AMERICAN MUSEUM
Novitates

PUBLISHED BY THE
AMERICAN MUSEUM
OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET
NEW YORK, N.Y. 10024 U.S.A.

NUMBER 2718 NOVEMBER 19, 1981

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Studies on the Paleozoic Selachian Genus *Ctenacanthus* Agassiz No. 1. Historical Review and Revised Diagnosis of *Ctenacanthus*, With a List of Referred Taxa

JOHN G. MAISEY[1]

ABSTRACT

Ctenacanthus Agassiz is a genus of elasmobranch, originally recognized by its dorsal finspines but now known from more complete remains. However, many other fossils, including isolated spines and complete fish, have been included in *Ctenacanthus*, although the spines differ from those of the type species, *C. major*, and from other presumably related species. Earlier diagnoses of *Ctenacanthus* are critically reviewed and the significance of previous diagnostic changes is discussed. It is concluded that *Ctenacanthus sensu lato* is paraphyletic. Some spines previously assigned to this taxon resemble living elasmobranch finspines, whereas others resemble hybodontid finspines. The fish described by Dean as *Ctenacanthus clarkii* should be referred to *C. compressus*. Both *C. clarkii* and *C. compressus* finspines are sufficiently like those of *C. major* for these species to remain within the genus. *Ctenacanthus compressus* is the only articulated Paleozoic shark so far described which can be assigned to *Ctenacanthus*. *Ctenacanthus costellatus* finspines are not like those of *C. major*, but instead resemble *Sphenacanthus* spines. *Goodrichthys eskdalensis* may be closely related to *Ctenacanthus*.

INTRODUCTION

The genus *Ctenacanthus* has been used as a catch-all taxon, rather like the old genus *Ammonites*, and is in need of revision. To many paleontologists *Ctenacanthus* includes primitive sharks with finspines somewhat like those in *Hybodus*, and "ctenacanth"

[1] Assistant Curator, Department of Vertebrate Paleontology, American Museum of Natural History.

ISSN 0003-0082 / Price $2.50

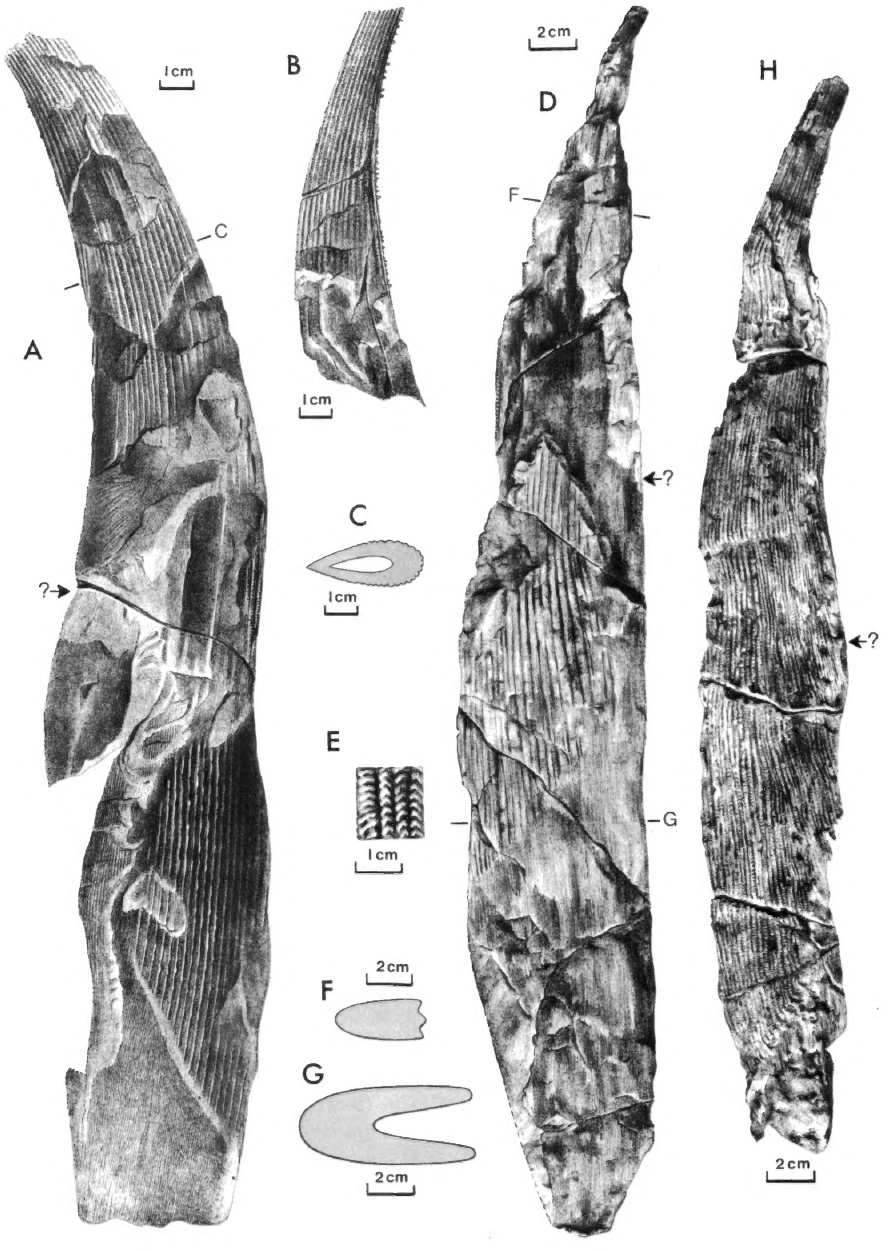


FIG. 1. A–C, *Ctenacanthus major* Agassiz, type, Bristol City Museum C4152. From Agassiz, 1837, table 4. D–H, *C. major* Agassiz. From Davis, 1883, plate XLII, BM(NH) P2534. Section (C) faces right, and is taken from (A), which shows the right side. Section (C) is distorted by crushing and is therefore unreliable. Specimen (B) is shown from the left side. Sections (F & G) facing left, and ornament detail (E) are from specimen (D), seen along with (H) from the left side.

sharks have often been treated as a monophyletic group, e.g., Brough (1935), Moy-Thomas (1936, 1939a, 1939b), Romer (1945), Moy-Thomas and Miles (1971), Maisey (1975) and Schaeffer and Williams (1977). Over the years numerous taxa, based on fin-

spines, have been added to *Ctenacanthus*. Some of these spines resemble *C. major*, the type species, and the present work seeks to restrict *Ctenacanthus* to include only those species founded on finspines that are similar to *C. major*. Over the years since Agassiz (1837) first described *Ctenacanthus* finspines, their diagnosis has been tinkered with until almost any Paleozoic phalacanthous shark can satisfy the definition of a "ctenacanth." In the course of my investigations it has become evident not only that "ctenacanths" (in the broad context that they have become known) are probably paraphyletic, but also that diagnosis of its finspines is so amended that it bears little resemblance to the admittedly poor original description. It is no longer possible to reconcile the type species, *C. major*, with generic diagnoses published after 1850.

In recent years the number of phalacanthous Paleozoic sharks known from fairly complete skeletal remains has grown enormously, although many of these have yet to be described. New finds of complete *Wodnika* (Schaumberg, 1977) from the German Kupferschiefer, and many as yet undescribed forms from the Carboniferous and Devonian of North America, cannot be evaluated critically until the "ctenacanth" problem is re-examined. In the first part of this work I review the literature dealing with *Ctenacanthus*, and attempt to show how successive authors have added progressively more confusion. Having trimmed *Ctenacanthus* of all but a central core of species based on finspines which closely resemble the type species, *C. major*, I will present a systematic revision of *Ctenacanthus* in the second part of this work.

EXPLANATION OF ILLUSTRATIONS

The figures in this paper are composites made both from specimens and original illustrations. In the course of preparing these figures it became apparent that there were many original discrepancies which needed rectifying or commenting on, and notes are given in the figure legends.

Where sections are shown horizontally (e.g., fig. 1C, F, G), their position on the related spine (e.g., fig. 1A) can be plotted. Where sections are vertical, either they were drawn at different scales to the spine and cannot be plotted accurately (e.g., fig. 3B, D, E, J), or space was unavailable to allow the section to be turned (e.g., fig. 6C). In general, original illustrations were faithfully reproduced, but the orientations and positions of sections, and level of posterior closure (indicated by a small arrow in lateral views) have been added. Sources of illustrations are indicated in the figure captions, all are reduced, and are not to scale.

HISTORICAL REVIEW

What is *Ctenacanthus*?

Ctenacanthus is a taxon founded on isolated dermal finspines (Agassiz, 1837). Spines referable to the type species of *Ctenacanthus, C. major*, have never been found associated with other remains. However, nobody has questioned the view that *Ctenacanthus* was a Paleozoic shark, somewhat like *Hybodus* from the Mesozoic, and a few fairly complete fossil sharks with finspines have been referred to *Ctenacanthus*. However, only one of these, a specimen of *C. clarkii* (Dean 1909), has a finespine with similar ornament to *C. major*, and therefore corroborates the view that *Ctenacanthus* was a shark (see below).

