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Skeletal anatomy of the Late Cretaceous shark, *Squalicorax* (Neoselachii: Anacoracidae)

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with 13 figures and 3 appendices

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Abstract: The paleobiology of the Cretaceous neoselachian shark, *Squalicorax*, has largely been based on isolated teeth. We examined partial and nearly complete skeletons of three species of *Squalicorax*, *S. falcatus* (AGASSIZ), *S. kaupi* (AGASSIZ), and *S. pristodontus* (AGASSIZ), that were collected from the U.S.A. These specimens suggest that the total body length (TL) of *S. falcatus* typically measured 1.8–2.0 m, and probably did not exceed 3 m. Moderate-sized individuals of *S. kaupi* and *S. pristodontus* perhaps measured about 3 m TL. Although *S. pristodontus* was the largest form among the three species examined, this taxon possessed a set of large jaws (with large but fewer teeth) relative to its body size compared to *S. falcatus* or *S. kaupi*. This suggests that tooth size is not an accurate indicator of the TL if one compares one *Squalicorax* species to another. Neurocranial features suggest that the vision of *Squalicorax* was not as acute as that of a contemporaneous macrophagous lamniform shark, *Cretoxyrhina mantelli* (AGASSIZ), but olfaction of *Squalicorax* may have been better than *C. mantelli*. The morphology of placoid scales suggests that *Squalicorax* was capable of fast swimming. New skeletal data support the view that the feeding dynamics of *Squalicorax* was similar to the modern tiger shark (*Galeocerdo* MULLER & HENLE). The present data do not allow for exact ordinal placement, but, contrary to some previous interpretations, *Squalicorax* can be excluded from the Hexanchiformes and Orectolobiformes. The taxon should more appropriately be placed within the Lamniformes or Carcharhiniformes.

Keywords: Anacoracidae • Chondrichthyes • Elasmobranchii • North America • paleobiology • *Squalicorax* • Upper Cretaceous

Kurzfassung: Bisher basierte die Kenntnis zur Paläobiologie des kretazischen Neoselachiers *Squalicorax* weitgehend auf isolierten Zähnen. Neue Untersuchungen an fast vollständigen sowie Teil-Skeletten von drei Arten der Gattung *Squalicorax (S. falcatus* (AGASSIZ), *S. kaupi* (AGASSIZ) und *S. pristodontus* (AGASSIZ)) aus verschiedenen Gebieten der U.S.A. zeigen, dass die Gesamtkörperlänge von *S. falcatus* im Durchschnitt 1,8–2,0 m betrug und wahrscheinlich 3 m nicht überschritt. Mittelgroße Individuen von *S. kaupi* und *S. pristodontus* maßen vermutlich etwa 3 m Gesamtlänge. *S. pristodontus* war die größte der drei untersuchten Arten und besaß verglichen mit *S. falcatus* oder *S. kaupi* im Verhältnis zur Gesamtkörpergröße relativ große Kieferknochen mit großen Zähnen, jedoch in einer geringeren Anzahl. Es zeigt sich, dass im Vergleich der Arten untereinander die Zahngröße kein besonders gutes Indiz zur Rekonstruktion der Gesamtkörperlänge ist. Merkmale des Neurocraniums belegen, dass das Sehvermögen von *Squalicorax* nicht so scharf war wie das des zeitgleich lebenden makrophagen lamniformen Hais *Cretoxyrhina mantelli* (AGASSIZ), jedoch der Geruchssinn von *Squalicorax* möglicherweise besser ausgebildet war als bei *C. mantelli*. Die Morphologie der Placoidschuppen deutet an, dass *Squalicorax* ein schneller Schwimmer war. Neue Daten zur Skelett-Morphologie bestätigen die Ansicht, dass das Fressverhalten von *Squalicorax* dem des rezenten Tigerhais (*Galeocerdo* MULLER & HENLE) ähnelte. Die vorliegenden Daten geben keine genauen Hinweise zur systematischen Einordnung von *Squalicorax*, allerdings kann eine Eingruppierung in die Hexanchiformes und Orectolobiformes, im Gegensatz zu früheren Ansichten, ausgeschlossen werden; eine Zuordnung zu den Lamniformes oder Carcharhiniformes kommt eher in Betracht.

Schlüsselwörter: Anacoracidae • Chondrichthyes • Elasmobranchii • Nord-Amerika • Paläobiologie • *Squalicorax* • Ober-Kreide

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Introduction

Remains of the extinct shark genus, *Squalicorax* WHITLEY, 1939 (Neoselachii: Anacoracidae), are common in Cretaceous marine deposits worldwide, including North and South America, Europe, Russia, Australia, Japan, and Africa (CAPPETTA 1987). However, the taxon is represented primarily by isolated teeth. Like other fossil elasmobranchs, this is due to the fact that their skeletal elements are primarily cartilaginous and not prone to fossilization.

Anacoracid sharks are the only pre-Cenozoic neoselachians with serrated teeth, which resemble those of carcharhiniform taxa, especially Recent *Galeocerdo* MULLER & HENLE, 1837 (e.g., see SCHWIMMER et al. 1997). This resemblance is thought to be a result of convergence rather than actual phyletic relationship (e.g., CAPPETTA 1987; SIVERSON 1992; WELTON & FARISH 1993). On the basis of tooth morphology, some researchers have envisioned *Squalicorax* as an active predator (e.g., GLIKMAN 1967; WOLBERG 1985a, b; WILLIAMSON et al. 1989; COMPAGNO 1990; FRICKHINGER 1995). Fossilized gastric contents and taphonomic evidence (e.g., tooth marks) have led others to believe that the shark was an opportunistic feeder (DRUCKENMILLER et al. 1993) or a scavenger (e.g., WILEY & STEWART 1977; SCHWIMMER et al. 1997; SHIMADA 1997a).

Aside from inferences that can be made based on the gastric residues and feeding marks, little is known about the paleobiology of *Squalicorax*. Basic information, such as body form and size, locomotion, and systematic position, remain to be determined. To learn more about this extinct shark, we examined all available partial or nearly complete skeletons of *S. falcatus* (AGASSIZ, 1843), *S. kaupi* (AGASSIZ, 1843), and *S. pristodontus* (AGASSIZ, 1843) collected from the Niobrara Chalk and Pierre Shale (Late Coniacian – Campanian) of Kansas, South Dakota, and Wyoming. In this paper, we review *Squalicorax* species of North America, describe the skeletal anatomy in the specimens examined, and discuss the body form, body size, feeding dynamics, and higher-level systematic position of this taxon based on anatomical evidence.

Squalicorax species of North America

The temporal range of *Squalicorax* (and the family Anacoracidae) spans much of the Cretaceous, from Late Albian to Late Maastrichtian time (CAPPETTA et al. 1993; NOUBHANI & CAPPETTA 1997). *Squalicorax* teeth are occasionally found in Paleocene or younger rocks (e.g., SHOURD & WINTER 1980), but these Cenozoic occurrences are considered to be reworked from underlying Cretaceous deposits (e.g., BURRIS 2001). Differences among species are based on variations in crown and root morphology. However, all species of *Squalicorax* can be described in a general way as having: an elongated mesial cutting edge and a much shorter distal cutting edge that forms a sharp, distally directed cusp; a short

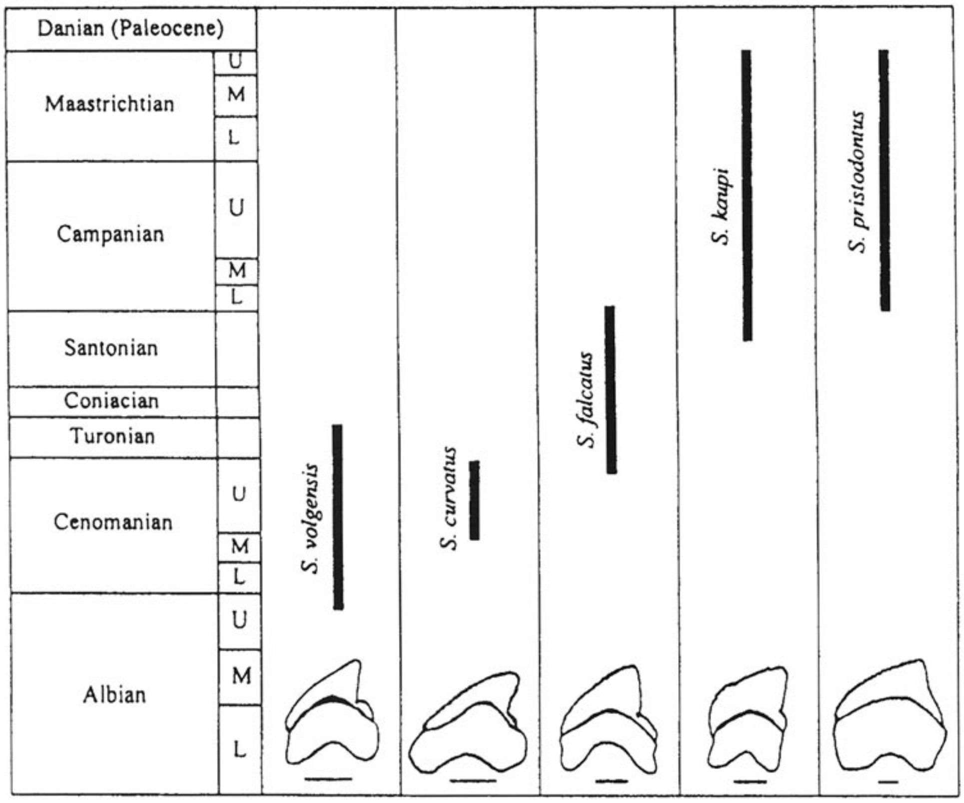


Fig. 1. Temporal distribution of five *Squalicorax* species in Cretaceous rocks of North America (see text for details). – Each illustrated tooth is a representative tooth of each species (mesial to the left; scale bar = 5 mm).

distal blade; and a labiolingually thin, weakly bilobate root that lacks a lingual nutritive groove. Here, we provide a brief review of North American species of *Squalicorax*.

WELTON & FARISH (1993: 120–121) illustrated teeth of "*Squalicorax* sp." from the Upper Albian of Texas, U.S.A., and these represent the oldest remains of the genus in North America. WELTON & FARISH's "*Squalicorax* sp." may be referable to *S. volgensis* (GLIKMAN in GLIKMAN & SHVAZHAITE, 1971), which is characterized by unserrated or weakly serrated teeth (see also SIVERSON 1996). CAPPETTA & CASE (1999) and CICIMURRI (2001) documented the occurrence of *S. volgensis* in Middle Cenomanian to Upper Turonian rocks.

