The Permo-Carboniferous genus *Sagenodus* and the beginning of modern lungfish

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Abstract

The lungfish *Sagenodus* is a widespread Permo-Carboniferous genus found in Europe and North America. Important localities in the U.S.A. include Middle Pennsylvanian coals near Linton, Ohio, Upper Pennsylvanian deposits near Robinson and Hamilton, Kansas, and Peoria, Illinois; Lower Permian sediments near Cameron, Ohio; and Lower Permian "Red Beds" of Texas and Oklahoma. At least three species of *Sagenodus* were present in North America (*S. copeanus, S. periprion, S. serratus*). *S. ohiensis* is represented solely by one skull.

Knowledge of the osteology of *Sagenodus* is enhanced by the study of well-preserved but disassociated elements from Robinson, Kansas (*S. copeanus*) and Little Bitter Creek, Texas (*S. serratus*). The orbital series is now known to be comprised of six elements and the sensory canal system is more complex than previously realized. The only known articulated skeleton of this genus, from Hamilton Quarry, Kansas, permits a restoration of the entire animal including the median fins. The dorsal and anal fins are not separate; there is instead, a continuous fin around the caudal end of the body, as found in other post-Devonian lungfishes.

Sagenodus is structurally intermediate between more primitive Devonian dipnoans and post-Paleozoic lungfishes. Evident trends can be seen in the reduction of bone (both number of bones and degree of ossification), the loss of cosmine, the nature of the scales, the structure and histology of tooth plates, and the configuration of the median fins. *Sagenodus* is a member of a euryhaline faunal assemblage that can be found from shallow marine to freshwater deposits.

Zusammenfassung

Der Lungenfisch *Sagenodus* ist im Permokarbon Europas und Nordamerikas weit verbreitet. Die mittelpennsylvanischen Kohlen bei Linton, Ohio, die oberpennsylvanischen Ablagerungen bei Robinson und Hamilton, Kansas, und Peoria, Illinois, die unterpermischen Sedimente bei Cameron, Ohio, und die unterpermischen "Red Beds" von Texas und Oklahoma sind die wichtigsten Fundstellen in den U.S.A. Drei *Sagenodus*-Arten treten in Nordamerika häufig auf (*S. copeanus, S. periprion* und *S. serratus*). *S. ohiensis* ist nur von einem einzigen Schädeldach bekannt.

Die Kenntnis der Osteologie von *Sagenodus* wird durch die Beschreibung der vorzüglich erhaltenen, aber isolierten Einzelelemente von Robinson, Kansas (*S. copeanus*) und von Little Bitter Creek, Texas (*S. serratus*) erweitert. Besonders zu erwähnen sind die Umrahmung der Orbita mit sechs Knochen und das Sinneskanalsystem der Kopfknochen, das komplexer als bisher angenommen ist. Das einzige bekannte artikulierte Exemplar der Gattung von Hamilton Quarry, Kansas, ermöglicht die Rekonstruktion des Gesamttieres einschliesslich der unpaaren Flossen. Dorsal- und Analflosse sind keine eigenständige Flossen, sondern sie bilden mit der Schwanzflosse einen einheitlichen Flossensaum um das Hinterende des Körpers wie in anderen postdevonischen Lungenfischen.

Sagenodus vermittelt in seiner Morphologie zwischen den primitiven devonischen und den fortschrittlichen postpaläozoischen Lungenfischen. Deutliche Entwicklungstendenzen auf moderne Lungenfische hin sind evident in der Knochenreduktion, was sowohl die Anzahl an Knochen als auch den Grad der Verknöcherung betrifft, im Verlust von Kosmin, in der Ausbildung der Schuppen, in der Struktur und Histologie der Zahnplatten und in der Gestaltung der unpaaren Flossen. *Sagenodus* gehört der euryhalinen Fauna an, die man in flachmeerischen bis Süsswasser-Ablagerungen des Permokarbons findet.

Introduction

The study of Recent and fossil lungfish provides an important data base for paleobiological and evolutionary studies. Lungfish are the primary example for a shift from a rapid to a slow rate of evolutionary change in vertebrates. They are, along with the actinistian *Latimeria*, the closest living relatives of the rhipidistians that gave rise to tetrapods. Our knowledge of fossil dipnoans largely focused on their superb Devonian record. This study of *Sagenodus* in North America attempts to redress this imbalance utilizing significant new material, the restudy of old specimens, as well as previous studies.

Sagenodus is a Permo-Carboniferous lungfish genus known from Europe and North America.

Owen (1867) erected the genus on histological features of Carboniferous tooth plates characterized by a low number of ridges. These tooth plates were originally assigned to *Ctenodus* by Agassiz, 1838, a genus with vaulted tooth plates and numerous ridges. The distinct nature of these two genera was not immediately recognized, and many *Sagenodus* species were still described as *Ctenodus* species (Atthey, 1868; T.P. Barkas, 1869; W.J. Barkas, 1877; Newberry, 1874; Cope, 1874, 1878) or as *Ceratodus* species (Cope, 1877; Fritsch, 1888). Woodward (1891) distinguished between tooth plates of *Ctenodus* with 12 or more roughly parallel ridges, and those of *Sagenodus* with fewer ridges, mostly 6 to 7 in radial arrangement. He synonymized with *Sagenodus* the genera *Petalodopsis* Barkas, 1874, *Ptyonodus* Cope, 1877, *Megapleuron* Gaudry, 1881, and *Hemictenodus* Jaekel, 1890 (partim) (full synonymy in Schultze, 1992: 203–211). *Megapleuron*, poorly known at the time, was reestablished by Schultze (1977). Woodward (1891) united many European species under *Sagenodus inaequalis* (*Ctenodus elegans, C. obliquus, C. imbricatus, C. ellipticus* Atthey, 1868, *Ctenodus monoceras* Barkas, 1869, *Ctenodus quadratus* Barkas, 1873, *Ceratodus barrandei* Fritsch, 1874, and *Petalodopsis mirabilis* Barkas, 1874). Since Waterston (1954) *Sagenodus quinquecostatus* Traquair, 1883, has also been included in *S. inaequalis* (full synonymy in Schultze, 1992: 212–216). A well-illustrated description of the genus was presented by Watson & Gill (1923). In North America Cope described many species of *Ceratodus* and *Ctenodus* (*Ceratodus vinslovii* Cope, 1875, *Ctenodus fossatus* and *C. gurleyanus* Cope, 1878, *Ctenodus heterolophus* and *C. vabasensis* Cope, 1883) that were placed in the genus *Sagenodus* by Woodward (1891). They were synonymized by Hussakof (1911) and placed with *S. serratus* by Romer & Smith (1934) (for full synonymy see Schultze, 1992: 222–224). Cope erected more species (*Ctenodus ohiensis* Cope, 1874, *Ceratodus paucicristatus* Cope, 1877, *Ctenodus dialophus, C. periprion,* and *C. porrectus* Cope, 1878) that hitherto have not been synonymized with *S. serratus*. The same is the case with *Sagenodus copeanus* Williston, 1899 and *Sagenodus ciscoensis* Romer & Smith, 1934. *Conchodus plicatus* Dawson, 1868, was placed into the genus *Ctenodus* by Woodward (1891) and into *Sageno-*

dus by Sternberg (1941); Baird (1978) agreed on the latter placement though we believe the specimen is too fragmentary for proper identification. It may be close to *S. periprion* (cf. Sternberg, 1941) or be a *Ctenodus* (cf. Woodward, 1891). Baird (1978) was correct to dismiss it as a nomen vanum. These are species based on tooth plates and, in the cases of *S. ohiensis* and *copeanus*, cranial remains; such material permits adequate comparisons with other species. We will not deal here with species based on scales because we do not believe that scales show features on which species can be satisfactorily distinguished.

We will describe Upper Pennsylvanian material of *S. copeanus* Williston, 1899 from the type locality, and *Sagenodus* material from a new Upper Pennsylvanian locality at Hamilton, Kansas. There will follow a comparison with Middle and Upper Pennsylvanian *Sagenodus* material from Linton and Cameron, Ohio, and Peoria, Illinois, before we extend the comparison to *Sagenodus* from Texas. Our goal is to describe features that can be used to diagnose North American species of *Sagenodus* and to determine the phylogenetic relationship of this genus to other dipnoan genera.

Materials and methods

The study is based on material listed in Appendix 1. The material of *Sagenodus copeanus* originates from the Upper Pennsylvanian of Kansas, that of *S. ohiensis* from the Middle Pennsylvanian of Ohio, that of *S. periprion* from the Lower Permian of Texas and Ohio, and that of *S. serratus* from the Middle Pennsylvanian of Ohio and the Lower Permian of Ohio, Oklahoma, and Texas. For comparison, material of *S. inaequalis* from the Upper Carboniferous of Czechia and England was studied.

The bones of *Sagenodus copeanus* occur in association with stromatolites (Chorn & Conley, 1978; Conley & Chorn, 1979; Sawin et al., 1985). The original description (Williston, 1899) was based on material recovered from stromatolites and surrounding matrix that were broken with a hammer. Acetic acid preparation (Toombs, 1948) is a much more effective way to produce large numbers of bones from the calcitic stromatolites. The bones occur dissociated from one another and are resistant to attack by acetic acid. They were impregnated with Campbells Cement after being exposed by dilute acetic acid. The junior author has prepared fossils from more than a ton of stromatolites since 1974, to assemble 697 (618 catalogued) bones and tooth plates that form the basis of the present study.

The *Sagenodus* material from Hamilton Quarry was collected by Walter Lockard, beginning in the mid 1960's (scales, parasphenoid, operculum, "angular", one tooth plate) and by

Drs. Royal and Gene Mapes, Athens, Ohio (complete specimen, Chorn & Schultze, 1989, and a nearly complete skull roof during the 1989 field season). The tooth plate was prepared with acetic acid using the transfer methods of Toombs & Rixon (1950) whereas only limited mechanical preparation has been done on the complete specimen and the skull roof.

Preliminary drawings of the specimens were done by the senior author with camera lucida attachment to a Wild M5 microscope, lucigraph and after photographs. Photographs were taken by the junior author.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, New York, U.S.A.

BMNH, The Natural History Museum, London, England

CMNH, Carnegie Museum of Natural History, Pittsburg, Pennsylvania, U.S.A.

FMNH, Field Museum of Natural History, Chicago, Illinois, U.S.A.

KUVP, Natural History Museum, University of Kansas, Lawrence, Kansas, U.S.A.

MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.

NMP, National Museum, Prague, Czechia

OSU, Orton Geological Museum, Ohio State University, Columbus, Ohio, U.S.A.

Sto, Paleozoologiska sectionen, Naturhistoriska Riksmuseet, Stockholm, Sweden

TMM, Vertebrate Paleontology Laboratory, University of Texas, Austin, Texas, U.S.A.

UCLA, Vertebrate Paleontology Collection, Dept. of Biology, University of California, Los Angeles, California, U.S.A.

UM, Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, U.S.A.

USNM, United States National Museum, Washington, DC, U.S.A.

Paleoecology

Sagenodus is frequently cited as a member of a freshwater vertebrate assemblage (e.g.: Olson, 1946, 1967, 1977; Romer, 1952, 1958; Lund, 1970, 1976; Carroll et al., 1972; Simpson, 1974; Baird, 1978; Hook & Baird, 1986, 1993; Hook & Ferm, 1988; Sander, 1989) comprising xenacanth sharks, palaeoniscoids, amphibians (*Eryops*, *Trimerorhachis*, *Lysorophus*, dissorophids etc.) and amniotes (pelycosaurs, *Seymouria*, *Diadectes*, *Captorhinus*, etc.). The dipnoan *Gnathorhiza*, actinistians (*Rhabdoderma*, *Spermatodus*), rhipidistians (*Ectosteorhachis*) and platysomids are associated in some localities (Table I). Invertebrates are poorly preserved or lacking; they are also considered to be freshwater indicators.

Nevertheless, marine occurrences of *Sagenodus* or of other members of the assemblage are known since the last century. The stromatolites of the type locality of *S. copeanus* were described as sponges (Beede, 1899) "associated with *Lingula, Productus* and a few pelecypods and gastropods" and the paleoenvironment as typical marine. Nevertheless, Baird (1966) assigned the stromatolites to freshwater environments, supposedly on the basis of the occurrence of trimerorhachid amphibians. Sawin et al. (1985) clearly demonstrated a shallow-marine depositional environment for the Robinson locality. The occurrence of growth series of bones of *S. copeanus* indicates that the lungfish lived in the region of the locality. The second locality of *S. copeanus*, Hamilton, Kansas, turned out to be a marine channel fill (Maples & Schultze, 1989; Cunningham, 1993; Schultze et al., 1994) after it was first described as stream or freshwater deposits (Bridge, 1976; Kaesler, 1989). Selective collecting of vertebrates and plants and selective interpretation of vertebrates or invertebrates guided the authors to a one-sided interpretation (Schultze, 1996). Comparison of total evidence (Maples & Schultze, 1989; Schultze & Maples, 1992) shows that we are dealing with a broadly adapted fauna of a region of very low topographic relief. The members of this fauna probably were euryhaline allowing them to cope with changing salinity and invade freshwater streams and ponds. A similar wide tolerance for fresh and brackish water is known in many extant marine fishes.

The *Sagenodus* localities of Kansas are not alone in representing deposits of shallow marine origin. In the following we will deal with earlier records of marine or brackish paleoenvironments of *Sagenodus* and associated members of the fauna. A very well analyzed locality with *Sagenodus* ("*Proceratodus hlavini*") is the late Pennsylvanian Kinney Brick Quarry of central New Mexico (Zidek, 1992). These nearshore marine or estuarine deposits are quite similar in faunal composition to Hamilton and Robinson of Kansas (Schultze & Maples, 1992). The East Manitou locality (N.E. of Frederick, Oklahoma) was interpreted as being of marine origin by Olson (1967), based on the occurrence of "*Orodus*-type shark teeth." Simpson (1974), who

recorded the first *Sagenodus* tooth plate from the locality, dismissed this evidence because he favored a freshwater origin of the deposits. Nevertheless, he recorded a broader faunal spectrum with platysomids, palaeoniscoids, *Acanthodes*, and *Hybodus*, which also are known from marine deposits. At other localities, Dalquest & Kocurko (1986) (see also Berman, 1970) recorded "a mixture of marine and terrestrial vertebrate fossils" together with nautiloids. They distinguished between marine indicators (*Ctenacanthus, Janassa, Luederia*, and ?*Platysomus*) and "terrestrial" (i.e. fluviatile) forms (*Lawnia*-like palaeoniscoids; *Schaefferichthys*, ?*Spermatodus*, *Gnathorhiza*, and tetrapods). *Xenacanthus*, which they expected in "terrestrial" strata, is restricted to the marine deposits. The problem with such a division of the vertebrate fossils is their co-occurrence in many localities in the Pennsylvanian and Lower Permian (Table I; Schultze & Maples, 1992). Sampling of complete faunas of localities demonstrate the co-occurrence of most of the so-called mixed vertebrate fauna with marine invertebrates (Schultze, 1985; Murry & Johnson, 1987; Olson, 1989). *Spirorbis*, an invertebrate often occurring together with the fauna, may serve as an example for one-sided interpretation. *Spirorbis* is universally known throughout its long fossil record as a marine life form. Only the Carboniferous is an exception where *Spirorbis* is thought to have inhabited fresh water based on its occurrence in presumed freshwater deposits (Schultze, 1996). Joggins is such a presumed freshwater locality with *Sagenodus* and *Spirorbis*; closer investigation has shown that agglutinated foraminifera and trace fossils indicate marine influence in an estuarine or tidal flats paleoenvironment (Archer et al., 1995).

All North American occurrences of *Sagenodus* are close to paleoshorelines. Considering the capability of many modern marine fishes to enter freshwater streams, we expect that Paleozoic fishes were also capable of entering the freshwater environment, and in any case the tidal flats and coastal plains as reconstructed for the Permian localities of Texas (Hentz, 1989). Olson (1958) mapped what he believed was a lake in the upper Arroyo Formation of north-central Texas. This lake may have been connected to the sea

through a channel entering from the south where the paleoshoreline was located. *Xenacanthus* occurs in the channel deposits and where the channel enters the lake. Probably the xenacanth sharks entered the channel and the lake from the sea, whereas the tetrapod remains are largely confined to lake sediments. This is consistent with the marine occurrence of *Xenacanthus* in Lower Permian deposits of Kansas (Schultze, 1985). We conclude that *Sagenodus* belonged to a euryhaline faunal assemblage that occurred in shallow marine to freshwater paleoenvironments.

Toomey & Cys (1977) described a marginal marine locality from the Lower Permian of New Mexico. This site resembles the Robinson locality in that it yields fish and tetrapod remains from a field of stromatolites. They recovered *Xenacanthus*, other shark teeth, *Acanthodes*, palaeonisciforms, a rhipidistian crossopterygian (? megalichthyid) and pelycosaurs. Invertebrates at the locality include *Spirorbis* and agglutinated foraminifera. Though *Sagenodus* was not collected, the vertebrates that were present often co-occur with this lungfish. Their presence in a marginal marine setting is additional evidence that this assemblage could inhabit marine or euryhaline paleoenvironments.

That faunal assemblage (Table I: %) comprises palaeonisciforms and xenacanths besides *Sagenodus* at 70-75% of the localities. In half of the localities, *Sagenodus* is accompanied by megalichthyid rhipidistians and trimerorhachids, diplo-caulids, and pelycosaurs. That indicates that these tetrapods are water based or using the water for food supply etc. (pelycosaurs). Lysorophids may belong to the water based group too. At about one third of the localities, *Sagenodus* occurs together with *Acanthodes*, *Orthacanthus*, hybodont and other sharks, eryopids, and *Spirorbis*. Cladodont teeth, *Janassa*, *Orodus* or other sharks occur together or alone in half of the localities. These taxa are taken as marine indicators. These are localities where *Spirorbis* often occurs.

Paleoenvironment and lungs

The occurrences of lungfish in fresh water is frequently connected with first occurrence of lungs,

and *Sagenodus* is cited as an early example of that transition (Campbell & Barwick, 1988: 223).

In contrast, the wide distribution of lungs within extant osteichthyans indicates that lungs are a primitive osteichthyan feature. Lungs are present in primitive actinopterygians (e.g. *Polypterus*), actinistians, lungfish, and tetrapods. However, Campbell & Barwick (1988) discounted the ability of early lungfish to breathe air. They maintain that early lungfish were living at depths in excess of 100 meters and consequently were unable to surface periodically to breathe air (Campbell & Barwick, 1988: 222). The Late Devonian *Griphognathus*, the chief example used by Campbell & Barwick, may have lived at 100 meter depths in the depositional environment at Gogo, Australia. However, *Griphognathus* was first described from shallow marine to lagoonal deposits near Kokenhusen, Latvia (Gross, 1956) and Bergisch-Gladbach, Germany (Schultze, 1969). The Early Devonian *Dipnorhynchus* and *Speonesydrion* occur with a diverse marine fauna of benthic invertebrates (Campbell & Barwick, 1988). The invertebrate fauna does not indicate water as deep as 100 meters. In addition, the Early Devonian *Uranolophus* was found in channel deposits in a coastal marine setting. The extant *Neoceratodus* possesses both lungs and a fully functional gill apparatus. Consequently, we see no reason to infer that primitive dipnoans lacked lungs.

Campbell & Barwick (1988) and Long (1993) use the long stalk of the parasphenoid, the shape of the ceratohyal, and the presence of a cranial rib to indicate a capacity to gulp air in some Late Devonian and all post-Devonian lungfish. They link air breathing in lungfish with their paleoenvironment. All air breathing lungfish are proposed to be freshwater forms, and the ability to burrow places *Gnathorhiza* as a sister taxon to the extant estivator, *Protopterus* (Long, 1993: fig. 10). It is a tenuous approach at best to connect a supposed function with a supposed paleoenvironment. Many of the supposed freshwater lungfish are marine or occur in both marine and freshwater environments. In contrast to the opinion of the three authors, *Fleurantia* and *Scaumenacia* occur in the shallow marine to estuarine paleoenvironment of Miguasha ("Escuminac Bay", see

Table 1. North American localities (number, see Fig. 1) of *Sagenodus* and co-occurring vertebrates, *Spirorbis*, and undoubted marine invertebrates (fusulinids, bryozoans, articulate brachiopods, crinoids, echinoids, conodonts); % = percentage of localities in which each taxon is present.

Nr. of locality	Sagenodus	Conchopoma	Gnathoriza	megalichthyid	Rhabdoderma	actinistian indet.	Palaeonisciformes	Platysomus	Acanthodes	Gyracanthus	"Xenacanthus"	Orthacanthus	Ctenacanthus	Janassa	Orodus	hybodont	cladodont	other sharks	microsaurs	dissorophid	trimerorhachid	Diplocaulus	lysorophid	eryopoid	pelycosaurs	diapsid	captorhinomorph	Spirorbis	marine invertebrates
1	x		x	x			x		x		x					x	x	x	x	x	x	x			x		x		x
2	x		x	x	x		x		x		x					x					x	x			x	x	x	x	x
3	x	x					x	x	x	x	x	x		x	x	x		x	x	x	x	x	x	x				x	
4	x						x	x	x		x	x		x	x	x				x					x	x			
5	x										x										x	x	x	x					
6	x		x				x				x	x				x	x	x			x	x							
7	x	x			x		x				x								x		x				x			x	
8	x	x		x	x		x	x			x					x	x				x	x						x	
9	x		x				x	x			x										x	x	x		x				
10	x						x				x										x	x	x		x				
11	x		x				x				x	x				x		x											
12	x										x		x						x			x		x				x	
13	x	x									x			x							x	x		x				x	
14	x																												
15	x		x	x			x			x	x					x	x												
16	x		x		x		x				x	x	x	x	x	x	x	x							x				
17	x		x	x		x					x										x	x			x	x			
18	x		x				x		x			x									x							x	
19	x																												
20	x			x	x	x	x		x		x	x				x			x		x	x						x	x
%	100	15	20	45	15	20	70	20	35	10	75	35	10	15	15	35	25	35	25	15	50	45	40	30	50	5	10	35	15

Schultze, 1996 and Cloutier et al., 1996). The paleoenvironment of *Howidipterus, Barwickia, Jarvikia,* and *Soederberghia* is usually seen as fresh water. However, Schultze & Cloutier (1996) demonstrate that it is at least influenced by marine conditions. *Megapleuron* and *Conchopoma* occur in the marine Essex fauna of Illinois (Schultze, 1975, 1977; Bardack, 1979; Maples & Schultze, 1989) and in deposits widely considered to be of freshwater origin at Linton, Ohio (Hook & Baird, 1986), and in Europe (Schultze, 1993). *Sagenodus* occurs in marine deposits as shown above. In addition, note that most if not all Devonian lungfish are marine, therefore the capability to live in a marine environment may have been inherited from a Devonian ancestor, whereas structual similarities between *Sagenodus* and *Neoceratodus* tell us little about the environmental physiology of *Sagenodus*.

Finally, like *Sagenodus, Gnathorhiza* is a common taxon in the marine deposits of Robinson (Schultze & Chorn, 1989; Schultze, 1996). *Gnathorhiza* also occurs at the seaward end of the estuarine deposits at Hamilton, Kansas (Schultze et al., 1994). In the Permian of Kansas, *Gnathorhiza* occurs in burrows in nearshore deposits (Schultze, 1985). Though this occurrence could represent estivation, it probably indicates an adaptation of *Gnathorhiza* to survive what was a tidal to supratidal area. This interpretation is supported by the occurrence of *Gnathorhiza* with a marine biota in the Lower Permian channel fill deposits near Peru, Nebraska (Ossian, 1974), in the marine section of the Arroyo Formation in Texas (Olson, 1989), as well as in the Robinson and Hamilton localities in Kansas. In any case, no recent phylogenetic analysis places *Gnathorhiza* as the sister taxon of the extant lepidosirenids. In
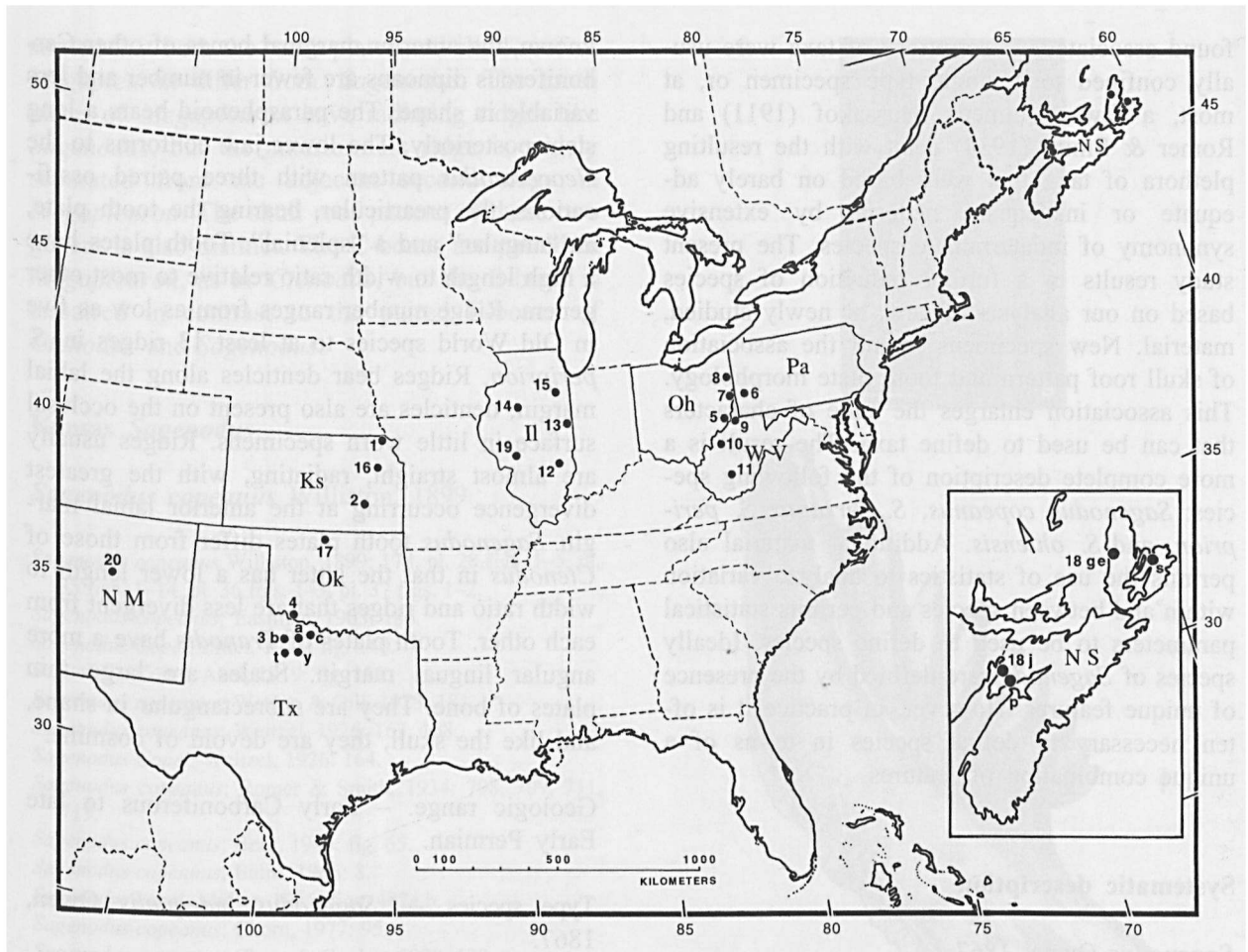
Fig. 1. North American localities of *Sagenodus*: (a) *S. copeanus*, Upper Pennsylvanian: 1, Robinson, Brown County, northeast Kansas; 2, Hamilton Quarry, Greenwood County, Kansas; (b) *S. periprion*, Lower Permian: 3, a, Archer, b, Baylor, c, Clay, t, Throckmorton, and y, Young County, Texas; 4, Tillman County, Oklahoma; 5, Cameron, Monroe County, Ohio; 6, Pittsburgh, Allegheny County, Pennsylvania; (c) *S. serratus*, Upper Pennsylvanian: 7, Linton, Jefferson County, Ohio; 8, Five Points, Mahoning County, Ohio (Hook & Baird, 1993); 11, Fayette County, West Virginia (Garton, 1978); 12, Falmouth, Jasper County, Illinois; 13, Vermilion River, Vermilion County, Illinois; 14, Peoria, Peoria County, Illinois; (d) *S. serratus*, Lower Permian: 3, Archer, Baylor, Throckmorton, and Young County, Texas; 4, Frederick, Tillman County, Oklahoma; 5, Cameron and Clark Hill, Monroe County, Ohio; 9, Marshall, Monongalia and Wetzel County, West Virginia

(Romer, 1952); 10, Wirt County, West Virginia (Romer, 1952); (e) *Sagenodus* sp.: Upper Pennsylvanian: 15, Pit 15, Kankakee County, Illinois; 16, Topeka, Shawnee County, Kansas; 17, Lower Permian; Pond Creek, Grant County, Oklahoma; 18, s, Upper Mississippian, Point Edward near Sydney, Cape Breton Island, Nova Scotia (Carroll et al., 1972: 50); ge, Namurian A, Lower Pennsylvanian; Grand Etang, Nova Scotia (Carroll et al., 1972: 42); j and p, Westphalian A, Lower Pennsylvanian; j, Joggins (Carroll et al., 1972: 74) and p, Parrsboro (Carroll et al., 1972: 64), Nova Scotia; 19, Upper Pennsylvanian; Carlinville, Illinois (*Proceratodus* of Romer & Smith, 1934); 20, Upper Pennsylvanian; Manzanita Mountains, New Mexico (*Proceratodus* of Zidek, 1975).
Il = Illinois; Ks = Kansas; NM = New Mexico; NS = Nova Scotia; Oh = Ohio; Ok = Oklahoma; Pa = Pennsylvania; Tx = Texas; WV = West Virginia.

conclusion, the possession of a lung is primitive for osteichthyans and thereby includes dipnoans. The more effective use of air breathing may have occurred in a coastal marine environment and is not an indicator of a freshwater paleoenvironment.

Determination of *Sagenodus* species

Previous systematic and taxonomic treatment of *Sagenodus* was based on descriptions of the skull and the tooth plates, both frequently of fragmentary nature. Often skull and tooth plates were not

found associated. Descriptions of taxa were usually confined to a single type specimen or, at most, a few specimens. Hussakof (1911) and Romer & Smith (1934) dealt with the resulting plethora of taxa that were based on barely adequate or inadequate material by extensive synonomy of indeterminate species. The present study results in a further reduction of species based on our analysis of new, or newly studied, material. New specimens permit the association of skull roof pattern and tooth plate morphology. This association enlarges the suite of characters that can be used to define taxa. The result is a more complete description of the following species: *Sagenodus copeanus*, *S. serratus*, *S. periprion*, and *S. ohiensis*. Additional material also permits the use of statistics to analyze variation within and between species and permits statistical parameters to be used to define species. Ideally species of *Sagenodus* are defined by the presence of unique features. However, in practice it is often necessary to define species in terms of a unique combination of features.

Systematic description

Sagenodus Owen, 1867

Synonyms. – *Ctenodus* Agassiz, 1838 (partim), *Petalodopsis* Barkas, 1874, *Ptyonodus* Cope, 1877, *Hemictenodus* Jaekel, 1890 (partim), *Proceratodus* Romer & Smith, 1934.

Emended diagnosis (see Hussakof, 1911). – Tooth-plated lungfish attaining a length of more than one meter. General body form similar to *Neoceratodus*, elongate with a diphycercal tail. Skull roof comprised of a massive B-bone, an unpaired C-bone, and paired E-bones in the medial series. Lateral to these lie paired elements – large I-bones, J, LM, and small N- and P-elements. Paired Z, Y, KX, and a circumorbital series of six paired bones form the lateral skull margin. The five-sided C-bone tapers posteriorly; it narrows to a point between the E-bones anteriorly. Shape of C and C's contact with other elements is distinctive for the genus. The snout is unossified and is bordered posteriorly by a series of small, polygonal marginal elements. Where

known, the anterior marginal bones of other Carboniferous dipnoans are fewer in number and less variable in shape. The parasphenoid bears a long stem posteriorly. The lower jaw conforms to the *Neoceratodus* pattern with three paired ossifications, the prearticular, bearing the tooth plate, an "angular" and a "splenial". Tooth plates have a high length to width ratio relative to most other genera. Ridge number ranges from as low as five in Old World species to at least 13 ridges in *S. periprion*. Ridges bear denticles along the labial margin; denticles are also present on the occlusal surface in little worn specimens. Ridges usually are almost straight, radiating, with the greatest divergence occurring at the anterior labial margin. *Sagenodus* tooth plates differ from those of *Ctenodus* in that the latter has a lower length to width ratio and ridges that are less divergent from each other. Tooth plates of *Tranodis* have a more angular lingual margin. Scales are large thin plates of bone. They are subrectangular in shape, and like the skull, they are devoid of cosmine.

Geologic range. – Early Carboniferous to late Early Permian.

Type species. – *Sagenodus inaequalis* Owen, 1867.

Comparison. – The tooth plates of *Ctenodus* have a high number of ridges (12 or more). Woodward (1891) used this to distinguish this genus from *Sagenodus* which was then thought to have a low number of ridges on the tooth plates. We now include tooth plates with high ridge counts comparable with *Ctenodus cristatus* and *C. interruptus* in the genus *Sagenodus*. The principle difference between the tooth plates of these two genera lies in the arrangement of the ridges. *Ctenodus* has roughly parallel ridges, whereas they are radially arranged in *Sagenodus*. The tooth plates may be more strongly arched in *Ctenodus*. Both genera are easily distinguished using the pattern of the skull roof. *Ctenodus* has paired C-bones, whereas *Sagenodus* has an unpaired median C-bone.

