

First articulated teleost fish from the Paleogene of West Antarctica

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Abstract: *Marambionella andreae* gen. et sp. nov. from the La Meseta Formation (Upper Eocene–?Lower Oligocene) on Seymour Island is the first fossil clupeid found in Antarctica and the first articulated teleost from the Antarctic Paleogene. It shows a mosaic of similarities and differences compared with various clupeid genera. This and the uncertainty about the polarity of characters within clupeids do not allow precise assessment of the phylogenetic relationships of *Marambionella*.

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Introduction

In 1988, during Argentinian-Polish studies on Seymour Island, a Polish geologist Professor A. Gaździcki discovered two nearly complete specimens of a fossil clupeid fish. The specimens, as well as other skeletal fragments and numerous isolated clupeid scales, come from the La Meseta Formation (Upper Eocene–?Lower Oligocene). According to Doktor *et al.* (1988) the material comes from the lowest part of the lithological sequence (Unit I of Elliot & Trautman 1982). When examining the clupeid remains, a few isolated scales of other teleosts were also found.

Upper Jurassic specimens of some Aspidorhynchidae (Richter & Thomson 1989) and an incomplete skull of the Upper Cretaceous Beryciformes (Grande & Chatterjee 1987) are the oldest fossil teleosts described from Antarctica. In addition disarticulated and fragmented skeletal material of Siluriformes (Grande & Eastman 1986), Gadiformes (Jerzmańska 1988) and of indeterminate teleost fishes (Woodward 1908, Grande & Eastman 1986, Jerzmańska 1988) is known from the Paleogene of the La Meseta Formation. The skeletons described below are thus the first articulated teleost fishes from the Paleogene Antarctica and the first clupeids from that region.

The earliest record of clupeids in vicinity of the Antarctic is an Upper Eocene otolith from southern Australia (Schwarzhan 1985). Of extant taxa *Sprattus fuegensis* (Jenyns 1842) with its southern distribution range reaching Tierra del Fuego lives closest to the Antarctic (Whitehead *et al.* 1985). Blaxter & Hunter (1982) reported that *Strangomera bentincki* (Norman, 1936) and *Ramnogaster arcuata* (Jenyns, 1842) occur within the Antarctic region but Whitehead (1985) suggested that the distributional records pertain to *Sprattus fuegensis*.

The following specimens were used for comparisons: *Sprattus sprattus* (L.), *Sardinella fimbriata* (Valenciennes 1847) (collection of the Zoological Institute, University of Wrocław), *Sardinella aurita* Valenciennes, 1847,

Sardinella sp. (Zoological Institute, Academy of Science, Leningrad).

All fossil specimens described here are housed in the Institute of Palaeobiology, Polish Academy of Science, Warsaw (abbreviated as ZPAL).

Systematic palaeontology

Subdivision TELEOSTEI (*sensu* Patterson & Rosen 1977)

Order CLUPEIFORMES (*sensu* Grande 1985)

Family CLUPEIDAE (*sensu* Grande 1985)

Genus *Marambionella* gen. nov.

Type species. *Marambionella andreae* sp. nov.

Derivation of name. Latin diminutive of the name Marambio (Argentine name for Seymour Island) where the genus was found.

Diagnosis. *Marambionella* differs from all other known clupeids in the following combination of characters: numerous, well-developed longitudinal striae forming two wedge-shaped areas in fronto-parietal region; elongated second supramaxilla with the lower part of the expanded portion larger than the upper, and with the ventral constriction anterior to the dorsal; large third infraorbital with a deeply incised anterior margin and elongated, sharply terminated anteroventral region; operculum devoid of radiating bone striae; relatively high number of vertebrae (*c.* 49) and of pleural ribs (*c.* 31); short last ray in the dorsal fin; heavy cycloid scales with one continuous and 3–5 interrupted vertical striae.

Marambionella andreae sp. nov.

(Figs 1–8)

Holotype. An almost complete specimen, without anterior end of dentary and end of caudal fin, and partly devoid of ventral body margin (P.III/1A).

Derivation of name. The species is named in honour of Polish geologist Andrzej Gaździcki who found the type specimen.

Diagnosis. As for genus.

Additional material. One incomplete specimen (P.III/1B), on the same slab as the holotype; 35 skeleton fragments on 23 slabs P.III/2–24; numerous accumulations of isolated scales on underside of 16 slabs.

Description. The skeletal fragments preserved suggest a form of a standard length not much different from that of the type specimen (Table I, Fig. 1). The bone thickness is variable. The bones of the skull roof are the thickest, as well as dentary, operculum and the neural process of the first preural centrum.

