# The anatomy of *Turinia pagei* (Powrie), and the phylogenetic status of the Thelodonti

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ABSTRACT: Little is known regarding the internal anatomy of thelodonts, with most of the available information coming from a single specimen, the holotype of Turinia pagei (Powrie). Previous descriptions have led to many partial, or conflicting interpretations. Herein, we describe fully the anatomy of T. pagei based on the holotype and additional material. T. pagei possessed a branchial system composed of eight pairs of gills, a buccal/nasohypophyseal region lined with minute denticles, comparable to buccopharyngeal denticles of sharks, and possessed a stomach which is preserved by sediment infill in the holotype specimen. Contrast between the petrological character of the gut infill and the sediment in which the animal is preserved suggests that the gut was infilled in vivo and that T. pagei was probably a deposit feeder. Phylogenetic analysis resolves T. pagei and the Galeaspida as sister-taxa, comprising a sister-group to the Osteostraci plus jawed vertebrates. In contrast to the view that has prevailed hitherto, thelodonts with a dorsoventrally compressed cross-sectional profile comprise a monophyletic group, of which T. pagei is the least derived member. The furcacaudiforms are resolved as an unnatural group, one taxon being the sister taxon to the 'conventional' thelodont clade, and the other, the sister taxon to this clade plus galeaspids, osteostracans and jawed vertebrates. The analysis agrees with the earlier view that thelodonts lack distinct synapomorphies, but we argue that distinct synapomorphies are not a requisite of monophyly.

KEY WORDS: 'agnathan', chordate, cladistics, homoplasy, palaeobiology, stem-gnathostome, thelodont, vertebrate.

'The discovery by Powrie (1870) of the first intact thelodont, "Cephalopterus" pagei, from the Lower Devonian of Scotland, did little to elucidate the relationships of the group. Instead, over the years, this specimen seems to have confused the issue' (Turner & van der Brugghen 1993, p. 127).

Thelodonts are extinct jawless vertebrates, which characteristically possess a dermal skeleton composed of thousands of microscopic scales that were commonly dispersed after death and the decay of supporting soft tissues. Thus, the fossil record of these animals is dominated by jumbled collections of scales that are recovered by acid dissolution of limestones (e.g. Turner 1973). Rarely, however, rapid burial, lack of current activity and absence of scavengers have combined to preserve the skeleton of these animals in such a way that the articulation of the scales has been affected only by decay of the internal organs and eventual collapse of the carcass. Such events are extremely rare but of great importance because it is only under these circumstances that the full variation of scale morphology can be fully appreciated (Märss & Ritchie 1998). Furthermore, it is precisely because such preservational events are so rare that we know so little about the anatomy and palaeobiology of this highly enigmatic group of vertebrates.

Although thelodonts are commonly considered to be jawless vertebrates, it has been suggested that these animals are more closely related to sharks than to any other group of extinct or extant vertebrates (Traquair 1899a; Turner 1991). In contrast, Janvier (1981, 1986, 1996a, b) has argued that thelodonts express only symplesiomorphic characters (shared-primitive characters) and no autapomorphic features. This has led to the interpretation of thelodonts as a paraphyletic ensemble, of which some members may be more closely related to crown-group gnathostomes than others (e.g. Forey & Janvier 1993, 1994; Wilson & Caldwell 1998; see Donoghue *et al.* 

2000 for a definition of crown-group and stem-groups concepts and how they are applied with respect to lower vertebrates). In contrast, Turner (1991) and Turner & van der Brugghen (1993) argued that all animals which possess thelodont-grade scales are united by a synapomorphy of scale histology and structure, although they concurred with the view of thelodonts as primitive crown-group gnathostomes, or as the sister-group of crown-gnathostomes.

Conventionally, thelodonts have been perceived as dorsoventrally compressed, with unsupported pectoral flaps, dorsal and anal fins, and a hypocercal tail (Turner 1991). However, whilst this bauplan may stand for most thelodonts, it does not encompass the recently discovered Furcacaudiformes (Wilson & Caldwell 1993), which also possess thelodontiform scales. The Furcacaudiformes are characterised by a deep, hump-backed and laterally-compressed body, approximately symmetrical tail, and lack the anal fins of dorso-ventrally compressed thelodonts (Wilson & Caldwell 1993, 1998; Caldwell & Wilson 1995). The existence of two distinct body forms of thelodontiform scale-bearing jawless vertebrates reinforces Janvier's (1981, 1996b) contention that, as conventionally perceived, the Thelodonti are a paraphyletic group. However, the lack of thelodont synapomorphies might result as much from absence of evidence as evidence of their absence. Considering the importance of thelodonts in scenarios currently being developed to explain the origin of jaws and teeth (e.g. Mallatt 1996; Smith & Coates 1998, 2001) the need to understand thelodont anatomy more fully has never been of greater importance.

#### 1. Turinia pagei (Powrie): a history of research

The first, and most complete articulated specimen of *Turinia* pagei was discovered in the Lower Old Red Sandstone of



interpretations	made by Turne.	r (1982, 1991, 1	992).									
Author	Powrie (1870)	Lankester (1870)	Traquair (1899a, b)	Kemna (1903)	Stensiö (1927)	Westoll (1945)	Stensiö (1958/1964)	Turner (1982)	Turner (1991)	Turner (1992)	Novitskaya & Turner (1998)	Herein
Affinity	ray-like	early shark/ray	derived shark, ancestor of	Thelodus	ray-like	neotenic osteostracan	heterostracan	thelodont	thelodont	thelodont	thelodont: basal	thelodont
Exposed surface	ventral	ventral	dorsal	dorsal	dorsal (implicitly)	ventral	dorsal	ventral	ventral & dorsal	Ι	dorsal	ventral
Mouth Anterior funnel	no evidence -	1 1	no evidence -	1 1		1 1	1 1	anterior buccal region	anterior flexible buccopharynx	anterior buccopharynx	sub-terminal olfactory bulbs and tracts	no evidence buccopharynx
Longitudinal ridge	?branchial apparatus	I	I	I	occipital region	aortic groove	occipitus	?pharynx	oesophagus and branchial arches	oesophagus and branchial arches	endocast of brain and pineal	oesophagus
Transverse ridges	?branchial apparatus	I	branchial skeleton	cartilaginous bracnhial skeleton	interbranchial ridges	roof of oralo- branchial chamber	branchial chambers and arches	branchial arches	branchial apparatus	branchial apparatus	branchial sacs and arches	branchial pouches and interbranchial rid ges
Number of oills/arches	7 or 8	I	8	8	> = 7	-	66	7 or 8	8	8	7 (?8)	8
Branchial	I	I	I	I	no evidence	I	?common	?separate	?separate	?separate	?separate	separate
Trunk infilling	I	I	I	I	oesophageal foramen	I	oesophageal foramen	gut	trunk musculature	oesophagous	stomach	stomach
Anal fin Caudal fin	no evidence 'entirely		no evidence heterocercal	1 1		1 1	1 1		present quite	present almost	?right of trunk ?hypocercal	no evidence ?hypochordal
Dorsal fin	no evidence	I	no evidence	I	I	I	I		symmetrical ?present	symmetrical 'small,	I	no evidence
Pectoral	fins	I	fin-folds	fins	fins/flaps	fins	fins	fins/flaps	flaps	fins and flaps	fins	flaps
Ventral fin	no evidence	Ι	no evidence	I	Ι	I	Ι	I	I	I	I	no evidence

**Table 1** A summary of the varying interpretation of features in the holotype specimen of *Turinia pagei* (NMS.G.1891.92.133); Novitskaya & Turner (1998) have also provided such a table but this does not include the interpretations made by Turner (1982, 1991, 1992).

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Turin Hill, near Forfar, Tayside (Fig. 1a-c). It was first formally described by Powrie (1870) and assigned the generic name Cephalopterus, although this was later identified as a junior homonym by Traquair (1896), who proposed the replacement name Turinia. Powrie interpreted the upper surface of this specimen as the ventral surface of the animal, the transverse ridges of the cephalothoracic region as the remains of a branchial apparatus (with 7-8 gills), and identified the presence of pectoral fins (see Table 1 for a history of changed interpretations of the holotype specimen). Lankester (1870) concurred with Powrie's interpretation of the orientation of the specimen, but this was later disputed by Traquair, who reinterpreted the upper surface of the specimen as the dorsal side of the animal, based entirely upon the assumption that the plesiomorphic condition of the vertebrate tail is heterocercal. Traquair (1899a, b) found no evidence of gills and preferred instead to interpret the transverse ridges of the cephalothorax as remains of branchial arches. Traquair (1899a) also synonymised Turinia with Thelodus on the basis of comparisons of scale morphology in the articulated holotype and isolated scales described earlier by Agassiz, but this synonymy has not received common acceptance. He suggested that vertebrates of this type were descendants of the elasmobranchs, and ancestors of cephalaspids such as Ateleaspis (a primitive osteostracan), drepanaspids, and finally, pteraspids.

Kemna (1903) concurred with Traquair (1899b) in using the caudal fin to interpret the holotype as presenting its dorsal surface, and attempted to evaluate evidence in favour of an interpretation of the transverse structures in the cephalothorax as either branchial arches or branchial pouches. Kemna (1903) also found no evidence for branchial openings.

Stensiö (1927) followed Traquair in his interpretation of the orientation of the holotype, but differed in that of the morphological structures preserved in the cephalothorax. To Stensiö, the cephalothorax represented a continuous visceral endoskeleton perforated caudally by a large oesophageal foramen, as in cephalaspids. Stensiö interpreted the longitudinal ridge that runs along the rostro-caudal axis of the cephalothorax as the occipital region of an endocranium, like that of heterostracans. However, this interpretation of the fossil is strongly biased by his support for an heterostracan affinity, and Stensiö made many suggestions for the positions of structures for which there is no evidence. While this bias is implicit in Stensiö's interpretation of the holotype, his suggestions for the presence of a mouth, olfactory organ, perichondral bone, labyrinth, orbitotemporal and ethmoidal regions of the brain, and mesodermal gills have sometimes been taken as fact by later authors. Stensiö further suggested that the fins of the cephalothorax might be interpreted as true pectoral fins or as simple fin flaps, dependent (respectively) upon whether each of the branchial chambers had separate openings to the outer surface, or whether the chambers possessed confluent efferent ducts that opened to a single pair of external branchial pores, as in heterostracans and Myxine.