Woodward (1891) and most authors up to Heyler (1969) synonymized *Megapleuron* Gaudry, 1881, with *Sagenodus*. Schultze (1977) demon-

strated that both the tooth plates and skull roof of *Megapleuron* differ from *Sagenodus*. The tooth plates of *Megapleuron* have radiating ridges like *Sagenodus*, but the anteriormost ridge is widely separated from the adjacent second ridge in *Megapleuron*. The skull roof pattern of these two genera is also distinct. The C-bones are paired in *Megapleuron*, as in *Ctenodus*, but the E-bone is unpaired in contrast to the paired E-bones of *Ctenodus* and *Sagenodus*.

Kansas *Sagenodus*

Sagenodus copeanus Williston, 1899

Sagenodus copeanus Williston, 1899: 178, pl. 28 figs. 1–5, pl. 35 figs. 1–14, pl. 36 figs. 1–3, pl. 37 figs. 1–2.
Sagenodus copeanus; Eastman, 1903: 186.
Sagenodus Copei; Zittel, 1918: fig. 140.
Sagenodus Copei; Abel, 1919: fig. 139.
Sagenodus copeanus; Watson & Gill, 1923: 181.
Sagenodus copeanus; Weitzel, 1926: 163, 168.
Sagenodus Copei; Weitzel, 1926: 164.
Sagenodus copeanus; Romer & Smith, 1934: 708, 709, 711, 719.
Sagenodus copeanus; Berg, 1940: fig. 65.
Sagenodus copeanus; Baird, 1966: 8.
Sagenodus copei; Müller, 1965: figs. 482a,b.
Sagenodus copeanus; Chorn, 1977: 95.
Sagenodus copeanus; Chorn & Conley, 1978: 139.
Sagenodus copeanus; Schultze et al., 1982: 48.
Sagenodus; cover page of Geotimes, 33(7), July 1988.
Sagenodus copeanus; Foreman & Martin, 1989: 133, 139.
Sagenodus cf. *copeanus;* Foreman & Martin, 1989: 138.
Sagenodus cf. *copeanus;* Schultze & Chorn, 1989: table 1.
Sagenodus copeanus; Schultze & Chorn, 1989: table 1.
Sagenodus copeanus; Chorn & Schultze, 1989: 173, 174.
Sagenodus sp.; Chorn & Schultze, 1989: fig. 1, 2.
Sagenodus copeanus; Chorn & Schultze, 1990: 22, table 2, fig. 6.
Sagenodus copeanus; Schultze, 1992: 218.
Sagenodus; Cunningham, 1993: table 1.
Sagenodus copeanus; Schultze, 1993: fig. 2.

Diagnosis. – Number of ridges on upper tooth plate 8-12 with 9 ridges being most common; 8-10 ridges on lower tooth plate with 8 or 9 ridges most common; high length/width ratio (4.6 for lower tooth plate, 3.8 for upper tooth plate); blunt posterior margin of lower tooth plate; narrow symphysis in long distance from tooth plate. Low angle between median and posteromedial border of bone E (120–130°) and between parasagittal
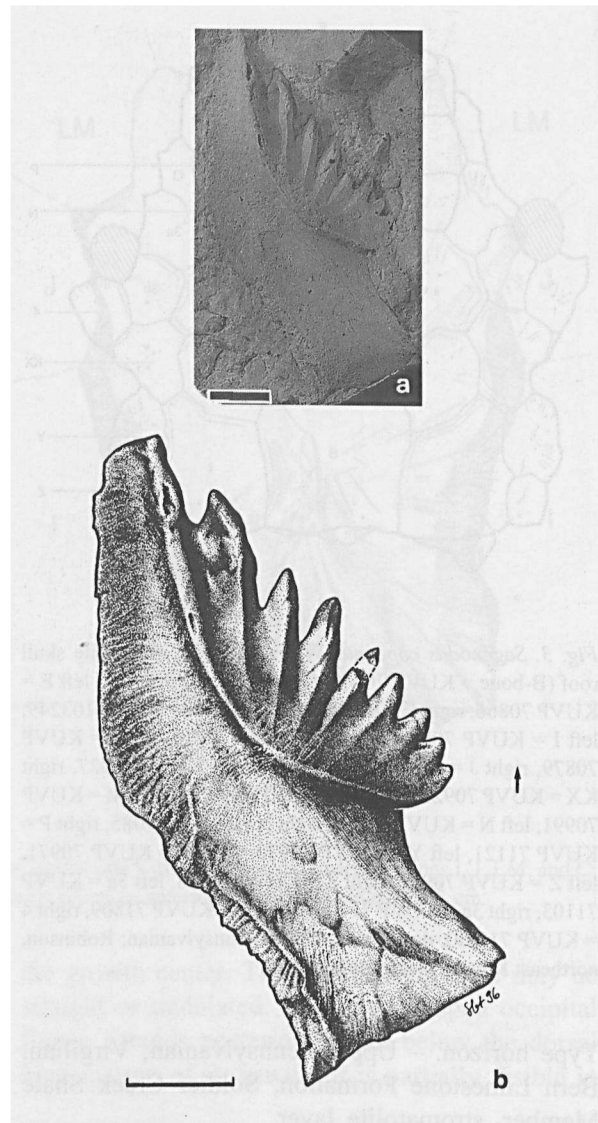

Fig. 2. Sagenodus copeanus Williston, 1899, left pterygoid with tooth plate = lectotype KUVP 55349a, cast of natural mold, palatal side: a, photo (dusted with NH₄Cl); b, drawing. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

ridges on ventral side of bone B (20–30°) compared to other species.

Lectotype. – KUVP 55349a and 55349b (Fig. 2; Williston, 1899: pl. 28 fig. 2), left pterygoid with tooth plate, from type series of Williston (1899).

Referred material. – See Appendix 2A.

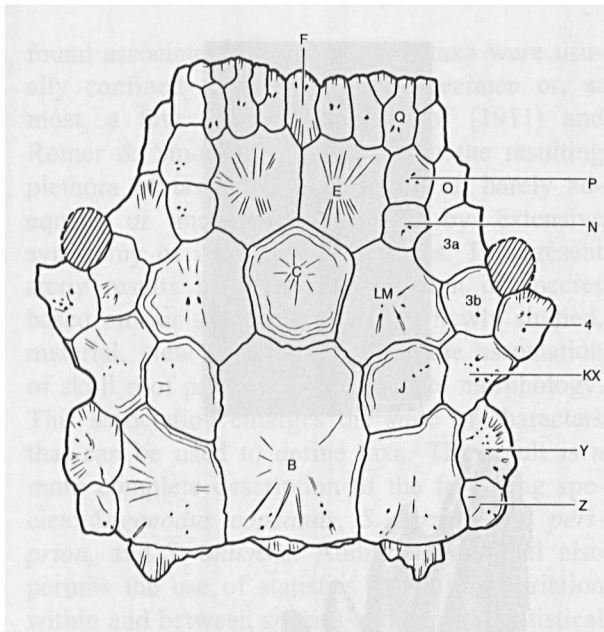Type locality. – Robinson, Brown County, northeast Kansas, U.S.A. (Fig. 1: 1).

Fig. 3. Sagenodus copeanus Williston, 1899, composite skull roof (B-bone = KUVP 70760, C-bone = KUVP 70779, left E = KUVP 70866, right E = KUVP 70867, F-bone = KUVP 103249, left I = KUVP 70899, right I = KUVP 70912, left J = KUVP 70879, right J = KUVP 70880, left KX = KUVP 70927, right KX = KUVP 70926, left LM = KUVP 70990, right LM = KUVP 70991, left N = KUVP 71086, right N = KUVP 71085, right P = KUVP 71121, left Y = KUVP 70970, right Y = KUVP 70971, left Z = KUVP 70947, right Z = KUVP 70948, left 3a = KUVP 71103, right 3a = KUVP 71105, right 3b = KUVP 71809, right 4 = KUVP 71099), dorsal side. Upper Pennsylvanian; Robinson, northeast Kansas. Scale equals 1 cm.

Type horizon. – Upper Pennsylvanian, Virgilian, Bern Limestone Formation, Soldier Creek Shale Member, stromatolite layer.

Sagenodus from Robinson

Locality. -- The type locality of *Sagenodus copeanus* Williston, 1899, represents an unusual, though not unique, association of vertebrate fossils and stromatolites; a similar occurrence was reported from the Lower Permian of New Mexico by Toomey & Cys (1977). The Robinson site is located on a creek bank where is exposed a carbonate layer composed chiefly of oncolites and columnar stomatolites that developed from them. This layer varies from zero to as much as 40 cm and lies between two shales. The closely spaced stromatolite heads trapped detrital material, including abundant skeletal remains of vertebrates and invertebrates. The chief vertebrate components of this fauna are lungfish, *Sagenodus* and *Gnathorhiza*, palaeoniscoids, *Acanthodes* and *Orthacanthus*. Several types of reptiles and amphibians are occasionally recovered and a trimero-

rhachid amphibian is a common component of the fauna. Invertebrates are largely or entirely represented by marine forms, usually of a fragmentary and sometimes juvenile nature. They include articulate brachiopods, corals, bryozoans, echinoderms, trilobites, bivalves, gastropods, and ostracods. There is general agreement that this locality represents an intertidal to subtidal depositional environment (Sawin et al., 1985). The extent to which this locality was influenced by the influx of fresh water remains controversial (Conley & Chorn, 1979; Schultze & Chorn, 1989).

Skull roof. – The dorsal skull roof (Fig. 3) of *S. copeanus* is a roughly rectangular and gently convex surface, dominated posteriorly by a large B-element. The primitive A-bone is lacking. Immediately in front of B lies an unpaired pentagonal C that is characteristic of the genus. Paired E-elements lie anterior to C. B is bordered laterally by paired I-, J-, and LM-elements; N and P are small bones that continue this series anteriorly to lie lateral to E. On the lateral margin of the skull, posterior to I-, J-, and LM-circumorbital bone 3b, lie KX, Y, and Z. Laterally there is a distinct notch in KX, that is partly bordered by Y, for the tabulate process of the operculum. Along the anterior margin of the ossified portion of the skull lie a row of small anteroposteriorly elongate elements; their variability is largely unknown and it is difficult to assign any individual bone to a specific position.

The circumorbital bones of *Sagenodus* are not well known in other species and will be described in some detail for *S. copeanus*. Here (Fig. 3) *S. copeanus* is restored with a smaller orbit than that figured by Watson & Gill (1923). The midpoint of the orbit of *S. copeanus* lies opposite the posterior margin of E. Both represent reconstructions and we doubt that these figures reflect a real difference in orbit position. The length of the composite skull roof upon which Fig. 3 is largely based is slightly less than 14 cm, roughly equal to the average length of material studied by Watson & Gill (1923: 166). The following description of individual bones of the skull roof focuses on their variability. Those illustrated in Fig. 3 may be regarded as representative of the species although not necessarily the most common type.

Most of the skull roof bones of *S. copeanus* from the Robinson locality are highly variable in thickness. For example, in C-bones of approxi-
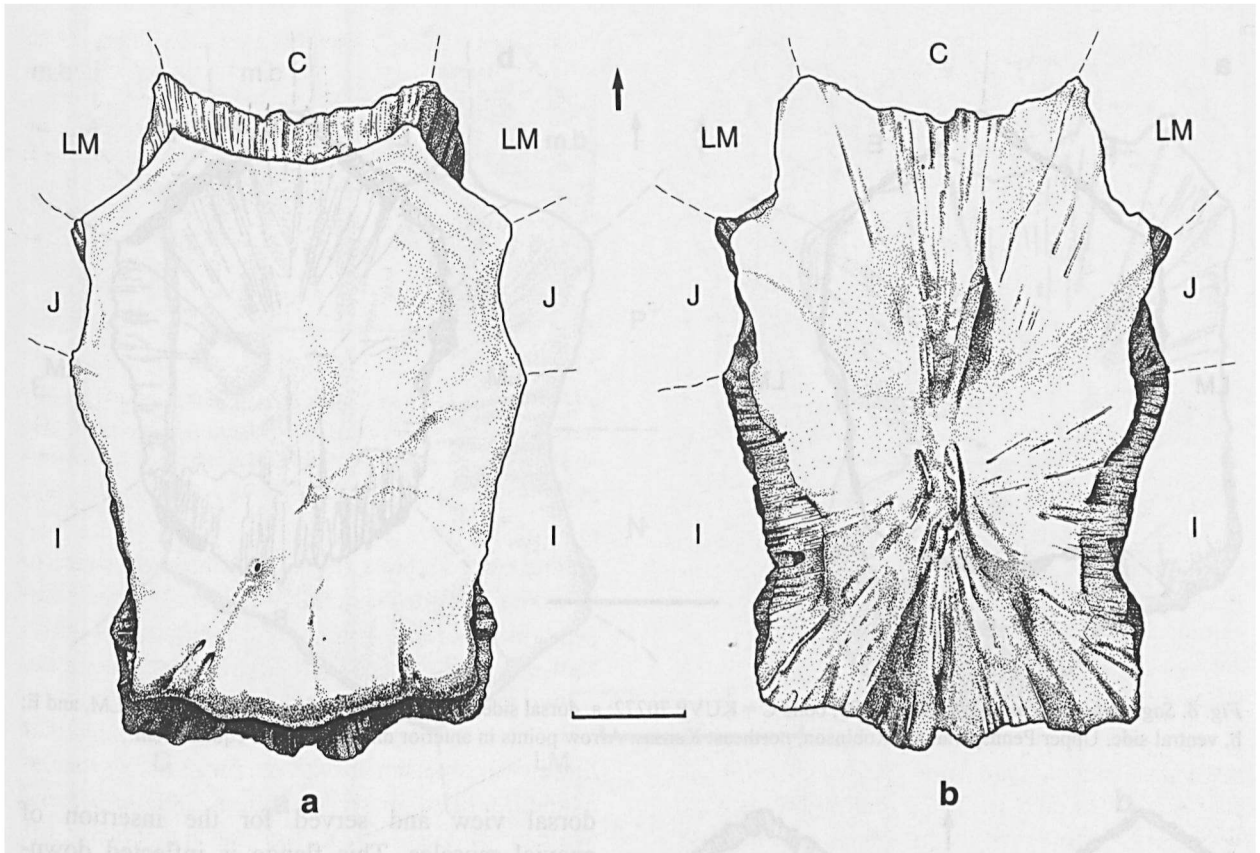
Fig. 4. *Sagenodus copeanus* Williston, 1899, bone B = KUVP 70759: a, dorsal side with indication of bordering bones I, J, LM, and C; b, ventral side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

mately equal length and width, one specimen may be three times the thickness of another. This condition will be discussed further in a subsequent paper.

Element B (Fig. 4) is commonly roughly rectangular and widest across its midpoint; anterior and posterior width are slightly less and approximately equal to each other. However, B is often tapered posteriorly to varying degrees; Fig. 5a (KUVP 70758) shows an extreme condition. B appears to be the most variable of all the larger skull roof bones. There is no constant correlation between width and length or between anterior or middle width and posterior width. The only exception is the correlation between middle and anterior width. KUVP 70757 (Fig. 5b) is unusual in lacking bilateral symmetry. Its left lateral margin encroached upon space normally occupied by J. Only few pores of the occipital commissure surface on the posterior third of the bone; they are arranged in two or three rows radiating from

the growth center. The hind margin of B may be straight or undulated. A well-developed occipital flange extends posteriorly from below the dorsal hind margin of B; usually it is partially visible in
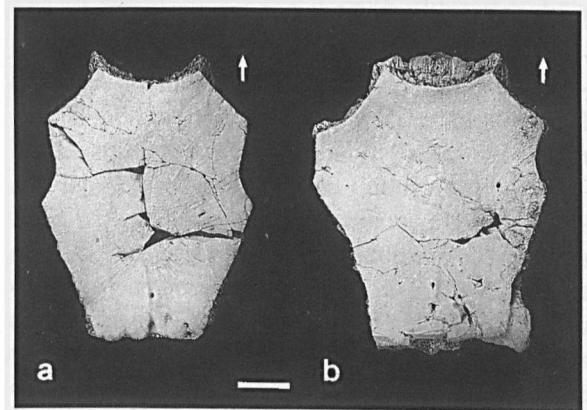
Fig. 5. *Sagenodus copeanus* Williston, 1899, dorsal side of bone B: a, KUVP 70758; b, KUVP 70757. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.
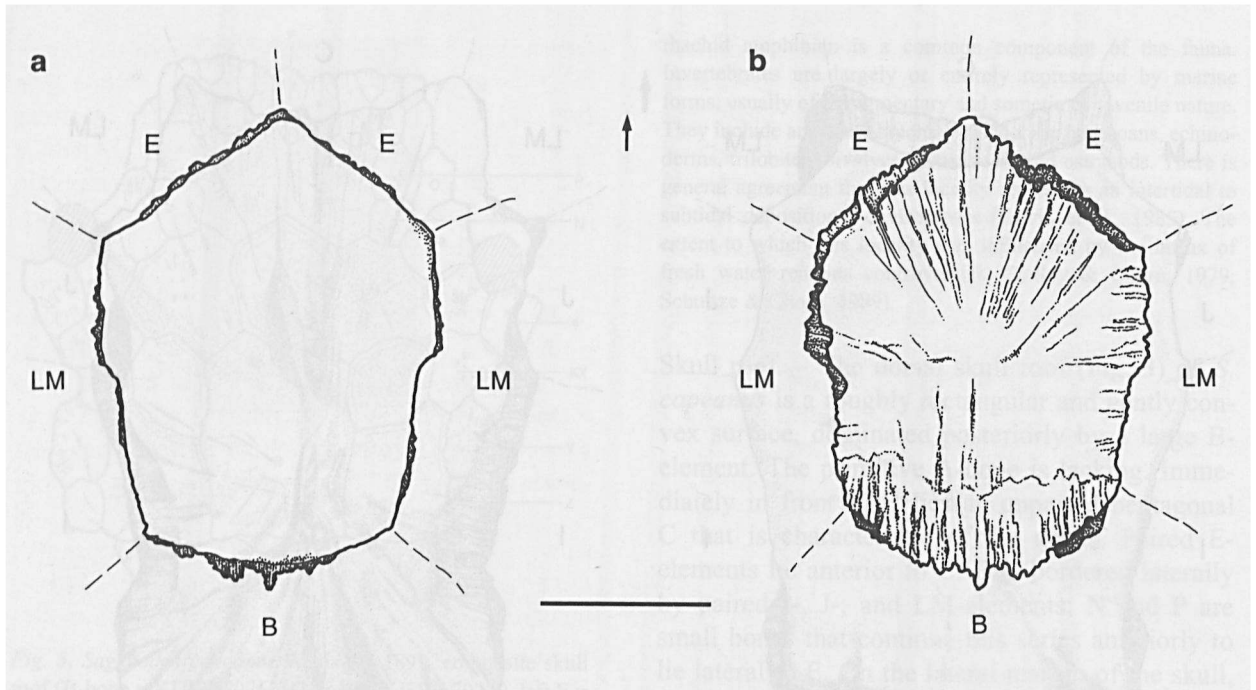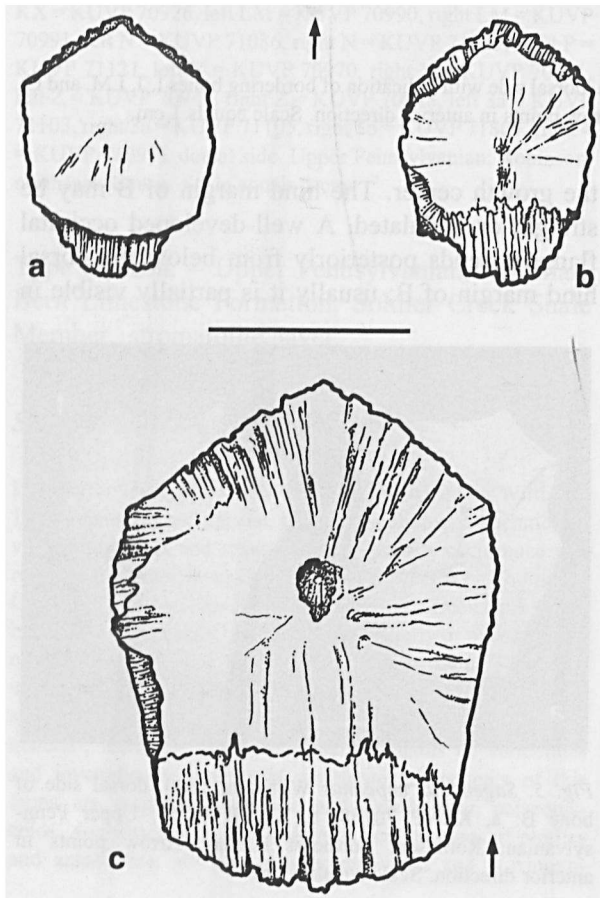
Fig. 6. Sagenodus copeanus Williston, 1899, bone C = KUVP 70772: a, dorsal side, with indication of bordering bones B, LM, and E; b, ventral side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

dorsal view and served for the insertion of epaxial muscles. This flange is inflected downward at a shallow angle in *S. copeanus*. B appears longer in ventral view because of the posterior extension of this shelf and a thin shelf which projects anteriad below C (Fig. 4b; see also Romer & Smith, 1934: fig. 4A). Posterolaterally the ventral surface of B is partially hidden by thin ventral lappets of I which flank B at the hind margin of the skull.

A salient feature of the ventral surface of B (Fig. 4b) is a shallow trough, variably bounded by two ridges. This structure lies in the midsagittal plane and represents the area of attachment of the chondrocranium with the dermal skull roof. The parasagittal ridges run roughly parallel near the middle of the bone but diverge anteriorly and posteriorly. These ridges may or may not terminate abruptly anteriorly. The anterior divergence

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Fig. 7. Sagenodus copeanus Williston, 1899, a-b, smallest bone C = KUVP 70763; a, dorsal side; b, ventral side; c, ventral side of bone C = KUVP 70775, with round pit for pineal organ. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.
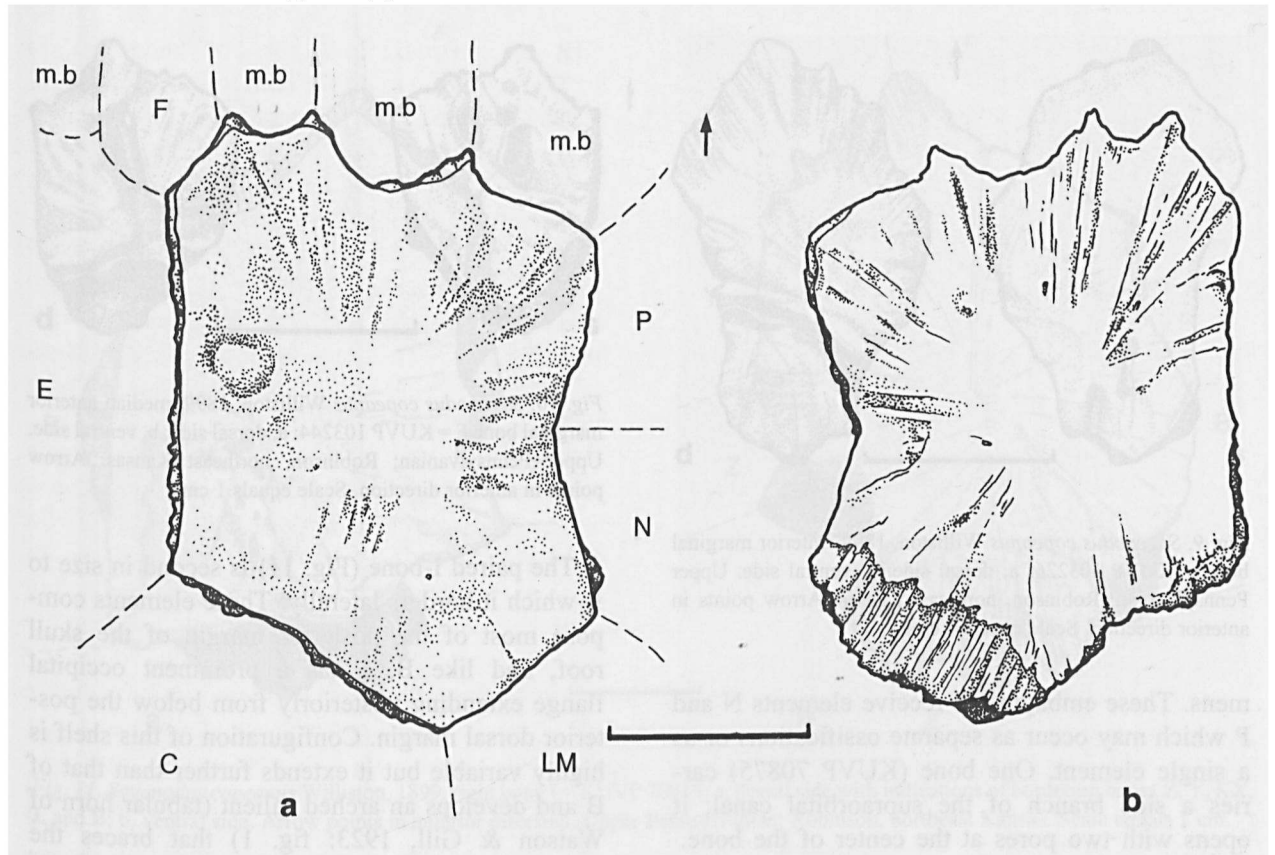
Fig. 8. *Sagenodus copeanus* Williston, 1899, right bone E = KUVP 70868: a, dorsal side with indication of bordering bones C, LM, N, P, marginal bones (m.b), F and E; b, ventral side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

was measured from radiographs for five specimens; they varied from 14 to 23 degrees.

The central unpaired element of the skull roof is C (Fig. 6a, b). It is pentagonal with the anterolateral corner distinctly angular. The bone may be nearly flat, slightly convex dorsally, or concave; some of the latter are slightly dished, others show a deep central depression. Increase in length is highly correlated with anterior and posterior width. As a variant KUVP 70773 is deeply notched at the right posterior corner. The ventral anterior margin projects forward below bone E. Interfingering projections for sutural attachment are particularly well developed deep along the hind margin, which in life was enveloped dorsally and ventrally by B. In the smallest example of C, a thin tongue projects posteriorly (Fig. 7a, b). An elongated (KUVP 70765, 70768) or round (KUVP 70775, Fig. 7c) pit for the pineal organ

appears on the ventral surface of several specimens.

Paired E-bones (Fig. 8a, b) lie anterior to C. The median, posteromedial, and posterolateral margins are more or less straight, the lateral border occasionally so. Projections of the posteromedial border interdigitate with the anterolateral border of bone C. Increase in the maximal length and length along the median line is closely correlated with anterior and posterior width. The intersection of the median and posteromedial borders of E is remarkably constant in *S. copeanus* at approximately 128 degrees. The anterior border is variably embayed to accommodate a small series of anterior marginal bones along the front of the skull roof. The lateral border usually has one or two shallow embayments; of eleven specimens this border is straight in two, with one embayment in four and two embayments in five speci-
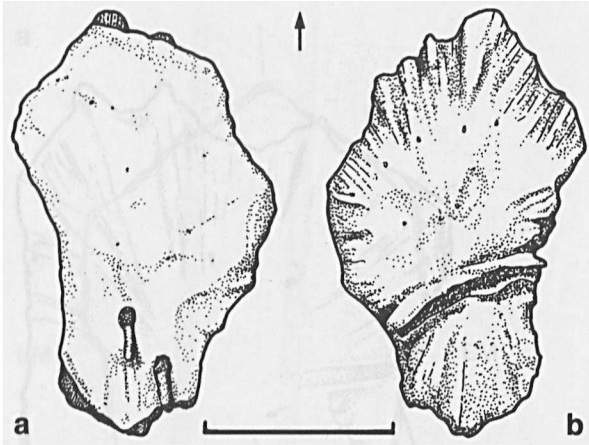
Fig. 9. Sagenodus copeanus Williston, 1899, anterior marginal bone = KUVP 103226: a, dorsal side; b, ventral side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.
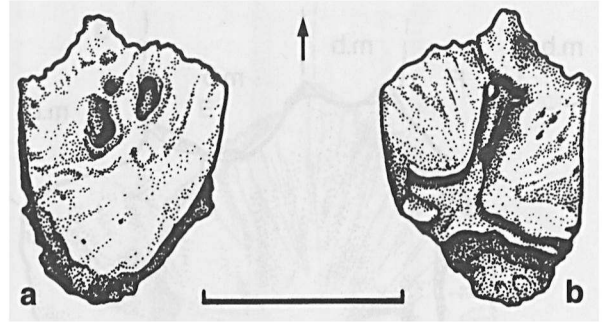

Fig. 10. Sagenodus copeanus Williston, 1899, median anterior marginal bone F = KUVP 103244: a, dorsal side; b, ventral side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

mens. These embayments receive elements N and P which may occur as separate ossifications or as a single element. One bone (KUVP 70875) carries a side branch of the supraorbital canal; it opens with two pores at the center of the bone.

The anterior marginal elements (Fig. 9), Q- and F-bones ("nasal and prenasal bones" in Watson & Gill, 1923) vary in size and shape. These bones are recognizable by the oblique path of the supraorbital canal on their ventral surface (Fig. 9b). The canal traverses the posterior half in the more lateral anterior marginal bones, and passes through the middle of the more medial anterior marginal bones. There is one median anterior marginal bone (= bone F, Fig. 10) in most cases, where the left and right supraorbital canals turn anteriorly (Fig. 10b). In a few cases, two elements occupy the median position. In addition, there are anterior marginal bones without a sensory canal. These lie lateral or anterior to the anterior marginal bones with the sensory canal. A few anterior marginal bones are wider than they are long, but most are elongated, up to twice as long as wide. Obvious fusion of elements as figured by Watson & Gill (1923: figs. 3B-D) were not observed, but one large bone (KUVP 103138) replaces many anterior marginal bones; its anterior fingered portion arches anteroventrally, following the curvature of the snout.

The paired I-bone (Fig. 11) is second in size to B which it borders laterally. These elements compose most of the posterior margin of the skull roof, and like B, I has a prominent occipital flange extending posteriorly from below the posterior dorsal margin. Configuration of this shelf is highly variable but it extends further than that of B and develops an arched salient (tabular horn of Watson & Gill, 1923: fig. 1) that braces the anocleithrum. The dorsal surface of I is gently arched. The pores of the occipital commissure open in the posterior half above and behind the canal. The number of pores is variable; they radiate away from the growth center in most specimens, though they are sometimes arranged in one double line like in Fig. 11a. Ventrally this element develops lappets that extend below B, J, Y, and to a lesser extent KX. In some specimens, KX and I have a vertical interdigitating contact. The posterolateral corner of I overlaps Z. Of 26 specimens, most more or less complete, none is remarkably different from the one figured. This is reflected in the close correlation between width and length and between anterior and posterior width.