Neurocranium: On nine heads, isolated or connected with parts of skeleton (P.III/3A–B, 6A, 7A–B, 9, 10A–B, 11), there are impressions of the skull roof with preserved bone fragments. On two specimens (P.III/3B, 7A) it is possible to see traces of a small supraoccipital separating the parietals and the ends of frontals (Fig. 2). In the fronto-parietal region there are well-developed, longitudinal striae forming two wedge-shaped areas which are separated by a smooth surface of the medial parts of the frontals and by the supraoccipital. On the anterior of the wedge, in the orbital region there are 2–4 longitudinal striae and a further 8 or 9 posteriorly. The

Table I. Measurements of the holotype of *Marambionella andreae* gen. et sp.nov.

	mm	Percentages of standard length
Standard length ¹	185	-
Head length	44	23.7
Maximal body depth at level of dorsal fin origin	c 50	c. 27.0
Predorsal length	c 90	c. 48.6
Prepelvic length	99	52.1
Preanal length	141	74.2
Caudal peduncle depth	20	10.5

¹ The length of fish excluding caudal fin from the anterior tip of the snout to the posterior end of the 3rd hypural plate.

length and pattern of the striae appear to be especially variable in the marginal part of the frontal surface (Figs. 2 & 3). The presence of a similar ornamentation on the heads in the holotype and specimen P.III/1B (preserved in lateral view, Fig. 1) can be assumed on the basis of another isolated head (P.III/3B). In the latter specimen both bones of the visceral cranium in lateral view and an imprint of the right frontal in dorsal view are visible. In the anterior part of the neurocranium (P.III/3B) the mesethmoid is visible, with lateral processes having broad bases and sharp ends. On two

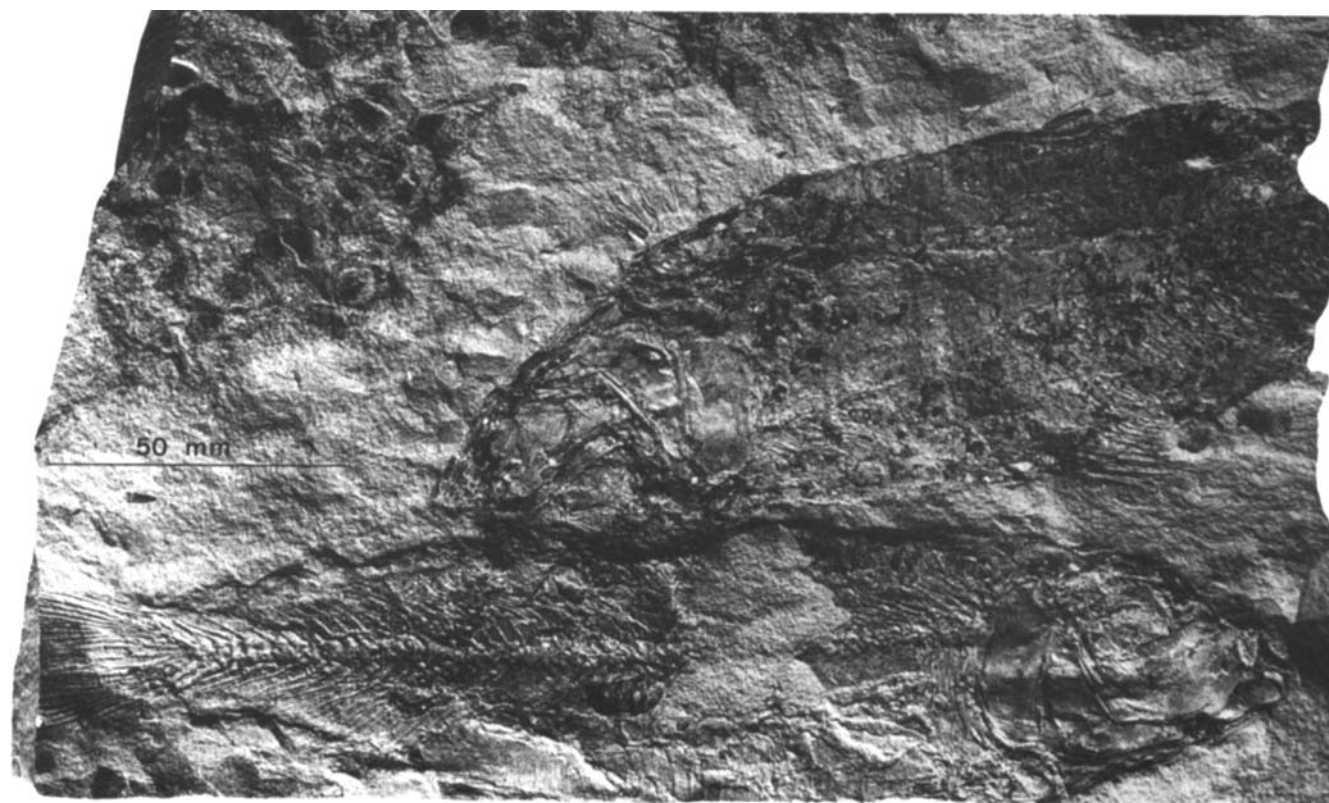


Fig. 1. *Marambionella andreae* gen. et sp.nov. Holotype P.III/ 1A (bottom) and paratype P.III/1B (top).