Westoll (1945) reinterpreted the anatomy of *T. pagei* as part of a re-examination of the relationships and palaeobiology of cephalaspids. He drew comparison between the general layout of the gills and cephalothorax of *T. pagei* and of cephalaspids, reverting to Powrie's original interpretation of the specimen as ventral-up based on the absence of dorsal anatomical structures. Transverse ridges in the cephalothorax were interpreted as impressions of a cartilaginous endoskeletal roof of an orobranchial chamber, after decay of the soft tissues. The absence of dorsal structures was attributed to the upper surface of the holotype representing solely the ventral dermal scales. Westoll was so impressed by the similarity in general layout of the branchial area in *T. pagei* and cephalaspids that he went on to suggest that *T. pagei* represented either a larval or neotenic cephalaspid, based largely on the absence of an unmineralised endoskeleton (*contra* Stensiö 1927).

Turner (in Allen et al. 1968) described a second, albeit partial, articulated specimen of T. pagei (BU 873) from the upper part of the Raglan Mudstone Formation (basal Devonian) exposed in Wilderness Quarry, Mitcheldean, Gloucestershire. The specimen was interpreted as a portion of the left margin of the cephalothorax, oriented ventral-up, preserving no trace of the pectoral fin/fin flap, and believed to preserve an outline trace of gill pouches. Turner (1982) provided a further description of the holotype in which she noted the absence of distinct nasal sacs and orbits, and the presence of a gut region immediately ventral to the cephalothorax, all assuming that the holotype is preserved in ventral aspect. In contrast to Stensiö and Westoll, Turner reinterpreted the longitudinal groove as a connection between buccal region, pharynx and gut; tiny scales on the outer margin of the branchial ridges were tentatively interpreted as covers to gill openings. Turner (1991) later interpreted the longitudinal ridge as the oesophagus and mid-line confluence of cartilaginous arches, thus preserving both dorsal and ventral anatomical features. In support, Turner cited an earlier suggestion (Turner 1982) that the preserved squamation was a mixture of both dorsal and ventral scales; the general paucity of scales was accounted for by post mortem redistribution. Turner reinterpreted the triangular sediment-infill of the posterior margin of the cephalothorax as having housed trunk musculature, and was also able to discern evidence of nasal sacs, pore-canal scales, dorsal and anal fins, and an almost symmetrical tail, similar to that of Loganellia scotica. The sedimentary infill of the rostral portion of the trunk was again re-interpreted by Wilson & Caldwell (1993) as the position of a gut. Märss & Ritchie (1998) described the squamation of the holotype specimen under the tentative interpretation that it is preserved in dorsal aspect.

Novitskaya & Turner (1998) considered the holotype to be preserved in dorsal aspect based in part on the inferred presence of 'imprints of the olfactory tracts and aspects of the brain' (Novitskaya & Turner 1998, p. 536). They also interpreted the presence of a pineal pit and macula, tentative evidence for division of the brain into telencephalon, mesencephalon (a distinct diencephalon is also distinguished), a cast of the myelencephalon, and two horizontal semicircular canals. These authors also observed evidence for branchial sacs, efferent branchial canals, and olfactory tracts leading to paired nasal sacs (i.e. olfactory bulbs) adjacent to, but separate from, an anterior mouth. The presence of olfactory organs with external openings separate from the mouth is important because, if correct, it contradicts the hypothesis that thelodonts possessed a common oral and nasohypophysial opening (van der Brugghen & Janvier, 1993; Janvier 1996a).

Despite the paucity of material on which our understanding of the anatomy of *T. pagei* is based, there is evidently considerable confusion over how the two existing articulated specimens should be interpreted. Below we provide a full redescription of the available material and assess existing interpretations of the anatomy of *T. pagei*.

#### 2. Systematic palaeontology

Chordata Bateson, 1886 Vertebrata Linnaeus, 1758 Gnathostomata Cope, 1889 Thelodonti Jaekel, 1911 Coelolepidae Pander, 1856

Remarks. The Linnean rank-free suprageneric classification above is based on our cladistic analysis and retains the Thelodonti as a high-level name for the monophyletic group which includes 'traditional' thelodonts plus Furcacauda heintzi. The family Coelolepidae was erected by Pander (1856) to include three newly described genera: Coelolepis, Pachylepis and Nostolepis. The latter is now widely considered to be an acanthodian (e.g. Moy-Thomas & Miles 1971) and the two first-named to be junior synonyms of Thelodus Agassiz, 1839 (Karatajute-Talimaa 1978). The family name has maintained a consistency of usage even though Jordan (1905) proposed the replacement name Thelodontidae. The family-group name Coelolepidae is here retained in accordance with ICZN Article 40 (ICZN 1999) and incorporates the monophyletic group of dorsoventrally flattened taxa traditionally considered as thelodonts, represented in our analysis by Turinia, Shielia, Loganellia and Phlebolepis, together with the type genus Thelodus. Adherents to Linnean rankings may prefer to elevate this group to the rank of Superfamily Coelolepidoidea. Our analysis (Fig. 9) suggests that the laterally compressed furcaudiforms constitute a paraphyletic assemblage which is less derived than the Coelolepidae, although it is recognised that this is not very well supported and that further work may demonstrate the monophyly of the Furcacaudiformes. Together, F. heintzi and the Coelolepidae, as the Thelodonti, constitute the sister group to the clade (Galeaspida (Osteostraci, jawed vertebrates)).

#### Genus Turinia Traquair, 1896, p. 262.

- 1870 *Cephalopterus* Powrie, pp. 298–9 [junior homonym of *Cephalopterus* Geoffroy Saint-Hilaire, 1809, the Amazonian umbrella bird].
- 1896 Turinia Traquair, p. 262.

#### Turinia pagei (Powrie), 1870 (Figs 1–8)

- \*v 1870 Cephalopterus Pagei, Powrie, pp. 298–9, pl. XIV, fig. 16.
- v 1896 Turinia Pagei; Traquair, p. 262.
  - 1976 *Turinia pagei* (Powrie); Turner, pp. 13–14 [synonymy to 1973].
    - 1978 Turinia pagei (Powrie); Karatajute-Talimaa, pp. 118–22, pls XXXIII-XXXV, pl. XXXVI, figs 1–18;
      p. XXXVII, figs 1–9; pl. XXXVIII-XXXIX; pl. XL, fig. 7; pl. XLII, figs 4, 5, 9; text-fig. 5; 26–1,2; 7–1,23.
- v 1982 *Turinia pagei* (Powrie); Turner, pp. 884–5, pl. 97, figs 1–3.
  - 1989 Turinia pagei (Powrie); Märss, fig. 176I2.
  - 1991 Turinia pagei; Turner, figs 1a; 5n, p; 6h; 7g.
  - 1992 *Turinia pagei*; Turner, pp. 22–4, 35–7
- v 1996a Turinia; Janvier, pp. 124-5, fig. 4.24D.
- v 1996 Turinia pagei; Mallat, fig. 13D.
- 1997 *Turinia pagei* (Powrie); Märss, pl. 1, figs 3–8; pl. 5, figs 1–3.
- v 1998 *Turinia pagei* (Powrie); Novitskaya & Turner, figs 1A, B; 3; 4.
- v 1998 *Turinia pagei* (Powrie); Märss & Ritchie, pp. 189, 191–3, fig. 49.

#### 3. Material

*Turinia pagei*: holotype (NMS.G.1891.92.133) from Turin Hill, near Forfar, Tayside; articulated but incomplete specimens (BU 872a, b; 873; 874; 875), Wilderness Quarry, Mitcheldean, Gloucestershire.

#### 4. Description

#### 4.1. NMS.G.1891.92.133 (holotype)

In the description and interpretation of this specimen we assume *a priori* that it is a vertebrate (based on the presence of scales composed of dentine), that it is preserved in either dorsal or ventral aspect (based on bilateral symmetry) and that the expanded portion of the anatomy represents rostral, whereas the tapering portion is caudal in relative orientation. Upper and lower, left and right are used in reference only to the specimens and do not refer to biological orientation.

The holotype (Figs 1–5) is 330 mm in length and 164 mm in maximum width and preserves a significant amount of threedimensional information, such that there is a 22 mm inflation of the cephalothorax, and 69 mm between the highest point on the cephalothorax and lowest point preserved of the tail. The cephalothorax, which dominates the anatomy, is 165 mm in maximum length. The trunk reaches a maximum width of 33 mm and, including the fin, is 160 mm in preserved length.



**Figure 2** Camera-lucida drawing of the salient features preserved in the holotype specimen of *Turinia pagei*; magnification  $\times 0.49$ . Interpretations of the structures are substantiated in section 5 of the text.

The caudal fin is incomplete, although the remains are articulated, and lie at approximately  $70^{\circ}$  to the horizontal (plane of the cephalothorax), reaching a maximum preserved spread of 50 mm. A counterpart has never been described and its whereabouts is unknown.

**4.1.1. Cephalothorax.** The distribution of scales over the surface of the cephalothorax is highly variable (compare Fig. 1a– c). Raised portions are marked by an absence of preserved scale cover, and also by a layer of sediment (identical to the sediment type surrounding the specimen) that lies between an upper layer of scales, preserved with the crowns uppermost, and a lower scale layer, where the pulp cavities face up. The apparent absence of scale cover from most of the upper layer is not a taphonomic feature (*contra* Turner 1991), as there are clear imprints of scale bases covering these areas (e.g. Fig. 3a), and they probably remain attached to the missing counterpart.

