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A NEW WORLD OCCURRENCE OF *NOTIDANODON LANCEOLATUS* (CHONDRICHTHYES, HEXANCHIDAE) AND COMMENTS ON HEXANCHID SHARK EVOLUTION

DOUGLAS J. LONG,[1] MICHAEL A. MURPHY,[2] AND PETER U. RODDA[3]

[1]Department of Integrative Biology and the Museum of Paleontology, University of California, Berkeley 94720,
[2]Department of Geology, University of California, Davis 95616, and
[3]Department of Geology, California Academy of Sciences,
San Francisco, 94118-4599

ABSTRACT—*Notidanodon lanceolatus* Woodward is reported from Late Aptian strata of northern California. This specimen, the oldest fossil cow shark (Hexanchidae) in the New World, greatly extends the geographic distribution of this species and confirms the eurytopic distribution of this genus. We suggest that cow shark teeth evolve in an orderly sequence in which the mesial edge of the tooth is at first smooth (*Notidanus muensteri*), then serrate (*Notidanus serratus, Notorynchus aptiensis*), and finally dentate (*Notidanodon lanceolatus*).

INTRODUCTION

A SINGLE FOSSIL specimen of the hexanchid cow shark, *Notidanodon lanceolatus* (Woodward), was recovered from the Late Aptian strata of the Budden Canyon Formation in Shasta County, northern California (Figures 1, 2). This is the earliest occurrence of fossil cow sharks in the New World, and extends the geographic range of the species, which was known only from England and northern Germany (Ward and Thies, 1987).

Two species of cow sharks currently live in the marine waters off California, *Notorynchus cepedianus* Ayres (sevengill shark) and *Hexanchus griseus* Rafinesque (sixgill shark). These and the sharpnose sevengill shark (*Heptranchias perlo* Rafinesque) are the extant genera of cow sharks in the family Hexanchidae. Some data on the ranges and ecologies of these recent species are available (Compagno, 1984; Ebert, 1986), but their evolution, paleoecology, and paleobiogeography are poorly known. In addition, these kinds of derivative studies are hampered by an inadequate and confusing taxonomic base to which our specimen permits only modest revision.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Order HEXANCHIFORMES Buen, 1926
Family HEXANCHIDAE Gray, 1851

Early workers grouped the unique multicuspate teeth of fossil hexanchids under the genus *Notidanus* Agassiz. Modern taxonomic revisions have divided *Notidanus* into many genera, but taxonomic relationships and the generic composition of the family Hexanchidae are still under discussion (Cappetta, 1975, 1987, 1990; Maisey, 1986; Maisey and Wolfram, 1984; Pfeil, 1983; Thies, 1987; Ward, 1979; Ward and Thies, 1987; Welton, 1979).

Genus NOTIDANODON Cappetta, 1975

The holotype of *Notidanodon pectinatus*, the type species of *Notidanodon*, is a lower anterolateral tooth collected from the White Chalk (Cenomanian to Santonian) in southern England (Agassiz, 1843, Pl. 36, fig. 3), but this specimen has been lost (Ward and Thies, 1987). *Notidanodon* is characterized by mesial and distal cusplets that are relatively large and well developed in contrast to other hexanchids, in which the mesial cusplets are absent or are present as serrations on the mesial face of the principal cusp (Figures 3, 4).

Besides the type species that ranges from the Cenomanian to Campanian, three other species have been referred to *Notidanodon*: *N. loozi* (Vincent), Thanetian; *N. dentatus* (Woodward), Campanian–Danian; and *N. lanceolatus* (Woodward), Early Hauteriverian–Albian. Ward and Thies (1987) considered some specimens of *N. pectinatus* to be *N. dentatus*, and some *N. dentatus* to be *N. loozi*, but until a full revision of these two species is completed, we will use the species designations for *Notidanodon* originally used by the authors.

NOTIDANODON LANCEOLATUS (Woodward, 1886)
Figures 3, 4

Referred material.—One specimen; California Academy of Sciences, Geology Collection CASG 63672.01.

Diagnosis.—Prominent, elongate, apically oriented principal cusp; enlarged and elongate mesial and elongate distal cusplets.