J (Fig. 12) is a paired, roughly shield-shaped element and in general the configuration is quite stable. This is corroborated by the close correlation of width measurements with maximum length. Of 19 examples only one deviated from the norm. KUVP 70894 reaches farther laterally to meet Y. This lateral portion is the most variable part of J. A branch of the supraorbital canal
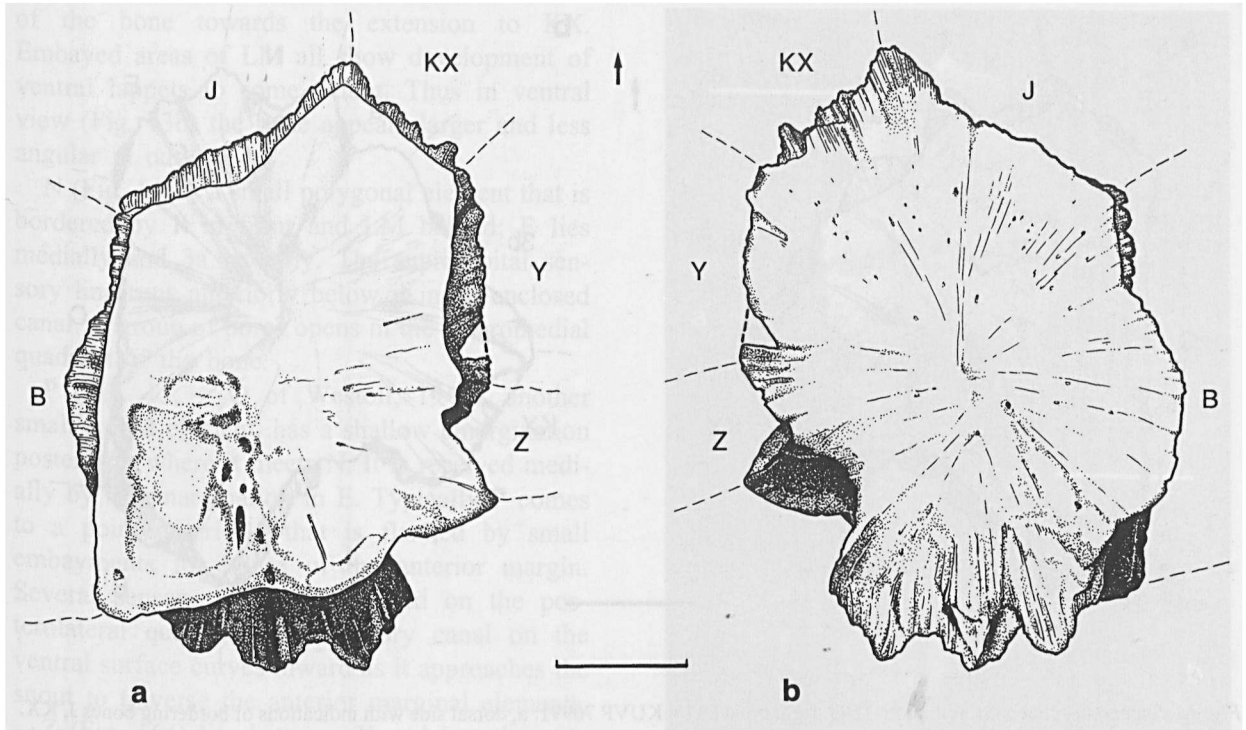
Fig. 11. Sagenodus copeanus Williston, 1899, right bone I = KUVP 70913: a, dorsal side with indications of bordering bones Z, Y, KX, J, and B; b, ventral side. Arrow points in anterior direction. Upper Pennsylvanian; Robinson, northeast Kansas. Scale equals 1 cm.
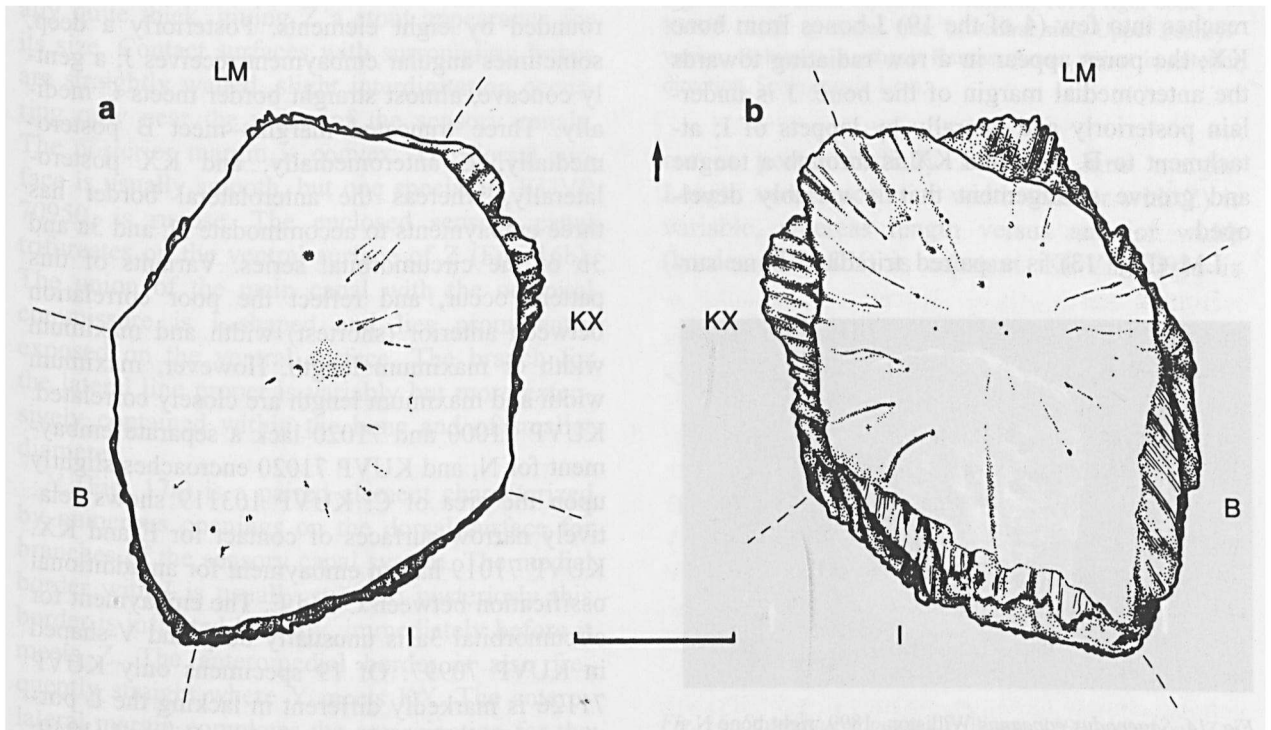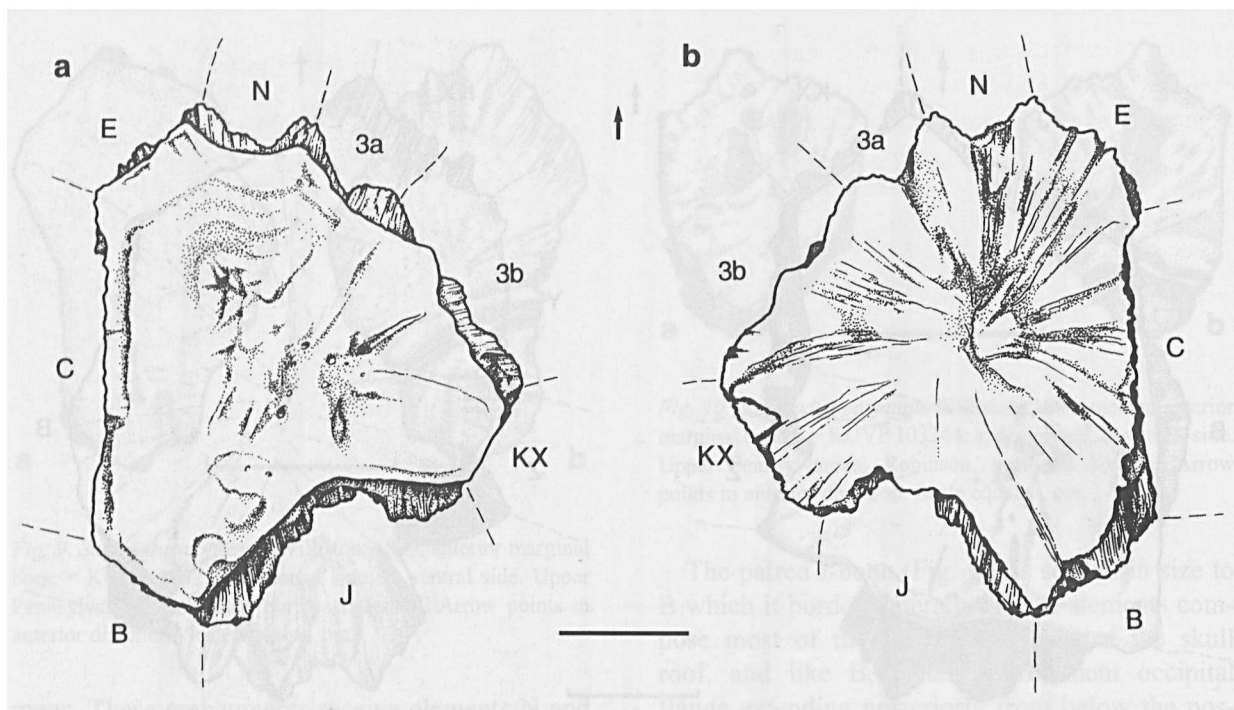

Fig. 12. Sagenodus copeanus Williston, 1899, right bone J = KUVP 70879: a, dorsal side with indications of bordering bones I, KX, LM, and B; b, ventral side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

Fig. 13. Sagenodus copeanus Williston, 1899, right bone LM = KUVP 70991: a, dorsal side with indications of bordering bones J, KX, 3b, 3a, N, E, C, and B; b, ventral side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

reaches into few (4 of the 19) J-bones from bone KX; the pores appear in a row radiating towards the anteromedial margin of the bone. J is underlain posteriorly and laterally by lappets of I; attachment to B, LM, and KX is through a tongue and groove arrangement that is variably developed.
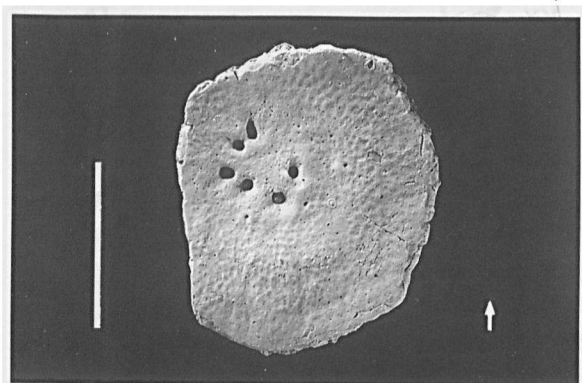
LM (Fig. 13) is a paired triradiate bone surrounded by eight elements. Posteriorly a deep, sometimes angular embayment receives J; a gently concave, almost straight border meets C medially. Three truncated margins meet B posteromedially, E anteromedially, and KX posterolaterally, whereas the anterolateral border has three embayments to accommodate N, and 3a and 3b of the circumorbital series. Variants of this pattern occur, and reflect the poor correlation between anterior (shortest) width and maximum width or maximum length. However, maximum width and maximum length are closely correlated. KUVP 71000 and 71020 lack a separate embayment for N, and KUVP 71020 encroaches slightly upon the area of C. KUVP 103119 shows relatively narrow surfaces of contact for E and KX. KUVP 71019 has an embayment for an additional ossification between C and E. The embayment for circumorbital 3a is unusually deep and V-shaped in KUVP 70997. Of 19 specimens only KUVP 71126 is markedly different in lacking the L portion, a condition also recorded by Westoll (1949: 150 ánd fig. 8A') for *Sagenodus*. The pores of the supraorbital canal open as a group off the center

Fig. 14. Sagenodus copeanus Williston, 1899, right bone N = KUVP 11086, dorsal side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

of the bone towards the extension to KX. Embayed areas of LM all show development of ventral lappets to some extent. Thus in ventral view (Fig. 13b) the bone appears larger and less angular in outline.

N (Fig. 14) is a small polygonal element that is bordered by P in front and LM behind; E lies medially and 3a laterally. The supraorbital sensory line runs anteriorly below it in an enclosed canal. A group of pores opens in the anteromedial quadrant of the bone.

P (Fig. 15; = Q of Westoll, 1949), another small paired element, has a shallow emargination posteriorly where it meets N. It is received medially by an emargination in E. Typically P comes to a point anteriorly that is flanked by small embayments for bones of the anterior margin. Several sensory pores are located on the posterolateral quadrant. The sensory canal on the ventral surface curves inward as it approaches the snout to traverse the anterior marginal elements.

Z (Fig. 16a) lies between Y and I at the posterolateral corner of the skull roof. It is a small bone, usually slightly longer than wide. It is usually quite thick, giving Z a stout appearance for its size. Contact surfaces with surrounding bones are straightly walled, slight interdigitation occurring only near the union of the sensory canals. The posterior margin is convex. The dorsal surface is usually smooth, but one specimen, KUVP 70950, is rugose. The enclosed sensory canal trifurcates on the ventral surface of Z (Fig. 16b). The union of the main canal with the occipital commissure is L-shaped and lies prominently exposed on the ventral surface. The branch for the lateral line proper is variably but more extensively contained within the bone and of smaller diameter.

Y (Fig. 17a) is a paired element characterized by numerous openings on the dorsal surface for branches of the sensory canal system. The medial border with I is usually straight; posteriorly this border is inflected laterally, immediately before it meets Z. The anteromedial border is also frequently straight where Y meets KX. The anterolateral margin completes the emargination for the tabulate process of the operculum. An embayment in the posteromedial corner receives Z. The lateral margin tends to be slightly irregular and
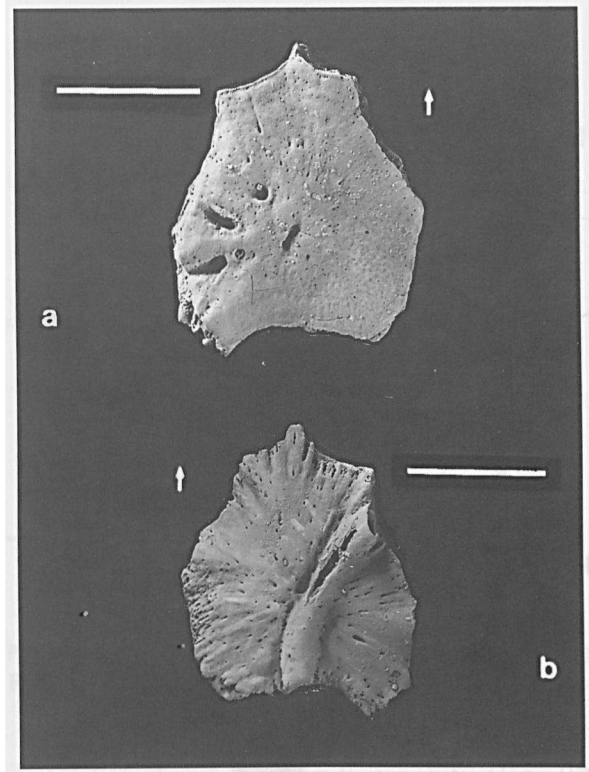

Fig. 15. Sagenodus copeanus Williston, 1899, right bone P = KUVP 11121: a, dorsal side; b, ventral side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

curves posteromedially near the hind margin. Length versus posterior width (border with Z) is variable, whereas length versus anterior width (border with KX) is constant. KUVP 70981 is
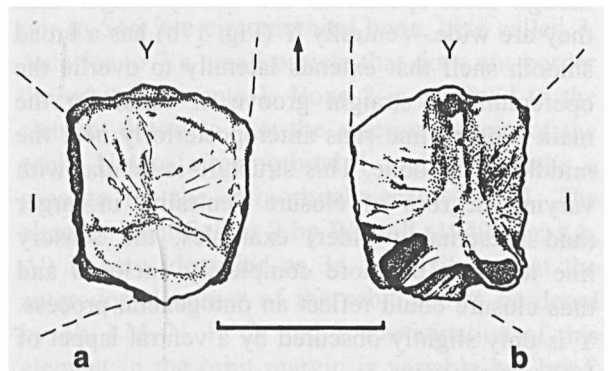

Fig. 16. Sagenodus copeanus Williston, 1899, right bone Z = KUVP 70951: a, dorsal side; b, ventral side; indications of bordering bones Y and I. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.
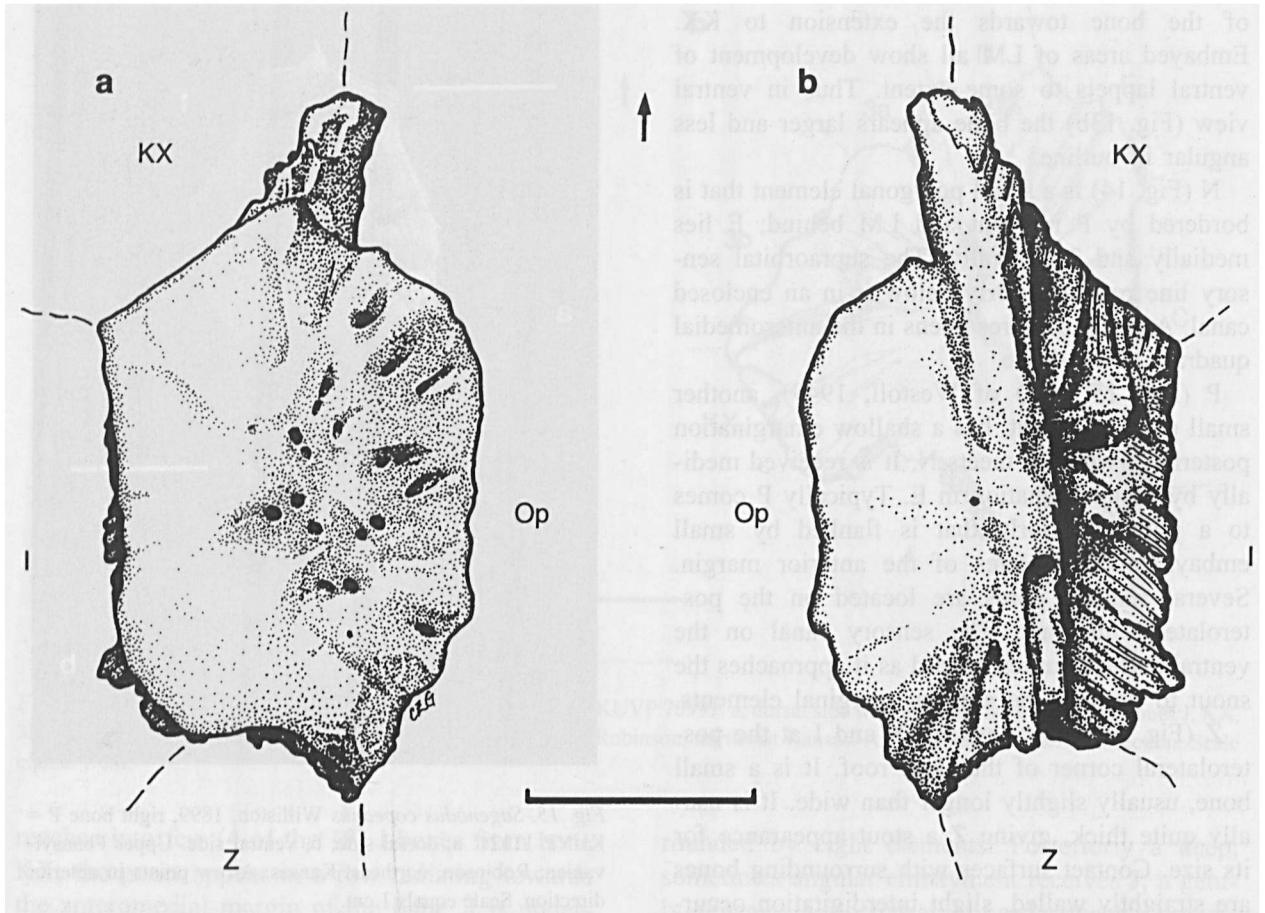
Fig. 17. *Sagenodus copeanus* Williston, 1899, right bone Y = KUVP 70988: a, dorsal side; b, ventral side; indications of bordering bones Z, operculum (Op), KX, and I. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

roughly as wide as its dorsal surface is long, although most specimens are clearly longer than they are wide. Ventrally Y (Fig. 17b) has a broad smooth shelf that extends laterally to overlie the operculum. A straight groove or canal for the main sensory line runs anteroposteriorly near the middle of the bone. This structure is tubular with varying degrees of closure ventrally; in larger (and presumably older) examples, the sensory line tends to be more completely enclosed and thus closure could reflect an ontogenetic process. Y is only slightly obscured by a ventral lappet of I in ventral view.

The only noteworthy variation from the above is represented by KUVP 70989. This element takes the form of Y+Z; however, it lacks the openings for the sensory canals to the dorsal surface which are so numerous in typical examples of Y.

The KX-bone (Fig. 18; = X+Y2 of Westoll, 1949) is a variable element in the skull roof of *S. copeanus*. Posterior width is quite variable in relation to maximum width and maximum length, whereas increase in maximum width is closely correlated with maximum length. Of 22 elements 10 are at least slightly unusual. Only the most aberrant will be mentioned here. Typically this paired bone is triradiate with truncated rami abutting LM and I; a third ramus projects laterally just anterior to a distinct notch for the tabulate process of the operculum. Anteriorly KX borders circumorbitals 3b and 4. Contact with 4 is usually almost straight but an embayment may be present in KX. Circumorbital 3b lies in an embayment
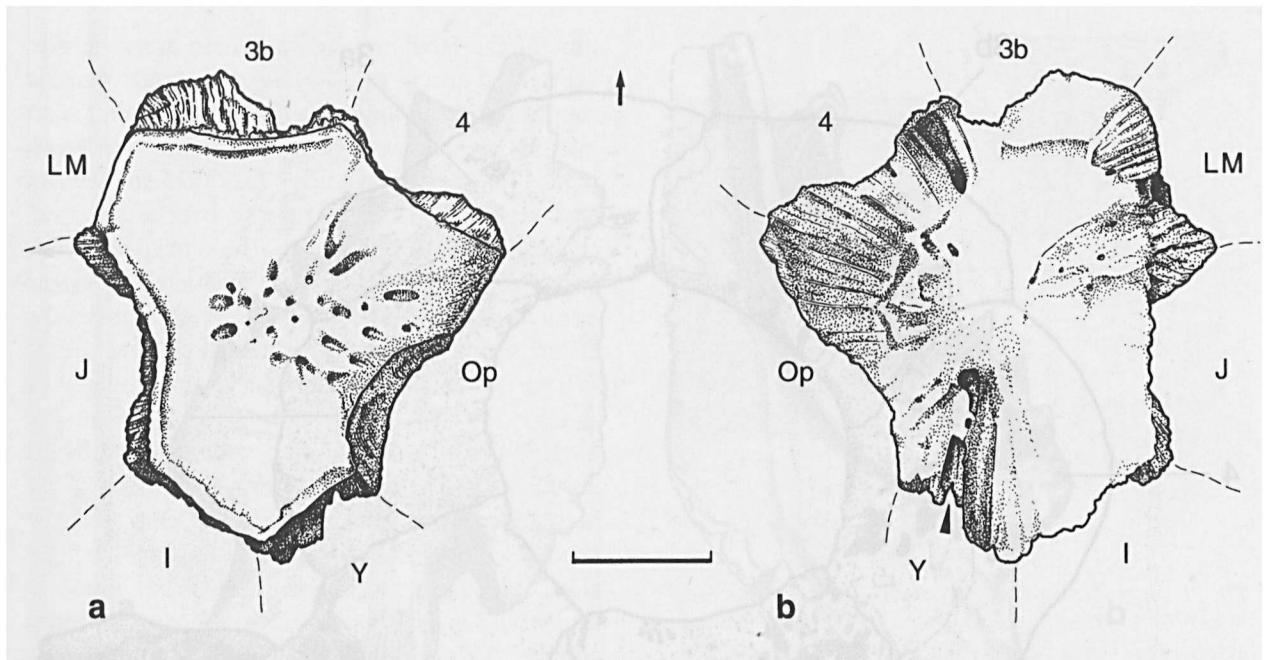
Fig. 18. Sagenodus copeanus Williston, 1899, right bone KX = KUVP 70944: a, dorsal side; b, ventral side; indications of bordering bones I, Y, operculum (Op), 4, 3b, LM, and J. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

and overlies a ventral lappet of KX. J also overlies a ventral lappet in an angular emargination on the medial side of KX. An anterior salient of Y extends along the posterolateral corner of KX to the opercular notch. Variants of the above include loss or shortening of the anteromedial ramus that abuts LM (KUVP 70945) such that there is a straight suture for J and LM, a condition similar to that figured by Westoll (1949: fig. 8A' left) for *Sagenodus*, where L (K of Westoll, 1949) is a separate ossification. Other variants show shortening of the abutment with I (KUVP 70936) or loss of all rami such that the bone approximates a hexagonal shape (KUVP 70933). KUVP 103121 lacks extensions towards both LM and I. KUVP 70938 is most unusual in having an embayment for an unknown bone immediately in front of the recess for the tabulate process of the operculum; an additional small bone may also have lodged between KX and circumorbital 4. KX has many openings of the sensory canal on the surface; the pores are grouped with the center towards the opercular notch.

Orbital region. – The orbit of *Sagenodus* has been little known except for the dorsal elements. The restoration shown here for *S. copeanus* (Fig. 19) should be reliable even though it is based on a composite reconstruction of the orbit. Six elements border the orbit. Bones of the cheek are lost with the exception of a series of small ossifications surrounding the preopercular sensory canal.

Circumorbitals 3b, 4, and 5+6 are present based on topographic relationships and, in the case of 5+6, the junction of the preopercular canal with the infraorbital canal. Immediately anterior to 5+6 is a circumorbital bone, here called 7. Anterior to 7 a small ossicle that does not border the orbit represents 1. Bone 2 is assigned to the element dorsal to 7 at the anterior margin of the orbit. Unlike circumorbital 1 and 7, it lacks a passage for the infraorbital sensory canal. The element identified as 2 by Westoll (1949: fig. 8A, A') is here identified as 3a. It is situated at the anterodorsal corner of the orbit and is bordered by 3b, LM, N, P, O, and 2. Participation of this element in the orbit margin is variable but brief. It sometimes carries a canal branch of the supraorbital.

Circumorbital 4 is readily distinguished by its squared-off posteroventral margin located diago-
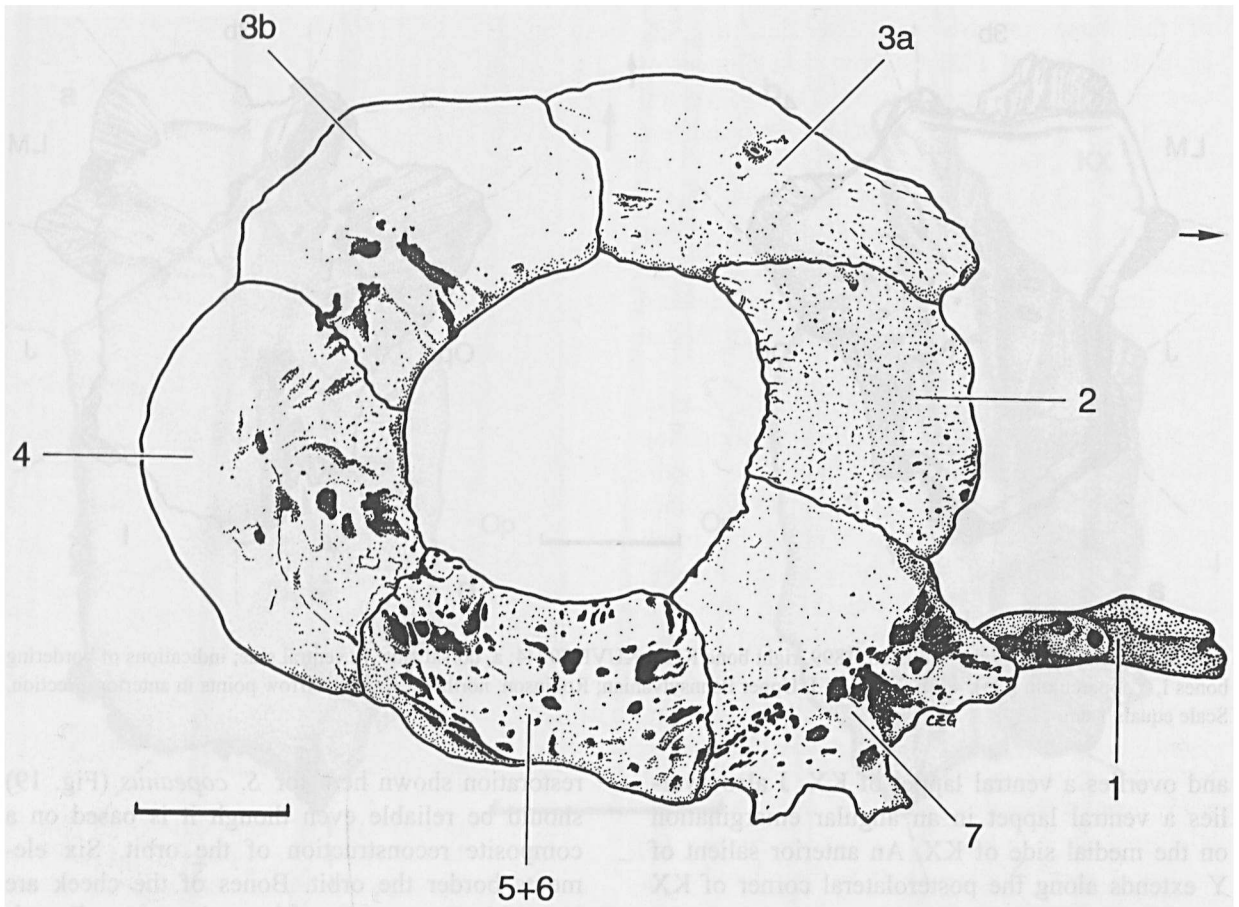
Fig. 19. Sagenodus copeanus Williston, 1899, circumorbital bones, lateral side; bone 1 = KUVP 103123, bone 2 = KUVP 71070, bone 3a = KUVP 71103, bone 3b = KUVP 71089, bone 4 = KUVP 71099, bone 5+6 = KUVP 71051, bone 7 = KUVP 71063. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

nally across the bone from the orbit. The bone usually shows numerous sensory pores. It meets KX posterodorsally, 3b anterodorsally, and 5+6 anteroventrally.

Circumorbital 5+6 makes up the ventral border of the orbit. It is rugose on the lateral surface and shows some sensory pores. Its length varies relative to the rest of the orbit and its depth is usually distinctly greater along the anterior border with bone 7. An opening is present ventrally for the preopercular sensory canal to join the infraorbital canal.

Circumorbital 7 lies at the anteroventral border of the orbit. Its anterior and posterior margins taper inwards toward the orbit. The lateral surface is relatively smooth but distal to the orbit the bone surface is quite uneven. This is caused by

several large sensory pores that are almost always arranged in a row (those seen in Fig. 19 are atypical in this respect). This line of pits and the area near the orbit are separated by a linear depression which may develop as a distinct groove. The anteroventral margin of 7 may be gently undulatory or show embayments (e.g. Fig. 19) formed by spurs of bone. Anteriorly this element meets bone 1 and dorsally bone 2; the union with these elements is usually confluent in smaller specimens and separated in larger specimens.

Contrary to the usual condition in Devonian dipnoans, bone 1 no longer enters the orbit. It is small and surrounds the anterior extension of the infraorbital sensory canal.

Circumorbital 2 lies at the anterior margin of the orbit. Characteristically it contains no large
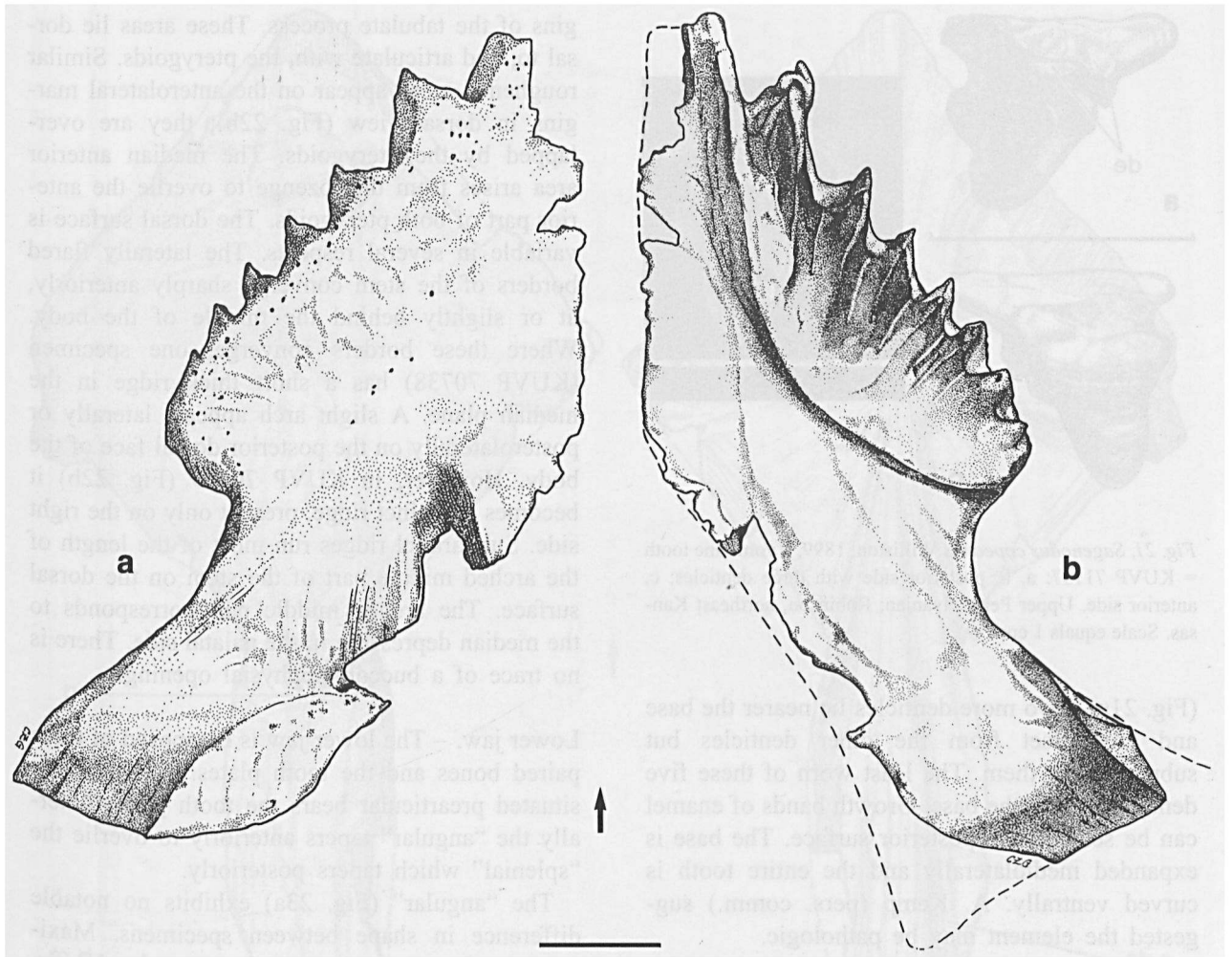
Fig. 20. Sagenodus copeanus Williston, 1899, left pterygoid = KUVP 70812: a, dorsal side; b, palatal side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

pits and it is not traversed by a sensory canal. Its shape is somewhat variable. The anterior margin is rough. The dorsal margin is bordered by bone 3a and may also meet bone O anterodorsally in some individuals.

Palatal region. – Paired pterygoids (Figs. 2, 20) bear the upper tooth plates. The pterygoids articulate with each other in the midline. Posteriorly they diverge and are separated by the parasphenoid. The pterygoids are quite thin anteriorly where they fuse with the tooth plates. Their delta-shaped quadrate ramus is relatively thick. Medially these rami overlie the anterolateral margins of the parasphenoid lozenge. The posterior mar-

gin of the pterygoids is inflected dorsally where it borders the gill chambers. The ventrolateral corner braces the quadrate. At this point each pterygoid bears a facet medial to the jaw articulation. This facet is strikingly similar to that of *Neoceratodus* (Watson & Gill, 1923: 174; pers. obs.).

