Thelodont scales from the Middle–Late Devonian Aztec Siltstone, southern Victoria Land, Antarctica

S. TURNER[1] and G.C. YOUNG[2]

[1]Queensland Museum, P.O.Box 300, S. Brisbane, Queensland 4101, Australia
[2]Bureau of Mineral Resources, PO Box 378, Canberra City, ACT 2601 , Australia

Abstract: A new fossil agnathan, *Turinia antarctica* sp. nov., based on numerous isolated scales, comes from the lower fish-bearing beds of the Aztec Siltstone. Scales from moraine at Mount Suess, originally described as selachian or psammosteid heterostracan, are referred to the new species which shows close affinity with *T. gondwana* from Bolivia and *T.* cf. *hutkensis* from Iran. Reassessment of the biostratigraphy of Middle Devonian turiniid scales suggests that the lower part of the Aztec Siltstone may be of Eifelian age.

Introduction

In the summer of 1911–12, during the British Antarctic 'Terra Nova' expedition (1910–13), Mr Frank Debenham of T.G. Taylor's party collected fossil fish remains from moraine near Granite Harbour. These were the first fossils of Devonian age, and the first fossil vertebrates, to be discovered on the Antarctic continent. They were described by A.S. Woodward in 1921. The fish came from samples of 'Beacon Sandstone' collected from the Mackay Glacier moraine of Gondola Ridge, but are now known to have been derived from the Aztec Siltstone of the Beacon Supergroup, from which an extensive fauna of Middle to Late Devonian fishes has been documented.

Included in the original collection were small scales which Woodward (1921, p. 51) described as 'very little mineralized', of white or bluish colour; 'in transparent sections their histological structure is perfectly observable'. He noted (1921, p. 56) that these 'minute fragments of dermal armour are scattered abundantly through various specimens of the rock, but most of them are shown only in broken section and so cannot easily be identified'. Woodward concluded that the 'majority seem to be shagreen granules referable either to primitive Ostracoderms or to Elasmobranchs'. The term 'ostracoderm' was used at that time for various armoured agnathans (jawless fishes) of the early and middle Palaeozoic.

Some of these 'denticles' described by Woodward were said to show in thin section a histological structure which he compared with the Late Devonian shark *Cladoselache*. There is only one published illustration of so called dermal tubercles of *Cladoselache*, by Woodward & White (1938);

the structure shown bears no resemblance to the thin sections of scales from Granite Harbour or other Antarctic material. In fact the scale, NHM P.9294, shown by Woodward & White is probably a pharyngeal denticle (Zangerl 1981) and might come from any one of several mid-Palaeozoic shark genera with complex multicuspid scales such as *Ctenacanthus* or *Stethacanthus*. Sharks subsequently identified in the Aztec fish fauna from associated teeth, spines and scales (Young 1982, 1989b, fig. 4E) have scales with a morphology typical of mid-Palaeozoic chondrichthyans.

A second denticle type was described by Woodward as having a conspicuous central pulp cavity, and Gross (1950, p. 72) suggested that these might belong to psammosteid heterostracans, a diverse group of Devonian agnathans which flourished particularly in the Baltic Province of Europe during the Middle/Late Devonian. Tarlo (1964, p. 91) re-examined the material, and concluded that 'they are probably heterostracan and are therefore likely to be psammosteid in nature'. At that time the psammosteids were the only heterostracans known to persist into the Upper Devonian. One of us (S.T.) examined the material in 1968 at the suggestion of Halstead (Tarlo) but then was persuaded that the scales were chondrichthyan because they did not show much similarity to known thelodont scales. Large turiniid scales with cruciform cross sections were not discovered until later.

New material from many localities in the Aztec Siltstone (Fig. 1) include scales with a different scale morphology from the sharks in the Aztec fauna (Young 1982). On the basis of histological structure, shown first by Woodward (1921, figs 14–22, reproduced here as Fig. 2), these scales clearly belonged to a turiniid thelodont agnathan. The presence of thelodonts in the Aztec fauna has already been noted in the literature (Grande & Eastman 1986, Halstead 1987, Long 1989, Turner 1984, 1986, and in Gagnier *et al.* 1988, Young 1981, 1987, 1988, 1989b). Here we describe
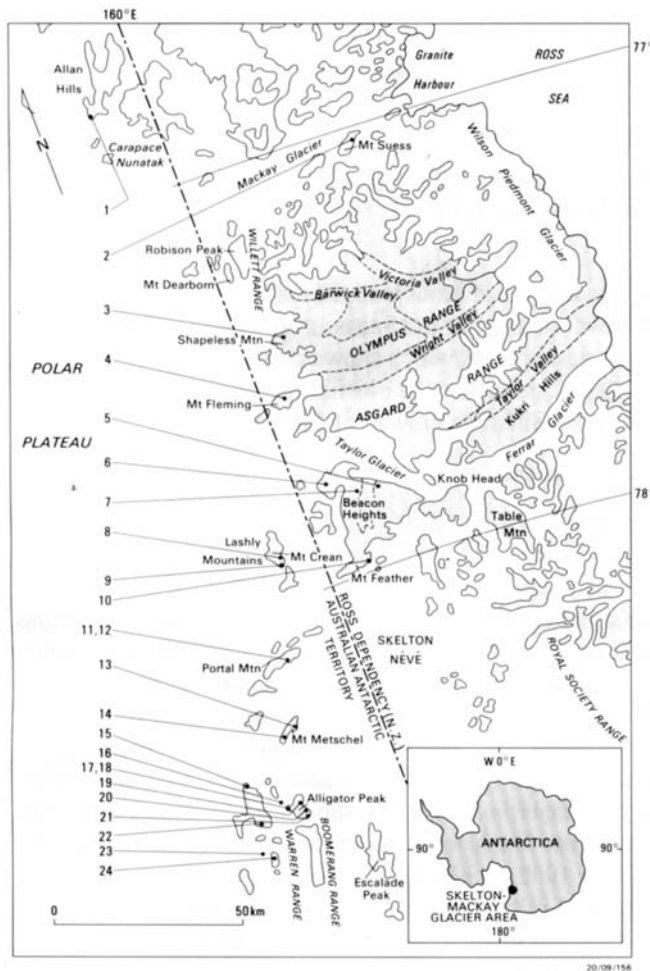
Fig. 1. Locality map for Devonian fish occurrences known from southern Victoria Land, Antarctica (after Young 1988). A new locality about 100 km south of those shown here has recently been recorded by Woolfe *et al.* (1990). *Turinia antarctica* sp. nov. comes from localities 2, Gondola Ridge, Mount Suess; 4, Mount Fleming; 8, Mount Crean; 12, Portal Mountain and 19, eastern face of Alligator Ridge, Boomerang Range.

these scales as a new species of the genus *Turinia*, based on new material and a redescription of Woodward's original specimens.

Material described or mentioned here is housed in the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra (prefix CPC), the Australian Museum, Sydney (prefix AMF), the Natural History Museum, London (prefix NHM P), the Field Museum of Natural History, Chicago (prefix PF), the Canterbury Museum, Christchurch (prefix AF), and in the private collection of C.T. McElroy, Sydney (prefix JK).

Previous investigations of the Aztec fish fauna

The first *in situ* fossil fish remains from the Aztec Siltstone were collected during the Trans-Antarctic Expedition of

1955–58 in the area of the Skelton Névé in southern Victoria Land (Gunn & Warren, 1962, White 1968). Other fossil localities from Beacon Heights, Mount Fleming, and Aztec Mountain were recorded by Matz & Hayes (1966), Helby & McElroy (1969), and Matz *et al.* (1972). The first significant collections of fossiliferous material were made under the New Zealand Antarctic Research Program (NZARP) by a Victoria University of Wellington Antarctic Expedition (VUWAE 13) in 1968-69 from the westernmost nunataks of the Transantarctic Mountains, between the Taylor and Mulock glaciers (McKelvey *et al.* 1972). Subsequent collections by another Victoria University expedition (VUWAE 15; 1970–71 field season), and a Canterbury Museum visit (NZARP, event 33; 1976–77) showed that the fossiliferous layer was widely distributed in southern Victoria Land. In the 1988-89 field season a new locality was found at Mount Hughes in the Cook Mountains about 100 km south of previously known exposures (Woolfe *et al.* 1990). Already described from the Aztec fauna are groenlandaspid arthrodires (Ritchie 1975), xenacanth sharks (Young 1982), bothriolepid antiarchs (Young 1988), acanthodians (Young 1989a), and crossopterygians (Young *et al.* in press). A dipnoan toothplate was illustrated by Campbell & Barwick (1987, fig. 2). Other taxa still to be described include palaeoniscoid osteichthyans, and some additional acanthodians and placoderms. The Aztec fauna has been reviewed by Grande & Eastman (1986) and Young (1989b, 1991). Based on current work the vertebrate fauna contains at least 21 genera and 30 species, making it one of the more diverse fossil faunas known from Antarctica.

Stratigraphic setting

The Palaeozoic and early Mesozoic Beacon Supergroup was subdivided by Harrington (1965) into the Devonian (or older?) Taylor Group, and the Victoria Group (Permo-Triassic). The Metschel Tillite, of possible Carboniferous age, occurs in some sections as a basal formation of the Victoria Group (McKelvey *et al.* 1970, 1972). Stratigraphical nomenclature for the Beacon Supergroup was summarized by McKelvey *et al.* (1972).

Two formations, formally defined by McKelvey *et al.* (1977: 832–836), contain Devonian fish remains; the Beacon Heights Orthoquartzite and the Aztec Siltstone. Only the Aztec Siltstone (uppermost Taylor Group) has so far yielded thelodont scales. In the type area at Aztec Mountain (Webb 1963), this formation comprises about 40 m of red and green siltstones exposed above the Beacon Heights Orthoquartzite. Subsequent fieldwork has shown the Aztec Siltstone to extend over an area about 200 km long and 50 km wide in the Skelton Névé – Mackay Glacier region (Fig. 1). It thins to the north from a maximum thickness of some 220 m in the southern Boomerang Range to a minimum of 40 m at Maya Mountain. This has been attributed to stripping of the upper strata by icesheet erosion during the late Palaeozoic

(McPherson 1978).

