

TURINIA PAGEI (POWRIE): A NEW RECONSTRUCTION OF THE SOFT ORGANS OF THE CEPHALOTHORAX

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The possible structure and mutual arrangement of some of the inner soft organs of *Turinia pagei* (Powrie) including the brain, pineal organ, olfactory sacs, semicircular canals, and branchial sacs are reconstructed. The details of morphology of departments of the brain and organisation of the branchial system are analysed. We interpret *T. pagei* as having paired nasal sacs and a telencephalon possessing well-developed olfactory tracts. Traces of the labyrinth are present at the level of the second and third gill pouches. In both these characters *T. pagei* was similar to heterostracans and early gnathostomes (placoderms, chondrichthyans). On the basis of a suite of characters including new data on the inner organisation of *Turinia* and *Lanarkia*, thelodonts represent a monophyletic group phylogenetically nearest to, and thus should be considered as the sister group of the gnathostomes. □ *Silurian, Devonian, agnathans, Thelodonti, brain, nasal sacs, stomach.*

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Thelodonts are extinct agnathan fishes (Late Ordovician-Late Devonian [early Frasnian]) which possess an exoskeleton of discrete dentinal scales with a base of acellular bonelike tissue (aspidin) which is capable of growth, and the production of simple to complex anchoring devices. The squamation is subdivided into several specialised scale areas. These characters were used by Turner (1991) to define the Thelodonti as a monophyletic group. Thelodonts are known mainly from isolated scales which are found abundantly in many deposits around the world. Taxa known from articulated specimens are few (although the number of specimens is large), preserved only in exceptional environments from the Silurian of Scotland, Norway, Canada and Estonia, and from the Early Devonian of Britain and Canada (Turner, 1976, 1982; Wilson & Caldwell, 1993; Caldwell & Wilson, 1995). Recent studies on the general morphology, squamation, and internal organisation of the thelodonts are providing new information on the nature of these fossil fishes, leading to diverse interpretations of the structures and consequently, different ideas about their relationships, some regarding them as monophyletic (e.g., Turner, 1991; Turner & van der Bruggen, 1993; van der Bruggen, 1993) and others as paraphyletic (van der Bruggen & Janvier, 1993; Wilson & Caldwell, 1993; Caldwell & Wilson, 1995). Closer scrutiny of the squamation and internal morphology seems to us to support the impressions of many early workers that

thelodonts are most like chondrichthyans, generally called 'sharks' in the older literature. This hypothesis was reiterated by Stetson (1931), supported by Novitskaya (1983, p. 148), and expanded on by Turner (1985, 1991). Most of these studies have been done on a wealth of old and new specimens of *Loganellia scotica* (Traquair), *Shielia taiti* (Stetson) and *Lanarkia* species from the classic Silurian Lagerstätte in the Southern Uplands, Scotland, which have now been newly described by Märss & Ritchie (1998), who also find evidence for gnathostome characters in the Silurian thelodonts. A suite of fossils from Arctic Canada, the so-called 'fork-tailed' thelodonts, is providing new insights into the range of variation in thelodont morphology (Wilson & Caldwell, 1993; Caldwell & Wilson, 1995) but these fossils have not yet been fully described and will not be considered here in detail.

In late 1994, the authors had the opportunity to review together thelodont collections held at the Queensland Museum and the data from new specimens. Among the studied materials was the cast of the holotype of *Turinia pagei* (Powrie) the original of which exhibits clearly the traces of soft inner organs on its surface (see e.g., Turner 1982, pl. 97). In addition, although not pointed out previously, the rounded clay mass just ventral to the cephalothorax is interpreted here as remains of stomach contents in this thelodont. The presence of a true stomach in thelodonts has only