Paired vomerine teeth are thought to have been present in *Sagenodus* (Atthey, 1875; Lund, 1970: fig. 9; Schultze, 1993: fig. 1c) and would have protruded from the palate anterior to the pterygoid tooth plates. A single specimen, KUVP 71137, is interpreted here as a vomerine tooth of *S. copeanus*. This element is roughly wedge-shaped with a row of three closely spaced denticles extending from the apex toward the base
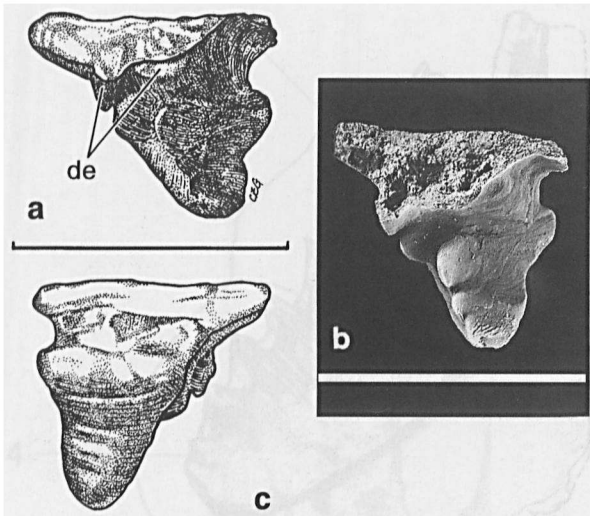
Fig. 21. Sagenodus copeanus Williston, 1899, ? vomerine tooth = KUVP 71137: a, b, posterior side with three denticles; c, anterior side. Upper Pennsylvanian; Robinson, northeast Kansas. Scale equals 1 cm.

(Fig. 21a). Two more denticles lie nearer the base and are offset from the other denticles but subparallel to them. The least worn of these five denticles lies at the base. Growth bands of enamel can be seen on the posterior surface. The base is expanded mediolaterally and the entire tooth is curved ventrally. A. Kemp (pers. comm.) suggested the element may be pathologic.

The parasphenoid (Fig. 22) is made up of a diamond-shaped body (the so-called lozenge), a tabulate anterior process, and a long posterior stem. The delta-shaped projections that comprise the body arch downward. The stem is constricted transversely where it joins the body; posteriorly it flares laterally in a gentle curve, then tapers to a blunt tip. In palatal view (Fig. 22a), a median depression, bordered laterally by parallel ridges, occupies most of the stem. Both ridges and depression are variably developed. Anterior to this depression a medial ridge rises abruptly, and it forms the posterior point of the diamond-shaped body. Width and anterior extent of the ridge are variable. The posterior terminus of this ridge marks the point of bifurcation of the dorsal aorta. At the anterior end of the parasphenoid the smooth ventral surface of the body forms a V, with an angle less than 90 degrees. Lateral and anterior to this V, roughened areas form the mar-

gins of the tabulate process. These areas lie dorsal to, and articulate with, the pterygoids. Similar roughened areas appear on the anterolateral margins in dorsal view (Fig. 22b); they are overlapped by the pterygoids. The median anterior area arises from the lozenge to overlie the anterior part of both pterygoids. The dorsal surface is variable in several respects. The laterally flared borders of the stem converge sharply anteriorly, at or slightly behind the middle of the body. Where these borders converge, one specimen (KUVP 70738) has a short thick ridge in the median plane. A slight arch appears laterally or posterolaterally on the posterior dorsal face of the body. However, in KUVP 70739 (Fig. 22b) it becomes a distinct ridge, present only on the right side. Subparallel ridges run most of the length of the arched middle part of the stem on the dorsal surface. The arched middle part corresponds to the median depression in the palatal side. There is no trace of a buccohypophysial opening.

Lower jaw. – The lower jaw is composed of three paired bones and the tooth plates. The medially situated prearticular bears the tooth plate. Laterally the "angular" tapers anteriorly to overlie the "splenial" which tapers posteriorly.

The "angular" (Fig. 23a) exhibits no notable difference in shape between specimens. Maximum depth and maximum length are closely correlated as size increases. The number of lateral pits for the oral sensory canal varies from 7 (with an 8th pit shared with the "splenial") in the largest specimen, to 4 (with a 5th shared) in the second largest "angular". Variation also occurs in the area of insertion for the adductor mandibulae, located between the ascending process and the tooth plate. In two specimens this area contains a deep pit dorsally. A shallow pocket is the usual condition. At the mediodorsal margin, a flattened ridge serves as support for the lateral portion of the tooth plate. The lingual face of the "angular" is concave (Fig. 23b). Though the surface is gently furrowed, a smooth narrow band extends anteriorly from the posterior margin. In only one specimen (KUVP 70857) is this band associated with a ridge on the posterior medial face of the bone. This ridge and the position of this band indicate that it formed the outer wall of the pas-
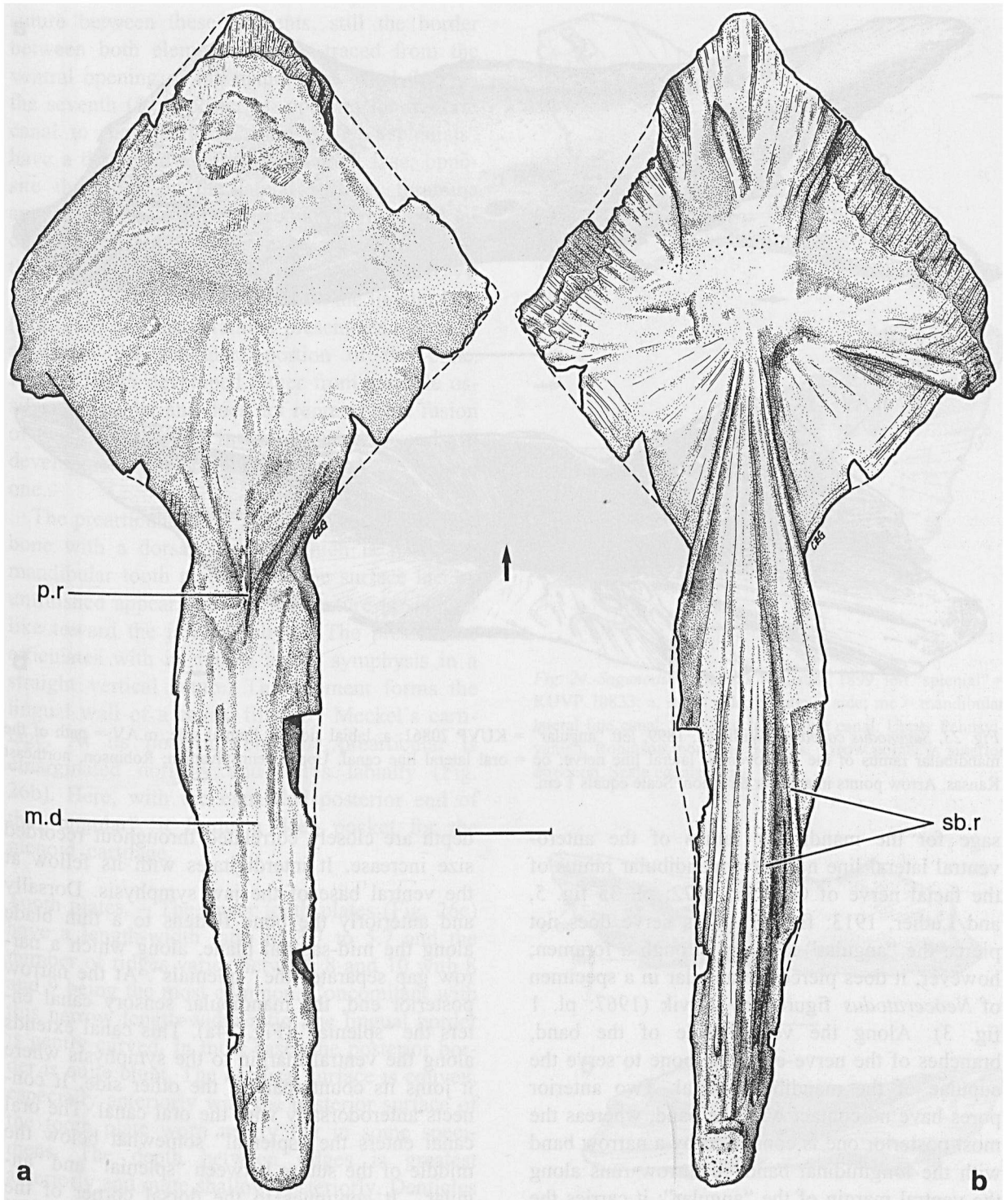
Fig. 22. Sagenodus copeanus Williston, 1899, parasphenoid = KUVP 70739: a, palatal side; b, dorsal side; m.d = median depression on palatal side of stem; p.r = posterior terminus of ridge on diamond-shaped body; sb.r = subparallel ridges on dorsal side of stem. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.
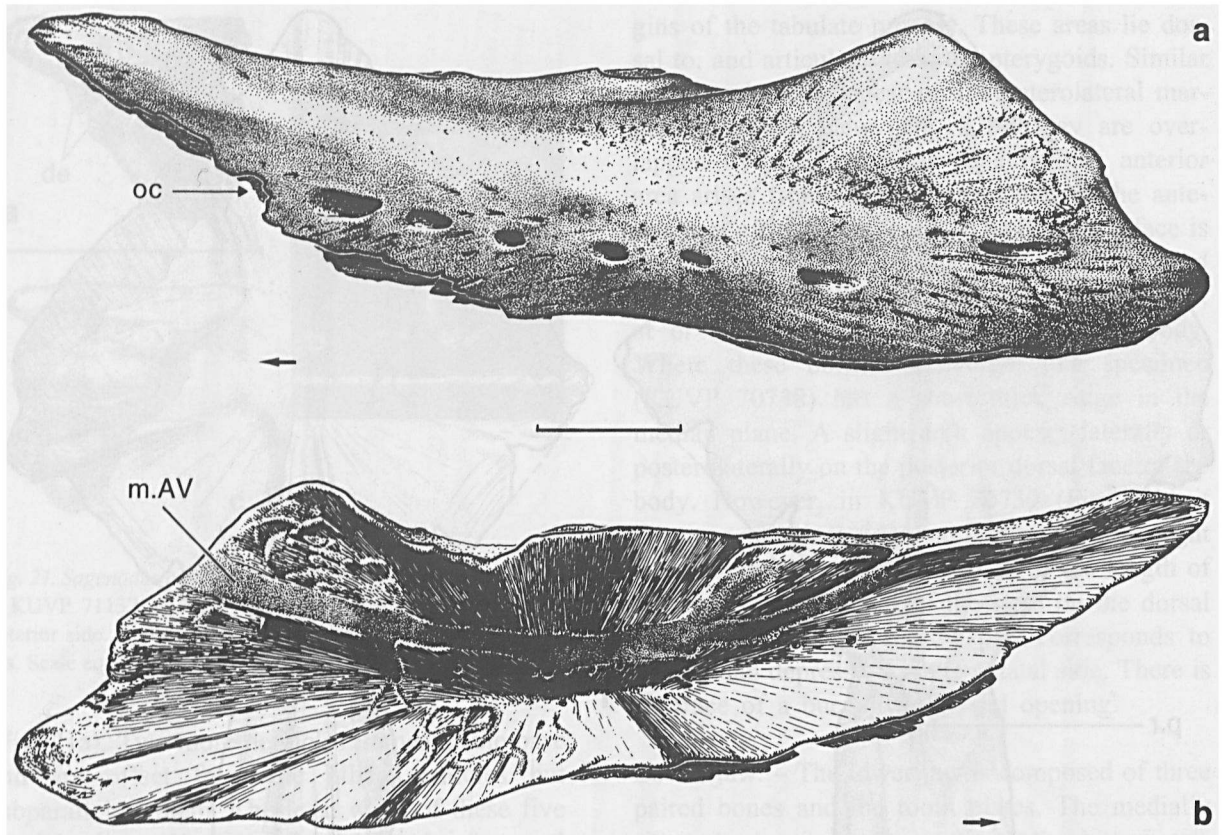
Fig. 23. *Sagenodus copeanus* Williston, 1899, left "angular" = KUVP 70861: a, labial side; b, lingual side; m.AV = path of the mandibular ramus of the anteroventral lateral line nerve; oc = oral lateral line canal. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

sage for the mandibular ramus of the antero-ventral lateral line nerve (= mandibular ramus of the facial nerve of Günther, 1872: pl. 35 fig. 5 and Luther, 1913: fig. 27). This nerve does not pierce the "angular" laterally through a foramen; however, it does pierce the angular in a specimen of *Neoceratodus* figured by Jarvik (1967: pl. 1 fig. 3). Along the ventral side of the band, branches of the nerve enter the bone to serve the cupulae of the mandibular canal. Two anterior pores have no contact with the band, whereas the most posterior one is connected by a narrow band with the longitudinal band. A furrow runs along the ventral margin of the "angular"; it carries the mandibular canal.

The "splenial" (Fig. 24) is more plate-like than the "angular" and is also concave on the lingual face (Fig. 24b). The shape of the bone does not change with size; maximum length and posterior

depth are closely correlated throughout recorded size increase. It interdigitates with its fellow at the ventral base of the jaw symphysis. Dorsally and anteriorly the bone flattens to a thin blade along the mid-sagittal plane, along which a narrow gap separates the "splenials". At the narrow posterior end, the mandibular sensory canal enters the "splenial" (Fig. 24a). This canal extends along the ventral margin to the symphysis where it joins its counterpart of the other side. It connects anterodorsally with the oral canal. The oral canal enters the "splenial" somewhat below the middle of the suture between "splenial" and "angular." It continues to the dorsal corner of the bone where it opens through a pore near the symphysis.

One lower jaw (KUVP 70845, Fig. 25) is remarkable in that "splenial" and "angular" form a single compound bone. There is no trace of a

suture between these elements, still the border between both elements can be traced from the ventral opening of the mandibular canal through the seventh (from posterior) opening for the oral canal to the anterodorsal tip. Other "splenials" have a thickened area on the lingual face; opposite this area, on the lateral surface, foramina appear as simple pits. Surrounding foramina incline away from this region and indicate that it is the center of growth for this element. KUVP 70845 lacks the thickened area on the lingual face (Fig. 25b) and the foramina present tend to radiate from the "angular" portion of the bone. KUVP 70845 developed either from a single ossification center and does not represent the fusion of two bones, or the fusion occurred so early in development that one center overtook the second one.

The prearticular (Fig. 26) is a thin strap-shaped bone with a dorsal shelf to which is fused the mandibular tooth plate. The bone surface has an unfinished appearance and the texture is sponge-like toward the jaw symphysis. The prearticular articulates with its fellow at the symphysis in a straight vertical suture. This element forms the lingual wall of a cavity filled by Meckel's cartilage. At its posterior end the prearticular is emarginated dorsally and flares labially (Fig. 26b). Here, with the expanded posterior end of the "angular", it forms a deep pocket for the glenoid cartilage.

Tooth plates. – The lower tooth plates (Fig. 26c) have a length-width ratio of 3.7 to 5.7 and the number of ridges varies between 8 and 10 with 8 and 9 being the most common. Concomitant with this narrow length-width ratio, the lingual border is gently curved. In most cases the posterior border is quite blunt. The occlusal surface is convex, especially anteriorly with the posterior surface of the tooth plate worn nearly flat in some specimens. The depth between ridges is greatest anteriorly and quite shallow posteriorly. Denticles were rapidly worn away and are preserved only on the labial margins of some ridges. Tooth ridges do not radiate from a single point. The prearticular meets the lingual margin to form an acute angle. The first (anterior) ridge is set off
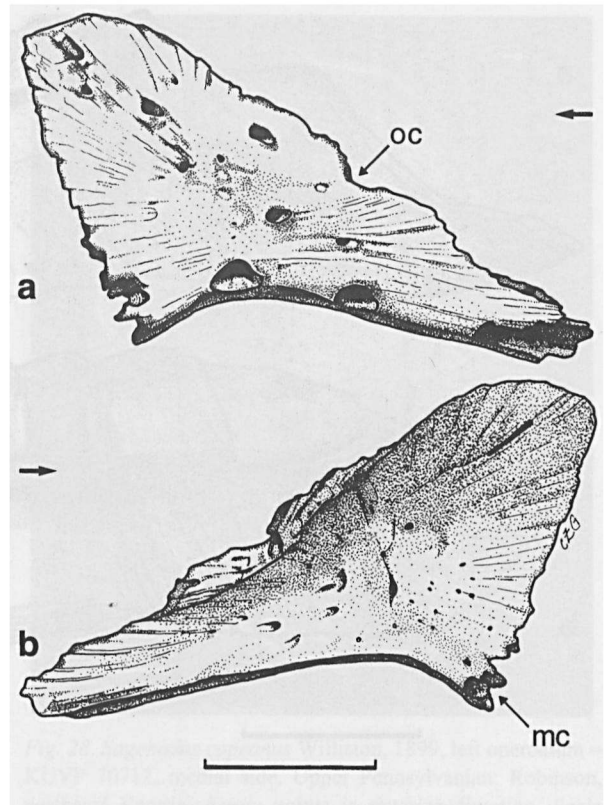

Fig. 24. Sagenodus copeanus Williston, 1899, left "splenial" = KUVP 70833: a, labial side; b, lingual side; mc = mandibular lateral line canal; oc = oral lateral line canal. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.
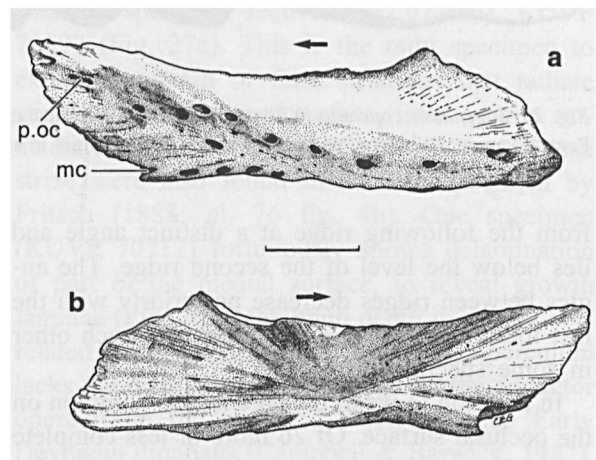

Fig. 25. Sagenodus copeanus Williston, 1899, left fused "splenial + angular" = KUVP 70845: a, labial side; b, lingual side; mc = mandibular lateral line canal; p.oc = pores of the oral lateral line canal. Upper Pennsylvanian; Robinson, northeast Kansas. Arrows point in anterior direction. Scale equals 1 cm.
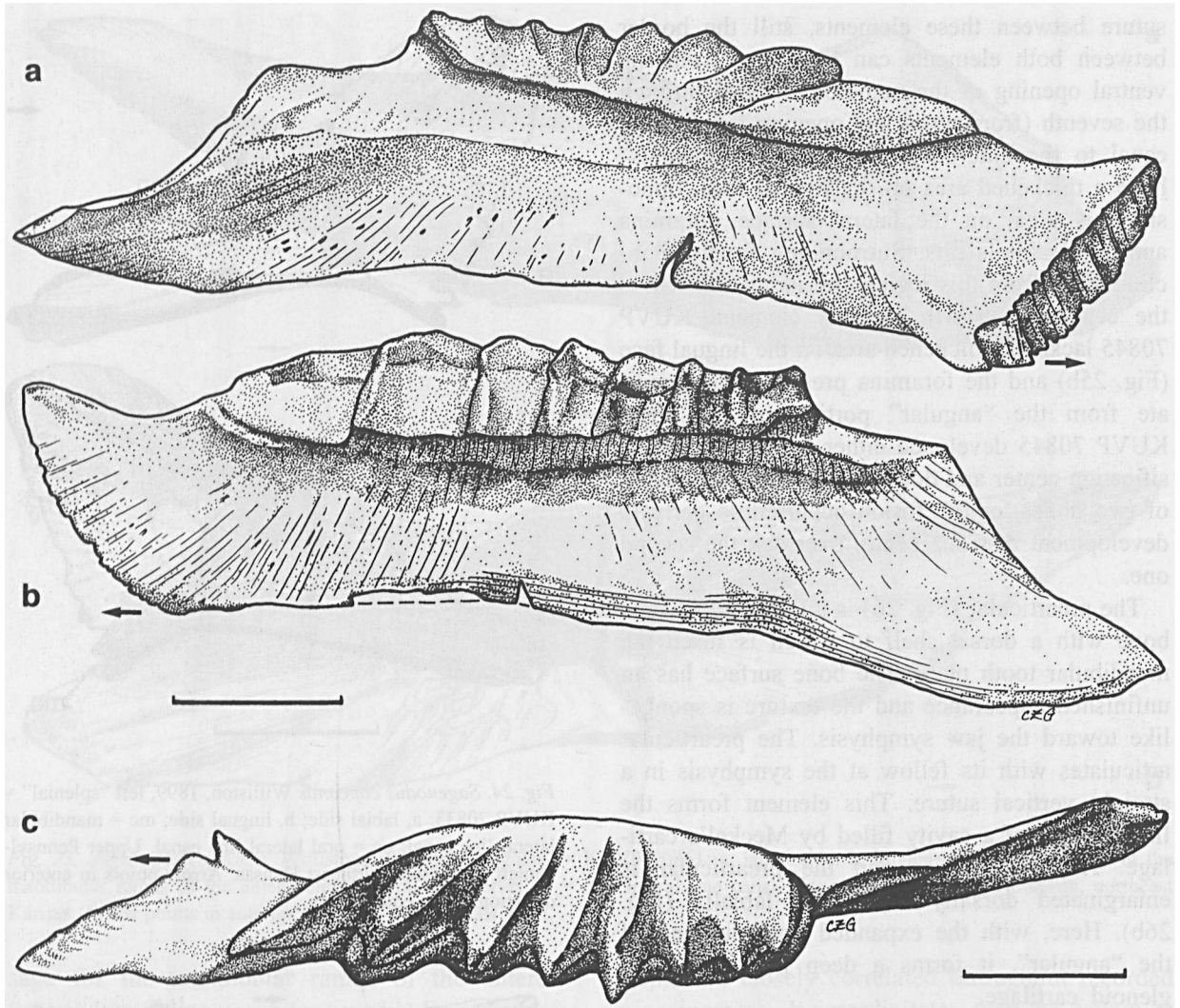
Fig. 26. Sagenodus copeanus Williston, 1899, left prearticular ✝ KUVP 70780: a, lingual side; b, labial side; c, dorsal view. Upper Pennsylvanian; Robinson, northeast Kansas. Arrows point in anterior direction. Scale equals 1 cm.

from the following ridge at a distinct angle and lies below the level of the second ridge. The angles between ridges decrease posteriorly with the last four ridges being subparallel with each other in some specimens.

In addition to wear, damage is also common on the occlusal surface. Of 26 more or less complete tooth plates, 8 or almost one third show a depression or gap in one of the ridges.

The upper, or pterygoid, tooth plate (Fig. 20b) is usually broader than the lower tooth plate, with a length-width ratio of 3.3 to 4.3. The number of ridges varies between 8 and 12 with 9 and 10

ridges being most common. The occlusal surface is mildly concave. Denticles are present only on the labial margin. The lingual margin approximates the curve of a circle in many specimens; in some, a shallow angle forms near the third ridge. Damage to upper tooth plates is rare in contrast to the lower. Only one specimen showed a small gap in a single ridge.

Upper and lower tooth plates occlude closely with ridges interdigitating. It follows from this alternation of ridges that the number of ridges should be similar for both upper and lower tooth plates.
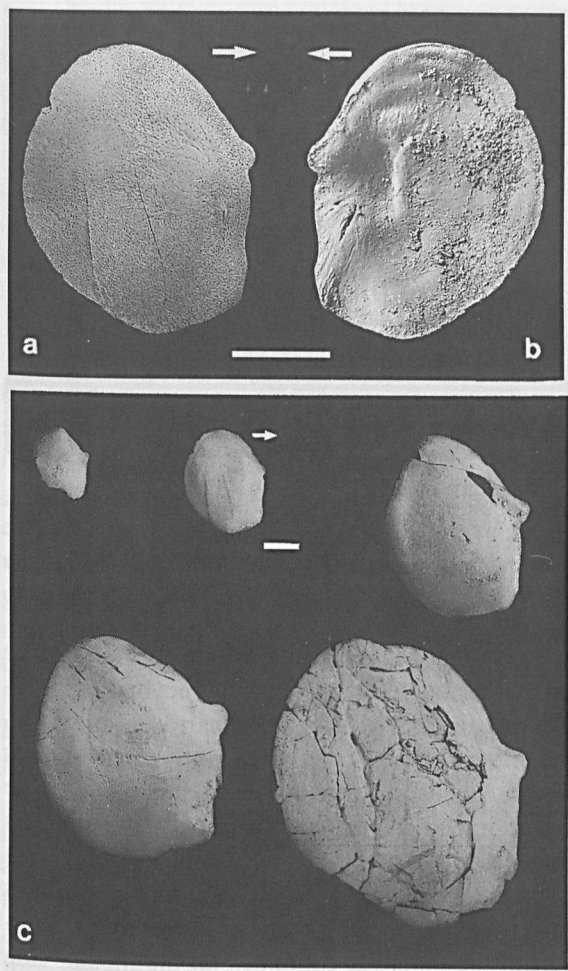
Fig. 27. Sagenodus copeanus Williston, 1899, a-b, right operculum = KUVP 70698; a, lateral side, b, medial side; c, size series of right opercula, from top left to bottom right: KUVP 70697, 70698, 70700, 70707, 70702. Upper Pennsylvanian; Robinson, northeast Kansas. Arrows point in anterior direction. Scale equals 1 cm.
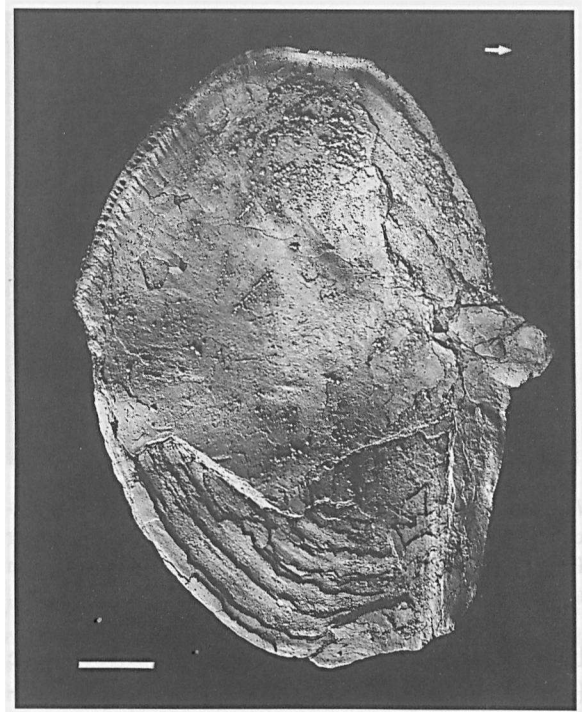

Fig. 28. Sagenodus copeanus Williston, 1899, left operculum = KUVP 70712, medial side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

Gill covers and branchial region. – The operculum (Fig. 27) is a stout bone of which more than 40 have been recovered. The bone is outwardly convex, with a regularly curved posterior and posteroventral margin. The dorsal margin is inflected inward immediately behind the tabulate process. The bone underlies a shelf formed by Y and abuts KX. The anterior margin ventral to the tabulate process is straight; here the posteroventral margin of bone KX and the posterior margin of bone 4 overlap the operculum. The anteroventral margin forms an angle of 115° with the anterior margin; it is straight or slightly embayed. Here the suboperculum underlies the operculum. The adult shape was attained in the smallest specimen recovered (2.07 cm), KUVP 70697 (Fig. 27c). This is the only specimen to exhibit a pattern of faint striations that radiate ventrally on the lateral surface, from a point immediately posterior to the tabulate process. These striae were also found in a small specimen by Fritsch (1888: pl. 76 fig. 4b). One specimen (KUVP 70712) fortuitously shows delamination of part of the medial surface, to reveal growth laminae (Fig. 28). Maximum depth is closely correlated with maximum length. The operculum lacks the distinct muscle scar left by the adductor operculi on the medial surface of some Early Devonian dipnoans (Campbell & Barwick, 1987). This muscle probably inserted on the edge of a shallow depression located posteroventral to the tabulate process (Fig. 27b). This depression is variably developed and is pronounced in only one small specimen, KUVP 70698. Three specimens
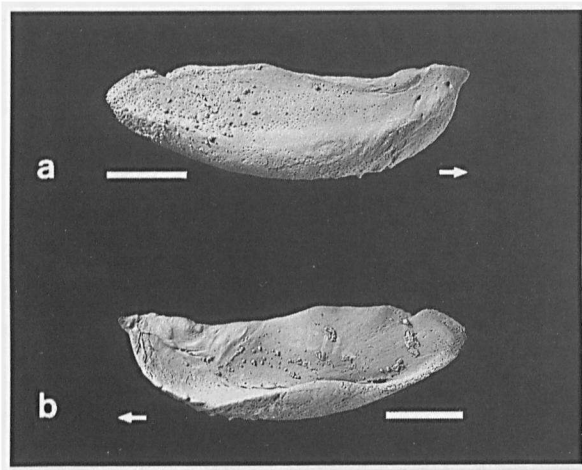
Fig. 29. Sagenodus copeanus Williston, 1899, right suboperculum = KUVP 71135: a, lateral side; b, medial side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrows point in anterior direction. Scale equals 1 cm.

Fig. 30. Sagenodus copeanus Williston, 1899, ceratohyal = KUVP 70718: a, lateral side; b, medial side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

have an additional depression on the medial face (KUVP 70707, 70716, and uncatalogued) posterior to the first one.

A suboperculum is present (Fig. 29). Its morphology is somewhat variable, underlying to large extent the anteroventral margin of the operculum; however, the exact orientation and position of the bone in the skull cannot be determined from dissociated material. The bone is plate-like, weakly convex laterally, and some specimens show a ridge that probably marked the ventral extent of the overlapping operculum. The largest specimen (KUVP 71135) has a ventral border that is inflected medially (Fig. 29b); several others show this to a much lesser degree. Watson & Gill (1923: fig. 16) described an element they thought could be a gular plate of *Sagenodus*. No similar examples occur in our collection and it is possible that these authors mistook a suboperculum for a gular plate. The element identified by Williston (1899: pl. 36 fig. 3) as a "subopercular (?)" is probably a partial operculum.

The ceratohyal (Fig. 30) is the only element known to ossify in the hyoid arch of *Sagenodus copeanus*. It is a perichondral ossification with thin walls. The central portion of the bone is constricted with only a narrow connection internally between the cartilage-filled posterior and anterior chambers. The anterior end flares and is ovate or approximately triangular in end view. A
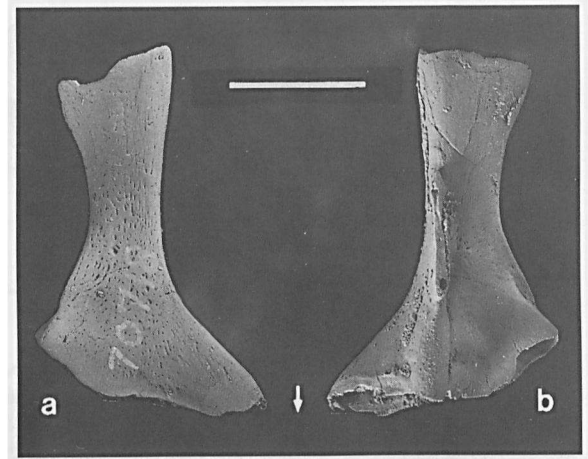
stout ridge appears on the posterior lateral surface and extends anteriorly somewhat beyond the midpoint of the bone. This ridge narrows anteriorly, becoming blade-like about halfway along its length, where it is pierced by a foramen. At the posterior end the ventral margin of the ridge is notched for a blood vessel. Some larger specimens have a tubular ossification to receive this vessel, on the medial surface, immediately adjacent to the notch. It continues on the medial side of the ceratohyal to the anterior end. The posterior end is flattened on the medial surface and expanded dorsoventrally. Posteriorly the ventral margin narrows to a sharp ridge, particularly so in the smallest specimen, KUVP 70718. Several specimens have a scar left by the mandibulohyoid ligament on the dorsolateral face, near the posterior margin. Williston (1899) was apparently first to tentatively identify this element correctly as the ceratohyal. Watson & Gill (1923) noted other interpretations in the literature and proposed that it was the quadrate (their fig. 11c and d) of *Sagenodus*.

Sensory canal system. – The sensory canal system in the skull of *S. copeanus* (Fig. 31) differs little from that figured by Westoll (1949: fig. 8A). However, the use of X-rays reveals a more elaborate pattern than previously recorded in other species of *Sagenodus*.

The main lateral line enters the skull roof through a small canal on the ventral surface of Z, at Z's posterior margin. It bifurcates and widens near the center of this element. From this point the cephalic division extends anteriorly and the occipital commissure medially. The sensory canal extends anteriorly below Y, in a ventrally opened or closed tube, as the cephalic division of the main lateral line.

The cephalic division sends numerous branches to the surface and lateral margin of Y, which is more extensively invested by the sensory canal system than any other bone. KX also shows numerous pores on the dorsal surface. As the sensory line extends forward it again becomes fully enclosed by bone within KX. It is in association with Y and KX that the enclosing canal attains its greatest diameter. Within KX, subsidiary canals may trend medially to penetrate J for a short distance, other branches run laterally to the edge of the skull roof. Slightly forward of the center of KX occurs the major bifurcation between the infraorbital and supraorbital sensory canal.

The supraorbital canal is slightly smaller in diameter than the infraorbital canal and trends anteromedially to enter LM. Near the middle of that bone the canal turns anteriorly, forming an angle of greater than 90°. From this point it runs forward in an approximately straight line through bones N and P. In P the canal curves anteromedially before entering the anterior marginal bones. The canal runs medially and somewhat anteriorly through a nearly enclosed tube on the ventral surface of the marginals. It passes below the posterior half of the lateral marginals and through the middle of the more medial elements in this series. The canal turns below the median element, or occasionally below two median bones.

The E-bone is normally without sensory canals but one example (KUVP 70875) shows a canal that must have run transversely from the supraorbital canal in P into the middle of the anterior end of E. From there a short branch extends posteriorly and another anteriorly, that bifurcates before reaching the anterior marginal bones.