Fossil localities

Full details for the 24 localities in Fig. 1 are given in Young (1988); here we comment on those localities which have yielded thelodont scales. MS and RS numbers cited are registered fossil localities in the 'Ross Sea Environs' Fossil Record File of the New Zealand Geological Survey.

2. *Gondola Ridge, Mount Suess (MS4)*. This is the original material collected from moraine of the Mackay Glacier at Gondola Ridge (Debenham 1921, Gunn & Warren 1962). Collections from the moraine on the south-east side of Gondola Ridge did not contain thelodonts (White 1968). Matz *et al.* (1972) ascribed these remains to their 'Windy Gully Formation' (basal Beacon Supergroup), but the faunal assemblage leaves little doubt that it came from basal beds of the Aztec Siltstone (Young 1988).

4. *Mount Fleming (MS228–230; RS 621, 622)*. Fish remains come from a siltstone bed 15 to 30 m below the disconformity at the top of the Aztec Siltstone (Matz & Hayes 1966). Matz *et al.* (1972: 356) recorded 'well-preserved Middle to Upper Devonian fish remains' from 'interbedded orthoquartzites and siltstone 61 m below the disconformity at Mount Fleming' within their 'Fortress Formation' (= Aztec Siltstone). The determinations are attributed (J.C. Bruner personal communication) to the late Dr R.H. Denison (ex Field Museum, Chicago). Although the museum lacks documentation for the Antarctic thelodont scales (on PF9600–9602), we assume they were part of the material recorded by Matz *et al.* (1972). Material collected in 1968–69 (McKelvey *et al.* 1972) from section 26 of Barrett & Webb (1973) contained no thelodont scales. However, the collection of M. A. Bradshaw (1976–77, NZARP Event 33, Canterbury Museum) from section H6 (unit 17) of Barrett & Webb (1973; 62 m above base) and that made by J. Bryan and K. Whitby in 1980-81, contains abundant well preserved scales (associated with *Bothriolepis* sp. indet. 3 of Young 1988).

8. *Mount Crean (MS5, MS6; RS 625—628)*. Thelodont scales come from units 3 and 5, but not from unit 8 of section L2 of Askin *et al.* (1971; measured up the south-eastern part of the outcrop). These units were placed within 23–42 m above the base of the Aztec Siltstone, but the section is interrupted by a dolerite dyke, making the stratigraphic levels for some fossiliferous horizons uncertain, as discussed by Young (1988). Thelodont scales are associated only with *Bothriolepis askinae, B. kohni*, and *B.* sp. indet. 4 and 5 from this locality (Young 1988).

12. *Portal Mountain (RS 634-637)*. Section P1 of Askin *et al.* (1971) includes the basal contact with the Beacon Heights Orthoquartzite. Thelodont scales have only been identified in unit 4, 7–16 m above the base of the formation,

associated with *Bothriolepis* sp. indet. 9; they are apparently absent from the fossiliferous horizons in unit 14, 44–53 m above base (see Young 1988, p. 13).

19. *Boomerang Range, east of Alligator Peak (MS237)*. This section is the only one measured in the region which includes the basal contact between the Aztec Siltstone and the Beacon Heights Orthoquartzite (section 5, Barrett & Webb 1973). Fish remains in the basal 4 m of section include thelodont scales, the most southerly known occurrence. Crossopterygian remains from here are described by Young *et al.* (in press).

Systematic description

THELODONTI

THELODONTIDA

Family TURINIIDAE Obruchev 1964

Remarks: The family Turiniidae currently contains three genera of thelodontids, *Turinia, Boreania* and *Australolepis*. The generic status of the latter has been questioned (Turner 1986, Turner in Gagnier *et al.* 1988) but the scales referred to *Australolepis*, Turner & Dring 1981 may represent an advanced turiniid condition. Turiniids had a squamation of small to large scales with a *Thelodus*-type histology (*sensu* Gross 1967). The range of scale form within the squamation, especially of body scales, is great. The crowns of the scales have simple crenulations in head (oral and some cephalopectoral) scales and, generally, high platforms with an ornament of lateral ridges in most body scales; scales referred to *Boreania* Karatajute-Talimaa 1985 are overall smaller and simpler in outline. The dentine encloses numerous straight dentine tubules which converge into one or up to three pulp cavities opening onto the base. Basal projections are common.

Regarding the genus *Australolepis*, the discovery of many new turiniid scale forms in Australian Lower and Middle Devonian rocks, some of which closely resemble *A. seddoni*, makes the generic distinction with *Turinia* Traquair 1896 less clear. One of the main features used to diagnose *A. seddoni* was the large wide open pulp cavity and fragile, deeply-dissected crowns. This scale form has now been found in samples with typical *T. australiensis* and other turiniid scales in central Australia. Young scales (in the growth range of one individual) always have a large wide-open pulp cavity; in fact such scales are only thin caps of dentine. What we see in *A. seddoni* and some of the other Australian turiniids may be neoteny in the squamation morphogenesis, so that occasionally older scales (in the growth series and stratigraphically older turiniids) can retain a wide open pulp cavity and do not acquire thick tumescent bases.

Genus *Turinia* Traquair 1896

Type species: *Turinia pagei* (Powrie 1870)

Diagnosis: Large thelodonts, at least 400 mm long, with a wide cephalothorax up to one quarter body length, which are slightly dorsoventrally-flattened with rounded anterior margin, and terminal or subterminal mouth. Slim triangular pectoral fins lateral to the cephalothorax have rounded posterior tips. Eyes are anterolateral. Eight pairs of branchial structures open venterolaterally on the cephalothorax. The post-pectoral trunk is fusiform. The tail is hypocercal or only slightly asymmetrical, apparently with rounded fin lobes. The squamation is complex with a wide range of scale variation and size (0.5–3.5 mm). Oral scales are rounded with crenulated or notched and ribbed crowns. Cephalopectoral scales are more elliptical, navicular and often asymmetrical. Postpectoral and other scales are navicular with lateral ridges and lappets or projections. Ribs under ventral crown surface posterior to the base common. Scale crowns are usually large relative to the base. Neck, moat-like with ornament of riblets or lappets common. Long anterior basal spur or projection developed on many scales. Pore canals can penetrate scales. The dentine tubules which tend to anastomose in mid-course may be enlarged at the junction with the pulp cavity. Small side lobes can occur within the pulp cavity. There are usually one, and up to three, long pulp canals (sometimes branched) and the same number of pulp openings which can occur on the side of the base. Upper Silurian (Ludlovian?) to Upper Devonian (lower Frasnian).

Remarks: Apart from the type species, *T. pagei* (see Turner 1976, 1982), other species are known only from scales; these are *T. australiensis* Gross 1971, *T. polita* Karatajute-Talimaa 1978, *T. hutkensis* Blieck & Goujet 1978, *T. pagoda* Wang, Dong & Turner 1986, *T. fuscina* Turner 1986, and *T. gondwana* Turner in Gagnier *et al.* 1988. '*T.*' *asiatica* Wang 1984 is not regarded as belonging to the genus. Oral scales from these species, as in all other thelodont genera, are remarkably similar, having simple rounded crowns with a smooth rounded top and crenulated edges which usually extend down to the neck. Those in *T. australiensis* (Turner *et al.* 1981) have very low crowns and almost no neck, but this distinctive feature may not be unique to this species; similar scales from Europe, which Turner compared to *T. australiensis*, have been referred to the species *Boreania minima* Karatajute-Talimaa 1985. Specific distinctions depend on morphology of a range of scales, especially post-pectoral scales, which can exhibit much variation.

Turinia antarctica sp. nov.

Figs 2–10

1921, 'Selachii(?)' 'primitive Ostracoderm or selachian dermal tubercles', Woodward, p. 56, Figs 14–22.
1950 '(?) Selachii (Dermal Tubercles)', Gross, p. 72
1964 'primitive ostracoderms or to elasmobranchs' 'probably psammosteid', Tarlo, p. 91.
1968 'supposed selachian dermal tubercles', White, p. 9.

1981 'probably thelodont scales', Young, p. 239.
1986 *Turinia* sp., Grande & Eastman, p. 113.
1986 *Turinia* sp., Turner, p. 58.
1986 turiniid, Wang, Dong & Turner, p. 315.
1987 'thelodonts', Halstead, p. 9.
1987 'thelodont agnathans', Young, p. 46.
1988 'turiniid thelodont scales', Young, pp. 12–17, text-figs 17–18, pl. 1, figs 4–6; pl. 3, figs 3, 5, 8–9.
1988 *Turinia* sp., Turner in Gagnier *et al.*, p. 280
1989a 'turiniid thelodont scales', Young, p. 21
1989b *Turinia* sp. nov. - 'turiniid thelodont scales', Young, p. 52–53, table 1, fig. 4C.
1989 'turiniid thelodontids', Long, p. 45.
1989 *Turinia* sp., Eastman & Grande, p.242.
1991 *Turinia* sp. nov., Young, p.543, fig. 15.

Material: Abundant scales, of which several hundred have been examined in detail, from the following list of specimens: NHM P.12561–562, P.12589, P.12590.1 [P.12590.2 was figured by Woodward (1921, fig. 33), as a palaeoniscoid scale], P.40678; AF 110, 120, 132, 139, 141, 149, 157–159, 162, 168, 170, 171, 173 175, 177, 242, 262; JK 102, 103; CPC 26411–415, 28588–614; AMF 54354, 459b, 55904, 55911; PF 9600–602.

Types: Material from Mount Fleming (Figs 3–7). Scale morphology varies on one individual, so nominating a single scale as holotype is not feasible.

Localities and Horizon: From the Aztec Siltstone at Granite Harbour (locality 2, Fig. 1), horizon unknown (NHM specimens); Mount Fleming (locality 4, Fig. 1), probably 61 m below the top of the Aztec Siltstone (PF 9600-602), unit 17, section H6 of Barrett & Webb (1973), 62 m above the base of the Aztec Siltstone (AF 110-177), and about 10 km east of Mount Fleming, horizon unknown (JK 102, 103); Mount Crean, Lashly Range (locality 8, Fig. 1), collecting sites MC1 (AMF 54354, 55904, 55911), MC 3 (CPC 28591) and MC 4 (CPC 26411-415, 28588-590) of Young (1988, fig. 4), also AF242, 249, 262, assumed to be within the lower 80 m of the Aztec Siltstone (section L2 of Askin *et al.* 1971); Portal Mountain (locality 12, Fig. 1), unit 4 of section P1 of Askin *et al.* (1971) (CPC 28592–614); Boomerang Range (locality 19, Fig. 1), basal 5 m of section 5 of Barrett & Webb (1973) (AMF 54459b).

