THE TAINOCERATIDAE (NAUTILIDA) OF THE CASPER FORMATION (L. PERMIAN) OF WYOMING

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***Tainoceras wyomingense, Metacoceras knighti,* and *Metacoceras sulciferum* from the Casper Formation (L. Permian) of Wyoming have been restudied. The syntypes of *M. knighti* and *M. sulciferum* contain specimens that are conspecific with the syntypes of *Tainoceras wyomingense.* This is supported by both the presence of ventral nodes and comparisons of morphometric ratios of the syntypes. Lectotypes of the three species are designated so that *T. wyomingense, M. knighti,* and *M. sulciferum* become synonyms. *T. wyomingense* is designated the senior synonym.**

INTRODUCTION

In the course of a study on some Illinois nautiloids, I had the opportunity to restudy most of the nautiloid material that Miller and Thomas (1) described from the Casper Formation (L. Permian) of Wyoming. This collection included the syntypes of *Metacoceras knighti*, *M. sulciferum*, and *Tainoceras wyomingense.* These three species have not been restudied except for brief mentions of *M. sulciferum* (2, 3) and the nearly verbatim reproduction of the original descriptions by Miller and Youngquist (4). I have found that Miller and Thomas (1) included specimens conspecific with the syntypes of *Tainoceras wyomingense* in the syntype series of both *Metacoceras knighti* and *M. sulciferum.* This error was probably due to the lack of knowledge about the ontogenetic variation of the two genera. This paper presents a study of ontogenetic variation found among the syntypes of the three species and a revision of their nomenclatural status.

MATERIAL AND METHODS

All measurments were made with calipers following Teichert (5) and are rounded to the nearest 1.0 mm. Abbreviations are: F, flank height; H, whorl height; W, whorl width; and V, ventral width. Ventral width was measured between lines established by the proximal bases of the ventrolateral nodes. Some measurements were estimated by measuring half the width or ventral width and multiplying that by two. Estimates were made only on specimens where the midpoint of the venter could be established by the presence of a morphological feature (*i. e.,* siphuncle, hyponomic sinus, or ventral nodes). All measurements were checked three times. Estimates varied by about ± 0.5 mm for small specimens (W< 25 mm) and ± 1.5 mm for larger specimens. Actual measurements averaged about 0.5 mm variation. All of the syntypes (SUI 1155-SUI 1163) of the three species were examined. Where possible more than one set of measurements were made for each specimen. The number of specimens included in each catalog number was 1155 (1), 1156 (12), 1157 (1), 1159 (4), 1160 (1), 1161 (1), and 1163 (5). The number of specimens too poorly preserved to measure was 1156 (6), 1158 (1), 1159 (1), and 1163 (1). A table of the raw data on which Figures 1A-F are based is available from the author. All the specimens examined are in the collections of the University of Iowa. The prefix, SUI, is not included for catalog numbers mentioned in the text.

RESULTS

Figures 1B, D, and F show that known *Tainoceras wyomingense* (those with ventral nodes or parts of such specimens) and known *Metacoceras* (those without nodes at sizes where *T. wyomingense* has nodes) have differing morphological proportions. The differences in ratios reflect differences in growth patterns of the two genera. F and V are not measurable on *T. wyomingense* until they are about 13 mm wide (Figures 1C-F). *Metacoceras* sp. have measurable F and V at a width of 8 mm and probably earlier *(Metacoceras* sp. Miller and Thomas is measurable at about 4 mm width). This difference is due to the late (after about 1.5 whorls) development of

