

# A NEW EARLY DEVONIAN THELODONT FROM CELTIBERIA (SPAIN), WITH A REVISION OF SPANISH THELODONTS

by HÉCTOR BOTELLA\*, JOSÉ I. VALENZUELA-RÍOS\* and PETER CARLS†

\*Department of Geology, University of Valencia, C./Dr Moliner 50, E-46100 Burjassot, Spain; e-mails: hecbose@postal.uv.es, Jose.I.Valenzuela@uv.es

†Institut für Umweltgeologie, Technische Universität Braunschweig, Pockelstrasse 3, D-38106 Braunschweig, Germany

Typescript received 10 May 2004; accepted in revised form 20 December 2004

**Abstract:** A revision of thelodont scales from the Lower Devonian of the Iberian Chains enables their grouping into two taxa: *Turinia pagei* and *T. nachoi* sp. nov. These taxa are clearly distinguishable by morphological and histological features; they also have a different stratigraphic range (*T. pagei* is restricted to Lochkovian strata, whereas *T. nachoi* sp. nov.

occurs within lower–middle Pragian rocks). The new species is represented by head, transitional (cephalopectoral) and trunk scales.

**Key words:** thelodonts, turiniids, Lower Devonian, Iberian Chains, systematic, Ibero-Armorica.

THELODONTS are an extinct group of Agnatha that ranged from the Middle–Upper Ordovician (Märss and Karatajütë-Talimaa 2002) to the Upper Devonian (Turner and Dring 1981). Typically they are within a size range of 15–30 cm. It is known that they show many different shapes: fusiform (e.g. *Phlebolepis*), flattened (e.g. *Turinia pagei*) or laterally compressed deep bodies (Furcacaucadiformes). They usually have one dorsal, one anal and paired pectoral fins, and a hypocercal caudal fin. Their entire body is covered by characteristic scales, with a crown of dentine and a growing base of acellular bone perforated by one or more pulp cavities.

Although some studies concerning their internal anatomy exist, very little is known thus far; this is mainly due to the fact that most articulated specimens found have only layers of scales, or their impressions, and the body outline. According to the restudy of the holotype of *Turinia pagei* (Novitskaya and Turner 1998; Donoghue and Smith 2001), this fossil preserves structures that are interpreted as gills, interbranchial arches associated with these, pharynx, prenasal sinus and nasopharyngeal duct, eye openings or nostrils, and a stomach. Evidence of internal mineralised skeletons in thelodonts has never been found. Consequently, it has been assumed that they had a cartilaginous skeleton. Analysis of the available articulated specimens shows that there are major morphological differences among the scales of different body areas (Märss 1986; Märss and Ritchie 1998). Isolated scales are more frequent in the fossil record, especially in Upper Silurian–Middle Devonian sediments, where they have

great biostratigraphic importance. In fact, most thelodont taxa are known from associations of these isolated scales. Turner (1997), following Gross (1967), Karatajütë-Talimaa (1978), Märss (1986) and Turner (1991), suggested the criteria for defining taxa based on associations of isolated scales, recommending that scales of different morphology (but with the same histological pattern) that consistently appear at the same stratigraphic levels should be classified as the same species. In addition, a squamation pattern that distinguishes the scales from different body parts, oral, cephalopectoral (a part of head and thorax), trunk (postpectoral and precaudal), and pinnal (fin) scales (Märss 1986), must be assembled (see also Turner 1999 for further categories). Additionally, we think that the ratio between supposedly different topological scales should be considered as an important characteristic.

Because complete specimens do not provide much more taxonomic information, the precise description and characterization of these scale associations could be sufficient to differentiate not only morphospecies but also biological species, although some observations must be made in this respect. Firstly, the number of distinguishable body areas proposed by Märss (1986) is based on *Phlebolepis elegans*, but some taxa could present a larger or a smaller number of distinguishable body areas (compare Caldwell and Wilson 1995; Märss and Ritchie 1998). Secondly, the morphological change between the different areas is not abrupt, and scales with intermediate morphologies are generally common. Thirdly, scales of the same area may have a different morphology (Karatajütë-Talimaa

2002). Finally, sometimes scales that belong to the same body area of two different taxa may have identical morphologies. For example, Karatajūtė-Talimaa (2002) observed that head, transitional and some types of trunk scales of *Turinia composita* (D and F) are morphologically identical to those of *T. pagei*. For these reasons, and in order to be able to identify different biological species, it is essential to characterise the squamation variation pattern as accurately as possible.

The aims of this paper are to present a taxonomic revision of all thelodont remains from the Iberian Chains and the Cantabrian Mountains (Spain), following the methodology proposed above, and to establish their stratigraphical range.

## THELODONT REMAINS FROM SPAIN

Thelodont remains are not very abundant among Lower Devonian fish microfossils from Spain. All the material currently known comes from the research activities of two working groups (Professor Peter Carls' group, at Braunschweig University, Germany, and Professor Valenzuela-Ríos' group at Valencia University, Spain) in three Celtiberian Lower Devonian formations: Luesma (d1), Nogueras (d2) and Santa Cruz (d3), whose main characteristics are as follows.

The Luesma Formation consists of alternating shales and quartzites with scarce limestone beds. The Silurian/Devonian boundary is located at the boundary between the d1bβ1 and d1bβ2 units, towards the middle part of the formation (Carls 1977). The sharp cut-off of siliciclastic sediments represents the start of the Nogueras Formation, which is composed of bioclastic limestones, marls and shales. The Lochkovian/Pragian boundary is located between the local boundary d2bα/d2bβ ('Leitbank A'). The Santa Cruz Formation consists of sandstones and shales with a few carbonate beds; the Pragian/Emsian boundary *sensu* the International Subcommission on Devonian Stratigraphy is located close to the base of the formation.

One of us (Carls) collected the first thelodont remains as a by-product of sampling programmes to obtain conodonts in the Axial Depression of the Cámaras River (ADCR) (Celtiberia; Text-fig. 1A–B). These remains consist of isolated scales from the Lochkovian part of the Luesma and Nogueras formations. In 1976, D. Goujet (Paris) undertook fieldwork together with Carls, and some of the material obtained was studied by Goujet and identified as *T. pagei* (Goujet and Blicek 1979; Goujet 1984). S. Turner examined part of this material (Turner 1984, pp. 194–196, fig. 5.1; Turner 1999) and identified scales of *T. pagei*, *T. polita*-type and turiniids similar to those of *T. australensis* and *T. fuscina* from eastern

Australia, in submember d1cγ of the Luesma Formation, and *Turinia* sp. cf. *T. pagei*, *Turinia* sp. cf. *T. australensis* and *Boreania minima* in submember d2bα (not d2cγ as printed) of the Nogueras Formation (except for *Boreania minima* all of these variations could now be included in the *T. pagei* type; S. Turner, pers. comm. 2004).

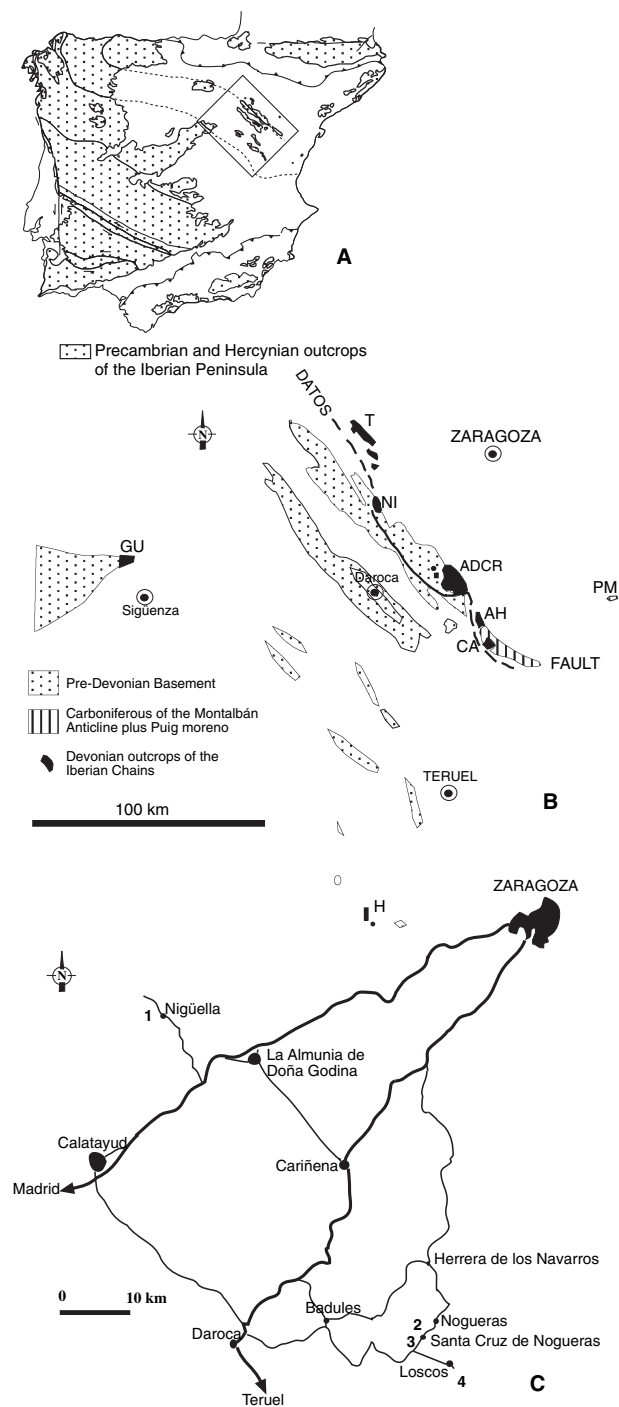
Mader (1986, fig. 4) mentioned the presence of *T. pagei* scales in the ADCR, near the Lochkovian/Pragian boundary. In addition, he recorded *T. pagei* from the upper part of Carazo Formation (Cantabria, northern Spain) in the middle Lochkovian, but this material was unavailable for study. Work in the ADCR since then has resulted in the collection of new material. Wang (1993) studied the microichthyoliths collected by P. Carls in the Luesma, Nogueras and Santa Cruz formations (Lochkovian–Pragian *sensu* Carls and Valenzuela-Ríos 2002) and recognised four thelodont taxa: *T. pagei* (lower Lochkovian–middle Pragian, in submembers d1cγ, d2bα, d2cβ and d3aβ), *Turinia?* sp. nov. A (lower Lochkovian–upper Lochkovian in d1cγ and d2bα), *Paraturinia dubia* (lower Pragian, submember d2cβ) and *Canonina* sp. (only two scales from middle Pragian, submember d3aβ). The 14 scales assigned by Wang (1993) to *Paraturinia dubia*, as he suggested, might not be a thelodontid, but a definitive assignation is not yet possible as our revision of these scales had to be based only on photographs.

