

A PLANT-AND-FISH ASSEMBLAGE FROM THE EOCENE LA MESETA FORMATION OF SEYMOUR ISLAND (ANTARCTIC PENINSULA) AND ITS ENVIRONMENTAL IMPLICATIONS

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Fossil floral remnants (leaves and shoots) belonging to *Cladophlebis* sp., *Dacrycarpus? tertiarius* (Berry) Zastawniak comb. n., *Araucaria nathorsti* Dusén, *Nothofagus* sp., *Knightiophyllum andreae* (Dusén) Zastawniak comb. n., *Dicotylophyllum* sp., and co-occurring with the clupeoid fish *Marambionella andreae* Jerzmańska and with other teleost remains were recovered from the lower part (Telm2) of the Eocene La Meseta Formation of Seymour Island (Antarctic Peninsula). This flora is indicative of a temperate climate and resembles mostly the present-day araucarian forest, with *Nothofagus* and Podocarpaceae, of the Argentine-Chilean borderland. The well-preserved floral assemblage, accompanied by clupeoid fish skeletons, together with sedimentological data, are all consistent with the estuarine origin of the La Meseta Formation.

Key words: Terrestrial flora, teleost fish, Eocene, Antarctica.

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INTRODUCTION

During the Argentine–Polish field work in 1988–89, 1991–92 and 1993–94 austral summers on Seymour (Marambio) Island, Antarctic Peninsula, a collection of terrestrial flora and teleost fishes was gathered by the Polish team from the lower part (Telm2) of the Eocene La Meseta Formation. The fossil site is located within a coastal cliff of the López de Bertodano Bay (locality ZPAL 9 on Text-fig. 1), stratigraphically belonging to SADLER's (1988) unit Telm2.

The Eocene terrestrial flora from the locality ZPAL 9 includes variably preserved impressions of leaves and shoots with no trace of plant tissue, identified on over 30 rock slabs. The complete specimens of a

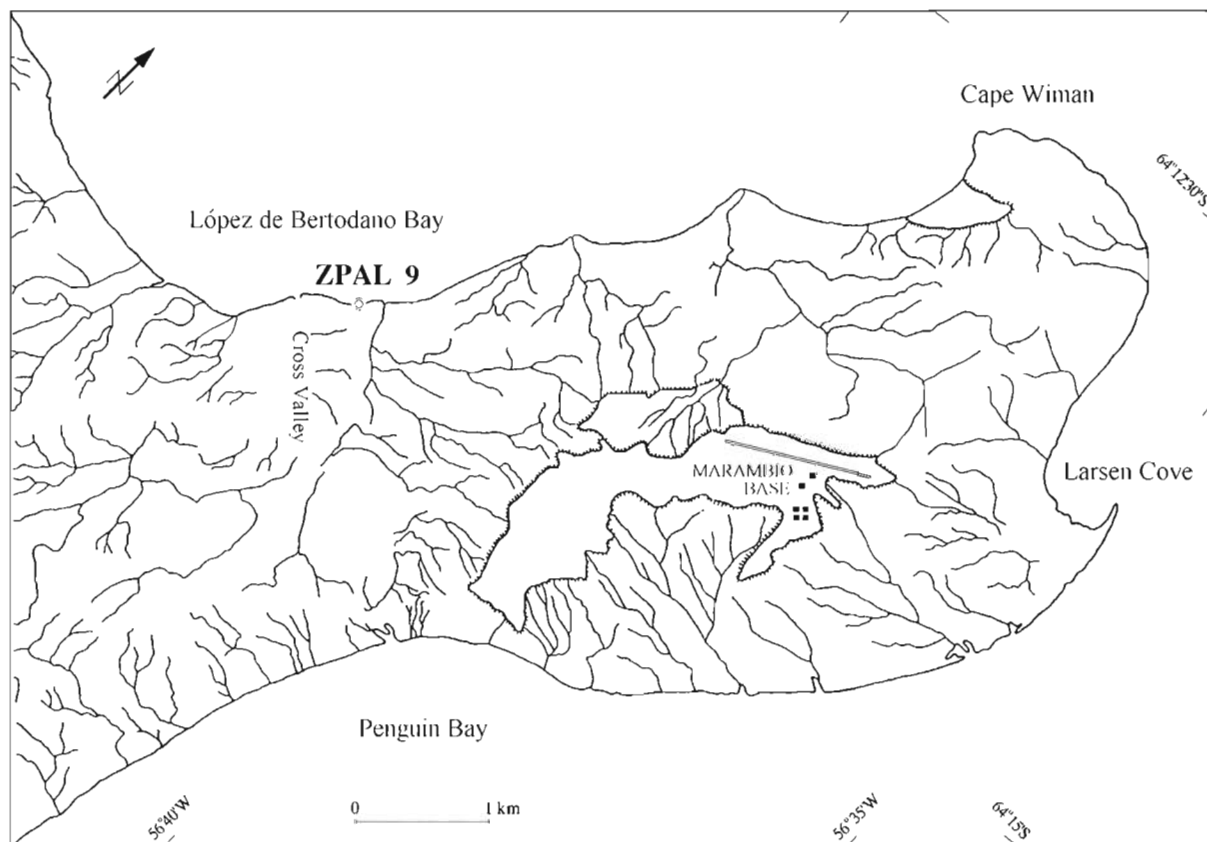


Fig. 1

Map of the northern part of Seymour Island showing the position of the plant-and-fish assemblage (ZPAL 9 site).

fossil clupeoid fish, other skeletal fragments and numerous isolated clupeoid scales (DOKTOR *et al.* 1988; JERZMAŃSKA 1991), as well as a few isolated scales of other teleosts were also found at the same locality. The leaves and fish remains are associated with pieces of coalified wood and articulated and broken bivalve shells.

M. DOKTOR, A. GAŹDZICKI and S.J. PORĘBSKI are responsible for stratigraphic and sedimentological data. E. ZASTAWNIAK is responsible for the paleontological determination and descriptions of the flora, whereas A. JERZMAŃSKA — for the teleost fish remains. All fossil specimens described and illustrated here are housed in the Institute of Paleobiology of the Polish Academy of Sciences, Warszawa (abbreviated as ZPAL PI.II and ZPAL P.III).

Acknowledgements. — The field work conducted on Seymour Island would not have been possible without logistic support from the Instituto Antártico Argentino (Buenos Aires) and Fuerza Aérea Argentina. Special thanks go to Dr. Andrzej TATUR who assisted one of us (AG) with collecting of fossils in the 1991–92 and 1993–94 austral summers. We would like to extend our appreciation to Mrs. Grażyna DZIEWIŃSKA for the photographs of fossils, to Dr. Jacek ŚWIDNICKI for the drawings of fish scales, and to Mr. Artur COPPING for linguistic verification of the English text. This paper has benefited from critical reviews by Dr. Rosemary A. ASKIN, Prof. Dr. Ryszard GRADZIŃSKI and Dr. Maria ZIEMBIŃSKA-TWORZYDŁO.

SEDIMENTOLOGICAL SETTING

The Eocene La Meseta Formation is a concave-down lens, 6 km wide and minimum 0.4 km thick, which caps the Antarctic Peninsula backarc succession on Seymour Island. The lens consists of fossiliferous, fine-grained sandstones and sandstone/mudstone heteroliths, with little or no interbeds of finer and

coarser lithologies. The La Meseta Formation is characterised by (1) its confinement to a major incision within the Cretaceous–Paleocene shelf succession (SADLER 1988), (2) intraformational multiple channeling associated with subtidal, intracoastal facies, (3) abundant indicators of tidal current activity, and (4) diverse biota comprised of both shallow-marine forms and well-preserved land-derived fossils, commonly bound to well-defined horizons intercalated with barren intervals. In light of this evidence, POREBSKI (1995) has recently reinterpreted the La Meseta Formation in terms of deposition within a compound-incised valley estuary which repeatedly developed above a major, linear NW–SE strike zone of fault-controlled subsidence. The estuary developed within a funnel-shaped valley affected by the hypersynchronous mesotidal regime of a semi-diurnal character.

DESCRIPTION OF THE FOSSIL SITE

The locality ZPAL 9 (Text-fig. 1; GPS coordinates: 64°14'57.660"S, 56°41'46.994"W; Jorge LUSKY – Instituto Antártico Argentino, Buenos Aires; personal communication, 1994) exposes unit Telm2 of SADLER (1988). In this area, Telm2 is 90–100 m thick. Towards the north, the unit is laterally replaced and erosively overlain by the veneroid-bearing channelised deposits of Telm3 interpreted as recording sedimentation within the estuary mouth and main estuary channel (POREBSKI 1995). Telm2 cropping out in the cliff consists of heterolithic strata which occur as rotated slide blocks, the infills of slide scars and incised channels, and major clinoform units (Text-fig. 2).

