THE SCOTTISH LOWER CARBONIFEROUS SHARK *ONYCHOSELACHE TRAQUAIRI*

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ABSTRACT. The discovery near Edinburgh of a second articulated specimen of a small Carboniferous hybodontiform shark has encouraged renewed anatomical study of the original Glencartholm specimen. This shark is not referable to *Tristychius arcuatus* Agassiz, 1837, as previous authors have suggested, but has recently been renamed *Onychoselache traquairi* Dick, 1978. *Onychoselache* has a tribasal pectoral fin similar to most hybodontiforms and neoselachians, not a dibasal fin as is often supposed. Furthermore, the structure of the head and tail are typically hybodontiform and, therefore, there is no justification for its subordinal separation from the hybodontids, as proposed by Moy-Thomas (1936).

IN 1888 Traquair briefly described the pectoral fin of a small shark from Glencartholm in Dumfriesshire, which he identified as *Tristychius arcuatus* Agassiz, 1837. He noted that the fin was remarkably modern in appearance compared with those of other known Palaeozoic sharks. Its basal cartilages were highly differentiated and very similar to those of Recent elasmobranchs. In fact, the fin appeared to have only two basal cartilages, a mesopterygium and a metapterygium, rather than the three typical of most Recent forms. He concluded that the propterygium was either very small or had fused to the mesopterygium. Traquair never published a full description of the specimen, which is now in the Royal Scottish Museum (RSM), Edinburgh. However, he appears to have had doubts about its similarity to *T. arcuatus*, and in 1903 referred it to *Tristychius minor* Portlock in a faunal list of the Glencartholm locality.

A more complete description of the specimen was given by Woodward (1924). He noted small '*Lophodus*'-like teeth and peculiar hooked denticles along the anterior margins of the pectoral fins, and also described its finspines. He accepted Traquair's (1888) identification as *T. arcuatus*, and concluded that sharks closely related to Mesozoic hybodonts were already present in the Lower Carboniferous.

The fish was redescribed by Moy-Thomas (1936), who prepared the posterior part of the specimen to expose the pelvic fins, anal fin, and base of the tail. He noted that the pectoral and caudal fins appeared to be more specialized than in hybodontids, and suggested that it should be included in a separate Suborder, Tristychii, of the Order Protoselachii (Moy-Thomas 1936, 1939).

Both Woodward (1924) and Moy-Thomas (1936) upheld Traquair's (1888) dibasal interpretation of the pectoral fin. However, one of us suggested recently that the mesopterygium was displaced and could be overlying and concealing the propterygium (Maisey 1975, fig. 2*b* inset). As in other sharks, the calcified cartilage elements are composed of a thin external layer of prismatic calcified cartilage surrounding a central core which, in life, was probably filled with non-calcified hyaline cartilage. A vertical section through a cartilage might, therefore, be expected to expose two layers of calcified cartilage. Where the mesopterygium of the Glencartholm specimen is damaged, however, it is possible to identify four layers of calcified cartilage, as if two cartilages were present. Confirmation of this possibility was provided when a new specimen of this fish was collected by Mr. S. P. Wood from the Wardie Shales near Edinburgh. This specimen (RSM 1974.23.14), studied by the other author (J. R. F. D.), shows quite clearly that three basal cartilages are present in each pectoral fin.

The Wardie specimen is slightly larger than the Glencartholm fish but there can be little doubt that the two are conspecific. Both have similar teeth and pectoral fins and both have the characteristic series of hook-like, anterior marginal pectoral denticles.

Unfortunately, other material collected by Mr. Wood from the Wardie Shales and elsewhere in the Scottish Oil Shale Group indicates that this fish cannot be *T. arcuatus* Agassiz. Its finspines are

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distinctly different from the holotype of *T. arcuatus* and, while they are similar to *T. minor*, the spine of the latter appears to be indistinguishable from immature spines of several contemporaneous shark species. Therefore, the Glencartholm specimen has recently been made the holotype of a new genus and species, *Onychoselache traquairi* (Dick 1978).

The reidentification of the Glencartholm fish, together with new information on the head and pectoral fins provided by the Wardie specimen, have encouraged us to produce a full redescription of *O. traquairi*. We have also been able to reconsider its relationships with other early sharks in the light of new data obtained from the study of *T. arcuatus sensu stricto* (Dick 1978).