In another area of Celtiberia, the Axial Depression of Niguella (NI) (Text-fig. 1B herein; see also Valenzuela-Ríos 1989), *T. pagei* appears in the upper Lochkovian, submember d2bα (Valenzuela-Ríos and Botella 2000). Botella and Valenzuela-Ríos (in press) reported this taxon from comparable levels in the ADCR.

Both working groups have thoroughly sampled these formations in six other areas of Celtiberia but, except for one scale of *T. pagei* from d2cβ in Henarejos, the other thelodonts found in Spain come from just two areas, ADCR, NI (Text-fig. 1A–B), which have comparable, but in some respects contrasting, sedimentary and faunal sequences (Carls and Valenzuela-Ríos 1999).

Thelodont scales have only been found in four sections of the Lower Devonian formations that include parts of the Luesma, Nogueras and Santa Cruz formations (Text-fig. 2): Poyales Este (submember d1cγ), Viñas (submember d2bα) and Sur barranco de Santo Domingo (submembers d2bα, d2cβ and d3aβ) in the ADCR, and Ni2 (submember d2bα) in NI (Text-fig. 1C). The ages of these records range from the late Lochkovian to middle Pragian (*sensu* Carls and Valenzuela-Ríos 2002). For a recent detailed geological and stratigraphical description of these two areas, see Carls and Valenzuela-Ríos (2002), and for a detailed faunal succession, see Carls (1999).

This paper is based on all available thelodont remains from Celtiberia. The material described is composed of isolated scales resulting from the dissolution of carbonate rocks with 5–10 per cent formic acid.



**TEXT-FIG. 1.** A, distribution of Precambrian and Palaeozoic rocks and location of the area studied. B, abridged geological map of Celtiberia showing Devonian and Carboniferous outcrops (modified from Carls and Valenzuela-Ríos 2002). GU, Guadarrama; H, Henarejos; T, Tabuenca; NI, Nigüella; ADCR, Axial Depression of the Cámaras River; PM, Puig Moreno; AH, Anadón-Huesa Devonian outcrops in the Montalbán Anticline; CA, Cabezos Altos Devonian outcrops in the Montalbán Anticline. C, Location of the studied sections. 1, Nigüella; 2, Poyales Este; 3, Viñas; 4, Sur Barranco de Santo Domingo.

## SYSTEMATIC PALAEOONTOLOGY

Our revision has enabled us to group all the thelodont remains from the Iberian Chains into two taxa that have different stratigraphic ranges, namely *T. pagei* and *T. nachoi* sp. nov., with just two indeterminate scales. All of the material is housed in the Museum of Geology, University of Valencia (MGUV).

Subclass THELODONTI Kiaer, 1932  
Order THELODONTIDA Stensjö, 1958  
Family TURINIIDAE Obruchev, 1964

Genus TURINIA Traquair, 1896

*Type species.* *Turinia pagei* (Powrie, 1870)

*Turinia nachoi* Botella and Carls sp. nov.  
Plates 1–2; Text-figure 3

v1993 *Turinia pagei* (Powrie); Wang (only material from d3aβ1), p. 81 text-figs 9a–c.

v1993 *Canonia* sp. Wang, p. 85 pl. 2, fig. 10.

*Derivation of name.* After Professor José Ignacio Valenzuela Ríos ('Nacho') for his outstanding contribution to Lower Devonian biostratigraphy and micropalaeontology in Spain.

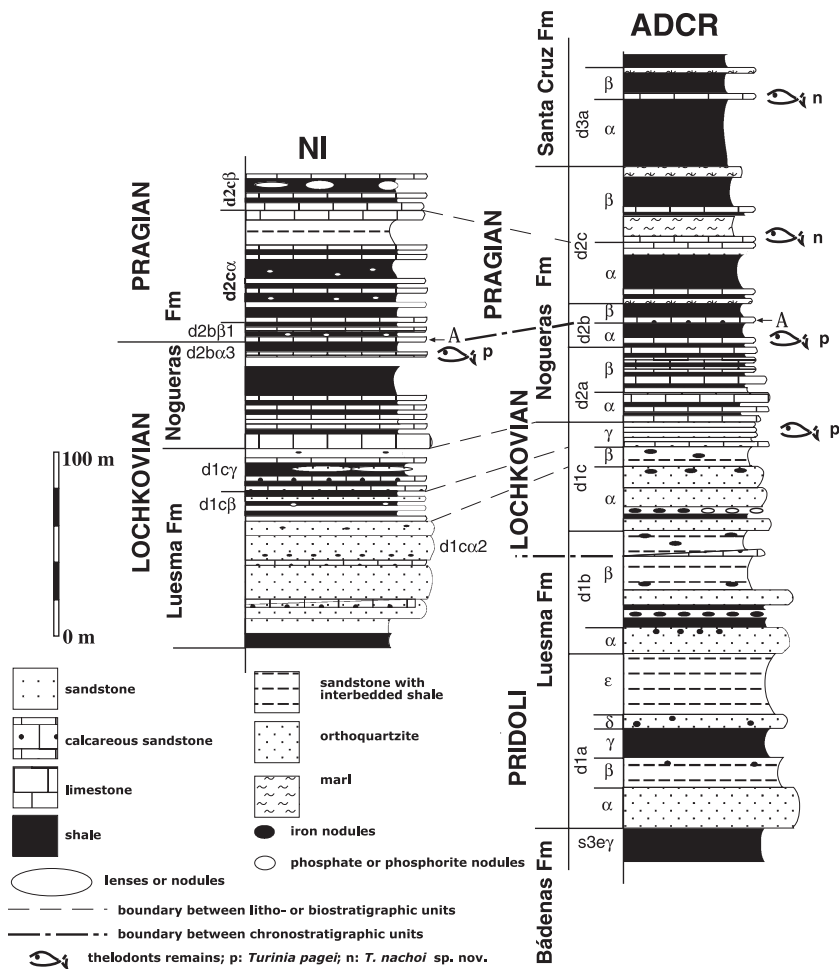
*Holotype.* Trunk scale MGUV-8108, Plate 2, figures 5–9.

*Additional material.* 59 isolated scales: MGUV 8101–8107, 8109, 15365–15416.

*Type locality and age.* Unit d3aβ1, Sur Barranco de Santo Domingo Section, ADCR, south of Aragón, Santa Cruz Formation, Lower Devonian, Pragian.

*Occurrence.* The upper part of the Noguerras Formation: unit d2cβ1 at Sur Barranco de Santo Domingo and Henarejos, and at the type locality (lower–middle Pragian).

*Diagnosis.* Turiniid species based on small isolated scales. The crown with four clearly distinguishable areas; one anterior, two lateral which are generally symmetrical, and one posterior. Each area is made of one main rib that bifurcates into two sharp, clearly marked secondary ribs that are further subdivided into two smaller ribs, resulting in a total of 16 minor ribs (in some of the transitional scales some of these ribs can be lost). These four main ribs converge posteriorly. The outline of the crown–base interface is rounded in oral scales, slightly navicular in transitional scales and rhombic with rounded edges in trunk scales. The base is wider than the crown at this



**TEXT-FIG. 2.** Litho-, bio- and chronostratigraphical correlation between Nigüella (NI) and the ADCR, with indication of levels that yielded the turiniids described in this work (modified from Carls and Valenzuela-Ríos 1999).

interface and develops a rounded ledge that surrounds the crown. The base shows one or more anterior spurs that in the head scales may not exist. A unique central pulp cavity is present. Dentine tubules arise individually from the pulp cavity and branch close to the crown surface. The base is composed of acellular bone.