Agassiz's (1837, p. 10) diagnosis of *Ctenacanthus* spines is as follows:

> Les *Ctenacanthus* sont d'immenses rayons très-comprimés, à base large, mais à cavité plus petite que celle des *Oracanthus*. La partie de ces rayons cachée dans les chairs paraît avoir été considérable. Au bord postérieur se voient quelques petites épines. La surface est ornée de stries longitudinales, plus rapprochées que celles des *Hybodes*, pectinées, c'est-à-dire crénelées transversalement et saillantes en forme de dents qui alternent d'une série a l'autre, mais qui semblent continuer à cause de leur obliquité.

The presence of an intramuscular part is characteristic of all elasmobranch dorsal finspines. It does not appear to be any more

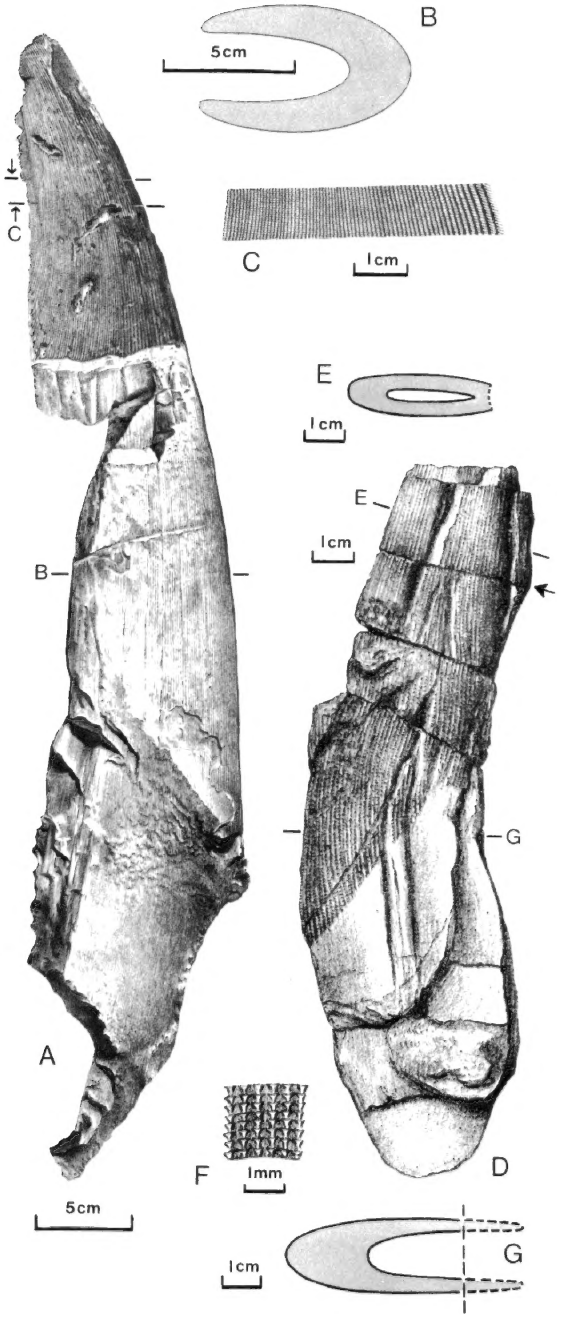


FIG. 2. A–C, *Ctenacanthus maximus* de Koninck. From de Koninck, 1878, plate 7, IRSNB P1305. Section (B) and ornament detail (C), both facing right, from specimen (A), seen from right side. Level of section not indicated in original, and drawn to a different (but indicated) scale, enabling its approximate level to be determined. D–G, *C. salopiensis* Davis. From Davis, 1883, plate CLIV. Section (G) facing left, was originally based on a restored outline of (D), seen from left side, and its posterior limits were imagined. Section (E), facing left, is incomplete and probably flattened.

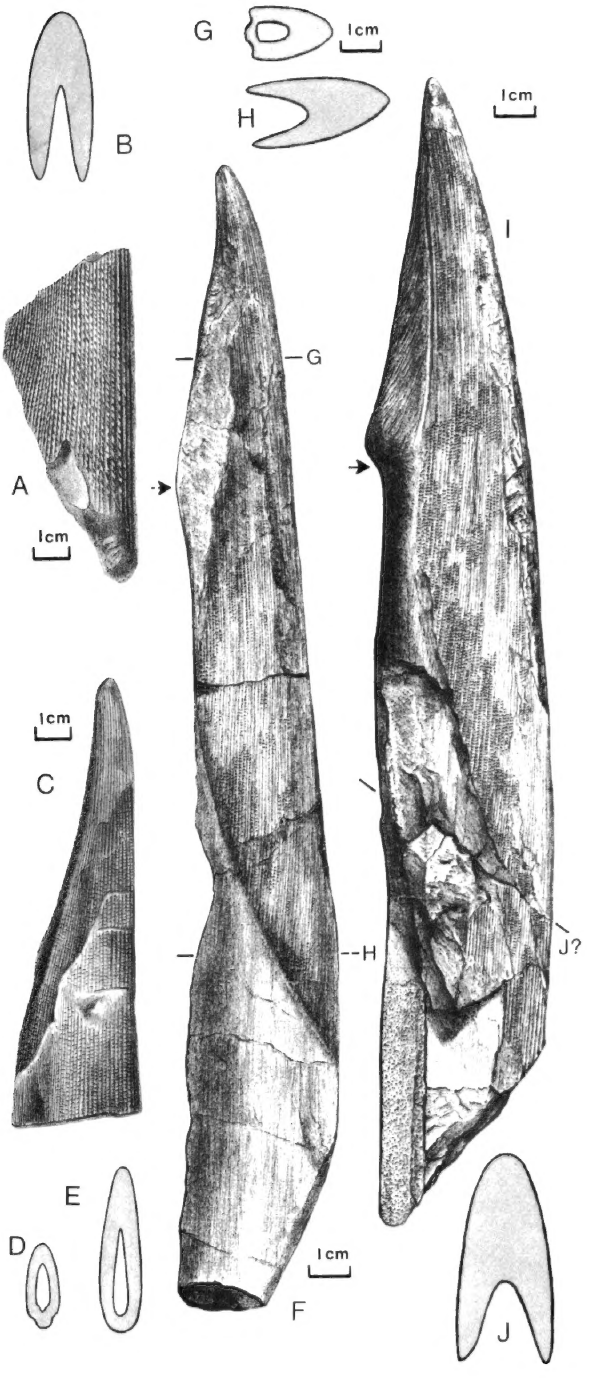
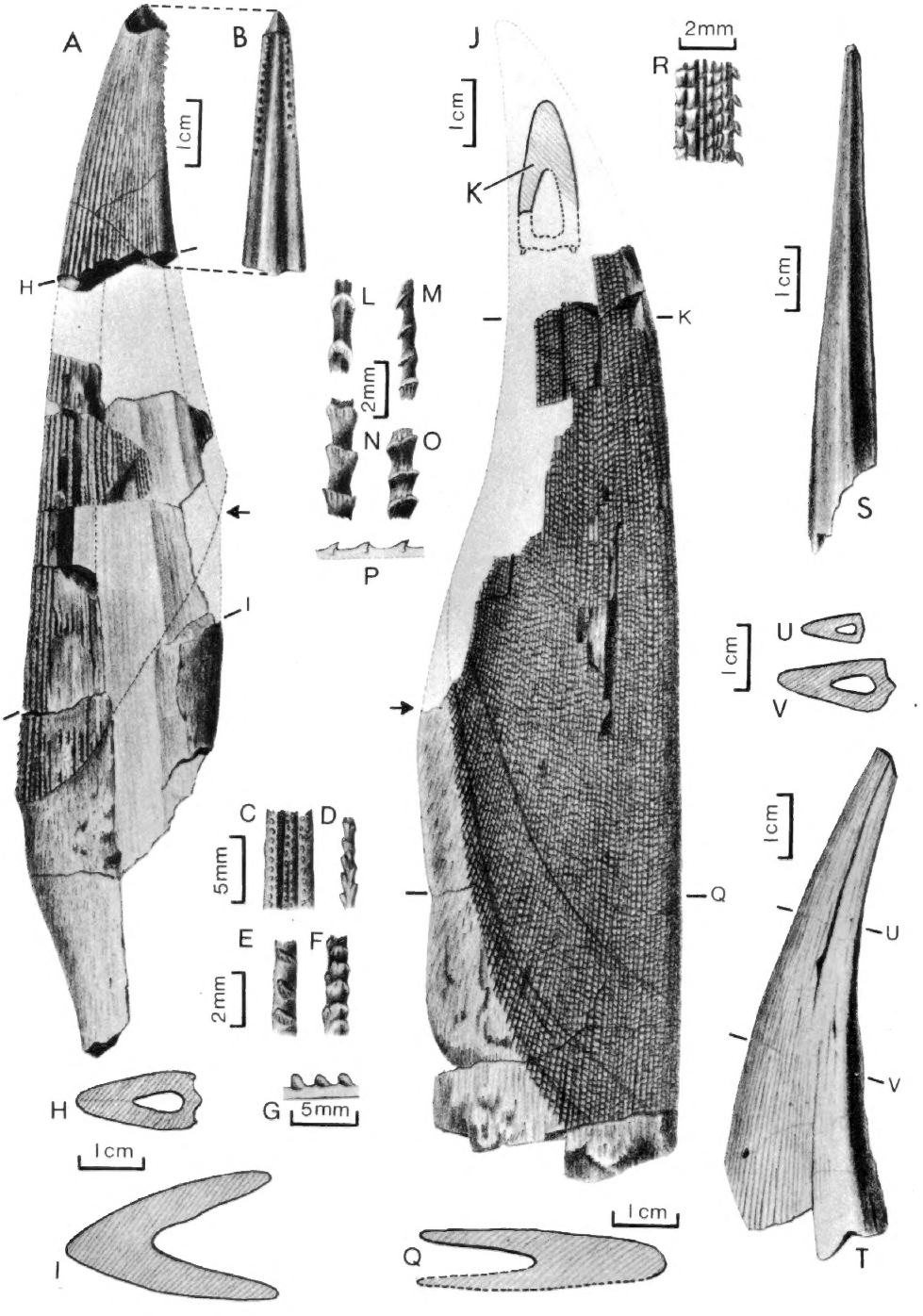


