

Systematics and description of the lungfish genus *Sagenodus* from the Carboniferous of the UK

Esther L. BEEBY^{1,2} (née SHARP), Timothy R. SMITHSON¹ and Jennifer A. CLACK^{1*}

¹ University Museum of Zoology, Cambridge, Downing Street, Cambridge, CB2 3EJ, UK.

Email: jac18@cam.ac.uk

² 25 Jays Mead, Wotton-under-Edge, Gloucestershire, GL12 7JF, UK.

*Corresponding author

ABSTRACT: The Carboniferous lungfish genus *Sagenodus* is reviewed from all available British specimens and described in detail for the first time. We identify two species exclusive to the UK: *Sagenodus inaequalis*, the type species, deriving from the late Carboniferous (=Pennsylvanian); and *Sagenodus quinquecostatus* derived from the early Carboniferous (=Mississippian). The genus is probably the most widespread of the known Carboniferous lungfish genera, but the British species have not been formally described since their discovery in the mid–late 19th Century. This work will provide data to help resolve existing questions about the position of *Sagenodus* in the phylogeny of Palaeozoic lungfishes, and provide a template for the recognition of isolated elements in museum collections and the finds from recent and future field work. The early Carboniferous species, *S. quinquecostatus*, shows a so far unique functional mechanism in which the lower tooth plates appear to rotate relative to the upper plates during jaw closure, implying a kinetic function at the symphysis or jaw joint.

KEY WORDS: *inaequalis*, jaw kinesis, Mississippian, Pennsylvanian, *quinquecostatus*, skull morphology, tooth plate morphology.

This study reviews and reassesses the two lungfish *Sagenodus* species from the UK: the type species of the genus, *Sagenodus inaequalis*, from the late Carboniferous (=Pennsylvanian); and a second species, *Sagenodus quinquecostatus*, from the early Carboniferous (=Mississippian) of the UK. *Sagenodus* was probably the most widespread of the Carboniferous lungfish genera and, consequently, is also one of the best known. It has a large distribution, with material known from Britain, Europe (the Czech Republic, France, and Germany), Russia, and the US. Its ecological diversity was relatively high, being found in freshwater to shallow marine deposits. It has a stratigraphic distribution from the Viséan (early Carboniferous) of the UK to the uppermost lower Permian (=Cisuralian) of the US and Germany (Schultze & Chorn 1997). Watson & Gill (1923) described *Sagenodus* as being the ‘most completely known lungfish’, and Schultze & Chorn (1997) referred to it as representing ‘the beginning of modern lungfish’, considering it structurally intermediate between Devonian and post-Palaeozoic lungfishes. *Sagenodus inaequalis*, as the type species, requires an updated account based on additional material. *Sagenodus quinquecostatus* was originally named in 1883 by Traquair, but was never fully described or diagnosed. We recognise it here as a separate species from *S. inaequalis*.

For much of the 19th Century little interest was shown in the structure of the skull roof of lungfishes, the majority of studies being confined to scales and tooth plates. For some time the only well-known skull roof material of any Carboniferous lungfish was that of *Sagenodus*. Where cranial material was included in descriptions it was largely dismissed as composed of numerous small bones of indeterminate arrangement and doubtful homology, but bearing a considerable resemblance to the skull roof of *Dipterus* (Watson & Gill 1923).

The genus *Sagenodus*, not originally clearly distinguished from the genus *Ctenodus*, was first characterised by Owen (1867) with the type species *S. inaequalis*. Owen’s description,



figures, and diagnosis were later claimed by Hancock & Atthey (1868) to be incorrect. Hancock & Atthey (1872) described, but did not figure, the skull roofs of *Ctenodus* and *Sagenodus* both as the genus *Ctenodus* (although they did distinguish differences between them), and both Barkas (1873a, b) and Miall (1880) figured, but did not describe, the skull roof of *Sagenodus*. *Sagenodus* was also described in some detail by Fritsch (1885–1889).

During the 1880s, Traquair (1881, 1883, 1890) briefly described the remains of a number of different lungfishes from the Blackband Ironstone of Burghlee (formerly Borough Lee), near Edinburgh, Scotland. Among them were tooth plates similar to those described by Hancock & Atthey (1868) as *Ctenodus obliquus* but sufficiently different for Traquair to propose the variety *quinquecostatus*. He subsequently elevated this to a new species (Traquair 1890), and although it was never formally diagnosed or figured, when the taxonomy of Carboniferous lungfish was more settled, Traquair (1903) named the Burghlee material *S. quinquecostatus*.

Owen’s designation of the genus was based upon a cross section of a juvenile palatal tooth plate, 6 mm in length and with six distinct ridges. Owen (1867) believed the specimen to represent teeth and a small portion of jaw, and likened his specimen with the extinct *Dictyodus* (now considered a synonym of *Sphyraneodus*, a relative of the scombroids; M. Friedman, pers. comm. 2004). He did not associate this specimen with any dipnoan groups, something with which Hancock & Atthey (1868) took particular issue, attributing the specimen to *C. obliquus*, or ‘perhaps, *C. elegans*’. While they were correct in asserting that the specimen belonged to a dipnoan, *C. obliquus* and *Ctenodus elegans* were eventually realised to be distinct from *Ctenodus* (Woodward 1891), and the name *Sagenodus* took precedence. Owen’s histological drawings show the distinctive petrodentine now known to be unique to lungfishes, so that, while the specimen cannot be assigned to any particular

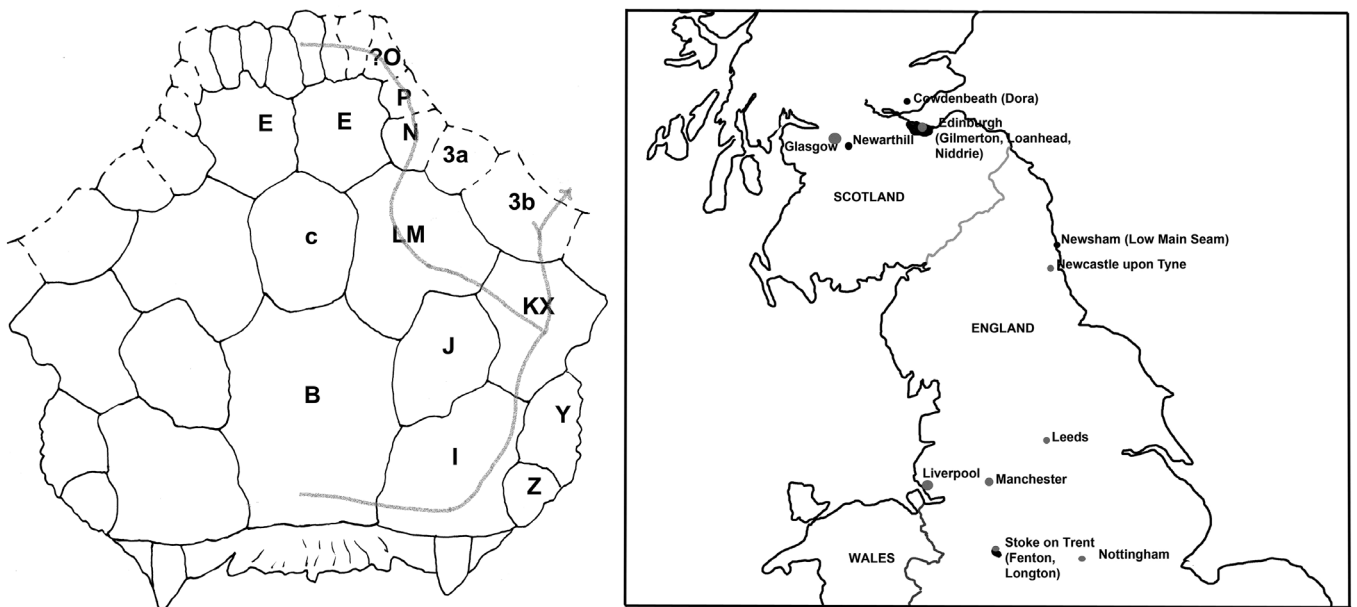


Figure 1 Left: *Sagenodus* skull roof reconstruction from Watson & Gill (1923) with addition of letter and numbering scheme from Forster-Cooper (1937). Right: Map of localities yielding *Sagenodus* specimen of the UK. Black areas indicate coal fields, black spots indicate localities, grey spots indicate major cities.

genus, at least its attribution to a major clade can be confirmed. Owen's type specimen comes from the Low Main Seam at West Cramlington, but both *Sagenodus* and *Ctenodus* occur in that seam at Newsham, Northumberland (Sharp & Clack 2013).

Although Owen did not state on which specimen his description was based, he later presented the specimen (NHMUK (BMNH) P 6246) to the British Museum, as listed by Woodward (1891, p. 259). Woodward defined the tooth plates of the genus as follows: 'Dental plates, above and below, triangular, irregularly ovate or elliptical in form, with few strong, outwardly directed ridges, more or less tuberculated or crenelated; vomerine teeth resembling a single ridge of a dental plate' (Woodward 1891, p. 256).

The description of *Sagenodus*, regarded by previous authors as probably representing several species, was finally addressed by Watson & Gill (1923). They gave the first accurate reconstruction of the skull roofs of both *Sagenodus* and *Ctenodus*, alongside those of *Uronemus* and *Dipterus*. Their reconstruction was a composite based upon a number of specimens and also incomplete in lacking the circumorbital bones. It was, however, based primarily upon a single specimen, NMS G 1878.45.7, a specimen further considered below. Although there are some inaccuracies in Watson & Gill's (1923) reconstruction, for the most part it is sound. They also illustrated individual bones of the skull, lower jaw, and pectoral girdle. They did not, however, give a detailed description of the assembled bones of the skull roof, stating instead that 'the figure renders unnecessary a detailed description of the form of the bones' (Watson & Gill 1923, p. 116). They also used a nomenclature that tried to homologue the bones with those of other sarcopterygians. Theirs remains the most recent description of the morphology of the three then known British Carboniferous genera that includes *Sagenodus*. We reproduce this reconstruction with Forster-Cooper's (1937) system of letters, numbers, and lateral line courses added (Fig. 1a).

More recently, Schultze & Chorn (1997) published a detailed description of the American species of *Sagenodus* based on acid-prepared, although disarticulated, material. They were the first to utilise the large numbers of available specimens to perform statistical analysis on the morphological variation found between the tooth plates of different species.

Our study has examined all the significant specimens of *Sagenodus* from the UK to provide an up-to-date account of the valid species. We conclude that two valid species can be diagnosed: *S. inaequalis* from the upper Carboniferous and *S. quinquecostatus* from the lower Carboniferous.

Institutional abbreviations. GNMHM (NEWHM) G = (Geology) Great Northern Museum; Hancock Museum, UK; KUVF = Kansas University Vertebrate Paleontology, USA; MM = Manchester Museum, UK; NMS G = (Geology) National Museums Scotland, UK; NHMUK (BMNH) P = (Pisces) Natural History Museum, London, UK; UMZC GN = (Gnathostome) or F (Fish), University Museum of Zoology, Cambridge, UK; NUFV = Nunavut University Fossil Vertebrates (currently housed at the University of Chicago, USA); BGS GSM = (Geological Sciences Museum) British Geological Survey, Keyworth, UK.

1. Material and methods

Many of the specimens had been partially prepared in the past, probably with a chisel and often to a very poor standard. This was often worst in type or figured specimens. A number of the specimens were subject to pyrite decay and were, therefore, stored in dry, low-humidity conditions. All preparation took place in the University Museum of Zoology, Cambridge, by ELS (now ELB), or by Sarah M. Wallace-Johnson (formerly Finney) at the University of Cambridge, Department of Earth Sciences, Brighton Building. Preparation included removing excess matrix, making sutures easier to interpret. In some specimens white paint was removed from sutures in order to ease interpretation. Some specimens from the National Museums Scotland had been coated in lacquer, supposedly to protect from pyrite decay. Where the specimens were not subject to decay, with the permission of National Museums Scotland, the lacquer was removed from the specimens using acetone and water.

In some cases, excess matrix was removed using either a pneumatic pen or modified dental mallet, and fine preparation was carried out using the dental mallet or a mounted 1 mm tungsten carbide needle. Prepared bone was consolidated using a solution of Paraloid B72 in acetone. For some specimens a

Texas Airsonic Inc. Jetsonic BW7 abrasive unit, using sodium bicarbonate, was used to remove a thin layer of sediment to allow surface detail to be prepared.

Drawings of specimens were made either from tracings of photographs or using a Wild stereomicroscope with a camera lucida. All the specimens to be prepared were first photographed in their original state with a Nikon D1 or Canon Powershot A80 digital camera. Photographs were processed and assembled using Adobe Creative Suites Photoshop, version 2017.1.1 or 2019.0.1.

Micro-computed tomography (CT) scanning was carried out on a Nikon Metrology XT H 225 ST High Resolution CT Scanner at the University of Cambridge Biotomography Center. The scan data were as follows: x-axis 606 pixels (slices); y-axis 1558 pixels; z-axis 1998 pixels; resolution 66.1041 µm; filter 1.5 mm copper; X-ray kV 180; X-ray uA 175; projections 1080; exposure 1415. Three-dimensional (3D) segmentation was carried out in Mimics Innovation Suite (biomedical.materialise.com/mimics; Materialise, Leuven, Belgium), and virtual sections of *S. quinquecostatus* NMS G 1886 82.11 taken from an ImageJ stack.

1.1. Specimens examined

Sagenodus inaequalis

NMS G 1878.45.7. Low Main Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Almost complete skull roof in dorsal view, missing circumorbital bones. Described and figured by Watson & Gill (1923), cited by Schultze & Chorn (1997).

NMS G 1878.45.13. Low Main Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Isolated parasphenoid.

NMS G 1878.45.21. Low Main Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Composite specimen with pectoral girdle elements. plates.

NMS G 1888.33.4. Low Main Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Right ceratohyal.

NMS G 1888.33.19. Low Main Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Isolated angular.

NMS G 1897.110.30. Virtuewell Coal Shale, Newarthill, Lanarkshire, upper Carboniferous, Langsettian (Westphalian A). Skull roof in dorsal view with tooth plates.

NMS G 1897.112.5. Virtuewell Coal Shale, Newarthill, Lanarkshire, upper Carboniferous, Langsettian (Westphalian A). Posterior part of skull roof in dorsal view, missing E-bones and rostral regions. Posterior circumorbital bones preserved. Described and figured by Watson & Gill (1923).

NMS G 1898.17.36. Virtuewell Coal Shale, Newarthill, Lanarkshire, upper Carboniferous, Langsettian (Westphalian A). Skull roof in visceral view and counterpart impression.

NMS G 1898.174.16. Virtuewell Coal Shale, Newarthill, Lanarkshire, upper Carboniferous, Langsettian (Westphalian A). Isolated left cleithrum.

NMS G 1898.154.23 and 24. Virtuewell Coal Shale, Newarthill, Lanarkshire, upper Carboniferous, Langsettian (Westphalian A). Skull roof and parasphenoid stalk, part and counterpart.

NMS G 1898.162.2.1. Virtuewell Coal Shale, Newarthill, Lanarkshire, Upper Carboniferous, Langsettian (Westphalian A). Skull roof and parasphenoid stalk, part and counterpart.

MM L10453. Low Main Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Isolated operculum.

NHMUK (BMNH) P 6246. Holotype. Low Main Coal Seam, West Cramlington, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Section of a prearticular tooth plate. Described and figured by Owen (1867).

GNMHH (NEWHM) G60.91. Low Main Coal Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Skull roof in dorsal view, posterior portion.

GNMHH (NEWHM) G60.99. Low Main Coal Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Isolated B-bone.

GNMHH (NEWHM) G61.24. Low Main Coal Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Scattered elements including tooth plates, skull roof bones, and opercula.

GNMHH (NEWHM) G61.34. Low Main Coal Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Composite specimen with anocleithrum, operculum, skull bones, and pterygoid with attached tooth plate.

GNMHH (NEWHM) G61.35. Low Main Coal Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Right lower jaw with prearticular tooth plate.

GNMHH (NEWHM) G61.36. Low Main Coal Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Isolated angular and splenial.

GNMHH (NEWHM) G61.44. Low Main Coal Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Isolated parasphenoid.

GNMHH (NEWHM) G61.46. Low Main Coal Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Left ceratohyal.

GNMHH (NEWHM) G172.32. Low Main Coal Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Left pterygoid and attached tooth plate.

GNMHH (NEWHM) G174.78. Low Main Coal Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Articulated posterior portion of skull roof in dorsal view and pectoral girdle elements in internal view.

UMZC GN 168. Low Main Coal Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Left prearticular tooth plate.

UMZC GN 159. Low Main Coal Seam, Newsham, Northumberland, upper Carboniferous, Duckmantian (Westphalian B). Right clavicle.

Sagenodus copeanus

KUVP 103259. *Sagenodus copeanus*. Hamilton Quarry, Kansas. Virgilian (Gzhelian) Upper Pennsylvanian. Skull roof in dorsal view.

KUVP 84201. *Sagenodus copeanus*. Hamilton Quarry, Kansas. Virgilian (Gzhelian) Upper Pennsylvanian. Complete specimen in dorsal and lateral view.

Sagenodus quinquecostatus

NMS G 1886 82.11. Burghlee Ironstone, Loanhead district, Scotland, lower Carboniferous, Serpukhovian (Pendleian). Skull roof and partial mandible, including vomerine and other tooth plates.

NMS G 1993.56.118. Dora Bone Bed, Cowdenbeath, Fife, Scotland, lower Carboniferous, Serpukhovian (Pendleian). Right pterygoid tooth plate. Figured by Smithson *et al.* (2019).

NMS G 1993.56.115. Dora Bone Bed, Cowdenbeath, Fife, Scotland, lower Carboniferous, Serpukhovian (Pendleian). Right prearticular tooth plate.

NMS G 1993.56.117. Dora Bone Bed, Cowdenbeath, Fife, Scotland, lower Carboniferous, Serpukhovian (Pendleian). Left pterygoid tooth plate.

NHMUK (BMNH) P 11506. Burghlee Ironstone, Loanhead district, Scotland, lower Carboniferous, Serpukhovian (Pendleian). Left pterygoid with tooth plate.

2. Systematic palaeontology

Osteichthyes Huxley, 1880

Sarcopterygii Romer, 1955

Dipnoi Müller, 1845

Sagenodontidae Jaekel, 1911

Genus *Sagenodus* Owen, 1867

Type species *Sagenodus inaequalis* Owen, 1867

Synonyms. *Ctenodus applantus* (*partim*) Romer, 1945; *Ceratodus barrandei* Frič, 1874; *Ctenodus caudatus* Barkas, 1877; *Ctenodus complantus* Fritsch, 1888; *Ctenodus elegans* Atthey, 1868; *Ctenodus ellipticus* Atthey, 1868; *Ctenodus imbricatus* Atthey, 1868; *Ctenodus monoceras* Barkas, 1873a; *Ctenodus obliquus* Atthey, 1868; *Ctenodus obtusus* Barkas, 1870; *Ctenodus quadratus* (*partim*) Barkas, 1873b; *Petalodopsis miribalis* Barkas, 1874; *Hemictenodus obliquus* Jaekel, 1890; *Sagenodus barrandei* Romer, 1945.

Other species (after Schultze 1992). *Sagenodus applantus* Fritsch, 1879*; *Sagenodus carbonarius* Romanowsky, 1864*; *Sagenodus copeanus* Williston, 1889*; *Sagenodus corrugatus* Atthey, 1868; *Sagenodus gaudryi* Author unknown*; *Sagenodus octodorsalis* Barkas, 1869; *Sagenodus ohioensis* Cope, 1874*; *Sagenodus periprion* Cope, 1878*; *Sagenodus serratus* Newberry, 1875.

Sagenodus carbonarius and *S. gaudryi* are considered here to be *nomina dubia* due to poor initial descriptions and lack of type material. The asterisks show those species that are not present in the UK, and which will not be considered further.

Diagnosis. Emended diagnosis after Schultze & Chorn (1997). Tooth-plated lungfish attaining a length of approximately 1 m. Apomorphic characters: massive B-bone pentagonal or septagonal, often with concave anterior margin, unpaired B-bone pentagonal with the following relations: bounded laterally by the paired I-, J-, and LM-bones, anteriorly by the C-bone. Pentagonal unpaired C-bone, bounded laterally by the LM-bones and anteriorly by the paired E-bones. Anterior to those, a single unpaired F-bone. J-bone does not contact C-bone. Tooth plates with a high length-to-width ratio relative to other genera, and between five and 13 ridges diverging lingually. Prearticular tooth plates narrower than pterygoid plates, with tooth ridge 1 angled dorsomedially, and widely separated from tooth ridge 2. Posteriorly placed ridge on cleithrum separating the branchial and postbranchial laminae.

Remarks. Schultze & Chorn (1997) gave a detailed diagnosis of *Sagenodus*, after Hussakof (1911). There seems to be little inter-specific variation in the structure of the skull roof, and any differences are very subtle. *Sagenodus* seems to have one of the most invariant skull roofs among Palaeozoic dipnoans. Specific differences are mainly to be found in their dentition. The lack of contact between the J- and C-bones is unusual among Palaeozoic lungfishes.

Type species. *Sagenodus inaequalis* Owen, 1867.

Holotype. NHMUK (BMNH) P 6246. Thin horizontal section of a mandibular tooth plate regarded here as non-diagnostic. Case 3800 was submitted on 30 April 2019 to the ICZN to change the holotype to NMS G 1878.45.7.

Proposed neotype. NMS G 1878.45.7. Articulated skull roof of *Sagenodus*.

Proposed neotype locality and horizon. Low Main Seam, Newsham, Northumberland, Duckmantian (Westphalian B), late Carboniferous.

Stratigraphic range of genus. Viséan to lower Permian.

Remarks. Tooth plates attributed to *Sagenodus* by Carpenter *et al.* (2014) from the Tournaisian of the Isle of Bute may not belong to this genus (Smithson *et al.* 2015). The tooth plate from the Tournaisian of Coldstream, Berwickshire, Scotland, thought by Smithson (pers. comm. in Schultze & Chorn 1997, p. 57) to be *Sagenodus*, has recently been named *Ballagadus caustrimi* (Smithson *et al.* 2015) and the two taxa are probably not closely related.

A number of specimens listed as '*Sagenodus*' were collected from Jarrow colliery in Ireland during the 19th Century, but they have never been examined or described. Specimens NHMUK PV OR41851 (a tooth plate) and NHMUK PV P41684 (B&C bones), and British Geological Survey GSL 1721 (rib and tooth plate) have been identified as *Sagenodus*, but their specific identity remains to be established.