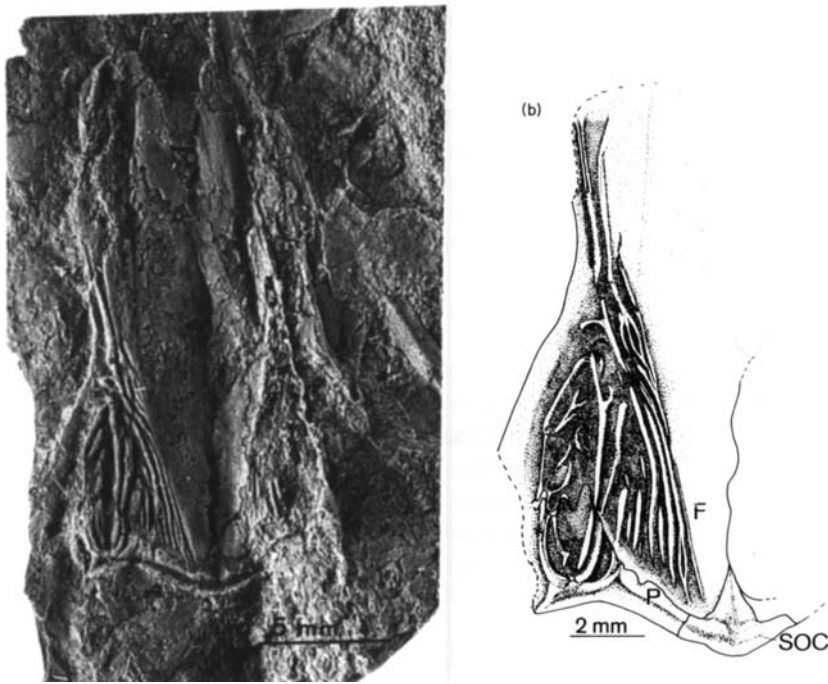


Fig.2. *Marambionella andreae* gen. et sp.nov. Left side of the skull roof with the fronto-parietal striae, P.III/3B. a. Latex peel from the natural mould. b. sketch reconstruction. F frontal; P parietal; SOC supraoccipital.

skulls (P.III/9, 10B) fragments of bones with a pitted surface are preserved, and in one place there is a trace of radial structure. Probably these are remnants of the prootic and the pterotic bullae.

Visceral cranium: The quadrate is inclined forwards, its condyle lying below the middle part of the orbit (Fig. 4). The lower jaw is *c.* 1.5 times longer than deep, with a stout dentary. In the upper jaw premaxillae are not visible in the fossils. Maxillae and the first supramaxillae are only partly preserved. The second supramaxilla is elongate, with the lower part of the expanded portion much larger than the upper and with the ventral constriction anterior to the dorsal one (the '*Harengula-Herklotsichthys*' form or '*Harengula*' shape of Whitehead 1964, 1968). The length of the posterior part of the second supramaxilla is *c.* 1.7 times its maximum depth. Of the circumorbital bones the third and largest infraorbital (Fig. 4) is the best preserved. There is also an isolated third infraorbital (Fig. 5). It is a thin bone with a fairly deep incision in its anterior margin, rounded ventral and posterior margins and an elongate, sharply terminated anteroventral region. On the bone surface a radial ornamentation is visible. The opercular bones (Figs. 1 & 4) are preserved in specimens P.III/1A–B, 6A, 14 & 24. On the large preoperculum there are radiating grooves in its mid part. The vertical limb is wider than the horizontal one. The operculum is heavily ossified and narrow, its height being *c.* 2.5 times its width in the lower part. Its anterior margin is vertical and the posterior margin is excavated; the upper edge is rounded and the lower one is nearly horizontal. The surface of the operculum is smooth, although in the holotype there are traces of very faint short striae in the anteroventral region. The suboperculum has a rounded posteroventral

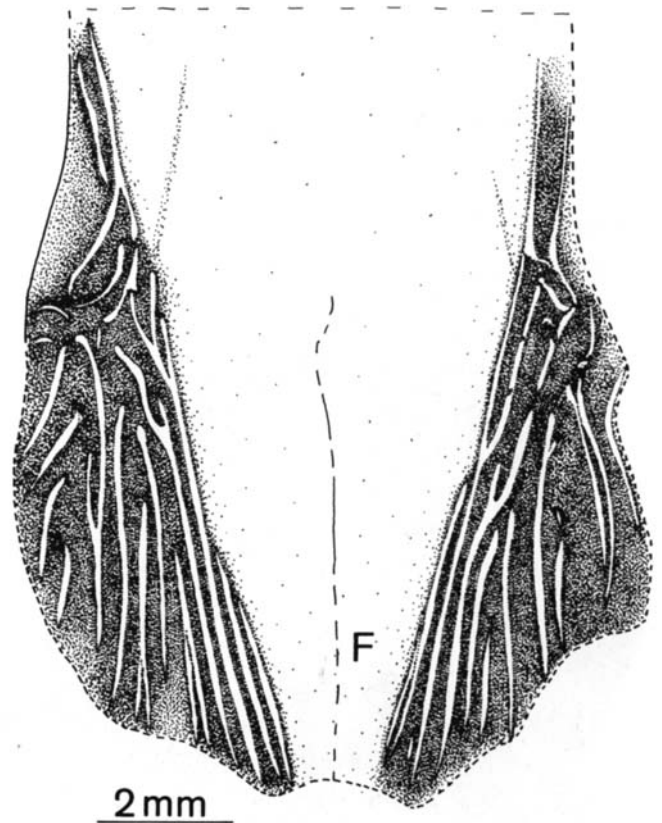


Fig.3. *Marambionella andreae* gen. et sp.nov. Sketch of the posterior part of the frontals, P.III/3A.