Description.—Specimen CASG 63672.01 is a single, complete labiolingually compressed tooth with a rectangular, mesodistally oriented root. Crown also mesodistally oriented and comprised of five mesial cusplets, one principal cusp, and four distal cusplets. Mesial cusplets apically or apicomesially inclined; principal cusp apically inclined; distal cusplets apicomesially inclined. Mesial cusplets increase in size distally. Cusp and cusplets possess a moderately convex labial and lingual crown face; smooth cutting edge present on mesial and distal keels of cusp and cusplets.

Discussion.—The long, apically oriented principal cusp and the large and elongate mesial and distal cusplets are the primary features that separate *N. lanceolatus* from other species of *Notidanodon* (Woodward, 1886; Ward and Thies, 1987). *Notidanodon lanceolatus* has been reported from England and northern Germany. The discovery of *N. lanceolatus* in northern California represents the first extra-European occurrence of the species and establishes a more global distribution. It is also the earliest hexanchid shark in the New World. Its Late Cretaceous congener, *N. pectinatus*, also has a global distribution having been reported from the Moreno Formation in central California (Applegate, 1965) and Seymour Island in the Antarctic Peninsula (Cione and Medina, 1987; Grande and Chattarjee, 1987).

Locality description and age of Notidanodon lanceolatus *in California.*—The nodule containing specimen CASG 63672.01 was found in the alluvial gravel of an unnamed gully (referred informally in the CAS locality register as "Shoup Ranch Gulch"), which is a tributary to Bee Creek, Ono quadrangle (USGS, 1981), Shasta County, California. Shoup Ranch Gulch (Figure 5) meanders for about 500 m generally along the strike of the bedding

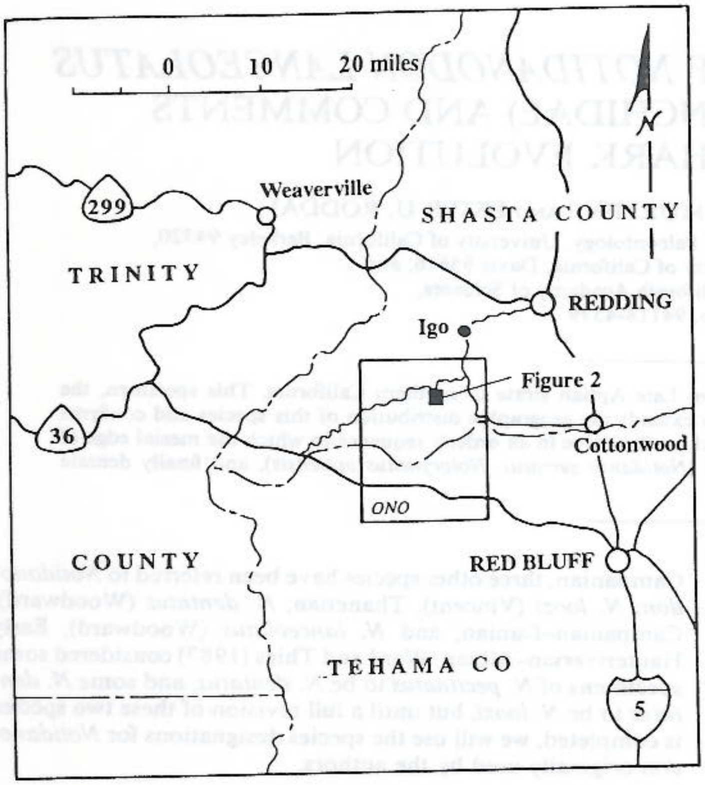

FIGURE 1—Location map showing the position of the 15′ Ono quadrangle (1949) in Shasta County, northern California.

in the upper Chickabilly Member of the Budden Canyon Formation (Murphy et al., 1964) and cuts a total of about 34 m of strata. The specimen was found in a meander near the top of the 34-m section (Figure 6). It could have come from anywhere in the interval, but typically the nodules break up before they are carried more than a few meanders downstream. In any case, the entire gully is within the Late Aptian *Eotetragonites wintunius* Zone (Popenoe et al., 1960).