Another, previously unrecorded, ramus of the supraorbital canal is almost invariably present and runs anterolaterally from the main canal in
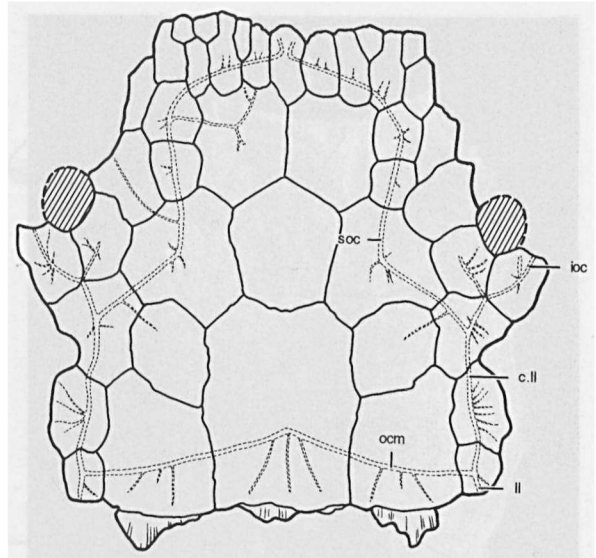

Fig. 31. Sagenodus copeanus Williston, 1899, composite skull roof, dorsal side, as in Fig. 3, course of the sensory canal system; c.ll = cephalic division of main lateral line canal; ioc = infraorbital lateral line canal; ll = main lateral line canal; ocm = occipital commissure; soc = supraorbital lateral line canal. Upper Pennsylvanian; Robinson, northeast Kansas.

LM immediately before the supraorbital canal enters N. Hence it proceeds diagonally across 3a to the edge of the bone in front of the orbit. Its diameter is somewhat less than the continuation of the supraorbital canal.

The infraorbital canal represents the ventrolateral arm of the sensory canal after the supraorbital canal branches. In *S. copeanus* the infraorbital canal extends from KX, exiting the bone approximately at the point of intersection of KX, 3b, and 4. Here the canal bifurcates, invading 3b for a short distance (a primitive feature found in Devonian lungfish, cf. Jarvik, 1980: fig. 333A, B). The infraorbital canal is restored entering the main body of 4 as in other *Sagenodus*. The infraorbital canal runs posterior and ventral to the orbit through 4, 5+6, 7, and 1. Small rami contact the surface at numerous points in 4, 5+6, and particularly along the anteroventral margin of element 7. The intersection with the preopercular canal is always present on the ventral border of 5+6. Element 1 is slender and much reduced. It has only a brief contact with element 7.

The oral canal passes through the "angular" and "splenial"; its pores form a row along the

Fig. 32. Sagenodus serratus (Newberry, 1874), bone B (= MCZ 8448-100), dorsal side, with posterior pit-line. Lower Permian; east of Throckmorton, Throckmorton County, Texas. Arrow points in anterior direction. Scale equals 1 cm.

middle of the lower jaw (Figs. 23–25). The oral canal enters the "angular" through a pore on the outside of the posterior end of the "angular", approximately at middepth. Usually one pore opens along the suture between "angular" and "splenial". The canal changes its direction to anterodorsal in the "splenial", where it ends with a pore close to the anterodorsal tip of the "splenial". One or two pores mark the connection between the oral and mandibular canal in the "splenial". The mandibular canal has pores only in the "splenial". It runs posteriorly in a furrow on the ventral margin of the "angular". Oral and mandibular canals connect to the infraorbital canal in bone 5+6. The intervening course through soft tissue may be surrounded by ossifications. Small ossifications bearing canals have been found but they cannot be assigned with certainty to the region.

The occipital commissure extends transversely

across the hind part of the skull, through Z, I, and B. Posteriorly directed subsidiary canals run to the hind margin of the skull in I and B. Typically there are three in B. Number and pattern are more variable in I but one ramus often extends laterally to exit the bone medial to the union of I with Z. Upon leaving I, the sensory canal enters an enclosed tube on the ventral surface of Z.

Watson & Gill (1923) and Westoll (1949) observed pit-lines in some specimens of *Sagenodus* from the British Isles. Pit-lines have not been reported previously from North American *Sagenodus*; however, one example of J (KUVP 70880) shows part of the anterior portion of the posterior pit-line, and examples of B from Texas (MCZ 8448-98 and -100, Fig. 32) show the posterior portion of the posterior pit-line on both sides.

Shoulder girdle. – The shoulder girdle of *S. copeanus* is stoutly constructed and comprises three paired elements: anocleithrum, cleithrum, and clavicle.

The anocleithrum (Fig. 33a) is a thin blade behind the skull roof and dorsal to the cleithrum. Its most robust portion is a narrow salient that projects anteriorly to articulate with the tabulate process of the I-element. It has an attachment area for a ligament. The attachment area lies at the end of the salient in adult specimens (KUVP 70262), but farther posterior near the center in small specimens (KUVP 103108). The ventral portion of the lateral surface is overlapped by the cleithrum. The sides of the anocleithrum converge ventrally to form a broadly rounded apex. Posteriorly the bone terminates in a sharper point that is notched ventrally. On the medial face of one specimen (KUVP 70862, Fig. 33b) two subparallel ridges trend dorsoventrally and a narrow straight ridge extends posteriorly just dorsal to the notch on the hind margin of the anocleithrum.

The largest component of the cleithrum (Fig. 34a) is the triangular, branchial lamina. It lies transversely in the posterior wall of the gill chamber. The branchial lamina is continuous with a thick lateral rim that forms a stout ridge on the posterior surface (Fig. 34b) of the cleithrum. On the lateral surface (Fig. 35) a pair of ridges run
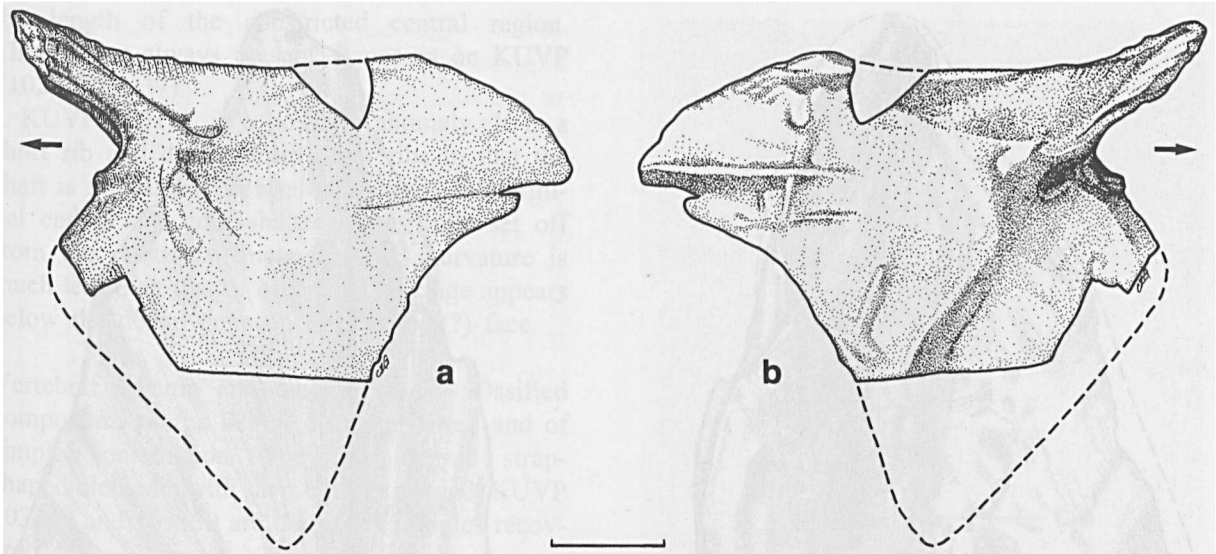
Fig. 33. Sagenodus copeanus Williston, 1899, left anocleithrum = KUVP 70862: a, lateral side; b, medial side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrows point in anterior direction. Scale equals 1 cm.

dorsoventrally; they are confluent with the two ridges on the ventrolateral face of the clavicle. These ridges on the cleithrum are subparallel but diverge dorsally. The area below the branchial lamina (Fig. 34a) is inflected anteriorly; it is received by a pouch in the articular process of the clavicle. Lateral to this area, the articular surface curves to form a ventrally directed process that wraps around the dorsolateral and posterior surface of the clavicle (Fig. 36b).

The cartilaginous scapulocoracoid left only faint impressions of its attachment on the ventral part of the posterior side of the cleithrum and the dorsal part of the posterior side of the clavicle. In cleithrum KUVP 70737 (Fig. 34b), an anomalous small spur of bone on the medial ridge marks the approximate dorsal extent of the attachment of the scapulocoracoid. Where the branchial lamina and the ventral process of the cleithrum form a right angle, the scapulocoracoid reaches over to the clavicle where it has only a small attachment area in the middle of the posterodorsal side.

The blade of the clavicle curves toward the ventral midline and terminates in a straight sharp edge. As it does so, the bone thins and its borders diverge. The branchial lamina forms a medially directed blade (Fig. 36a). A groove is present on the medial face in the area between the blade and the branchial lamina. Dorsolaterally the bone thickens and an attachment process for the clei-

thrum extends medially at a steep angle to the blade. The anterior face of the dorsal end is concave and dorsomedially the attachment process forms a pocket to receive the cleithrum. The area of attachment between these elements is triangular in shape and wraps around the dorsal end of the clavicle onto its posterior face. Laterally two ridges (Fig. 35) appear along the dorsal half of the ventral surface of the clavicle, and diverge to form a trough toward the area of attachment with the cleithrum.

The clavicle of *S. copeanus* resembles that of *Neoceratodus* in that two ridges are present on the lateral surface of the clavicle in *Neoceratodus*. Position and blade-like nature of the branchial lamina are also similar but this lamina is relatively smaller in *S. copeanus*. The clavicles of these two dipnoans also differ in several ways. That of *Neoceratodus* shows the reduction of bone mass that characterizes the entire skeleton of this genus. The blade of the clavicle is straplike and the posterior lip of the blade is folded anteriorly. In *S. copeanus* the blade is triangular in ventral view and the posterior edge is only slightly inflected medially.

Ribs. – Ribs tend to be well developed in most dipnoans and *Sagenodus* is no exception. A typical rib is constructed of dense bone around a narrow canal. They are round or ovate in cross-
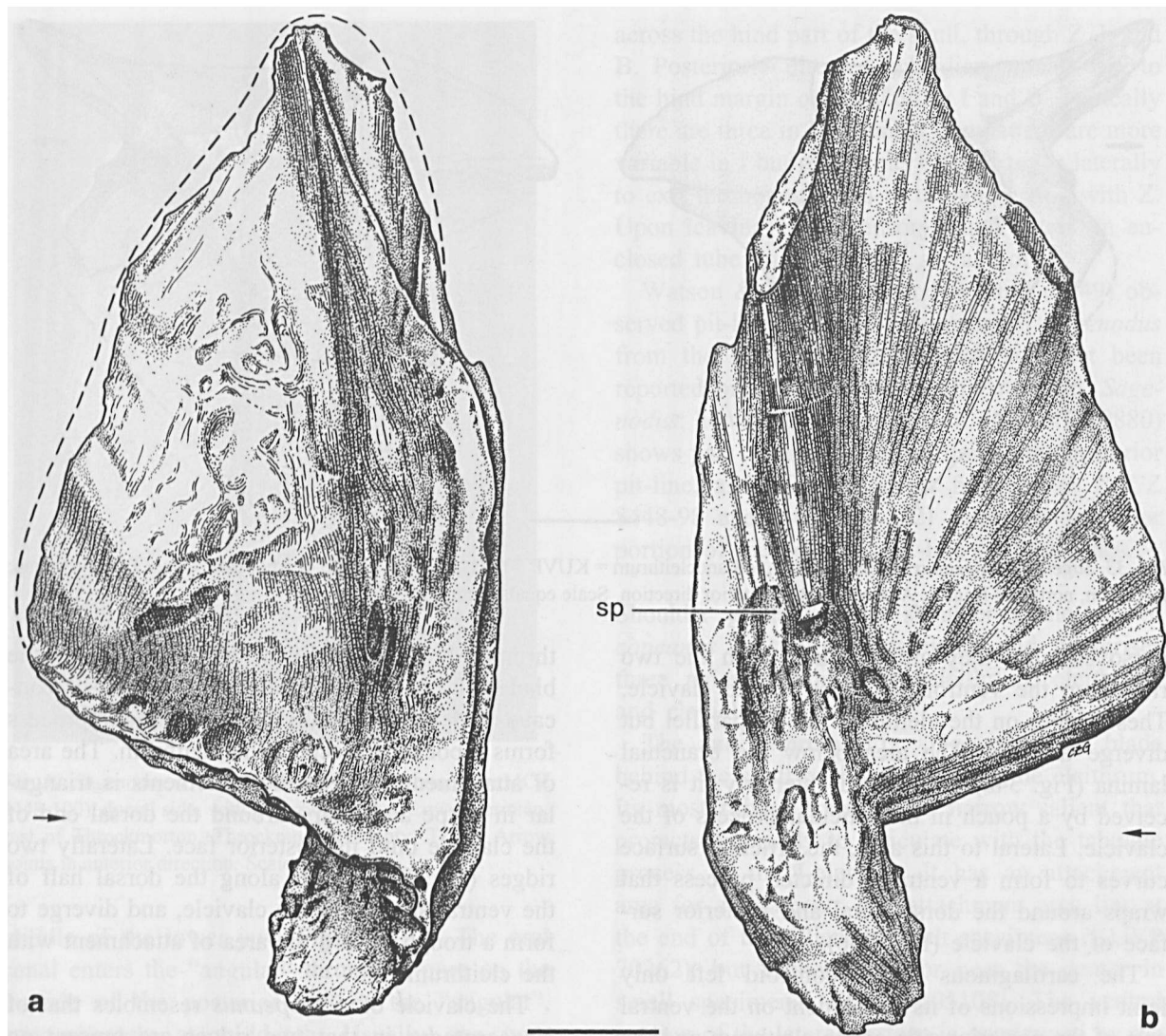
Fig. 34. Sagenodus copeanus Williston, 1899, left cleithrum = KUVP\70737: a, anterior side; b, posterior side; sp = small spur (= dorsal extent of attachment of scapulocoracoid). Upper Pennsylvanian; Robinson, northeast Kansas. Arrows point laterad. Scale equals 1 cm.

section, tapering slightly to a cartilage-filled tip (open because the cartilage is not calcified or ossified) ventrally. The shaft is gently curved with the curvature increasing dorsally toward the flared, cone-shaped end near the vertebral column. Individual ribs may lie in a single plain or deviate slightly from this condition. The inner curvature is more or less uninterrupted, while the outer curvature is reflected dorsally, forming an obtuse angle where the shaft joins the terminal cone. A groove is sometimes present distal to the terminal end. Swellings are occasionally found on the shaft (Rothschild & Martin, 1993: fig. 19-4, representing *S. copeanus* ribs from Robinson lo-

cality). They are comparable to those figured by Fritsch (1888: pl. 79), and are thought to represent healed fractures.

A feature found only in lungfishes is the enlarged first, or cranial rib, thought to facilitate hyoid depression (Bemis, 1987). KUVP 71021 and 71022 are the most complete. This rib is a thin-walled tube, compressed and expanded at both ends to form flattened ends. These ends are joined by a narrow shaft and lie at approximately 45° to each other. They are perichondrally ossified and filled with cartilage, but hollow for most of their length in fossil condition. A narrow ridge is developed on the medial surface and trending

the length of the constricted central region. Though not always present, it occurs on KUVP 71021 (Fig. 37).

KUVP 103128 is a possible anomaly. It is a short rib and differs from other ribs in that the shaft is not tapered ventrally. Dorsally the terminal end is still cone-shaped but is little set off from the relatively thick shaft. Its curvature is much less than that of other ribs. A ridge appears below the dorsal cone on the anterior(?) face.

Vertebral column and median fins. – Ossified components of the neural arch are paired and of simple construction. They are curved strap-shaped elements with their ends expanded. KUVP 103129 and 103130 are the only examples recovered.

Little can be said about the median fins based on dissociated material, therefore the following description is brief and tentative. The longest elements are the spinous component of the neural arch and the haemal arch and spine. The neural spines may be of delicate construction with a narrow space between the two openings at the proximal end. One element (KUVP 103132) is expanded proximally in the transverse plain, constricted at the center of the shaft, and moderately expanded in the median plain at the open-ended distal tip. Another (KUVP 71027) is similar except that the spine is approximately tubular above the proximal bifurcation.

Haemal arches and spines ossify as a single unit, are more robust than neural spines, and have a deep V-shaped bifurcation proximally. Distally the shaft tends to be flattened in the transverse plain. Anomalies may occur, such as the fusion of two haemal spines along much of their length (KUVP 103133, Fig. 38). One specimen (KUVP 71028) has a scoop-shaped expansion on the distal end.

Sagenodus from Hamilton Quarry

Material. – See Appendix 2B.

Locality. – Quarry 3 km east of Hamilton, Greenwood County, central eastern Kansas, U.S.A. (Fig. 1: 2). The preservation of
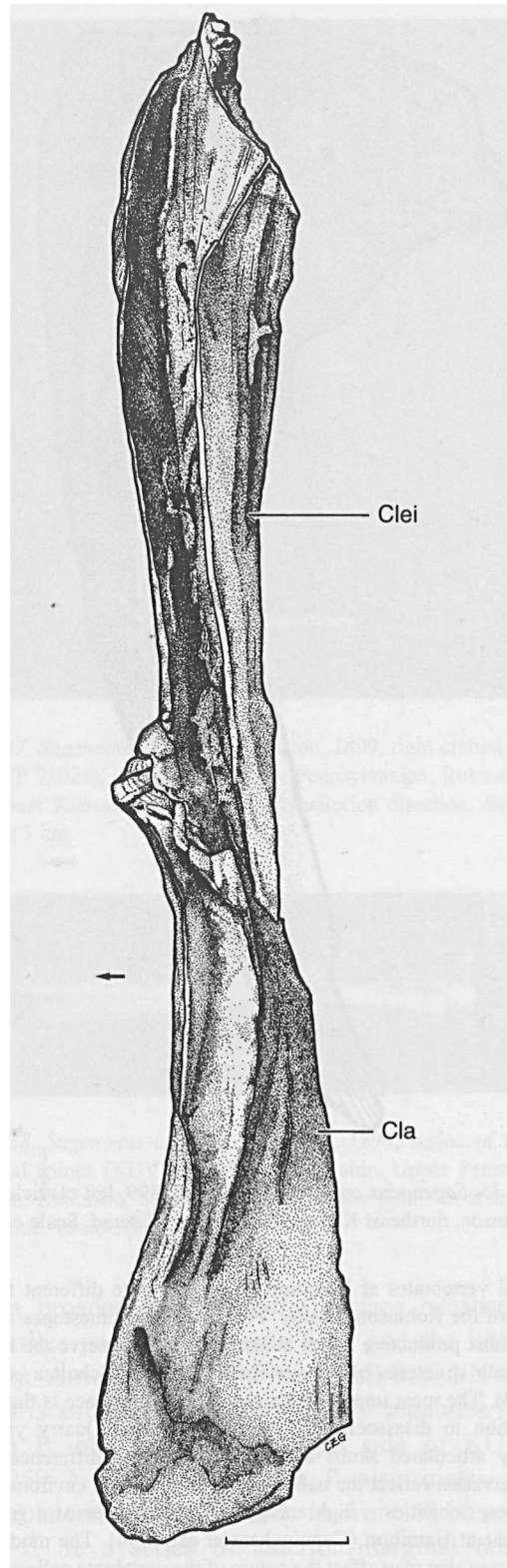

Fig. 35. Sagenodus copeanus Williston, 1899, left cleithrum (KUVP 70737, Clei) and clavicle (KUVP 70964, Cla), in lateral view. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.
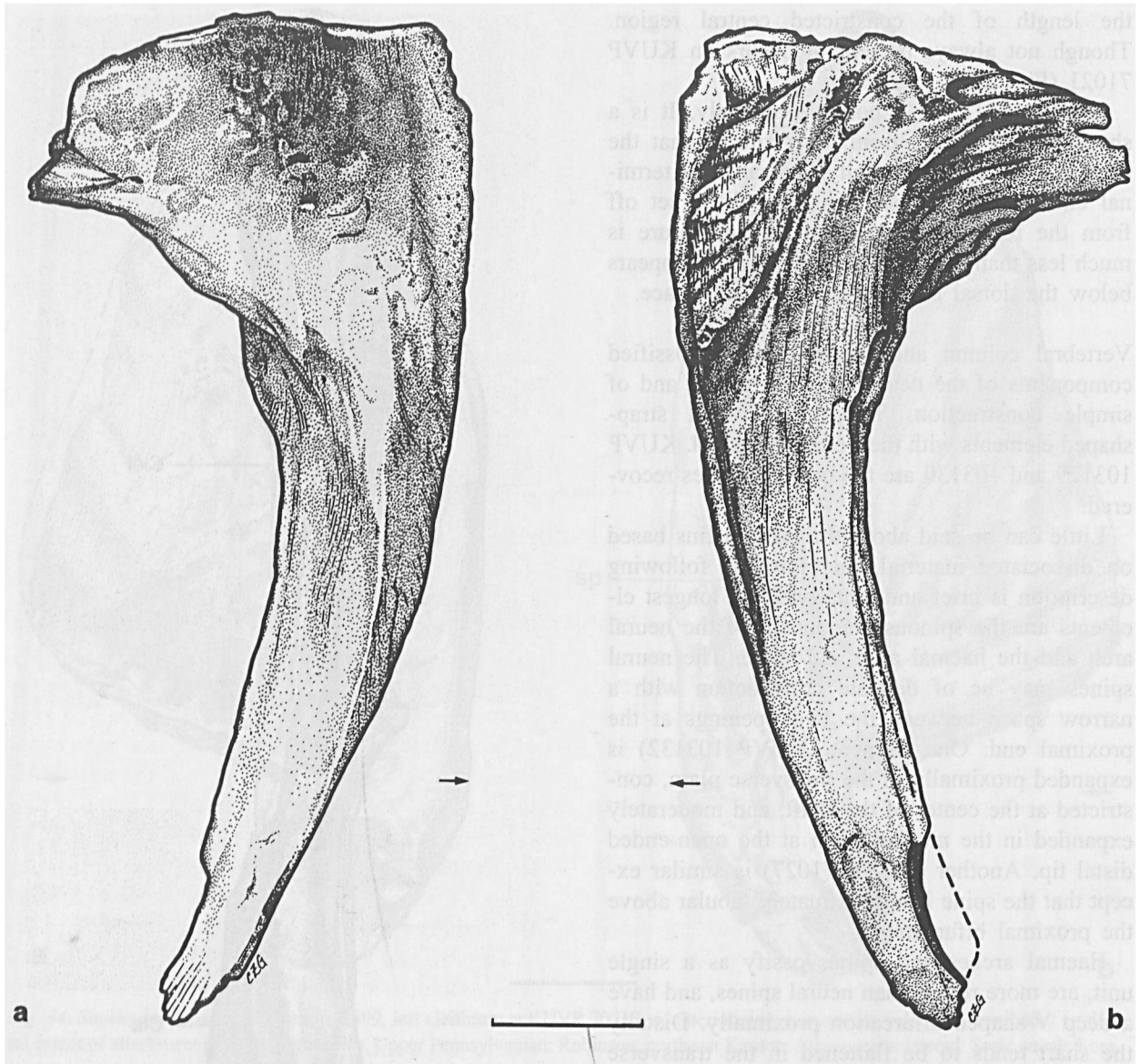
Fig. 36. Sagenodus copeanus Williston, 1899, left clavicle = KUVP 70964: a, anterior side; b, posterior side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrows point laterad. Scale equals 1 cm.

fossil vertebrates at Hamilton Quarry is quite different from that of the Robinson locality. Fine laminated limestones form the most productive layers at Hamilton and preserve the most delicate structures of the vertebrate skeleton (Schultze et al., 1994). The most important preservational difference is that, in addition to disassociated elements, Hamilton Quarry yields many articulated skulls and skeletons. These differences in preservation reflect the nature of the depositional environment at these localities – high energy at Robinson versus a gentle current at Hamilton (Cunningham et al., 1994). The mode of recovery also may affect the nature of the vertebrate collections from these two sites. For example, the scales of *Sagenodus* are typical of lungfish in being extensively subdivided. These scales would disintegrate rapidly when exposed by acetic acid,

the technique used on almost all specimens from Robinson. However, intact *Sagenodus* scales are often found on the bedding planes of the fine laminated limestones from Hamilton Quarry. Taken together, material from these two sites complements each other; isolated elements from Robinson can be studied in three dimensions and the articulated complete skeleton from Hamilton permits the restoration of entire *Sagenodus* (Fig. 39).

Complete specimen (Fig. 39). – The complete specimen, KUVP 84201 (Chorn & Schultze, 1989: fig. 2, and the cover of Geotimes, 33(7), July 1988), is flexed into a U-shape with the skull

drawn laterally and dorsally toward the tail. The caudal and posterior abdominal regions are preserved in lateral view, whereas the main portion of the abdominal region and the head are compressed dorsoventrally. Most of the bones of the skull roof are attached to the counterpart with only the ventral surface visible. On the left lateral side, portions of pterygoid, prearticular, and angular are visible in section. The opercula are flattened out into the horizontal plain. Behind the left operculum, the anocleithrum and the dorsal portion of the cleithrum are visible.

The complete specimen reached a total length of 35 to 36 cm. The isolated elements from Hamilton Quarry are all larger than the corresponding elements in the articulated specimen. Most of these elements derived from individuals that were two or three times the size of the articulated specimen. Assuming isometric growth, larger individuals were approximately 1 m in total length. Head length (snout to posterior margin of bone B) is approximately equal to abdominal body depth, or one seventh of total length. The abdomen is slightly· longer than the caudal region without including the fin rays at the tip of the caudal fin. These proportions give the fish an elongated body shape.

Skull roof. – The isolated skull roof (KUVP 103259, Fig. 40; Schultze, 1993: fig. 2) preserves all but the most lateral elements in the posterior half and, on the left side, the whole suite of bones between the orbits and the median anterior marginal bones in the anterior half of the skull. The lateral canal-bearing bones of the posterior half are preserved on the skull of the complete specimen (KUVP 84201), seen in dorsal view on the right. Their counterparts on the left and the median cranial elements are seen in ventral view. The rectangular median B-bone, the largest of the skull roof, is surrounded by bones I, J, LM, and C. The unpaired median C-bone is met anteriorly by the paired E-bone. Anteriad the I-bone extends laterally, so that it surrounds bone J posterolaterally and reaches bone KX. Bone J is smaller than the I- and the LM-bone; in ventral view it appears even smaller. The LM-bone has a triradiate appearance on the outside, whereas it ap-
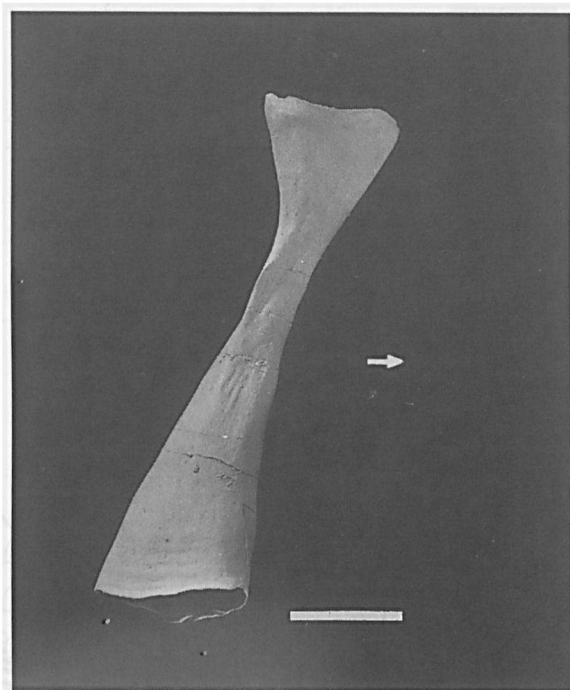
Fig. 37. Sagenodus copeanus Williston, 1899, right cranial rib (KUVP 71021), medial side. Upper Pennsvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

Fig. 38. Sagenodus copeanus Williston, 1899, fusion of two haemal spines (KUVP 103133), lateral side. Upper Pennsylvanian; Robinson, northeast Kansas. Arrow points in anterior direction. Scale equals 1 cm.

pears broader on the ventral surface because it underlies portions of bones I, C, and the lateral bones. Anterior to LM lie the small bones N and P. N is smaller than P and usually separates LM from P; however, on the right side of KUVP 103259 N is so small that P also meets the anterolateral margin of LM. In front of bones P and E lie a series of anterior marginal bones (bones Q to F). In KUVP 103259, a median unpaired anterior marginal bone (bone F) lies in front of the suture between the paired E-bones,

Fig. 39. Sagenodus copeanus Williston, 1899, restoration of entire specimen, lateral side, after KUVP 84201. Upper Pennsylvanian; Hamilton, central eastern Kansas. Scale equals 1 cm.
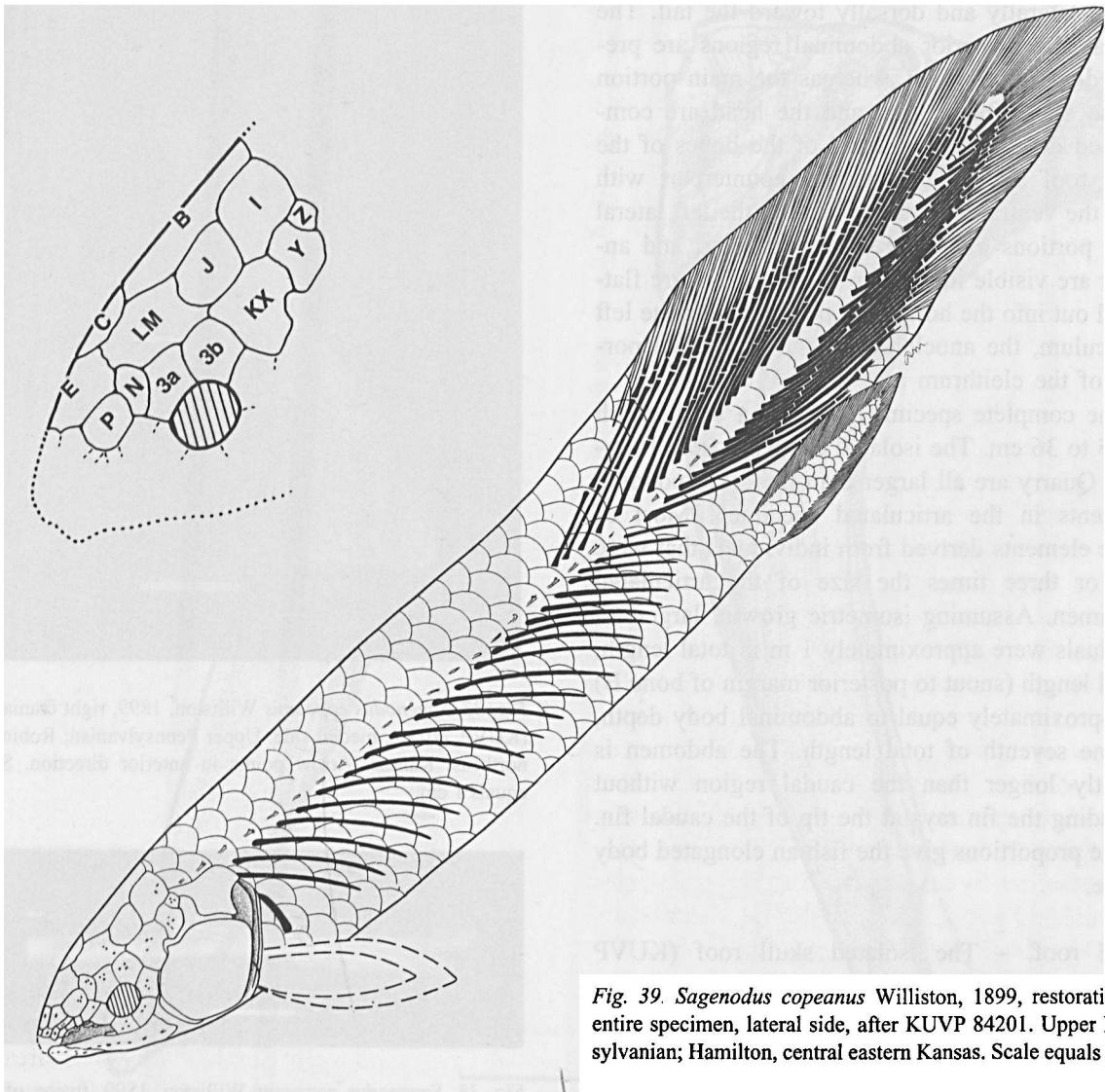
whereas a pair of anterior marginal bones occupies this position in KUVP 84201. The elongated anterior marginal bones are preceded anteriorly by irregularly shaped marginal bones that are usually of smaller size. The lateral line bearing bones, lateral to bones I and J, are not preserved in KUVP 103252, but their length can be determined by the emargination at the lateral margin of bones I and J; bone Z reaches approximately one half to three quarters the length of bone Y. Bones Y and KX form the notch for the tabulate process of the operculum. In front of the notch, bone KX has a straight margin that aligns with the operculum.

The circumorbital bones 3a and 3b lie between the orbit and bones KX, LM, N, and P; 3a being longer than 3b. On the left side of KUVP 84201, we see the inside of bone 4 covered partly by the operculum; other circumorbital bones are not preserved. Anterior to bone 3a and lateral to bone P, a series of small bones with lateral line canal pores form a continuous arcade with the anterior marginal bones.

The lateral line canals of the isolated skull are traceable by pores or, as in the case of the occipital commissure, by the canal itself (Fig. 40), visible because the dorsal layers of the bone adhered to the counterpart. The occipital commissure is

inclined slightly forward from the growth center of bone I towards the growth center of bone B. In both I-bones, one branch of the canal runs posteriorly from the growth center. The occipital commissure joins the main lateral line canal in bone Z. The cephalic division of the main lateral line canal passes through Y (with many pore openings) into KX where it bifurcates into the supraorbital and infraorbital canal. A branch of the infraorbital canal extends into bone 3b where it opens to the surface through several pores. The infraorbital canal cannot be followed because only the inside of bone 4 is exposed on KUVP 84201. Sensory canal pores extend into the posterolateral arm of the triradiate LM. The supraorbital canal continues from LM to N and P into the anterior marginal bones where both sides meet in a median unpaired bone (F), or in median paired anterior marginal bones. In skull roof KUVP 103259, the supraorbital canal seems to pass from P into O and then into lateral marginal bones so that it forms a half circle before entering the marginal bone in front of bone E. This reconstruction of the course of the supraorbital canal is supported by the lateral position of the canal in isolated P-bones of *Sagenodus copeanus* from Robinson; the anterior end of the canal is directed anterolaterally on the inside of the P-bones. From pores in bones 3a, it can be assumed that the supraorbital canal gives off subsidiary canals into bone 3a from LM, or N.