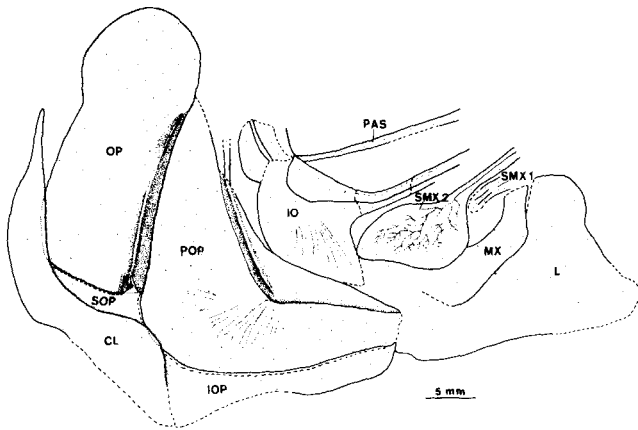


Fig. 4. *Marambionella andreae* gen. et sp.nov. Visceral cranium and cleithrum in medial view as preserved in P.III/1A-B. Dashed lines indicate restoration. CL cleithrum; IO infraorbital; IOP interoperculum; L lower jaw; MX maxilla; OP operculum; PAS parasphenoid; POP preoperculum; SOP suboperculum; SMX supramaxilla.

edge. The interoperculum is long and expanded posteriorly. The branchiostegal rays are only partly preserved; in one specimen (P.III/14A) only the three anterior ones with the 'clupeoid projections' of McAllister (1968) are present.

Pectoral girdle and fin: Poorly preserved; in specimens P.III/1A-B only the outline of the cleithrum is visible and



Fig. 5. *Marambionella andreae* gen. et sp.nov. Isolated third infraorbital P.III/2.

there appear to be 16 rays in the fin.

Pelvic girdle: Poorly preserved (P.III/1A-B); the pelvic fin originates anterior to the level of the middle of the dorsal fin and somewhat nearer to the anal fin than to the pectoral base. The state of preservation of the rays is not sufficient for accurate counts.

Vertebral column: Not well preserved in any of the specimens. Even in the nearly complete holotype a mid section of c. 27 mm is destroyed, where it is estimated that 10 vertebrae are missing. Hence the number of vertebrae would be 47, from the first preural centrum bearing the parhypural to the level of the posterior margin of operculum. Clupeids have two vertebrae immediately behind the head bearing no ribs (Grande 1982a). Thus the total number of preural vertebrae is c. 49, including 16 well preserved caudal vertebrae. There are c. 31 pleural ribs. Their traces are visible in the anterior and posterior part of the abdominal cavity of the holotype (Fig. 1) and in specimen P.III/15A.

Traces of the first five posterodorsally inclined predorsal bones are preserved in the holotype but there were almost certainly more in life.

Dorsal fin: Originates nearer to the snout tip than to the caudal fin base. It has about 19 rays (P.III/1B). There is a long, narrow dorsal fin stay posterior to the last pterygiophore.

Anal fin: Preserved in the holotype and partly in specimens P.III/5. Its origin is equidistant between the pelvic and the caudal bases, and it has about 19 rays. It can not be stated if the last two anal rays were enlarged.

Caudal skeleton: The reconstruction (Fig. 6a) is based on three specimens (P.III/20, 21A, 23A). A heavily ossified neural process of the first preural centrum is broad and short, with two shallow, longitudinal depressions in the distal part of lateral surface. More anterior preural centra have long neural spines with tapered ends. The haemal spines of the second to fourth preural vertebrae are long; the first two of them are broad. The first uroneural bears a thin lamina and is fused to the first preural centrum. The second uroneural is more slender and extends posteriorly beyond the first. The right and left second uroneurals are visible in specimen P.III/20 (Fig. 6b). The first ural centrum is small and fused with the second narrow hypural. The second ural centrum is elongate. The parhypural is not fused to the first preural centrum. A trace of the hypurapophysis is visible. The first and third hypurals are broad. The third uroneural and the epurals are not visible.

Scales: Large fragments of squamation are preserved on three specimens (P.III/1A-B, 5). Isolated single scales are rare. Thick accumulations of isolated scales (Fig. 7a) were found on under surface of some slabs (P.III/3, 4, 6-11, 13, 16-17, 19-23). The scales are large, roundish, and measure c. 8-9 mm in diameter. The posteriormost vertical stria of each scale is continuous (Fig. 7b); anteriorly, there are commonly 3-4, and sometimes 5 interrupted striae. Posterior parts of the scales lack perforation. The inner lamellar layer of the scales is much thicker than in extant clupeids.