Sagenodus inaequalis Owen, 1867

Differential diagnosis. Differs from *S. copeanus* in B-bone less posteriorly constricted and J-bones of a more angular and variable shape. Tooth plates never more than eight ridges. Teeth are fused into shearing ridges, with little evidence of individual teeth except in the most labial regions, where there are typically one or two unfused teeth. Pterygoid tooth plates broadly ovate in shape, with a length-to-width ratio of between 1:7 and 2:8, tooth ridge angle between 50° and 70°. Tooth ridges of equal lateral extent. Prearticular tooth plates elongate, with length-to-width ratio of between 2:9 and 3:8, tooth ridge angle c.90°. Ridge 1 is longer than the other ridges. Typically fewer tooth ridges than American species and length-to-width ratio of tooth plates is also less.

Stratigraphic range of species. 'Middle Coal Measures', upper Carboniferous, Langsettian–Bolsovian (Westphalian A–C) of England and Scotland.

UK localities. Low Main Seam, Newsham, Northumberland (type locality); Newarthill, Lanarkshire; Fenton and Longton, Staffordshire (Figure 1b; see also Panchen 1970 for a map of UK early Late Carboniferous localities).

Remarks. Schultze & Chorn (1997) described the American species of *Sagenodus* as having tooth plates with the following approximate proportions:

Sagenodus copeanus: upper tooth plates 8–12 ridges, length-to-width ratio 3:8; lower tooth plates 8–10 ridges, length-to-width ratio 4:6.

Sagenodus serratus: upper tooth plates 6–9 ridges, length-to-width ratio 2:6; lower tooth plates 6–9 ridges, length-to-width ratio 3:9.

Sagenodus periprion: upper tooth plates 10–12 ridges, length-to-width ratio 3:7; lower tooth plates 11–13 ridges, length-to-width ratio 4:1.

Sagenodus quinquecostatus Traquair, 1883

Synonyms. *Ctenodus obliquus* var. *quinquecostatus* Traquair, 1883; *Hemictenodus quinquecostatus* Traquair, 1890.

Differential diagnosis. Differs from *S. inaequalis* in smaller estimated body length up to 0.4 m. Pterygoid tooth plates fan-shaped, tooth ridge angle up to c.160°. Length-to-width ratio 3:3. Typically five tooth ridges present, separated by deep grooves; some specimens have an accessory sixth ridge immediately behind the fifth with no groove between. Unworn teeth are small, laterally compressed, and recurved. They are often fused and worn to narrow ridges on the lingual part of the tooth plate. Limited increase in tooth size along the tooth ridges. Prearticular tooth plates long and narrow, tooth ridge angle c.90°. Length-to-width ratio 3:8. Typically four tooth ridges. Tooth ridge 1 long, remaining tooth ridges short,

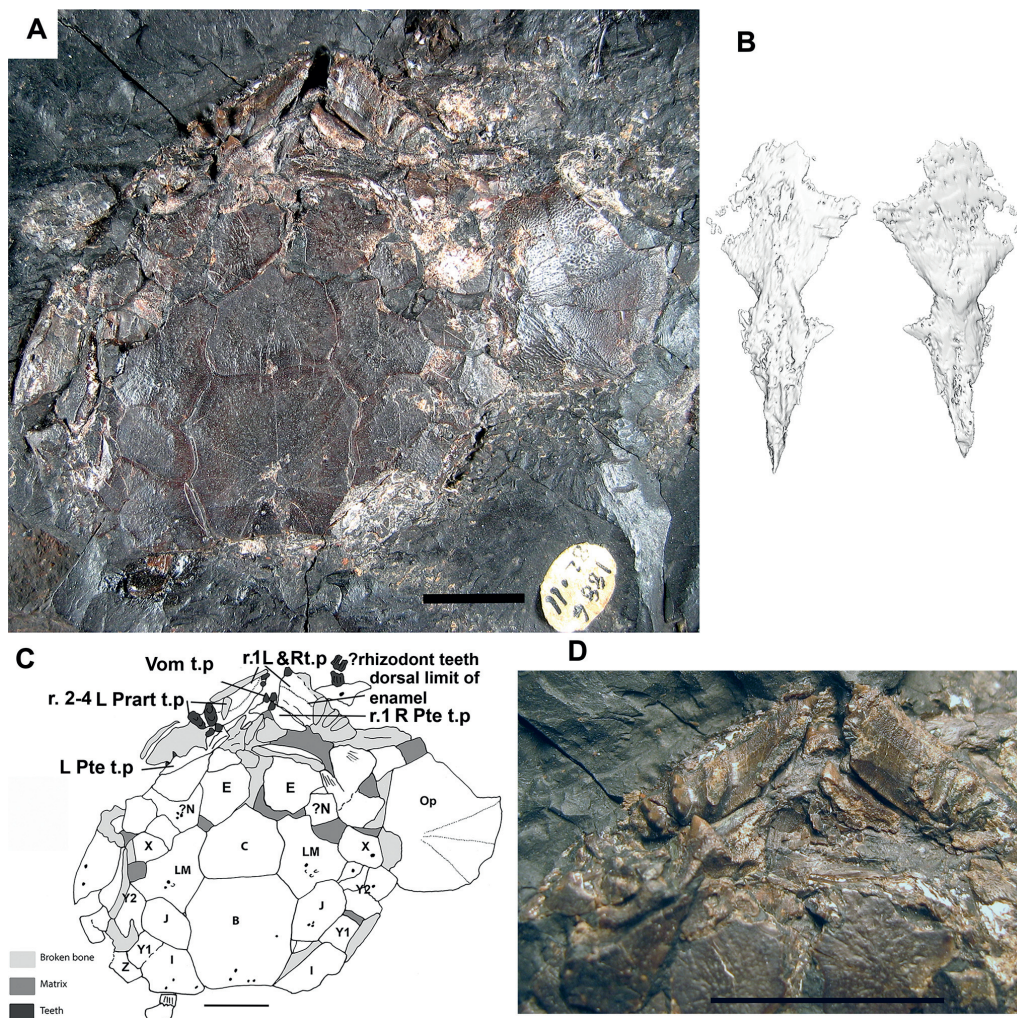


Figure 2 *Sagenodus quinquecostatus*. Skull of lectotype NMS G 1886 82.11: (A) photograph of dorsal surface showing skull roof and tooth plates; (B) image from micro-CT scan showing parasphenoid, left, internal (visceral) view, right, external (buccal) view; (C) drawing of holotype skull; (D) close-up of holotype skull showing tooth plates. Abbreviations: L = left; Prart t.p = prearticular tooth plate; Pte t.p = pterygoid tooth plate; R = right; t.p = tooth plate; Vom = vomer. Scale bars = 10 mm.

separated by shallow grooves, with little divergence between them and set almost at right angles to tooth ridge 1. Teeth on tooth ridge 1 fused to a worn, sharp blade lacking enamel, bearing two or three teeth at the labial end. Remaining tooth ridges bear up to four small, laterally compressed, recurved teeth showing little wear.

Lectotype specimen. NMS G 1886.32.11 (Figs 2, 3). Skull preserved in dorsal view, showing full complement of skull roofing bones, right operculum, mandibles, and upper and lower tooth plates. Vomerine tooth plate present with three teeth, the central of which is larger.

Type locality and horizon. Burghlee Ironstone (also known as Blackband Ironstone of Borough Lee, Rumbles Ironstone, or Loanhead Ironstone Number 3 (see Smithson 1985; Andrews & Carroll 1991; Smithson *et al.* 2019)), Loanhead (Burghlee Colliery), Midlothian, Scotland. Pendleian, early Serpukhovian, early Carboniferous.

Stratigraphic range of species. Brigantian (Viséan) to Pendleian (Serpukhovian), early Carboniferous.

Other localities. Relatively common lungfish found at four localities in eastern Scottish Midland Valley–Gilmerton, Loanhead, Dora, and Niddrie (Figure 1b; see also Smithson *et al.* 2019 for a map of late Early Carboniferous localities).

Remarks. From the collections of specimens nominated by Traquair (1883, 1890) as *S. quinquecostatus*, we have chosen an almost complete skull with its four tooth plates as

a lectotype. The additional specimens become paratypes. We are satisfied that the material represents the genus *Sagenodus*, but the associated tooth plates differ sufficiently from those of *S. inaequalis* to be recognised as a separate species. We retain the name given to this species by Traquair (1883). *Sagenodus quinquecostatus* occurs in the early Carboniferous, whereas *S. inaequalis* occurs in the late Carboniferous.

Sagenodus quinquecostatus is the earliest known occurrence of the genus. It displays the diagnostic *Sagenodus* pattern of skull roofing bones, and is similar to *S. inaequalis* in parasphenoid shape, lower jaw morphology, and the narrow prearticular tooth plates with angled tooth ridge 1. Only on this ridge are the teeth fused into a sharp blade; the other ridges bear laterally compressed teeth showing little wear. The orientation of tooth ridge 1 suggests that during food processing each mandible could rotate either medially along its long axis (clockwise on the left, anticlockwise on the right), to bring the ridge 1 into occlusion with the ridges 1 and 2 on the pterygoid plate, or the reverse, to bring the more posterior ridges into occlusion with those on the pterygoid. This is a form of kinesis not previously described in lungfish, and is discussed in more detail below.

Sagenodus quinquecostatus is one of six lungfish taxa found in the Burghlee Ironstone (Smithson *et al.* 2019) and, judging by the number of specimens in the Natural History Museum, London, and National Museums Scotland, was probably the

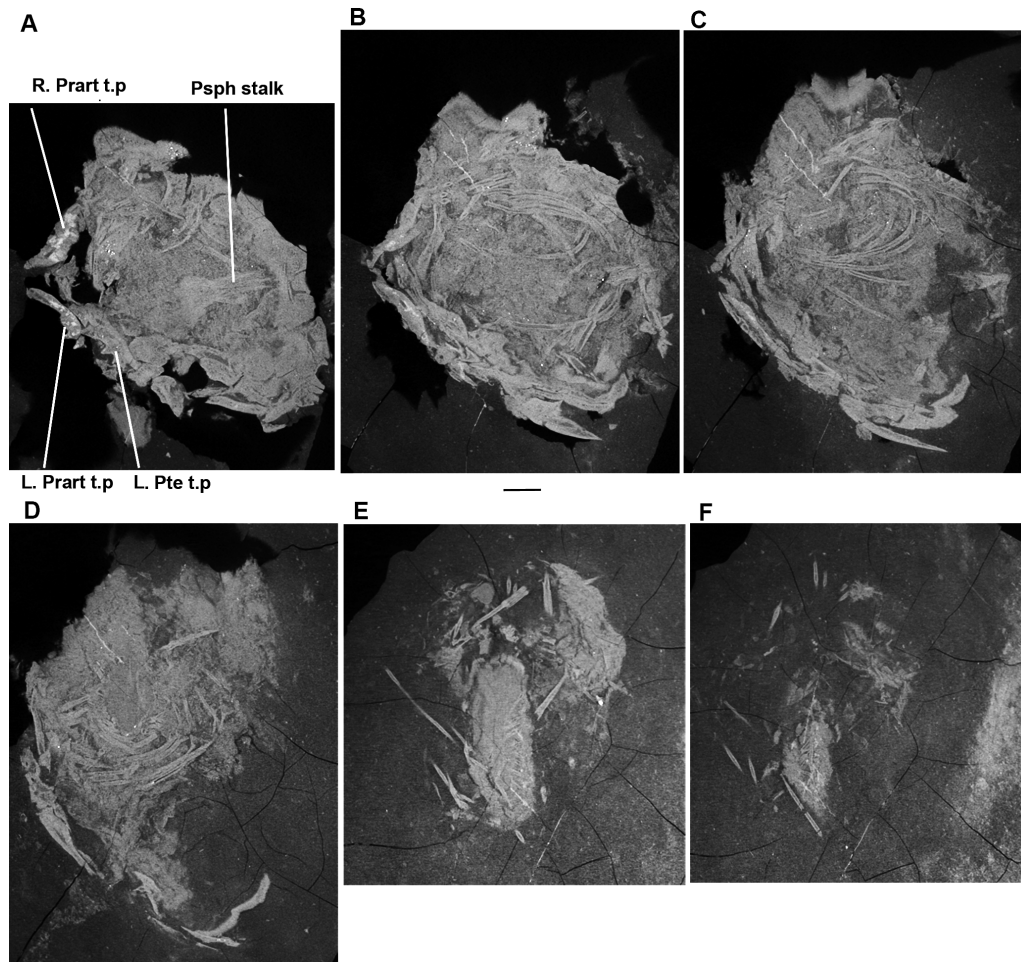


Figure 3 *Sagenodus quinquecostatus*. Slices from micro-CT scans from ImageJ of lectotype NMS G 1886 82.11: (A) slice 42 showing parasphenoid stalk, tooth plates, and unidentified bones; (B, C) slices 54 and 59 showing ribs and unidentified bones; (D) slice 89 showing ribs and fin rays; (E, F) slices 137 and 148 showing fin rays. Slices go from dorsal to ventral horizontally through the specimen. Abbreviations: Psph = parasphenoid; Prart t.p = prearticular tooth plate; Pte t.p = pterygoid tooth plate; R = right; L = left. Scale bars = 10 mm.

second most common after *Ctenodus interruptus*. At Dora it is found with *Uronemus splendens* (Smith *et al.* 1987) and at Gilmerton and Niddrie it is found with *C. interruptus* (Henrichsen 1972).

As well as an almost complete skull roof with four tooth plates, the specimen also preserves a parasphenoid, an operculum, and some postcranial material revealed by micro-CT scan (Figs 2, 3). The latter consists of a series of ribs at a mid-level in the specimen, and, more externally, an array of fin rays. We find it hard to envisage how this distribution could come about, unless the specimen represented a compacted skeleton that was perhaps enclosed in a burrow at the time of death. We discuss this further below.

3. Description

The skeletal elements described below pertain to both UK species of *Sagenodus* unless otherwise stated. The tooth plates are described separately, and differ between *S. inaequalis* and *S. quinquecostatus*.

3.1. Dermal skull roof

The skull roof of *Sagenodus* is somewhat square and the bones form a slightly convex surface. The bones of *Sagenodus* are much less ornamented than those of *Ctenodus* (Sharp & Clack 2013), and in most specimens the union between the cranial bones is less secure, although the posterior series are often found in articulation. In many articulated skulls, the ventral

lappets that underlie the dermal skull roof are rarely seen. As in many dipnoans, there is a degree of intraspecific variation in the configuration of the skull roof, although *Sagenodus* seems to be the most consistent.

The most prominent element of the skull roof is the B-bone, the midline element, which lies at the posterior margin of the skull roof and bears the occipital sensory canal. There is no A-bone. Anterior to the B-bone lies the single C-bone. This five-sided element is highly characteristic of the genus, as is the shape of the contact it makes with its surrounding bones. In *S. quinquecostatus*, the C-bone is relatively wider and the B-bone relatively shorter than in *S. inaequalis* (Fig. 2). In other respects, the bone relationships are similar as far as can be judged. In front of the C-bone are the paired E-bones, and anterior to this lies the single unpaired F-bone. Lateral to this midline series are the paired I-, J-, and LM-bones. These are similarly large elements and, together, these bones form the majority of the skull roof area. Lateral to the E-bones lie the small N- and P-bones, which carry the supraorbital canal forwards onto the rostral mosaic. Lateral to the I-bone lies the Z-, Y-, and KX-bones. These bones form the lateral margins of the posterior part of the skull roof. The KX-bone bears a prominent notch laterally, continuous with the margin of the Y-bone, where it bears the operculum. A similar feature is seen in *Limnichthys*, where it occurs on the separate X-bone (Challands *et al.* 2019). Anterior to the E-, N-, and P-bones is a series of small elongate bones, which do not conform to a conserved pattern. In those specimens that preserve them, they vary in shape, number, and arrangement; they are sometimes

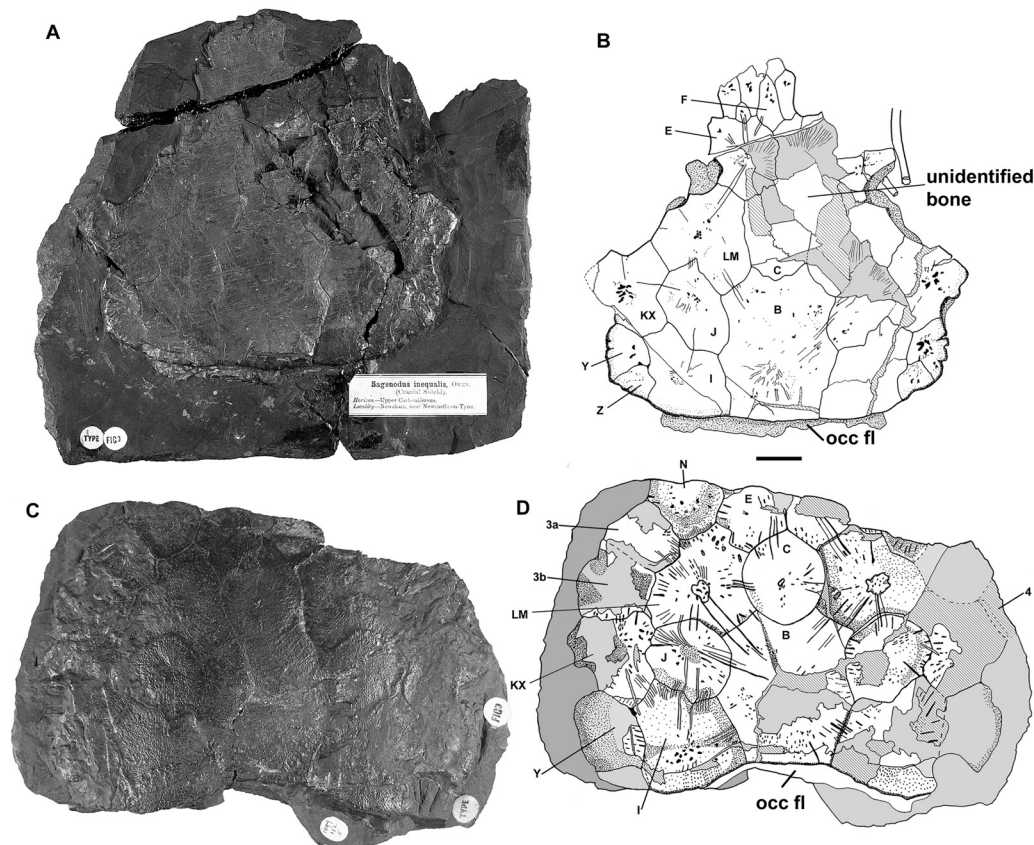


Figure 4 *Sagenodus inaequalis* skull specimens. (A, B) NMS G 1878.45.7 proposed neotype: (A) photograph of specimen in dorsal view; (B) interpretive drawing. (C, D) NMS G 1897.112.5: (C) photograph of specimen in dorsal view; (D) interpretive drawing. Scale bar = 10 mm.

found united together, independent of the named skull roof bones, and are, therefore, termed the 'prenasal bones' or rostral mosaic.

The circumorbital bones are poorly known from British deposits, although they have been described for the American species *S. copeanus*, and Schultze & Chorn (1997) claimed the genus had a smaller orbit than reconstructed by Watson & Gill (1923). The following description of the skull roof of *Sagenodus* is based on data mainly from NMS G 1878.45.7 (Fig. 4a, b) and a number of others such as NMS G 1897.112.5 (Fig. 4c, d). Because *Sagenodus* is based only upon the cross section of a tooth plate of uncertain generic identity, we have applied to the International Commission on Zoological Nomenclature to designate NMS G 1878.45.7 as the lectotype of the genus *Sagenodus*. This constitutes Case 3800 submitted to the Commission.

The B-bone is the largest bone of the skull roof and its relative dominance makes it a unique characteristic of this genus. It is roughly rectangular in shape and the bone is constricted in three places: at its posterior point, around its mid-length, and anteriorly. This posterior constriction is less prominent in specimens of *S. inaequalis* than in *S. copeanus*. The anterior margin of the B-bone tapers into two curved prongs, and the concave anterior margin so formed could be a derived feature in dipnoans relating to the acquisition of a single C-bone. This is more obvious in NMS G 1878.45.7 (Fig. 4a, b) than in some other specimens (e.g., GNMHM G 60.99, Fig. 5a–d). The contact between the B-bone and C-bone is one of the more variable features within *Sagenodus* (e.g., Fig. 5e, f). The relative extent of the anterior part of the B-bone compared with the total length of the bone is also variable.

The posterior margin of the B-bone is gently convex, curves ventrally, and, in some specimens, there is evidence of an occipital flange projecting posteriorly from its ventral margin,

although in NMS G 1878.45.7 (Fig. 4) it is somewhat damaged. The posterior region of the B-bone carries the occipital sensory line canal (occipital commissure of Schultze & Chorn 1997). This is typically seen opening as pores on the posterior third of the surface of the B-bone. This is illustrated in Figure 5e, f, although the B-bone is often broken along the path of this canal, which, in some cases, is clearly visible. Pores or pits are often found at the centres of radiation of many bones, and some are probably related to lateral lines passing beneath. Parallel and sub-parallel grooves and ridges radiate from this position to the J- and I-bones, indicating direction of growth. There is considerable variation in the extent to which the path of the lateral line canals can be traced. As in all Palaeozoic dipnoans (Miles 1977), the lateral line canals pass through the centre of ossification of the bone and then give rise to a network of tubules, which disseminate throughout the bone.

The B-bone is almost unique for bones of the skull roof in that it has been found isolated, allowing the visceral surface to be seen in relief. Figure 5a–d illustrates GNMHM G 60.99, which shows the visceral surface of the B-bone as significantly different in both shape and anterior extent to that seen from the dorsal surface of the bone. The anterior expansion of the visceral surface exceeds that of the dorsal surface and, laterally, the bone also occupies a slightly greater area. In addition, there are overlap areas at the antero- and postero-lateral corners of the bone where the lappets of the adjacent bones such as the I-bone and LM-bone overlap with the B-bone.