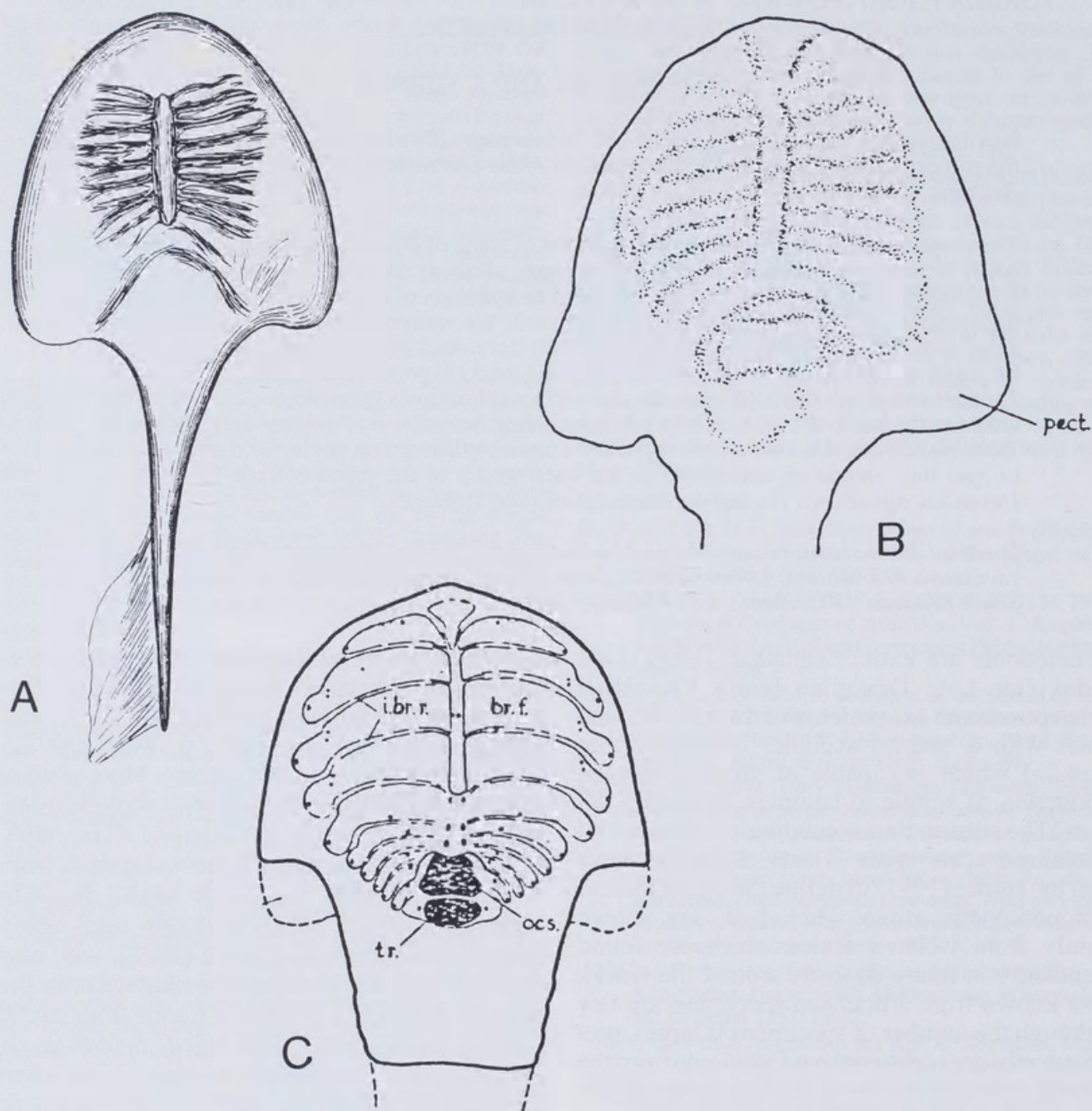


FIG. 1. Comparison of two former different interpretations of the holotype of *Turinia pagei*: A, Powrie, 1870, as 'ventral view'; B, Westoll 1945, as a 'larval cephalaspid' with his drawing of the outline of the cephalothorax 'after Traquair, 1899a'; compared with C, a cephalaspid based on Stensiö (1927) figures of *Kiaeraspis*, showing conformation of roof of branchial cavity etc.; Westoll figured 'br f'=branchial fossa, 'i br r'=interbranchial ridge, oes=oesophagus, pect=pectoral fin, tr=opening for truncus arteriosus.

recently been verified by Wilson & Caldwell (1993) and van der Bruggen (1994).

Turinia pagei was discovered and first described by Powrie (1870, Fig. 1a); the specimen is preserved in fine-grained Lower Devonian sandstone from Turin Hill, Forfar, Scotland. We concentrate on this example because it is one of the few complete specimens of a Devonian thelodont and because, unlike other complete thelodonts mentioned above, this specimen is

preserved as a natural mould in three-dimensions with friable remnants and impressions of scales present. The range of scale variation can be compared with that of other articulated but incomplete specimens of *T. pagei* (e.g., Traquair, 1899; Ørvig, 1969; Turner in Allen et al., 1968) and with isolated scales from numerous marine and marginal or non-marine localities from around the former Old Red Sandstone continent (e.g., Gross, 1967; Turner, 1973; Karatajute-Talimaa, 1978).

TABLE 1. Differences of interpretation of the holotype of *Turinia pagei* in earlier literature compared with the present study. Abbreviations: ant.=anterior; cart.=cartilaginous; d=dorsal; interbr.=interbranchial; longit.=longitudinal; oesoph.=oesophagial; pters.=pteraspid; v= ventral.

Author	Identity	View	Mouth	Eyes	Nasal sacs	Longit. ridge	Brain	Otic	Branch-ial sacs	Branch-ial arches	Branch-ial openings	Gut	Pectoral appendage	Tail	Other
Powrie 1870	own family ray-like	v	ant.	?	?	branch-ial skeleton	-	-	-	7/8 'exposed'	-	-	fins	'entirely below'	no ventral, anal or dorsal fins
Lankester 1870	early shark/ray	v?	-	-	-	-	-	-	-	-	-	-	-	-	-
Traquair 1899	<i>Thelodus</i> Heterostraci shark origin	d	?	?	-	-	-	-	-	8 cart. skeleton	-	-	lateral fin-folds	heterocercal broken off	no ventral, anal or dorsal fins
Kemna 1903	<i>Thelodus</i>	d	-	-	-	-	-	-	8 'poches' OR	8 arcs?	none	-	fins	-	branch-ial skeleton
Stensiö 1927	Heterostraci	d	cf. pters.	?small cf. pters.	cf. pters.	occipital region	'solid' endocranium	not shown cf. pters.	mesodermal sacs 7+	undivided interbr. ridges	no sign	oesoph. foramen	not certain	-	cartilage perichondral bone (thin)
Westoll 1945	larval cephalaspid	v	-	none	-	aortic groove cf. <i>Kiaeraspis</i>	-	-	-	paired pockets	interbr. ridges	-	-	-	roof branch-ial chamber
Stensiö 1958/1964	Heterostraci	d	-	echancrure	-	-	occipital region endocranium	labyrinth	8 'fosses'	visceral arches interbr. ridges 1- [0?] shows 9	8 extra-branch-ial atria	oesoph. foramen conduit for branch-ial vessels	-	-	hyoid arch mandibular
This Paper	thelodont basal gnathostome	d	sub-terminal	?	paired	see brain	endocast present with pineal	trace paired between br. 2/3	7 (8?)	long, narrow	separate ?	stomach present	fins	uncertain hypocercal	perichondral bone implied