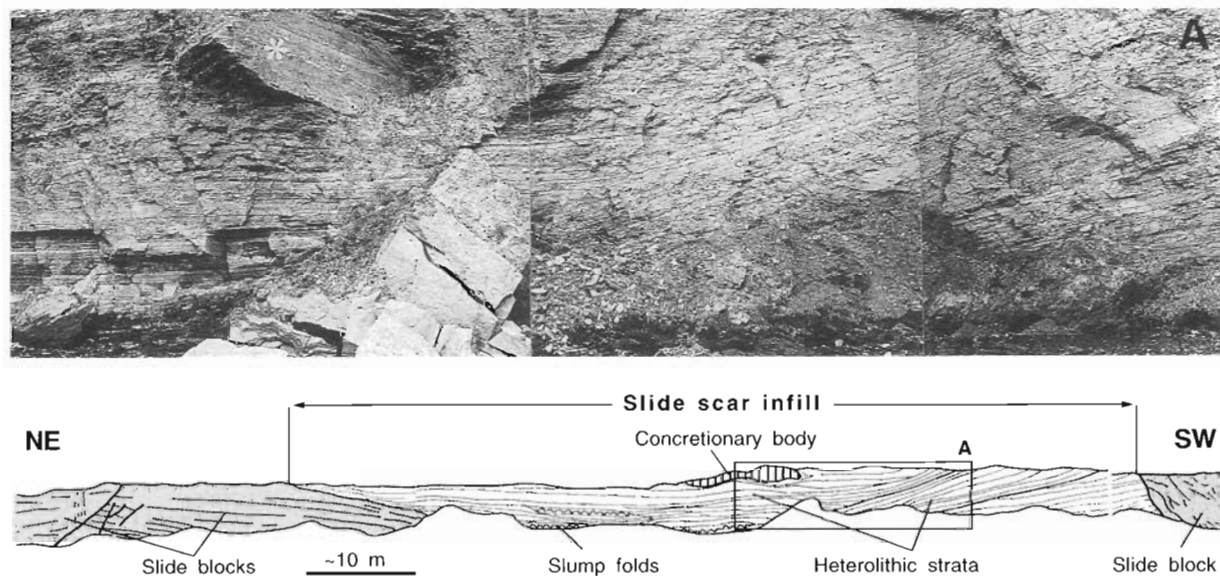


Fig. 2

Panoramic fragment of Telm2 coastal exposure, showing the distribution of slide blocks, slide-scar infill and the location of the studied fossil fish-and-plant locality (ZPAL 9). Photographic inset shows the onlapping contact of the horizontally bedded heterolithic fill (VAS) onto the inclined heterolithic strata (IHS). The fish and flora remains were found in the concretionary body (asterisked).

Slide zone. The lower part of the exposed section consists of a series of tilted blocks separated by high-angle discontinuities. The blocks consist of a finely laminated to lenticularly bedded mud-dominated heterolith which shows little or no internal contortions. Bedding in the tilted blocks dips 5–27°SSW. The boundary high-angle discontinuities appear as normal faults inclined 30–60°, mostly trending WNW–ESE and showing N–ly throws. Some of the faults cut through the entire outcrop (height 5–8 m); however, most faults appear to be truncated by the overlying channel-fill deposits. The rotated blocks are believed to represent the foot of a rotational slide mass which was emplaced towards the NNE, *i.e.*, towards the valley axis. This gravity collapse produced a hummocky topography of upthrown edges of tilted blocks and slide detachments, with constructional depressions or slide scars in-between. This topography, with

a visible relief of 5–8 m, was filled first by locally developed debris-flow deposits, and later affected predominantly by tidal processes which resulted in heterolithic strata arranged in vertical accretion and lateral accretion patterns.

The scar infill. The scar infill which contains the studied fossils (Text-fig. 3) is located on a slide block tilted 27°SSE, which also forms the northern margin to the onlapping scar infill (Text-fig. 2). The southern margin, ca. 100 m apart, is cut by a brecciated inverse fault zone which apparently post-dates the scar, although it is believed to have been caused by an intraformational event as well. The infill itself comprises inclined heterolithic strata (IHS — THOMAS *et al.* 1987) overlain by a vertically accreted heterolith (Text-figs 2–3).

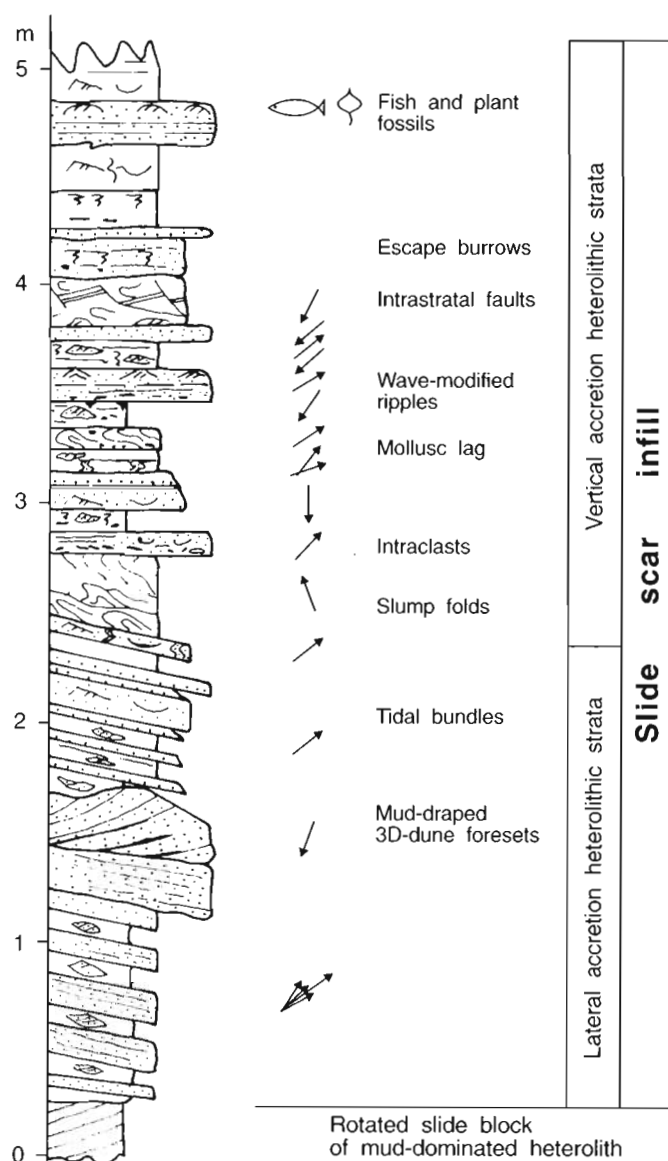


Fig. 3

Stratigraphic log showing the lithofacies development, paleocurrent directions and interpretation of the studied ZPAL 9 fossil site.

The IHS body is minimum 5 m high and 40 m wide. It consists of planar to slightly convex-up foreset beds, 3–20 cm thick, with tangential toes which onlaps to the N the inclined scar bottom. The beds consist of parallel laminated to flaser cross-laminated silty to fine sandstone alternating with dark gray silt-laminated sandy mudstone and cm-thick mud layers. The latter commonly show minute, sand-filled shrinkage (syneresis?) cracks. Foreset dip angle varies between 10 and 18° and tends to increase upwards. The



Fig. 4

Details of the vertical accretion strata in the slide scar infill (compare Text-fig. 3), showing horizontal tidal couplets in the wavy and linsen bedded intervals.

azimuth of dips varies little around the mean towards 047° . Two reactivation surfaces (convex-up truncations) were identified, spaced at ca. 5 m, one carrying isolated asymmetrical dunes located ca. 1 to 3 m above the IHS toes. The dunes are up to 0.2 m high and 30 m in spacing, and consist of silty sand with mud-draped cross-strata directed towards 170° , *i.e.*, obliquely up the foreset slope. Bioturbation is low to absent, although the IHS facies in the nearby outcrops abounds locally in *Scolicia* meniscate burrows resembling the *Echinocardium* press structures known from the heterolithic infill of modern mesotidal channels (VAN DER BERG 1981).

The IHS body is overlain by the vertical accretion strata (VAS). They are subhorizontally bedded, dipping 3°E , and show uplapping terminations with both the northern scar wall and the IHS body (Text-fig. 2). The VAS fill begins with a coherent slump of heterolithic folds verging towards 350° which indicates slumping down the IHS body. The slump is overlain by rhythmic sandstone/mudstone alternations corresponding to tidal couplets (Text-fig. 4), intercalated at random with somewhat thicker sandstones and thin zones of slump folding and intrastratal faulting (Text-fig. 3).

Sand is very fine to fine grained, well to moderately sorted, and locally abounds in mudstone and coaly intraclasts and dispersed mollusc shells. Mud ranges between silty sand and sandy silt, which are commonly packed with carbonized plant matter and dark pellets. Sand beds are normally a few cm in thickness, have sharper bases than tops, and commonly show loaded bases. Internally, the beds are parallel laminated and ripple cross-laminated, often passing laterally into isolated ripple lenses enclosed in mud. The ripples tend to be asymmetrical and commonly exhibit mud flaser linked upwards with the overlying mud bed to form mud offshoots. Symmetrical ripple forms with unidirectional cross-laminae are also present, suggesting some oscillatory component in the otherwise dominant unidirectional currents.

Mud layers range from mm-thick flasers on ripple foresets and toes, through cm-thick drapes which are often cracked and laterally traceable to mud flake concentrates, to dm-thick composite unit showing linsen bedding and finely silt-laminated portions. Such a mud-dominated heterolith commonly reveals subvertical sand-filled dykelets, mm to cm in dimension, which display irregular, crenulated margins and resemble syneresis casts (PLUMMER and GOSTIN 1981; ASTIN and ROGERS 1991). Bioturbation is repre-

sented by numerous horizons of animal escape structures, small, sand-filled *Skolithos* and a bifurcating, Y-shaped burrow, similar to *Polykladichnus irregularis* FÜRSICH (FÜRSICH 1981).

Evidence of reversing flow is ubiquitous in the heterolithic facies, although opposing cross-laminae in the adjacent sets (herringbone cross-stratification) was rarely observed. The paleoflow directions deduced from cross-lamination in strongly bipolar, with the dominant NE-directed mode (mainly in the wavy-bedded intervals) and the secondary SW-directed mode (mainly in the linsen-bedded intervals). Such an asymmetry in the flow strength and direction is typical for tidal currents as the result of mutually evasive ebb-flood pathways (NIO *et al.* 1980), and points to the dominance of the ebb flow in the studied locality. Near the top of the exposed VHS fill there occur irregular, carbonate-cemented concretionary body which yielded the clupeoid fish skeletons and scales accompanied by plant remains (Text-fig. 3).