It is in the anterior portion of the bone that the discrepancy in extent between dorsal and ventral surfaces is most obvious. The anterior third of the ventral surface of the bone is highly ridged and grooved (NMS G 1898.17.36, Fig. 6a). In those specimens that show an impression of the ventral surface of the skull roof, the suture between the B- and C-bones is very

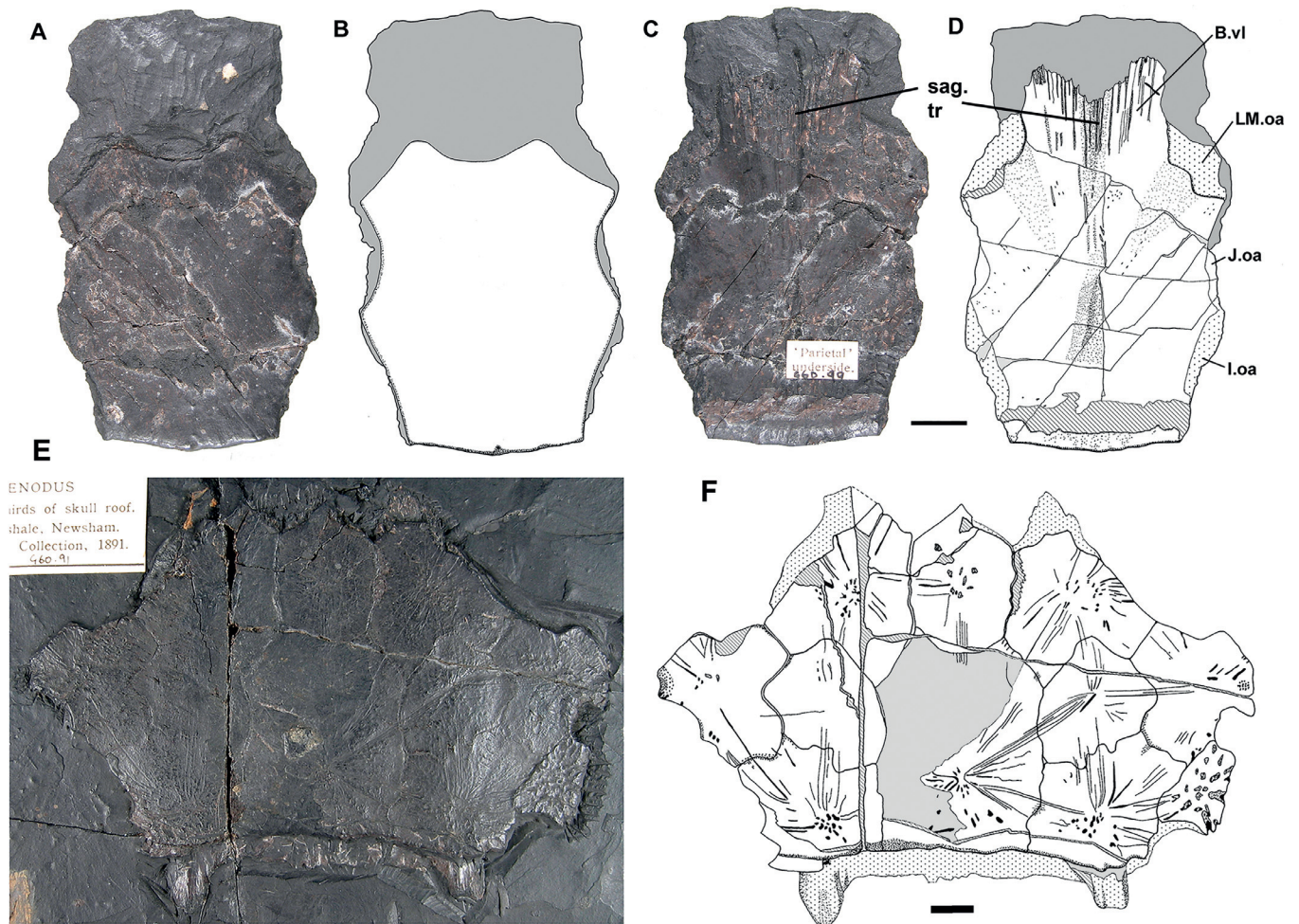


Figure 5 *Sagenodus inaequalis* skull specimens. (A–D) GNMHM 60.99 B-bone: (A) dorsal view; (B) interpretive drawing; (C) ventral view; (D) interpretive drawing. (E, F) GNMHM 60.91 skull roof: (E) dorsal view; (F) interpretive drawing. Abbreviations: B.v.l = ventral lappet of B-bone; I.oa = I-bone overlap; J.oa = J-bone overlap; LM.oa = LM bone overlap. Scale bars = 10 mm.

difficult to see clearly (Fig. 6b, c) because the degree of interdigitation is so tight.

Schultze & Chorn (1997) noted a trough in the mid-sagittal plane of the ventral surface of the B-bone of *S. copeanus*, which was bordered, to a greater or lesser extent, by two radiating ridges. This depression is also found in specimens of *S. inaequalis* and, as reported for the North American genus, its bounding ridges are of variable prominence and extent. GNMHM G 60.99 (Fig. 5a–d) has a subtle trough but no evidence of parasagittal ridges, whereas the impression of the skull roof seen in NMS G 1897.110.34 (not figured, ELS, pers. obs. 2006) suggests that the trough was more pronounced. Only in NMS G 1898.162.2.1 (Fig. 6b, c) are the sagittal ridges well developed. It seems likely that these troughs and ridges in life would have contacted the median cristae, by which the braincase would have been suspended from the ventral surface of the skull roof. This cannot be confirmed as the form of the braincase in most post-Devonian dipnoans is not known.

Anterior to the B-bone is the single median C-bone. In contrast with *Ctenodus*, this bone is unpaired in *Sagenodus*, a derived feature within the lungfishes. It is slightly larger than half the size of the B-bone and, where the E-bones are preserved, the C-bone is slightly longer. While the junction between the posterior and lateral margins is fairly smooth, that between the anterior and lateral margins is at a distinct angle. The lateral margins taper slightly posteriorly, meaning that the bone is broader anteriorly. Again, the overall shape of the bone in *S. inaequalis* does seem much more variable

than that described for *S. copeanus*, some examples being more rounded in their proportions (Fig. 4c, d) while others are longer than they are broad (e.g., Fig. 4a, b). In keeping with the B-bone, the posterior margin of the C-bone is convex, although the degree of curvature varies. The anterolateral margin forms an obtuse angle and the anterior margin forms a similar angle, which nestles between the posteromedial margins of the paired E-bones.

There are pores visible at the centre of the C-bone in some specimens, as well as lines from the centre of radiation, which straddle the boundary between the B- and C-bones. The visceral surface of the bone is seen in NMS G. 1898.17.36 and NMS 1898.162.2.1 (Fig. 6). Although there is a tightly knit association between the B- and C-bone, the contact between the two bones is difficult to define in that view (Fig. 6). There is no sufficient evidence of the pit for the pineal organ described by Schultze & Chorn (1997).

The E-bones lie anterior and slightly lateral to the C-bone. Together, these paired elements occupy the same width of the skull roof as the single B-bone and are approximately five-sided, although the shape of the anterior margin is extremely variable. It is not common for the E-bones to be preserved. Only two specimens (Figs 6, 7) show them in articulation with the rest of the skull roof, although they are quite fragmentary. These paired bones meet in a straight line medially and then diverge posteriorly, as they are separated by the anterior portion of the C-bone. Both the posteromedial and posterolateral margins are fairly straight in dorsal view. The lateral margin has two embayments to receive, posteriorly,

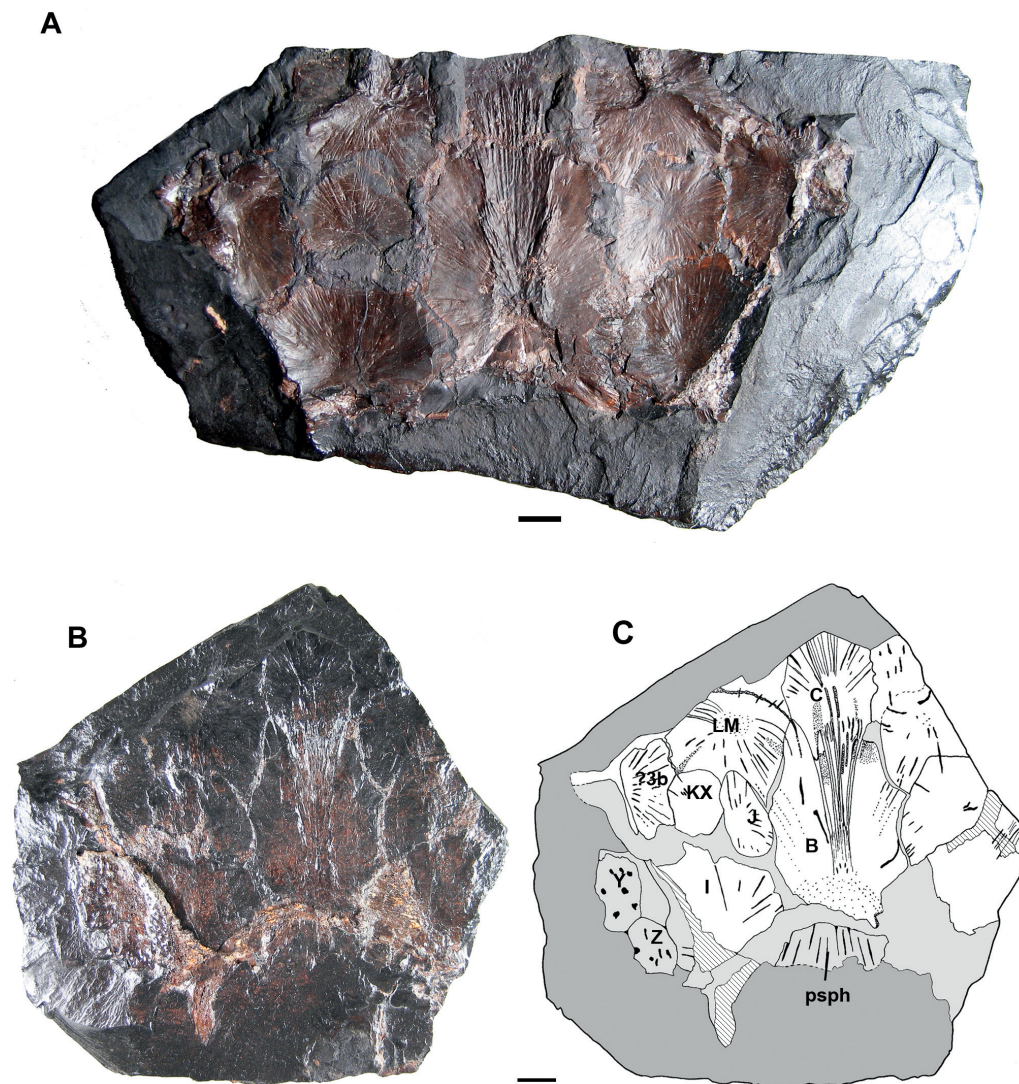


Figure 6 *Sagenodus inaequalis* skull specimen. (A) NMS G. 1898.17.36, inner surface of skull roof. (B, C) NMS 1898.162.2.1: (B) impression of surface; (C) interpretive drawing of same. Scale bars = 10 mm.

the N-bone and, anteriorly, the P-bone. The anterior margin also receives the 'prenasal bones' of Watson & Gill (1923, fig. 1, p. 164) and, centrally, the single F-bone. Watson & Gill (1923, p. 167, fig. 3) illustrated an isolated bone that they considered as an E-bone (their 'nasal'). The E-bones carry branches of accessory canals from the LM-bones; accessory branches also pass from the E-bone into the anterior prenasal bones (Fig. 4).

Anterior to the E-bones are the prenasal bones. Only one specimen has these bones in articulation with a partially complete skull roof (NMS 1878.45.7, Fig. 4a, b). Watson & Gill (1923, p. 167, fig. 3) also illustrated what they considered to be isolated or partially isolated prenasal bones of *Sagenodus* from Newsham, although there is no way to associate these bones unequivocally with *Sagenodus*, because *Ctenodus* also occurs at this locality. The prenasal bones and the F-bone carry the supraorbital canal, evidenced by the presence of a series of sensory pores visible on the dorsal surface. They have been reported as being fused in some specimens (Watson & Gill 1923) or replaced by a single bone in one specimen of *S. copeanus* (Schultze & Chorn 1997).

The extent of these rostral bones can be quite large, as shown by a specimen of *S. copeanus* from the upper Pennsylvanian Hamilton Quarry in Kansas (Fig. 7). This specimen lacks the lateral bones of the skull roof, but it is clear that the skull has a considerable anterior extent, making it appear longer than

it is wide, in contrast to square skull roof typically described for *Sagenodus* (Schultze & Chorn 1997). Not only does the specimen illustrate the marginal N- and P-bones, but it also illustrates the crescentic O-bone, not known in *S. inaequalis*. In addition, it is clear that there are multiple rows of small elements present anterior to the E-bones, and that more than one row of these bones carries the sensory pores of the supraorbital canal.

Lateral to the B-bones lie the paired I-bones ('tabulars' of Watson & Gill 1923). These are relatively large bones, smaller only than the B- and LM-bones (although in *S. copeanus*, the I-bones are consistently larger than the LM-bones). These elements form most of the posterior width of the skull roof and only the lateral corner of the posterior margin is occupied by bone Z. As with the B-bone, the I-bones also have a ventral occipital flange on the posterior margin of the skull, which articulates with the anocleithrum ('tabular horns' of Watson & Gill 1923). While in NMS G 1878.45.7 (Fig. 4) this flange is equal in posterior extent to that of the B-bone, in most specimens it is usually large and extends further in a posterior direction (Fig. 5e, f), though they are never as extensive or of the same size as those found on the I-bones of *Ctenodus*.

Each I-bone is approximately equal in width to the B-bone, and at maximum length extend forward for more than half the length of this median element. The anterior margin of the I-bone begins at the most lateral extent of the B-bone and turns

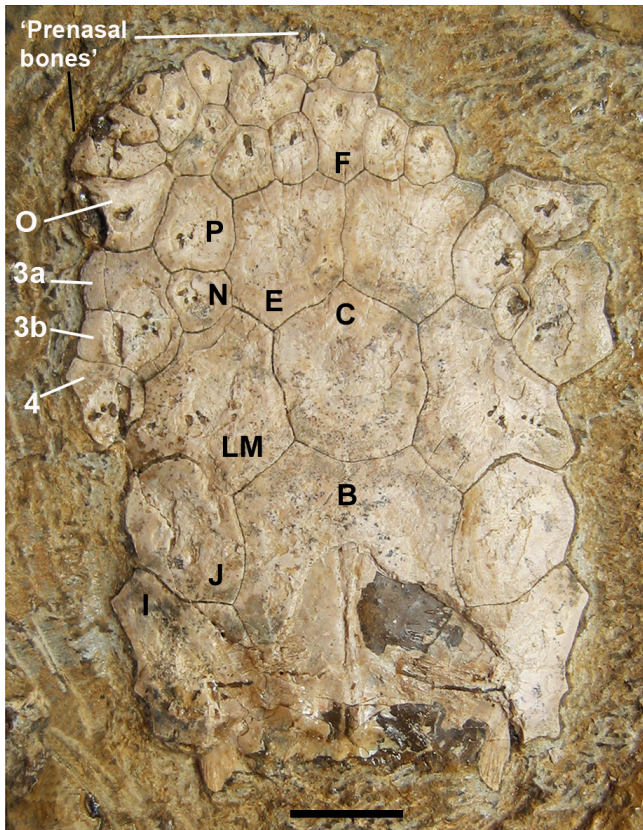


Figure 7 *Sagenodus copeanus* skull roof. KUVP 103259 with bone lettering and numbering applied. Scale bar = 10 mm.

laterally at about 90°. It continues for about half the width of the bone and then turns forward at an oblique angle. The most anterior point of the I-bone is where it meets the postero-medial corner of the KX-bone and the posterolateral corner of the J-bone. From this point the margin follows that of the KX-bone until it meets the Y-bone, where it turns posteriorly (Fig. 4). The lateral margin of the I-bone is undulating, with two shallow embayments to receive the Y- and Z-bones. Although the specimens of I-bones are broadly similar, the shape of the anterior margin varies between specimens and within a single specimen, from almost straight to undulating.

Continuing from B-bone, the I-bones carry the occipital commissure, which traverses the posterior third of the bone into the Z-bone (Fig. 8). There are numerous pores on the surface of the posterior half of the bone (Fig. 4). The bone also has branches of the occipital lateral line shown in Figure 8e, a composite reconstruction based on the part and counterpart specimens NMS 1898.154.23 and 24. Overall, the I-bone of *Sagenodus* is much larger and more prominent a member of the skull roof than the equivalent bone in *Ctenodus*.

Anterior to the I-bones are the paired J-bones ('inter-temporals' of Watson & Gill 1923). Of the major bones of the skull roof, these seem to be the most variable in their shape and relationship with the surrounding bones. Those in *S. copeanus* are described as being 'shield shaped' (Schultze & Chorn 1997, p. 22) and resemble a lozenge, but those of *S. inaequalis* are more rounded and vary considerably in the extent to which they penetrate the KX- and LM-bones (Figs 4, 8). Medially, they occupy the anterior half of the lateral margin of the B-bone, which they contact via a curved margin. In anterior extent the J-bones can be slightly shorter, equal in length, and, in some cases, extend further forward than the B-bone (Fig. 4).

Posteriorly, the contact with the I-bones can be tightly interdigitated or a simple contact. Laterally, the margin of the

bone bows outwards to form an angular convex margin with the medial margin of the KX-bone. Similarly, the anterior margin forms an obtuse angle with the posterior margin of the LM-bone and it is these lateral and anterior margins that are the most variable. For example, in NMS G 1878.45.7 (Fig. 4) the lateral margin forms a gentle curve with the KX-bone and a sharp prong penetrates the LM-bone, whereas GNMHM G 60.91 (Fig. 5e, f) demonstrates a lateral margin which invades the KX-bone to a much greater extent. The J-bones of NMS G 1897.112.5 (Fig. 4) are sub-circular and penetrate very little into the LM-bones.

Although there are no isolated examples of J-bones, evidence from impressions of the visceral surface of the skull roof suggests that the ventral anterior and lateral extent of the bones is somewhat greater than that seen in dorsal view. In some specimens the J-bone carries an extension of the supraorbital canal from the KX-bone.

The J-bone represents a major difference between the morphology of *Sagenodus* and *Ctenodus*. As noted, *Sagenodus* has a single median C-bone, in contrast with the paired C-bones of *Ctenodus*. In *Ctenodus*, the J-bones contact the C-bone over a large area. This is not the case in *Sagenodus*: here the J-bones and C-bone are prevented from contact by the large anterior extent of the B-bone, which is in contact with the LM-bone. Whether this is a result of the increased size of the B-bone, or a result of the loss of paired C-bones, is impossible to know.

The LM-bones are the second largest elements in the skull roof of *S. inaequalis*. They are three-lobed and bounded by the B-, C-, E-, J-, KX-, N-, 3a-, and 3b-bones. The largest of the three lobes points posteromedially and is bounded by the J- and C-bones, forming a junction with the B-bone. The anterior lobe meets the E-bone and the posterolateral lobe meets the KX-bone. Posteriorly, the bone is embayed where it receives the J-bone (Fig. 4). Laterally and anteriorly the bone is bordered by the N-bone and two bones of the orbital series, 3a and 3b; these bones are contacted via three shallow embayments, which give this margin a variable and zig-zig appearance. The only specimen that illustrates these contacts in full is NMS G 1897.112.5 (Fig. 4c, d).

The supraorbital canal is prominent in the LM-bone; large pores offset from centre towards the KX-lobe are visible. In larger specimens these pores are raised relative to the rest of the bone (Fig. 4c, d). Specimens NMS G 1897.110.34 and NMS G 1898.154.23/24 (Fig. 8) show that the supraorbital line traverses the LM-bone and that from it the lateral line passes into the N-, KX-, J-, and B-bones, where it splits into the postorbital and infraorbital canals.

Westoll (1949) described a specimen lacking the L-portion of the LM-bone, probably NHMUK (BMNH) P 7719, which has an extra bone between the Y- and LM-bones. There are some lateral line pores on this accessory bone, suggesting that it could indeed be a separate L-bone. It is not unusual for the skull roofs of dipnoans to be polymorphic, though it is less common in the post-Devonian dipnoans.

The N-bone is the most anterior bone in the lateral series that can be readily characterised, although it is only known from a minority of specimens of *S. inaequalis*, being more commonly preserved in the American *S. copeanus*. Only two specimens with the N-bone in articulation with other skull roof bones have been examined in the course of this study (Figs 4c, d, 8a, b). The posterior margin of the N-bone forms a V between the 3a- and LM-bones, the margins with both being gently undulating and convex with respect to the N-bone. Medially, it is bordered by the E-bone and fits into the posterior of two notches on the lateral margin. The anterior margin of the N-bone is straight, as far as it is possible to tell, at its junction with the P-bone.

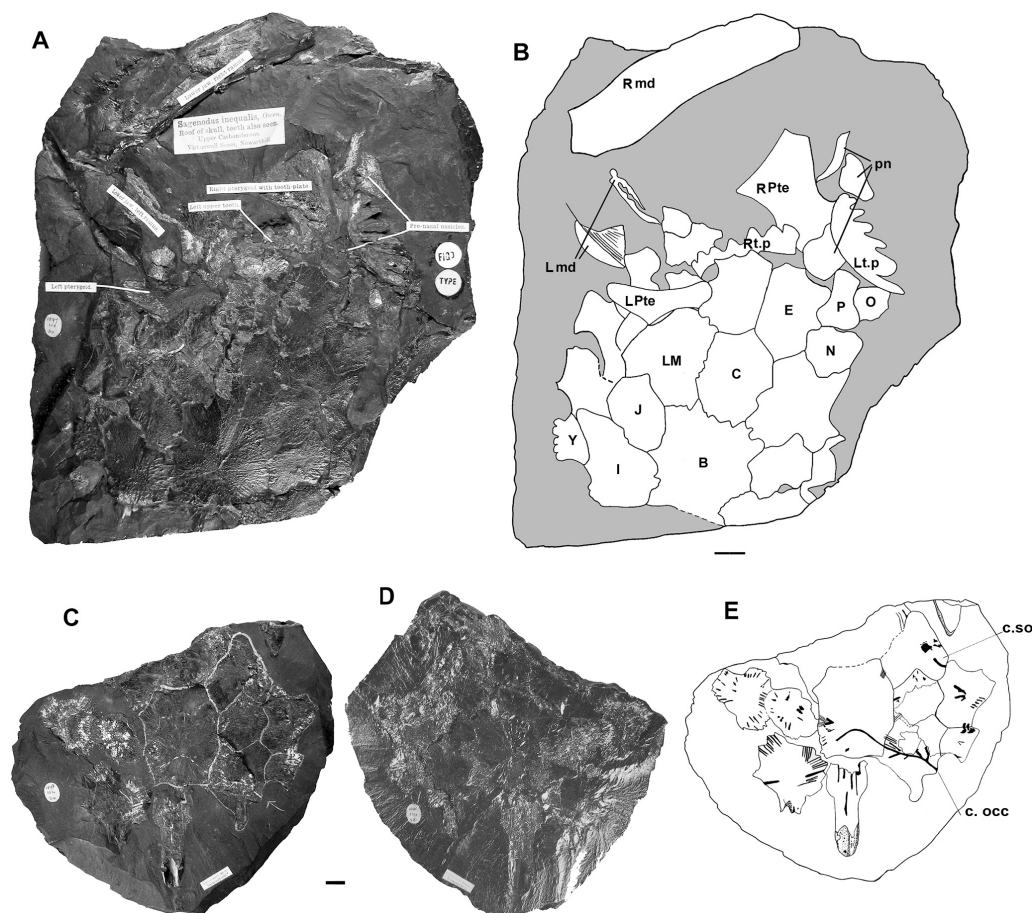


Figure 8 *Sagenodus inaequalis* skull specimens. (A, B) NMS G 1897.110.30: (A) photograph of skull roof; (B) interpretive drawing. (C–E) NMS G 1898.154.23/24 part and counterpart: (C, D) visceral skull roof in part and counterpart; (E) interpretive drawing. Abbreviations: c.occ = occipital canal; pl.p = posterior pit line; Rmd = right mandible; Lmd = left mandible; RPte = right pterygoid; LPte = left pterygoid; pn = prenasal bones; Rt.p = right prearticular plate; Lt.p = left prearticular plate; c.so = supraorbital canal. Scale bars = 10 mm.