The traces of the endoskeleton and various inner organs are either rarely preserved in thelodonts or, because of the nature of their preservation, are difficult to interpret. Despite being known for over 160 years, the group remains enigmatic and was until recently poorly characterised. Turner (1991) proposed the monophyly of the Thelodonti based on features of gross and scale morphology (see also Forey, 1984). Ideas about the inner organisation of thelodonts have been mostly reduced to creation of very generalised schemes which had as their foundation information from only a few specimens. Various interpretations of the preserved structures of the holotype and only complete specimen of *T. pagei* have been given (e.g., Powrie, 1870; Traquair, 1899; 1906; Westoll, 1945; Stensiö, 1927, 1964; Fig. 1, Table 1). The present study of the cast of the holotype *T. pagei* concludes that the arrangement of ridges and hollows shown on the cephalothorax can be interpreted as various endoskeletal features and soft organs allowing a

new reconstruction (Fig. 2a). The new data from the holotype of *T. pagei* concern mainly the brain, nasal sacs and branchial system. This information diminishes the gaps in our knowledge of the internal organisation of the thelodonts. We thus regard the latter as being significant for the further study of the problem of phylogenetic relationships of the ancient agnathan and gnathostome vertebrates.

The first turiniid thelodont was found in the classic Old Red Sandstone area of the northern hemisphere in deposits which until recently were thought to be non-marine sediments. The type specimen, '*Cephalopterus*' *pagei*, was discovered by Powrie in 1870 in the Lower Devonian of Turin Hill, eastern Scotland. That year both Powrie and Lankester considered that the holotype was preserved in ventral view; Powrie interpreted seven or eight pairs of 'exposed' branchial arches and thought it 'strangely allied to the modern Rays' (see Powrie's restoration in Fig. 1a); Lankester (1870) noted the resemblance to the

ventral surface of a cephalaspid but thought that the fossil was an early representative of the sharks and rays. Traquair (1899) was the first to seriously consider the significance of *T. pagei* in the light of new Silurian thelodonts he was also studying. He had renamed the holotype *T.* (Turner, 1976) and, in 1899, gave a full description of the specimen, reverting to the type genus *Thelodus*. He noted the absence of jaws and teeth and deduced that the arrangement of ridges and grooves was simply an indication of the presence of a cartilaginous branchial skeleton. Contrary to Powrie he did not believe that the branchial arches were exposed but, because he believed that the thelodont tail was heterocercal, he interpreted the fossil as preserved in dorsal view exhibiting eight pairs of cartilaginous arches, the last pair tending backwards in a reversed V-shape. Kemna (1903) went on to study *T. pagei* by comparison with other thelodonts ('coelolepids') known at the beginning of the 20th century. He surveyed the history of *T. pagei* and noted the differences of opinion on the determination of the visible side of the holotype. Kemna, following Traquair's (1899) opinion on the caudal fin, interpreted it as the dorsal side. While giving arguments pro and contra the interpretation of the branchial structures as visceral or branchial arches, he left the question open for further discussion. Subsequently, there have been several interpretations of the morphology of *T. pagei* and its systematic position compared to other thelodonts and in the overall interrelationships of agnathans (e.g., Westoll, 1945; Stensiö, 1927, 1964; Karatajute-Talimaa, 1978; Turner, 1982, 1991; Janvier, 1996). Information on the soft organs, however, is almost absent from the preceding literature. A brief interpretation of some of them was given by Stensiö (1958, 1964). Stensiö considered *T. pagei* as separate from other thelodonts; he placed it within the Heterostraci based on the configuration of the branchiae and the possession of an endocranium. Westoll (1945), however, preferred to return to the similarity to cephalaspids, notably *Kiaeraspis* (Fig. 1b, c). However, in considering the Turiniidae, Stensiö gave his main attention to the exoskeleton, which is not the subject of this paper. Only on the plate illustrating the holotype did he interpret the morphology of the branchial apparatus (e.g., Stensiö 1964, fig. 89) where he distinguished at least eight pairs of branchial sacs. His hypothesis will be considered further below in connection with analysis of questions remaining in the reconstruction of the inner organs of *T. pagei*.

As will be apparent in our description of the soft parts which follows we now interpret the cephalothorax of the holotype as being preserved in dorsal view because of the imprints of the olfactory tracts and aspects of the brain.