Diagnosis: Scale species *sensu* Turner (1976); thelodontid with large scales up to 3.0 mm. Scales from oral region rounded with up to 14 crenulations subdivided by wide to narrow troughs. The crown tops can be planar. The crown ribs extend from the neck groove nearly onto the mid point of the rounded crown surface. Cephalopectoral scales are similar but rounded anteriorly and more angular to posterior; bases are as big as crowns and can be deep and straight-sided with an anterior process angled downward. Trunk scales (postpectoral) are long, and relatively high, with the crown and base elongated in the horizontal plane. The anterior

crown rim is generally divided into three or four doubled-ribbed sections; rarely it is expanded forwards and downwards into an anterior crown prong. The crown tends to expand outwards and backwards from the narrow neck-base interface. It is flattened with a central raised portion of elliptical shape, usually made up of three or four ribs with shallow troughs between; small riblets may be found at the anterior rim of the crown. The posteriormost tip of the central platform may be placed about one-third to one-half of the way down the crown where it converges with the raised edges of the one to three lateral segments; the tip may elongate into a small ridge which extends to the posterior end of the crown. One to four pairs of narrow lateral flanges flank the mid portion separated by relatively wide troughs. Major crown ribs are often subdivided with narrow troughs and ornamented with small tubercles. On the ventral side of the crown there are further, usually five to ten, subdivided ribs, the median pair of which flanks the posterior tip of the base. A smooth neck region surrounds the anterior crown with a wide trough. The crown in some scales is high and slender at the crown-neck interface then curves posteriorly. The base in body scales is usually wider than the crown; typically it is elongated in the horizontal plane into one (or rarely two) long anterior processes which may be up to half scale length and which may extend forwards and down. The pulp cavity is also elongated tending to form a long elliptical or slit-like, and rarely a keyhole shaped opening in the posterior part of the base.

Remarks: The scales of this species share many features, particularly in the tiered complexity of their crowns, with those of *Turinia gondwana* of Bolivia, with some scales from the Cravens Peak Beds of western Queensland (Turner *et al.* 1981, Turner 1986, fig. 3K), with some of *Turinia hutkensis*, and with scales from New South Wales described as *Turinia* sp. cf. *T. hutkensis* by Young & Gorter (1981). With the latter they also share the tendency (seen in the Granite Harbour examples) to produce small scales that are cruciform in section. The subdivided ribbing on the crowns is also seen in *Turinia pagoda* and *Turinia hutkensis* (though in the latter species the ridges and troughs seem more rounded and wider) and in turiniid scales from South Australia (Long *et al.* 1988). The high and narrow set of the crown on the neck and base and the angular bend and expansion posteriorly of the crown in some scales are features shared with *Turinia pagoda* and a scale from Thailand (horizon uncertain but might be Lower or Middle Devonian, Blieck *et al.* 1984), with turiniid scales from the lower Eifelian of north-east Iran (Turner & Janvier 1979), and to some extent in *Turinia gondwana*, as well as with turiniid scales from New South Wales and South Australia (Young & Gorter 1981, Long *et al.* 1988). However, the scales of *Turinia antarctica* are differentiated by the relatively greater complexity of the crown ribbing, especially the wide expansion of double-ribbed sections on the posterior crown, with extra ribs and flanges more apparent, and in the presence of tuberculated ribs seen clearly on many crowns.

The relatively good preservation of the scales, with few broken and with fragile crown peaks intact, suggest little transportation after death. Scales at some localities seem to be all of the same growth generation, with bases and pulp cavities of about the same level of development. These might have come from only a few individuals, bearing in mind that each thelodont had a possible squamation of several thousand scales at any one time in its life (Turner 1991).

Description

We deal first with Woodward's specimens, even though better material is now available from other localities. Woodward's illustrations (1921, pl. 1. figs 14–22) are reproduced here as Fig. 2. One oval specimen (Fig. 2b) 'bears a trace of three prominences or flutings on one side', and a smaller rhombic scale (Fig. 2c) 'exhibits a fluting or sinuosity on two contiguous sides'. Both of these specimens are comparable with cross-sections of turiniid head scales which in all species are very similar (see e.g. Karatajute-Talimaa 1978). The specimen in Woodward's fig. 16 (Fig. 2e) is a
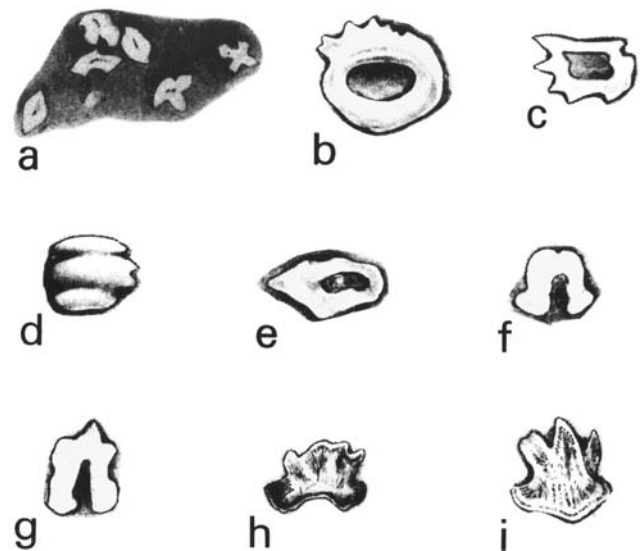

Fig. 2. *Turinia antarctica* sp. nov. Reproduction of original illustrations from Woodward (1921, pl. 1, figs 14–22); **a.** sagittal and transverse sections of NHM P. 12561; **b.** oblique section of possible head scale, NHM P. 12589; **c.** transverse section of possible cephalopectoral scale, from NHM P. 12561; **d.** dorsal view of crown of trunk scale, NHM P. 12561; **e.** transverse section through base of trunk scale, NHM P.12590.1; **f.** sagittal section of possible transitional scale, NHM P. 12561; **g.** sagittal section of trunk scale, NHM P. 40678; **h.** thin section of trunk scale, NHM P. 12562; **i.** thin section of trunk scale, NHM P. 12562. Note that **b–c** and **e–g** show the typically large pulp canal and cavity of turiniid thelodontids. All approximately the same size as illustrated by Woodward - **a,b** x 6; **e** x 12; **c, h–i** x 14; **d, f–g** x 15.

turiniid trunk scale in sagittal section. Of specimens shown in vertical section (Figs 2g, f–i), the last two show nicely the curving remnants of Sharpey's fibres in the base as well as the simple branching dentine tubules which are typical of most thelodontid scales. Two of the scales in his fig. 19 (Fig. 2a) do not have typical turiniid scale outlines but rather those of more specialized scales with deeply indented crowns seen in some advanced turiniids (e.g. Turner et al. 1981, Young et al. 1987); the other four show transverse sections through the base and one vertical section, Fig. 2d shows the upper rounded surface of crown in part with 'a large median lobe and two comparatively small lateral lobes'. Woodward thought this specimen, particularly, suggested a compound scale, such as occurs in Cladoselache.

Woodward described thin sections of the scales with 'only a slight trace of the obliterated pulp cavity', but, the pulp cavity is apparent in most of the figured scales (Fig. 2a–c, e–g). Woodward stated (1921, p.57) that 'the microscopic

structure is typically Elasmobranch ... each large cusp showing a trace of an original pulp-cavity from which fine calcigerous tubes radiate to the periphery, while coarse tubes diverge into the upper part of the base, and the lower part of the base exhibits only a concentric structure'. Fig. 2i portrays the vertical section through the anterior end of a turiniid body scale with a tripartitite crown; the 'cusps' are not fused nor are there traces of a tripartite pulp cavity. The microstructure is certainly not typical of elasmobranch scales, which normally have one or more neck canals, a relatively high and narrow neck and, usually, a rhombic base. None of these features is apparent in the scales figured.

Woodward tentatively referred some scales to Cladoselache because the crowns were lobed. However, no histological work had been done on this genus at that time for comparison (Dean 1909), and, as discussed above, the only published section of a Cladoselache scale is unlike the Antarctic material. Cladoselache scales are more complex, being multicuspid and composite (Zangerl 1981). In their simple outlines, histological structure of simple orthodentine cap and basal tissue free of cells or cavities, and in the absence of neck canals, the Granite Harbour scales are typically thelodontid.

Of the more recent collections, those from Mount Fleming (Figs 3–7) are best preserved, mostly as detailed natural moulds in sandstone or siltstone, and illustrate the total morphological range of the species. Other material is dealt with by locality. Associated with the turiniid scales from Mount Fleming are shark scales, like those of Antarctilamna described by Young (1982), and an unusual ornamented complex scale or plate that might belong to a chondrichthyan (Young & Turner 1990).