PALEOBOTANY

The first elaboration of Tertiary plant remains from Seymour Island appeared in DUSÉN's (1908) publication, in which he described the impressions of leaves and shoots gathered during the 1901–03 Swedish South Polar Expedition led by Otto NORDENSKJÖLD. The recognized plant-bearing strata (see ANDERSSON 1906, p. 44) belong to the Paleocene Cross Valley Formation (ELLIOT and TRAUTMAN 1982; CASE 1988) and the Eocene La Meseta Formation (CASE 1988).

HICKEY's (1973, 1979) terminology has been used in leaf descriptions.

TAXONOMIC DESCRIPTION

Class **Polypodiopsida** MEYEN, 1987

Family unknown

Genus *Cladophlebis* BRONGNIART, 1849

Cladophlebis sp.

(Pl. 33: 3; Text-fig. 5: 4)

Material. — One fragment of frond (ZPAL Pl.II/4).

Description. — Frond pinnate, coriaceous. Preserved pinna ca. 3 cm long and 3 cm wide. Shape and length of the whole frond unknown. Pinnules pinnately arranged, attachment adnate, shape of pinnules linear-lanceolate, 1.4 × 0.4 cm. Margin entire, more or less straight, subparallel for most of the pinnule length, apex blunt. Space between pinnules ca. 3 mm wide. Only one vein entering each pinnule from the rachis at 60°. Costa straight, persisting to pinnule apex. Venation of the next orders invisible.

Remarks. — The generic name defines this type of fern frond, in the opinion of T.N. TAYLOR and E.L. TAYLOR (1993), as characteristic of osmundaceous ferns. A closer determination of the extant fragment and also its relation to present-day ferns is impossible. Conspicuous, however, is the state of preservation of the specimen, which suggests considerable toughness of the frond.

Class **Pinopsida** MEYEN, 1987

Family **Podocarpaceae** NEGER, 1907

Genus *Dacrycarpus* (ENDLICHER) DE LAUBENFELS, 1969

Dacrycarpus? tertiarius (BERRY) ZASTAWNIAK comb. n.

(Pl. 32: 1)

1928. *Fitzroya tertiaria* BERRY: p. 13, pl. 2, figs 2–4.

1938. *Fitzroya tertiaria* BERRY: p. 60, pl. 12, fig. 2.

1940. *Podocarpus tertiarius* (BERRY) FLORIN: FLORIN, p. 39.

Material. — Impression of the tip of a branching shoot (ZPAL Pl.II/6).

Description. — Leafy twigs 1.5–2 mm wide, branching, covered with imbricate leaves with broadly decurrent bases. At the tip of the stems there is oval widening (male strobili?).

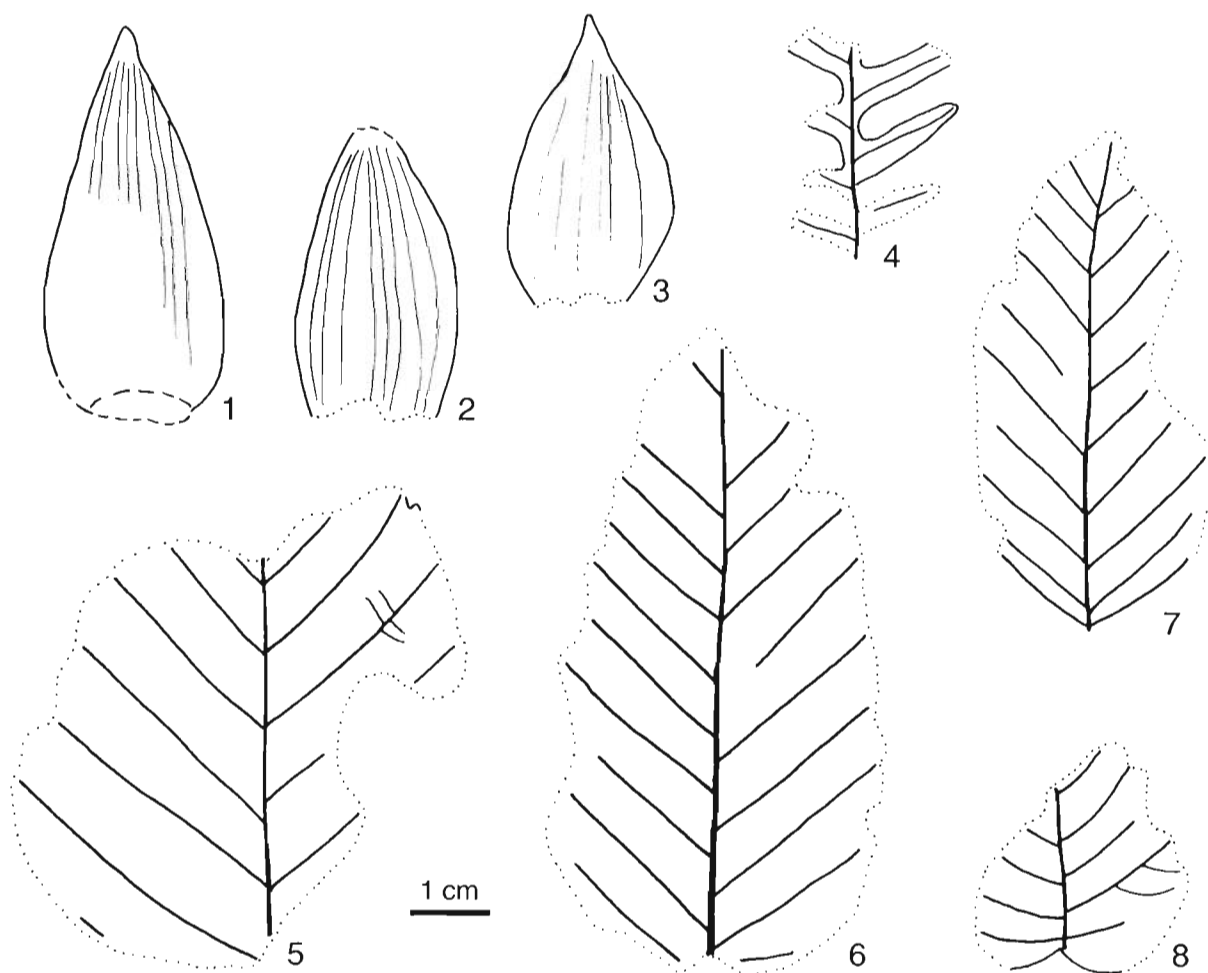


Fig. 5

Leaves of *Araucaria nathorsti* DUSÉN: 1 — ZPAL Pl. II/19, 2 — ZPAL Pl. II/2, 3 — ZPAL Pl. II/20; frond of *Cladophlebis* sp.: 4 — ZPAL Pl. II/4; leaves of *Nothofagus* sp.: 5 — ZPAL Pl. II/22, 6 — ZPAL Pl. II/25, 7 — ZPAL Pl. II/7, 8 — ZPAL Pl. II/14.

Remarks. — Judging from the nature of the foliage and the arrangement of the twigs, the illustrated specimen from the locality ZPAL 9 represents the same coniferous plant that BERRY (1928, 1938) named *Fitzroya tertiaria*. FLORIN (1940) revised that determination and included this species in the genus *Podocarpus* from section *Dacrycarpus*, comparing it to modern *Podocarpus dacrydioides* A. RICHARD from New Zealand. As a consequence DE LAUBENFELS' (1969) revision, the name *Dacrycarpus* is binding for this group of species of the Podocarpaceae, necessitating a new combination for the fossil taxon.

At the tips of the shoots there are apparent oval widenings which resemble the pollen cones in today's *Dacrycarpus dacrydioides* (A. RICHARD) DE LAUBENFELS.

It should be emphasized, however, that any determination of the specimen from the locality ZPAL 9, not supported by studies of the anatomic structure of cuticles, cannot be totally reliable. This is particularly true in the case of fossil remains of the family Podocarpaceae, in which some genera are hard to tell from one another on the basis of sterile shoot morphology alone, e.g. *Dacrycarpus* and *Dacrydium* (DE LAUBENFELS 1969). The most recent study of fossil remains of *Dacrycarpus* (WELLS and HILL 1989) indicated that this genus was much more differentiated in the Tertiary of the Australasian region than it is now. At present this species is dominant in lowland swampy forest in New Zealand, reaching an altitude of 600 m and occurring also in relatively cool conditions, retaining its dimorphic foliage (ALLAN 1961).

Family **Araucariaceae** STRASBURGER, 1872Genus *Araucaria* JUSSIEU, 1789Section *Colymbea* ENDLICHER, 1847*Araucaria nathorsti* DUSÉN, 1907

(Pl. 32: 3–5; Text-fig. 5: 1–3)