Raised areas include a rostro-medial, cone-shaped sediment infill (Fig. 3a, b) that begins 8 mm from the rostral margin, with a width of 30 mm, and tapers to 14 mm, over a length of 35 mm. This infill is also distinguished by the presence of extremely small (c. 0.5 mm in length) tear-drop shaped scales, overlain by a patchy distribution of larger (>1 mm) equidimensional scales which are oriented crown-up (Fig. 3b). The smaller scales taper in a forward-pointing orientation and are aligned obliquely to the rostro-caudal axis of the animal, converging about the midline. The portions of the cephalothorax lateral to the funnel-shaped structure (Fig. 3a) are low-lying, exhibit no evidence of sediment infill, and there is a greater complement of *in-situ* scale cover, scales are approximately 1 mm in diameter and equidimensional. These scales taper to a thin band caudo-laterally, which skirts the central raised portion of the cephalothorax.

The mid-line of the raised cephalothorax continues caudally from the funnel-shaped structure to a longitudinal ridge (slightly offset to the left; Figs 3a, 4a, b) which runs the length of the cephalothorax, along a shallow medial trough, to a cone-shaped, marl-filled area at the core of the rostral portion of the trunk (63 mm, tapering from 58 mm to 3 mm). The longitudinal ridge appears to be divided into segments corresponding to adjacent transverse structures that dominate the cephalothorax (Fig. 4a, b); six rostral divisions are clearly discernible, with a further two faintly preserved at the caudal end of the cephalothorax (designated 1 to 8 from rostral to caudal). The transverse structures are gently sigmoidal in outline, increasing in size from 1 to 6, and again decreasing from 6 to 8; they vary in orientation through approximately  $60^{\circ}$ , from slightly rostro-lateral (1), to strongly caudo-lateral (8). The shape of the transverse structures differs on left and right halves of the holotype, and this appears to have resulted from slight collapse of the specimen onto the left margin (as viewed) where scales are most poorly articulated. As a result, the right half of the specimen appears to be in a better state of preservation (Fig. 4a). The transverse segments to the right of the mid-line are further divisible into medial, lateral and outer portions; the lateral divisions are only faintly segmental and connect to form a rostro-caudal ridge (Figs 1c, 4a). The ridge continues beyond the segmentation, to the rostral margin of the animal (parallel to the rostral cone-shaped sedimentary infill), and can tentatively be traced continuing caudally along the margin of the sedimentary infill of the trunk. The inner portion of the segments appears to be connected to the longitudinal ridge, which occupies a shallow medial trough (Fig. 4a, b), from which they expand and inflate laterally. The outer portion of the transverse segments is characterised by deep clefts (Fig. 4a, c, d) that grade into the flat, low-lying lateral to caudo-lateral extensions of the cephalothorax on both left and right sides. The clefts are lined with

very small scales (c. 0.5 mm in length, comparable to those occupying the cone-shaped sedimentary infill at the mid-rostrum; Fig. 4d) that taper rostro-medially and are overlain by large equidimensional scales or partial sediment cover bearing the impression of such scales (c. 2 mm in diameter). Transverse structures to the left of the longitudinal ridge are more sigmoidal in outline (Fig. 1), but this appears artefactual as the break in slope along the outer-lateral margin of the cephalothorax corresponds to the intermittent lateral ridge connecting the segments on the right side of the specimen.

Clefts in the outer portions of the transverse segments result in an indented margin to the up-standing cephalothorax. The low-lying, lateral and caudo-lateral extensions of the cephalothorax bear caudo-laterally oriented scales that are rhombic in outline (Fig. 4c, upper right), with their crowns facing into the sediment; they diminish in size caudally and medially. The outline of the cephalothorax is delimited by caudally oriented scales; the scales form a sharp, natural edge with crowns directed away from the animal. The caudal margin of the cephalothorax is strongly concave (Figs 1, 4a, b) and tapers dramatically to the trunk and tail (Fig. 5a, c).

**4.1.2. Trunk.** The rostral portion of the trunk overlaps with the outline of the cephalothorax (Figs 1, 5a). The core of the trunk is dominated by a sedimentary infill (Figs 1, 5a-c), some of which appears to have been prepared away at some stage and subsequently glued back into place. This sediment is much finer than the matrix which surrounds the specimen, and the presence of scale-base imprints over the surface of the infill (Fig. 5a) suggests that it occupies the interior of the trunk. The margins of the sedimentary infill are sharp and distinct (Fig. 5a, b), and the structure tapers from 54 mm to approximately 5 mm over 116 mm, terminating abruptly. The remainder of the trunk through to the tail is represented by a concentration of scattered scales of uniform morphology (see Märss & Ritchie 1998; Fig. 5c), with a slight scatter to right, immediately rostral to the tail, and a prominent ridge constituting its left margin.

**4.1.3. Tail.** Most of the tail is missing and only a small portion of a fin is preserved, which exhibits a distinct lower margin (Fig. 5c). Scales within this preserved portion have a lath-like outline and are organised into zones. The caudal margin of the fin is not preserved.

#### 4.2. NMS.G.1891.92.134

This specimen is simply a patch of articulated scales, preserving no anatomical features (also figured by Ørvig 1969, fig. 2a). The equidimensional shape of the scales suggests that this specimen represents a portion of the cephalothorax.

## 4.3. Wilderness Quarry Specimens (BU 872a, b; 873; 874; 875)

**4.3.1. General.** These specimens almost certainly represent fragments of a single articulated animal although extensive preparation of many areas prevents relative reorientation of the fragments.

**4.3.2. BU 872a, b** (part and counterpart or adjacent fragments; Fig. 6). The specimens comprise a patch of scales that can be oriented based on the direction in which the scales taper. The scales are well to poorly articulated, from a finite right margin to a truncated irregular left margin, respectively. Close to the anteriormost preserved margin, scales are oriented with crowns facing out, in a manner directly comparable to the marginal scales which border the antero-lateral fins in the holotype of *Turinia pagei*; scale orientation and diminution in size are also comparable to the extent that this patch of scales is identified as an antero-lateral fin. In comparison with the fins of the holotype, both dorsal and ventral scale layers are present



**Figure 3** Holotype of *Turinia pagei* (Powrie) (NMS.G.1891.92.133): (a) buccopharyngeal region, frame width 52 mm; (b) centre-field of B at higher magnification, frame width 50 mm; interpretations of the morphology are given in Figure 2.



**Figure 4** Holotype of *Turinia pagei* (Powrie) (NMS.G.1891.92.133): (a) branchial region on right (sinistral) side, frame width 108 mm; (b) detail of the pharyngeal region, frame width 50 mm; (c) efferent gill openings, frame width 31 mm; (d) denticles in efferent region of gill, frame width approximately 15 mm; interpretations of the morphology are given in Figure 2.



**Figure 5** Holotype of *Turinia pagei* (Powrie) (NMS.G.1891.92.133): (a) overview of stomach, frame width 120 mm; (b) caudal portion of digestive tract, frame width 57 mm; (c) fin in caudal region, frame width 157 mm; interpretations of the morphology are given in Figure 2.



**Figure 6** Specimen BU 873 of *Turinia pagei* (Powrie) from Wilderness Quarry; maximum length of figured portion in foreground 131 mm; background figure is a close-up of the squamation in the lower portion of the foreground figure; frame height 24 mm.

and it is possible to discern variation in scale shape, which is not possible on the holotype. The breakdown in scale articulation at the truncated left margin of BU 872a, b corresponds to the outer portion of the cephalothorax in the holotype.

**4.3.3. BU 873.** The main specimen described by Turner (*in* Allen *et al.* 1968; Fig. 7a–c) is a well-articulated patch of

scales and exhibits a considerable amount of three-dimensionality, although whether this is representative of original anatomy is unclear. Like the preceding specimen, BU 873 can be oriented on the basis of scale orientation. The scales range from equidimensional to slightly greater in length than width, which by comparison with scale size and shape distribution in the holotype, and in other thelodonts (cf. Märss & Ritchie 1998), suggests that this specimen represents a portion of the cephalothorax. Generally, only a single layer of scales is discernible, but there is limited evidence for a small patch of overlying scales encapsulating a pocket of sediment on the anterior portion of the specimen; the scales of the two layers face in opposing orientations. Outliers of siltstone are reminiscent of the transverse portions of the cephalothorax of the holotype. However, these outliers remain because of the undulating nature of surface on which the scales are preserved and they do not appear to represent anatomical features (Fig. 7b-c).

**4.3.4. BU 874.** This specimen is a small (c. 15 cm<sup>2</sup>; Fig. 7d) patch of scales which range from good to extremely poor articulation. The scales are slender (approximately two to three times as long as they are wide) and exhibit evidence of opposing layers, where articulated. Scale shape suggests that this specimen represents either a portion of an anterolateral fin or a portion of the trunk.

**4.3.5. BU 875.** Two layers of scales (Fig. 7e–g) that are separated by a pocket of sediment that tapers in thickness from 16 to 0 mm (Fig. 7f), one side exhibiting better scale articulation than the other (Fig. 7e *versus* Fig. 7g). There is also evidence for at least one layer of scales which joins the intervening scale layers at approximately  $45^{\circ}$  (Fig. 7f). Scales range in size from approximately 2 mm to <0.5 mm in maximum length and length: width ratio varies from 1:1 to 2:1.

**4.3.6. Additional fragments.** Several additional fragments are also known, although these are limited to two thin sections and small fragments preserving patches of scales no more than  $1 \text{ cm}^2$ ; it has not proved possible to relate these to any of the larger fragments.

#### 5. Interpretation

#### 5.1. General

It is clear from the presence of asymmetry in the holotype that it is necessary to consider taphonomy before interpreting the preserved anatomical features. Indeed, it is apparent from previous interpretations of the holotype that differing authors' opinions have arisen from the failure to dissociate the interpretation of preserved structures, from the anatomical features that can be assumed to be present based upon the preserved structures (e.g. Powrie 1870 *versus* Traquair 1899b).