Palatal region. – Two incomplete parasphenoids have been collected; KUVP 103262 has been prepared with acetic acid. In both specimens, the stem is preserved best but is not complete. The lozenge was damaged in preparation. The stem is flanked dorsally by laterally flared borders which converge anteriorly towards the midpoint of the lozenge. On the dorsally arched dorsal side of the stem is a concavity bordered by subparallel ridges. This depression terminates anteriorly behind a median ridge that extends onto the lozenge.

Lower jaw. – The left prearticular, KUVP 103261 (Fig. 41), was prepared with acetic acid using the transfer method of Toombs & Rixon (1950). It is
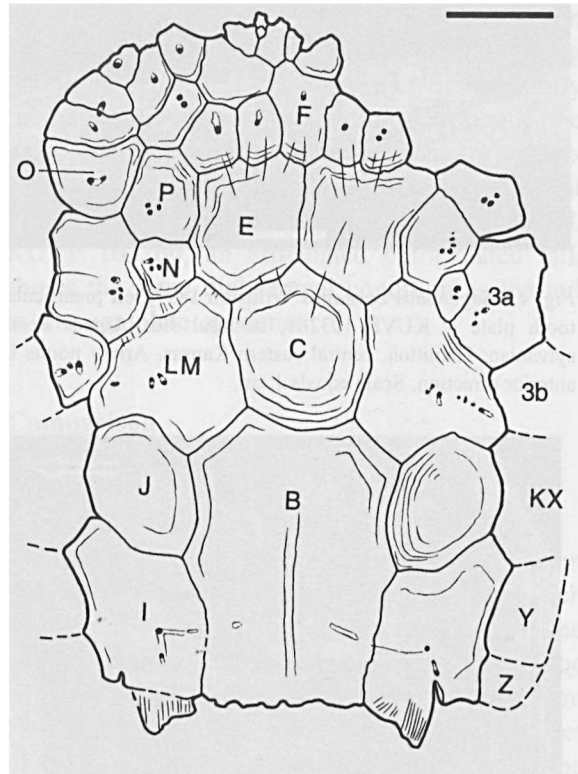

Fig. 40. Sagenodus copeanus Williston, 1899, skull roof = KUVP 103259, dorsal side (B, C, E, F, I, J, KX, LM, N, O, P, Y, Z, 3a, 3b, skull roofing bones). Upper Pennsylvanian; Hamilton, central eastern Kansas. Scale equals 1 cm.

nearly three times (2.9) longer than the length of the prearticular visible in longitudinal section in the complete specimen, KUVP 84201. The tooth plate sits on an elongated prearticular that ends anteriorly with a symphysial attachment area for the opposing prearticular. The dorsal margin of the prearticular slopes down from the median anterodorsal tip towards the attachment area of the tooth plate. The tooth plate extends linguad and labiad over the prearticular; on the labial side tooth plate and prearticular form a shelf that extended over the "angular". The posterior part of the prearticular is broken and displaced ventrally. Minimum length, based on this broken specimen of KUVP 103261, was 70 mm.

The tooth plate is narrow and long (length-width ratio of 4 : 1). There are eight well-developed ridges separated by deep valleys plus two small ridges at the posterior end. Each ridge shows denticles on its ventrolateral margin, the largest denticle lying most ventral and labial. The
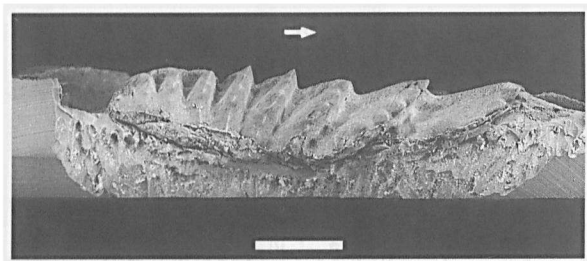
Fig. 41. Sagenodus copeanus Williston 1899, left prearticular tooth plate = KUVP 103261, occlusal side. Upper Pennsylvanian; Hamilton, central eastern Kansas. Arrow points in anterior direction. Scale equals 1 cm.
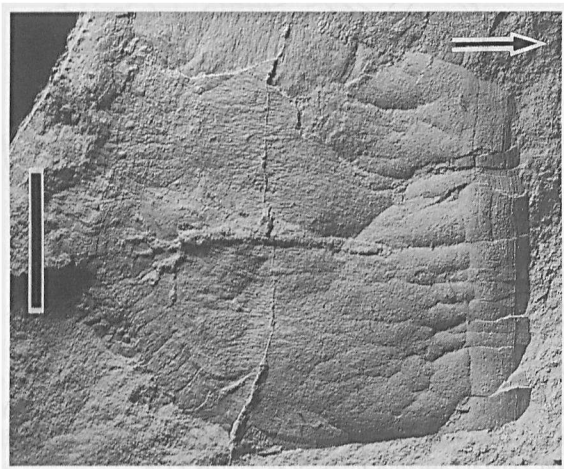

Fig. 42. Sagenodus copeanus Williston, 1899, lateral line scale = KUVP 103266a. Upper Pennsylvanian; Hamilton, central eastern Kansas. Arrow points in anterior direction. Scale equals 1 cm.

superficial enamel covers the lateral sides of the ridges, but it does not reach ventrally as far as the last, most ventral denticle except on the first ridge. On the surface of the tooth plate, the enamel is abraded and pleromic tissue exposed.

The main part of one right "angular", KUVP 103282, shows the medial surface and the impression of it on the counterpart. The dorsoventrally widened posterior part slopes posteroventrally in two distinct embayments with a posterior elevation in the middle of the slope. The course of the nervus facialis can be traced along the medial face of the "angular."

Gill cover. – The medial surface of an isolated right operculum, KUVP 103281, shows a shallow

depression ventral to the tabulate process as in specimens from Robinson. Anterior to the tabulate process, the border is straight; it forms a right angle with a somewhat concave anteroventral border for the articulation with the suboperculum. Posterior and dorsal borders are convex.

Both left and right operculum are placed lateral to the head on the complete specimen. The tabulate process enters a notch formed by the posterolateral margin of bone KX and the anterolateral margin of bone Y. The straight margin anterior to the tabulate process articulates with bone KX and the postorbital bones 4 and 5+6. The suboperculum is not visible.

Scales. – The scales are the most common isolated elements (25 isolated scales) of *Sagenodus* at Hamilton (Fig. 42). The rounded scales of *Sagenodus* have the typical composition of modern lungfish scales, including radial striae that are cut by furrows into irregular plates (Kerr, 1955). These plates are elongated and rectangular in the anterior covered region of the scale, and nearly square at the posterior exposed field of the scale. The surface of the scales is smooth with concentric growth lines. At the posterior margin the radial striae appear more distinct. The scales are elongated with a straight anterior margin in the anterior flank region; otherwise they have a rounded anterior and posterior margin. The isolated scales range in length from 22.5 to 37 mm, compared to a maximum of 16 mm in the anterior abdominal region of the articulated specimen.

The lateral line scales (Fig. 42) show the branching of the lateral line canal in the exposed field of the scales. The lateral line canal opens to the surface through many small pores in addition to the main opening between the lateral line scales.

The natural relationships of the abdominal scales are obscured by lateral spreading caused by dorsoventral compression of the body. Fortunately, in some regions a partially correct overlapping of scales is preserved. Twenty plus scale rows are estimated for the abdominal region, based on scale size and preserved overlapping. Segments of the ribs appear between scales; they are reconstructed in Fig. 39 in a one to one rela-

tionship with the scale rows. However, this rela-
tionship cannot be definitely established with the
specimen in hand.

Caudal region. – The caudal region begins in
front of the base of the pelvic fin with a haemal
arch and spine that is thicker than the ribs. The
caudal region shows the internal support for the
caudal fin very nicely. Ventral to the notochord,
a series of haemal arches with spines is followed
distally by two ventral radials, a proximal long
radial and a short distal radial that is covered
partially by the bases of the fin rays. Dorsal to the
notochord, the same number of neural elements
and radials are present. Neural spines are present
but their number and shape cannot be determined
throughout most of the abdominal region because
they are obscured by scales. The proximal dorsal
radials are longer than the distal ones which are
covered by the bases of the fin rays. Scales are
present lateral to the notochord and diminish in
size towards the tip of the diphycercal tail. There
are approximately as many neural and haemal
arches and spines as there are scale rows. There
are 27-28 scale rows or body segments in the
caudal region. The scales lateral to the notochord
carry the lateral line; these scales are preserved in
more or less original contact in the anterior cau-
dal and posterior abdominal region. Single lateral
line canals appear in scales along the abdominal
region. The lateral line canal and its branchings
are filled with clear calcite.

Of the paired fins, only the pelvic fin is pre-
served; it was mistakenly interpreted as the anal
fin by Chorn & Schultze (1989). Fin rays sur-
rounding an elongated lobe with small scales are
visible on part and counterpart. The pelvic fin lies
below the third haemal arch and at the level of
the anterodorsal extension of the caudal fin. The
length of the pelvic fin corresponds to the depth
of the body at its insertion, and is approximately
one seventh the total body length (snout to poste-
rior tip of caudal fin). There is a continuous fin
web supported by fin rays around the caudal re-
gion beginning dorsal to the base of the pelvic fin
and ending ventrally at a point about half the
length of the caudal region behind the pelvic fin.
The fin rays overlap each other in the dorsal fin

web of the caudal fin, but there is no interruption
within the fin rays or within the supporting
radials to separate a dorsal or anal fin. Ventrally
the caudal fin rays do not extend forward to the
most anterior ventral radial; the first fin rays at-
tach to the sixth distal radial. This arrangement
may indicate that the anal fin was not formed.
KUVP 103260, an articulated but isolated tail,
shows the same diphycercal condition as the tail
in the complete specimen.

Comparison

Sagenodus from Robinson and Hamilton

The occurrence of isolated elements at Robinson
locality affords us the opportunity to study each
bone from all aspects. The reconstruction of the
skull roof from these isolated elements can be
compared with the articulated skull roofs from
Hamilton Quarry. As noted previously, the bones
of the articulated skull roof are smaller than the
isolated bones recovered from Hamilton Quarry.
All bone measurements from the articulated skull
roofs from Hamilton Quarry are also at the lower
end of the size range of comparable bones from
the Robinson locality. Only one smaller I-bone,
one smaller C-bone and one smaller operculum
were recovered from Robinson. However, width/
length ratios still correspond; the bones from
Hamilton appear on or close to the regression line
established from the more numerous material of
Robinson. An exception is the B-bone of KUVP
103259 from Hamilton; it is much smaller than
any B-bone from Robinson, being slightly more
than half the length (58%) of the smallest B-bone
from Robinson. This is the only bone which does
not fall close to the regression line of bones es-
tablished from Robinson. It is longer relative to
its width compared with most Robinson B-bones.
This may indicate that the posterior skull roof
grows wider relative to length with age. Never-
theless, with only one exception, width/length
ratios of different bones are not distinct between
the articulated skull roofs from Hamilton and the
reconstructed skull roof from Robinson.

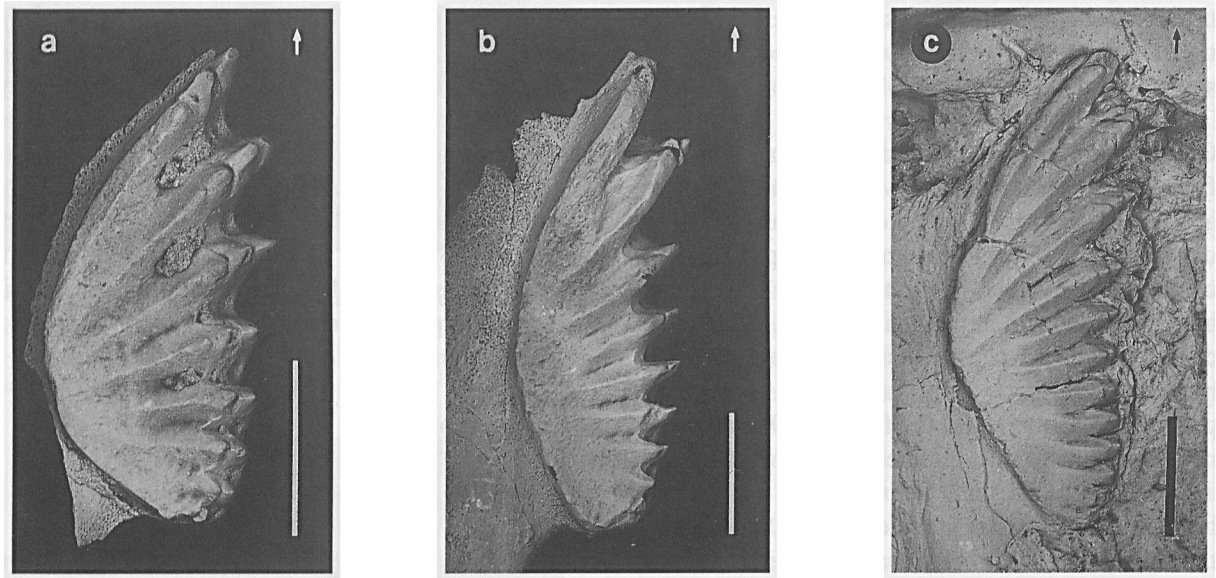The shapes of single bones from Hamilton and

Fig. 43. Left upper (pterygoid) tooth plates, occlusal side: a, *Sagenodus serratus* (MCZ "GGG"-162); b, *S. copeanus* (KUVP 70812); c, *S. periprion* (MCZ 9183 – 199). Specimens dusted with NH_4Cl. Arrows point in anterior direction. Scales equal 1 cm.

Table II. Tooth plate data of the three North American species of *Sagenodus*. Greatest width of upper tooth plates were measured between ridges 3 and 4, and of lower tooth plates between ridges 4 and 5.

|	Upper jaw				Lower jaw			
	length	width	ridges	L/W	length	width	ridges	L/W
S. serratus								
Mean	3.48	1.33	7.59	2.61	3.50	0.92	7.54	3.87
SD	1.01	0.38	0.61	0.21	0.65	0.22	0.64	0.45
Min.	0.95	0.4	6	1.94	0.97	0.31	6	3.13
Max.	5.48	2.08	9	3.13	4.47	1.39	9	5.16
n	116				65			
S. copeanus								
Mean	3.51	0.93	9.67	3.80	3.50	0.77	8.68	4.64
SD	0.89	0.23	1.05	0.30	0.67	0.20	0.72	0.57
Min.	1.65	0.42	8	3.29	2.36	0.44	8	3.68
Max.	4.55	1.16	12	4.27	4.95	1.22	10	5.71
n	15				22			
S. periprion								
Mean	4.32	1.15	10.75	3.73	4.58	1.11	11.86	4.14
SD	1.07	0.19	0.95	0.41	0.74	0.18	1.07	0.39
Min.	3	0.94	10	3.19	3.5	0.81	11	3.62
Max.	5.25	1.36	12	4.2	5.77	1.33	13	4.66
n	4				7			
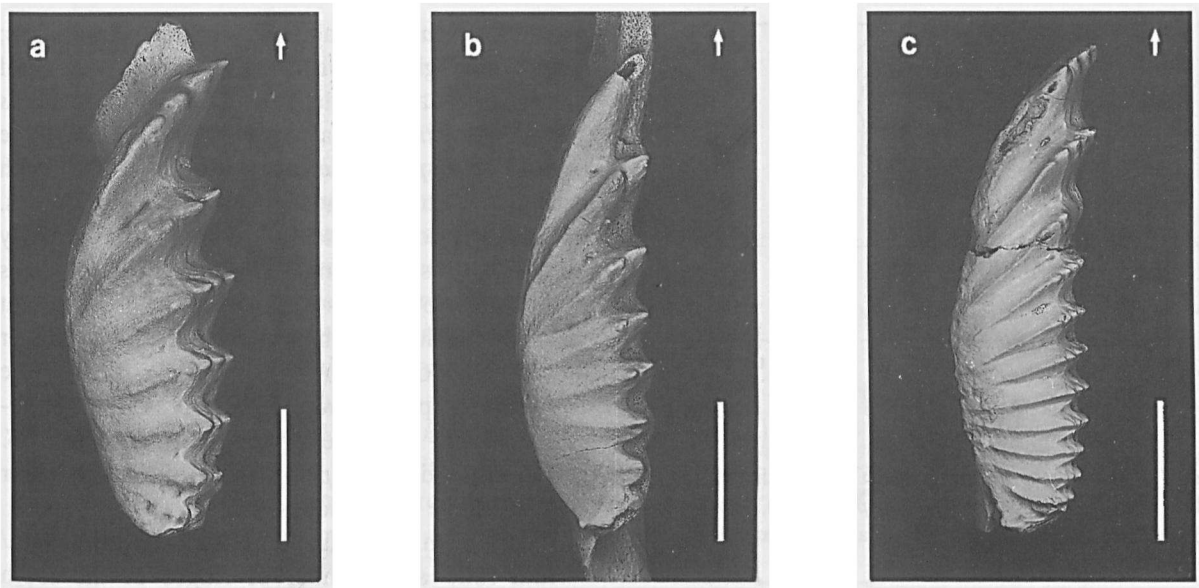
Fig. 44. Right lower (prearticular) tooth plates, occlusal side: a, *Sagenodus serratus* (MCZ 13907-121); b, *S. copeanus* (KUVP 70798); c, *S. periprion* (MCZ 8468-193). Specimens dusted with NH$_4$Cl. Arrows point in anterior direction. Scales equal 1 cm.

Robinson localities are not markedly different, taking into account the variation of bones collected at the Robinson locality. The most conspicuous difference between skull roofs from Hamilton and the reconstruction from Robinson is in the shape of the anterior marginal bones. The row just in front of the E-bones is more elongate in the reconstruction than in the detached skull roof from Hamilton (KUVP 103259), except for the median bone. This is the most variable region of the skull roof, and in the complete specimen from Hamilton, these bones are elongated as reconstructed in the skull roof from Robinson. The isolated operculum and the opercula of the complete specimen, KUVP 84201, are identical in shape with those from Robinson. The muscle imprint of the adductor operculi is clearly expressed in the small isolated operculum from Hamilton and the smallest operculum from Robinson.

Sagenodus *tooth plates*

Species of the genus *Sagenodus* can be separated on characteristics of their tooth plates. The well-preserved prearticular tooth plate, KUVP 103261,

from Hamilton Quarry has eight ridges with two incipient ones on its heel, and consequently it falls within the range of the prearticular tooth plates from Robinson. With its high length/width ratio, it closely compares to the larger prearticular tooth plates from Robinson. It follows from this comparison that the specimens from both localities cannot be distinguished morphologically and therefore the *Sagenodus* specimens from Hamilton Quarry are assigned to *S. copeanus*.

Tooth plates of *S. copeanus* tend to be narrower than those of *S. serratus* (Table II; Figs. 43a, b; 44a, b; 45). Both the number of ridges and the length/width ratio overlap at the lower end of the range with that of *S. serratus* except for the length/width ratio of the upper tooth plates which is significantly higher in *S. copeanus*. The greatest width lies between ridges 4 and 5 of the lower tooth plates in *S. copeanus*, but between ridges 3 and 4 in *S. serratus*. The angles between ridges of tooth plates of *S. copeanus* fall within the range of variation of *S. serratus*; the angle cannot be used to distinguish both species. In *S. copeanus* the distance between the anterior end of the lower tooth plate and the prearticular symphysis is relatively greater than that of *S. serratus*. The width of the symphysis is also narrower in *S. copeanus*
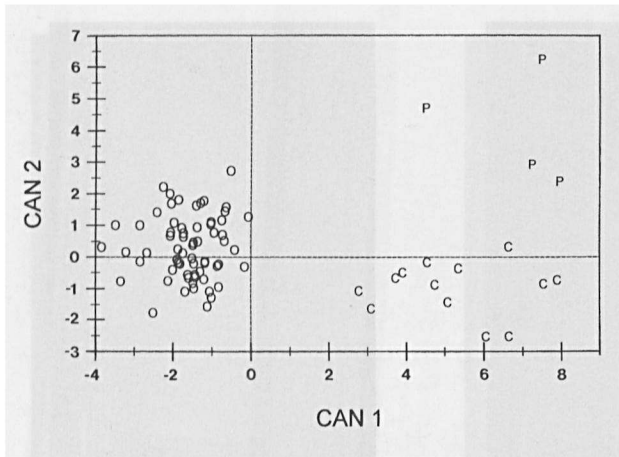
Fig. 45. Comparison of length/width ratio with number of ridges in tooth plates of *Sagenodus copeanus* (C), *S. periprion* (P), and *S. serratus* (O) plotted on canonical axes from discriminant function analysis.

(Fig. 46). The skull roof of *S. serratus* (MCZ 8600) is essentially similar to that of *S. copeanus*, and the two species cannot be distinguished from each other based on skull roof morphology.

The number of ridges on *S. copeanus* tooth plates also overlaps on the upper end of its range

Fig. 46. Symphysis of prearticular: a, *Sagenodus serratus* (MCZ 8601–4, Lower Permian; Little Bitter Creek, Young County, Texas); b, *Sagenodus copeanus* (KUVP 70800, Upper Pennsylvanian; Robinson, northeast Kansas). Arrows point in anterior direction. Scale equals 1 cm.

with *S. periprion* (Table II; Figs. 43a, c, 44a, c; 45). The angles between ridges of tooth plates of *S. periprion* are smaller than those of *S. copeanus* and *S. serratus* with a broad zone of overlap. The ridges of *S. periprion* more closely parallel each other in contrast to those of the other two species. The lower tooth plates of *S. periprion* usually have the posterior end sharply tapered, whereas the lower tooth plates of *S. copeanus* have a blunt terminus. The length/width ratio of the lower tooth plates of *S. periprion* is lower, that of the upper tooth plates about the same as in *S. copeanus* (Table II). The upper tooth plates of *S. copeanus* and *S. periprion* differ in that the latter usually have more ridges.

A discriminant function analysis of length/width ratio and number of ridges of the tooth plates shows a clear separation of these three *Sagenodus* species (Fig. 45). The horizontal canonical axis represents a summation of the variables, whereas the vertical canonical axis contrasts length/width ratio to number of ridges. As the data of the specimens of each species cluster together, there is no overlap between the three species.
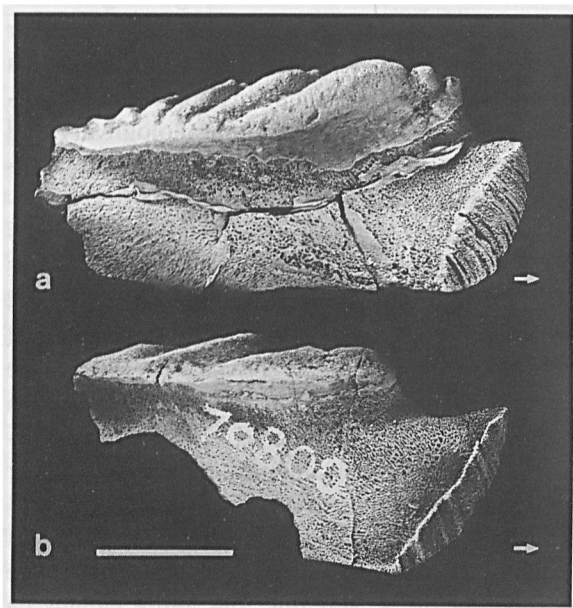
Sagenodus serratus and *S. periprion*

In the 1930's, Carnegie Museum field parties led by John Burke made substantial collections of *Sagenodus* from near Cameron, Monroe County, Ohio (Fig. 1: 5 = locality 6 of Moran, 1952). The material, with few exceptions, comprised disassociated bones and tooth plates from a grey shale in the Washington Group, Dunkard Series, Lower Permian. Tooth plate morphology indicates that two species of *Sagenodus* are represented: *S. periprion* and, less frequently, *S. serratus* (one upper tooth plate and one pterygoid with tooth plate). Much of this material is well preserved, though more subject to distortion and crushing than bones from Robinson, Hamilton, Kansas, and Little Bitter Creek, Texas. Bones from the Cameron locality are indistinguishable in most respects from those of *S. serratus* from Texas and *S. copeanus* from the Robinson locality. Detailed description of the shape and relative position of

Cameron specimens would be redundant. Instead, we focus on what few differences can be seen. Enough elements were recovered to construct a composite skull roof (Fig. 47), as was done for the Robinson material of *S. copeanus*. With two species present at the Cameron locality, the possibility of combining elements from both, in one composite skull roof, is real. Nevertheless, this reconstruction should represent a reasonably accurate view of a *S. periprion* skull roof. The only known difference in skull proportions is the change from relatively short, wide C and E elements in *S. serratus* and *S. copeanus* to longer, narrower elements in some of the Cameron specimens. Shorter C-bones from Cameron may represent individual variation or, more probably, belong to *S. serratus*. In thickness Cameron skull roof elements are comparable to, or thinner than, those of *S. serratus* from Texas. Two Cameron C-bones are quite thin for their size, measuring 1.3 and 1.4 mm at the center of growth. *S. copeanus* skull bones show extreme variation in thickness; however, no C-bone from Robinson is comparably thin and some are much thicker. Many Cameron skull roof elements show a pattern of concentric growth lines and several of these bones have a radiating pattern of fine grooves on the dorsal surface.

The B-bones from Cameron vary in several ways from those of *S. copeanus*. The angle formed by the parasagittal ridges on the ventral surface is more obtuse in all but one of the Cameron B-bones. These ridges diverge from 14 to 23 degrees in *S. copeanus* versus 28 to 40 degrees in B-bones presumed to be *S. periprion* (Fig. 48a, b). One incomplete B-bone from Cameron shows ridge divergence of less than 10 degrees. This is a very low figure and one which may come from an element of *S. serratus*. *S. serratus* (Fig. 48c) shows a wider range of variation than other North American *Sagenodus*. Two B-bones from Cameron, one complete and one a posterior fragment, have three or four deep grooves that extend posteriorly from the level of the occipital commissure. They have carried branches of the sensory canal that are roofed by bone in other specimens. The complete B-bone also has a single groove extending anterolaterally toward, but not quite contacting LM.
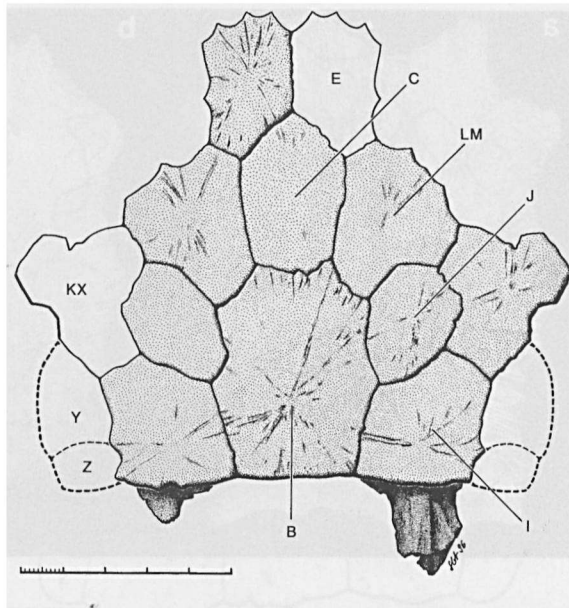

Fig. 47. Sagenodus periprion (Cope, 1878), composite skull roof, dorsal side (B-bone = CMNH 8504, C-bone = CMNH 8512, left E = CMNH 8513, left and right I = CMNH 8510, left and right J = CMNH 8543, right KX = CMNH 8511, left and right LM = CMNH 8511). Lower Permian; Cameron, Pennsylvania. Scale equals 1 cm.

Few "angular" bones are preserved from Cameron but the most complete (CMNH 8574) appears to be slightly more elongated anteroposteriorly than those of *S. copeanus* and *S. serratus*. This elongation accompanies the long narrow tooth plates of *S. periprion* and is consistent with the elongation of the anterior skull elements, C and E. This "angular" bone is more strongly concave on the medial surface than other North American *Sagenodus*.

Skull roofs of *Sagenodus* (including *S. ohiensis*)

The skull roof pattern of *Sagenodus copeanus* closely resembles *Sagenodus* material from the Late Pennsylvanian of England and North America as well as a skull (MCZ 8600) of *S. serratus* from the Early Permian of Texas.

The skull MCZ 8600 (Fig. 49) is dorsoventrally flattened. The left operculum covers the left side of the skull roof. Circumorbital bones lie in front of the operculum. Some of the anterior marginal
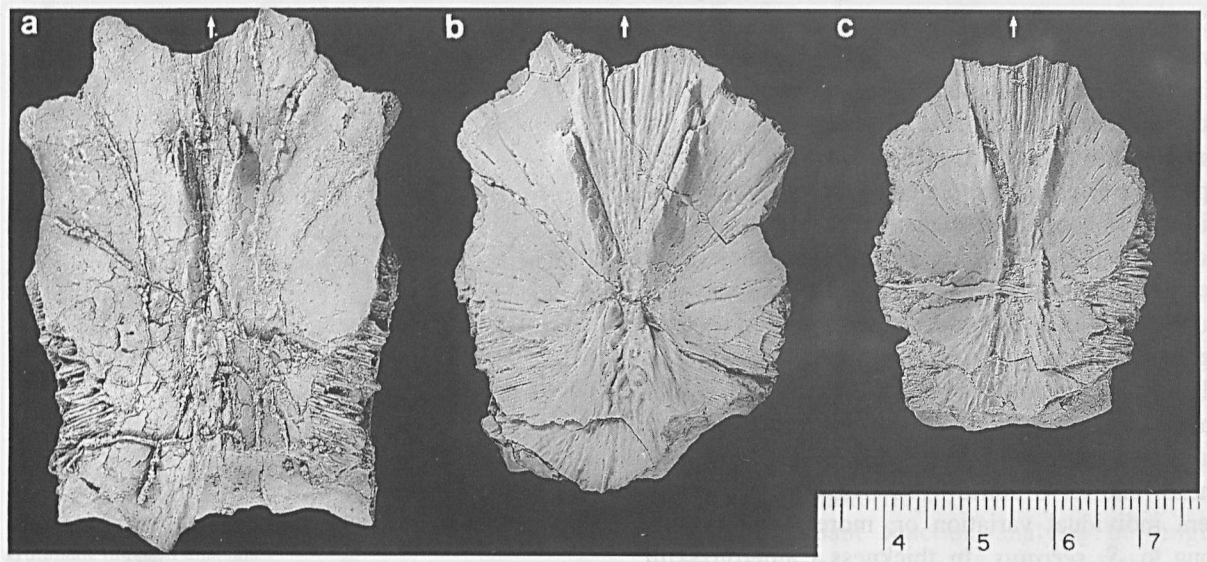
Fig. 48. Ventral side of bone B: a, *Sagenodus copeanus* (KUVP 70760); b, *S. periprion* (CMNH 8504 – 142); c, *S. serratus* (MCZ 8448 – 102). Arrows point in anterior direction. Scales equal 1 cm.

bones are pushed backwards over the E- and P-bones by the left shoulder girdle which is displaced anterior to the skull. On the palatal side, the parasphenoid and pterygoid tooth plates are pressed against the ventral side of the skull roof. The bones of the skull roof show the typical *Sagenodus* pattern. An unpaired elongate B-bone is preceded by a pentagonal median C-bone. The B-bone is narrower relative to its length when compared with *S. copeanus*, whereas measurements and relations of the C-bone fall within the range of *S. copeanus*. The E-bones compare well in shape and size with *S. copeanus*. The anterior marginal bones in front of the E-bones are fewer in number and shorter than in the composite specimen of *S. copeanus* reconstructed from Robinson, but they are similar to specimen KUVP 103259 from Hamilton. These differences are unimportant because the anterior marginal bones of *Sagenodus* are so variable in size and shape. They carry numerous pores associated with the supraorbital canal. In the series of elements from I to P, the right I-bone is only partially preserved, whereas the left one is covered by the operculum so that the shape of I can only be reconstructed and measurements cannot be taken. Anteromedial to I, the J-bone is somewhat elongated in medial-anterolateral direction; it is shorter in comparison

with its width than most J-bones of *S. copeanus*, but the difference is insignificant. The LM-bone compares closely in size and shape with that of *S. copeanus*. Pores associated with the supraorbital canal mark its passage from LM anteriorly into two small bones (N and P) of variable size and shape. Bone N is smaller than P. Bones KX to O are preserved in the most lateral series of the skull roof. The two posterior bones, Z and Y, are missing. The proportions of the KX-bone fall within the range of variation of *S. copeanus*. Bone O is convex posteriorly where it meets bone 3a; it widens by a third anteriorly. Bone O carries pores of a subsidiary branch of the supraorbital canal.