Abbreviations used in text and text-figs. MC, Meckel's cartilage; MSP, mesopterygium; MTP, metapterygium; NCR, neurocranium; PAX, pectoral fin axis; PQ, palatoquadrate; PRP, propterygium; R, radials; SC, scapulocoracoid; apq, articular process of palatoquadrate; cor, coracoid region of scapulocoracoid; dent, denticles; dfm, diazonal nerve foramen; fm, foramen magnum; pop, postorbital process; scp, scapular region of scapulocoracoid.

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES
Subclass ELASMOBRANCHII
Order HYBODONTIFORMES incertae familiae
Genus ONYCHOSELACHE Dick, 1978

Type and only known species. O. traquairi Dick, 1978.

Revised diagnosis. Small (160–250 mm long) hybodontiform sharks having a series of about twelve or fourteen large, hook-like denticles along the anterior margin of each pectoral fin; similar denticles present on head, sometimes fused at their bases into multicuspid scales. Teeth low-crowned and tumid, with deep roots lacking a lingual torus. Finspines with three or four thin costae each side; the hindmost finspine more recurved and stouter than the anterior one.

Onychoselache traquairi Dick, 1978

Holotype. RSM 1885.54.1, from the Glencartholm Volcanic Beds, C_2/S_1 Zone, Viséan (Lower Carboniferous) on the banks of the River Esk, near Glencartholm, Dumfries District (Galloway and Dumfries Region), Scotland.

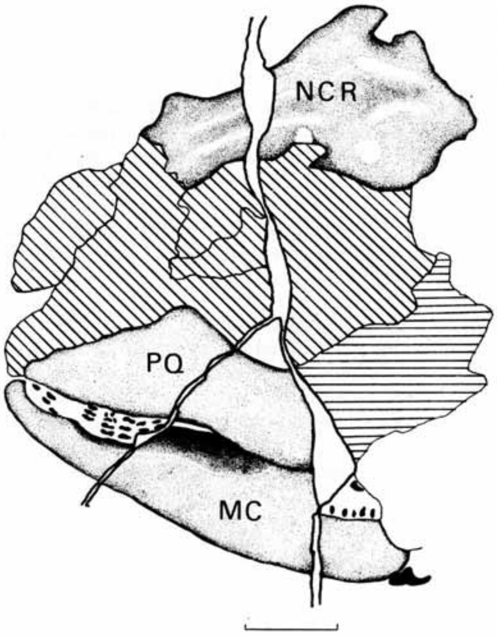
Referred material. RSM 1974.23.14A/B from nodule bed 7 (Wood 1975), Wardie Shales, C_2/S_1 Zone, Viséan, on the seashore between Granton Harbour and Trinity Bridge, Wardie, Edinburgh, Scotland.

Preservation. The Glencartholm specimen is preserved in a calcareous shale, while the Wardie specimen is in a clay-ironstone nodule. Because of the delicate state of both specimens, little additional preparation has been possible. The former is exposed in lateral view and is almost complete except for the tip of the tail. The latter specimen is exposed dorsoventrally, but extends only to the start of the pelvic region, to the base of the second dorsal finspine. The Wardie specimen is slightly the larger, suggesting a fish of about 250 mm total length compared with about 165 mm for the holotype.

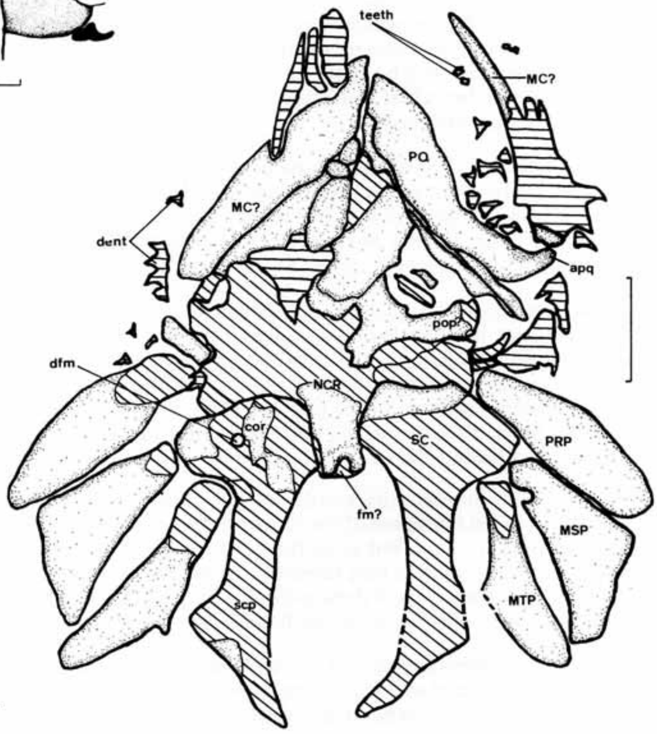
Description

Neurocranium and Jaws. The head of the holotype is badly crushed and has not previously been described. Like the trunk, it is exposed in lateral view, so that the left palatoquadrate, the right Meckel's cartilage, and parts of the roof and left side of the neurocranium can be identified (text-fig. 1). The neurocranium is about 24 mm long. The orbits lie almost midway along its length and are surmounted by marked supraorbital ridges.