Abdominal scutes: Impressions of high ascending arms are visible in the holotype, between the base of pectoral fin and the anal region. There are 19 scutes in front of the base of ventral fins, and 13 posterior to it. A few scutes are preserved on skeleton fragments (P.III/12–13, 15A) and on skeleton P.III/1B (Fig. 1). A partial reconstruction of their shape is given in Fig. 8.

Comparison

The inclusion of *Marambionella* in the Superfamily Clupeoidea and higher categories of clupeomorphs has been based on those diagnostic characters, listed by Grande (1985), which are visible in the specimens examined:

Clupeomorpha— abdominal scutes present (Figs 1 & 8); second hypural fused with the first ural centrum and a free first hypural (Fig. 6a); the presence of ossified bullae is only probable.

Clupeiformes— parietals completely separated by the supraoccipital (Fig. 2).

Clupeoidei— fusion of the first uroneural with the first preural centrum (Fig. 6a); no lateral line scales.

Grande (1985) recognized three superfamilies of Clupeoidei: Engrauloidea, Pristigasteroidea and Clupeoidea. *Marambionella* may be excluded from the first two superfamilies by its lack of the relevant diagnostic characters (Table II).

Clupeoidea— The high ratio of pleural ribs to preural vertebrae in *Marambionella* (approximately 0.63) is within the range of this superfamily (Table II) as opposed to 0.56 or less in the other clupeomorphs (Grande 1985). The superfamily contains two families: Clupeidae and Chirocentridae.

Clupeidae: the state of preservation of the specimens examined does not show the condition of the postcleithra in *Marambionella*. This is significant because the only diagnostic

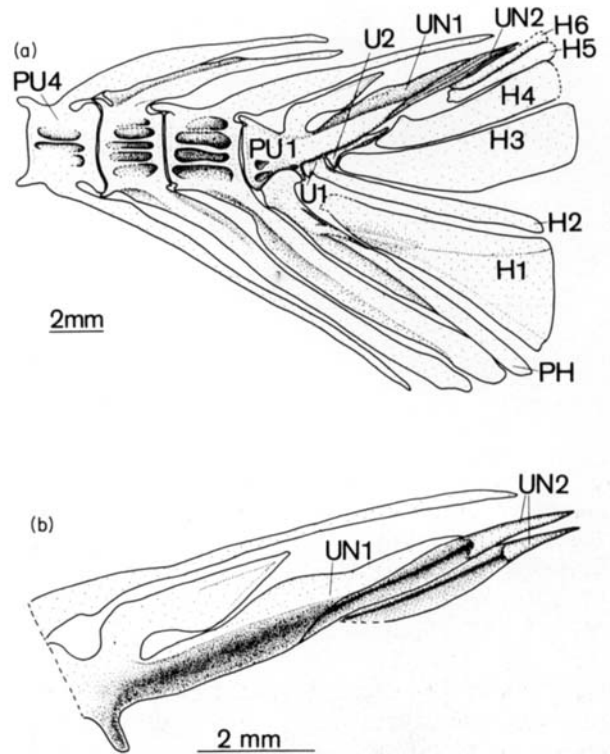


Fig. 6. *Marambionella andreae* gen. et sp. nov.

a. Reconstruction of caudal skeleton based on P.III/20, 21A, 23A. b. Right and left second uroneurals, P.III/20. H hypural; PH parhypural; PU preural centrum; U ural centrum; UN uroneural.

character of clupeids mentioned by Grande (1985) is the presence of two long rod like postcleithra. According to Whitehead (1985, p. 25) the family, as constituted at present, is probably an artificial assemblage, being defined largely on the shared absence of those special attributes that characterize the other clupeoid families.

Hence the inclusion of *Marambionella* in the family Clupeidae has been based on negative evidence, i.e. it does not show characters of neither the chirocentrids nor other families.

The detailed osteology of members of the Clupeidae is well known for only a few species. Most descriptions of clupeid species and genera contain mainly morphometric data and meristic information. In the case of fossil forms they are most often based on few, and sometimes even poorly preserved specimens. At the same time, even in extant forms, such characters as e.g. the number of rays in the dorsal and anal fins '...are relatively difficult to count in many species of clupeids (Berry 1964)'. Other characters, such as the number of gill rakers on the first branchial arch are practically impossible to estimate in fossil forms. Of the few osteological characters (structure of skull, pectoral girdle, axial skeleton) used in the clupeid classification, only opercular bones and

Table II. Comparison of diagnostic characters of Engrauloidea, Pristigasteroidea, Clupeoidea (according to Grande 1985) and *Marambionella*.