FIG. 3. *Ctenacanthus tenuistriatus* Agassiz. A–E, from Agassiz, 1837, table 3. (A), Bristol specimen, no catalogue number, now lost. (C), composite from BM(NH) P495, 2225; F–J, from Davis, 1883, plate XLIII, BM(NH) P3109. Levels of sections (B, D, E) facing upward and drawn from (A & C) and (J), drawn from (I), cannot be accurately determined; (J) may be a very oblique section through a fracture shown in (I). Drawing (C) is not a specimen but represents an original composite. Spines (A, C, F, I) are all seen from the right side.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"considerable" in *C. major* than in the majority of other elasmobranch finspines. Evidently Agassiz was most impressed by the ornamentation pattern as a taxonomic character. It is difficult to formulate a diagnosis based simply on these characteristics, but others appear in the description of *C. major* (Agassiz, 1837, p. 11, repeated here in part):

> Toute sa surface est ornée de gros plis longitudinaux, entre lesquels se trouvent des sillons arrondis et des plis transverses et obliques très-rapprochés, qui forment par leur saillie une sorte de dentelure sur les côtés de chaque sillon. Au bord postérieur du rayon, et vers sa pointe seulement, on remarque quelques petites épines, ou plutôt quelques rides plus saillantes en forme de peigne sur le sillon marginal. Ses côtés sont comprimés et légèrement bombés sur le milieu. Sa coupe transversale, fig. 3, est ovale, arrondie du côté de la face postérieure du rayon et tranchante à son bord antérieur. La ligne de démarcation entre la partie sillonnée du rayon, qui était visible extérieurement et sa base lisse qui était cachée dans les chairs, est très-oblique. Le canal de la partie postérieure de la base est très profond et se prolonge en forme de cavité ovale jusque vers l'extrémité du rayon.

The principal diagnostic features of a *Ctenacanthus* finspine based on Agassiz's description seem to be the style of ornamentation and shape in cross-section. It is in relation to these particular features that subsequent authors have amended their diagnoses the most. Even Agassiz (1837) did not restrict the genus to finspines with ornament like that of *C. major,* as his next species, *C. brevis,* is based on another finspine which is covered by rows of large, rounded, striated tubercles. He never examined the specimen on which *C. brevis* was founded before publication, although he was aware of its ornamentation. His plate 2, figure 2 was copied from a drawing he received from Buckland.

I have examined the large type specimen of *C. major* (C4152, Bristol City Museum, England). Unfortunately, much of the Bristol collection was destroyed during the Second World War, and other specimens referred to *C. major* by Agassiz (1837) cannot be located. Specimen C4152 is badly crushed and few diagnostic features are visible. The shape in cross-section is critical, and I have tried to compare the type of *C. major* with other referred specimens and other, similar taxa. The cross-section of the spine shown by Agassiz (1837, plate 4, reproduced in fig. 1C here) is crushed and its anterior margin should be rounded rather than sharp. However, it is possible to verify that the posterior wall is convex, as Agassiz (1837, p. 11) stated, and not concave as most subsequent authors have said. Other finspines which are referred to *C. major,* and in which the posterior wall is convex, include BM(NH) P3109, 3313, and P2224 (not clearly, and only at the apex). Most specimens in the British Museum (Natural History) referred to *C. major* are from northern England, whereas the type specimen comes from the Avon

←

FIG. 4. A–I, *Ctenacanthus varians* St. John and Worthen. From St. John and Worthen, 1875, plate 14. Sections (H & I), facing left, are not transverse but appear to be drawn from broken surfaces as indicated on (A), left side. Details (C–G) were approximately located in the original; (C) is from near the ornament base anteriorly; (D) is from the tenth rib, low down on the right side; (E) is near to the base, close to the posterolateral margin; (F) is from the middle of the right side, close to the base; (G) shows some marginal denticles near the apex. View (B) is of the posterior wall. J–V, *C. speciosus* St. John and Worthen. From St. John and Worthen, 1875, plate 14. Section (K) can be accurately located on (J) but lack of space precluded showing section horizontally. Sections (U & V), facing left, are probably oblique. Details (L–P) were taken "from various parts" and cannot be accurately positioned; presumably (P) shows marginal denticles. Detail (R) is misleading, as it had nothing to do with the specimen shown, but pertains to some other referred specimens. Spine (J) seen from right side; (T) from left side; (S) = posterior view.

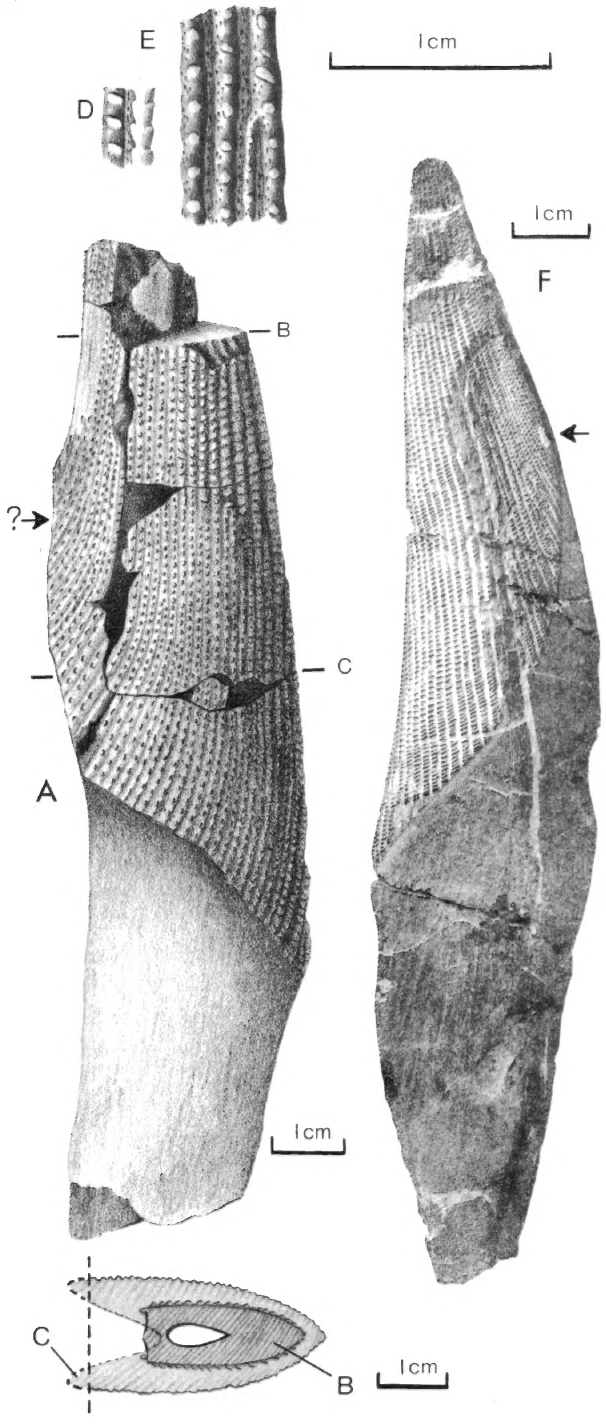


FIG. 5. *Ctenacanthus spectabilis* St. John and Worthen. A–E from St. John and Worthen, 1875, plate 15; F, from Eastman, 1902, plate 5. Section (C) is imaginary and seems too large for the level shown because it was originally intended to fit a restored outline silhouetted out in the present figure. Section (B) is drawn from a broken end. Detail (D) is from (A), right side; (F) is from left side (different specimen).

Gorge, near Bristol, England, although all are from lower Carboniferous limestones. Consequently there is some doubt as to their conspecificity. Other finspines which are probably referable to *C. major,* and which have a convex posterior wall, include the following: BM(NH) P9790, P495 (paratype of *C. tenuistriatus*; see below for further discussion of this specimen); BM(NH) P2523 (holotype of *C. salopiensis*); BM(NH) P3440, P34432, P34431, P2522, P213, and P23822 (*Ctenacanthus* sp.). Some other fragments are indeterminate because the posterior wall is not preserved, e.g., BM(NH) P34433 (a finspine base), P34441 and P34877.

