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Studies on the Paleozoic Selachian Genus *Ctenacanthus* Agassiz: No. 2. *Bythiacanthus* St. John and Worthen, *Amelacanthus,* New Genus, *Eunemacanthus* St. John and Worthen, *Sphenacanthus* Agassiz, and *Wodnika* Münster

JOHN G. MAISEY[1]

ABSTRACT

Some of the finspines originally referred to *Ctenacanthus* are reassigned to other taxa. Several characteristically tuberculate lower Carboniferous finspines are referred to *Bythiacanthus* St. John and Worthen, including one of Agassiz's original species, *Ctenacanthus brevis*. Finspines referable to *Bythiacanthus* are known from western Europe, the U.S.S.R., and North America. *Amelacanthus,* new genus, is described on the basis of finspines from the United Kingdom. Four species are recognized, two of which were originally assigned to *Onchus* by Agassiz, and all four of which were referred to *Ctenacanthus* by Davis. *Eunemacanthus* St. John and Worthen is revised to include some European and North American species. *Sphenacanthus* Agassiz is shown to be a distinct taxon from *Ctenacanthus* Agassiz, on the basis of finspine morphology, and its widespread occurrence in the Carboniferous of North America is demonstrated. Similarities are noted between the finspines of *Sphenacanthus* and *Wodnika,* and both taxa are placed provisionally in the family Sphenacanthidae. A new species of *Wodnika, W. borealis,* is recognized on the basis of a finspine from the Permian of Alaska.

INTRODUCTION

The present paper is the second in a series of reviews of the Paleozoic chondrichthyan *Ctenacanthus*. The first paper (Maisey, 1981) reexamined Agassiz's (1837) genus *Ctenacanthus* in an attempt to restrict this taxon to sharks with finspines that closely resemble those of the type species, *C. major*. Agassiz (1837) described some other

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spines which were referred to *Ctenacanthus*, although their morphology and ornament patterns differ greatly from those of *C. major*. Only one of Agassiz's (1837) other *Ctenacanthus* species, *C. tenuistriatus*, is left in that genus by Maisey (1981). However, various spines have been referred to *Ctenacanthus* by previous authors, with the result that the genus had become reduced to an almost undiagnosable state; in particular, *Sphenacanthus* has been greatly confused with *Ctenacanthus*. The present work therefore reviews finspines that were included in *Ctenacanthus* by Agassiz (1837) but were excluded by Maisey (1981), and also includes a review of the genus *Sphenacanthus*.

ACKNOWLEDGMENTS

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BYTHIACANTHUS ST. JOHN AND WORTHEN

HISTORICAL NOTE: The type species of *Ctenacanthus* (Agassiz, 1837) is *C. major*. The second species he described, *C. brevis*, is based on a dorsal finspine which is very different from that of *C. major* in shape and ornamentation. Instead of being long and slender, the spine of *C. brevis* is squat and broad, and is ornamented by large round, striated tubercles arranged in closely spaced series down the spine, instead of the fine pectinated ribs seen on *C. major* spines. Since the spines of *C. brevis* and *C. major* are so different, retaining *C. brevis* in the genus *Ctenacanthus* is unjustified. Recent squaloid and heterodontid finspine morphology and ornamentation does not vary below generic level. This is apparently also true of hybodont finspines (Maisey, 1978).

Agassiz (1837) never saw the finspine on which his description of *C. brevis* was based before its publication, although it is known which specimen this was and it can still be located (see below and fig. 2B, C). He knew the specimen only from a drawing sent by the Reverend William Buckland, his colleague.

Finspines similar to those in *C. brevis* were later described from North America and referred to a new genus, *Bythiacanthus* St. John and Worthen (1875). Comparison of the original descriptions with other finspines referred to *Bythiacanthus* in the American Museum of Natural History suggest that Agassiz's (1837) *C. brevis* should provisionally be referred to *Bythiacanthus*.

AMENDED DIAGNOSIS: Elasmobranch recognized by having dorsal finspines of stout build, rhomboidal outline in lateral view; thick walls of trabecular osteodentine; anterior face rounded, strongly to moderately compressed laterally, posterior wall convex, level of posterior closure very high and the posterior wall correspondingly short; in transverse section the trunk wall much thickened anteriorly; ornament of longitudinal rows of rounded, striated tubercles, usually

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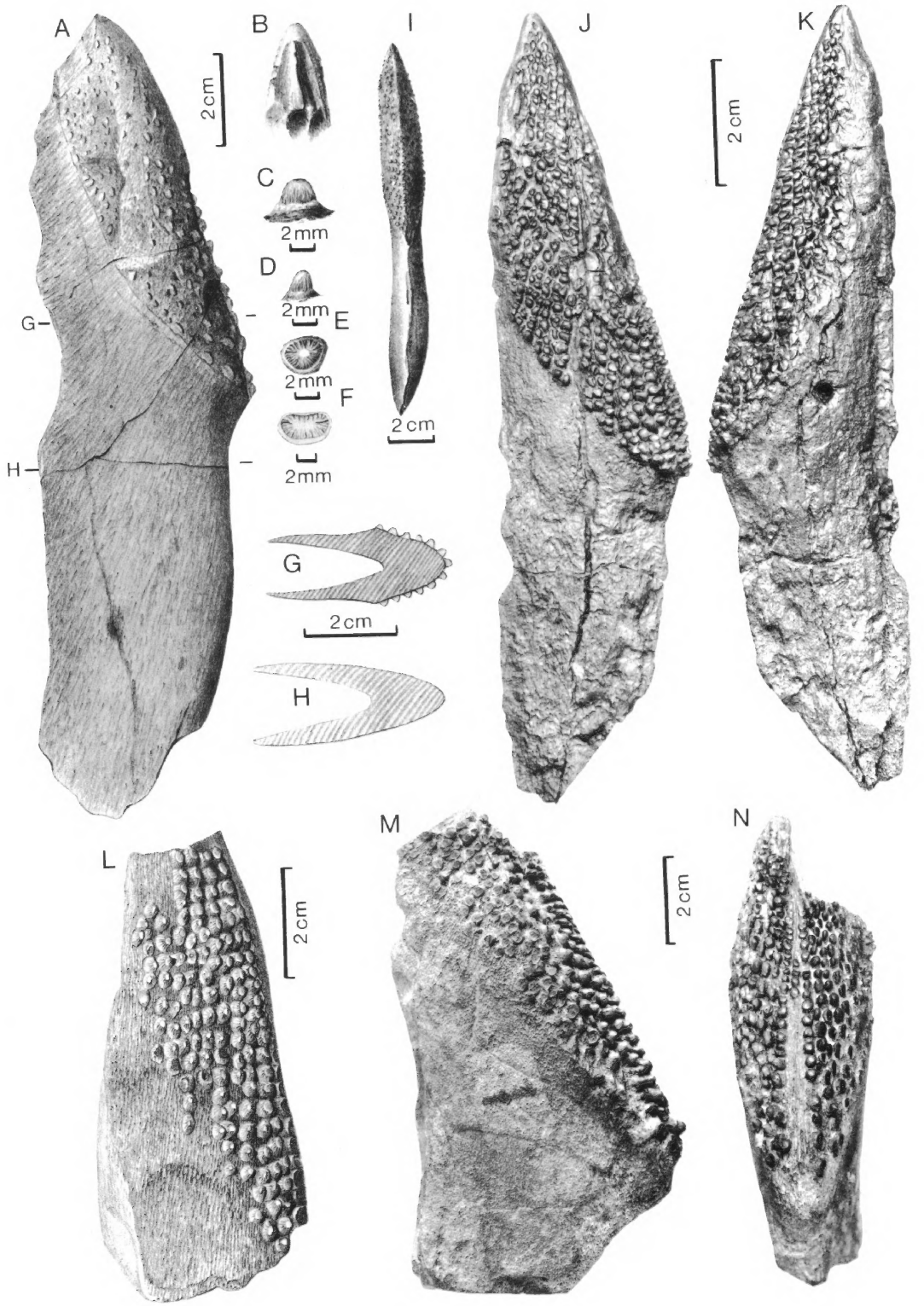
FIG. 1. A–I, *Bythiacanthus vanhornei*; holotype, from St. John and Worthen (1875) pl. 17, no. 1. J–L, *Bythiacanthus siderius* (Leidy); J–K, AMNH 1826, St. Louis Limestone, Alton, Illinois; L, the holotype PAN S 22:17 7835, "Sub-Carboniferous," Glasgow, Tennessee; from Leidy (1873) pl. 32, no. 59.

M–N, *Bythiacanthus* off. *ianishevskyi* AMNH 9594 (reversed to facilitate comparison with other specimens); Waverly sandstone, ?Marion Co., Kentucky.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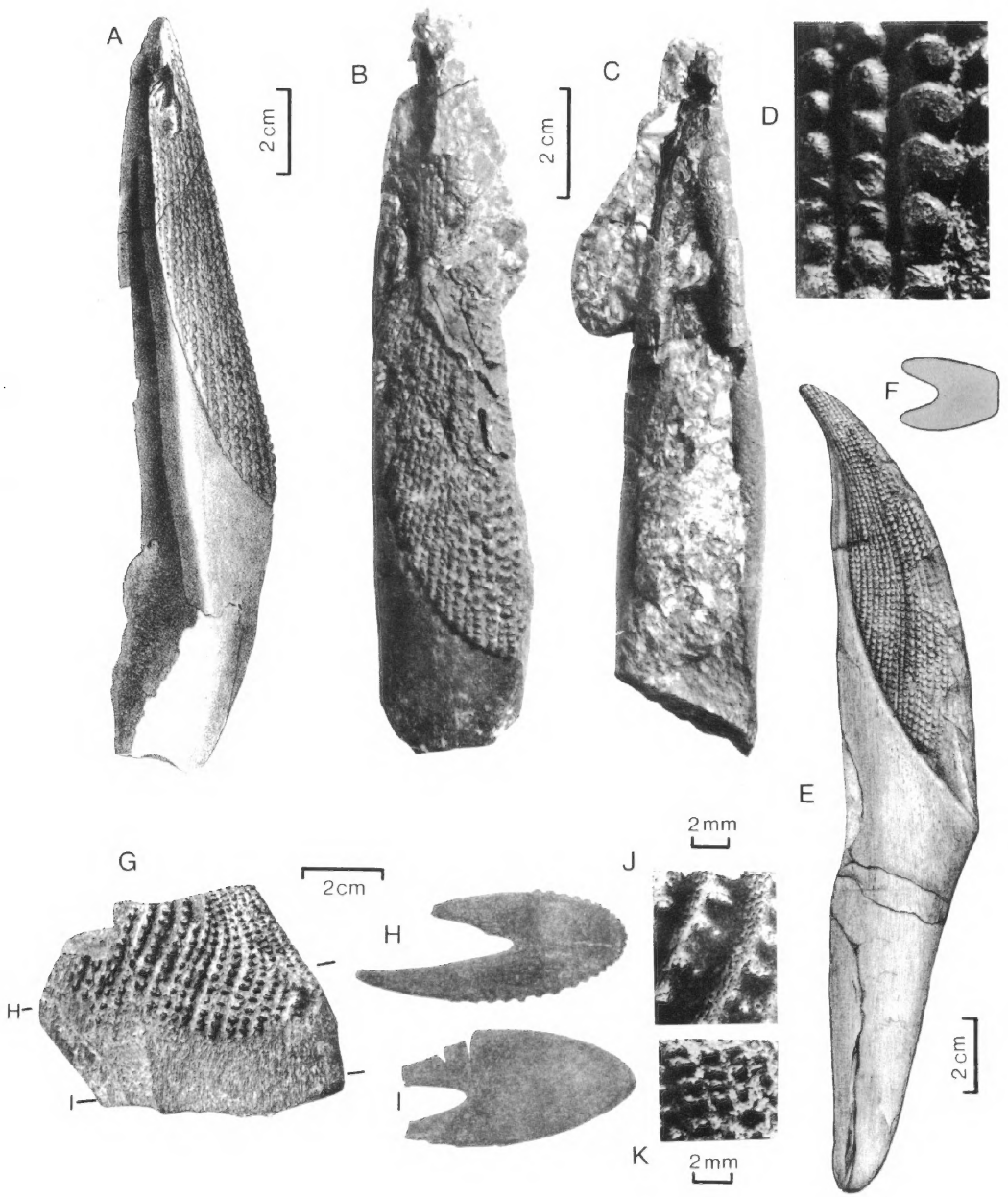