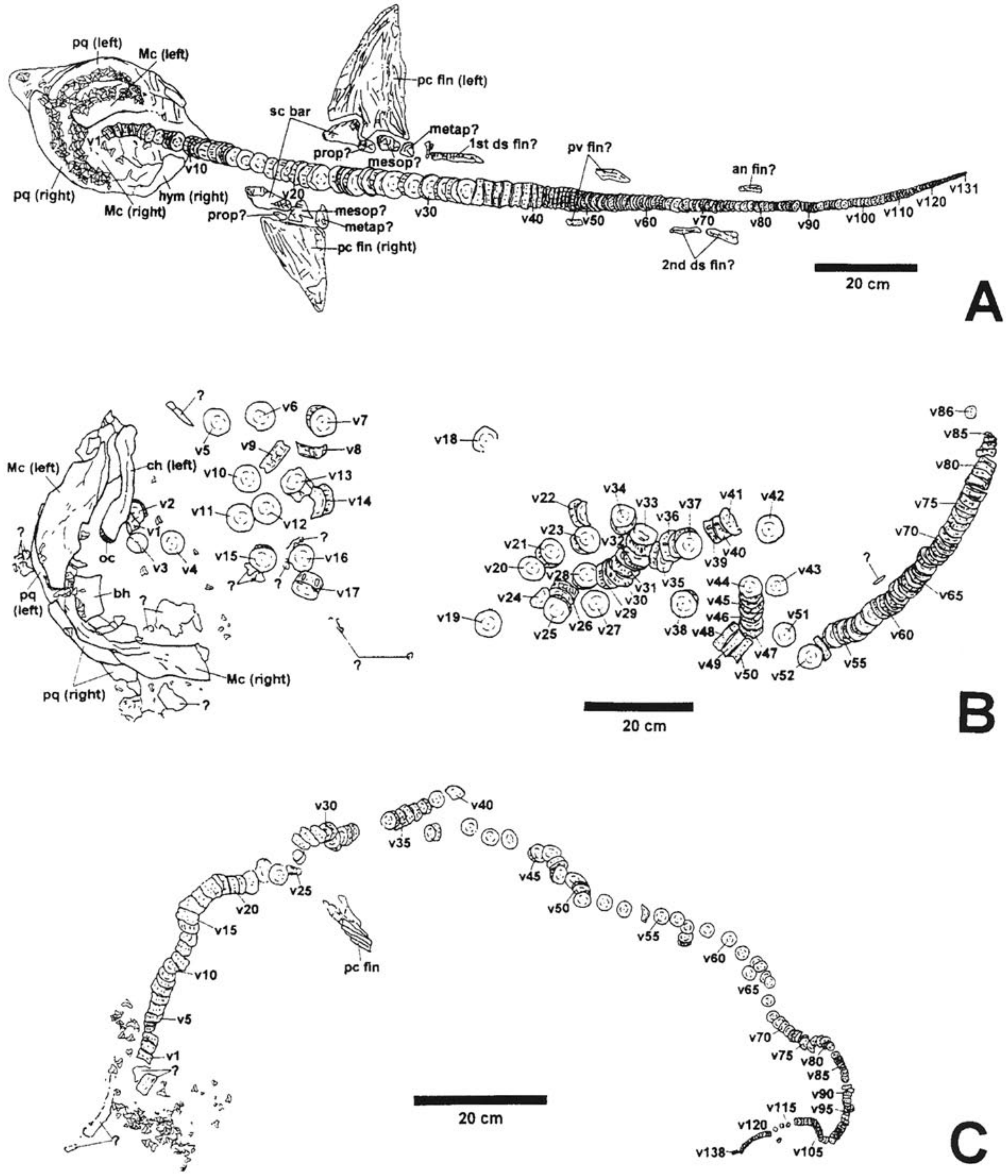


Fig. 2. Partial and nearly complete skeletons of *Squalicorax falcatus*. – **A**: USNM 425665. – **B**: LACM 120090. – **C**: LACM 143537 (exact order of vertebrae is partly uncertain in B and C). – Key to lettering: an fin, anal fin; bh, basihyal; ch, ceratohyal; ds fin, dorsal fin; hym, hyomandibula; Mc, Meckel's cartilage; mesop, mesopterygium; metap, metapterygium; pc fin, pectoral fin; pq, palatoquadrate; prop, propterygium; pv fin, pelvic fin; sc bar, scapulocoracoid bar; v, vertebra.

However, the inclusion of WELTON & FARISH's "*Squalicorax* sp." would extend the stratigraphic range of the species from the Upper Albian to the Upper Turonian (Fig. 1).

Squalicorax curvatus (WILLISTON, 1900) is a Cenomanian species that is characterized by teeth with crowns that strongly curve distally and have a convex labial face. CAPPETTA & CASE (1999) believe that some teeth referred to *S. curvatus* should in fact be assigned to *S. baharijensis* (STRÖMER, 1927). The stratigraphic range of these taxa is from the Middle Cenomanian to the Upper Cenomanian (CAPPETTA & CASE 1999; CICIMURRI 2001; Fig. 1).

Teeth of *Squalicorax falcatus* have been reported from Upper Cenomanian to Lower Campanian rocks in North America (WILLIAMSON et al. 1993; MARTIN et al. 1998; Fig. 1) and show a considerable degree of morphological variation. This variation could be indicative of multiple species (WELTON & FARISH 1993), or simply dignathic, ontogenetic, or sexual heterodonty within a single species. For the purpose of this study, we adhere to WELTON & FARISH's (1993) treatment of the species, in which teeth of *S. falcatus* consist of a broad morphological range, including forms like CAPPETTA & CASE's (1999) "*Squalicorax* sp. 1" and "*Squalicorax* sp. 2".

Squalicorax kaupi is known from Upper Santonian to Upper Maastrichtian rocks in North America (CASE 1979; WILLIAMSON et al. 1989; Fig. 1), and it often occurs with *S. pristodontus* (CASE 1979; LAUGINIGER 1988). The youngest occurrence of *S. pristodontus* is Upper Maastrichtian (CASE 1979), whereas its oldest record is represented by Early Campanian specimens from the uppermost Niobrara Chalk of Kansas (HAMM et al. 2003; Fig. 1).

Thus far, *Squalicorax falcatus*, *S. kaupi*, and *S. pristodontus* are the only anacoracid sharks in which skeletal remains are known. Other *Squalicorax* species, and species of other anacoracid genera (*Microcorax* CAPPETTA & CASE, 1975, *Pseudocorax* PRIEM, 1897, and *Paracorax* CAPPETTA, 1977), are represented only by their teeth (for review, see CAPPETTA 1987). Therefore, elucidating the phylogenetic interrelationships of anacoracid taxa is difficult based on this limited evidence and is beyond the scope of this paper. Nevertheless, as noted by others, all *Squalicorax* species are probably closely related to each other phylogenetically (e.g., BILELO 1969; CAPPETTA 1973, 1987; MEYER 1974; WOLBERG 1985a, b; WELTON & FARISH 1993). For example, CAPPETTA (1987) stated that there was a gradual transition between *Squalicorax* species, with *S. falcatus* giving rise *S. kaupi*, and then *S. kaupi* to *S. pristodontus*. This interpretation is based on the following observed morphological trend through time: teeth become larger and labiolingually thinner; the cusp becomes more erect; the mesial cutting edge becomes highly convex; the transition between the distal cutting edge and distal blade becomes less distinct; serrations become coarser and more complex; and the root becomes thinner and higher (CAPPETTA 1987; WELTON & FARISH 1993).

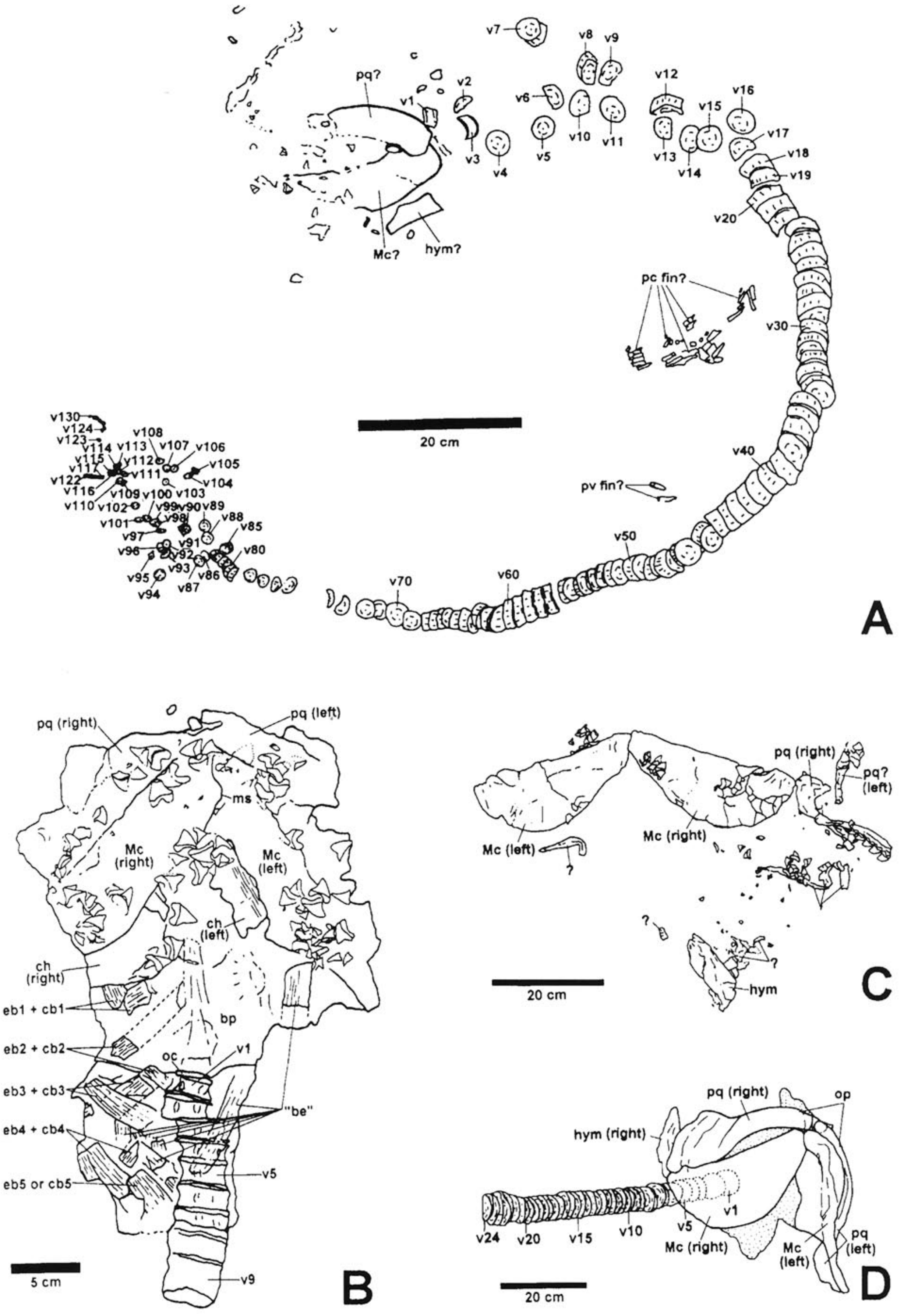
Material and methods

Squalicorax specimens in the following institutions in the United States were examined: American Museum of Natural History (AMNH), New York; Cincinnati Museum Center (CMC), Cincinnati, Ohio; Sternberg Museum of Natural History, Fort Hays State University (FHSM), Hays, Kansas; University of Kansas Museum of Natural History (KUVP), Lawrence; Los Angeles County Museum of Natural History, California (LACM); Museum of Geology, South Dakota School of Mines and Technology (SDSM), Rapid City; University of Colorado Museum (UCM), Boulder; United States National Museum of Natural History (USNM), Washington D.C.; and Geology Museum, Department of Geology and Geophysics, University of Wisconsin at Madison (UW-Madison), Madison.

The specimens we examined come from Upper Coniacian to Middle Campanian rocks of Kansas, South Dakota, and Wyoming, U.S.A. The following specimens were extensively studied: USNM 425665, LACM 120090, LACM 143537, LACM 135929, CMC VP-5722, FHSM VP-2213, KUVP 69712, and SDSM 34975 (Figs. 2–4). Additional specimens are listed in Appendix 1, but these consist mostly of fragmentary skeletal remains that offered little informative skeletal data. Because of the difficulty in identifying skeletal material without associated teeth, we focused primarily on those specimens that were associated with at least one tooth (Appendix 1). Specimens consisting only of teeth are not included here because of the obvious lack of desired data.

We follow COMPAGNO (1999b) for extant shark taxonomy. Skeletal terminology follows primarily COMPAGNO (1988, 1990, 1999a). For extinct shark taxonomy, we generally follow CAPPETTA (1987), but the morphological variation of teeth among species of *Squalicorax* appears to overlap, making the separation of one species from another difficult (FOWLER 1911; LAUGINIGER 1986; WILLIAMSON et al. 1993). Thus, for the identification of the three *Squalicorax* species we examined (*S. falcatus*, *S. kaupi*, and *S. pristodontus*), we follow the classification scheme of WELTON & FARISH (1993).