Character	Superfamily	<i>Marambionella</i>
Suspensorium inclined:	Engrauloidea Obliquely backwards	Forwards
Predorsal bones inclined:	Pristigasteroidea Vertically or anterodorsally	Posterodorsally
Interlobar notch in third hypural:	Lost	Present
Pleural ribs to preural vertebrae ratio:	Clupeoidea 0.47–0.71	c. 0.63

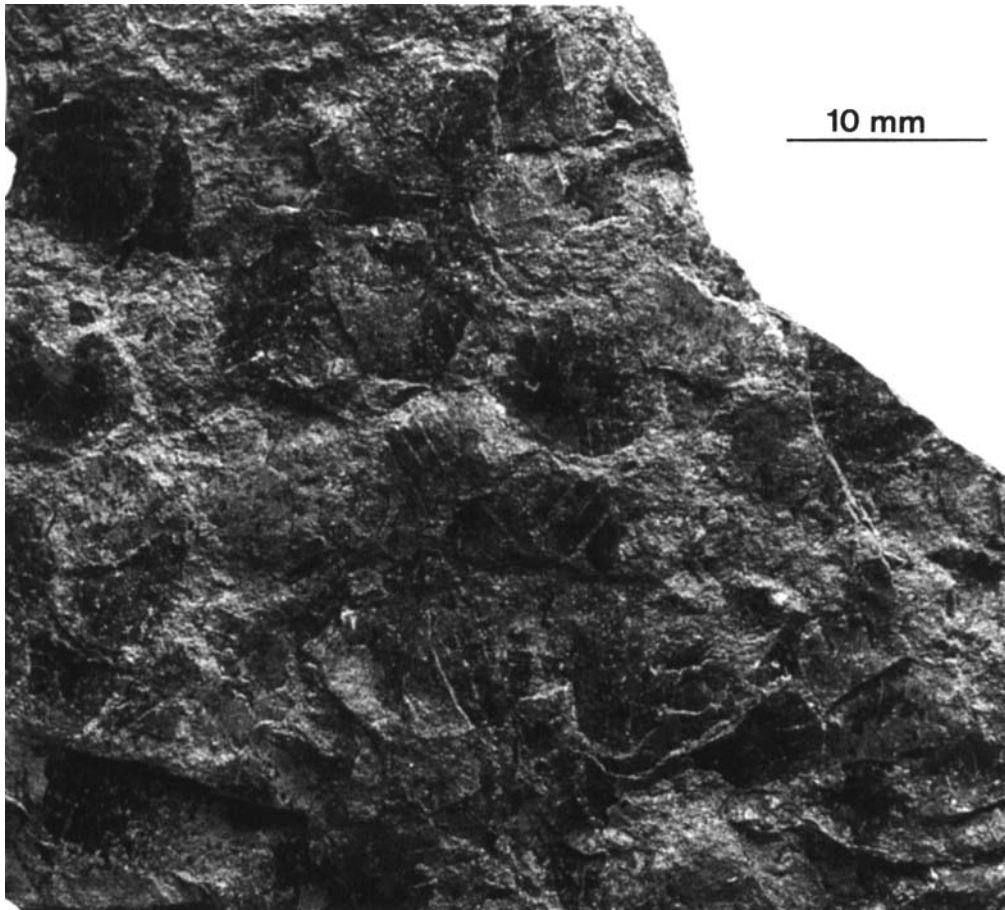


Fig. 7. *Marambionella andreae* gen. et sp.nov.
 a Accumulation of isolated scales P.III/21. b. Enlarged sketch of an isolated scale P.III/16.

number of vertebrae are most often described by paleontologists. More complete data on fossil and extant Clupeiformes were given by Grande (1982a, b, 1985). In

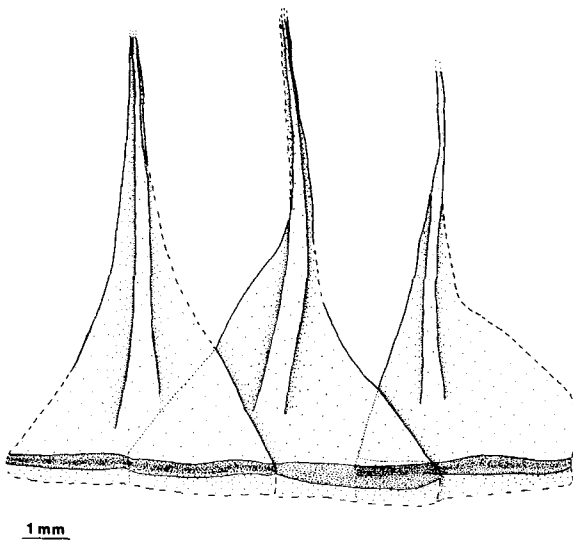


Fig. 8. *Marambionella andreae* gen. et sp.nov. Partial reconstruction of abdominal scutes, right side in medial view; based on specimens P.III/15A, 12, 13.

the latter paper he listed fossil genera and species classified with Clupeidae, excluding some from the family. The Clupeidae comprise five subfamilies: Dussumieriinae, Pellonulinae, Dorosomatinae, Alosinae and Clupeinae (Grande 1985, Whitehead 1985).