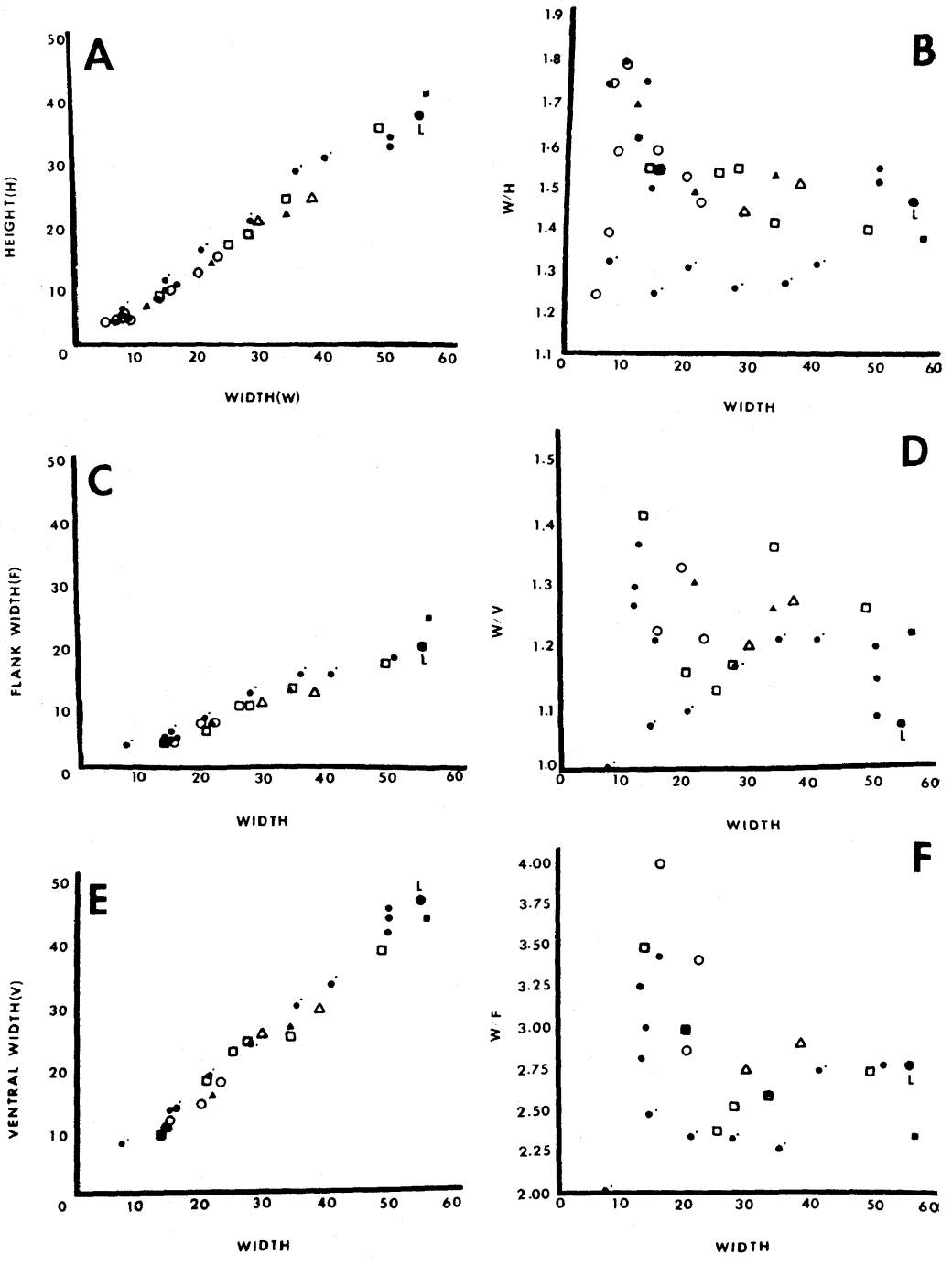

FIGURE 1. Scatter diagrams of measurements of Tainoceratidae from the Casper Formation owing relationships of various parameters to width. Symbols: open circle, 1159; closed circle, 1156 *Tainoceras*); closed circle with dot, 1156 (*Metacoceras*); open triangle, 1161; closed triangle, 1160; pen square, 1163; closed square, 1155; closed circle accompanied by L, lectotype *Tainoceras knighti.*

the ventrolateral and umbilical shoulders in *T. wyomingense* versus the earlier (at the end of the first half whorl) development of these in *Metacoceras* sp. The ventrolateral shoulders of the *Metacoceras* develop first while in *T. wyomingense* the umbilical shoulders appear first. Since the whorl happens to be widest at the first developed shoulder in each case, the W/V of *Metacoceras* sp. is 1.0 at first whereas that of *T. wyomingense* is 1.25 initially. W/F also differs. Since *T. wyomingense* does not develop ventrolateral shoulders until more than one whorl has been completed, they have a larger W/F than *Metacoceras* sp., which has measurable flanks at three-quarters of a whorl. The rate of increase in width is not constant in *T. wyomingense.* It increases more rapidly in the first 1.5 whorls than in the later ones. This is reflected in the peaks of W/H, W/V, and W/F (Figures 1B, D, and F). These peaks are either lacking or occur at an earlier stage in *Metacoceras* sp.