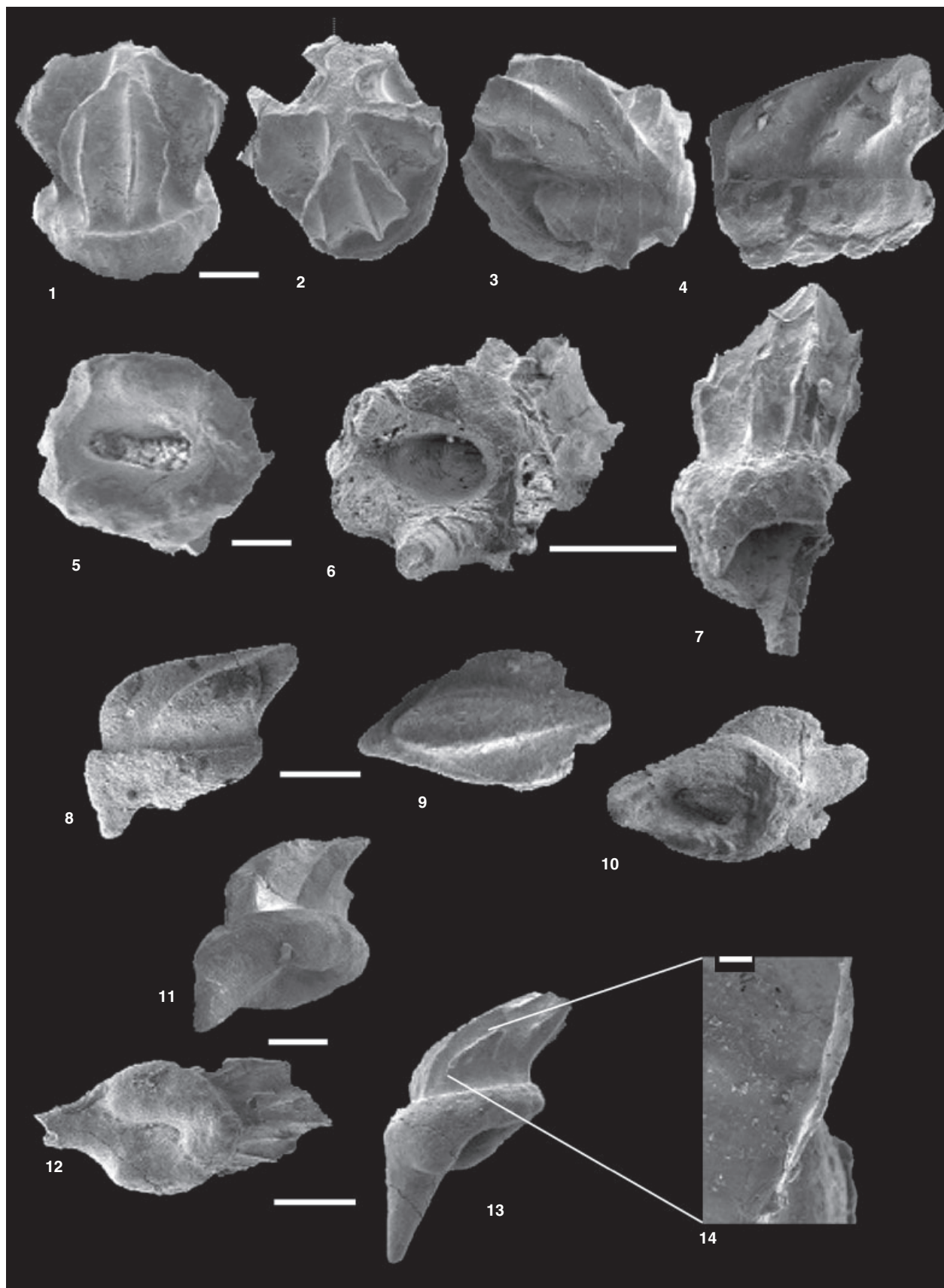
*Description*

The collection of scales includes head, transitional (cephalo-pectoral) and trunk scales.

*Head scales* (Pl. 1, figs 1–7). These have a very high crown, which is symmetrical in crown view, and with four clearly distinguishable areas that are alike in both shape and size. Each area is formed by four ribs with the following arrangement from top to bottom: a single rib starts from the central point that bifurcates a little below; each of these two ribs bifurcates further. The four areas converge upwards at a central point, which can also be slightly displaced posteriorly (Pl. 1, figs 1–2 and 3–4, respectively). The clearly marked ribs are sharp, the crown becomes narrower towards the neck (Pl. 1, figs 1, 7) and the base is short and slightly wider than the crown, and may or may not have spur-shaped projections on the anterior part. Some cephalic scales have up to three of this type of projection (Pl. 1, figs 6–7); this has not been

**EXPLANATION OF PLATE 1**

Figs 1–14. *Turinia nchoi* sp. nov. 1–7, head scales. 1–2, MGVU 8101 (1 lateral view, 2 crown view); 3–5, MGVU 8102 (3 crown view, 4 lateral view, 5 basal view); 6–7, MGVU 8103 (6 basal view, 7 lateral view). 8–14, transitional scales. 8–10, MGVU 8104 (8 lateral view, 9 crown view, 10 basal view); 11, MGVU 15365 anterolateral view; 12–14, MGVU 8105 (12 basal view, 13 lateral view, 14 detail of the crown surface). Scale bars for 1–5, and 11, 100 μm; 6–10, 12–13, 250 μm; 14, 25 μm. All scales from Sur Barranco de Santo Domingo Section, ADCR, south of Aragón, Spain, Santa Cruz Formation, Pragian (1–7, 11–14 from unit d3aβ1, 8–10 from unit d2cβ1).



observed in the other topological types of the new species. The base shows a pulp opening in both juvenile and mature scales.

*Transitional scales* (Pl. 1, figs 8–14). The crown is arched, longer and extends more posteriorly than the base, and has an acute end. Commonly the main ribs converge at this end (Pl. 1, figs 8, 13), although in some cases the ribs from both lateral areas do not reach this point. Some specimens differ as a result of erosion or breakage of the lateral flanks (Pl. 1, fig. 9); these can potentially be confused with *Canonia* (compare Vieth 1980, pl. 3, figs 1, 3) or with trident-like scales of some other turiniids, like *T. fuscina* (compare Turner 1986, fig. 2K, R–U). In transitional scales of *T. nachoi* the secondary ribs seem to have disappeared, but can be seen under higher magnification using an electron microscope (Pl. 1, fig. 14). The base is short, deep and thick, and has a short, spur-like, anterior projection (Pl. 1, figs 8, 11, 13).

*Trunk scales* (Pl. 2, figs 1–13). These are narrow and have a strongly arched crown, which is positioned posteriorly. The four areas of the crown converge at three different points that are aligned along an anteroposterior axis, which gives a laminated aspect to the upper part of the crown (Pl. 2, fig. 8). The crown has many thin, sharp and bifurcating ribs close to the neck (Pl. 2, fig. 9). The base outline is rhombic with rounded edges (Pl. 2, figs 6, 13), and an anterior spur (occasionally very long, up to three times the crown length) (Pl. 2, figs 11–12) is consistently present. The pulp opening is small and can even be closed (Pl. 2, figs 6, 13). In scales where the crown has been broken transversally, the typical bifurcated-rib pattern is also observed (Pl. 2, fig. 10).

A transitional gradient can be drawn between the three types of scales, from the head (anteriormost scales in the body) with ribs that converge at a central point of the crown to the most posterior scales where the convergence point has been displaced posteriorly. Anterior spur(s) of head scales, when present, are always orientated downwards (Pl. 1, fig. 7); towards more posterior scales, this spur becomes larger and progressively is orientated forwards (Pl. 1, fig. 11; Pl. 2, figs 1, 4–7, 11–13).

*Histology.* As no single thin section provides complete information regarding histological characters, in part related to poor preservation, reconstruction of the scale is based on the interpretation of several thin sections (Text-fig. 3). The crown is composed of orthodentine enclosed by a thin layer of enamel-like tissue. The base is made of acellular tissue (probably aspidine). Only one pulp cavity is present.

A few narrow, scattered dentine tubules arise individually (not in bunches) from the central pulp cavity into the crown. Most are straight, but a few are sinuous. Commonly, tubules bifurcate distally close to the crown surface; these branches are short,

straight and few in number. Pulp canals are not developed. Evidence of Sharpey's fibres is present at the base.

Growth lines occur in both the base and the crown. The central open pulp cavity is high, narrow and arched following the curvature of the crown. In mature scales the pulp opening can be closed.

*Remarks.* *T. nachoi* has mainly monolithic scales with a high crown. The crown ribs reach the crown-base interface. The base has a pulp opening and, occasionally, a very long, spur-like anterior projection. The dentine tubules are narrow and long. According to these characteristics, we place it within the Turiniidae (see Turner *et al.* 1995).