FIG. 2. A–F, *Bythiacanthus brevis* (Agassiz); A, from Agassiz (1837) tab. 2, no. 2; B, C, the holotype C 4154 (photographs courtesy of Bristol City Museum and Art Gallery, England). Compare with A which was originally copied from Buckland's drawing of this specimen; D, detail of ornament from another specimen, BM(NH) P2226; E, F, from Davis (1883) pl. XLIII, no. 3; this appears to be specimen BM(NH) P2226.

G–K, *Bythiacanthus ianishevskyi* (Khabakob); from Khabakob (1926) pl. III, nos. 5–10.

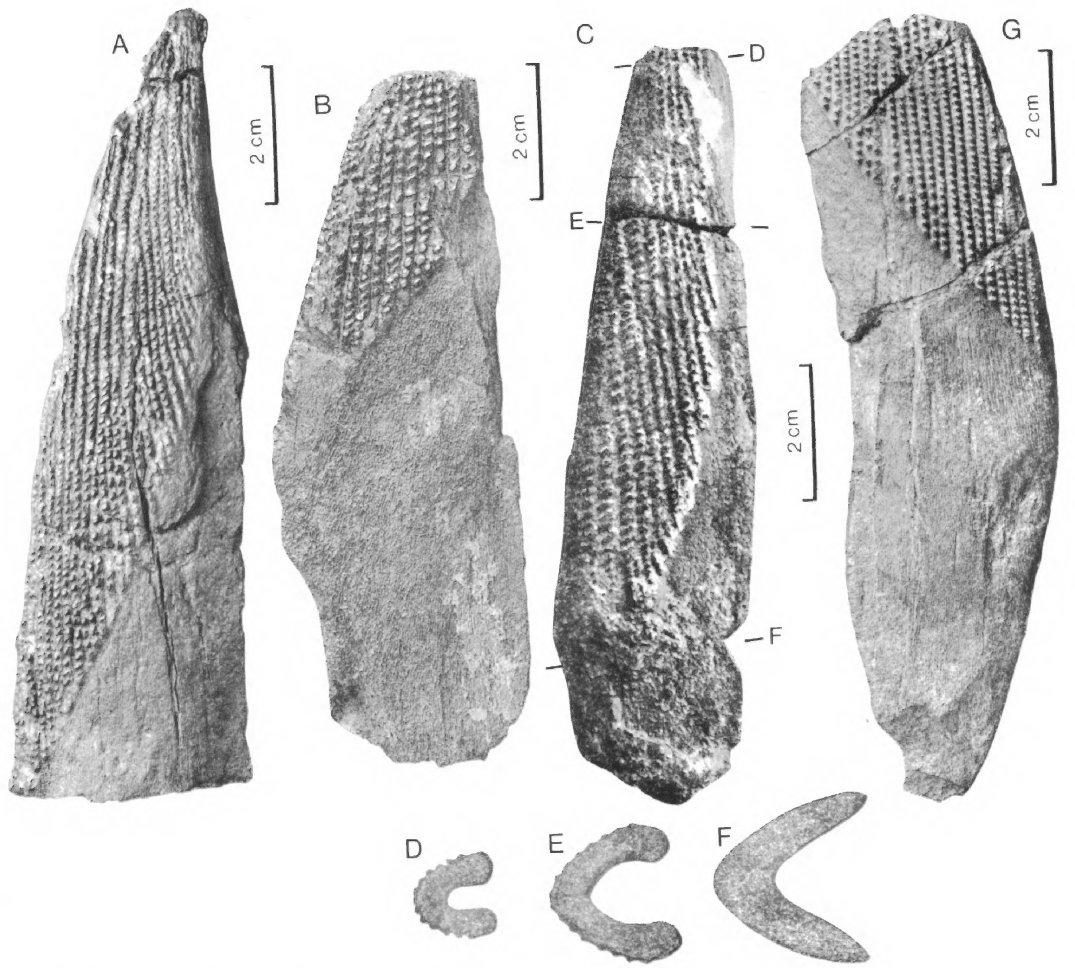

FIG. 3. A, B, *Bythiacanthus solidus* (Eastman); A, the holotype, USNM 3383; B, paratype, from Eastman (1903) pl. 7, no. 3.

C–F, *Bythiacanthus peregrinus* (Khabakob); from Khabakob (1928) pl. III, nos. 1–4.

G, *Bythiacanthus lucasi* (Eastman); from Eastman (1902) pl. 6, no. 1.

less than their own diameter apart; rows increased proximally by primary bifurcation anteriorly and by being inserted between other rows marginally.

TYPE SPECIES: *Bythiacanthus vanhornei* St. John and Worthen, 1875, p. 445, St. Louis Limestone, Alton, Illinois.

REFERRED SPECIES: *Ctenacanthus brevis* Agassiz, 1837, p. II; *C. ianishevskyi* Khabakob, 1928, p. 23; *C. lucasi* Eastman, 1902, p. 80; *C. peregrinus* Khabakob, 1928, p. 25; *Asteracanthus siderius* Leidy, 1873, p. 313; *C. solidus* Eastman, 1902, p. 90; *Incertae sedis,* aff. *Bythiacanthus*; *Glymmatacanthus irishii* St. John and Worthen, 1875, p. 447; *G. rudis* St. John and Worthen, 1883, p. 249; *G. petrodoides* St. John and Worthen, 1883, p. 250.

DISCUSSION: Leidy (1873, p. 313) referred a coarsely tuberculated finspine, PAN S 22:13 7835, from the "Sub-Carboniferous" of Glasgow, Tennessee, to a new species,

Asteracanthus siderius. Apart from the presence of tubercles, however, there is nothing to suggest that this spine is referable to *Asteracanthus,* which is otherwise a Mesozoic taxon and which has distinctive hybodontid finspines (Maisey, 1978). Leidy's (1873) specimen of a spine resembles that of *Bythiacanthus vanhornei,* described by St. John and Worthen (1875, p. 445), who suggested that these spines might belong to the same species. Another almost complete finspine, AMNH 1826, closely resembles Leidy's (1873) specimen, and is referred to *Bythiacanthus siderius*. Finspines referred to this taxon are more densely covered by tubercles than those in *B. vanhornei.* Because of the differences in their tubercle arrangement and density, I disagree with St. John and Worthen's (1875) suggestion that these species are synonymous (fig. 1A–L).

Agassiz's (1837) figure of "*Ctenacanthus*" *brevis* is reproduced here (fig. 2A), along with illustrations of the actual specimen (fig. 2B, C). This represents the first time that the type specimen has been properly figured. The coarsely tuberculate ornament is shown in detail (fig. 2D). It agrees closely with that of *Bythiacanthus* finspines. In transverse section, *B. siderius* and *B. vanhornei* finspines are laterally compressed, whereas those of *B. brevis* are rounded and little compressed. All these finspines have an extremely high level of posterior closure, so that the posterior opening is very long and the complete posterior wall is short. In all cases the posterior wall is convex. *Bythiacanthus brevis* finspines are stout, thick walled, and strongly recurved toward the tip.

Tubercles on these spines are arranged in rows which increase in number proximally by two methods; bifurcation of new rows from a primary row anteriorly; and marginal introduction of new rows posterolaterally (cf. *Sphenacanthus* marginal rib insertion pattern described below).

Bythiacanthus vanhornei and *B. siderius* finspines are laterally compressed, but are very deep anteroposteriorly. This is evident in transverse sections (e.g., fig. 1G, H). Other finspines with similar ornamentation but relatively even deeper cross-sections are also known.

Bythiacanthus solidus (Eastman, 1902, p. 90) is based on finspines USNM 3383 (the holotype) and USNM 4833 (paratype). Eastman's (1902, fig. 13) transverse section is taken near the base of the type finspine, but does not indicate the full depth of the spine anteroposteriorly. Eastman (1902, pl. 2, fig. 3) did not otherwise figure the type specimen, which is illustrated here (fig. 3A). The ornament of the holotype is slightly less pronounced than that of the paratype (fig. 3B), and is similar to the ornament of *B. lucasi,* also described by Eastman (1902, p. 80, pl. 6, fig. 1, also text-fig. 9). The ornamentation of *B. solidus,* however, is less regular than that of *B. lucasi* (fig. 3G). A primary row of tubercles is present anteriorly on finspines of both species. Both are provisionally referred to *Bythiacanthus* although their ornamentation is more regular than in the type species, *B. vanhornei.*

Bythiacanthus ianishevskyi (Khabakob, 1928, p. 23) is also founded on a fragmentary finspine with coarse, tuberculate ornament and an extremely deep anteroposterior dimension in transverse section (fig. 2G–K). Another finspine of equally peculiar shape is AMNH 9594, apparently from the Waverly Sandstone of Marion Co., Kentucky (fig. 1M, N). This spine is referred to *Bythiacanthus* and is probably close to *B. ianishevskyi.*

Bythiacanthus peregrinus (Khabakob, 1928, p. 25) is provisionally included here because of similarities in the finspine ornamentation in *B. brevis, B. solidus,* and *B. lucasi.* In transverse section *B. peregrinus* finspines resemble those of *B. brevis* quite closely, and these species may eventually prove to be synonymous. Khabakob's (1928) illustrations are shown in figure 3C–F.