DISCUSSION

All of the syntypes (1159-1163) of *T. wyomingense* are conspecific. But at least two of the syntypes (1156.A; 1156.B) of *Metacoceras knighti* and one syntype (1158) of *M. sulciferum* are certainly conspecific with *T. wyomingense.* These all have ventral nodes. Although the greatly reduced ventral nodes of these specimens are not visible on the plate figures, they may be seen if the specimens are examined. The other syntypes of the *Metacoceras* species that are conspecific with *T. wyomingense* are either too young to have ventral nodes developed or are living chambers from mature specimens that have lost the nodes. Most of the small specimens that Miller and Thomas (1) included in 1156 appear from Figures 1B, D, and E to be conspecific with *T. wyomingense.* Of the large specimens only 1155 approaches *Metacoceras* more closely than *Tainoceras.* The large ones included in 1156 all appear to be *T. wyomingense.* The figured syntype (Miller and Thomas, 1, Pl. 97, figs. 4-5) 1157 of *M. sulciferum* was received too late to permit including data from it in Figure 1. But near the adoral end, the specimen measures W, 22 mm; H, 15 mm; F, 8 mm; and V, 17 mm. The ratios are W/H = 1.47, W/V = 1.29, and W/F = 2.75. These data make the specimen more closely resemble *T. wyomingense* than *Metacoceras* sp. Specimen 1157 is too small to have ventral nodes developed.

The details of the ontogeny of the ornamentation of *T. wyomingense* are difficult to interpret owing to the variable preservation of the specimens. The lateral nodes mentioned by Miller and Thomas (1, p. 731) are present only on one crushed specimen and appear to be an artifact of preservation. The first sign of ornamentation is the appearance of transverse lateral plicae at the end of the first whorl. The ventral and dorsal ends then become the ventrolateral and umbilical nodes respectively; and the midlateral portion is lost. This pattern is similar to the one observed for *T. monilifer by* Tucker (6).

The lectotypes (designated below) of *Tainoceras wyomingense, Metacoceras knighti* and *M. sulciferum* are conspecific. Although both *M. knighti* and *M. sulciferum* have page priority over *T. wyomingense*, I believe that preservation of *T. wyomingense* as senior would better serve the stability of nomenclature. The combination *T. wyomingense* has been used several times, while the combinations *T. knighti* and *T. sulciferum* have not previously been published. In accordance with the first revisor principle (Art. 24, I. C. Z. N., XV) the binomial *Tainoceras wyomingense* has priority over the binomials *Tainoceras knighti* and *Tainoceras sulciferum.*

SYSTEMATIC PALEONTOLOGY

Family TAINOCERATIDAE Hyatt, 1883

Genus TAINOCERAS Hyatt, 1883

TAINOCERAS WYOMINGENSE Miller and Thomas

Plate 1, figs. 2, 3, 8.

Metacoceras knighti Miller and Thomas (1, p. 728-729); Miller and Youngquist (4, p. 112-113).

Metacoceras sulciferum Miller and Thomas (1, p. 729-730), Pl. 97, figs. 4, 5; Miller and Youngquist (4, p. 113-114), Pl. 47, figs. 4, 5.

Tainoceras wyomingense Miller and Thomas (1, p. 732-733) Pl. 96, fig. 13, Pl. 97, fig. 6, Pl. 98, figs. 3, 4; Miller and Youngquist (4, p. 92-93) Pl. 7, fig. 7, Pl. 25, figs. 3, 4, Pl. 47, fig. 6; Kummel (3, p. 25) Fig. 7d; Kummel (7, p. K391).

