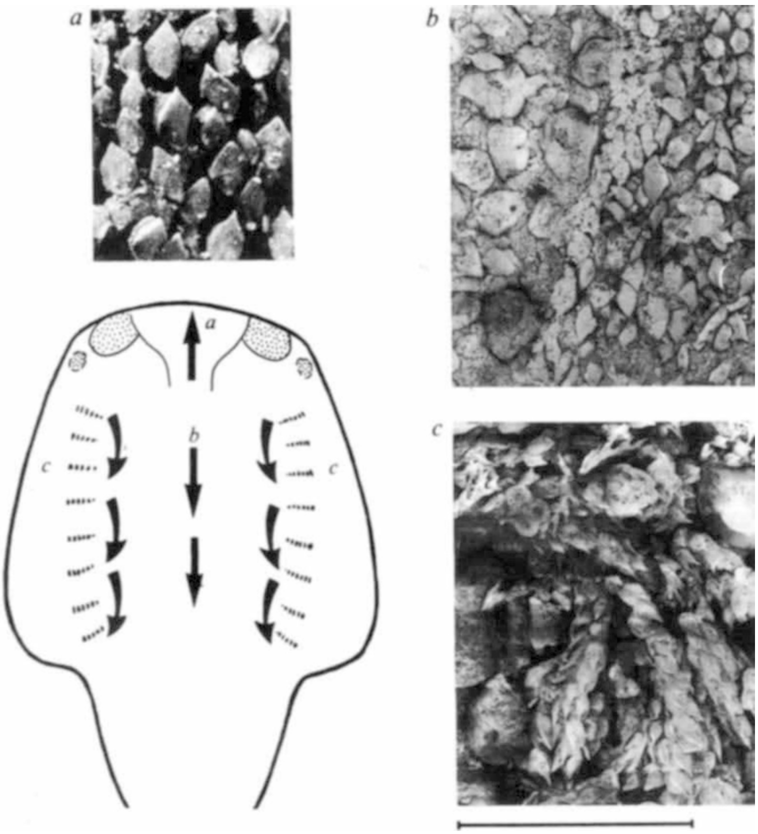
Denticles in thelodonts

SIR — Thelodonts are the most enigmatic of all Palaeozoic jawless vertebrates, because their internal skeleton was not ossified and their exoskeleton was made up of minute scales which were often dispersed during decay. Scotland is one of the few places where articulated thelodonts are found, where they occur in 425-million-year old Silurian rocks. Acid preparation carried out by W. V. B. on some well-preserved Scottish thelodonts has yielded for the first time peculiar internal assemblages of minute denticles or denticle-bearing plates, which recall some of the pharyngeal dermal elements of jawed vertebrates and were hitherto unrecorded in any jawless vertebrate. Some of these thelodont dermal elements have recently been mentioned[1–3], but we are now able to describe their precise distribution inside the animal, and provide a possible explanation of their function.

The internal denticles fall into three types: (1) located inside the snout, consisting of minute, forward-pointing denticles (*a* in the figure); (2) located further back in the centre of the head, consisting of somewhat similar, but backward-pointing denticles (*b*); and (3) located near the presumed branchial openings, consisting of slender cusped denticles, often fused into thin, curved series arranged side by side (*c*). This discovery of an extensive exoskeletal covering in the mouth and pharynx of a jawless vertebrate raises several questions. Did other Palaeozoic jawless vertebrates, in particular the armoured forms, or 'ostracoderms', also possess such internal denticles, hitherto unnoticed? Or were some thelodonts more closely related to jawed vertebrates, as recently suggested on other grounds[4,5]?

The denticles of the second and third type can easily be interpreted as pharyngeal denticles or tooth whorls associated with the gill bars or with the extrabranchial ducts. Similar tooth whorls occur in Palaeozoic sharks, for example[6]. More puzzling are the forward-pointing denticles in the snout, which cannot be regarded as buccal denticles or teeth because of their orientation. However, similar forward-pointing denticles or tubercles are observed on the wall of the large median dorsal duct of galeaspids (a group of Palaeozoic armoured jawless vertebrates[5]), which was for intake of respiratory water. The role of such structures, directed against the water flow, may have been either to repel ectoparasite larvae or to convey part of the water flow toward the nasal cavities. If this analogy is correct, thelodonts may have had some kind of large terminal inhalent duct, comparable in structure and function to that of extant hagfishes, a condition which is currently regarded as primitive for vertebrates, but lost in lampreys and jawed vertebrates[5]. The co-existence of such a large median inhalent duct connected with the nasal sacs, and pharyngeal denticles or tooth whorls, are what would be expected in a theoretical pre-gnathostome.



Outline of the head of the thelodont *Loganellia*, from the Silurian of Scotland, showing the position and orientation of the three types of internal denticles (*a*–*c*). In *b*, the much larger external head scales are exposed in basal view on the left side. Nasal cavities and eyeballs stippled. Scale bar, 1 mm.

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Protein structure and introns

SIR — In the view of Gilbert[1,2] and others, genes encoding modern proteins arose by the intron-mediated assembly of ancestral RNA genetic units encoding protein structural motifs. A recent boost for this model came from the discovery in the triose phosphate isomerase (TIM) gene of a mosquito[3] of a novel intron mapping to a position predicted several years earlier[4]. This is interpreted to be a rare survivor of an intron which was present in the assembly of an ancestral TIM gene billions of years ago, an intron which was generally lost in most descendant species. There is, however, a very simple alternative explanation for mapping between intron position and protein structure which requires neither the invocation of coincidence nor an ancient, gene-assembly origin for introns.

It is widely believed that, very early on, RNA was used as both genetic storage material and cellular effector molecule. Labile RNA 'genes' might have enhanced their stability by adopting folded tertiary structures, capable of being unfolded during translation. As in the Gilbert model, these genes would have encoded small protein structural motifs able to associate in various combinations to form multisubunit complexes, equivalent to modern proteins, with selectable functions.

Complex continuous genes could then