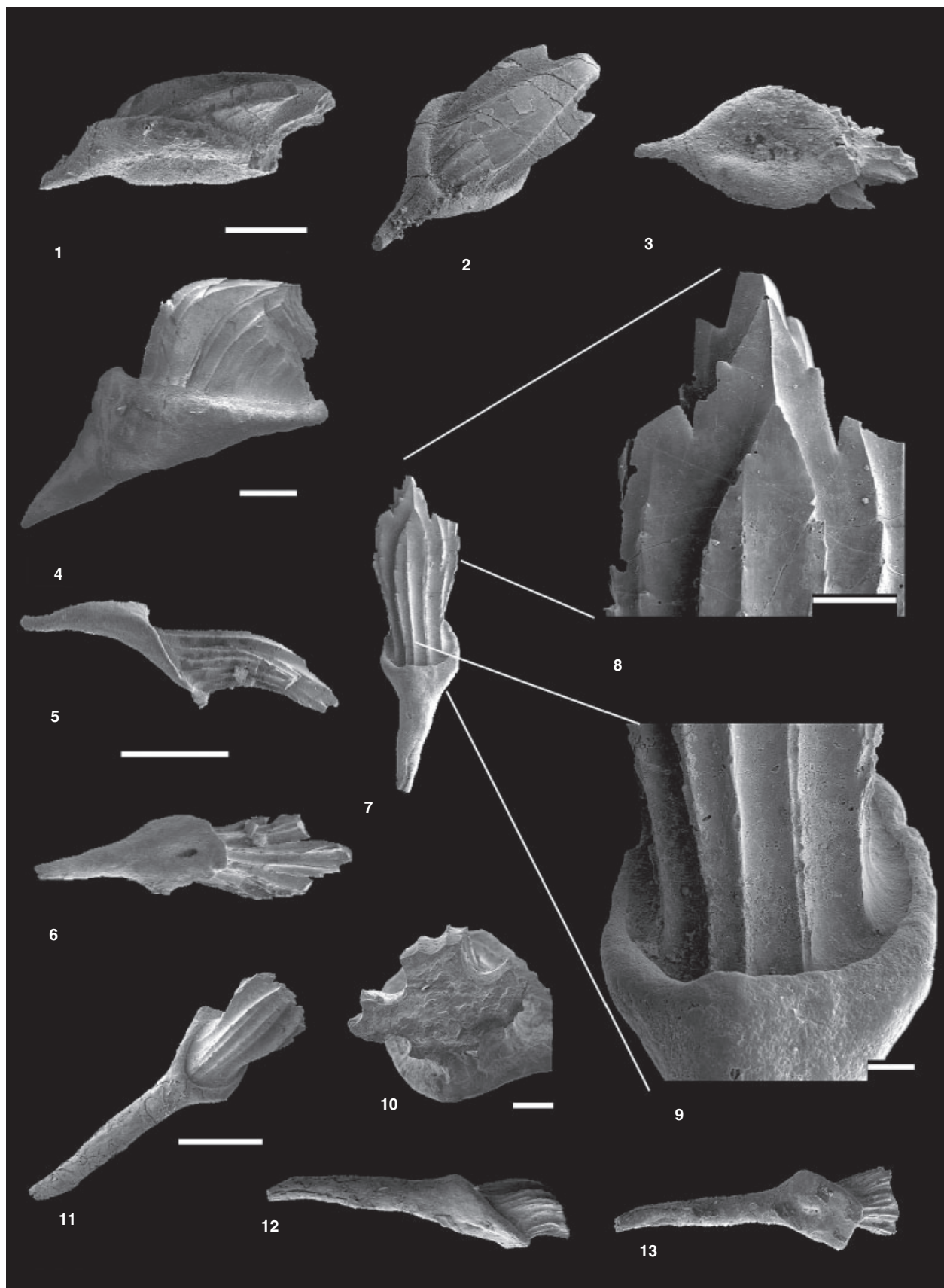
The morphological variation in the pattern of scales along the body of *T. nachoi* is similar to the other species of *Turinia*. This pattern consists of rounded head scales, navicular transitional scales, and torch-shaped trunk scales with rounded rhombic bases and an anterior spur-like projection. This variation is observed in *T. pagei* (Gross 1967, pl. 7, figs 1–10; Karatajūtė-Talimaa 1978, pl. 33, figs 1–9; pls 34–35; pl. 36, figs 1–17; pl. 37, figs 1–9; pls 38–39; pl. 40, fig. 7), *T. polita* (Karatajūtė-Talimaa 1978, pl. 40, figs 1–6; pl. 41; pl. 42, fig. 1), *T. australiensis* (Gross 1971; Turner 1997, figs 3–4), *T. antarctica* (Turner and Young 1992; Turner 1997, fig. 7), *T. fuscina* (Turner 1986, fig. 2B–H, J–U), *T. gondwana* (Gagnier *et al.* 1988, figs 3–4), *T. composita* (Karatajūtė-Talimaa 2002, fig. 1), *T. gavinyoungi* (Turner 1995, fig. 3), *T. hutkensis* (Blieck and Goujet 1978, pl. 61, figs 1–14) and perhaps also in *T. pagoda*, but insufficient material is available from the species (Wang *et al.* 1986) to confirm this; according to Märss (1999) it might belong to *Boothialepis*.

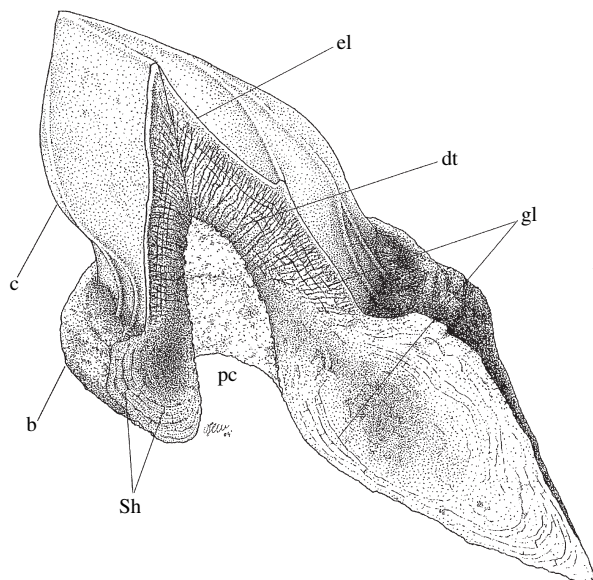
*T. nachoi* is similar to *T. hutkensis* and *T. gavinyoungi* in having closely spaced double ribs, some head scales with more than one anterior spur orientated downwards (Turner 1995, fig. 3u–v), and well-differentiated crown areas (five or more in *T. gavinyoungi* and four in *T. pagei*), and in the overall laminated aspect of the trunk scale crowns. Furthermore, the histology of *T. gavinyoungi* (Turner 1991, 1995) is close to *T. nachoi*, mainly in the morphology and distribution of dentine canals, suggesting a close phylogenetic relationship between them. However, *T. nachoi* does not have the fine riblet ornamentation that is present on the main ribs of *T. gavinyoungi* and *T. australiensis*.

*T. nachoi* is also similar to representatives of *Australolepis* (Turner and Dring 1981) in the small size of the

## EXPLANATION OF PLATE 2

Figs 1–13. *Turinia nachoi* sp. nov., trunk scales. 1–3, MGUV 8106 (1 lateral view, 2 crown view, 3 basal view); 4, MGUV 8107, lateral view; 5–9, MGUV 8108, holotype (5 lateral view, 6 basal view, 7 frontal view, 8 detail of the apical part of the crown surface, 9 detail of the crown-base interface); 10–13, MGUV 8109 (10 broken crown view, 11 frontal view, 12 lateral view, 13 basal view), this scale was broken during photographing. Scale bars for 1–4, 250  $\mu\text{m}$ ; 5–7, 11–13, 500  $\mu\text{m}$ ; 8, 10, 100  $\mu\text{m}$ ; 9, 50  $\mu\text{m}$ . All scales from unit d3a $\beta$ 1, Sur Barranco de Santo Domingo Section, ADCR, south of Aragón, Spain, Santa Cruz Formation, Pragian.





**TEXT-FIG. 3.** *Turinia nachoi* sp. nov.; reconstruction of the scale microstructure based on thin sections of specimens MGVU 15413–16; b, base; c, crown; dt, dentine tubules; el, enamel-like tissue layer; gl, growth layers; pc, pulpar cavity; Sh, canals for Sharpey's fibres.

scales and the presence of sharp, bifurcated ridges and ornamentation in the ventral part of the crown (Turner and Dring 1981, fig. 4A–D, G, J; Turner 1997, fig. 8A–B). However, the emended diagnosis of *Australolepis seddoni* (Trinajstić 2001, p. 239) shows many differences from *T. nachoi*; for example, the latter lacks the small tubercles (cf. Trinajstić 2001, fig. 2b, f), multidigitate lappets (cf. Trinajstić 2001, fig. 2a, g–h, k), acute apices (cf. Trinajstić 2001, fig. 3e) and fine ribbed microornamentation (cf. Trinajstić 2001, fig. 2b, i) that are present in *Australolepis seddoni*. In addition, the number of separate scale morphology regions in *A. seddoni* is greater than has been observed in *T. nachoi* (cf. Trinajstić 2001, fig. 4).