The type species of *Glymmatacanthus, G. irishii,* is based on a fragmentary finspine, USNM 13537. Its flattened shape in transverse section, and ornamentation pattern are reminiscent of *Bythiacanthus* (fig. 4D–G). Another species also founded on a similar fragment of spine, is *G. rudis* (fig. 4A–C). *Bythiacanthus* and *Glymmatacanthus* are

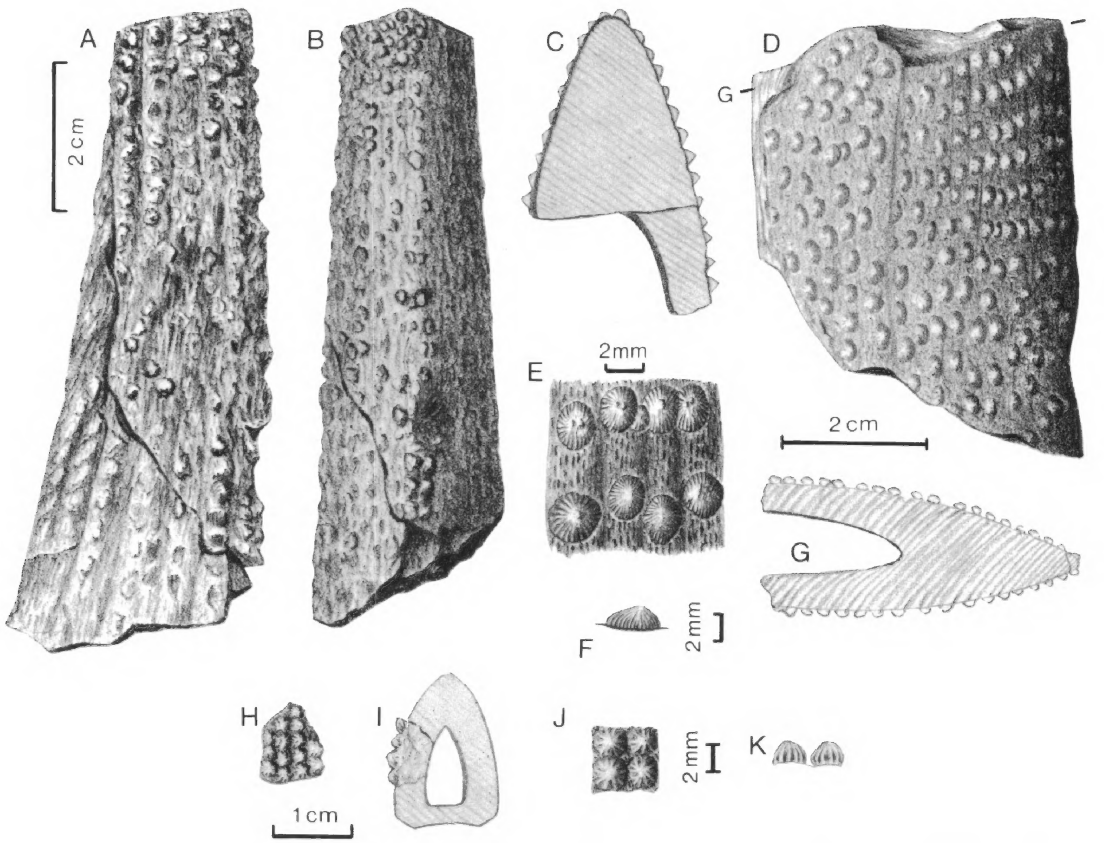

FIG. 4. A–C, *Glymmatacanthus rudis*; from St. John, Worthen and Miller (1883) pl. XXV, no. 1; section C is diagrammatic and cannot be located accurately on original specimen USNM 13504.

D–G, *Glymmatacanthus irishii*; from St. John, Worthen and Miller (1875) pl. 17, no. 2; specimen now USNM 13537.

H–K, *Glymmatacanthus petrodoides*; from St. John, Worthen and Miller (1883) pl. XXV, no. 2.

provisionally retained as separate taxa, but may prove to be synonymous. Some species, such as *G. petrodoides* St. John and Worthen (1883, p. 250) are based on very fragmentary material about which little can be said (fig. 4H–K).

ARTICULATED OR ASSOCIATED REMAINS

None of the finspines discussed here has been described from associated or articulated remains. Therefore, the relationships of taxa based on these remains are highly speculative. An as yet undescribed shark, FMNH PF 8170, from the Mecca Shales (Pennsylvanian) of Indiana, however, has coarsely tuberculate finspines which may ally it to *Bythiacanthus*. There is some similarity between *Bythiacanthus* finspines and those of *Goodrichthys eskdalensis* (Moy-Thomas, 1936, pl. II). Both have an extremely high level of posterior closure, and a relatively short ornamented region. Whether these similarities are of systematic significance is unknown.

AMELACANTHUS, NEW GENUS *EUNEMACANTHUS* ST. JOHN AND WORTHEN

HISTORICAL NOTE: *Amelacanthus*, new genus, is defined on the basis of finspines. Four species from the British lower Carbon-

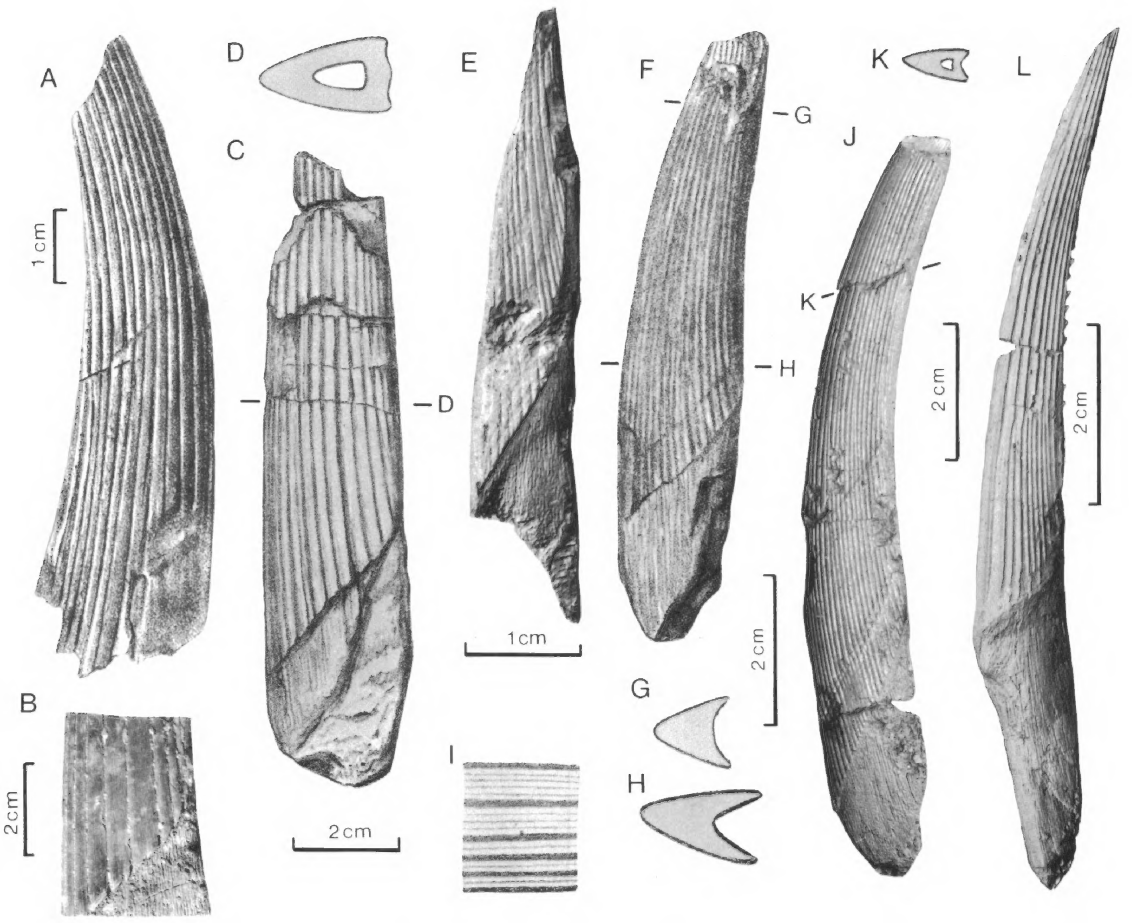

FIG. 5. A–E, *Amelacanthus sulcatus* (Agassiz); A, from Agassiz (1837) tab. 1, no. 6; B, detail of ornament from BM(NH) P2670; C, D, from Davis (1883) pl. XLV, no. 3; specimen now BM(NH) P2670; E, from peel of BM(NH) P2871.

F–I, *Amelacanthus plicatus* (Davis); from Davis (1883) pl. XLV, no. 4.

J, K, *Amelacanthus laevis* (Davis); from peel of BM(NH) P2531.

L, *Amelacanthus pustulatus* (Davis); from peel of BM(NH) P2529, reversed to facilitate comparison with other specimens.

iferous are recognized, two of which were originally referred to *Onchus* (Agassiz, 1837), and all four of which were referred to *Ctenacanthus* by Davis (1883). These species are readily distinguished from *Ctenacanthus major* by the extensive shiny enameled layer over much of the smooth finspine ornament.

The genus *Eunemacanthus* is based on a finspine which was originally referred by Newberry and Worthen (1866) to *Ctenacanthus,* but which was subsequently removed to the new genus (St. John and Worthen, 1883). Agassiz (1837) listed *C. heterogyrus* finspines but these were only later described and figured (McCoy, 1855). This species is probably referable to *Eunemacanthus* on the basis of its finspine morphology (see below).

AMELACANTHUS, NEW GENUS

DIAGNOSIS: Elasmobranch recognized by slender, slightly recurved finspines; anterior

margin acute but rounded; sides divergent posteriorly but almost flat, giving a subtriangular outline in section; posterior wall concave or flat, rarely with a low rise mesially; ornament of broad, smooth costae (ribs) with narrow intercostal grooves; costae heavily enameled and usually displaying growth lines; primary bifurcation of costae occurs at the anterior margin, but a distinct anterior rib may be absent; posterolateral margins armed apically by small, usually downcurved and rounded or pointed denticles.