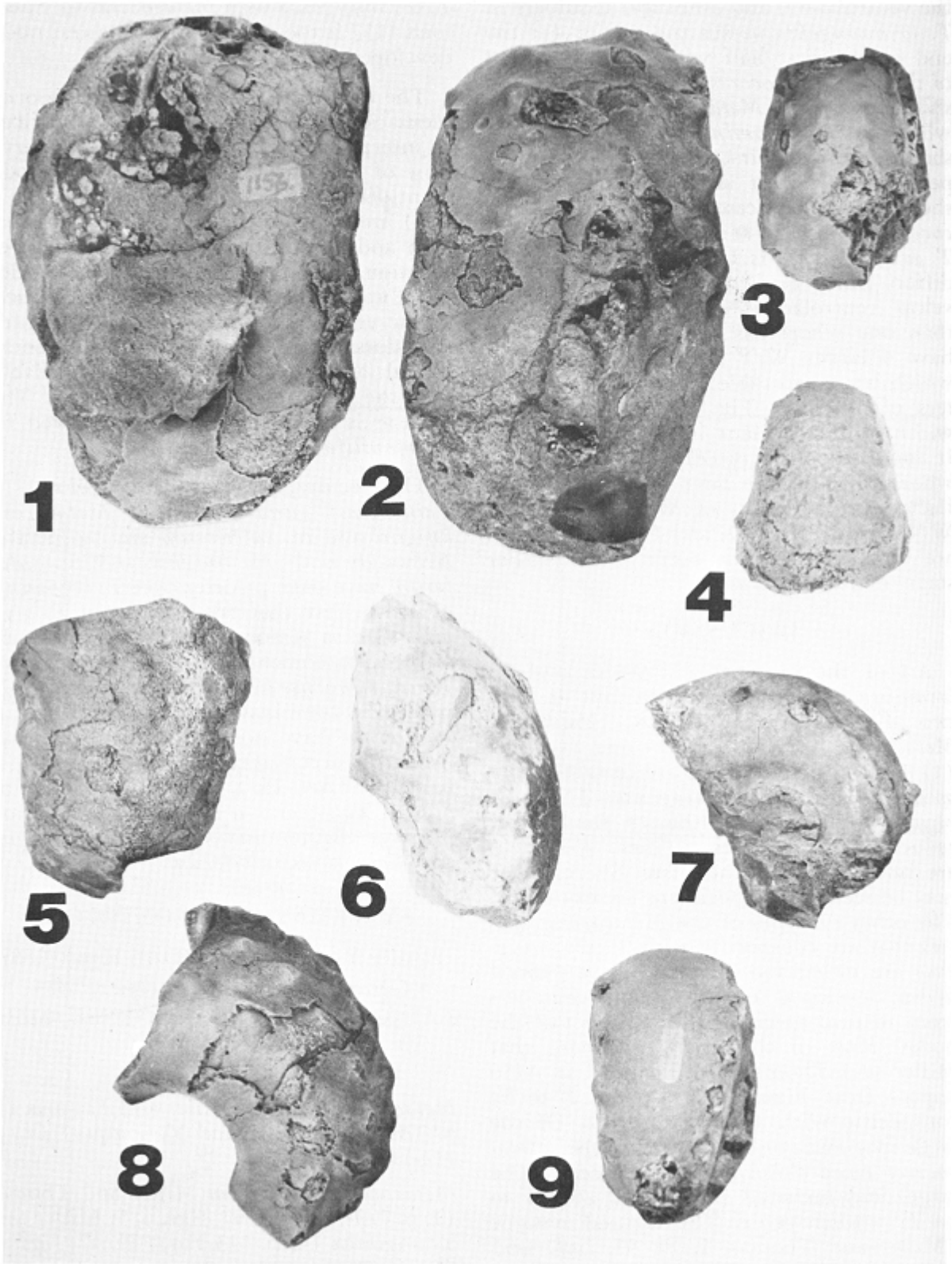

PLATE 1, FIGURE 1. *Tainoceras knighti* (Miller and Thomas). Ventral view of the lectotype (1156.A) with the adoral end toward the top, × 0.9. FIGURES 2, 3, 8. *Tainoceras wyomingense* Miller and Thomas. 2, ventral view of a mature paralectotype (1163.A), × 0.9; 3, ventral view of a juvenile paralectotype (1163.B), × 1; 8, lateral view of the lectotype of *Tainoceras wyomingense* (1161), × 1. FIGURE 4. *Tainoceras sulciferum* (Miller and Thomas). Ventral view of the lectotype, × 0.9. FIGURES 5-7, 9. *Metacoceras* sp. 5, 6, ventral and lateral views of two different specimens (1156.C and 1156.D respectively), × 0.9; 7, 9, ventral and lateral views of another specimen (1156E.), × 1.

Lectotype. — 1161 (Plate 1, fig. 8) is designated lectotype of *Tainoceras wyomingense* Miller and Thomas.

Description. — The description of this species follows that of Miller and Thomas (1) but is modified by additional information from the lectotype and paralectotypes of *Tainoceras knighti.*

The conch, which forms about four volutions, is subdiscoidal, nautiliconic, and rather large at maturity. The lectotype at its adoral end is 25 mm high and about 38 mm wide. One of the paralectotypes attained a maximum diameter of 60 mm and an estimated height and width of 25 and 35 mm respectively. The whorls are depressed and are octagonal in cross section. Ventral, ventrolateral, and dorsolateral sides of the conch are relatively narrow compared to the lateral and dorsal sides. Except near the adapical end where the conch is subcircular in cross section, the adapical portion of the conch is elliptical, being strongly depressed dorsoventrally and very broadly rounded laterally; the dorsal side of the conch is less strongly convex than the ventral side. The conch is rapidly expanded orally and at the adoral end of the first volution it is 9 mm wide and 5 mm high. At the end of the second volution it is 15 mm wide and 10 mm high.