Some scales of *T. nachoi* were attributed to *T. pagei* by Wang (1993, fig. 9A–C) but they are clearly different. None of the characteristic morphologies of *T. nachoi* is present in scales of *T. pagei* (cf. Gross 1967, pl. 7, figs 1–10; Karatajūtė-Talimaa 1978, pl. 33, figs 1–9; pls 34–35; pl. 36, figs 1–17; pl. 37, figs 1–9; pls 38–39; pl. 40, fig. 7); additionally, scales of

*T. pagei* never appear associated with *T. nachoi*. The scales of *T. nachoi* are smaller, and have marked double ribs and four distinguishable areas in the crown that are never present in *T. pagei*. The base of *T. nachoi* is never as globose or as deep as some specimens referable to *T. pagei* (see Karatajūtė-Talimaa 1978, pl. 35, fig. 5; pl. 37, fig. 1). The typical smooth, flat crowns of *T. pagei* do not occur in *T. nachoi*.

Following our morphological and histological examination of the *Canonia grossi* material studied by Vieth (1980, pl. 3) in the Museum of Göttingen University, the Celtiberian scales that were formerly attributed to *Canonia* sp. by Wang (1993, pl. 2, fig. 10) are now identified as transitional scales of *T. nachoi* sp. nov.

#### *Turinia pagei* (Powrie, 1870)

Plate 3; Plate 4, figures 1–10

- v1993 *Turinia pagei* (Powrie); Wang (only scales of this taxon in levels d1cγ and d2bα), p. 81, pl. 1, figs 3–11; pl. 2, figs 11–14; pl. 17, figs 1–2; text-fig. 9d.
- v non1993 *Turinia pagei*; Wang (material from d3aβ1), p. 81, text-fig. 9a–c.
- v 1993 *Turinia?* sp. A; Wang, p. 84, pl. 2, figs 6–9; text-fig. 10.
- 1984 *T. pagei*; Turner, p. 194, fig. 5.1a, f–g.
- 1984 *T. sp. cf. T. australensis*; Turner, p. 194, fig. 5.1c–e.

This list is restricted to Spanish material; for a complete record see Karatajūtė-Talimaa (1978), Turner (1976), Märss and Ritchie (1998) and Donoghue and Smith (2001).

*Material studied.* 103 isolated scales: MGVU 8111–8129, 14282–14365.

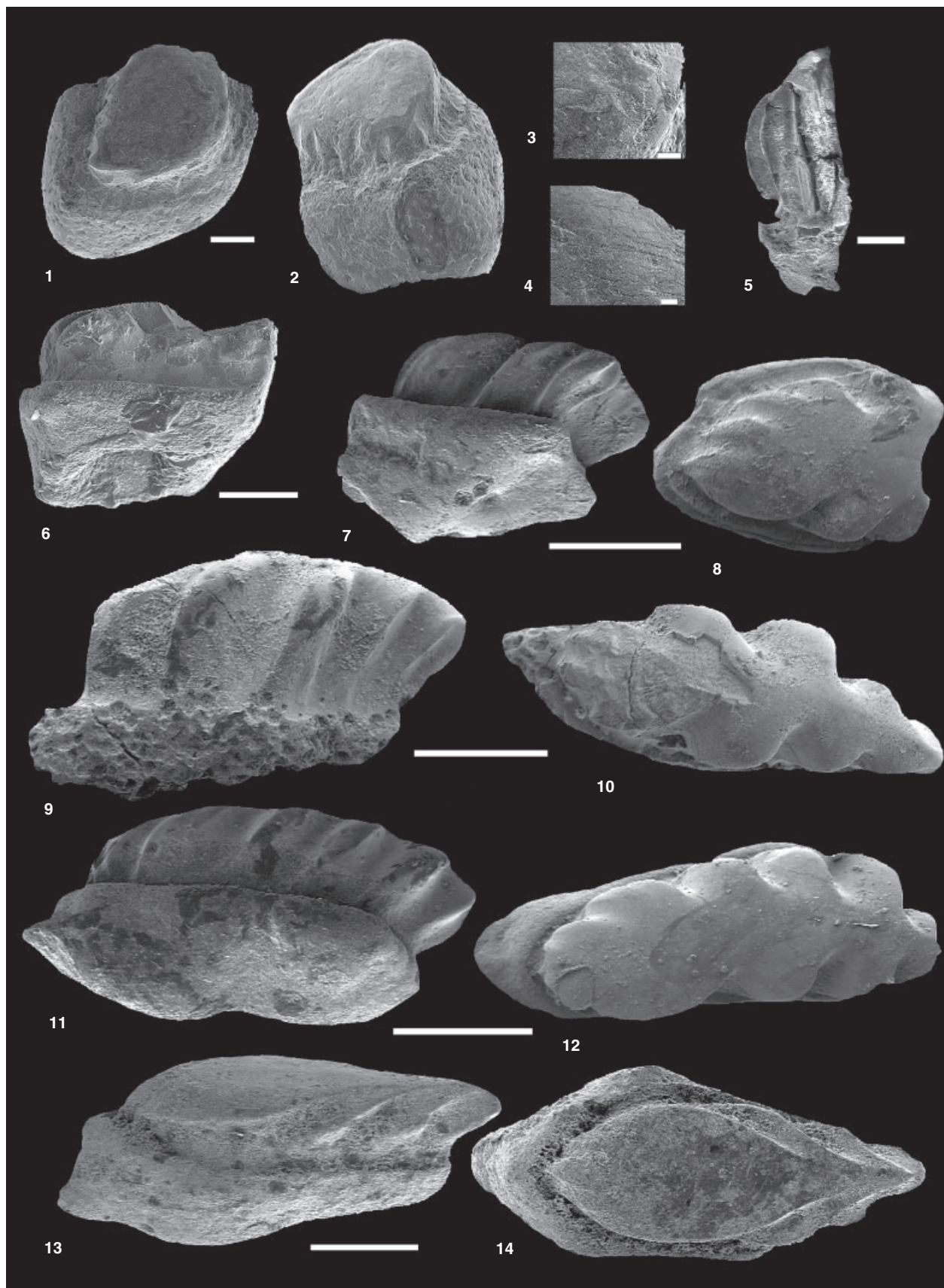
*Occurrence.* In the eastern Iberian Chains from lower Lochkovian (submember d1cγ Poyales North-West section) to upper Lockovian (submember d2bαf, Poyales Este, Viñas, Henarejos and Nigiella 2 sections).

#### *Description*

*Rostral scales* (Pl. 3, figs 1–4). These are relatively small with a low, flat, smooth crown and a rounded margin; they can also be

#### EXPLANATION OF PLATE 3

Figs 1–14. *Turinia pagei* (Powrie 1870). 1–4, rostral scale, MGVU 8125 (1 crown view, 2 lateral view, 3–4 detail of the crown surface showing abrasion marks, see text). 5–6, head scales; 5, MGVU 8121 in frontal view; 6, MGVU 8120 in laterobasal view. 7–14, transitional scales. 7–8, MGVU 8122 (7 lateral view, 8 crown view); 9–10, MGVU 8123 (9 lateral view, 10 crown view); 11–12, MGVU 8128 (11 laterobasal view, 12 crown view); 13–14, MGVU 8129 (13 lateral view, 14 crown view). Scale bars for 1–2, 100 μm; 3, 25 μm; 4, 10 μm; 5, 7–14, 500 μm; 6, 250 μm. All scales from unit d2bα2, Viñas section, ADCR, south of Aragón, Spain, Nogueras Formation, Lochkovian.



grooved (Pl. 3, figs 1–2). Neck short. Base deep and strongly bowed with a small central pulp opening; generally larger than the crown and with a rounded margin, lacking any groove.

*Head scales.* Among the Celtiberian scales, only three typical head scales (*sensu* Gross 1967, pl. 7, figs 8–10; Karatajūtė-Talimaa 1978, pl. 35; pl. 36, fig. 2; pl. 37, figs 4–5) have been found (Wang 1993, pl. 1, fig. 7 and MGUV 8131–2, Pl. 3, figs 5–6 herein). The specimen MGUV 8131 (Pl. 3, fig. 5) has a longitudinally broken crown; it is high, with more than ten very deep and clearly marked ribs. The ribs are widely spaced and the grooves between them are deeper than in those illustrated by Gross (1967) and Karatajūtė-Talimaa (1978). Although the base is also broken, it is possible to extrapolate that it was deep and compact. A large pulp cavity would have been located in the centre of the scale.

*Transitional scales* (Pl. 3, figs 7–14; Pl. 4, figs 1–3; see also Wang 1993, pl. 1, figs 6, 8–11; pl. 2, figs 11–14). These scales are navicular-shaped, sometimes very narrow (Pl. 3, figs 10, 12) and can be arched (Pl. 3, fig. 12); the last of these is possibly related to their location on the body. The crown has a typical oak-leaf shape, with 10–12 ribs, which can be arched backwards; as a consequence the anterior ribs become higher and thicker, and the posterior ones shorter (Pl. 3, figs 13–14). From the top view, the crown ribs can be symmetrically distributed (Pl. 3, figs 12–14; Pl. 4, fig. 3) or alternate (Pl. 3, fig. 10). The base is thick, compact and shallow, and sometimes has a short, thick anterior spur. The pulp opening is small and central, although in mature scales it can be completely closed (Pl. 3, figs 8, 11).