The *Notidanodon lanceolatus* tooth and the ammonites are found in limestone nodules, commonly with abundant fragments of wood, many burrowed by teredinid bivalves. The limestone nodules vary in size and shape and they tend to be concentrated at certain stratigraphic horizons, in places coalescing into more or less continuous beds. The predominant lithology is a dark-gray, massive mudstone that locally shows evidence of intensive bioturbation. Rare benthic shelly faunal elements (as yet unstudied) include the bivalve *Pinna* sp., the anchurid gastropod *Drepanochilus* sp., and other small gastropods and nuculanid bivalves.

Although the presence of *Pinna* sp. and the heavily bioturbated sediments could suggest a shallow marine environment, most of the ammonite families present, Phylloceratidae, Lytoceratidae, Tetragonitidae, and Desmoceratidae, belong to groups that have been associated with deep-water environments (Ward and Signor, 1983, and references therein). The ammonite fauna, the lack of shallow-water sedimentary structures, the presence of early diagenetic nodules and concretions, and abundant plant remains suggest a deep, quiet-water environment, several kilometers offshore and near a large deltaic system.

EVOLUTION OF *NOTIDANODON*

Early hexanchid evolution is inferred from isolated teeth found in Jurassic marine deposits of Europe (Ward and Thies, 1987; Cappetta, 1987, 1990) and complete specimens from the upper Jurassic Solenhofen Limestone of southwest Germany (Maisey, 1986). The generic designation of the Late Jurassic hexanchids has changed many times in recent years (*Notidanus,* Woodward, 1886, Cappetta, 1990; *Notidanoides,* Maisey, 1986, Ward and Thies, 1987; *Eonotidanus,* Pfeil, 1983, Cappetta, 1987; *Paranotidanus,* Ward and Thies, 1987). Cappetta (1990) revised and synonymized several Late Jurassic hexanchids into one genus with two species, *Notidanus muensteri* Agassiz (Figure 7.1, 7.2)

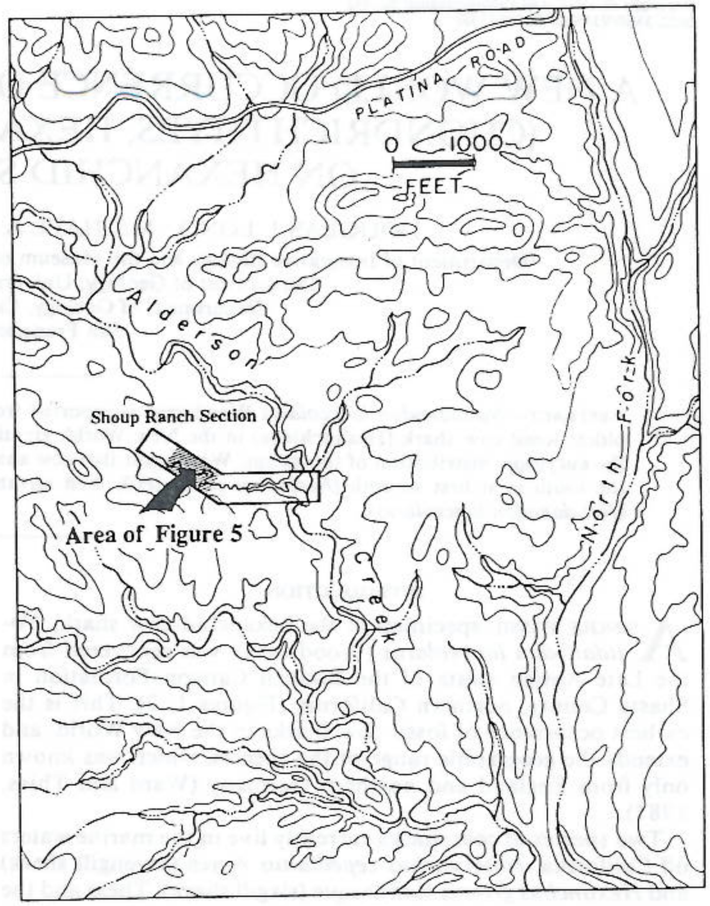

FIGURE 2—Location map showing the area of the Shoup Ranch Section on topographic map of the Ono quadrangle and the position of Figure 5 (cross-hatched area).