DESCRIPTION

The type specimen of *T. pagei* is the natural cast of an intact animal not deformed in any way. The counterpart apparently was not found. Table 2 displays measurements of *T. pagei*. The total length was taken from the middle of the anterior border of the head to the (broken) end of the lower lobe of the caudal fin; the maximum width is across on the level of postero-lateral points of the lateral brim. The caudal peduncle was taken across the narrowest point in front of the tail. As preserved, the anterior part of the body is relatively flat. The well-developed lateral brim (of the pectoral fin) starts just posterior to a slight bulge in the outline of the specimen, interpreted here as the possible position of the orbit, shown in Fig. 2a with a dashed line. Alternatively, the eyes might be placed directly on the antero-lateral border of the cephalothorax in a more lateral position and thus, as Traquair (1899) noted, they are not preserved. The pectoral extension (variously called the 'flap' or 'fin' in the literature; here we use the term 'fin') thus starts a little in front of the first pair of raised ridges or branchial structures, which we interpret as branchial sacs (see below), becoming larger in a caudal direction. This lateral rim of the fin is flatter than the raised central portion of the large cephalothorax. The cephalothorax in thelodonts usually comprises around one-quarter to one-third of total body length (Turner, 1991); at least the latter in the case of *T. pagei*. The external border of the lateral brim is rounded. The postero-lateral lobes of the fin have a rounded-triangular form. Behind the widest part of the lateral brim and cephalothorax the body tapers suddenly to a quite narrow peduncle. On the type specimen in between the lateral brim (distal pectoral lobes of the fin) at the posterior part of the cephalothorax can be seen a large rounded mass preserved as a darker clay-like sediment. The configuration of the median fins is not clear but there is a probable anal fin preserved on the right hand side of the specimen. The upper lobe of the tail fin is short, the lower lobe is well formed and elongated but not complete as the rock is broken (or trimmed) at this point. These lobes are apparently rounded. They are connected by a series of undulations which might represent a tail web. The tail fin is apparently hypocercal.

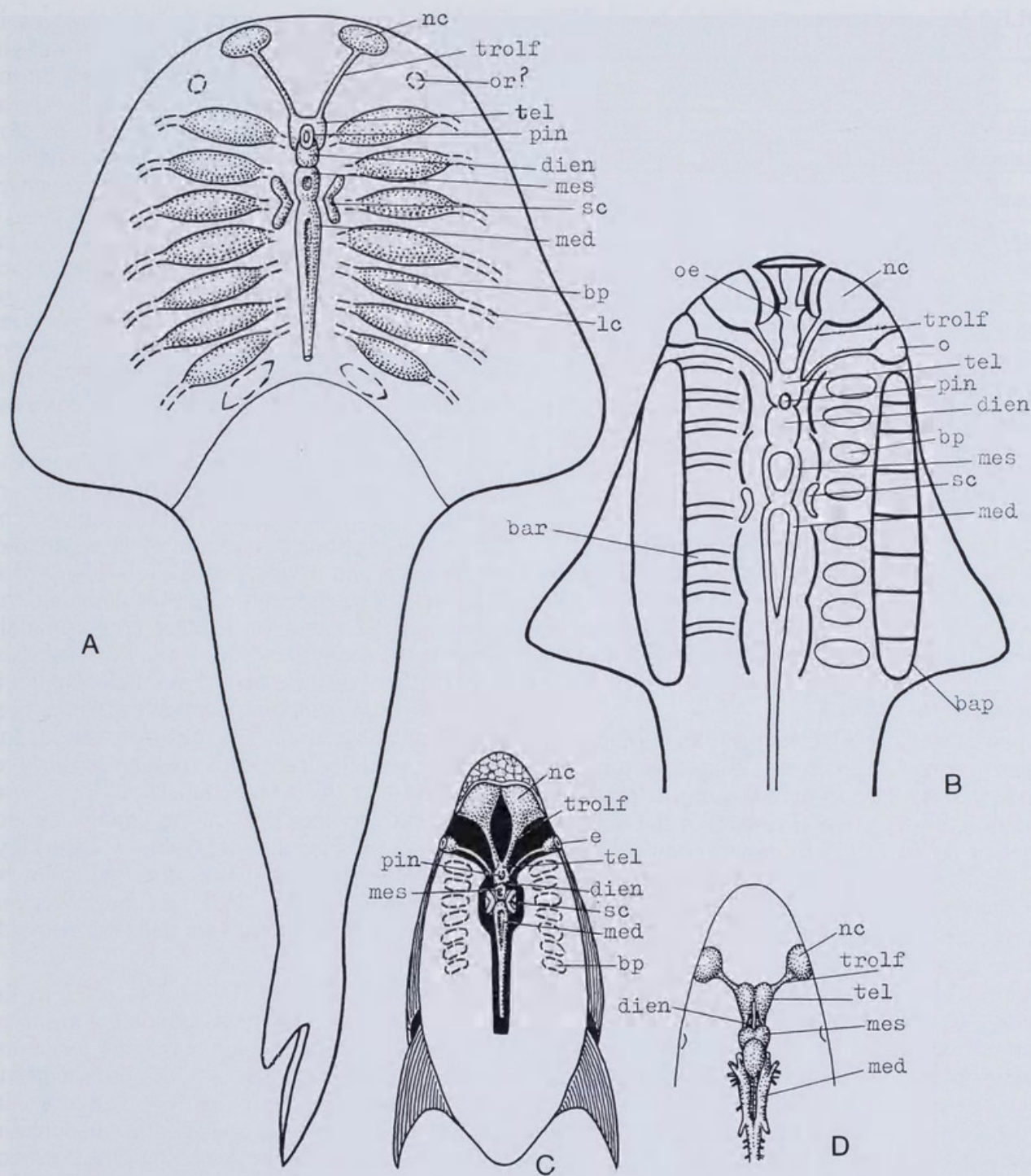


FIG. 2. Diagrammatic representation of the inner organisation of thelodonts, heterostracans and sharks. A, stylised drawing of main features of *Turinia pagei* (Powrie) based on the cast of the holotype, National Museums of Scotland RSM 1891. 92. 133. B, *Lanarkia horrida* (from Turner & van der Bruggen, 1993). C, pteraspid heterostracan of *Podolaspis* type (modified from Novitskaya, 1993). D, shark, *Squalus acanthias* (simplified from Marinelli & Strenger, 1959). Abbreviations: bap=branchial apparatus or row with branchial compartments; bar=possible position of visceral arch; bp=possible branchial pouch; dien=diencephalon; lc=lateral branchial canal; med=medulla (myelencephalon); mes=mesencephalon; nc=nasal capsule; oe=oesophagus; or=orbit; pin=pineal macula (probable position in thelodonts: A, B); sc=location of semicircular canals (uncertain in thelodonts: A, B); tel=telencephalon; trolf=olfactory tracts.