Agassiz (1837) also described and figured three other *Ctenacanthus* species on the basis of finspines: *C. brevis,* which he admittedly never examined; *C. ornatus,* probably an acanthodian spine fragment from the Devonian Old Red Sandstone (Pageau, 1969); and *C. tenuistriatus* (fig. 3A–E). The last is close to *C. major* (suggested as a synonym by Agassiz, 1837, and proposed as such by Woodward, 1891).

I am indebted to Dr. Michael Crane, City of Bristol Museum and Art Gallery for his invaluable assistance in attempting to resolve certain problems connected with *C. tenuistriatus*. Of the two specimens described and figured by Agassiz, plate 3, figures 7, 8 (C and A respectively here), the Bristol specimen (A) has long since disappeared. In a letter to me Dr. Crane wrote:

> E. B. Tawney annotated our copy of *Poissons Fossiles,* circa 1870, marking those specimens which were, or should have been, in the collection. There is a note against this specimen to indicate that it was in the collection, or that Tawney had evidence to suggest that it should have been. The MS "Bristol Philosophical Institution Catalogue of Fragments of Fossil Fishes selected by Dr. Agassiz 1834" does not list this species . . . . None of our later indexes of type and figured specimens made any reference to the original of this figure of *C. tenuistriatus* (*C. major*). If we did have it, and I am by no means certain that we did, it has not been recognized in the collections.

Fortunately, the other (Egerton) specimen (C) survives as BM(NH) P495, P2225. However, Agassiz (1837) and Woodward (1891) disagree as to the relationship of the Egerton and Bristol specimens; Agassiz stated that the Egerton spine was the upper part of a similar spine to the Bristol one; Woodward said that the Bristol specimen is actually part of the Egerton fossil. At the time of this writing the Bristol specimen has not been located.

Another species also based on a finspine, *C. heterogyrus,* was figured but not described by Agassiz (1837; see McCoy, 1855, p. 625, for a description), and still another taxon (*Onchus sulcatus*) was later included in *Ctenacanthus* by Davis (1883) and Woodward (1891). Neither of these taxa has "comblike" pectinate ornament typical of *C. major. Ctenacanthus heterogyrus* has coarse, irregular enameled ribs, and *C. sulcatus* has smooth, broad, enameled ribs. Both spines have a concave or flat posterior wall. Evidently there has been uncertainty over the systematic limits of *Ctenacanthus* since its first description. Trautschold (1874a, 1874b) added to the confusion by describing some orthocone cephalopods from Russia as *C. major* (Khabakob, 1928).

After Agassiz (1837), the next diagnosis of *Ctenacanthus* finspines seems to be McCoy's (1855, p. 624): "Fin-spines of moderate and large size, compressed, gradually tapering, moderately arched backwards; anterior face narrow, rounded; posterior face concave, with a moderate cavity, the lateral edges bordered by two rows of curved denticles inclined downwards. Surface marked with strong, longitudinal ridges and furrows, pectinated by transverse scales or tubercles. The concealed base of moderate size, rapidly tapering, finely striated."

An important change was thus made, and retained by all subsequent diagnoses, namely that the finspine has a concave posterior face. This is not true for spines of *C. major, C. tenuistriatus,* and *C. brevis* all of which are convex or ridged posteriorly. McCoy (1855) described *C. crenatus,* represented by a fragmentary spine lacking any part of the posterior wall. Davis (1883) was unable to relocate this specimen and it has never been recovered. Another finspine, *C. denticulatus,* was described and figured by McCoy

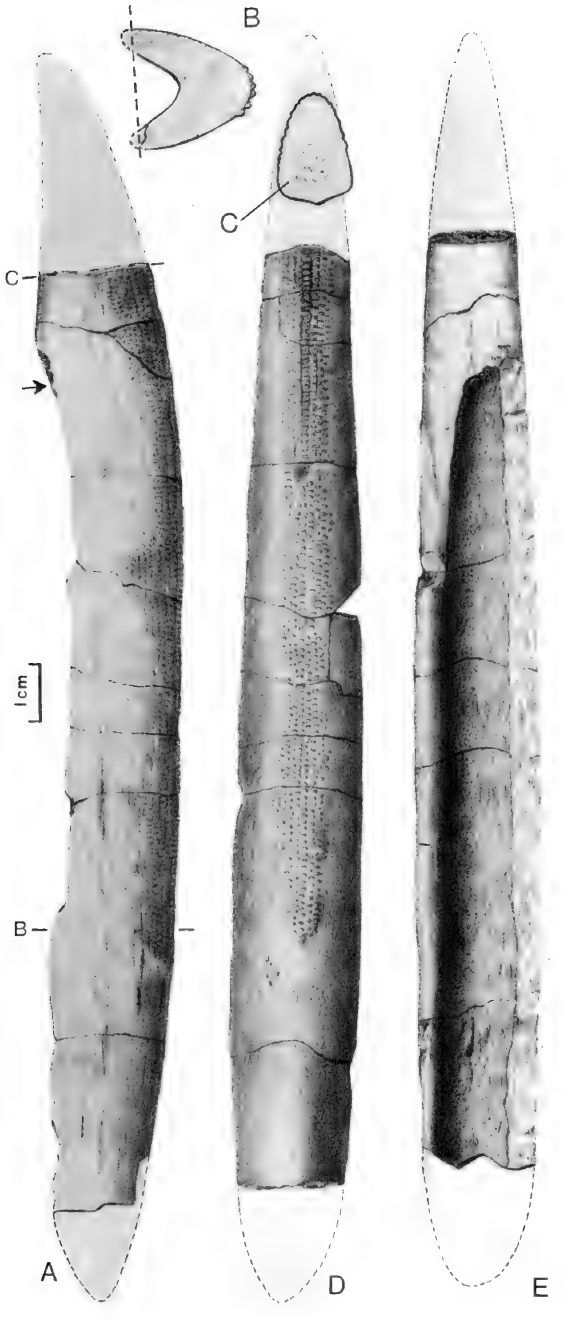


FIG. 6. A–E, *Ctenacanthus harrisoni* St. John and Worthen. From St. John and Worthen, 1883, plate XXIII. (A) = right side; (D) anterior; (E) = posterior. Section (C) can be plotted accurately on (A) but space precluded showing section horizontally. The original restored posterior profile of (A) was very inaccurate and is silhouetted out; the level of posterior closure is probably higher (arrowed) than St. John and Worthen suggested.

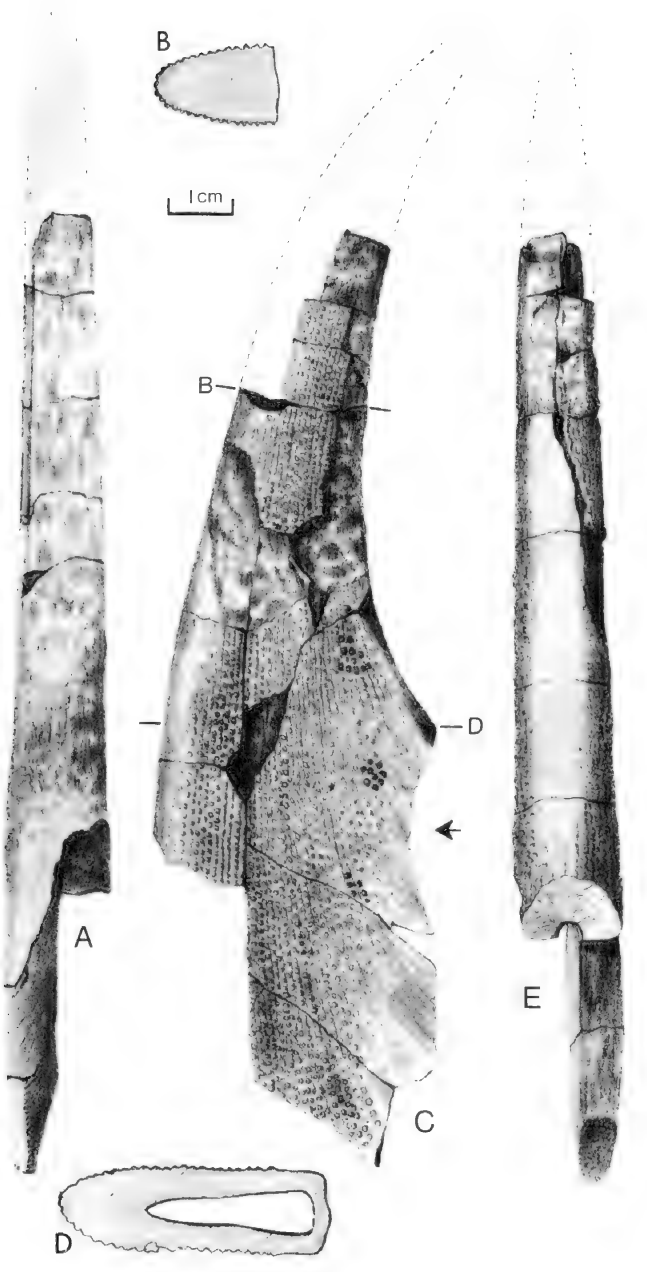


FIG. 7. A–E, *Ctenacanthus deflexus* St. John and Worthen. From St. John and Worthen, 1883, plate XXII. (A) and (E), whilst appearing to be the same length as (C), seem to be drawn at odd angles so that reference points such as broken surfaces and fractures do not line up. (A) = posterior; (C) = left side; (E) = anterior.