TYPE SPECIES: *Onchus sulcatus* Agassiz, 1837, vol. 3, p. 8, pl. 1, fig. 6; *Onchus sulcatus* Agassiz; Agassiz, 1837, p. 8; *Ctenacanthus sulcatus* (Ag); Davis, 1883, p. 343; *C. sulcatus* (Ag); Woodward, 1891, p. 101.

TYPE: Bristol Museum C4154 lower Carboniferous Limestone; Gloucestershire, Shropshire, and Armagh.

REFERRED SPECIES: *C. plicatus* (Agassiz, 1837); *C. laevis* Davis, 1883, p. 341; *C. pustulatus* Davis, 1883, p. 344.

DISCUSSION: The finspines referred here to *Amelacanthus* differ profoundly from those of *Ctenacanthus* in their ornamentation. Instead of numerous pectinated or transversely tuberculated ribs (typical of *Ctenacanthus*) the finspines of *Amelacanthus* are ornamented by broad, smooth costae separated by narrow intercostal grooves. The costae are surfaced by a shiny, thick outer enameloid layer. Agassiz (1837) did not refer any of these finspines to *Ctenacanthus*. This was not because of the differences in their ribbed ornamentation, however, but because he thought these spines lacked posterolateral denticles. Two species were referred to *Onchus*; *O. sulcatus* and *O. plicatus* (the latter by name only). Davis (1883, p. 343) mentioned that Agassiz subsequently received a finspine of *O. sulcatus* in which marginal denticles were present, and Davis also confirmed the presence of these denticles on finspines of this and the other species. On the strength of this discovery, Davis (1883) referred *O. sulcatus* and *O. plicatus* to *Ctenacanthus*. The possibility that posterolateral marginal denticles might be useless as a generic character does not seem to have been considered. Two other species, *C. laevis* and *C. pustulatus*, were also recognized on the basis of enameled finspines similar to those of *O. sulcatus* and *O. plicatus*. All these species are referred here to *Amelacanthus*, new genus.

The principal differences between the finspines referred here to *Amelacanthus* are the number and breadth of costae and the angles at which the lateral faces of the spines diverge. In *Amelacanthus sulcatus* the finspines have about 15 costae per side, with a somewhat broader anterior rib from which three or four lateral ribs arise by primary bifurcation (fig. 5A–E). Finspines of *A. sulcatus* are about twice as deep as broad in transverse section (Davis, 1883, fig. 3A). The lateral faces diverge from the leading edge of the finspine at approximately 30 degrees (fig. 5D). Finspines referred to *A. laevis* are similar to those of *A. sulcatus* in transverse section (fig. 5K), and the anteriormost lateral costae arise by primary bifurcation from the anterior rib, but there are more ribs (approximately 24 per side). The posteriormost ribs are continuous down to the ornament base in *A. laevis* finspines (fig. 5J). In *A. sulcatus*, however, the posteriormost one or two ribs terminate at the posterolateral margins above the ornament base (marginal offlap of ribs; fig. 5C). Finspines of *A. sulcatus* and *A. laevis* are of similar size and the differences noted are probably not growth related; different taxa are undoubtedly represented.

Finspines of *Amelacanthus plicatus* are somewhat broader posteriorly than those of *A. sulcatus* and *A. laevis*, and in transverse section have the form of an equilateral triangle (fig. 5F–I). A distinct anterior (primary) rib is absent. Lateral ribs increase in number basally by bifurcation rather than by intercalation of new ribs. As a result of this, the anterior margin is "formed by the repeated inosculation of the lateral ridges" (Davis, 1883, p. 342). In other respects *A. plicatus* finspines resemble those of *A. sulcatus* and *A. laevis*, and are most like *A. laevis* finspines in having about 20 costae per side proximally and half that number distally.

Finspines referred to a fourth species, *Amelacanthus pustulatus*, are distinguished

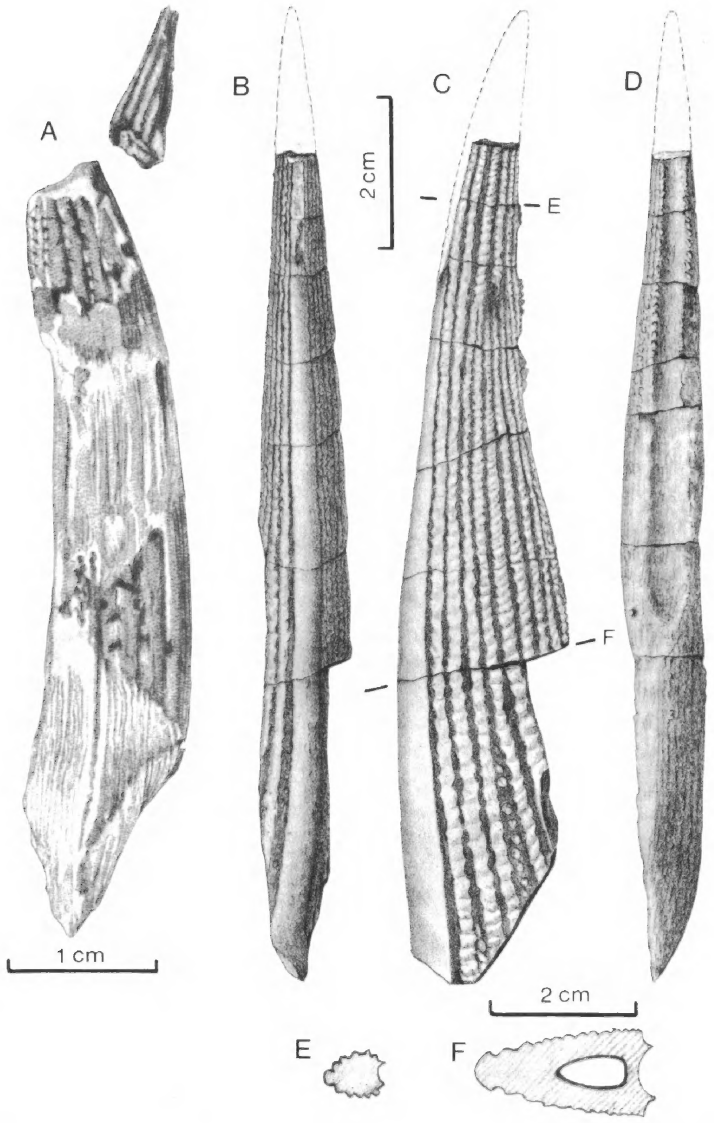

FIG. 6. A–F, *Eunemacanthus costatus* (Newberry and Worthen); A, from Newberry and Worthen (1866) pl. XII, no. 5; B–F, from St. John, Worthen and Miller (1883) pl. XXIII, no. 2.

from the others by its ribs, which are narrower than the intercostal grooves (fig. 5L). About nine or ten ribs are present on each side, their number increasing proximally by lateral intercalation and anterior primary bifurcation. Between some of the more anterior ribs are a few discrete enameled tubercles. Posterolateral (marginal) denticles are present on finspines of *A. sulcatus, A. plicatus,* and *A. pustulatus*. These denticles are unusual in *A. pustulatus* in being directed upward, rather than downward as in most Paleozoic shark finspines.

EUNEMACANTHUS
ST. JOHN AND WORTHEN

AMENDED DIAGNOSIS: Elasmobranch recognized by stout, elongate and laterally compressed finspines; anterior margin broad, oc-

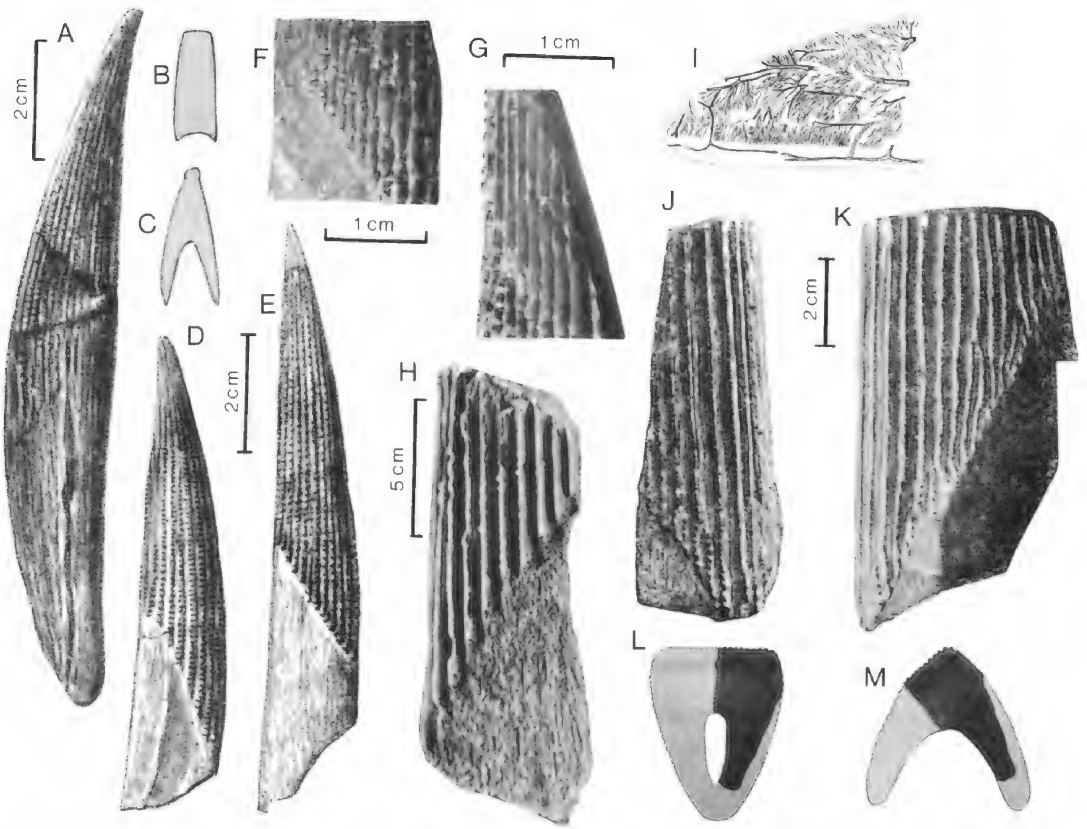

FIG. 7. A–I, *Eunemacanthus heterogyrus* (McCoy); A–E, from Davis (1883) pl. XLIV, nos. 1–3; F, G, details of ornament from BM(NH) P2228; H [Royal Mus., Bruxelles] P1321; I, sagittal section through apex of BM(NH) 2528 to show heavy abrasion of dentine.