#### 5.2. Orientation

Interpretation of the rostral-caudal orientation of the holotype can safely be assumed based on the remains of a tail which clearly distinguishes the caudal pole. However, the dorsoventral orientation of the holotype, as noted above, is more contentious. Based on the assumption that the plesiomorphic condition of the tail in vertebrates is heterocercal, and that *Turinia* is a primitive fish, Traquair (1899b) used the shape of the tail to determine that the holotype presented its dorsal surface. However, aside from changed views of vertebrate symplesiomorphies, there is not enough of the tail preserved to determine its shape, and so this criterion cannot be used to determine dorso-ventral orientation. Above the preserved fin web is a portion of the trunk which has traditionally been interpreted as a second lobe of the caudal fin (Fig. 1a, c). While the preserved portion of the fin web is largely two-dimensional, this



**Figure 7** Main specimens of *Turinia pagei* (Powrie) from Wilderness Quarry: (a–c) BU 873: (a) overview of specimen exhibiting putative gill pouches along right margin, maximum length of figured portion of specimen 153 mm; (b, c) close-up of putative gill pouches reveals that the structures are outliers of siltstone which remain due to the undulating nature of surface on which the specimen is preserved, (b) lateral view, (c) plan view, both views are of a portion of the specimen measuring 85 mm in length; (d) BU 874, maximum length of specimen 110 mm; (e–g) BU 875, maximum length of specimen 106 mm: (e) view of upper surface; (f) side view exhibiting at least two layers of scales, (g) lower surface.

overlying 'lobe' is preserved in considerable relief (Figs 1a, c, 5c), defining the left margin of the trunk, and possibly represents the position of the notochord, thus indicating the chordal 'lobe'. Nevertheless, the portion of the animal extending beyond the edge of the block, may represent more than just the tips of the dorsal and ventral caudal fin lobes. Indeed, there is an absence of scales comparable to those comprising the fin web surrounding the opposing 'lobe', and it is likely that the caudal fin was, thus, strongly asymmetrical. Therefore, the caudal fin was either hyperchordal, and the holotype is preserved dorsal-up, or else the caudal fin was hypochordal and the holotype is preserved ventral-up. Comparison with other thelodonts is instructive, because their tails are usually either symmetrical, with dorsal and ventral lobes equally developed, or nearly so (Cometicercus, Drepanolepis, Furcacauda, Pezopetallichthys, Loganellia, Shielia, Sphenonectris), or else hypochordal, and the ventral lobe most strongly developed (Lanarkia, Phlebolepis). If the tail of T. pagei is hypochordal, the holotype is preserved ventral-up. Corroborative evidence would be useful, and this may occur in the form of the sedimentary infill of the trunk (Figs 1, 2, 5a, b). This has been identified as a possible gut trace by Turner (1982) and Wilson & Caldwell (1993), an oesophagus by Turner (1992), and a stomach by Novitskaya & Turner (1998). The significance of this sedimentary infill will be expanded upon below, but at present it is important to note that it tapers rapidly, extending caudally as a narrow channel surrounded on all sides by trunk scales, and that it terminates abruptly at the left margin of the trunk (Fig. 5b). We cannot conceive of any other internal cavity of similar dimensions which might become infilled by sediment, or one that might terminate in such a caudal position; thus, we concur with the interpretation of a stomach and gut trace. By implication, the termination of the gut trace close to, but not at, the left margin of the trunk, must indicate a cloaca, or at least its proximity. Given that the anus and distal portion of the digestive tract are situated ventrally in all other vertebrates, we can interpret the left margin of the trunk at this point as ventral or close to ventral. If the cephalothorax is presented in ventral aspect, the tail has been rotated by 20°. Conversely, if the cephalothorax is presented in dorsal aspect, the tail would have to have been rotated through a minimum of  $160^{\circ}$ . It would be unreasonable to assume rotation of the tail through more than  $90^{\circ}$  (such that the dorso-ventral plane of the tail lies parallel to the horizontal plane of the cephalothorax), and further rotation would lead to a greater degree of disruption in the digestive tract and trunk than is observed. This provides affirmation that the holotype of T. pagei is oriented ventral-up.

#### 5.3. Cephalothorax

Features of the cephalothorax preserved in relief are also distinguishable from other portions of the anatomy by sedimentary infill (compare Fig. 1b to Fig. 1a, c). Further, because the infilling sediment is comparable to the matrix surrounding the animal, and separates two opposing layers of scales, it is most likely that features preserved in relief are internal body cavities. However, the opposing scale layers are almost certainly dorsal and ventral (Turner 1982), suggesting that the upper surface of the holotype is at the base of a rock bed, rather than the top, and that the opposing scale layer has collapsed after decay of supporting soft tissue and unmineralised cartilage, and/or that the intervening layer of sediment retained the threedimensional shape of the animal until compaction.

The rostral margin of the holotype lacks any indication of the presence of openings (Figs 1, 2, 3a, b), such as a mouth, nasohypophysial foramina or orbits, that might be indicated by a gap in squamation or by the presence of specialised scales. The conspicuous indentations in the rostrolateral margins of the cephalothorax (Figs 1, 2) may, however, represent the position of eyes or nostrils. The rostral position of the cone-shaped sedimentary infill (Fig. 3a, b) leads to three possible interpretations: an oral cavity, a prenasal sinus and nasopharyngeal duct, or both. The lack of a distinct rostral margin to the structure, and the lack of firm evidence for a mouth and/or nasohypophysial foramen elsewhere, prevents resolution of these alternatives. The caudal tapering of the sedimentary infill is coincident with an increase in relief and increase in scale size, from the minute scales that occupy the rostro-lateral portion, to progressively larger scales that are more characteristic of the dominant cephalothoracic squamation. This change is likely to be the result of a 'cut-effect' as the preserved upper surface of the holotype passes through different layers of anatomy.

The cone-shaped structure continues caudally and appears to be connected to the longitudinal medial ridge, although the ridge is offset to the left and preserved in greater relief (Figs 3a, 4a, b). Tentative evidence of connection between the longitudinal ridge and the transverse structures, which are preserved in even greater relief, indicates that these should be considered together. It is most likely that the transverse structures represent a branchial apparatus, although detailed interpretation of these ridges and grooves has been one of the major areas of dispute. The presence of broad convex ridges with acute intervening troughs corroborates the interpretation of these features as internal moulds. Both Stensiö (1927) and Westoll (1945) interpreted them as internal moulds of a continuous endoskeleton. Westoll (1945) also contended that the holotype is ventral-up, and the structures represent impressions of the roof of the branchial endoskeleton. However, if this was the case, impressions of the branchial fossae would be preserved as broad and concave transverse troughs, not ridges. Alternatively, the structures could represent an internal cast of the animal's external morphology, infilled by sediment and the remains of the animal after death and decay of the supporting tissues. Another possibility is that the transverse structures represent the mould of a cast of external morphology of the endoskeleton alone. However, internal cavities were clearly infilled by sediment during or shortly after death, and so from the competing hypotheses it is most likely that the transverse structures represent internal moulds of gill pouches, or of branchial fossae and interbranchial ridges on the floor of an unmineralised endoskeleton. Whichever interpretation is chosen, the convex transverse ridges clearly reflect the presence of gills, and the intervening troughs, the presence of interbranchial ridges or arches. Preservation in relief by sedimentary infill, connection to the branchial chambers, and the rostral naso/oral-cavity, all indicate that the longitudinal ridge represents an internal cavity. This does not preclude existing interpretations as an endocast of various portions of the brain (Stensiö 1927, 1958, 1964; Novitskaya & Turner 1998), if it represents a post mortem infilling of a braincase and nerve canals. Alternative interpretations, including a dorsal aorta (Westoll 1945), pharynx (Turner 1982), or oesophagus (Turner 1991, 1992), are all equally plausible if the same biostratinomic scenario is envisaged. Indeed, as Turner (1991, 1992) has suggested, the longitudinal ridge could represent a composite of anatomical structures. It is possible to prune this list through consideration of the arguments presented in their support. Novitskaya & Turner (1998) asserted that specific structures are olfactory bulbs, semi-circular canals, or divisions of the prosencephalon, mesencephalon and rhomencephalon; no reasoning is provided to indicate how they reached their conclusions. As the holotype is preserved ventral-up, it is highly unlikely that the longitudinal ridge represents an endocast of the brain. Aside from this, the nature of connection of the structure to the branchiae makes a brain endocast-interpretation unlikely, unless one is willing to accept that the connections represent 3–4 mm diameter canals through an unmineralised endoskeleton for the branchial nerves. Furthermore, connection of the longitudinal ridge to the rostral naso/oral opening (not a pair of olfactory bulbs and tracts contra Novitskaya & Turner 1998) further precludes the interpretation of a brain endocast. Both Stensiö (1927) and Westoll (1945) considered the ridge to represent an aortic groove which occupies a similar medial position in osteostracans, where it has been interpreted as having housed an oesophagus and dorsal aorta (Janvier 1985a). However, Stensiö rejected this interpretation because of the relatively wide diameter and tapering nature of the ridge. In turn, Westoll (1945, p. 346) viewed 'Stensiö's objections to be unjustified in view of the absence of other structures that should also occur on his theory', and maintained the interpretation of the ridge as an aortic groove. Given the sedimentary infill of the branchial chambers, longitudinal ridge, and connecting ramifications of the longitudinal ridge, a more likely interpretation of this structure is part of the respiratory system, rather than as e.g., the aorta dorsalis, arteria branchialis afferens and arteria communicans. Therefore, the obvious interpretation of a median canal with connections to the branchial pouches, is a pharynx and afferent branchial ducts, respectively. The possibility that this structure represents a ventral aorta cannot be ruled out entirely, although it appears likely that the sedimentary infilling of internal body chambers is restricted to the respiratory system, and given the biostratinomic scenario proposed it is unlikely that the ventral aorta would become infilled by sediment.