The traces of some soft organs are clearly preserved on the dorsal side of the holotype. These are discussed below.

THE BRAIN. In his explanations of inner structures of *T. pagei*, Stensiö (1964, p. 272, fig. 89: 'r.oc') noted the existence of a thickening formed

TABLE 2. Main measurements of *Turinia pagei* - RSM 1891.92.133.

Character measured	Measurement (mm)	Ratio
medial total length (mtl)	320	
cephalothorax length (cl)	120	mtl/cl = 2.67
maximum width (mw)	155	mtl/mw = approx. 2
length of pineal organ (po)	5	
width of po	1-1.5	
length of pineal macula (pm)	8-9	
width of pm	7	
width at level of po	95	mw/po = 1.6
width of caudal peduncle (cp)	30	
length of lower caudal lobe (ll)	45	mtl/ll = approx. 7.5
maximum width of lateral brim (lb)		mw/lb = 5

by the occipital region of the endocranium. This thickening continues forward into the otic region of endocranium. Our study of the cast of the holotype shows that the traces of the compartments of the brain can be distinguished in this thickening. Here we propose the following interpretation of the brain.

A pair of shallow but clear grooves is visible on the anterior part of the head. They diverge from the region situated in front of the pineal organ (see below), continue in the direction of the anterior border of the head and terminate not far from it (Fig. 2a, Fig. 3, trolf). We equate these grooves with the tracti olfactorii of modern sharks and other diplorhinal animals, for example, *Lanarkia* (Turner & van den Bruggen, 1993; Fig. 2b), and the Palaeozoic heterostracans (Fig. 2c), by comparison with their position relative to the pineal organ and the anterior border of the head, and by their length. The position of anterior ends of olfactory tracts indicates the place of the paired nasal sacs which were situated near the anterior border of the head on either side of the presumed just ventral mouth opening. The bulbous shape of the nasal sacs is apparent. The telencephalon is not distinguishable but it is possible to estimate its place indirectly, based on the position of the pineal organ and, therefore, from the position of the diencephalon. The pineal organ was situated on a level of the anterior pair of the branchial sacs. Its trace has the appearance of elongated oval pit bordered by a low convex border visible on the surface of the cast. The dimensions of the pit and pineal macula (including convex border) are shown in Table 2. The position of pineal macula indicates that of the diencephalon

since, as far as it is known, the pineal organ in agnathans is always associated with the diencephalon. The preserved surface shown on the cast becomes somewhat lower in front of the diencephalon. In all probability the telencephalon in *T. pagei* was placed in the region of this depression, that is, the upper surface of telencephalon was lower than the upper surface of diencephalon. Alternatively, the depression might be the back of the mesencephalon which is often opposite gill pouch #1 in gnathostomes (Mallatt, pers. comm.). The posterior limit of diencephalon is marked by a weak groove behind the pineal macula. Thus the posterior edge of the diencephalon is placed approximately on the level between the first and the second pairs of branchial sacs.

The natural casts of the mesencephalon and myelencephalon or their endocranial casts are visible on the holotype of *T. pagei* behind the diencephalon although the limit between the mesencephalon and myelencephalon is poorly distinguished. The junction of mesencephalon and myelencephalon was on a level approximately between the second and third pairs of branchial sacs. Further back the cast of myelencephalon is seen distinctly, extending back as far as the posterior branchial region. The traces of anterior and posterior semicircular canals are seen on the level of second and third branchial sacs (Fig. 3, sc. (lab.)), but the imprints of the canals are not perfectly clear. The possible position of the labyrinth in the same place was also indicated by Stensiö (1964, fig. 89, 'lab?') although our numeration of the branchial sacs does not coincide with his.

BRANCHIAL STRUCTURE. The casts of the branchial sacs are clearly visible on the holotype of *T. pagei*. The branchial sacs were large and situated overall transversally. They diminished in size in a caudal direction (Figs 3-4). The branchial sacs are situated near to one another. Seven pairs of them are clearly distinguishable. The presence of the eighth most posterior pair is not definite but the possible position is indicated in Fig. 2a. The anterior pair of branchial sacs is the largest, oriented transversally and obliquely; their lateral ends are directed forward. The orientation of sacs changes from anterior to posterior: the lateral ends of posterior branchial sacs are directed obliquely and back.