J–M, *Eunemacanthus? venator* (Khabakob); J–L from Khabakob (1928) pl. IV, nos. 1–3; M, alternative restoration of section, avoiding need for ribs on posterior wall (cf. L).

cupied by a wide, enameled rib; sides nearly flat, but with a slight convexity; posterior surface concave; ornamentation of thick, irregular enameled ribs interrupted by transverse ridges, sometimes discontinuous; intercostal areas sometimes occupied by irregularly dispersed tubercles or short lengths of ribbing; primary bifurcation occurs anteriorly; marginal denticles occur apically.

TYPE SPECIES: *Ctenacanthus costatus* Newberry and Worthen, 1866, p. 120, pl. XII, fig. 5; Carboniferous, St. Louis Limestone, Alton, Illinois; *Ctenacanthus costatus* Newberry and Worthen, 1866, p. 120; *Ctenacanthus excavatus* St. John and Worthen, 1875, p. 428; *Eunemacanthus costatus* (Newberry and Worthen); St. John and Worthen, 1883, p. 246.

REFERRED SPECIES: *Ctenacanthus heterogyrus,* McCoy, 1855, p. 625 (syn. *C. dubius* Davis, 1883, p. 340; see Woodward, 1891, p. 101); *Eunemacanthus keyti* Branson, 1916, p. 655; *Ctenacanthus venator* Khabakob, 1928, p. 28.

DISCUSSION: Although Newberry and Worthen's (1866) species was designated the type of *Eunemacanthus* by St. John and Worthen (1883), it is predated by *Ctenacanthus heterogyrus* which is similar in many respects. This species was named by Agassiz (1837, p. 177), but was only later described (McCoy, 1855, p. 625). *Eunemacanthus heterogyrus* finspines seem sufficiently distinct

from *E. costatus* to continue separating them specifically.

Eunemacanthus costatus finspines are moderately recurved posteriorly, taper fairly rapidly, and have a wedge-shaped transverse section (fig. 6). The anterior rib is particularly broad, being almost semicircular in section, and the spine therefore has a blunt leading edge. St. John and Worthen's (1883) description of the ornamentation is clear and is not repeated here.

Eunemacanthus heterogyrus finspines are similarly shaped as those in *E. costatus,* but in many specimens the appearance of a broad leading edge is further exaggerated by remarkably heavy abrasion (fig. 7A–I). The ribs are somewhat less crenulated than in the type specimen, although this is not apparent from published figures. In fact, there is considerable variation in the ornamentation that has been illustrated. In McCoy (1855, pl. III, fig. 32), rather beaded or crenulated ribs are indicated, whereas they are depicted (somewhat diagrammatically) as straight bars by De Koninck (1878, pl. VI, fig. 3; cf. fig. 7H here). Davis (1883, pl. XLIV, figs. 1–3) illustrates strongly pectinate finspines, with fairly regular ribbing. Finspines of *E. heterogyrus* in the British Museum (Natural History) are much more irregularly ornamented (fig. 7F, G). Irregular tubercles and short costae are much more common in *E. heterogyrus* than in *E. costatus*. The marginal denticles also differ, the finspines of *E. costatus* being recurved upward slightly, and those of *E. heterogyrus* being more rounded.

An inner layer of nontrabecular dentine completely fills the finspine central cavity apically in *E. heterogyrus,* perhaps to counter the effects of heavy in vivo apical abrasion; a longitudinal section illustrates how extensive both the abrasion and the secondary dentine are (fig. 7I). *Eunemacanthus costatus* has not been sectioned, and it is not known whether a comparable plug of dentine is developed.

Eunemacanthus keyti is founded on a tiny scrap of finspine (Branson, 1916, p. 655, pl. IV, fig. 1, text-fig. 1), and is here included with misgivings since the posterior wall is convex rather than concave (possibly a result of crushing), although the irregular, enameled ribs are similar to *E. costatus*.

Ctenacanthus excavatus St. John and Worthen (1875, p. 428) is based on fragments from the tips of finspines, probably *E. costatus*. The fewer number of ribs is probably growth related (see Maisey, 1975, 1978).

Ctenacanthus dubius Davis (1883, p. 340) similarly can be regarded as an *E. heterogyrus* finspine at an earlier state of development.

Ctenacanthus venator Khabakob (1928, p. 28) is known only by a fragment from the midregion of a finspine (fig. 7J–M). The ornamentation is said to be "smooth-ribbed," but whether it is enameled or not is not mentioned. The posterior wall of the spine is apparently concave. I have not examined the specimen and provisionally must accept Khabakob's conclusion that it is "nearly allied to the English *Ctenacanthus heterogyrus* McCoy." However, I have reservations about including *C. venator* here, since the published figures are very reminiscent of *Sphenacanthus* spp. (see following section and figs. 8–11). Khabakob's (1928, fig. 2) transverse section is unlikely to be accurate, since it shows lateral ribbing extending onto the posterior wall, unlike other elasmobranch dorsal finspines (fig. 7L). An alternative restoration of the transverse section is shown in figure 7M.

All the finspines under discussion are characteristically ornamented with heavily enameled costae, and (apart from *E. keyti*) have a concave posterior wall. None of them is known from articulated or even associated remains, so their relationships are to a large extent untestable. However, in both characteristics just mentioned, these finspines resemble those of Recent squaloids and heterodontids, and differ profoundly from those of hybodontids. They are similar also to finspines of *Palaeospinax* and *Nemacanthus,* fossil genera which I have argued elsewhere (Maisey, 1977) are closely allied to living elasmobranchs. I therefore suggest that *Amelacanthus* and *Eunemacanthus* are allied to neoselachians and not to hybodontids

or *Ctenacanthus*. *Nemacanthus* characteristically has a broad anterior enameled rib, and numerous rounded tubercles arranged in more or less vertical rows laterally. Marginal denticles are frequently but not invariably present. The finspines of *Geisacanthus bullatus* St. John and Worthen (1875, p. 441, pl. XVII, figs. 3, 4) have larger, vertically striated tubercles (diameters exceeding that of the anterior rib, unlike *Nemacanthus* which has rather smaller tubercles), which are arranged in definite axial series. *Geisacanthus* finspines may therefore represent a morphological intermediate between those of *Eunemacanthus* and *Nemacanthus*, although a phylogenetic relationship based on these similarities would be highly speculative.

None of the finspines referred to *Amelacanthus* or *Eunemacanthus* have been found associated with other remains. However, these spines are considered to pertain to sharks, rather than to some other fish, because of the presence of distinct ornamented (distal) and unornamented (basal) parts (see Maisey, 1975 for details).

Eunemacanthus seems to have had a fairly wide distribution. *Amelacanthus* is more restricted. Outside Great Britain and Northern Ireland, *Amelacanthus* is recognized in North America on the basis of a fragmentary finspine, University of Nebraska State Museum no. 82410.

SPHENACANTHUS AGASSIZ AND *WODNIKA* MÜNSTER

HISTORICAL NOTE: *Ctenacanthus* and *Sphenacanthus* are Paleozoic chondrichthyan taxa, recognized by dorsal finspines. These spines were originally described by Agassiz (1837), but the descriptions are founded in each case upon rather poor specimens. However, many better preserved spines have subsequently been referred to these taxa, and some are associated with skeletal remains. Unfortunately, over the years *Sphenacanthus* has become almost lost as a synonym of *Ctenacanthus*. In part, this is undoubtedly due to Thomson's (1869) confusion of *Sphenacanthus* with the type species of *Ctenacanthus*, *C. major*, and to Newberry's (1873) revision of *Ctenacanthus* which was based on *Sphenacanthus* finspines that had been sent him from Scotland and which had previously been misidentified as *C. major* (Maisey, 1981). Confusion over the identity of *Ctenacanthus* and *Sphenacanthus* has also resulted in referral of a wide variety of finspines, with differing ornamentation and other morphological characters, to *Ctenacanthus* (e.g., Davis, 1883). In fact *Ctenacanthus* and *Sphenacanthus* finspines are readily distinguishable. It is now clear that Newberry's (1873) *Ctenacanthus marshi* finspine is referable to *Sphenacanthus*, and that it represents the first published (but by no means the only) occurrence of *Sphenacanthus* from Carboniferous deposits of North America.

During the course of the present investigation, it became evident that *Sphenacanthus* finspines closely resemble those of *Wodnika*, a Permian shark now known from many complete skeletons (Schaumberg, 1977 and in prep.). Since these genera may be closely related, a discussion of *Wodnika* has been added here.

I will attempt to distinguish between *Sphenacanthus* and *Ctenacanthus* by presenting diagnoses of their finspines. Associated remains of both genera are known (Dick, 1978; Maisey, 1981), and other characters such as tooth morphology support the continued separation of these taxa. In the present work, however, my primary concern is with finspine morphology, and discussion of other anatomical features will be minimal.

WHAT IS *SPHENACANTHUS*?

The following is the diagnosis of *Sphenacanthus* presented by Agassiz (1837, p. 5):

"This genus is founded on a single spine, from the freshwater Burdiehouse Limestone, in the collection of the Royal Society of Edinburgh. As in *Gyracanthus* it has well-defined grooves and ridges; but rather than being arranged obliquely across the spine as in that genus, the grooves and ridges of the Sphenacanth extend longitudinally from the