The *Marambionella* differs from members of the Dussumieriinae in lacking the W-shaped abdominal scutes (Grande 1985). Among Pellonulinae the Eocene *Knightia* Jordan 1907 somewhat resembles *Marambionella* in the ornamentation of the skull roof and thick scales. However, like other members of the subfamily it differs from *Marambionella* in the lack of the first supramaxilla and in a lower number of preural vertebrae (Grande 1982b, 1985). Within the Dorosomatinae, *Dorosoma* Rafinesque 1820 is the only genus with two supramaxillae and it differs from *Marambionella* in the structure of its dorsal and anal fin and in the shape of the third infraorbital (Nelson & Rothman 1973).

A comparison between *Marambionella* on the one hand and Alosinae and Clupeinae on the other is very difficult because of the lack of diagnostic osteological characters in those subfamilies (Grande, 1985) and because of still debatable relationships between their genera (Whitehead 1967, 1985, Nelson 1970). The state of preservation of the present specimens limits comparison of *Marambionella* with the

alossine and clupeine genera to details of the ornamentation of the fronto-parietal region, shape of the second supramaxilla, the number of vertebrae (Table III) and structure of the scales.

Marambionella displays the highest degree of resemblance to *Hilsa* Regan 1917, *Escualosa* Whitley 1940, *Amblygaster* Bleeker 1849 and *Sardinella* Valenciennes 1847 in the number and pattern of the strong longitudinal fronto-parietal striae but it differs from them in the shape of the second supramaxilla (Table III).

Marambionella shares the second supramaxilla of 'Harengula'-shape: with *Herklotsichthys* Whiteley 1951, *Harengula* Valenciennes 1847 and the Miocene *Eosardinella* Sato 1966. But these three genera all have a lower number of fronto-parietal striae (Table III). Other Clupeinae with the same shape of the second supramaxilla have a very poorly ornamented skull roof (*Lile* Jordan & Evermann 1896, *Platanichthys* Whitehead 1968) and some genera of Dussumieriinae have a smooth skull roof (Whitehead 1985, Whitehead *et al.* 1966).

The number of vertebrae in *Marambionella* is similar to that in some species of *Sardinella* (Table III) and of other genera of Dussumieriinae, Dorosomatinae, Alosinae and Clupeinae (McGowan & Berry 1984, Grande 1985).

The scale structure of *Marambionella* differs from that found in *Hilsa* and most species of *Sardinella* in the lack of perforation on the exposed part of the scale (Whitehead 1985). *Marambionella* shares the single continuous and the low number of interrupted striae with *Amblygaster*, with most species of *Sardinella* and numerous other clupeid genera. This contrasts with all striae being continuous in *Herklotsichthys* and *Harengula* (Chan 1965, Whitehead 1964, 1985), and the longitudinally elongated scales with all

striae interrupted in the Miocene *Eosardinella* (Sato & Uyeno 1985). The heavy scales distinguish *Marambionella* from all extant clupeids. The above analysis shows that both the mosaic of similarities and differences between those forms and the lack of information on the polarity of characters and detailed classification within clupeids do not allow reconstruction of phylogenetic relationships of *Marambionella*.

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References

- BERRY, F.H. 1964. Review and emendation of: Family Clupeidae, by Samuel F. Hildebrand (Fishes of the Western North Atlantic, ed. H.B. BIGELOW. *Memoir of the Sears Foundation for Marine Research* No. 1, 257-454.) *Copeia*, No. 4, 720-730.
- BLAXTER, J.H.S. & HUNTER, J.R. 1982. The biology of the clupeoid fishes. *Advances in Marine Biology*, **20**, 1-223.
- CHAN, W.L. 1965. A systematic revision of the Indo-Pacific clupeid fishes of the genus *Sardinella* (Family Clupeidae). *Japanese Journal of Ichthyology*, **12**, 104-118.
- DOKTOR, M., GAŹDZICKI, A., MARENSSI, S.A., POREBSKI, S.J., SANTILLANA, S.N. & VRBA, A.V. 1988. Argentine-Polish geological investigations on Seymour (Marambio) Island, Antarctica, 1988. *Polish Polar Research*, **9**, 521-541.
- ELLIOT, D.H. & TRAUTMAN, T.A. 1982. Lower Tertiary strata on Seymour Island, Antarctic Peninsula. In CRADOCK, C., ed. *Antarctic geoscience*. Madison: University Wisconsin Press, 287-297.
- GRANDE, L. 1982a. A revision of the fossil genus *Diplomystus*, with comments on the interrelationships of clupeomorph fishes. *American Museum Novitates*, No. 2728, 34 pp.
- GRANDE, L. 1982b. A revision of the fossil genus *Knightia*, with a description of a new genus from the Green River Formation (Teleostei, Clupeidae). *American Museum Novitates*, No. 2731, 22 pp.
- GRANDE, L. 1985. Recent and fossil clupeomorph fishes with materials for revision of the subgroups of clupeoids. *Bulletin of the American Museum of Natural History*, **181**, 231-372.
- GRANDE, L. & CHATTERJEE, S. 1987. New Cretaceous fish fossils from Seymour Island, Antarctic Peninsula. *Palaeontology*, **30**, 829-837.
- GRANDE, L. & EASTMAN, J.T. 1986. A review of Antarctic ichthyofaunas in the light of new fossil discoveries. *Palaeontology*, **29**, 113-137.
- JERZMAŃSKA, A. 1988. Isolated vertebrae of teleostean fishes from the Paleogene of Antarctica. *Polish Polar Research*, **9**, 421-435.
- MCALLISTER, D.E. 1968. Evolution of branchiostegals and classification of teleostome fishes. *Bulletin of the National Museum of Canada*, **221**, 239 pp.
- MCGOWAN, M.F. & BERRY, F.H. 1984. Clupeiformes: development and relationships. In MOSER H.G. *et al.*, eds. *Ontogeny and systematics of fishes*. Special Publication of the American Society of Ichthyologists and Herpetologists, No. 1, 108126.