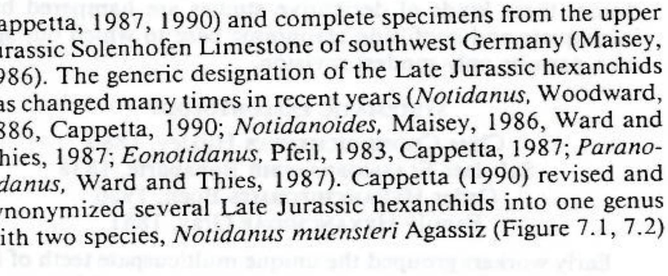

FIGURE 3—Photograph of the California *Notidanodon lanceolatus* Woodward specimen (CASG 63672.01). A lower anterolateral tooth.

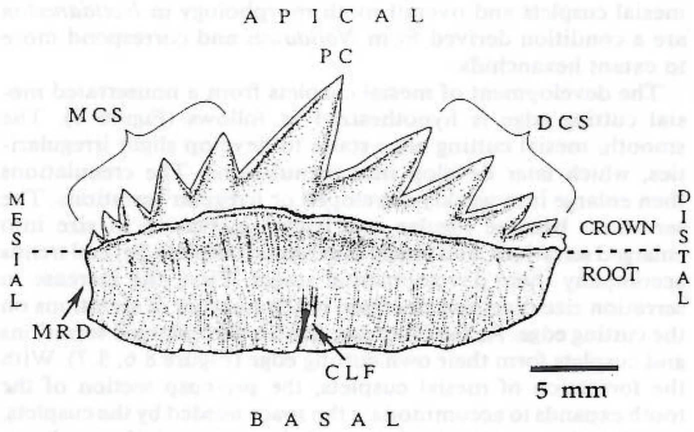

FIGURE 4—Illustration of the *Notidanodon lanceolatus* Woodward tooth showing morphological terms used in this study. MRD, mesial root depression; MCS, mesial cusplets; PC, principal cusp; DCS, distal cusplets; CLF, central lingual foramen.

and *N. serratus* Fraas (Figure 7.3). The dentition of *Notidanus* shows the primitive pattern from which the tooth morphology of Cretaceous hexanchid sharks can be derived. Like all hexanchids, Jurassic *Notidanus* exhibits both dignathic heterodonty (differences between teeth in the upper and lower jaws) and monognathic heterodonty (differences between anterior and posterior teeth in a single jaw). The teeth of *Notidanus* consist of a laterally compressed root and crown with a distally inclined principal cusp and two to four distal cusplets. These characters constitute the basic dental pattern of all hexanchid sharks. Based on tooth morphology, anatomy, and stratigraphic position, *Notidanus* is the ancestral stock of hexanchid sharks. *Notidanus muensteri* usually has a smooth cutting edge on the mesial face of the principal cusp, but some specimens may have a slightly irregular or weakly serrated cutting edge (Cappetta, 1990; Quenstedt, 1858). *Notidanus serratus* has weak to well-developed serrations on the lower mesial cutting edge of the principal cusp, a character that is interpreted here as advanced over *Notidanus muensteri.* Serrations on the cutting edge of teeth are thought to be a derived condition in all groups of sharks (Applegate, 1967; Compagno, 1988). Pfeil (1983) also surmised that hexanchid teeth with a serrate mesial cutting edge are derived from an ancestral form with a smooth cutting edge. If these assumptions are correct, *Notidanus serratus* should descend from *Notidanus muensteri* and succeed it stratigraphically even though our present data are too limited to show this pattern.

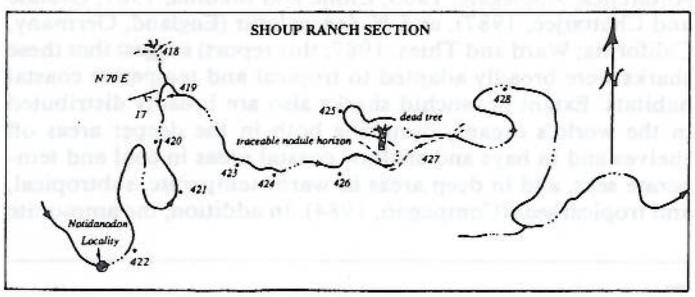

FIGURE 5—Pattern of Meanders in Shoup Ranch Gulch showing relative positions of collecting localities of *Notidanodon lanceolatus* Woodward and associated ammonites. Relative stratigraphic positions are shown in Figure 6.