Transitional scales are morphologically connected, by means of intermediate shapes, to trunk scales (Pl. 3, figs 13–14; Pl. 4, fig. 4).

*Trunk scales* (Pl. 4, figs 4–10). These have a flat crown with a pointed rear edge that juts out from the base. The ridges are located on the lateral edges and in the ventral part of the crown. The base has a long anterior spur, which is very displaced anteriorly, and a pulp opening located in a central position. These scales are like those described by Gross (1967, pl. 7, figs 1–4) and Karatajūtė-Talimaa (1978, pl. 34, figs 1, 3; pl. 36, figs 4, 10, 12; pl. 37, figs 2–3; pl. 38, figs 4–6). Some scales (Pl. 4, fig. 5) have a crown that is higher and not flat. They exhibit long ribs that reach the neck on the anterior margin. These scales are similar to those described by Karatajūtė-Talimaa (1978, pl. 34, fig. 4; pl. 36, fig. 15; pl. 39, fig. 7).

*Histology.* *T. pagei* from the eastern Iberian Chains shows no histological difference from the species described by Gross (1967) and Karatajūtė-Talimaa (1978).

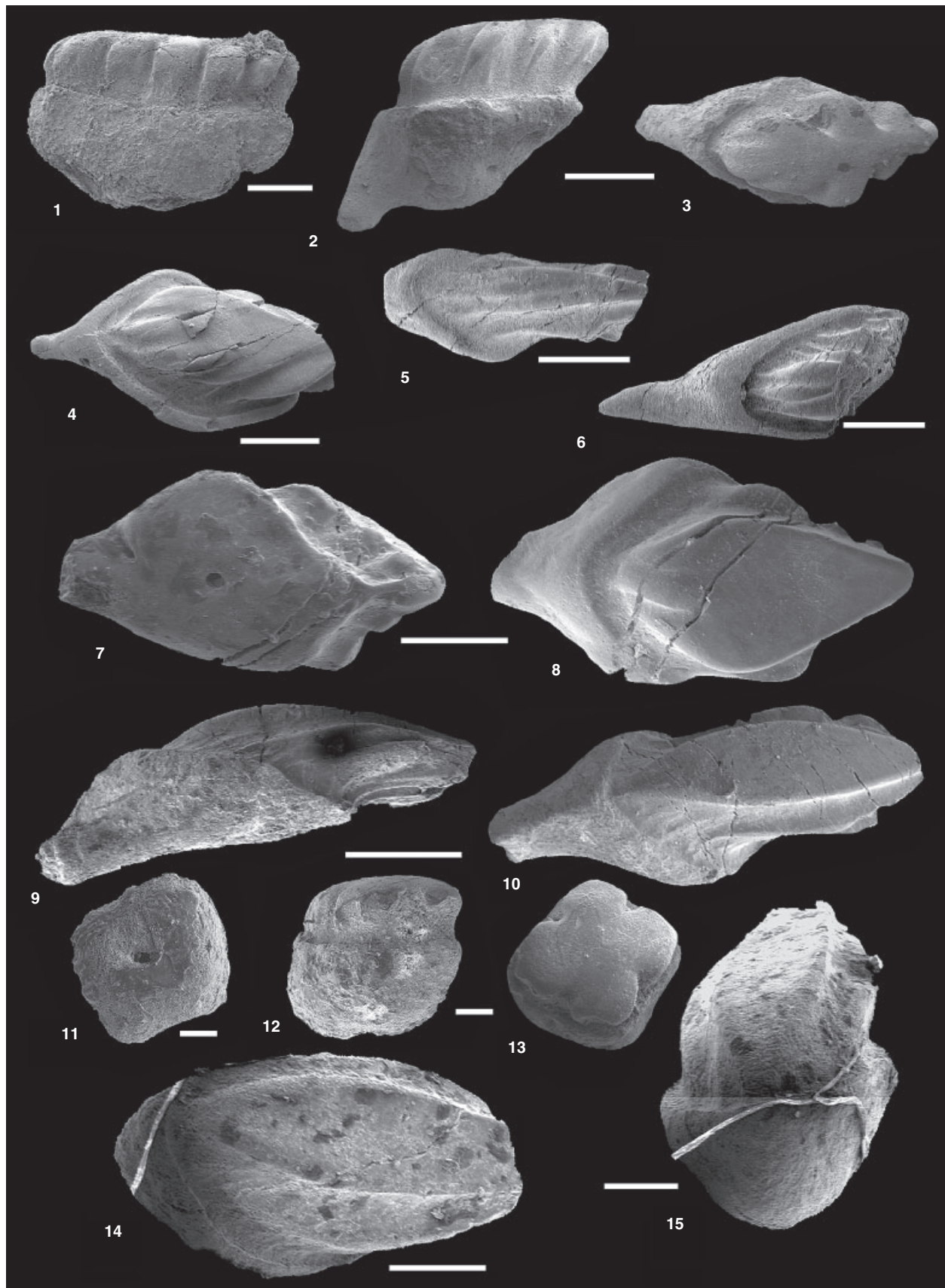
*Remarks.* The general morphology and histological type of these scales allow their referral to *T. pagei*, in which we also include Wang's material classified as *T?* n. sp. A. The latter has a flat crown and lateral ribs that give a serrated aspect to the crown edge. They are similar to some forms of *T. pagei* previously documented by Karatajūtė-Talimaa (e.g. compare Wang 1993, pl. 2, figs 6–9 with Karatajūtė-Talimaa 1978, pl. 37, figs 1–2, 3m). Additionally, *T?* sp. A (*sensu* Wang) always occurs with *T. pagei*. The material documented by Turner (1984, 1999) from the d1c and d2b (*sic*) also probably corresponds to *T. pagei*. Rostral scales are rare (only two specimens have been found); they would have occupied an anterior position, near the mouth opening. Their shape could be modified by usage. Based on the existence of fine-grained sediment in the stomach but not in the branchial region of the holotype Donoghue and Smith (2001) concluded that *T. pagei* was a deposit feeder. Following this interpretation, we think that the flat crown morphology could be due to continuous wear of the oral scales because of their contact with the sediment. Some marks that indicate wear-related abrasion have been observed in these scales (Pl. 3, figs 3–4), which are rare in comparison with the other scale types. Therefore, rostral scales could have originally been small head scales that were subsequently modified by wear during feeding. This process could have occurred in other species as well; for instance, in *T. australensis* the crown erosion of head scales like those illustrated by Turner (1997, fig. 3E, I; head scales) would have produced morphologies like those in her figure 3B–C (oral scales). Karatajūtė-Talimaa (1978, pl. 34, figs 5–9; pl. 36, fig. 8) figured similar scales among those of *T. pagei*.

Transitional scales as long, narrow and arched as those described here have not been figured by other authors. They are the most abundant forms in our material. This contrasts markedly with the material studied by Gross (1967) in which head scales are the most abundant, and with the Canadian Arctic assemblage (Vieth 1980) that we examined, in which trunk scales are the most numerous.

#### EXPLANATION OF PLATE 4

Figs 1–10. *Turinia pagei* (Powrie 1870). 1–3, transitional scales. 1, MGUV 8127 (lateral view); 2–3, MGUV 8119 (2 lateral view, 3 crown view). 4–10, trunk scales. 4, MGUV 8117 (crown view); 5, MGUV 8116 (crown view); 6, MGUV 8115 (frontal view, crown is broken); 7–8, MGUV 8113 (7 basal view, 8 crown view); 9–10, MGUV 8112 (9 lateral view, 10 frontal view).

Figs 11–15. *Thelodonti* gen. and sp. indet. 11–13, MGUV 8111 (11 basal view, 12 lateral view, 13 crown view); 14–15, MGUV 8110 (14 crown view, 15 frontal view). Scale bars for 2–10, 14, 500  $\mu\text{m}$ ; 1, 15, 250  $\mu\text{m}$ ; 11–13, 100  $\mu\text{m}$ . All scales from unit d2bz2, Viñas section, ADCR, south of Aragón, Spain, Nogueras Formation, Lochkovian.



BOTELLA *et al.*, Turinia, Thelodonti

In our material the morphological variability within trunk and transitional scales, which is similar to that presented by Gross (1967), is not as great as that figured by Karatajūtė-Talimaa (1978), or as observed in the material from Göttingen attributed to *T. pagei* by Vieth (1980), and restudied by us, which also shows considerable variation within trunk and transitional scales. The differences among topological scale types and the morphological variations found could indicate that within the scales of *T. pagei*-type more than one biological species is represented, as others have pointed out previously (Märss and Ritchie 1998).

Thelodonti gen. and sp. indet.

Plate 4, figures 11–15

*Description.* MGUV 8128 (Pl. 4, figs 11–13) is a small scale with a low crown that has four notches at the margins giving a cross-like aspect in upper view (Pl. 4, fig. 13); these notches start from the base (Pl. 4, fig. 12). Neck low and weak. Base deeper than the height of the crown, has a rhombic outline with rounded edges and one pulp opening in central position (Pl. 4, fig. 11). MGUV 8129 (Pl. 4, figs 14–15) has a bowed base with a rounded-navicular outline, and a small central pulp opening. Neck is restricted to a narrow groove and the crown has four ribs that converge at a posterior point that stands out beyond the base (posteriormost part of the scale is broken).