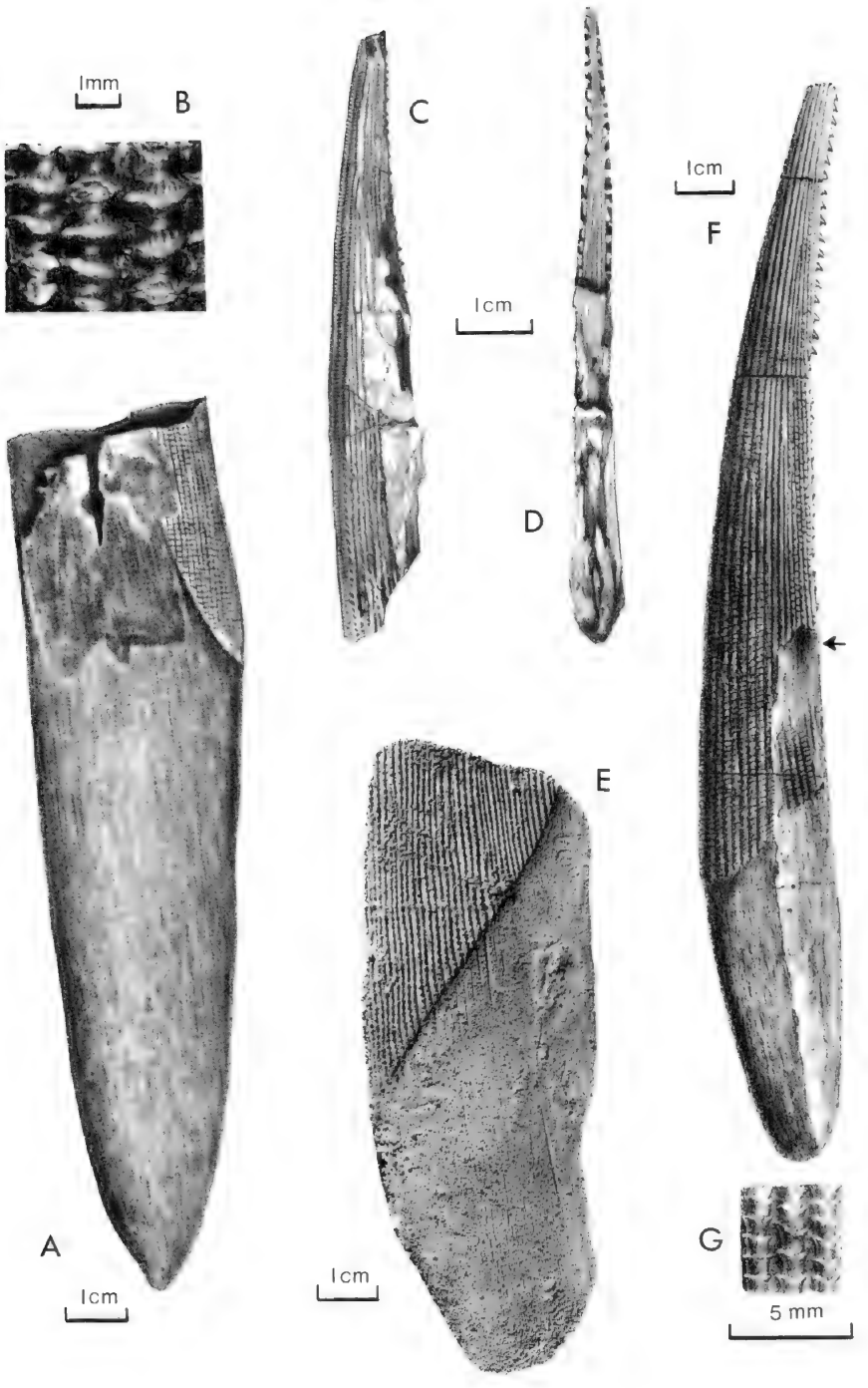


FIG. 8. (A, B) *C. littoni* Newberry; (A) from Newberry, 1889, plate XXV, spine base, right side. (B) from AMNH 1050, the holotype, detail of ornament. (C, D) *C. angulatus* Newberry and Worthen. From Newberry and Worthen, 1866, plate XII; (C) left side; (D) posterior wall. (E) *C. randalli* Newberry. From peel of AMNH 6675, the holotype. (F, G) *C. denticulatus* McCoy. From Sedgwick and McCoy, 1855, plate 3K; (F) left side. (G) ornament detail.

(1855, see fig. 8F–G, here). *Ctenacanthus denticulates* resembles *C. major* in ornamentation and gross morphology; here, too, the posterior wall bears a median convexity and is not concave. *Ctenacanthus distans* McCoy (1855) is based on an elongate, slender and laterally compressed finspine which, following the erection of *Acondylacanthus* by St. John and Worthen (1875) was referred to that genus by Davis (1883) and Woodward (1891). *Ctenacanthus heterogyrus* spines were also described by McCoy (1855) having been figured already by Agassiz (1837). With regard to the shape of the posterior wall of *Ctenacanthus* finspines, McCoy (1855) was more influenced by *C. heterogyrus* (with atypical ornament, see above) and *C. distans* (subsequently removed to another genus) than by Agassiz's (1837) description of *C. major* spines and McCoy's own specimen of *C. denticulatus*. Of all the "ctenacanths" so far considered, four species including the type have finspines with a convex or ridged posterior wall (*C. major, C. tenuistriatus, C. denticulatus, C. brevis*), and all but *C. brevis* have pectinate ornamentation. I have so far been unable to come up with an explanation for McCoy's (1855) departure from the original diagnosis. It is somewhat easier to follow the next development, however, as it is better documented in the literature and I have been able to examine critical specimens.

Newberry (1873) took McCoy's (1855) diagnosis almost verbatim, but noted the inconsistencies with Agassiz's (1837) description of *C. major* finspines. Newberry procured specimens of finspines identified as *C. major*. These survive in the American Museum of Natural History (AMNH 523 and 524). They are not referable to *C. major*, but are spines of another genus, *Sphenacanthus*. Moreover, these spines were apparently collected from the Scottish Coal Measures, not from the Carboniferous Limestone of England. No spines referable to *C. major* have ever been found in the Scottish Coal Measures, although in part these formations are of equivalent age (Mississippian) to the Carboniferous Limestone. *Sphenacanthus* finspines have irregular, widely spaced ribs, sometimes with scattered tubercles but never closely pectinated like those in *C. major*, and the spine is concave or flat posteriorly. Newberry's (1873) *C. marshi* finspine is referable to *Sphenacanthus*. Thus, by an unfortunate coincidence Newberry was sent some comparative material, which happened to be congeneric with his specimen of *C. marshi*, but which was misidentified as spines of the type species of *Ctenacanthus, C. major*. It has not been possible to locate the source of the misidentified Scottish spines at this time. Bearing in mind that Newberry's (1873) concept of *Ctenacanthus* finspines was based on specimens referable to *Sphenacanthus*, one can see why he wrote (p. 327):

> In the general character of the surface markings, these spines resemble those figured and described by Agassiz under the name of *Ctenacanthus major*; and they agree also with Agassiz's description so far as regards the ornamentation but not in regard to form or the "acute posterior margin"—the latter being a most anomalous feature in the spines of *Ctenacanthus*, all of which, so far as I know have a flattened posterior surface . . . . I have some large and massive spines from the Coal Measures of Scotland, which, with nearly identical surface markings, are twice as long as these, and they have the posterior margins, not acute, as Prof. Agassiz represents his specimens of *Ctenacanthus major*, but broadly concave, as in the specimens before us. The spines come to me as *Ctenacanthus major*, and suggest the probability that Prof. Agassiz was misled by the imperfect exposure of the specimen he figures, and that if this were properly developed it would show a flattened, striated posterior surface, as do the other species of the genus.