The neurocranium of RSM 1974.23.14 is exposed in ventral view (text-fig. 2). Its occiput lies between the two coracoid parts of the pectoral girdle. The only feature of the neurocranium which can be distinguished further forward is a long process running laterally towards the left palatoquadrate. This is probably a postorbital process similar in structure to that of *T. arcuatus sensu stricto* (Dick 1978). Both specimens suggest that the otico-occipital region was proportionately as short as that of *Hybodus basanus* (Woodward 1916).



TEXT-FIG. 1. *Onychoselache traquairi*, RSM 1885.54.1. Braincase and jaws. Diagonal hatching is damaged cartilage. Horizontal hatching is an area of broken cartilage and denticles. Scale bar = 5 mm.



TEXT-FIG. 2. *Onychoselache*, RSM 1974.23.14A. Jaws, braincase, pectoral girdle, and pectoral basals. Scale bar = 10 mm.

The palatoquadrate of RSM 1885.54.1 is badly damaged posteriorly. Its anterior end is shallow and its jaw symphysis, which must have underlain the ethmoid region of the neurocranium, would have been narrow. A well-developed orbital process is present beneath the orbit on RSM 1885.54.1. The articular region of the left palatoquadrate is exposed on RSM 1974.23.14. The jaw is lying on its side, with the articular process for the lower jaw projecting laterally (text-fig. 2, apq). Although the otic process is incomplete, there is no suggestion of a long and deep quadrate region like that of most Palaeozoic sharks (Schaeffer 1967, 1975). The jaw may have been similar in shape to that of *T. arcuatus* (Dick 1978, fig. 10A–D) and probably terminated beneath the postorbital process of the neurocranium.

The right Meckel's cartilage is exposed in mesial aspect on the holotype. Part of a deep dental furrow for the tooth families can be seen beneath the orbital process of the palatoquadrate. The lower jaw deepens posteriorly, but its articular surface is obscured.

Branchial arches. Nothing is preserved of the branchial arches in RSM 1974.23.14, and very little can be identified in the holotype. However, Woodward (1924, fig. A, br) noted the presence of a few long, thin cartilages, lying horizontally along the body above the left scapulocoracoid, which he identified as branchial rays. He suggested that the pectoral girdle of the holotype was slightly displaced, but Moy-Thomas (1936, fig. 12) restored the coracoid region of the scapulocoracoid running beneath the branchial arches and almost extending forward to the back of the jaw. This results in an unnaturally high position for the branchial arches, whose ventral elements would still have lain well above the level of the jaw articulation.

We believe, for reasons explained below, that the left scapulocoracoid of the holotype has been displaced forward so that most of the branchial cartilages have been lost. Those cartilages identified by Woodward (1924) as branchial rays may in fact be the pharyngobranchial elements of the gill arches, displaced forwards and upwards by the scapulocoracoid until they came to lie in the horizontal plane. Alternatively, they may be hyoid rays similar to those of *T. arcuatus* (Dick 1978), but it is far more likely that both branchial and hyoid rays would be lost before the much stouter visceral arches to which they were attached.

Vertebral column. The axial skeleton of both specimens is similar, although the Wardie specimen's vertebral column is partly disarticulated. There are no vertebral centra and presumably the notochord was unconstricted. The neural arches, ribs, and haemal arches are calcified; the neural arches are stout, but the ribs are long and slender. Those of the Wardie specimen are apparently broken, and consequently appear shorter than in the holotype.

Dorsal fins. Moy-Thomas (1936, p. 776) noted the presence of a single, short radial cartilage behind the triangular basal of the second dorsal fin. While the poor preservation of this region makes interpretation difficult, there is probably at least one more radial and there may even have been a series of cartilages similar to those in *Hybodus hauffianus* (Woodward 1916, fig. 2).

The internal structure of the first dorsal fin of the Wardie specimen is obscured by its displaced finspine. Most of the second dorsal fin is also missing, and only a small part of its basal cartilage can be identified behind the base of the finspine.