The N-bone carries the supraorbital canal forwards onto the P- and rostral bones, confirmed by the presence of sensory pores at the centre of the bone. Both Westoll (1949, p. 151, fig. 8A) and Schultze & Chorn (1997, p. 18, fig. 3) illustrated the N-bone as being entirely separated from the orbital margin by the 3a-bone. This does not appear to be the case in NMS G 1897.112.5 (Fig. 4c, d), in which the 3a- and N-bones are of roughly similar size and shape. Because the areas lateral to these bones are not present on either specimen, it is not possible to comment on the status of the anterior orbital bones.

The P-bones lie anterior to the N-bones. The presence of these bones is suggested by two distinct notches in the lateral margin of the E-bones, the posterior of which accommodates the N-bone and the anterior P-bone. Unfortunately, there is no fully articulated evidence of the P-bone in any specimens of *S. inaequalis*. NMS G 1897.110.30 (Fig. 8) has a bone preserved anterior to the N-bone, but it is slightly disarticulated. The bone is slender, with a length 1.5 times that of its width. It is a little constricted about its centre, but has a posterior margin which fits roughly with that of the N-bone behind it. The medial margin seems straighter than might be supposed by examining the E-bone.

Lateral to this bone is a slightly shorter and stouter element of unknown identity. It is probable that it is the O-bone but, as this bone is unknown in all other specimens of *S. inaequalis*, it cannot be confirmed. This identification is supported by its position anterior to the N-bone and in close association with the P-bone. The alternative bone, which might be seen to lie

lateral to the P-bone, is the 3a-bone, although it would be expected for the bone to be placed equidistantly between the N- and P-bones. The lack of information regarding these anterolateral skull roof bones means that it is useful to examine the conditions found in specimens of other species of *Sagenodus*, in particular that of the better known *S. copeanus*.

Observation of *S. copeanus* (KUVV 103259, Fig. 7) illustrates a distinct individual bone occupying the anterior half of the E-bones and lying lateral to them, probably a P-bone. This bone is twice the length of the N-bone and slightly wider than its neighbour. Anteriorly, it is associated with two 'prenasal bones', and, laterally, it contacts the O-bone. Posteriorly, it has a small area of contact with orbital bone 3a, comprising half of the anterolateral and lateral margin of this bone, together with the N-bone. The P-bone carries the supraorbital canal forwards into the 'prenasal' bone, and this is supported by the presence of sensory pores on its surface in this specimen.

The Z-bones are the most posterolateral bones in the dermal skull roof of *Sagenodus*, forming the back corners of the skull roof of this genus (Fig. 4a, b). The Z-bones are small but thick elements of a generally rounded shape, having a convex, crenelated posterior margin and a pitted dorsal surface. The Z-bones nestle between I- and Y-bones. It is through the Z-bones, on their ventral surface, that the main lateral line canal enters the skull and bifurcates into two branches. That passing medially, and parallel with the posterior margin of the skull roof, is the occipital commissure; that passing

anteriorly through the marginal bones of the skull roof is the cephalic division of the main lateral line.

Because of the bulk of the lateral line canal, the dorsal surface of the Z-bones are pocked with numerous sensory pores. There are no known examples of the ventral surface of a Z-bone of *S. inaequalis* so it is not possible to comment on its morphology. Personal observation (ELS, 2006) of specimens of *S. copeanus* confirms the description given by Schultze & Chorn (1997), which stated that the sensory canals were carried on the ventral surface enclosed within bone. This gives the ventral surface of the bone the appearance of a flat surface with a Y-shaped cylinder on it.

The Y-bone lies anterior and slightly lateral to the Z-bone, forming part of the lateral margin of the skull roof. It is generally trapezoid in shape, its lateral margin being the longest (Fig. 4). As described, it articulates posteriorly with a Z-bone and this margin is concave with respect to the Y-bone. Medially, the border with the I-bone is straight and the union between the two takes up the anterior half of the I-bone. The anterior margin of the Y-bone is formed by the junction with the KX-bone, and this is a straight but oblique border, moving anterolaterally. Thus, the most anterior extent of the Y-bone is pointed, but also somewhat laterally placed. The lateral margin, crenelated as in the B-bone, is gently convex. It passes posterolaterally, and then posteriorly in a curve, which is confluent with the lateral margin of the X-bones.

The anterior portion of the lateral margin is confluent with the notch in the KX-bones, which receives the tabulate process of the operculum. On the dorsal surface the bone is highly pitted and dimpled (Fig. 4), evidence of the high density of sensory canal elements present in this bone. The ventral surfaces of the Y-bones are poorly known for *S. inaequalis*, but the lateral extent seems to be greater in ventral view, presumably forming a region of overlap for the operculum. Observation of the visceral surface of the Y-bone of *S. copeanus* shows a distinct bony structure running anteroposteriorly down the mid-point of the bone, which exceeds both the anterior and ventral extent of the dorsal surface: it would have contained the main sensory line.

The KX-bones ('squamosal', Watson & Gill 1923; 'X-intertemporal', Ahlberg 1991; 'X + Y2', Westoll 1949) are three-lobed and similar in shape and orientation to the LM-bones, although they are smaller (Fig. 4). They form the most lateral extent of the skull table, articulating laterally with the tabulate process of the operculum. The three lobes have straight, truncated distal margins, and the posterior lobe fits between the J- and Y-bones. This lobe has a straight margin with the I-bone (Fig. 4). All margins are smooth with little interdigitation. Posterolaterally, there is a distinct notch in which the operculum is housed, and the lateral border also abuts this bone with a concave boundary. The lateral margin of KX- is posteriorly excluded from the lateral wall of the skull by the anterior projection of Y-, although these bones form a smooth notch in the skull wall.

Anterolaterally, the KX-bone meets the orbital bone 4 in a straight margin, although this bone is not known in articulation for *S. inaequalis*. Anteriorly, there is a concave margin into which fits the 3b-bone, and, anteromedially, the bone contacts the LM-bone. The medial contact with the J-bone occupies the entire lateral extent of J- and this contact is angular with the margin of the KX-bone, forming a concave surface of more than 90°.

The KX-bone is the point of bifurcation of the lateral line ventrally into the infraorbital lateral line canal, and continuing anteriorly into the LM-bone as the supraorbital lateral line canal. Accessory canals also penetrate into the J-bones (Fig. 5), something which is characteristic of the K-bone in *Dipterus* (Forster-Cooper 1937; Westoll 1949), hence its identification

with the X-bone here. NMS 1898.17.36 (Fig. 6) shows a ventral thickening, which suggests that the lateral line was buried deep within the KX-bone. There are numerous pores on the dorsal surface, which are set slightly off-centre towards the opercular notch (Fig. 4).

3.2. Orbital region

Until the description of *S. copeanus*, the orbital region of *Sagenodus* was very poorly known. This is still the case for *S. inaequalis*, with few circumorbital bones known in detail and only two known in articulation with the skull roof – i.e., the dorsal elements 3a and 3b. The specimen that preserves these elements best is NMS G 1897.112.5 (Fig. 4c, d), although 3a is seen in NMS G 1897.110.30 (Fig. 8a, b). Even in the well-known North American species the reconstruction of the orbit from Schultze & Chorn (1997) was based on isolated elements, making any reconstruction tentative. There is no evidence of cheek bones in any specimens known for this genus and they are, therefore, assumed not to have been preserved.

Of the two orbital bones known with certainty for *S. inaequalis*, 3a and 3b are both in articulation with the LM-bone (Fig. 4c, d). The posterior element, the 3b-bone, is associated along its posterior margin with the KX-bone and is concave here. It seems that the union between these bones was not strong and they are usually disarticulated. The sutures seem to lack interdigitation and are found with some matrix between the bones. The medial margin meets the LM-bone and is broadly straight and anteromedially directed. The area around this junction is elevated relative to the more proximal areas of the bones, and this is seen, to a smaller degree, on the sutures between the other orbital elements and their neighbours. Although the dorsal surface of the bone is obscured by matrix in NMS G 1897.112.5 (Fig. 4a, b), there is a pitted and rugose surface, which becomes depressed laterally, and probably represents overlap areas for the adjacent 3-bones.

The anteromedial margin of the 3b-bone meets the 3a-bone in an oblique, straight junction. It is the anterodorsal element of the skull roof and was described by Westoll (1949, p. 151, fig. 8) as bone 2. Its medial margin fits within a concavity in the LM-bone and is consequently angularly convex. The anteromedial margin meets the N-bone and this border is undulating. The anterolateral margin, presumably with the 2-bone, is oblique and seems straight in its most anterior portions, turning posteriorly and becoming confluent with the lateral margin of the 3b-bone. The 3a-bone is also pitted and grooved in the visible areas. Both the 3a- and 3b-bones carry pores of the sensory canal, the 3b-bone carrying a short dorsal branch of the infraorbital sensory canal. GNMHM G 60.91 (Fig. 5e, f) suggests that the 3a-bone carries a small accessory branch of the supraoccipital canal, which enters it from the LM-bone.

The size and position of the left 3a-bone in NMS G 1897.112.5 is somewhat unusual. In other reconstructions of the species, as well as in examined specimens of *S. copeanus*, *S. serratus*, and *S. ohioensis*, the anterior extent of the 3a-bone causes it to sit lateral to the N- and P-bones, thus excluding them from the orbital margin (Fig. 4c, d). In NMS G 1897.112.5, however, the N-bone is larger than reconstructed elsewhere, and the 3a-bone is offset posterolaterally, with its anterior point reaching only to the midpoint of the N-bone. Although the lateral margin of the 3a-bone is broken, there is no reason to suppose that much bone is missing. It seems that *Sagenodus* is the only known dipnoan in which the dorsal margin of the orbit is composed of two bones, both distinct from those at the anterior and posterior orbital margins.

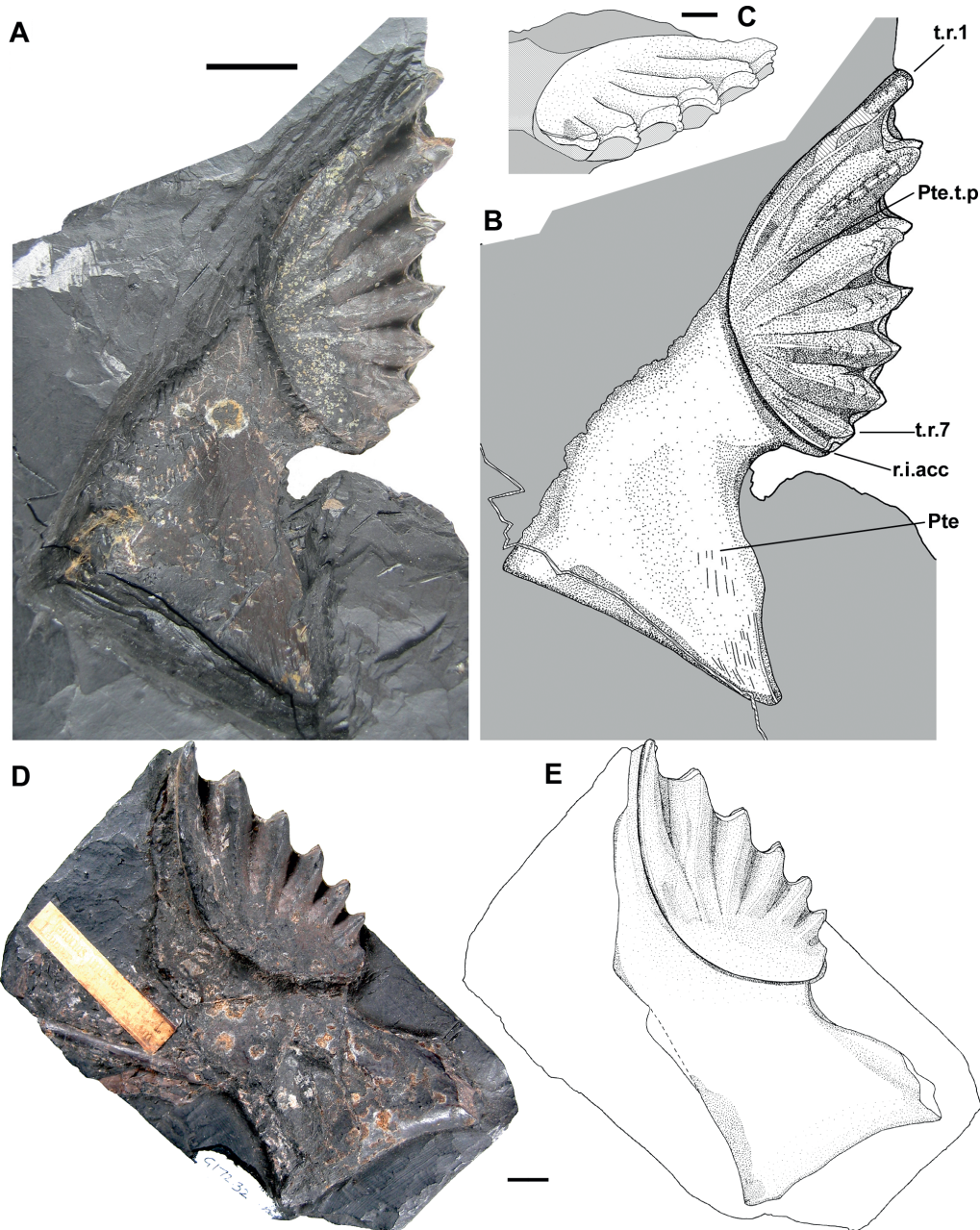


Figure 9 *Sagenodus inaequalis* pterygoids and associated tooth plates. (A, B) GNMHM G 61.34 left pterygoid: (A) photograph; (B) interpretive drawing. (C) Drawing of tooth plate showing wear pattern. (D, E) GNMHM G 172.32: (D) photograph; (E) interpretive drawing. Abbreviations: Pte.t.p = pterygoid tooth plate; r.i.acc = accessory ridge; t.r.1 = tooth ridge 1; t.r.7 = tooth ridge 7. Scale bars = 10 mm.

The other bones of the orbit are unknown in articulation with skull roof material of *S. inaequalis*; however, there is little reason to suppose that the orbital region of *S. inaequalis* is significantly different from that of *S. copeanus* or *S. serratus* (Schultze & Chorn 1997).

3.3. Palate

The palate of *Sagenodus*, as in *Ctenodus* (Sharp & Clack 2013), is composed of paired pterygoids, the upper tooth plates, and the median parasphenoid. Quadrates are not preserved. In addition, there is evidence of the presence of vomerine tooth plates in *S. quinquecostatus* (see below). The tooth plates will be described separately below.

The pterygoids of *Sagenodus* conform closely to the form of those seen in *Ctenodus*, and good examples of pterygoids of *Sagenodus* and its associated tooth plate are shown in Figure 9. Anteriorly, the medial margin is sub-parallel with that of the tooth plate, where the two pterygoids articulate in

the midline of the palate. Posterior to this, the medial margin turns laterally at an angle of approximately 140° , and from this point the two pterygoids are separated by the parasphenoid.

The posterior portion of the pterygoid is offset laterally with respect to the tooth plate and is a characteristic 'delta-shape'. The medial region here has an 'unfinished' surface, and at this point the pterygoid would have been underlain by the parasphenoid. The pterygoids of *Sagenodus* have a less curved medial margin than those of *Ctenodus* (Sharp & Clack 2013). Anterior to this, however, the body of the parasphenoid would overlie the paired pterygoids to a degree. Lateral to this region is the quadrate ramus, and although it is always preserved in a single plane, in life this lateral corner of the pterygoid would be angled ventrally and abut the quadrate. The anterior portion of the pterygoid near the midline of the palate seems quite thin (although the bones are not known in isolation for the British genera), but posteriorly the quadrate ramus is very robust.

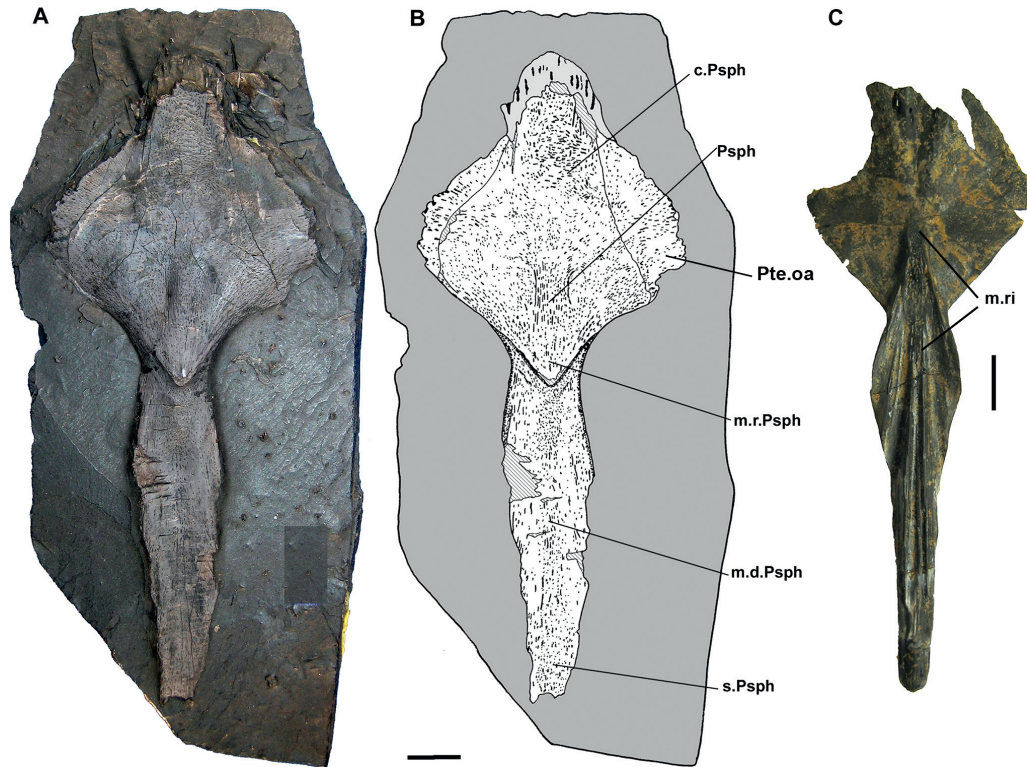


Figure 10 *Sagenodus* spp. parasphenoids. (A, B) *Sagenodus inaequalis* NMS G 1878.45.13 parasphenoid in buccal view: (A) photograph; (B) interpretive drawing. (C) *Sagenodus copeanus* KUV 70738 parasphenoid in visceral view. Abbreviations: Psph = parasphenoid; c.Psph = corpus of the parasphenoid; m.d.Psph = median depression of the parasphenoid; m.r.Psph = median ridge of the parasphenoid on the buccal surface; Pte.oa = pterygoid overlap area; s.Psph = stalk of the parasphenoid; m.ri = median ridge on the visceral surface. Scale bars = 10 mm.

The parasphenoid of *Sagenodus* is relatively smaller and less extensive than that of *Ctenodus*. Again, it is divided into the distinct corpus and stem, and in *Sagenodus* the stem is narrower than that of *Ctenodus* (Sharp & Clack 2013), and the lateral margins are scarcely flared. At their point of contact there is a slight constriction of the stem. The parasphenoid of *Sagenodus* is illustrated in buccal view in Figure 10a, b. There were no available specimens that preserve the visceral surface of the parasphenoid for *S. inaequalis*, and that in Figure 10c is of *S. copeanus*. The parasphenoid of *S. quiquecostatus* is similar as far as can be seen (Fig. 2b) from micro-CT scan reconstructions, except that the stem has much more extensive lateral flare on the margins and a much more strongly tapering component on the visceral surface of the corpus.

The corpus is roughly diamond shaped, with somewhat concave lateral margins. The anterior margin of the corpus makes an angle of between 85° and 90°, and the anterior tabulate process has a gently curved anterior margin. Similarly, the lateral angles of the parasphenoid corpus are at approximately 90°, making the body more square than described for *S. copeanus* (Schultze & Chorn 1997). The margins of the corpus are irregular and ‘unfinished’ at the area of overlap with the pterygoids; the surface of the tabulate process bears anteroposteriorly oriented ridges.

The buccal surface of the parasphenoid varies in its texture: some specimens show a smooth surface, others are broadly smooth but ornamented with pits and grooves, something that is prominent in GNMHM G 61.44, which has an area of dense pustulate ornament on the posterior half of the corpus. The lateral ‘wings’ of the corpus are less ornamented, where the pterygoids would overlap (Fig. 10). The overlapping pterygoids would arch ventrally, allowing the quadrate ramus to contact the quadrate. Similarly, the lateral angles of the

parasphenoid arch downward, although the preservation does not permit this to be seen. Instead, many specimens of parasphenoid are broken in the lateral regions.

Where the stem and the corpus meet there is a ridge, as the posterior corner of the corpus is elevated relative to the rest of the bone. This ridge thins anteriorly and continues forward onto the corpus for a third of its length, and is bordered laterally by two depressions. This is in contrast to the prominent ridge of the corpus seen in *Ctenodus* (Sharp & Clack 2013). The median ridge in *S. copeanus* forms a smooth transition with the parasphenoid stem.

The stem of the parasphenoid makes up almost half of the total length of the bone, and is ornamented with small pits and grooves parallel to the orientation of the stem. Its margins flare laterally for part of its length, after which they begin to converge again, meeting in a rounded posterior termination. The most conspicuous feature of the parasphenoid is the median depression, bordered by parallel ridges (Fig. 10). This depression is not seen to an equal extent in all specimens but is present, to some degree, in all of those studied.

The visceral surface of the parasphenoid is not known for *S. inaequalis* but is known for other species. A poorly preserved example is seen in *S. quiquecostatus* (Figs 2, 3). The anterior portion of the stem of *S. copeanus* (ELS, pers. obs. 2006) bears very prominent ridges on the lateral margins, which continue onto the corpus and converge near the centre. The stem is characterised by a number of somewhat radiating ridges, running anteroposteriorly, for most of its length (Fig. 10). It is interesting to note that the parasphenoid stem of *S. copeanus* is longer in relation to the body than seen in *S. inaequalis*. Similarly, the anterior stem is more flared than found in *S. inaequalis* but similar to those seen in *Ctenodus* (Sharp & Clack 2013) and *S. quiquecostatus*.