Fig. 3. Partial skeletons of *Squalicorax falcatus* and *S. kaupi*. – **A**: LACM 135929, *S. falcatus* (exact order of vertebrae is partly uncertain). – **B**: CMC VP-5722, *S. falcatus*. – **C**: FHSM VP-2213, *S. kaupi*. – **D**: KUVP 69712, *S. kaupi* (stipple = possible neurocranium). – Key to lettering: be, branchial elements; bp, basal plate of neurocranium; cb, ceratobranchial; ch, ceratohyal; eb, epibranchial; hym, hyomandibula; Mc, Meckel's cartilage; ob, orbital process; oc, occipital centrum; pc fin, pectoral fin; pq, palatoquadrate; v, vertebra.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Anatomical description

Neurocranium

COMPAGNO (1990: fig. 10) illustrated a nearly complete neurocranium of *Squalicorax "falcatus"* (LACM 16056; Fig. 5) which was purportedly associated with teeth and jaw fragments. This specimen was not available for us to study. However, COMPAGNO's (1990) illustration suggests that the width of the skull is almost as broad as the cranial length, and the anterior (precerebral) fontanelle opens widely along the anterior margin of the skull. A pair of laterally projected preorbital processes forms the widest points, whereas paired postorbital processes are not prominent. A well-defined supraorbital crest (shelf) is present between the preorbital and postorbital processes. Much of the cranial roof and basal plate are flat, but there is an indication of the presence of the tripodal rostrum (formed by a medial rostral cartilage and a pair of lateral rostral cartilages) and "ectethmoid processes" (COMPAGNO 1990; for further discussion, see below). Based on the position of the "processes", the nasal capsules must have been large, taking up about 40 % of the cranial length. The anteroposterior length of the orbital region is about the same as that of the nasal region, whereas the otic region takes up only about 20 % of the cranial length. The presence of a suborbital shelf is uncertain. Likewise, the presence of hyomandibular fossa cannot be determined from COMPAGNO's (1990) illustration, but it is presumably positioned on the lateroventral corner of the short otic region

CMC VP-5722 (*Squalicorax falcatus*) preserves a posterior part of the flat basal plate of the neurocranium (Fig. 3B). The lateral edges are missing but the cranium is broad, and the posterior edge does not extend posteriorly beyond the occipital centrum. Parts of the neurocranium are preserved in three other specimens, USNM 425665, LACM 120090 (*S. falcatus*; Figs. 2A–B), and KUVP 69712 (*S. kaupi*; Fig. 3D), but they do not offer further information on neurocranial anatomy.

Splanchnocranium

Labial cartilages

The mandibular arch of extant sharks is accompanied by at most three labial cartilages per side (MAISEY 1983). In the specimens we examined, labial cartilage was either not preserved or could not definitively be identified as such. A 5 cm-long, rod-like piece of cartilage, that may be one of the labial cartilages, is located near the paired Meckel's cartilages of SDSM 34975 (*Squalicorax pristodontus*; Fig. 4); however, because the specimen was significantly disarticulated, this element could be from another part of the skeleton.

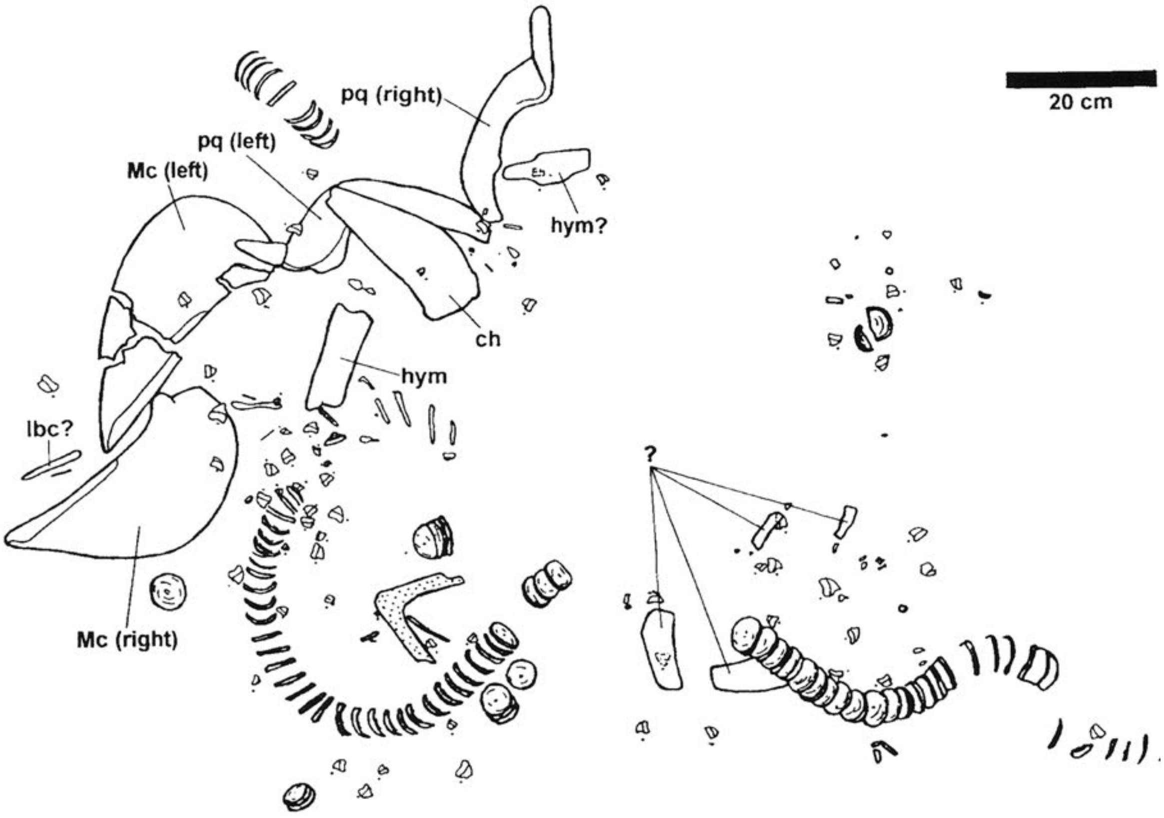

Fig. 4. Partial skeleton of *Squalicorax pristodontus* (SDSM 34975). – Key to lettering: ch, ceratohyal; hym, hyomandibula; lbc, labial cartilage; Mc, Meckel's cartilage; pq, palatoquadrate. Stippled item = dentary of marine turtle.

Mandibular arch

Owing to their high level of calcification, many of the specimens we studied include the upper pair of palatoquadrates and lower pair of Meckel's cartilages. In most cases, the jaws are preserved so that the original anteroposterior curvature was flattened, but there is little dorsoventral distortion (Figs. 2A–B, 3B–D, 4). This taphonomic condition indicates that the jaws of *Squalicorax* were broad laterally and that the mouth was wide. Specimens with the jaws connected at their symphyses (Figs. 2A–B, 3B, D) show the upper jaw overbiting the lower jaws, indicating that the shark had a subterminal mouth. Jaw cartilages of *S. pristodontus* (Fig. 6) are robust and thicker than those of similar sized *S. falcatus* or *S. kaupi*.

The preservation of USNM 425665 and LACM 120090 suggests that the jaw cartilages of *Squalicorax falcatus* were gently arched (Figs. 2A–B). The best sources of information regarding the jaw morphology of the genus comes from specimens of *S. kaupi* and *S. pristodontus* (Figs. 3C–D, 4, 6). The palatoquadrate of these taxa consists of a gently curved, long palatine process and an expanded quadrate process with a thick, prominent quadrate ridge (Figs. 3D, 6). The cartilage of the palatine process is deep and thick, and a low process is located on its dorsal side, 40 % of the way from the symphysis. We interpret the low process as the orbital process, which would presumably have articulated with the anterior part of the basal plate of the skull. The symphysis of each palatoquadrate of SDSM 34975 (*S. pristodontus*) has a deep, squared end, suggesting a tight connection between these elements. In addition, a short, ventrally directed projection is located at the mesioventral edge of the palatoquadrate symphysis (Figs. 6, 7). Such a ventral projection, here referred to as the "mesioventral process", may have served as a supplementary area for the attachment of jaw-connecting ligaments.

The Meckel's cartilage of *Squalicorax kaupi* and *S. pristodontus* is deep, being more than twice the depth of the palatine process of the palatoquadrate (Figs. 3C–D, 6). The posterior 80 % of the Meckel's cartilage is particularly expanded for massive quadratomandibularis muscles (sensu MOTTA & WILGA 1995), which would have originated from an expanded quadrate process of the palatoquadrate. The anterior portion of the Meckel's cartilage exhibits mesiodistal curvature and the symphysis tapers to a rounded point. The symphysial surface shows that the connection between the lower jaws was not as tightly held as in the upper jaws. The Meckel's cartilage is thickest near the symphysis and quadratomandibular joint. A weak mandibular knob (sensu WU 1994), which would have articulated with the hyoid arch, is located near the quadratomandibular joint.

USNM 425665 (*Squalicorax falcatus*; Fig. 2A) preserves many teeth in situ on its jaws, but a detailed description of its dentition would be premature because the oral region requires further preparation (note: the specimen is currently a fixed part of a permanent exhibit). Nevertheless, there are at least 15 tooth rows on the left palatoquadrate and at least 13 tooth rows on the right Meckel's cartilage (Fig. 8). These numbers do not include rows of small teeth that can be considered symphysial teeth (sensu SHIMADA 2002). This specimen and FHSM VP-2213 (*S. kaupi*; Fig. 3C) show that adjacent teeth do not overlap each other (Fig. 9). This condition is called a "juxtaposed dentition" (WELTON & FARISH 1993). In SDSM 34975 (*S. pristodontus*), the anterior 60 % of the lingual side of both the palatoquadrate and

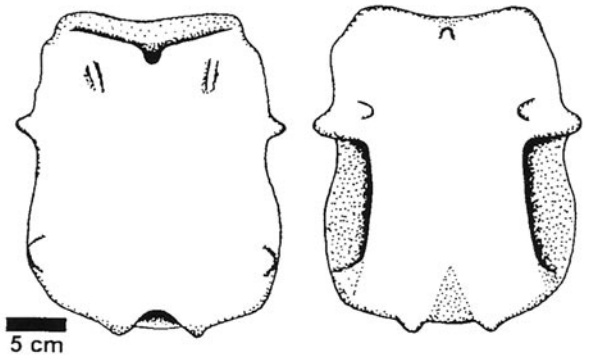

Fig. 5. Dorsal (left) and ventral (right) views of neurocranium of *Squalicorax* "*falcatus*" (after COMPAGNO 1990: fig. 10). – Anterior to the top.

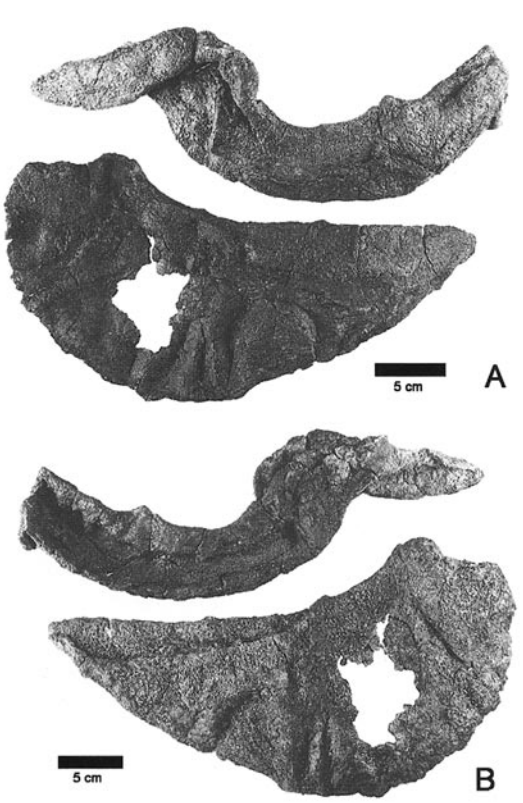

Fig. 6. Photographs of right palatoquadrate (top) and right Meckel's cartilage (bottom) of *Squalicorax pristodontus* (SDSM 34975; cf. Fig. 4). – **A**: labial view (anterior to the right); **B**: lingual view (anterior to the left).

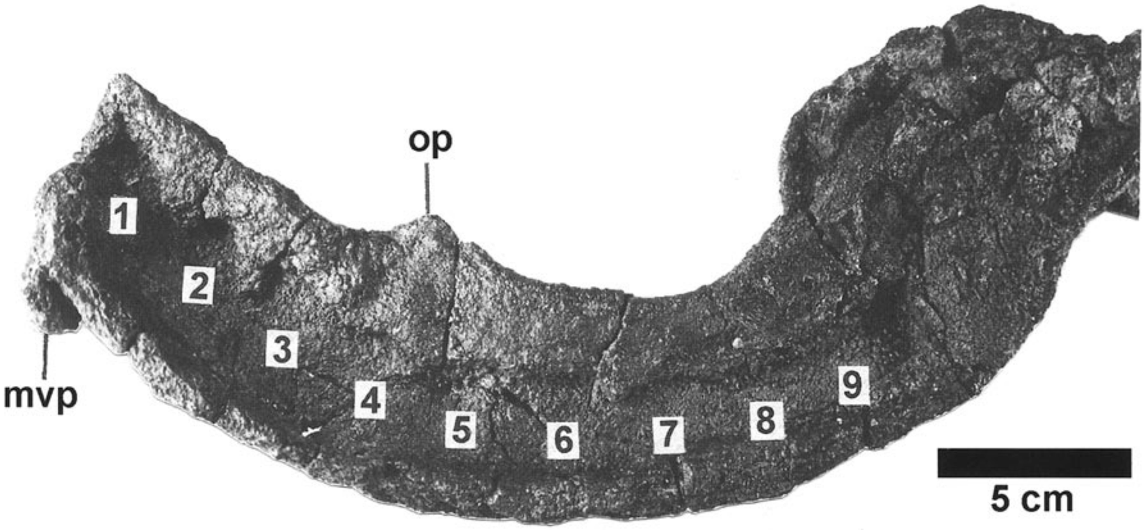

Fig. 7. Detail of right palatoquadrate (lingual view; cf. Fig. 6B) of *Squalicorax pristodontus* (SDSM 34975; cf. Fig. 4). – Numbers 1 through 9 represent position of nine tooth rows. – Key to lettering: mvp, mesioventral process; op, orbital process.