British material from Newsham was figured by Watson & Gill (1923: fig. 1) and modified in the circumorbital region by Westoll (1949: fig. 8). A North American specimen was figured by Romer & Smith (1934: fig. 4B) from the Late Pennsylvanian (Lower Carbondale group) near Peoria, Illinois (Fig. 1: 13). Note that in both figure and text, dorsal and ventral surfaces are reversed (Westoll, 1949). Cranial roof elements from Newsham, Peoria, Robinson, Hamilton, and Texas probably are indistinguishable from each other. Despite the close resemblance among these forms, skull roof pattern can be used to distin-

guish some skull roof material from the Permo-Carboniferous Dunkard group in Ohio (*S. periprion*) and the type and only known specimen of *S. ohiensis* from the Middle Pennsylvanian of Linton, Ohio (Cope, 1874: pl. 45; Newberry, 1889: fig. 3; Hussakof, 1916: fig. 2). *S. serratus* from the Middle Pennsylvanian of Linton, Ohio (Fig. 1: 7), is based on an upper tooth plate (AMNH 481+482). Besides several upper tooth plates, the Linton coal deposits yield four partial skull roofs. Specimens BMNH P.7773 and Sto 4518a, b show bones with smooth surfaces and the arrangement typical of *Sagenodus*. They are assigned here to the species *S. serratus*. AMNH 8645 (Schultze, 1977: fig. 10) reveals only the ventral surface and also is assigned to *S. serratus*. The surface of the skull bones of the holotype of *S. ohiensis* (assigned to *S. serratus* by Hook & Baird, 1986, and Schultze, 1992), has a rugose ornament of grooves and furrows, an unusual, if not unique ornamentation for a lungfish (Fig. 50; Cope, 1874: pl. 45 fig. 2), but similar to the skull ornament of early tetrapods. The proportions of the skull bones are very different as well. The C-bone is oval-shaped and short, the E-bones are narrow and the LM-bones very broad. The angle between median and posteromedial border of bone E measures 120°, comparable to *S. copeanus*. The length to posterior width ratios of C (1.5) and E (1.9) of *S. ohiensis* fall on or near the regression line of *S. periprion*. However, the long narrow B-bone and the wide I-, J-, and LM-bones differ from *S. periprion*. Bone B has convex lateral borders without concave embayments for bones LM, I, and J as in other species of *Sagenodus* (Figs. 2, 31, 40, 47, 49). The lateral portion of bone J is very short. The suture between bones I and J moves posteromediad to the center of I, so that the medial portion of J is much longer than the lateral portion. If the shape of bone J is correctly interpreted, this would be a very distinctive feature of *S. ohiensis*. The bone pattern places the specimen within the genus *Sagenodus*. Nevertheless, the ornament and the bone proportions distinguish it from all known *Sagenodus* species. This skull roof stands as the holotype and only known specimen of *Sagenodus ohiensis*. None of the tooth plates from Linton,
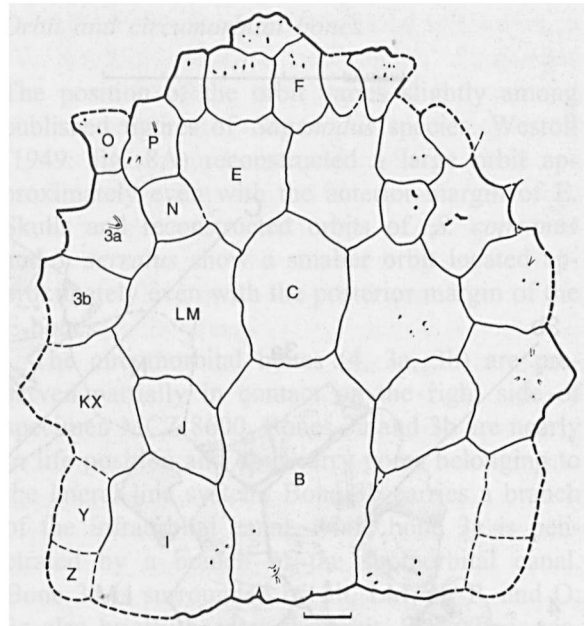

Fig. 49. Sagenodus serratus (Newberry, 1874), skull roof = MCZ 8600, dorsal side (B, C, E, F, I, J, KX, LM, N, O, P, Y, Z, 3a, 3b, skull roofing bones*)*. Lower Permian; Little Bitter Creek, Young County, Texas. Scale equals 1 cm.

Ohio, are associated with the single skull roof of *S. ohiensis*. Without the recovery of additional specimens it is unknown whether *S. ohiensis* represents a rare lungfish or an anomalous skull of *S. serratus*.

One other important specimen was discussed and figured by Romer & Smith (1934). This is a nearly complete skull roof of *Sagenodus* from the Lower Carbondale Formation (Westphalian) near Peoria, Illinois. Specimen FMNH UC 2061 consists of a fine impression of dorsal and ventral surfaces of a skull roof preserved in coal. Also recorded is most of an operculum, an "angular", and parts of two tooth plates. Some bone is present including the posterior half of a C-bone, now detached from the coal. The arrangement and dimensions of the roof elements are comparable to those of *S. copeanus* and *S. serratus*. It was to *S. serratus* that the Peoria skull roof was referred by Romer & Smith (1934), though this assignment is uncertain considering how little of the tooth plates remains. The divergence of the anterior parasagittal ridges on the ventral surface of the B-bone is 19°. The specimen is an excellent
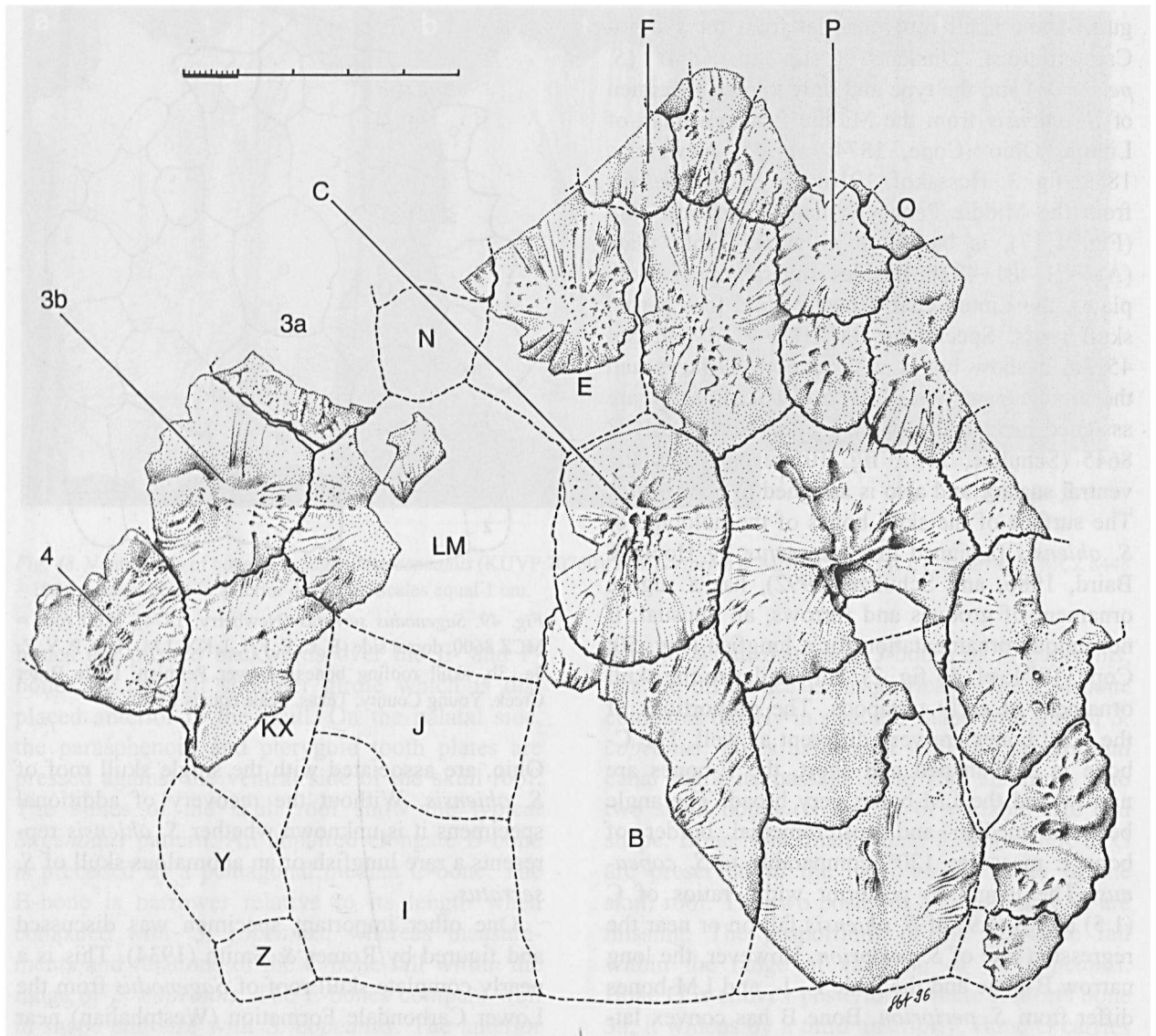
Fig. 50. Sagenodus ohiensis (Cope, 1874), skull roof = AMNH 8540G, 8541G, 8522G + 8531G, dorsal side (B, C, E, F, I, J, KX, LM, N, O, P, Y, Z, 3a, 3b, 4, skull roofing bones*).* Upper Pennsylvanian; Linton, Jefferson County, Ohio. Scale equals 1 cm.

example of a skull roof variant noted by Westoll (1949: fig. 8A') where one bone occupies the area normally taken by elements N and P. Westoll also noted that Romer & Smith (1934: fig. 4 A, B) reversed the dorsal and ventral surfaces of the skull roof in both figure and text. Subsequently, Schultze (1977: fig. 10) described and figured as dorsal, the ventral surface of a posterior part of a skull roof of *S. serratus* (AMNH 8645) from Linton, Ohio. The Peoria skull roof is noteworthy in that the bones are thinner than those of any other known specimen of *Sagenodus*. The C-bone

and parts of surrounding elements are approximately 1 mm thick in a skull roof approximately 8 cm in length. Such a thin skull roof is seen in *Neoceratodus* but falls far short of the extreme examples of C in *S. copeanus*. The thinness of bones in coal deposits, such as the Peoria and Linton specimens, may be the effect of partial dissolution of bone in that depositional environment (R. Zangerl, pers. comm.). However, such thin bones occur also in calcareous deposits such as those found at Robinson, Kansas (*S. copeanus*) and at Cameron, Ohio (*S. periprion*). Another
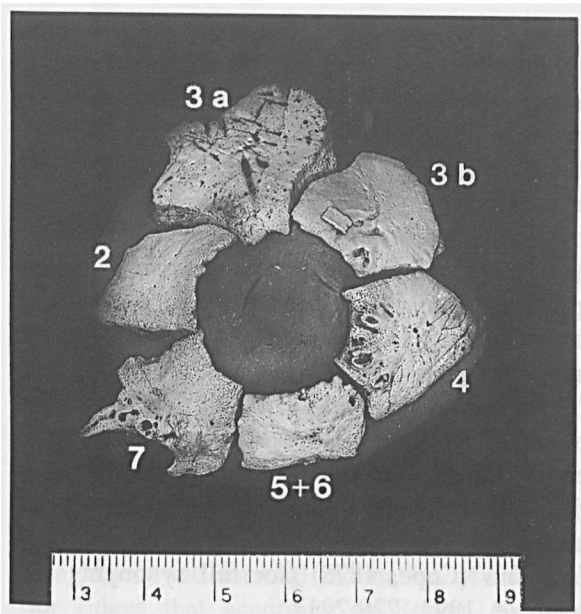
Fig. 51. Sagenodus serratus (Newberry, 1874), circumorbital bones, lateral side (bone 2 = MCZ 13907, bone 3a = MCZ 8601, bone 3b = MCZ 13907, bone 4 = MCZ 8601, bone 5 + 6 = MCZ 13907, bone 7 = MCZ 13907). Lower Permian; Little Bitter Creek, Young County, Texas. Arrow points in anterior direction. Scale equals 1 cm.

remarkable feature of the Peoria skull roof is that the supraoccipital commissure runs through a groove on the ventral surface of the skull roof. In other *Sagenodus* it courses through an enclosed canal. The only other specimen known to us to have a groove for this commissure is that of *S. serratus* (AMNH 8645) mentioned above. Perhaps the space required for this commissure, coupled with the thinness of the skull roof elements, precluded the complete envelopment of the commissure by the I and B bones.

CMNH 26583 from the Cameron locality represents one of the most unusual variations found in *Sagenodus*. The specimen is a partial skull only partially articulated and still in a shale matrix. It cannot definitely be assigned to species. Four articulated roofing bones are revealed in dorsal view. They are KX, Y, I, and LM and their configuration indicates that this skull lacked a J-bone on the right side. I, KX, and LM have expanded into the area normally filled by J where they meet each other in a triradiate suture each third of which represents approximately 120 degrees.

Orbit and circumorbital bones

The position of the orbit varies slightly among published figures of *Sagenodus* species. Westoll (1949: fig. 8A) reconstructed a large orbit approximately even with the anterior margin of E. Skulls and reconstructed orbits of *S. copeanus* and *S. serratus* show a smaller orbit located approximately even with the posterior margin of the E-bones.

The circumorbital bones (4, 3a, 3b) are preserved partially in contact on the right side of specimen MCZ 8600. Bones 3a and 3b are nearly in life position and both carry pores belonging to the lateral line system. Bone 3b carries a branch of the infraorbital canal, while bone 3a is penetrated by a branch of the supraorbital canal. Bone 3a is surrounded by 3b, LM, N, P, and O; 3a also briefly borders the orbit. Bone 3b is visible where it borders KX, LM, and 3a, but is covered on its ventrolateral surface by bone 4 which is turned inner-side up. The right bone 7 has been displaced to the left margin of the specimen, with its inside surface facing up. On the left side, all circumorbital bones are preserved, but not in articulation. Bone 7 lies on bone 3a, bone 5+6 partially on bone 7 and O, and bone 4 partially on bone 3a. Bone 3b lies on the inner side of the skull roof above the outer surface of the operculum. Fig. 51 shows the reconstructed arrangement of the circumorbital bones. The number of circumorbital bones and the general size and participation in the orbit margin is comparable between *S. serratus* (Fig. 51) and *S. copeanus* (Fig. 19); even bone 7 possesses the same processes, of which one leads the infraorbital canal to bone 1.

Other North American *Sagenodus*

With the exception of *S. ohiensis*, which is based on a skull roof, North American species of *Sagenodus* are based on tooth plates or scales. Scales of *Sagenodus*, *Ctenodus*, and *Megapleuron* are very similar to each other and it is not possible to assign isolated scales to genus, nor is it possible to relate species erected on scales with taxa based on tooth plates. We consider all *Sage-*

nodus species based on scales or isolated bones to be nomina dubia, i.e. *Sagenodus occidentalis* (Newberry & Worthen, 1866) (nomen vanum after Baird, 1978), *S. quadratus* (Newberry, 1873), *S. reticulatus* (Newberry & Worthen, 1870), *S. browniae* Cope, 1897, *S. conchiolepis* Cope, 1897, *S. foliatus* Cope, 1897, *S. lacovianus* Cope, 1897, *S. magister* Cope, 1897, *S. quincunciatus* Cope, 1897, and *S. textilis* Hay, 1899.

Romer & Smith (1934) synonymized several species of *Sagenodus* with *S. serratus*. We have, for the most part, followed their conclusions. However, unlike Romer & Smith, we do not consider the fragmentary type of *S. paucicristatus* to be diagnostic and the name is therefore a nomen dubium. In addition, *Ctenodus reticulatus* Newberry, 1874 of Linton, Ohio, based on a tooth plate with seven ridges (AMNH 9143; Hay, 1900, suggested the new name *Sagenodus jugosus*) also may be conspecific with *S. serratus*. Romer & Smith (1934) recognized four species of *Sagenodus* from the Texas Permian: *S. ciscoensis*, *S. dialophus*, *S. periprion*, and *S. porrectus*.

The type of *S. dialophus* is a left lower tooth plate. Though incomplete anteriorly, all or part of 13 ridges are present. Romer & Smith (1934) estimated that a total of 15 ridges were present in the complete tooth plate; however, we believe that 13 ridges were all that were present. A count of 13 ridges places *S. dialophus* within the upper part of the range of *S. periprion*. The type also has a high length to width ratio comparable to that of *S. periprion*; however, since the type is incomplete the exact ratio is unknown. From what little data is afforded by the holotype, we conclude that *S. dialophus* cannot be successfully distinguished from *S. periprion* and is therefore a junior synonym of the latter. Both taxa were proposed by Cope (1878) with *S. periprion* having page priority.

There are three cotypes of *S. ciscoensis*. The broad pterygoid tooth plate has eight ridges and a posterior heel. The angle formed between the anterior and posterior half of the tooth plate along the buccal margin appears to be pathological. Though this angle is described by Romer & Smith (1934) as "very sharp", it falls within the range of variation found in *S. serratus* tooth plates from

Texas. The estimated length/width ratio falls within the values of *S. serratus*. The preserved partial prearticular plate has deep valleys between the widely spaced ridges of which five are preserved. All these features indicate that *S. ciscoensis* is a synonym of *S. serratus*.

After placing *S. ciscoensis* and *S. dialophus* in synonymy with *S. serratus* and *S. periprion*, respectively, two valid species of *Sagenodus* are recognized in the Permian of Texas: *S. periprion* and *S. serratus*.

S. periprion (Cope, 1878): high ridge count for tooth plates (upper 10-11, lower 11–13), high length/width ratio (Table II: 4.1 for lower tooth plate, 3.7 for upper tooth plate), tapered posterior margin of lower tooth plate. Synonyms: *S. dialophus* (Cope, 1878) (for full synonymy see Schultze, 1992: 220-221).

S. serratus (Newberry, 1874): low number of ridges on tooth plates (upper 7-9, lower 7-9), low length/width ratio (Table II: 3.9 for lower tooth plate, 2.6 for upper tooth plate), tapered posterior margin of lower tooth plate; symphysis in short distance from tooth plate. Synonyms: *S. porrectus* (Cope, 1878), *S. fossatus* (Cope, 1878), *S. gurleyanus* (Cope, 1878), *S. heterolophus* (Cope, 1883), *S. vabasensis* (Cope, 1883), *S. vinslovi* (Cope, 1875), *S. ciscoensis* (Romer & Smith, 1934) (for full synonymy see Schultze, 1992: 221–224), *Proceratodus carlinvillensis* Romer & Smith, 1934, and *?P. hlavini* Zidek, 1975. Kemp (1996) referred *Proceratodus* to *Sagenodus* because the characters used by Romer & Smith (1934) and Zidek (1975) to distinguish the two genera are characters associated with wear. *Proceratodus carlinvillensis* is based on one left pterygoid tooth plate from the Pennsylvanian of Carlinville, Illinois. The tooth plate carries seven ridges and has a length/width ratio comparable to *S. serratus*. Kemp (1996) compared the tooth plate with *S. inaequalis*, a European species with long, radiating ridges. Short ridges are common to North American species of *Sagenodus* (Fig. 43). They are a function of narrow tooth plates, less radiating ridges and wear, and not a sign of pathological development. *Proceratodus hlavini* is based on one left prearticular tooth plate from the Pennsylvanian of the Manzanita Mountains,

New Mexico (Zidek, 1975). The tooth plate carries seven ridges. It conforms in all respects to tooth plates of *S. serratus*, except being much narrower; therefore an assignment as *Sagenodus* sp. is suggested.

Outside the Permian of Texas, the tooth plates of *S. serratus* from the Middle Pennsylvanian of Ohio have a ridge count identical to that of *S. porrectus*. The tooth plates also have the same length/width ratio. On this basis and contrary to Schultze (1992), *S. porrectus* Cope, 1878, must be considered to be a junior synonym of *S. serratus* Newberry, 1874.

Complete, or nearly complete, upper and lower tooth plates from the Cameron locality, Ohio, are similar to the type of *S. periprion* and exhibit the straightness and forward inclination of the anterior ridges that according to Romer & Smith (1934) are distinctive features of *S. periprion*. These upper tooth plates also have a fairly high ridge count (11 in the only nearly complete specimen, CMNH 8500). Romer (1952) tentatively recognized the affinities of some of the Cameron, Ohio specimens when he referred to them as *Sagenodus* cf. *periprion*.

In conclusion we recognize only four species of *Sagenodus* from North America. *Sagenodus copeanus* is morphologically intermediate between *S. serratus* and *S. periprion*. *S. ohiensis* is known from one skull roof, characterized by tetrapod-like surface ornamentation and a unique pattern of cranial elements. The type species, *Sagenodus inaequalis*, from Europe is distinguished by long radiating ridges from North American species with short ridges.

Stratigraphic and paleogeographic distribution

The first occurrence of the genus *Sagenodus* is recorded from the uppermost Lower Carboniferous (Mississippian) of England, Scotland, and Nova Scotia (Fig. 52). Smithson (pers. comm.) mentions a tooth plate from the Tournaisian of Coldstream, Berwickshire, Scotland. The latest occurrence of *Sagenodus* is recorded from the uppermost Lower Permian of Texas, West Virginia, eastern Pennsylvania, and Germany (Ber-

man, 1968; Romer, 1952; Schultze, 1993). Hence, the genus has a recorded range of 70 million years, and a range of 100 million years if the Tournaisian record is included. Thus *Sagenodus* is a very long ranging dipnoan genus in contrast to Devonian genera and even to other post-Devonian genera, with the exception of *Ceratodus* with a longer stratigraphic range.

Sagenodus also is second only to *Ceratodus* in geographic range and is the most widely distributed lungfish of the Permo-Carboniferous (Schultze, 1993). In the Early Carboniferous, there is still a marine connection between Russia, England, Scotland, and Nova Scotia (Ziegler, 1989). If, as we believe probable, *Sagenodus* was tolerant of marine conditions, this connection could account for the early distribution of the genus. In the Namurian the marine connections disappear. *Sagenodus*-bearing deposits of the Westphalian and Stephanian basins in England, Scotland, and central Europe are widely believed to be of continental origin and are layed down in fresh water. Accepting these reconstructions, *Sagenodus* may have entered these basins by rivers from marine to fresh or brackish-water habitats.

There is a big time gap (about 20 million years) between the first occurrence of *Sagenodus* in Nova Scotia (aquatic connections to the Midwest) and its first occurrence in Illinois and Ohio. There are still records of *Sagenodus* from the Westphalian of Nova Scotia (Joggins and Parrsboro; Carroll et al., 1972), but there was no aquatic connection to the Midwest at that time. It is most probable that *Sagenodus* spread to the Midwest in the late Early to early Late Carboniferous. *Sagenodus* spread over time from the east (Pennsylvania to Illinois) to the west (Kansas) and south (Texas and Oklahoma) during the Pennsylvanian and Early Permian, and continued to exist in the eastern part of the Midwest through the latest Pennsylvanian. The expansion is possible through the shallow sea of the Midwest.

The paleogeographic distribution of *Sagenodus* extends through Czechia, Germany, England, Scotland, and Ireland in Europe. In North America the range extends from Nova Scotia to New Mexico through Pennsylvania, West Virginia, Ohio, Illinois, Kansas, Oklahoma, and

Texas. Records of *Sagenodus* from Nova Scotia are cited by Carroll et al. (1972). The New Mexico record of *Sagenodus* is represented by a lower tooth plate and a partial prearticular previously attributed to *Proceratodus* (cf. Zidek, 1975).

Phylogenetic relationships

Thomson & Campbell (1971) and Miles (1977) placed *Sagenodus* as the Paleozoic lungfish closest to modern (Mesozoic and Cenozoic) lungfish. Bemis (1984) generally followed Miles (1977), but Bemis placed *Megapleuron* as the sister taxon of *Sagenodus* instead of *Straitonia*, and *Megapleuron* and *Sagenodus* as close relatives of modern lungfish. The cladistic analyses by Marshall (1987), Schultze & Marshall (1993), and Schultze & Bolt (1996) placed *Sagenodus* in a polychotomy with all other Permo-Carboniferous lungfish except *Conchopoma* (Marshall, 1987: fig. 5), in a sequence between *Ganopristodus*, *Megapleuron*, and a group of taxa consisting of *Straitonia*, *Tranodis*, and *Ctenodus* (Schultze & Marshall, 1993: fig. 7) or a sequence of *Straitonia*, *Tranodis*, and *Megapleuron* (Schultze & Bolt, 1996: fig. 7). In contrast, Campbell & Barwick (1990) place the sister taxa *Straitonia* and *Sagenodus* at the base of all post-Devonian lungfish.

The instability in the phylogenetic relationships of lungfish, especially of Late Paleozoic dipnoans, is mainly a function of the nature of the characters (Schultze & Marshall, 1993). All analyses show a high homoplasy index. That indicates that there are not enough characters to define monophyletic units. That is the reason why the selection of taxa included in an analysis strongly influences the hypotheses of relationships of the taxa to each other.

With this in mind, we included all Permo-Carboniferous taxa except *Parasagenodus*, a few post-Paleozoic and four Devonian taxa, in our analyses. We generated eight trees by using PAUP 3.1.1. (unweighted and unordered characters, DELTRAN character-state optimization) with 47 characters (Appendix 3) and 18 taxa

(Appendix 4: data matrix), of which the Devonian genera *Dipterus* and *Rhinodipterus* were placed in the outgroup (Fig. 53: tree length = 121 steps, consistency index = 0.579, homoplasy index = 0.421). *Delatitia* appears at the base of all post-Devonian taxa, and the typology of the cladograms between *Delatitia* and *Megapleuron* is the same for all eight trees. *Sagenodus* is imbedded within the Permo-Carboniferous taxa. It is neither the most basal taxon of all post-Devonian lungfish nor the sister taxon to all post-Permian lungfish. The eight trees differ in the placement of *Scaumenacia*, *Phaneropleuron*, *Dipterus*, and *Rhinodipterus* to each other and in the arrangement above *Megapleuron*. Above *Megapleuron*, two typologies each in four trees appear (Fig. 54). *Palaeophichthys* is separated from *Gnathorhiza*, and *Paraceratodus* from *Neoceratodus* in typology A (Fig. 54a). In contrast, typology B shows a sister-group relationship between *Palaeophichthys* (*Gnathorhiza* + *Ptychoceratodus*) and *Paraceratodus* (*Neoceratodus* + *Lepidosiren*). The placement of *Ptychoceratodus* is unusual, but appears in both typologies. Typology B agrees better with the stratigraphic appearance of the taxa, and corresponds except for the placement of *Ptychoceratodus* with accepted phylogenies; therefore typology B has been drawn in Fig. 53.

Characters that define all post-Devonian lungfish according to Campbell & Barwick (1990: fig. 1 C8), already occur in the Late Devonian lungfish *Phaneropleuron* and *Scaumenacia* (loss of cosmine; no ossification of snout, dentary, and chondrocranium; formation of a parasphenoid stalk; reduction from four to two infradentaries). A large pulp cavity is known only from a few post-Devonian genera so that its presence is not certain at the transition to post-Devonian genera. Loss of bone A in connection with the shift of the occipital commissure to bone B, a parasphenoid with lozenge and long stalk, and a diphycercal caudal fin including dorsal and anal fins are characters that distinguish all post-Devonian taxa (except *Conchopoma*) from Devonian taxa. The node 8 (*Sagenodus* as the sister taxon of all remaining Permo-Carboniferous and post-Permian taxa) is characterized by the loss of bone D, presence of bone LM, a single bone 1, and a parasphenoid

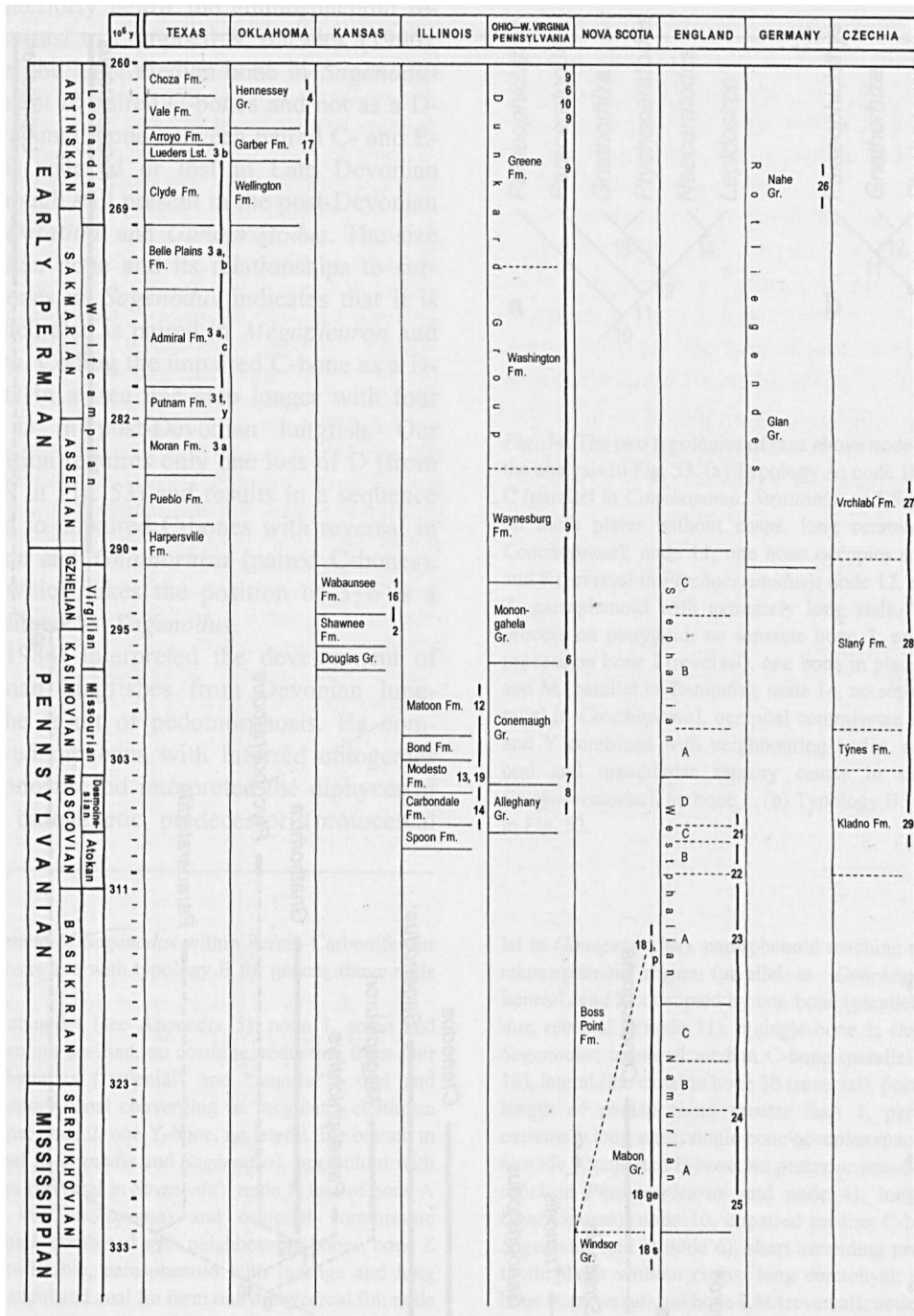| 10⁶ y			TEXAS	OKLAHOMA	KANSAS	ILLINOIS	OHIO—W. VIRGINIA PENNSYLVANIA	NOVA SCOTIA	ENGLAND	GERMANY	CZECHIA
260	EARLY PERMIAN	ARTINSKIAN / Leonardian	Choza Fm. / Vale Fm. / Arroyo Fm. / Lueders Lst. 3 b / Clyde Fm.	Hennessey Gr. 1,4 / Garber Fm. 17 / Wellington Fm.			Dunkard Group 9,6,10,9,9 / Greene Fm. 9			Rotliegendes / Nahe Gr. 26	
269		SAKMARIAN / Wolfcampian	Belle Plains Fm. 3 a, b				Washington Fm.			Glan Gr.	Vrchlabí Fm. 27
282		ASSELIAN	Admiral Fm. 3 a, c / Putnam Fm. 3 t, y / Moran Fm. 3 a / Pueblo Fm. / Harpersville Fm.				Waynesburg Fm. 9				
290	PENNSYLVANIAN	GZHELIAN / Virgilian			Wabaunsee Fm. 1,16 / Shawnee Fm. 2 / Douglas Gr.		Monongahela Gr. 6	Stephanian C			Slaný Fm. 28
295		KASIMOVIAN / Missourian				Matoon Fm. 12		Stephanian B			Týnes Fm.
303		MOSCOVIAN / Desmoinesian / Atokan				Bond Fm. / Modesto Fm. 13,19 / Carbondale Fm. 14 / Spoon Fm.	Conemaugh Gr. / Alleghany Gr. 7,8	Stephanian A			Kladno Fm. 29
311								Westphalian D 21 / Westphalian C 21 / Westphalian B 22			
323		BASHKIRIAN						Westphalian A 23 / Boss Point Fm. 18 j, p			
333	MISSISSIPPIAN	SERPUKHOVIAN						Namurian C / Namurian B 24 / Mabon Gr. 18 ge / Namurian A 25 / Windsor Gr. 18 s			