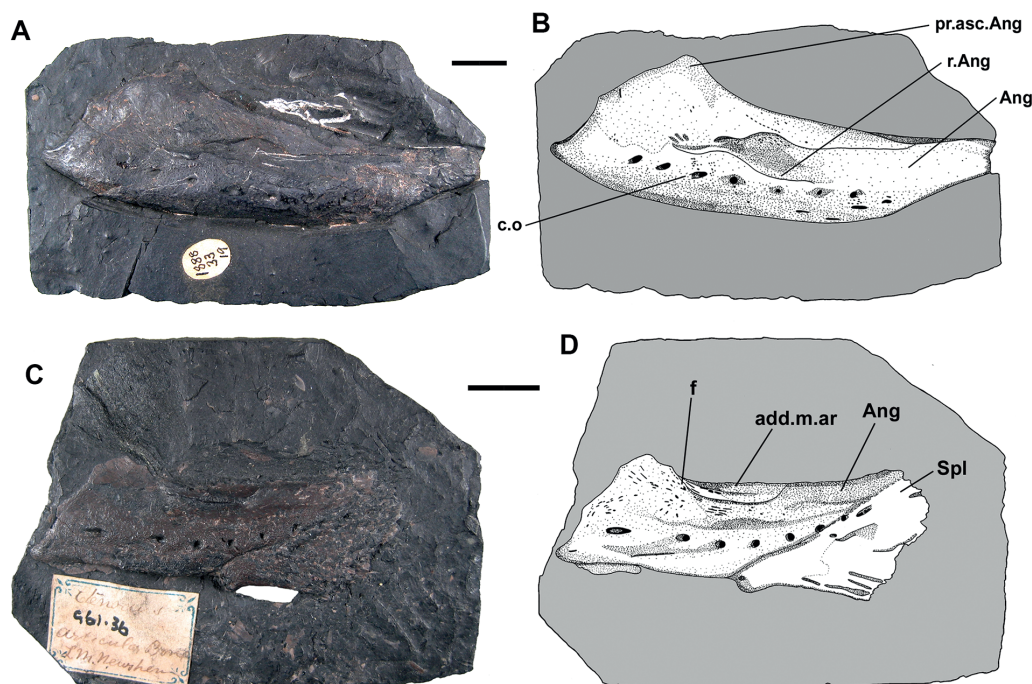


Figure 11 *Sagenodus inaequalis* lower jaw elements. (A, B) NMS G 1888.33.19 right angular in lateral view: (A) photograph; (B) interpretive drawing. (C, D) GNMHHM G 61.36 right angular and splenial in lateral view: (C) photograph; (D) interpretive drawing. Abbreviations: Ang = angular; add.m.ar = area of attachment for the adductor mandibulae; pr.asc.Ang = ascending process of the angular; c.o = oral sensory canal; f = foramen; r.Ang = ridge of angular; Spl = splenial. Scale bars = 10 mm.

3.4. Lower jaw

The lower jaw of *Sagenodus* comprises three paired bones, angular, splenial, and prearticular, and the paired tooth plates. Laterally, the angular is a curved bone that tapers anteriorly and articulates with the splenial. Medially, the tooth plate is borne on the prearticular. Both the mandibular and oral lateral lines are carried on the lower jaw. It is very uncommon for these three elements of the lower jaw to be found in articulation and, for *S. inaequalis*, such preservation has not been observed.

The angular is the largest element of the lower jaw and is situated laterally in the mouth, forming most of the external area (Figs 11, 12). It is a curved triangle in shape, being deepest posteriorly and tapering to a truncated point anteriorly. Its posterodorsal margin is divided into two areas by a subtle angle on the margin. The most posterior region of this margin forms a gentle and shallow notch into which the unossified articular would have fitted. Moving dorsally from here is a second region, found as a notch in some specimens or as a plain surface in others. This margin leads to the highest point of the angular, the ascending process situated at approximately one quarter of the length of the bone. From here, the dorsal margin of the bone descends, steeply at first, and then in a more shallow concave arc, tapering to its most anterior point. This margin is notably more curved than the dorsal margin of the angular of *Ctenodus* (Sharp & Clack 2013).

The dorsal margin of the bone anterior to the ascending process is the region for the attachment of the adductor mandibulae. Schultze & Chorn (1997) described some specimens of *S. copeanus* with a deep pit in this region. GNMHHM G 61.36 (Fig. 11) does have an expanded flattened region in front of the ascending process, which might be equivalent in function. The internal face of the angular is unknown in that specimen. Posterior to this region, and anterior to the ascending process of the angular, is a small pit, seen only in GNMHHM G 61.36 (Fig. 11). While it is difficult to interpret, its position corresponds to that described by Jarvik (1980) as the foramen for the ramus intermandibularis and mandibularis trigemini.

The ventral margin of the angular forms either a shallow curve or is sub-horizontal. The most posterior point of the bone is a rounded prong, confluent dorsally with the articular facet. The curved ventral surface turns dorsally upon the point of contact with the splenial. If the angular is isolated this region can be easily identified by this change of direction of the margin of the bone, as well as the somewhat 'unfinished' surface on the anteroventral regions of the bone.

The angular possesses two branches of the lateral line: the oral canal, which passes dorsally through the middle of the bone onto the splenial, and the mandibular canal, which traverses the ventral portion of the angular onto the splenial. These lateral line canals open to the surface via pores which are seen to a lesser or greater extent on different specimens. The oral canal is the most prominent, and is usually represented by six or seven pores on the angular, whereas the mandibular canal is more elusive on the angular, only represented by a few thin and elongate pores on the ventral margin of GNMHHM G 61.35 (Fig. 12). Schultze & Chorn (1997) refer to the mandibular canal as being found in a gutter, but there is no evidence for that here.

The lateral face of the angular is, broadly speaking, convex, but there is a notable thickening ventrally in the region of the lateral line canals. This is bordered by a distinct dorsal undulating margin, above which the bone becomes distinctly less thick. It is presumed that this thickening contained the lateral line canal. This ridge is much more developed in the two larger specimens illustrated here. The smaller example of an angular (Fig. 11) from a presumed sub-juvenile shows some thickening, but to a lesser extent. This thickened ridge was not described for *S. copeanus*, and was not noted upon personal investigation (ELS 2006) to be as well developed as that in *S. inaequalis*.

The medial face of the angular is concave (Fig. 12). There is a distinct medial furrow, bordered ventrally by a large and well-defined ridge, which is thickest just ventral to the furrow, thinning into another smaller furrow below that. Schultze & Chorn (1997) described this as carrying the mandibular canal.

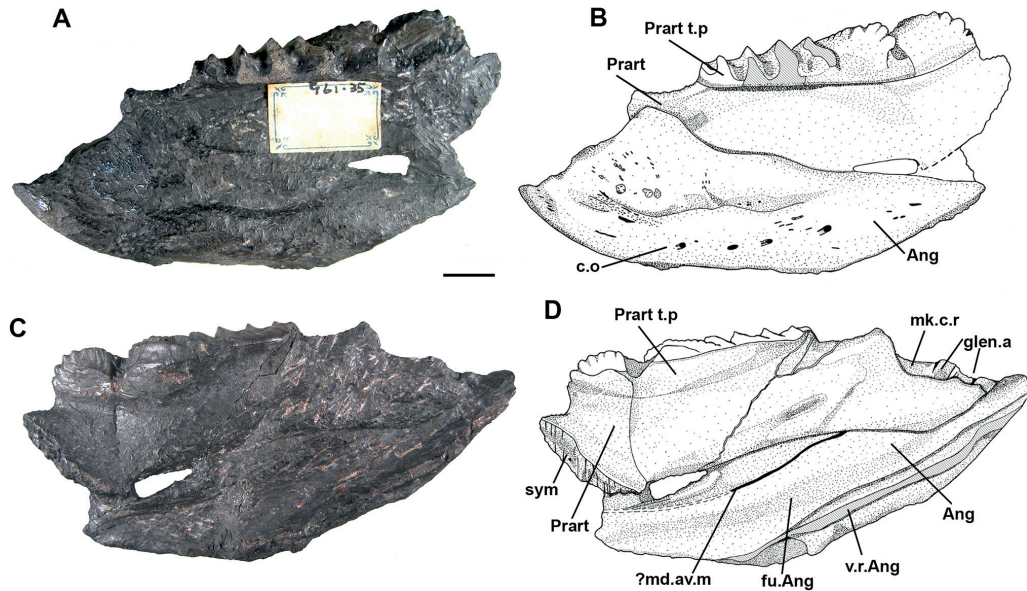


Figure 12 *Sagenodus inaequalis* lower jaw elements. (A–D) GNMHM G 61.35 right angular, prearticular, and prearticular tooth plate in lateral view: (A) photograph; (B) interpretive drawing; (C, D) specimen in lingual view: (C) photograph; (D) interpretive drawing. Abbreviations: Ang = angular; glen.a = area of glenoid; fu.Ang = furrow of the angular; md.av.m = path of the mandibular ramus of the anteroventral lateral line nerve; mk.c.r = area that receives the Meckelian cartilage; Prart = prearticular; Prart t.p = prearticular tooth plate; sym = symphyseal region of mandible; v.r.Ang = ventral ridge of the angular. Scale bar = 10 mm.

As the ridge extends posteriorly it becomes confluent with the ventral margin of the angular, eventually forming the posterior prong of the angular.

Schultze & Chorn (1997) also described the path of the mandibular ramus of the anteroventral lateral line nerve. It is not possible to confirm the presence of that path on GNMHM G 61.35, although there is some evidence of a canal (subsequently filled with matrix), which may represent the path of this nerve in *S. inaequalis* (Fig. 12).

The junction of the angular with the splenial is illustrated in a single specimen, GNMHM G 61.36 (Fig. 11), which was figured by Watson & Gill (1923, fig. 14, p. 180). Posteriorly, the junction is straight, becoming more intimate as the margin rises anterodorsally. Halfway along this junction it becomes difficult to see the detail of the relationship. Schultze & Chorn (1997) described the angular as overlying the splenial, but that does not seem to be certain in *S. inaequalis*.

The splenial is situated anterior to the angular. It is a triangular bone that tapers posteriorly, articulating with the anterior taper of the angular. Its anterior margin is roughly straight, with an 'unfinished' margin that articulates with its partner ventrally at the symphysis of the lower jaw (Fig. 12), indicating that the symphysis was not firmly sutured. The posterior point of the splenial is truncated and articulates incompletely with the most anteroventral point of the angular. From there, its dorsal and ventral margins rise dorsally in parallel, although the splenial remains ventral to the articular throughout its length. The ventral border of the splenial is asymmetrically convex, the longer ascending portion of the arc being posterior in position and the shorter descending portion being anterior.

The anterior margin of the bone is anteriorly inclined. This angle varies between specimens, being between 110° and 120° from the ventral margin. While it appears from the specimens that both the angular and splenial are on the same plane, this is not the case. The splenial is oriented at an oblique angle to the angular so as to meet its antimeres at the anteroventral midline of the jaws such that the splenial is positioned anteriorly, ventrally, and medially to the angular.

As with the angular, the splenial carries the mandibular and oral branches of the lateral line (Fig. 11). The mandibular

canal continues along the ventral margin of the bone, received from the angular at its most posterior point, and extends forward until it meets the canal of its antimeres at the symphysis. The oral canal enters the splenial approximately halfway along its union with the articular, and the splenial is also thickened in the region of this canal. Both these bones have incomplete pores, which unite at the suture. The oral canal passes into the splenial and then extends dorsally, subparallel to the junction of the two and opening through a pore in the dorsal corner of the splenial. There is an accessory branch connecting the mandibular and oral canals together, shown by the presence of one large sensory pore between the two. The inner face of the splenial is unknown in this species, though in *S. copeanus* it is concave. Only one splenial of *S. inaequalis* has been found in articulation with any other bone of the lower jaw (Fig. 11).

The prearticular is a long narrow, almost parallel-sided bone, which occupies the whole of the inner surface of the lower jaw. It lies lingually to the angular and splenial and slightly dorsal to both, forming the pocket in which the Meckel's cartilage would have been situated. GNMHM G 61.35 (Fig. 12) shows the angular and the prearticular, although the latter bone is dorsally and anteriorly offset to its orientation in life.

The prearticular has a tight union with its tooth plate and in most cases it is not possible to see any suture between them due to fusion during development. It is less common to see these tooth plates disarticulated than it is to find disarticulated pterygoid tooth plates. The prearticular has a dorsal shelf onto which the tooth plate sits, although the tooth plate extends considerably further labially than the bone itself, forming a dorsal overhang between the ventral surface of the tooth plate and the lateral wall of the prearticular. Internally, the extent of the tooth plate is not so marked, and the lingual margin of the tooth plate is confluent with that of the prearticular, forming a smooth curve between the two elements.

Posterior to the tooth plate, the prearticular is extremely thin, flaring a little at its most posterior point. The dorsal margin has one emargination directly posterior to the tooth plate, which ends posteriorly in a pointed dorsal spur. Behind this, the dorsal margin has another, much more distinct,

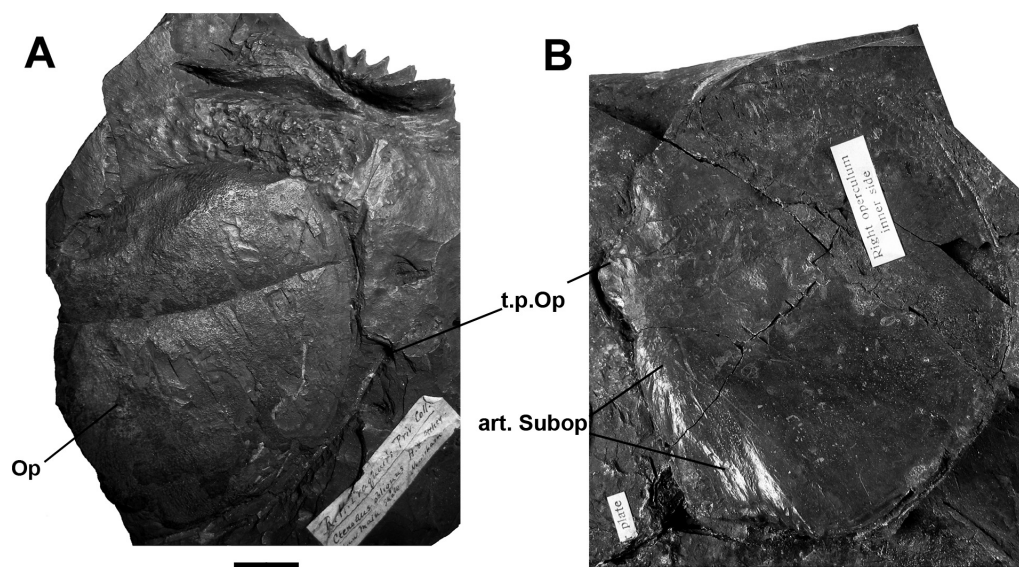


Figure 13 *Sagenodus inaequalis* opercular bones. (A) MM L10453 left operculum in external view; (B) GNMHM G 61.34 right operculum in internal view. Abbreviations: art. Subop = articulation for suboperculum; Op = opercular bone; t.p.Op = tabulate process of the operculum. Scale bars = 10 mm.

emargination in which the dorsal margin drops to below the level of the tooth plate (Fig. 12). This deep notch is associated with a similar one at the posterior extent of the angular and, together, they receive the unossified articular (Schultze & Chorn 1997), forming the articular surface of the lower jaw. Posterior to this, there is another small dorsal spur, and the margin then proceeds posteriorly until forming the tapered posterior margin of the prearticular.

The ventral margin of the bone is gently undulating and broadly concave until meeting its anterior margin. When viewed laterally, the margin of the bone turns anterodorsally at an oblique angle, eventually meeting the dorsal margin of the bone. If viewed medially, the ventral margin meets the symphyseal surface. The symphyseal surface is an elongated oval in shape and, like that of the splenial, is 'unfinished'. In the region of the symphysis, the whole of the prearticular turns inwards and, to a small extent, ventrally. The result of this is that, if viewed from the front, the symphyseal margin (Fig. 12) is oriented so that the most anterior portion is dorsally and laterally situated, whereas the posterior end is ventrally and medially located.

The prearticular tooth plate is approximately two thirds the length of the prearticular. It does not sit symmetrically along the length of the prearticular, but instead occupies an anterior position, much as the pterygoid tooth plate does on the pterygoid.

3.5. The branchial region

The branchial region of *Sagenodus* is poorly known and the only elements described and identified with certainty here are the operculum and ceratohyal. Schultze & Chorn (1997) state that these are the only elements of the branchial skeleton to ossify in *Sagenodus*. As with *Ctenodus*, it is assumed that the branchial region of *Sagenodus* conforms in its nature closely to the configuration seen in *Neoceratodus* (Rosen *et al.* 1981).

There is little to distinguish the operculum of *Sagenodus* from that of *Ctenodus* (Sharp & Clack 2013) and the basal Carboniferous genus *Limnichthys* (Challands *et al.* 2019). The bone is large and robust; it is outwardly convex and its posterior margin forms a regular curve. For this genus the only specimen in which the operculum has been found in natural articulation with the KX-bone is NMS G 1886.82.11,

the lectotype specimen of *S. quinquecostatus* (Fig. 2). Although this operculum is not entirely complete, it is more regularly rounded than those of *S. inaequalis*, which typically have a slightly greater dorsoventral diameter than anteroposterior diameter. The outer surface is pitted and there are striations radiating outwards from the tabulate process. The posterior portion also exhibits a triangular segment of finer ornament more similar to that found on the operculum of *S. inaequalis*.

Figure 13 illustrates adult opercula of *Sagenodus*, identified in association with other elements of *Sagenodus*. Similar to *Ctenodus*, the operculum articulates anteriorly with the KX- and Y-bones via the tabulate process, a rounded protuberance that sits in the notch between the former bones of the skull roof. The tabulate process is positioned in a slightly dorsal position on the anterior margin of the operculum (Fig. 13). Dorsal to it, the margin is straight, and above this the margin is inflected again before the major curve of the operculum begins. It is in this region, dorsal to the tabulate process, that the KX- and Y-bones overlie the operculum.

Ventral to the tabulate process the margin becomes straight and turns posteroventrally at a shallow angle, and then posteriorly, forming an angle of approximately 120°. On the internal face of the operculum these margins border a depressed triangular region, which is the region of articulation between the operculum and the suboperculum.

The ceratohyal is the only known element of the hyoid arch of *Sagenodus* because, as with *Neoceratodus*, it is the only element to ossify. It was well described for *S. copeanus* (Schultze & Chorn 1997), and here is identified and described for *S. inaequalis* for the first time. The identity of the ceratohyal in *Sagenodus* spp. has been debated. Examples have been described by, among others, Watson & Gill (1923) as a quadrate (Fig. 14a) and, according to them, by Fritsch (1885–1889) as both a scapula and a femur. Williston (1899) gave it its correct identification. As a member of the hyoid arch, the ceratohyal is principally an endoskeletal ossification. Its preservation is based upon the fact that it is surrounded by a perichondral ossification. For *S. copeanus*, for which there is 3D acid-etched preparation, this can be observed in great detail; the anterior and posterior ends of the bone are hollow (ELS, pers. obs. 2006). This structure can be inferred, rather than observed directly, in British specimens, as illustrated in Figure 14.

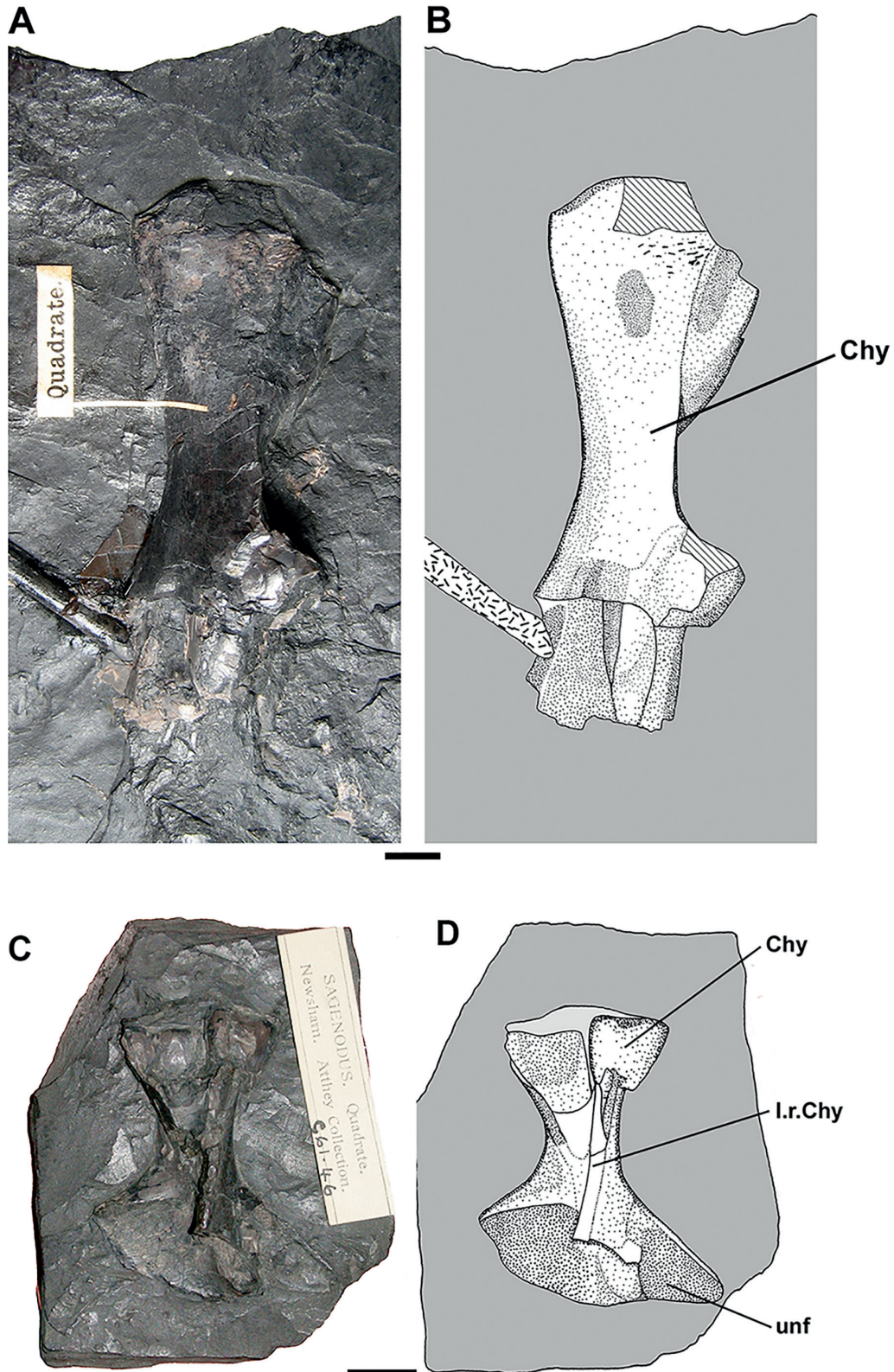


Figure 14 *Sagenodus inaequalis* ceratohyals. (A, B) NMS G 1888.33.4 right ceratohyal in oblique view: (A) photograph; (B) interpretive drawing. (C, D) GNMHM G 61.46 left ceratohyal in lateral view: (C) photograph; (D) interpretive drawing. Abbreviations: Chy = ceratohyal; l.r.Chy = ridge on left ceratohyal; unf = unfinished region. Scale bars = 10 mm.