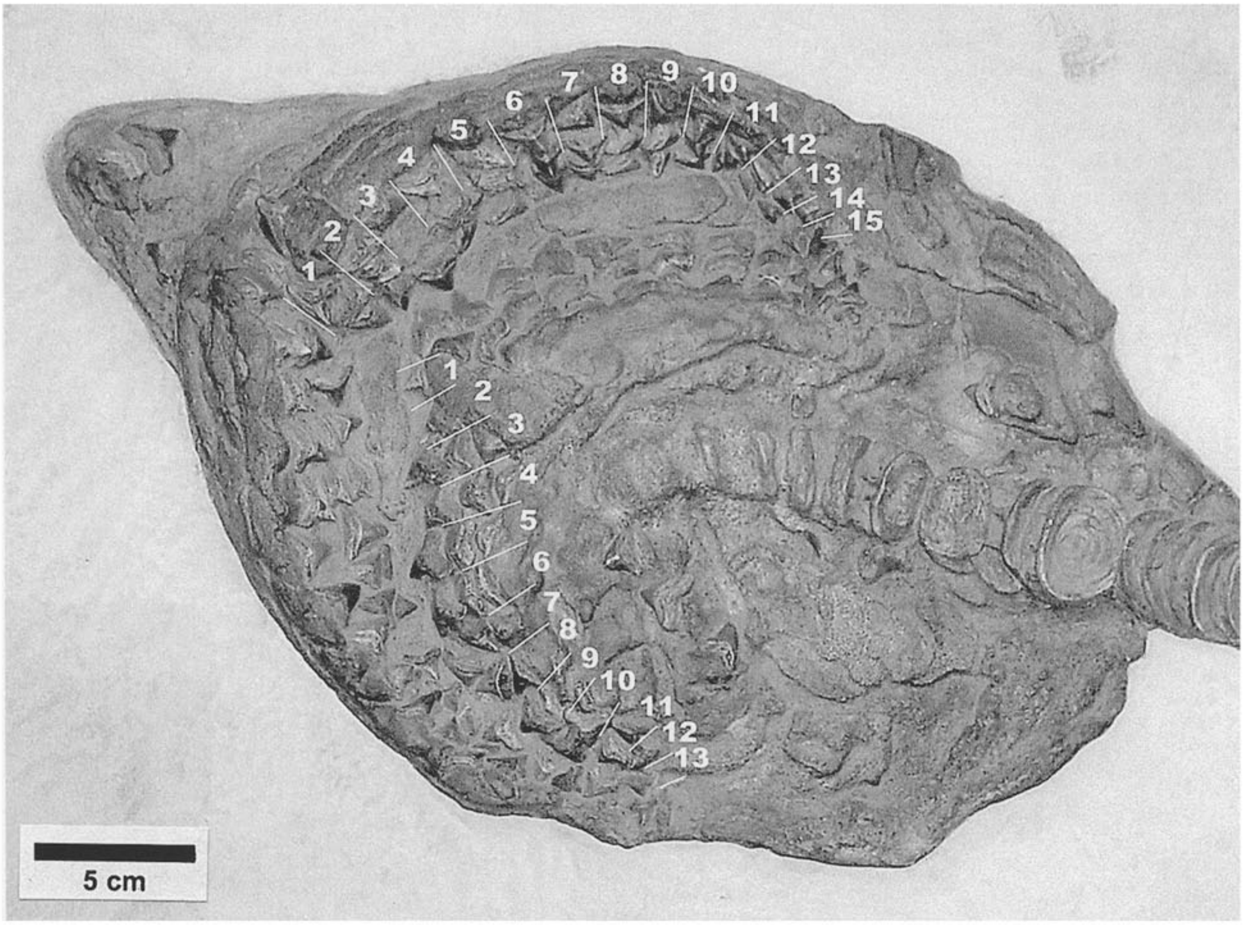

Fig. 8. Photograph of "head" of *Squalicorax falcatus* (USNM 425665; cf. Fig. 2A) showing the maximum number of upper tooth rows (upper serial numbers on left palatoquadrate) and lower tooth rows (lower serial numbers on right Meckel's cartilage) recognized in the specimen. Note: serial numbers have no implication to specific tooth types.

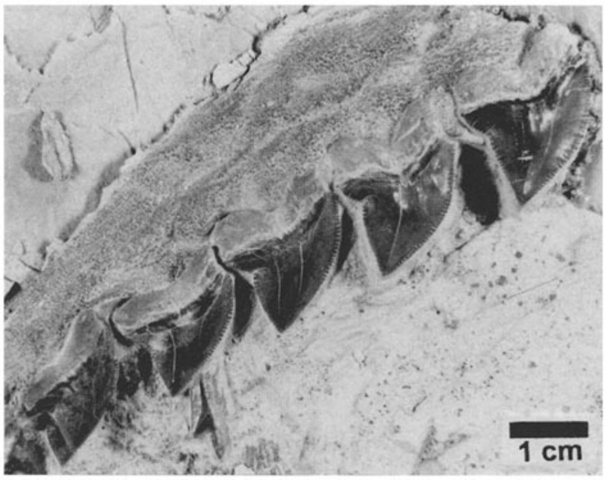

Fig. 9. Photograph of right palatoquadrate with articulated teeth (labial view) of *Squalicorax kaupi* (FHSM VP-2213; cf. Fig. 3C).

Meckel's cartilage forms a deep trough along their occlusal margin, which would have been occupied by developing teeth in life (Fig. 6B). Although the teeth were disarticulated in the specimen, shallow pits are visible in the trough of the palatoquadrate (Fig. 7), indicating at least nine, probably juxtaposed, tooth rows in the upper jaw of *S. pristodontus*. In addition, SHIMADA (1994) noted that the dentition in FHSM VP-2213 (*S. kaupi*) possesses the function of cutting sensu stricto (sensu CAPPETTA 1987) characterized by only one functional dental series (Fig. 9).

Hyoid Arch

The hyoid arch of elasmobranchs consists of paired hyomandibulae, paired ceratohyals, and unpaired basihyal. Several *Squalicorax* specimens preserve at least one hyomandibula (Figs. 2A, 3A, C–D, 4), and the morphological variation of this element among the three species is not substantial. In general, the hyomandibula is rectangular, and the length is about three times greater than the width. It is short relative to the size of the mandibular arch, measuring only about 43–50 % of the mesiodistal length of the Meckel's cartilage. A ceratohyal preserved in SDSM 34975 (*S. pristodontus*; Fig. 4) is long (over 60 % of the length of the Meckel's cartilage) and cleaver-shaped, and its presumed anterior end is narrower than the posterior end. A basihyal preserved in LACM 120090 (*S. falcatus*; Fig. 2B) shows that its width is about 40 % of the length of the ceratohyal. It has a straight posterior margin and slightly concave lateral edges, which presumably articulated with the anterior tip of the ceratohyals. The morphology of its anterior margin is uncertain.

Branchial arches

CMC VP-5722 (*Squalicorax falcatus*) is the only specimen with a set of branchial arch elements preserved (Fig. 3B). A series of presumed epibranchials and ceratobranchials, each represented by an elongate cartilaginous piece, is preserved, especially on the right side between the ceratohyal and the level of the seventh vertebra. The number of preserved pieces and their distribution suggest that there were five branchial arches.

Vertebral column

Vertebral centra of *Squalicorax* are amphicoelous, with numerous concentric lamellae around the primary double-cone calcification (see WELTON & FARISH 1993: figs. 25A, D, 26B). The centra are usually well calcified but prone to distortion, possibly because the "double-cones" are supported by very few radial cartilage plates (e.g., see APPLEGATE 1970: fig. 179B). The centra in the trunk region are circular, whereas those in the caudal region, especially the ones toward the terminal end, tend to be elongated dorsoventrally. The centra are thin, with their anteroposterior length measuring only about 25–30 % of their diameter in the trunk region. The articular surfaces of each centrum are nearly flat due to their shallow concavities.

Information on the organization of centra within the vertebral column comes primarily from specimens of *Squalicorax falcatus*, in particular USNM 425665, LACM 135929, and LACM 143537 (Figs. 2A, C, 3A). The total vertebral count in the three specimens is 131, 130, and 138 centra, respectively. Morphological variation between adjacent centra is subtle throughout the vertebral column, and the transition between precaudal and caudal vertebrae is difficult to ascertain. However, based on these specimens, the diameter of centra diminishes abruptly somewhere between the 70th and 85th vertebrae (Appendix 2). Therefore, the precaudal-caudal transition is thought to occur in that area. COMPAGNO (1988) stated that *Squalicorax* had a precaudal count of over 90 centra but did not provide supporting evidence for his view. The largest centra are located between the 10th and 30th vertebrae (Appendix 2). This is also true for KUVP 69712 (*S. kaupi*) in which the largest centra are the 11–13th vertebrae.

ROZEFELDS (1993) and KRIWET & OPPERMANN (1997) each reported a string of asterospondylic vertebrae with associated placoid scales of a possible anacoracid. ROZEFELDS' (1993) specimen came from the Lower Cretaceous of Australia, and KRIWET & OPPERMANN's (1997) specimen occurred in the Upper Cretaceous of Spain. Because these specimens were not associated with teeth, their exact taxonomic identity remains tenuous. However, we believe neither ROZEFELDS' (1993) specimen nor KRIWET & OPPERMANN's (1997) specimen belongs to *Squalicorax* because the anteroposterior length of vertebral centra in those specimens is not as compressed as that in *Squalicorax* specimens we examined (based on ROZEFELDS' fig. 2 and on photographs presented to K.S. by KRIWET in 1997).

Fins

Pectoral fin

COMPAGNO (1990) described the pectoral fin of *Squalicorax "falcatus"* as plesodic without providing any illustration. Examination of USNM 425665 (*S. falcatus*), which preserves both the right and left pectoral fins, confirm that they are plesodic (Fig. 2A). The fins are triangular (see also FRICKHINGER 1995: 180), although their edges appear to be incomplete. The exact number of fin radials is uncertain, but there are at least 14. We could not confirm the presence of distal inter-radials. The specimen also preserves a probable propterygium, mesopterygium, and metapterygium. The outline of each of these elements is not clear, but the mesopterygium appears to be the largest element among the three. A small portion of the scapulocoracoid bar is preserved at the base of each pectoral fin. The fins are slightly displaced in position, but the scapulocoracoid bar appears to have crossed the vertebral column ventrally at about the 20th to 25th vertebrae, which is approximately 31 % of the total body length from the snout. The fin span (distance between the distal fin tips) is about 30 % of the total body length. Additional specimens of *S. falcatus*, LACM 143537 and 135929 (Figs. 2C, 3A), retain one incompletely preserved pectoral fin that consists of several broken fin radials. The proximal end of the fin is located near the 25th vertebra. Available specimens of *S. kaupi* and *S. pristodontus* furnish no information on pectoral fins.

Pelvic fin

USNM 425665 and LACM 135929 (*Squalicorax falcatus*; Figs. 2A, 3A) preserve a pair of cartilaginous pieces along the vertebral column at the level of the 46th–51st vertebrae (Fig. 2A). Based on their position within the skeleton, these paired structures appear to be parts of the pelvic fins. However, their exact morphology is uncertain due to their poor preservation. LACM 120090 (*S. falcatus*) preserves a small cartilaginous piece near the 60th vertebra that may be part of one of the pelvic fins (the posteriormost "?" mark in Fig. 2B). There is no sign of a pelvic bar in any of these specimens.