The interbranchial grooves in the surface of the holotype are most strongly pronounced at their caudo-lateral margin where each branchial pouch tapers caudally and the squamation is characterised by minute denticles which point rostrally and towards the gill pouch (Fig. 4). It is unlikely that these comprise branchial covers as they are overlain by large ventral (crownup) scales. Alternatively, these patches of minute scales might be associated with gill septa, or represent gill operculae which are themselves covered by normal squamation; either way, they were clearly located internally. Adaxially to the lateral limit of the branchial pouches, the faintly segmented ridge which extends rostrally to the position of the putative eye of Turner (in Mallatt 1996), and caudally to the margin of the gut trace, is an area preserved in higher relief than the branchial pouches with a sharp lateral margin (Figs 1a, 4a); it is most likely to represent the presence of an unmineralised endoskeleton.

There is no evidence for an internal skeletal component to the lateral flap-like extensions to the caudolateral margins of the cephalothorax (a sub-triangular depression is clearly present in the right fin/flap of the holotype, but it is difficult to interpret; Fig. 1c); there is no zonation within the squamation that might indicate underlying fin radials (cf. Jarvik 1980), and no ridges that might indicate the presence of an endoskeleton in any form.

#### 5.4. Trunk

The relevance of the sedimentary infill of the rostral portion of the trunk has been alluded to above; it belongs to the digestive tract and is probably a stomach. Moreover, the stomach is infilled by silt-grade sediment that is much finer, and of different petrological composition, to that which surrounds the holotype, and fills the naso/oral cavity and respiratory system (Figs 1, 5a, b). This sediment cannot, therefore, have been washed into the carcass post mortem and must represent in vivo stomach contents, thus providing evidence for deposit 27

feeding in Turinia pagei, and by implication, other thelodonts (see below). While this evidence is clearly circumstantial, it represents the best evidence presented for the interpretation of feeding strategies in a non-conodont stem-gnathostome (see Purnell 2001). As aforementioned, the gut trace extends caudally and provides a rostral limit for the position of the anus, and a useful means by which the holotype can be oriented. The lack of uniformity of scale morphology throughout the trunk region, and specifically in the region where scales are most poorly articulated, means that there is an absence of evidence for the presence of dorsal, anal or lateral fins/fin flaps. Any interpretation of the lateral flaps as true fins must remain equivocal.

#### 5.5. Tail

From what little is preserved of it, the caudal fin is demonstrably asymmetrical. However, as noted above, it is not obvious that the preserved fin web, which is truncated by the edge of the block, actually represents a portion of the caudal fin, and the possibility that it represents a dorsal fin cannot be rejected on the available evidence. Nevertheless, the preserved fin is composed from minute (<0.5 mm length) lath-shaped scales (see Märss & Ritchie 1998) which exhibit zonation.

#### 6. Comparison to other thelodonts

Comparison of the anatomy of Turinia pagei with other thelodonts is difficult because the holotype of T. pagei exhibits a uniquely three-dimensional preservation; all other thelodonts, with the exception of the stomachs of the Furcacaudiformes (Wilson & Caldwell 1993, 1998), are preserved as flat layers of scales (e.g. Märss & Ritchie 1998). T. pagei has traditionally been interpreted as conforming to the group of thelodonts which, in vivo, were dorso-ventrally compressed in crosssectional profile (Turner 1991, 1992); we find no evidence to contradict this in our re-examination of the known material. The bauplan of dorso-ventrally compressed thelodonts is relatively stable; all members for which the anatomy is well constrained (Loganellia, Shielia, Lanarkia, Phlebolepis) exhibit a blunt rostral margin, rostrally situated mouth/nasohypophysial opening, rostro-laterally situated orbits, eight branchial pouches, lateral appendages in an approximately pectoral position, dorsal and anal fins, and a caudal fin that is either symmetrical, or (to a greater or lesser degree) has a more strongly developed ventral lobe (although not all features have necessarily been described from all taxa). Some exceptions to this overall bauplan exist in Shielia taiti and Lanarkia lanceolata, both of which possess paired ventral fins/flaps in addition to paired fins/flaps in a pectoral position; S. taiti lacks an anal fin/flap, and the ventral fins/flaps occur in a pectoral position (Märss & Ritchie 1998). Therefore, the absence of evidence for dorsal and anal fins/flaps in T. pagei might be a preservational artefact rather than evidence of their absence.

#### 6.1. Buccopharyngeal/nasohypophyseal opening and branchial system

The funnel-shaped outline of the bucco/nasal cavity in Turinia *pagei* is closely comparable to the field of forward-pointing denticles at the rostral margin of Loganellia scotica (van der Brugghen & Janvier 1993) and the funnel-shaped bucco/nasal cavity in Lanarkia (Märss & Ritchie 1998, fig. 43E). The absence of evidence for a prenasal sinus distinct from a mouth may be a preservational artefact, but many tens of articulated thelodonts have now been examined, belonging to seventeen species, and there is mounting evidence of absence. This condition is unparalleled amongst hagfish, lampreys and

primitive crown-group gnathostomes, possibly indicating a thelodont synapomorphy. However, amongst stem-gnathostomes, the nasal openings in heterostracans have also been interpreted as opening into the buccal cavity. Again, this is based largely on lack of evidence for separate oral and nasal openings, but is supported by the close topological relationship with rostral impressions in the dorsal shield of cyathaspids, which have been interpreted as the position of olfactory organs (Whiting & Halstead Tarlo 1965; Halstead Tarlo & Whiting 1965; Novitskaya 1971, 1983, 1993; see also Janvier 1993, 1996a). Trying to weigh up the arguments over the condition in thelodonts is more problematical because the exoskeleton is not fused, and so even an overwhelming absence of evidence cannot readily be used as evidence of absence. For instance, despite the numerous specimens of Phlebolepis elegans, a great many of which exhibit complete articulation of their exoskeleton, none has yet been discovered in which the external gill openings can be discerned (Märss 1986); regardless of whether the gills possessed individual efferent openings, or whether the efferent branchial ducts were confluent and they possessed a single pair of external openings (as in *Myxine* and heterostracans sensu stricto), external efferent branchial openings must have been present.

A critical test of the hypothesis that thelodonts possessed a common buccopharyngeal/nasohypophyseal opening (van der Brugghen & Janvier 1993; Janvier 1996a) would be evidence for the presence of olfactory organs adjacent to the known buccopharyngeal opening. Novitskaya & Turner (1998) interpreted the presence of such structures in the holotype specimen of *T. pagei*, but it is clear from our reinvestigation of this specimen that no evidence exists; the structures interpreted by Novitskaya & Turner (1998) are the margins of the oral/ nasohypophyseal opening (e.g. Turner 1982).

Other than the position of the efferent branchial openings, there is little evidence for the position and extent of the branchial pouches in thelodonts other than *T. pagei*. However, some specimens do exhibit dark organic films which have been taken by previous authors to represent the remains of a branchial system. Stetson (1931) described the presence of eight serially arranged sub-rounded dark patches in the holotype of *Shielia taiti* (GSE 3903), which he compared to the gill arches in elasmobranch embryos. Stetson (1931) also noted that Traquair (1905) had described the presence of structures indicative of branchial pouches in specimens questionably assigned to *Lanarkia*. Märss & Ritchie (1998) have since demonstrated that, in both instances, the structures coincide with patches of denticles, and it is likely that they represent operculae of efferent gill openings.

## 7. The systematic position of *Turinia pagei* and status of the Thelodonti

In an attempt to resolve the relationships of *Turinia pagei* we have modified the data matrix compiled by Donoghue *et al.* (2000) to include a number of extra characters. A number of additional changes were also made, including the exclusion of very poorly known taxa (*Eriptychius* and pituriaspids), and a number of character scores were also modified based upon new or more complete data. The data matrix and character descriptions can be found in the Appendix (section 11); for detailed comments on character descriptions, the reader is directed to Donoghue *et al.* (2000).

The dataset was subjected to parsimony analysis using PAUP 3.1.1 (Swofford 1993) and character evolution was resolved using MacClade 3.0.5 (Maddison & Maddison 1992). Bootstrap values were obtained using a 1,000,000 repli-

cate 'fast' stepwise addition search in PAUP\* 4.0b4a (Swofford 1999); these values were corroborated in a 10,000 replicate random stepwise addition bootstrap analysis in PAUP 3.1.1. Bremer Support values were obtained using Tree Rot (Sorensen 1996).

Analysis of a dataset excluding all thelodont taxa yielded three equally most-parsimonious trees that differ in resolution of the clade (Euphanerops, Jamoytius, Anaspida); the strict consensus of these trees is presented in Figure 8a (ci(e) =0.6954; ri = 0.7196; 180 steps). Analysis of a dataset including T. pagei yields six equally most-parsimonious trees that differ in the placement of T. pagei; one where T. pagei is resolved as the sister-group to the clade (Galeaspida (Osteostraci, jawed vertebrates)), and the other where T. pagei and Galeaspida are resolved as sister-taxa; the strict consensus of all six trees is presented in Figure 8b (ci(e) = 0.6648; ri = 0.6935; 188 steps). A posteriori reweighting according to retention indices derived from the preceding unweighted analysis yielded three equally most-parsimonious trees that differ only in the topology of the clade (Euphanerops, Jamoytius, Anaspida); T. pagei and Galeaspida are resolved as sister taxa (Fig. 8c; ci(e) = 0.8146; ri = 0.8611; 109.4000 steps). In order to test the hypothesis that the Thelodonti is paraphyletic (Janvier 1981), codings for other thelodont taxa were included encompassing the diversity of bodyforms of taxa known from articulated remains. Branchand-bound analysis of this dataset yielded three equally mostparsimonious trees (ci(e) = 0.6489; ri = 0.7155; 193 steps; Fig. 8d) that differ in the topology of a monophyletic (Euphanerops, Jamoytius, Anaspida); the majority of thelodont taxa group together as a clade, constituting a sister group to (Galeaspida (Osteostraci, jawed vertebrates)). Sphenonectris turnerae is the only thelodont with a phylogenetic position distinct from the clade. A posteriori reweighting has no effect upon relationships.