Table III. Comparison of select characters of *Marambionella* and some clupeine and alosine genera.

Genera	Number of fronto-parietal striae	Second supramaxilla	Vertebrae
<i>Marambionella</i>	8-9	'Harengula' shape	c. 49
Clupeinae:			
<i>Amblygaster</i>	7-14 ⁴	'Sardinella' shape ^{4,5}	43-44 ⁶
<i>Sardinella</i>	7-14 ⁴	'Sardinella' shape ^{4,5}	42-48 ⁶
<i>Escualosa</i>	8-9 ³	Subrectangular ³	39-40 ⁶
<i>Herklotsichthys</i>	3-7 ⁴	'Harengula' shape ⁵	39-44 ⁶
<i>Harengula</i>	3-5 ¹	'Harengula' shape ⁵	40-43 ⁶
<i>Eosardinella</i>	4-5 ⁷	'Harengula' shape ⁷	47 ¹
Alosinae:			
<i>Hilsa</i>	7-14 ⁴	Paddle shaped ² posteriorly	43 ⁶

References:

- 1) Whitehead 1964
- 2) Whitehead 1965
- 3) Whitehead 1967
- 4) Whitehead 1985
- 5) Whitehead *et al.* 1966
- 6) Grande 1985
- 7) Sato & Uyeno 1985

- NELSON, G.J. 1970. The hyobranchial apparatus of teleostean fishes of the families Engraulidae and Chirocentridae. *American Museum Novitates*, 2410, 30 pp.
- NELSON, G. & ROTHMAN, M.N. 1973. The species of gizzard shads (Dorosomatinae) with particular reference to the IndoPacific region. *Bulletin of the American Museum of Natural History*, 150, 133-206.
- RICHTER, M. & THOMSON, M.R.A. 1989. First Aspidorhynchidae (Pisces: Teleostei) from Antarctica. *Antarctic Science*, 1, 57-64.
- SATO, Y. & UYENO, T. 1985. On the clupeid fish, *Eosardinella hishinaiensis*, from Miocene beds in Sado Island, Japan. *Memoirs of the National Science Museum Tokyo*, 18, 57-63. [In Japanese].
- SCHWARZHANS, W. 1985. Tertiäre Otolithen aus South Australia und Victoria (Australien). *Paleoichthyologia*, 3, 60 pp.
- WHITEHEAD, P.J.P. 1964. *Herklotsichthys* Whitley, 1951 to replace *Harengula* Valenciennes, 1847 for Indo-Pacific species (Pisces: Clupeidae). *Annals and Magazine of Natural History*, Series 13, 6, 237-284.
- WHITEHEAD, P.J.P. 1965h. A preliminary revision of the IndoPacific Alosinae (Pisces: Clupeidae). *Bulletin of the British Museum (Natural History)*, *Zoology*, 12, 117-156.,
- WHITEHEAD, P.J.P. 1967. The clupeoid fishes described by Lacepède, Cuvier & Valenciennes. *Bulletin of the British Museum (Natural History)* *Zoology*, Supplement 2, 180 pp.
- WHITEHEAD, P.J.P. 1968. A new genus for the South American clupeid fish, *Lile platana* Regan. *Journal of Natural History*, 12, 477-486.
- WHITEHEAD, P.J.P. 1985. Chirocentridae, Clupeidae and Pristigasteridae. In FAO species catalogue. Clupeoid fishes of the world. *FAO Fisheries synopsis*, No. 125, 7, Pt. 1, 303 pp.
- WHITEHEAD, P.J.P., BOESEMAN, M. & WHEELER, A.C. 1966. The types of Bleeker's Indo-Pacific clupeoid and clupeoid fishes. *Zoologische Verhandelingen, Leiden*, No. 84, 1-152.
- WHITEHEAD, P.J.P., SMITH, P.J. & ROBERTSON, D.A. 1985. The two species of sprat in New Zealand waters *Sprattus antipodum* and *S. muelleri*. *New Zealand Journal of Marine and Freshwater Research*, 119, 261-271.
- WOODWARD, A.S. 1908. On fossil fish-remains from Snow Hill and Seymour Islands. *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901-1903*, 3, *Geologie und Paläontologie*, (1916), 4, 1-4.