Figure 14 illustrates the external/lateral face of the ceratohyal. That illustrated in Figure 14a, b (NMS G. 1888.33.4) is the only specimen associated with other good *Sagenodus* material but is less well preserved, missing both the anterior and posteriormost portions. It is also seen in an oblique view, broadly dorso-medially, and tentatively interpreted as a right ceratohyal. The other specimen, GNMHM G 61.46 (Fig. 14c, d) was illustrated

by Watson & Gill (1923, p. 177) and is cautiously identified here as a left ceratohyal in lateral view.

Although it is common for such material to be compressed and distorted, these specimens are both crushed and collapsed, evidence of the hollow nature of the bone without its cartilaginous interior. The only region of the bone that is relatively unaffected is the middle portion and, in particular, the lateral

ridge that runs along the constricted region between the two expanded ends. That the bones are somewhat crushed shows how thin the perichondral layer of bone was. The form of the bone is that of an hourglass – both the anterior and posterior ends are flared and the middle constricted. The posterior end is considerably more flared, particularly in what is believed to be the dorsal direction.

The lateral face of the ceratohyal is characterised by the presence of a prominent ridge (Fig. 14d). Although this ridge is incomplete and damaged, it appears that its posterior extent is true. How far this ridge proceeded anteriorly is difficult to interpret, but it may have reached halfway onto the anterior flare and was probably approximately half the total length of the bone. Miles (1977) described a distinct ‘crest’ on the lateral face of the ceratohyal of *Chirodipterus australis*, which he interpreted as separating the insertion areas for the levator and interhyoideus muscles. Despite this similarity there is no clear region of insertion of muscles either above or below this ridge and, as a consequence, an inference of muscle insertions must be regarded with some caution.

The posterior region of the ceratohyal is the most compressed region of the bone, although it is not clear to what extent this region would have been flattened in life. The expanded posterodorsal process appears to have a depressed and ‘unfinished’ region indicating continuation in cartilage or other tissue; Miles (1977) suggested that the hyosuspensory ligament would have inserted here, a possible interpretation of this feature. The ceratohyal was probably suspended by such a structure from the braincase, and the interpretation of this region for attachment does not seem unreasonable. It is, however, impossible to infer to what posterior extent the ceratohyal was composed of cartilage. Similarly, the anterior region of the ceratohyal would have articulated with the endochondral hypohyal, and would itself be partly endochondral and lacking in perichondral ossification. This area of bone is also partly crushed in the specimens. The dorsal surface of the ceratohyal is smooth, and is ornamented with fine pits and small grooves.

3.6. Postcranium: appendicular skeleton

The first described element of pectoral girdle of *Sagenodus inaequalis* was the clavicle, by Hancock & Atthey (1872). After this, descriptions of the pectoral girdle were by Miall (1880), Fritsch (1885–1889), and by Watson & Gill (1923) somewhat schematically. Schultze & Chorn (1997) described the pectoral girdle of *S. copeanus* in some detail on the basis of three-dimensionally preserved material. There are no such well-preserved specimens of the pectoral girdle of *S. inaequalis*, although, generally, the elements agree with those described in the latter. The biggest problem of identifying elements is that of association, especially in cases where more than one genus is known from a locality. In the case of *Sagenodus*, it is possible to compare material that is in doubt with better preserved material from other localities.

There are no complete specimens of anocleithra (‘post-temporal’ of Watson & Gill 1923) known for *Sagenodus*, and incomplete ones are rare. The anocleithrum is the only element of the pectoral girdle that has not been found in articulation with other undoubted elements of *Sagenodus* and, therefore, the identification of the following element (Fig. 15a, b) GNMHM G 61.64 is made by comparison with the anocleithrum of *S. copeanus* (Schultze & Chorn 1997). A similarly shaped lungfish anocleithrum from the Tournaisian of Scotland is figured in Clack *et al.* (2019, fig. 8D).

The anocleithrum is a large, flat bone consisting anteriorly of a single projecting ‘ramus’, which articulates with the

I-bone and, posteriorly, of a broad, ventrally projecting ‘corpus’ (Fig. 15a, b). The anterior part of the ramus is missing and, consequently, the attachment area for the ligament is not found. Unlike that illustrated by Schultze & Chorn (1997), there is no marked difference in the angle between the dorsal margins of the anterior ramus and the corpus of the anocleithrum. This margin approximates to horizontal for two thirds of its length, after which it turns dorsally briefly and then makes a rounded posterior margin. There is also no evidence of the posterior notch described by Schultze & Chorn (1997).

The anterior ramus bears a ridge, broken in places, which extends posteriorly, becoming less prominent and more rounded towards the posterior region of the corpus in external view. The whole dorsal region of the anocleithrum is raised relative to the ventral region, on which the cleithrum overlapped. Ventral to the anterior ramus is a large notch, below which the margin of the bone turns ventrally, and then posteriorly, to meet the posterior margin of the corpus in what is reconstructed as a smoothly rounded apex.

The lateral (external) face of the corpus preserves a number of ridges of varying prominence. The most pronounced of these is that which lies parallel with the dorsal ridge, and between the two is a striated trough, which may have borne some form of blood vessel. It is possible that this ridge marks the most dorsal extent of the overlap of the cleithrum, which has been identified in some Devonian lungfishes (ridge 1 of Jarvik 1980). Another ridge is seen on the posteroventral margin of the corpus. Two smaller, parallel ridges at the centre of the corpus make an anteroventral-posterodorsal angle. The anocleithrum has a smooth surface, which indicates (Jarvik 1980) deep burial of the bone within the skin.

A more commonly found element is the cleithrum – a large, triangular bone, whose large blade is orientated laterally and lies against the back wall of the gill chamber. As with the anocleithrum, it is sometimes difficult to assign specimens to a genus – for example, in material from Newsham, which preserves both *Sagenodus* and *Ctenodus* (Sharp & Clack 2013). There are a few examples of cleithra known in association with identifiable specimens of *S. inaequalis*. Specimen GNMHM G 174.78 (not figured) includes a poorly preserved cleithrum associated with well-defined skull roof material from Newsham. It provides the general shape of the cleithrum and, although showing no further detail, allows identification of other cleithra from this species. On one face of the block is a prearticular tooth plate that is readily attributable to *Sagenodus*. NMS G 1898.174.16 (Fig. 15c, d) is a better-preserved left cleithrum in posterior/internal view, from the Virtuewell Coal Shale from Newarthill in Lanarkshire from which there is no record of *Ctenodus*. The bone is broadly triangular in shape, the most conspicuous feature being the broad branchial lamina (Fig. 15d). This thin blade broadens laterally into a thickened ridge, which in life would be confluent with a similar ridge laterally placed on the external portion of the clavicle. Lateral to this is a smaller partially exposed ‘lateral’ lamina (Fig. 15d). The dorsal margin of the bone is rounded, and for a quarter of the height of the branchial lamina the lateral and medial margins are parallel. The medial margin then broadens in two steps, until it turns laterally at approximately 45°, meeting the articular process of the cleithrum. The branchial lamina is broadly concave in posterior view with the surface gently undulating; it has small, radiating ridges on the surface of the bone, which become more ornamented ventrally. This ornament continues onto the articular process of the cleithrum, suggesting that the bone was not deeply embedded but close to the skin.

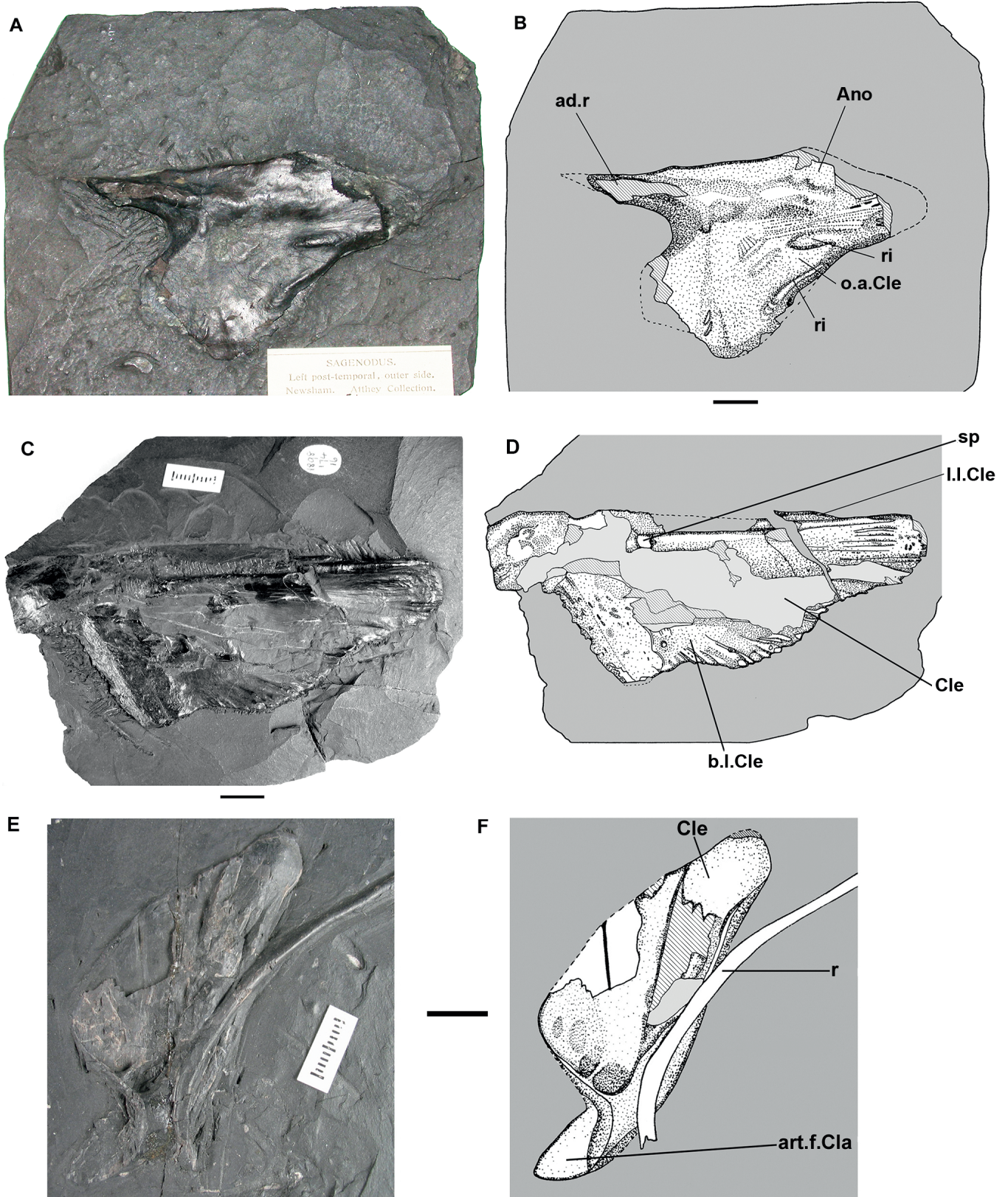


Figure 15 *Sagenodus inaequalis* shoulder girdle elements. (A, B) GNMHM G 61.64 left anocleithrum in external view: (A) photograph; (B) interpretive drawing. (C, D) NMS G 1898.174.16 left cleithrum in internal view: (C) photograph; (D) interpretive drawing. (E, F) NMS G 1878.45.21 left cleithrum in external view: (E) photograph; (F) interpretive drawing. Abbreviations: ad.r = dorsal ramus of the anocleithrum; Ano = anocleithrum; art.f.Cla = articular facet for clavicle; b.l.Cle = branchial lamina of the cleithrum; Cle = cleithrum; l.l.Cle = lateral lamina of the cleithrum; o.a.Cle = overlap area for the cleithrum; ri = ridge; sp = spur of Schultze & Chorn (1997); r = rib. Scale bars = 10 mm.

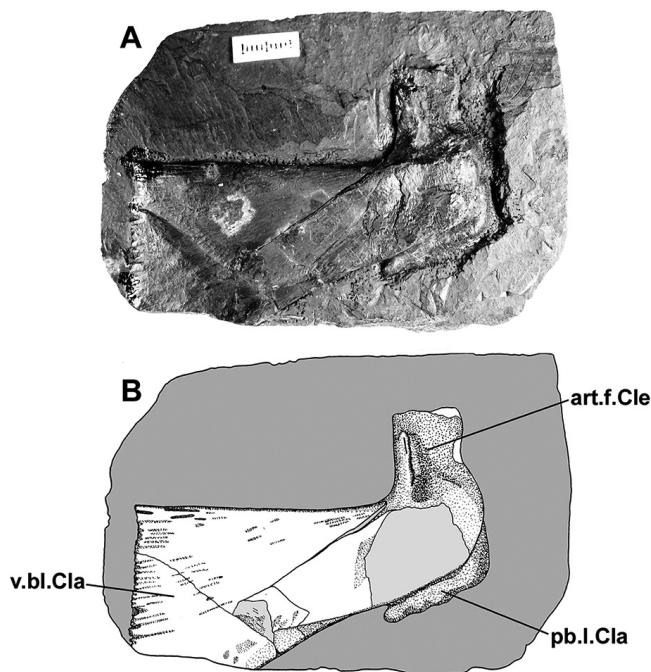


Figure 16 *Sagenodus inaequalis* right clavicle. UMZC GN 159: (A) photograph; (B) interpretive drawing. Abbreviations: art.f.Cle = articular facet for clavicle; pb.l.Cla = postbranchial lamina of the clavicle; v.bl.Cla = ventral blade of the clavicle. Scale bar = 10 mm.

In *S. copeanus*, the articular process of the cleithrum turns slightly medially, and Schultze & Chorn (1997, p. 39) described it as being 'inflected anteriorly', but that feature is not seen in our specimens. The ventral part of the articular process is incomplete in NMS G 1898.174.16 (Fig. 15c, d), although in life this would articulate with the clavicle. As illustrated by Schultze & Chorn (1997, fig. 34, p. 40), there is what appears to be a 'small spur' (Fig. 15d) on the lateral ridge of the cleithrum, which the authors claim is the most dorsal extent of the cartilaginous scapulocoracoid.

The external aspect of the cleithrum is shown in GNMHM G 61.64 (Fig. 15a, b) and the internal in NMS G 1878.45.21 (Fig. 15e, f). The dorsal part of the bone is rounded and the shape of the branchial lamina conforms broadly to that of a scalene triangle. From this view the ventral margin of the branchial lamina is thickened, and in the area where the blade meets the lateral ridge there are two distinct hollows, presumably for the insertion of a ligamentous connection to the hyoid apparatus and cranial ribs. The anterior surface of the branchial lamina is unornamented, and thickens laterally to form a second lateral ridge, in *S. copeanus*, which Schultze & Chorn (1997) claimed was sub-parallel to the ridge visible from posterior view. It has not been possible to verify this in our material.

The ventral ridge of the branchial lamina becomes confluent with that of the lateral ridge, and extends laterally onto the articular process. Medially, this thickened ridge ceases abruptly and the rest of the bone is thin. The concavity made at this junction is the articular facet, and it is here that the cleithrum receives the clavicle.

The clavicle is also poorly known from articulated specimens of *Sagenodus*. There are two poorly preserved clavicles present on the composite specimen GNMHM G 174.78, giving the general bone form and illustrating that the clavicle is of roughly the same length as the cleithrum. There are also poorly preserved specimens in disarticulation with material attributable to *Sagenodus* from a number of other specimens, but those best preserved are found in isolation. The clavicle is the

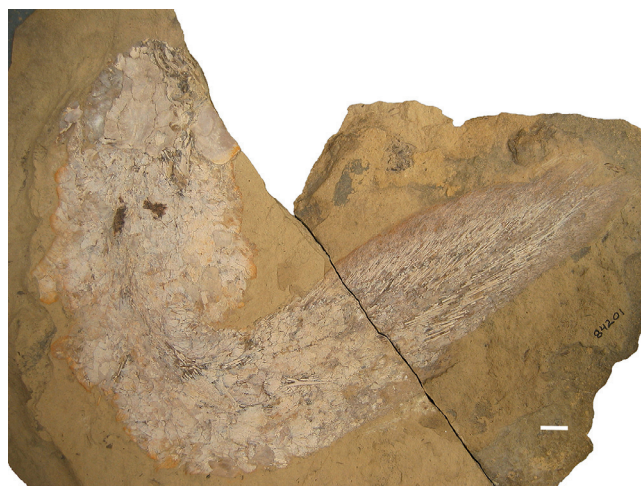


Figure 17 *Sagenodus copeanus* KUVP 84201, entire fish. Scale bar = 10 mm.

pectoral girdle element, which is typically most deformed by preservation. The 3D nature of the bone is missing in most specimens, and the blade appears flat rather than curved. The clavicle of *Sagenodus* is illustrated in Figure 16 (right internal view).

The most prominent feature of this bone is the large anterior and ventrally directed blade. It is broad and diverges along its length, terminating in an abrupt and straight margin, in contrast to *Ctenodus* whose blade has roughly parallel margins. The internal surface of this distal margin is gently scalloped and the surface of the bone lightly ornamented with striations. In life the blade would be curved so that the distal margin is rotated by approximately 150° relative to the articular surface. Dorsoposteriorly, the clavicle thickens and the margin of the blade is raised above the small, medially oriented branchial lamina. The articular facet, which contacts the cleithrum, is posteriorly placed, and the bone is ornamented here. Two ridges on the medial edge of the clavicle would be confluent with those found on the cleithrum.

3.7. Postcranium: axial skeleton

The axial skeleton of *Sagenodus* is poorly known. There are few known 'whole-body' specimens, none of which are of the British species, although the lectotype of *S. quinquecostatus* retains an array of associated ribs, revealed by micro-CT scans (Fig. 3). The best of the articulated specimens is a small individual from the Hamilton quarry in Kansas: KUVP 84201 (Fig. 17). It was described by Chorn & Schultze (1989), reconstructed by Schultze & Chorn (1997, p. 44, fig. 39). There is little reason to suppose that the postcranial skeleton of British *Sagenodus* species are different in any important respect from that specimen, and cannot be described further.

3.8. The tooth plates

The tooth plates of *Sagenodus* are probably the most widely known of any genus in the Palaeozoic in terms of numbers. This is evidence not only of the geographically wide distribution of this genus but also of the highly hard-wearing and durable nature of these plates, much more so than genera with tooth plates composed of denticle fields or less fully consolidated tooth rows. Although *Sagenodus* was defined on the basis of tooth plate histology, it is relatively uncommon for a tooth plate to be found in articulation with skull roof material: rather, these elements are often found disarticulated and scattered on blocks with other skull roof elements, and it is

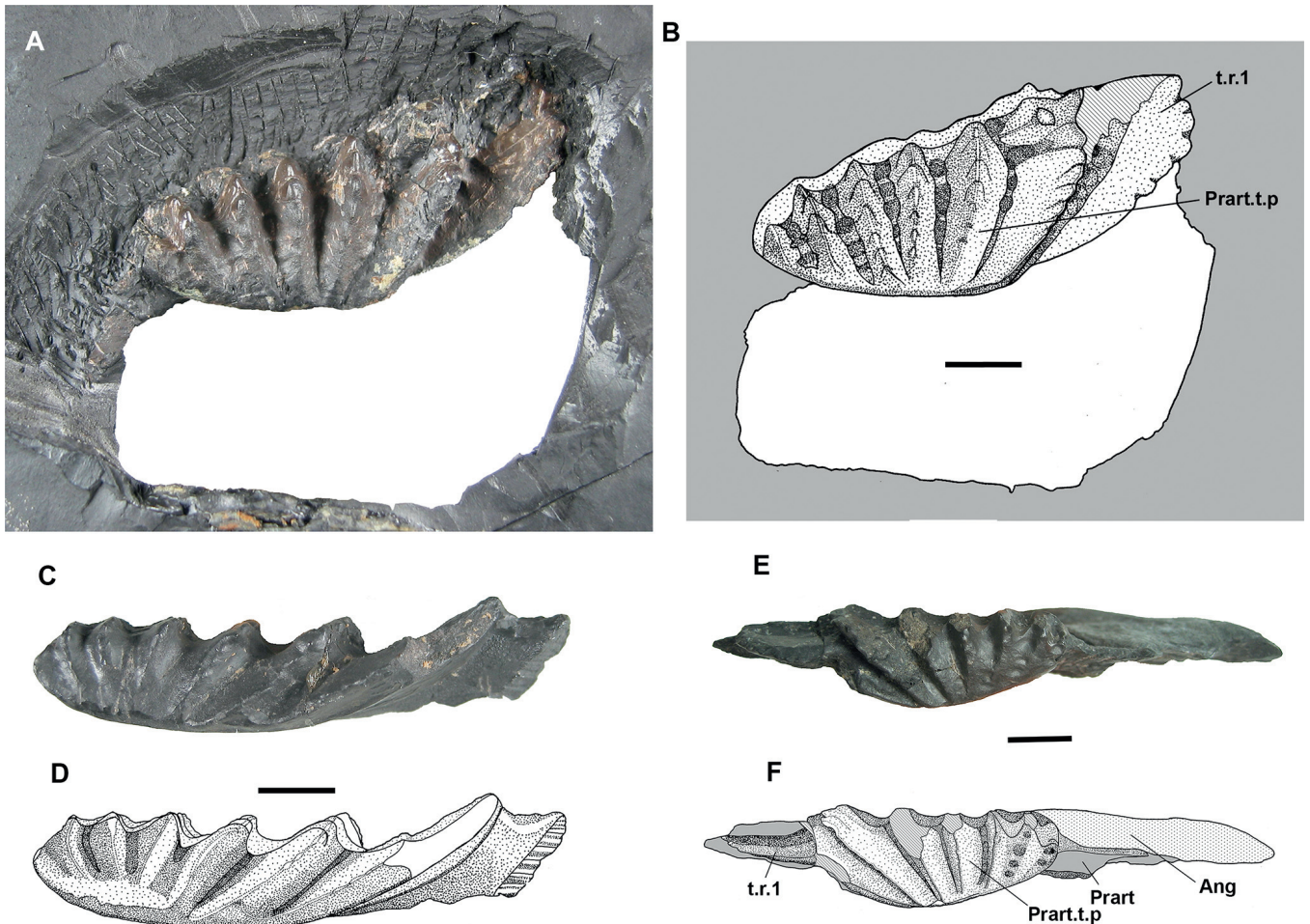


Figure 18 *Sagenodus inaequalis* prearticular tooth plates. (A, B) GNMHM G 61.34 left prearticular tooth plate in buccal view: (A) photograph; (B) interpretive drawing. (C, D) UMZC GN 168 left prearticular tooth plate in buccal view: (C) photograph; (D) interpretive drawing. (E, F) GNMHM G 61.35 right angular, prearticular, and prearticular tooth plate in buccal view: (E) photograph; (F) interpretive drawing. Pale shading represents prearticular; mechanical stippling, angular; hatching, broken bone. Abbreviations: Ang = angular; Prart = prearticular; Prart.t.p = prearticular tooth plate; t.r.1 = tooth ridge 1. Scale bars = 10 mm.

through such associations that the tooth plates of *Sagenodus* are identified.