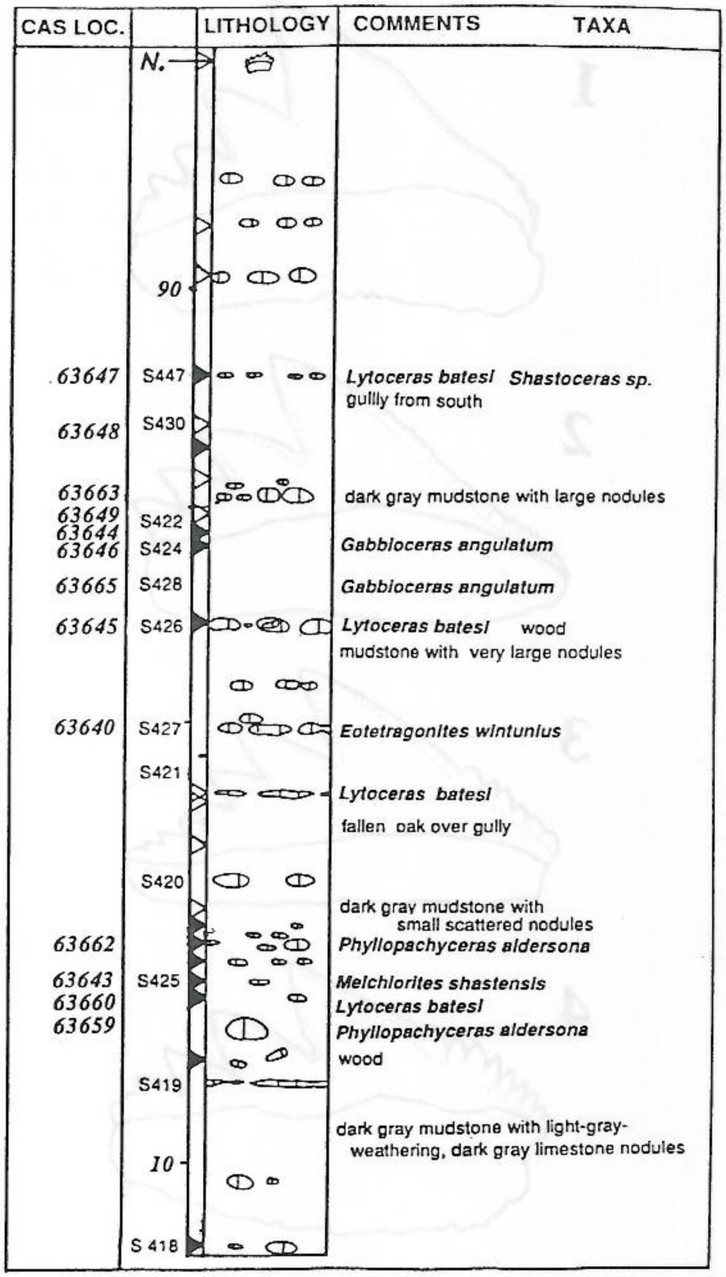

FIGURE 6—Columnar section showing position of *Notidanodon lanceolatus* Woodward in the Shoup Ranch Section. *Notidanodon lanceolatus* was found in stream gravel at the position indicated (N) on the section and must have been derived from the *Eotetragonites wintunius* Zone in the relatively limited outcrop that lies upstream from the discovery locality. The same gravel deposit also contained abundant specimens of *Lytoceras batesi.*

In the Early Cretaceous, the trend established in *Notidanus* continued in two genera, *Notorynchus* and *Notidanodon. Notorynchus aptiensis* Pictet (Valanginian or Hauterivian to Albian) (Figure 7.4) shows the large principal cusp and shows an increase in the size, numbers, and regularity of the mesial serrations and the distal cusplets. *Notidanodon lanceolatus* (Figures 3, 4, 7.5) takes this trend one stage further with an overall increase in tooth size and a transformation of the mesial serration into mesial cusplets. Thies (1987) thought the enlarged