Whereas specimens of *Squalicorax kaupi* with preserved pelvic fins are unknown, one specimen of *S. pristodontus* (SDSM 34975) possesses a set of isolated cartilaginous pieces that may be parts of the pelvic fins (indicated by "?" in Fig. 4). The specimen preserves only 78 vertebrae, which are partially articulated, and the possible pelvic fin elements were located near the 56–60th vertebrae as preserved (i.e., counted from the anterior part of the specimen). Thus far, we have not been able to identify claspers in any of the specimens we examined.

Dorsal fins

USNM 425665 (*Squalicorax falcatus*) is the only specimen we examined that preserves probable basal cartilage of the first and second dorsal fins (Fig. 2A). The probable first dorsal fin base is found immediately posterior to the left pectoral fin. It is preserved only as a 12 cm-long, narrow, cartilaginous piece that parallels the vertebral column at the level of the 30–35th verebrae. The preserved portion probably represents the posterior end of the first dorsal fin base, and the anteroposterior length was likely longer than 12 cm. The preserved portion of the probable second dorsal fin base measures 12 cm in anteroposterior length, and it occurs near the 65–75th vertebrae. The overall morphology of the two fins is uncertain.

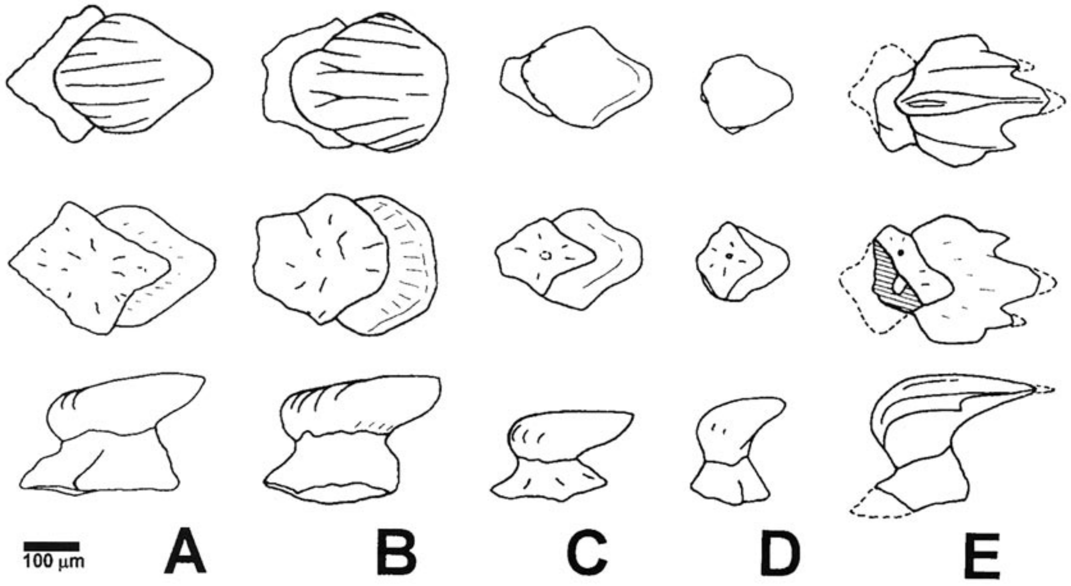

Fig. 10. Morphological variation of placoid scales (five examples, A–E) from head region of *Squalicorax falcatus* (CMC VP-5722; cf. Fig. 3B). Top row, apical view; middle row, basal view; bottom row, side view. – All anterior to the left.

Anal fin

USNM 425665 (*Squalicorax falcatus*) preserves a probable anal fin base near the 76–80th vertebrae. It measures about 4 cm in anteroposterior length, but its exact shape is uncertain. Remains of the anal fin are not preserved in any of the other specimens we examined.

Caudal fin

The exact morphology of the caudal fin in *Squalicorax* is uncertain. However, vertebral measurements of USNM 425665 (see above) suggest that the caudal fin begins somewhere between the 70th and 85th vertebrae. There is no perceived change in the angle of the vertebral column at the presumed precaudal-caudal transition.

Placoid scales

APPLEGATE (1970: figs. 176A–F) illustrated some placoid scales of *Squalicorax falcatus* and noted a high degree of variation in their morphology. Some scales possessed a crown with five to six fingerlike posterior projections, some had a smooth crown surface with one posterior projection, and yet others exhibited a crown with three keels. The original positions of the scales were uncertain, and the exact sizes of illustrated scales were not clearly indicated.

Many scattered placoid scales (Fig. 10) were collected from matrix around the head region of CMC VP-5722 (*Squalicorax falcatus*; Fig. 3B). Each scale consists of a crown and a root in which the former is positioned slightly posterior to the latter. The length and width of each crown are no more than 350 and 300 µm, respectively, and the size of each root is about the same as or slightly less than the crown. The base of each root is relatively flat, and there may be one distinct foramen at its center. Despite considerable variation, the scales can be classified broadly into two types. The most common type (here referred to Type 1) is characterized by a massive crown with a massive root, and both parts have a rounded rhombic outline when viewed apically and basally (Figs. 10A–D). The crown of large scales of this type has seven or eight distinct, parallel to sub-parallel keels that extend from the anterior edge, whereas smaller scales tend to show less distinct, shorter, and fewer keels. If distinct keels are present, the spacing between two adjacent keels is about 30 µm on average. Another morphotype (Type 2) has a palmate crown with three to eight (but five on average), posteriorly directed projections (Fig. 10E). A keel usually accompanies each projection.

Several presumed pharyngeal denticles (Fig. 11) were collected from the matrix around jaw elements of FHSM VP-2213 (*Squalicorax kaupi*; Fig. 3C). Their size and shape are similar to each other, and they somewhat resemble Type 1 scales of *S. falcatus*. However, the apical surface is flat and keel-less, and seven or eight blunt ridges occur along the anterior face of the crown (Figs. 11A, C). A pair of foramina is located on the posterior surface of the root in some samples (one side is shown in Fig. 11C). The root base usually shows a foramen at the center (Fig. 11B).

Discussion

Body form

Previous restorations of the body shape of *Squalicorax* are considered to be tenuous because they were based solely on dental morphology (WILLIAMSON et al. 1989; ROTHSCHILD & MARTIN 1993; SCHWIMMER 1997). APPLEGATE (1970) considered *Squalicorax* to be a pelagic form simply because of the worldwide distribution of its teeth. However, some general statements can be made from the skeletal material we examined, and inferences can be made on the overall shape of the body. Much of this is based on nearly complete and partial skeletons of *S. falcatus*, but some information was gleaned from the remains of *S. kaupi* and *S. pristodontus* we studied.

A wide neurocranium, inferred presence of a short tripodal rostrum, and laterally expanded nature of the mandibular arch (Fig. 12A; also see above) suggest that *Squalicorax falcatus* had a broad head with a flat dorsal surface and a short, blunt snout (i.e., not a conical head; cf. "snout pointed" in FRICKHINGER 1995: 180). The mouth was subterminal, gently curved, and probably located immediately posterior to large nasal capsules and below the orbits. Large nasal capsules indicate well-developed olfactory sense.

Modern pelagic sharks with a fusiform body generally have circular vertebral centra, whereas true benthic

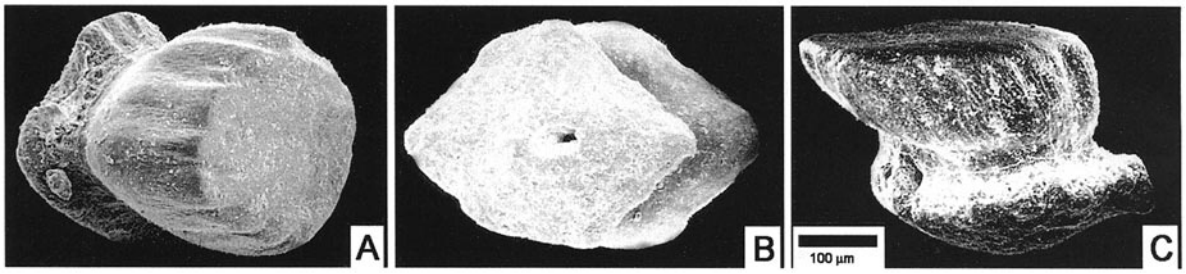

Fig. 11. Scanning electron micrographs of placoid scales of *Squalicorax kaupi* (FHSM VP-2213; cf. Fig. 3C; scales were sampled near jaw cartilages; figured specimens represent three different samples). – **A**: apical view (slightly oblique; anterior to the left); **B**: basal view (anterior to the left); **C**: side view (anterior to the right).

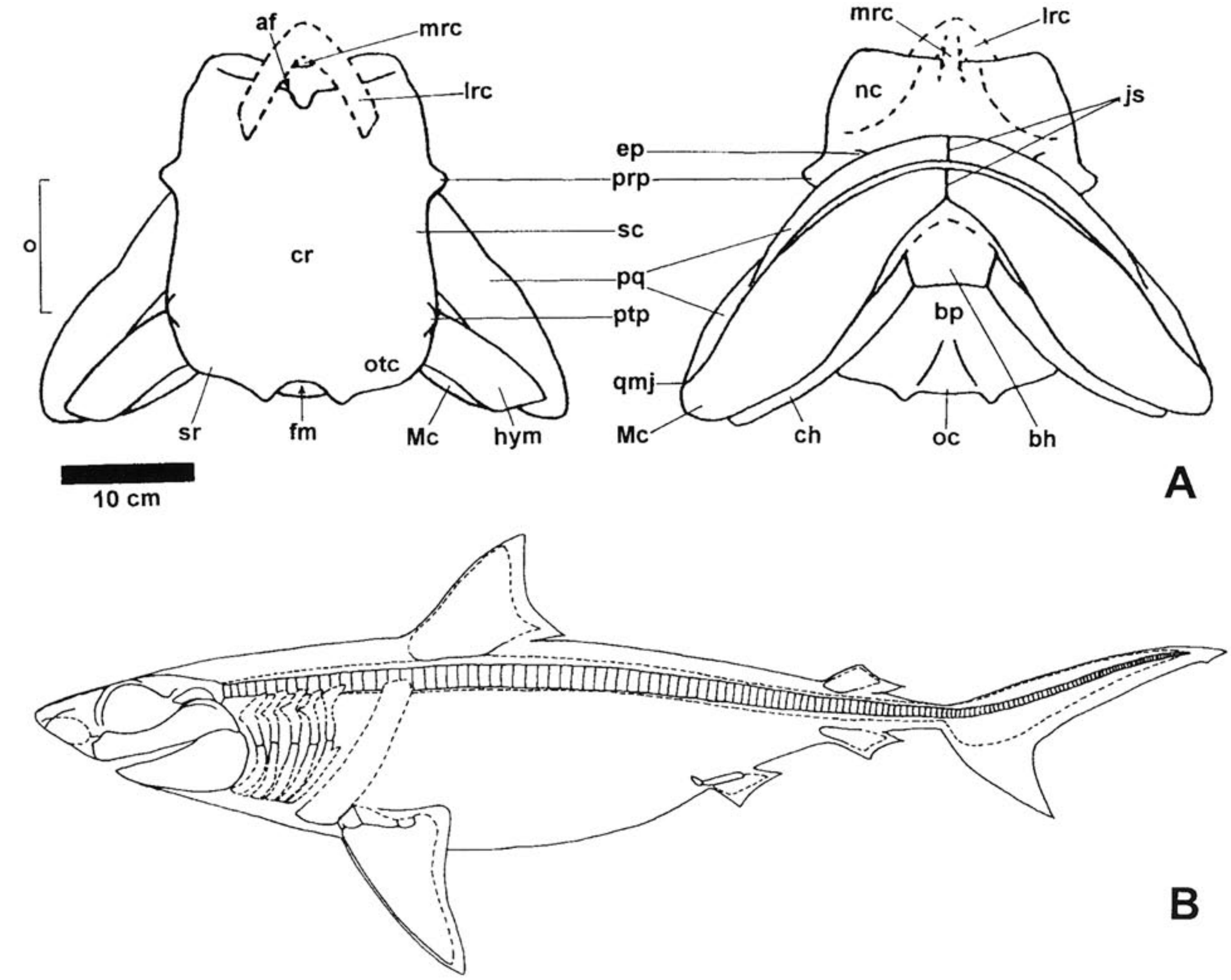

Fig. 12. Tentative skeletal reconstruction of *Squalicorax falcatus*. – **A**: Cranial skeleton based on combination of COMPAGNO's (1990: fig. 10; cf. Fig. 5) and this study (anterior to the top; left, dorsal view; right, ventral view). – **B**: Entire skeleton of two-meter-long individual (broken lines for skeletal elements and solid line for body outline are hypothetical; solid lines within body outline represent skeletal parts preserved in specimens examined or inferred from Fig. 5; fin positions are primarily based on USNM 425665 [cf. Fig. 2A]). – Key to lettering: af, anterior fontanelle; bh, basihyal; bp, basal plate of neurocranium; ch, ceratohyal; cr, cranial roof; ep, ectethmoid process; fm, foramen magnum; hym, hyomandibula; js, jaw symphysis; lrc, lateral rostral cartilage; Mc, Meckel's cartilage; mrc, medial rostral cartilage; nc, nasal capsule; o, orbit; oc, occipital centrum; otc, otic capsule; pq, palatoquadrate; prp, preorbital process; ptp, postorbital process; qmj, quadratomandibular joint; sc, supraorbital crest; sr, sphenopterotic ridge.

sharks, such as *Squatina*, have dorsoventrally compressed vertebral centra (see APPLEGATE 1967; COMPAGNO 1977). The largest centra in *Squalicorax* are circular, and we therefore infer that this shark had a fusiform body with a circular girth at the trunk region.