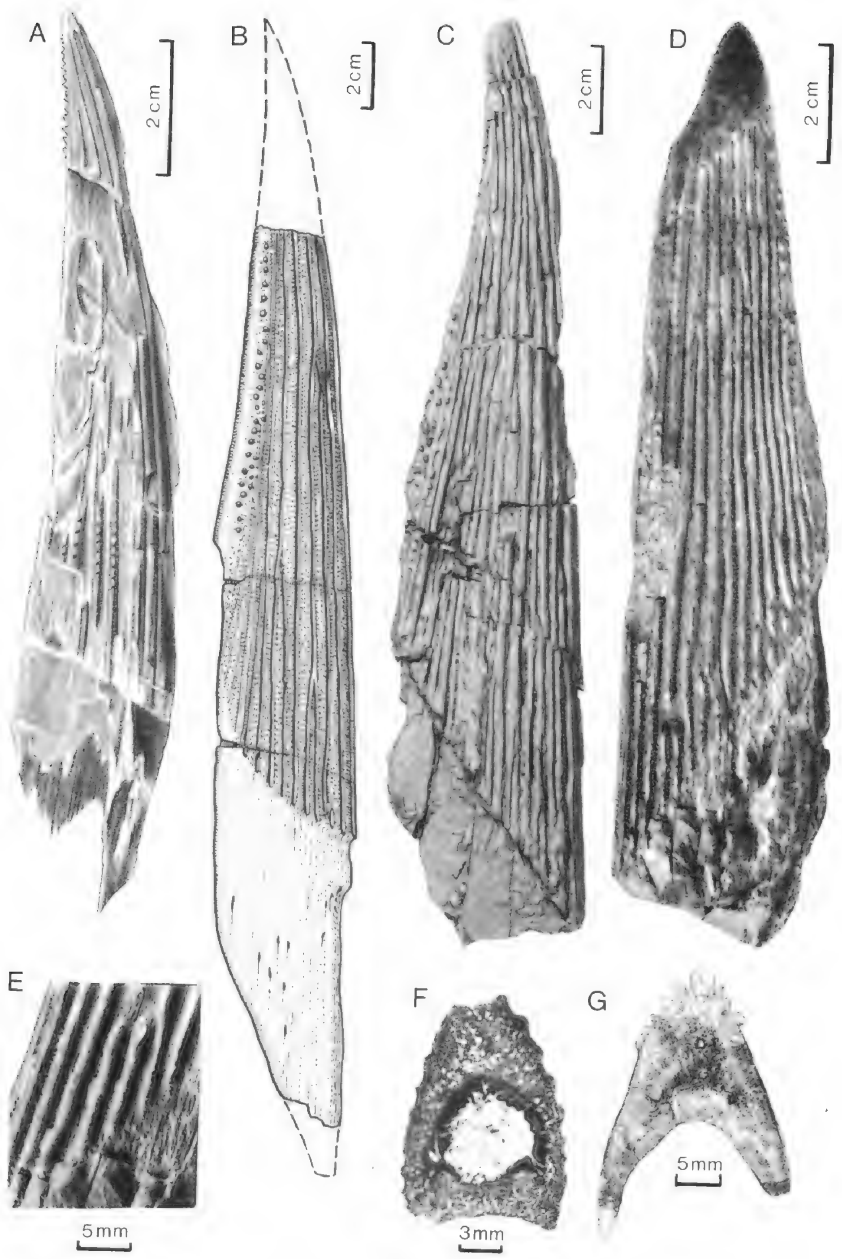

FIG. 8. A, *Sphenacanthus serrulatus* Agassiz; from Agassiz (1837) tab. 1, no. 11; B–G, *Sphenacanthus hybodoides*; B, drawing of BM(NH) P5572 (reversed for ease of comparison); C, AMNH 9591; D, BM(NH) P8172; E, detail of ornament from BM(NH) P8172; F, BM(NH) Wild Coll. slide no. 459; section above level of posterior closure; G, BM(NH) P10016, section below level of posterior closure.

base to the apex of the spine, which is rounded on its sides and anterior margin, but cut squarely on its posterior face. These characters draw it much to the hybodes

[hybodonts] from which it differs in that instead of large teeth in its posterior border, only a delicate crenellation is noted. . . . This spine is shaped like a wedge which tapers gradually to its extremity, and which is round on three of its faces and cut squarely on its fourth. The truncated side is smooth, and on its margins a slight serration is noted. The ridges which project on the sides and anterior border are gradually lost on the posterior margin towards the tip; they are rounded on the anterior margin and on the sides of the tip of the spine; while, on the sides of the middle and lower part, particularly on the posterior margins, they are slightly crenellated."

Agassiz (1837) commented on the similarities between the ribbing of *Sphenacanthus* and *Hybodus* finspines, but also noted that large downcurved posterior denticles (characteristic of hybodontid finspines) are absent from *Sphenacanthus* spines. The fine crenulation of some of the ribs in *S. serrulatus* is rarely seen in other finspines referred to *Sphenacanthus*.

Although it is true that the ribbing of *Sphenacanthus* finspines resembles that of *Hybodus,* the arrangement and modes of increase in the number of ribs is different in these taxa. In *Sphenacanthus* finspines, new ribs appear down the posterolateral margins and subsequently run onto the lateral spine wall (figs. 8A, C, D; 9A; 10A, D, E; 11A, B). This mode of increase, which I term "marginal rib insertion," is apparently confined to *Sphenacanthus*. It can be seen in several examples figured here and is apparent in Agassiz's (1837) type specimen (fig. 8A). Marginal ribs pass distally into posterolateral denticle rows which are always present. In addition to marginal rib insertion, rib numbers increase down the length of the spine both by bifurcation and intercalation. Like *Hybodus* and unlike *Ctenacanthus,* there is no primary rib down the anterior midline of a *Sphenacanthus* finspine. Unlike *Hybodus* finspines, those of *Sphenacanthus* lack a lateral field of fine, narrow ribs. In large *Sphenacanthus* finspines there are frequently as many as 20 to 25 ribs per side. As in hybodontid finspines the ribbing is not completely smooth, and there are rugosities and nodal points which in some spines are organized into a definite pattern suggestive of pauses

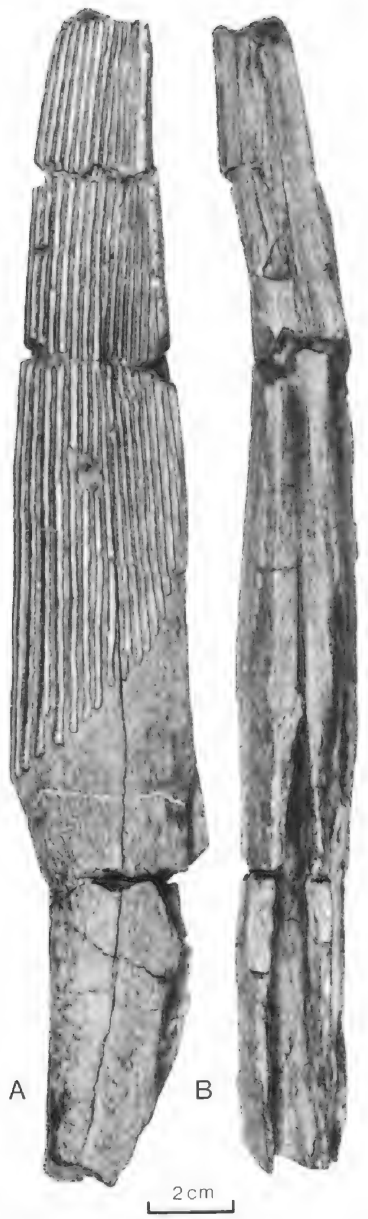

FIG. 9. A, B, *Sphenacanthus hybodoides*? AMNH 523, one of Newberry's specimens originally misidentified as *Ctenacanthus major.*

and interruptions in finspine development. The nodes of one rib often correspond with nodes on adjacent ribs, giving rise to a discontinuous growth line (varix) across all the ribs but not intercostally (figs. 8D; 9A; 10A, D, E). These varices are as important as growth lines in interpreting morphogenetic processes of fossil finspines, and were used in an earlier study of hybodontid finspines (Maisey, 1978). Although each rib is independent of its neighbors, development of all the ribs was clearly governed by a single, synchronized developmental pattern. Some spines of *S. hybodoides* have numerous beadlike nodes along the ribs, especially on the more lateral ones but sometimes more anteriorly, e.g., BM(NH) P 3117, P 3119. *Sphenacanthus nodosus* finspines are strongly beaded. Generally, the ribs of *Sphenacanthus* finspines lack a shiny enameloid layer, except at the nodes; one of Newberry's specimens from the Scottish Coal Measures, AMNH 523, has more completely enameled ribs than most *Sphenacanthus* finspines.

Marginal denticles of *Sphenacanthus* finspines extend from near the spine tip to just above the level of posterior closure, as in many other Paleozoic finspines. These marginal denticles sometimes comprise several short series, so that the marginal "row" may consist of several sections (figs. 8B, C, D; 10D). Each of these short denticle series is proximally continuous with one of the marginally inserted ribs. The developmental implication of this denticle arrangement is that the marginal row was not the product of a single scleroblastic center, but that after an initial period of denticle formation the marginal scleroblastic tissue was displaced around onto the lateral surface of the spine, by a newly differentiated scleroblastic primordium, as the dimensions of the spine increased proximally. Thus the marginal denticles and marginally inserted ribs of *Sphenacanthus* finspines may be regarded as a product of several *anlagen*. This pattern of rib insertion provides an important difference between *Sphenacanthus* and typical hybodontid finspines (e.g., *Hybodus, Acrodus, Asteracanthus*). The *Sphenacanthus* pattern, beginning with an interrupted series of denticles and becoming more continuous, is the opposite of the usual hybodontid pattern where the ribs are initially continuous but become discontinuous later in development (discussed in detail by Maisey, 1978).

Following Agassiz's (1837) description of *S. serrulatus,* Egerton (1853) erected two further species, also based on finspines, named *S. hybodoides* and *S. nodosus.* Stratigraphically these were younger than *S. serrulatus,* being from the upper rather than lower Carboniferous. The majority of *Sphenacanthus* finspines in collections are of Pennsylvanian age. The holotype of *S. nodosus,* BM(NH) P3121, has more regularly beaded ribbing than typical *S. hybodoides.* Such regular beading is also apparent on BM(NH) P2223 (two finspines) and P2120. Woodward (1889, p. 242) made *S. nodosus* a synonym of *S. hybodoides,* using the argument that one was probably founded on a posterior finspine and the other on an anterior spine. This speculation is unfounded, however, since no specimens show this to be the case, and both species are therefore provisionally retained here.

Some *S. hybodoides* finspines have been crushed so that their posterior wall seems convex, e.g., BM(NH) P3232, P5552. However, all uncrushed *Sphenacanthus* finspines have a flat or slightly concave posterior wall, and lack a median keel or ridge. An incomplete spine, *S. hybodoides* BM(NH) P8172 has heavy but symmetrical abrasion of its apex, presumably acquired during life (fig. 8D). Egerton (1853, p. 281) noted similar abrasion of the holotype of *S. nodosus,* BM(NH) P3121. Transverse sections through the apical region of *Sphenacanthus* finspines reveal thick deposits of non-trabecular circumpulpar dentine (e.g., fig. 8F), which in some cases completely plugs the spine central cavity apically. In these sections another peculiar feature of *Sphenacanthus* finspines is evident. Anterior to the spine central cavity is a prominent region of spongy trabecular dentine, in which the denteonal trabeculae are much thinner than elsewhere (fig. 8F, G).