Fig. 52. Stratigraphic distribution of *Sagenodus*: 1–20, locality numbers as in Fig. 1; 21, Longton, North Staffordshire, England; 22, Bellsdyke Pit, Airdie, Lanarkshire, Scotland, and Newsham, Northumberland, England; 23, Newarthill, Lanarkshire, Scotland; 24, Niddrie, Edinburgh, Midlothian, Scotland; 25, Loanhead, Midlothian, Scotland (Henrichsen, 1972); 26, Sobernheim, Rhineland-Palatine, Germany (Schultze, 1993); 27, Kostálov, Czechia; 28, Kounov, Kroucová, and Zábor, Czechia; 29, Nýřany, Czechia (Zajíc & Štamberg, 1985). Time scale after Harland et al. (1990). Fm. = Formation; Gr. = Group.
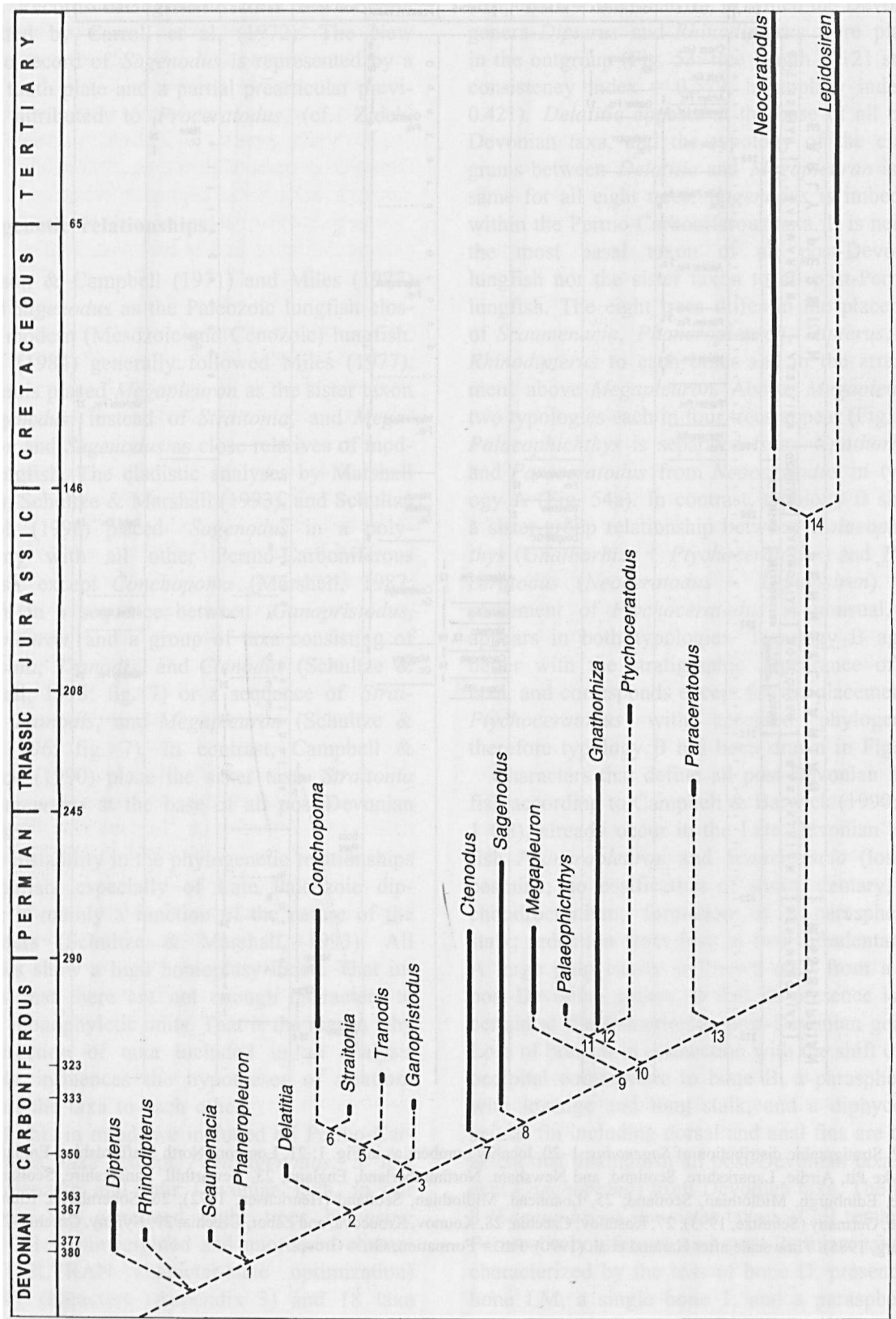
reaching anteriorly below the ethmosphenoid region. In contrast to Campbell & Barwick (1990), we interpret the large median bone in *Sagenodus* as replacement of paired C-bones and not as a D-bone. D is a small bone between paired C- and E-bones. It is reduced or lost in Late Devonian lungfish, though still present in the post-Devonian *Ctenodus, Delatitia,* and *Ganopristodus.* The size of the median bone and its relationships to surrounding bones in *Sagenodus* indicates that it is bone C which also is paired in *Megapleuron* and *Gnathorhiza.* Coding the unpaired C-bone as a D-bone results in a tree one step longer with four losses of D in post-Devonian lungfish. Our homologization requires only one loss of D (from node 7 to 8 in Fig. 53) and results in a sequence from paired to unpaired C-bones with reversal in *Megapleuron* and *Gnathorhiza* (paired C-bones). The bone which takes the position of 5+6 is a character unique to *Sagenodus.*

Bemis (1984) interpreted the development of post-Devonian lungfishes from Devonian lungfishes as the result of pedomorphosis. He compared derived dipnoans with inferred ontogenies of early dipnoans and interpreted the diphycercal tail as an ontogenetic predecessor (protocercal
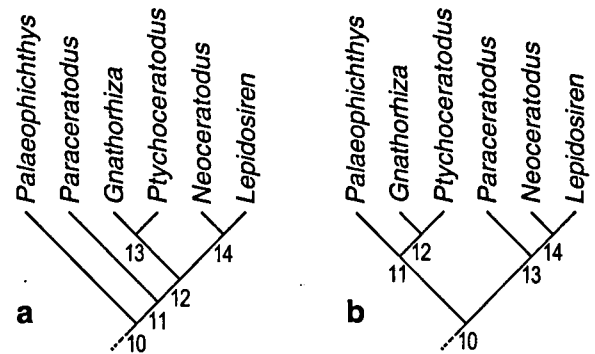

Fig. 54. The two typologies of taxa above node 9 resulting from the analysis in Fig. 53. (a) Typology A: node 10, unpaired bone C (parallel in *Conchopoma, Straitonia,* and *Sagenodus*), ridges on tooth plates without cusps, long ceratohyal (parallel in *Conchopoma*); node 11, one bone occupies space of bones E and F (reversal in *Ptychoceratodus*); node 12, no separate bone Z, parasphenoid with extremely long stalk, short ascending process on pterygoid; no separate bone 3; node 13, posterior process on bone I (reversal), one bone in place of bones K, L, and M (parallel in *Tranodis*); node 14, no separate bone J (parallel in *Conchopoma*), occipital commissure in skin, bones C and Y combined with neighbouring bones, one infradentary, oral and mandibular sensory canals in skin (parallel in *Ptychoceratodus*), no bone 1. (b) Typology B: node 10 to 14 as in Fig. 53.

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Fig. 53. Placement of *Sagenodus* within Permo-Carboniferous genera (consensus tree with typology B for genera above node 9, cf. Fig. 54).

Characters at nodes (see Appendix 5): node 1, snout and chondrocranium not ossified, no cosmine, reduction from four to two infradentaries ("splenial" and "angular"), oral and mandibular sensory canal converging in "angular", cleithrum without cosmine; node 2, one Y-bone, no lateral line branch in bone 3 (reversal in *Tranodis* and *Sagenodus*), operculum with tabulate process (reversal in *Straitonia*); node 3, loss of bone A (reoccurrence in *Conchopoma*) and occipital commissure through B, bone L combined with neighbouring bones, bone Z included in skull table, parasphenoid with lozenge and long stalk, dorsal, caudal and anal fin form one diphycercal fin; node 4, no posterior process on bone I (parallel in *Phaneropleuron* and node 9); node 5, loss of bone D (parallel in *Phaneropleuron,* most *Scaumenacia* and node 8), Y combined with bone X; node 6, unpaired median C-bone (parallel in *Sagenodus* and node 10); node 7, oral sensory canal in "angular" and mandibular canal in ventral groove, large pulp cavity, two bones 3 (parallel in *Delatitia*), no bone 8; node 8, loss of bone D (parallel in *Phaneropleuron,* most *Scaumenacia* and node 5), bone M combined with neighbouring bones (paral-

lel in *Ganopristodus*), parasphenoid reaching anteriorly below ethmosphenoid region (parallel in *Conchopoma*), place of bones L and M occupied by one bone (parallel in *Ganopristodus,* reversal at node 11), a single bone 1; characterization of *Sagenodus*; unpaired median C-bone (parallel at nodes 6 and 10), lateral line canal in bone 3b (reversal), posterior to anterior length of parasphenoid greater than 1, parasphenoid with extremely long stalk, single bone occupies space of bones 5 and 6; node 9, unpaired E-bone, no posterior process on bone I (parallel in *Phaneropleuron* and node 4), long clavicle (also *Conchopoma*); node 10, unpaired median C-bone (parallel in *Sagenodus* and at node 6), short ascending process, ridges on tooth plates without cusps, long ceratohyal; node 11, single bone X (reversal), no bone LM (reversal); node 12, no separate bone Z (parallel at node 14), bone KLM present (parallel in *Tranodis*), posterior process on bone I (reversal); node 13, one bone in place of bones E and F (parallel in *Gnathorhiza*); node 14, occipital commissure in skin, bones J and C combined with neighbouring bones, no separate bone Z (parallel at node 12), no separate bone Y (parallel at node 5), parasphenoid with extremely long stalk (parallel in *Sagenodus* and *Gnathorhiza*), one infradentary, oral and mandibular sensory canals in skin (parallel in *Ptychoceratodus*), no bone 1.

tail) of the heterocercal tail (protocercal and diphycercal tails differ in formation and internal morphology). Loss of cosmine (loss of ganoin and dentine in actinopterygians) and loss of ossification of the endocranium is typical of all osteichthyan groups as well as the loss of calcification of the endocranium in lineages of chondrichthyans and placoderms. The loss of ossification may indicate that fishes adapted to a more efficient Ca-P-physiology and restricted the deposition of Ca-P-salts to the external (dermal) cover. The phylogenetic replacement of lepidotrichia by actinotrichia, which are the ontogenetic predecessor of lepidotrichia in modern lungfish, may be a case of pedomorphosis as Bemis (1984) demonstrates.

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Appendix 1. Studied material of *Sagenodus*

Sagenodus copeanus from the Upper Pennsylvanian: (a) Robinson locality, Brown County, Kansas (Fig. 1: 1): KUVP 785, 55348-55400 (old collection described by Williston, 1899), 70697-71137, 72471, 103101–103258; (b) Hamilton Quarry, Greenwood County, Kansas (Fig. 1: 2): KUVP 81393, 81394, 83748, 84201, 103259–103283, 120139.

Sagenodus inaequalis from the Pennsylvanian: (a) Newsham, Northumberland: AMNH 7608 (pterygoid with tooth plate), 7808 (prearticular with tooth plate); MCZ 1217 (pterygoid with tooth plate), 1218 (two lower tooth plates), 1222 (lower tooth plate), 1225 (upper and lower tooth plates), 1226 (2 lower and 2 upper tooth plates), 1227 (lower tooth plate), 1230 (upper tooth plate), 1231 (upper tooth plate), 1234 (two upper tooth plates), 1238 (upper tooth plate), 1241 (upper tooth plate); (b) Kounová, Czechia: NMP M 1223 (*S. barrandei*).

Sagenodus ohiensis from the Middle Pennsylvanian of Linton, Jefferson County, Ohio (Fig. 1: 7): AMNH 8540G + 8541G and counterpart 8522G + 8531G (partial skull roof, holotype of *Ctenodus ohiensis*; Cope, 1874: pl. 45, fig. 2; Hussakof, 1916: fig. 2).

Sagenodus periprion from the Lower Permian: (a) Texas (Fig. 1: 3): AMNH 7234 (holotype *Ctenodus dialophus*, lower tooth plate), 7470 (upper tooth plate), 7474 (holotype *Ctenodus periprion*, upper tooth plate), USNM 11679 (upper tooth plate), 419727 (lower tooth plate); (b) Cameron, Monroe County, Ohio (Fig. 1: 5): CMNH 8500-8515, 8543, 26583 (isolated skull bones and tooth plates: 8500 = 22 tooth plates, 8502 = 1 upper tooth plate, 8503 = 16 skull bones, E, LM, Y, 4, 3a, and pieces, 8504 = 10 B-bones, 8505 = 30 opercula, 8506 = 6 clavicles, 8509 = 8 posterior ends of pterygoids, 8510 = 5 I-bones, 8511 = 1 B-bone, 9 KX-bones, 4 LM-bones, 8512 = 5 C-bones, 1 posterior end of pterygoid, 1 bone fragment, 8513 = 1 E-bone, 8514 = 3 "angulars", 8515 = 4 ceratohyals, 8543 = 8 J-bones, 26583 = partial skull roof + operculum); (c) Rattlesnake Canyon, Archer County, Texas (Fig. 1: 3a): MCZ 8454 (1 upper tooth plate), TMM 40030-103 (upper tooth plate), 40030-2104 (lower tooth plate), UM 11674 (1 upper tooth plate); (d) N.W. of Dean, Clay County,Texas (Fig. 1: 3c): MCZ 28457 (1 lower tooth plate); (e) E. of Rendham, Baylor County, Texas (Fig. 1: 3b): MCZ 8464 (2 upper tooth plates; (f) S.W. of Dundee, Archer County, Texas (Fig. 1: 3a): MCZ 8465 (1 lower tooth plate); (g) W. of Williams Ranch, Baylor County, Texas (Fig. 1: 3b): MCZ 8468 (1 upper and 1 lower tooth plate); (h) Pittsburgh, Allegheny County, Pennsylvania (Fig. 1: 6): CMNH 19127 (1 upper tooth plate; Lund, 1970, fig. 7A); (i) Clark Hill, Monroe County, Ohio (Fig. 1: 5): MCZ 9183 (pterygoid with tooth plate).

Sagenodus serratus from the Middle Pennsylvanian: (a) Linton, Jefferson County, Ohio (Fig. 1: 7): AMNH 4817482 (holotype of *S. serratus*, 1 upper tooth plate), 1887 + 9142 (formerly 7468, upper tooth plate), 7463 (upper tooth plate), 8645 (posterior skull roof; Schultze 1977: fig. 10), 9134 (formerly 7464, holotype of *Ctenodus reticulatus* and *S. jugosus*, upper tooth plate), 9143 (formerly 7461, upper tooth plate), BMNH P. 7773 (skull roof; Watson & Gill, 1923: fig. 6C), OSU 4463 (upper tooth plate), Sto 4518a, b (disarticulated skull roofing bones), Hamilla collection (pterygoid with upper tooth plate); (b) Vermilion River, Vermilion County, Illinois (Fig. 1: 13): FMNH UF407 (1 upper and 1 lower tooth plate, and pieces); (c) S.E. of Falmouth, Jasper County, Illinois (Fig. 1: 12): FMNH UC1799 (*Proceratodus* cf. *carlinvillensis* Romer

& Smith, 1934, pterygoid tooth plate and bone fragments); (d) Peoria, Peoria County, Illinois (Fig. 1: 14): FMNH UC2061 (skull roof; Romer & Smith, 1934: fig. 4B).

Sagenodus serratus from the Lower Permian: (a) N.E. of Frederick, Tillman County, Oklahoma (Fig. 1: 4): KUVP 103140 (upper tooth plate), 103141 (lower tooth plate); (b) Little Bitter Creek, Young County, Texas (Fig. 1: 3y): MCZ 8442 (1 lower tooth plate), 8600 (skull and 3 splenials), 8601 (9 B-bones, 8 C-bones, 14 E-bones, 40 I-bones, 22 J-bones, 23 LM-bones, 32 KX-bones, 34 Y-bones, 1 Z-bone, 1 articulated LM+J and 1 articulated I+JK, 27 anterior marginals, more than 35 circumorbitals, 9 splenials, 3 angulars, 1 parasphenoid, 1 operculum, 1 clavicle, 1 cleithrum, 8 lower and 13 upper tooth plates), 13907 (1 I-bone, 3 J-bones, 5 Y-bones, 7 N-bones, 4 anterior marginals, 11 circumorbitals, 59 lower and 70 upper tooth plates), 8904 (1 E-bone, 7 J-bones, 1 N-bone, 10 circumorbitals, 3 lower and 12 upper tooth plates); (c) Cottonwood Creek, Archer County, Texas (Fig. 1: a): MCZ 8447 (1 C-bone, 1 lower and 1 upper tooth plate); (d) E. of Throckmorton, Throckmorton County, Texas (Fig. 1: 3t): MCZ 8448 (18 B-bones, 2 parasphenoids), FMNH UC2205 (holotype of *S. ciscoensis*, 1 upper and 1 lower tooth plate); (e) Black Flat, Archer County, Texas (Fig. 1: 3a): MCZ 8451 (1 upper tooth plate); (f) Rattlesnake Canyon, Archer County, Texas (Fig. 1: 3a): MCZ 8454 (1 lower tooth plate), TMM 40030-17 (1 upper tooth plate), 40030-44 (1 upper tooth plate), 40030-106 (1 lower tooth plate), 42497-12 (1 upper tooth plate), 42498-3 (2 upper tooth plates), 42501 (1 upper tooth plate); (g) N.E. of Dundee, Archer County, Texas (Fig. 1: 3a): MCZ 8458 (1 lower tooth plate); (h) E. of Rendham, Baylor County, Texas (Fig. 1: 3b): MCZ 8463 (1 LM-bone, 3 circumorbitals); (i) SPRR Survey A-431, Archer County, Texas (Fig. 1: 3a): MCZ 8466 (1 lower and 1 upper tooth plate); (j) W. of Williams Ranch, Baylor County, Texas (Fig. 1: 3b): MCZ 8468 (1 ? vomer, 4 upper tooth plates); (k) W.S.W. of Dundee, Archer County, Texas (Fig. 1: 3a): MCZ 8665 (2 upper tooth plates); (l) Cameron, Monroe County, Ohio (Fig. 1: 5): CMNH 8500 (1 upper tooth plate), 8501 (1 upper tooth plate); (m) Tit Mt., Archer County, Texas (Fig. 1: 3a): TMM 40031-43 (1 upper tooth plate), 40031-56 (1 lower tooth plate); (n) S. of Fulda, Baylor County, Texas (Fig. 1: 3b): AMNH 341 (upper tooth plate); (o) N. of Dundee, Archer County, Texas (Fig. 1: 3a): AMNH 9835 (upper tooth plate); (p) E. of Lake Kemp, Baylor County, Texas (Fig. 1: 3b): UCLA VP 431 (upper tooth plate; Berman, 1968: 833); (q) without precise locality, Texas (Fig. 1: 3): AMNH 5286 (holotype of *Ctenodus angustus*, lower tooth plate), 7235 (holotype of *Ctenodus porrectus*, upper tooth plate), 7473 (holotype of *Ctenodus heterolophus*, upper tooth plate), USNM 409697 (1 upper tooth plate), 409705 (1 lower tooth plate), 419729 (1 upper tooth plate), 427669 (1 upper tooth plate), 427670 (2 upper and 2 lower tooth plates), 427671 (8 upper and 2 lower tooth plates); (r) Clark Hill, Monroe County, Ohio (Fig. 1: 5): MCZ 9183 (lower tooth plate).

Sagenodus indet. from the Upper Pennsylvanian: Topeka, Shawnee County, Kansas (Fig. 1: 16): KUVP 127054 (tooth plate).

Sagenodus indet. from the Lower Permian: Cameron, Monroe County, Ohio (Fig. 1: 5): CMNH 26583 (block with disarticulated bones I, KX, L and Y).

Appendix 2. Material of *S. copeanus* (KUVP nr.)

A. Material from Robinson, Brown County, Kansas:

Skull roofing bones: B-bone 55381, 55363, 70747-70760 (70752-3 sectioned, 70757 = Fig. 5b, 70758 = Fig. 5a, 70759 = Fig. 4, 70760 in Figs. 3, 48a), 103131 sectioned; C-bone 70761-70779 (70762, 70769 sectioned, 70763 = Fig. 7a, b, 70772 = Fig. 6, 70775 = Fig. 7c, 70779 in Fig. 3), 86251 sectioned; C-, E- and LM-bones in articulation 55371; E-bone 55355 (Williston, 1899: pl. 35 fig. 8), 70866-70878 (70866 and 70867 in Fig. 3, 70868 = Fig. 8, 70870, 70875 sectioned), 86253 sectioned, 103111; anterior marginal bone (with supraorbital canal), 55374, 71119, 71122, 86255, 103142-103226 (Fig. 9); anterior marginal bone (without supraorbital canal) 103227-103243; median anterior marginal bone F (with supraorbital canal of both sides) 103244 (Fig. 10)-103258 (103249 in Fig. 3); I-bone 55373, 55383, 70899-70924 (70899 and 70912 in Fig. 3, 70913 = Fig. 11); J-bone 70879 (Fig. 12 and in Fig. 3)-70898 (70880 in Fig. 3, 70881, 70893 sectioned); parts of J-, LM- and KX-bones in articulation 55353 (Williston, 1899: pl. 35 fig. 6); LM-bone 55354 (Williston, 1899: pl. 35 fig. 7), 55356 (Williston, 1899: pl. 35 fig. 9), 55357 (Williston, 1899: pl. 35 fig. 10), 55358 (Williston, 1899: pl. 35 fig. 12), 55359 (Williston, 1899: pl. 35 fig. 13), 70990 (in Fig. 3)-71000 (70991 = Fig. 13 and in Fig. 3), 71014, 71015, 71017-71020, 103119, 103120; M-bone 71126; N-bone 71084-71087 (71085 and 71086 in Fig. 3, 71086 = Fig. 14); P-bone 71118, 71120, 77121 (= Fig. 15 and in Fig. 3), 71123, 103118; Z-bone 70947-70958 (70947 and 70948 in Fig. 3, 70951 = Fig. 16), 71029; Y-bone 70970-70988 (70970 and 70971 in Fig. 3, 70988 = Fig. 17), 71030, 103112; Y+Z-bone 70989; KX-bone 55360 (Williston, 1899: pl. 35 fig. 14), 55370, 70926-70946 (70926 and 70927 in Fig. 3, 70944 = Fig. 18), 103121; X-bone in part 71125; unidentified skull bone 103138. Casts of sectioned specimens available.

Circumorbital bones: 1-bone 103123 (in Fig. 19); 2-bone 71065-71072 (71070 in Fig. 19) and three uncatalogued; 3a-bone 71016, 71100-71117 (71103 in Fig. 19 and in Fig. 3, 71104 sectioned, 71105 in Fig. 3), 103126, 3a-bone in part 71124; 3b-bone 71088-71098 (71089 in Figs. 3 and 19), 103125; 4-bone 55368, 55369, 71073-71083, 71099 (in Figs. 3 and 19), 103116, 103117; 5+6-bone 71031-71051 (in Fig. 19), 86252 sectioned, 103122; 7-bone 71052-71064 (71063 in Fig. 19), 103124, 103127; unidentified circumorbital 86254 sectioned.

Palatal region: parasphenoid 55365, 55399 (Williston, 1899: pl. 35 fig. 3), 70738-70746 (70739 = Fig. 22), 103105 and nine uncatalogued pieces; pterygoid fragment 55385; tooth plate with pterygoid 55390, 70811-70814 (70812 = Figs. 20, 43b), 103101; upper tooth plate 55391, 70815-70827, 103102, 103103; vomerine tooth 71137 (Fig. 21).

Lower jaw: "angular" 785, 55364, 70846-70861 (Fig. 23), 103109 and five uncatalogued pieces; "angular" + "splenial" 70845 (Fig. 25); "splenial" 70828-70844 (70833 = Fig. 24), 103110 and six uncatalogued pieces; prearticular 55348 (Williston, 1899: pl. 28 figs. 1, 1a), 55392, 70780 (Fig. 26)-70810 (70798 = Fig. 44b, 70800 = Fig. 46b).

Opercular and branchial regions: operculum 55361 (Williston, 1899: pl. 36 fig. 2), 55362 (Williston, 1899: pl. 36 fig. 3), 55386, 55389, 55398 (Williston, 1899: pl. 35 fig. 1), 70697-70716 (70698 = Fig. 27; 70712 = Fig. 28), 103113–103115 and many (over 15) uncatalogued pieces; suboperculum 55394, 55395, 71127-71136 (71135 = Fig. 29); ceratohyal 55351 (Williston, 1899: pl. 28 figs. 3, 3a,b), 55384, 70717-70729 (70718 = Fig. 30), 103104.

Shoulder girdle: anocleithrum 55352 (Williston, 1899: pl. 35 fig. 4), 55367, 55372, 70862 (Fig. 33)-70865, 103108 and four uncatalogued pieces; cleithrum 55366, 55396, 70730-70737 (= Figs. 34, 35), 103107 and nine uncatalogued pieces; clavicle 70959-70969 (70964 = Figs. 35, 36), 103106 and 12 uncatalogued partial clavicles.

Postcranial elements: cranial rib 71021 (= Fig. 37)-71026; rib 103128, 103136, 103137, 127055–127057 (right, middle, left specimen respectively in Rothschild & Martin, 1993: fig. 19-4); neural arch 103129, 103130; neural spine 71027, 103132; haemal arch with spine 71028; two haemal arches and spines fused 103133 (Fig. 38); radial 103134, 103135; scale fragment 72471.

B. Material from Hamilton, Greenwood County, Kansas:

Complete specimen: 84201 (Fig. 39; Chorn & Schultze, 1989: fig. 2, and cover of Geotimes, 33(7), July 1988) with counterpart.

Skull roof: 103259 (Fig. 40) with counterpart (Chorn & Schultze, 1990: fig. 6; Schultze, 1993: fig. 2).

Palatal region: parasphenoid 81394, 103262.

Lower jaw: left prearticular with tooth plate 103261 (Fig. 41; Chorn & Schultze, 1989: fig. 1) with imprint; "angular" 103282 with counterpart.

Opercular region: right operculum 103281.

Scales: 81393, 83748, 103263–103280 (103266a = Fig. 42), 120139.

Caudal fin: 103260.

Appendix 3. Characters and character states used in the phylogenetic analysis (PAUP 3.1.1)

Skull roof

1. Bone D: 0 = present, 1 = absent.
2. Bone J: 0 = present, 1 = fused.
3. Occipital commissure passing: 0 = through I-A-I, 1 = through I-B-I, 2 = above bones.
4. Bone C: 0 = paired, 1 = unpaired, 2 = fused.
5. Bone E: 0 = paired, 1 = unpaired, 2 = EF.
6. Posterior process of bone I: 0 = present, 1 = absent.
7. Snout: 0 = covered with cosmine, 1 = not covered with cosmine.
8. Bone I: 0 = present, 1 = fused.
9. Bone K: 0 = single, 1 = fused.
10. Bone L: 0 = two bones, 1 = single, 2 = fused.
11. Bone M: 0 = single, 1 = fused.
12. Bone Z: 0 = posterior to Y, 1 = between Y and I, 2 = absent.
13. Bone Y: 0 = two bones (Y_1, Y_2), 1 = one bone, 2 = no separate Y.
14. Bone X: 0 = present, 1 = absent.
15. Relationship between cephalic division of main lateral line canal and bone 3: 0 = reaching into 3, 1 = not in 3.
34. Bone ZY: 0 = absent, 1 = present.
35. Bone XY: 0 = absent, 1 = present.
36. Bone KX: 0 = absent, 1 = present.
37. Bone KL: 0 = absent, 1 = present.
38. Bone KLM: 0 = absent, 1 = present.
39. Bone LKJ: 0 = absent, 1 = present.
40. Bone LM: 0 = absent, 1 = present.

Palatal region

16. Position of parasphenoid: 0 = below otico-occipital region, 1 = below ethmosphenoidal and otico-occipital regions.
17. Relation between posterior to anterior length of parasphenoid: 0 = <1, 1 = about 1, 2 = >1.
18. Shape of parasphenoid: 0 = plough-shaped, 1 = with lozenge, 2 = anterior border round.
19. Stem of parasphenoid: 0 = short, 1 = prominent, 2 = long, 3 = extremely long.
20. Ascending process: 0 = absent, 1 = short, 2 = long.

Lower jaw

21. Number of infradentaries: 0 = 4, 1 = 2, 2 = 1.
22. Course of oral and mandibular canals: 0 = parallel in two bones, 1 = converging in one bone, 2 = oral canal in bone, mandibular canal in gutter, 3 = both above bone.
23. Ridges of tooth plates: 0 = with cusps, 1 = without cusps.
24. Pulp cavity: 0 = small, 1 = large.
32. Tooth plate: 0 = absent, 1 = with radiating ridges, 2 = with parallel ridges.

Gill region

25. Cranial rib: 0 = lacking, 1 = present.
26. Ceratohyal: 0 = short and stout, 1 = long.
29. Tabulate process on operculum: 0 = without, 1 = with.

Postcranial region

27. Mobility of clavicle: 0 = no to little, 1 = mobile (long clavicle).
28. Cosmine on cleithrum and clavicle: 0 = with, 1 = without.
30. Dorsal fin(s): 0 = two, 1 = one, 2 = fused with caudal fin.
31. Anal fin: 0 = present, 1 = absent.
33. Caudal fin: 0 = heterocercal, 1 = diphycercal.

Cheek region

41. Bone 3: 0 = single, 1 = two bones, 2 = absent.
42. Bone 8: 0 = single, 1 = fused, 2 = absent.
43. Bone 5+8: 0 = absent, 1 = present.
44. Bone 5: 0 = single, 1 = fused, 2 = absent.
45. Bone 5+6: 0 = absent, 1 = present.
46. Bone 6: 0 = single, 1 = fused, 2 = absent.
47. Bone 1: 0 = two bones, 1 = single, 2 = absent.

Appendix 4. Data matrix of characters 1–47 (cf. Appendix 3)

		Dipterus	*Rhinodipterus*	*Scaumenacia*	*Phaneropleuron*	*Conchopoma*	*Delatitia*	*Ctenodus*	*Ganopristodus*	*Straitonia*	*Tranodis*	*Sagenodus*	*Megapleuron*	*Palaeophichthys*	*Gnathoriza*	*Paraceratodus*	*Ptychoceratodus*	*Neoceratodus*	*Lepidosiren*
1	D	0	0	0/1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1
2	J	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1
3	occ	0	0	0	0	0	0	1	1	1	1	1	1	?	1	2	1	3	3
4	C	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	2	2
5	E	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	1	2	2
6	plp	0	0	0	1	1	0	0	1	?	1	0	1	1	0	1	0	1	1
7	snout	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
8	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
9	K	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
10	L	0	1	0	1	2	0	2	2	2	2	2	2	2	2	2	2	2	2
11	M	0	0	0	?	0	?	0	1	0	0	1	1	?	1	1	1	1	1
12	Z	0	0	1	0	1	0	1	1	1	1	1	1	1	2	1	2	2	2
13	Y	0	0	0	0	2	1	0	1	2	2	1	1	1	1	1	2	2	2
14	X	0	1	1	0	1	1	0	1	1	1	1	1	0	2	1	0	1	1
15	1.3	0	1	0	?	1	1	1	1	1	0	0	?	?	1	?	?	?	1
16	psp	0	0	0	?	1	?	0	0	?	0	1	1	?	1	?	1	1	1
17	l.psp	0	0	?	?	0	?	2	?	?	1	2	0	?	1	?	?	0	0
18	s.psp	0	0	?	?	2	?	1	1	?	1	1	1	?	2	?	?	1	1
19	stem	0	0	?	?	1	?	2	2	?	2	3	2	2	3	?	?	3	3
20	apr	0	0	0	?	0	?	0	0	?	0	0	0	?	1	?	2	2	1
21	ide	0	0	1	?	1	?	1	1	?	1	1	?	1	1	?	1	2	2
22	omc	0	0	1	?	1	?	2	?	?	1	2	?	?	2	?	3	3	3
23	ridg	0	0	0	0	?	0	0	0	?	0	0	0	1	1	?	1	1	1
24	pulp	0	0	0	?	0	?	1	0	?	?	1	?	?	1	?	?	1	1
25	cri	1	1	1	?	1	?	?	?	?	0	1	1	?	1	?	?	1	1
26	ch	0	?	?	?	1	?	0	0	?	?	0	?	1	1	?	?	1	1
27	clav	0	0	0	0	1	?	?	0	?	?	0	1	1	1	?	?	1	1
28	clei	0	0	1	1	1	?	?	1	?	1	1	1	1	1	1	?	1	1
29	op	0	0	0	0	1	1	1	1	0	?	1	1	?	1	?	?	1	0
30	df	0	0	1	1	2	?	?	2	2	?	2	2	2	?	2	?	2	2
31	af	0	0	0	0	1	?	?	1	1	?	1	1	1	1	1	?	1	1
32	tp	1	1	1	1	0	1	2	0	?	1	1	1	1	1	?	1	1	1
33	cf	0	0	0	0	1	?	?	1	1	?	1	1	1	1	1	?	1	1
34	ZY	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
35	XY	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0
36	KX	0	1	1	0	0	1	0	1	0	0	1	1	1	1	1	1	1	1
37	KL	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0
38	KLM	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0
39	LKJ	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
40	LM	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	1
41	3	0	0	0	0	0	1	1	0	?	0	1	?	?	2	?	?	2	2
42	8	0	0	0	?	1	?	2	?	?	0	2	?	?	1	?	?	2	2
43	5+8	0	0	0	?	1	?	0	?	?	0	0	?	?	1	?	?	0	0
44	5	0	0	0	?	1	?	?	?	?	0	1	?	?	1	?	?	0	2
45	5+6	0	0	0	?	0	?	?	?	?	0	1	?	?	0	?	?	0	0
46	6	0	0	0	?	0	?	?	?	?	0	1	?	?	0	?	?	0	2
47	1	0	0	0	?	?	?	?	?	?	?	1	?	?	1	?	?	2	2

Appendix 5. Distribution of character states in Fig. 53 (character$^{\text{state}}$, homoplasies in italics)

Node 1: 7^1, 21^1, 22^1, 28^1.
Node 2: 13^1, 15^1, 29^1.
Node 3: 3^1, 10^2, 12^1, 18^1, 19^2, 30^2, 31^1, 33^1.
      Node 4: *6^1*.
      Node 5: *1^1*, *13^2*, 35^1, 36^{1-0}.
      Node 6: *4^1*
Node 7: 22^2, 24^1, 41^1, 42^2.
Node 8: *1^1*, 11^1, 16^1, 40^1, 47^1.
      Sagenodus: *4^1*, 15^{1-0}, 17^2, *19^3*, 44^1, 45^1, 46^1.
Node 9: 5^1, *6^1*, 27^1.
Node 10: *4^1*, 20^1, 23^1, 26^1.
      Node 11: 14^{1-0}, 40^{1-0}.
      Node 12: 6^{1-0}, 12^2, 38^2.
Node 13: 5^2.
Node 14: 2^1, 3^3, 4^2, *12^2*, *13^2*, *19^3*, 21^2, 22^3, 47^2.