The majority of thelodonts are thus united as a clade entirely by homoplasy. While we recognise that homoplasy is often important in resolving relationships (e.g. Källersjö et al. 1999), it is possible that the grouping of thelodonts is an artefact of a sampling strategy in which all the thelodonts are analysed at species level, while the vast majority of the remaining terminal taxa are higher taxa (usually families). It may, therefore, be preferable to use multiple species rather than individual higher taxa as terminal taxa (e.g Wiens 1998), but this is often impractical when conducting analysis of palaeontological material. In such circumstances it is necessary to use higher taxa as phena because most fossil species are incompletely known; the problems of dealing with missing data are exacerbated when conducting phylogenetic analysis of fossil and living taxa (as is the case here). Each of the phena represented by higher taxa in the primary dataset were subsequently replaced by two or more phena representative of a lower taxonomic level. It proved impractical to analyse the resulting dataset using the branch-and-bound search option of PAUP due to excessive computation time and, in consequence, the more approximate heuristic search options were adopted; in all heuristic searches, ten replicate random addition searches were undertaken. This analysis of the dataset yielded 37 equally most-parsimonioustrees, the strict consensus of which provides little resolution of the relationships of thelodonts to the heterostracomophs (heterostracans plus Astraspis and the arandaspids) galeaspids, and osteostracans plus jawed vertebrates (Fig. 9a; ci(e) = 0.6158; ri = 0.7892; 205 steps). However, there is consensus support for a monophyletic group composed from all thelodont taxa bar Sphenonectris turnerae. A posteriori reweighting resolves (in comparison with unweighted analysis) the thelodont clade as a sister group to the clade (Galeaspida(Osteostraci, jawed vertebrates); S. turnerae is resolved

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**Figure 8** (A) Strict consensus tree arising from branch-and-bound analysis of the data set using many higher taxa as phena and excluding thelodonts; 3 trees @ 180 steps, ci(e) (consistency index excluding uninformative characters) 0.6954, ri (retention index) 0.7196. (B) Strict consensus tree including *Turinia pagei* (Powrie); 6 trees @ 188 steps, ci(e) 0.6648, ri 0.6935. (C) Strict consensus tree using the same parameters as B, with *a posteriori* weighting using retention indices derived from the preliminary unweighted analysis (base weight of 1000); 3 trees @ 109.4000 steps, ci(e) 0.8146, ri 0.8611. (D) Strict consensus tree arising from analysis of an augmented dataset including five additional thelodont phena; 3 trees @ 193 steps, ci(e) 0.6489, ri 0.7155.

as a sister taxon to both clades (Fig. 9b; ci(e) = 0.6877; ri = 0.8490; 143.64639 steps).

Bremer support and bootstrap values for the trees presented in Figure 9 indicate that individual clades are not well supported, a common feature of cladistic analyses of stemgnathostomes (Donoghue *et al.* 2000; Freedman in press). Nevertheless, the topology of trees arising from recent analyses exhibit a remarkable degree of consistency, even when phena otherwise represented by higher taxa are replaced by multiple phena of lower rank. The results of the above analyses support a thelodont clade, albeit united solely on homoplasy.

It has been argued on numerous occasions that the Thelodonti do not constitute a monophyletic clade because they fail to exhibit distinct synapomorphies (Karatajute-Talimaa 1978; Janvier 1981, 1986, 1993, 1996a, b; Forey & Janvier 1993, 1994), despite attempts to identify them. Forey (1984) raised the possibility that thelodonts may be united on the arrangement of pectoral flaps and efferent gill openings, a possibility now precluded by the character states in the Furcacaudiformes. Alternatively, Turner (1991) and Gagnier (1993) argued that thelodonts may be united on the presence of an acellular scale attachment process but, as Janvier (1996a, b) has observed, such a structure is not developed in all thelodonts and is present in other groups such as the anaspids. Unfortunately, in the debate over thelodont monophyly, all authors have failed to distinguish between two quite distinct arguments.



**Figure 9** Strict consensus trees of a dataset where higher taxon phena are replaced by multiple phena of lower rank: (A) unweighted; 37 trees @ 205 steps, ci(e) 0.6158, ri 0.7892; (B) *a posteriori* reweighted analysis using retention indices derived from the preliminary unweighted analysis (base weight of 1000); 3 trees @ 143.64639 steps, ci(e) 0.6877, ri 0.8490, rc. Statistical support for both trees is given in (A) as bootstrap values and (B) as Bremer Support (clade decay) values.

Firstly, do thelodonts constitute a monophyletic group? If so, do thelodonts share any uniquely derived characters? The second debate does not arise unless it can be demonstrated that thelodonts constitute a monophyletic group. Monophyly is a statement about relationship and membership; the shared-derived characters that unite a monophyletic group may characterise it, or diagnose it, but characters do not define a monophyletic group (Ghiselin 1984; Sober 1988; de Queiroz & Gauthier 1990; Smith 1994).

Unequivocal homoplastic character changes occurring on the node subtending the thelodont clade plus its sister clade include: (26) a switch from sensory lines in grooves to canals, and (44) acquisition of a dorsal fin. The thelodont clade itself is united by only one unequivocal character change: (47) acquisition of paired lateral fin folds; characters 44 and 47 are the most significant distinguishing characters that separate Sphenonectris turnerae from the thelodont clade. The thelodonts traditionally interpreted as dorso-ventrally compressed are united to the exclusion of a paraphyletic 'Furcacaudiformes' by the presence of opercular flaps associated with gill openings (32). Turinia pagei is resolved as a sister-taxon to the remaining members of this clade, which are in turn united by a switch from orthodentine to mesodentine comprising the dermal skeleton (69). The terminal clade Loganellia + Phlebolepis is united by the presence of a distinct anal fin (45). Table 2 lists character attributes at the node subtending all thelodonts under (a) ACCTRAN (accelerated transformation) and (b) DELTRAN (delayed transformation) optimisations for the consensus tree presented in Figure 9b.

Given that thelodonts (or a subclade thereof) have traditionally been allied to the heterostracans (Traquair 1899a, b, 1905; Stensiö 1927, 1932, 1958, 1964; Berg 1940; Obruchev 1964; Moy-Thomas & Miles 1971; Halstead 1982; Novitskaya & Karatajute-Talimaa 1989) it is pertinent to consider the character changes that occur on the node subtending (thelodonts (galeaspids (osteostracans, jawed vertebrates)), to the exclusion of the heterostracans. Only one unequivocal (homoplastic) character change occurs and this is a switch from multiple to single odontodes comprising individual dermal scales and plates. The view expressed by Stensiö (1964, p. 374), 'Les Thelodonti semblent donc étroitement apparentés aux Heterostraci par leur organisation générale", still stands, though we must now view these similarities as symplesiomorphies rather than as an indication of close kinship.

#### 7.1. Thelodont intrarelationships

Many early workers (Westoll 1945; Ørvig 1968) considered thelodonts as a group of unrelated forms possessing a primitive micromeric exoskeleton, and this was supported by Janvier (1981), who interpreted thelodonts as a paraphyletic stemgroup. Utilising histological differences, Karatajute-Talimaa (1978, figs 20, 21) recognised two independently evolved groups of thelodonts, the katoporids, composed of mesodentine, and the thelodontids, composed of orthodentine. This division was expanded upon by Turner (1991), who revised the histological interpretations of thelodonts. Three principle groups were recognised, with the loganiids identified as the sister-group to katoporids + thelodontids (Turner 1991, fig. 10). Wilson & Caldwell (1998) undertook a cladistic analysis incorporating the Furcacaudiformes. A strict consensus of 33 equally most-parsimonious trees resolved the Furcacaudiformes as the sister-group to the jawed vertebrates + nonfurcacaudiform thelodonts, but did not resolve relationships within the latter group.

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Table 2Reconstructed character attributes for the node subtending the Thelodonti, according to the tree topology in Figure 9b and under acceler-<br/>ated transformation (ACCTRAN) or delayed transformation (DELTRAN) optimisations; character states in bold signify differences between<br/>optimisations.

	Character	ACCTRAN	DELTRAN
1	Neural crest	present	present
2	Brain	present	present
3	Olfactory peduncles:	present	present
4	Pineal organ	present and uncovered	present and uncovered
5	Pituitary	divided	divided
6	Adenohypophysis	segmented and compartmentalised	segmented and compartmentalised
7	Optic tectum:	present	present
8	Cerebellum:	present	present
9	Pretrematic branches of branchial nerves	present	absent
10	Flattened spinal chord	absent	absent
11	Dorsal and ventral spinal roots united	present	absent
12	Mauthner cells	present	present
13	Synaptic ribbones in retinal receptors	present	present
14	Nasal opening(s)	single, median	single, median
15	Nasohypophysial opening serving respiration	absent	absent
16	Single nasohypophysial opening	present	present
17	Position nasohypophysial opening	dorsal	dorsal
18	Olfactory organ	paired	paired
19	Extrinsic eye musculature	present	present
20	Semi-circular canals	two	two
21	Vertical semicircular canals forming loops	present	present
22	Externally open endolymphatic ducts	present	absent
23	Neuromasts	present	present
24	Electroreceptive cells	present	present
25	Sensory line distribution	head and body	head and body
26	Sensory line condition	enclosed in canals	enclosed in canals
27	Pouch-shaped gills	present	present
28	Symmetrically disposed gills	present	present
29	Elongate branchial series	absent	absent
30	Gills openings arranged in slanting row	nresent	present
31	Position of gill openings	lateral	lateral
32	Opercular flaps	absent	absent
33	Endodermal gill lamellae	absent	nresent
34	Gill lamellae with filaments	nresent	present
35	Mouth posaition	terminal	terminal
36	Velum absent	present	absent
37	Atrium and ventricle of heart	in close proximity	in close proximity
38	Closed pericardium	present	present
39	Open blood system	present	present
40	Paired dorsal aortae	absent	absent
40	I arge lateral head vein	nresent	absent
42	True lymphocytes	present	present
43	Subapopeurotic vascular plexus	present	present
44	Dorsal fin	present	present
45	Distinct anal fin	absent	absent
46	Unnaired fin ray supports	nresent	nresent
47	Paired lateral fin folds	absent	absent
48	Constricted pectorals	absent	absent
40	Tail morphology	diphycercal	diphycercal
50	Preanal median fold	absent	absent
51	A bility to synthesise creatine phosphatase	nresent	nresent
52	Visceral arches fused to neurocranium	present	present
53	Horny teeth	absent	absent
54	Trematic rings	absent	absent
55	Arcualia	present	nresent
56	Cartilagenous conula assoc, with tongue muscles	absent	absent
57	Chondroitin 6 sulpahet in cartilage	present	present
58	Braincase with lateral walls	present	present
50	Neuroaranium alosed dorsally	present	absent
59	Occiput analoging nerves IX and X	present	absent
61	Annular cartilage	absont	absent
62	Trunk darmal skalaton	nresent	ausult
62	Derichondral hone	absent	absent
64	Calcified cartilage	absent	absent
65	Calcified dermal skeleton	auselli	ausull
600	Lamellar agnidin	present	present
00 67	Callular hana	abaant	present
0/	Centural Dolle	ausent	ausent
0ð 60	Dentine type	orthodentine	orthodentine
70	Enomol/oid	abaant	abaant
70	Enamei/010	absent	absent
/1	r mee-rayered exoskeleton		
12	Odentede composition of teath/coales/denticles	ausent	ausefil
15	Scale shape	diamond shaned	diamond shared
/4	Scale shape	diamond-snaped	diamonu-snapeu