The umbilicus is rather large and perforate. The diameter of the umbilicus is equal to about 35% the diameter of the conch. The umbilical perforation is oval and about 5 mm long and 3 mm wide. The umbilical walls are steep and the umbilical shoulders are subangular. Umbilical nodes are present where the conch has a width of 26 mm and possibly as early as 1.5 whorls (15 mm wide). The umbilical nodes are thickenings of the test and thus are not visible on the internal mold of all but the largest specimens and they may be easily destroyed by abrasion of the shell. The umbilical nodes become more and more obliquely elongated as the conch grows and on the living chambers of mature individuals are up to 6 mm long and 2-4 mm high.

Each growth line forms a broad, moderately deep, rounded, ventral sinus and on each side of it, a broad, low, gently rounded, lateral salient. Growth lines are essentially straight and directly transverse on the umbilical walls. The adapical portions of the conch are smooth or nearly so, but near the midpoint of the second volution transverse lateral plicae develop. The ventral and dorsal ends become the ventrolateral and umbilical nodes respectively, whereas the center portion is lost. The ventrolateral nodes increase in size as the size of the conch increases. Near the middle of the second volution two rows of similar nodes are gradually developed on the venter. These nodes continue to enlarge and to become progressively less longitudinally elongated and more conical with growth. Where the nodes begin to disappear they are slightly laterally elongated. In the last 3.5-4 whorls, the ventral nodes become reduced in size and are obsolete on the living chambers of mature individuals.

The camerae are moderate in length. The suture pattern and siphuncle are as described by Miller and Thomas (1).

Occurrence.— *Stenopoceras* beds of the Casper Formation, in Gilmore Canyon, about 8 miles southeast of Laramie, Wyoming.

TAINOCERAS KNIGHTI (Miller and Thomas)

Plate 1, fig. 1.

Synonomy identical to *Tainoceras wyomingense.*

Syntypes. — This species was based on 19 specimens (1155, n = 1; 1156, n = 18). Two of these are *Metacoceras* (1156.C; 1156. D). Two others (1156.E; 1156.L) also appear to be *Metacoceras* (Text-figs. 1D, F). Two others (1156.P; 1156.Q) are fragments from inner whorls of *Stenopoceras abundum* Miller and Thomas. Morphological data indicate that the remaining 13 are conspecific with *T. wyomingense.*

Lectotype. — 1156.A (Plate 1, fig. 1) is designated lectotype of *Metacoceras knighti* Miller and Thomas.