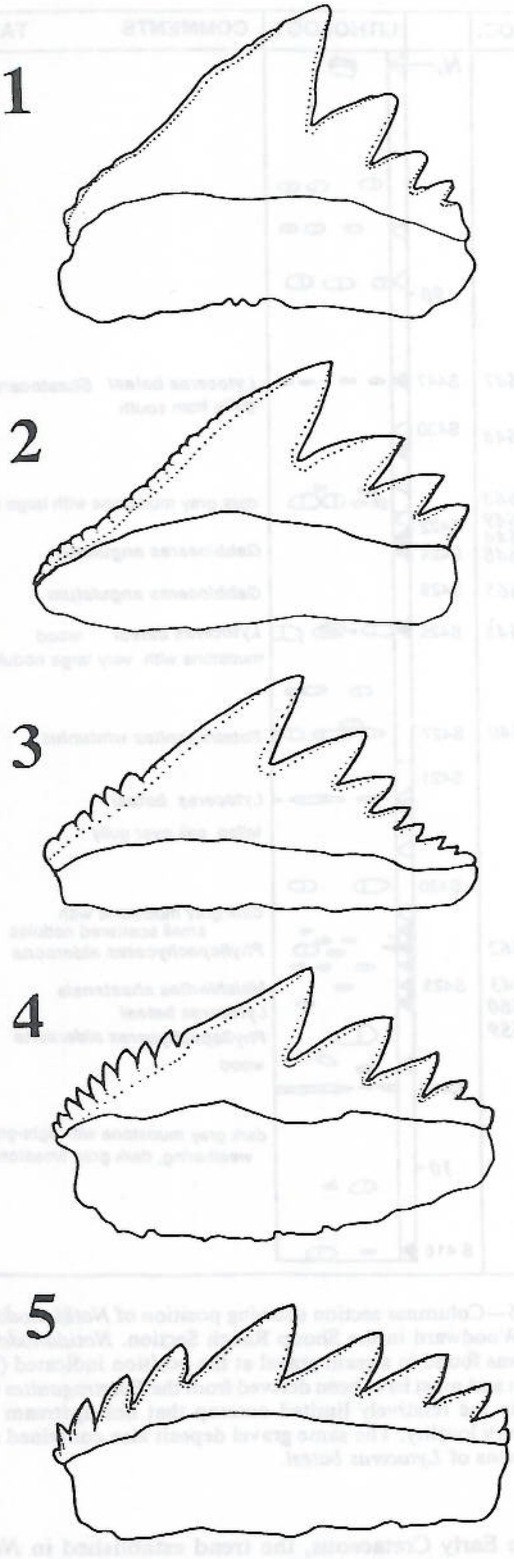

FIGURE 7—Evolutionary sequence of the development of mesial cusplets in Mesozoic hexanchid sharks. *1, Notidanus muensteri* Agassiz (Upper Jurassic) with a relatively smooth mesial cutting edge. *2, N. muensteri* with a weakly serrated cutting edge. *3, N. serratus* Fraas (Upper Jurassic) with a serrated lower cutting edge. *4, Notorynchus aptiensis* Pictet (Upper Cretaceous) with enlarged, even serrations on the lower cutting edge. *5, Notidanodon lanceolatus* Woodward (Upper Cretaceous) with large mesial cusplets. (*1* redrawn from Cappetta, 1990; *2* and *3* redrawn from Quenstedt, 1858; *4* and *5* redrawn from Thies, 1987.) Teeth not drawn to scale.

mesial cusplets and overall tooth morphology in *Notidanodon* are a condition derived from *Notidanus* and correspond more to extant hexanchids.

The development of mesial cusplets from a nonserrated mesial cutting edge is hypothesized as follows (Figure 8). The smooth, mesial cutting edge starts to develop slight irregularities, which later develop into crenulations. The crenulations then enlarge into weakly developed or irregular serrations. The serrations become regular and larger, increasing in size into enlarged serrations, and finally into mesial cusplets. Several trends accompany these developmental stages. First, the increase in serration size dictates a decrease in the number of serrations on the cutting edge. As they increase in size, the enlarged serrations and cusplets form their own cutting edge (Figure 8.6, 8.7). With the formation of mesial cusplets, the pre-cusp section of the tooth expands to accommodate the space needed by the cusplets, and they become less horizontal and more vertical in order to attain an apical orientation. The development of mesial cusplets and enlargement of the pre-cusp section of the tooth results in an increase in the mesiodistal length of the tooth.