Unfortunately, the preservation of material still does not allow us to answer the question of how the branchial sacs of *T. pagei* opened to the outside. We still cannot determine whether they had separate branchial openings or individual canals

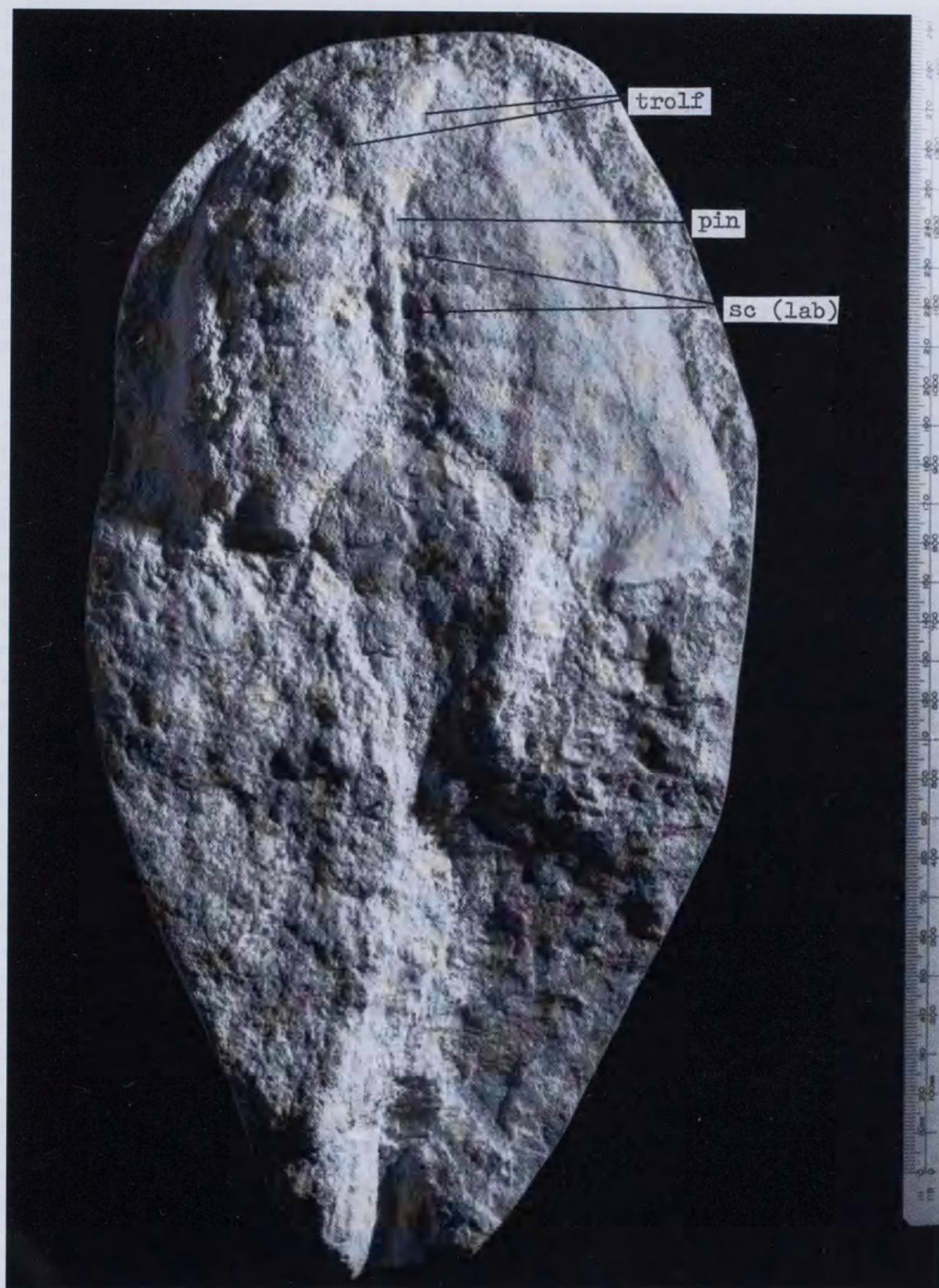


FIG. 3. Photograph of the cast of the holotype of *Turinia pagei* (Powrie) exhibiting the position of olfactory tracts (trolf), brain, pineal organ (pin), possible semicircular canals (sc (lab)). Impressions of brain stem and branchial sacs can be seen. Holotype (RSM1891.92.133; Museum of Scotland, Edinburgh) from the Early Devonian (Lochkovian) Old Red Sandstone of Turin Hill, Forfar (Scotland).

leading out to a common atrial canal. The slight thickening which is seen on the lateral brim of *T. pagei* was interpreted as the anterior branchial canal by Stensiö (1964, 'conduit branchial antérieur'). Such an interpretation sat well with his idea of *T. pagei* being an heterostracan. Our investigations show, however, that this canal was not continuous but consisted of short separated segments (Fig. 4, icbr). The curved imprints, which were explained by Stensiö (1964, fig. 89) as extrabranchial atria, are seen to be more lateral relative to each branchial sac. Similar imprints or natural casts can be seen in many heterostracans (e.g., Novitskaya, 1983). In all probability these imprints represent the traces of individual branchial canals leading from the branchial sacs. In some thelodonts, for example in *Phlebolepis elegans* (Ritchie, 1968), and the recently discovered fork-tailed thelodonts (Wilson & Caldwell, 1993), the branchial sacs each opened out separately.

As already noted, the casts of the branchial sacs in *T. pagei* are situated near to one another. If this state was not due to posthumous alteration such as contraction, the branchial arcs (arches) appear to have been very long and narrow and subequal in size. The first visceral arch was apparently situated immediately behind the eye. In *T. pagei*, the posterior arches were shorter than the more anterior ones. As with the pharyngeal arrangement in modern primitive sharks, this pattern matches well with the extrabranchial cartilages of sharks (Mallatt, pers. comm. 1996).