All galeomorph sharks (sensu COMPAGNO 1973) have five pairs of gill slits along the lateral sides of the body immediately behind the mouth (COMPAGNO 1984). The hyoid arch and five branchial arches border the gill slits. CMC VP-5722 (*Squalicorax falcatus*) preserves a ceratohyal followed by a series of (at least) five branchial arch elements on the right side of the body (Fig. 3B), suggesting that this shark also had five pairs of gill slits.

In galeomorph sharks, five pairs of gill slits occur either entirely in front of pectoral bases or partially above the pectoral bases (see COMPAGNO 1984). None of the *Squalicorax* specimens we examined preserved both the pectoral fins and branchial arches together. Thus, the exact location between these skeletal structures is uncertain. However, we think that the branchial arches did not extend beyond 30 % of the total body length from the snout, judging from the position of the base of triangular pectoral fins in USNM 425665.

COMPAGNO (1990: 373) stated that *Squalicorax* had a "caudal fin with strong ventral lobe", but he did not provide any evidence. The exact outline of the caudal fin is not preserved in the examined specimens. However, except for the abrupt decrease in the diameter of the centra, the vertebrae at the presumed precaudal-caudal transition in *S. falcatus* specimens show no appreciable change in morphology or in the angle of the vertebral column. This condition suggests that the caudal fin had a low aspect ratio: i.e., a highly asymmetrical (heterocercal) tail with large dorsal lobe and small ventral lobe.

In USNM 425665, the location of the base of the first dorsal, pelvic, second dorsal, anal, and caudal fins ranges from 30?–49 %, 58–64 %, 68–75 %, 75–78 %, and 72–80 %, respectively, of the total body length from the tip of the snout (note: "30 %" for the anterior margin of the first dorsal fin is speculative based on the position of the pectoral fins). THOMSON & SIMANEK (1977) found that the range of positions for most fins is narrow in extant sharks. For example, in modern *Galeocerdo*, the first dorsal, pelvic, second dorsal, anal, and caudal fins range, or is placed at, 29–45 %, 52–61 %, 62–72 %, 63–73 %, and 76 %, respectively, of the total body length from the snout tip (taken from the illustration in COMPAGNO 1984: 504). The value for the second dorsal and anal fins in *Galeocerdo* appears to be off slightly from the range in *Squalicorax falcatus*, but otherwise the fin positions in *Galeocerdo* are comparable to that in *S. falcatus*. The total vertebral count of *Galeocerdo* ranges from 216 to 234 (COMPAGNO 1988), which is much greater than that of *S. falcatus* (i.e., 130–138). However, the differences in vertebral count apparently do not influence the fin positions in relation to the rest of the body.

Body size

Literature discussing the body size of *Squalicorax* species is limited. STEWART (1978: 14) stated that *S. falcatus* was "a rather small lamniform". Later, STEWART (1993) noted that *S. falcatus* measured 1.8–3.0 m total length (TL). FRICKHINGER (1995) illustrated USNM 425665, noting that the specimen length is approximately 188 cm. SCHWIMMER et al. (1997) indicated implicitly that the total length of *S. kaupi* is much less than 5.0 m, and explicitly that "*S. kaupi* specimens" measuring 1.2 cm (presumably tooth height) were sharks less than 3.0 m TL. SCHWIMMER et al. (1997: 76) also noted that, based on LACM 120090 (Fig. 2B), the maximum TL of *S. falcatus* was perhaps around 3.5 m. WALKER & WARD (1992: 200) noted that the typical *S. pristodontus* measured 2.5 m TL, but their basis is unclear.

The entire vertebral column is preserved in three similar-sized specimens of *Squalicorax falcatus*, LACM 135929, LACM 143537, and USNM 425665. If the length of each vertebral column is added to the cranial length (estimated based on the anterior extent of the distribution of teeth in some cases), these specimens measure about 1.8–2.0 m TL (Figs. 2A, C, 3A). For each of these specimens, we measured the crown height, the total height of the largest tooth, and the diameter of the largest centrum (Appendix 3). The maximum vertebral diameters and the estimated TL values were averaged among these three specimens, and the relationship between these values was used to estimate the TL of: "large" *S. falcatus*, "large" *S. kaupi*, "moderate size" *S. pristodontus*, "large" *S. pristodontus*, and possible gigantic *Squalicorax* (*S. pristodontus*?). An assumption was made that the diameter of the largest vertebral centrum in each specimen in question has the same size relation to the TL as the relationships between the mean diameter and mean TL from the three *S. falcatus* individuals.

Based on the relationship among the mean maximum vertebral diameter (40 mm), the mean estimated TL (192 cm), and the size of their preserved teeth, LACM 135929, LACM 143537, and USNM 425665 are considered moderate-sized individuals for the species. LACM 120090 is a partial skeleton of *Squalicorax falcatus* (Fig. 2B), which represents the largest individual of the species among the specimens examined. The largest vertebra in this specimen is about 45 % larger than the mean maximum vertebral diameter of the three moderate-size individuals (Appendix 3). This suggests that this individual was about 278 cm in TL.

The largest skeleton of *Squalicorax kaupi* examined, KUVP 69712 (Fig. 3D), appears to be a moderate- to large-sized individual for the species based on a few teeth preserved. The largest vertebra in the specimen is 55 % larger than the average maximum vertebral diameter of the three *S. falcatus* individuals (Appendix 3), giving an estimated TL of 298 cm.

Squalicorax pristodontus is assumed to be the largest form among *Squalicorax* species based on the height of its teeth, which reach almost 30 mm (see WELTON & FARISH 1993). On the basis of their preserved teeth, SDSM 34975 (Fig. 4) and 47682 are moderate and large *S. pristodontus* individuals, respectively. Because the largest vertebrae in SDSM 34975 and 47682 are respectively about 13 % and 60 % greater than the mean maximum vertebral diameter of the three *S. falcatus* individuals, they would measure about 216 and 307 cm TL, respectively (Appendix 3). Thus, the present skeletal data support the view that *S. pristodontus* is the largest of the three species examined, exceeding 3 m in TL.

Although we limited our study to partial and nearly complete specimens, one additional specimen, SDSM 47683, is noteworthy. The specimen consists of 10 associated shark vertebrae collected from Middle Campanian rocks of southwestern Fall River County, South Dakota. These vertebrae are gigantic, measuring 10 cm in diameter. Their morphology is identical to that of *Squalicorax* we examined, and the largest vertebra in the specimen is about 2.5 times larger than the average maximum vertebral diameter of the *S. falcatus* specimens mentioned above (Appendix 3). If in fact the vertebrae belong to *Squalicorax* (presumably *S. pristodontus*), the TL of this individual would have measured approximately 480 cm.

Assuming that the above TL estimations are reasonable, we examined the jaw size in relation to TL using *Squalicorax* specimens in which at least one complete or nearly complete Meckel's cartilage was preserved. The mesiodistal length along the jaw surface between the mandibular symphysis and mandibular knob of the Meckel's cartilage was measured for the following four specimens (Appendix 3): USNM 425665 (*S. falcatus*), LACM 120090 (*S. falcatus*), KUVP 69712 (*S. kaupi*), and SDSM 34975 (*S. pristodontus*). The jaw length is about 10.5–12.6 % of the TL in *S. falcatus* and *S. kaupi*, whereas it is about 15.7 % of the TL in *S. pristodontus*. In other words, compared to *S. falcatus* or *S. kaupi*, *S. pristodontus* appears to have possessed a set of large jaws relative to its body size.

We concede that correlations between the TL and tooth size, and between the TL and vertebral size may be biased for several reasons: the sample size is small (n = 3), the range of estimated TL is narrow (only 20 cm), and the tallest teeth of the original dentition may not be represented in LACM 135929 and 143537 (*Squalicorax falcatus*). In addition, teeth of *S. pristodontus* are the largest of the three species examined (see WELTON & FARISH 1993), and its jaws were large relative to its body size (see above) and apparently accommodated fewer tooth rows (ca. nine rows, as opposed to at least 13 rows in *S. falcatus*). These facts suggest that the relationship between the TL and tooth size is species specific in this genus.

Feeding dynamics

Various lines of evidence suggest that *Squalicorax* was an opportunistic feeder or scavenger like *Galeocerdo*, which perhaps has the most generalized diet among Recent sharks (COMPAGNO 1984). The documented diet of *Squalicorax* includes various osteichthyan and chondrichthyan fishes, marine tetrapods (turtles, mosasaurs, and plesiosaurs), and bloat-and-float dinosaurs (e.g., DRUCKENMILLER et al. 1993; STEWART 1993; SCHWIMMER et al. 1997; SHIMADA 1997a). New anatomical data provide some additional insights into the feeding dynamics of *Squalicorax*.

SHIMADA (1997b) described a neurocranium of another Late Cretaceous shark, *Cretoxyrhina mantelli* (AGASSIZ, 1843) (Lamniformes: Cretoxyrhinidae). The neurocranium exhibited remarkably large orbits with limited room for the nasal capsules. This led SHIMADA (1997b) to suggest that *C. mantelli* had acute vision. Unlike *C. mantelli*, the neurocranium of *Squalicorax* possesses nasal capsules that are almost as large as the orbits. This condition suggests that the vision of *Squalicorax* was not as acute as in *C. mantelli*, but the olfactory capabilities were better developed. These interpretations are consistent with the proposed feeding style of *C. mantelli* and *Squalicorax*. *Cretoxyrhina mantelli*, regarded as a predatory shark that attacked large active marine vertebrates (teleosts, turtles, mosasaurs, and possibly plesiosaurs: SHIMADA 1997a; SHIMADA & HOOKS 2004), would have required acute vision to effectively hunt for prey, whereas *Squalicorax* as a scavenger would have required acute olfaction to detect distantly located carcasses.

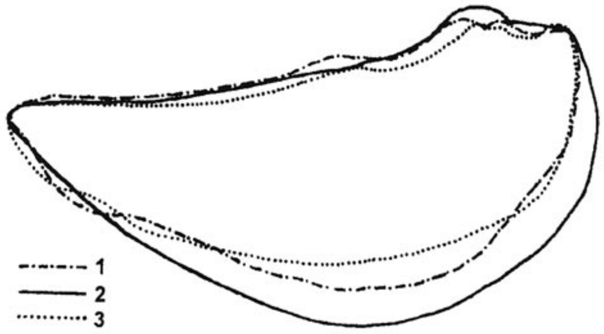

Fig. 13. Outline of Meckel's cartilage of three shark taxa. – Line 1: *Squalicorax kaupi* (FHSM VP-2213; cf. Fig. 3C). – Line 2: *S. pristodontus* (SDSM 34975; cf. Figs. 4, 6). – Line 3: Modern tiger shark (4.8 m TL *Galeocerdo*: Jaws International collection). – Anterior to the left; for comparison, jaw sizes are adjusted at dorsomesial and dorsodistal corners of each Meckel's cartilage.

When we compared *Squalicorax* to *Galeocerdo*, we found that the Meckel's cartilage of *Galeocerdo* is more similar to that of *S. kaupi* than that of *S. pristodontus* (Fig. 13). Although a slight ventral expansion of the surface area is seen in *S. kaupi*, the cartilage of *S. pristodontus* greatly expands ventroposteriorly. Thus, *Squalicorax* had a larger surface area for the attachment of the quadratomandibularis muscle (sensu MOTTA & WILGA 1995) than *Galeocerdo*. The larger muscle mass in turn suggests that the biting force of *Squalicorax*, especially *S. pristodontus*, was greater than that of extant *Galeocerdo* of similar size.