Anal fin. In the holotype this was described by Moy-Thomas (1936, p. 777), who identified two small cartilages behind the region of the pelvic fins and beneath the haemal arches. The specimen is broken between the cartilages, but as in the dorsal fins, cartilage appears to be more extensive than his restoration suggests, and may represent the remains of a single, proximal basal plate of the anal fin. Beneath these fragments of damaged cartilage, there are traces of one or two further poorly calcified elements. These may be radial cartilages which articulated with the basal plate.

Caudal fin. As Moy-Thomas (1936) observed, several of the haemal arches lying midway between the anal fin and the hind edge of the specimen are stout and elongated in comparison with those more anteriorly, but from this point they diminish in size caudally. These cartilages are much broader and less numerous than the neural arches above them. They are also much longer, and several of the longest (possibly up to eight or ten) may be jointed once along their length. There can be little doubt that these cartilages represent hypural elements of the caudal fin.

Moy-Thomas (1936) was uncertain about the structure of the caudal fin because of the apparent downturning of the vertebral column towards the edge of the specimen. There appears, however, to be no reason why the caudal fin of *Onychoselache* should not have been slightly heterocercal; the position in which the holotype is preserved may quite easily have been caused by flexion of the trunk muscles after death. The hypural cartilages indicate the presence of a small hypocaudal lobe, probably similar in shape to that of *Tristychius* and *Hybodus*.

Pectoral girdle. This consists of a pair of large, separate, scapulocoracoid cartilages. In RSM 1974.23.14 these have been crushed so that they now lie in the horizontal plane of the nodule, and are exposed along their entire length.

Each scapulocoracoid consists of a broad ventral coracoid region, to which the fin articulates, and a long, thin, scapular process. The proximal region of the process projects outwards slightly and has a concave lateral margin. It turns mesially through an angle of about 45° just over half-way along its length. Woodward (1924, p. 340) believed that this point, which may be termed the dorsolateral angle of the scapular process, formed the original point of articulation of the pectoral fin. It is clear, however, from the Wardie specimen (text-fig. 2) that this is not the case.

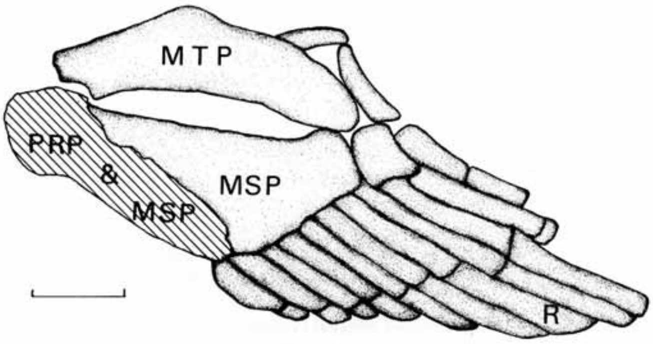
The apices of the two scapular processes in the Wardie specimen approach each other towards the midline of the body. In the Glencartholm specimen the left process lies above the level of the notochord, and it therefore seems possible that in life the apices of the two processes terminated very close on either side of the base of the first dorsal finspine.

The coracoid region is slightly better preserved in the Wardie specimen. Seen in section, it is approximately square; ventrally, a short plate runs inwards, terminating short of the midline. The lateral coracoid wall runs outwards from the base of the scapular process to develop articular processes for the three basal cartilages of the pectoral fin. Unfortunately, the articular region is damaged or hidden in both specimens. A single foramen is present on the coracoid's lateral surface in the Wardie specimen. This was undoubtedly for the passage of the brachial artery and diazonal nerves to the pectoral fin. By analogy with Recent sharks, it is probable that a further lateral foramen was present and that the two foramina lay above and below the articular region of the scapulocoracoid. A mesial foramen, by which the artery and nerves would have entered the scapulocoracoid, is not identifiable.

Woodward (1924) and Moy-Thomas (1936) disagreed about the original orientation of the pectoral girdle. Whereas Woodward considered the pectoral fin of the Glencartholm specimen to have been displaced, having originally articulated with the girdle at its broadest point, Moy-Thomas (1936) doubted that the girdle had been disturbed significantly and reconstructed the fin and girdle just as they are preserved.

Neither of these restorations of the pectoral girdle is very satisfactory, and a comparison of the two specimens suggests yet another interpretation. While the pectoral fin basals clearly have a short area of articulation on the coracoid region of the girdle, Woodward (1924) was probably correct in considering the girdle to have been displaced. In both specimens the coracoid region appears to have swung anterodorsally upon a point of rotation high up the scapular process. In the Wardie specimen this movement has been so marked that the scapulocoracoids now lie horizontally with their coracoid region crushed against the occiput of the neurocranium (text-fig. 2). Displacement of the coracoid region would also explain the condition of the branchial arches, and how the pectoral fins of both specimens have been displaced forwards. This has led, in the Glencartholm specimen, to the overlapping of the pro- and mesopterygia and, in the Wardie specimen, to the dislocation of the propterygia which now lie in front of the coracoids.