Samples presumably collected in the 1960s (see above) include three pieces of grey sandstone (PF9600-9602, designated as 'Beacon Sandstone') containing thelodont scales preserved either as friable, cream-coloured broken scales, or as natural moulds within the quartzitic sandstone. There are oral, cephalopectoral and trunk scales (Fig. 3). Oral scales tend to have deep bases when seen in side view (Fig. 3b–c). The rounded crown has four or more rounded ribs which may be subdivided (Fig. 3b). The anterior base may be enlarged (Fig.3b). A well-preserved cephalopectoral crown (Fig. 3a) shows a wide crown with a rounded triangular central section narrowing posteriorly, with minor riblets anteriorly. Two deep grooves on either side are flanked by lateral lappets which in turn bear two lateral spurs seen on the left side. The trunk scales are of various kinds presumably from postpectoral, precaudal and pinnal regions (sensu Märss 1982). Many exhibit anteriorly-displaced bases and long anterior basal spurs which may be downturned at the distal tip (Fig. 3d). Some crowns are tricuspidate or with lateral spurs elongated posteriorly and separated from a narrow central region by deep troughs (Figs 3e, g). Others have many lateral spurs or ventral crown riblets (Fig. 3f). All have large pulp openings and a large pulp canal extending well
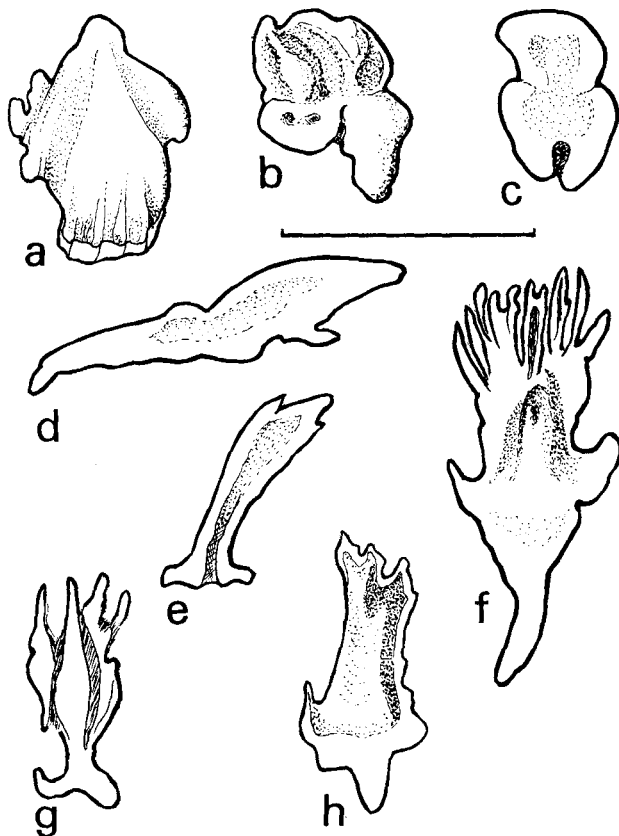

Fig. 3. Turinia antarctica sp. nov. Scales from Mount Fleming (from PF 9600, 9602); a. crown of cephalopectoral scale PF9600. 1; b. oral or cephalopectoral scale in lateral view PF9600.2; c. cephalopectoral scale in sagittal section PF9602.1; d. trunk scale in transverse section PF9602.2; e. pinnal? scale in sagittal section PF9602.3; f. trunk scale in transverse section PF9602.4; g. crown and neck of trunk or precaudal scale PF9602.5; h. cephalopectoral or trunk scale in oblique section PF9600.3. Scale bar = 1 mm.
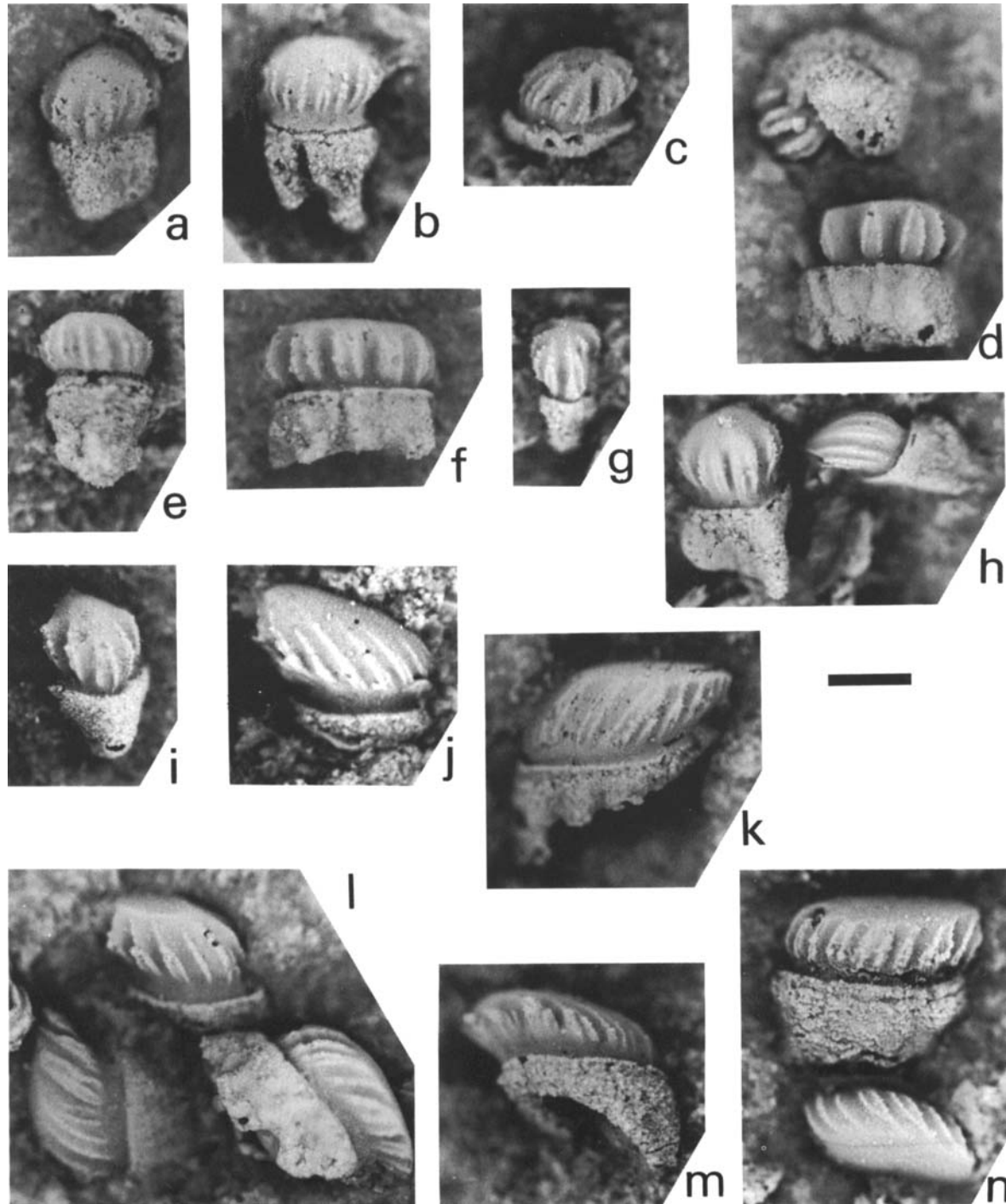
Fig. 4. *Turninia antarctica* sp. nov. Head and transitional scales from the cephalopectoral region. Mount Fleming (all from AF168). **a. b.** oral/head scale in anterior view, AF168. 1–2; **c.** oral/head scale from anterior showing planed off crown tip, AF168.3; **d.** oral/head scale in lateral view clearly showing tuberculated ribs, AF168.4, possible head scale above, AF168.5; **e.** oral/head scale in lateral view, AF168.6; **f.** oral/head scale in lateral view, AF168.7; **g.** oral/head scale from anterior, AF168.8; **h.** oral/head scale in lateral view clearly showing tuberculated ribs, AF168.9 (left); pospectoral trunk scale to right, AF168.10; **i.** transitional (cephalopectoral of Märss 1982) scale to right, AF168.11; **j.** cephalopectoral scale from anterior, AF168.12; **k.** cephalopectoral scale in lateral view, AF168.13; **l.** three cephalopectoral scales in lateral view, upper one showing planed off crown, AF168.14-16; **m.** cephalopectoral scale from posterior basolateral view, AF168.17; **n.** two cephalopectoral scales in lateral (upper) and crown (lower) views showing planed off crown in upper, AF168.18-19. Scale bar = 0.5 mm.
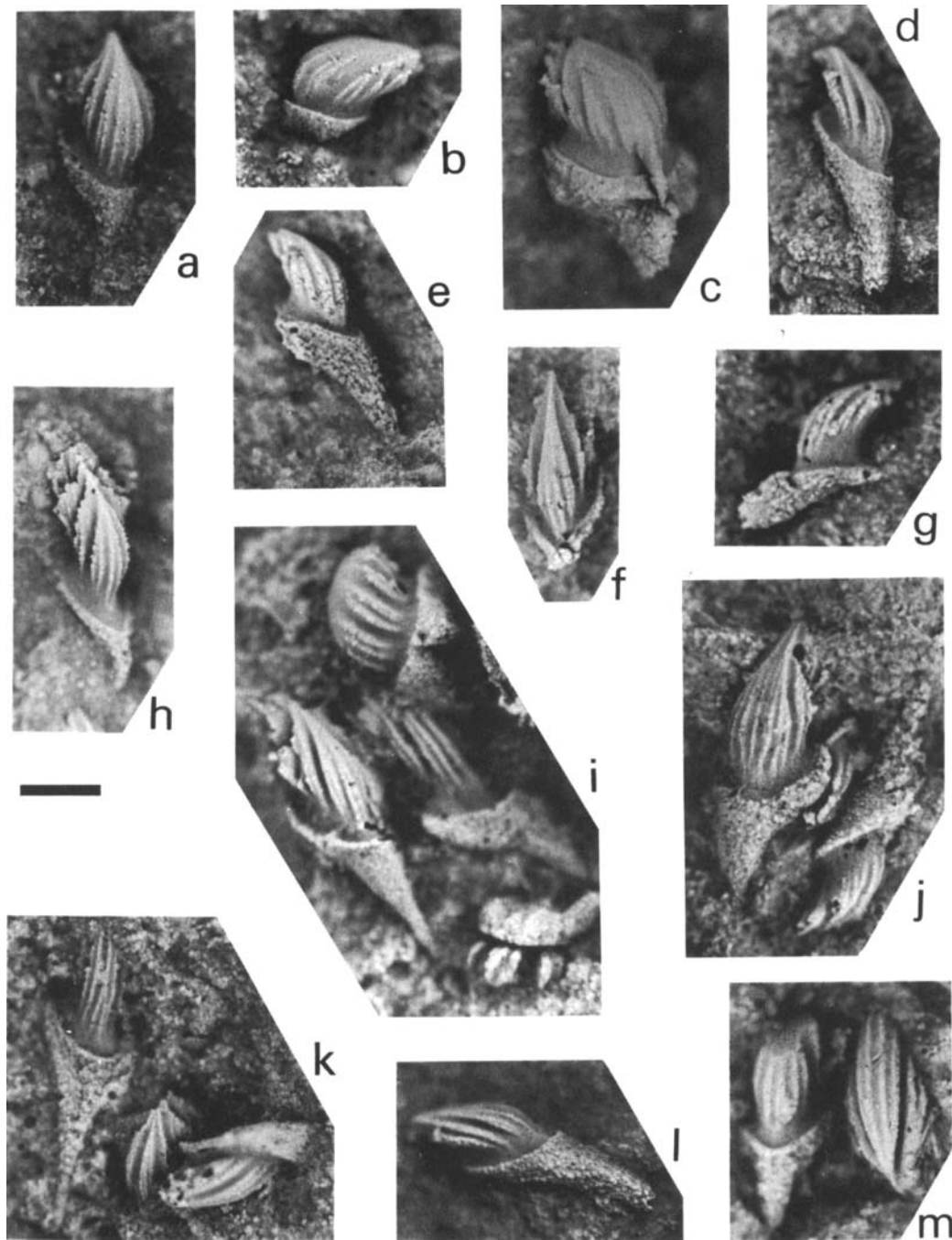
Fig. 5. *Turinia antarctica* sp. nov. Postpectoral and possible pinnal or precaudal scales. Mount Fleming (all from, AF168).
a. postpectoral scale in anterior view, AF168.20; **b.** cephalopectoral? or postpectoral scale in lateral view, AF168.21;
c. postpectoral scale in anterior view showing unique anterior crown spur, AF168.22; **d.** postpectoral scale in lateral view, AF168.23; **e.** postpectoral scale in lateral view, AF168.24; **f.** precaudal? scale in crown view, AF168.25; **g.** postpectoral scale in lateral view, AF168.26; **h.** postpectoral or precaudal scale in anterior view clearly showing complex tiered crown with tuberculated ribs, AF168.27; **i.** postpectoral or precaudal scale in anterior view (left), cephalopectoral scales in lateral view (top and bottom), pinnal? scale in lateral view (middle right), AF168.28–31; **j.** postpectoral scale in anterior view (left), pinnal? scale in lateral view (middle), postpectoral scale in lateral view (right, upside down), AF168.32–34; **k.** pinnal? scale in anterior view (left), postpectoral scale crown in anterior view (middle), postpectoral scale in lateral view (right, upside down), AF168.35–37; **l.** postpectoral scale in lateral view, AF168.38; **m.** postpectoral scale in anterior view showing planed off crown (left), postpectoral scale crown (right), AF168.39–40. Scale bar = 0.5 mm.