1907. *Araucaria nathorsti* DUSÉN; p. 105, pl. 12, figs 1–13.1908 ?*Araucaria imponens* DUSÉN; p. 11, pl. 1, figs 16–17.1969. *Araucaria nathorsti* DUSÉN; MENENDEZ, pl. 10, fig. 9.**Material.** — Six impressions of leaves, three of them complete (ZPAL Pl.II/2, 10, 16–17, 19–20).**Description.** — The dimensions of the whole leaves are 3.9×2.2 cm, 5.4×2.4 cm and 4.0×2.2 cm, the breadths of the others are 2.1–2.2 cm. They are lanceolate or narrowly ovate, slightly asymmetric, widest in the lower half; apex acute, leaf attachment broad, without petiole; margin entire. Leaves coriaceous, without major vein or keel, with prominent, numerous, unbranched, parallel veins.**Remarks.** — The impressions of *Araucaria* leaves found in the material studied correspond perfectly with the species *Araucaria nathorsti* DUSÉN, described from the Punta Arenas region in the southern part of the Patagonian Upland in South America (DUSÉN 1907). So numerous were the impressions of leaves and shoots of *Araucaria* in a layer of lignites and clayey shales at this locality that an araucarian horizon has been distinguished in the geological profile. Very many impressions of leaves of *Nothofagus subferruginea* (DUSÉN) TANAI (= *Fagus subferruginea* DUSÉN) were also found underneath, at the same site. DUSÉN (1907) acknowledged that the modern species most closely related to the fossil one is *Araucaria imbricata* PAVON [= *A. araucana* (MOLINA) K. KOCH].Later, DUSÉN (1908) described a new fossil species, *Araucaria imponens* DUSÉN, from Seymour Island on the basis of one nearly complete leaf. A 6 cm length of this leaf is preserved, 1.2 cm in width. DUSÉN (1908) compared *A. imponens* to the modern South American species *Araucaria brasiliensis* A. RICHARD [= *A. angustifolia* (BERTOLINI) KUNTZE] and the Australian *A. bidwilli* HOOKER. According to FLORIN (1940, p. 32) *A. imponens* belongs to section *Colymbea* ENDLICHER. This species could possibly lie within the range of variation of *A. nathorsti*.Leafy shoots and detached leaves of *Araucaria nathorsti* are also known from the Tertiary of Rio Negro (BERRY 1928), the Eocene of Puerto Altamirano and Mina Martha, Golfo de Skyring as well as Bahia Slogget in Tierra del Fuego and Estancia Leleque at Lelej near Choila (determinations by T.G. HALL 1909, quoted after FLORIN 1940, p. 38) and also from the Tertiary of Pico Quemado, Rio Negro, Argentina (MENENDEZ and CACCAVARI 1966; MENENDEZ 1969).The great similarity of *A. nathorsti* to the modern species *A. araucana* suggests its membership in section *Colymbea*, but HILL and BIGWOOD (1987) doubt whether the section can be precisely established on the basis of purely vegetative remains. The latest find of *Araucaria* leaves represents the fossil species *Araucaria hastiensis* described by HILL and BIGWOOD (1987) from the Eocene of Tasmania. The structure of the fossil leaf cuticle indicates, in the author's opinion, that it belongs to the section *Colymbea* or *Bunya*.At present, *Araucaria angustifolia* (BERTOLINI) KUNTZE grows in the mountains of southern Brazil and Argentina, whereas *A. araucana* (MOLINA) K. KOCH occurs in Chile, south-western Argentina and on the western slopes of the Andes at an altitude of 500 to 1800 m. In moist depressions it forms mixed forests with *Nothofagus* and *Podocarpus* (HUECK 1966). The climatic conditions prevailing in the Chilean-Argentine araucarian forests are characterized by a mean annual temperature of 10–15°C and an annual precipitation of 600–1200 mm (HUECK and SEIBERT 1972).Class **Magnoliopsida** CRONQUIST, TAKHTAJAN *et* ZIMMERMANN, 1966Subclass **Hamamelidae** TAKHTAJAN, 1966Family **Nothofagaceae** KUPRIANOVA, 1962Genus *Nothofagus* BLUME, 1850*Nothofagus* sp.

(Pl. 32: 6–7; Pl. 33: 4; Text-fig. 5: 5–8)

Material. — Four fragments of leaves (ZPAL Pl.II/7, 14, 22, 25).**Description.** — The only leaf impression which is nearly complete measures 6.5×3.3 cm, and is elliptical with a rounded-cuneate base. Another preserved specimen is 8.5 cm long and 3.6 cm wide, and

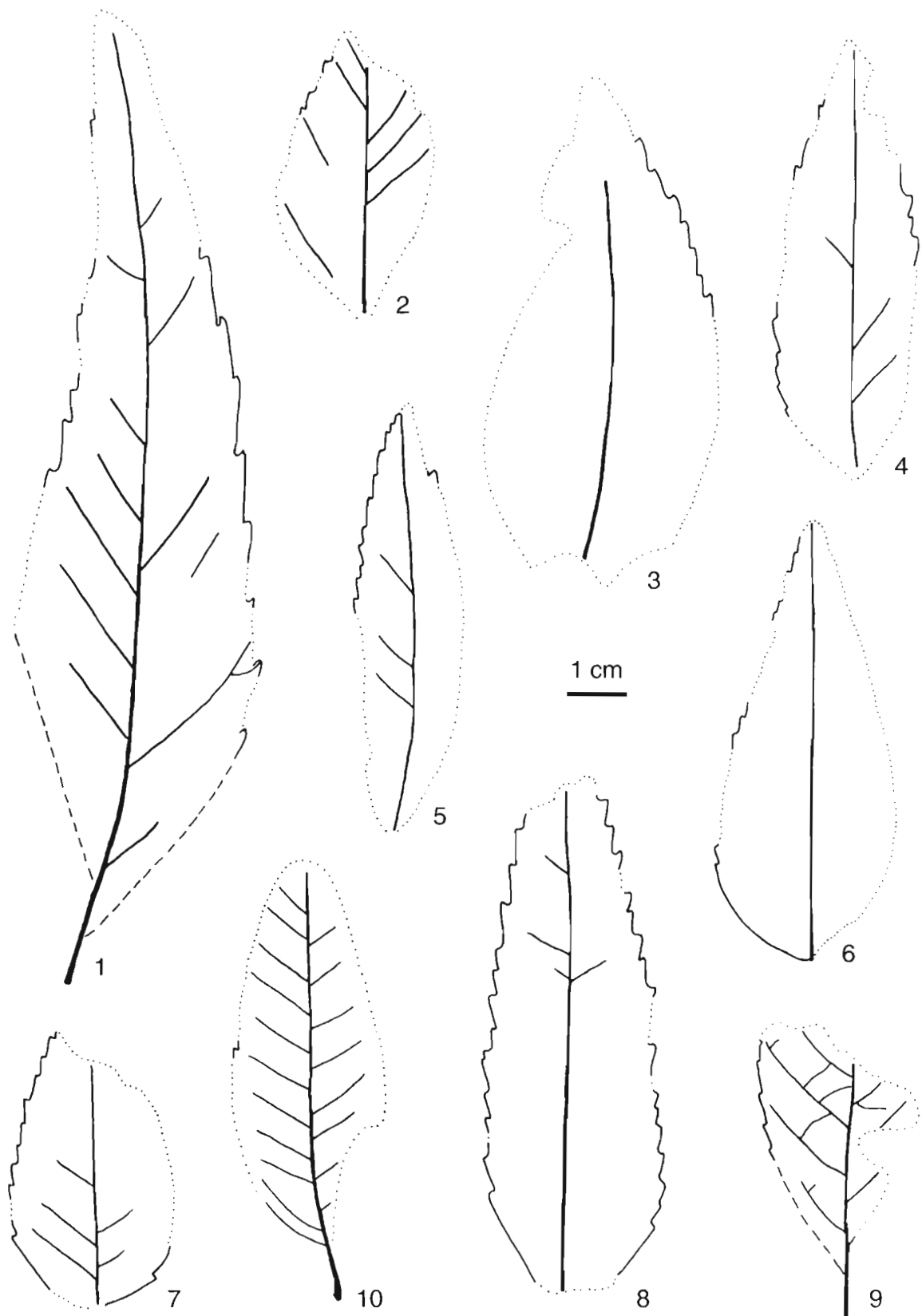


Fig. 6

Leaves of *Knightiophyllum andreae* (DUSÉN) ZASTAWNIAK comb. n.: 1 — ZPAL Pl.II/5a, 2 — ZPAL Pl.II/11, 3 — ZPAL Pl.II/9, 4 — ZPAL Pl.II/12, 5 — ZPAL Pl.II/23, 6 — ZPAL Pl.II/24, 7 — ZPAL Pl.II/15, 8 — ZPAL Pl.II/1, 9 — ZPAL Pl.II/21; leaf of *Dicotylophyllum* sp.: 10 — ZPAL Pl.II/8.

still another is part of a very wide leaf, about 6.8 cm in width. One impression shows the lower part of a leaf, 3 cm wide, with cordate base. In none of the specimens is the leaf margin preserved. The venation is pinnate, probably craspedodromous, the midvein straight with secondary veins running parallel, at fairly regular intervals. In one case the outer secondary veins are visible.

Remarks. — Because of their characteristic, parallel and regular secondary venation these leaves have been included in the genus *Nothofagus*. Leaves of this type are frequent in the Tertiary of West Antarctica, beginning with the Upper Cretaceous (ZASTAWNIAK 1981; ZASTAWNIAK *et al.* 1985; BIRKENMAJER and ZASTAWNIAK 1986; ZASTAWNIAK 1994). The poor state of preservation and lack of cuticular remains do not permit more detailed taxonomic studies nor comparison with Recent species. It should be mentioned that the only Tertiary species from that region, with similar venation and relatively large leaves, is *Nothofagus subferruginea* (DUSÉN) TANAI, frequent in the Tertiary of West Antarctica and South America (TANAI 1986), the modern counterpart of which is the South American deciduous *N. alessandri* ESPINOSA from the subgenus *Fuscospora* HILL *et* READ.

Subclass **Rosidae** TAKHTAJAN, 1966

Family **Proteaceae** DE JUSSIEU, 1789

Genus *Knightiophyllum* gen. n. ZASTAWNIAK

Knightiophyllum andreae (DUSÉN) ZASTAWNIAK comb. n.

(Pl. 33: 1a–b, 2; Text-fig. 6: 1–9, Text-fig. 7: 1–3)

Type species: *Knightiophyllum andreae* (DUSÉN) ZASTAWNIAK comb. n.

1908. *Knightia andreae* DUSÉN; p. 7, pl. 1, figs 7, 9, 11.

1908. *Illiciphyllum* sp. (1); DUSÉN, p. 5, pl. 2, fig. 14.

1908. *Illiciphyllum* sp. (2); DUSÉN, p. 6, pl. 2, fig. 16.

1988. *Nothofagus* sp.; CASE, fig. 4a–c.