In all probability the pectoral girdle sloped posterodorsally, with the scapular process lying at an angle of about 60 to 70° to the horizontal axis of the body. Ventrally, a gap for the branchial arches would have been present between the back of the jaws and the coracoid region of the girdle.



TEXT-FIG. 3. Pectoral fin of RSM 1885.54.1. The propterygium is partially concealed by a damaged area. Scale bar = 5 mm.

Pectoral fin. The pectoral fins of the Glencartholm specimen are distorted, but enough of their structure can be determined (text-fig. 3) to show that they were very similar to those of the Wardie specimen. In the latter, both pectoral fins are exposed (text-fig. 4) with the basal and radial cartilages well spread out. Apart from the slight forward displacement of the propterygia, the basal cartilages lie much as they would have done in life.

Three large basal cartilages articulate proximally on the scapulocoracoid. All three are remarkably long, running nearly half the length of the fin, and terminating distally at approximately the same level. Their length suggests that they projected laterally into the fin well beyond the limits of the body wall. Over most of their surface the basals are quite thin, but each is stiffened by a stout marginal ridge along one side.

The propterygium is narrow and shaped like the blade of a palette knife. The proximal margin is about 2·5 mm broad and appears to have been slightly concave to receive the articular process of the coracoid. Immediately distal to the well-developed articular cotylus, the propterygium has a short neck region. Beyond this, the anterior surface develops a long, blade-like margin which curves convexly towards the bluntly pointed propterygial apex. The posterior surface of the propterygium is also convex, but considerably straighter than the anterior edge and, as it runs proximally, it thickens to form a stout marginal ridge.

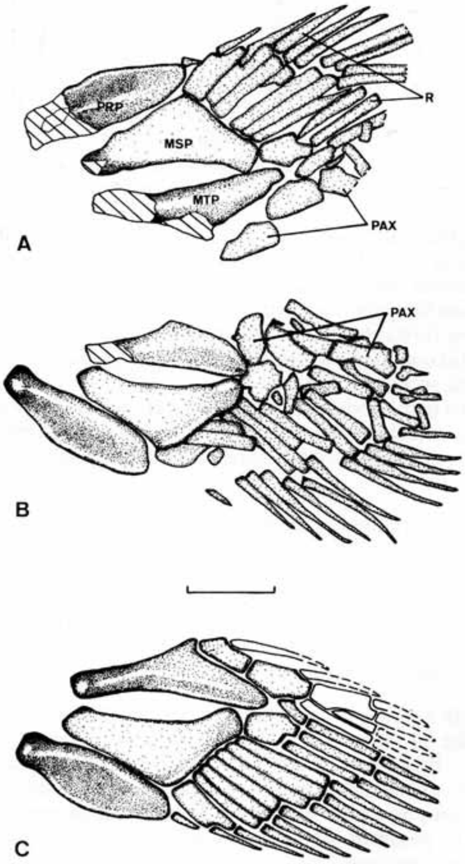
The mesopterygium is an approximately triangular cartilage, with a broad distal margin, to which the majority of the fin's radial cartilages articulate. Proximally it develops a short (about 2 mm wide) posteromesially facing articular margin for the scapulocoracoid. The anterior margin is straight, running approximately parallel with the posterior margin of the propterygium, while its thickened posterior margin is concave.

The metapterygium has a short, thick shaft proximally. It is curved so that both ends meet the mesopterygium, but the elements diverge centrally. The metapterygial apex is acute. There is a small posterodistally directed process at the broadest point of the cartilage, just over half-way from its proximal end (text-fig. 4A).