into the scale (Figs 3c–f, h). The narrowness of the crown/neck interface is well shown in Figs 3e & g.

The scales illustrated in Figs 4–6 are selected from some 350 preserved as impressions on a single piece of greyish green siltstone (AF 168) which also contains remains of *Bothriolepis* (*B.* sp. indet. 3 of Young 1988, pl. 1, figs 4,5), acanthodians, and a porolepiform rhipidistian scale (Young *et al.* In press). Thelodont scales are scattered around the larger fossils; most are aligned parallel with the long axis of the bothriolepid plate, with others at right angles. Smaller scales (less than 0.5 mm) are rare; one such oral scale is shown in Fig. 7b. Typical turiniid oral scales with a circular outline are seen in Figs 4a–g. In these, 7–14 main ribs around the crown rim are usually subdivided by narrow grooves and separated by deeper troughs. The tuberculated ribs are shown clearly in Figs 4a, c–g. The bases of these scales are usually deep and may be elongated in the vertical plane (Figs 3b, e & g).

The more common cephalopectoral scales (Figs 4 h–n) are relatively high, with an elongate oval crown having a rounded anterior border coming to an angular posterior point. The 12–14 subdivided ribs on the crown extend from the top down to the neck-base interface. The ribs are often split in midsection (Fig. 4l). Rib tubercles are shown in Figs 4 h & k. The bases are generally smaller than the crown but can be elongated into an anterior process which tends to be angled downwards (Figs 4k & m).

Large, elongate trunk scales are most common (Figs 5, 6c–f, 7f–i). The crown and base are usually elongated in the horizontal plane (e.g. Figs 5d, i, k–l). The crowns expand outwards and backwards in many scales (Figs 5c, h, i, 7f–i) with multidigitate lappets common (Figs 5d, 7d, f–i). Tricuspidate forms, possibly precaudal scales, are shown in Figs 5f & 5m. As a consequence of elongation, the neck-base interface has become narrow in some scales, possibly typical of the pinnal region (Figs 5g, k). Possible pinnal scales also have narrow crowns with finer ribbing (Fig. 5k (left), 7e). The complex crown structure is seen in most well-preserved scales. There is a central raised portion of elliptical or triangular shape with three to five main ribs which can be subdivided anteriorly (Figs 5a, c–d, f, h–m, 7c–d, g–i). In some scales the central platform ends in front of the posterior point of the crown where it can converge with the raised edges of the one or two lateral segments (Figs 5a, c, h, i, l, 7d). The posterior tip of the central platform may then elongate into a small ridge which extends to the posterior end of the crown (Figs 5 a, i, m). One specimen (Fig. 5c) has a median anterior process which extends forwards and downwards from the anterior crown rim over the neck/base interface. One (Fig. 5f) to four pairs of narrow lateral flanges (Figs 5c, h, i, 7h) flank the mid portion, separated by relatively wide troughs. Tubercles on the main ribs are shown in Figs 5 a, c, h. Complex anterior-posterior tiering of the crown is shown in Figs 5 c, i and particularly in 5h. The anterior crown is surrounded by a smooth wide trough (Figs 5a, c–m). The

base in most scales is shallow and placed well forward (Figs 5 d–e, g–m), often long and narrow with a long anterior process (Figs 5a, d–e, g–m) of up to two-thirds scale length (Figs 5d, k–l). Fig. 6 shows basal views of scales. Typical of oral scales is a rounded torus with a small central pulp opening (Figs 6a–b); trunk scales have commonly three to five, sometimes more, subdivided ribs on the ventral side of the crown, the median or median pair of which merges into the posterior tip of the base (Figs 6c–f). In some trunk scales, the pulp cavity is a long elliptical opening or trench in the posterior part of the base (Figs 6c–f). Subdivided anterior processes occur (Figs 6c (lower) & 7g).

Many scales from all regions have planar crown tops but especially oral and cephalopectoral scales (Figs 4 c, e, k–l, n (upper), 5m (left), 7a). This may denote scales from the underside of the body or from the ventral fin tips where abrasive wear to the erupted crowns could have occurred during life.

A range of scales from Mount Crean is illustrated in Figs 7j–l & 8. All scales in Fig. 8 are preserved as moulds on two hard sandstone samples which were etched in hydrochloric acid to prepare impressions of mixilateral and posterior ventrolateral plates referred to *Bothriolepis* sp. indet. 4 (CPC 26223, 225; see Young 1988, fig. 27B, pl. 5, figs 7, 8). Numerous less well preserved scales (in calcareous siltstone, so not acid-etched) occur in other Mount Crean samples, for example associated with *Bothriolepis kohni* from MC1, and with *B. askinae* from MC3 (e.g. Young 1988, pl. 3, figs 3, 5).

Among the illustrated examples, cephalopectoral scales (Figs 7j–k, 8c–d, f–h) show the same general features as those from Mount Fleming. In some, the troughs (Figs 7l, 8h) seem deeper giving a 'Christmas tree' effect. The subdivided ribs of the crown in Fig. 8d appear to develop small swellings at the mid point. Trunk scales show the deep trough around the crown (Fig. 8a) with the long anterior process and crown in a single plane (Figs 8b, e). One trunk scale (CPC 28590) shows a rudimentary three-tiered crown (Figs 7g, 8g). Except for CPC 28588 (Fig. 8d), most of these scales lack clear tuberculation along the ribs; they may have been abraded, since they occur in a coarser matrix than those just described from Mount Fleming.

Scales from Portal Mountain (Fig. 9) are preserved in a fine calcareous siltstone matrix; they have been partly exposed by mechanical preparation. In overall morphology they are typical of turiniid scales and several are very similar to cephalopectoral scales of the type species, *T. pagei*, figured by Ørvig (1969, fig. 2). Scales (Fig. 9b) with anterior basal elongation and subdivided bases (Fig. 9d) are found. One cephalopectoral scale (Fig. 9f) has a large, diamond-shaped flat crown with a crenulated margin; the base is largely obscured by matrix. Another (Fig. 9e) has a gently convex crown surface with five anterior ribs on the central portion and two pairs of lateral ribs. Another (Fig. 9c) is a large navicular scale with a convex surface, the base partly broken

and obscured by matrix.

Other less well-preserved examples from unit 4, section P1, of Portal Mountain include oral, cepholopectoral and trunk scales, which exhibit various features described above from other localities. Typical turiniid head scales (e.g. CPC26592, 595–598, 600–601, 605) include some with rounded tops (CPC26592, 26601), crowns with simple undulating ribbed outlines and with the ribs bifurcating towards the outer rim (CPC26600), ribs extending down to a shallow neck groove (CPC26595), or an ascending crown surface seen in lateral profile with acutely angled lateral ribs (CPC26596–7). The anteriorly-placed bases have long or bifurcated anterior processes (CPC26598, 26605). Some resemble the tricuspidate crown form illustrated in Figs 3g or 5j.

The most southerly known occurrence of *T. antarctica* sp. nov. is a single scale (Fig. 9g) from the Boomerang Range (locality 19, Fig. 1), preserved on specimen AMF 54459, an articulated but incomplete osteolepid (see Young *et al.* In press, Fig.19B). This small scale (crown about 0.5 mm long), which could be an oral or pinnal scale, has six ridges converging to a point on the anterior central portion, with a pair of lateral ribs posterior to this (Fig. 9g). The base is obscured by matrix. There is no evidence that it is not conspecific with scales described above from the northern localities.