Newberry went on to admit that if Agassiz were correct about the shape of the posterior wall of the *C. major* finspine, the new form (*C. marshi*) would be distinct. However, it is clear that he thought Agassiz was wrong. Ironically, Agassiz (1837) had already described and figured a finspine of *Sphenacanthus* unfortunately from a much poorer specimen than Newberry's. Since Newberry's (1873) account sounded authoritative, and some attempt had been made by him to ex-

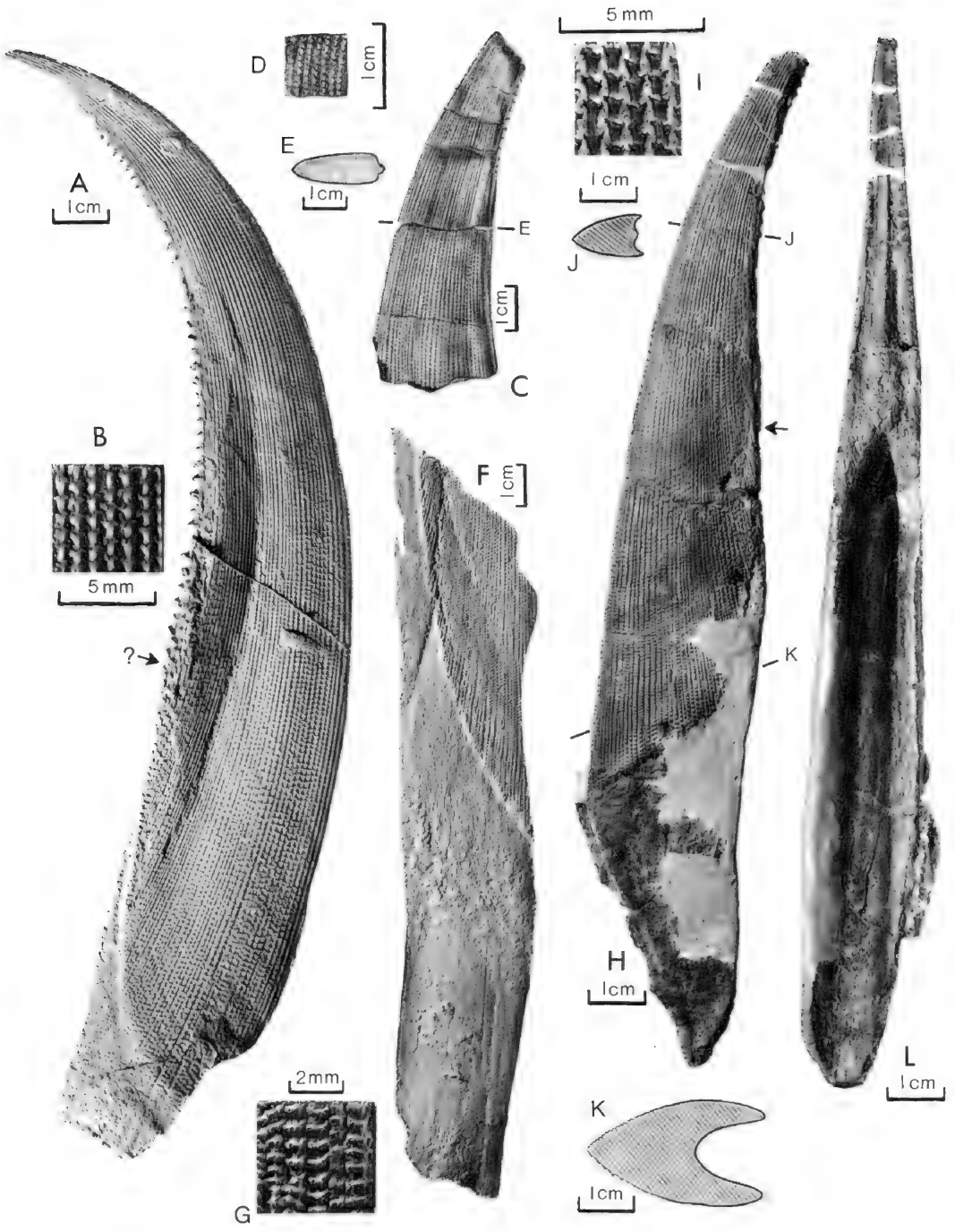


FIG. 9. (A–G) *C. compressus* Newberry. (A, B) from peel of AMNH 225; (C–E) the holotype, AMNH 140, from Newberry, 1889, plate XXIII; (F–G) from peel of AMNH 189. (A, F) from right side, photographed from peels; (C) from left side. (F, G) is Dean's (1909) specimen, identified there as *C. clarkii*. (H–L) *C. clarkii* Newberry; (H, I, L) from AMNH 220, the holotype; (J, K) from Newberry, 1889, plate XXVI, to same scale as (H & L), but posterior outline of (J) is modified to indicate posterior ridge; (H) left side; (L) posterior view; sections (J & K) face left.

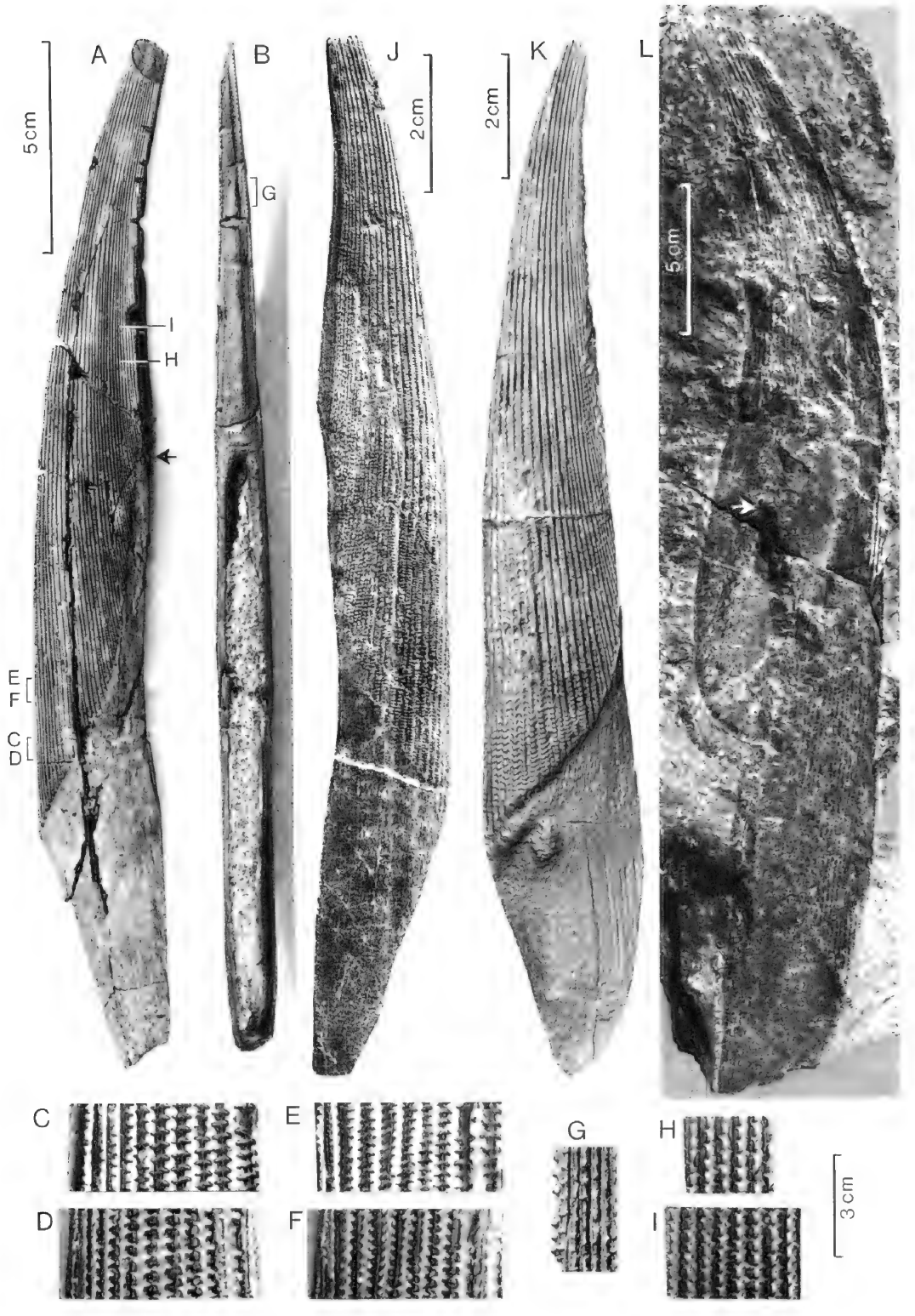
amine finspines (but not the type specimen) of the type species of *Ctenacanthus, C. major,* his conclusions have had a strong influence on subsequent researchers (see below). In a forthcoming paper dealing with other "ctenacanth" spines (Maisey, in prep.), *Sphenacanthus* will be revised and Newberry's specimens will be illustrated and shown to be referable to that genus.

Having gone to these lengths to discredit Agassiz's (1837) observations, it is inexplicable that Newberry should then refer other finspines to *Ctenacanthus* in which the posterior wall is convex or ridged. In the same volume, Newberry (1873, p. 326; also 1889, p. 286) described a new species based on finspines, as *C. vetustus.* The type specimen, AMNH 351, is a well-preserved finspine lacking only its distal end. It has smooth lateral ribs, only the anterior ribs being pectinated (not, however, like the pectinations of *C. major,* but coarser and more irregular). However, a recent find suggests that the type specimen of *C. vetustus* is a posterior finspine and that the anterior one has beaded or coarsely pectinate lateral ribs (Hlavin, 1976). The ornamental pattern and shape in transverse section of *C. vetustus* finspines preclude it from the genus *Ctenacanthus*; a new genus has been proposed for this species (Hlavin, 1976), but it has yet to be described formally.