DISCUSSION

On the whole, the organisation of the visceral system in *T. pagei* has overall similarity to that of heterostracans and some other agnathans (Gagnier, 1995). Such common traits are observed in the presence of a few branchial sacs, in their form and disposition, in the presence of individual (for each sac) lateral canals and in the simple structure of cartilaginous non-differentiated branchial arches. Whether similar characters were inherent also in the most archaic vertebrates is still in debate. To a certain degree the finds of Ordovician vertebrates in Australia (*Arandaspis*: Ritchie & Gilbert-Tomlinson, 1977) confirm this. Some current analyses have led to the conclusion that cephalaspids, with their highly specialised morphology are the sister-group of gnathostomes and that thelodonts are paraphyletic (e.g., Forey & Janvier, 1994). However, we consider that the *T.* pattern seems to show what some regard as the primitive gnathostome condition (e.g., Novit-

skaya, 1983; Gagnier, 1995). The arrangement is comparable with living early gnathostome embryos with first gill arch and pouch just behind the eye, second arch (the hyoidean) just in front of the otic capsule and so on (e.g., Mallatt, 1996). Thus, the primitive vertebrate pattern might be a high number of paired branchial structures, as in galeaspids and some Ordovician forms (Gagnier, 1995; Janvier, 1996). A small number of eight paired branchial structures, as seen in *Turinia*, which might functionally have been only seven pairs; this recalls the suggested pre-gnathostome pattern (Mallatt, 1996) which is close to that seen in modern primitive chondrichthyans such as *Heptranchias* and *Chlamydoselachus*.

Consideration of the morphology of *T. pagei* indicates the internal organisation of one thelodont, although to understand some organs, principally the branchial system, we need more precise data. At the same time the new interpretation makes it possible to compare *T. pagei* with *Lanarkia horrida*, another thelodont in which the soft organs have recently been reconstructed on the basis of good new material (Turner & van der Bruggen, 1993). Comparison shows that *Turinia* and *Lanarkia* were similar in the main pattern of their inner organisation. The presence of possible well developed long olfactory tracts and paired, separate large nasal sacs of gnathostome type in both thelodonts are the most significant common characters. From our study of *T. pagei*, it is clear that the reconstruction of the labyrinth in *L. horrida* was probably placed too far back by Turner and van den Bruggen (1993; the brain configuration needs to be slightly altered to abut the semicircular canals with the level of the 2nd and 3rd gill pouches. However, as shown on the comparative scheme (Fig. 2), both thelodonts are similar in the characteristics of the cephalothorax to heterostracans and basal gnathostomes. The same position of the telencephalon in relation to the upper surface of diencephalon is found in heterostracans (Novitskaya, 1974, 1983) and lampreys (Marinelli & Strenger, 1954; Fontaine, 1958). The pineal organ was situated on a level of the anterior pair of the branchial sacs, as in heterostracans (Novitskaya, 1983, fig. 64). The posterior limit of diencephalon occupies a similar position in heterostracans, e.g., *Poraspis pompeckji* (Novitskaya, 1983, pl. 4, figs 2, 3). Because the labyrinth is not clearly seen, it is possible that the semicircular canals were placed somewhat deeper in the endoskeleton in *T. pagei* than in some other early vertebrates. In heterostracans, for example, the semicircular canals retain very clear