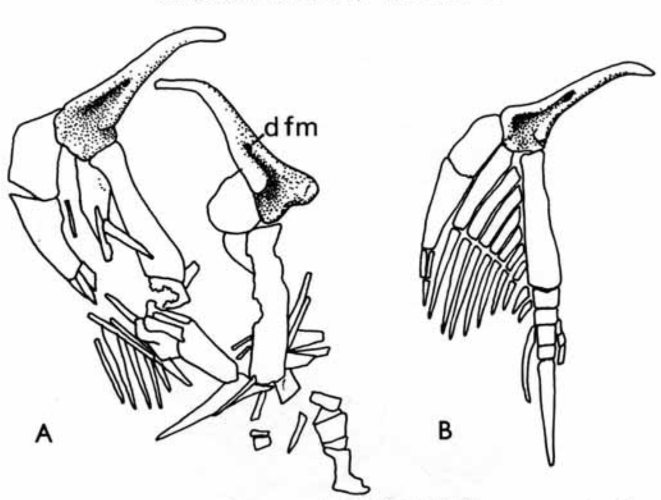
The radials of the pectoral fin probably extended to the fin margin, as at their tips there are many large denticles which probably lay along the fin's leading edge. The radials of both pectoral fins of the Wardie specimen are slightly displaced, but comparison permits an accurate reconstruction of the fins to be made.

The propterygium bears a single, short, unjointed radial, which can be seen lying displaced in the right pectoral fin. The mesopterygium bears ten radials along its lateral margin. The first eight are jointed once along their length. The proximal portions of the anteriormost two radials are fused (text-fig. 4A). While the lateral margins of the proximal parts of the next six are closely apposed, they do not appear to be fused. The final pair is jointed twice; again, their most proximal portions form a small, irregularly shaped cartilage which lies against the apical margins of both the meso- and metapterygial basals. This last pair of radials must have approached the distal apex of the fin at their tips.

The region of the metapterygial radials is extremely distorted in the Glencartholm specimen, and even in the Wardie specimen their arrangement is uncertain, although there is clearly a series of small cartilages forming a short 'axis'. Two 'axial' elements articulate with the posterodistal margin of the metapterygium; these both lie between the notch made by the posterodistal process of the metapterygium and its apex (text-fig. 4C). The second of these cartilages bore at least one, and probably two, radials along its 'pre-axial' margin near its apex. The first radial was jointed twice, the second probably only once. Both these first two 'axial' cartilages also appear to have borne a single short radial along their posterior margins. Distally, the second 'axial' cartilage articulated with a third 'axial' element, which probably bore about three radials near its apex.



TEXT-FIG. 4. Pectoral fins of RSM 1974.23.14 (counterpart). A, right fin; B, left fin; C, reconstruction of left fin. Scale bar = 10 mm. Pectoral scales omitted.



TEXT-FIG. 5. A, pelvic skeleton of RSM 1885.54.1; B, reconstruction interpreting the 'axial' cartilage as an intromittent 'clasper'.

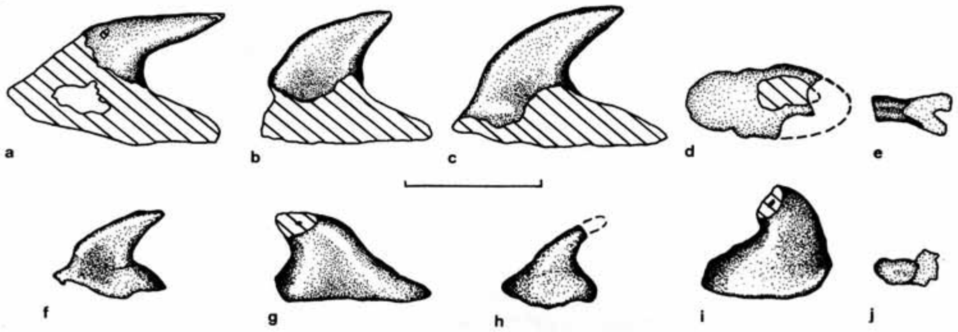
Pelvic girdle. The pelvic girdle and fins of the Glencartholm specimen lie disarticulated beneath the second dorsal fin, while those of the Wardie specimen are missing. The two halves of the pelvic girdle are unfused and much smaller than the scapulocoracoids. Each of the two cartilages has a long, curved process arising from the expanded articular region. The process probably lay horizontally within the body, projecting forwards and inwards towards the midline of the body. Its base has an elongate fossa, penetrated at one end by a foramen (text-fig. 5A), which probably allowed the diazonal nerves to reach the ventral surface of the fin.

The articular region has a pair of expanded articular facets at its antero- and posterolateral corners for the enlarged first pelvic radial and the basipterygium respectively. Between the facets, the lateral margin of each pelvic girdle cartilage is slightly concave for the articulation of the second pelvic radial cartilage.