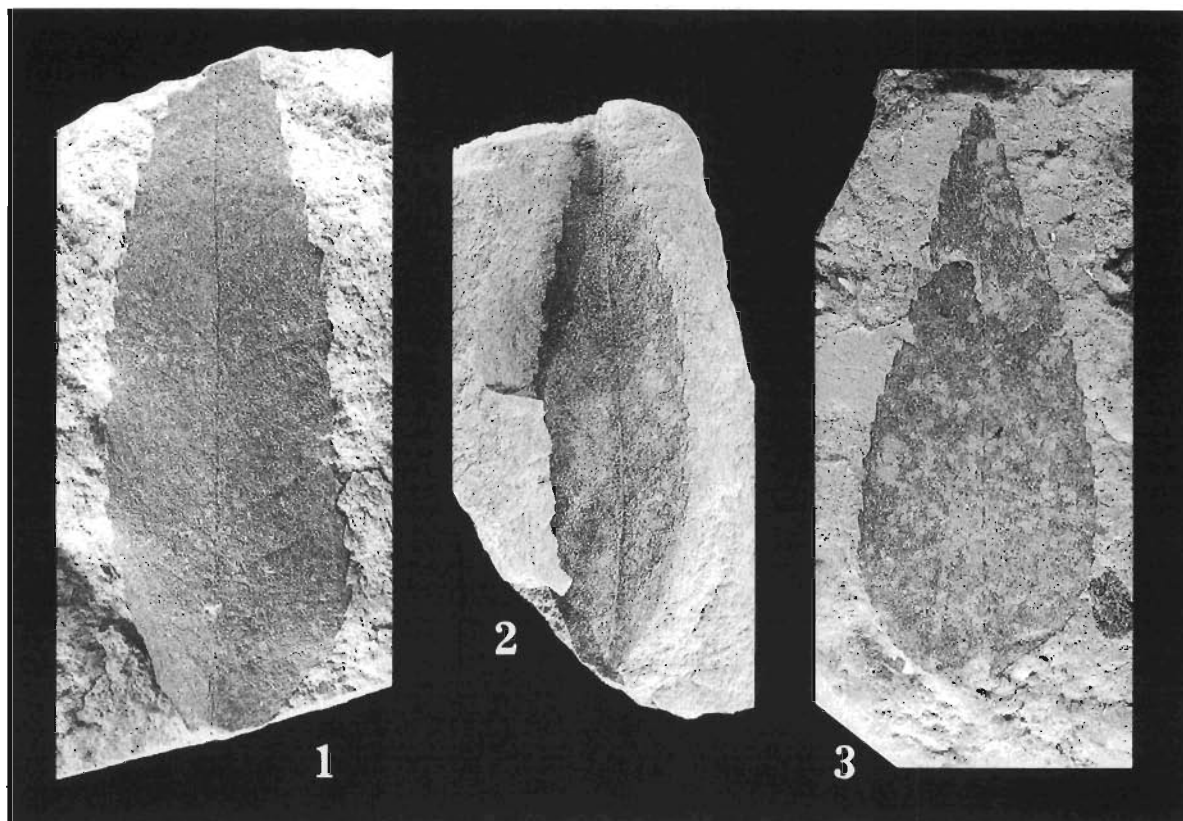


Fig. 7

Knightiophyllum andreae (DUSÉN) ZASTAWNIAK comb. n., leaf impression: 1 — ZPAL Pl.II/1; impression of narrow elliptical leaf: 2 — ZPAL Pl.II/23; impression of narrow ovate leaf: 3 — ZPAL Pl.II/24. All natural size.

Diagnosis. — Leaves petiolate, slightly asymmetric, lanceolate, narrowly ovate or elliptic, base cuneate or rounded, margin crenate, tooth type cunonioid, sinuses +/- rounded, spacing irregular, series simple. Venation pinnate, semicraspedodromous, secondary veins straight or slightly curved, tertiary veins partially percurrent. Texture coriaceous.

Material. — Nine leaf impressions, two with twin impressions (ZPAL Pl.II/1, 5a–b, 9, 12, 15, 21, 23–24, 26a–b).

Description. — Leaves slightly asymmetric, from 6.0–16.4 cm long and 1.9–4.3 cm wide, petiole 8 mm long. Leaves lanceolate, narrowly ovate or elliptic, widest in the lower half. Base cuneate or rounded, asymmetric, apex acute or acuminate. Margin crenate, tooth types cunonioid, sinuses +/- rounded, spacing irregular, series simple. Venation pinnate, semicraspedodromous. Midvein stout, straight, on one specimen curved. Secondary veins straight or slightly curved, full number unknown. Some percurrent tertiary veins visible. Texture coriaceous.

Remarks. — The leaf impressions of this fossil taxon are distinguished by their characteristic shape and the crenation of their leaf margins. Leaf remains of this type were described by DUSÉN (1908) from Seymour Island. They were correspondingly large, up to 12 cm long, lanceolate, with similarly shaped margins, coriaceous but with obscure venation. DUSÉN (1908) compared them to the modern New Zealand *Knightia excelsa* R. BROWN from the family Proteaceae and drew attention to its peculiar isolated position among all the plant remains described by him from that fossil flora.

It is impossible to check the affiliation of the leaf remains described to the genus *Knightia* on the basis of leaf impressions alone. For this reason an artificial genus, *Knightiophyllum*, was created. However, we cannot expect to settle the question of whether it belonged to the family Proteaceae until some other better-preserved finds are at our disposal in the future. However, it should be noted, relatively large numbers of pollen grains of the family Proteaceae have been found in the sediments of the La Meseta Formation (ZAMALOA *et al.* 1987), even pollen grains similar to *Knightia excelsa* pollen type (ASKIN personal communication, 1995).

The leaf specimens from the La Meseta Formation on Seymour Island, recognized by CASE (1988, p. 527) as “large-leaved species of *Nothofagus* typical of this locality”, bear morphological features which agree with those of *Knightiophyllum andreae*.

Dicotyledones incertae sedis

Genus *Dicotylophyllum* BANDULSKA, 1923

Dicotylophyllum sp.

(Pl. 32: 8; Text-fig. 6: 10)

Material. — One leaf impression (ZPAL Pl.II/8).

Description. — Leaf lanceolate, about 7 cm long and 2.5 cm wide, petiole 1 cm long. Base cuneate, apex damaged. Venation pinnate, midvein stout, slightly curved at leaf base. Secondary veins, at least 10 in number, regular, parallel, with a straight course and a moderate angle of divergence except for the basal secondary vein, which is parallel to the base margin. Type of venation in the leaf margin area unknown; margin dentate, but only one small tooth is visible.

Remarks. — The specimen found represents an unrecognized dicotyledonous plant.

COMPARISON

The presence of ferns, conifers, represented by both families typical of the Tertiary of the Southern Hemisphere, Araucariaceae and Podocarpaceae, and dicotyledons with the dominant species *Knightiophyllum andreae* and leaves of *Nothofagus*, all described earlier by DUSÉN (1908) and CASE (1988) from Seymour Island, was confirmed in the fossil flora from the ZPAL 9 site.

With regard to plant taxa, the fossil flora studied by DUSÉN (1908) is much more heterogeneous than that studied here. Ferns are represented much more abundantly with only one taxon found at site ZPAL 9. As far as coniferous plants are concerned, the same families are present in both floras, namely Araucariaceae (one leaf of *Araucaria imponens*) and Podocarpaceae. In this latter case, however, the genera are different, that is *Acmopyle* PILGER and *Prumnopitys* PHILIPPI (see FLORIN 1940, p. 32; ZASTAWNIAK *et al.* 1985, p. 150). Conifers are not very numerous and, as at site ZPAL 9, they are outnumbered by the Angiospermae.

Two genera of angiosperms occur in both localities: *Knightiophyllum* and *Nothofagus*. At the studied site (ZPAL 9), there is only one more angiospermous genus present (*Dicotylophyllum* sp.). In DUSÉN's (1908) material angiosperms are very heterogeneous and, particularly noteworthy, it provides evidence of the presence of more thermophilous, laurel-leaved forms.

CASE's (1988) study deals with leaf remains from the Paleocene Cross Valley Formation on Seymour Island and gives more or less the same picture of the vegetation as DUSÉN's (1908) publication, *i.e.*, a high representation of ferns, the presence of fossil leaves of *Nothofagus* and remains of Podocarpaceae. The evidence in CASE's (1988) publication about the occurrence of laurel-leaved forms in the Cross Valley Formation however, is missing.

The material studied by CASE (1988) from the Eocene La Meseta Formation (site RV 8425 located close to our locality ZPAL 9) contains leaf remains with carbon film, fragments of coalified wood, mollusc shells and starfish remains. The fossil plants are represented by large leaves of *Knightiophyllum andreae* (non *Nothofagus*), fronds of at least two types and section of a shoot of "an araucarian conifer" (CASE 1988).

It should also be noted that palynological studies of the La Meseta Formation on Seymour Island (ZAMALOA *et al.* 1987) evidenced the presence of pollen grains of Araucariaceae, Podocarpaceae, Proteaceae (numerous) and *Nothofagus* (very numerous).

FISH PALEONTOLOGY

The Eocene La Meseta Formation on Seymour Island is the only known locality for Tertiary teleost fishes in Antarctica (GRANDE and EASTMAN 1986; JERZMAŃSKA 1988, 1991; EASTMAN and GRANDE 1991; JERZMAŃSKA and ŚWIDNICKI 1992; EASTMAN 1993). The fish fauna collected from the locality ZPAL 9 include a rich assemblage of clupeoids (Text-figs 8–10) and a few gadiform and beryciform scales (Text-figs 11–13).