Other finspines were subsequently described by Newberry in which the posterior wall was also ridged or convex, and which were all referred to *Ctenacanthus.* These include *C. furcicarinatus* Newberry (1875, p. 54), *C. wrighti* Newberry (1884, p. 206; also 1889, p. 66), *C. gurleyi* Newberry (1897, p. 290), *C. compressus* Newberry (1878, p. 191), *C. randalli* Newberry (1889, p. 105), *C. clarkii* Newberry (1889, p. 168), *C. angustus* Newberry (1889, p. 181), and *C. littoni* Newberry (1889, p. 201). Previously *C. angulatus* had also been described (Newberry and Worthen, 1866, p. 118). Only some of these species are represented by finspines which closely resemble *C. major,* the type species of *Ctenacanthus,* in their detailed morphology and ornament pattern. These include *C. angulatus* (fig. 8C, D), *C. angustus, C. clarkii* (fig. 9H–L), *C. compressus* (fig. 9A–G), *C. littoni* (fig. 8A, B), and *C. randalli* (fig. 8E). Among those excluded from *Ctenacanthus* are "*Ctenacanthus*" *vetustus,* "*C.*" *furcicarinatus,* "*C.*" *wrighti* and "*C.*" *gurleyi.* "*Ctenacanthus*" *vetustus* has already been discussed, but it is worth mentioning here that its finspines have been found associated with "*Orodus*"-like teeth (Hlavin, 1976), which differ from the cladodont teeth of the only articulated *Ctenacanthus* recognized here, *C. compressus* (=*C. clarkii* of Dean, 1909, see below). "*Ctenacanthus*" *furcicarinatus* finspines have smooth ribbing, interrupted only by numerous transverse ridges similar to the non-pectinate ribs of "*C.*" *vetustus.* According to Newberry (1875, p. 54), "*C.*" *furcicarinatus* spines were associated with "*Orodus*"-like teeth, and partial skeletons (unfortunately never recovered) were reported by quarrymen. "*Ctenacanthus*" *wrighti* is based on the apical part of a remarkably straight finspine, which has an angular cross-section and ridged, straight ribs. "*Ctenacanthus*" *gurleyi* is excluded from *Ctenacanthus* because a holotype was never designated and Newberry (1897) did not figure it. However, Newberry's description fits that of a *Ctenacanthus* finspine. The large size and stratigraphic horizon (St. Louis "beds," Indiana) suggest that these *C. gurleyi* may be synonymous with *C. major.*

Barkas (1877) compared *Ctenacanthus* and *Hybodus* finspines in some detail, and noted many morphological similarities. However, these similarities are common to all primitive shark finspines, and his conclusions that *Ctenacanthus* is a synonym of *Hybodus* and that (p. 155) "we must therefore abolish the genus *Ctenacanthus* . . ." made on the basis of these similarities, cannot be upheld. Barkas (1877) was unaware of detailed but consistent differences in the morphological and ornamental patterns of *Hybodus* and *Ctenacanthus* finspines; moreover, subsequent discoveries of more complete fossils show that these genera possessed different types of teeth, scales, and other skeletal characters.

De Koninck (1878) described some fin-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spines from the lower Carboniferous of Belgium, including some large specimens which were referred to a new species, *C. maximus*. However, de Koninck admitted: "Elle a quelque resemblance avec le *C. tenuistriatus* Ag.," the main difference being the greater number of ribs in *C. maximus* finspines (probably a growth-related factor). Both *C. maximus* and *C. tenuistriatus* are probably synonymous with *C. major* (Woodward, 1891, p. 98). De Koninck's (1878, p. 67) comment that *C. furcicarinatus* of Newberry (1875) is a variety of *C. tenuistriatus* cannot be upheld, since as discussed above, *C. furcicarinatus* finspines have a different ornament pattern. De Koninck (1878, p. 65) maintained the view that "le côté postérieur est concave" in his diagnosis of *Ctenacanthus* finspines, in contradiction of his specimens.

Davis (1883) repeated McCoy's (1855) diagnosis of *Ctenacanthus*, commenting that: "The Agassizian conception of the genus *Ctenacanthus* has been enlarged by various authors so as to include a number of specimens, like *Ctenacanthus* (?) *distans* McCoy, which it is very probable pertained to quite a different type of fish. The inclusion of such species has also been made by some American paleontologists . . . . These specimens differ in no respect from some which have been described as *Leptacanthus* Ag. and *Acondylacanthus* St. J. & W., whilst they present great divergence from the Ctenacanthoid Type." He proposed removing such anomalous forms from *Ctenacanthus* and restricting the genus to Agassiz's parameters.

Although Davis's action was desirable, he countered progress by the substituting of other anomalous forms, e.g., finspines of *C. laevis, C. pustulatus, C. dubius, C. plicatus,* and *C. rectus,* many of which have extensive, smooth enameled ribbing and no trace of pectination, and all of which have a concave posterior wall. He was undoubtedly influenced by Agassiz's (1837) inclusion of *C. heterogyrus, C. sulcatus,* and *C. plicatus* (by name only), all of which are represented by heavily enameled, posteriorly concave finspines. Woodward (1891, p. 102) commented that *C. laevis* may pertain to another genus, *Acondylacanthus* (proposed by St. John and Worthen, 1875). However, this is unlikely in view of the differing ornamentation patterns and the shorter length of *C. laevis* finspines. The inclusion of smooth, enameled forms by Agassiz (1837), McCoy (1855) and Davis (1883) led Woodward (1891, p. 97) to publish a shorter, modified and now all-embracing diagnosis of *Ctenacanthus*: "Dorsal finspines robust, often attaining to a large size, laterally compressed; sides of exserted portion ornamented with longitudinal ridges, usually crenulated or denticulated, rarely smooth; posterior face flat or concave, with a series of small denticles upon each margin."

He drew attention to the association of similar finspines and teeth in *Ctenacanthus costellatus* Traquair (1884). Indeed, he had earlier (Woodward, 1889, p. 242) placed this species in *Sphenacanthus,* presumably on similarities of the dorsal finspines ("ornamented by robust longitudinal ridges, in part nodose . . . ." p. 241). Discovery of the *C. costellatus* specimen was important because it was the first record of a complete associated phalacanthous selachian skeleton from the Paleozoic. It has generally been regarded as a *Ctenacanthus* (Traquair, 1884; Brough, 1935; Moy-Thomas, 1936) although the finspines are not covered by dense pectinations and are concave posteriorly. Therefore, *C.*

←

FIG. 10. A–J, *Ctenacanthus venustus*. A–I, the type specimen, MCZ 5183. This has not been previously figured, although Eastman (1902, fig. 10) gave some line drawings of transverse sections. Another referred specimen (J) was illustrated instead (USNM 3385). (A), left side; (B), posterior view. (C–I), ornament details; (G), shows marginal denticles; position of details shown on (A & B). K, *C. nodocostatus* peel (AMNH 8026) of the type specimen (Buffalo Museum E2083), left side. L, *C. major,* Bristol City Museum, C4152, holotype; photo of specimen courtesy of Bristol City Museum.

costellatus is not referable to the genus *Ctenacanthus,* but may be allied to *Sphenacanthus* (Woodward, 1889; Maisey, in prep.).

In North America, the anterior half of an upper Devonian phalacanthous shark was referred to *C. clarkii* Newberry (1889) by Dean (1909). Another shark, *Goodrichthys eskdalensis,* was also considered to be a "ctenacanth" (Moy-Thomas, 1936; Moy-Thomas and Miles, 1971). These discoveries seemed to settle the question of which tooth type the "ctenacanths" possessed, for all three have supposedly "cladodont" teeth. *Goodrichthys eskdalensis* has smooth unornamented teeth and pectinated ribbing on its finspines. However, the extent of this ornamentation is greatly reduced in comparison with *Ctenacanthus major.* Apart from this difference, *Goodrichthys* finspines resemble those of *C. major,* and these fishes may therefore be closely related taxa.

The anterior dorsal finspine is preserved as an impression in Dean's (1909) specimen, AMNH 189, which was referred to *C. clarkii.* I have compared a peel from this impression with Newberry's (1889) type specimens of *C. clarkii* and *C. compressus,* and also with other specimens in both the American Museum and the Cleveland Museum of Natural History (fig. 9). There is sufficient variation among finspines referred to *C. clarkii* and *C. compressus* to suggest that both species are represented by anterior and posterior finspines. It seems to me that Dean's (1909) specimen should be referred to *C. compressus* rather than to *C. clarkii,* since its finspine is characteristically compressed in transverse section (fig. 9F, G). The base of this spine's ornamented region is very oblique to the main axis of the spine. Another finspine referred to *C. compressus,* AMNH 225 (fig. 9A, B) has a more transverse base to its ornamented region, as do two other spines in the Cleveland Museum, CMNH 6064 and 5395. The type specimen of *C. clarkii,* AMNH 220, is a finspine with a fairly transverse base to its ornament (fig. 9H). Other spines which may be referred to *C. clarkii,* such as CMNH 6140, have a more oblique ornament base. Thus similar variation in the lower limits of ornamentation in both *C. compressus* and *C. clarkii* is demonstrable. Comparison with articulated fossil sharks ("*C.*" *costellatus, Hybodus* spp.) suggests that this variation reflects the different angles that anterior and posterior finspines are inserted. The articulated specimen of *C. compressus,* AMNH 189, shows the more obliquely inserted condition of "*C.*" *costellatus* and *Hybodus* spp. finspines.

More importantly, however, in many respects both *C. clarkii* and *C. compressus* finspines agree closely with *C. major* in terms of ornamentation pattern and other morphological features. Therefore, whichever species is represented by Dean's (1909) specimen, it can be referred to *Ctenacanthus* with some confidence. Recent discovery of similar sharks from the Cleveland shale will, when described, provide an important contribution to our knowledge of *Ctenacanthus.* This in turn should provide more accurate limits as to what may be termed a "ctenacanth."