Pelvic fin. The disarticulated cartilages of the pelvic fin are quite accurately figured by Moy-Thomas (1936, fig. 14), but a number of additional elements can be identified (text-fig. 5A). Although the condition of the pelvic fins of the Glencartholm specimen provide little objective evidence for any particular restoration of the fin, we have used the analogy of the pelvic fin of *Tristychius arcuatus* (Dick 1978, fig. 22) to propose a slightly different interpretation (text-fig. 5B) from that of Moy-Thomas (1936, fig. 15). We suggest that the specimen may be interpreted as a male with a long metapterygial axis and a long clasper cartilage.

Scales. The bodies of both specimens are generally devoid of scales. Each has a series of large, hooklike denticles (text-fig. 6) along the anterior margin of its pectoral fins. First described by Woodward (1924, p. 340), they extend from the apex of the propterygium to the distal tip of the pectoral fin. Their smooth, enamelled cusps curve mesially towards the fin insertion. The denticles have a round basal plate composed of osteodentine. The Wardie specimen also has one or two small rounded denticles along the posterior margin of the pectoral fin like those described by Woodward (1924) in the Glencartholm specimen.

In addition, there are a number of large, hooklike denticles on the heads of both specimens. These are similar in structure to those on the anterior margin of the pectoral fin, but many of their basal plates are fused together to produce multicuspid dermal rods. These are more completely exposed in

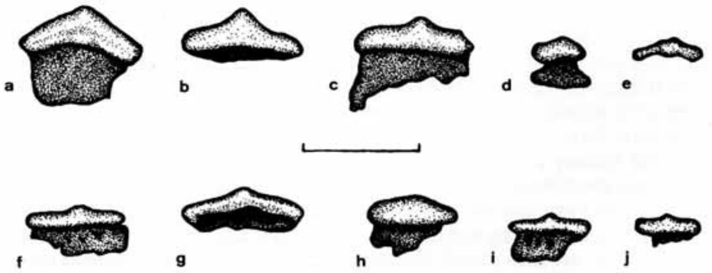


TEXT-FIG. 6. Denticles from the pectoral fins of RSM 1974.23.14 (*a–e*) and RSM 1885.54.1 (*f–j*). All are from the anterior margins of the fin, except *e* and *j*, which come from near the posterior margins. Diagonal hatching indicates broken surfaces. Scale bar = 1 mm.

the Wardie specimen, where they lie along the lateral surface of the jaws and possibly also above the gill arches (text-fig. 2); these are considered too large to be pharyngeal denticles. In the Glencartholm specimen there are single, large hook-denticles at the articulation of the jaws and above the posterior corner of the orbits.

Teeth. Teeth are preserved in both specimens and have been described in the Glencartholm specimen (Woodward 1924; Moy-Thomas 1936). There were at least fifteen tooth families in each jaw ramus, each containing four or more teeth. In the Wardie specimen the teeth lie loose near the front of the jaws. They are slightly larger than those of the Glencartholm specimen, but they have the same basic structure (text-fig. 7). In general, tooth crowns of the Wardie specimen are slightly less worn, possibly because they were positioned lingually in the replacement file and were therefore not functional.

To Woodward's (1924) description of the teeth the following may be added. All the teeth are extremely small (slightly less than 1 mm in length) and would probably be missed if they were lying isolated in matrix. Tooth roots clearly had neither a lingual nor a labial torus, but the crowns bear a small bulge on what is probably their lingual surface. This lingual button probably acted as a spacer, as in certain *Hybodus* and *Acrodus* spp. (Reif 1976).



TEXT-FIG. 7. Teeth from RSM 1974.23.14 (*a–e*) and RSM 1885.54.1 (*f–j*). Teeth (*a–d*) in lateral view, but it is uncertain whether lingual or labial surfaces are shown. Tooth (*e*) shows the occlusal surface. Approximate positions of others are as follows: (*f*) upper jaw, file 2 or 3; (*g*) lower file 5; (*h*) upper file 2 or 3; (*i, j*) upper file 8 or 9. Scale bar = 1 mm.

Dorsal finspines. Both finspines of the Glencartholm specimen are apparently in poorer condition than when they were first described. Those of the Wardie specimen are poorly exposed. Although detailed comparison with the type specimen of *T. arcuatus* is difficult, it differs from *Onychoselache* finspines in at least four respects.

(i) Size: *Onychoselache* finspines are under 40 mm long, whereas those of *Tristychius* range up to 150 mm, the majority being 70–80 mm long.

(ii) Outline in lateral view: *Tristychius* finspines are very long and slender, with gentle posterior recurvature. *Onychoselache* finspines are rather deeper anteroposteriorly, resulting in a stubby appearance. The posterior spine is fatter and more recurved than the anterior, and looks quite different from the holotype of *T. arcuatus*.