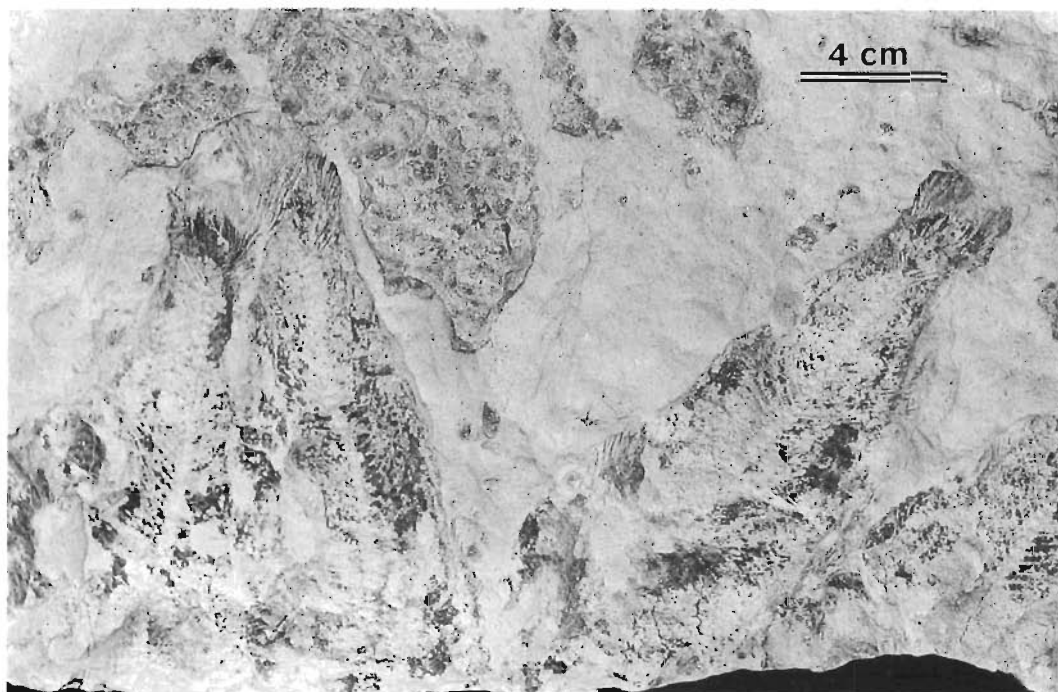


Fig. 8

Field photograph of four skeletons of *Marambionella andreae* JERZMAŃSKA, 1991 preserved on a bedding plane (locality ZPAL 9).

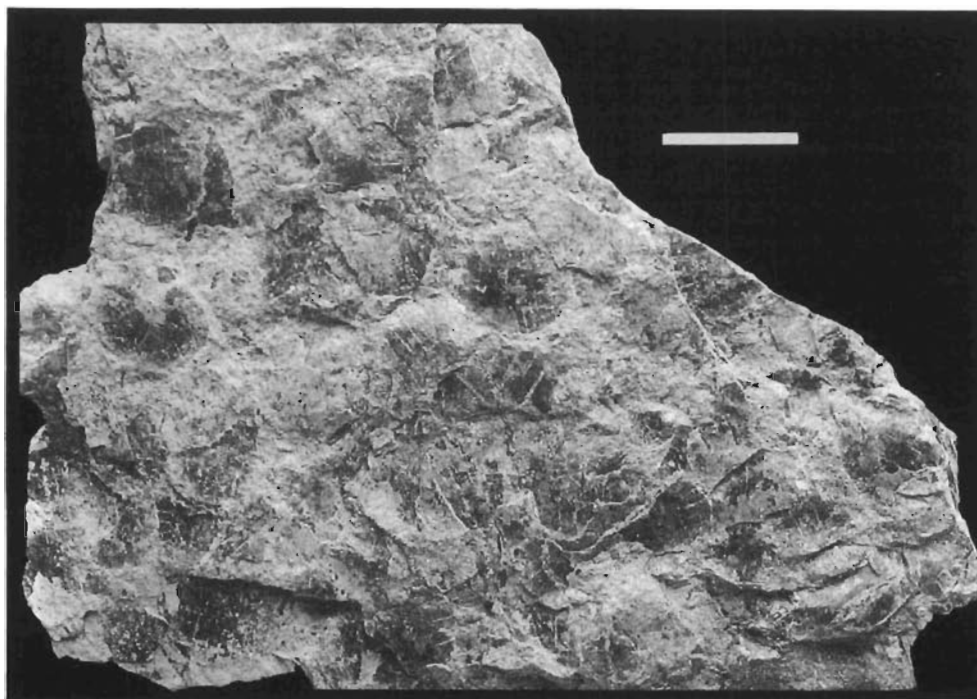


Fig. 9

Accumulation of isolated scales of *Marambionella andreae* JERZMAŃSKA, 1991 on a bedding plane (ZPAL P.III/21) see JERZMAŃSKA (1991). Scale bar is 1 cm long.

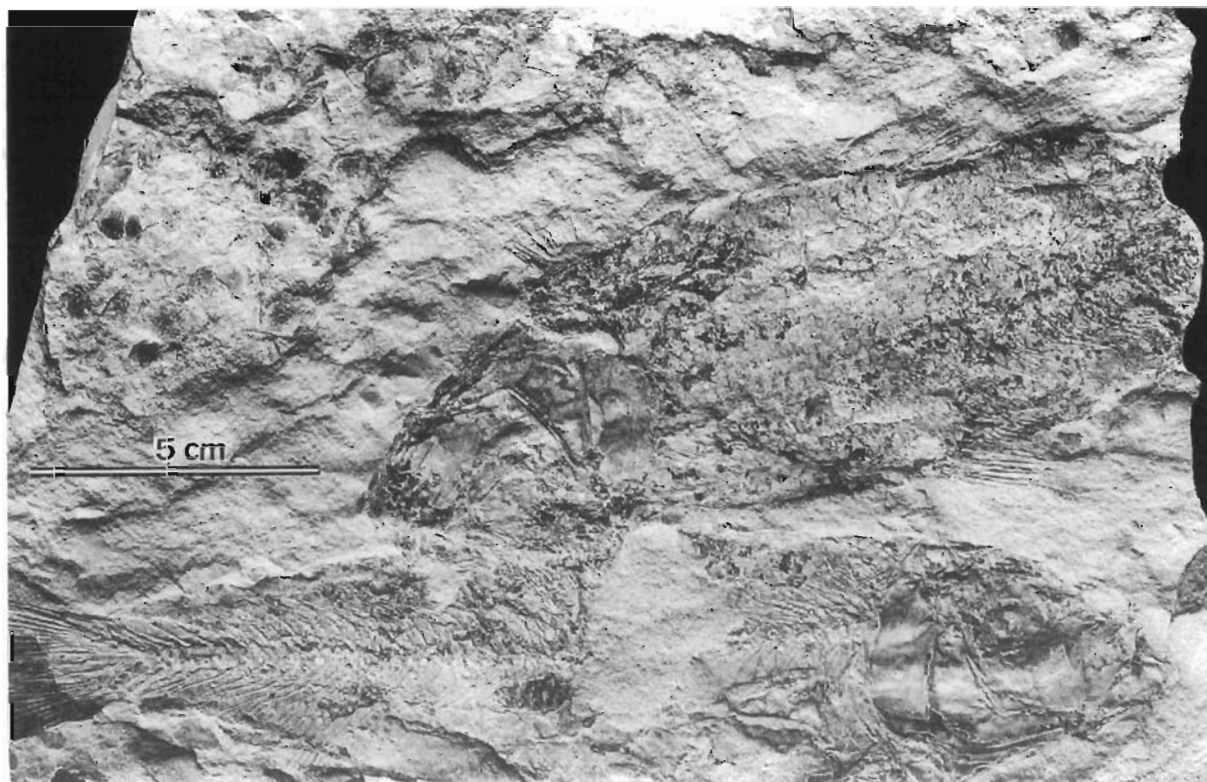


Fig. 10

Two skeletons of *Marambionella andreae* JERZMAŃSKA, 1991 (ZPAL P.III/1a-b) see JERZMAŃSKA (1991).

Order Clupeiformes (*sensu* GRANDE, 1985)Family **Clupeidae** (*sensu* GRANDE, 1985)Genus *Marambionella* JERZMAŃSKA, 1991*Marambionella andreae* JERZMAŃSKA, 1991

(Text-figs 8–10, 14)

Remarks. — An abundant complete or nearly complete skeletons (Text-figs 8, 10, 14), large fragments of skulls and complete postcranial skeletons; few isolated cranial bones, large numbers of isolated scales (Text-fig. 9), accumulated on a bedding plane (see JERZMAŃSKA 1991).

Order Gadiformes GOODRICH, 1909 (COHEN, 1989)

Family unknown

(Text-figs 11–12)

Material. — Among the abundant scales of *Marambionella andreae*, there were few small, isolated scales of gadiform fishes of uncertain affinities. They are represented by: three isolated, oval cycloid scales on a bedding plane (Text-figs 11–12) with *M. andreae* (ZPAL P.III/10f, 19b).

Dimensions. — The specimen ZPAL P.III/10f — an almost complete scale about 4 mm long and about 2.8 mm wide (Text-fig. 11); ZPAL P.III/19b — two adjacent scales, the larger (Text-fig. 12) being about 3.3 mm long and about 2.1 mm wide, while the smaller about 1.5 mm long and about 1.0 mm wide.

Remarks. — All these scales have an oval focus and numerous circuli, arranged according to the following patterns: The specimen ZPAL P.III/10f (Text-fig. 11) has all circuli running parallel to the rounded edge of the scale in the anterior field, below the acentric focus; in the posterior field, the median circuli, below the focus, are obliquely oriented and converging towards the centerline of the scale at sharp angles; numerous lateral circuli of the posterior field are, however, almost parallel to the edge of the scale. Both scales of the specimen ZPAL P.III/19b have almost centrally located foci, and the circuli of right and left parts of the anterior field converge along the midline at stright angles, while the pattern of circuli in the posterior field and in lateral parts resembles that of ZPAL P.III/10f (Text-fig. 11).

The structures, described above, resemble most the scales of some Phycidae, including Recent species *Phycis chesteri* (GOODE *et* BEAN, 1878) and *Urophycis chuss* (WALBAUM, 1792) *fide* DAVID (1956), as well as some Merluccidae (*Merluccius hubbsi* MARINI, 1933; author's own observations).