Description of Lectotype. — The lectotype is a fragment of a living chamber that was about 55 mm wide and 38 mm high at midlength. The specimen is 98 mm along the venter. It probably represents a fully mature specimen of the species. The ornamentation consists of six rows of nodes, two on the venter and one on each of the ventrolateral and umbilical shoulders. The ventral nodes are indistinct and are present only

where the test is preserved on the right side of the lectotype. Large conical ventrolateral nodes are only slightly longitudinally elongated. The interval from the crest of one node to the crest of the next is about 20 mm at midlength. The umbilical nodes are thickenings of the test and are only barely visible on the exfoliated left side of the shell. The ones on the right side are obliquely elongated and closely spaced. Growth lines, camerae, and siphuncle are not visible.

Discussion. — Discussion of Figures 1A-F indicates that the lectotype of *T. knighti* is conspecific with *T. wyomingense.* The ventral nodes are small but this should be so on a specimen of this size (W = 50 mm at adapical end). At this same size, a paralectotype of *T. wyomingense* (Plate 1, fig. 2) has very reduced nodes as well.

Occurrence. — Identical to that of *Tainoceras wyomingense.*

TAINOCERAS SULCIFERUM (Miller and Thomas)

Plate 1, fig. 4

Synonomy identical to *Tainoceras wyomingense.*

Syntypes. — This species was based on two specimens both of which are *Tainoceras wyomingense* juveniles.

Lectotype. — 1158 is designated lectotype of *Metacoceras sulciferum* Miller and Thomas.

Description of Lectotype. — The lectotype is a fragment of about half a volution that measures 50 mm along the venter. It is 26 mm wide at its adoral end and 20 mm wide at the adapical end. Since the umbilical wall is not visible, it is not possible to measure the height accurately. Midventrally there is a sulcus that is bordered on each side by longitudinal ridges. These ridges become divided into nodes adorally. The test is poorly preserved so that accurate measurement of the ventral nodes is impossible. Longitudinally elongated ventrolateral nodes are spaced at about 6-mm intervals as measured crest to crest. Irregularly spaced umbilical nodes are present. Since the test appears to have been abraded, the nodes may have been more prominent.

Discussion. — Kummel (3) and Reed (2) have both suggested that *Metacoceras sulciferum* could have been ancestral to the line that led to *Tainionautilus.* These speculations were based on the sulcate venter that Miller and Thomas (1) thought was characteristic of *M. sulciferum.* However, sulcate venters are not rare among species of *Metacoceras.* Pennsylvanian species such as *M. cornutum*, *M. perelegans*, and *M. mutabile* Miller and Owen all have concave zones on the venter. Although *Tainonautilus* may have evolved from some species of *Metacoceras*, *M. sulciferum* is not a good choice since the description was based on juvenile *Tainoceras wyomingense.*

Occurrence. — Identical to *Tainoceras wyomingense.*

Genus METACOCERAS Hyatt, 1883 METACOCERAS sp. Plate 1, figs. 5-7, 9.

Metacoceras sp. Miller and Thomas (1, p. 730-732), Pl. 96, figs. 10, 11; Miller and Youngquist (4, p. 116-117), Pl. 7, figs. 4-6.

Metacoceras knighti Miller and Thomas (1, p. 728-729), Miller and Youngquist (4, p. 112-113).

Metacoceras cheneyi Miller and Youngquist (8, p. 2, 6), P1. 1, figs. 16-18; Miller and Youngquist (4, p. 107-108), Pl. 45, figs. 1-3, Pl. 46, figs. 6-8.

Discussion. — Material from the Casper Formation available to me is too meager to base a description on. Until more complete specimens are collected and the relationships of these and *M. cheneyi* are understood, this species of *Metacoceras* is better left undescribed. Material presently available includes 1153, 1154, 1156.C-.E, and 1156.L.

Occurrence. — Identical to that of *Tainoceras wyomingense.*

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