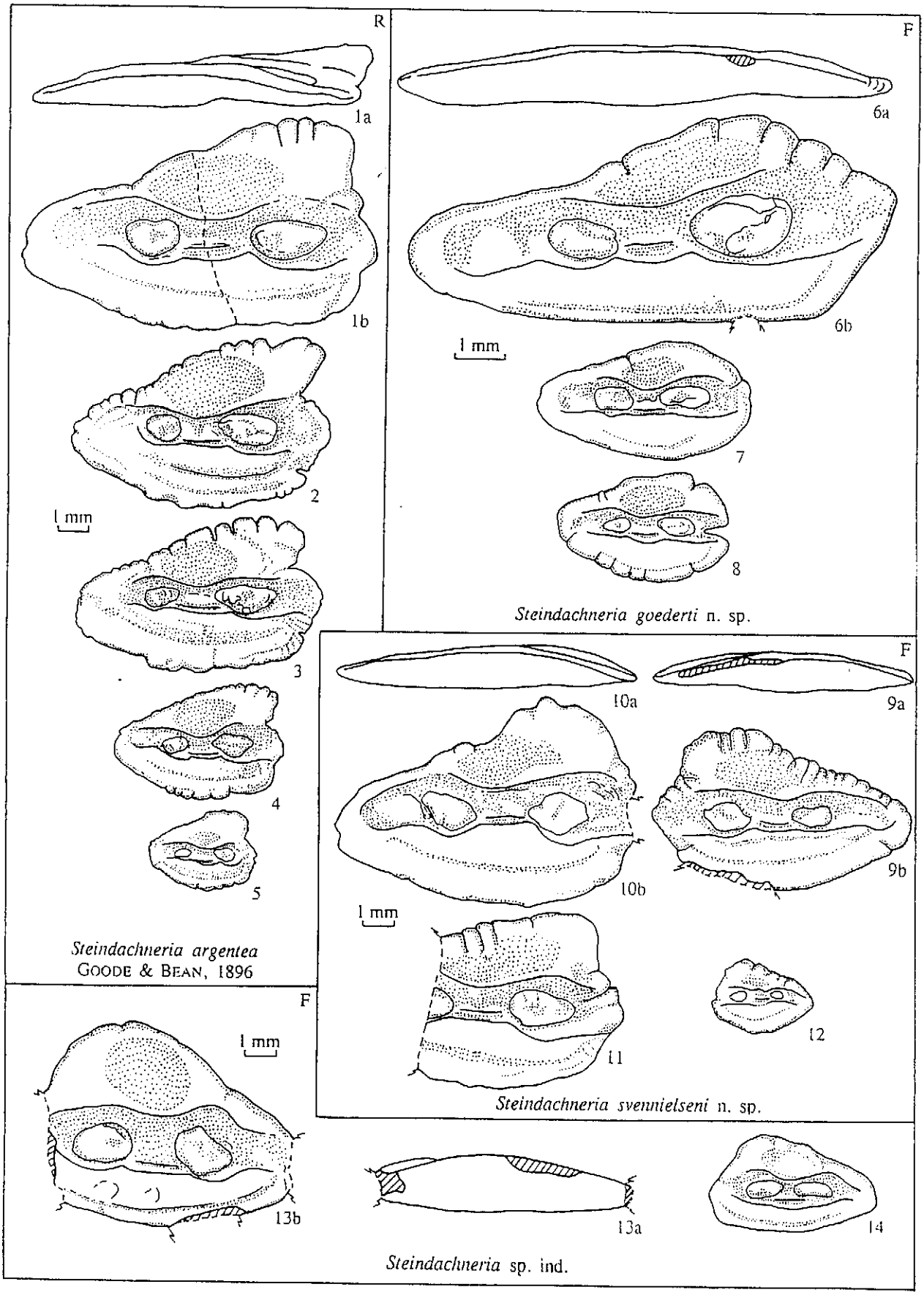
All figured specimens are deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB). The fossil otoliths bear numbers of the collection of types and figured fossil fish specimens of the IRSNB. The Recent otoliths are part of the reference collection of Recent otoliths, at the same Institution. The latter collection is arranged in systematic order without numbering; therefore, such specimens, when figured, bear only the notition "coll. IRSNB".
The abbreviations F and R in the upper right corner of each compartment of the plates indicate if the figured specimens in that compartment are fossils (F) or Recent (R). In the text of the explanations, L stands for left otolith and R for right otolith. The annotations Fig. a and b are used to indicate respectively ventral and inner (= mesial) views. Figures without letter show inner views.

Figs. 1-5: *Steindachneria argentea* GOODE & BEAN, 1896
L, Recent, Caribbean, (coll. IRSNB).

Figs. 6-8: *Steindachneria goederti* n. sp.
L, Astoria Formation, Canyon River, Washington State, 6 = holotype (IRSNB P 6924), 7-8 = paratypes (IRSNB P 6925-6926).

Figs. 9-12: *Steindachneria svennielseni* n. sp.
9 and 12 = R, 10-11 = L, Navidad Formation, ? Tortonian; 9-11 = Matanzas, 12 = Punta Perro, 9 = holotype (IRSNB P 6927), 10-12 = paratypes (IRSNB P 6929-6930).

Figs. 13-14: *Steindachneria* sp. ind.
R, Termo Fora Formation, 13 = Valle Ceppi (IRSNB P 6931), 14 = Sciolze (IRSNB P 6932).


R
1a
1b
2
1 mm
3
4
5
Steindachneria argentea
GOODE & BEAN, 1896
F
6a
6b
1 mm
7
8
Steindachneria goederti n. sp.
F
10a
9a
10b
9b
1 mm
11
12
Steindachneria svennielseni n. sp.
F
1 mm
13b
13a
14
Steindachneria sp. ind.