None of the scales from Portal Mountain or the Boomerang Range shows the fine tuberculations and subdivided ribs and lappets seen in scales from Mount Fleming and Mount Crean. This is attributed to poor preservation. The similar overall morphology observed from all localities prompts us to regard all the available material as belonging to one new species.

Histology and morphogenesis

The scales exhibit typical thelodontidid histology (*sensu* Gross 1967). Thin sections of scales from Mount Crean (Fig. 10) show typical orthodentine with fine dentine tubules directly radiating from the pulp canal with fine bunches at their distal ends. On the outer surface is a thin clear enameloid layer. Proximally, the dentine tubules tend to coalesce and be funnel-shaped (Fig. 10a, c), a feature seen in some other advanced thelodontidids (e.g. Karatajute-Talimaa 1978). The base is formed of clear aspidin-like tissue

Fig. 6. *Turinia antarctica* sp. nov. Ventral view showing base of scales. Mount Fleming (all from, AF168). **a. b.** oral scale with deep base, AF168.41-42; **c.** two postpectoral scales with elongate anterior basal spurs, bifurcate in lower, AF168.43-44; **d.** postpectoral scale with elongate rather flattened base, AF168.45; **e.** two postpectoral scales with elongate bases, right in lateral view, AF168.46-47; **f.** pospectoral scale with narrow elongate anterior basal process, AF168.48. Scale bar = 0.5 mm.
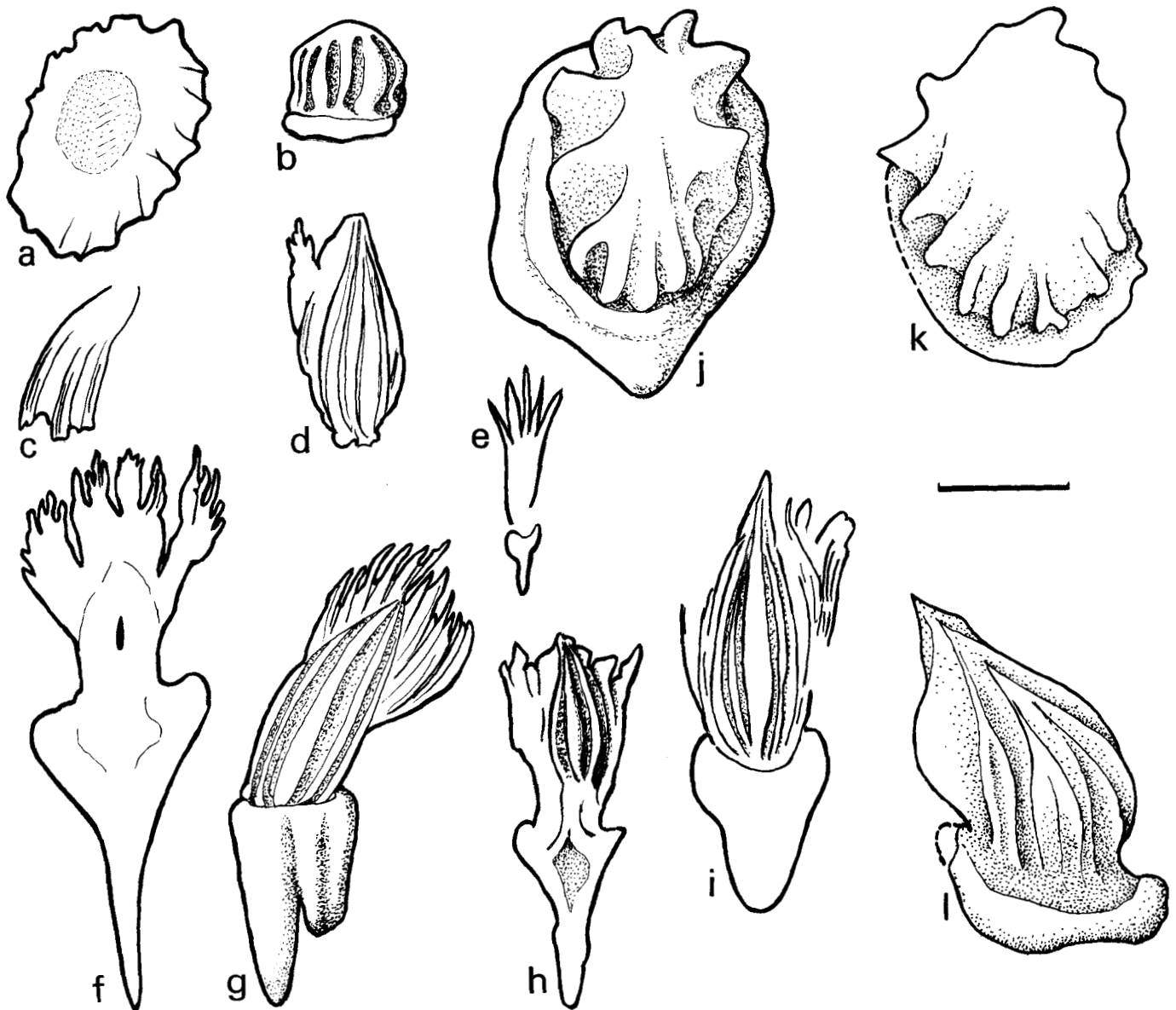
Fig. 7. *Turinia antarctica* sp. nov. Specimens from Mount Fleming (a–i, from, AF110, 139, 157, 170, 175), and Mount Crean (j, AF249, k, l with CPC 26225); **a.** head scale in crown view showing planed off top, AF175.1; **b.** oral? scale in lateral view, AF110b.1; **c.** detail of anterior crown of postpectoral scale in lateral view, AF175.2; **d.** detail of crown of postpectoral scale in dorsal view, AF157 (obverse).1; **e.** outline of pinnal? scale in dorsal view, AF139.1; **f.** postpectoral or precaudal scale in transverse section, AF110b.2; **g.** postpectoral or precaudal scale in dorsal view with transverse section of base, AF157 (obverse).2; **i.** postpectoral or precaudal scale in dorsal view, AF170.1; **j.** cephalopectoral scale in dorsal view, AF249.1; **k.** head or cephalopectoral scale in dorsal view, CPC28590.1; **l.** postpectoral scale in anterior view showing complex tiered crown, CPC28590.2. Scale bar = 0.5 mm.

penetrated by few tubules, which held Sharpey's fibres in life, particularly concentrated in the anterior process (Fig.10d). Neck canals, as would be found in shark scales, are absent. Growth lines can be seen in the cross section (Figs 10a–c).

Many of the scales described by Woodward show large pulp cavities (Figs 2b–c, e–g), also seen in some scales from Mount Fleming (Figs 3 d–e, h, 4k?, m, 6c, 7h) and at Portal Mountain (Fig. 9d). In most thelodontidid scales this would denote morphogenetically young scales (not necessarily from juvenile animals). In certain turiniids, however, especially those from younger horizons, there was a tendency to retain a large pulp cavity throughout the life of the scale. Then, although the base developed, the crown was left as a relatively thin structure. A single elongated pulp cavity placed well back on the base is a particular feature of several trunk scales. Most scales have deep or elongated bases suggesting that all came from the same generation of scale formation and possibly from animals of the same age. The
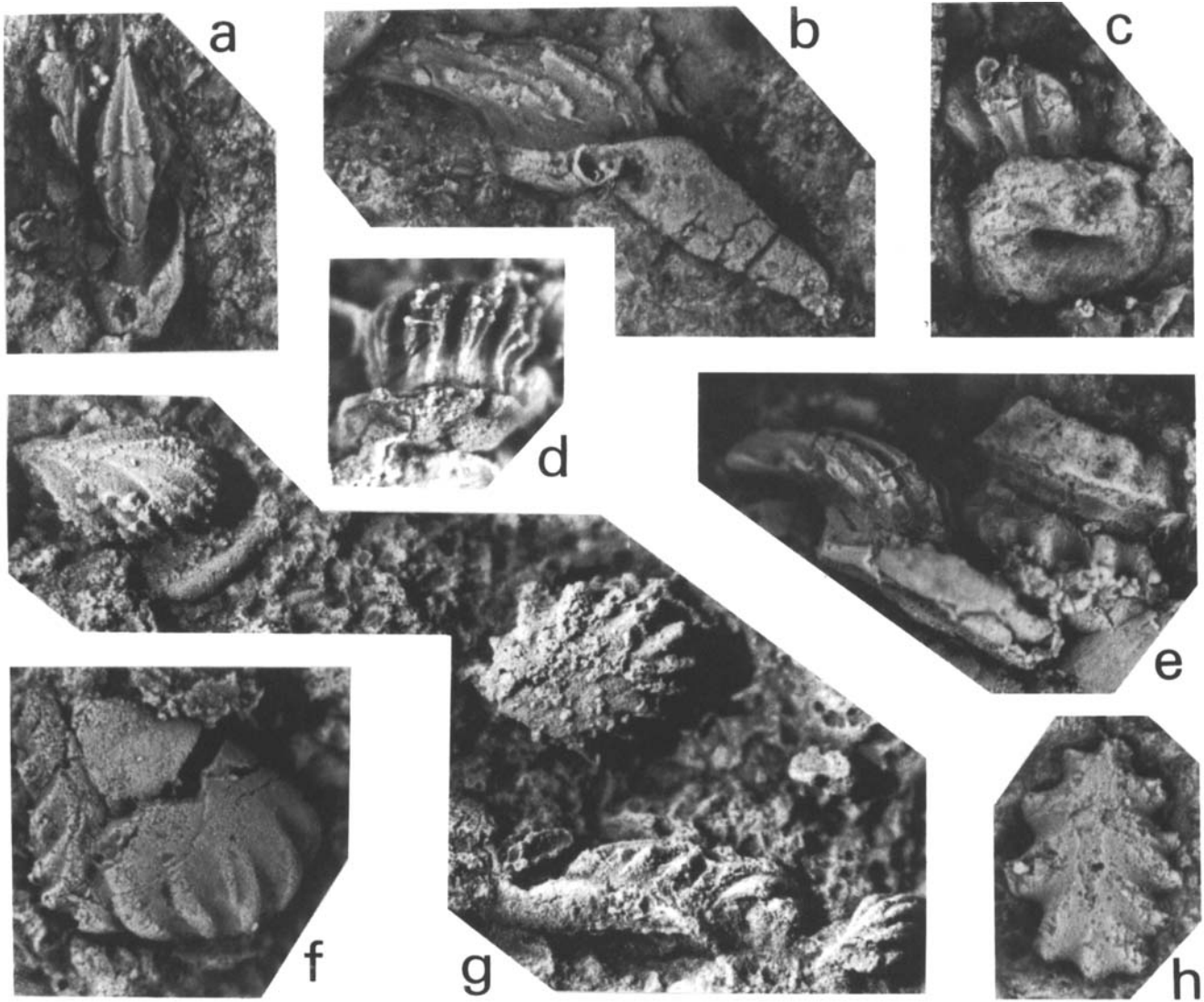
Fig. 8. *Turinia antarctica* sp. nov. Specimens from Mount Crean; **a.** precaudal? scale in dorsal view, CPC 26411; **b.** postpectoral scale in lateral view, CPC26412; **c.** head scale in lateral view, CPC 26413; **d.** cephalopectoral scale in lateral view, CPC 28588; **e.** postpectoral scale (left) and head scale (right, upside down) in lateral view, the latter showing a possible resorption feature of the neck/base interface, CPC 26414; **f.** cephalopectoral scale in anteriodorsal view, CPC 28589 **g.** three cephalopectoral scales (upper left anterodorsal, CPC 28590.2, middle upper crown and middle lower lateral views) and one oral or pinnal? scale (lower right) in crown view; **h.** oral or pinnal? scale in crown view, CPC 26415. Scale bar = 0.5 mm.