Fig. 11
Cycloid scale of Gadiformes (ZPAL P.III/10f).

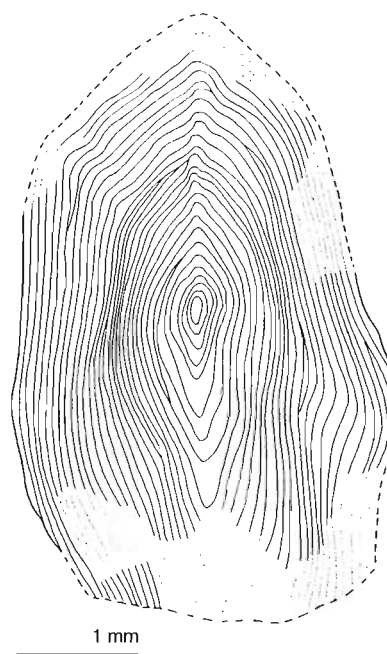


Fig. 12
Cycloid scale of Gadiformes (ZPAL P.III/19b).

Order **Beryciformes** REGAN, 1909

Family unknown

(Text-fig. 13)

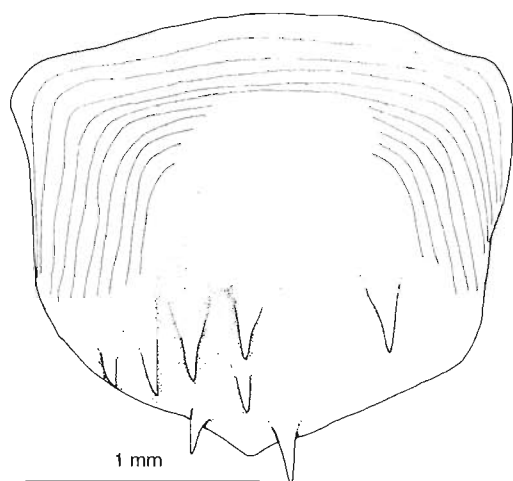


Fig. 13

Ctenoid scale of Beryciformes (ZPAL P.III/18b).

Material. — Five ctenoid scales on a bedding plane of rock samples with remains of *Marambionella andreae* (ZPAL P.III/8, 13, 16, 18 and 25), including two with partially preserved spines on the posterior field (ZPAL P.III/16 and 18). Of the other three only anterior and both lateral fields are visible.

Dimensions. — Maximum width of the best preserved scale (ZPAL P.III/18b) at the anterior margin — 2.1 mm; maximum medial length — 1.9 mm. The other, less complete scales are of similar size.

Remarks. — All specimens have highly visible smooth medial area. Numerous circuli are parallel to the anterior and both lateral edges. On smooth posterior field, preserved only in two specimens (ZPAL P.III/16 and 18b), there were numerous sharply pointed spines (Text-fig. 13). These multiple spines and the pattern of circuli near the anterior and lateral edges differentiate the scales from those of Recent and fossil gadiform species belonging to the family Macrouridae (DAVID 1956; IWAMOTO and STEIN 1974).

Instead, these structures resemble the pattern of circuli and spines in some Recent species of beryciform family Trachichthyidae, e.g. *Paratrachichthys prosthemus* JORDAN and FOWLER 1902 *vide* (GON 1987), and those near the dorsal fin of *Paratrachichthys sajademalensis* KOTLYAR, 1979 and *Hoplostethus natalensis* KOTLYAR, 1978 (KOTLYAR 1980). Thus the ctenoid scales described above have been assigned to the Beryciformes.

Beryciformes are known from Antarctica only from the Late Cretaceous strata of Seymour Island (GRANDE and CHATTERJEE 1987). These remains consist of a fragmentary cranium and a poorly preserved scale of *Antarctiberyx seymouri* GRANDE *et* CHATTERJEE, 1987, belonging to the family Trachichthyidae.

DISCUSSION

DEPOSITIONAL CONDITIONS

The lithofacies spectrum points to deposition of the studied part of Teln2 within a relatively protected, central estuarine basin (POREBSKI 1995). It was dominated by tidal activity and influenced by a periodic fluvial inflow, as indicated by the common occurrence tidal bundles accompanied by plant matter in various decay stages, ranging from the perfectly preserved laeaves and shoots, tree logs and coalified fragments. The abundance of the complete leaves suggests a forest growing by the estuary shore, from where they could possibly have fallen down directly into the water or were transported over very short distances before being rapidly buried in the sediment. The leaves must have been rather tough and leathery preventing their disintegration into small fragments and ensuring their long term survival.

The co-occurrence of such preserved terrestrial flora with the marine clupeoid fishes (Text-fig. 14), together with the ample evidence of tidal activity, point to vigorous interaction between marine processes and a fluvial inflow, as would occur in a tide-dominated estuary. This is further corroborated by the common occurrence of the syneresis? cracks pointing to salinity fluctuations through incursions of fresh water (BURST 1965). The low-diversity trace fossil assemblage combining elements of the *Skolithos* and the *Cruziana* facies (POREBSKI 1995) is similar to that recorded in the subnormal saline conditions of the present-day Georgia estuaries (HOWARD and FREY 1975). Clupeoid fishes are known to penetrate far inland in West African estuaries (BEADLE 1972, p. 57).

The scales of *Marambionella andreae* were probably accumulated by the action of bottom currents removing them from the fish skin. The mass occurrence of the *M. andreae* scales may indicate a seasonal



Fig. 14

Bedding plane showing the plant-and-fish assemblage from the locality ZPAL 9 revealing ?*Knightiophyllum* sp. (A), *Murambionella andreae* (B) and clupeoid scales (arrowed). ZPAL PI.II/13.

appearance of large schools of this species possibly related to their spawning areas. Such behaviour is corroborated by many Recent clupeoid species spawning in shallow nearshore waters, estuaries and even in rivers (BLAXTER and HUNTER 1982).

Deposition over the ZPAL 9 site took place on ebb-dominated, shallow subtidal to intertidal?, mixed flats which backed to the SW the central estuarine channel. The absence of unequivocal signs of emersion points to a subtidal setting, whereas the rarity of megaripples suggests the predominance of non- to broadly channelised flows over protected shallow flats or in a deeper, tidal-dominated lagoon. A more open, offshore setting is unlikely, because of the absence of hummocky cross-stratification, scarcity wave-generated structures as well as the limitation of bioturbation and fauna to discrete horizons. The site under consideration records a two-phase deposition within a constructional channel formed in a response to voluminous gravity failure which affected the southwestern bank of the central estuarine basin (POREBSKI 1995). The gravity collapse resulted in the rugged topography of rotated slide blocks and intervening lows. A NE-SW or ENE-WSW striking scar was initiated in the hangingwall of a NW-ly rotated slide block and was immediately subjected to active tidal discharges. The early infill phase reflects the asymmetrical filling of the scar through lateral accretion nucleated around the upthrown edge of the slide block to form

the IHS body analogous to the point bar of a meandering tidal channel. The subsequent VAS phase reflects a rather rapid abandonment of the scar and switch to deposition from less energetic, ebb-dominated tidal flows which accompanied the formation of the plant-and-fish assemblage.

CLIMATIC IMPLICATIONS

The past studies of the Late Cretaceous and Tertiary leaf floras from King George Island (South Shetland Islands, West Antarctica), documented a distinct thermophilous element which in the leaf physiognomy is expressed by whole margins and brochidodromous or camptodromous venation (BIRKENMAJER and ZASTAWNIAK 1986, 1988, 1989a, b; TOKARSKI *et al.* 1987; ZASTAWNIAK 1994). This element is also prominent in the Paleocene floras of Seymour Island, evidenced in the material of DUSÉN (1908) and CASE (1988) from the Cross Valley Formation.

Younger, Oligocene floras of the *Nothofagus*–Podocarpaceae type from King George Island show a different character (ZASTAWNIAK 1981; ZASTAWNIAK *et al.* 1985). They document a distinctly cooler climate (BIRKENMAJER and ZASTAWNIAK 1989a, b).

The laurel-leafed element has not been found both in the materials from the ZPAL 9 site and in other localities within the Eocene La Meseta Formation (CASE 1988). In this respect the picture of the La Meseta Formation vegetation seems to correspond better to the cool-temperate vegetation from the Oligocene of King George Island (ZASTAWNIAK 1981; ZASTAWNIAK *et al.* 1985). On the other hand, however, such large leaves of *Knightiophyllum andreae* or *Nothofagus* as those found at the ZPAL 9 locality must have belonged to plants growing in more favourable climatic conditions than during the Oligocene of King George Island.

To sum up, the Eocene flora from the La Meseta Formation (ZPAL 9 site) indicates a temperate type of climate, somewhat warmer than in the Oligocene. Since the laurel-leafed element is present in the Paleocene Cross Valley Formation leaf flora studied by DUSÉN (1908) and absent in the locality ZPAL 9 flora, this latter seems to indicate cooler conditions. Nevertheless, this conclusion is equivocal in the light of the palynological results of the older, Paleocene deposits of Seymour Island. In ASKIN's (1988) opinion, they indicate cool-temperate, moist conditions reconstructed on pollen spectra. These reveal the domination of the pollen grains of Podocarpaceae accompanied by Araucariaceae and *Nothofagus*, as well as spores of mosses and ferns, and pollen grains of Angiospermae including Proteaceae, Loranthaceae, Myrtaceae, Casuarinaceae, Ericales, and Liliaceae. ASKIN (1988) has suggested that the vegetation was similar to that of the present-day lowland rain forest of southern Chile, and a similar conclusion can be invoked for the flora from the ZPAL 9 site. The latter flora resembles the present-day araucarian forests with *Nothofagus* accompanied by Podocarpaceae trees. Such forests grow in the Argentine–Chilean borderland between 30 and 40°S at altitudes ranging from 600 to 1800 m. The mean annual temperature in this area is +10 to +15°C, the winter temperature reaching -5°C on the Chilean side and -20°C on the Argentine side. The annual rainfall ranges between 600 and 1200 mm and the snow cover remains for many months (HUECK 1966; HUECK and SEIBERT 1972).