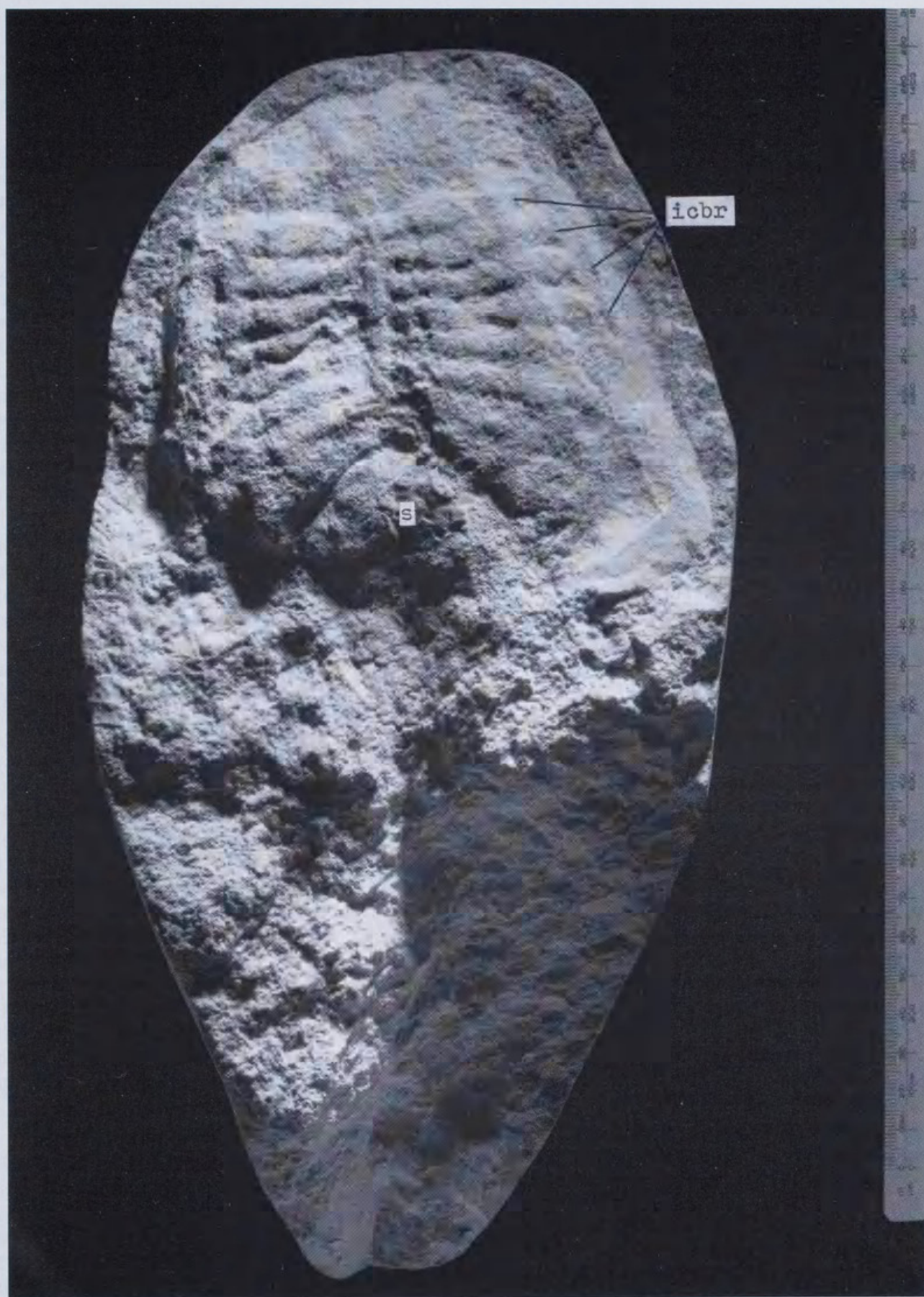


FIG. 4. Photograph of the cast of the holotype of *Turinia pagei* (Powrie). Different direction of light makes the traces of branchial apparatus clearer: icbr=individual branchial canals; s=position of stomach contents.

traces which can be seen in cyathaspids such as *P. pompeckji* (Brotzen), *P. cylindrica* Kiaer, *Komalaspis della nitida* (Kiaer) (e.g., Stensiö, 1964, figs 81A,B-82A,B; Novitskaya, 1983, pl. IV, figs 2, 3).

The comparison of thelodonts and heterostracans shows that the visceral arch situated immediately behind the eye in *T. pagei* corresponds to the mandibular arch of heterostracans. This structure was homologised to that of lower gnathostomes (using a shark embryo) by Novitskaya (1983). The second arch is compared to the hyoidean in sharks, the following to the first branchial arch and so on (Novitskaya 1983, fig. 71, p.133). The similarity of thelodonts, heterostracans and basal gnathostomes in the disposition of the named visceral arches and the large nasal sacs, leads us to consider the visceral skeleton as homologous in all three groups.

The presence of these characters in the morphology of the named groups and the evidence from the holotype of *T. pagei* testify that a common nasohypophysial duct of cephalaspid type did not form in their ontogenesis (contra van der Bruggen & Janvier, 1993). Furthermore, the type of ontogenesis (development) in thelodonts was fundamentally similar to that of heterostracans and basal gnathostomes. The method of reconstructing the developmental type of an agnathan on the basis of their morphology was earlier demonstrated by Novitskaya & Karatajute-Talimaa (1989) and Novitskaya (1993).

SUMMARY

The organisation of the visceral skeleton, the number of branchial sacs (at least seven or at most eight pairs), and the position of the anterior pair relative to the pineal organ, are similar in *Turinia* and *Lanarkia*. The characters noted here, as with some others concerning the internal morphology and the exoskeleton (Novitskaya, 1983; Turner, 1991), are similar also in these thelodonts and in heterostracans. At the same time the presence of external openings of branchial sacs ventral to the pectoral fin-lobes, now known in some thelodonts, separates them from the specialised heterostracans which possessed a common removal branchial canal with one common external opening or atrium.

The mouth in *T. pagei* was apparently anterior and just ventral, flanked by paired nasal capsules. No evidence for a nasohypophysial organ is seen. The branchial row which began just behind the eyes, was relatively foreshortened with openings in all probability ventral to the pectoral fins as

known in *Phlebolepis elegans* and *Loganellia scotica*.

In *T. pagei* the morphology of the divisions of the brain (diencephalon, mesencephalon, myelencephalon) is simple and similar to that in such groups of vertebrates as lampreys, heterostracans, and arthrodires (e.g., Novitskaya, 1993). In the morphology and disposition of these brain compartments, *T. pagei* is generally similar to *Lanarkia*. The brain is homologous with that in heterostracans and in lower gnathostomes (e.g., chondrichthyans). The pineal organ was preserved but there was no nasohypophysial organ. The paired semi-circular canals are placed in the region of the branchiae 2 and 3. Other characters such as the presence of specialised denticles lining the mouth and pharyngeal region, morphological style and complexity of the external squamation, presence of a stomach (see e.g., Fig. 4, s), indicate close similarity between thelodonts and chondrichthyans.

In agreement with the above-mentioned similarities between thelodonts and lower gnathostomes (in morphology of olfactory organ, telencephalon, in apparent absence of a common nasohypophysial organ) we believe that thelodonts shared a similar type of ontogenesis (see Novitskaya & Karatajute-Talimaa, 1989). This, and the presence of external removal openings for each pair of branchial sacs, seen in some thelodonts (but not here in the holotype of *T. pagei*), provides the basis for considering them as the group most similar to basal gnathostomes in the main traits of organisation. Among Palaeozoic agnathans the thelodonts are thus considered to be the group phylogenetically nearest to gnathostomes (chondrichthyan fishes). This idea has been considered previously by both authors on the basis of other material and other characters (Novitskaya, 1983; Turner, 1991). A recent cladistic analysis of early vertebrates arrived at a similar conclusion that places thelodonts as the sister group of gnathostomes (Gagnier, 1995). The new data on the internal organisation of *T. pagei* presents evidence supporting this hypothesis.

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