## AGE AND ENVIRONMENT OF CELTIBERIAN THELODONTS

In Celtiberia the Silurian/Devonian boundary is located within the upper part of member d1b $\beta$ , the so-called d1b $\beta$ 2 fauna (Carls 1977). Important elements of this fauna are the homalonotid trilobite *Acastella heberti* that clearly indicates the Devonian (see discussion in Carls and Valenzuela-Ríos 1999), brachiopods such as *Platyorthis* sp. D ex gr. *monnieri*, *Podolella renselaeroides* and *Howellella mercurii*. The record of the conodont *Icriodus woschmidti* and a new species of the recently erected conodont genus *Zieglerodina* (Murphy *et al.* 2004) confirm the Devonian age for these strata.

The lowest record of *T. pagei* in Celtiberia is from the first levels of submember d1c $\gamma$  (Poyales E; Text-fig. 1C), which consists of 13 m of quartzitic sandstones, calcareous sandstones, arenaceous shales and arenaceous bioclastic shelly limestones (coquinas) with abundant bryozoan colonies. The rich brachiopod, trilobite and conodont fauna indicates an early Lochkovian age (base of the trilobite *Acastella tiro* Zone); in terms of conodont biozonation, this unit correlates with some levels below the *Lanea omoalpa-L. eleanorae* Zone of Murphy and Valenzuela-Ríos (1999). The next record of *T. pagei*

comes from d2b $\alpha$ 2, which consists of 5 m of bioclastic limestone beds with abundant *Schizophoria* sp. W and uncinulidae. These beds are rich in brachiopods, and include the incoming of *Hysterolites gandli*. Conodonts are represented by *Icriodus* and *Pelekysgnathus*. Above this unit is a shaly and sandy interval (d2b $\alpha$ 3) 8 m thick that is, in turn, overlain by bed 'A', which indicates the base of the Pragian. Therefore, the range of *T. pagei* in Celtiberia encompasses most of the Lochkovian except for the earliest part. This range is within the global range of *T. pagei*.

It is important to note that records of *T. pagei* are limited to the two cited units d1c $\gamma$  and d2b $\alpha$ 2. All the levels in between have been sampled at a fine scale and other abundant fish remains have been found, but not turiniids (Mader 1986; Wang 1993; Valenzuela-Ríos and Botella 2000; Botella and Valenzuela Ríos 2002).

This discontinuous record could be related to faunal migration pulses. Carls and Valenzuela-Ríos (1999) have observed that the Lochkovian and Pragian shallow marine waters of Celtiberia were rapidly invaded by cosmopolitan faunas belonging to other groups, for example conodonts, during times of moderate deepening, but that afterwards they had difficulties in flourishing. This can probably be linked to the nature of the basin during the Early Devonian; these rapid deepenings would then be quickly compensated for by terrigenous inputs from nearby sources (Carls 1999). The record of numerous fish taxa is fairly continuous in the ADCR and NI (Wang 1993; Valenzuela-Ríos and Botella 2000), whereas *T. pagei* is only recorded from two levels that coincide with pulses of cosmopolitan faunal invasions; this suggests that *T. pagei* could have been involved in colonising processes in this basin, but long-term colonisation was prevented by the rapid environmental changes that took place there. This suggestion might be supported by the wide geographical distribution of *T. pagei* in Cantabria (Mader 1986), Scotland (Powrie 1870), the Welsh Borderland (Turner 1973), northern France (Goujet and Blicke 1979), Belgium (Blicke and Goujet 1991), the Baltic region and Podolia (Karatajūtė-Talimaa 1978; Talimaa 2000), the central Urals (Märss 1997), Spitzbergen (Ørvig 1969; Goujet and Blicke 1977, 1979), the Canadian Arctic (Vieth 1980) and Idaho, USA (Dehler and Elliott 2002), together with the faunal and lithological continuity of the Mauro-Ibero-Armorican Basin.

The levels from which *T. pagei* is recorded, together with the excellent preservation of the scales, which do not show signs of having been transported, indicate that this species lived in very shallow waters close to the coast, as indicated by the associated palaeochannels and other sedimentary structures. In general the Early Devonian facies of Celtiberia indicate a typical shelf environment (see Carls 1999).

Records of *T. pagei* are mainly associated with tentaculitids, brachiopods, remains of phyllocarids, and especially conodonts and remains of acanthodians (*Gomphonchus*, *Nostolepis*, *Machaeracanthus*, *Cheiracanthoides*), chondrichthyans (*Leonodus carlsi*, *Iberolepis aragonensis*, *Lunalepis leonensis*) and placoderms.

*T. nachoi* sp. nov. occurs in submembers d2c $\beta$  and d3a $\beta$ , together with a rich fauna of brachiopods dominated by *Acrospirifer beaujeani* and *Euryspirifer*, and with the conodont *Icriodus curvicauda*. The age of these levels is early–middle Pragian. It is possible that parts of these levels represent period of clearer water and slightly deeper conditions on the platform than those in which *T. pagei* lived (Carls 1999).

Apart from the taxa mentioned, numerous fish remains occur together with *T. nachoi* but in contrast to the *T. pagei* association, these are mainly chondrichthyans (*Leonodus carlsi*, *Lunalepis leonensis*, *Cladolepis* sp., *Celtiberina maderei*, *Nogueralepis teruelensis*) and sarcopterygians (*Onychodus* sp.), the lack of acanthodians being remarkable. Therefore, there are differences not only in the ages of the *T. pagei* and *T. nachoi* occurrences but also in their faunal environmental associations.

*Acknowledgements.* We thank Dr Susan Turner and Dr Valentine Karatajūtė-Talimaa for their comments on our material. Dr Karatajūtė-Talimaa loaned some scales of *T. pagei* from Podolia for comparative purposes. Dr Helga Groos-Uffnerde facilitated the study of Vieth's collection housed at Göttingen and Prof. Hans-Peter Schultze and Dr Gloria Arraitia helped with the study of Gross' collection stored in Berlin. Oscar Sanisidro carefully drafted the histological reconstruction of Text-figure 3. Scientific comments by Dr Susan Turner and Dr Tiu Maars, editorial comments by Dr Lyall I. Anderson, and the editorial and linguistic help of Prof. David J. Batten improved this paper. We thank all four for their effort and assistance. This work has been partially financed by the 'Programa de Estancias breves del FPI-MCYT' (HB), the Alexander von Humboldt-Stiftung (JIV-R) and the Project BTE 2003–01609 'Ministerio de Ciencia y Tecnología y Fondo Europeo de Desarrollo Regional FEDER'. This work is a contribution to IGCP Project 499: 'Devonian land-sea interaction: evolution of ecosystems and climate'.

## REFERENCES

- BLIECK, A. and GOUJET, D. 1978. A propos de nouveau matériel de Thélodontes (Vertébrés Agnathes) d'Iran et de Thaïlande: aperçu sur la répartition géographique et stratigraphique des Agnathes des "régions gondwaniennes" au Paléozoïque moyen. *Annales de la Société Géologique du Nord*, **97**, 363–372.
- — 1991. Les vertébrés du Devonien Inférieur d'Arville et de Nonceveux (Belgique). *Annales de la Société Géologique du Nord*, 2<sup>o</sup> Serie, **1**, 67–78.
- BOTELLA, H. and VALENZUELA-RÍOS, J. I. 2002. Análisis comparativo de microvertebrados fósiles del límite Lochkoviense/Praguense (Devónico Inferior) en la Depresión Axial del río Cámaras (Cordillera Ibérica, provincia de Teruel). *Teruel*, **88-89** (for 2000–2002), 45–68.
- CALDWELL, M. W. and WILSON, M. V. H. 1995. Comparison of the body form and squamation of 'fork-tailed' agnathans with that of conventional thelodonts. *Geobios, Mémoire Spécial*, **19**, 23–29.
- CARLS, P. 1977. The Silurian-Devonian boundary in north-eastern and central Spain. 143–158. In MARTINSSON, A. (ed.). *The Silurian-Devonian boundary*. IUGS Series A, **5**, Stuttgart, 349 pp.
- 1999. El Devónico de Celtiberia y sus fósiles. *Memorias de las VI Jornadas Aragonesas de Paleontología* (25 Años de Paleontología Aragonesa', Homenaje al Prof. Leandro Sequeira), pp. 101–164.
- and VALENZUELA-RÍOS, J. I. 1999. Similitudes y diferencias estratigráficas entre el Pridoliense-Praguense celtibérico y armoricano. *Revista Española de Paleontología*, **14** (2), 115–128.
- — 2002. Devonian-Carboniferous rocks from the Iberian Cordillera. 299–314. In GARCÍA-LÓPEZ, S. and BASTIDA, F. (eds). *Palaeozoic conodonts from northern Spain*. Instituto Geológico y Minero de España, Serie Cuadernos del Museo Geominero, **1**. Madrid, 438 pp.
- DEHLER, C. M. and ELLIOTT, D. K. 2002. Marine-to-non-marine microvertebrate correlation in Lower Devonian strata of central-eastern Idaho. *Rocky Mountain Geological Society of America Meeting, Cedar City, Utah, Abstracts with Programs*, **34** (4), 52.
- DONOGHUE, P. C. J. and SMITH, M. P. 2001. The anatomy of *Turinia pagei* (Powrie), and the phylogenetic status of the Thelodonti. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **92**, 15–37.
- GAGNIER, P., TURNER, S., FRIMAN, L., SUAREZ-RIGLOS, M. and JANVIER, P. 1988. The Devonian vertebrate and mollusc fauna from Seripona (Dept. of Chuquisaca, Bolivia). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **176**, 269–297.
- GOUJET, D. 1984. Les poissons placodermes du Spitsberg. Arthroires Dolichothoraci de la Formation de Wood Bay (Dévonien Inférieur). *Cahiers de Paléontologie*, **1984**, 316 pp.
- and BLIECK, A. 1977. La faune de Vertébrés de l'horizon «Vogti» (Groupe de Red Bay, Spitsberg). Comparaison avec les autres faunes ichthyologiques du Dévonien inférieur européen. *Compte Rendus de l'Académie des Sciences, Serie D, Sciences Naturelles*, **284** (16), 1513–1515.
- — 1979. Les Vertébrés de l'Assise des Schistes et Grès de Pernes (Dévonien du Nord de la France). *Extrait des Annales de la Société Géologique du Nord*, **98**, 263–277.
- GROSS, W. 1967. Über Thelodontier-Schuppen. *Palaeontographica, Abteilung A*, **127**, 1–67.
- 1971. Unterdevonische Thelodontier- und Acanthodier-Schuppen aus Westaustralien. *Paläontologische Zeitschrift*, **45**, 97–106.