We present descriptions of the tooth plates of *S. inaequalis* and *S. quinquecostatus* as examined in this study. The tooth plates of *S. quinquecostatus* differ significantly from those of *S. inaequalis*.

3.8.1. Tooth plates of *S. inaequalis*. The pterygoid tooth plates of *S. inaequalis* are the most widely known, although prearticular tooth plates have occasionally been mistaken for them. Examples of the pterygoid tooth plates are illustrated in Figure 9. They are ovate, with a length-to-width ratio of between 1:7 and 2:8. This is lower than the prearticular tooth plates, which are typically narrower than their opposing pair. The pterygoid tooth plates of *S. inaequalis* examined in this study have, on average, a lower length-to-width ratio than those *Sagenodus* species from the US.

The lingual margin forms a smooth curve, which extends from the tip of ridge 1 to that of the most posterior or accessory ridge. The anterior third of the lingual margin is almost straight and is parallel with the lingual margin of the pterygoid. The maximum medial extent of the lingual margin of the tooth plate is just posterior to half of the maximum length of the tooth plate, whereas the maximum lateral extent of the lingual margin is slightly posterior to this at approximately two thirds of the way back. The labial margin, while undulating by virtue of the tooth ridges, is not symmetrical with the

lingual one as it forms a much less laterally extensive arc. The tooth ridges radiate from a point approximately two thirds along the length of the lingual edge, and their distal ends form a smooth convex curve from which no tooth ridge projects much further than any other. The tooth ridge angle varies between 50° and 70° , depending on the number of tooth ridges. The tooth ridge angle increases with increasing tooth ridge number.

The number of tooth ridges varies within the genus (Schultz & Chorn 1997). In *S. inaequalis*, the ridge numbers vary from 6 to 8. The morphology of the ridges themselves also varies. In all examined specimens there are teeth remaining on the labial margin of the tooth plate (Fig. 9). Some specimens show almost complete tooth fusion into solid ridges (Fig. 9c, d), whereas other specimens retain a greater number of distinct teeth on the ridges (Fig. 9a, b). It is very unusual for teeth to remain on the most lingual areas of the tooth plate; this region of the occlusal surface is often entirely worn away, with little ridge detail remaining.

The occlusal surface is gently concave, although this is variable amongst specimens. Similarly concave pterygoid tooth plates are present in *Ctenodus* species, and relate to occlusal relations with convex prearticular plates (Smithson *et al.* 2015; Clack *et al.* 2018). The most lingual areas are usually significantly more concave than the outer regions, and in some specimens the labial portion of the tooth plate is

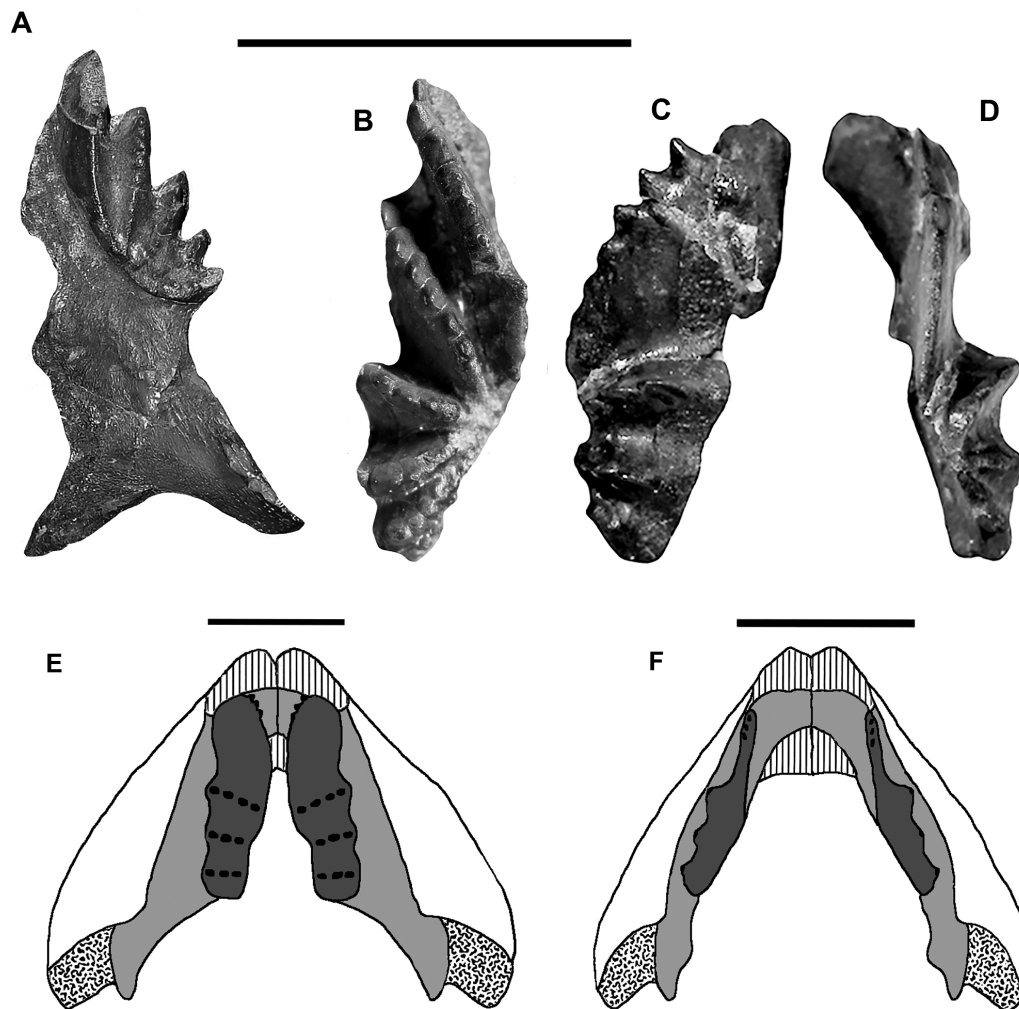


Figure 19 *Sagenodus quinquecostatus* tooth plates. (A) NHMUK (BMNH) P 11506 left pterygoid tooth plate. (B) NMS G 1993.56.118 right pterygoid tooth plate. (C, D) NMS G 1993.56.115 right prearticular tooth plate: (C) view with ridge 1 held approximately horizontally and more posterior ridges approximately vertically; (D) view with ridge 1 approximately vertical. (E, F) Diagrams of the two positions of the tooth plates in *S. quinquecostatus* based on the type specimen NMS G 1886.32.11 and the right prearticular of NMS G 1993.56.115: (E) jaws in position as in (C) for rear tooth plates to occlude (medial rotation); (F) jaws in position as in (D) for ridge 1 to occlude (lateral rotation). Tooth plates, dark grey; tooth cusps, black; prearticular, light grey; splenial, vertical hatch; angular, white. Scale bars = 10 mm (A–D); 5 mm (E, F) (scale bars are placed above their respective images).

somewhat convex. Similarly variable is the level of tooth wear seen on the occlusal surface, and this does not seem to be correlated with either size or collection locality.

Prearticular tooth plates (Figs 12, 18) are often mistaken for pterygoid tooth plates when not associated with the prearticular bone itself. Their general shape is more variable than that of the pterygoid tooth plates, although they consistently have a higher length-to-width ratio of between 2:9 and 3:8. The tooth ridge angle is $c.90^\circ$, slightly greater than that of the pterygoid tooth plates.

One characteristic feature of the prearticular tooth plates of *Sagenodus* is that tooth ridge 1 is longer than the other ridges and is often inclined anteriorly, so that the most anterior furrow is asymmetrical to a large degree (Fig. 18c–f). In *S. inaequalis*, tooth ridge 1 also tends to preserve the teeth along more of its length than the other ridges and is commonly broken with its anterior portion missing. A similar disparity in the size of ridge in some Late Devonian lungfishes was noted by Clack *et al.* (2018). However, the individual teeth remain preserved on all the prearticular tooth ridges more commonly than on the pterygoid tooth plates, although they are often worn. The prearticular tooth plates are more

often found incomplete and seem to break or damage more readily than the pterygoid tooth plates.

Although the prearticular tooth plates are also oval in outline, they tend to be a more elongate oval. The lingual margin forms a shallow curve, the middle section of which is almost straight in a number of specimens. This curve becomes more distinct at the lingual margin of tooth ridge 1. In contrast, with the exception of tooth ridge 1, the labial margin is straighter than that of the pterygoid tooth plate, making the maximum width of the tooth plate fairly constant throughout its length. While the ridges do radiate, this is less distinct in the more posterior ridges, and the angle between the anterior ridges is greater. It is only lingual to the more posterior ridges that there is any significant wear on the occlusal surface.

The number of ridges on the prearticular tooth plate is variable similarly to those on the pterygoid tooth plate. Again, the ridge number varies between 5 and 8, and there seems to be a fairly close correspondence between the number of ridges on both the upper and lower plates. Although this seems intuitive since there would have been a close occlusal relationship between the upper and lower tooth plates, it is not the case in some Devonian forms (Clack *et al.* 2018). Both the

depth, width, and angle of the furrows between ridges is greater for the more anterior ridges, and the furrows are also more symmetrical in the posterior regions of the tooth. The furrows often contain a row of isolated depressions, suggestive of occlusion with the pterygoid tooth plates, although no specimens have been studied for this genus where occluding tooth plates can be identified with certainty. The tooth plate is convex to occlude with the concave pterygoid plate.

3.8.2. Tooth plates of *Sagenodus quinquecostatus*. Individual pterygoid tooth plates of *S. quinquecostatus* are relatively common in the late Early Carboniferous of Scotland (Fig. 19a), and incomplete specimens are preserved on the lectotype NMS G 1886.82.11 (Fig. 2). They differ from those of *S. inaequalis* in never having more than six tooth ridges and typically having five. They are distinctly fan-shaped, with a greater length-to-width ratio of 3:3.

Two morphs of the pterygoid tooth plate are known. One morph has blunt cone-like teeth that are usually worn into blades, especially at the lingual end of the tooth ridge, and has a tooth ridge angle of $c.90^\circ$ (Fig. 19a). The other has more laterally compressed teeth showing less wear and with a much greater tooth ridge angle of up to $c.160^\circ$ (Fig. 19b). Both morphs have been found at Loanhead, the morph with blunt cone-like teeth has been found at Niddrie, and the morph with laterally compressed teeth has been found at Dora and Gilmerton. They may represent two different species but, in the absence of any additional evidence, we here treat all the material as belonging to *S. quinquecostatus*.

Prearticular tooth plates are very rare. They are preserved on the lectotype (Fig. 2) and a small individual tooth plate, NMS G 1993.56.115, was collected from the Dora Bone Bed, Cowdenbeath (Smithson 1985) (Fig. 19c, d). They differ from those of *S. inaequalis* in having no more than four tooth ridges. Tooth ridge 1 is long, orientated almost at right angles to the short posterior ridges. The teeth on tooth ridge 1 are fused into a sharp blade on the lectotype specimen, but some individual teeth are still present on the small Dora specimen. The posterior tooth ridges bear up to four unworn teeth. In the lectotype specimen, the mesial side of the dorsal surface of the tooth plate is covered with a layer of enamel. This extends from the lingual edge to cover approximately two thirds of the plate. The labial margin is very clear and forms a distinct boundary between the open texture of the bone on the lateral side of the tooth plate and the smooth enamel-covered mesial side. The enamel surrounds the teeth on the posterior tooth ridges but has been worn away along most of the length of tooth ridge 1 (Fig. 2). Specimen BGS GSM 4556, *S. inaequalis*, also shows distinctive enamel. Its length-to-width ratio of 3:8 is similar to that of some *S. inaequalis* specimens, and the tooth ridge angle of 90° is also similar.

Until now, the presence of vomerine teeth in *Sagenodus* has been assumed, as in *Neoceratodus* (Kemp 1977), and isolated vomerine tooth plates have been inferred to be those of *Sagenodus* (Watson & Gill 1923; Atthey 1868). The only vomerine tooth plate associated with skull material is preserved on the lectotype specimen of *S. quinquecostatus* NMS G 1886.82.11 (Fig. 2). The specimen has been dorsoventrally compressed to such an extent that the prearticular tooth plates appear anterior to the dermal skull roof in semi-articulation with the pterygoid tooth plates. Anterior to the E-bones, and between the tooth plates, is a single element orientated similarly to the pterygoid tooth plates. This element has three distinct cusps in a row, the enamel clearly visible. A closer view is illustrated in Figure 2e.

Although the view of the bone is obscured, the vomerine tooth plate appears to differ from that described by Schultze & Chorn (1997) for *S. copeanus*, all teeth being in a single plane. It comprises a single row of three teeth and the associated

bone. The central tooth is larger than those flanking it, although the tip is incomplete. The left lateral margin of the vomer is not visible and, therefore, it is not possible to say with certainty the total number of teeth that the vomer bears. Lund (1970) described the vomer of *Sagenodus periprion* as having five or more teeth (cusps).

4. Other taxa

The following British taxa are listed amongst Schultze's (1992) currently valid species list. The first three were described as *Ctenodus*, but Woodward (1891) synonymised them into *Sagenodus*. Most of these derive from the Low Main Seam, Newsham, Northumberland, and are late Carboniferous in age.

Sagenodus caudatus Barkas, 1877 (syn. *Ctenodus caudatus*)

This taxon was erected by Barkas (1877) on the basis of a single tooth plate specimen from the Northumberland Coal Measures. He described it as resembling *Ctenodus ellipticus* (*S. inaequalis*), although smaller and with a long projection from one (the anterior) extremity. The plate had four ridges, the most anterior of which he described as being 'broad and inclined forward, projecting beyond the outer margin'. Also noted is a ridge running from the back of the prolongation along the centre of the underside of the tooth plate.

Based on Barkas' (1877) figure, as well as the presence of this horizontal ridge, it seems likely that the specimen is that of a lower tooth plate and that the 'prolongation' is the 'prearticular' bone. The small size of the specimen and the number of ridges is an indication that the specimen is that of a juvenile and almost certainly *S. inaequalis* and, therefore it is proposed that *C. caudatus* be synonymised with *S. inaequalis*. This is supported by the supposed resemblance to *C. ellipticus*, also a synonym of *S. inaequalis*.

Sagenodus corrugatus Atthey, 1868 (syn. *Ctenodus corrugatus*)

This species was also based upon a single tooth plate from the Collingwood Pit in Northumberland, and transferred to *Sagenodus* by Woodward (1891). This specimen was described as large, slightly convex, with nine 'somewhat irregular, rounded' ridges. The spaces between the ridges were noted as large, and Atthey commented on the fact that the 'tubercles' along the external border were indistinctly and irregularly tuberculated. The specimen is held in the collections of the Great Northern Museum (Hancock Museum) and was examined in the course of this study. Its size, general shape, and number of ridges suggests that the specimen represents an example of *Ctenodus* – most likely *Ctenodus cristatus*, as it is from the Carboniferous of Northumberland – contrary to Woodward's (1891) suggestion of *Sagenodus*.

Sagenodus octodorsalis Barkas, 1869 (syn. *Ctenodus octodorsalis*)

Sagenodus octodorsalis, previously *C. octodorsalis*, was described by Barkas (1869) on the basis of a single tooth plate and was never illustrated. It is described as having eight ridges free from denticulations, with rudimentary tubercles at the extremities of ridges one to six. The grooves between the ridges are broad, and their bases are shallow and smoothly rounded. The presence of eight ridges suggests that it likely belongs to *Sagenodus*, and the fact that these ridges are without 'tubercles' supports that. *Sagenodus octodorsalis* is, therefore, synonymised with *S. inaequalis*.

5. Discussion

5.1. Phylogenetic considerations

Sagenodus has been considered by some authors (e.g., Schultze & Chorn 1997) to occupy an unusual position within the Dipnoi, being in many ways structurally intermediate between

the Devonian and post-Palaeozoic lungfishes, and has been used as an outgroup for later taxa and for comparison on many occasions. However, several cladistic analyses of lungfishes have been prepared in recent years, in which the position of *Sagenodus* has been variable. Lloyd *et al.* (2011) were among the first to produce comprehensive parsimony analyses using various criteria to identify character changes throughout the group. In that study, only *S. inaequalis* was used, based on the 1923 work by Watson and Gill, rather than the more recent study of *S. copeanus* by Schultze & Chorn (1997). In addition, for *Ctenodus*, only *Ctenodus romeri* was included, which has subsequently been placed in a separate genus, *Occludus* (Smithson *et al.* 2015). This taxon, consisting only of isolated tooth plates, was used rather than Watson & Gill's (1923) descriptions of the more complete *C. cristatus*. In their analyses, Lloyd *et al.* (2011) found *Sagenodus* to fall below *Ctenodus*, the latter being clustered with *Tranodis* and *Straitonia* plus *C. romeri*.

Pardo *et al.* (2014), describing a new lower Permian genus, *Persephonichthys* from the USA, used a dataset consisting of this taxon with mainly Devonian and a few Carboniferous taxa. Whereas *Persephonichthys* clustered with *Neoceratodus* and Lepidosireniformes, *S. copeanus* clustered with a number of Devonian taxa such as *Adelargo*, *Howidipterus*, and *Barwickia*. *Ctenodus* was not included in their dataset.

Kemp *et al.* (2017), using a different and less comprehensive dataset, found *Sagenodus* to fall one node above *Ctenodus*, both appearing basal to all their other included post-Devonian taxa.

In an analysis of most Devonian and a range of Carboniferous taxa, Clack *et al.* (2018) found *Sagenodus* to fall above a clade including *Ctenodus* (*C. interruptus*, *C. allodens*), *Delatitia*, and the newly described Devonian taxon *Celsiodon*. That study also included a newly discovered but then un-named taxon from the Tournaisian of Scotland. This taxon, named *Limanichthys*, was included in another analysis by Challands *et al.* (2019) in which *Sagenodus* was found to cluster most often with Carboniferous taxa, although in one of their analyses it occurred in a polytomy with many Devonian taxa and some Carboniferous ones. One conclusion of those two studies was that some Late Devonian taxa show characters more typical of Carboniferous ones. They also corroborate the impression that *Sagenodus* is more derived than *Ctenodus* in reducing the number of dermal skull bones, and in the reduction of individual cusps on the tooth ridges, in which it more closely resembles *Neoceratodus*. Nonetheless, its position among other taxa remains equivocal.

We hope that the new data provided by this study will assist further phylogenetic analyses of lungfishes in the future.

5.2. Comparisons with other Carboniferous taxa

In Britain in the Mississippian, *Sagenodus* is one of a number of lungfish taxa of varying sizes and dentitions. These range from those with strongly diverging tooth ridges, those with almost parallel tooth ridges, to those with a single main tooth ridge (Smithson *et al.* 2015). They seem to have been adapting to changing conditions following the end-Devonian mass extinction, and were beginning to exploit different food types and habitats. In the later Mississippian, at the locality known as Loanhead, at least six different taxa were present (Smithson *et al.* 2019), again showing a variety of feeding mechanisms, of which *S. quinquecostatus* was one. By the Pennsylvanian, in the coal swamps of the UK, *Sagenodus* is one of just two lungfish taxa, the other being *Ctenodus*, which has a very different pattern of skull roofing bones and tooth plates from *Sagenodus*. Elsewhere in the Carboniferous, *Conchopoma*, which has a denticulated palate rather than tooth plates, occurs in the

Mississippian at Loanhead, Scotland (Smithson *et al.* 2019), the Pennsylvanian at Mazon Creek (Marshall 1988), and also in the early Permian (Schultze 1975).

Sagenodus shares with other Carboniferous lungfish a reduced number of skull roofing bones. *Sagenodus*, *Straitonia* (Sharp & Clack 2013), and *Conchopoma* (Schultze 1975) have a single midline C-bone and have lost the D-bone. This is part of a trajectory of reducing dermal and endochondral bone ossification in lungfish skeletons, possibly as a result of paedomorphosis (Bemis 1984).

The early Permian genus *Gnathorhiza* has been suggested to have formed aestivation burrows, although only skulls with no postcranial material have been found within the burrow casts (Berman 1976). Lungfish of the genus *Sagenodus* have not yet been found in burrows, and have been considered not to have aestivated (Schultze & Chorn 1997; Huttenlocker *et al.* 2018). Small *et al.* (2006), who also commented on aestivation burrows in lungfishes, drew their conclusions from the fact that although two genera of lungfishes had been found in burrows, specimens of *Sagenodus* were not mentioned, and presumably were not found at their locality. The argument by Huttenlocker *et al.* (2018), therefore, was founded on the absence of evidence. McCahon & Miller (2015) found burrows of *Gnathorhiza* in the lower Permian of Kansas, some of which did contain articulated and disarticulated postcranial elements, such as ribs.

We not only suggest that the specimen of *S. quinquecostatus* described above could have been preserved in a burrow, but also possibly in the close contemporary *Straitonia* (Sharp & Clack 2012). In the latter, the postcranium was well preserved, and curved round head to tail. This is a similar position to that of aestivating specimens of *Protopterus* (specimen UMZC F 4441). We find it hard to envisage a situation that could produce preservation such as that in *S. quinquecostatus* except as an individual that was in a burrow.

5.3. Jaw kinesis in *Sagenodus*

In extant lungfish like *Neoceratodus* the pterygoid and prearticular tooth plates are very similar (Kemp 1977). They are securely attached to the pterygoid and prearticular bones, which, in turn, are firmly sutured to the surrounding bones of the skull and mandibles (JAC, pers. obs. 2018, UMZC F 4381). The jaw joint is a simple hinge and there is no evidence of cranial kinesis. The same is true for most Devonian lungfish, but in some the pterygoid and prearticular tooth plates are subtly different from each other (Clack *et al.* 2018), and in others the skulls are poorly ossified (Cloutier 1996). Carboniferous lungfish also have poorly ossified skulls, with most of the endochondral parts missing from their fossils, and the upper and lower tooth plates are often quite different from each other (Smithson *et al.* 2015, 2019). *Sagenodus* is one of the Carboniferous lungfish showing the greatest disparity in tooth plate morphology. The pterygoid tooth plates are fan-shaped with vertical tooth ridges, whereas the prearticular plates are narrower and more rectangular, with the anterior-most tooth ridges angled anteromedially. Furthermore, tooth ridge 1 is longer than the others, and the posteriormost tooth ridges are relatively short.