presence of incremental lines suggest growth over several timespans (years or seasons). One scale (Fig. 8e) shows a distinct groove below the neck-base interface, which appears to be a resorption feature, not previously noted in thelodont scales. This might be a pathological condition caused when the scale erupted through the epidermis and some infection occurred.

Discussion

Comparisons with other turiniid species

The new species resembles *T. hutkensis* from Iran, in the tripartite subdivision of the crown and in having secondary ridges on the primary. It differs in having sharp rather than rounded primary ridges, which are separated by wide rather than narrow grooves. The subdivision tends to be concentrated in the midpart of the main rib, a feature also seen in some scales of *T. gondwana*. Another difference from *T. hutkensis* is the tendency in *T. antarctica* to have a narrow lower part of the crown, which may either rise straight up from the base before inflecting back (e.g. Fig. 5g), or extend straight back in the same plane as the long anterior process (e.g. Figs 5l, m).

T. antarctica resembles some scales from the lower Eifelian Khush–Yeilagh Formation, Oriental Alborz, Iran, especially the posteriorly expanded scale referred to as '*Skamolepis*-like'
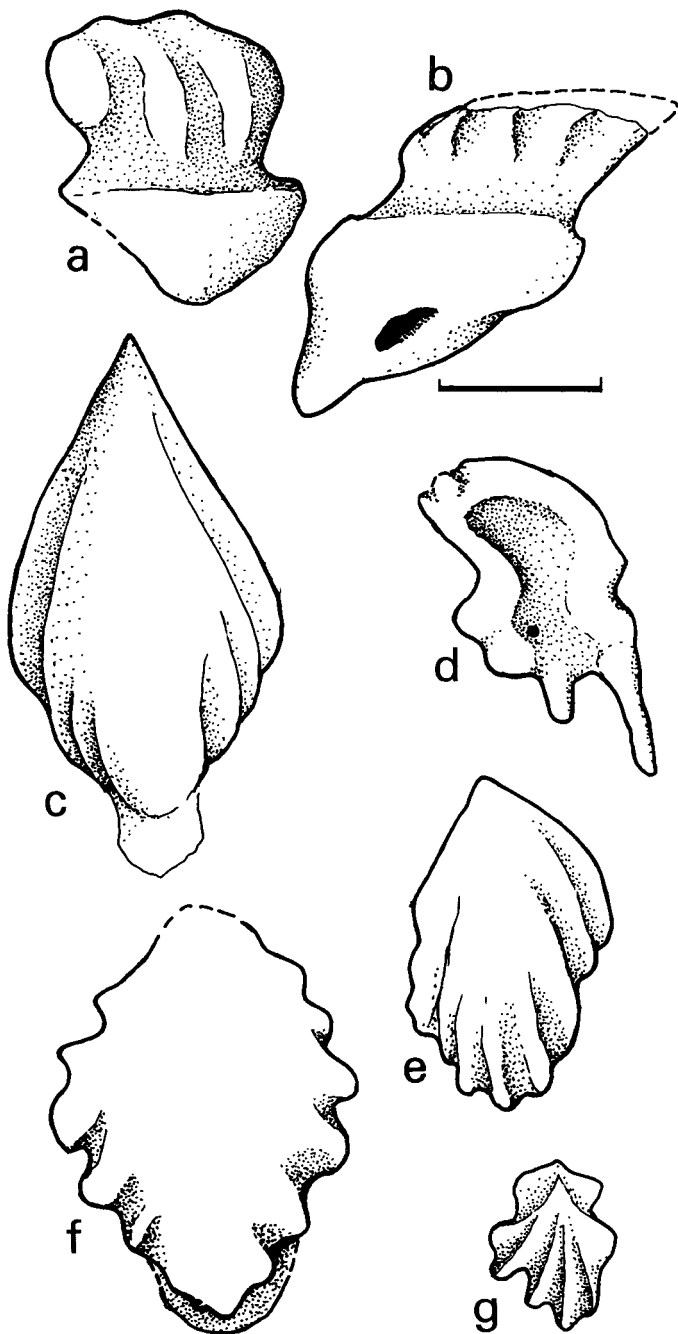
Fig. 9. *Turinia antarctica* sp. nov.? Specimens from Portal
Mountain (a–f) and Boomerang Range (g); **a.** head scale in
lateral view, CPC 28601; **b.** transitional/cephalopectoral or
just postpectoral scale in lateral view, CPC 28598; **c.** crown
of postpectoral scale in dorsal view, CPC 28613;
d. cephalopectoral? scale in sagittal section, CPC 28605;
e. crown of cephalopectoral scale in dorsal view, CPC28600;
f. cephalopectoral scale in dorsal view, CPC 28606; **g.** crown
of oral or pinnal? scale in dorsal view AMF 54459b.
Scale bar = 0.5 mm.

Fig. 10. *Turinia antarctica* sp. nov. Photomicrographs of
specimens in thin section from Mount Crean (CPC 28591); all
x 64; **a.** sagittal section of cephalopectoral scale with large
pulp cavity; **b.** transverse section of trunk scale showing
scalloped profile of crown and incremental lines in dentine;
c. sagittal section of trunk scale; **d.** sagittal section of trunk
scale with elongated anterior basal process.

by Turner & Janvier (1979, fig. 1). Similarities include the
horizontally-placed and elongated bases, large pulp cavities,
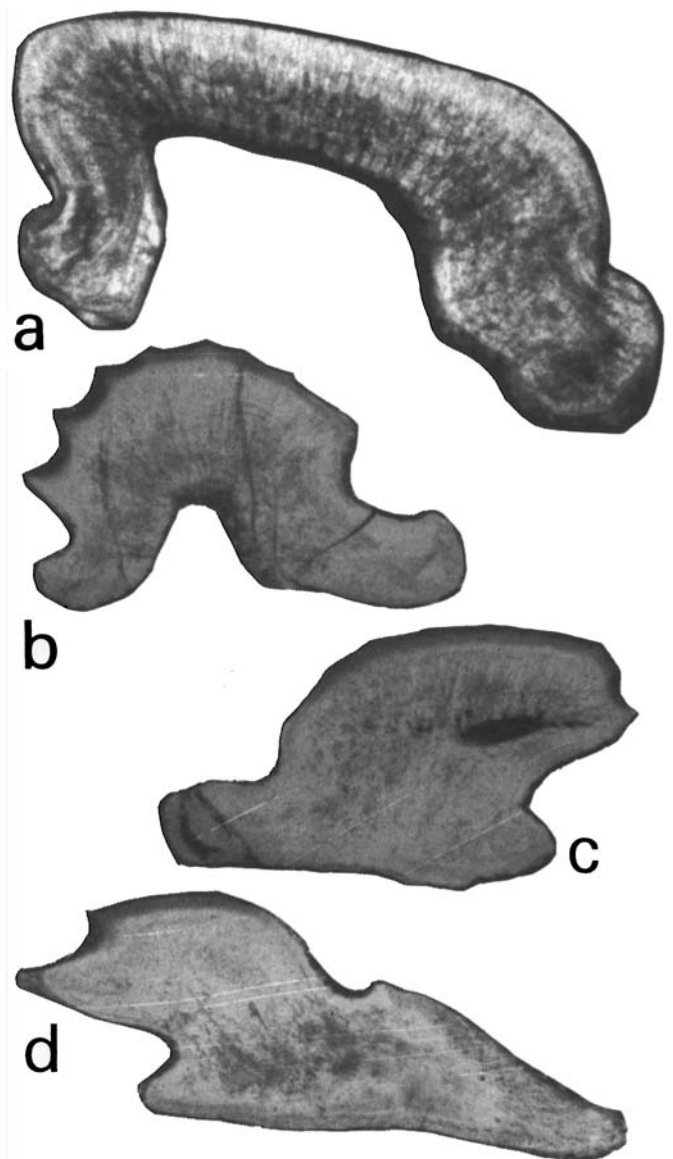a central ribbed portion to the crown, and the series of lateral

ridges and ventral crown ribs.

The tendency for a three-tiered crown is also seen in
T. gondwana, but this species has coarser and more rounded
ribs (Gagnier *et al.* 1988). Other resemblances to the
Bolivian specimens, which suggest that these two species
were closely related, include large size, extreme horizontal
elongation with long, often double anterior processes,
expanded crowns with bifurcated ribbing and foreshortened
midsection, and the elongation of the pulp opening in trunk
scales. However, in *T. gondwana* the crowns are less

complex, and the pulp opening invariably exhibits a keyhole-like shape, whereas in *T. antarctica* it is a simple elongation (e.g. Figs 6c–e).