The same morphologic progression is also found in the ontogeny of extant hexanchid sharks. During the development of *Notorynchus* and *Hexanchus,* there is an increase in the number of distal cusplets, the robustness of the principal cusp and cusplets, and the size and numbers of mesial serrations, all in proportion to the tooth as a whole (Welton, 1979). In addition, Compagno (1988) suggested that a change from serrations to cusplets can occur as a result of positive allometry in the growth of an individual through successive generations of replacement teeth. Thus, ontogenetic change mirrors the phylogenetic progression.

PALEOBIOGEOGRAPHY

Notidanus muensteri and *N. serratus* were sympatric and contemporaneous taxa that inhabited the tropical eastern Tethys Seaway. In the Early Cretaceous, the European seas differentiated into a relatively shallow tropical Tethys Sea and the sea north of Tethys became temperate (Thies, 1987). This climatic change is indicated by a differentiation of the Cretaceous biota. Thies (1987) also asserted that *Notorynchus aptiensis* was the predominant hexanchid shark in Tethys, while *Notidanodon lanceolatus* was dominant in the Cretaceous North Sea. It is difficult to see the rationale for this position, because all of the localities for *Notorynchus aptiensis* are in the area of the postulated Cretaceous North Sea and one of them is the same at which *Notidanodon lanceolatus* is also found (Thies, 1987, fig. 2).

The global distributions of the few known Cretaceous specimens of *Notidanodon dentatus* (Europe and New Zealand; Ward, 1979; Ward and Thies, 1987), *N. pectinatus* (Europe, California, Antarctica; Applegate, 1965; Cione and Medina, 1987; Grande and Chattarjee, 1987), and *N. lanceolatus* (England, Germany, California; Ward and Thies, 1987; this report) suggest that these sharks were broadly adapted to tropical and temperate coastal habitats. Extant hexanchid sharks also are broadly distributed in the world's oceans, occurring both in the deeper areas off shelves and in bays and shallow coastal areas in cool and temperate seas, and in deep areas in warm-temperate, subtropical, and tropical seas (Compagno, 1984). In addition, the ammonite

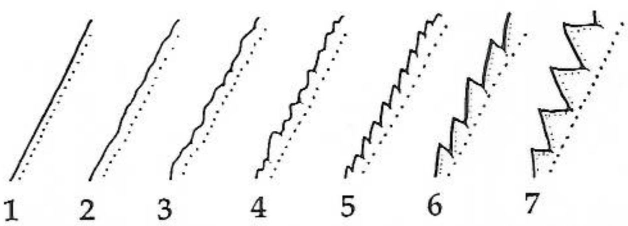

FIGURE 8—Developmental stages of the formation of mesial cusplets from a smooth cutting edge. *1*, smooth cutting edge; *2*, cutting edge with slight irregularities; *3*, with crenulations; *4*, with irregular serrations; *5*, with regular serrations; *6*, with enlarged serrations; *7*, with mesial cusplets (expanded after Pfeil, 1983).

fauna associated with *N. lanceolatus* in northern California was broadly distributed in the Tethyan region, having species in common with the French Vocontien and Clansayes areas and the Caucasus. The entire assemblage of sharks, lytoceratid, desmoceratid and phylloceratid ammonities, and abundant woody fragments with associated small gastropods and teredinid bivalves suggests a normal marine habitat that was influenced by a large river system on the nearby land area.

Notidanodon probably occupied several levels of the trophic ladder. Dietary studies of extant hexanchid sharks show they are primarily opportunistic predators on a variety of invertebrates, bony fishes, and sharks, but they are also scavengers (Ebert, 1986; Compagno, 1984). The direct association of *Notidanodon* teeth with the skeletons of marine reptiles (Cione and Medina, 1987; Applegate, 1965) supports the idea that *Notidanodon* was also an opportunistic scavenger.

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