The wear on tooth ridge 1 of the prearticular plate seen in *S. quinquecostatus* (Fig. 19) and *S. inaequalis* (Fig. 12), and the pits between the posterior tooth ridges of the pterygoid plate of *S. inaequalis* (Fig. 9b) show that both parts of the tooth plate were involved in the bite. The different orientation of the anterior and posterior tooth ridges on the prearticular tooth plates suggests kinesis must have occurred to ensure occlusion took place during different phases of jaw action.

For the anterior tooth ridges to occlude, ridge 1 would have to move from its resting orientation to a more vertical one. In order to achieve this, the mandibles would need to rotate medially along their long axes. By contrast, the posterior tooth ridges, which are set at 90° from those of ridge 1, and the jaws would need to rotate in the opposite direction to enable occlusion.

One explanation for this pattern of occlusion is a simple kinetic mechanism controlled by the shape of the jaw joint and involving movement at the symphysis. The jaw rami of *Sagenodus* are not firmly sutured together, unlike those of most Devonian lungfish. Examples in which they are strongly sutured or fused include the Early and Middle Devonian lungfish like *Paleadaphus* (Traquair 1878) and *Dipterus* (Jarvik 1967), the Late Devonian *Chirodipterus australis*, *Holodipterus gogoensis* (Miles 1977), and *Uranolophus wyomingensis*, (Schultze & Campbell 1986), or extant forms (JAC, pers. obs. 2018, *Neoceratodus* UMZC F 4381). In those with an unsutured mandibular symphysis, in one part of the jaw action, the mandibles could have rotated medially along their long axis, opening the symphysis ventrally, and turning tooth ridge 1 towards the frontal plane (a horizontal position) and the posterior ridges into the sagittal plane (vertical) (Fig. 19e). In a second part of the jaw action, the anterior tooth ridges would initially remain horizontal before the mandibles rotate laterally, closing the symphysis, and turning tooth ridge 1 into the sagittal plane (vertical), to occlude between ridge 1 and 2 of the pterygoid plate and the posterior ridges into the frontal plane and occupy a lateral position (Fig. 19f). In this way, the tooth plates can perform two very different biting actions. In an action probably aided by the rotation of the mandibles, the anterior ridges sliced and the posterior ridges ground. Other lungfish were probably able to process food in a similar way using a heterodont arrangement of laterally compressed teeth on a long tooth ridge 1 and blunt cones on the posterior ridges, as in *Clackodus angustulus* (Smithson *et al.* 2019), but *Sagenodus* is the only Carboniferous lungfish that we know of which appears to have developed such a complex jaw kinesis. This may account for the longevity of the genus, ranging from the late Early Carboniferous (=late Mississippian) to the lower Permian, c.40 my.

Although this type of action has never been documented in lungfishes before, a similar kind of action has been noted both in some actinopterygians (Gosline 1987) and a chondrichthyan (Coates *et al.* 2019). In the actinopterygians *Epinephelus* and *Tautoga*, the lower jaws swing apart at the symphysis, twisting the jaws along their long axes. In the Carboniferous chondrichthyan *Tristychius*, it is mainly the ceratohyal and basihyals that perform a similar action to that described above for *Sagenodus* jaws, with a contribution to the action by Meckel's cartilage. In both cases, the effect is to improve suction feeding. Although the specific arrangement of tooth plates in *Sagenodus* do not suggest that this jaw action was used for suction feeding, it does seem to have been using a similar sequence of actions, but to bring about two phases of a specialised food processing cycle.

Our interpretation of kinesis in the lungfish jaw mechanics raises some profound questions. It implies that some lungfishes in the Palaeozoic differed quite considerably both from those of recent taxa and many of those from the Devonian period. In all three recent genera and most of those from the Devonian, the lower jaw elements meet at a sutured or even fused symphysis, and in the fossils, the lower jaws are usually found as a unit. These have been assumed to be the model for interpreting all lungfish taxa. However, it has been noted (Clack *et al.* 2018) that some Devonian forms must have had a form of kinetic mechanism that allowed the tooth plates to

function effectively, with essentially horizontal or concave tooth plates on the pterygoid and convex tooth plates on the prearticular. Such an arrangement is found in the Carboniferous genus *Ctenodus* (Sharp & Clack 2013), and in the complete dentition of a specimen from the Late Devonian of Nunavut NUFV 794 (Clack *et al.* 2018). However, in the latter, the mechanics of the jaw action must have been somewhat different from that in *Sagenodus*, because in the Nunavut specimen, rather than being concave, the pterygoid plate was flat whereas the prearticular plate was strongly convex. A complete set of tooth plates from a single individual exists, and could be used for the basis of a biomechanical study in that taxon. Unfortunately, the specimens of *S. quiquecostatus* do not at present include sufficient data to test our ideas. Although all four plates are in position in the holotype specimen, they are not readily rendered from the micro-CT scan data.

Alongside this observation goes another – that often among both Late Devonian and Carboniferous lungfish, the quadrates and articulars are usually not fossilised – and presumed quadrates described by Watson & Gill (1923) were correctly identified as ceratohyals by Williston (1899). Presumably because they were unfossilised, quadrates and articulars are not otherwise described in Carboniferous taxa, although there are no comments to the effect that they are missing that we have been able to find in the literature. The two lower jaw rami are often found separately, or only a single ramus is visible. Examples include the Late Devonian *Celsiodon* and new taxa D and H (Clack *et al.* 2018), the mid-Pennsylvanian *Conchopoma* (Schultze 1975; Marshall 1988), the mid-Pennsylvanian *Paleophichthys* (Schultze 1994), and the Triassic *Ptychoceratodus* (Schultze 1981). We assume that had the symphysis been strongly sutured or even fused, the structure would have been maintained, and the preservation is likely to have shown that. The symphyseal region often appears 'unfinished', connected only by cartilage. It is during the Late Devonian and Carboniferous periods that lungfishes appear to have progressively lost the ossification of the neurocranium and postcranial skeleton (Bemis 1984). This process could have allowed experimentation with parts of the endoskeleton associated with feeding.

To support the contention that 'some Carboniferous lungfishes did things differently' from modern or other fossil representatives, we also note that some Carboniferous taxa including *Clackodus* (Smithson *et al.* 2019) appear to have produced their tooth plates by a somewhat different developmental mechanism from that seen in *Neoceratodus* or *Andreyevichthys*. The latter genera had only a single pioneer tooth to produce their cusps, whereas *Clackodus* and others appear to have had two.

The possibility of kinesis in Palaeozoic lungfishes warrants further study. Our finding supports the idea that not all Palaeozoic lungfishes can be interpreted in respect of the feeding mechanism in terms of a modern analogue. More broadly, it calls into question the universal applicability of the 'Extant Phylogenetic Bracket' principle (Witmer 1995).

6. Acknowledgements

We thank the following curatorial staff for their assistance with access to specimens: in the UK, Paul Shepherd, British Geological Survey, Keyworth; Rebecca Smith, Manchester Museum; Bobbie Paton, Mike Taylor, and Stig Walsh, National Museums Scotland; Steve McLean, Sylvia Humphrey, Great Northern Museum Hancock Museum; Per Ahlberg, Sally Young, Martha Richter, Sandra Chapman, and Emma Bernard, Natural History Museum London; Dan Pemberton, Mathew Lowe, Rod Long, and Mike Dorling, Sedgwick Museum,

Cambridge; and Matt Lowe, University Museum of Zoology, Cambridge (formerly of the Sedgwick Museum, Department of Earth Sciences, University of Cambridge). Outside of the UK, the following curators and collections managers facilitate study of specimens in their care: Bill Simpson and Matt Friedman, Field Museum, Chicago, Illinois; John Chorn and Desui Miao, Natural History Museum, and Hans-Peter Schultze, Kansas University Museum, Lawrence, Kansas; Amy Henrici, Dave Berman, and Norm Wuerthele, Carnegie Museum, Pittsburgh, Ohio. We thank Keturah Smithson for micro-CT scanning at the Cambridge Biotomography Centre. Sarah Wallace-Johnson (formerly Finney), Head Conservator in the Department of Earth Sciences, University of Cambridge, provided and oversaw the use of airbrasive equipment. We also thank Dr Tom Challands, an anonymous referee, and Dr Stig Walsh for helpful comments to improve the paper, and for careful editing of the text.

7. References

- Ahlberg, P. E. 1991. A re-examination of sarcopterygian interrelationships, with special reference to the porolepiformes. *Zoological Journal of the Linnean Society* **103**, 241–87.
- Andrews, S. M. & Carroll, R. L. 1991. The Order Adelospondyli: Carboniferous lepospondyl amphibians. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **82**, 239–75.
- Atthey, T. 1868. Notes on the various species of *Ctenodus* obtained from the shales of the Northumberland coal field. *Annals and Magazine of Natural History 4th Series* **1**, 77–87.
- Barkas, T. P. 1869. Notes on some curious dentition of Coal-Measure fishes. *Scientific Opinion* **2**, 479–80.
- Barkas, T. P. 1870. *Ctenodus obtusus* (n. sp.). *English Mechanics and World Science* **12**, 160.
- Barkas, T. P. 1873a. Illustrated guide to the fish, amphibian, reptilian, and supposed mammalian remains of the Northumberland Carboniferous strata. London: W. M. Hutchings. 117 pp.
- Barkas, T. P. 1873b. Remains of *Ctenodus*. *English Mechanics and World Science* **18**, 68.
- Barkas, W. J. 1874. On the microscopical structure of fossil teeth from the Northumberland true coal measures. *Monthly Review of Dental Surgery* **2**, 533–39.
- Barkas, W. J. 1877. On the genus *Ctenodus*. *Journal of the Proceedings of the Royal Society of New South Wales* **10**, 99–110.
- Bemis, W. E. 1984. Paedomorphosis and the evolution of the Dipnoi. *Paleobiology* **10**, 293–307.
- Berman, D. S. 1976. Occurrence of *Gnathorhiza* (osteichthyes: Dipnoi) in aestivation burrows in the lower Permian of New Mexico with description of a new species. *Journal of Paleontology* **50**, 1034–39.
- Carpenter, K. K., Falcon-Lang, H. J., Benton, M. J. & Henderson, E. 2014. Carboniferous (Tournaisian) fish assemblages from the Isle of Bute, Scotland: systematics and palaeoecology. *Palaeontology* **57**, 1215–40.
- Challands, T. J., Smithson, T. R., Clack, J. A., Bennett, C. E., Marshall, J. E. A., Wallace-Johnson S. M. & Hill, H. 2019. Lungfish survivor of the end-Devonian extinction and an early Carboniferous dipnoan radiation. *Journal of Systematic Palaeontology* **17**, 1825–46. doi: 10.1080/14772019.2019.1572234.
- Chorn, J. & Schultze, H. P. 1989. A complete specimen of *Sagenodus* (Dipnoi) from the Upper Pennsylvanian of the Hamilton Quarry, Kansas. In Mapes, G. & Mapes, R. H. (eds) *Regional geology and palaeontology of Upper Paleozoic Hamilton quarry area in south-eastern Kansas*. Kansas Geological Survey Guidebook, Series 6.
- Clack, J. A., Challands, T. J., Smithson, T. R. & Smithson, K. Z. 2018. Newly recognized Famennian lungfishes from east Greenland reveal tooth plate diversity and blur the Devonian-Carboniferous boundary. *Papers in Palaeontology* **5**, 261–75.
- Clack, J. A., Bennett, C. E., Davies, S. J., Scott, A. C., Sherwin, J. & Smithson, T. R. 2019. A Tournaisian (earliest Carboniferous) conglomerate-preserved non-marine faunal assemblage and its environmental and sedimentological context. *PeerJ* **1**, article 1. doi: 10.7717/peerj.5972.
- Cloutier, R. 1996. Dipnoi (Akinetia: Sarcopterygii). In Schultze, H.-P. & Cloutier, R. (eds) *Devonian fishes and plants of Miguasha, Quebec, Canada*, 198–226. München: Verlag Dr Friedrich Pfeil.
- Coates, M. I., Tietjen, K., Olsen, A. M. & Finarelli, J. A. 2019. High-performance suction feeding in an early elasmobranch. *Science Advances* **5**, eaax2742.
- Cope, E. D. 1874. Description of a species of *Ctenodus*. *Proceedings of the Academy of Natural Sciences of Philadelphia* **1874**, 91–92.
- Forster-Cooper, C. 1937. The Middle Devonian fish fauna of Achanarras. *Transactions of the Royal Society of Edinburgh-Earth Sciences* **59**, 223–39.
- Frič, A. 1874. Ueber die entdeckung eines lurchfisches: *Ceratodus barandei* in der Gaskohle des Rakonitzer Beckens. *Sitzungsberichte der Königl. Böhmischen Gesellschaft der Wissenschaften (in Prag)* **1874**, 193–95.
- Fritsch, A. 1879. *Fauna der Gaskohle und der Kalksteine der Permformation Bohems*. Band 1. Prague: Selbstverlag. pp. 1–92.
- Fritsch, A. 1885–1889. *Fauna der Gaskohle und der Kalksteine der Permformation Bohems*, 2. *Stegocephali (Schluß), Dipnoi, Selachii (Anfang)*. Prague: Selbstverlag. pp. 1–114.
- Gosline, W. A. 1987. Jaw structures and movements in higher teleostean fishes. *Japanese Journal of Ichthyology* **34**, 21–32.
- Hancock, A. & Atthey, T. 1868. Notes on the remains of some reptiles and fishes from the shales of the Northumberland coal field. *Transactions of the Natural History Society of Northumberland and Durham* **3**, 66–120.
- Hancock, A. & Atthey, T. 1872. A few remarks on *Dipterus* and *Ctenodus*, and on their relationship to *Ceratodus forsteri*, Krefft. *Transactions of the Natural History Society of Northumberland and Durham* **4**, 397–407.
- Henrichsen, I. G. C. 1972. A catalogue of fossil vertebrates in the Royal Scottish Museum, Edinburgh. *Geology* **3**, 1–26.
- Hussakof, L. 1911. The Permian fishes of North America. *Carnegie Institution of Washington Publications* **146**, 155–75.
- Huttenlocker, A. K., Henrici, A., Nelson, W. J., Elrick, S., Berman, D. S., Schlotterbeck, T. & Sumida, S. S. 2018. A multitaxic bone bed near the Carboniferous Permian boundary (Halgaito Formation, Cutler Group) in Valley of the Gods, Utah, USA: vertebrate paleontology and taphonomy. *Palaeogeography, Palaeoclimatology, Palaeoecology* **499**, 72–92.
- Huxley, T. H. 1880. On the applications of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* **1880**, 649–62.
- Jaekel, O. 1911. *Die wirbeltiere*. Berlin: Börntrager. 252 pp.
- Jarvik, E. 1967. On the structure of the lower jaw in dipnoans: with a description of an early Devonian dipnoan from Canada *Melanchnathus canadensis* gen. et sp. nov. *Journal of the Linnean Society (London)* **47**, 155–83.
- Jarvik, E. 1980. Basic structure and evolution of the vertebrates. Volume 1. London, New York, Toronto, Sydney, San Francisco: Academic Press. 575 pp.
- Kemp, A. 1977. The pattern of tooth plate formation in the Australian lungfish *Neoceratodus forsteri* Krefft. *Zoological Journal of the Linnean Society* **60**, 223–58.
- Kemp, A., Cavin, L. & Guinot, G. 2017. Evolutionary history of lungfishes with a new phylogeny of post-Devonian genera. *Palaeogeography, Palaeoclimatology, Palaeoecology* **471**, 209–19.
- Lloyd, G. T., Wang, S. C. & Brusatte, S. L. 2011. Identifying heterogeneity in rates of morphological evolution, discrete character change in the evolution of lungfish (Sarcopterygii; Dipnoi). *Evolution* **66**, 330–48.
- Lund, R. 1970. Fossil fishes from southwestern Pennsylvania. Part I, fishes from the Duquesne Limestone (Conemaugh, Pennsylvanian). *Annals of Carnegie Museum* **41**, 231–61.
- Marshall, C. R. 1988. A large, well preserved specimen on the Middle Pennsylvanian lungfish *Conchopoma edesi* (osteichthyes: Dipnoi) from Mazon Creek, Illinois, USA. *Journal of Vertebrate Paleontology* **8**, 383–94.
- McCahon, T. J. & Miller, K. B. 2015. Environmental significance of lungfish burrows (*Gnathorhiza*) within lower Permian (Wolfcampian) paleosols of the US midcontinent. *Palaeogeography, Palaeoclimatology, Palaeoecology* **425**, 1–12.
- Miall, L. C. 1880. On some bones of *Ctenodus*. *Proceedings of the Yorkshire Philosophical Society* **7**, 289–99.
- Miles, R. S. 1977. Dipnoan (Lungfish) skulls and relationships of the group – a study based on new species from the Devonian of Australia. *Zoological Journal of the Linnean Society* **61**, 1–328.
- Müller, J. 1845. Über den Bau und die Grenzen der Ganoiden, and über das natürliche System der Fische. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin* **1844**, 117–216.
- Newberry, J. S. 1875. Descriptions of fossil fishes. *Report of the Geological Survey of Ohio* **2**, 1–64.
- Owen, R. 1867. On the dental characters of genera and species, chiefly of the fishes from the lower main seam and shales of coal, Northumberland. *Transactions of the Odontological Society of Great Britain* **5**, 323–75.
- Panchen, A. L. 1970. In Kuhn, O. (ed.) *Handbuch der Paläoherpetologie, part 5a (Anthracosauria)*. Stuttgart: Gustave Fischer Verlag.

- Pardo, J. D., Huttenlocker, A. K. & Small, B. J. 2014. An exceptionally preserved transitional lungfish from the Lower Permian of Nebraska, USA, and the origin of modern lungfishes. *PLoS ONE* **9**. e108542. doi:10.1371/journal.pone.0108542.
- Romer, A. S. 1945. The Late Carboniferous vertebrate fauna of Kounova (Bohemia) compared with that of the Texas Redbeds. *American Journal of Science* **243**, 417–42.
- Romer, A. S. 1955. Herpetichthyes, Amphibioidei, Choanichthyes or Sarcopterygii? *Nature* **176**, 126.
- Rosen, D. E., Forey, P. L., Gardiner, B. G. & Paterson, C. 1981. Lungfishes, tetrapods, paleontology, and plesiomorphy. *Bulletin of the American Museum of Natural History* **167**, 159–276.
- Schultze, H.-P. 1975. Die Lungenfisch-Gattung *Conchopoma* (pisces, Dipnoi). *Senckenbergiana lethaea* **56**, 191–231.
- Schultze, H.-P. 1981. Das Schädeldach eines ceratodontident Lungenfisches aus der Trias Süddeutschlands (Dipnoi, Pisces). *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* **70**, 1–31.
- Schultze, H.-P. 1992. Fossilium catalogus, Dipnoi. Amsterdam: Kugler Publications. 464 pp.
- Schultze, H.-P. 1994. *Palaeophichthys parvulus* Eastman, 1908, a gnathorhizid dipnoan from the Middle Pennsylvanian of Illinois, USA. *Annals of the Carnegie Museum* **63**, 105–13.
- Schultze, H.-P. & Campbell, K. S. W. 1986. Characterization of the Dipnoi, a monophyletic group. *Journal of Morphology Supp.* **1**, 25–37.
- Schultze, H.-P. & Chorn, J. 1997. The Permo-Carboniferous genus *Sagenodus* and the beginning of modern lungfish. *Contributions to Zoology* **67**, 9–70.
- Sharp, E. L. & Clack, J. A. 2012. Redescription of the lungfish *Straitonia waterstoni* from the Viséan of Lothian, Scotland. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **102**, 179–89.
- Sharp, E. L. & Clack, J. A. 2013. A review of the Carboniferous lungfish genus *Ctenodus* Agassiz, 1838 from the United Kingdom, with new data from an articulated specimen of *Ctenodus interruptus* Barkas, 1869. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **104**, 169–204.
- Small, B., Pardo, J. & Huttenlocker, A. K. 2006. Taxonomic diversity of estivating species in the lowest Permian of North America: onset of seasonality and comments on physiological plasticity. *Journal of Vertebrate Paleontology* **26**(Suppl. to part 3), 126A.
- Smith, M. M., Smithson, T. R. & Campbell, K. S. W. 1987. The relationships of *Uronemus*: a Carboniferous dipnoan with highly modified tooth plates. *Philosophical Transactions of the Royal Society, London B* **317**, 299–327.
- Smithson, T. R. 1985. Scottish Carboniferous amphibian localities. *Scottish Journal of Geology* **21**, 123–42.
- Smithson, T. R., Richards, K. R. & Clack, J. A. 2015. Lungfish diversity in Romer's Gap: reaction to the end-Devonian extinction. *Palaeontology* **59**, 29–44.
- Smithson, T. R., Challands, T. J. & Smithson, K. Z. 2019. Traquair's lungfish from Loanhead: dipnoan diversity and tooth plate growth in the late Mississippian. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **109**, 49–59.
- Traquair, R. H. 1878. On the genera *Dipterus*, *Palaeodaphus*, *Holodus* and *Cheirodus*. *Annals and Magazine of Natural History* **5**, 1–17.
- Traquair, R. H. 1881. Notice of new fish remains from the Blackband Ironstone of Borough Lee, near Edinburgh. *Geological Magazine* **8**, 34–37.
- Traquair, R. H. 1883. Notice of new fish remains from the Blackband Ironstone of Borough Lee, near Edinburgh. No. IV. *Geological Magazine* **10**, 542–44.
- Traquair, R. H. 1890. List of the fossil Dipnoi and Ganoidei of Fife and the Lothians. *Proceedings of the Royal Society of Edinburgh* **17**, 385–400.
- Traquair, R. H. 1903. On the distribution of fossil fish-remains in the Carboniferous rocks of the Edinburgh district. *Transactions of the Royal Society of Edinburgh* **40**, 687–707.
- Watson, D. M. S. & Gill, E. L. 1923. The structure of certain Palaeozoic Dipnoi. *Journal of the Linnean Society of London, Zoology* **35**, 163–216.
- Westoll, T. S. 1949. On the evolution of the Dipnoi. In Jepsen, G. L., Mayr, E. & Simpson, G. G. (eds) *Genetics, paleontology, and evolution*, 121–84. Princeton: Princeton University Press.
- Williston, S. W. 1899. A new species of *Sagenodus* from the Kansas coal measures. *Kansas University Quarterly* **8**, 175–81.
- Witmer, L. M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In Thomason, J. J. (ed.) *Functional morphology in vertebrate paleontology*, 9–33. New York: Cambridge University Press.
- Woodward, A. 1891. *Catalogue of the fossil fishes in the British museum part II*. London: British Museum of Natural History. 576 pp.

MS received 14 June 2019. Accepted for publication 17 October 2019