#### Table 2(continued)

	Character	ACCTRAN	DELTRAN
75	Oak-leaf shaped ornament	absent	absent
76	Oral plates	absent	absent
77	Pharyngeal denticles	present	absent
78	Dermal head covering in adult state	micromeric	micromeric
79	Large unpaired dorsal and ventral head plates	absent	absent
80	Endoskeletal head shield encapsulating gills	present	present
81	Sclerotic ossicles	absent	absent
82	Ossified endoskeletal sclera encapsulating eye	absent	absent
83	Blood volume	< 10%	< 10%
84	Haemoglobins $< O_2$ affinity and $>$ Bohr effect	present	present
85	Nervous regulation of heart	present	present
86	Heart response to catecholamines	present	present
87	High blood pressure	present	present
88	Hyperosmoregulation	present	present
89	High proportion of serine and theronine collagen	present	present
90	Lactate dehydrogenase 5	present	present
91	Pituitary control of melanophores	present	present
92	Pituitary control of gametogenesis	present	present
93	High metabloic rate	present	present
94	Ion transport in gills	present	present
95	Typhlosole in intestine	present	present
96	Spleen	present	present
97	Collecting tubules in kidneys	present	present
98	Condensed and discrete pancreas	present	present
99	A islet cells in endocrine pancreas	present	present
100	Male gametes shed directly through coelom	absent	present
101	Forward migration of postotic myomeres	absent	absent
102	Sexual dimoprhism	present	present
103	Larval phase	absent	present
104	Pelvic paired fins/flaps	absent	absent
105	Sensory fields	absent	absent
106	Horizontal component to caudal fin	absent	absent
107	Single pair of branchial openings	absent	absent
108	Position of notochord in tail fin	hypochordal	hypochordal
109	Jaws	absent	absent

Unrooted analysis of the thelodont ingroup using our dataset yields four equally most-parsimonious trees in which the furcacaudiform taxa are resolved as more closely related to each other than either is to any other taxon; the interrelationships of non-furcacaudiforms are unresolved. This result corroborates the conclusions of Wilson & Caldwell (1998). However, in contrast to Wilson & Caldwell (1998), rooted analysis resolves the Furcacaudiformes as paraphyletic with respect to non-furcacaudiforms. Furthermore, rooted analysis also resolved the interrelationships of non-furcacaudiform taxa, with *Turinia pagei* as the sister-group of (*Shielia (Loganellia, Phlebolepis*)).

#### 8. Flaps, fins and limbs

Like so much regarding the state of understanding of thelodont anatomy, the question of homology between the 'anterolateral appendages' and pectoral fins in osteostracans, pituriaspids and crown-group gnathostomes remains unresolved through the absence of direct evidence. Internal anatomical characters have only been preserved in the holotype of *Turinia pagei* by virtue of sedimentary infilling of the branchial system, and the presence of an extensive (unmineralised) cephalothoracic endoskeleton has been only tentatively interpreted. There is no evidence that would support homology of the anterolateral appendages with pectoral fins.

Märss & Ritchie (1998) reviewed the anatomy of *Shielia taiti*, which exhibits paired posterolateral appendages in addition to an anterolateral pair. If these represent homologues of crowngnathostome pelvic fins, as suggested by Märss & Ritchie (1998) and Mallatt (1997), *S. taiti* would add further weight to the hypothesis that thelodonts are paraphyletic. However, like the anterolateral appendages, the posterolateral appendages lack evidence of zonation that might be taken as evidence of fin rays (e.g. Jarvik 1980). A potential test of homology is the topological relationship between the putative pelvic fins and the site of the anus. Paired fins are patterned by the *Hox* family of homeotic genes (Shubin *et al.* 1997; Coates & Cohn 1998) which are expressed no further rostrad than the hindbrain, and no further caudad than the anus; theoretically, paired appendages caudal to the anus cannot be homologues of pelvic fins. In *S. taiti*, the posterolateral paired fins lie rostral to the presumed site of the anus (T. Märss pers. comm. 1998; Märss & Ritchie 1998, fig. 24) and, thus, pass one test of homology with true paired fins.

The distribution of characters and topological relationships of taxa presented in Figure 9c, d suggest that the pectoral flaps of thelodonts are not homologous to the constricted pectorals of jawed vertebrates and osteostracans (note: although Tremataspis is herein resolved as plesiomorphic for osteostracans, ACCTRAN optimisations suggests that the paired pectoral fins of osteostracans and jawed vertebrates are homologous; but see Forey 1987; this probably arises because no other non-cornuate osteostracan taxa were included in the analysis - see Janvier 1985a, b). That fins should evolve independently so many times belies the possibility that either the topological relationships of anaspids (sensu lato), thelodonts, osteostacans and jawed vertebrates, presented herein, are incorrect, or else there is a developmental basis upon which fins are likely to arise more than once. Coates & Cohn (1998) argue that the origin of fins is linked to staggered Hox gene expression which they contend is linked to differentiation of the gut. It is interesting to note that in the taxa in which paired fins are present, but deemed independently evolved with respect to jawed vertebrates, evidence exists for a differentiated gut (Stensiö 1939 for anaspids; Wilson & Caldwell 1993, 1998 and herein for thelodonts), although no evidence exists to support the view that a differentiated gut was not present in taxa known not to possess paired fins.

#### 9. Pharyngeal denticles, teeth and scales

With the discovery of composite denticles in the pharynx and associated with the efferent gill openings of thelodonts (van der Brugghen & Janvier 1993; Wilson & Caldwell 1998), Smith & Coates (1998, 2001) have attempted to dissociate debates over the origin of jaws and the origin of dentalpatterning. However, as Smith & Coates (2001) note, the distribution of these characters on existing phylogenetic schemes 'highlights a fundamental problem' with their hypothesis for the origin of vertebrate dentitions. In a phylogenetic context, the hypothesis that the lodont pharyngeal denticles are homologous to the teeth of jawed vertebrates fails the test of secondary homology (Patterson 1982; de Pinna 1991) because thelodonts and jawed vertebrates are relatively distantly related and the intervening taxa all lack structures that could be homologised with teeth. Indeed, it implies that the putatively homologous patterning mechanisms responsible for polarisation of patterning and replacement in the pharyngeal denticles of thelodonts were acquired independently of jawed vertebrates.

The only thelodont taxon known to possess a pharyngeal skeleton composed from composite scales is *Loganellia scotica*, which is recognised herein as amongst the most derived of thelodonts incorporated into the analysis. This exacerbates the fundamental problem identified by Smith & Coates (2001) as it requires an even greater edentate interval of gnathostome phylogeny than that originally identified by these authors. Although pharyngeal denticles are also known from *Turinia pagei*, the only other thelodont (other than *L. scotica*) known to possess composite odontodes is *Pezopetallichthys ritchei*, in which the denticles occur in association with the efferent gill openings (Wilson & Caldwell 1998), and thus are presumably external in position.

#### **10.** Conclusions

(1) The holotype is preserved in ventral aspect. Tranverse structures are interpreted as gills and their associated interbranchial ridges or arches. The eight pairs of transverse structures are connected medially by a longitudinal ridge that is interpreted as a pharynx. A caudally tapering structure could be interpreted as a mouth, a prenasal sinus and nasopharyngeal duct, or both. Indentations in the rostro-lateral margins may represent the position of eyes or nostrils. A patch of siltstone in the trunk of the holotype is interpreted as an internal body cavity: a stomach and gut. The absence of scales over substantial areas of the holotype is not attributed to processes of decay since the impressions of scales bases are present.

(2) The oral/buccopharyngeal cavity and internal surfaces of the efferent gill openings are lined with denticles, comparable to the condition found in *Loganellia* (Turner 1991; van der Brugghen & Janvier 1993; Märss & Ritchie 1998). Comparable structures are present in chondrichthyans (Nelson 1970; Reif 1985), although their function is unknown.

(3) There is no evidence in the available material for the presence of: a brain, olfactory sacs, pineal organ, pineal foramen, common efferent branchial ducts, dorsal aorta, dorsal fin, anal fin, morphology of caudal fin, true fins, or position of opening to oral/buccopharyngeal cavity.

(4) The presence of fine-grained sediment filling the stomach and gut, but not the buccopharyngeal area, of the holotype, provides support for the interpretation of *Turinia pagei* as a deposit feeder.