Eastman's (1902, 1907, 1908) analyses of *Ctenacanthus* are essentially biostratigraphic, but he also fitted his characters to some largely untestable preconceived notions about anterior and posterior finspines. *Ctenacanthus* was reduced to an almost undiagnosable state (Eastman, 1902): "It is customary to recognize *Ctenacanthus* as a distinct genus, for although the spines are indistinguishable from those of *Hybodus,* they are not associated with *Hybodus*-like teeth in the Devonian and Carboniferous, none having been found in rocks older than the Mesozoic." *Hybodus* and *Ctenacanthus* finspines are, in fact, readily distinguishable (for an account of hybodontid finspines see Maisey, 1978). Moreover, hybodontid finspines, teeth, and cephalic spines are now recorded from Permian and Carboniferous strata (Romer, 1942; Berman, 1970; Nielsen, 1932; Patterson, 1967; Zidek, 1969; Lund, 1970; Chorn and Conley, 1978). Eastman (1907) commented that *Ctenacanthus* finspines were probably common to more than one genus of shark. However, his reference to "spines indistinguishable from those of

this genus in *Cladoselache* . . ." is apparently based on misidentification of Dean's (1909) *Ctenacanthus* specimen as *Cladoselache*; spines of *Cladoselache* were unknown at that time.

Very little progress was made with "ctenacanth" sharks until recently. An image of some ancestral hybodont had crystallized, and "ctenacanths" took on a quite undeserved air of respectability. For example, Moy-Thomas (1939a, p. 6) wrote: "The Hybodontii . . . resemble the Ctenacanths . . . in the angles of the dorsal fin-spines and internal skeleton of the dorsal fins, the position of the anal fin, and the tribasal pectoral fin . . . there does seem to be no doubt that the hybodonts are descended from the ctenacanths, and the latter from the cladoselachians."

SYSTEMATIC REVISION OF *CTENACANTHUS*

Since the genus *Ctenacanthus* is founded on isolated fossil finspines, the diagnosis which follows is confined to features of these spines, even though at least one referred species is known from fairly complete material. The morphological and ornament pattern of *Ctenacanthus* finspines is unique and can be described on a phenetic basis. It must be emphasized that it is not yet possible to distinguish derived from primitive characters in my description.

GENUS *CTENACANTHUS* AGASSIZ, 1837

Elasmobranch dorsal finspines, gradually tapering and recurved posteriorly, anterior face narrow and rounded, lateral face slightly convex, posterior face with a pronounced proximal median ridge or convexity separated from the posterolateral margins by a flat or slightly concave area; apically the posterior ridge dies away; cross-section from two to three times as deep as broad; ornament of numerous closely spaced fine longitudinal ribs, some of which arise by primary bifurcation of a median rib anteriorly (although this rib is indistinguishable from others in terms of pattern of ornamentation), ribs closely pectinated with minute transverse tuberculations, each one somewhat variable in shape but often striated vertically, and projecting laterally from the raised ribs so there is a space beneath each tubercle; tubercles of adjacent costae almost touch and may interlock like teeth on a zipper; posterolateral margins ornamented apically by a row of low, posteriorly directed denticles, sometimes downcurved, but lacking any denticles more medially on the posterior face; spine trunk composed mainly of trabecular dentine but lacking any ordered vascularization other than a median canal anterior to the central cavity; inner lamellar layer usually only weakly developed.

Type Species: *Ctenacanthus major* Agassiz, 1837; lower Carboniferous Limestone, Avon Gorge section, Bristol; Bristol City Museum C4152.

SYNONYMS: *C. tenuistriatus* Agassiz; Agassiz, 1837, III, p. 11; *C. tenuistriatus* Ag.; de Koninck, 1878, p. 67; *C. maximus* de Koninck; de Koninck, 1878, p. 68; *C. tenuistriatus* Ag.; Davis, 1883, I, p. 334; *C. salopiensis* Davis; Davis, 1883, I, p. 339.

The following records are of fossils misidentified as *C. major*:

C. major Ag.; Thomson, 1869, p. 102 (*Sphenacanthus*, see Woodward, 1889, p. 242).
C. major Ag.; Newberry, 1873 (*Sphenacanthus*).
C. major Ag.; Trautschold, 1874a, 1874b (cephalopod, see Khabakob, 1928, p. 31).

REFERRED TAXA:

(i) Species which may be synonymous with *C. major*:

C. varians St. John and Worthen, 1875, p. 422 (syn. *C. speciosus* St. John and Worthen, 1875, p. 424; see Eastman, 1902).
C. varians St. John and Worthen, var. *russakovi* Khabakob, 1928, p. 26.
C. spectabilis St. John and Worthen, 1875, p. 420 (see also Eastman, 1902, p. 87).
C. harrisoni St. John and Worthen, 1883, p. 236.
C. deflexus St. John and Worthen, 1883, p. 234.

(ii) Other referred species:

C. angulatus Newberry and Worthen, 1866, p. 118.

C. angustus Newberry, 1889, p. 181 (see also Hussakof, 1908, p. 45).
C. clarkii Newberry, 1889, p. 168 (see also Hussakof, 1908, p. 45; Dean, 1909, p. 249).
C. cliftonensis Branson et al., 1938, p. 122.
C. compressus Newberry, 1878, p. 191.
C. denticulatus McCoy, 1848, p. 116 (see also McCoy, 1855, p. 625; Davis, 1883, p. 338; Woodward, 1891, p. 100).
C. littoni Newberry, 1889, p. 201 (see also Hussakof, 1908, p. 45).
C. nodocostatus Hussakof and Bryant, 1918, p. 159.
C. randalli Newberry, 1889, p. 105 (see also Eastman, 1907a, p. 77; 1907b, p. 154; Hussakof, 1908, p. 46).
C. venustus Eastman, 1902, p. 81.

CONCLUSIONS

The type specimen of *Ctenacanthus major,* Bristol City Museum C4152, must be regarded as the type of *Ctenacanthus* Agassiz (1837). Of Agassiz's other species, only *C. tenuistriatus* has finspines like those of *C. major. Ctenacanthus brevis* is excluded on the grounds that its ornamentation pattern differs profoundly from that of the type species, and its shape is also different. *Ctenacanthus ornatus* is also excluded since the holotype is very fragmentary and there is some evidence of acanthodian affinities (Pageau, 1969). "*Onchus*" *sulcatus* and *C. heterogyrus* are excluded since they are based on finspines with smooth, enameled ribs and a concave posterior wall, as do some other species later described by Davis (1883).

Ctenacanthus brevis is represented by stout, thick-walled finspines, with a high level of posterior closure and coarse, tuberculate ornament. It closely resembles some other species in these respects, e.g., *C. ianishevskyi* Khabakob (1928, p. 23), *C. lucasi* Eastman (1902, p. 80), and *C. solidus* (*ibid.,* p. 90). It is also similar to *Bythiacanthus vanhornei* St. John and Worthen (1875, p. 445), *B. siderius* (Leidy, 1873, p. 313) and to *Glymmatacanthus* spp., e.g., St. John and Worthen (1875, p. 447; 1883, pp. 249–250). The latter genus is, however, extremely ill-defined and founded on fragments of tuberculated dermal armor which may not be from elasmobranchs.

Several Mississippian species are based on finspines with extensive enameled ornament and a concave posterior wall, including *C. heterogyrus, C. sulcatus, C. plicatus, C. laevis, C. pustulatus, C. dubius,* and *C. rectus.* In these respects these spines resemble those of Recent squaloids and heterodontids, and those of the Liassic *Palaeospinax* and Triassic *Nemacanthus.*

I have argued above that few "*Ctenacanthus*" finspines described in the past are actually referable to Agassiz's (1837) genus. Some of the more highly enameled spines may pertain to sharks with neoselachian affinity. Other spines are notably like those of Mesozoic hybodontids, e.g., *C. vetustus, C. furcicarinatus.* Thus without even a lengthy discussion of innumerable finspines, it is possible to identify, within the species referred to *Ctenacanthus,* forms which are referable (however tentatively) to neoselachians or to hybodontids. At present there is insufficient data to test such relationships. Future studies may reveal which of these finspine characters are important as synapomorphies with other taxa.

ACKNOWLEDGMENTS

I particularly thank Ms. Lorraine Meeker and Mr. Chester Tarka for producing the excellent composite figures, often from rather indifferent original plates or specimens. The work involved in their construction was considerable, since the originals were frequently not scaled correctly and were misleading.

The following have also provided me with access to specimens or have supplied useful information; S. M. Andrews (Royal Scottish Museum, Edinburgh), M. D. Crane (Bristol Museum), J. Dick (University of Newcastle-upon-Tyne), C. L. Forbes (Sedgwick Museum, Cambridge), N. Hotton (National Museum of Natural History, Smithsonian Institution), P. Janvier (Université Paris), C. Patterson (British Museum, Natural History), P. Sartenaer (Institut Royal des Sciences Naturelles de Belgique), C. Schaff (Museum of Comparative Zoology, Harvard University), K. S. Thomson (Yale University), and

M. Williams (Cleveland Museum of Natural History). I also thank Drs. Donn Rosen, Bobb Schaeffer, and Michael Williams for their comments on the manuscript.

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