The mandibular arch is not fused to the neurocranium in sharks, and the upper jaw protracts considerably in some taxa (MOTTA & WILGA 2001; WILGA et al. 2001). Sharks with kinetic jaws, such as many carcharhinoids and lamnoids, possess long, posteriorly-directed hyomandibulae that swing laterally and transmit thrust to move the mandibular arch forward (MOSS 1972, 1977; FRAZZETTA 1994; MOTTA & WILGA 1995). On the other hand, sharks with less kinetic jaws, such as squaloids and orectolobids, have short hyomandibulae, restricting jaw kinesis (MOSS 1977; but note that some have developed an alternative mechanism for jaw protrusion; see WU 1994). The length of the hyomandibulae in *Squalicorax* can be described as moderate (about, or slightly less than 50 % of the mesiodistal length of the Meckel's cartilage), and we believe *Squalicorax* could protract its jaws to some extent, more than squaloids and orectoloboids.

Upon biting, sharks with serrated teeth, such as *Galeocerdo*, twist their head and body side-to-side rapidly, producing a sawing action with the teeth (SPRINGER 1961; RANDALL 1992). Great stresses are exerted on the upper jaws, but the knoblike orbital processes on the palatoquadrates probably accommodate lateral strain by sliding along either side of the neurocranium near the anterior portion of the orbital region (SPRINGER 1961).

Squalicorax had a dental series with a function of cutting sensu stricto in which the dentition rested on gently curved jaws. *Squalicorax* most likely twisted its head and body side-to-side to produce a highly effective sawing action when feeding. Lateral strains applied to the anterior part of the jaws were probably taken up by the orbital processes, which braced to the neurocranium, whereas strains at the posterior end of jaws were probably taken up by the broad hyomandibulae.

Placoid scales of "fast swimming sharks" generally exhibit grooves bordered by keels (REIF & DINKELACKER 1982) and show interkeel distances of <100 µm (RASCHI & TABIT 1992). Scales of sharks are known to show ontogenetic "growth" through replacement, but the interkeel spacing in "fast swimming sharks" remains relatively constant through ontogeny even with an increased number of keels (RASCHI & ELSOM 1986). Sharks that are considered to be "more sluggish" (e.g., *Galeocerdo*) possess scales having an interkeel distance that exceeds 100 µm (up to 275 µm), and the number of keels is maintained despite ontogenetic increase in scale size (RASCHI & ELSOM 1986). The interkeel distance in *Squalicorax* (at least in *S. falcatus*) is around 30 µm, suggesting that *Squalicorax* was capable of fast swimming.

Higher-level systematics

Overview

The familial placement of *Squalicorax* has been debated for well over 100 years. For example, the genus has been assigned to Squalidae (DIXON 1850), Notidanidae (LERICHE 1929), Isuridae (BERTIN & ARAMBOURG 1958), and Lamnidae (FOWLER 1911). Some have even suggested that *Squalicorax* be placed within Cetorhinidae (WHITE 1936, 1937; GREGORY 1951a, b: fig. 8.35; BERG 1958). CASIER (1947) erected the family Anacoracidae to include isolated *Squalicorax* teeth (later expanded to include other similar-toothed taxa), and most recent researchers consider this a well-established neoselachian taxon (COMPAGNO 1977; CAPPETTA 1987; WELTON & FARISH 1993). The relationships among different genera within the family remain uncertain (see GLIKMAN 1958, 1980; CAPPETTA 1987).

To date, the ordinal classification of *Squalicorax* is unresolved. Anacoracids are usually placed in Lamniformes (WOODWARD 1889, 1902–1912; LERICHE 1902; BERG 1958; BERTIN & ARAMBOURG 1958; GLIKMAN 1964; JANVIER & WELCOMME 1969; THIES & REIF 1985; WOLBERG 1985a, b; CAPPETTA 1987; COMPAGNO 1990; SIVERSON 1996). However, some researchers have placed Anacoracidae (or *Squalicorax*) into Hexanchiformes (LERICHE 1906; CASIER 1947; BLOT 1969; HERMAN 1977), Orectolobiformes (APPLEGATE 1970), or Carcharhiniformes (MAISEY 1984). The anatomical data presented in this paper are insufficient to elucidate the systematic relationships among different *Squalicorax* species, but no evidence refutes the placement of the genus into Anacoracidae. Here, we review the systematic position of *Squalicorax* at the ordinal level based on available anatomical data.

Squalicorax: not a hexanchiform

The teeth of *Squalicorax kaupi* and *S. pristodontus* possess a labiolingually flattened root that is weakly bilobate and does not have lingual nutritive grooves (see WELTON & FARISH 1993). A similar root morphology is seen in hexanchiform sharks, which led CASIER (1947) to classify this shark into the non-galeomorph (squalomorph) taxon, Hexanchiformes. CAPPETTA (1987) later discredited this idea by pointing out that "more primitive species" (e.g., *S. falcatus*) have a root that is uncharacteristic of hexanchiforms in being more massive and obviously bilobate.

One purported anatomical feature has been presented as an indicator that *Squalicorax* be placed within Hexanchiformes. COMPAGNO (1990: fig. 10) illustrated the ventral side of the neurocranium of *Squalicorax* "*falcatus*" (Fig. 5) and highlighted what was interpreted as a pair of ectethmoid processes ("ep"? of Fig. 12A). If indeed they are ectethmoid processes (sensu CARVALHO 1996) which are apomorphic and do not occur outside of Neoselachii, their presence indicates that *Squalicorax* belongs to the superorder Squalea (= non-galeomorph neoselachians), which includes Hexanchiformes (SHIRAI 1992, 1996; CARVALHO 1996). However, as pointed out by CARVALHO (1996), the definition of "ectethmoid processes" varies among researchers, and non-homologous processes may occur on the ventral surface of the neurocranium. The assertion that *Squalicorax* was a non-galeomorph shark is unconvincing because the exact nature of the "ectethmoid process" remains uncertain, and we found no other skeletal evidence to suggest that the taxon was a squalomorph shark.

Although we do not know the number of gill slits in Jurassic hexanchiforms, Recent taxa have six or seven pairs of gill slits (COMPAGNO 1984), and our study indicates that *Squalicorax* had five pairs. There are several other features that indicate *Squalicorax* was not a hexanchiform shark. For example, modern hexanchiforms possess only one dorsal fin (COMPAGNO 1984), whereas *Squalicorax* appears to have had two. Pectoral fins of hexanchiforms are aplesodic (COMPAGNO 1977), whereas those of *Squalicorax* were plesodic. Furthermore, the heavily calcified nature and overall morphology of *Squalicorax* jaws is more similar to jaws of modern galeomorphs (especially some derived lamniforms and carcharhiniforms) than to hexanchiforms (for lists of comparative modern specimens, see SHIMADA 2002: appendices 1, 2).

Galeomorph sharks include Heterodontiformes, Orectolobiformes, Lamniformes, and Carcharhiniformes (CAPPETTA 1987). Based on rigorous phylogenetic analyses, the monophyly of galeomorphs has been defended (SHIRAI 1996; CARVALHO 1996), and the most undisputed synapomorphy uniting galeomorph taxa is the presence of "short otic capsules" (COMPAGNO 1973, 1977; SHIRAI 1996; CARVALHO 1996). COMPAGNO's (1990: fig. 10) illustration of the neurocranium of *Squalicorax "falcatus"* (Figs. 5, 12A) shows a short otic region (i.e., indicative of short otic capsules), suggesting that *Squalicorax* was a galeomorph shark.

Squalicorax: not an orectolobiform

APPLEGATE (1970: 427) stated that *Squalicorax* was possibly "a direct ancestor of the primitive orectolobids", but he did not provide any supporting evidence for this statement. The order Orectolobiformes was not formally described until two years later (APPLEGATE 1972) and, to our knowledge, this is the only statement that implies *Squalicorax* was an orectolobiform shark.

One skeletal feature supporting the monophyly of Orectolobiformes is the distally expanded pectoral mesopterygium and metapterygium and the distinctive gap between them (SHIRAI 1996). USNM 425665 (*S. falcatus*) preserves a probable mesopterygium and metapterygium in each pectoral fin. The elements appear to be short but their exact morphology is unclear, and we could not confirm the presence or absence of a gap between them.

DINGERKUS (1986: 231) stated that the neurocranium of orectolobiform sharks has "a simple, ventrally originating rostral process", and "a median fontanelle, posterior to the anterior fontanelle". Based on COMPAGNO's (1990: fig. 10) illustration of the neurocranium of *Squalicorax*, the rostrum in *Squalicorax* originates from the dorsal side of the skull as paired lateral rostral cartilages (see also Fig. 12A). Furthermore, the *Squalicorax* skull does not exhibit a median fontanelle, unless one considers its possible fusion to the anterior fontanelle, as in a few orectolobiform genera (DINGERKUS 1986). In addition, the hyomandibulae of *Squalicorax* are moderately elongate and more like those in derived lamniforms and carcharhiniforms (e.g., MOSS 1972; FRAZZETTA 1994; MOTTA & WILGA 1995) than those in orectolobiforms (e.g., MOSS 1977; WU 1994). For these reasons, we do not believe *Squalicorax* was an orectolobiform shark.

Squalicorax: a carcharhiniform or a lamniform?

Teeth of *Squalicorax* resemble those of the carcharhiniform taxon, *Galeocerdo* (CAPPETTA 1987; SIVERSON 1992; WELTON & FARISH 1993; SHIMADA 1994), and MAISEY (1984: 49) considered *Squalicorax* a member of Carcharhiniformes on the basis of crown morphology ("blade-like serrated teeth with a strongly asymmetrical main cusp"). However, CAPPETTA (1987) placed *Squalicorax* into Lamniformes based on the root morphology (i.e., moderately compressed, bilobate root with distinct lobes), and most subsequent researchers have followed CAPPETTA's view. The similarity in crown morphology between *Squalicorax* and *Galeocerdo* is interpreted as a result of convergent evolution because the root morphology and tooth histology differ between these taxa (CAPPETTA 1987; WELTON & FARISH 1993).

COMPAGNO (1990), SHIRAI (1996), and CARVALHO (1996), each presented a set of synapomorphies of Lamniformes based on skeletal and non-skeletal data. The only synapomorphy common among the three studies was the "ring" type intestinal valve. This character is not useful for fossil shark systematics because soft tissue, such as the intestine, is rarely preserved in the fossil record. The most recent phylogenetic analysis discussing the systematic position of Carcharhiniformes is that of SHIRAI (1996). SHIRAI (1996) listed only three synapomorphies uniting the modern carcharhiniforms, of which only one of them was a skeletal character (his Character 70): i.e., a feature of claspers in male. Because no claspers have been recognized in preserved skeletons of *Squalicorax*, this character does not contribute to the ordinal placement of the genus.

Whereas carcharhiniform taxa have orthodont teeth that are characterized by an internal pulp cavity (CIGALA-FULGOSI & MORI 1979; COMPAGNO 1988), teeth of *Squalicorax* have an osteodont histology (WELTON & FARISH 1993), as do all lamniforms (GLIKMAN 1967: pl. 5 fig. 19; CAPPETTA 1977). The absence of a pulp cavity in *Squalicorax* was noted long ago (e.g., WOODWARD 1889; WILLISTON 1900; LERICHE 1902), and this characteristic remains the most convincing evidence among many researchers that *Squalicorax* was not a carcharhiniform shark. COMPAGNO (1988) argued that *Squalicorax* was a lamniform shark because of the osteodont tooth histology.

In diagnosing the superfamily Anacoracoidea, GLIKMAN (1967: 343) noted that the adjacent tooth roots abut each other and do not overlap. Likewise, WELTON & FARISH (1993: 14) cited *Squalicorax* as an example of "juxtaposed dentition", but neither report presented any supporting evidence for these statements. However, SHIMADA (1994) confirmed the juxtaposed tooth row arrangement in *Squalicorax* (Fig. 9). Juxtaposed dentition (WELTON & FARISH 1993) is a form of "independent dentition" (COMPAGNO 1988) in the sense that tooth bases do not overlap. Juxtaposed-independent row arrangements are also seen in some non-galeomorph sharks such as hexanchiforms, but all lamniforms have this arrangement (SHIMADA 2002). On the other hand, all carcharhiniforms have tooth bases that overlap (COMPAGNO 1988).