Correlation within the Aztec Siltstone

Young (1988) erected a scheme of six biostratigraphic zones based on *Bothriolepis* species, with the lower two zones defined in part on association with turiniid scales. It was noted that these lower assemblages are only well known from northern localities (2,4,8,12, Fig. 1), whereas the upper three zones (*karawaka*, *Pambulaspis*, and phyllolepid zones) are documented only at southern localities (13–24, Fig. 1), where the fossiliferous horizons occur near the top of the sequence. Assuming that the zones were not diachronous, the suggested relative positions in the sequence of lower and upper zones was based on assessment of the length of the middle *portalensis* zone, only well documented at Portal Mountain. The proposed biostratigraphic zonation could be tested by new fossil discoveries at the southern localities from the lower part of the Aztec sequence, which should correspond to one or more of the lower biostratigraphic zones documented from the northern localities. The single turiniid scale of *T. antarctica* sp. nov. (AMF 54459b), subsequently identified from the lowest fossiliferous horizon in the Boomerang Range (locality 19, Fig. 1), now confirms the presence of a basal thelodont assemblage at southern localities. However, new collections containing antiarchs must be made to establish which of the two lowest zones in Young's scheme are represented.

Previous age assessment of the Aztec fish fauna

All expert opinion has agreed on a Devonian age for the Aztec fish fauna, but its precise age within the Middle-Late Devonian remains uncertain. Woodward (1921) first proposed a Late Devonian age, and Gross (1950) reached the same conclusion. White (1968, p. 6) suggested an age 'nearer the top of the Middle Devonian rather than the base of the Upper'. Ritchie (1969, 1975) added phyllolepid and groenlandaspid placoderms to the faunal list, and proposed a younger Late Devonian age. Young (1982) suggested correlations with south-eastern Australia based on sharks in the Aztec fauna, and now supported by the occurrence of the acanthodian *Culmacanthus* (Long 1983, Young 1989a). Young (1988, p. 19) noted the unique overlap of turiniid thelodonts and *Bothriolepis* at the base of the Aztec succession, suggesting an age as old as early Givetian. It is possible that most or all of the Aztec Formation is of Givetian age (Young 1989b), with the upper assemblage (phyllolepid zone of Young 1988) approaching the Givetian-Frasnian boundary.

A microflora, ascribed a Frasnian age by Helby & McElroy (1969), is the only other direct non-vertebrate evidence of age from the Aztec Siltstone. This assemblage is dominated by the spore *Geminospora lemurata*, for which Playford

(1983) suggested a biostratigraphic range from early(?) or middle Givetian to late Frasnian or (?) early Famennian. However, Balme (1988) has recently suggested an Eifelian-middle Frasnian range for this form, and both Richardson & McGregor (1986) and Streel *et al.* (1987) place the *lemurata* zone in the early Givetian. Another poorly preserved palynomorph assemblage from the Terra Cotta Sandstone member of the basal New Mountain Sandstone of the Taylor Group was assigned a Pragian–Emsian age by Kyle (1977), and provides a provisional maximum age constraint for the Aztec assemblage. The palynomorph assemblage occurs only 80 m above the base of the sequence at Table Mountain, where only the lower 240 m of Taylor Group sediments are preserved. However, some 900 m of section separates this horizon from the Aztec fish fauna (composite figure based on thicknesses given in McKelvey *et al.* 1977).

New evidence of age provided by Turinia antarctica sp. nov.

Scales of *T. antarctica* sp. nov. only occur in the lower part of the Aztec succession and, as previously discussed (Young 1988, 1989a, b), this evidence implies an early appearance for the associated placoderms, *Bothriolepis* and *Groenlandaspis*, both of which are recorded from near the base of the Aztec Siltstone. This situation can be compared with Eifelian occurrences of *Bothriolepis* in China (e.g. Pan 1981), the association of a bothriolepid with turiniid scales from the ((?)Eifelian–Givetian) Hatchery Creek fauna of New South Wales (Young & Gorter 1981), and the diversity of Early–Middle Devonian groenlandaspids in western New South Wales (Ritchie 1975). Young (1988) concluded that a lower limit (within the Middle Devonian) for the age of the Aztec fish fauna could not yet be established, and the new thelodont evidence presented here supports an older age.

Similarities between *T. antarctica*, *T. gondwana* from Bolivia, and the turiniid scales from north-eastern Iran discussed above, suggest close links between these faunas. In the Iranian section a bone-bed just below the thelodont-bearing layer (KH2 of Blieck *et al.* 1980, K2 of Goujet & Janvier 1984) contains a rich vertebrate fauna of placoderms (holonematids, groenlandaspids, a pachyosteomorph resembling *Leptosteus*, coccosteids, an arctolepid, a petalichthyid or phlyctaeniid, the antiarch *Hyrcanaspis*, ptyctodont tooth plates), acanthodians including *Gyracanthus* spines, elasmobranch spines, a dipterid, onychodontids, holoptychiids, and osteolepids (Blieck *et al.* 1980, Janvier & Pan 1982). The chondrichthyan spine (Blieck *et al.* 1980, pl.1, fig. 20) resembles those of *Antarctilamna* described by Young (1982, fig. 5) from Antarctica and south-east Australia, and recorded in Bolivia by Gagnier *et al.* (1988). A vertebrate fauna about 20 m above the thelodont-bearing layer in Iran was considered to be Eifelian or early Givetian by Goujet & Janvier (1984); charophyte oogones and poorly-preserved conodonts associated with the thelodonts were regarded as

late Emsian-Eifelian by Hamdi (Goujet & Janvier 1984, Young 1987).

T. gondwana from Bolivia (Seripona) occurs in a bone-bed assigned by Gagnier *et al.* (1988) to the upper part of the Catavi Formation, previously regarded as Upper Silurian on sedimentological evidence. Gagnier *et al.* (1988) suggested a late Early or early Middle Devonian age on the vertebrate evidence. The overlying beds, provisionally referred to the Santa Rosa Formation, were said to contain Devonian palynomorphs. The top of the Seripona sequence has a fauna similar to that from the Emsian-Eifelian Icla Formation (Gagnier *et al.* 1988, pp. 271, 272). Subsequently, Gagnier *et al.* (1989) presented new evidence that the bone-bed containing *T. gondwana* represents the lowermost part of the Santa Rosa Formation, from which chitinozoans suggest a Lochkovian-Pragian age. However, of at least 11 vertebrate taxa in the Bolivian fauna, only three are common at generic level to the Aztec fauna (*Turinia*, the shark *Antarctilamna*, and the acanthodian *Gyracanthus*, which may be related to *Gyracanthides* from the Aztec fauna). The latter is the only climatiid acanthodian in the Aztec fauna, whereas the Seripona fauna also contains several new species referred to *Climatius*, the ichnacanthid *Gomphonchus*, and *Nodonchus*, *Onchus*, and *Sinacanthus*. The other acanthodians from the Aztec fauna are diplacanthids (*Antarctonchus*, *Byssacanthoides*, *Culmacanthus*), and not closely related to the Seripona acanthodians. Add to this the placoderms (the most abundant fossils in the Aztec fauna, but not yet known from Seripona) and osteichthyans (palaeoniscoids, dipnoans, and several rhipidistians) which occur in the lower part of the Aztec Siltstone, and it is clear that the differences between the two vertebrate assemblages are substantial. The differences may be due partly to environmental conditions - the associated bivalve *Palaeoneilo* at Seripona suggested a tidal marsh environment to Gagnier *et al.* (1988), whilst the Aztec Siltstone is regarded as a braided stream deposit by McPherson (1978). The apparent close relationship between the *Turinia* species in the two faunas might indicate that these represent a non-marine component.

Younger thelodonts (*Australolepis seddoni*) from a marine assemblage in the Givetian-Frasnian Gneudna Formation of Western Australia (Turner & Dring 1981) are of different morphology and may represent a separate species lineage (cf. Goujet *et al.* 1984, who initially suggested similarities between the Seripona *Turinia* and *A. seddoni*). If, as previously suggested, the Aztec turiniid represents the youngest known occurrence in a non-marine deposit, then by comparison with the Seripona assemblage, we suggest that this turiniid morphotype was long-ranging, compared to other elements of the faunas, with the exception of antarctilamnid chondrichthyans. Refinement of this provisional biostratigraphic assessment will depend on discovery of new faunas of intermediate age, which should contain similar turiniids, but with different faunal associations. It is noteworthy that neither arthrodires nor antiarchs have yet

been confirmed to occur in South America, even though they are one of the most common and diverse elements in Middle Devonian vertebrate assemblages of other continents.

Summary and conclusions

It seems that during the late Early to Middle Devonian several new turiniids with complex three-tiered and elongated scales developed along the Gondwana shelf and shorelines, some perhaps confined to non-marine environments. The oldest appears to be *Turinia gondwana* in Bolivia in a Lochkovian–Pragian deposit. A suite of turiniids (not all formally described as yet) from various localities in central and eastern Australia apparently range from late Emsian to Eifelian in age (Long *et al.* 1988). There are resemblances between these and the Eifelian and Givetian turiniids from Iran (Turner & Janvier 1979) and those from the Eifelian and Givetian of western Yunnan (Wang *et al.* 1986). This turiniid morphotype occurs in Iran, Thailand and western Yunnan and could be expected from other Gonwana localities; it seems to persist into the late Givetian–early Frasnian as *T. hutkensis* (Blieck & Goujet 1978, P. Janvier personal communication, 1988, on age of *hutkensis*-bearing sediments). *Turinia antarctica*, described here, shares features in common particularly with *T. gondwana*, but also with turiniid scales from the lower Khush-Yeilagh Formation of north-eastern Iran, from the Hatchery Creek Conglomerate of New South Wales, the Cravens Peak Beds of the Georgina Basin and sediments in the Amadeus and eastern Officer basins of Australia. The thelodont evidence does not exclude an age for the lower part of the Aztec Siltstone as old as Lochkovian-Pragian. However, an Eifelian or slightly younger age is considered more likely, taking into account the evidence of other elements in the fauna from the top of the Aztec sequence which point to an age as young as early Upper Devonian.

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