(iii) Posterior hook-denticles: a double row is present in both genera, but they are feeble in *Onychoselache* and nothing like as well developed as in *Tristychius*.

(iv) Costae: *T. arcuatus* typically has five costae per side apically, with a single costa anteriorly. *Onychoselache* has only four per side. Costal number is a variable feature in many fossil finspines, e.g. *Hybodus*, *Acrodus*, whereas in many modern examples it is constant, e.g. *Deania*, *Etmopterus*, and *Centrophorus*. Its significance is therefore uncertain in *Onychoselache*. The extent of lateral costae may be more important. In *T. arcuatus* only the anteriormost ribs reach the level of insertion; the lateral ribs terminate well above this level. In *Onychoselache* they terminate together at the level of insertion. In both forms, however, there are traces of a dermal vascular network similar to that found in Mesozoic hybodontid finspines (Maisey 1978).

Discussion. Onychoselache shares the following, apparently derived, features with Mesozoic hybodontids (*Hybodus*, *Acrodus*, *Asteracanthus*, etc.):

(i) finspines having posterior retrorse hooklike denticles and widely spaced lateral costae with intercostal vascular impressions;

(ii) tooth histology (Moy-Thomas 1936);

(iii) presence of enlarged head scales (although morphologically simpler in *Onychoselache* than typical hybodontid cephalic spines);

(iv) certain features of dorsal and pelvic fins;

(v) calcified ribs (Maisey 1975).

T. arcuatus is similar in features (i), (ii), (iv), and (v), but apparently lacks enlarged head spines (Dick 1978). Both fishes are here regarded as early hybodontiforms, but the following autapomorphies of *Onychoselache*, together with the differences in their finspines, seem to justify their generic separation:

(vi) dentition—low, tumid crowns and deep roots;

(vii) retrorse pectoral denticle series.

Onychoselache may be primitive in retaining plesodic pectoral fins; *Tristychius* and Mesozoic hybodontids were aplesodic.

The following features are shared by *Onychoselache*, *Tristychius*, Mesozoic hybodontids and neoselachians (including the earliest well-known form, *Palaeospinax*):

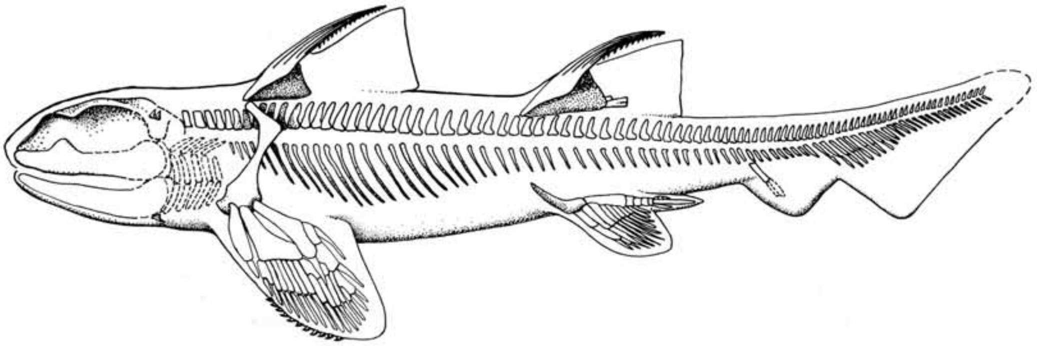
(viii) a concentrated scapulocoracoid articulation;

(ix) tribasal pectoral fins;

(x) palatoquadrate lacking a 'cleaver-shaped' quadrate region.

The retrorse pectoral denticles of *Onychoselache* are morphologically similar to posterior denticles of hybodontiform dorsal finspines, for which there is evidence of secondary fusion to the finspine trunk (Maisey 1978). It is interesting to note that the pectoral fins of a second early chondrichthyan group, the iniopterygians, are also armed (perhaps convergently) with numerous retrorse denticles anteriorly (Zangerl and Case 1973). In both *Onychoselache* and iniopterygians, pectoral scales extend down over the radials but not over the basal elements.

We concur with Woodward (1924) that the fish now known as *Onychoselache* is allied to Mesozoic hybodontids. So far we have been unable to demonstrate any derived features shared only by *Tristychius* and *Onychoselache*, and consequently refrain from placing *Onychoselache* in any family at



TEXT-FIG. 8. Restoration of *Onychoselache* skeleton.

present. Text-fig. 8 shows an outline restoration of *Onychoselache*. Reinterpretation of the pectoral fin from new material suggests that subordinal separation, as proposed by Moy-Thomas (1936, 1939), is unnecessary.

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