A unique heterodonty, referred to as the "lamnoid tooth pattern", occurs in modern macrophagous lamniforms due to the occurrence of a hollow inflation called the "dental bulla", which is located at the mesialmost portion of each jaw cartilage (COMPAGNO 1990; SHIMADA 2002). SHIMADA (2002) regarded the presence of dental bullae as a synapomorphy of Lamniformes, assuming that its absence in the two microphagous forms, *Megachasma* TAYLOR et al., 1983, and *Cetorhinus* (GUNNERUS, 1765), is a secondary loss. COMPAGNO (1988) indicated that the dentition of *Squalicorax* does not exhibit the lamnoid tooth pattern, and our study suggests that at least *S. pristodontus* lacks dental bullae (Figs. 6B, 7). Although the lack of this feature suggests that *Squalicorax* does not belong to Lamniformes, it could represent a secondary loss due to dental specialization with a function of cutting sensu stricto, which does not exist in extant lamniforms. If *Squalicorax* is a lamniform, then it would be the only macrophagous lamniform without the dental bullae.

COMPAGNO (1990: fig. 10) indicated the presence of a tripodal rostrum in the neurocranium of *Squalicorax "falcatus"* (Fig. 12A) and noted that *Squalicorax* pectoral fins are plesodic. The tripodal rostrum can be found in both Lamniformes and Carcharhiniformes (COMPAGNO 1973, 1977, 1999b), and, although plesodic pectoral fins occur in several species of these two orders (SHIRAI 1996), COMPAGNO (1990) listed this as a shared feature of derived lamnoids. In addition, the *Squalicorax* neurocranium somewhat resembles that of the extant lamniform, *Megachasma pelagios* TAYLOR et al., 1983. However, as noted by COMPAGNO (1990), the resemblance may simply be superficial (i.e., homoplasious).

The vertebral count in sharks can vary without any specific evolutionary trend, but it can be a useful tool for shark classification (SPRINGER & GARRICK 1964). The range of the count in *Squalicorax falcatus* (i.e., 130–138) is comparable to many carcharhiniform species (e.g., SPRINGER & GARRICK 1964; COMPAGNO 1988), whereas it is low for most lamniforms (except for taxa, such as *Mitsukurina* JORDAN, 1898, and *Cetorhinus*: e.g., SPRINGER & GARRICK 1964; CAPPETTA 1980; GOTTFRIED et al. 1996; SHIMADA 1997b). If indeed *Squalicorax* is a lamniform, it is noteworthy that no modern lamniform with known vertebral counts has a range of 130–138. COMPAGNO (1990) noted the *Cetorhinus*-like structure in centra of *Squalicorax*; however, it must be noted that the vertebral calcification pattern is not phylogenetically informative because the same pattern is seen in other unrelated shark taxa (COMPAGNO 1988; CARVALHO 1996; WELTON & FARISH 1993).

Summary

A wealth of paleobiological information of *Squalicorax* was obtained through our examination of the skeletal remains of *S. falcatus*, *S. kaupi*, and *S. pristodontus* that were collected from Kansas, South Dakota, and Wyoming, U.S.A. The specimens suggest that *S. falcatus* generally did not reach 3 m TL, whereas moderate-sized individuals of *S. kaupi* and *S. pristodontus* measured 3 m TL. *Squalicorax pristodontus* is the largest taxon among the three species examined, but it is unlikely that the taxon reached 5 m TL. The comparison with *S. falcatus* or *S. kaupi* suggests that *S. pristodontus* possessed a set of large jaws relative to its body size. This observation, combined with the fact that *S. pristodontus* generally has larger teeth and fewer tooth rows than *S. falcatus* and *S. kaupi*, suggests that one cannot adequately extrapolate the TL of a *Squalicorax* individual using the relationship between the TL and tooth size of other *Squalicorax* species (i.e., the quantitative relationship is species specific in this genus).

Compiled anatomical data also provide some insights into the lifestyle and feeding strategies of *Squalicorax*. Based on the size of the orbit with respect to that of nasal capsule, *Squalicorax* probably depended more on olfaction than vision compared to the contemporaneous macrophagous lamniform shark, *Cretoxyrhina mantelli*. Placoid scales have several keels on their crown top, and the small interkeel distance indicates that *Squalicorax* was capable of fast swimming. Like Recent *Galeocerdo*, *Squalicorax* was probably able to protract its jaws and fed by twisting its head and body from side-to-side to provide a sawing motion of the dentition.

Despite the ample anatomical data presented here, the ordinal placement for *Squalicorax* remains uncertain. Nevertheless, our study suggests that the taxon was not a member of Hexanchiformes or Orectolobiformes. Characteristics such as osteodont tooth histology, non-overlapping teeth on the jaws, and plesodic fins suggest that *Squalicorax* was a lamniform shark. On the other hand, non-laminiform characteristics such as the apparent lack of dental bullae, the possible absence of lamnoid tooth pattern, and similar vertebral count may indicate the shark was a carcharhiniform. Due to the fact that there are no compelling characteristics supporting *Squalicorax* as a carcharhiniform, we adhere to the view that *Squalicorax* belongs to Lamniformes. Perhaps, as COMPAGNO (1988: 404) stated, *Squalicorax* was a lamnoid with carcharhinoid-like adaptations.

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Appendix 1

List of examined *Squalicorax* skeletal specimens associated with teeth

Squalicorax falcatus (or *S*. cf. *S. falcatus*)

CMC VP-5722, *S. falcatus*, cranial region with at least 104 teeth and 30+ vertebrae, Smoky Hill Chalk Member of Niobrara Chalk, southeastern Gove County, Kansas (Figs. 3B, 10).

KUVP 34916, *S.* cf. *S. falcatus*, many vertebrae and multiple teeth, Smoky Hill Chalk Member of Niobrara Chalk, Phillips County, Kansas (discussed by STEWART 1978).

LACM 16056, *S. "falcatus"*, nearly complete neurocranium allegedly with teeth and jaw fragments, presumably from Smoky Hill Chalk Member of Niobrara Chalk, Logan County, Kansas (available only through data presented by COMPAGNO 1988, 1990; see Figs. 5, 12A).

LACM 120090, *S. falcatus*, partial skeleton with at least 42 teeth, Smoky Hill Chalk Member of Niobrara Chalk, Kansas (Fig. 2B).

LACM 135929, *S. falcatus*, partial skeleton with at least 24 disarticulated teeth, Smoky Hill Chalk Member of Niobrara Chalk, Kansas (Fig. 3A).

LACM 143536, *S. falcatus*, ca. 20 disarticulated teeth, scattered scales, and some cartilage pieces, Smoky Hill Chalk Member of Niobrara Chalk, Kansas.

LACM 143537, *S. falcatus*, partial skeleton with at least 70 disarticulated teeth, Smoky Hill Chalk Member of Niobrara Chalk, Leoti, Wichita County, Kansas (Fig. 2C).

USNM 425665, *S. falcatus*, nearly complete skeleton, Smoky Hill Chalk Member (?) of Niobrara Chalk, Kansas (Figs. 2A, 8; also illustrated in FRICKHINGER 1995: 180).

UW-Madison catalogue number NS.1509.34, *S. falcatus*, partial skeleton with at least 50 disarticulated teeth, Smoky Hill Chalk Member of Niobrara Chalk, Logan County, Kansas (discussed by DRUCKENMILLER et al. 1993).

Squalicorax kaupi (or *S*. cf. *S. kaupi*)

AMNH 11746, *S. kaupi*, jaw fragment with at least 3 teeth, Pierre Shale, northeastern Niobrara County ("Mule Creek Junction"), Wyoming.

FHSM VP-2213, *S. kaupi*, jaw elements with partially articulated teeth, Niobrara Chalk, Rooks County, Kansas (Figs. 3C, 9, 11; discussed by SHIMADA 1994).

KUVP 229, *S. kaupi*, 42 teeth, scales, and some cartilage pieces, Niobrara Chalk?, Kansas?.

KUVP 55188, *S.* cf. *S. kaupi*, 26 disarticulated teeth and some cartilage pieces, Niobrara Chalk, Kansas.

KUVP 55190, *S. kaupi*, 6 vertebrae and multiple teeth, Niobrara Chalk, Logan County ("Buttle Creek"), Kansas.

KUVP 69712, *S. kaupi*, anteriormost 24 vertebrae and jaw elements with at least 3 teeth, Pierre Shale, Wyoming (Fig. 3D).

LACM 128007, *S. kaupi*, 45 disarticulated teeth and ca. 20 vertebrae, Smoky Hill Chalk Member of Niobrara Chalk, Logan County, Kansas.

UCM 36322, *S. kaupi*, at least 43 teeth and cartilage pieces, Sharon Springs Member of Pierre Shale, Red Bird, Niobrara County, Wyoming.

Squalicorax pristodontus

SDSM 34975, *S. pristodontus*, partial skeleton, ca. 60 cm above the top of the Ardmore Bentonite, Sharon Springs Member of Pierre Shale, southwestern Fall River County ("Wallace Ranch"), South Dakota (Figs. 4, 6, 7).

SDSM 47682, *S. pristodontus*, seven disarticulated teeth and five vertebrae, at the contact between the Gammon Ferruginous Member and Ardmore Bentonite, Sharon Springs Member, Pierre Shale, southwestern Fall River County ("Wallace Ranch"), South Dakota.

UCM 70757, *S. pristodontus*, 51 disarticulated teeth and cartilage pieces, Sharon Springs Member of Pierre Shale, Red Bird, Niobrara County, Wyoming.

Appendix 2

Diameter (in mm) of vertebral centra in four specimens of *Squalicorax falcatus*. – *, extensive disarticulation; ( ), severe distortion. Note significant change in diameter between v70 and v85.

v	USNM 425665 (Fig. 2A)	LACM 120090 (Fig. 2B)	LACM 135929 (Fig. 3A)	LACM 143537 (Fig. 2C)
1	27	–	20+	22
5	33	50^*	25	25
10	40	50^*	29	25
15	40	50^*	32	31
20	50	50^*	35	31
25	53	50*	50	(22)
30	50	58^*	49	30
35	49	57^*	45	29
40	47	45^*	45	23
45	40	50^*	34	23
50	37	50^*	34	23
55	33	48	31	22
60	30	46	(36)	22
65	27	45	30	19
70	24	44	30	19
75	20	43	24	18
80	20	34	20	12
85	19	20	13	12
90	19	20	13	12
95	19	–	12	12
100	19	–	11	12
105	19	–	11	10
110	18	–	11	9
115	13	–	8	7
120	12	–	4	7
125	8	–	4	5
130	6	–	4	5
13X	6	–	–	5

Appendix 3

Some basic measurements used for discussion. Code: 1, complete axial skeleton of *Squalicorax falcatus* offering approximate TL (asterisk under 1' = average value based on three specimens); 2, "large" incomplete *S. falcatus* skeleton; 3, "large" incomplete *S. kaupi* skeleton; 4, incomplete *S. pristodontus* specimen; 5, possible *Squalicorax* (*S. pristodontus*?) vertebrae. – Abbreviations: mCH, maximum vertical crown height of tallest tooth preserved (in mm); mTH, maximum vertical tooth height of tallest tooth preserved (in mm); mD, maximum diameter of largest centrum preserved (in mm); %mD, maximum diameter of largest centrum preserved relative to average diameter of three *S. falcatus* skeletons in terms of percentage (i. e., 40 mm = 100 %); TL, total body length (in cm); McL, mesiodistal length of Meckel's cartilage between mandibular symphysis and mandibular knob (in cm); %McL, mesiodistal length of Meckel's cartilage relative to TL in terms of percentage. Note that each specimen may not necessarily preserve the tallest teeth of its original dentition.

Code	Specimen	mCH	mTH	mD	%mD	TL	McL	%McL
1	USNM 425665	11.0	18.0	44	–	200	21	10.5
1	LACM 135929	10.5	16.5	41	–	195	–	–
1	LACM 143537	8.0	13.5	35	–	180	–	–
1'	–	–	–	40^*	100	192^*	–	–
2	LACM 120090	11.0	17.5	58	145	[278]	35	12.6
3	KUVP 69712	13.5	–	62	155	[298]	34	11.4
4	SDSM 34975	12.0	22.0	45	113	[216]	35	16.2
4	SDSM 47682	18.0	27.0	64	160	[307]	–	–
5	SDSM 47683	–	–	100	250	[480]	–	–