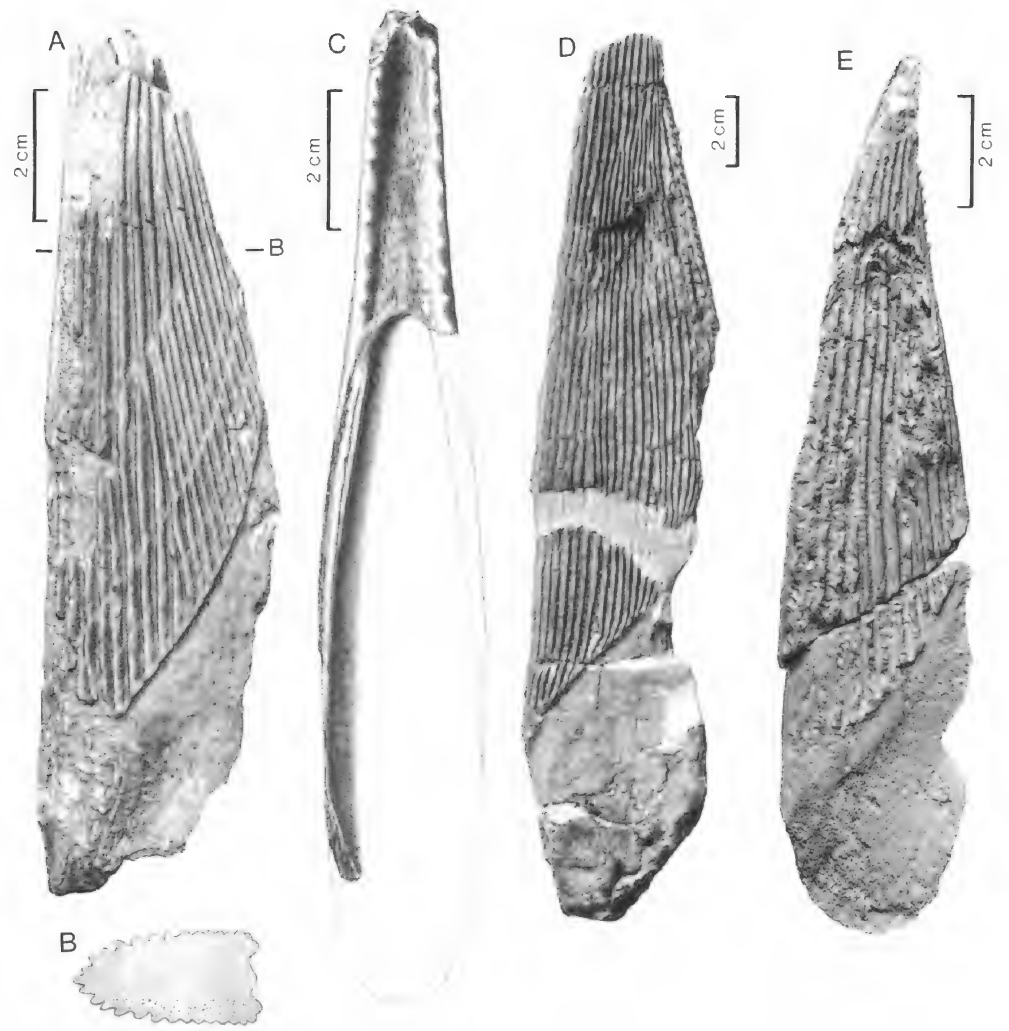

FIG. 10. A–C, *Sphenacanthus marshi* (Newberry); A, the holotype, from peel of YPM 2873; B, C, from Newberry (1873) pl. 36, no. 3; D, *Sphenacanthus hybodoides*? AMNH 524, the other Newberry specimen originally misidentified as *Ctenacanthus major*, for comparison with *S. marshi*; E, *Sphenacanthus* off. *marshi*, from peel of USNM 299644, Kinderhook Fm., ?Iowa (St. John Coll.).

Historically, the next species of *Sphenacanthus* to be described (as *Ctenacanthus*) was Newberry's (1873) *C. marshi*. I have examined the holotype, Peabody Museum no. 1896, and a cast (AMNH 1166) of a referred specimen. The pattern of ornamentation (particularly the rib arrangement and marginal insertion pattern), straight posterior margin and concave posterior wall are characteristic of *Sphenacanthus* finspines. I have no doubt that Newberry's (1873) specimen is referable to this genus (fig. 10A–C).

In an attempt to compare his material with the type species of *Ctenacanthus, C. major,* Newberry acquired two specimens (now AMNH 523, fig. 9; and 524, fig. 10D). These finspines are from the Scottish Coal Measures and are referable to *Sphenacanthus,*

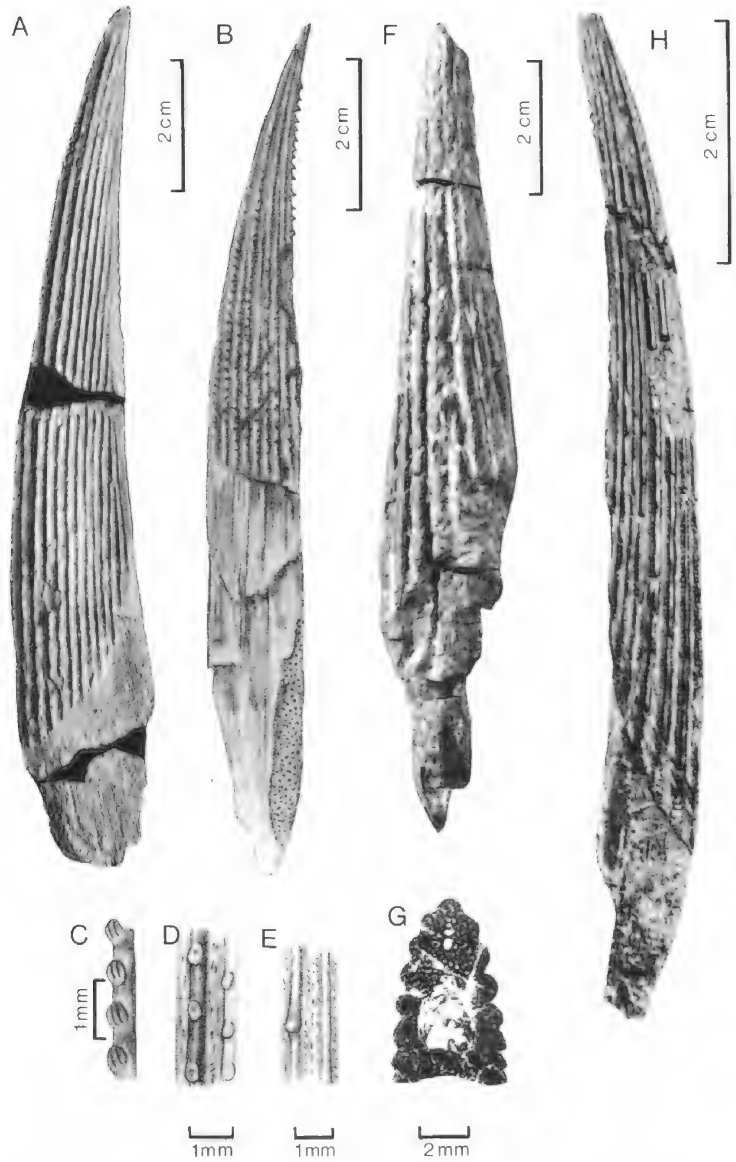

FIG. 11. A, *Sphenacanthus aequistriatus* (Davis); peel of holotype, BM(NH) P7705; B–E, *Sphenacanthus costellatus* (Traquair), from Traquair (1884) pl. II, nos. 2–5; F, *Wodnika borealis,* new species, the holotype, USNM 299646, Permian, Siksikput Fm., Lisburne Hills, Alaska; G, H, *Wodnika striatula* section and finspine in Schaumberg coll.

perhaps *S. serrulatus* (although AMNH 524 is more like the nodular finspines of *S. hybodoides*). Unfortunately, Newberry's Scottish specimens were misidentified as finspines of *C. major*. Newberry's (1837) concept of *C. major* was therefore based upon finspines of *Sphenacanthus,* the genus to which his "*C. marshi*" finspines coinci-

dentally belong. It is worth repeating Newberry's (1873, p. 327) remarks in the light of this discovery:

> 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 this genus.

I cannot agree that the ornament of Newberry's (1873) specimens resembles that of *C. major* finspines; he was probably allowing the misidentified referred specimens from Scotland to influence him more than Agassiz's (1837) diagnosis. I cannot trace any correspondence to suggest who supplied Newberry with misidentified material. However, some significance may be attached to Thomson's (1869) paper, in which *Sphenacanthus hybodoides* finspines were misidentified as belonging to *Ctenacanthus major.*

Sphenacanthus hybodoides is generally regarded as a Pennsylvanian species like *S. marshi.* However, Newberry's Scottish specimens (if their locality data are accurate) and several new discoveries in North America suggest that very similar spines also occur in the Mississippian. These finds may broaden the range of *S. hybodoides* and *S. marshi* and these species may eventually prove to be synonymous. Four other North American finspines referable to *Sphenacanthus* are:

CM26049, a finspine with a concave posterior wall, marginal tubercles and several faint ribs.

CM26816-8, a slab containing, among various teeth, a finspine referable to *Sphenacanthus.*

USNM 299644, a finspine from the Kinderhook Formation of ?Iowa, collected by Orestes St. John (fig. 10E). At present it is not possible to assign these spines to new species; provisionally all are referred to *S. marshi.*

Davis (1879a, p. 185) proposed another species, *Ctenacanthus aequistriatus,* which is also founded on a finspine, BM(NH) P 7705, from the lower Coal Measures (Pennsylvanian) of Lowmoor, Yorkshire. There are only about a dozen ribs per side; these are straighter and much more regular than in other *Sphenacanthus* finspines (fig. 11A). Each rib is very thin, with no pectinations, beading, or varices. The ornament terminates abruptly at its lower end. Marginal denticles are present and several ribs are introduced marginally. Another specimen, BM(NH) P15504, from Bradford, Yorkshire, is similar to the holotype, but is incomplete (only an apical piece a few inches long is preserved). The posterior wall of these spines is concave. In view of the distinctive ornamentation, *S. aequistriatus* is retained here as another *Sphenacanthus* species (agreeing with Woodward, 1889, p. 244).

Ctenacanthus minor Davis (1879b, p. 531) was referred to *Sphenacanthus* by Woodward (1889, p. 244); it is probably an immature *Sphenacanthus* finspine, since it has smooth ribs and a concave posterior wall, and is only 1.4 inches long. As an immature specimen, this spine would not be expected to display the marginal rib insertion pattern which, as discussed above, would develop progressively as the finspine enlarged. In all probability *S. minor* is not a valid species, and may be synonymous with *S. hybodoides* which is found in the same horizon.