- KARATAJŪTĖ-TALIMAA, V. N. 1978. *Silurian and Devonian thelodonts of the USSR and Spitsbergen*. 'Mokslas', Vilnius, 334 pp. [In Russian].
- 2002. Lower Devonian (Lochkovian) thelodonts from the October Revolution Island (Severnaya Zemlya Archipelago, Russia). *Geodiversitas*, **24**, 791–804.
- KIAER, J. 1932. The Downtonian fauna of Norway. I. Anaspidia, with a geological introduction. *Skrifter Videnskapselskapet I, Matematiske-Naturvidenskapslige Klasse*, **6**, 1–139.
- MADER, H. 1986. Schuppen und Zähne von Acanthodien und Elasmobranchien aus dem Unter-Devon Spaniens (Pisces). *Göttinger Arbeiten zur Geologie und Paläontologie*, **28**, 1–59.
- MÄRSS, T. 1986. Squamation of the thelodont agnathan *Phlebolepis*. *Journal of Vertebrate Paleontology*, **6**, 1–11.
- 1997. Vertebrates of the Pridoli and Silurian–Devonian boundary beds in Europe. *Modern Geology*, **21**, 17–41.
- 1999. A new Late Silurian or Early Devonian thelodont from the Boothia Peninsula, Arctic Canada. *Palaentology*, **42**, 1079–1099.
- and KARATAJŪTĖ-TALIMAA, V. N. 2002. Ordovician and Lower Silurian thelodonts from Severnaya Zemlya Archipelago (Russia). *Geodiversitas*, **24**, 381–404.
- and RITCHIE, A. 1998. Articulated thelodonts (Agnatha) of Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **88**, 143–195.
- MURPHY, M. A. and VALENZUELA-RIOS, J. I. 1999. *Lanea* new genus, lineage of Early Devonian conodonts. *Bollettino della Società Paleontologica Italiana*, **37**, 321–334.
- — and CARLS, P. 2004. On classification of Pridoli (Silurian)–Lochkovian (Devonian) Spathognathodontidae (conodonts). *University of California Riverside, Campus Museum Contribution*, **6**, 1–25.
- NOVITSKAYA, L. I. and TURNER, S. 1998. *Turinia pagei* (Powrie): a new reconstruction of the soft organs of the cephalothorax. *Memoirs of the Queensland Museum*, **42**, 533–544.
- OBRUCHEV, D. V. 1964. Agnathan and fishes. In ORLOV, Y. O. (ed.). *Fundamentals of palaeontology*, **11**. Nauka, Moscow, 522 pp. [In Russian].
- ØRVIG, T. 1969. Vertebrates from the Wood Bay Group and the position of the Emsian–Eifelian boundary in the Devonian of Vestspitsbergen. *Lethaia*, **2**, 273–328.
- POWRIE, J. 1870. On the earliest known vestiges of vertebrate life; being a description of the fish remains of the Old Red Sandstone rocks of Forfarshire. *Edinburgh Geological Society, Transactions*, **1**, 284–301.
- STENSIÖ, E. A. 1958. Les Cyclostomes fossiles ou Ostracodermes. 173–425. In GRASSE, P.-P. (ed.). *Traité de Zoologie*, **13**. Masson et Cie, Paris, 924 pp.
- TALIMAA, V. 2000. Significance of thelodonts (Agnatha) in correlation of the Upper Ordovician to Lower Devonian of the northern part of Eurasia. 69–80. In BLIECK, A. and TURNER, S. (eds). *Palaeozeic vertebrate biochronology and global marine/non-marine correlation. Final report of IGCP 328 (1991–1996)*. Courier Forschungsinstitut Senckenberg, **223**, 575 pp.
- TRAQUAIR, R. H. 1896. The extinct vertebrate animals of the Moray Firth area. 235–285. In HARVIE-BROWN, J. A. and BUCKLEY, T. E. (eds). *A vertebrate fauna of the Moray Basin*. David Douglas, Edinburgh, Volume 2, 309 pp.
- TRINAJSTIC, K. 2001. A description of additional variation seen in the scale morphology of the Frasnian thelodont *Australolepis seddoni* Turner and Dring, 1981. *Records of the Western Australian Museum*, **20**, 237–246.
- TURNER, S. 1973. Siluro-Devonian thelodonts from the Welsh Borderland. *Journal of the Geological Society, London*, **129**, 557–584.
- 1976. Thelodonti (Agnata). 1–35. In WESTPHAL, F. (ed.). *Fossilium Catalogus I, Animalia*. Dr W. Junk B. V., Gravenhage.
- 1984. Studies of Palaeozoic Thelodonti (Craniata: Agnatha). Unpublished PhD thesis, University of Newcastle-upon-Tyne, 223 pp.
- 1986. Vertebrate fauna of the Silverband Formation, Grampians, Western Victoria. *Proceedings of the Royal Society of Victoria*, **98** (2), 53–62.
- 1991. Monophyly and interrelationships of the Thelodonti. 87–119. In CHANG, M.-M., LIU, Y.-H. and ZHANG, G.-R. (eds). *Early vertebrates and related problems of evolutionary biology*. Science Press, Beijing, 514 pp.
- 1995. Devonian thelodont scale (Agnatha, Thelodonti) from Queensland. *Memoirs of the Queensland Museum*, **38**, 677–685.
- 1997. Sequence of Devonian thelodont scale assemblages in East Gondwana. 295–315. In: *Paleozoic sequence stratigraphy, biostratigraphy, and biogeography: studies in Honor of J. Granville (Jess) Johnson*. Geological Society of America, Special Paper, **321**, v+401 pp.
- 1999. Wenlock–Lochkovian (Gedinian) thelodont assemblages and their possible ecological significance. 42–78. In BOUCOT, A. J. and LAWSON, J. D. (eds). *Palaeoecommunities: a case study from the Silurian and Lower Devonian*. International Geological Correlation Programme, Project Ecostratigraphy, Final Report. Cambridge University Press, Cambridge, 895 pp.
- and DRING, R. S. 1981. Late Devonian thelodonts (Agnatha) from the Gneudna Formation, Carnarvon Basin, Western Australia. *Alcheringa*, **5**, 39–48.
- VERGOOSSEN, J. M. J. and YOUNG, G. C. 1995. Fish microfossils from Irian Jaya. *Memoirs of the Association of Australasian Palaeontologists*, **18**, 165–178.
- and YOUNG, G. C. 1992. Thelodont scales from the Middle–Late Devonian Aztec Siltstone, southern Victoria Land, Antarctic. *Antarctic Science*, **4**, 89–105.
- VALENZUELA-RÍOS, J. I. 1989. El Paleozoico de Nigüella (nota preliminar). *Azara*, **1**, 35–43.
- and BOTELLA, H. 2000. Datos preliminares sobre la fauna de vertebrados (Pisces) del Devónico Inferior de Nigüella (Cadenas Ibéricas). *Geogaceta*, **28**, 153–156.
- VIETH, J. 1980. Thelodontier-, Acanthodier- und Elasmobranchier-Schuppen aus dem Unter-Devon der Kanadischen Arktis (Agnatha, Pisces). *Göttinger Arbeiten zur Geologie und Paläontologie*, **23**, 1–69.
- WANG, R. 1993. Taxonomie, Palökologie und Biostratigraphie der Mikroichthyolithen aus dem Unterdevon Keltiberiens, Spanien. *Courier Forschungsinstitut Senckenberg*, **161**, 1–205.
- WANG, S.-T., DONG, Z.-Z. and TURNER, S. 1986. Discovery of Middle Devonian Turiniidae (Thelodonti: Agnatha) from Western Yunnan, China. *Alcheringa*, **10**, 315–325.