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PLATE 32

Plant impressions from the Eocene La Meseta Formation (Telm2), Seymour Island (locality ZPAL 9).

Dacrycarpus? tertiarius (BERRY) ZASTAWNIAK comb. n. 133

Fig. 1. Impression of *Dacrycarpus? tertiarius* twigs with imbricate leaves and longitudinal section of the shoot fragment of *?Araucaria* sp. (bottom), natural size, ZPAL Pl.II/6.

?Araucaria sp.

Fig. 2. Enlargement of *?Araucaria* sp. from Fig. 1, $\times 1.5$.

Araucaria nathorsti DUSÉN 135

Fig. 3. Leaf impression; $\times 2$, ZPAL Pl.II/2.

Fig. 4. Whole leaf impression, natural size, ZPAL Pl.II/20.

Fig. 5. Whole leaf impression, natural size, ZPAL Pl.II/19.

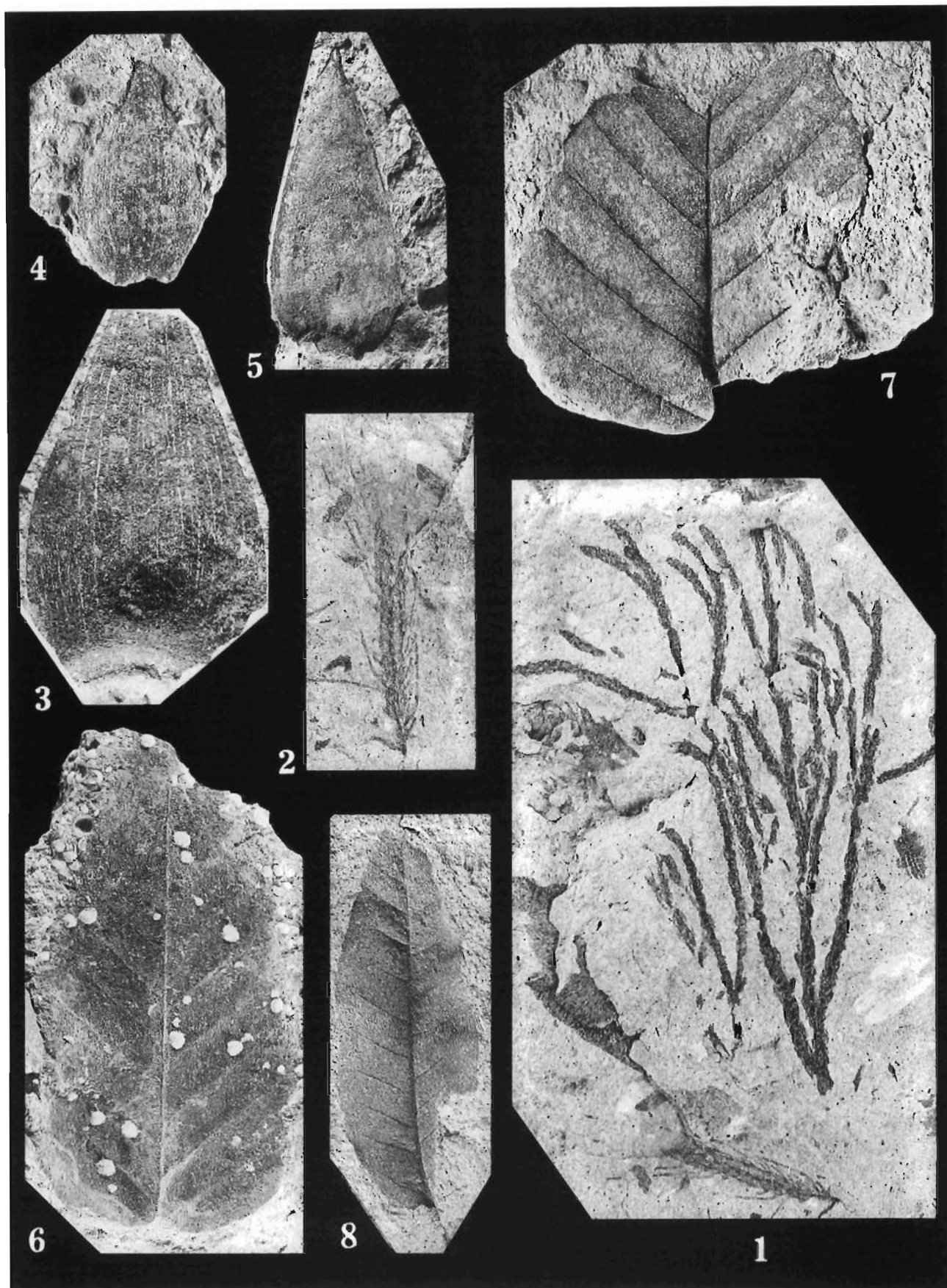
Nothofagus sp. 135

Fig. 6. Leaf impression with bivalves on the surface, natural size, ZPAL Pl.II/25.

Fig. 7. Impression of large leaf, natural size, ZPAL Pl.II/22.

Dicotylophyllum sp. 138

Fig. 8. Leaf impression, natural size, ZPAL Pl.II/8.



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PLATE 33

Plant impressions from the Eocene La Meseta Formation (Telm2), Seymour Island (locality ZPAL 9).

Knightiophyllum andreae (DUSÉN) ZASTAWNIAK comb. n. 137

Fig. 1. Twin impressions, natural size; a – ZPAL Pl.II/5b, b – ZPAL Pl.II/5a.

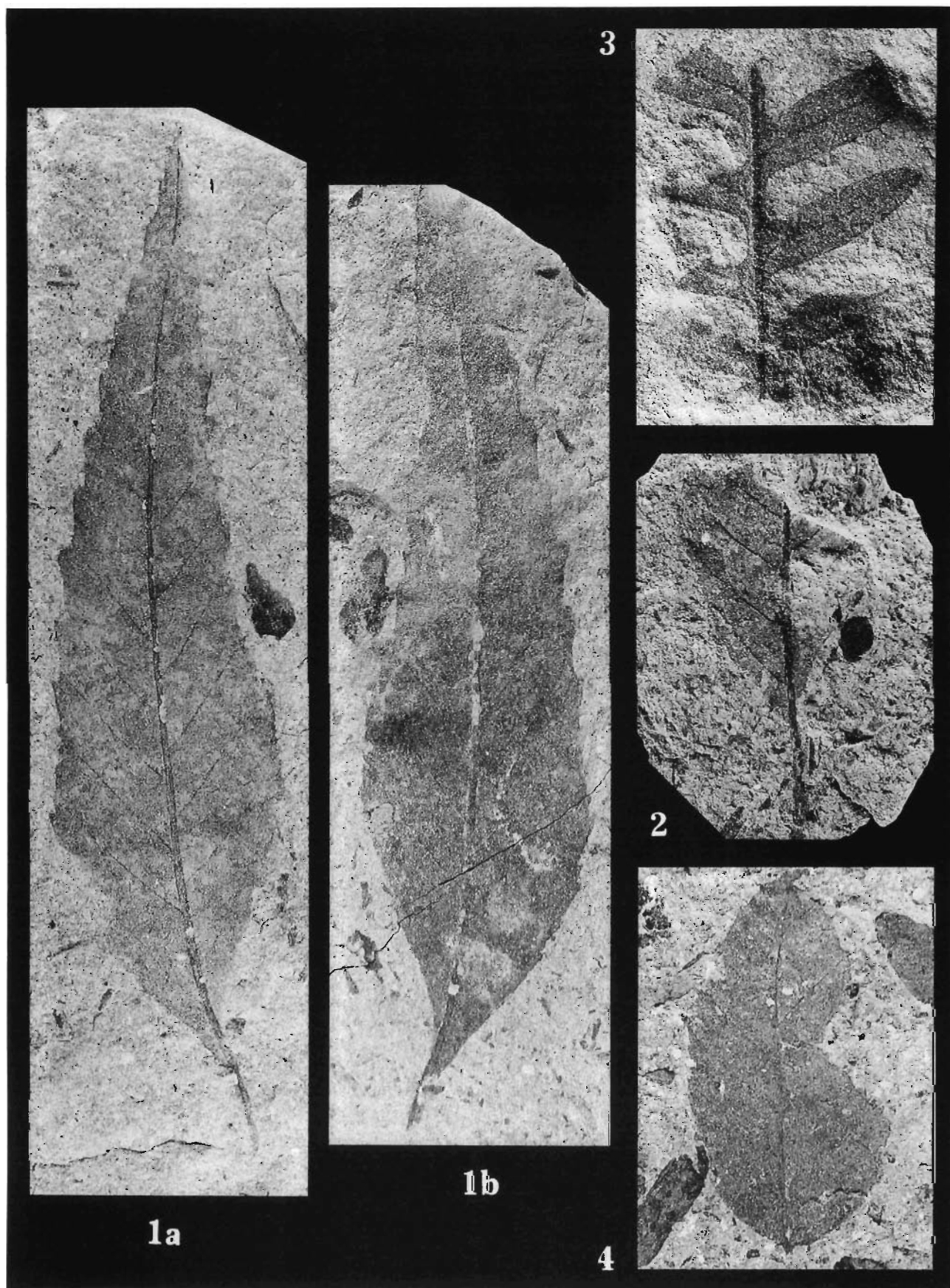
Fig. 2. Impression of basal part of leaf with long petiole, natural size, ZPAL Pl.II/21.

Cladophlebis sp. 133

Fig. 3. Fragment of frond, × 2, ZPAL Pl.II/4.

Nothofagus sp. 135

Fig. 4. Impresssion of the almost whole leaf, natural size, ZPAL Pl.II/7.



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