A complete fossil shark *Ctenacanthus costellatus* from the lower Carboniferous of Eskdale, Dumfriesshire, was described by

Traquair (1884, p. 4), who noted that its finspines (fig. 11B–E here) "perhaps approach(es) most nearly the *Sphenacanthus serrulatus* of Agassiz than any other." Traquair recorded the presence of marginal denticles on the finspine of Agassiz's (1837) holotypes of *S. serrulatus,* and on the basis of this similarity with *Ctenacanthus* made *Sphenacanthus* a synonym of that genus. Woodward (1889, p. 242) was also impressed by similarities between *S. serrulatus* and *C. costellatus*. This genus, however, was not distinguished on the basis of finspine morphology by Woodward (1889, p. 241): "finspines of this fish are indistinguishable from those named *Ctenacanthus* by Agassiz." Instead, the distinction was based on an extremely tenuous proposal that teeth like those of *C. costellatus* are absent in formations yielding *Ctenacanthus* finspines! Woodward (1889) thus created a non sequitur whereby two taxa are distinguished by a negative character, which is unrelated to the means by which the taxa were originally separated. Although this method of distinguishing *Ctenacanthus* from *Sphenacanthus* is unjustifiable, these taxa are nevertheless distinguishable by differences in their finspine morphology and ornament patterns. On the basis of these features, the shark described by Traquair (1884) is closer to *Sphenacanthus* than to *Ctenacanthus*.

As mentioned above, there are problems with which species of *Sphenacanthus* should be considered distinct and which should be placed in synonymy. Thomson (1869) described some associated *Sphenacanthus* finspines, "*Cladodus*" *mirabilis* teeth and shagreen (as *Ctenacanthus major*). Dick (1878, p. 103) mentions undescribed associated remains of *S. serrulatus* as having teeth which are easily confused with those of *Tristychius arcuatus,* although *S. serrulatus* teeth differ from those referred to *S. hybodoides* and *S. costellatus*. Thus, there is some evidence that these *Sphenacanthus* species are valid. So far, no associated remains from North America have been referred to *Sphenacanthus*.

SPHENACANTHUS AGASSIZ

REVISED DIAGNOSIS: Shark recognized by its finspines, which are gradually tapered and slightly recurved posteriorly, often with a straight posterior profile; anterior face acutely rounded, lateral faces slightly convex to flat, posterior face strongly concave and lacking a pronounced median ridge or convexity; cross-section approximately twice as deep as broad; ornament of prominent raised costae a variable distance apart, but intercostal grooves generally as wide as or wider than costae; no primary anterior rib and primary bifurcation is characteristic; costae branch irregularly, are sometimes nodose and discontinuous, and new ones sometimes appear by intercalation and often by addition to the marginal ribs; ribs smooth or nodose, never closely pectinated but sometimes beaded with small, well-spaced tuberculations which may be thinly enameled and striated; posterolateral margins ornamented by a row of low, posteriorly directed tubercles or denticles, produced in part by tubercle series related to marginally inserted costae; spine trunk composed of trabecular dentine with a prominent spongy region anteriorly, but lacking any ordered vascularization other than a median canal anterior to the central cavity; an inner lamellar, nontrabecular layer is characteristically well developed.

TYPE SPECIES: *Sphenacanthus serrulatus* Agassiz, 1837.

SYNONYM: *Ctenacanthus serrulatus* (Ag); Traquair, 1884, p. 6.

OTHER REFERRED SPECIES: *S. hybodoides* (Egerton); Egerton, 1853, p. 280; *S. nodosus* (Egerton); Egerton, 1853, p. 281; *S. marshi* (Newberry); Newberry, 1873, p. 326; *S. aequistriatus* (Davis); Davis, 1879a, p. 185; *S. minor* (Davis); Davis, 1879b, p. 531; *S. costellatus* (Traquair); Traquair, 1884, p. 3.

GENUS *WODNIKA* MÜNSTER (1843)

AMENDED DIAGNOSIS: Small Permian phalacanthous shark attaining lengths of

about 100 cm.; finspines smooth-ribbed, lacking pronounced posterior denticles, and with concave posterior wall; teeth low, rounded, tumid, with crowns of tubular dentine apparently lacking an outer enameloid layer, approximately eight or nine replacement files in each half-ramus of the jaws; axial skeleton poorly calcified; caudal fin with single series of small dorsal arcualia and longer jointed hypural radials; body scales apparently compound and possibly of growing type (detailed morphology not yet known).

TYPE SPECIES: *Wodnika striatula* Münster, 1843.

Much of the generic diagnosis above is based on Schaumberg's (1977) revision of *Wodnika striatula*.

Wodnika borealis, new species

DIAGNOSIS: *Wodnika* known only from a dorsal finspine, which differs from that of *W. striatula* only in the following respects; posterolateral ribs as broad as the anterior ribs, and all ribs stouter and more closely spaced than in *W. striatula*; lateral ribbing bifurcates from an anterior primary rib.

It is also noteworthy that *W. borealis* may have attained a slightly greater size than *W. striatula*, since the holotype of *W. borealis* is a finspine which, when complete, probably measured over 150 mm. in length whereas *W. striatula* finspines are generally somewhat shorter. *Wodnika borealis* also comes from a different geographical region from *W. striatula*, and considerably extends the known distribution of the genus.

HOLOTYPE: USNM 299646; Permian, Siksikpuk Formation, Lisburne Hills, Point Hope Quadrangle, 21 ft. above Lisburne-Siksikpuk contact in stream valley, about 3 miles N of Mt. Itsalik, Alaska, coll. K. J. Bird, 1972; figure 11F.

ARE *SPHENACANTHUS* AND *WODNIKA* RELATED?

Wodnika is a small Permian shark originally recognized by its teeth (Münster, 1843), but now known from a number of complete and partial skeletons (Schaumberg, 1977). The teeth are of rounded, non-cuspidate durophagous morphology, with a punctate surface to the crown and (according to a personal communication from W.-E. Reif, Tübingen) without an enameloid outer layer.

Although these teeth were originally assigned to hybodontids (*Acrodus* Münster, 1840, p. 123; *Strophodus* Münster, *op. cit.*, p. 123; 1843, p. 50), the tooth morphology differs in some respects from typical *Acrodus*, and the postcranial and dermal skeleton of *Wodnika* also differs from that of hybodontids. For example, *Wodnika* lacks cephalic spines and a calcified rib cage, and its scales are not of hybodontid morphology. Moreover, its finspines are distinguishable from those of Mesozoic hybodontids (see Maisey, 1978). *Wodnika* finspines are ornamented by several fairly smooth, broad ribs, interrupted only by varices (fig. 11H). No marginal denticles are known, and marginal insertion of new ribs is also unknown. The posterior wall of the spine is concave (fig. 11G); its anterior wall is thick and spongelike, but not so extensively spongy as in *Sphenacanthus*. While the ribbing of *Wodnika* and hybodontid finspines is similar, it also agrees with the ribbing of *Sphenacanthus* in general appearance, and the shape and internal morphology of *Wodnika* and *Sphenacanthus* finspines seen in sections agree closely (cf. figs. 8F, 11G). *Wodnika* and *Sphenacanthus* differ in their tooth morphology; in the absence of marginal rib insertion and denticles from *Wodnika* finspines and in stratigraphic occurrence. While these two genera are still considered to be distinct, similarities in their finspines suggest that *Wodnika* and *Sphenacanthus* be referred to a higher taxon, termed here the family Sphenacanthidae.

By grouping *Wodnika* and *Sphenacanthus* together into a higher taxon, on the basis of similarities in their finspines, the systematic position of these two taxa is no longer as problematic as it was. They differ from hybodontid sharks and from *Ctenacanthus* in

several respects, and are probably not closely related to either. Tooth morphology in *Wodnika* is very different from that of *Sphenacanthus*, and the total amount of dental variation among different taxa presently included within the Sphenacanthidae is as great as that known within the Hybodontidae. It is therefore concluded that the tendency toward a durophagous habitus occurred independently in *Wodnika* and in hybodontids such as *Acrodus* and *Asteracanthus*.

CONCLUSIONS

Only two of Agassiz's (1837) *Ctenacanthus* species based on finspines are retained in that genus: *Ctenacanthus major* (the type species) and *C. tenuistriatus* (a synonym of *C. major*). Thus only one species of *Ctenacanthus* described in that work is still considered valid (Maisey, 1981). Of the remaining species given by Agassiz (1837), *C. ornatus* is not an elasmobranch but is probably an acanthodian (Pageau, 1969). The other species, *Ctenacanthus brevis*, is referred here to *Bythiacanthus* St. John and Worthen (1875). Two species were referred to the genus *Onchus* by Agassiz (1837) but later described as *Ctenacanthus* by Davis (1883), along with two other species. All four of these species are now placed in a new genus, *Amelacanthus*. Agassiz (1837) listed (but did not describe) another *Ctenacanthus* species, *C. heterogyrus*, which was later described by McCoy (1855). This species is now placed within the genus *Eunemacanthus*. The finspines of *Amelacanthus* and *Eunemacanthus* have thick enameloid layers and most have a concave posterior wall, features that suggest affinity with neoselachians.

Whereas some taxa previously included in *Ctenacanthus* can be assigned elsewhere, another previously distinct Agassizian genus, *Sphenacanthus*, has become undeservedly reduced to a synonym of *Ctenacanthus*. Finspines of *Sphenacanthus* differ from those of *Ctenacanthus*, however, and a revised diagnosis of *Sphenacanthus* (based on its finspines) is proposed. Similarities with *Wodnika* suggest these genera are closely allied to each other.

It is interesting to note that the few tolerably complete Paleozoic phalacanthous sharks known at present may not be closely related to one another, contrary to a popular belief. *Ctenacanthus compressus* and *C. clarkii* are referred to *Ctenacanthus* with some degree of confidence (Maisey, 1981). "*Ctenacanthus*" *costellatus* is probably more closely allied to *Sphenacanthus* and is provisionally placed in that genus (see also Woodward, 1889). In some respects *Goodrichthys eskdalensis* finspines resemble those of *Ctenacanthus* (e.g., ornament pattern) but in other respects are similar to those of *Bythiacanthus* (e.g., level of posterior closure). An undescribed Pennsylvanian form may be closely allied to *Bythiacanthus*. Other "ctenacanths" show evidence of affinity with Mesozoic hybodontids (Maisey, 1981 and in prep.). *Amelacanthus* and *Eunemacanthus* finspines are similar in some respects to those of *Nemacanthus* and *Palaeospinax*; the latter genus is well known from articulated remains (Maisey, 1977) and has affinity with Recent sharks. It is therefore no longer possible to group all phalacanthous Paleozoic sharks into a single "ctenacanth" category, even though the interrelationships of these sharks are poorly understood. We must instead recognize "ctenacanths" to be a non-monophyletic group containing members of various lineages, the interrelationships of which will hopefully become better known.

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