(5) A phylogenetic analysis resolves thelodonts as a clade Thelodonti (albeit without any uniquely derived characters) comprised of *Furcacauda heintzi*, plus a monophyletic group composed of 'traditional' thelodonts, the Coelolepidae. Within this latter clade, *T. pagei* is the plesiomorphic sister-taxon to (*Shielia taiti* (*Loganellia, Phlebolepis*)). The furcacaudiform *Sphenonectris turnerae* is resolved as a sister-taxon to (Thelodonti (Galeaspida (Osteostraci, jawed vertebrates))) and thus, the Furcacaudiformes are an unnatural group and thelodontiform scales diagnose a grade rather than a clade.

(6) The resolution of the lodont interrelationships provides a systematic framework within which interpretation of equivocal aspects of the lodont anatomy can be constrained.

(7) ACCTRAN character state optimisation on a consensus tree indicates that the paired pectoral flaps of thelodonts and paired pectoral fins of jawed vertebrates are not homologous and, furthermore, the pharyngeal denticles of thelodonts are not homologous to the teeth of crown-group gnathostomes.

#### 11. Epilogue

In closing, we return to the epigram quoted from Turner & van der Brugghen (1993). The holotype of *T. pagei* has not confused discussion over the relationships of thelodonts, rather it is the disparate, incomplete and inconsistent interpretations of the specimen that have been the source of confusion.

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#### 13. Appendix

#### 13.1. Character descriptions

More complete character descriptions with comments can be found in Donoghue *et al.* (2000).

1. Neural crest: absent = 0, present = 1; 2. Brain: absent = 0, present = 1; 3. Olfactory peduncles: absent = 0, present = 1; 4. Pineal organ: absent = 0, present and covered = 1, present and uncovered = 2; 5. Pituitary divided to adenohypophysis and neurohypophysis: absent = 0, present = 1; 6. Adenohypophysis: absent = 0, simple = 1, segmented and compartmentalised = 2; 7. Optic tectum: absent = 0, present = 1; 8. Cerebellum: absent = 0, present = 1; 9. Pretrematic branches in branchial nerves: absent = 0, present = 1; 10. Flattened spinal chord: absent = 0, present = 1; 11. Ventral and dorsal spinal nerve roots united: absent = 0, present = 1; 12. Mauthner fibres in central nervous system: absent = 0, present = 1; 13. Synaptic ribbons in retinal receptors: absent = 0, present = 1; 14. Number of nasal openings: none = 0, paired = 1, single median = 2; 15. Nasohypophyseal opening serving respiration (nasopharyngeal duct): absent =0, present =1; 16. Single nasohypophysealopening: absent = 0, present = 1; 17. Position of nasohypophysealopening: None = 0, terminal = 1, dorsal =2; 18. Olfactory organ: absent = 0, paired = 1, unpaired = 2; 19. Extrinsic eye musculature: absent = 0, present = 1; 20. Presence/absence and number of semicircular canals in labyrinth: none = 0, one = 1, two = 2, three = 3; 21. Vertical semicircular canals forming loops, well separate from the vestibular division of the labyrinth: absent = 0, present = 1; 22. Externally open endolymphatic ducts: absent = 0, present = 1; 23. Sensoryline system with neuromasts: absent = 0, present = 1; 24. Electroreceptive cells: absent = 0, present = 1; 25. Sensory-line grooves or canals: absent = 0, present on head only = 1, present on head plus body = 2; 26. Sensory-line: absent = 0, enclosed ingrooves = 1, enclosed in canals = 2; 27. Pouch-shaped gills: absent = 0, present = 1; 28. Gills alternate = 0, symmetrical = 1; 29: Elongate branchial series: more than 10 gill pouches/ slits = 0, fewer than 10 = 1; 30: Gill openings lateral and arranged in slanting row: absent = 0, present = 1; 31: Position of gill openings: gills opening laterally = 0, ventrally = 1; 32: Opercular flaps associated with gill openings: absent = 0, present = 1; 33: Endodermal gill lamellae: absent = 0, present = 1; 34: Gill lamellae with filaments: absent = 0, present = 1; 35: Mouth terminal = 0 or ventral = 1; 36. Velum: absent =0, present = 1; 37. Relative position of atrium and ventricle of heart: well separated = 0, close to each other = 1; 38. Closed pericardium: absent = 0, present = 1; 39. Open blood system: absent = 0, present = 1; 40. Paired dorsal aortae: absent = 0, present = 1; 41. Large lateral head vein: absent =0, present = 1; 42. True lymphocytes: absent = 0, present = 1; 43. Subaponeurotic vascular plexus: absent = 0, present = 1; 44. Dorsal fin: separate dorsal fin absent = 0, present = 1; 45. Anal fin separate: absent = 0, present = 1; 46. Unpaired fin ray supports closely set: absent = 0, present = 1; 47. Paired lateral fin folds: absent = 0, present = 1; 48. Constricted pectorals: absent = 0, present = 1; 49. Tail shape: no distinct lobes developed = 0, ventral lobe much larger than dorsal =1, dorsal lobe much larger than ventral = 2, dorsal and ventral lobes approximately equally developed = 3; 50. Preanal median fold: absent = 0, present = 1; 51. Ability to synthesise creatine phosphatase: absent = 0, present = 1; 52. Visceral arches fused to the neurocranium: absent = 0, present = 1; 53. Horny teeth: absent = 0, present = 1; 54. Trematic rings: absent = 0, present = 1; 55. Arcualia: absent = 0, present = 1; 56. Cartilaginous copula associated with tongue protractor and retractor muscles: absent = 0, present = 1; 57. Chondroitin 6-sulphate in cartilage: absent = 0, present = 1; 58. Braincase with lateral walls: absent = 0, present = 1; 59. Neurocranium entirely closed dorsally and covering the brain: absent = 0, present =1; 60. Occiput enclosing vagus and glossopharyngeal: enclosure

of cranial nerves IX and X, absent = 0, present = 1; 61. Annular cartilage: absent = 0, present = 1; 62. Trunk dermal skeleton: absent = 0, present = 1; 63. Perichondral bone: absent =0, present = 1; 64. Calcified cartilage: absent = 0, present = 1; 65. Calcified dermal skeleton: absent = 0, present = 1; 66. Lamellar aspidin: absent = 0, present = 1; 67. Cellular bone: absent = 0, present = 1; 68. Dentine absent: = 0, present = 1; 69. Dentine absent = 0, mesodentine = 1, orthodentine = 2; 70. Enamel/oid: absent = 0, (monotypic) enamel = 1, enameloid (bitypic enamel) = 2; 71. Three-layered exoskeleton consisting of a basal lamella, middle spongy (or cancellar) layer and a superficial (often ornamented) layer: absent = 0, present = 1; 72. Cancellar layer in exoskeleton, with honeycomb-shaped cavities: absent = 0, present = 1; 73. Composition of the scales/denticles/teeth: absent = 0, made up by a single odontode = 1, made up by several odontodes = 2; 74. Scale shape: scale absent = 0, diamond-shaped = 1, rod-shaped = 2; 75. Oak-leaf-shaped tubercles: absent = 0, present = 1; 76. Oral plates: absent = 0, present = 1; 77. Denticles in pharynx: absent = 0, present = 1; 78. Dermal head covering in adult state: absent = 0, small micromeric = 1, large (macromeric)dermal plates or a shield = 2; 79. Large unpaired ventral and dorsal dermal plates on head: absent = 0, present =1; 80. Massive endoskeletal head shield covering the gills dorsally: absent = 0, present = 1; 81. Sclerotic ossicles: absent = 0, present = 1; 82. Ossified endoskeletal sclera encapsulating the eye: absent = 0, present = 1; 83. Blood volume: more than 10% of body volume = 0, less than 10% of body volume = 1; 84. Haemoglobins with low O2 affinity and significant Bohr effect: absent = 0, present = 1; 85. Nervous regulation of heart: absent = 0, present = 1; 86. Heart response to catecholamines: absent = 0, present = 1; 87. High blood pressure: absent = 0, present = 1; 88. Hyperosmoregulation: absent =0, present = 1; 89. High proportion of serine and theronine collagen: absent = 0, present = 1; 90. Presence of lactate dehydrogenase 5: absent = 0, present = 1; 91. Pituitary control of melanophores: absent = 0, present = 1; 92. Pituitary control of gametogenesis: absent = 0, present = 1; 93. High metabolic rate: absent = 0, present = 1; 94. Ion transport in gills: absent = 0, present = 1; 95. Typhlosole in intestine: absent = 0, present = 1; 96. Spleen: absent = 0, present = 1; 97. Collecting tubules in kidneys: absent = 0, present = 1; 98. Condensed and discrete pancreas: absent = 0, present = 1; 99. A islet cells in the endocrine pancreas: absent = 0, present = 1; 100. Male gametes shed directly through the coelom: absent = 0, present = 1; 101. Forward migration of postotic myomeres: absent = 0, present = 1; 102. Sexual dimorphism: absent = 0, present = 1; 103. Larval phase: absent = 0, present = 1; 104. Pelvic fins/flaps: absent= 0, present = 1; 105. Sensory fields: absent = 0, present = 1; 106. Horizontal caudal fin: absent = 0, present = 1; 107. Single confluent branchial opening: absent = 0, present = 1; 108. Chordal disposition relative to tail development: isochordal = 0, hypochordal = 1, hyperchordal = 2; 109. Jaws: absent = 0, present = 1.

Cephalochordata

Tunicata

Petromyzontida

Athenaegis

cvathaspid

pteraspid Astraspis

Mvxinoidea

Pharyngolepis Rhyncholepis

Euphanerops

Iamovtius

A teleaspis

Zenaspis

Arandaspida

11132112321232200013111222011001230222212010101201002123111211110113010210001230272222222011220000200112222222 11123112320001131112223232322120012010101201002123111211110113000122202312202012322222 

Polybranchiaspidida

cg Chondrichthyes

Loganellia

Cladoselache

Arthrodira

Acanthothoraci

Eugaleaspidiformes

Tremataspi

Sphenonectris turnerae

Phlebolepis elegans

Sheilia taiti

Turinia pagei

Conodonta

Furcacauda heintzae

Heterostraci

Galeaspida

Osteostraci

Anaspida

awed vertebrates

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